



Research Paper

Young individuals, deciduous dentition, and rooted teeth of Late Miocene Mesotheriidae (Notoungulata) from central Argentina: new data and interpretations on a long debate [☆]



Esperanza Cerdeño ^{a,b,*}, Claudia I. Montalvo ^c, Santiago Hernández Del Pino ^{a,b,d}, Renata Sostillo ^{b,c}, Gabriela I. Schmidt ^{b,e}, Matías A. Armella ^{b,f}, Rodrigo L. Tomassini ^{b,g}

^a Paleobiología y Paleocología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT-CONICET-Mendoza. Avda. Ruiz Leal s/n, M5500 Mendoza, Argentina

^b Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

^c Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina

^d Laboratório de Paleontologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3900, Monte Alegre - Ribeirão Preto, São Paulo, Brazil

^e Laboratorio de Paleontología de Vertebrados, Centro de Investigación Científica y de Transferencia Tecnológica a la Producción (CICYTP, CONICET, Gob. ER-UADER), Diamante, Entre Ríos, Argentina

^f Instituto Superior de Correlación Geológica (INSUGEO-CONICET), Yerba Buena, and Facultad de Ciencias Naturales e Instituto Miguel Lillo (IML), Universidad Nacional de Tucumán (UNT), San Miguel de Tucumán, and Facultad de Ciencias Exactas y Naturales (FaCEN), Universidad Nacional de Catamarca (UNCa), Catamarca, Argentina

^g Instituto Geológico del Sur (INGEOSUR), Departamento de Geología, Universidad Nacional del Sur-CONICET, Avda. Alem 1253, 8000 Bahía Blanca, Buenos Aires, Argentina

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ABSTRACT

Unpublished material of *Tytopheriopsis chasicensis* (Notoungulata, Mesotheriidae) from the Late Miocene Arroyo Chasicó locality (Buenos Aires Province, Argentina; Cerro Azul Formation) reveals ontogenetic changes in the cheek teeth (lingual grooves and proportions) among young individuals. Additionally, the specimen MD-CH-07-04 bears a rooted upper premolar. This sample sheds new light on the long-standing controversy regarding the deciduous/permanent mesotheriine premolars, but also raises new questions. No specimen considered as young (bearing an 'extra' premolar) has proved to be rooted through X-ray or CT-scan images. Among the compared mesotheriines from La Pampa Province, two specimens (Mesotheriinae indet. from Telén and Laguna Chillhué) show revealing features: one presents a rooted p4 and the other bears a permanent premolar (p4) positioned below and lingually to the rootless dp4, similarly to the holotype of '*Pseudotytherium carlesi*' (Huayquerías of Mendoza Province). Interpreting the rooted teeth is difficult, but their deciduous condition is herein discarded: in MD-CH-07-04, due to the occlusal morphology of both the rooted P4 and the accompanying molars compared with young individuals with P2; in the rooted p4 from Telén, its morphology is similar to that of other compared p4 without roots, and the mandibular bone does not indicate a very juvenile condition. The specimen from Laguna Chillhué and the holotype of "*P. carlesi*" are the first mesotheriines described with both deciduous and corresponding permanent premolars altogether. A better interpretation of these scarce cases of rooted and deciduous premolars would be possible with further findings and the revision of other large samples from single localities.

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1. Introduction

Mesotheriidae is a family of South American native ungulates included in the order Notoungulata, being the largest representa-

tives of the suborder Typotheria (e.g., Croft et al., 2020). They are known from the early Oligocene, but particularly from the late Oligocene Deseadan age to the Pleistocene (Cerdeño, 2018; Croft et al., 2020). Paleogene mesotheriids are gathered as trachytherines and represented by the genus *Trachytherus*, but recognized as a paraphyletic group (Billet et al., 2008; Shockey et al., 2016; Armella and Deforel, 2023). The remaining taxa constitute the subfamily Mesotheriinae that shows greater diversity and geographi-

[☆] Corresponding editor: Laurent Marivaux.

* Corresponding author.

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

cal distribution (Cerdeño et al., 2018; Armella and Deforel, 2023). Even though the best record of the family comes from Argentina, mesotheriids are also known from Bolivia, Peru, and Chile. In fact, based on the record of *Trachytherus*, Shockey et al. (2016) proposed a small geographical area encompassing western Bolivia and southern Peru as the ancestral area for mesotheriid diversification. The family is mainly characterized by: euhyposodont (following Mones, 1982; equivalent to hypselodont, elodont, or ever-growing) incisors with buccal enamel; protohyposodont (very high-crowned, indeed) cheek teeth in trachytherines and euhyposodont in mesotheriines (with trilobed upper molars); and postcranial elements associated with a digging behavior or semi-fossorial habits (Shockey et al., 2016; Fernández-Monescillo et al., 2018). Compared to most tyotherians, mesotheriines are characterized by the loss of some teeth, with dental formula in adults being 1-0-2-3/2-0-1-3. Specimens preserving three upper premolars and two lower premolars have been interpreted differently as juvenile individuals with deciduous teeth (Francis, 1960, 1965; Fernández-Monescillo et al., 2022a, 2022b) or still-young individuals with permanent dentition (Cerdeño and Schmidt, 2013). Given these contrasting interpretations, only new material – particularly juvenile specimens and ontogenetic series – will help to clarify this issue.

The present contribution arose from the study of unpublished specimens from the early Late Miocene Arroyo Chasicó locality (Buenos Aires Province; Fig. 1), which leads us to revisit the mentioned long-standing controversy. Arroyo Chasicó is a paradigmatic Late Miocene locality in the Pampean region of Argentina – La Pampa and Buenos Aires provinces – with abundant remains of Mesotheriinae. This material from Arroyo Chasicó not only provides a good sample of young individuals revealing ontogenetic changes, but also includes a specimen with a rooted premolar. The faunal assemblage from Arroyo Chasicó was classically ascribed to the Arroyo Chasicó Fm. that was reinterpreted as part of the Cerro Azul Fm. (Folguera and Zárate, 2009). This assemblage was, in turn, the basis of the Chasicóan South American Land Mammal Age or Stage/Age (Tortonian; Pascual et al., 1965; Cione and Tonni, 1995). Based on radiometric ages (using impact glasses [‘escorias’] and detrital zircons) and high-resolution magnetostratigraphic profiles, the fossiliferous levels at this locality are assigned to the interval 9.7–8.7 Ma (Zárate et al., 2007; Sanz-Pérez et al., 2024). Among the materials used for comparison in

this study, many specimens come from the Cerro Azul Fm. at several localities in La Pampa Province (Late Miocene–Early Pliocene; Piñero et al., 2021; Sanz-Pérez et al., 2024), as well as other Neogene remains from different Argentinean areas (Fig. 1). The compared samples have provided another specimen with a rooted premolar and two specimens that present a permanent premolar along with the corresponding deciduous tooth. Altogether, the studied material challenges the interpretation of these specimens within the young (non-fully adult) Late Miocene mesotheriines.

2. Material and methods

The studied specimens from Arroyo Chasicó belong to the paleontological collections of museums of the Buenos Aires Province in Monte Hermoso, Punta Alta, and Mar del Plata towns (see institutional abbreviations below). Other revised specimens involved in this study belong to several Argentinean institutions also listed in the institutional abbreviations below, particularly those from the Cerro Azul Fm. housed at the Paleontological Collection of the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa.

Mesotheriid materials from Arroyo Chasicó are attributable to *Tyotheriopsis chasicóensis*, the species defined by Cabrera and Kraglievich (1931) for this locality; none of the revised materials leads to propose the presence of a second mesotheriid taxon. Other compared and discussed specimens, concerning roots, ‘extra’ premolars or young condition, belong to different taxa (*T. silveyrai*, *Pseudotyotherium subinsigne*, *Mesotherium cristatum*, and Mesotheriinae indet.) and come from different stratigraphic levels, as detailed throughout the text. The list of revised unpublished (except one) materials from Arroyo Chasicó and three other localities (total number of specimens: 59) are given in Appendix A.

Morphological descriptions and measurements follow previous papers on Mesotheriidae systematics (Croft et al., 2004; Cerdeño et al., 2018; Armella et al., 2025). Dental measurements are shown in Appendix B. We have identified several wear/ontogenetic stages that mostly concern variation in the occlusal morphology of premolars and accompanying molars among the young individuals without deciduous dentition, following Cerdeño and Schmidt’s (2013) criterion, considering juvenile those bearing deciduous teeth (or referred to as such in bibliography). In some cases, the presence of trabecular bone and open sutures also helped to establishing the young condition of the specimens.



Fig. 1. Geographic distribution of Miocene–Middle Pleistocene localities with Mesotheriidae remains mentioned in the text.

Some specimens were subjected to X-ray radiography and/or computed tomography studies to check the possible presence of roots. For radiographies, we received collaboration of private odontologists in Santa Rosa (La Pampa Province) and Mendoza cities. Medical CT scanning using a GE Medical System Discovery STE scanner, housed at Fundación Escuela de Medicina Nuclear (FUESMEN, Mendoza), generated sequences of DICOM images with 500 × 500 pixels resolution and a slice distance of 0.55 mm.

Institutional Abbreviations: Argentina: **CRILAR-Pv**, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, Vertebrate Paleontology Collection, Anillaco; **GHUNLPam**, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa; **IANIGLA-PV**, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Vertebrate Paleontology Collection, Mendoza; **MACN-Pv**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Vertebrate Paleontology Collection, Ciudad Autónoma de Buenos Aires; **MCH-P**, Museo Condor Huasi, Paleontological collection, Belén; **MCNAM-PV**, Museo de Ciencias Naturales y Antropológicas ‘J. C. Moyano’, Mendoza; **MD-CH**, Museo Municipal de Ciencias Naturales ‘Carlos Darwin’ (locally known as ‘Museo Darwin’), Chasicó collection, Punta Alta; **MHAS**, Museo del Hombre de Antofagasta de la Sierra, Antofagasta de la Sierra; **MLP-PV**, collection of the División Paleontología de Vertebrados, Museo de La Plata, La Plata; **MMH-CH**, Museo Municipal de Ciencias Naturales ‘Vicente Di Martino’, Chasicó collection, Monte Hermoso; **MMP**, **M/S**, Museo Municipal de Ciencias Naturales ‘Lorenzo Scaglia’, Museum/Scaglia collections, Mar del Plata.

