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DIATOMS (BACILLARIOPHYTA) FROM DIFFERENT BENTHIC HABITATS WITHIN SEVEN UPLAND LAKES IN THE LAGUNA SAN RAFAEL NATIONAL PARK, CHILE

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ABSTRACT

Diatom assemblages from 18 samples from 7 lakes along an altitudinal gradient (200 - > 1000 m a.s.l.) in the Laguna San Rafael National Park, on the eastern side of the Patagonian ice cap, were analysed. Over 190 taxa from 38 genera were found and identified to species or variety wherever possible. Some taxa could not be allocated to known species. The diatom floras of the lakes differed considerably, with the lake environment showing a stronger effect on the assemblage than did the habitat type in two lakes (Alpha and Hielo Azul). However, the highest similiarities were found between epiphytic samples from four lakes, Oxbow lake, Lagos Leones, Alpha and Quito. A few cosmopolitan species were found in almost all the lakes, but many taxa were restricted to one or two lakes. Assemblage data from all samples was subjected to TWINSPAN revealing three major groups of assemblages, discriminated primarily by two cosmopolitan species and several acidophilic taxa. Fuller water chemistry was available for four lakes allowing the relationships between diatoms and water chemistry to be analysed using CANOCO. None of the environmental gradients were large, but DCCA discriminated clearly between the lakes, placing Buena Vista and Cachorro far apart, as they have no taxa in common. Alpha and Quito fell inbetween, but separated from each other because they share only a few, uncommon, taxa.

Key words: Diatoms, Benthic habitats, Laguna San Rafael National Park, Chile.

RESUMEN

Diatomeas (Bacillariophyta) de diferentes hábitats bénticos dentro de siete lagos de altura en el Parque Nacional Laguna San Rafael, Chile. Se analizó una colección de 18 muestras de Diatmeas colectadas en 7 lagos distintos a lo largo de un gradiente de altitud (200 ->1000 m.s.n.m.n.) del Parque Nacional Laguna San Rafael, al Este del campo de hielo patagónico norte. Se encontraron más de 190 taxones de 38 géneros que fueron indentificados a especies o variedades cuando esto fue posible. Algunos taxones no pudieron ser asociados a ninguna especie conocida. La flora de diatomeas de los lagos difirió considerablemente; en dos lagos (Hielo Azul y Alpha) el medio ambiente lacustre tuvo mayor efecto sobre los ensambles que el tipo de hábitat. Sin embargo, las mayores similitudes fueron encontradas entre muestras de epifitas de cuatro lagos, Oxbow, Lagos Leones, Alpha y Quito. Algunas especies cosmopolitas fueron encontradas en casi todos los lagos, pero la mayoría de los taxones se restringieron sólo a uno o dos lagos. Los datos de los ensambles fueron procesados utilizando TWINSPAN, cuyo análisis reveló la existencia de tres grupos principales de ensambles discriminados principalmente en dos especies cosmopolitas y varios taxones acidófilos. En cuatro de los lagos cuyas características químicas del agua eran conocidas se pudieron analizar las relaciones entre la química del agua y las diatomeas (usando CANOCO). Ninguno de los gradientes medioambientales fueron importantes, sin embargo el DCCA discriminó claramente entre los lagos, separando considerablemente los lagos Cachorro y Buena Vista ya que no presentan taxones en común. Alpha y Quito se ubicaron en una situación intermedia, pero separados entre ellos, ya que sólo comparten unos pocos taxones inusuales con los demás.

Palabras clave: Diatomeas, Hábitats bénticos, Parque Nacional Laguna San Rafael, Chile.

INTRODUCTION

Diatoms are perhaps the most species-rich and widely distributed microalgal group occurring in freshwater and marine environments throughout the world. Because many taxa have well-defined or restricted ecologies, diatoms have long been recognised as potential bioindicators and various diatom-based biomonitoring systems have been developed (Kolkwitz & Marsson 1908, Kolbe 1927, Hustedt 1938, 1938/1939, Lange-Bertalot 1978, Descy 1979, CEMAGREF 1982, Leclerq & Maquet 1987, Lecointe *et al.* 1993, Round 1993, Kelly & Whitton 1995). Because their siliceous cell walls are also well preserved in lake-sediments, diatoms have also been used in palaeoenvironmental studies, reconstructing past lake-histories and climate (Allott *et al.* 1992, Bennion *et al.* 1995, Sayer *et al.* 1999). However, because few diatom taxa are truly cosmopolitan, their use as biomonitors must always be preceded by base-line studies that incorporate floristic surveys and environmental data collection. There have been relatively few studies that include diatoms from southern Chile (Krasske 1939a,b, 1949, Rivera 1983, Lange-Bertalot *et al.* 1996, Rumrich *et al.* 2000), and virtually no detailed ecological studies. This work therefore contributes to establishing a baseline data set on diatom diversity in the area, that could later be used to develop a water quality monitoring system within the LSRNP.

The Darwin Initiative (LSRNP biodiversity research programme) facilitated the collection of diatom samples and water chemistry from a range of aquatic habitats at different altitudes in the Laguna San Rafael National Park, southern Chile, in January–March 1998. The field work was concentrated in the Leones and Nef Valleys, on the eastern side of the North Patagonian ice cap, with the aim of obtaining biodiversity, habitat and water chemistry data (Cox 1999). Seven lakes within which different types of substratum had been sampled were subjected to more detailed analysis to investigate the relationships between site, substratum and diatom assemblages.

METHODS

During the course of three Raleigh International expeditions to the Laguna San Rafael National Park between 28th January and 20th March 1998, diatom and water samples were collected from a range of lakes (Cox 1999). The diatom floras of seven lakes (Table 1) were studied in more detail, with particular reference to different benthic habitats within the lakes.

TABLE 1. Details of site locations, altitude and field measurements.

Site	date	longitude	latitude	altitude m a.s.l.	temperature °C.	pH	alkalinity mg/l $CaCO_3$
Oxbow Lake	11.02.98	72°50'20"W	47°07'50"S	202	23.0	6.7	-
Lago Leones	28.01.98	73°06'20"W	46°43'15"S	310	10.8	6.4	14.0
Lago Quito	16.02.98	73°00'50"W	47°08'40"S	370	18.5	7.2	17.0
Laguna Cachorro	04.02.98	73°06'30"W	46°44'50"S	430	11.7	6.6	10.2
Lago Alpha	13.02.98	72°54'30"W	47°07'30"S	500	14.0	7.0	24.0
Lago Buena Vista	22.02.98	73°10'05"W	47°05'40"S	740	19.9	5.9	2.0
Lago Hielo Azul	22.02.98	73°11'20"W	47°04'25"S	1048	8.1	6.6	9.0

Field methods

Diatoms were sampled from a range of surfaces in the shallow littoral of the lakes, including the soft surficial sediments (<1cc volume), rock scrapes, submerged mosses, and the surface of submerged macrophytes. Samples were transferred to small glass vials and preserved with Lugol's iodine. Water temperature, pH and alkalinity (Table 1) were measured in the field. 100mls of water were also taken at each lake for chemical analysis. The samples were filtered on site and frozen on arrival at the NHM.

Laboratory methods

Water samples were analysed for major cations and anions using ion chromatography and ICP mass spectroscopy (Table 2). Diatom samples were washed with distilled water and then cleaned of organic material by heating with 50% nitric acid. Cleaned and rinsed diatoms were mounted in Naphrax to make permanent slides for light microscopy, or on stubs for scanning electron microscopy. A complete set of slides is held in the Natural History Museum, London, and another set has been lodged at the Museo Nacional de Historia Natural, Santiago, Chile.

TABLE 2. Concentrations of anions and cations in filtered and unfiltered lake water.
Ion chromatography(F – Mg) was not carried out on unfiltered samples, which are shown on the second line for each lake. No water samples were obtained for the Oxbow Lake and Lago Leones, and the filtered sample for Lago Hielo Azul was missing.

Site	F ppm	Cl ppm	NO_3 ppm	PO_4 ppm	SO_4 ppm	Na ppm	K ppm	Ca ppm	Mg ppm	Cr ppb	Mn ppb	Ni ppb	Cu ppb	Zn ppb	As ppb	Se ppb	Pb ppb
Oxbow lake	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lago Leones	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lago Quito	<0.01	0.44	0.08	0.28	0.74	1.10	0.23	5.82	1.34	1.36	10.8	0.27	0.62	16.2	0.21	0.19	nf
										1.74	0.88	0.01	0.32	8.11	0.15	0.12	nf
Laguna Cachorro	<0.01	0.23	<0.02	0.07	8.59	0.59	1.04	7.04	0.59	0.59	2.39	0.66	0.23	4.27	0.09	nf	nf
										0.76	1.32	0.65	0.42	5.15	0.15	nf	nf
Lago Alpha	<0.01	0.77	0.25	0.08	0.42	1.61	0.46	7.68	1.19	2.87	1.61	0.53	2.78	24.3	0.65	0.57	nf
										3.52	0.46	0.17	0.17	15.4	0.85	0.64	nf
Lago Buena Vista	0.01	0.34	0.08	<0.05	<0.01	0.49	0.08	0.31	0.07	2.14	1.95	nf	0.22	8.42	0.01	0.04	nf
										5.00	1.02	nf	0.01	2.25	nf	nf	nf
Lago Hielo Azul										1.17	7.59	nf	nf	10.7	0.03	0.27	0.02

NH_4, Li and Cd were below detection limits in all samples.

The slides were initially examined under a Leica ATC 2000 microscope using oil immersion at x1000 magnification. Diatom valves were identified to species level as far as possible, and counted along one or more eyepiece transects per slide, counting 300–400 valves per sample / slide. The locations of taxa of particular interest were recorded with the use of an England Finder and subsequently re-examined using a Leica DMLB microscope, transmitted light Differential Interference Contrast (DIC), and images were captured digitally. A variety of texts were used to identify the taxa, including: Krammer (1997a,b), Krammer & Lange–Bertalot (1986, 1988, 1991a & 1991b), Krasske (1939a, 1949), Lange-Bertalot *et al.* (1996), Lange-Bertalot & Krammer (1989), Lange-Bertalot & Metzeltin (1996), Lange-Bertalot & Moser (1994), Metzeltin & Lange-Bertalot (1998), Rumrich *et al.* (2000), Williams & Round (1987). Nevertheless a number of taxa could not be identified to known species and require further taxonomic investigation.

Statistical analyses

All diatom abundances were expressed as percentages of the total diatom count for each sample. Shannon-Wiener diversity (H') and evenness (E) were calculated for each sample using the following equations:

$H' = - S (p_i . \ln p_i)$ and $E = H' / \ln S$

where p_i is the proportion of the total sample represented by species i, and S is the total number of taxa in the sample. Diversity (H') values range from 0 – 4 (highest) and evenness (E) from 0 – 1 (most even). Samples were also compared using the Bray-Curtis similarity measure, (or dominance identity, DI [Engelberg 1987]) using the equation:

$$D1, 2 = \sum qi$$

Where D1, 2 is the dominance identity between samples 1 and 2 and qi is the smaller of the two relative abundances of species i. D can vary between 0% and 100%, with 0 indicating total dissimilarity and 100 absolute agreement between the two samples.

Diatom assemblages were classified into ecological groups using Two Way Indicator Species Analysis (TWINSPAN for DBOS, version 3.2), a hierarchical classification technique based on the concept that a group of samples constituting a community type will have a corresponding group of species that characterise that community type i.e. indicator species. TWINSPAN incorporates quantitative data by considering the different abundance levels of the same species to be different species, which it calls pseudo-species. Therefore, a single recorded species at 4 different abundances in four different habitats may have four pseudo-species. The first division is crude and based on reciprocal averaging (as in CA) where the 1st ordination axis is divided at its centroid. Each sample is then classified into one of two groups (positive on the right hand side and negative on the left). Species are given a score according to their degree of preference for one side of the dichotomy or the other. Highly preferential species are those that are at least three times more common on one side and are given a score of one (rare species are downweighted). Borderline cases can occur and are sites close to the point in the ordination where the initial division occurred. Each new group undergoes the same process until a certain number of divisions have been performed or the group is too small to divide further. Once the samples have been classified into ecological groups, the species are classified according to their overall fidelity to the groups and a two-way, site by species matrix is produced from which a dendogram can be produced (Jongman *et al.*, 1995). The cut levels used in the construction of pseudospecies were 0.1%, 2.1%, 4.1% and 7.1% and the dendogram was drawn using Microsoft Excel 2000.

