SEPARATION OF MALLOMONAS DUERRSCHMIDTIAE SP. NOV. FROM M. CRASSISQUAMA AND M. PSEUDOCORONATA: IMPLICATIONS FOR PALEOLIMNOLOGICAL RESEARCH

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ABSTRACT

A new species, Mallomonas duerrschmidtiae, with characteristics common to both Mallomonas crassissquama (Asmund) Fott and Mallomonas pseudocoronata Prescott, is described from acidic lakes low in specific conductance and total phosphorus concentration. Characteristics of scales, bristles and spines serve to separate the three taxa. The length and area of scales of M. duerrschmidtiae are significantly larger than those of M. crassissquama but smaller than those of M. pseudocoronata. Although the anterior submarginal ribs of scales of M. duerrschmidtiae may become extended to form short wings, the scales lack the large forward projecting anterior wings characteristic of scales of M. pseudocoronata. Features of the dome and junction between the arms of the V-rib and anterior submarginal ribs also serve to distinguish between the three species. Cells of M. duerrschmidtiae also possess long, smooth and thick spines on their posterior scales and lack helmet bristles. M. duerrschmidtiae has different maxima along pH, temperature, specific conductance, total phosphorus and seasonal gradients than either M. crassissquama or M. pseudocoronata. Discriminant analysis, based on nine morphological characters, was used to successfully classify body scales of the three species. The importance of M. duerrschmidtiae as a bioindicator in future lake monitoring and paleolimnological inference studies is discussed.

Key index words: ecology; Mallomonas crassissquama; Mallomonas duerrschmidtiae sp. nov.; Mallomonas pseudocoronata; morphology; paleolimnology; scaled chrysophytes.

Mallomonas crassissquama (Asmund) Fott was originally described by Asmund as a variety of Mallomonas acaroides Perry emend. Iwano and later raised to the rank of species by Fott (1962). The primary differences between M. crassissquama and M. acaroides are that the former taxon has a well developed meshwork of ribs on the shield and possesses domeless body scales and posterior scales with spines (Siver and Skogstad 1988). Both species can have either serrated and/or helmet bristles. Mallomonas pseudocoronata Prescott also has scales that resemble those of M. crassissquama in morphology but differ in being unusually large and possessing a well defined anterior wing.

Isolated scales of M. pseudocoronata that lack wings due to breakage are difficult to separate from those of M. crassissquama (Smol et al. 1984a). The degree of ribbing on the scale shields of M. crassissquama (Siver and Skogstad 1988) and M. pseudocoronata (Nicholls 1987) can vary from very dense to virtually absent. In addition to morphologically similar scales, cells of M. crassissquama and M. pseudocoronata have caudal scales with spines, although those of the latter are significantly longer (Asmund and Kristiansen 1986, Nicholls 1987). The bristles of M. pseudocoronata differ from those of M. crassissquama in being shorter, smooth and lacking the characteristic helmet tip (Asmund and Kristiansen 1986).

Mallomonas crassissquama, one of the most commonly encountered and widely distributed species of Mallomonas (Kristiansen 1975, Takahashi 1978, Nicholls 1982, Siver and Skogstad 1988), is found over a wide range of environmental conditions (Siver and Skogstad 1988). In addition, M. crassissquama dominates paleo-environments, commonly accounting for over 90% of the total number of scales (Smol et al. 1984a, Christie and Smol 1986, Charles et al. 1987). Despite its widespread abundance, the importance of M. crassissquama declines below a pH of 5.0 (Smol et al. 1984a, Smol 1986, Siver and Skogstad 1988, Siver 1989a, Eloranta 1989). In paleolimnological studies, decreases in M. crassissquama are often correlated with a decrease in lakewater pH below 5.0–5.5, making this taxon a critical indicator organism in acid deposition research (Christie and Smol 1986, Hartmann and Steinberg 1986, Charles and Smol 1988). However, in contrast to most findings, Dixit et al. (1988a) found scales that they identified as M. crassissquama in the surface sediments of

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MALLONAS DUERRSCHMIDTIAE SP. NOV.

729

lakes from the Sudbury region with a pH below 5. Because of its importance in paleo-environments throughout the world, *M. crassiquama* will remain a key organism in future research.

Except for being recorded from the sediments of one European lake (Smol 1988) and in Lake Biwa, Japan (Ito 1988), *M. pseudocoronata* is essentially restricted to North American localities (Wijek 1984, Siver 1990). It is distributed primarily along the alkaline end of the pH scale (Asmund and Hilliard 1961, Charles and Smol 1988, Dixit et al. 1988a, b, Siver 1989a). Thus, *M. pseudocoronata* also represents a pH indicator species and one useful in palaeolimnological research.