Anatomical Abbreviations: **DP/dp**, upper/lower deciduous premolar; **I/i**, upper/lower incisor; **M/m**, upper/lower molar; **P/p**, upper/lower premolar.

3. Results

3.1. Young Mesotheriinae individuals from Arroyo Chasicó

One character traditionally used to identify juvenile individuals (i.e., with deciduous dentition) among mesotheriines is the presence of an ‘extra’ premolar in the jugal series, thus showing three instead of the two upper premolars (P3–4) and two instead of one lower premolar (p4) of full adult individuals. However, Cerdeño and Schmidt (2013) rejected the deciduous condition of this ‘extra’ and its accompanying premolars in several specimens, referring to these individuals as young, but not juvenile, hypothesizing that the P2/p3 would be lost early in their life time. In addition, specimens with P2 do not show the same morphology of the accompanying premolars and molars, reflecting different wear stages among them. In this sense, another feature that has been proved to vary with wear is the presence of one or two lingual grooves in P3 and P4, although a well-developed lingual groove in P4 of adults is also established as a taxonomic character shared by genera such as *Pseudotypotherium* and *Mesotherium* in Argentina, and *Caragatypotherium* in Chile (Francis, 1965; Cerdeño and Montalvo, 2001; Flynn et al., 2005).

3.1.1. Upper dentition

Description: Within the *Typotheriopsis chasicoensis* sample from Arroyo Chasicó, two maxillary fragments, MMH-CH 86-09-87 and MMH-CH 85-04-125, have three high-crowned premolars, as it occurs in the previously studied MLP-PV 55-IV-28-14 from the same locality (Cerdeño and Schmidt, 2013). The presence of P2 correlates with a general size of these specimens that is clearly smaller than that of adult individuals (Fig. 2(A); Appendix B), with minimal overlapping that may reflect individual variation (possibly including sexual dimorphism). This size difference supports a younger ontogenetic stage of the former specimens; moreover,

our comparisons allow establishing a relative ontogenetic sequence between them and with respect to other already studied young mesotheriines, as reflected in Table 1.

MMH-CH 86-09-87 (Fig. 3(A, B)) presents relatively longer and narrower jugal teeth than MMH-CH 85-04-125 (Fig. 3(C, D)), and the general size is smaller in the former, including the I1 (length of I1 = 9.6 mm vs. 11.8 mm). In MMH-CH 86-09-87 (Fig. 3(A)), P2 is subtriangular, barely wider than long; P3 is extended mesially at the parastyle area and there are two lingual lobes, the anterior much narrower (mesiodistally) than the posterior, separated by a neat lingual groove; the lingual length occupied by these two lobes is clearly shorter than the ectoloph; and P4 is long with undulate lingual wall, in which three lobes are observed, but the mesial groove is much shallower than the distal groove; the morphology of P4 resembles that of M1–2 (M3 is incomplete), in which the median lobe projects lingually and the distal groove is more open and deeper than the mesial groove. In MMH-CH 85-04-125 (Fig. 3(C)), P2 is very short and wide; P3 is more subrectangular, less mesio buccally expanded, and with a deeper lingual groove than in MMH-CH 86-09-87; and P4 is also shorter, with more triangular, well-delimited median lobe. The molars in MMH-CH 85-04-125 are also shorter, with the median lobe less expanded lingually, closer to the adult morphology, but the M3 presents an evident lingual groove in the third lobe. Differences in cheek-tooth size are reflected in Appendix B. The commented differences in morphology and size lead to consider MMH-CH 86-09-87 to be ontogenetically younger than MMH-CH 85-04-125 (Table 1). Neither the former nor the latter revealed the presence of roots through X-ray or CT-scan images. Besides, MMH-CH 85-04-125 is composed of two fragments that let see the posterior area of P4 inside the bone; even though it is not well preserved, no root is observed but part of the buccodistal corner of the curved crown continuing deep in the maxilla.

The isolated tooth MMH-CH 86-09-76 (Fig. 3(E, F)) is quite similar to the P4 of MMH-CH 86-09-87 and it is included in the stage 2 (Table 1). The preserved crown, basally open, shows that the tooth becomes slightly shorter and wider with wear, with more tightened lobes; the mesial groove persists at the level of crown breakage, which might indicate that the tooth is a slightly worn molar if the groove continues basally, but the preserved fragment is too short to be sure of this persistence.

The specimen MLP-PV 55-IV-28-14 from Arroyo Chasicó (Cerdeño and Schmidt, 2013; Fig. 3(G, H)) has P2–3 without neat grooves (just a smooth mesial concavity) and P4 with two lingual grooves, the mesial one very shallow; the molars are proportionally wider, with large median lobe, slightly projected lingually in M1–2; a lingual groove is present in the third lobe of M3 (as in MMH-CH 85-04-125), which is barely discernible in M1–2. In an ontogenetic scale, MLP-PV 55-IV-28-14 would be slightly older than MMH-CH 85-04-125, but within the same wear stage 3 (Table 1). Dimensions of the latter are slightly smaller, but close (Appendix B).

Remarks: The described upper dentition can be initially compared with young individuals already published by Cerdeño and Schmidt (2013). Following a relative ontogenetic sequence, the youngest individual would be MCH-P 24, associated upper teeth of Mesotheriinae indet. (Fig. S1(A–C), Appendix C) from Villavil (Late Miocene, Chiquimil Fm., El Jarillal Mb., Catamarca Province), whose crowns are relatively short, and they may represent teeth that have just begun to erupt (stage 0; Table 1), as some show a certain wear degree. The following two stages would include the specimens MACN-Pv 9531 from Farola Monte Hermoso (*Pseudotypotherium exiguum*; Early Pliocene, Monte Hermoso Fm., Buenos Aires Province), MLP-PV 37-III-7-1+5 (holotype of ‘*P. carhuense*’ = *P. subinsigne*; Cabrera, 1939; Cerdeño and Montalvo, 2001) from Adolfo Alsina (‘Epecuén Fm.’ = Cerro Azul Fm., Buenos Aires

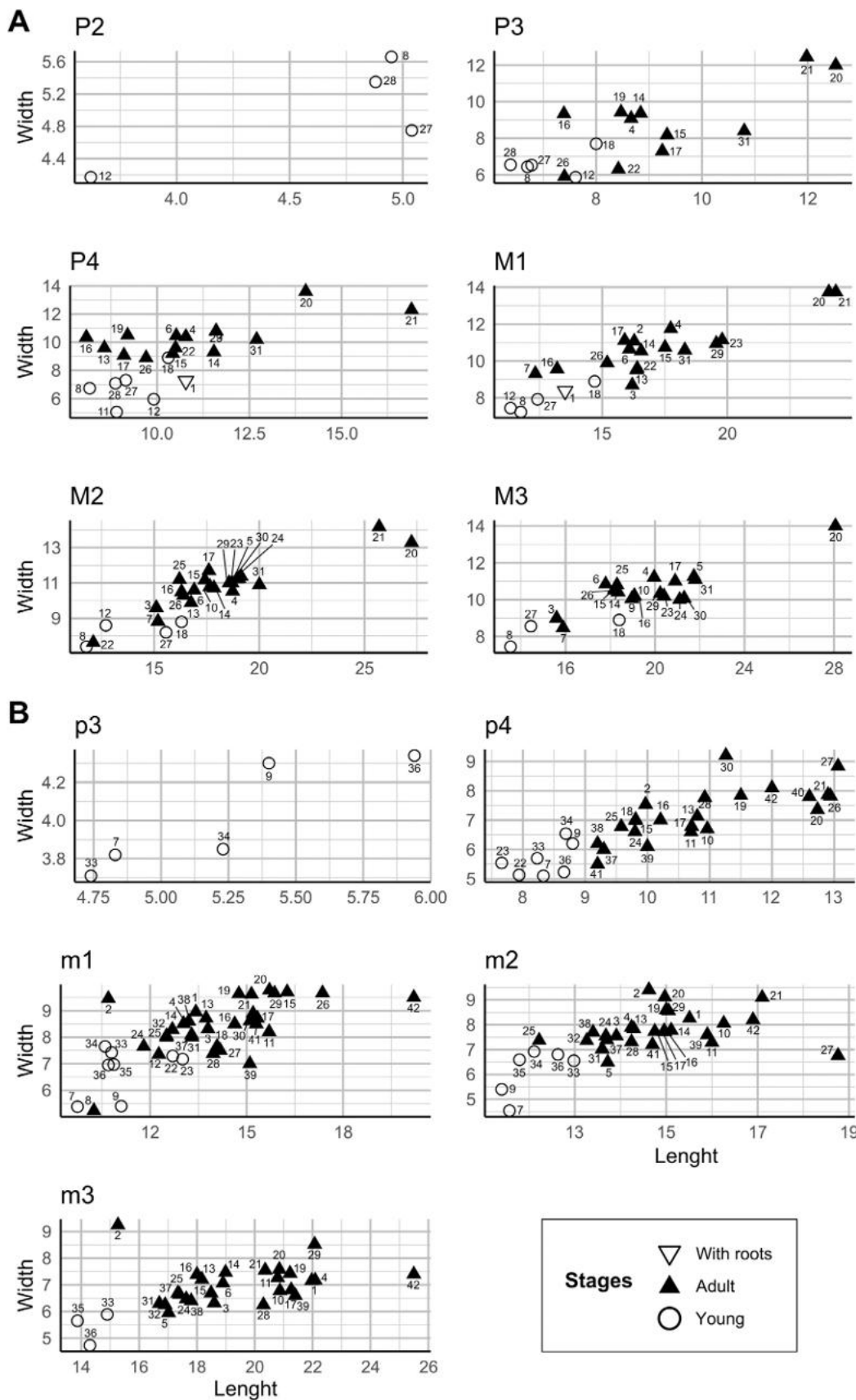


Fig. 2. Scatter plots of upper (A) and lower (B) cheek teeth (P2–M3/p3–m3) of *Typotheriopsis chascoensis* from Arroyo Chasicó locality, differentiating young and adult individuals, and the rooted specimen, as well as the holotype of *T. chascoensis* (numbers 31 and 42 for upper and lower teeth, respectively). Numbers correspond to specimens detailed in [Appendix B](#).

