VI.1. PHYTOPLANCTON
VI.1a. The diatoms

SIMONE SERVANT-VILDARY

Introduction

The diatoms of Lake Titicaca are known solely on the basis of studies of Frenguelli (1939), Richerson *et al.* (1977, 1986), Theriot *et al.* (1985) and Carney *et al.* (1987) in the Peruvian side of the lake, and by Liberman and Miranda (1987) in the Bolivian part.

The flora described here was established from samples taken at eleven stations in the Bolivian part of the lake. This work however, like the others mentioned above, still gives a very limited picture in both time and space of this component of the flora. The physical and chemical conditions vary at hourly and daily time scales, in part due to the high altitude of the lake, and the response of the flora to these changes may be correspondingly rapid. For this reason it is difficult, without regular sampling and measurements during the day and at larger time scales, to establish a representative and exhaustive inventory of the total diatom flora in this environment.

Methods

The diatoms studied were fixed in formol and first observed without additional preparation of the samples. They were then treated and cleaned in order to eliminate the organic material and better observe the frustules with an optical microscope.

The days and hours of collection are indicated in lines 2 and 4 of Table 1, for 11 stations indicated in Fig. 1. Diatons were collected with plankton nets in the surface waters; only sample 10 consists of washed epiphytes from Characaea macrophytes at stations 1 and 10. Also listed in Table 1 are certain physical and chemical parameters measured at the time of collection, or calculated from about fifty measurements made in Lago Pequeno or Lago Grande during the same months as the sampling (Iltis, 1987).

C. Dejoux and A. Iltis (eds.), Lake Titicaca, 163–175.

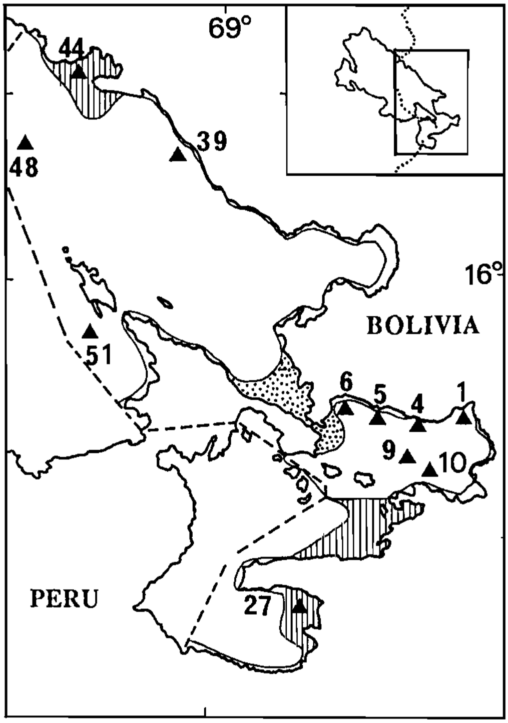


Figure 1. Sampling locations in the Bolivian part of Lake Titicaca.

The diatom flora

As has been previously discussed by the above mentioned authors, the pelagic diatom flora does not appear to be species rich. We have found 101 species, and only 38 are abundant. This may appear relatively few for such an extensive system. The number of truly planktonic species is quite low in relation to the number of taxa at shallow stations which include benthic, epiphytic and facultative planktonic species (see Table 2). The most species-rich genera are *Navicula*, *Nitzschia*, *Fragilaria* and *Cyclotella*, and the most abundant are *Cyclotella* and *Fragilaria*. Frenguelli (1939) identified 118 species at 7 stations, but he considered that only 38 species really were present in the lake water. Carney *et al.* (1987) list 50 species found in the lake, 25 of which are abundant.

The analysis of our samples allows us to distinguish six groups based on the species composition:

1. (Stations 44 and 48). This group is dominated by the planktonic stelligeroid *Cyclotella*. Station 44, distinguished by its more turbid waters, is characterised by greater species richness which is especially due to epiphytes such as *Achnanthes delicatula* and *Amphora pediculus*.

Table 1. Physical and chemical characteristics of the stations studied. 1) Stations; 2) Dates of sampling and measurements of temperature, pH, transparency and conductivity; 3) Dates which were used for calculations of averages: 3a) days, 3b) months and years; 4) Hours of sampling; 5) Depth (m) of water column at sampling location; 6) Transparency at time of sampling; 7) Average transparency; 8) Temperature in °C at time of sampling; 9) Average of temperatures; 10) pH of surface water at time of sampling; 11) Average pH; 12) Conductivity in S cm^{-1} at 25°C at time of sampling; 13) Average conductivity. Average values are based on fifty measurements made on the dates listed in line 3a.

