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Original article

Milk molars or extra premolars in Mesotheriinae (Mesotheriidae, Notoungulata): New insights into an old controversy☆

Esperanza Cerdeño [a,*], Gabriela I. Schmidt [b]

[a] Departamento de Paleontología, IANIGLA, Centro Científico Tecnológico CONICET-Mendoza, Avenida Ruiz Leal s/n, 5500 Mendoza, Argentina
[b] Laboratorio de Paleontología de Vertebrados, CICYTTP – CONICET, Materi y España, E3105BWA Diamante, Entre Ríos, Argentina

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ABSTRACT

A recently recovered specimen of Mesotheriinae (Mesotheriidae, Notoungulata) from the late Miocene-early Pliocene of La Rioja Province (Argentina), CRILAR Pv 433, corresponds to an individual with three upper premolars, which appears to be an "anomaly" among mesotheriines. The detailed study of this specimen, however, brings up an old controversy on the interpretation of different mesotheriine specimens with three upper or two lower premolars. After being described as different taxa, these were later considered to be juvenile representatives of other known species. The three upper or two lower teeth were interpreted as the milk molars DP2–4 and dp3–4, respectively, which would be replaced in adult life by two upper (P3–4) and one lower (p4) permanent premolars. The new material leads us to set up a different interpretation. In our opinion, all these specimens actually preserve the permanent dentition, corresponding to different ontogenetic stages of more or less young individuals. This consideration implies the necessity of a deep systematic revision of the whole subfamily, keeping in mind this new point of view and the ontogenetic variation within a species. Therefore, the presence of P2/p3 is not enough to define a different taxon at this moment. Pending this taxonomic revision, the dental morphology of CRILAR Pv 433 resembles both *Typotheriopsis* (e.g., upper premolars with one labial sulcus) and *Pseudotypotherium* (e.g., P4 with lingual groove, wide median lobe of M3) as these two late Miocene genera are currently characterized. Furthermore, P2/p3 could be expelled soon in the lifetime of individuals, and even the presence of P2/p3 could be a variable character within the same taxon; if so, this might reflect an evolutionary trend to the loss of a dental element within mesotheriines, but the revision of a large sample is necessary to support or reject these hypotheses.

1. Introduction

The first fossil mammals from the Salicas Formation, La Rioja Province, Argentina, were studied by Tauber (2005), adding data to the poor mammal record of the Neogene deposits of this area. This author listed a fossil assemblage encompassing some xenarthrans, rodents, and notoungulates. Recently, a new collection from the El Degolladito area allowed a more detailed study on systematic, biochronological, and paleobiogeographical aspects of the mammal fauna from the Salicas Formation (Brandoni et al., 2012); the details on geographic provenance and stratigraphic correlations are described in this paper. Tauber (2005) assigned the faunal remains to the Huayquerian Age (late Miocene) and Brandoni et al. (2012) established correlations with the well-known Neogene beds of the Andalhuala and Chiquimil formations, in Catamarca Province. They considered that the Salicas assemblage can roughly correspond to the range from 6.02 to 6.68 Ma obtained for these levels (Marshall and Patterson, 1981), closer to the recently proposed Huayquerian/Montehermosan boundary for the Northwest of Argentina (Reguero and Candela, 2011).

Among the remains from El Degolladito, there is a well preserved maxillary fragment (CRILAR Pv 433) of a mesotheriid notoungulate mammal, previously determined as cf. *Pseudotypotherium*, but even considered as a possible new taxon by the presence of a P2 in its dental formula (Schmidt, 2011; Brandoni et al., 2012).

The presence of three upper premolars – and two lower ones – in members of the Subfamily Mesotheriinae was broadly discussed decades ago (Kraglievich, 1934, 1940; Cabrera, 1937a, b; Patterson, 1952) with two different interpretations: (i) species with extra premolars (P2 and p3), or (ii) juvenile individuals with dP2 and dp3 of other known species whose adults present only two upper (P3–4) and one lower (p4) premolars. Francis (1960) summarized this old controversy and concluded himself that some specimens actually showed deciduous teeth (DP2–4/dp3–4) together with

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* Corresponding author.
E-mail address: espe@mendoza-conicet.gob.ar (E. Cerdeño).

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permanent molars, and that DP2/dp3 would not be replaced by permanent premolars, resulting in an adult formula with just P3–P4/p4 and three molars. This condition could be that observed in CRILAR Pv 433, that is DP2–4 and M1–3, but some factors argue for another interpretation (P2–M3).

The determination as cf. *Pseudotypotherium* previously achieved by Brandoni et al. (2012) is discussed herein. Taking into account the new-presented perspective (Sections 4 and 5), an accurate taxonomic identification is not possible without a whole revision of the subfamily, which is far beyond the aim of this paper, in which we deepen the study of CRILAR Pv 433 and argue for the presence of three upper premolars in some mesotheriines.

2. Material and methods

This study is mainly focused on a cranial fragment from the El Degolladito area stored at the Paleontological collection of the Centro Regional de Investigación de La Rioja (CRILAR), La Rioja Province, Argentina. This specimen, CRILAR Pv 433, is very fragmented but has most of the palate preserved, with right and left I1, the right tooth row (P2–M3), and the incomplete left M2 and M3, as well as a small part of the right zygomatic arch (Fig. 1(A)). Other mesotheriid remains from the same locality, not directly associated with this palate, are CRILAR Pv 422, a lower left premolar (?p4), and CRILAR Pv 432, an incomplete right upper molar (?M3). A morphological and metrical study was performed, following previous works on this group of notoungulates (Francis, 1960, 1965; Cerdeño and Montalvo, 2001; Cerdeño et al., 2012, among others).