Several researchers have reported a form, identified as *M. crassiquama*, consisting of scales and cells that bear a striking resemblance to *M. pseudocoronata*. The scales are large and generally heavily silicified (Jacobsen 1985, Asmund and Kristiansen 1986, Siver and Skogstad 1988); the cells have very prominent posterior spines and bristles lacking helmet tips (Asmund and Kristiansen 1986, Kristiansen 1986). Jacobsen (1985) suggested that this taxon was restricted to northern regions. Kling and Kristiansen (1983) also found this organism but identified it as an immature or underdeveloped form of *M. pseudocoronata*.

We now have enough evidence to show that the form is a separate taxon and should be described at the species level. The new species bears characteristics of both *M. crassiquama* and *M. pseudocoronata* and probably accounts for most, if not all, reports of *M. crassiquama* from waterbodies with a pH less than 5 (e.g. Dixit et al. 1988a). Since the new species is distributed differently along environmental gradients than either *M. crassiquama* or *M. pseudocoronata*, critical taxonomic verification is paramount.

The purpose of this paper is to describe *Mallomonas duerrschmidtiae* sp. nov. and compare its cell, scale and ecological characteristics with those of the closely related taxa *M. crassiquama* and *M. pseudocoronata*.

MATERIALS AND METHODS

A total of 489 water samples (399 from Connecticut and 90 from the Adirondack Mountain region of New York) from 66 localities (45 from Connecticut and 23 from the Adirondacks) were analyzed with scanning electron microscopy (SEM) for the presence of *M. duerrschmidtiae*, *M. crassiquama* and *M. pseudocoronata*. Samples were collected with a horizontal van Dorn bottle from a depth of 1 m. A minimum of 411 of the samples was also analyzed for temperature, pH, specific conductance and total phosphorous concentrations. Temperature and specific conductance were measured in the field using a YSI model 33 SCT meter. Methods of analyses for pH and total phosphorous determinations were as described by Siver and Skogstad (1988) and Siver and Hamer (1989). Detailed methods for the collection and preparation of samples for observation with SEM were as described in previous papers (Siver 1987, 1988).

Frequency graphs were prepared to help describe the distribution of the three taxa with respect to seasonal, temperature, pH, specific conductance and total phosphorous gradients. Weighted mean values of pH, temperature, specific conductance and total phosphorus were calculated for each taxon with the equation:

\[
\text{weighted mean factor} = \frac{\sum P(X_i)}{\sum P_i}
\]

where \( P_i \) = the frequency of occurrence of the taxon in the \( i \)th interval, \( X_i \) = the midpoint of the \( i \)th interval, and \( n \) = the number of intervals. The intervals for each variable were as illustrated in Figures 26–28. Calculations of weighted mean pH values were determined from pH measurements (geometric mean of hydrogen ion concentrations) (see Middleton and Rovers 1976). The reader is referred to the work of Jongman et al. (1987) for discussion of the use of weighted averages in ecological studies.

Discriminant analysis (DA) was used to classify 57 isolated body scales into one of three mutually exclusive groups of taxa, *M. duerrschmidtiae*, *M. crassiquama*, or *M. pseudocoronata* and to classify the 41 samples of *M. duerrschmidtiae* and *M. crassiquama* into their respective groups. Standardized measurements of nine predictor variables (total scale area, form factor, length, width, pore area, rim area, dome area, V-rib angle and the angle formed between the arm of the V-rib and the anterior submarginal rib) were used to develop the discriminant functions in both cases. All measurements were determined from scanning electron micrographs using a digitizer. The anterior wing of scales of *M. pseudocoronata* was not included in area, length and form factor measurements. The value for pore area was determined by averaging the area for all pores found on the shield of a given scale. Form factor is a dimensionless ratio that compares the area of the scale to its perimeter using the following relationship:

\[
\text{Form factor} = \frac{(4\pi A)}{P^2}
\]

where \( A \) = area of the scale and \( P \) = perimeter of the scale. The ratio is normalized so that the form factor of a circle \( = 1 \) and of a line \( = 0 \). A discriminant function score was determined for each of the 57 samples based on the nine scale characteristics and used to classify each sample into the taxon for which its score was closest. Analysis of variance was used to identify significant differences (\( a = 0.05 \) level) in scale characteristics between the three taxa. Statistical analyses were done on a VAX 8550 computer using the statistical package SPSSX (Version 3.0, Norusis 1985).

RESULTS

*Mallomonas duerrschmidtiae* sp. nov.