For those lakes with full water chemistry (Quito, Cachorro, Alpha, Buena Vista), the relationship of diatom distribution and abundance to environmental variables was investigated using multivariate ordination techniques in the software program, CANOCO Version 4 (ter Braak & Smilauer 1998). To determine whether the species data showed a unimodal or linear response and the strength of this response, the indirect exploratory ordination technique of Detrended Correspondence Analysis (DCA) was applied. This operates on species data alone by constructing theoretical environmental variables and produces a graphical summary of the major patterns of variation within the species data. Detrending was via segments, species were square-root transformed and rare species downweighted. DCA determines the maximum variance between site and species data, with the greatest amount of variation represented by axis 1 of the ordination. If a linear response is obtained, the data should be subjected to a Principle Components Analysis (PCA), whilst a unimodal response should be subjected to a simple Correspondence Analysis (CA)(also called reciprocal averaging or RA). DCA can flatten out some of the variation, leading to a loss of ecological information (Jongman *et al.* 1995). Thus, CA determines the effect of the detrending on the data (using interspecies distances and bi-plot scaling, square root transformation of species abundances and down-weighting of rare species) and also explains any correlation between species and sites. In a CA, species and site scores are maximally correlated with each other and are shown simultaneously along the same axes. Data can then be examined via Canonical (or Constrained) Correspondence Analysis (CCA), and its detrended form DCCA. Both CCA and DCCA allow examination of both species and environmental data as linear combinations of each other and statistical testing of the environmental variables (and hypotheses) to determine a minimum set of variables that explain most of the variation in the species data. Variables are only significant at the 5 % significance level where $p \leq 0.05$, via 999 unrestricted Monte Carlo Permutations. DCCA ordination was based on inter-sample distances with Hill's scaling. In strongly unimodal data Hill's scaling allows the species point in the biplot to be interpreted as the optimum of its unimodal response (ter Braak & Smilauer, 1998). Species data were square root transformed, rare species downweighted and environmental data were standardised prior to entry into the program. Detrending was via 2nd order polynomials. The ordination gradients were drawn using Microsoft Excel 2000.

RESULTS

Lake characteristics

The lakes in this study cover an altitudinal gradient of over 800m, ranging from 202m to 1048m a.s.l. Most of the lakes are clear, with good light penetration (Kelly Jackson, pers. comm.), although no secchi depth readings were taken. Some of the lakes are not completely isolated, having inflows and / or outflows e.g. Leones, Cachorro and Alpha, while others are fed by glacial meltwater, e.g. Buena Vista. Water temperature ranged between 8.1°C and 23°C and did not necessarily decrease with increasing altitude, although the highest temperature was measured in the lowest lake, and the lowest temperature in the highest lake (Table 1). All lakes have slightly acidic to circumneutral pH, ranging from 5.9 to 7.2, lowest in Buena Vista and highest in Quito. Alkalinity, a measure of the total concentration of alkaline salts, ranged from 2 to 24 mg/l $CaCO_3$, Buena Vista and Alpha having the lowest and highest alkalinity, respectively. Fuller water chemistry was obtained for four lakes (Table 2) and shows considerable variation in some major cations and anions, although generally all are nutrient poor. Buena Vista has the lowest concentration of ions, Cachorro the highest, with a particularly high value for sulphate (8.59 ppm).

Diatom assemblages

TABLE 3. Summary of sample type from lakes

Lake	Sample	Type	Slide number
Oxbow lake	macrophyte	epiphytic (P)	BM 99792
Oxbow lake	rock scrape	epilithic (R)	BM 99793
Lago Leones	mud sample	epipelic (S1)	BM 99773
Lago Leones	not recorded	epilithic? (R?)	BM 99774
Lago Leones	mud sample	epipelic (S2)	BM 99775
Lago Leones	macrophyte	epiphytic (P)	BM 99776
Lago Quito	root scrape	epipelic (S)	BM 99795
Lago Quito	macrophyte	epiphytic (P)	BM 99796
Laguna Cachorro	rock scrape	epilithic (R)	BM 99779
Laguna Cachorro	macrophyte	epiphytic (P)	BM 99780
Lago Alpha	plant surface	epiphytic (P)	BM 99769
Lago Alpha	mud surface	epipelic (S1)	BM 99770
Lago Alpha	mud	epipelic (S2)	BM 99771
Lago Buena Vista	macrophyte	epiphytic (P)	BM 99826
Lago Buena Vista	mud	epipelic (S)	BM 99827
Lago Hielo Azul	moss	epiphytic (P)	BM 99822
Lago Hielo Azul	rock scrape	epilithic (R)	BM 99823
Lago Hielo Azul	sediment	epipelic (S)	BM 99824

Table 3 shows the types of sample taken from the lakes and Table 4 shows the percentage abundances of the more abundant taxa (91) in the different lake samples. A full list of taxa (195) encountered is given in Appendix 1 and most of these are illustrated in Figs 5-187. Many taxa are restricted to one or a few lakes, with almost half the taxa occurring in only one sample or one lake (Table 4), while a few taxa were very widely distributed. *Cymbella microcephala* Grunow was most widespread, occurring in 14 samples and all lakes except Buena Vista, while *Achnanthes minutissima* Kützing (including its varieties) and *Cymbella simonsenii* Krammer were found in 13 and 8 samples, 6 and 4 lakes, respectively. Total species number, diversity (H') and evenness (E) varied with lakes and substratum (Table 4). Thus, Cachorro epiphyton had the fewest taxa (10), while Leones had the most (37) in a putative epilithic sample. The latter also had the highest value of H' (2.83), but the Oxbow epiphyton had the lowest value of H' (0.99). Although H' is related to the number of taxa in a sample, it is also affected by the relative contributions of the taxa and decreases with increasing unevenness. Thus E was lowest for the Oxbow epiphyton (0.36), but highest for Buena Vista epiphyton (0.83) in which 6 taxa each had relative abundances over 10%.

TABLE 4. Diatom assemblages from different habitats within the lakes.
Values are percentage abundances, but only taxa with at least 2% abundance in any habitat are included. + indicates that the taxon was present <2%.

Species	**Oxbow**		**Leones**				**Quito**		**Cachorro**		**Alpha**			**Buena Vista**		**Hielo Azul**		
	P	**R**	**P**	**R?**	**S1**	**S2**	**P**	**S**	**P**	**R**	**P**	**S1**	**S2**	**P**	**S**	**P**	**R**	**S**
Cyclotella stelligera	-	-	-	-	-	-	+	-	-	-	+	4.6	2.3	-	-	-	-	-
Aulacoseira granulata	-	5.9	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hannaea arcus	-	-	-	3.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fragilaria capucina	-	-	-	26.3	-	-	-	-	-	-	-	-	-	-	-	-	5.2	+
F. capucina var. *capucina*	-	-	-	-	-	-	-	-	28.7	10.6	-	-	-	-	-	-	-	-
F. capucina #1	-	-	-	-	-	-	-	-	+	65.5	-	-	-	-	-	26.3	-	-
F. capucina #4	-	-	-	-	-	-	-	-	50.5	-	-	-	-	-	-	-	-	-
F. vaucheriae	-	-	-	13.4	-	-	-	-	-	-	-	-	-	-	-	4.0	-	-
F. vaucheriae?	-	-	-	2.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. similis	+	4.0	-	-	-	-	-	-	12.5	-	-	-	-	-	-	-	-	-
Fragilaria / Synedra sp.	-	-	-	-	-	-	+	+	3.2	-	-	-	-	-	-	-	+	-
Staurosira construens var. #1	-	2.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diatoma mesodon	-	-	-	4.0	-	-	-	-	-	-	-	-	-	-	-	9.9	+	-
Meridion circulare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.1	-	-
Synedra acus / Synedra radians	-	-	-	-	-	-	-	-	-	7.6	-	-	-	-	-	-	-	-
Eunotia bilunaris	-	-	+	-	-	-	-	-	-	-	-	-	-	19.3	10.4	-	11.5	-
E. bilunaris? girdle view	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-
E. bilunaris var. *mucophilia*	-	-	-	-	-	-	-	-	-	-	-	-	-	12.6	6.0	-	+	-
E. bilunaris var. *mucophilia* #2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.1	-	-	-
E. diodon	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	10.5
E. exigua	-	-	-	-	-	4.0	-	-	-	-	-	-	-	-	5.6	-	-	-
E. exigua #2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-
E. intermedia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.3	-	+	-
E. muscicola var. *muscicola*	-	-	-	+	-	-	-	-	-	+	-	-	-	-	2.3	-	-	-
E. naegeli	-	-	+	-	-	3.5	-	-	-	-	-	-	-	-	6.1	-	-	-
E. nymanniana	-	-	-	-	-	-	-	-	-	-	-	-	-	10.4	+		-	-
E. paludosa var. *paludosa*	-	-	-	-	-	18.6	-	-	-	-	-	-	-	3.2	2.3	-	-	-
E. subarcuatoides	-	-	-	-	-	26.4	-	-	-	-	-	-	-	+	-	-	-	-
E. tecta	-	-	-	-	-	-	-	-	-	-	-	-	-	11.6	+	-	+	-
Eunotia #1	-	-	-	-	-	-	-	-	-	-	-	-	-	3.0	-	-	-	-
Eunotia #2	-	-	-	-	-	2.0	-	-	-	-	-	-	-	-	-	-	-	-

Species	Oxbow		Leones				Quito		Cachorro		Alpha			Buena Vista		Hielo Azul		
	P	R	P	R?	S1	S2	P	S	P	R	P	S1	S2	P	S	P	R	S
Anomoeoneis vitrea	-	+	-	-	-	-	25.9	-	-	-	-	-	-	-	-	-	-	-
Cymbella difficilis	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	+	-	-	-
C. falaisensis	10.1	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
C. microcephala	3.0	31.5	33.5	3.0	+	-	32.6	27.0	+	4.5	18.0	18.2	12.5	-	-	-	20.6	15.7
C. simonsenii	+	-	6.0	-	+	+	5.7	+	-	-	7.2	4.0	-	-	-	-	-	-
Encyonema neogracile	-	+	2.5	-	-	-	7.1	-	+	-	5.3	4.3	+	-	-	-	-	-
E. minutum	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	3.8	3.4	9.0
E. supergracile	-	+	-	-	+	-	-	7.0	-	-	-	-	-	-	-	-	-	-
E. triste	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	4.0	+	5.4
Gomphonema gracile	-	-	-	-	-	-	-	6.2	-	-	-	-	-	-	-	-	-	-
G. gracile var. #2	-	-	-	-	-	-	-	-	-	-	3.6	-	-	-	-	-	-	-
G. parvulum var. #1	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
G. parvulum var. #2	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
G. parvulum var. & fo. *parvulum*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-
G. parvulum (girdle view)	-	-	-	6.8	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Achnanthes chlidanos	-	-	-	-	66.7	-	-	-	-	-	-	-	-	-	-	25.5	3.9	-
A. coarctata var. *coarctata*	-	-	-	-	5.1	-	-	-	-	-	-	-	-	-	-	-	-	-
A. minutissima	76.4	20.5	32.0	-	2.0	-	6.7	-	-	+	30.5	9.9	2.3	-	-	-	12.0	30.7
A. minutissima var. *jackii*	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	7.0	-
A. minutissima var. #2	+	-	-	-	-	-	-	51.1	-	-	-	-	-	-	-	-	-	-
Achnanthes subatomoides	-	2.1	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Cavinula pseudoscutiformis	+	11.5	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Frustulia rhomboides	-	+	-	+	-	-	-	-	-	-	-	-	19.2	10.4	20.8	-	6.3	-
F. rhomboides var. *crassinervia*	-	-	-	-	-	-	7.6	-	-	-	-	+	-	9.4	2.8	-	-	-
Brachysira brebissonii	-	-	4.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B. brebissonii / neoexilis	-	-	-	-	-	-	-	-	-	-	23.9	-	2.3	-	-	-	-	-
B. brebissonii var. #1	+	+	-	-	-	-	-	-	-	-	-	14.9	-	-	-	-	-	-
B. brebissonii var. #2	-	-	-	-	-	-	-	-	-	-	-	3.0	-	-	-	+	+	-
B. brebissonii var. #3	-	+	+	-	-	-	4.3	-	-	-	-	-	-	15.3	-	-	-	-
B. neoexilis	-	-	-	-	+	-	-	-	-	-	-	-	38.5	+	22.0	-	14.9	-
Brachysira sp. #1	-	-	-	-	-	-	-	+	-	-	-	28.1	-	-	-	-	-	-
Pinnularia microstauron	-	-	-	-	-	11.1	-	-	-	-	-	-	-	-	-	-	-	-
P. stomatophora	-	-	-	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pinnularia #1	-	-	-	-	5.1	-	-	-	-	-	-	-	-	-	-	-	-	-
Caloneis #1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9.3	+	+
Navicula halophiloides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.4
N. longicephala var. *longicephala*		-	-	-	-	-	5.5	-	-	-	-	-	-	-	-	-	-	-
N. protracta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	+
N. radiosa	+	+	+	-	-	-	2.1	-	-	-	-	-	-	-	-	-	-	-
Navicula #1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.0
Stauroneis phoenicenteron	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-
S. wislouchii	-	-	-	2.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stauroneis #1	-	-	-	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kobayasia subtilissima	-	-	-	-	-	8.6	-	-	-	-	-	-	-	-	+	-	-	+
Amphora veneta	-	-	-	-	6.8	-	-	-	-	-	-	-	-	-	-	-	-	2.3
Nitzschia alpina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.0
N. amphibioides	-	-	-	-	-	-	-	-	2.1	-	-	-	-	-	-	-	-	-
N. bacillum	-	+	-	-	-	-	-	-	-	3.5	3.0	-	3.5	-	-	-	6.3	+
N. bacillum / lacuum	-	3.3	-	-	+	-	+	-	-	-	-	5.0	8.3	-	-	-	-	-
N. frustulum var. *frustulum*	-	-	-	-	-	-	-	-	-	-	3.9	3.0	-	-	-	-	-	-

