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Systematics and biostratigraphic implications of a new notoungulate assemblage (Mammalia, Pan-Perissodactyla) from the India Muerta Formation (Late Miocene), Northwestern Argentina

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SYSTEMATICS AND BIOSTRATIGRAPHIC IMPLICATIONS OF A NEW NOTOUNGULATE ASSEMBLAGE (MAMMALIA, PAN-PERISSODACTYLA) FROM THE INDIA MUERTA FORMATION (LATE MIOCENE), NORTHWESTERN ARGENTINA

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Abstract. The fossils of the India Muerta Formation (Neogene, Tucumán Province, Northwestern Argentina) include several vertebrate groups, mainly metatherian, xenarthran, and notoungulate mammals. Nevertheless, these remains have been scarcely mentioned in the literature, being mostly noted in faunistic lists, without a focus on taxonomic or morphological aspects. Additionally, most of the biostratigraphic or paleobiogeographic considerations, which are based merely on lithostratigraphic inferences, have suggested a correlation mainly with the Andalhuala (Late Miocene–Pliocene) and the Corral Quemado (Pliocene) formations, both units corresponding to the Santa María sedimentary basin of the Calchaquí valleys of Northwestern Argentina. Here, we present a study of a notoungulate assemblage recently recovered from levels of the India Muerta Formation, clarifying the geological context and correlating fossil levels with western outcrops. Our study identifies remains grouped systematically as two toxodontids, one mesotheriid, and four hegetotheriids, some of which represent the first records for the unit and/or the region. The sedimentological analysis suggests that this fauna developed in a paleoenvironment corresponding to a complex of braided to meandering fluvial systems. Based on these new data, the fossiliferous levels of the India Muerta Formation reinforce a Late Miocene (Tortonian) age. Consequently, our chronological proposal leads to a closer correlation between the India Muerta Formation and the Las Arcas and Chiquimil formations, which immediately underlie the Andalhuala Formation in western valleys. These inferences agree with previous radioisotopic analyses and, hence, the evidence yielded by the presence of these newly documented notoungulates stands as our most reliable basis for stratigraphic correlation.

Key words. Choromoro basin. NWA. *Ocnerotherium*. *Hemihegetotherium torresi*. Astragalus. Deciduous teeth. Tortonian.

Resumen. SISTEMÁTICA E IMPLICANCIAS BIOESTRATIGRÁFICAS DE UN NUEVO ENSAMBLE DE NOTOUNGULADOS (MAMMALIA, PAN-PERISSODACTYLA) DE LA FORMACIÓN INDIA MUERTA (MIOCENO TARDÍO), NOROESTE ARGENTINO. Los fósiles de la Formación India Muerta (Neógeno, Tucumán, noroeste argentino) incluyen varios grupos de vertebrados, principalmente mamíferos metaterios, xenartros y notoungulados. Sin embargo, estos restos han sido escasamente mencionados en la literatura, siendo mayormente incluidos en listas faunísticas, sin discutirse aspectos taxonómicos o morfológicos. Además, la mayoría de las consideraciones bioestratigráficas o paleobiogeográficas, basadas en inferencias litoestratigráficas, sugieren principalmente una correlación con las formaciones Andalhuala (Mioceno Tardío–Plioceno) y Corral Quemado (Plioceno), ambas parte de la cuenca sedimentaria de Santa María, en los valles Calchaquíes del noroeste argentino. Aquí se estudia una asociación de notoungulados recuperados recientemente en la Formación India Muerta, estableciendo su contexto geológico y correlacionando los niveles fósiles con afloramientos occidentales. Nuestro estudio identifica dos restos asignados a Toxodontidae, un Mesotheriidae y cuatro Hegetotheriidae, algunos de los cuales representan los primeros registros para la unidad y/o la región. El análisis sedimentológico sugiere que esta fauna se desarrolló en un paleoambiente correspondiente a un sistema fluvial entrelazado a meandriforme. Estos nuevos datos sustentan una edad Mioceno Tardío (Tortoniense) para los niveles fosilíferos de la Formación India Muerta. En consecuencia, la propuesta cronológica derivada de nuestro estudio conduce a una correlación más estrecha entre la Formación India Muerta y las formaciones Las Arcas y Chiquimil, inmediatamente subyacentes a la Formación Andalhuala en los valles occidentales. Estas inferencias concuerdan con análisis radioisotópicos previos y, por lo tanto, la evidencia arrojada por la presencia de estos notoungulados recientemente documentados se erige como nuestra base más confiable para la correlación estratigráfica.

Palabras clave. Cuenca Choromoro. NOA. *Ocnerotherium*. *Hemihegetotherium torresi*. Astrágalo. Dientes deciduos. Tortoniense.

Since the 19th century, the Neogene fossil record of Northwestern Argentina (hereafter NWA) has been known and investigated based mostly on vertebrate remains coming from western outcrops, such as those of the Santa María and El Cajón valleys (Catamarca and Tucumán provinces). In part, this is related to the fact that these sedimentary sequences (largely comprising the Santa María Group) are well exposed and extensive, characterizing the Sierras Pampeanas geological province. Additionally, as the geochronological constraints of these areas have been deeply studied, they have become the reference for the most complete geochronological and paleoenvironmental Neogene scheme of NWA (see Esteban *et al.*, 2017, 2019; Georgieff *et al.*, 2017; Zapata *et al.*, 2019; and references therein). Conversely, the outcrops located on the eastern side of the Calchaquíes ranges (Fig. 1), which are usually isolated and have extensive vegetation cover, have been scarcely studied.

During recent decades, several works have focused on the eastern foreland basins of NWA, mainly with the aim of characterizing their sedimentological and geochronological aspects as well as their relationships with western units (Cristallini *et al.*, 2004; Iaffa *et al.*, 2011a, 2011b, 2013; Zapata *et al.*, 2019; Armella *et al.*, 2020). In addition, new fossil finds have resulted in an integrated perspective of the Neogene vertebrate fauna of NWA (*e.g.*, Powell *et al.*, 2012; García-López & Babot, 2015; Albino, 2017; Alonso, 2018; Armella *et al.*, 2018, 2019). In this context, one of the eastern units that has yielded several fossils is the India Muerta Formation (Late Miocene–Early Pliocene [Zapata *et al.*, 2019]; Choromoro Basin, Tucumán Province; Fig. 1.1–1.2).

The vertebrate fossil record of the India Muerta Formation includes fishes, turtles, snakes, and crocodilians (Babot & Ortiz, 2008; Powell *et al.*, 2012; Powell & Ortiz, 2014; Albino, 2017). However, mammalian remains are the most abundant, including metatherians, xenarthrans, and notoungulates (García-López & Babot, 2015). Despite this relative diversity, these fossils have been scarcely mentioned in the literature; mostly, they have been noted

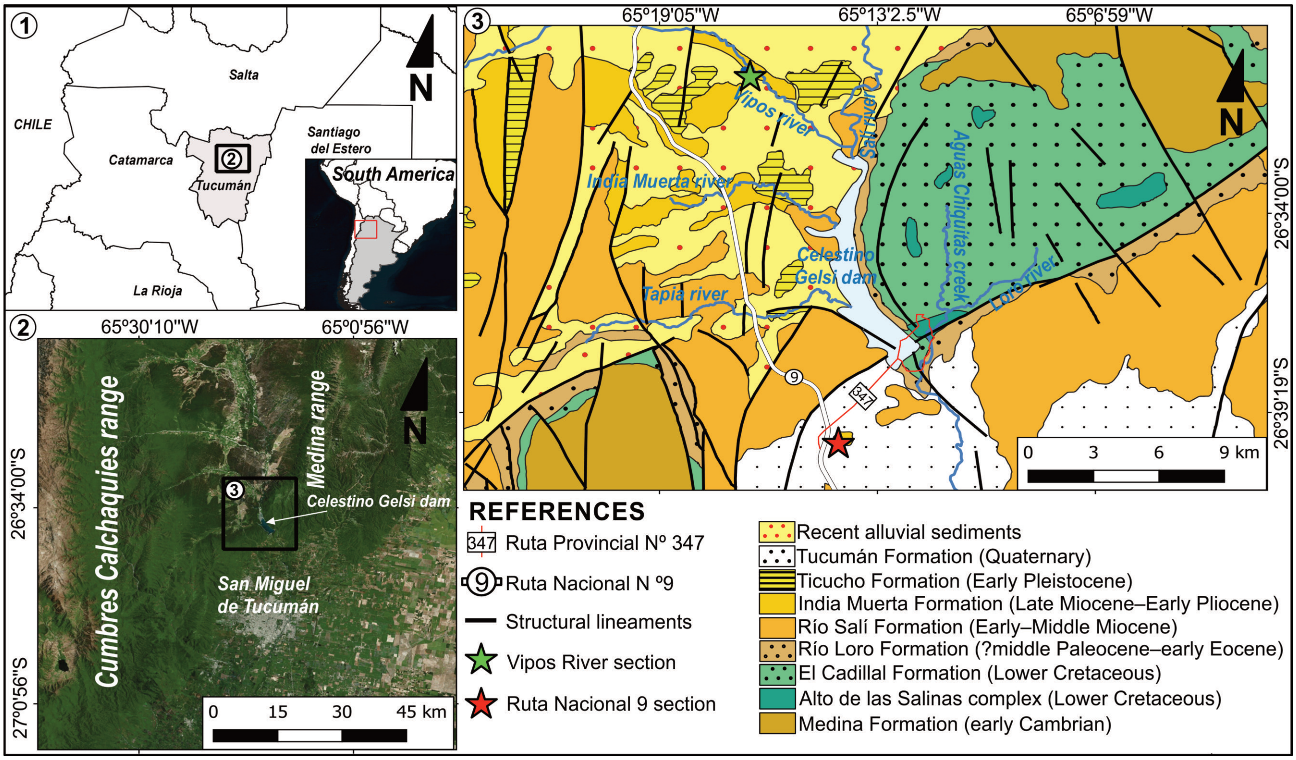

Figure 1. 1–2, Location of the Choromoro basin in the Department of Tafí Viejo, Tucumán Province (Argentina); **1,** general geographic location; and **2,** detailed location; **3,** geologic map of the study area showing the relative extensions of the lithostratigraphic units that crop out around the Celestino Gelsi Dam (El Cadillal locality).

in faunistic lists, without a focus on taxonomic or morphological aspects (Powell & Ortiz, 2014). Also, given that the fossil levels are isolated and lack continuity even between geographically close sites, most biostratigraphic and paleobiogeographic considerations are based merely on lithostratigraphic inferences. Such approaches have suggested a correlation mainly with the Andalhuala Formation (Late Miocene–Pliocene) but also with the Corral Quemado Formation (Pliocene), both included in the Santa María Group and cropping out in western basins of NWA (Bossi *et al.*, 1998; Georgieff *et al.*, 2014).

Recent fieldwork in the India Muerta Formation has led to fossil discoveries with accurate stratigraphic locations. Among them, specimens of Notoungulata (Mammalia, Pan-Perissodactyla) are the most abundant. These herbivorous placental mammals evolved from the early Paleocene to the Late Pleistocene (Paula-Couto, 1952; Barnosky & Lindsay, 2010; Croft *et al.*, 2020; but see MacFadden, 2005), becoming abundant in most Cenozoic continental biotas. The fact that notoungulates are well represented in several Neogene outcrops of Argentina, particularly in western localities of NWA, make them important elements for biostratigraphical inferences (*e.g.*, Tomassini *et al.*, 2013; Woodburne *et al.*, 2014).

The focus of the present contribution is the detailed study of a notoungulate assemblage, including cranial and postcranial remains, recently recovered from levels of the India Muerta Formation. We also describe stratigraphic profiles aimed at partially clarifying the geological context and correlating fossil levels with western outcrops. Our results provide new information about the diversity of notoungulates in NWA that are useful for biostratigraphic studies.

Geographic and stratigraphic context

The Choromoro valley is located 25 km north of the city of San Miguel de Tucumán (Tucumán Province) and is geologically characterized by a Cretaceous/Cenozoic depocenter known as the Tapia-Trancas Basin (Guido & Sesma, 2014) (Fig. 1.1). The Paleogene and Neogene–Quaternary sedimentation overlies in discordance the El Cadillal Formation (Lower Cretaceous). The Paleogene is represented by the Río Loro Formation (?middle Paleocene–early Eocene; Bossi *et al.*, 1998; González *et al.*, 2000; Georgieff *et al.*, 2014; Gelfo *et al.*, 2020). At the study area, the Neogene–Pleistocene units correspond to the Choromoro Group that, from base to top, is composed of the Miocene Río Salí and India Muerta formations. These units are overlain by the Ticucho Formation (Early Pleistocene), and the Quaternary is represented by the Tucumán Formation and recent aulluvial materials (González *et al.*, 2000; Georgieff *et al.*, 2014) (Fig. 1.3).

Bossi (1969) first identified the India Muerta Formation based on outcrops located on the cliffs of the India Muerta River. However, its type profile was described on the cliffs of the Vipos River, with a thickness of 700 m. The India Muerta Formation is composed of an alternation of thick gray sandstone banks, thin sandstones with cross-stratification, and massive and bioturbated light brown siltstones. This unit overlies the Río Salí Formation, showing a gradual transition and incorporating features such as green siltstone horizons, white tuffs, and color changes from light brown to reddish brown. Newer studies have divided the India Muerta Formation into lower and upper sections based on absolute U-Pb dating and studies of the regional evolution of the basin (Zapata *et al.*, 2019). Absolute radioisotopic ages indicate a maximum age of 9.82 ± 0.11 My for the Lower India Muerta Section (LIMS) and a minimum of 3.7 ± 0.11 My for the Upper India Muerta Section (UIMS). The LIMS was deposited paraconformably on top of the Río Salí Formation and is characterized by a change from saline lacustrine to ephemeral fluvial deposits. The UIMS is interpreted as a more permanent fluvial system, with a maximum age of ~3 My (Zapata *et al.*, 2019). Paleoenvironmentally, Bossi (1969), Bossi *et al.* (1998), and Georgieff *et al.* (2014) proposed a fluvial system of meandering rivers with gently sloping floodplains furrowed by rivers with sandy beds that were surrounded by silty, undifferentiated vertical accretionary deposits with sporadic ephemeral lagoons.

MATERIALS AND METHODS

The studied remains are stored at the PVL of the Facultad de Ciencias Naturales e Instituto Miguel Lillo (Tucumán Province, Argentina). The taxonomic and anatomical study was carried out mostly through direct comparisons, using type specimens stored in the aforementioned collection and at the MLP (Buenos Aires Province, Argentina), MACN (Ciudad Autónoma de Buenos Aires, Argentina), and the FMNH (Chicago, USA). Additionally, we consulted historical literature and papers focused on toxodontid, mesotheriid, and hegetotheriid notoungulates (*e.g.*, Cabrera & Kraglievich, 1931; Pascual, 1965; Cifelli, 1983; Cerdeño & Bond, 1998; Cerdeño & Montalvo, 2002; Croft & Anaya, 2006).

Descriptions, comparisons, and measurements of specimens followed the usual terminology and methodology for each notoungulate group (Madden, 1990; Cerdeño & Bond, 1998; Cerdeño & Montalvo, 2002). Terminology for the basicranium follows O'Leary (2010) and MacPhee (2014) and references therein. Tarsal terminology follows Cifelli (1983), Szalay (1985), and Shockey & Flynn (2007). Dimensions as absolute values and by means of bivariate plots were used to evaluate size variation among specimens.

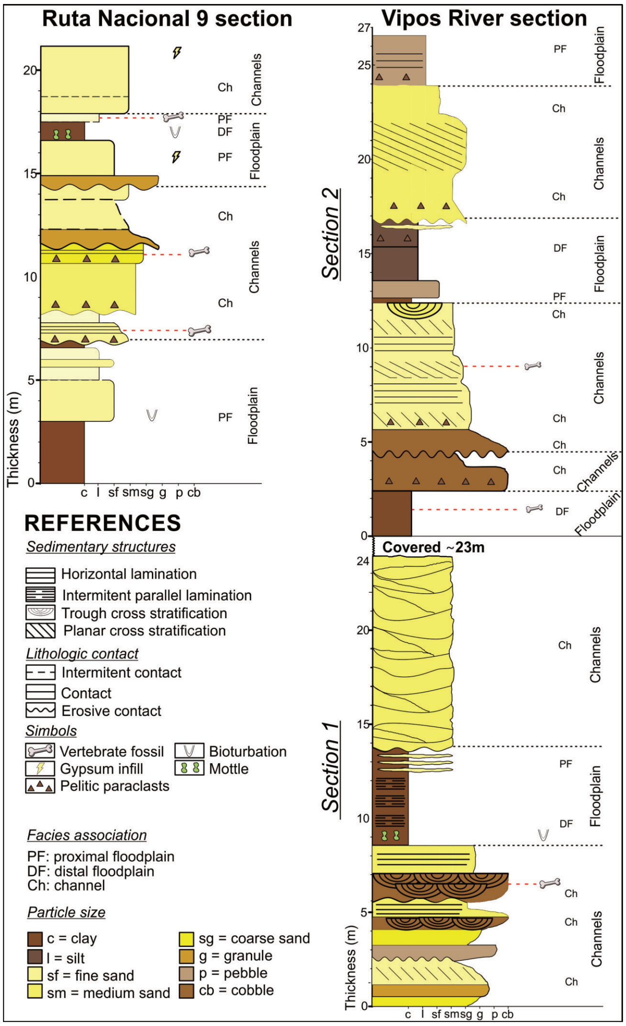

Figure 2. Sections of the India Muerta Formation showing the different facies associations.

