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A methodology for the determination of pollen sources in studies of Patagonian camelid coprolites

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ABSTRACT

Pollen studies on Patagonian camelid coprolites (Argentina) focus on palaeodiet analyses and palaeoenvironmental reconstructions. The elucidation of the source of pollen in coprolites is a main issue to interpret what and how past facts happened. The aim of this work is to evaluate the source of the pollen contained in both modern *Lama guanicoe* feces and camelid coprolites to evaluating the post-depositing contamination. Pellets were separated into outer and inner parts, and pollen extraction was made of each for analysis. As to pollen concentration, differences probably linked to the pollination season were found between both parts of the feces. The presence of certain taxa only in the outer part could be due to postdepositional contamination. Coprolites evidenced more *Nothofagus* anemophilous pollen concentration in the outer surface of feces and certain taxa were only registered in a single part. A separate pollen analysis of the outer and inner parts of modern feces and coprolites yields information referred to contamination by environmental pollen; thus, the items conforming part of the diet of the vegetation area not consumed by the organisms can be discriminated.

1. Introduction

The finding of Holocenic coprolites ascribed to camelids in caves from the Argentine Patagonia (sites CCP5 and CCP7, Perito Moreno National Park) gave rise to questions about the seasonality in the site use of camelids and men (Martínez Tosto and Yagueddú, 2012; Martínez Tosto et al., 2012, 2013; Velázquez et al., 2014), of palaeodiets and of the contribution of the analysis of coprolites to environmental studies.

Since *Lama guanicoe* (camelid) was the main subsistence resource of hunter-gatherers (Borrero, 2001; Miotti and Salemme, 1999), the knowledge of palaeodiets, action range and seasonality in the use of caves/eaves could yield information on the mobility dynamics of these groups.

Pollen studies on coprolites focus on palaeodiet analyses and environmental reconstructions (Reinhard and Bryant, 1992; Carrión et al., 2001, 2004; Horrocks et al., 2003; Burry et al., 2008; Martínez Tosto et al., 2012; Velázquez et al., 2015, 2010; Wood et al., 2012). Various authors point out that a main issue is the elucidation of the source of the pollen content. For instance, pollen grains in coprolites of herbivores are related to their diet and the plant availability in the environment. In this way, the presence of pollen in herbivore, can be the result of:

1) diet of anthers, leaves, stems, flowers and fruits, ingested with pollen grains adhered to the organs surface (Bryant and Holloway, 1983)
2) water drinking with suspended pollen grains coming either from pollen rain or aquatic plants,
3) air inhalation,
4) pollen depositing over the feces surface after deposition, mainly pollen grains with anemophilous dispersion (Carrión et al., 2001, 2005). This happens because once the deposition has occurred, *mucus* surrounding feces acts as a pollen trap from the pollen rain (Chaves, 2000) (Fig. 1): it is the post-depositional pollen contamination.

The concentration and preservation of pollen within coprolites are influenced by many factors: a) type of plant pollination (zoophilous, anemophilous, hydrophilous or autopollination); b) physiology of the organisms digestive system; c) organisms' feeding habits or behavior and d) preservation environment, like temperature, humidity and acidity.

On the other hand, studies of modern feces together with coprolite analyses and experimental studies allow for comparisons and contribute to the necessary information to interpret what and how past facts happened (Fernández-Jalvo et al., 2010; Gil-Romera et al., 2014). In studies of modern diets and palaeodiets, and the analysis of fresh feces and coprolites it is important to ascertain the origin of pollen and spores to contribute information to other ecological matters of organisms (Fig. 1).

