Leftover prey remains: a new taphonomic mode from the Late Miocene Cerro Azul Formation of Central Argentina

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LETHAIA

Montalvo, C.I., Tomassini, R.L. & Sostillo, R. 2015: Leftover prey remains: a new taphonomic mode from the Late Miocene Cerro Azul Formation of Central Argentina. *Lethaia*, DOI: 10.1111/let.12140.

The Cerro Azul Formation (La Pampa Province, Argentina) comprises a rich vertebrate fauna of small mammals dominated by notoungulates and rodents. The fauna pertains to the Late Miocene specifically to the Huayquerian Stage/Age. Taphonomic analysis of micro-mammals from Estancia Ré locality evidenced that the faunal assemblage was accumulated by the activity of a predator. This assemblage was compared with others from the Cerro Azul Formation in Telén and Caleufú localities (La Pampa Province), previously interpreted as products of predator activities. These microfossil accumulations differ from assemblages attributed to pellets and faeces produced by modern predators (nocturnal and diurnal bird raptors and carnivore mammals). However, due to their anatomical representation, degree of bone breakage and presence of tooth marks, they are interpreted as accumulations of uneaten prey remains discarded by the predator. The predator involved could not be determined with certainty, although the presence of tooth marks in some skeletal remains and the presence of coprolites in Telén and Caleufú suggest that it could be a carnivore mammal. Similarities in the accumulation mechanism, patterns of preservation and sedimentary contexts in the three assemblages support the recognition of a new taphonomic mode, termed 'leftover prey remains'. □ *Argentina, Cerro Azul Formation, Late Miocene, leftover prey remains, micro-mammals, taphonomic mode.*

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Only a few papers on Neogene faunal assemblages of Argentina include detailed taphonomic evaluations that provide insights into conditions favouring their accumulation and preservation (Bown & Larriestra 1990; Tauber 1997a,b; Tomassini & Montalvo 2010a, b, 2013; Tomassini 2012; Tomassini *et al.* 2014). In central Argentina, some faunal assemblages from the Late Miocene Cerro Azul Formation (Linares *et al.* 1980; Folguera & Zárate 2009) have been taphonomically analysed (Montalvo 2002b, 2004b; Montalvo *et al.* 2005, 2008; Verzi *et al.* 2008). Most of these assemblages are composed by micro-vertebrate remains and are particularly interesting because of the richness and diversity of the small mammals. Taphonomic information suggests they are accumulations produced by predators, and several of these accumulations supported previous biochronological proposals for the Cerro Azul Formation (e.g. Verzi *et al.* 2008).

A rich vertebrate fauna composed mainly of micro-mammals was recovered from deposits of the Cerro Azul Formation at Estancia Ré locality, Conhelo Department, northern La Pampa Province, Argentina (Fig. 1A). The assemblage includes numerous remains of diverse groups of micro-mammals (Marsupialia, Notoungulata and Rodentia), macro-mammals (Xenarthra, Cingulata and Folivora, Notoungulata and Litopterna) and one Squamata (Reptilia). The identified taxa indicate this unit is assignable to the Late Miocene and specifically to the Huayquerian Stage/Age (Cerdeño & Montalvo 2001; Urrutia *et al.* 2008; Olivares *et al.* 2012; Albino *et al.* 2013; Sostillo *et al.* 2014).

In this contribution, the taphonomic attributes of the micro-mammal assemblage from Estancia Ré locality are analysed. The results are compared with other micro-mammal assemblages from the Late Miocene Cerro Azul Formation exposed at Caleufú and Telén localities (Fig. 1A), which have been previously studied (Montalvo 2002b, 2004b; Montalvo *et al.* 2008; Verzi & Montalvo 2008). The preservation patterns and the accumulation mechanism of the remains, coupled with sedimentary context of the bone bearing horizons, point to particular taphonomic mode (*sensu* Behrensmeyer 1988) for the three assemblages.
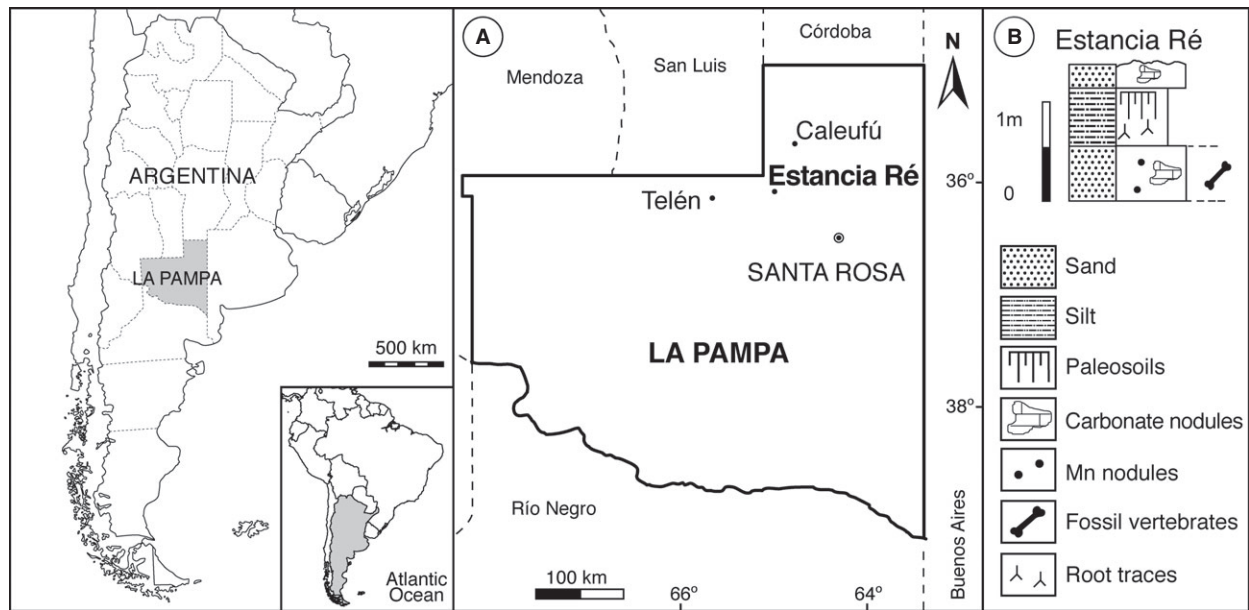
Fig. 1. A, geographical location of Late Miocene deposits of Cerro Azul Formation in La Pampa Province, Argentina. B, stratigraphical column in Estancia Ré locality.

