

CELL WALL MORPHOLOGY AND SYSTEMATIC IMPORTANCE OF *THALASSIOSIRA RITSCHERI* (HUSTEDT) HASLE, WITH A DESCRIPTION OF *SHIONODISCUS* GEN. NOV.

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The centric diatom order Thalassiosirales includes all diatoms with a fulloportula (strutted process), a feature now recognized as a synapomorphy for the lineage. Within Thalassiosirales, *Thalassiosira* is perhaps the most taxonomically and morphologically diverse genus, and at least two distinct morphological groups have been recognized within it. Group “A” *Thalassiosira* species, which include the type species, *T. nordenskioldii*, have short inward and long outward extensions of the strutted processes and a labiate process on the valve mantle. Group “B” species have exceptionally long inward and reduced outward extensions of the strutted processes, and a labiate process on the valve face. We collected and cultured *Thalassiosira ritscheri*, which has a combination of group A and B characters. It has a labiate process on the valve face and reduced outward extensions of the strutted processes. We show for the first time that *T. ritscheri* has short inward, A-type extensions of the strutted processes. A phylogenetic interpretation of these conditions suggests a close relationship between *T. ritscheri* and the traditionally held group “B” species. Species diagnosed by the autapomorphic condition of a labiate process away from the valve mantle, including many group “B” *Thalassiosira* species, are transferred into *Shionodiscus* gen. nov.

INTRODUCTION

The centric diatom order Thalassiosirales includes all diatoms with a fulloportula (strutted process, SP), a feature now recognized as a synapomorphy for the lineage (Theriot & Serreyssol 1994). This interpretation is congruent with phylogenetic analysis of SSU rDNA data (Medlin & Kaczmarska 2004). Thalassiosirid diatoms are among the most abundant and diverse diatoms in the plankton of large rivers and reservoirs, freshwater lakes, brackish and estuarine waters, nearshore marine waters, and open ocean habitats (Hasle & Syvertsen 1997, Stoermer & Julius 2003). With nearly 400 names, *Thalassiosira* is one of the most taxonomically diverse genera within Thalassiosirales (according to the computerized database of verified diatom names at the California Academy of Sciences, E. Fourtanier and J.P. Kociolek, pers. comm.), and not surprisingly, it is among the most morphologically diverse genera as well. With few exceptions (Theriot *et al.* 1987), the generic level classification of Thalassiosirales is phenetic, a fact which has been verified consistently by phylogenetic analysis of SSU rDNA sequence data (most recently by Medlin & Kaczmarska 2004). Consistent with phylogenetic results, morphological data further suggest that no single character or combination of characters can be interpreted as derived and therefore indicative of monophyly of *Thalassiosira* (Theriot & Serreyssol 1994, Hasle & Syvertsen 1997).

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At least two distinct morphological groups have been recognized within *Thalassiosira* on the basis of SP ultrastructure and location of the rimoportula (labiate process, LP) (Hasle 1968, Hasle & Syvertsen 1997). One group (group "A", Hasle 1968, Hasle & Syvertsen 1997) has morphological features most similar to the type species, *T. nordenskiöldii* Cleve. Most species in this group have short inward and long outward extensions of the SP's, and an LP on the valve mantle (Hasle 1968, Hasle & Syvertsen 1997). A second group (group "B", Hasle 1968, Hasle & Syvertsen 1997) has exceptionally long inward and little or no outward extensions of the SP's, and an LP on the valve face (Hasle 1968, Fryxell & Hasle 1979a, Hasle & Syvertsen 1997, Shiono & Koizumi 2000). This group also has been referred to informally as the "*T. trifulta* group" (Shiono & Koizumi 2000).

We collected and cultured one species, *Thalassiosira ritscheri* (Hustedt) Hasle, which appears to have a combination of group A and B characters. *Thalassiosira ritscheri* has an LP on the valve face and reduced outward extensions of the SP's, but little if anything is known about the inward extensions of the SP's in this species (Hasle & Heimdal 1970, Johansen & Fryxell 1985, Hasle & Syvertsen 1997). Existing photographs of *T. ritscheri* are either equivocal or suggestive of A-type SP morphology (Hasle & Heimdal 1970, Johansen & Fryxell 1985). In any case, the position of the LP and reduced outward extensions of the SP's suggest a possible relationship of *T. ritscheri* with group B *Thalassiosira* species. The purpose of our study was to thoroughly document the cell wall morphology of *T. ritscheri* and to interpret its features in a phylogenetic framework, with particular reference to the group A and B classification. Finally, we propose the transfer of *T. ritscheri* and many group B *Thalassiosira* species into a new genus, *Shionodiscus* gen. nov.