Species	Oxbow		Leones				Quito		Cachorro		Alpha			Buena Vista		Hielo Azul		
	P	R	P	R?	S1	S2	P	S	P	R	P	S1	S2	P	S	P	R	S
N. gracilis	-	-	6.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. intermedia #2	-	-	-	-	-	27.7	-	-	-	-	-	-	-	-	-	-	-	-
N. lacuum	4.7	-	3.5	-	-	-	+	-	-	-	-	-	10.4	-	-	-	-	-
N. palea / gracilis	-	-	-	-	3.0	-	-	-	-	-	-	-	-	-	-	-	-	-
N. perminuta	-	-	7.7	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stenopterobia curvula	-	-	-	-	-	3.5	-	-	-	-	-	-	-	-	-	-	-	-
Epithema turgida	-	-	-	-	-	-	-	3.1	-	-	-	-	-	-	-	-	-	-
Unknown sp. #5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.0	-	-
Unknown sp. #8	-	4.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5
Total number taxa in sample	16	29	15	37	17	17	21	11	10	17	13	19	22	15	24	16	24	23
Shannon-Wiener diversity	0.99	2.34	1.82	2.83	1.44	2.10	2.06	1.42	1.25	1.34	1.92	2.20	2.05	2.24	2.50	2.12	2.47	2.34
Evenness	0.36	0.70	0.67	0.78	0.51	0.74	0.68	0.59	0.54	0.47	0.75	0.76	0.66	0.83	0.79	0.77	0.78	0.75

The most taxon rich genera were *Eunotia* Ehrenberg (26 taxa), *Nitzschia* Hassall (18), *Navicula* Bory (17), *Fragilaria* Lyngbye (14), *Gomphonema* Agardh (12), *Achnanthes* Bory (11), *Cymbella* Agardh (10) and *Brachysira* Kützing (8), although many taxa were rare. Thus the generic ranking of taxa with >2% abundance in any sample was *Eunotia* (16), *Nitzschia* (10), *Fragilaria* (8), *Brachysira* (7), *Achnanthes* (6), *Gomphonema* (6), *Navicula* (5), *Cymbella* (4) and *Encyonema* (4). Some lakes were dominated by particular genera, e.g. Cachorro had high abundances of *Fragilaria* spp. (>70%), compared to about 40% in Leones and 30% in Hielo Azul. Buena Vista epiphyton contained abundant *Eunotia* (>60%), *Frustulia* Rabenhorst (~20%) and *Brachysira* (~15%) spp. The same genera were found in slightly different proportions on sediments in Buena Vista (*Eunotia* <50%, *Frustulia* >20%, *Brachysira* >20%). *Eunotia* only occurred in two other lakes, Leones and Hielo Azul, on sediments in the former (>50%), and rock and sediment in the latter (~10% in each). *Frustulia* was also found in Quito epiphyton (~7%), Alpha epipelon (~19%) and Hielo Azul epilithon (~6%), whereas *Brachysira* was plentiful in Alpha epiphyton (~24%) and epipelon (40-45%). It also occurred in Hielo Azul epilithon (~15%) and to a lesser extent in Leones and Quito epiphyton (<5%). These genera, and particularly *Eunotia*, often occur in lower pH waters, and their dominance in Buena Vista is almost certainly a reflection of the lower pH (Table 1) and ionic concentrations (Table 2) in that lake.

Relationship between diatom assemblages and lakes

Fig. 1 shows the relationships between all 18 samples determined by TWINSPAN, with the indicator taxa for the different groups in the dendrogram. There are three major groups of samples, Group A, Groups B-D, Groups E and F, and one group containing a single sample (G). Group G (Leones S2) is separated from the others at the first level by the presence of *Cocconeis placentula* Ehrenberg. At the next level, the distribution of 5 taxa, *Frustulia rhomboides* (Ehrenberg) De Toni, *Brachysira neoexilis* Lange-Bertalot *F. rhomboides* var. *crassinervia* (Brébisson) Ross, *Eunotia bilunaris* (Ehrenberg) Mills and *Eunotia tecta* Krasske, separates two groups of sites (E+F and A-D). Group E is separated from group F at level 3 by the presence of *Encyonema supergracile* Krammer & Lange-Bertalot. Thus, group F comprises the Buena Vista assemblages plus Hielo Azul R, while the epiphytic (P) assemblages from Leones and Quito together with Alpha S2 comprise group E. On the other side of the level 2 separation, group A (containing Leones S1, Leones P, Cachorro R and Hielo Azul P) is separated from groups B-D by the absence or low abundance of *C. microcephala* and *A. minutissima*. Group B (Cachorro R and Hielo Azul S) is separated off at level 4 by the presence of *Cymbella naviculiformis* Auerswald, while the final division between groups C and D is made on the presence of *Cyclotella stelligera* Cleve & Grunow in the latter (Alpha P and S1). Although TWINSPAN groups both Oxbow and both Buena Vista assemblages together (groups C and F respectively), these groups also contain assemblages from other lakes, and similarly groups A, B and E contain assemblages from different lakes.

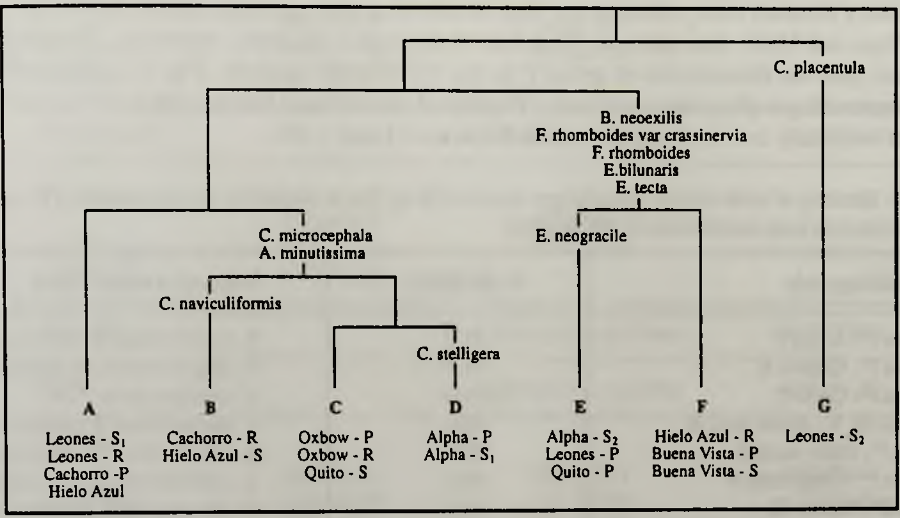

FIGURE 1. TWINSPAN dendogram showing the hierarchical clustering of sites (A-G). The taxa that discriminate between the groups are shown at the appropriate separation point on the diagram. Note that *C. microcephala* and *A. minutissima* are also abundant in group E.

The species associated with each group are listed as follows:

Group A: *AchnChil, AchnCoCo, AchnGerm, AchnLanc, AchnMiJa, AchnMinu, AchnSuba, AldaPsBr AmphVene, AulaGran, BracBre2, BracMino, BracNeoe, CaloSp1, CaviPseu, CymbCiCy, CymbCymb, CymbMicr, CymbSimo, DiatMeso, EncyNeog, EncySupa, EncyTris, EunoBiSu, EncyMinu, EunoMuMu, EunoPect, FragBent, FragCapu, FragCap1, FragCaCa, FragCapV, FragSp2, FragSp3, FragCap4, FragGerm, FragSyne, FrusRhom, FrusVulg, GompGra1, GompPar1, GompPar2, GompPaPa, GompParv, GompPata, HannArcu, HannArAr, MeriCirc, MeriCiCo, NaviAngu, SellPuPu, NaviSp3, NaviTriv, NeidAfLo, NitzAmpi, NitzBaLa, NitzClau, NitzDiMe, NitzInte, NitzPaGr, NitzPerm, PinnSp1, PinnSp2, PinnStom, SellPuPu, StauPhoe, StauSp1, StauWisl, SuriPsCo, UKSp4, UKSp5.*

Group B: *AchnCoar, AchnMinu, AchnSuba, AchnVene, CaloSp2, CaviPseu, CymbCySi, CymbMicr, CymbNavi, EncyMinu, EncyTris, EpitSp1, FragCapu, FragCap1, FragCaCa, FrusRhSa, GompAcum, GompParv, NaviHalo, NaviHass, NaviPerm, NaviProt, NaviSp1, NaviSp2, NaviStau, NaviSubl, NaviSubm, NeidHerc, NaitzAlpi, NitzBaci, PinnGiMi, Sp1, StauSuat, SyneArRa.*

Group C: *AchnMinu, AchnMin2, AchnSp2, AulaGran, BracBr1, BracBr3, BracSp1, BracVitr, CaviPseu, CyclSp2, CymbFals, CymbMicr, CymbSimo, CymbSp1H, EncyNeog, EncyMinu, EncySupa, EpitHynd, EpiTuHy, EunoBiSu, FragSimi, FragSyne, FrusRhom, GompAcum, GompClav, GompPar3, NaviRadi, NitzBaci, NitzBaLa, NitzFru3, NitzLacu, PseuBre2, PseuBre3, PseuPseu, RhopGibb, SellLaLa, StauCons, StauCon1, StauConN, StauLeDu, StauPiPi, UKSp8.*

Group D: *AchnMinu, BracBre1, BracBre2, BracBrNe, BracSp1, CyclStell, CymbCist, CymbMicr, CymbSimo, EncyMinu, EncyNeog, FrusRhCr, GompAcum, GompGra1, GompGra2, NitzBac1, NitzBaLa, NitzFrFr, NitzInt1, PseuBrev, SellSemi, SyneUlna, TabeFloc.*

Group E: *AchnSp1, AchnMinu, AmphPell, BracBreb, BracBre3, BracBrNe, BracNeoe, BracVitr, CratHali, CyclStell, CyclSp1, CymbCiCy, CymbFals, CymbMicr, CymbSimo, CymbSp1H, DiplSubo, EncyNeog, EunoBilu, EunoGird, EunoNaeg, FragExig, FragTene, FragSyne, FrusRhom, FrusRhCr, FrusVuNe, GompAcum, NaviAngu, NaviMart, NaviMini, NaviPseV, NaviRadi, NitzBaci, NitzBaLa, NitzDipp, NitzFrus, NitzGrac, NitzLacu, NitzPerm, PinnGibb, RhopGibb, StauPinn, StauSual, UKSP2, UKSp3, UKSp6.*

Group F: *AchnChil, AchnGerm, AchnMiJa, AchnMinu, BracBre2, BracBre3, BracNeoe, CaloSp1, CymbDiff, CymbMicr, DiatMeso, EncyMinu, EncyTris, EunoArcu, EunoBilG, EunoBilu, EunBiMu2, EunoBiMu, EunoBiSu, EunoExig, EunoExi2, EunoInci, EunoInte, EunoNaeg, EunoPaPa, EunoSp1, EunoSp3, EunoSchw, EunoSuba, EunoSub2, EunoTect, EunoVali, FragCapu, FragSyne, FrusRhom, FrusRhCr, GompParG, MeriCiCo, NaviProt, NaviSubl, NaviStau, NeidAffi, NeidAppl, NeidSp1, NitzBaci, NitzInte, SellSemi, UKSp7.*

Group G: *CoccPlac, CymbDiff, CymbSimo, EunoDiod, EunoExig, EunoNaeg, EunoSuba, EunoSubM, EunoSp2, NaviLoLo, NaviMini, NaviSubl, NitzInte, StauKreg, StauCurv.*

Whereas TWINSPAN separates groups largely on a presence-absence basis, the Bray-Curtis similarity measure incorporates abundance into its calculation. The ranking of the most similar assemblages using the latter is shown in Table 5 with the taxa making the largest contribution to the measure. It is clear that the widespread and abundant taxa, *C. microcephala* and *A. minutissima* account for much of the similarity between sites, although the high abundances of *B. neoexilis* and *F. rhomboides* in Alpha, Buena Vista and Hielo Azul account for a few of the higher similarity measures. The latter taxa are associated with the delimitation of group F in the TWINSPAN analysis (Fig. 1). Nevertheless, many pairs of assemblages show little similarity; 25 pairs of assemblages had no species in common, and 56 pairs had extremely low similarity measures, between 0.1 and 5.0%.