In order to stratigraphically locate the fossil levels, we described two detailed profiles of the India Muerta Formation located in two sections with relatively low vegetation coverage: Ruta Nacional 9, located at 26° 39′ 28.6″ S, 65° 14′ 09″ W, and Vipos River, located at 26° 29′ 38.3″ S, 65° 16′ 6.5″ W (Fig. 1.3). The descriptions of the sedimentary facies of the outcrops were made following the criteria of Miall (1996), which uses a capital letter for the texture of the sedimentary rock and a lowercase letter for its sedimentary structure. The acronyms were made as simple as possible to allow a more orderly reading, as pointed out by Bridge (1993). Facies associations (Tab. 1) for interpretation of fluvial systems were made following the criteria of Miall (1996), Sánchez-Moya & Sopeña (2010), and Viseras & Fernández (2010). The measurements of the studied sections were taken considering lower and upper beds that showed lateral continuity and could be tracked in the field. The descriptions of the profiles include lithology, grain size, contacts, sedimentary struc-tures, presence of fossils, and color of each stratum, as illustrated in Figures 2 and 3.

Institutional acronyms. AMNH, American Museum of Natural History, New York, USA; **FMNH,** The Field Museum, Chicago, USA; **GHUNLPam,** Cátedra Geología Histórica, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, La Pampa, Argentina; **LIEB-PV,** Laboratorio de Investigaciones en Evolución y Biodiversidad-Colección Paleontología de Vertebrados, Esquel, Argentina; **MACN-A,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"-Colección Nacional Ameghino, Ciudad Autónoma de Buenos Aires, Argentina; **MACN-PV,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" -Colección Nacional de Paleovertebrados, Ciudad Autónoma de Buenos Aires, Argentina; **MNHN-BOL-V,** Museo Nacional de Historia Natural-Bolivia-Departamento de Paleontología de Vertebrados, La Paz, Bolivia; **MLP,** Museo de La Plata, La Plata, Argentina; **MMP,** Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Argentina; **PVL,** Colección Paleontología de Vertebrados

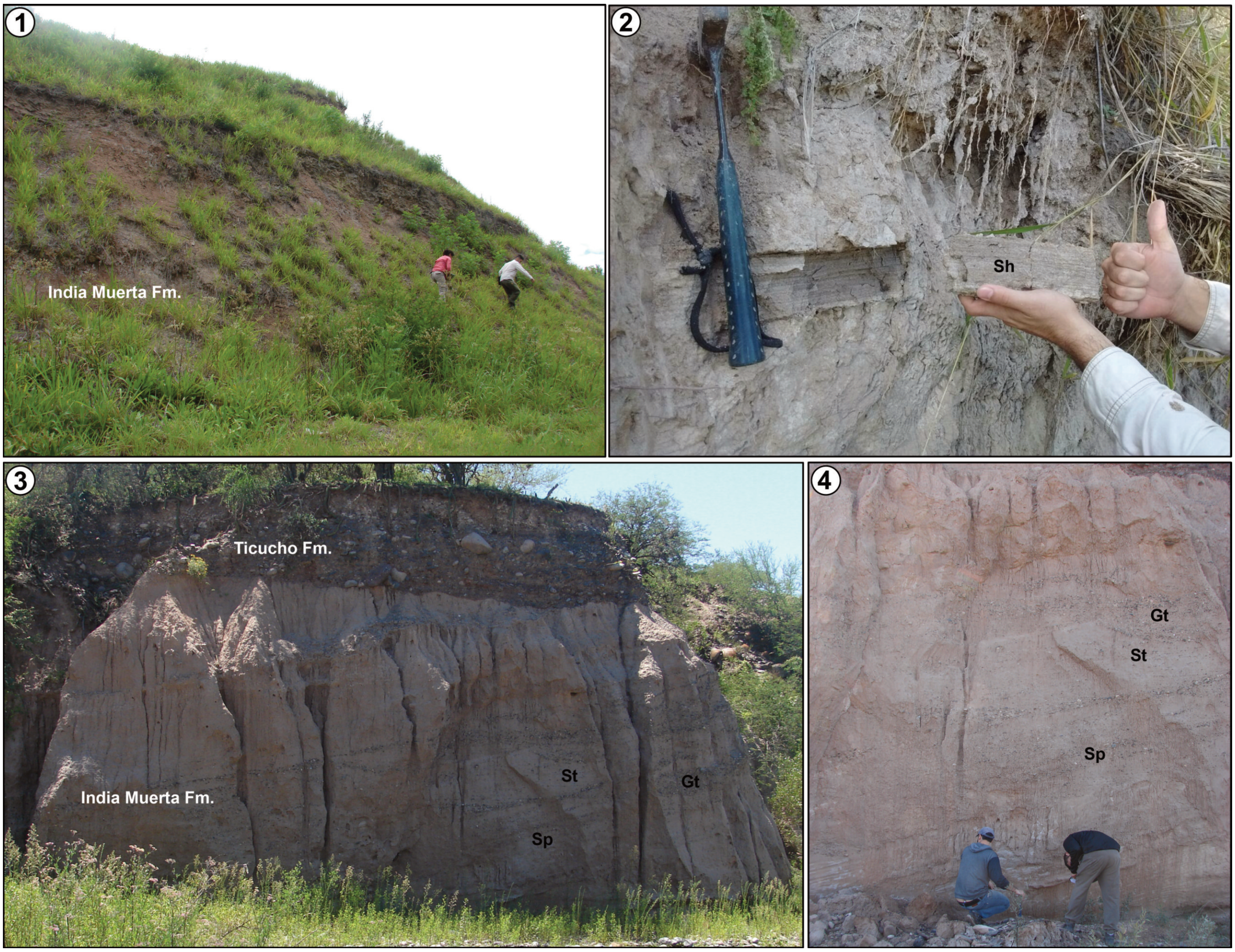

Figure 3. Sections and facies recognized in the study area. **1,** outcrops of the India Muerta Formation at the Ruta Nacional 9 section; **2,** detail of facies (sandstone with horizontal lamination); **3,** outcrops of the India Muerta and Ticucho formations at the Vipos River sections; **4,** detail of facies (sandstone with planar cross stratification, sandstone with trough cross stratification, and conglomerate with trough cross stratification). See Table 1 and Figure 2 for profiles and facies associations and paleoenvironmental interpretations.

TABLE 1 – Facies associations and their main interpretations.

Facies	Facies association	Paleoenvironmental interpretation
Cm, Lm, Sg, Sm	Proximal floodplain	Floodplain with crevasse lobes.
Cm, Cho	Distal floodplain	Floodplain with ponds and bioturbations.
Sm, Sh, Sp, Si, St, Sg, Gg, Gi, Gt	Channels	Channel with longitudinal/lateral bars. Amalgamated channels.

Sedimentary structure abbreviations: g, graduated; h, horizontal lamination; i, inverse graduated; m, massive; o, mottled; p, planar cross stratification; t, trough cross stratification. **Lithology abbreviations:** C, claystone; G, conglomerate; L, siltstone; S, sandstone.

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Anatomical abbreviations. I/i, upper/lower incisor; **IAM,** internal auditory meatus; **M/m,** upper/lower molar; **P/p,** upper/lower premolar.

RESULTS

Stratigraphy of the fossil-bearing levels of the India Muerta Formation

Ruta Nacional 9 section

This section is located north of San Miguel de Tucumán city, on the margins of the Ruta Nacional N° 9, at its junction with the Ruta Provincial N° 307, in the locality of El Cadillal (Figs. 1.2–1.3, 2, and 3.1–3.2). This is the site of the India Muerta Formation that has yielded a variety of vertebrate fossils.

Composition and interpretation. In general terms, the Ruta Nacional 9 section is composed of claystones, fine to coarse sandstones, and conglomerates (Figs. 2 and 3.1–3.2); facies and facies associations are summarized in Table 1. The section is interpreted as a braided to meandering fluvial system with floodplains and channel areas. The floodplains can be classified as proximal and distal with respect to the relative distance to the main channels of the depositional system. The distal areas are characterized by mottled claystone banks, without the development of sedimentary structures. The proximal areas are associated with layers of claystone, intercalated with relatively thin banks of sandstones related to the development of crevasse lobes. The channels association are: i) channels with longitudinal bars composed of conglomerates and sandstones normally graduated with horizontal lamination and paraclasts; and ii) amalgamated channels composed of massive sandstones with pelitic paraclasts. This section has provided a large number of fossil specimens, including fishes, turtles, snakes, crocodilians, metatherians, cingulates, rodents, and notoungulates.

Vipos River section

The sedimentary sequence studied is located on the margins of the Vipos river (Fig. 1.3). These sediments crop out on the northern margin of the river cliffs and show a good exposure and continuity in almost all of the section. The outcrop was described in two sections related vertically with a short discontinuity between them, due to coverage (Fig. 2). Facies and facies associations are summarized in Table 1.

Composition and interpretation. In general terms, some of the interpreted facies associations correspond to a channel zone context, while others are explained as floodplains. Vipos River section 1 (Fig. 3.3) is interpreted as a fluvial system with stable channel areas with sandy-conglomerate facies interspersed with plains containing pelitic materials. Floodplains are mainly composed of massive claystones that intercalate at the top with centimeter to decimeter-scale (5–15 cm) facies of massive sandstone. The channel facies associations are: i) minor braided channels with longitudinal bars composed of coarse sandstone to conglomerate that end with normal graduated coarse sandstones with parallel stratification; and ii) deep braided amalgamated channels composed of alternating normal to inverse graduated pebbly sandstones amalgamated with coarse sandstones and trough cross-stratified conglomerates (Fig. 3.3–3.4).

Vipos River section 2 is also interpreted as a braided/meandering fluvial system with alternating channel and floodplain areas (Fig. 3.3). The floodplains facies associations are: i) distal areas with ponds composed of massive claystone facies up to 3 m thick; and ii) proximal areas with crevasse lobes composed of massive claystone with finely laminated sandstones facies with clay paraclasts. Channel facies associations present better development of longitudinal/lateral bars, and it is possible to distinguish different types of channels: i) braided minor channels composed of alternating massive to laminated to cross-stratified sandstones with clay paraclasts; and ii) deep channels composed of coarse to medium sandstone with cross trough stratification (Fig. 3.3–3.4) with clay paraclasts.

SYSTEMATIC PALEONTOLOGY

PAN-PERISSODACTYLA Welker *et al.*, 2015
NOTOUNGULATA Roth, 1903
TOXODONTIA Owen, 1853
TOXODONTIDAE Gervais, 1847
TOXODONTINAE Trouessart, 1898

Ocnerotherium Pascual, 1954

Type species. *Ocnerotherium intermedium* Pascual, 1954. Late Miocene–Early Pliocene, San Luis and Buenos Aires provinces, Argentina.

Holotype. MLP 52-IX-17-1, incomplete right maxilla with

P1-3 and isolated P4, and right mandibular fragment with m2–3 (Pascual, 1954).

Ocnerotherium sp.

Figure 4.1–4.4; Table 2

Referred material. PVL 4653, right M1.

Locality and horizon. Lower section of the India Muerta Formation, Ruta Nacional 9, near the bridge to El Cadillal locality, Tafí Viejo Department, Tucumán Province, Argentina (Figs. 1 and 2). Late Miocene (Tortonian).

Description. The right M1, PVL 4653, presents small fractures, and the posterior edge of the protocone is partially broken (Fig. 4.1). However, the general morphology and the main features are well preserved. Measurements are given in Table 2.

In occlusal view, the ectoloph of PVL 4653 is almost straight; the parastyle is rounded and points mesiobuccally, and the paracone area is robust (Fig. 4.1). The mesial face is obliquely oriented and slightly convex near the protocone. The protocone area extends distolingually, where a small portion is broken. Lingually, the anterior fold is deep and oriented parallel to the mesial face. Adjacent to the anterior fold, there is a marked distal lingual sulcus that extends along the crown. The hypocone is rounded at the distal face, although not globose, and is straight at its mesiolingual face, forming an acute lingual face with a small and shallow concave area that extends along the crown. The base is similar to the occlusal face, with the anterior fold and sulcus well-developed (Fig. 4.2). The enamel covers the buccal face and partially covers the mesial and lingual faces, while the parastyle, protocone, and distal face are devoid of enamel (Fig. 4.3–4.4). The mentioned features, along with the molar wear, allow us to infer that it belongs to an adult individual.

Comparisons. Several features observed in PVL 4653, such as the deep anterior fold, the presence of a distal sulcus or concavity, and the arrangement of the enamel bands, are shared with *Toxodon* Owen, 1837, *Pisanodon* Zetti, 1972, *Mixotoxodon* van Frank, 1957, *Ocnerotherium*, and *Paratrigodon* Cabrera & Kraglievich, 1931. Moreover, the anterior fold and the distal sulcus are particularly observed in M1–2 of *Paratrigodon euguii* Cabrera & Kraglievich, 1931 (*e.g.*, MMP 5262; Pascual, 1965, fig. 9), M1 of *Mixotoxodon larensis* van Frank, 1957 (*e.g.*, AMNH 48864; van Frank, 1957, fig. 9), M1-2 of *Pisanodon nazari* Cabrera & Kraglievich, 1931 (*e.g.*, MLP 12-1667), M1–2 of adult and juvenile specimens of *Toxodon* (*e.g.*, MACN-PV 8598 and MLP 12-1174, respectively), and M1–2 of *Ocnerotherium* (*e.g.*, MLP 52-IX-17-1, holotype; Pascual *et al.*, 1966, pl. LXXX and LXXXI). However, both structures vary among these taxa, mainly in the development of the distal sulcus. *Paratrigodon euguii* (MMP 5262) presents a shallow distal sulcus in the M1, while it is a slight concavity in the M2; in turn, the M1–2 mesial faces, near the protocone area, are mostly straight to slightly concave. In *M. larensis* (AMNH 48864), the anterior fold and distal sulcus of M1 are similar to PVL 4653, but M1 differs in its hypocone morphology (straight distal and convex mesiolingual faces, forming a rounded lingual edge). In turn, in *M. larensis* there is a small projection of enamel in the mesial face, at the level of the protocone. These features differ from the specimen of the India Muerta Formation. Concerning *Pi. nazari* (MLP 12-1667), the remains probably belong to a juvenile individual (*sensu* Cabrera & Kraglievich, 1931), in which the M1 shows a distal sulcus deeper than in PVL 4683 and a well-rounded lingual edge between the anterior fold and the distal sulcus. The M2 of *Pi. nazari* (MLP 12-1667) differs from PVL 4653 in the presence of a concave ectoloph, acute buccodistal edge, straight distal face, and a rounded lingual edge of the hypocone. These differences distinguish the M1–2 of *Toxodon* (adult MACN-PV 8598 and a juvenile MLP 12-1174) from PVL 4653.

Finally, the M1–2 of the holotype of *O. intermedium* (MLP 52-IX-17-1) and PVL 4683 share the following features: almost straight ectoloph, mesial face obliquely oriented and slightly convex, rounded distal face, anterior face of the hypocone straight with a small and shallow concave area, and similar development of distal sulcus and anterior fold.

