



## The significance of modern diatoms as paleoenvironmental indicators along an altitudinal gradient in the Andean piedmont of central Argentina

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### ABSTRACT

The objectives of this study were to (a) analyze the distribution pattern of diatom assemblages in freshwater systems from central-western Argentina, (b) investigate the key climatic and limnological factors affecting the species distributions, and (c) evaluate the extent and limitations of diatoms as Quaternary paleoenvironmental indicators in the area. Diatoms were sampled and physical and chemical variables were quantified in a total of 45 lotic and lentic sites. Altitude, annual precipitation, and summer (January) temperature data were obtained from a world climate database. Previously published data from an adjacent region was incorporated into the modern dataset. Environmental variables significantly influencing diatom assemblage composition were identified through partial canonical correspondence analyses (CCAs). In order to assess the degree of analogy between modern and fossil assemblages, the modern analog technique (MAT) was applied. Diatom taxa showed distinct abundance patterns in relation to altitude, with a shift from communities dominated by periphytic and benthic taxa in lower sites to communities dominated by small benthic–tychoplanktonic taxa in high elevated waterbodies. The pH was the strongest variable explaining the variance within the diatom dataset, followed by log-conductivity and summer air temperature. The comparison of modern diatom assemblages with fossil sequences allowed reconstruction of the evolution of shallow, lentic and vegetated habitats. A good analogy between modern and Pleistocene diatom assemblages was found. The strong relationship between diatoms and climate-driven environmental variables, such as pH, conductivity and summer temperature, enhances the importance of the diatom floras as paleoclimatic indicators in the area and encourages future development of quantitative inference models for the region.

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### 1. Introduction

Diatoms have played a major role in the reconstruction of past climate changes, being used as proxy indicators to infer Holocene climate variability in every continent (Mackay et al., 2003). The majority of recent diatom-based paleoclimatological studies apply quantitative multivariate techniques to reconstruct past environmental variables related to climate, either directly, such as surface-water temperature (e.g. Vyvermann and Sabbe, 1995; Rosén et al., 2000; Bigler and Hall, 2002) and air temperature (e.g. Korhola et al., 2000), or indirectly by reconstructing, for example, salinity (e.g. Fritz et al., 1991; Laird et al., 1996; Gasse et al., 1997; Verschuren et al., 2000), dissolved organic carbon (DOC; Pienitz et al., 1999), conductivity (e.g. Davies et al., 2002), and pH (e.g. Psenner and Schmidt, 1992; Koinig et al., 1998). Studies based on qualitative information provided by assessing changes in diatom species and assemblages, especially with respect to their habitat,

survival strategies and autoecologies, are also common (e.g. Smol, 1988; Bradbury et al., 2002). Reconstructions based on all these methods rely on the general assumption that the past environmental requirements of the fossil diatom taxa have remained similar to those of their closest living representatives. In this way, the environmental information obtained from living organisms can be used as analogs and extrapolated to the fossil record, particularly in Quaternary research.

Paleoclimatic reconstructions in Southern South America are mostly restricted to the Andes, while the eastern lowlands have been sparsely covered (Villalba et al., 2009). Diatom-based paleoclimatic studies are particularly scarce for central-western Argentina, an area characterized by the presence of numerous sedimentary alluvial successions of late Pleistocene and Holocene origin. Although a series of efforts focusing on reconstructing past climatic variability have recently been carried out in the area, they were based mainly in stratigraphic, sedimentological (Zárate and Mehl, 2008; Mehl, 2010; Tripaldi, 2010; Tripaldi et al., 2010), palynological (Páez et al., 2010), and malacological (De Francesco et al., 2007; De Francesco and Hassan, 2009) data. Despite the abundance and diversity of diatoms present in these sediments (De Francesco and Dieguez, 2006), no studies dealing with diatoms and their environmental significance have been conducted in the

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region. Moreover, the lack of information on the distribution and ecology of diatoms in modern environments of central-western Argentina significantly restricts the quality and extent of diatom-based paleo-environmental reconstructions in the area.

De Francesco and Hassan (2009) studied the distribution of mollusks in a combined lotic–lentic dataset of 45 sites from central-western Argentina (Mendoza and San Luis Provinces) and analyzed their usefulness as modern analogs of Pleistocene and Holocene mollusk assemblages from the region. In the present contribution, the distribution of modern diatoms in the same 45 sites was analyzed and compared with fossil diatom assemblages in the mollusk-bearing sediments described by De Francesco and Hassan (2009), in order to assess and compare their paleoecological significance. In particular, the present work aims to: (a) analyze the distribution pattern of diatom assemblages in freshwater systems, (b) investigate the key climatic and limnological factors affecting the species distributions, and (c) compare Quaternary and modern diatom assemblages in order to reconstruct past habitats and to evaluate the value of diatoms as paleobioindicators in the area.

## 2. Study area

The study area lies within the South American Arid Diagonal, a region considered to have been climatically sensitive to the latitudinal shifts of the Pacific and Atlantic anticyclonic centers during the late Pleistocene and Holocene (Abraham de Vazquez et al., 2000). The climate of the region is semiarid with a main annual rainfall of 250 mm in the eastern piedmont (Capitanelli, 2005). Regionally, the area is cut across by several fluvial systems (Tunuyán, Diamante, and Atuel rivers) with their headwaters located in the high Andes Cordillera (Fig. 1). The

river water discharges depend mainly on glacial melting and winter precipitation of Pacific origin. When reaching the piedmont, the rivers form very extensive and complex alluvial fans that are well exposed for several kilometers along river banks (Zárate, 2002).

The sampling area extends from a height of about 2100 m a.s.l. in the Andean Cordillera to 400 m a.s.l. in the eastern plains (see De Francesco and Hassan, 2009). The region is characterized by a predominance of fluvial environments (rivers, streams, and springs), with a few isolated natural lakes (e.g., Laguna Blanca, Laguna Llancanelo, Laguna Sosneado), and artificial lentic environments (e.g., Presa del Tigre and Presa Nihuil dams). Salt mines are also present locally (e.g., Salinas Diamante, Salina La Horqueta).

## 3. Materials and methods

### 3.1. Modern dataset

In total, 45 sites were selected to represent the maximum heterogeneity of aquatic environments in the area (Fig. 1), that is, the whole range of variation in altitude, morphology, substrate, and flow (e.g., streams, rivers, shallow lakes, ponds, springs, dams and canals). The basins of Río Tunuyán, Río Diamante, Río Atuel, and Río Grande were included. At each site, current velocity, water temperature, pH, and conductivity were quantified. Current velocity was measured using a neutrally buoyant sphere and calculating the time it took the sphere to move 5 m. Temperature, pH, and conductivity were measured with field instruments. Aquatic vegetation cover at each sampling site was estimated visually, and a nominal variable was erected for statistical purposes (0 = no vegetation, 1 = sparse vegetation cover, and 2 = dense vegetation cover). One subsurface water sample (1 L) was

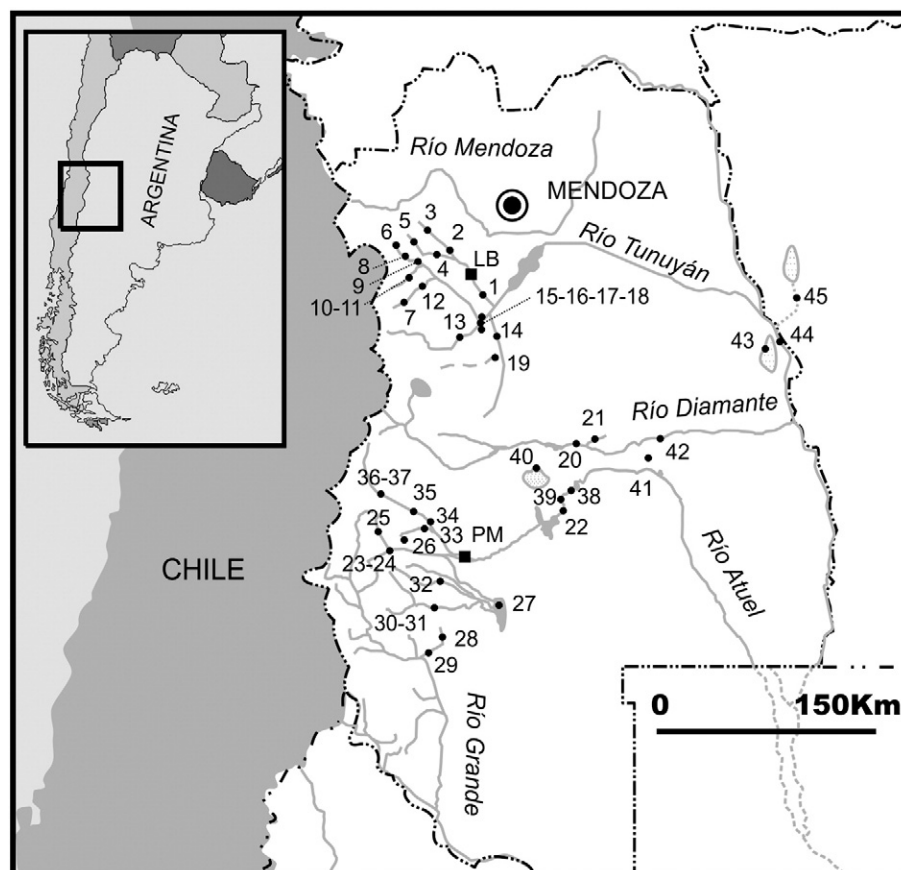


Fig. 1. Location map of modern (circles) and Quaternary (squares) study sites in central-western Argentina.

