

The genus *Semiorbis* (Eunotiaceae, Bacillariophyta) in North America

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The genus *Semiorbis* was erected by R.M.Patrick in 1966 as monotypic based on the relatively rare taxon *Semiorbis hemicyclus*. Defining characters for *Semiorbis* include strongly arcuate valves, short eunotioid raphe branches, well-developed external costae with spine-like projections on the virgae, lack of rimoportulae, and a broader dorsal mantle. New populations of *Semiorbis* were found in the central USA (Wisconsin) on Outer Island, Apostle Islands National Lakeshore, along southeast Lake Superior, from a lake in New Jersey (USA), and from a small arctic lake in Nunavut, Canada. The population in Outer Lagoon, a shallow embayment cut off from Lake Superior by a long-shore bar, provided documentation of living cells and colonies of *Semiorbis*. We examined the morphology, ecology, and taxonomy of these new populations using light and scanning electron microscopy, traditional morphometrics, and sliding landmarks shape analysis. We compared these populations to European populations of *Semiorbis hemicyclus* and North American populations of *Semiorbis rotundus* and *Semiorbis catillifera*. We determined that the population found in Wisconsin represents a new species herein described as *Semiorbis eliasiae* Edlund, D.R.L.Burge, N.A.Andresen & VanderMeulen *sp. nov.*, the New Jersey (USA) population is *Semiorbis rotundus*, and the Nunavut (Canada) population represents a North American population of the generitype *Semiorbis hemicyclus*.

Keywords: diatoms, Eunotiales, new species, taxonomy, shape analysis, biogeography

Introduction

Semiorbis is based on a taxon described by Ehrenberg (1841), *Synedra hemicyclus* Ehrenberg, from the Degernä fossil deposit in Sweden. This taxon has been variously placed in *Eunotia* Ehrenberg, *Ceratoneis* Ehrenberg, *Pseudoeunotia* Grunow, *Amphicampa* (Ehrenberg) Ralfs, and was eventually designated as the generitype of *Semiorbis* R.M.Patrick (*Semiorbis hemicyclus* (Ehrenberg) R.M.Patrick in Patrick & Reimer 1966). *Semiorbis* is usually associated with low pH and low alkalinity waters (Camburn & Charles 2000), and its frustules are characterized by strongly arcuate valves, well-developed external transapical costae, no rimoportulae, and frustules with slightly amphoroid symmetry (Edlund & Burge 2015).

Recent work by Reid & Williams (2010) confirmed the monophyly of the genus and recognized two additional taxa within *Semiorbis*, including a new species from the eastern United States, Canada, and Japan called *Semiorbis rotundus* G. Reid & D.M. Williams, and a species transferred from *Eunotia*, *Semiorbis catillifera* (Morrow) G.Reid & D.M.Williams, that was earlier described from

Florida (USA; Morrow et al. 1981). *Semiorbis hemicyclus* was suggested to be limited in distribution to low pH and low conductivity waters in northwest Europe and Greenland. Many reports of *Semiorbis* in North America, although usually identified as *S. hemicyclus*, can be identified as *S. rotundus* (Eardley-Wilmot 1928, Patrick & Reimer 1966, Davis et al. 1983, Camburn et al. 1984–1986, 2000, Dixit & Dickman 1986, Elner & Ray 1987, Dixit et al. 1988, Hamilton et al. 1992, Fallu et al. 2000, Pienitz et al. 2003, Siver et al. 2005, Edlund et al. 2013).

We studied several North American populations of *Semiorbis* from Nunavut (Canada) and New Jersey, Florida, and Wisconsin (USA) and a population from Kristiansund, Norway. We examined the valve morphology of these four disparate populations using traditional morphometrics, light microscopy, and shape analysis, to determine the identity of each population. Based on the results, four *Semiorbis* species could be separated including one new species: *Semiorbis eliasiae* Edlund, D.R.L.Burge, N.A.Andresen & VanderMeulen *sp. nov.*, described herein. We further document the valve ultrastructure of *S. eliasiae*

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Associate editor: Patrick Rioual

(Received 17 August 2020; accepted 14 December 2020)

as well as its protoplast and colony arrangement based on living material. The presence of *S. hemicyclus* in North America is confirmed and it is therefore recognized as a circumboreal and holarctic taxon.

Material and methods

The following slides and material were examined:

Science Museum of Minnesota, MBE 712, USA, New Jersey, Burlington County, Bass River State Forest, Lake Absegami, *Sphagnum* squeezings along shore towards outlet. Taxa include *Tabellaria* spp., *Eunotia* spp., *Frustulia* spp., *Actinella punctata*, *Aulacoseira* spp., *Brachysira* spp., and *Semiorbis*. Coll: M.B. Edlund, 23 April 1995

BR IX-36-C10, Walker Arnott (n° 856). Norway, Christiansund (Kristiansund), Pond at Fisco. Predominant taxa include *Semiorbis* together with several species in the genera *Brachysira*, *Eunotia*, and *Actinella*.

Science Museum of Minnesota, MBE 2351, Canada, Nunavut, Lake #3, 0–1 cm surface sediment from a pond, 65.12446°N, –107.394°W, water depth 3.6 m, temperature 11.2 °C, specific conductivity 52 $\mu\text{S cm}^{-1}$, dissolved oxygen saturation 105.5%, pH 5.20, 21.54% sediment organic content (Porinchu *et al.* 2009, Westover *et al.* 2009). Predominant taxa include *Psammothidium marginulatum* (Grunow) Bukhtiyarova & Round, *Stauroforma exiguiformis* (Lange-Bertalot) R.J.Flower, V.J.Jones & Round, *Frustulia* spp., *Encyonema* spp., *Aulacoseira nivalis* (W.Smith) J.English & Potapova, *Brachysira brebissonii* R.Ross, *Chamaepinnularia mediocris* (Krasske) Lange-Bertalot, and a small-celled *Semiorbis* sp. at 3.5% abundance. Coll: VI-03, Karlyn Westover, 07 August 2004.

ANSP GC-65337, USA, Wisconsin, Apostle Island National Lakeshore, Outer Island Lagoon, sediment core, 0–1 cm depth. Coll: M.B. Edlund, J.R. Hobbs, J. Elias, 25 July 2007.

ANSP GC-53770, holotype for *Semiorbis catillifera*, USA, Florida, Walton County, Rocky Creek, Elgin Air Force Base.

