



Early-to-Middle Holocene environmental reconstruction in the southern Puna (26° S, Argentina) from camelid coprolite records

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ABSTRACT

Paleoenvironmental records in the eastern Andes (16–26° S), broadly indicate a gradual trend towards aridity from the Early to the Middle Holocene with certain chronological discrepancies. Even under this adverse climatic scenario, the archaeological record suggests the presence of hunter-gatherers in the southern Argentinian Puna associated with the availability of resources for their subsistence, even during drier than present periods. Herbivore coprolites contain multiple proxies that provide independent records of paleovegetation and paleoenvironments. Among them, plant tissue fragments and pollen grains, offer a powerful and complementary insight on past vegetation changes and their relationship with climatic conditions during the Holocene, particularly in the southern Argentine Puna. Thus, in this work camelid coprolites recovered from the archaeological site Quebrada Seca 3 (QS3) were analyzed using microhistological and palynological techniques to reconstruct the diet of these herbivores but also to infer vegetation and environmental changes from the Early to Middle Holocene (ca. 9600–6100 cal yrs BP) in the southern Argentine Puna (26°S). Results of both records show similar patterns in the percentages and species richness (especially those growing in wetlands) within and between coprolites dating to the Early Holocene (9600–8000 cal yrs BP) which suggest an environmental stability during this period. Around 8000 cal yrs BP, an increased variability in the richness of grasses, shrubs, dwarf shrubs, annual herbs and sedges species shows the gradual establishment of dry conditions, peaking around 6100 cal yrs BP. By this time, variability in the plant content of coprolites reflects seasonality in the assemblages due to the presence/absence of annual herbs either in the pollen or microfragment records. Therefore, it is likely that coprolites were from different animals that were hunted at different times of the year, supporting the evidence that QS3 has been occupied for short intervals of time after 7200 cal yrs BP when environmental conditions were extremely arid. The complementary analysis of the microfragments and pollen records preserved in coprolites provide valuable, complementary and alternative archive for herbivorous diet and for vegetation and environmental reconstructions, reinforcing that multiproxy approaches are necessary to obtain maximum information from coprolite studies.

1. Introduction

The Middle Holocene in the Central Andes is a period of great interest due to the establishment of hyper-arid conditions on a regional scale, and the consequences they could have on human societies (Núñez et al., 2013; Barberena et al., 2017; Santoro et al., 2017). Paleoenvironmental records in the eastern Andes (16–26° S), broadly indicate a gradual trend towards aridity from the Early to the Middle Holocene with certain chronological discrepancies (Tchilinguirian and Morales, 2013; Tchilinguirian and Olivera, 2014; Tchilinguirian and Olivera, 2014; Grana

et al., 2016a). Even under this adverse climatic scenario, the archaeological record suggests the presence of hunter-gatherers in the southern Argentinian Puna associated with the availability of resources for their subsistence, even during periods of great environmental dryness (Aschero and Martínez, 2001; Pintar, 2009; Martínez et al., 2010a; Mondini et al., 2011), when other areas were abandoned, for more than 3000 years, as occurs in the Atacama Desert in northern Chile (Núñez et al., 2002; Grosjean et al., 2005, 2007).

In Antofagasta de la Sierra (henceforth, ANS, Fig. 1), at the southern Argentinian Puna (26°S), several archaeological sites were identified

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with sedimentary sequences, indicating human presence during the Early and Middle Holocene (Aschero et al., 1991; Elkin, 1996; Pintar, 2004; Martínez et al., 2010a, 2010b). The Quebrada Seca 3 site (henceforth, QS3, Fig. 1b.) is one of them, and was used as a residential site during the Early Holocene and as a logistic site during the Middle Holocene (Pintar and Rodríguez, 2015). Camelid coprolites were recovered from different archaeological levels of QS3 dating to the Holocene which suggest that after animals were hunted, their carcasses were transported to the site (Elkin, 1996; Mondini, 2013; Mondini and Elkin, 2014; Urquiza and Aschero, 2014). Therefore, it is possible to predict that the cleaning of the intestinal tracts was carried out *in situ* (Elkin, 1996), allowing the guano to be deposited within the site as part of the sedimentary/archaeological sequence. This is supported by the fact that in the archaeological levels from which the coprolites were recovered, fragmented bone remains were also found, possibly as a result of processing and discarding tasks (Elkin, 1996).

Beyond the archaeological relevance of the coprolites found in QS3, they constitute a key archive on which to reconstruct not only the diet of these herbivores but also to infer vegetation and environment changes. Paleoenvironmental reconstructions based on coprolites are scarce in the southern Argentinian Puna, (Martínez et al. 2010b; Martínez et al., 2004; Mosca Torres et al. 2018; Petrih et al., 2021), compared with other areas in Argentina, such as Patagonia (Fugassa et al., 2010; Velázquez et al., 2010, 2014, 2015, 2020; Beltrame et al., 2012, 2015; Martínez Tosto and Yagueddú, 2012; Caruso Fermé et al., 2018; among others). In particular, camelid coprolites records, are an important source of evidence not only for paleodiet reconstructions, but paleoenvironments in arid and semi-arid regions (Mosca Torres et al., 2018; Petrih et al., 2021). On one hand, camelids are generalist herbivores, including in their diets perennial annual grasses, seasonal dicotyledonous herbs, shrubs, and cacti as well as species of wetlands and river or stream courses (sedges and associated grasses; Puig et al., 2001; Borgnia et al., 2010; Castellaro et al., 1999; Mosca Torres and Puig, 2010). On the other hand, these animals were the main resource in the diet of the inhabitants of ANS (Elkin, 1996; Aschero and Hocsman, 2011; Mondini and Elkin, 2014), therefore bones, fleece and coprolites of wild camelids such as vicuña (*Vicugna vicugna*) and guanaco (*Lama guanicoe*), were preserved in most of the archaeological sites of ANS throughout the Holocene (Elkin, 1996). At the end of the Middle Holocene domesticated species coprolites were also incorporated to the sequences due to the use of the llama (*Lama glama*) by human societies (Olivera, 1997; Urquiza and Aschero, 2014).

Herbivore coprolites preserve past evidence through different proxy records (plant remains, pollen, phytoliths, ancient DNA, parasites, isotopes, among others) which provide independent data of paleovegetation and paleoenvironments (Birks and Birks, 2000; Wood et al., 2012; Jørgensen et al., 2012; Wood and Wilmshurst, 2016; Velázquez et al., 2019; Shillito et al., 2020). These are especially useful when there is good stratigraphic and chronological control of the archaeological sites (Hastorf and Wright, 1998; Betancourt and Saavedra, 2002; Ghosh et al., 2008; Wood et al., 2012; Marinova et al., 2013; Velázquez et al., 2015). Microbotanical remains, such as plant tissue microfragments and pollen grains, offer a powerful and complementary insight on the past vegetation and its relationship with the environment and the human culture (e.g. ecological knowledge, landscape use and natural resources management; Dilkes-Hall et al., 2020). Pollen assemblages preserved in coprolites reflects the composition and dynamics of the vegetation at a regional level (Bryant and Holloway, 1983; Reinhard and Bryant, 1992; Carrión et al., 2004; Caruso Fermé et al., 2018) while the changes observed in the microfragment record are of local relevance and would complement the regional inferences evidenced in the pollen record (Jørgensen et al., 2012; Wood et al., 2012; Rawlance et al., 2016; Mosca Torres et al., 2018; Llano et al., 2020; Petrih et al., 2021).

