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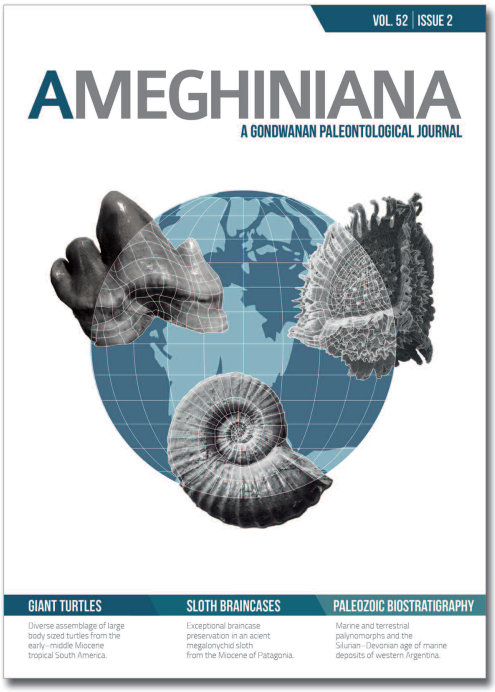

NEW INFORMATION ON THE INTERATHERIID *ANTOFAGASTIA TURNERI* GARCÍA-LOPEZ AND BABOT (MAMMALIA, NOTOUNGULATA) FROM NORTHWESTERN ARGENTINA

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NEW INFORMATION ON THE INTERATHERIID *ANTOFAGASTIA TURNERI* GARCÍA-LOPEZ AND BABOT (MAMMALIA, NOTOUNGULATA) FROM NORTHWESTERN ARGENTINA

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Key words. Interatheriidae. Eocene. Geste Formation. Intraspecific variation.

Reddish sandstone beds of the Geste Formation (middle–late Eocene) yielded an interesting and abundant record of fossil vertebrates. Since the earliest records in this unit almost three decades ago (Alonso and Fielding, 1986), several sauropsids, metatherians, and eutherians have been identified (López, 1997; Goin *et al.*, 1998). In spite of this diversity the taphonomic features of this stratigraphic unit have proved to be problematic, as all specimens are represented by fragments that, in several cases, lack enough diagnostic information (García-López and Babot, 2014). Nevertheless, at least five new mammalian species have been described and several previously known genera have been identified (López, 1995, 1997; López and Bond, 1995; Goin *et al.*, 1998; Reguero *et al.*, 2008; García-López and Babot, 2014). In this sense, the Geste Formation is –after the Lumbrera Formation– the richest and most productive Paleogene fossil mammal- bearing unit in northwestern Argentina.

Even though the Geste Formation is exposed at several locations along the Argentinean Puna, the localities of Pozuelos salt flat (Salta) and particularly Antofagasta de la Sierra (Catamarca) are the only sites where fossil-bearing beds have been found. Fossil remains of Notoungulata are abundant at these sites, particularly those of Interatheriidae (Typotheria) such as. *Punapithecus minor* López and Bond, 1995, which has been the only member of this family known for northwestern outcrops for almost 20 years. These records from the Geste Formation are remarkable because interatheriids are absent in other Paleogene units from northwestern Argentina (López and Bond, 1995; García-López and Babot, 2014).

Recently, another interatheriid was described for this unit. *Antofagastia turneri* García-López and Babot, 2014, was collected in deposits located near the town of Antofagasta de la Sierra. This species is a small basal interatheriid (Fig. 1) only slightly larger than *Punapithecus minor*. It shows brachydont upper molars with a narrow lingual sulcus and an oblique central fossa, among other features. The holotype is a fragment of a left maxilla with part of P4 and M1 and a very worn but complete M2–3 still showing several teeth features. Recent fieldwork at the type locality resulted in the recovery of two new specimens of this taxon. These specimens are represented by a maxillary fragment bearing teeth and an incomplete upper molar, both showing a lesser degree of wear than the holotype. In this contribution, I present these specimens and discuss the new features observed and their relevance in a phylogenetic and taxonomic context. Additionally, I analyze the morphology of two mandibular fragments bearing lower dentition, which show some traits that suggest that they might be referred to the genus *Antofagastia* García-López and Babot (2014). This study brings new information regarding intraspecific and ontogenetic variation, representing a valuable tool to assess the diagnostic features present in fossil fragments and isolated dental pieces.

