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Diatoms of the Northeastern Gulf of Mexico: Light and Electron Microscope Observations of *Sulcatonitzschia*, a new Genus of Nitzschioid Diatoms (Bacillariales: Bacillariaceae) with a Transverse Sulcus

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DIATOMS OF THE NORTHEASTERN GULF OF MEXICO: LIGHT AND ELECTRON MICROSCOPE OBSERVATIONS OF *SULCATONITZSCHIA*, A NEW GENUS OF NITZSCHIOID DIATOMS (BACILLARIALES: BACILLARIACEAE) WITH A TRANSVERSE SULCUS

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ABSTRACT: During a systematic investigation of phytoplankton assemblages in the northeastern Gulf of Mexico (GOM) in the aftermath of the Deepwater Horizon blowout we encountered a population of diatoms morphologically similar to *Nitzschia ossiformis* (Taylor) Simonsen located about 75 km offshore and concentrated at a depth of 60–120 meters. The density of individuals in the population was sufficient to make detailed observations using light and electron microscopy. Our specimens were frequently united into short ribbon-like colonies. This, plus features of the fine structure of valve (biseriate striae, raphe canal without pores and flush with the valve surface) suggest the GOM population is more closely related to *Fragilariopsis* than to *Nitzschia sensu stricto*. The presence of a unique feature, described here for the first time, a transverse sulcus in the exterior surface of one of the poles, coupled with the characteristic shape of the valve, suggest our taxon cannot be accommodated in *Fragilariopsis*, or any other genus hitherto known within the family Bacillariaceae. We, therefore, propose a new genus, *Sulcatonitzschia* for this diatom and any other nitzschioid diatom with a transverse sulcus, with a new species, *Sulcatonitzschia novossiformis* as the generitype. Published descriptions suggest that some populations identified as *Nitzschia ossiformis* may be conspecific with *S. novossiformis*, but the type of *N. ossiformis* as delineated by Taylor is not. Examination of the fine structure of the valves is necessary to resolve these relationships.

KEY WORDS: *Nitzschia ossiformis*, *Synedra ossiformis*, transverse sulcus, phytoplankton

INTRODUCTION

The coastal zone of the northeastern Gulf of Mexico (GOM) is in many ways an ideal system for studying diatom biodiversity. The region includes the outlets of 5 major river systems – the Escambia, Choctawhatchee, Apalachicola, Ochlockonee, and Suwannee – as well as the outlets of numerous smaller rivers and streams. In the west, these empty into a series of brackish lagoons and large bays bounded by barrier islands. In the east, the local physiography prevents the formation of barrier islands. Instead, the coastal region is dominated by swamps and marshes (Pennock et al. 1999, Livingston 2001). Between and within the 2 subregions is a broad assemblage of marine habitats including saltwater marshes and tidal creeks, oyster beds, seagrass beds, unvegetated submerged sediments, intertidal mud flats and sandy beaches, all of which are impacted by significant inputs of freshwater from the various rivers and streams (Livingston 2001).

Offshore, the topography is dominated by DeSoto Canyon, a break in the continental shelf bringing the 100 m contour within 35 kilometers of the coast, the steepest increase in depth in the region and serving to separate the sedimentary regime of the western panhandle of Florida from that of the West Florida Shelf (Longhurst 2007). Here, the mixing of near-shore waters influenced by riverine systems, especially the Mississippi to the west and the Apalachicola in the center, with off-shore surface waters brought in by the Loop Current, and deeper waters moving up DeSoto Canyon, lead to a region with rel-

atively high levels primary of productivity (Qian et al. 2003, Salmerón–García et al. 2011, Murawski et al. 2016). While relatively well studied from an oceanographic point of view, systematic studies of seasonal variations in the composition of the phytoplankton at the species scale are scarce (Murawski et al. 2016). The most detailed studies are those of Curl (1959) and Saunders and Fryxell (1972).

In April of 2010, the Deepwater Horizon drilling rig exploded, causing a massive oil spill in the northern GOM; by the time the flow was stopped in September, about 4.9 million barrels of oil had been released directly into the GOM (McNutt et al. 2012). Attempts to assess the impacts of this spill in the northeastern GOM were hampered by the lack of base-line data, especially with respect to the phytoplankton (Murawski et al. 2016). The present study is a part of a larger project with the goal of reassessing the status of photosynthetic communities along the northwest coast of Florida. Overall, phytoplankton samples were collected from a consistent set of stations off the coast of the western panhandle of Florida over a period of 4 years. While we are still analyzing the complete set of samples, at this point we have spatial and distributional data on 80+ species of coccolithophores, 130+ species of diatoms, and 22 species of dinoflagellates (Nienow et al. 2013, Agbali 2014, Avery 2014, Cruz 2015, Nienow et al. 2017).

Included in the off-shore samples is a diverse assemblage of planktonic nitzschioid diatoms of the genera *Alveus* Kacz-

mariska & Fryxell, *Fragilariopsis* Hustedt, *Nitzschia* Hassall, and *Pseudo-nitzschia* Peragallo. One of these, present only in deep water stations, was a form morphologically similar to *Nitzschia ossiformis* (Taylor) Simonsen, but differing in its mode of colony formation and some morphological and morphometric details. The new form was present in sufficient numbers to allow a detailed examination of its valve structure using light, scanning, and transmission electron microscopy (LM, SEM, and TEM, respectively). Our observations revealed the presence of a unique structure, a transverse groove, or sulcus, in the exterior of one pole of a valve, not found in any other nitzschioid diatom. We consider this structure to be distinctive, necessitating the designation of a new genus, *Sulcatonitzschia*, within the family Bacillariaceae, with the new species *Sulcatonitzschia novossiformis* as the generic type. Here, we provide a taxonomic description of the new genus and species, and compare it with closely related nitzschioid genera.

MATERIALS AND METHODS

Collection stations were established along 3 transects extending from Pensacola Bay, Choctawhatchee Bay, and St. Andrew Bay, all located in the western panhandle of Florida; 2 additional stations were located farther from shore, directly over DeSoto Canyon, GOM (Figure 1). Details of the station locations and sampling program can be found in Nienow et al. (2017). In brief, stations were sampled during 19 cruises between January 2011 and June 2014, as weather permitted. At each station, whole water samples were collected at 20 to 25 m

intervals from the surface to a depth of 150 m, with additional samples taken from 200 m, 400 m, and from near the bottom, as appropriate, using a rosette of Niskin bottles attached to a carousel sampler. Up to 1000 mL of each sample was filtered through a 0.45 μm nitrocellulose filter during the transit to the next station. Filters were immediately rinsed with a 0.02 mM borate solution (pH = 8.3) and air-dried. Net plankton samples were collected at each station using a 25 μm mesh net towed vertically from a depth of up to 100 m and fixed immediately with Lugol's iodine.

