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New light on the endemic South American pachyrukhine *Paedotherium* Burmeister, 1888 (Notoungulata, Hegetotheriidae): Taphonomic and paleohistological analysis

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A B S T R A C T

Paedotherium is a small notoungulate endemic of South America, very abundant in the Neogene assemblages of the Argentine Pampas. Numerous specimens of this taxon were recovered in the Arroyo Chasicó Formation (Late Miocene), following a strict control of their stratigraphic provenance. In this context, a detail taphonomic and paleohistological study were performed, and the results obtained were compared with the information of other Neogene assemblages of Argentina previously studied, in order to interpret the relevance of this taxon in the biocoenosis and taphocoenosis corresponding to this lapse. Before burial, specimens were affected by diverse biostratinomic processes, according to the particular characteristics of each preservational context. After burial, the specimens were modified by the same fossil-diagenetic processes. Similar patterns of preservation were identified in specimens of *Paedotherium* recovered in other Neogene fluvial deposits of the Argentine Pampas. Based on the bone microstructure, it was possible to differentiate juvenile and adult individuals belonging to different Neogene species of *Paedotherium*. The mandibles of this taxon maintained the same ontogenetic growth strategy throughout the Late Cenozoic. This work provides novel data on paleoecological and paleobiological features of this taxon.

1. Introduction

The vertebrate fauna from the Neogene of Argentine Pampas is among the richest and most diverse of South America (Cione and Tonni, 2005). Particularly, the Pachyrukhinae (Notoungulata, Hegetotheriidae), an endemic South American group, are a major component of many assemblages (e.g. Tomassini et al., 2013, 2014; Montalvo et al., 2008, 2016). They comprise small herbivorous species (estimated body mass ranging from 1.8 to 2.2 kg approximately; Elissamburu, 2012) with cranial and postcranial morphology that resembles extant leporids and some caviomorph rodents, probably adapted to open and semiarid environments (Cerdeño and Bond, 1998; Reguero et al., 2007; and references therein).

Among pachyrukhines, *Paedotherium* Burmeister, 1888 includes three well-represented species, *P. minor* Cabrera, 1937, *P. typicum* Ameghino, 1887 and *P. bonaerense* Ameghino, 1887, with a temporal range that comprises the interval Late Miocene-Early Pleistocene (Cerdeño and Bond, 1998). Recently a new species, *P. kakai* Reguero et al., 2015, was defined for the Late Miocene based on a single specimen. Several studies related to the systematic, phylogeny, paleobiology and paleoecology of this taxon were performed (see Tomassini et al., 2014; Reguero et al., 2015; Cerdeño et al., 2016; and references therein).

In the last ten years numerous vertebrate fossils were recovered from the fluvial deposits of the Arroyo Chasicó Formation (Late Miocene), following a strict control of their stratigraphic provenance. In this context, the main goal of this paper is to analyze from a taphonomic viewpoint the specimens of *Paedotherium* belonging to this collection, and interpret the possible biostratinomic and fossil-diagenetic histories. Additionally, according to histological characteristics, new paleobiological data related with growth patterns and bone remodeling are provided. The results obtained are compared with the information of other Neogene assemblages of the Argentine Pampas with presence of *Paedotherium*, which have

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been previously studied (e.g. Montalvo, 2004; Montalvo et al., 2008, 2016; Tomassini and Montalvo, 2010, 2013; Tomassini, 2012; Tomassini et al., 2013, 2014), in order to interpret the relevance of this taxon in the biocoenosis and taphocoenosis corresponding to this lapse.

2. Geographic and stratigraphic setting

The accumulation of the Late Miocene-Pliocene continental deposits in central Argentina occurred after the regression of the Paranense Sea. The sequences registered in this region comprise homogeneous sediments consisting of brown silts and sandy silts, commonly defined as loess and loess-like deposits, with pedogenetic features throughout and paleosol levels (Zárate, 2005; Folguera and Zárate, 2009; Folguera et al., 2015).

Arroyo Chasicó is a classic fossiliferous site of Argentina, located at the southwestern of the Buenos Aires Province (Fig. 1a), recognized due the abundance and diversity of vertebrate remains (e.g. Bondesio et al., 1980; Cione and Tonni, 2005); also, it constitutes the type locality of the Arroyo Chasicó Formation (sensu Pascual, 1961). Based on lithological and paleontological criteria two members were recognized in this formation, Vivero Member in the lower portion and Las Barrancas Member in the upper portion (Fidalgo et al., 1978, 1987; Bondesio et al., 1980). From a biostratigraphic point of view two units were defined, both corresponding to the Late Miocene; the fauna of the Vivero Member was assigned to the *Chasicotherium rothi* Biozone (Lower Chasicoan Stage/Age), whereas the fauna of the Las Barrancas Member was assigned to the *Chasicotatus ameghinoi* Biozone (Upper Chasicoan Stage/Age) (Cione and Tonni, 2005).