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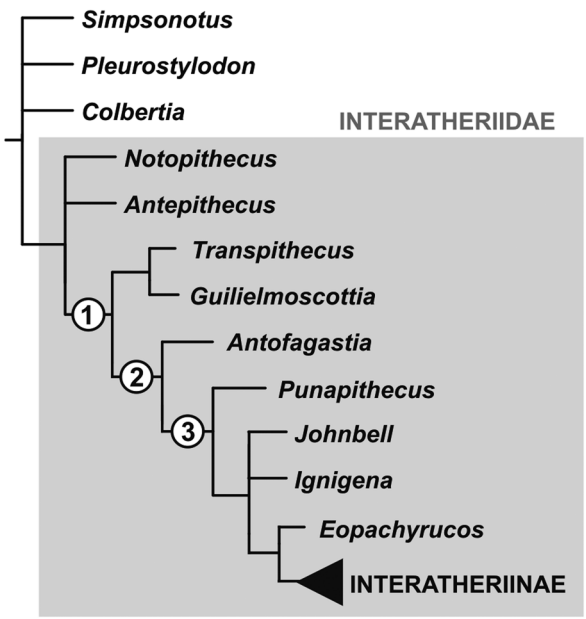

Figure 1. Cladogram showing the phylogenetic arrangement of the basal interatheriids and the distribution of some characters after García-López and Babot (2014). **1,** P1 with vertical mesiolabial crest, lingual sulcus well expressed although narrow on M1–2, and p4 molariform and p3 enlarged but smaller than molars; **2,** paracone/parastyle inflection absent or reduced on M1–3 and very small size; **3,** lingual sulcus on M1–2 well developed, persistent, relatively wide, and well expressed on the lingual wall, and hypocone present on M3.

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

SYSTEMATIC PALEONTOLOGY

Order Notoungulata Roth, 1903

Suborder Typotheria Zittel, 1893

Family Interatheriidae Ameghino, 1887

Genus ***Antofagastia*** García-López and Babot, 2014

Type species. *Antofagastia turneri* García-López and Babot, 2014; original designation. Late Eocene from northwestern Argentina.

Antofagastia turneri García-López and Babot, 2014
Figure 2

Referred specimens. MHAS 062, fragment of left maxilla with M1 and almost complete M2; MHAS 063, incomplete right M1.

Geographic occurrence. Antofagasta de la Sierra, Catamarca Province, Argentina (26°03′ 24.86″ S, 67°24′ 16.53″ W).

Stratigraphic occurrence. Middle section of the Geste Formation (*sensu* Alonso, 1992). Late Eocene.

