



First record of a Late Holocene fauna associated with an ephemeral fluvial sequence in La Pampa Province, Argentina. Taphonomy and paleoenvironment



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ABSTRACT

The first Late Holocene mammal assemblage (mainly micromammals) of La Pampa Province was found in Quehué paleontological site, associated with an ephemeral fluvial sequence. Taphonomical features of the collected materials were evaluated in order to increase the knowledge of the ancient vertebrate communities of this area and to interpret the origin of the assemblages. Field data and taphonomic analysis of the specimens, suggested the recognition of three assemblages with different taphonomic histories: 1) large to medium sized mammals; 2) micromammals found inside burrows or associated with them; and 3) discrete accumulations of micromammals and other microvertebrates (amphibians, reptiles and birds). Additionally, the paleoenvironmental analysis based mainly on the record of small mammals reflected the predominance of semi-arid conditions associated with a mosaic of open shrub steppe, grasslands and xerophytic forests of Espinal, similar to the present one in the Quehué valley area. However, the presence of *Lestodelphys halli* in the Quehué site during the Late Holocene (~1.2 ky BP), suggests a more heterogeneous environment and perhaps relative colder and drier than current times, which are featured by more mesic conditions and anthropic activities, mainly agriculture and livestock during the last centuries.

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1. Introduction

Quaternary vertebrate faunas from central Argentina are among the richest and most diverse of South America. It is well-known that the Pampean Region of Argentina has provided the basis for the chronobiostratigraphic continental scheme of South America (Cione and Tonni, 2005; Cione et al., 2015). The record of small mammals recovered in the last decades largely increased the knowledge of the communities inhabiting the area during this interval. However, detailed taphonomic studies that supply information for the understanding of the origin of the assemblages are

still scarce (e.g. Pardiñas, 1999, 2001, 2004; Cenizo and De los Reyes, 2008; Montalvo et al., 2012; Quintana, 2015; Tomassini et al., 2017). It is worth highlighting that there are no studies of Late Holocene fauna records toward the western Pampean Region (i.e. La Pampa Province). In addition, paleoenvironmental studies in La Pampa Province are scarce, including a sedimentological and palynological analysis of Salina Anzoátegui in the south-east (Schäbitz, 1994) and a sedimentological analysis of Quehué valley in the central-east (Mehl, 2011; see below).

The fauna analyzed in this contribution comes from the middle levels of a Late Holocene sedimentary sequence that crops out at Quehué paleontological site. This is the first Late Holocene record for La Pampa Province. The aim of this paper is to analyze the taphonomic features of the materials recovered from the fluvial

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deposits of this site to interpret the origin of the assemblages. The taphonomic study provides new information on the preservation of skeletal remains in different contexts within fluvial environment and serves as a frame of reference for the analysis of similar assemblages recovered from Holocene paleontological and archaeological sites. In addition, on the basis of the record of small mammals, a paleoenvironmental analysis is presented.

2. Geographic and stratigraphic setting

The Quehué paleontological site is located in the Quehué valley (~37°S, 65°W, La Pampa Province; Fig. 1a), in the western part of the Pampean Region known as Dry Pampas. The climate of the Pampean Region is determined by the Atlantic anticyclone, which reduces its effects regionally from northeast to southwest. This results in a heterogeneous climate, which changes gradually from humid in the northeastern area (mean annual precipitation of 1200 mm; mean annual temperature of 18 °C) to dry sub-humid in the southwestern area (mean annual precipitation of 600 mm; mean annual temperature of 14 °C; Burgos, 1968). Quehué valley is included in the Espinal Phytogeographic Province (Fig. 1a), dominated by xerophytic forest (*Prosopis caldenia*), but also having grasslands (*Stipa* spp.), creosote bushes (*Larrea* spp.) scrublands (*Condalia microphylla* and *Prosopis flexuosa*), and deforested agricultural land and pastures (Cabrera, 1976). This area is characterized by the presence of strigiform birds such as *Tyto alba* (barn owl), *Athene cunicularia* (burrowing owl), *Bubo virginianus* (great horned owl) and *Asio flammeus* (short-eared owl). It also includes several mammal species such as the white-eared opossum (*Didelphys albiventris*), cougars (*Puma concolor*), wild cats (*Leopardus* spp. and *Puma yagouaroundi*), armadillos (*Chaetophractus* spp.), foxes (*Lycalopex gymnocercus*), grisons (*Galictis cuja*), skunks (*Conepatus chinga*) and numerous rodents.

The Late Quaternary alluvial sequence of the Quehué valley crops out with a lateral continuity of several hundred meters and a 3-m-average thickness forming a terrace along the banks of the Quehué ephemeral creek, that drains approximately 30 km of the valley (from ~37°06'42"S - 64°52'27"W to ~37°01'16"S - 64° 31' 46"W; Fig. 1b). The present-day talweg of the stream is located at the stratigraphic contact between Late Quaternary and Late Miocene (Cerro Azul Formation) deposits (Fig. 1e); the last one, also forming the structural plain in which the Quehué valley has been carved.

In the area of the Quehué paleontological site, where fossil specimens were found, the lower section of the Late Quaternary sequence, named Unit 1 in this contribution (Lithofacies 1 in Mehl and Zárate, 2008, Fig. 1c; d), exhibits horizontally laminated clayey silts and an incipient spongy pedological structure -paleosol- on its top most part. Some megamammals, i.e. Toxodontidae indet. (Notoungulata) and *Neosclerocalyptus* sp. (Xenarthra, Glyptodontidae), were recovered from the base of this sequence (Montalvo et al., 2007; Bargo et al., 2010). Recently, two mandible fragments assigned to *Hippidion* sp. (Equidae, Perissodactyla) were also recovered in this level. The sedimentary organic matter content on the topmost part of the paleosol was dated and yielded an age of 9040±580 ¹⁴C years BP, indicating a minimum age for the soil -close to the end of soil forming processes due to the burial- (Mehl and Zárate, 2008).

Unit 1 is covered by massive silty very fine sands with common calcium carbonate clasts, corresponding to the Unit 2 (Lithofacies 3 in Mehl and Zárate, 2008, Fig. 1e); it shows an undulate and abrupt lower limit with sandy-clayey silts clasts cemented by calcium carbonate, indicating a likely drier and warm atmosphere (Mehl, 2011). Laminated and/or massive infilled burrows with a tunnel average diameter of 8 cm were recorded in this level (Fig. 1f).

Vertebrate specimens recovered from Unit 2 are evaluated in this paper (Fig. 1g and h). The topmost part of this unit is slightly harder and has faint red oxidation color (poorly developed soil). The sedimentary organic matter content was dated and yielded an age of 1258±75 ¹⁴C years BP (Mehl and Zárate, 2008).

Units 1 and 2 were aggraded from water flows transporting silt and fine sand as suspended load (Mehl and Zárate, 2008). The generation of sedimentary aggradation processes in a fluvial environment of ephemeral characteristics suggests seasonal or sporadic water availability in the fluvial valley (Mehl, 2011). The development of pedogenetic processes in the topmost part of the silty sand deposits of Unit 2 would indicate a new period of better conditions and stability, possibly associated with regional reconstructions of the climatic event of the Medieval Climatic Anomaly (MCA) (Mehl, 2011).

The basal part of Unit 2 exhibits a lateral change to a paludal deposit of limited areal distribution, defined here as Unit 2a (Lithofacies 2 in Mehl and Zárate, 2008, Fig. 1d). An age of 8083±73 ¹⁴C years BP was obtained based on sedimentary organic matter content (Mehl and Zárate, 2008). It indicates deposition in a temporary waterlogged environment in some moment during the Early Holocene. The deposit of Unit 2a is cover by sediments of the upper part of Unit 2.

The predominantly fluvial sequence of Unit 1, 2 and 2a was buried by a silty very fine sand cover of eolian genesis according to regional evidences (Lithofacies 4 in Mehl and Zárate, 2008, Fig. 1d). Likely this eolian aggradation process, could be related to the climatic conditions of the Little Ice Age (LIA) (Mehl, 2011).

3. Materials and methods

Vertebrate specimens were recovered from Unit 2 which is the fossiliferous unit and objective of this paper. Field observations suggested the existence of assemblages with different taphonomic histories preserved in a single deposit; thus, sampling, collection of materials, and taphonomic evaluation were made considering this context. The specimens are housed in the collection of the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa (acronym GHUNLPam), La Pampa Province, Argentina.

