The stomatocyst of Mallomonas acaroides v. muskokana (Chrysophyceae) *

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Abstract

The stomatocyst of Mallomonas acaroides v. muskokana is described based on observations made from both live populations and surface sediment remains. The cyst is slightly ovate in shape, covered with evenly spaced, ornamented spines and has a short cylindrical collar with a variable apex and internal annulus surrounding the pore. The spines have a thickened base, a cylindrical middle section and a flattened apex with a ring of finger-like projections. Several immature stages of development are described and the stomatocyst is compared to those described for phylogenetically similar species. Complementary investigations of stomatocysts from both living (planktonic) and sediment collections can greatly facilitate the identification of stomatocyst morphotypes.

Introduction

A feature common to all species within the algal class Chrysophyceae sensu Hibberd (1976) is the formation of a siliceous resting stage known as the stomatocyst. This cyst may be formed through either an asexual and/or sexual process (Skuja, 1950; Sandgren, 1981; Cronberg, 1986; Sandgren and Flanagan, 1986). Stomatocysts generally range in diameter from ca. 4 to 30 µm (Sandgren & Carney, 1983), are oval or spherical, and exhibit wide variation in their structure and ornamentation. The overall structure of the stomatocyst, especially of the pore-collar complex and cyst body, is considered of great taxonomic significance (Hibberd, 1977; Skogstad, 1984; Sandgren & Carney, 1983), and many species are believed to form species-specific stomatocysts (Cronberg, 1986). The size and shape of stomatocysts tends to be quite stable (Cronberg, 1986; Sandgren, 1989) while the degree of ornamentation for some species, may be related to the physiological state of the organism during encystment (Sandgren, 1983).

Stomatocyst microfossils are becoming increasingly important in paleolimnological research (Smol, 1991) for inferring historical changes in lakewater conditions (e.g. Adam & Mahood, 1981; Battarbee et al., 1980; Carney & Sandgren, 1983; Smol, 1985; Duff & Smol, 1988; Rybak, 1986, 1987). However, because the morphologies of the stomatocysts are described for only ca. 5% of the known morphotypes (Cronberg, 1986; Duff & Smol, 1988), their use is currently limited.

Mallomonas acaroides v. muskokana, recently described by Nicholls (1987), has been shown to be an important component of the phytoplankton flora (Siver, 1988; 1989b) and microfossil assemblages (Smol et al., 1984; Charles & Smol, 1988) of softwater acidic lakes in the Adirondack
Mountain region. This taxon has been reported from similar habitats in Ontario (Nicholls, 1987; Dixit et al., 1988) and Connecticut (Siver, 1989b) and was noted to be abundant in both clear and humic-stained lakes (Siver, 1988). Siver (1989b) demonstrated that the distribution of *M. acaroides* v. *muskokana* was clearly distinct from *M. acaroides* v. *acaroides* along a pH gradient, and that pH and water temperature strongly dominated the first factor in a principal component analysis for v. *muskokana*. Hence, *M. acaroides* v. *muskokana* is not only a valuable indicator of pH, but may also be important in paleoclimate research. The purpose of this paper is to describe the morphology of the stomatocyst of *M. acaroides* v. *muskokana*.

**Materials and methods**

The collection of live material and subsequent preparation for analysis with scanning electron microscopy (SEM) were as described in previous papers (Siver, 1987; Siver, 1988).

A core from Little Echo Pond (see below) was taken at the point of maximum depth using a modified KB type gravity corer (Brinkhurst, 1969; Glew, 1988) and subsampled with a close interval core extruder (Glew, 1988). A subsample from the 0.25–0.5 cm interval was acid cleaned and washed according to the procedure used by Smol (1983), diluted and dried onto a piece of aluminum foil. The aluminum foil sample was prepared for observation with SEM in the same manner as the live collections (see Siver, 1987).

The methods for measuring the total phosphorus content, specific conductance and pH were as described previously (Siver, 1988).

