Studies on the diatom genus *Stenopterobia* (Bacillariophyceae) including descriptions of two new species

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Abstract: During an investigation of freshwater diatoms from highly acidic ponds scattered along the Atlantic Coastal Plain of North Carolina we encountered a large number of specimens from the genus Stenopterobia. All of the specimens were representative of straight, not sigmoidal-shaped, taxa and collectively ranged in length from ca. 10 µm to over 200 µm. In the process of making species determinations we examined type material for four species of Stenopterobia originally described by Lewis (1864) from Saco Pond, a small spring-fed waterbody nestled in the White Mountains of New Hampshire. The four species, Stenopterobia baileyi (Lewis) Brébisson ex Van Heurck, Stenopterobia anceps (Lewis) Brébisson ex Van Heurck, Stenopterobia delicatissima (Lewis) Brébisson ex Van Heurck, and Surirella intermedia Lewis (=Stenopterobia curvula (W. Smith) Krammer), were originally placed by Lewis within the genus Surirella. We examined seven permanent slides archived at the Academy of Natural Sciences of Philadelphia that contained material collected by Lewis. In addition, we collected new material from Saco Pond, including a sediment core, and examined these samples using SEM. We also examined type material for another species, Stenopterobia cuspidata (Hustedt) Vyverman, using SEM. We concluded that the North Carolina collections contained five species, two described as new (Stenopterobia gracilis sp. nov. Siver & Camfield and Stenopterobia fusiformis sp. nov. Siver & Camfield), two representing organisms originally described by Lewis (S. baileyi and S. delicatissima), and the fifth recently described from Cape Cod (Stenopterobia pseudodelicatissima Siver & Hamilton). New characters, including externally capped areolae, valve face coverings, and laterally opened girdle bands, are described for the genus. Lastly, lectotypes for three of Lewis' taxa were selected.

Key words: Atlantic Coastal Plain, Bacillariophyceae, lectotype, F.W. Lewis, Stenopterobia, Surirella.

Résumé : Au cours d'une recherche sur les diatomées d'eau douce des étangs fortement acides, distribués le long de la plaine côtière de l'Atlantique, en Caroline du Nord, les auteurs ont rencontré une grande quantité de spécimens du genre Stenopterobia. Tous les spécimens correspondent à des taxons rectilignes, non sigmoïdes, dont les dimensions se situent globalement autour de 10 µm à plus de 200 µm. Au cours de l'identification, les auteurs ont examiné le matériel type de quatre espèces de Stenopterobia, originalement décrites par Lewis (1864) et provenant de Saco Pond, une petite étendue d'eau alimentée par une source prenant naissance dans les White Mountains du New-Hampshire, aux USA. Lewis a originalement placé ces quatre espèces dans le genre Surirella : S. baileyi (Lewis) Brébisson ex Van Heurck, Stenopterobia anceps (Lewis) Brébisson ex Van Heurck, Stenopterobia delicatissima (Lewis) Brébisson ex Van Heurck, et Surirella intermedia Lewis (=Stenopterobia curvula (W. Smith) Krammer). Les auteurs ont examiné de plus, sept montages permanents archivés à l'Academy of Natural Sciences de Philadelphie, et contenant du matériel récolté par Lewis. Ils ont aussi récolté du nouveau matériel de Saco Pond, incluant une carotte de sédiments, et ils ont examiné ces échantillons en microscopie électronique par balayage (SEM). Ensuite, ils ont étudié le matériel type d'une autre espèce, le Stenopterobia cuspidata (Hustedt) Vyverman, en SEM. Ils concluent que les collections de la Caroline du Nord contiennent cinq espèces, dont deux décrites comme nouvelles espèces (Stenopterobia gracilis Siver & Camfield et Stenopterobia fusiformis Siver & Camfield), deux représentant des organismes déjà décrits par Lewis (S. baileyi et S. delicatissima), et une cinquième espèce récemment décrite de Cap Cod (Stenopterobia pseudodelicatissima Siver & Hamilton). On décrit de nouveaux caractères pour le genre, incluant des auréoles extérieurement recouvertes, des couverts opposés aux valves et des bandes enveloppantes ouvertes latéralement. Enfin on a sélectionné des lectotypes pour trois des taxons de Lewis.

Mots-clés : plaine côtière de l'Atlantique, Bacillariophyceae, lectotype, F.W. Lewis, Stenopterobia, Surirella.

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Introduction

Stenopterobia de Brébisson ex Van Heurck 1896 is a small genus of freshwater diatoms in the family Surirellaceae found predominately as motile forms in acidic, poorly buffered, and oligotrophic waterbodies (Patrick and Reimer

1966; Krammer 1989; Round et al. 1990). As originally proposed by Brébisson (in Van Heurck 1896), species within Stenopterobia are distinguished from those in the closely related genus Surirella by the narrow and elongated shape of the frustule and the fact that at least some taxa have a sigmoid configuration in valve view. Other species are not sigmoidal, but rather straight and linear to linear-lanceolate in outline. In general, the structure of the valve and raphe system in Stenopterobia species is considered to be less complex and distinct from that of Surirella (Krammer 1989; Round et al. 1990). In a recent cladistic analysis of taxa within the family Surirellaceae based on morphometric characters, Stenopterobia was found to represent a monophyletic clade most closely related to the Robustae section of Surirella (Ruck and Kociolek 2004). In that study, the primary characters that supported the Stenopterobia clade included areolae without internal coverings, multiseriate striae, and possession of dilated raphe ends at both valve poles (Ruck and Kociolek 2004).

In a presentation made to the Academy of Natural Sciences in Philadelphia on 29 December 1863, and subsequently published in the Proceedings of the Academy in 1864, F.W. Lewis described four narrow and elongated species of Surirella: Surirella *baileyi* (Lewis) Van Heurck, Surirella intermedia Lewis (=Stenopterobia curvula (W. Smith) Krammer), Surirella anceps (Lewis) Brébisson ex Van Heurck, and Surirella delicatissima (Lewis) Brébisson ex Van Heurck. The new species were collected by Lewis from the marsh end of a small, shallow, spring-fed pond situated in the White Mountains of New Hampshire, known as Saco Pond. Lewis was particularly intrigued with the narrow and elongated nature of the valves, to the point that he referred to them as "transitionary" within Surirella and noted a resemblance to the more elongated genera Nitzschia and Synedra. Two of the Saco Pond species were sigmoidal (S. intermedia and S. anceps) and the other two, straight and linear forms. Not surprising, de Brébisson established Stenopterobia (in Van Heurck 1896) based largely on the narrow and elongated nature of Lewis' four species and transferred all four taxa into his newly erected genus. Recently, Krammer (in Lange-Bertalot and Krammer 1987) reported S. intermedia to be conspecific with Nitzschia curvula W. Smith (Smith 1856) and transferred it into Stenopterobia using the epithet "curvula" because it has taxonomic priority. Stenopterobia anceps and S. baileyi are believed to be endemic to North America, while S. delicatissima and S. curvula are widespread and cosmopolitan species (Krammer 1989).

As part of a larger project aimed at surveying diatoms and scaled chrysophytes in ponds along eastern North America, we encountered a significant number of *Stenopterobia* specimens in waterbodies along the Atlantic Coastal Plain of North Carolina. All of the specimens were straight forms that collectively ranged in length from ca. 10 μ m to over 200 μ m and clearly represented a number of different species. To sort out specimens and make species determinations it was necessary for us to examine type material from Saco Pond as well as type material for *Stenopterobia cuspidata* (Hustedt) Vyvermann. The objective of this contribution is to present our findings, including details on the designation of lectotypes for three of Lewis' original species and de-

scriptions for new character traits of *Stenopterobia* and two new species within this genus.

Materials and methods

Planktonic, periphytic, and surface sediment samples were collected from 27 freshwater waterbodies along the Atlantic Coastal Plain of North Carolina in May and June 2001. Plankton samples were collected with a 10 µm mesh net from the center of each waterbody. Representative periphyton samples were collected from microhabitats around the perimeter of each waterbody and stored in whirl-pack bags. Surface sediments were taken from the deep point of each lake using a Glew gravity corer (Glew 1989) and sectioned on site with a mechanical extruder (Glew 1988). Water samples for chemical analyses were taken at a depth of 1 m from the center of each waterbody. The Secchi disk depth and geographic coordinates were taken with a 20 cm black and white disk and a Trimble Geoexplorer GPS unit, respectively. Specific conductance and temperature were measured with a Hydrolab DataSonde 4A. Chemical analyses followed the procedures of Ahrens and Siver (2000) or as modified by Lott and Siver (2005). In addition to the physical and chemical data presented within this study, data for all study locations can be found at the web site, silicasecchidisk.conncoll.edu.