Mammals were classified as small (micromammals, <1 kg), medium (1–44 kg) and large (>45 kg) according to the categories proposed by Martin and Steadman (1999), commonly used in archaeology and paleontology. Taphonomic features were analyzed with a Leica MS 5 binocular light microscope. Some specimens were 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).

Frequency and diversity of taxa in each assemblage were estimated with the following indexes. NISP (number of identified specimens per taxon), MNI (minimum number of individuals) and MNE (minimum number of elements), according to Badgley (1986). MNI was calculated on the basis of the most abundant element per taxon, except for Dasypodidae. In this latter case, a MNI = 1 was considered for each of the identified species, because of the large amount of osteoderms present in the carapace and the high degree of disarticulation and dispersion of these elements (Montalvo, 2004). In the micromammal assemblage recovered inside burrows or associated with them, each association of specimens recorded was considered as MNI = 1.

The index isolated teeth/isolated vertebrae (Behrensmeyer, 1975; Behrensmeyer and Dechant Boaz, 1980), provides a criterion for determining if a group of bones was selectively biased before burial, and can be considered as an indicator of the degree of hydrodynamic sorting. The groups proposed by Voorhies (1969),

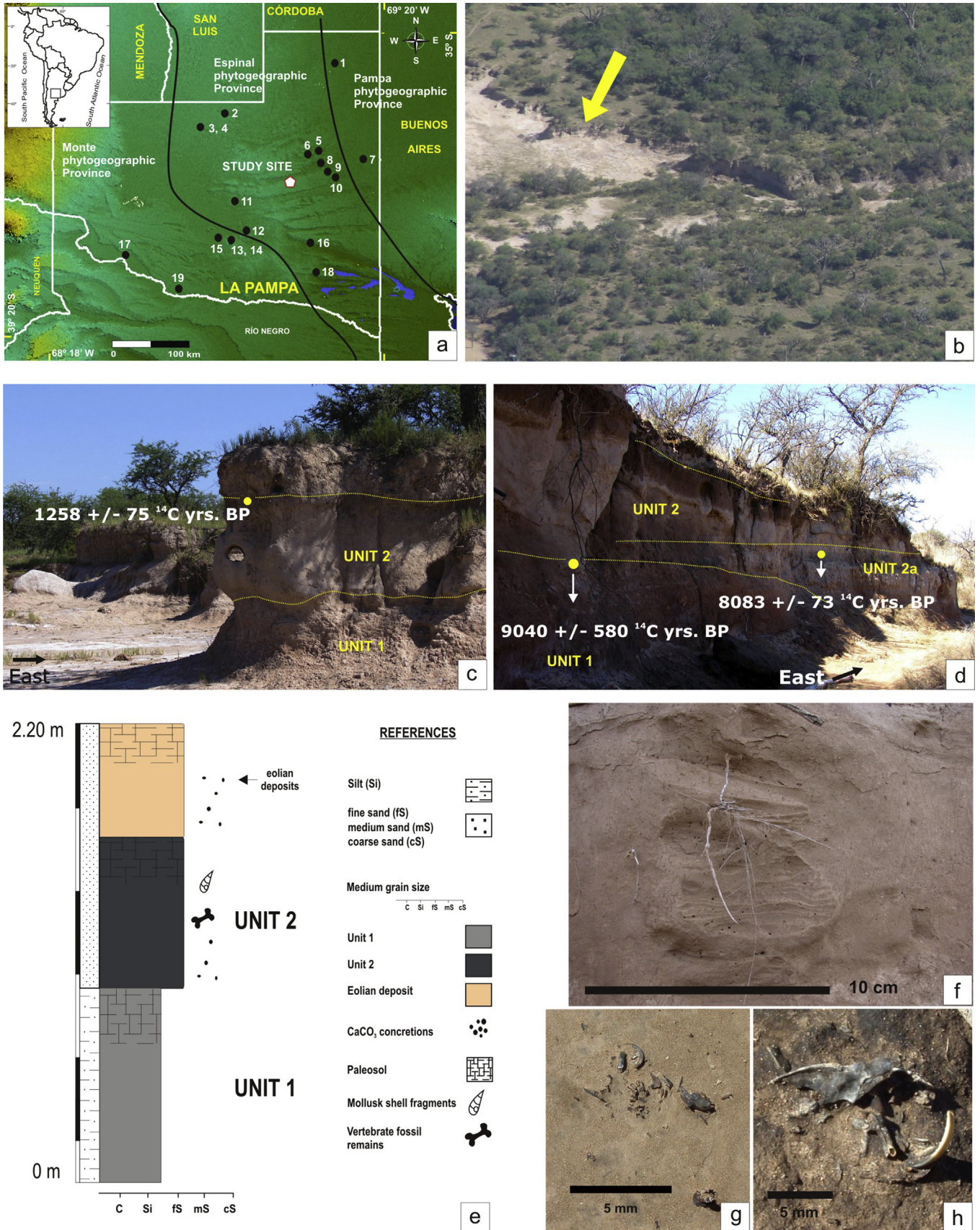


Fig. 1. **a.** Location map showing phytogeographic provinces, Quehué paleontological site and recent owl pellet samples: 1. Alta Italia; 2. Estancia La Elenita; 3, 4. Curru-Mahuida; 5. Viviero Forestal Provincial; 6. Laguna Don Tomás; 7. Colonia San Miguel; 8. Bajo Giuliani; 9. Cantera Santa Rosa; 10. Reserva Parque Luro; 11. Estancia Arco Iris; 12. Estancia Los Ranqueles; 13, 14. Parque Nacional Lihué Calel; 15. Estancia La Manuela; 16. Estancia Luan Cura Hué; 17. Casa de Piedra; 18. Cuchillo Có; 19. Gobernador Duval. **b.** Panoramic view of the Quehué valley at the study area (see arrow). **c.** View of the outcrops near the study area showing units 1, 2 and 4, and chronology of the section. **d.** View of outcrops, near the study area, showing units 1-4, and chronology of the section. **e.** Stratigraphic column of Quaternary units at the study area, showing the bearing level. **f.** Cross section of burrow in Unit 2. **g, h.** Discrete accumulations of micromammals in Unit 2.

according to the susceptibility of the different skeletal elements to be mobilized by water, allow evaluating the hydrodynamic sorting. These two methodologies were calculated in the large to medium sized mammal assemblage.

3.1. The following taphonomic attributes were analyzed

- Articulation degree, according to the classification proposed by Behrensmeier (1991): articulated, disarticulated but associated, and disarticulated and isolated.
- Breakage degree, whether the specimens (cranial and postcranial element were complete or incomplete. The type of fractures (smooth transverse, spiral and stepped; sensu Marshall, 1989) was analyzed in the incomplete specimens.
- Weathering degree, the following categories were considered for micromammals (modified from Andrews, 1990); 0: unweathered specimens (without alteration); 1: specimens showing surface slight splitting, parallel to the fibrous structure; 2: specimens showing more intense splitting, but little exfoliation. For medium to large mammals, the categories proposed by Alcalá (1994) were considered; 1: intact specimens; 2: specimens showing surface loss of bone material; and 3: specimens showing deep loss of bone material.
- Abrasion degree, following the categories proposed by Alcalá (1994); 1: intact specimens; 2: rounded specimens; and 3: polished specimens.
- Impregnation degree, considers the presence or absence of color changes due to the precipitation of manganese oxides. Different types of pigmentation caused by oxides impregnations have been distinguished following the classification proposed by Marín Arroyo et al. (2008); Type 0: typical light coloration; Type 1: light surface and small, dark brown, circular and internal stains; Type 2: uniformly light brown tone and glossy appearance; Type 3: uniformly dark brown tone and matt appearance; Type 4: uniformly black with occasional irregular bluish stains superimposed on the black pigmentation.
- Presence or absence of tooth marks and other bioerosive marks.