From a methodological point of view, plant tissues microfragments preserved in coprolites are generally able to be identified at a greater taxonomic resolution (up to the species level) than pollen (Birks and Birks, 2000; Riley, 2008, 2012; Jørgensen et al., 2012; Shillito et al., 2020). This is particularly relevant for sites located in vegetation units where species within a family/genus grow under completely different ecological/environmental conditions. In areas dominated by grasses (Poaceae family) for example, the microhistological analysis provides key data at the species level while the pollen analysis data could just give insights at the family or genus level (see Appendix 1 for examples). On the other hand, even its higher taxonomic resolution, the microhistological identification of several dicotyledonous species preserved in coprolites is difficult to achieve because they are highly digestible (Jørgensen et al., 2012; Shillito et al., 2020). On the contrary, pollen grains in coprolites are well preserved and pollen assemblages includes a large number of taxa belonging to dicotyledonous plants allowing them to be typically identified to genus level (Martínez Tosto and Yagueddú, 2012; Velázquez and Burry, 2012; Wood et al., 2012; Velázquez et al., 2015). Based on the latter, the complementary analysis of pollen and plant tissue microfragment records provide a valuable tool to recognize and quantify plants that are sensitive to increased (decrease) aridity

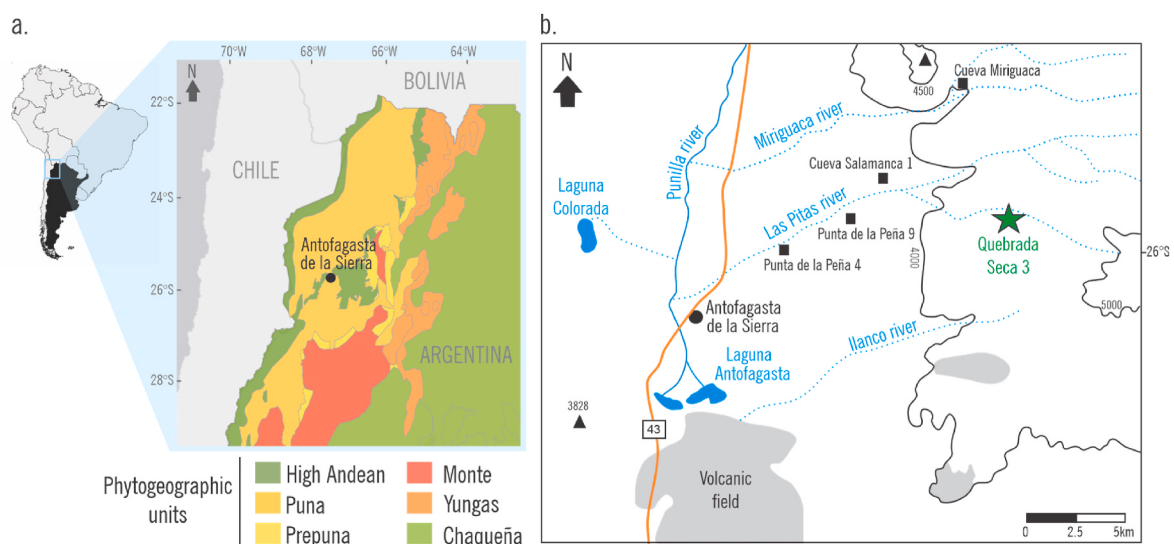


Fig. 1. Location of the study site. (a) Vegetation map of the northwest of Argentina showing the location Antofagasta de la Sierra (ANS) in the southern Puna (modified from Oyarzabal et al., 2018). (b) Location of the archaeological site Quebrada Seca 3 eastwards of ANS (modified from Mosca Torres et al. 2018).

such as annual herbs (several shrubs and various species of grasses) as well as those that only grow in wetlands or river edges (many sedges and grasses) in the Puna and High Andean regions. Moreover, once paleovegetation is reconstructed based on these records, environmental conditions at the local and regional scales may be inferred.

This study aims to reconstruct the paleodiet of camelids to infer paleoenvironmental conditions in the Southern Puna (26°S, Argentina) from the Early to the Middle Holocene based on the joint analysis of plant tissue microfragments and pollen records preserved in camelid coprolites recovered from the Quebrada Seca 3 archaeological site. The results are further integrated and discussed at the regional scale with selected records located on the eastern side of the Andes.

1.1. Paleoenvironmental background

At millennial and centennial timescales, there is agreement on the paleoclimatic conditions that existed in the Central Andes (16–23°S) during the Early and Late Holocene (eg. Grosjean and Nuñez, 1994, 2003; Yacobaccio and Morales, 2005; Quade et al. 2008, Tchilinguirian and Olivera, 2014). Following the Late Pleistocene much wetter than present conditions were recorded at the regional scale. The Early Holocene was also wet but showed a gradual trend towards aridity. Widespread arid conditions established and prevailed during the Middle Holocene, as suggested by different records of both Andean slopes (Valero Garcés et al., 1996; Grosjean, 2001; Grana and Morales, 2005; Zárate et al., 2005; Latorre et al., 2006; Quade et al., 2008, Huguin and Restifo, 2012, among others). However, several authors state that the aridification process was not homogeneous, particularly in the Northwest of Argentina (Tchilinguirian, 2011; Mondini, 2013; Tchilinguirian and Morales, 2013; Tchilinguirian and Olivera, 2014). Paleorecords from the eastern Andes (16–26°S) reflect these temporal patterns (Fig. 2) showing the onset of moisture decrease around 8000–7000 cal yr BP. Thus, pollen and geomorphological records from Yavi (22°S) reflect a sharp change around 8000 cal yr BP (Kulemeyer et al., 1999; Lupo, 1998 in Tchilinguirian and Morales, 2013) while soil development (16°–26°S; Morales, 2011) and alluvial sedimentation evidence (16°–21°S; Servant and Servant-Vildary, 2003) is not so conclusive. Nevertheless, both records indicate drier than present conditions around 6900 cal yrs BP and 6200 cal yrs BP, respectively. On the other hand, the multiproxy record of Pastos Chicos (23°S; Tchilinguirian et al., 2014), Lapao ravine (23°S; Yacobaccio and Morales, 2005; Morales, 2011), and Laguna Colorada (26°S; Tchilinguirian and Olivera, 2014) show an asynchronous moisture change from wetter to drier than present conditions at 6000, 7000 and 8000 cal yrs BP, respectively (Fig. 2). Chronological discrepancies could be related to the latitudinal location of the sites but also to the archive and proxy analyzed (Tchilinguirian, 2011; Tchilinguirian et al., 2014).

At the local scale, paleoenvironmental reconstructions based in multiproxy records, such as sedimentology, geomorphology, isotopes, diatoms and ostracods reflect that arid conditions prevailed in ANS during the Middle Holocene (Olivera et al., 2006; Tchilinguirian and Olivera, 2014) even there are still some divergences (Tchilinguirian, 2011). These differences could be related to the intensity, frequency and timing associated to the paleoenvironmental reconstructions (Grana et al., 2016a; Olivera et al., 2015; Tchilinguirian and Olivera, 2014) as well as the variability in the sensitivity of the analyzed archives/proxies (Tchilinguirian, 2011; Tchilinguirian and Olivera, 2014). Thus, the multiproxy records of ANS reflect a mosaic distribution of water resources on an intra and inter-basin scale (Tchilinguirian and Morales, 2013; Grana et al., 2016a). Paleohydrological changes of varied magnitude were observed in two of the main rivers, Las Pitás and Miriguaca (Fig. 1b), that generated favorable local conditions for human occupation associated with the river wetlands (Grana et al., 2016b). Grana et al. (2016b) inferred two paleoenvironmental phases during the arid Middle Holocene for Las Pitás and Miriguaca basins, characterized by different magnitudes of environmental changes and local