TABLE 5. Ranking of most similar assemblages based on Bray-Curtis similarity measure showing the most abundant taxon or taxa contributing to the measure.

Assemblage pair	**% similarity**	**important taxon / taxa**
Leones P : Alpha P	57.0	*A. minutissima, C. microcephala*
Leones P : Oxbow R	54.4	*C. microcephala, A. minutissima*
Leones P : Quito P	50.0	*C. microcephala*
Hielo Azul R : Hielo Azul S	48.0	*A. minutissima, C. microcephala*
Alpha P : Hielo Azul S	47.7	*A. minutissima, C. microcephala*
Leones P : Hielo Azul S	46.3	*A. minutissima, C. microcephala*
Quito P : Oxbow R	42.1	*C. microcephala, A. minutissima*
Alpha S2 : Buena Vista S	41.3	*B. neoexilis, F. rhomboides*
Oxbow R : Alpha P	40.9	*A. minutissima, C. microcephala*
Alpha P : Alpha S1	40.8	*C. microcephala*
Alpha S2 : Hielo Azul R	39.5	*C. microcephala, B. neoexilis*
Oxbow P : Leones P	39.2	*C. microcephala, A. minutissima*
Oxbow R : Hielo Azul S	38.0	*A. minutissima, C. microcephala*
Quito P : Alpha P	36.5	*C. microcephala, A. minutissima*
Quito P : Alpha S1	36.1	*C. microcephala, A. minutissima*
Oxbow R : Hielo Azul R	35.4	*C. microcephala, A. minutissima*
Oxbow P : Alpha P	34.9	*A. minutissima, C. microcephala*
Leones P : Alpha S1	34.5	*C. microcephala, A. minutissima*
Oxbow P : Hielo Azul S	33.6	*C. microcephala, A. minutissima*
Oxbow R : Alpha S1	33.6	*C. microcephala, A. minutissima*
Leones P : Hielo Azul R	33.1	*C. microcephala, A. minutissima*
Alpha P : Hielo Azul R	33.0	*C. microcephala, A. minutissima*
Hielo Azul R : Buena Vista S	32.5	*B. neoexilis, E. bilunaris*

Comparing within-lake assemblages using the Bray-Curtis similarity measure (Table 6) revealed that there was extemely low similarity (<4%) between different habitats within Leones and Quito, whereas in Alpha and Hielo Azul some habitat comparisons showed >40% similarity. In the other lakes between habitat similarities were between 20-30%. This suggests that, in many cases, the substratum type had a marked effect on the diatom assemblage, rather than water chemistry being the overriding factor. Even in the lake with the lowest pH (Buena Vista), where a more specialised flora might have been expected, similarity between habitats is still below 30%. However, if similarity is calculated using genus rather than species abundances, within lake assemblages show greater similarity (Table 6) than within habitat comparisons (Table 7). Assemblage similarity is particularly high in Buena Vista (83.4%) and Cachorro (>80%) in which several species of *Eunotia* and *Fragilaria*, respectively, contribute significantly to the flora, whereas in Quito, Leones and Oxbow, similarity does not exceed 45%.

TABLE 6. Bray-Curtis similarity measures for within-lake assemblage comparisons. Values are % similarity based on species (or genus) abundances, where 0 indicates total dissimilarity and 100 indicates total similarity.

Hielo Azul			
	epiphyton	epipelon	
epilithon	11.1 (37.7)	48.0 (61.1)	
epipelon	8.5 (38.1)		
Buena Vista:		epipelon v. epiphyton	27.6 (83.4)
Alpha			
	epipelon 1	epipelon 2	
epiphyton	40.8 (72.1)	22.9 (50.4)	
epipelon 2	23.2 (69.2)		
Cachorro		epiphyton v. epilithon	24.0 (80.6)
Quito		epiphyton v. epipelon	0.0 (44.1)
Leones			
	epilithon?	epipelon 1	epipelon 2
epiphyton	3.0 (13.4)	3.8 (40.9)	1.7 (22.6)
epipelon 2	0.0 (13.1)	0.5 (15.1)	
epipelon 1	2.0 (15.4)		
Oxbow		epiphyton v. epilithon	25.5 (45.7)

Relationship between diatom assemblages and substrata

Table 7 shows that the greatest similarities were found between epiphytic samples from different lakes, e.g. Leones P and Alpha P (57%), Leones P and Oxbow P (54.4%), and Leones P and Quito P (50%). This reflects the high abundance of *A. minutissima* in these samples (Table 5). The similarities between Alpha P and Oxbow P and Quito P were also relatively high, 34.9% and 36.5% respectively. On the whole similarities between epipelic and epilithic samples from different lakes were lower, although Buena Vista S and Alpha S2 had a similarity measure of 42.3% (predominantly *F. rhomboides* and *B. neoexilis*), and Oxbow R and Hielo Azul R had a similarity measure of 35.4% (predominantly *C. microcephala* and *A. minutissima*). There was also little grouping of same habitat assemblages within the TWINSPAN groups, except Cachorro P and Hielo Azul P in group A, and Leones P and Quito P in group E.

TABLE 7. Bray-Curtis similarity measures for between lake but within habitat comparisons. Values are % similarity based on species (or genus) abundances, where 0 indicates total dissimilarity and 100 indicates total similarity. Figures in parenthesis are based on generic identity only.

Epiphytic samples	Oxbow	Leones	Quito	Cachorro	Alpha	Hielo Azul
Hielo Azul	0.0 (22.1)	0.0 (24.1)	0.0 (18.8)	12.1 (31.3)	0.0(29.4)	0.0 (0.3)
Buena Vista	0.0 (0.3)	0.8 (6.2)	11.8 (24.3)	0.0 (0.0)	0.0 (16.3)	
Alpha	34.9 (50.7)	57.0 (65.4)	36.5 (64.8)	1.8 (4.5)		
Cachorro	1.4 (4.3)	1.8 (4.5)	2.1 (2.1)			
Quito	6.1 (24.0)	50.0 (54.9)				
Leones	39.2 (52.5)					
Epipelic samples	Leones S1	Leones S2	Quito	Alpha S1	Alpha S2	Buena Vista
Hielo Azul	4.0 (44.8)	1.7 (23.9)	22.3 (65.1)	25.9 (34.4)	16.3 (24.3)	2.0 (14.7)
Buena Vista	0.5 (3.0)	6.1 (42.8)	0.0 (1.9)	0.3 (23.4)	42.3 (45.1)	
Alpha S2	6.8 (12.9)	0.0 (19.9)	12.5 (19.0)	23.2 (69.2)		
Alpha S1	5.6 (19.0)	0.5 (10.9)	21.3 (40.5)			
Quito	2.5 (55.5)	0.5 (3.0)				
Leones S2	0.5 (15.1)					
Epilithic samples	Oxbow	Leones	Cachorro			
Hielo Azul	35.4 (58.2)	12.5 (21.2)	9.0 (17.3)			
Cachorro	5.3 (16.2)	3.5 (53.8)				
Leones	4.5 (17.8)					

Relationship between diatoms and lake environment

Species data and sites were first analysed using DCA (Fig. 2) which showed long gradients (axis 1 = 6.8 standard deviations (S.D.) and axes 2 = 3.05 S.D), indicating a strong to very strong unimodal response with a good spread of species and site scores. The eigenvalues for axes 1 and 2 are measured in standard deviation units (s.t.u.) ($\lambda_1 = 0.88$, $\lambda_2 = 0.53$) showing that axis 1 describes most of the variance in the data and implies a high ß-diversity (species turnover rate from one habitat to the next). This may have a geographical basis as the altitudinal gradient of each lake increases with gradient length on axis 1. Axes 1 and 2 together explain 30% of the total cumulative percentage variance of the species data, with only an additional 3.6% being explained by all 4 axes. The total inertia in the species data is described by the sum of all unconstrained eigenvalues, 4.7.

Cachorro is separated from Buena Vista by more than 4 s.t.u. on the first axis indicating that these two lakes should have no species in common. This can be confirmed by comparing their assemblages in Table 4. Cachorro is also separated from Alpha by between 3-4 s.t.u., indicating that they have only a few species in common, i.e. *C. microcephala* and *Nitzschia bacillum* Hustedt, although only Cachorro R has both taxa. Species at the edges of the plot are deemed to be rare and in low abundance e.g. *C. naviculiformis*, *Fragilaria* # 3, *Cymbella difficilis* Krasske, *Amphipleura pellucida* Kützing and *Nitzschia dippelii* Grunow are all found in only 1 site and at less that 2% abundance. It is also clear that Buena Vista is unlike all the other lakes, with *Eunotia* spp. being the most abundant taxa, and with high abundances of a few species of *Brachysira* and *Frustulia*. *Fragilaria* is similarly most abundant in Cachorro. Meanwhile, considering individual habitats, the separation of Quito S from Buena Vista S, and Alpha S1 and P from Buena Vista S and P, by 4 or more s.t.u., suggests that the same habitat types may have few, if any, species in common. This is borne out by the original species counts and the summary in Table 4. In an attempt to interpret the 2nd axis, species with a high score (> 4 s.t.u.) and with a low score (< 1 s.t.u) were compared. There appears to be a split between those taxa "preferring" more acid conditions e.g. *Eunotia*, and those "preferring" more alkaline e.g. *Epithemia* Brébisson ex Kützing, *Nitzschia*. This suggests pH as the factor accounting for differences in relative abundances and assemblage composition between lakes. Thus, DCA reveals a clear difference in diatom assemblage structure between the lakes, and between similar habitats from different lakes. Although the cause of the differences cannot be deduced from the DCA, it provides clues when examined in relation to the measured environmental variables, e.g. altitude and pH.

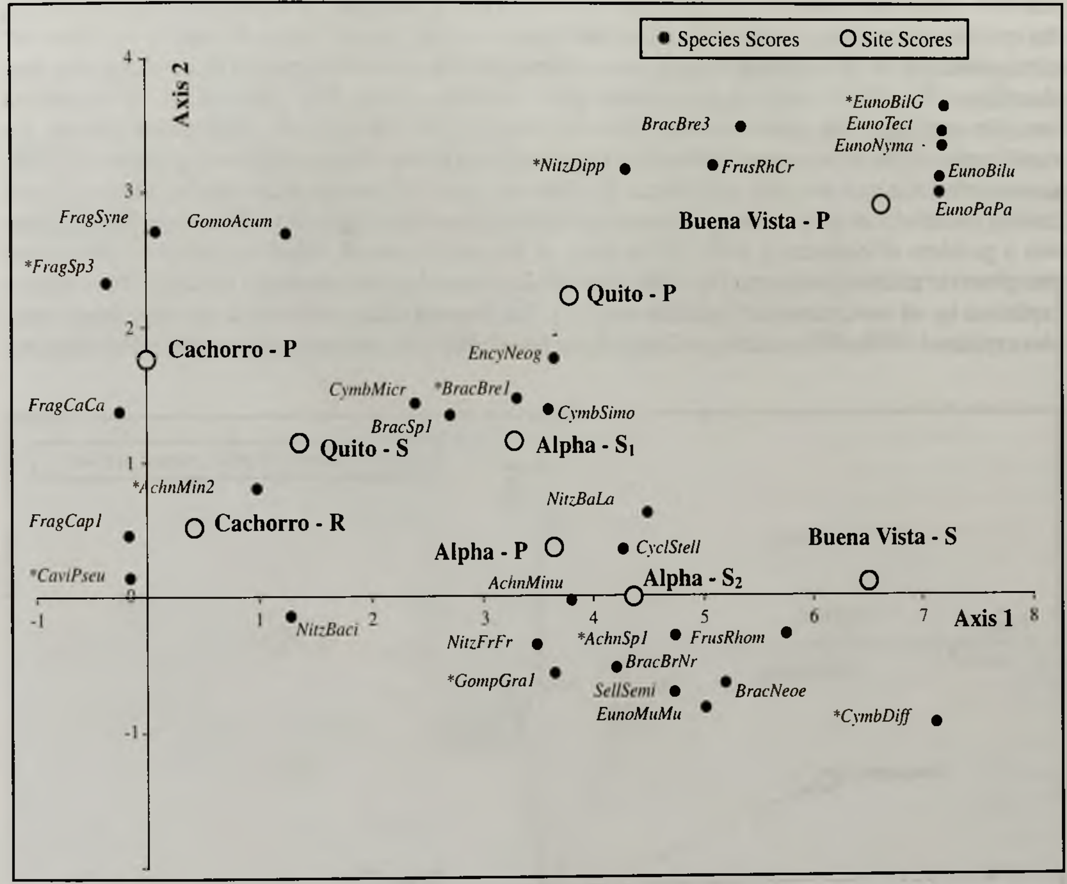

FIGURE 2. DCA of 9 sample sites within 4 lakes (species & sites). Those species marked with an asterix (*) consist of an assemblage of species with the identifying taxa underlined as follows:
***AehnSp1**: AmphPell, CratHali, CymbCiCy, DiplSubo, FusVuNe, NaviAngu, NaviMart, NaviPseV, NitzFrus, StauSual, UKSp2, UKSp3.*
***AchnMin2**: AchnSp2, EncySupa, EpitTuHy, GompGrac, RhopGibb.*
***BracBre1**: BracBre2, CymbCist, DiplElli, EncyMinu, PseuBrev, StauCoVe, SyneUlna.*
***CaviPseu**: CymbCySi, CymbNavi, EpitSp1, NaviHass, NaviLapi, NaviPerm, NaviStau, NeidHerc, PinnGiMi, StauSuat, SyneArRa.*
***CymbDiff**: EunBiMu2, EunoBiSu, EunoExig, EunoExi2, EunoInte, EunoNaeg, EunoSchw, EunoVali, NaviProt, NaviSubl, NeidAffi, NeidAppl, NeidSp1, NitzInte.*
***EunoBilG**: EunoBiMu, EunoInci, EunoSuba, EunoSub2, EunoSp1, UKSp7.*
***FragSp3**: FragCap4, FragBent, NitzAmpi, NitzDiMe, PinnSp2.*
***GompGra1**: GompGra2, NitzBac1, NitzInt1, TabeFloc.*
***NitzDipp**: BracVitr, CyclSp1, CymbFals, EunoGird, FragExig, FragTene, NaviRadi, PinnGibb, StauPinn, UKSp6.*

