Morphological variation and ecology of *Mallomonas crassisquama* (Chrysophyceae)

Peter A. Siver and Ashbjørn Skogstad

*Mallomonas crassisquama* is one of the most common and widely distributed species of *Mallomonas*. In this study we compare the morphology and ecology of the species based on 309 collections from 67 localities in Connecticut (U.S.A.) and Norway. The taxon produces a very complex siliceous coat consisting of four scale and two bristle types all of which have considerable structural variation. A new variety, *M. crassisquama* var. *papillata* is described. Bristle production was found to be temperature dependent where cells formed serrated or helmet bristles under cold or warm conditions, respectively. *M. crassisquama* was found to exist over wide temperature, conductivity, phosphorus and pH ranges, however, was absent in samples with a pH <5.5.

P. A. Siver, Dept. of Biological Sciences, Western Connecticut State Univ., Danbury, CT 06810, USA. - A. Skogstad, Dept. of Biology, Div. of Limnology, Univ. of Oslo, P.O. Box 1027, Blindern, N-0315 Oslo 3, Norway.

**Introduction**

*Mallomonas crassisquama* (Asmund) Fott was first described by Asmund (1959) as a variety of *M. acaroides* and later raised to the species rank (Fott 1962). *M. crassisquama* differs from *M. acaroides* Perty emend. Iwanoff in the presence of a well developed ribbed meshwork on the shield, presence of domeless body scales, and caudal scales with spines, although apparently transitional forms are often observed between these two taxa.

Fine structural differences in the siliceous armor of scaled chrysophytes, used to delineate taxa, are revealed with the use of electron microscopy. However, what degree of variation in the siliceous armor should be allowed at the form, variety and species ranks (cf. Kristiansen 1981)? Differences in scale ultrastructure may exist within a single cell, in a population or between populations from different localities (Kristiansen 1979). Often slight differences in scale design are given form, variety or even species ranking. However, the variability in scale and bristle structure seen in published micrographs of *M. crassisquama* is quite large (Asmund 1959, Takahashi 1978 and Asmund & Kristiansen 1986).

*M. crassisquama* is one of the most widely distributed and often encountered *Mallomonas* taxa (Kristiansen 1975, Takahashi 1978, Smol 1979, Nicholls 1982). Because of its widespread distribution *M. crassisquama* scales would be present in the sediments of many lakes and recent work suggests that its disappearance may indicate increasing lake acidity (Smol et al. 1984a, 1984b).

The purpose of this paper is to present the morphological variability and ecological preferences of *M. crassisquama* and the description of a new variety.

**Materials and methods**

A total of 309 (220 from Connecticut and 89 from Norway) collections from 67 localities (40 from Connecticut and 27 from Norway) were analyzed for *Mallomonas crassisquama*. A minimum of 264 of the samples were also tested for temperature, pH, conductivity and total phosphorus levels (Tab. 1).
Tab. 1. The total number of analyzed collections made within different range intervals for temperature, pH, total phosphorus and conductivity.

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>pH</th>
<th>Total phosphorus µg P-1</th>
<th>Conductivity µS</th>
</tr>
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<tr>
<td>Range Number</td>
<td>Range Number</td>
<td>Range Number</td>
<td>Range Number</td>
</tr>
<tr>
<td>0-3 40</td>
<td>&lt;5.5 10</td>
<td>0-10 57</td>
<td>20-40 89</td>
</tr>
<tr>
<td>3-6 26</td>
<td>5.5-6 23</td>
<td>10-20 81</td>
<td>40-60 52</td>
</tr>
<tr>
<td>6-9 34</td>
<td>6-6.5 56</td>
<td>20-30 45</td>
<td>60-80 26</td>
</tr>
<tr>
<td>9-12 24</td>
<td>6.5-7 72</td>
<td>30-40 34</td>
<td>80-100 18</td>
</tr>
<tr>
<td>12-15 27</td>
<td>7-7.5 39</td>
<td>&gt;40 47</td>
<td>100-120 26</td>
</tr>
<tr>
<td>15-18 33</td>
<td>7.5-8 35</td>
<td>120-180 32</td>
<td>&gt;180 24</td>
</tr>
<tr>
<td>18-21 47</td>
<td>&gt;8 40</td>
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<td></td>
</tr>
<tr>
<td>&gt;21 46</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