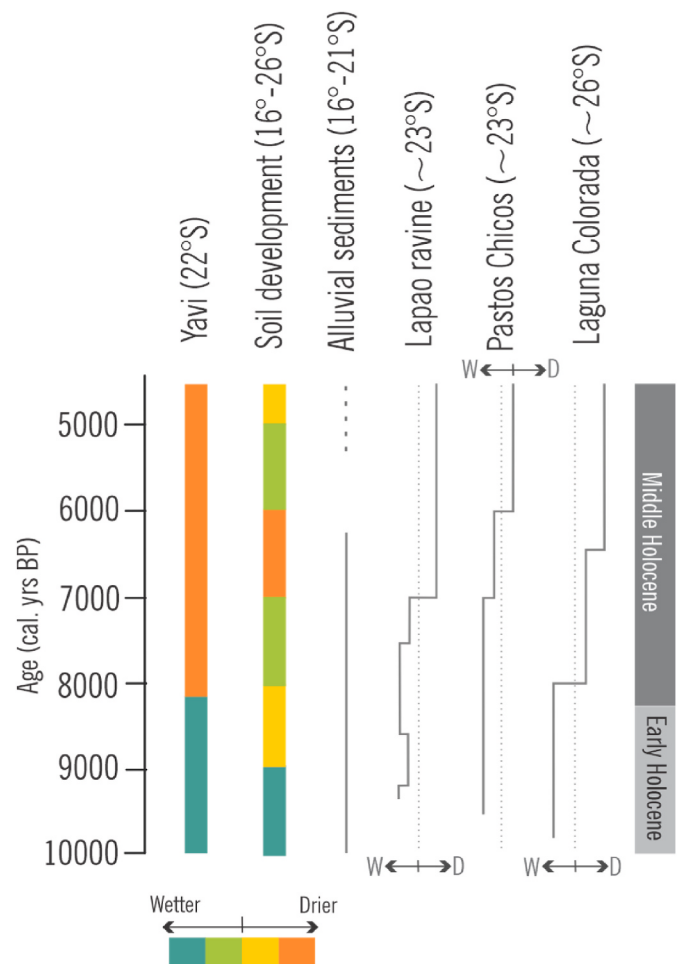


Fig. 2. Early/Middle Holocene paleoclimatic inferences from records located at the eastern side of the Andes: Yavi (22°S; Kulemeyer et al., 1999; Lupo, 1998 in Tchilinguirian and Morales, 2013); Soil development (16°–26°S; Morales, 2011); Alluvial sediment (16°–21°S; Servant and Servant-Vildary, 2003); Lapao ravine (23°S; Yacobaccio and Morales, 2005; Morales, 2011); Pastos Chicos (23°S; Tchilinguirian et al., 2014) and; Laguna Colorada (26°S; Tchilinguirian et al., 2005 in Tchilinguirian and Morales, 2013). (Modified from Tchilinguirian and Morales, 2013).

chronological discrepancies. Information obtained for Las Pitás river states that before 6700 cal yrs BP streamflow conditions prevailed associated with high-energy channels, whereas ca. 6700–4800 cal yrs BP, less humid conditions were observed with periodic debris flows separated by episodes of marsh formation as indicated by the sedimentary and diatom records (Grana et al., 2016a, 2016b). From an archaeological point of view, the water availability along this river through time was key for maintaining high productive environments for the hunter-gatherers inhabiting the Southern Puna (Tchilinguirian and Morales, 2013).

2. Study area

The archaeological site Quebrada Seca 3 (QS3) is located 15 km east of Antofagasta de la Sierra (ANS, Catamarca, Argentina) in the southern Puna of Argentina (>3,500 m asl; 22°–27°S; 65°10′–68°50′W; Fig. 1). The climate in ANS is arid/semiarid with intense nocturnal frosts and scarce rainfall (0–200 mm/yr) mainly occurring during the summer (70% from November to March; Viale et al., 2019) when mid- and upper-level easterly wind brings moist air that feed convective storms over the eastern side of the Andes (Garreaud, 1999; Falvey and Garreaud, 2005). Winter precipitation (~30%) is linked to the incursion of

cold fronts sourced from the Pacific Ocean that crosses to the eastern side of the Andes (Viale et al., 2019).

The environment where ANS is located is called Salt or Desert Puna (Troll, 1958), characterized by extensive areas of salt flats associated with average annual evapotranspiration around 550 mm (negative water balance; Grana et al., 2016b), intense solar radiation due to the altitude and great daily thermal amplitude (Olivera, 1988; Yacobaccio, 1998). The landscape of this region has shallow undulating plains interrupted by igneous and metamorphic rock outcroppings as well as sedimentary rock sequences and volcanic chains (González, 1992). Phytogeographically, this area corresponds to the Puna Province with minor areas belonging to the High Andean Province (Oyarzabal et al., 2018, Fig. 1a). Vegetation is dominated by shrub and grass steppes associated with herbaceous, halophile and psammophile communities. Three main plant communities are distinguished, the *tolar*, *pajonal* and *vega* although Haber (1991) defines others considering the conjunction of ecological and economic criteria that determine the forage potential of the environment, such as *quebrada* (ravine) slopes and river vegetation.

Below 3800 m asl, the *tolar* develops characterized by shrub steppes and low vegetation cover (Aguirre, 2012; Rodríguez, 2013a; Pintar and Rodríguez, 2015). It is dominated by shrub species as *Parastrephia lucida*, *Aloysia deserticola*, *Neosparton ephedroides*, *Senecio viridis* and *Atriplex* sp., accompanied by species of *Lycium* and *Baccharis* genera and herbaceous plants that grow in the shade of them (Rodríguez, 2008; Cuello, 2006; Rodríguez, 2013a; Pintar and Rodríguez, 2015). Above 3800 m asl, the High Andean steppe or *pajonal*, is characterized by the dominance of grass species of *Festuca* and *Pappostipa* that grow in sandy soils, along with annual herbs of the Malvaceae family and shrubby species of *Adesmia*, *Baccharis*, *Senecio* and *Fabiana* (Cuello, 2006; Pintar and Rodríguez, 2015). The *vegas* are wetlands with the highest primary productivity of the salt Puna (Tchilinguirian and Olivera, 2014) where species of Poaceae, Juncaceae and Cyperaceae families are dominant in association with shrubs and other small species towards the edges (Cabrera et al., 1980; Elkin, 1996). This environment occupies less than

1% of the salt Puna area and they are associated with rivers, salt flat margins and lagoons (Tchilinguirian and Olivera, 2014). Finally, the vegetation community of the *quebrada* slopes is dominated by *Fabiana brioides*, *Baccharis tola* and *Parastrephia quadrangularis*, along with annual herbs (Cuello, 2006; Pintar and Rodríguez, 2015).

The local fauna includes vicuñas (*Vicugna vicugna*), which mainly graze in the *pajonal* and *vegas* while the llamas (*Lama glama*) mostly feed on *vegas* grasses and shrubs (Pintar and Rodríguez, 2015; Mosca Torres et al., 2018). Several rodent and bird species also inhabit the area, for example the chinchilla (family Chinchillidae) and suris (*Rhea pinnata*) along with foxes (*Pseudalopex culpaeus* and *Pseudalopex griseus*) and the puma (*Puma concolor*) which are the main predators (Olivera and Elkin, 1994).

2.1. Archaeological site of Quebrada Seca 3

The archaeological site QS3 is a rock shelter at the base of an ignimbrite cliff in a high ravine. It is located at the southern margin of the Quebrada Seca valley, at 4100 m asl (Aschero et al., 1991). The main channel of the ravine is a tributary of the Las Pitas River, which in turn flows into the Punilla River (Fig. 1b). This ravine is surrounded by watercourses or *vegas* that are not permanent, therefore its flows vary according to climatic conditions, water tables and seasons (Mohn, 2010). In front of QS3, at the bottom of the ravine there is the *vega* of Quebrada Seca that extends for about 100 m wide. The site QS3 has an area under cover of 9 m × 5 m with an exterior and an interior sector designated as overhang and cave, respectively (Fig. 3a; Aschero et al., 1991; Elkin, 1996).

