

PRESERVATION OF *CYCLOTELLA* *MENEHINIANA* KÜTZING (BACILLARIOPHYCEAE) ALONG A CONTINENTAL SALINITY GRADIENT: IMPLICATIONS FOR DIATOM-BASED PALEOENVIRONMENTAL RECONSTRUCTIONS

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Abstract. In order to elucidate the effect that physico-chemical lake characteristics exert on diatom valve preservation, the taphonomic signatures of the target taxon *Cyclotella meneghiniana* Kützinger was assessed in twenty five shallow lakes of the Pampa plain of Argentina. Fragmentation and dissolution indices were quantitatively related to environmental variables by means of univariate and multivariate techniques (Generalized Linear Models, Redundancy Analysis and Canonical Correspondence Analysis). Valves showed signs of fragmentation and dissolution, and different stages of taphonomic damage were recognized. Dissolution significantly increased with salinity, pH, carbonate and bicarbonate concentrations. Environmental constraints on valve fragmentation were less clearly identified in the dataset. Besides its key role on valve preservation, salinity also accounted for a significant, although lower, percentage of the variation in diatom composition of death assemblages. These results encourage the use of diatom taphonomy as an indicator of past salinity fluctuations in Pampean shallow lakes. Taphonomic profiles can be used to reconstruct past environmental fluctuations, as well as to identify assemblages subjected to significant taphonomic biases. Combining diatom taphonomy and community paleoecology constitutes a promising tool for maximizing their respective strengths while downweighing their limitations.

Key words. Taphonomy. Diatoms. Shallow Lakes. Community Paleoecology.

Resumen. PRESERVACIÓN DE *CYCLOTELLA MENEGHINIANA* KÜTZING (BACILLARIOPHYCEAE) A LO LARGO DE UN GRADIENTE DE SALINIDAD CONTINENTAL: IMPLICANCIAS PARA LOS ESTUDIOS PALEOAMBIENTALES BASADOS EN DIATOMEAS. Con el fin de identificar los forzantes ambientales que controlan la preservación de las diatomeas en los lagos someros, se estudió la preservación de las valvas de una especie indicadora de diatomea, *Cyclotella meneghiniana* Kützinger, en veinticinco lagos someros de la Región Pampeana Argentina. A tal fin, se calcularon índices de disolución y fragmentación, los cuales se relacionaron cuantitativamente con las características ambientales de los lagos estudiados a través de técnicas estadísticas multivariadas. Las valvas mostraron signos de disolución y fragmentación, pertenecientes a distintos estadios de alteración tafonómica. La disolución se correlacionó significativa y positivamente con la salinidad, el pH, y las concentraciones de carbonato y bicarbonato. Los forzantes ambientales que controlan la fragmentación de los frústulos no fueron claramente identificados en el set de datos. La salinidad explicó también un porcentaje significativo, aunque menor, de la varianza en la composición taxonómica de los ensambles de muerte. Los resultados obtenidos alientan el uso de los atributos tafonómicos de las valvas de diatomeas como indicadores de fluctuaciones pasadas de salinidad en estos lagos. Los cambios en el estado de preservación a lo largo de las sucesiones sedimentarias pueden utilizarse para identificar fluctuaciones ambientales en el pasado, además de proveer herramientas para la identificación de ensambles alterados tafonómicamente. Combinar la tafonomía con los estudios paleoambientales basados en la composición taxonómica de los ensambles constituye una herramienta potencial para maximizar las fortalezas de ambas disciplinas, a la vez que su combinación minimiza sus respectivas limitaciones.

Palabras clave. Tafonomía. Diatomeas. Lagos Someros. Paleoecología.

THE study of diatoms as a tool to understand Holocene environmental changes in the Pampean Region has significantly increased during the last decade (García-Rodríguez *et al.*, 2009; Stutz *et al.*, 2010; Hassan, 2013; Hassan *et al.*, 2011, 2012, 2014). In these studies, the shifts in the com-

position of sedimentary diatom assemblages during the last ca. 5000 cal. years BP were addressed and interpreted as a consequence of past changes in salinity and the nutrient status of the lakes. Diatom records evidenced a shift from brackish-saline and low trophic conditions during the

middle Holocene towards freshwater-eutrophic ones developed since *ca.* 1500–1200 cal. years BP (Hassan, 2013; Hassan *et al.*, 2014). This paleoenvironmental evolution was also recorded by mollusk and pollen records, and related to changes in the paleoclimatic dynamics as well as the sea influence associated with the last transgressive-regressive cycle (De Francesco *et al.*, 2013; Stutz *et al.*, 2014).

In a recent contribution, Hassan *et al.* (2014) reported noticeable changes in the diatom preservation associated with the observed shifts in the assemblages composition. The preservation of diatoms in two Holocene sedimentary successions was evaluated by considering the degree of dissolution and fragmentation of valves of *Cyclotella meneghiniana* Kützinger, a centric diatom selected as target taxon given its abundance in both sequences (Hassan *et al.*, 2011). As diatom preservation is strongly dependent on valve morphology and, consequently, on taxonomy (Barker, 1992; Ryves *et al.*, 2009), the use of a target taxon such as *C. meneghiniana* allowed the assessment of the changes in preservation independently of the assemblage composition. This taxon had already been used as an indicator of diatom dissolution not only because of its abundance in modern and past environments but also for its moderate sensitivity to dissolution and its easily recognizable valves, which can be identified even under very poor preservation conditions (Barker, 1992).

The observed changes in the preservation of *C. meneghiniana* during the Holocene were mainly explained as a consequence of past variations in salinity (Hassan *et al.*, 2014). In fact, the worst preservation of *C. meneghiniana* was recorded in assemblages indicative of brackish to hypersaline conditions, in some cases associated with subaerial exposure. Previous experimental and field-based studies conducted in the Northern Hemisphere indicated that pH, temperature, salinity and ionic strength are the most significant factors affecting frustule dissolution in saline environments (*e.g.*, Lewin, 1961; Flower, 1993; Barker *et al.*, 1994; Ryves *et al.*, 2006). This pattern was also supported by recent experimental essays focused on local diatom assemblages, which revealed a significant influence of NaCl and HCO₃Na concentrations on the dissolution rates of *C. meneghiniana* (Díaz and Hassan, 2016). However, although experimental and fossil evidences suggest that the dissolution of valves increased in saline lakes, no attempts of ex-

ploring the extent of this relationship in modern Pampean lakes have been made. This is particularly important for South American studies, where, although taphonomic research has grown significantly in the last years (Ritter *et al.*, 2016), little is known about diatom preservation along the prevailing environmental gradients.

The Pampean plains of Argentina are dominated by numerous shallow waterbodies, which are far more abundant than deepwater systems (Diovisalvi *et al.*, 2015). Most of these lakes are small (< 500 ha in surface area and up to *ca.* 4 m deep) and characterized by salinities ranging from oligo- to hypersaline (Giorgi *et al.*, 2005). Diatom assemblages are abundant and diverse in these lakes, and their composition is strongly related to gradients of conductivity, pH and nutrients (Hassan *et al.*, 2009, 2011, 2012). Given the high relative abundances exhibited by *C. meneghiniana* in many of these lakes, they provide a unique opportunity to study diatom preservation along natural salinity gradients in continental settings.