Samples for phytoplankton and chemical analysis were taken at a 1 meter depth. During summer stratification, when possible, integrated epilimnetic samples were used for analysis. Either net (6 or 10 µm mesh) or centrifuged samples were used to analyze for *M. crassiqua* populations. Half of each sample was immediately fixed with Lugol's solution (Connecticut samples) or glutaraldehyde in Na-cacodylate buffer to a final concentration of 2% and 0.1 M respectively, at pH 7.0 (Norwegian samples). Temperature was measured with a YSI model 33 SCT (Connecticut) or a Fluke 2175A (Norway) meter. The pH was analyzed with a Fisher Accumet (Connecticut) or a Radiometer 29 (Norway) pH meter. Conductivity was measured with a YSI model 33 SCT (Connecticut) or a platinum electrode connected to a Philips GM 4249 (Norway) meter. Total phosphorus was analyzed on oxidized samples using the stannous chloride method (Franson 1980) (Connecticut) or after the method of Goitomer et al. (1978) (Norway).

Both live (refrigerated prior to observation) and fixed samples were used to study *M. crassiqua* populations. Samples from Norwegian localities were prepared for SEM and TEM observation as previously described by Skogstad (1984) and observed with a Jeol JSM-35C (SEM) or Siemens EL microscope IA (TEM). Connecticut samples were prepared for SEM observation by air drying a portion of each sample onto a piece of aluminum followed with two distilled water rinses. Each sample was then mounted onto an aluminum stub with apiezon wax, coated with gold using a Polaron E5100 sputter coater and observed with a Coates and Welter field emission SEM.

Results

General

Live cells are ovoid in shape, range in size from 10-29 x 6-18 µm and are covered with siliceous scales and bristles. The anterior portion of the cell, from which the majority of bristles originate is usually wider than the posterior spine bearing end. Scales range in size from 2.7-6.0 x 1.9-3.8 µm. Bristles can be of two types (see below) and range in length from 8-30 µm.

Scale morphology

Four basic types of scales, each found in a specific position on the cell, comprise the scale coat of *M. crassiqua* cells. Going from the anterior to the posterior of a given cell 1) anterior domed scales 2) body scales with domes 3) body scales without domes or spines and 4) posterior spined scales (Fig. 1). The apical scales and posterior spined scales (Fig. 2), located at the extreme ends of the cells, are asymmetric in shape. Because of the shape of the dome, body scales with domes (Figs 3 & 4) are also asymmetric, however, less so than the apical and spined scales. Domeless body scales (Figs 1 & 5) are symmetrical in shape and often have several papillae on the distal most end.

Shield reticulation is generally as described by Asmund and Kristiansen (1986). A large degree of variation in shield reticulation was found between populations (Figs 2, 3, & 6), cells from the same population or scales on a given cell (Fig. 7). Most scales have a ribbing pattern that forms a secondary layer consisting of large pores (Figs 3 & 4). Shells with virtually no or very little shield reticulation are most commonly found on the apical scales and posterior spined scales (Fig. 2). The denser the shield reticulation, the easier windows are observed (Figs 1 & 3). Flange ribs are usually parallel to one another (Fig. 3), however, they may fork, become connected with perpendicular ribs (Fig. 6) or form a reticulated pattern similar to that found on the shield. On all scales the minute base plate pores are lacking in extreme peripheral regions (Fig. 4).

The amount of overlap or thickness of the rim and V-rib (here referred to as canopying) varies, however, is usually greatest on more silicified scales with well-developed secondary layers. In some cases the degree of canopying obscures both the parallel ribs of the flange.
Figs 1-8. *Mallomonas crusisquama*. - Fig. 1. Whole cell denoting scale and bristle orientation. The relative position of domed and domeless body scales and caudal spined scales can be seen (3,500×). - Fig. 2. A group of body and caudal scales with little shield reticulation. Note the asymmetrical caudal scale with small spine (7,000×). - Fig. 3. Single domed body scale with extensive shield reticulation. Note the window at the base of the shield and the asymmetrical dome with the U-shaped doorways (15,000×). - Fig. 4. Single domed body scale. The scale is symmetrical except for the dome area. Note the position of the minute base plate pores (6,700×). - Fig. 5. Group of scales showing symmetrical domeless body scales and domes with both ridges and raised papillae (4,100×). - Fig. 6. Isolated scale with a smooth dome. Note the connection of several adjacent flange rims with perpendicular struts (15,000×). - Fig. 7. Close-up of the posterior position of a cell. Note scale with little reticulation interposed between those with large degree of reticulation (15,000×). - Fig. 8. Herbally silted scales with parallel ridges on the dome. Note the series of minute teeth lining the doorways (6,700×).
Figs. 9-12. *Mallomonas leucas.* Fig. 9. Bristle with helmet on the distal end (15,000×). Fig. 10. Serrated bristles (8,000×). Fig. 11. Helmet bristle with additional tooth located above the helmet but below the needle tip (23,000×). Fig. 12. A single scale and short serrated bristle with recurved hooks (250×). Figs. 13-16. *Mallomonas leucas* var. *pallina.* Fig. 13. Whole cell, denoting identity of scale-like structures as found on the type. Labeled as Fig. 14 (20,000×). Fig. 15. High magnification of the scale-like structures, showing the inner and outer plates (14,000×). Fig. 16. Raised papillae, clearly evident in this under-explored aspect.
Fig. 17. The frequency of occurrence of *Mallomonas crassissquama* in all lakes sampled with water (A) temperatures ranging between 0 and 27°C, (B) pH values ranging between 4.5 and 9.5, (C) conductivity values ranging between 18 and 418 μS, and (D) total phosphorus levels ranging between 0 and 372 μg P L−1 at the time of collection.

