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SOME ASPECTS OF MORPHOLOGICAL VARIATION IN *STEPHANODISCUS NIAGARAE* (BACILLARIOPHYCEAE)¹

Edward Theriot and Eugene F. Stoermer

Great Lakes Research Division, University of Michigan, Ann Arbor, Michigan 48109

ABSTRACT

Valves of *S. niagarae* var. *niagarae* Ehr. and *S. niagarae* var. *magnifica* Fricke from geographically dispersed sediment and plankton collections were observed by light microscopy and scanning electron microscopy (LM and SEM). Measurements made by LM can be arranged so that means and ranges of diameter, areolar density, or stria density intergrade from one population into the next. Mean diameter is negatively related to increasing areolar and stria densities. No unique features observable by SEM distinguish the two described varieties. Thus, *S. niagarae* var. *magnifica*, having large diameter valves with low areolar and stria densities, may represent one end of a trend in overall variation in *S. niagarae*. At the opposite extreme are the populations with small valves and high areolar densities which are often erroneously referred to as *S. astraea*. Type material of *S. niagarae* lies intermediate to these forms. Three populations considered in this study have distinct morphological characteristics. Valves from Yellowstone Lake sediments have spine placements distinctly different from valves of all other populations. Specimens from Lake Superior have nearly flat central areas. Ribs of valves from Grand Traverse Bay (Lake Michigan) are covered with granules.

Key index words: diatoms, polymorphism; diatoms, ultrastructure; diatoms, phytogeography; *Stephanodiscus*; *Thalassiosiraceae*

The centric diatom genus *Stephanodiscus* Ehr. was erected with the description of *S. berolinensis* Ehr. and *S. niagarae* Ehr. (9). Ehrenberg (1845) did not formally designate a generitype or a holotype for either species but apparently intended to base the genus on *S. berolinensis*: "Der *Stephanodiscus niagarae* ist eine ausgezeichnete grosse Art dieser erst im vorigen Jahre bei Berlin mit einer kleineren Art (*S. berolinensis*) entdeckten Gattung." Authentic mate-

rial of *S. berolinensis* has either been lost or exists unlabeled in the Ehrenberg Collection of the Paleontological Museum in Berlin (Museum für Naturkunde der Humboldt-University zu Berlin). The lake from which it was first collected is now within the city limits of Berlin, and the ecology and flora of the lake are undoubtedly altered. Authentic material of *S. niagarae* exists in the Ehrenberg Collection. Also, the Academy of Natural Sciences of Philadelphia and the Farlow Herbarium (Harvard University, Cambridge, Mass.) have material attributed to J. W. Bailey (ANSP 42768 and Bailey 1793, respectively) believed to be derived from the original Niagara Falls material from which *S. niagarae* was described.

There is some question in the literature on the taxonomic affinities and range of variation in *S. niagarae*. A variety, *S. niagarae* var. *magnifica* Fricke, was described from fossil material in Mexico (31). Distinctions between the two taxa are not generally made in the recent phycological literature. Cleve-Euler (1951) made the combination *S. astraea* var. *niagarae*, based on supposed similarities to *S. astraea* (Ehr.) Grun. a combination not accepted by most authors.

Both described varieties of *niagarae* flourish in naturally and culturally eutrophied waters, but are reduced in abundance in waters receiving high amounts of chlorides and industrial pollution (36). The taxa occur in lakes and rivers throughout North America (e.g. 2,38). Also, extant material has been reported from Russia (15) and West Java (14). Fossil material has been reported from locations in North America, Russia (16), Europe (6) and Japan (24).

A significant amount of interpopulational variation was encountered in this study. In spite of this, most populations could be identified as one or the other of the described varieties. However, three

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populations were distinguishable from both described varieties and are perhaps worthy of varietal status themselves.

Variation and inadequate typification of this and other *Stephanodiscus* species often cause misidentification of *S. niagarae*. Small valves, especially, are commonly mistaken for *S. astraea*. The purpose of this paper is to describe the morphology of morphotypes of the *S. niagarae* complex to aid in its identification, and to provide a basis for further studies on this and related taxa.