North American material was prepared by oxidation in 30% H_2O_2 ; material was rinsed 4–5x with distilled H_2O , dried onto No. 1 coverglasses, and mounted on microslides with Zrax (MicrAP, Philadelphia). North American material was examined using an Olympus BX50 light microscope equipped with differential interference contrast (DIC), oil immersion optics capable of 1000x at NA 1.40, and a QImaging 5.0 system. Norway material was examined on an Olympus BX53 microscope equipped with DIC and oil immersion optics capable of 1000x at NA 1.40, and an Olympus UC30 imaging system. Cleaned

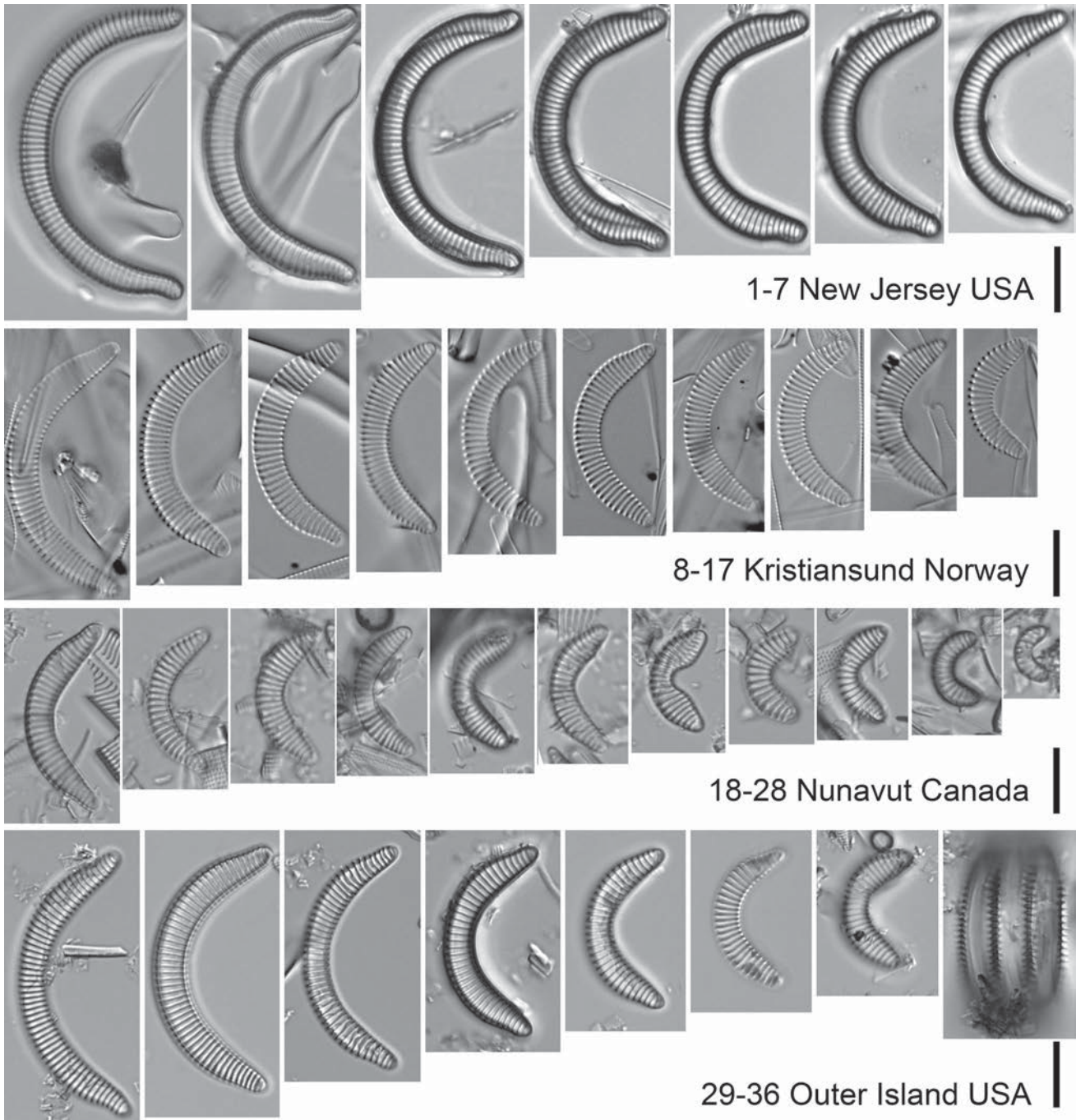
material from the Outer Island (Wisconsin, USA) population was further dried onto coverslips that were then mounted on aluminium stubs, coated with 20 nm of Au, and examined at 15–20 kV accelerating voltage in a JEOL-JSM-6060LV SEM, with specimens examined for internal ($n = 5$) and external ($n = 5$) valve morphology.

Morphometrics (length, breadth, stria count and density per 10 μm) and valve curvature on the dorsal margin (Bixby & Zeek 2010) were measured or calculated for at least 25 valves per population. We also applied sliding landmarks shape analysis using four fixed (two at maximum length, two at central breadth) and 16 sliding landmarks to define valve shape across the size series ($n = 25$ –50 valves per population) for each taxon (see examples of landmark placement in Fig. 49). The 20 landmarks were digitized using tpsDig v 2.28 (Rohlf 2016). Using tpsRelw v 1.65 (Rohlf 2016), landmarks were centred and aligned using the Procrustes method to remove size variation as a factor of shape change (Rohlf & Slice 1990). Principal component analysis (tpsRelw v 1.65) was used to identify the major variation in shape change; scores along the principal component axes of variation are referred to as relative warps (RW). The axis scores for RW1 and RW2 were compared to each other and to valve length to relate valve shape change to ontogeny associated with size diminution. Valve terminology follows Reid & Williams (2010).

Results

Among the five populations of *Semiorbis* (Figs 1–48, Table 1), there is variability in valve size, shape, and dorsal curvature. Valves in the New Jersey (USA) population are 33–45 μm long, 3.8–5.6 μm broad, have a stria density of 8–12 per 10 μm , and valve curvature ranges from 0.05 to 0.12 (Figs 1–7). The population from Kristiansund, Norway has valve lengths of 18.7–37.4 μm , breadth 3.4–4.7 μm , stria density of 8–16 per 10 μm , valve curvature from 0.04 to 0.10, and weakly rostrate ends in larger valves (Figs 8–17). The Nunavut (Canada) population has many very small valves; overall valve lengths are 9–28 μm , breadth 2.5–4.6 μm , stria density of 11–14 per 10 μm , very weakly rostrate ends in larger valves, and valve curvature from 0.06 to 0.20 (Figs 18–28). The Outer Island (Wisconsin, USA) population has a wide range of valve sizes with length 16.5–40 μm , breadth 3.6–5.7 μm , stria density 8–12 per 10 μm , rostrate ends in longer valves, and curvature from 0.05 to 0.12 (Figs 29–36). The population from Outer Island, Wisconsin (USA), also gave us the opportunity to document live cells and colony morphology of *Semiorbis* (described below; using live material from surface sediment, 0–1 cm, collected by Joan Elias, 31 August 2011, 47°00'27.1"N, –90°27'34.8"W).