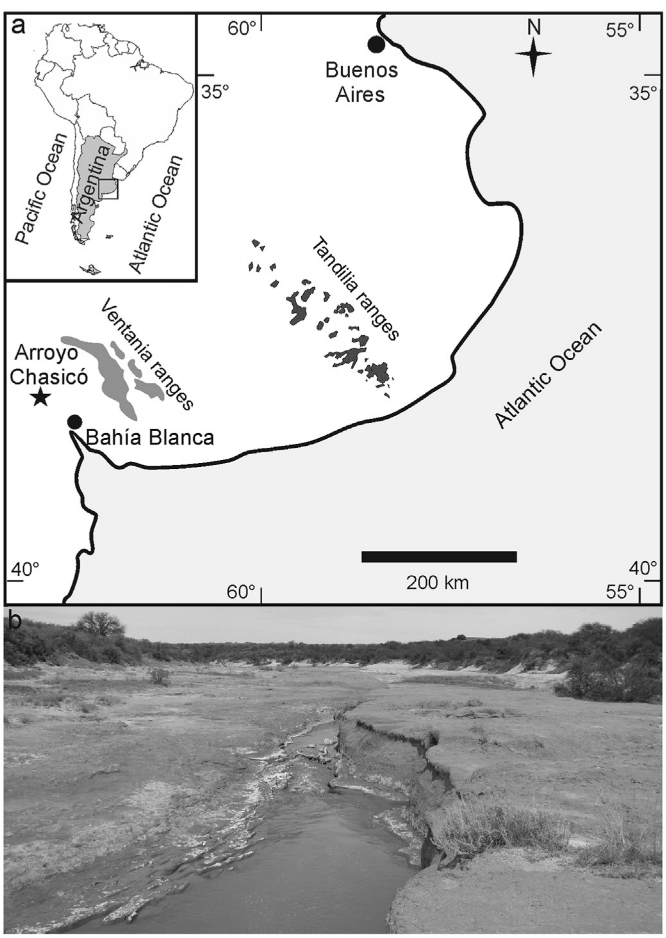

Fig. 1. a. Location map showing Arroyo Chasicó locality, Buenos Aires Province, Argentina. **b**. Detail of the Arroyo Chasicó Formation outcrops in their type locality.

After a detailed stratigraphic and sedimentological work, Zárate et al. (2007) modified the previous scheme and propose a new framework that included three facies associations instead of two members (Fig. 2; Table 1). Facies Association 1 comprises very fine sandstones, with very well-defined planar cross-bedding of low to medium angle inclination, observable in lenticular sets (facies Sp). Carbonate deposits are very abundant. This facies association represents a channel-bar deposit, consisting of three episodes of aggradation, probably originated by a braided to meandering system. Facies Association 2 includes sandy siltstones with poorly-defined cross-bedding (facies FSp), and massive sandy siltstones with intraclasts of siltstones and very fine sandstones (facies FSm). Carbonate deposits are very common. This facies association represents high-density flows accumulated in a marginal channel and/or floodplain environment. Facies Association 3 is mainly represented by mudstones with well-defined fine horizontal stratification (facies Fh). In local depressions, also includes sandy siltstones horizontally bedded (facies FSh) and massive mudstones (facies Fm). Mottles of iron are abundant, but carbonate deposits are less abundant than in the other facies associations. This facies association represents low-energy conditions of sedimentation in a swampy environment. In all facies associations, paleosols (facies P) were identified.

The succession was the result of episodic sedimentation in a fluvial environment of a mixed-load stream under progressively decreasing energy. The volcaniclastic composition of the deposits, indicates that the fluvial system drained the westward region by the Andean foothills (Zárate et al., 2007). Based on a radiometric age of 9.23 ± 0.09 Ma, obtained from impact glass (escoria) registered in the facies Sp, and high-resolution magnetostratigraphic profiles, Zárate et al. (2007) suggest: 1) facies associations 1 and 2 were accumulated between 9.43 and 9.07 Ma; 2) facies association 3 is younger than 9.02 Ma. However, the total duration of sedimentation remains unconstrained and could have extended to 8.7 Ma.

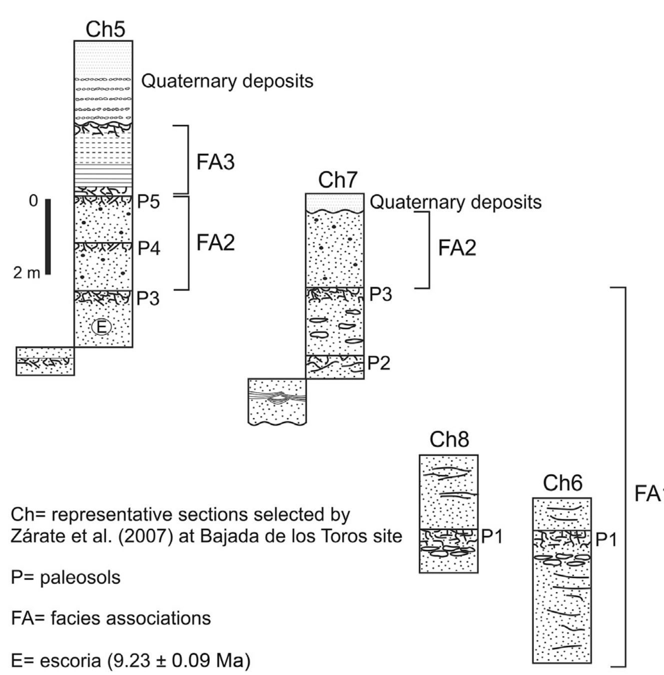

Fig. 2. Sections of the Arroyo Chasicó Formation showing the different facies associations (modified from Zárate et al., 2007).

Table 1
Facies and paleoenvironmental interpretation of the Arroyo Chasicó Formation (sensu Zárate et al., 2007) at its type locality (Arroyo Chasicó). *Paedotherium* remains studied herein were recovered from facies Sp, FSm, FSh and Fh.

Facies associations	Code	Facies	Sedimentary structures	Interpretation
3	Fh	Mudstone	Horizontal stratification	Swamp, floodplain
	Fm	Mudstone	Massive	
	FSh	Sandy siltstone	Horizontaly beddded	Crevasse
	P	Clayey silstone to mudstone	Pedogenic structure	Paleosol
2	FSm	Sandy siltstone	Massive	Overbank deposit, floodplain
	FSp	Sandy siltstone	Coarse cross bedding	Marginal channel
	P4, P5	silstone to mudstone	Pedogenic structure	Paleosol
1	Sp	Very fine sandstone	Planar cross bedding	Channel bar
	P1, P2, P3	Silty sandstone to mudstone	Pedogenic structure	Paleosol

3. Materials and methods

Outcrops of the Arroyo Chasicó Formation studied herein are discontinuously exposed along the lower reach of Chasicó Creek, within the 8–10 m high cliffs on both sides of the creek (Fig. 1b). The fossiliferous sites Estancia Norma Alicia, Bajada de los Toros, La Isla, La Cascada and Vivero von Humboldt, covering a length of 10 km approximately, were visited during the field seasons of the years 2005, 2006 and 2007.