On shore, net plankton samples were concentrated by sedimentation. A portion of the concentrated material was cleaned with nitric acid/potassium dichromate and rinsed 10 times with de-ionized water. For light microscopy (LM), aliquots of the cleaned material were air-dried onto glass coverslips, then mounted on glass slides in Naphrax and observed with a Olympus BX60 light microscope (Olympus, Tokyo, Japan) equipped with differential interference contrast (DIC) optics and a Canon EOS Rebel digital camera (Canon, Tokyo, Japan) configured for remote viewing. The same microscope system was used to observe water mounts of Lugol's-fixed material. For scanning electron microscopy (SEM), aliquots of cleaned material were dried onto circular glass coverslips mounted on SEM stubs using carbon tape, sputter-coated with gold/palladium using a Denton Vacuum Desk IV sputter-coater (Moorestown, New Jersey, USA), and examined with a JEOL 6480 LV (JEOL, Tokyo, Japan) scanning electron microscope. For quantitative analyses, a portion of each rinsed and air-dried

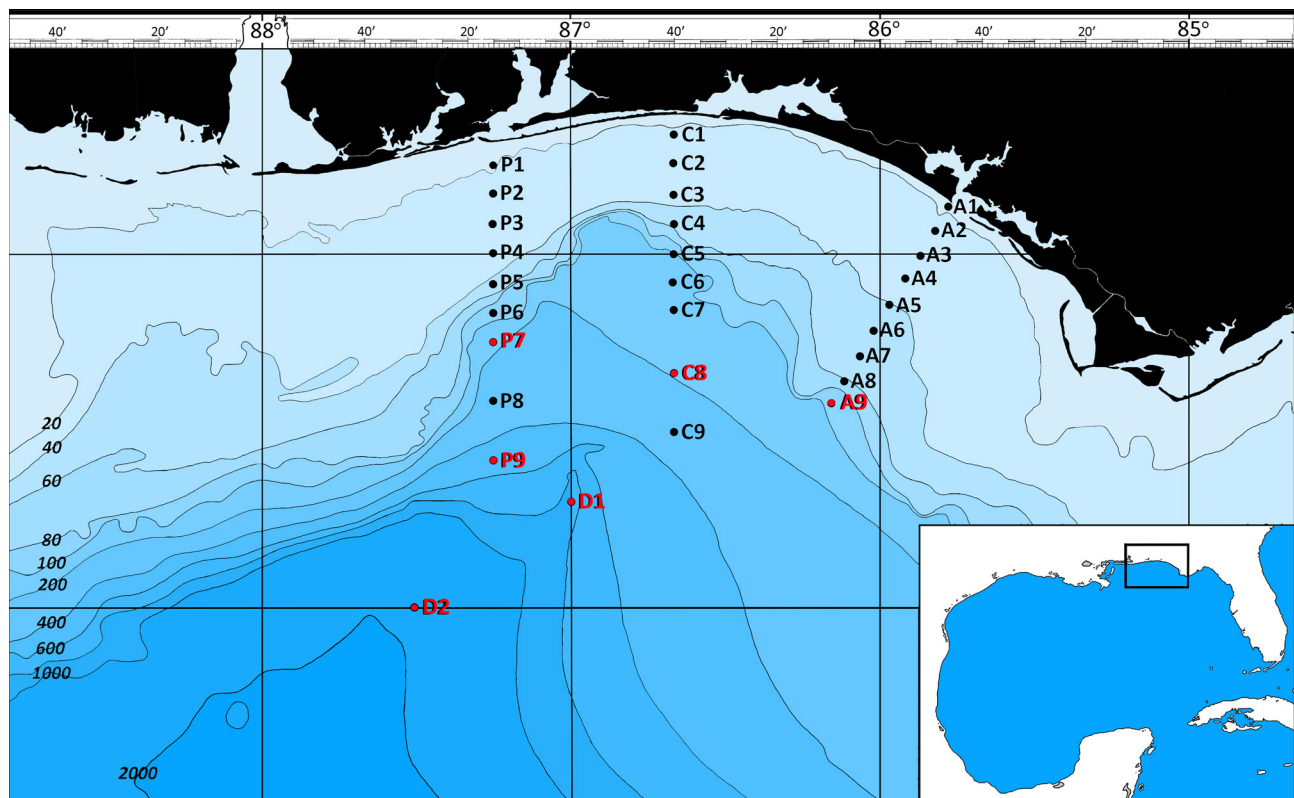


FIGURE 1. Stations sampled in the northeastern Gulf of Mexico during this project. Stations where populations of *Sulcatonitzschia novossiformis* were observed are indicated in red. Contours redrawn from NOAA (2013) Chart 11006 Gulf Coast - Key West to Mississippi River (<http://www.charts.noaa.gov/PDFs/11006.pdf>).

filter was mounted on an SEM stub with carbon tape, sputter-coated with gold-palladium and observed with SEM using the same system. For transmission electron microscopy (TEM), small aliquots were air-dried onto formvar-coated copper grids; grids were examined using a FEI 120CM Bio-Twin TEM located at Florida State University. Measurements were taken from the LM, SEM, and TEM images using tools available in Adobe Photoshop (San Jose, California, USA).

Terminology used for structures observed in LM and SEM follows that of Anonymous (1975), von Stosch (1975), Ross et al. (1979), Mann (1981), and Cox (2004). The classification system follows that of Cox (2015).

RESULTS

Materials Collected

The new species was collected from 6 stations during 7 cruises between March 2012 and May 2014 (Figure 1). Specifics of the collections are listed in Table 1.

Description of Genus and Species

PHYLUM: Bacillariophyta Karsten

CLASS: Bacillariophyceae Haeckel

SUBCLASS: Bacillariophycidae D. G. Mann

ORDER: Bacillariales Hendey

FAMILY: Bacillariaceae Ehrenberg

GENUS: *Sulcatonitzschia* J.A. Nienow & A.K. S.K. Prasad gen. nov.

Description. Cells solitary or in short ribbon-like chains, linear to lanceolate in valve view, rectangular in girdle view. Plastids two, arranged symmetrically about the medial transapical plane. Valves mostly isopolar, inflated at the center and at the poles. Externally, a transverse sulcus present at one pole of the valve and a wing-like ridge (thickening) at the other pole. Striae composed of 2 or more rows of poroid areolae. Marginal canal raphe is present; the canal more or less flush with the surface of the valve, exterior wall of the canal without poroids. Central nodule present or absent, exterior terminal raphe fissures absent. Conopeum absent. Cingulum composed of open bands, the valvocopula perforated with a single row of poroids, copulae hyaline. Marine, planktonic.

Sulcatonitzschia can be distinguished from other planktonic nitzschoid diatoms by the presence of a transverse sulcus at one pole and a wing-like ridge at the other pole of the valve.

Etymology: The name incorporates the diagnostic feature of a transverse sulcus (from the Latin *sulcatus* = furrowed) in a nitzschoid valve.

TYPE SPECIES: *Sulcatonitzschia novossiformis* J.A. Nienow & A.K.S.K. Prasad *sp. nov.*

Description: Based on measurements of 35 specimens. Cells

TABLE 1. Stations and collections where *Sulcatonitzschia ossiformis* was observed.

