



Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Palynological analysis of extinct herbivore dung from Patagonia, Argentina

Nadia Jimena Velázquez ^{a,*}, Lidia Susana Burry ^b, Martín Horacio Fugassa ^c

^a CONICET -Laboratorio de Palinología y Bioantropología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3250, CP (7600) Mar del Plata, Argentina

^b Laboratorio de Palinología y Bioantropología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3250, Mar del Plata, Argentina

^c CONICET - Laboratorio de Paleoparasitología y arqueología contextual, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3250, Mar del Plata, Argentina

ARTICLE INFO

Article history:
Available online xxx

Keywords:
Mylodontidae
Coprolites
Palynological analysis
Paleodiet

ABSTRACT

Dung pollen studies can contribute information to the paleodiet and paleoenvironmental knowledge during the Pleistocene–Holocene transition. In this study, pollen analysis of extinct megaherbivore dung dated at $10,530 \pm 620$ BP was performed. Random samples from extinct herbivore dung, level 18, were collected from the archaeological excavation Cerro Casa de Piedra 7 (CCP7) (Argentine Patagonia). These samples were ascribed to ground sloths, Family Mylodontidae. Pollen extraction was carried out by acetolysis. The results were compared with microhistological analyses of feces and with sedimentary pollen analysis of the site. The diet items mainly consisted of Poaceae together with Apiaceae, Caryophyllaceae, Apiaceae *Azorella* type, Asteraceae subf. Asteroideae, *Nassauvia*, *Perezia*, *Acaena*, Ericaceae/*Empetrum* and *Ephedra*. A taxonomic coincidence between the palynological and microhistological analyses that permitted the determination of diet items was observed. The Poaceae and Apiaceae dominance allows supposing the grass steppe and the *Nothofagus* undergrowth as food areas for megaherbivores. The greater diversity of pollen grains in feces than in sediments due to the contribution of taxa with zoophilous pollination (regularly scarce or absent in sedimentary studies) demonstrates the value of dung analysis to paleoenvironmental reconstructions.

© 2015 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

The end of Pleistocene – start of Holocene extinct South American fauna consisted of great mammals including ground sloths (*Myodon darwini*), mastodons (*Haplomastodon*), horses (*Hippidion saldiasi*), camelids (*Paleolama*, *Lama gracilis*, *Macrauchenia patachonica*), felids (*Panthera onca mesembrina*, *Smilodon*) and canids (*Duscycyon avus*). They coexisted with some currently living species: *Lama guanicoe* (guanaco), *Felis concolor* (puma), foxes (*Pseudalopex culpaeus*, *P. griseus*) and *Hippocamelus bisulcus* (huemul) (Miotti and Salemme, 1999; Borrero, 2001). The causes of extinction of the Pleistocene fauna have been much discussed (Markgraf, 1985; Ferigolo, 1996–1997; Borrero, 2008). Among them

are the introduction of pathogens, the aborigine hunting pressure, and post glacial climate changes, including the cold and dry climate pulse coincident with the “Antarctic Cold Reversal” (12.2–15.3 ka) (Cione et al., 2003; Sugden et al., 2005). Markgraf (1985) also mentions paleoenvironmental changes south of Patagonia at the end of Pleistocene. These changes would have affected the resource availability for animals.

Paleodiet studies can contribute information to the ecological interactions in the Pleistocene–Holocene transition. A way of knowing the food resources of past faunas is through the study of fossil traces such as feces. Feces can be found dehydrated or mineralized as coprolites, which possess remains of non-digested diet items or inclusions. Among them are pollen grains, plant remains, phytolites, hairs, parasites and fossil DNA traces. The analysis of coprolites allows for the study of paleodiets, paleoenvironment, parasitism, and site use seasonality (Reinhard and Bryant, 1992; Carrión et al., 2001, 2004, 2005; Horrocks et al.,

* Corresponding author.

E-mail address: nvelazquez@mdp.edu.ar (N.J. Velázquez).

2003, 2008; Chaves and Reinhard, 2006; Riley, 2012; Wood et al., 2012; among others). Studies on pollen grains and plant remains of both camelids and presumed human coprolites found in Parque Nacional Perito Moreno (Argentine Patagonia) have offered information on their main diet items during the Holocene, and also on the site use seasonality and the environmental characteristics (Velázquez et al., 2010; Martínez Tosto and Yagueddú, 2012; Martínez Tosto et al., 2012; Velázquez and Burry, 2012; Velázquez et al., 2014).

One of the problems in palynological studies of coprolites is to elucidate the source of pollen. Among the possible mechanisms of incorporation of pollen to feces are ingestion of flowers, fruits and leaves with pollen adhered to them; water-ingest; inhaling; and pollen rain after deposition of feces (D'Antoni and Togo, 1974; Carrión et al., 2004).

Coprolites from herbivores represent a sample of ancient resources and landscapes. Among extinct megaherbivores, *Mylodon* guano has been reported in layers of different sites of Patagonia (Moore, 1978; Markgraf, 1985). *Mylodon darwini*, a strong megaherbivore, had a thick skin covered with long hairs and dermal ossicles forming a shell. It had a relatively slow walk, and had a small number of predators (Brandoni et al., 2010).

Few pollen studies have been done on feces of the Patagonian *Mylodon darwini*. Moore (1978) studied pollen and plant macroremains from a *Mylodon* guano deposit (ca. 12,400 BP) in the cave Última Esperanza (Última Esperanza, Chile), now a steppe environment. The results reveal that the diet consisted of grasses (Poaceae) and cyperaceans (Cyperaceae). In the same site, Markgraf (1985) analyzed cuticle remains and pollen grains from several layers of *Mylodon* feces (between 13,470 ± 180 and 10,832 ± 400 BP), having found 80–95% grasses and 5–20% cyperaceans, and some herbs in the most ancient layer; on the other hand, in the most modern layer (10,832 ± 400 BP) the pollen spectrum showed dominance of Asteraceae and dicotyledonean herbaceous taxa, and low values of grasses.

As for the paleoenvironmental changes that could have affected the resource availability, Markgraf (1985) reported between 11,000 and 10,000 BP a transition from a mesic and cold environment, with a grass steppe poor in species, to a more arid and warmer environment, with a shrubby steppe rich in species, and taxa typical of more arid conditions, *Berberis*, *Empetrum* and *Perezia*. In this sense, the feeding habits of the megaherbivores seem to correspond to the vegetation type dominating the area.

