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Multivariate analysis of diatoms and water chemistry in Bolivian saline lakes

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Abstract

Diatom assemblages are described from surface sediments in thirteen salt lakes located in the southern Bolivian Altiplano. Factor analysis of correspondences and cluster analysis are used to classify the diatom assemblages. New methods are proposed to establish the qualitative and quantitative relationships between diatom floras and ecological parameters. Diatom assemblages are linked more to the ionic elements than to the salinity, pH, depth, temperature or elevation. Environmental variables are divided into three modalities which allow considerations of many different variables not under the same units.

Introduction

Diatoms in hypersaline lakes from South America have been little studied (Hustedt, 1927; Frenguelli, 1936; Patrick, 1961; Lopez, 1980; Servant-Vildary, 1978, 1983, 1984). However, stratigraphy (Servant & Fontes, 1978; Fernandez, 1980), geochemistry, (Carmouze *et al.*, 1978; Miranda, 1978; Risacher, 1978a; Risacher & Eugster, 1979; Ballivian & Risacher, 1981), clay neoformation (Badaut *et al.*, 1979), hydrobiology (Iltis *et al.*, 1984), ornithology (Hurlbert & Keith, 1979), geocryology (Hurlbert & Chang, 1984, 1988) have been subjects of deep interest. Dissolution and transformation of diatoms in the sites studied are intense and begin in the three first centimeters of the sediments (Badaut *et al.*, 1979).

The objective of the research presented in this paper is to provide information concerning the response of diatoms to salt concentrations in order to reconstruct past environments. It involves, (1) an inventory of the diatom species, (2) a classification of the lakes based on the diatom flora using correspondence factor and cluster analysis, (3) an ordering of the species inside a cluster, using an 'interpreting help' method to determine the degree of relation of the subdominant or scarce species to a given milieu, (4) the determination of the ionic elements which mostly influence a diatom assemblage; using the 'variables/classes' and 'classes/variables' contributions program, (5) the quantification of the chemical variables, using a 'interactions species/ionic variables' program which puts into the same graph, samples and/or species and ionic elements whose concentration is expressed in categories (Roux, 1985).

Description of the sites studied

The volcanic area, called Lipez, is broken up into a large number of small salt lakes located at between 4000 and 5000 m of altitude. The climate is characterized by strong winds, high insolation and evaporation (1400 mm year^{-1}), and low pluviosity (100–200 mm year^{-1}). Average daily air and water temperature amplitude is in the order of 15 °C. Rain water additions were negligible in the two years of our study. Similar general climatic conditions affect to the 13 lakes (Fig. 1), which have waters in a wide range of salinities.

The ionic composition of the lakes mainly depends on the nature of the surrounding rocks, the interactions between water and sediments and the origin of influent waters. Ballivian & Risacher (1981) based a chemical classification on these three parameters and separated the lakes into four groups.

1. *Na-SO_4-Cl lake*: Hedionda is essentially fed by spring waters. Chiar Kota is fed by running water from the north, whose composition is already of high salinity (TDS: 1.88 g l^{-1}). There is deposition of gypsum near the margins. Honda is fed by water springs whose chemical composition is affected by the volcanic and sedimentary rocks. There are deposits of halite on the margins. Lakes Pujio and Puripica Chico are very small; see Hurlbert & Keith (1979) and Hurlbert & Chang (1983) for details. Ballivian is isolated from Ramaditas basin by a high sill, but they could have been connected during highest water-level periods. Ramaditas is fed by running water springs from the south, and diffuse springs in the north-western and eastern margins. Laguna Verde is characterized by lack of salt deposits in the margins.

2. *Na-SO_4 lakes*: Canapa and Chulluncani are the northernmost studied lakes in this series. Canapa is a very small lake, evaporites are thick and the underground water is independent of the superficial lake. The lake is fed by spring water in the northern part and by the Tapaquillcha River in the eastern part. Chulluncani, fed by a small river, is only 15 cm deep, and can be completely dry. There are thenardite deposits on the margins.

3. *NA-Ca-Cl lakes*: The lake surface of Pastos Grandes is small compared to the evaporitic crust. It is composed of a 'central lake' and marginal lakes which can reunite after the wet season to form a continuous ring around the salar. The lake is fed by small rivers and spring waters. Laguna Colorada typically belongs to the sodium chloride group. Although the chemical characteristics are variable within the lake according to the chemistry of inflow waters, only one sample was studied. However, as the water supply is bicarbonated, a sample for diatom study was taken outside the lake, near the natron deposits. Unfortunately, no chemical analyses at the same sample site was available, so we used the nearest water sample CLD 4 which gives the best idea of the outside water chemistry.

4. *Na-CO_3 lake*: In Cachi Laguna, 90% of its water supply comes from the western part of the lake. The sample for diatom study was taken from the part of the lake where surficial water has a subterranean origin.

Detailed discussions about seasonal and inter-annual variations of chemistry and diatom floras are given in Iltis *et al.* (1984).

Materials and methods

Sampling and chemical analysis

Water samples from the water column near the shoreline were collected with plastic bottles and preserved with chloroform. Surface sediment samples were collected at the same sites (Fig. 1) and time (May and November 1978) as water samples, and preserved with formalin (4%), both at room temperature in Paris. The problem of poor representativeness by dissolution and transformation of diatoms was avoided using these diatoms samples collected just in the water-sediment interfaces.

Thirty diatom samples and the corresponding water data were used for multivariate analysis. Samples of water and sediment were submitted to acid digestion in order to obtain clean and free of organic matter diatom frustules. The number of

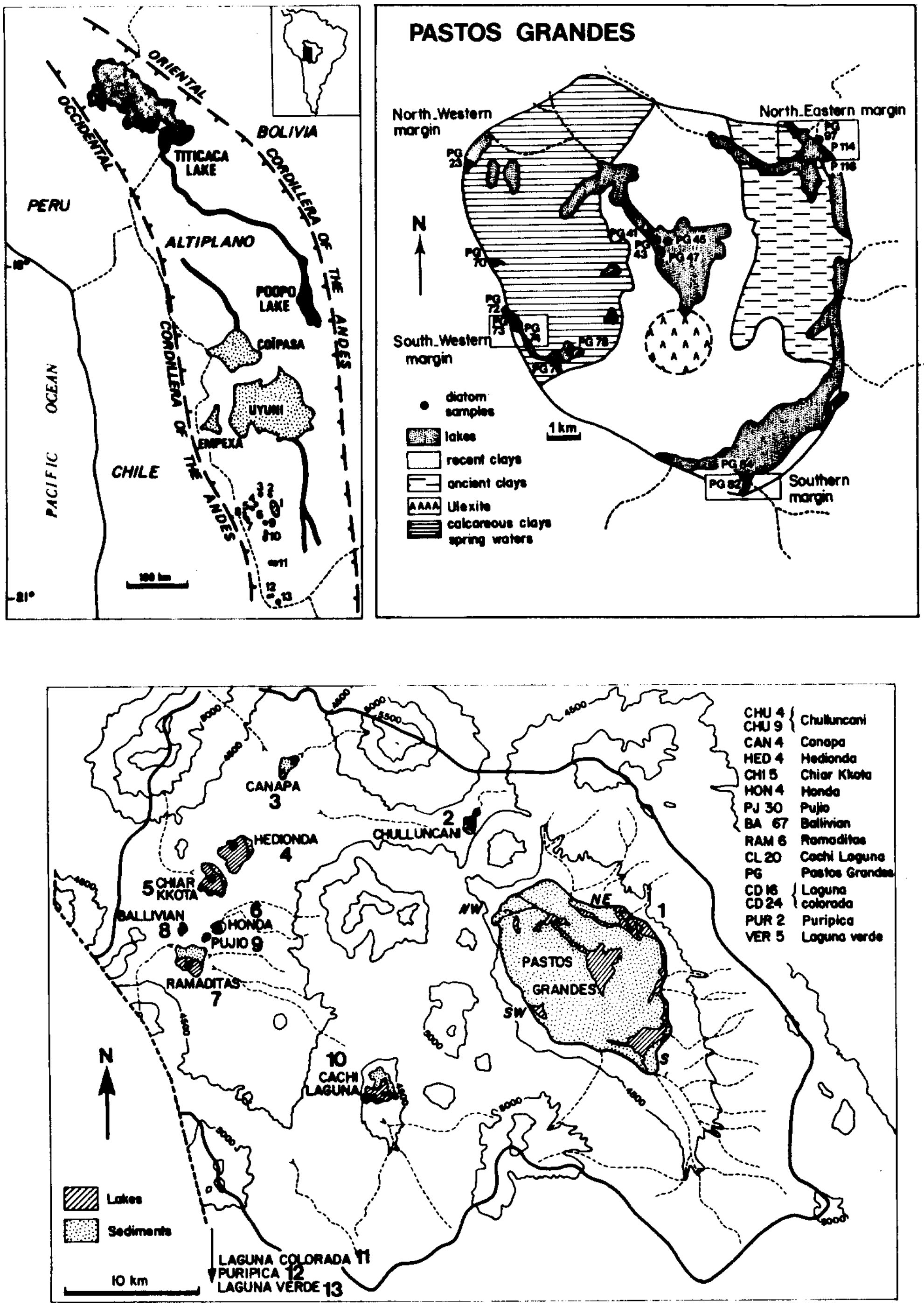


Fig. 1. Geographical location of the sites studied. Samples for diatom analysis with the list of the codes are located for the small lakes in the lower part, and for Pastos Grandes in the right upper part.

frustules counted in each samples varied between 251 and 4500, including subliving diatoms from surface sediments and living diatoms from the water column.

Water analysis to determine sodium, potassium, lithium, calcium and magnesium (Na, K, Li, Ca, Mg), chloride (Cl), sulphate (SO_4) and silicate (Si) were done in the laboratory several months after sample collection.

Codification of the samples is explained by the following examples. Diatom sample BA67 from Lake Ballivian is chemically characterized by the corresponding water sample, named BAL1. In the largest lake, Pastos Grandes, all the samples are named with four characters: the first or the two first letters of the lake name, 'P' or 'PG', followed by two (PG41) or three numbers (P114). They are characterized by the corresponding water samples called PAG. Analytical methods used are: atomic absorption spectroscopy to determine sodium, potassium, lithium, calcium and magnesium; mercurium thiacyanate colorimetry for chloride; indirect colorimetry with methylthymol blue upon excess of Ba after precipitation of $BaSO_4$ for sulfate; colorimetry with ammonium molybdate for silicium.

Statistical analysis

1. *The factor analysis of correspondences* (FAC) (Greenacre, 1984; Lebart *et al.*, 1984) or reciprocal averaging (Hill, 1973), is currently used for species and sample data (Gauch, 1982). In this case we have used this same method for processing the chemical data. It is an extension of principal components analysis (PCA) well suited to deal with either categorical variables or count variables. Its main feature is to take into account the margins of the data table, that is the sum of the scores for species and for samples. The underlying distance function is said to be double weighted. For the distance between samples i and i′, the formula is:

$$D^2_{ii'} = \Sigma_j \frac{1}{x_j} \left(\frac{x_{ij}}{x_i} - \frac{x_{i'j}}{x_{i'}} \right)^2$$

where

x_{ij} is the score of species j in sample i

$x_i = \Sigma_j \times ij$ = sum of scores of sample i

$x_j = \Sigma_i \times ij$ = sum of scores of species j

2. *The cluster analysis*: in order to make up groups of samples and species we used a cluster analysis (Ward, 1963). It is an hierarchical agglomerative process based on the variance of the intragroup distances.

Instead of a direct processing of the species percentage table, we computed the usual Euclidean distances on samples from their factor analysis coordinates. Taking into account the 6 most significant axis, summarizing a variance of 58%, we eliminate the random fluctuations of the abundances and rely upon an overall more stable process.

3. *Variables/classes and classes/variables contributions program.* After having condensed the samples into groups or classes of homogeneous flora, we felt it necessary to determine whether some chemical variables were responsible for these different assemblages. The computations performed consist in decomposing the generalized sum of squares interclasses deviations (SSID):

$$SSID = \Sigma J \, \Sigma k \; nk \, (\bar{x}_{kj} - \bar{x}_j)^2$$

where:

nk = number of samples in group k

x_{kj} = mean value of variable j within group k

x_j = mean value of variable j over all samples.