Station	Location	Date of Collection	Type of Sample	Depth/ Length of Tow	Slide/ Stub number
Station P7 Pensacola Bay Transect	29°45' N, 087°15' W	17 March 2012	vertical plankton tow	100 meters	wet mount
		2 June 2013	vertical plankton tow	100 meters	wet mount
Station P9 Pensacola Bay Transect	29°25' N, 087°15' W	5 May 2012	vertical plankton tow	100 meters	Slides BP-1940a, BP-3313a-g, BP-3314a-e Stub 2514
		5 May 2012	filtered whole water	60 meters	Stub 1945
			filtered whole water	80 meters	Stub 1946
		8 July 2012	filtered whole water	125 meters	Stub 2328
		6 April 2013	vertical plankton tow	100 meters	Stub 2838
		1 May 2014	filtered whole water	75 meters	Stub 3310
Station C8 Choctawhatchee Bay Transect	29°40' N, 086°40' W	7 May 2012	filtered whole water	80 meters	Stub 1983
Station A9 Saint Andrews Bay Transect	29°34.75' N, 086°09.5' W	6 May 2012	vertical plankton tow	85 meters	Stub 2524
Station D1 DeSoto Canyon	29°40' N, 086°40' W	6 May 2012	filtered whole water	80 meters	Stub 1445
Station D2' DeSoto Canyon	29°17.6' N, 087°0.0' W	15 October 2012	filtered whole water	100 meters	Stub 2600

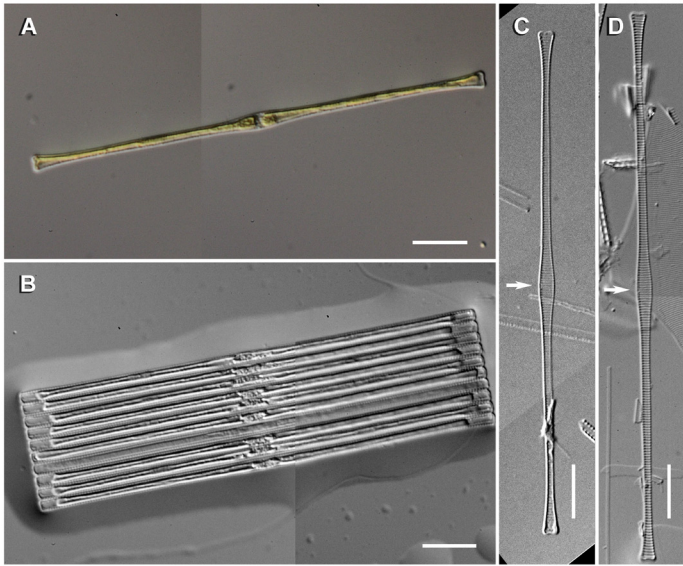


FIGURE 2. Light microscopy images of *Sulcatonitzschia novossiformis* from the Gulf of Mexico using Differential Interference Contrast (DIC). A. Valve view, preserved material. Note the 2 plate-like plastids, one in each half. B. Girdle view, preserved material. A ribbon-like colony of 10 cells. C. (holotype) and D. Valve views, acid-cleaned material. The canal raphe in both images is on the left side of the valve, arrows indicate the central interspace. Scale bars = 10 μ m.

solitary or united into short ribbon-like colonies (Figures 2A, 3A), ribbon-like colonies sometimes separating to form tight zig-zag colonies (Figure 3B). Individual cells with 2 plate-like plastids arranged symmetrically about the median transapical plane (Figure 2A). Valves linear, inflated at the center and at the poles (Figures 2A, 2C, 2D, 4A, 5A, 6A), 62–102 μ m long, 2.3–3.1 μ m wide at the widest point in the center. Inflated apices with distinct concavity, giving them the appearance of the head of a bone. A transverse sulcus is present in the exterior surface of one of the apices, and short, almost wing-like, extensions on the other (Figures 3C–3D, 4C–4D, 6C–6F, 7A–7B, 8C). The transverse sulcus takes the form of a shallow groove replacing the endmost stria, about 0.2 μ m wide, 0.2 μ m deep, and extending across the entire valve face. Away from the apices, the valve face is relatively flat, separated from the valve mantle on one side by the eccentric canal raphe and associated structures, and on the other by a thin hyaline rim (Figures 4B–4D, 6C–6F). Transverse striae are parallel, the number of striae in 10 μ m ranging from 21–24. The striae are composed of 2 rows of circular poroid areolae, 6 to 7 in 1 μ m, occluded by hymenes with hexagonal arrays of small pores (Figure 7C–7F). Canal raphe just visible along the margin in light microscopy of cleaned valves (Figure 2C, 2D); in SEM, raphe system not raised above the surface of valve (Figures 6B–6F). Density of fibulae is about equal to the density of striae. Median fibulae are distant from each other creating a larger central interspace (Figures 2C, 2D, 4B, 5B, 6B). Longitudinal ridges connecting bases of fibulae can be seen clearly; flanges extending from fibulae absent (Figures 5B–5D). Internally, the 2 branches of the raphe meet in a small central nodule (Figure 5B) and end in simple helictoglossae

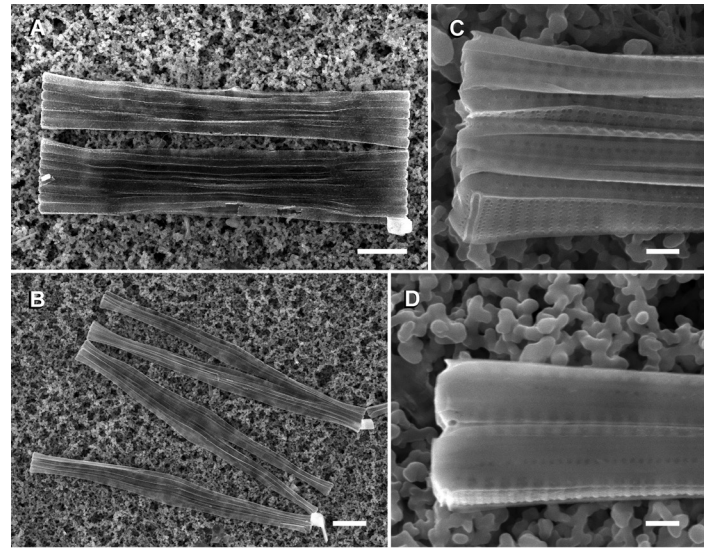


FIGURE 3. Scanning electron microscopy images of filtered, rinsed, and air-dried *Sulcatonitzschia novossiformis* from the Gulf of Mexico showing colony formation. A. Ribbon-like colony with 14 cells. B. Colony beginning to separate, giving rise to zigzag chains. C–D. Details of colonies. Note the transverse grooves in the lower-most cells in Figures C and D and the absence of conspicuous pads of mucilage. Scale bars = 10 μ m in A and B, 1 μ m in C and D.

