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Human subsistence and environmental stability during the last 2200 years in Epullán Chica cave (northwestern Patagonia, Argentina): A perspective from the zooarchaeological record

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ABSTRACT

The faunal content from Epullán Chica archaeological site (ECh, thereafter), a small cave located in northwestern Patagonia, Argentina, was studied from taphonomic and paleoenvironmental points of view. This cave is placed in the ecotone between Monte desert and the Patagonian steppe, in the middle Limay River basin, was occupied since the end of the Late Holocene. Zooarchaeological evidence retrieved from ECh is diverse, including fresh-water mollusk shells (*Diplodon chilensis*), eggshell and bone fragments of Rheidae, bones and teeth of large (*Lama guanicoe*), medium (e.g., *Chaetophractus villosus*, *Conepatus chinga*), and micro-sized (several species of sigmodontine and caviomorph rodents) mammals. Most of the recorded taxa were the result of human exploitation. However, owl pellets preserved in the sediments, and other taphonomic signatures, clearly indicate that avian predators are responsible for part of the micromammal record. Micromammal abundances during the last 2.2 ka BP are suggestive of a relative environmental stability around ECh, at least until the beginning of the last century. In this sense, Late Holocene landscapes were dominated by open steppe areas and large rocky outcrops, with minor changes in humidity and temperature during this period.

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1. Introduction

In general, zooarchaeologists study the past interaction between fauna and humans on the base of the faunal remains recovered from archaeological sites (Lyman, 1994). This interaction may have taken place in different types of hunting or fishing and domestication processes, as well as in rituals, taboos, totems, symbols, and arts (Binford, 1981; Lyman, 1994; Russell, 2011, and references therein). Nevertheless, some faunal remains could have been naturally (i.e., without human participation) incorporated in the archaeological record by its own deaths *in situ*, by predators and/or by post-depositional agents such as running water and strong winds (e.g., Andrews, 1990; Lyman, 1994). Taphonomy is the discipline which study the processes involved in the transition of the organisms from the biosphere into the lithosphere, providing crucial data on the depositional and post-depositional agents that have participated in the formation of the assemblages (Andrews, 1990; Lyman, 1994). Distinguishing faunal remains accumulated by birds of prey, carnivore mammals, and humans are essential to envisage reliable paleoenvironmental models and evaluate natural action vs. human subsistence (Andrews, 1990; Pardiñas, 1999a,b). In this sense, jointly zooarchaeology, taphonomy, and paleoecology can shed light on the subsistence patterns of the hunter–gatherers and their relationships with the landscape (Lyman, 1994; Pardiñas, 1999a,b).

The archaeological researches in northwestern Patagonia have integrated different kinds of analysis (e.g., geoarchaeological,

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chronostratigraphical, paleoecological, zooarchaeological and taphonomical) from numerous archaeological sites with Late Pleistocene and Holocene sequences, mostly located through the main hydric basins such as the Colorado, Neuquén and Limay Rivers (Barberena et al., 2015, and references therein). One of this archaeological sites, Epullán Grande cave [LL], with an entire Holocene sequence and located in the middle Limay River basin, has been studied from archaeological, geological, biological, zooarchaeological and paleoecological perspectives (e.g., Crivelli Montero and Fernández, 1996; Prieto and Stutz, 1996; Crivelli Montero et al., 1996a,b; Pardiñas, 1999a,b; Palacios, 2005, 2008; Villarosa et al., 2006; Fernández, 2007; Cordero, 2009, 2010; Pardiñas and Teta, 2013). Zooarchaeological studies of the early strata of LL revealed a human subsistence mostly focused on the consumption of large-sized mammals (*Lama guanicoe* [guanaco]), complemented by large-sized birds (*Rhea pennata* [lesser rhea]), medium (*Lycalopex griseus* [South American grey fox] and *Lycalopex culpaeus* [culpeo], *Conepatus chinga* [Molina's hog-nosed skunk] and *Chaetophractus villosus* [hairy armadillo]) and micro-sized mammals (*Ctenomys* spp. [tuco-tucos], and the cavies *Galea leucoblephara* [common yellow-toothed cavy] and *Microcavia australis* [southern mountain cavy]) (Crivelli Montero et al., 1996a; Pardiñas, 1999a,b; Cordero, 2009, 2010; Pardiñas and Teta, 2013). On the other hand, the paleoecological contributions from LL depicted by the micromammal record pointed out a marked stability with some minor changes through the entire Holocene sequence (Crivelli Montero et al., 1996a; Pardiñas, 1999a; Pardiñas and Teta, 2013).

Nonetheless, a smaller archaeological cave site, Epullán Chica (ECh, thereafter), with a rich zooarchaeological record of Late Holocene, located about 100 m east from LL and excavated in 1989/1992, remained unstudied until recently. The present zooarchaeological study focuses on the taxonomic identification and taphonomic analysis of faunal remains recovered from ECh, in order to assess the main agents responsible of the bone accumulations, distinguishing both natural and anthropic processes. In addition, a paleoenvironmental analysis is presented based on the micromammal record retrieved from this cave site. We consider this task as a first step to understand the role of fauna of ECh from a zooarchaeological point of view, the importance of the use of this cave regarding LL, and a better knowledge of the paleoenvironmental conditions at the time of its deposition, providing data about the subsistence patterns of the Late Holocene hunter–gatherers of the middle Limay River basin.

2. Regional setting

ECh (40°23′10″S, 70°11′44″W, 680 m asl) is an archaeological site located in the Cañadón del Tordillo. It was ~5 km north of the Limay River (Collón Curá Department, southern Neuquén Province, Argentina) (Fig. 1); nowadays, it is ~2 km north of the Piedra del Águila reservoir. It opens to the north in a rocky outcrop of volcanic tuffs of the Collón Curá Formation. From a phytogeographic point of view, ECh is located in the Monte-Patagonian Ecotone and near the Occidental District of the Patagonian Phytogeographic Province at the middle part of the Limay River basin (sensu León et al., 1998). Annual precipitation is around 180 mm, and consequently the environment is semiarid. Its plant composition includes Monte shrubs such as *Prosopis*, *Schinus*, and *Larrea*, and Patagonian shrubs such as *Mulinum*, *Senecio*, *Chuquiraga*, and herbs such as *Distichlis*, *Stipa*, *Poa* and *Cortaderia selloana* (Schult. and Schult. f.) Asch. and Graebn that mostly grow in humid locally areas known as "mallines" (León et al., 1998). Several volcanoes in the north Patagonia Andean cordillera have produced explosive eruptions during the Quaternary (e.g., Villarosa et al., 2006). The volcanic materials form thick tephra deposits, which have been recorded in the archaeological sites located in the upper and middle Limay River basin, such as Traful I, LL and ECh, and that were associated with the Nahuel Huapi white tephra, an event with radiocarbon dates ranging ca. 1950–2500 cal BP (Villarosa et al., 2006).

3. Materials and methods

3.1. Archaeological site, stratigraphy, and chronology

ECh is about 5 m wide at the mouth, 3.5 m long and covers ~11 m^2; maximum depth of the fill was 1.40 m. Twenty archaeological 1 m × 1 m squares, covering the entire surface of the cave, were dug, although not all of them reached bedrock. The excavated volume was about 13 m^3 and the sediments were sieved through 3 mm-sized mesh.

