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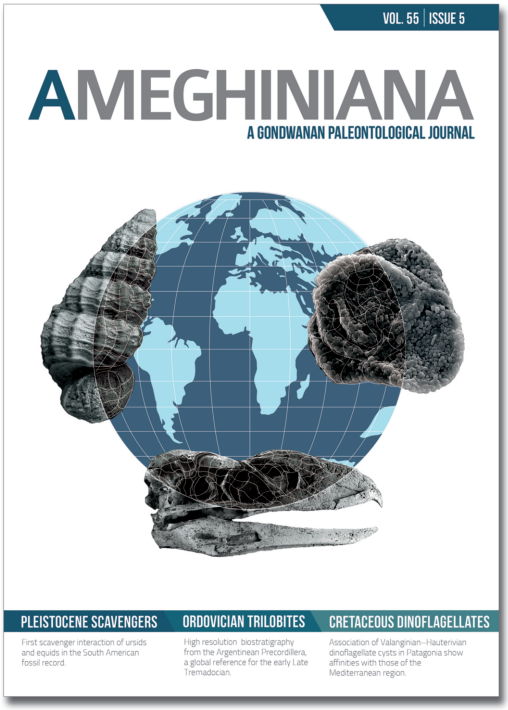

AN EVALUATION OF THE DENTAL FEATURES USED TO DISTINGUISH *TYPOTHERIOPSIS* FROM *PSEUDOTYPOTHERIUM* (MESOTHERIIDAE, NOTOUNGULATA): REAPPRAISALS AND PROPOSALS REGARDING THEIR SYSTEMATIC VALUE

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AN EVALUATION OF THE DENTAL FEATURES USED TO DISTINGUISH *TYPOTHERIOPSIS* FROM *PSEUDOTYPOTHERIUM* (MESOTHERIIDAE, NOTOUNGULATA): REAPPRAISALS AND PROPOSALS REGARDING THEIR SYSTEMATIC VALUE

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Palabras clave. Mesotheriinae. Sistemática. Dientes. Neógeno tardío. Argentina.

MESOTHERIIDAE is a clade included in the Order Notoungulata that lived from the early Oligocene (Tinguiririan South American Land Mammal Age—SALMA) to the early–middle Pleistocene (Ensenadan SALMA) (Flynn *et al.*, 2005; Cerdeño *et al.*, 2012). Throughout the Neogene, this group is represented in several South American localities (see Armella *et al.*, 2018), displaying a high diversity in size and cranial morphology (*e.g.*, Townsend and Croft, 2010; Cerdeño *et al.*, 2012).

The Mesotheriinae records in the late Neogene of Argentina are mostly grouped in two genera: *Typotheriopsis* Cabrera and Kraglievich, 1931 and *Pseudotypotherium* Ameghino, 1904 (Francis, 1965; Cerdeño and Montalvo, 2001). They are well-known and frequent in late Miocene and Pliocene outcrops from the Northwest and Central regions of this country (see Cerdeño and Montalvo, 2001; Armella *et al.*, 2018 for a summary). Since their establishment, both genera were poorly diagnosed. *Typotheriopsis* was based on badly preserved cranial and mandibular remains (*i.e.*, *Typotheriopsis chasicoensis* Cabrera and Kraglievich, 1931) that were superficially described. For its part, the type of the type species of *Pseudotypotherium* (*i.e.*, *Pseudotypotherium pulchrum* Ameghino, 1904) consists of a complete mandible belonging to a juvenile individual, with deciduous last premolars (**dp3**–**dp4**) (Kraglievich, 1934). This fact was posteriorly reflected in a problematical taxonomy and supernumerary species. It was not until the studies of Francis (1960, 1965) and Cerdeño and Montalvo (2001) that the diversity of *Typotheriopsis* and *Pseudotypotherium* was partially clarified and reorganized taking into account, among other things, ontogenetic variability.

Francis (1965) proposed several dental differences between *Typotheriopsis* and *Pseudotypotherium*, such as: the proportion and orientation of the first upper incisor (**I1**), the degree of overlapping among the cheek-teeth, the general shape of the last upper premolar (**P4**) and the first lower incisor (**i1**), the ratio of the lower incisors (**i1**–**2**) and the diastema divergence. In particular, the widely accepted dental feature traditionally considered to distinguish *Pseudotypotherium* from *Typotheriopsis* is the presence of a lingual groove in the P4 but with some recognized variations (Pascual *et al.*, 1966; Cerdeño and Montalvo, 2001; Flynn *et al.*, 2005; Cerdeño and Schmidt, 2013). Furthermore, Francis (1965, p. 24) mentioned a great-sized palate attributable to *Pseudotypotherium* without the P4 lingual groove. Other features, some of which were proposed to differentiate other mesotheriine genera, such as the differences in lower den-

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tition (see Villarroel, 1974), were mostly dismissed and considered as homogeneous traits or referable to intraspecific variation (Cerdeño and Montalvo, 2001; Cerdeño and Schmidt, 2013; but see Flynn *et al.*, 2005, on lower molars). Moreover, lower dentition features were considered non-informative at the generic level (see Townsend and Croft, 2010). As a consequence, when the available materials are mostly composed of isolated or incomplete dentitions, it is not possible to determine to which genus the remains belong.