MATERIALS AND METHODS

Specimens were examined from 11 collections made in 8 lakes in the United States. Samples were collected from surface sediments of the South Arm of Yellowstone Lake, Wyoming, by B. Shero (Medaille College, Buffalo, N.Y.) and a core of Lake Erie sediments at 6 and 20 cm below surface sediments by V. R. Frederick (Great Lakes Laboratory, State University of Buffalo). Plankton samples were collected from the open waters of Lake Superior, Michigan; Green Bay and Grand Traverse Bay, Lake Michigan; and Saginaw Bay, Lake Huron, by the Great Lakes Research Division, University of Michigan (GLRD). Plankton samples from Teal Lake, Michigan; Lake Erie, Pennsylvania; and West Lake Okoboji, Iowa, were donated from the personal collections of R. Kreis (GLRD), B. Glover (GLRD), and E. F. Stoermer, respectively. Material on slide ANSP 42768 is the basis for our concept of *S. niagarae*. We point out that because Lake Erie is the only significant water source for the Niagara River, any planktonic diatom discovered in the river probably originated in Lake Erie and that Frederick's and Glover's collections are modern collections from Erie.

Light and scanning electron microscopic (LM, SEM) observations and micrographs were made on material which was either incinerated (38), or acid-cleaned by allowing the material to remain overnight in approximately equal volumes of sample and concentrated nitric acid, or by the method of Patrick and Reimer (1969), and then washed in distilled water to remove the acid. Cleaned material was air-dried on a cover slip and warmed to remove adsorbed water. For LM, material was embedded in Hyrax (refractive index 1.71) and observed and photographed at 950 $\times$ with a Leitz Ortholux microscope fitted with a double diaphragm, 1.40 N.A. immersion condenser and 1.40 N.A. APO objective. For SEM, cover slips with material were affixed to stubs with double stick tape. Latex spheres (1.109 μ m, E. Fullam Co.) were dried on the cover slip for internal calibration of magnification, and the entire preparation was coated with gold in a Technics D-C Hummer sputter system. For transmission electron microscopy (TEM), specimens from Saginaw Bay were fixed, sectioned and photographed by Dr. L. Sicko-Goad and D. Lazinsky (GLRD). Samples were fixed in the field in 3% glutaraldehyde in 0.05 M cacodylate buffer, pH 7.2. The samples were held on ice until returned to the laboratory (ca. 6 h), then rinsed in buffer and post-fixed in 1% OsO₄ in the same buffer for 1 h. They were then dehydrated through a graded ethanol-propylene oxide series and embedded in Epon 812 (20). Sections were cut on a diamond knife, collected on 300 mesh copper grids, stained with uranyl acetate (34) and examined in either a Zeiss EM 95-2 or JEOL JEM 100B electron microscope.

With the exception of ANSP 42768, all material examined (as Hyrax slides, cleaned material, SEM stubs, and TEM grids) are housed at GLRD (Stoermer collection). When the amount of available material permitted, duplicate Hyrax slides were deposited in the University of Michigan Herbarium.

Measurements were taken via LM from the first nine valves encountered in a level plane of focus in each sample. Areolar density was measured from the level of spine insertion towards

the center along the stria most directed left. Using this stria as a center, stria density was measured along a line tangent to spine insertion. The number of rows of areolae at the level of spine insertion in the center stria and each of the four nearest striae were recorded and averaged.

RESULTS

Terminology used conforms to proposals of the International Symposium of Recent and Fossil Diatoms (1) and to an amendment of that report (27). Except as noted, reported observations are applicable to all specimens examined.

The valves are strongly arched and appear undulate in girdle view in the LM (Fig. 1). As in other *Stephanodiscus* taxa the areolae are arranged in radiating striae separated by raised hyaline costae (Figs. 2a-7). In the central area the striae are uniseriate and occasionally appear wavy or lose definition entirely (Fig. 7). Towards the margin striae become biseriate. The striae end in 2 or more rows of areolae (Figs. 2a-8). The areolar pattern may become disorganized near the margin, obliterating the ends of the costae (Figs. 4, 8). Areolae on the mantle are more densely packed than those of the valve face (Figs. 7, 8). From 8 to 13 areolae are located in a vertical row from the junction of the face and mantle to the valve margin.

Foramina of the loculate areolae appear round or angular in the SEM (Figs. 8, 9) and round in high focus in LM (Fig. 2b). Atypically, they may be partially or completely closed by aggregates of granules or small "hoods" (Fig. 10). In deep focus in LM, areolae appear hexagonal; areolar chamber size being inversely proportional to areolar density (Figs. 2a, 3, 4). Convex cribra close the internal opening of the areolae (Fig. 11a). Pores in the vella are visible only with TEM and are themselves partially occluded by rices (Fig. 11b). The rices together have the appearance of a small ring supported by several struts within the cribrum pore (Fig. 11b).