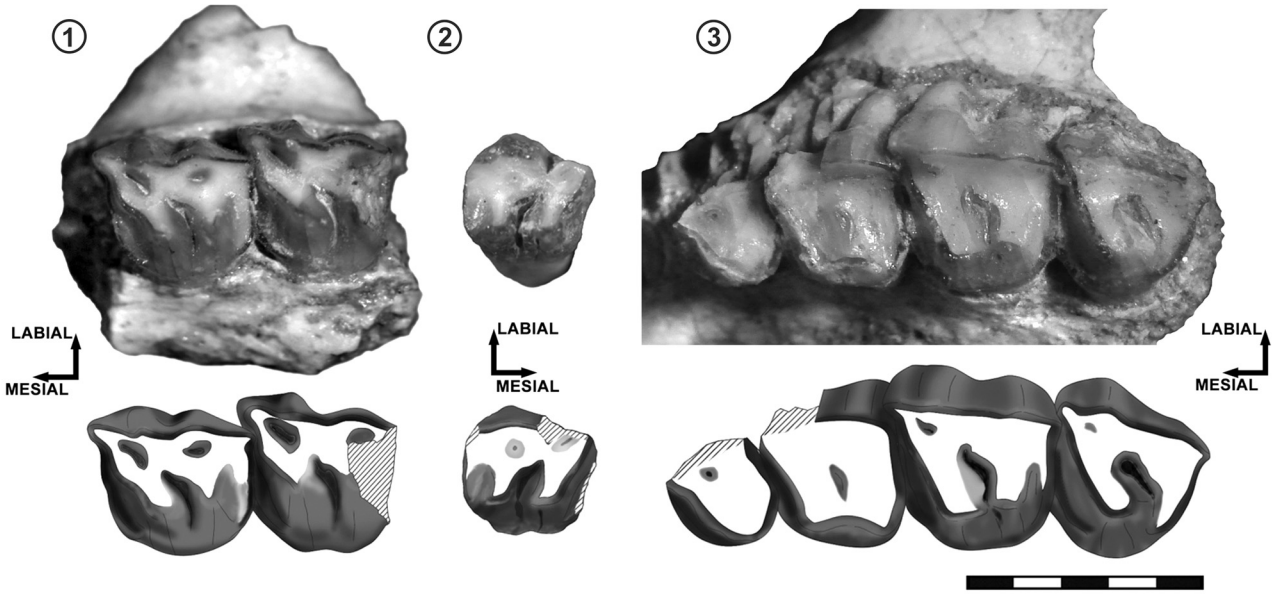

Figure 2. *Antofagastia turneri*; **1, MHAS** 062, left maxillary fragment with M1 and M2 in occlusal view; **2, MHAS** 063, incomplete right M1 in occlusal view; **3, MHAS** 003 (holotype), left maxillary fragment with incomplete P4 and M1–3 in occlusal view. Scale bar= 5 mm.

Description. These specimens are slightly smaller than the holotype of *Antofagastia turneri*; dental measurements are detailed in Table 1. The teeth in specimen MHAS 062 are almost complete and only the most distal part of the M2 is missing. Given the low degree of wear, almost all the features usually present in Paleogene typotherians are visible on MHAS 062 (mesiolabial and distolabial fossettes, central fossa, mesial and distal cingula, etc.). On the other hand, the tooth MHAS 063 is incomplete and shows a more advanced wear stage and some weathering. This tooth preserves approximately the 80% of the crown surface, lacking the mesiolabial and distolabial corners. Both fossettes are present, although the surface of the mesiolabial fossette is incomplete and the distolabial fossette is almost erased by wear. The mesial cingulum is also heavily worn by transport. All other features are the same for both specimens.

The M1 is present in both specimens. The mesiolabial fossette is larger than the distolabial fossette and bean-shaped in early wear stages (with a mesiolingual concavity). It is also oblique, and mesiolabially-distolingually oriented. The distolabial fossette is much smaller and slightly shallower than the former. Additionally, it is more mesiodistally oriented when it is not worn; under more advanced wear (as in MHAS 063) this fossette becomes very small and rounded. The central fossa is also visible and in all new specimens it is very similar to the fossa described for M2 in the holotype of *Antofagastia turneri* (see García-López and Babot, 2014). This structure is oblique and shallow and is lingually connected to a faint lingual sulcus. The parastyle is prominent on the M1 (this cusp is only preserved in the specimen MHAS 062) and is separated from the labial fold of the paracone by a shallow sulcus. The labial sulcus separating paracone and metacone fold is also shallow and wide. The metastyle is conspicuous (in MHAS 063 it is reduced by transport) and overlaps distally with the parastyle of the M2. In occlusal view, the protocone is larger than the hypocone. The protoloph shows a small mesial inflection in MHAS 062, differing from MHAS 063 and the holotype, which have no inflection. The mesial cingulum is small although it is clearly visible and ends at the mesiolingual corner of the protocone. The distal cingulum shows the same development and is located at the same height as the mesial cingulum. As already mentioned, the lingual sulcus is very narrow in occlusal view and poorly expressed on the lingual wall of the tooth.