The site sedimentary sequence presents a remarkable series of occupations along the Holocene, with four main units spanning the period between ca. 9410 ± 120 yrs BP and 2480 ± 60 yrs BP (Fig. 3b; Elkin, 1996; Aschero and Martínez, 2001). The units were numbered from top to bottom including layers 0/lens 1x, layer 1 and layer 2a and 2 b. Layer 0 is a loose silty-sandy surface layer with guano. It contains some plant and faunal remains, and carbonaceous sediments of apparent

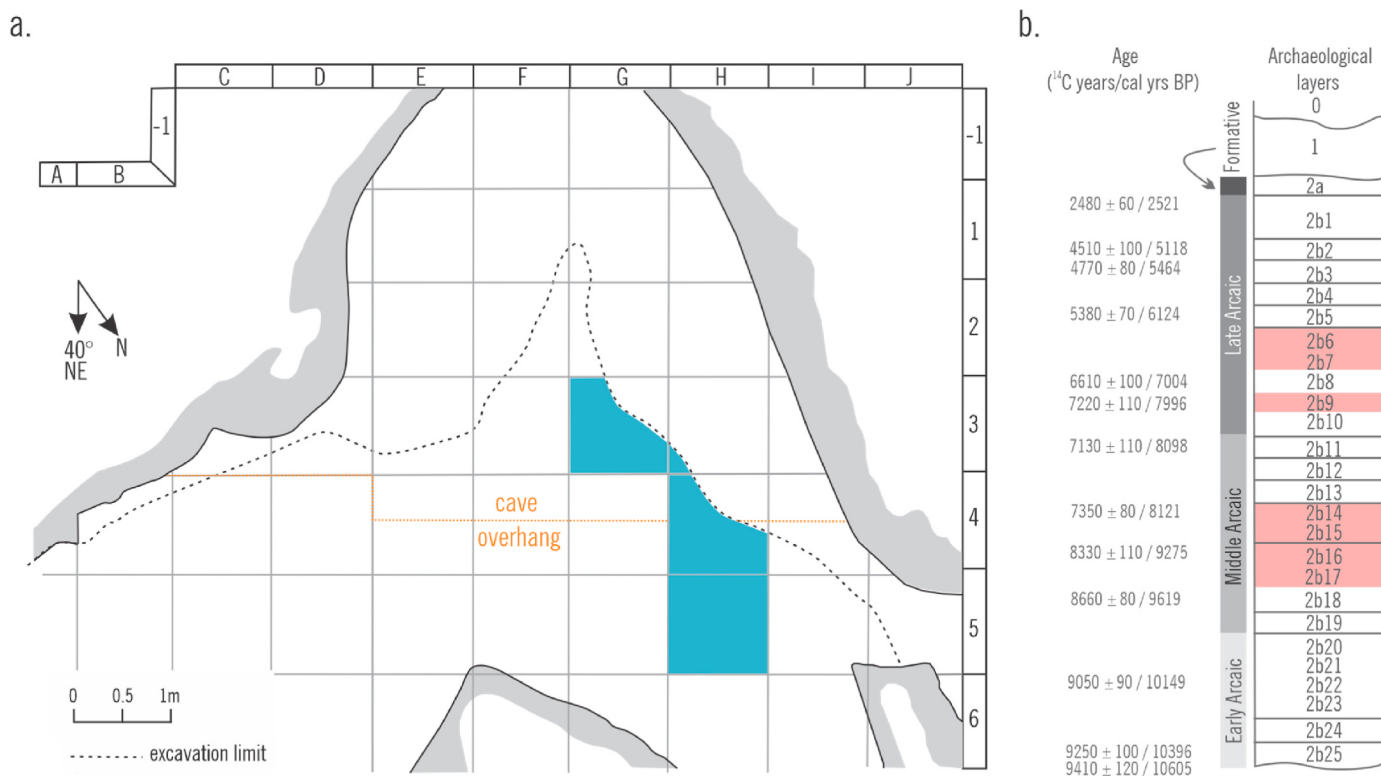


Fig. 3. (a) Level floor of the layer 2 b of QS3. Squares in blue indicate the sectors (letter and number) from which coprolites analyzed in this study were found (modified from Rodríguez, 1998). (b) Chronology of the archaeological site QS3. Rectangles in pink indicate the levels from which coprolites were found.

anthropogenic origin; Layer 1 is a compact silty-sandy sediment, archaeologically sterile; Layer 2a is a non-compacted sandy sediment of gray to light brown coloration at the top with few anthropogenic remains; Layer 2 b is a light brown sandy to sandy-loamy silty sediment layer with important anthropogenic evidences (Aschero et al., 1991; Elkin, 1996). Within the latter layer, 25 occupation levels were differentiated and dated between 4510 ± 100 yrs BP (level 2b2) and 9410 ± 120 yrs BP (level 2b25) (Fig. 3b; Aschero et al., 1991), with just a 510 yrs gap of occupation between the early and late Middle Holocene (Pintar and Rodríguez, 2015). Most of the radiocarbon dates were made on charcoal remains extracted from combustion structures and the results are generally consistent with the stratigraphic sequence (Table 1; Elkin, 1996). This long sequence of occupation is of great importance for the region because it makes QS3 one of the oldest sites with frequent occupations throughout the Holocene. Even in the middle Holocene, QS3 functioned as a logistical camp (where hunting parties retooled and maintained their hunting equipment), whereas other areas of the Puna show no signs of human settlements (Elkin, 1996; Pintar, 1996 in Mohn, 2010; Mondini, 2013; Pintar and Rodríguez, 2015).

The environment around QS3 is related to the plant communities of the *pajonal*, *tolar*, *quebrada* slopes and *vega*, which provide a good variety of species for firewood, lining and medicinal use, among others (Rodríguez, 2008). Archaeobotanical studies in QS3 revealed the presence of several plant taxa belonging to different vegetation communities from levels 2b17, 2b15 (Early Holocene), 2b10 and 2b8 (Middle Holocene) (Pintar and Rodríguez, 2015). Specimens of the *vega* and *pajonal* were more abundant in the earliest levels, species of the *quebrada* slopes, *tolar* and lower *pajonal* were more used during the Middle Holocene, while species of the *vega* were less utilized (Rodríguez, 2004). The record of these species shows that the occupants of QS3 knew the plants that developed in their surroundings and were capable of modifying their ranges of action to obtain them even in times of extreme aridity (Pintar and Rodríguez, 2015). At this point it is important to highlight that the species found at the site are part of the current plant communities on the area, so it is inferred that during climatic fluctuations there were increases or decreases in abundance but not in plant richness (Rodríguez, 2013b; Apóstolo et al., 2019). However, this record is limited to species that were functional to human groups, either as part of the subsistence economy such as the use of some species before and after the domestication process (Babot, 2016; 2004, 2011; Aguirre, 2007; 2012; Rodríguez, 2013b.), as well as for their use and transformation for other purposes (fuel, making artifacts, beds, etc.; Rodríguez, 1998, 2000, 2004, 2005, 2013b; Rodríguez and Rúgulo de Agrasar, 1999; Rodríguez, 1998; Aguirre, 2012; Rodríguez, 2014).

