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# Morphotype variations in subfossil diatom species of *Aulacoseira* in 24 Michigan Lakes, USA

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Diatom assemblages preserved in lake sediment records can provide proxy data of past environmental changes in biological conditions. In order to investigate past changes in the environment of north-central Michigan, diatom assemblages were studied in sediment cores retrieved from 24 lakes. Diatoms were analyzed from the 'top' and 'bottom' of each core to reconstruct land-use changes in this area. *Aulacoseira* taxa were identified and evaluated with light and scanning electron microscopy. Results of these observations showed the presence of some variability of the morphological features within North American species populations. Diatom species composition in surface sediments and differences between tops and bottoms corresponded to changes in land use surrounding the lakes, ranging from predominantly forest and rangeland to urban and agriculturally impacted. Diatom-inferred past conditions revealed that the observed morphotypes probably represent taxa with different ecological preferences. The main factors influencing the variability of these morphotypes are changes in the trophic status of the lakes.

**Key words:** diatom, *Aulacoseira*, ultrastructure, sediment, distribution, morphotype, Michigan lakes

## Introduction

In the last few decades, lakes within large watersheds adjacent to the Great Lakes have been of considerable interest (WOLIN and STOERMER 2005). Information on changes due to human activities is imprinted in the lacustrine sediment composition (STOERMER et al. 1985, FRITZ et al. 1993, BRADBURY et al. 2002) and inferences of past conditions are possible (STOERMER and SMOL 1999). Following changes in diatom assemblages allows the distinguishing of natural disturbances from those caused by the development of the many coastal areas of the Great Lakes (ENACHE and PRAIRIE 2002).

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Species within aquatic ecosystems change with the surrounding environment. Algae go through such changes faster than other organisms (BARINOVA et al. 2008) and are considered sensitive indicators of past and current changes. Studies of past environmental conditions are limited to inorganic biological remnants such as diatom frustules and other preserved proxies of past conditions.

In sediments, diatoms are abundant and well preserved (STOERMER and SMOL 1999), and diatom species respond sensitively to anthropogenic alterations in land use and cover and resulting changes in nutrient concentration and conductivity (DIXIT et al. 2001). Many reconstructions of lake history based on sub-fossil diatoms have used changes in ratios of centric and pennate diatoms in sediments (e.g. WOLIN and DUTHIE 1999, STONE and FRITZ 2004). Centric diatoms dominate lacustrine sediments (STOERMER and SMOL 1999) and the genus *Aulacoseira* has been reported in most lakes (ZOHARY 2004, WOLIN and STOERMER 2005). Changes in *Aulacoseira* species can bring region-specific understanding in freshwater habitats (USOLTSEVA and LIKHOSHWAY 2007). Closely related species have been lumped in many studies because fine level distinctions in taxonomy are too challenging without extensive taxonomic experience.

The goals of this study were first to trace coarse changes in centric and pennate diatom species composition between 'top' and 'bottom' sediments and second to compare the dominant *Aulacoseira* species and diatoms were analyzed from the 'top' and 'bottom' of each core. The 'top/bottom' comparison approach has been used in palaeolimnological reconstruction of recent climate change and extensive catchment land-use changes in different locations (DIXIT et al. 1999, MESSERLI et al. 2000, YANG et al. 2002, 2008).

## Materials and methods

Sediment cores were retrieved from 24 lakes in the Muskegon River watershed, Michigan (STEVENSON et al. 2007). The Muskegon River watershed drains approximately 2,723 square miles of land and is located in north-central Michigan. The river is approximately 219 miles long from its source at Houghton and Higgins Lakes down to its mouth at Muskegon Lake and, eventually, Lake Michigan. The Muskegon River watershed is one of the largest watersheds in the State of Michigan (http://www.cevl.msu.edu/mrweap/mRiver Map.html). Lakes were sampled at their deepest point, in the deepest basin (GLEW et al. 2001). Glew Corer was used for sediment retrieval. Lake metrics were measured and summarized as part of the Muskegon Watershed project.

In this study, tops were the surface sediment, bottoms were the deepest intact sediment retrieved by the corer. Using a knife, tops and bottoms were sliced and represented 1cm of sediment (V. LOUGHEED personal communication). Preparation of diatom samples followed standard methods (BATTARBEE 1986).

Diatom relative abundances were determined by subsampling and acid-cleaning a subsample of the sediment algal sample. Subsamples of cleaned diatoms were mounted on microscope slides using NAPHRAX® as mounting medium. A minimum of 600 diatom valves were identified and counted at 1000 times magnification using a Leica DMLB microscope and differential interference contrast optics. Samples were scanned for *Aulacoseira* species after enumeration of 600 valves. SEM observations were made with acid-cleaned, gold-coated specimens and a scanning electron microscope (SEM, JEOL, Japan Electron Optics Laboratories) 6400V with a LaB6 emitter (Noran EDS) at the Center for Advanced Microscopy at Michigan State University.

Diatoms were identified primarily with the use of HUSTEDT (1927–1966), KRAMMER and LANGE-BERTALOT (1986, 1988, 1991a, b), PATRICK and REIMER (1966, 1975), as well as more recent or more specific references such as the PIRLA Diatom Iconograph (CAMBURN et al. 1986, KRAMMER 1991a, b, SIVER and KLING 1997, CRAWFORD and LIKHOSHWAY 1998, LIKHOSHWAY and CRAWFORD 2001, HOUK and KLEE 2007) and Diatoms of North America (SIVER et al. 2005).

*Aulacoseira* species have been identified by the following characters: frustule dimensions (ranges in valve diameter and pervalvar axis length); areolar rows on the mantle in 10 µm; form and ultrastructure of the areola-type and vola-covered occlusions; form and structure of the linking spines; form and structure of the separation spines; structure of the ringleist – shallow or deep; thick, thin or hollow; number, position and form of the rimoportula; type of the external opening of the rimoportula; other species features – presence of spines; granulae, etc.

The following community characteristics were calculated for each sample: richness (total number of taxa observed in a site); Shannon-Weaver diversity index $H= -\Sigma_{(i-s)}p_i\log(p_i)$, where $p_i$ is the proportion of the total count arising from the $i^{th}$ species (SHANNON and WEAVER 1949); evenness (equitability)=H'/ln(richness) (PIELOU 1969) and Simpson's dominance index (SIMPSON 1949), which measures the likelihood of two randomly chosen individuals in a sample being the same species.

The correlation coefficients ($r^2$) were used to identify relationships between physicochemical variables in top and bottom-reference sites. Significant correlations of more than 50% were discussed.

All statistical analyses were performed with SYSTAT ® 10 (WILKINSON 1989).

