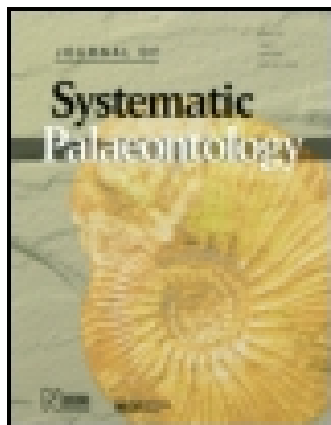


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Journal of Systematic Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tjsp20>

Notoungulate faunas of north-western Argentina: new findings of early-diverging forms from the Eocene Geste Formation

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Published online: 04 Jul 2014.

To cite this article: D. A. García-López & M. J. Babot (2014): Notoungulate faunas of north-western Argentina: new findings of early-diverging forms from the Eocene Geste Formation, *Journal of Systematic Palaeontology*, DOI: [10.1080/14772019.2014.930527](http://dx.doi.org/10.1080/14772019.2014.930527)

To link to this article: <http://dx.doi.org/10.1080/14772019.2014.930527>

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Notoungulate faunas of north-western Argentina: new findings of early-diverging forms from the Eocene Geste Formation

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(Received 7 October 2013; accepted 26 March 2014)

Vertebrate-bearing deposits of the Geste Formation (Late Eocene) crop out in the Puna of Catamarca and Salta, north-western Argentina, and have yielded specimens of a variety of clades. Among these, mammals have particular importance since their record shows some taxonomic peculiarities when compared with that of adjacent units. Here we describe new material that includes Notoungulata of generalized morphology, two morphotypes of basal typotherians, and two interatheriid taxa (including *Antofagastia turneri* gen. et sp. nov.). These findings increase the variety of groups and provide new information about previously known taxa for this unit. Three phylogenetic analyses with different taxonomic contexts were performed. The first analysis includes the specimen referred to as ‘Typotheria indet. A’ in a data matrix of Paleogene notoungulates containing taxa traditionally referred as ‘Oldfieldthomasiidae’. The specimen is grouped together with three ‘oldfieldthomasiids’ (*Maxschlosseria*, *Ultrapithecus* and *Dolichostylocodon*) in the resulting tree. The second analysis involves specimens referred to as ‘Typotheria indet. B’, ‘archaeohyracids’, mesotheriids and hegetotheriids. The results show these fossils to be part of a basal polytomy of ‘early archaeohyracids’. Finally, a third analysis was conducted with Interatheriidae as the ingroup which recovered *Antofagastia turneri* at the base of a node including extra-Patagonian forms of non-interatheriine interatheriids plus *Eopachyrucos* and interatheriines. Although *Antofagastia*, *Punapithecus* and Chilean extra-Patagonian forms share some features, such as small size, they do not comprise a distinct clade. The notoungulate record of the Geste Formation shows some singularities in the context of north-western Argentinean Paleogene units, the presence of interatheriids and ‘archaeohyracids’ being the most striking of these. The differences exhibited can be partially explained by temporal factors, since recent isotopic data points to a Late Eocene age for this unit. Biogeographical isolation represents another possible explanation, because these levels appear to be deposited in an isolated geographical and geological context, suggesting intermontane basin deposition or local wedge-top basins.

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Keywords: Eocene; Notoungulata; Interatheriidae; Geste Formation; phylogeny; faunal singularities

Introduction

The middle and late Paleogene represents a complex and crucial time in mammal evolutionary history around the world. During this time, the ecological and taxonomic changes undergone by different lineages, correlated with dramatic climatic changes, shaped the identity of major groups that evolved during the Neogene and persisted to the present day. The Eocene–Oligocene boundary is crucial in this chain of events and is documented worldwide by nearly synchronous faunal events known as the Grande Coupure (in Europe: Stehlin 1909), the Mongolian Remodelling (in Asia: Meng & McKenna 1998), and the Patagonian Hinge (Goin *et al.* 2010, *in press*).

In this context, South American native mammals, which additionally evolved in relative isolation, show a clear diversification and began to develop trends of

‘modernization’ towards the end of the Eocene, at the beginning of the Second Faunal Stratum recognized by several authors (Simpson 1980; Flynn & Wyss 1998; Croft *et al.* 2008). This morphological evolution is particularly well documented in the Order Notoungulata whose representatives are conspicuously present in almost all fossil mammal associations recorded across the Cenozoic.

Among the extra-Patagonian Paleogene localities in Argentina, the north-western outcrops have yielded an outstanding record of fossil vertebrates, particularly mammals. Several units, such as the Mealla (Paleocene: Pascual *et al.* 1978, 1981; Quattrocchio *et al.* 1997; Gelfo *et al.* 2009), Maíz Gordo (Late Paleocene–Early Eocene: Pascual *et al.* 1981; Volkheimer *et al.* 1984; Quattrocchio & Volkheimer 1990) and particularly Lumbrera (Eocene) formations have been explored in recent decades. They have yielded crocodiles, turtles, boids, fishes and a rich

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and in some cases exceptionally preserved fauna of mammals including metatherians (Sparassodonta, Bonapartheriiformes) and native ungulate groups ('Condylarthra', Litopterna, Astrapotheria and Notoungulata) (Pascual *et al.* 1978, 1981; Bond & Vucetich 1983; Babot *et al.* 2002; Deraco *et al.* 2008; Argot & Babot 2011; García-López & Powell 2009, 2011). Other north-western Argentinean geological units have received less attention, despite their palaeontological and biostratigraphical relevance. In this context, one of the most interesting units is the Geste Formation, given the singularities of its mammalian fauna.

The Geste Formation crops out in several localities of the Argentinean Puna. Alonso (1992) divided the outcrops surrounding the Pozuelos salt flat (Quebrada El Paso, Salta Province) into three members according to their lithological nature (considered informal divisions by Carrapa & DeCelles 2008). The fossil-bearing unit is the middle member, characterized by reddish coarse-grained sandstones and mudstones alternating with lenticular conglomeratic bodies. Sediment grain size increases upwards towards the common conglomerates (Alonso 1992; Reguero *et al.* 2008; Carrapa & DeCelles 2008). This section, also present in the locality of Antofagasta de la Sierra (Catamarca Province; Fig. 1), has yielded a diverse fauna

of fossil vertebrates (crocodiles, snakes, lizards and several mammals: López 1997; Babot *et al.* 2012). Although fragmentary, notoungulates are abundant in this unit; taxa referred to as 'Oldfieldthomasiidae', 'Archaeohyracidae' and Interatheriidae have been reported, along with diverse material regarded as notostylopids, isotemnids and notohippids (López 1995, 1997; López & Bond 1995; Reguero *et al.* 2008).

The Geste Formation has been traditionally referred to the Mustersan SALMA (Late Eocene), mainly based on biochronological data (Pascual 1983; Alonso *et al.* 1988; López 1997; Goin *et al.* 1998), although a Barrancan sub-age (late Middle Eocene) has been recently proposed from isotopic data and palaeontological studies (del Papa *et al.* 2010; Powell *et al.* 2011). Other proposals, controversial and unsupported by reliable evidence, have argued for an older age (middle Late Paleocene) for the Geste Formation (Marshall *et al.* 1997; Sempere *et al.* 1997).

Recent fieldwork conducted at Antofagasta de la Sierra led to the discovery of new notoungulate specimens including interatheriids and other forms related to early-diverging representatives of the order. In this paper, we analyse anatomical, taxonomic, and phylogenetic aspects of these fossils. These new data emphasize certain singularities of the fossil fauna of the Geste Formation in

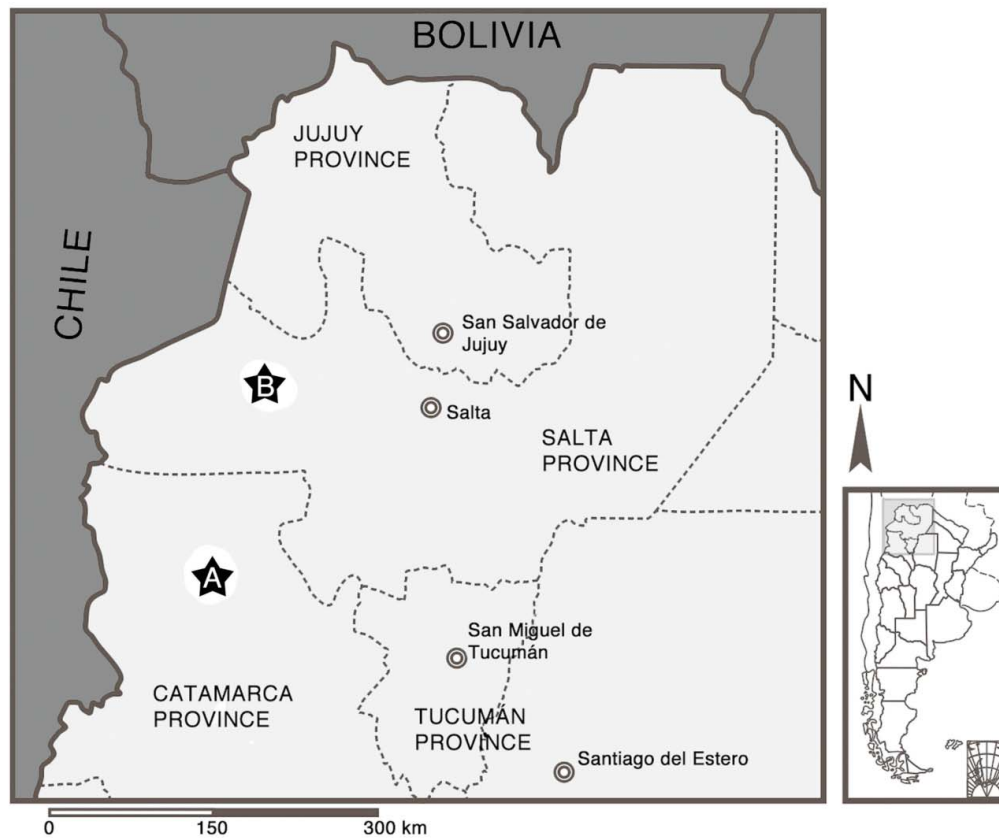


Figure 1. Map showing the location of the main outcrops of the Geste Formation discussed on the text. A = Antofagasta de la Sierra; B = Quebrada El Paso.

relation to the faunas of adjacent geological units (e.g. Lumbrera Formation), providing additional evidence on the age of these levels and new information about the morphology of early forms of some of the most representative families of Notoungulata (i.e. Interatheriidae).

Material and methods

Institutional abbreviations

MHAS: Museo del Hombre de Antofagasta de la Sierra, Catamarca, Argentina; **MLP:** Museo de La Plata, Buenos Aires, Argentina.

Other abbreviations

DP: upper deciduous premolar; **P:** upper premolar; **M:** upper molar; **m:** lower molar; **SALMA:** South American Land Mammal Age.

Material

The material included in this paper was collected during several field seasons conducted in 2009–2013. Some remains were collected directly in the field, but others were recovered using screen-washing techniques performed with a 0.1 mm mesh and analysing the sediments under binocular microscope.

Terminology

The terminology used in the anatomical description follows mainly Smith & Dodson (2003) and some terms commonly used for notoungulate dentition (e.g. crochet and entolophid). We retain the names of some groups currently recognized as paraphyletic for practical reasons.

Phylogeny

We conducted three phylogenetic analyses in order to determine the position of most of the specimens described here including the new taxon *Antofagastia turneri*. Each analysis was developed taking into account the taxonomic context of the specimens involved in order to gain resolution and, in the case of the more fragmentary specimens, obtain a preliminary idea of their relationships within a concrete framework. All analyses were carried out using Tree Analysis Using New Technology (TNT) Goloboff *et al.* (2008) with the traditional search option, using the tree bisection reconnection swapping algorithm and under equal weights (EW) and implied weights (IW) methods (Goloboff 1993). The IW function was used under different concavities (K).

Specimen MHAS 002 (Typotheria indet. A) was included in an unpublished data matrix developed by one of us (DAGL) as part of his PhD dissertation (García-

López 2009). This matrix comprises 44 craniodental characters (Supplemental Appendix 1) and 14 taxa including the informal taxon *Campanorco* and some well-known Paleogene and Neogene forms. Additionally, four representatives of Notostylopidae and ‘Henricosborniidae’ were included as outgroups. All characters were treated as non-additive.

The three specimens referred to as ‘Typotheria indet. B’ were included in the data matrix published by Billet *et al.* (2009). Characters treated as additive are the same as those specified by these authors. The matrix includes several taxa of ‘Archaeohyracidae’, Mesotheriidae and Hegetotheriidae, including *Oldfieldthomasia debilitata* and *Notopithecus adapinus* as outgroups. Additionally, the ‘archaeohyracid’ *Punahyrax bondesioi* from the Geste Formation (Reguero *et al.* 2008) was also included in the analysis.