Elsewhere, pollen analysis have been done from coprolites of extinct herbivores: Shasta ground sloth (*Nothrotheriops shastense*) in the USA (Thompson et al., 1980); mountain goat (*Myotragus balearicus*) in the Balearic Islands, Spain (Alcover et al., 1999; Welker et al., 2014) and camelid (*Paleolama major*) in Bahia, Brazil (Marcolino et al., 2012). Their diet items were determined and the contribution of the studies to paleoenvironmental reconstructions discussed. The aim of this study is to perform a palynological study of extinct herbivore dung dated at 10,530 ± 620 BP and to discuss its contribution to the diet and paleoenvironmental knowledge of Cerro Casa de Piedra 7 (Argentine Patagonia) during the Pleistocene–Holocene transition.

2. Regional setting

Cerro Casa de Piedra 7 (CCP7) (47°57'S 72°05'W, 900 masl) is located in a transitional strip between the Andean forest and the Patagonic steppe, in the valley of Lake Burmeister, Perito Moreno National Park (PMNP), Santa Cruz Province, Argentina. The climate in PMNP is from temperate-cold to cold in summer and glacial during the rest of the year, with predominant western winds. The mean annual temperature is lower than 4 °C, with a marked

seasonality (temperatures can reach –30 °C minimum in winter and 15 °C maximum in summer). Precipitation oscillates from near 600 mm in the west to 400 mm in the east (Aschero, 1981–1982; Paruelo et al., 1998).

Nowadays on the hillsides of the Andes, between 850 and 1200 masl, a *Nothofagus pumilio* and *Nothofagus antarctica* forest grows, in addition to small woods of *N. antarctica* and *N. betuloides*, shrub and herbaceous vegetation associated with forest e.g. *Escallonia*, *Berberis*, *Fuchsia magellanica* and species belonging to the genera *Osmorhiza*, *Acaena* and *Perezia*. Toward the east, at approximately 800 masl a *Verbena tridens*, *Berberis*, *Mulinum spinosum* and *Chilolotrichium* shrub-steppe grows, and also a *Nardophyllum obtusifolium* steppe with *Festuca pallescens*, together with *Stipa ibari*, *Poa ligularis*, *Carex*, *Cerastium arvense*, *Adesmia lotoides*, *Nassauvia darwini*, *Acaena pinnatifida* and *M. spinosum* occur. At 300 masl develops the *F. pallescens* steppe with *P. ligularis*, *Rytidosperma picta*, *Stipa*, *Carex*, *Colobanthus lycopodioides*, *Armeria maritima*, *A. pinnatifida*, *Polygala darwiniana*, *Nassauvia darwini*, *Perezia recurvata*, *Mulinum microphyllum*, and *N. obtusifolium*, *Senecio filaginoides* and *Berberis heterophylla* shrubs; in addition, high altitude semi-deserts with dense patches of *E. rubrum*. Further, *Caltha sagittata*, *Plantago barbata*, *Acaena magellanica* and Cyperaceae wetland meadows grow (Movia et al., 1987; Mermoz, 1998; Ferreyra et al., 2008) (Fig. 1). The vegetation in front of Cerro Casa de Piedra is dominated by *Empetrum rubrum* that forms dense myrtle fields (“murtillar”) together with *Gaultheria mucronata*, *Nardophyllum obtusifolium*, *Acaena*, *Azorella monantha*, *Senecio filaginoides*, *Mulinum spinosum* and *Adesmia boronoides*. Some sectors contain *Festuca pallescens* grass steppe and *Nothofagus pumilio* seedlings from the forest.

Geomorphological studies in the PMNP area suggest that lakes Belgrano and Burmeister could be relicts of a large paleo-basin, that could have reached 100 m above the present level of lake Belgrano (800 masl). The level would have risen several times, the oldest during the early Holocene (González, 1992). The formation of this paleo-lake together with the vegetation changes would have affected the availability of space and the access to the different resource organisms that inhabited the region (Civalero and Aschero, 2003).

2.1. Site Cerro Casa de Piedra 7

CCP7 is the only cave from Cerro Casa de Piedra hill (Fig. 2) that has yielded evidence of the Pleistocene–Holocene transition. It presents a stratigraphic sequence and a human occupation dated between ca. 10,690 ¹⁴C BP (Aschero et al., 2008) and 3480 ± 70 ¹⁴C BP (LP 300) (Civalero and Aschero, 2003). Palynological studies of sediments from the stratigraphic sequence have revealed a Poaceae dominance of 60–80% in a ca. 10,530 ± 620 BP level, thus determining a grass steppe-type physiognomy (Mancini, 2007).

Six random samples (M15-1, M15-2, M15-E, M15-F, M15-G and M15-H) from an extinct herbivorous dung level were collected from the CCP7 archaeological excavation, Area 1, microsector D11B, level 18 (2) (Table 1). The sediment is sandy-limestone, reddish, of wet appearance and carbonate (De Nigris, 2004) (Fig. 3a). A single date of 10,530 ± 620 BP (UGA 7385) with no human association is reported (Civalero and Aschero, 2003; Aschero et al., 2008). The dating was done over a dung sample from level 18(2) (Fig. 3b). Samples from extinct herbivorous dung were ascribed to ground sloths, Family Mylodontidae, Gill 1872 (Merino pers. comm. in Aschero et al., 2008). In this level, archaeofaunistic remains of guanaco (*Lama guanicoe*) (Civalero and De Nigris, 2005) were recovered, but no bone remains attributable to Mylodontidae have been found. Moreover, coprolites of carnivores (foxes and pumas), omnivores (presumably

humans), and herbivores (camelids) have been encountered. Radiocarbon age was calibrated and corrected for the Southern Hemisphere (Hogg et al., 2013) using the program Calib, version 7.0.2 (Stuiver et al., 2005).

Table 1
Mylodontidae dung samples from CCP7.

Sample	Weight (g)	Pollen sum	Undetermined
M15-1	0.07	232	4
M15-2	0.36	200	3
M15-E	0.35	137	6
M15-F	0.41	39	2
M15-G	0.51	268	4
M15-H	0.45	243	2

3. Materials and methods: pollen extraction

Every sample was weighed and a tablet of *Lycopodium clavatum* spores (Batch N° 124961, mean = 12,542 spores/tablet) was added in order to calculate pollen concentration (number of pollen grains/g of sample) (Stockmarr, 1971). Then, the samples were rehydrated in 0.5% trisodium phosphate (TSP) (after Callen and Cameron, 1960) and filtered through a 260 µm mesh. The residue was preserved for microhistological analysis (Yaguéddú et al., 2013) and the filtrate was used in this work.