Each stratum was described, given a unique number in a continuous sequence beginning with 1, and its stratigraphic position recorded by noting its physical relationship with the adjacent strata (Harris, 1989). Because the sediments of ECh were extremely friable, what made it risky to cut successive sections, only one profile, limited to the lower half of the sedimentary deposit, was exposed (Fig. 1). In addition, many burrows were spotted and, whenever possible, they were excavated separately, but contamination cannot be discounted. In consequence, it was considered safer to organize the data horizontally, according to levels below datum, each 5 cm thick. These levels were grouped in four temporal units according to depth, differences sediment, and radiocarbon dates (Fig. 1). The latter were obtained from charcoal samples processed at the Laboratorio de Tritio y Radiocarbono (LATYR), Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata (LP) and Beta Analytic (Beta). Calibration for the Southern Hemisphere was made through SHCal04 14c using CALIB 6.0.1 program, in conjunction with Stuiver and Reimer (1993). The basic fill of the cave is a pale yellowish sand derived from the weathering of the tuff forming the ceiling and walls and eolic sand of the same nature, since bedrock outcrops in the vicinity are also of tuffs of the Collón Curá Formation. In spite of this apparently homogeneous sediment, each unit ("U") presented particular characteristics: UI = comprised between bedrock (−175 cm) to −125 cm from datum. Bedrock was covered by tobaceous sand, the characteristic sediment of the rock shelter. A pit in the rock floor was partly filled by a hearth, which burnt sediments and clasts. A charcoal sample taken from this hearth indicated 2220 ± 50 ^{14}C BP (357–284 cal. BC; Lab-code Beta 54772). A later patch of charcoals and burnt sediment was identified as a hearth of which a charcoal sample was dated to 2200 ± 60 ^{14}C BP (211–91 cal. BC; Lab-code Beta 54771). Subsequently, a conspicuous tephra stratum some 18 cm thick was deposited, which was partially covered by a hearth dated 1980 ± 50 ^{14}C BP (17–132 cal. AD; Lab-code LP 2881). A significant burrow beginning in UII reached bedrock (see Fig. 1). UII = ranging from −125 to −80 cm. Most of the fill of this unit consists of the characteristic sediment and sand mixed with grass remains and some tephra. A thick, stratified hearth ~1 m wide oxidized the sediment on which it rested, was dated on 1740 ± 60 ^{14}C BP (318–423 cal. AD; Lab-code LP 2870). Some vegetable lenses were identified and the aforementioned burrow cut across the sediments. UIII = comprised between −80 and −60 cm. Most of the fill of this unit consists of the characteristic sediment. A group of charcoals, which did not form a combustion feature, was dated to 1510 ± 80 ^{14}C BP (534–664 cal. AD; Lab-code LP 2903). A hearth indicated 1680 ± 80 ^{14}C BP (376–539 cal. AD; Lab-code LP 2904). Another hearth was poorly defined and scarce in charcoal. Other strata contain tephra and vegetal remains, lens of grass, and were

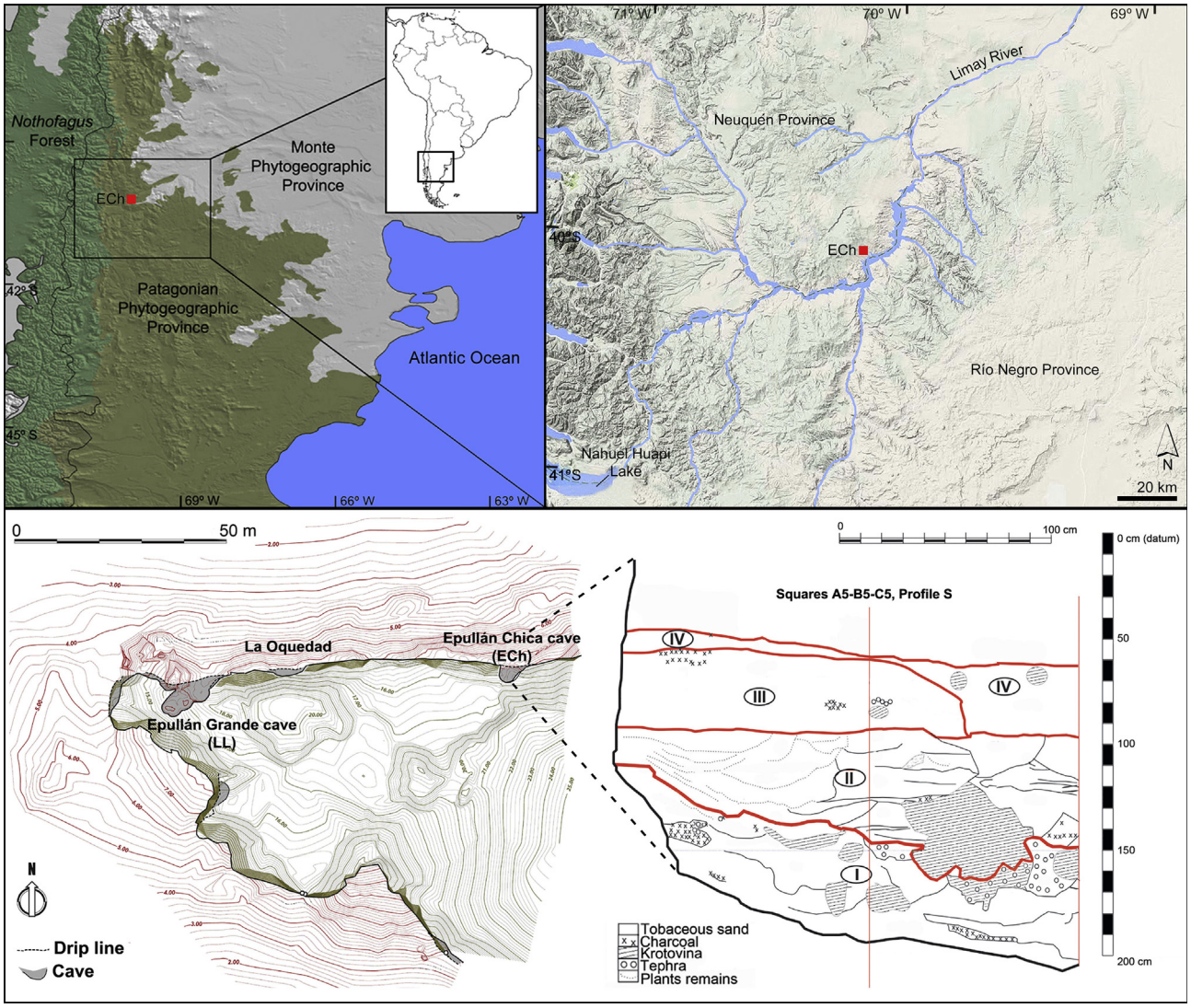

Fig. 1. Map of the study area, northwestern Patagonia (above), Argentina, with the locations of archaeological site superimposed on the main phytogeographic units; the rocky formation and stratigraphic profile (below). The rocky formation was drawn by Luis Teira.

affected by burrows. UIV = ranging from −60 to −25 cm. One stratum forms most of the volume of this unity and is mainly composed by the characteristic sediment of the cave. A modern (20th century) metal knife was recovered from this stratum at 60 cm below datum. Other relevant strata contain sand mixed with grass remains and some tephra, poorly defined hearths and lenses of vegetal remains. Burrows traversed the sediments.

On the basis of the chronostratigraphic studies, the zooarchaeological materials are assigned to Late Holocene temporal units, as follow: UI = ca. 2.2–2 ka BP (minimum number of individuals (MNI) = 398); UII = ca. 2–1.7 ka BP (MNI = 754); UIII = ca. 1.7–1.5 ka BP (MNI = 111); UIV = ca. 1.5 ka BP-20th century (MNI = 113). In addition to zooarchaeological remains, other types of archaeological materials were recovered, including lithic artifacts, plant remains (*Larrea nitida* Cav., *Mulinum spinosum* (Cav.) Pers. *Schinus polygamus* (Cav), *Colliguaja integerrima* Gill. and Hook., *Cortaderia selloana*, *Austrocactus* aff. *A. bertinii* (Cels) Britton & Rose, *Stipa* sp., and *Bromus* sp.), rock art and cordage (unpublished data). The studied materials of ECh were temporarily deposited for study in the CIAFIC (Centro de Investigaciones en Antropología Filosófica y Cultural, Buenos Aires).

3.2. Taphonomic and quantitative zooarchaeological analysis

A total of 9178 zooarchaeological remains from ECh cave were examined under magnification. Taxonomic identifications were made by comparison with voucher specimens housed in the mammals collection of the Museo de Ciencias Naturales de La Plata (Buenos Aires), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires) and Centro Nacional Patagónico (Puerto Madryn, Chubut), and with specific literature (e.g., Pacheco Torres et al., 1986; Pearson, 1995; Vizcaíno et al., 1995; Fernández et al., 2011). The taxonomic identification of micromammal was only based on skulls, mandibles and teeth; taxonomy of rodents follows Patton et al. (2015). On behalf of the analysis of eggshells of Rheidae, the methodology proposed by Apolinaire and Turnes (2010) was followed. This methodology makes the distinction between the two species of Rheidae (*Rhea americana* [greater rhea] and *R. pennata*) based on the pores count of the eggshells per 1 cm^2. The number of pores for *R. pennata* is less than 65 per cm^2 and for *R. americana* is more than 70 per cm^2 (Apolinaire and Turnes, 2010). For this purpose, a sample of each archaeological unit was taken (UI = 15, UII = 25, UIII = 29 and UIV = 9).