**Results**

*Description of the Stomatocyst*

Stomatocysts are slightly ovate, range in length from 12.9 μm to 16 μm (not including surface projections), have a mean size of 13.7 ± 0.77 μm × 12.9 ± 1.0 μm (n = 20), a well defined collar, and they possess ornamented spines distributed over the surface (Figs. 1–4). Spines are straight, roughly perpendicular with the cyst body, have a mean length of 1.1 μm and range in length from 0.8 μm to 1.6 μm. Spines are evenly spaced, approximately 1.7 μm apart, although a range of 0.9 μm to 2.8 μm was observed (Figs. 1–4); spines are often less dense in the region immediately surrounding the collar (Figs. 1–2). Each spine is wider at the base, tapers to a more or less cylindrical middle section and terminates in a flared, flattened top (Figs. 3–5). A whorl of 7 to over 20 small finger-like projections radiate from the flattened top of each spine (Figs. 3–5). The base of the spine is circular or more rarely elliptical (Fig. 3). Each spine has a circular depression centrally positioned on the flattened top, suggesting that the distal portion is hollow (Figs. 3–5). However, spines broken off at the base appear to be solid structures.

The collar is simple, circular, with a cylindrical outer margin, a concave inner margin and a variable apex (Figs. 1, 3). Mature specimen have a very narrow annulus surrounding the pore. The diameter of the collar consistently measured between 1.8 μm and 2.0 μm and it had a mean height of 0.5 μm (Fig. 3). The collar to stomatocyst diameter ratio is 1 : 7. The pore is also circular, centrally positioned within the collar and has a mean diameter of 0.93 μm.

Several stages in the development of the cyst were also observed (Figs. 2, 6). Immature cyst walls consist of a series of closely spaced, almost circular pores (Fig. 6), equally distributed over the entire surface; spines and other surface projections are lacking. This stage of development is referred to as the honeycomb stage (Skogstad, 1984). A further advanced stage of development was represented by a stomatocyst where the honeycomb pattern was only slightly discernible due to a thin deposition of silica, the spines lacked the ring of finger-like projections and only the outline of the collar was completed (Fig. 2).
Figs. 1–6. Stomatocyst of *Mallomonas acaroides* v. *muskokana*. Fig. 1–3 represent specimens from the surface sediments (0.25–0.5 cm) of Little Echo Pond; Fig. 4–6 represent live cells from Bigelow Pond (see text for details). Fig. 1. Mature stomatocyst showing the arrangement of spines on the surface and the rather small cylindrical collar. Note the lower density of spines in the region of the collar. Scale bar = 5 μm. Fig. 2. Slightly immature stomatocyst with partially developed spines and collar. Scale bar = 5 μm. Fig. 3. Close up of the collar-pore region and surface of a mature stomatocyst. Note the saucer-shape of the collar and the underlying outline of the honeycomb pattern. Several elongated spine bases can be seen. Scale bar = 2 μm. Fig. 4. Intact cell. Fully developed spines can be observed beneath the scales. Scale bar = 2 μm. Fig. 5. Close up of the wall of a mature stomatocyst showing the details and spacing of the spines. Note the central depression on the flattened distal surface of each spine. Scale bar = 2 μm. Fig. 6. Immature stomatocyst at the honeycomb stage of development. Note the closely spaced pores and the lack of surface projections. Scale bar = 2 μm.
Identification of the original specimen

Based on the guidelines developed by the International Statospore Working Group (Cronberg & Sandgren, 1986), the following formal designation in provided:

_P.A. Siver stomatocyst no. 13_
_Biological affinity: Mallomonas acaroides v. muskokana_ Nicholls

_Micrograph:_ Siver, P.A. 1989. Journal of Paleo-Limnology. Fig. 1 (P.A. Siver micrograph no. A292)

_Origin:_ Surface sediments (0.25–0.5 cm) of Little Echo Pond, Franklin County, New York, USA (44° 18’ 20” N, 74° 21’ 33” W)