Recovery was by direct collection of the in situ remains that were visible in each level; following a strict control of their stratigraphic provenance. All remains were collected, including microvertebrates specimens (mammals, anurans and reptiles with estimated body masses <5 kg), large mammals specimens (with estimated body masses >5 kg) and splinters (fragments smaller than 3 cm with undetermined anatomic and taxonomic adscription).

In this work, a taphonomic and paleohistological analysis of *Paedotherium* specimens recovered from the Arroyo Chasicó Formation were performed. The bearing levels correspond to the facies Sp, FSm, FSh and Fh, according to the scheme proposed by Zárate et al. (2007) for this formation. The materials are housed in the Museo Municipal de Ciencias Naturales "Carlos Darwin" (Punta Alta, Buenos Aires Province), under the acronym MD-CH.

Taphonomic features were analyzed with a Leica MS 5 binocular light microscope. Some specimens were also photographed using a JEOL 35 CF SEM scanning electron microscope, belonging to the Unidad de Administración Territorial del Centro Científico y Tecnológico CONICET Bahía Blanca (CCT-CONICET-BB).

Anatomical representation was determined by the following indexes (Badgley, 1986): NISP (number of identified specimens per taxon), MNE (minimum number of skeletal elements) and MNI (minimum number of individuals). The MNI was calculated based on mandibles.

Paedotherium is considered as a micromammal based on their estimated body mass (<2 kg; Elissamburu, 2012). Specimens were assigned to two age classes, based on the dental ontogeny and the degree of ossification. Juvenile individuals include specimens with emerging teeth and/or immature bone, with exposed areas of trabecular bone, whereas adult individuals include specimens with permanent teeth and/or mature bone (Montalvo et al., 2016; Cerdeño et al., 2016).

The following taphonomic features were analyzed on the remains:

1. Articulation. Whether the specimens were articulated, disarticulated but associated, or disarticulated and isolated (Behrensmeyer, 1991).
2. Breakage. Whether the specimens were complete or incomplete. Four categories were used for skull breakage, including broken skulls without zygomatic region, only maxillae and premaxillae, isolated premaxillae, and isolated maxillae (Andrews, 1990). Four categories were also used for mandible breakage, including broken ascending ramus, missing ascending ramus, missing ascending ramus and symphysis, and ventral border of the dentary broken (Andrews, 1990). In both cases, skull and mandibles, we determined the type of fractures considering stepped fractures with crenulated edges and smooth transverse fractures. The type of fracture was also evaluated in long bones (humeri, radii, ulnae, femora and tibiae), considering longitudinal, stepped, spiral and smooth transverse fractures (Marshall, 1989).
3. Predation/scavenging. Considers specimens with puncture marks (e.g. Binford, 1981; Lyman, 1994).
4. Weathering. Considers unaltered specimens (category 0), and specimens with splitting (category 1), chipping and/or flaking (category 2) (Andrews, 1990).
5. Abrasion. Considers unaltered specimens (category 1), and specimens with rounding (category 2) and/or polishing (category 3) (Alcalá, 1994).
6. Impregnation, encrustation, and corrosion. Considers specimens with fossil-diagenetic modifications produced by different processes (e.g. Lyman, 1994; Montalvo et al., 2016).

The original bone microstructure was evaluated based on the analysis of thin longitudinal and transverse sections of seven hemimandibles assigned to *P. minor*, made at the second molar (m2) level. The specimens studied belong to juvenile (NISP = 2) and adult (NISP = 5) individuals. The sections were performed at the Laboratorio de Petrotomía of the INGEOSUR (CONICET), Departamento de Geología, Universidad Nacional del Sur (UNS), following the methodology proposed by Tomassini (2012), and were observed under a Nikon Eclipse E400 POL petrographic polarizing microscope.

4. Results

4.1. Taphonomy

Several specimens (NISP = 690) assigned to microvertebrates (mammals, anurans and reptiles) and large mammals were recovered in the last years from the different facies of the Arroyo Chasicó Formation, following a strict control of their stratigraphic provenance. In this context, 137 specimens belonging to this collection (19.85% of the whole sample) were assigned to *Paedotherium*. This taxon is the most abundant in the sample. The MNE was 120 and the MNI was 39 (Table 2). Juvenile individuals were recorded in all facies, with low percentages (Table 2). Some well-preserved skulls and mandibles, all of them belonging to adult individuals, displayed characters that allowed their assignment to *P. minor*; the single species represented in this formation.

Only cranial elements, including mandibles (40.88%), isolated

Table 2
Indexes of the *Paedotherium* assemblage from the facies of the Arroyo Chasicó Formation. The values obtained evidence some differences between the different environmental contexts. Percentages of juvenile individuals, calculated based on the MNE, were low in all facies.

Indexes	Facies Sp (channel bar)	Facies FSm (floodplain)	Facies FSh (crevasse)	Facies Fh (swamp)
NISP	22	37	30	48
MNE	18	30	29	43
MNI	6	13	7	13
%juvenile	5.55	16.67	6.90	6.98

molars (22.63%) and maxillae (10.22%), were predominant. Other elements presented very low percentages or were absent (scapulae, radii, fibulae, metapodials and ribs). The values showed important variations between different facies in relation to the frequency of the skeletal elements represented (Fig. 3). It is worth highlighting that most of the postcranial elements belonging to micromammals recovered in these deposits are incomplete and present an extreme degree of breakage, and others (e.g. metapodials, ribs, vertebrae, phalanges) are difficult to identified from a taxonomic viewpoint; therefore, they usually can be classified only as Mammalia indet. (Tomassini, personal observation).

Few articulated specimens (sensu Behrensmeyer, 1991) were recorded from facies FSm and Fh (Table 3). They were represented by maxillae and diverse elements of the limbs (Fig. 4a). All the specimens recovered from facies Sp and FSh were disarticulated and isolated (sensu Behrensmeyer, 1991).