Geological setting

Deposits of the Cerro Azul Formation are discontinuously exposed in scattered localities of eastern La Pampa Province and western Buenos Aires Province (Argentina). They generally consist of sparse outcrops, restricted to the bottom and hillslopes of topographic depressions and valleys. The Cerro Azul Formation is composed predominantly of brown silts and sandy silts primarily of aeolian origin (loess deposits), which have been reworked by aqueous agents (loess-like deposits). Palaeosols are common throughout the sequence and include abundant carbonate nodules and rhizoconcretions. The detailed description of the geology and stratigraphy of this formation is provided by Folguera & Zárate (2009, and references therein). A Late Miocene age has been attributed to the succession on the basis of its vertebrate fossil content (Verzi *et al.* 2008; and references therein). Five biozones, covering the Chasicoan–Late Huayquerian interval, have been recognized for this formation, based mainly on the anagenetic pattern of change in the octodontoid rodent lineages (Octodontidae and Echimyidae). The different evolutionary grade of these rodents suggests chronological differences among localities (Verzi *et al.* 2008, 2011; Sostillo *et al.* 2014).

Outcrops of the Cerro Azul Formation in the Estancia Ré locality (S 36°06′52,61″,W 64°59′35,13″) are thin (1.5 m) and limited surface exposure (5200 m^2 approximately). The section is characterized by reddish brown to reddish silts and sandy silts.

Three levels were identified, and the remains were exhumed from the lowest sandy silts deposits which contain calcareous concretions and rounded manganese nodules (Fig. 1B). The outcrops of Telén locality are homogeneous, 6 m thick, and mostly composed of carbonate-cemented siltstones and fine-grained sandstones (Montalvo *et al.* 2008). At Caleufú, the exposures are composed of sandy silts that are weakly stratified, 0.8–1 m thick, cemented by carbonates, and with abundant scattered calcareous concretions and rounded manganese nodules (Verzi & Montalvo 2008). The levels of Cerro Azul Formation in the three localities were interpreted as loess-like deposits with immature palaeosols and little diagenetic alteration.

Materials and methods

The material studied is housed in the paleontological collection of the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa (UNLPam) with the acronym GHUNLPam (Departamento de Geología, UNLPam).

Only the micro-mammals were studied in our taphonomic analysis because they are the largest group of vertebrates and the most diverse in the assemblage. Taxonomic identifications were made by comparison with specimens of the GHUNL-Pam palaeontological collection. The taphonomic features were analysed with a Leica Ms5 stereomicroscope.

Following the methodology proposed by Vizcaíno & Fariña (1999) and Montalvo (2004b), remains corresponding to taxa with body masses <5 kg were assigned to micro-mammals. These specimens were then 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 2004b).

The taxonomic and anatomical representations of micro-mammals were determined through the following indices: NR (number of recovered remains, represents the sum of undetermined fragments and specimens identified anatomically and taxonomically), NISP (number of identified specimens per taxon), MNI (minimum number of individuals) and MNE (minimum number of skeletal elements).

The following taphonomic attributes were analysed on the remains:

- Articulation degree; whether the skeletal elements were articulated, disarticulated but associated, or disarticulated and isolated (Behrensmeyer 1991).
- Breakage degree; whether skeletal elements are complete or incomplete. In the latter, the type of fracture was evaluated (smooth transverse, spiral and stepped; Marshall 1989). Four categories were used for skull breakage, including broken skulls without zygomatic region, only maxillae and premaxillae, isolated pre-maxillae and isolated maxillae. Mandibles were assigned to one of the four categories, including broken ascending ramus, missing ascending ramus, missing ascending ramus and symphysis, and ventral border of the dentary broken. In all categories, molar retention was evaluated.
- Weathering degree; considers remains without alteration and remains with slight splitting and/or cracks on their surface (Andrews 1990).
- Abrasion degree; it considers unaltered remains and remains with rounding and polishing (Alcalá 1994).
- Impregnation degree; it describes the presence or absence of manganese oxides on the outer surface.
- Corrosion degree, it considers the presence or absence of areas modified by dissolution, with or without change of the surface colour.
- Bioerosion degree; it describes modifications of the outer surface due to biological activity.
- The presence or absence of calcareous crusts and concretions associated with the remains.