and the window (Fig. 8). The tips of the V-rib bend 30–45°* and form ridges that extend along the distal perimeter of the scale. The ridges either meet and fuse in the domeless body scales (Fig. 1), become extended and form the spines on posterior scales (Figs 2 & 7), or end at the dome in the domed scales (Fig. 3).

The scales are imbricated in a spiral fashion with their longitudinal axes perpendicular to the longitudinal axis of the cell (Fig. 1). The distal portion of each scale rests on the rims of the scales in front so that only the V-rib, shield and dome areas are exposed (Fig. 1). Scales, especially larger ones, are often curved with the concave portion being against the cell membrane, in order to conform to the cell shape. The concave U-shaped opening to the underside of the dome (see below) is along the lower distal margin, giving the scales an asymmetrical shape and allowing the bristle to be positioned 90° to the scale axis but parallel to the cell axis (Figs 1 & 7). Spines are parallel to the cells longitudinal axis (Fig. 1), range in length from 0.15 μm to 8 μm, and extend slightly upwards from the longitudinal scale axis.

Dome structure

Domes are either smooth (Fig. 6) or sculptured with parallel ridges (Fig. 8) or raised papillae. In some instances, both ridges and raised papillae can be found on the same dome (Fig. 5). Many of the domes, especially the sculptured ones, have a series of teeth that line the doorway and in some instances become expanded to form a short lateral wing (Fig. 8). In several populations smooth and papillae domed scales were found on the same cell.

**Bristle morphology**

As reported by Asmund and Kristiansen (1986) cells in this study had either helmet bristles (Fig. 9), serrated (needle) bristles (Fig. 10) or both. The distal end of each bristle type is usually slightly recurved and tapered to form a needle-like tip. Shafts of helmet bristles are serrated or smooth. In two populations, the bristles had an additional tooth on the concave side above the helmet but below the distal tip (Fig. 11). The distal teeth usually point towards the bristle tip, however, sometimes the proximal teeth form recurved hooks (Fig. 12). Serrated bristles are generally shorter in length than helmet bristles.

*Mallomonas crassissquama* (Asmund) Fott var. papillosa Siver and Skogstad var. nov.

Differt a var. *crassissquama* papillis squamarum prominenteribus, uniserialibus, secus costas submarginalis anterior et intra cristas V-formis.

Holotype: Fig. 13. Deposited at the Limnological Department, Biological Institute, University of Oslo, Blindern. Collected in Lake Dæløvann on 14.08.79.

The variety differs from the type by possessing very prominent papillae on its scales (Figs 13–16). The papil-
Fig. 18. The occurrence of *Mallomonas crassiquama* cells with either serrated or helmet bristles at water temperatures ranging between 0 and 27°C.

lae are deposited in a single row along the inner side of the V-rib and extend along both anterior branches of the submarginal ribs.

If the papillae were removed from the scales of var. *papillosa* the organism would be identical in structure to the type. The overall scale complement (asymmetric apical domes scales, domed body scales, domed or domeless body scales and caudal spinous scales), shield meshwork and presence of spines agrees with that of the type. Thus, we feel the organism should be described at the variety level.