taken at each site to assess for concentrations of nitrate ( $\text{NO}_3^-$ ), phosphate ( $\text{PO}_4^{3-}$ ), and silica ( $\text{SiO}_2$ ) following standard methods (APHA, 1992) within fifteen days of collection. A subsample (ca. 0.5 kg) was taken for grain size analysis (using the dry-sieving technique) and organic content. The former was quantified as the proportion of gravel (>2 mm in diameter), coarse sand (2 mm–500  $\mu\text{m}$ ), medium sand (250–499  $\mu\text{m}$ ), fine sand (125–249  $\mu\text{m}$ ), very fine sand (62–124  $\mu\text{m}$ ), and mud (silt and clay, <62  $\mu\text{m}$ ). The organic content of each sample was estimated using the loss-on-ignition method (LOI) for 4 h at 550 °C and water content was calculated by drying the sediment for 24 h at ca. 105 °C (Heiri et al., 2001). Altitude was recorded for each sample and general precipitation and summer (January) temperature values were derived from the climate database WorldClim (Hijmans et al., 2005) using the DivaGis 7.1.7.2 program (Hijmans et al., 2009). This climate database contains values of altitude, monthly precipitation and temperature for a  $0.5^\circ \times 0.5^\circ$  grid, and allows plotting monthly and annual values at that scale.

Samples for diatom analysis were collected with 20 mm diameter  $\times$  100 mm length plastic tubes from the littoral zone of each site. The top 1 cm of sediment was scraped with a spatula and placed into 100 mL plastic vials. In streams with stony beds, sampling was performed by collecting the surface sediment and all stones present in a  $10 \times 10$  cm square. The epilithon was removed from the surface of large stones with a toothbrush. In the laboratory, 5 g of dry sediment was oxidized with hydrogen peroxide (30%) and cleaned with hydrochloric acid (10%) followed by repeated washing with distilled water until reaching neutral pH, and diluted to a total volume of 100 mL. After complete homogenization, a subsample was transferred to a coverslip and air-dried. Permanent drop slides were mounted with Naphrax®. On each slide at least 300 diatom valves were counted in random transects at  $1000\times$  magnification. Diatom species were identified according to standard floras (Krammer and Lange-Bertalot, 1986, 1988; Rumrich et al., 2000; Lange-Bertalot, 2001).

Additionally, diatom and environmental data from 10 shallow lakes previously studied in the adjacent La Pampa province (Espinal region) were integrated to the current dataset in order to increase its accuracy and regional representativity. For details on the location of the sites and the methodologies applied see Hassan et al. (2012).

### 3.2. Fossil datasets

In order to assess the paleoenvironmental significance of modern diatoms, the dataset was used to interpret fossil diatom assemblages from a Pleistocene (La Bomba; De Francesco et al., 2007) and a Holocene (Puesto Moya; De Francesco and Dieguez, 2006) alluvial succession from Mendoza province. The La Bomba (LB) succession is located in the proximity of Río Tunuyán, whereas Puesto Moya (PM) is situated in southern Mendoza (Fig. 1).

#### 3.2.1. La Bomba (Pleistocene)

This alluvial succession ( $33^\circ 28' \text{ S}$ ,  $69^\circ 03' \text{ W}$ ) crops out on the right margin of the Arroyo La Estacada, a tributary of Río Tunuyán (in the area of modern sites 1 and 2; Fig. 1). The succession was analyzed in detail by De Francesco et al. (2007). The stratigraphic section, mainly composed of fine sands, interbedded with levels of silty clays and organic matter, records the interval between ca. 35  $^{14}\text{C}$  ka years B.P. and 31  $^{14}\text{C}$  ka years B.P. (Table 3) and has a total height of 3 m. Samples for fossil diatom analysis were collected from the main sedimentological units (De Francesco et al., 2007), which included 14 discrete levels.

#### 3.2.2. Puesto Moya (Holocene)

This alluvial succession crops out on the right bank of the Río Atuel in southern Mendoza ( $35^\circ 15' \text{ S}$ ,  $69^\circ 14' \text{ W}$ ), in the proximity of Laguna Llanquanelo, in an area of broad meandering sections. Mollusk assemblages were previously analyzed in detail by De Francesco and Dieguez (2006) and De Francesco and Hassan (2009). The section

has a total height of 4.67 m, of which only the uppermost 1.3 m was sampled for diatom analysis at 10 cm intervals that included 12 discrete levels. These levels covered the interval between ca. 2890 and 790  $^{14}\text{C}$  years B.P. (Table 3). For further information on stratigraphy and mollusk paleoecology see De Francesco and Dieguez (2006).

### 3.3. Data analyses

Standard product–moment correlation analyses were conducted to identify strongly intercorrelated environmental variables, allowing some of them to be omitted from subsequent statistical analyses. To correct their skewed distributions, conductivity and LOI data were log transformed, as  $\log(x+1)$ . Diatom relative abundance data were square root transformed prior to statistical analyses in order to stabilize their variances (Bigler et al., 2006).

In order to determine whether a unimodal or linear response model was the most appropriate for the dataset, the gradient length of the first canonical axis was calculated through detrended correspondence analysis (DCA). In general, if the gradient length is greater than 2 standard deviation (SD) units, a unimodal response model is considered more appropriate. A linear response model is more suited to a gradient length smaller than 2 SD units. Since the gradient length for the training set was of 5.88 SD units, a unimodal model, i.e. canonical correspondence analysis (CCA, ter Braak, 1986), was used to analyze the relationship between diatom assemblage composition and environmental variables. A series of partial CCAs, run with one explanatory variable at a time, was used to separate the total variation in diatom data into components that represent the unique contributions of individual environmental variables, the contribution of covariance between variables and the unexplained variance (Bocard et al., 1992). The percentage variance explained by each variable was calculated, and the statistical significance was assessed by ANOVA permutation tests (Legendre and Legendre, 1998; Oksanen et al., 2011). CCA was then performed based on the whole set of significant variables.

Diatom zones in the fossil sequences were defined using constrained hierarchical clustering based on Bray–Curtis distance matrices, with clusters constrained by sample order. The statistical significance of the diatom zones was assessed through the broken stick model (Bennett, 1996). DCA results were also used to estimate species turnover through the fossil sequences (Eilertsen et al., 1990). DCA calculates the length of the species gradients (DCA axis 1 scores), which describe the degree of species turnover, with half change in species composition occurring at approximately 1.0–1.4 standard deviation (SD) units, and complete turnover of species indicated by gradient lengths higher than 4 SD (Heino and Soininen, 2005). The modern analog technique (MAT) was applied in order to assess the degree of analogy between modern and fossil assemblages. MAT is useful for detecting fossil samples that have close modern analogs within the available modern training set. The basic idea is to compare numerically, using the squared chord distance (SCD) as the dissimilarity measure, the fossil assemblages with the ten most similar modern samples. A critical value with which to compare the fossil samples is determined by calculating the mean minimum dissimilarity coefficient (DC), and the 90% confidence interval for the modern samples (i.e. each sample in the calibration set is compared with all other modern samples to determine the sample to which it had a minimum DC). Any fossil samples with minimum DCs falling within the extreme 10% range of the modern dataset were deemed to have a very poor or no modern analog (Laird et al., 1998). Finally, CCA based on modern samples with fossil samples kept passive were run in order to identify the main environmental gradients influencing the composition of fossil assemblages with modern analogs.

All analyses and graphs were performed using the software R version 2.12.2 (R Development Core Team, 2011), including the packages “vegan” version 1.17–8 (Oksanen et al., 2011), and “rioja” version 0.5–6 (Juggins, 2009).

**Table 1**  
 Values obtained for environmental variables in the 45 sampling sites. Cond: conductivity (mS/cm). T: water temperature (°C). Depth (cm). Cu: current velocity (m s<sup>-1</sup>). Veg: vegetation cover. Hard: hardness (mg L<sup>-1</sup> of CaCO<sub>3</sub>). Hum: humidity (%). LOI: organic content (%) estimated using the loss-on-ignition method. Categories of grain size (gravel, CS: coarse sand, MS: medium sand, FS: fine sand, VFS: very fine sand, and mud) are expressed in %. Concentrations of ions are expressed in mg L<sup>-1</sup>. Alt: altitude (m), Prec: mean annual precipitation (mm), SumT: summer temperature (°C).

