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Diversity and geographic distribution of *Chlorococcales* (*Chlorophyceae*) in contrasting lakes along a latitudinal transect in Argentinean Patagonia

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Abstract The present study focuses on the geographic distribution and biodiversity of the *Chlorococcales* in Patagonian lakes, covering a latitudinal transect. Two different approaches are considered (a) a review of the historical records of *Chlorococcales* in Patagonia and (b) the analysis of the morphology-based species diversity, ecological remarks, and geographic distribution of the chlorococcalean species recorded in 33 aquatic environments during surveys 2007 and 2008. A total of 308 chlorococcalean species were recorded throughout a 60-year period in Patagonian freshwater systems, encountering the highest chlorococcalean richness in lakes and shallow lakes located in the more intensively sampled areas. In our surveys 2007–2008, 72 chlorococcalean taxa were registered, among which 80% are worldwide distributed, about 19% are restricted to cold temperate areas in both hemispheres and one species (*Pediastrum patagonicum*) is one of the taxa probably endemic for Patagonia. The chlorococcalean richness in relation to the environmental factors, revealed that it is directly correlated with the trophic status of the water bodies (chl *a*: $r = 0.52$ and DIN: $r = 0.47$; $P < 0.05$). The latitude was inversely correlated with the species richness ($r = -0.40$; $P < 0.05$), and the chlorococcalean biodiversity of the Andean lakes (mean value: 3.64) was significantly lower ($P = 0.0022$) than that of the lakes from the Patagonian Plateau (mean value: 9.62). In this study we observed a decreasing trend in the biodiversity of *Chlorococcales* with increasing latitude, which fits in the existing ecological pattern described for different groups of organisms.

Keywords Argentinean Patagonia · Biodiversity · Biogeography · *Chlorococcales* · Lakes

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Introduction

Patagonia is a very interesting region in the world that still remains relatively undisturbed and presents vast extensions of land without human presence. It is one of the main lacustrine regions in South America, hosting a great variety of freshwater systems. The deepest lakes are situated in the Andean Patagonia and Tierra del Fuego, whereas in the Patagonian Plateau lakes are shallower (Quirós and Drago 1999).

The studies on micro-algae of the Argentinean Patagonian lakes were initiated in mid-XXth century (Guarrera and Kühnemann 1949; Seckt 1950–1956) and included mostly floristic papers. Latter on, K. Thomasson provided a series of articles regarding the phytoplankton community of several Araucarian lakes (Thomasson 1955, 1956, 1957, 1959, 1963). In the 70s and 80s further algal floristic studies were conducted in different lakes of the region (Maglianesi et al. 1973; García de Emiliani and Schiaffino 1974; Tell 1975, 1979a, b; Tell and Mosto 1976; Guarrera 1977; Guarrera and Ferrario 1979; Echenique et al. 1988; Izaguirre 1988; Izaguirre and del Giorgio 1989), among which there is a very important contribution regarding the *Chlorococcales* from Tierra del Fuego that involved surveys carried out during several years (Tell and Mosto 1982). During the last two decades, the limnological studies held in Patagonian lakes included not only a floristic approach, but also ecological remarks on the algal assemblages (Tell 1979b; Izaguirre et al. 1990; Tell and Mataloni 1990; Izaguirre 1991, 1993; Guarrera and Echenique 1992; Diaz and Pedrozo 1993; Juárez and Vélez 1993; Queimaliños 1993; Díaz 1994; Mataloni 1994; Díaz et al. 2000). All together, the above mentioned papers reveal a high richness of *Chlorococcales* in different types of Patagonian aquatic environments.

In spite of the abundant literature on freshwater algae from Patagonia, there are few studies focusing on biogeographic aspects. In this sense, one contribution is that of Tell (1995) which reports data on the geographic distribution of some freshwater algae from Tierra del Fuego. Another study, held by Maidana et al. (2005) analysed the latitudinal variation in the diversity of diatoms along a transect from Patagonia to Antarctica based on the morphological concept of species, observing a decreasing pattern in the species number with increasing latitude. The biogeographic studies involving micro-algae are relevant to elucidate the controversy between the ubiquity hypothesis of the microorganisms (Fenchel et al. 1997; Finlay 2002; Fenchel and Finlay 2004) and the existence of geographical distribution patterns and endemism in these organisms (Foissner 2006, 2008; Logares 2006). According to Foissner (2008) the study of protist species number and distribution has two main challenges. The first one should resolve why the endemic species do not spread world-wide as the majority of other species. The second one, in agreement with Weisse (2008), should focus on the development of a species concept reconciling morphologic, genetic and ecological features.

The present study focuses on the geographic distribution and biodiversity of the *Chlorococcales* in Patagonian lakes, covering a latitudinal transect from Neuquen Province (37.76°S) to Tierra del Fuego (63.41°S). Two different approaches are considered in this paper: (a) a review and numerical analysis of the historical records of *Chlorococcales* in Patagonia obtained from data of the literature; (b) the analysis of the morphology-based species diversity, ecological remarks, and geographic distribution of the chlorococcalean species recorded in 33 aquatic environments during surveys 2007 and 2008.

Materials and methods

Historical review of the records of *Chlorococcales* in Patagonia

The historical review of the records of *Chlorococcales* species in Patagonia was based on all the existent data since the earliest papers in 1949. A total of 34 papers published during 60 years were consulted. In each case, we annotated the different species records, the type of environment and the geographical position where they were encountered. The publications are indicated in the Introduction. We analysed the number of chlorococcalean records for different freshwater systems (lakes, shallow lakes, pond, rivers, streams, reservoirs and peat bogs), and for the different Argentinean Patagonian Provinces following an increasing latitudinal transect (Neuquen, Rio Negro, Chubut, Santa Cruz and Tierra del Fuego).

Survey 2007–2008 in South Argentinean Patagonia

The water bodies studied in 2007 and 2008 are located along a latitudinal Patagonian transect from the south of Chubut Province (45.37°S) to Tierra del Fuego Province (63.41°S), Argentina. Following the classification given by Quirós and Drago (1999) the water bodies are included in two of the recognized Geographical Lake Regions of Argentina: the "Andean Patagonia Region" and the "Patagonian Plateau Region".