## Results

Lakes varied in depth from Sapphire Lake with 2.2 m to Fremont and Ryerson Lakes with more than 20 m. Total anthropogenic land use varied from less than 4% for 3 lakes to more than 80% in Fremont Lake. Diatom species composition in surface sediments and differences between tops and bottoms corresponded to the current land use surrounding the lakes, which ranged from predominantly forest (Goose and Long Lakes, Missauke county) and rangeland to urban and agriculturally impacted (Cadillac Lake, Wexford county). Particular combinations of size, depth and human impact conditions allowed the classification of 13 lakes with good conditions, 8 lakes with fair and 3 lakes with poor conditions. For example, the shallow and eutrophic Brooks Lake with only 23% total land use had the highest cultural eutrophication index and was classified as poor (Tab. 1).

We identified 153 diatom species. Centric diatoms were dominant in 55% of the 'top' sediment counts and in 92% of the 'bottom' sediment counts. *Aulacoseira* species were present in all lakes and dominant in top and bottom counts. No community diversity attributes were significantly different in 'top' and 'bottom' counts. Mean Shannon diversity was close to 1 in both 'top' and 'bottom' counts. Shannon diversity was highest in the 'top' sediment count for Goose Lake (a good quality lake) and the 'bottom' sediment count of Round Lake (a fair quality lake). In the three lakes with poor quality, diversity significantly de-

**Tab. 1.** Lake Identity and characteristics. Number abbreviations correspond to numbers in map 1. T_LAND – total land use, where 0% land use means no human alteration or 100 % forest; depth in m; S_CTP – sum of total P in ppb; CEI – Cultural eutrophication; A_OLIGo – Algae as percent oligotrophic taxa according to Stevenson's Mid Atlantic trophic index; Lake_IBI – Lake index of biological indicator and Lake condition (Muskegon watershed web).

| N | Lake | County | T_LAND | Depth | S_CTP | Secchi | CEI | A_Oligo | Lake_IBI | Lake Condition |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Baptist Lake | Newaygo | 0.53 | 14.33 | 14.31 | 5.77 | –0.42 | 0.06 | 52.02 | Good |
| 2 | Brooks Lake | Newaygo | 0.22 | 4.13 | 16.30 | 0.93 | 1.03 | 0.00 | 8.91 | Poor |
| 3 | Cadillac Lake | Wexford | 0.76 | 3.75 | 24.60 | 1.58 | 0.71 | 0.01 | 14.68 | Poor |
| 4 | Doc and Tom Lake | Clare | 0.34 | 6.33 | 16.59 | 2.50 | 0.04 | 0.04 | 62.78 | Good |
| 5 | Fremont Lake | Newaygo | 0.83 | 20.67 | 19.75 | 3.82 | 0.62 | 0.03 | 29.45 | Fair |
| 6 | Goose Lake | Missauke | 0.03 | 3.50 | 13.44 | 1.91 | 0.06 | 0.13 | 72.83 | Good |
| 7 | Haymarsh Lake | Mecosta | 0.07 | 8.67 | 16.33 | 3.08 | 0.05 | 0.02 | 36.99 | Fair |
| 8 | Hess Lake | Newaygo | 0.42 | 3.80 | 13.70 | 0.60 | 1.42 | 0.00 | 8.47 | Poor |
| 9 | Hillsview Lake | Mecosta | 0.13 | 10.30 | 14.40 | 2.00 | 0.77 | 0.12 | 38.01 | Fair |
| 10 | Horsehead Lake | Mecosta | 0.34 | 13.33 | 14.20 | 3.50 | –0.18 | 0.04 | 42.70 | Good |
| 11 | Little Whitefish Lake | Newaygo | 0.20 | 12.00 | 22.90 | 3.62 | –0.30 | 0.01 | 47.24 | Good |
| 12 | Long Lake C | Clare | 0.31 | 17.70 | 10.10 | 5.10 | –0.50 | – | 49.35 | Good |
| 13 | Long Lake M | Missauke | 0.04 | 5.00 | 12.89 | 2.83 | –0.01 | 0.02 | 59.65 | Good |
| 14 | McCoy Lake | Osceola | 0.61 | 8.33 | 33.01 | 2.58 | 0.07 | 0.08 | 53.75 | Good |
| 15 | Pickerel Lake | Newaygo | 0.34 | 19.25 | 21.10 | 4.13 | –0.02 | 0.00 | 29.29 | Fair |
| 16 | Rogers Dam Pond | Mecosta | 0.48 | 4.40 | 34.36 | 1.53 | 0.64 | 0.06 | 33.38 | Fair |
| 17 | Round Lake | Mecosta | 0.41 | 12.50 | 23.83 | 2.67 | 0.40 | 0.03 | 33.71 | Fair |
| 18 | Ryerson Lake | Newaygo | 0.48 | 24.17 | 22.79 | 5.17 | –0.16 | 0.03 | 40.80 | Good |
| 19 | Sapphire Lake | Missauke | 0.21 | 2.20 | 15.00 | 1.50 | –0.11 | 0.07 | 57.78 | Good |
| 20 | School Section Lake | Mecosta | 0.40 | 7.00 | 20.94 | 3.57 | –0.23 | 0.06 | 54.82 | Good |
| 21 | Second Lake | Newaygo | 0.65 | 12.33 | 13.76 | 3.37 | 0.26 | 0.04 | 36.13 | Fair |
| 22 | Silver Lake | Clare | 0.27 | 14.92 | 13.76 | 4.67 | –0.34 | 0.33 | 64.77 | Good |
| 23 | Townline Lake | Mecosta | 0.46 | 11.43 | 14.20 | 2.90 | 0.32 | 0.07 | 43.45 | Good |
| 24 | Winfield Lake | Newaygo | 0.64 | 14.33 | 33.67 | 1.95 | 0.90 | 0.03 | 19.67 | Fair |

**Tab. 2.** Community attributes in top and bottom sediment sites. SE – standard error; *p* – significance level.

| Attributes | Bottom | | | | Top | | | | p |
|---|---|---|---|---|---|---|---|---|---|
| | mean | ±SE | min | max | mean | ±SE | min | max | |
| Diversity | 1.01 | 0.045 | 0.42 | 1.4 | 1 | 0.059 | 0.19 | 1.4 | ns |
| Richness | 46 | 2.55 | 21 | 69 | 43 | 2.36 | 17 | 63 | ns |
| Evennes | 0.26 | 0.009 | 0.14 | 0.337 | 0.26 | 0.013 | 0.07 | 0.341 | ns |
| Simpson's dominance | 0.736 | 0.009 | 0.663 | 0.863 | 0.737 | 0.013 | 0.659 | 0.934 | ns |

creased with an increase in human influence 1.01 (± 0.00001 SE 'bottom') to 0.89 (± 0.001 SE 'top'). Baptist Lake had the lowest diversity in both 'top' and 'bottom' counts, so lake quality alone was not a good predictor of diatom sediment diversity. Simpson's index did not differ between top and bottom (mean 0.74 for both) even though the dominant taxa changed. In 'bottom' sediment samples, taxa observed in counts varied from 21 to 69 taxa (evenness 0.14 to 0.34), while in the 'top' 1 cm sediment species ranged from 17 to 63 diatom taxa (evenness 0.06 to 0.34, Tab. 2). A fairly diverse *Aulacoseira* bottom community reduced to *A. subarctica* and *A. ambigua* in the top samples. The main factors influencing the variability of these morphotypes were changes in the trophic status of the lakes (Tab. 3).

