Journal of Arid Environments 97 (2013) 160–169

Contents lists available at SciVerse ScienceDirect

Journal of Arid Environments

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

Paleoenvironmental reconstruction of central-western Argentina from analysis of Late-Pleistocene mammal droppings

Eduardo Martinez Carretero [a,*], Alejandro Garcia [b], Mariana Dacar [c]

[a] Geobotánica y Fitgeografía (IADIZA-CONICET), Av. Adrián Ruiz Leal s/n°, 5500 Mendoza, Argentina
[b] CONICET-Fac. Filosofía, Humanidades y Artes, UNSJ, Ignacio de la Roza 230 (Oeste), 5400 San Juan, Argentina
[c] GIB-IADIZA (CONICET), Av. Adrián Ruiz Leal s/n°, 5500 Mendoza, Argentina

ARTICLE INFO

Article history:
Received 16 May 2012
Received in revised form
6 March 2013
Accepted 5 June 2013
Available online

Keywords:
Ancient mammals
Argentina
Fecal pellets
Paleoecology
Pleistocene

ABSTRACT

Plant macrofossils studied in coprolites from small-sized, medium-sized and large mammals, dated by ^{14}C to ca. 30.8–24 and 9 kybp, allowed to record changes in local vegetation and its relation with geomorphological units. Paleobotanical samples were determined using microhistological analysis. We found that plant associations and the vegetation–geomorphology relation were similar in the two periods analyzed. According to this study, the Monte plant formation would reflect certain stability during the analyzed period in arid central-western Argentina, although this does not imply the absence of variations in plant structure.

1. Introduction

Reconstruction of the paleoclimate of southern South America for the last glacial cycle provides valuable information related to global climate change. The analysis of faunal feces is a fruitful means for the reconstruction of environmental conditions in the past. Small and medium-sized mammals are important components of the faunal communities in South America; however their fossil record is still scarce. In America, paleoenvironmental studies of feces and contents of caves of small mammals (rodents) have been conducted in desert areas of the United States and northern Chile (Betancourt et al., 1990; Latorre et al., 2001, 2002, 2006) including the last 40 ^{14}C kybp. Microhistological and DNA studies were made on feces from large mammals from different places in the USA (Phillips, 1984; Poinar et al., 1998; Thompson et al., 1980). In South America, instead, paleoenvironmental reconstructions for the Pleistocene have mostly focused on pollen (Heusser, 1983; Markgraf et al., 1992; Páez et al., 2008; Zárate and Páez, 2002) and glacier studies (Porter, 1981; Rabassa and Clapperton, 1990). The present knowledge of Late Quaternary environmental change in subtropical central-western Argentina is fragmentary, particularly because dated records from feces are scarce, pollen analyses are mostly restricted to the Holocene, and a general model of Pleistocene glacial advances is not yet available.

The paleoecological record obtained from recent stratigraphic excavations at the site Gruta del Indio (Mendoza), central-western Argentina, reveals the presence of coprolites from small, medium-sized and large mammals, this record being unique in South America. Analyzing this record represents the first contribution to the reconstruction of paleoenvironmental conditions of the late Pleistocene in the area around 34° S, based on microhistological studies (García and Martínez Carretero, 2010; Martínez Carretero et al., 2009). The archaeological material from Gruta del Indio's first excavations was examined by Lagiglia (1956, 1977; Semper and Lagiglia, 1968), while D'Antoni (1976) and D'Antoni and Markgraf (1977) made paleoclimatic considerations from pollen analyses. New excavations carried out since 1997, within the dripline of the cave, at the limit between squares R8 and R9, provided a stratigraphic profile that is basically coincident with the one proposed by Lagiglia (1977). Plant samples obtained provide information about paleoenvironmental and biogeographical evolution in the area for the period 30.8–9 ^{14}C kybp.

* Corresponding author. Geobotany and Phytogeography, Av. Adrián Ruiz Leal s/n°, 5500 Mendoza, Argentina. Fax: +54 261 5244101.
E-mail addresses: mcarrete@mendoza-conicet.gob.ar, mcarrete@lab.cricyt.edu.ar (E. Martinez Carretero), alegarcia@unsj.edu.ar (A. Garcia), mdacar@mendoza-conicet.gob.ar (M. Dacar).

0140-1963/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jaridenv.2013.06.005

2. Study area, stratigraphy and chronology

The site Gruta del Indio is located in the area known as Rincón del Atuel at 34° 45′S–68° 22′W, in central-southern Mendoza, Argentina. The area around the site is constituted by a basaltic outcrop next to the Atuel River, located 20 m above the alluvial plain. Under the outcrop, water erosion formed a cave which was later filled with gravel, sand and slime, dominant elements in the profile (Semper and Lagiglia, 1968), and with finer illuviated materials.

Vegetation of the studied area corresponds mostly to the Monte and Cardonal phytogeographic provinces (Martínez Carretero, 2004; Roig et al., 1995) (Fig. 1). Based on the present work, plant communities in the study area were classified as: a) Monte communities (*Larrea divaricata–Larrea cuneifolia*, Roig, 1989); b) Monte riparian communities (*Senecio–Proustia cuneifolia*, Roig, 1989); and c) Communities on xeric rocky slopes of the Cardonal (*Dolichlasium lagascae*, Roig and Martinez Carretero, 1998). In the comparative table (Table 2) species were arranged according to these plant communities.

The sedimentary profile exposed by the excavation shows four layers. Upper Layers 1 and 2 consist of yellowish brown, fine slimy sediment, differing only in the grade of cohesion (Fig. 2). Layer 3 is the only one having fecal pellets of extinct Pleistocene mammals, along with feces of extant species, such as those of *Lagidium viscacia*. Pleistocene megafauna bones, wood fragments and a few small chalcedony flakes (supposed to correspond to Layer 2 or upper part of Layer 3) are also present. Layer 3 is composed of brown (10 YR 5/3) fine sediment with small fragments of basaltic rock fallen from the ceiling of the cave. Both color and composition of sediments are homogenous throughout the layer, showing no signs of alteration by post-depositional agents (such as burrowing rodents, ants, and geological displacements). The presumably vertical movement of the small flakes (García and Lagiglia, 1999) suggests that alteration processes occurred in the excavation area, although they must have been quite restricted, as shown by the integrity of megafauna feces and by the absence of both inclination in rock and wood fragments and intrusion of sediments different from those of Layer 3. Feces are isolated, not forming a midden, generally in horizontal position and showing high level of integrity. This integrity, however, decreases from the upper to the bottom part of Layer 3. Lagiglia previously (1956) indicated the presence on the site of remains of large mammals attributed to *Megatherium* sp. and *Mylodon listai*, including some big feces now exhibited in the Museum of Natural History of San Rafael. The mammal pellets analyzed in this study are smaller (Fig. 3), and similar to those of *Hippidion* sp. found in Gruta Los Morrillos (Gambier, 1995). Taking also into account that bones of *Hippidion* have been identified in the record of Gruta del Indio (García, 2003), we assigned our dung samples to this taxon. Finally, Layer 4 presents a dark sand deposit with neither cultural nor faunal remains.

