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Observations on valve structures of *Navicula directa* (Wm. Smith) Ralfs *in* Pritchard and *Navicula glaciei* V. Heurck from rocky substrates in Antarctic Peninsula

Luciano Felício Fernandes[1,2] and Leticia Knechtel Procopiak[1]

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ABSTRACT - (Observations on valve structures of *Navicula directa* (Wm. Smith) Ralfs *in* Pritchard and *Navicula glaciei* V. Heurck from rocky substrates in the Antarctic Peninsula). The diatoms *Navicula directa* and *N. glaciei* were examined under light and electron microscopes for investigating their frustule morphology. Further, variations associated to size reduction of the cells were recorded for *N. glaciei*. Samples were collected on rocks of Admiralty Bay and Elephant Island, Antarctic Peninsula. *N. directa* shows lanceolate valves with conspicuously parallel striae and composed of lineate areolae occluded by hymenes. Its raphe system has distal endings surrounded by helictoglossae, which are raised and supported by silica bridges. This structure also gives rise to a chamber, bordered by the valve apex edge. An accessory rib lies along with the raphe sternum. *N. glaciei* bears parallel striae tending to radiate near the apices. The central area is expanded towards the valve edge; in small specimens, it turns quadrangular. The raphe system is straight with distal endings bearing helictoglossae. *N. glaciei* was abundant in the samples, indicating that hard bottoms are true habitats and an additional seeding source of cells to the phytoplankton community during the ice melting in Austral spring.

Key words: Bacillariophyta, taxonomy, benthic microalgae, *Navicula*, Antarctica

RESUMO - (Observações sobre a estrutura das valvas de *Navicula directa* (Wm. Smith) Ralfs *in* Pritchard e *Navicula glaciei* V. Heurck de substratos rochosos na Península Antártica). As diatomáceas *Navicula directa* e *N. glaciei* foram examinadas em microscopia eletrônica para investigar sua morfologia e variações associadas à redução de tamanho da célula. As amostras foram coletadas em rochas da Baía do Almirantado e Ilha Elefante, Península Antártica. *N. directa* apresenta valvas lanceoladas com estrias fortemente paralelas e compostas por aréolas lineoladas ocluídas por hymenes. O sistema de rafe possui terminações com helictoglossa, a qual encontra-se elevada em relação ao restante da valva, e sustentada por barras de sílica. Este arranjo também origina uma câmara, limitada pela margem dos ápices da valva. Uma costela projetada está presente ao longo do sternum da rafe. *N. glaciei* apresenta valvas com superfície provida de estrias radiais, tendendo a paralelas na região central de valvas menores. A região central é expandida em direção à borda da valva; em exemplares menores ela torna-se quadrangular. *N. glaciei* foi abundante nas amostras, indicando que substratos rochosos são habitats ocupados pela espécie e uma fonte adicional de células para a comunidade fitoplanctônica durante o derretimento de gelo na primavera Austral.

Palavras-chave: Bacillariophyta, taxonomia, microalgas bênticas, *Navicula*, Antártica

Introduction

Benthic microalgae are widespread organisms, contributing with the bulk of primary production of microphytobenthos in soft and hard marine substrates around the world, and sometimes surpassing the biomass contribution of phytoplankton cells (McIntire & Moore 1977, Charpy-Roubaud & Sournia 1990, Underwood 1994). In Antarctica, the ecological and taxonomic works carried out focusing on benthic microalgae are limited (Gilbert 1991, and see reviews of White et al. 1993 and Knox 1994). Instead, the ice-algae (diatom dominated) communities are well known by their high productivity in austral spring and during the ice melting, when they enhance the primary productivity of the pelagic community by releasing cells to the water column (Whitaker 1977, Everitt & Thomas 1986, El-Sayed & Fryxell 1993). Few important works dealing on microphytobenthic primary production and the biomass seasonality were produced

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[1] Departamento de Botânica, Setor de Ciências Biológicas, Centro Politécnico, Universidade Federal do Paraná, Caixa Postal 19031, 81531-990 Curitiba, PR, Brasil.

[2] Corresponding author: lucfel@bio.ufpr.br

in Antarctic neritic regions, all of them studying soft bottoms environments (sand, gravels or mud), also pointing out the dominance of diatoms within the benthic community (White et al. 1993). These studies found that diatoms play an important role in the organic carbon flux of littoral ecosystems in different sites of Antarctica. On the other hand, hard bottom substrates have been overlooked, although comprising a substantial surface bottom area in the Antarctic continental shelf (Knox 1994). Some recent works were produced showing that epilithic diatoms are relevant contributors to phytoplankton biomass when cells are resuspended to the water column (Krebs 1983, Ahn et al. 1994, 1997, Kang et al. 1997a, Klöser 1998). Ligowski (2000) recorded a large biomass of benthic diatoms being consumed by the krill *Euphausia superba* Dana during summer in Admiralty Bay, pointing out the importance of these microalgae to the pelagic community as this crustacean plays a key role in the Antarctic ecosystem.

In the same way, taxonomic studies dealing on diatom inhabiting hard substrates are scarce. In the majority of the pioneer works, few samples from rocky bottoms were collected, and the somewhat preliminary species descriptions have hampered positive or reliable identification of many taxa (Karsten 1906, Van Heurck 1909, Mangin 1915, Peragallo 1921, Mann 1937).

The diatom genus *Navicula* Bory is one of the most important components within the microbiota of eponthic (that is, ice related) communities in Antarctica (Medlin & Pridlle 1990) as well as in Arctic (Poulin & Cardinal 1982a). Regarding the Antarctic microflora, species of *Navicula* are common to dominant in both seasonal pack ice and permanent ice surrounding the continent. During the ice retreating, many cells can be found in the water column, thus enhancing phytoplankton biomass and productivity, and affecting the pelagic food chain during the austral summer (Medlin & Pridlle 1990, El-Sayed & Fryxell 1993).