Despite the similarities between PVL 4653 and *O. intermedium*, a few features (such as a distolingually elongated hypocone and a narrow paracone) highlight the gracile morphology of the toxodontid from the India Muerta Formation compared to the holotype of *O. intermedium* (MLP 52-IX-17-1; Pascual *et al.*, 1966, pl. LXXX and LXXXI). Regarding dimensions (Tab. 2), PVL 4653 is smaller than the M1 and M2 of *O. intermedium* (MLP 52-IX-17-1) and an

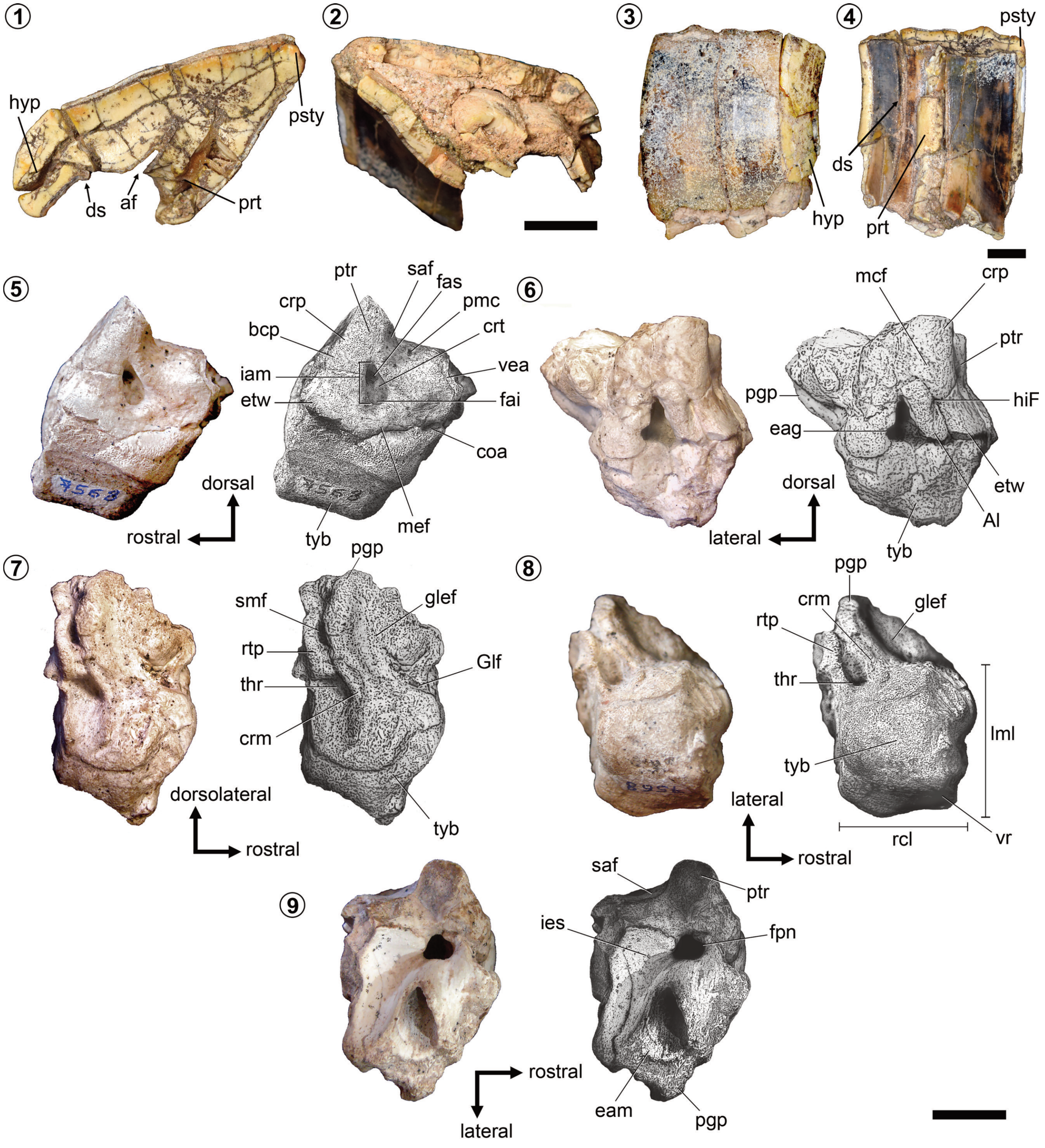

Figure 4. Toxodontidae specimens from the India Muerta Formation, Late Miocene (Tafí Viejo Department, Tucumán Province, Argentina). **1–4,** ***Ocnerotherium*** sp. **PVL 4653**, right M1; **1,** occlusal, **2,** basal, **3,** buccal, and **4,** lingual views. **5–9,** Toxodontidae indet. **(PVL 7568)**, right basicranial fragment; **5,** medial (intracranial), **6,** rostral, **7,** ventromedial, **8,** ventral, and **9,** dorsal views. Abbreviations: **af**, anterior fold; **Al,** alisphenoid; **bcp,** bump on *crista petrosa*; **coa,** cochlear aqueduct; **crm,** *crista meatus*; **crp,** *crista petrosa*; **crt,** *crista transversa*; **ds,** distal sulcus; **eag,** ectotympanic-alisphenoid gap; **eam,** external acoustic meatus; **etw,** epitympanic wing; **fai,** *foramen acusticum inferius*; **fas,** *foramen acusticum superius*; **fpn,** *foramen pneumaticum*; **glef,** glenoid fossa; **Glf,** Glaserian fissure; **hiF,** *hiatus Fallopii*; **hyp,** hypocone; **iam,** internal auditory meatus; **ies,** inner surface of the epitympanic sinus; **lml,** lateromedial length of the tympanic bulla; **mcf,** petrosal contribution to the middle cranial fossa; **mef,** medial flange; **pgp,** postglenoid process; **pmc,** petromastoid canal; **prt,** protocone; **psty,** parastyle; **ptr,** petrosal; **rcl,** rostrocaudal length of the tympanic bulla; **rtp,** retrotympanic process; **saf,** subarcuate fossa; **smf,** stylomastoid foramen; **thr,** tympanohyal recess; **tyb,** tympanic bulla; **vea,** vestibular aqueduct; **vr,** vertical ridge. Scales= 10 mm.

adult specimen of *Toxodon* (MACN-PV 8598) but larger than *Pi. nazari* (MLP 12-1667) and a juvenile specimen of *Toxodon* (MLP 12-1174) (Tab. 2). Differences between PVL 4653 and *O. intermedium* cannot be directly attributable to ontogenetic stage, given that both seem to belong to adult individuals. The scarcity of remains prevents a deeper taxonomic evaluation.

Toxodontidae indet.
Figure 4.5–4.9

Referred material. PVL 7568, right basicranial fragment.

Locality and horizon. India Muerta Formation, Ruta Nacional 9, near the bridge to El Cadillal locality, Tafí Viejo Department, Tucumán Province, Argentina (Figs. 1 and 2). Late Miocene (Tortonian).

Description. This fragment corresponds to the right auditory region, including incomplete petrosal, squamosal, and ectotympanic bones, forming a series of structures, including the tympanic bulla, epitympanic sinus, and auditory meatus.

The petrosal is partially preserved, as it is broken at the level of the subarcuate fossa, lacking the dorsal part of it and the entire mastoid area. Moreover, only the cerebellar aspect of the petrosal is visible, as the ectotympanic and squamosal bones are firmly attached to it, hiding the tympanic and squamosal aspects, respectively. This cerebellar exposure measures 17.65 mm from the petrosal rostral tip to the caudal edge of the cochlear aqueduct (see below). The zone of the IAM and the rostroventral half of the subarcuate fossa are well preserved (Fig. 4.5). The latter is wide, moderately shallow, and shows well-defined rostral edges, semicircular in outline. Near the center of the preserved concavity, there is a small aperture that may correspond to the petromastoid canal (for the subarcuate artery). Rostroventrally, the edge of the subarcuate fossa is pressed against the IAM, resulting in a subtriangular outline for this latter structure. Within the IAM, there is a deep *crista transversa* that separates the *foramen acusticum superius*, the primary exit of the facial nerve (cranial nerve VII), from the *foramen acusticum inferius*, the former being smaller than the latter. The *foramen acusticum inferius* contains two separated concavities filled with sedimentary matrix that correspond to the *tractus spiralis foraminosus*, for the passage of the cochlear fibers of the vestibulocochlear nerve (cranial nerve VIII), and the *foramen singulare*, for the vestibular fibers of the same element. Rostrally, there is a small, flattened protuberance that corresponds to the dorsal (or cerebellar) side of the epitympanic wing, a structure closing the tympanic cavity ventrally. Caudally, the zone of the epitympanic wing is followed by an irregular edge, firmly attached to the medial side of the tympanic bulla. This is the medial flange of the petrosal, also generally described in studies of the tympanic aspect. Following the line of this

TABLE 2 – Dimensions (in mm) of M1 and M2 of PVL 4653, identified as *Ocnerotherium* sp., and other toxodontid specimens discussed in the text.

Specimen	M1		M2	
	L	W	L	W
PVL 4653	43.69	21.39	-	-
Pisanodon nazari MLP 12-1667 (holotype)	36.37	15.66	38.92	16.18
Ocnerotherium intermedium MLP 52-IX-17-1 (holotype)	58.93	32.00	60.24	32.22
Toxodon sp. MACN-PV 8598	45.22	24.06	52.70	24.06
Toxodon sp. MLP 12-1174	36.44	18.32	35.42	15.86

Abbreviations: L, length; W, width.

flange, there is a small notch pierced by an oblong aperture, the cochlear aqueduct. More dorsally, and near the ventral edge of the subarcuate fossa, there is a slit integrated within a vertical crest on the petrosal surface. This is the vestibular aqueduct for the endolymphatic duct and accompanying vein.

The rostral area of the cerebellar aspect bears the *crista petrosa* and the petrosal contribution to the middle cranial fossa (Fig. 4.5–4.6). The former is smooth and wide and, hence, not well defined. There is a subtle bump on the *crista petrosa*, near the roof of the IAM, at the level of the separation between the latter and the subarcuate fossa (Fig. 4.5). Gabbert (2004) reports the presence of a tentorial ossification that runs from a similar position to that observed here for the previously mentioned bump. Such an ossification has been observed in other notoungulates (Martínez *et al.*, 2016, 2020; García-López & Cohen, 2021), but there is no sign of it in PVL 7568. The part of the middle cranial fossa is not concave (hence, there is no clear fossa for the trigeminal ganglion). Laterally, this area bears a small aperture, formed between the petrosal and a small preserved part of the alisphenoid, firmly attached to the former (Fig. 4.6). This aperture may be the *hiatus Fallopii*, for the greater petrosal nerve.

The ectotympanic bone (Fig. 4.5–4.8) forms the tympanic bulla, which is ventrally prominent in this case (in ventral view, the rostrocaudal length of the bulla equals 17.60 mm and the lateromedial length equals 22.45 mm; Fig. 4.8). The surface of the bulla is somewhat irregular, with several crests and bulges (Fig. 4.6–4.8); its wall seems to be very thick, and it is firmly attached to the surrounding preserved elements (petrosal, alisphenoid, and squamosal). There is a vertical ridge on the rostromedial corner of the bulla, which defines a roughly sharp edge (Fig. 4.8). Lateral to this ridge there is a vertical concavity, limited dorsally by a large gap between the ectotympanic and alisphenoid (Fig. 4.6). The aperture leads to the tympanic cavity and seems to be natural although possibly enlarged by breakage and loss of part of the ectotympanic. This may be interpreted as the exit for the Eustachian tube and other structures leaving the tympanic cavity. Laterally, the ectotympanic forms most of the tympanohyal recess (*vagina processus hyoidei*; housing the tympanohyal projection of the petrosal), which is a large and rounded aperture (Fig. 4.7–4.8). The tympanohyal recess is limited rostrally by the medial end of the *crista meatus* and medially and caudally by a horizontal crest of the ectotympanic, which laterally contacts the ventral tip of the retrotympanic process of the squamosal (Fig. 4.7–4.8). The tympanohyal recess also marks the medial end of a groove formed between the retrotympanic process of the squamosal and the external acoustic meatus of the ectotympanic. Near its midpoint, this groove contains the stylomastoid foramen (Fig. 4.7), the final exit of the facial nerve from the basicranium. This position is typical in notoungulates, given the presence of the large bulla and hypertrophied squamosal elements. The external acoustic meatus shows a ventral *crista meatus* (as it is usual for notoungulates). This structure is very strong in this specimen (Fig. 4.7–4.8), similar to that observed in Toxodontia in terms of length and arrangement (*e.g.*, *Coquenia* Deraco *et al.*, 2008; *Periphragnis* Roth, 1899; *Nesodon* Owen, 1847).

The preserved squamosal area in PVL 7568 includes part of the postglenoid process (Fig. 4.6–4.9), the retrotympanic process (Fig. 4.7–4.8), the roof of the external acoustic meatus, and the epitympanic sinus (Fig. 4.9), the latter being opened dorsally due to breakage. Only the medial half of the postglenoid process is present, being low and not particularly prominent (considerably smaller than the retrotympanic process) as in toxodontids. The lateral area of the postglenoid process is absent; however, there is a depression (probably housing a foramen) and a notch on the medial side of the squamosal, near the rostrolateral wall of the tympanic bulla (Fig. 4.7–4.8). The nature of the depression remains unclear. As for the notch, this is probably part of the Glaserian fissure, since the squamosal contributes to the lateral wall of this aperture, as in other notoungulates (Patterson, 1936; Gabbert, 2004; Billet *et al.*, 2008, 2009; García-López, 2011; García-López *et al.*, 2018). The base of the postglenoid process is pressed against the *crista meatus*, following the same slope (Fig. 4.7–4.8). Caudally, the retrotympanic process is considerably larger than the postglenoid process, although more rostrocaudally compressed. The retrotympanic process is pressed against the *crista meatus*; however, both structures are separated, leaving a groove (Fig. 4.5) where the stylomastoid foramen (lateral) and the tympanohyal recess (medial) are present. The caudal wall of the retrotympanic process is flattened (Fig. 4.8) and was probably pressed against the jugular process (= paraoccipital process) of the exoccipital, which is not preserved in PVL 7568. This flat surface shows some grooves and a foramen, which is difficult to assess given the lack of the surrounding elements. Finally, the inner surface of the epitympanic sinus is exposed dorsolaterally (it is usually covered in notoungulates by the epitympanic theca of the squamosal; see MacPhee, 2014). This surface is smooth and (at least the preserved part) surrounds the external auditory meatus dorsally (Fig. 4.9). An aperture is clearly visible, located dorsal to the medial end of the auditory meatus (and hence, dorsal to the *crista tympanica* of the ectotympanic). This aperture is the *aditus* of the epitympanic sinus (also called *foramen pneumaticum*; see MacPhee, 2014), which marks the connection between the sinus and the proper tympanic cavity.

Comparisons. Although this specimen is not associated with dental remains, its features point indisputably to the identification of PVL 7568 as a Notoungulata. The presence of an elongated osseous external auditory meatus, well-developed *crista meatus*, and hypertrophied epitympanic sinus are common characters to most notoungulates, particularly Neogene representatives. As for its affinities at a family level, the scenario is somewhat more problematic. Towards the end of the Miocene, only hegetotheriids, interatheriids, mesotheriids, and toxodontids are documented for outcrops of NWA (Esteban *et al.*, 2017; Zimicz *et al.*, 2018; Armella & Bonini, 2020). Of these, the first three present a different general arrangement. Hegetotheriids and interatheriids are generally smaller than mesotheriids and toxodontids, and the studied basicranial fragment is too large to correspond to one of those groups in this context. Besides this, in the case of hegetotheriids, hegetotheriines show a vestigial *crista meatus*, and pachyrukhines have long but more gracile structures, in addition to a very globose and smooth tympanic bulla and epitympanic theca. Interatheriids also have a more inflated bulla, in addition to cancellous bone on the wall of this structure and lesser development of the *crista meatus* and retrotympanic process. Mesotheriids, in turn, display some similarities with PVL 7568, such as the length of the *crista meatus*, the relatively smaller postglenoid process, and the large retrotympanic process (*e.g.*, *Pseudotypotherium* Ameghino, 1904, PVL 2764, MACN-PV 2925). Nevertheless, the heavily crested surface of the tympanic bulla, the prominent rostral edge of the tympanohyal recess, and the more vertical arrangement of the former structures distinguish the morphology of this family from the material here studied. Moreover, the petrosal morphology is also different, considering published data on the specimen MNHN-BOL-V 006906 (tentatively assigned to *Trachytherus* Ameghino, 1889; see Billet *et al.*, 2008). In that specimen, the cerebellar surface shows several differences, such as the rounded IAM, a less developed epitympanic wing area, and a shallower subarcuate fossa with less defined edges.

However, when the morphology of the tympanohyal recess is evaluated, PVL 7568 shows a strong resemblance to typotherians. Billet (2011) established that most typotherians show a projection of the ectotympanic that forms the caudal edge of the tympanohyal recess, which is formed by the jugular process (exoccipital) in other notoungulates. Hence, the presence of the former condition in PVL 7568 may favor affinities with Typotheria. Nevertheless, as the jugular process is not preserved, the true superficial condition of that part of the skull is hard to assess, since this element would have hidden the ectotympanic extension caudal to the tympanohyal recess in ventral view.

Finally, toxodontids usually show a long and robust *crista meatus* and a large retrotympanic process. Additionally, the surface of the bulla is more limited and relatively smoother than in mesotheriids (although more irregular than in hegetotheriids and interatheriids), and the tympanohyal process and stylomastoid foramen are arranged in a groove between the *crista meatus* and the retrotympanic process. In this sense, the morphology observed in PVL 7568 matches with this general arrangement. Additionally, the cerebellar side of the petrosal resembles that of the specimen FMNH 13110 (*Adinotherium ovinum* Owen, 1853; see Gabbert, 2004) regarding the close position of the subarcuate fossa and IAM, the subtriangular outline of the latter, and the development of the epitympanic wing area. Given this evidence, we consider that this basicranial fragment corresponds to a Toxodontidae indet. Unfortunately, a more accurate identification rests on the availability of more comprehensive surveys focused on cranial features of

Notoungulata, which are currently limited to some groups (particularly when the auditory region is considered).