MATERIALS AND METHODS

During the 18th Korean Antarctic Program (KARP) expedition, data on surface hydrography and phytoplankton (including chlorophyll *a*, quantitative and qualitative data on community assemblages) were acquired at 31 stations around the South Shetland Islands and northwestern Weddell Sea from 19 December 2004 to 2 January 2005. Surface temperature and salinity were measured at each station. Water samples were collected on the "up" casts with a Seabird rosette unit equipped with 2-liter PVC Niskin bottles. Samples for quantitative phytoplankton analyses were fixed and filtered onboard R/V Yuhzorgoologiya. Aliquots of 250 ml of discrete water samples were preserved with 25% glutaraldehyde (final concentration 1% of total volume). Phytoplankton were enumerated according to the HPMA method (Kang & Fryxell 1991). Chlorophyll *a* concentrations were measured with a Turner Design field fluorometer (TD 700). Phytoplankton net samples were collected with vertical net tows (20 µm mesh) from 100 m to surface at each station. From this sample, one aliquot was used to isolate live cells for culture, and the remaining sample was preserved with 25% glutaraldehyde (2% final concentration by volume). The culture of *T. ritscheri* used in this study was isolated from a sample taken at station LC01 (60.0023°S, 52.2554°W).

Cells were isolated under a dissecting microscope with a Pasteur pipette drawn out over a flame to a small (ca. 100 µm) diameter tip. Cells were rinsed at least twice in sterile f/2 medium (Guillard & Ryther 1962, Guillard 1975) before transfer into a culture tube with sterile f/2 medium. Cells were grown at 4°C on a 16:8 light-dark cycle, harvested during exponential growth, and rinsed with distilled water several times. Rinsed cells were dried onto a coverglass and mounted onto a microscope slide with Naphrax or filtered onto a 0.22 µm nitrocellulose filter, which then was dried and prepared for observation with a field emission scanning electron microscope (FE-SEM). Another aliquot of rinsed cells was boiled in 30% hydrogen peroxide for one hour, and then rinsed several times before preparation for FE-SEM

observation. Light microscope observations were made with a Zeiss Axioskop, and FE-SEM observations were made with a Hitachi S-4500 FE-SEM.

RESULTS

Hydrography and phytoplankton biomass

Mean temperature, salinity, and total chl-*a* concentration during the whole cruise period were 1.71°C, 33.97 psu, and 0.92 mg chl-*a*-m⁻³, respectively. Dominant phytoplankton were nano-sized (<20 µm) phytoflagellates (e.g. *Phaeocystis antarctica* Karsten [motile stage], *Cryptomonas* spp., *Gymnodinium* spp., and *Pyramimonas* spp.) and small diatoms (e.g. *Minidiscus chilensis* Rivera, *Fragilariopsis pseudonana* (Hasle) Hasle, and *F. cylindrus* (Grunow) Krieger). Nanoplanktonic phytoplankton accounted for greater than 89% of total chl-*a* concentration. Mean chl-*a* concentration of the micro-sized phytoplankton (>20 µm) such as *Thalassiosira* spp. accounted for 11% of the total chl *a*.