The Florida (USA) *Semiorbis* sample has valves that are 17–40 μm long, 4.8–5.3 μm broad, with stria density of 12–13 per 10 μm , and are much less arched, have a slightly

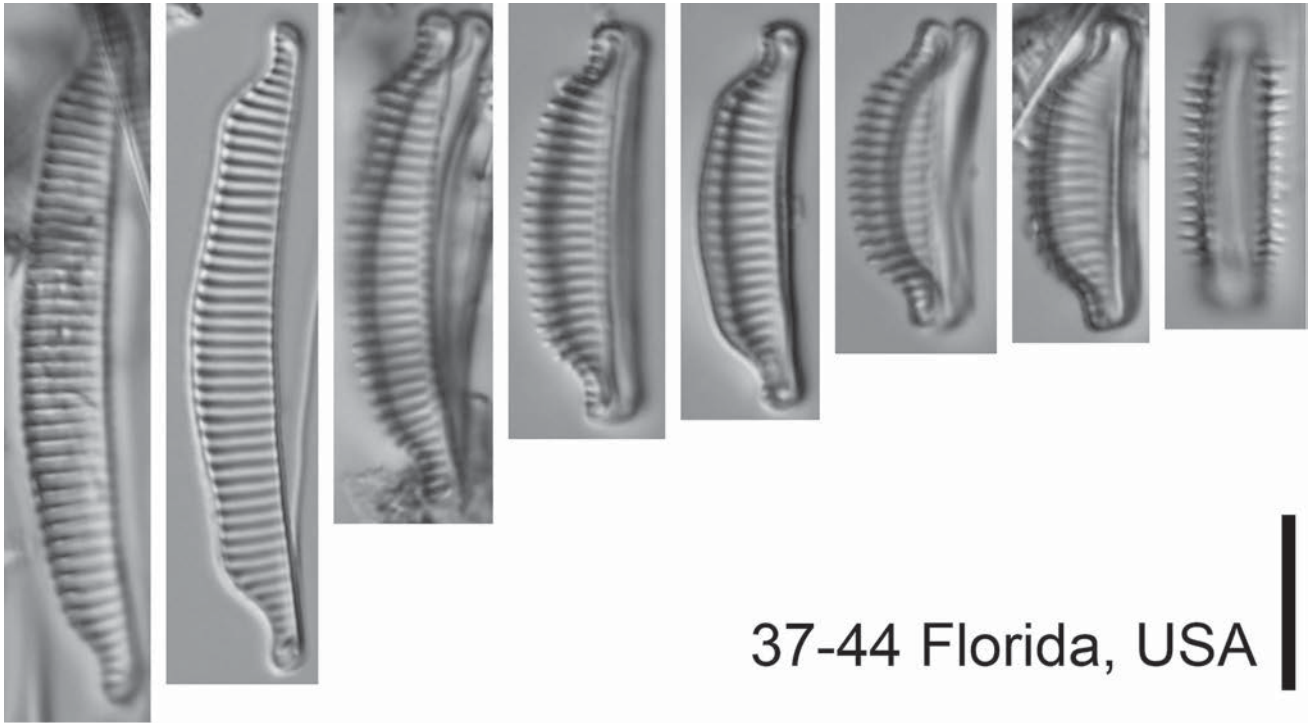


Figs 1–36. Light micrograph size series of *Semiorbis* populations. All figures at same magnification. Scale bars are 10 μm . **Figs 1–7.** *Semiorbis rotundus* from Lake Absegami, New Jersey (USA), (Science Museum of Minnesota, MBE 712A). **Figs 8–17.** *Semiorbis hemicyclus* from Kristiansund, Norway (BR IX-36-C10, Walker Arnott, n° 856). **Figs 18–28.** *Semiorbis hemicyclus* from Nunavut, Canada, (Science Museum of Minnesota, MBE 2351A). **Fig. 24** an aberrant valve. **Figs 29–36.** *Semiorbis eliasiae* from Outer Island Lagoon, Apostle Islands National Lakeshore, Wisconsin (USA), (ANSP GC-65337). Holotype is Fig. 30. Isotypes are Figs 31 (ANSP GC-65338), 32 (CANA 128904).

scalloped dorsal margin, and strongly rostrate ends compared to other *Semiorbis* populations (Figs 37–44). These characteristics clearly identify the Florida (USA) population as *S. catillifera* (Morrow et al. 1981, Reid & Williams 2010, Burge & Edlund 2016). Because of this clear distinction, *S. catillifera* was left out of further morphometric

analyses, but we include a size series of light micrographs to allow comparison with other taxa.

Bivariate plots of valve breadth, valve curvature, stria density, and total stria count against valve length did not provide clear separation of any populations (Fig. 45). *Semiorbis* from New Jersey had the longest valve



37-44 Florida, USA

Figs 37–44. Size series of *Semiorbis catillifera* from Rocky Creek, Eglin Air Force Base, Walton County, Florida, United States, (ANSP GC-53770). Scale bar is 10 μ m.

lengths and generally least curvature, whereas valves from Nunavut were shorter and more curved. *Semiorbis* from Norway and Outer Island had a similar range of lengths and curvature, but the Norway valves were generally narrower for a given valve length. All populations had similarly variable stria densities. Total stria count was strongly correlated to valve length but provided no clear separation among populations.

Relative Warp (RW) axes 1 and 2 scores were calculated for specimens from the New Jersey (USA), Outer Island (USA), Nunavut (Canada), and Norway populations. Relative Warp axis 1 captures the overall valve shape (Fig. 46). At the negative end of RW axis 1 valves are more uniformly shaped. That is, if they were ‘straightened’ they would be linear with parallel margins to even slightly panduriform. At the positive end of RW axis 1, valves are more tapered from the valve centre to the apices, i.e. if valves at the positive end of RW axis 1 were ‘straightened’ they would be lanceolate. Valves from Outer Island (USA) plot most negatively on RW axis 1, valves from Norway and New Jersey (USA) plot closest to the origin of RW axis 1, and valves from Nunavut (Canada) plot most positively.