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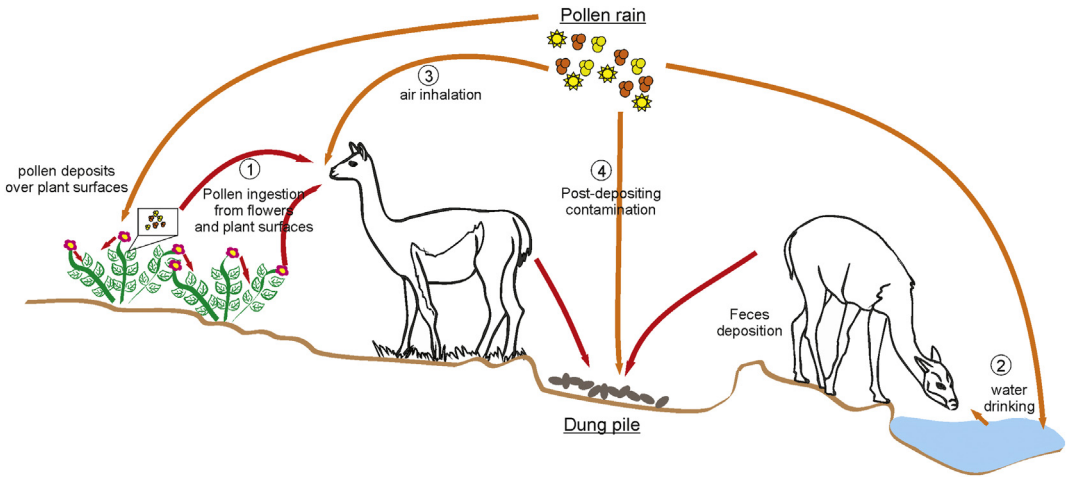

Fig. 1. Different input pollen routes to *Lama guanicoe* feces.

The aim of this work is to evaluate the source of the pollen contained in modern *Lama guanicoe* feces and camelid coprolites. The hypothesis posed is that the feces surface is contaminated with pollen coming from the pollen rain.

2. Regional setting

The Perito Moreno National Park (PMNP) is located in central-west Santa Cruz, in the Andes Mountain Range, Río Chico Department (Fig. 2).

The climate, influenced by the South Pacific Anti-cyclone, is temperate-cold to cold in summer and glacial the rest of the year, with predominant western winds. Mean annual temperatures are less than 4 °C, with a sharp seasonality (in winter, temperatures can reach −30 °C, and in summer 15 °C). Annual precipitations in the park range from near 600 mm in the west to 400 mm in the east (Aschero, 1981–1982; Paruelo et al., 1998).

Phytogeographically, the park is located in the Deciduous Forest District of the Subantarctic Province and in the Central District of the Patagonic Province (Cabrera, 1976). The area of study consists of caves located in Cerro Casa de Piedra (CCP) (47°57′S; 72°05′O, 900 m asl), east of the Andes Mountain Range, in a transitional belt between the mountain range forest and the Patagonic steppe, in the Roble River basin and Lake Burmeister. The hill has a series of eaves and caves, among which are the sites Cerro Casa de Piedra cave 5 (CCP5) and 7 (CCP7), 600 m from the Roble River southern margin (Fig. 3a).