The Andean Patagonia Region is characterized by large and deep lakes, which range from ultraoligotrophic to oligotrophic. The distinctive characteristic of the landscape results from a combination of a glacial origin and a later strong fluvial erosion that together with the hard rock composition, accounts for the typical very dilute waters of the lakes. Deep lakes are usually elongated in an east–west orientation as determined by the shape of the glacial valleys that hold them (Díaz et al. 2000). Some shallow lakes are also present in this region, which are typically smaller.

The Patagonian Plateau is a complex landscape mainly characterized by a basaltic plateau and tectonically uplifted pebble fans (Iriondo 1989); this arid region contains different types of water bodies: large artificial lakes that are fed by allochthonous exorheic rivers or originated in the Andes, permanent natural lakes located in depressions and temporary waters. Most of the lakes of this region range from mesotrophic to eutrophic (Quirós and Drago 1999). According to Quirós and Cuch (1985) total phosphorous and phytoplankton chlorophyll *a* of the lakes of the Patagonian Plateau are higher compared with those registered in the Andean lakes. In Tierra del Fuego (Insular Patagonia) some lakes are placed near the mountains and belong to the Andean Patagonian Region, while others are placed in the Patagonian Plateau of the island, among which most of those of the South-eastern are humic-stained lakes. The climate of Patagonia varies from "Andean humid cold" in the West to "Patagonian arid" towards the East, with mean annual precipitations ranging from 800 to 200 mm respectively.

In our study we selected 33 water bodies, located in both limnological regions including deep lakes, shallow lakes and small ponds. Samples were collected during two springtime campaigns in South Argentinean Patagonia (SAP): Chubut and Santa Cruz Provinces (November 2007); Tierra del Fuego Province (October 2008). The following parameters were measured in each of the water bodies with portable instruments: temperature, pH, and conductivity with Horiba D-54 (Horiba, Japan), and dissolved oxygen (DO) with HI 9146 Hanna (Hanna Instruments, USA). Water transparency was recorded using a Secchi disk.

At the deep lakes integrated samples were collected within the euphotic zone from the surface to 5 m; at the shallow lakes water was obtained sub-superficially. Samples for nutrient analyses and chlorophyll *a* (chl *a*) were immediately filtered through Whatman® GF/F filters. Phosphate, nitrate and ammonia concentrations were determined from the filtered water using a Hach™ DR/2800 spectrophotometer and their corresponding kits of reagents (the detection limit for all nutrients being 0.001 mg L^{-1}) following the techniques described in APHA American Public Health Association (2005). Aliquots of filtered water were acidified and stored at 4°C for the analysis of dissolved organic carbon (DOC), which was determined using a high temperature Pt catalyst oxidation method (Shimadzu TOC-5000) following the recommendations of Sharp et al. (1993). Chlorophyll *a* concentrations were estimated using 90% acetone HPLC grade with two 15 min sonication steps separated by an overnight storage at 4°C and pigment analysis was carried out by spectrophotometry using the equations given by Nusch (1980). Phytoplankton samples were collected in each water body for the analysis of the biodiversity (fraction >2 μm). Two types of samples were obtained: (a) filtered through 15 μm-pore size net and preserved with 4% formalin; (b) non-filtered samples fixed with 1% acidified Lugol's iodine solution and maintained in the dark at 4°C. The taxonomic determination of *Chlorococcales* was carried out using a light microscope (Zeiss) under × 1000 magnification. The classification of the species was based on the criteria of Komárek and Fott (1983), Hegewald et al. (1988), and also relevant articles published by Tell and collaborators for the Patagonia (e.g. Mosto 1976; Tell 1974, 1975, 2001, 2004, 2009; Tell and Mosto 1976, 1982; Tell and Mataloni 1990).

Results

Historical review of the records of *Chlorococcales* in Patagonia

A total of 312 chlorococcalean species were recorded throughout the 60-year period in Patagonian freshwater systems. The complete floristic list is presented in a supplementary table linked to Table 2, in which the bibliographic source for each of the records is indicated. From the analyses of the information obtained, it can be seen that the number of species varies in relation to the type of aquatic system and the geographical position. There exists a higher number of records of chlorococcalean species for lentic environments (both deep and shallow lakes), followed by rivers and streams. As regards the geographical distribution of the recorded species, the highest richness coincides with the more intensively sampled provinces (Rio Negro and Tierra del Fuego).

Survey 2007–2008 in South Argentinean Patagonia

Environmental conditions of the studied freshwater systems

Water temperatures varied considerably among the aquatic systems even though they were all sampled in springtime: the range encountered for this variable fluctuated between 4.5 and 27.0°C (Table 1). The small and shallow ponds exhibited the highest temperatures and the widest range, from 7.3 to 27.0°C. In the shallow lakes temperatures varied from 7.8 to 17.3°C, whereas the deep lakes presented the lowest values ranging from 4.5 to 12.8°C. The conductivity values in the three different types of aquatic systems fluctuated from low (around 50 μS cm^{-1}) to relatively high (around 4500 μS cm^{-1}), being the only exception the extremely high conductivity (25800 μS cm^{-1}) registered in Shallow Lake 32 (Laguna

Table 1 Geographic position and main limnological characteristics of different freshwater systems of South Argentinean Patagonia surveyed during spring-times 2007–2008