Approximately 1-2 mL of each concentrated plankton sample was air dried onto heavy-duty aluminum foil on the day of collection. For the purposes of this study, aliquots of all periphyton collections from a given waterbody were mixed into a combined sample. The surface sediment (0-1 cm) samples and combined periphyton samples were oxidized with a sulfuric acid - potassium dichromate solution according to Marsicano and Siver (1993), and an aliquot from each resulting slurry was air-dried onto both aluminum foil and glass cover slips. The aluminum foil samples were used for observation with SEM according to the procedures of Siver (1987). Essentially, samples were attached to an aluminum stub with Apiezon® wax, coated with a gold and palladium mixture for 1 min with a Polaron model E5100 sputter coater and observed with a Leo 982 SEM. Glass cover slips were mounted onto glass slides with Naphrax mounting medium, observed with a Leica DMR light microscope equipped with differential interference contrast (DIC) and reflected interference contrast optics (Siver and Hinsch 2000) or an Olympus BX-51 light microscope and imaged with a Sony DKC-ST5 digital camera. Specimens of the two new species selected as holotypes and isotypes were lightly encircled with a diamond scribe and deposited into herbaria as described below. Aliquots from the slurries have been deposited at the California Academy of Sciences (CAS) and the Canadian Museum of Nature (CANA). A minimum of 25 specimens of each species of Stenopterobia found in the samples was measured to establish morphometric ranges. The terminology used in this paper follows Ross et al. (1979), Krammer (1989), and Ruck and Kociolek (2004).

As part of our study we found it necessary to examine type material for three straight forms, *S. delicatissima*, *S. baileyi*, and *S. cuspidata*. In the process of examining this material, we were also able to inspect specimens of three sigmoid species of *Stenopterobia* with SEM. Two of these taxa, *S. anceps* and *Surirella intermedia*, were originally described by Lewis (1864) and the third, Stenopterobia pelagica Hustedt, by Hustedt (1942). Richard Crawford (Alfred Wegener Institute) kindly supplied us with a small liquid sample (preserved with glycerin) of type material for S. cuspidata from the Hustedt collection: AS1320 Celebes, Wallacea Expedition, Wawontoa See. This material was rinsed several times with distilled water, dried onto aluminum foil and prepared for observation with SEM as outlined above. For the four species originally described by Lewis (1864), we examined seven slides archived at the Academy of Natural Sciences in Philadelphia (ANSP) that were made from type material taken from the original locality, Saco Pond, as noted below, and in Table 1. Eduardo Morales and Marina Potapova, both at ANSP, helped us to locate these slides for examination. These individuals also searched the ANSP diatom herbarium records and determined that no original material remained that could be used for observation with SEM. In an attempt to obtain material of the Stenopterobia species originally described by Lewis that could be examined with SEM, we traveled to and sampled Saco Pond in September 2005. During that visit we collected numerous samples from all habitats of the waterbody and took a gravity core from the center of the pond that measured 31 cm in length. Our thinking was that in the event the organisms were no longer resident in the pond, we may be able to find specimens within layers of the core deposited close to the time Lewis made his original trip in the 1860's. Although we were not able to secure funds to date the core, it is highly likely based on similar cores from New England that bottom sections are over 100 years old.

Results

Comments and findings on permanent slides archived at ANSP

Seven slides archived at the ANSP with material from Saco Pond were examined as part of this study (Table 1, Figs. 1-7). Six of the slides are in the Febiger Collection and one (44940) within the General Collection, although the latter originated from the G.A. Fisher Collection. Of the six in the Febiger Collection, three (2350, 2645, 2646) are noted to have been prepared by F.W. Lewis, two (4320, 4321) prepared by Febiger from material collected by Lewis and one (2338) does not list details of who collected the material or prepared the slide. There is confusion on some of the records associated with these permanent slides regarding the location of Saco Pond and the date. Some list Saco Pond in the State of Maine and others question whether it is in New Hampshire (Table 1). There is no question that Saco Pond, the headwaters of the Saco River, is situated in New Hampshire. Corrections to this effect were noted on several cards by F. Keeley, formerly a curator at the ANSP. Some of the confusion may be due to the fact that the Saco River eventually flows from New Hampshire into Maine. It is also unclear whether the dates found on a few of the slides or associated cards pertain to the time the material was collected or when the slide was actually prepared. All of the dates found were listed as 1863 or later changed to this year. In the original publication presented to the ANSP on December 29, 1863 and published in 1864, Lewis noted that he made the collections "about three years ago" leading us to believe that the material he used was most likely collected in 1860.

All three of the slides prepared by Lewis (2350, 2645, 2646) have similar diatom assemblages and appear to represent the same sample. The assemblages are especially rich in Eunotia and Frustulia, with lesser contributions from Tabellaria, Neidium, Pinnularia, Encyonema, and Stenopterobia, and are consistent with an acidic environment. All four of the Stenopterobia species originally described by Lewis from Saco Pond under the genus Surirella: S. bailevi, S. intermedia, S. anceps, and S. delicatissima were found on slides 2645 and 2646, and all species except S. baileyi were found on on slide 2350. In addition to Stenopterobia taxa, all three slides contained specimens of Actinella punctata Lewis, also originally described from Saco Pond by Lewis. Other notable species included Semiorbis hemicyclus (Ehrenberg) Patrick, Frustulia bahlsii Edlund & Brant, Eunotia serra Ehrenberg, and Fragilariforma constricta (Ehrenberg) Williams & Round. It is not clear what type of mounting medium was used to prepare these slides, but it is thicker around the edges of the cover slip relative to the center and is best viewed with phase contrast as opposed to DIC. Unfortunately, we were unable to focus on specimens from slides 2350 and 2645 with a $100 \times$ oil-immersion lens, consistent with similar attempts made by ANSP scientists; owing to the slightly curved nature of the preparation (lower in the center and higher around the margins) coupled with the small size of the cover slip, the margin of the lens comes to rest on the preparation before the proper working distance can be achieved.

The diatom assemblages on slides 2338 and 44940 appear to represent the same material, as noted above on the three slides prepared by Lewis. There is no record of who made slide 2338 or collected the material found on it. This slide also differs from the other six in that the material was not cleaned prior to preparation, as indicated by the organic matter and whole tests of amoeba found on the slide. The handwriting on the small label found on slide 2338 appeared to match that on the three slides prepared by Lewis and on letters originally written by him and archived at the ANSP library. Although we can't be certain, it is probable that Lewis also prepared this slide. The handwriting on slide 44940 differs from that on 2338 and the slides known to be prepared by Lewis. As was the case for slides 2350 and 2645, we could not focus on specimens on slide 44940 with a $100 \times$ oil-immersion lens.

The diatom assemblages on the last two slides prepared from Lewis' material by Febiger, slides 4320 and 4321, appear to represent a different habitat from Saco Pond relative to the other five. Although many of the same diatom taxa are found on these slides, the relative proportions differ considerably from the other five slides, and both of the slides prepared by Febiger contain significant numbers of sponge spicules. The clarity of these two preparations is superior to the others and each contained circled specimens. There is a notation on the slide made by C.W. Reimer that says "*Stenopterobia anceps* (Lewis) (good cells)" along with a scribed circle containing several whole specimens as well as parts of others (see below). Slide 4321 also contained an enscribed circle with a large, centrally located specimen of *Frustulia bahlsii*, a taxon denoted by Lewis (1865) as the sporangial

Collection	Number	Preparer	Remarks	Locality	Other
Febiger	2338	i		Saco, Maine	Scribed circle of Stenopterobia delicatis- sima, this study
Febiger	2350	F.W. Lewis	Fine washing	Saco Pond, N.H.	
Febiger	2645 ^a	F.W. Lewis	Semi-fossil	Saco Pond, Me; N.H. (Keeley)	Scribed circle of S. delicatissima, this study
Febiger	2646	F.W. Lewis	Semi-fossil (Mixed)	Saco Pond, Me; N.H. (Keeley)	Scribed circles of selected lectotypes for S. delicatissima (arrow) and Surirella baileyi, this study
General Collection (From G.A. Fisher Collection)	44940		Collection of? #1367	New Hampshire? (Maine), Saco Pond	Existing ink mark on cover slip; no obvious specimen noted
Febiger	4320	C. Febiger	Collected by Lewis (1863 ^b)	Saco Pond, N.H. ?	Scribed circles of <i>Stenopterobia anceps</i> made by C.W.Reimer (arrow) and in this study. Lectotype selected within existing circle
Febiger	4321	C. Febiger	Collected by Lewis (1863)	Saco Pond, N.H. ?	Existing scribed circle surrounding speci- men of <i>Frustulia bahlsii</i>

We circled three specimens of S. delicatissima, one of S. bailevi, and one of S. anceps on four different slides (Table 1). Approximate positions of all seven scribed circles (five from this study and two existing ones) are indicated in Figs. 2-4, 6, and 7. Two of the S. delicatissima specimens are circled on slides prepared by Lewis (Fig. 4 on 2646 and Fig. 3 on 2645) and the third (Fig. 2) on slide 2338 that we believe was also made by Lewis (see above). Owing to the nature of the preparations, the fact that many specimens were not parallel with the cover slips, and since some slides could not be viewed with higher magnification, it was difficult to find particularly revealing specimens. Of the specimens circled, the one on slide 2338 (Figs. 21–23) yields the most detail for S. delicatissima. However, because we are not certain whether slide 2338 represents type material, we decided to select the circled specimen on slide 2646 (Fig. 20) as the lectotype for S. delicatissima.