Several ^{14}C dates were obtained through analyses of megafauna feces from R8/R9 performed by the Tritium and Radiocarbon Laboratory (Latyr) of La Plata University. Each sample consisted of a single pellet or two adjacent megafauna excrements. The absolute stratigraphic coherence of coprolite dates (Garcia and Lagiglia, 1999) minimizes eventual differences related to the high standard deviations obtained. Table 1 shows the occurrence of two periods of sediment and pellet deposition for Layer 3. The radiocarbon dates indicate that the record of the oldest period in R8-R9 begins at least

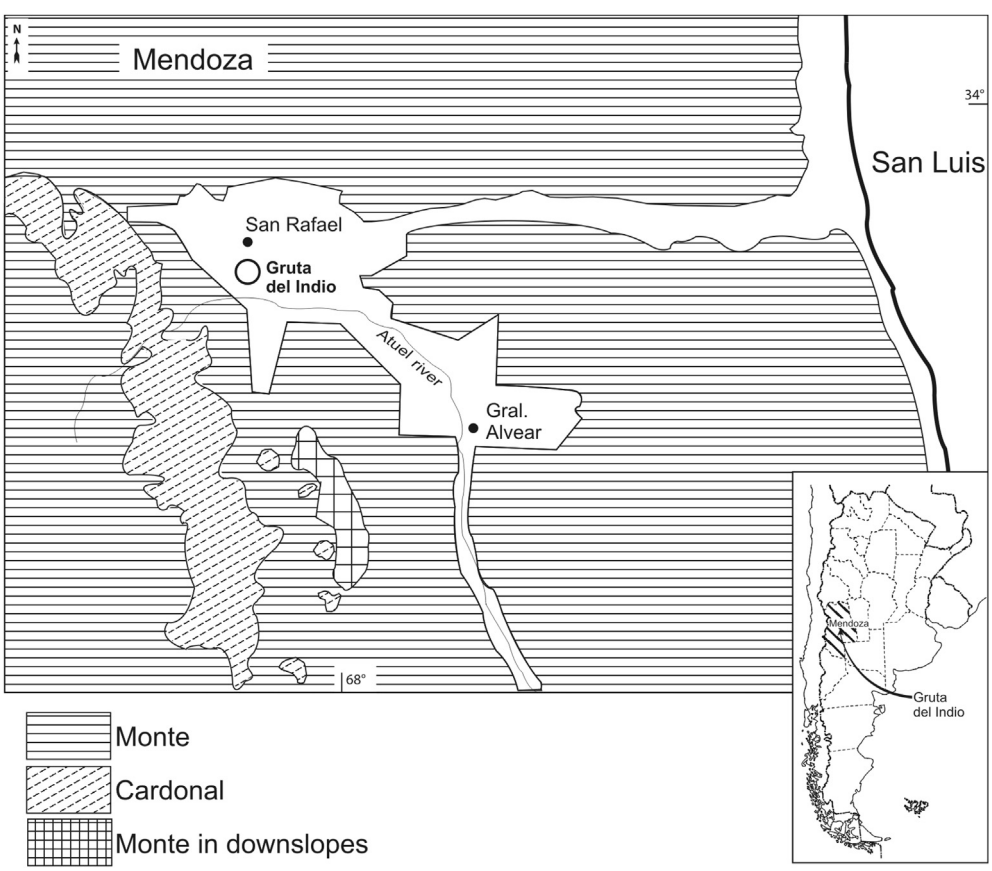

Fig. 1. Vegetation map of Gruta del Indio area.

Table 1
Chronological summary and stratigraphic levels of Layer 3 in Gruta del Indio.

Stratigr. Level	Lab. n°	Date (uncal)	Approx. age used in text
5	LP 925	8990 ± 90	9 ky
6	LP 1075	24,140 ± 510	24 ky
8	LP 1072	28,670 ± 720	28.7 ky
9	LP 929	30,200 ± 800	30.2 ky
10	LP 918	30,800 ± 700	30.8 ky

LP = Latyr, La Plata, Buenos Aires, Argentina.

by 30.8 and ends by 24 ^{14}C kybp, whereas the younger one has been dated to ca. 9 ^{14}C kybp (García, 2003). According to the analyses of samples from other zones of the site, the beginning of Layer 3 dates to at least 37.6 ^{14}C kybp (Beta 152587) (García, 2003). Also, some previous dates from dung samples taken by Austin Long and Humberto Lagiglia at the upper part of Layer 3 gave results ranging from 12375 ± 115 (A-9571) to 10900 ± 185 (A-9493) (Long et al., 1998), which reduces the chronological hiatus at a site scale.

3. Sampling and method

Excavation was carefully carried out with brush and metal trowel, on a 1.2 m^2 area partially comprising squares R8 and R9. Remains were grouped on artificial levels, whose thickness (from 6 to 14 cm in Layer 3) and inclination depended on that of the recorded components (mainly megafauna dung pellets) and on the spatial relationships between them. Once the sediment of Layer 2 was removed, Layer 3 was excavated through Levels 3–11 (Fig. 2); considering the general tendency to horizontality in the deposition, Level 4 surely included a part of the sediments corresponding to Level 3 that were compressed by rocks fallen from the ceiling. Each of the excrements was recovered and put into individual nylon bags.

Feces were analyzed separately and classified according to origin as proceeding from small mammals (S; rodents), medium-sized mammals (M; *L. viscacia*), and large mammals (L; *Hippidium* sp.). Only those levels from which at least a group of five coprolites could be obtained were analyzed. Each coprolite was regarded as a basic sampling unit. Two 3-g samples were randomly obtained from each coprolite. This material was prepared for microscopic analysis using the methodology proposed by Dacar and Giannoni (2001). This methodology consists of a CO_3HNa pretreatment that facilitates sample handling, and allows for better observations of seed cuticle, starch and epidermis than the traditional methodology (Baumgartner and Martin, 1939; Dusi, 1949; Holechek, 1982; Johansen, 1940; Williams, 1969; etc.). The relative frequency of appearance of different taxa was quantified for each of the 50 randomly chosen fields, at 400× under an optical microscope. Plant macrofossils including seeds, leaves, flowers, and fruits were then identified by comparison to a reference collection from the Geobotany and Phytogeography Herbarium (MERL). Reference materials were prepared for different species of each genus. Paleobotanical and current local floras were compared with the presence analysis. When known, the photosynthetic path (C3, C4) was indicated for each species. Genus and species frequency for each sample were adjusted to the 1–5 scale, with 1 being <5 (very rare), 2 being 6–10 (rare), 3 being 11–15 (common), 4 being 16–20 (abundant), and 5 being >21 (dominant). Relative abundance was plotted accordingly for each taxon. Isolated counts were also considered. Plant species nomenclature follows a published catalogue of the Argentine Republic (Zuloaga and Morrone, 1996).