Navicula directa (Wm. Smith) Ralfs *in* Pritchard 1861 is less abundant than *N. glaciei*, but common in ice-algae and bottom samples from different sites of Antarctica and the Arctic (Cleve 1883, 1895, Mann 1925, Cleve-Euler 1953, Watanabe 1988, Kang et al. 1997b, Poulin & Cardinal 1982b), sometimes found in plankton samples (Heiden & Kolbe 1928, Hendey 1964). This bipolar species is easily recognizable due to its large size and conspicuous parallel striae on the valve face (Manguin 1960, Hendey 1964). Since its original description in 1853, the species has been regularly recorded in temperate to cold regions. Although papers dealing on its frustule morphology under light microscope are abundant (Cleve 1895, Van Heurck 1896, Peragallo & Peragallo 1897-1908, Cleve-Euler 1953, Frenguelli & Orlando 1958, Manguin 1960, Hendey 1964, Macchiavello 1972), electron microscopy studies are scarce in the modern literature (see review of Gaul et al. 1993). To date, we have found some scanning electronmicrographs taken by Wasell & Hakansson (1992, figures 89-93) that we believe refer to *N. directa*.

Navicula glaciei Van Heurck was first described by Van Heurck (1909) and, since then, has been regularly recorded in the literature as an abundant endemic diatom living in Antarctic ice habitats (Krebs 1983, Watanabe 1988, Kang et al. 1997a). However, despite its importance, the valve structure of this diatom was not further studied until the work of Whitaker & Richardson (1980). These authors investigated the biochemical composition of the cells, also providing a good account on the frustule morphology of *N. glaciei* under the scanning electron microscope, though some structures like cingulum and raphe system have remained to be further detailed.

This paper is the first of a taxonomic series designed to study benthic (epilithic and epiphytic) diatoms of the Antarctic region. In this report, *Navicula directa* and *N. glaciei* were examined under scanning electron microscopy in order to elucidate their valve structures. The variations in morphology of *N. glaciei* valves arising from the reduction after successive cell divisions were also investigated to complement the data given by Whitaker & Richardson (1980).

Material and methods

Field material was collected in 18 stations along the littoral shore of Admiralty Bay and Elephant Island in November/December 1994 (figure 1), during the XIII Brazilian Expedition to Antarctica (PROANTAR XIII). Samples were collected around Martel Cove at Admiralty Bay (62º05'S and 58º24'W), near the Antarctic Brazilian Station Comandante Ferraz (EACAF), from eulittoral and sublittoral regions by scrapping the substrate with a tooth-brush after collecting the rocks. Sublittoral samples were collected in 2 and 14 meters depth by SCUBA diving. Additional

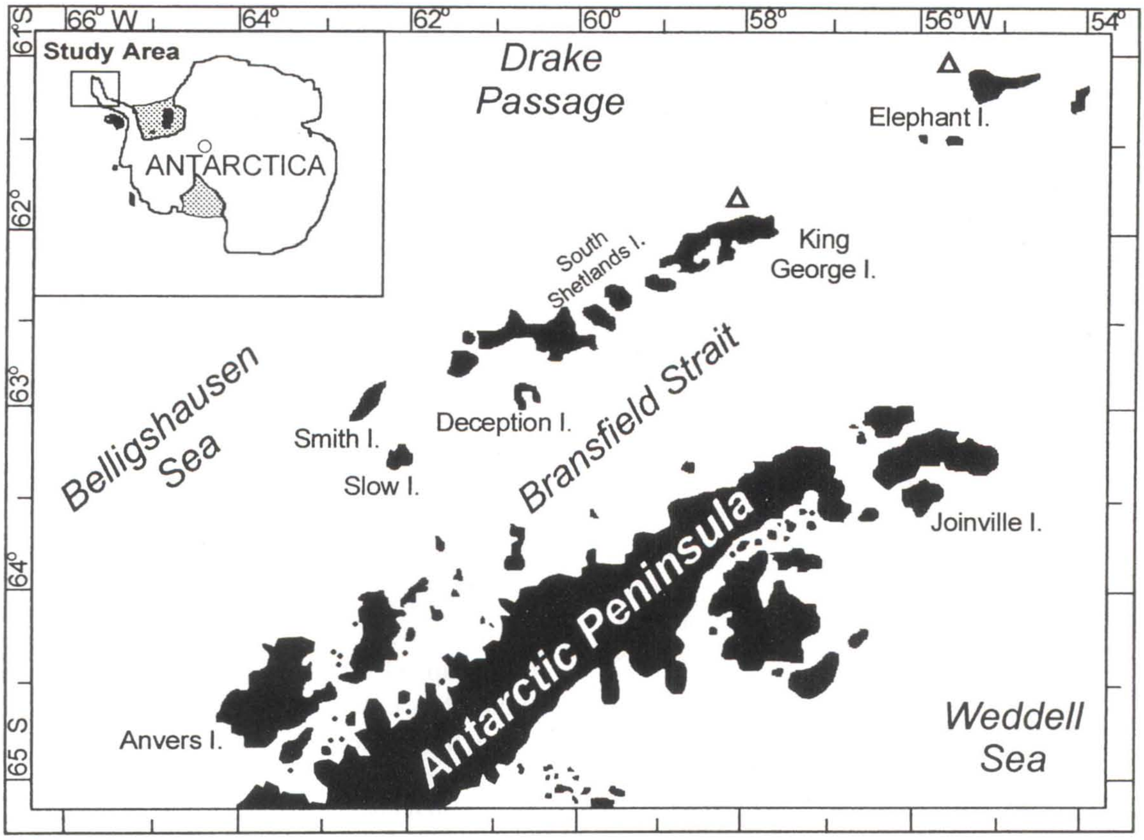


Figure 1. Map of the study area, showing the Antarctic Peninsula and the locations (Δ) where the samples were collected during the PROANTAR XIII, Nov/Dec 1994.

samples were also collected around Elephant Island (61º05'S and 55º20'W), from eulittoral and shallow sublittoral regions. Rocks were washed with filtered seawater and the resulting material was concentrated in flasks for preservation with formaldehyde until 1% final fixative concentration.The use of a small boat allowed the detailed coverage of the entire shore of Martel Cove in order to detect some eventual sharp development of epilithic diatoms.