In order to determine whether the micromammal assemblage was accumulated by predators, specimens were evaluated according to the taphonomic methodology proposed by Andrews (1990) and Fernández-Jalvo and Andrews (1992), which includes the

following indexes and analyses:

- Assessment of the relative abundance of skeletal elements considering the representation of each element in the context of the $MNI = MNE_i / (E_i \times MNI) \times 100$, where MNE_i is the minimum number of a given skeletal element in the sample, and E_i is the expected number of that skeletal element in an individual.
- Calculation of indexes of proportion of elements: relation between cranial and postcranial elements (femora + humeri)/(mandibles + maxillae) = $f + h / md + mx$, and relation between proximal and distal limb elements (tibiae + ulnae)/(femora + humeri) = $t + u / f + h$.
- Evaluation of the postcranial breakage degree (femora, humeri, radii, tibiae and ulnae; complete or proximal and distal portions), comparing the number of complete specimens against the number of proximal, shaft, and distal portions.
- Analysis of the degree of digestive corrosion, performed mainly on teeth, proximal portions of femora, and distal portions of humeri. Differences among modifications by digestion in teeth of the rodents Cricetidae, Ctenomyidae and Caviidae were evaluated according to the methodology proposed by Fernández et al. (2017).

Small mammals have been widely used as indicators of paleo-environmental conditions since they are abundant and diverse in the archaeological and paleontological records. Most taxa have relatively narrow environmental requirements, being frequently associated with particular microenvironments. Paleocological inferences are usually based on presence/absence of some species and/or relative changes of their frequencies (e.g. Andrews, 1990; Pardiñas, 1999).

Taking into account that taphonomic and taxonomic evidences suggest strigiform birds as the main producers of the discrete accumulations of microvertebrates (see Discussion), paleoenvironmental reconstruction was based on comparisons between both fossil and living small mammal assemblages derived from pellets samples produced by *Tyto alba* and *Athene cunicularia* that were recovered from nest and roosting sites at precise localities of Monte, Espinal and Pampa biomes (La Pampa Province) (Table 1, Fig. 1a). Correspondence analysis was performed in order to explore species and samples ordination in multivariate space selecting those fossil and current small mammal samples with $MNI \geq 50$, after

Table 1
Recent owl pellet samples (*Tyto alba* and *Athene cunicularia*) from La Pampa Province. Samples are listed from north to south (expressed in MNI). ID corresponds to numbers used in Fig. 1a. Abbreviations: **Aa.** *Akodon azarae*. **Ad.** *Akodon dolores*. **Ca.** *Calomys* spp. **Ct.** *Ctenomys* spp. **Et.** *Eligmodontia typus*. **Gg.** *Graomys griseoflavus*. **Gl.** *Galea leucoblephara*. **Ma.** *Microcavia australis*. **Nl.** *Necromys lasiurus*. **Of.** *Oligoryzomys flavescens*. **Ol.** *Oligoryzomys longicaudatus*. **Ra.** *Reithrodon auritus*. **Tp.** *Thylamys pallidior*. **P.** Pampa phytogeographic Province. **E.** Espinal phytogeographic Province. **M.** Monte phytogeographic Province.

ID	Localities	Aa	Ad	Ca	Ct	Et	Gg	Gl	Ma	Nl	Of	Ol	Ra	Tp	Total	Owl	References
1	Alta Italia (P)	4	4	296	0	0	0	0	0	0	3	0	2	0	305	<i>Tyto</i>	Massoia and Vetrano (1988)
2	Estancia La Elenita (E)	11	3	131	0	0	19	0	0	0	0	0	1	0	154	<i>Tyto</i>	Tiranti (1988)
3	Curru-Mahuida (E)	0	1	10	72	3	0	1	0	0	0	0	0	11	98	<i>Athene</i>	Solaro et al. (2012)
4	Curru-Mahuida (E)	31	68	158	18	17	5	0	0	4	1	0	0	14	285	<i>Tyto</i>	Solaro et al. (2012)
5	Vivero Forestal Provincial (E)	10	1	52	1	0	2	0	0	0	2	0	3	0	61	<i>Tyto</i>	Tiranti (1988)
6	Laguna Don Tomás (E)	1	0	1	3	0	0	0	0	0	0	0	0	0	4	<i>Athene</i>	Montalvo and Tejerina (2009)
7	Colonia San Miguel (P)	0	0	54	0	0	0	0	0	0	0	0	0	0	54	<i>Tyto</i>	Tiranti (1988)
8	Bajo Giuliani (E)	12	11	114	1	69	5	0	1	0	6	0	47	4	258	<i>Tyto</i>	De Santis et al. (1983)
9	Cantera Santa Rosa (E)	5	1	47	3	212	6	0	0	0	5	0	11	0	285	<i>Tyto</i>	Tiranti (1994)
10	Reserva Parque Luro (E)	11	71	155	1	78	20	1	0	0	6	0	6	7	345	<i>Tyto</i>	Tiranti (1994)
11	Estancia Arco Iris (E)	1	2	9	0	7	0	0	0	0	0	0	1	3	22	<i>Tyto</i>	Tiranti (1988)
12	Estancia Los Ranqueles (E)	7	45	47	7	53	34	1	0	0	2	3	4	10	206	<i>Tyto</i>	Tiranti (1988)
13	Parque Nacional Lihué Calel (M)	5	149	46	56	17	34	1	3	0	0	8	8	14	336	<i>Tyto</i>	Fracassi et al. (2004)
14	Parque Nacional Lihué Calel (M)	0	1	19	56	17	3	0	1	0	0	0	8	4	109	<i>Athene</i>	Tommaso et al. (2009)
15	Estancia La Manuela (M)	0	5	4	38	35	23	1	1	0	0	0	2	8	117	<i>Athene</i>	Tommaso et al. (2009)
16	Estancia Luan Cura Hué (E)	99	47	93	23	76	11	1	0	0	18	0	11	47	327	<i>Tyto</i>	Tiranti (1992)
17	Casa de Piedra (M)	0	72	0	11	130	58	7	5	0	0	0	1	16	300	<i>Tyto</i>	Montalvo et al. (1985)
18	Cuchillo Có (E)	5	6	134	0	66	26	0	0	0	0	0	8	10	250	<i>Tyto</i>	Tiranti (1992)
19	Gobernador Duval (M)	0	2	2	2	17	1	0	0	0	0	0	1	4	29	<i>Tyto</i>	Tiranti (1988)

exploration of sample-size effects on their taxonomical structures. This evaluation was made on a data matrix of relative abundances (%MNI). Statistical analysis was made using the program PAST (PAleontological Statistics), version 3.12.

4. Results

The Late Holocene specimens studied herein (NISP = 1099) come from the middle portion of the sedimentary sequence (Unit 2). Specimens of amphibians, reptiles and birds, not included in the taphonomic analysis, were also recovered from the same level. The field taphonomic evaluation of these specimens and their disposition in the sedimentary sequence allowed distinguishing three assemblages: 1) large to medium sized mammals; 2) small mammals (micromammals) recovered inside burrows or associated with them; and 3) discrete accumulations of micromammals and other microvertebrates.

4.1. Large to medium sized mammals

4.1.1. Taxonomic structure

This assemblage is composed by xenarthrans, artiodactyls, carnivores and rodents. Xenarthrans are represented mostly by osteoderms that belong to different species of Dasypodidae (Table 2, Fig. 2a–c), and three fragments of mandibles assigned to Dasypodidae indet. The remaining taxa include by Canidae, Camelidae, Chinchillidae and Caviidae (Table 2, Fig. 2d–g).

The assemblage is characterized by a MNI of 11 (Table 2). Without considering Dasypodidae osteoderms, NISP is 75 and MNE is 64. NISP and MNE of Dasypodidae osteoderms is 106, including 49 isolated osteoderms, and four sets of 10, 10, 15 and 22 associated osteoderms each one.

4.1.2. Taphonomic signature

The 33% of the specimens correspond to cranial elements (maxillae, mandibles and isolated teeth), while the remaining percentage includes diverse postcranial elements. The anatomical representation indicates that vertebrae (31%), metapodials (14%) and mandibles (12%) are the most frequent elements; other elements present very low percentages or are absent (Fig. 3). The index isolated teeth/isolated vertebrae is 1.5. All the skeletal elements belonging to the groups proposed by Voorhies (1969) are

represented. Disarticulated and isolated specimens (sensu Behrensmeyer, 1991) are dominant (79%); while the rest, including osteoderms of the different species of Dasypodidae and vertebrae of small indeterminate mammals, are disarticulated but associated (sensu Behrensmeyer, 1991). Incomplete specimens represent 22.66% of the sample; 60% of them presents smooth transverse fractures, 23% stepped fractures and 17% spiral fractures. Complete specimens (77.44%) include isolated molars, osteoderms, vertebrae, metapodials and femora. One palate with both P4-M3 series assigned to *Lama* sp., presents its right portion (including the dental series) collapsed and displaced backward, resulting in the breakage of this area of the palate (Fig. 2e). None of these specimens show signs of digestions. Tooth marks are absent.