Table 1

Studied and compared specimens of young individuals (upper dentition) of Mesotheriinae and description of recognized ontogenetic stages. Abbreviations: *E.*, *Eutypotherium*; *P.*, *Pseudotypotherium*; *R.*, *Rusconitherium*; *T.*, *Tyotheriopsis*. The slash (/) separates the preserved teeth of each series of the specimen. * Third lobe of M3 with posterolingual groove. References and comments: ^a Cerdeño and Schmidt (2013); ^b Fernández-Monescillo (2022b); ^c Cerdeño and Montalvo (2001); ^d this work; ^e labelled as such; ^f mesotheriids from Salicas Fm. after Ruiz-Ramoni et al. (2023); ^g Sostillo et al. (2021); ^h Sostillo et al. (2025). Locality and horizon of each specimen are indicated in the text and/or Appendix A.

Specimens from Arroyo Chasicó	Specimens from other sites	Dental series	Taxon	Wear stage	Description
	MCH-P 24	Associated P–M	Mesotheriinae indet. ^a	0	Just erupted teeth (two with some wear degree); long and narrow occlusal face; relatively low crown with open base
	MACN-Pv 9531	P2–M2	<i>P. exiguum</i> ^b	1	Presence of P2; P3 bilobed; all teeth high and with open base; P2–4 and M relatively long and narrow in occlusal view; rather open lingual grooves in P and M; molars with median lobe lingually projected
	MLP-PV 37-III-7-1+5	P2–M2	' <i>P. carhuense</i> ' (= <i>P. subinsigne</i>) ^c	2	Presence of P2; P2–3 relatively shorter than in stage 1; rather open lingual grooves in P and M; molars with median lobe lingually projected
MMH-CH 86-09-87		I1, P2–M3*	<i>T. chasicoensis</i> ^d	2	
MMH-CH 86-09-76		P4?	<i>T. chasicoensis</i> ^d	2	
	MLP-PV 29-IV-15-3	(P2–3)–P4–M1/P2	' <i>P. studeri</i> ' ^e	2	
	MLP-PV 62-XII-4-11+12	P2–M1/M1–3	<i>Pseudotypotherium</i> sp. ^e	3	Triangular P2; P3 subtriangular with smooth lingual undulation or more rectangular with lingual groove; trilobed P4; more tightened molar lobes
MMH-CH 85-04-125		I1, P2–M3	<i>T. chasicoensis</i> ^d	3	
MLP-PV 55-IV-28-14		I1, P2–M3/ I1, P2–M1	<i>T. chasicoensis</i> ^d	3	
	GHUNLPam 814	P3–M3	<i>P. subinsigne</i> ^g	3	
	CRILAR-Pv 55	P4	<i>Tyotheriopsis</i> sp. ^e	3?	
	CRILAR-Pv 433	I1, P2–M3	<i>Tyotheriopsis</i> sp. ^e	4	P2–3 short and wide; tight, bifurcate lingual groove in P4
	GHUNLPam 21104	P2–4	<i>P. subinsigne</i> ^g	4	
MMP 538-M		I1, P3–M2/ I1, P3–M3	<i>T. chasicoensis</i> ^d	5	Without P2; subtriangular P3, with a wide concavity to undulate mesiolingual face; short or insinuated lingual groove in P4 in <i>Tyotheriopsis</i> , but persistent in <i>Pseudotypotherium</i> ; distolingual corner of P4 at a right angle. [See text about GHUNLPam 6753]
	GHUNLPam 6753	P3–M2	<i>T. chasicoensis</i> ^g	?	
	GHUNLPam 9154	I1, P3–M3/ I1, M1–3 (P2?)	<i>T. silveyrai</i> ^g	5	
	GHUNLPam 21137	P3–M2	<i>P. subinsigne</i> ^g	5	
	GHUNLPam 18551	P3–M1/P3–M3	<i>P. subinsigne</i> ^g	5	
	GHUNLPam 12826	P3–M3/P3–M3	<i>P. subinsigne</i> ^g	5	
	GHUNLPam 18756	I1, P3–M3/ I1, P4–M3	<i>P. subinsigne</i> ^g	5	
MD-CH-07-04		Rooted P4–M1–3	<i>T. chasicoensis</i> ^d	3/4	By comparison of accompanying molars
	GHUNLPam 14011	Rooted? P2–3	Mesotheriinae indet. ^h	4?	

Province), and MLP-PV 62-XII-4-11+12 (labelled *Pseudotypotherium* sp.) from Laguna Chillhué (Cerro Azul Fm., La Pampa Province) evaluated by Cerdeño and Schmidt (2013).

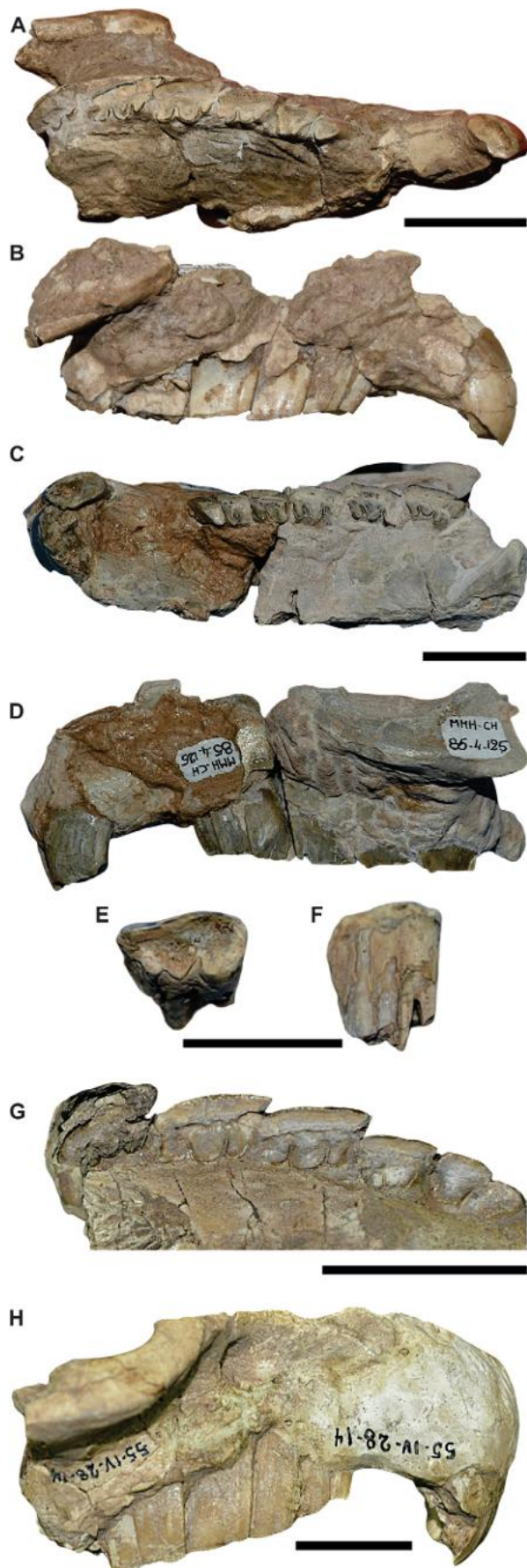
MACN-Pv 9531 (Fig. S1(D, E), Appendix C) is here assigned to stage 1 (Table 1); it shows the entire height of the crowns, evidencing the lack of roots and the open bases in all teeth (P2–M2), as well as the progressive change in the development of the lingual groove along the crown (Cerdeño and Schmidt, 2013); on the occlusal surface, P2 and P3 are elongate, the latter with undulate ectoloph and separated lingual lobes.

MLP 37-III-7-1+5 (Fig. S1(F, G), Appendix C) is similar to MACN-Pv 9531 but more worn, with P2–3 less elongate, but P3 without lingual groove, and is here considered as stage 2 (Table 1). Considering P4–M2, this specimen is similar to the described MMH-CH 86-09-87 and MMH-CH 86-09-76 from Arroyo Chasicó, although MMH-CH 86-09-87 presents a lingual groove in P3. Also comparable to the latter is MLP-PV 29-IV-15-3 (remains of P2–3 and P4–M1; Fig. S1(H, I), Appendix C) from the 'Araucanian' (Late Miocene) of Catamarca Province (labelled "*P. studeri*? 'Araucaniano', Monte Hermoso? Methfessel? collection" but confirmed as coming from Catamarca by the curator of MLP, M. Reguero, to EC, October 27, 2011). In this case, the third lobe of P4 presents a smooth lingual concavity, less evident in M1; this P4 is similar to that of MLP 37-III-7-1+5.

The stage 3 (Table 1) includes MLP-PV 62-XII-4-11+12 (Fig. S1(J, K), Appendix C), in which the lobes of P4 and molars are more tightened, although the median lobe still projects lingually in

molars. We also include in this stage the described MMH-CH 85-04-125, in which, however, the P3 still maintains a distinct lingual groove (Fig. 3(C)). A similar lingual projection in molars is also observed in GHUNLPam 814 from Loventué (Cerro Azul Fm.; La Pampa Province; Fig. S1(L), Appendix C), in which the P4 (occlusally broken) reveals a lingual groove bifurcated at the end, creating a small triangular median lobe enclosed by the adjacent lobes. This difference from the P4 in MLP-PV 62-XII-4-11+12 could be due to the level of breakage in GHUNLPam 814, which is well below the occlusal level of the molars.

In the stage 4, we include specimens with P2, but with P3–4 and the molars displaying different features from those described above (Table 1). This is the case of the cranial fragment CRILAR-Pv 433 (Fig. S1(M), Appendix C) of *Tyotheriopsis* sp. from El Degolladito (Salicas Fm., La Rioja Province; Ruiz-Ramoni et al., 2023), which was the trigger for the previous review by Cerdeño and Schmidt (2013). In this specimen, the P2 is short and wide (resembling that of MMH-CH 85-04-125), the P3 does not have lingual groove, the P4 has a lingual groove bifurcated at its end (as in GHUNLPam 814); however, the molars do not have projecting median lobe or wide grooves (contrary to the youngest specimens), and no molar shows a distolingual groove in the third lobe. This specimen did not show roots after X-ray images. Similarly, GHUNLPam 21104 from Algarrobo del Águila (Cerro Azul Fm.; La Pampa Province; Fig. S1(N), Appendix C) preserves incomplete P2–4 that allow observing a similar bifurcated groove in P4. These teeth were initially considered as deciduous (Cerdeño and Montalvo, 2001),



but later interpreted as permanent (Cerdeño and Schmidt, 2013; Sostillo et al., 2021).