Light microscope observations of Thalassiosira ritscheri

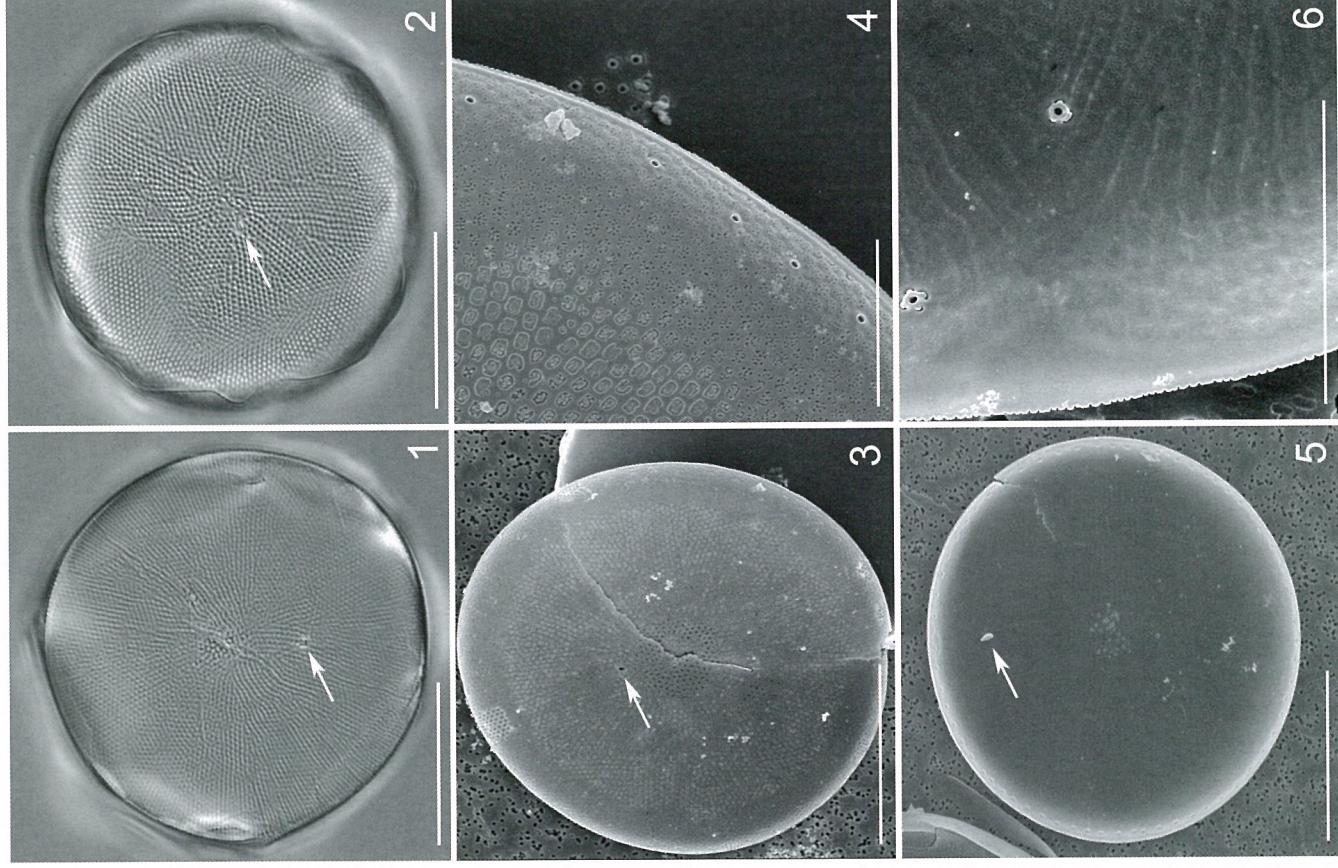
Cells are approximately 44–48 µm in diameter (Figs 1, 2), which is at the lower end of the size range of naturally occurring populations (Johansen & Fryxell 1985). Areolae, approximately 15 in 10 µm, occur in fascicles. Areolar size and density are uniform across the valve face (Figs 1, 2). A central cluster of SP's is evident, though difficult to discern in most specimens (Figs 1, 2). The prominent LP is radially oriented, and its position on the valve face varies from subcentral (adjacent to the central cluster of SP's; Fig. 2) to midway between the center and valve margin (Fig. 2). Mantle SP's are difficult to resolve in the light microscope. Inability to resolve prominent inward extensions in the light microscope (e.g. Figs 51a, 60a, 67a, and 68a in Johansen & Fryxell 1985) would suggest that *T. ritscheri* has short inward (A-type) extensions of the SP's.