*Aulacoseira* taxa from the 'bottom' sediment counts were negatively correlated with depth, cultural eutrophication, and increase in total phosphorus where pennate diatoms dominated the community. In the 'top' diatom community *Aulacoseira* taxa were positively correlated with depth and oligotrophic conditions (Tab. 4).

**Tab. 3.** Relative abundance (RA) of *Aulacoseira* species in top and bottom sediment samples of the 24 Michigan lakes.

| Taxon | RA top, mean (range) | RA bottom, mean (range) |
|---|---|---|
| *Aulacoseira ambigua* (Grunow) Simonsen | 0.22<br>(0.006–0.54) | 0.11<br>(0.003–0.29) |
| *Aulacoseira granulata* (Ehrenberg) Simonsen | 0.02<br>(0.002–0.13) | 0.02<br>(0.001–0.08) |
| *Aulacoseira granulata* morphotype *curvata* | | 0,003 |
| *Aulacoseira italica* (Ehrenberg) Simonsen | 0,003 | 0,003 |
| *Aulacoseira nygaardii* (Camburn) Camburn et Charles | | 0,003 |
| *Aulacoseira perglabra* (Østrup) Haworth | | 0,08 |
| *Aulacoseira pseudoamericana* (Camburn) Siver et Kling | | 0,08 |
| *Aulacoseira subarctica* (Müller) Haworth | 0.19<br>(0.003–0.52) | 0.11<br>(0.002–0.68) |
| *Aulacoseira valida* (Grunow) Krammer | | 0,003 |

**Tab. 4.** Correlations between algal groups and lake dimensions. Percent *Aulacoseira* in 'top' and 'bottom' samples, other Centric and Pennate diatoms and factors as abbreviated in table 1.

| | DEPTH | S_CTP | SECCHI | CEI | A_Oligo | LAKE_IBI | Au_T | Centr-T | Pen_T | Au_B | Centr-B | Pen_B |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DEPTH | 1.00 | | | | | | | | | | | |
| SUMCTPPPB (S_CTP) | 0.23 | 1.00 | | | | | | | | | | |
| SECCHI | –0.48 | 0.51 | 1.00 | | | | | | | | | |
| CULTURALEUT (CEI) | 0.11 | **0.99** | **0.65** | 1.00 | | | | | | | | |
| (A_Oligo) | **0.91** | –0.18 | –0.67 | –0.29 | 1.00 | | | | | | | |
| LAKE_IBI | **0.57** | –0.12 | **–0.91** | –0.29 | **0.59** | 1.00 | | | | | | |
| *Aulacoseira* -top (Au_T) | **1.00** | 0.26 | –0.47 | 0.14 | **0.90** | **0.58** | 1.00 | | | | | |
| Other centrics-top (Centr-T) | 0.42 | **0.98** | 0.41 | **0.95** | 0.01 | –0.04 | 0.44 | 1.00 | | | | |
| Pennate-top | **0.50** | **–0.56** | –0.38 | **–0.56** | **0.76** | 0.06 | 0.47 | –0.39 | 1.00 | | | |
| *Aulacoseira* -bottom (Au_B) | **–0.83** | **–0.73** | 0.02 | **–0.64** | **–0.54** | –0.30 | **–0.85** | **–0.85** | –0.06 | 1.00 | | |
| Other centrics-bottom (Centr-B) | 0.33 | 0.24 | 0.45 | 0.35 | –0.45 | –0.01 | 0.35 | 0.04 | 0.19 | 0.19 | 1.00 | |
| Pennate-bottom | **0.73** | **0.68** | 0.24 | **0.65** | 0.48 | –0.06 | **0.74** | **0.80** | 0.23 | **–0.92** | –0.41 | 1.00 |

## *Aulacoseira* species descriptions

*Aulacoseira ambigua* (Grunow) Simonsen (SIMONSEN 1979; **Pl. 1, Figs. 1–10**)

*Basionym*: *Melosira crenulata* var. *ambigua* Grunow (VAN HEURCK, H., 1880–1885)

*Melosira ambigua* (Grunow) O. Müller

*Aulacoseira ambigua* (Grunow) Simonsen (KOBAYASI and NOZAWA 1981: Figs. 1–22)

*Melosira ambigua* (Grunow) O. Müller var. *ambigua* (CAMBURN and KINGSTON 1986: 20, Pl. I, Figs. 1–5)

*Aulacoseira ambigua* (Grunow) Simonsen (SIVER and KLING 1997: 1808, Figs. 1–12)

*Aulacoseira ambigua* (Grunow) Simonsen (CAMBURN and CHARLES 2000; 13, Pl. 1, Figs. 18–22)

*Aulacoseira ambigua* (Grunow) Simonsen; (SIVER et al. 2005: 33, Pl. 1, Figs. 22, 25–27, Pl. 3, Fig. 3)

Valve diameter ranges of 4–14 µm; the height of valve mantle 5.50–14 µm; the areolae on the mantle are in spiral rows 16–20 in 10 µm. The areolae have circular form with deep-seated vela. The linking spines are notched bifid, and terminate each mantle costa. The ringleist is hollow (Pl. 1, Fig. 10). The rimoportulae are two per valve, without stalk. They are located on the ringleist (LIKHOSHWAY and CRAWFORD 2001). Their external openings are large, visible in LM (Pl. 2, Fig.5). The separating spines are longer, pointed (LE COHU 1991).

Ecology: known from mesotrophic to eutrophic environments, dominant in shallow lakes (VAN DAM et al. 1994, TRIFONOVA and GENKAL 2001, BARINOVA et al. 2008). This taxon disappeared from the top of Cadillac Lake (being with 29% RA) in the bottom sediment, and remained in low abundance in Doc and Tom Lake (both lakes with poor conditions). A 15-fold increase from bottom to top was observed in Fremont Lake. This taxon was not observed in any lake classified as 'Good' (Tab. 1).