New material of *Punapithecus* (MHAS 004–012) and the holotype and unique specimen of *Antofagastia turneri* (MHAS 003) were analysed using a data matrix taken from Hitz *et al.* (2006), with some modifications based on personal observations and literature (see Supplemental Appendix 2). We added three new characters – 14, 15 and 16 (mesial inflection in M1-2 protoloph, lingual sulcus on M1-2, and central fossa on M1-2, respectively) – and modified the scoring of characters 3, 7, 12 and 13 of Hitz *et al.* (2006). The matrix includes 46 craniodental characters scored in 23 taxa (Supplemental Appendix 2). Three of these taxa were used as the outgroup: the Paleocene genus *Simpsonotus*, the most basal notoungulate for which a complete skull is known (Billet 2011; García-López & Powell 2011); the Eocene basal toxodont *Pleurostygodon*; and the Eocene basal typotherid *Colbertia*. In this case, all characters were treated as non-additive.

Support indices were calculated for all analyses with TNT: Bremer (for analyses under equal weights) and symmetric resampling functions (Goloboff *et al.* 2008; Ramírez 2005).

Specimens studied and bibliographical references consulted for phylogenetic analyses are listed in Supplemental Appendix 3.

Systematic palaeontology

Order **Notoungulata** Roth, 1903

Notoungulata indet.

(Fig. 2)

Material. MHAS 001, incomplete trigonid and talonid of right m1 or m2.

Occurrence. Antofagasta de la Sierra, Catamarca Province, Argentina (26° 03' 43" S, 67° 24' 27" W). Middle Section of the Geste Formation (*sensu* Alonso 1992); Late Eocene.

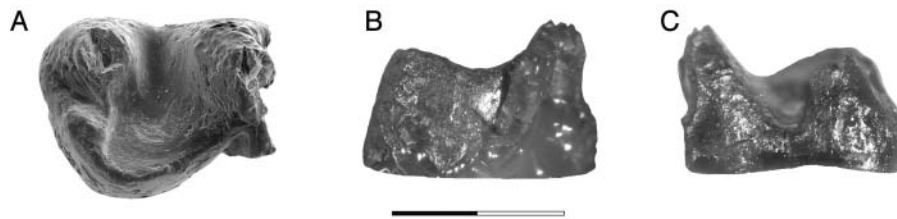


Figure 2. Notoungulata indet., MHAS 001, incomplete trigonid and talonid of right m1 or m2; Geste Formation, Antofagasta de la Sierra, Catamarca Province, Argentina. **A**, occlusal view; **B**, lingual view; **C**, labial view. Scale bar equals 2 mm.

Description. Only the distolingual part of the trigonid is preserved. The apex of the metaconid is broken and therefore its morphology is not clearly visible. The labial sulcid is deep. The cristid obliqua connects with the protolophid at its middle transverse length and extends distally into a hypolophid that shows a gentle angle at the level of the hypoconid. The hypoconulid is located on the distal side of the tooth and is more developed than the hypoconid but smaller than the entoconid. The talonid basin is wide and shallow and the entoconid is bunoid, being broken near the apex. It presents a faint entolophid (slightly bended distally) that reaches the hypolophid between the hypoconid and the hypoconulid. The sulcid between this latter cusp and the entoconid is conspicuous and well developed.

Remarks. The small size of this tooth matches with the average size of most interatheriids recorded in the Geste Formation (see below). Nevertheless, the strong bunodont condition in this specimen prevents its inclusion in that family. The same criterion can be applied to rule out affinities with ‘Archaeohyracidae’ (e.g. *Eohyrax*, *Punahyrax*, *Archaeohyrax*), which also exhibit morphologies very different from this tooth (e.g. isolated fossettids, more advanced lophodonty). Among early-diverging notoungulates, the occlusal pattern of this molar resembles *Henricosbornia* in the small size, incipient lophodonty, wide and shallow talonid basins, and faint and distally shifted entolophids. No previous mention has been made of fossils referred to ‘Henricosborniidae’ in the Geste Formation, so this cryptic record shows the presence of a more diverse array of generalized forms.

Suborder **Tyotheria** Zittel, 1893

Tyotheria indet. **A**

(Fig. 3A)

Material. MHAS 002, fragment of right mandible with m1 and m2.

Occurrence. Antofagasta de la Sierra, Catamarca Province, Argentina (26° 03' 43" S, 67° 24' 27" W). Middle Section of the Geste Formation (*sensu* Alonso 1992); Late Eocene.

Description. The molars are brachydont and much larger than in MHAS 001. Both teeth are virtually identical in morphology, their size being the only clear difference, with m1 smaller than m2 (Table 1). Additionally, the first molar shows more advanced wear. The trigonid and the talonid are about the same size in occlusal view. The metaconid is the highest cusp and lacks the small cusp usually attached to the mesial wall in Paleogene forms and identified by some authors as a paraconid (Pascual *et al.* 1978). The zone of the protoconid is only visible in m2; it is connected mesially with a small, hook-like paracristid pointing lingually. The mesial cingulid is well developed and reaches the base of the mesial wall of the metaconid. This structure is coalescent with the paracristid in m1 (which exhibits greater wear, as noted above) but is completely independent from this cristid in the m2. The cristid obliqua connects with the protolophid at its mid-length (slightly labially) and the labial sulcid is deep and narrow. There are no labial cingulids on these molars. The hypolophid is well developed and the hypoconid is not conspicuous. The hypoconulid is small and located at the distal wall of the molars. In both teeth the talonid basin is shallow, although it is very narrow given the great size of the entoconid (in occlusal view). The m2 shows a small cingulid at the lingual end of the talonid basin, which is absent in the m1. As previously mentioned, the entoconid is a large cusp connected to the hypolophid by a well-developed entolophid. In the m2, the entoconid shows a very small cristid on its mesiolabial wall that projects into the talonid basin. Despite its great areal development, the entoconid is low (much lower than the metaconid). A small but conspicuous sulcid separates the entoconid from the hypoconulid. This zone is not clearly visible in the m1 but the m2 presents a small but conspicuous distolingual cingulid at the base of the sulcid.

Remarks. The greater development of lophs distinguishes this specimen from more basal forms (usually referred to as ‘Henricosborniidae’) and its morphology differs in several aspects from notostylopids (e.g. more expanded entoconid, greater size of the trigonid, absence of a paraconid or accessory cusp located at the mesiolabial wall of the metaconid). Moreover, the expanded

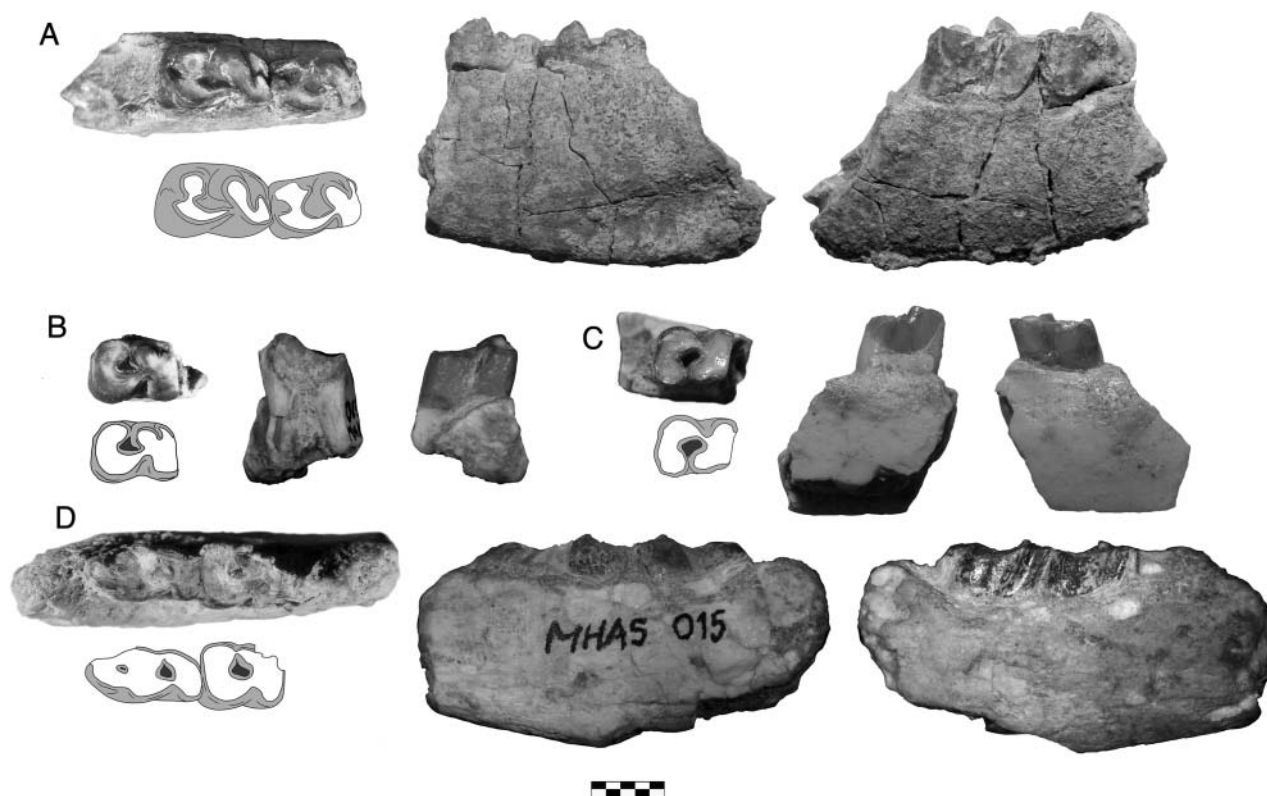


Figure 3. Indeterminate typotherian remains from the Geste Formation, Antofagasta de la Sierra, Catamarca Province, Argentina. **A**, *Typotheria* indet. A MHAS 002, fragment of right mandible with m1 and m2 in occlusal, lingual and labial views; **B–D**, *Typotheria* indet. B; **B**, MHAS 013, right m1 or m2 in occlusal, lingual and labial views; **C**, MHAS 014, fragment of left mandible with m1 or m2 in occlusal, lingual and labial views; **D**, MHAS 015, fragment of right mandible with incomplete m1 and complete m2–3 in occlusal, lingual and labial views. Scale bar equals 5 mm.

entoconid and the narrow talonid basin are also features that separate the fossil from early representatives of *Toxodontia* such as isotemnid, which have been recorded previously in the Geste Formation (López 1995, 1997).

Table 1. Dental measurements (in mm) of specimens referred to *Typotheria* indet. A and *Typotheria* indet. B. Abbreviations: L, length; W, width.

Typotheria indet. A						
	m1		m2		m3	
	L	W	L	W	L	W
MHAS 002	6.73	4.14	7.93	4.84	—	—

Typotheria indet. B						
	m1 or m2		m2		m3	
	L	W	L	W	L	W
MHAS 013	6.58	4.58	—	—	—	—
MHAS 014	5.57	4.43	—	—	—	—
MHAS 015	—	—	5.70	4.61	7.95	3.78

Among *Typotheria*, affinities with intertheriids and ‘archaeohyracids’ are ruled out by their higher hypsodonty and lophodonty, development of fossettids, and lesser development of cingulids. Within early-diverging typotherians, some forms traditionally referred as ‘oldfieldthomasiids’ (e.g. *Oldfieldthomasia*, *Maxschlosseria* and *Dolichostylodon*) are similar to specimen MHAS 002, showing a large entoconid (although not connected to the trigonid), narrow talonid basin, small or absent accessory cusp on the metaconid (‘paraconid’), small paracristid and well-developed mesial cingulid.

Typotheria indet. B
(Fig. 3B–D)

Material. MHAS 013, right m1 or m2. MHAS 014, fragment of left mandible with m1 or m2. MHAS 015, fragment of right mandible with distal fragment of m1 and complete m2 and m3.

Occurrence. Antofagasta de la Sierra, Catamarca Province, Argentina (26° 03' 43" S, 67° 24' 27" W). Middle Section of the Geste Formation (*sensu* Alonso 1992); Late Eocene.