Only 2.80% of the specimens shows surface loss of bone material related with weathering, represented by slight splitting parallel to the fibrous structure (category 2, sensu Alcalá, 1994). There are no specimens with abrasion evidence (category 1, sensu Alcalá, 1994). Impregnation with manganese oxides is present in all the specimens, most of them (80%) assigned to Type 1 (sensu Marín Arroyo et al., 2008), while the remaining can be included in Type 4 (sensu Marín Arroyo et al., 2008).

4.2. Micromammals associated with burrows

4.2.1. Taxonomic structure

Specimens of this assemblage were recovered inside the burrows or associated with them (Fig. 1f). The assemblage is composed exclusively by rodents, including the caviomorphs *Ctenomys* sp. (88%) and *Galea leucoblephara* (4%), and the cricetid *Reithrodon auritus* (8%) (Table 2). Specimens of *Ctenomys* are fragmentary, being very difficult their identification at species level. *Ctenomys azarae*, *C. talarum* and possibly also *C. mendocinus* are currently present in the area of the Quehué valley (Bidau, 2015). The NISP of the assemblage is 160, the MNE is 144 and the MNI is 25 (Table 2). Only one individual was considered from each burrow.

4.2.2. Taphonomic signature

The 55.63% of the specimens correspond to cranial elements (maxillae, mandibles and isolated teeth), while the remaining percentage includes diverse postcranial elements. There is a high frequency of mandibles, maxillae, isolated teeth and vertebrae (mainly of *Ctenomys* sp., the best represented taxon) (Fig. 4). The

Table 2

Fossil site taxonomic structure and minimum number of individuals (MNI) obtained in each assemblage. LMM: Large to medium sized mammals; MB: Micromammals associated with burrows; MA: Micromammals accumulations.

Order	Family	Taxon	Assemblages			
			LMM	MB	MA	
Xenarthra	Dasypodidae	<i>Chaetophractus villosus</i>	1			
		<i>Chaetophractus</i> cf. <i>C. vellerosus</i>	1			
		<i>Zaedyus pichiy</i>	1			
Artiodactyla	Camelidae	<i>Lama</i> sp.	2			
Carnivora	Canidae	<i>Lycalopex gymnocercus</i>	1			
Rodentia	Chinchillidae	<i>Lagostomus</i> sp.	4			
		<i>Dolichotis</i> sp.	1			
			<i>Microcavia australis</i>			9
			<i>Galea leucoblephara</i>		1	2
		Ctenomyidae	<i>Ctenomys</i> sp.		22	59
		Cricetidae	<i>Reithrodon auritus</i>		2	15
			<i>Calomys</i> cf. <i>C. laucha-C. musculus</i>			1
			<i>Graomys griseoflavus</i>			4
			<i>Akodon dolores</i>			2
			<i>Eligmodontia typus</i>			2
Didelphimorphia	Didelphidae	<i>Thylamys pallidior</i>			2	
		<i>Lestodelphys halli</i>			2	
		Total MNI	12	25	99	



Fig. 2. Large to medium-sized mammals assemblage. **a.** *Chaetophractus* cf. *C. vellerosus*, mobile osteoderms (GHUNLPam 14753). **b.** *Chaetophractus villosus*, mobile (left) and fixed (right) osteoderms (GHUNLPam 14965). **c.** *Zaedyus pichiy*, mobile osteoderms (GHUNLPam 14775). **d.** *Lycalopex gymnocercus*, premolar in lateral view (GHUNLPam 19138). **e.** *Lama* sp., palate with right and left molariform series in occlusal view (GHUNLPam 27063). **f.** *Lagostomus* sp., left hemimandible with m2-m3 in labial view (GHUNLPam 19115). **g.** *Dolichotis* sp., palate with left P4-M1 (GHUNLPam 6743). Micromammals discrete accumulations. **h.** *Ctenomys* sp., skull in ventral view with incisors and right Dp4-M2 (GHUNLPam 14757). **i.** *Microcavia australis*, skull in ventral view with left P4-M3 and right P4-M2 (GHUNLPam 12707). **j.** *Galea leucoblephara*, right hemimandible with p4-m2 in labial view (GHUNLPam 14747). **k.** *Reithrodon auritus*, right hemimandible with incisor and m1-m3 in occlusal view (GHUNLPam 14750). **l.** *Graomys griseoflavus*, left hemimaxilla with M1-M2 in occlusal view (GHUNLPam 12621). **m.** *Eligmodontia* sp., left hemimandible with incisor and m1-m3 in occlusal view (GHUNLPam 19079). **n.** *Calomys* cf. *C. laucha-C. musculus*, right hemimandible with incisor and m1-m2 in occlusal view (GHUNLPam 12603). **o.** *Akodon dolores*, right hemimandible with incisor and m1 in occlusal view (GHUNLPam 12627). **p.** *Thylamys pallidior*, left hemimaxilla with P3-M4 in occlusal view (GHUNLPam 14598). **q.** *Lestodelphys halli*, right hemimandible with p1-m4 in labial view (GHUNLPam 19120). Scales = 5 mm.

other elements are absent or in very low values (Fig. 4).

The average of the relative abundance is 13.02%. The relationship between cranial and postcranial elements (20.31) shows a deficit of postcranial bones, and relationship between proximal and distal elements of the limbs (38.46) reflects loss of distal bones.

The specimens of all individuals are disarticulated but

associated (sensu Behrensmeyer, 1991). The 90% of the specimens are incomplete; 50% of them present smooth transverse fractures, 32% stepped fractures and 18% spiral fractures. Complete specimens only include vertebrae and hemimandibles.

None of the specimens shows signs of weathering (category 0), abrasion (category 1, sensu Alcalá, 1994) tooth marks and digestive

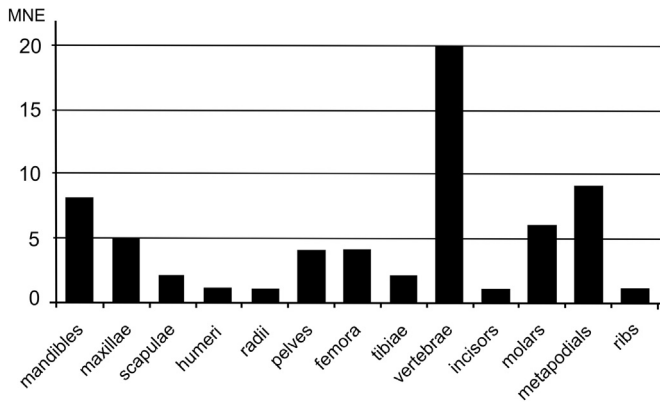


Fig. 3. Minimum number of elements (MNE) identified in the fossil large to medium sized mammals assemblage (except Dasypodidae osteoderms).

corrosion. Most of the specimens (70%) display evidence of impregnation with manganese oxides, mainly included in Type 3 and Type 4 (sensu Marín Arroyo et al., 2008).

4.3. Micromammals and other microvertebrates accumulations

4.3.1. Taxonomic structure

This assemblage is dominated by caviomorph rodents including *Ctenomys* sp. (59.60%), *Microcavia australis* (7.10%) and *Galea leucoblephara* (5.10%), followed by cricetid rodents including *Reithrodon auritus* (15.10%), *Graomys griseoflavus* (4.10%), *Akodon dolores* (2%), *Eligmodontia typus* (2%) and *Calomys* cf. *C. laucha-C. musculus* (1%), and the marsupials *Thyllamys pallidior* (2%) and *Lestodelphis halli* (2%) (Table 2, Fig. 2h–q). Scarce fragmentary specimens of other vertebrates were identified (but not included in the taphonomic analysis), belonging to anuran amphibians, squamate reptiles and passerine birds. This assemblage is characterized by a NISP of 831, MNE of 762 (Table 3) and MNI of 99 (Table 2). Juveniles are represented by 27 individuals (*Ctenomys* sp. = 70.30%;

M. australis = 22.22%; other taxa = 7.48%).

4.3.2. Taphonomic signature

Specimens were found as discrete irregular accumulations in the bearing level (Fig. 1g and h), but disarticulated and isolated (sensu Behrensmeyer, 1991). Each accumulation was composed of numerous specimens corresponding to more than one individual and more than one taxon.