Observations of valves under scanning electron microscopy (SEM) and light microscopy (LM) were performed after cleaning cells with conventional methods (Hasle & Fryxell 1970), and with Naphrax as the mounting medium for permanent glass slides. Samples were examined in a Phillips XL-30 electron microscope, housed at the Electron Microscopy Center/UFPR. Terminology followed Ross et al. (1979), Round et al. (1990) and Cox (1999).

Permanent slides are deposited at the Herbarium of Federal University of Paraná (UPCB) under the numbers UPCB-43995 to UPCB-44012.The slides where the species occurred are indicated following the species description, and their corresponding stations are described.

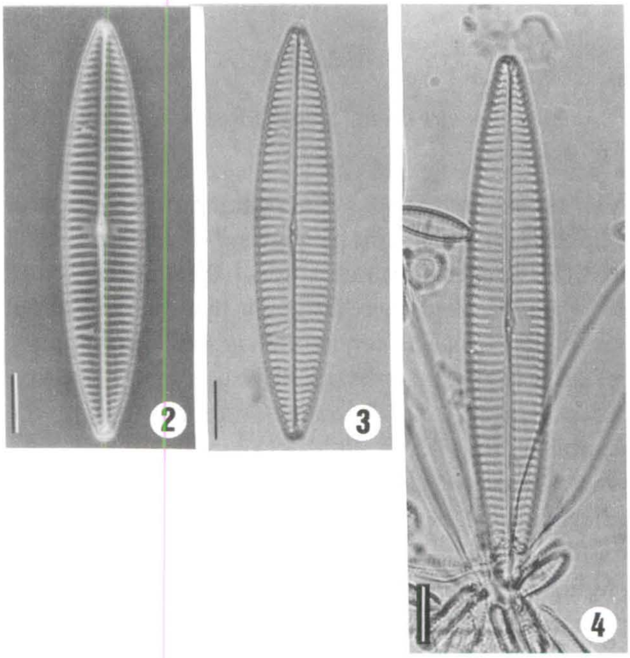
Results

Navicula directa (Wm. Smith) Ralfs *in* Pritchard
Figures 2-12

Valves are lanceolate with slightly rostrate apices (figures 2-4); 41-66 µm apical axis, 7-11 µm transapical axis. Striae clearly parallel, 8 in 10 µm, composed of elongate lineate pores occluded by hymenes in internal view (figure 6). The central area is small and circular, resulting from the shortening of the two central opposite striae (figures 2-5). The raphe system is straight; the central endings being slightly expanded (figures 2-4). On the primary side of the valve there is an accessory rib lying along the raphe sternum and born at the middle of the raphe branch, extending until the apices (figure 7). In this region, the raphe sternum of the primary side of the valve coarsely overlaps another one (figures 8-9). The helictoglossa is very pronounced and surrounded by two silica bridges arising from the valvar margin (figures 7-8). This arrangement leads to the formation of a space (or chamber) possessing a few apical areolae (figures 7-8). Externally, the central raphe endings are slightly expanded and turned to the same side of the valve (figures 2-4). The terminal endings are bent (not illustrated, but see Wasell & Hakansson, 1992). Internally, the central raphe endings are simple, not expanded (figure 6). Virgae are conspicuously thickened, leaving the areolae and vimines in depressions (figures 8-9). Cingulum not observed. Some valves (figures 10-12) resembling *N. directa* and that we have ascribed as *Navicula* sp. (*directa*?) show the raphe system modified when compared to the pattern described above. The silica bridges of the valvar edge (supporting the helictoglossae) are not fully developed (figure 11). The raphe sternum thickening at the primary side of the valve is more evident (figure 12) and its associated accessory rib (figure 11) is more conspicuous than in the valves described above. Moreover, the apices are subacute, not rounded as in *N. directa*.

References: Van Heurck 1896: 189, t. 25, figure 722; Peragallo & Peragallo 1897-1908: 91, t. 12, figure 6; Poulin & Cardinal 1982b: 2836-2837, figure 10.

Occurrence in the samples: Elephant Island, eulittoral or shallow sublittoral (UPCB-43995, UPCB-43996, UPCB-43998, UPCB-43999, UPCB-44005).



Figures 2-4. *Navicula directa*, LM. Scales = 10 µm.