The quantity, $nk\,(\bar{x}_{kj} - \bar{x}_j)$, which weights the deviation of group k from the overall mean of variable j, may be regarded as the share of variable j and class k in the SSID. But such a figure is easier to group when expressed as a ratio. We computed two types of ratios, filling up two different tables as follows.

In the first table we put up the ratios (as percentages):

$$100\,(\bar{x}_{kj} - \bar{x}_j)^2/\Sigma J\,(\bar{x}_{kj} - \bar{x}_j)^2$$

For each particular group k, these figures allow for determining the most discriminant variables. The second table is filled with the following values:

$$100\, nk\,(\overline{x}_{kj} - \overline{x}_j)^2 / \Sigma k\, \Sigma nk\,(\overline{x}_{kj} - \overline{x}j)^2$$

which indicates the most typical class with regard to a particular variable J.

4. *Variables/classes and classes/variables interactions program*. This program is used to quantify the ionic variables which mostly influence each group of samples and each species. We have separated the values of each chemical variable into three classes or modalities corresponding to low, medium, high concentrations. Each of them becomes a new variable, a *category*, and a new table is built up, the rows of which are the species and the columns are the categories. Each cell (i, j) of the table contains the mean percentage of species i, among all the samples falling in the category j. In other words the cells of the table are made of mean floristical abundances, but the columns of the table represents modalities (low, medium, and high) of chemical variables. In this way, we enforce the factor analysis of correspondences (FAC) to work out the relationship between species and chemical variables. This method gives us the possibility to see in the same graph both the classes and the chemical variables, ordinated from lower (1) to higher values (3).

Combining the methods (CA, CVC, CVI and FAC), we can determine the chemical variables which characterize each cluster and we can quantify the relative role of a chemical variable on the cluster but also on each sample and each species. This method also computes and submits to factor analysis the environmental data which are not in the same units, such as pH, depth, temperature, elevation.

Results

The diatom flora

Ninety four Pennatophycideae species (Table 2) were identified in the 30 samples. Good preservation of the frustules can be observed (Fig. 9–56) which indicates that dissolution of the frustules in the sediment water interface can be neglected and that our samples can be considered as good representatives of the sampling sites. Basic environmental data are given in Table 1.

According to many authors (Frenguelli, 1945; Krammer, 1980; Krammer & Lange-Bertalot, 1985, 1986; Osada & Kobayasi, 1985), the species identified can be distributed in four general groups: Endemic, athalassic and/or sea-related, athalassic saltwater and fresh-oligohaline species.

Most of the species are linked to low water level habitats. Most of them are benthic, epiphytic and aerophilous. There are no euplanktonic species but some of them can tolerate depth variations (eurytopic) and can be planktonic or tychoplanktonic: *Ceratoneis arcus*, *Fragilaria brevistriata*, *Fragilaria pinnata*, *Synedra rumpens*, *Nitzschia palea*. The pH is always higher than 7, thus most of species have to be alkaliphilous or alkalibiontic, but some are pH-indifferent.

(i) Comparisons between published and local affinities to the salinity.

Achnanthes linearis, *Amphora libyca*, *Cymbella affinis*, *Cymbella norvegica*, *Neidium apiculatum*, *Neidium bisulcatum*, *Rhopalodia gibba* considered as halophobous or oligohalines were only found in the low salinity samples (PG72, PG74, PG82, PG97, PG23). The local ecological affinity agrees with the literature data.

Few species were found in samples with salinities between 10 and 30 g l^{-1} (RAM6, VER5, HON4, CAN4, CHU9, PG70, PG73, PG76, PG41, PG43). *Achnanthes chilensis* mesohalobous according to Hustedt (1927), is abundant in VER5, 13.5 g l^{-1}, but two oligohalines species live here in saline waters: *Caloneis silicula* in CAN4 13.8 g l^{-1} and *Amphora ovalis* in CHU9 11.2 g l^{-1}.

Among the species restricted to the hyperhaline samples (BA67, HED4, PJ30, PUR2, CHI5, CHU4, CL20, CD16, CD24, PG78, P114, P116, PG45, PG47), *Mastogloia smithii amphicephala* was considered as mesohalobous by De Wolf

Table 1. Physical and chemical characteristics of the sites studied. Lakes BA-Ballivian, RAM-Ramaditas, VER-Laguna verde, PJ-Pujio, HON-Honda, CHI-Chiar Kkota, CAN-Canapa, CHU-Chulluncani, CD-Laguna Colorada, CL-Cachi laguna, PG and P-Pastos Grandes. Numbers after the lake code mean the samples chemically well characterized. Elev.: Elevation (m), W. Long.: West longitud, SW Lat.: Southwest latitude, Water L.: water level (cm), Temp.: temperature (°C), Dens.: density g cm^{-3}, pH, Alk: alkalinity (meq l^{-1}), ionic contents (mM l^{-1}), TDS: total dissolved salts (g l^{-1}).

Diatom s. Water s.	BA67 BAL1	RAM6 RAM5	VER5 VER2	HED4 HED3	PJ30 PUJ5	PUR2 PUR4	HON4 HON3	CHI5 CHI4
Elev.	4117	4120	4350	4120	4110	4393	4110	4112
W. Long.	68°05	68°05	67°48	68°03	68°04	67°30	68°04	68°04
SW. Lat.	21°38	21°38	22°48	21°34	21°37	22°31	21°37	21°35
Water L.	–	30	<100	20	100	100	20	20
Temp.	5	1	2	8	1	4	6	8
Dens.	1.03	1.02	1.01	1.05	1.02	1.02	1.01	1.05
pH	8.18	8.15	8.72	8.5	8.85	8.52	8.28	8.05
Alk	4.88	2.93	7.25	10	7.22	7.8	4.4	8.05
Cl	620	392	182	693	400	430	290	1090
SO_4	59.4	32	24	186	45	48.5	27.1	42.5
B	13.9	7.12	11.6	21.7	13.4	22	5.27	23.1
Si	0.9	1.48	1.02	0.983	0.933	0.735	1.13	1.23
Na	591	330	196	885	435	415	293	900
K	43.5	26.3	7.88	53.7	26.1	44	25.3	63.9
Li	3.67	1.7	5.26	17.6	5.33	15.7	6.77	25.4
Ca	29.9	34.2	5.44	13	9.98	11.6	4.99	33.4
Mg	24.9	13.4	10.8	26.7	8.64	11.3	5.76	46.9
TDS	45.2	29	13.5	72.3	35.9	32.7	25.6	69.4

Diatom s. Water s.	CAN4 CAN3	CHU4 CHU3	CHU9 CHU2	CD16 CLD4	CD24 CLD33	CL20 CAL19
Elev.	4140	4430		4278		4495
W. Long.	68°01	67°53		67°47		67°57
SW. Lat.	21°·	21°32		22°11		21°43
Water L.	15	15		20		
Temp.	6	5	8	6	10	21
Dens.	1.009	1.087	1.008	1.08	1.04	1.02
pH	9.18	8.8	10.2	8.4	8.5	10.38
Alk	2.15	35	11.4	31.5	12.9	355
Cl	63.4	1240	55.5	1830	831	128
SO_4	52.8	277	45.4	61.1	62.3	38.6
B	23.1	1.2	88.7	56.6	2403	13.2
Si	1.12	0.783	0.667	1.63	1.16	5.75
Na	156	1310	101	1770	865	460
K	5.42	327	46	109	54	73
Li	2.81	3.24	0.396	28.2	1205	7.8
Ca	1.62	18.2	4.99	6.48	2.57	0.06
Mg	1.4	78.2	2.18	37.2	15.7	6.03
TDS	13.8	144.4	11.2	120.35	59.16	36.27

Table 1. (continued).

Pastos Grandes: Central lake

Diatom s. Water s.	PG23 PAG22	PG41 PAG40	PG43 PAG30	PG45 PAG44	PG47 PAG48
Elev.	4400				
W. Long.	67°47				
SW. Lat.	21°39				
Temp.	1	4	6	5	5
Dens.	1.001	1.02	1.01	1.073	1.211
pH	9.35	8.52	8.05	7.4	7.2
Alk	1.51	4.25	3.21	9.08	22.9
Cl	19.7	470	227	1730	5470
SO_4	0.75	4.84	2.6	13.2	25.6
B	0.323	5.55	2.63	26.8	87.3
Si	1.37	1.13	0.617	0.733	1.12
Na	19.6	403	196	1480	4480
K	1.1	26.1	12.8	101	363
Li	0.692	16.9	7.57	72.1	236
Ca	0.612	8.98	4.99	27.4	77.3
Mg	0.453	10.9	5.43	4.53	143
TDS	1.4	26.7	14.2	103	371.2

Pastos Grandes: W–N lake W–S lake

Diatom s. Water s.	PG70 PAG69	PG72 PAG72	PG74 PAG74	PG73 PAG73	PG76 PAG75	PG78 PAG77
Temp.	5	10	1	1	10	10
Dens.	1.009	1	1.009	1.001	1.01	1.098
pH	8.42	6.95	8.15	7.85	8.35	7.91
Alk	5.09	3.3	5.13	4.2	3.85	9.42
Cl	204	2.54	190	16.9	234	2420
SO_4	2.76	1.09	3.15	1.35	3.18	30.4
B	2.77	0.092	2.36	0.27	2.96	29.6
Si	1.3	1.33	2.1	1.08	1.15	1.22
Na	174	3.48	170	15.2	196	2000
K	13.6	0.422	10.2	1.23	14.8	128
Li	6.12	0.073	6.12	0.56	8.29	86.5
Ca	4.99	1.27	4.74	0.815	4.99	37.4
Mg	3.7	0.831	5.68	2.28	5.43	49.4
TDS	13.1	0.6	12.1	1.54	14.3	144.1

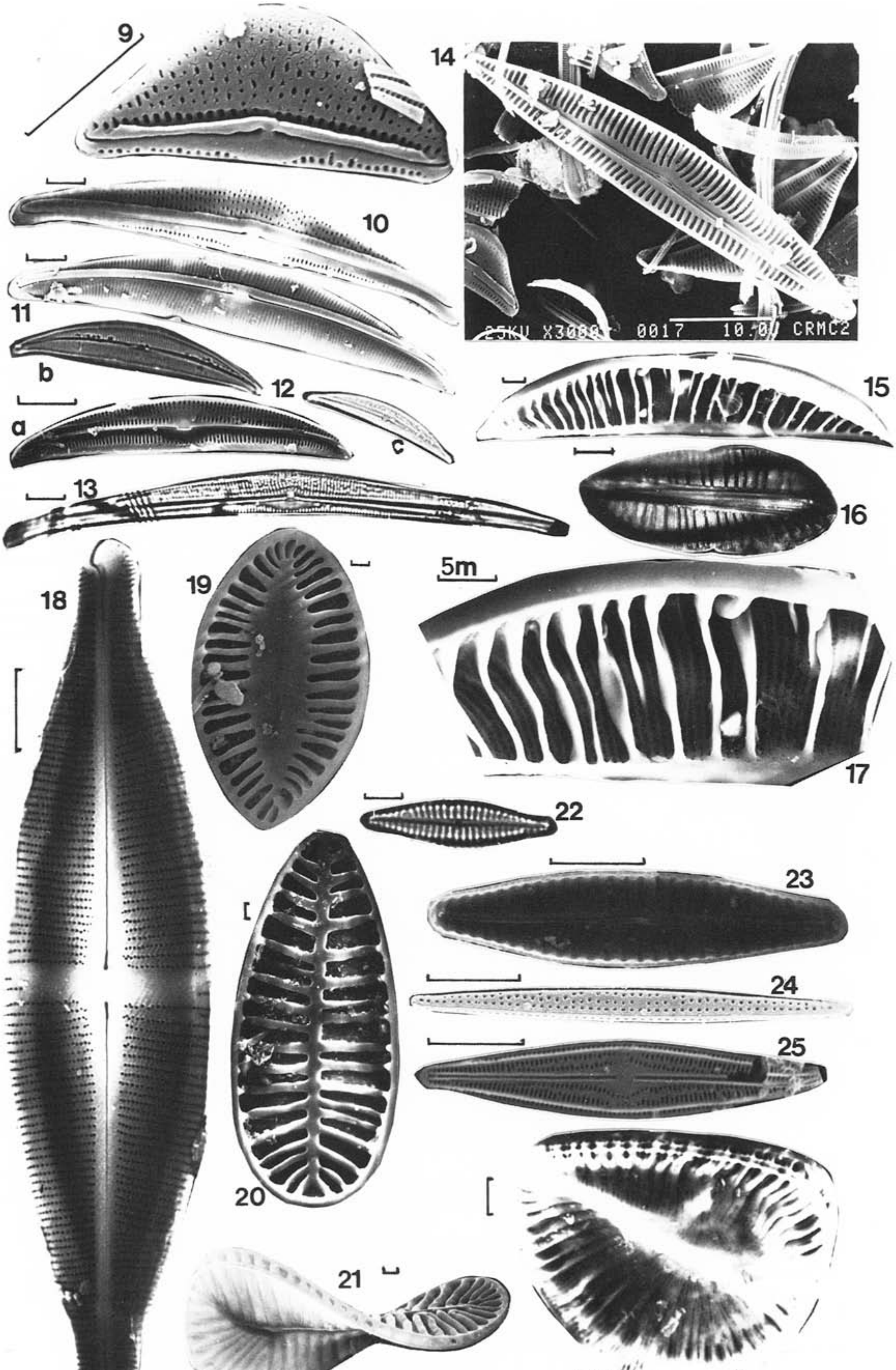
Pastos Grandes: Southern lake Eastern lake

