

The separation of *Mallomonas acaroides* v. *acaroides* and v. *muskokana* (Synurophyceae) along a pH gradient

by

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With 1 table and 2 figures

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Abstract: The use of "fossil" algal assemblages to reconstruct the historical pH levels in lakewaters has become the primary means of assessing the acidification rates of lakes over long time periods. *Mallomonas acaroides* is a valuable indicator species for pH that has been used in such inference models, however, there is some debate concerning the actual distribution of the species with respect to a pH gradient. In this paper, two varieties of *M. acaroides*, v. *acaroides* and v. *muskokana*, were found to be clearly separated along a pH gradient. Variety *acaroides* was alkalibiontic in nature, with a maximum distribution and a weighted mean pH above 8.0. Variety *muskokana* was acidobiontic in nature with a maximum frequency of occurrence and a weighted mean pH below 5.5. Variety *muskokana* was found to be restricted to warmer water temperatures. Principal component analysis was used to document the importance of pH and temperature in controlling the distribution of these two taxa. It is proposed that the discrepancies reported in the literature concerning the occurrence of *M. acaroides* with respect to pH were due to the combination of records of both varieties.

Introduction

Many of the morphological characteristics originally used to separate different varieties of *Mallomonas acaroides* have been shown to be of no taxonomic significance (Asmund 1959) or within the accepted range of variation for v. *acaroides* as originally emendated by Ivanov (Asmund & Kristiansen 1986). For example, *M. acaroides* is capable of producing serrated bristles, helmet bristles or both on individual cells. Fott (1962) recognized this difference at the variety level with the type producing only helmet bristles. Cells with only serrated bristles or both bristle types constituted different varieties. However, in their recent monograph on *Mallomonas* Asmund and Kristiansen (1986) considered these differences in the types of bristles produced to be within the accepted limits for the type and invalidated varieties differentiated solely on the basis of bristle type. Although *Mallomonas acaroides* v. *inermis* Fott, still recognized as a legitimate taxon, lacks helmet bristles, it also differs from the type in possessing smaller, domeless posterior scales.

Recently, Nicholls (1987) described a new variety from Ontario, *v. muskokana*, that differs from *v. acaroides* and *v. inermis* on the basis of scale and bristle morphology. Variety *muskokana* is separated from *v. acaroides* primarily because it has domed scales that are sculptured with raised papillae and ridges, domeless posterior scales, helmet bristles with a distinctive subapical tooth on the side of the shaft opposite of the cleft, and other features (Nicholls 1987). Although *v. muskokana* is similar to *v. inermis* with the presence of domeless scales, it differs from the latter by possessing helmet bristles, differently structured toothed bristles and larger scales with highly ornamented domes. In addition, Nicholls (1987) suggested that *v. muskokana* was restricted to dilute softwater localities, while *v. acaroides* was found in more alkaline habitats.

Mallomonas acaroides has recently been demonstrated to be an important component of the microfossil assemblages in sediments from Adirondack lakes that have been adversely affected by acid deposition (Smol et al. 1984 and Charles & Smol in press). Charles & Smol (in press) reported *M. acaroides* to have an abundance weighted mean pH of 5.25 and suggested that according to Hustedt's (1939) system it was an acidobiontic species. Such a classification as an acidobiont was in direct contrast with the results from previous workers who reported *M. acaroides* from more alkaline localities (Asmund 1959; Cronberg & Kristiansen 1980; Roijackers & Kessels 1986; Kristiansen 1986). The purpose of this paper is to show that in addition to being separated on the basis of morphological features, *v. muskokana* and *v. acaroides* are also clearly separated along a pH gradient.

Material and methods

A total of 332 collections (293 from Connecticut and 39 from the Adirondack Mountain region of New York) from 62 localities (45 from Connecticut and 17 from the Adirondacks) were analyzed for *Mallomonas acaroides*. Plankton net samples (10 μ m) and water samples were taken from the center of the lake at a 1m depth or at 0.5 m along shore. A portion of each water sample was concentrated with centrifugation for eight minutes at 2000 rpm and used with the net sample for analysis.

One ml portions of each sample were dried onto separate pieces of aluminum foil, rinsed 2 \times with distilled water, trimmed and mounted onto aluminum stubs with apiezon wax, coated with gold for 4.5 minutes using a Polaron sputter coater, and observed with a Coates and Welter field emission SEM.

The specific conductance and temperature of the water were measured with a YSI model 33 SCT meter. The pH was measured in the field with a Fisher Accumet model 640A meter. Total phosphorus was measured after acid digestion with the stannous chloride method (Franson 1980).