Specimens of *S. baileyi* were particularly rare on the slides. We were not able to focus with an $100 \times \text{oil-immersion}$ lens on most of the specimens and most (e.g., Fig. 93) were difficult to focus clearly. One specimen, a nonconstricted form enscribed on slide 2646 (Figs. 95 and 97), was particularly revealing and we selected it as the lectotype for *S. baileyi*. Two scribed circles are on slide 4320, one made as part of this study and another pre-existing circle made by C.W. Reimer. As noted below, we selected a specimen of *S. anceps* contained within the circle made by C.W. Reimer as the lectotype (Figs. 106–109).

Comments and findings on type material for *Stenopterobia cuspidata* from the Alfred Wegener Institute

Stenopterobia cuspidata was originally described from Lake Wawontoa (=Lake Lontoa), Celebes, by Hustedt (1942) within the genus Surirella and later transferred to Stenopterobia (Vyverman 1989). Two subspecific taxa, Surirella cuspidata f. constricta Hustedt (Hustedt 1949) and Stenopterobia cuspidata var. giluwensis Vyverman (Vyverman 1989), were subsequently described from the Belgium Congo and Papua New Guinea, respectively, and differ minimally from the type. Although light micrographs of S. cuspidata are rare, the ones presented by Simonsen (1987) as the lectotype for S. cuspidata (Simonsen 1987; plate 442, Figs. 1-5) and of the holotype for f. constricta, along with one presented by Bramberger et al. (2006) of S. cuspidata, are of high quality. Therefore, given the very small quantity of type material available to us, we elected to prepare the entire aliquot for observation with SEM. The sample had a number of interesting diatom taxa, including several Surirella species, S. pelagica and we were fortunate to find one (albeit broken) specimen of Hustedt's S. cuspidata (Figs. 127-129). Stenopterobia pelagica was described by Hustedt (1942) from Lake Mahalone, Celebes, and noted by him as also present in three other lakes, including material from Lake Wawontoa. SEM images of S. pelagica from Hustedt's Lake Wawontoa material are illustrated in Figs. 130-132.

Figs. 1–12. Figs. 1–7 are images of the seven slides of Saco Pond material archived at ANSP and examined as part of this study. The black circles indicate positions of scribed specimens. See Table 1 and the text for details. Figures 8–12 are light microscopy (LM) images of representative specimens printed at the same scale of the five species of *Stenopterobia* found in coastal North Carolina ponds, *Stenopterobia pseudodelicatissima* (Fig. 8), *Stenopterobia delicatissima* (Fig. 9), *Stenopterobia fusiformis* (Fig. 10), *Stenopterobia gracilis* (Fig. 11) and *Surirella baileyi* (Fig. 12). Scale bar = 20 μm.



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Figs. 13–18. SEM micrographs of *S. curvula* taken from the Saco Pond core depicting various stages of deterioration of the valve face cover and mantle rib wings. Fig. 13. Specimen with a complete valve face covering and fully formed mantle rib wings. Note that the raphe opening is not covered. Fig. 14. The apex of the same specimen illustrated in Fig. 13 showing the portion of the valve not typically covered. Figs. 15–18. Various stages of breakdown or peeling away of the valve face covering. Note that the mantle rib wings are still intact on the specimens in Figs. 15 and 16. Pieces of the covering remain attached to the transverse ribs on some specimens (Fig. 16) and often form a short canopy on others (Figs. 17 and 18). Scale bars = 1 μ m in Figs. 13, 14, 16, and 17; 2 μ m in Fig. 15; and 10 μ m in Fig. 18.



Figs. 19–39. Images of *S. delicatissima* from the ANSP slides (Figs. 19–26), original drawings by Lewis (Figs. 27 and 28 reprinted from Lewis (1864)) and from the Saco Pond sediment core (Figs. 29–39). The specimen in Fig. 20 represents the lectotype circled on ANSP slide 2646. Figures 22 and 23 represent different focal planes of the same specimen and the specimen in Fig. 24 is in girdle view. Note that longer specimens tend to become more linear-shaped with more protracted apices. Scale bar = $10 \mu m$.



Figs. 40–45. SEM images of *S. delicatissima* from the type locality, Saco Pond, New Hampshire. External (Figs. 40 and 41) and internal (Fig. 42) views of whole valves depicting overall shape and distribution of alar canals. Specimen in Fig. 42 is slightly constricted along the median region of the valve. Figs. 43–45. Close-ups of the valve surfaces from three specimens depicting the median region, multiseriate striae, transverse ribs, and keels. Note the areolae can be rimmed (Figs. 43 and 44) or covered (Fig. 45). Scale bars = 500 nm in Fig. 44; 2 μ m in Figs. 43 and 45; and 10 μ m in Figs. 40–42.



Figs. 46–51. SEM images of *S. delicatissima* from the type locality, Saco Pond, New Hampshire. Figs. 46 and 47. External and internal views of the valve apex showing the positions of the funnel-shaped thickenings originating from the raphe ribs (Fig. 46; arrow) and the terminal raphe endings (Fig. 47). Fig. 48. Internal view depicting the striae, median region and alar canals. Figs. 49–51. Girdle view of a whole frustule illustrating the laterally-opened girdle bands, mantle ribs, keel, and distal raphe fissure. Scale bars = 1 μ m in Fig. 50; 2 μ m in Figs. 46–48 and 51; and 10 μ m in Fig. 49.



			Alar-canal density	Rib density	
Faxon	Length (µm)	Width (µm)	(no./100 µm)	(no./10 µm)	Reference & material
S. delicatissima	38-55	4-5	65-72		Our measurements from ANSP slides; Saco Pond
S. delicatissima	34–68	3.5 - 5	68-78	30–35	Our material from Saco Pond
S. delicatissima	38-72	4-5.5	60-70	30	(Ruck and Kociolek, 2004), bog in Minnesota
S. delicatissima	34-55	5-6	50-60		(Siver et al. 2005), ponds on Cape Cod
S. delicatissima	24-60	3.5 - 5	55-64	29–34	This study, coastal North Carolina waterbodies
S. pseudodelicatissima	10-15	3-4.5	100-130	40-45	(Siver and Hamilton 2005), ponds on Cape Cod
S. pseudodelicatissima	10 - 16	3.2-4	120-135	42-50	This study, coastal North Carolina waterbodies
S. gracilis	63-156	46	75-85	30–35	This study, coastal North Carolina waterbodies
S. fusiformis	65-125	4.8-6	100 - 105	32–34	This study, coastal North Carolina waterbodies
S. baileyi	82-131	8.5 - 10	40-43		Our measurements from ANSP slides; Saco Pond ^a
S. baileyi	80–204	8-11	40-46	20–25	This study, coastal North Carolina waterbodies ^b
Surirella cuspidata	120	10	Ι		Original paper, (Hustedt 1942)
Surirella cuspidata f. constricta	100 - 160	7			Original paper, (Hustedt 1949)
S. cuspidata v. giluwensis	85-120	9–10	40–55	20–25	Original paper, (Vyverman 1989)
Note: Since a single striae is found by "Based on measurements from six spe ^b Based on measurements from 88 spec	etween each pair of valve scimens. scimens.	ribs, the rib density is eq	uivalent to striae density. We	were not able to estim	ate rib density from ANSP slides (see text for details).

cal features that are typical and well established for *Stenopterobia* taxa (e.g., Krammer 1989; Round et al. 1990; Ruck and Kociolek 2004; Siver and Hamilton 2005) and consistent with our findings (Table 2, Figs. 13–132). Valves are narrow, linear to lanceolate with large length to width ratios and are either sigmoid (e.g., Fig. 106) or straight (e.g., Figs. 8–12) in outline. Apices range from being rounded and blunt (Fig. 31) to narrow and highly protracted (e.g., Figs. 55 and 74). The raphe encircles the valve margin and is situated on a keel that is elevated a short distance from the valve surface by alar canals that alternate with fenestral openings (Fig. 113). Each fenestral opening contains one to several fenestral bars. The valve face is generally undulate, crossed with transapical external ribs or costae (referred to as Type II costae in Ruck and Kociolek 2004), and has a median region that can range from being very narrow (e.g., *S. curvula*) to a wide hyaline zone (e.g., *S. pseudo-delicatissima*). We define the median area to be the portion of the face not transversed with areolae (Fig. 61). The exter-