Based on this, we reanalyzed the dental features of *Typotheriopsis* and *Pseudotypotherium* samples to evaluate their relevance in a taxonomic framework and to help identify fragmentary material and isolated dental mesotheriine pieces as well.

***Institutional abbreviations*. FMNH,** Field Museum of Natural History, Chicago, USA; **GHUNLPam,** Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina; **MACN,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; **MLP,** Museo de La Plata, La Plata, Argentina; **MMP,** Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Argentina; **PVL,** Colección Paleontología Vertebrados Lillo, San Miguel de Tucumán, Argentina.

***Anatomical abbreviations*. d,** deciduous; **I/i,** upper/lower incisors; **M/m,** upper/lower molars; **P/p,** upper/lower premolars.

MATERIALS AND METHODS

The study comprises qualitative and morphometric analyses (see Supplementary Online Information). For both, the anatomical terms follow classical papers (*e.g.*, Francis, 1965; Villarroel, 1974; Cerdeño and Montalvo, 2001) and more recent contributions (Flynn *et al.*, 2005; Townsend and Croft, 2010; Cerdeño and Schmidt, 2013). We used adults and some subadults, which show a more advanced teeth wear stage, to avoid morphological changes related to ontogeny (Francis, 1965; Cerdeño and Schmidt, 2013). In this sense, we omitted the type of the type species of *Pseudotypotherium* from the analysis concerning p4 due its representation by a juvenile individual (with dp3–dp4).

In order to work with a more reliable taxonomical framework, we firstly explore sets of features in specimens with complete dental series and associated cranial and mandibular materials. Then, we assess their consistency and taxonomical value in the whole studied sample (including isolated cranial, mandibular and dental remains). This was important considering the controversy inherent to the diagnostic value of lower dentition traits (see Townsend and Croft, 2010). Moreover, it enables the evaluation of the morphological variability and the tentative taxonomic assignment of the analyzed sample. The dental dimensions were used to evaluate average and range values, and confidence intervals. Additionally, the Student's t test was performed to determine if there are significant differences between the mean of the two taxa. The variables analyzed (see raw measurements in Supplementary Online Information) were measured on digital images using the measure tool of tpsDig software (Rohlf, 2013). We photographed ventral views of the skulls and dorsal views of the mandibles orientated along the alveolar plane (Fig. 1).

RESULTS

Upper dentition

Typotheriopsis and *Pseudotypotherium* differ in many of the features of upper dentition. The major axis of I1 is narrower in *Typotheriopsis* than it is in *Pseudotypotherium* (Fig. 2.1; Tab. 1), the extreme values are similar but there is no overlapping. Contrary to Francis (1965), we did not observe marked differences related with I1 orientation, as Cerdeño and Montalvo (2001) and Flynn *et al.* (2005) also observed.

Regarding cheek-teeth, they are wider (P4 and M2) or in almost all cases wider (M1 and M3) in *Typotheriopsis* than they are in *Pseudotypotherium* (Fig. 2.2; Tab. 1). As Francis (1965) mentioned, *Typotheriopsis* has a triangular P4 which is wider in its distal region while, in *Pseudotypotherium*, it is oval and wider in its middle region (Fig. 1.1–2; Tab. 1). In consistency with previous researchers (*e.g.*, Francis, 1965; Cerdeño and Montalvo, 2001; Flynn *et al.*, 2005; Cerdeño and Schmidt, 2013), our analysis supports the systematic value of the lingual groove of P4; however, it exhibits different degrees of development (see Cerdeño and Montalvo, 2001, p. 69). Particularly, the specimen MLP 65-VII-29-32, referred to *Typotheriopsis*, shows a lingual groove of P4 poorly developed, raising some reconsideration concerning this trait. Beyond this, we considered this feature as highly reliable to distinguish *Typotheriopsis* from *Pseudotypotherium* in almost all cases, as also Flynn *et al.* (2005, p. 66–67) stated.