3. Materials and methods

Twenty camelid coprolites recovered from seven archaeological levels (layer 2 b) from Quebrada Seca 3 (QS3) dating from the Early to Middle Holocene were analyzed (Table 1). The zoological origin of the

coprolites was determined by the morphology, compatible with that of vicuña (*Vicugna vicugna*) feces. Coprolites were measured and weighted separately following the protocol of Velázquez et al. (2019). Three subsamples were obtained and weighted from each coprolite by separating the external part (subsampling E) from the internal part (subsampling I) by scraping the cortex with a scalpel. The third subsample was obtained by joining part of subsamples E and I (subsampling M). Micro-histological analysis was performed using subsamples M, whereas subsamples I were used for palynological analysis to avoid potential contamination airfall pollen grains.

Each subsample M was processed for identification of plant fragments using the microhistological technique described by Duci (1949) with some modifications to suit the vegetation of arid areas. This technique consists of the identification of plant fragment tissues under a microscope, using diagnostic characteristics suitable for the differentiation of the species under study. These characteristics usually comprise epidermal cells, stomata, hairs and trichomes (Pelliza de Sbriller, 1993) and constitute reference standards that allow the taxonomic determination of plant fragments. Fragments observed in the coprolites were identified comparing with a modern plant reference collection that consisted of plant material collected in study area and herbarium specimens of the Instituto Superior de Estudios Sociales (ISES) (CONICET-Tucumán) and Herbario Ruiz Leal of IADIZA (CONICET Mendoza). Six microscope slides were made for each subsample M, and 85 fields per slide were systematically examined using a microscope at 100–400x magnification. Plant identification was generally performed up to the genus level and to species level when possible.

For the identification and quantification of plant fragments, the presence of at least two recognizable diagnostic structures was considered. In the case of a species of the Poaceae family, if the fragment presented only silica cells, it was not identifiable and was considered as “Poaceae indeterminate”. On the other hand, a fragment that presented, for example, stomata and cell pairs, was identifiable and therefore quantifiable. This criterion was established so as not to overestimate easily identifiable species. In the case of dicotyledonous species with stellate trichomes (and other types of trichomes or diagnostic glandular hairs that are easily detached from the tissues), the presence of 3 of these structures was considered as a record. Finally, non-epidermal plant fragments (lacking structures for their identification) were ignored since all plant species present them.

Nineteen subsamples I were processed following summarized standard methods for pollen extraction (Faegri and Iversen, 1989). Samples were hydrated in distilled water (2 h), KOH 10% 100 °C (10 min), sieving by 120 µm mesh, three distilled water washes and acetolysis. The pollen basic sum included 300 pollen grains from local communities which were identified aided by reference pollen books and papers (Heusser, 1971; Markgraf and D'Antoni, 1978) and the reference collection of the Laboratorio de Paleocología del Cuaternario (IANIGLA, CCT CONICET Mendoza). Both, plant fragments and pollen percentages were calculated and plotted using TGView 1.7.16 (Grimm,

Table 1
Radiocarbon dates from the archaeological site Quebrada Seca 3.

Level	Number of analyzed coprolites	Age (14C years)	Age (cal. yrs BP)	2σAge range (cal. yrs BP)	Period ^a	Material	Laboratory number	Reference
2b5	–	5380 ± 70	6124	5942–6285	MH	charcoal	Beta 59,927	Aschero, 1993–94
2b6 (base) ^a	5	–	–	–	MH	–	–	–
2b7 ^a	3	–	–	–	MH	–	–	–
2b8	–	6160 ± 100	7004	6746–7255	MH	charcoal	AC 1117	Elkin (1996)
2b9	1	7220 ± 60	7996	7868–8170	MH	charcoal	SMU 2364	Elkin (1996)
2b14	3	7350 ± 80	8121	7972–8325	MH	charcoal	Beta 59,928	Elkin (1996)
2b15 ^a	4	–	–	–	EH	–	–	–
2b16	1	8330 ± 110	9275	9015–9521	EH	charcoal	LP 267	Elkin (1996)
2b17	3	8660 ± 80	9619	9475–9891	EH	charcoal	Beta 77,747	Elkin (1996)

^a These levels have no date. Typological indicators were used to assign these levels to the Middle Holocene (MH). ^a MH: Middle Holocene; EH: Early Holocene.

2011).

The chronological control of the archaeological sequence was based on radiocarbon dates published previously (Table 1; Aschero, 1993-1994; Elkin, 1996). Radiocarbon dates were calibrated at two-sigma with the calibration curve for the Southern Hemisphere (SHCal20; Hogg et al., 2020) using Calib 8.1.0 (Stuiver et al., 2021).

4. Results

Microhistological and palynological analyses show similar assemblages and diversity changes among archaeological levels (Figs. 4 and 5). However, taxonomical resolution and species richness observed were variable between both techniques.

Thirty-five species in 20 genera of eleven families were identified through the microhistological technique: sixteen grasses, ten shrubs, five herbs, three sedges, one cactaceae and one unidentified dicotyledonous species. Plant fragments assemblages observed in coprolites from archaeological levels 2b17, 2b16, 2b15, and 2b14 dated between 9600 and 8100 cal yrs BP are similar. Poaceae species were the most frequent, with a dominance of *Deschampsia eminens* (65–95%), associated with *Cinnagrostis velutina*, *C. chrysophylla*, *Festuca weberbaueri* and *F. chrysophylla* with lower values (<10%) (Fig. 4). Among shrubs, six species were represented with low percentages (<8%), such as *Adesmia* sp. (Fabaceae), *Lycium* sp., *Lycium chanan* (Solanaceae), *Junellia seriphoides* (Verbenaceae), *Baccharis polifolia* and *Ocyroe armatha* (Asteraceae). The Juncaceae *Oxichloe andina* was the second important species in level 2b15 after *D. eminens*, whereas Cyperaceae species (*Carex macrorrhiza* and *Phylloscirpus* sp.) were less frequent (<5%) in the four levels.

Changes in both percentages and species richness begin to be noticed from levels 2b9 to 2b6 (7996 to before 6124 cal yrs BP). Poaceae species were still dominant, but unlike the earliest levels, a greater richness of grasses is observed in the last ones. Level 2b7 has a higher richness of Poaceae species than 2b9 and 2b6 levels, whereas the 2b6 level has higher percentages and richness of shrubs than 2b7 and 2b9 levels. Sedges were more abundant in 2b6 than in 2b7, whereas these species were absent in level 2b9. In addition, a great intra-level variability is observed in samples of level 2b6 (Fig. 4).

Among grasses, *Deschampsia eminens* is still important in 2b9 (50%), but its values begin to decrease at 2b7 until it is almost absent in 2b6 at expenses of *Festuca chrysophylla* that increase from 5 to 40%, associated to other grasses such as *Festuca* sp., *F. weberbaueri*, *F. nardifolia* and

F. orthophylla (<18%), *Cinnagrostis* sp., *C. velutina*, *C. chrysophylla* (<15%) and *Pappostipa* sp., *P. chrysophylla* and *P. frigida* (~20%). *C. curvula*, *Festuca* sp., *F. orthophylla*, *Pappostipa* sp., and *P. frigida* were only observed in coprolites of level 2b7, whereas *Puccinellia frigida* was exclusive in samples of level 2b6.

Percentages of the shrubs *Pycnophyllum* sp., *Adesmia* sp., *Lycium chanan*, *Junellia seriphoides*, *Aloysia deserticola*, *Parasterphia lucida* and *Fabiana* spp., were higher in level 2b6 than in level 2b7, whereas only two shrub species (*Adesmia* sp., and *Fabiana* spp.) were present in level 2b9 at very low percentages. Three herb species were recorded in all the sequence in very low percentages (<5%), *Hoffmannseggia glauca*, *Phacelia* sp. (level 2b7) and *Phacelia setigera* (level 2b6). Finally, one undetermined dicotyledonous taxa (Taxa A) was recorded exclusively in level 2b6 with percentages under 15%.