Findings and comments on the genus Stenopterobia

The following account summarizes the major morphologi-

face by alar canals that alternate with fenestral openings (Fig. 113). Each fenestral opening contains one to several fenestral bars. The valve face is generally undulate, crossed with transapical external ribs or costae (referred to as Type II costae in Ruck and Kociolek 2004), and has a median region that can range from being very narrow (e.g., S. curvula) to a wide hyaline zone (e.g., S. pseudodelicatissima). We define the median area to be the portion of the face not transversed with areolae (Fig. 61). The external ribs normally extend from the margin of the median area across the valve face and attach to the keel (containing the raphe canal), but on some species the ribs also cross the median area. The most common condition is one where pairs of slightly thicker ribs align with the alar canals and fuse with the sides of the keel (Figs. 60 and 63). Between each pair of thickened ribs is one to circa five ribs that also originate at the median region, but run under the keel and fuse with similarly aligned mantle ribs to form the fenestral bars. The fenestral bars are of similar width to the valve ribs. The series of external ribs found on the valve face is mirrored along the mantle (Fig. 63), with pairs of thicker ribs fusing with the alar canals and supporting the outer side of the keel alternating with ribs that fuse to form the fenestral bars. Transapical striae, consisting of small circular areolae, are found between the external ribs (Figs. 43 and 44) and continue onto the alar canals and mantle. There are two to three rows of areolae between each pair of ribs that have been collectively referred to as a single multiseriate stria (e.g., Krammer 1989; Ruck and Kociolek 2004). When three rows of areolae are present, the middle row is often shorter and terminates short of the median region. The pattern of external ribs, striae, and alar canals (referred to as keel punctae in older literature) are more or less equally spaced over the majority of the valve, but often become somewhat disorganized near the apices, especially on valves with highly protracted ends (Fig. 46). The raphe is situated atop the keel between a pair of thickened ridges (Fig. 114). At the apex of the valve, the raphe ridge closest to the valve face flares to form a thickening that continues around the apex and fuses with its counterpart on the other side of the valve (Fig. 46). This thickening, referred to as a "flap" in Ruck and Kociolek (2004), is often better developed on straight forms. The distal raphe fissures most often bend down onto the mantle and usually hook around the end of the outer raphe ridge (Figs. 51 and 116). Internally, the raphe ends are simple, terminate at the apex and are discontinuous (Fig. 132, insert).

In addition to the morphological features noted above, we have observed four hitherto unreported or rarely mentioned

Table 2. Morphometrics of *Stenopterobia* species dealt with in this paper based on our measurements and those taken from the literature.



Figs. 52–58. Size declination series for *S. gracilis* from North Carolina sites (Figs. 52–56) and close-ups of the valve surface using RIC. Note the slender, linear shape of the valve and the protracted nature of the apices. Valves can be slightly constricted (e.g., Figs. 53, 55, and 56). The specimen in Fig. 55 represents the holotype deposited at the CAS. Scale bars = $10 \mu m$. Larger scale bar is for Figs. 57 and 58 only.

Figs. 59–64. SEM images of *S. gracilis* from the type locality, Bay Tree, North Carolina. Fig. 59. Whole valve depicting the linear margins and protracted and needle-shaped apices. Figs. 60–62. Specimens depicting the relatively wide median region (Fig. 61; arrows), transverse ribs, keel, and short multiseriate striae. Although the striae terminate at the margin of the median area, the ribs originate at the very center of the valve. Externally, the areolae can be rimmed (Fig. 60), capped (Fig. 62), or both forms can be found on the same valve (Fig. 61). Various stages of development of the mantle rib wings are observed on Figs. 62–64. Note that in this species, wings are normally present only on the ribs that are not aligned with alar canals. Scale bars = 1 μ m (Figs. 60, 61, and 63); 2 μ m in Figs. 6 and 64; and 20 μ m in Fig. 59.



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Figs. 65–70. SEM images of *S. gracilis* (Figs. 65 and 66) and *S. pseudodelicatissima* (Figs. 67–70) based on specimens from localities in North Carolina. Close-ups of the valve apex (Fig. 65) and internal structure (Fig. 66). Note the thickened raphe ribs, wide median region, and short striae. Fig. 67. Whole frustule depicting the lanceolate shape of the valve, arrangement of alar canals, and position of the keel. Figs. 68 and 69. Close-ups of the specimen in Fig. 67. Note the wide median region, short striae, and the nature of the transverse ribs and flared raphe rib around the valve apex. Fig. 70. Internal view showing the striae and alar canals. Scale bars = 1 μ m in Fig. 69; 2 μ m in all others.



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Figs. 71–85. Size declination series for *S. fusiformis* (Figs. 71–78), and *S. pseudodelicatissima* (Figs. 80–85), and a close-up of the former taxon using RIC optics (Fig. 79). Figures 75 and 76 are of the same specimen and represent the holotype on slide deposited at CAS. Figures 77 and 79 represent an isotype specimen circled on a slide deposited at Canadian Museum of Nature. Specimens illustrated in Figs. 74 and 78 are isotypes on slides in P.A. Siver's personal collection. Scale bars = 10 µm.



Figs. 86–91. SEM images of *S. fusiformis* from North Carolina sites. Fig. 86. Whole frustule depicting the lanceolate shape and the long protracted apices of the valve. Note the slight twisting of the apices. Fig. 87. Close-up of the frustule in Fig. 86 illustrating the relatively unornamented nature of the valve surface. Fig. 88. Close-up of the apex of the frustule in Fig. 86 showing the relatively wide nature of the alar canals, short fenestral openings, and distal raphe fissures. Fig. 89. Close-up of the valve surface depicting the short striae consisting of only a few areolae and thinly silicified ribs. This specimen has rimmed areolae. Figs. 90 and 91. Girdle views of two valves illustrating numerous and laterally opening bands. These specimens have externally capped areolae. Scale bars = 1 μ m in Figs. 89–91; 2 μ m in Figs. 87 and 88; and 20 μ m in Fig. 86.



Figs. 92–98. Images of *S. baileyi* from Lewis' original drawing (Fig. 92 reprinted from Lewis (1864)), ANSP slides (Figs. 93, 95, and 97), and North Carolina sites (Figs. 94, 96, and 98). Specimens in Figs. 92–94 and 95–96 represent constricted and nonconstricted forms, respectively. Figures 97 and 98 are close-ups of the specimens in Figs. 95 and 96, respectively. Note the pairs of transverse ribs that attach to the alar canals. The specimen in Figs. 95 and 97, circled on ANSP slide 2646, is selected as the lectotype. See text for details. Scale bar for Figs. 92–96 (black) = 10 μ m; scale bar for Figs. 97 and 98 (white) = 5 μ m.



Figs. 99–110. Size declination series for *S. baileyi* from North Carolina sites (Figs. 99–105) and images of *S. anceps* (Figs. 106–109) circled on ANSP slide 4320 (Fig. 110) selected as the lectotype. Scale bar for whole valves = $20 \mu m$ (Figs. 99–106); scale bar for close-ups = $10 \mu m$ (Figs. 107–109).



Figs. 111–116. SEM images of *S. baileyi* from North Carolina. Fig. 111. Inside view of a whole valve. Fig. 112. Close-up of the external valve surface denoting the structure of the transverse ribs. Note that the transverse ribs originate at the center of the valve, often connect to neighboring ribs and are sometimes branched. Figs 113–115. Views of the keel–raphe complex, mantle, and fenestral ribs. The single black arrow on Fig. 113 points to the raphe slit on the keel, the white arrow to an alar canal, and the double black arrows denote a fenestral opening. The multiseriate striae consist of areolae with rims and continue only a short distance onto the mantle. Note that the mantle ribs can possess lateral wings (e.g., Fig. 115) and that the raphe is bordered by thick ribs. Fig. 116. Close-up of the end of the valve depicting the manner in which the raphe ribs become thicker and reinforce the apex. Scale bars = 500 nm in Fig. 115; 1 μ m in Figs. 113 and 114; 2 μ m in Figs. 112 and 116; and 20 μ m in Fig. 111.



characters for Stenopterobia. First, we found numerous specimens, including ones of S. delicatissima, S. pseudodelicatissima, S. gracilis, and S. fusiformis that had capshaped discs covering the exterior surface of the areolae, both on the valve face as well as on the mantle (e.g., Figs. 45, 50, 61, 63, 68, and 90). In each population examined, we could usually find valves with or without the coverings as well as ones with rimmed areolae, the latter presumably representing the remains of the cap. The most common condition was that all areolae on a single specimen would either contain coverings or lack them, making it difficult to determine whether they represented two different morphotypes. However, if enough valves are examined, ones with areolae containing and lacking caps can usually be found (Fig. 61). To date, we have only observed capped areolae on straight forms. Second, we observed specimens of S. delicatissima from the type locality (Saco Pond) as well as in North Carolina sites that had girdle elements that opened in a lateral position, more or less midway along the valve (Fig. 50). Copulae that open laterally have also been observed for S. pseudodelicatissima, S. gracilis, and S. fusiformis (Fig. 90) and we suspect this may be the case for at least all of the straight forms within the genus.

Third, we found numerous valves of S. curvula from Saco Pond where the majority of the valve face was essentially covered with an intact thin layer of silica that we refer to simply as a valve face covering (Figs. 13-15). The valve face covering spans the surface of the valve except near the apices where small openings can be found (Fig. 14) and along the raphe slits (Figs. 13-17). The covering, in effect, forms a tunnel-like cavity between it and the valve face. We also noted various stages of degradation of the valve face covering where it would peel away (Figs. 15 and 16) usually from the center of the valve towards the margins. Where the covering was in direct contact with the transverse ribs, parts of the covering would often remain, yielding various types of thickenings and designs (Figs. 16 and 17). On other valves, part of the covering would sometimes persist along the valve margin forming a short canopy over part of the valve face (Figs. 17 and 18). The various degrees of degradation of the valve face covering can yield strikingly different images when observed with light microscopy (LM), sometimes obscuring the true identity of the specimen.