Complete specimens were very scarce in all facies (Table 3), represented by astragali, calcanea, femora, phalanges and isolated molars. Fragments of maxillae, with all teeth or some of them, were the most frequent portion of the skulls. Mandibles mainly included body fragments without the ascending ramus, but retained all teeth or most of them. Both maxillae and mandibles showed stepped fractures with crenulated edges and smooth transverse fractures. Long bones recovered from facies Sp and FSh only showed stepped fractures, while those recovered from facies FSm and Fh displayed longitudinal, stepped, spiral and smooth transverse fractures.

Marks identified as punctures were recorded in specimens from all facies (Table 3). The affected specimens, all of them disarticulated and isolated, were represented by mandibles and limb elements (humeri, ulnae, tibiae, calcanea) belonging to adult individuals. These marks penetrate the full thickness of compact bone and, in some specimens, present crushing of this type of bone into the damage feature. Most of them are circular or oval (Fig. 5c–h), although in some cases also present irregular shapes (Fig. 5a and b). Size was variable, the average length was 1.86 mm (range = 0.82–4.12 mm) and average width was 1.18 mm (range = 0.77–1.79 mm). They are located in different portions of the specimens and occur mostly isolated, only one ulna (Fig. 5a and b) and one mandible (Fig. 4e and f) presented marks on both sides of the bone.

Specimens with evidence of weathering were recovered from facies FSm, FSh and Fh (Table 3), including mandibles, maxillae, isolated molar and tibiae. Bone elements showed slight splitting parallel to the fibre structure, while molars (both isolated and retained in the alveoli) presented splitting of the dentine (category 1, sensu Andrews, 1990) (Fig. 4b).

Signs of abrasion were recognized in specimens from all facies (Table 3), represented mainly by isolated molars and mandibles. Most of them presented a slight rounding on the edges and ridges (category 2; sensu Alcalá, 1994) (Fig. 4c), while others, recovered from facies FSh, displayed a more pronounced rounding and an intense polishing of the outer surface (category 3; sensu Alcalá, 1994) (Fig. 4d).

Evidences of impregnation, encrustation and corrosion were recognized in specimens from all facies (Table 3). No patterns reflecting differential alteration were recognized among different skeletal elements. Impregnation with manganese oxides is represented by dark spots with dendritic habit, covering diverse sectors

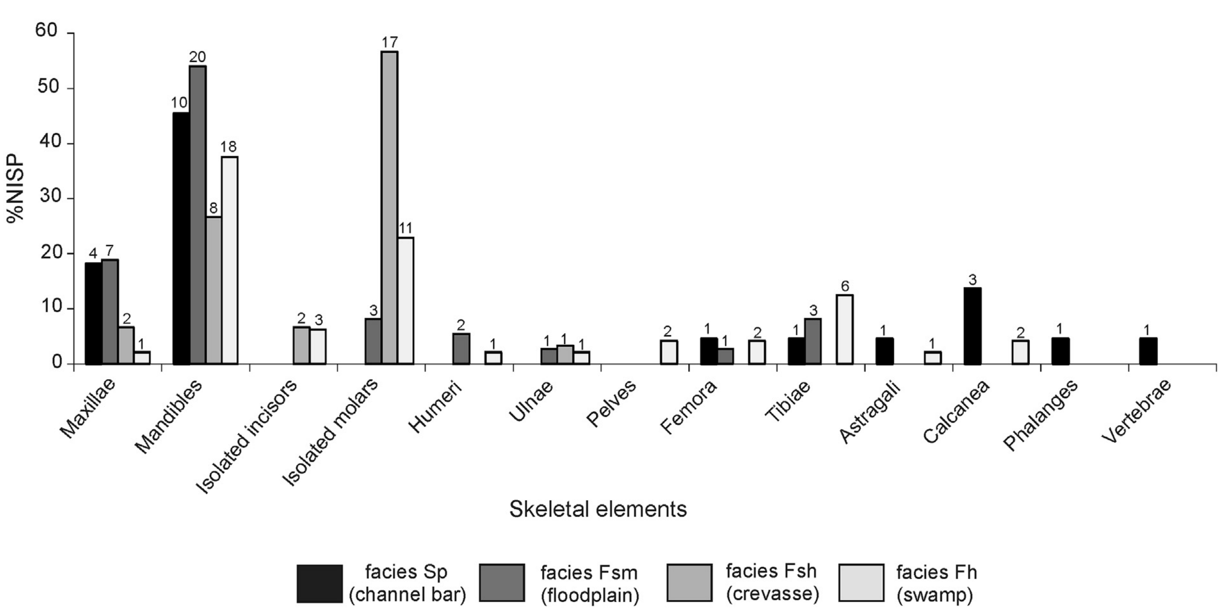

Fig. 3. Skeletal elements distribution from the different facies of the Arroyo Chasicó Formation. Numbers above the bars represent the raw data. The values obtained evidence differences between the different environmental contexts.

Table 3
Pre and post-burial modifications recorded in the *Paedotherium* specimens from the facies of the Arroyo Chasicó Formation. The values obtained evidence some differences between the different environmental contexts. Percentages were calculated based on the MNE.

Taphonomic features	Facies Sp (channel bar)	Facies FSm (floodplain)	Facies FSh (crevasse)	Facies Fh (swamp)
Articulation	0%	13.33%	0%	10.41%
Completeness	16.67%	3.33%	6.90%	9.30%
Predation/scavenging	5.55%	26.66%	3.45%	9.30%
Weathering				
Category 0	100%	70%	75.86%	88.37%
Category 1	0%	30%	24.14%	11.63%
Abrasion				
Category 1	61.11%	93.33%	37.93%	79.07%
Category 2	38.89%	6.67%	48.28%	20.93%
Category 3	0%	0%	13.79%	0%
Impregnation	27.78%	36.67%	65.52%	20.93%
Encrustation	72.22%	53.33%	13.79%	46.51%
Corrosion	16.67%	36.67%	51.72%	23.25%