Cellula ellipsoides vel obovoides, ante setis, post spinis longis in caudam convergentibus munia, corpore cum cauda 20.9–29.3 μm longo. Squamae tetragoneae, anticae cupulatae, mediae aliae cupulatae aliae cupulis crentes, posticae spinigerae, onnes in helices dispositae axibus earum cum axe longitudinali cellularis angulos rectos formantibus. Squamae mediae magnae, 4.7–8.6 μm longae, ellipticae, paulum curvae, cum superficie cellularis ita congruentes. Squamae anticae et posticae asymmetricae proper cupulis illorum oblique insertae et harum spinis retro directas. Quaerum squama laminam basalem perforatum et limbum posteriorem et crista V-formem praebens. Scutum strato secundario tectum et costis reticulatae connexis poros magnos eingentibus formatum. Rami cristae V-formis curvi, cum costis submarginibus anterioribus confluentes, ita marginem non attingentes. Costae submarginales antiores saepe super aquamarin in albas breves surgentes. Cupula parva foroce setae tenui, duae vel quartus costas parallelas, complures papillos, alii serratae parvam supra ostium prominentem praebens. Limbus posterior tigliis brevisibus seriatis suffultus cum cum crista


V-formi conjunctibus, interdum sub eo plus minuens occulit. Limbi anteriores angustae, laeves. Spinae crassae, 5.7–9.7 μm longae, in apices acutae attenuate. Setae costatae, dentibus in unum cuique seriem dispositae serratae, 6.2–9.9 μm longae.

Die 20 Maii anni 1986 in stagno parco Polliaq Pond regionis Franklin County civitatise americanae New York sub numero A1 ab auctore lecta. Figura 1 typica monstrata.

Cells are 20.9 μm × 29.3 μm, elliptical to obovate, with bristles covering the anterior ½ to ⅞ of the cell and a posterior group of scales with long spines (Figs. 1–3). The cell coat consists of four types of scales arranged from the anterior to posterior of the cell in the following order: domed anterior, domed body, domeless body and posterior spined (Figs. 1–3). Body scales are spirally arranged with their longitudinal axes perpendicular to the longitudinal axis of the cell. Each scale is overlapped by the scale positioned behind it in the same spiral row and by the scales in the spiral row above it (Figs. 1–3). The apical scales, which form the anterior-most ring of scales, are highly asymmetric due to the position of the dome on the left side of the scale and a large serrated wing projecting from the left side of the dome; the wings collectively form a ring around the flagellar opening.

Body scales are large, range in length from 4.7–8.6 μm, are usually highly silicified and curved such that the concave (ventral) surface conforms to the shape of the cell (Figs. 4–7). The domes of body scales have a small rounded lip or wing on the right side of the dome lining the U-shaped bristle opening, giving the scale a slight asymmetry (Fig. 4). Like the anterior domed scales, posterior spined scales are strongly asymmetrical due to the continuation of the submarginal ribs into a long spine such that the spine is oriented parallel to the longitudinal axis of the cell (Fig. 3).

Body scales are elliptical and consist of a perforated base plate, posterior rim and V-rib. The posterior rim and V-rib are strongly hooded, forming extensive canopies (Figs. 4–6). The arms of the V-rib curve and are continuous with the anterior submarginal ribs; the latter either terminate at the sides of the dome (Fig. 4), meet and fuse in the domeless scales (Fig. 5), or become extended and form the spines on posterior scales (Fig. 3). The anterior submarginal ribs are often extended above the plane of the scale, forming short wings (Fig. 7). Domes are relatively small, have a shallow bristle cavity and are most often marked with two to four parallel ribs positioned on the left side of the dome and oriented parallel to the longitudinal axis of the cell (Figs. 4–6). Domes may also be ornamented with raised papillae (Fig. 4). The right anterior submarginal rib often continues across the dome and terminates above the bristle opening (Fig. 4). The shield consists of a secondary layer of interconnecting ribs forming large pores (Figs. 1–7). The thicker the secondary ribs, the smaller are the diameters of the pores. The posterior flange consists of a series of short struts that connect the V-rib with the posterior rim (Fig. 4); a series of circular pores alternates with the struts. On some scales the canopy of the posterior rim extends to the V-rib, completely obscuring the posterior flange (Fig. 6). Anterior flanges are narrow and unornamented.

The spines are long (mean = 7.8 μm), range in length from 5.7–9.7 μm, are smooth and thick and taper to a sharp point. Bristles are short, range in length from 6.2–9.9 μm, and are ribbed and unilaterally serrated (Fig. 8). On some bristles the proximal teeth are recurved. No additional morphological structure of scales or bristles could be discerned using TEM.

The species is named in honor of Dr. Monika Dürrschmidt.

Comparison of Cell and Scale Features with M. crassissquama and M. pseudocoronata

Many characteristics of M. duerrschiitae are similar to those of M. crassissquama and/or M. pseudocoronata. The overall morphology of the cells and scales and the types, orientations and arrangements of scales are similar for all three taxa. Like M. duerrschiitae, cells of M. crassissquama (Figs. 9, 10) and M. pseudocoronata (Figs. 17, 18) are elliptical to obovate with a slightly wider anterior end and a tapered posterior portion with spines. Cell length (not including the spines) of M. duerrschiitae (mean = 18.8 ± 3.0 μm) is slightly smaller than either M. crassissquama (mean = 22.1 ± 2.2 μm) or M. pseudocoronata (mean = 22.7 ± 1.9 μm). Mallomonas crassissquama and M. pseudocoronata also have cells with domed anterior (Figs. 15, 20), domed body (Figs. 11, 12, 19, 21) and posterior spined (Figs. 14, 22) scales arranged in a spiral fashion with their longitudinal axes perpendicular to the longitudinal axis of the cell (Figs. 9, 17).