*Aulacoseira granulata* (Ehrenberg) Simonsen (SIMONSEN 1979; **Pl. 2, Figs. 1–6**)

Basionym: *Gallionella granulata* Ehrenberg 1841

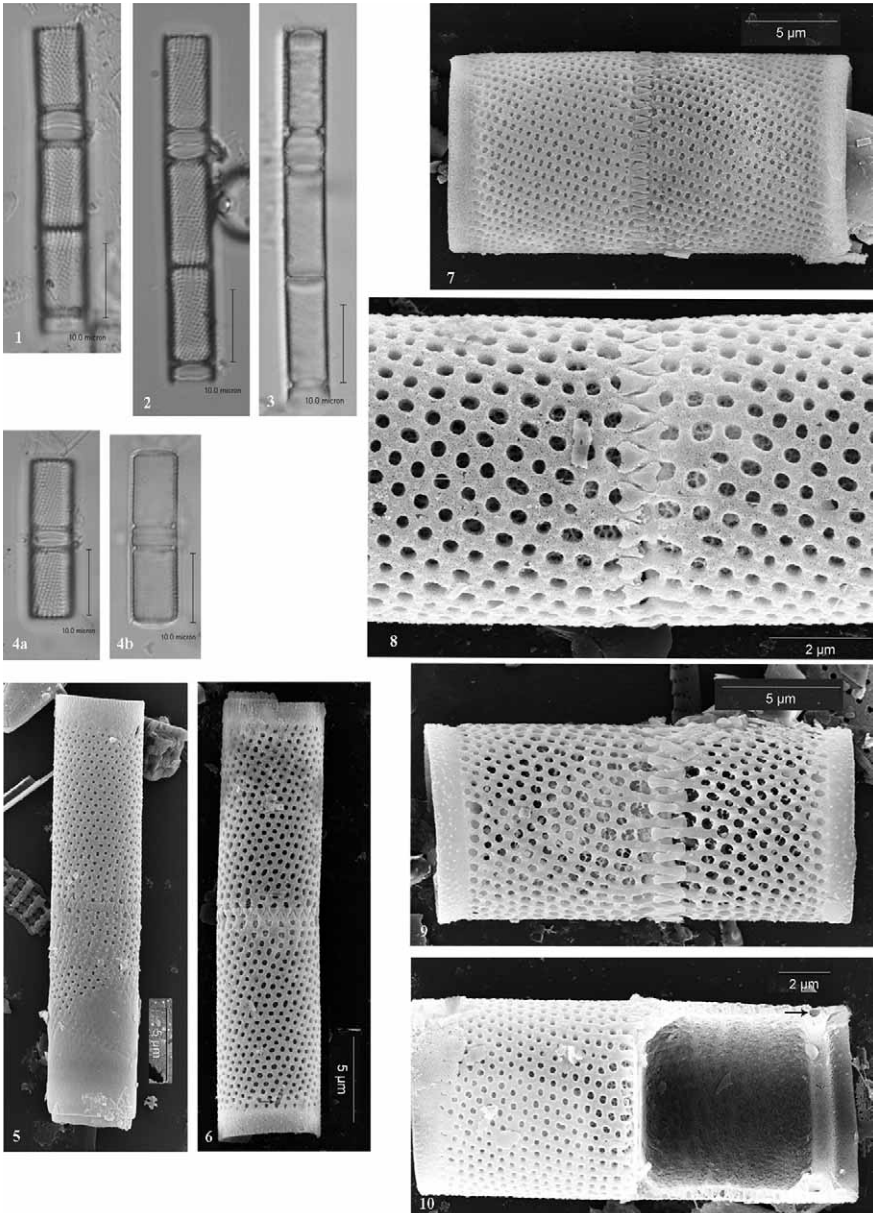
*Melosira granulata* (Ehrenberg.) Ralfs (PRITCHARD 1861: 820)

*Melosira granulata* (Ehrenberg.) Ralfs (STOERMER et al. 1981: 348, Pl. 2, Figs. 21–33)

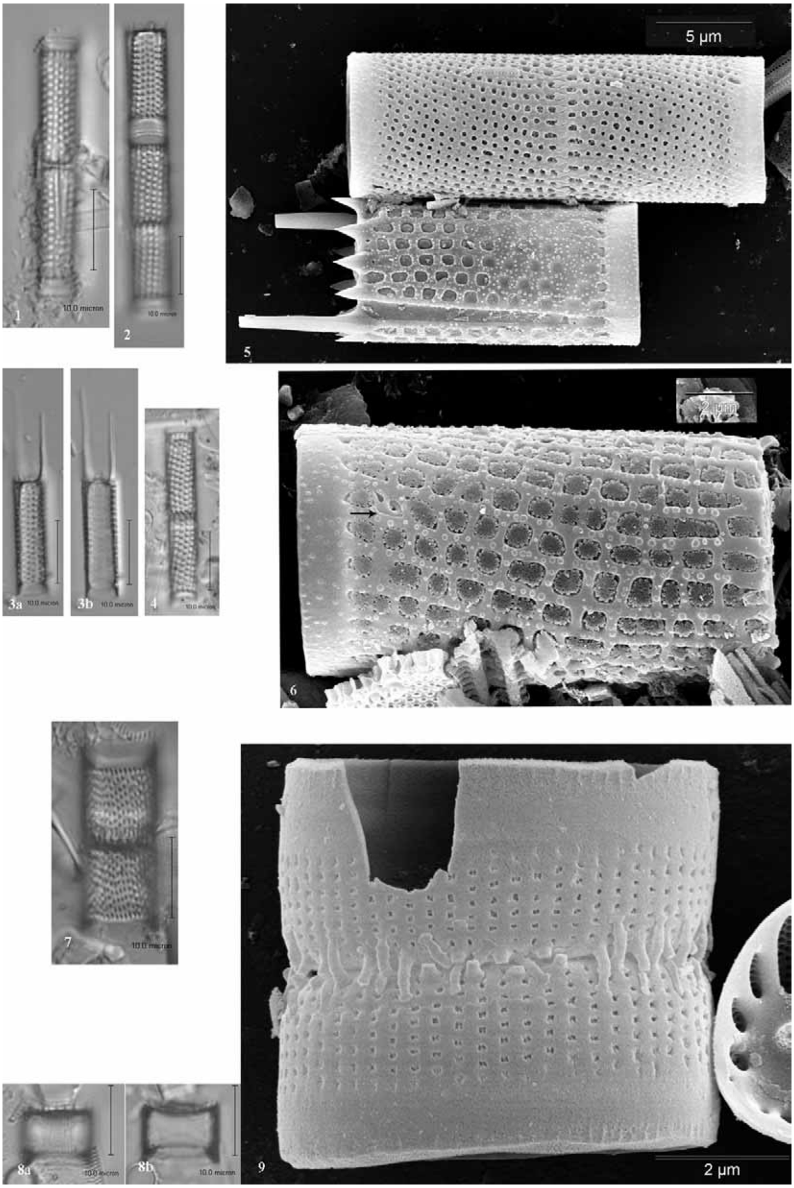
*Aulacoseira granulata* (Ehrenberg) Simonsen (SIVER and KLING 1997: 1813, Figs. 23–28)

Valve diameter ranges of 3–11.50 µm; the height of valve mantle 10–17 µm; the areolae on the mantle are in straight or spiral rows 10–15 in 10 µm. The areolae are coarse, round to square, covered with velar complex (CRAWFORD and LIKHOSHWAY 1998). The velar plate occurs on the outside. The linking spines are notched triangular. The rimoportulae are found on the valve face/mantle junction, near the ringleist (Pl. 1, Fig. 5). The external opening is large, visible in LM (LIKHOSHWAY and CRAWFORD 2001). Internally, the rimoportula has tightly curved stalks lying close to the mantle surface (LIKHOSHWAY and CRAWFORD 2001). The separating spines are conical with varying length, from short to almost the length of the valve mantle.