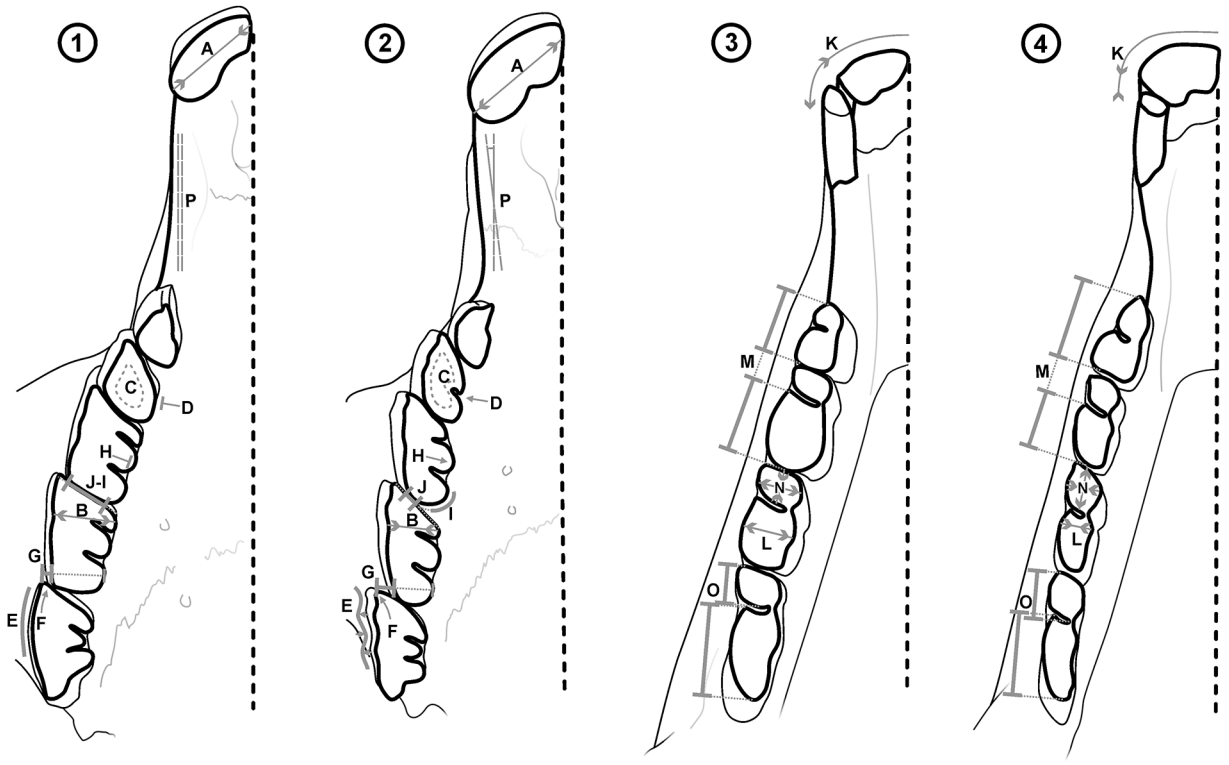

Figure 1. Schematic upper (**1, 2**) and lower (**3, 4**) dentition morphology. **1, 3,** ***Typotheriopsis***. **2, 4,** ***Pseudotypotherium***. Highlighted differences are labelled with letters, which correspond to Table 3.