All the skeletal elements were represented in this sample (Table 3). The 51.70% of the specimens correspond to cranial elements (maxillae, mandibles and isolated teeth), while the remaining percentage includes diverse postcranial elements. The anatomical representation indicates a high frequency of mandibles, maxillae, femora and humeri (Table 3).

The average of the relative abundance is 18.38%. The relationship between cranial and postcranial elements ($f + h / md + mx = 58.28$) shows loss of postcranial bones, and the relationship between proximal and distal elements of the limbs ($t + u / f + h = 16.46$) reflects a high deficit of distal bones.

Incomplete specimens represent 72.97% of the sample. Complete skulls are not preserved, and the most frequent portions are maxillae and rostra. Complete mandibles are very scarce; instead, mandibles lacking the coronoid processes and/or the condyles are very frequent. Some mandibles (5.66%) show breakage at the base of the alveolar sockets near the ventral border. Among the postcranial elements, humeri, femora, tibiae, vertebrae and metapodials are preserved complete.

The postcranial elements evaluated for breakage degree (Andrews, 1990) are shown in Table 4. The 49.09% of the specimens are complete. The 66% of the incomplete specimens shows spiral or stepped fractures and 34% presents smooth transverse fractures or combinations of different types of fractures.

Several specimens show signs of digestive corrosion (Table 5, Fig. 5), mainly light. In 11% of *Ctenomys* molars, the enamel surface presents slight pitting. In 10% of Caviidae molars, digestion is visible because the labial and lingual corners of the teeth are rounded and the protruding angles flattened. In 9% of Cricetidae molars, matt

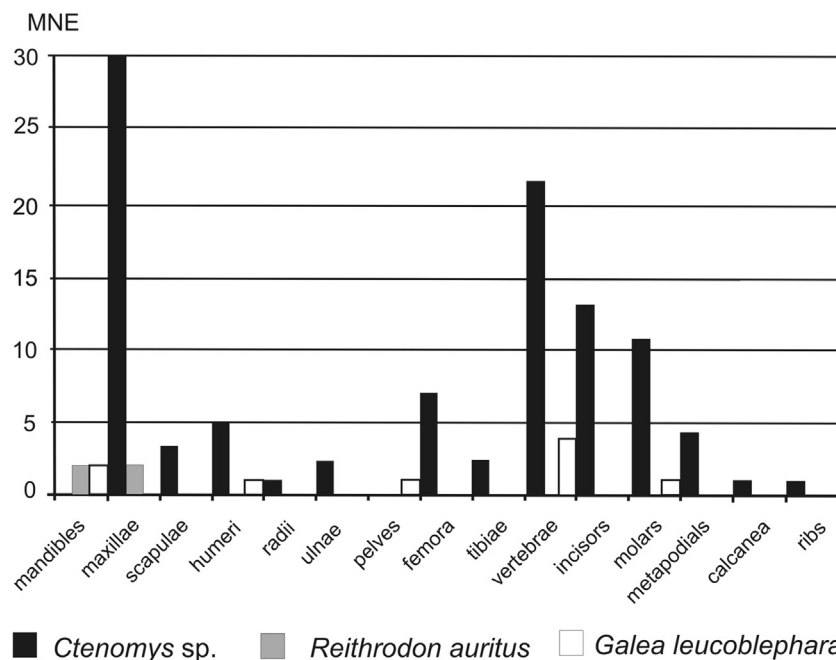


Fig. 4. Minimum number of elements (MNE) obtained in the fossil micromammals associated with burrows assemblage.

Table 3

Minimum number of elements (MNE) and relative abundance (Rel. Ab.) obtained in the micromammals discrete accumulations, based on a MNI = 99.

Elements	MNE	Rel Ab.
mandible	159	80.30
maxilla	131	66.16
scapula	15	7.58
humerus	77	38.89
radius	5	2.53
ulna	8	4.04
pelvis	29	14.65
femur	92	46.46
tibia	20	10.10
vertebra	71	1.99
incisor	57	14.39
molar	42	2.65
metapodial	32	0.58
calcaneus	3	1.52
astragalus	3	1.52
Rib	18	0.76
Total	762	
Average		18.38

enamel is visible in lateral view. No molar of these taxa display the dentin affected by digestion.

None of the specimens shows signs of weathering (category 0) or abrasion (category 1, sensu Alcalá, 1994). Most of the specimens (90%) display evidence of impregnation with manganese oxides, mainly included in Type 4 but also in Type 2 and Type 3 (sensu Marín Arroyo et al., 2008).

5. Discussion

5.1. Taphonomic history

Fluvial dynamic is recorded along the Late Pleistocene and Holocene at the Quehué valley (Calmels et al., 1996), featured by the occurrence of the ephemeral course of the Quehué creek (Mehl and Zárate, 2008). In the rather narrow overbank area of the Quehué creek, the Late Quaternary is recorded by deposits from suspension loads (Unit 1) and from traction fluid flows (Unit 2), that were stabilized by pedogenic processes, one at the beginning of the Holocene (9040±580 ¹⁴C years BP) and the other at the Late Holocene (1258 ± 75 ¹⁴C years BP). After the last period of soil formation, aeolian deposition partially covered the fluvial valley and the surrounding structural plain. An episode of incision cut the Late Pleistocene and Holocene sedimentary sequence and determined the present-day talweg of the Quehué creek, where also Late Miocene deposits crop out (Mehl and Zárate, personal communication).

As mentioned above, field observations (e.g. disposition in the sedimentary sequence) and preservational features suggest different taphonomic histories for the Late Holocene vertebrate specimens recovered from Unit 2. In this context, three assemblages were identified.

Table 4

Breakage degree of different limb bones of the micromammals discrete accumulations.

	Femur		Humerus		Tibia		Ulna		Radius	
	MNE	%	MNE	%	MNE	%	MNE	%	MNE	%
Complete	38	41.30	37	48.05	8	40.00	0	0	0	0
Proximal	49	53.26	12	15.58	6	30.00	8	100	5	100
Distal	5	5.44	28	36.37	6	30.00	0	0	0	0

Table 5

Percentages of digestive corrosion in postcranial elements (proximal femora and distal humeri) and teeth (incisors and molars) belonging to the micromammals discrete accumulations.

	% absent	% light	% moderate	% heavy	% extreme
Femur	50.58	33.33	12.64	3.45	0
Humerus	72.31	26.15	1.54	0	0
Molar	89.58	10.42	0	0	0
Incisor	92.98	5.27	1.75	0	0

5.1.1. Large to medium sized mammals assemblage

In this assemblage (NISP = 181), specimens from 11 individuals were recovered, which were assigned to xenarthrans, artiodactyls, carnivores and rodents, whose body mass vary approximately between 3 and 90 kg. Dasypodid osteoderms were the dominant skeletal elements (NISP = 106), frequency consistent with their abundance in each carapace, and also vertebrae, the most abundant elements in mammal skeletons, were numerous.

Among the skeletal elements easily transported by water flows (groups I and I-II of Voorhies, 1969) there were pelvis, ribs, scapulae, metapodials and vertebrae. Among vertebrae, noteworthy, only four of them were isolated, the rest were, although disarticulated, forming small accumulations that may have been mobilized when they still had connective tissues or most likely underwent little transport and dispersion. Mandibles and maxillae were recorded as well, which are resistant to transport (groups II-III and III of Voorhies, 1969). Although in low frequency, skeletal elements belonging to the different groups proposed by Voorhies are represented in this assemblage, suggesting that the hydrodynamic sorting was not very important. As well, the isolated teeth/isolated vertebrae index (1.5) also suggests a low degree of hydrodynamic sorting. Similar values were reported by different authors for floodplain deposits (see Behrensmeyer, 1975; Badgley, 1986; Tomassini and Montalvo, 2013). These results agree with the low energy interpreted for the environmental context in which the specimens were preserved.