Diatom s. Water s.	PG82 PAG81	PG84 PAG83	PG97 PAG96	P114 PAG124	116 PAG115
Temp.	10	15	10	10	7
Dens.	1	1.14	1	1.16	1.17
pH	9.62	7.46	8.92	6.95	7.5
Alk	0.523	9.7	1.36	7.68	13.1
Cl	1.78	3770	4.23	4330	4450
SO_4	0.146	35.1	0.052	33.8	33.1
B	0.065	37.4	0.1	50.4	48.1
Si	0.567	1.18	0.8	0.6	1.12
Na	1.82	3350	3.7	3520	4000
K	0.113	165	0.322	251	3520
Li	0.05	97.3	0.17	167	124
Ca	0.152	41.1	0.312	59.4	62.3
Mg	0.132	51.4	0.305	105	85.6
TDS	0.19	225.3	0.40	255.23	267.36

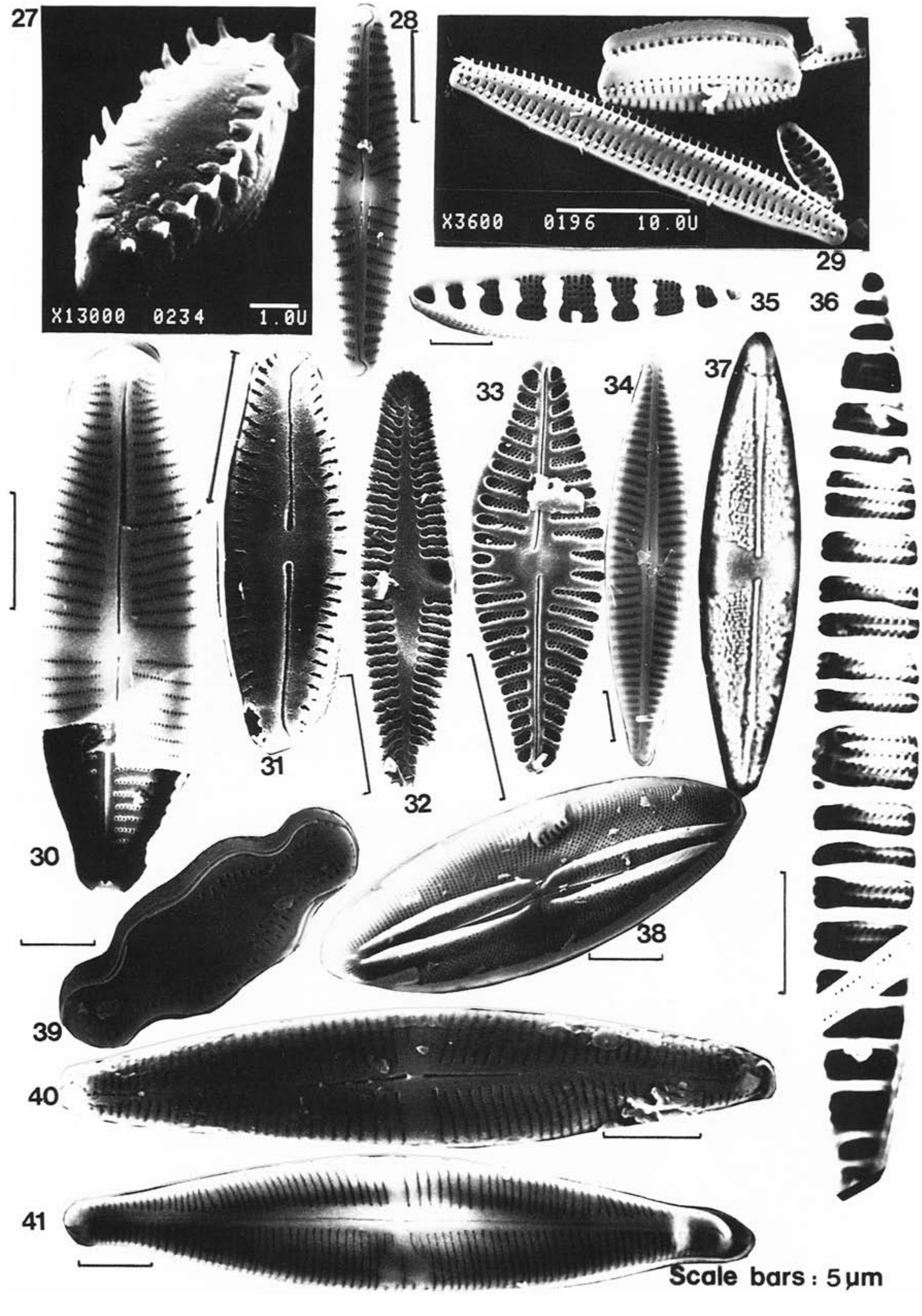
Table 2. The diatom flora. Column 1, Ecology: E = endemic species, A = athalassic saltwater species, M = marine or sea-related species, F = freshwater species. O = oligohaline species. Column 2, Alphabetical list of taxa. Column 3, Codes of taxa.

Ecology	Taxa	Codes	Ecology	Taxa	Codes
FO	*Achnanthes arenaria* Amossé	AL	FO	*N. gastrum* Ehrenberg	NG
AM	*A. breviceps* Agardh	ABR	F	*N. mutica binodis* Hustedt	NMB
EA	*A. chilensis* Hustedt	ACI	F	*N. mutica nivalis* (Ehr.) Hustedt	NMN
A	*A. delicatula* (Kütz) Grunow	AD		*N.* nov. sp.	NNS
FO	*A. linearis* W. Smith	ALI	F	*N. pseudolitoricola* Häkansson	NLI
FO	*A. speciosa* Hustedt	AS	FO	*N. pseudolanceolata* Lange-Bertalot	NL
EA	*Amphora atacamae* Frenguelli	AAM	FO	*N. pupula* Kützing	NPP
EA	*A. boliviana* Patrick	ABE	AM	*N. pygmaea Kützing*	NPY
EA	*A. boliviana f. elongata*	ABE	FO	*N. rhynchocephala* Kützing	NR
EA	*A. carvajaliana* Patrick	AC		*N.* sp.	NS
EA	*A. chilensis* Hustedt	ACI	F	*Neidium apiculatum* Reimer	NEA
FO	*A. libyca* Rhrenberg	AY	F	*N. bisulcatum* (Lagerstedt) Cleve	NEB
AM	*A. lineolata* Ehrenberg	AML	EA	*Nitzschia accedens chilensis* Patrick	NAC
FO	*A. ovalis* Kützing	AO	FO	*N. alpina* Hustedt	NA
E	*A. platensis* Frenguelli	AP	AM	*N. denticula* Grunow	ND
AM	*Anomoeoneis sphaerophora*		A	*N. epithemioides* Grunow	NE
	var. *angusta* Frenguelli	ASA	AM	*N. frustulum* (Kütz.) Grunow	NF
AME	*A. sph. navicularis* (O. Muller) Frenguelli	ASN	AM	*N. grunowii* (Cleve) Hasle	NIG
AM	*A. sph. platensis* Frenguelli	ASP	FO	*N. hantzschiana* Rabenhorst	NIH
AM	*A. sph. polygramma* (Ehr.) O. Muller	ANS	AM	*N. hungarica* Grunow	NHU
AM	*Brachysira aponina* Kutzing	BA	OA	*N. inconspicua* Grunow	NI
FO	*Caloneis silicula* (Ehr.) Cleve	CS		*N. minutula* Grunow	NM
	C. sp.	CSP		*N.* nov. sp.	NINS
AM	*C. westii* (W. Smith) Hendey	CW	AM	*N. palea* (Kütz.) W. Smith	NPA
FO	*Ceratoneis arcus* Kützing	CA	AM	*N. punctata* (W. Smith) Grunow	NP
FA	*Cocconeis placentula* Ehrenberg	CP	AM	*N. pusilla* (Kutz.) Grunow	NPU
FO	*Cymbella affinis* Kützing	CYA	AM	*N. quadrangula* Lange-Bertalot	NQ
FO	*C. lunata* W. Smith	CYL	A	*N. valdecostata* Lange-Bertalot	NV
FO	*C. norvegica* Grunow	CYN	FO	*Opephora martyi* Heribaud	OM
	C. sp.	CYS	F	*Pinnularia bogotensis* Grunow	PB
AM	*Denticula elegans* Kützing	DE	FO	*Rhopalodia gibba* (Ehr.) O. Muller	RG
AM	*D. elegans f. valida* Pedicino	DEV	EA	*R. wetzeli* Hustedt	RW
AM	*D. thermalis* Kützing	DT	A	*Scoliopleura peisonis* Grunow	SP
A	*Entomoneis alata* Kützing	AAL	F	*Stauroneis anceps* Ehrenberg	SA
F	*Fragilaria brevistriata* Grunow	FB	A	*S. bathurstensis* Giffen	SB
F	*F. contruens venter* (Ehr.) Grunow	FCV	A	*S. gregorii* Ralfs	SG
F	*F. elliptica* Schumann	FE	A	*S. legleri* Hustedt	STL
FO	*F. pinnata* Ehrenberg	FP		*S.* spd.	SSPD
F	*F. zeilleri* Heribaud	FZ		S. sp.	SSP
F	*Gomphonema parvulum* Kützing	GP	EA	*Surirella chilensis* Janish	SC
F	*Hantzschia amphioxys maior* Grunow	HN	FO	*S. oregonica* Ehrenberg	SO
	H. nov. sp.		A	*S. ovata utahensis* Grunow	SOU
EA	*Mastogloia atacamae* Frenguelli	MA	A	*S. peisonis* Hustedt	SUP
	M. smithii amphicephala Grunow	MSA	EA	*S. sella* Hustedt	SUS
A	*Navicula cari cincta* (Ehr.) Lange-Bertalot	NCC	EA	*S. wetzeli* Hustedt	SW
AM	*N. cincta* (Ehr.) Kützing	NCI	A	*Synedra pulchella* Kützing	SYP
FO	*N. cryptocephala* Kützing	NC	FO	*S. rumpens* Kützing	SYR