Mammals were divided into three size-categories: micro (<1 kg; Didelphimorphia, Ctenomyidae, Caviidae, Cricetidae), medium (between 1 and 20 kg; Dasypodidae, Mustelidae, Mephitidae, Canidae and Felidae) and large-sized (>20 kg; *L. guanicoe*, see Table 1). Average masses for each taxon were taken from Redford and Eisenberg (1992). Bone and teeth remains were identified according to the following measures of taxonomic abundance and skeletal parts (Grayson, 1991): NSP (total number of specimens), NISP (number of identified specimens per taxon; Payne, 1975), MNE (minimum number of elements; Mengoni Goñalons, 1999), MAU% (standardized minimum number of animal units, Binford, 1984) and MNI (White, 1953). The MNI for eggshells of Rheidae was calculated according to the average of 71.37 g per individual (Bonomo et al., 2008).

During the field work, an evaluation of the contextual archaeological record was made in order to identify burrows and articulated skeletons, which suggest natural death *in situ* or fossorial activities of some taxa such as *Ctenomys* and *C. villosus*. In order to contextualize the archaeofaunistic assemblage, the modification of the bone surfaces related to depositional and post-depositional processes (e.g., weathering, diagenetic, rodent and root action) was recorded (e.g., Behrensmeyer, 1978; Lyman, 1994; Quintana, 2007). The weathering stages proposed by Behrensmeyer (1978) were grouped in absence (stage 0), low (stages 1–2), medium (stage 3) and high (stages 4 and 5) levels. The difference of bone mineral density (BMD) in the skeletal elements would favor the destruction of some bones or parts of them and survival of others (Elkin, 1995). The non-parametric Spearman's test was applied in order to explore the correlation between the part representations of the sample (expressed in MAU%) and the BMD proposed for camelids (Elkin, 1995). This analysis was not performed with the bone remains of Rheidae because of their low number.

Bone modifications generated by natural predators were analyzed, such as carnivore mammals and birds of prey. For large and medium-sized mammals, mechanical (holes, pits, furrows, gnawing) and digestive action were considered (e.g., Mondini, 2003). For micromammals, the classification proposed by Andrews (1990) and Fernández-Jalvo and Andrews (1992) was followed. This classification makes the distinction between five categories of modification of skeletal and teeth remains (i.e., light, intermediate, moderate, heavy and extreme), that broadly correspond to strigiform, falconiform and accipitriform birds and carnivore mammals. According to Andrews (1990), these categories are based both on the degree of modification by digestive corrosion

Table 1
Relative abundance of taxa recovered from ECh for each temporal unit.

			UI		UII		UIII		UIV	
		W (kg)	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Mollusca	*Diplodon chilensis*	0.002	3	1	1	1	–	–	2	1
Reptilia	Iguanidae indet. 1		1	1	–	–	–	–	–	–
	Iguanidae indet. 2		2	1	–	–	–	–	1	1
Aves	Aves indet.		1	–	1	–	–	–	1[a]	–
	Rhea sp.	15–30	1	1	5	1	2	1	2	1
	Rhea sp. (eggshells)	0.07	1057	7	1796	13	319	2	511	3
	Rhea pennata (eggshells)		13	–	17	–	19	–	4	–
	Rhea cf. *R. pennata* (eggshells)		–	–	2	–	1	–	–	–
	Rhea americana (eggshells)		–	–	3	–	7	–	4	–
	Rhea cf. *R. americana* (eggshells)		–	–	2	–	–	–	–	–
	Cyanoliseus patagonus	0.25	–	–	–	–	–	–	1[a]	1
Mammalia	Mammalia indet.		29	–	10	–	11	–	66	–
	Mammalia indet. (large)		47	–	74	–	12	–	25	–
	Mammalia indet. (medium–large)		2	–	14	–	–	–	6	–
Camelidae	*Lama guanicoe*	118	56	2	64	2	20	2	22	1
	Mammalia indet. (medium)		–	–	8	–	–	–	1	–
	Mammalia indet. (medium–small)		16	–	4	–	–	–	–	–
Dasypodidae	Dasypodidae indet.		–	–	–	–	–	–	2	–
	Chaetophractus villosus	2.37	82	3	15	1	2	1	182	2
	C. villosus (osteoderms)		178	–	49	–	12	–	1072	–
Canidae	*Lycalopex* sp.		1	1	1	1	–	–	–	–
	Lycalopex griseus	3.99	–	–	–	–	17	1	–	–
Mustelidae	Mustelidae indet.		4	1	–	–	–	–	–	–
	Galictis cuja	1.58	–	–	1	1	–	–	1	1
Mephitidae	*Conepatus chinga*	1.75	1	1	–	–	–	–	1	1
Felidae	Felidae indet.		1	1	–	–	–	–	–	–
	Leopardus geoffroyi	3.59	–	–	–	–	–	–	1	1
Ctenomyidae	*Ctenomys* sp. 1	0.18	204	88	432	174	71	30	56	28
	Ctenomys sp. 2	0.50	1	1	–	–	–	–	–	–
Caviidae	*Microcavia australis*	0.26	24	11	43	25	7	5	4	2
	Galea leucoblephara	0.22	9	6	15	10	3	2	1	1
Cricetidae	*Akodon iniscatus*	0.02	3	3	10	7	1	1	1	1
	Abrothrix olivacea	0.02	13	8	22	13	2	2	–	–
	Abrothrix hirta	0.03	3	3	1	1	–	–	1	1
	Chelemys macronyx	0.04	–	–	3	1	–	–	–	–
	Phyllotis xanthopygus	0.06	237	81	505	182	44	22	41	18
	Loxodontomys micropus	0.06	4	3	1	1	–	–	1	1
	Eligmodontia sp.	0.02	195	83	382	138	20	12	31	16
	Reithrodon auritus	0.08	209	70	427	149	69	29	68	28
	Euneomys chinchilloides	0.08	17	10	23	12	–	–	3	2
Didelphidae	*Thylamys pallidior*	0.02	17	11	48	22	2	2	2	2
	Total		2431		3979		641		2114	
	Total NSP		2431		3988		642		2117	

[a] Feather.

and frequencies of affected elements. On the other hand, taphonomic evidences of human activities were evaluated, such as cut marks, pounding, scraping, intentional fracture, percussion marks and thermoalteration (e.g., Binford, 1981; Shipman et al., 1984; Blumenschine et al., 1996; Mengoni Goñalons, 1999; Pardiñas, 1999b; Medina et al., 2012). Based on color and texture of the bone surfaces and the uniformity of the attributes, the characterization of the type of thermoalteration such as burned, carbonized and calcined, was assessed (Shipman et al., 1984; Stiner et al., 1995). In order to assess marrow consumption only breakage of long bones was considered.

3.3. Micromammals as paleoenvironmental indicators

Micromammals have been widely used as indicators of paleoenvironmental conditions since they are abundant and diverse in the archaeological and paleontological records. Most of these taxa have relatively narrow environmental requirements, being frequently associated to particular microenvironments (e.g., Pardiñas, 1999a). Paleoecological inferences are usually based on presence/absence of some species and/or relative changes of its frequencies. Our analysis of bone remains and taxonomic profiles of the samples suggests that the main taphonomic agents that produced the ECh deposits were owls, as those which were involved in the genesis of the micromammal samples in the nearby LL (Crivelli Montero et al., 1996a; Pardiñas, 1999a,b; Pardiñas and Teta, 2013). Based on these findings, paleoenvironmental reconstruction was supported on comparisons between both fossil and recent micromammals assemblage derivate from owl pellets samples (Andrews, 1990; Pardiñas, 1999a,b). Comparisons focused on exploring the paleoenvironmental significance of archaeological samples were performed using a wide range of recent owl pellet samples produced by *Bubo virginianus magellanicus* (Magellanic horned owl) and *Tyto alba* (barn owl) that were recovered from nest and roosting sites across the study area, including a three-year sample of fresh owl pellets produced by *T. alba* in the vicinity of ECh (Cañadón del Tordillo, 40°23′28″S, 70°11′48″W, Pardiñas et al., 2003; Pardiñas and Teta, 2013).

4. Results

4.1. Taxonomic structure

High richness of taxa was recorded, including one mollusk, at least two species of lizards, three of birds and no less than 20 species of mammals (Table 1). The assemblage (NISP = 9165 and MNI = 1376) includes bone and teeth remains of mammals, birds and reptiles (58.98%), eggshells (40.90%), feathers (0.02%) and mollusk shells (0.06%).