	Lat. (°S)	Long. (°W)	Temp. (C°)	pH	Cond. (μS cm^{-1})	chl *a* (μg l^{-1})	PO_4 (ppm)	DIN (ppm)	DOC (ppm)	Kd (m^1)
Lake 1 (Musters)	45.55	69.14	12.60	7.84	310	2.62	0.38	0.23	10.80	1.15
Pond 2	45.57	69.11	15.50	8.40	490	4.75	0.06	0.41	19.30	2.53
Pond 3	45.60	69.00	14.10	8.05	110	9.68	0.20	0.42	13.50	2.27
Lake 4 (Colhue Huapi)	45.37	68.95	10.00	8.68	1350	47.01	1.78	0.28	8.20	28.52
Lake 5 (Pueyrredón)	47.38	71.97	8.90	7.26	130	0.41	0.05	0.07	7.60	0.19
Lake 6 (Posadas)	47.45	71.81	10.00	7.84	210	0.38	0.07	0.05	6.10	0.09
Pond 7	47.34	70.99	27.00	8.30	1810	17.02	14.10	0.10	17.00	1.17
Lake 8 (Ghio)	47.27	71.51	12.80	8.20	4760	0.11	0.84	0.04	42.00	0.34
Pond 9	47.20	71.60	20.70	8.20	4110	18.35	15.80	0.05	64.10	3.42
Pond 10	47.46	71.87	15.60	8.20	50	3.00	0.04	0.12	6.10	1.77
Shallow Lake 11	48.69	71.15	10.10	8.20	560	19.56	0.18	0.06	33.70	7.04
Shallow Lake 12	48.68	71.13	13.60	8.20	4600	5.43	0.10	0.03	43.50	1.73
Shallow Lake 13	48.63	71.14	17.30	8.30	230	36.67	0.10	0.18	44.00	ND
Lake 14 (Cardiel)	48.99	71.13	11.00	9.30	4360	0.76	1.39	0.10	11.80	0.23
Pond 15	49.26	72.89	7.30	7.30	80	1.78	0.96	0.16	7.00	0.49
Lake 16 (Lago del Desierto)	49.08	72.89	8.20	6.90	20	0.20	0.15	0.14	5.10	0.12
Pond 17	49.13	72.93	14.80	7.00	50	0.29	0.27	0.17	11.00	0.61
Pond 18	49.59	72.30	12.30	8.15	380	3.87	0.26	0.34	5.40	0.42
Pond 19	49.59	72.31	13.60	8.30	560	3.17	0.15	0.17	11.70	0.54
Lake 20 (Viedma)	49.39	72.87	8.30	6.70	40	1.02	0.25	0.04	5.50	1.62
Lake 21 (Argentino)	50.31	72.80	10.00	6.90	40	0.17	0.13	0.17	4.00	1.31
Pond 22	50.32	72.79	12.30	8.06	610	8.00	0.24	0.07	17.00	3.06
Lake 23 (Roca)	54.83	68.56	4.50	7.60	78	0.41	0.10	0.08	50.20	1.50
Lake 24 (Laguna Negra)	54.84	68.59	6.10	6.90	66	0.68	0.07	0.13	17.80	0.80
Lake 25 (Escondido)	54.68	67.81	4.50	7.36	103	0.12	0.04	0.07	5.10	0.64

Table 1 continued

	Lat. (°S)	Long. (°W)	Temp. (C°)	pH	Cond. (µS cm^{-1})	chl *a* (µg l^{-1})	PO_4 (ppm)	DIN (ppm)	DOC (ppm)	Kd (m^1)
Lake 26 (Fagnano)	54.59	67.62	6.70	7.50	85	0.41	0.02	0.07	12.00	0.69
Pond 27	54.60	67.63	8.30	6.50	205	0.10	0.08	0.08	7.10	3.30
Shallow Lake 28 (Victoria)	54.78	67.70	7.20	7.40	55	0.10	0.03	0.06	5.60	1.77
Pond 29	54.87	67.35	8.20	7.93	110	0.34	0.08	0.04	24.80	2.98
Pond 30	54.85	68.58	13.40	8.14	1284	0.51	0.03	0.08	10.80	2.16
Shallow Lake 31 (San Luis)	53.92	67.60	10.70	8.10	313	0.29	0.17	0.08	17.10	2.06
Shallow Lake 32 (De los Cisnes)	53.79	67.78	12.70	8.98	25800	0.31	0.40	0.13	6.90	2.73
Lake 33 (Yehuin)	54.36	67.78	8.00	8.00	197	0.10	0.04	0.14	9.30	0.40

Lat Latitude, *Long* longitude, *Temp* temperature, *Cond* conductivity, *chl a* chlorophyll *a*, PO_4 dissolved reactive phosphate, *DIN* dissolved inorganic nitrogen, *DOC* dissolved inorganic carboc, *Kd* vertical attenuation coefficient de los Cisnes); the glacial lakes located in the Andean region exhibited the lowest conductivities. As for pH, waters were characterized to be circumneutral (6.5) to alkaline (9.3), corresponding the highest value to Lake Cardiel.

Ponds, shallow lakes and lakes presented in general similar concentrations of nitrogenous forms: $N–NO_3$ ranged from non detectable to 0.18 mg L^{-1}, and $N–NH_4$ from non detectable to 0.41 mg L^{-1}. The highest $N–NH_4$ concentration was found in Ponds 2 and 3 from Chubut. As regards $P–PO_4$, differences were observed in the ranges for the different types of aquatic systems; the concentration of this nutrient in lakes oscillated from 0.02 mg L^{-1} (Lake Fagnano) to 1.80 mg L^{-1} (Lake Colhue Huapi), in shallow lakes from 0.02 to 0.40 mg L^{-1} (Shallow Lake 32), whereas the ponds exhibited the greatest difference, ranging from 0.03 to 15.80 mg L^{-1} (Pond 9). The DOC concentrations were also highly variable in ponds (5.4–64.1 mg L^{-1}), and the extreme value was observed for Pond 22 (2326 mg L^{-1}). In shallow and deep lakes DOC concentrations varied from 4.0 to 50.2 mg L^{-1}, registering the highest value in Lake Ghio.

Light penetration as reflected by Kd values, was highly variable in the sampled aquatic systems, ranging from extremely low (0.04 m^{-1}) to very high (28.52 m^{-1}), corresponding the lowest figures to the oligotrophic Andean lakes and the highest ones to the shallow lakes located in the Patagonian Plateau, with an extreme light attenuation in Lake Colhue Huapi.

Floristic and biogeographical remarks

Table 2 shows the distribution of the species of the sampling period 2007–2008 in the different freshwater bodies. A total of 72 chlorococcalean taxa were registered. Spindle-shaped cells are represented by solitary and colonial entities. Among the free living unicellular forms two genera are present: *Monoraphidium* and *Schroederia*. Twelve species of the first genus were previously mentioned for South Argentinean Patagonia (SAP), among them we have encountered ten in our survey: *M. arcuatum, M. caribeum, M. circinale, M. contortum, M. griffithii, M. indicum, M. komarkovae, M. minutum, M. subclavatum* and *M. tortile*. Almost all of these entities are worldwide distributed. *M. arcuatum, M. circinale,* and *M. contortum* are the species best represented in SAP, being present in eleven, five and ten sites respectively.