FE-SEM observations

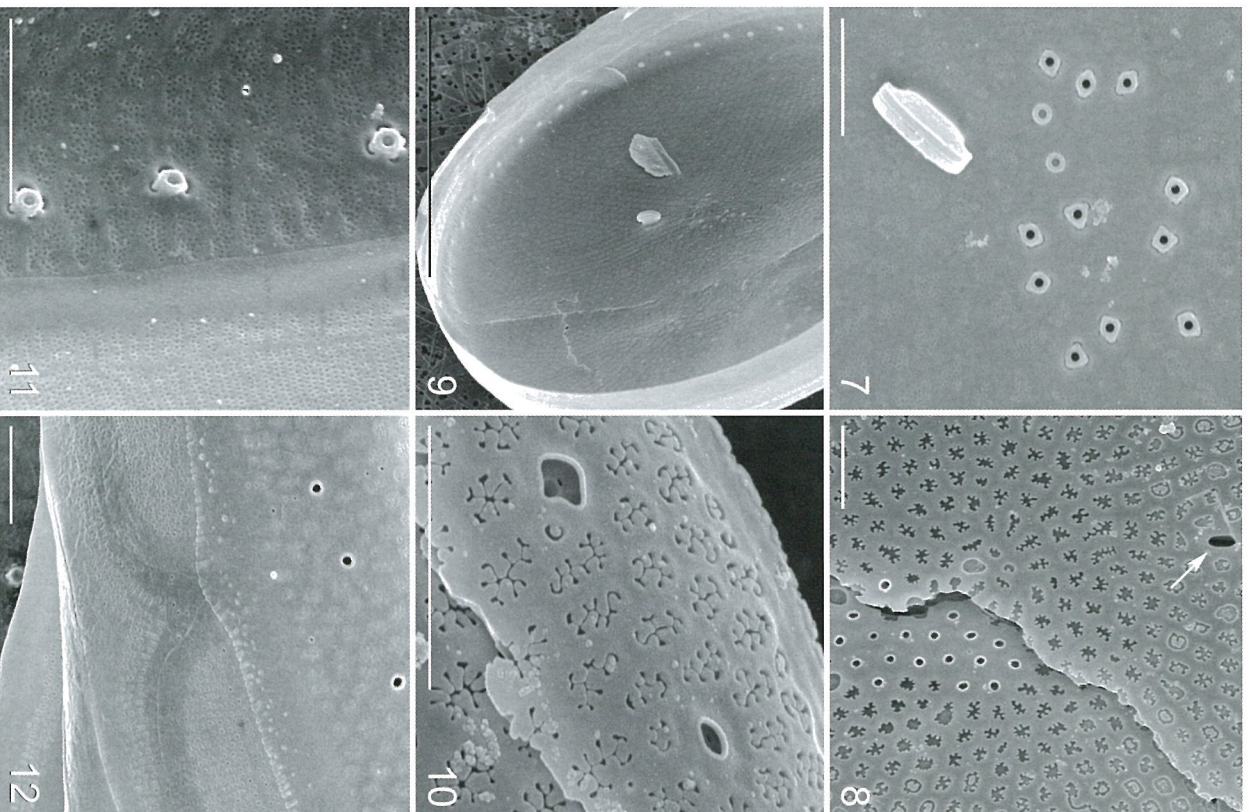
External foramina are partially occluded by irregular, sometimes fingerlike projections (Figs 3, 4). Internally, cribra appear as flat, undifferentiated pore fields (Figs 5, 6).

As indicated previously (Johansen & Fryxell 1985, Hasle & Syvertsen 1997), *T. ritscheri* has a central cluster of SP's, which range in number from approximately 10–30 in our culture specimens (Figs 5, 7, 8). Some specimens had a few SP's scattered on the valve face. Central area SP's are surrounded externally by a hyaline area (Fig. 8), and the outward extension is little more than a slightly raised rim (Fig. 8). Internally, central area SP's are operculate with short, A-type extensions (Fig. 7). Central area SP's have 2–4 satellite pores, each type equally common in our culture specimens (Fig. 7). Opercula are small, rounded tabs located immediately above the satellite pores (Fig. 7). Satellite pores are surrounded by small, sometimes slightly raised cowlings (Fig. 7). FE-SEM observations confirm that *T. ritscheri* has a single ring of SP's on the valve mantle (Figs 3–5, 9). Outward extensions of the mantle SP's consist of slightly raised rims, similar to the valve-face SP's (Figs 4, 10). Mantle SP's have four satellite pores, very rarely three (Figs 6, 11).