About the margin, a thickened rim completely encircles the very edge of the valve and extends slightly beyond the mantle forming a small step (Fig. 12). There are vertical "scratches" in this rim at irregular intervals.

There are three types of processes on every valve. From two to nine strutted processes occur in the central area (Fig. 13). Each takes the place of an areola in a stria (Fig. 14). Strutted processes occur also on the mantle (Figs. 8, 13, 15) and are almost always associated with a spine. A narrow costa about half the length of the mantle depth separates the two processes (Figs. 8, 10, 12). Strutted processes on the mantle always have three satellite pores, whereas central strutted processes generally have two (Figs. 14, 16). Satellite pores extend past the basal siliceous layer along the central tube into the interior of the cell. They appear to be wholly occluded at the internal end (Fig. 17). Some micrographs suggest a narrow passage into the biological interior but we

FIGS. 1-6. Specimens illustrating the range of size and character variation in populations of *S. niagarae* sensu lato. FIGS. 1, 3, 4. Specimens typical of *S. niagarae* var. *niagarae*. FIG. 1. Girdle view; recent plankton from Green Bay, Lake Michigan. FIG. 3. Valve view photographed at low focus, ANSP 42768. FIG. 4. Valve view photographed at low focus; recent plankton from Saginaw Bay, Lake Huron. FIGS. 2a, b. Specimens typical of *S. niagarae* var. *magnifica*; recent plankton from Lake West Okoboji, Iowa. FIG. 2a. Valve view photographed at low focus. FIG. 2b. Segment of same specimen photographed at high focus. FIGS. 5, 6. Specimens from variant populations which have not been described. FIG. 5. Valve view photographed at high focus. Note that the loculi of the central areolae are in the same plane of focus as the foramina of the striae areolae, an indication of the flatness of the valve center; modern plankton from Lake Superior. FIG. 6. Valve view photographed at high focus; surficial sediments from Yellowstone Lake, Wyoming. Specimen shown in Fig. 3 is mounted in Canada balsam, all others mounted in Hyrax. Scale = 10 μ m.

have not been able to demonstrate this conclusively. Spines occur at the junction of the valve face and mantle at every second to third rib (Figs. 3-5, 7). Because the mantle slopes strongly, spine placement appears submarginal in LM. This is not so obvious in smaller (ca. 25-35 μ m diameter) specimens. Spines are tapered, with a sharply pointed, flattened or pinched appearance at the tip (Fig. 8). Three to

seven labiate processes are inserted at or near the level of spine insertion (Figs. 7, 8, 10, 18, 20, 21). Their external expression superficially resembles the spines and they are difficult to distinguish via LM. However, they are shorter, straighter and less tapered than spines and are inserted at a slightly different angle than the spines.

Three populations share a majority of valve fea-

NOTE: abbreviations used in Figs. 7-21: S = spine, L = labiate process, M = mantle strutted process, C = central strutted process

FIGS. 7-14. Ultrastructure of the valve of *S. niagarae* sensu lato. FIG. 7. Typical valve morphology. Arrows mark suture. Saginaw Bay. FIG. 8. Detail of mantle and valve of 7. FIG. 9. Detail of central area areolae, Lake Erie. FIG. 10. Detail of mantle and valve with areolae with obstructed foramina. Green Bay. FIG. 11a. Longitudinal section of striae areolae, Saginaw Bay. FIG. 11b. Cribrum in cross section. Long axis of areola is perpendicular to page. Note rices within cribrum pores. Saginaw Bay. FIG. 12. Detail of mantle illustrating thickened rim at the margin. Arrows mark suture. Saginaw Bay. FIG. 13. Biological interior, Saginaw Bay. FIG. 14. Detail of central strutted process, Biological interior, Yellowstone Lake. Scale = 5 μm (Figs. 7, 13); 1 μm (Figs. 8, 9, 10, 11a, 12, 14); 0.25 μm (Fig. 11b).

FIGS. 15-18. Ultrastructure of the valve of *S. niagarae* sensu lato. FIGS. 19-21. Atypical population valve morphology. FIG. 15. Detail of mantle and valve face. Biological interior. Green Bay. FIG. 16. Cross section of mantle strutted processes from a grazing section of the mantle area. Saginaw Bay. FIG. 17. Longitudinal section of mantle strutted process. Saginaw Bay. FIG. 18. Longitudinal section of labiate process and spines. Saginaw Bay. FIG. 19. Lake Superior valve with relatively flat central area. FIG. 20. Detail of thickened spines and labiate process of Yellowstone Lake valve. FIG. 21. Grand Traverse Bay valve. Note large granules on costae and in central area. Scale = 1 μ m (Figs. 15-18, 20); 5 μ m (Figs. 19, 21). Arrows indicate latex spheres in Figs. 20 and 21.

tures with other material but also have characteristics clearly distinguishing each from all other populations. Valves from Lake Superior are only slightly arched in the center (Figs. 5, 19). All Yel-

lowstone Lake valves have spines at every third and/or fourth costa (Figs. 6, 20). The spines and labiate processes of these valves are exceptionally thickened at the bases and so are heavily tapered (Fig. 20).