Considering the three species of *Schroederia* mentioned for SAP, our samples only include *S. indica,* being present exclusively in Lake Colhue Huapi. This record enlarges the geographical distribution of this species to South American cold waters. Colonial straight spindle-shaped cells forms include three genera: *Ankistrodesmus*, *Fusola* and *Quadrigula*. Fifteen *Ankistrodesmus'* species were previously mentioned for SAP, among them only *A. fusiformis, A. gracilis* and *A. spiralis* are present in our samples. The three species are widely distributed over the world. In our samples they are poorly represented in lakes and ponds of the continental Patagonian Plateau. The only species of the genus *Fusola* recorded for the region is *F. viridis*, and it is mentioned for the first time for SAP. It was present in two lakes of the Patagonian Plateau: Musters and Cardiel. Two species of the genus *Quadrigula* were recorded for SAP; in the present survey we only found *Q. lacustris*. It is an interesting species, not frequently encountered, mainly known for temperate and cold waters. Komárek and Fott (1983) point out that the species probably belongs to the genus *Pseudoquadrigula*.

Spherical cells enclosed within mucilage (*Eutetramorus*-like) are represented by three genera: *Coenocystis*, *Eutetramorus* and *Sphaerocystis*. Most of the species of these genera are well known in Europe, but less known in the Southern hemisphere. Few species of this

Table 2 Distribution of the chlorococcalean species encountered in the different freshwater systems of South Argentinean Patagonia during surveys 2007–2008

	Lake 1 (Musters)	Pond 2	Pond 3	Lake 4 (Colhue Huapi)	Lake 5 (Pueyrredón)	Lake 6 (Posadas)	Pond 7	Lake 8 (Ghio)	Pond 9	Pond 10	Shallow Lake 11	Shallow Lake 12	Shallow Lake 13	Lake 14 (Cardiel)	Pond 15	Lake 16 (Lago del Desierto)	Pond 17
Ankistrodesmus fusiformis		x											x				
Ankistrodesmus gracilis				x									x				
Ankistrodesmus spiralis							x						x				
Botryococcus braunii									x			x					
Botryosphaerella sudetica								x									
Chlorella sp.	x			x	x		x						x				
Coelastropsis costata																	
Coelastrum astroideum			x														
Coelastrum indicum	x																
Coelastrum microporum																	
Coenocystis planctonica								x				x					
Coenocystis subcylindrica																	
Crucigenia quadrata																	
Crucigeniella rectangularis															x		
Dictyosphaerium pulchellum	x		x	x	x												

Table 2 continued

	Lake 1 (Musters)	Pond 2	Pond 3	Lake 4 (Colhue Huapi)	Lake 5 (Pueyrredón)	Lake 6 (Posadas)	Pond 7	Lake 8 (Ghio)	Pond 9	Pond 10	Shallow Lake 11	Shallow Lake 12	Shallow Lake 13	Lake 14 (Cardiel)	Pond 15	Lake 16 (Lago del Desierto)	Pond 17
Dictyosphaerium tetrachotomum var. *tetrachotomum*													x			x	
Didymocystis bicellularis													x				
Eremosphaera eremosphaeria	x																
Eutetramorus fotti	x							x									x
Eutetramorus nygardii																x	
Eutetramorus planctonicus																	
Fusola viridis	x													x			
Kirchneriella contorta				x													
Kirchneriella irregularis																	
Lagerheimia subsalsa													x				
Lobocystis planctonica	x							x		x				x		x	
Micractinium pusillum		x															
Monoraphidium arcuatum	x	x	x				x	x			x	x	x	x			
Monoraphium caribeum			x	x													
Monoraphidium circinale	x	x	x		x	x											
Monoraphidium contortum	x	x	x	x	x	x					x	x	x	x			
Monoraphidium griffithii	x	x									x		x				
Monoraphidium indicum		x	x		x												

Table 2 continued

	Lake 1 (Musters)	Pond 2	Pond 3	Lake 4 (Colhue Huapi)	Lake 5 (Pueyrredón)	Lake 6 (Posadas)	Pond 7	Lake 8 (Ghio)	Pond 9	Pond 10	Shallow Lake 11	Shallow Lake 12	Shallow Lake 13	Lake 14 (Cardiel)	Pond 15	Lake 16 (Lago del Desierto)	Pond 17
Monoraphidium komakovae													x				
Monoraphidium minutum		x											x				
Monoraphidium subclavatum		x					x										
Monoraphidium tortile		x															
Oocystidium ovale				x													
Oocystis borgei								x									
Oocystis lacustris				x		x	x					x	x	x			x
Oocystis marsonii																	x
Oocystis naegelli	x																
Oocystis parva	x								x	x							
Oocystis submarina																x	
Pediastrum boryanum	x	x		x									x				
Pediastrum boryanum var. longicorne																	
Pediastrum integrum																	
Pediastrum kawraiskyi	x			x									x		x		
Pediastrum mustersii	x			x		x											
Pediastrum patagonicum	x			x													

Table 2 continued

	Lake 1 (Musters)	Pond 2	Pond 3	Lake 4 (Colhue Huapi)	Lake 5 (Pueyrredón)	Lake 6 (Posadas)	Pond 7	Lake 8 (Ghio)	Pond 9	Pond 10	Shallow Lake 11	Shallow Lake 12	Shallow Lake 13	Lake 14 (Cardiel)	Pond 15	Lake 16 (Lago del Desierto)	Pond 17
Pediastrum simplex v. sturmii	x																
Planktosphaeria gelatinosa				x													
Quadrigula lacustris																	
Raphidocelis mucosa													x				
Scenedesmus acuminatus													x				
Scenedesmus cf. acutiformis		x															
Scenedesmus acutus													x				
Scenedesmus circunfusus							x										
Scenedesmus ecornis							x										x
Scenedesmus intermedius		x															
Scenedesmus opoliensis																	
Scenedesmus quadricauda		x					x										
Scenedemus spp.		x					x										
Schroederia indica				x													
Sphaerocystis schroeteri							x						x				

Table 2 continued

	Lake 1 (Musters)	Pond 2	Pond 3	Lake 4 (Colhue Huapi)	Lake 5 (Pueyrredón)	Lake 6 (Posadas)	Pond 7	Lake 8 (Ghio)	Pond 9	Pond 10	Shallow Lake 11	Shallow Lake 12	Shallow Lake 13	Lake 14 (Cardiel)	Pond 15	Lake 16 (Lago del Desierto)	Pond 17
Tetraedron aff. Pentaedricum													x				
Tetrastrum komarekii					x												
Tetrastrm sp.				x													
Westella botryoides	x			x				x						x			
Willea vilhelmii																	
Willea sp.																	