Other specimens likely represent an older wear stage 5 (Table 1) within the sample of young individuals, closer to the adult individuals (young adults), as they do not present P2, which would have been expelled and the corresponding alveolus reabsorbed. For instance, MMP 538-M (Fig. S2(A, B), Appendix C) from Arroyo Chasicó still shows a short groove in P4 and the median lobe of M1 (incomplete on M2) is slightly projected lingually. It is assumed that the short groove of the premolars would eventually disappear with increased wear in *Typotheriopsis* (vs. *Pseudotypotherium*). GHUNLPam 21137 (Fig. S2(C), Appendix C) from Caleufú (Early Pliocene, Cerro Azul Fm., La Pampa Province), assigned to *P. subinsigne* (Sostillo et al., 2021), shows the P3 with a smooth lingual concavity and an acute, short groove on its mesial face, and a well-marked paracone fold; P4 with a short, well-marked, mesially oriented lingual groove; and M2 with a slightly projected median lobe. Similar morphologies are observed in other specimens of *P. subinsigne* from the Late Miocene Cerro Azul Fm. in La Pampa Province: GHUNLPam 18551 (P3–4 and incomplete molars) from Salinas Grandes de Hidalgo (Fig. S2(D), Appendix C); GHUNLPam 12826 from Don Mariano, with P3–M3 (Fig. S2(E), Appendix C); and GHUNLPam 18756 (Fig. S2(F), Appendix C) from Jacinto Araoz, the latter with a relatively large size (Appendix B). In turn, GHUNLPam 9154 (Appendix B; Fig. S2(G, H), Appendix C) from Quehué (La Pampa Province), assigned to *Typotheriopsis silveyrai* (Sostillo et al., 2021), has short and wide P3 and subtrapezoidal P4, both premolars without lingual groove and with undulate mesial wall, and M1 with median lobe slightly projected. Also from La Pampa, GHUNLPam 6753 (Fig. S2(I), Appendix C) from Cerro La Bota, assigned to *T. chasicensis* (Montalvo et al., 2019), shows a similar tooth morphology (P3–M2) to that of GHUNLPam 9154. However, in this case, the specimen is notably small and the maxilla presents trabecular bone, which differs from the previous specimens established as wear stage 5, including MMP 538-M that belongs to the same taxon (*T. chasicensis*) and the same age (Chasicóan Stage/Age). This could represent a particular case that complicates even more the observed variation among young individuals, as it shows dental features of a young adult, but a size and bone features of a much younger individual.

The adults of *Typotheriopsis* lose the lingual groove of premolars, as supported by specimens such as MMP 475-M, MMP 495-M, MD-CH-06-142, and MMH-CH-83-03-127 from Arroyo Chasicó (Appendix B; Fig. S3(A–E), Appendix C), and GHUNLPam 9954 from Algarrobo del Águila (Sostillo et al., 2021: fig. 5a). In contrast, adults of *Pseudotypotherium* maintain a single lingual groove in P4 as in MMP 323-M of *P. exiguum* from Farola Monte Hermoso (Fernández-Monescillo et al., 2022b; Fig. S3(F), Appendix C).

The described wear variation among young individuals correlates with the changes observed throughout the tooth crowns in the specimen MACN-Pv 9531 of *P. exiguum* from Farola Monte Hermoso (Cerdeño and Schmidt, 2013). Another specimen that clearly shows this marked change is the isolated P4 CRILAR-Pv 55 (Fig. S3 (G, H), Appendix C) from El Degolladito (Salicas Fm., La Rioja Province; *Typotheriopsis* sp.), in which the three well-developed lobes on the occlusal surface transform into a subtriangular tooth with-

Fig. 3. Upper dentition of young specimens of *Typotheriopsis chasicensis* from Arroyo Chasicó locality. A, B. MMH-CH 86-09-87, right cranial fragment with I1 and P2–M3, in ventral and lateral views. C, D. MMH-CH 85-04-125, left cranial fragment with I1 and P2–M3, in ventral and lateral views. E, F. MMH-CH 86-09-76, left P47, in occlusal and lingual views. G, H. MLP-PV 55-IV-28-14, right cranial fragment with I1 and P2–M3, in ventral and lateral views. Scale bars: 20 mm (A–D, G, H), 10 mm (E, F).

out grooves at the opposite side, with a tiny, ephemeral fossette. The occlusal morphology of this tooth is similar to that of MMH-CH 85-04-125 and would also represent the wear stage 3 (Table 1).

3.1.2. Lower dentition

Description: The revised lower dentition includes four young individuals bearing the ‘extra’ premolar (p3), represented by the mandibular fragments MMH-CH 83-03-114, MMH-CH 83-03-117, MD-CH-05-194, and MMH-CH s/n, a quite complete mandible without a collection number. To these specimens, we add MD-CH-05-39, which has two anterior alveoli and m1–3 of comparable size to the molars of the other specimens (Appendix B), and MMH-CH-85-4-124, based on its small size, although p3 is lacking (see below).

In MMH-CH 83-03-114 (Fig. 4(A, B)), the p3 is subtriangular, buccally undulated with a marked angle, and with a distolingual fold (opposite to the buccal angle) that fades basally along the crown; the enamel is lacking on the lingual face. This premolar is clearly shorter than the p4. The latter has a deep, open-V-shaped buccal groove and a smoother lingual groove at the same level; the trigonid is short, but does not narrow mesially, at least on the occlusal surface; the talonid is wider than the trigonid, almost as wide as that of m1, but shorter (Appendix B). The lingual enamel in p4–m3 is thin and covered with cement. CT-scan images of MMH-CH 83-03-114 do not reveal premolar roots or tooth germs.

In MMH-CH 83-03-117 (Fig. 4(C–E)), the preserved portion of the p3 is the basal, subtriangular part of the tooth that shows a fine line of enamel at the breakage level on the buccal side, covered with cement, which evidences that it is part of a high crown that narrows basally. It has a more regular triangular section than that in MMH-CH 83-03-114, which can be expected because the observed section is at a rather basal position of a tooth that is supposed to be expelled before reaching the adult stage (Cerdeño and Schmidt, 2013). The p4 shows enamel extended well beyond the p3 breakage level (Fig. 4(E)), which evidences a euhipodont crown. Both mentioned specimens are considered here as wear stage 1 (Table 2).

MD-CH-05-194 (Fig. 4(F)) is very fragmented, but several teeth are well preserved, including the incisors. The p3 is subtriangular, longer than wide, with an acute, short buccal groove and a smooth lingual concavity; the tooth can be observed mesially to its basal end, and there is no evidence of roots. The p4 shows a short, buccally angled trigonid and a wide talonid. The premolars are somewhat greater than those of the previously described specimens (Appendix B), which likely indicates a slightly more advanced ontogenetic stage (wear stage 2; Table 2).

The mandible MMH-CH s/n is relatively complete (Fig. 4(G)), with both dental series (i1–2, p3–m3). X-ray and CT-scan images of this specimen do not reveal premolar roots or tooth germs. It is slightly larger than MMH-CH 83-03-114 and 117, with relatively wider teeth. Teeth of MMH-CH s/n are more similar to those of

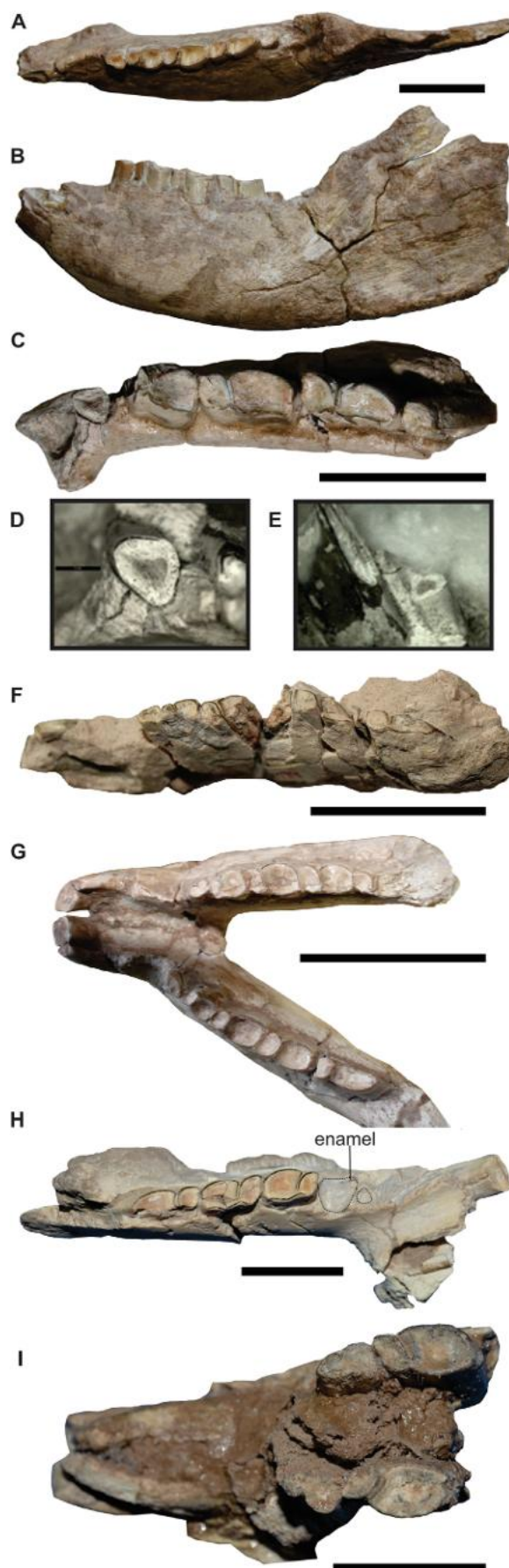


Fig. 4. Lower dentition of young specimens of *Typotheriopsis chasicocoensis* from Arroyo Chasicó locality. **A, B.** MMH-CH 83-03-114, left mandible with remains of i2 and p3–m3, in occlusal and lateral views. **C.** MMH-CH 83-03-117, right mandibular fragment with broken p3, p4–m2 and fragment of m3. **D, E.** Detail of the p3 (D) and p3–4 (E) of MMH-CH 83-03-117, showing the enamel of p3 at the breakage level, in occlusal view, and the buccal height of the crown of p4. **F.** MD-CH-05-194, right mandibular fragment with i1–2 and p3–m3 (m1–2 incomplete), in occlusal view. **G.** MMH-CH s/n, incomplete mandible with right and left i1–2 and p3–m3, in occlusal view. **H.** MD-CH-05-39, mandibular fragment with part of the symphysis and left i1, alveoli of i2, p3–4, and m1–3, in occlusal view. **I.** MMH-CH-85-04-124, mandibular fragment with both series i1–2 and p4–m1, occlusal view. Scale bars: 20 mm.