The primary differences among the three taxa lie in the characteristics of the scales, bristles and spines.

Figs. 1–8. Mallomonas duerrschiitae. Figs. 1–3. Whole cells showing anterior domed, domed body, domeless body and posterior spined scales and bristles. Note the imbricated nature of the scales. Scale bars = 5 μm. Fig. 4. Domed body scale depicting the continuation of the arms of the V-rib with the anterior submarginal ribs. Note the ridge and papillate markings on the dome and point of emergence of the bristle. Scale bar = 2 μm. Fig. 5. Isolated domed and domeless body scales and bristles. Scale bar = 5 μm. Fig. 6. Domed body scales. Note the parallel ridges and short wing on the dome and the curved nature of the scale. Scale bar = 2 μm. Fig. 7. Close up of an intact cell showing the imbricated nature of the scales. Note the extension of the anterior submarginal ribs into wings. Scale bar = 2 μm. Fig. 8. Uniserrated bristles with ribs. Scale bar = 5 μm.
Figs. 17–22. *Mallomonas pseudorontata*. Figs. 17, 18. Whole cells depicting the overlapping nature of the scales. Note the protruding anterior wings and long posterior spines. Scale bar = 10 μm for Figure 17 and 5 μm for Figure 18. Fig. 19. Domed body scale lacking secondary markings on the shield. Scale bar = 2 μm. Fig. 20. Group of anterior and domed body scales. Note the asymmetrical nature of the anterior scales. Scale bar = 5 μm. Fig. 21. Domed body scales with exceptionally long wings. Note that the base of the wing is attached to the base plate and is not an extension of the anterior submarginal ribs. Scale bar = 5 μm. Fig. 22. Posterior spined scale. Note the asymmetry and the ribs on the spine. Scale bar = 5 μm.

Figs. 9–16. *Mallomonas crassissima*. Figs. 9, 10. Whole cells showing domed body, domeless body and posterior spined scales and bristles. Note the alignment of scales into spiral rows. Scale bar = 10 μm for Fig. 9 and 5 μm for Fig. 10. Fig. 11. Domed body scale with a relatively weak secondary reticulation and a smooth dome. Scale bar = 2 μm. Fig. 12. Domed body scale with a relatively heavy reticulation on the shield and papillae on the dome. Scale bar = 2 μm. Fig. 13. Anterior domed scales. Note the relatively large dome and extension of the left anterior submarginal rib into a short wing along the dome. Scale bar = 2 μm. Fig. 14. Asymmetric spined posterior scale. Scale bar = 2 μm. Fig. 15. Domed scale with serrated bristle. Note the recurved hooks on the proximal end of the shaft. Scale bar = 2 μm. Fig. 16. Non-serrated helmet bristle. Scale bar = 2 μm.
Not including the wing, the length, width and area of body scales of *M. pseudocoronata* are significantly larger than those of *M. crassissquama* (Fig. 23A, C, D). Body scales of *M. crassissquama* rarely have the larger dimensions of *M. pseudocoronata* scales. The length, width and area of body scales of *M. duersschmidtiae* are between those of *M. crassissquama* and *M. pseudocoronata* (Fig. 23A, C, D). Scales of *M. duersschmidtiae* are often similar in length to those of *M. pseudocoronata* but have a significantly smaller width, similar to that of *M. crassissquama*. As a result, body scales of *M. duersschmidtiae* have a mean surface area larger than those of *M. crassissquama* but smaller than those of *M. pseudocoronata*.

Three additional features of the scales separate the three taxa. First, scales of *M. pseudocoronata* have a forward projecting anterior wing that originates on the anterior flange along the outer boundary of the anterior submarginal ribs and projects upward at a 45–60° angle from the plane of the base plate (Figs. 19, 21). On body scales the wings fuse anterior to the dome along a median axis running parallel to the longitudinal axis of the scale (Fig. 19). On anterior domed scales the wings are smaller and may not fuse anterior to the dome (Fig. 20). On posterior scales the wings merge and become continuous with the spine (Fig. 22). Scales of *M. crassissquama* lack the characteristic wing. As stated above, body scales of *M. duersschmidtiae* may have short wings, but they differ from those of *M. pseudocoronata* in that they originate on and are extensions of the anterior submarginal ribs (Figs. 4, 7). In addition, they do not extend and fuse anterior to the dome.

The second major difference in the architectural structure of the scales is the point of juncture of the V-rib with anterior submarginal ribs. As described for *M. duersschmidtiae*, the arms of the V-rib curve and become continuous with the anterior submarginal ribs on the scales of *M. pseudocoronata* (Figs. 19–21). On scales of *M. crassissquama* the juncture between the anterior submarginal ribs and the V-rib is angular, and the two structures are not curved and continuous (Figs. 11, 12). Generally, the arms of the V-rib on body scales of *M. crassissquama* extend past the point of fusion with the anterior submarginal ribs and terminate at the perimeter of the scales. Such an extension of the V-rib to the perimeter of the scale is not found on body scales of *M. duersschmidtiae* or *M. pseudocoronata*.