Six fragments of shells of *Diplodon chilensis* (freshwater mussel) were found in UI, UII and UIV. Two morphotypes of Iguania were recovered in UI (dentaries with monocuspidate and tricuspidate teeth), and one species in UIV (dentary with tricuspidate teeth). Two fragments of indeterminate diaphysis and a feather of unidentified birds were recorded in UI, UII, and UIV, respectively. In addition, one feather of the psitacid *Cyanoliseus patagonus* (burrowing parrot) belongs to UIV. Regarding Rheidae, scarce skeletal elements were recovered. Two humeri were found in UIV, a vertebra and a medial phalanx were observed in UIII, a distal fragment of the tarsometatarsus and four phalanges were found in UII and one phalanx in UI. In the avifaunistic assemblages, mostly fragments of eggshells of Rheidae were found. Although the analyzed eggshell samples were scarce, *R. americana* was recorded since the UII. Eggshells of *R. pennata* were more abundant than those of *R. americana* in UII and UIII. However, both species had similar eggshells abundances in UIV (Table 1). Currently, the southernmost distribution of *R. americana* reaches northern Patagonia (Tambussi and Acosta-Hospitaleche, 2002), from the Atlantic coast to the eastern and northeastern edge of Neuquén Province (Handford and Mares, 1982). Historically, F. Moreno observed this species in the northeast of Chubut Province in 1876–1877 (Moreno, 1879, p.76). In archaeological contexts of the latest Holocene, *R. americana* was recorded in the lower basin of Limay River (Borrero, 1981, p.118) and in the middle/lower basin of Negro River (Prates, 2008). The finding of eggshells of *R. americana* in ECh, located in the middle basin of Limay River, constituted the southernmost record for the species during the Late Holocene. This suggests that the past Holocene distribution of this species could have been wider than the present one.

Some fragmentary remains were assigned to unidentified Mammalia. Several bones and tooth remains of *L. guanicoe* was found through the sequence (Table 1). Fig. 2a shows that the representation of the anatomic units (MAU%) of *L. guanicoe* was similar in all of units, being skulls, forelimbs (mostly humeri and radii/ulnae) and hindlimbs (mainly femora and tibiae) the more representative anatomical units. The absence or low representation of some anatomical units could be related to the absence of diagnostic features due to fragmentation, making it difficult an assignment to more precise anatomical categories. Although a positive correlation between MAU% and BMD is observed in *L. guanicoe*, the values are low and statistically non-significant, suggesting that the differential preservation of the bones has not played a prominent role in the formation of the assemblages (UI $rs = 0.35$ $p > 0.05$; UII $rs = 0.098$ $p > 0.05$; UIII $rs = 0.228$ $p > 0.05$; UIV $rs = 0.153$ $p > 0.05$).

C. villosus NISP is very high, since most of the specimens are osteoderms. Discarding the individual that died naturally in its burrow (see section 4.2), *C. villosus* is better represented in UI (MNI = 3), with a greater number of elements of the different regions of the skeleton (mostly skulls, followed by vertebrae, ribs, forelimbs and hindlimbs).

Regarding the carnivorous mammals, a fragment of femur of *Lycalopex* sp., fragmentary remains of a skull of a Mustelidae, a scapula of *C. chinga* and a fragment of scapula of Felidae were identified in UI. A fragment of femur of *Lycalopex* sp. and a humerus of *Galictis cuja* (lesser grison) were found in UII. A large portion of vertebral column and articulated basipodia of *L. griseus* were recovered in UIII. A radius of *G. cuja*, a mandible of *C. chinga* and a mandible of *Leopardus geoffroyi* (Geoffroy's cat) were found in UIV.

The taxonomic identification of micromammals and their abundances are detailed in Table 1. Recorded taxa include one didelphid marsupial, *Thylamys pallidior* (mouse opossum), nine sigmodontine rodents, *Akodon iniscatus* (Patagonian grass mouse), *Abrothrix olivacea* (olive grass mouse), *Abrothrix hirta* (long-haired grass mouse), *Chelemys macronyx* (Andean long-clawed mouse), *Reithrodon auritus* (coney-rat), *Phyllotis xanthopygus* (yellow-rumped pericote), *Loxodontomys micropus* (southern pericote), *Eligmodontia* sp. (silky desert mouse) and *Euneomys chinchilloides* (chinchilla rat), and three caviomorph rodents, *M. australis*, *G. leucoblephara*, and *Ctenomys*. Based mostly on metric features, we were able to recognize two morphotypes within *Ctenomys*: a smaller one, largely dominant (*Ctenomys* sp. 1), and a much larger, although scarce form (*Ctenomys* sp. 2.). In coincidence with our findings, several authors highlighted the presence of two morphotypes of *Ctenomys* in the archaeological sequences of Traful I and LL caves. *Ctenomys sociabilis* (social tuco–tuco) and *Ctenomys* cf. *C. maulinus* (Maule tuco–tuco) are larger than the widespread *Ctenomys haigi* (Haig's tuco–tuco), being referred as those larger forms in Traful I and LL caves, respectively (Pearson and Pearson, 1993; Pardiñas, 1999a; Chan et al., 2005; Pardiñas and Teta,

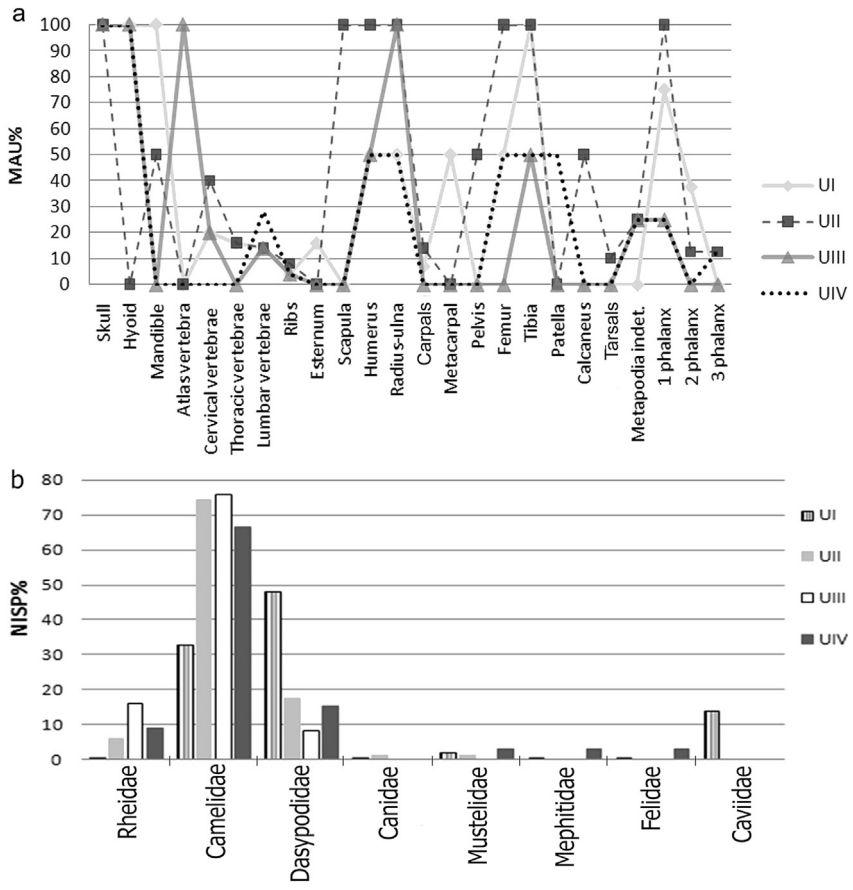

Fig. 2. a, standardized minimum number of animal units (MAU%) of *Lama guanicoe* through the sequence of ECh. b, taxonomic abundance (NISP%) at family level with evidence of anthropic accumulation through the sequence.

2013). Based on morphological characteristics and current records, we suggest that our *Ctenomys* sp. 1 is referable to *C. haigi*.

4.2. Natural taphonomic processes

Concerning the analysis of natural bone modifications (except micromammals, see below), a low incidence of processes that could have affected the bones through the sequence during the deposition and post-deposition were observed (Table 2). In fact, no carnivore tooth marks were found. However, burrows of animals were detected during the excavation (Fig. 1). In this sense, several bones were found articulated without evidence of human and predator activity, pointing a natural death *in situ*. In fact, an almost entire articulated skeleton of *C. villosus* (NISP = 1192) was recovered in UIV, suggesting that it could have died naturally in its burrow (Fig. 3a). In addition, a nearly entire vertebral column (Fig. 3b) and elements of autopodium articulated of *L. griseus* was recorded in UIII. Weathering in bone remains was not noted in most levels (Table 2). Other post-depositional processes such as root, rodent and trampling marks, and manganese oxide impressions (Fig. 3c) were observed in some units (Table 2).