	Pond 18	Pond 19	Lake 20 (Viedma)	Lake 21 (Argentino)	Pond 22	Lake 23 (Roca)	Lake 24 (Laguna Negra)	Lake 25 (Escondido)	Lake 26 (Fagnano)	Pond 27	Shallow Lake 28 (Victoria)	Pond 29	Pond 30	Shallow Lake 31 (San Luis)	Shallow Lake 32 (De los Cisnes)	Lake 33 (Yehuin)
Ankistrodesmus fusiformis																
Ankistrodesmus gracilis																
Ankistrodesmus spiralis																
Botryococcus braunii		x		x	x		x							x		x
Botryosphaerella sudetica														x		
Chlorella sp.																
Coelastropsis costata		x														
Coelastrum astroideum	x	x														
Coelastrum indicum																

Table 2 continued

	Pond 18	Pond 19	Lake 20 (Viedma)	Lake 21 (Argentino)	Pond 22	Lake 23 (Roca)	Lake 24 (Laguna Negra)	Lake 25 (Escondido)	Lake 26 (Fagnano)	Pond 27	Shallow Lake 28 (Victoria)	Pond 29	Pond 30	Shallow Lake 31 (San Luis)	Shallow Lake 32 (De los Cisnes)	Lake 33 (Yehuin)
Coelastrum microporum						x										
Coenocystis planctonica																
Coenocystis subcylindrica	x													x		
Crucigenia quadrata						x										
Crucigeniella rectangularis	x	x	x													
Dictyosphaerium pulchellum			x													
Dictyosphaerium tetrachotomum var. *tetrachotomum*																
Didymocystis bicellularis																
Eremosphaera eremosphaeria																
Eutetramorus fotti	x	x		x		x								x		
Eutetramorus nygardii			x						x							
Eutetramorus planctonicus	x	x	x				x									
Fusola viridis																
Kirchneriella contorta																
Kirchneriella irregularis												x				

Table 2 continued

	Pond 18	Pond 19	Lake 20 (Viedma)	Lake 21 (Argentino)	Pond 22	Lake 23 (Roca)	Lake 24 (Laguna Negra)	Lake 25 (Escondido)	Lake 26 (Fagnano)	Pond 27	Shallow Lake 28 (Victoria)	Pond 29	Pond 30	Shallow Lake 31 (San Luis)	Shallow Lake 32 (De los Cisnes)	Lake 33 (Yehuin)
Lagerheimia subsalsa																
Lobocystis planctonica																
Micractinium pusillum																
Monoraphidium arcuatum												x		x		
Monoraphium caribeum																
Monoraphidium circinale																
Monoraphidium contortum																
Monoraphidium griffithii												x				
Monoraphidium indicum																
Monoraphidium komakovae																
Monoraphidium minutum																
Monoraphidium subclavatum																
Monoraphidium tortile																
Oocystidium ovale																
Oocystis borgei																
Oocystis lacustris	x	x	x					x						x		x

Table 2 continued

	Pond 18	Pond 19	Lake 20 (Viedma)	Lake 21 (Argentino)	Pond 22	Lake 23 (Roca)	Lake 24 (Laguna Negra)	Lake 25 (Escondido)	Lake 26 (Fagnano)	Pond 27	Shallow Lake 28 (Victoria)	Pond 29	Pond 30	Shallow Lake 31 (San Luis)	Shallow Lake 32 (De los Cisnes)	Lake 33 (Yehuin)
Oocystis marsonii																
Oocystis naegelli																
Oocystis parva				x				x	x					x		
Oocystis submarina																
Pediastrum boryanum	x	x										x				
Pediastrum boryanum var. longicorne													x			
Pediastrum integrum	x	x														
Pediastrum kawraiskyi												x		x	x	
Pediastrum mustersii														x		
Pediastrum patagonicum														x		
Pediastrum simplex v. sturmii																
Planktosphaeria gelatinosa		x			x	x					x					
Quadrigula lacustris	x					x										
Raphidocelis mucosa																
Scenedesmus acuminatus																
Scenedesmus cf. acutiformis																
Scenedesmus acutus																
Scenedesmus circunfusus																

Table 2 continued

	Pond 18	Pond 19	Lake 20 (Viedma)	Lake 21 (Argentino)	Pond 22	Lake 23 (Roca)	Lake 24 (Laguna Negra)	Lake 25 (Escondido)	Lake 26 (Fagnano)	Pond 27	Shallow Lake 28 (Victoria)	Pond 29	Pond 30	Shallow Lake 31 (San Luis)	Shallow Lake 32 (De los Cisnes)	Lake 33 (Yehuin)
Scenedesmus ecornis																
Scenedesmus intermedius																
Scenedesmus opoliensis												x				
Scenedesmus quadricauda																
Scenedemus spp.																
Schroederia indica																
Sphaerocystis schroeteri																
Tetraedron aff. Pentaedricum																
Tetrastrum komarekii																
Tetrastrm sp.																
Westella botryoides														x		x
Willea vilhelmii									x					x		x
Willea sp.																x

group were recorded for Argentina, all of them distributed in temperate and cold waters. Three species of the first genus were mentioned for SAP, two of them present in our samples: *C. planctonica* and *C. subcylindrica*. *C. planctonica* constitutes a new record from SAP, being present in Lake Ghio and a shallow lake of the Patagonian Plateau. *C. subcylindrica* also constitutes a new record from SAP, being present in one pond and one shallow lake, from Santa Cruz and Tierra del Fuego respectively. Three out of four species of *Eutetramorus* recorded for SAP were present in our samples: *E. fotii, E. nygardii,* and *E. planctonicus*. The first species is the most widely distributed of the genus, and in our samples it was also largely distributed, being present in eight water bodies. According to Komárek and Fott (1983) *E. nygardii* is only known from Greenland′s ultra-oligotrophic lakes; probably this is the first record for the Southern hemisphere. Agreeing with Komárek and Fott's (loc. cit) data, in our samples it was also present in three Andean oligotrophic lakes. Probably, also *E. planctonicus* constituted the first record for the South hemisphere; it was recorded in two ponds and two lakes.

Curved cells enclosed within mucilage (*Kirchneriella*-like) are represented by the genera *Kirchneriella* and *Raphidocelis*. Couté and Tell (in press) describe the species and the geographical distribution of *Kirchneriella* in Argentina. Eight species of this genus were previously mentioned for SAP, among them only two were encountered by us: *K. contorta* and *K. irregularis*. Although both species are cosmopolitan, they were present only once in our samples. The genus *Raphidocelis* comprises only two or three species rarely mentioned for the North Hemisphere, being poorly known in the Southern one. *R. mucosa* was recorded only once in a shallow lake of the Patagonian Plateau.