Navicula glaciei Van Heurck
Figures 13-24

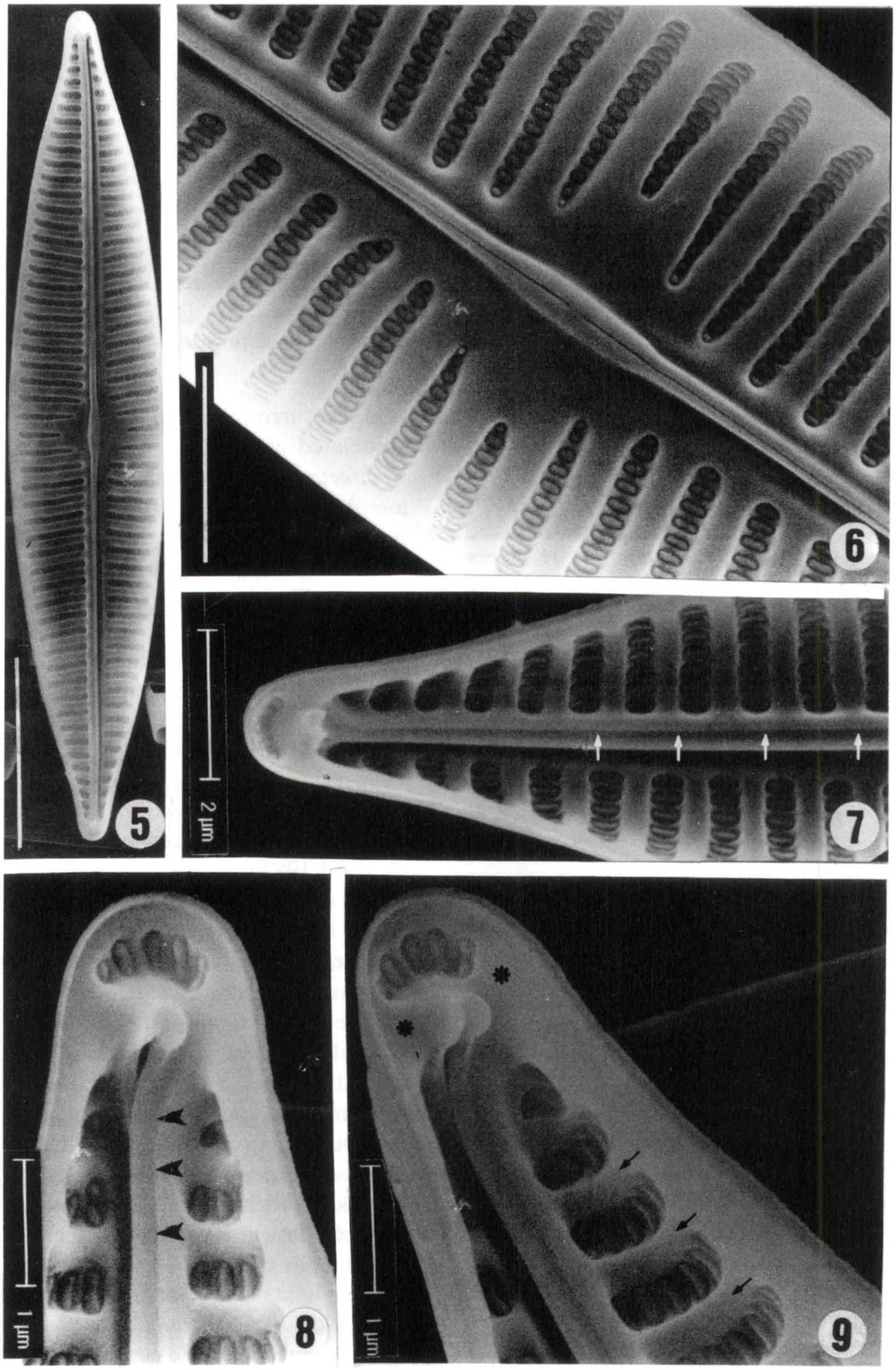
Valves lanceolate to elliptical (small forms) with rounded to slightly rostrate apices (figures 13-20); 6-27 µm apical axis, 3-7 µm transapical axis. The surface is areolated; areolae being elongate and poroidal, occluded by hymenes (not illustrated), and arranged in radiate striae (12-16 in 10 µm) (figures 13-16). In small valves, the striae show a tendency to become parallel near the center, besides having smaller number of striae (less than 8 in 10 µm, figures 19-20) and areolae. At the connection between the mantle and the valve face there is a continuous row of areolae (not illustrated), each one more elongated than those of the surface. The central area is quadrangular (smaller valves) or bow tie shaped (that is, expanded towards the margin), and it is interrupted near the margin by 1-2 shorter striae (figures 17-20). A single row of apical pores surrounds the terminal ending (figure 21). Externally, the raphe system is straight, having hooked terminal endings (figures 17, 21). The raphe sternum expands in a terminal area bordering the terminal ending (figure 21). Internally the central raphe endings are separated by the central nodule (figure 18). Near the pole, raphe sternum is projected to the primary side, in such a way the ending opens laterally (figure 22). Terminal endings are slightly bent and not expanded, bearing a helictoglossa (figure 22). A triangle-like terminal area borders the helictoglossa. The cingulum is composed by 1-2 bands (figure 23), each one complemented by a small U-shaped band (figures 23-24).

References: Van Heurck 1909: 11, t. 1, figure 13; Whittaker & Richardson 1980: 250-257, figures 4a-i; Poulin & Cardinal 1982b: 2830, figure 28; Watanabe 1988: 227-228, figures 16-17.

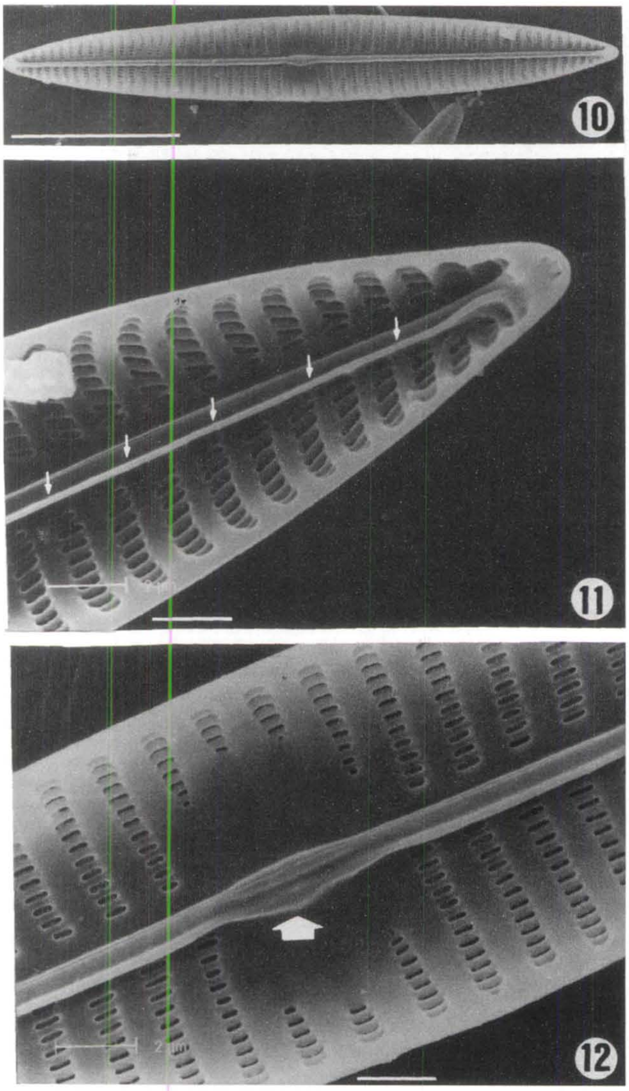
Occurrence in the Stations: Elephant Island, eulittoral or shallow sublittoral (UPCB-43995, UPCB-43996, UPCB-43998, UPCB-43999, UPCB-44005). Brazilian Antarctic Station EACAF, Martel Cove at Admiralty Bay, sublittoral 2 meters depth (UPCB-43997).