TYPOTHERIA Zittel, 1892
MESOTHERIIDAE Alston, 1876
MESOTHERIINAE Simpson, 1945

Mesotheriinae indet.
Figure 5.1–5.2

Referred material. PVL 4655, left upper premolar fragment.
Locality and horizon. India Muerta Formation, Ruta Nacional 9, near the bridge to El Cadillal locality, Tafí Viejo Department, Tucumán Province, Argentina (Figs. 1 and 2). Late Miocene (Tortonian).
Description. Initially, PVL 4655 was cataloged (original inventory book in the PVL) as an incisor fragment belonging to a Rodentia indet. However, after cleaning and preparation, we noticed that PVL 4655 is in fact a buccal wall of a left upper postcanine tooth, whose morphology resembles the cheek teeth of Mesotheriidae (Fig. 5.1). PVL 4655 presents a conspicuous parastyle column, differentiated from the ectoloph by a marked sulcus that extends along the crown (Fig. 5.1–5.2). Overall, the ectoloph (mesiodistal length = 11.38 mm) is convex but it shows slight undulations.
Comparisons. The conspicuous parastyle column is more often observed in premolars than molars of mesotheriines, such as *Typotheriopsis chasicoensis* Cabrera & Kraglievich, 1931 (MLP 12-1666) (mesiodistal length of P3 = 10.46 mm, P4 = 11.55 mm), *Typotheriopsis silveyrai* Cabrera, 1937 (MLP 36-XI-10-2) (mesiodistal length of P3 = 8.25 mm, P4 = 9.48 mm), Mesotheriinae indet. (PVL 4817) (mesiodistal length of P3 = 10.98 mm, P4 = 11.52 mm), and *Eutypotherium superans* Ameghino, 1904 (MACN-A 1079) (mesiodistal length of P3 = 6.68 mm, P4 = 9.35 mm). Unfortunately, there are no additional features or remains to better define the taxonomy. Beyond that, the reassessment of PVL 4655 and its referral to Mesotheriinae represents the first record of this subfamily in this area.

HEGETOTHERIIDAE Ameghino, 1894
"HEGETOTHERIINAE" Ameghino, 1894

Hegetotheriinae is a paraphyletic assemblage according to the analysis by Seoane & Cerdeño (2019).

Hemihegetotherium Rovereto, 1914

Type species. *Hemihegetotherium achataleptum* Rovereto, 1914. Late Miocene, Mendoza, Catamarca, San Juan, and La Pampa provinces, Argentina (Cerdeño & Contreras, 2000; Cerdeño & Montalvo, 2002; Sostillo *et al.*, 2021).
Holotype. MACN-PV 8491, almost complete skull with right P4–M3 and left P2–M3, and left mandibular fragment with m1–3 (Rovereto, 1914).

Hemihegetotherium torresi (Cabrera & Kraglievich, 1931)
Figure 5.3–5.4; Table 3

Holotype. MLP 27-VIII-1-1, both maxillary fragments, incomplete mandible, and postcranial remains (Cabrera & Kraglievich, 1931).
Referred material. PVL 7567, left mandibular fragment with p2—m1 and part of the trigonid of m2.
Locality and horizon. India Muerta Formation, Ruta Nacional 9, near the bridge to El Cadillal locality, Tafí Viejo Department, Tucumán Province, Argentina (Figs. 1 and 2). Late Miocene (Tortonian).
Description. PVL 7567 is badly preserved with a clearly broken area in the mandibular ramus at the level of contact between p4 and m1 (Fig. 5.3–5.4). Tooth crowns are also broken, but intraalveolar outlines are preserved, allowing us to analyze the morphology.

The mandibular ramus is low, although it increases in height distally (Fig. 4.3). All teeth are bilobed due to the marked buccal fold and increase in dimensions distally (Fig. 4.4; Tab. 3). Overall, anterior lobes (trigonids) are slightly smaller than the posterior lobes (talonids). In p2, both lobes are triangular with acute buccal faces, and the lingual face of the trigonid presents a small concave area. Both p3 and p4 are molariform, trigonids present rounded mesial and buccal faces, talonids are markedly acute, and lingual faces are convex. The m1 closely resembles the p4 in size and morphology except for a slight concave area in the lingual face of the talonid, near the distolingual corner.
Comparisons. PVL 7567 is larger than Pachyrukhinae taxa and similar in size to hegetotheriines. It differs from

Hegetotherium Ameghino, 1887 (MACN-A 631, MACN-A 632, MACN-A 3336-37, MLP 12-1806) in having the distolingual corner of m1 not lingually projected, and from *Hegetotheriopsis* Kramarz & Paz, 2013 (MACN-PV CH2015, MACN-PV CH2014) by the presence of m1 without lingual inflection. Further, PVL 7567 differs from *Sallatherium* Reguero & Cerdeño, 2005 in having p3 with an anterior lobe shorter than the posterior one (Reguero & Cerdeño, 2005,

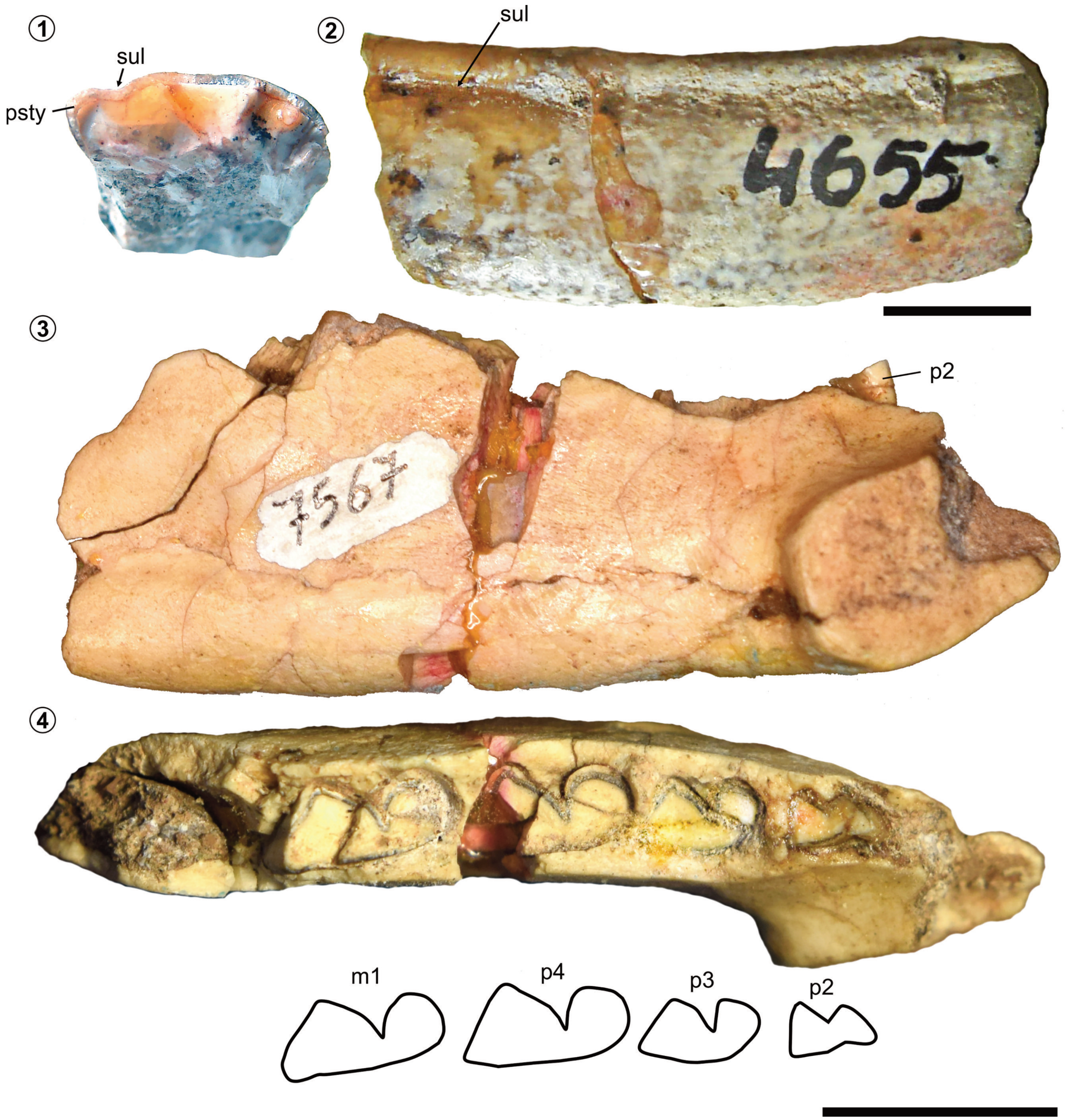

Figure 5. Mesotheriidae and Hegetotheriidae specimens from the India Muerta Formation, Late Miocene (Tafí Viejo Department, Tucumán Province, Argentina). **1–2,** Mesotheriinae indet. **PVL 4655**, left upper premolar fragment; **1,** occlusal view; and **2,** detail of a sulcus that extends along the crown. Scale= 5 mm. **3–4,** ***Hemihegetotherium torresi*** **PVL 7567**, left mandibular fragment with p2–m1; **3,** medial view; and **4,** occlusal view with a detail of tooth outlines. Abbreviations: **psty,** parastyle; **sul,** sulcus. Scale= 10 mm.

TABLE 3 – Dimensions (in mm) of lower postcanine teeth of PVL 7567, identified as *Hemihegetotherium torresi*, and other *Hemihegetotherium* species.

Specimen	p2		p3		p4		m1		m2		m3		p2/3 relative length (%)
	L	W	L	W	L	W	L	W	L	W	L	W	
PVL 7567	4.34	2.62	5.52	3.27	7.92	4.14	7.97	3.94					78.62
H. tantillum													
LIEB-PV 7181*	4.30	2.70	5.80	3.40	6.20	3.50	7.40	3.60	7.20	3.60			74.13
LIEB-PV 7144	5.10	3.50	7.10	4.00	7.40	4.60			8.50	4.70	10.60	4.10	71.83
LIEB-PV 7101					7.20	4.20	7.40	4.30	7.60	4.10	9.80	3.90	
LIEB-PV 5246			5.90	3.70	7.30	4.30							
Mean	4.70	3.10	6.27	3.70	7.03	4.15	7.40	3.95	7.77	4.13	10.20	4.00	
Min	4.30	2.70	5.80	3.40	6.20	3.50	7.40	3.60	7.20	3.60	9.80	3.90	
Max	5.10	3.50	7.10	4.00	7.40	4.60	7.40	4.30	8.50	4.70	10.60	4.10	
H. trilobus													
MNHN-BOL-V 003671 (l)*	5.20	3.70	7.10	4.80	8.80	5.50	8.90	5.40	9.40	5.60	12.00	5.00	73.23
MNHN-BOL-V 003671 (r)*	5.50	4.00	7.30	5.00	8.70	5.70	8.90	5.50	9.00	5.50	12.20	4.90	75.34
MNHN-BOL-V 003650	5.30	3.60	6.40	4.40	7.60	4.70	8.10	5.40	8.20	5.00	11.00	4.30	82.81
MNHN-BOL-V 006387			8.00	4.80	8.30	5.00	8.70	5.10	8.60				
MNHN-BOL-V 006390					8.00	5.10	8.00	5.00	8.60	5.30	10.90	4.50	
Mean	5.33	3.77	7.20	4.75	8.28	5.20	8.52	5.28	8.76	5.35	11.53	4.68	
Min	5.20	3.60	6.40	4.40	7.60	4.70	8.00	5.00	8.20	5.00	10.90	4.30	
Max	5.50	4.00	8.00	5.00	8.80	5.70	8.90	5.50	9.40	5.60	12.20	5.00	
H. achataleptum													
MLP 31-XI -12-6	5.14	3.09	12.66	7.27	12.90	7.62	13.85	7.70					40.60
MLP 70-IV-30-2					8.26	4.59	8.85	5.06					
MACN-PV 8156	4.54	3.07	8.42	5.07	9.14	5.15	8.93	4.74	9.55	4.29			53.91
MACN-PV 8491*							12.85	7.08	13.19	7.56	15.98	6.42	
MLP 36-XI-10-1 (r)	5.00	2.70	11.90	7.00	13.00	7.30	12.40	6.50	12.70	6.70			42.01
MLP 36-XI-10-1 (l)			11.40	6.30	11.40	6.50	12.00	7.00	12.70	6.60			
GHUNLPam 5675	5.10	2.80	9.00	5.50	9.30	5.30	11.00	5.40	10.90	5.60			56.66
GHUNLPam 14095			9.13	5.07	9.27	5.59	9.90	5.45	10.20	5.30	11.00	5.03	
Mean	4.95	2.92	10.42	6.04	10.47	6.01	11.22	6.12	11.54	6.01	13.49	5.73	
Min	4.54	2.70	8.42	5.07	8.26	4.59	8.85	4.74	9.55	4.29	11.00	5.03	
Max	5.14	3.09	12.66	7.27	13.00	7.62	13.85	7.70	13.19	7.56	15.98	6.42	
H. torresi													
MLP 27-VIII-1-1*	3.04	1.95	6.04	3.64	6.23	4.63	6.99	3.99	7.77	3.89	9.18	3.84	50.33
GHUNLPam 8045					8.00	4.00	8.20	4.80					
GHUNLPam 5307							7.87	3.94					
Mean	3.04	1.95	6.04	3.64	7.12	4.32	7.69	4.24					
Min	3.04	1.95	6.04	3.64	6.23	4.00	6.99	3.94	7.77	3.89	9.18	3.84	
Max	3.04	1.95	6.04	3.64	8.00	4.63	8.20	4.80	7.77	3.89	9.18	3.84	

Abbreviations: L, length; l, left; Max, maximum; Min, minimum; r, right; W, width; *, holotypes. Measurements of *H. tantillum* from Vera (2019), *H. trilobus* from Croft & Anaya (2006), and *H. achataleptum* and *H. torresi* from Cerdeño & Montalvo (2002), Armella (2019), and Sostillo *et al.* (2021).

fig. 2) and from *Prohegetotherium* Ameghino, 1897 (MACN-PV 16609; Cerdeño & Reguero, 2015, fig. 5) in having sharp talonid corners of p2–m1 and p3 without a lingual concavity or sulcus. PVL 7567 is similar to *Hemihegetotherium* (MACN-PV 8491, MACN-PV 8156, MLP 31-XI-12-6, MLP 70-IV-30-2, MLP 76-VI-12-93, and MLP 76-VI-12-22) in having p3–m1 with convex lingual faces, presence of p2 notably smaller than p3, and straight distal faces of p2–m1.

So far, *Hemihegetotherium* is known by four species mainly differentiated by size: *Hemihegetotherium trilobus* Croft & Anaya, 2006 and *Hemihegetotherium tantillum* Vera, 2019 from the Middle Miocene of Bolivia and Middle to Late Miocene of Argentina, respectively, and *H. torresi* and *H. achataleptum* (*e.g.*, Cerdeño & Contreras, 2000; Cerdeño & Montalvo, 2002; Armella, 2019; Sostillo *et al.*, 2021) from the Late Miocene of Argentina. In this context, PVL 7567 differs from *H. tantillum* (Vera, 2019, fig. 4) in having p2 with a distal face straight rather than concave, trigonid of p3–m1 buccally rounded, shorter trigonid than talonid in p3, and m1 without mesial narrow expansion in the trigonid and distolingual expansion in the talonid. *Hemihegetotherium trilobus* is mainly characterized by the presence of a sharply trilobed m3 (a feature shared with *H. tantillum*) and a proportionately larger p2 (p2 length < 67% p3 length in *H. torresi* and *H. achataleptum*, > 73% p3 length in *H. trilobus*; Croft & Anaya, 2006). Unfortunately, the m3 is not preserved in PVL 7567; however, we noticed that its p2 is proportionately large (78.62%). Moreover, in the process of comparing p2 proportions among *Hemihegetotherium* species (Tab. 3), we discovered that both *H. trilobus* and *H. tantillium* also share this condition (*i.e.*, proportionately larger p2, > 73% p3 length; not discussed by Vera, 2019). Finally, Late Miocene *Hemihegetotherium* taxa are mainly distinguished by their size: *H. torresi* is smaller than *H. achataleptum*. In this sense, PVL 7567 is considerably smaller (based on p4 and m1 dimensions) than *H. achataleptum* and similar in size to *H. torresi* (Fig. 6; Tab. 3). Furthermore, the scatterplots of p4 and m1 show that the dimensions of PVL 7567 are closer to *H. torresi* and *H. tantillum* than to *H. trilobus* and *H. achataleptum* specimens (Fig. 6). On this basis and considering the inferred age of fossil levels of the India Muerta Formation, we assign PVL 7567 to *H. torresi*. Beyond that, it is important to note that there is a clear overlapping among the dimensions of all taxa, except a few *H. achataleptum* specimens that are particularly large, a fact that highlights that this feature needs to be reconsidered as a dimorphic or intraspecific trait rather than diagnostic.