(Figure 5C, 5D). No terminal fissures were visible externally. No pores could be seen on the exterior wall of the raphe canal (Figures 6B–6D). Striae continue onto the mantle as 2 large pores on both the proximal (Figure 6C, 6D) and the distal sides of the valve (Figure 6E, 6F). Rows and clusters of small spines

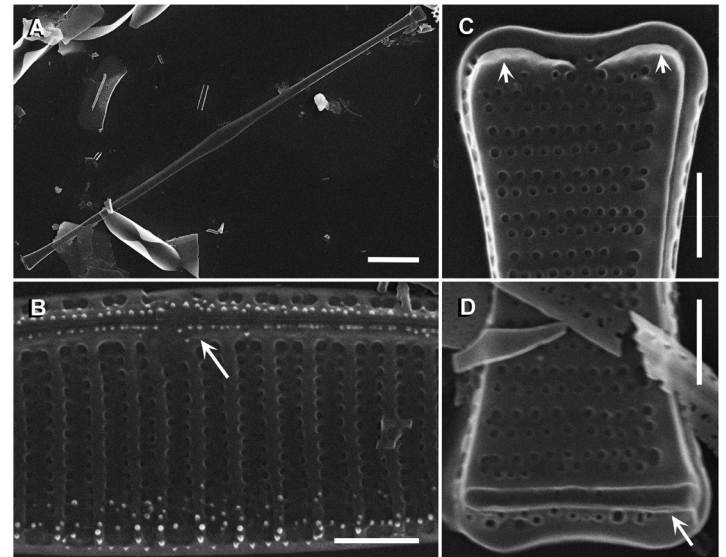


FIGURE 4. Scanning electron microscopy images of the valve exterior of acid-cleaned *Sulcatonitzschia novossiformis* from the Gulf of Mexico. A. Complete valve. B. Detail of central region with a large central interspace (arrow), parallel striae composed of 2 rows of areolae. The valve face is bordered by the canal raphe on one side and a narrow hyaline band of silica on the other. Small spines or spinules can be seen along the border of the valve face. C and D. Details of the 2 valve ends. A transverse groove is seen at one end in D (arrow), but not in C; instead there are two small wing-like projections (arrows). Scale bars = 10 μ m in A, 1 μ m in B–D.

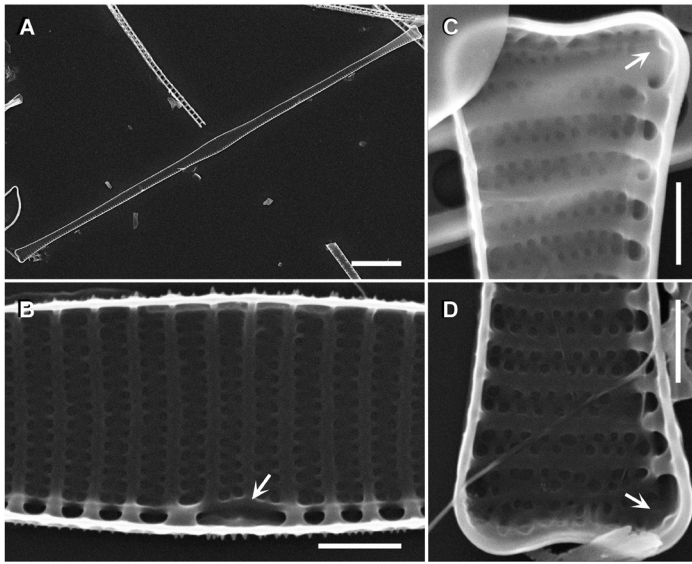


FIGURE 5. Scanning electron microscopy images of the valve interior of acid-cleaned *Sulcatonitzschia novossiformis* from the Gulf of Mexico. A. Complete valve. B. Detail of the central area showing the central node (arrow) and the enlarged central area. C and D. Details of the valve ends. Note the helictoglossae in the lower corners of the valves (arrows). The interior of the transverse groove is not apparent at either end. Scale bars = 10 μm in A, 1 μm in B-D.

are found bordering the raphe and along the distal valve face/valve mantle interface in central portion of the valve (Figures 4B, 6B). Epicingulum composed of one or more open bands, the first of which (the valvocopula) is marked by a row of large pores, about 40 in 10 μm (Figures 3C, 3D, 6C, 6F). The other copulae, when present, appear to be hyaline. A diagrammatic representation of the structures is provided in Figure 8.

Taxonomic Summary

Holotype: Slide VSU-3314a (ANSP-GC59337). The holotype specimen is located at England Finder coordinates F28-3 and is illustrated as Figure 2C here.

Isotypes: Slide VSU-3314a (ANSP-GC59337), England Finder coordinates Q34-2; and slide VSU-3313e, England Finder coordinates F34-4; VSU-3314b, England Finder coordinates L35-3, Q32-2, and Q34-2; VSU-3314e, England Finder coordinates M34-2, R34-4, all stored in the AKSKP collection, Florida State University, Tallahassee, FL.

Type locality: 29°25'N, 87°15'W. Northeastern GOM. Station P9. Collected on 5 May 2012 with a 25- μm mesh plankton net. At a depth of 60 m, where the highest concentration of cells was located, the water temperature was 21.3°C and the salinity was 36.4.

Etymology: The epithet *novossiformis* refers to the similarity of this diatom to *Nitzschia ossiformis*.

Remarks

Sulcatonitzschia novossiformis was observed most frequently in samples collected during the months of April and May, from stations at least 75 km from shore. It appears to be more common deep in the euphotic zone; *S. novossiformis* was observed in whole water samples from depths between 60–125 m. *Sulcatonitzschia novossiformis* was never seen in large num-