To assess the effect of the detrending, CA and CCA analyses were performed, but both showed an arch in the data. (Detrending hides or corrects this.) According to Jorgman *et al*; (1995), this effect often happens when axis 1 of the CA explains most of the species data, because CA will not then detect a true 2nd gradient. Rearranging the species scores in ascending order in a data matrix revealed a clustering that confirmed the DCA. The results of the CCA were similar to the CA. The arch effect in the CCA ordination may have been the result of over-fitting a small data set, which can be corrected by DCCA.

In the DCCA the eigenvalues for the first two axes are λ_1 0.85 and λ_2 0.50. Together, they explain just 30% of the total cumulative percentage variance of the species data, although they explain 64 % of the species-environment relationship. The total inertia in the species data and sum of all canonical eigenvalues is 4.48 (the same as in the CCA) and describes the variance in species dispersion rather than abundance. The DCCA ordination is shown as two plots for clarity. Fig. 3 shows the environmental variables and Fig. 4 the species and samples. The results of the Monte Carlo permutation tests for the significance of the first canonical axis in explaining most of the dispersion gave a p-value of 0.005, showing that this axis is highly significant. Furthermore, a test of the significance of all canonical axes (testing the relationship between species and environment) was also highly significant (p = 0.005). There was a problem of colinearity with all but three of the environmental variables (chloride, nitrate and phosphate) in addition to the small number of samples compared to environmental variables. The variance explained by all environmental variables was 2.11, but forward selection showed that only three variables explained 100% of the variance to a significant level (chloride, potassium and calcium). Nevertheless,

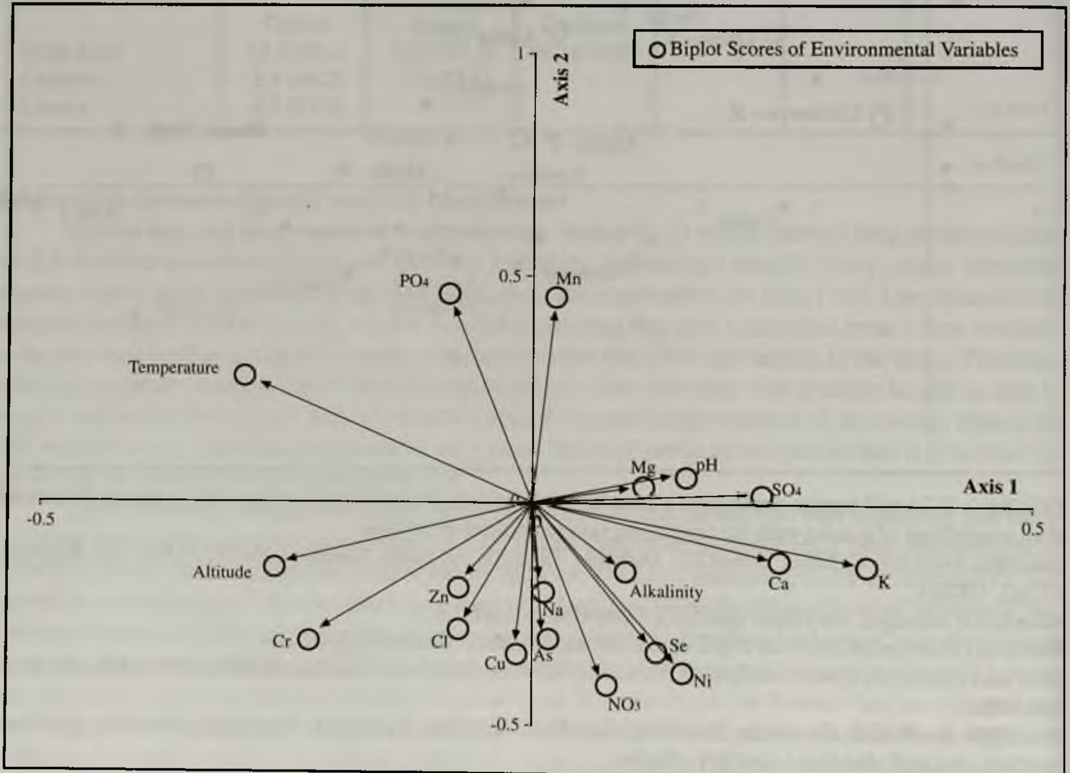

FIGURE 3. DCCA of the environmental variables for 9 sample sites within 4 Lakes. NB The scale is the same as in Figure 4 but has been expanded for clarity.

because the arrangement of species in the ordination is not affected greatly by intercorrelations, all variables were plotted in Fig. 3. The lengths of the arrows indicate the strength of the correlations between environmental variables and species, and as all arrows are very short, any correlation is weak. Arrows parallel to axes indicate a correlation with that axis. From Fig. 3 it can be seen that manganese, sodium, arsenic and copper correlate closely with axis 2, whilst sulphate correlates closely with axis 1. Since sites and species are fitted onto the axes simultaneously, superimposing Fig. 3 over Fig. 4 shows that species and samples in the lower left quadrant of the plots are associated with metals and altitude, whilst those in the lower right quadrant are associated with alkalinity.

By examining the relative contribution of each species to the total cumulative variance in the ordination it is possible to determine which species have a stronger influence on the ordination. Species with larger variances have a stronger influence. The highest contributing species (for axes 1 and 2) are *Fragilaria capucina* #1, and *Fragilaria capucina* var. *capucina* Desmazieres, followed by *Eunotia paludosa* var. *paludosa* Grunow, *E. bilunaris* and *F. rhomboides*. The species contributing least were *Cymbella simonsenii* Krammer, *Encyonema neogracile* Krammer and *Eunotia muscicola* var. *muscicola* Krasske. All species contributed more to ordination axis 2 than 1.

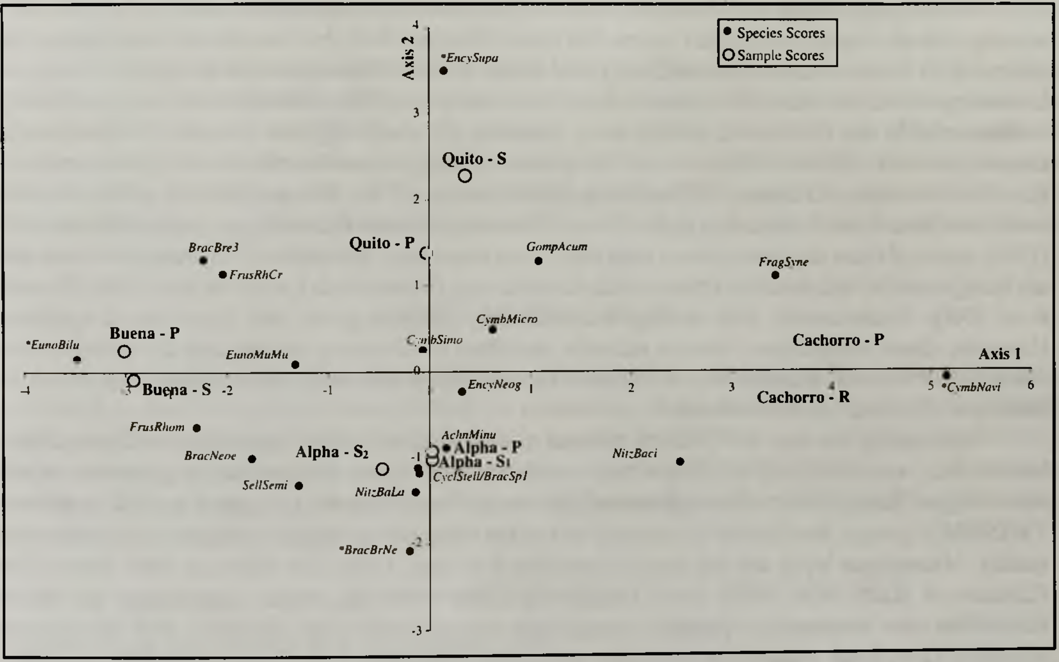

FIGURE 4. DCCA of 9 sample sites within 4 lakes (species & sites). Those species marked with an asterix (*) consist of an assemblage of species with the identifying taxa underlined as follows:
EunoBilu: *CymbDiff, EunoBilG, EunoBilu, EunBiMu2, EunoBiMu, EunoBiSu, EunoExig, EunoExi2, EunoInci, EunoInte, EunoSuba, EunoSub2, EunoNaeg, EunoPaPa, EunoSp1, EunoSchw, EunoTect, EunoVali, NaviProt, NaviSubl, NeidAffi, NeidAppl, NitzInte, UKSp7.*
EncySupa: *AchnMin2, AchnSp2, BracVitr, CyclSp2, CymbFals, EpitTuHy, EunoGird, FragExig, FragTene, GompGrac, NaviRadi, NitzDipp, PinnGibb, RhopGibb, StauPinn, UKSp6.*
CymbiNavi: *CaviPseu, CymbCySi, EpitSp1, FragCap1, FragCaCa, FragSp3, FragCap4, FragBent, NaviHass, NaviLapi, NaviPerm, NaviStau, NeidHerc, NeidAmph, NitzDiMe, PinnGiMi, PinnSp2, StauSuat, SyneArAr.*
BracBrNe: *AchnSp1, AmphPell, BracBre1, BracBre2, CratHali, CymbCist, CymbCiCy, DiplElli, DiplSubo, EncyMinu, FrusVuNe, GompGrac, GompGra2, NaviAngu, NaviMart, NaviPseuV, NitzBac1, NitzInt1, NitzFrus, NitzFrFr, PseuBrev, StauCoVe, StauSual, SyneUlna, TabeFloc, UKSp2, UKSp3.*

Examining the positions of particular lakes, Buena Vista lies near the top of the altitude gradient and distant from the top of the pH gradient, while Cachorro lies at the opposite end of axis 1, near the top of the sulphate gradient. The distance between these sites imply that they have very few species in common, borne out by the similarity measure which is 0.0 for three of the four possible comparisons, 0.25 for the fourth. Alpha and Quito lie nearer the centre of the plot, on opposite sides of axis 1. Quito falls near the top of the manganese gradient while the position of the Alpha assemblages reflects the higher concentrations of copper, arsenic, sodium and chloride at that site. The different assemblages from each lake fall in slightly different positions because of the contrasting contributions of species to those assemblages. Thus, the positions of the two Buena Vista sites reflect the differing contributions of their most abundant species, *F. rhomboides*, *B. neoexilis* and *E. bilunaris*, and the proximity of Quito S to *Encyonema supergracile* Krammer reflects its occurrence in that sample only. The widespread taxa, *C. microcephala* and *A. minutissima* fall near the origin, on the positive part of axis 1, being found in all lakes except Buena Vista.

DISCUSSION

As this study comprised 18 samples from only seven lakes, it cannot be considered an exhaustive investigation of diatoms within the Laguna San Rafael National Park, but nevertheless some interesting points can be drawn. The restriction of many taxa to one or a few lakes was striking, although it was also interesting to find that two cosmopolitan species occurred in over 70% of the samples, sometimes at high abundances. On the other hand, several taxa, including *Cymbella difficilis* Krasske, *E. supergracile*, *Encyonema triste* (Krasske) Krammer and *Gomphonema patagonicum* Krasske, have only been recorded from South America (Krammer 1997a,b, Lange-Bertalot *et al.* 1996). Krasske (1939a,b, 1949) described many new taxa from S. America, and southern Chile in particular. According to Lange-Bertalot *et al.* (1996), some of these are synonymous with taxa found elsewhere, but an increasing number of new taxa are being recorded and described from South America only (Metzeltin & Lange-Bertalot 1998, Rumrich *et al.* 2000). Unfortunately little ecological information has been given with these new descriptions. However, closer comparison between recently described S. American species and the unknown taxa (especially *Frustulia*, *Eunotia* and *Brachysira* specimens) in this study will be necessary before the identity of the latter can be resolved.