The dominance of disarticulated and isolated specimens indicates that, in most cases, the exposure time was enough for the separation and dispersion of the different bones present in the carcass. The presence of some small accumulations composed by disarticulated but associated specimens, including parts of armadillo carapaces and vertebrae of Mammalia indet., suggests a relatively rapid burial. Muñoz (2015) stated that armadillo carapaces delay the disarticulation of other skeletal elements acting as protective structures. However, in this assemblage there are no other skeletal elements of armadillos apart from three mandibles, which are elements that disarticulate in early stages (Muñoz, 2015); the presence of just portions of carapaces suggests that individuals were already in final stages of disarticulation and anatomical elements removed from the assemblage.

The large-medium sized mammals assemblage constitute an accumulation related with action of surface flows -water (Rogers and Kidwell, 2007). However, complete specimens prevailed, suggesting they were not affected by destructive taphonomic processes. Among incomplete specimens, most of them showed

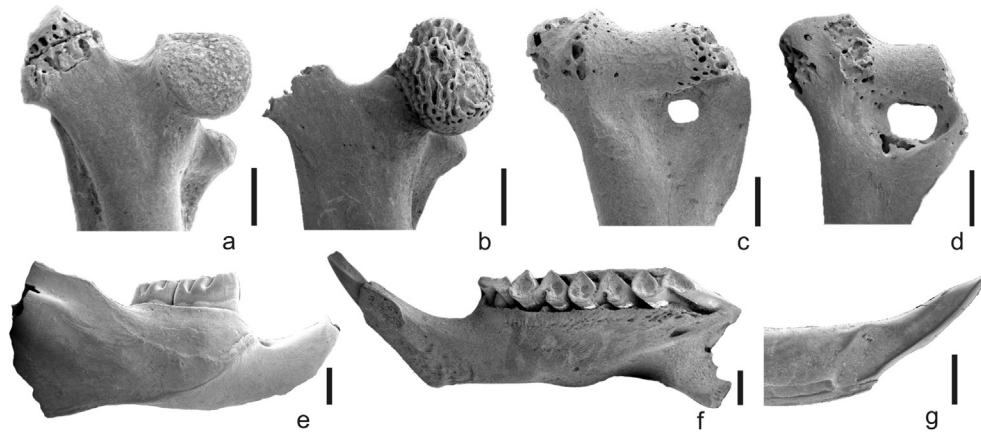


Fig. 5. Digestive corrosion in specimens belonging to the micromammals discrete accumulations. **a, b.** Rodent proximal femora with digestive corrosion, moderate and heavy respectively. **c, d.** Rodent distal humeri with light digestive corrosion. **e.** *Graomys griseoflavus* hemimandible (GHUNLPam 12615), molars without evidence of digestion. **f.** *Microcavia australis* hemimandible (juvenile, GHUNLPam 12609), incisor and molars without evidence of digestion. **g.** Rodent incisor with moderate digestive corrosion.

smooth transverse fractures that may be interpreted as produced during fossil-diagenetic stage, once the bones were already mineralized. On the other hand, fractures related to the biostratigraphic stage (stepped and spiral fractures) are scarce; distortion recorded in the palate of *Lama* sp. (Fig. 2e). could have been originated by the trampling produced by other mammals.

Some specimens showed evidences of weathering (e.g. slight splitting), that indicate exposition to atmospheric agents. The little amount of affected specimens, all of them with low intensities, suggests that exposure time was relatively short.

Specimens from this assemblage did not show signs of abrasion that could be related to water transport. However, the abundance of disarticulated and isolated specimens and the low representativity of skeletal elements for each recorded taxon, accumulated in an environmental context subject to sporadic flooding, suggest that bones may have been mobilized after burial.

5.1.2. Micromammals associated with burrows

This assemblage included specimens (NISP = 160) belonging to 25 individuals, recovered inside burrows or associated with them. Three rodent taxa (whose body mass is below 1 kg) were recorded, *G. leucoblephara*, *R. auritus* and *Ctenomys* sp.; the latter supplied the highest values of MNI and MNE. The anatomical representation showed a high percentage of cranial elements; maxillae and mandibles are preserved in most individuals. The postcranial elements are scarce and the distal limb bones have very low representativity.

All specimens were disarticulated but associated, both those recorded inside the burrows and those associated with them. This suggests that each individual was buried relatively quick.

Incomplete specimens prevailed, as evidence of the action of diverse destructive taphonomic processes. Fractures recorded were produced both on fresh bones (e.g. spiral and stepped) and mineralized remains (e.g. smooth transverse).

The presence of smooth transverse fractures and low values of relative abundance of skeletal elements of each individual may be related to different post-burial destructive processes; among them, the mobilization due to digging rodents (see Bocek, 1986), load generated by the overlying sediments, and the erosion of the bearing levels. Finally, a bias linked to the location of each burrow in relation to the current bed of the creek, may be proposed. Burrowers prefer well drained soils in upland areas; consequently, in areas under seasonal flooding, burrowers were absent (see

Voorhies, 1975). Probably over time, the studied deposits were subject to sporadic flooding, which could have caused the loss of some remains.

The absence of marks related to predation, particularly corrosion by digestive acids, rule out the participation of predators or scavengers in the origin of this assemblage. Also, the specimens had no evidences of weathering, possibly because of the protection of the burrow. The finding of individuals constituted by disarticulated but associated specimens, added to the absence of signs of abrasion, allows inferring that if there was mobilization of bones, this was very scarce.

These results are coincident with previous taphonomic studies performed by Peña (1997) and Tomassini et al. (2017) in Pliocene and Holocene burrows, respectively, of the Pampean Region. These authors indicated that the specimens recovered inside burrows were mostly articulated or associated, with good preservation degree (mostly complete, and without signs of weathering and abrasion); in both cases skull and mandibles were frequent, and in less degree bones of the limbs.

According to the available evidence, some burrows are interpreted to have acted as traps (see Behrensmeier and Hook, 1992; Tomassini et al., 2017). In this context, it can be interpreted that some individuals could have died inside the burrows, probably trapped during eventual flooding events.

It has been proposed that the burrowing habit might increase the chances for fossilization (Voorhies, 1975). *Ctenomys* sp., the most frequent taxon of this assemblage, is a fossorial rodent. Their living populations are composed of semi-isolated demes, occupying patches of habitat where soil hardness and particle size provides suitable conditions for burrowing activities (Busch et al., 2000; Mora et al., 2007). In Quehué site, sedimentological features of the bearing level agree with those of the environments in which the species of *Ctenomys* dig their burrows, and the diameters of the tunnels of the burrows that could be measured coincide with those of modern ones (Antinuchi and Busch, 1992). *Galea leucoblephara* often utilized the abandoned burrows of larger mammals, such as armadillos (*ChaetophRACTUS* spp.), plains vizcacha (*Lagotomus maximus*) and tuco tuco (*Ctenomys* spp.) (see Rood, 1972). *Reithrodon auritus* can excavate tunnel systems, but sometimes used burrows dug by *Ctenomys* (Pardiñas and Galliari, 2001). In this context, it can be proposed that individuals of *Ctenomys* sp. were the producers of the burrows, whereas the individuals of *G. leucoblephara* and *R. auritus* would be occasional occupants.

5.1.3. Micromammals and other microvertebrate accumulations

This assemblage (NISP = 831) is composed by 99 individuals of several species of rodents and marsupials (but also other microvertebrates: anurans, reptiles, and birds), included disarticulated and isolated specimens recovered in small discrete accumulations (Fig. 1g and h). According to the disposition of the specimens in the bearing level, and their taphonomic features, the accumulations were interpreted as disaggregated pellets produced by a predator.

Specimens without digestion evidences prevailed in the sample. Most affected specimens showed a light degree of corrosion. These characteristics coincide with the accumulations of small mammals generated by strigiform birds (Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Fernández et al., 2017). On the basis of the strigiforms inhabiting today in the Quehué valley, the data were compared to those of *Tyto alba*, *Athene cunicularia* and *Bubo virginianus*. Comparison (discriminating by taxon) between these living strigiforms (see Fernández et al., 2017) and the Late Holocene sample, in relation to the modifications produced by digestion, reflected that the latter had a little higher percentages of molars of Cavidae and *Ctenomys*. In this regard, *A. cunicularia* and *B. virginianus* produce accumulations with higher percentages of modifications by digestive corrosion than *T. alba* (Andrews, 1990; Gómez, 2007; Montalvo and Tejerina, 2009; Montalvo et al., 2015).