A lot of species and infraspecific taxa of the genus *Pediastrum* were described over the world, mainly in the North hemisphere, most of them widely distributed but others recorded only from circumscriptive regions (Komárek and Jankovská 2001; Tell 2004). It is interesting to point out that two cases of endemism for the South hemisphere are known: *P. marvillense* (Grande Terre, Kergelen islands) and *P. patagonicum* (lake Musters, Argentinean Patagonia). Twenty five species of *Pediastrum* were previously mentioned for SAP, among them only seven were sampled by us: *P. boryanum, P. boryanum* var. *longicorne, P. integrum, P. kawraisky, P. mustersii, P. patagonicum* and *P. simplex* var. *sturmii*. Among these entities, three recent species (*P. kawraisky, P. mustersii, P. patagonicum*) and a fossil one (*P. leonensis*) are characterized by the lobes of the external cells oriented in different planes (Tell 2004; Tell and Zamaloa 2004). A review of the long list of species of *Pediastrum* described over the world shows that this type of morphology is only present in these four species. It is worth to note that all four species were recorded for SAP, where two of them are endemic (the recent *P. patagonicum* and the fossil *P. leonensis*). *P. kawraisky* presents a distribution restricted to colder regions in the North and South hemispheres, usually associated with peaty habitats. In the South hemisphere its distribution is restricted below the 45.55°S. In our samples it is widely distributed in seven water bodies, six of which are located at different latitudes in the Patagonian Plateau. *P. mustersii* was first described by Tell and Mataloni (1990) from lake Musters (45.55°S–69.14°W), and several times mentioned later for temperate waters of the North and South hemisphere. In our samples it was recorded in three lakes and one shallow lake, from Chubut Province to Tierra del Fuego. *P. patagonicum* was also first described by Tell and Mataloni (loc. cit.) for Lake Musters, being at the moment recorded in two lakes from Chubut Province and one shallow lake from Tierra del Fuego. Populations of the three living species of *Pediastrum* with lobes in the external cells oriented in different planes were only found together in the lakes Musters, Colhue Huapi and San Luis. Lakes Musters and Colhue Huapi, although of different origin, are located very close to each other in the

Patagonian Plateau; San Luis is a shallow lake of the plateau of Tierra del Fuego Island, placed near Río Grande city. Contrarily, *P. boryanum* is worldwide distributed, and it was recorded in our samples in several lakes, shallow lakes and ponds. *P. boryanum* var. *longicorne* was only recorded in one pond of the insular Patagonia. *P. integrum*, which has a similar geographical distribution to *P. kawraisky,* was registered in our survey in two ponds from Santa Cruz Province. *P. simplex* var. *sturmii* was only present in Lake Musters, being the first record for Argentina.

The genus *Desmodesmus* was separated from *Scenedesmus* by An et al. (1999), and corroborated by Van Hannen et al. (2002). Tell (2009) published a revision of the perforated *Scenedesmus* and *Desmodesmus* for Argentina. Among the *Chlorococcales* these genera include the largest number of species and infraspecific entities. Many of them are well known and widely distributed, but others were rarely recorded over the world. All the records of *Scenedesmus* from SAP were mentioned previously to 1999; therefore none of the entities were registered under the name *Desmodesmus*. Sixty-eight species of *Scenedesmus* were previously mentioned for SAP, among them we have only encountered eight: *S. acuminatus, S.* cf. *acutiformis, S. acutus, S. circumfusus, S. ecornis, D. intermedius* (syn. *S. intermedius*), *D. opoliensis* (syn. *S. opoliensis*) and *D. quadricauda* (syn. *S. quadricauda*). *S. ecornis* and *D. quadricauda* were recorded in two ponds in Continental Patagonia; the six remaining species were recorded only once and may be consider "rare" in the region. Anyway, all the recorded species are well known and widely distributed over the world. We think that many of the species of *Scenedesmus* previously mentioned from SAP before this article need taxonomical confirmation. The neighbor genus of *Scenedesmus*, *Didymocystis* is represented by only one species, *D. bicellularis,* recorded only once in a shallow lake of the Patagonia Plateau. This species was frequently recorded from many sites of Central and Eastern Europe.

Lagerheimia subsalsa and *Tetraedron* aff. *pentaedricum* are two planktonic coccoid algae recorded only once in our samples. On the other hand, the small unicellular *Planktosphaeria gelatinosa* was recorded in five water bodies from the Continental and Insular Patagonia. *Crucigeniella rectangularis, Crucigenia quadrata* and *Tetrastrum komarekii* are small coenobia sporadically present in few lakes. The genus *Willea* includes only three or four worldwide recognized species, which are rarely mentioned. *W. vilhelmii* was encountered in three sites of the Insular Patagonia. *Willea* sp. (Komárek and Fott 1983 p. 775, Pl. 216:1) agrees with the entity found by us in lake Yehuin. It was previously recorded from Germany and Sweden. Probably it is a new species restricted to circumpolar regions.

Tell (2001) compiled the mentioned species of *Coelastrum* for Argentina, including those of SAP. Seven species of *Coelastrum* were previously mentioned for SAP; among them three were recorded by us: *C. astroideum, C. indicum,* and *C. microporum.* Although all these three species are widely distributed, *C. astroideum* was recorded just in three sites and *Coelastrum indicum,* and *C. microporum* in only one. The neighbor genus *Coelastropsis* comprises only one well recognized species, *C. costata.* It was rarely mentioned and shows a geographical distribution restricted to North Europe and the South of South America. In our samples *C. costata* was present in only one pond.