The third distinguishing feature used to separate body scales is the structure of the dome. The area of the dome is similar for *M. crassissquama* and *M. duersschmidtiae*, but both have larger domes than *M. pseudocoronata* (Fig. 23E). Despite the similar surface area, domes of *M. crassissquama* are raised further above the plane of the scale and have a more pronounced bristle cavity than those of *M. duersschmidtiae* (compare Figs. 4, 12). In addition, domes of scales of *M. crassissquama* are usually smooth (Fig. 11) or marked with raised papillae (Fig. 12), whereas those
of *M. duerrschiidiae* have parallel ribs and sometimes additional papillae (Figs. 4–6). Domes on body scales of *M. pseudocoronata* are small, shallow, unornamented, round or triangular in shape and generally surrounded by the wing (Figs. 19, 21).

*Mallomonas duerrschiidiae* (Fig. 3) and *M. pseudocoronata* (Fig. 22) have long and thick spines averaging 7.8 µm and 9.4 µm in length, respectively (Fig. 23B). Spines of *M. crassisquama* are smaller and average only 2.2 µm in length (Figs. 14, 23B). Spines of *M. duerrschiidiae* and *M. crassisquama* are smooth, whereas those of *M. pseudocoronata* are most often ribbed (Fig. 22). All three species can possess bristles that are ribbed. Those of *M. duerrschiidiae* (Fig. 8) and *M. crassisquama* (Fig. 15) are unilaterally serrated, have a distal tip that is slightly recurved and tapered to a point and proximal teeth that are often recurved. The bristles of *M. pseudocoronata* are similar in shape but generally lack serrations. Bristles of *M. duerrschiidiae* and *M. pseudocoronata* are similar in length but significantly smaller than those of *M. crassisquama* (Fig. 23F). Cells of *M. crassisquama* may also have helmet bristles that are long and either smooth or serrated (Fig. 16).

**Table 2.** Classification results of discriminant function analysis for separating isolated scales from three taxa (I) and two taxa (II).

<table>
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<th>Predicted group</th>
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Percent correctly classified = 93%

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<td>2. <em>M. duerrschiidiae</em> sp. nov.</td>
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Percent correctly classified = 100%

**Fig. 24.** Scatterplot of the numerical values for the first and second canonical discriminant function scores for body scales of *M. duerrschiidiae*, *M. crassisquama*, *M. pseudocoronata*.

**Discriminant Analysis of Isolated Scales**

The initial discriminant analysis (DA) extracted a two factor model, based on nine morphological characters, for distinguishing among isolated scales of the three taxa (Table 1, Fig. 24). Function #1 was dominated by scale area, dome area and the size of the angle between the arm of the V-rib and the anterior submarginal rib, whereas the form factor, scale width and scale area dominated function #2 (Table 1). Function #1 clearly separated scales of *M. pseudocoronata* from those of *M. duerrschiidiae* and *M. crassisquama*, whereas function #2 was necessary to distinguish between the latter two taxa (Fig. 24). Using the two factor model, 93% of the isolated scales were correctly classified into their respective groups (Table 2). Three scales of *M. duerrschiidiae* were incorrectly classified as *M. crassisquama* and one of *M. crassisquama* as *M. duerrschiidiae*; all scales of *M. pseudocoronata* were correctly classified.

A second DA was done to extract a single factor model to distinguish between scales of only *M. duerrschiidiae* and *M. crassisquama* (Table 1, Fig. 25). The variables most effective in separating scales from these two groups were scale area and form factor. Scale width, pore area, dome area and V-rib/submarginal rib angle were also important (Table 1). This model was even more effective in separating scales from the two taxa (Fig. 25) and correctly classified all 41 samples (Table 2).

**Ecology**

*Mallomonas duerrschiidiae*. *M. duerrschiidiae* was found over relatively narrow environmental gradients. In Connecticut and Adirondack waterbodies *M. duerrschiidiae* was found primarily during the spring and fall with peak frequencies of 17% and 15%, respectively (Fig. 26A). However, it was present in only 4% of the collections made from...
under the ice and 3% of those made during the summer. As a result, *M. duersschmidtiae* has a relatively low weighted mean temperature of 12.4°C, a maximum occurrence between 9-18°C and is much rarer at extreme temperatures (Fig. 26B).

*Mallomonas duersschmidtiae* is also restricted to acidic softwater lakes low in specific conductance and total phosphorus levels (Fig. 26). This species was found in 26% of the collections from waters of pH 5 and 5.5; its frequency of occurrence diminished rapidly below and above this interval (Fig. 26C). *Mallomonas duersschmidtiae* is best described as a true acidophilous taxon because it is found almost exclusively below a pH of 7, has a preference for pH values between 5 and 6 and has a weighted mean pH of 5.76.