Mesotheriine material used for comparison includes maxillary fragments or isolated teeth belonging to the collections of Museo de La Plata (MLP); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires; Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa (GHUNLPam), Santa Rosa; and Museo Condor Huasi (MCH-P), Belén, Catamarca, Argentina. The specimens, their origin and references, if any, are detailed in Table 1.

Abbreviations (text and tables): DP/dp, upper/lower milk molars; Fm., Formation; I, upper incisor; L, length; l., left; M, upper molar; Max., maximum; P/p, upper/lower premolar; r., right; W, width. DP and dp in quotes (text and Table 1) denote the supposed condition of milk molars previously assumed for the mentioned teeth, but presently questioned by the authors.

3. Description of the Mesotheriinae from El Degolladito

The zygomatic arch of CRILAR Pv 433 starts at the level of the anterior part of M1. The posterior border of the zygomatic plate is

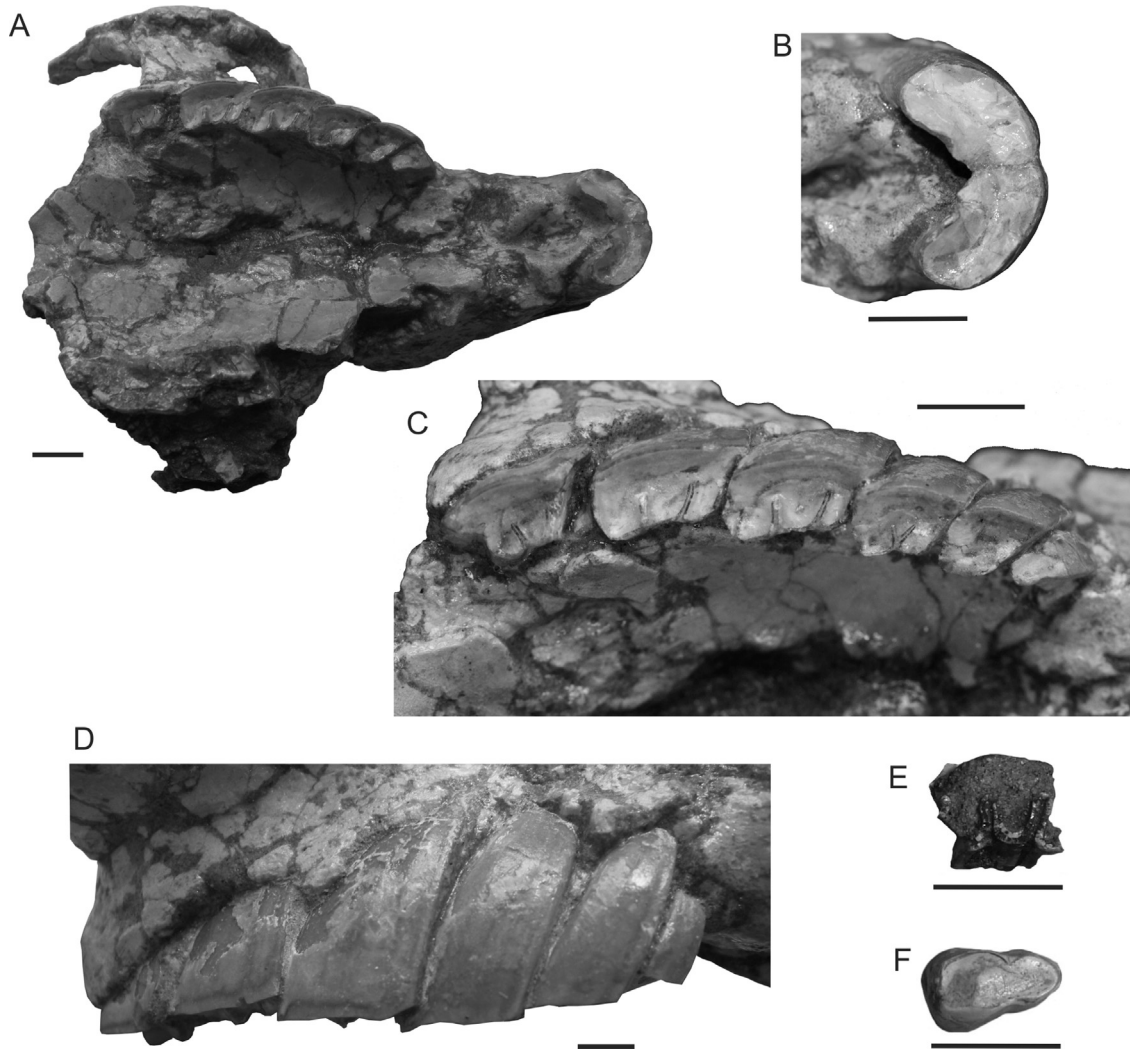

Fig. 1. Mesotheriidae from El Degolladito, Salicas Formation (La Rioja Province, Argentina). **A–D**. CRILAR Pv 433, cranial fragment with right and left I1, and right P2–M3; A, ventral view; B, detail of incisors; C, detail of the cheek teeth, occlusal view; D, labial view of the cheek tooth row. **E**. CRILAR Pv 432, upper right?M3 (anterior face to right). **F**. CRILAR Pv 422, lower left?p4 (anterior face to right). Scale bars: 10 mm.