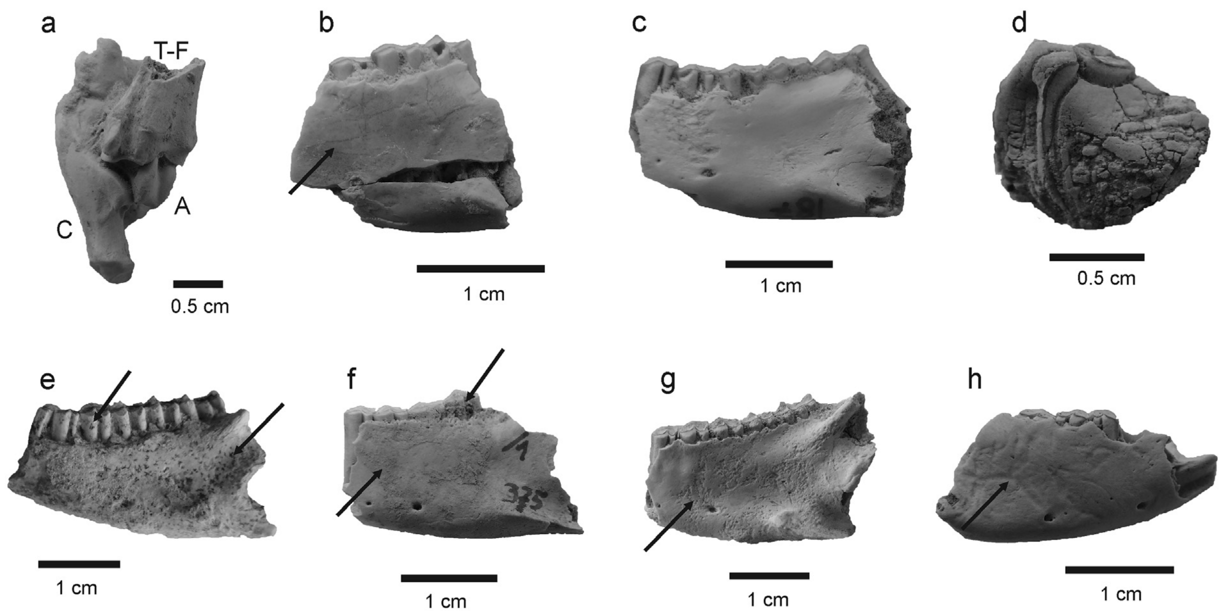

Fig. 4. Taphonomic features recorded in the *Paedotherium* specimens. **a**. Tibia (T–F), calcaneus (C) and astragalus (A) (MD-CH-06-61) articulated. **b**. Mandible (MD-CH-06-420) showing slight splitting (arrow). **c**. Mandible (MD-CH-06-187) showing slight rounding of the edges. **d**. Mandible (MD-CH-06-318) showing rounding of the edges and polishing of the outer surface. **e**. Mandible (MD-CH-06-137) showing black spots of manganese oxides (arrows). **f**. Mandible (MD-CH-06-375) showing thin calcareous coatings (arrows). **g**. Mandible (MD-CH-06-383) showing degradation of the compact bone layer (arrow). **h**. Mandible (MD-CH-06-104) showing root traces (arrow).

of the outer surface (Fig. 4e). Encrustation is represented by calcareous coatings with variable thickness, covering partially the outer surface (Fig. 4f). Corrosion is represented by changes of color in the outer surface and degradation of the compact bone layer (Fig. 4g); also, in facies FSm (NISP = 2) and Fh (NISP = 1) specimens with root traces (Fig. 4h), assigned to the ethological category Corrosichnia (see Mikuláš, 1999; Montalvo, 2002), were recorded.

Corrosion also produced slight obliteration of the original bone microstructure, generally limited to small areas. Most of the cavities (e.g. vascular canals, osteocyte lacunae) generated by degradation of the organic matter were infilled with manganese oxides.

4.2. Paleohistology

Based on the analysis of thin sections, typical microstructural elements of the mammalian bone tissue were recognized. In this context, there are some differences between juvenile and adult individuals related to the characteristics of collagen fibers, vascular canals and osteocyte lacunae.

4.2.1. Adult individuals

The internal layer is represented by parallel-fibered bone tissue (Fig. 6a and b). This type of bone tissue shows closely-packed collagen fibers, with the same orientation and, generally, mutually parallel. Sparse simple primary vascular canals are present, mutually parallel, and they follow the orientation of the collagen fibers. Osteocyte lacunae are numerous, flattened, and mainly spatially well-organized in the matrix, with their main axis oriented parallel to the collagen fibers.

The middle layer, separate from the internal layer by a reversal line, is represented by compacted cancellous bone tissue (Fig. 6a and b). This type of bone tissue shows a chaotic spatial organization, with convoluted appearance. Layers of lamellar bone tissue are deposited around bony trabeculae. Numerous vascular canals are present. Also, there are some primary osteons showing their typical constitution, which includes a canal surrounded by concentric bone lamella with a centripetal disposition. Osteocyte lacunae are numerous, globular or flattened, and spatially well-organized in the zones with lamellar bone tissue.