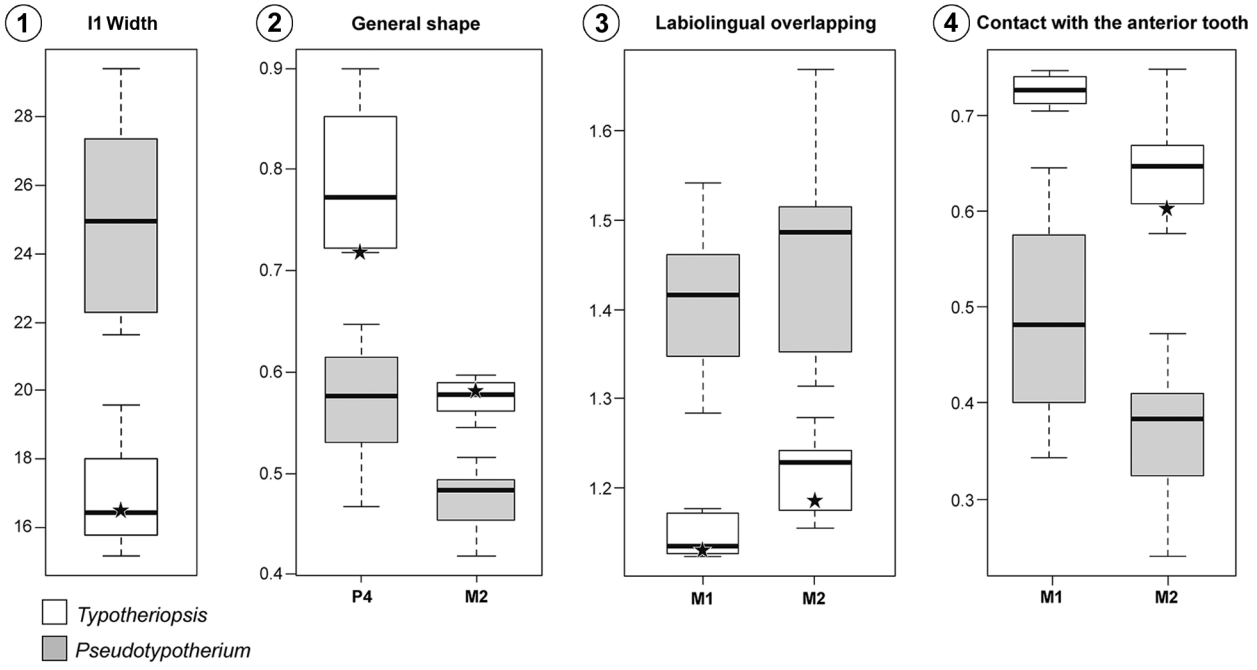

Figure 2. Boxplots of the most reliable traits on the upper dentition. Box midline represents medians, and box floor and roof are first and third quartile, respectively. Whiskers represent cases laying within 1.5 times the interquartile range. Black stars indicate the position of the type of ***Typotheriopsis chasicoensis***. **1,** Upper incisor width (**A**); **2,** general shape (**B**); **3,** labiolingual overlapping of molars (**G**); **4,** contact with anterior tooth (**J**). The letters in bold correspond to Table 3 and Figure 1.

TABLE 1 – Comparisons between* Typotheriopsis *and* Pseudotypotherium *of selected upper dentition measurements and ratios.

Tooth	Feature	Equation	Typotheriopsis						Pseudotypotherium					
			N	Mean	SD	Min	Max	CI	N	Mean	SD	Min	Max	CI
I1	**Width (in mm)****	I1W	3	**17.05**	2.27	15.15	19.56	±5.64	14	**25.05**	2.73	21.63	29.39	±1.58
P3	General shape**	P3W/P3L	6	0.76	0.04	0.71	0.84	±0.05	27	0.66	0.06	0.58	0.78	±0.02
P4	**General shape****	P4W/P4L	6	**0.80**	0.08	0.72	0.90	±0.08	27	**0.57**	0.05	0.47	0.65	±0.02
	Contact with anterior tooth*	P3con/P4mf	5	0.66	0.06	0.57	0.71	±0.07	25	0.50	0.05	0.41	0.61	±0.02
M1	General shape**	M1W/M1L	6	0.56	0.04	0.52	0.60	±0.04	31	0.49	0.04	0.42	0.56	±0.01
	Labiolingual overlapping†**	M1wph/P4df	6	**1.15**	0.02	1.12	1.18	±0.02	28	**1.40**	0.07	1.29	1.54	±0.03
	Contact with the anterior tooth**	M1con/M1mf	4	**0.73**	0.02	0.70	0.75	±0.03	29	**0.49**	0.10	0.34	0.65	±0.04
M2	**General shape****	M2W/M2L	8	**0.58**	0.02	0.55	0.60	±0.02	26	**0.48**	0.03	0.42	0.52	±0.01
	Labiolingual overlapping†**	M2wph/M1df	7	**1.22**	0.05	1.16	1.28	±0.04	25	**1.46**	0.10	1.31	1.67	±0.04
	Contact with the anterior tooth**	M2con/M2mf	7	**0.65**	0.06	0.58	0.75	±0.05	25	**0.36**	0.07	0.24	0.47	±0.03
M3	General shape*	M3W/M3L	7	0.53	0.03	0.50	0.59	±0.03	25	0.50	0.04	0.44	0.57	±0.02
	Labiolingual overlapping**†	M3wph/M2df	8	1.14	0.10	0.93	1.27	±0.08	25	1.36	0.12	1.10	1.54	±0.05

**Student's t test indicates significant differences between means at alpha= 0.05. **Student's t test indicates significant differences between means at alpha= 0.001. †Following Flynn* et al. *(2005). See Supplementary Online Information for more details and equation abbreviations.*
*Abbreviations: **CI**, confidence interval at alpha= 0.05; **Max**, maximum; **Min**, minimum; **N**, sample size; **SD**, standard deviation. In **bold**, the most reliable traits for systematical proposes (i.e., without any overlapping and with high differences according both, confidence interval and extreme values, for each sample).*