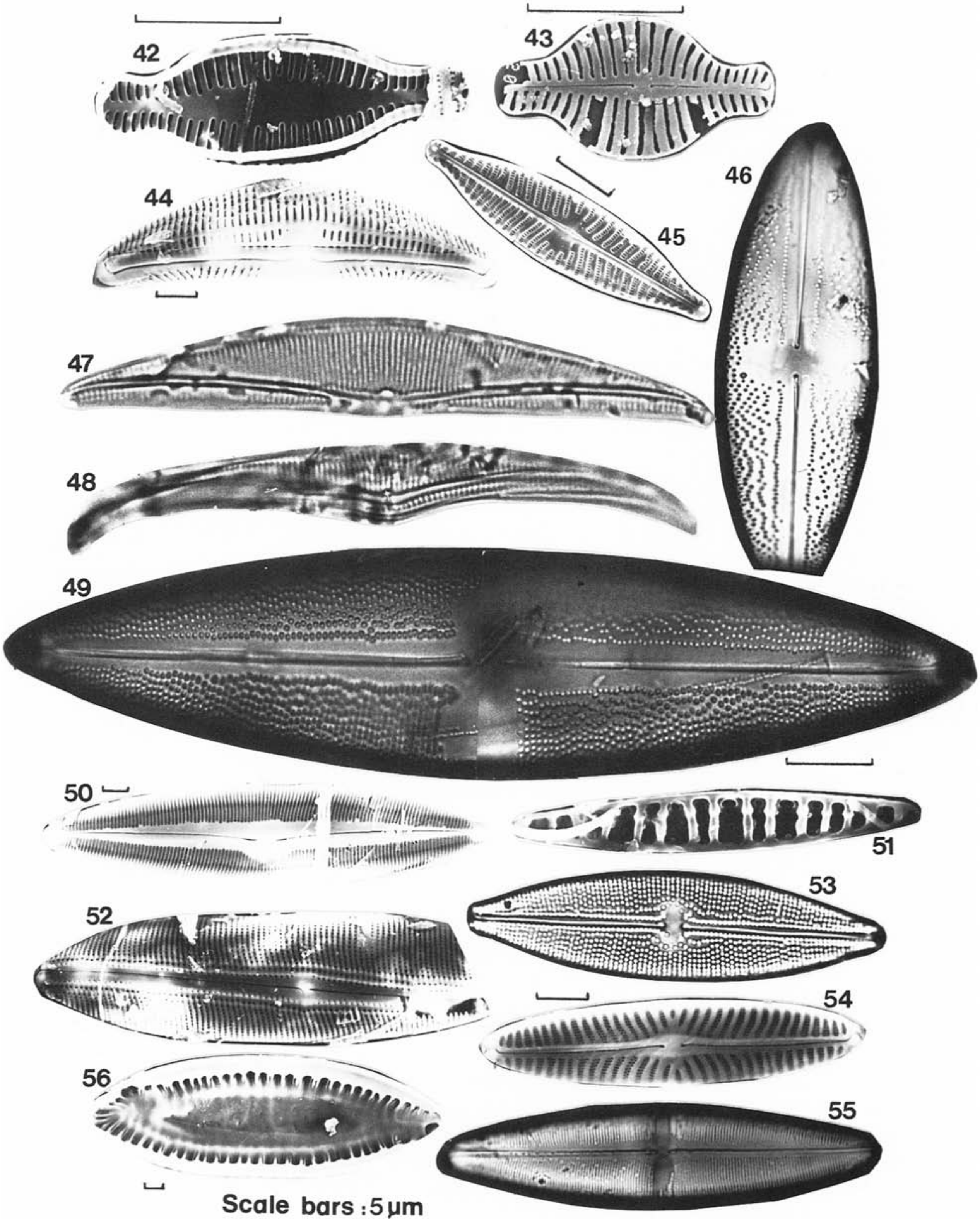
Figs. 9–26. 9, *Amphora carvajaliana* Patrick; 10, *Amphora boliviana* Patrick; 11, *Amphora atacamae* Frenguelli, a: external valve view, b: LM; 12, *Amphora atacamae* Frenguelli, a: internal valve view, b: LM, c: this small form is called var. *minor* in the countings (Table 4); 13, *Amphora boliviana* Patrick, var. *elongata* in the countings; 14, *Cymbella gracilis* (Ehr.) Kützing, *Cymbella lunata* in Table 4; 15–17, *Rhopalodia wetzeli* Hustedt, 15, internal valve view, 16, LM, 17, detail of the costae; 18, *Stauroneis bathurstensis* Giffen, 19, *Surirella sella*, Hustedt; 20, *S. wetzeli* Hustedt; 21, *S. wetzeli*, twisted specimen; 22, *Navicula* sp., *Navicula* nov. sp. in Table 4; 23, *Navicula* sp., internal valve view; 24, *Nitzschia* sp., 25, *Brachysira aponina* Kützing; 26, *Surirella ovata* var. *utahensis* Grunow. ⟶



Scale bars : 5 µm



Figs. 27–41. 27, ***Fragilaria brevistriata*** Grunow; 28, *Navicula cincta* (Ehr.) Kützing; 29, ***Fragilaria zeilleri*** Heribaud; 30, ***Stauroneis anceps*** Ehrenberg; 31–32, ***Achnanthes chilensis*** Hustedt, 31, external view of the hypovalve, 32, internal view of the epivalve; 33, ***Achnanthes delicatula*** (Kütz.) Grunow; 34, ***Navicula pseudolanceolata*** Lange-Bertalot; 35, ***Denticula elegans*** f. *valida* Pedicino; 36, ***Denticula thermalis*** Kützing; 37, ***Stauroneis*** sp.; 38, ***Navicula pygmaea*** Kützing; 39, ***Navicula mutica binodis*** Hustedt; 40–41, ***Stauroneis legleri*** Hustedt.



Figs. 42–56. 42–43, *Achnanthes arenaria* Amossé, 42: internal view of the epivalve, 43: external view of the hypovalve; 44, *Amphora libyca* Ehrenberg; 45, *Navicula cryptocephala* Kützing; 46, *Anomoeoneis sphaerophora* var. *polygramma* (Ehr.) O. Müller; 47–48, *Amphora lineolata* Ehrenberg, 49, *Anomoeoneis sphaerophora* var. *platensis* Frenguelli; 50, Caloneis westii (W. Smith) Hendey; 51, *Denticula elegans* Kützing; 52, *Scoliopleura peisonis* Grunow; 53, *Mastogloia smithii* var. *amphicephala* Grunow (cf. *M. patens* Frenguelli); 54, *Navicula cari* var. *cincta* (Ehr.) Lange-Bertalot (cf. *N. cari* (Ehr.) Ralfs); 55, *Stauroneis gregorii* Ralfs (cf. *S. amphioxys* Gregory); 56, *Surirella chilensis* Janish.

Table 3. Relative abundances of diatom taxa, the basic units for the analysis (in per mil).

Taxa	Samples																													
	BA67	RAM6	VER5	HED4	PJ30	PUR2	HON4	CH15	CAN4	CHU4	CHU9	CL20	CD24	CD16	PG70	PG23	PG41	PG43	PG45	PG47	PG72	PG73	PG76	PG74	PG78	PG82	PG84	PG97	P114	P116
Achnanthes breviceps	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	18	0	0
Achnanthes chilensis	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Achnanthes delicatula	0	0	0	0	12	0	0	0	0	0	0	0	0	1	0	9	12	45	12	0	0	0	0	0	0	0	0	0	4	0
Achnanthes arenaria	23	5	5	0	0	0	126	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Achnanthes linearis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0
Achnanthes speciosa	40	1	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
Amphiprora alata	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphora libyca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphora atacamae	0	0	0	8	34	19	10	0	17	0	0	0	0	31	7	0	44	67	0	49	0	0	31	0	115	7	87	0	4	18
Amphora atacamae minor	0	0	0	0	0	3	0	13	0	0	0	0	0	0	0	0	45	45	0	22	0	0	0	0	53	0	0	0	0	38
Amphora boliviana	10	0	4	0	0	0	2	0	0	0	1	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphora boliviana elongata	0	0	0	0	0	0	0	0	0	0	6	0	0	0	27	8	0	0	6	13	0	32	0	39	0	0	2	0	0	0
Amphora carvajaliana	23	0	0	874	541	632	715	895	0	96	0	0	1	64	126	8	60	61	24	31	5	15	52	18	13	11	14	0	0	0
Amphora chilensis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphora lineolata	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0
Amphora ovalis	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphora platensis	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomoeoneis sphaerophora angusta	0	0	0	2	2	0	0	0	0	7	1	0	2	1	7	0	0	0	0	0	0	0	0	0	0	2	0	6	0	0
Anomoeoneis sphareophora polygramma	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomoeoneis sphaerophora platensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	44	0	0	0	0	0	0
Anomoeoneis sphaerophora navicularis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0
Brachysira aponina	3	39	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caloneis silicula	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caloneis sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
Caloneis westii	1	1	0	0	0	0	0	0	0	0	0	0	0	0	23	28	0	0	0	0	0	31	0	33	0	2	2	0	0	0
Ceratoneis arcus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cocconeis placentula	0	10	37	0	4	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Cymbella affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
Cymbella lunata	44	5	0	0	118	0	25	13	0	0	0	0	0	1	10	2	0	0	6	0	0	94	34	80	26	0	0	0	0	0
Cymbella norvegica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	0	0
Cymbella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Denticula elegans	47	23	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Denticula elegans valida	0	7	148	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Denticula thermalis	6	5	1	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fragilaria brevistriata	0	0	0	0	0	0	0	0	40	15	0	0	0	0	346	735	47	0	0	94	0	66	4	56	13	0	0	0	104	52
Fragilaria construens venter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	83	0	0	0	0	0	0	14	17	0	17	0	18	0
Fragilaria elliptica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	73	120	58	0	11	0	0	0	0	0	0	0	0
Fragilaria pinnata	0	0	0	0	0	0	0	0	17	0	0	0	0	0	7	0	15	0	24	13	0	0	0	0	0	123	0	0	0	90
Fragilaria zeilleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	6	0	0	0	0	0	18	0	426	0	0	0	0
Gomphonema parvulum	0	0	0	0	0	0	0	0	23	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	18	0	0
Hantzschia amphioxys major	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	6	4	0
Hantzschia nov. sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	120	0	0	6	0	2	0	130	4	0
Mastoglia atacamae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	5	0	0	12	0	0	156	78	177	6	2	8	12	0	6
Mastoglia smithii amphicephala	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Navicula cari cincta	0	0	0	0	0	3	0	16	5	0	0	0	0	1	0	1	6	0	0	4	0	0	0	0	0	0	65	0	69	0
Navicula cincta	0	0	0	0	0	6	0	0	92	7	15	0	23	10	23	1	0	6	0	9	500	99	62	189	8	196	12	40	34	22
Navicula cryptocephala	16	5	2	4	12	89	12	1	63	0	0	0	1	51	15	8	89	73	54	85	0	0	46	12	123	78	27	320	90	92
Navicula gastrum	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Navicula mutica binodis	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	125	0	0	0	0	2	6	54	4	6
Navicula mutica nivalis	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	2	0	110	0	3
Navitula nov. sp.	3	5	0	0	59	16	15	0	0	0	0	0	0	228	20	0	121	214	192	255	0	0	31	0	126	19	434	0	324	236
Navicula pseudolitoricola	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	4	0	2	0	0	0
Navicula pseudolanceolata	0	0	0	0	0	0	1	0	260	514	13	0	13	0	0	0	0	0	0	0	0	161	0	0	0	0	0	0	0	0
Navicula pupula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4	0	0	0
Navicula pygmaea	1	1	0	0	0	0	0	1	0	0	0	0	0	0	3	12	0	6	0	0	0	0	0	0	0	2	0	0	0	0
Navicula rhynchocephala	6	3	4	22	38	79	38	0	0	0	0	0	0	55	70	0	103	129	177	27	15	0	256	56	331	0	0	60	60	110
Navicula sp.	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	11	3	16	0	4	0	0	0	6	0	0	0	0	0	0
Neidium apiculatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Neidium bisulcatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Nitzschia accedens chilensis	0	0	14	0	0	0	2	1	0	0	0	0	0	62	3	1	57	85	12	73	0	0	4	0	22	9	71	0	18	82
Nitzschia alpina	0	0	0	0	0	0	0	0	0	0	0	0	37	48	0	1	0	0	0	22	0	0	0	0	0	0	0	0	0	0
Nitzschia denticula	0	0	0	0	0	0	0	3	23	0	0	0	1	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0
Nitzschia epithemioides	0	0	0	0	0	0	0	0	17	0	0	0	0	17	0	0	28	101	66	54	0	0	0	0	17	7	90	0	41	73
Nitzschia frustulum	0	0	0	0	0	0	0	0	0	0	4	0	0	0	35	0	15	0	18	0	30	0	0	4	13	16	14	60	13	0
Nitzschia grunowii	6	0	2	0	24	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Nitzschia hantzschiana	13	14	0	0	19	66	7	0	0	15	0	0	0	0	0	0	0	0	0	0	185	51	0	14	0	14	0	0	0	0
Nitzschia hungarica	0	0	0	4	0	29	0	0	150	47	26	0	0	13	0	5	0	11	12	4	0	23	46	6	13	34	6	50	4	6
Nitzschia inconspicua	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60	0	0
Nitzschia minutula	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nitzschia nov. sp.	654	839	711	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	4	0	0	0	0	0	0
Nitzschia palea	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	9	0	0	0	0	0	0	0	0	0	0	70	0	0	0
Nitzschia punctata	0	0	2	0	16	0	0	0	0	0	0	0	0	0	10	1	3	0	0	0	0	60	25	4	4	2	10	0	0	6
Nitzschia pusilla	0	0	2	0	0	0	0	0	0	0	8	23	3	0	0	0	12	11	24	145	0	0	0	0	0	0	87	0	106	139
Nitzschia quadrangula	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	12	0	0	0	116	0	0	0	0	0	0	0
Nitzschia valdecostata	0	0	0	0	8	19	0	0	80	0	0	0	1	0	20	0	0	0	0	0	0	0	0	14	0	12	0	0	0	0
Opephora martyi	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	19	0	0	4	0	0	0	0	0	0	0	12	8	3	3
Pinnularia bogotensis	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	11	0	18	0	4	2	6	0	0
Rhopalodia gibba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0
Rhopalodia wetzeli	3	0	0	0	0	0	0	6	0	0	0	0	0	0	15	0	6	22	36	4	0	0	34	0	4	2	11	6	4	3
Scoliopleura peisonis	0	10	0	19	20	6	13	26	0	0	0	0	0	0	10	0	0	11	12	0	0	18	31	0	17	2	0	0	0	0
Stauroneis anceps	0	1	0	0	0	0	0	1	0	0	0	0	0	0	20	24	22	11	12	18	0	31	52	4	58	9	4	0	0	0
Stauroneis bathurstensis	0	0	0	0	16	13	12	3	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stauroneis gregorii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	8	0	0	0
Stauroneis legleri	0	0	0	14	0	0	0	0	123	7	0	778	5	440	0	0	22	0	0	0	0	0	0	0	0	0	42	6	8	15
Stauroneis spd.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	2	0	0	0
Stauroneis sp.	0	0	0	0	0	0	0	0	0	0	0	196	0	0	0	2	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Surirella chilensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	7	0	26	0	0	0	0	0	0
Surirella oregonica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	4	0	21	13	82	0	0	0	0	0	0
Surirella ovata utahensis	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Surirella peisonis	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Surirella sella	60	30	19	8	48	0	19	10	0	1	0	0	2	1	90	1	0	1	8	1	0	42	14	104	4	1	0	6	0	0
Surirella wetzeli	0	0	0	152	4	20	1	1	48	268	4	0	0	0	35	1	3	6	36	2	0	39	15	35	1	1	2	0	4	0
Synedra pulchella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Synedra rumpens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	18	4	0
Total frustules	590	1102	700	982	469	604	856	1076	347	251	478	514	888	577	495	1404	627	354	333	444	400	517	402	423	452	821	938	330	431	552