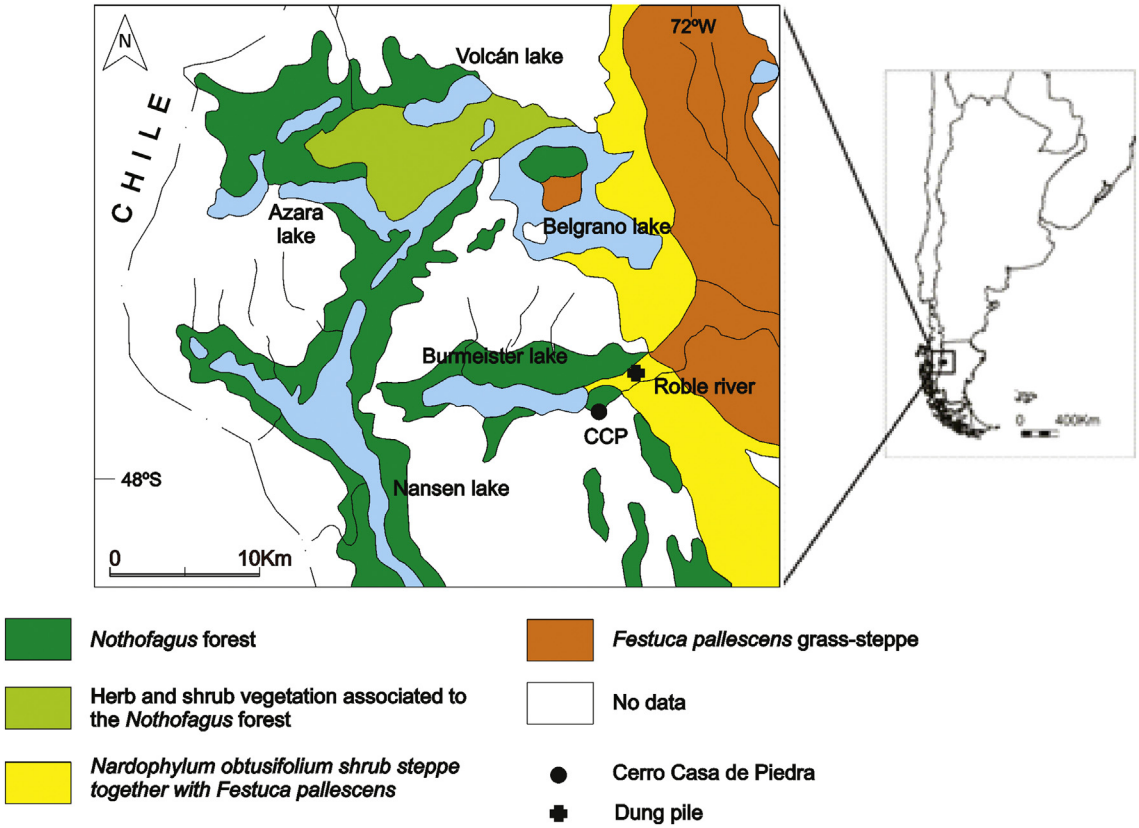

Fig. 2. Map of the Perito Moreno National Park vegetation units, province of Santa Cruz (modified from Movia et al., 1987), and Cerro Casa de Piedra location.

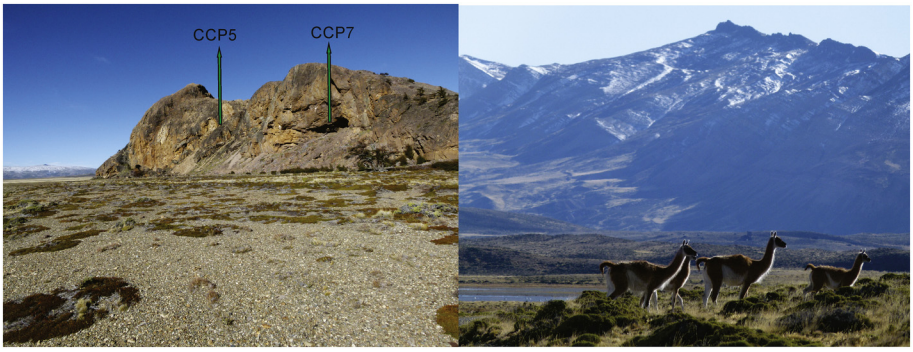

Fig. 3. a. Cerro Casa de Piedra 5 and 7, b. *Lama guanicoe* in Perito Moreno National Park.

Vegetation around CCP from the base of the hill to the Roble River is dominated by an *Empetrum rubrum* fringe which makes up a dense murtillar with *Gaultheria mucronata*; a *Festuca pallescens* grass steppe in some sectors; an *Azorella monanthos* murtillar and scattered adults and shoots of *Nothofagus pumilio* trees; and a shrub steppe with *Nardophyllum obtusifolium*, *Mulinum spinosum*, *Senecio filaginoides* and *Adesmia boronioides* predominance. Along the Roble River shore, a grass-shrub steppe dominated by *Nardophyllum obtusifolium* together with grasses and *Acaena* is observed.

3. *Lama guanicoe*

The guanaco (Fig. 3b) is a pseudo-ruminant species which grazer and browser habits could partly explain its wide distribution and its great adaptability for living in different environments (Wheeler, 1991). During the reproductive season, the guanaco populations make up three basic social units: polygamous family groups (one male and its harem together with juveniles), non-reproductive male groups and solitary males (Franklin, 1982). The group composition outside the reproductive season varies according to the environmental conditions.

4. Materials and methods

Pollen from 12 modern feces of *Lama guanicoe* were collected in a dung pile at the Valley of Roble River (Fig. 2) during summer, fall, winter and spring 2010. This modern feces model was used as an analog of camelid coprolites. Twenty eight camelid coprolites were analyzed from CCP5 and CCP7 (Velázquez and Burry, 2012; Velázquez et al., 2010, 2014).

All pellets were weighed; diameter and width measures were registered; shape, texture and color of every feces were determined; and surface inclusions were observed under the stereomicroscope (Chame, 2003; Jouy-Avantin, 2003).

To evaluate the post-depositing contamination produced by anemophilous pollen, pellets were divided into outer and inner subsamples by scraping the cortex away with a scalpel. Then, each of the samples was weighed.