Concerning molar morphology, the ectoloph is straighter in *Typotheriopsis* than it is in *Pseudotypotherium*, and this latter genus is more similar to *Mesotherium* (early Pleistocene genus, the last mesotheriid representative) (*e.g.*, MACN-Pv 2924). The M1 and M2 parastyles of *Typotheriopsis* point mesially, while they are oriented mesiolabially in *Pseudotypotherium* (Fig. 1.1–2). Related to this, the labiolingual overlapping is less marked in *Typotheriopsis* than it is in *Pseudotypotherium* (a difference particularly marked for M1 and M2; Fig. 2.3, Tab. 1). In nearly all cases, *Typotheriopsis* has an M1–2 median lobe with its lingual edge reaching the level of the adjacent lobes (anterior and posterior) while, in *Pseudotypotherium*, the lingual exposure of its median lobe exceeds the level of the adjacent lobes (see also Villarroel, 1974, p. 251). Nevertheless, this feature displays some variability probably related with ontogenetic traits (*e.g.*, the left M1 of the *Typotheriopsis* specimen MLP 67-XII-27-1 shows a similar condition to that of *Pseudotypotherium*) (see Cerdeño and Schmidt, 2013).

On the other hand, the P4, the M1, and the M2 of *Typotheriopsis* have straight distal faces; as a result, there is a large contact area between P4/M1 and M1/M2 (Tab. 1; Fig. 2.4). In contrast, *Pseudotypotherium* shows distal faces that are markedly globose and a thereby small contact area between P4/M1 and M1/M2 (Tab. 1; Fig. 2.4). It is important to note that this condition is also observed in P3/P4 and M2/M3 but in a less evident manner, and there is some superposition of range values between both genera (Tab. 1).

Lower dentition

Francis (1965) stated that *Typotheriopsis* shows a subtriangular i1 in cross-section, which is approximately twice the i2, while *Pseudotypotherium* presents a more trapezoidal-shaped i1, which is more than twice than the i2. Later, Cerdeño and Montalvo (2001, p. 70) highlighted that size differences show some degree of overlapping between these taxa; however, they validated the morphological differences. In this sense, the results of our analysis are consistent with the latter.

Concerning the lower cheek-teeth, contrary to previous

Table 2 – Comparisons between **Typotheriopsis** *and* **Pseudotypotherium** *of selected lower dentition measurements and ratios.*

Tooth	Feature	Equation	Typotheriopsis						Pseudotypotherium					
			N	Mean	SD	Min	Max	CI	N	Mean	SD	Min	Max	CI
p4	General shape**	p4wlobP/p4l	6	0.58	0.04	0.53	0.62	0.04	15	0.49	0.04	0.45	0.57	0.02
	Posterior lobe shape	p4wlobP/p4LlobP	6	1.02	0.06	0.96	1.10	0.06	16	0.95	0.11	0.76	1.16	0.06
	Anterior lobe shape**	p4wlobA /p4LlobA	6	0.95	0.12	0.81	1.09	0.13	15	0.68	0.06	0.58	0.80	0.03
	p4/m1 relative length**	p4l/m1LlobP	7	**0.97**	0.10	0.82	1.07	0.09	15	**1.32**	0.10	1.17	1.48	0.05
m1	General shape**	m1wlobP/m1l	10	0.51	0.06	0.45	0.63	0.04	20	0.39	0.03	0.29	0.43	0.02
	Posterior lobe shape*	m1wlobP /m1LlobP	10	0.70	0.08	0.63	0.87	0.05	20	0.60	0.04	0.50	0.66	0.02
	Anterior lobe shape**	m1wlobA/m1LlobA	8	**1.27**	0.09	1.15	1.43	0.08	19	**0.89**	0.07	0.76	1.05	0.04
	Posterior lobe width (in mm)*	m1wlobP	10	8.62	1.70	6.52	11.71	1.22	20	7.23	1.37	4.82	11.26	0.64
m2	General shape**	m2wlobP/m2l	8	0.45	0.04	0.38	0.50	0.03	20	0.32	0.02	0.28	0.38	0.01
	Posterior lobe shape**	m2wlobP/m2LlobP	8	0.68	0.05	0.61	0.74	0.04	20	0.55	0.04	0.49	0.64	0.02
	Anterior lobe shape**	m2wlobA/ m2LlobA	9	**1.01**	0.07	0.90	1.11	0.05	21	**0.75**	0.06	0.65	0.86	0.03
	Relative width of the m2 posterior lobe to the m3 posterior lobe*	m2wlobP/m3wlobP	7	1.11	0.05	1.03	1.16	0.05	20	0.96	0.09	0.77	1.21	0.04
	Posterior lobe width (in mm)*	m2wlobP	8	7.51	1.15	6.48	9.42	0.96	21	6.32	1.25	4.17	10.09	0.57
m3	General shape	m3wlobP/m3l	7	0.31	0.05	0.25	0.39	0.04	17	0.27	0.02	0.23	0.34	0.01
	Posterior lobe shape	m3wlobP/m3LlobP	7	0.46	0.06	0.38	0.56	0.06	17	0.43	0.04	0.36	0.53	0.02
	Anterior lobe shape**	m3wlobA/m3LlobA	7	**0.99**	0.07	0.92	1.14	0.07	20	**0.71**	0.04	0.63	0.80	0.02
	Lobes proportion**	m3LlobP/m3LlobA	7	**2.31**	0.14	2.15	2.57	0.13	17	**1.78**	0.14	1.41	2.03	0.07
	Posterior lobe width (in mm)	m3wlobP	7	7.10	1.17	5.69	8.48	1.08	20	6.62	1.35	4.11	10.81	0.63