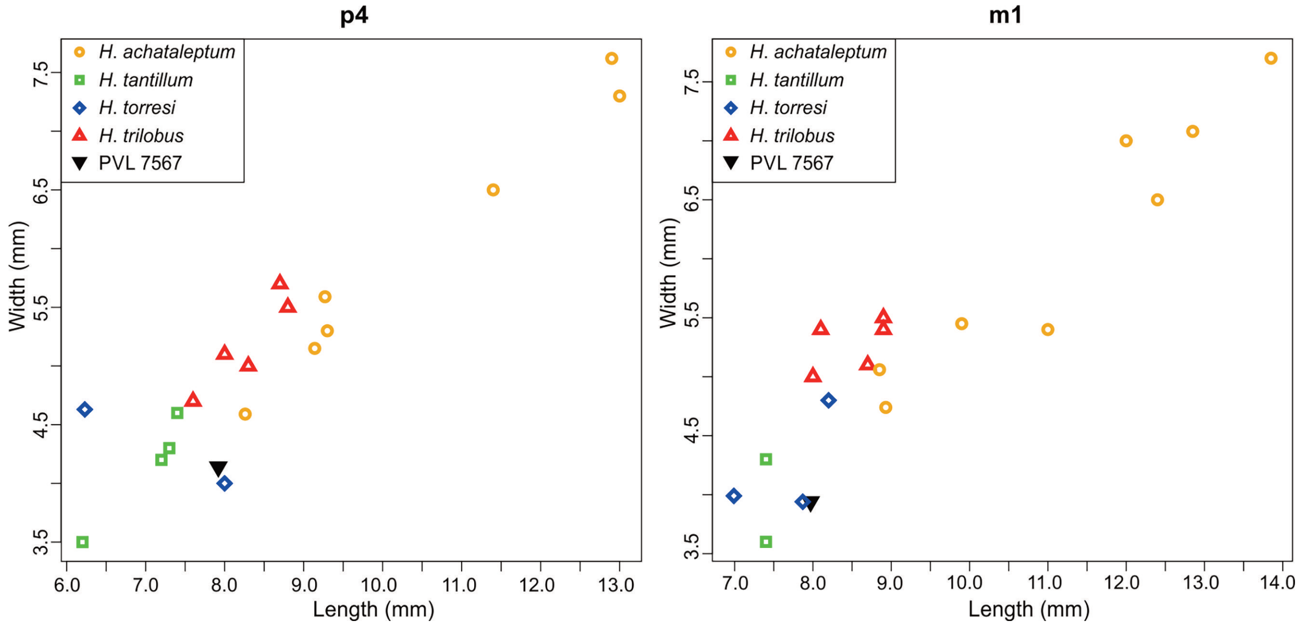

Figure 6. Scatter plot (length *vs.* width) of p4 (left) and m1 (right) of specimens of ***Hemihegetotherium*** (colored by species) and **PVL 7567**. See Table 3 for specimen catalog numbers and measurements.

PACHYRUKHINAE Lydekker, 1894

Paedotherium Burmeister, 1888

Type species. *Paedotherium insigne* (*P. bonaerense*) Burmeister, 1888. Late Miocene to Early Pleistocene, Buenos Aires, La Pampa, and Córdoba provinces, Argentina.

Holotype. MACN-A 1184, palatal fragment with incisors and two rows of cheek-teeth (Cerdeño & Bond, 1998).

Paedotherium sp. indet. A

Figure 7.1–7.4; Table 4

Referred material. PVL 7558, left mandibular fragment with p4-m1.

Locality and horizon. India Muerta Formation, Ruta Nacional 9, near the bridge to El Cadillal locality, Tafí Viejo Department, Tucumán Province, Argentina (Figs. 1 and 2). Late Miocene (Tortonian).

Description. In this mandibular fragment, p4 and m1 present a deep buccal groove, hence, both teeth are bilobed (Fig. 7.1). The anterior lobes are buccolingually narrower than the posterior ones. Lingual faces are slightly convex.

Comparison. The bilobed and molar-like premolar of PVL 7558 represents a difference with respect to *Tremacyllus* Ameghino, 1891, the other Pachyrukhinae genus recorded in the Late Miocene of NWA. In turn, among *Paedotherium* species, a molar-like p4 is present in *P. bonaerense* and *Paedotherium minor* Cabrera, 1937 but is not observed in *Paedotherium typicum* (Ameghino, 1887). According to dental dimensions (Tab. 4), while PVL 7558 is in the size range of *P. bonaerense* and *P. minor*, it is closer to the *P. bonaerense* average (see Cerdeño & Bond, 1998, tabs. 5 and 6). However, the lack of more acute diagnostic information precludes more taxonomic details.

Paedotherium sp. indet. B

Figure 7.1–7.4; Table 4

Referred material. PVL 7565, left maxillary fragment with DP1–4.

Locality and horizon. India Muerta Formation, Ruta Nacional 9, near the bridge to El Cadillal locality, Tafí Viejo Department, Tucumán Province, Argentina (Figs. 1 and 2). Late Miocene (Tortonian).

Description. This specimen is well preserved (Fig. 7.2–7.3). It shows a conspicuous diastema, suggesting the absence of a canine. As for the rest of dental pieces, they represent the deciduous dentition, with DP1–4 (see comparisons below). Tooth size increases distally, and each tooth presents a broad layer of cement, mostly on the lingual face (Fig. 7.3; Tab. 4). Enamel fully covers the buccal face and partially covers the mesial and lingual faces, while the paracone and distal faces are devoid of enamel. The occlusal surfaces of DP1–4 present a remnant of a median enamel fossette, which is visible as a small fossette located at the level of the protocone in DP1–2, and as a longitudinal enamel band buccally located in DP3 and still barely visible in DP4 (Fig. 7.3). DP1–3 are imbricated and approximate isosceles triangles in outline, with two long sides (buccal and lingual) and a shorter base (distal) with rounded corners. Ectolophs are convex with a shallow concave area near the distobuccal edge. The lingual faces of DP1 and DP2 present mesiolingual and distolingual concave areas. The latter form a shallow groove in DP2 and DP3 (Fig. 7.3). DP3 presents a more convex lingual face than DP1 and DP2. Distal faces are straight. DP4 is quadrangular with rounded edges, except in the parastyle and metastyle (acute edges). Although the ectoloph and the distal face of DP4 resemble the morphology of DP1–3, the mesial and lingual faces are well-distinguished, and both are convex without grooves. In lateral and occlusal views, the P4 can be seen below the deciduous tooth. The buccal and distal faces of P4 are similar to those of DP4 (Fig. 7.3–7.4). Lingual and mesial faces are not visible.

Comparisons. The presence of a conspicuous diastema suggests the absence of the canine and thus, affinities with Late Miocene pachyrukhines. Among these forms, genus *Tremacyllus* is characterized by the presence of large post-incisor grooves, which are absent in PVL 7565, allowing its identification as a representative of the genus *Paedotherium*.

The preserved teeth of this specimen were initially interpreted as P2–M1 (see Alonso, 2018), matching the upper dental formula of Pachyrukhinae (1-0-3-3; Cerdeño & Bond, 1998). Moreover, the low degree of molarization of premolars and presence of lingual grooves on them were the basis for referring PVL 7565 to *Paedotherium* cf. *P. minor* (Alonso, 2018). However, after cleaning and preparation, we

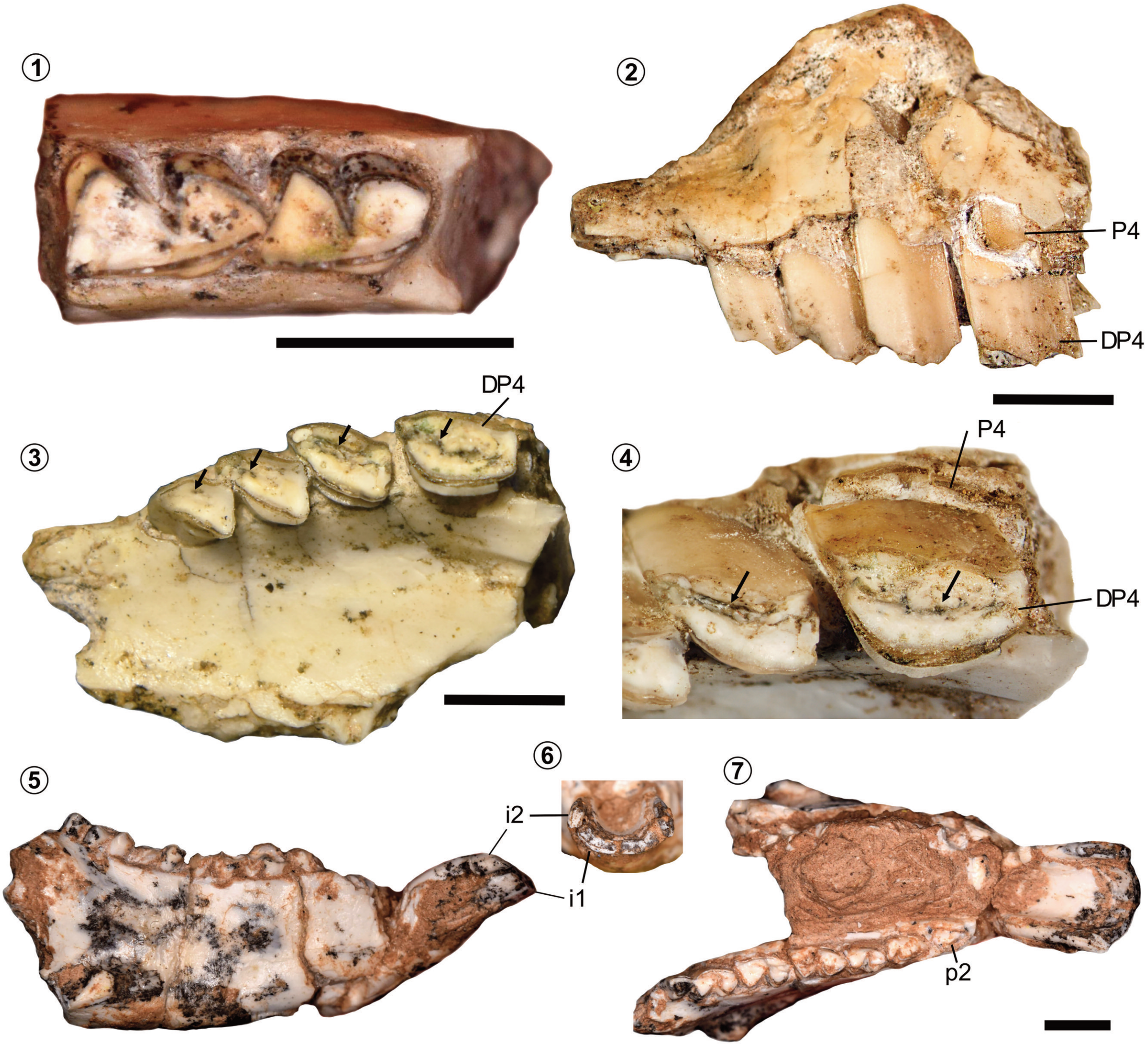

Figure 7. Hegetotheriidae, Pachyrukhinae specimens from the India Muerta Formation, Late Miocene (Tafí Viejo Department, Tucumán Province, Argentina). **1,** ***Paedotherium*** sp. indet. A, **PVL 7558**, left mandibular fragment with p4–m1 in occlusal view. **2–4,** ***Paedotherium*** sp. indet. B, **PVL 7565**, left maxillary fragment with DP1–4; **2,** lateral; and **3,** occlusal views; **4,** a detail of **PVL 7565** in oblique (slightly lateral) occlusal view showing P4 below DP4 (no scale). Arrows indicate remnants of enamel fossettes. **5–7,** ***Tremacyllus incipiens***, **PVL 7559**, mandibular body with complete right dentition (2-0-3-3); **5,** lateral view; **6,** occlusal view of incisors; and **7,** cheek teeth. Scales= 5 mm.

noted a tooth below the supposed M1, which led us to reconsider the dental loci represented. Cerdeño *et al.* (2016) studied a large sample of juvenile remains of *Paedotherium* and *Tremacyllus* from La Pampa Province (Argentina) and recognized several ontogenetic stages according to the degree of wear and the replaced deciduous teeth. Taking this information into account, we now consider that the tooth below the last dental piece of PVL 7565 represents a DP4, given that a deciduous cheek tooth is positioned over the apex of the corresponding permanent tooth (*i.e.*, P4 in the specimen of the India Muerta Formation). Cerdeño *et al.* (2016) also inferred a distal to mesial direction of tooth replacement for *Paedotherium* specimens; therefore, we consider the anterior teeth of PVL 7565 to represent DP1–DP3. This is supported by the occlusal morphologies of these teeth, which show fossettes (see description above).

TABLE 4 – Dimensions (in mm) of *Paedotherium* indet. PVL 7565 and PVL 7558 and *Tremacyllus incipiens* PVL 7559.

Specimen	DP1		DP2		DP3		DP4									
	L	W	L	W	L	W	L	W								
PVL 7565	3.23	2.85	3.89	3.44	4.28	3.12	4.76	3.62								
	i1		i2		p2		p3		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
PVL 7558	-	-	-	-	-	-	-	-	4.18	2.83	4.88	2.97				
PVL 7559	4.31	1.28	2.01	1.48	2.29*	1.06*	2.56	1.89	3.54	2.29	4.25	2.44	4.21	2.73	5.23	2.28

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

Hence, based on the presence of deciduous teeth, immature trabecular bone (see Cerdeño *et al.*, 2016), and permanent P4 visible below the DP4, we can confirm that PVL 7565 represents a young individual. In this context, this specimen is remarkable for the presence of DP1, which is an uncommon condition among Pachyrukhinae taxa.

The presence of four premolars in PVL 7565 is shared with hegetotheriines and Deseadan Pachyrukhinae taxa (such as *Propachyrucos* Ameghino, 1897 and *Prosotherium* Ameghino, 1897). However, a large diastema without signs of a canine, small size (Tab. 4), and the morphology of DP4/P4 of PVL 7565 allow us to discard its affinities with hegetotheriines or Deseadan Pachyrukhinae. The development of an extra tooth has not been recorded hitherto among post-Deseadan pachyrukhines, but it has been observed in other typotherian notoungulates, such as Mesotheriidae taxa (Francis, 1960; Cerdeño & Schmidt, 2013), even in sub-adult and adult individuals. In this context, we maintain the identification of PVL 7565 as a representative of the genus *Paedotherium* but modify its assignment to *Paedotherium* sp. Hence, this is an individual placed between the second and third ontogenetic stage established for upper dentitions of that genus (*sensu* Cerdeño *et al.*, 2016) and represents the first record of an extra deciduous tooth for *Paedotherium*. Reviewing more samples is still necessary to deepen the knowledge of these developmental patterns.

Tremacyllus Ameghino, 1891

Type species. *Pachyrukhos impressus* (Ameghino, 1888). Late Miocene–Late Pliocene, Mendoza, Buenos Aires, La Pampa, San Luis, and Córdoba provinces, Argentina (Cerdeño & Bond, 1998; Sostillo *et al.*, 2018; Armella *et al.*, 2022).

Tremacyllus incipiens Rovereto, 1914

Figure 7.5–7.7; Table 4

Holotype. MACN-PV 8163, articulated skull (Rovereto, 1914).

Referred material. PVL 7559, mandibular body with complete right dentition (2-0-3-3) and left i1–2 and p2.

Locality and horizon. India Muerta Formation, outcrops along Vipos River, Tafí Viejo Department, Tucumán Province, Argentina (Figs. 1 and 2). Late Miocene (Tortonian).

Description. PVL 7559 is relatively well preserved, and the crowns of all teeth are present except p2 (Fig. 7.5–7.7). Tooth wear and the eruption stage of m3 indicate that PVL 7559 represents an adult individual.

In lateral view, i1–2 are procumbent (Fig. 7.5). The first incisor is buccolingually flattened, convex, and mesiodistally longer than i2 (Tab. 4). The second incisor is elliptical and presents a marked curvature in lateral view, convex to the occlusal plane (Fig. 7.6). Premolars are bilobed (due to a conspicuous buccal groove), imbricated, and increase in size distally (Fig. 7.7). The anterior lobes are slightly smaller than the posterior lobes, except in p3, and show more rounded buccal edges than the posterior ones. Lingual faces are convex. The p4 is slightly molarized, and it presents a rounded mesial face compared to m1. Both m1 and m2 are similar, slightly imbricated, and resemble the premolar morphology, but m2 has a slight concavity near the disto-lingual corner (Fig. 7.7). By contrast, m3 is trilobed, with the two more anterior lobes similar to that of m2, and the third lobe is a seemingly more isolated structure, given the presence of a strong lingual groove. Also, the third lobe of the m3 has a shallow groove on its distal face (Fig. 7.7).