The M2 is partially preserved in specimen MHAS 062, lacking the posterior part of the crown (including parastyle and distal cingulum). This tooth is very similar and shows almost the same features described by García-López and Babot (2014). Differences observed (*e.g.*, size, development of lingual sulcus and parastyle/paracone sulcus, etc.) will be discussed below. The only structure here preserved and not visible in the holotype is the distolabial fossette. Although not complete, it reveals that this structure is large at this wear stage and shows a similar arrangement to that present in the first upper molar.

Table 1. Measurements (in mm) of the specimens mentioned in the text. Upper teeth are indicated with upper case and lower teeth are indicated in lower case.

Specimen	***M1***		***M2***			
	L	***W***	***L***	***W***		
MHAS 062	*3.31*	*3.17*	*~3.45*	*3.35*		
	p4		***m1***		***m3***	
	L	***W***	***L***	***W***	***L***	***W***
MLP 86-V-6-6	*3.26*	*2.06*	*3.54*	*2.24*	-	-
MHAS 064	-	-	-	-	*4.15*	*2.13*

Abbreviations: ***L,*** *length;* ***W,*** *width.*

cf. ***Antofagastia***

Figure 3

Referred specimens. MLP 86-V-6-6, left mandibular fragment with p4 and m1; MHAS 064, right mandibular fragment with m3.

Geographic occurrence. Both specimens come from Antofagasta de la Sierra, Catamarca Province, Argentina. The coordinates for MLP 86-V-6-6 are 26°04′ S and 67°26′ W (following López and Bond, 1995) and for MHAS 064 are 26°03′ 43″ S, 67°24′ 27′ W.

Stratigraphic occurrence. Middle section of the Geste Formation (*sensu* Alonso, 1992). Late Eocene.

Description. Both specimens show a moderate degree of wear. Dental measurements are given in Table 1.

The specimen MLP 86-V-6-6 was already described by López and Bond (1995) as *Punapithecus minor*. It should be noted that these authors first mentioned the specimen as bearing a p4 and m1 but later in the same contribution they mention the same specimen as bearing p3 and p4 (see López and Bond, 1995, p. 96). García-López and Babot (2014) mentioned MLP 86-V-6-6 as bearing p4 and m1. The latter interpretation is herein supported and the apparent contradiction of López and Bond (1995) is considered to be due to a misprint or typing error. The p4 shows a relatively high molarization evidenced mostly by the large occlusal surface of the talonid compared to the trigonid (a feature already pointed by the mentioned authors and discussed below). Additionally, the trigonid shows a subtriangular outline in occlusal view, which is a common feature of interatheriid molars (Hitz *et al.*, 2006; García-López and Babot, 2014). The paralophid is well developed, reaching the lingual wall of the tooth. The metalophid is almost transverse (or barely oblique). Both lingual and labial sulcids are