Ecology: known from mesotrophic to highly eutrophic environments, dominant in shallow lakes (VAN DAM et al. 1994, SIVER and KLING 1997, TRIFONOVA and GENKAL 2001, BARINOVA et al. 2008).



**Pl. 1.** *Aulacoseira ambigua* (Grun.) Simonsen **Fig. 1** – girdle view – LM, Round Lake, top sediments; **Figs. 2, 3** – girdle view with cross-section focus – LM, Silver Lake, bottom sediments; **Figs. 4 a, b** – girdle view with cross-section focus – LM, Cadillac Lake, top sediments; **Fig. 5** – sibling valves, showing spiral rows of areolae with external openings of the rimoportulae, SEM, Round Lake, top sediments; **Figs. 6, 7** – sibling valves, SEM, Cadillac Lake, top sediments; **Fig. 8** – detail of linking spines – triangular with bicuspid ends, SEM, Cadillac Lake, top sediments; **Fig. 9** – sibling valves with dissolution, see the prominent form of the linking spines – the ends are clavate, SEM, McCoy Lake, bottom sediments; **Fig. 10** – inner surface of the girdle, the Ringleist is hollow, SEM, Cadillac Lake, top sediments.



**Pl. 2.** *Aulacoseira granulata* (Ehrenber) Simonsen. **Fig. 1** – girdle view – LM, Ryerson Lake, top sediments; **Fig. 2** – girdle view – LM, Second Lake, top sediments; **Figs. 3a, b** – girdle view with cross-section focus – LM, Ryerson Lake, bottom sediments; **Fig. 4** – girdle view – LM, Haymarsh Lake, bottom sediments; **Fig. 5** – *Aulacoseira ambigua* (above) and *A. granulata* (below) with long pointed separating spines, SEM, Cadillac Lake, top sediments; **Fig. 6** – *A. granulata*, external opening of the rimoportula arrowed, SEM, Cadillac Lake, top sediments; **Fig. 7** – *A. italica* (Ehrenberg) Simonsen, LM, Horsehead Lake, top sediments; **Figs. 8 a, b** – *A. nygaardii* (Camburn) Camburn and Charles, girdle view with cross section focus, LM, McCoy Lake, bottom sediments; **Fig. 9** – *A. nygaardii* (Camburn) Camburn and Charles, sibling valves with T-shaped tips of the spines, SEM, McCoy Lake, bottom sediments.

*Aulacoseira granulata* mophotype *curvata* (Hustedt) Krammer

*Basionym*: *Melosira granulata* var. *curvata* Grunow (VAN HEURCK, H., 1880–1885)

*Aulacoseira granulata* mophotype *curvata* (Hustedt) Krammer (KRAMMER 1991a: Figs. 6–8, 19)

Valve diameter ranges 5–7.50 µm; the height of valve mantle 12.50–16.50 µm; the areolae on the mantle are in straight or spiral rows 12 in 10 µm.

Ecology: known from mesotrophic to eutrophic environments as *A. granulata* (VAN DAM et al. 1994) typical of shallow lakes (TRIFONOVA and GENKAL 2001). In Muskegon lakes we found it in Townline Lake, which has good conditions.

*Aulacoseira italica* (Ehrenberg) Simonsen (SIMONSEN 1979; **Pl. 2, Fig. 7**)

*Basionym*: *Gallionella italica* Ehrenberg 1838

*Melosira italica* (Ehrenberg) Kützing (KÜTZING 1884: 55, Pl. 2, Fig. 4)

*Aulacoseira italica* (Ehrenberg) Simonsen (KOBAYASI and NOZAWA 1981: Figs. 1–11)

*Aulacoseira italica* (Ehrenberg) Simonsen (KRAMER 1991b: Fig. 44)

*Aulacoseira italica* (Ehrenberg) Simonsen emend. Crawford, Likhoshway et Jahn (CRAWFORD et al. 2003: 17, Figs. 2–14)

Valve diameter ranges of 8–11 µm; the height of valve mantle 9–14 µm; the areolae on the mantle are in straight or sinistrorse spiral rows 16–18 in 10 µm. The areolae are subcircular, or, more usually, elongated to fine slits (CRAWFORD et al. 2003). The velum, a spongiform plate, occurs on the inner aperture. The rimoportulae are usually two per valve and positioned 4–5 areolae distant from the ringleist. Ringleist is solid, narrow and shallow (CRAWFORD et al. 2003). The linking spines are large and T-shaped. The separation spines are the same length as linking spines, but are pointed and are rarely found on each valve.

Ecology: Known from mesotrophic to eutrophic environments, dominant in shallow lakes (VAN DAM et al. 1994, TRIFONOVA and GENKAL 2001).

*Aulacoseira nygaardii* (Camburn) Camburn et Charles (CAMBURN and CHARLES 2000; **Pl. 2, Figs. 8–9**)