The fourth structure was the formation of a thin wing-like expansion on each mantle rib (Figs. 13–16, 63, and 115). This character has been observed for *S. gracilis*, *S. baileyi*, and *S. curvula*. The wings often abutted each other forming thin slits between each pair of ribs. Typically, frustules of *S. curvula* with valve face coverings had fully formed mantle wings (Figs. 13–16), but we also observed valves with mantle rib wings that lacked valve face coverings. The mantle rib wings were also observed to peel away yielding the more cylindrical nature of the ribs. Frustules of *S. baileyi* also had mantle wings, but we never observed a frustule with a valve face covering.

Species descriptions of taxa found in North Carolina waterbodies

Stenopterobia delicatissima (Lewis) Brébisson ex Van Heurck 1896 (Figs. 19–51)

BASIONYM: Surirella delicatissima Lewis 1864.

LECTOTYPUS: Here designated as the circled specimen on ANSP Slide 2646. The specimen is illustrated in Fig. 20.

The following description of *S. delicatissima* is based on LM observations of all available slides of material collected by Lewis from the type locality, Saco Pond, New Hampshire, and archived at the ANSP, as well as LM and SEM observations of recent collections made from Saco Pond as part of this study.

Valves are slender, linear-lanceolate to linear with triangular-shaped and pointed apices (Figs. 19-42) and keels elevated from the valve surface by short alar canals (Fig. 50). The apices can be protracted and needle-like, especially on longer valves. Valves can be slightly constricted centrally (Figs. 27 and 42) and frustules appear slightly linear-lanceolate in girdle view with bluntly rounded ends (Figs. 24 and 49). The external valve surface consists of thickened and evenly-spaced ribs that extend from the median area across the valve face and connect with the keel (Figs. 43-45). Pairs of ribs that are slightly thicker fuse with the alar canals and connect more or less along the sides of the keel. Between each pair of thickened ribs is one to three less silicified ribs that run under the keel, fuse with aligning ribs from the mantle to form fenestrae that attach to the undersurface of the keel. There are two to three rows of areolae between adjacent ribs forming a single multiseriate stria (Figs. 43-45 and 48). If three rows of areolae are present, the central one is usually shorter and situated towards the outside of the valve. Externally, the areolae are either capped with domed coverings (Figs. 45, 50, and 51) or are ringed with a thickened rib which represent the remains of the caps (Figs. 43 and 44). Internally, the areolae are unoccluded (Figs. 47 and 48). The pattern of ribs and areolae can become unorganized along the narrow protracted apices (Fig. 46). The median area is narrow, linear-lanceolate and usually extends no more than ca. 20% of the valve width (Figs. 43-45). The raphe is situated between two narrow ridges aligned atop of the keel (Figs. 43 and 50). At the apex of the valve, the raphe ridge closest to the valve face (i.e., the top rib) flares to form a funnel-shaped thickening, which fuses with its counterpart from the other side of the valve (Fig. 46). The distal raphe fissure bends down onto the mantle near the apex of the valve (Fig. 51). Internally, the distal ends of the raphe meet at the apex, but are not continuous (Fig. 47). Three to five hyaline and laterallyopened copulae comprise the cingulum (Figs. 50 and 51). Length, 34-68 µm; width, 3.5 to 5 µm; alar canals, 65-78/ 100 μm; external ribs, 30-35/10 μm.

Stenopterobia gracilis Siver & Camfield sp. nov. (Figs. 52–66)

DESCRIPTIO: Cellulae longae, graciles, et lineares cum maxime ductis apicibus. Valvae leviter constringeri centraliter; frustula rectangulares ad leviter lanceolatos aspectu cingulari. Externus, frons cum aequaliter dipositis costis extendens ex mediarea ad limbum. Costae latae, planae ad mediaream, tenuiores fit et plures cylindrical ad limbum. Costae binatim ad canales alares coniungunt. Diversae frondis costae cum similaribus costis innascens secus limbum formare breves fenestras coniungunt. Costae limbi expansae lateraliter et saepe inter se adiacent. Striae breves, ex duabus ad tribus **Figs. 117–122.** SEM images of *S. baileyi* from North Carolina sites. External (Fig. 117) and internal (Fig. 118) valve structure. Note the relatively small alar canal openings. Figs. 119–121. Close-ups of the alar canals and structure of the mantle. Note the areolae covering the external surface of the alar canals. Fig. 122. Internal view of the valve apex. Note the terminal raphe endings and that the alar canals have merged to form a single opening. Scale bars = 500 nm in Fig. 120; 1 μ m in Fig. 119; 2 μ m in Figs. 117, 121, and 122; and 5 μ m in Fig. 118.



Figs. 123–126. SEM images of *S. anceps* from the type locality, Saco Pond, New Hampshire. Figs. 123 and 124. External valve surface depicting the broadly rounded apex, arrangement of evenly spaced transverse ribs originating from a thick median ridge and the keel. Note that the pairs of ribs attaching to the alar canals are thickened relative to those attaching to the fenestrae. Figs. 125 and 126. Internal views of the same valve illustrating the small openings to the alar canals, the median region underlying the external marginal ridge and the multi-seriate striae. Scale bars = 2 μ m in Figs. 124 and 126; 20 μ m in Figs. 123 and 125.



series punctarum consistunt, ca. 1/4 frondis et continuant deorsum secus limbum transeunt. Extra, areolae alteruter tholiformes obtegentes vel crassilabra habent. Interne, areolae inobterunt. Mediarea ca. 1/2 latitudis frondis. Raphe sita inter duas angustas cristas in carinam. Ad apicem, raphocrista propius frondi formare infundibularem spissescentem flagrat, qua cum se pare ex alio latu valvae coniungit. Distalis raphis fissura deorsum in limbum ad apicem valvae curvat. Copulae laeves, hyalinae et apertae secus medium frustuli. Longitudo: 63–156 µm; latitudo: 4–6 µm; canalis alaris: 75–85/100 µm; costae externe: 30–35/10 µm.

HOLOTYPUS: Here designated as the circled specimen on microscope slide marked "F", deposited at the California Academy of Sciences, San Francisco, California (CAS # 222036). This specimen is illustrated in Fig. 55.

ISOTYPI: Here designated as the circled specimen on microscope slide marked "D" deposited at Canadian Museum of Nature, Ottawa, Ontario (CANA 80022) and the circled specimen on slide marked "E" in P.A. Siver's personal collection.

TYPE MATERIAL: Cleaned surface sediment material deposited at

CAS (# 625115) and the Canadian Museum of Nature, Ottawa, Ontario (CANA 79750). Collector: P.A. Siver, June 2001.

TYPE LOCALITY: Bay Tree Lake, Bladen County, North Carolina, $34^{\circ}40'$ 59.36"N 78°24' 58.77"W.

ETYMOLOGY: The specific epithet refers to the long, thin, and narrow shape of the valve.

Valves are long, slender, linear with highly protracted apices (Figs. 52–59). Valves can be slightly constricted centrally and frustules are rectangular to slightly lanceolate in girdle view. The external valve surface consists of thickened and evenly-spaced transverse ribs that extend from the center of the valve across the valve face and connect with the keel (Figs. 60–62). The ribs are broad and flat within the median area and become thinner and more cylindrical along the striae. Pairs of ribs fuse along the alar canals connecting to the sides of the keel, alternating with ribs that fuse with mantle ribs along the undersurface of the keel to form short fenestrae (Figs. 60–62). The mantle ribs that align with the fenestrae are expanded laterally, often abutting each other (Figs. 62–64). Striae are short, consist of two to three rows

Figs. 127–132. SEM images of *S. cuspidata* (Figs. 127–129) and *S. pelagica* (Figs. 130–132) based on material from the Hustedt collection, AS1320. Fig. 127. A portion of a *S. cuspidata* valve with a constricted median region and a triangular-shaped apex. Figs. 128 and 129. Close-ups of the specimen in Fig. 127 depicting the evenly spaced transverse ribs, keel, fenestral openings, and distal raphe fissures. Fig. 130. Whole specimen of *S. pelagica* illustrating the slight sigmoidal nature and needle-like apices of the valve. Fig. 131. Close-up of the external valve surface. Note the evenly spaced and evenly thickened transverse ribs, narrow median region, and multiseriate striae. Fig. 132. External and internal (insert) views of the valve apex depicting the raphe structure. Note that the distal raphe fissures terminate on the valve surface. Scale bars = 1 μ m in Fig. 131; 2 μ m in Figs. 128, 129, and 132; 20 μ m in Fig. 127; and 50 μ m in Fig. 130.