The skeletal elements were also classified according to their transport susceptibility, both by water or wind, considering the groups proposed by Dodson (1973), and Cheme Arriaga *et al.* (2012).

To assess the possibility that the micro-mammal remains represent an accumulation produced by predators, the taphonomic methodology proposed by Andrews (1990) and Fernández-Jalvo & Andrews (1992) was used, which includes the following analyses:

- Calculation of the relative abundance of different skeletal elements, considering the representativeness of each element in the context of the minimum number of individuals, as follows: MNEi/ (EixMNI) × 100, where MNEi is the minimum number of particular skeletal elements for the sample and Ei is the expected number of this skeletal element in a given individual. Because of the great taxonomic diversity of micro-mammals and the quantitative differences of certain skeletal elements (e.g. teeth, vertebrae and metapodials) in the different taxa of the assemblage, only those elements represented by two units (e.g. paired skeletal elements) in the complete skeleton were evaluated (e.g. mandibles, maxillae and femora).
- Calculation of the index that evaluates the ratio of cranial and post-cranial elements [(femora + humeri) / (mandibles + maxillae)], and the index that analyses ratios of proximal and distal elements of the limbs [(tibiae + ulnae) / (femora + humeri)]. Indexes that refer to molar and incisor loss and isolated incisor and molars were not evaluated because of the taxonomic diversity of the assemblage, including taxa with different number of teeth, which hindered the evaluation.
- The degree of post-cranial breakage was evaluated for humeri, femora, ulnae and tibiae, comparing the number of complete remains against the number of proximal, shaft and distal fragments.
- Evaluation of the degree of digestive corrosion, based on evidence of modifications produced by digestive acids.
- Presence of other types of marks on the surface of the remains (e.g. punctures, scores).

Results

All the variables evaluated in the assemblage of Estancia Ré are summarized in Table 1. More than half of the fossil remains are undetermined fragments, both anatomically and taxonomically. The NISP of micro-mammals was 965, this total includes at least 14 taxa that belong to Marsupialia,

Table 1. Taphonomic variables evaluated for Estancia Ré, Telén and Caleufú assemblages.

Quarry data	Estancia Ré	Caleufú	Telén
Size of accumulation	5200 m^2	1590 m^2	48000 m^2
Spatial density (remains/m^2)	0.70	4.1	0.25
Assemblage data			
Number of recovered remains (NR)	3416	6516	11647
Number of identified specimens per taxon (NISP)	1757	3049	5598
Micromammals	85%	98%	78%
Number of coprolites	–	66	2
Micromammals assemblage			
Minimum number of skeletal elements (MNE)	904	1554	2123
Minimum number of cranial elements	597	1029	1185
Minimum number of postcranial elements	307	525	938
Number of taxa	14	16	26
Minimum number of individuals (MNI)	161	275	244
Average relative abundance	19.69%	17.43%	21.99%
(Femur+humerus/mandible+maxilla) × 100	14.35	12.63	17.59
(Tibia+ulna/femur+humerus) × 100	66.67	88.23	126.62
Juvenile individuals	11.18%	30.44%	2.78%
Bone features			
Incomplete cranial elements	100%	100%	100%
Incomplete postcranial elements	95%	92%	90%
Evidence of weathering	0.63%	>5%	>5%
Evidence of Mn impregnation	93.80%	95%	98%
Evidence of corrosion	12.61%	21.55%	18%
Remains with marks	1.21%	2.40%	1.60%
Articulated elements	0.88%	2.72%	0.25%

Table 2. Number of identified specimens (NISP), and minimum number of individuals (MNI) of different micromammals identified in Estancia Ré assemblage.

Taxa	NISP	MNI
Didelphimorphia		
Thylamys zetti	1	1
Thylatheridium sp.	1	1
Didelphidae indet.	2	2
Notoungulata		
Paedotherium minor	328	39
Tremacyllus sp.	5	5
Rodentia		
Reigechimys octodontiformis	21	16
Pampamys emmonsae	6	6
Neophanomys sp.	1	1
Phtoramys sp.	2	2
Octodontoidea indet.	5	5
Abrocoma antiqua	10	4
Palaeocavia sp.	32	15
Caviidae indet.	72	11
Lagostomus (Lagostomopsis) sp.	55	13
Rodentia indet.	56	40
Mammalia indet.	368	–

Notoungulata and Rodentia, and post-cranial elements assigned to Mammalia indet. The hegetotheriid *Paedotherium minor* represents 33.98% of the sample, being the most abundant taxon. Rodents reach 26.95% and are represented mainly by the chinchillid *Lagostomus* (*Lagostomopsis*) sp., the caviid *Palaeocavia* sp. and other undetermined representatives of the same family, and the echimyid *Reigechimys octodontiformis* (Table 2). Eighteen juvenile individuals were identified, 14 of which were assigned to *P. minor* (Fig. 2A). The MNE was 904 (Table 3) and the MNI was 161 (Table 2), the latter calculated on mandibles, the most abundant elements of the assemblage (35.61%).