Table 2

Studied and compared specimens of young individuals (lower dentition) of Mesotheriinae and description of recognized ontogenetic stages. Abbreviations: *P.*, *Pseudotytheriopsis*; *T.*, *Tyotheriopsis*. The slash (/) separates the preserved teeth of each series of the specimen, except for the case dp4/p4 in which it indicates the presence of both teeth. References: ^a Rovereto (1914), Kraglievich (1934); ^b this work; ^c Sostillo et al. (2021); ^d Cabrera (1939), Cerdeño and Montalvo (2001); ^e Ruiz-Ramoni et al. (2023); ^f Romano et al. (2023). Locality and horizon of each specimen are indicated in the text and/or Appendix A.

Specimens from Arroyo Chasicó	Specimens from other sites	Dental series	Taxon	Wear stage	Description
	MACN-Pv 8480	i1–2, dp?3–dp4/p4–m1–3	<i>P. carlesi</i> ^a	0	Presence of dp3 (or p3), dp4 and germ of p4
	GHUNLPam 2304	i1–2, dp?3–dp4/p4	Mesotheriinae indet. ^b	0	altogether, and worn m1–3
MMH-CH 83-03-114		i1–2, p3–m3	<i>T. chasicoensis</i> ^b	1	Presence of p3, subtriangular, buccally undulated
MMH-CH 83-03-117		p3–m2 and trigonid of m3	<i>T. chasicoensis</i> ^b	1	with a marked angle; p4 with deep, open buccal groove. Narrower molars than in stage 2
	GHUNLPam 8234	p3–4	Mesotheriinae indet. ^b	1	
	MLP-PV 37-III-7-1	p3–m1	<i>P. carhuense</i> ^d	1	
	CRILAR-Pv 422	P4	<i>Tyotheriopsis</i> sp. ^e	1?	
MMH-CH s/n		i1–2, p3–m3/ i1–2, p3–m3	<i>T. chasicoensis</i> ^b	2	Presence of p3, subtriangular, with acute buccal
MD-CH-05-194		i1–2, p3–m3	<i>T. chasicoensis</i> ^b	2	groove. Molars wider than in stage 1, with
MD-CH-05-39		Alveoli of p3–4, and m1–3	<i>T. chasicoensis</i> ^b	2	tightened grooves
	GHUNLPam 152	p3–m3	<i>P. subinsigne</i> ^c	2	
	GHUNLPam 14335	p3–4	Mesotheriinae indet. ^c	2?	
	MACN-Pv 8481	p3–m1	<i>P. carlesi</i> ^a	2	
	IANIGLA-PV 545	i1–2, p3–m2	<i>P. subinsigne</i> ^f	2	
MMH-CH-85-04-124		i1–2, p4–m1/ i1–2, p4–m1	<i>T. chasicoensis</i> ^b	3	Without p3; small size.
	GHUNLPam 18756	p4–m3/p4–m3	<i>P. subinsigne</i> ^c	3	Without p3 (associated with skull stage 5 of upper teeth)
	MCH-P 198	Alveolus of p3 without tooth remains, p4–m3	<i>Tyotheriopsis</i> sp.	3?	Alveolus present but without p3 (see text)
	GHUNLPam 9522	Alveolus of p3–rooted p4	Mesotheriinae indet. ^b	?	Deep alveolus for p3; shallow buccal groove in p4

MD-CH-05-194 (Appendix B) and are thus considered to be at a comparable ontogenetic stage (Table 2). The morphology of the p3 is discussed in the following section.

In MD-CH-05-39 (Fig. 4(H)), there are two alveoli anterior to m1, with sediment partially hiding their outline and covering some remains of premolars. The alveolus for the p4 is longer buccally than lingually, and the end of the symphysis reaches its level, as in MMH-CH s/n. Inside this alveolus, remains of the p4 show some dentine and a thin line of buccal enamel, showing that this part of the tooth is not a root. The alveolus for p3 is smaller and roughly subtriangular. This specimen is also considered at wear stage 2 (Table 2).

MMH-CH-85-04-124 (Fig. 4(I)) is distorted and very incomplete, but preserves right and left i1–2 (both i2 are displaced lingually relative to the respective i1) and p4–m1. Its preservation makes it difficult to accurately discard the existence of p3; the p4 is more triangular than in the previous specimens, mesially pointed, with marked, short buccal groove. The m1 is slightly larger than in MMH-CH s/n, but the p4 is shorter (Appendix B). The morphology and size of p4 point to a relatively older individual that may have lost (or close to losing) the p3; therefore, this specimen is considered to belong to stage 3 (Table 2).

The homogeneity of the lower dentition makes it more difficult to establish an ontogenetic sequence compared to the upper dentition. As stated above and based on size, we consider MMH-CH 83-03-114 and MMH-CH 83-03-117 to be the youngest individuals (stage 1) of this sample from Arroyo Chasicó, followed by MD-CH-05-194, MMH-CH s/n, and MD-CH-05-39 (stage 2), and finally MMH-CH 85-04-124 as stage 3 (Table 2). However, differences in size are not so evident, except for the narrower molars of the first two specimens (Fig. 2(B); Appendix B).

Remarks: The comparison of the described lower dentition shows that the p3 of young individuals presents two main

morphologies. In MMH-CH 83-03-114 (Fig. 4(A, B)), the buccal wall is smoothly concave, in contrast to the short, marked buccal groove and the acute fold that appear in the p3 of GHUNLPam 152 (Fig. S4(A), Appendix C) from Loventué (La Pampa Province), GHUNLPam 8234 (Fig. S4(B, C), Appendix C) from Telén (La Pampa Province; Mesotheriidae indet.), MLP-PV 37-III-7-1 (Fig. S4(D), Appendix C) from Adolfo Alsina (Buenos Aires Province; Cerdeño and Montalvo, 2001; *P. carhuense* = *P. subinsigne*), MACN-Pv 8481 (Fig. S4(E), Appendix C), labelled *P. carlesi* (= *P. subinsigne*; Kraglievich, 1934), from the Huayquerías de San Carlos (Mendoza Province; from levels now considered lower Tunuyán Fm., Early Pliocene; Romano et al., 2023), and IANIGLA-PV 545 (Fig. S4(F, G), Appendix C) from the Early Pliocene Tunuyán Fm. in Huayquerías del Este (Mendoza Province; *P. subinsigne*; Romano et al., 2023). The acute groove is also present but less conspicuous in the described MMH-CH s/n (Fig. 4(G)), in which both p3 are slightly different to each other, and the trigonid is relatively large in the right p3 compared with the mentioned specimens. As noted in the previous section, this mandible is considered to be at an older wear stage (2) than MMH-CH 83-03-114 (stage 1; Table 2). The younger condition of MMH-CH 83-03-114 discards that the mentioned difference in the p3 outline is due to a higher degree of wear in MMH-CH 83-03-114. A taxonomic implication is also possible, as the material from Arroyo Chasicó belongs to *Tyotheriopsis chasicoensis*, while GHUNLPam 152, MACN-Pv 8481, and IANIGLA-PV 545 are assigned to *P. subinsigne*. However, MMH-CH 83-03-114 and MMH-CH s/n likely represent individual variation within the Arroyo Chasicó sample. Based on the p4 and molars, the compared specimens GHUNLPam 8234 (with trabecular bone) and MLP-PV 37-III-7-1 are more similar to the former and are included in wear stage 1 (Table 2), while GHUNLPam 152, MACN-Pv 8481, and IANIGLA-PV 545 are closer to MMH-CH s/n

and are, thus, considered as wear stage 2 (Table 2). Minor differences among them are insufficient to differentiate other stages.

In addition, the mandible of *Tyotheriopsis* sp. MCH-P 198 (Fig. S4(H), Appendix C), from the Late Miocene–Early Pliocene Andalhuala Fm. (Quebrada de Juijuil, Catamarca Province; Armella, 2019), preserves the alveoli of ‘extra’ premolars. Nevertheless, after cleaning these areas, no evidence of a tooth appeared, suggesting that these teeth were lost shortly before the death of the individual. The p4 presents a deep buccal groove that, along with a relatively smooth lingual groove, defines a rounded talonid and a subrectangular trigonid. This specimen is tentatively assigned to the wear stage 3 (Table 2).

The described lower dentitions do not allow observing directly how the crown varies. However, this aspect can be analyzed in CRILAR-Pv 422 (Cerdeño and Schmidt, 2013), a p4 that shows a long occlusal outline, with relatively long and subrectangular talonid; on the opposite side (Fig. S4(I–K), Appendix C), instead, the talonid is proportionally shorter, wider, and more rounded, and the buccal groove is deeper, features that are typical of adult individuals (e.g., MMH-CH 86-09-51 from Arroyo Chasicó; Fig. S4(L), Appendix C). This opposite morphology of CRILAR-Pv 422 is more similar to that of the p4 in the previous specimens assigned to the wear stage 2, which implies that the occlusal outline of CRILAR-Pv 422 corresponds to a younger individual and it is tentatively considered as stage 1 (Table 2). In the mandible GHUNLPam 18756 (associated to the skull fragment; see Section 3.1.1) of *P. subinsigne*, which lacks p3, the p4 has a rather narrow and short talonid (Fig. S4(M), Appendix C).

All mentioned specimens come from Late Miocene–Early Pliocene levels, but the presence of p3 is also observed in older mesotheriines, such as the specimen MLP-PV 12-2323, labelled *Eutyotherium lehmannitschei*, from the Middle Miocene of Laguna Blanca (Chubut Province) (EC, personal data; Kraglievich, 1930; Appendix B; Fig. S4(N), Appendix C) and *Rusconitherium mendocense* (MCNAM-PV 4005) from the Early Miocene of Divisadero Largo and Potrerillos localities (Mendoza Province; Cerdeño et al., 2018; Appendix B). In the latter, the p3 is simple, subcylindrical, while in MLP 12-2323, the p3 is more developed, with short and narrow trigonid, well differentiated by lingual and buccal grooves from the wider talonid. Cabrera (1937) mentioned that he had opened the bone of this mandible and checked that all teeth presented their base open to the bottom of their respective alveoli, which supported for the author the adult condition of the individual vs. the juvenile with deciduous premolars.