*Basionym*: *Melosira nygaardii* Camburn 1986

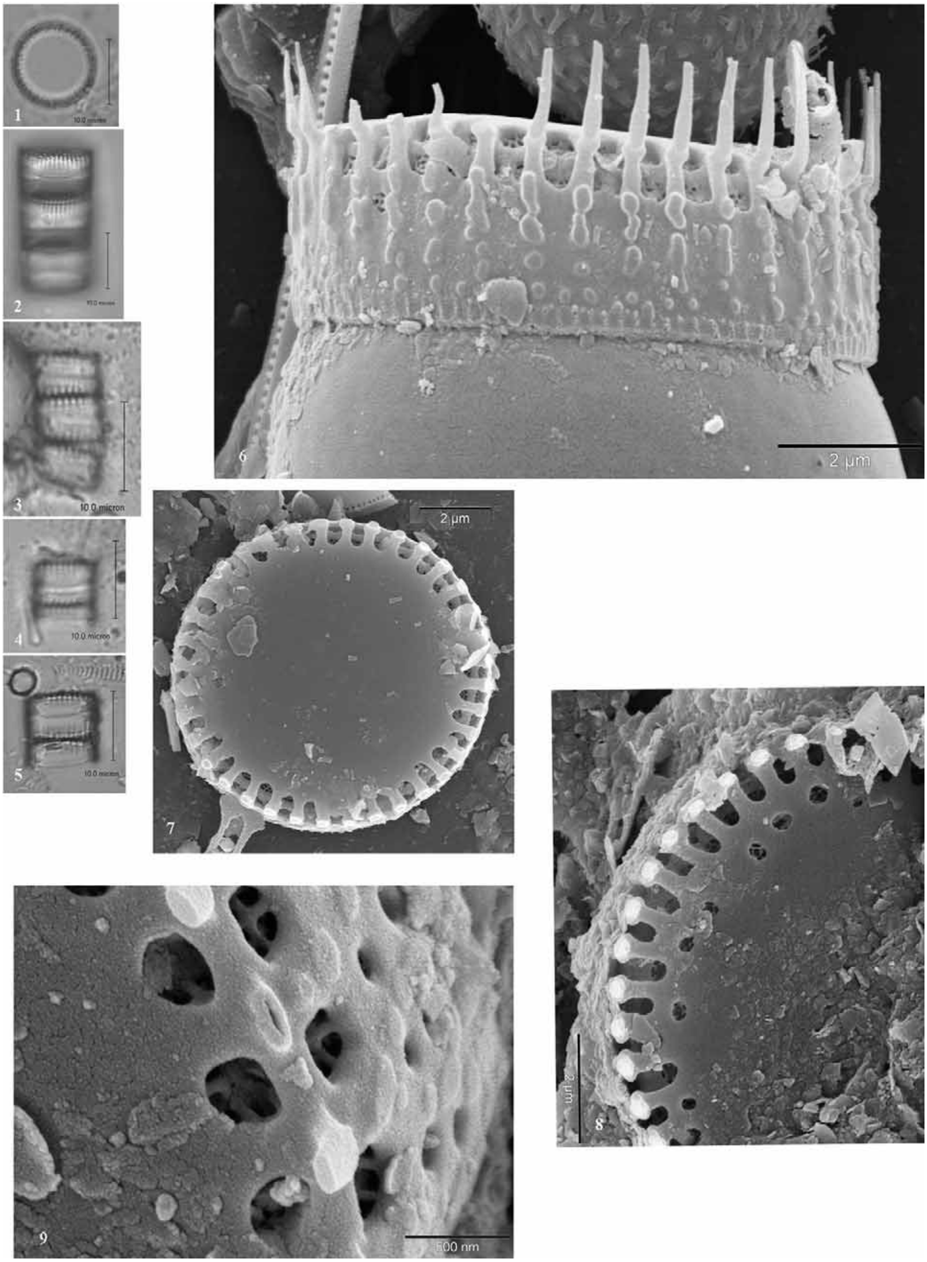
*Aulacoseira nygaardii* (Camburn) Camburn et Charles (CAMBURN and CHARLES 2000: 14, Pl. 3, Figs. 9, 16–22)

*Aulacoseira nygaardii* (Camburn) Camburn et Charles (SIVER and HAMILTON 2005: 258, Figs. 1–16)

*Aulacoseira nygaardii* (Camburn) Camburn et Charles (SIVER et al. 2005: 35, Pl. 1, Figs. 11–16, Pl. 2, Figs. 6–8)

Valve diameter 10 µm; the height of valve mantle 6 µm; the areolae on the mantle are in straight rows 22 in 10 µm. The areolae are circular to rectangular; the position of the velum (type 'rotae') is attached down into the base of areola (SIVER and HAMILTON 2005). The ringleist is very shallow. The linking spines are short, with equal length and T-shaped endings.

Ecology: known from acidic, nutrient-poor waters (SIVER and HAMILTON 2005, SIVER et al. 2005) this taxon was rare in our study and appeared in the 'bottom' sediment of McCoy Lake.



**Pl. 3.** *Aulacoseira perglabra* (Østrup) Haworth. **Fig. 1** – valve view, LM, McCoy Lake, bottom sediments; **Figs. 2, 3, 4, 5** – girdle view – LM, McCoy Lake, bottom sediments; **Fig. 6** – girdle view, see the long and narrow linking spines, SEM, McCoy Lake, bottom sediments; **Fig. 7** – valve view with peripheral ring of elongated areolae, the second (inner) ring is partial with smaller and cruciate areolae with vela, SEM, McCoy Lake, bottom sediments; **Fig. 8** – valve view with more regular second peripheral areolar ring, SEM, McCoy Lake, bottom sediments; **Fig. 9** – The velum of the areola, SEM, McCoy Lake, bottom sediments.

*Aulacoseira perglabra* (Østrup) Haworth (HAWORTH 1988; **Pl. 3, Figs. 1–9**)

*Basionym*: *Melosira perglabra* Østrup 1910

*Melosira perglabra* Østrup (CAMBURN and KINGSTON 1986: 28, Pl. 4, Figs. 59–65, Pl. 5, Figs. 77–78)

*Aulacoseira perglabra* (Østrup) Haworth (SIVER and KLING 1997: 1818, Figs. 48–53, 60–63)

*Aulacoseira perglabra* (Østrup) Haworth (CAMBURN and CHARLES 2000: 14, Pl. 4, Figs. 1–8)

*Aulacoseira perglabra* (Østrup) Haworth (SIVER et al. 2005: 1, Figs. 7–10, 23–24: 2, Figs. 3–5)

Valve diameter ranges 5.50–13.50 µm; the height of valve mantle 1.50–4.00 µm; the areolae on the mantle are in very short rows (12–21 in 10 µm) and are normally obscured by the overlapping spines of the sibling valve. The areolae are covered by vela. The rimoportula is single, small, and sits in a narrow band as in LIKHOSHWAY and CRAWFORD (2001). There is a lack of any noticeable ringleist (SIVER and KLING 1997). The linking spines are long and narrow, with flat ending as shown in CRAWFORD and LIKHOSHWAY (1998, Fig. 11).

They are carried on buttresses spanning the margin of the face and mantle. On the valve face there is one peripheral ring of elongated areolae that extends onto the mantle, but sometimes smaller crucial areolae form second (inner) partial ring.

Ecology: known from oligotrophic conditions (SIVER and KLING 1997, TRIFONOVA and GENKAL 2001) this taxon was not observed in 'top' sediment samples. We found it in 'bottom' sediments of McCoy Lake.

*Aulacoseira pseudoamericana* (Camburn) Siver et Kling (SIVER and KLING 1997; **Pl. 4, Figs. 1–9**)

*Basionym*: *Melosira pseudoamericana* Camburn 1986

Valve diameter ranges 8.50–13.00 µm; the height of valve mantle 3.00–6.00 µm; the mantle is unornamented. The valve face is ornamented with two, sometimes three, peripheral rings of small and irregularly arranged areolae. The single rimoportula is positioned near the junction of the valve face and mantle (SIVER and KLING 1997). The ringleist is very shallow. The linking spines are spatulate with apiculate tips (Pl. 4, Fig. 5), or long and narrow – similar to *Aulacoseira perglabra* (Østrup) Haworth (Pl. 3, Fig. 6).