Coprolite pollen records from archaeological levels 2b17, 2b16, 2b15 and 2b14, dated between 9600 and 8100 cal yrs BP are similar (Fig. 5). They are dominated by Poaceae (90–100%) associated with trace values (<2%) of Asteraceae Asteroideae (*Senecio* and *Baccharis* types), Fabaceae (*Adesmia* type) and Solanaceae. Pollen assemblages from layer 2b9 (7996 cal yrs BP) are still dominated by Poaceae but up to 80% at expenses of the increase of the associated pollen types such as Asteraceae Asteroideae (*Artemisia* type; 10%), Asteraceae Asteroideae (*Senecio* and *Baccharis* types) and Fabaceae (*Adesmia* type) under 5%. Layer 2b7 (6100–7000 cal yrs BP) pollen assemblages present lower values of Poaceae (55–65%) but still dominating together with Asteraceae Asteroideae (*Senecio* and *Baccharis* types; <5%), Asteraceae Asteroideae (*Artemisia* type; 5–30%), Asteraceae Mutisiae (<5%) and Solanaceae (20%). Finally, pollen assemblages from fecal pellets recovered from layer 2b6 (6100–7000 cal yrs BP) are highly variable and the most diverse from the whole record. They are co-dominated by Poaceae (40 µm; 20–60%) and Poaceae (25 µm, 40%) and Juncaceae/Juncaginaceae (5–65%) along with Asteraceae Asteroideae (*Senecio* type), Fabaceae (*Adesmia* type), Brassicaceae, Solanaceae, *Aloysia*, *Phacelia*, Apiaceae (*Azorella* and *Mulinum* types), Montiaceae (*Calandrinia* type) and Malvaceae under 20%.

5. Discussion

5.1. Paleoenvironmental reconstruction

The results of microhistological and palynological records show similar patterns in the percentages and species richness in the earliest

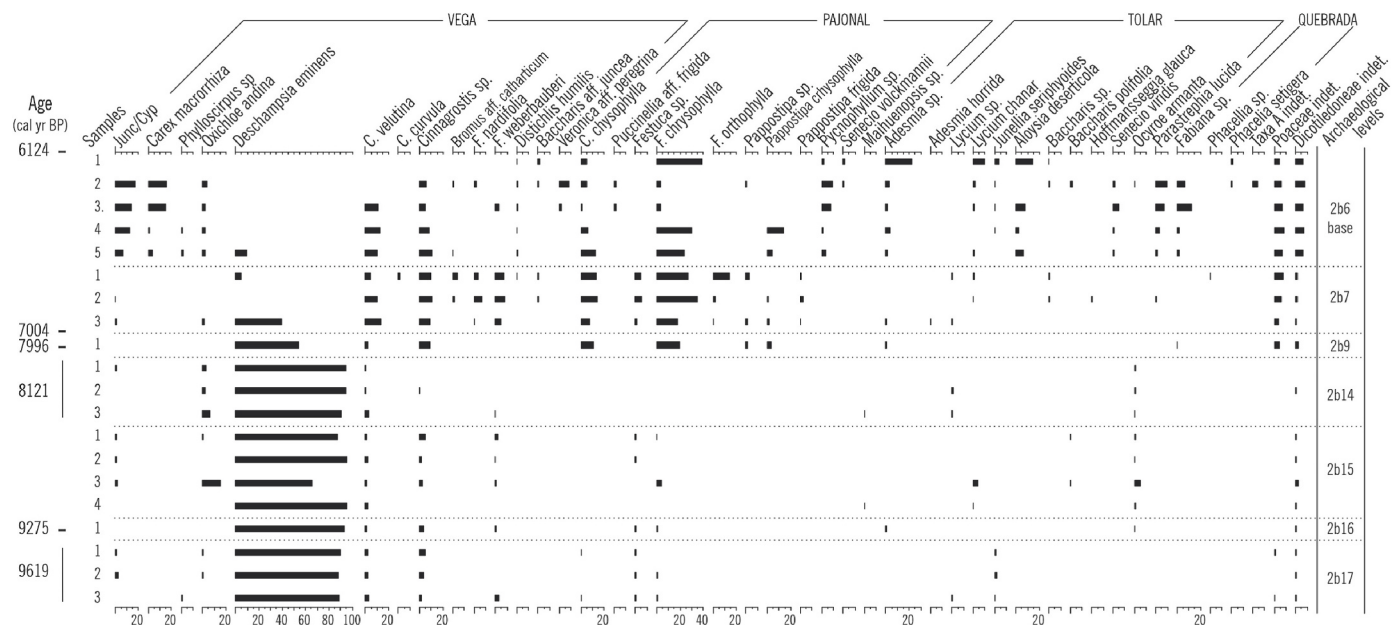


Fig. 4. Percentage diagram of microfragments from Q3S camelid coprolites.

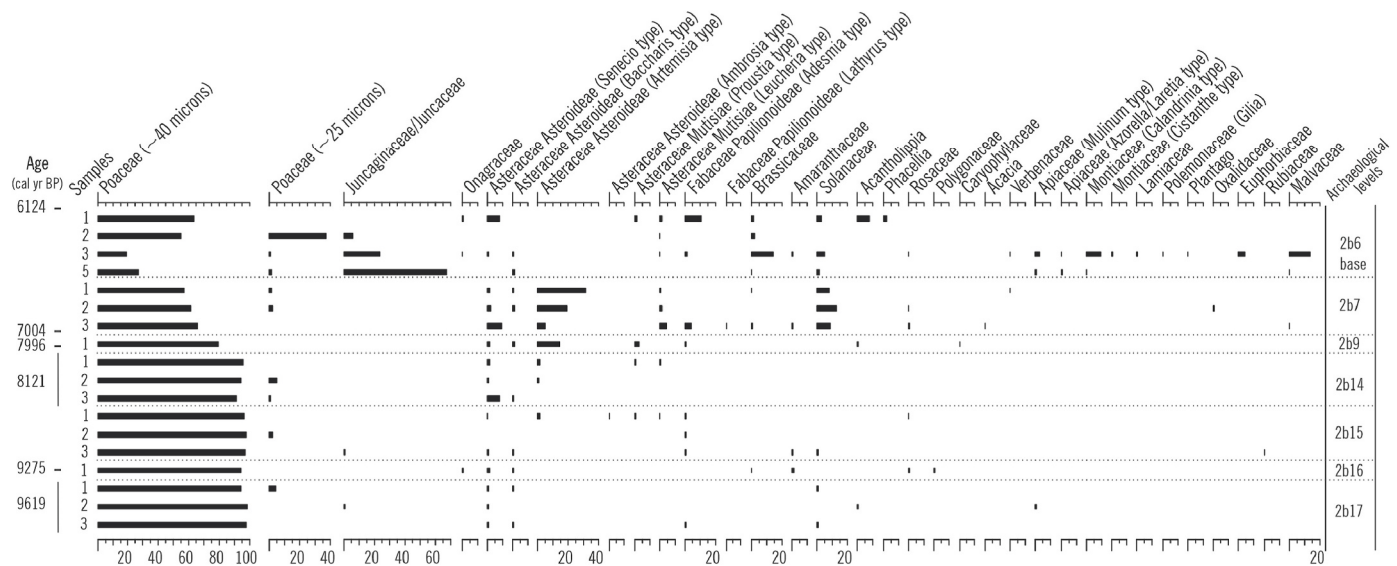


Fig. 5. Percentage diagram of pollen from QS3 camelid coprolites.

archaeological levels (2b17, 2b16, 2b15 and 2b14) since 9619 until 7996 cal yrs BP (Figs. 4 and 5). From ca. 8000 cal yrs BP (level 2b9) there is an increase in the richness of grasses, shrubs, dwarf shrubs, annual herbs and sedges species, being more noticeable in the level 2b6, ca. 6124 cal yrs BP (Figs. 4 and 5). At this level there was also an important species variability among coprolites that could reflect seasonal changes in the environmental vegetation.