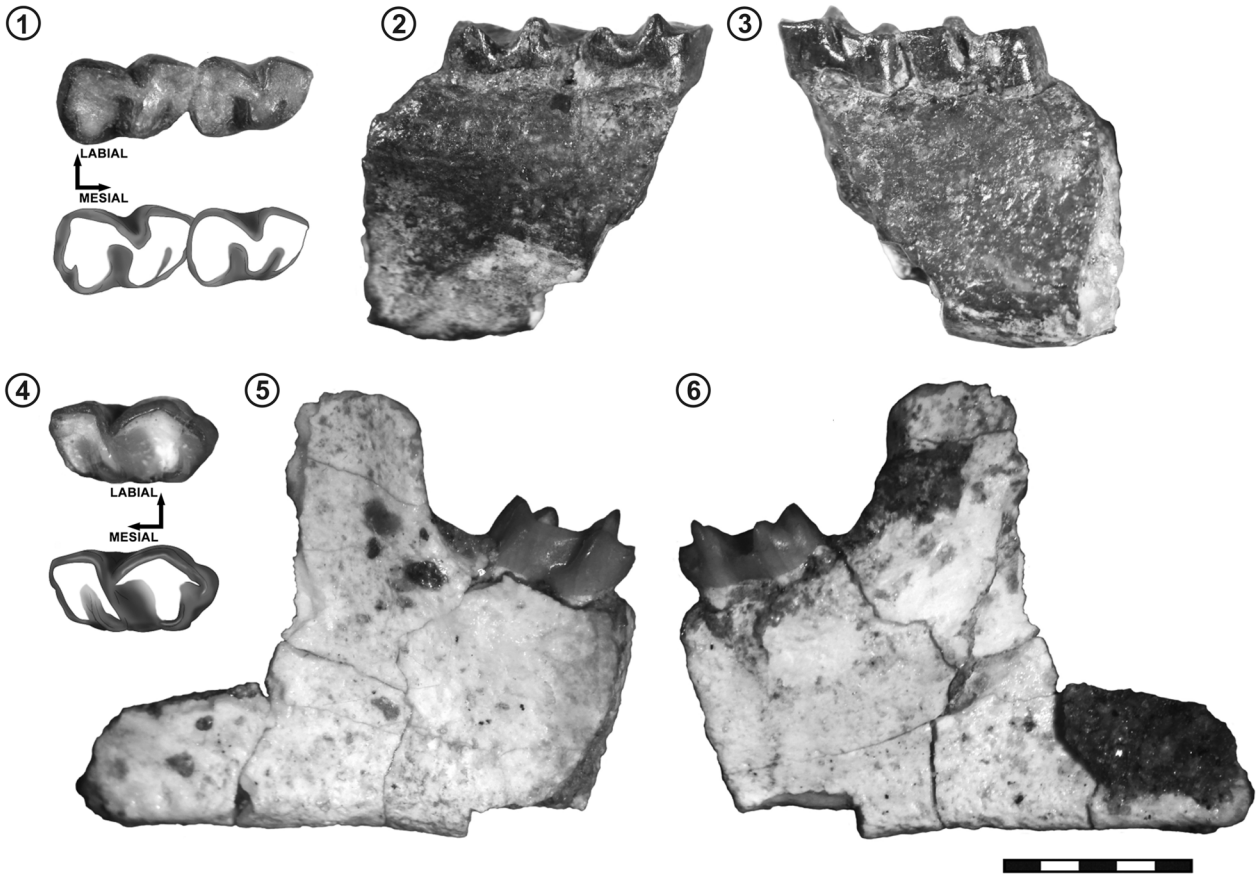

Figure 3. cf. *Antofagastia*; **1–3, MLP** 86-V-6-6, detail of p4 and m1 in occlusal view and mandibular fragment in medial and lateral view; **4–6, MHAS** 064, detail of m3 in occlusal view and mandibular fragment in lateral and medial view. Scale bar= 5 mm.

deep, the lingual sulcid being more posteriorly placed. The hypolophid forms an angle near the distolabial corner of the tooth. The entoconid is very wide and shows a raised lingual edge. The m1 is similar to the p4, but larger and more robust. Likewise, the labiolingual extension of the paralophid is smaller in this case. Finally, the presence of a small but conspicuous hypoconulid represents another difference with the premolar but all other features are very similar. I was unable to identify an "anterior spur of metaconid (paraconid)" (López and Bond, 1995, p. 94) on the m1 in this specimen.

The material MHAS 064 bears only an m3. This tooth is similar to the m1 in many features (small labiolingual extension of paralophid, lack of "anterior spur" or accessory cuspule on the metaconid, angulated hypolophid, well-developed labial sulcid, wide entoconid with raised lingual edge) but presents a larger talonid with a distally elongated hypoconulid and a conspicuous talonid labial sulcus, as usual for the third lower molar in Paleogene notoungulates. Otherwise, the lack of a lingual sulcid should be mentioned as a singular trait; the zone of this structure on the lingual wall is closed by a shallow crest running from the distal wall of the metaconid to the mesial edge of the entoconid.