Discussion

Navicula directa fits well into the circumscription of *Navicula* Bory as recently proposed by Cox (1999), and it has two diagnostic characters: striae strongly parallel in all the valve face and a complex raised helictoglossa surrounded by two silica bridges arising

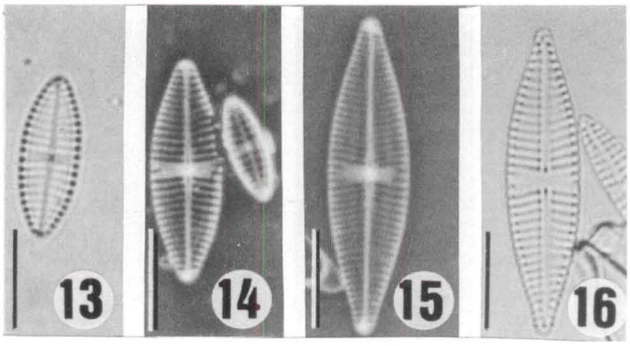


Figures 5-9. *Navicula directa*, SEM, internal views. 5. Whole valve showing parallel striae pattern. 6. Central region of valve, note central raphe endings and areolae occluded by hymenes. 7. Apex of valve, note accessory rib (arrows) on raphe sternum. 8. Apex of valve showing helictoglossa, note raphe sternum (arrowheads) on the primary side overlapping the raphe ending. 9. Same valve apex, tilt 30°, note silica bridges (indicated by *) supporting the helictoglossa and the chamber with a single row of areolae; virgae are evident (arrows), separating striae. Scales: figure 5 = 10 µm, figures 6, 8 and 9 = 1 µm, figure 7 = 2 µm.



Figures 10-12. *Navicula* sp. (*directa*?), SEM, internal views of modified raphe structure.10: Whole valve.11. Apex of valve illustrating accessory rib (arrows) on raphe sternum, note the helictoglossa and compare with figure 11. 12. Central region of valve showing thickening of raphe sternum (arrow). Scales: figure 10 = 20 µm, figure 11and 12 = 2 µm.

from the valvar edge. Such a structure is found in several species of *Navicula* (e.g., Cox 1977, Reichardt 1992) and in related genera of Naviculaceae Kützing emend. D.G. Mann such as *Pseudogomphonema* Medlin, *Rhoikoneis* Grunow and *Trachyneis* Cleve (Cox 1979, Round et al. 1990, Medlin 1991). Medlin (1991) even considered these genera as a phylogenetic group with close affinity, sharing the same areolae construction and a similar raphe system bearing the complex helictoglossae and the accessory rib along the raphe sternum. In *Donkinia* Ralfs *in* Pritchard, Family Pleurosigmataceae Mereschkowsky, the