Few associated or articulated specimens were recovered (*sensu* Behrensmeyer 1991). They were represented by mandibles and maxillae of *P. minor* (Fig. 2B), and vertebrae and metapodials of Mammalia indet. Most remains showed no weathering signs (category 0, *sensu* Andrews 1990), and only 0.63% showed slight splitting of bone parallel to fibre structure (Fig. 2C) (category 1, *sensu* Andrews 1990). Only one specimen showed abrasion signs, evidenced by rounding edges and polish of the outer surface (category 2, *sensu* Alcalá 1994).

Only metapodials, calcanea and astragali were preserved complete (Fig. 2D). Among the incomplete remains, 94.55% showed smooth transverse fractures (Fig. 2E); spiral and stepped fractures (Fig. 2F) are uncommon, occurring only 5.45% of the bones (*sensu* Marshall 1989). All skulls and mandibles were incomplete. Some fragments of palates preserved both dental series (Fig. 2G); but the most frequent portions were maxillary fragments with all, or some of the teeth. Mandibles were mainly represented by body fragments; the absence of the articular condyle, the coronoid process or the whole posterior portion was frequent, in many cases with stepped fractures (Fig. 2H). In rodent mandibles, the loss of incisors is common, whereas mandibles of *P. minor* are commonly badly broken, lacking the posterior portion.

More than 90% of the remains had surficial stains. Of those stained, 47.40% were dark coloured over the entire surface, whereas the remaining presented isolated dark spots, with dendritic habit and different magnitudes (Fig. 2I, J).

Varying degrees of corrosion were identified in 12.61% of the remains, evidenced by slight signs of rounding on the edges, changes in colour and partial loss of the compact bone layer (Fig. 2K). Root traces
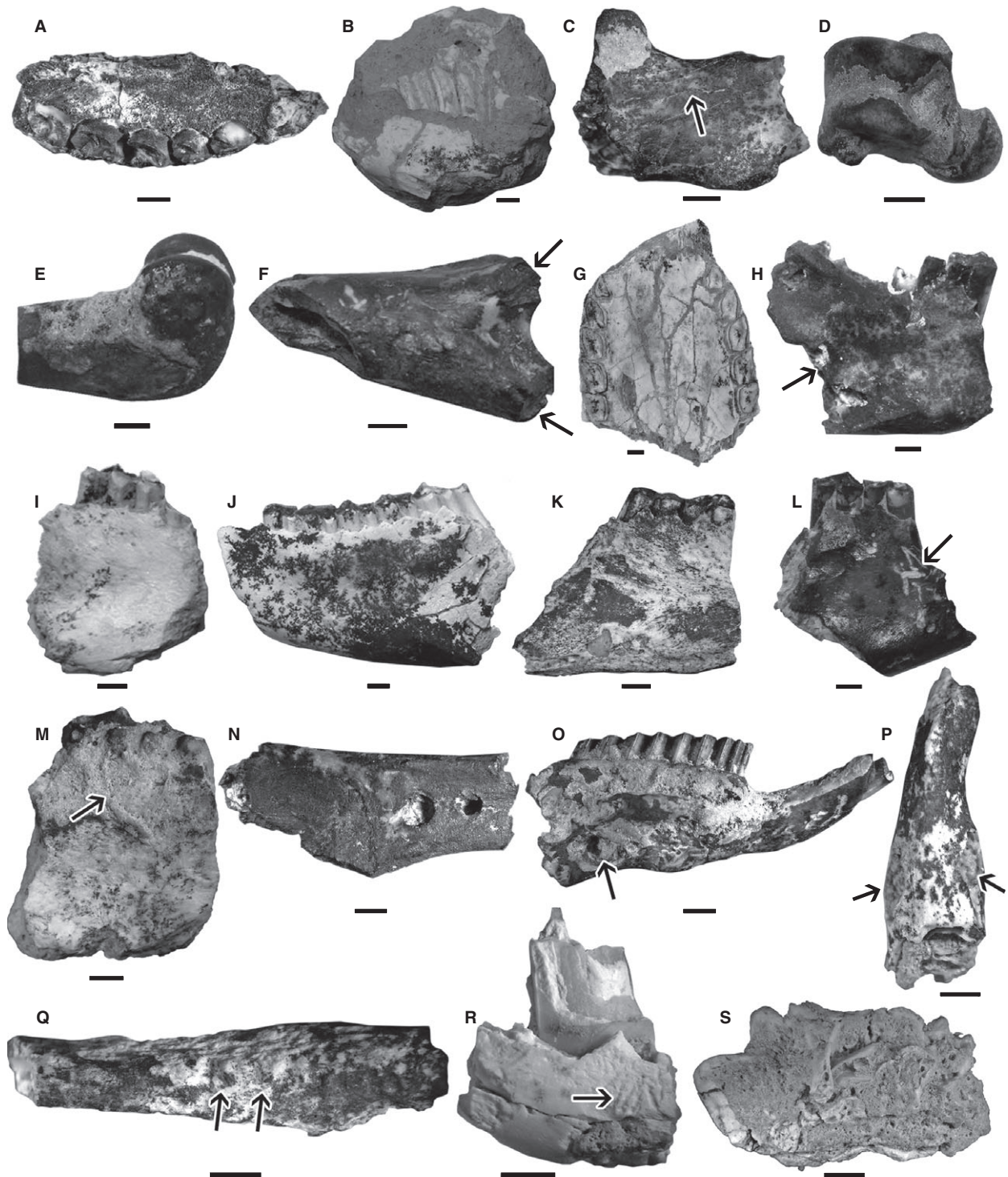
Fig. 2. A, left maxilla of juvenile specimen of *Paedotherium minor*. B, articulated specimen of *P. minor* partially included in calcareous concretion. C, bone fragment with slight splitting of bone parallel to fibre structure. D, astragali with a calcareous micro-crystalline coating. E, smooth transverse fracture on femora. F, spiral fracture on distal humerus. G, complete palate of *P. minor*. H, mandible of *P. minor* with stepped fracture. I, J, mandibles of *P. minor* showing different degrees of impregnation. K, mandible of *P. minor* showing corrosion with change of colour. L, mandible of *P. minor* with Corrosichnia. M, mandible of *P. minor* with rhizoliths. N–P, specimens with circular marks. Q, R, specimens with parallel marks. S, coprolite recovered from Caleufú. Scale bars = 2 mm.