Table 1
List of specimens included in the comparative study of CRILAR Pv 433. Some specimens might have been included in some studies, but were not detailed (e.g., Francis, 1960).

Specimen and origin	Material	Reference or collection label
MLP 55-IV-28-14 ([a]) Arroyo Chasicó Fm., Campo de Torres, Buenos Aires	Palatal fragment with I1 (right I1 incomplete), left P2–M1, and right P2–M3 (M3 broken)	Labelled *Typotheriopsis* sp. (not labelled as juvenile)
MLP 37-III-7-1+5 ([b]) Adolfo Alsina, "Epecuén Fm.", Buenos Aires	Right "DP2–4" and M1–2, and mandibular fragments with right "dp3", fragment of m1 and left "dp4"–m3	*Pseudotypotherium carhuense* Cabrera, 1939. Francis (1965); Zetti (1972): juvenile of *Typotheriodon grandis* Cabrera, 1939
MLP 29-IV-15-3 ([b]) Monte Hermoso? (in schedula)	Maxillary fragment with left "DP4"–M1 and right "DP2"	Labelled *P. studeri* Moreno and Mercerat, 1891. Species defined for Catamarca Province
MLP 62-XII-4-11+12 ([b]) Laguna Chillhué (=Valle Argentino), Cerro Azul Fm., La Pampa	Right "DP2–4"–M1 and left M1–3	Labelled *Pseudotypotherium* sp. from Valle Argentino. Cerdeño and Montalvo (2001)
GHUNLPam 21104 ([b]) Cerro de los Guanacos, Cerro Azul Fm., La Pampa	Left maxillary fragment with "DP2–4" ("DP2" broken)	Cerdeño and Montalvo (2001)
GHUNLPam 8624 ([b]) Laguna Chillhué, Cerro Azul Fm., La Pampa	Isolated left "DP4"	Cerdeño and Montalvo (2001)
GHUNLPam 814/1([b]) Loventué, Cerro Azul Fm., La Pampa	Isolated left P4	Cerdeño and Montalvo (2001)
MCH-P 24 ([b]) Villavil, Chiquimil A Formation, Catamarca	Four unworn or barely-worn isolated upper teeth	No more data
MACN PV 9531 ([c]) Barranca Monte Hermoso, Buenos Aires	Maxillary fragment with right "DP2–4"–M2	Labelled *Typotheriodon* (juvenile)

([a]) Chasicoan, ([b]) Huayquerian, and ([c]) Montehermosan South American Mammal Ages.

smoothly concave, reaching the middle level of M3 (Fig. 1(A)). The length of this plate is around 37.4 mm.

The right and left I1 form an approximate right angle (longitudinal axes at 92°) and occupy a maximum transverse diameter – between their outer sides – of 22.3 mm. Their contact surface is 6.7 mm long. Each incisor is kidney-shaped, smoothly convex labially, and presents a wide median lingual groove and a second one more mesially placed, leaving a marked fold between them (Fig. 1(A, B)).

The outstanding feature of this specimen is the presence of three premolars (Fig. 1(A, C)), which implies the presence of a P2 in this mesotheriine individual. This P2 is smaller than P3 and P4, but well-developed and subtriangular in outline, with a very short lingual face; its anterior face is almost straight, but with a faint concavity; the posterior face is shorter and straighter; the ectoloph is short, hardly convex. The P2 is slightly more labiolingually inclined than P3 (Fig. 1(C)). The P3 is subtriangular in outline, but with smoothly convex posterior and labial walls, and the parastyle is hardly distinct. The P4 is a more quadrangular tooth, with a well-defined, narrow, Y-shaped lingual groove, and a parastyle projecting over the P3. The ectoloph of the P4 is relatively longer than that of the P3. The parastylar groove is little marked in both premolars and molars.

The M1 and M2 have a large middle lobe, reaching the lingual level of the anterior lobe, the posterior one being slightly more projected lingually. On M3, the anterior lobe is directed more posteriorly; the middle lobe is barely shorter than the others, but slightly more triangular in outline. The parastyle is wide and pointed anteriorly, projecting over the M2. The metastyle of the M3 projects backward and contributes to the sharply concave posterior face.

There are remnants of a cement layer on the ectoloph, lingual wall, and grooves of each tooth. In labial view, the missing bone of the maxilla at the basal level of P2–M1 allows seeing the hypsodont crowns of these teeth (Fig. 1(D)). Dental dimensions of CRILAR Pv 433 indicate a small-medium mesotheriid (Table 2). The whole cheek tooth series is smoothly convex, and there is a small difference of width along the palate. The index of imbrication (following Flynn et al., 2005) between M1 and M2 is 1.20.

The dental morphology of CRILAR Pv 433 resembles both *Typotheriopsis* Cabrera and Kraglievich, 1931 (e.g., premolars with one labial sulcus) and *Pseudotypotherium* Ameghino, 1904 (e.g., P4 with lingual groove, wide median lobe of M3) based on current characterization of these two late Miocene genera (Cerdeño and Montalvo, 2001), but both are supposed to lack the P2 (Section 4).

Table 2
Measurements (in mm) of CRILAR Pv 433 from El Degolladito, La Rioja Province, Argentina. Approximate values within parentheses.