In the present contribution, we addressed the taphonomic signatures of *C. meneghiniana* valves in 25 modern Pampean lakes representing a strong salinity gradient. Their preservation was evaluated through the analysis of frustule fragmentation and dissolution, and quantitatively related to environmental variables through the application of multivariate techniques. Our final aim was to elucidate the effect that physico-chemical lake characteristics exert on valve preservation in order to provide tools for the interpretation of the environmental significance of past diatom taphonomic signatures. The results will allow the combination of taphonomy and community composition to provide insights into the formation of diatom death assemblages in shallow lakes, as well as to provide tools to improve the quality of future paleoenvironmental studies in the area.

MATERIAL AND METHODS

Field and Laboratory methods

Study Sites. The study was based on the analysis of diatom samples obtained from previously studied datasets (Hassan *et al.*, 2009, 2011, 2012), as well as unpublished samples deposited in the diatom collection of the Group of Ecology and Paleoecology of Continental Aquatic Environments (University of Mar del Plata, Argentina). From the available samples, only those containing proportions of *C. meneghiniana*

> 5% were used in this study. A total of 25 shallow lakes located across the Pampa plain of Argentina were selected following this criterion (Fig. 1; Tab. 1). The proportional abundances of diatom taxa in these 25 shallow lakes are provided as Supplementary Online Information.

Diatom analyses. The original samples from the 25 Pampean shallow lake surface sediments were re-examined by G.S. Hassan to assess diatom preservation. The samples were prepared following the procedure of Renberg (1990), which, compared with more traditional methods, reduces damage to valves (Hassan *et al.*, 2014). After complete homogenization, a subsample was transferred to a coverslip and air dried for 1 h. Permanent slides were made using Naphrax®. On each slide, the preservation of 50 randomly selected *C. meneghiniana* valves was evaluated using a Leica DM500 light microscope (LM) at 1000X magnification. Two taphonomic variables, (1) degree of fragmentation and (2) dissolution (*sensu* Ryves *et al.*, 2009, see below), were determined for each sample in a three-grade scale. For each variable, specimens were classified as good (0= best preservation; < 10% alteration), fair (1= intermediate, between 10 and 50%

alteration) and poor (2= poorest; > 50 % alteration).

The obtained taphonomic variables were used to calculate F dissolution (F_d) and breakage (F_b) indices (Ryves *et al.*, 2009, 2013), which compare the ratio of undamaged valves (undissolved/unbroken) to all counted valves. These indices vary from 0 to 1, with $F=1$ indicating that all valves are perfectly preserved and $F=0$ indicating that all valves appear dissolved/broken under LM. To maximize potential information from more dissolved valves, the Diatom Dissolution Index (DDI, Ryves *et al.*, 2006) was applied, which compares the assemblage with its dissolution endpoint:

$$DDI = \frac{\sum_{s=3}^{s=1} ns * (S - 1)}{N * (S_{max} - 1)}$$

where n is the number of valves in the preservational stage S (good, fair or poor) and N is the total number of valves that were classified. S_{max} is the highest dissolution stage that the valves in the assemblage can reach. DDI varies from 0 (perfect preservation) to 1 (all valves at the highest dissolu-

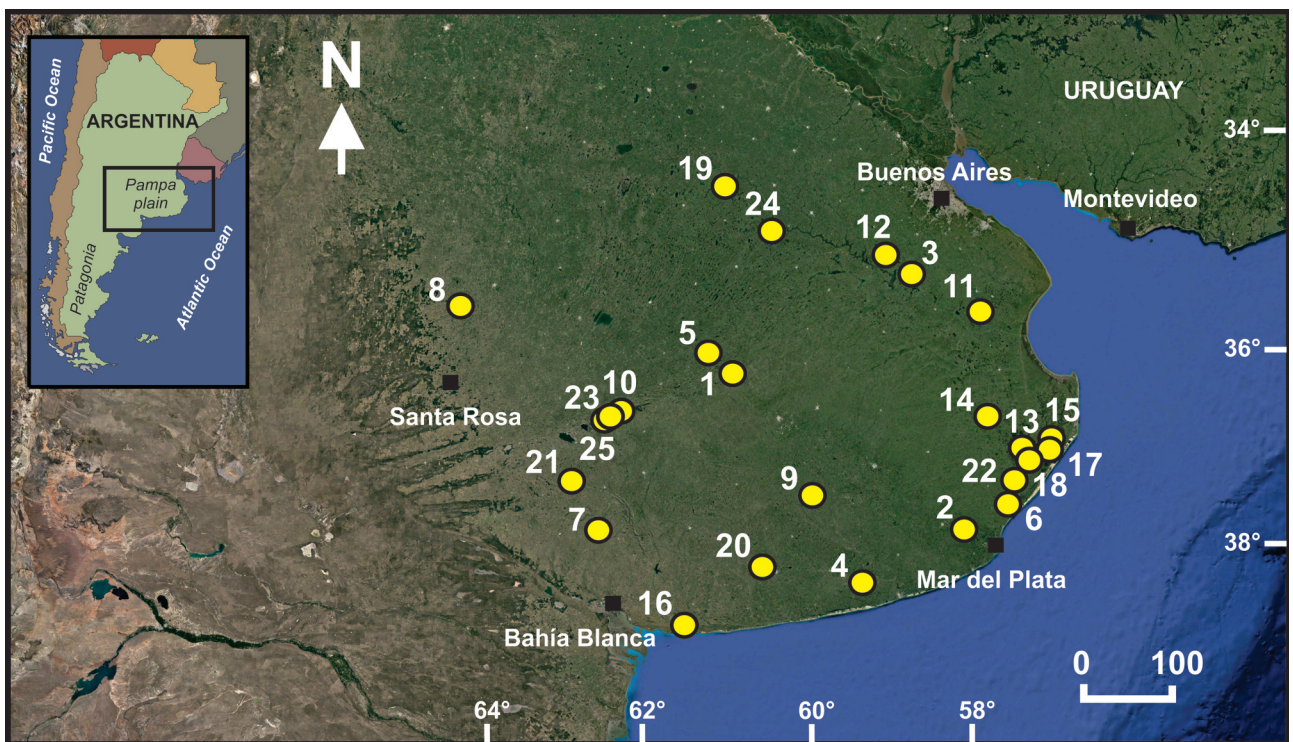


Figure 1. Location map of study sites in the Pampa plain of Argentina. Lakes are ranked in order of increasing salinity (see Tab. 1 for references on lake characteristics) (satellite image from Google Maps; Landsat/Copernicus 2016).

TABLE 1 – Summary of environmental information for the 25 studied lakes. The original source of environmental data is provided.