(1982) and halophile by Hustedt (1927), *Amphiprora alata* as mesohalobous by De Wolf (1982) and Frenguelli (1936), *Anomoeoneis sphaerophora polygramma* as oligohalobe by De Wolf (1982), *Surirella ovata utahensis* as euryhaline by Wornardt (1964), *Anomoeoneis sphaerophora navicularis* as brackwasser by Cholnoky (1968), *Navicula pupula* as oligohaline by Hustedt (1959).

The last group concerns the halophobous or oligohaline species which are here living in saline waters and, consequently, must be considered as euryhalines: *Cymbella lunata*, *Fragilaria brevistriata*, *Gomphonema parvulum*. Six freshwater diatoms occur in small quantity in only one high salinity sample. They are considered as allochtonous: *Hantzschia amphioxys maior*, *Ceratoneis arcus*, *Navicula mutica nivalis*, *Navicula mutica binodis*, *Pinnularia bogotensis*, *Synedra rumpens*.

These general comments show that we cannot use only published ecological data for past reconstructions because even for some well-known species, local adaptation to salinity is variable. It is recommended to use living diatoms from the area where paleoecological studies take place. But, even in the best conditions, the applicability of our own data is limited 'to lakes that have remained within the represented ranges of environmental modern parameters' as suggested by Anderson *et al.* (1986).

(ii). Relationships between salinity, number of species and diversity in the Lipez area.

It is generally admitted that the number of species and the diversity are lower in salt than in fresh-

Table 4. Pastos Grandes lake: relation between salinity changes and number of species, salinity changes and dominant species. 2a) No relation between salinity and number of species along a gradient of salinity in the SW margin. 2b, c, d,e) The low salinity samples are characterized by different dominant oligohaline species according to the area. Decrease in number or disappearance of these oligohaline species are observed; they are replaced by a meso-polyhalobous species (*Navicula* nov. sp.) when the salinity increases.

a. South-western area					
Samples	PG72	PG73	PG74	PG76	PG78
Salinity $g\,l^{-1}$	0.6	1.6	12.1	14.4	144
Number of species	9	25	26	21	23
b. South-western area					
Samples	PG72	PG73	PG74	PG76	PG78
Salinity $g\,l^{-1}$	0.6	1.6	12.1	14.3	144
% *Navicula* nov. sp.	0	0	0	3.1	12.6
% *Nitzschia hantzschiana*	18.5	1.4	5.1	0	0
c. Southern area					
Samples	PG82	PG84			
Salinity $g\,l^{-1}$	0.19	225			
% *Navicula* nov. sp.	1.9	43.4			
% *Fragilaria zeilleri*	42.6	0			
d. North-eastern area					
Samples	PG97	P114	P116		
Salinity $g\,l^{-1}$	0.4	255	267		
% *Navicula* nov. sp.	0	32.4	23.6		
% *Navicula cryptocephala*	32	9	9.2		
e. North-western area					
Samples	PG23	PG43	PG41	PG45	PG47
Salinity $g\,l^{-1}$	1.4	14.2	26.7	103	371
% *Navicula* nov. sp.	0	21	12.1	19.2	25.5
% *Fragilaria brevistriata*	73.5	0	4.7	0	9.4

water lakes. In the Bolivian freshwater montane lakes, several hundred species were identified (Servant-Vildary, 1986), against 94 in these saline lakes.

In low salinity samples the Shannon diversity index is generally higher (3.7) than it is in high salinity samples (0.8). However, no defined relationship correlation was observed between decreasing Shannon diversity index and increasing salinity. In Pastos Grandes, on the southern margin, the index value is the same (3.39) in a very low salinity sample PG82 (0.4 g l^{-1}), and in a very high salinity sample PG84 (225 g l^{-1}). Correlation between decreasing number of species and increasing salinity, generally emphasized by many authors, has not been observed in Pastos Grandes. Along a salinity gradient there from the NE margin to the centre, no correlation appeared (Table 4a).

(iii). Relationships between salinity and dominant species.

Different salinities are not often linked to different dominant species. Most of these lakes are characterized by two or three species which represent more than 70% of the total flora. Same dominant species are found in lakes with different salinities. Thus, *Amphora carvajaliana* is the dominant species in five lakes, CHI5, HED4, PJ30, PUR2, HON4, the salinity of which is respectively 77, 72, 35, 32, 25 g l^{-1}. Furthermore, the changes of the salinity observed between 1980 and 1983 are not related either to diatom assemblage composition or to dominant species: In Hedionda, the measured salinity was 72 g l^{-1} in 1980 and 57 g l^{-1} in 1983 and *Amphora carvajaliana* was still the dominant species, the same phenomenon has been observed for Honda (salinity from 25 to 21 g l^{-1}), Puripica (salinity from 32 to 28 g l^{-1}) and Chiar Kkota (salinity from 77 to 119 g l^{-1}). It appears that other parameters in addition to salinity control the growth of a few species.

Different dominant species are found in low salinity samples, as for example in Pastos Grandes below 1.4 g l^{-1}. This can be explained by the origin and chemistry of the freshwater inputs in the lake. *Nitzschia hantzschiana* is dominant in the western part of the lake, *Fragilaria zeilleri*, in the southern part, *Navicula cryptocephala*, in the north-eastern part and Fragilaria brevistriata in the north-western part (Table 4b, c, d, e).

As freshwater-oligohaline conditions change to meso-polyhaline conditions, the relative abundance of freshwater diatoms slowly decreases and saltwater diatoms slowly increase. In Pastos Grandes, the percentage of *Navicula* nov.sp. increases when the salinity increases, at the same time the freshwater-oligohaline species disappear or decrease.

Our observations show that strong modifications of the diatom flora can be explained by the salinity only when it crosses the limit between fresh-oligohaline to meso-hyperhaline conditions (around 2 g l^{-1}). Within these limits, the diatom flora changes are better explained by other parameters.

Classification of the lakes, based on the diatom flora

(i). Definition of groups (or classes) of samples.

The FAC applied to the relative abundances of the 94 taxa (Table 3) in the 30 samples (j = 94 and i = 30) produces 10 factors which account for 78,8% of the distributional variance of the species data base. The factor matrix gives the composition of each sample in terms of the ten factors. There is an important difference between the 4th

Table 5. Factor analysis of correspondences of taxa, inertia values.

Axis	Eigenvalues	Inertia	Cumulate inertia
1	0.86	13.31	13.31
2	0.70	10.77	24.08
3	0.64	9.94	34.02
4	0.60	9.24	43.26
5	0.48	7.44	50.70
6	0.46	7.06	57.76
7	0.38	5.96	63.72
8	0.37	5.72	69.44
9	0.33	5.12	74.56
10	0.27	4.23	78.79

and the 5th axis, but the first five axes have 50.70% of the variance (Table 5).

Factors 1 and 2 represent 24.08% of the total variance. According to these two factors two groups are separated from all others. Along axis 1, group 1 (VER5, BA67, RAM6); group 1 explains 88% of the factor 1. Along axis 2, group 2 (CL20, CD16) explains 88% of the factor 2 (Fig. 2).

In the space defined by axis 3 and 4 (Fig. 3) the remaining 25 samples, located close to the origin

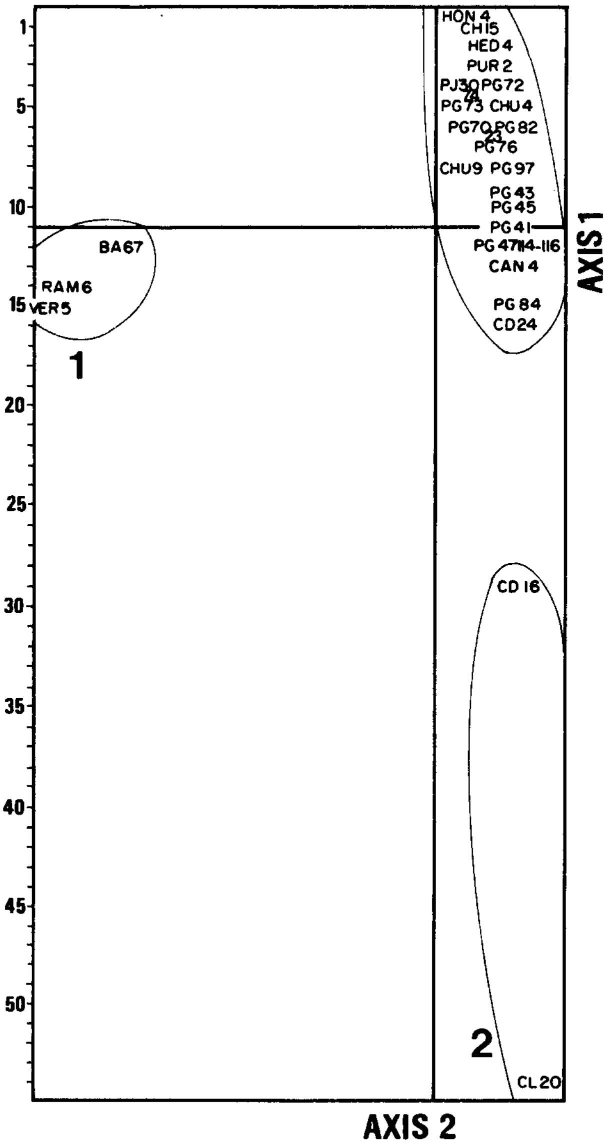


Fig. 2. Projection of the samples points on factorial plane 1–2.