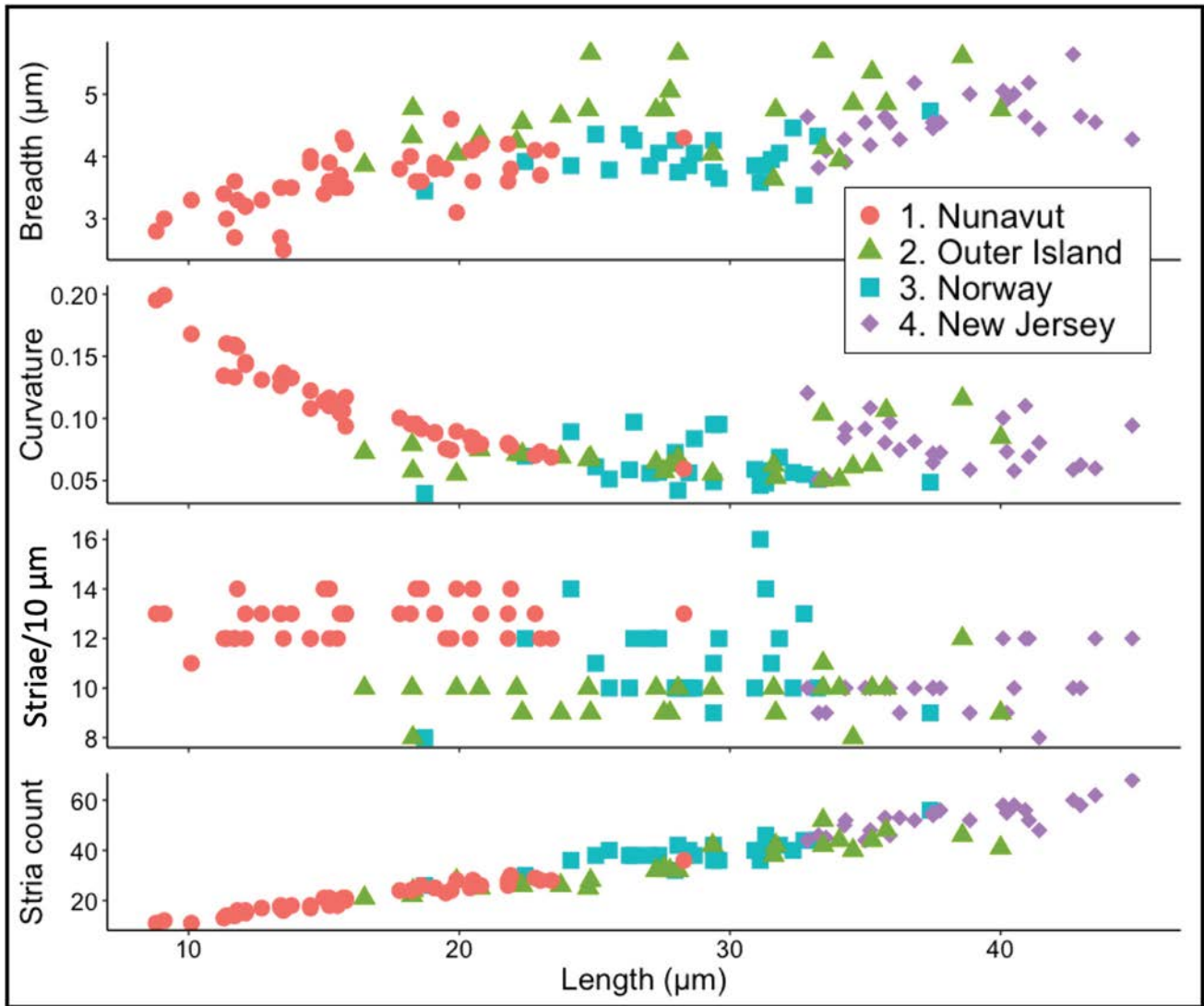
Relative Warp axis 2 captures variation in the depth of valve curvature (Fig. 46). At the negative end of axis 2 the valve curvature is deeper, whereas at the positive end of Axis 2 the valve curvature is shallower. Outer Island (USA) valves plot most negatively on RW axis 2, whereas valves in the Norway population plot most positively.

Nunavut (Canada) and New Jersey (USA) valves are distributed along the full range of RW axis 2.

A bivariate plot of RW axis 1 against RW axis 2 scores for all populations shows that the Outer Island (USA) population is readily separable from other *Semiorbis* populations (Fig. 46). The other three populations overlapped in morphospace with the Nunavut (Canada) population plotting most positively on RW axis 1 and Norway plotting most positively on RW axis 2.

A bivariate plot of RW axis 1 against valve length provides further separation of the populations (Fig. 47). The Outer Island (USA) population continues to plot most negatively on RW axis 1 with lengths from 15 to 35 μ m. The New Jersey (USA) population is strongly positive on RW Axis 1 and plots among the longer valve lengths of 32–46 μ m. The Nunavut (Canada) and Norway populations form a continuum along both axes, from short valves with high RW axis 1 scores to long valves with low RW axis 1 scores.

Based on our morphometric analyses of valve metrics and shape (Figs 48–50), we recognize three species of *Semiorbis* in addition to *S. catillifera*. The longer length and strongly curved valves of the New Jersey (USA) population are readily separable based on length and RW axis 1 and easily identified as *S. rotundus* (Reid & Williams 2010). We identify the Nunavut (Canada) population as *S. hemicyclus*, representing the shorter end of a size continuum that includes the overlapping and longer valves of the Norway population of *S. hemicyclus*. In comparisons



Figs 45. Distribution of valve breadth (top panel, μm), valve curvature (second panel, μm^{-1}), stria density (third panel, striae/ $10\mu\text{m}$), and total stria count (bottom panel) against valve length (μm) in four populations of *Semiorbis* ($n = 25\text{--}50$ valves per population, red circle – Nunavut, Canada; green triangle – Outer Island, USA; blue square – Kristiansund, Norway; purple diamond – New Jersey, USA).

of RW axis 1 to valve length and to RW axis 2, specimens from the Outer Island (USA) population are clearly separated by their more parallel-sided and deeply curved valves of medium length. We were not able to assign the Outer Island (USA) population to a known species and describe it as new.

Semiorbis eliasiae Edlund, D.R.L.Burge, N.A.Andresen & VanderMeulen *sp. nov.* (Figs 29–36, 51–53)

Holotype: Circled specimen on slide (Fig. 30, ANSP GC-65337).