Between 9600 and 8100 cal yrs BP, the pollen record shows high percentages of grasses, that according to the microhistological record corresponds almost exclusively to the presence of *Deschampsia eminens*, a species that grows in flooded sites and wetlands of ANS (Rodríguez, 1998; Rodríguez and Rúgulo de Agrasar, 1999; Rodríguez, 2013a). The high percentages of *D. eminens* indicates that the animals fed mainly in the *vega* as well as the low values of other species that do not develop in that environment. Therefore, it could be inferred that the animals were hunted in the *vega* or in its surroundings as mentioned by Pintar (2008), and slaughtered in the site (Elkin, 1996; Urquiza and Aschero, 2014). It is important to clarify that the *vega*, is the only environment that can be used by families (territorial groups), solitary individuals (territorial animals) and bachelor groups (groups without territory) simultaneously without conflicts between territorial and non-territorial males, although the time spent in the *vega* by territorial males in vigilance is greater than outside of it (Mosca Torres et al., 2015). During the wet season or when resources are relatively abundant, the vicuña consumes high-quality forage species of the *vega* and spends large part of its time in this environment (Borgnia et al., 2010; Mosca Torres and Puig, 2010; Mosca Torres et al., 2012). So, the lack of variability in both records, within and between fecal pellets, from levels dating back to the Early and Early-Middle Holocene, reflect a similar foraging behavior of vicuñas which implies an environmental stability during this period. Moreover, the predominance of grasses of the *vega* reflect that wet conditions prevailed during the Early Holocene as was recorded previously in the Salt Puna of Catamarca (Tchilinguirian and Morales, 2013; Tchilinguirian and Olivera, 2014).

Around 8000 cal yrs BP (layer 2b9), Poaceae still dominated the pollen assemblages but a slight increase in pollen percentages of Asteraceae Asteroideae (*Artemisia* type; 10%) states the onset of the major change for the whole record. Even though, the increase in Asteraceae was not observed in the microhistological record, but an increase in the diversity grasses species consumed was recorded. *D. eminens* continues to be the most consumed, associated to *Festuca chrysophylla* from the *pajonal*, along with *Cinnagrostis* sp., and *C. chrysophylla*, species that also grow in the *vega* of Quebrada Seca locality. This

increase in the consumption of other species of grasses would indicate a decrease in the availability of *D. eminens*, probably associated to the onset of dry conditions. Given that only one coprolite was recovered from layer 2b9, this inference is not as robust as in other levels where more coprolites were analyzed.

After ca. 7004 and before ca. 6124 cal yrs BP, pollen grains and plant fragments of grasses still dominate, but their percentages are the lowest for the whole record. In contrast, there is an increase in the percentages of pollen types and fragments of shrubs, dwarf shrubs and annual herbs belonging to the *tolar*, together with high Andean steppe and *vega* species, that indicates a clear change in the foraging behavior of vicuñas that has not precedent in the last 2000 cal yrs. Thus, pollen assemblages of coprolites from layer 2b7 indicates that vicuñas ate grasses but also *tolar* shrubs such as Asteraceae Asteroideae, Asteraceae Mutisiae and Solanaceae. Indeed, microhistological analysis show a strong decrease (or absence) of *D. eminens*, at expenses of the increase in the diversity of other grass species of the *vega* and *pajonal*. So, both records point out the gradual establishment of dry conditions which onset was inferred in level 2b9.

In contrast to level 2b7, pollen assemblages from level 2b6 present a higher diversity of pollen types from shrubs, dwarf shrubs, annual herbs and Juncaginaceae species in several samples. Microhistological results support the pollen record and complement the information regarding of species of Poaceae, Juncaceae and Cyperaceae families. There is also a remarkable variability among samples of this level that was observed in both, the pollen and microhistological records. Indeed, it is likely that the coprolites were from different animals that were hunted at different times of the year. The percentages increase of pollen types from annual herbs such as Brassicaceae, Montiaceae, Euphorbiaceae and Malvaceae types in sample 3 of level 2b6, would be related to more humid conditions that allowed the growth of these species. In contrast, high percentages of pollen types and tissue fragments of shrubs as *Adesmia*, *Lycium chanoir* and *Fabiana* sp., *Junellia seriphioides* and *Aloysia deserticola* in sample 1 of level 2b6, together with the high consumption of *F. chrysophylla* and the scarce presence of annual herbs and species of the *vega*, would reveal more arid conditions. The decrease in the record of *D. eminens* would respond to the progressive increase in aridity during the Middle Holocene that produced a retraction of the *vega* and/or a decrease of water holes/springs (Olivera et al., 2006; Tchilinguirian, 2011; Tchilinguirian and Morales, 2013; Grana et al., 2016b). This could explain the decrease in vegetation cover that led to the disappearance (or low availability) of grass species which apparently were replaced by an increase of sedges (Juncaceae and Cyperaceae). Change of plant

community in response to the most arid conditions, would force a radical change of the vicuña foraging behavior. Actually, this change in the diet is supported by Mosca Torres and Puig (2010) who reported that under drought conditions, vicuñas become less selective in obtaining food and behave opportunistically when food availability decline or is of low forage quality, broaden their dietary niche.

So both, the pollen and microhistological records from QS3 revealed a major environmental change to more arid conditions around 8000 cal yrs BP that finally intensified after ca. 7004 and before ca. 6124 cal yrs BP. Our results are in agreement with other evidences in the area (26°S) such as the Laguna Colorada record where the water body dried up and wind erosion occurred around 8400 cal yrs BP and 6500 cal yrs BP (Fig. 2) (Tchilinguirian and Olivera, 2014). Besides, similar dry conditions established slightly later, ca. 5900 BP, in the middle course of the Las Pitas River (Grana et al., 2016b). An important pattern that arises from this sites located at the same latitude, is that the change towards drier conditions seems to have been in “two steps” through time. It is probably that differences in the chronology between records depend on local characteristics of the sites (geomorphology, topography and altitude) that condition somehow microclimatic (temperature and humidity) conditions (Tchilinguirian and Olivera, 2014; Tchilinguirian and Morales, 2013) or the response time of the analyzed proxies. If compared at a regional scale, the main change timing agrees with the Yavi record (22°S; Kulemeyer et al., 1999; Lupo, 1998) and predates the Lapao ravine (23°S; Yacobaccio and Morales, 2005; Morales, 2011) and Pastos Chicos (23°S; Tchilinguirian et al., 2014) which occurred around 7.200 cal yrs BP. However, even the chronologic differences and that it seems not to be a latitudinal-related pattern of change, the regional expression of the wet-to-dry conditions suggest a common and regional in scale driver probably associated to the South American Summer Monsoon dynamics.

5.2. Archaeological implications

The expansion of the vega close to site during the Early Holocene, led to an increase in forage availability for the vicuña, the main food resource of hunter-gatherers. Therefore, it is possible that a large number of animals congregated in this habitat facilitating the hunting of adult animals, as well as offspring (Elkin, 1996). When the humidity begins to decrease, the availability of subsistence resources for both, animals and inhabitants of Quebrada Seca, also decreases. Therefore, changes occur in the plant community of the environment, which would lead to changes in the foraging strategies of the vicuña and, possibly, in hunting strategies of hunter-gatherer (Aschero and Matínez, 2001).