Regarding the micromammal assemblages, the finding of 22 almost intact pellets preserved in all stratigraphic temporal units (UI = 2; UII = 10; UIII = 4; UIV = 6), together with light digestive corrosion on < 5% of micromammals teeth in all temporal units (Table 2, Fig. 3d and e). These taphonomic evidences suggest that the main accumulator agent of ECh cave was a strigiform belonging to the Category I (Light modification), probably *T. alba*. In connection with this, a suitable site for an owl roost was detected on the wall inside the cave. The finding of seven scat fragments indicates a low participation of carnivore mammals in the genesis of the vertebrate assemblages of this cave (Andrews, 1990). Moreover, no weathering evidences were found, and most of the micromammal bones (70%) were broken with irregular surfaces (Fig. 3f), probably by trampling, a common post-depositional taphonomic processes in caves with restricted circulation space (e.g., Andrews, 1990; Pardiñas, 1999b).

4.3. Anthropic processes

Several taxa recorded at ECh showed evidences of human exploitation (*e.g.*, cut marks, thermoalterations in bones and eggshells, flake scars, tools; Figs. 4 and 5). Among birds, a fragment of an unidentified shaft from UII was calcined (Table 3). A high degree of thermoalteration (carbonization and calcination) in all bones of Rheidae (Table 3) was observed through the sequence (except UIV). A shaft of humerus of *Rhea* sp. in UIV presents cut marks that can be associated to defleshing. Also, a high proportion of fragments of Rheidae eggshells with thermoalteration (between 15% and 63%) were recovered from all units (Table 3).

Several evidences of anthropic modification were recognized through the sequence across the different size categories of unidentified mammals (i.e., large, large–medium, and medium–small-sized) (Table 3). A high percentage of thermoalteration, between 27% and 53% depending on the category (except medium–small-sized mammals in UI with 6.25%), was observed (Table 3). In these categories, the proportions of those with low (burned) to high thermoalteration (carbonized and calcined) were

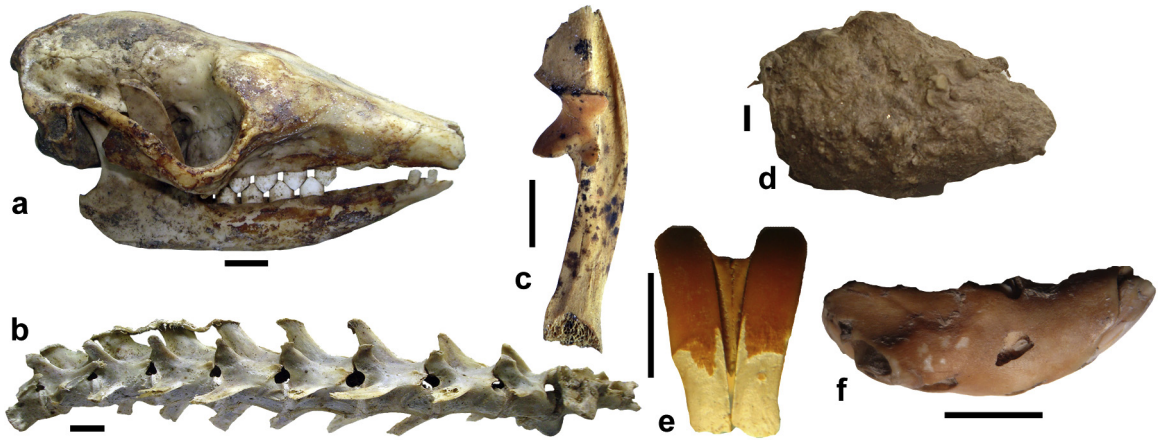

Fig. 3. Examples of natural taphonomic processes at Epullán Chica. a, articulated skull of *Chaetophractus villosus* (UIV). b, articulated part of spinal column of *Lycalopex* cf. *L. griseus* (UIII). c, ulna of *C. villosus* showing manganese oxide impressions (UI). d, pellet preserved (UII). e, upper incisives of *Ctenomys* showing digestive corrosion (UI). f, mandible of *Ctenomys* with marks of trampling and diagenetic action (UI). Scales a–c: 1 cm; scales d–f: 5 mm.

similar, with 48.78% and 51.21%, respectively. Cut marks in these categories of mammals were observed through the sequence. For large-sized unidentified mammals the percentages of fresh fractures range from 7.7% to 64% (Table 3). Three long bones from UI show flake scars and were intentionally fractured, plausibly to obtain bone marrow.

In carnivore mammal bones, cut marks were observed (Table 3), including those inferred as a consequence of defleshing in a shaft of femur of *Lycalopex* sp. in UII, and in a shaft of humerus of *G. cuja* in UIII. Furthermore, in UIV skinning marks in the labial surface of a mandible of *L. geoffroyi* were recorded (Fig. 4a and b).

Concerning dasypodids, a high percent of thermoalterated specimens of *C. villosus* (ca. 50% in UI and UII, and 20–30% in UIII and UIV, Table 3) were observed (discarding the individual that has died naturally in its burrow). In terms of NISP, the osteoderms were the most frequently thermoalterated bones through the sequence (UI = 80.91%, UII = 80.55%, UIII = 100%, and UIV = 100%), followed by skull remains (UI = 9.92% and UII = 8.33%), distal elements of limb bones (UI = 6.10% and UII = 5.55%) and other endoskeletal elements (UI = 3.05% and UII = 5.55%). This major proportion of thermoalterated exoskeletal elements agrees with the experimental cooking by hot charcoal of *C. villosus* (cf. Frontini and Vecchi, 2014). In UI seven elements of *C. villosus* with cut marks were recorded: one mandible, one rib, two ulnae, one radius, one pelvis (Fig. 4c and d), and one tibia-fibula. Also, in UIII one cut mark on the ventral surface of an osteoderm of *C. villosus* was recorded.

For *L. guanicoe* the proportion of specimens with cut marks varies between 9% and 21% (Table 3). Through the sequence various processing activities such as skinning (in proximal phalanges from UII and UIV), disarticulation, butchering (in UI, UII and UIV), and defleshing (in UI, UII and UIII) on several elements of the axial and appendicular skeleton were identified. In addition, the percentage of long bones of *L. guanicoe* with fresh fractures was similar through the sequence (Table 3, Fig. 4e), varying from 50% in UIV to 76% in UI. Also, 20% of those bones fractured in UI showed flake scars, which likely resulted from actions aimed at the consumption of bone marrow. A high proportion of specimens of *L. guanicoe* with thermoalteration (from 17.86% in UI to 50% in UII) was observed through the sequence (Table 3), most of them in the category of carbonized (Fig. 4f) (UI = 80%, UII = 84.37%, UIII = 75% and UIV = 85.71%). The other percentages correspond to remains with partial burning. This high level of thermoalteration (mostly carbonization) possibly indicates the discarding of remains in hearths.

Mollusks are represented by a fragmentary engraved shell of *D. chilensis* in UI (Fig. 4g). Its maximum width is 19 mm. In its inner face, three series of engravings were performed: A) two parallel zigzagging lines, wider than the rest, were scratched; B) a series of thin lines which crisscross at roughly right angles, plus some oblique lines; C) another zigzag rested on a straight line, with an intermediate width between those of A and B. Since the object is incomplete, it is not possible to decide whether it was a pendant. Many examples of engraved portable objects of stone (mainly schist), eggshell and mollusk shells are known from Patagonia. The motifs are usually geometric and rather simple, although sometimes they combine to form more complex patterns (Losada Gómez, 1980). Many engraved stones and shells from Patagonia feature zigzags (Losada Gómez, 1980; Fernández and Ramos, 2008; Crivelli Montero and Palacios, 2010). The rock art and the paintings decorating the fur mantles worn by the historical Patagonian hunter–gatherers are also geometric (Crivelli Montero and Palacios, 2010). Zigzags were painted or engraved in several sites of Southwestern Río Negro: Loncomán, Paredones del Río Pichileufú, Cuadro Leleque, Comallo I, Calcatreo I (Boschín, 2009) and Casa de Piedra de Ortega (unpublished data).

Table 2
Natural bone modifications in different units of Epullán Chica. R = root marks; Mg = manganese oxide; T = trampling marks; Ro = rodent marks; Ca = carnivore marks; Dc = digestive corrosion; W = weathering.

Unit	R	%	Mg	%	T	%	Ro	%	Ca	Dc[a]	%	W (absence)	W (low)	W (medium)	W (high)
I	–	–	7	0.28	2	0.08	–	–	–	10	4.8	98.34%	1.65%	–	–
II	–	–	–	–	2	0.05	1	0.02	–	10	4.6	96.17%	3.18%	0.63%	–
III	–	–	2	0.3	–	–	–	–	–	93	4.9	100%	–	–	–
IV	4	0.19	1	0.04	–	–	–	–	–	45	4.8	96.15%	3.85%	–	–

[a] Only for micromammals.