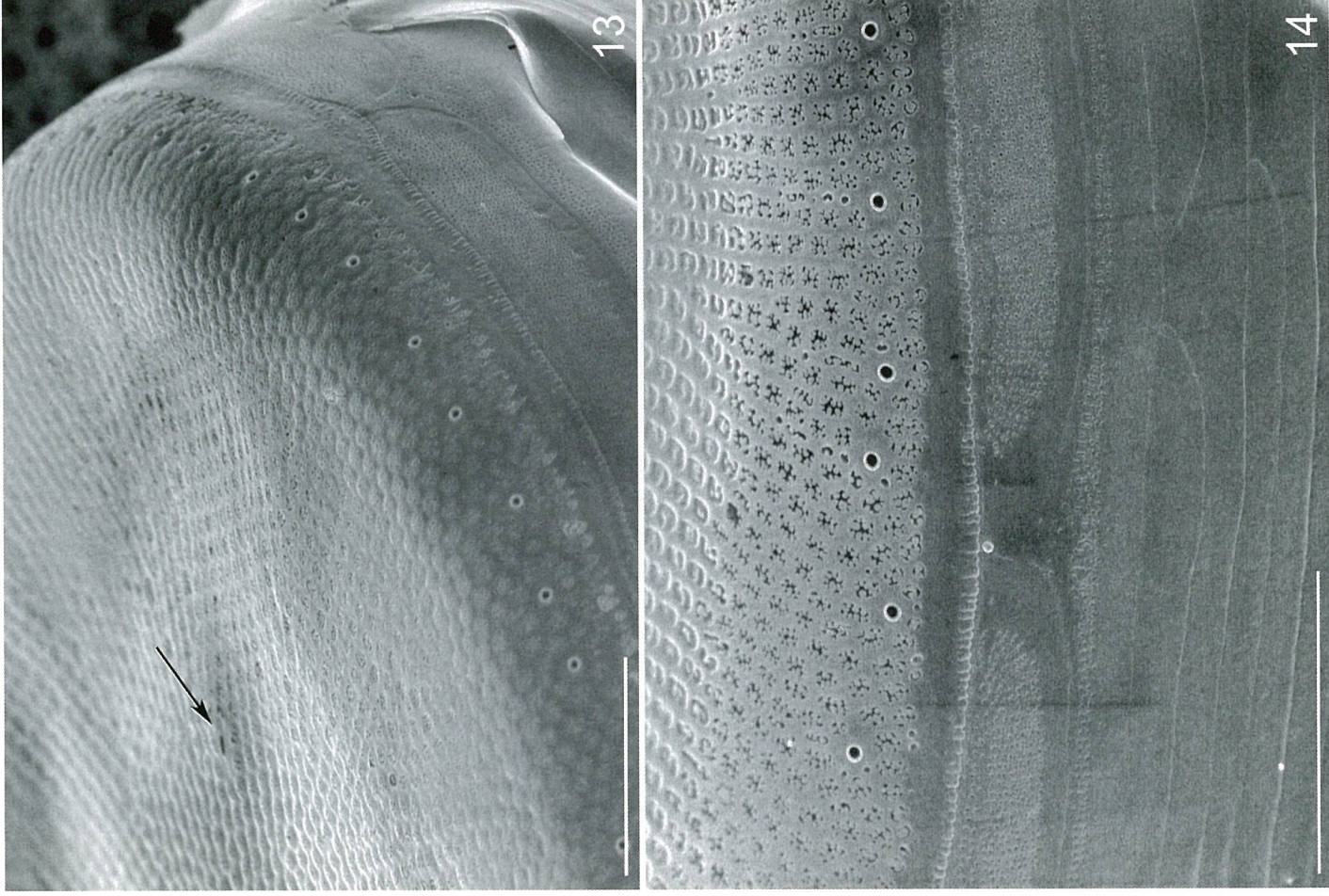
The LP is radially oriented and on a short stalk (Figs 5, 7, 9). Externally, the LP appears as a radially oriented, slit-like aperture between the valve center and margin (Figs 3, 8). The girdle bands are discontinuous (open), and the valve bears a prominent antingula at the first girdle band opening (Fig. 12). The first girdle band opening is located on the side of valve bearing the LP (Fig. 13). Subsequent girdle bands are right-hand spiraled. The first two girdle bands have multiple rows of simple, round pores, and the remaining bands are imperforated pleurae (Figs 12–14).



Figs 1–6. Cell wall morphology of *Thalassiosira ritischeri* with light microscopy (Figs 1, 2) and field emission microscopy (Figs 3–6). Arrows indicate the position of the labiate process. **Figs 1, 2.** Light micrographs showing the variable position of the labiate process on the valve face. **Fig. 3.** External view of valve. **Fig. 4.** External view of valve margin showing areolar structure and reduced outward openings of the mantle strutted processes. **Fig. 5.** Internal view of valve. **Fig. 6.** Internal view of valve margin showing flat cribra arranged in fascicles, a mantle strutted process, and a strutted process on the valve face. Scale bars = 20 μm (Figs 1–3, 5); 5 μm (Figs 4, 6).



Figs 7–12. Field emission micrographs of *Thalassiosira ritscheri*. **Fig. 7.** Internal view of the central cluster of strutted processes and adjacent labiate process. **Fig. 8.** External view of the central cluster of strutted processes surrounded by hyaline area. The arrow indicates the outward opening of the labiate process. **Fig. 9.** Internal view of valve showing single ring of mantle strutted processes. **Fig. 10.** External view of mantle strutted process openings, which consist of a slightly raised rim. The rim is not fully formed on the leftmost strutted process, exposing at least one satellite pore. **Fig. 11.** Internal view of mantle strutted processes with three or four satellite pores. **Fig. 12.** External view of valvar antiligula, first girdle-band opening, and ligula of the second girdle band. The first two girdle bands are perforated by several rows of regularly spaced, subcircular pores. Scale bars = 2 μm (Figs 7, 8, 10–12); 20 μm (Fig. 9).