Taxon/waterbody	рН	Specific conductance $(\mu S \cdot cm^{-1})$	Secchi disk depth (m)	Color (Pt–Co units)	Total phosphorus $(\mu g \cdot L^{-1})$
S. fusiformis					
Great Lake	4	94	0.31	125	30
Long Pond	3.9	85	0.31	192	32
S. gracilis					
Bay Tree Lake	4.6	68	1	23	13
White Lake	4.8	62	NA	2	6
Jones Lake	4	71	1.06	117	7
Salters Lake	4.1	62	0.77	125	16
Horseshoe Lake	4	49	1.13	192	7
Patsy Pond	4.7	72	1.22	58	14

Table 3. Physical and chemical properties of the waterbodies harboring S. fusiformis and S. gracilis.

Note: All waterbodies are situated on the Atlantic Coastal Plain of North Carolina.

of areolae, traverse about 1/4 of the valve face and continue down along the mantle (Figs. 60-64). Externally, the areolae possess domed coverings (Figs. 61-64), however, the caps can become eroded leaving a thickened rim around the pore (Figs. 60, part of 61). Internally, the areolae are unoccluded (Fig. 66). The pattern of ribs and areolae is less organized along the protracted apices (Fig. 65). The median area is wide covering circa 1/2 of the valve face (Figs. 60-62 and 66). The alar canals are narrow, about 0.4 µm wide (Fig. 66). The raphe is situated between two narrow ridges aligned along the top of the keel (Figs. 61-63). At the apex of the valve, the raphe ridge closest to the valve face (i.e., the top rib) flares to form a funnel-shaped thickening, which fuses with its counterpart from the other side of the valve (Fig. 65). The distal raphe fissure curves down onto the mantle at the apex of the valve. Copulae are smooth, hyaline and open along the middle of the frustule. Length, 63-156 µm; width, 4–6 µm; alar canals, 75–85/100 µm; external ribs, 30-35/10 µm.

Stenopterobia gracilis has been found in six waterbodies along the North Carolina coastal plain, including five closely situated sites in the Bladen Lakes State Forest region (Table 3). These localities are highly acidic, poorly buffered, rich in humic substances, with moderate concentrations of total phosphorus, and low transparency as measured with a Secchi disk (Table 3).

Stenopterobia fusiformis Siver & Camfield sp. nov. (Figs. 71–79 and 86–91)

DESCRIPTIO: Valvae longae, lanceolatae cum maxime ductis acicularibus apicibus ut rationem habeat ad ca. 1/2 lontitudinem valvae. Margines ductorum apicum paralleli et torquati facti sunt. Externa frons aequaliter dipositarum, tenuium transversarum costarum quarum extendunt ex mediaarea ad carinam consistit. Costae binatim secus canaliz alaris coniungunt et ad latus caminae connectunt. Diversae frondis costae cum limbi costis secus subter superficiem caminae formare fenestras coniungunt. Fenestrae et al.ares canales per brevis in tantem ut carina paene in frondem requiescitur. Limbus vadosus. Striae per brevis, cicrumscriptae ad ambitum frondis, et duabus serierum punctarum consistunt. Extra, areolae tholiformes obtegentes habent, tamen, pilei relinquens crassibrum circum porum possunt roderi. Interne, areolae inobterunt. Mediarea lata, circum 1/2 ad 3/4 latitudem frondis. Raphe sita inter duas angustas cristas parallelas super carina. Distalis raphis fissurae deorsum ex carina ad apicem valvae inclinant et ad planum frondis terminant. Copulae tenues, hyalinae, ad decem per frustulum et apertae lateraliter prope centrum valvae. Longitudo: $65-125 \ \mu m$; latitudo: $4.8-6 \ \mu m$; canalis alaris: $100-105/100 \ \mu m$; costae externe: $32-34/10 \ \mu m$.

HOLOTYPUS: Here designated as the circled specimen on microscope slide marked "A", deposited at the California Academy of Sciences, San Francisco, California (CAS # 222037). This specimen is illustrated in Figs. 75–76.

ISOTYPI: Here designated as the circled specimen on microscope slide marked "D" deposited at the Canadian Museum of Nature, Ottawa, Ontario (CANA 80023) and illustrated in Figs. 77 and 79, and the circled specimens on slides marked "B" and "C" in P.A. Siver's personal collection and illustrated in Figs. 74 and 78, respectively.

TYPE MATERIAL: Cleaned composite periphyton sample deposited at CAS (# 625116) and the Canadian Museum of Nature, Ottawa, Ontario (CANA 880024). Collector: P.A. Siver, June 2001.

TYPE LOCALITY: Great Lake, Croatan National Forest, North Carolina, 34°51′34.44″N, 77°03′07.67″W.

ETYMOLOGY: The specific epithet refers to the spindle shape of the frustule.

Valves are long, lanceolate with highly protracted needlelike apices that account for circa 1/2 of the length of the valve (Figs. 71-78 and 86). The margins of the protracted apices become parallel and often twist (Fig. 86). The external valve surface consists of evenly-spaced transverse ribs that extend from the median area to the keel (Figs. 79 and 89). The ribs are thin and difficult to discern with LM except with reflected interference contrast optics (Fig. 79). Pairs of ribs fuse along the alar canals and connect to the sides of the keel. These ribs alternate with ones that align with mantle ribs along the undersurface of the keel to form fenestrae (Figs. 90 and 91). The fenestrae and alar canals are very short, such that the keel almost rests on the valve surface (Fig. 90). The valve mantle is shallow. Striae are very short, restricted to the periphery of the valve face, and consist of two rows of areolae (Fig. 89). There are one to four areolae per row. Externally, the areolae possess domed coverings (Figs. 87, 90, and 91); however, the caps can become eroded leaving a thickened rim around the pore (Fig. 89).

Internally, the areolae are unoccluded. The median area is wide, covering circa 1/2 to 3/4 of the valve face. The raphe is situated between two narrow ridges aligned along the top of the keel (Figs. 87–89). The distal raphe fissures bend down from the keel at the very apex of the valve and terminate near the plane of the valve face (Fig. 88). Copulae are thin, hyaline, and open laterally near the center of the valve. There can be many, often up to 10, copulae per frustule (Figs. 90 and 91). Length, 65–125 μ m; width, 4.8–6 μ m; alar canals, 100–105/100 μ m; external ribs, 32–34/10 μ m.

Stenopterobia fusiformis has been observed in two waterbodies, Great Lake and Long Pond, situated on the North Carolina coastal plain (Table 3). Both localities are highly acidic, poorly buffered, humic-stained, and with moderate concentrations of total phosphorus and shallow Secchi disk depths (Table 3).

Stenopterobia pseudodelicatissima Siver & Hamilton (Figs. 67–70 and 80–85)

Valves are short, elliptical-lanceolate with keels elevated only a short distance from the valve surface and acute, rounded apices (Figs. 80-85, 67, and 70). The median area of the valve, both internally and externally, consists of a wide hyaline region that extends across at least 1/2 the width of the valve and conforms to the shape of the valve (Fig. 68). Externally, the transverse ribs are short, thinly silicified, and are positioned between the margin of the median area and the keel (Fig. 68). The pairs of ribs that align with the alar canals are slightly thicker than ribs that form with adjoining mantle ribs to form the fenestrae (Figs. 68 and 69). Most often, there is only a single rib between each pair of alar canal ribs. The same arrangement of ribs, either aligning with the alar canals or attaching to fenestrae, is found on the mantle side of the wing. The striae are short, alternate with the ribs and consist of two or three rows of areolae (Figs. 66 and 68). The areolae are covered externally with a siliceous cap (Figs. 68 and 69) and are unoccluded on the internal valve surface (Fig. 66). The raphe is situated between two narrow ridges aligned atop of the keel (Figs. 68 and 69). At the apex of the valve, the raphe ridge closest to the valve face (i.e., the top rib) flares to form a funnelshaped thickening that connects with its counterpart on the other side of the valve and extends over the valve apex (Fig. 69). The distal raphe fissure bends down onto the mantle at the point where the top raphe ridge begins to flare. Three to four hyaline copulae comprise the cingulum. Length, 10 to 16 µm; width, 3.2 to 4 µm; alar canals, 120 to 135/100 µm; external ribs, 42-50/10 µm.

Stenopterobia baileyi (Lewis) Brébisson ex Van Heurck 1896 (Figs. 92–105 and 111–122)

BASIONYM: Surirella baileyi Lewis 1864.

SYNONYM: : Surirella arctissima Schmidt 1877.

LECTOTYPUS: Here designated as the circled specimen on ANSP Slide 2646. The specimen is illustrated in Figs. 95 and 97.