Lake	ID	Cond (mS/cm)	TDS (ppt)	Hardness	pH	Temp (°C)	O ₂ (%)	Depth (cm)	Secchi (cm)	CO ₃ ²⁻	HCO ₃ ⁻	Cl ⁻
1 - Blanca Grande	BGDE	0.75	0.37	229.0	7.75	24.3	109.5	140	10	0.0	520.0	55.3
2 - La Brava	LBRA	0.83	0.41	211.8	8.38	–	–	–	–	66.3	439.6	99.4
3 - San Miguel del Monte	SMON	0.87	0.43	189.0	8.20	24.2	140.0	250	15	0.0	333.0	91.0
4 - Tupungato	TUPU	1.04	0.52	221.5	8.95	14.4	–	20	–	0.0	710.5	790.0
5 - Cabeza de Buey	CBUEY	1.08	0.54	176.0	10.02	–	–	–	–	495.0	218.0	117.0
6 - Nahuel Rucá	NRUC	1.14	0.54	457.8	8.52	24.9	55.5	79	11	26.1	747.3	193.8
7 - Las Encadenadas	ENCA	1.54	0.77	272.5	8.29	24.9	105.3	120	10	0.0	532.5	264.0
8 - Monte Nieves (Solaro)	SOLA	1.80	0.90	186.0	10.50	22.2	–	–	14	154.2	288.0	670.0
9 - San Antonio	SANT	1.85	0.92	155.2	8.95	22.0	78.0	80	15	131.3	2282.6	504.0
10 - Alsina	ALSI	1.89	0.95	150.0	8.70	25.6	105.1	–	10	61.6	614.0	181.0
11 - Chis Chis	CHIS	1.98	0.99	229.0	8.23	24.2	140.0	250	15	0.0	627.0	368.0
12 - Lobos	LOBO	2.21	1.10	275.0	7.75	25.7	118.9	160	10	0.0	333.0	410.0
13 - Los Carpinchos	CARP	4.00	2.00	817.2	8.39	26.1	36.4	91	10	69.8	944.0	957.6
14 - Kake Huincul	KAKE	4.01	2.00	1140.0	7.74	26.3	84.3	150	15	0.0	400.0	1420.0
15 - Salada Grande	SDAG	5.88	2.93	588.4	8.56	21.3	–	–	–	80.5	446.2	2271.8
16 - Sauce Grande	SAUC	6.25	3.12	1641.6	8.50	25.2	124.0	150	10	92.0	1177.3	1600.0
17 - Los Horcones	HORCO	6.48	3.23	652.8	9.15	24.7	–	–	–	152.1	310.0	2080.6
18 - Las Mostazas	MOST	6.70	3.34	1499.7	8.62	23.8	130.3	125	36	108.6	948.4	1894.0
19 - Gómez	GOME	6.96	3.47	357.0	8.79	27.8	102.9	–	10	41.1	990.0	11828.0
20 - La Tigra	TIGR	7.11	3.55	289.0	9.24	–	–	–	–	1104.0	1666.0	828.0
21 - Puan	PUAN	7.57	3.78	127.0	9.33	24.1	89.9	400	–	77.0	2700.0	6610.0
22 - Hinojales San Leoncio	SLEO	9.67	4.83	–	9.07	–	–	15	–	–	–	–
23 - Cochicó	COCHI	15.53	7.75	644.0	9.35	26.3	97.6	160	–	462.0	2255.3	1210.1
24 - Bragado	BRAGA	16.17	8.07	12125.0	8.61	28.4	128.0	40	–	71.8	676.0	17673.0
25 - Monte	MONT	26.40	13.18	160.6	9.25	–	127.5	–	–	2198.2	2774.3	558.7

Cond= Conductivity. TDS= Total dissolved solids. Hardness is expressed as mg L⁻¹ of CaCO₃. Temp= Temperature. O₂= Dissolved oxygen. Concentrations of CO₃²⁻ (carbonates), HCO₃⁻ (bicarbonates) and Cl⁻ (chloride) are expressed in mg L⁻¹.

tion stage). Additionally, the Diatom Fragmentation Index (DFI) was also calculated by applying the same equation to fragmentation data (Hassan *et al.*, 2014). A fifth taphonomic variable, the Total Taphonomic Grade (TTG), was calculated as the average of DDI, DFI, F_d and F_b as a way to synthesize all taphonomical attributes in a single index.

Numerical methods

Univariate Analyses. Generalized Linear Models (GLM) were applied in order to evaluate the effects of environmental parameters on the taphonomic variables used to define diatom preservation within sites. In contrast to linear regression analyses, GLM can deal with residuals that do not conform to a normal distribution. The GLM coefficients and

standard errors were estimated with the logit link function and the quasibinomial variance function because taphonomic variables are proportions and dispersion is frequently smaller than one (Tomašových and Zuschin, 2009). Chemical variables were $\log(x+1)$ transformed previous to GLM tests. GLM analyses and regression graphs were performed in R version 3.3.2 (R Development Core Team 2016), using the package "car" version 2.1-4 (Fox and Weisberg, 2011).

Multivariate Analyses. A Redundancy Analysis (RDA) was used to quantify the relationship between environmental and taphonomic variables in a multivariate space. RDA is a constrained ordination technique based on linear (Euclidean distance) relationships between variables which allows a direct analysis of the relationship between biological and environmental components (ter Braak, 1994). In order to display quantitative changes in DDI values across the RDA