The subsamples were placed in 15 ml conical tubes, a tablet of *Lycopodium clavatum* spores (Batch No. 124961, mean = 12,542 spores/tablet) (Stockmarr, 1971) was added to ensure no loss of material during the extracting process and to calculate pollen concentration (number of pollen grains/g of subsample). Later, they were rehydrated with 0.5% trisodium phosphate dodecahydrate and stored in refrigerator for 72 h (Callen and Cameron, 1960). Subsequently, the subsamples were filtered through a 260 μm mesh. Remains trapped in the mesh were kept for microhistological studies. The filtrate was used for pollen extraction.

Pollen extraction of every pellet subsample was made (D'Antoni, 1979; Faegri and Iversen, 1989) as follows:

a) concentration of filtrate by 2500 rpm centrifugation for 5 min;
b) dehydration with pure acetic acid;
c) elimination of the cellulosic material by acetolysis (the acetolytic mixture is made of 9:1 ratio of acetic anhydride to sulfuric acid) (Erdtman, 1943; Faegri and Iversen, 1989).

Finally, the obtained residue was concentrated by 2500 rpm centrifugation for 5 min and the subsamples were stored in Kahn tubes.

4.1. Identification and counting of pollen types

Semi-permanent slides were made (D'Antoni, 1979) and microscope observations done with an optical binocular microscope (400×; 1,000×). The identification and pollen counting was made using specialized bibliography (Heusser, 1971; Markgraf and D'Antoni, 1978; Moore et al., 1991) and the reference pollen collection of both the Palynology Laboratory and the Palynology and Bioanthropology Group (Universidad Nacional de Mar del Plata, Argentina). The Instituto de Botánica Darwinion, Argentina (http://www.darwin.edu.ar) nomenclature system was used. The pollen sum included all pollen and spore types, and a sum of at least 200 grains for statistical significance (Sobolik, 1988).

The concentration of every pollen type was calculated. Pollen concentration is an absolute measure of the number of pollen grains per sample unit (Benninghoff, 1962; Maher, 1981) calculated by the following formula:

$$X = a\,b/c\,p$$

Where a is the number of added foreign marker (spores of *Lycopodium clavatum*), b is the number of pollen grains counted, c is the number of spores of L. *clavatum* counted and p is the weight of the sample (D'Antoni, 1979).

Concentration diagrams were made of the dominant pollen types in the outer and inner subsamples. Pollen concentration data were used to compare the abundance of every pollen type in the outer and inner subsamples. These absolute data allowed for the independence of the abundance of the rest of taxa, as the percentage data.

To evaluate similarities and differences in pollen concentration of outer and inner subsamples of coprolites correspondence analyses with programs R (R Development Core Team, 2011), were done. The pollen concentration of dominant types was used for correspondence analysis.

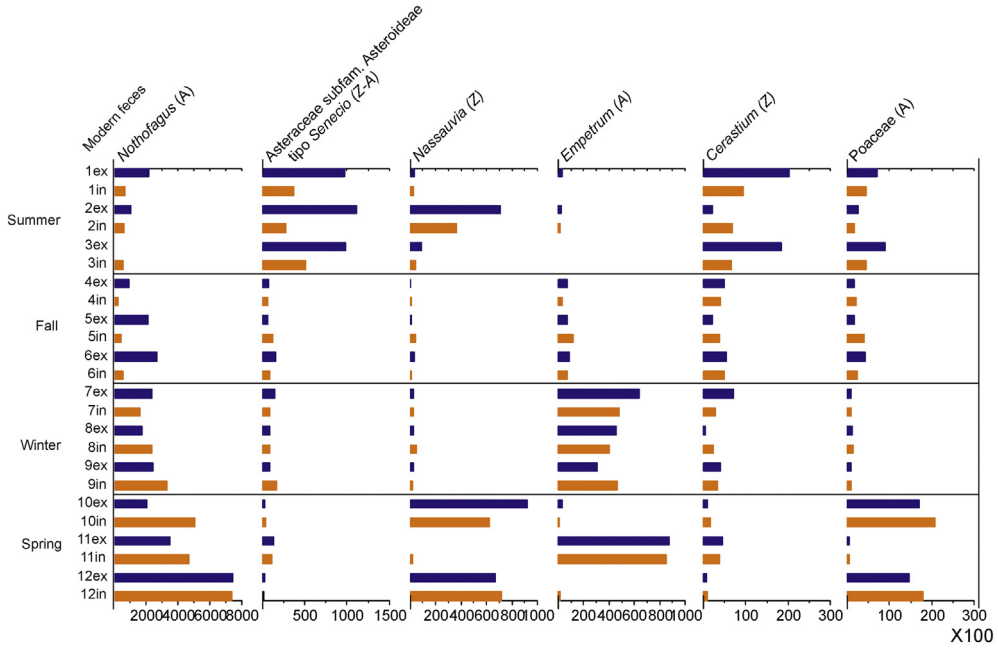

Fig. 4. Diagram of pollen type concentrations: guanaco modern feces. ex: outer subsample, in: inner subsample. (A): anemophilous, (Z): zoophilous.