Description. The molar in MHAS 013, identified as m1 or m2, shows moderate wear. In occlusal view, the mesio-lingual length of the trigonid is much reduced and its outline is kidney-like (distally concave). Most of the occlusal features of the trigonid have disappeared through wear and no fossettids are visible; nevertheless, the lingual ends of the protolophid and paralophid are separated by a small sulcid. The distal wall of the protolophid is concave and the metaconid is the highest cusp of the tooth. The hypolophid joins the protolophid almost on its middle labiolingual length; the labial sulcid is deep. The talonid is lower than the trigonid but its occlusal surface is larger. The hypoconid and hypoconulid are not conspicuous, the entolophid is very developed, and the entoconid is expanded mesially, joining the distal wall of the metaconid, and isolating a wide and relatively deep trigonid–talonid fossettid. There is no labial sulcid or cingulid on the talonid.

The tooth preserved in MHAS 014 (also identified as m1 or m2) is similar to the molar in MHAS 013, although crown height is greater. The wear observed in MHAS 014 is similar to that of the m2 preserved in MHAS 015 and the trigonid is featureless, with no fossettids or sulcids. The metaconid is also the highest cusp in this specimen, although it exhibits an anterior projection that runs mesially as a crest, which is lacking in MHAS 013. Finally, the trigonid–talonid fossettid is significantly deeper in this case and, on the labial wall of the tooth, the sulcid shows a small, cusp-like cingulid at its base, near the neck of the tooth.

Specimen MHAS 015 preserves both m2 and m3. The m2 is very similar to MHAS 014 and, as already pointed out, shows a similar wear stage. The m3 is highly affected by wear, preventing a full description of this tooth. However, the crown is complete (except for some missing parts of the enamel layer on the lingual wall) and some features can be noted. As usual in notoungulates, the m3 is clearly longer (mesiodistally) than the anterior molars, mainly due to the greater development of the hypoconulid. On the trigonid, a shallow lingual sulcid is still visible on the internal wall. On the labial wall, the surface is smooth and convex, without grooves, and the sulcid is deep. As on previous molars, there is a well-isolated trigonid–talonid fossettid but, additionally, there is a small entolophid–hypoconulid fossettid located on the distolingual surface of the talonid. Finally, there is a shallow but conspicuous labial sulcid on the distolabial wall of the talonid. Dental measurements are shown in Table 1.

Remarks. The specimens referred as *Tytopheria* indet. B differ from *Tytopheria* indet. A mainly in their greater hypsodonty. This is recognizable by the complete isolation of a deep talonid fossettid on the teeth identified here as m1 or m2 and m2. In *Tytopheria* indet. A the talonid basin is much shallower and its bottom is lingually open

(a more advanced wear stage will not isolate a talonid fossettid, or this will be faint and not as deep as in *Tytopheria* indet. B). Additionally, the presence of a mesial cingulid and a very small lingual cingulid located near the neck of the teeth in *Tytopheria* indet. A is a clear difference.

The morphology of these specimens is similar to that present in several taxa known as ‘archaeohyracids’. This Paleogene group, traditionally referred as a family of *Tytopheria* or *Hegetotheria* clades (depending on the systematic approach), is nowadays considered as paraphyletic or even polyphyletic (Croft *et al.* 2003; Reguero *et al.* 2008; Billet *et al.* 2009; Billet 2011). ‘Archaeohyracids’ represent the most abundant notoungulates in the Geste Formation outcrops after interatheriids (see below). Most specimens recovered in this unit during our fieldwork can be assigned to the genus *Punahyrax*, the only taxon recognized so far of this unnatural cluster in north-western Argentina (Reguero *et al.* 2008).

Assignment of the elements here described as *Tytopheria* indet. B is based on certain differences observed between this material and *Punahyrax*. These differences include the position of the entolophid in all molars, which is more transverse in the new material than in *Punahyrax* (and in fact, also than in Patagonian forms such as *Pseudhyrax* and *Eohyrax*), the development of an entolophid–hypoconulid fossettid in the m3 (absent in *Punahyrax*), and the development of the talonid in m3, which is proportionally shorter in *Punahyrax* (in the new material, these proportions are more similar to those found in *Eohyrax* and *Pseudhyrax*). It is noteworthy that the size of these teeth is similar to *Punahyrax* but crown height is less than in this genus and Patagonian representatives; in this sense, given these differences and those noted previously, the presence of a new taxon of ‘Archaeohyracidae’ in the Geste Formation cannot be discounted. Nevertheless, in view of the fragmentary nature of the material described here, new findings are necessary to confirm or reject this view.

Family **Interatheriidae** Ameghino, 1887

Genus *Antofagastia* gen. nov.

(Fig. 4)

Type species. *Antofagastia turneri* sp. nov.

Diagnosis. As for the type and only known species.

Derivation of name. From the locality of Antofagasta de la Sierra, Catamarca Province, Argentina.

Antofagastia turneri sp. nov.

(Fig. 4)

Diagnosis. Small Interatheriidae with brachydont dentition, narrow (although somewhat persistent) lingual sulcus, and faint fossettes in the upper molars. It shows the

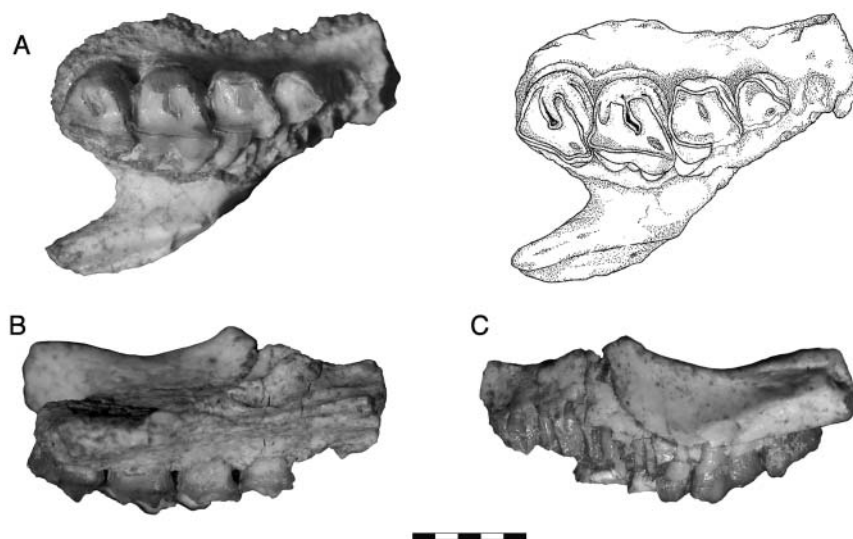


Figure 4. *Antofagastia turneri* gen. et sp. nov., holotype, MHAS 003, Geste Formation, Antofagasta de la Sierra, Catamarca Province, Argentina. Fragment of left maxilla with incomplete P4, almost complete M1 and complete M2–3 in **A**, occlusal view; **B**, medial view; **C**, lateral view. Scale bar equals 5 mm.

typical condition of the zygoma present in Interatheriidae, with the jugal excluded from the orbit by the zygomatic process of the maxilla and the presence of a small descending process (Hitz *et al.* 2006). This taxon differs from *Eopachyrucos* and members of Interatheriinae (*sensu* Hitz *et al.* 2006) in its brachydont premolars and molars, and from *Johnbell*, *Ignigena*, *Eopachyrucos* and interatheriines in its molars, which are wider than long. Additionally, it differs from *Notopithecus*, *Antepithecus*, *Guilielmoscottia*, *Transpithecus*, *Eopachyrucos* and interatheriines by its smaller size. Considering only the basal Interatheriidae, it differs from *Notopithecus* in the absence of a medial labial fossette and the posteriormost insertion of the zygoma (level of P4 in *Notopithecus* and M1 in *Antofagastia*), and from *Punapithecus* by its greater size. A weak mesial inflection of the M1 protoloph (see Fig. 4A) distinguishes *Antofagastia* from *Punapithecus*, *Notopithecus*, *Antepithecus*, *Transpithecus* and *Johnbell*. *Antofagastia* has a narrower lingual sulcus and almost flat lingual wall on the upper molars (i.e. the lingual sulcus is poorly expressed on this wall, see Fig. 4A) compared to the condition in *Punapithecus*, *Guilielmoscottia*, *Transpithecus*, *Johnbell* and *Ignigena*. It also differs from *Punapithecus*, *Johnbell* and *Ignigena* in the presence of a more persistent and oblique central fossa (additionally, this structure is shallower than in *Antepithecus*, *Guilielmoscottia* and *Transpithecus*) and from *Notopithecus*, *Antepithecus* and *Transpithecus* by its less persistent labial fossettes (particularly the mesiolabial fossette). Shallower labial inflections on the ectoloph (parastyle/paracone inflection; paracone/metacone inflection) distinguish *Antofagastia* from *Notopithecus*, *Guilielmoscottia* and *Transpithecus*, and the late formation of the entoloph (at least after the

disappearance of the distolabial fossette) distinguish it from *Antepithecus* and *Transpithecus*. *Antofagastia* differs from *Guilielmoscottia*, *Transpithecus*, *Johnbell* and *Ignigena* by the presence of a well-developed mesial cingulum on the upper molars.

Derivation of name. The species epithet honours Juan Carlos M. Turner, an Argentinean geologist who defined the Geste Formation and whose work in north-western units led to fundamental contributions to the geology of his country.

Material. Holotype: MHAS 003, fragment of left maxilla preserving most of the zygomatic process, the orbital process, and dentition; it includes an incomplete P4, almost complete M1, and complete M2–3.

Occurrence. Antofagasta de la Sierra, Catamarca Province, Argentina (26° 03' 43" S, 67° 24' 27" W). Middle Section of the Geste Formation (*sensu* Alonso 1992); Late Eocene.

Description. Given the erupted teeth (with M3 completely emerged) and the wear stage, the specimen is recognized as an advanced adult. Dental measurements are shown in Table 2.

Maxilla. The fragment of maxilla preserves a small portion of the facial and palatal processes, the complete orbital process, and most of the zygomatic process. The facial process exhibits the floor of the infraorbital canal whose anterior opening, the infraorbital foramen, is located at the level of the third premolar. The orbital process forms the floor of the orbit; posteromedially to the maxillary foramen (the posterior opening of the

Table 2. Dental measurements (in mm) of *Antofagastia turneri* and new specimens of *Punapithecus minor* described here. Some specimens of *P. minor* are too damaged and were not included. Abbreviations: L, length; W, width.

<i>Antofagastia turneri</i>												
	M1		M2		M3							
	L	W	L	W	L	W						
MHAS 003	~3.44	3.75	4.17	4.14	3.88	4.05						
<i>Punapithecus minor</i>												
	P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W
MHAS 004	—	—	—	—	2.20	2.35	2.71	2.46	2.84	2.60	—	—
MHAS 005	2.12	1.79	2.42	2.27	2.60	2.78	2.98	3.05	3.03	3.32	2.95	2.72
MHAS 006	1.77	1.47	2.32	1.86	—	—	—	—	—	—	—	—
MHAS 007	—	—	—	—	2.52	2.67	—	—	—	—	—	—
MHAS 008	—	—	—	—	—	—	3.03	2.67	3.04	2.71	—	—
MHAS 009	—	—	—	—	2.30	2.39	—	—	—	—	—	—
MHAS 012	2.12	1.41	—	—	—	—	—	—	—	—	—	—

infraorbital canal) the maxilla bears two small foramina. The zygomatic process extends from the middle extension of the M1 ectoloph to the distal border of the M2. Here the maxilla exhibits a small descending process. On the ventrolateral edge of the zygomatic arch there is a flat area anteroposteriorly elongated which represents the origin of the deep masseter muscle. This area is dorsally bounded by a well-developed crest that reaches the descending process anteriorly. On the dorsal border of the zygomatic process, immediately posterior to the ventral border of the orbit, there is a raised surface identified as the jugal bone. This element has the same position, aspect, and extension present in other interatheriids.

Dentition. The check teeth are brachydont and all dental pieces exhibit advanced wear. The fourth premolar is partially preserved, the labial third being lost; nevertheless, several features are still visible. The tooth shows a low molarization. The protocone, the only visible cusp (Fig. 4A, B), is slightly shifted mesially. The mesial cingulum is well developed and is restricted to the mesial face of the crown, not reaching the lingual side of the protocone. The central fossa is small, slightly elongated mesiodistally and mesially shifted. Distally to the protocone there is an area with exposed dentine produced by the fusion of the distal cingulum with the occlusal surface.

All molars are subtriangular. This shape is emphasized on the third molar due to the typical reduction of the hypoconid. In occlusal view, the M1 is similar in size to the M3, and both are smaller than the M2.