From the morphological and functional point of view, the genera *Dictyosphaerium*, *Lobocystis*, *Westella*, *Botryococcus.,* and *Botryosphaerella*, present many features in common. Nine entities of *Dictyosphaerium* were previously mentioned for SAP, among them only two were encountered by us: *D. pulchellum* and *D. tetrachotomum* var. *tetrachotomum. D. pulchellum* is worldwide distributed; in our samples it was present in three lakes and ponds of the Patagonian Plateau and two Andean lakes. *D. tetrachotomum* var. *tetrachotomum* presents a restricted distribution in temperate and cold waters, and in our samples it was only recorded in two sites. We agree with Komárek and Fott (1983) who think that the tropical finding of this species must still be revised. *Lobocystis planctonica* is widely distributed over the world, but in Argentina it was occasionally mentioned above the parallel 45.37°S. Contrarily, in the cold waters of the Patagonian Plateau it was frequently encountered in lakes and ponds. Taking into account the a recent paper by Stoyneva (2008), the records of different species of *Lobocystis* in SAP should be revised, since the presence or absence of radiating structure in the mucilage would be an important character for morphologically defining the species of this genus; in our material the specimens fit with the original description given for *L. planctonica* in Komárek and Fott (1983). *Westella botryoides* is restricted to temperate and cold waters of the North and South hemisphere, and in our samples it was present in six sites of the Continental and Insular Patagonia. *Botryococcus braunii* is cosmopolite; in our samples it was largely distributed in eight water bodies of the Continental and Insular Patagonia. *Botryosphaerella sudetica* is known from peat bogs and distrophic and oligotrophic cold waters from the North hemisphere; in our samples it was recorded in one lake from Santa Cruz Province and one shallow lake of Tierra del Fuego.

The morphospecies and infraspecific forms belonging to the genus *Oocystis* present some difficulties for their taxonomical identification. The morphological characters that define the infra-generic taxa are often variable and not well established. Eighteen species of *Oocystis* were previously mentioned for SAP, among them six were found by us: *O. borgei*, *O. lacustris*, *O. marsonii*, *O. naegelli*, *O. parva* and *O. submarina*, all of them largely distributed over the world. *O. borgei* was recorded only in lake Ghio. *O. lacustris* was the species most extensively distributed in our samples, being found at thirteen sites. *O marsonii* was found only in one pond near the Andean mountains. *O. naegelli* was recorded in Lake Musters, *O. parva* in seven lakes, shallow lakes and ponds, and *O. submarina* in Lago del Desierto. The taxonomic review of Stoyneva et al. (2007) on tropical *O. lacustris* and related species showed a great morphological variability in *O. lacustris* and they found that the diacritical features of the species *O. parva*, *O. marssonii*, *O. borgei*, and *O. lacustris* overlap; thus the authors identified all these specimens as a single species (*O. lacustris*) proposing that the other taxa were synonyms. Taking into account this study, we consider that a further revision of all the recorded *Oocystis* in Patagonia would be necessary in order to analyse the morphological variability of the genus in this region.

The neighbor genus *Oocystidium* comprises just two species described in the bibliography, being one of them, *O. ovale*, present in lake Colhue Huapi. This species is rare in our samples but largely distributed over the world.

In South America, *Dictyosphaerium tetrachotomum, Raphidocelis mucosa, Westella botryoides, Botryosphaerella sudetica, Pediastrum kawraisky, P. patagonicum, Willea vilhelmii, Willea* sp. (Komárek and Fott 1983, p. 775, Pl. 216:1), and *Coelastropsis costata* were encountered in our samples but are not recorded over the parallel 45.37°S. The same happened with the species *Enallax alpina, E. coelastroides, Pediastrum taylori*, *Scotiella antarctica*, and the *Scendesmus'* species and infraespecific species described from Tierra del Fuego by Mosto (Tell and Mosto 1982) *S. fuegiensis*, *S. guarrerae*, *S. latocostatus* f. *major* and *S. ushuaiensis.* We do not include in this list all the mentioned species of *Trochiscia* because we consider that they need taxonomical revision. The absence of the mentioned species above the parallel 45.37°S means that they have a noticeable geographic restriction, not being able to prosper in other environmental conditions, in particular not in

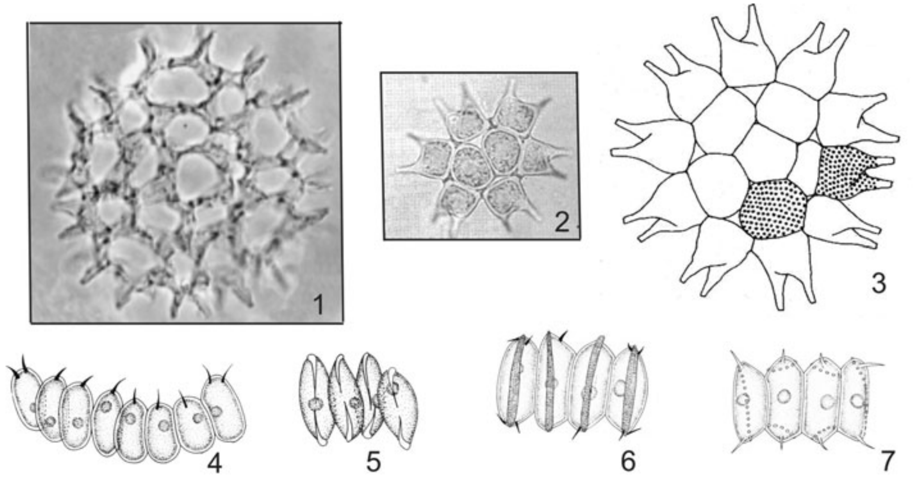

Fig. 1 Probable chlorococcalean endemic species for South Argentinean Patagonia. (1) *Pediastrum leonensis* Tell et Zamaloa (after Tell and Zamaloa 1994) (fossil); (2) and (3) *P. patagonicum* Tell et Mataloni (after Tell and Mataloni 1990); (4) *Scenedesmus fuegiensis* Mosto in Tell and Mosto (after Tell and Mosto 1982); (5) *S. guarrerae* Mosto in Tell and Mosto (after Tell and Mosto 1982); (6) *S. latocostatus* f. *major* Mosto in Tell and Mosto (after Tell and Mosto 1982); (7) *S. ushuaiensis* Mosto in Tell and Mosto (after Tell and Mosto 1982). Reproduced from Tell and Mosto (1982); Tell and Mataloni (1990) and Tell and Zamaloa (2004)

warmer climates. The mentioned *Scenedesmus* species together with *P. patagonicum*, which are probably endemic taxa, as well as the fossil *P. leonensis* are illustrated in Fig. 1.

The analysis of the chlorococcalean richness in relation to the environmental factors, revealed that the species richness of this group in the aquatic environments of SAP is directly correlated with the trophic status of the water bodies (chl a: $r = 0.52$ and DIN: $r = 0.47$; $P < 0.05$), The pH of the water was also positively correlated with chlorococcalean species richness ($r = 0.36$; $P < 0.05$).