When using diatoms as indicators of water quality, epilithic assemblages have usually be chosen, because they are considered to show closer correlation with water quality than epiphytic or epipelic assemblages (Round 1993). Although the epilithic assemblages from the different lakes fall in different TWINSPAN groups, the data set is too small to test the reliability of epilithic samples to monitor water quality. Macrophyte hosts are not usually considered to have a selective effect on their diatom flora (Cattaneo & Kalff 1978, 1979, 1980, Eminson & Moss 1980) but, rather surprisingly, the highest similarities were obtained for epiphytic assemblages from different lakes. However, with the exception of Buena Vista, these assemblages usually contained high abundances of the cosmopolitan species, *A. minutissima* and *C. microcephala*. *A. minutissima* often occurs in disturbed habitats and is an early coloniser of surfaces (Round 1990, Cox 1991) while *C. microcephala* is usually associated with well-aerated habitats. However, according to Krammer (1997b) while the latter is found in oligotrophic, acidic and low conductivity waters in northern Europe, it occurs in calcium-rich, moderate conductivity waters in central Europe and North America. Its ecological distribution in the LSRNP lakes is closer to the latter than the former, particularly given its absence from the most acidic lake, Buena Vista. (The existence of contrasting ecological races may also indicate the need for taxonomic revision.) The higher abundances of *A. minutissima* and *C. microcephala* on plants and rocks compared to the higher abundances of *F. rhomboides* and *B. neoexilis* on sediments may also reflect habit differences. *A. minutissima* frequently attaches by mucilage stalks whereas *Frustulia* and *Brachysira* spp. occur as actively motile, free-living individuals, that are able to survive in more mobile sediments. Species of *Eunotia*, *Brachysira* and *Frustulia* are often found in more acidic habitats. This pattern is maintained in this survey and supported by the ordination analysis.

DCCA can be a useful tool for exploring the relationships between species data and environmental variables, but because the present data set is small with short environmental gradients, care must be taken in interpreting the results. When performing DCA, CA and CCA there is a proviso that the number of environmental variables should be smaller than the number of sites, otherwise the species-environment correlation may yield values close to 1, even if none of the variables affect the species (ter Braak & Smilauer, 1998). This was not the case in this study but the results should still be interpreted carefully, as they remain little more than generalisations. The discrepancy between the sizes of the species and environmental data sets may have been an additional cause of the arch effect in the CA and CCA. It is possible to reduce the number of variables for CCA and DCCA, but there is an inevitable loss of information. However, in CANOCO the use of forward selection, or stepwise analysis of environmental variables via Monte Carlo permutations, allows the environmental variables to be reduced to their minimum while still explaining most of the variance. This is still no guarantee that the best set of variables will be selected as the problem of colinearity remains and multiple comparisons can produce significant, but false, results. Nonetheless, the tests are a reasonable measure of the analyses and how well each variable fits the species data.

The taxonomic diversity and floristic contrasts between different lakes in this small study indicate that there is much scope for using diatoms as environmental indicators. The number of unknown taxa is a further spur to investigating the flora in greater depth, and seeking to clarify the biogeography of diatom species. As more lakes are investigated in detail it will be possible to build up a local data set as the basis of a monitoring system for the park, using diatoms as indicators of environmental change. Causes of the latter may include increased human activity in the park and external factors such as climate change and increased UV radiation.

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APPENDIX 1. TOTAL SPECIES LIST.

Order follows taxonomic treatment in Round, Crawford & Mann (1990). Taxa with * occurred at >2% abundance in at least one sample.

Coscinodiscaceae (centric diatoms)

- *Cyclotella stelligera* Cleve & Grunow *
- *Cyclotella* #1
- *Cyclotella* #2
- *Aulacoseira granulata* (Ehrenberg) Simonsen *

Fragilariophyceae (araphid pennate diatoms)

- *Hannaea arcus* (Ehrenberg) Patrick *
- *Hannaea arcus* var. *arcus*
- *Fragilaria* bent
- *Fragilaria capucina* Desmazieres *
- *Fragilaria capucina* #1 *
- *Fragilaria capucina* var. *capucina* *
- *Fragilaria exigua* Grunow in Cleve & Möller
- *Fragilaria germainii* Lange-Bertalot & Reichardt
- *Fragilaria similis* Krasske *
- *Fragilaria tenera* (W. Smith) Lange-Bertalot
- *Fragilaria vaucheriae* (Kützing) Petersen *
- *Fragilaria* cf. *vaucheriae* *
- *Fragilaria* #2
- *Fragilaria* #3
- *Fragilaria* #4 *
- *Fragilaria / Synedra* sp. *
- *Staurosirella leptostauron* var. *dubia* (Grunow) comb. nov.
- *Staurosirella pinnata* (Ehrenberg) Williams & Round
- *Staurosirella pinnata* var. *pinnata*
- *Staurosira construens* Ehrenberg var. #1 *
- *Staurosira construens* var. nov.
- *Staurosira* cf. *construens*
- *Staurosira construens* fo. *venter*
- *Pseudostaurosira brevistriata* (Grunow in Van Heurck) Williams & Round
- *Pseudostaurosira brevistriata* var. #2
- *Pseudostaurosira brevistriata* var. #3
- *Pseudostaurosira pseudoconstruens* (Marciniak) Williams & Round
- *Diatoma mesodon* (Ehrenberg) Kützing *
- *Meridion circulare* (Greville) Agardh *
- *Meridion circulare* var. *constrictum* (Ralfs) Van Heurck
- *Synedra acus* Kützing / *S. radians* *
- *Synedra ulna* (Nitzsch) Ehrenberg
- *Tabellaria flocculosa* (Roth) Kützing

Bacillariophyceae (raphid diatoms)

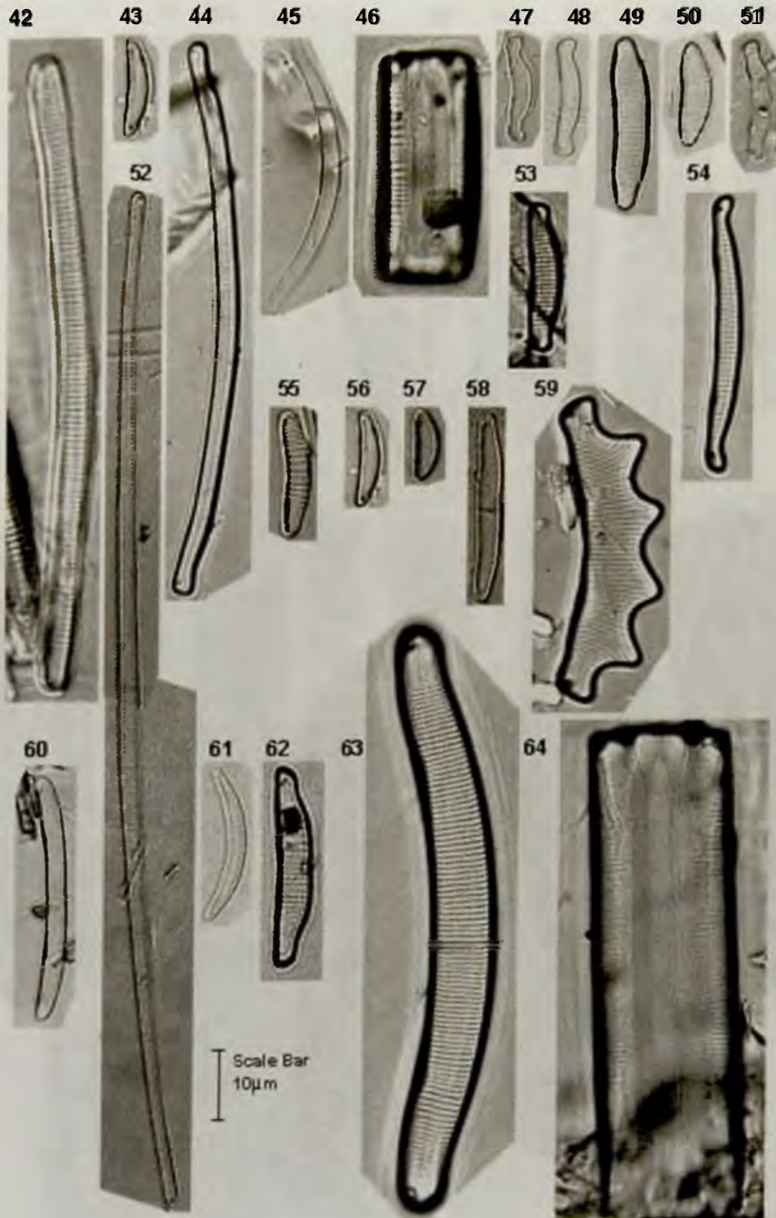
- *Eunotia arcus* Ehrenberg
- *Eunotia bilunaris* (Ehrenberg) Mills *
- *Eunotia bilunaris* var. *subarcuatoides*
- *Eunotia bilunaris* var. *mucophilia* Lange-Bertalot & Nörpel *
- *Eunotia bilunaris* var. *mucophilia* #2 *
- *Eunotia bilunaris* ? (girdle view only) *
- *Eunotia diodon* Ehrenberg *
- *Eunotia exigua* (Brébisson) Rabenhorst *

Eunotia exigua #2 *
Eunotia incisa Gregory
Eunotia intermedia (Krasske) Lange-Bertalot & Nörpel *
Eunotia muscicola var. *muscicola* Krasske *
Eunotia naegeli Migula *
Eunotia nymanniana Grunow *
Eunotia paludosa var. *paludosa* Grunow *
Eunotia pectinalis (Dillwyn) Rabenhorst
Eunotia schwabei Krasske
Eunotia subarcuatoides Alles, Nörpel & Lange-Bertalot *
Eunotia subarcuatoides – malformed
Eunotia subarcuatoides #2
Eunotia tecta Krasske *
Eunotia valida Hustedt
Eunotia #1 *
Eunotia #2 *
Eunotia #3
Eunotia sp. (girdle view)
Anomoeoneis vitrea (Grunow) Ross *
Cymbella cistula (Ehrenberg) Kirchner
Cymbella cistula / cymbiformis
Cymbella cymbiformis Agardh
Cymbella cymbiformis / simonsenii
Cymbella difficilis Krasske *
Cymbella falaisensis (Grunow) Krammer & Lange-Bertalot *
Cymbella microcephala Grunow *
Cymbella naviculiformis Auerswald
Cymbella simonsenii Krammer *
Cymbella #1 (*helvetica* type)
Encyonema neogracile Krammer *
Encyonema minutum (Hilse in Rabenhorst) D.G. Mann *
Encyonema supergracile Krammer & Lange-Bertalot *
Encyonema triste (Krasske) Krammer *
Gomphonema acuminatum Ehrenberg
Gomphonema clavatum Ehrenberg
Gomphonema gracile Ehrenberg *
Gomphonema gracile var. #1
Gomphonema gracile var. #2 *
Gomphonema parvulum (Kützing) Kützing *
Gomphonema parvulum var. #1 *
Gomphonema parvulum var. #2 *
Gomphonema parvulum var. #3
Gomphonema parvulum var. *parvulum* fo. *parvulum* *
Gomphonema parvulum? (girdle view only)
Gomphonema patagonicum Krasske
Achnanthes chlidanos Hohn & Hellermann *
Achnanthes coarctata var. *coarctata* (Brébisson) Grunow *
Achnanthes coarctata var. *constricta* Krasske
Achnanthes germainii Manguin
Achnanthes lanceolata (Brébisson) Grunow
Achnanthes minutissima Kützing *