FIG. 22. The relationship between mean areolar density and mean diameter. Abbreviations: LOK = West Lake Okoboji, SUP = Lake Superior, JB = ANSP 42768, YSL = Yellowstone Lake, GTB = Grand Traverse Bay, GRN = Green Bay, TEAL = Teal Lake, SAG = Saginaw Bay, ERIE = Lake Erie, CR6 and CR20 = Lake Erie core at 6 cm and 20 cm depth, respectively.

FIG. 24. Means and ranges of diameter by location. Abbreviations as in Fig. 22.

Large granules on the costae characterize valves from Grand Traverse Bay (Fig. 21).

Plots of the means and ranges of measurements made by LM reveal considerable interpopulational variation as well as several interesting character correlation patterns. First, there is a negative correlation between mean diameter and mean areolar density (Fig. 22). Second, as areolar density increases to 13 per 10 μm the stria count remains relatively constant while there is an irregular fluctuation in the number of rows of areolae per stria (Fig. 23). Above 13 areolae per 10 μm there is a rapid increase in average stria density and a reduction in the number of rows of areolae per stria (Fig. 23). Finally, there is no clear discontinuity in any single character plotted against location except perhaps for diameter. Valves from Lake Okoboji average much larger than those of ANSP 42768 with little overlap in size (Fig. 24). Interestingly, valves from the modern Lake Erie plankton collection are much finer in overall measurements than core material or ANSP 42768.

FIG. 23. The relationship between mean areolar density, mean stria density and mean number of rows of areolae per stria. Abbreviations as in Fig. 22. The numbers below the plotted areolar and stria density data are the mean number of areolar rows.

DISCUSSION

We are familiar with three studies including descriptions and/or micrographs of *S. niagarae* to which we may compare our results. Observations and measurements made on Japanese fossil material using TEM are generally in accord with our own (24). However "an annulus of pointed or T-shaped spinules about 10 μm long" (we assume these are spines) were observed about the margin (24). Spines on valves we observed were never that long, nor were they T-shaped. Furthermore the areolae were reportedly "closed outwards by a sieve membrane and occluded inwards by a cover membrane" (24). It was not clear what was meant by a "cover membrane". As a comparison we can only offer the thin siliceous membranes that occasionally obstruct the foramina of our specimens. In our specimens of *S. niagarae* and in all other *Stephanodiscus* species with loculate areolae, the cribra (Okuno's sieve membrane) close the areolae on the internal surface of the valve (4,7,11,19,29). Perhaps Okuno (1964) did not correctly interpret the structure because of the two-dimensional nature of TEM observations. Differences in spine length and shape also suggest that we are dealing with different taxa. Other scanning electron micrographs of Asian diatoms captioned as *S. niagarae* (16) are questionable. Plate 14, Figure 11 (in 16) illustrates a *Stephanodiscus* with a short spine at every rib and a flat valve face. This more closely resembles *S. tenuis* Hust. or *S. hantzschii* Grun. and we regard this as a misidentification. The valve in Plate 4, Figure 5 (in 16) is arched in the center as in most of our North American material, but differences exist. The valve mantle appears shallower than in our material and each rib appears to extend well into the mantle region, again suggesting a misidentification. No spines are visible but they may have been broken off or dissolved in this fossil material. SEM's of material from sediments of sev-

eral Minnesota lakes (4) are in agreement with our own.