Pollen extraction was carried out by acetolysis (9 parts of acetic anhydride:1 part sulfuric acid) (Faegri and Iversen, 1989). Identification and counting of pollen types were carried out under an optical microscope (1000× magnification). Specialized bibliography and the pollen collection of the Palynology Laboratory (Universidad Nacional de Mar del Plata, Argentina) were used as references (Heusser, 1971; Markgraf and D'Antoni, 1978; Moore et al., 1991).

Table 2
Pollen concentration (grains/g) from Mylodontidae dung samples. (A): anemophilous pollen, (Z): zoophilous pollen. *some herbs.

		M15-1	M15-2	M15-E	M15-F	M15-G	M15-H
Herbs	Poaceae (A)	45,503	15,794	5502	8832	16,049	17,580
	Lamiaceae (Z)	1011	1089	0	421	511	0
	Fabaceae <i>Adesmia</i> type (Z)	1517	0	300	421	0	628
	Caryophyllaceae (Z)	506	545	400	0	1124	1570
	<i>Colobanthus</i> type (Z)	0	0	0	0	0	628
	<i>Cerastium</i> type (Z)	0	0	100	0	0	628
	<i>Valeriana</i> (Z)	0	181	200	0	511	314
	Cheno/Am (A)	0	0	200	0	102	0
	Brassicaceae (mostly Z, some A)	0	181	0	0	102	0
	Verbenaceae (Z)	506	0	0	0	0	0
	Iridaceae (Z)	0	0	0	0	0	314
	<i>Armeria</i> (Z)	0	181	0	0	0	0
	<i>Polygala</i> (Z)	0	181	0	0	0	0
	<i>Plantago</i> (A)	0	0	0	0	0	314
	Shrubs	Apiaceae (Z)*	40,447	10,348	800	841	307
Apiaceae <i>Azorella</i> type (Z)		3539	0	300	0	204	1570
Asteraceae subf. Asteroideae (A y Z)		8595	2542	1801	421	2760	13,499
<i>Nassauvia</i> (A y Z)		2528	726	1601	841	2351	5965
<i>Perezia</i> (Z)		1517	726	300	0	409	1256
<i>Acaena</i> (mostly Z)		4045	1997	0	1682	1227	3767
<i>Empetrum</i> /Ericaceae (A)		0	363	100	0	511	7848
<i>Ephedra</i> (A)		2528	726	700	421	409	1256
Anacardiaceae (Z)		0	0	0	0	0	3767
Solanaceae (Z)		0	0	100	0	0	0
Trees		<i>Nothofagus</i> (A)	1517	181	0	0	409
	<i>Podocarpus</i> (A)	0	0	100	0	0	0
	Undetermined	2022	544	600	841	409	2825
	Total pollen concentration	115,781	36,305	13,104	14,721	27,395	75,658

The percentage and concentration of every pollen type, and the total pollen concentration were calculated. Pollen spectra were graphed in percentage diagrams using the program TGView 2.02 (Grimm, 2011). The results were compared with those of microhistological analyses of the Mylodontidae sample M15-1 (Yaguéddú et al., 2013). Furthermore, pollen spectra of this work and of sedimentary pollen analysis of site CCP7 (Mancini, 2007) were compared.

4. Results

The calibrated age (BP) of a dung sample, level 18 (2) was between 13,546–10,490 (2σ) and 12,883–11,312 (1σ). The samples consisted of flattened fragments; in some cases a sandy surface was observed. Plant fragments were included (Fig. 4). The samples were from 0.07 g to 0.51 g.

The pollen sum ranged between 137 and 268 pollen grains. A single sample alone showed a pollen sum as low as 39 pollen grains (Table 1).

A total of 26 pollen types were identified. The percentage pollen diagram of samples showed dominant pollen types of herbs like Poaceae (up to 59%) and shrubs such as Apiaceae (35%), Asteraceae subf. Asteroideae (18%) and *Nassauvia* (12%).

Poaceae reached the highest percentage in each sample. Arborescent taxa such as *Nothofagus* were identified in three samples with a maximum of 1.5%. *Podocarpus*, with 0.7%, was only present in sample M15-E. Moreover, the xerophytic taxon *Ephedra*, with 1.5–5% was identified in every sample. The undetermined pollen grain percentage in samples was less than 5% (Fig. 5).

In general, the total pollen concentration was low. The highest total pollen concentration was 115,781 grains/g. At the same time, the lowest total pollen concentration was 13,104 grains/g. The pollen concentration of dominant pollen types were: Poaceae (45,503 grains/g); Apiaceae (40,447 grains/g); Asteraceae subfam. Asteroideae (13,499 grains/g) and *Nassauvia* (5965 grains/g) (Table 2).

5. Discussion

5.1. Probable diet items

Considering the concentration and dispersion mechanisms, plant pollen types found in the Mylodontidae feces (level 18) from CCP7 could indicate plant consumption or contamination of the ingested food (Velázquez and Burry, 2012). On the other hand, the possibility of post-deposition contamination from pollen rain could not be discarded. However, the presence in feces of plant fragments belonging to taxa coincident with those of pollen might be evidence that would reinforce the consumption hypothesis.

In general, the results of this study agree with the microhistological analyses of sample M15-1 by Yagueddú et al. (2013). Taxa Poaceae, Apiaceae, Ericaceae, *Perezia*, *Colobanthus* and *Armeria* are coincident in both studies; nevertheless, the microhistological analysis showed a larger abundance of grasses (Poaceae) than dicotyledonean species, while the palynological study rendered similar Poaceae and dicotyledonean (mainly family Apiaceae) abundance (Table 3).

Microhistological analysis allowed for the determination of species of the grass group (Yagueddú et al., 2013) whereas the feces pollen analysis recognized all the families or genera that were identified in the microhistological analysis, not all of them at the same taxonomic level, which shows that the pollen spectrum contains all items consumed by Mylodontidae. Nevertheless, the palynological study showed larger taxa diversity than the microhistological one in a proportion of 26/19. This extra pollen could be due to different factors: a) ingestion of leaves, flowers, and fruits that had pollen grains adhered to them, b) ingestion of water with pollen in it, and c) post-depositional feces contamination.