Figs 13, 14. Field emission micrographs of *Thalassiosira ritscheri*. **Fig. 13.** External view showing the relative position of the first girdle band opening to the labiate process (arrow). **Fig. 14.** External view showing right-hand spiral orientation of consecutive girdle bands. The first two girdle bands bear several rows of pores, whereas subsequent bands are imperforated. Scale bar = 5 μm .

DISCUSSION

Thalassiosira ritscheri is the only described species in Thalassiosirales that we know of with this combination of characters: fasciculate striae, a LP on the valve face, one marginal ring, and one central cluster of SPs that are A-type inwardly and B-type outwardly. The position of the LP on the valve face and the reduced outward extensions of the SPs suggest a close relationship to group B *Thalassiosira* species, which are further characterized by exceptionally long inward extensions of the SPs. Until now, the internal ultrastructure of the SPs in *T. ritscheri* was undocumented, and our observations clearly indicate that they are A-type, with short, "normal" sized inward tubes and satellite pores covered by tabular opercula. The fossil diatoms *T. bipora* Shiono and *T. depressa* Shiono appear to be close relatives of *T. ritscheri*. All three species have an LP on the valve face, short (A-type) SPs internally, and reduced (B-type) SP extensions externally. *Thalassiosira baldanffi* Bodén has a central SP cluster and an LP away from the mantle and so might also be a close relative of *T. ritscheri*, with a few important differences. *Thalassiosira baldanffi* has regularly spaced occluded processes (Bodén 1993), which are absent in *T. ritscheri*. Also, the LP in *T. baldanffi* is located at the junction of the valve face and mantle, not on the valve face.

Although possession of a central SP cluster is common among taxa with an LP on the valve mantle (e.g. *T. rotula* Meunier and *T. antarctica* Comber), *T. ritscheri* is the only described species we are aware of with both a central SP cluster and an LP decidedly on the valve face (Hasle & Syvertsen 1997). Several group B taxa have multiple central SPs, which are typically organized into a modified ring (*T. endoseriata* Hasle and G. Fryxell and *T. poro-irregularata* Hasle and Heimdal) or one or more distinct rows (*T. trifulla* G. Fryxell and *T. poroseriata* (Ramsfjell) Hasle).

At first glance, the unique combination of characters in *T. ritscheri* suggests incongruence with the A–B classification of *Thalassiosira* species. Presence of fasciculate striae and short inward extensions of the SPs ally *T. ritscheri* with group A species. An LP on the valve face and reduced outward extensions of the SPs, however, suggest a close relationship to group B species. This appearance of incongruence might simply reflect the fact that the original A–B classification did not distinguish between phylogenetically ancestral (plesiomorphic) and derived (apomorphic) character states.

Evidence from phylogenetic analysis of SSU rDNA sequences suggests that *Lauderia* and *Porosira* are the sister clade to the remaining Thalassiosirales. These taxa typically have a labiate process within or near the mantle and operculate SPs with short inward extensions. These features are common to most *Thalassiosira*, including the type species, *T. nordenskiöldii*. This evidence suggests that A-type features are plesiomorphic and B-type are apomorphic, including the LP location well onto the valve face. The combination of plesiomorphic and apomorphic characters in *T. ritscheri* is consistent with the interpretation of it being the sister species to a clade of the traditionally held group B species. That is, the valve-face LP would diagnose a clade of *T. ritscheri* and all group B species. Within this large clade of *Thalassiosira* species that have an LP on the valve face is a sub-clade of the traditionally held group B species diagnosed by exceptionally long inward extensions of the SPs. Operculate SPs with short inward extensions place *T. ritscheri* at the base of the group B clade. Trifulate SPs are further interpreted as apomorphic relative to operculate strutted processes, which suggests that "trifulate" species (e.g. *T. ostrupii* and *T. trifulta*) form an even less inclusive clade within group B. This interpretation is consistent with the fossil record, as elegantly demonstrated by Shiono (2001), who proposed that the trifulate SP is derived relative to the operculate SP, on the basis of stratigraphic superposition.

Although most group B species fit this hypothesis well, the character combinations present in some species suggest true conflict from a phylogenetic perspective. For example, *T. confusa* Makarova has reduced outward SP extensions and long, trifulate-type inward SP

extensions, but it has a LP located at the edge of the valve face rather than towards the center. The two SP characters (long inward extension and trifoliate structure) suggest that the single feature of the LP position near the valve face–mantle junction is a phylogenetic reversal. Thus, *T. confusa* is most parsimoniously placed with other group B species.