	Lago Mayor (east)				Lago Menor (south)	Lago Menor (north)					Characea
1)	48	51	39	44	27	6	5	4	9	1	10
2)	17/10/86	17/12/86	27/6/85	17/10/86	9/12/85	24/4/86	14/12/88	11/12/85	9/12/86	27/6/85	24/2/87
3a)	14-18/	9-11/	26-29/	14-18/	-	21-23/	-		9-11/	26-29/	-
3b)	10/86	12/86	6/85	10/86	-	4/86	-	12/85	12/86	6/85	-
4)	9.25	12.40	17.25	7.25	12.12	16.55	14.45	7	7.30	9	10.50
5)	140	150	80	8	3	25	40	10	6	3.5	3
6)	11.5	13	10.5	5	3	5.5	5.5	-	4.5	3.5	3
7)	12.39	11.94	11.77	12.39	-	5.63	-	4	4.45	4.66	-
8)	12.1	13.5	12.8	12.3	16.3	14.6	15.1	-	14.5	8.9	15
9)	12.8	13.7	12.6	12.8	-	14.7	-	14.1	15.3	10.7	-
10)	-	8.22	-	-	9	8.28	8.42	-	8.4	-	8.4
11)	8.31	8.48	-	8.31	-	8.40	-	8.31	8.68	-	-
12)	1500	1500	1700	1450	960	1450	1500	-	1525	1610	1400
13)	-	1501	-	1490	-	1368	-	1500	1521	-	-

2. (Station 27). This is distinguished from all the others by the abundance of *Cocconeis*, including *C. titicacaensis*, and also *Nitzschia admissoides* and *Fragilaria capucina*. This flora may depend on the low conductivity measured at this station, or it may simply represent a shallow environment colonized by aquatic plants which are a preferred substrate for *Cocconeis*.
3. (Stations 1 and 39). This community is distinguished by the almost exclusive presence of *Cyclotella andina*. These two stations are quite different in depth (80 and 3.5 m) and temperature (12.6 and 8.9°C); the only common factor is that they were both sampled in June 1985. Theriot et al. (1985) also indicated that densities of *C. andina* increased at two stations which were quite different in depth (147 m and 14 m) between May and August in the Peruvian Lago Grande. According to these authors, thermal stratification was disrupted during this period and limiting nutrients increased as a result of mixing from bottom waters. Thus the abundance of this species in June 1985 could be explained by this factor.
4. (Stations 5, 6 and 51). This group is characterised by a predominance of *Fragilaria crotonensis*, while *C. andina* is rare. These are deep-water stations, at 25, 40, and 150 m, respectively. *F. crotonensis*, which is present in large chains (Figs. 22, 23), is clearly planktonic here. Another species, *Entomoneis palludosa* var. *salina*, has been found only at station 5. Its presence cannot be explained since its preferred ecological habitats are meso- to euhaline.

Table 2. Diatoms found at the eleven stations examined. Semi-quantitative evaluation of the abundance of each species: 6 – very abundant; 5 – abundant; 4 – frequent; 3 – rare; 2 – very rare; 1 – present; 0 – absent.