Among species of *Mallomonas*, *M. duersschmidtiae* is one of the most restricted along a specific conductance gradient, having been found only in waterbodies of less than 43 µS (Fig. 26D). It had a maximum occurrence below 20 µS and a weighted mean of 18 µS. In addition, *M. duersschmidtiae* was recorded mostly between 5–10 µg P·L⁻¹, and was lacking in all collections with a total phosphorus concentration greater than 20 µg P·L⁻¹ (Fig. 26E). Although this taxon was abundant in a few slightly colored localities, it had a distinct preference for clearwater lakes and was lacking from all darkly stained bogs.

*Mallomonas crassiquama*. *M. crassiquama* was common during each month of the year and found in a minimum of 19% of collections from any given month (Fig. 27A). Although it was slightly more abundant during spring and late fall, *M. crassiquama* did not exhibit any clear preference for a given season. Even though *M. crassiquama* had a weighted mean temperature of 13°C, it was common over the entire gradient (Fig. 27B), resulting in a large standard deviation of 7°C.

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**Fig. 25.** Frequency distribution plot of the canonical discriminant function scores for body scaled of *M. duersschmidtiae* and *M. crassiquama* based on a one factor model.

**Fig. 26A–F.** Frequency distributions for *M. duersschmidtiae* along various environmental gradients. A) Season, B) temperature, C) pH, D) specific conductance, F) total phosphorus, F) weighted mean values.

*Mallomonas crassiquama* was found over a wide pH range; however, it had a maximum occurrence in waters between pH 6.5–7.5 (Fig. 27C). Eleven percent of the collections between pH 5–5.5 had specimens of *M. crassiquama*. The frequency of occurrence increased steadily to 50% in the 6.5–7 pH interval and then declined gradually to where it was again found in only 11% of the collections between pH 8.5–9 (Fig. 27C). This taxon was noticeably absent below pH 5 and above pH 9, had a weighted mean pH of 7 and is best described as pH indifferent.

*Mallomonas crassiquama* was found in a wide variety of lake types ranging from ultraoligotrophic to eutrophic and clearwater to humic, although it was lacking in all acidic bog localities. It had a weighted mean total phosphorus concentration of 22 µg P·L⁻¹; however, it was as abundant above 40 µg P·L⁻¹ as it was below 5 µg P·L⁻¹ (Fig. 27E). Likewise, populations of *M. crassiquama* were observed over a wide range of specific conductance values from 18–219 µS (Fig. 27D), and it had a weighted mean of 96 µS. Although *M. crassiquama* was found in an average of 36% of all collections ranging from 20–180 µS, it occurred in only 7% and 5% of the collections less than 20 µS and greater than 180 µS, respectively.

*Mallomonas pseudocoronata*. Populations of this species, found in 10% of all collections, began to develop during the spring when water temperatures rose above approximately 12°C, were maintained throughout the summer and disappeared by mid-autumn (Fig. 28A). Whole cells were found in 14%
of the samples made from March through October, whereas only isolated scales were found in 2% of the 127 collections made from November through February. As a result, *M. pseudocoronata* has a relatively high weighted mean temperature of 18.1°C.

*M. pseudocoronata* was found in 18% of the collections above pH 6.5, was not found below pH 5.8 (Fig. 28C), and had a weighted mean pH of 7.7. *Mallomonas pseudocoronata* was found over a large specific conductance gradient; however, it was significantly less frequent in waterbodies with low specific conductance (Fig. 28D). It had a maximum occurrence between 100–120 µS where it was recorded in 32% of the samples and a weighted mean specific conductance of 112 µS. *Mallomonas pseudocoronata* was sporadically distributed over a total phosphorus gradient being found as often in lakes below 10 µg P·L⁻¹ as it was in those above 35 µg P·L⁻¹ (Fig. 28E). In general, *M. pseudocoronata* was found in oligotrophic, mesotrophic and eutrophic lakes, avoided the hypereutrophic localities, had a preference for clearwater habitats and was absent in all darkly stained humic samples.

**DISCUSSION**

Based on cell, scale and ecological characteristics, *M. duersschmidtiae* is easily separated from *M. crassiquama* and *M. pseudocoronata*. Whole cells of *M. duersschmidtiae* and *M. pseudocoronata* can be distinguished from those of *M. crassiquama* based on the significantly longer posterior spines and shorter bristles. In addition, cells of *M. duersschmidtiae* and *M. pseudocoronata* lack helmet bristles, and the protruding wings of scales are easily seen on cells of *M. pseudocoronata*. Isolated body scales are also easily separated based on characteristics of the dome, junction of the arms of the V-rib and anterior submarginal ribs and the presence/absence of an anterior wing. Isolated body scales that are separated into three groups using dome, V-rib/submarginal rib angle and wing characteristics can also be successfully grouped using discriminant analysis based on a combination of additional measurable characteristics. Other parameters that were useful in separating isolated scales included the area of the scale, form factor, area of the dome and the size of the angle between the arm of the V-rib and the anterior submarginal rib. The results of the discriminant analyses clearly support the idea that *M. duersschmidtiae* is indeed a separate taxon. The extent and magnitude of the differences between *M. duersschmidtiae* and either *M. crassiquama* or *M. pseudocoronata* are similar to or greater than those used to separate other species of *Mallomonas* at the species level (Asmund and Kristiansen 1986). Thus, we conclude that *M. duersschmidtiae* is best described at the species level.