were present in 3.76% of the materials (Fig. 2L) and assigned to the ethological category Corrosichnia (Mikuláš1999).

A calcareous micro-crystalline coating covering part of the outer surface (Fig. 2D) was present on 11.5% of the remains and 8.3% were totally or

Table 3. Minimum number of skeletal elements (MNE) of micromammals in Estancia Ré assemblage.

Skeletal elements	MNE
Mandibles	322
Maxillae	138
Isolated teeth	137
Scapulae	8
Humeri	18
Ulnae	20
Pelves	26
Femora	48
Tibiae	24
Calcanea	21
Astragali	22
Metapodials	85
Vertebrae	35

partially encased in calcareous concretions (Fig. 2B). In three specimens of *P. minor,* rhizoliths development was identified (Fig. 2M).

The average of relative abundance of micro-mammals skeletal elements, calculated on a MNI of 161, was low, and only mandibles and maxillae are well represented. Among the post-cranial elements, the representation of femora is outstanding (Table 4). The ratios of representation of different parts of the skeleton are shown in Table 1. Table 5 shows the percentage of the different portions of the main long bones, all of which were incomplete.

No clear evidence of corrosion by digestive acids was found in the analysed remains. However, different types of marks were present. Some were circular

Table 4. Relative abundance of micro-mammal skeletal elements considering the MNI of 161.

Skeletal elements	% relative abundance
Mandibles	100.00
Maxillae	38.82
Scapulae	2.48
Humeri	5.59
Ulnae	6.21
Pelves	8.07
Femora	14.91
Tibiae	7.45
Calcanea	6.52
Astragali	6.83
Average	**19.69**

Table 5. Breakage of postcranial elements in the micro-mammals of Estancia Ré assemblage.

	% Femur	% Humerus	% Tibia	% Ulna
Proximal	47.92	16.67	25	100
Distal	45.83	50	62.50	0
Shaft	6.25	33.33	12.50	0

punctures with irregular margins, with an average length of 1.94 mm (range = 3.90–0.45 mm) and an average width of 1.54 mm (range = 3.00–0.30 mm). In two specimens, these puncture marks were present on both sides of the bones (Fig. 2N–P). Other marks included elongated and parallel scoring with U-shaped cross-section, generally on the margins of the element (Fig. 2Q,R).

Discussion

Taphonomic analysis

The taphonomic features of the Estancia Ré assemblage were compared with those of Caleufú and Telén (Table 1). Estancia Ré assemblage is from small area (5200 m^2), with a density of 0.70 remains/m^2. This value is larger than that obtained in Telén and much smaller than that of Caleufú. In the three localities, almost 50% of the recovered remains were indeterminable both anatomically and taxonomically.

Micro-mammal remains from Estancia Ré represented approximately 85% of the total specimens. This value is higher than that of Telén and lower than that of Caleufú. In turn, Estancia Ré has a lower taxonomic diversity than the other two localities.

The comparison of the percentages of each skeletal element in the three assemblages showed cranial materials are the most common elements and the only ones to exceed 10% frequency. Mandible percentages are also relatively common in the three localities (Fig. 3).

The minimum number of individuals calculated for Estancia Ré was lower than that recorded for Caleufú and Telén. The most frequent taxon in the
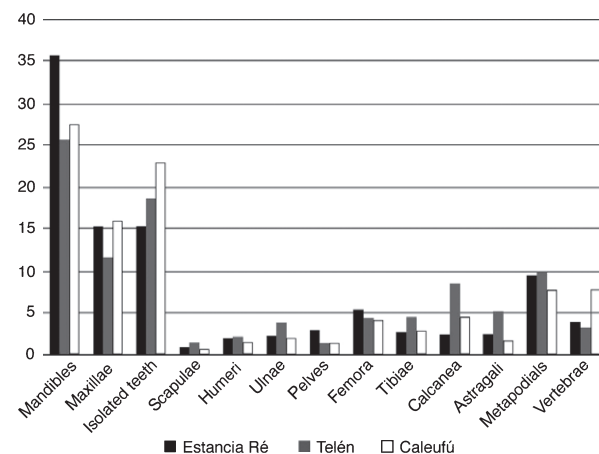

Fig. 3. The percentage of skeletal elements (MNE) from Estancia Ré, Telén and Caleufú assemblages.

three localities was *Paedotherium minor* (Estancia Ré, MNI = 39; Caleufú, MNI = 96; Telén, MNI = 120), representing between 24% and 49% of the total specimens. On the other hand, in Estancia Ré, the number of individuals interpreted as juveniles was higher than in Telén but much lower than in Caleufú.