	44	48	39	51	6	4	1	9	27	5	10
Achnanthes delicatula Kützing	3	1	.	.	.	.	.	.	.	.	.
Achnanthes hungarica Grunow	.	.	.	.	.	1	.	.	.	.	.
Achnanthes lanceolata Brebisson	1	.	.	.	.	.	.	.	.	.	.
Achnanthes minutissima Grunow	1	.	.	.	1	2	.	1	.	.	.
Achnanthes saccula Carter	1	.	.	.	.	.	.	.	.	.	.
Amphora inariensis Krammer	.	.	.	.	.	1	.	.	.	.	.
Amphora lybica Ehrenberg	1	.	.	.	.	.	.	.	1	.	.
Amphora pediculus (Kütz.)Grunow	3	.	.	.	.	1	.	.	.	.	.
Amphora veneta Kützing	.	.	.	.	.	1	.	.	.	.	1
Anomoeoneis serians (Breb.)Cleve	.	.	.	.	.	.	.	.	.	.	1
Caloneis bacillum (Grun.)Cleve	1	1	.	.	.	.	.	.	.	1	.
Caloneis molaris (Grun.)Krammer	.	.	.	.	.	1	.	.	.	.	.
Cocconeis placentula Ehrenberg	2	1	.	.	.	3	.	.	2	.	1
Cocconeis titicacaensis Frenguelli	.	.	.	.	.	.	.	.	4	.	2
Cyclotella andina Theriot Carney & Richerson	3	1	6	.	1	1	6	.	.	2	.
Cyclotella atomus Hustedt	.	1	.	.	.	.	.	.	.	.	.
Cyclotella iris Brun & Heribaud	.	1	.	.	.	.	.	.	.	.	.
Cyclotella kützingiana Thwaites	1	2	.	.	.	.	.	.	.	.	.
Cyclotella meneghiniana Kützing	.	.	.	.	1	2	.	.	.	1	.
Cyclotella stelligera Cleve & Grunow	6	6	1	.	2	2	.	.	1	1	.
Cyclotella s. var. glomerata (Bach.)Haworth & Hurley	1	3	.	.	.	.	.	.	1	.	.
Cyclotella s. var. pseudostelligera (Hust.)Haworth & Hurley	3	2	.	.	.	.	.	.	.	.	.
Cymatopleura solea (Breb.)W.Smith	1	.	.	.	.	.	.	.	1	.	.
Cymbella cistula (Ehr.) Kirchner	.	.	.	.	.	1	.	.	1	.	1
Cymbella c. var. maculata (Kütz.)Van Heurck	.	.	.	.	.	.	.	.	1	.	.
Cymbella cymbiformis Agardh	.	.	.	.	.	.	.	.	2	.	.
Cymbella falaisiensis (Grun.)Krammer & Lange-Bertalot	.	.	.	.	.	.	.	1	.	.	2
Cymbella gracilis (Ehr.) Kützing	.	.	.	.	.	.	.	.	1	.	.
Cymbella microcephala Grunow	.	.	.	.	.	2	.	2	.	.	1
Cymbella minuta Hilse	.	.	.	.	.	.	.	.	.	.	1
Cymbella pusilla Grunow	.	.	.	.	.	.	.	.	.	.	2
Denticula elegans Kützing	.	.	.	.	.	1	.	.	.	.	1
Entomoneis paludosa var. subsalina (Cl.)Krammer	.	.	.	.	.	.	.	.	.	5	.
Epithemia sorex Kützing	.	.	.	.	.	1	.	.	1	.	.
Epithemia zebra (Ehr.)Kützing	1	1	.	.	.	1	.	.	.	1	4
Fragilaria brevistriata Grunow	.	.	.	.	.	1	.	.	.	.	.
Fragilaria capucina Desmazières	.	.	.	.	.	4	.	.	2	.	1
Fragilaria c.var. vaucheriae Lange-Bertalot	2	.	.	.	.	.	.	.	6	.	.
Fragilaria construens (Ehr.)Grunow	.	.	.	.	.	2	.	.	.	.	.
Fragilaria c. subrotundata Mayer	1	.	.	.	.	.	.	.	.	.	.
Fragilaria crotonensis Kitton	.	1	.	1	6	.	.	.	.	6	1
Fragilaria famelica Lange-Bertalot	.	.	.	.	.	.	.	.	1	.	.
Fragilaria lapponica Grunow	.	.	.	.	.	2	.	.	.	.	.
Fragilaria pinnata Ehrenberg	.	.	.	.	1	3	.	.	.	1	.
Fragilaria p. var. lancettula (Schum.)Hustedt	.	.	.	.	1	.	.	.	.	.	.
Fragilaria tabulata Lange-Bertalot	1	.	.	.	.	.	.	.	.	.	.
Fragilaria ulna Lange-Bertalot	.	.	.	.	.	2	.	.	.	.	3
Frustulia vulgaris Thwaites	1	.	.	.	.	.	.	.	.	.	.
Gomphonema acuminatum var. coronata (Ehr.)W.Smith	.	1	.	.	.	.	.	.	.	.	.
Gomphonema angustatum (Kütz.)Rabenhorst	.	.	.	.	.	.	.	.	1	.	.
Gomphonema parvulum (Kütz.) Kützing	.	.	.	.	.	1	.	.	2	.	.
Gomphonema valentinica Nik	.	.	.	.	.	.	.	.	1	.	1
Gyrosigma acuminatum (Kütz.)Rabenhorst	1	.	.	.	.	1	.	.	.	.	.
Hantzschia amphioxys (Ehr.)Grunow	.	.	.	.	.	.	.	.	1	.	.
Mastoglia atacamae Hustedt	.	.	.	.	.	.	.	.	.	.	1
Mastoglia smithii Thwaites	.	.	.	.	.	2	.	.	.	.	6
Navicula anglica Ralfs	1	1	.	.	.	.	.	.	.	.	.
Navicula bahusiensis (Grun.)Grunow	1	.	.	.	.	.	.	.	.	.	.

Table 2. Continued.