	I1 [r./l.]	P2	P3	P4	M1	M2 [r./l.]	M3 [r./l.]
L	15/15.3	4.8	8.5	10.5	13.9	15.0/(15.6)	(15.7)/16.4
W	9.4/8.8	7.0	8.6	7.5	8.7	8.4/(9)	7.9/8.7
L I1–M3	100	–	–	–	–	–	–
L P2–P4	26.3	–	–	–	–	–	–
L M1–M3	43.1	–	–	–	–	–	–
Max. palatal L	(104)	–	–	–	–	–	–
Palatal W	–	26.0	–	35.5	–	38.9	38.0
L diastema	23.4	–	–	–	–	–	–

The upper molar CRILAR Pv 432 (Fig. 1(E)) has incomplete anterior and posterior lobes. The median lobe is well-developed, nearly reaching the same lingual level as the other two. The preserved enamel on the distal face suggests that it would correspond to the inflexion present on the M3. The length of the preserved molar is 10.35 mm.

The lower tooth CRILAR Pv 422 is roughly subtriangular in outline (Fig. 1(F)). A shallow labial groove separates the trigonid and talonid, the former being shorter and more rounded than the latter. Opposite to the labial groove, the lingual wall shows a shallow depression throughout the crown height. The occlusal surface presents a smooth concavity on each lobe, the posterior one being deeper due to wear. Tooth dimensions are: length, 11.1 mm; anterior width, 4.9 mm; and posterior width, 7.1 mm. These dimensions are below the minimum value established by Cerdeño and Montalvo (2001) for the p4 sample of mesotheriines and approach those considered by these authors to be dp4. Taking into account the following discussion (Sections 4 and 5), both CRILAR Pv 422 and the supposed dp4 in Cerdeño and Montalvo (2001) could correspond to permanent premolars (p4), reflecting ontogenetic size variation. CRILAR Pv 422 closes the specimens of *Typotheriopsis chasicoensis* Cabrera and Kraglievich, 1931 studied by Cerdeño (2000), but with a more rounded anterior lobe.

Both teeth, CRILAR Pv 432 and CRILAR Pv 422, are tentatively assigned to the same taxon as CRILAR Pv 433, although the accurate identification of this taxon is not possible at present, as stated in Section 1.

4. Comparisons

Due to the presence of three upper premolars in CRILAR Pv 433, the comparison is focused on several specimens showing the same condition, previously assumed to correspond to the deciduous dentition (see Section 1), as well as some isolated teeth also considered to be milk molars (Table 1). Concerning size, CRILAR Pv 433 matches better as a whole with the supposed juvenile specimens described by Cerdeño and Montalvo (2001: table 1) than with adults, but proportions are rather different. Dimensions of the whole studied sample reflect a similarity in size among all the specimens with respect to the considered adult ones (Cerdeño and Montalvo, 2001, and pers. obs.), which support their younger, but not necessarily juvenile condition.

Specimens MLP 37-III-7-1+5, MLP 29-IV-15-3, and MACN PV 9531 differ from CRILAR Pv 433 because their "DP4" has a well-developed, broad median lobe and are relatively longer teeth (Fig. 2(A–D)). In turn, their M1 is also different as it has a projected median lobe and the lingual grooves are wider than that observed on CRILAR Pv 433. This occlusal morphology is also observed on the isolated teeth from Villavil (MCH-P 24; Fig. 2(E, F)). The P2 of