The M1 is almost complete, lacking only the paracone and parastyle. This molar is heavily worn; it has lost the

mesiolabial and distolabial fossettes. In this wear stage the central fossa is small, shallow, and transversely developed. The protocone exhibits an angular mesiolingual edge. The protoloph is wide and mainly transverse. The apex of the hypocone is slightly higher than the protocone and is more labially located; the zone between both cusps presents a shallow concavity on the lingual wall. The mesial cingulum is weakly developed and does not reach the lingual side of the crown. The distal cingulum is completely fused with the metaloph and is located at the same level as the mesial cingulum. The metacone apex is rounded and the labial fold is wide. The metastyle is vestigial and it is indicated only by a subtle convexity against the mesial wall of the M2 parastyle.

The second molar is less affected by wear than the M1, conserving the mesiolabial fossette, in which the main axis is oblique (mesiolabial–distolingual). Thus, the differences evident in the following description are mainly due to different wear stages. The crista 1 (running mesiolingually from the ectoloph joining the protoloph and isolating the mesiolabial fossette; see Billet 2011) is very wide at this stage, constraining the mesial extension of the central fossa. There is no sign of the distolabial fossette. The central fossa is slightly more oblique than in M1, narrow, and shallow. On the labial border of this last fossa there is an inflection that indicates the position of the crista 2 (see Billet 2011). The central fossa is connected with a narrow lingual sulcus running transversely between the protoloph and metaloph, and is thus not fully isolated lingually. In occlusal view, the protocone is much larger than the hypocone and its mesiolingual edge is also angular. The

protoloph is more oblique than in the M1 but is also wide. The apex of the hypocone shows almost the same height as the protocone but is shifted slightly labially. The mesial cingulum is poorly developed but is slightly more conspicuous than in the M1; it surrounds the mesiolingual zone of the base of the protocone reaching the lingual side of the tooth. The distal cingulum is narrow and is separated from the metaloph at this wear stage. The parastyle is well developed and imbricated with the metastyle of the precedent tooth. A faint sulcus separates the parastyle from the labial fold of the paracone. The paracone is the highest cusp on the M2 at this wear stage and its labial fold is wide, representing almost 50% of the total length of the ectoloph. The metacone is much lower than the paracone and its labial fold is narrower. The labial sulcus separating the paracone and metacone fold is shallow and wide. The metastyle is more developed and more distally extended than on the M1.

The third molar is triangular in outline. In occlusal view, there is a tiny mesiolabial fossette; the distolabial fossette is absent. The crista 1 is very wide and the crista 2 is represented as a small inflexion on the central fossa. The central fossa is larger than in the preceding molars (as expected from a less worn molar) and notably oblique. The outline of the central fossa is a narrow triangle with a short side bounded by the crista 1. On its distolingual apex the fossa is connected with a short but well-defined lingual sulcus which surrounds the distal base of the protocone. This cusp is dominant and is even more developed (relatively to other cusps) than in the preceding molars. The protoloph is slightly narrower than in the M2. As previously mentioned the hypocone is absent. The mesial cingulum is broader than on the M2; in the same way, the distal cingulum is sharper and shorter. This latter cingulum is coalescent with a reduced metaloph. The parastyle is smaller than in the M2 and is less imbricated. Although the apex of the paracone is broken, it can be observed that the labial fold of this cusp is fused with the labial fold of the parastyle. The metacone is not differentiated on the ectoloph. The metastyle is broken but the outline of the tooth indicates that it was distally prominent.

Genus *Punapithecus* López & Bond, 1995

Punapithecus minor López & Bond, 1995

(Fig. 5)

Material. MHAS 004, fragment of left maxilla with P4–M2. MHAS 005, fragment of right maxilla with root of P1 and complete P2–M3. MHAS 006, fragment of right maxilla with P2 and P3. MHAS 007, fragment of left maxilla with incomplete P3 and P4. MHAS 008, fragment of left maxilla with M1 and M2. MHAS 009, fragment of right maxilla with P4 and incomplete M1 and M2. MHAS 010, fragment of right maxilla with incomplete M1–3. MHAS 011, fragment of right maxilla with P4 and

incomplete M1. MHAS 012, fragment of left maxilla with P2 and incomplete P3 and P4.

Occurrence. Antofagasta de la Sierra, Catamarca Province, Argentina (26° 03' 43" S, 67° 24' 27" W). Middle Section of the Geste Formation (*sensu* Alonso 1992); Late Eocene.

Remarks. We found intraspecific variation among the new material presented here and those originally described by López & Bond (1995). Part of this variation can be explained by wear degree. According to our observations, four wear stages can be identified (Fig. 5). We based these stages (1, 2, 3 and 4) on molar morphology given the lack of a complete ontogenetic series for premolars. The features mentioned for each stage are constant for all molars and there is no evident wear gradient between M1 and M3 (except for certain differences observed in some specimens and detailed below).

Stage 1: The lingual sulcus is connected to a small and shallow central fossa. This fossa is faint and subtriangular. Both labial fossettes are present. M3 unknown (e.g. MLP 88-V-10-1; MHAS 008; Fig. 5A, B).

Stage 2: The central fossa narrows and only the lingual sulcus remains. The lingual fossettes are still present. M3 unknown (e.g. MHAS 004; Fig. 5C).

Stage 3: The distolabial fossette disappears in all molars and the mesiolabial fossette is vestigial on the M1. The lingual sulcus is slightly tilted mesially (e.g. MLP 86-V-6-5; Fig. 5D).

Stage 4: Both labial fossettes are missing (the distolabial fossette persists on the M3 of the specimen MHAS 005). The lingual sulcus is clearly tilted mesially (e.g. MLP 88-V-10-3, MHAS 005, MHAS 009 and MHAS 010; Fig. 5E–H).

The overall size of the specimens is also a source of variation (Table 2) and some specimens are larger than the rest (Fig. 6). The differences in size cannot be explained by age, since the biggest specimens exhibit wear stages 1 and 4 (MLP 88-V-10-1 and MHAS 005). Therefore, there is some intraspecific variation regarding size, although it is constrained within a small range and, in fact, is less than the differences in molar size observed for other interatheres such as *Federicoanaya* and *Santia-gorothia* (see Fig. 6 and Hitz *et al.* 2008).

An additional observation can be made on specimen MLP 86-V-6-6 (originally included in the hypodigm of *Punapithecus minor*), referred to as a left mandibular fragment with p4 and m1 (Fig. 7). The morphology of the teeth in this material matches with the features mentioned by López & Bond (1995), including the fact that the talonid is more developed than the trigonid on the p4 (a diagnostic feature for the species according to those authors). Nevertheless, this specimen is clearly larger than other specimens of *Punapithecus* (see López & Bond 1995, p. 96) and does not match with any maxillary fragment

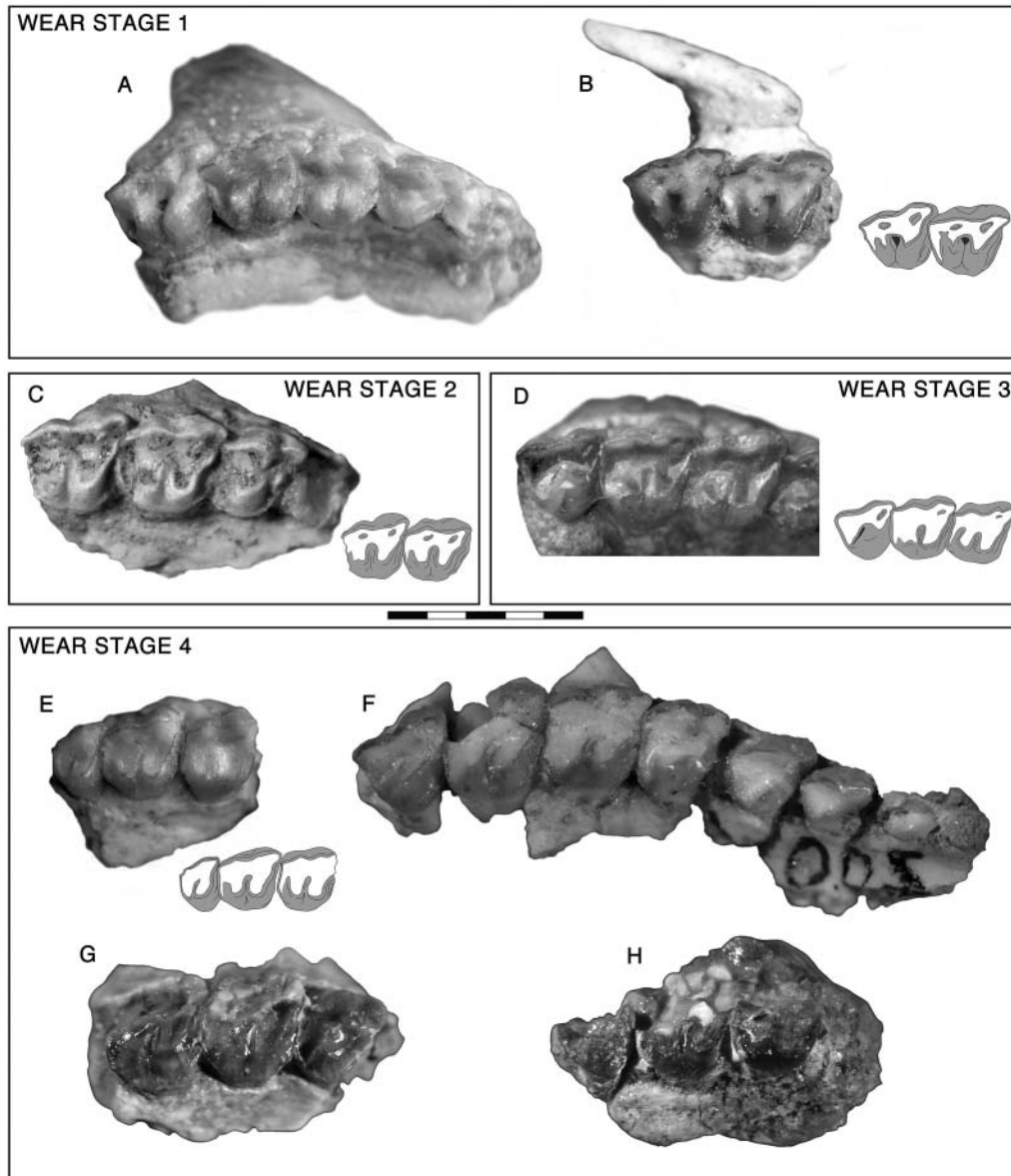


Figure 5. Wear stages in *Punapithecus minor*, Geste Formation, Antofagasta de la Sierra, Catamarca Province, Argentina. **A**, MLP 88-V-10-1, fragment of right maxilla with DP2–M2; **B**, MHAS 008, fragment of left maxilla with M1–2; **C**, MHAS 004, fragment of left maxilla with P4–M2; **D**, MLP 86-V-6-5, holotype, detail of molars; **E**, MLP 88-V-10-3, fragment of right maxilla with M1–3; **F**, MHAS 005, fragment of right maxilla with root of P1 and complete P2–M3; **G**, MHAS 009, fragment of right maxilla with P4 and incomplete M1 and M2; **H**, MHAS 010, fragment of right maxilla with incomplete M1–3. Images B, C, and D are flipped horizontally for comparative purposes. All specimens are shown in occlusal view. Scale bar equals 5 mm and is valid for all images (except drawings).

assigned to this taxon. The overall size is more typical of specimens of a size close to *Antofagastia*. Given the lack of information on its lower teeth we cannot refer this material to the new genus nor to any other known interatheriid taxa. Nevertheless, we consider that the strong difference in size between this specimen and other fossils referred to *Punapithecus minor* is enough to rule out the inclusion of MLP 86-V-6-6 in this species.

Phylogenetic analysis results

The analysis including the specimen referred as *Typotheeria* indet. A (MHAS 002) yielded 46 maximum parsimony trees (MPT) of 114 steps under EW, and five equally parsimonious trees of maximum fit (score = 7.66667) under IW. Strict consensus trees and support values for both methods are shown in [Figure 8](#).