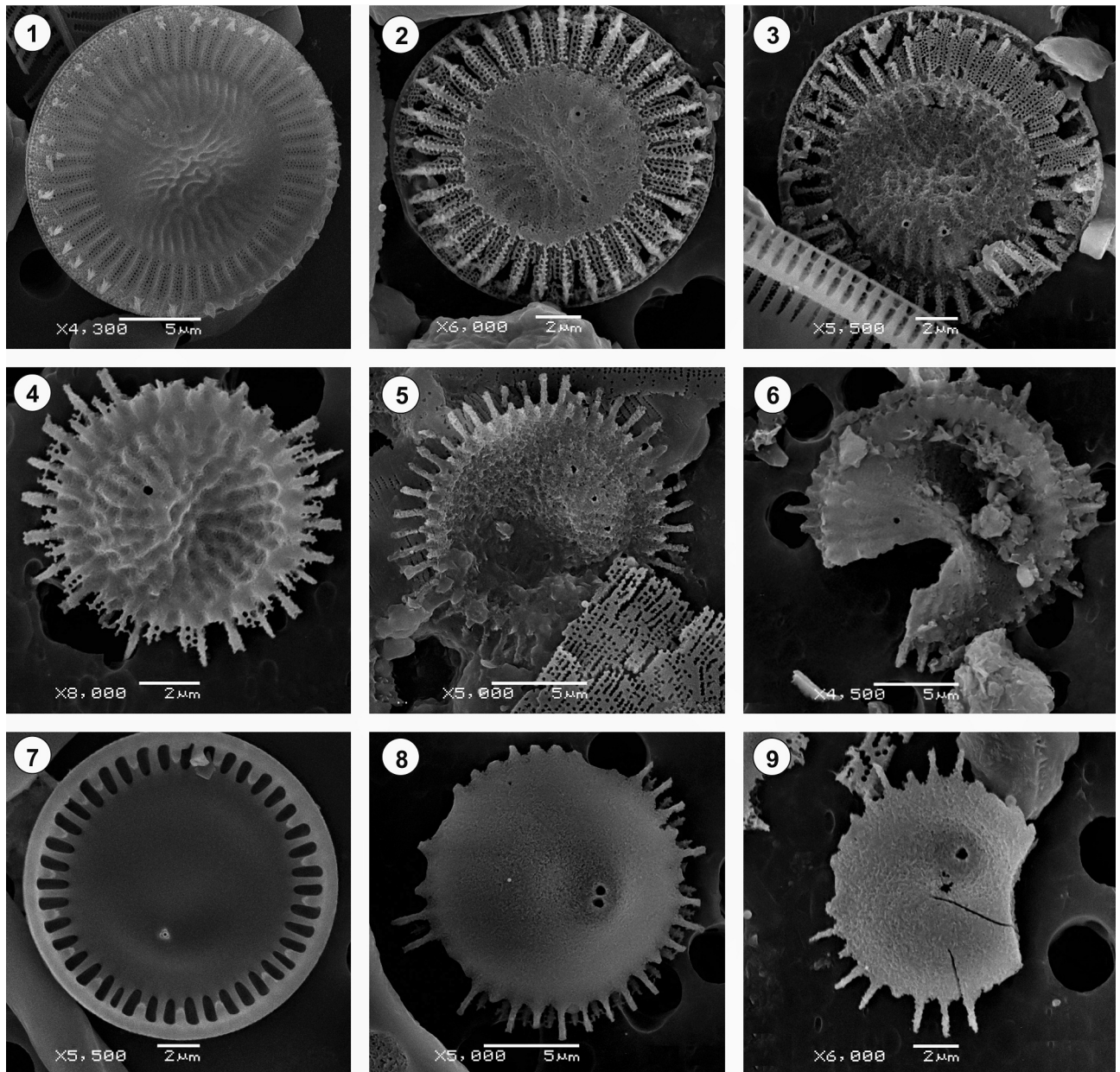


Figure 2. Scanning Electron Microscope (SEM) microphotographs of *Cyclotella meneghiniana* valves; 1, Pristine valve, external surface view; 2–6, Valves showing increasing dissolution, external surface view; 7, Pristine valve, internal surface view; 8–9, Valves showing increasing dissolution, internal surface view. Scale bars and magnification are shown for each picture individually.

plot, a dissolution trend surface was fitted to the ordination diagram using a GLM model based on a quasi-binomial distribution. Samples with missing values in the explanatory variables were set as passive samples. A series of partial RDAs, run with one explanatory variable at a time, were used to calculate the percentage of variance explained by each environmental variable (Borcard *et al.*, 1992). The statistical significance of RDA results was assessed by applying Monte Carlo tests (reduced model) involving 999 permutations. RDA was performed using the program CANOCO version 4.5 (ter Braak and Šmilauer, 1998).

Comparison of taphonomic and biological patterns. The relationship between intersample taphonomic distances (Manhattan distances) and species compositional similarities

(Bray-Curtis dissimilarities) was evaluated through Pearson linear correlation coefficient using PAST v. 3.14 (Hammer *et al.*, 2001). In order to compare the amount of variation explained by environmental variables in both datasets, a Canonical Correspondence Analysis (CCA) was performed. CCA was also applied to assess the explanatory power of taphonomic indices in constraining diatom assemblage compositions. CCA is a multivariate method that assumes unimodal distributions of biological data along environmental gradients and allows us to elucidate the relationships between biological assemblages of species and known variations in environmental variables (ter Braak, 1986). A series of partial CCAs, run with one explanatory variable at a time, was used to calculate the percentage of variance

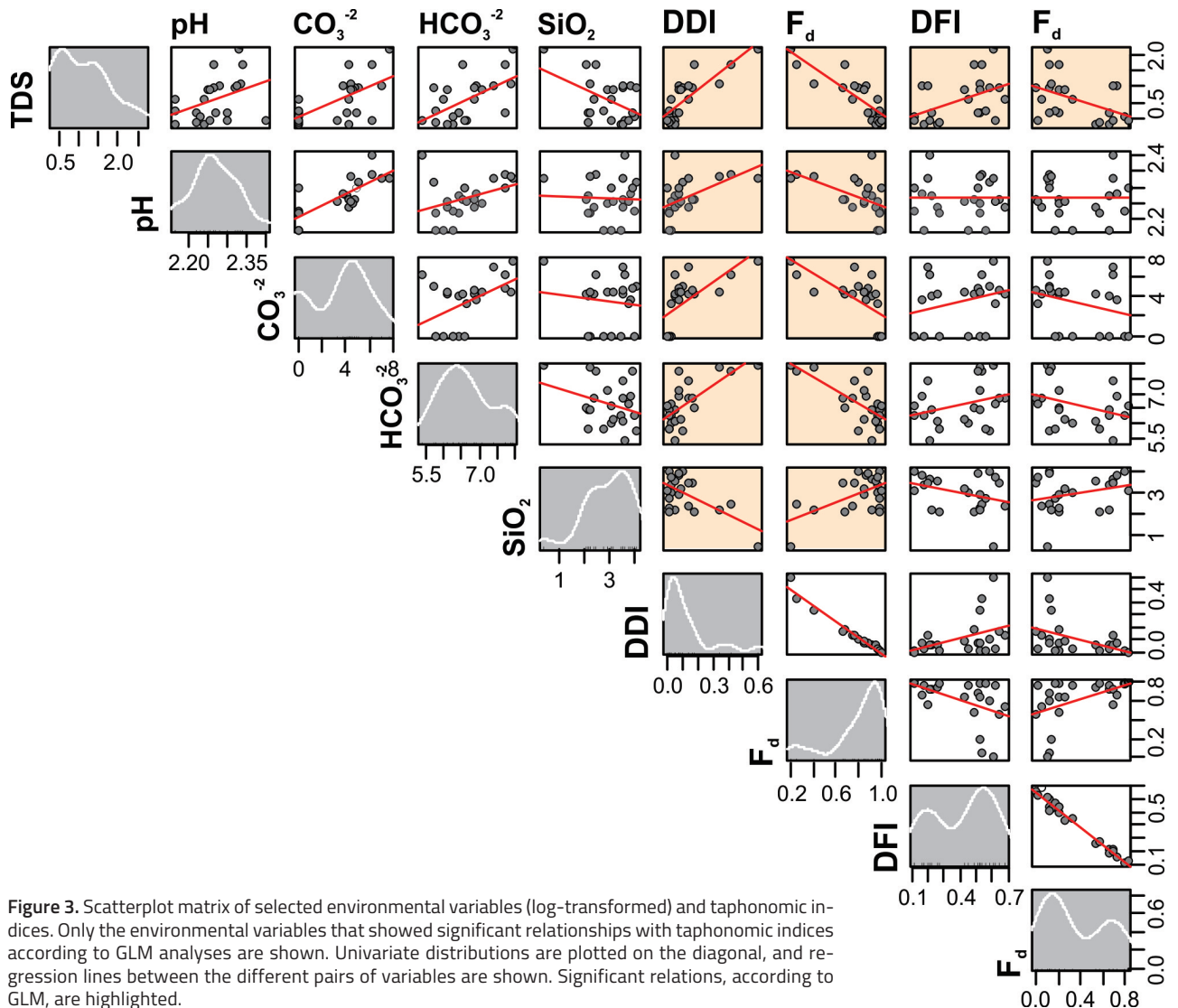


Figure 3. Scatterplot matrix of selected environmental variables (log-transformed) and taphonomic indices. Only the environmental variables that showed significant relationships with taphonomic indices according to GLM analyses are shown. Univariate distributions are plotted on the diagonal, and regression lines between the different pairs of variables are shown. Significant relations, according to GLM, are highlighted.