	44	48	39	51	6	4	1	9	27	5	10
Navicula capitata var. hungarica (Grun.)Ross	.	.	.	.	.	1	.	.	.	.	.
Navicula c. var. capitata Ehrenberg	1	.	.	.	.	.	.	.	.	.	.
Navicula cohnii (Hil.)Lange-Bertalot	.	.	.	.	.	1	.	.	.	.	.
Navicula cryptotenella Lange-Bertalot	.	.	.	.	.	2	.	2	.	.	3
Navicula cuspidata (Kütz.)Kützing	.	.	.	.	.	1	.	.	.	.	.
Navicula halophila (Grun.)Cleve	.	.	.	.	.	1	.	.	.	.	1
Navicula kotschyi Grunow	1	.	.	.	.	.	.	.	.	.	.
Navicula margalithii Lange-Bertalot	.	.	.	.	.	1	.	1	.	.	.
Navicula minuscula var. muralis (Grun.)Lange-Bertalot	1	.	.	.	.	.	.	.	.	.	.
Navicula mutica Kützing	.	.	.	.	.	1	.	1	.	.	.
Navicula pseudoanglica Lange-Bertalot	1	.	.	.	.	.	.	.	.	.	.
Navicula pseudolanceolata var. denselineolata Lange-Bertalot	.	.	.	.	.	.	.	6	.	.	1
Navicula pupula var. pupula Kützing	.	.	.	.	.	1	.	.	.	.	.
Navicula radiosa Kützing	.	.	.	.	.	3	.	2	.	.	1
Navicula rhynchocephala Kützing	.	.	.	.	.	.	.	.	.	1	.
Navicula subrotundata Hustedt	1	4	.	.	.	.	.	.	.	.	.
Navicula tenera Hustedt	2	.	.	.	.	.	.	.	.	.	.
Navicula tripunctata (O.Mull.)Bory	.	.	.	.	.	.	.	.	.	1	.
Navicula viridula (Kütz.)Ehrenberg	1	.	.	.	.	.	.	.	.	.	.
Navicula vulpina Kützing	.	.	.	.	.	1	.	.	.	.	.
Nitzschia acidoclinata Lange-Bertalot	.	.	.	.	.	6	.	1	.	.	1
Nitzschia admissoides Cholnoky	.	.	.	.	.	.	.	.	6	.	.
Nitzschia amphibia Grunow	1	.	.	.	.	1	.	.	3	.	.
Nitzschia denticula Grunow	.	.	.	.	.	.	.	.	2	.	5
Nitzschia dissipata (Kütz.)Grunow	1	.	.	.	.	.	.	.	.	.	.
Nitzschia eglei Lange-Bertalot	.	.	.	.	.	1	.	.	.	.	.
Nitzschia frustulum Kützing	.	.	.	.	.	1	.	1	.	.	.
Nitzschia gracilis Hantzsch	.	.	.	.	.	1	.	.	.	.	.
Nitzschia hantzschiana Rabenhorst	1	.	.	.	.	4	.	.	.	2	.
Nitzschia hungarica Grunow	1	.	.	.	.	1	.	.	.	.	.
Nitzschia intermedia Hantzsch	2	.	.	.	.	.	.	.	.	.	.
Nitzschia mediocris Hustedt	1	.	.	.	.	1	.	.	.	.	.
Nitzschia microcephala Grunow	1	.	.	.	.	1	.	.	.	.	.
Nitzschia palea (Kütz.) W.Smith	.	.	.	.	.	1	.	.	.	.	.
Nitzschia p. var. debilis (Kütz.)Grunow	1	.	.	.	.	5	.	.	.	.	.
Nitzschia recta Hantzsch	2	.	.	.	1	.	.	.	.	.	.
Nitzschia sp.	.	.	.	.	.	.	.	2	.	.	2
Nitzschia valdestriata Aleem & Hustedt	1	.	.	.	.	1	.	.	.	.	.
Pinnularia borealis Ehrenberg	.	.	.	.	.	1	.	.	.	.	.
Pinnularia divergentissima (Grun.)Cleve	1	.	.	.	.	.	.	.	.	.	.
Rhoicosphenia abbreviata (Ag.)Lange-Bertalot	1	.	.	.	.	1	.	.	.	.	.
Stephanodiscus dubius (Fr.)Hustedt	.	1	.	.	.	.	.	.	.	.	.
Stephanodiscus hantzschii Grunow	2	.	.	.	.	.	.	.	.	.	.

5. (Stations 4 and 10, considered as one station). These communities have in common *Fragilaria ulna*, *Mastogloia smithii* and *M. atacamae* which are not present, or only quite rarely, at other stations. Also in these associations are other species such as *Nitzschia denticula* and *Nitzschia palea debilis* which can, like the above two species, adapt to waters relatively high in salts (Servant-Vildary and Roux, 1990).
6. (Station 9). This final group is similar to the previous, but is distinguished by the abundance of *Navicula pseudolanceolata*. The growth of this species at only this station cannot be explained, since stations 4, 9 and 10 are located quite close to each other in thern Lago Pequeño.