Although both serrated and helmet bristles were found on var. *papillosa* most cells had only serrated bristles. Some of the bristles were almost devoid of serrations. The papillae range up to 0.3 μm in height above the scale base plate and they are very prominent in SEM (Fig. 14); however, they are easily overlooked and difficult to observe in TEM because of their position on heavily silicified structures (Fig. 15). Posterior scales on some cells lack papillae (Fig. 16). The size of var. *papillosa* cells, scales and bristles falls within the range for the type.

The phytoplankton community of Lake Dælivann is very rich in species, the most dominant of which are: *Chrysocromulis parva*, *Rhodomonas lacustris*, *Cryptomonas* spp., *Synedra* spp., *Asterionella formosa*, *Chrysococcus triporus*, *Epipyxis polymorpha*, *Staurastrum chaetoceras* and *Dinobryon sociale* var. *americana*. The physical-chemical conditions of the water when *M. crassiquama* var. *papillosa* was found were 15 to 16°C, pH of 7.5, 38 μg tot-P l⁻¹, 172 μS and 30 mg Pt l⁻¹. *M. crassiquama* var. *papillosa* has also been found in Linge Lake, Northwestern Ontario, Canada (H. Kling, pers. comm.).

Ecology

The collections represented a wide range of environmental conditions (Tab. 1). Temperature ranged from 1 to 27°C, pH from 4.5 to 9.5, conductivity from 18 to 418 μS and total phosphorus from nondetectable to 372 μg P l⁻¹. *Mallomonas crassiquama* was found in 30% and 39% of the Connecticut and Norwegian samples, respectively (33% of the total). Although rarely abundant, it was a common member of the phytoplankton flora in 10% and 8% of the Connecticut and Norwegian samples, respectively, and found over a wide range of environmental conditions (Fig. 17).

*Mallomonas crassiquama* found during all months of the year, was eurythermal occurring between 1–27°C (Fig. 17A). In addition, it had a wide tolerance to pH (Fig. 17B), conductivity (Fig. 17C) and total phosphorus levels (Fig. 17D). Although *M. crassiquama* was found in an average of 35% of all collections from 20 to 180 μS, it occurred in only 8% of the collections with greater than 180 μS (Fig. 17C). It was also absent from all collections below pH 5.5 (Fig. 17B). *M. crassiquama* was found in clear and humic stained lakes as well as in woodland oligotrophic and recreational eutrophic lakes.

Tab. 2. The distribution of *Mallomonas crassiquama* cells with only serrated (S) bristles, only helmet (H) bristles or both (B) in three Connecticut (USA) lakes.

<table>
<thead>
<tr>
<th>Date</th>
<th>°C</th>
<th>Bristle Type</th>
<th>Date</th>
<th>°C</th>
<th>Bristle Type</th>
<th>Date</th>
<th>°C</th>
<th>Bristle Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 22, 1984</td>
<td>17</td>
<td>H</td>
<td>June 5, 1984</td>
<td>20</td>
<td>B (mostly helmet)</td>
<td>June 5, 1984</td>
<td>17</td>
<td>H</td>
</tr>
<tr>
<td>Nov. 14, 1984</td>
<td>8.5</td>
<td>B</td>
<td>Nov. 7, 1984</td>
<td>9.5</td>
<td>?</td>
<td>Sept. 12, 1984</td>
<td>19.5</td>
<td>H*</td>
</tr>
<tr>
<td>Jan. 5, 1985</td>
<td>1</td>
<td>S</td>
<td>March 27, 1985</td>
<td>8</td>
<td>S</td>
<td>March 27, 1985</td>
<td>7.5</td>
<td>S</td>
</tr>
</tbody>
</table>

* Isolated helmet bristles only, no whole cells found.
Morphological variability vs. environmental conditions

Many attempts were made to correlate morphological differences with environmental parameters. The best correlation dealt with bristle morphology which was found to be a temperature dependent phenomenon (Fig. 18). Cells possessing only serrated bristles were found to be cold water forms mainly occurring at temperatures below 12°C while organisms with only helmet bristles were found mostly in warmer water above 15°C. Cells with both bristle types occurred from 9 to 20°C. Serrated bristles from cold water populations were often short in length and restricted to the anterior half of the cell. Populations of cells with either serrated or helmet bristles were often found in the same lake at different times of the year. For example, in each of the three lakes, the bristle morphology of cells from six populations correlated well with temperature (Tab. 2). Populations in Bigelow Pond and Westside Lake always had scales with raised papilae on their domes regardless of the bristle type. Cells in Tyler Lake had scales with either smooth domes or domes with papilae.