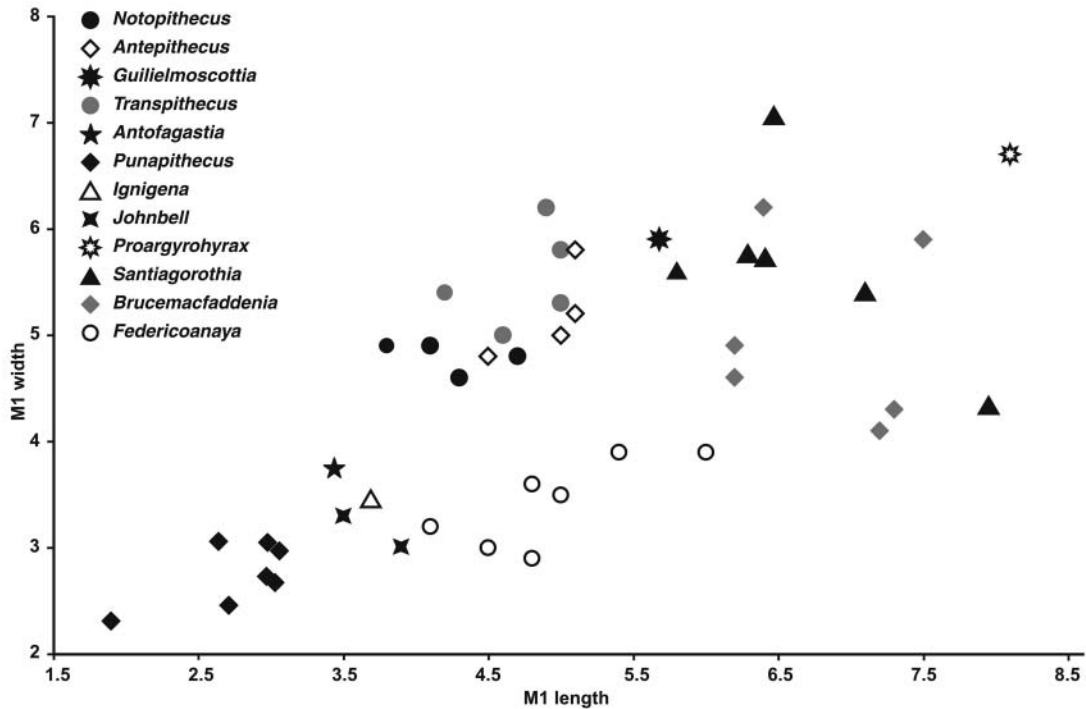


Figure 6. Bivariate plot of several interatheriid taxa comparing the size of M1. Measurements were taken directly from studied material and from Simpson (1967), Hitz *et al.* (2006, 2008) and Vera (2012).

In accordance with the more comprehensive analyses of Billet (2010, 2011), the family Oldfieldthomasiidae forms a paraphyletic cluster. In turn, members of this traditional group integrate two monophyletic groups identified as nodes A and B in Figure 8. Node A includes *Oldfieldthomasia* and *Acoelodus* and is supported by four synapomorphies under EW: ‘face pattern’ present in upper molars but ephemeral and with relatively shallow fossettes (character 10: state 1), presence of mesostyle (character 17: state 1), conspicuously long rostrum (character 33: state 1), and low rostrum (character 34: state 0). Among these, characters 10 and 17 represent autapomorphies for the clade. Under IW the number of synapomorphies is three (with character 34 excluded from them) and the number of autapomorphies is also three. Node B includes *Maxschlosseria*, *Ultrapithecus*, *Dolichostylodon* and

Tytopheria indet. A. Under EW this group is defined by the following synapomorphies: prominent metastyle in M1 extending far beyond the posterior edge of the distal cingulum in occlusal view (character 13: state 1), strong and high parastyle in M1 with prominent and well-developed column and overlapping with P4 (character 14: state 1), well-developed metacone column on M1–2 ectoloph, clearly wider than the paracone column in occlusal view (character 15: state 2), protocone larger than the hypocone in M1–2 (character 18: state 1), well-developed mesiolingual cingulum on m1–2 (character 26: state 0), labial sulcid on m1–2 reaching the coronal base (neck) (character 30: state 1), trigonid and talonid subequal in size in m2 (character 31: state 1), and weak and slender zygoma (character 41: state 0). Among these, characters 14 and 15 represent autapomorphies. Under IW the synapomorphies

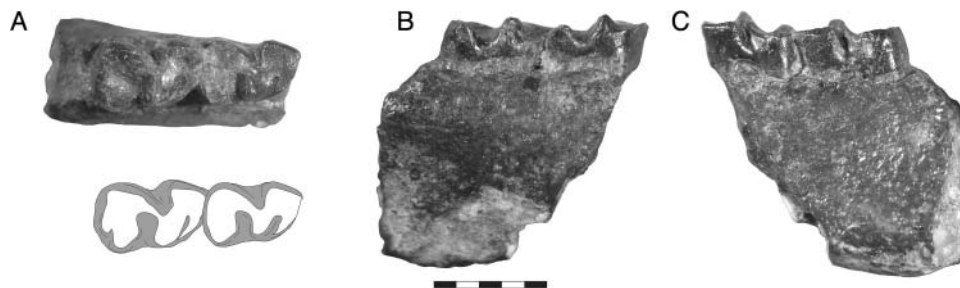


Figure 7. MLP 86-V-6-6, left mandibular fragment with p4 and m1, referred to *Punapithecus minor* by López & Bond (1995). **A**, occlusal view; **B**, lingual view; **C**, labial view. Scale bar equals 5 mm.

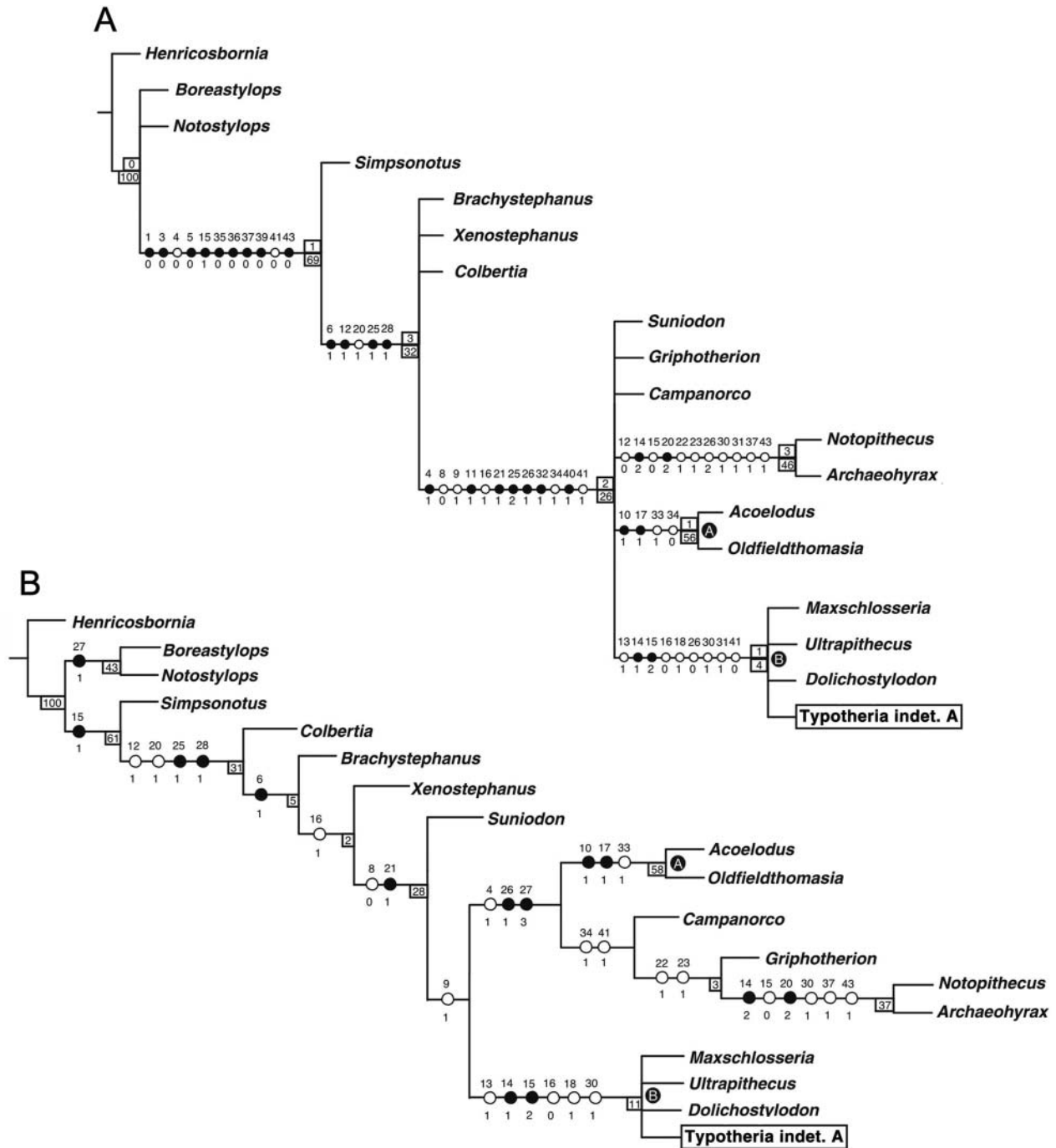


Figure 8. Phylogenetic position of *Typotheria indet. A* (MHAS 002). **A**, strict consensus tree (114 steps) under equally weighted characters; **B**, tree (score = 7.66667) under implied weights. Circles on nodes represent synapomorphies; black circles indicate autapomorphic features and white circles homoplastic synapomorphies. Upper numbers represent character number and lower numbers character states. Numbers enclosed in boxes indicate Bremer support (top) and symmetric resampling values (bottom).

(and autapomorphies) are the same excluding characters 26, 31 and 41.

The analysis for *Typotheria indet. B* yielded 16 MPT of 63 steps under EW, and five equally parsimonious trees of maximum fit (score = 2.0238) under IW. Strict consensus trees and support values for both methods are shown in Figure 9. The node including ‘archaeohyracids’, mesotheriids

and hegetotheriids is supported by four autapomorphies in both cases; these are the same as those listed by Billet *et al.* (2009) as unambiguous synapomorphies. *Punahyrax* and *Typotheria indet. B* are part of a polytomy basal to this clade. *Typotheria indet. B* is defined by two character states in both methods (EW and IW): presence of a small fossettoid between m3 entolophid and hypolophid

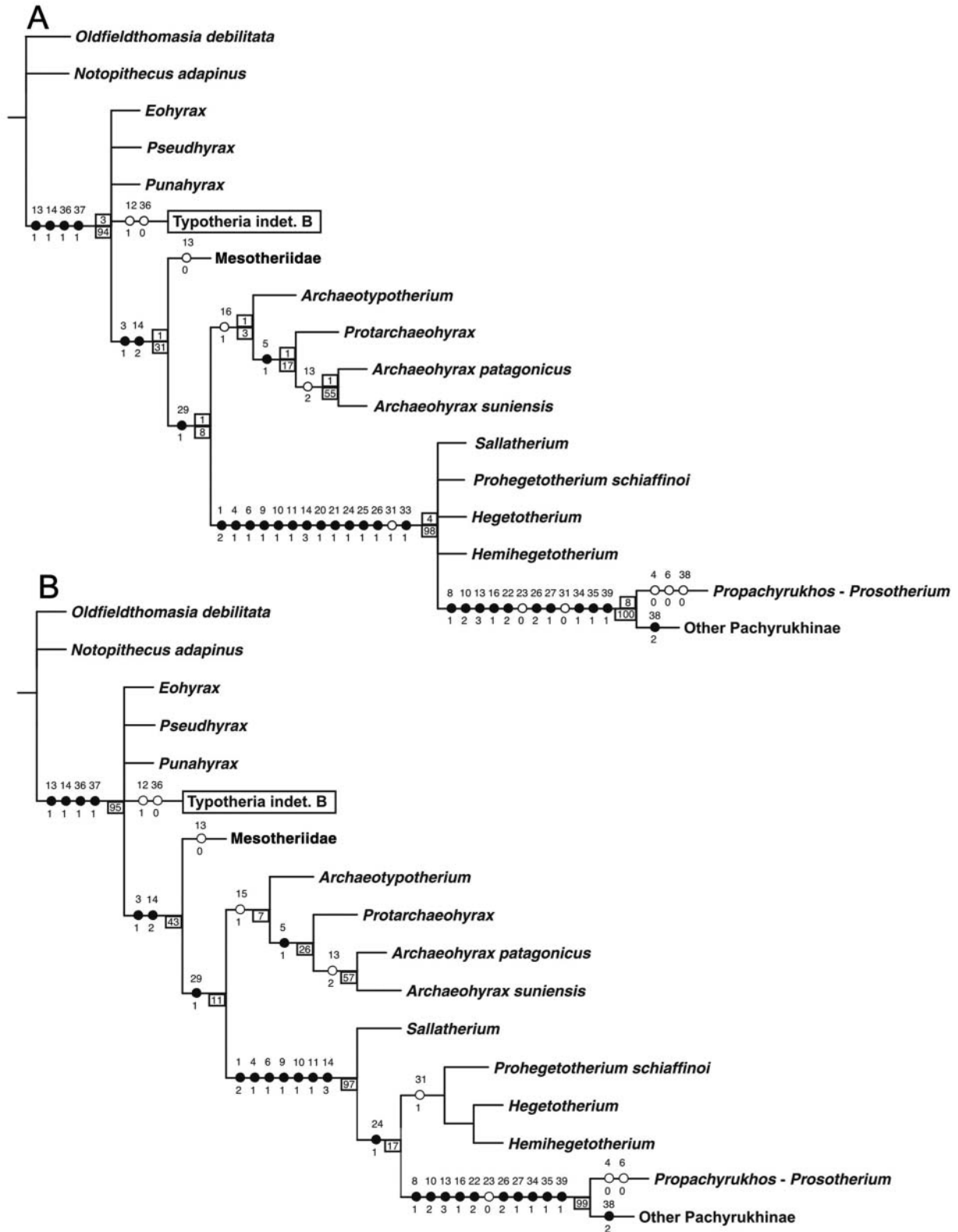


Figure 9. Phylogenetic position of *Typotheria indet. B* in the context of ‘Archaeohyracidae’, Mesotheriidae and Hegetotheriidae. **A**, strict consensus (63 steps) under equally weighted characters; **B**, tree (score = 2.0238) under implied weights. Circles on nodes represent synapomorphies; black circles indicate autapomorphic features and white circles indicate homoplastic synapomorphies. Upper numbers represent character number and lower numbers character states. Numbers enclosed in boxes indicate Bremer support (top) and symmetric resampling values (bottom).