Three features warrant further investigation. First, the satellite pores of strutted processes of *Stephanodiscus* species often, if not always, appear occluded in SEM (unpublished observations, 28). Observations on *S. niagarae* suggest that small passages resolvable only with TEM, exist into the satellite pore, but this was not confirmed. Secondly, *ricae* have been previously observed within the cribriform pore of *S. niagarae* var. *magnifica* from Lake Okoboji (7) and illustrated but not discussed for *S. astraea* var. *minutula* (Kütz.) Grun. (10). It may be of widespread occurrence in this genus, but because of its small size and delicate structure it is generally overlooked or destroyed by standard valve cleaning techniques. Our unpublished electron micrographs of longitudinal sections of the areolae suggest the presence of a thin siliceous membrane supporting the *ricae* within the cribriform. If this is the case then the areolae would not be a complete perforation of the basal siliceous layer. The cribriform pores in *Thalassiosira eccentrica* (Ehr.) Cleve (Centrales: Thalassiosiraceae) reportedly are not perforations of the basal siliceous layer, but are sites of extremely thin (12 nm) silicification (30). These features may provide another link among genera of the family Thalassiosiraceae. Finally, another areolar substructure deserves attention. Obstructed foramina occur occasionally not only on *S. niagarae* but also on *S. alpinus* Hust. (unpublished observations), *S. tenuis* Hust. and *S. binderanus* var. *oestrupii* (35). In the latter two species the occurrence of foraminal obstructions was limited to valves apparently specialized for colony separation. The significance of this feature for non-filamentous species is unknown. Valves with obstructed foramina do not characterize any population but were found on each of several preparations along with valves of normal areolar morphology.

The number and location of strutted processes, labiate processes and spines are given considerable weight in the classification and identification of *Stephanodiscus* species (11,19). In *S. niagarae* the placement and number of strutted processes in the central area may be so variable that there is little taxonomic information associated with that feature. The association between spines and marginal strutted processes, including the distance separating the two, is very constant and most important in the identification of the entire *S. niagarae* complex (Figs. 7, 19, 21). That the labiate processes are distinguishable from spines in external view in SEM and in LM makes them somewhat useful in identification, although their number appears quite variable within and between populations. Moderate to large valve diameters and very robust spines are also characteristic of all populations. The submarginal placement of the spines is useful in identifying larger specimens but may be difficult to detect on smaller specimens. Incomplete or inaccurate statements con-

cerning this feature have apparently caused misidentification of *S. niagarae*. Spine placement is generally considered an important distinguishing character for identification of *S. astraea* and *S. niagarae* (e.g. 38). We have examined many North American collections purported to have been *S. astraea*. All medium to large *Stephanodiscus* valves observed in those collections are more correctly identified as *S. niagarae*.

It is extremely difficult to make a comparison of *S. niagarae* and *S. astraea* sufficient to hypothesize their evolutionary relationship because of nomenclatural and morphological uncertainties about the true identity of *S. astraea*. Ehrenberg (1844) described *Discoplea? astraea*. That same year Kützting (1844) described *Cyclotella rotula*. Kützting (1849) then made the combination *Cyclotella astraea* of *D.? astraea* and *C. rotula*, implying Ehrenberg (1844) preceded Kützting (1844). We cannot absolutely substantiate that, but the forward of Kützting's book is dated July, 1844, whereas Ehrenberg (1844) is dated 27 June. Grunow (in 5) placed *C. astraea* (Ehr.) Kütz. in *Stephanodiscus*, accepting Kützting's (1849) treatment of the specific epithet. Hendey (1964) did not explain why he made the combination *S. rotula* (Kütz.) Hendey citing *C. rotula* Kütz. and *S. astraea* (Kütz. ex Ehr.) Grun. in synonymy. It is not clear if he was confused by Kützting's (1849) subsequent transfer of *Discoplea rotula* Ehr. to *Cyclotella*, illegally retaining the epithet, as *Cyclotella rotula* (Ehr.) Kütz. It is entirely possible that *D. astraea* and *C. rotula* Kütz. are entirely different species, making Hendey's combination correct but his synonymy incorrect. Considerable morphological variability has been reported for *S. astraea*. Hendey (1964) reported that *S. rotula* from coastal waters in England has a spine at the end of each rib. Håkansson (1976) reported irregular spine placement on valves from Swedish lakes and that central strutted processes were entirely lacking, and illustrates variable placement of marginal strutted processes. One valve has strutted processes well below the spines as in *S. niagarae*; two others, immediately below the spines. Skabichevsky (1973) found statistically significant differences in spine pattern, diameter and areolae counts among populations from different locations in Russia. Our unpublished observations on isotype material of *Cyclotella rotula* Kütz. confirm that it is a genuine *Stephanodiscus* according to the criteria of Round (1970). But it is distinct from both Hendey's and Håkansson's material, having a ring of central strutted processes and irregular spine placement. Clearly type material of *D. astraea* must be examined and *S. astraea* reevaluated before determining evolutionary relationships between *S. astraea* and *S. niagarae*.