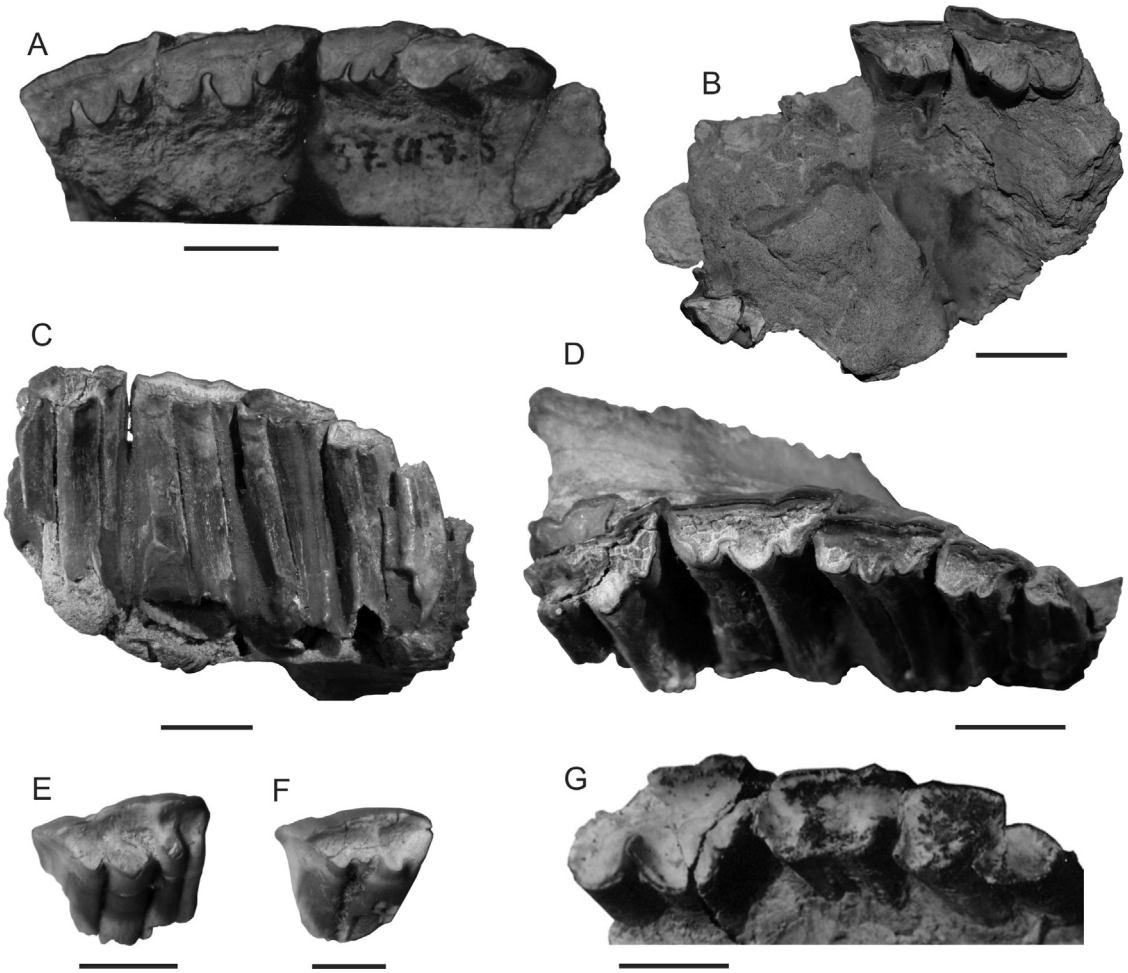

Fig. 2. A. "*Pseudotypotherium carhuense*", MLP 37-III-7-1+5 (holotype), right "DP2–4" and M1–2, occlusal view. **B**. "*P. studeri*", MLP 29-IV-15-3, maxillary fragment with left "DP4"–M1 and right "DP2", occlusal view. **C**, **D**. MACN PV 9531, maxillary fragment with right P2–M2, lingual (C) and occlusal (D) views. **E**, **F**. MCH-P 24, isolated upper molars (?), occlusal views (anterior face to left). **G**. *Pseudotypotherium* sp., MLP 62-XII-4-11+12, right "DP2–4"–M1 (left M1–3 of this individual not figured), occlusal view. Scale bars: 10 mm.

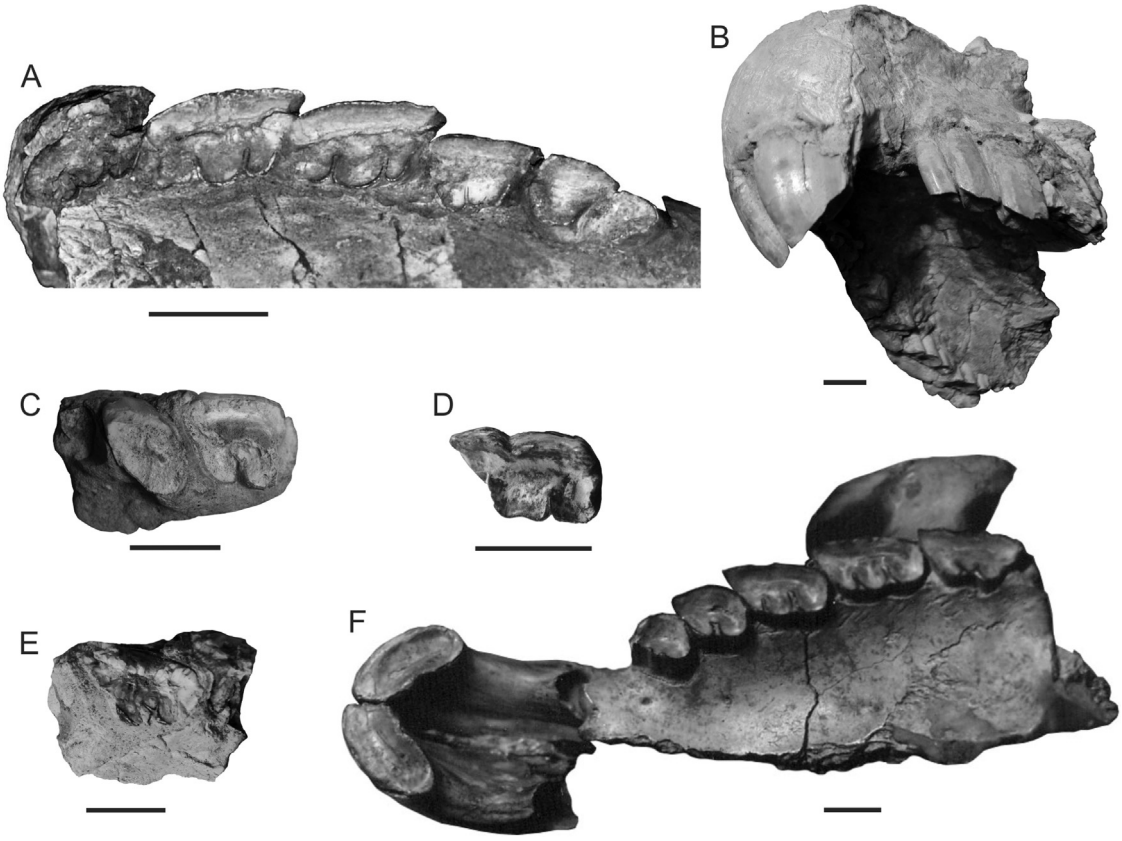

Fig. 3. A, **B**. *Typotheriopsis* sp., MLP 55-IV-28-14; A, detail of right P2–M3 (M3 broken); B, anterolateral view of the whole fragment with I1, left P2–M1, and right P2–M3. **C**. GHUNLPam 21104, left maxillary fragment with "DP2–4" ("DP2" broken). **D**. GHUNLPam 8624, left P4 (anterior face to left). **E**. GHUNLPam 814/1, left P4 (anterior face to left). **F**. MLP 12-1695, maxilla with both I1 and left P4–M3. Scale bars: 10 mm.