5. Results

5.1. Post depositing contamination of modern feces and coprolites

5.1.1. Lama guanicoe modern feces

In the pollen concentration diagram representing the most important anemophilous and zoophilous pollen types found in modern feces (Fig. 4) more pollen concentration was observed in the outer subsample for the anemophilous taxa *Nothofagus* and Poaceae, and for the zoophilous taxa Asteraceae subf. Asteroideae, *Nassauvia* and *Cerastium*.

Also, taxa with low pollen concentration present only in a single subsample (outer or inner) were identified: Asteraceae subf. Mutisioideae, *Perezia*, Iridaceae, *Podocarpus*, *Chiliotrichum*, Rosaceae, *Acaena*, *Armeria maritima*, *Rumex*, Fabaceae, *Polygala*, Apiaceae, *Mulinum*, *Azorella*, Asteraceae subf. Cichoroideae, Juncaceae, *Loasa*, Caryophyllaceae, *Silene*, *Gunnera*, Ericaceae, Cyperaceae and *Polypodium* spores.

5.1.2. Camelid coprolites from sites CCP5 and CCP7

Variations were observed between the coprolites' outer and inner subsamples from site CCP5, being pollen more concentrated in the outer subsample (Fig. 5). The *Nohofagus* pollen concentration was usually greater in the outer part. On the other hand, taxa only present in one of the subsamples were registered in low concentration: Apiaceae, *Azorella*, *Colobanthus*, *Acaena*, Lamiaceae, *Valeriana*, Iridaceae, *Gaultheria*, Caryophyllaceae, *Silene*, Rosaceae, *Podocarpus*, *Perezia*, Pteridophyta, *Rumex*, Caryophyllaceae, Cheno/Am, Anacardiaceae,

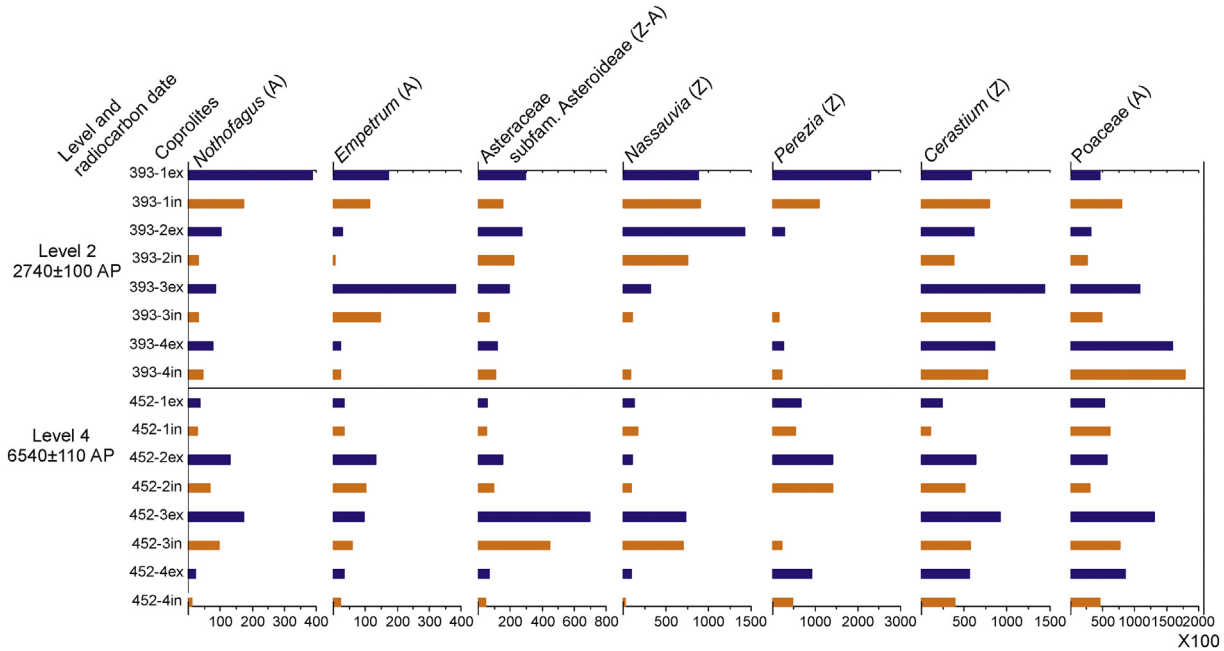

Fig. 5. Diagram of pollen type concentrations: coprolites from site CCP5. Blue: outer subsample and orange: inner subsample. (A): anemophilous, (Z): zoophilous. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