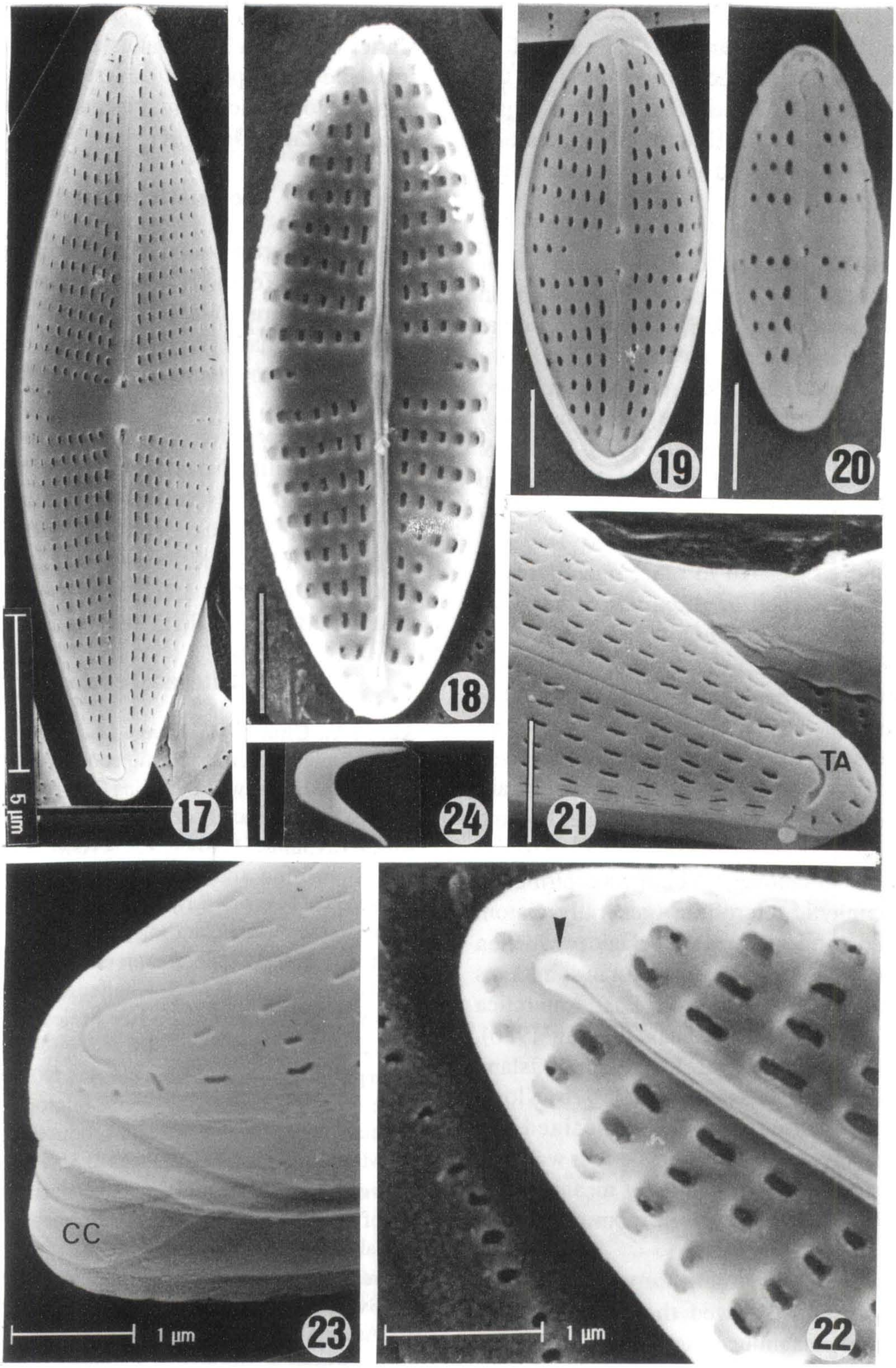


Figures 13-16. *Navicula glaciei*, LM, note very small valve at the right side of figure 14. Scales = 10 µm.

bridges surrounding the helictoglossa and the associated chambers are not so developed as in *N. directa*. In her comprehensive review on the valve morphology of *Navicula* Bory, Cox (1999) mentioned this is a structure rarely found in the genus, also illustrating (figure 87) the internal apex of *Navicula arenaria* Donkin, where the helictoglossa is not so complex as in *N. directa*.

In the literature, the dimensions of *N. directa* are quite variable, with apical axis oscillating from 40 to 200 µm, and the transapical axis from 7 to 18 µm, and with 4 to 11 striae in 10 µm (Castracane 1886, Cleve 1895, Van Heurck 1896, Peragallo & Peragallo 1897-1908, Cleve-Euler 1953, Frenguelli & Orlando 1958, Manguin 1960, form b, Hendey 1964, Poulin & Cardinal 1982b). We were not able to illustrate the details of external raphe endings of *N. directa* under SEM, although we were allowed to analyze the pictures and describe those structures. Wasell & Hakansson (1992) have also shown them in three pictures (their figures 91-93) named *Navicula* sp. Basically, the terminal endings are bent, approaching the valve apices, and the central ones are turned to the same side, each one with a pore-like structure.

Our SEM observations on the morphology of *Navicula glaciei* were coincident with those of Whitaker & Richardson (1980), but some further details on raphe structure were found such as the structure of the raphe endings and the cingulum. In addition, the size limits of the valves were expanded, and the morphological variations occurring as the cells diminish in size were reported. In general, striae gradually tend to become parallel, and the valve contour shows an elliptical shape. The central area changes from expanded towards the edge to almost quadrangular in shape, according to a progressive valve reduction. In the literature, *N. glaciei* varied from 15.6 to 28.0 µm



Figures 17-24. *Navicula glaciei*, SEM, external (figures 17, 19-21, 23-24) and internal views (figures 18, 22). 17. Large valve, note bow tie shaped central area and subrostrate apices. 18. Elliptical valve with rounded apices, note raphe ending interrupted at center. 19-20. Small valves bearing quadrangular central areas and smaller number of striae and areolae. 21. Valve apex illustrating hooked terminal endings surrounded by hyaline terminal area (TA); a single row of areolae is also present at the edges. 22. Valve apex showing helictoglossa (arrowhead), note triangular terminal area. 23. Apex of frustule showing bands of cingulum and a complementary copula (CC). 24. Complementary copula isolated. Scales: figure 17 = 5 µm, figures 18, 19, 20, 21 and 24 = 2 µm, figures 22 and 23 = 1 µm.

apical axis, 4.8 to 7.2 µm transapical axis and had 16 to 22 striae in 10 µm (Van Heurck 1909, Frenguelli & Orlando 1958, Whitaker & Richardson 1980). On the other hand, Poulin & Cardinal (1982b) found larger specimens in southwestern Hudson Bay, Canadian Arctic, their valves ranging from 29 to 42 µm apical axis, 7 to 13 µm transapical axis and 14 to 15 striae in 10 µm.

N. directa has been typically found in ice or bottom sediment habitats, sometimes in the plankton (Mann 1925, Cleve-Euler 1953, Poulin & Cardinal 1982b). *N. glaciei* has been recorded as exclusive from ice and frequently dominant, also being released into the water column during the ice melting in spring/summer (Whitaker 1977, Watanabe 1988, Tucker & Burton 1988, McMinn 1996, Kang et al. 1997a, b). In this work, however, *Navicula glaciei* was very abundant on rocks sampled in Admiralty Bay and Elephant Island, associated to other quantitatively important species, such as *Achnanthes brevipes* Agardh, *Parlibellus delognei* Cox and *Synedra* sp. (L.K. Procopiak & L.F. Fernandes, unpublished data). Such findings suggest that hard substrates are another true habitat occupied by *N. glaciei*, and not merely a contamination from the melted ice. One could even speculate that bottom rocks would be a relevant seeding source of living cells into the water column and then to the ice, during the seawater-freezing period in austral autumn. Moreover, the biomass contribution of epilithic/epiphytic microflora (generally diatom dominated) and its relevance to the pelagic production during summer was already pointed out in some sites of Antarctica, like Davis Station, East Antarctica (Everitt & Thomas 1986, Thomas & Jiang 1986), Maxwell Bay and Poter Cove, King George Island (Ahn et al. 1994, 1997, Kang et al. 1997b, Klöser 1998). These authors have hypothesized the mechanisms involved in inoculating the cells would be their transfer to the water column by means of cell resuspension through wind-driven mixing and tidal effects.