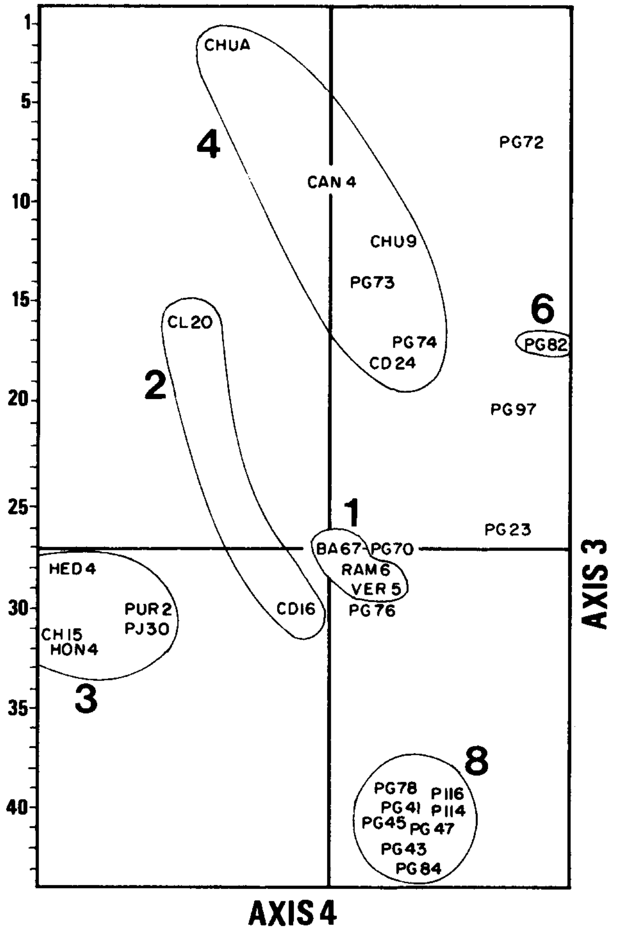


Fig. 3. Projection of the samples points on factorial plane 3–4.

of axis 1 and 2, are distributed in 4 groups. Axis 3 is explained by group 3 composed of HED4, CHI5, HON4, PUR2, PJ30 which accounts for 56% of the inertia and by group 6 composed of one sample PG82 (8% of the inertia) opposed to the former one. Factor 3 explains 64% of the total inertia. Axis 4 is explained by group 4 composed of CHU4, CAN4, CHU9, PG73, PG74, CD24 (39% of the inertia) opposed to the group 8 composed of PG78, PG41, PG45, PG47, PG43, P116, P114, PG84 (38% of the inertia). Factor 4 is explained by 77% of the total inertia.

Group 5 (PG23, PG70) which explains 29% of the total inertia, is opposed to group 7 (PG72, PG97), which explains 50% of the inertia, along axis representing factor 5 (Fig. 4), which accumu-

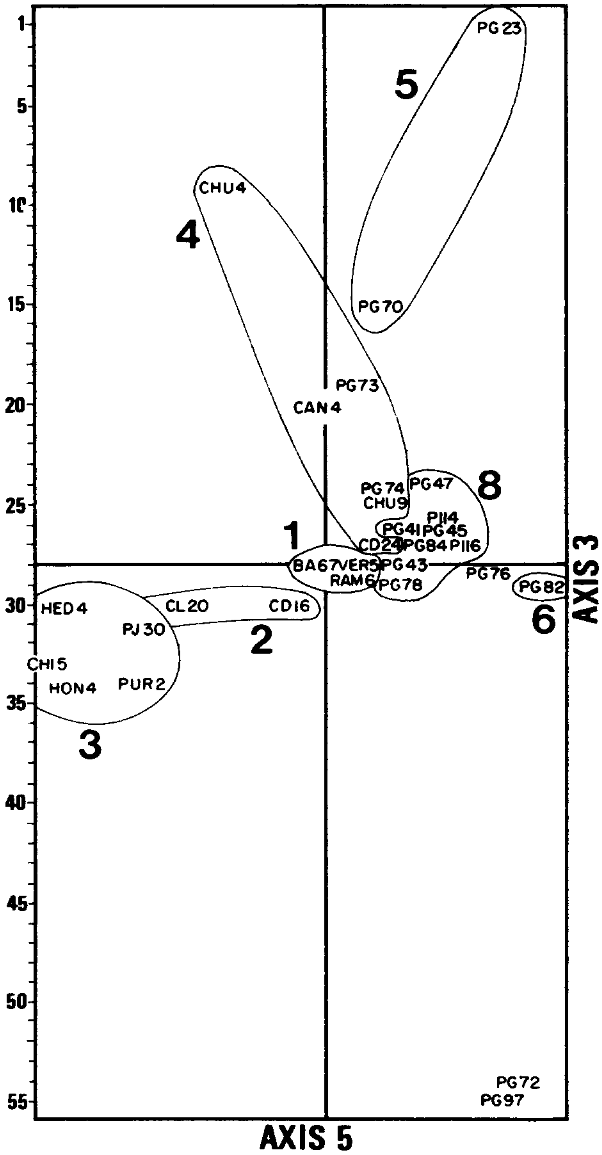


Fig. 4. Projection of the samples points on factorial plane 3–5.

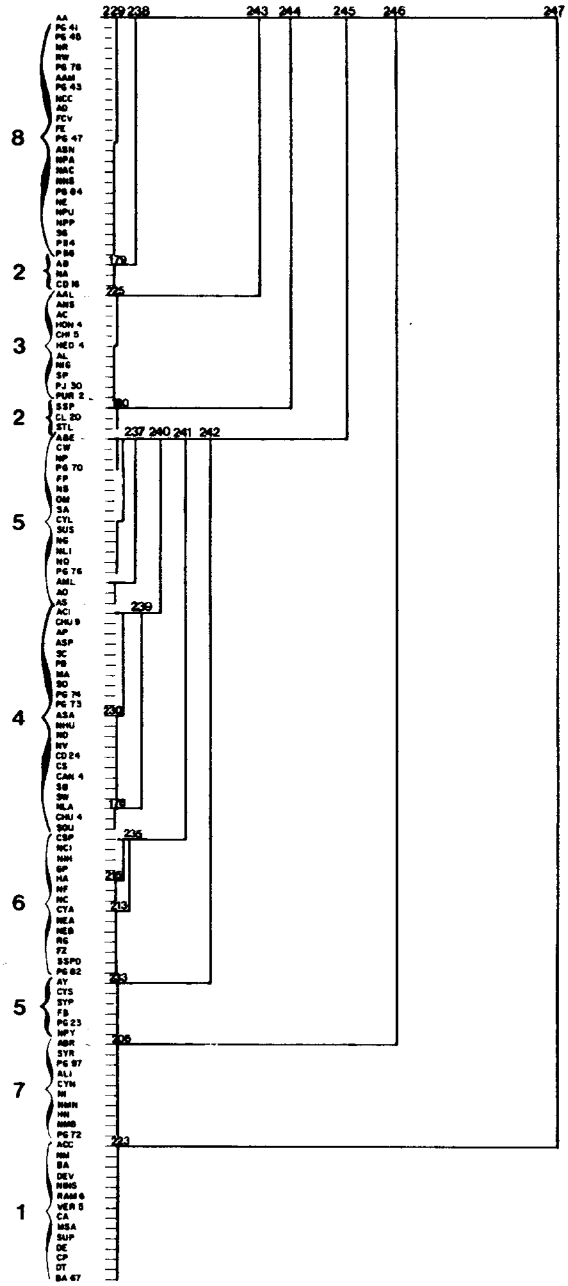


Fig. 5. Cluster Analysis (CA) of samples and taxa. Codes for taxa are given in Table 2.

lates 79% of the inertia. Considering the five first factors, only sample PG76 cannot easily be related to any factor.

(ii). Diatom species ordination.

Cluster analysis of taxa yielded 8 major groups (Fig. 5) composed by species and samples linked by a node: group 1 (node 223), group 2 (244), group 3 (node 225), group 4 (node 239), group 5 (node 237), group 6 (node 235), group 7 (node 206), group 8 (node 229). In order to show the relationships between species and samples in a group, we are able to calculate the values of all the nodes which compose a group. The values are obtained by

$$\Sigma\ CA/\Sigma \text{ components of each node}$$

where CA is the absolute contribution which represents the part of each variable in the variance of the considered axis.

These values give the exact degree of the contribution of each species in each group of samples and the degree of its relation to a sample or to another species. The species are classified according to the degree of correlation: strongly correlated species are named 'characteristic', moderately correlated, 'accompanying species', weakly correlated 'ubiquitous species' (Fig. 6).

For example, in group 1 (Fig. 6,1) samples RAM6 and VER5 are very close; they are characterized by NINS, *Nitzschia nov.sp.* and DEV, *Denticula elegans valida*. ACC, *Achnanthes chilensis*, NM, *Nitzschia minutula*, BA, *Brachysira aponina* are slightly related, and can be considered as 'accompanying species'. Sample BA67 is slightly related to RAM6 and VER5, and is characterized by DT, *Denticula thermalis*. CA, *Cymbella affinis*, MA, *Mastogloia smithii amphicephala*, SUP, *Surirella peisonis*, DE, *Denticula elegans* and CP, *Cocconeis placentula* are slightly related, and are considered as 'accompanying species'.