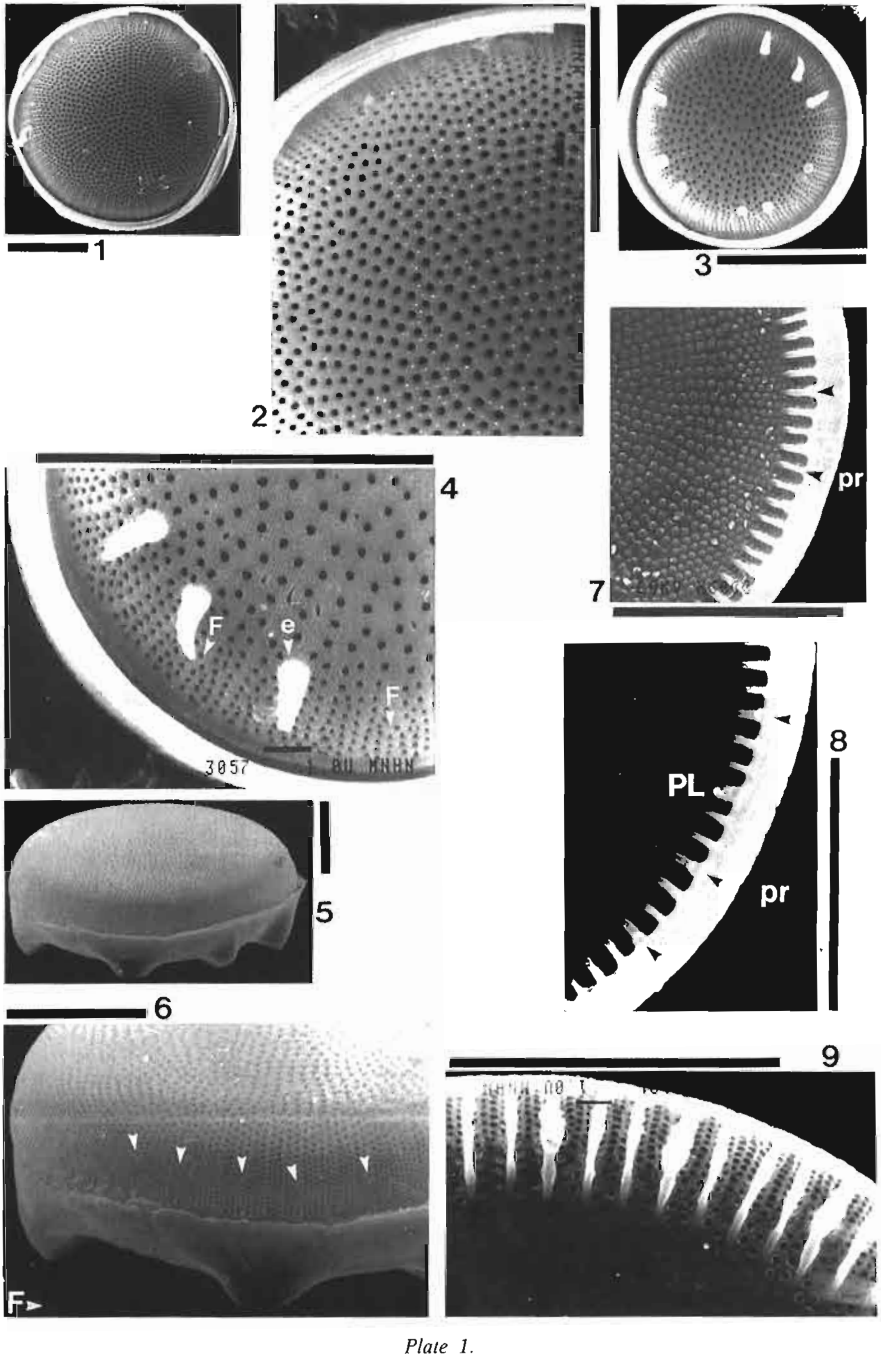
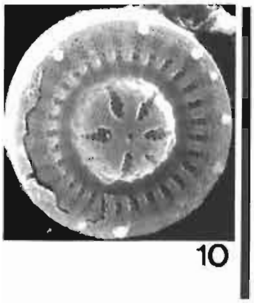


Plate 1.



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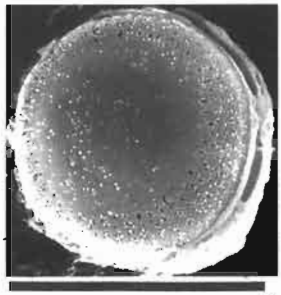

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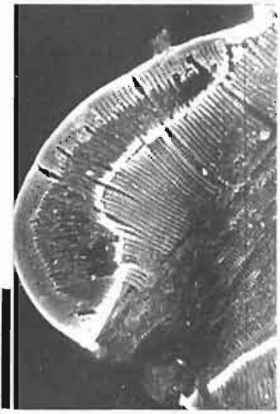

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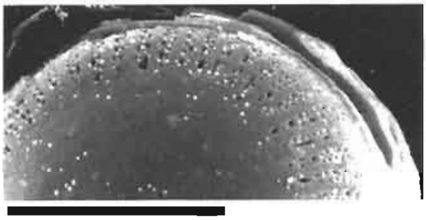

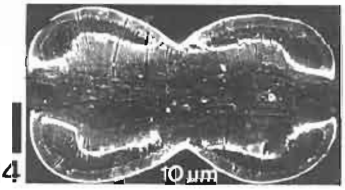

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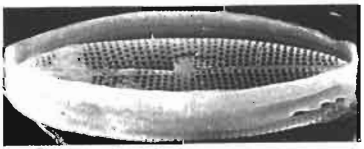

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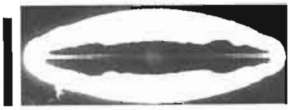

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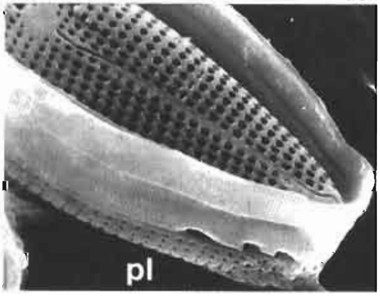

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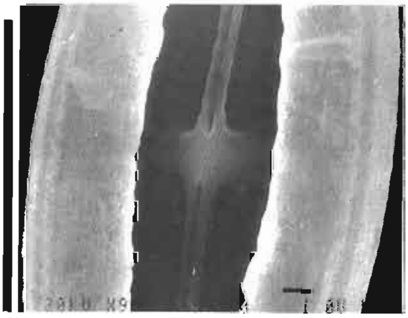

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Plate 2.