Site	Cond	pH	T	Depth	Cu	Veg	Cl <sup>-</sup>	SO <sub>4</sub> <sup>2-</sup>	NO <sub>3</sub> <sup>-</sup>	PO <sub>4</sub> <sup>3-</sup>	F <sup>-</sup>	CO <sub>3</sub> <sup>2-</sup>	HCO <sub>3</sub> <sup>-</sup>	SiO <sub>2</sub>
1—A° La Estacada	1.15	8.16	21.2	33	0.30	0	66.0	610.0	14.80	0.21	0.54	0.0	216.3	46.4
2—A° Puente El Zampal	1.41	8.24	16.7	34	0.30	0	112.0	795.0	7.93	0.10	1.69	0.0	370.0	63.3
3—A° Puente Roto	1.40	8.31	25.8	43	0.60	0	112.0	650.0	10.00	0.12	1.70	0.0	216.3	34.0
4—A° Guajardino	1.01	8.05	20.7	27	0.55	1	66.0	455.0	11.34	0.04	1.93	0.0	340.0	18.5
5—A° Guajardino (nac.)	0.33	8.25	13.5	6	0.00	2	13.1	123.0	6.80	0.01	1.45	0.0	123.6	10.7
6—Río Las Tunas	0.30	8.25	22.8	25	1.50	0	13.1	127.0	0.00	0.00	0.67	0.0	69.5	10.8
7—A° Torrecillas 1	0.17	8.10	16.7	32	1.00	1	19.8	19.6	0.50	0.00	1.12	0.0	108.1	12.6
8—Río Las Tunas 2	0.10	7.89	19.9	125	0.00	2	59.3	376.0	0.50	0.00	2.89	0.0	340.0	62.8
9—Río Las Tunas 3	0.64	8.06	18.2	40	1.00	2	26.3	280.0	0.50	0.00	1.76	0.0	231.7	48.0
10—A° del medio 1	1.69	7.91	18.8	15	0.00	2	85.7	20.2	0.50	0.94	2.15	0.0	494.4	86.5
11—A° del medio 2	0.75	8.05	17.1	150	0.27	2	39.5	286.0	5.35	0.22	1.24	0.0	239.4	56.3
12—A° Torrecillas 2	0.51	8.16	15.6	80	0.27	1	29.6	176.0	5.35	0.00	1.48	0.0	216.3	42.5
13—A° Vista Flores	1.21	7.87	16.0	6	0.10	1	145.0	525.0	0.50	0.21	0.70	0.0	409.4	61.4
14—Río Tunuyán	0.82	8.22	18.2	200	1.50	0	102.2	393.0	5.50	1.18	1.03	0.0	154.5	16.5
15—A° Guiñazu	0.74	8.10	16.5	49	0.43	2	26.3	324.0	0.00	2.54	1.54	0.0	301.2	48.7
16—A° Caroca	0.81	7.88	17.0	75	1.00	2	59.3	204.5	0.50	0.00	2.38	0.0	224.0	54.6
17—Acequia Claro	0.76	8.10	16.7	15	0.67	2	52.7	202.7	3.75	1.56	1.51	0.0	193.1	53.0
18—A° Claro	1.18	7.93	18.1	50	0.67	1	115.4	481.0	2.46	1.89	1.91	0.0	278.1	52.8
19—A° Yaucha	0.21	7.90	10.1	43	1.35	0	9.9	46.7	3.65	0.40	0.00	0.0	231.7	20.0
20—Presa del Tigre	0.71	7.71	19.0	20	0.38	2	85.7	315.0	0.00	0.17	1.62	0.0	131.3	12.7
21—A° Gaby	0.76	8.17	19.3	85	0.16	2	98.9	117.0	11.70	0.00	1.17	0.0	168.0	11.6
22—Presa Nihuil	1.16	8.04	18.3	20	0.00	2	165.0	67.8	3.75	0.00	1.17	0.0	168.0	11.0
23—Los Molles	0.79	7.81	21.6	26	0.00	2	115.4	68.8	4.97	0.00	1.55	0.0	594.0	34.5
24—Río Salado	2.05	7.85	14.9	150	1.00	0	646.4	17.8	3.23	0.00	1.45	0.0	92.7	9.7
25—Vertiente Molles	0.62	7.47	14.5	3	1.00	0	214.0	11.2	0.96	0.00	0.64	0.0	610.0	16.5
26—Niña Encantada	0.76	7.72	11.7	55	0.67	2	26.3	392.0	12.8	0.00	0.70	0.0	231.0	28.5
27—Llananelo	8.68	7.87	19.9	25	0.00	0	427.4	1670.0	1.41	0.00	2.42	0.0	139.0	5.6
28—A° Agua Botada	0.59	7.92	19.9	10	0.75	0	13.2	174.0	0.00	0.00	2.35	0.0	471.0	41.3
29—Baños Grande	1.05	7.34	14.3	15	0.00	2	58.2	253.2	0.00	0.00	0.76	0.0	410.0	35.5
30—Río Malargüe	0.55	8.00	16.5	150	0.35	0	49.4	156.0	0.00	0.17	0.75	0.0	285.0	42.6
31—Vertiente Malargüe	0.72	7.93	16.0	5	0.10	2	27.0	124.0	0.00	0.00	1.30	0.0	278.0	38.0
32—A° El Chacay	0.34	8.10	11.2	28	1.10	2	10.0	114.0	0.00	0.00	0.40	0.0	162.2	17.0
33—Laguna Blanca	3.97	8.04	15.6	60	0.00	0	465.0	90.0	0.00	0.00	4.88	0.0	84.0	21.2
34—A° Sosneado	0.79	8.11	14.3	14	0.17	2	39.5	256.0	0.00	0.00	0.69	0.0	160.0	34.4
35—Vertiente Sosneado	0.80	8.24	19.3	7	0.17	2	26.3	342.0	0.00	0.08	1.45	0.0	226.0	50.7
36—Laguna Sosneado 1	0.22	9.40	22.3	20	0.10	2	46.1	79.5	0.00	0.13	0.50	50.8	58.6	43.7
37—Laguna Sosneado 2	0.22	9.00	15.9	50	0.00	2	49.4	58.1	0.00	0.00	0.00	50.2	67.0	32.6
38—Vertiente Cañon	2.11	8.19	18.9	10	0.17	0	178.1	690.0	11.86	0.60	1.61	0.0	595.0	17.8
39—Río Atuel	1.47	7.55	19.8	50	0.67	0	185.0	692.0	0.00	0.00	0.61	0.0	243.0	22.2
40—Salinas Diamante	30.00	7.55	16.1	15	0.00	0	30000	51530	0.00	0.00	1.88	0.0	150.8	13.2
41—Las Aguaditas	1.86	7.81	15.5	50	0.10	2	335.7	680.0	1.37	0.00	0.52	0.0	360.0	37.8
42—Montecomán	1.40	8.11	18.4	150	0.67	0	234.1	4775.0	2.51	0.05	0.84	0.0	234.6	36.6
43—Salina La Horqueta	9.83	8.26	20.8	35	0.00	0	2440.0	4405.0	0.00	0.27	0.05	0.0	142.0	10.0
44—Río Desaguadero	1.70	8.17	19.9	150	0.40	0	442.0	118.0	0.00	0.30	0.00	0.0	217.8	16.4
45—A° Bebedero	16.00	7.66	20.6	20	0.00	0	7717.0	2140.0	0.00	0.02	1.39	0.0	150.8	72.7