Phylogenetic interpretations of character states used for classification of *Thalassiosira* species are generally consistent with stratigraphic studies of the genus (Shiono & Koizumi 2001). We believe this body of evidence is sufficient to warrant raising the group B *Thalassiosira* species to generic status, and we therefore propose a new genus, *Shionodiscus* gen. nov., to include *Thalassiosira* species with the autapomorphic conditions of a LP on the valve face, SP's with longer extensions inwards (including but not limited to species with trifoliate strutted processes), and reduced or absent outward extensions of the SP's.

Diagnosis

Order: Thalassiosirales Glezer & Makarova 1986

Family: Thalassiosiraceae Glezer & Makarova 1986

Shionodiscus Alverson, Kang et Theriot, gen. nov.

Thalassiosira Cleve affine, a quo rimoportula semper semota a margine, typice in facie valvae, aliquando ad oram faciei; fuloportulis typice extensionibus intrisecis longis et semper extensionibus extrinsicis parvis aut absentibus.

Akin to *Thalassiosira* Cleve, from which it differs by the labiate process always being distant from the margin, typically on the valve face, sometimes at the edge of the face; with strutted processes typically with long inward extensions and always with outward extensions reduced or absent.

Etymology: *Shionodiscus* is named in honour of Dr Masamichi Shiono, whose efforts have contributed greatly to our understanding of the stratigraphic history and evolution of this group of diatoms.

Typus generis: *Shionodiscus oestrupii* (Ostenfeld) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Coscinosira oestrupii* Ostenfeld 1900. *Iagttagelser over Overfladevandets Temperatur, Saltholdighet og Plankton paa islandke og grønlandske Skibsrouter i 1899*: p. 52.

Synonym: *Thalassiosira oestrupii* (Ostenfeld) Hasle 1972. *Taxon* 21(4): p. 544.

New nomenclatural combinations for *Shionodiscus*

Shionodiscus bioculatus (Grunow) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Coscinodiscus bioculatus* Grunow 1884. Wien 28: p. 107, Pl. 3(C), Fig. 30.

Synonym: *Thalassiosira bioculata* (Grunow) Ostenfeld 1903. *Botany of the Færøes Part 2*: p. 564, Fig. 120.

Shionodiscus bioculatus var. *exiguus* (Grunow) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Coscinodiscus bioculatus* var. *exigua* Grunow 1884. Wien 28: p. 108, Pl. 4(D), Fig. 2.

Synonym: *Thalassiosira bioculata* var. *exigua* (Grunow) Husted 1928. *Dr L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz* 7(1): p. 332.

- Shionodiscus biporus* (Shiono) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira bipora* Shiono 2000. *Diatom Research* 15(1): p. 139, Figs 25–27.
- Shionodiscus centrus* (Shiono) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira centra* Shiono 2000. *Diatom Research* 15(1): p. 132, Figs 1, 2.
- Shionodiscus confusus* (Makarova) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira confusa* Makarova 1975. *Novitates Systematicae Plantarum Non Vascularium* 12: p. 149, Pl. 1, Figs 1, 2.
- Shionodiscus depressus* (Shiono) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira depressa* Shiono 2000. *Diatom Research* 15(1): p. 135, Fig. 13.
- Shionodiscus endoseriatus* (Hasle & G. Fryxell) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira endoseriata* Hasle & G. Fryxell in G. Fryxell & Hasle 1977. *Beihft zur Nova Hedwigia* 54: p. 78, Figs 45–49.
- Shionodiscus exceptiuinculus* (Shiono) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira exceptiuincula* Shiono 2001. *Diatom Research* 16(1): p. 84, Figs 1, 2.
- Shionodiscus freguelli* (Kozlova) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira freguelli* Kozlova 1967. *Novitates Systematicae Plantarum Non Vascularium* 1967: p. 58, Fig. 6.
- Shionodiscus freguellopsis* (Fryxell & Johansen) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira freguellopsis* Fryxell & Johansen in Johansen & Fryxell 1985. *Phycologia* 24(2): p. 168, Figs 6, 67, 68, 71, 81.
- Shionodiscus gracilis* (Karsten) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Coccolindiscus gracilis* Karsten 1905. *Deutsche Tiefsee-Expedition* 2(2): p. 78, Pl. 3, Fig. 4.
- Shionodiscus gracilis* (Karsten) Hustedt 1958. *Deutsche Antarktische Expedition 1938/39* 2: pp. 109, 110, Figs 4–7.**
- Shionodiscus gracilis* var. *expectus* (VanLandingham) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira expecta* VanLandingham 1978. *Catalogue of the Fossil and Recent Genera and Species of Diatoms and their Synonyms. Part VII. Rhodicosphenia through Zygoceeros*: p. 3995.
- Shionodiscus gracilis* var. *expecta* G. Fryxell & Hasle 1979. *Phycologia* 18(4): p. 384.**
- Shionodiscus delicatula* Hustedt 1958. *Deutsche Antarktische Expedition 1938/39* 2: p. 110, Figs 8–10 (*non* Ostentfeld 1907).**
- Shionodiscus latimarginatus* (Makarova) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira latimarginata* Makarova 1975. *Novitates Systematicae Plantarum Non Vascularium* 12: p. 150, Pl. 1, Figs 3, 4.
- Shionodiscus oestrupii* var. *planus* (Jousé) Alverson, Kang et Theriot, *comb. nov.***
 Basionym: *Thalassiosira oestrupii* var. *plana* Jousé 1968. *Novitates Systematicae Plantarum Non Vascularium* 1968: p. 15, Pl. 1, Figs 8, 9.