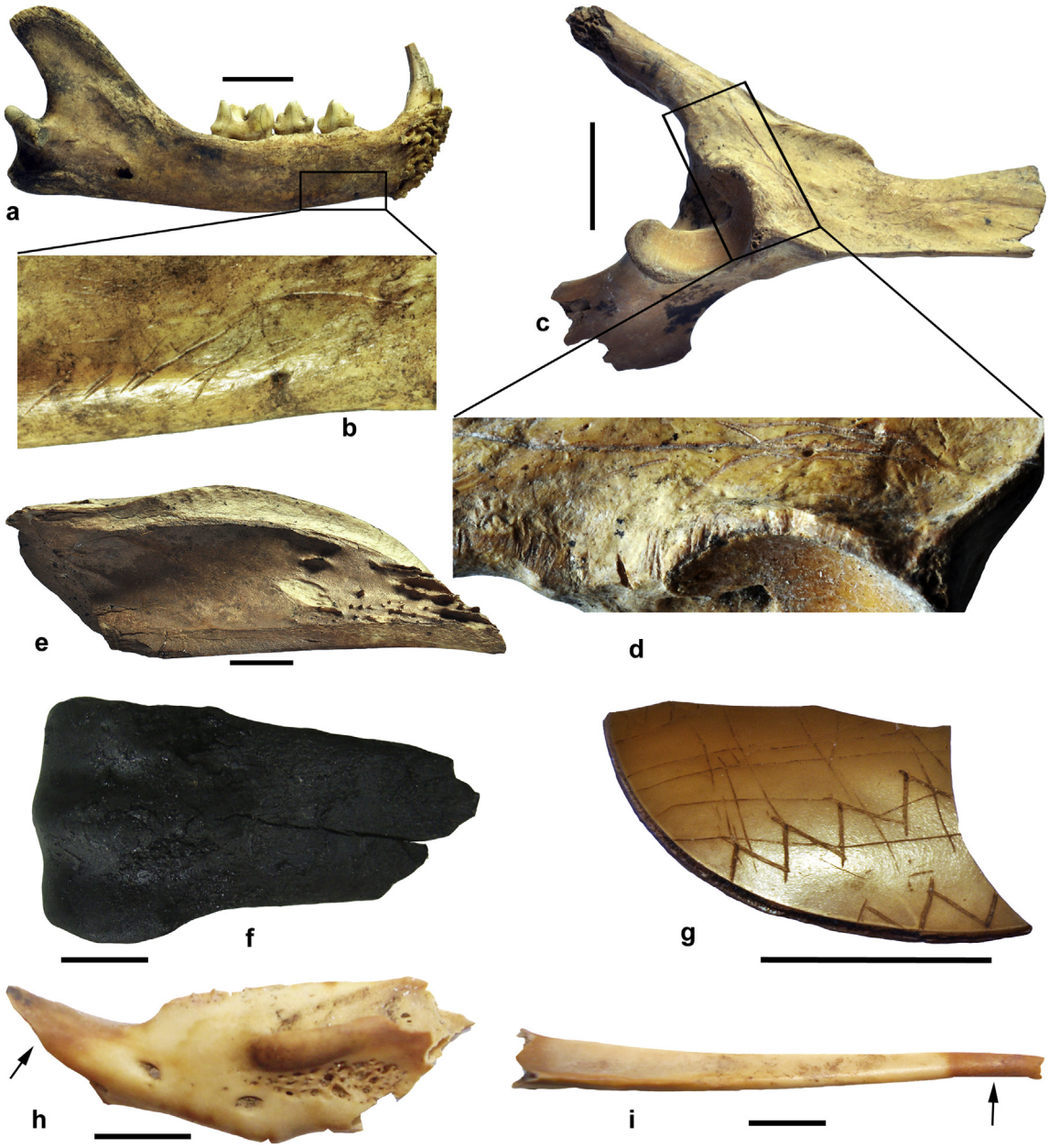

Fig. 4. Examples of anthropic action. a, mandible of *Leopardus geoffroyi* (UIV). b, detail of the cut mark area of the previous picture. c, pelvis of *Chaetophractus villosus* showing cut marks in acetabulum (UI). d, detail of the cut mark area of the previous picture. e, fragment of shaft of long bone of *Lama guanicoe* showing fresh breakage (UIII). f, distal epiphysis of metapodial of *L. guanicoe* with thermoalteration signals (UIV). g, fragment of shell of *Diplodon chilensis* with incisions (UI). h, mandible of *Microcavia australis* with light burnt on the incisor alveolus (UI). i, tibia of *M. australis* showing light burnt on the distal extremity (UI). Scales a–g: 1 cm; scales h and i: 5 mm.

At least a mandible and a tibia of the caviomorph *M. australis* (UI) show extremities which are partially thermoalterated (Fig. 4h and i). The burnt pattern on both elements are coincident with the taphonomic results of previous archaeological observations and experimental works performed by Pardiñas (1999b) and Medina et al. (2012), respectively, suggesting human consumption on part of the larger rodents in the earlier occupations of the cave.

Bone artifacts were recovered in UI and UII (Table 3, Fig. 5). A fragment of shaft of tibia of *L. guanicoe* with shiny surface and retouching on the extreme was identified in UI. It was possibly used as a flaker (Fig. 5a and b). A proximal fragment of metacarpus of *L. guanicoe* with a longitudinal fracture, tapered edges and blunt tip was found in UII (Fig. 5c–e), was also likely used as a flaker. Finally, a fragment of long bone of unidentified mammal with the extreme sharpened recovered from UI (Fig. 5f and g) was probably used as a borer.

4.4. Ethnographic sources of use of fauna at Patagonia

As well as food, a variety of resources were obtained from the fauna. A brief summary of the documentary evidence concerning species found in the excavation of ECh follows.

Cloaks were made generally of *L. guanicoe* skins, as almost every witness has recorded (Cox, 1863, p. 183; Musters, 1964, pp. 246–247; Perea, 1989, p. 21; Priegue, 2007, pp. 27–33). Mantles of *Lycalopex*, *Puma*, *Leopardus*, *Rhea* and *Conepatus* were also prepared, but mainly for trade. Those of *Rhea* and *Lycalopex* were easily broken and demanded hard work; they were, as the *Conepatus*

Fig. 5. Bone tools recovered from Epullán Chica. a, flaker made in tibia of *Lama guanicoe* (UI). b, detail of the modified area of picture a. c, flaker made in metacarpal of *L. guanicoe* (UII). d, detail of dorsal part of the polished area of picture c. e, detail of the ventral part of picture c. f, borer of long bone of Mammalia indet (UI). g, detail of the polished area of picture f. Scales: 1 cm.

mantle, luxury items (Musters, 1964, p. 198 and 319; Moreno, 1879, p. 66; Aguerre, 2000, pp. 130–131; Priegue, 2007, p. 33). Exceptionally, mantles of *Ctenomys* were also prepared (Priegue, 2007, p. 30), in one example including pieces of sigmodontine rodents (cf. the "quillango" exposed in the museum of the Salesiana Mission in Río Grande, Tierra del Fuego). The skins were anointed with grease and a paste or liver of *Rhea*, Dasypodidae or other animals (Priegue, 2007, p. 27). Diapers for the infants were made of a piece of the untanned skin of a neonate *L. guanicoe* (Hilger, 1957, p. 273; Priegue, 2007, p. 42). The usual dwellings were tents (*toldos*): a framework of posts covered with processed, painted and sewn 20–50 *L. guanicoe* hides (Musters, 1964, p. 126; Claraz, 1988, p. 72; Perea, 1989, pp. 20–21). Moreover, leather, sinews, tendons, nerves and veins of *L. guanicoe* and *Rhea* were employed for sewing, making ropes, pouches, coverings for the bolas and toys (Cox, 1863, p. 94 and 162½; Hilger, 1957, p. 360; Perea, 1989, p. 37; Aguerre, 2000, pp. 141–142; Priegue, 2007, p. 33 and 75). Animal blood enters with sand or ash into the mix serving to make the bolas which are utilized for managing livestock (Perea, 1989, p. 35; Priegue, 2007, p. 75). A kind of flute was made making holes to the thigh-bone of a *L. guanicoe* (Musters, 1964, p. 136). Wool was taken from the hunted *L. guanicoe* and woven (Hilger, 1957, p. 375 and 377) or employed to stuff pillows or toys (Musters, 1964, p. 126; Aguerre, 2000, pp. 141–142). Dried dung of *L. guanicoe* served in the preparation of the paint for mantles (Perea, 1989, p. 62). Animal grease was employed to make candles (Priegue, 2007, p. 53). *Rhea* or *L. guanicoe* marrow was used to form a skin cream (Aguerre, 2000, p. 112 and 113). *Rhea* eggs were stored in pits (Zeballos, 1960, p. 373). Cavies were cooked directly on hot charcoal (Aguerre, 2000, p. 127). *Rhea* feathers were one of the most important trade item in the historical period (Cox, 1863, p. 166 and 188; Moreno, 1879, p. 76 and 95; Musters, 1964, p. 197; Claraz, 1988, p. 124; Aguerre, 2000, pp. 127–128; Priegue, 2007, p. 38). They also adorned the head of the performers of the *loncomeo*, a male dance (Cox, 1863, p. 162½; Musters, 1964, p. 136). The armors of Dasypodidae were useful work-baskets in which women kept bodkins, sinews and other elements for sewing (Musters, 1964, p. 127 and 268). *Conepatus* was kept as a pet, and was very tame (Musters, 1964, pp. 279–280). Children suffering from stomachache were treated with toasted Rheidae pepsin and water. Raspings of *L. guanicoe* bezoars were boiled in water and drunk against heart disease (Musters, 1964, p. 196; Priegue, 2007, pp.74–75).