Delineating *S. niagarae* var. *magnifica* and *S. niagarae* var. *niagarae* on the basis of material examined is difficult. We were not able to demonstrate an obvious discontinuity in any single character seg-

regating the specimens into groups conforming to standard concepts of the two taxa. Fricke's (in 31) original illustrations separate the two taxa only on the basis of size. Even though there is some overlap in size there is a large increase in mean diameter of the Lake Okoboji population over material on ANSP 42768. Because of this and because the size range of the Lake Okoboji population falls within the size range suggested by Fricke's illustrations we tentatively regard this material as *S. niagarae* var. *magnifica*. Examination of type material as well as specimens from a broader geographical area is warranted.

Because diameter is such a critical character it is important to discuss variation in this feature in relationship to Margalef's (1969) well known theory of size variation in centric diatoms. Margalef (1969) hypothesized that, in general, a centric diatom species will become reduced in diameter when exposed to increasingly eutrophic conditions. More complete analysis of *S. niagarae* from a Lake Erie core provides some support for this theory (Theriot and Stoermer, unpublished data). Also valves from more eutrophic localities in the Great Lakes (Lake Erie, Saginaw Bay and Green Bay) are smaller than those from oligotrophic Lake Superior and Grand Traverse Bay (Fig. 24). Since diameter is correlated with other characters which are themselves inter-correlated, the trophic status of a lake may influence overall valve morphology. Margalef's hypothesis would not have predicted the large valves of highly eutrophic West Lake Okoboji. This may indicate genetic distance between *S. niagarae* var. *magnifica* and the nominate variety, or it may be that size control is by some particular environmental factor, generally but not always, associated with eutrophy.

Differences observed with SEM and LM other than size do not relate to standard concepts of the two described varieties, but do characterize several local populations. Further investigations of Yellowstone Lake, Lake Superior and Grand Traverse Bay populations may warrant the description of new varieties of *S. niagarae*.

Because the functional morphology of valve features is incompletely understood, the reason for the variation encountered and associated competitive advantages are unclear. Variation encountered may be the result of variable phenotypic expression of a single genotype in response to varying environmental conditions. Silica concentrations (3), salinity (12, 25, 32), nitrogen and phosphorus concentrations and temperature (37) can control polymorphism in uni-algal cultures of centric diatoms. It is also possible that isolation and subsequent differentiation has occurred. Makarova (1976) felt that this mechanism accounted for morphological variation witnessed in various members of the genus *Thalassiosira*, particularly within *T. eccentrica* (Ehr.) Cleve. Skabichevsky (1973) hypothesized the same mechanism to account for variation in *Stephanodiscus* as-

traca. Murphy and Guillard (1976), using gel electrophoresis, demonstrated differences among clones of *Thalassiosira pseudonana* Hasle and Heimdal isolated from different environments, noting small morphological differences among clones. It is hard to imagine that there is no function associated with characteristic valve features and that selection does not act on them. If two populations of a species are sufficiently isolated, evidence for differentiation is expected from not only biochemical but also morphological studies. Evidence for small, discrete changes in morphology over geographic space within the *S. niagarae* complex and Murphy and Guillard's (1976) observations argue that prior complete, detailed morphological studies will enhance the understanding of taxonomic data gathered with biochemical methods.

There are suggestions of a multivariate relationship between morphology and ecological factors in *S. niagarae* and related taxa. We are presently investigating the application of multivariate statistical methods to such problems in this and other *Stephanodiscus* taxa.

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MUCILAGE TUBE MORPHOLOGY OF THREE TUBE-DWELLING DIATOMS AND ITS DIAGNOSTIC VALUE¹

Eileen J. Cox

Botany School, South Parks Road, Oxford, OX1 3RA, United Kingdom

ABSTRACT

Colonies of *Berkeleya rutilans* (Trent.) Grun., *Navicula pseudocomoides* Hendey and *N. ramosissima* (C. A. Ag.) Cleve were examined using light and electron microscopy to elucidate the structure of their mucilage tubes. Each species was found to have a characteristic tube construction which could be used for identification. A summary of features on which these species can be recognized was compiled.

Key index words: *Berkeleya*; diatoms; identification; mucilage tubes; *Navicula*

Although a number of early workers, Dillwyn (1802–1809), Agardh (1817, 1824, 1830), Greville (1823–1828), Harvey (1841), Smith (1856) and Grunow (1880a, b) used the gross features of the mucilage tube colonies produced by a number of naviculoid diatoms as a means of identification and classification, such practise has fallen into disrepute.

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