Discussion

Because the cell shape and size, dome structure and bristle morphology of Mallomonas crassissquama are similar to M. acaroides several authors have questioned the validity of M. crassissquama as a separate species, especially since the amount of shield reticulation can overlap between the two taxa (Anderson 1978, Kristiansen 1975, Wee 1982). In the original description Asmund (1959) stated that there was not always a clear cut difference between M. crassissquama and M. acaroides var. striatula Asmund (= M. acaroides var. acaroides). Recently, authors have separated M. crassissquama from M. acaroides on the basis of the presence of posterior spines (Kristiansen 1979, Cronberg & Kristiansen 1980, Nicholls 1982, Asmund & Kristiansen 1986). Clearly, since bristle and dome morphology can be similar in M. crassissquama and M. acaroides and the degree of shield reticulation can overlap, isolated bristles or domed scales with little reticulation may not be sufficient to make a correct species determination. In cases where the shield reticulation is well developed the distinction may be based on isolated scales, however, the presence of domeless body scales and spined posterior scales will clearly distinguish the taxon (Asmund & Kristiansen 1986).

It has been suggested that the formation of helmet bristles in M. crassissquama is related to the maturation stage of the cell (Harris 1970, Takahashi 1978, Nicholls 1982) where helmet bristles are formed by mature cells; immature cells form only serrated bristles. Asmund and Hilliard (1961) questioned this hypothesis and believed that further investigations were needed. We have shown that bristle morphology in M. crassissquama is clearly a temperature dependent phenomenon where cold and warm water populations produced only serrated or helmet bristles, respectively.

Little is known about temporal variation in scaled chrysophytes (Kristiansen 1979). Asmund (1959) found M. tonsurata Teiling em. Krieger to have shorter and coarser bristles during summer. Even though M. crassissquama is often reported in taxonomic surveys rarely do authors cite both the bristle type and lakewater temperature. The information available from the literature supports our findings that bristle morphology is temperature dependent. Asmund and Hilliard (1961) found M. acaroides var. crassissquama Asmund populations with only (or mainly) serrated or helmet bristles in cold and warm water, respectively; in several instances both bristle types were reported. In addition, Asmund and Kristiansen (1986) and Jacobsen (1985) have reported M. crassissquama cells with apical tufts of short, smooth non-helmet bristles from cooler subarctic and arctic lakes. In this study, cells with similar bristle features, except for the presence of serrations, were restricted to cold conditions.

Populations with both bristle types were most often found during periods of rapid temperature changes, the spring and fall, and probably represent an intermediate form. It also seems likely that if a given cell could shed or replace "old" bristles with "new" ones, it may be able to change its bristle complement. This dynamic aspect of bristle production could explain how cells with a majority of one bristle type may possess a few bristles of the other type. Perhaps the longer helmet bristles are produced during warmer months to as a compensation for lower water viscosity.

Conditions could exist that may tend to mask the true temperature/bristle morphology relationship. For example, since M. crassissquama is eurythermal cells formed at one temperature could survive and be collected at temperatures other than those under which it formed. If this occurred, cells with serrated or helmet bristles may be found at warmer or cooler temperatures than expected.

Like Mallomonas crassissquama, the closely related species M. acaroides is capable of producing serrated bristles, helmet bristles or both on individual cells. We feel that bristle morphology in M. acaroides may also be temperature dependent as was found in M. crassissquama. In a careful study of M. acaroides var. striatula (= M. acaroides var. acaroides) from Danish lakes, Asmund (1959) noted that only serrated bristles were present in cold water populations while a greater abundance of helmet bristles were seen with increasing temperatures. Asmund even remarked that the organisms with only serrated bristles may be cold water forms.

Since the var. papillosa was found in only one of the 309 collections, which represented a wide range of environmental regimes, it seems unlikely that the papilae formed in response to ecological conditions. It is possible that a similar variation in bristle complement ver-
sus temperature may exist in var. *papillosa* as was found in var. *crassisquama*, however, more observations must be made.

It is of interest that Péterfi and Momeu (1976) described a variety (var. *papillosa*) of the related taxon *M. acaroides* based, in part, on the presence of small papillae located on the dome and along both anterior margins. In 1983, Momeu and Péterfi raised this taxon to species rank, *M. strictopteris*. The prominence of the papillae in *M. strictopteris* may have been underestimated with TEM as was the case with *M. crassisquama* var. *papillosa*. Perhaps *M. strictopteris* and *M. crassisquama* var. *papillosa* represent an example of parallel evolution.