Ca <sup>2+</sup>	Mg <sup>2+</sup>	Hard	Hum	LOI	Gravel	CS	MS	FS	VFS	Mud	Alt	Prec	SumT
44.0	64.3	378.0	19.98	1.90	76.24	2.77	1.19	2.97	6.23	10.59	860.11	290.07	30.5
49.7	125.7	648.0	21.67	2.02	76.24	2.77	1.19	2.97	6.23	10.59	923.91	291.35	30.3
38.3	114.0	571.0	20.01	1.65	76.24	2.77	1.19	2.97	6.23	10.59	936.82	291.19	30.3
35.6	48.7	292.0	20.80	1.19	41.51	5.31	11.42	18.51	11.76	11.47	927.29	294.15	30.4
10.0	38.1	184.0	57.87	7.87	0.00	0.00	25.55	25.57	24.02	24.85	1080.29	294.95	29.8
16.8	34.0	184.0	8.35	1.32	74.56	15.08	8.88	1.33	0.13	0.02	1143.94	313.55	29.1
12.0	17.7	104.1	20.00	1.70	63.35	9.51	7.72	9.88	5.12	4.42	1178.51	325.46	28.8
38.9	1.6	606.0	42.65	4.70	0.00	0.76	1.60	12.75	37.85	47.02	927.29	294.15	30.4
34.9	68.5	373.0	40.00	5.00	0.00	0.76	1.60	12.75	37.85	47.02	908.40	299.20	30.4
103.5	200.0	1095.0	40.97	7.99	17.95	8.23	18.93	17.84	16.19	20.85	932.93	304.17	30.2
22.0	63.8	321.0	68.61	5.31	0.00	0.93	13.48	24.31	23.09	38.19	932.93	304.17	30.2
22.2	79.0	385.0	27.01	2.37	0.00	0.00	0.05	2.16	26.40	71.39	943.61	305.98	30.1
33.8	88.0	451.0	41.78	7.81	3.79	1.84	6.88	19.93	19.30	48.25	965.35	325.49	29.8
21.2	68.0	336.0	20.81	0.85	52.15	0.29	2.13	17.04	18.34	10.05	892.96	309.13	30.3
23.2	43.6	240.0	37.89	4.27	7.80	10.23	20.14	26.36	16.54	18.92	868.19	296.22	30.4
28.2	83.8	420.0	46.22	3.53	8.05	5.21	14.61	19.73	18.43	33.96	871.48	297.95	30.4
23.2	27.6	173.0	35.80	2.55	8.80	6.91	13.27	25.46	19.72	25.83	874.35	301.60	30.4
28.5	50.4	281.4	35.80	2.55	8.80	6.91	13.27	25.46	19.72	25.83	874.35	301.60	30.4
17.2	28.1	160.0	20.74	0.88	0.00	0.57	15.70	50.96	24.47	8.29	973.86	340.97	29.6
20.5	63.1	314.0	9.92	1.00	74.56	15.08	8.88	1.33	0.13	0.02	914.45	329.29	30.0
35.1	58.8	333.0	24.34	3.95	0.45	3.74	7.56	35.08	30.52	22.64	863.36	332.00	30.1
76.3	105.6	630.0	10.55	1.15	74.56	15.08	8.88	1.33	0.13	0.02	1300.47	291.28	28.3
31.8	58.4	323.0	49.89	4.32	23.58	19.35	15.14	13.62	10.15	18.16	1938.09	551.37	23.7
62.4	52.5	375.0	22.80	1.74	0.00	0.59	22.80	57.20	14.21	11.78	1932.78	550.87	23.7
62.4	43.6	338.0	4.67	1.21	94.81	3.18	1.05	0.69	0.18	0.08	1956.42	561.20	21.4
133.0	1.08	337.0	47.58	3.33	23.58	19.35	15.14	13.62	10.15	18.16	2092.91	529.73	22.7
90.0	89.7	598.0	34.19	2.95	0.27	5.05	8.45	21.52	23.08	41.63	1336.05	233.34	28.4
16.0	53.2	262.0	9.92	0.65	61.60	26.34	8.14	3.30	0.41	0.21	1969.40	335.13	24.2
25.2	97.0	467.3	67.52	8.45	11.94	13.47	26.31	26.58	12.49	9.20	1593.40	328.37	26.0
27.2	42.2	244.0	21.33	2.23	63.34	9.51	7.73	9.88	5.12	4.42	1538.11	301.56	26.8
13.3	51.5	248.0	26.66	2.23	0.00	1.61	16.60	26.89	26.12	28.78	1537.62	301.30	26.8
5.97	44.0	198.0	7.61	0.96	64.81	8.08	6.85	10.13	4.29	5.83	1425.43	281.53	27.6
43.0	356.0	1546.6	19.46	0.94	22.20	8.31	34.65	34.39	0.22	0.21	1637.78	410.61	26.1
27.2	83.2	415.0	24.49	2.38	26.36	13.68	19.22	24.04	9.41	7.29	1612.77	389.67	26.2
36.5	60.5	343.6	17.09	1.69	26.69	11.64	12.69	26.69	13.14	7.14	1790.29	468.26	25.3
17.2	24.3	144.4	56.09	5.58	0.00	1.04	10.99	28.30	34.54	25.13	2112.55	618.47	22.0
18.0	26.2	154.4	64.74	5.84	3.24	7.12	14.88	22.90	25.12	26.74	2137.21	618.23	22.0
21.3	69.7	344.2	17.16	1.18	67.28	27.56	3.68	0.71	0.31	0.46	934.26	309.73	29.1
33.6	172.0	800.3	10.62	1.30	44.37	40.82	11.74	2.21	0.39	0.48	1068.24	304.53	29.1
260.0	1858.5	8391.6	20.38	1.37	5.27	7.28	6.86	18.78	41.04	20.77	1290.50	307.70	28.3
22.6	200.6	892.6	21.12	3.52	38.26	17.07	18.17	14.77	5.67	6.06	552.87	301.00	32.2
34.0	72.6	387.6	27.31	1.78	0.00	0.00	1.82	28.27	49.10	20.81	523.90	298.00	32.6
51.8	324.0	1481.5	15.94	1.04	9.24	16.30	7.54	34.95	22.54	9.42	411.07	375.47	33.6
29.8	158.4	734.5	27.06	1.95	0.00	0.00	0.05	2.36	29.79	67.80	410.08	416.30	33.6
345.0	695.0	3764.0	32.95	5.44	0.00	1.68	32.62	21.54	23.04	21.12	402.73	459.47	33.4

4. Results

4.1. Environmental variables

The standard product–moment correlation analysis indicated that altitude, precipitation and summer temperature were strongly correlated ( $p < 0.001$ ). Also, grain size variables, LOI and water content exhibited high correlations ( $p < 0.001$ ). Hence, the original matrix of 20 environmental variables (Table 1) was reduced to a set of 11. These were: log-conductivity, water temperature, pH, current velocity, vegetation cover,  $\text{NO}_3^-$ ,  $\text{PO}_4^-$ ,  $\text{SiO}_2$ , medium sand, log-LOI, and summer temperature. Data on  $\text{PO}_4^{3-}$  and  $\text{SiO}_2$  concentrations were not available for sites from La Pampa. Hence, these variables were excluded from CCA.

4.2. Modern dataset

Samples from three of the 45 Mendoza sites did not contain diatom frustules (sites 38, 39, and 41). A total of 191 taxa were recorded in the surface sediments of the remaining 42 sites. The distribution of the most abundant taxa (>2%) is presented along the altitudinal gradient (Fig. 2). Overall, diatom taxa showed distinct abundance patterns in relation to altitude. Species arrangement allowed the identification of taxa characteristic of lower altitudes, which were located on the left side of the diagram and also species typical of higher elevations, which were located on the right-hand side. Taxa such as *Cocconeis placentula*, *Tryblionella compressa*, *Halamphora* sp., *Navicula recens* and *Rhoicosphenia curvata* were common in the lower altitude sites. *Staurosirella pinnata*, *Staurosira venter*, *Hannaea arcus*, *Diatoma moniliforme*, *Achnanidium minutissimum*, and *Fragilaria* sp. were dominant in higher elevation waterbodies (Fig. 2).

In La Pampa province, diatom assemblages were less diverse and dominant taxa were strongly related to the environmental characteristics of the waterbodies (Hassan et al., 2012). *Hippodonta hungarica*, *Hantzschia amphioxys* and *Nitzschia amphibia* were highly abundant in lakes with conductivities below 1 mS/cm, while lakes with higher conductivities (3–15 mS/cm) were mainly dominated by *Planothidium delicatulum*, *Cyclotella meneghiniana* and *Amphora copulata* (see Hassan et al., 2012 for details).

Partial CCA showed that pH and log-conductivity were the strongest variables explaining variance respectively 4.57% and 4.1% ( $p = 0.005$ ) of the explained diatom variance within the joint Mendoza–La Pampa dataset (Fig. 3), followed by summer-T (3.15%,  $p = 0.025$ ). The rest of the environmental variables did not explain significant portions of the diatom variances and were excluded from the analysis. The CCA ordination of Mendoza and La Pampa samples based on the reduced set of 3 environmental variables was significant ( $p = 0.005$ ), and explained 16% of the diatom assemblage variance. The first two axes captured 7 and 11% of the variance in species composition, or 50 and 83% of the species–environment relationship, respectively (Table 2). The species–environment correlations of CCA axis 1 (0.93) and axis 2 (0.89) were high and indicated a strong relationship of diatom taxa to environmental variables.