A total of 207 collections were surveyed from the literature that listed all scaled chrysophyte species present and the lake-water pH. Specimens that could be identified as *Mallomonas acaroides v. acaroides* via micrographs were found in 31 (15%) of these collections. Distributional data for both varieties from the Connecticut and Adirondack samples and for *M. acaroides v. acaroides* from the literature survey were used to prepare frequency distribution plots and weighted mean pH values. The means were weighted according to the frequency of the taxon in each of 9 pH intervals using the following equation:

$$\text{pH} = \sum_{i=1}^9 \text{Pi (Xi)/} \sum_{i=1}^9 \text{Pi}$$

where pH = weighted mean pH; Pi = frequency of the taxon in the ith pH interval and; Xi = pH mid-point of the ith interval. The pH intervals included <5, >8.5 and the seven 0.5 gradations in between 5 and 8.5. Principal components analysis, based on temperature, pH, specific conductance and total phosphorus records, was used to extract a two-factor model that explained the maximum percentage of the total variability in the dataset.

Results

Populations of *Mallomonas acaroides* were found in 16% of the collections from the Connecticut and Adirondack localities. However, populations (n = 37) with anterior domed scales with ribs and papillae (Fig. 1 a, b), domeless posterior scales (Fig. 1 c) and helmet bristles with a single subapical tooth located opposite of the opening of the helmet (Fig. 1 d), characteristics of v. *muskokana*, were restricted to softwater localities with pH values below 7.1. Populations (n = 15) equivalent to v. *acaroides* (see Asmund & Kristiansen 1986) and lacking the above morphological features, were found primarily in more alkaline habitats that were often also eutrophic in nature.

Mallomonas acaroides v. *muskokana* was found in 12% of the collections from Connecticut waterbodies. However, it was much more common in the Adirondacks where it was observed in 65% of the lakes; this taxon was found in all samples with a pH<5.5, including all of the humic stained bog lakes. In both Connecticut and the Adirondacks, v. *muskokana* had a maximum frequency of occurrence between a pH of 4.5 and 5.5 (Fig. 2 a). Its occurrence decreased significantly as the pH increased above a pH of 5.5 and it was not found above a pH of 7.1. The weighted mean pH for v. *muskokana* was 5.3. A total of 74% and 68% of the variance in the temperature and pH data, respectively, for v. *muskokana* were explained in a one factor model using principal component analysis (PCA) (Table I). Whole cells of v. *muskokana* were observed from late spring through early fall.

Table I: The results of a principal component analysis based on temperature, pH, specific conductance and total phosphorus records, for *Mallomonas acaroides* v. *acaroides* and v. *muskokana*. The percentage of the total variability in the dataset explained by the first and second principal components is given. In addition, the percentage of the total variability for the parameters controlling the first and second principal components is listed.

Taxon	n	% Total variance explained by a 2-factor model	% Variability explained per parameter	
			First PC	Second PC
<i>M. acaroides</i> v. <i>acaroides</i>	15	77	83-pH 76-Conductance	99-Temperature
<i>M. acaroides</i> v. <i>muskokana</i>	37	70	74-Temperature 68-pH	66-Total phosphorus 58-Conductance