(character 12: state 1) and trigonid fossettid absent in lower molars (character 36: state 0).

The analysis performed to resolve the position of *Antofagastia* and *Punapithecus* yielded 16 trees under EW (90 steps) and one tree under IW (score = 4.46230). In both cases the topology is basically the same; however, the analysis under IW shows greater resolution (resolving the position of *Notopithecus* and *Antepithecus* and some nodes within Interatheriinae). Strict consensus trees for both analyses and support values are shown in Figure 10. Interatheriidae (node A in Fig. 10) is defined by the same eight characters proposed by Hitz *et al.* (2006). Among basal interatheriids, *Guiliemoscottia* and *Transpithecus* form a monophyletic group (node C in Fig. 10) defined by anterior cingulum absent and posterior cingulum high on crown, merging early with wear on P2–4 (character 11: state 1), and anterior cingulum absent on M1–3 (character 19: state 1). *Antofagastia turneri* is located at the base of node D (Fig. 10) as sister taxon of the rest of Interatheriidae excluding *Notopithecus*, *Antepithecus* and node C. Node D is defined by two synapomorphies: paracone/parastyle inflection on M1–3 absent or reduced (character 12: state 1) and very small size (character 46: state 1; autapomorphy). *Punapithecus* is the most basal taxon within the immediately less inclusive clade (node E) and sister group of node F which matches with node 2 of Hitz *et al.* (2006, fig. 6). The arrangement of *Eopachyrucos* plus Interatheriinae is almost the same as that of these authors and, given the scope of the present contribution, will not be discussed here.

Discussion

The phylogenetic context of several groups of Paleogene notoungulates remains obscure in several points, despite some recent efforts (Billet 2010, 2011). A number of traditionally accepted groups have proved to be paraphyletic, including most of those in which various notoungulates from the Geste Formation are included. Interatheriidae is, in fact, the only group recognized as natural among the family-level taxa mentioned in this contribution.

Along with the fact that many notoungulate remains found in the Geste Formation show generalized morphologies, with similar forms being difficult to distinguish, an additional problem is the very fragmentary nature of the material recovered. In most cases, the information contained in the specimens is very scarce and diagnostic features are rarely preserved, preventing generic or specific assignment or the unambiguous recognition of new taxa. Despite this fact, we included some of the new specimens in the different phylogenetic analyses in order to obtain a wider view of the role played by the notoungulates of the Geste Formation in the evolutionary history of this group.

Below we discuss the phylogenetic position of the new fossils referred as *Typrotheria* indet. A and B, and the interatheriid *Antofagastia turneri*. Additionally, we discuss some singularities of the entire notoungulate record of the Geste Formation and the age of this unit.

Phylogenetic position of *Typrotheria* indet. A and *Typrotheria* indet. B

The Family Oldfieldthomasiidae was proposed by Simpson (1945) as part of his suborder Toxodonta (currently known as Toxodontia). Later, he reassigned the family to *Typrotheria* (Simpson 1967) and for several years ‘oldfieldthomasiids’ represented the most basal members of this suborder. In later decades, ‘morphological groups’ were proposed within the family, mainly separating Patagonian from non-Patagonian forms (Bond 1981; López 1995; Montalvo & Bond 1998). Nevertheless, the integrity of Oldfieldthomasiidae was not questioned until the work of Cifelli (1993) who raised the possibility of the paraphyly of the group. Later, López & Bond (2003) recognized the paraphyly of the group and proposed the erection of a new, unnamed family comprising some taxa traditionally referred as ‘oldfieldthomasiids’: *Colbertia*, *Brachystephanus*, *Xenostephanus*, *Allalmeia* and some species of *Maxschlosseria*. More recently, the phylogenetic position of representatives of this family was assessed by López (2008) and García-López (2009), each proposing different arrangements for these taxa. Finally, in an extensive phylogeny of Notoungulata, Billet (2010, 2011) proposed formally the paraphyly of Oldfieldthomasiidae.

As mentioned before, the analysis published in the current paper is based on the unpublished data matrix built by one of us (DAGL) for a PhD dissertation (García-López 2009) and the results are basically the same. Two monophyletic groups were recovered. Specimen MHAS 002 is grouped together with *Dolichostylodon*, *Ultrapithecus* and *Maxschlosseria*. This result is intriguing for two reasons. The first is that *Suniodon catamarcensis*, the other ‘oldfieldthomasiid’ recorded from the Geste Formation in Antofagasta de la Sierra (López 1995), is not included in that group, discarding the possibility that MHAS 002 belongs to this species (note that the type specimen and all other specimens referred to *S. catamarcensis* are represented by upper dentition, while MHAS 002 is a mandibular fragment). The second reason is that this monophyletic group was previously recovered in another contribution (García-López 2009), where the possibility of a new family-level arrangement within the paraphyletic ‘Oldfieldthomasiidae’ was considered. However, the very low support for this arrangement (Fig. 8) prevents us from accepting conclusively this finding. Further work focused on members of the unnatural group ‘Oldfieldthomasiidae’ should be carried out, including the revision and evaluation of the validity of known species

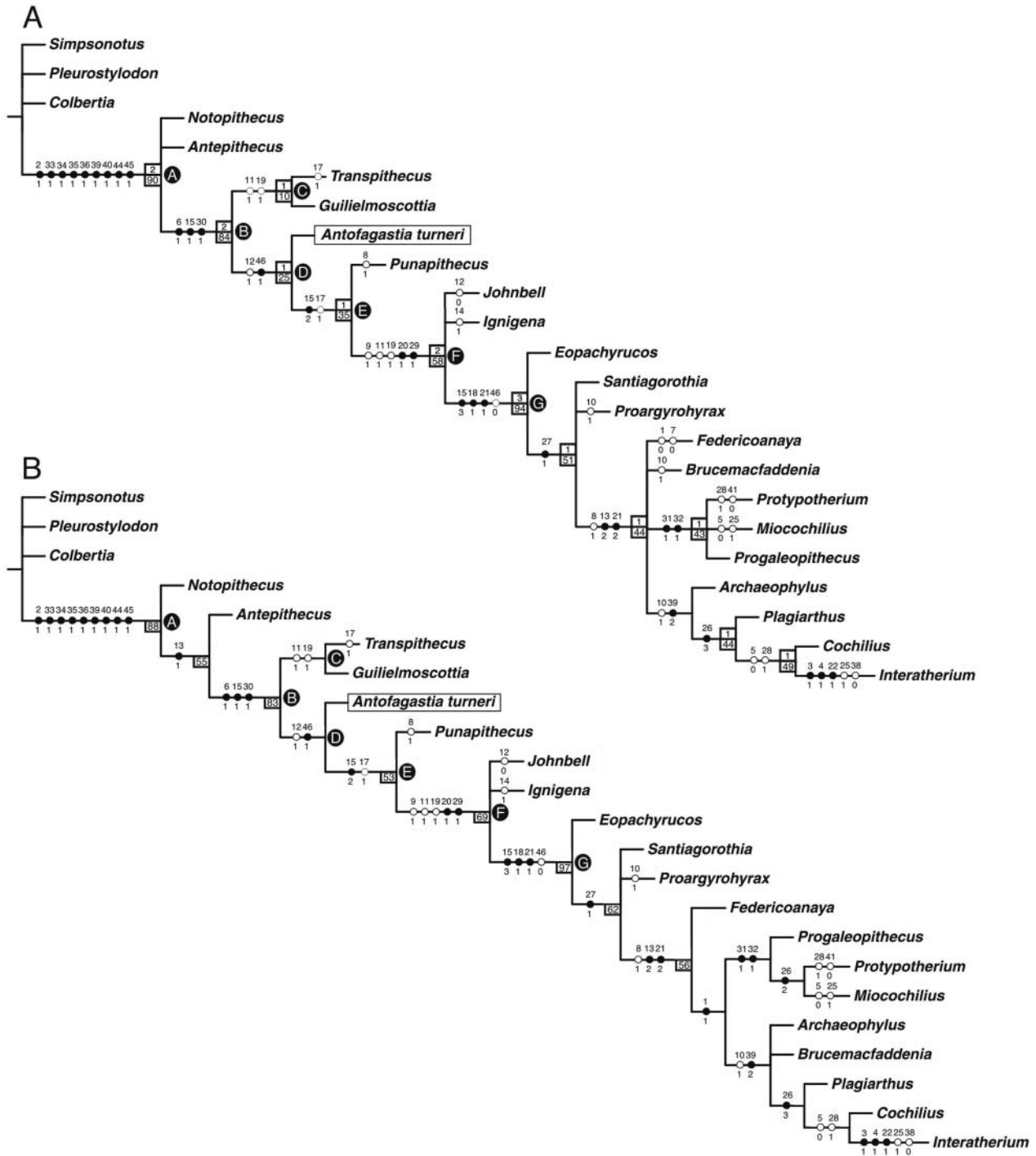


Figure 10. Phylogenetic analysis of Intertheriidae. **A**, strict consensus (90 steps) under equally weighted characters; **B**, tree (score = 4.46230) under implied weights. Circles on nodes represent synapomorphies; black circles indicate autapomorphic features and white circles homoplastic synapomorphies. Upper numbers represent character number and lower numbers character states. Numbers enclosed in boxes indicate Bremer support (top) and symmetric resampling values (bottom).

and the recovery of more complete and better-preserved specimens. Even so, these results imply that, as for other taxa, a mosaic of forms coexisted in this area, with some diversity of basal representatives and a complex biostratigraphical framework.

In the light of our results, the specimens referred as *Typotheria* indet. B and *Punahyrax bondesioi* occupy a basal position in the context of the ‘Archaeohyracidae’, Mesotheriidae and Hegetotheriidae. In the case of *Punahyrax*, this partially agrees with previous approaches that

have shown this taxon in a basal position in a similar context (Reguero *et al.* 2008). In the original analysis performed by Billet *et al.* (2009), mesotheriids were nested between *Eohyrax* and *Pseudhyrax* (referred to as ‘early archaeohyracids’ in the present contribution) and a clade formed by the ‘late archaeohyracids’ and hegetotheriids. In this new approach, Typotheria indet. B is part of the same polytomy in which *Punahyrax* is included along with the ‘early archaeohyracids’. It should be noted that any of the possible resolutions of this polytomy show Typotheria indet. B as sister taxon of the group Mesotheriidae + ‘late archaeohyracids’ + hegetotheriids. The poor resolution obtained (at least for this node) prevents us from making further statements, and only future findings of more complete specimens of this morphotype will provide the data necessary to solve this problem.

Phylogenetic position of *Antofagastia turneri*

As was already pointed out, the data matrix used for the analysis of intertheriids was taken from Hitz *et al.* (2006) with some modifications (see Supplemental Appendix 2). The results here obtained are very similar to those obtained by these authors: Intertheriidae is recovered and supported by the same synapomorphies detailed by Hitz *et al.* (2006) (see node A in Fig. 10). Nevertheless, this new analysis yielded a more resolved tree, especially for the relationships between basal intertheriids. The analyses performed considering equally weighted characters and under IW show mainly the same arrangements but differ in the degree of resolution (resolving the position of *Notopithecus* and *Antepithecus* for basal intertheriids, and partially resolving some nodes within more derived intertheriines under IW). *Notopithecus* and *Antepithecus* are located as the most basal intertheriids, with *Notopithecus* being the most basal genus in the IW analysis. This arrangement was discussed by Hitz *et al.* (2006), and the basal position of *Notopithecus* is congruent with the traditional phylogenetic framework (Cifelli 1993; Hitz *et al.* 2000; Billet 2010, 2011).