The CCA ordination plot showed that the composition of surface sediment assemblages differed significantly between the Mendoza and La Pampa provinces (Fig. 3A). The first axis showed positive correlations with pH ( $r = 0.91$ ), and summer temperature ( $r = 0.51$ ). Accordingly, sites were ordinated along this axis following mainly pH and temperature gradients, with shallow lakes from La Pampa and Mendoza located towards the right and the center of the plot, respectively. The second was positively correlated with log-conductivity ( $r = 0.81$ ). Consequently, sites were ordinated along axis 2 following ionic strength

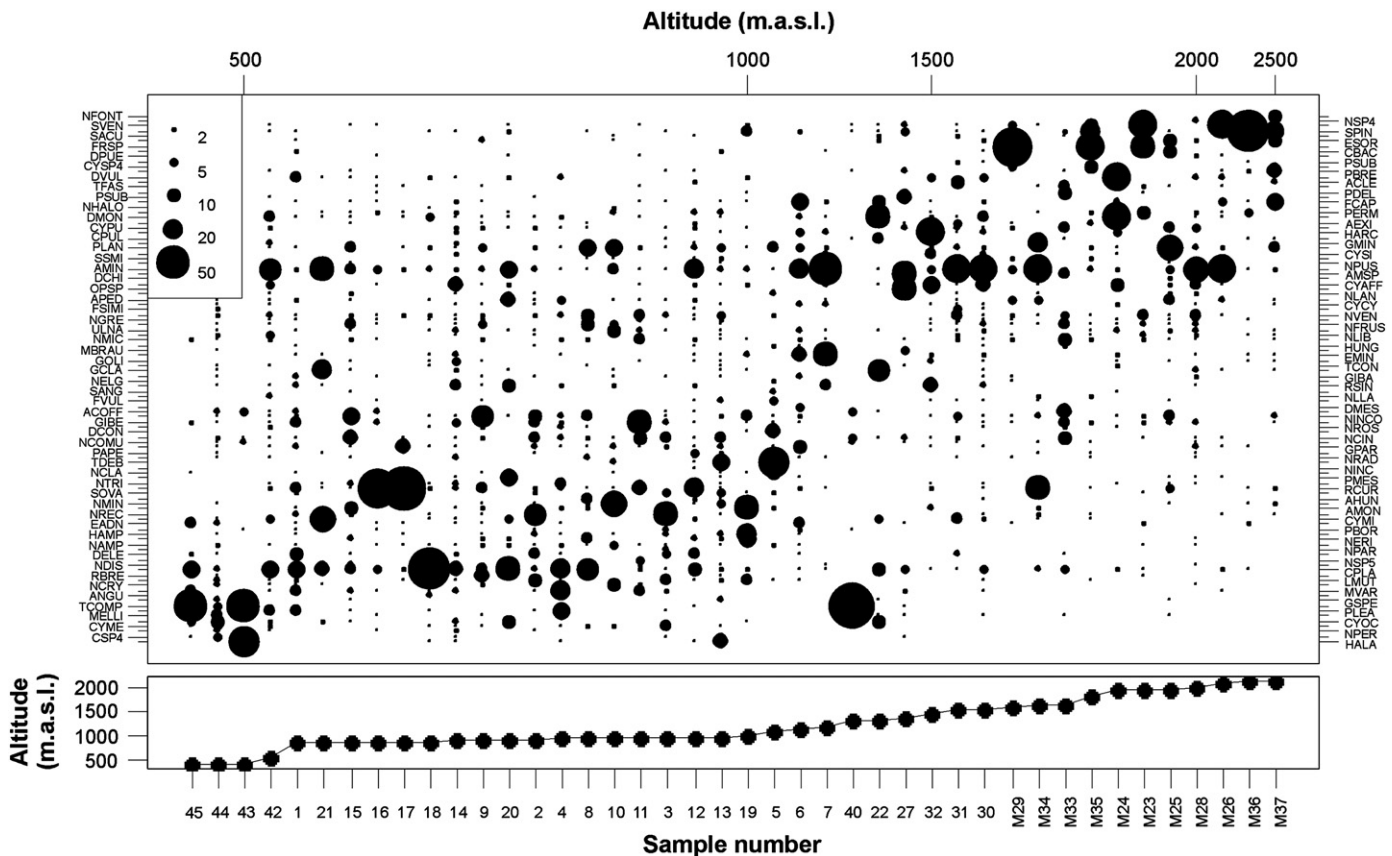
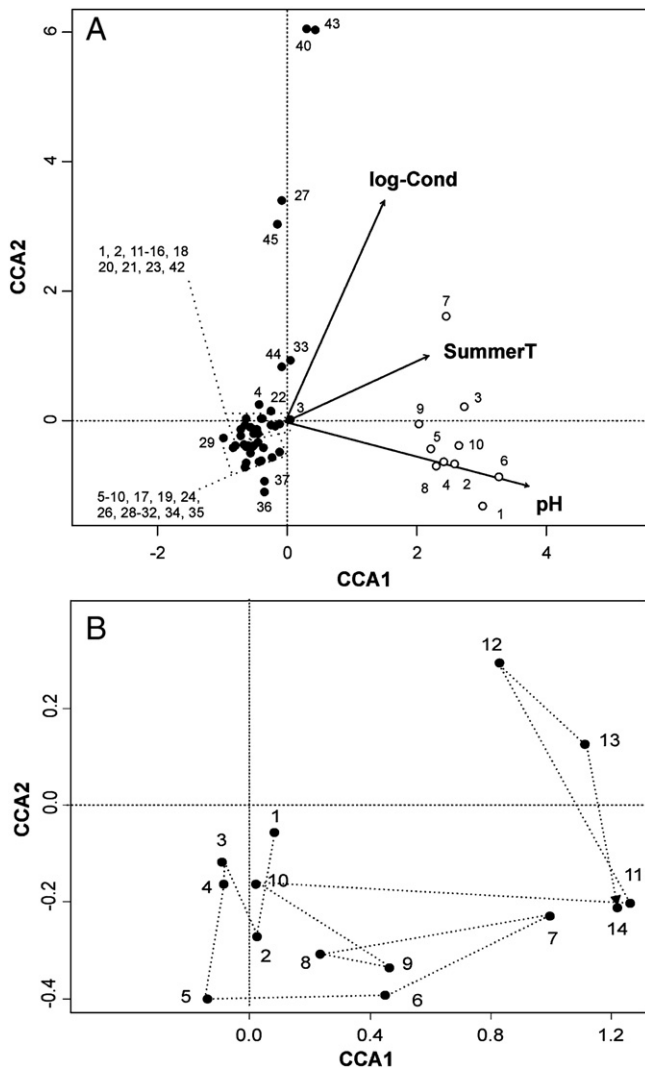


Fig. 2. Distribution of dominant diatom taxa along the studied altitudinal gradient. For diatom name abbreviations see Table 4.



**Fig. 3.** Canonical correspondence analysis (CCA) ordination plot showing (A) the relationship between environmental variables and sampling sites from Mendoza (black circles), and La Pampa (white circles), (B) passive ordination of fossil samples in the CCA ordination space of the modern dataset La Bomba section.

gradients, with saline and brackish sites located towards the top of the diagram (Fig. 3A).

### 4.3. Fossil diatom assemblages

#### 4.3.1. La Bomba (Pleistocene)

All samples analyzed in the La Bomba succession contained diatoms. A total of 58 taxa were identified, from which only 18 reached relative frequencies >2% in at least one sample and were plotted in Fig. 4.

Three significant diatom zones were defined according to cluster analysis (Fig. 4): the base of the sequence (LB1: up to 250 cm) was characterized by the dominance of the fresh/brackish taxa *Pseudostaurosira brevistriata* (epiphytic), and *Staurosira venter* (tychoplankton), accompanied by the brackish epiphytic *Planothidium delicatulum*. The composition of the assemblages was homogeneous in this zone, as indicated by the small range observed in DCA scores (−1.2 to −0.7). The middle section (LB2: 260–120 cm depth) was characterized by an increase in the percentages of *Cyclotella meneghiniana*, *Planothidium delicatulum* and *Gomphonema minutum*. Overall, this zone was dominated by brackish to brackish/freshwater taxa from a mixture of habitats (plankton, epiphytes and benthos). DCA scores were more variable in this zone, ranging between −0.7 and 0.5, indicating shifts in diatom composition

**Table 2**

Summary statistics for the first two axes of CCA, with the 3 selected environmental factors.

Ordination results	Axis	
	1	2
Eigenvalues ( $\lambda$ )	0.521	0.345
Species–environment correlation	0.935	0.895
Cumulative % variation of species data	6.9	11.0
Species–environment relationship	49.9	83.0
Sum of all $\lambda$	7.565	
Sum of all canonical $\lambda$	1.043	
Test of significance of the first canonical axis $p=0.005$		
Test of significance of all canonical axis $p=0.005$		

The significance of canonical axes is indicated based on 199 unrestricted ANOVA like permutations.

among samples. The top of the sequence (LB3) was also dominated by the brackish/freshwater planktonic species *C. meneghiniana*, but accompanied mainly by brackish benthic and epiphytic taxa such as *Navicula cincta*, *Halammphora coffaeiformis*, *Halammphora veneta* and *Nitzschia vitrea*. DCA scores were higher and remained relatively constant in this zone, and ranged between 1 and 1.5 SD, indicating that diatom assemblages remained fairly similar within this zone, but were very different from the ones at the base of the sequence.

According to MAT results, most La Bomba levels presented analogs in the modern dataset. Samples from the base of the sequence were analogous to sites 23 (Los Molles pond) and 26 (Niña Encantada lake) from Mendoza. Samples from the middle and top parts of the succession were analogous to lakes from La Pampa (10–La Brava and 1–El Cañadón). Passive ordination of La Bomba levels into the CCA plot showed a turning from freshwater and cooler conditions at the base of the sequence, to more saline and warm conditions at the top (Fig. 3B). According to these results, it can be stated that the La Bomba succession registered the evolution of a very shallow lake or pond of freshwater characteristics towards brackish and more alkaline conditions.