The assemblage of Estancia Ré has a low average of representativeness (<20%) of the different skeletal elements according to the MNI, and only the relative abundance of mandibles and maxillae is outstanding. Among the post-cranial material, femora have the best representation. The curve of skeletal representativeness of Estancia Ré is similar to those recorded in Telén and Caleufú (Fig. 4). At all the three localities, ratios of representation of: (1) cranial elements were higher than for any other anatomical region, and (2) proximal limb elements (femora and humeri) were better represented than distal limb elements (tibiae and ulnae).

The percentage of articulated specimens of Estancia Ré was low, intermediate between those in Telén and Caleufú. In the three localities, disarticulated and isolated remains prevail. These data indicate that few remains preserved the connective tissues during burial.

In all the three localities, the only some skeletal elements that were complete are structurally dense (e.g. metapodials). The percentage of incomplete skeletal elements was very high in the three localities. All skulls were incomplete, and only fragments of maxillae were frequent; mandibles were relatively complete albeit lacking the posterior portion. All long bones were broken, and proximal portions of ulnae and femora, and distal portions of humeri and tibiae prevailed.

The most common type of fracture in all three localities was smooth transverse indicating they were produced after bones lost their organic components (Gifford-Gonzalez 1989; Andrews & Fernández-Jalvo 1997). However, spiral and stepped fractures were identified, which are produced when the bone is still

fresh (Gifford-Gonzalez 1989; Andrews & Fernández-Jalvo 1997). Activities of predators/scavengers and trampling prior to the burial are the processes that cause spiral fractures (Gifford-Gonzalez 1989) and could be explain the predominance of complete small anatomical elements (Andrews 1990). However, other diagnostic characters (e.g. lines and grooves) indicative of trampling were not observed.

Few micro-mammal remains of the three localities showed any evidence of weathering by atmospheric agents. The elements from Estancia Ré presented good preservation of their surface, and in the cases in which it was affected, modifications may be clearly attributed to processes other than weathering (e.g. corrosion). These features suggest, such as stated for Caleufú and Telén, that most materials was quickly buried (Behrensmeyer 1978; Andrews 1990).

Only a one element at Estancia Ré was abraded. In the three assemblages, mandibles and maxillae were the dominant bones, and other elements included in different groups according to their transport susceptibility are also represented (Dodson 1973; Cheme Arriaga *et al.* 2012). The presence of bones with low (mandibles) and high (maxillae, vertebrae) susceptibility to transport indicates neither water nor wind played a role in the development of the assemblage.

The abundance of remains with black outer surface is notable often in dendritic pattern in the three localities. The enrichment with manganese and subsequent precipitation as oxides is one of the main processes by which the materials are impregnated and acquire a dark colour (e.g. Shahack-Gross *et al.* 1997; López-González *et al.* 2006; Marín Arroyo *et al.* 2008). The manganese soluble form (Mn^{++}) is transported by water circulating through the sediments. However, an increase in the pH and Eh conditions of the micro-environment of preservation results in the precipitation of manganese oxides (Diez *et al.* 1999; López-González *et al.* 2006; Marín Arroyo *et al.* 2008).

Evidence of corrosion, traces produced by roots, micro-crystalline calcareous coatings, total or partial inclusion in calcareous concretions and development of rhizoliths are all present at Estancia Ré. These characteristics are associated with the soil processes in which the remains were accumulated (Montalvo 2004b). All these attributes were also present on bones at Telén and Caleufú (Montalvo 2002a, 2004b; Montalvo *et al.* 2005, 2008).

Finally, and as it was reported for Caleufú and Telén (Montalvo 2004b; Montalvo *et al.* 2008), no clear signs of digestive action were identified in any skeletal element of Estancia Ré. However, a few specimens showed two types of marks on the outer surface (scoring and punctures). Such marks were
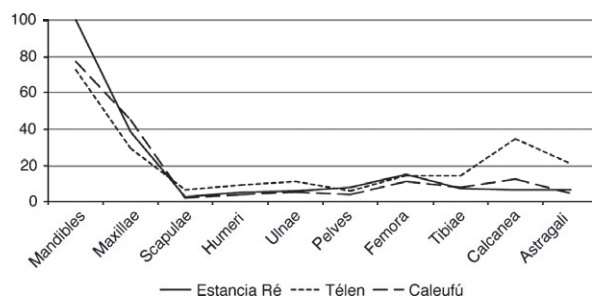

Fig. 4. Relative abundance of skeletal elements identified in Estancia Ré, Telén and Caleufú assemblages.

also identified in the remains of Caleufú and Telén. Punctures are similar to those produced by pressure of teeth in assemblages of bones gathered by modern predators (Lyman 1994) and may be related to predation by carnivore mammals (Mondini 2003). Lloveras *et al.* (2011) pointed out that the presence of punctures with irregular margins, such as those observed in many elements of the studied assemblages, may indicate the action of mammals. The described scoring may also be attributed to the activity of predator mammals (Andrews & Fernández-Jalvo 1997; Mondini 2003; Domínguez-Rodrigo & Barba 2006). In relation to this, it is noteworthy that coprolites were recovered in Caleufú and Telén (Fig. 2S), and those of Caleufú were interpreted carnivorous mammal coprolites (Montalvo 2004a).