3.2. Mesotheriinae with rooted premolars

The existence of roots in the mesotheriine dentition has been barely mentioned (Patterson, 1952), insufficiently studied, or even unintentionally ignored (Francis, 1960, 1965). Nevertheless, the specimen MD-CH-07-04 from Arroyo Chasicó bears a rooted premolar, whose interpretation (P4 or DP4?) is the crux of the matter. Starting with this specimen, we also include here a few other cases of mesotheriines proved or suspected to bear rooted premolars in order to present a more complete panorama on this character.

3.2.1. Arroyo Chasicó

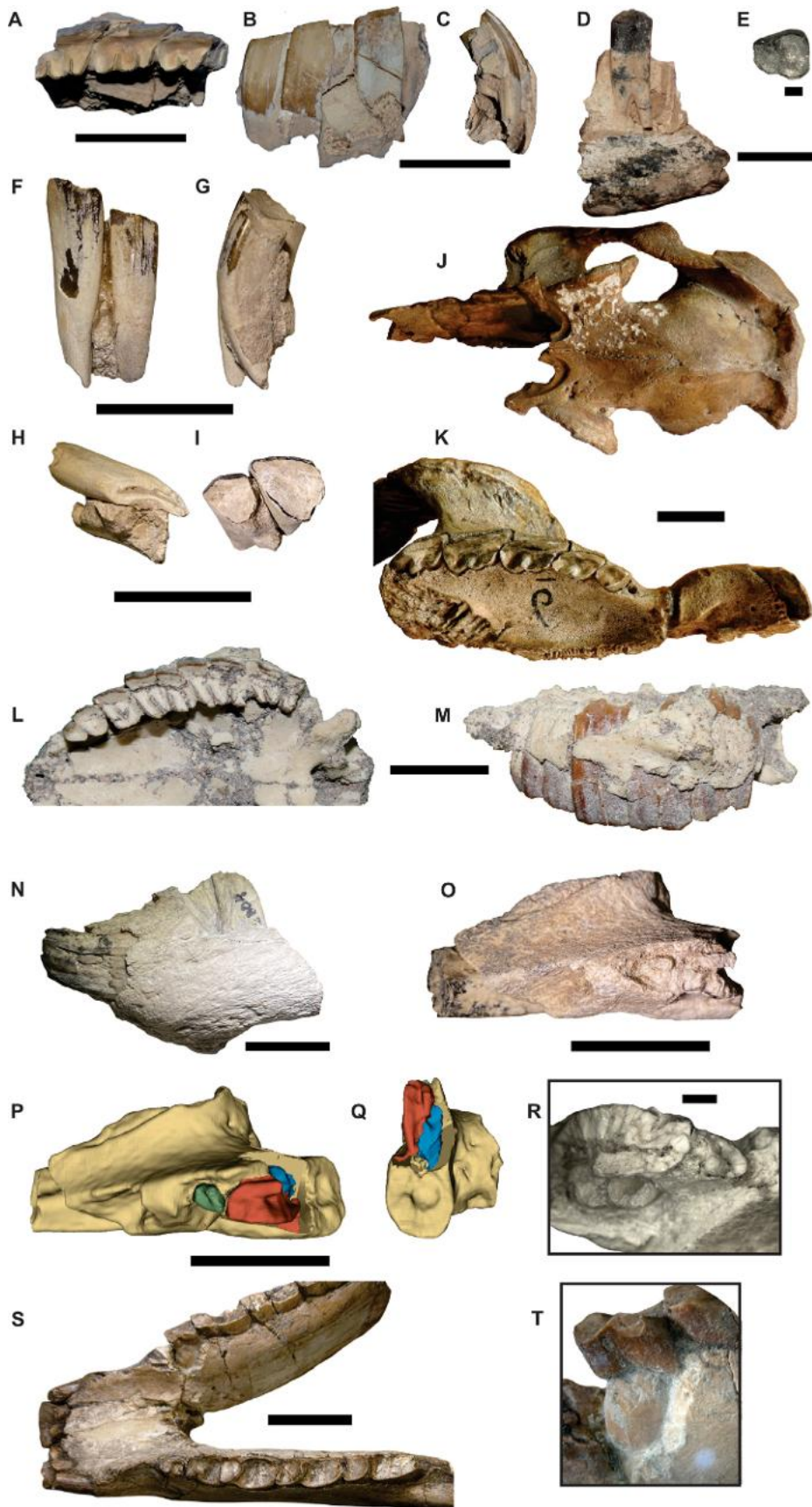
MD-CH-07-04 (Fig. 5(A–C)) is a right maxillary fragment with three teeth. The two posterior teeth are easily identified as M1 and M2 (the latter distobuccally incomplete), due to their trilobed occlusal morphology, with a large median lobe with parallel sides; euhypsodont, longer than wide teeth (Appendix B), with the parastyle overlapping the distobuccal corner of the anterior tooth; both molars have a smooth paracone fold, better marked in M2 due to

the slightly more evident concavity that follows this fold. In contrast to these molars, the anterior preserved tooth shows well-developed roots, observable due to the breakage of the maxillary bone (Fig. 5(C)). This premolar is shorter than the molars and shows a bifurcated lingual groove that delimits a small, triangular median lobe. The small size of MD-CH-07-04, the presence of a small median lobe in the premolar, and some trabecular bone observable in the maxilla points to a young individual, although based on the molar morphology it would not be as young as some specimens described in Section 3.1. The a priori ‘logical’ interpretation of the rooted premolar as deciduous becomes inconsistent when comparing this specimen with the young individuals described in Section 3.1, with premolars (including ‘extra’ P2) and accompanying molars (Cerdeño and Schmidt, 2013). The size of MD-CH-07-04 is intermediate between that of the youngest individuals (e.g., MMH-CH 85-04-125, MMH-CH 86-09-76, MMH-CH 86-09-87) and that of the adults (e.g., MMH-CH 83-03-116, MMH-CH 83-03-127, MD-CH-06-142, MCNAM-PV 3211, among others) from Arroyo Chasicó (Fig. 2(A)).

Within the large sample from Arroyo Chasicó, including previously published specimens and the presently revised collections, only one specimen, MD-CH-07-04, can be accurately considered as bearing a rooted tooth. The median lobe of the rooted P4 is similar to that observed in the P4 of different Late Miocene specimens considered as young individuals, but not evidenced as rooted teeth (Section 3.1). A similar but more developed median lobe is present in the described MMH-CH-85-4-125 from the same locality, while a more similar development is observed in *Tyotheriopsis* sp. CRILAR-Pv 433 (Fig. S1(M), Appendix C) from the Salicas Fm. (Cerdeño and Schmidt, 2013; Ruiz-Ramoni et al., 2023), without evidence of roots, and the specimens assigned to *Pseudotyotherium subinsigne* from La Pampa Province (Cerdeño and Schmidt, 2013; Sostillo et al., 2021) such as GHUNLPam 814 (Loventué; Fig. S1(L), Appendix C) and GHUNLPam 21104 (Fig. S1(N), Appendix C). A few studied specimens of *P. exiguum* from Farola Monte Hermoso stored in MMH do not show this kind of P4, but it appears in two specimens (MLP-PV 48-XII-16-220 and MLP-PV 12-1680) from this locality figured by Fernández-Monescillo et al. (2022b).

3.2.2. Telén, central-western La Pampa Province (Cerro Azul Fm., Late Miocene)

The accidental removal of a fractured portion of mandibular bone in GHUNLPam 9522 from Telén has revealed that the preserved premolar (p4 in Cerdeño and Montalvo, 2001, Mesotheriinae indet.) has two well-developed roots (Fig. 5(D)) well deep into the alveolus (20.5 mm from the occlusal border to the root bifurcation). No other tooth is preserved, but the bone reveals an anterior deep alveolus corresponding to an ‘extra’ premolar (Fig. 5(D)). The rooted p4 shows a short, slightly buccomesially-oriented trigonid and a wider talonid with convex buccal and lingual walls. The buccal groove is shallow, ending far from the lingual side (Fig. 5(E)). In this feature, this p4 differs from other compared young individuals with a deeper groove, such as GHUNLPam 8234 (euhypsodont and with trabecular bone; Fig. S4(B, C), Appendix C), also from Telén, and MMH-CH 83-03-117 from Arroyo Chasicó (see Section 3.1.2), both with p3. Neither the occlusal morphology of p4 nor the mandibular bone in GHUNLPam 9522 indicates a very young individual, but the presence of p3 points to a young condition. The p4 GHUNLPam 9522 is barely wider than those of young individuals from La Pampa Province (see Section 3.1.2), including GHUNLPam 8234 (Telén), GHUNLPam 152 (Loventué), and GHUNLPam 14335 (Salinas Grandes de Hidalgo; Fig. S4(O, P), Appendix C), but all of them are slightly larger than those from Arroyo Chasicó with p3 (Appendix B).



3.2.3. Salinas Grandes de Hidalgo, central-eastern La Pampa Province (Cerro Azul Fm., Late Miocene)

GHUNLPam 14011 preserves left P2–3 (considered as DP2–3 of Mesotheriinae indet. in Sostillo et al., 2021, 2025) with a small fragment of bone in between, which are characterized by the narrowing of the crowns to their base, well observable in both teeth (Fig. 5(F–I)). The P2 is more curved vertically than the P3 (Fig. 5(G)). Both have a layer of cement covering the enamel (Fig. 5(F, G)); the latter is observed buccally to a high level, and it is not easy to ascertain whether the last and narrower part correspond to a root (Fig. 5(G, H)). In occlusal view (Fig. 5(I)), the P2 has a smooth paracone fold rather centrally placed on the ectoloph; the tooth is barely shorter than wide and lingually rounded; the P3 is more subtriangular, with better developed parastyle, and the mesial face smoothly undulating. Enamel lacks in most part of the mesial face of P2 and in a smaller section in P3. This occlusal morphology is similar to that of P2–3 in MLP 55-IV-28-14 from Arroyo Chasicó (see Cerdeño and Schmidt, 2013, and Section 3.1), which are slightly smaller (Appendix B). The occlusal outline in GHUNLPam 14011 is also similar to that of P3–4 in MMP 495-M from Arroyo Chasicó, a specimen that let see the open base of both premolars and the molars with adult morphology (Fig. S3(B, C), Appendix C), and whose size is slightly smaller than that of GHUNLPam 14011 (Appendix B). The rooted condition in GHUNLPam 14011 is thus not as certain as in the previous cases.