MACN PV 9531 has its crown lower than that of P3 as it happens in CRILAR Pv 433.

MLP 62-XII-4-11+12 (Fig. 2(G)) exhibits "DP2–4" that are rather different from MLP 37-III-7-1+5 and CRILAR Pv 433. The "DP4" has a long, trilobed parastyle, but the lingual grooves are faint, in contrast with MLP 37-III-7-1+5, MACN PV 9531 or Villavil specimens, although it is also a relatively long tooth. The P4 of CRILAR Pv 433 is relatively shorter, more trapezoidal in outline, and with a much reduced median lobe. The "DP3" of MLP 62-XII-4-11+12 is also somewhat shorter than those of MLP 37-III-7-1+5 and MACN PV 9531, with less undulating ectoloph. All of these have a small labial fold and are relatively longer than the P3 of CRILAR Pv 433. These differences also apply to the respective "DP2" and P2, the tooth of CRILAR Pv 433 being clearly shorter and more triangular in outline. The M1–2 of MLP 62-XII-4-11+12 have a large, projected median lobe, but the grooves are more closed than in the other MLP and MACN specimens; in this individual, the preserved left M3 is very inclined and its crown increases distally – i.e., with more advanced wear – indicating a subadult age. Another interesting feature of M1–M2 is the fourth lobe showed by MCH-P 24 (Fig. 2(E)). Compared with MLP 37-III-7-1+5 (Fig. 2(A)) and MACN PV 9531 (Fig. 2(D)), the general occlusal morphology is similar by the elongation of the parastyle and the development of the median lobe, but these two specimens do not present a fourth lobe. Considering how the outline of the teeth can change, as seen in MACN PV 9531, we think that MCH-P 24 may represent an earlier ontogenetic stage; it will become trilobed with more advanced wear.

The specimen MLP 55-IV-28-14 (Fig. 3(A, B)) from the Arroyo Chasicó Formation appears closer to CRILAR Pv 433 by the triangular outline of its "DP2–3". Its "DP4" is trilobed, but the separation of the two first lobes is subtle by means of a rather short anterior lingual groove. This condition is similar to that of MLP 37-III-7-1+5, but the latter has wider, open lingual grooves and the tooth is more elongated. MLP 55-IV-28-14 also shows that the "DP2" crown is lower than that of "DP3" as it happens in CRILAR Pv 433 and MACN PV 9531. Its incisors are similar too, but they bear just a median lingual groove.

In the case of GHUNLPam 21104, the "DP2" (broken) is rather triangular, and the "DP3" is more similar to the P3 of CRILAR Pv 433 and MLP 55-IV-28-14 than to the "DP3" of the other compared specimens, but preserves a small labial fold and has less developed parastyle (Fig. 3(C)). The "DP4", in turn, is also closer to the P4 of CRILAR Pv 433 by its more quadrangular outline and the even more reduced Y-shaped median lobe. In contrast, the "DP4" GHUNLPam 8624 (Fig. 3(D)) presents a projected parastyle and a long anterior lingual lobe.

Another specimen considered to be juvenile is that of the Pleistocene *Mesotherium cristatum* Serrés, 1867 figured by Patterson (1952: fig. 1), which shows a small anterior alveolus, from which the author described the "DP2" as a simple, semi-cylindrical tooth.

All these comparisons reveal some morphological variations among the known supposed juvenile mesotheriine specimens, not only in the "deciduous dentition" but also in the accompanying permanent molars. We interpret these variations as due to ontogeny, but within individuals with permanent dentition. Some taxonomic differentiation is not discarded among these specimens, but it is evident that a deep revision of a much larger sample of mesotheriines is needed to achieve an accurate taxonomic interpretation of these variations.

5. Ontogenetic variations

Among the compared specimens, MACN PV 9531 lacks the lingual maxillary bone; it allows observing how the crown design changes throughout the tooth (Fig. 2(C)). Both the "DP3" and the "DP4" have a lingual groove that clearly differentiates an anterior lobe in the occlusal surface, but it fades out along the high crown. As a result, the "DP3" loses their lingual groove and the "DP4" becomes bilobed. Similarly, the "DP2" reduces its anterior projection and becomes a shorter and wider tooth, more similar to the occlusal outline of the P2 of CRILAR Pv 433. Tooth proportions vary from relatively longer to relatively wider along the crown. Consequently, features formerly considered to represent milk molars (e.g., long occlusal face, parastyle expanded, broad lingual grooves) are here demonstrated to change with wear, achieving the "typical" premolar occlusal morphology. Accompanying permanent molars also show this ontogenetic variation, changing their proportions and the extent of the lingual grooves.

Trying to establish detailed ontogenetic stages is not easy due to the relatively scarce material and the uncertainty that all belong to the same taxon, but some successions among the studied specimens can be approached. In this sense, MACN PV 9531 and MLP 37-III-7-1+5 would be rather young individuals, the former maybe younger by the presence of a lingual groove in "DP3". The specimen MLP 29-IV-15-3 is similar to them, but teeth are a little wider, which implies a more advanced wear stage. MLP 62-XII-4-11+12, MLP 55-IV-28-14 and CRILAR Pv 433 are more aged individuals, with proportionally shorter and wider teeth, and narrower lingual grooves. Concerning the other compared specimens, the isolated "DP4" GHUNLPam 8624 could represent an intermediate stage between MACN PV 9531 and MLP 37-III-7-1+5, as it has an elongated parastyle, but the lingual anterior groove is barely marked. In turn, GHUNLPam 21104 is an older individual, similar to CRILAR Pv 433 by the short and wide teeth. Likely, from a certain age on, the occlusal outline would be more stable along the crown.