5. Discussion

5.1. Paleoenvironmental reconstruction based on micromammals

Taphonomical analysis suggests that most of the micromammal remains found at ECh were incorporated by a little destructive strigiform bird, possible *T. alba*. This owl is usually found in caves, inhabiting open environments and displaying an opportunistic trophic behavior, feeding mostly on micromammals within a foraging area of about 1–5 km (e.g., Taylor, 2004). Most of the microvertebrates recorded at ECh are within the prey size range of this owl (e.g., Bellocq, 2000). Based on these finding, we made a comparison between recent and past owl pellet samples in order to carry out paleoenvironmental interpretations (e.g., Andrews, 1990; Pardiñas, 1999a).

Micromammalian assemblages of ECh show a remarkable similitude along the four studied units, suggesting only minor environmental changes along the last 2.2 ka. Four species were dominant (*Ctenomys* sp.1, *R. auritus*, *P. xanthopygus*, and *Eligmodontia* sp.), with constant proportions (~10–30%) throughout the sequence (Fig. 6). Other micromammals were also found throughout the entire stratigraphic profile (*T. pallidior*, *A. iniscatus*, *M. australis* and *G. leucoblephara*) but in lower proportions (<5%). Species with discontinuous records includes *A. olivacea*, *A. hirta*, *L. micropus*, and *E. chinchilloides*. Finally, the sigmodontine *C. macronyx* and the caviomorph *Ctenomys* sp.2 were restricted to the UII and UI, respectively (Table 1).

Table 3
Taxa with evidence of anthropic exploitation. TA = thermoalteration; LB = long bones; FF = fresh fracture; NFS = Negative flake scars.

	NISP	Cut marks	%	Tools	%	TA	%	LB	FF	%	NFS	%
UI												
Diplodon chilensis	3	–	–	1	33.33	–	–	–	–	–	–	–
Rhea sp.	1	–	–	–	–	1	100	–	–	–	–	–
Rhea sp. (eggshells)	1057	–	–	–	–	160	15.13	–	–	–	–	–
Mammalia indet. (large)	47	20	42.55	–	–	20	42.55	47	15	32	3	20
Mammalia indet. (medium–large)	2	1	50	1	50	–	–	–	–	–	–	–
Lama guanicoe	56	8	14.29	1	1.79	10	17.86	21	16	76	1	6.3
Mammalia indet. (medium–small)	16	–	–	–	–	1	6.25	–	–	–	–	–
Chaetophractus villosus	260	7	2.69	–	–	131	50.4	–	–	–	–	–
Microcavia australis	24	–	–	–	–	2	8.3	–	–	–	–	–
UII												
Aves indet.	1	–	–	–	–	1	100	–	–	–	–	–
Rhea sp.	5	–	–	–	–	5	100	–	–	–	–	–
Rhea sp. (eggshells)	1796	–	–	–	–	1124	62.58	–	–	–	–	–
Mammalia indet. (large)	74	15	20.27	–	–	39	52.70	71	19	27	–	–
Lama guanicoe	64	7	10.94	1	1.56	32	50	28	16	57	–	–
Mammalia indet. medium	8	1	12.50	–	–	–	–	–	–	–	–	–
Mammalia indet. (medium–small)	4	–	–	–	–	2	50	–	–	–	–	–
Chaetophractus villosus	64	–	–	–	–	36	56.3	–	–	–	–	–
Lycalopex sp.	1	1	100	–	–	–	–	–	–	–	–	–
Galictis cuja	1	1	100	–	–	–	–	–	–	–	–	–
indet.	9	–	–	–	–	1	11.11	–	–	–	–	–
UIII												
Rhea sp.	2	–	–	–	–	2	100	–	–	–	–	–
Rhea sp. (eggshells)	319	–	–	–	–	182	57.05	–	–	–	–	–
Mammalia indet.	11	–	–	–	–	3	27.27	–	–	–	–	–
Mammalia indet. (large)	13	–	–	–	–	–	–	13	1	7.69	–	–
Lama guanicoe	19	4	21.05	–	–	8	42.1	9	5	55.5	–	–
Chaetophractus villosus	14	1	7.14	–	–	4	28.57	–	–	–	–	–
UIV												
Rhea sp.	2	1	50	–	–	–	–	–	–	–	–	–
Rhea sp. (eggshells)	511	–	–	–	–	141	27.59	–	–	–	–	–
Mammalia indet.	66	5	7.58	–	–	18	27.27	36	14	38.8	–	–
Mammalia indet. (large)	25	6	24	–	–	10	40	25	16	64	–	–
Mammalia indet. (medium–large)	6	1	16.67	–	–	–	–	2	1	50	–	–
Lama guanicoe	22	2	9.09	–	–	7	31.82	14	7	50	–	–
Mammalia indet. (medium)	1	–	–	–	–	–	–	1	1	100	–	–
Dasypodidae indet.	2	–	–	–	–	2	100	–	–	–	–	–
Chaetophractus villosus	62	–	–	–	–	13	21	–	–	–	–	–
Leopardus geoffroyi	1	1	100	–	–	–	–	–	–	–	–	–

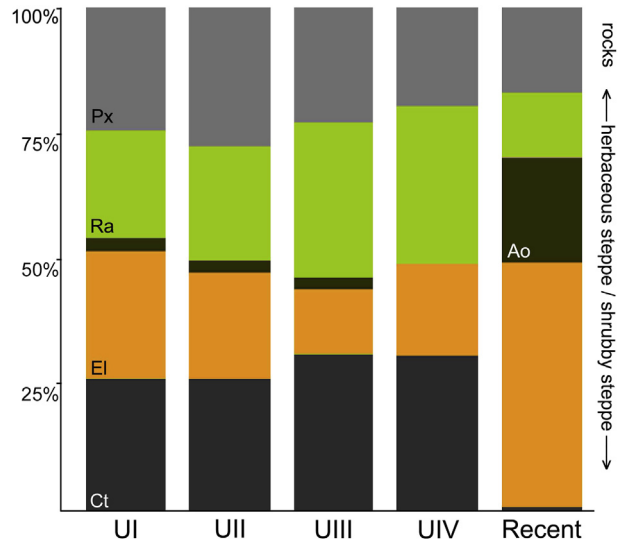

Fig. 6. Histogram showing the proportions of the most abundant micromammals species (expressed as percentage of the minimum number of individuals [MNI]) recovered at ECh and recent owl pellet sample. Abbreviations: *Phyllotis xanthopygus* (Px); *Reithrodon auritus* (Ra); *Eligmodontia* spp. (El); *Ctenomys* sp. 1 (Ct); *Abrothrix olivacea* (Ao).

The four predominant species suggest the development of open areas of shrubby to herbaceous steppes, intermixed with large rocky outcrops (Pardiñas et al., 2003). This basic taxonomic signature along with the continuous presence of *T. pallidior*, *A. iniscatus*, *M. australis* and *G. leucoblephara* are suggestive of conditions similar to those of the Monte-Patagonian ecotone for the last 2.2 ka, as was defined for other archaeological sites in northwestern Patagonia for the latest Holocene (Pardiñas et al., 2003; Fernández et al., 2012; Pardiñas and Teta, 2013). In line with these findings, other elements typically allied to the Monte desert (e.g., *Akodon dolores* [Dolores grass mouse], *Graomys griseoflavus* [gray leaf-eared mouse]) were not found in ECh. The influence of Patagonian elements, usually linked to conditions more humid and cooler than those of the Monte, is depicted by the interrupted presence of taxa such as *A. olivacea*, *A. hirta*, *E. chinchilloides* or *L. micropus* between 2.7 and 2 ka. In congruence, the pollen record of LL revealed a mixed scrubby-herbaceous steppe around 2.2 ka (Prieto and Stutz, 1996).