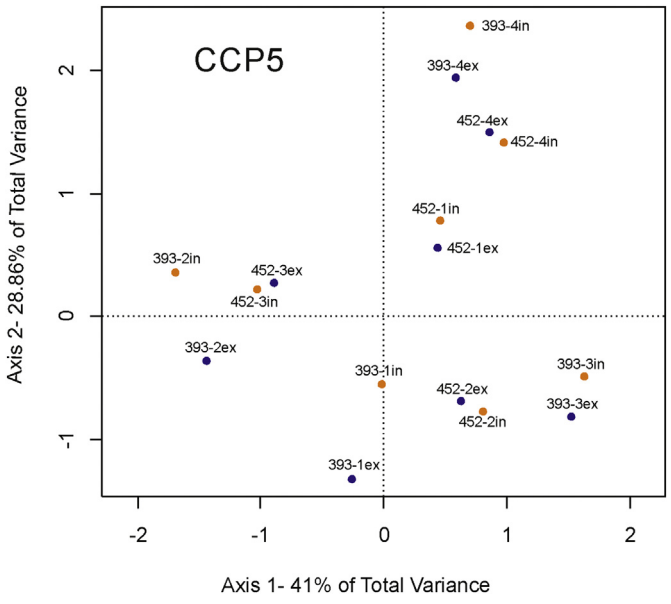

Fig. 6. Correspondence analysis of outer and inner subsamples of coprolites from CCP5. Blue: outer subsample and orange: inner subsample. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Schinus, Fabaceae, *Adesmia*, Rubiaceae, Cyperaceae, *Armeria maritima*, Brassicaceae, *Plantago*, Asteraceae subf. Cichoroideae, Solanaceae, *Berberis* and *Polypodium*.

Axes 1 and 2 of the correspondence analysis accounted for 41% and 28.86% of the total variance, respectively, in the coprolites' outer and inner subsample concentration data. Pollen concentrations of both outer and inner subsamples were different (Fig. 6).

Pollen concentration differences between subsamples were observed for coprolites from site CCP7, mainly in *Nothofagus* and Poaceae. The *Nothofagus* pollen concentration was greater in the outer part (Fig. 7). Also, taxa were registered in a single subsample: *Gaultheria*, Asteraceae subf. Mutisioideae, *Perezia*, Apiaceae, *Azorella*, Caryophyllaceae, *Cerastium*, *Silene*, Asteraceae subf. Cichoroideae, *Armeria*, *Rumex*, Brassicaceae, *Podocarpus*, *Adesmia*, *Lycium*, Fabaceae, Rosaceae, *Acaena*, *Valeriana*, Apiaceae, *Mulinum*, Solanaceae, Malvaceae, *Podocarpus*, Cactaceae, Iridaceae, *Misodendrum*, Lamiaceae, *Chiliotrichum*, Juncaceae, Lamiaceae, *Nassauvia*, *Loasa*, Bromeliaceae and *Polypodium*.

The correspondence analysis, accounted for 50.82% of variance with axis 1 and 17% with axis 2 (Fig. 8). Pollen concentrations from both surface and inner subsamples were different.

6. Discussion

6.1. Post-depositional pollen contamination

6.1.1. Lama guanicoe modern feces

As to the abundance of types Asteraceae subf. Asteroideae, *Nassauvia* and *Cerastium*, the differences between outer and inner subsamples observed in summer feces could be linked with the pollination season of species of these genera, and genus *Senecio* (Asteraceae subf. Asteroideae). These taxa pollinate during summer (Arroyo Kalin et al., 1981; Ferreyra et al., 2006) hence able to carry pollen to the feces surface after deposition (see Figs. 1 and 4).