Comparisons. PVL 7559 presents a general morphology and a dental formula typical of Late Miocene Pachyrukhinae. Also, it presents imbricated premolars, the p4 is slightly molarized, and the general size is more similar to *Tremacyllus* rather than *Paedotherium*. To date, two species are recognized in this genus: *Tremacyllus impressus* (Ameghino, 1888) and *T. incipiens* (Cerdeño & Bond, 1998; but see Sostillo *et al.*, 2018). Recently, Armella (2022) and Armella *et al.* (2022) studied a large *Tremacyllus* sample, where tooth sizes and P4 and upper premolars morphology were proposed as diagnostic traits to distinguish both taxa. Although PVL 7559 does not preserve the upper dentition, the large sizes of p4–m2 (see Armella, 2022) agree with the dimensions of *T. incipiens* (13.07–15.08% larger than *T. impressus*). In turn, the most conspicuous feature is the posterior lobe of p4, which is mesiodistally longer and less acute in PVL 7559 compared to specimens referred to *T. impressus* (*e.g.*, MACN-A 10277, MACN-PV 2434, MACN-A 1672-73). On these bases, we refer the specimen of the India Muerta Formation to *T. incipiens*.

Pachyrukhinae indet.
Figure 8.1–8.5

Referred material. PVL 7566, left astragalus.

Locality and horizon. India Muerta Formation, Ruta Nacional 9, near the bridge to El Cadillal locality, Tafí Viejo Department, Tucumán Province, Argentina (Figs. 1 and 2). Late Miocene (Tortonian).

Description. The astragalus is almost complete but shows superficial abrasion marks evidenced by well-rounded edges. Also, there is a breakage at the level of the dorsal astragalar foramen (see below). In dorsal view, the tibial trochlea is excavated and asymmetric, with the lateral crest more developed than the medial one (Fig. 8.1). The trochlear concavity leads anteriorly to a deep trochlear fossa, which is smooth and bounded by the anterior end of the lateral trochlear crest. The astragalar neck is shorter than the astragalar body, representing almost 24% of the total length of the astragalus (Tab. 4). It is slightly tilted, causing the medial displacement of the astragalar head. The oblique dorsal crest (nuchal crest) is robust, sigmoid, posterolaterally-anteromedially oriented, and occupies the entire surface of the neck (Fig. 8.1). The astragalar head is spherical, wider than the neck, and a shallow groove surrounding the head allows the distinction of both structures (Fig. 8.1). The navicular facet occupies the entire anterior surface of the astragalar head and extends onto the medial surface (Fig. 8.2).

In plantar view, the astragalus shows eroded edges around the tibial trochlear region; nevertheless, the articular facets are well-preserved (Fig. 8.2). The ectal facet is pear-shaped, with the major axis anteroposteriorly oriented. It is represented by a relatively deep concavity that is laterally extended (forming a lateral process), which is facing mainly the plantar aspect (Fig. 8.2). In contrast, the sustentacular facet is convex, oval, and occupies the plantar surface of the astragalar neck. This facet exhibits well-defined edges, without contacting the navicular facet due to the presence of a deep and broad sulcus between them (Fig. 8.2). The interarticular sulcus is deep, broad, and anterolateral-posteromedially oriented. In its posterior area, the inferior astragalar foramen is circular and large, and it opens plantarly (Fig. 8.2). The edges of the superior astragalar foramen, mainly dorsal, are broken, but it seems to open posteriorly (Fig. 8.3). It is connected with the inferior astragalar foramen. On the medial area, the astragalar medial plantar tuberosity (medial protuberance in Cifelli, 1993; medial process in Shockey & Flynn, 2007; tibial protuberance in Vera, 2012) is eroded but seems to be quite small, not connected with the navicular facet (Fig. 8.2–8.3).

In medial view, the facet for the medial malleolus of the tibia is smooth and larger than the astragalar medial plantar tuberosity (Fig. 8.4). The attachment for the tibioastragalar ligament is located between both structures, being a shallow depressed area. In lateral view, the fibular facet is flat, crescent-like (with a blunter posterior end), and well-projected laterally (Fig. 8.5). The attachment for the fibuloastragalar ligament is a deep and conscripted oval-shaped depression with the major axis anteroposteriorly oriented.

Comparisons. The presence of an astragalar neck that is constricted and well differentiated from the head and the body, the oblique dorsal crest, the astragalar medial plantar tuberosity (*sensu* Cifelli, 1983, 1993), the medially extended navicular facet (*sensu* Bergqvist, 1996), and the steeply inclined ectal facet of the astragalus (Shockey *et al.*, 2012), results in the identification of PVL 7566 as a notoungulate. In turn, the size and general morphology of PVL 7566 (*e.g.*, spherical astragalar head, lateral process well-developed, astragalar neck length and orientation) lead us to include it within Hegetotheriidae, Pachyrukhinae (see Kraglievich, 1926 and Vera & Ercoli, 2018). Among pachyrukhine astragali diversity, PVL 4566 shares several features with *Paedotherium* species (*e.g.*, *P. bonaerense* MACN-PV 6436; *P. typicum* MLP 52-IX-30-43, and *Paedotherium* sp. MLP 12-1791; Fig. 8.6–8.8), such as spherical to hemispherical astragalar head medially displaced, medial extension of the navicular facet, asymmetric trochlea, parallel lateral and medial crests, trochlear fossa well-marked, sigmoid oblique crest, lateral process well-developed, small astragalar medial plantar tuberosity circumscribed to the posterior area, wide and deep interarticular sulcus, and sustentacular facet on neck surface without contacting navicular facet. In turn, there are differences between the specimen from the

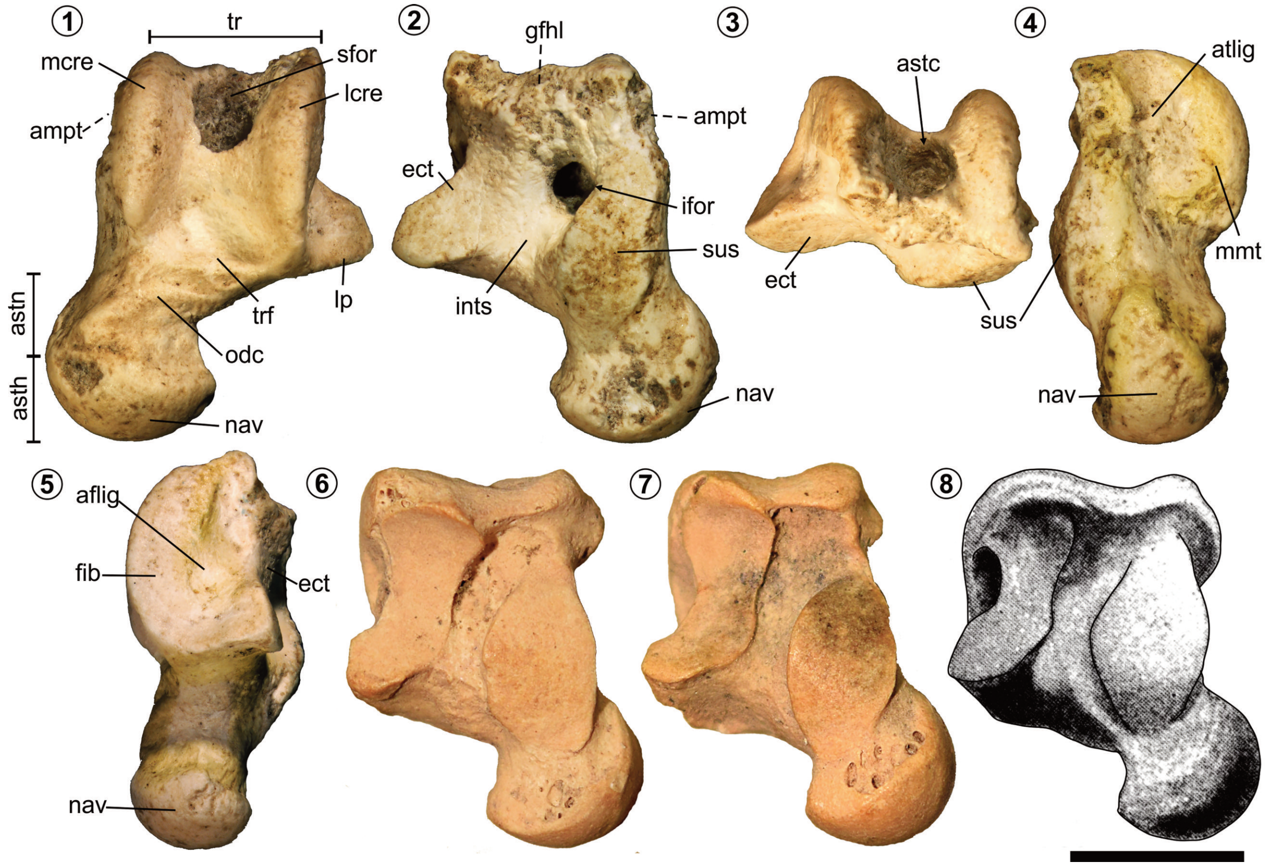

Figure 8. 1–5, Left astragalus bone of Pachyrukhinae indet. **PVL 7566** from the India Muerta Formation, Late Miocene (Tafí Viejo Department, Tucumán Province, Argentina); **1,** dorsal; **2,** plantar; **3,** proximal; **4,** medial; and **5,** lateral views. **6,** ***Paedotherium*** sp. **MLP 12-1791**, right astragalus in plantar view (reversed). **7,** ***Paedotherium typicum*** **MLP 52-IX-30**, right astragalus in plantar view (reversed). **8,** ***Paedotherium bonaerense*** **MACN-PV 6436**, left astragalus in plantar view (from Kraglievich, 1926, pl. VII). Abbreviations. **aflig,** attachment for the fibuloastragalar ligament; **ampt**; astragalar medial plantar tuberosity; **astc,** astragalar canal; **asth,** astragalar head; **astn,** astragalar neck; **atlig,** attachment for the tibioastragalar ligament; **ect,** ectal facet; **fib,** fibular facet; **gfhl,** groove for the tendon of the flexor hallucis longus muscle; **ifor,** inferior astragalar foramen; **ints,** interarticular sulcus; **lcre,** lateral crest; **lp,** lateral process; **mcre,** medial crest; **mmt,** facet for the medial malleolus of the tibia; **nav,** navicular facet; **odc,** oblique dorsal crest (nuchal crest or tibial stop); **sfor,** superior astragalar foramen; **sus,** sustentacular facet; **tr,** tibial trochlea; **trf,** trochlear fossa. Scale= 5 mm.

TABLE 5 – Updated faunal list of the India Muerta Formation, Late Miocene.

Taxa	Reference
ACTINOPTERYGII Klein, 1885	
SILURIFORMES Fink & Fink, 1996	
Siluriformes indet.	Alonso,2018
REPTILIA Laurenti, 1768	
TESTUDINES Linnaeus, 1768	
Testudines indet.	Powell & Ortiz (2014)
SERPENTES Linnaeus, 1958	
MACROSTOMATA Müller, 1831	
BOIDAE Gray, 1825	
Gaimanophis Albino, 1996	
Gaimanophis powelli Albino, 2017	Albino (2017)
CROCODYLIA Owen, 1842	
EUSUCHIA Hyxley, 1875	
Eusuchia indet.	Powell & Ortiz (2014)
MAMMALIA Linnaeus, 1758	
METATHERIA Huxley, 1880	
SPARASSODONTA Ameghino, 1894	
BORHYAENOIDEA Ameghino, 1894	
Stylocynus Mercerat, 1917	
aff. *Stylocynus* sp.	Babot & Ortiz (2008)
POLYDOLOPIMORPHIA Ameghino, 1897	
BONAPARTHERIIFORMES Goin & Candela, 2004	
ARGYROLAGIDAE Ameghino, 1904	
Microtragulus Ameghino, 1904	
Microtragulus sp. indet.	García-López & Babot (2015)
EUTHERIA Huxley, 1880	
XENARTHRA Cope,1889	
CINGULATA Illiger, 1811	
GLYPTODONTIDAE Gray, 1869	
PLOHOPLOHORINI Castellanos, 1932	
Cocinocercus Cabrera, 1939	
cf. *Cocinocercus* sp.	Powell & Ortiz (2014)
LOMAPHORINI Hoffstter, 1958	
Lomaphorus Ameghino, 1889	
Lomaphorus sp. indet.	Alonso (2018)
DASYPODIDAE Gray, 1821	
EUPHRACTINI Winge, 1923	
Paleuphractus Kraglievich, 1934	
? *Paleuphractus*	Alonso (2018)
RODENTIA Bowdich, 1821	
HYSTRICOGNATHI Tullberg, 1899	
CAVIIDAE Fischer de Waldheim, 1817	
DOLICHOTINAE Pocock, 1922	
Orthomyctera Rovereto, 1914	
Orthomyctera sp. indet.	Alonso (2018)
PANPERISSODACTYLA Welker *et al.*, 2015	
NOTOUNGULATA Roth, 1903	
TOXODONTIA Owen, 1853	
TOXODONTIDAE Gervais, 1847	
Toxodontidae indet.	This contribution
TOXODONTINAE Trouessart, 1898	
Ocnerotherium Pascual, 1954	
Ocnerotherium sp.	This contribution
TYPOTHERIA Zittel, 1892	
MESOTHERIIDAE Alston, 1876	
MESOTHERIINAE Simpson, 1945	
Mesotheriinae indet.	This contribution
HEGETOTHERIIDAE Ameghino, 1894	
“HEGETOTHERIINAE” Ameghino, 1894	
Hemihegetotherium Rovereto, 1914	
Hemihegetotherium torresi (Cabrera & Kraglievich, 1931)	This contribution
PACHYRUKHINAE Lydekker, 1894	
Pachyrukhinae indet.	
Paedotherium Burmeister, 1888	
Paedotherium sp. indet. A	
Paedotherium sp. indet. B	This contribution
Tremacyllus Ameghino, 1891	
Tremacyllus incipiens Rovereto, 1914	Alonso, 2018; this contribution

India Muerta Formation and *P. typicum* MLP 52-IX-30-43 and *Paedotherium* sp. MLP 12-1791 (Fig. 8.6–8.7): PVL 7566 has a wider trochlea, and the ectal facet is laterally well-extended and, as a result, the lateral process is more developed than in mentioned specimens. While these differences could be related to intra- or interspecific variation, the most singular feature of PVL 7566 is the presence of astragalar foramina (Fig. 8.1–8.5). These structures have been not observed in other pachyrukhines (Fig. 8.6–8.8) and are considered unusual among Neogene notoungulates (Shockey & Flynn, 2007). It is important to highlight that, although broken areas near the superior astragalar foramen could overestimate its development, the presence of smooth walls into the astragalar canal and the development of the inferior astragalar foramen support our interpretations of these uncommon structures. However, an anomalous condition should not be discarded for this individual. On these bases, we refer PVL 7566 to Pachyrukhinae indet. until more postcranial studies contribute to identifying more diagnostic traits.

DISCUSSION AND CONCLUSIONS

The fossil record of the India Muerta Formation comprises several vertebrate remains (Tab. 5); mammals represent most of the documented material including mainly xenarthrans (Glyptodontidae, Dasypodidae), metatherians (Borhyaenoidea, Argyrolagidae), rodents (Caviidae), and notoungulates (Powell *et al.*, 2012; Powell & Ortíz, 2014; García-López & Babot, 2015; Albino, 2017). This represents a remarkable diversity, especially considering the limited area of the outcrops compared to other highly fossiliferous units from NWA. Moreover, the paleoenvironments interpreted in this work (braided to meandering fluvial systems) agree with the habitats that would have been occupied by the general fauna, which also includes turtles, crocodilians, fishes, and snakes (Tab. 5).

Nevertheless, the age of the India Muerta Formation has been a matter of some debate, and there is a series of factors that preclude an accurate chronological assignment for it (*e.g.*, scattered outcrops not deeply correlated, vegetative cover that deteriorates and hides the outcrops, inaccurate stratigraphic control of the paleontological material, among others). Added to this, the fragmentary nature of most of the recovered fossils precludes, in certain cases, achieving a high taxonomic resolution. In this context, the study of this assemblage has resulted in sufficient knowledge to recognize that the notoungulates of the India Muerta Formation include taxa that are unusual for the region and/or display singular features.