Ecology: this taxon was rare and appeared in bottom sediments of McCoy Lake, where trophic conditions are good. Previously this taxon was reported together with *A. perglabra* in oligotrophic environments (SIVER and KLING 1997).

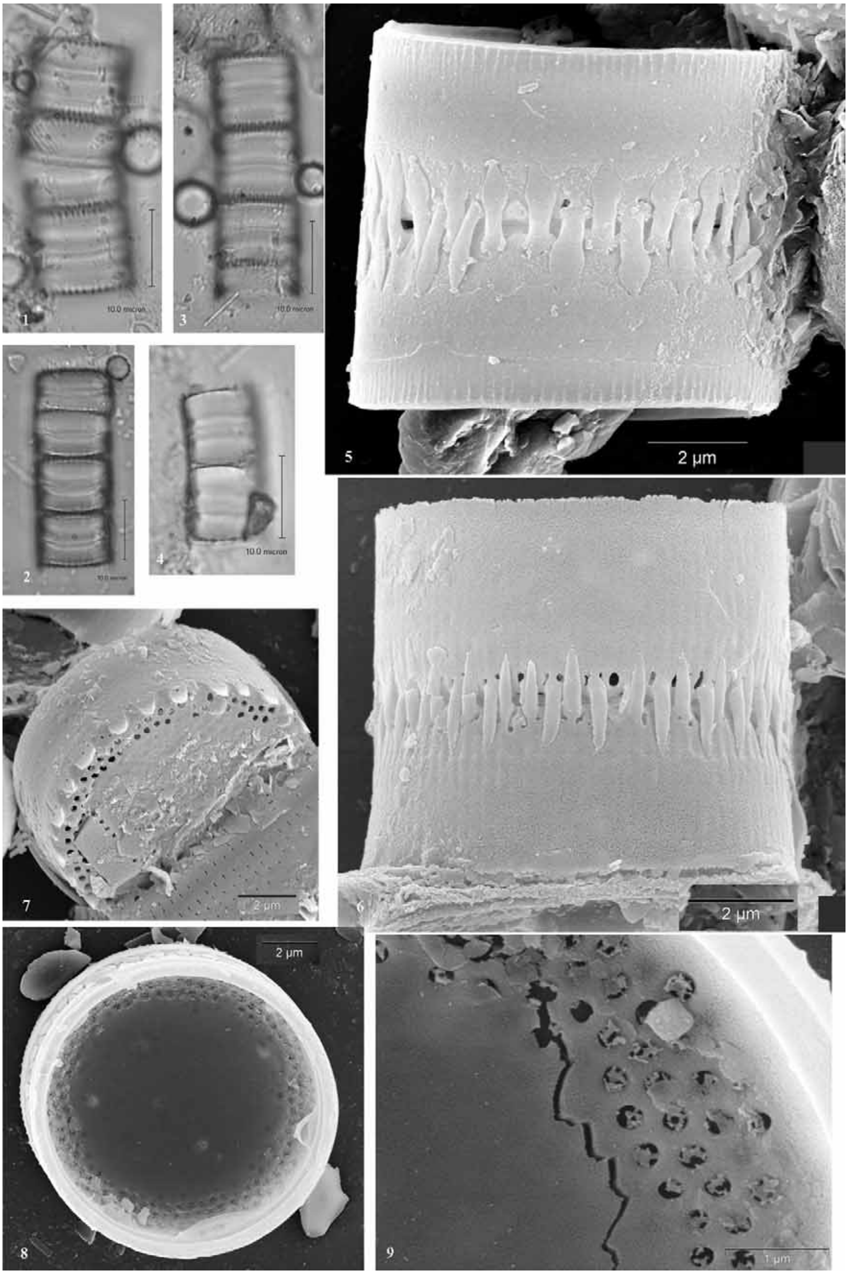
*Aulacoseira subarctica* (O. Müller) Haworth (HAWORTH 1988; **Pl. 5, Figs. 1–11**)

*Basionym*: *Melosira italica ssp. subarctica* O. Müller 1906

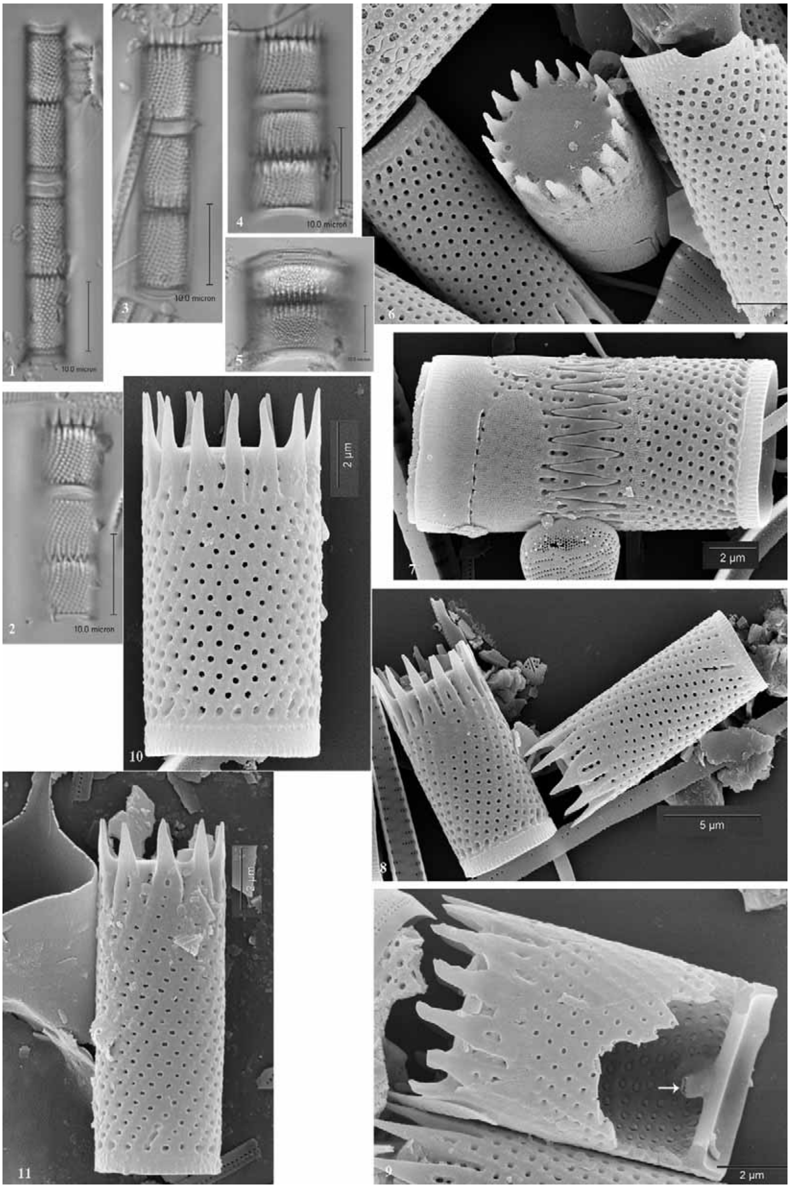
*Melosira italica* ssp. *subarctica* O. Müller (CAMBURN and KINGSTON 1986: 24, Pl. 2, Figs. 34–35, 37–40)