The external layer, separate from the middle layer by a reversal

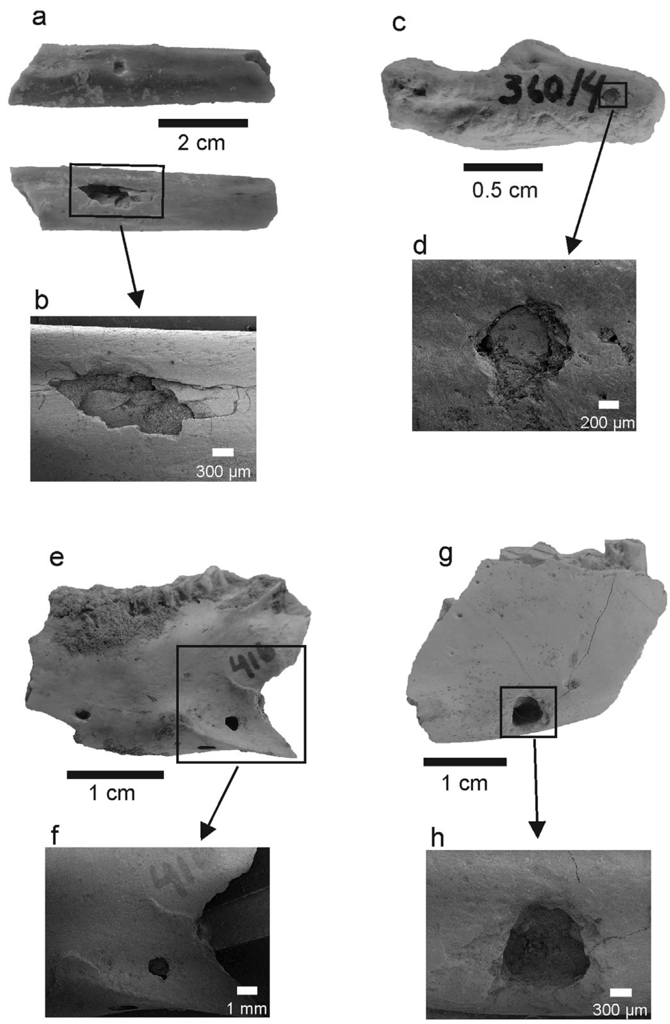

Fig. 5. Specimens of *Paedotherium* with puncture marks. **a**. Marks present on both sides of a tibia shaft (MD-CH-06-190), with different shapes. **b**. Detail of the mark, showing an irregular shape. **c**. Mark presents on the proximal portion of a calcaneus (MD-CH-06-360). **d**. Detail of the mark, showing a circular shape. **e**. Marks present on both sides of the lower portion of a mandible (MD-CH-06-416). **f**. Detail of the marks, showing circular shapes. **g**. Mark presents on the lower portion of a mandible (MD-CH-06-324). **h**. Detail of the mark, showing circular shape.

line, is represented by lamellar bone tissue (Fig. 6a and b). This type of bone tissue shows a high spatial organization with presence of thin successive lamellae. The number of lamellae is variable; each of them presents closely-packed collagen fibers mutually parallel, but with different orientation from one lamella to the next. Sparse simple primary vascular canals are present, mutually parallel and following the orientation of the collagen fibers. Osteocyte lacunae are numerous, flattened, and spatially well-organized in the matrix, with their main axis oriented parallel to the collagen fibers.

4.2.2. Juvenile individuals

The internal layer is represented by parallel-fibered bone tissue, with similar characteristics to those mentioned in adult individuals (Fig. 6c and d). The external layer displayed a poor preservation degree, which greatly hinders its description; however, primary cortical bone including large resorption cavities, some of them surrounded by layers of lamellar bone tissue, could be identified (Fig. 6c and d).

5. Discussion

Numerous remains of *Paedotherium* were recovered from different facies of the Arroyo Chasicó Formation. Specimens belonging to juvenile and adult individuals were identified. This taxon is one of the most abundant mammals in many Neogene assemblages of the Argentine Pampas, represented by *P. minor* in the Arroyo Chasicó (Late Miocene, Chasicoan Stage/Age) and Cerro Azul (Late Miocene, Huayquerian Stage/Age) formations, and by *P. bonaerense* and *P. typicum* in the Monte Hermoso Formation (Early Pliocene, Montehermosan Stage/Age) and the Playa San Carlos, Playa Los Lobos (Late Pliocene, Chapadmalalan Stage/Age), Punta Martínez de Hoz and Punta San Andrés (Late Pliocene, Marplatan Stage/Age) aloformations (e.g. Cerdeño and Bond, 1998; Tomassini, 2012; Tomassini et al., 2013, 2014; Montalvo et al., 2008, 2016; Cerdeño et al., 2016).

In several of these units, *Paedotherium* usually appears inside burrows or associated with them (e.g. Genise, 1989; Elissamburu et al., 2011; Tomassini, 2012; Beilinson and Taglioretti, 2013). Taking into account that this particular environmental context protects the bones from destructive processes (e.g. weathering, trampling, water transport) (see Voorhies, 1975), it is possible to consider that the fossorial habits proposed for this taxon (see Cerdeño and Bond, 1998; Elissamburu, 2004; Elissamburu et al., 2011) would have favored, in many cases, the preservation of their remains.

The specimens studied in this work mainly included mandibles, maxillae and isolated teeth, which constitute the most diagnostic skeletal elements of this taxon. The absence or low percentages of some postcranial elements are probably related to the poor preservation that shows the micromammals remains in this formation and, therefore, to biases in the taxonomic determinations. However, taking into account the environmental contexts analyzed, we do not discard that sorting by different processes (e.g. activity of predators/scavengers, water transport) could have influenced in the final skeletal representation.

The absence of articulated or associated specimens in the channel bars (facies Sp) and crevasses (facies Fsh) deposits could be related with the high energy of these environmental contexts and its capacity to disarticulate, transport and scatter the bones. The scarce articulated specimens recorded from floodplain (facies FSm) and swampy (facies Fh) deposits reflect that, in the environmental contexts with low energy, some bones were buried quickly and with presence of connective tissue. The occurrence of different articulation degrees in some facies indicates that bones were gradually buried.

The high degree of breakage recorded in specimens from all facies indicates that most bones were affected by diverse destructive processes throughout the taphonomic history. Longitudinal, stepped and spiral fractures are related to biostratinomic processes, while smooth transverse fractures are related to fossil-diagenetic processes. Montalvo (2004) indicated that the mandibles of *Paedotherium* are particularly susceptible to be broken, due to their long and narrow shape.