Origin of the accumulation

The diversity of taphonomic features described above have provided the following characteristic traits: (1) high density of remains in a small area; (2) predominance of disarticulated elements; (3) high frequency of cranial elements and low frequency of post-cranial elements; (4) preferential preservation of some regions of the cranial and post-cranial elements; (5) marks interpreted as tooth marks; (6) presence of spiral fractures; (7) almost total absence of abrasion; and (8) no evidence of wind or water transport. These taphonomic characteristics suggest that the assemblage of micro-mammals recovered from the Late Miocene levels of the Cerro Azul Formation, in the locality of Estancia Re, was accumulated due to the activity of predators.

The taxonomic representation suggests a selection of prey towards certain taxa [*Paedotherium minor* and the rodents *Lagostomus* (*Lagostomopsis*) sp., *Palaeocavia* sp. and *Reigechimys octodontiformis*] and, in addition, towards juvenile individuals.

The micro-mammal assemblage of Estancia Ré has the same taphonomic signatures as those of Telén and Caleufú, whose origin was also related to predation processes (Montalvo 2002b, 2004b; Montalvo *et al.* 2008). However, no clear evidences of modifications produced by digestive acids were found in any of these assemblages, as expected in accumulations produced by a predator (Korth 1979; Andrews 1990).

Comparisons between fossil assemblages and modern accumulations produced by different predators are a tool to identify, at least in broad categories, the possible agent (Cochard 2008; Lloveras *et al.* 2010). Considering the modern accumulations of micro-mammal skeletal elements from disaggregation of faeces and pellets, Andrews (1990) classified

predators in three groups: owls, diurnal raptors and mammalian carnivores. Owl pellets result in minimal modification of the bones of the ingested prey. These accumulations have good anatomical representation, the skeletal elements are rarely broken, and evidences of digestive action are absent or minimal (Andrews 1990). Although in the materials of Estancia Ré, Telén and Caleufú, no evidence of digestive action was identified, the strong differences found in the anatomical representation, indexes of representativeness, types of breakage and the presence of remains with tooth marks argue against these birds as producers of these accumulations.

Diurnal raptors and carnivore mammals produce accumulations of digested remains with percentages of anatomical representation with low averages, better representativeness of cranial elements and a high degree of breakage of cranial and post-cranial remains. In these cases, there are always a high percentage of bones with clear and, in general, strong and extreme evidence of digestive action (Andrews 1990). Even though small, delicate bones can be destroyed by digestive processes, decreasing its preservation potential (Lloveras *et al.* 2010), the complete absence of remains with evidence of corrosion by digestion in Estancia Ré, Telén and Caleufú assemblages is significant. Also of significance, is that at all these sites of juvenile individuals were preserved (as well as avian remains in the two latter localities), which, by their nature, tend to be quickly destroyed (Behrensmeyer *et al.* 2003). Given these comparisons, the absence of evidence of digestive action allows to discard the possibility that the three assemblages correspond to accumulations originated by disaggregation of faeces or pellets (*sensu* Mellet 1974; Mayhew 1977).

The study of modern predators shows that many of them accumulate uneaten portions of their prey in nests, perches, latrines and den entrances (Andrews & Evans 1983; Andrews 1990). Such behaviour, observed in some raptor birds and mammalian carnivores, can occur when the prey are larger than the predator or as a mechanism of storage when prey is abundant (Andrews 1990). In such cases, the accumulated skeletal elements do not present evidence of digestive corrosion and, occasionally, may have marks related to the handling of the prey. Although some observations on modern predators indicate the possibility of mixing between eaten and uneaten skeletal elements, usually these studies report only the origin of the samples (e.g. nests, latrines) without differentiating these two types of remains (e.g. Lloveras *et al.* 2012). So far, the studies that differentiate between eaten and uneaten small mammal remains from a single predator are scarce

(e.g. Montalvo & Tallade 2009, 2010; Lloveras *et al.* 2012; Rodríguez-Hidalgo *et al.* 2013). Concerning the accumulations of small mammal remains not eaten by mammalian carnivores and raptor birds, studies are focused on anatomical representation, degree of breakage and the presence of tooth or beaks marks (Table 6).

These examples exhibit clear differences (mainly in anatomical representation) among uneaten bone samples produced by different predators. Even the accumulations of undigested remains of a single predator may also show different features in the anatomical representation and degree of breakage of the skeletal elements, which are attributed to variations of behaviour (Rodríguez-Hidalgo *et al.* 2013).

In the assemblages of the Late Miocene here studied, there are clear differences in the involved taxa (both prey and predator) with any modern accumulation. Also, when comparing modern and fossil accumulations, it is important to consider the influence of the processes affecting fossils, both before and after the burial, which overprints the above attributes. All these issues hinder the interpretation of the origin of these accumulations. However, the data obtained in the three localities, particularly the absence of corrosion by digestion, suggest that the micro-mammal assemblages correspond to accumulations formed by non-ingested prey remains. This implies, in turn, that the predator performed a selective use of certain portions of the body of the prey.