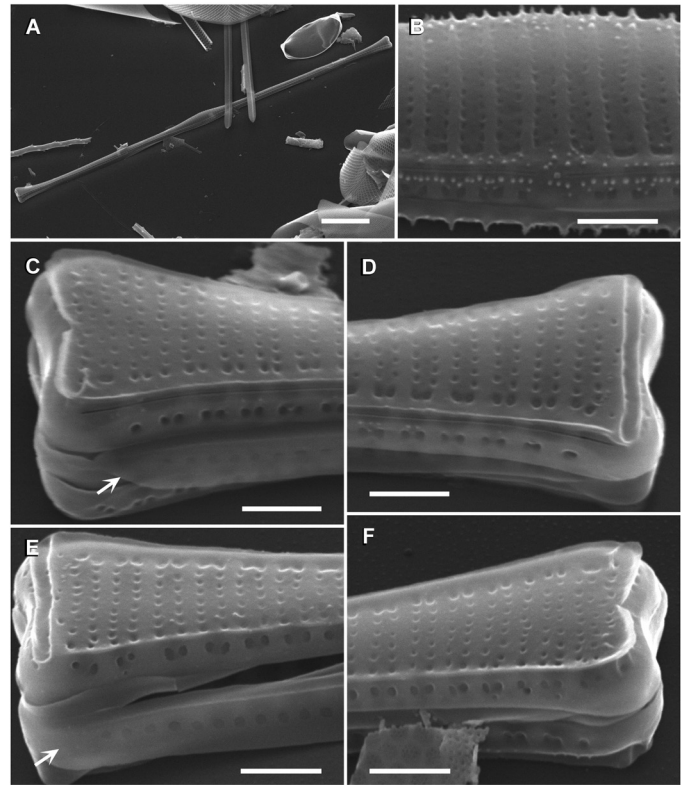


FIGURE 6. Scanning electron microscopy images of the mantle and epicingulum of acid-cleaned *Sulcatonitzschia novossiformis* from the Gulf of Mexico. Angle of Tilt (AOT) 45°. A. Complete valve. B. Detail of the central area showing the central raphe ends and central interspace. Note the rows of spinules bordering the raphe and along the distal edge of the valve face. C. and D. Details of the 2 valve ends, C with a slight wing-like extension and D with a transverse sulcus. In both images, the striae continue on the mantle below the raphe canal as 2 large pores. The valvocopula, arrow in C, is open near the end of the valve and marked by a single series of large pores. E. and F. The same valve, rotated 180° around the medial pervalvar axis and tilted 45° to show the distal mantle. Striae continue on the mantle beyond the ridge at the valve face-valve mantle interface as 2 large areolae, similar to the proximal mantle. The valvocopula can be seen most clearly in E (arrow). Scale bars = 10 μm in A, 1 μm in B-F.

bers—the largest observed concentrations were about 3,300 cells/L in May 2012, from a depth of 60 m. Significant co-occurring species include the diatoms *Nanoneis longta* Li & Gao emend Nienow, *Neodelphineis indica* (Taylor) Tanimura and *Pseudo-nitzschia* spp., and the coccolithophores *Emiliania huxleyi* (Lohmann) Hay & Mohler and *Florisphaera profunda* Okada & Honjo. *Nanoneis longta* (Nienow et al. 2017) and *Florisphaera profunda* (Quinn et al. 2005) are both recognized as showing a preference for the lower euphotic zone.

DISCUSSION

Position of *Sulcatonitzschia* within the Bacillariaceae

The basic features of *Sulcatonitzschia* — more or less linear valve outline, a marginal canal raphe and 2 chloroplasts placed on opposite sides of the nucleus — establish its position in the family Bacillariaceae (Cox 2015) and would justify its placement in the genus *Nitzschia*. However, *Nitzschia* is a large genus with poorly delineated boundaries (Mann 1978, 1986, Round

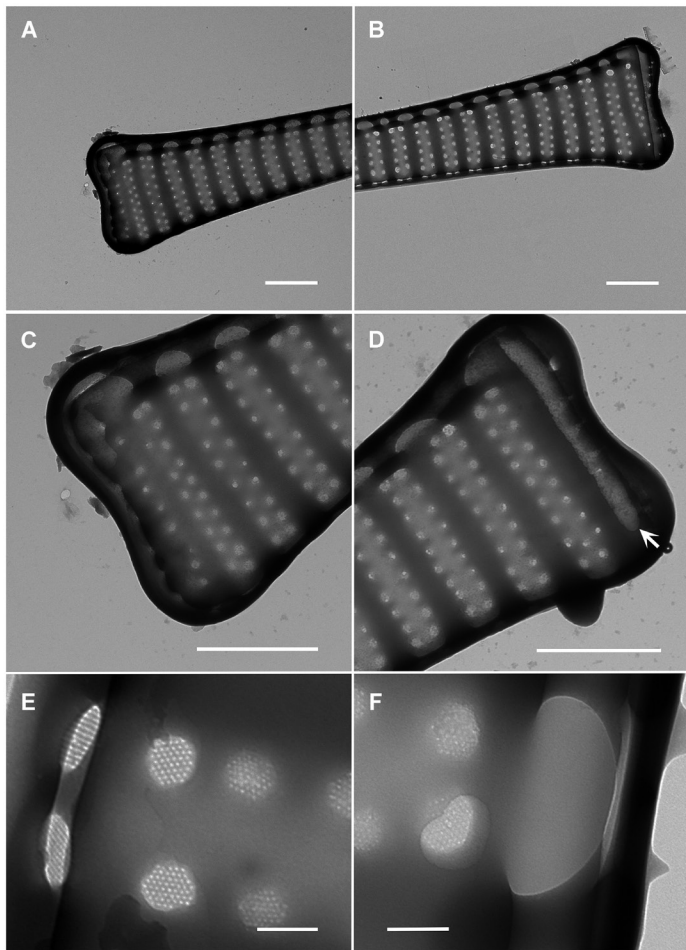


FIGURE 7. Transmission electron microscopy images of acid cleaned *Sulcatonitzschia novossiformis* from Gulf of Mexico. A-B. Low magnification images of the 2 ends of the same valve. C-D. Details of the valve ends. The transverse groove can be seen in D (arrow). E. Detail of areolae illustrating the array of small pores in the hymenes. F. Detail of the wall of the canal raphe, without perforations. Scale bars = 1 μm in A-D, 0.1 μm in E-F.

et al. 1990), and at least 845 validly described species (Guiry and Guiry 2020). Many authors, beginning with Grunow (1862), have attempted to bring order to the genus by separating species into groups, sections, subgenera and/or new genera, sometimes with contradicting interpretations (see Hasle 1972, 1993, Mann 1978, 1986). Currently, there are 19 (Cox 2015) to 24 (Guiry and Guiry 2020) genera recognized in the family, with a number of them either previously included as sections of the genus *Nitzschia* (e.g., *Fragilariopsis*, *Grunowia* Rabenhorst, *Perrya* Kitton, *Psammodyctyon* Mann, *Pseudo-nitzschia*, and *Tryblionella* Smith) or based on unique features of individual species of the genus (*Alveus*). Important features used to distinguish genera include: habit, valve symmetry, structure and position of the raphe system, fine structure of areolae and striae, and other details of the valve structure. An examination of these features as observed in *Sulcatonitzschia*, especially the presence of a transverse sulcus at one end of the valve and a marginal wing at the other, justify its position as a separate genus in the family.