In the present work, visual observations of rocks from the study sites showed the existence of a brownish pellicle containing attached cells recovering the entire rock surface. Light microscope examination confirmed that most of the epilithic community was dominated by the diatoms *Navicula glaciei*, *Achnanthes brevipes*, *Synedra* sp., *Parlibellus delognei* and, in some sites, *Melosira* spp. Therefore, judging from the significant density of *Navicula glaciei* and other associated species recorded around Martel Cove and Elephant Island, we suspect they could be an important contributor for both the microphytobenthic community and the phytoplankton inhabiting the study region.

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Literature cited

Ahn, I.Y., Chung, H., Kang, J.S. & Kang, S.H. 1994. Preliminary studies on the ecology of neritic marine diatoms in Maxwell Bay, King George Island, Antarctica. The Korean Society of Phycology 9: 37-45.

Ahn, I.Y., Chung, H., Kang, J.S. & Kang, S.H. 1997. Diatom composition and biomass variability in nearshore waters of Maxwell Bay, Antarctica, during the 1992/1993 austral summer. Polar Biology 17: 123-130.

Castracane, C.A. 1886. Report on the scientific results of the Voyage of H.M.S. Challenger during the years 1873-76; Botany, v. II, Her Majesty's Government, London, 178 p.

Charpy-Roubaud, C. & Sournia, A. 1990. The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans. Marine Microbial Food Webs 4: 31-57.

Cleve, P.T. 1883. Diatoms collected during the expedition of the "Veja". Ur Vega-Expeditionens ventenskapliga iakttageler, Stockholm, pp. 455-525.

Cleve, P.T. 1895. Synopsis of the naviculoid diatoms. Konglica Svenska Vetenskapsakademiens Handlinglar. Reprint A. Asher & Co., Amsterdam, v. 27, pp. 1-223, t. I-IV.

Cleve-Euler, A. 1953. Die Diatomeen von Schweden und Finland. Teil III. Monoraphideae, Biraphideae 1. Konglica Svenska Vetenskapsakademiens Handlinglar, v. 4, pp. 1-255.

Cox, E.J. 1977. Raphe structure in naviculoid diatoms as revealed by the scanning electron microscope. Nova Hedwigia 54: 261-274.

Cox, E.J. 1979. Symmetry and valve structure in naviculoid diatoms. Nova Hedwigia 64: 193-206.

Cox, E.J. 1999. Studies on the diatom genus *Navicula* Bory. VIII. Variation in the valve morphology in relation to the generic diagnosis based on *Navicula tripunctata* (O.F. Müller) Bory. Diatom Research 14: 207-237.

El-Sayed, S.Z. & Fryxell, G.A. 1993. Phytoplankton. In: E.I. Friedmann (ed.). Antarctic Microbiology, Wiley-Liss Inc., New York, pp. 65-122.

Everitt, D.A. & Thomas, D.P. 1986. Observations of seasonal changes in diatoms at inshore localities near Davis Station, East Antarctica. Hidrobiologia 139: 3-12.

Frenguelli, J. & Orlando, H.A. 1958. Diatomeas y silicoflagelados del sector Antártico Sudamericano. Instituto Antártico Argentino, Buenos Aires, Publicación 5, 191 p.

Gilbert, N.S. 1991. Microphytobenthic seasonality in near-shore marine sediments at Signy Island, South Orkney Islands, Antarctica. Estuarine, Coastal and Shelf Science 33: 89-104.

Gaul, U., Geissler, U., Henderson, M., Mahoney, R. & Reimer, C.W. 1993. Bibliography on the fine-structure of diatom frustules (Bacillariophyceae). Proceedings of the Academy of Natural Sciences of Philadelphia 144: 69-283.

Hasle, G.R. & Fryxell, G.A. 1970. Diatoms: cleaning and mounting for light and electron microscope. Transactions of American Microscopical Society 89: 469-474.

Heiden, H. & Kolbe, R. W. 1928. Die marinen Diatomeen der deutschen Südpolar-Expedition 1901-1903. In: Deutsche Südpolar-Expedition, Erich von Gruyter & Co., Berlin, 8 (Heft V), pp. 450-715.

Hendey, N.I. 1964. An introductory account of the smaller algae of British coastal waters. 5: Bacillariophyceae (diatoms). Fishery investigations - Series IV. Her Majesty's Stationery Office, London, 317 p.

Kang, J.S., Kang, S.H., Lee, J.H., Chung, K.H. & Lee, M.Y. 1997a. Antarctic micro- and nano-sized phytoplankton assemblages in the surface water of Maxwell Bay during the 1997 austral summer. Korean Journal of Polar Research 8: 35-45.

Kang, S.H, Kang, J.S., Chung, K.H., Lee, M.Y., Lee, B.Y., Chung, H., Kim, Y. & Kim, D.Y. 1997b. Seasonal variation of nearshore Antarctic microalgae and environmental factors in Marian Cove, King George Island, 1996. Korean Journal of Polar Research 8: 9-27.

Karsten, G. 1906. Das phytoplankton des Antarktischen Meeres nach dem Material der deutschen Tiefsee-Expedition 1898-1899. In: C. Chun (ed.). Wissenschaftiliche Ergebnise der deutschen Tiefsee - Expedition auf dem Dampfer "Valdivia" 1898-1899, Frommannsche Buchdruckerei, Jena, Band II, Teil II, pp. 1-136.

Klöser, H. 1998. Habitats and distribution patterns of benthic diatoms in Potter Cove (King George Island, Antarctica) and its vicinity. Berichte zur Polarforschung 299: 95-105.

Knox, G.A. 1994. The biology of the Southern Ocean. Cambridge University Press, London, pp. 193-220.