*Aulacoseira subarctica* (O. Müller) Haworth (SIVER and KLING 1997: 1811, Figs. 13–22)

*Aulacoseira subarctica* (O. Müller) Haworth (CAMBURN and CHARLES 2000: 15, Pl. 4, Figs. 23–31)



**Pl. 4.** *Aulacoseira pseudoamericana* (Camburn) Siver et Kling. **Figs. 1–4** – girdle view – LM, McCoy Lake, bottom sediments; **Figs. 5, 6** – sibling valves, unornamented mantle and spatulate spines with apiculate tips, SEM, McCoy Lake, bottom sediments; **Fig. 7** – valve view with peripheral, irregularly arranged areolae, SEM, McCoy Lake, bottom sediments; **Fig. 8** – valve inside view with internal projections of the rimoportulae, very shallow ringleist, SEM, McCoy Lake, bottom sediments; **Fig. 9** – valve inside view, detail with the peripheral rings of areolae, SEM, McCoy Lake, bottom sediments.



**Pl. 5.** *Aulacoseira subarctica* (O. Müller) Haworth. **Fig. 1** – girdle view – LM, Second Lake, top sediments; **Figs. 2, 3, 4** – girdle view – LM, Ryerson Lake, top sediments; **Fig. 3** – girdle view – LM, Ryerson Lake, bottom sediments; **Fig. 5** – girdle view – LM, Hillsview Lake, bottom sediments; **Fig. 6** – valves of *A. ambigua* and *A. subarctica* – on the valve face of *A. subarctica* there are a few areolae, located close to the margin, SEM, Pickerel Lake, bottom sediments; **Fig. 7** – sibling valves with clearly overlapping cingulae, SEM, Pickerel Lake, bottom sediments; **Figs. 8, 9, 10** – girdle view, the isomorphic spines are of equal length; see, arrowed, the external opening of the rimoportula (with curved stalk), located near the well developed ringleist, SEM, Pickerel Lake, bottom sediments; **Fig. 11** – girdle view – a long narrow valve, left – ligula shaped cingulum, SEM, Ryerson Lake, top sediments.

Valve diameter ranges 4–22.5 µm; the height of valve mantle 6–15 µm; the areolae on the mantle (14–25 in 10 µm) are in spiral pervalvar rows. The areolae are small with deep-set vela (CRAWFORD and LIKHOSHWAY 1998). The rimoportulae are two per valve, without stalk. They are found near the ringleist (Fig. 9) and their external openings are large and visible in LM (LIKHOSHWAY and CRAWFORD 2001). The ringleist is well developed. To our knowledge only isomorphic spines have been described for this taxon (GIBSON et al. 2003, WOLFE and EDLUND 2005). All spines are pointed and of equal length.

Ecology: similarly to literature findings of abundance in oligotrophic conditions (VAN DAM et al. 1994, SIVER and KLING 1997, TRIFONOVA and GENKAL 2001, TUJI and HOUKI 2004, BARINOVA et al. 2008), this taxon was abundant in both top and bottom sediment in lakes of good and fair trophic conditions, but appeared only in the bottom sediment of Brooks and Hess Lakes, classified as lakes with poor conditions.

*Aulacoseira valida* (Grunow) Krammer 1991

*Basionym*: *Melosira crenulata* var. *valida* Grunow (VAN HEURCK 1880–1885)

*Melosira italica* var. *valida* (Grunow) Hustedt 1927

*Melosira italica* var. *valida* (Grunow) Hustedt (CAMBURN and KINGSTON 1986: 25, Pl. 2, Fig. 36)

*Aulacoseira valida* (Grunow) Krammer (KRAMMER 1991b: Figs. 23–29, 31, 36–39)

*Aulacoseira valida* (Grunow) Krammer specimens conspecific with *Aulacoseira italica* (Ehrenberg) Simonsen (SIVER and KLING 1997: 1815, Figs. 42–45)

*Aulacoseira valida* (Grunow) Krammer (CAMBURN and CHARLES 2000: 15, Pl. 5, Figs. 1–4).

*Aulacoseira valida* (Grunow) Krammer (SIVER et al. 2005: 40, Pl. 3, Figs. 1–2).

Valve diameter 8 µm; the height of valve mantle 10 µm; the areolae on the mantle are 12 in 10 µm, formed dextrorse spirals. Areolae become enlarged longitudinally towards the valve mantle (HOUK and KLEE 2007). The rimoportula is located in the inner side of the ringleist (LIKHOSHWAY and CRAWFORD 2001). The linking spines are long, relatively thick, with T-shaped enlarged distal edge.

Ecology: This taxon, reported from neutral to mesotrophic conditions (SIVER et al. 2005) was rare and appeared in bottom sediments of McCoy Lake.

## Discussion

Within diatom communities from Michigan lake sediment cores we saw a 44% decrease in *Aulacoseira* species diversity from bottom to top sediment layers. No other diatom group, such as centric diatoms or pennate diatoms, experienced such a decrease. Diatom species composition between tops and bottoms corresponded to the current land use surrounding the lakes, which ranged from predominantly forest and rangeland to urban and agriculturally impacted. Inferred past conditions revealed that the observed morphotypes probably represent taxa with different ecological preferences. 'Bottom' *Aulacoseiras* like *A. granulata* and *A. italica* did not change with human influence, while *A. subarctica* and *A. ambigu*a increased in abundance. *Aulacoseira granulata* morphotype *curvata*, *A. nygaardii*, *A. perglabra* and *A. pseudoamericana* were absent in the 'top' sediment and were replaced with *A. ambigua* and *A. subarctica*. The main factors influencing the variability of these morphotypes were changes in the trophic status of the lakes.

Diatom-inferred indices for changes in lake water levels and trophic status have been based on species presence or absence (WOLIN 1996). In this study we linked *Aulacoseira* species with the trophic status of lakes in Michigan, where good quality lakes are abundant. Species such as *A. nygaardii*, *A. perglabra* and *A. pseudoamericana* that occurred frequently in bottom sediments were absent in the top sediment and were replaced predominantly with *A. ambigua*. In poor quality lakes, *A. subarctica* disappeared in the top sediment. We concentrated on centric diatoms and *Aulcoseira*, but changes in pennate diatoms remain unclear.

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