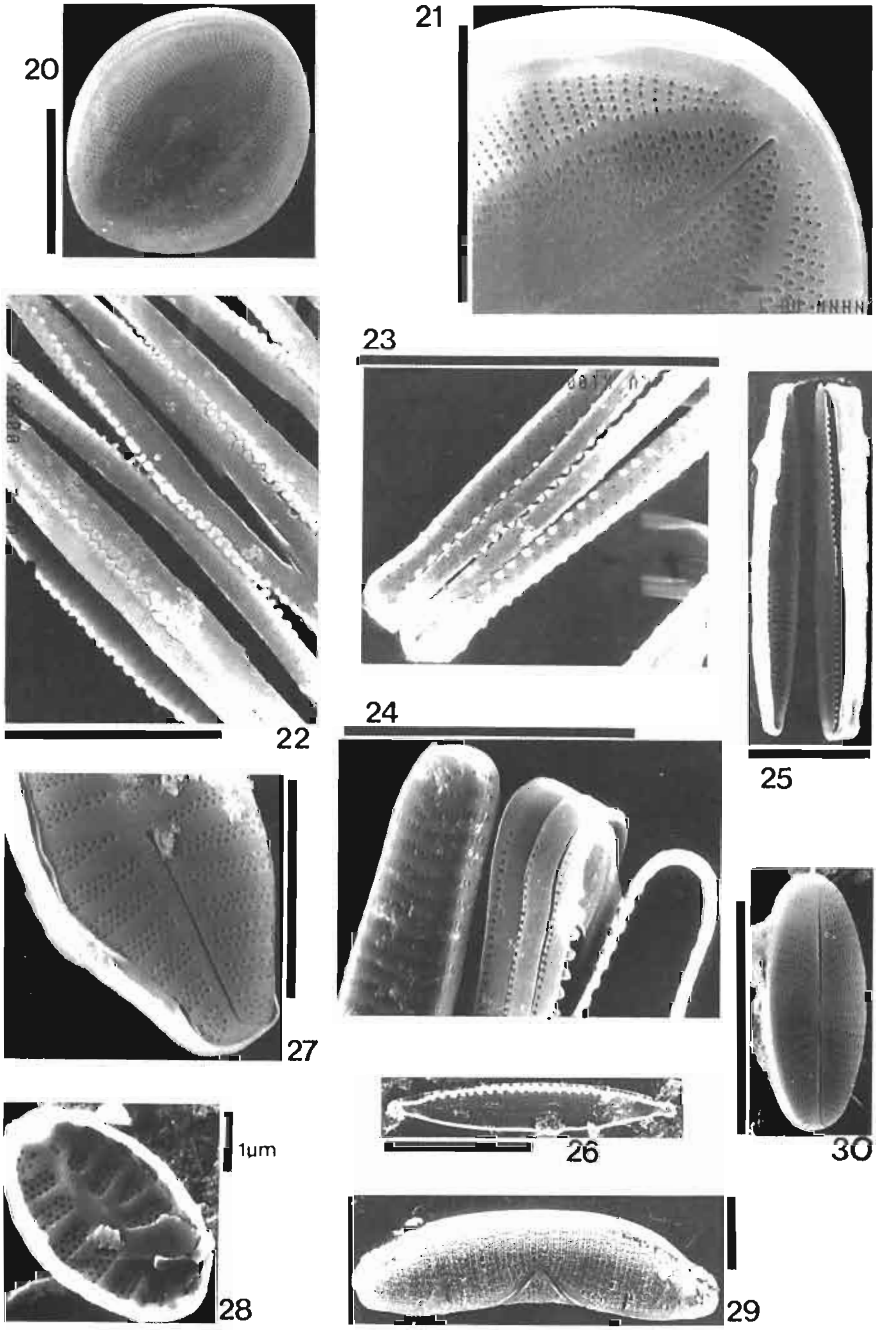

Plate 3.

Morphological observations on certain taxa

We consider here only abundant or characteristic species; the complete list of species found is given in Table 2.

Amphora pediculus (*Kütz.*) Grunow

This species is abundant at station 44 and rare at station 4. Despite its small size, it is easy to observe the punctae on the striae. The predominant form is identical to that described by Krammer (1980, Plate 6, Fig. 42). Larger and longer forms, in which the punctae on the striae are finer, are rarer. This species lives in well oxygenated running waters, so its presence at station 44 can be explained by the proximity to the outflow of Suches river. At station 4 some larger forms with less rudimentary pores may be *A. inariensis*. Krammer (1980) indicates this species is found in lightly acid (pH = 6.8) freshwaters. Here it is found at a more elevated pH. This is a typically northern alpine species, but it is rare.

Cocconeis titicacaensis Frenguelli

Found by Frenguelli in Lake Titicaca, it does not appear to have been found by others to date and thus may be one of the rare endemic species. Frenguelli indicated that it was very abundant near the port of Guaqui and rare in Lago Grande. In our samples, it is also quite abundant at station 27 near Guaqui, and it is also present as epiphytes washed from Characeae at stations 1 and 10 in northern Lago Pequeno. We observe, as Frenguelli, that the smaller forms are round and the strial density of the hypotheca is high (close to 30 in 10 µm – Fig. 20). The larger forms are more oval and the strial density is much lower (between 20 and 24). The hyaline space of the hypotheca, which is located midway between the raphe and the marginal border, may continue, according to Frenguelli, beyond the terminal pores of the raphe to a linear space to the apices. This character could not be seen clearly despite the large numbers of individuals observed (Fig. 21). On the contrary, we have noted small ridges irregularly arranged around the inferior valve in the interstrial spaces.