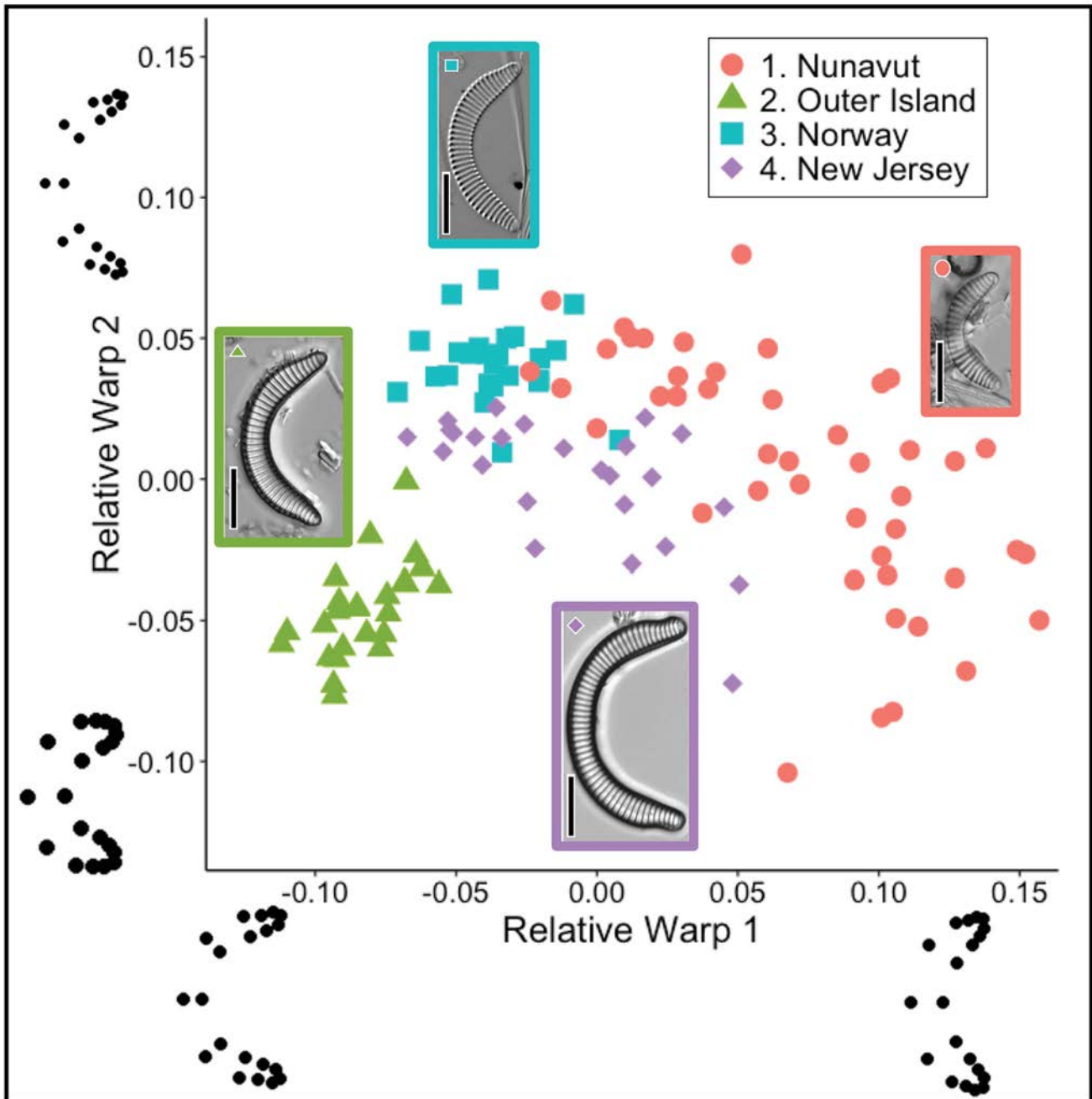
Isotypes: Circled specimen on slide (Fig. 31, ANSP GC-65338). Circled specimen on slide (Fig. 32, CANA-128904).

Type locality: USA, Wisconsin, Apostle Islands National Lakeshore, Outer Island Lagoon, $47^{\circ}00'27.1''\text{N}$, $-90^{\circ}27'$

$34.8''\text{W}$. Surface sediment from core, 0–1 cm, collected by M.B. Edlund, J.R. Hobbs, Joan Elias, 25 July 2007 (ANSP material GCM-5771, CANA material 128904).

Paratype: USA, Wisconsin, Apostle Islands National Lakeshore, Outer Island Lagoon, $47^{\circ}00'27.1''\text{N}$, $-90^{\circ}27'34.8''\text{W}$. Surface sediment from core, 29–30 cm (sediment deposited ca. 1968), collected by M.B. Edlund, J.R. Hobbs, Joan Elias, 25 July 2007 (ANSP GC-65339 and GCM-5772, CANA slide and material 128905).