The ornamentation of the stomatocyst documented for _M. acaroides v. muskokana_ is very similar, if not identical, to that described for _M. acaroides v. acaroides_ Perty emend. Ivanov (Asmund & Kristiansen, 1986; Cronberg, 1980 – as _M. acaroides v. striatula_). The structure and spacing of the spines and the collar-pore complex are virtually the same in both varieties. However, the diameter reported for stomatocysts of _v. acaroides_ (16–24 µm) was larger than that documented here for _v. muskokana_. Cronberg (1980) reported an immature stomatocyst for _v. acaroides_ lacking spines and with a smooth wall. Such a stomatocyst may represent a developmental stage between the honeycomb-stage (Fig. 6) and the formation of spines (Fig. 2) (ala Sandgren, 1989). The spine ornamentation of the stomatocyst of _M. acaroides v. muskokana_ also appears similar to that of _Mallomonas crassiquama_ (Asmund) Fott (Gretz et al., 1979; Asmund & Kristiansen, 1986) and _Mallomonas pseudocoronata_ Prescott (Smol, 1984). The average diameter of cysts of _M. crassiquama_ (15 µm) and _M. pseudocoronata_ (17 × 15 µm) are also similar to that of _v. muskokana_ (13.6 µm). The stomatocyst of _M. pseudocoronata_ has a short and cylindrical collar, similar to that of _v. muskokana_. The concave inner portion of the collar, described here for _v. muskokana_, has not been reported for _M. pseudocoronata_ (Smol, 1984), although that shown in Fig. 7 of Smol (1984) appears similar.

Ecological background information

The ecology of _Mallomonas acaroides v. muskokana_ was recently described by Siver (1988, 1989) and need not be elaborated upon in detail here. Essentially, _M. acaroides v. muskokana_ is acidobiotic in nature, with an abundance weighted mean pH below 5.5, and is restricted to habitats characterized by warmer water temperature. Populations of this taxon are usually first detected in late spring when the water temperature reaches between 10 and 15 °C, they form maximal concentrations in mid-summer and then disappear by mid-autumn. Cyst formation was observed on October 17, 1987 in Bigelow Pond and October 3, 1987 in Polliwog Pond at 14 and 13 °C, respectively. In addition, similar cysts were observed in a phytoplankton sample from Little Echo Pond on November 8, 1986 at 8 °C; no live cells of _M. acaroides v. muskokana_ were found in the sample. Immature honeycomb-stages (e.g., Fig. 6) were observed only in the Bigelow Pond sample.

Because the details of the mature stomatocysts were primarily described from specimens found in surface sediments from Little Echo Pond, it was selected as the original locality. Little Echo Pond is situated at an elevation of 480 m in the Adirondack Mountains of New York State, Franklin County, within the Fish Creek Ponds State Campground (44° 18’ 20” N, 74° 21’ 33” W). It is a small (2.3 acres) humic stained, seepage bog lake with a maximum depth of 4.6 m and a mean depth of 3.3 m. The pH, specific conductance and total phosphorus levels measured during 1986 ranged from 3.95–4.24, 25–40 µS and 11–19 µg-P l−1, respectively.

Polliwog Pond is a clear water, acidic lake (pH range: 5.42–5.68) located close to Little Echo Pond (see Siver, 1988, for map). Bigelow Pond is slightly humic in nature, acidic (pH range: 5.5–6.5) and situated in Bigelow State Park, Town of Union in the State of Connecticut. Both Polliwog and Bigelow are softwater lakes low in specific conductance and total phosphorus levels.
Discussion

The use of both live collections and surface sediment remains proved most valuable in describing the features of the somatocyst of Mallomonas acaroides v. muskokana, and several stages of development of the cyst wall. Live plankton collections are obviously needed in order to link a characteristic morphotype to a known species. However, typically only a small proportion of cells in a given population are observed undergoing encystment. The problem of observing cysts from live collections using SEM is further complicated because a smaller sample size is used and the species-specific scales may become disarticulated from the cyst. The result is that of the many cyst morphotypes that have been described, only a small percentage are linked to specific organisms (Cronberg, 1986). In this study the unique surface detail of the somatocyst of M. acaroides v. muskokana was observed from live, intact cells; many more somatocysts were then subsequently identifiable from the surface sediments of a lake where the organism was known to be a dominant member of the phytoplankton community. In this case, Little Echo Pond was especially attractive because its extant flora and surface sediments were overwhelmingly dominated (e.g. > 99% of total scales) with only M. acaroides v. muskokana and Synura sphagnicola (Korsh.) Korshikov. Cells or scales of taxa with similar cysts, such as M. acaroides v. acaroides, M. crassiquama, and M. pseudocoronata, were not observed in the plankton nor in a thorough examination of the top 10 cm of sediment from Little Echo Pond. Since scale preservation in Little Echo Pond was good and only scales of M. acaroides v. muskokana were found, it was concluded that the many cysts observed in the surface sediments that matched those from living populations represented M. acaroides v. muskokana. Analyses of cysts from plankton tows and from surface sediment samples, as done in this study and followed by Cronberg (1980), should prove a very useful protocol for the identification of unknown somatocysts. However, caution must be exercised if scale remains from species with similar cysts are also present in the sediment samples.