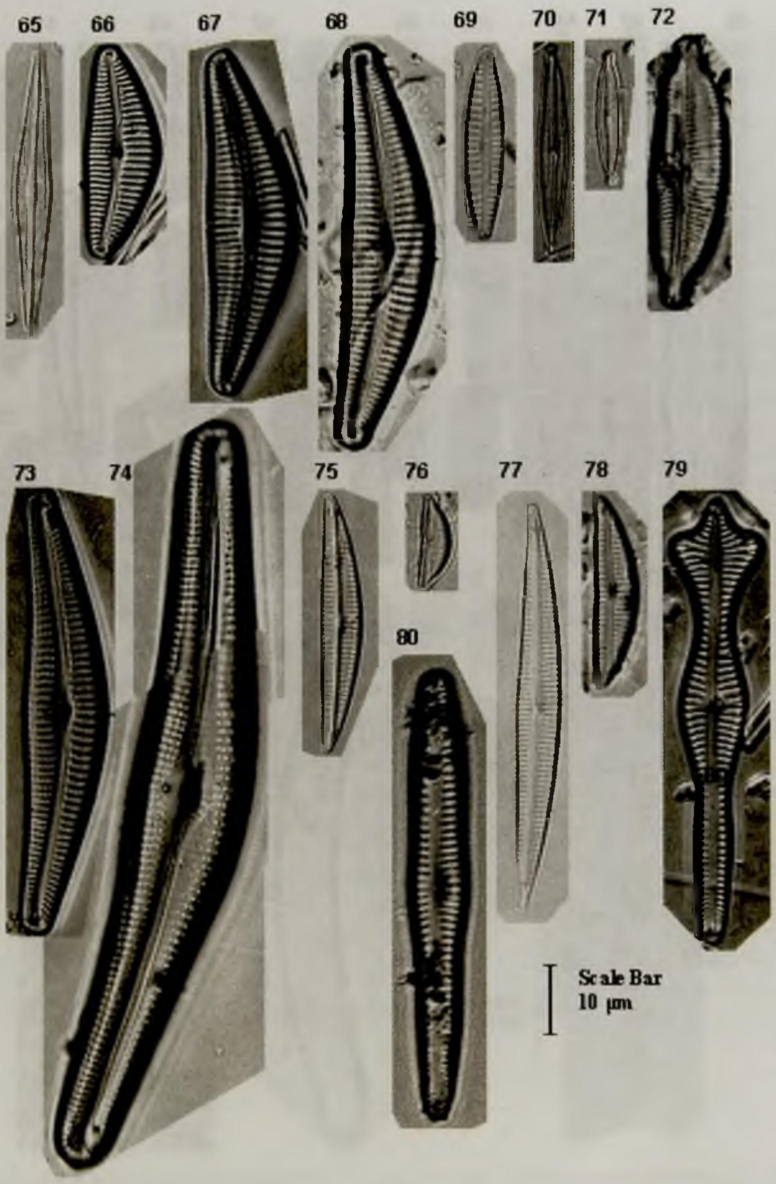
Achnanthes minutissima var. *jackii* (Rabenhorst) Lange-Bertalot *
Achnanthes minutissima #2 *
Achnanthes subatomoides (Hustedt) Lange-Bertalot *
Achnanthes #1
Achnanthes #2 *
Cocconeis placentula Ehrenberg
Cavinula pseudoscutiformis (Hustedt) D.G. Mann *
Amphipleura pellucida Kützing
Frustulia rhomboides (Ehrenberg) De Toni *
Frustulia rhomboides var. *crassinervia* (Brébisson) Ross *
Frustulia saxonica Rabenhorst
Frustulia vulgaris (Thwaites) De Toni
Frustulia vulgaris / neomondana
Brachysira minor (Krasske) Lange-Bertalot & Moser
Brachysira brebissonii Ross in Hartley *
Brachysira brebissonii #1 *
Brachysira brebissonii #2 *
Brachysira brebissonii #3 *
Brachysira brebissonii / neoexilis *
Brachysira neoexilis Lange-Bertalot *
Brachysira #1 *
Neidium affine (Ehrenberg) Pfitzer
Neidium affine var. *longiceps* (Gregory) Cleve
Neidium apiculatum Reimer
Neidium hercynicum A. Mayer
Neidium #1
Sellaphora laevissima var. *laevissima* (Kützing) D.G. Mann
Sellaphora pupula var. *pupula* (Kützing) Mereschkowsky
Sellaphora seminulum (Grunow) D.G. Mann
Pinnularia gibba Ehrenberg
Pinnularia gibba / microstauron
Pinnularia microstauron (Ehrenberg) Cleve *
Pinnularia stomatophora Grunow *
Pinnularia viridis (Nitzsch) Ehrenberg
Pinnularia #1 *
Pinnularia #2
Caloneis #1 *
Caloneis #5
Diploneis elliptica (Kützing) Cleve
Diploneis subovalis Cleve
Adlafia bryophila (Petersen) Moser, Lange-Bertalot & Metzeltin / *pseudobryophila*
Navicula angusta Grunow
Navicula halophiloides Hustedt *
Navicula hassiaca Krasske
Navicula lapidosa Krasske
Navicula longicephala Hustedt var. *longicephala* *
Navicula martinii Krasske
Navicula minima Grunow
Navicula perminuta Grunow
Navicula protracta (Grunow) Cleve *
Navicula pseudoventralis Hustedt

Navicula radiosa Kützing *
Navicula subalpina Reichardt
Navicula submolesta Hustedt
Navicula trivialis Lange-Bertalot
Navicula #1 *
Navicula #2
Navicula #3
Craticula halophila (Grunow ex Van Heurck) D.G. Mann
Stauroneis kriegerii Patrick
Stauroneis phoenicenteron (Nitzsch) Ehrenberg *
Stauroneis wislouchii Poretzky & Anisimowa *
Stauroneis #1 *
Kobayasia subtilissima (Cleve) Lange-Bertalot *
Amphora veneta Kützing *
Nitzschia alpina Hustedt *
Nitzschia amphibioides Hustedt *
Nitzschia bacillum Hustedt *
Nitzschia bacillum #1
Nitzschia bacillum / lacuum *
Nitzschia clausii Hantzsch
Nitzschia dippelii Grunow
Nitschia dissipata var. *media* (Hantzsch) Grunow *
Nitzschia frustulum (Kützing) Grunow *
Nitzschia frustulum var. *frustulum* *
Nitzschia frustulum #3
Nitzschia gracilis Hantzsch *
Nitzschia intermedia Hantzsch
Nitzschia intermedia #1
Nitzschia intermedia #2 *
Nitzschia lacuum Lange-Bertalot *
Nitzschia palea (Kützing) W. Smith / *N. gracilis* Hantzsch *
Nitzschia perminuta (Grunow) M. Peragallo *
Stenopterobia curvula (W. Smith) Krammer *
Surirella pseudolinearis var. *constricta* (Grunow) Hustedt
Epithemia hyndmanii W. Smith
Epithema turgida (Ehrenberg) Kützing / *E. hyndmanii* W. Smith *
Epithemia sp. #1
Rhopalodia gibba (Ehrenberg) O. Müller
Unknown #2
Unknown #3
Unknown #4
Unknown #5 *
Unknown #6
Unknown #7
Unknown #8 *
Sp. #1 *
Sp. #2

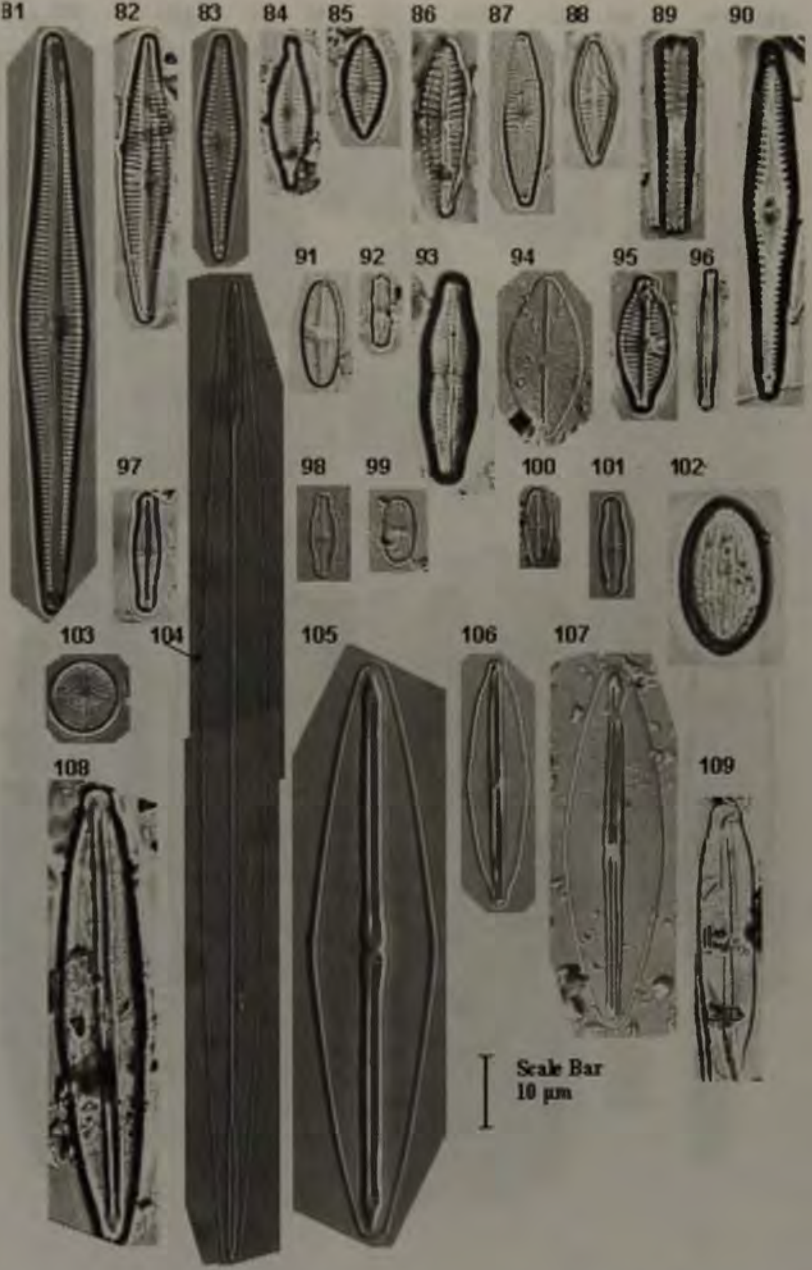
FIGURAS 5-41. **5**. *Cyclotella stelligera*, **6**. *Cyclotella* #1, **7**. *Cyclotella* #2, **8**. *Aulacoseira granulata*, **9**. *Hannaea arcus*, **10**. *H. arcus var. arcus*, **11**. *Fragilaria* bent, **12**. *F. capucina*, **13**. *F. capucina* #1, **14**. *F. capucina* var. *capucina*, **15**. *F. exigua*, **16**. *F. germanii*, **17**. *F. similis*, **18**. *F. tenera*, **19**. *F. vaucheriae*, **20**. *F.* cf. *vaucheriae*, **21**. *Fragilaria* #2, **22**. *Fragilaria* #3, **23**. *Fragilaria* #4, **24**. *Fragilaria/Syndera* sp., **25**. *Staurosirella leptostauron* var. *dubia*, **26**. *S. pinnata*, **27**. *S. pinnata* var. *pinnata*, **28**. *Staurosira construens*, **29**. *S construens* var. nov., **30**. *S.* cf. *construens*, **31**. *S. construens* fo. *venter*, **32**. *Pseudostaurosira brevistrata*, **33**. *P. brevistrata* var. #2, **34**. *P. brevistrata* var. #3, **35**. *P. pseudoconstruens*, **36**. *Diatoma mesodon*, **37**. *Meridion ciculare*, **38**. *M. circulare* var. *constrictum*. **39**. *Synedra acus/S. radians*, **40**. *S. ulna*, **41**. *Tabellaria flocculosa*.