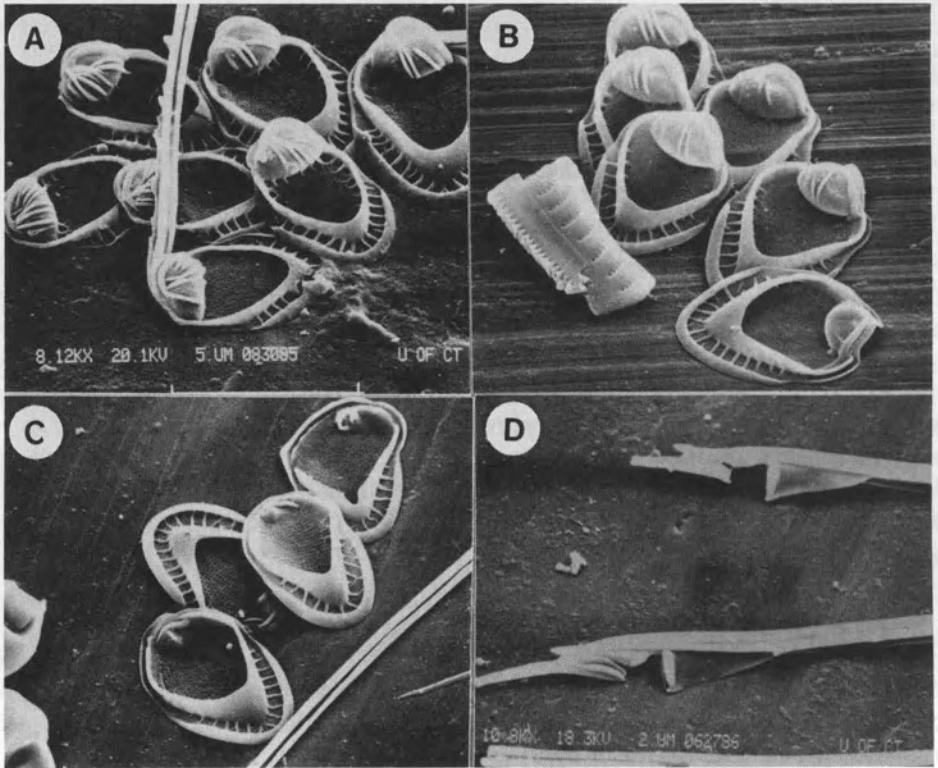


Figure 1: Scanning electron micrographs of *Mallomonas acaroides* v. *muskokana*. A. and B. Typical domed scales. Note the sculptured domes, ornamented with ridges and raised papillae (A = 5.350 \times and B = 5.350 \times). C. Characteristic appearance of posterior domeless scales (C = 4.650 \times). D. Typical helmet bristle morphology. Note the subapical tooth on the side opposite of the cleft (D = 6.870 \times).

Mallomonas acaroides v. *acaroides* was rare in Connecticut localities, being found in only 3% of the collections. This organism was not found in the Adirondack samples. Variety *acaroides* had a maximum frequency of occurrence at the 8.5 to 9.0 interval and was found in progressively lower percentages of the collections as the pH decreased (Fig. 2 b). A similar distributional pattern was observed for v. *acaroides* using pH records from the literature (Fig. 2 c). The weighted mean pH values for v. *acaroides* calculated from results in the study and from the literature were 8.1 and 8.4, respectively. The lake-water pH and specific conductance were the most important parameters controlling the distribution of v. *acaroides* (Table I). A total of 83% of the variation in the pH data was explained in a one-factor model using PCA (Table I). Variety *acaroides* was not restricted to warm water temperatures as was v. *muskokana*.

The high degree of occurrence of *Mallomonas acaroides* v. *muskokana* in Adirondack localities, also documented by Charles and Smol (in press), was most likely the result of the predominance of softwater acidic waterbodies (Schofield 1976; Whitehead et al. 1986). In the Connecticut study lakes, the distribution of *M. acaroides* v. *muskokana* was also restricted to acidic localities low in alkalinity. Since the majority of the Connecticut study lakes had greater pH and alkalinity levels than those in the Adirondacks, the lower frequency of occurrence of v. *muskokana* in Connecticut is not surprising.

Discrepancies in the literature concerning the distribution of *Mallomonas acaroides* with respect to pH must be resolved since this organism is being used in paleolimnological inference models (e.g. Charles & Smol in press). Although Smol et al. (1984) and Charles and Smol (in press) reported *M. acaroides* as an acidobiont, Roijackers and Kessels (1986) and Kristiansen (1986) reported this taxon from localities with much higher pH values. It is now clear that the conflicting reports were the result of comparing distributional records for two morphologically distinct taxa. The organism reported in 70% of the sediment assemblages by Charles and Smol (in press) were of v. *muskokana* (Smol personal communication); to date v. *acaroides* has not been recorded from Adirondack waterbodies (Siver 1988). Since v. *muskokana* is primarily distributed below a pH of 7.0 (Fig. 2 a) and has a weighted mean of 5.3, it is clearly a true acidobiont. On the other hand, since v. *acaroides* was restricted to pH conditions above 7 and had a weighted mean greater than 8 in both Connecticut lakes and the literature review, it is best classified as an alkalibiontic taxon. The separation of both v. *muskokana* and v. *acaroides* with respect to a pH gradient is consistent with the comments made by Nicholls (1987).

The importance of the lakewater pH in controlling the distributions of both *Mallomonas acaroides* v. *acaroides* and v. *muskokana* was documented by principal component analysis (Table I). In addition to pH, the water temperature was also an important factor regulating the occurrence of v. *muskokana*. Thus, the occurrence of v. *muskokana* in a given lake is dependent on the pH, however, it will be found primarily during the warmer months. Because v. *acaroides* was found over a much wider temperature range, the water temperature was not as important a factor in controlling its distribution. Variety *acaroides* would be most likely found in waterbodies with a high pH during most of the year.

The role pH plays in governing the distributions of *Mallomonas acaroides* v. *acaroides* and v. *muskokana* is clear. The effects of other factors, especially those that covary with pH, will be evaluated only with further study. Care in distinguishing between the two varieties is mandatory.

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