TABLE 2 – *Taphonomic indices.*

Lake		DDI	F_d	DFI	F_b	TTG
1 - Blanca Grande	BGDE	0.02	0.96	0.18	0.66	0.10
2 - La Brava	LBRA	0.05	0.94	0.26	0.54	0.15
3 - San Miguel del Monte	SMON	0.01	0.98	0.27	0.56	0.14
4 - Tupungato	TUPU	0.00	1.00	0.12	0.82	0.06
5 - Cabeza de Buey	CBUEY	0.05	0.92	0.21	0.68	0.13
6 - Nahuel Rucá	NRUC	0.02	0.96	0.62	0.02	0.32
7 - Las Encadenadas	ENCA	0.01	0.98	0.11	0.80	0.06
8 - Monte Nuevas (Solano)	SOLA	0.13	0.80	0.21	0.64	0.17
9 - San Antonio	SANT	0.07	0.88	0.51	0.12	0.29
10 - Alsina	ALSI	0.05	0.92	0.22	0.66	0.13
11 - Chis Chis	CHIS	0.01	0.98	0.53	0.20	0.27
12 - Lobos	LOBO	0.01	0.98	0.56	0.16	0.28
13 - Los Carpinchos	CARP	0.14	0.74	0.68	0.04	0.41
14 - Kakel Huincul	KAKE	0.02	0.96	0.45	0.32	0.23
15 - Salada Grande	SDAG	0.09	0.84	0.43	0.26	0.26
16 - Sauce Grande	SAUC	0.08	0.84	0.53	0.20	0.30
17 - Los Horcones	HORCO	0.10	0.80	0.59	0.12	0.34
18 - Las Mostazas	MOST	0.17	0.66	0.65	0.00	0.41
19 - Gómez	GOME	0.07	0.86	0.16	0.72	0.11
20 - La Tigra	TIGR	0.14	0.76	0.20	0.68	0.17
21 - Puan	PUAN	0.34	0.40	0.52	0.14	0.43
22 - Hinojales San Leoncio	SLEO	0.23	0.60	0.37	0.42	0.30
23 - Cochicó	COCHI	0.42	0.26	0.54	0.12	0.48
24 - Bragado	BRAGA	0.18	0.68	0.49	0.20	0.33
25 - Monte	MONT	0.60	0.20	0.61	0.10	0.60

DDI: Diatom Dissolution Index, F_d : F dissolution index, DFI: Diatom Fragmentation Index, F_b : F fragmentation index.

explained by each environmental variable (Borcard *et al.*, 1992). The statistical significance was assessed by unrestricted Monte Carlo tests (full model) involving 999 permutations using the program CANOCO version 4.5 (ter Braak and Šmilauer, 1998).

RESULTS

Preservation of C. meneghiniana

Valves of *C. meneghiniana* showed signs of both frag-

mentation and dissolution. Distinct stages of valve dissolution were observed under a Scanning Electronic Microscope (SEM), allowing us to recognize morphological changes exerted by chemical dissolution (Fig. 2). Pristine valves are characterized by a central disk undulated and striated by grooves, and usually with one to three central processes. The central area is surrounded by a distinctive marginal ring of striae formed by irregular areolae and separated by costae (Fig. 2.1: outer view; Fig. 2.7: inner view). In a first

TABLE 3 – Results of Generalized Linear Models using logit link function and quasibinomial variance function showing the significance of the relationship between taphonomic indices and chemical variables.

	DDI	Slope	St. error	t-test	p-value
pH	8.7360	3.4820	2.509	0.01960	*
Salinity	1.6606	0.2174	7.638	9.40e-08	***
HCO ₃ ⁻	1.3038	0.2764	4.717	0.00011	***
SiO ₂	0.8909	0.2280	-3.907	0.00081	***
CO ₃ ²⁻	0.5409	0.1106	4.890	6.89e-05	***
Cl ⁻	0.3305	0.1899	1.740	0.09575	
NO ₃ ⁻	0.5377	0.3274	1.642	0.11478	

	F _d	Slope	St. error	t-test	p-value
pH	-9.305	3.787	-2.457	0.0220	*
Salinity	1.8824	0.2635	-7.145	2.82e-07	***
HCO ₃ ⁻	1.3904	0.3091	-4.498	0.00018	***
SiO ₂	0.8765	0.2911	3.011	0.00665	**
CO ₃ ²⁻	0.5371	0.1283	-4.186	0.00038	***
Cl ⁻	0.4211	0.1888	-2.231	0.03620	*
NO ₃ ⁻	0.4868	0.3671	-1.326	0.19840	

	DFI	Slope	St. error	t-test	p-value
pH	-1.536	2.436	-0.631	0.5350	
Salinity	0.5349	0.2270	2.357	0.0273	*
HCO ₃ ⁻	0.3674	0.2181	1.685	0.1062	
SiO ₂	0.2909	0.1907	-1.525	0.1420	
CO ₃ ²⁻	0.0810	0.0672	1.206	0.2405	
Cl ⁻	0.1927	0.1063	1.812	0.0836	
NO ₃ ⁻	0.3772	0.2183	1.728	0.0980	
Secchi	0.1319	0.3864	-0.341	0.7380	
Depth	0.2131	0.2269	0.939	0.3630	

	F _b	Slope	St. error	t-test	p-value
pH	2.174	3.701	0.587	0.563	
Salinity	0.9040	0.3873	-2.334	0.0287	*
HCO ₃ ⁻	0.6552	0.3622	-1.809	0.0841	
SiO ₂	0.4450	0.3295	1.352	0.1908	
CO ₃ ²⁻	0.1291	0.1029	-1.255	0.2230	
Cl ⁻	0.3336	0.1802	-1.851	0.0776	
NO ₃ ⁻	0.6265	0.3848	-1.628	0.1180	
Secchi	0.1643	0.5784	-0.284	0.781	
Depth	0.3826	0.3799	-1.007	0.331	

The p-values in bold represent the significant results for $p < 0.001$ (***), $p < 0.01$ (**), and $p < 0.05$ (*).

stage, dissolution affects the intercostal areas, enlarging the areolae and destroying the boundaries among adjacent ones although the marginal rim usually remains (Figs. 2.2–3). In a more advanced stage of dissolution, the marginal rim is totally dissolved and the structure of the intercostal areas is completely lost but costae remain (Fig. 2.4–5). The final stages of dissolution are mainly evidenced as a featureless disc in which costae are dissolved or just vestigial and the processes remain enlarged (Fig. 2.6, 2.8–9). This highly dissolved stage, however, still allows a reliable taxonomic recognition of *C. meneghiniana*.