All the skeletal elements were represented, but the average of relative abundance was low (18.38%). For *T. alba*, Andrews (1990) obtained averages between 27.20% and 63.20%. For *A. cunicularia*, Gómez (2007) reported an average of 35.45% and Montalvo and Tejerina (2009) of 55.62%, in both cases based on samples from the Pampean Region. For a sample of *B. virginianus* from Mendoza Province, Montalvo et al. (2015) reported an average of 47.80%. The values of modern samples of strigiforms are higher than those of Quehué site, which is reflected in the curve of anatomical representation (Fig. 6). Samples are coincident in the good representativity of cranial elements (mandibles and maxillae were abundant). Differences in the representation of some skeletal elements and averages could be related to the loss of most fragile bones (scapulae, radii, ulnae) or smallest (autopodial elements, vertebrae, ribs). The evaluated indexes for Quehué site showed a better representation of cranial elements and a higher loss of distal bones with respect to modern samples.

Incomplete specimens prevailed in this assemblage. Percentage

of complete limb bones was high (41.10%), similar to that of *B. virginianus* (40%, Montalvo et al., 2015), but lower than those of *T. alba* (96.60%, Gómez, 2007) and *A. cunicularia* (71.40%, Gómez, 2007; 73.77%, Montalvo and Tejerina, 2009). An important percentage of specimens showed fractures probably produced before burial (66%); even so, the post-burial fractures must also be taken into account, because they may have affected complete specimens or may have masked previous fractures.

Based on these evidences, it is proposed that the discrete accumulations of micromammals and other microvertebrates studied herein were produced by the predatory activity of strigiforms. Although the different taphonomic variables do not indicate an owl species in particular, the habits and behaviors of the species that currently inhabit the area can shed light on the accumulator agent. *A. cunicularia* occurs in open areas, nests and rests in burrows excavated by itself or by mammals such as the plains vizcacha *Lagostomus maximus* (Marks et al., 1999); this behavior might increase the chances for pellets preservation. The taxonomic structure recorded in the assemblage of Quehué site mostly coincides with *A. cunicularia* trophic activity known for La Pampa Province (Tommaso et al., 2009; Solaro et al., 2012; see Table 1). Coincidentally, correspondence analysis is consistent to order the assemblage of Quehué site close to those of *A. cunicularia* (Fig. 7). Unlike most owls (e.g. *T. alba* and *B. virginianus*), *A. cunicularia* is often active during the day, thus usually preys on diurnal rodents such as juveniles of *Ctenomys* spp., *G. leucoblephara* and *M. australis* (Marks et al., 1999); in agreement with these observations, in the sample of Quehué site there were several juvenile individuals (28%).

Quintana (2015) studied the taphonomic features of bones recovered from disaggregated modern pellets of *T. alba* and stated that post-depositional processes affect them early, but a prolonged period of exposure is required for them to be expressed. No evidence of weathering, trampling, and abrasion were recognized in the assemblage of Quehué site; hence, a rapid burial of pellets can be proposed.

Finally, impregnation by manganese oxides produced modifications in specimens of the three assemblages. In the large to medium sized mammals assemblage a low percentage of specimens was affected (20%), whereas in the other two assemblages the amount of affected specimens was very high (>80%). Precipitation

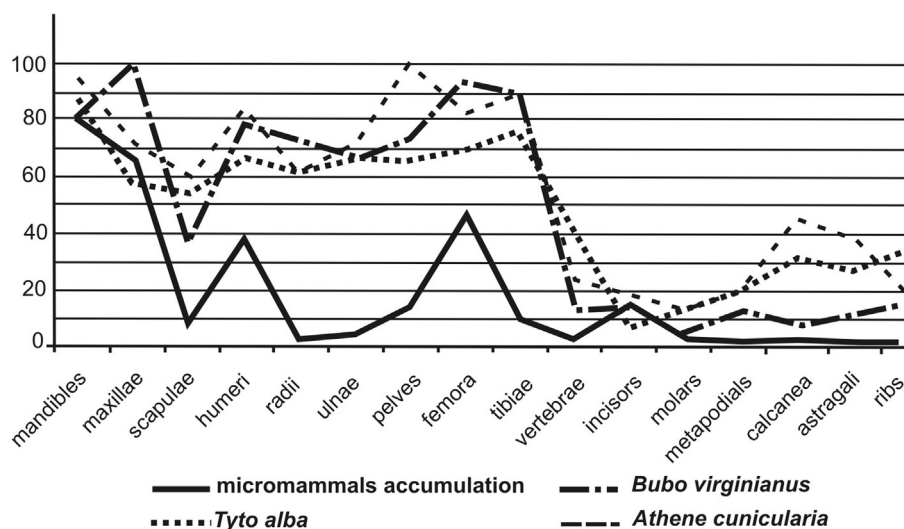


Fig. 6. Relative abundance of skeletal elements identified in the micromammals discrete accumulations of the Quehué site compared with average data from *Tyto alba* (Andrews, 1990), *Athene cunicularia* (Montalvo and Tejerina, 2009) and *Bubo virginianus* (Montalvo et al., 2015).