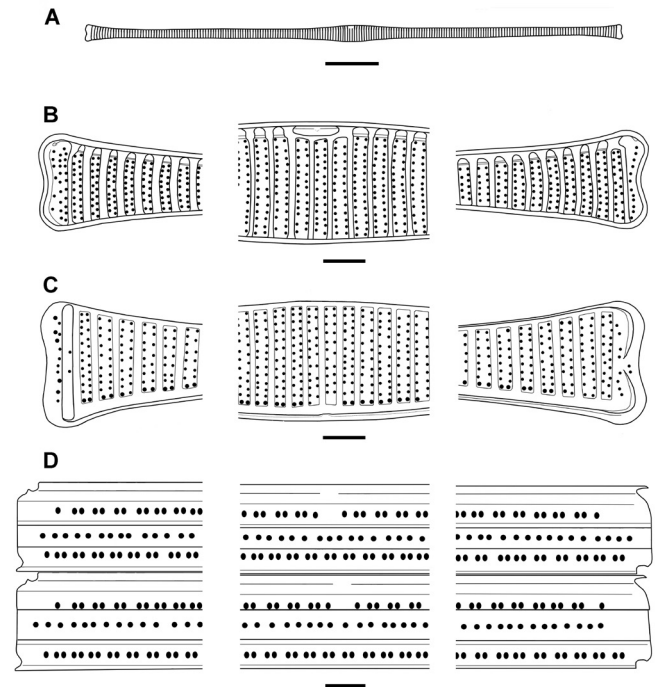


FIGURE 8. Schematic diagrams of *Sulcatonitzschia ossiformis*. A. Complete valve as viewed in light microscopy. B. Details of the interior of the 2 poles and the center of a valve. The sulcus is located at the left-hand pole. C. Details of the exterior of the 2 poles and the center of the valve. The sulcus is located at the left-hand pole, the wing-like extension at the right-hand pole. D. Details of the 2 poles and the center of a short chain composed of two sibling valves in girdle view. Scale bars 10 μm in A, 1 μm in B-D.

The majority of nitzschioid diatoms are benthic forms associated with bottom sediments, with planktonic forms restricted to a few genera. Previously described genera with species recorded as planktonic include *Alveus*, *Bacillaria* Gmelin, *Cylindrotheca* Rabenhorst, *Fragilariopsis*, *Neodenticulata* Akiba & Yanagisawa, *Nitzschia*, and *Pseudo-nitzschia* (Hasle and Syvertsen 1996, Kaczmarska and Fryxell 1996). Because *Sulcatonitzschia* is also planktonic, it may be useful to examine the features of *Sulcatonitzschia* in comparison to these genera (Table 2).

Colony Formation

A characteristic feature of *Sulcatonitzschia* is the ability to form colonies of 10–20 cells. On occasion we did observe zigzag colonies (see Figure 3B), but these are not analogous to the zigzag colonies seen in *Thalassionema*—there was no evidence of the mucilaginous pads responsible for colony formation in *Thalassionema*, and reported by Taylor for *N. ossiformis* (Taylor 1966). It is possible that the absence of these pads could be an artifact of sample preparation, but we have seen mucilage pads in samples prepared in the same manner linking members of *Thalassionema* and *Neodelphineis indica* (Taylor) Hasle into colonies (J.A. Nienow, unpub.). The zigzag colonies in *Sulcatonitzschia* are more likely the result of the partial breakup of ribbon-like chains, especially since each zig or zag typically contains multiple cells linked along the valve face. We did not see any structural elements of the valve that could be used to

TABLE 2. Comparison of features used to distinguish genera of nitzschioid diatoms with planktonic members.

Character	<i>Sulcatonitzschia</i> ¹	<i>Alveus</i> ²	<i>Bacillaria</i> ^{3,4,11}	<i>Cylindrotheca</i> ^{5,11}	<i>Fragilariopsis</i> ^{6,11}	<i>Neodenticula</i> ^{7,8}	<i>Nitzschia</i> ^{9,10,11}	<i>Pseudonitzschia</i> ^{6,11}
habitat	marine; plankton	marine; plankton	freshwater & brackish; benthos (plankton)	(freshwater) brackish to marine; benthos (plankton)	marine; benthos, plankton	marine; plankton	freshwater, brackish, marine; benthos, plankton	marine; plankton
habit	solitary or short ribbon-type chains	solitary	motile colonies	solitary	ribbon-type chains	ribbon-type chains	solitary or in gelatinous colonies	stepped chains
valve outline	linear	lanceolate to linear	linear, with tapered apices	spindle-shaped with drawn-out ends	elliptical to linear-lanceolate	linear, linear-elliptical, elliptical	various, linear to sigmoid	elongate, linear to lanceolate
structure of striae	biseriate	biseriate; alveolate	uni- to biseriate	striae absent	biseriate	irregular rows of areolae	various, usually uniseriate	uni- to multiseriate
position of raphe system	eccentric, even with valve	eccentric	central, above valve surface	central to eccentric	eccentric, even with valve surface	eccentric, even with valve surface	central to eccentric, raised above valve surface	eccentric, even with valve raised above valve surface
number of fibulae compared to interstriae	about the same as interstriae	about the same as interstriae	fewer than interstriae	NA	about the same as interstriae	about the same as interstriae	equal to or fewer than interstriae	equal to or fewer than interstriae
pores in outer wall of raphe system	absent	absent	present	absent	absent	absent	present or absent	absent
conopeum	absent	absent	absent	absent	absent	absent	absent or present	absent
diagnostic features	transverse sulcus at one valve, wing-like extension at other	heavily silicified valves with alveolate striae	tongue-and-groove system in the external valve surface	weakly silicified; cylindrical cross section; valves often twisted	ribbon chains, some species heteropolar	presence of primary pseudosepta	absence of characters used to distinguish other genera	stepped chains, some species heteropolar

¹present study; ²Kaczmarek and Fryxell 1996; ³Schmid 2007; ⁴Jahn and Schmid 2007; ⁵Reimann and Lewin 1964; ⁶Hasle 1993; ⁷Poulin et al. 2010; ⁸Akiba and Yanagisawa 1986; ⁹Mann 1978; ¹⁰Mann 1984; ¹¹Lundholm et al. 2002.

hold sibling cells together. However, the presence of zigzag colonies suggests that the cells are more strongly attached at the poles and that some feature of the pole is responsible for ribbon formation. A likely candidate would be the transverse sulcus. It is possible that mucilage is transported to the sulcus by the raphe and then fills the sulcus; in this respect it is noteworthy that the raphe ends near one edge of the sulcus. The mucilage then contacts the expanded wing-like extension of the adjacent cell, forming a connection. The small spines and spinules along the margins of the central region of the valve may help to maintain the structure, not by direct linkage, but by increasing the resistance to shear forces.

Most nitzschioid diatoms, including *Alveus*, *Cylindrotheca* and planktonic species of *Nitzschia sensu stricto*, are solitary (Round et al. 1990). As a consequence, some authors have used the mode of colony formation to help distinguish groups and genera within the Bacillariaceae (Mann 1978). Mann (1978) catalogued 7 types of colonies with the family. In 4 of the types the cells are clearly united by mucilage: stipitate and stellate colonies where the cells joined by mucilage secreted from one

end of the cell; colonies with cells embedded in a common amorphous mucilage; and colonies of cells forming mucilaginous tubes. The stellate colonies are structured by mucilage pads similar to what Taylor (1966) described for *Synedra ossiformis* (= *N. ossiformis*). The next 3 types of colonies catalogued by Mann (1978) involve more direct contacts between the valves of neighboring cells. The first of these, motile colonies of variable shape, are characteristic of the genus *Bacillaria*. In this case the cells move back and forth along the valves of their neighbors, sometimes in a coordinated fashion, switching from ribbon-like colonies to fully extended stepped chains. Colonies of this sort are easily recognized in live material because of their constant movement. In preserved material, colonies are caught in varying stages between the 2 extremes.