An interesting result of the analysis is the grouping of the Patagonian forms *Transpithecus* and *Guilielmoscottia* in a basal monophyletic group (node C) defined by two synapomorphies (see Results). *Transpithecus* was recently revised and restricted to the Barrancan subage of the Casamayoran SALMA (Vera 2012) while *Guilielmoscottia* is a Mustersan genus (Simpson 1967; Reguero & Prevosti 2010). A close relationship between these two taxa has not been recovered in any previous cladistic analyses (e.g. Hitz 1997; Hitz *et al.* 2006, 2008), although Simpson (1967) considered this possibility. *Guilielmoscottia* was originally included in Archaeopithecidae, a precociously hypsodont family of poorly known notoungulates. However, Simpson (1967, p. 75) observed that “*Guilielmoscottia* (...) may be more closely related to

Transpithecus than to *Archaeopithecus*” and both genera had to be considered as part of ‘Notopithecinae’. Later in the same contribution he remarked “*Transpithecus* is still closer to the Mustersan *Guilielmoscottia* to which it is probably ancestral” (p. 101). Additionally, he proposed some morphological bases for these statements: “among other known forms it [*Guilielmoscottia*] most closely resembles the Casamayoran *Transpithecus* and could be derived from the latter by accentuating the peculiar character of the inner lobes of the molars, carrying this forward in attenuated form to the premolars, and having M3 more triangular or ‘terminalized’.” Although these features are only vaguely stated by Simpson, apparently the synapomorphies that support node C in the present analysis partially concur with the observations made by him. Particularly the feature ‘M3 more triangular’ can be considered as included within character 19 (state 1), which refers to the absence of an anterior cingulum on M1–3 since the absence of the cingulum gives a ‘more triangular’ occlusal outline to the tooth. However, it should be noted that this feature defining node C is homoplastic (as the other character supporting the node): it also defines node F including *Ignigena* and *Johnbell* plus *Eopachyrucos* and Intertheriinae. The addition of more detailed craniodental data is necessary to confirm the validity of this clade in future studies.

The immediate less inclusive group in the cladogram (node D) includes *Antofagastia* plus node E in Figure 10. Two synapomorphies diagnose node D, character 12 and 46, of which character 46 is an autapomorphy. Character 12 refers to the paracone/parastyle inflection on upper molars; after the detailed revision of the taxa involved in the analysis, we changed the scoring for *Archaeophylus*, *Federicoanaya*, *Brucemacfaddenia*, *Proargyrohyrax*, *Johnbell* and *Punapithecus* (see details in Supplemental Appendix 2). Character 12 was considered by Hitz *et al.* (2006, node 2) as a synapomorphy for a clade comprising *Johnbell*, *Ignigena*, *Eopachyrucos* and Intertheriinae. In this context, the expression of state 1 of this character (absent or reduced inflection) occurs earlier, in a more basal position than previous analyses. Character 46, related to the size of M1, has received some attention in previous publications. Hitz *et al.* (2006, character 43) observed that very small size was a feature common to three taxa – *Punapithecus*, *Ignigena* and *Johnbell* – noting that these were extra-Patagonian forms. Nevertheless, this feature does not diagnose any clade in their analysis and according to their results its distribution is due to convergence. Even so, they mention the possibility that small body size is associated with biogeographical provincialism, temporal distribution, or clinal variation. The inclusion of *Antofagastia turneri* brings a new basis for its interpretation. This new taxon represents a very small form considering the definition of character 46 (mesiodistal and labiolingual length of M1 < 4 mm), being similar

in size than *Johnbell* and *Ignigena* and hence larger than *Punapithecus*. Unlike the results of Hitz *et al.* (2006), very small size represents an autapomorphy in our analysis, defining part of the stem lineage of the tree. Character 46 also occurs as a synapomorphy in node G (*Eopachyrucos* plus Interatheriinae), where it suffers a reversal (1 → 0). Hitz and colleagues considered that the small size of northern interatheriids (*Punapithecus*, *Johnbell*, *Ignigena*, and now, *Antofagastia*) “may reflect minor geographic provincialism or clinal variation” (Hitz *et al.* 2006, p. 27). It should be noted that the theoretical bases of provincialism used by these authors are not entirely accurate. This pattern, involving the congruent distribution of several taxa in a restricted area, cannot be established from the currently available fossil record. Even so, considering only the pattern of distribution of the small size condition in our phylogenetic hypothesis, we can point out that this is not geographically associated; the same result was obtained in the phylogeny performed by Hitz *et al.* (2006). Small north-western Argentinean and Chilean forms do not constitute a monophyletic group and central Chile shows more faunistic affinities with Patagonia than with north-western Argentina, sharing some taxa (e.g. *Santiagorothia*) and being geographically closer. Regarding clinal variation, we also consider that the knowledge of fossil faunas of north-western Argentina is still too poor to make any conclusive assertion about this hypothesis.

The temporal distribution of small forms, also considered by Hitz *et al.* (2006), can be also questioned since given the possible Casamayoran age of the levels where *Ignigena* was found, this range would be too wide (Casamayoran–Tinguirirican) and largely overlaps the temporal distribution of larger interatheriids (Fig. 11). Nevertheless, it should be noted that if recent age assignments for the Geste Formation that point to a Barrancan depositional age are confirmed (Powell *et al.* 2011; Herrera *et al.* 2012), this would concentrate most small forms in the late Casamayoran or Barrancan stage (but see discussion below on the age of the Geste Formation for other interpretations).

The phylogeny recovered here shows that the validity of synapomorphies can be variable in the light of new discoveries, as previously concluded by Hitz *et al.* (2006). The definition of intra-familial clusters (e.g. subfamily Interatheriinae) is liable to modification as new materials become known, and this is particularly true for families such as Interatheriidae where several, mostly basal taxa are only known from dental remains. Character distribution along the most distal nodes here considered (node F, node G and Interatheriinae) shows some differences compared to previous analyses, particularly Hitz *et al.* (2006). Node F encompassing Chilean forms (*Ignigena* and *Johnbell*) plus *Eopachyrucos* and Interatheriinae matches node 2 of the consensus tree shown by these authors. This node is supported in our analysis by five apomorphies, two of

which are autapomorphic. Characters 9 (state 1; P2–4 metacone ectoloph very low or almost flat), 20 (state 1; M1–3 longer than wide), and 29 (state 1; m1–3 bilobed) match with the features supporting the node in Hitz *et al.* (2006), being characters 20 and 29 autapomorphies in our results. However, character 12, as was noted above, appears more basal in our analysis (node D) than in the results of Hitz *et al.* (2006) and two other synapomorphies were added to node F: character 11 (state 1; cingula on P2–4) and 19 (state 1; anterior cingulum absent on M1–3). The definition of node G (*Eopachyrucos* plus Interatheriinae) is different from that of Hitz *et al.* by the absence of one synapomorphy (related to character 7; parastyle/paracone inflection on upper premolars) and the addition of two new ones: character 15 (state 3; lingual sulcus on M1–2 completely persistent) and character 46 (interpreted as a regression to state 0; moderate to large size). Finally, it is striking that in our results Interatheriinae is only defined by one unequivocal synapomorphy (character 27, state 1; bilobed p3–4), also recovered by previous authors (Hitz *et al.* 2000, 2006). Nevertheless, other features that reflect cranial differences were not recovered as synapomorphies in our analysis, although such features were considered as provisional diagnostic characters by Hitz *et al.* (2006).

Notoungulate record of the Geste Formation and chronological considerations

Previous contributions have noted the great relevance of the Paleogene record of notoungulates from north-western Argentina for understanding the early history of several lineages in this group (Reguero *et al.* 2008; García-López 2009; Deraco *et al.* 2009; García-López & Powell 2011). Multiple early-diverging taxa were recorded in the north-western provinces, and the lack of genera shared with Patagonian localities indicates some degree of faunal singularity. Genera like *Simpsonotus*, *Colbertia*, *Punahyrax*, *Coquenia* and *Griphotherion* represent a wide taxonomic mosaic within the order and occupy key basal positions for different lineages (Reguero *et al.* 2008; Deraco *et al.* 2009; García-López 2009; Billet 2010, 2011; García-López 2011; García-López & Powell 2011). Hence, north-western Argentina represents a major area for the preservation of early members of different groups, particularly tyotherians.

Apparently, Interatheriidae would be a *prima facie* exception to this framework, since the most basal and ancient representatives (from the Riochican SALMA) are recorded in Patagonian outcrops and the interatheriid record in the north-western provinces is very scarce. Nevertheless, increased knowledge of this family and the new records reported here and in previous studies shed new light on their Paleogene history. Extra-Patagonian forms, including north-western Argentinean taxa, are

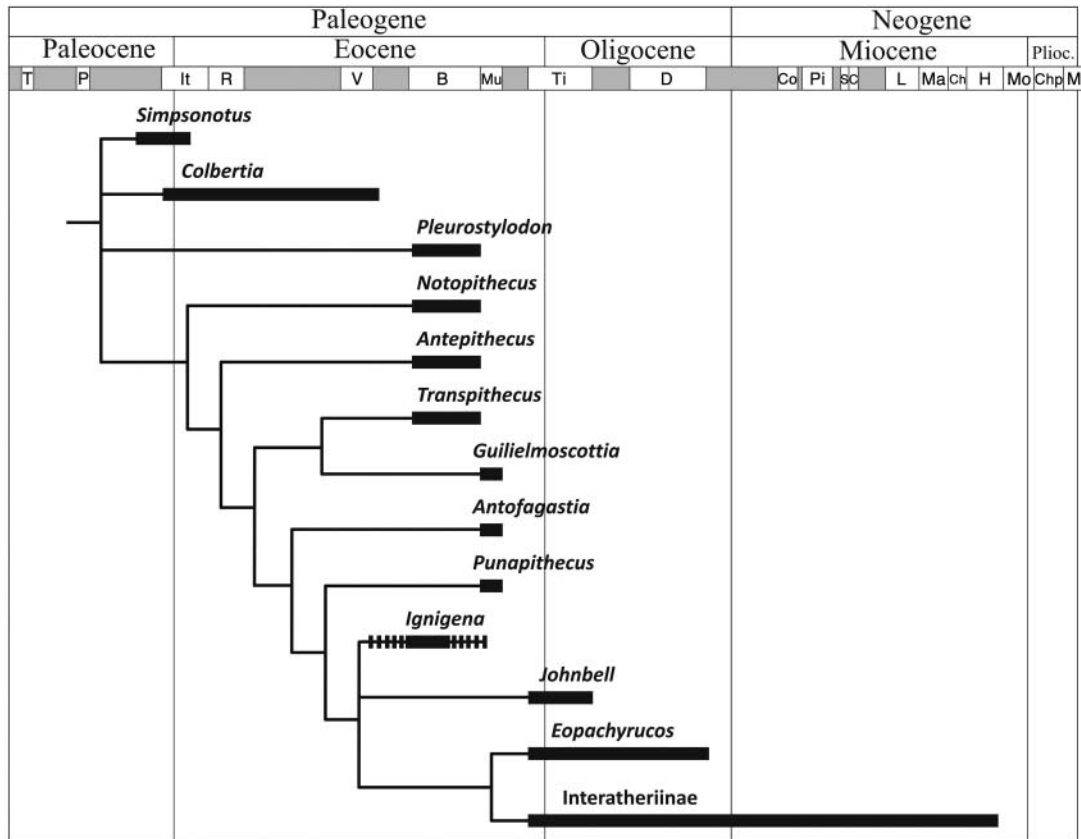


Figure 11. Temporal distribution of basal intertheriids. South American Land Mammal Ages after Goin *et al.* (2012). Abbreviations: B, Barrancan; C, ‘Colloncuran’; Ch, Chasicuan; D, Deseadan; H, Huayquerian; It, Itaboraian; L, Laventan; M, Marplatan; Ma, ‘Mayoan’; Mo, Montehermosan; Mu, Mustersan; P, Peligran; Pi, ‘Pinturan’; S, Santacrucian; T, Tiu-pampán; Ti, Tinguirirican; V, Vacan.

concentrated in a significant segment of the stem leading to Interatheriinae, where some morphological novelties (such as smaller body size) are expressed and where the beginnings of certain changes in the evolutionary history of the group are visible (e.g. changes in degree of hypsodonty reflected in the loss or modification of features such as fossettes and cingula). These changes determine the sequential appearance of characters once thought to emerge near or at the base of Interatheriinae.