Notwithstanding these issues, the taxa that are recognized allow us to gather pertinent information for biostratigraphic assessments. The presence of *Ocnerotherium* represents the first record of the genus in NWA. So far, Neogene toxodontids of the region mainly comprise specimens morphologically close to *Xotodon* Ameghino, 1887 and *Calchaquitherium* Nasif, Musalem, & Cerdeño, 2000, which mostly occur in western valleys (*e.g.*, Santa Maria and Villavil-Quillay valleys). In this sense, the record of *Ocnerotherium* constitutes a novel and relevant element since, although it does not allow an assignment at the specific level, the stratigraphic range of this genus is relatively restricted. It was originally defined as monotypic by Pascual (1954) based on the species *Ocnerotherium intermedium*, whose holotype (MLP 52-XI-17-1) was collected in Barrancas del Retama, Ayacucho Department, San Luis Province (Argentina), at levels known as "*Estratos de Los Llanos*", initially assigned to the Pliocene. Later, new fossils referred to *O. intermedium*, as well as other faunistic elements recorded in contemporary levels, were used as the basis for the establishment of the Chasicoan age, in which *Ocnerotherium* is a conspicuous member (*e.g.*, Pascual, 1965; Pascual *et al.*, 1996; Contreras & Baraldo, 2011). Currently, the Chasicoan age is mostly accepted as corresponding to the Tortonian (Late Miocene; Cione & Tonni, 2005; Zárate *et al.*, 2007). This scenario leads us to consider the record of *Ocnerotherium* as a relatively reliable element to infer the age of the fossiliferous levels of the India Muerta Formation. Nevertheless, a more recent record of this taxon should be mentioned: Linares (2004) documented *Ocnerotherium* remains in the Urumaco Formation (Venezuela) and suggested that they could represent a different species, but he did not provide anatomical details beyond the smaller size of the fossils. The fossiliferous levels of the Urumaco Formation were assigned by this author to the Huayquerian age, which would extend the temporal range of the genus. However, the lack of morphological detail prevents confirming the assignment provided by Linares (2004) and, therefore, precludes extending the biochron of *Ocnerotherium* with confidence. Based on this, we consider that the record of *Ocnerotherium* in the India Muerta Formation represents a relevant element to constrain the temporal range of the fossiliferous levels to the Tortonian.

Regarding other notoungulate finds, the scarce and fragmentary mesotheriid remains do not allow us to reach a taxonomic level lower than subfamily, which is not useful for biostratigraphic inferences in this case. Nevertheless, it is important to note that this occurrence represents the first report of Mesotheriidae in Neogene units cropping out in eastern areas of NWA. This is an interesting point given that findings of mesotheriids are relatively frequent in western outcrops of NWA (*e.g.*, Las Arcas, Chiquimil, and Andalhuala formations; Armella *et al.*, 2018), western and Pampean Neogene units of Argentina (*e.g.*, Huayquerías and Cerro Azul formations; Cerdeño, 2018), as well as in Miocene units of Bolivia (*e.g.*, Townsend & Croft, 2010).

The Hegetotheriidae are well represented in the India Muerta Formation by both hegetotheriines and pachyrukhines. Among hegetotheriines, *Hemihegetotherium torresi* (documented in the Late Miocene; see Cerdeño & Montalvo, 2002; Croft & Anaya, 2006; Vera, 2019; Sostillo *et al.*, 2021) allows us to constrain the temporal range of the fossil-bearing levels, indicating that these represent the earliest part of the Late Miocene (Tortonian). As for *Ocnerotherium*, the identification of this specimen as *H. torresi* represents the first record of this species in NWA.

Finally, regarding Pachyrukhinae, both *Paedotherium* and *Tremacyllus incipiens* have a wide temporal range that spans the Chasicoan through Marplatan (Early Pleistocene) ages (Cerdeño & Bond, 1998). Thus, the identification of these taxa in the India Muerta Formation is not useful for biostratigraphic inferences. In addition, *Paedotherium* and *T. incipiens* are widely recorded in Neogene outcrops of southwestern valleys of NWA (Esteban *et al.*, 2017; Armella *et al.*, 2022).

On the other hand, it should be noted that some unusual features are present in some Pachyrukhinae specimens recovered from the India Muerta Formation. PVL 7565 (*Paedotherium* sp. indet. B) retains a DP1, an additional tooth that has not been observed so far in other juvenile specimens of the genus. This constitutes a morphological particularity, interpreted here as related to intraspecific variation, although it cannot be completely discarded as a taxonomically significant trait. Another specimen, PVL 7566, an isolated astragalus identified as Pachyrukhinae indet., also presents particular features, such as the presence of the superior astragalar foramen. However, as mentioned previously, these are isolated cases within a small sample and may represent individual anomalies.

In summary, based on the Notoungulata fauna, the fossiliferous levels of the India Muerta Formation most likely correspond to the Late Miocene. While this is in concordance with previous contributions (*e.g.*, Powell & Ortiz, 2014; Albino, 2017), new data presented here favor a more precise age assignment to the early Late Miocene (Tortonian). Moreover, previous studies (*e.g.*, Bossi, 1969; Bossi *et al.*, 1998; Powell *et al.*, 2012; García-López & Babot, 2015) have correlated the India Muerta Formation—at least partially—with the Andalhuala Formation (cropping out in the western valleys of Catamarca and Tucumán provinces), given that this latter unit spans part of the Late Miocene–Early Pliocene interval (*ca.* 7.1 to 3.6 My; Georgieff *et al.*, 2017). This proposal is partially supported by the presence of *Paedotherium* and *Tremacyllus* but not by *H. torresi* and *Ocnerotherium*, whose affinities point to early forms present at higher latitudes. Consequently, the biochronological proposal derived from our study leads to a closer correlation between the India Muerta Formation and Las Arcas and Chiquimil formations (*ca.* 9.0 to 7.0 My), immediately underlying the Andalhuala Formation in western valleys. As the fossil assemblage here studied and the described sections are related to the upper part of the LIMS, these inferences are congruent with the U-Pb radioisotopic date of 8.43 ± 0.08 My (Tortonian) indicated by Zapata *et al.* (2019).

It is important to emphasize that the vertebrate fossil record of the India Muerta Formation includes a great diversity of taxa in addition to notoungulates (see Powell *et al.*, 2012; Powell & Ortiz, 2014; García-López & Babot, 2015; Albino, 2017; Tab. 5) and hence, further studies will probably contribute significantly to constraining the proposed temporal range and environmental background. Until then, the evidence yielded by the presence of these newly documented South American native ungulates stands as our most reliable basis for correlations with other units in the context of the radioisotopic dates.

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REFERENCES

Albino, A. M. (1996). Snakes from the Miocene of Patagonia (Argentina). Part I: The Booidea. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, *199*, 417–434.

Albino, A. (2017). A new species of *Gaimanophis* (Serpentes, Boidae) from the Miocene of northwestern Argentina with remarks on the Neogene boids of South America. *Comptes Rendus Palevol*, *16*(3), 278–283.

Alonso, G. E. (2018). *Bioestratigrafía y paleoambientes de la Formación India Muerta (Grupo Choromoro, Mioceno tardío?), provincia de Tucumán* [Unpublished Undergraduate Thesis]. Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán.

Ameghino, F. (1887). Enumeración sistemática de las especies de mamíferos fósiles coleccionados por Carlos Ameghino en los terrenos eocenos de Patagonia austral y depositados en el Museo de La Plata. *Boletín del Museo de La Plata*, *1*, 1–26.

Ameghino, F. (1887). Observaciones generales sobre el orden de mamíferos extinguidos sudamericanos llamados Toxodontes (Toxodontia) y sinopsis de los géneros y especies hasta ahora conocidos. *Obras Completas y Correspondencia Científica*, *5*, 355–431.

Ameghino, F. (1888). Lista de las especies de mamíferos fósiles del Mioceno superior de Monte Hermoso hasta ahora conocidas. *Obras Completas y Correspondencia Científica*, *5*, 481–496.

Ameghino, F. (1889). Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas de la Academia Nacional de Ciencias de Córdoba*, *6*, 422–433.

Ameghino, F. (1891). Mamíferos y aves fósiles argentinos: especies nuevas. Adiciones y correcciones. *Revista Argentina de Historia Natural*, *1*, 240–259.

Ameghino, F. (1897). Mammifères crétacés de l'Argentine. (Duxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*). *Boletín del Instituto Geográfico Argentino*, *18*, 406–429, 431–521.

Ameghino, F. (1904). Nuevas especies de mamíferos cretáceos y terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina*, *57*, 162–175, 327–341.

Armella, M. A. (2019). *Sistemática, bioestratigrafía y paleobiogeografía de los Notoungulados del Neógeno del Noroeste argentino* [PhD Thesis]. Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán. Retrieved from https://ri.conicet.gov.ar/handle/11336/87493

Armella, M. A. (2022). Tooth size variation in assemblages of *Tremacyllus* (Hegetotheriidae, Notoungulata): insights into geographical gradients, systematics, and sexual dimorphism. *Journal of Mammalian Evolution*, *29*(1), 113–128.

Armella, M. A. & Bonini, R. A. (2020). Biostratigraphic significance of the presence of *Protypotherium* cf. *P. antiquum* Ameghino 1885 (Interatheriidae, Notoungulata) in the late Miocene of Northwestern Argentina. *Journal of South American Earth Sciences*, *102*, 102676. http://doi.org/10.1016/j.jsames.2020.102676

Armella, M. A., Ercoli, M. D., Bonini, R. A., & García-López, D. A. (2022). Detecting morphological gaps in teeth outlines of a Pachyrukhinae (Hegetotheriidae, Notoungulata) lineage: systematic and palaeobiogeographical significance of the records from Northwestern Argentina. *Comptes Rendus Palevol*, *22*(16), 323–348.

Armella, M. A., García-López, D. A., Babot, M. J., Deraco, V., Herrera, C. M., Saade, L., & Bertelli, S. (2020). Postcranial remains of basal typotherians (Mammalia, Notoungulata) from the Eocene of northwestern Argentina. *Acta Palaeontologica Polonica*, *65*(2), 413–428.

Armella, M. A., García-López, D. A., & Esteban, G. I. (2019). Paleobiogeografía del Orden Notoungulata en el Neógeno del Noroeste Argentino: análisis integral de los registros de la región. *Actas del 5° Simposio del Mioceno-Pleistoceno del Centro y Norte de Argentina* (pp. 165–168). Jujuy.

Armella, M. A., Nasif, N. L., & Cerdeño, E. (2018). Small-sized mesotheriines (Mesotheriidae, Notoungulata) from Northwestern Argentina: Systematic, chronological, and paleobiogeographic implications. *Journal of South American Earth Sciences*, *83*, 14–26.

Babot, M. J. & Ortiz, P. E. (2008). Primer registro de Borhyaenoidea (Mammalia, Metatheria, Sparassodonta) en la provincia de Tucumán (Formación India Muerta, grupo Choromoro; Mioceno tardío). *Acta geológica lilloana*, *21*(1), 34–48.

Barnosky, A. D. & Lindsey, E. L. (2010). Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change. *Quaternary International*, *217*(1), 10–29.

Bergqvist, L. P. (1996). *Reassociação do póscrânio ás espécies de Ungulados da Bacia de S. J. de Itaboraí (Paleoceno), Estado do Rio De Janeiro, e Filogenia dos 'Condylarthra' e Ungulados Sul-Americanos com base no póscrânio* [Unpublished Thesis]. Universidade Federal do Rio Grande Do Sul.

Billet, G. (2011). Phylogeny of the Notoungulata (Mammalia) based on cranial and dental characters. *Journal of Systematic Palaeontology*, *9*(4), 481–497.

Billet, G., De Muizon, C., & Mamani Quispe, B. (2008). Late Oligocene mesotheriids (Mammalia, Notoungulata) from Salla and Lacayani (Bolivia): implications for basal mesotheriid phylogeny and distribution. *Zoological Journal of the Linnean Society*, *152*(1), 153–200.

Billet, G., Patterson, B., & De Muizon, C. (2009). Craniodental anatomy of late Oligocene archaeohyracids (Notoungulata, Mammalia) from Bolivia and Argentina and new phylogenetic hypotheses. *Zoological Journal of the Linnean Society*, *155*(2), 458–509.

Bossi, G. E. (1969). Geología y estratigrafía del sector sur del valle de Choromoro. *Acta geológica lilloana*, *10*, 17–64.

Bossi, G. E., Gavriloff, I. J., & Esteban, G. I. (1998). Terciario. Estratigrafía, Bioestratigrafía y Paleogeografía. In M. Gianfrancisco, M. E. Puchulu, J. Durango de Cabrera, & G. F.

Aceñolaza (Eds.), *Geología de Tucumán* (pp. 87–108). Publicación Especial del Colegio de Graduados en Ciencias Geológicas de Tucumán.

Bridge, J. S. (1993). Description and interpretation of fluvial deposits: a critical perspective. *Sedimentology*, *40*(4), 801–810.

Burmeister, C. V. (1888). Relación de un viaje a la Gobernación de Chubut. *Anales del Museo Nacional de Buenos Aires*, *3*, 175–252.

Cabrera, A. (1937). Notas sobre el suborden Typotheria. *Notas del Museo de La Plata*, *2*, 17–43.

Cabrera, A. (1939). Sobre vertebrados fósiles del Plioceno de Adolfo Alsina. *Revista del Museo de La Plata*, *2*(6), 3–35.

Cabrera, A. & Kraglievich, L. (1931). Diagnosis previas de los ungulados fósiles del Arroyo Chasicó. *Notas Preliminares del Museo de La Plata*, *1*, 107–113.

Cerdeño, E. (2018). Updated synthesis of South American Mesotheriidae (Notoungulata) with emphasis on west-central Argentina. *Revue De Paléobiologie*, *37*(2), 421–431.

Cerdeño, E. & Bond, M. (1998). Taxonomic revision and phylogeny of *Paedotherium* and *Tremacyllus* (Pachyrukhinae, Hegetotheriidae, Notoungulata) from the late Miocene to Pleistocene of Argentina. *Journal of Vertebrate Paleontology*, *18*(4), 799–811.

Cerdeño, E. & Contreras, V. H. (2000). El esqueleto postcraneal de *Hemihegetotherium* (Hegetotheriidae, Notoungulata) del Mioceno superior de Puchuzum, San Juan, Argentina. *Revista Española de Paleontología*, *15*(2), 171–179.

Cerdeño, E. & Montalvo, C. (2002). Los Hegetotheriinae (Hegetotheriidae, Notoungulata) del Mioceno superior de la provincia de La Pampa, Argentina. *Revista del Museo Argentino de Ciencias Naturales nueva serie*, *4*(1), 35–43.

Cerdeño, E., Montalvo, C. I., & Sostillo, R. (2016). Deciduous dentition and eruption pattern in late Miocene Pachyrukhinae (Hegetotheriidae, Notoungulata) from La Pampa Province, Argentina. *Historical Biology*, *29*(3), 359–375. http://doi.org/10.1080/08912963.2016.1164532

Cerdeño, E. & Reguero, M. (2015). The Hegetotheriidae (Mammalia, Notoungulata) assemblage from the late Oligocene of Mendoza, central-western Argentina. *Journal of Vertebrate Paleontology, 35*(2), e907173. http://doi.org/10.1080/02724634.2014.907173

Cerdeño, E. & Schmidt, G. I. (2013). Milk molars or extra premolars in Mesotheriinae (Mesotheriidae, Notoungulata): new insights into an old controversy. *Geobios*, *46*(3), 195–202.

Cifelli, R. L. (1983). Eutherian tarsals from the late Paleocene of Brazil. *American Museum Novitates*, *2761*, 1–31.

Cifelli, R. L. (1993). The phylogeny of the native South American ungulates. In F. S. Szalay, M. J. Novacek, & M. C. McKenna (Eds.), *Mammal Phylogeny*, *Placentals* (pp. 195–216). Springer-Verlag.

Cione, A. & Tonni, E. (1995). Bioestratigrafía y cronología del Cenozoico Superior de la región pampeana. In M. Alberdi, G. Leone, & E. Tonni (Eds.), *Evolución biológica y climática de la Región Pampeana durante los últimos cinco millones de años. Un ensayo de correlación con el Mediterráneo Occidental* (pp. 49–74). Monografías del Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas.

Contreras, V. H. & Baraldo, J. A. (2011). Calibration of the Chasicoan-Huayquerian stages boundary (Neogene), San Juan, western Argentina. In J. A. Salfity & R. A. Marquillas (Eds.), *Cenozoic Geology of the Central Andes of Argentina* (pp. 111–121). SCS Publishers.

Cristallini, E. O., Comínguez, A. H., Ramos, V. A., & Mercerat, E. D. (2004). Basement double-wedge thrusting in the northern Sierras Pampeanas of Argentina (27°S) –Constraints from deep seismic reflection. In K. R. McClay (Ed.), *Thrust Tectonics and Hydrocarbon Systems* (pp. 65–90). American Association of Petroleum Geologists Memoir 82.

Croft, D. A. & Anaya, F. (2006). A new middle Miocene hegetotheriid (Notoungulata: Typotheria) and a phylogeny of the Hegetotheriidae. *Journal of Vertebrate Paleontology*, *26*(2), 387–399.