On the other hand, it is possible that the lesser number of taxa from the microhistological analysis could be attributable to the fact that some plant fragments did not remain in the feces, having disintegrated in the megaherbivore during the digestive system passage. The pollination type of the taxa found in the feces pollen spectra is another indication to infer either diet or contamination. The presence of zoophilous pollen types would indicate consumption, as these taxa possess both low production and pollen dispersal, which determine a low contamination

Table 3

Main diet indicator taxa identified in pollen and plant fragments from Mylodontidae subfossil feces, CCP7.

	Pollen	Plant fragments (Yagueddú et al., 2013)
Poaceae (A)	X	X
Caryophyllaceae (Z)	X	X
Apiaceae (Z)	X	X
Apiaceae <i>Azorella</i> type (Z)	X	X
Asteraceae subf. Asteroideae (Z)	X	–
<i>Nassauvia</i> (Z)	X	–
<i>Perezia</i> (Z)	X	X
<i>Acaena</i> (Z)	X	–
Ericaceae/ <i>Empetrum</i> (A)	X	X
<i>Ephedra</i> (A)	X	–

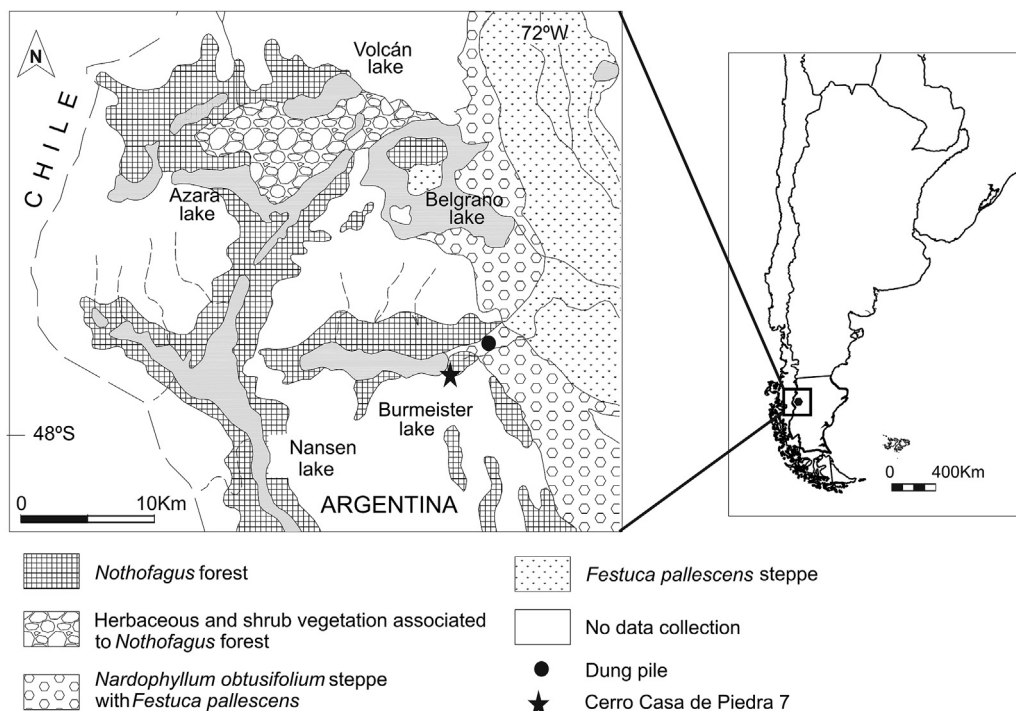


Fig. 1. Map of Perito Moreno National Park (PMNP), Santa Cruz province, showing the areas of the vegetation units (modified from Movia et al., 1987) and the location of Cerro Casa de Piedra 7 (CCP7) (after Velázquez et al., 2014).



Fig. 2. Cerro Casa de Piedra, Parque Nacional Perito Moreno, Santa Cruz, Argentina (Photograph taken by Velázquez, N.J.).

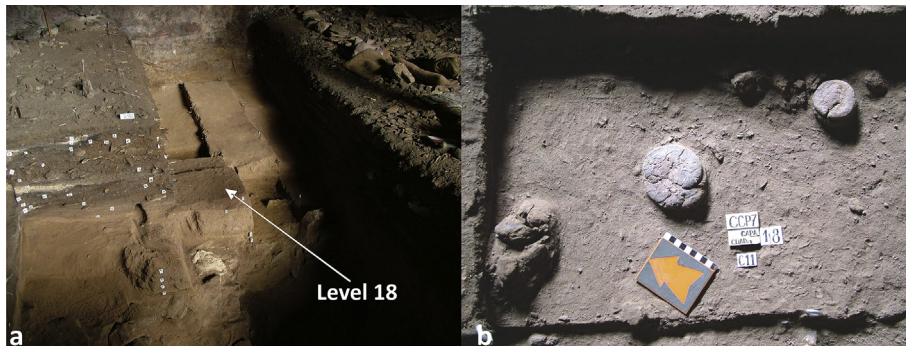


Fig. 3. a. Base of the CCP7 excavation, layer XVIII, where Mylodontidae feces were found; b. Guano from Mylodontidae megaherbivores (courtesy of Civalero, M.T.).

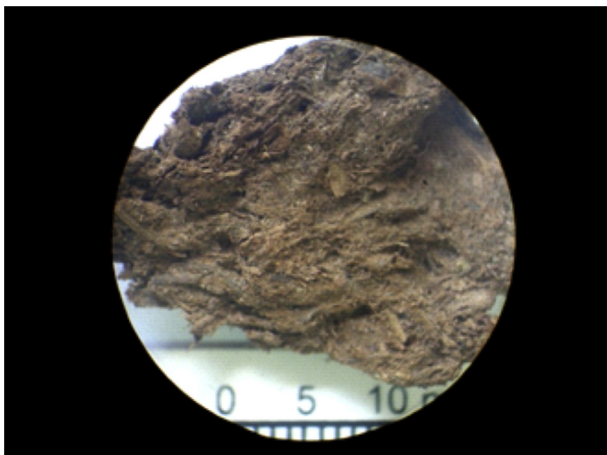


Fig. 4. Mylodontidae feces sample, M15-H (Velázquez, N.J.).

probability from food or feces (Bryant and Holloway, 1983; Pearsall, 2000).