Shionodiscus oestrupii var. *venrickae* (G. Fryxell & Hasle) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Thalassiosira oestrupii* var. *venrickae* G. Fryxell & Hasle 1980. *American Journal of Botany* 67(5): p. 810, Figs 11–19.

Shionodiscus perpusillus (Kozlova) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Thalassiosira perpusilla* Kozlova 1967. *Novitates Systematicae Plantarum Non Vasculares* 1967: p. 60, Figs 12, 13.

Shionodiscus poro-irregularis (Hasle & Heimdal) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Thalassiosira poro-irregularis* Hasle & Heimdal 1970. *Beihfte zur Nova Hedwigia* 31: p. 573, Figs 55–64, 71, 72.

Shionodiscus poroseriatus (Ramsfjell) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Coscinosira poroseriata* Ramsfjell 1959. *Nytt Magazin for Botanikk* 7: p. 175, Pl. 1, Fig. g and Pl. 2, Fig. a.

Synonym: *Thalassiosira poroseriata* (Ramsfjell) Hasle 1972. *Taxon* 21(4): p. 544.

Shionodiscus praeoestrupii (Dumont, Baldauf & Barron) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Thalassiosira praeoestrupii* Dumont, Baldauf & Barron 1986. *Micropaleontology* 32(4): p. 373, Pl. 1, Fig. 2.

Shionodiscus ritscheri (Hustedt) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Coscinodiscus ritscheri* Hustedt 1958. *Deutsche Antarktische Expedition 1938/39* 2: pp. 117, 118, Figs 44–46.

Synonym: *Thalassiosira ritscheri* (Hustedt) Hasle 1968. *Nytt Magazin for Botanikk* 15(3): p. 196.

Shionodiscus tetraoestrupii (Bodén) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Thalassiosira tetraoestrupii* Bodén 1993. *Terra Nova* 5(1): p. 65, Pl. 1, Fig. D.

Shionodiscus tetraoestrupii var. *reimeri* (Mahood & Barron) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Thalassiosira tetraoestrupii* var. *reimeri* Mahood & Barron 1995. *A Century of Diatom Research in North America: A Tribute to the Distinguished Careers of Charles W. Reimer and Ruth Patrick*. p. 2, Fig. 23.

Shionodiscus trifultus (G. Fryxell) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Thalassiosira trifulta* G. Fryxell in Fryxell & Hasle 1979. *Nova Hedwigia Beiheft* 64: p. 16, Figs 1–24.

Shionodiscus variantius (Shiono) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Thalassiosira variantia* Shiono 2001. *Diatom Research* 16(1): p. 86, Figs 13, 14.

Shionodiscus voeringensis (Bodén) Alverson, Kang et Theriot, *comb. nov.*

Basionym: *Thalassiosira voeringensis* Bodén 1992. *Stockholm Contributions in Geology*. 42(3): p. 201, Pl. 4, Figs 1a–c.

It is clear from morphology and existing phylogenetic analyses of SSU rDNA sequences that *Thalassiosira* is not a natural evolutionary lineage. In the absence of a densely sampled and well-resolved phylogeny of Thalassiosirales, one useful strategy toward establishing a

more natural classification of this group is to interpret cell wall and other characteristics in a phylogenetic framework. This type of analysis can be applied to single characters as easily as it can to entire suites of characters. All classifications are dynamic, testable hypotheses, and those based on sound phylogenetic principles are much more likely to withstand rigorous testing.

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