In addition to morphological characteristics of cells and siliceous components, the three taxa were also separated along environmental gradients. *M. duersschmidtiae* was most common in the spring and autumn between temperatures of 9–18°C, was rare
above 20° C and was restricted to acidic lakes low in specific conductance and total phosphorus. In comparison, *M. pseudocoronata* was more abundant during the warmer months, had a higher weighted mean temperature and was mostly distributed along the higher end of both pH and specific conductance gradients. Cells of *M. crassiquama* were commonly found during every month of the year and over a wide temperature and total phosphorus gradient. However, the maximum occurrence of *M. crassiquama* along a pH gradient was between that of *M. duerrschmidtiae* and *M. pseudocoronata*, and the three taxa are best described as circumneutral, acidophilous and alkaliphilous, respectively. Both *M. crassiquama* and *M. pseudocoronata* were rare in waterbodies with a specific conductance below 20 μS where *M. duerrschmidtiae* was most abundant. In addition, unlike *M. crassiquama* and *M. pseudocoronata*, *M. duerrschmidtiae* was rarely encountered in eutrophic lakes, and all three taxa were lacking from acidic bog lakes. Thus, the different habitat requirements of the three taxa lend further support that they are indeed separate species.

A review of the literature supports the fact that *M. crassiquama* has a wide ecological tolerance (Siver and Skogstad 1988), having been found in ultraloiotrophic (Eloranta 1986), oligotrophic (Battarbee et al. 1980, Wawrzyniak and Andersen 1985, Eloranta 1986, Siver and Skogstad 1988), eutrophic (Asmund 1959, Momeu and Péterfi 1983, Siver and Skogstad 1988), clearwater (Asmund 1959, Eloranta 1989) and humic stained (Battarbee et al. 1980, Eloranta 1985, 1989) lakes. *Mallomonas crassiquama* has been found in collections from each season and has a wide temperature tolerance (Asmund 1959, Asmund and Hilliard 1961, Takahashi 1978, Roijackers and Kessels 1986, Siver and Skogstad 1988). Similar ranges in pH of 5.5–9.3 (Siver and Skogstad 1988), 6.3–8.6 (Asmund and Hilliard 1961), 5.5–9.0 (Takahashi 1978), 4.7–7.8 (Smol et al. 1984a), 6.2–7.5 (Roijackers and Kessels 1986), 5.4–8.0 (Cronberg and Kristiansen 1980) and 4.8–7.2 (Eloranta 1989) have been reported for *M. crassiquama*. This taxon has also been observed to be lacking in localities with a pH less than 5 (Cronberg and Kristiansen 1980, Smol 1986, Siver and Skogstad 1988, Eloranta 1989). Siver (1989a) calculated a weighted mean pH of 6.6 from literature values, supporting the idea that *M. crassiquama* is best described as pH indifferent (Takahashi 1978, Roijackers and Kessels 1986). Asmund (1959) and Roijackers (1981) noted that *M. crassiquama* had a slight preference for alkaline waters, whereas Momeu and Péterfi (1983), Eloranta (1985, 1989) and Charles and Smol (1988) reported a preference for slightly acidic localities. Many paleolimnological studies have correlated a decrease in *M. crassiquama* with a concurrent drop in inferred lakewater pH below 5.0, presumably caused by acidic deposition, confirming the idea that this species disappears at low pH (e.g. Battarbee et al. 1980, Smol 1980, Smol et al. 1984b, Christie and Smol 1986, Hartmann and Steinberg 1986, Dixit et al. 1988b).

The few literature records for *M. pseudocoronata* confirm the idea that it is found primarily between spring and autumn, is alkaliphilic in nature and very rare below pH 6 (Siver 1989a). Ito (1988) observed active populations only during the warm summer, and Wawrzyniak and Andersen (1985) recorded *M. pseudocoronata* in 33% of collections made from northern boreal regions during late spring and summer. The weighted mean pH values of 7.37 and 7.35 reported by Charles and Smol (1988) and Dixit et al. (1988a), respectively, were virtually the same as the 7.3 value reported in an earlier communication (Siver 1989a). In addition, Dixit et al. (1987) reported *M. pseudocoronata* to have a preference for circumneutral to alkaline lakes in Quebec. Wee and Gabel (1989) found this species between a pH of 7.7–8.7 in Iowa localities, and Asmund and Hilliard (1961) observed it between pH 7.2–8.6 in Alaska.