Despite the remarkable homogeneity of the ECh micromammalian samples, some minor variations could be explained by the influence of major climatic events occurred towards the Late Holocene. For example, the presence of *L. micropus* and *C. macronyx* at 2.2–1.7 ka is broadly coincident with the neoglacial reactivations, the spread of forest element to the east and changes in fire regimes documented in the region for this period, suggesting a change toward more cooler and humid conditions, possibly associated with

the interannual climate variability of El Niño-Southern Oscillation (e.g., Rabassa and Clapperton, 1990; Whitlock et al., 2006). In the same period, *Eligmodontia* decreased in abundance, while *R. auritus* increased, indicating an increase of the herbaceous steppe cover in detriment of shrubby steppes. In this sense, the UI and UII are characterized by the presence of several Patagonian elements (e.g., *A. hirta*, *E. chinchilloides* or *L. micropus*), as can be expected under this inferred climatic scenario. The absence of these same taxa in the UIII is suggestive of a smooth change towards more arid conditions around 1.7–1.5 ka. This scheme is broadly coincident with those inferred by Pardiñas et al. (2005, see also Teta et al., 2005; Pardiñas and Teta, 2013), who suggested – based on the micromammal samples of several archaeological sites across northwestern Patagonia – a more humid and cooler climate around 2.7–2 ka, followed by the expansion of shrubby steppes under more arid conditions between 1.9 and 1 ka.

The high proportions of the fossorial rodent *Ctenomys* at ECh clearly contrast with its scarcity in recent samples (Pardiñas and Teta, 2013: Table 4, locality #2). Previous authors highlighted that past *Ctenomys* populations of Patagonia were considerably larger and wider extended than those in modern times (see Pardiñas and Teta, 2013, and references therein). The main cause of the reduction, and even the local extirpation, of *Ctenomys* is perhaps related to the introduction of sheep and the consequent overgrazing and soil compaction. Within this context, habitat reduction by volcanic eruptions could be accompanied by the decrease of *Ctenomys* spp. in some areas of western Patagonia (e.g., Chan et al., 2005; Pardiñas and Teta, 2013). More recently, *A. olivacea* also disappeared from several localities in northern Patagonia, perhaps as a result of a general trend towards more arid and warmer conditions and the advance of the Monte vegetation during the last centuries (e.g., Pardiñas et al., 2012; Udrizar Sauthier and Pardiñas, 2014; Teta et al., 2014). The recent increase of *A. iniscatus* and *Eligmodontia* sp., the decrease of *P. xanthopygus* and *R. auritus* and the range expansion of some opportunistic species such as *Calomys musculinus* (drylands vesper mouse), *Akodon dolores and Oligoryzomys longicaudatus* (Long-tailed pygmy rice rat) are indicative of the human impact over the region during the last century, broadly characterized by the increase of shrubby areas with large patches of bare soils and the loss of herbaceous cover.

5.2. Human subsistence at Epullán Chica cave and surroundings

The zooarchaeological analysis has revealed that the economy of the Late Holocene hunter–gatherers of ECh was quite diversified. This type of subsistence has persisted until historic times. The main faunal resources obtained by humans who inhabited ECh were *L. guanicoe*, *C. villosus* and eggs of Rheidae (Fig. 2b). On the other hand, carnivores seem to have been an occasional resource, possibly obtained not only for their nutrients (e.g., defleshing marks in *Lycalopex* sp. and *G. cuja*) but also for their skins, evident from skinning marks in the mandible of *L. geoffroyi*, and corroborated by ethnographic sources. The consumption of eggs of Rheidae (including *R. pennata* and *R. americana*) could have been a seasonal practice, as rheids lay eggs mainly between August and January (Martella and Navarro, 2006), although ethnographic sources refer the storage of Rheidae eggs in pits, a common practice still today. The exploitation of the faunal resources at the site across the different periods seems to reflect a basically unchanging environment during the last 2.2 ka, as suggested by the micromammals record.

Considering the proximity between LL and ECh, it is possible to interpret that toward the Late Holocene, both cave sites could have been complementary dwellings and that they could have been inhabited by the same groups of humans. Similarity in art expressions, lithic artifacts, cordage, bone tools, faunal and plants exploitation, although with lower degree of intensity in ECh (its use by burrowing animals, absence of pottery, and fewer defined hearths and lithic tools), are good supports of these assumptions (Crivelli Montero and Fernández, 1996; Crivelli Montero et al., 1996a,b; Pardiñas, 1999a,b; Palacios, 2005, 2008; Fernández, 2007; Cordero, 2009, 2010; unpublished data). In addition, archaeobotanical studies carried out at LL indicated processing and consumption of the cactus *Austrocactus* aff. *A. bertinii* since 7 ka, and its storage since 5 ka (Crivelli Montero et al., 1996b; Fernández, 2007). In similar way, but in a much lower intensity, evidence of its processing was observed at ECh (unpublished data).

The zooarchaeological record of the Early and Mid-Holocene sequences of LL may help to understand the dynamics of the hunter–gatherers' subsistence system previous to ECh occupation. Although the Late Holocene faunal sequence of LL remains mostly unpublished, zooarchaeological studies of LL revealed a human subsistence similar to that recorded in ECh, mostly focused on the consumption of large-sized mammals (*L. guanicoe*), and an increase through the time of complementary source of food integrated by large-sized birds (*R. pennata*), medium (*L. griseus* and *L. culpaeus*, *C. chinga* and *C. villosus*), and micro-sized mammals (the tuco-tucos *Ctenomys* spp., and the cavies *G. leucoblephara* and *M. australis*) (Crivelli Montero et al., 1996a; Pardiñas, 1999a,b; Cordero, 2009, 2010).

Considering the evidence obtained in both caves, it is suggested that the Late Holocene regional hunter–gatherers were turning toward seminomadic conditions (sensu Binford, 1980), living within well-defined territories, reducing their residential mobility and intensifying in correspondence their economy (Cordero, 2012). The process of intensification in the exploitation of resources may take place when human hunting and foraging efficiency decreases over time, as a consequence of an imbalance between a stable environmental carrying capacity and an increasing human demography, which led to gradual reductions in residential mobility (e.g., Broughton, 1994). The practice of storing ochre and vegetable food after ca. 6 ka, the increasing number of archaeological sites of the Limay River basin from ca. 2 ka, the adoption of pottery and the bow and arrow some time later, a wider range of animal species in the diet and longer stays, suggested both by the richer contexts and a more careful preparation of the living surfaces by spreading straw, are good support for these assumptions (Crivelli Montero, 2010).

Although new technologies (as bow and arrow), an increased logistical mobility, and more exploitation of lower ranked resources could compensate for these limitations, a greater diversity of the exploited species for food, and confections of furs and bone tools (e.g., Alero Carriqueo and Cueva y Paredón Loncomán archaeological sites; Cordero, 2010), have been noted. In sum, the zooarchaeological data of ECh are consistent with those evident on a regional scale in other sites of the Limay River central basin (Cordero, 2010, 2012).

6. Conclusions

The taphonomic analysis of ECh suggests a palimpsest between different kinds of predators (owls for micromammals) and humans (for micro, medium and large-sized vertebrates). However, some species of middle mammals could have died in their burrows inside the cave. According to the recorded micromammals, Late Holocene environments around to ECh mostly consist in open shrubby areas intermixed with large rocky outcrops, depicting a great stability during the last 2.2 ka BP. The zooarchaeological analysis of ECh has revealed diversified economy of Late Holocene hunter–gatherers with great stability in the use of faunal resources through the

sequence, in consonance with the evidence of other sites of the Limay River middle basin. Apparently, when ECh was an element of the settlement system, the regional hunter–gatherers were intensifying their economy, reducing the residential mobility toward seminomadic conditions. The main sources of animal protein for the occupants of ECh were *L. guanicoe*, dasypodids and rheid eggs; perhaps with other aims, medium-sized mammals (felids, mustelids, mephitids, cavids, etc) were also exploited. The mollusk shells and some long bones of *L. guanicoe* provide information about the use of tools and symbolic aspects of the material culture in the middle valley of the Limay River in the Late Holocene. Finally, the absence of pottery, fewer lithic tools and hearths, less consumption of cactus without storing, and the use of the cave by burrowing animals, could be interpreted as the secondary use (of ECh regarding LL) by humans who inhabited the Cañadón del Tordillo, focusing on processing of several animals.

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