DISCUSSION

The new specimens referred to *Antofagastia turneri* show the same combination of characters that differentiate the holotype from other basal interatheriids and from the Interatheriinae. Nevertheless, specimens MHAS 062 and MHAS 063 exhibit some differences that I attribute to intraspecific variation. The first difference is related to size. Both new specimens are slightly smaller than the holotype (see Tab. 1; note that MHAS 063 was not measured given the high weathering of the crown, although it was directly compared). Although the low number of specimens does not allow a statistical analysis in order to test the significance of this variation, the differences in size are consistent with the variation observed in other basal interatheriids and also in interatheriines (Fig. 4).

Other differences can be explained by wear, which varies with the age of the individual. MHAS 062 shows almost no wear, and in MHAS 063 the wear degree is considerably lower regarding the holotype (Fig. 2). García-López and Babot (2014) proposed four wear stages for the sample of specimens of *Punapithecus minor*. Extrapolating this conceptual framework to *Antofagastia turneri*, the holotype can be compared to wear stage 3 of *P. minor*, while MHAS 062 is referable to wear stage 1 or 2 and MHAS 063 is referable to wear stage 2.

Several morphological differences observed in the teeth are caused by wear degree. The most obvious is the presence of the distolabial fossette, which is absent in the holotype of *Antofagastia turneri*. This fossette is mesiodistally elongated in early wear stages but, as wear advances, it turns rounded and very shallow until it finally disappears before the inclusion of the distal cingulum in the occlusal surface. On the other hand, the mesiolabial fossette shows some changes in outline and size, although it maintains an oblique orientation and is relatively persistent.

Another difference is related to the development of the parastyle/paracone sulcus. This sulcus is clearly present in specimen MHAS 062 –albeit very shallow– but it is absent in the holotype. The development of this structure along the labial wall of the teeth shows that the sulcus becomes shallower toward the neck, thus explaining the poorly-developed structure in older individuals.

Additionally, in the specimen MHAS 062 the mesial cingulum is apparently more developed than in the holotype and MHAS 063. Nevertheless, this difference can be also explained by wear, since the holotype of *Antofagastia turneri* presents a wear facet running over the mesial edge of the cingulum, thus narrowing its surface. Regarding specimen MHAS 063, it lacks great part of the cingulum, presumably because of transport, and thus it cannot be compared.

Apart from size, other traits observed in the new specimens represent intraspecific variation that cannot be explained by wear. Specimen MHAS 062 presents a slightly deeper lingual sulcus and a conspicuous mesial inflection of the protoloph. Both features are poorly expressed in the holotype of *Antofagastia turneri*. The greater development of the lingual sulcus, although clearly visible, is still moderate and does not present the same development than other forms such as *Punapithecus* López and Bond, 1995. On the other hand, the presence of the mesial inflection in the protoloph (and the intraspecific variation associated to this trait) was also observed in that genus. At this point it should be noted that in the specimen MHAS 063, which shows a