The development of the somatocyst wall is a continuous process generally thought to proceed in two phases (Sandgren, 1989). The inner wall of the cyst is formed during the initial phase and results in a complete and solid structure, except for the pore (Sandgren, 1989). A general thickening of the primary cyst wall, as well as the development of the collar and body ornamentation (if present), is formed during the second phase (Sandgren, 1980a; Cronberg, 1980; Skogstad, 1984; Sandgren, 1989). Thus, immature somatocysts that lack a full compliment of ornamentation can be found. In this study three stages in the development of the somatocyst wall were observed. The most immature stage (Fig. 6) was of a cyst with a honeycomb-like surface and lacking spines. The formation of a reticulated or honeycomb-like pattern on the cyst wall has also been documented for Mallomonas intermedia Kisselew (Skogstad, 1984) and Mallomonas caudata (Sandgren, 1980b; 1989; Cronberg, 1988). As reported for M. intermedia (Skogstad, 1984), the honeycomb pattern observed in M. acaroides v. muskokana may represent the actual pattern of silicification during the formation of the primary cyst wall. A thin layer of silica is subsequently deposited over the honeycomb design during the secondary silicification phase, although the honeycomb pattern can still be discerned under the thin layer on mature cysts (Figs. 3 and 5). The reticulated pattern observed on cysts of M. caudata differs from those of either M. intermedia or M. acaroides v. muskokana in that it represents a true secondary layer of ornamentation (Sandgren, 1989) and is a component of the mature cyst (Cronberg, 1988; Sandgren, 1989).

A second more advanced stage of development (Fig. 2) was of a cyst with a relatively smooth wall and partially formed spines and collar. This specimen, presumably represents a stage of development during the secondary phase of silicification after the thin layer was deposited over the honeycomb pattern, but prior to completion of the spines and collar. These observations support the
idea that the secondary surface ornamentation and collar are formed after the primary wall layer is completed as documented by Sandgren (1989). The most ornamented stage and presumably the most advanced cyst (Fig. 1), had well developed spines and a fully formed collar.

*Mallomonas acaroides* v. *acaroides*, *M. acaroides* v. *muskokana* and *M. crassiquama* are in the same series within the genus; *M. pseudocoronata* is placed within a different section, primarily because of the presence of an anterior wing on the scales (Asmund & Kristiansen, 1986). Based on available information, the stomatocysts of the four taxa share similarities, especially regarding the morphology of the spines; this supports the idea that the four taxa may be phylogenetically related. Further work is needed in order to compare other features of mature cysts (i.e., the collar) as well as developmental stages. It will also be interesting to see if other closely related species form structurally similar cysts.

As a result of a continuous maturation process of stomatocyst formation, it is likely that several different morphotypes representing the same taxon would be found in sediment remains. Many unanswered questions concerning the factors governing the formation of stomatocysts remain. What factors are most influential in determining the degree to which a given stomatocyst becomes ornamented? Sandgren (1983) found that water temperature played a significant role in the ornamentation of stomatocysts in Dinobryon cylindricum Lam. The amount of available silica may also be important. Another unanswered question is "What is the relationship between cyst morphology and viability?" Do mature and immature cysts contribute equally to the benthic seed populations of a species? It seems most probable that the formation of a mature and viable stomatocyst is a complex physiological process that would be directly or indirectly effected by a myriad of factors (Sandgren, 1981). Such questions will best be addressed by laboratory culture work and will greatly enhance the use of stomatocysts in paleolimnological research.

Sudden changes in environmental conditions have been suggested to trigger the formation of resting stages in many algae (as reviewed by Sandgren, 1981). A sudden change is often linked to stomatocyst formation in scaled chrysophytes (Cronberg, 1980; Cronberg, 1986; Smol, 1984). The limited observations made in this study suggest that stomatocyst formation in *M. acaroides* v. *muskokana* is correlated with a decrease in water temperature. Clearly, experimental work is needed in order to document the factors resulting in cyst formation.

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References