#### 4.3.2. Puesto Moya (Holocene)

Only 8 of the 12 samples analyzed from the Puesto Moya succession contained diatoms. These levels comprised the interval between 110 and 40 cm depth where a total of 77 diatom taxa were identified, with only 27 species reaching relative abundances >2% and being plotted in Fig. 5.

According to cluster analysis, four significant diatom zones were delimited (Fig. 5): the base of the sequence (PM1: between 110 and 95 cm) was dominated by the fresh/brackish aerophilic taxa *Nitzschia amphibia* and *Denticula elegans*, the brackish benthic *Diploneis chilensis*, and the brackish/freshwater epiphytic *Rhopalodia gibberula*. DCA scores were ca. −0.5. Zone 2 (PM2) comprised only one sample, at 80 cm depth, characterized by an increase in the relative abundance of the fresh/brackish tycho planktonics *Staurosira venter* and *Pseudostaurosira*

**Table 3**

Radiocarbon dates for (A) La Bomba, and (B) Puesto Moya profiles.

Depth (m)	Material	$^{14}\text{C}$ age B.P.	Lab. no.
(A)			
0.10	Mollusk shells	31,570 ± 440	AA61397
1.85	Mollusk shells	31,520 ± 520	AA61398
2.20	Mollusk shells	35,460 ± 740	AA61399
2.65	Mollusk shells	35,170 ± 670	AA61400
(B)			
1.10	Organic sediments	2890 ± 32	AA73239
1.00	Mollusk shells	1727 ± 34	AA73233
0.82	Organic sediments	1238 ± 33	AA73238
0.45	Organic sediments	904 ± 33	AA73237
0.40	Mollusk shells	793 ± 33	AA73234

**Table 4**  
List of dominant diatom species, their authorities and codes used in Fig. 2.

Diatom taxa	Authority
ACLE	<i>Karayevia clevei</i> (Grunow) Round & Bukhtiyarova
ACOFF	<i>Halamphora coffaeformis</i> (Agardh) Kützing
AEXI	<i>Achnanthes exigua</i> Grunow
AHUN	<i>Lemnicola hungarica</i> (Grunow) Round & Basson
AMIN	<i>Achnantheidium minutissimum</i> (Kütz.) Czarnecki
AMON	<i>Amphora montana</i> Krasske
AMSP	<i>Amphora</i> sp. Cholnoky
ANGU	<i>Aulacoseira granulata</i> var. <i>angustissima</i> Müller
APED	<i>Amphora pediculus</i> (Kütz.) Grunow
ATAC	<i>Halamphora atacamae</i> (Frenguelli) Levkov
CBAC	<i>Caloneis bacillum</i> (Grunow) Mereshkowsky
CPLA	<i>Cocconeis placentula</i> Ehrenberg
CPUL	<i>Ctenophora pulchella</i> (Ralfs) Williams and Round
CSP4	<i>Caloneis</i> sp. –
CYAFF	<i>Cymbella affinis</i> Kützing
CYCY	<i>Cymbella cymbiformis</i> Agardh
CYME	<i>Cyclotella meneghiniana</i> Kützing
CYMI	<i>Encyonopsis microcephala</i> (Grunow) Krammer
CYOC	<i>Cyclotella ocellata</i> Pantocsek
CYPU	<i>Cymbella pusilla</i> Grunow
CYSI	<i>Encyonema silesiacum</i> (Bleisch) Mann
CYSP4	<i>Cyclotella</i> sp. –
DCHI	<i>Diploneis chilensis</i> (Hustedt) Lange-Bertalot
DCON	<i>Diadesmis contenta</i> (Grunow ex Van Heurck) Mann
DELE	<i>Denticula elegans</i> Kützing
DMES	<i>Diatoma mesodon</i> (Ehr.) Kützing
DMON	<i>Diatoma moniliformis</i> Kützing
DPUE	<i>Diploneis puella</i> (Schumann) Cleve
DVUL	<i>Diatoma vulgare</i> Bory
EADN	<i>Epithemia adnata</i> (Kütz.) Brébisson
EMIN	<i>Encyonema minutum</i> (Hilse in Rabenhorst) Mann
ESOR	<i>Epithemia sores</i> Kützing
FCAP	<i>Fragilaria capucina</i> Desmazières
FRSP	<i>Fragilaria</i> sp. –
FSIMI	<i>Frankophila similioides</i> Lange-Bertalot & Rumrich
FVUL	<i>Frustulia vulgaris</i> (Thwaites) De Toni
GCLA	<i>Gomphonema clavatum</i> Ehrenberg
GIBA	<i>Rhopalodia gibba</i> (Ehr.) Müller
GIBE	<i>Rhopalodia gibberula</i> (Ehr.) Müller
GMIN	<i>Gomphonema minutum</i> (Agardh) Agardh
GOLI	<i>Gomphonema olivacea</i> (Horn.) Dawson ex Ross & Sims
GPAR	<i>Gomphonema parvulum</i> (Kützing)
GSPE	<i>Gyrosigma spencerii</i> (Bailey) Griffith and Henfrey
HALA	<i>Halamphora</i> sp. Rabenhorst
HAMP	<i>Hantzschia amphioxys</i> (Ehr.) Grunow
HARC	<i>Hannaea arcus</i> (Ehr.) Patrick
HUNG	<i>Hippodonta hungarica</i> (Grun.) Lange-Bertalot, Metzeltin & Witkowski
LMUT	<i>Luticola mutica</i> (Kütz.) Mann
MBRAU	<i>Mastogloia braunii</i> Grunow
MELLI	<i>Mastogloia elliptica</i> (Agardh) Cleve
MPUM	<i>Mastogloia pumila</i> (Cleve) Cleve
MVAR	<i>Melosira varians</i> Agardh
NAMP	<i>Nitzschia amphibia</i> Grunow
NCIN	<i>Navicula cincta</i> (Ehr.) Ralfs
NCLA	<i>Nitzschia clausii</i> Hantzsch
NCOMU	<i>Nitzschia communis</i> Rabenhorst
NCRY	<i>Navicula cryptocephala</i> Kützing
NDIS	<i>Nitzschia dissipata</i> Hustedt
NELG	<i>Placoneis elginensis</i> (Gregory) Cox
NERI	<i>Navicula erifuga</i> Lange-Bertalot
NFONT	<i>Nitzschia fonticola</i> (Grunow) Grunow
NFRUS	<i>Nitzschia frustulum</i> (Kütz.) Grunow
NGRE	<i>Navicula gregaria</i> Donkin
NHALO	<i>Craticula halophila</i> (Grunow) Mann
NINC	<i>Navicula incertata</i> Lange-Bertalot
NINCO	<i>Nitzschia inconspicua</i> Grunow
NLAN	<i>Nitzschia lanceolata</i> Smith
NLIB	<i>Navicula libonensis</i> Schoeman
NLLA	<i>Navicula cryptotenella</i> Lange-Bertalot
NMIC	<i>Nitzschia microcephala</i> Grunow
NMIN	<i>Eolimna minima</i> (Grunow) Lange-Bertalot
NPAR	<i>Nitzschia parvula</i> Smith
NPER	<i>Navicula peregrina</i> (Ehr.) Kützing
NPUS	<i>Nitzschia pusilla</i> Grunow

**Table 4** (continued)

Diatom taxa	Authority
NRAD	<i>Navicula radiosa</i> Kützing
NREC	<i>Navicula recens</i> (Lange-Bertalot) Lange-Bertalot
NROS	<i>Navicula rostellata</i> Kützing
NSP4	<i>Navicula</i> sp.4 –
NSP5	<i>Navicula</i> sp.5 –
NTRI	<i>Navicula tripunctata</i> (Müller) Bory
NVEN	<i>Navicula veneta</i> Kützing
OPSP	<i>Ophephora</i> sp. –
PAPE	<i>Pinnularia appendiculata</i> (Agardh) Cleve
PBOR	<i>Pinnularia borealis</i> Ehrenberg
PBRE	<i>Pseudostaurosira brevistriata</i> (Grun.) Williams & Round
PDEL	<i>Planothidium delicatulum</i> (Kütz.) Bukhtiyarova & Round
PERM	<i>Nitzschia perminutum</i> (Grunow) Peragallo
PLAN	<i>Planothidium lanceolatum</i> (Bréb. ex Kütz.) Lange-Bertalot
PLEA	<i>Pleurosira laevis</i> (Ehr.) Compère
PMES	<i>Pinnularia gibba</i> var. <i>mesogongyla</i> (Ehr.) Hustedt
PSUB	<i>Pseudostaurosira subsalina</i> (Hustedt) Morales
PSUB	<i>Pinnularia subcapitata</i> Gregory
RBRE	<i>Rhopalodia brebbisonii</i> (Ehr.) Müller
RCUR	<i>Rhoicosphenia curvata</i> (Kütz.) Grunow ex Rabenhorst
RSIN	<i>Reimeria sinuata</i> (Greg.) Kociolek & Stoermer
SACU	<i>Ulnaria acus</i> (Kütz.) Aboal
SANG	<i>Surirella angusta</i> Kützing
SOVA	<i>Surirella ovalis</i> Brébisson
SPIN	<i>Staurosirella pinnata</i> (Ehr.) Williams & Round
SSMI	<i>Stauroneis smithii</i> Grunow
STAC	<i>Stauroneis tackei</i> (Hust.) Krammer & Lange-Bertalot
SVEN	<i>Staurosira venter</i> (Ehr.) Hamilton
TCOMP	<i>Tryblionella compressa</i> (Bailey) Poulin
TCON	<i>Tryblionella constricta</i> Gregory
TDEB	<i>Tryblionella debilis</i> Arnott
TFAS	<i>Tabularia fasciculata</i> (Agardh) Williams & Round
ULNA	<i>Ulnaria ulna</i> (Nitzsch) Compère