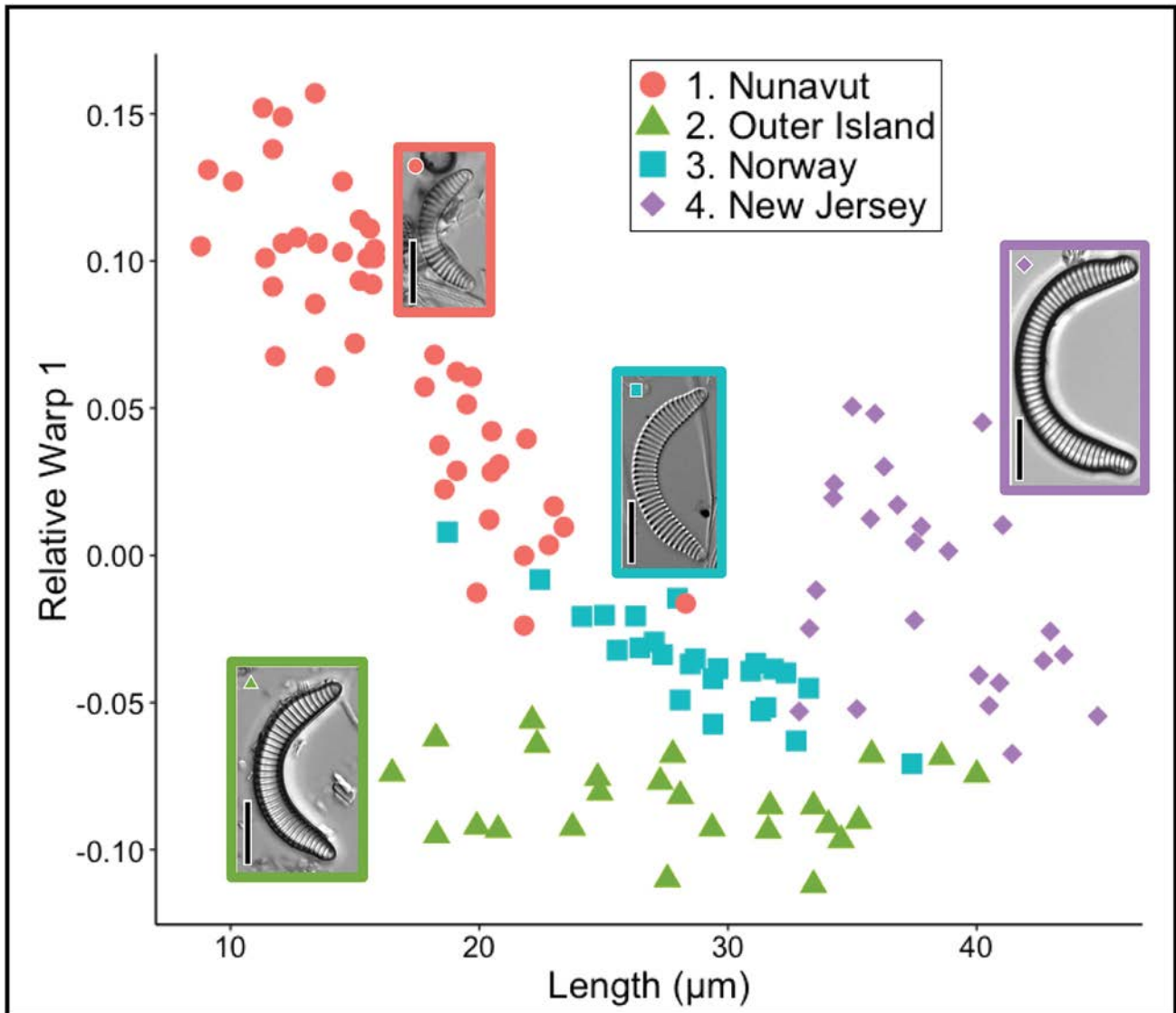
Etymology: This species honours Joan Elias, retired, National Park Service, Great Lakes Inventory and Monitoring Network (GLKN), who initiated an innovative biomonitoring programme using diatoms on the inland GLKN lakes including Outer Lagoon on Outer Island at the Apostle Islands National Lakeshore (USA).



Figs 46. Distribution of valve shape descriptors Relative Warp 1 plotted against Relative Warp 2 in four populations of *Semiorbis* ($n = 25\text{--}50$ valves per population, red circle – Nunavut, Canada; green triangle – Outer Island, USA; blue square – Kristiansund, Norway; purple diamond – New Jersey, USA). Representative specimens of each population shown in coloured box. Outlines at the maximum and minimum of each axis represent shape variation captured by Relative Warps 1 and 2.

Description: Cells lunate with dorsal sides slightly broader compared to ventral sides, lanceolate in girdle view (Figs 29–36). Cells arranged in colonies constructed of four to many cells adjoined at their valve ends in circular groups with their dorsal mantles and cingula facing outward. Cells with a centrally located nucleus and two plate-like valve-appressed chloroplasts in each cell. Storage bodies common and likely polyphosphate (libroplasts) or chryso-laminarin (Figs 48–50). Valves lunate with somewhat

broader dorsal mantles (Fig. 53), slightly rostrate ends, parallel margins that may be slightly constricted mid-valve in smaller specimens, and conspicuous external transapical costae (Figs 29–36). Valve length $16.5\text{--}40.5\text{ }\mu\text{m}$, breadth $3.6\text{--}5.7\text{ }\mu\text{m}$, stria or transapical costa density $8\text{--}12$ per $10\text{ }\mu\text{m}$, and dorsal curvature from 0.05 to 0.12 . In scanning electron microscopy, transapical costae terminating dorsally and ventrally in short, flat spines at the face-mantle junction. Costae continuing onto the valve mantle



Figs 47. Relative Warp 1 plotted against valve length (μm) in four populations of *Semiorbis* ($n = 25$ per population, red circle – *S. hemicyclus* from Nunavut, Canada; green triangle – *S. eliasiae* from Outer Island, USA; blue square – *S. hemicyclus* from Kristiansund, Norway; purple diamond – *S. rotundatus* from New Jersey, USA). Representative specimens of each population shown in coloured box.

(Figs 51–53). A short raphe slit present at each valve end, externally starting on the ventral mantle and curving onto the valve face at each end (Fig. 52), internally limited to the ventral mantle and terminating in a small helicoglossa (Figs 54–55, 57). No rimoportulae present (Figs 55, 57). One stria between neighbouring costae (Fig. 53), striae uniseriate, sometimes becoming biseriate toward the face-mantle junction, and continuing onto the valve mantle (Figs 53, 56). Areolae without external occlusion, internally occluded by a hymen (Fig. 56). Cingulum of 3–4 split bands, each with a single row of areolae (Figs 52–53).

Diagnosis: *Semiorbis eliasiae* differs from *S. rotundus* by being shorter, with less rostrate apices, and less deeply arched valves. *Semiorbis hemicyclus* can have much shorter valves than *S. eliasiae* and the valve centre is often

the broadest part of the valve in the former. *Semiorbis eliasiae* also has somewhat coarser costa/stria density compared to *S. hemicyclus* of similar length. Valve ontogeny during the life history of *S. hemicyclus* and *S. eliasiae* is strongly controlled by shape as defined by Relative Warp 1. Relative Warp 1 changes dramatically along length in *S. hemicyclus* in contrast to the highly constrained valve shape across valve length in *S. eliasiae*. In short, valves of *S. eliasiae* have a more consistent valve shape along the full range of lengths; if the valves were straightened, *S. eliasiae* would have linear to slightly panduriform valve margins compared to linear to lanceolate margins in *S. hemicyclus*.

Ecology: Known distribution to date is limited to surface sediments and core material from Outer Lagoon on

Table 1. Morphometrics for five populations (ordered as in results) and type material of *Semiorbis* species including valve length, breadth, stria density, total stria count, and dorsal valve curvature calculated using Bixby & Zeek (2010).