Interestingly, the latitude was inversely correlated with the species richness ($r = -0.40$; $P < 0.05$). The biogeographical trend is illustrated in Fig. 2. On the other hand, the species richness of the Andean lakes (mean value: 3.64) was significantly lower ($P = 0.0022$) than that of the lakes from the Patagonian Plateau (mean value: 9.62).

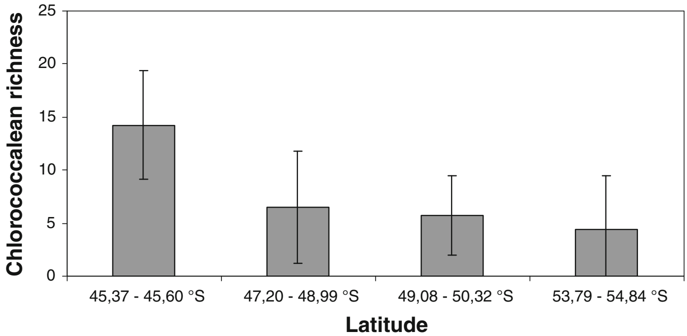

Fig. 2 Chlorococcalean richness for different latitudinal intervals from South Argentinean Patagonia. Data corresponds to spring-time surveys 2007–2008

Discussion

The analysis of the chlorococcalean flora obtained from the surveys 2007–2008 would confirm Tell's suggestions (1995), who stressed that the geographic and climatic characteristics of Patagonia and, in particular those of Tierra del Fuego, are more comparable with the ones of other world regions than with those of the rest of the Argentinean territory. Therefore, its algal microflora shows more similarities with that from some cold regions of the North hemisphere than with the rest of South America. Many species registered in the North hemisphere, would have not been able to prosper under the conditions of the tropical and subtropical zone, and may then be again found in the Patagonia region. This distribution leads to think about an ample dispersion of propagules by means of the wind or migratory birds, which would be successful in their growth and development when they find a propitious habitat. In most of the species registered here, the favorable factors would mainly be given by conditions of low temperatures in the entire region and, in particular, dystrophic conditions in Tierra del Fuego, with predominance of acid waters and dissolved humic substances. On the other hand, human introductions as a way of propagule dispersion should not be disregard. Human vectors are among the transport process involved in the dispersion of microorganisms, which can operate over long distances (Vincent 2000). For example, the species *Schroederia indica* encountered in Lake Colhue Huapi, was not previously registered in Patagonia, and its records correspond mainly to tropical and warm habitats, and never reported for the American continent (Komárek and Fott 1983). The presence of this species in a single site in Patagonia could indicate a discontinuous dispersion mediated by human vectors.

Among the species registered in the studied lakes nearly 80% are worldwide distributed, about 19% are restricted to cold temperate areas in both hemispheres, and a single taxa (*Pediastrum patagonicum*) was only found in particular environments of Patagonia, suggesting that it is endemic. Nevertheless, if we consider all the studies carried out by Tell (see Tell and Mosto 1982), other four chlorococcalean species were only found in Patagonia: *Scenedesmus fuegiensis*, *S. guarrerae*, *S. latocostatus* f. *major* and *S. ushuaiensis*. Our results are in agreement with Coesel and Krienitz (2008) remarks. These authors state that although most of the *Chlorococcales* are cosmopolite, many cases of endemism are also mentioned in the literature.

Taking into account the two current models regarding the protist distribution: the "ubiquity model" (Finlay et al. 1996; Fenchel and Finlay 2004) and the "moderate endemicity model" (Foissner 2006, 2008), our results seem to support the second position since some species are presumably endemic as they were only reported for Patagonia. According to Foissner (2008) there is no doubt about the existence of endemic protists. His estimations resulting from morphological and/or molecular species concept of well studied protistan groups showed a 30% of endemic species. Among the reasons that this author wields for the restricted distribution of some taxa, the main would be an insufficient time to spread for young species, the existence of specific ecological demands and the lack of the production of resting propagules that can withstand long range dispersal.

In this study we observed a decreasing biodiversity pattern of *Chlorococcales* with increasing latitude, reinforcing the ecological pattern described for different groups of organisms (Willig et al. 2003; Pimm and Brown 2004). Particularly, this trend was observed along a Patagonian-Antarctic transect for freshwater diatoms (Maidana et al. 2005). Furthermore, Convey (2001) recognized a progressive loss of species richness in the macro and micro biota from Sub Antarctica to Continental Antarctica. Contrarily, analyzing the historical floristic list (Supplementary Table), the latitudinal decrease richness is not evident because the sampling effort was not the same at the different latitudes. Clearly, those provinces more intensively sampled (Rio Negro and Tierra del Fuego) exhibit the highest number of records. We consider that many of the historical records should be revised since most of the species were identified using literature exclusively from the Northern hemisphere and without taking into account that the local flora may present phenotypic variability. On the other hand many species proceed from fixed material only sporadically collected. Finally, during the last 20 years many of the recorded taxa were revised, changing their taxonomical affiliation. Thus, it is difficult to compare the historical records with our floristic list.

Our results showed a significant positive correlation between the *Chlorococcales*' species richness and the indicators of trophic status of the lakes. In this sense, Komárek and Fott (1983) highlighted the success of this algal group in eutrophic and mesosaprobic freshwaters. Nevertheless, some small chlorococcalean species may also be well represented in nutrient-poor waters since their small cells have a high surface-area-to-volume ratio, and thus and advantage in the nutrient uptake (Happey-Wood 1988). In general terms, the diversity of the phytoplankton community was found to be positively correlated with a moderate eutrophication, but it is important to point out that in very poor waters the low diversities may be also influenced by the randomness of many rare species (Margalef 1983).

Many authors have stressed the importance of the molecular tools in the biodiversity and biogeographic studies of protists (Coesel and Krienitz 2008; Weisse 2008). Nevertheless, although we recognize the importance of the molecular approaches, the comparison of morphospecies proceeding from different regions may be a good means to understand their biogeographical distribution. On the other hand, as Weisse (2008) observes, "there is no molecular gold standard for protist taxonomy to solve the species problem…". In conclusion, both molecular and morphological approaches constitute a good way to approach the understanding of the diversity, linkage and biogeography.

Biodiversity and biogeographic studies of free-living protists (as in our case the chlorococcalean algae) are fundamental to increase the knowledge of their biology, that as stated by Cotterill et al. (2008), will only advance from intensive inventories and field studies of these microorganisms across the world′s habitats.

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