*subsalina*, accompanied by the epiphytic *Halamphora* sp., and *Cymbella pusilla*. The DCA score of this sample was significantly higher (1.3), indicating a very different composition of diatom assemblages. PM3 was located between 85 and 65 cm depth, and dominated by the same diatom assemblages recorded in PM1. The DCA scores decreased again to negative values similar to those of the base (–0.5). The uppermost zone (PM4) grouped samples between 65 and 40 cm, and was characterized by a high diversity. Diatom assemblages were dominated by *Cocconeis placentula*, *Rhopalodia musculus*, *C. pusilla*, *Nitzschia perminuta*, *Navicula peregrina*, *Staurosirella pinnata*, *Cyclotella meneghiniana*, *D. elegans*, *Staurosira venter* and *Halamphora* sp. DCA scores were positive and ranged between 0 and 0.7.

The application of MAT analysis showed that only two fossil samples from Puesto Moya (levels 5 and 8) had analogs within the modern dataset. Their closest analogs were fluvial sites from Mendoza, such as the Desaguadero and Tunuyán rivers, followed by El Zampal and La Estacada streams. All these sites were characterized by low conductivities (<1.7 mS/cm) and values of pH~8.

## 5. Discussion

### 5.1. Modern diatom distribution

The composition of the diatom assemblages in the surface sediment samples of central-western Argentina showed environmentally driven patterns of change along the sampling transect. The most apparent trend observed was a shift from communities dominated by periphytic (e.g. *Cocconeis placentula* and *Rhoicosphenia curvata*) and benthic taxa (e.g. *Tryblionella compressa*) in the lower altitude sites to those dominated by small taxa considered to be benthic–tychoplanktonics (e.g. *Staurosirella pinnata*, *Staurosira venter*, *Hannaea arcus* and *Achnantheidium minutissimum*) in the higher elevation waterbodies. Several studies in mountainous regions have demonstrated a zonation



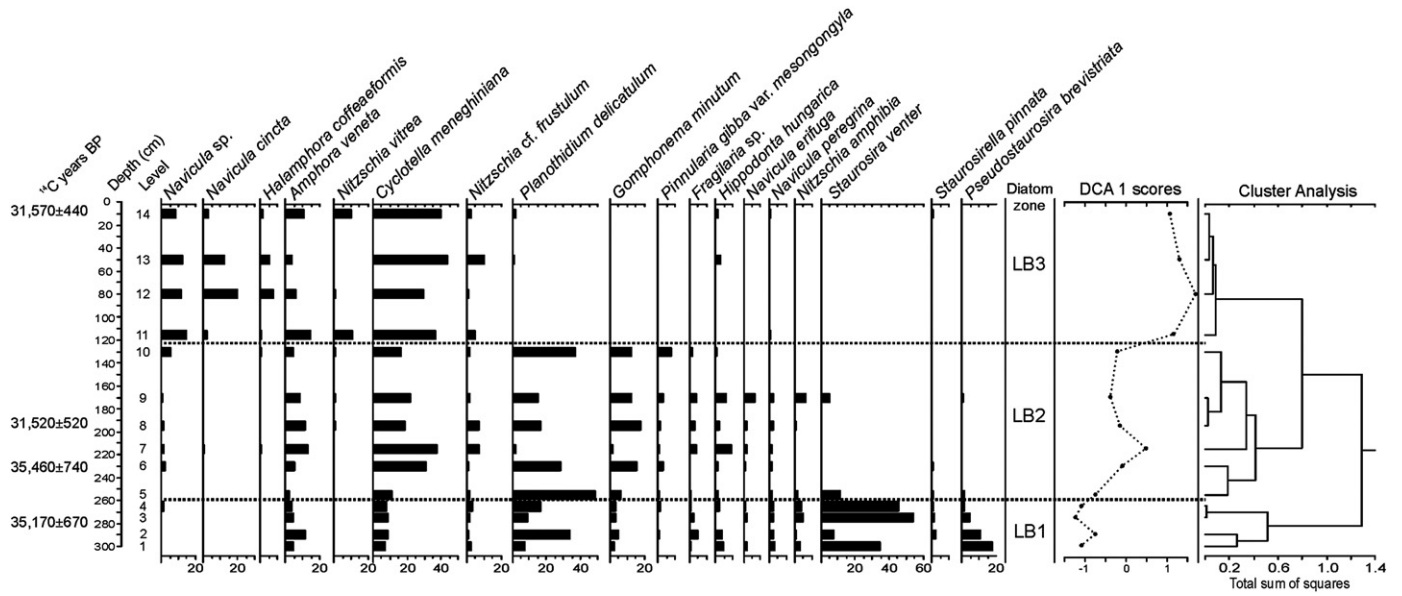


Fig. 4. Frequency diagram of diatom composition at La Bomba succession.

of diatom assemblages along altitudinal gradients, both in lotic and lentic environments. In studies performed in lakes, small periphytic and tychoplanktonic taxa such as *Staurosira construens*, *S. pinnata*, *Pseudostaurosira brevistriata* and *A. minutissimum* became dominant in lakes above 1000–1500 m a.s.l. (Lotter et al., 2010). Studies of streams showed that motile, epipellic or episammic diatoms such as *Navicula* spp. and *Nitzschia* spp. characterize lower altitude sites, whereas *Fragilaria* spp. and *Achnanthes* spp., which are attached to the substrate, characterized higher sites. Particularly *Hannaea arcus*, which was found in high altitude streams in the present study, has been related to cool fast flowing mountain streams (Hansen et al., 2006). Hence, increasing

abundance of fragilarioid taxa is a phenomenon frequently observed with increasing altitude, which is likely related to the fact that the growing season at high altitudes is considerably shorter due to prolonged snow and ice-cover. As ice-melt starts at the shores, these marginal areas provide suitable habitats for the development of fragilarioid taxa, which are more adaptable and competitive under harsh or fluctuating environmental situations (see Lotter et al., 2010 and references therein).

pH was the strongest environmental variable explaining a significant portion of the variance of diatom assemblages in our dataset. Although pH has been stated as one of the most important controlling