Current plant communities were floristically surveyed over the area within 300 m of the Gruta del Indio site, considering that the foraging area for small rodents usually is <100 m (Pearson and Ralph, 1978). Puig et al. (1998) found evidence of selective feeding by *Lagidium* on plants growing in rocky outcrops, so local vegetation is well sampled in its fecal pellets. The current local landscape comprises the top of the outcrop, the north-facing rocky edge, the talus, the temporary river and the extensive sandy plain. Ten plots (10 × 10 m^2 or on occasions 2 × 5 m^2) were delimited in each sub-environment. All plants inside these plots were identified and surveyed. Surveys were grouped taking into account the different sub-environments found (Table 2). As samples come from animal diets and the joint analysis of different coprolites, grouped by age, was based on the habitat preference of each animal group, they have high sampling value.

A data matrix (Table 2) was made from the current and paleobotanical information obtained, and standardized by columns (representing different levels and ages). In standardizing, the older the level a higher loss of material by deterioration was assumed, so the algorithm $y_1 = x_1/x$ was used (MC Cune and Grace, 2002).

Both paleobotanical and current floras were statistically analyzed using cluster and principal components analyses (Benzécri, 1973).

4. Results

We identified a total of 47 plant macrofossil taxa. A total of 37 taxa were identified to species, the rest to genus or family level (e.g., Chloridea). The genus and species frequency for each sample is observed in Fig. 4. Fig. 5 shows the frequencies, in percentages, grouped by life form, according to the chronology defined from paleobotanical materials in Gruta del Indio. In the current local flora, with 35 species recorded, 80% of them belonged to the Monte and 11% to the Cardonal; whereas in fossil records (27 plants, 17 at specific level) 51.9% belonged to the Monte region, 3.7% to the Cardonal, and 7.4% are of wide distribution. The remaining 37%, determined only at genus level, does not admit of phytogeographical assignment.

The clustering obtained reflects the same vegetation communities mentioned above. Three clusters resulted from the analysis (Fig. 6).

Cluster 1 gathered medium-sized mammals dated at <9 kybp to the current top of outcrop and lowland samples. Cluster 2 shows two sub-clusters: 2a links riparian and talus vegetation with small mammal samples, and 2b with large mammal samples, both dated at ca 9 kybp and between 24 and 30.2 ^{14}C kybp. Cluster 3 includes large mammal samples dated at 28.6 kybp and 30.8 kybp ^{14}C related to riparian, talus and lowland vegetation.

Data ordination was performed through the Principal Components Analysis, without axis rotation. This analysis allows for distribution of data along two variation axes. Axis I is related to water availability in the substrate, distinguishing the saxicolous plant communities in the top of outcrop from riparian and talus vegetation. Axis II is associated with preferences for these plant taxa exhibited by small, medium-sized and large mammals. This analysis also resulted in three clusters coincident with those obtained from the cluster analysis (Fig. 7).

Considering the percentage of presence of life forms present (Raunkjaer, 1937), according to sampling levels, nanophanerophytes are present throughout the period analyzed, and appear as the most conspicuous life form in large mammal samples. Chamaephytes are part of the diet of large mammals. Small and large mammals show preference for hemicryptophytes. The specific level is difficult to reach in paleobotanical hemicryptophytes, which limits the analysis; however, the same genera occur in the current

Table 2
Table of presence between current and paleobotanical local flora.

	Outcrop	Basament	Low land	Talus	Riparian	M4	M5	L3	L4	L6	L7a	L8a	L8b	L8c	L8d	L7b	L7c	7d	L9	L10a	L10b	S4	S6	L5	S5	S8	w5	w6	w7	Chorogical type	Life form
*Ephedra triandra**	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Lycium chilense ovalifolium**	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Condalia microphylla**	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
Glandularia crithmifolia	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	C
*Aloysia gratissima**	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Zuccagnia punctata**	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Larrea divaricata**	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	M	N
*Lecanophora heterophylla**	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	M	C
*Tephrocactus aoracanthus**	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	S
*Bulnesia retama**	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Trichocereus candicans**	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	S
*Lycium tenuispinosum**	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Larrea cuneifolia**	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Senna aphylla**	.	1	1	1	.	.	.	1	1	1	1	1	1	1	1	1	1	.	1	1	1	.	.	1	.	.	.	.	.	M	C
Prosopis flexuosa depr.*	.	.	1	.	.	.	.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.	M	N
*Pappophorum caespitosum**	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	1	1	1	1	1	.	.	.	M	H
Acantholippia seriphioides	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	1	.	.	.	.	.	M	C
*Bouteloua sp.**	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	M	H
*Capparis atamisquea**	.	.	.	1	.	.	1	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	M	N
Prosopidastrum globosum	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	M	.
*Stipa sanluisensis**	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	H
Clematis montevidensis	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Cp
Bowlesia tropaeolifolia	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	T
*Schinus fasciculata**	.	.	.	.	1	.	.	1	.	1	.	.	.	1	.	.	1	.	1	1	.	.	.	1	.	.	.	.	.	M	N
Senecio gilliesianus	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
Baccharis salicifolia	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Salvia gilliesii**	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	N
*Geoffroea decorticans**	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Digitaria californica**	.	.	.	1	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	H
*Aristida adscensionis ?**	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	M	H
*Buddleja mendozensis**	1	1	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	N
*Cercidium praecox**	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	M	N
Eupatorium patens	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	M	N
*Hyalis argentea**	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	M	C
Caesalpinia gilliesii	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	N
Ligaria cuneifolia	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	E
Chenopodium papulosum	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	1	.	.	1	1	1	.	.	.	.	.	.	
Chloridea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	.	.	.	.	H
Poa ?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	H
Fabiana sp.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Senecio sp.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lycium sp.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Panicum ?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	H
Setaria sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	H
Hordeum sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	H
Stipa sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	H
Bromus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	H

L: Large mammals, M: Medium-sized mammals, S: Small mammals, w: wood, *: megathermic species. Life form: N: nanophanerophyte, C: chamaephyte, S: suculent, H: hemicryptophyte, T: therophyte, E: epiphyte, Cp: climbing phanerophyte. Chorological type: M: Monte, C: Cardonal.

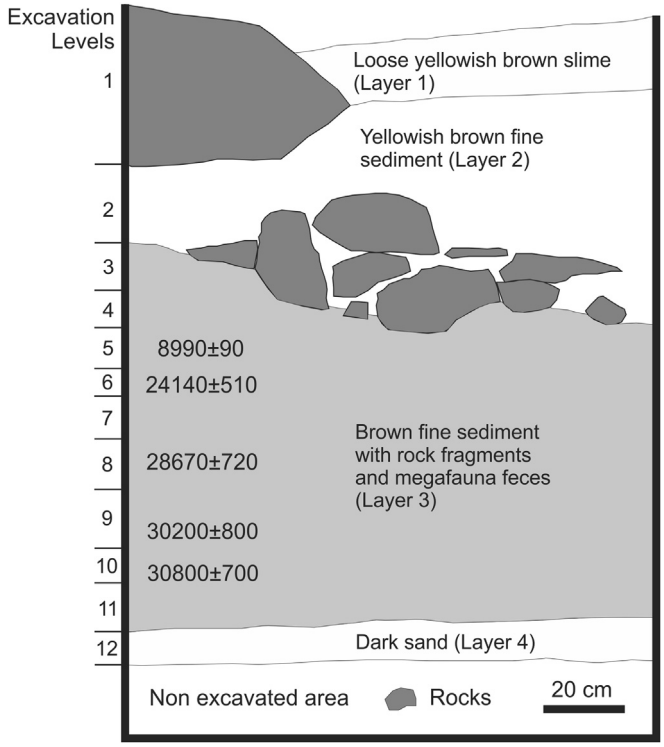

Fig. 2. Stratigraphic profile and levels from excavation of pit R8/9, and approximated vertical position of datings.

local flora. Climbing phanerophytes are absent from paleobotanical samples. The analysis of current life forms indicates dominance of nanophanerophytes and hemicryptophytes. Fossil floral records reveal that nanophanerophytes and chamaephytes are present in 50% of the paleobotanical flora dated to ca. 30.8 ^{14}C kybp.