In general, fall and winter feces showed no differences in the pollen concentration of all taxa found, enabling to pose two hypotheses: 1) in those seasons, pollen production and release are low, meaning less contribution to pollen rain, and therefore, to the feces surface, and 2) even though mucus covering feces can act as a pollen trap (Alcover et al., 1999; Chaves, 2000), the time passed from the fecal deposition to the sampling could have been insufficient to increase concentrations in the outer surface of feces (Velázquez and Burry, 2012). Other alternative is that, the fall-winter snowfall does not allow the pollen adherence to the surface. To corroborate this hypothesis empiric studies are necessary, as suggested by Fernández-Jalvo et al. (2014).

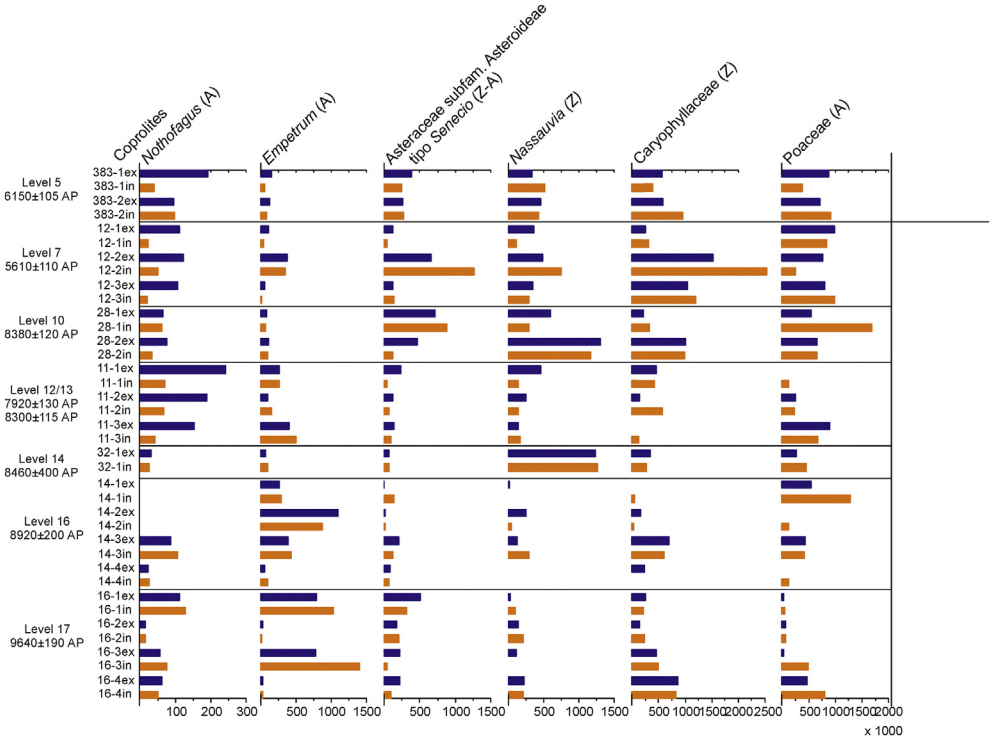

Fig. 7. Diagram of pollen type concentrations: coprolites from site CCP7. Blue: outer subsample and orange: inner subsample. (A): anemophilous, (Z): zoophilous. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

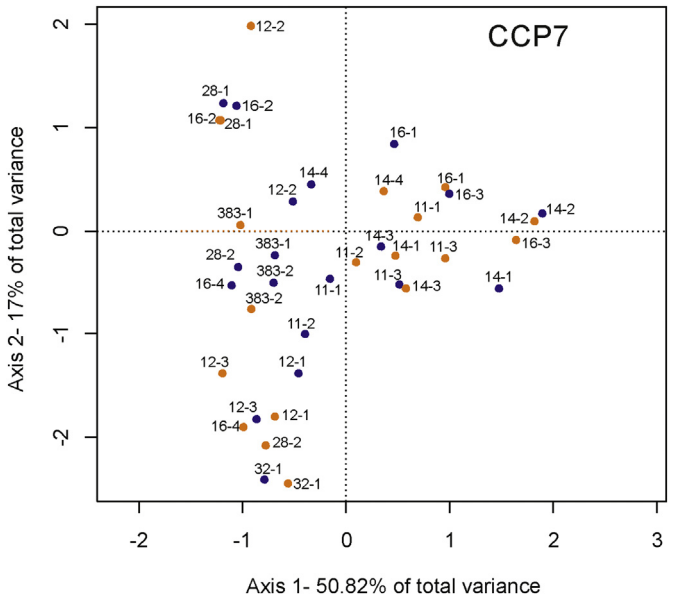

Fig. 8. Correspondence analysis of outer and inner subsamples of coprolites from CCP7. Blue: outer subsample and orange: inner subsample. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

On the other hand, the presence in feces of certain taxa, although in low concentration, in the outer part and their absence in the inner part, could evidence a post-depositional contamination. For example, pollen deposited on the feces' surface may have been refloated from surface deposits by the strong Patagonian winds.