The taphonomic signature of the valves varied between lakes, fragmentation indices being more variable than dissolution indices (Fig. 3; Tab 2). DDI values ranged between 0 (Lake Tupungato) and 0.6 (Lake Monte), whereas the proportion of valves showing no sign of dissolution (F_d) ranged between 1 (Lake Tupungato) and 0.2 (Lake Monte). DFI values ranged between 0.11 (Lake Las Encadenadas) and 0.68 (Lake Los Carpinchos). The least fragmented valves were found in Lake Tupungato (F_d = 0.82), while the most fragmented were recorded in Lake Las Mostazas (0). Dissolution and fragmentation indices were low ($r = 0.398$ for DDI vs DFI, $r = 0.44$ for F_d vs F_b) but significantly ($p < 0.05$) correlated among them (Fig. 3), suggesting that a significant part of the fragmentation evidenced by *C. meneghiniana* valves was a consequence of the weakening produced by silica dissolution.

Chemical variables and taphonomy

Univariate Analyses. GLM results indicated that the dissolution of *C. meneghiniana* is significantly related to water chemistry (Tab. 3). DDI significantly increased with salinity, pH, carbonate and bicarbonate concentrations, whereas the proportion of undissolved valves showed a negative significant correlation with those variables (Fig. 3). Both variables were also significantly correlated with silica content, DDI being higher while F_d lower in lakes with low silica concentrations (Fig. 3; Tab. 3). Environmental constraints on valve fragmentation were less clearly identified in the dataset. The GLM test indicated only a marginally significant and positive relationship between salinity and fragmentation. The addition of physical variables (depth and Secchi depth; Tab. 3) resulted in non-significant correlations.

Multivariate Analyses. The relationship between taphonomic and environmental indices is summarized in the RDA plot (Fig. 4). The first two axes of RDA accounted for 77% of the total variance in diatom preservation (Tab. 4). According to partial RDA, salinity (as logTDS) was the strongest environmental variable that explained significant percentages of the variance (33.3%, $p < 0.001$), followed by bicarbonates (25.7%, $p < 0.01$) and carbonates (9.9%, $p < 0.05$; Tab. 4). None of the remaining environmental variables included in the analysis explained the significant proportions of taphonomic variations. The examination of the RDA plot showed that DDI, DFI and TTG were negatively correlated with axis 1 (which explained 70% of the variation), while F_d and F_b showed the opposite pattern (Fig. 4). Among the taphonomic variables, DDI was the most highly correlated with salinity, carbonates and pH, showing a strong relationship with the increasing dissolution along the environmental gradients of these variables (Fig. 4).

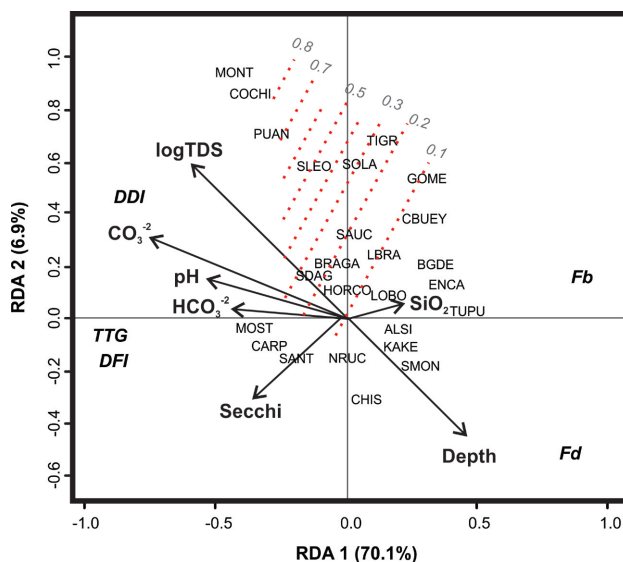


Figure 4. RDA triplot of sites, taphonomic and environmental variables. Site abbreviations can be found in Table 1. Dotted lines indicate values of the DDI attribute surface.

TABLE 4 – Summary statistics for the constrained ordinations based on taphonomic (RDA) and compositional (CCA) datasets. The percentage of variance explained by single environmental variables was calculated on the basis of partial constrained ordinations.

	Taphonomy (RDA)		Compositional (CCA)	
	Axis		Axis	
Ordination results	1	2	1	2
Eigenvalues (λ)	0.701	0.066	0.590	0.445
Explained variation (cumulative)	70.02	76.61	16.21	28.43
Pseudo-canonical correlation	0.923	0.617	0.998	0.971
Explained fitted variation (cumulative)	90.95	99.5	24.44	42.86
Total variation	2.36		3.64	
% of variance explained	77%		66.3%	
Gradient length (SD)	0.6		3.9	
Partial ordinations results	% of variance explained			
Salinity (TDS)	33.3***		11.7●	
HCO ₃ ⁻²	25.7**		4.6	
CO ₃ ⁻²	9.6*		5.2	
SiO2	9.5		5.3	
pH	9.2		4.5	
Secchi Depth	10.1		5.9	
Depth	0.5		8.1	

The significance of canonical axes is indicated based on 999 unrestricted Monte Carlo permutations ($p < 0.1$ •, $p < 0.5$ *, $p < 0.01$ **, $p < 0.001$ ***).

Taphonomic vs. biological patterns

The correlation between the variation in the preservation of *C. meneghiniana* and the variation in the composition of the assemblages was positive and significant ($r = 0.64$, $p < 0.05$; Fig. 5). CCA results indicated that salinity accounted for 11.7% of the variation in the diatom composition although it was only marginally significant ($p = 0.07$; Tab. 4). Carbonates and bicarbonates did not exhibit significant relationships with compositional data. The use of taphonomic indices as explanatory variables in CCA yielded negative results as none of the indices explained significant portions of the diatom compositional variance ($p > 0.1$).

DISCUSSION

Cyclotella meneghiniana as indicator of the preservation state of diatom assemblages

The taphonomic analysis of *Cyclotella meneghiniana* indicated a high susceptibility of the valves to dissolution and fragmentation. The usefulness of target taxa (such as *C. meneghiniana*) as proxies for dissolution of the entire assemblages has been previously emphasized, particularly as their use reduces the need to evaluate the preservation of each taxon separately to obtain a dissolution value for the sample (Ryves, 1994). In an early example, Barker *et al.* (1990) and Barker (1992) calculated the ratio of pristine to dissolved *C. meneghiniana* valves (*i.e.*, valves without mar-

ginal areolae), which proved to be a useful index of preservation for comparing experimentally dissolved samples. Overall, as the dynamics of diatom dissolution deeply rely on frustule architecture, consequently being highly dependent on taxa morphology, the usefulness of *C. meneghiniana* as an indicator of diatom preservation in Pampean lakes becomes particularly relevant. Its sensibility to taphonomic factors, together with its widespread distribution both in modern and fossil samples of the region (*e.g.*, Hassan *et al.*, 2011, 2014), encourages its application as a reliable index of preservation both in neo and paleoenvironmental research based on diatom assemblages.