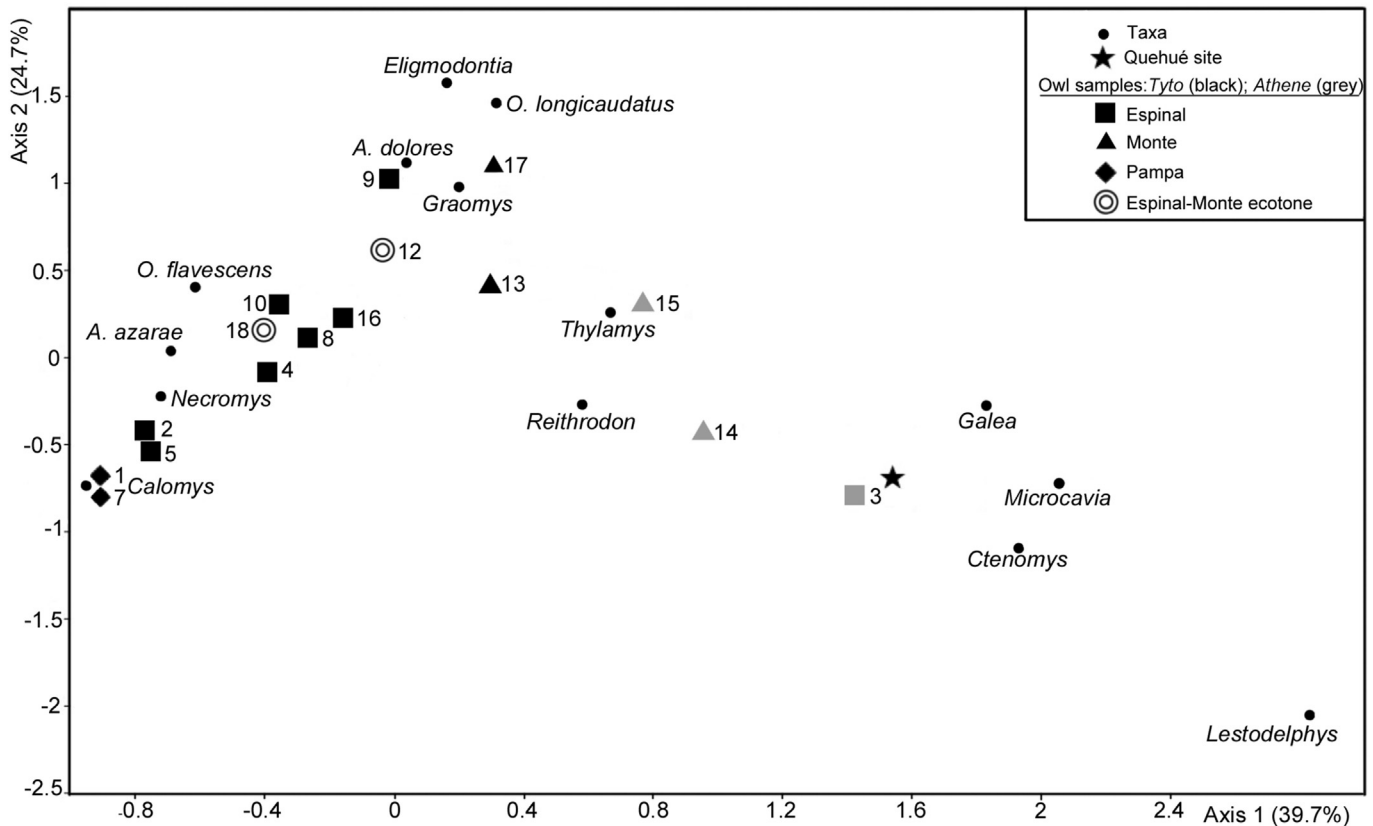


Fig. 7. Correspondence analysis of micromammals fossil assemblage from Quehué site and recent owl pellet samples from La Pampa Province. Percentages of both axes show the variance. Numbers are those used in Table 1 as ID. Note: Espinal (1 and 11) and Monte (19) owl pellet samples were excluded because of their low values (MNI < 50).

of manganese oxides is one of the main fossil-diagenetic processes by which specimens become impregnated and acquire a dark color (e.g. López-González et al., 2006; Marín Arroyo et al., 2008). The most frequent origin of these impregnations is related to the high concentrations of manganese present in the water that circulates by the fossiliferous levels (Pfretzschner and Tütken, 2011). As occurs in other fossil assemblages of the Pampean Region, the most affected fossils are the smallest ones (Tomassini et al., 2014; Montalvo et al., 2016). It is interpreted that the specimens of the three assemblages were modified by the same post-burial processes.

5.2. Paleoenvironmental interpretation

Correspondence analysis based on taxonomic identifications and recent pellets results ordered the modern samples by phyto-geographic units (with the exception of the sample of *A. cunicularia* from Curru-Mahuida locality) and by owl species (Fig. 7). In fact, the main factor (axis 1, 39.7% of the variance) shows samples associated with the Pampa and Espinal towards the left, and with the Monte desert towards the middle. The sample of Quehué site is close to those recent pellet samples of *A. cunicularia* from Monte and Espinal, possibly due to the greater proportion of the caviomorph rodents *Ctenomys*, *Galea* and *Microcavia*, and other small mammals typically allied (e.g. *G. griseoflavus*, *A. dolores*, *E. typus* and *T. pallidior*) but not exclusive of these phyto-geographic units (see also Table 1). This is supported by the presence in the bearing level of medium and large mammal taxa (*Lama* sp., *L. gymnocercus*, *Dolichotis* sp., *Lagostomus* sp., *C. villosus*, *Chaetophractus* cf. *C. vellerosus* and *Z. pichiy*), which currently also inhabit in these two

phyto-geographic units. In addition, the occurrence of *R. auritus* suggests the development of open, herbaceous steppe environments associated with water bodies. On the other hand, the sample of Quehué site is separated from small mammal samples of the Pampa phyto-geographic unit, located in the eastern fringe of La Pampa Province (Fig. 1a), because this latter is mainly composed by the sigmodontine rodents *Calomys* spp., *A. azarae* and *O. flavescens* (see also Table 1).

The isolation of *L. halli*, considering both axes of the correspondence analysis, is coherent with the single record in the fossil sample of the Quehué site. The other species found in the sample of Quehué site (including small, medium and large-sized mammals) are currently present in the area (e.g. Redford and Eisenberg, 1992; Siegenthaler et al., 2004; Patton et al., 2015). Nowadays, the vast majority of current localities with presence of *L. halli* (>90%) corresponds to Patagonian steppe, where cool and dry climatic conditions are dominant (e.g. Formoso et al., 2016; and references therein). The main exceptions correspond to the Monte of the north of Río Negro Province, Mendoza Province and south of La Pampa Province. There are two records of *L. halli* in the last-mentioned province, one in a rocky area with abundant grass cover at Parque Nacional Lihué Calel (37°57'S, 65°33'W), and the other at Laguna La Amarga (38°12'S, 66°05'W) 40 km south from Parque Nacional Lihué Calel (Birney et al., 1996; Teta et al., 2009). These modern populations of *L. halli* were considered relicts of those that were more widely distributed earlier in the Holocene; thus, they appear to be more vulnerable to becoming extinct (e.g. Formoso et al., 2016). Therefore, the presence of this marsupial in the Quehué site enlarges its known distribution in La Pampa Province ca. 130 km to the NE, and corroborates its wider geographic extension

during the Late Holocene.

In surrounding regions (e.g. humid Pampa, Mendoza and Patagonia), there are also several Holocene records of *L. halli* (e.g. Fernández, 2010; Fernández et al., 2016; Tomassini et al., 2017; see also Formoso et al., 2016, and references therein). In addition, in coincidence with the Quehué site, two Late Holocene archaeological sites located in the Monte desert (Agua de La Mula, 35°22'S, 68°15'W, Mendoza Province, ~1.6–1 ky BP; Cueva Galpón, 41°09'40"S, 65°47'32"W, Río Negro Province, ~3.3–1.9 ky BP), recorded similar taxonomic composition of the small mammal assemblages, with the local extinction of *L. halli* (Fernández, 2010; Fernández et al., 2016).

Possibly the present retraction of this marsupial has combined the effects of the most recent anthropic impact with climatic variations, including the general increase in moisture and temperature in Central Argentina (Viglizzo et al., 1995; Formoso et al., 2016). The impact of recent climatic fluctuations, such as MCA (relatively warmer and wetter) or LIA (relatively colder and drier), would have been expressed as minor variations in the frequencies of some taxa and/or in the expansion/retraction of others (e.g. Fernández, 2010; Fernández et al., 2016). Sedimentary deposits with ages consistent with the regional timing for both climatic episodes were detected in the Quehué valley (Mehl, 2011). The sedimentological and palynological records of Salina Anzoátegui in southeastern La Pampa Province (39°00'S, 63°46'W) allowed to recognize the Espinal phytogeographic unit, with minor variations from the middle Holocene until recent times, suggesting persistent arid to semi-arid conditions (e.g. Schäbitz, 1994). In this context, the anthropic impact and the more mesic conditions could have played a major role in the retraction of *L. halli* in the dry Pampa. The progressive development of agricultural and livestock activities in the Pampean and Patagonian regions, mainly during the last 200 years, has yielded an overexploitation of pastures, an increase of open areas with bare soil and bushes (e.g. Perelman et al., 1997).

6. Conclusions

Numerous vertebrate remains (mainly mammals) were recovered from Late Holocene fluvial deposits of the Quehué valley, La Pampa Province. The disposition of the specimens in the bearing level and the taphonomical features allowed differentiation of three assemblages, with different biostratigraphic histories.

Large to medium sized mammals, is an attritional assemblage formed by specimens mobilized probably during flooding events. The assemblage of micromammals associated with burrows, includes well preserved specimens of individuals that would have died inside the burrows (produced by *Ctenomys* sp.) or near them. Micromammals and other microvertebrates discrete accumulations, the most numerous in amount of specimens and individuals, were interpreted as produced by the disaggregation of pellets generated by a strigiform, possibly *A. cunicularia*. These two latter involve very short intervals, endorsing the idea that the taxa included were coetaneous. According to the results obtained, burial was very rapid in the three assemblages; even so, it may be suggested that the micromammals associated with burrows were the ones that suffered the most rapid burial, following by the micromammals of the discrete accumulation and finally the large to medium sized mammals.

The paleoenvironmental analysis based on the small mammals displayed semi-arid conditions associated with a mosaic of open shrub steppe, grasslands and xerophytic forests of Espinal, similar than today at the Quehué valley. This hypothesis is also supported by the presence of medium and large fossil mammals, and by other studies (e.g. sedimentology, palynology). However, the presence of *L. halli* in the Quehué site during the Late Holocene (~1.2 ky BP),

suggests a more heterogeneous environment and perhaps relative colder and drier than current times, which are featured by more mesic conditions and anthropic activities mainly agriculture and livestock during the last centuries.

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