More relevant are stepped chains and ribbon- or band-like colonies present in some truly planktonic forms. Stepped chains are a distinguishing feature of the planktonic genus *Pseudo-nitzschia* (Hasle 1993); stepped chains have not been observed in *Sulcatonitzschia*. Ribbon-like colonies are more widespread, occurring in several genera including *Cymbellonitzschia*,

Denticula Kützing, *Fragilariopsis*, *Grunowia* Rabenhorst, and *Neodenticula* Akiba & Yanagisawa (Mann 1978, Round et al. 1990, Hasle 1993, Poulin et al. 2010); of these only *Fragilariopsis* and *Neodenticula* contain marine planktonic members. Valves of the planktonic species *Neodenticula seminae* (Simonsen & Kanaya) Akiba & Yanagisawa include a series of thicker costae (primary pseudosepta) separated from each other by thinner costae (secondary pseudosepta; Akiba and Yanagisawa 1986, Poulin et al. 2010), a feature visible in light microscopy but not seen in *Sulcatonitzschia*. This leaves *Sulcatonitzschia* most closely allied with *Fragilariopsis* on the basis of habit and colony formation.

Fine Structure of the Valve

The fine structure of the valve has long been used to separate genera and subgroups within the Bacillariaceae (Mann 1978). Members of the genus *Cylindrotheca* represent an extreme in the family. Members of *Cylindrotheca* are characterized by long, acicular, spirally twisted frustules, and very weakly silicified valves with numerous girdle bands (Reimann and Lewin 1964, Round et al. 1990, Hasle and Syvertsen 1996). The most common pattern in *Nitzschia* consists of single rows of poroid areolae (striae) alternating with transverse costae (interstriae), neither interrupted by any sort of sternum, with or without a marginal ridge (Mann 1978); the planktonic marine species *N. bicapitata* Cleve (Hasle 1964, plate 5, figure 7) and *N. braarudii* Hasle (Hasle 1964, plate 2, figure 1) display this pattern (Hasle 1964, Hasle and Syvertsen 1996). A similar pattern is common in what is now known as *Tryblionella* Wm. Smith; here single, but sometimes multiple, rows of poroids alternate with transverse costae, as above, but there is usually some sort of a sternum and a ridge on the distal margin (Mann 1978). In a third group, at least a portion of the valve is loculate; this type of construction is uncommon among the Bacillariaceae (Mann 1978), but is a characteristic of *Psammodictyon* Mann (Round et al. 1990). More directly relevant to the current discussion are 2 systems with bi- to multi-seriate striae with (Mann's pattern 4) or without (Mann's pattern 2) a central sternum and a pronounced marginal ridge (Mann 1978). Pattern 2 occurs in *Sulcatonitzschia*, *Fragilariopsis*, *Pseudo-nitzschia*, (Hasle 1964, 1993, Mann 1978, Lundholm et al. 2002), and *Neodenticula* (Akiba and Yanagisawa 1986, Poulin et al. 2010), as well as the planktonic species *Nitzschia sicula* (Castracane) Hustedt (Hasle 1964, 1972, Mann 1978, Hasle and Syvertsen 1996). Both primary pseudosepta and cross-bars, characteristic of *Neodenticulata*, are absent from *Sulcatonitzschia*, *Fragilariopsis*, *Pseudo-nitzschia* and *Nitzschia sicula*. In light of this structure it is somewhat surprising that the genera *Neodenticula*, *Fragilariopsis*, and *Pseudo-nitzschia* appear to be closely related phylogenetically (Hasle and Syvertsen 1996, Lundholm et al. 2002, Poulin et al. 2010).

Poroids in *Fragilariopsis*, *Pseudo-nitzschia* and *Sulcatonitzschia* are occluded by hymenes of various structure. In *Sulcatonitzschia* the openings in the hymenes are arranged in a hexagonal pattern. This is a common pattern in species of *Fragilariopsis*, although species with circular or scattered arrangements are also known (Lundholm and Hasle 2010). In *Pseudo-nitzschia*

the hymenes are often divided into sectors, however, the openings within a sector tend to be arranged in a hexagonal pattern (Mann 1978, Lundholm et al. 2002, 2012, Cavalcante 2011). In other species of *Nitzschia*, the openings in the hymenes are arranged in circular, hexagonal, or scattered patterns (Mann 1978, see figures 545–547, figure 565, figure 562, respectively).

The structures of the raphe and the raphe canal in *Fragilariopsis*, *Pseudo-nitzschia*, and *Sulcatonitzschia* show some differences with those of *Nitzschia* sensu stricto. The exterior of the raphe canal in all 3 is more or less even with the valve surface, while in most species of *Nitzschia* sensu stricto the exterior of the raphe is raised into a keel, which may be covered by a conopeum (Mann 1978, Hasle 1993, Lundholm et al. 2002). It should be kept in mind that this is not a universal feature of *Nitzschia*; in the planktonic species *N. sicula*, common in the GOM, the raphe system is even with the valve surface and lacks a conopeum (Hasle and Syvertsen 1996, plate 75, figures a–d). In addition, the exterior of the raphe canal of *Fragilariopsis*, *Pseudo-nitzschia*, and *Sulcatonitzschia* is free of pores and poroids, while in many species of *Nitzschia* sensu stricto the exterior of the raphe canal is perforated by pores; these pores are absent in *N. sicula* (Hasle and Syvertsen 1996, plate 75, figures a–d). Terminal fissures are also absent in these 3 genera, while common in species of *Nitzschia* (Mann 1978). The raphe of *Sulcatonitzschia* possesses a central nodule; this feature is variable in *Fragilariopsis*, *Nitzschia*, and *Pseudo-nitzschia* (Mann 1978, Hasle and Syvertsen 1996, Lundholm et al. 2002) and may be more useful for distinguishing species rather than genera.

The cingulum of *Sulcatonitzschia* is composed of one or more open copulae. The valvocopula is marked by a single row of large pores. When present, the other copulae appear to be hyaline. This is a common cingulum-type observed in the genus *Fragilariopsis* (Lundholm et al. 2002, Cefarelli et al. 2010), although species with striated copulae are known (Lundholm and Hasle 2010). In *Pseudo-nitzschia*, both the valvocopulae and copulae tend to be striated (Villac et al. 2005, Stonik et al. 2011, Lundholm et al. 2012).

In summary, on the basis of valve structure, *Sulcatonitzschia* appears to belong to the general group composed of *Fragilariopsis*, *Pseudo-nitzschia*, *Neodenticula* and some species of *Nitzschia* (Mann 1978, Hasle and Syvertsen 1996, Lundholm et al. 2002, Poulin et al. 2010). Members of the group share bi- to multiseriate striae composed of poroid areolae occluded by hymenes, eccentric canal raphe systems not raised above the surface of the valve, with the exterior walls of the canal free of poroids, and raphes without terminal exterior fissures. The members differ in the type of colony formation (solitary vs. stepped chains vs. ribbon-type chains) and in details of the valve structure—the presence of pseudosepta in *Neodenticulata*, and a transverse sulcus at one end of *Sulcatonitzschia*.