Even though other pollen studies on modern feces discard the outer subsamples, thus not allowing to consider the post-depositional contamination (Moe, 1983; Bjune, 2000; Scott et al., 2003), according to our results, the analysis of different parts of a pellet could give information about the origin of pollen within feces. Therefore, if the objective of pollen studies of coprolites was to complement environmental information of a region, when discarding the outer part the quantification of those taxa absent in the inner part of the feces would be lost.

6.1.2. Camelid coprolites from sites CCP5 and CCP7

Pollen concentration differences between subsamples observed in correspondence analysis could be due to post-depositing contamination (Figs. 1, 6 and 8). Coprolites from sites CCP5 and CCP7 evidenced more *Nothofagus* pollen (anemophilous dispersion) concentration in the outer subsamples (Figs. 5, 7). These concentration differences of the *Nothofagus* type were also observed in presumably human coprolites from CCP7 (Burry et al., 2008). These results allow inferring that those grains could have been deposited over the feces after deposition through the wind entering the cave or, during the coprolite undergrounding, by addition of the cave's surface pollen sediment. On the other hand, the *Nothofagus* pollen found in the inner subsamples could have been consumed together with fodder after its deposition on plant leaves (Alcover et al., 1999), as established in leaves and stems samples of *Empetrum rubrum*, with *Nothofagus* grains adhered to their surface (Martel et al., 2015).

The modern and fossil camelid feces surface showed anemophilous pollen contamination after depositing. The same results have been found in a study of coprolites of a hyena from the Kalahari Desert, South Africa (Gil-Romera et al., 2014). The permanence of non-consumed pollen over the coprolites surface could have been helped by the mucus covering feces, an excellent pollen trap (Chaves, 2000). The largest Poaceae pollen concentration in the inner part of certain coprolites would indicate that this taxon was part of the camelid diet. This hypothesis is sustained with the finding of plant fragments of *Festuca pallescens* and *Stipa speciosa* in coprolites of the same archaeological layers as the studied in this work (Velázquez et al., 2010; Velázquez, 2016).

As for the identified zoophilous pollen types no differences have been found between the outer and inner parts of coprolites; the concentration values were sometimes larger in the inner subsample and sometimes in the outer. These taxa are likely to be diet items, since it is supposed that if they are part of the voluntary consumption they should be distributed in the interior as well as in the surface of the feces during the making up of the fecal mass in the organism's digestive tract.

A separate pollen analysis of the outer and inner parts of modern feces and coprolites yields information referred to contamination by environmental pollen; thus, the items conforming part of the diet of the elements of the vegetation area not consumed by the organisms can be discriminated. For this reason, it is recommended that in modern and coprolite feces, processing and separate analysis of the surface and inner parts be implemented. In this way, the information is kept to contribute and complement palaeoenvironmental reconstructions (Gil-Romera et al., 2014), in addition to making contributions to palaeoecological studies of organisms.

7. Conclusions

The analysis of summer guanaco's feces showed pollen concentration variations between the outer and inner subsamples because taxa like Asteraceae subf. Asteroideae, *Nassauvia* and *Cerastium* adhere to the feces surface after deposition of feces.

These differences could be linked with the pollination season of these taxa.

However, fall and winter feces showed similarities in the pollen concentration of all taxa found. The reason could be a low pollen production in fall and winter.

The analysis of pollen coprolites from sites CCP5 and CCP7 evidenced *Nothofagus* anemophilous pollen contamination in the outer part.

These taxa could have been deposited over the feces after deposition through the wind entering the cave or, during the coprolite undergrounding, by addition of the cave's surface pollen sediment. Also, the largest Poaceae pollen concentration in the inner part could indicate that this taxon was part of the camelid diet.

These results indicate that the analysis of the different parts of a pellet gives relevant information about the origin of pollen within feces. This methodology can be implemented in coprolite studies to contribute to the environmental information of a region and the palaeodiet reconstruction.

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