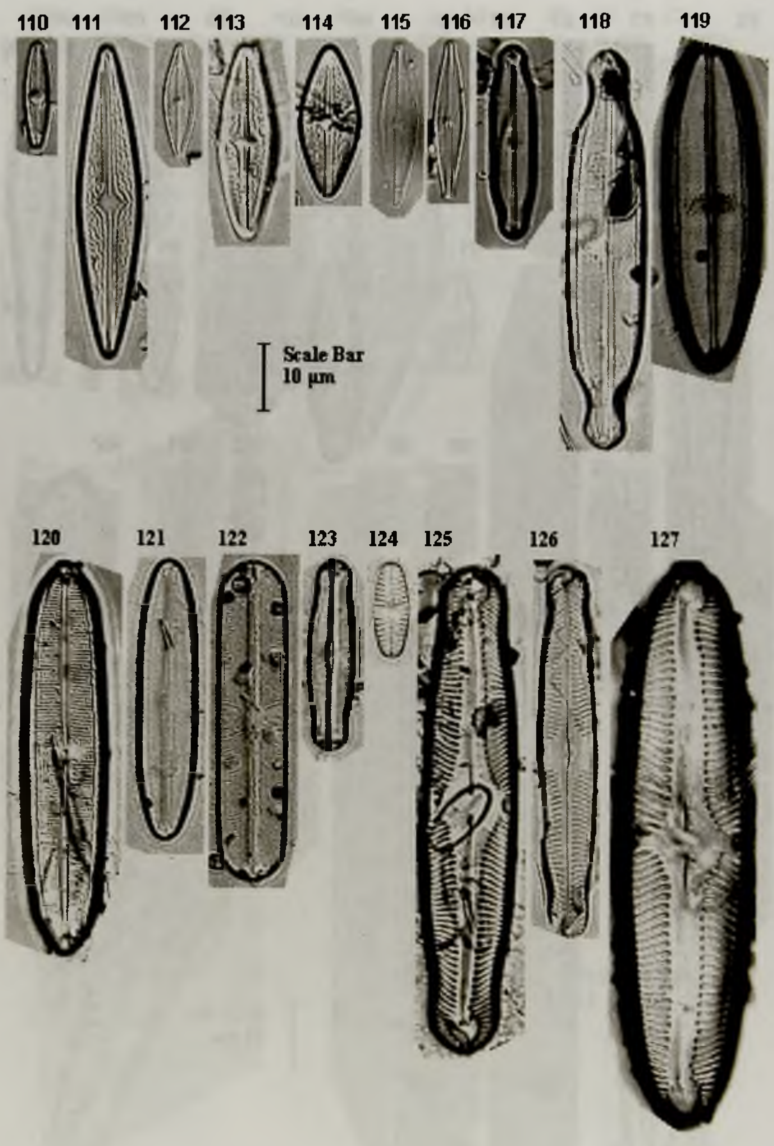
FIGURAS 42-64. **42.** *Eunotia bilunaris*, **43.** *E. bilunaris* van *subarcuatoides*, **44.** *E. bilunaris* var. *mucophilia*, **45.** *E. bilunaris* var. *mucophilia* #2, **46.** *E. bilunaris* (girdle), **47.** *E. exigKd*, **48.** *E. exigua* # 2. **49.** *E. incisa*, **50.** *E. intermedia*, **51.** *E. muscicola* var. *muscicola*, **52.** *E. naegeli*, **53.** *E. nymanniana*, **54.** *E. paludosa* var. *paludosa*, **55.** *E. pectinalis*, **56.** *E. subarcuatoides*, **57.** *E. subarcuatoides* (malformed), **58.** *E. subarcuatoides* # 2, **59.** *E. tecta*, **60.** *E. valida*, **61.** *Eunotia* #1, **62.** *Eunotia* #2, **63.** *Eunotia* #3, **64.** *Eunotia* sp. (girdle).



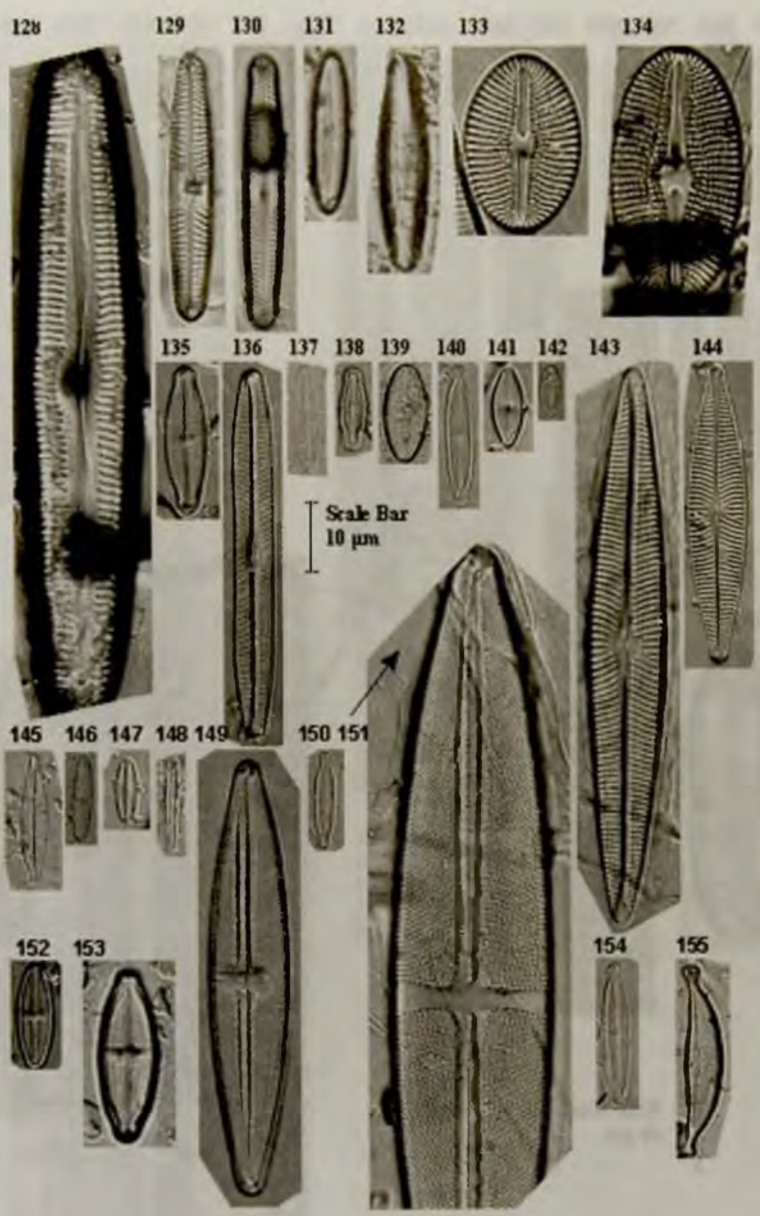
FIGURAS 65-80. 65. *Anomoeoneis vitrea*, 66. *Cymbella cistula*, 67. *C. cistula/cymbiformis*, 68. *C. cymbiformis*, 69. *C. difficilis*, 70. *C. falaisensis*, 71. *C. microcephala*, 72. *C. naviculiformis*, 73. *C. simonsenii*, 74. *Cymbella* # 1 (helvicta type), 75. *Encyonema neogracile*, 76. *E. minutum*, 77. *E. supergracile*, 78. *E. triste*, 79. *Gomphonema acuminatum*, 80. *G. clavatum*.



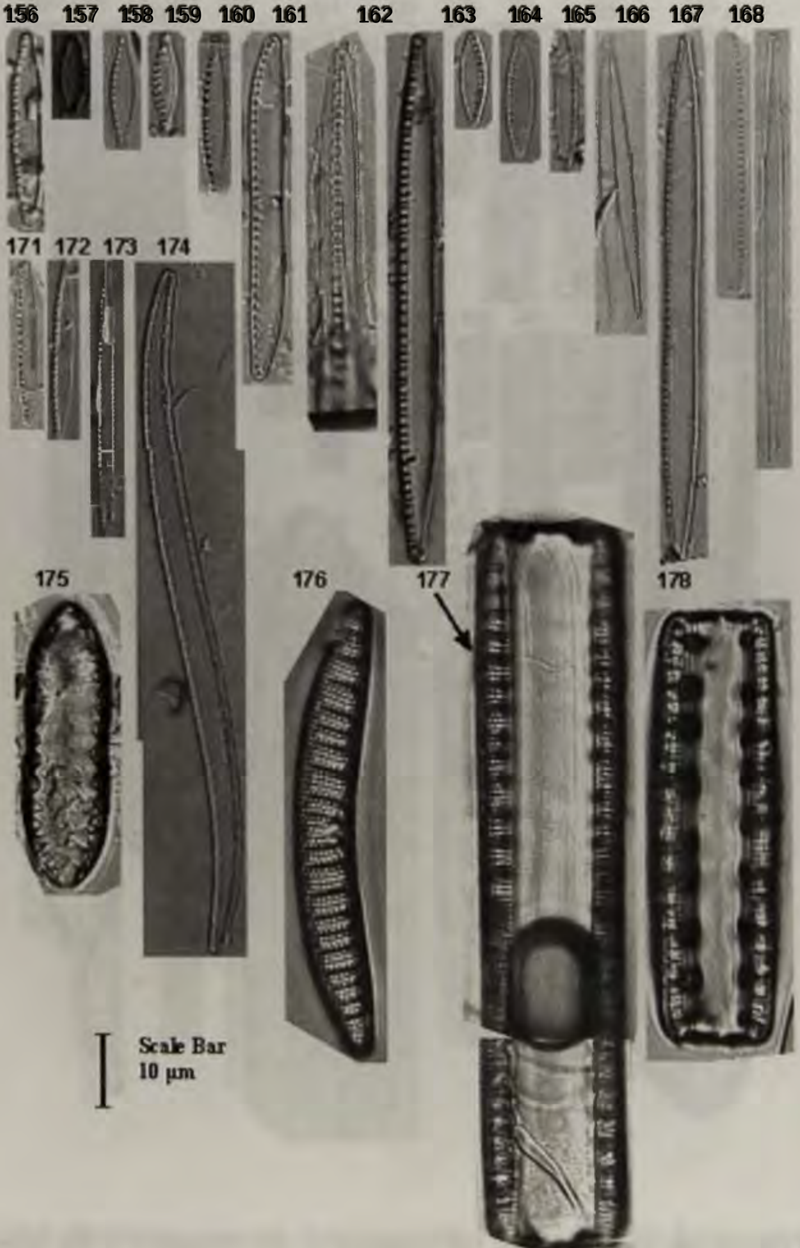
FIGURAS 81-109. 81. *Gomphonema gracile*, 82. *G. gracile* var. #1, 83. *G. gracile* var. #2, 84. *G. parvulum*, 85. *G. parvulum* var. #1, 86. *G. parvulum* var. #2, 87. *G. parvulum* var. #3, 88. *G. parvulum* var. *parvulum* fo. *parvulum*, 89. *G. parvulum* ? (girdle), 90. *G. patagonicum*, 91. *Achnanthes chlidanos*, 92. *A. coarctata* var. *coarctata*, 93. *A. coarctata* var. *constricta*, 94. *A. germartii*, 95. *A. lanceolata*, 96. *A. minutissima*, 97. *A. minutissima* var. *jackii*, 98. *A. minutissima* #2, 99. *A. subatomoides*, 100. *Achnanthes* #1, 101. *Achnanthes* #2, 102. *Cocconeis placentula*, 103. *Cavinula pseudoscutiformis*, 104. *Amphipleura pellucida*, 105. *Frustulia rhomboides*, 106. *F. rhomboides* var. *crassinerva*, 107. *F. saxonica*, 108. *F. vulgaris*, 109. *F. vulgaris/neomondana*.



FIGURAS 110-127. **110.** *Bracysira minor*, **111.** *B. brebissonii*, **112.** *B. brebissonii* **#1**, **113.** *B. brebissonii* **#2**, **114.** *B. brebissonii* **#3**, **115.** *B.brebissonii/neoexilis*, **116.** *B. neoexilis*, **117.** *Neidium affine*, **118.** *Neidium affine* var. *longiceps*, **119.** *N. apiculatum*, **120.** *N. hercynicum*, **121.** *Nedium* **#1**, **122.** *Sellaphora laevissima* var. *laevissima*, **123.** *S. pupula* var. *pupula*, **124.** *S. seminulum*, **125.** *Pinnularia gibba*, **126.** *P. gibba/microstauron*, **127.** *P. microstauron*.



FIGURAS 128-155. 128. *Pinnularia viridis*, 129. *Pinnularia* # 1, 130. *Pinnularia* # 2, 131. *Caloñéis* # 1, 132. *Caloñéis* # 5, 133. *Diploneis elliptica*, 134. *D. subovalis*, 135. *Adlafia bryophila*, 136. *Navícula angusta*, 137. *N. halophiloides*, 138. *N.hassiaca*, 139. *N. lapidosa*, 140. *N. longicephala* var. *longicephala*, 141. *N. martinii*, 142. *N. minima*, 143. *N. radiosa*, 144. *N. subalpina*, 145. *N. submolesta*, 146. *N. trivalis*, 147. *Navícula* # 1, 148. *Navícula* # 2, 149. *Navícula* # 3, 150. *Stauroneis kreigerii*, 151. *S. phoenicenteron*, 152. *S. wislouchii*, 153. *Stauroneis* # 1, 154 *Kobayasia subtilissima*, 155. *Amphora veneta*.



FIGURAS 156-178. 156. *Nitzschia alpina*, 157. *N. amphibiodes*, 158. *N. bacillum*, 159. *N. bacillum* # 1, 160. *N. bacillumAacuum*, 161. *N. clausii*, 162. *N. dippelii*, 163. *N. dissipata* var. *media*, 164. *N.ffustulum*, 165. *N.ffustulum* vat.*ffustulum*, 166. *N.ffustulum* #3, 167. *N. gracilis*, 168. *N. intermedia*, 169. *N. intermedia* #1, 170. *N. intermedia* # 2, 171. *N. lacuum*, 172. *Ni palea*, 173. *N. perminuta*, 174. *Stenopierobia cumula*, 175. *Surirella pseudolinearis* var. *constricta*, 176 *Epithemia hyndmanii*, 177. *E. turgida/E. hyndmanii*, 178. *Epithemia* sp # 1,

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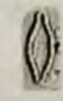

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FIGURAS 179-187. 179. *Rhopalodia gibba*, **180.** *Unknown* #2, **181.** *Unknown* #3, **182.** *Unknown* #4, **183.** *Unknown* # 5, **184.** *Unknown* # 6, **185.** *Unknown* #7, **186.** *Unknown* # 8, **187.** *Sp* # 1.