Paleobotanical samples respond to both selective sampling and environmental preference of each animal group. *L. viscacia* lives exclusively in rocky habitats and feeds primarily on saxicolous plant species. Caviomorph rodents prefer environments with deep and relatively loose soils, like lowlands and taluses, whereas large mammals dwell in larger areas, foraging on grasses, shrubs and low trees. The paleobotanical material presented here demonstrates these environmental preferences (Table 2).

Fig. 3. Coprolite from extinct large mammal.

In agreement with plant taxa distribution, chorological types were defined as Monte and Cardonal. Taking the chorological position of each species into account (Table 2), Monte plant species are present in all samples, and those from Cardonal are found mostly in samples from medium-sized mammals. Most plant species belong to the Monte phytogeographical province, except for *Salvia gilliesii*, *Stipa sanluisensis* and *Buddleja mendozensis* which belong to Cardonal and constitute the vegetation of warm xeric slopes adjoining the Monte vegetation.

5. Discussion

From the analysis of presence, life forms, plant community scheme, and current phytogeographic zonation, *Prosopis flexuosa* var. *depressa*, *Pappophorum caespitosum*, *Capparis atamisquea*, *Cercidium precox* ssp. *glaucum*, *Prosopidastrum globosum*, among others, emerge as indicative species of a warm and dry environment, typical of the Monte, during the periods between ca. 8–9 ^{14}C kybp and ca. 24–30.8 ^{14}C kybp. Coprolite floras contain perennial C3 shrubs (*Senna aphylla*, *P. flexuosa* var. *depressa*, *L. divaricata*), C4 summer-flowering perennial grasses (*P. caespitosum*, *Bouteloua* sp., *Digitaria californica*), and C4 annual grasses (*A. adscensionis*). *Pappophorum* is common in Argentina and southern Peru, and scarce in Chile, whereas *P. caespitosum* is a common grass in the Monte (Argentina). On the whole, the C4 photosynthetic path is dominant, indicating plant species adapted to environments of high temperature, high solar radiation, and low water availability.

In addition, close to feces, small stem portions of *L. divaricata*, *P. flexuosa* and *Cercidium praecox* ssp. *glaucum* were recovered at levels 5, 6, and 7. Each of these species is syntaxonomically characteristic of a class and association. According to Braun-Blanquet (1950, 1979), characteristic species are helpful in determining the floristic individuality of a plant community, apart from representing the highest value indicative of the ecological conditions in each community, i.e. its stability. One more important aspect to take into consideration is the presence of woody parts and fruits of these plant species, which reveals plant community stability in allowing ecesis. Paleoecological contributions normally do not address the vegetation–landform relationship (Cole, 1982; Van Devender and Spaulding, 1979); however, in this study the indicative value of plant species was recognized as a relevant factor in paleoenvironmental reconstruction. Midden or coprolite analyses are generally considered to underrate the extent of shrublands and grasslands and overlook the mosaic aspects of vegetation distribution induced by landforms (Webb and Betancourt, 1990). Moreover, fossil differential conservation and the plant-collecting behavior of each animal species make data interpretation difficult. Nevertheless, analysis of samples per age and animal body size (small, medium-sized or large) permit obtaining a more comprehensive vegetation sampling along the archaeological profile, minimizing sampling biases. The paleobotanical evidence analyzed agrees with the selective plant collection and environmental preference shown by each animal group. This is due to food-storing habits and a strong territoriality, especially for medium and small-sized mammals. Thus, fecal pellets of medium-sized mammals (*L. viscacia*) living exclusively in rocky environments, and whose diet is based on saxicolous plant species (belonging to *D. lagascae* and *Senecio–Proustia* communities), indicate the past existence of these habitats. Large mammals explore more extensive areas and forage on grasses, shrubs, and low trees, so their feces reveal their preference for lowland plant species (which include elements of the *L. divaricata–L. cuneifolia* community). Small mammals (caviomorphs) that inhabit areas with deep and relatively loose soils prefer riparian and talus vegetation. In conclusion, the flora composition of mega-, meso- and microfauna feces points