Valves are long and linear, becoming linear–lanceolate with size reduction, with protracted and triangular-shaped apices (Figs. 92–105). Valves can be slightly constricted centrally (Figs. 92–94, 102, and 103) and frustules are rectangular in girdle view. The external valve surface consists

of closely spaced transverse ribs that extend from a narrow median line across the valve face and connect with the keel (Figs. 112 and 117). The ribs are broad, flat, and often fuse with adjacent ribs near the median line. The pairs of ribs that fuse along the alar canals remain evenly thickened across the valve face (Fig. 112) and are readily observed with light microscopy (Figs. 95-98), whereas the ribs between canals become significantly thinner as they fuse with mantle ribs to form the fenestrae (Figs. 112 and 117). Two to five ribs are found between each pair of alar canals (Figs. 113 and 114). The mantle ribs can be expanded laterally, often becoming close to abutting each other (Fig. 115). Striae consist of two to three rows of rimmed areolae that continue a short distance onto the mantle (Figs. 113, 114, and 118). Internally, the areolae are unoccluded (Figs. 119 and 121). The pattern of ribs and areolae is less organized along the protracted apices. The alar canals are about 0.6 µm wide and extend several microns above the valve surface where they connect to the keel (Figs. 113, 118, 120, and 121). The raphe is situated between two narrow ridges on top of the keel and slightly off-centered toward the mantle side of the valve (Figs. 114 and 115). The raphe ridges thicken around the apex of the valve at the point where the distal raphe fissure curves down onto and back along the mantle forming a fish hook design (Fig. 116). Internally, the raphe ends are discontinuous (Fig. 122). Length, 80-204 µm; width, 8-10.5 µm; alar canals, 40-46/100 µm; external ribs, $20-25/10 \mu m$.

Notes on additional species of Stenopterobia

Stenopterobia anceps (Lewis) Brébisson ex Van Heurck (Figs. 106–109 and 123–126)

LECTOTYPUS: Here designated as the circled specimen on ANSP Slide 4320. The specimen is illustrated in Figs. 106–109.

We observed numerous specimens of *S. anceps* both on ANSP slides of Lewis' original material from Saco Pond and from collections we made from this same locality.

Valves are long, sigmoid-shaped, with parallel sides and broadly rounded apices (Fig. 106). The valve surface is undulated (Figs. 107-109 and 126) and traversed with closely spaced and thin ribs (Figs. 123 and 124). The ribs originate along a centrally positioned ridge, cross the valve face and attach to the keel (Fig. 124). Pairs of ribs fuse along the alar canals where they become slightly flared and connect to the sides of the keel (Fig. 124). Two to five ribs are found between each pair of alar canals; these ribs align with mantle ribs along the undersurface of the keel and form short fenestrae. The alar canals are widely spaced (Figs. 125 and 126), small and positioned directly below the keel such that they are not readily observed with light microscopy (Fig. 109). Striae lie between the transverse ribs, consist of two to three rows of small areolae, and are continuous onto the mantle. We have never observed coverings on the areolae. The raphe is situated between a pair of ridges atop of the keel (Fig. 124).

Stenopterobia pelagica Hustedt (Figs. 130–132)

We used SEM to observe specimens of S. pelagica within

the Lake Wawontoa material and provide a few comments on the valve structure of this taxon. Valves are narrow and linear with highly protracted and sigmoidal apices (Fig. 130). The external valve surface consists of evenly spaced and evenly thickened transverse ribs originating from a narrow median region and extending across the valve face ultimately attaching to the keel (Fig. 131). The pairs of ribs attaching to the alar canals are not readily discernable from those situated between the canals (Fig. 131). Striae are multiseriate and consist of two rows of areolae. Areolae had slightly thickened rims and we did not observe external siliceous caps. Externally, the distal raphe fissures bend down off of the keel and terminate on the valve face and the raphe ribs do not merge along the apical region (Fig. 132). Internally, the raphe ends are simple and discontinuous (Fig. 132, insert).

Discussion

In the original description of S. delicatissima from Saco Pond, New Hampshire, Lewis (1864) noted the taxon to be a minute and variable species with linear to linear-lanceolate valves, inconspicuous marginal alar canals, and delicate striae. Given the structure of the valve, the striae he noted would correspond to the external ribs or costae. It is interesting that although Lewis (1864) noted valves to be only "sometimes centrally constricted", he illustrated this feature in his only drawing of the valve face (Fig. 27). Even though a range in valve size was not given in the original paper, the drawings of S. delicatissima are approximately 37 μ m \times 3.5 μ m (Plate I, Fig. 4*a* in Lewis (1864) = Fig. 27, this paper) and 41 µm (Plate I, Fig. 4b in Lewis (1864) = Fig. 28, this paper). Further, his drawing shows the apices to be attenuated, forming a more or less triangular shape, but not as highly protracted as sometimes depicted in more recent works (e.g., Krammer and Lange-Bertalot 1988; Ruck and Kociolek 2004).

Our examination of Saco Pond material included seven archived slides from ANSP, including ones prepared by Lewis or that contained material he collected, along with recently collected periphytic samples and sections taken every 2 cm from a 31 cm sediment-core retrieved from the type locality. Our findings of S. delicatissima, based on all of these Saco Pond samples, can be summarized as follows: The majority of the Saco specimens matched the brief description given by Lewis (1864) as well as the general shape depicted in his drawings. Specimens were linear to linearlanceolate and a small percentage were slightly constricted in the center of the valve. Many of the Saco Pond specimens had attenuated triangular-shaped apices similar to those on the drawing made by Lewis (1864), but others had more protracted apices. The range in valve outline is consistent with some recent studies from North America, including Camburn and Charles (2000); Fallu et al. (2000); Ruck and Kociolek (2004), and Siver et al. (2005), as well as material from Germany examined by Krammer (1989).

Saco Pond specimens of *S. delicatissima* ranged in size from 34–68 μ m × 3.5–5 μ m, had alar canal densities between 68–80/100 μ m, and external rib densities ranging from 30–35/10 μ m. The range in valve size of the Saco Pond specimens is reasonably consistent with ones reported

by Siver et al. (2005) for populations examined on Cape Cod and by Ruck and Kociolek (2004) based on a population from a bog in Minnesota, but does not extend to the 100 μ m length listed by Krammer and Lange-Bertalot (1988). The density of external ribs (=striae density) is very similar to that observed by Ruck and Kociolek (2004). The alar-canal density is slightly higher than those reported by Ruck and Kociolek (2004) and Siver et al. (2005), but not unreasonably so. The ultrastructural characteristics of the Saco Pond specimens are similar to those depicted for *S. delicatissima* by Krammer (1989), Ruck and Kociolek (2004), and Siver et al. (2005) and we conclude that all of these populations represent the same species. We do not believe that all of the specimens illustrated in Krammer and Lange-Bertalot (1988) are representative of *S. delicatissima*.

Based on the concept of *S. delicatissima* presented above, *S. fusiformis* and *S. gracilis* clearly represent different taxa. Valves of *S. fusiformis* are significantly longer with highly protracted and often twisted apices and have a higher alarcanal density relative to *S. delicatissima*. Valves of *S. fusiformis* have short rows of areolae restricted to the valve margins, a wide central hyaline region and shorter, less robust external ribs as compared with *S. delicatissima*. The overall design of the valve surface of *S. fusiformis* is more similar to that of *S. pseudodelicatissima* (this paper and Siver and Hamilton 2005), although the overall shapes and sizes of these taxa are significantly different.

It is more difficult to separate S. gracilis from S. delicatissima since the basic valve ultrastructure is similar for both taxa. The density and distribution of ribs on the valve face and mantle and their attachments to the keel are virtually identical. The height of the keel above the valve surface, structure of the raphe and density of alar canals is also similar and both organisms can produce capped areolae and possess girdle bands that open laterally near the middle of the valve. Despite the similarities between S. gracilis and S. delicatissima, the two taxa can be differentiated on the basis of four characters. First, the most obvious difference is the significantly longer valves of S. gracilis. The extremely long and slender nature of valves of S. gracilis was a consistent feature of all populations examined, and the maximum range in valve length was double that of S. delicatissima. Second, valves of S. gracilis are linear, never lanceolate, and the apices always highly protracted and never bluntly rounded. Third, the mantle ribs on the valves of S. gracilis were consistently expanded into wings, a feature we did not observe on S. delicatissima, nor could we find this character noted in the literature. Fourth, although the width of the central hyaline region is variable on S. delicatissima, it is more consistent and wider on S. gracilis.

Although we could easily identify the specimens from our North Carolina sites, referred to in this paper as *S. baileyi*, we are not entirely sure that these populations are indeed this taxon. Based on the light micrographs illustrated in Simonsen (1987), we initially identified our specimens as *S. cuspidata* and we remain convinced that both taxa are closely related. However, in the process of studying the Lewis material from Saco Pond, we were able to find six specimens of the taxon originally described by Lewis as *S. baileyi* and it became apparent to us that the North Caro-

lina specimens may indeed represent this species. Based on LM, our North Carolina specimens match those of S. baileyi from the Lewis slides (e.g., compare Figs. 93-96) and we have no reason to conclude otherwise. Both have a similar valve shape, including constricted and unconstricted forms, similar valve face structure, and rib and alar canal densities. The specimens of S. baileyi we studied on the Lewis slides ranged in size from 82–132 μ m \times 8.5–10 μ m, within the size range of the North Carolina specimens. Unfortunately, there is no original Lewis material at the ANSP that could be examined with SEM and, to date, we have not been unable to find specimens of S. baileyi in our recent collections made from Saco Pond. Although it would obviously be ideal to examine more specimens of S. baileyi, especially with SEM, we see no reason not to conclude that the North Carolina populations are indeed equivalent to Lewis' S. baileyi and we elect, in lieu of establishing a new species, to use this epithet for this taxon.