The Family Apiaceae has zoophilous pollination. Its high pollen concentration in feces (40,447 grains/g) and the presence of plant fragments in sample M15-1 indicate that Apiaceae has been an item of the Mylodontidae diet. In particular, fragments of *Osmorhiza* and *Azorella* were identified (Yagueddú et al., 2013). *Osmorhiza chilensis* is a rosette-shaped mesophytic herb that inhabits the humid undergrowth of *Nothofagus pumilio* (Dimitri, 1974). This fact suggests that sloths resorted to the undergrowth in search of herbs. However, according to Mancini (2007), the forest was not much developed in the area next to Cerro Casa de Piedra.

The Family Asteraceae subf. Asteroideae is a taxon with numerous species. It can show zoophilous or anemophilous pollination, and most species, independently of their pollination type, have a large pollen production. In this subfamily, the shrub *Nardophyllum obtusifolium* grows together with *Festuca pallescens* conforming a grass-shrub steppe in the area close to Cerro Casa de Piedra. *Senecio filaginoides* is another species of the subfamily, also inhabiting the steppe. A high concentration of subfamily Asteraceae has been registered in the pollen spectrum. However, no

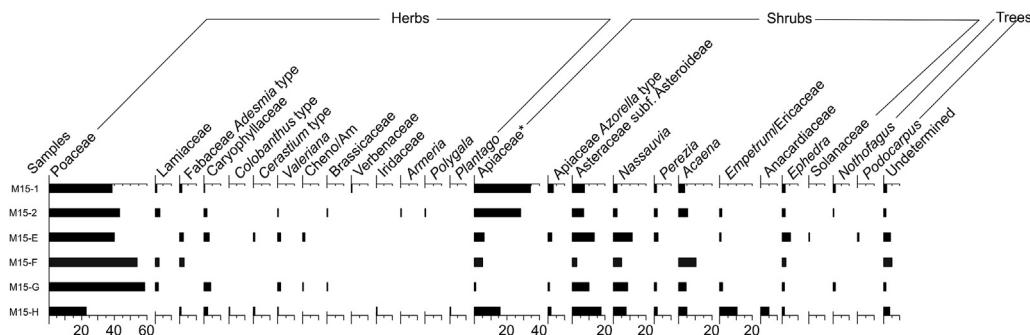


Fig. 5. Pollen diagram of Mylodontidae subfossils feces samples from CCP7 site. *some herbs.

plant fragments have been identified in feces that could help recognize this taxon as part of the Mylodontidae diet. Therefore, the high pollen concentration of Asteraceae subfam. Asteroideae in feces could be due to pollen grains adhering to the food consumed.

On the other hand, the genus *Nassauvia* which includes both zoophilous and anemophilous species of low pollen production is another possible item of the Mylodontidae diet. Nowadays, this taxon grows in the Patagonian semi-desert unit (Ferreyra et al., 2008).

Moreover, the zoophilous taxon *Acaena* was found in most samples with a concentration reaching 4045 grains/g, thus suggesting this item could be part of the diet. Other zoophilous taxa present in the majority of samples, although in low concentration, were Caryophyllaceae, *Cerastium* type, Lamiaceae, Fabaceae *Adesmia* type and *Valeriana*.

In addition, the *Ephedra* pollen grains show anemophilous dispersion, but being its pollen production low would allow inferring that this taxon has been consumed. Currently, in the PNPM *Ephedra frustillata* grows in the hillsides (Ferreyra et al., 2008). As for the Ericaceae/*Empetrum* grains, they show anemophilous pollination; they were present in low concentration in almost all samples, exception made of sample 15H, which reached a high concentration (7848 grains/). Likewise, Yaguéddú et al. (2013) identified *Gaultheria* (Ericaceae) plant fragments in M15-1, thus suggesting this item could be part of the diet.

According to the results of this study, half of the analyzed samples showed that the Poaceae pollen concentration is similar to that of Apiaceae. This suggests that not only grasses were part of the diet, but Apiaceae shrubs and *Osmorhiza* herbs were also important components. In addition, Markgraf (1985) observed pollen grains from both shrubby plants and grasses in *Mylodon* feces found in the site Cueva del Milodón, even though they were non-dominant in pollen spectra, save the youngest sample. Coincidentally, the microhistological analysis carried out in one of the CCP7 sample evidenced a greater percentage of grasses than dicotyledoneans, suggesting that grasses could be a main item of the megaherbivores diet. On the other hand, Poaceae shows a larger pollen concentration than the rest of samples. These results support the hypothesis of the grazing habits of megaherbivores, which agree with the results registered by Moore (1978) and Markgraf (1985), although shrubs or dicotyledonean herbaceous taxa should not be discarded as a diet item.

As regards to the habitat of *Mylodon*, the Poaceae dominance on the one hand, and the presence of Apiaceae on the other, allows supposing the use of the grass-steppe as well as the *Nothofagus pumilio* undergrowth -where *Osmorhiza* inhabits-for feeding. The possible diet items are summarized in Table 3.

The taxa represented in the pollen spectrum and absent in the plant fragments spectrum, such as *Nothofagus* and *Podocarpus*, would show the grains coming from the pollen rain that could have

been adhered to plants consumed, incorporated to water drunk by the animal, or otherwise, they could have been deposited over the feces surface after deposition.

5.2. Coprolites pollen analysis vs. sedimentary pollen analysis

The high Poaceae percentage (up to 59%) found in the megaherbivore feces agree with the results of the sedimentary pollen study of the same archaeological level (18). In the latter, Mancini (2007) suggests that a grass-steppe had developed in the area ca. 10,530 ± 620 BP. Moreover, the presence of *Nothofagus*, *Podocarpus*, Asteraceae subfam. Asteroideae, *Nassauvia*, *Empetrum rubrum*, Apiaceae *Azorella* type, *Acaena*, *Ephedra*, Fabaceae, Chenol/Am, Brassicaceae, *Plantago* and Lamiaceae pollen types registered in the Mylodontidae feces analysis agree with taxa identified in sediments (Mancini pers. comm.; Mancini 2007; Velázquez et al., 2010). However, a greater diversity was identified in feces than in sediments, indicating the importance of studies on fossil feces to paleoenvironmental reconstructions, for they contribute information not represented in the sedimentary pollen spectrum (Chaves, 2000; Velázquez et al., 2010). Thus, in this work the presence of taxa *Perezia*, Solanaceae, Anacardiaceae, Caryophyllaceae, *Colobanthus* and *Cerastium* type, *Armeria*, *Valeriana* and *Polygala*, has been registered, most of them with zoophilous dispersal (Table 2) and none present in sediments.