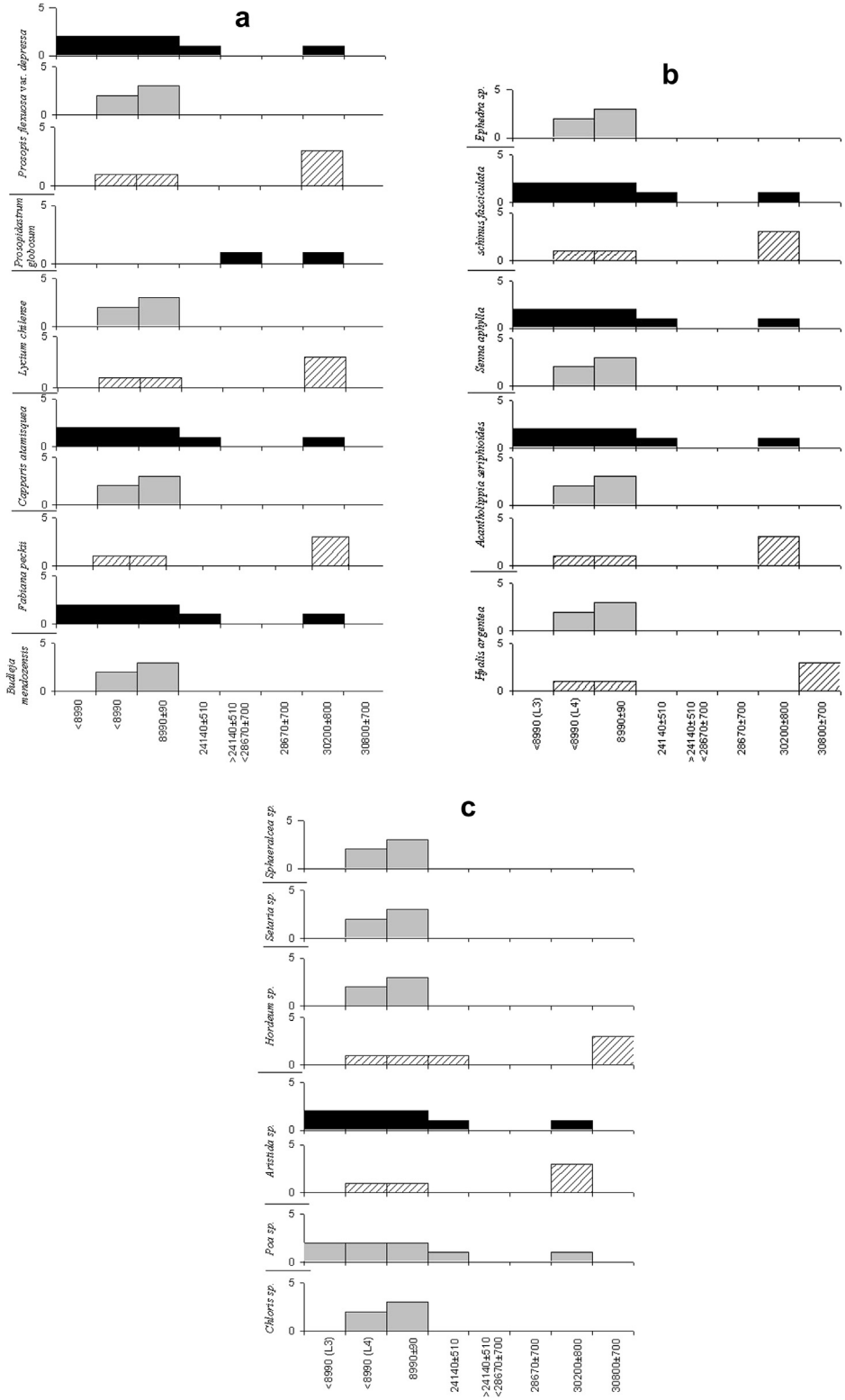

Fig. 4. Genus and species frequency from plants found in coprolites from Gruta del Indio. a: nanophanerophyte, b: chamaephyte, c, d: hemicryptophytes, e: others ▬ Large mammals, ▨ Small mammals ▭ medium-sized mammals.

to an environment with physiographic components (outcrop, talus, and lowlands/riverbanks) similar to the present ones, although this does not imply the existence of quite the same landscapes.

Unfortunately, despite offering the only record of coprolites for the Pleistocene–Holocene transition in the Argentine Monte, the excavated area of Gruta del Indio is lacking in sediments corresponding to the period between ca. 9 and ca. 24 ^{14}C kybp, so it is hard to come to a conclusion as to the probable environmental changes in this period. As mentioned above, this hiatus is smaller when considering the whole site, and it would have ended by 12.5

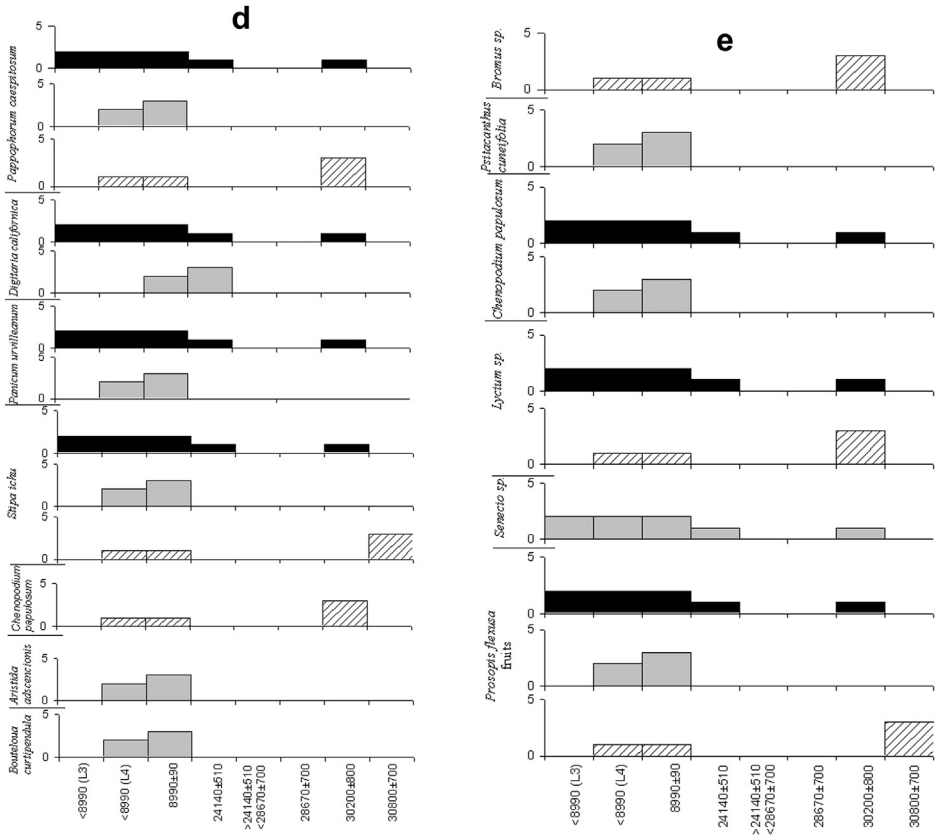

Fig. 4. (*continued*).

instead of ca. 9 ^{14}C ky ago. Studies on environmental conditions for that period in other arid regions show similar results, pointing to conditions dominated by increasing temperature and dryness. According to Markgraf et al. (1992), environmental conditions in the southern hemisphere toward 18 kybp were drier than in the present time, which favored wind erosion by sand-dune formation. Kiage and Liu (2006) mention for Eastern Africa two periods of desiccation between 21 and 12.5 kybp, two events of drought at approximately 8.3 and 5.2 kybp, and the beginning 4 ky ago of the arid period that extends up to the present. Polyak et al. (2012) indicate, for the Carisbad Cavern (USA), a terminal Pleistocene drought between 14.5 and 12.9 kybp, briefly interrupted by the Younger Dryas, and a rapid transition from cool moist Late Glacial to warm dry Holocene. Besides, Wang et al. (2012) have recognized fire occurrences on the Chinese Loess Plateau, during the Last Glacial Maximum (22.3–14.6 kybp), when the climate was drier and with a more continuous grass cover. Zárate and Fasano (1989) report an aeolian episode for central Argentina dated at 11 kybp, with probable loss of material due to wind erosion. For central Chile (Laguna Tagua Tagua, 30°–40°S), Heusser (1990), by using pollen analysis, suggested intervals of relative aridity during the Holocene and Pleistocene, and ice age climate with restricted seasonality for the late Pleistocene, which constituted a transition toward the semiarid Mediterranean climate. Latorre et al. (2002), analyzing middens in the absolute desert of Atacama, reported a relative to moderate increase in precipitation during the middle Holocene, compared to the hyperaridity of the early and late Holocene. Betancourt et al. (2000), in the Atacama desert, found a lack of middens in the 35–22 kybp interval, which possibly reflects increased aridity and decreased midden production rather than decay of older middens.

In general, these studies link the periods of greater aridity with erosion processes. In the case of Gruta del Indio, due to the absence of specific geological studies, it is very difficult to support the lack of deposition of sediment and organic material between ca 12.5 and 24 ^{14}C kybp. Instead, it is more likely that during that period (at least in its final moments) there has been a marked predominance of the erosive agents over the depositional ones, with the consequent elimination of the top part of Layer 3. At least in some areas of the site, this erosive process would have ended about 12.5 ^{14}C ky ago, as would indicate the first datings of the post-hiatus record currently available. The similarity of the sediments prior and posterior to the hiatus and the disturbing action of the megafauna could explain the homogeneity of Layer 3 and the lack of a visible erosive discordance.