Croft, D. A., Gelfo, J. N., & López, G. M. (2020). Splendid innovation: the extinct South American native ungulates. *Annual Review of Earth and Planetary Sciences*, *48*, 259–290.

Deraco, M. V., Powell, J. E., & López, G. (2008). Primer leontínido (Mammalia, Notoungulata) de la Formación Lumbrera (Subgrupo Santa Bárbara, Grupo Salta-Paleógeno) del noroeste argentino. *Ameghiniana*, *45*(1), 83–91.

Esteban, G., Georgieff, S., Nasif, N., Ibáñez, L., & Bonini, R. (2019). Marco estratigráfico, paleontología de vertebrados y paleoambientes del Plioceno de Catamarca, Tucumán y Santiago del Estero, Argentina. *Opera lilloana*, *52*, 348–366.

Esteban, G., Nasif, N., Armella, M., & Madozzo Jaén, M. C. (2017). Los vertebrados del Neógeno tardío de Catamarca y Tucumán: Actualización de su registro y cronología. In C. M. Muruaga & P. Grosse (Eds.), *Ciencias de la Tierra y Recursos Naturales del NOA. Relatorio del 20° Congreso Geológico Argentino* (pp. 754–766). Asociación Geológica Argentina.

Francis, J. C. (1960). Análisis de algunos factores de confusión en la sistemática genérica de los Mesotheriinae (Notoungulata, Typotheria). *Ameghiniana*, *2*(2), 29–36.

Gabbert, S. L. (2004). The basicranial and posterior cranial anatomy of the families of the Toxodontia. *Bulletin of the American Museum of Natural History*, *285*, 177–190.

García-López, D. A. (2011). Basicranial osteology of *Colbertia lumbrerense* Bond, 1981 (Mammalia: Notoungulata). *Ameghiniana*, *48*(1), 3–12.

García-López, D. A. & Babot, M. J. (2015). A late Miocene Argyrolagidae (Mammalia, Metatheria, Bonapartheriiformes) from northwestern Argentina. *Ameghiniana*, *52*(3), 314–323.

García-López, D. A., Babot, M. J., González, R., & Scanferla, A. (2018). Cranial anatomy of an Eocene notoungulate mammal from northwestern Argentina with special reference on the ear region. *Historical Biology*, *30*(7), 957–975.

García-López, D. A. & Cohen, L. (2021). Comments on the petrosal morphology of *Griphotherion peiranoi* García-López and Powell, 2011, an Eocene typotherian (Mammalia, Notoungulata) from Northwestern Argentina. *Libro de Resúmenes del 12° Congreso de la Asociación Paleontológica Argentina* (pp. 119). Buenos Aires.

Gelfo, J. N., García-López, D. A., & Bergqvist, L. P. (2020). Phylogenetic relationships and palaeobiology of a new xenungulate (Mammalia: Eutheria) from the Palaeogene of Argentina. *Journal of Systematic Palaeontology*, *18*(12), 993–1007.

Georgieff, S. M., Ibáñez, L. M., Vides, M. E., Anis, K. B., & Nieva, S. M. (2014). Paleógeno y Neógeno de Tucumán: estratigrafía y paleoambientes sedimentarios. In S. Moyano, M. E. Puchulu, D. S. Fernández, S. Nieva, & G. Aceñolaza (Eds.), *Geología de Tucumán* (pp. 106–123). Colegio de Graduados en Ciencias Geológicas de Tucumán.

Georgieff, S. M., Muruaga, C. M., Ibañez, L. M., Spagnuolo, C., Bonini, R., Esteban, G., Nasif, N., & del Pero, M. A. (2017). Estilos de deformación, cronoestratigrafía y evolución paleoambiental de las unidades neógenas de las Sierras Pampeanas Noroccidentales de Catamarca y Tucumán, Argentina. In C. M.

Muruaga & P. Grosse (Eds.), *Ciencias de la Tierra y Recursos Naturales del NOA. Relatorio del 20° Congreso Geológico Argentino* (pp. 254–268). Asociación Geológica Argentina.

González, O. E., Viruel, M. E., Mon, R., Tchilinguirian, P., & Barber, E. L. G. (2000). Hoja Geológica 2766-II San Miguel de Tucumán. *Dirección Nacional del Servicio Geológico*, *Boletín 245*, 1–124.

Guido, E. Y. & Sesma, P. J. (2014). Geografía Física. In S. Moyano, M. E. Puchulu, D. Fernández, G. Aceñolaza, M. E. Vides, & S. Nieva (Eds.), *Geología de Tucumán* (pp. 29–48). Colegio de Graduados en Ciencias Geológicas de Tucumán.

Iaffa, D. N., Sabat, F., Bello, D., Ferrer, O., Mon, R., & Gutierrez, A. A. (2011a). Tectonic inversion in a segmented foreland basin from extensional to piggyback settings: the Tucuman basin in NW Argentina. *Journal of South American Earth Science*, *31*(4), 457–474.

Iaffa, D. N., Sabat, F., Muñoz, J. A., Mon, R., & Gutierrez, A. A. (2011b). The role of inherited structures in a foreland basin evolution. The Metán Basin in NW Argentina. *Journal of Structural Geology*, *33*(12), 1816–1828.

Iaffa, D. N., Sabat, F., Muñoz, J. A., & Carrera, N. (2013). Basin Fragmentation Controlled by Tectonic Inversion and Basement Uplift in Sierras Pampeanas and Santa Bárbara System, Northwest Argentina. *Geological Society of London*, *Special Publications*, *377*(1), 101–117.

Kraglievich, L. (1926). Sobre el conducto humeral en las vizcachas y paquirucos Chapadmalenses con descripción del *Paedotherium imperforatum*. *Anales del Museo Nacional de Historia Natural "Bernardino Rivadavia"*, *34*, 45–88.

Kraglievich, L. (1934). *La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron*. Imprenta "El Siglo Ilustrado".

Kramarz, A. G. & Paz, E. R. (2013). Un Hegetotheriidae (Mammalia, Notoungulata) basal del Mioceno temprano de Patagonia. *Revista Mexicana de Ciencias Geológicas*, *30*(1), 186–195.

Linares, O. J. (2004). Bioestratigrafía de la fauna de mamíferos de las formaciones Socorro, Urumaco y Codore (Miocene medio-Plioceno temprano) de la región de Urumaco, Falcon, Venezuela. *Paleobiología Neotropical*, *1*, 1–26.

MacFadden, B. J. (2005). Diet and habitat of toxodont mega-herbivores (Mammalia, Notoungulata) from the late Quaternary of South and Central America. *Quaternary Research*, *64*(2), 113–124.

MacPhee, R. D. E. (2014). The serrialis bone, interparietals, "X" elements, entotympanics, and the composition of the notoungulate caudal cranium. *Bulletin of the American Museum of Natural History*, *384*, 1–69.

Madden, R. H. (1990). *Miocene Toxodontidae (Notoungulata, Mammalia) from Colombia, Ecuador and Chile* [Unpublished thesis]. Duke University.

Martínez, G., Dozo, M. T., Gelfo, J. N., & Marani, H. (2016). Cranial morphology of the late Oligocene Patagonian notohippid *Rhynchippus equinus* Ameghino, 1897 (Mammalia, Notoungulata) with emphases in basicranial and auditory region. *PLoS ONE*, *11*(5), e0156558. https://doi.org/10.1371/journal.pone.0156558

Martínez, G., Dozo, M. T., Vera, B., & Cerdeño, E. (2020). Paleoneurology, auditory region, and associated soft tissue inference in the late Oligocene notoungulates *Mendozahippus fierensis* and *Gualta cuyana* (Toxodontia) from central-western Argentina. *Journal of Vertebrate Paleontology*, *39*(6), e1725531. https://doi.org/10.1080/02724634.2019.1725531

Mercerat, A. (1917). Notas sobre algunos carnívoros fósiles y actuales de la América del Sud. *Estudios*, *12*, 1–430.

Miall, A. D. (1996). *The Geology of Fluvial Deposits.* Springer-Verlag.

Nasif, N., Musalem, S., & Cerdeño, E. (2000). A new toxodont from the late Miocene of Valle del Cajón (Catamarca, Argentina) and taxonomic remarks on the Family Toxodontidae (Notoungulata). *Journal of Vertebrate Paleontology*, *20*, 591–600.

O'Leary, M. A. (2010). An anatomical and phylogenetic study of the osteology of the petrosal of extant and extinct artiodactylans (Mammalia) and relatives. *Bulletin of the American Museum of Natural History*, *335*, 1–206.

Owen, R. (1837). A description of the cranium of the *Toxodon platensis*, a gigantic extinct mammiferous species, referable by its dentition to the Rodentia, but with affinities to the Pachydermata and the herbivorous Cetacea. *Proceedings of the Geological Society of London*, *2*, 541–542.

Owen, R. (1847). Notices on some fossil Mammalia of South America. *Report of the 16° Meeting of the British Association of the Advancement of Science* (pp. 65–67). London.

Owen, R. (1853). Description of some species of the extinct genus *Nesodon*, with remarks on the primary group (Toxodontia) of the hoofed quadrupeds to which that genus is referable. *Philosophical Transactions of the Royal Society of London*, *143*, 291–309.

Pascual, R. (1954). Adiciones a la fauna de la Formación de Los Llanos de San Luis y su edad. *Revista del Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata*, *1*(2), 113–121.

Pascual, R. (1965). Los Toxodontidae (Toxodonta, Notoungulata) de la Formación Arroyo Chasicó (Plioceno inferior) de la provincia de Buenos Aires. Características geológicas. *Ameghiniana*, *4*(4), 101–132.

Pascual, R., Ortega-Hinojosa, E. J., Gondar, D., & Tonni, E. P. (1966). IV Vertebrata. In A. V. Borrello (Ed.), *Paleontografía Bonaerense* (pp. 1–202). Comisión de Investigación Científica de la Provincia de Buenos Aires.

Pascual, R., Ortiz Jaureguizar, E., & Prado, J. L. (1996). Land mammals: paradigm for Cenozoic South American geobiotic evolution. *Münchner Geowissenschaftliche Abhandlungen*, *30*(A), 265–319.

Patterson, B. (1936). The internal structure of the ear in some notoungulates. *Field Museum of Natural History, Geological Series*, *6*, 199–227.

Paula-Couto, C. de. (1952). Fossil mammals of the beginning of the Cenozoic in Brazil. Notoungulata. *American Museum Novitates*, *1568*, 1–16.

Powell, J. E., García-López, D. A., Babot, M. J., Herrera, C., Ortiz, P. E., & Albino, A. (2012). Vertebrados de la Formación India Muerta (Neógeno, provincia de Tucumán). Consideraciones cronológicas y paleoambientales. *Ameghiniana, Suplemento Resúmenes*, *49*(4), 15R.

Powell, J. E. & Ortiz, P. E. (2014). Los vertebrados fósiles de la provincia de Tucumán. In S. Moyano, M. E. Puchulu, D. S. Fernández, S. Nieva, & G. Aceñolaza (Eds.), *Geología de Tucumán* (pp. 208–227). Colegio de Graduados en Ciencias Geológicas de Tucumán.

Reguero, M. A. & Cerdeño, E. (2005). New late Oligocene Hegetotheriidae (Mammalia, Notoungulata) from Salla, Bolivia. *Journal of Vertebrate Paleontology*, *25*(3), 674–684.

Roth, S. (1899). Apuntes sobre la geología y paleontología de los Territorios del Río Negro y Neuquén (diciembre de 1895 a junio de 1896). *Revista del Museo de La Plata*, *9*, 141–197.

Rovereto, C. (1914). Los estratos araucanos y sus fósiles. *Anales del*

Museo Nacional de Historia Natural de Buenos Aires, *25*, 1–247.

Sánchez-Moya, Y. & Sopeña, A. (2010). Sistemas aluviales de baja sinuosidad. In A. Arche (Ed.), *Sedimentología: del proceso físico a la cuenca sedimentaria* (pp. 225–259). Consejo Superior de Investigaciones Científicas, Madrid.

Seoane, F. D. & Cerdeño, E. (2019) Systematic revision of *Hegetotherium* and *Pachyrukhos* (Hegetotheriidae, Notoungulata) and a new phylogenetic analysis of Hegetotheriidae. *Journal of Systematic Palaeontology*, *17*(19), 1635–1663.

Shockey, B. J. & Flynn, J. J. (2007). Morphological diversity in the postcranial skeleton of Casamayoran (? Middle to Late Eocene) Notoungulata and foot posture in notoungulates. *American Museum Novitates*, *3601*, 1–26.

Shockey, B. J., Flynn, J. J., Croft, D. A., Gans, P., & Wyss, A. R. (2012). New leontiniid Notoungulata (Mammalia) from Chile and Argentina: comparative anatomy, character analysis, and phylogenetic hypotheses. *American Museum Novitates*, *3737*, 1–64.

Sostillo, R., Cerdeño, E., & Montalvo, C. I. (2018). Taxonomic implications of a large sample of *Tremacyllus* (Hegetotheriidae: Pachyrukhinae) from the late Miocene Cerro Azul Formation of la Pampa, Argentina. *Ameghiniana*, *55*(4), 407–422.

Sostillo, R., Montalvo, C. I., Cerdeño, E., Schmidt, G. I., Folguera, A., & Cardonatto, M. C. (2021). Updated knowledge on the Notoungulata (Mammalia) from the late Miocene Cerro Azul Formation, La Pampa Province, Argentina. *Historical Biology*, *33*(8), 1247–1265.

Szalay, F. S. (1985). Rodent and lagomorph morphotype adaptations, origins, and relationships: some postcranial attributes analyzed. In W. P. Luckett & J. L. Hartenberger (Eds.), *Evolutionary relationships among rodents: a multidisciplinary analysis. NATO Advanced Science Institutes (ASI) Series, volume 92* (pp. 83–132). Springer.

Tomassini, R. L., Montalvo, C. I., Deschamps, C. M., & Manera, T. (2013). Bioestratigraphy and biochronology of the Monte Hermoso Formation (early Pliocene) at its type locality, Buenos Aires Province, Argentina. *Journal of South American Earth Sciences*, *48*, 31–42.

Townsend, B. & Croft, D. A. (2010). Middle Miocene mesotheriine diversity at Cerdas, Bolivia and a reconsideration of *Plesiotypotherium minus*. *Paleontologia Electronica*, *13*(1), 1–36.

van Frank, R. (1957). A fossil collection from Northern Venezuela, 1. Toxodontidae (Mammalia, Notoungulata). *American Museum Novitates*, *1850*, 1–38.

Vera, B. (2012). Revisión del género *Transpithecus* Ameghino, 1901 (Notoungulata, Interatheriidae) del Eoceno medio de Patagonia, Argentina. *Ameghiniana*, *49*(1), 60–74.

Vera, B. (2019). A new species and the record of *Hemihegetotherium* (Notoungulata, Hegetotheriidae) in the Middle to Late Miocene of Patagonia, Argentina. *Journal of South American Earth Sciences*, *93*, 23–35.

Vera, B. & Ercoli, M. D. (2018). Systematic and morphogeometric analyses of Pachyrukhinae (Mammalia, Hegetotheriidae) from the Huayquerías, Mendoza (Argentina): biostratigraphic and evolutionary implications. *Journal of Vertebrate Paleontology*, *38*(3), e1473410. https://doi.org/10.1080/02724634.2018.1473410

Viseras, C. & Fernández, J. (2010). Sistemas aluviales de alta sinuosidad. In A. Arche (Ed.), *Sedimentología: del proceso físico a la cuenca sedimentaria* (pp. 261–298). Consejo Superior de Investigaciones Científicas.

Woodburne, M. O., Goin, F. J., Bond, M., Carlini, A. A., Gelfo, J. N., López, G. M., Iglesias, A., & Zimicz, A. N. (2014). Paleogene land mammal faunas of South America; a response to global climatic changes and indigenous floral diversity. *Journal of Mammalian Evolution*, *21*(1), 1–73.

Zapata, S., Sobel, E. R., del Papa, C., Muruaga, C., & Zhou, R. (2019). Miocene fragmentation of the Central Andean foreland basins between 26 and 28°S. *Journal of South American Earth Sciences*, *94*, 102238. https://doi.org/10.1016/j.jsames.2019.102238

Zárate, M. A., Schultz, P. H., Blasi, A., Heil, C., King J., & Hames, W. (2007). Geology and geochronology of the type Chasicoan (late Miocene) mammal-bearing deposits of Buenos Aires Province (Argentina). *Journal of South American Earth Sciences*, *23*(1), 81–90.

Zetti, J. (1972). *Los mamíferos fósiles de Edad Huayqueriense (Plioceno medio) de la región pampeana* [PhD Thesis]. Universidad Nacional de la Plata. Retrieved from http://sedici.unlp.edu.ar/handle/10915/4949

Zimicz, N., Payrola, P., & del Papa, C. (2018). New, Late Miocene mammalian assemblage from the Palo Pintado Formation (Northwestern Argentina). *Journal of South American Earth Sciences*, *81*, 31–44.

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