Besides its susceptibility and widespread distribution, the use of *C. meneghiniana* as taphonomic target taxa is also furthered by its exhibition of easily identifiable stages on the dissolution process, with its valves remaining recognizable even in the most advanced dissolution stages. As previously stated by several authors, the initial stages of diatom dissolution yield valves relatively transparent under the light microscope, mainly as a result of the enlargement of structural pores and the thinning of the cell walls. Poorly silicified traits are lost in the next stages of dissolution, leaving behind stronger central areas and thicker frustule parts (Barker, 1992; Ryves, 1994). In the case of *Cyclotella* species, the more delicate marginal areas disappear first, leaving a relatively featureless disc behind (*e.g.* *C. caspia* Grunow (Battarbee, 1988); *C. meneghiniana* (Barker, 1992), Fig. 2 this study; *C. bodanica* Eulestein (Barker *et al.*, 1994); *C. minuta* (Skvortzov) Antipova (Battarbee *et al.*, 2005); *C. choctawhatcheeana* Prasad (Ryves *et al.*, 2009)). In the case of Pampean lakes, where no other morphologically similar *Cyclotella* species are found, these discs can be confidently assigned to *C. meneghiniana* in isolation, even in the absence of specimens dissolved to a lesser extent in the same samples. Under these circumstances, where dissolution can bias the diatom counts toward the more resistant and recognizable taxa (such as *C. meneghiniana*; Barker *et al.*, 2002), compositional diatom data may become hard to correct and interpret, thus enhancing the importance of understanding the environmental constraints of taphonomic traits in diatom analyses. In this context, the taphonomic analysis of *C. meneghiniana* constitutes a useful and simple tool for assessing the environmental significance of diatom remains even under poorly conditions of preservation.

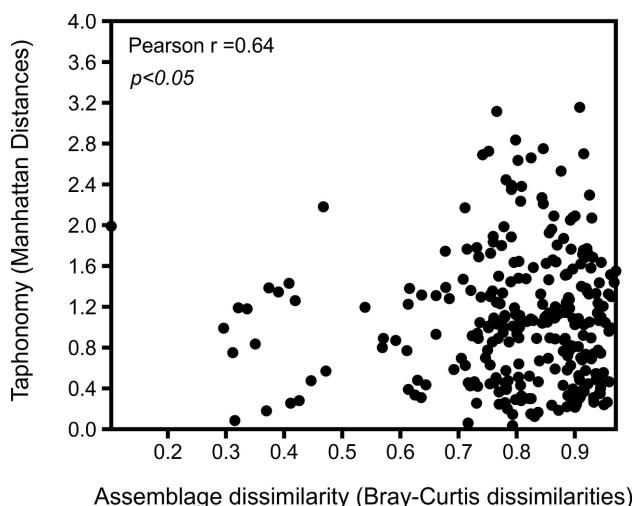


Figure 5. Scatterplot showing correlation between dissimilarities in species composition and *C. meneghiniana* preservation. The Pearson r and the significance of the relationship is shown.

Environmental controls on diatom preservation

The results of the GLM analyses indicated that the dissolution of *C. meneghiniana* is significantly related to water chemistry and particularly to salinity, carbonate, bicarbonate, pH and silica concentrations. These variables explained 77% of the variation in the preservation of *C. meneghiniana* in the dataset, according to RDA. These results are consistent with previous experimental and field studies conducted in the Northern Hemisphere showing that, although diatom dissolution occurs both in freshwater and saline environments, it is in the latter where its strongest effects are evidenced (Barker, 1992; Ryves *et al.*, 2006; Roubex *et al.*, 2008). Although silica dissolution is positively correlated with salinity (Ryves *et al.*, 2006 and references therein), the chemical causes of this interaction are not clearly understood (Roubex *et al.*, 2008). Frustule dissolution is higher in solutions with low silica concentration (*i.e.*, unsaturated; Flower and Ryves, 2009) and is therefore controlled by the combined properties of the solution in which the silica is immersed, the sedimentary matrix and the nature of the silica particles themselves (Barker *et al.*, 1994). Moreover, biological factors such as the role of bacteria in dissolving silica and removing the protective organic coatings of the frustules (Roubex *et al.*, 2008), invertebrate bioturbation and grazing may also influence dissolution (see Ryves *et al.*, 2006 and references therein). Furthermore, it has been experimentally demonstrated that living cells of *C. meneghiniana* grow thicker in lower salinities, showing well-developed costae and spines as well as numerous siliceous granules along the valve mantle. Cells grown at higher salinities develop thin valves with poorly developed costae and spines, and lack siliceous granules along the valve mantle (Tuchmann *et al.*, 1984). Hence, besides the differences in the post-mortem dynamics of silica solubility, the preservation of diatoms along salinity gradients also seems to be driven by the intrinsic properties of the valves and differential growth.

The role of carbonates in diatom dissolution has been recognized in previous contributions (Barker *et al.*, 1994; Ryves *et al.*, 2006). Carbonate concentrations explained a significant portion of the dissolution variance in the lakes from North America (Ryves *et al.*, 2006) whereas Na₂CO₃ solutions induced a strong dissolution of the frustules in controlled experiments (Barker *et al.*, 1994; Díaz and Hassan,

2017). Poor preservation associated with high carbonate concentration has been related to elevated pH, because it increases the dissolution of silicic acid (Newberry and Schelske, 1986; Barker, 1992; Flower, 1993). High pH is usually correlated with carbonate concentrations in lakes (*e.g.*, Hassan *et al.*, 2011). However, the explanatory power of pH in the present study was significantly lower than carbonates and bicarbonates, which coincide with previous results (Ryves *et al.*, 2006).

Environmental constraints on valve fragmentation were less clearly identified in the Pampean dataset. The causes of fragmentation of diatom frustules have been relatively poorly studied (*e.g.*, Haberyan, 1985; Ryves *et al.*, 2006). Higher fragmentation has been associated with high energy environments such as littoral and shallow lacustrine zones (Round, 1964; Flower and Nicholson, 1987). The effect of grazing has also proven to be significant in causing frustule breakage (Haberyan, 1985). Therefore, biological and physical environmental variables, such as fetch, depth, wind speed and grazers abundance, may play a key role in explaining diatom fragmentation. From these, only depth was included in the Pampean dataset; however, according to GLM results, it did not show a significant relationship with fragmentation. Fragmentation showed a significant relationship with dissolution, implying that at least a part of it can be facilitated by the debilitation of the valves caused by the dissolution of the cell wall. Moreover, early fragmentation caused by environmental constraints can favor the further dissolution of the fragments by increasing their exposed surface (Barker *et al.*, 1994). This can explain the positive and significant (although low) relation between salinity and fragmentation observed in this dataset. Overall, fragmentation is caused by a complex interaction between several physical and biological variables that our data set seems to have partially overlooked.