Cyclotella andina Theriot, Carney & Richerson

Many specimens observed from the Bolivian part of Lake Titicaca are morphologically quite similar to those described by Theriot *et al.*, 1985. We insist on only three differences: 1) there is not a ring of silica (Fig. 9) at the base of the ribs on the inside (Theriot *et al.*, Fig. 13); 2) the labiate process is effectively on the same rib as the strutted process, but it does not have the same form; according to Theriot *et al.* (Fig. 14) it is an elongate tube, somewhat separate from the strutted process, while it is round and appears attached to the rib by some type of "spokes" (Fig. 8); 3) the cingulum (Theriot *et al.*, Fig. 11) consists of several copulae (Figs. 1 to 3), but in some individuals this could be covered by a thick leaf of silica with 8 peduncles; only 4 can be seen in Fig. 5. This structure is unknown, and we are uncertain whether it is some specialization of the mantle, a modification of the cingulum, or some structure underneath the cingulum and thus invisible most of the time.

As indicated by Theriot *et al.* (1985), the dimensions of this species are quite variable, but in station 1 where this taxon can represent 100% of the diatom flora, the larger forms are more frequent.

The stelligeroid *Cyclotella* group. Haworth, 1986

The genus *Cyclotella* is the most varied and abundant in the pelagic flora of Lake Titicaca. The stelligeroid group being particularly well represented in at stations 44 and 48.

We are in agreement with Haworth (1986) that there exists continuous variation within this group. We thus follow this author who proposes combining these taxa within the species *stelligera*, maintaining the following varieties in order not to lose ecological information: *C. stelligera* var. *stelligera*, *C. stelligera* var. *glomerata*, *C. stelligera* var. *pseudostelligera*. All these varieties pertain to type 1 defined by Servant-Vildary (1986) and are characterised by simple chambers (*C.s.* var. *stelligera*) or alveolar depressions (*C.s.* var. *pseudostelligera*) widely opened toward the inside.

These varieties are present together at stations 44 and 48, though *C. s. stelligera* (Fig. 10) predominates. According to Haworth (1986), this form grows best in waters of high silica content, while *C.s. pseudostelligera* grows better in more silica-poor waters.

Cymbella cistula var. *maculata* (Kutz.) H. van Heurck

First noted by Frenguelli (1939) in Lake Titicaca, it was later found by Manguin (1964) in bogs of highland Peru and by Pierre (1986) in highland lakes of Bolivia. Based on Fig. 11 of this last author, this variety belongs to the group of *Cymbella cistula* without papillae (Lange-Bertalot, 1986). But as this author has observed, separation of this variety solely on the basis of the absence of the stigma is very tenuous. Still, the Bolivian forms present a rather special morphology. Much shorter than the type species, they are also much more arched (with sub-rostrated extremities) than the varieties depicted by Hustedt (1930) and Van Landingham (1964). It may be useful to record these differences, at least for Andean forms, since they may reflect particular ecological adaptations such as to temperature conditions.

Entomoneis paludosa var. *subsalina* Cleve

This species name has been chosen over *E. alata* because of the high number of striae per 10 μm. The striae of the wings and the cell are equally punctuated by a line of simple pores, which are not altered by the line of union between the wing and cell; this line is lightly sinuous (Figs 13–15).

At station 5 this species is second in abundance after *Fragilaria crotonensis* (Fig. 15). It has not been found at another station. Presented here is a particularly fragile skeleton which is somewhat fragmented. Given its frequency, it does not appear to be transported. The species is cosmopolitan in waters of moderate conductivity; the subsalina variety is in waters of higher dissolved salts. Its presence in only station 5 is inexplicable.

The genus *Fragilaria* Lyngbye

This genus is both abundant and species rich in Lake Titicaca. We adopt the nomenclature of Lange-Bertalot (1980) which groups the species and varieties of this genus with those of *Synedra*. The list of synomyms is provided here to demonstrate the variety of forms which are found in the lake; we refer to the figures published by Lange-Bertalot (1980) listed after the taxa to provide fuller information:

1) *Fragilaria capucina vaucheriae* includes: *Fragilaria intermedia* (L-B, Figs 35–38), *Exilaria vaucheriae* (L-B, Fig. 31), at station 27.
2) *Fragilaria capucina* includes: *Synedra sumpens* var. *familiaris* (L-B, Fig. 50) at station 44. *Synedra rumpens rumpens* (L-B, Figs 61–62) at station 27. *Synedra vaucheriae* (L-B, Figs 121–116 (?)) and *Synedra rumpens* (L-B, Fig. 42) at station 4.
3) *Fragilaria tabulata* includes: *Fragilaria fonticola* (L-B, Fig. 157), *Synedra tabulata* (L-B, Figs 160, 167, 168, 173) at station 44.
4) *Fragilaria ulna* includes: *Synedra acus angustissima* (L-B, Fig. 194) at station 4; *Fragilaria construens oregona* (L-B, Fig. 193) at stations 4 and 10.