Our data also lead to a revision of the paleoclimatic sequence available for the area, made through the analysis of the pollen collected in other profiles of Gruta del Indio (D'Antoni, 1983). According to this author the main environmental change would have happened at approximately 10 ^{14}C kybp, when the vegetation in nearby areas showed variations in dominance of certain plant species, as Monte species began to prevail over Patagonian species, with phreatophytes dominating the riparian vegetation. The period dated between 32 and 27.5 kybp is indicative of a transition to a Patagonian environment; between 27.5 and 24 kybp a thermal increase favored the expansion of the Monte, though in an ecotone with Patagonian species; between 15.5 and 12.5 kybp Patagonia is present again, and finally as of 12.5 kybp the Monte became definitely established (D'Antoni, 1980). Our data allow discussing this information. The portion of D'Antoni's pollen diagram that corresponds to most of the late Pleistocene was based on age interpolation for Layer 3, the beginning and end of which were marked by

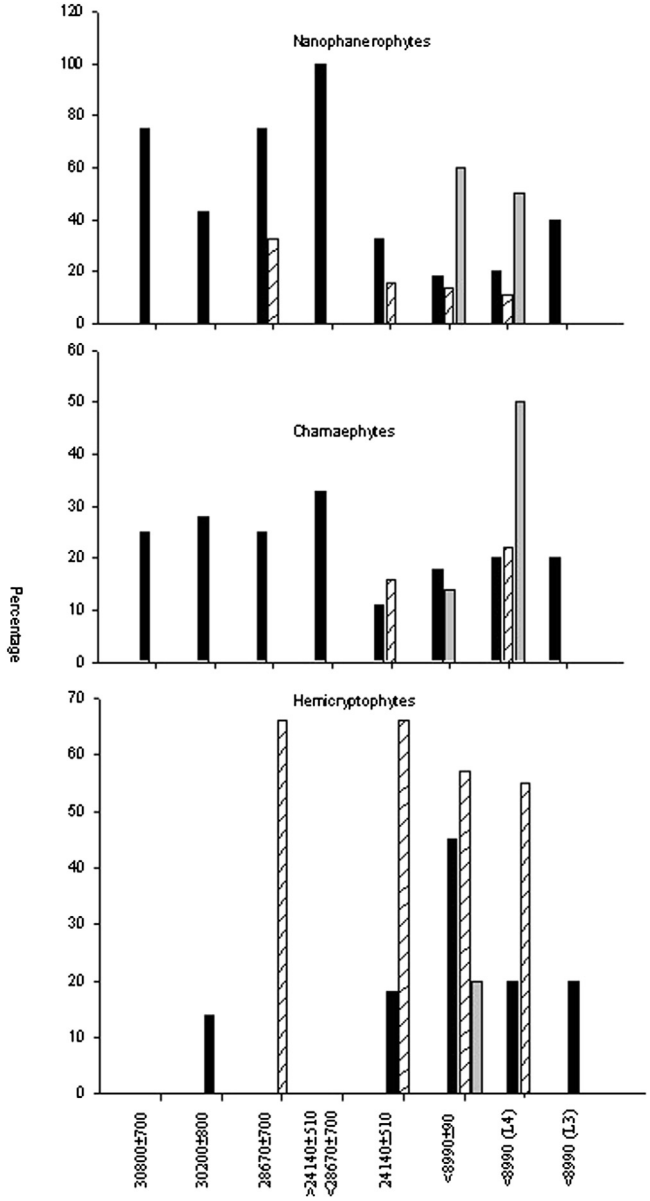

Fig. 5. Percent variation in life forms (Nanophanerophytes, Chamaephytes, Hemicryptophytes) over the period studied. ■ Large mammals, ▨ Small mammals ▭ Medium-sized mammals.

ages of >32–11.8 ± 180 kybp (D'Antoni, 1980), and on the assumption of a constant deposition rate. However, our recent datings of large mammal feces reveal that the bottom of Layer 3 is >37.6 ky old (Beta 152587). Likewise, deposition would not have been constant, since both stratigraphic studies of recent excavations and the currently available set of dates show a hiatus between ca. 9–12 and ca. 24 ^{14}C kybp (García and Lagiglia, 1999). This change in the stratigraphic and chronological framework limits interpretation of the typical pollen sequence on the site, as proposed in 2007 from our preliminary data (García and Martínez Carretero, 2010), and supported later by the reinterpretation of pollen associations from Gruta del Indio (Páez et al., 2010). Moreover, considering the current phytogeographical assignments of plant species included in the pollen diagram, however, there appear some relevant differences. The genera *Acantholippia*, *Aloysia*, *Salvia* and *Thymophylla* are regarded as Patagonian, but in fact they belong to the Monte, along with the genera *Schinus* and *Gutierrezia*, which

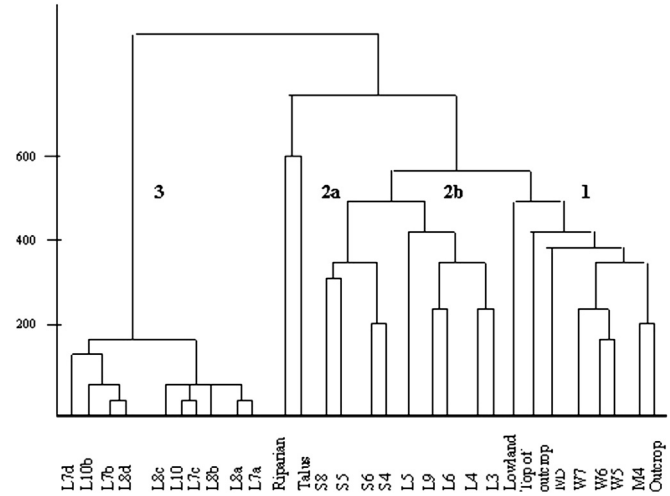

Fig. 6. Clustering per sampling level. L: large, M: medium-sized, S: small mammals.

reveals the presence of the Monte in the area. Of the other genera included in the diagram, only *Maytenus* (riparian genus) is considered to be Patagonian. *Budleja* might be *Buddleja mendozensis*, usually accompanied by plant species typical of warm rocky environments; *Buddleja araucana*, currently located 250 km south of the study area, is Payunian. However, *Budleja* is not accompanied by meso or microthermal species in the pollen diagram, on account of which indicated changes would not be so accurate. As for *P. flexuosa*, the species referred to is very likely the shrub variety *P. flexuosa* var. *depressa*, widely distributed over the study area and difficult a pollen-based differentiation from the typical variety. All these data claim a reinterpretation of the regional pollen framework, and support the scenario presented here, with a group of Monte megathermal species dominating the flora of most late Pleistocene times at Rincón del Atuel.