Linking taphonomy and compositional data

The positive correlation between the variation in the preservation of *C. meneghiniana* and the composition of the assemblages suggests the existence of common causal environmental stressors in the structuration of both patterns. Two causes can explain this relationship: 1) the inter-specific variation in preservation, related to the intrinsic properties of frustules that can cause differential preservation

and the consequent changes in the composition of the species along environmental gradients; and 2) the same environmental factors can affect both the distribution and preservation of the taxa, *i.e.* by altering the taphonomic signature of frustules and also shifting the species composition of the assemblages according to their optima and tolerances.

The existence of environmental factors affecting both the distribution and preservation of the diatom taxa was evidenced by ordination results. Salinity explained significant portions of variance in both taphonomic and compositional analyses, although its effect on the composition of the assemblages was only marginal and lower. These results are comparable to those yielded in previous studies of Central Argentina, in which log-Conductivity accounted for 4.8% of the variance in diatom assemblage compositions (Hassan *et al.*, 2011). Our findings indicate that, although this environmental factor influences the structuring of the composition of diatom life assemblages in Pampean shallow lakes, it plays a stronger and more significant role in the preservation of their frustules after deposition in death assemblages. The effect of salinity in diatom metabolism and the consequent impact on diatom community compositions has been largely recognized (Fritz, 2007). Nevertheless, the full understanding of this relationship in arid and semi-arid lakes is obscured by the impact of salinity on the development of frustules (Tuchmann *et al.*, 1984) and its further preservation. In a recent work conducted on diatom life assemblages (*i.e.*, cells showing intact chloroplasts; Hassan, 2015) in three Pampean shallow lakes representing a short conductivity gradient (0.3–7.5 mS/cm; Hassan, 2015), the percentage of variance on diatom compositions explained by this environmental variable was similar both in life and death assemblages (9.85 and 12.26%, respectively), therefore suggesting a dominance of pre-mortem influence of this environmental variable in structuring diatom assemblages at low salinities. Whether these percentages remain similar at high salinities, where the strongest taphonomic effects are observed, is unknown.

The lack of explanatory power of taphonomic indices in CCA indicates that the effect of preservation in structuring diatom assemblages is low. These results suggest that, even when salinity altered the preservation of the valves, particularly by leaving identifiably dissolution marks, this effect was not strong enough to destroy whole valves or

shift species composition in most of the studied lakes. This result is not surprising as the number of sites characterized by high salinities was relatively low: only three sites exceeded the value of 5 ppt (Lakes Cochicó, Bragado and Monte, Tab. 1), which has been experimentally demonstrated to exponentially catalyze *C. meneghiniana* dissolution (Roubeix *et al.*, 2008). Moreover, the dominance in these three lakes of highly silicified, resistant taxa (*C. meneghiniana*, *Campylodiscus clypeus* Ehrenberg and *Denticula elegans* Kützing) supports the possibility of a taphonomic bias against more delicate species. Yet, although salinity showed to drive frustule dissolution along the studied gradient, examples of highly destructive lakes where differential taxa dissolution can bias specific composition were relatively scarce in the dataset. Under these circumstances, DDI seems to be a more sensitive indicator of salinity differences among lakes than the shifts in the relative abundances of diatom taxa, providing a useful tool to infer past changes in salinity for paleoenvironmental studies.

Paleoenvironmental implications

The strong relationship between the dissolution of *C. meneghiniana* valves, salinity and carbonate gradients enhances the paleoenvironmental significance of dissolution trends along the fossil record. Ideally, dissolution profiles can be used as records of diatom taphonomic history, and related to fluctuations in past salinity and alkalinity. In saline lakes, periods of increased dissolution may indicate increased salinity and alkalinity, which can be indirectly related to climate and lake level changes (Ryves *et al.*, 2006). In fact, the strong environmental dependence of diatom preservation found in the present study allows the paleoenvironmental interpretation of taphonomic histories in highly fluctuating and very shallow lakes such as the numerous waterbodies that are characteristic of the South American Pampas.

Additionally, the taphonomic history of the diatom fossil record provides valuable information to assess the quality of the paleoenvironmental inferences that can be made from fossil assemblages. Sedimentary levels dominated by highly dissolved and fragmented diatom valves are very likely indicative of poor community composition preservation and, consequently, of unpredictable errors when used in qualitative or quantitative environmental reconstructions

(Ryves *et al.*, 2009). Stratigraphic intervals strongly affected by dissolution may have, in fact, lost part of the diatom assemblage, thus leading to the preservation of the most resistant frustules (Hassan *et al.*, 2014). Therefore, the inclusion of taphonomic profiles as routine analyses in diatom-based reconstructions provides an independent source of data for evaluating the quality and confidence of the inferences made from compositional data.

In the light of these new results, the reexamination of the previously published taphonomic history of *C. meneghiniana* in Holocene sediments of Nahuel Rucá and San Leoncio (Hassan *et al.*, 2014) suggests strong fluctuations of past salinity and hardness in these lakes. The increased dissolution values exhibited by *C. meneghiniana* indicate the occurrence of brackish environments in these lakes by ca. 1500 cal. years BP, with modern conditions developing during the last ca. 200 cal. years BP. DDI values for these levels reached up to 0.7, indicating the prevalence of highly destructive environments with salinity and hardness values lying on the upper reaches of the studied modern gradient. The community composition corresponding to these moments of increased salinity should be interpreted with caution, as the inferred destructive conditions could have significantly biased the proportions of taxa towards resistant species. As suggested by our results, dissolution data for those levels would be a more confident source of environmental data than community composition, enhancing the significance of studying taphonomic histories in these lakes.

CONCLUSIONS

The results obtained in the present contribution signaled a high influence of environmental gradients on diatom preservation in Pampean shallow lakes. This was particularly evident in saline and alkaline lakes, where diatom valves were highly susceptible to dissolution and fragmentation. Consequently, the results allowed us to elucidate the environmental significance of the taphonomic signatures of *C. meneghiniana* valves, providing insights into the paleoenvironmental value of diatom taphonomic histories. Moreover, the strong relationship between the preservation and the composition of the assemblages found in the dataset suggested the existence of common causal environmental stressors in the structuration of both patterns, enforcing the value of taphonomy as an independent source of paleoenvironmental research.

In the light of these results, it is worth noting that combining diatom taphonomy and community paleoecology constitutes a promising tool for maximizing their respective strengths while downweighing their limitations: whereas taphonomy allows the assessment of the confidence of the autoecological inferences, the optima and tolerances of the taxa could lead to an understanding of the environmental factors causing the taphonomic signature of valves. Moreover, if fossil studies are accompanied by local and regional analyses on actualistic taphonomy, the potential information provided by preservational profiles significantly increases. By increasing actualistic and experimental data, taphonomic information can be used to gain paleoecological information, and not simply to assess the loss of information from the fossil record.

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