Krebs, W.N. 1983. Ecology of marine neritic diatoms, Arthur Harbor, Antarctica. Micropaleontology 29: 267-297.

Ligowski, R. 2000. Benthic feeding by krill, *Euphausia superba* Dana, in coastal waters off west Antarctica and in Admiralty Bay, South Shetland Islands. Polar Biology 23: 619-625.

Macchiavello, J.C.M. 1972. Estudio diatomologico del Mar de la Flota, de Puerto Paraíso y observaciones en el Mar de Bellingshausen. In: Contribución del Instituto Antártico Argentino, Directorio Nacional del Antártico, Buenos Aires, v. 155, pp. 1-105.

Mangin, L. 1915. Phytoplankton de l'Antarctique, "Expedition du Porquoi pas?" In: Deuxième Expedition Antarctique Française (1908-1910), commandée par le Dr. Jean Charcot, Paris, 95 p.

Manguin, E. 1960. Les diatomées de la Terre Adélie campagne du "Comandant Charcot" 1949-1950. Annales des Sciences Naturales, Botanique et Biologie Végétale 12: 223-363.

Mann, A. 1925. Marine diatoms of the Canadian Arctic expedition, 1913-18. In: Report of the Canadian Arctic expedition 1913-18, F.A. Acland, Ottawa, v. IV: Botany, part F: marine diatoms, 33 p.

Mann, A. 1937. Diatoms. Australasian Antarctic Expedition 1911-14, Scientific Reports. v. 1, pp. 1-82.

McIntire, C.D. & Moore, W.M. 1977. Marine littoral diatoms - Ecological considerations. In: D.W. Werner (ed.). The biology of diatoms. Botanical Monographs, v. 13. University of California Press, Berkeley, pp. 333-371.

McMinn, A. 1996. Preliminary investigation of the contribution of fast ice algae to the spring phytoplankton bloom in Ellis Fjord, eastern Antarctica. Polar Biology 16: 301-307.

Medlin, L.K. 1991. Evidence for parallel evolution of frustule shape in two lines of pennate diatoms from the epiphyton. Diatom Research 6: 109-124.

Medlin, L.K. & Priddle, J. 1990. Polar marine diatoms. British Antarctic Survey/NERC, London, 214 p.

Peragallo, H. & Peragallo, M. 1897-1908. Diatomées marines des France et des districts maritimes voisins. M. J. Tempére, Grez-sur-Loing, Paris, 493 p. and Atlas.

Peragallo, M. 1921. Diatomées d'eau douce et Diatomées d'eau salée. In: Deuxième Expédition Antarctic Française (1908-1910), commandée par Dr. J. Charcot, Masson et Cie. Éditeurs, Paris, pp. 1-98.

Poulin, M. & Cardinal, A. 1982a. Sea ice diatoms from Manitounuk Sound, southeastern Hudson Bay (Quebéc, Canada). I. Family Naviculaceae. Canadian Journal of Botany 60: 1263-1278.

Poulin, M. & Cardinal, A. 1982b. Sea ice diatoms from Manitounuk Sound, southeastern Hudson Bay (Quebéc, Canada). II. Naviculaceae, genus *Navicula*. Canadian Journal of Botany 60: 2825-2845.

Reichardt, E. 1992. *Navicula jakovljevicii* Hust. (Bacillariophyceae) Morphologie und taxonomische überlegungen. Diatom Research 7: 293-301.

Ross, R., Cox, E.J., Karayeva, N.I., Mann, D.G., Paddock, T.B.B., Simonsen, R. & Sims, P.A. 1979. An amended terminology for the siliceous components of the diatom cell. Beiheft Nova Hedwigia 64: 513-533.

Round, F.E., Crawford, R.M. & Mann, D.G. 1990. The diatoms. Biology and morphology of the genera. Cambridge University Press, Cambridge, 747 p.

Thomas, D.P. & Jiang, J.L. 1986. Epiphytic diatoms of the inshore area near Davis station. Hydrobiologia 140: 193-198.

Tucker, M.J. & Burton, H.R. 1988. The inshore marine ecosystem off Vestfold Hills, Antarctica. Hydrobiologia 165: 129-139.

Underwood, G.J.C. 1994. Seasonal and spatial variation in epipelic diatom assemblages in the Severn estuary. Diatom Research 9: 451-472.

Van Heurck, H. 1896. A treatise on Diatomaceae. Wm. Wesley & Son, London, 558 p.

Van Heurck, H. 1909. Diatomées. Resultats du voyage du S.Y. "Belgica" en 1897-1899 sous le commandetement de A. de Gerlache du Gomery. In: Rapports Scientifiques: Botaniques, Expedition Antarctique Belgique, J.E. Buschmann, Anvers, v. 5, pp. 1-129.

Wasell, A. W. & Hakansson, H. 1992. Diatom stratigraphy in a lake on Horseshoe Island, Antarctica: a marine-brackish-fresh water transition with comments on the systematics and ecology of the most common diatoms. Diatom Research 7: 157-194.

Watanabe, K. 1988. Sub-ice microalgal strands in the Antarctic coastal fast ice near Syowa station. The Japanese Journal of Phycology 36: 221-229.

Whitaker, T.M. 1977. Sea ice habitats of Signy Island (South Orkneys) and their primary productivity. In: G.A. Llano (ed.). Adaptations within Antarctic ecosystems. Proceedings of the 3rd SCAR Symposium on Antarctic Biology, Washington, D.C. Smithsonian Institute, Washington, pp. 75-82.

Whitaker, T.M. & Richardson, S. 1980. Morphology and chemical composition of a natural population of an ice-associated antarctic diatom *Navicula glacei.* Journal of Phycology 16: 250-257.

White, D.C., Smith, G.A., Guckert, J.B. & Nichols, P.D. 1993. Nearshore benthic marine sediments. In: E.I. Friedmann (ed.). Antarctic Microbiology. Wiley-Liss Inc., New York, pp. 219-240.