In summary, results obtained at Gruta del Indio allow advancing significantly on diverse aspects related to the paleoenvironmental reconstruction of central west Argentina. On the one hand, they

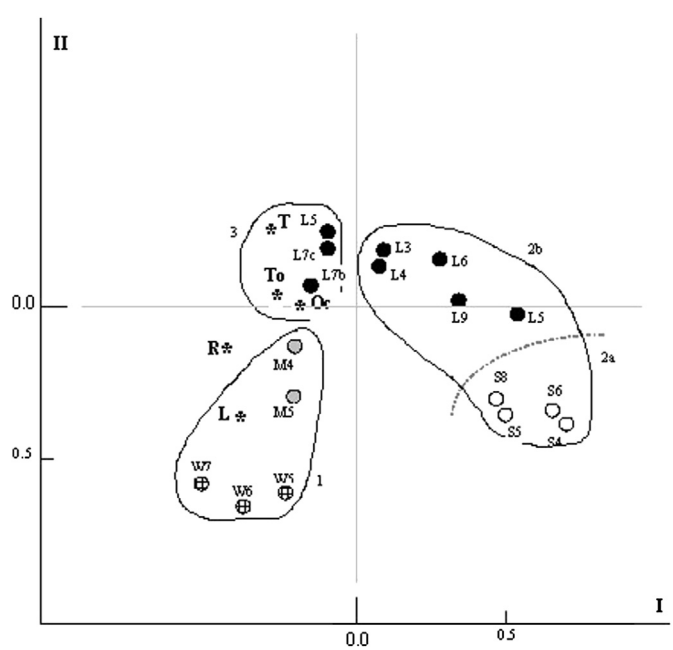

Fig. 7. Arranging of data through Principal Components Analysis.

determine the predominance of xeric Monte formation since ca. 31 kybp, and contribute to characterizing its components; on the other hand, they permit to enhance the perspectives generally applied at continental scale by adding the analysis of geoforms, from the marked territoriality of the mesofauna and their dietary habits, suggesting the continuity of similar geotopes throughout the analyzed period and evidencing a certain environmental stability. Finally, our paper constitutes a relevant input to the current discussion about the regional paleoenvironmental model.

6. Conclusions

Like at present, our results show a prevalence of Monte xeric vegetation in Gruta del Indio and the surrounding area for the periods 31–24 and ca. 9 ^{14}C kybp, and arid conditions similar to the current ones, within a similar local geomorphology, and with similar regional plant zonation. These data, along with the significant floristic similarity recorded, provide no evidence of significant vegetation changes, despite the occurrence of the Last Glacial Maximum during the intermediate hiatus. The long distance of the study area from the ice front (more than 200 km) possibly explains the lack of influence of that glacial advance on the local flora, and the fact of not having found significant modifications on the profile of the cave and related geotopes. During this interval there could have been entrance of microthermal Patagonian elements, but this situation would not have meant floristic change in the megathermal shrubby vegetation.

Acknowledgments

To Dr. L.A. Borrero (CONICET), and Dr. W. Volkheimer (IANIGLA) for their opinion and comments, and to N. Horak (IADIZA) for the English version. To Antorchas Foundation (A-13740/1-43, A-13887/1-40), and to SeCTyP-UNCuyo and CONICET for the economic support. We appreciate the valuable suggestions of the anonymous reviewers.