As noted above, we further believe that the species described by Hustedt (1942) from Celebes as S. cuspidata is closely related to S. baileyi and differs from it in a few subtle ways. The single specimen of S. cuspidata we found in the type material clearly matches the concept of this species as presented in Simonsen (1987), but the fact remains that the description of this taxon is based on examination of only a handful of specimens (Simonsen 1987; Krammer and Lange-Bertalot 1988; Bramberger et al. 2006). The general pattern of ribs on the valve surface and mantle, as well as the striae and alar canal densities, of the specimen of S. cuspidata we examined with SEM are similar to those of our North Carolina taxon (i.e., S. baileyi). However, our North Carolina specimens have more protracted apices, ribs that commonly fuse to neighboring ribs close to the median line, and shorter striae that are often composed of three rows of areolae and extend further down onto the mantle. For these reasons, and because the description of S. cuspidata is based on such a limited numbers of specimens from another region of the world, we conclude that it would be premature at this time to synonomize S. cuspidata with S. baileyi. We also recognize that such a synonomy may never be possible.

Van Landingham (1978) listed *Surirella arctissima* as a synonym for *S. baileyi*, a conclusion with which we agree. In this regard, it is worth mentioning that the card associated with slide 2645 at the ANSP contains the following note: "Mr. Keeley has examined Temper and Peragallo slide No. 372 and finds the ringed specimen of *Surirella Baileyii* (note misspelling) to be correctly identified and identical with what is usually called *Surirella arctissima*." As noted by Van Landingham (1978), Lewis' original description has taxonomic priority for this species.

Although our study did not focus on sigmoidal taxa, we offer a few comments on *S. anceps* and *S. pelagica*. The specimens of *S. anceps* that we observed from type material and from newly collected samples from Saco Pond clearly match Lewis' original description for this species (Lewis 1864). He particularly noted the small, often "inconspicuous" alar canals and the fact that the striae (ribs) extended from a well defined central space across the valve surface. Based on our observations of Saco Pond material, we consistently found specimens of *S. anceps* to be wider and possess more rounded and less attenuated apices as

compared with those of *S. curvula*. These findings also match the images of both species presented in Camburn and Charles (2000) and those of *S. curvula* in Ruck and Kociolek (2004). Lastly, it is worth noting that valve shape and the ultrastructural features of *S. pelagica* are quite similar to those of *Surirella densestriata* (Hustedt) Krammer, and we believe further work is needed to identify distinguishing characters for these two taxa.

In the course of this project we designated lectotype specimens for three of the four species of Stenopterobia described by Lewis from Saco Pond, originally S. delicatissima, S. baileyi, and S. anceps. The fourth taxon, S. intermedia, is conspecific with S. curvula, a species described earlier by W. Smith in 1856. Choosing a lectotype from the Lewis material for the common and widespread species S. delicatissima was difficult because of the relatively few specimens found on the slides, and because of the poor conditions of the slides it was not possible to examine and image specimens with a high magnification oil-immersion lens. Nonetheless, we selected the specimen illustrated in Fig. 20 as the lectotype for S. delicatissima from Slide 2646, a preparation that was made by Lewis from material he personally collected from the type locality. Selecting a lectotype for S. baileyi was equally difficult owing to the rare nature of the taxon and the poor conditions of the slides. After a thorough examination of all of the slides, we found only six specimens of S. baileyi. Two of the six specimens had valves that were slightly constricted, but were difficult to image (e.g., Figure 93 from slide 2645). As a result, we selected a lectotype from Slide 2646 (Fig. 95) that was not centrally constricted, but represented the specimen that best displayed the characteristics of the valve. As noted above, Slide 4320 prepared by Febiger from Lewis material contained a scribed circle and a note made by C.W. Reimer indicating that the slide contained good specimens of S. anceps. Within the circle are several whole valves of S. anceps, along with several broken pieces. We selected a whole valve of S. anceps located within, but near the edge, of the existing scribed circle as the lectotype (Figs. 106-109).

Stenopterobia delicatissima is widely distributed (Krammer 1989) and it is no surprise that we have observed it in numerous regions along the east coast of North America. In contrast, we have not observed populations of either S. fusiformis or S. gracilis outside of the rather restricted coastal North Carolina localities in which they have been found. We have described a number of other interesting and unique species from these pocosin waterbodies, including Eunotia croatana Siver, Hamilton, & Morales, Eunotia pseudofragilaria Siver, Hamilton, & Morales (Siver et al. 2006), and Nupela scissura Siver, Hamilton, & Morales (Siver et al. 2007), and it is worth noting that Scherer (1988) and Gaiser and Johansen (2000) also described new diatom species from similar habitats along this region of the Atlantic Coastal Plain. It therefore seems highly possible that a small, but nonetheless distinct, element of the diatom flora from this region of the Atlantic Coastal Plain is endemic to the area.

We observed *S. fusiformis* in all of the plankton samples from each of the lakes in which it was found. The linear– lanceolate shape with elongated and needle-like apices of S. fusiformis valves is similar to other diatoms, such as Nitzschia acicularis (Kützing) W. Smith and Nitzscia draveillensis Coste & Ricard, that are known planktic forms. The presence of planktic forms within Stenopterobia is interesting since the genus is known to primarily contain attached forms (Krammer 1989; Round et al. 1990; Rumrich et al. 2000). Similarly, unlike the vast majority of species in the genus *Eunotia* that are typically attached organisms, E. croatana and E. pseudofragilaria also represent planktic species. The presence of planktic species from raphe-bearing attached genera supports the hypothesis of Siver et al. (2006) that the extreme acidity and humic stained nature of these lakes has historically inhibited the growth of plankton from other algal groups, making this habitat available for attached taxa able to evolve morphotypes better adapted for such an existence.

Although fully formed valve face coverings and mantle rib wings have not been previously reported for Stenopterobia, parts of these intriguing structures have certainly been observed. For example, remnants of both structures can be seen on specimens representing type material for S. curvula (see Figs. 1, 2, 4, and 9 of Krammer 1989), on valves of S. densestriata (see Plate 197, Figure 7 of Rumrich et al. 2000), on the mantle of S. cf. denestriata (see Plate 59, Figure 10 of Ruck and Kociolek 2004) and most likely represent the "mushroom-like" projections noted by Round et al. (1990). In fact, in his description of S. curvula, Krammer (1989) referred to remnants of these structures as "very fine and frail structural elements" and further noted that "The fenestral openings between the alar canals in the wings are also covered by fine membranes. Some remnants of these membranes can usually be observed." It is worth noting that, to date, the valve face covering has only been observed on sigmoid taxa.

The functions of the valve face covering and mantle rib wings are not known. It is also unclear whether some cells produce these structures during wall formation while others do not, or if all cells make coverings and subsequently loose them. What is clear is that these structures are common on at least some Stenopterobia species, they form a cavity through which water could presumably collect and that the frustule probably remains motile since the raphe slits remain open. Perhaps the structures provide a means to get rid of excess silica. Krammer (1989) noted that the fine structural elements on the external ribs of S. curvula were easily destroyed during cleaning, a possibility also mentioned by Ruck and Kociolek (2004). This was not the case in our study. Even though all of the specimens imaged in our work with SEM were boiled in a mixture of H₂SO₄ and potassium dichromate, we consistently found intact coverings, even on older specimens recovered from the very bottom of the sediment core from Saco Pond. Therefore, these coverings can remain intact on acid cleaned frustules.

Like the valve face covering, it is not known if all *Stenopterobia* species can form areolae that are externally covered with a siliceous cap. In our study, this character was definitively observed only on straight forms. Interestingly, other genera within the Family Surirellaceae, including *Surirella*, *Cymatopleura*, and *Campylodiscus*, have areolae with caps or thickened rims, but these are on the internal, not external, valve surface. In fact, in a phylogenetic

study using morphometric characters, Ruck and Kociolek (2004) noted that the genus *Stenopterobia* formed a monophyletic group supported, in part, by the lack of internal coverings on the areolae. Thus, not only is it intriguing that the surface of the valve containing areolae coverings is apparently reversed in some *Stenopterobia* relative to other members of the family, but this character may further aid in splitting straight and curved species.

Pennate diatoms with girdle bands that open laterally are not common (Round et al. 1990). Based on our findings, straight forms of *Stenopterobia* clearly possess bands that open laterally, which makes sense for taxa with such protracted apices. At least some other members of the Surirellaceae, including *Surirella ovalis* Brébisson (Ruck and Kociolek 2004), also have such girdle bands and its possible that this trait is more widespread within this family than currently realized.

In summary, five species of the genus *Stenopterobia*, all representing straight morphotypes, are discussed from highly acidic localities along the Atlantic Coastal Plain of North Carolina. Two of these taxa are described as new species, two represent organisms originally described by Lewis (1864), and the fifth is a recently described species from Cape Cod (Siver and Hamilton 2005). We were further able to provide modified descriptions for *S. delicatissima* and *S. baileyi*, both originally identified by Lewis (1864) as well as brief comments on three sigmoidal forms, *S. curvula, S. anceps*, and *S. pelagica*.

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