Dry conditions recorded by the palynological record during the Middle Holocene, show the presence of pollen belonging to annual herbs which would indicate the occurrence of short humid periods or a marked seasonality with a well-developed humid season. In this sense, Pintar (2014a) argued that around 7200 cal yrs BP, brief occupations in QS3 were evidenced in level 2b8 through lithic and camelid remains which were correlated with short wet pulses recorded in Laguna Colorada and the Miriguaca River (Tchilinguirian and Morales, 2013; Grant et al., 2016b). Indeed, Grant et al. (2016a) stated that after 6700 cal yrs BP conditions of decreased moisture were observed in Las Pitas river, although there was always availability of surface water. Therefore, it is possible that QS3 were occupied for short intervals of time (seasonally?) after 7200 cal yrs BP due to the greater availability of resources in the area than elsewhere in the Salt Puna (Aschero and Hocsman, 2011). This would explain not only the presence of coprolites in levels 2b7 and 2b6 (between ca. 7300 to ca. 6100 cal yrs BP), but also the record of annual herbs preserved in the coprolites of those levels and the richness variability among coprolites of level 2b6. The presence of resources associated with the availability of water during the driest period of the Holocene, implies that this sector of the Puna would have been a “fluvial oasis” (*sensu* Bruniard, 1999 in Pintar, 2014b) allowing the human occupation of QS3 as a logistical base yearlong but discontinuously

during the Middle Holocene. This inference is also supported by Pintar (2014a) who re-examined the conditions surrounding Cueva Salamanca 1, other archaeological site located in Las Pitas basin (Fig. 1b), to which Quebrada Seca is a tributary. Therefore, these evidences suggest that the presence of “ecological refuges” (*sensu* Grosjean et al., 1997) would be restricted to the Atacama Desert (Chile), where human occupations decreased, and dispersed to previously unoccupied areas with seasonal and/or variable wetlands and springs.

6. Conclusions

The local environmental patterns recorded by the microfragment and pollen records preserved in coprolites from QS3 shed light on those discrepancies in timing, direction and magnitude of past environmental changes based on other archives/proxies. While the pollen record of camelid coprolites is sensitive to short-term wet events and may underestimate dry periods (Tchilinguirian and Morales, 2013; Grosjean et al., 2003), the microhistological record clearly shows dry phases through the taxonomic identity of moisture-tolerant grass and shrub species. Therefore, this work demonstrates that the combination of the microhistological and palynological records in order to reconstruct paleodietary and paleoenvironmental changes provided a more accurate and detailed approach of the vegetation dynamics due to climatic fluctuations from the Early to the Middle Holocene. Changes in vegetation dynamics are reflected in the variations on diversity and richness of the species recorded by both analysis techniques. Future coprolite analyses of other archaeological sites of the study area dating back to the Early and Middle Holocene, could support/refute the “ecological refuge” or “fluvial oasis” hypotheses mentioned in this study. Moreover, the coprolite analysis together with the palynological analysis of sedimentary sequences encompassing the Late Holocene, will provide a more detailed insight into the paleoenvironment evolution of the Salt Puna throughout the last 10,000 years.

CRediT authorship contribution statement

M. Eugenia Mosca Torres: Writing – original draft, Writing – review & editing, Visualization, Supervision, Methodology, Investigation, Formal analysis, Conceptualization, Software. **M. Eugenia de Porras:** Writing – review & editing, Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Visualization, Writing – original draft. **Carlos A. Aschero:** Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

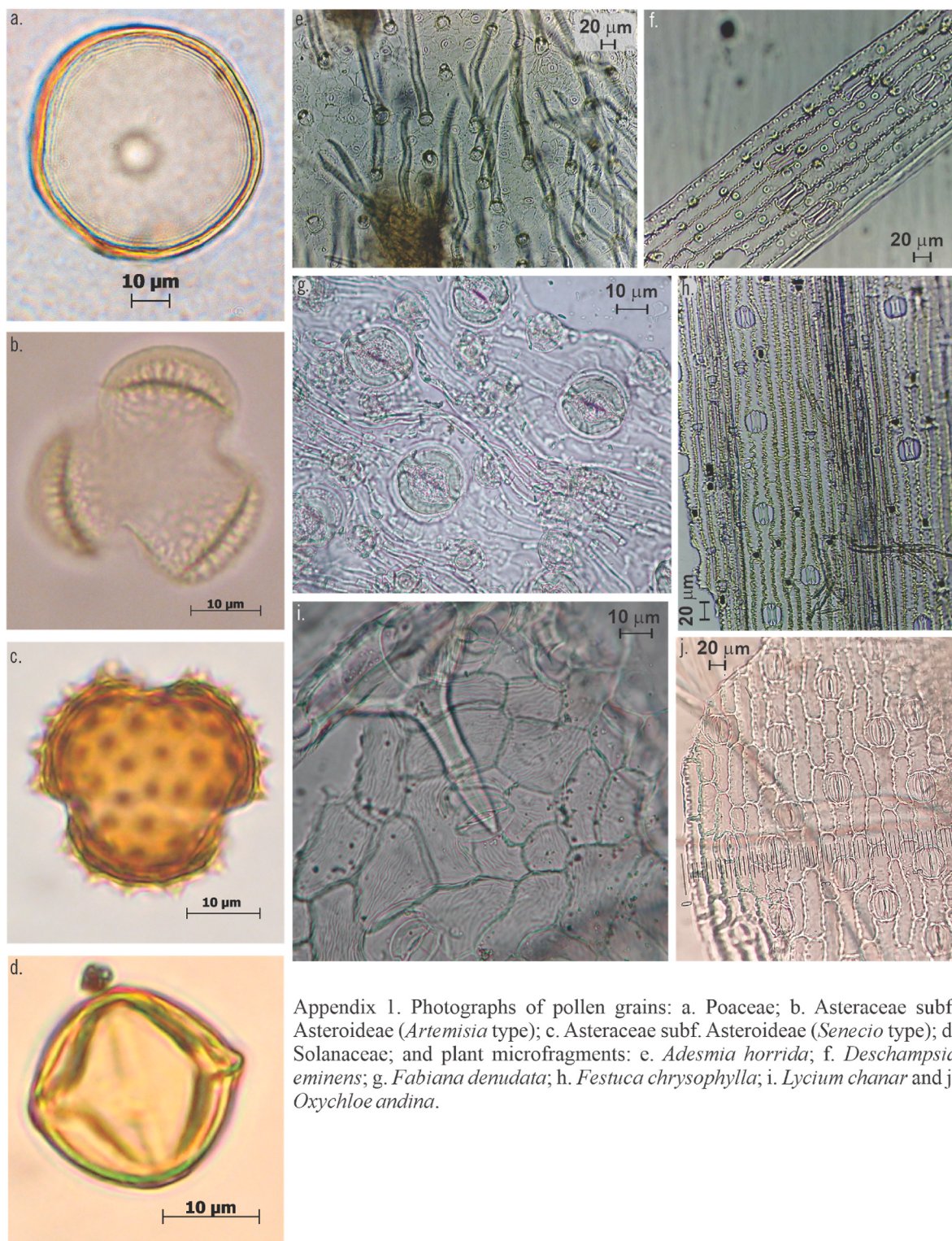
Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix 1. Photographs of pollen grains: a. Poaceae; b. Asteraceae subf. Asteroideae (*Artemisia* type); c. Asteraceae subf. Asteroideae (*Senecio* type); d. Solanaceae; and plant microfragments: e. *Adesmia horrida*; f. *Deschampsia eminens*; g. *Festuca chrysophylla*; i. *Lycium chanaar* and j. *Oxychloe andina*



Appendix 1. Photographs of pollen grains: a. Poaceae; b. Asteraceae subf. Asteroideae (*Artemisia* type); c. Asteraceae subf. Asteroideae (*Senecio* type); d. Solanaceae; and plant microfragments: e. *Adesmia horrida*; f. *Deschampsia eminens*; g. *Fabiana denudata*; h. *Festuca chrysophylla*; i. *Lycium chanaar* and j. *Oxychloe andina*.

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