In group 2 on factor 2 (Fig. 6,2), the components of node 244 are separated in two subgroups. The first sub-group (node 180) is highly related to factor 2 defined by the sample CL20. It is characterized by SSP, *Stauroneis sp.* and STL, *Stauroneis legleri*, both species being strongly related to this sample. The second sub-group with sample CD16 is relatively well related to CL20 by node 244. It is characterized by NA, *Nitzschia alpina* and by AB, *Amphora boliviana*. Although its contribution to axis 2 is clear, it is also related to

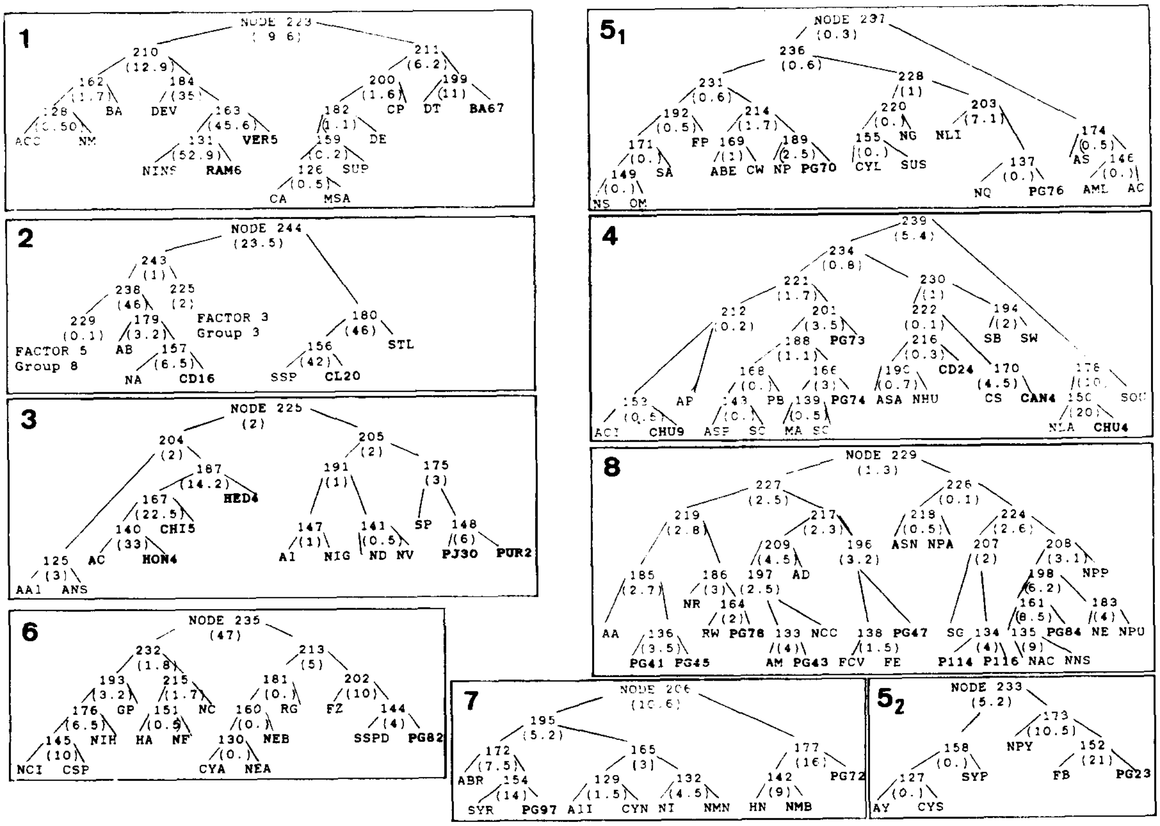


Fig. 6. Hierarchical classification of samples and taxa in Groups 1 to 8. Main values of the nodes are in brackets.

factor 5 by node 229 and to factor 3 by node 225. Sub-group 2 is slightly related to group 3 by co-occuring species AB, *Amphora boliviana* by the node 243 and slightly related to group 8 by the same species. We can conclude that the accompanying species are co-occuring species. This fact explains the close position of sub-group 2 to the group 8 in the hierarchical classification (Fig. 5). Similar comments can be done about group 5 (Figs. 5 and 6).

Table 6. Chemical variables/classes, classes/chemical variables contributions program. A – The positive correlation indicates the ion which mostly affected the considered group of samples, the negative correlation indicates the ion which, by its low content or its lack, mostly separates the considered group from the others. B – The positive correlation indicates the most typical group with regard to a variable.

A – Chemical variables/classes contributions.

	Positive correlation		Negative correlation	
	Strong	Weak	Strong	Weak
Group 1	SO_4, Cl	Na, Ca	Alk	Si, K
Group 2	Alk	Na, K	Cl	Ca, Si, SO_4
Group 3	SO_4, Na	–	Alk	Cl, Si
Group 4	SO_4	K	Cl, Na	–
Group 5	Cl	Na, Alk, Li	SO_4	–
Group 6	Si, Alk	–	Cl	Na, SO_4
Group 7	Alk, Si	Ca	Cl, Na	SO_4
Group 8	Cl	Na	SO_4	Alk, Si

B – Classes/Chemical variables contributions

	Positive contribution		Negative contribution	
	Strong	Weak	Strong	Weak
Alk	2, 7, 6	5	8	3, 1
Ca	7, 1	6	2	8, 3, 4
Cl	8	5	7, 4	2, 3
K	4, 2	–	7	1, 6, 8, 5
Mg	7, 1	4, 6	2, 8	5, 3
Na	8	3, 2, 1, 5	7, 4	6
Si	6, 7	–	–	8, 3, 1, 2, 4
SO_4	4	3, 1	8	5, 7, 6
Li	5	8	–	1, 4, 3, 2, 7, 6

Diatom assemblages as affected by chemical variables

(i). The variables/classes, classes/variables contributions method

For each of the 8 clusters of samples, we determined its correlation (positive or negative) with each ionic variable (Table 6).

Group 1 is essentially influenced by sulfate and chloride and to a lesser degree by sodium and calcium and is characterized by low alkalinity and to a lesser extent by the absence of silicium and potassium, in contrast with groups 2, 6 and 7 which are positively influenced by alkalinity. Group 1 is close to groups 3 and 8 by low alkalinity and silicium content, but differs from

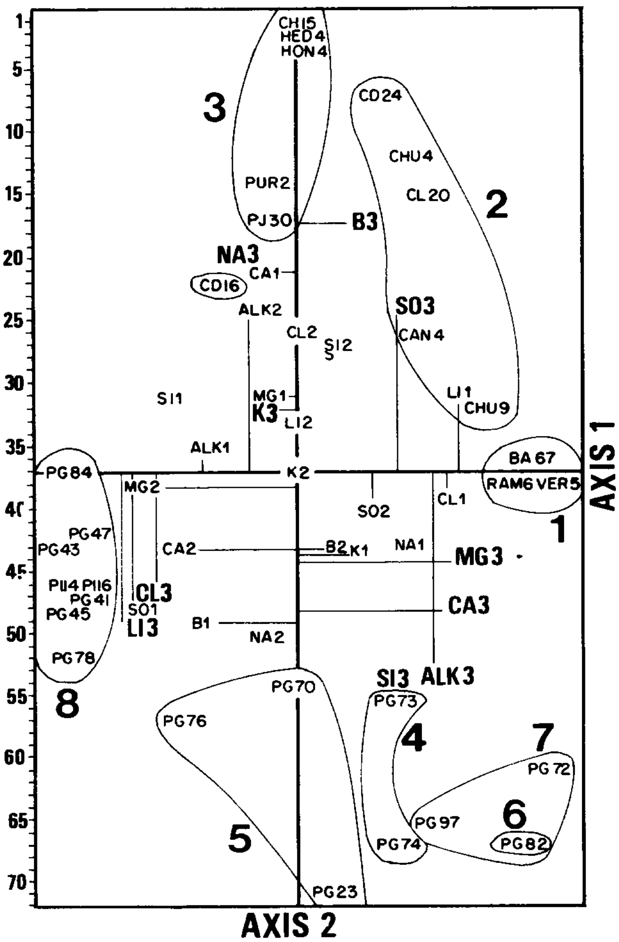


Fig. 7. Projection of samples and chemical variables points on factorial plane 1–2.

class 8 by sulfate. Highly related to sulfate, it is however less determined by this anion than group 4 is, and less related to chloride as group 8 is. Finally, the diatom assemblage of group 1 is linked to the presence of chloride and sulfate, but under a lower concentration of sulfate than is needed by the diatom assemblage of group 4; as well as by a concentration of chloride than is needed by group 8 (Table 6a).

(ii). The interactions species/ionic variables method
We use this method to quantify the ionic variables related to each cluster, and then present a FAC graph of the established relations (Fig. 7). We can

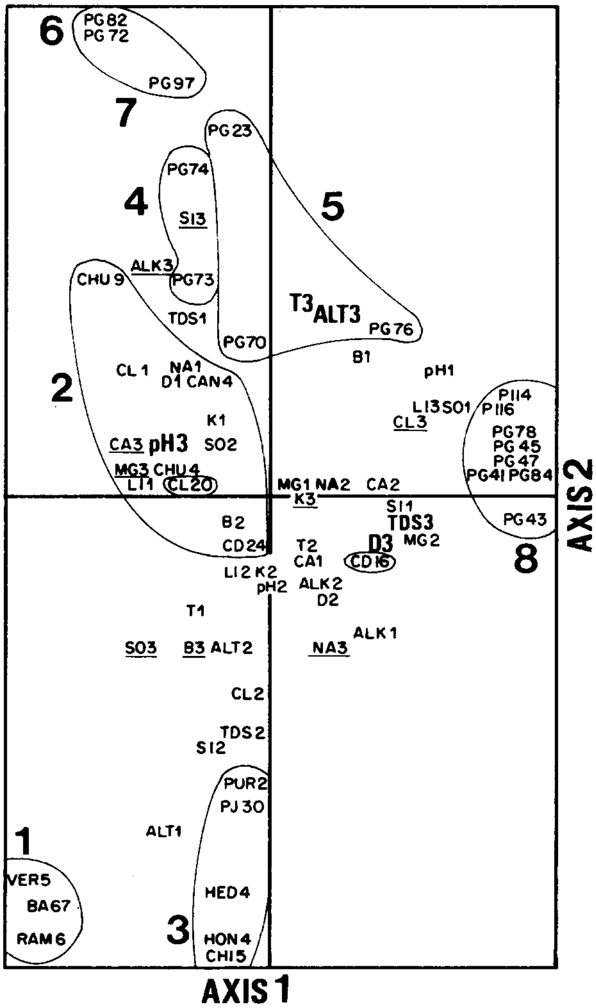


Fig. 8. Projection of samples, chemical variables, salinity TDS, physical parameters depth (D), pH (PH), temperature (T) and elevation (ALT) points on factorial plane 1–2.

observe that the results are similar to those obtained by the former method, but the advantage is that the results can be shown in a graph were the ionic components are quantified using for low content values <34%, category 1, medium content, values between 34 and 68% (category 2), and high content, values >68% (category 3).

The last step of these different approaches is to verify if the ionic contents are really the main factors influencing the composition of diatom assemblages. For such a purpose we use another FAC where other environmental variables such as total dissolved salts (TDS), and physical parameters such as temperature, (T), altitude, (ALT), pH (pH) and depth (D) are included and split into three modalities as for ionic components (Fig. 8).

Comparing the results obtained with only the ionic variables (Fig. 7) to those obtained with all the environmental factors (Fig. 8), it is clear that the last parameters are only secondary factors, because they do not strongly modify the clusters neither their location on the main factorial axis. The composition of each cluster is similar and it is related to the same ionic elements in both analyses. The ordination along axis 1 and axis 2 in both graphs has changed a little. Opposition along axis 1 between clusters 1 and 8 and along axis 2, between cluster 3 and clusters 5, 6 and 7 are unchanged, cluster 4 remains intermediate, but there is a shift of cluster 1 along axis 2 due to parameter altitude.

Discussion

We may suppose that eurytherm species are the best adapted to the hard climatic conditions as wide daily temperature variations occur in the Lipez area.

Qualitative and quantitative relationships between diatom species, groups of samples and environmental variables obtained by different statistical approaches are summarized in Table 7 together with measured data and ecological informations.

Group 1 is characterized by *Nitzschia* nov. sp. whose development is due to high content of

Table 7. Groups of environmental parameters and species set up using measured published and inferred data for each group of samples. Classes of salinity, pH and temperature are according to Lowe's system (1973). Line 1, 8 groups of samples (classes) obtained from FAC of taxa. Line 2, samples which composed the groups 1 to 8. Line 3, characteristic species. Line 4a, accompanying species. Line 5, depth. Line 6, salinity. Line 7, pH: Acb = % of acidobiontic species, Ac = % of acidophilous species, Ind = % of pH-indifferent (circumneutral) species, Al = % of alkaliphilous species, Alb = % of alkalibiontic species, U = % of species whose affinity to pH is unknown. Line 8, groups of species according to temperature: TE = true eurytherms (tolerate temperature fluctuations of 20 °C or over), ME = mesoeurytherms (tolerate fluctuations of about 15 °C), MEW = warm (living in waters from 20 to °C), MST = temperature (15–25 °C), MSC = cold (10–20 °C), ES = Eustenotherms (tolerate temperature fluctuations of about 5 °C), ESW = warm (living at or over 25 °C), EST = temperate (15–25 °C), ESC = cold (at or below 15 °C), U-unknown affinity to temperature. Line 9, elevation.