With respect to the isolated teeth MCH-P 24, they represent a much younger stage, as they are hardly worn. In addition, these teeth have a shorter crown, and one could think that they actually are milk molars. However, the similarity of the figured tooth (Fig. 3(E)) with the M1 of MACN PV 9531 and MLP 37-III-7-1+5, together with the uncertainty of their position in the tooth row, lead us to interpret them as permanent teeth just erupting, and thus from an individual clearly younger than MACN PV 9531.

On the other hand, the apparent lack of true milk molars among mesotheriids seems to be unusual compared with other notoungulate families. This can be due to a general taphonomic bias, but it also indicates the need of a very complete revision of mesotheriids, which could confirm the existence of deciduous dentition within the collections.

6. Discussion

Once exposed the similarities and differences among the known mesotheriid specimens with three upper premolars, we note several features that support the condition of permanent teeth in CRILAR Pv 433. In the first place, as far as we know among ungulates, milk molars that are normally replaced by permanent premolars are not high-crowned teeth, while CRILAR Pv 433 has very hypsodont teeth. Comparing with other euhypsodont notoungulates, personal observations of juvenile individuals of the genus *Paedotherium* Burmeister, 1888 (Hegetotheriidae) reveal short delicate crowns that appear covering the corresponding permanent tooth (e.g., GHUNLPam 19389, 21373, 21517); in addition, the permanent molars of young individuals show little wear, with some differentiation of cusps. In a group closer to mesotheriines such as the Trachytheriinae, Billet et al. (2008) described the deciduous premolars as rectangular teeth that became more quadratic in advanced stages of wear. These authors exposed the ontogenetic variation both of deciduous and permanent teeth of *Trachytherus alloxus* Billet, De Muizon and Mamaní Quispe, 2008, but did not allude to any relative difference in their crown height.

On the other hand, CRILAR Pv 433 shows a degree of wear on all teeth congruent with a permanent dental series (Fig. 1(C)); i.e., no significant differences in occlusal features are observed between premolars and molars to assume that CRILAR Pv 433 has the series DP2–4 and M1–3. These differences are observed in other notoungulates where deciduous and permanent molars are found in a single series (Madden, 1997; Billet et al., 2008). Furthermore, if the three anterior cheek teeth of CRILAR Pv 433 were milk molars, when these "high-crowned" teeth (at least DP3–4) were replaced by permanent premolars, the M1–3 should be so worn that they would necessarily show stronger wear differences with respect to P3–4 than those actually observed in adult mesotheres without P2.

In addition, in different ungulates (e.g., litopterns, fossil and extant perissodactyls) and even in some other groups such as caviomorph rodents (at least in taxa with normal tooth replacement; G. Vucetich, pers. com.), milk molars are usually long and narrow teeth, while the premolars of CRILAR Pv 433 are relatively wider teeth, particularly the P2.

In summary, none of the described features of CRILAR Pv 433 leads us to consider it as a juvenile individual with a deciduous dentition. Therefore, one can assume that it represents a mesotheriine species characterized by the presence of a P2. At this point, we return to the old controversy and discuss the previously compared remains (Section 4).

The most complete specimens compared, i.e., those with supposed milk molars together with permanent molars, share with CRILAR Pv 433 the high-crowned teeth and the congruent degree of wear on the whole preserved dental series, which leads us to interpret all of them (and as an extrapolation all mesotheriines with three upper and two lower premolars) as corresponding to individuals with a permanent dentition. At the same time, the observed differences among them may represent different ontogenetic stages from subadult to adult conditions. Taking into account this variation and the euhypsodont condition of these teeth, it can be assumed that the replacement of their milk molars would have happened very soon in the life time of these mammals.

Changes in size and morphology along the tooth crown with wear have been demonstrated for different euhypsodont or hypsodont notoungulates such as the archaeohyracids (Croft et al., 2003; Billet et al., 2009; Cerdeño et al., 2010), toxodontids (e.g., Madden, 1997) or Trachytheriinae mesotheriids (Billet et al., 2008), as well as other mammals such as the hydrochoerid rodents (Vucetich et al., 2005, 2011; Deschamps et al., 2009). Something similar happens in mesotheriines, as actually already supported by Francis (1965) with respect to the change in crown diameters. Among mesotheres, Ameghino (1889: pl. 19, fig. 5) figured a molar of "*Typotherium maendrum*" in which the parastyle diminishes to the base of the crown, becoming a shorter tooth. Croft et al. (2004) established an ontogenetic variation in the early Miocene mesotheriine *Eotypotherium chico* Croft, Flynn and Wyss, 2004, but see comments in Cerdeño (2007: p. 771) about this particular case. In addition, a slight morphological variation of the M1 median lobe of another early Miocene mesotheriine was pointed out by Cerdeño (2007).