Location/taxon	Length (μm)	Breadth (μm)	Stria density no. per 10 μm	Total stria no.	Dorsal curvature (μm^{-1})	Reference
New Jersey, USA <i>Semiorbis rotundus</i>	32.8–44.9	3.8–5.6	8–12	44–68	0.05–0.12	This study
Kristiansund, Norway <i>S. hemicyclus</i>	18.7–37.4	3.4–4.7	8–16	26–56	0.04–0.10	This study
Nunavut, Canada <i>S. hemicyclus</i>	8.8–28.3	2.5–4.6	11–14	11–36	0.06–0.20	This study
Outer Island, USA <i>S. eliasiae</i>	16.5–40.0	3.6–5.7	8–12	21–52	0.05–0.12	This study
Florida, USA <i>S. catillifera</i>	17.0–40.0	4.8–5.3	12–13	21–46	–	This study
<i>S. catillifera</i> (type)	10.0–42.0	2.8–6.1	11–14	20–54	–	Morrow et al. (1981)
<i>S. rotundus</i> (type)	21.0–44.0	4.0–5.2	12–13	29–66	–	Reid & Williams (2010)
<i>S. hemicyclus</i>	22.0–46.0	3.8–5.0	11–14	37–78	–	Reid & Williams (2010)

Outer Island, Apostle Islands National Lakeshore (USA). *Semiorbis* can be found in Outer Lagoon sediments deposited since the 1950s with its greatest abundance in the surface sediments (> 6% abundance; Edlund et al. 2013). Outer Lagoon is a small (0.22 km²) shallow (< 1.4 m deep) lake separated from Lake Superior by a long-shore sand bar. Water quality of Outer Lagoon (Elias & Damstra 2012) is characterized as circumneutral (pH 6.4), with low nutrients (total P 11.6 $\mu\text{g L}^{-1}$, total N 0.675 mg L^{-1}), low productivity (chlorophyll-a 1.4 $\mu\text{g L}^{-1}$), low alkalinity (6 mg L^{-1}), low specific conductivity (24 $\mu\text{S cm}^{-1}$), and moderately coloured (DOC 15 mg L^{-1}).

Discussion

The genus *Semiorbis* is found in northern hemisphere low pH and low alkalinity habitats but is uncommonly reported (Camburn et al. 1984–1986, Camburn & Charles 2000, Fallu et al. 2000, Siver et al. 2005, Reid & Williams 2010, Edlund & Burge 2015). We document four species from North America: *S. rotundus*, *S. catillifera*, *S. hemicyclus*, and the new species *S. eliasiae*. The last taxon was documented in the living condition and shown to form spherical colonies, like *S. hemicyclus* (Cleve-Euler 1953) and *S. rotundus* (Kobayasi & Nagumo 1978). Cells have a centrally located nucleus and two plate-like valve-appressed chloroplasts per cell, accompanied by storage bodies probably or polyphosphate (libroplasts) or chrysolaminarin. Live *S. eliasiae* collections were from surficial lake sediments; others have reported *Semiorbis* associated with filamentous algae (Cox 1996). Among the eunotioid diatoms, the *S. eliasiae* cytoplasmic arrangement is shared by many taxa including *Eunotia arcus*, *E. serra*, and *E. monodon* Ehrenberg (Heinzerling 1908, Cox 1996) and *Actinella* (Uherkovich 1986, Beals 2011, de Castro Canani et al. 2018). We also confirmed the absence of rimoportulae in the genus and the presence of internal hymenate areolae occlusions (Moss et al. 1978); within

the Eunotiales the hymenes are apparently easily lost during preparation (Edlund et al. 2000, Reid & Williams 2010).

Because of its rarity, species recognition within *Semiorbis* has to date been limited to morphological data. Reproductive and molecular data have not been reported for *Semiorbis* to support or refine species recognition. Here we supplemented traditional morphometrics by applying sliding landmark shape analysis to show morphological separation of three similar strongly arched *Semiorbis* taxa. Among the many methods used for shape analysis (Pappas et al. 2014), sliding landmarks shape analysis was developed to detect variation and differences among organisms and structural shapes (Rohlf & Slice, 1990), and has been applied to analysis of siliceous algae using both light and scanning electron micrographs (e.g. Beszteri et al. 2005, English & Potapova 2012, Siver et al. 2013). Key findings have supported the separation of closely related taxa, provided morphological support for molecular phylogenies, enabled new species recognition, and defined species-level ontogenies from multiple temporal samples (English & Potapova 2012, Burge et al. unpubl.). Whereas *S. catillifera* is easily distinguished among *Semiorbis* taxa by traditional morphometrics, it was only by combining traditional morphometrics with sliding landmarks shape analysis, similar to English & Potapova (2012), that we could discern the ontogenetic patterns that readily differentiate the three strongly arched *Semiorbis* species.

Reid & Williams (2010) did a monographic study of *Semiorbis* and documented three species including *S. hemicyclus*, *S. catillifera*, and a new species, *S. rotundus*. The latter taxon was documented in eastern North America and Japan. One conclusion reached by Reid & Williams (2010) was that the generitype, *S. hemicyclus*, was not found in North America, but was limited to the Old World. Our analysis suggests that *S. hemicyclus* is present in North America. The population from Nunavut (Canada) clearly