*Mallomonas crassisquama* is almost always reported as being the most common and widely distributed species of *Mallomonas* (Kristiansen 1975, Takahashi 1978, Battarbee et al. 1980, Wujek et al. 1981, Nicholls 1982, Kling & Kristiansen 1983 and Smol et al. 1984a). Its cosmopolitan distribution is related to its tolerance of a wide range of environmental parameters. Live *M. crassisquama* cells were found between 1 to 27°C which also represented the temperature range for all collections (Fig. 17A). Other researchers have found similar temperature ranges (Asmund 1959, Battarbee et al. 1980). Although Asmund (1959) reported var. *crassisquama* to have a temperature optimum between 10 to 15°C our data do not indicate such an optimum.

In this study, *M. crassisquama* was often found in oligotrophic lakes, in agreement with observations made by Battarbee et al. (1980) and Smol et al. (1983). However, healthy populations also occurred in more eutrophic lakes. In fact, 22 populations were found in lakewater with greater than 20 μg P L⁻¹. In a later study, Smol et al. (1984a) reported a total phosphorus range of 2.4 to 40 μg P L⁻¹ and a mean of 8.4 μg P L⁻¹ which is in agreement with our results.

*M. crassisquama* populations were found in 35 percent of the collections representing waters with a conductivity between 20 and 180 μS indicating a wide tolerance range (Fig. 17C). A significantly lower percentage (8%) of the samples collected from waters with a conductivity greater than 180 μS contained *M. crassisquama* indicating that although it can tolerate high conductivity it does not favor it. In addition, this taxon was found over a large alkalinity range and in very clear as well as in humic stained lakes.

In agreement with Smol et al. (1984b) we also found *M. crassisquama* to have a wide pH tolerance; populations were found between pH 5.5 and 9.3. Although this study included only 10 samples with a pH <5.5, none of these contained *M. crassisquama*, supporting the hypothesis that this taxon is limited at lower pH values. In addition, in a recent survey of acidic lakes located in the Adirondack region of New York state (U.S.A.), *M. crassisquama* was not found in any of the 10 samples below a pH of 5.1 (Siver, unpubl. data). Thus, we agree with Smol et al. (1984a, 1984b) that a lowering of the lake water pH below 5 will result in the disappearance of *M. crassisquama*.

Unlike bristle types, the degree of shield reticulation and dome morphology, both of which vary considerably in *M. crassisquama*, were not found to be environmentally controlled. Since scales with little or no reticulation may be juxtaposed to scales with a well-developed ribbed pattern, we feel this characteristic should not be used as a taxonomic criterion to further delineate forms or varieties.

Unsculptured domes or ones with papillae are most often reported for *M. crassisquama* (Asmund 1959, Asmund & Hilliard 1961, Battarbee et al. 1980). Asmund and Hilliard (1961) believed the papillae on the dome was a feature that "may be potentially present in every population." We feel this may be true, especially since both smooth and papillae domed scales were found on the same cell. Domes with a short wing have also been reported to occur especially on apical scales (Asmund 1959, Momeu & Péterfi 1983, Asmund & Kristiansen 1986). In this study several populations had domed body scales with short wings.

Kristiansen (1979) stated that since 3 to 4 types of scales can be found on one cell the whole scale cover must be considered in any taxonomic description. In addition, since large variation in scale design exists in some species (e.g. *M. crassisquama*) yet others have quite uniform structure (e.g. *Synura uvella*), Kristiansen (1981) posed the question — how small differences should be recognized to be of taxonomic value? We feel that scale polymorphism should be addressed and included in a species description. For example, since shield, dome and flange structure is quite variable in *M. crassisquama* we feel it should not be used to further delineate taxonomic units but rather, the variation be noted as part of its description. If, however, further information shows the structures to be genetically controlled, then species variety or formae determinations could be made.

In some instances isolated scales, especially larger heavily silicified ones were found to have a striking resemblance to wingless *M. pseudocoronata* Prescott scales. In these cases, species determinations were considered valid only after whole cells or groups of scales and bristles were found. Several investigations have also noted the possible resemblance of isolated *M. crassisquama* scales to wingless *M. pseudocoronata* scales (Kling & Kristiansen 1983, Smol et al. 1984b, Jacobsen 1985). Perhaps *M. crassisquama* is evolutionarily closely related to *M. pseudocoronata*.

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