Punctures marks are similar to those produced by carnivore mammals, as a result of the direct pressure generated by teeth on bone surface (Binford, 1981; Lyman, 1994; Pobiner, 2008; Lloveras et al., 2011). This type of mark could have been originated at the time of death of the animal, associated with predation, or after their death, related with scavenging. Stepped fractures with crenulated edges, both in maxillae and mandibles, and spiral fractures in long bones, are other evidences usually associated to the activity of predators/scavengers (Gifford-Gonzalez, 1989; Pobiner, 2008; Montalvo et al., 2016). The activity of predators/scavengers probably contributed to the disintegration and scattering of bones. The absence of punctures marks in specimens assigned to juvenile

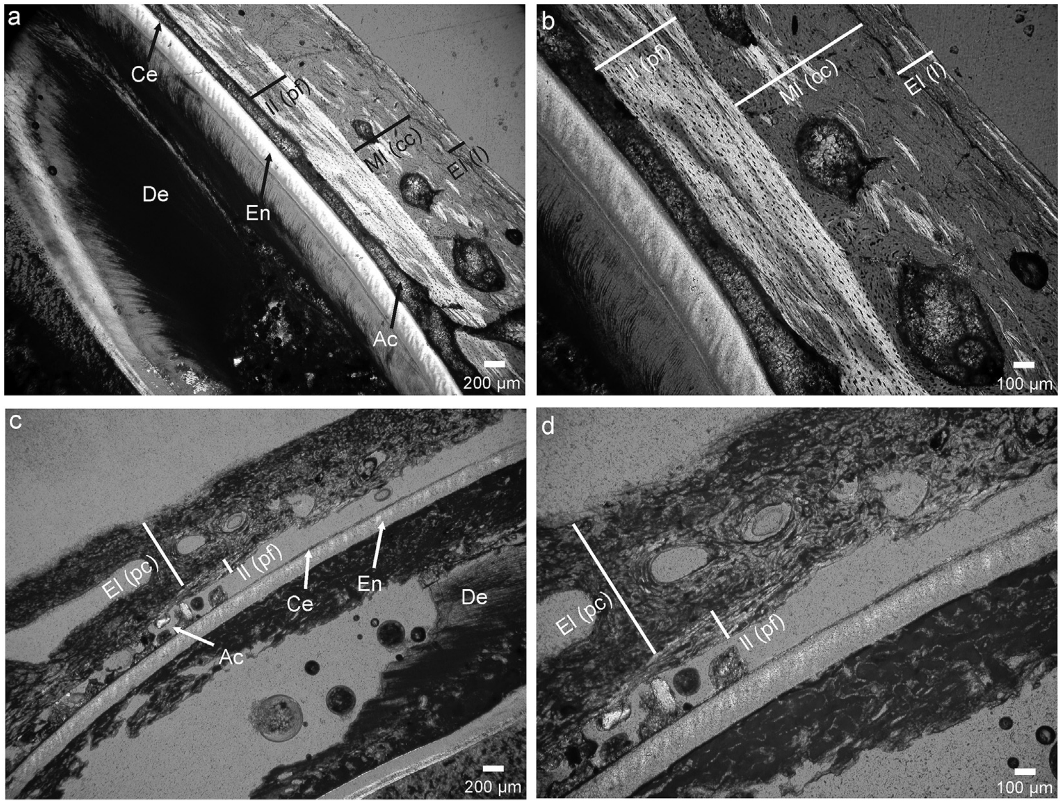

Fig. 6. Paleohistological features of *Paedotherium* mandibles. Different bone tissues were identified. **a**. Adult individual (MD-CH-06-184) showing internal (parallel-fibered bone tissue), middle (compacted cancellous bone tissue) and external (lamellar bone tissue) layers. **b**. Closer view of the bone tissue. **c**. Juvenile individual (MD-CH-06-158) showing internal (parallel-fibered bone tissue) and external (primary cortical bone) layers. **d**. Closer view of the bone tissue. Abbreviations: **Ac**, alveolar cavity; **cc**, compacted cancellous bone tissue; **Ce**, cementum; **De**, dentine; **El**, external layer; **En**, enamel; **Il**, internal layer; **Ml**, middle layer; **l**, lamellar bone tissue; **pc**, primary cortical bone; **pf**, parallel-fibered bone tissue.

individuals could be related to the fact that bones of juvenile mammals present lower structural densities (Lyman, 1994) and, therefore, it tend to be easily destroyed.

In some cases, different characteristics of the punctures marks (e.g. size, shape, location) can provide information about the taxonomic identity of the producer (e.g. Andrews and Fernández-Jalvo, 1997; Domínguez-Rodrigo and Piqueras, 2003). However, it also needs to be taken into consideration the fact that similar marks can be originated by diverse producers and that the same producer can generates different marks (Bromley, 1996). In this context, possible producers recorded in levels of the Arroyo Chasicó Formation include the Sparassodonta marsupials *Chasicostylus castroi* Reig, 1957, *Pseudolycopsis cabrerai* Marshall, 1976, *Lycopsis viverensis* Forasiepi et al., 2003 and Thylacosmilidae indet. (Suárez and Goin, personal communication).

The presence of punctures marks in specimens recovered from channel bars (facies Sp) and crevasses (facies Fsh) deposits allows to suggest that, before burial, some bones were mobilized from the surrounding floodplain. In this sense, diverse authors (e.g Korth, 1979; Badgley, 1986) mentioned that the accumulations originated in these environmental contexts can include prey remains that were reworking by the fluvial dynamic.

In several fossiliferous localities of the Cerro Azul Formation with micromammals specimens accumulated by the activity of predators (Estancia Ré, Telén and Caleufú), *P. minor* was the most frequent taxon, representing between 24% and 49% of the whole samples (Montalvo et al., 2016; and references therein). In this context, marks produced by teeth were recorded in several specimens, but the absence of digestive corrosion signs, the degree of breakage, the type of fractures recorded, and the anatomical representation indicate that the assemblages represent accumulations of uneaten body parts. The identification of punctures and scorings marks and the presence of coprolites in these accumulations support the interpretation of carnivore mammals as the producers; Sparassodonta and Didelphimorphia marsupials were proposed as the possible producers (Montalvo et al., 2008, 2016).

Several coprolites containing remains of *Paedotherium* sp., rodents and fishes were recovered in the Monte Hermoso Formation, all of them assigned to carnivore mammals (Tomassini and Montalvo, 2010). Also, several isolated cranial and post-cranial elements of *P. bonaerense* recovered from this formation show punctures and scoring with sizes and shapes that allow their assignment to Sparassodonta and Didelphimorphia marsupials (Tomassini, personal observation).