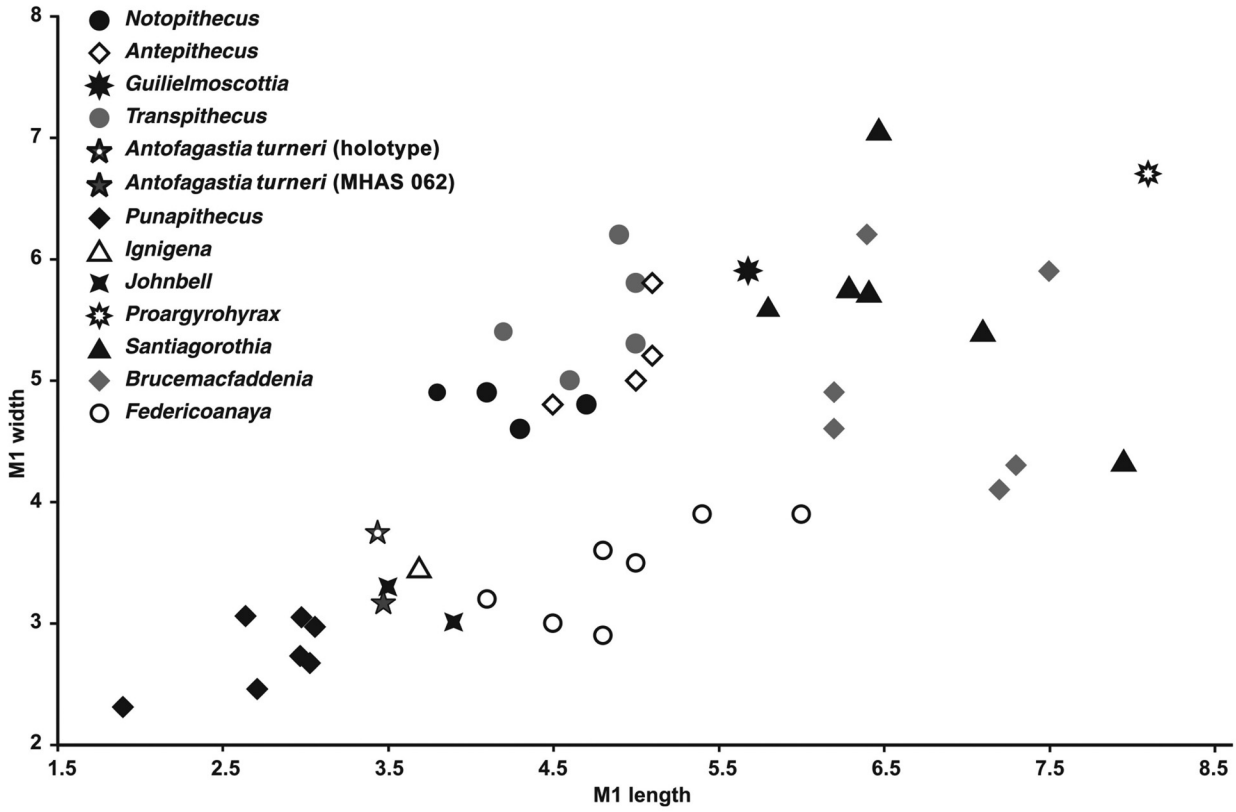

Figure 4. Bivariate plot of interatheriid taxa including MHAS 062 and comparing the size of M1. Modified from García-López and Babot (2014).

wear stage intermediate between MHAS 062 and the holotype, this mesial inflection is very subtle (as in the holotype). Some of the traits showing intraspecific variation are implied in some of the characters coded in the data-matrix presented by García-López and Babot (2014). Nevertheless, these variations do not imply changes in codification since they are relatively subtle.

Upper teeth are generally preferred for defining new genus –and species– rank taxa in Paleogene forms. Since the Geste Formation is represented by high-energy sediments, the fossil specimens that can be found are always fragmentary and in some cases heavily damaged by transport. This fact implies that there are little or no chances of finding complete or even partial skulls associated with either upper or lower dentition. Maxillary fragments with upper teeth are abundant in outcrops of the Geste Formation and represent the basis for the proposal of most taxa for this unit, as *Suniodon* López, 1995; *Punapithecus* and *Antofagastia* (note the important exception of *Punahyrax* Reguero, Croft, López, and Alonso, 2008, which was mostly described on the basis of lower teeth). Mandible fragments with teeth and isolated lower dental pieces are also abundant, but upper and lower teeth are not found in association. Thus, one faces the problem of referring lower teeth to taxa mostly diagnosed by traits of the upper dentition. In this regard, the only evidences available to relate lower and upper teeth are occlusal morphology and relative size. Morphology can easily indicate the inclusion of a specimen in a given family; however, this line of evidence is weaker at a generic and/or specific level, particularly considering that the knowledge on Paleogene forms for several lineages is still poor and scattered. At this point, relative size could be a more reliable source of information.