Also within mesotheriids, Billet et al. (2008) described in detail the crown tooth changes of the thrachytheriine *T. alloxus*, both in premolars and molars. Besides the increasing width of the teeth with wear, these authors stated some morphological changes,

including the reduction of the median lobe in molars. In mesotheriines, at least in their revised late Mio-Pliocene representatives, the trilobed molar condition remains in full adults; changes concerning the number of lobes in molars refer to the above-commented fourth lobe that can be present in the youngest individuals (MCH-P 24).

One of the observed differences among the revised specimens concerns the lingual groove of P4 ("DP4"). Most of the discussed material comes from the late Miocene of Argentina, where only two genera have been identified: *Typotheriopsis* and *Pseudotypotherium*. The main difference between them is based on the absence or presence, respectively, of a lingual groove in P4 (Pascual et al., 1966; Cerdeño and Montalvo, 2001; Tauber, 2005). Actually, when available material is mostly composed of isolated or incomplete dentitions, it is not possible to determine which genus is present (Cerdeño and Montalvo, 2001). Considering just that character, CRILAR Pv 433 resembles *Pseudotypotherium* (Brandoni et al., 2012). Both *Pseudotypotherium* and the Pleistocene *Mesotherium* are characterized by a clearly bilobed P4, with a wide groove (Francis, 1965; Cerdeño and Montalvo, 2001; Flynn et al., 2005; Townsend and Croft, 2010), but other taxa also have a short, little marked lingual groove in P4, such as *Eutypotherium lehmannistchei* Roth, 1902 (early Miocene of Argentina) or *Caraguatypotherium munozi* Flynn et al., 2005 (late Miocene of Chile). Even though the adult specimens of the Argentinean *Pseudotypotherium subinsigne* (Rovereto, 1914) present some variation in the development of the lingual groove, the presence of a bifurcation in this groove has been previously observed only in three specimens: GHUNLPam 21104 and GHUNLPam 814/1 from the Cerro Azul Formation (La Pampa), and MLP 12-1695 from Monte Hermoso, Buenos Aires Province (Cerdeño and Montalvo, 2001: p. 69). The first one has been already commented above as a possible juvenile specimen (Fig. 3(C)). GHUNLPam 814/1 (Fig. 3(E)) was recognized as an incompletely preserved P4 whose lingual groove bifurcates in a similar way to that of CRILAR Pv 433, and being hardly more open lingually. In turn, MLP 12-1695 is an adult maxilla with P4–M3 (together with the incisors), in which the P4 has a different aspect: the bifurcation is hardly insinuated and the lingual groove is relatively wide, with rather parallel sides (Fig. 3(F)). [It is worth noting that MLP 12-1695 shows a lingual fold in the I1 similar to that of CRILAR Pv 433.] Furthermore, the well-formed but short Y-shaped groove of the P4 of CRILAR Pv 433 actually recalls the one observed in some molars (M1) of early Miocene mesotheriines such as *Altitypotherium chucalensis* Croft, Flynn and Wyss, 2004, from the Chucal Formation (Chile) and the Mariño Formation (Mendoza, Argentina; cf. *A. chucalensis*; Cerdeño, 2007), as well as the specimens from the Chichinales Formation (Río Negro, Argentina; Paz et al., 2011). Consequently, it seems that the lingual groove of P4 should be treated as a more complicated feature than its mere presence or absence, and its phylogenetic significance better evaluated.

In summary, both the presence of a P2 (and p3) and the morphology of the lingual groove in P4 are two characters that must be reconsidered under a new point of view in the context of mesotheriines. We cannot discard a possible taxonomic differentiation based on these two features, but a deep revision of all known mesotheriines becomes necessary with this new perspective in mind. The presence of a P2 (or p3) by itself does not seem to be enough at this moment to define accurately a new taxon, as specimens with P2 also present differences among them, even though most are identified as ontogenetic changes. In addition, a last hypothesis is that the P2 (and p3) could be expelled relatively soon in the life time of the individuals, as it has been stated for the canine and P1 of some trachytheriine mesotheriids (Billet et al., 2008). This is partially supported by the crown height of P2, high but clearly shorter than that of P3. If so, individuals with three upper (or two lower) premolars would have only two (or one) at an older age. Another possibility is that the presence of the P2 (and p3) is a variable character within a same taxon, which would maybe reflect an evolutionary trend to the loss of a dental element within mesotheriines. As already said, a very deep revision of mesotheriines will support or reject these hypotheses.

7. Conclusions

The specimen CRILAR Pv 433 from the Salicas Formation, La Rioja Province, Argentina, is recognized as a member of Mesotheriinae with permanent dentition, including three premolars (P2–P4). The comparison of CRILAR Pv 433 with other specimens previously considered to bear the deciduous dentition (DP2–4) allows us to propose that all of them are actually bearing permanent premolars. Morphological variations among them, especially referred to the development of lingual grooves on premolars and accompanying molars and to the change in occlusal outline, are interpreted as due to different ontogenetic stages from young (but without milk molars) to adult individuals.

This new interpretation, together with the observed morphological differences of the lingual groove of P4, leads to the necessity of a full revision of the systematics of the Subfamily Mesotheriinae. At this moment, the presence of three upper and two lower premolars is not enough to establish a different taxon based uniquely on this character. The P2 (and p3) may be expelled relatively soon in the life time of the individuals, or their presence may even be a variable character within a same taxon, possibly reflecting an evolutionary trend to the disappearance of P2/p3 within a phylogenetic lineage. In the present context of Mesotheriinae knowledge, and pending their taxonomic revision, the specimen CRILAR Pv 433 resembles both *Typotheriopsis* and *Pseudotypotherium*.

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