Although it is not possible so far to determine the kind of predator involved, the presence of tooth marks on some remains and the record of coprolites in the same levels, in Telén and Caleufú, suggest it was a small mammalian carnivore. Possible carnivore mammals could be Marsupialia (Sparassodonta and Didelphimorphia), recorded in several Late Miocene assemblages of La Pampa (Goin *et al.* 2000; Montalvo *et al.* 2008).

Assemblages produced by predators have a local spatial resolution and a temporal resolution between 10^{-2} and 10^2 years (Behrensmeyer & Hook 1992; Behrensmeyer & Chapman 1993), depending on the behaviour of the predator (Mellet 1974; Brain 1980; Andrews 1990). The specimens of micro-mammals recovered in Estancia Ré, as well as those of Telén and Caleufú, present characteristics indicating homogeneity in the processes that affected them before and after burial, which supports the contemporaneity of each assemblage and suggests their accumulation in a very short lapse. This information support previous biochronological proposals for the Cerro Azul Formation, which indicate that the assemblages from several localities of La Pampa Province represent different short intervals within

Table 6. Taphonomic attributes analyzed on uneaten small mammal remains accumulated by carnivore mammals and raptor birds.

Citation	Prey	Predator	Anatomical representation	Average relative abundance	Complete remains	Degree of breakage	Marks	% marks
Álvarez *et al.* (2012)	Leporids	*Leopardus geoffroyi* (Geoffroy's cat)	Prevalence of mandibles, maxillae, pelves, femora and tibiae. Ribs: absent. Low representativeness of vertebrae and scapulae.	40.20%	88.8%	Skulls mainly broken, but maxillae were preserved. Mandibles represented by dentary.	Tooth marks.	19.80%
Rodríguez-Hidalgo *et al.* (2013)	Leporids (two samples)	*Lynx pardinus* (Iberian lynx)	Prevalence of postcranial elements. Cranial remains: scarce. Greater survival of hindlimbs over forelimbs.	Sample A: 56.83% Sample B: 18.39%	37.6%	Predominance of distal portions of the limbs.	Tooth marks.	0.90%
Lloveras *et al.* (2012)	Leporids	*Vulpes vulpes* (red fox)	Prevalence of tibiae and metatarsals. Cranium, incisors, upper molars, femora, scapulae and ribs: absent.	25.60%	89%	Skulls: broken. Mandibles represented by dentary.	Tooth marks.	9.50%
Montalvo & Tallade (2009, 2010)	Rodents	*Caracara plancus* (crested caracara)	Prevalence of mandibles and maxillae.	8.79%	High degree of integrity mainly in cranial elements.	Predominance of proximal portions of the limbs.	Attributed to action of the beak or claws.	4%

the Huayquerian Stage/Age (Verzi *et al.* 2008, 2011; Sostillo *et al.* 2014). The presence of the Echimyidae *Reigechimys octodontiformis* suggests that the Estancia Ré assemblage is younger than that of Telén, where *R. plesiodon* is present, and older than Caleufú, where *Reigechimys* has not been recorded, but other taxa indicate it is assignable to the latest Miocene (Verzi *et al.* 1994, 2008; Montalvo *et al.* 2008; Verzi & Montalvo 2008; Sostillo *et al.* 2014).

Conclusions

Considering the recorded characteristics (high density of remains in a stratigraphically limited unit, abundance of micro-mammal individuals, high diversity of taxa, estimated body masses <5 kg), the small mammal assemblages of Estancia Ré, Telén and Caleufú (La Pampa Province, Argentina), from the Late Miocene levels of the Cerro Azul Formation, can be defined as micro-fossil bonebeds (*sensu* Eberth *et al.* 2007; Rogers & Kidwell 2007). The notoungulate *Paedotherium minor* and the caviid and chinchillid rodents prevail in all of them.

The remains of Estancia Ré were affected by diverse processes occurred before and after burial and display similar taphonomic histories to those interpreted in previous studies for Telén and Caleufú. The attributes recognized in the three localities support the proposal of accumulations originated by the activity of a predator, which have a local spatial resolution and represent short intervals. The absence of digestive corrosion marks in remains from the three localities indicates that the assemblages represent accumulations of uneaten body parts. This feature indicates assemblages are not scatological accumulations or accumulations formed by a mix of eaten and uneaten remains. Some evidences (e.g. coprolites, tooth marks) support the interpretation of carnivore mammals as the agents that produced these accumulations.

The similarity of taphonomic signatures, coupled with the similarities in the sedimentary context at all three localities, indicate that bonebeds are product of a single taphonomic mode (*sensu* Behrensmeyer 1988), 'leftover prey remains'. Beyond the temporal differences between the localities (Telén, Estancia Ré and Caleufú), this taphonomic mode demonstrates the processes were present repeatedly though time in different areas of the same region.

This analysis provides a framework for the evaluation of new fossil assemblages with similar characteristics that contrast with previously recognized taphonomic modes, such as faeces and pellets (*sensu* Behrensmeyer & Hook 1992) that include micro-vertebrate assemblages formed by the accumulation of digested skeletal elements.

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