López and Bond (1995) referred five specimens bearing lower dentition to *Punapithecus minor*. Analyzing the measurements given in that contribution, it can be observed that

the specimen MLP 86-V-6-6 is larger than others. This fact was already noted by García-López and Babot (2014), who pointed out that the size observed in this material was more consistent with taxa such as *Antofagastia*. It should be mentioned that several specimens with lower dentition have been collected over the last years in the Geste Formation. The resulting sample includes mostly small specimens with a size agreeing with that expected for *Punapithecus*. Only specimen MHAS 064 is larger, consistent with that observed for MLP 86-V-6-6. Since the same pattern is found in maxillary fragments, with smaller specimens easily referred to *Punapithecus* and larger specimens belonging to the genus *Antofagastia*, it is tempting to separate the sample of lower teeth following the same systematic reasoning. This is the main reason why specimens MLP 86-V-6-6 and MHAS 064 are better compared to *Antofagastia*. Additionally, these lower teeth occlude clearly with the upper ones referred to this genus and the wear facets on each side match (*e.g.*, mesial surface of entoconid dorsomesially oriented against the distal surface of protocone ventrodistally oriented). This fact provides some morphological evidence supporting this idea.

If specimens MLP 86-V-6-6 and MHAS 064 effectively belong to the genus *Antofagastia* some characters should be commented. One of the diagnostic traits mentioned by López and Bond (1995) for *Punapithecus minor* was the fact that the talonid was larger than the trigonid in the third and fourth lower premolar. This feature is present in the fourth lower premolar in MLP 86-V-6-6 (referred here as cf. *Antofagastia*) and indicates an advanced molarization. Moreover, this trait is unusual among Paleogene forms and similar to some Neogene taxa. In this regard, *Antofagastia* and *Punapithecus* would share this character, although it should be mentioned that it is actually not particularly marked in *Punapithecus*; in fact, Hitz *et al.* (2006) considered that the talonid was subequal to the trigonid in this taxon (see character 23 of that contribution). Despite this similarity and the fact that *Antofagastia turneri* resembles *Punapithecus minor* in several traits, most characters shared are considered plesiomorphic features, and a phylogenetic analysis performed including these interatheriids from northwestern Argentina does not indicate a close relationship among them (see García-López and Babot, 2014). Nevertheless, it cannot be ignored that specimen MLP 86-V-6-6 actually shows a p4 with a talonid slightly larger than the trigonid; *i.e.*, it shows one of the characters considered diagnostic by López and Bond (1995). As new evidence is added and new materials are found, it is possible that future analyses may show a closer position of these two taxa, or even indicate that they represent two species of the same genus.

CONCLUSIONS

The features observed in the new specimens of *Antofagastia turneri* indicate some degree of intraspecific variation. This pattern was already observed in *Punapithecus minor* and other interatheriids (Vera, 2012) and should be carefully considered, particularly in the case of taxa based on isolated dental pieces or other fragmentary material.

On the other hand, mandible fragments bearing lower teeth are here referred as cf. *Antofagastia* mainly considering differential size observed in the sample of interatheriids recovered from outcrops of the Geste Formation. At this point, small and large pieces can be considered as referable to *Punapithecus* and *Antofagastia*, respectively.

Shedding light on the apparently "cryptic" history of extra-Patagonian interatheriids from Argentina surely will clarify some points of the evolutionary path of this interesting family of typotherians. Although the Geste Formation has proved to be very productive, yielding several notable fossils, the study of taphonomic features on material from this unit faces several obstacles, such as sampling biases and very fragmentary material. Recently found fossil- bearing outcrops of this unit may offer new lines of evidence and must be explored. Likewise, the exploration of neighboring units of similar age (*i.e.*, Lumbrera, Quebrada de los Colorados, and Casa Grande formations) should also provide evidence in order to elucidate questions related to the singular presence of interatheriids in the Geste Formation and other faunal peculiarities.

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