A greater abundance of Apiaceae grains was found in feces than in sediments. This suggests that this family is part of the Mylodontidae diet. According to Bryant and Holloway (1983), the proportion of entomophilous types in sediments is low. Greater entomophilous taxa percentages in coprolites than in sediments indicate taxon intake.

The presence of *Ephedra* and *Nassauvia*, pollen types that currently grow in the semi-desert, suggest that in the area close to CCP7 more arid conditions prevailed during the Pleistocene–Holocene transition than today. Nowadays, the semi-desert develops in a plateau, east of the PMNP, with rainfall less than 200 mm. However, in spite of the presence of taxa in low concentration and growing in arid conditions, feces pollen spectra indicate, as in sediments, the dominance of Poaceae.

The palynological and microhistological of presumed human coprolites in the archaeological level 18, CCP7 (Burry et al., 2013; Martínez Tosto et al., 2013) agree with our results as far as grasses' dominance and presence of shrubs (*Azorella monantha*, *Empetrum rubrum*, Asteraceae subfam. Asteroideae, Caryophyllaceae, *Nassauvia*, *Acaena*, Fabaceae and Solanaceae) are concerned. These findings reinforce the identification of pollen grains of plants growing ca. 10,530 BP; further, some of these plants were consumed by the megaherbivore and humans. As for the Poaceae dominance for the Pleistocene–Holocene transition, the Mylodontidae feces pollen spectra coincide with the contemporary

sedimentary pollen spectra of site CCP7 as well as of other sites of southwestern Santa Cruz between 45° and 50° S (Mancini, 1998, 2009; Mancini, 2002).

6. Conclusions

The Mylodontidae feces pollen analysis results of site CCP7 show a Poaceae dominance that indicates the grazing habit of the Patagonian megaherbivores ca. 10,530 BP. Nevertheless, shrubs or dicotyledonean herbaceous taxa should not be discarded in relation to its environmental availability. These results are compatible with those of the coprolite microhistological analysis from PNPM (Yaguéddú et al., 2013), and the coprolite pollen analysis of Cueva del Milodon in Chile (Moore, 1978; Markgraf, 1985). The taxonomic coincidence between palynological and microhistological analyses permitted the determination of diet items. However, the palynological analysis showed more taxonomic diversity than the microhistological. The reason could be found in diverse factors: contribution of pollen grains to feces through a) adherence to leaves, flowers, or fruits of plants not consumed by megaherbivores, b) deposition of pollen grains on the water consumed by the megaherbivore, or c) post-depositional contamination of feces. Shrub taxa were also identified in high concentrations. They were present in the microhistological analysis and the species were adapted to zoophilous pollination, suggesting that they could also be part of the Mylodontidae diet.

The greater diversity of pollen grains in feces than in sediments demonstrates the value of the study of coprolites to paleoenvironmental reconstructions due to the contribution of taxa with zoophilous pollination, regularly scarce or absent in sedimentary studies. In this way, the paleoenvironmental information of Cerro Casa de Piedra in the Pleistocene–Holocene transition becomes enriched.

Acknowledgments

Our most grateful thanks to Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET); Universidad Nacional de Mar del Plata (UNMDP), Project (EXA-UNMDP 654/2015); Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT), Fondo para la Investigación Científica y Tecnológica (FONCYT), Project (PICT N° 04-12262, 12-2316); Matilde Trivi de Mandri for helping in the writing; Teresa Civalero and Carlos Aschero for providing the samples and their valuable comments which helped to improve the manuscript; Agustín Barrere, Horacio Barrere, Perito Moreno National Park park-rangers and National Parks Administration for helping in the field work. We are also grateful to Jose S. Carrión and anonymous reviewers for their useful comments. This work is part of the doctoral thesis of Nadia Jimena Velázquez.