3.2.4. Barranca Camet, near Mar del Plata, southeastern Buenos Aires Province (Ensenada Fm., Early–Middle Pleistocene)

Patterson (1952) described the juvenile skull MMP 6-S (Fig. 5(J, K)) of *Mesotherium cristatum*, explaining that the P3 could be extracted from the maxilla and showed two roots. However, the tooth is presently well attached and roots cannot be seen with the naked eye; unfortunately, we have not been able to obtain X-ray or CT images so far. The small alveolus anterior to this tooth could correspond to a reduced missing P2. The skull is clearly juvenile based on the trabecular bone and visible sutures and the teeth also show features of a young individual: lingual groove of P4 (present in adults) bifurcated at its end, delimiting a tiny median lobe, molars proportionally long, and M3 with small median lobe.

3.2.5. Vega Chacras, Antofagasta de la Sierra, Catamarca Province (Potrero Grande Fm., Early Miocene)

During the development of this work, a specimen with three rooted premolars (MHAS 161; Fig. 5(L, M)) was found in Early Miocene levels of Catamarca Province (Armella et al., 2023, 2025). Despite some similarities with Late Miocene young individuals, MHAS 161 is interpreted as an adult of a new taxon, *Ichhutharium wayra* Armella et al., 2025, that represents the earliest diverging Mesotheriinae and combines ancestral and derived dental and palatal features.

3.3. Mesotheriinae with milk dentition

Francis (1960) stated that milk molars of mesotheriines have open roots (though it would be their base, not true roots) and continue their growth long after the eruption and use of the three per-

manent molars; this author indicated that several specimens (upper and lower dentition without details) showed the germ of the true premolar at the bottom of the alveolus, but he did not specify which these specimens were. A few years later, Francis (1965) confirmed his previous statements about the mesotheriines and the proposed synonymies (not under discussion here), and referred to the studied material as that stored in the museums of La Plata, Buenos Aires, and Mar del Plata until the end of 1960, but he did not provide illustrations. According to Cerdeño and Schmidt's (2013) interpretation, the classically assumed deciduous teeth within mesotheriines would be permanent teeth. Despite this, the revised material now reveals two cases in which a permanent premolar is present together with the erupted one, and thus the latter can consequently be assumed as deciduous.

GHUNLPam 2304 (Fig. 5(N–R)) from Laguna Chillhué (Cerro Azul Fm.; La Pampa Province) is a mandibular fragment showing trabecular bone and bearing i1, alveolus of i2, and two broken premolars (previously interpreted as deciduous – dp3–4 – by Cerdeño and Montalvo, 2001, and considered as Mesotheriinae indet.; not revised by Sostillo et al., 2021). Some bone on the buccal side was removed (Fig. 5(N)), and the enamel can be seen on the buccal face of the trigonid more basally than what seemed to be a bifurcation of roots in the second tooth, which led us to discard its rooted condition. Nevertheless, the CT images of this specimen (Fig. 5(P, Q)) revealed a potential tooth located basally and lingually to this second tooth (assumed as dp4). For better verification, we removed a fragment of lingual bone, and the tooth (p4) appeared at sight (Fig. 5(R)). It is worth highlighting that this p4 is displaced lingually from the base of dp4, the latter not showing roots. Similarly, the first premolar (dp3?) narrows basally, but there is not a clear differentiation of a root, either at naked eye or in the CT image, where no germ is suggested.

The second case is the holotype of '*Pseudotytherium carlesi*', MACN-Pv 8480, from the Huayquerías de San Carlos area in Mendoza Province (Rovereto, 1914). It is a mandible with complete right and left dental series, with 'extra' premolars. This specimen was interpreted as a juvenile (with deciduous dentition) of *P. subinsigne* by Kraglievich (1934), but neither he nor subsequent authors described any tooth germ. When we requested a photograph of the specimen in the MACN collection, we realized the partially removed lingual bone between the two right premolars, discovering a tooth basally and lingually placed to the second (a priori p4, but now dp4) (Fig. 5(S, T)). It would be worth checking if this condition also exists on the left side, as the bone does not present any particular thickening to suggest its presence. Neither tomography nor X-ray images are available at this moment for the '*P. carlesi*' specimens. The dental measurements of MACN-Pv 8480 (after Rovereto, 1914) reveal similar dimensions to the other specimen assigned to '*P. carlesi*', MACN-Pv 8481, and to other young individuals, with the p4 slightly wider (Appendix B); with respect to GHUNLPam 2304, the comparable dimensions are slightly larger in MACN-Pv 8480.

The comparison of both specimens with a germ shows that the outline of the first premolar (dp3?) in GHUNLPam 2304 is subtriangular, without a marked buccal angle, while in '*P. carlesi*', both the buccal and lingual walls are convex (left tooth). The dp4 of GHUNLPam 2304 has a more angled buccal face of the trigonid.

Fig. 5. A–M. Rooted or potentially rooted teeth of Mesotheriinae. A–C: MD-CH-07-04, right maxillary fragment of *Tyotheriopsis chasicensis* from Arroyo Chasicó, with rooted P4 and M1–2, in occlusal, buccal, and mesial views; D, E: GHUNLPam 9522, right mandibular fragment of Mesotheriinae indet. from Telén, with alveolus of p3 and rooted p4, in buccal and occlusal views; F–I: GHUNLPam 14011, left (rooted?) P2–3 of Mesotheriinae indet. from Salinas Grandes de Hidalgo, in buccal, mesial, linguo-basal, and occlusal views; J, K: MMP 6-S, cranial fragment of *Mesotherium cristatum* from Barranca Camet, with right i1, anterior alveolus (P2?) and P3 (rooted?)–M3, in dorsal and ventral views; L, M: MHAS 161, palate of *Ichhutharium wayra* from Vega Chacras, showing the left series P2–M3, all premolars rooted, in ventral and lateral views. N–T. Mesotheriinae specimens with dp4 and p4. N–R: GHUNLPam 2304, mandibular fragment of Mesotheriinae indet. from Laguna Chillhué, with left i1–2 and p3–4, in lateral (N) and occlusal (O) views, CT images in occlusal (P) and distal (Q) views, and detail of the dp4 and the exposed p4 germ (R); S, T: MACN-Pv 8480, incomplete mandible of *Pseudotytherium subinsigne* ('*P. carlesi*') from Huayquerías de San Carlos area, in occlusal view and detail of the exposed p4 by the erupted premolars. Scale bars: 20 mm (A–D, F–P, S), 3 mm (E, R); no scale (Q, T).

In this tooth, the short trigonid, wider talonid, and shallow buccal groove are similar to the rooted premolar GHUNLPam 9522 or the p4 of specimens such as GHUNLPam 152 from Loventué (Section 3.1.2). The exposed p4 in GHUNLPam 2304 shows a bilobed morphology (trigonid and talonid), which is not clearly observed in MACN-Pv 8480. In addition, the relative position of the tooth differs, being placed more anteriorly in the latter (it surpasses the trigonid of the dp4) than in the former (barely surpassing the trigonid-talonid groove of dp4).

In both cases, the first preserved premolar could be assumed to be a dp3; however, the interpretation of the first cheek tooth in different notoungulates is a matter of debate (see Section 4). On the other hand, the outline of erupted premolars in GHUNLPam 2304 is similar to those of MMH-CH 83-03-114 (Fig. 4(A, B)), the former with more closed buccal groove (both teeth occlusally incomplete). However, the CT images of MMH-CH 83-03-114 do not reveal a germ tooth that would lead to interpreting the premolars as deciduous.

4. Discussion

Morphological and metrical variations in mesotheriines linked with ontogenetic stages have been mentioned in different opportunities, but mainly associated with the consideration of juvenile (with deciduous dentition) vs. adult individuals (Francis, 1960), as exposed in previous sections, or even concerning a particular character within a sample such as the presence of fossettes in premolars (e.g., CRILAR-Pv 55, see Section 3.1.1; and GHUNLPam 14335, Fig. S4(O, P), Appendix C; Croft et al., 2004; Armella et al., 2025).

The Late Miocene sample from Arroyo Chasicó and the compared specimens from other localities/ages allow us to propose a relative ontogenetic sequence of young individuals that is summarized in Tables 1, 2. This variation of young individuals was described by Cerdeño and Schmidt (2013) based on several available materials, contrasting with the previous criterion (juvenile with deciduous teeth vs. adults). The sample here studied reinforces the interpretation of young individuals for specimens previously considered juvenile, mainly those bearing an 'extra' premolar (P2/p3). At the same time, new questions arise about the characteristics of the deciduous teeth in mesotheriines, especially counting on some specimens with rooted premolars and tooth germs. Examples provided by Cerdeño and Schmidt (2013) and the new ones described in Section 3.1 do not support the idea that the 'extra' premolars are deciduous teeth.

Until now, an indirect proof of deciduous dentition in mesotheriines was provided by Gomes Rodrigues et al. (2017a, 2017b), who described P3–4 germs (deciduous not preserved) in MMHN Bol V 3349 of the early Middle Miocene *Microtyotherium choquecotense* from Bolivia. These authors assumed that these two premolars are replacing three deciduous teeth, an assumption that would not be valid for mesotheriines where the P2 is present as interpreted by Cerdeño and Schmidt (2013). The latter authors hypothesized that the upper P2 and the lower p3 would be expelled relatively early in life, partially based on their clearly shorter crown compared with the following premolars (P3–4/p4).

The new data presented here provide the first cases of a germ being present together with the erupted tooth (see comment in Section 3.3 on Francis' [1960] statements about the presence of germs), GHUNLPam 2304 (Fig. 5(N–R), Mesotheriinae indet.) and the holotype of '*P. carlesi*' MACN-Pv 8480 (Fig. 5(S, T), *P. subinsigne*). This discovery raises doubts about the presence of germs in specimens that have not been evaluated through X-ray or CT-scan images, such as the case of the specimen MACN-Pv 8481 (Fig. S4

(E), Appendix C) assigned to '*P. carlesi*', in which p3 is present. Nevertheless, other young individuals for which such images exist (e.g., MMH-CH 86-09-87, MMH-CH 85-04-125, MMH-CH 83-03-114, MMH-CH s/n, and CRILAR-Pv 433) have not revealed any evidence of the presence of germs. Altogether, the evidence presented here prevents the establishment of a conclusive pattern on the mesotheriine deciduous dentition.