Because the three species are differentially distributed along pH, temperature, specific conductance, total phosphorus and seasonal gradients, they will undoubtedly be valuable in future lake monitoring and paleolimnological reconstructing efforts. In the past, *Mallomonas duerrschmidtiae* has inevitably been confused and included with *M. crassiquama*, especially in studies from regions with a predominance of softwater acidic localities low in specific conductance and total phosphorus. A few of the collections from the study of *M. crassiquama* made by Siver and Skogstad (1988) contained *M. duerrschmidtiae*. In a study of surface sediments from lakes in the Adirondacks, Smol et al. (1984a) initially combined records for *M. duerrschmidtiae* with those of *M. crassiquama* but now realize that the former taxon is much more common that the latter (Cumming and Smol, pers. commun.). Kling and Kristiansen (1983, Figs. 30, 32) and Jacobsen (1985, Figs. 7–9) identified scales of *M. duerrschmidtiae* as *M. pseudocoronata* and *M. crassiquama* forma, respectively.

Critical taxonomic verification is mandatory in all ecological studies, especially paleolimnological ones, where the relative numbers of taxa are used to infer a specific environmental condition. This has been demonstrated most effectively in the use of microfossil diatom and chrysophyte assemblages to infer historical pH levels (Charles 1985, Charles and Smol 1988). Typically, relationships between surface sediment assemblages and contemporary pH conditions from a set of lakes in a given region are utilized in a multiple regression analysis (e.g. Charles and Smol 1988), or more recently, canonical correspondence analysis (e.g. Stevenson et al. 1989, Dixit et al. 1989) to derive an inference model. The inference model is then used to reconstruct the pH downcore through time (e.g. Anderson et al. 1986). Such an approach has been successfully applied to lakes in different regions (e.g. the Adirondacks, Charles 1985; Sud-
bury, Dixit et al. 1988a) and yielded $R^2$ and SE values as significant as 0.94 ± 0.28 (Charles 1985). In addition, Siver and Hamer (1990) developed an inference model based on living populations of chrysophytes for use in detecting contemporary changes in lakewater pH.

The fine-tuning of inference models utilizing scaled chrysophytes will rely, in part, on improvements in the taxonomy of the organisms used to build the models (Davis and Smol 1986). For example, *M. acaroides* v. *mushokana* Nicholls was shown to be ecologically separated from the type, v. *acaroides*, along a pH gradient (Siver 1989b). Such a distinction will provide for more significant models in regions where both species are encountered. Likewise, because *M. duersschmidtia* has a much lower weighted mean pH and is more common in waterbodies close to pH 5 than either *M. crassinqua* or *M. pseudocoronata*, critical taxonomic separation is mandatory. Dixit et al. (1988a) found *M. crassinqua* below a pH of 5.0 in surface sediments of several lakes in the Sudbury area, contradicting the large body of evidence that supports the idea that this taxon disappears below pH 5.0. However, the scale pictured by Dixit et al. (1988a) representing *M. crassinqua* is actually that of *M. duersschmidtia*, indicating that the two taxa were mixed in the counts. This supports the idea that reevaluating collections for taxonomic discrepancies may help to solve apparent contradictions in the literature and eventually yield additional information of ecological importance.

Most paleolimnological studies that have utilized scaled chrysophytes for ecological inference have enumerated the isohaline scales using light microscopy (e.g. Smol et al. 1984a, Christie and Smol 1986, Charles and Smol 1988). Even though the presence of any species of *Mallomonas* should be verified with electron microscopy, with practice isolated scales of *M. duersschmidtia* can be accurately separated from those of *M. crassinqua* with light microscopy by observing the structural differences at the juncture of the V-rib and submarginal rib. In addition, other features such as the size of scales and characteristics of bristles and spines could be used to support a taxonomic decision.

Although multivariate statistical analyses utilizing morphological characteristics have been used to separate taxa in other algal groups, for example, the diatoms (Theriot and Stoermmer 1984a, b), this study represents the first attempt for the scaled chrysophytes. Models derived from discriminant analysis based on measurements of body scales accurately classified isolated scales. Principal component analysis (PCA) was also used to analyze the data. In PCA analysis the variance is maximized between all cases, regardless of their group (in this case species) assignments. Therefore, the principal axes will not necessarily represent the most appropriate linear combination of the original variables for separating the taxonomic groups. The first factor derived from discriminant analysis will always represent the best linear combination of the original variables for use in distinguishing among groups. In our study PCA did not separate the taxonomic units along the first two axes as well as did the discriminant analysis.

In summary, *M. duersschmidtia* is easily distinguished from other related species of *Mallomonas* on both morphological and ecological grounds. Since it is also restricted along various environmental gradients and is often an important member of the phytoplankton flora, it represents an excellent organism for use in ecological inference.

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