References

- Alcover, J.A., Perez-Obiol, R., Yll, E., Bover, P., 1999. The diet of *Myotragus balearicus* Bate 1909 (Artiodactyla: Caprinae), an extinct bovid from the Balearic Islands: evidence from coprolites. *Biological Journal of the Linnean Society* 66, 57–74.
- Aschero, C.A., 1981–1982. Nuevos datos sobre la arqueología del Cerro Casa de Piedra, sitio CCP5 (Parque Nacional Perito Moreno, Santa Cruz, Argentina). *Intersecciones en Antropología* 14 (2), 267–284.
- Aschero, C.A., Bozzuto, D., Civalero, M.T., Nigris, M.D., Vruno, A.D., Dolce, V., Fernández, N., González, L., Sacchi, M., 2008. Nuevas evidencias sobre las ocupaciones tempranas de Cerro Casa de Piedra 7. In: Morello, F., Prieto, A., Martinic, M., Bahamondes, G. (Eds.), *Arqueología de Fuego-Patagonia. Levantando piedras, desenterrando huesos y develando arcanos*. Centro de Estudios del Cuaternario Antártico (CEQUA), Punta Arenas, Chile, pp. 569–576.
- Borrero, L.A., 2001. El poblamiento de la Patagonia: Toldos, milodones y volcanes. Emecé, Buenos Aires.
- Borrero, L.A., 2008. Extinction of Pleistocene megamammals in South America: the lost evidence. *Quaternary International* 185, 69–74.
- Brandoni, D., Ferrero, B.S., Brunetto, E., 2010. *Myodon darwini* Owen (Xenarthra, Mylodontinae) from the Late Pleistocene of Mesopotamia, Argentina, with remarks on individual variability, paleobiology, paleobiogeography, and paleo-environment. *Journal of Vertebrate Paleontology* 30 (5), 1547–1558.
- Bryant Jr., V.M., Holloway, R.G., 1983. The role of palynology in archaeology. In: Schiffer, M.B. (Ed.), *Advances in Archaeological Method and Theory*, vol. 6. Academic Press, New York, NY, pp. 191–219.
- Burry, L.S., Velázquez, N.J., Martínez Tosto, A.C., Yaguéddú, C., Fugassa, M.H., 2013. Estudios palinológicos, paleobotánicos y parasitológicos en coprolitos holocénicos de Patagonia, Argentina. XIV Simpósio Brasileiro de Paleobotânica e Palinología, 5° Encontro latinoamericano de fitólitos, 13–16 de mayo de 2013. In: Mendonça, C.B.F., Gonçalves-Esteves, V., Carvalho, M.A., Scheel-Ybert, R. (Eds.), *Conservação do patrimônio paleobotânico e palinológico, Série Livros 49*. Museu Nacional, Rio de Janeiro, Brasil, p. 43.
- Callen, E.O., Cameron, T.W.M., 1960. A prehistoric diet revealed in coprolites. *New Scientist* 8, 35–40.
- Carrión, J.S., Yll, E.I., Riquelme, J.A., 2004. Perspectivas del análisis polínico de coprolitos y otros depósitos biogénicos útiles en la inferencia paleoambiental. In: *Miscelánea en Homenaje a Emiliano Aguirre: Paleontología*. Museo Arqueológico Regional, Madrid, pp. 128–139.
- Carrión, J.S., Riquelme, J.A., Navarro, C., Munuera, M., 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 176, 193–205.
- Carrión, J.S., Gil, G., Rodríguez, E., Fuentes, N., García-Antón, M., Arribas, A., 2005. Palynology of badger coprolites from Central Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 226, 259–271.
- Chaves, S.A.M., 2000. Estudo palinológico de Coprólitos pré-históricos Holocenos coletados na toca do Boqueirão do sítio da Pedra Furada-contribuições paleoentológicas, paleoclimáticas e paleoambientais para a região sudeste do Piauí-Brasil. *Revista do Museu de Arqueologia e Etnologia*. Universidade de São Paulo 10, pp. 103–120.
- Chaves, S.A.M., Reinhard, K.J., 2006. Critical analysis of coprolite evidence of medicinal plant use, Piauí, Brazil. *Palaeogeographic, Palaeoclimatology, Palaeoecology* 237, 110–118.
- Cione, A.L., Tonni, E.P., Soibelzon, L.H., 2003. The Broken Zig-Zag: Late Cenozoic large mammal and tortoise extinction in South America. *Revista del Museo Argentino de Ciencias Naturales* 5 (1), 1–19.
- Civalero, M.T., Aschero, C.A., 2003. Early occupations at Cerro Casa de Piedra 7, Santa Cruz Province, Patagonia Argentina. In: Miotti, L., Salemme, M., Flegenheimer, N. (Eds.), *Where the South Winds Blow: Ancient Evidence for Paleo South Americans*. Center for the Studies of the First American (CSFA) and Texas A&M University Press, Texas, pp. 141–147.
- Civalero, M.T., De Nigris, M.E., 2005. Explotación de fauna y tecnología lítica en Cerro Casa de Piedra 7 (Santa Cruz, Argentina). *Relaciones de la Sociedad Argentina de Antropología* 30, 105–122.
- D'Antoni, H.L., Togo, J., 1974. Análisis polínico de coprolitos animales: su aplicación en arqueología. In: III Congreso Argentino de Arqueología Salta, pp. 1–16.
- De Nigris, M.E., 2004. El consumo en grupos cazadores recolectores: un ejemplo zooarqueológico de Patagonia Meridional. *Sociedad Argentina de Antropología*, Buenos Aires, first ed.
- Dimitri, J.M., 1974. Pequeña flora ilustrada de los Parques Nacionales andino-patagónicos. *Anales de Parques Nacionales* Tomo XIII, 1–122.
- Faegri, K., Iversen, J., 1989. In: Faegri, K., Kalland, P.E., Krzywinski, K. (Eds.), *Textbook of Pollen Analysis*, fourth ed. J. Wiley & Sons, Chichester, 328pp.
- Ferigolo, J., 1996–1997. Late Pleistocene South American land mammal extinctions: the infection hypothesis. *Quaternary of South America and Antarctic Peninsula* 12, 279–310.
- Ferreira, M., Rivas, C., Mirabeli, M., Morosini, F., Fernández, A., 2008. Flora, vegetación y fauna altoandinas en el Parque Nacional Francisco Perito Moreno. Final report.
- Gill, T., 1872. Arrangement of the Families of Mammals, with Analytical Tables. In: *Smithsonian Miscellaneous Collections*, Washington, vol. 11, 6+ 98 pp.
- González, M.A., 1992. Paleoaambientes del Pleistoceno Tardío/Holoceno Temprano en la Cuenca de los Lagos Belgrano y Burmeister (47°40'/48' Sur, 72°30'Oeste), Santa Cruz. *Informes Técnicos*. Fundación Carl C. von Cullenius 9, pp. 1–7.
- Grimm, E.C., 2011. *Tilia Software*, 1.7.14. Research and Collection Center, Springfield, Illinois.
- Heusser, C.J., 1971. *Pollen and Spores from Chile. Modern Types of Pteridophyta, Gymnospermae and Angiospermae*. University of Arizona Press, Tucson.
- Hogg, A.G., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Heaton, T.J., Palmer, J.G., Reimer, P.J., Reimer, R.W., Turney, C.S.M., Zimmerman, S.R.H., 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. *Radiocarbon* 55, 1889–1903.
- Horrocks, M., Irwin, G.J., McGlone, M.S., Nichol, S.L., Williams, L.J., 2003. Pollen, phytoliths and diatoms in prehistoric coprolites from Kohika, Bay of Plenty, New Zealand. *Journal of Archaeological Science* 30, 13–20.
- Horrocks, M., Salter, J., Braggins, J., Nichol, S., Moorhouse, R., Elliott, G., 2008. Plant microfossil analysis of coprolites of the critically endangered kakapo (*Strigops habroptilus*) parrot from New Zealand. *Review of Palaeobotany and Palynology* 149, 229–245.
- Mancini, M.V., 1998. Vegetational changes during Holocene in the extra-Andean Patagonia, Santa Cruz province, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 138, 207–219.