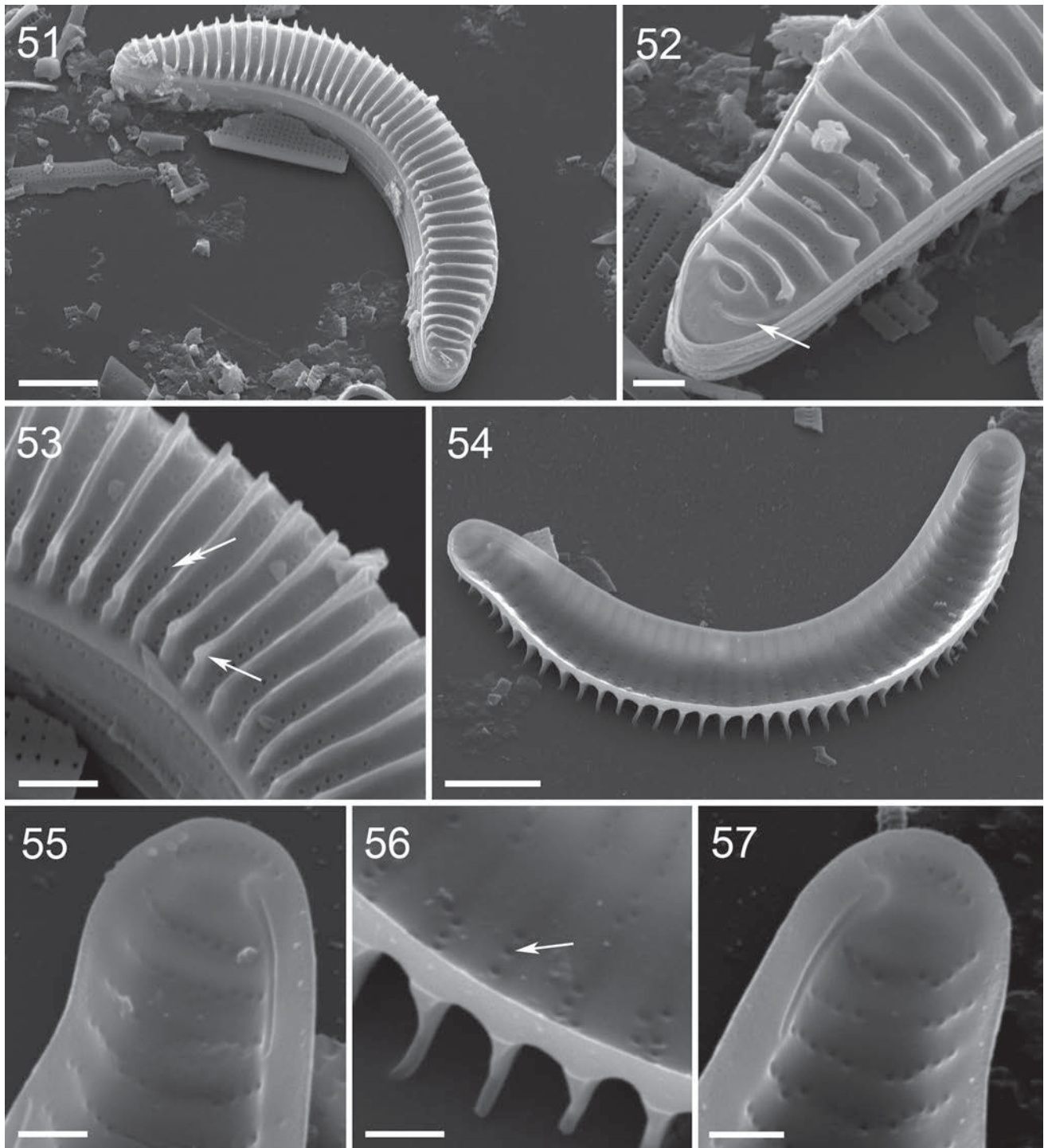


Figs 48–50. Live colonies of *Semiorbis eliasiae* comprise four – many cells adjoined in circular colonies along the ventral sides of their ends with the dorsal margins oriented to the outside of the colony. Cells have a central nucleus (N), two valve-appressed chloroplasts (C), and prominent storage bodies (S) of polyphosphate (libroplasts/volutin) or chrysolaminarin. Recently divided cells also visible (D). Scale bars 10 μm . Scale bar for Figs 49, 50 in Fig. 50b.

represents the shorter end of the *S. hemicyclus* morphological continuum, and in fact extends the lower length range of *S. hemicyclus* to 8.8 μm , well below other published values (22–48 μm ; Reid & Williams 2010). Larger cells from Nunavut (Canada) are well represented in the morphoserries of the Norway population of *S. hemicyclus*. As such, *S. hemicyclus* appears to have a broader size range and a circumboreal and holarctic distribution (Fallu et al. 2000).

In contrast, the distributions of other *Semiorbis* appear more restricted. *Semiorbis catillifera* has been collected only from the type locality, as periphyton in a shallow, slightly acidic stream in western Florida (USA; Morrow et al. 1981, Burge & Edlund 2016). Similarly, *S. eliasiae* has been conclusively documented only from its type locality, Outer Lagoon, a long-shore embayment along the Lake Superior shoreline of Outer Island (USA). Paleoecological

analysis of a 73-cm sediment core from Outer Lagoon suggests that this embayment has been isolated from Lake Superior for ~ 700 years. *Semiorbis eliasiae* can be found in Outer Lagoon sediments deposited since the 1950s with its greatest abundance in the surface sediments ($> 6\%$ abundance; Edlund et al. 2013). The fate of this nearshore aquatic habitat is questionable. In September 2014, a large storm breached the long-shore bar separating the lagoon from Lake Superior and inundated Outer Lagoon. By July 2020, about one-third of the original lagoon had been re-isolated from Lake Superior with a new long-shore bar. However, it is anticipated that other reports of '*Semiorbis hemicyclus*' in North America (e.g. Camburn & Charles 2000, pl. 15, fig. 21) will, upon closer examination, expand the range of *S. eliasiae* to include other low conductivity, slightly acidic to circumneutral habitats in north temperate North America.



Figs 51–57. Scanning electron micrographs of *Semiorbis eliasiae* from Outer Island Lagoon, Apostle Islands National Lakeshore, Wisconsin (USA), (ANSP GCM-5771). **Fig. 51.** External view of frustule with slight amphoroid symmetry showing prominent transapical costae. **Fig. 52.** External valve end showing raphe slit (arrow) ending distally on the valve face and punctate cingula bands. **Fig. 53.** External valve has transapical costae that end dorsally and ventrally in flat spines (arrow) and separate rows of areolae aligned in uniseriate striae (double arrow). Cingulum bands with a single row of areolae. **Fig. 54.** Internal view of valve. **Fig. 55.** Internal view of valve end of specimen in Fig. 54 showing short raphe branch terminating distally in a helictoglossa and lack of rimoportula. **Fig. 56.** Internal view of mid-valve of specimen in Fig. 54 showing areolae internally occluded by hymenes (arrow) and arranged in uniseriate striae that can become biserial on both valve mantles. **Fig. 57.** Other end of valve in Figs 54–55 also shows internal raphe and lack of rimoportula. Scale bars 5 μm (Figs 51, 54), 1 μm (Figs 52, 55–57), 2 μm (Fig. 53).

Acknowledgements

Special thanks to Joan Elias of NPS-GLKN, Karlyn Westover of Indiana State University, and Mark Spahr for collecting and sharing samples, to Matthew Julius, St. Cloud State University, for providing SEM facilities, and to an anonymous reviewer and associate editor for improving the manuscript. Sadly, Dr Norman Andresen passed away shortly before this manuscript was submitted.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the National Park Service Great Lakes Inventory and Monitoring Network (NPS-GLKN) under [Grant numbers P10AC00280, P15AC00368, and J2105100003/0002].

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