1 GROUPS			1	2	3	4	Units
2 SAMPLES			RAM 6, VER5, BA 67.	CL 20, CD 16.	HED 4, HON4, PUR 2, PJ 30, CHI 5.	(1) CHU 4, CD 24, CAN 4, CHU9. (2) PG 73, PG 74.	
3 CHARACTERISTIC SPECIES			Nitzschia nov. sp. Denticula elegans valida Denticula thermalis	Stauroneis leglerì. Stauroneis sp.	Amphora carvajaliana	Navicula pseudolanceolata Surirella ovata utahensis Anomoeoneis sphaerophora angusta Nitzschia hungarica Caloneis silicula	
4 FELLOW SPECIES			Brachysira aponina Nitzschia minutula Achnanthes chilensis Mastogloia smithii amphicephala Caloneis arcus Surirella peisonis Denticula elegans Cocconeis placentula	Amphora boliviana Nitzschia alpina	Amphiprora alata Anomoeoneis sphaerophora polygramma Nitzschia denticula Nitzschia valdecostata Nitzschia grunowii Scoliopleura peisonis Achnanthes lemmermanii	(1) Stauroneis bathurstensis Surirella wetzeli Amphora platensis Amphora chilensis (2) Mastogloia atacamae Surirella oregonica Surirella chilensis Anomoeoneis sphaerophora Pinnularia bogotensis (1) FIRST SUB_GROUP (2) SECOND SUB_GROUP	
5 DEPTH	A	range	30-100	20-50	20_100	15-20	cm
		mean	65	35	40	17	
	B	a	36.4	—	—	52	%
		e	0.8	—	96.3	0.22	
		b	41.2	—	0.92	23	
		l	—	—	0.01	—	
		p	—	—	—	5.4	
		E	21.2	—	—	17.2	
		U	0.4	100	2.7		
	C	D 1				+	modalities 1 → <20cm
		D 2	+	+	+		2 → 20-30
		D 3					3 → >30
6 SALINITY	A	range	13 to 45	36 to 120	25 to 77	1.6 to 144	g/l
		mean	29	78	48.2	40.3	
	B	<0,2	—	—	0.05	5.43	%
		0,2-10	0.4	—	0.2 - 10	—	
		10-20	14.1	—	—	—	
		20-30	31	70.3	96.4	90.1	
		>30	31	—	—	—	
		Eurys	20.8	—	2.7	0.25	
		U	12	29.7	0.71	2.4	
		(ions)	SO_4^{--}(2), Cl^-(1), Ca^{++}(3), Mg^+(3), Na^+(1) NINS: Ca^{++}(3), Mg^+(3) DEV: Alk(3) Ca^{++}(3) Mg^+(1)	B^+(3), K^+(3), Na^+(3) SO_4^{--}(3), Si(2), Alk(2), Ca^{++}(1), Mg^+(1), Li(1) STL: B^+(3), Mg^+(1) SO_4^{--}(2) SSP: Alk(3), Si(3) SO_4^{--}(2)	SO^{--}(3), Na^+(3), B(3), Alk(2), Si(2) Cl^-(2), Ca^{++}(1) AC: Cl^-(2), Li(2), Na^+(3), Si(2), SO_4^{--}(3)	for the first sub.group: SO_4^{--}(3), B(3), Si(2), Li(1), K(3) for the second sub. group: Si(3) NLA: Li(1), Alk(2), SO_4^{--}(3), Cl^-(1)	
	C	TDS 1				+	modalities 1 → 0.2-20 g/l
		TDS 2	+	+	+		2 → 20-50
		TDS 3					3 → >50
7 pH	A	range	8.18 to 8.78	10.3	8.05 - 8.85	7.8 to 10.2	
		mean	8.35		8.4	8.7	
	B	Acb	—	—	—	—	%
		Ac	—	—	—	—	
		Ind	—	3	—	—	
		Al	30	15.5	0.7		
		Alb	1.33	—	0.32	0.89	
		U	68.6	81.5	99	99.11	
	C	pH 1					modalities 1 → 6.9-7.5
		pH 2	+	+	+		2 → 7.5-8.5
		pH 3				+	3 → 8.5-10.3
8 TEMPERATURE	A	range	1. to 5	6_21	1_8	1 - 10	°C
		mean	2.6	13.5	6	5.1	
	B	TE	26.1		0.2		%
		ME MEW	—				
		ME MET	—				
		ME MEC	—				
		MS MSW	—				
		MS MST	1.33		1.4		
		MS MSC	—			0.25	
		ES ESW	—				
		ES EST	—				
		ES ESC	31.4	-			
		U	41	100	98.4	99.75	
	C	T1	+		+	+	modalities 1 → 1-4°C
		T2		+			2 → 4-8
		T3					3 → 8-20
9 ELEVATION		range	4117-4350	4278-4495	4110-4393	4140 - 4400	m
		mean	4195	4386	4169	4312	
		Alt 1	+		+		modalities 1 → 4100-4200m
		Alt 2		+		+	2 → 4200-4300
		Alt 3					3 → >4300

Table 7. (continued).

1 GROUPS			5	6	7	8	Units
2 SAMPLES			1rst sub.group: PG 70, PG 76 2nd sub-group: PG 23	PG 82	PG 72, PG 97.	PG 84, PG 41, PG 45, PG 43, PG 47, P 114, P 116.	
3 CHARACTERISTICS SPECIES			(1) Nitzschia punctata Nitzschia quadrangula Navicula pseudolittoricola (2) Fragilaria brevistriata Navicula pygmaea	Fragilaria zeilleri .	Navicula mutica binodis Hantzschia nov. sp. Achnanthes breviceps	Navicula nov. sp. Nitzschia epithemioides Nitzschia accedens chilensis Nitzschia pusilla Amphora atacamae Amphora atacamae minor Navicula cari cincta Fragilaria construens venter. Fragilaria elliptica Stauroneis gregorii	
4a ACCOMPANYING SPECIES			(1) Navicula gastrum Surirella sella Cymbella lunata (2) Synedra pulchella Cymbella sp. Amphora lybica	Neidium bisulcatum Neidium apiculatum Cymbella affinis Rhopalodia gibba Stauroneis spd	Achnanthes linearis Cymbella norvegica Synedra rumpens Navicula mutica nivalis Nitzschia inconspicua	Navicula pupula Achnanthes delicatula Anomoeoneis sphaerophora navicularis Nitzschia palea	
4b UBIQUIST SPECIES			Navicula sp. Amphora ovalis Achnanthes speciosa Amphora boliviana elongata Amphora lineolata Caloneis westii Opephora martyi Stauroneis anceps Fragilaria pinnata	Gomphonema parvulum Nitschia hantzschiana Navicula cincta Nitzschia frustulum Hantzschia amphioxys			
5 DEPTH	A	range	20-20				cm
		mean	20	20	20	100	
	B	a	—	0.29	25	—	%
		e	57	—	3.7	1.3	
		b	11.6	29.2	1.2	0.14	
		I	5.1	—	—	17.4	
		p	—	—	—	2.3	
		E	2.9	6.7	20.4	18.1	
		U	11.6	63.7	49.5	60.3	
	C	D 1	+	+	+		modalities 1 → <20cm 2 → 20-30 3 → >30
		D 2					
		D 3				+	
6 SALINITY	A	range	1.4-14.3		0.4 to 0.6	13-324	g/l
		mean	9.6	0.19	0.5	169	
	B	<0.2	—	—	—	—	%
		0.2-10	10.9	3.4	96.2	11.7	
		10-20	28.5	—	—	—	
		20-30	—	—	3.75	—	
		> 30	—	—	0	51.6	
		Eurys	58.7	29		18.1	
		U	1.85	63.7		8.5	
			for the first sub-group: CL⁻(3), Li(3), Na⁺(2), B⁺(1) for the second sub-group: Si(3), Alk(3) NP: Ca⁺⁺(2), B⁺(1), Cl⁻(3) NQ: Ca⁺⁺(2), Cl⁻(3), K⁺(3) FB: Si(3), Alk(3), B⁺(2), Mg(2)	Si(3), Alk(3), Ca⁺⁺(3), Mg⁺(3). FZ: Alk(3), Ca⁺⁺(3), K⁺(1), Si(3), SO₄⁻⁻(2).	Alk(3), Si(3), Ca⁺⁺(3), Mg⁺(3). NMB: Alk(3), Cl⁻(1), Ca⁺⁺(3), Si(3), Mg⁺(3)	Cl⁻(3), Na⁺(3), Li(3) NNS: SO₄⁻⁻(1), Si(1), Alk(1), B⁺(1), Na⁺(3), Li(3), Ca⁺⁺(3), Cl⁻(3)	
	C	TDS 1	+	+	+		modalities 1 → 0.2-20g/l 2 → 20-50 3 → >50
		TDS 2					
		TDS 3				+	
7 pH	A	range	8.4 to 9.35		6.95-8.92	6.95-9.7	
		mean	8.7	9.62	7.93	7.9	
	B	Acb	—	—	—	—	%
		Ac	4.7	—	—	—	
		Ind	5.1	—	62	2.46	
		Al	53.05	29.5	—	19.4	
		Alb	1.96	1.9	23.7	—	
		U	30.14	68.4	14.1	77.9	
	C	pH 1	+			+	modalities 1 → 6.9-7.5 2 → 7.5-8.5 3 → 8.5-10.3
		pH 2					
		pH 3		+	+		
8 TEMPERATURE	A	range	1.10		10	5-15	°C
		mean	5.3	10	10	8.8	
	B	TE	63.1	33.8		27.5	%
		ME MEW	—	—		—	
		ME MET	—	—		—	
		ME MEC	—	—		—	
		MS MSW	—	—		—	
		MS MST	—	—		3.7	
		MS MSC	2.96	2	3	—	
		ES ESW	—	—		—	
		ES EST	—	—	3	—	
		ES ESC	5.5	2.9	16.6	—	
		U	28	63.7	75.8	68.5	
	C	T 1					modalities 1 → 1-4°C 2 → 4-8 3 → 8-20
		T 2				+	
		T 3	+	+	+		
9 ELEVATION		range					m
		mean	4400	4400	4400		
		Alt 1					modalities 1 → 4100-4200m 2 → 4200-4300 3 → > 4300
		Alt 2					
		Alt 3	+	+	+	+	

calcium (CA3) and magnesium (MG3). As indicated by measured values, this group is related to higher concentration of sulfate (SO2) than chloride (Cl1), to medium salinity (TDS2), (the measured salinity is $29\,g\,l^{-1}$) to medium pH (pH2), (the measured pH 8.35) to low temperature (T1), (the measured temperature is 2.6 °C) and low elevation. Except for depth and salinity, where 41% of benthic and 31% of polyhalobous species are present and give good ecological information which correspond to those obtained from measured data, the other ecological parameters should not have been determined with only ecological informations from literature because 68.1% of the species have unknown pH affinity and 41% of the species have unknown temperature affinity. This lack of ecological data is due to the abundance in this group of *Nitzschia* nov. sp. (Fig. 24) whose ecology is unknown.

Group 2: ecological data are lacking for depth, pH and temperature. Data upon salinity affinity of characteristic species of *Stauroneis* were given by Patrick (1961).

Group 3: there is a complete lack of data for temperature and pH, but some useful ones have been found concerning depth and salinity affinities.

Group 5, 6, 7: Based only on published ecological data, depth and salinity should have been determined (essentially separation between groups 5, 6, 7 and group 8), but without any possibility of quantification. The low salinity groups 5, 6 and 7 contain different 'characteristic' oligohaline species *Fragilaria brevistriata*, *Fragilaria zeilleri* and *Navicula mutica binodis*, each one is related to the chemistry of the freshwater. *Fragilaria brevistriata* develops in high concentrations of silica, high alkalinity and medium concentration of boron; *Fragilaria zeilleri* develops better in relation to silica, high alkalinity and calcium; *Navicula mutica binodis* develops better in high alkalinity, silica, calcium and magnesium. Thus, differences in the development of the three oligohaline species should be mainly related to differences in the concentrations of boron, calcium, and magnesium.

Group 8: Based only on ecological data, only depth and salinity should have been determined. As indicated by measured data, this group is characterized by high salinity, with high concentration of chloride, sodium and lithium. The development of characteristic species *Navicula* nov. sp. is due to high content of calcium.

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