- Mancini, M.V., 2002. Vegetation and climate during the Holocene in Southwest Patagonia, Argentina. *Review of Palaeobotany and Palynology* 122, 101–115.
- Mancini, M.V., 2007. Cambios paleoambientales en el ecotono bosque-estepa: Análisis polínico del sitio Cerro Casa de Piedra 7, Santa Cruz (Argentina). In: Morello, F., Martinić, M., Prieto, A., Bahamonde, G. (Eds.), *Arqueología de Fuego Patagonia. Levantando piedras, desenterrando huesos y develando arcanos*. Ediciones CEQUA, Punta Arenas, Chile, pp. 89–94.
- Mancini, M.V., 2009. Holocene vegetation and climate changes from a peat pollen record of the forest-steppe ecotone, Southwest of Patagonia (Argentina). *Quaternary Science Reviews* 28, 1490–1497.
- Marcolino, C.P., dos Santos, I.R.M., Cozzuol, M.A., Cartelle, C., Trindade Dantas, M.A., 2012. Diet of *Palaeolama major* (Camelidae) of Bahia, Brazil, inferred from coprolites. *Quaternary International* 278, 81–86.
- Markgraf, V., 1985. Late Pleistocene faunal extinctions in southern Patagonia. *Science* 228, 1110–1112.
- Markgraf, V., D'Antoni, H.L., 1978. Pollen Flora of Argentina. Modern Spore and Pollen Types of Pteridophyta, Gymnospermae and Angiospermae. The University of Arizona Press, Tucson.
- Martínez Tosto, A.C., Yaguéddú, C., 2012. Identificación de microrrestos vegetales en un coprolito humano del sitio Cerro Casa de Piedra, Santa Cruz, Argentina. *Magallania* 40 (1), 333–339.
- Martínez Tosto, A.C., Burry, L.S., Civalero, M.T., 2012. Aportes paleobotánicos en la reconstrucción de paleodietas. Análisis de coprolitos del Cerro Casa de Piedra, Santa Cruz. *Revista del Museo de Antropología* 5, 163–170.
- Martínez Tosto, A.C., Burry, L.S., Arriaga, M.O., Civalero, M.T., 2013. Estudio paleobotánico en coprolitos del Holoceno y su utilización como indicadores del uso del espacio. In: Bárcena, J.R., Martín, S.E. (Eds.), *Arqueología Argentina en el Bicentenario de la Asamblea General Constituyente de 1813*. XVIII Congreso Nacional de Arqueología Argentina La Rioja, 22 al 26 de abril de 2013, pp. 19–20.
- Mermoz, M., 1998. Mapa preliminar de vegetación Parque Nacional Perito Moreno, Dirección Nacional de Conservación de Áreas protegidas. Delegación Regional Patagonia, Bariloche.
- Miotti, L., Salemme, M., 1999. Biodiversity, taxonomic richness and generalist-specialists economical systems in Pampa and Patagonia regions, southern South America. *Quaternary International* 53/54, 53–68.
- Moore, D.M., 1978. Post-glacial vegetation in the South Patagonian territory of the giant ground sloth, *Myiodon*. *Botanical Journal of the Linnean Society* 77, 177–202.
- Moore, P.D., Webb, J.A., Collinson, M.E., 1991. *Pollen Analysis*, second ed. Blackwell, London.
- Movia, C., Soriano, A., León, R., 1987. La vegetación de la Cuenca del Río Santa Cruz (provincia de Santa Cruz, Argentina). *Darwiniana* 28, 9–78.
- Paruelo, J.M., Beltrán, A., Jobbágy, E., Sala, O.E., Golluscio, R.A., 1998. El clima de la Patagonia: 442 patrones generales y controles sobre los procesos bióticos. *Ecología Austral* 8, 85–101.
- Pearsall, D., 2000. *Paleoethnobotany. A Handbook of Procedures*, second ed. Academic San Diego. 700 pp.
- Reinhard, K.J., Bryant, V.M.J., 1992. Coprolite analysis: a biological perspective on archaeology. In: Shiffer, M. (Ed.), *Advances in Archaeological Method and Theory* 4. University of Arizona Press, Tucson, pp. 245–288.
- Riley, T., 2012. Assessing diet and seasonality in the Lower Pecos canyonlands: an evaluation of coprolite specimens as records of individual dietary decisions. *Journal of Archaeological Science* 39 (1), 145–162.
- Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13, 615–621.
- Stuiver, M., Reimer, P.J., Reimer, R.W., 2005. CALIB 5.0 [www program and documentation].
- Sugden, D.E., Bentley, M.J., Fogwill, C.J., Hulton, N.R., McCulloch, R.D., Purves, R.S., 2005. Late-glacial glacier events in southernmost South America: a blend of northern and southern hemispheric climatic signals? *Geografiska Annaler: Series A, Physical Geography* 87 (2), 273–288.
- Thompson, R.S., Van Devender, T.R., Martin, P.S., Foppe, T., Long, A., 1980. Shasta ground sloth (*Nothrotheriops shastensehoffstetteri*) at Shelter Cave, New Mexico: environment, diet, and extinction. *Quaternary Research* 14, 360–376.
- Velázquez, N.J., Burry, L.S., 2012. Palynological analysis of *Lama guanicoe* modern feces and its importance for the study of coprolites from Patagonia Argentina. *Review of Palaeobotany and Palynology* 184, 14–23.
- Velázquez, N.J., Burry, L.S., Mancini, M.V., Fugassa, M.H., 2010. Coprolitos de camélidos del Holoceno como indicadores paleoambientales. *Magallania* 38 (2), 213–229.
- Velázquez, N.J., Burry, L.S., Fugassa, M.H., Civalero, M.T., Aschero, C.A., 2014. Palynological analysis of camelid coprolites: seasonality in the use of the site Cerro Casa de Piedra 7 (Santa Cruz, Argentina). *Quaternary Science Reviews* 83, 143–156.
- Welker, F., Duijm, E., van der Gaag, K.J., van Geel, B., de Knijff, P., van Leeuwen, J., Mol, D., van der Plicht, J., Raes, N., Reumer, J., Gravendeel, B., 2014. Analysis of coprolites from the extinct mountain goat *Myotragus balearicus*. *Quaternary Research* 81 (1), 106–116.
- Wood, J.R., Wilmshurst, J.M., Wagstaff, S.J., Worthy, T.H., Rawlence, N.J., Cooper, A., 2012. High-resolution Coproecology: using coprolites to reconstruct the habits and habitats of New Zealand's extinct upland Moa (*Megalapteryx didinus*). *PLoS ONE* 7, 1–13.
- Yaguéddú, C., Velázquez, N.J., Arriaga, M.O., 2013. Estudios paleobotánicos en heces subfósiles de Mylodontidae de Patagonia. XIV Simpósio Brasileiro de Paleobotânica e Palinologia. 5º Encontro latinoamericano de fitólitos, Rio de Janeiro, 13-16 de mayo de 2013. In: Mendonça, C.B.F., Gonçalves-Esteves, V., Carvalho, M.A., Scheel-Ybert, R. (Eds.), *Conservação do patrimônio paleobotânico e palinológico, Série Livros* 49. Museu Nacional, Rio de Janeiro, Brasil, p. 189.