The possible consideration of a retained deciduous dentition in adults does not seem to be supported. The interpretation of an upper/lower first premolar as a deciduous tooth in different groups (e.g., interatheres, octodontoid rodents, among others) is mostly based on the great degree of wear of this tooth with respect to the permanent jugal series and the observation of different ontogenetic stages. Nevertheless, mesotheriids with P2/p3 do not show an incongruent wear degree of these teeth with respect to the following, as previously evidenced by Cerdeño and Schmidt (2013) and in this work.

On the other hand, the specimens with confirmed rooted premolars (Section 3.2) do not support their interpretation as deciduous teeth, even though they belong to individuals assumed to be young. As already explained, the morphology and proportions of the accompanying molars in MD-CH-07-04 from Arroyo Chasicó (*T. chasicensis*) do not justify that the P4 is deciduous, particularly when compared with young individuals without roots (e.g., MACN-Pv 9531 or CRILAR-Pv 433; see Section 3.1.1). The aspect of molar morphology and the congruent degree of wear of the entire jugal series was already exposed by Cerdeño and Schmidt (2013) with respect to CRILAR-Pv 433 and the compared specimens. The case of GHUNLPam 9522 from Telén limits the comparison because of the lack of teeth accompanying the rooted p4; the young condition of this individual would be supported by the presence of the (high) alveolus of p3. The other cases of rooted teeth exposed above are less conclusive in which concerns Late Miocene specimens, while the older *Ichhutharium wayra*, MHAS 161, corresponds to a different, older group of mesotheriines that bears three permanent, rooted premolars (Armella et al., 2025).

Ever-growing teeth evolved in four families of notoungulates (Madden, 2015; Gomes Rodrigues et al., 2017a): Mesotheriidae, Hegetotheriidae, Toxodontidae, and Interatheriidae (only some basal interatheriines develop roots in very old individuals); these groups also share an eruption pattern in which the three molars erupt before the permanent premolars. In addition, the acquisition of euhiposodont teeth would be related to the ingestion of dust and grit while eating plants near the soil, due to the abundance of abrasive materials from the volcanic activity (Pascual and Ortiz-Jaureguizar, 1990; Strömberg et al., 2013). The euhiposodont teeth increased the duration of crown growth, which would postpone the time for reaching the maximum tooth length, and this delay is reflected in the tooth-size difference between young and adult individuals, mainly among mesotheriids and toxodontids (Gomes Rodrigues et al., 2017a, 2017b).

On the other hand, the interpretation of the first premolar in the cheek-tooth row as deciduous or permanent is often unclear, even in extant mammal species (Smith, 2000). Within trachytherine mesotheriids, Billet et al. (2008) described a large sample of *Trachytherus alloxus* from Salla (Bolivia; late Oligocene), in which they recognized the presence of small P1 and p1 (absent in old specimens) in specimens with deciduous dentition (Billet et al., 2008: fig. 14B, app. 1), while deciduous DP/dp1 are not mentioned. The protohiposodont permanent dentition of this taxon develops roots in old individuals, and roots are also mentioned for their anterior deciduous teeth; deciduous premolars are easily differentiated (relatively long and narrow teeth; presence of fossettes/fossettids; and well-developed parastyles). When DP2–4 are in use, the M1 is slightly worn and M2 is pointing; when P2–4 are erupting, M2 is

little worn and M3 is pointing (Billet et al., 2008); no specimen was described with deciduous premolars and their permanent counterparts simultaneously.

Concerning Hegetotheriidae (the sister group of Mesotheriidae according to Billet, 2011), Cerdeño et al. (2017) described the deciduous dentition of *Paedotherium* (Pachyrukhinae) from the Late Miocene–Early Pliocene of central Argentina, and observed that DP2–4 are high-crowned, rootless, and covering the apex of the euhypodont permanent premolars; the degree of wear and height of the crown allowed establishing the pattern of replacement. This genus lacks P1, but Armella et al. (2024) have recently described a DP1 in a specimen from the Late Miocene of Tucumán Province. As stated by Cerdeño et al. (2017), morphological similarities between deciduous and permanent premolars in *Paedotherium*, particularly when worn, can lead to misinterpretations. This suggests that in some cases, relying solely on external tooth morphology may be insufficient to distinguish deciduous from permanent dentition. This may help explain the lack of identified deciduous teeth despite the abundance of certain taxa, consistent with the observations made here for mesotheriines.

Among other typotherian notoungulates, archaeohyracids are well represented by large samples of *Archaeohyrax suniensis* from the Oligocene of Salla, Bolivia (Billet et al., 2009) and Quebrada Fiera, Mendoza, Argentina (Cerdeño et al., 2010), and *Pascualhyrax irqi* from the Eocene of Salta (Ferro et al., 2023), in all cases recognizing different ontogenetic stages and the deciduous dentition. Teeth are protohypodont, with small I2–P1/c–p1, but without DP/dp1, and show a significant change of proportions along the crown in upper cheek teeth. The DP/dp2–4 are protohypodont and rooted (Billet et al., 2009). As in trachytherines, archaeohyracids show well-differentiated deciduous teeth and the ontogenetic stages evidence how their wear increases while the molars successively erupt, and the permanent premolars are clearly less worn than molars (M2 erupts with DP4 still present).

Intertheriids also show a dual interpretation of the first premolar, as described by different authors concerning diverse species (Vera and Cerdeño, 2014; Fernández et al., 2021, 2023). This first tooth (DP/dp1 or P/p1) and the other deciduous teeth are brachydont, with roots, and heavily worn compared with the remaining tooth series (occlusal morphology of DP/dp2–4 can be similar to that of P/p2–4 in taxa such as *Interatherium*, but still differentiated by being brachydont and rooted; Fernández et al., 2021). Also, Vera et al. (2017) described late Oligocene specimens in which permanent premolars develop roots whereas molars do not.

The precedent paragraphs evidence variations concerning deciduous dentitions among typotherian notoungulates. In the studied mesotheriines, particularly in the large sample from Arroyo Chasicó, we also observe a significant variation concerning different aspects. On the one hand, specimens with rooted premolars seem to belong to young individuals, but not as young as other specimens without roots. Up to now, there are too few examples of rooted premolars in mesotheriines to confidently interpret an evolutionary pattern within the subfamily and hypothesize its causes; we can neither discard that they represent cases of ancestral state retention within the group. Variations within the young sample are also evident, concerning the reduction of lingual grooves in premolars (MMH-CH 85-04-125 would be an exception as its P3 has a groove deeper than in relatively younger specimens), the change in proportions, and the lobes of the molars becoming tighter and more regular. On the other hand, the two specimens with a p4 germ do not particularly differ from other young specimens with p3 in which germs are not detected. In addition, the position of the germ, basal but also lingual to the dp4, is not usual in other notoungulates or even other ungulates (e.g., perissodactyls) where replacement is known.

5. Conclusions

The studied sample of mesotheriines, assigned to *Typpotheriopsis chasicoensis*, from the early Late Miocene Arroyo Chasicó locality includes several specimens considered as young individuals, but without deciduous teeth. These specimens add to other studied Late Miocene materials, and allow us to establish a more detailed relative ontogenetic sequence for their upper dentitions and, to a lesser degree, for the lower ones.

This sample from Arroyo Chasicó has also provided the first specimen (MD-CH-07-04) with a rooted upper premolar among Late Miocene mesotheriines. In turn, within the compared sample, the mandibular fragment GHUNLPam 9522 (Mesotheriinae indet.) from Telén (La Pampa Province) has revealed the first case of a rooted lower premolar. Other possible rooted teeth are less conclusive, such as GHUNLPam 14011 (Mesotheriinae indet.) from Late Miocene Salinas Grandes de Hidalgo locality and MMP 6-S (*Mesotherium cristatum*) from the Early–Middle Pleistocene Barranca Camet locality. These rooted premolars are herein discarded as deciduous teeth. The roots of the P4 of MD-CH-07-04 are morphologically different from the rooted premolars (P2–4) of the recently described *Ichhutherium wayra* from the Early Miocene Vega Chacras locality, Catamarca Province (Armella et al., 2025).

On the other hand, the specimens GHUNLPam 2304 from Laguna Chillhué (Mesotheriinae indet.; Late Miocene; La Pampa Province) and MACN-Pv 8480 (holotype of ‘*Pseudotyppotherium carlesi*’ = *P. subinsigne*) from Huayquerías de San Carlos (Early Pliocene; Mendoza Province) show a p4 germ, supporting the deciduous condition of the respective erupted premolar. The germ is placed basally and lingually to the dp4 in both cases, but its relative position and the observed outline are not the same. The interpreted dp4 show an occlusal morphology similar to that of the permanent p4 in other specimens without germs, differing from that observed in the trachytherine mesotheriids, and closer to the condition in the hegetotheriid *Paedotherium* and other typotherians such as *Interatherium*.

Interpreting the rooted and deciduous teeth analyzed here is challenging. At the moment, we consider them individual cases within large samples, mainly concerning the Arroyo Chasicó sample. The described cases of roots and germs do not show a clear pattern, as each comes from different sites, ages, and/or taxon. In this sense, the analysis of another large sample from a single locality (e.g., Farola Monte Hermoso) could be likely significant. In any case, our research reveals the need for further investigation and a more constant application of X-ray or CT scans. Only new findings will provide better support for individual variation, evolutionary patterns, or taxonomic implications.

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CRedit authorship contribution statement

Esperanza Cerdeño: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Claudia I. Montalvo:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Santiago Hernández Del Pino:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Renata Sostillo:**

Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Gabriela I. Schmidt:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Matías A. Armella:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Rodrigo L. Tomassini:** Writing – review & editing, Writing – original draft, Project administration, Investigation, Funding acquisition.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices A-C. Supplementary information

Supplementary information (including a list of revised specimens, upper and lower dental measurement tables, and Figs. S1–S4) associated with this article can be found, in the online version, at: <https://doi.org/10.1016/j.geobios.2025.09.001>.

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