Evidences of weathering registered in specimens from facies FSm, FSh and Fh reveal that they were affected by atmospheric agents, such as sun, wind, rain and temperature changes, among others. The occurrence of different weathering stages in each facies indicates that bones were gradually buried. The identification of slight modifications suggests a short time of exposition at the surface.

Marks of abrasion reflect the friction produced by sedimentary particles in movement on bone surface. The differences recorded in this case are related with the characteristics of the bearing levels. The highest percentages of specimens affected and the highest intensities were obtained in the crevasses (facies FSh) and channel bars (facies Sp) deposits, suggesting that the time of interaction between remains and sediment was extensive or that the intensity was high; which is consistent with the high energy of these environmental contexts. On the contrary, the lowest percentages of specimens affected (always with low intensities) were obtained in the floodplain (facies FSm) and swampy (facies Fh) deposits, suggesting that the residence time under abrasive conditions have been short or that the intensity was low; which is consistent with the low energy of these environmental contexts.

Processes of impregnation, encrustation and corrosion reflect the interaction between the specimens and the substrate in which they were buried and preserved. The impregnation with manganese oxides indicates alkaline and oxidizing conditions during dry periods. Encrustation is related with precipitation of carbonatic salts and indicates alkaline conditions during dry periods. Corrosion is probably associated to the action of humic acids during wet periods. Trace fossils assigned to Corrosichnia suggests a temporary shallow burial in a substrate supporting vegetation.

Specimens assigned to adult individuals showed a good preservation degree of the original bone microstructure, even those with evidences of post-burial corrosion, while specimens assigned to juvenile individuals displayed a poor preservation degree. This difference is probably related with the type of bone tissue represented in each ontogenetic stage. In both cases, it seems to be that the permineralization (sensu Fernández-López, 2000) with manganese oxides favored the preservation of some microstructural elements (e.g. vascular canals, osteocyte lacunae).

Similar pre and post-burial modifications were also described in specimens of *Paedotherium* recovered from other Neogene fluvial deposits of the Argentine Pampas (e.g. Cerro Azul Formation, Montalvo, 2004; Montalvo et al., 2008, 2016; Monte Hermoso Formation, Tomassini, 2012; Tomassini and Montalvo, 2013; Tomassini et al., 2014). Despite the particular characteristics of each fossiliferous locality, it is worth highlighting that these assemblages show clear similarities in their taphonomic histories.

Paleohistology is an issue scarcely considered in the study of Cenozoic mammals, particularly for notoungulates (Kolb et al., 2015; and references therein). In this context, thin sections performed in mandibles of *P. minor* from the Arroyo Chasicó Formation, previously assigned to juvenile and adult individuals based on macroscopic characters, revealed a variety of bone tissues.

Both age classes displayed an internal layer of parallel-fibered bone tissue with low vascularization, which indicates slow apposition rates. Juvenile individuals are also characterized by: 1) an external layer of primary cortical bone, with low degree of bone modelling; and 2) lack of lamellar bone tissue layer. These features suggest early ontogenetic stages (Enlow, 1962; Francillon-Vieillot et al., 1990; Chinsamy-Turan, 2011). Adult individuals are also characterized by: 1) a middle layer of compacted cancellous bone tissue, that represents the compaction of a region that previously consisted of spongy bone by processes of bone modelling, associated to the growth of the skeletal element; and 2) an external layer of lamellar bone tissue, which indicates slow apposition rates and low growth rates. These features suggest late ontogenetic stages (Enlow, 1962, 1963; Francillon-Vieillot et al., 1990; Chinsamy-Turan, 2005, 2011).

The differences recorded in the samples studied are fundamentally related with the age of the individuals and represent diverse events (e.g. growth rate, bone modelling) occurred throughout the life of the organism. A decrease in growth rate during ontogeny is interpreted for the mandibles of this taxon. Thus, the histological analysis support the ontogenetic determinations based on macroscopic observations of the skeletal elements.

Similar histological features were also recognized in mandibles belonging to juvenile and adult individuals of *P. minor* and *P. bonaerense*, from the Cerro Azul and Monte Hermoso formations respectively (Montalvo, 2004; Tomassini, 2012; Tomassini et al., 2014; Garrone et al., 2016). This pattern allows inferring that different species of *Paedotherium* maintained the same ontogenetic growth strategy throughout the Late Cenozoic, at least in this skeletal element.

6. Conclusions

The high frequency of *Paedotherium* specimens in many fossil assemblages of the Argentine Pampas, suggests that this taxon was an important component in the Neogene communities of the region. In this context, the data obtained in this study provide new information on paleoecological and paleobiological features of this small notoungulate endemic of South America.

The specimens of *Paedotherium* recorded in the fluvial deposits of the Arroyo Chasicó Formation showed different taphonomic histories. Before burial, specimens were affected by diverse biostratinomic processes, including disarticulation and scattering, predation/scavenging, weathering and abrasion. Differences are related with the particular characteristics of each deposit. After burial, specimens were modified by the same fossil-diagenetic processes, including impregnation, encrustation and corrosion.

Taphonomic characteristics observed in other Neogene fluvial deposits of the Argentine Pampas reflect a similar pattern of preservation for the specimens of *Paedotherium*. The burrows produced by this taxon constituted a relevant environmental context for the preservation of their skeletal elements. This paper provides a framework for the analysis of other Cenozoic micromammal assemblages with presence of *Paedotherium*.

Considering the evidences recorded in several formation of central Argentina, it is possible to consider that the species of *Paedotherium* were a habitual component in the diet of different predators and/or scavengers. This information contributes to the knowledge on the trophic relationships of the Neogene communities.

Paleohistological analysis provides a further perspective on the structure and ontogenetic growth of the *Paedotherium* mandible throughout the Late Cenozoic. Based on the bone microstructure, it was possible to differentiate juvenile and adult individuals belonging to different Neogene species of *Paedotherium*. This type of study constitutes an additional proxy for the determination of ontogenetic stages in taxa whose classification is difficult based on macroscopic characters or when the remains have high breakage degrees.

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