**Student's t test indicates significant differences between means at alpha= 0.05. **Student's t test indicates significant differences between means at alpha= 0.001. See Supplementary Online Information for more details and equation abbreviations.*
*Abbreviations: **CI**, confidence interval at alpha = 0.05; **Max**. maximum; **Min**. minimum; **N**. sample size; **SD**. standard deviation. In **bold**. the most reliable traits for systematical proposes (*i.e., *without any overlapping and with high differences according both, confidence interval and extreme values, for each sample).*

statements, our analysis found certain significant differences between *Typotheriopsis* and *Pseudotypotherium*. In almost all cases, the posterior lobes of the lower cheek-teeth are wider in *Typotheriopsis* than they are in *Pseudotypotherium*; however, there is some degree of overlapping in the values (Tab. 2). In almost all cases, the relative width among the posterior lobe of the molars decreases from m1 to m3 (m1 > m2 > m3) in *Typotheriopsis* (Tab. 2). Conversely, *Pseudotypotherium* specimens present a similar or smaller posterior lobe width of m2 than that of m3 (m1 > m2 ≤ m3). However, there are specimens (*e.g.*, GHUNLPam 19868, GHUNLPam 8230, GHUNLPam 8303) referable to *Pseudotypotherium*, which show proportions similar to those of *Typotheriopsis.* A valuable feature to distinguish both genera is the relationship between the p4 total length and the m1 posterior lobe length, which is similar in *Typotheriopsis* and, in contrast, in *Pseudotypotherium,* it is defined by the former being always larger than the latter (Fig. 3.1; Tab. 2).

On the other hand, *Typotheriopsis* shows an anterior lobe of the molars that is wider and shorter than that of *Pseudotypotherium.* Particularly, the relationship between width and length of the anterior lobes reveals that this lobe is approximately equidimensional in the case of the m2 and m3 in *Typotheriopsis* while, in the m1, it is wider than it is long (Fig.