In the context of north-western Argentina, the relationships of the fossil record of the Geste Formation with surrounding Paleogene units remain debatable. The most striking singularity is related to the abundance of interatheriid and ‘archaeohyracid’ remains (particularly in Antofagasta de la Sierra; Table 3). These groups represent by far the most abundant notoungulate fossils in this locality and have not yet been recorded in the probably contemporaneous Lumbreira, Casagrande and Quebrada de los Colorados formations (Pascual *et al.* 1981; del Papa *et al.* 2010; Powell *et al.* 2011). This fact has been noted by previous authors, at least for the Lumbreira Formation (López & Bond 1995), and can be explained by sampling

bias, differences in age, biogeographical barriers, or a combination of these factors.

There is no doubt that a bias affects sampling of the Geste Formation. The fossils found in this unit are disarticulated and highly fragmented, showing clear signals of transport and size selection (average size about 15 mm). In this sense, the probability for the preservation of medium-sized or large mammals is low, although their presence in these outcrops is documented mainly by isolated teeth, of, for example, isotemnid, notohippids (see López 1997) and large sparassodont metatherians (Goin *et al.* 1998; Powell *et al.* 2011). In other words, fossils of medium to large mammals are generally reduced to unidentifiable fragments, while the remains of smaller mammals can preserve much more diagnostic information, allowing satisfactory assignment. This bias means that the abundance of small interatheriid and ‘archaeohyracid’ specimens in the Geste Formation does not necessarily indicate that they were really the most abundant notoungulate taxa in this unit. Interestingly, the same kind of bias has been noted in the Paleogene locality of Contamana, Perú (Antoine *et al.* 2012). In this case,

Table 3. South American native ungulates from the Geste Formation outcropping at Antofagasta de la Sierra, Catamarca province (AdSa) (26° 03' 35.8" S, 67° 24' 22.1" W), and the surroundings of the Pozuelos salt flat, Salta (Po) (24° 30'–24° 45' S, 66° 35'–66° 45' W).

Taxa	Recovered specimens	Locality	References
Order 'Condylarthra'			
cf. <i>Ernestokokenia</i>	1	AdSa	López (1997)
Order Litopterna			
Litopterna indet.	1	AdSa	Armella (2014)
Order Pyrotheria			
Family Pyrotheriidae			
Genus <i>Propyrotherium</i>			
<i>Propyrotherium</i> sp.	1	AdSa	López (1997)
Order Astrapotheria			
Family Astrapotheriidae			
Gen et sp. indet.	1	AdSa	López (1997)
Order Notoungulata			
Family Notospylopidae			
Gen et sp. indet.	2	AdSa	López (1997)
Family ?Notostylopidae	1	AdSa	López (1997)
Suborder Toxodontia			
Family Isotemnidae			
Gen. et sp. indet.	2	AdSa	López (1997)
Gen. et sp. indet.	1	AdSa	Armella (2014)
Gen. et sp. indet.	1	AdSa	Unpublished data
Family Notohippidae			
cf. <i>Pampahippus</i>	1	AdSa	López (1997)
Gen. et sp. indet.	1	AdSa	Unpublished data
Suborder Typotheria			
Family Oldfieldthomasiidae			
Genus <i>Suniodon</i>			
<i>Suniodon catamarcensis</i>	2	AdSa	López (1995)
<i>Suniodon</i> sp.	1	AdSa	Unpublished data
Family Oldfieldthomasiidae			
Genus <i>Colbertia</i>			
<i>Colbertia</i> sp.	1	AdSa	López (1995, 1997)
Gen. et sp. indet.	1	AdSa	López (1995, 1997)
Gen. et sp. indet.	1	AdSa	Unpublished data
Family Interatheriidae			
Genus <i>Punapithecus</i>			
<i>Punapithecus minor</i>	19	AdSa; Po	López & Bond (1995); this contribution
Genus <i>Antofagastia</i>			
<i>Antofagastia turneri</i>	1	AdSa	This contribution
Gen et sp. indet.	3	AdSa	Armella (2014)
Gen et sp. indet.	1	AdSa	Unpublished data
Family Archaeohyracidae			
Genus <i>Punahyrax</i>			
<i>Punahyrax bondesioi</i>	15	AdSa; Po	Alonso (1992); López (1997); Reguero <i>et al.</i> (2008); this contribution
Gen et sp. indet.	2	AdSa	Unpublished data
Typotheria indet. A	1	AdSa	This contribution
Typotheria indet. B	3	AdSa	This contribution
Notoungulata indet.	1	AdSa	This contribution

'archaeohyracids' and basal interatheriids are also the most complete and identifiable specimens.

However, as pointed out previously, 'archaeohyracids' and interatheriids have not yet been recorded in

neighbouring Eocene formations of north-western Argentina, and so their presence in Eocene outcrops of the Puna is notable. An additional argument can be made pointing to taphonomic peculiarities preventing the preservation of

small-sized taxa, or sampling biases in these surrounding units, with fossil sampling focusing on large vertebrates. Nevertheless, it should be noted that the fossilization potential of units such as Lumbrera and Casagrande is very high and very complete small-sized specimens other than interatheriids and ‘archaeohyracids’ have been found in these deposits (e.g. Pascual 1980a, b; García-López & Powell 2009). In summary, it can be concluded that the presence of these two groups in the Geste Formation represents a true faunal singularity for this unit in the region.

Chronological factors can also be considered as explanations for these faunal differences. The age of the Geste Formation has been extensively discussed in different contributions. Several earlier authors have listed biostratigraphical evidence supporting a Mustersan SALMA assignation for this unit (e.g. Alonso & Fielding 1986; López 1997; Goin *et al.* 1998), followed with reservation in recent studies (Reguero *et al.* 2008). This evidence includes the presence of Patagonian Mustersan taxa, such as *Propyrotherium*, the ‘evolutionary degree’ of north-western Argentinean metatherians and native ungulates, and the shared record of ungulates (e.g. an isotemnid; see Bond & López 1995) between the Geste Formation and other alleged Mustersan SALMA units of north-western Argentina (i.e. the Casa Grande Formation). The single record of *Propyrotherium* in the Geste Formation is highly doubtful, as noted by Reguero *et al.* (2008) and therefore does not represent good support for this age assignment. We consider the ‘evolutionary degree’ of the taxa as a vague concept, often not well defined, and not a valuable tool to assess the age of Paleogene units within short periods (such as the Barrancan–Mustersan span) since the number of apomorphic states present in a taxon is linked to different and complex factors, not just time. Finally, the common record of an isotemnid in the Geste and Casa Grande formations is not considered as conclusive since it has yet to be published and no other mention is made in recent publications. Moreover, it should be noted that the Mustersan SALMA assignation for Casa Grande has been challenged and the formation was correlated with older units (see below). For all these reasons, we believe that the biochronological evidence for assignment of the Geste Formation to the Mustersan SALMA is not conclusive.

Recent palaeontological contributions have hypothesized stratigraphical correlation of the Geste, Lumbrera, Casa Grande and Quebrada de Los Colorados formations due to the common presence of the peculiar dasypodid *Pucatherium parvus* (Powell *et al.* 2011; Herrera *et al.* 2012; Herrera 2013). Given this correlation, all these units were assigned to the Barrancan subage (late Middle Eocene) on the basis of an isotopic date of 39.9 Ma from a top bed of the Lumbrera Formation (del Papa *et al.* 2010) and the presence of taxa also found in Barrancan Patagonian outcrops (Herrera 2013). Therefore, this new direct

biochronological information points to an older age for the Geste Formation. However, the biostratigraphical value of dasypodids was only recently considered and needs to be assessed in the future.

Other authors have correlated the Geste Formation with different units on the basis of lithological evidence, ranging from the earlier Eocene (Marshall *et al.* 1997; Sempere *et al.* 1997) to the Late Eocene (Voss 2002). Finally, and more importantly, recent isotopic dating focused on the Geste Formation has yielded ages ranging from the Middle to Late Eocene. DeCelles *et al.* (2007) and Carrapa & DeCelles (2008) published U-Pb detrital zircon ages for several samples taken from the Geste Formation near the Pozuelos salt flat. They found the age of the mammal-bearing levels to range from 37.3 ± 1.5 to 35.4 ± 0.55 Ma, which is partially coincident with the Mustersan SALMA.

In summary, among different lines of evidence used to assess the age of the Geste Formation, biochronological evidence should not be ignored but seems to be relatively inconclusive. Trust must be placed on isotopic dating data, which points to a Late Eocene age for vertebrate-bearing levels of the Geste Formation. Given this chronological framework, the Geste Formation is younger than neighbouring Eocene units (e.g. Lumbrera Formation). This could explain, in some measure, the faunal differences noted above and support an extra-north-western Argentinean early evolution scenario at least for Interatheriidae, with these forms reaching this region subsequently.

Even assuming chronological differences with surrounding Paleogene units, palaeobiogeographical factors should not be ignored when explaining the faunal singularities of the Geste Formation. These deposits formed in an isolated context (in contrast to other Puna plateau deposits, such as those located in Southern Bolivia), suggesting intermontane basin deposition or local wedge-top basins (Carrapa & DeCelles 2008). This geological framework, together with probable regional and local high-relief uplift that had occurred by the Late Eocene or earlier (DeCelles *et al.* 2007; Carrapa & DeCelles 2008; Barnes & Ehlers 2009), could indicate that biogeographical barriers were an important factor acting on notoungulate distributions, producing clear environmental contrasts.

Conclusions

Despite the fragmentary nature of the fossil material found in outcrops of the Geste Formation, a wide diversity of basal forms in several suprageneric clades has been described. Specimen MHAS 002 (*Typrotheria* indet. A) is part of an unnamed clade which groups several taxa traditionally referred as ‘Oldfieldthomasiidae’ and including

Patagonian and non-Patagonian forms. Material referred to as *Typotheria* indet. B is placed within a polytomy of 'early archaeohyracids' in our analysis (which also includes *Eohyrax*, *Pseudohyrax* and *Punahyrax*). New specimens are referred to the species *Punapithecus minor*. These specimens and those previously known show different degrees of wear that were interpreted as four stages related to ontogenetic changes. *Antofagastia turneri* represents a new genus and species of basal interatheriids diagnosed by a combination of characters including small size, small central fossa, a particular configuration of the lingual sulcus, and cheek teeth wider than long. In a phylogenetic context, this record and the new information recovered for *P. minor* contribute to the resolution of phylogenetic relationships among basal interatheriids and add new data about character distribution in these forms.

The record of interatheriids and 'archaeohyracids' in north-western Argentina is restricted to the Geste Formation. In a phylogenetic context, these forms and those recorded in central Chile are located in a segment of the phylogenetic stem leading to Interatheriinae, where certain changes in the evolutionary history of the group are first expressed (e.g. increased hypsodonty). This highlights the importance of the north-western Argentinean fossil record for the study of early diversification of several notoungulate lineages.

Even though a taphonomic bias can be identified in the sampling of Geste Formation outcrops, the presence of interatheriids and archaeohyracids represents a faunal singularity in this unit. This difference with adjacent formations can also be due to chronological factors or biogeographical barriers. Given the apparent contradictions between isotopic dating and recent biostratigraphical evidence, age assessment of the Geste Formation remains unclear and it is possible that age differences among the Geste, Lumbrera, Casa Grande and Quebrada de los Colados formations may be relatively slight. On the other hand, recent structural hypotheses interpret the Geste Formation as being deposited as an isolated unit in the context of the early uplift of the Puna plateau. This suggests the possibility of the existence of biogeographical barriers separating the fauna of the Geste Formation from surrounding coetaneous units and explaining its distinctive nature.

Acknowledgements

We thank A. Kramarz (Museo Argentino de Ciencias Naturales 'Bernardino Rivadava'), J. Powell (Colección Paleontología de Vertebrados Lillo, Universidad Nacional de Tucumán) and M. Reguero (Colección Paleontología de Vertebrados, Museo de La Plata) for access to collections in their care. D. Croft and G. Billet made valuable

comments and suggestions that greatly helped to improve this contribution. R. Hitz and G. Billet kindly provided photographs of some of the taxa used in this study (*Ignigena*, *Johnbell*, *Plagiathrus* and *Ultrapithecus*), R. González made the drawing of the holotype of *Antofagastia turneri*, and M. Armella and F. Zannier provided valuable assistance during fieldwork. We also thank H. Carrizo and R. Grau for logistic support, and the Secretaría de Ganadería de Catamarca and Minera del Altiplano for housing our research team in the field. This study was supported by the Fundación Miguel Lillo [project code IPA-P1]; Agencia de Promoción Científica y Tecnológica [project code PICT 407].

Supplemental material

Supplemental material for this article can be accessed here: <http://dx.doi.org/10.1080/14772019.2014.930527>

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