Fragilaria capucina Desm

We note (Figs 24–25) the presence of a saw-like structure on the internal border of the valvocopula. This structure is similar to those described by Kobayasi (1979) for *F. pseudogaillonii* (Fig. 9), in the genus *Diploneis* at Charaña by Servant-Vildary and Blanco (1984) (Plate 1, Fig. 9, and Plate 5, Figs 2 & 3), and by Idei and Kobayasi (1986), (Fig. 19). The internal thickening located at the extreme of the valve can be discerned over the central specimen of Fig. 24. This could be related to the "ligula" described by Idei and Kobayasi (1968) for *Diploneis parma*. More detailed studies are needed to describe this structure which to date has been little noticed in the genus *Fragilaria*.

Fragilaria crotonensis Kitton

There is no particular morphological character which distinguishes the morphotype here from the forms in the other parts of the world. This species is present in large chains (Fig. 15). Enlarged at the center in valve view, cells are connnected only at these points (Fig. 22) thanks to the adaptation of the teeth. These expand and take the form of blades at the center of the frustule, while they are much smaller toward the extremes of the frustules (Fig. 23) where there is paper-like cohesion between individuals.

This taxon is extremely abundant at stations 5 and 6 near the Chua Depression. It can live in shallow areas, close to aquatic macrophytes, and can be transported to areas of greater depth and float near the surface because of its colonial morphology.

Gomphonema cf. valentinica Nik

This species is very small, elongate and sharp, almost isopolar in valve view, and with very rudimentary striae. It attaches to plants with a particularly resistant mucilagenous tube; this firm attachment provides protection against predators. Its presence in sample 10 indicates that it lives attached to Characeae. The study of this form deserves more study since some individuals do not have the rectangular hyaline area which characterises this species.

Mastogloia atacamae Hustedt

This is rare in the Characeae epiphyte samples (stations 1 and 10), and is associated with *Mastogloia smithii* which predominates (Figs 16 to 19).

This species belongs to the group of *M. elliptica*, but is distinguished by a higher strial density of rather oblique striae and a larger central area, characterised by alternatively large and short striae, and by a number of more elevated chambers.

It has been found in the fossil state (Servant-Vildary, 1984) in the Charana formation of presumed late Pliocene age, in a highly saline paleoenvironment. Hustedt (1927) described it from the Loa formation, where it was associated with many species typical of environments with high salt concentrations. The presence of this species in relatively fresh waters indicates that, like many species of the genus *Mastogloia*, it can adapt to a wide range of salinities.

Conclusions

In addition to the relatively low species diversity indicated above, the diatom flora composition appears highly cosmopolitan. With the exception of three species (*Cocconeis titicacaensis*, *Cyclotella andina*, *Mastogloia atacamae*) which can currently be considered as endemic, all the other taxa appear to have extensive geographical distributions. We cannot at present compare this flora with those of other aquatic systems in Bolivia. The principal studies realized to date in this country have concerned superficial or quaternary sediments of small mountain bogs or saline lakes of the southern Altiplano. These systems are generally quite shallow and favor benthic pennate diatoms over pelagic species. Still, cores taken by Pierre and Wirrmann (1986) from deep high- altitude lakes of the Bolivian Cordillera have demonstrated that during the recent Quaternary in these lakes there existed a flora which alternated between *Cyclotella stelligera* and *Fragilaria construens* plus *F. pinnata*, the two most abundant genera today in Lake Titicaca.

The incomplete observations of this study also make clear the substantial spatial variability in species composition of the diatoms. The few available data on environmental factors such as pH, temperature, conductivity and other chemical variables still do not allow interpretations in terms of these factors. However, it is possible to hypothesize that water depth, the presence or absence of rooted aquatic vegetation, and the water transparency in relation to proximity to the river outflows are some of the more important factors which influence diatom community composition.

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Edited by

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KLUWER ACADEMIC PUBLISHERS
DORDRECHT / BOSTON / LONDON

Library of Congress Cataloging-in-Publication Data

Lake Titicaca : a synthesis of limnological knowledge / edited by C.
Dejoux and A. Iltis.
p. cm. -- (Monographiae biologicae ; v. 68)
Includes indexes.
ISBN 0-7923-1663-0 (HB : alk. paper)
1. Limnology--Titicaca Lake (Peru and Bolivia) 2. Aquatic
resources--Titicaca Lake (Peru and Bolivia) I. Dejoux, Claude.
II. Iltis, A. III. Series.
QP1.P37 vol. 68
[QH128]
574 s--dc20
[574.5'26322'098412] 92-7958

ISBN 0-7923-1663-0

Published by Kluwer Academic Publishers,
P.O. Box 17, 3300 AA Dordrecht, The Netherlands.

Kluwer Academic Publishers incorporates
the publishing programmes of
D. Reidel, Martinus Nijhoff, Dr W. Junk and MTP Press.

Sold and distributed in the U.S.A. and Canada
by Kluwer Academic Publishers,
101 Philip Drive, Norwell, MA 02061, U.S.A.

In all other countries, sold and distributed
by Kluwer Academic Publishers Group,
P.O. Box 322, 3300 AH Dordrecht, The Netherlands.

Printed on acid-free paper

Printed in the Netherlands