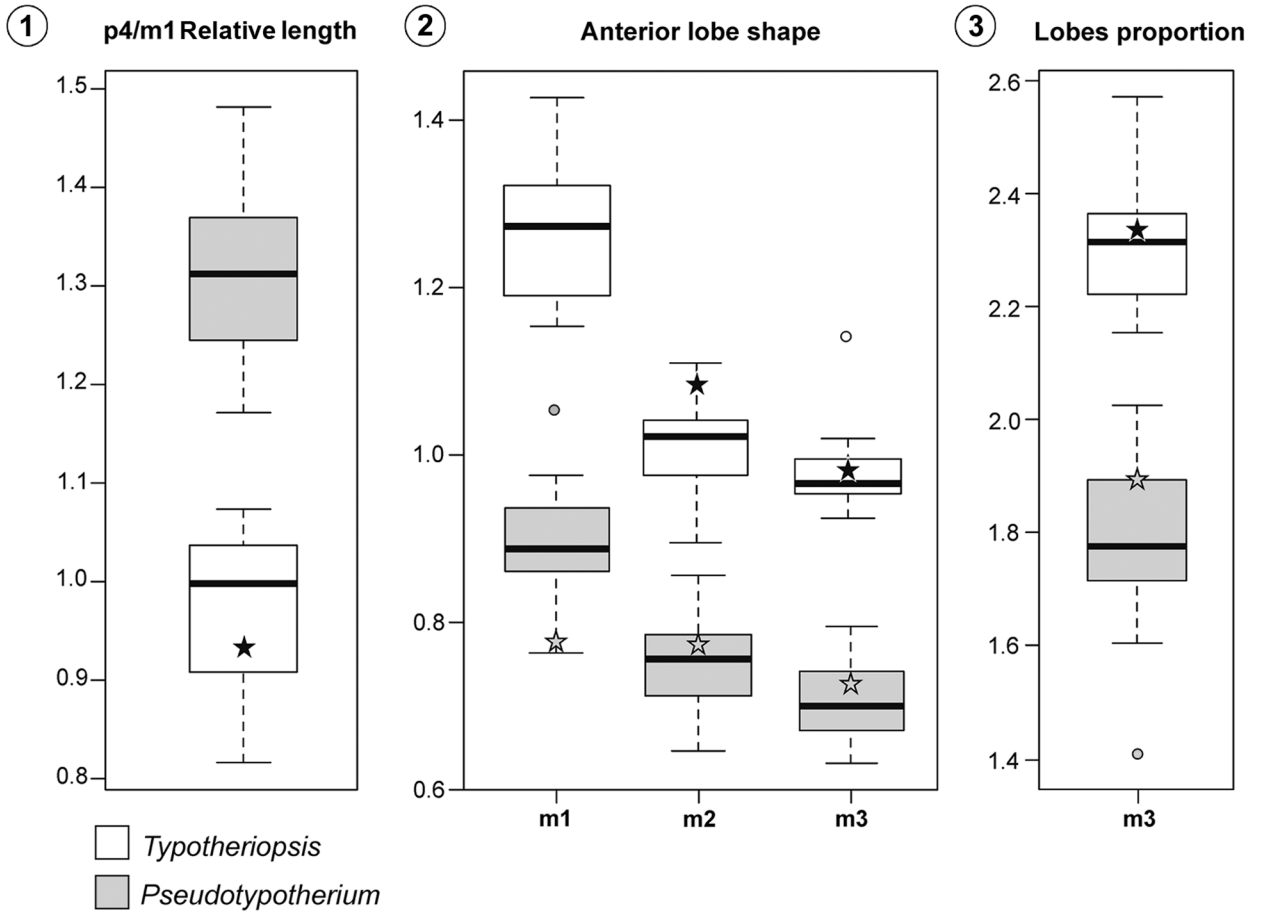

Figure 3. Boxplots of most reliable traits on the lower dentition. Box midline represents medians, and box floor and roof are first and third quartile, respectively. Whiskers represent cases laying within 1.5 times the interquartile range. Small dots out of the whiskers must be considered outliers. Black and grey stars indicate the position of the type of ***Typotheriopsis chasicoensis*** and ***Pseudotypotherium pulchrum***, respectively. **1,** Relationship between the length of **p4** and the length of the posterior lobe of **m1** (**M**); **2,** shape of anterior lobe of molars (**N**); **3,** proportion of **m3** lobes (**O**). The letters in bold correspond to Table 3 and Figure 1.

3.2; Tab. 2). In contrast, *Pseudotypotherium* presents the anterior lobe of molars that is longer than it is wide although, in some cases (*e.g.*, MLP 12-2284, MACN-Pv 7962), the m1 shows an anterior lobe approximately equidimensional (Fig. 3.2; Tab. 2). In turn, the length of the posterior lobe of the m3 is always much more than twice the anterior lobe length in *Typotheriopsis* while lesser or just twice the anterior lobe in *Pseudotypotherium* (maximum value in one specimen GHUNLPam 8230) (Fig. 3.3; Tab. 2). Although the length of the posterior lobe of m3 could be affected by ontogeny (see Cerdeño and Schmidt, 2013), it was observed in both the adult and the subadult specimens that were sampled.

Finally, we observed parallel upper diastemata in *Typotheriopsis* that proved different from those of *Pseudotypotherium*, where they tend to diverge in the anterior region, probably in relation with the increasing size of its I1 (Fig. 1.1–3). This pattern is less clear in the lower diastemata, with intermediate conditions in both genera (Fig. 1.2–4).

DISCUSSION AND CONCLUSIONS

According to Francis (1965), the most conspicuous difference between *Typotheriopsis* and *Pseudotypotherium* is the absence or presence (respectively) of the lingual groove of P4. Our analysis supports this trait as a powerful tool to distinguish *Typotheriopsis* from *Pseudotypotherium* as it is consistent throughout the complete sample. Nevertheless, we agree with previous researchers regarding the varying development of this groove (Flynn *et al.*, 2005; see also Cerdeño and Schmidt, 2013). The *Pseudotypotherium* specimen without a groove that was mentioned by Francis (1965,

Table 3 – List of teeth features with diagnostic value to identify **Typotheriopsis** *and* **Pseudotypotherium** *remains.*