Comparison of *Sulcatonitzschia novossiformis* with *Synedra ossiformis*

The South African Survey frigate *Natal* undertook 9 oceanographic cruises between April 1962 and March 1963 in the south western Indian Ocean in support of the Indian Ocean

Expedition (IOC 1963). A total of 98 net plankton samples were collected during 4 of these cruises, yielding 414 taxa of phytoplankton, including 238 diatom taxa (Taylor 1966). Among these was a narrowly elongate diatom with inflated, slightly concave apices, which gave it a distinctive bone-like shape (Taylor 1966). Colony formation (cells united into loose zig-zag chains by mucilage pads located at the apices), the presence of mucilage pores at each end of a valve, and the presence of narrow pseudoraphe convinced Taylor he was observing a synedroid diatom, and so he placed the new taxon in the genus *Synedra* and gave it the name *Synedra ossiformis* in reference to the characteristic shape of the valves, designating a line drawing of 2 united frustules as the type of the species (Taylor 1966, p. 440, plate 91(4), figure 34).

A few years later Simonsen encountered a diatom with the same general appearance in phytoplankton samples collected off the eastern coast of Africa in the vicinity of Mombasa and off the western coast of India south of Mumbai during the cruise of the *R/V Meteor* in the Indian Ocean in 1964–65 (Simonsen 1974). However, instead of mucilage pores at the apices and a pseudoraphe down the center of the valve, Simonsen's form was marked by the presence of a canal raphe with a prominent central nodule. In spite of the differences in the descriptions of the 2 forms, Simonsen assumed that the diatom he observed was conspecific with the diatom Taylor (1966) observed, and that the differences were the result of the difficulty of observing the detailed structure of the very narrow valves. Under this assumption, the presence of a canal raphe necessitated the transfer of Taylor's species from *Synedra* to *Nitzschia* under the new combination *Nitzschia ossiformis* (Taylor) Simonsen (Simonsen 1974, plate 40, figure 3). *Nitzschia ossiformis* has been reported several times since the initial observations of Taylor and Simonsen, but never in large numbers, either as *S. ossiformis* (Perissinotto 1992) or *N. ossiformis* (Kaczmarek et al. 1986, Boden and Reid 1989, Licea 1992, Treppke 1995, Lui 2008). We are unaware of any studies of the fine structure of valves of either *S. ossiformis* or *N. ossiformis*.

There remains a concern that the diatoms observed by Taylor and Simonsen are, in fact, distinct entities belonging to different genera. Taylor (1966), in his description of *Synedra ossiformis*, clearly notes the presence of a narrow central area as “a fine linear pseudoraphe [that] is almost indistinguishable from delicate longitudinal striae of equal thickness” (Taylor 1966, p. 441) and mucilage pores at each apex. Longitudinal striae of the sort described and illustrated by Taylor usually result from a regular, relatively coarse, arrangement of areolae within transverse striae (Taylor 1966, plate 91(4), figure 34). This type of structure is not consistent with the figure provided by Simonsen (Simonsen 1974, plate 40, figure 3). Nor does it match the 6–7 areolae in 1 µm (60–70 in 10 µm) observed in *Sulcatonitzschia novossiformis*. In addition, Simonsen (1974) makes no mention of Taylor's observations of mucilage pores. The implicit assumption made by Simonsen was that 2 diatoms with the same size, distinctive shape, and striae density found in relatively close proximity both in time and space probably belong to the same species. Under

this assumption, the discrepancies in the descriptions, especially Taylor's failure to note the presence of a canal raphe, could be attributed to the difficulties involved in resolving key features of the valve accompanying the techniques used by Taylor. For systematic work with diatoms Taylor examined cells cleared by passage through a series of alcohols, then mounted in Hyrax, not acid cleaned valves as is the standard practice (Taylor 1966, p. 437). Taylor did clean some aliquots of his phytoplankton samples with acid for observation using electron microscopy, but it does not appear that he was able to observe *S. ossiformis*, probably because of the small numbers of cells in the sample (Taylor 1966). It is also possible that Taylor's observations are correct, and that he did indeed observe a synedroid diatom inhabiting subantarctic waters, distinct from the nitzschoid diatom observed by Simonsen (1974) in equatorial waters. It is unfortunate that all we have to work with is a line drawing, with all of its inherent assumptions and interpretations (Taylor 1966, plate 4, figure 34), as the type of *Synedra ossiformis*, and a single photograph (Simonsen 1974, plate 40, figure 3) to justify its transfer. Unless and until archived material from the original samples can be located and critically examined, we will be left with a lingering doubt concerning the synonymy of the 2 taxa. In this context, it should be noted that Kato and Suto (2018) recently described a new species, *Thalassionema bifurcum* Kato et Suto from Pleistocene sediments, with concave apices, similar to those in *N. ossiformis* and *S. novossiformis*.

The taxon observed in the present study clearly cannot be reconciled with the description and illustrations provided by Taylor (1966) for *Synedra ossiformis*. However, it is similar in size, shape and the density of striae to the descriptions and measurements provided by Simonsen (1974), Kaczmarek et al. (1986), and Licea (1992) for *Nitzschia ossiformis*. It is possible that diatoms described in these papers are actually members of *Sulcatonitzschia*. Detailed observations of the fine structure and the confirmation of the presence of a transverse sulcus are necessary to confirm this hypothesis. Our attempts to locate specimens of *N. ossiformis* in material collected by Simonsen during the cruise of the *R/V Meteor*, currently included in the Hustedt Diatom Collection at the Alfred Wegener Institute (2020), at the Helmholtz Centre for Polar and Marine Research (<https://www.awi.de/en/science/biosciences/polar-biological-oceanography/main-research-focus/hustedt-diatom-study-centre/database.html>), were unsuccessful. Until these observations can be completed, it is better to keep *Sulcatonitzschia novossiformis* and *Nitzschia ossiformis* separate.


In summary, *Sulcatonitzschia* shares numerous features with members of the genus *Fragilariopsis*, including: the formation of ribbon-like colonies; cells with a degree of heteropolarity in the fine structure of the valve, but not the gross outline; raphe canals free of poroids on the exterior walls; raphe canals not raised above the surface of the valve; raphes without terminal fissures, striae composed of 2 or more rows of poroids occluded by hymenes with a hexagonal array of openings; and a cingulum composed of a valvocopula with a single row of pores and hyaline copulae. In spite of these similarities, *Sulcatonitzschia*


novossiformis cannot be accommodated in *Fragilariopsis*. The valve outline – long and thin, with inflated ends – and, more importantly, the presence of a transverse sulcus at one pole of the valve, are too far removed from the norms for the genus. Furthermore, the transverse sulcus in *Sulcatonitzschia* is unique among the Bacillariaceae.

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