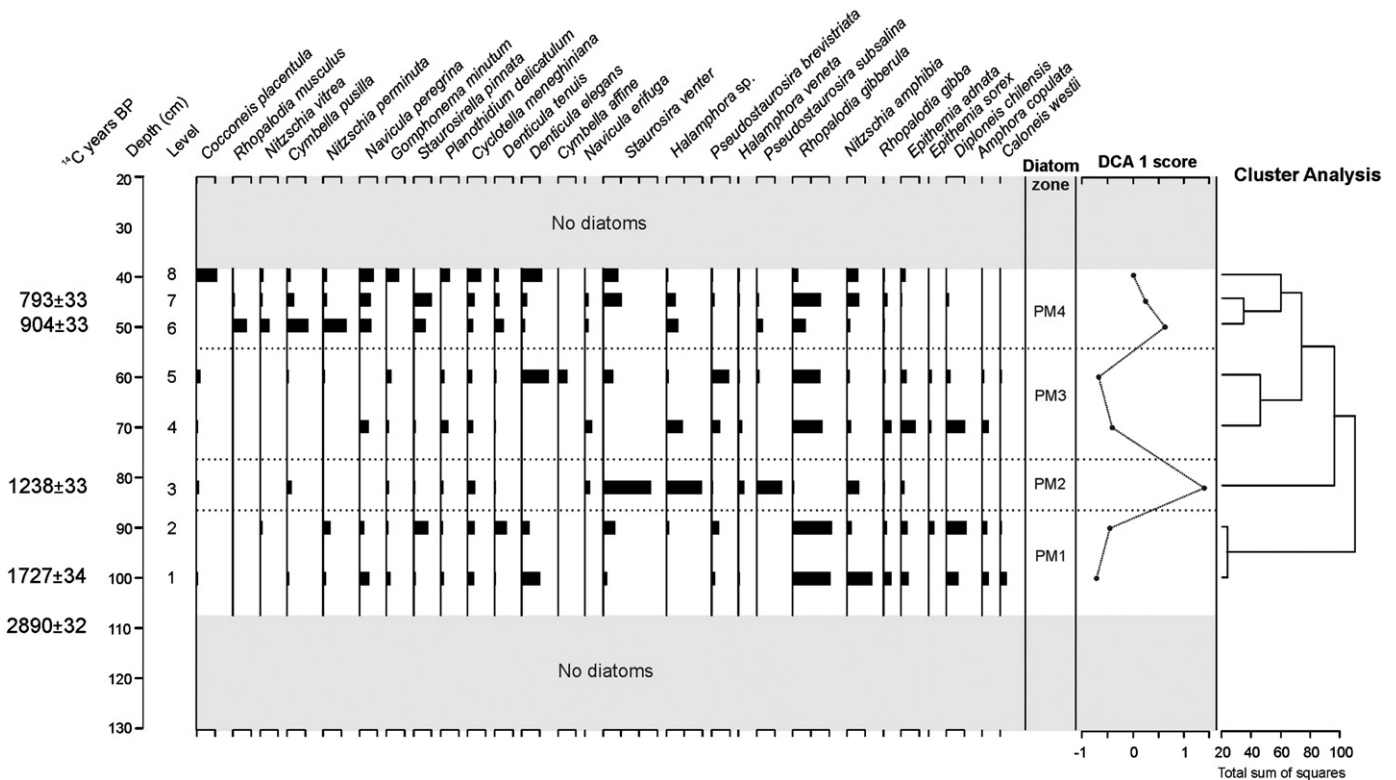


Fig. 5. Frequency diagram of diatom composition at Puesto Moya succession.

variables on species composition in freshwater systems, there is no detailed ecophysiological understanding on how it influences the growth and competitive abilities of individual diatom taxa. However, it is well known that pH controls many chemical and biochemical processes and reactions including the carbonate–bicarbonate balance in lakes, the availability of nutrients for algal uptake, the solubility of metals and the activity of enzymes such as the phosphatases (Battarbee et al., 2001). The strong relationship between pH and diatoms observed in central-western Argentina is in agreement with results of numerous previous studies (e.g. Gasse and Tekaiia, 1983; Davis and Anderson, 1985; Dixit et al., 1988; Weckström et al., 1997; Bigler and Hall, 2002; Denys, 2006; Ginn et al., 2007). As diatoms respond sensitively to changes in pH, diatom pH transfer functions have been commonly applied in acidification studies (e.g. Davis et al., 1983; Battarbee and Charles, 1987; Wäckstrom et al., 2003). More recently, this approach has also been used in climate change reconstruction (Boyle, 2008). The link between climate changes and pH is complex and depends on the prevailing source (Wolin and Stone, 2010). In lakes from central Argentina, water chemistry is mostly driven by evaporative processes (Drago and Quirós, 1996; Hassan et al., 2012), which lead to increased salt concentrations and pH values during drier and warmer periods (Echaniz et al., 2006, 2008). Hence, the strong relationship between diatom assemblages and pH found in this study poses an indirect approach to paleoclimate reconstructions. Quaternary fluctuations in pH values inferred from diatom analysis in central Argentina can thus be interpreted as indirect indicators of past moisture and temperature changes.

Conductivity was the second important environmental variable in explaining diatom variance in our dataset. Diatom-inferred salinity/conductivity methods are now being used extensively, separately or in combination with other proxy methods, for climate change studies (Battarbee, 2000). Diatoms are especially good indicators of salinity, and have been used extensively for the purposes of climate reconstruction from closed basin lake sediments (Fritz, 2007). As the ionic concentration and composition of inland water bodies are affected by changes in effective moisture (precipitation minus evaporation:  $P - E$ ), changes in the composition of diatom species that vary in their salinity tolerances provide a tool for the reconstruction of past climate (Fritz, 2007). Hence, in the last decade several diatom–salinity training sets for different geographical regions have been constructed for paleoclimatological purposes (Fritz et al., 1991; Gasse et al., 1995; Wilson et al., 1996; Gell, 1997; Reed, 1998). In the case of our dataset, the strong conductivity gradient displayed by lentic environments encourages the future development of training sets that allow developing quantitative diatom-based conductivity reconstructions in central Argentina.

Summer temperature also explained a significant portion of diatom assemblage variance. Given the large altitudinal range of our study sites, it is not surprising that altitude-correlated environmental parameters such as air or water temperature explained a high proportion of variance in the diatom datasets. This result is in agreement with previously published surface sediment datasets from several regions of the world (Pienitz et al., 1995; Vyvermann and Sabbe, 1995; Lotter et al., 1997; Weckström et al., 1997; Rosén et al., 2000; Bigler et al., 2006). However, as diatoms are not directly exposed to air temperatures during their life-cycle, the fact that air temperature explained more variance than water temperature measurements in our dataset constitutes an unexpected finding. Similar results have been reported in other datasets, and explained by the fact that single spot water temperature measurements provide a poor approximation of monthly mean values (Bigler et al., 2006). Despite this limitation, several diatom–air temperature transfer functions have been developed (Pienitz et al., 1995; Vyvermann and Sabbe, 1995; Lotter et al., 1997; Weckström et al., 1997; Rosén et al., 2000; Bigler et al., 2006). In fact, this development has been encouraged because performance statistics of the diatom–temperature transfer functions are usually comparable to those based

on other proxy-indicators (e.g., chironomids, pollen) from the same training-sets (e.g., Lotter et al., 1997; Rosén et al., 2000). However, the relationship between diatoms and climate may be complex and probably temperature is related to a combination of several other factors (Pienitz et al., 1995; Lotter et al., 1997). As a consequence, the diatom estimated optima and tolerances for air temperature should be considered as relative rather than absolute values.

## 5.2. Paleoenvironmental reconstructions

The radiocarbon chronology of the stratigraphic interval analyzed in the La Bomba section indicates that the water body developed during part of the Marine isotope stage 3, a period characterized by a general tendency to global warming (Espizúa, 1999). The diatom record of La Bomba, which suggests a relatively humid and mild interval, is in agreement with these regional patterns. This interpretation is also consistent with a mollusk-based reconstruction, which proposed the presence of a lentic habitat with nil or very low water velocity (De Francesco and Hassan, 2009). Moreover, the sedimentary evidence suggested a relatively low energy environment, which also agrees with the excellent preservation and high abundance of mollusk shells found in the profile (De Francesco et al., 2007). Furthermore, the diatom record showed a tendency for increasing ionic strength and temperature towards the top of the section, thus providing a more detailed record of environmental change during this period. Overall, the La Bomba section records the evolution of a shallow lentic water body, that shifted from freshwater and circumneutral pH at ca. 35,000 years B.P. to a brackish and alkaline environment towards 31,000 years B.P. This change in water chemistry would likely have been driven by an increase in temperature, as suggested by the strong relationship between diatoms and summer temperature, which would have in turn increased the evaporation rates leading to more saline conditions. The suggested increased evaporation rate is also supported by the  $\delta^{18}\text{O}$  values obtained from fossil mollusk shells, which showed more enriched values than those that occur in modern samples (De Francesco et al., 2007; unpub. data).

In Puesto Moya, diatom assemblages were restricted to the lapse between ca. 1700 and 800 years B.P. The presence of aerophilous taxa, such as *Nitzschia amphibia* and *Denticula elegans*, indicates a very shallow environment probably subjected to periods of desiccation. The dominance of fresh to brackish taxa supports the presence of a very shallow environment of freshwater to slightly brackish conditions. This interpretation coincides with the previous mollusk based reconstruction, which suggested the presence of a very shallow lentic habitat with nil or very low water velocity and freshwater conditions, not connected to the main fluvial system (De Francesco and Hassan, 2009). These changes may be related to past meander cutoff events from the river, which would have led to the formation of oxbow lakes. Unfortunately, there is a lack of good analogs between the Puesto Moya samples and the modern dataset, which prevented detailed paleoenvironmental reconstruction.

## 6. Conclusions

This paper constitutes the first report on the distribution of modern and Quaternary diatoms from the Andean piedmont of central Argentina. The results obtained provide useful analogs for paleoenvironmental reconstructions of past water bodies, as demonstrated by the good analogy between modern and Pleistocene diatom assemblages. Outstandingly, the strong relationship between diatoms and climate-driven environmental variables such as pH, conductivity and summer temperature, enhances their importance as paleoclimatic indicators in the area and encourages the future development of quantitative inference models for the region.

Given the scarcity of local ecological information, it becomes clear that further studies on South American freshwater diatoms need to be conducted in order to increase the accuracy of diatom-based

paleoenvironmental reconstructions. The future expansion of the study area, and the integration of this dataset with others constructed from lakes located in adjacent regions, would not only solve the analogy problems between fossil and modern assemblages but could also increase the potential for reliable quantitative reconstructions of later Quaternary climates in southern South America.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, <http://dx.doi.org/10.1016/j.palaeo.2012.11.002>. These data include Google maps of the most important areas described in this article.

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