Feature		**Typotheriopsis**	**Pseudotypotherium**
Upper teeth			
*A**	*I1 width*	*Shorter than 20 mm*	*Larger than 20 mm*
*B***	*P4-M3 width*	*Wider (P4, M2) or in almost all cases wider (M1, M3)*	*Narrower (P4, M2) or in almost all cases wider narrower (M1, M3)*
*C**	*P4 general shape*	*Triangular, wider in its distal region*	*Oval, wider in its middle region*
*D**	*P4 lingual groove*	*Absent or markedly reduced*	*Present and well defined*
*E***	*Molar ectoloph*	*Straighter*	*Undulated*
*F***	*Molar parastyle*	*Pointed mesially*	*Mesiolabially directed*
*G**	*Labiolingual overlapping of molars*	*Less (M2, M1) or in almost all cases less (M3)*	*More (M2, M1) or in almost all cases more (M3)*
*H***	*Median lobe exposure of M1-M2*	*In almost all cases reach the level of the adjacent lobes*	*In almost all cases surpass the level of the remaining lobes*
*I***	*Shape of the distal face of P4 and M1*	*Flattened*	*Globose*
*J***	*Contact with the anterior tooth (P4/M1 and M1/M2)*	*Extended*	*Reduced*
Lower teeth			
*K**	*Shape of i1 in cross section*	*subtriangular-shaped*	*In almost all cases trapezoidal-shaped*
*L****	*p4-m3 posterior lobe*		
	- Absolute width	*In almost all cases wider*	*In almost all cases narrower*
	- Relative width among them	*Progressive and marked increasing of the width from m3 to m1 (m1 > m2 > m3)*	*With m3 and m2 frequently similar or even lower m2 width (m1 > m2 ≤ m3)*
*M***	*p4/m1 relative length*	*p4 similar or shorter than m1 posterior lobe*	*p4 significantly larger than m1 posterior lobe*
*N***	*Shape of anterior lobe of molars*	*Equidimensional m3 and m2, and wide m1*	*Narrow m3 and m2, and narrow or equidimensional m1*
*O***	*Proportion of m3 lobes*	*Posterior lobe length larger than twice the anterior*	*Posterior lobe length similar or lower than twice the anterior*
Diastemata			
*P***	*Divergence*	*Parallel upper diastemata*	*Anteriorly diverging upper diastemata*

** Features with diagnostic value recognized by previous authors and supported in this study. ** The new reliable traits confirmed throughout the whole sample. *** New feature that shows a strong pattern but with some exceptions.*

p. 24) was neither figured nor identified by a collection number; thus, it could not be examined in the consulted repositories.

As previously mentioned, there are somewhat debatable features, considered mainly homogeneous, and minor tools to distinguish both genera: the morphology of incisors and cheek-teeth, molar overlapping and diastemata divergence. The detailed analysis herein performed on a wide sample of specimens has enabled the reappraisal of some of them and the recognition of new informative traits in order to distinguish *Typotheriopsis* from *Pseudotypotherium* (Tab. 3).

Firstly, our analysis supports the presence of size variation in the upper incisors without overlapping ranges between both genera. Nevertheless, we did not observe differences related to the incisor orientation and the lower incisors size (conversely to Francis, 1965). Moreover, we agree with previous authors (*i.e.*, Francis, 1965; Cerdeño and Montalvo, 2001; Flynn *et al.*, 2005) regarding the mor-

phological differences in the lower incisors (Tab. 3).

Additionally, we note differences related with the ectoloph and the overlapping of upper molars (ectoloph straighter and lower overlapping in *Typotheriopsis* than in *Pseudotypotherium*, particularly M1 and M2; Figs. 1.1–2, 2.3, Tab. 1). Likewise, the lingual exposure of the M1–2 median lobe presents differences between both genera (at the level of the adjacent lobes in *Typotheriopsis* and exceedingly in *Pseudotypotherium*). Although this morphology could vary ontogenetically (Cerdeño and Montalvo, 2001; Cerdeño and Schmidt, 2013), the extension of the median lobe appears to be different in the two studied taxa, to some extent, and useful for its recognition.

In addition, our analysis recovered subtle differences regarding diastemata divergences, and an unambiguous distinction was only possible in well-preserved specimens. In this sense, our proposal is contrary to that of Francis (1965, p. 22, 24), who only suggested differences in the lower diastemata (parallel in *Typotheriopsis* and posteriorly convergent in *Pseudotypotherium*). Instead, we observed almost similar lower diastemata in both genera and, conversely, main differences in the upper ones (parallel in *Typotheriopsis* and posteriorly convergent in *Pseudotypotherium*). Furthermore, this latter observation is interesting considering previous works (*i.e.*, Cerdeño and Montalvo, 2001 and Flynn *et al.*, 2005) establishing an ambiguous condition for both genera (parallel or gently convergent upper and lower diastemata).

In summary, this contribution reevaluates previously recognized taxonomical features and deals with new characters (Tab. 3). This expanded set of features allowed us to work on the identification at the generic level, in some cases for the first time, of incomplete or disassociated remains (see Supplementary Online Information). The use of the herein proposed set of traits in larger samples would help distinguish mesotheriine species and assess their diversity during the late Neogene.

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