References

Baumgartner, L.L., Martin, A.C., 1939. Plant histology as an aid in squirrel food-habits studies. Journal of Wildlife Management 3, 266–268.
Benzécri, J.P., 1973. L'analyse des données-II. L'analyse des correspondences. Dunod, Paris.
Betancourt, J.L., Van Devender, T.H., Martin, P.S. (Eds.), 1990. Packrat Middens. The Last 40,000 Years of Biotic Change. University of Arizona Press, Tucson.
Betancourt, J.L., Latorre, C., Rech, J.A., Quade, J., Rylander, K.A., 2000. A 22,000 year record of monsoonal precipitation from northern Chile's Atacama desert. Science 289, 1542–1546.
Braun-Blanquet, J., 1950. Sociología Vegetal. Estudio de las comunidades vegetales. Acme Agency, Buenos Aires.
Braun-Blanquet, J., 1979. Fitosociología. Bases para el estudio de las comunidades vegetales. Blume, Barcelona.
Cole, K., 1982. Late Quaternary zonation of vegetation in the eastern Grand Canyon. Science 217, 1142–1145.
D'Antoni, H., 1976. Paleoecología de la Gruta del Indio (San Rafael, Mendoza) y sus correlaciones. Ph. D. thesis. Fac. Cs. Nat. y Museo, Universidad Nacional de La Plata, Argentina.
D'Antoni, H., 1980. Los últimos 30 mil años en el sur de Mendoza, Argentina. In: III Coloquio sobre Paleobotánica y Palinología. Memorias. SEP INAR, México, pp. 83–108.
D'Antoni, H., 1983. Pollen analysis of Gruta del Indio. Quaternary of South America and Antarctic Peninsula 1, 83–103.
D'Antoni, H., Markgraf, V., 1977. Dispersión del polen actual en Argentina en relación con la vegetación. In: Presented at the III Coloquio sobre Paleobotánica y Palinología. Museo Nacional de Antropología, D.F. México.
Dacar, M., Giannoni, S.M., 2001. A simple method for preparing reference slides of seed. Technical Notes. Journal of Range Management 54 (2), 191–193.
Dusi, J.L., 1949. Method for the determination of food habits by plant microtechniques and histology and their application on cottontail rabbit food habits. Journal of Wildlife Management 13 (3), 295–298.
Gambier, M., 1995. Hallazgo de fauna extinta en Los Morrillos. Revista Ansilta 10, 16–20. San Juan.
García, A., 2003. On the coexistence of man and extinct Pleistocene megafauna at Gruta del Indio (Argentina). Radiocarbon 45 (1), 33–39.
Garcia, A., Lagiglia, H., 1999. A 30,000 year-old megafauna dung layer from Gruta del Indio (Mendoza, Argentina). Current Research in the Pleistocene 16, 116–118.
García, A., Martínez Carretero, E., 2010. Observaciones sobre la reconstrucción paleoambiental del Rincón del Atuel. In: Papú, O. (Ed.), Actas E-ICES 5. Comisión Nacional de Energía Atómica, Mendoza, pp. 129–133.
Heusser, C.J., 1983. Quaternary pollen record from Laguna de Tagua Tagua, Chile. Science 219, 1429–1432.
Heusser, C.J., 1990. Ice age vegetation and climate of subtropical Chile. Palaeography, Palaeoclimatology, Palaeoecology 80, 107–127.
Holechek, J.L., 1982. Sample preparation techniques for microhistological analyses. Journal of Range Management 35 (2), 267–268.
Johansen, D.A., 1940. Plant Microtechnique. McGraw-Hill, Book Co., New York, N.Y.
Kiage, L., Liu, K., 2006. Late Quaternary paleoenvironmental changes in East Africa: a review of multiproxy evidence from palynology, lake sediments, and associated records. Progress in Physical Geography 30 (5), 633–658.
Lagiglia, H., 1956. Estudios arqueológicos en el Rincón del Atuel, Dto. de San Rafael (Mza.). Anales de Arqueología y Etnología XII, 229–288. Mendoza.
Lagiglia, H., 1977. Arqueología y ambiente natural de los valles del Atuel y Diamante. Ph. D. thesis. Fac. Cs. Nat. y Museo, Universidad Nacional de la Plata.
Latorre, C., Betancourt, J., Rylander, K., 2001. Cambios vegetacionales durante los últimos 45.000 años en el Desierto de Atacama (22°–24°S), norte de Chile. In: XIII Reunión Anual de la Sociedad Botánica de Chile. Gayana, vol. 58(1).
Latorre, C., Betancourt, J., Rylander, K., Quade, J., 2002. Vegetation invasions into absolute desert: a 45,000 yr rodent midden record from the Calama-Salar de Atacama basins, northern Chile (lat 22°–24° S). GSA Bulletin 114 (3), 349–366.
Latorre, C., Betancourt, J., Arroyo, M.T.K., 2006. Late Quaternary vegetation and climate history of a perennial river canyon in the Río Salado basin (22°S) of Northern Chile. Quaternary Research 65, 450–466.
Long, A., Martin, P., Lagiglia, H., 1998. Ground Sloths and humans at Gruta del Indio. Argentina. Radiocarbon 40 (2), 693–700.
Markgraf, V., Dodson, J.R., Kershaw, A.P., Mcglone, M.S., Nicholls, N., 1992. Evolution of late Pleistocene and Holocene climates in the circum-South Pacific land areas. Climate Dynamics 6, 193–211.
Martínez Carretero, E., 2004. La Provincia Fitogeográfica de La Payunia. Boletín Sociedad Argentina de Botánica 39 (3–4), 195–226.
Martínez Carretero, E., García, A., Dacar, M., 2009. Evidence of late-Pleistocene Monte formation in central west Argentina. Current Research in the Pleistocene 26, 139–141.
MC Cune, B., Grace, J., 2002. Analysis of Ecological Communities. MjM Software Design, United States of America.
Páez, M., Rojo, L., Navarro, D., Zárate, M., Quintana, F., Willie, M., Schäbitz, F., 2008. Late Holocene paleoenvironments in arid and semiarid regions of Argentina (33°–35° S and 50° S). In: 4th Alexander von Humboldt International Conference. The Andes: Challenge for Geosciences, Santiago de Chile.
Páez, M.M., Navarro, D., Rojo, L.D., Guerci, A., 2010. Vegetación y paleoambientes durante el Holoceno en Mendoza. In: Zárate, M., Gil, A., Neme, G. (Eds.), Condiciones paleoambientales y ocupaciones humanas durante la transición Pleistoceno-Holoceno y Holoceno de Mendoza. Sociedad Argentina de Antropología, Buenos Aires, pp. 175–210.
Pearson, O.P., Ralph, C.P., 1978. The Diversity and Abundance of Vertebrates along an Altitudinal Gradient in Peru. In: Memorias del Museo de Historia Natural "Javier Prado", vol. 18, pp. 5–80.
Phillips III, A., 1984. Shasta ground sloth extinction. Fossil packrat midden evidence from the western Grand Canyon. In: Martin, P.S., Klein, R. (Eds.), Quaternary Extinctions. A Prehistoric Revolution. The University of Arizona Press, Tucson, pp. 148–158.
Poinar, N.H., Hofreiter, M., Spaulding, W.G., Martín, P.S., Stankiewicz, A., Bland, H., Evershed, R., Possnert, G., Pääbo, A., 1998. Molecular Coproscopy: dung and diet of the extinct ground slot *Nothrotheriops shastensis*. Science 281, 402–406.
Polyak, V., Asmeron, Y., Burns, S.J., Lachniet, M., 2012. Climatic backdrop to the terminal Pleistocene extinction of North American mammals. Geology 40 (11), 1023–1026.
Porter, S., 1981. Pleistocene glaciation in the southern Lake District of Chile. Quaternary Research 16, 263–292.
Puig, S., Videla, F., Cona, M., Monge, S., Roig, V., 1998. Diet of the Mountain vizcacha (*Lagidium vizcacha* Molina, 1782) and food availability in northern Patagonia, Argentina. Zeitschrift für Saugetierkunde 63, 228–238.
Rabassa, J., Clapperton, C.H., 1990. Quaternary glaciations of the southern Andes. Quaternary Science Review 9, 153–174.
Raunkjaer, C., 1937. Plant Life Form. Claredon Press, Oxford.
Roig, F., 1989. Ensayo de detección y control de la desertificación en el W de la ciudad de Mendoza desde el punto de vista de la vegetación. In: Roig, F. (Ed.), Detección y control de la desertificación. Conferencias, trabajos y resultados del Curso Latinoamericano. UNEP-IADIZA-CONICET, Mendoza, pp. 196–232.
Roig, F., Martínez Carretero, E., 1998. La vegetación puneña en la provincia de Mendoza, Argentina. Phytocoenologia 28 (4), 565–608.
Roig, F., Martinez Carretero, E., Méndez, E., 1995. Mapa de Vegetación de la Provincia de Mendoza. Multequina 5. addenda.
Semper, J., Lagiglia, H., 1968. Excavaciones arqueológicas en el Rincón del Atuel (Gruta del Indio) Departamento de San Rafael (Mendoza). Revista Científica de Investigaciones 1 (4), 89–158.
Thompson, R.S., Van Devender, T.R., Martin, P.S., Foppe, T., Long, A., 1980. Shasta ground sloth (*Nothotheriops shastense* Hoffstetter) at Shelter Cave,

New Mexico: environment, diet, and extinction. Quaternary Research 14, 360–376.
Van Devender, T.R., Spaulding, W.G., 1979. Development of vegetation and climate in the southwestern United States. Science 204, 701–710.
Wang, X., Zhongli, D., Peng, P., 2012. Changes in fire regimes on the Chinese Loess Plateau since the last glacial maximum and implications for linkages to paleoclimate and past human activity. Palaeography, Palaeoclimatology, Palaeoecology 315–316, 61–74.
Webb, R.H., Betancourt, J.L., 1990. The spatial and temporal distribution of radiocarbon ages from packrat middens. In: Betancourt, J.L., Van Devender, Th., Martin, P.S. (Eds.), Packrat Middens. The Last 40,000 Years of Biotic Change. University of Arizona Press, Tucson, pp. 59–84.
Williams, O.B., 1969. An improved technique for identification of plant fragments in herbivore feces. Journal of Range Management 22, 51–52.
Zárate, M., Fasano, J.L., 1989. The Plio–Pleistocene record of the central eastern Pampas, Buenos Aires province, Argentina: the Chapadmalal case study. Paleogeography, Paleoclimatology, Paleoecology 72, 27–52.
Zárate, M., Páez, M., 2002. Los paleoambientes del Pleistoceno-Holoceno en la Cuenca del Arroyo La Estacada, Mendoza. In: Trombotto, D., Villalba, R. (Eds.), IANIGLA, 30 Años de Investigación Básica y Aplicada en Ciencias Ambientales. Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina, pp. 117–121.
Zuloaga, F., Morrone, O. (Eds.), 1996. Catálogo de las Plantas Vasculares de la República Argentina. Missouri Botanical Garden, Missouri.