



Fossil species of *Mallomonas* from an Eocene Maar Lake with recessed dome structures: Early attempts at securing bristles to the cell covering?

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With 5 figures and 1 table

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Abstract: The genus *Mallomonas*, the largest within the Class Synurophyceae, consists of motile, unicellular, freshwater heterokonts that are covered with an outer layer of overlapping siliceous scales. The scales are flat, circular to oval structures with taxonomically distinct designs. In addition to scales, the cell coverings of most *Mallomonas* species contain a second siliceous component known as a bristle. Bristles are composed of a long thin shaft and a flattened proximal foot. The foot of the bristle is fastened under the distal end of a scale in such a way as to allow the shaft to radiate out from the cell and rotate on its axis. For many species, the distal scale margin is distinctly raised, forming a hollow space that secures the bristle foot, and an inverted U-shaped opening from which the shaft emerges. This structure is called the dome. We describe three fossil species of *Mallomonas* from an Arctic Eocene maar lake that contain domes that are recessed to varying degrees back from the distal scale margin. This design is not known in the modern flora and we hypothesize that it represents an early attempt at securing bristles to the scale coat.

Key words: *Mallomonas*, siliceous scales, bristles, dome, Eocene, fossil.

Introduction

Organisms within the Class Synurophyceae (synurophytes) are motile, unicellular or colonial, freshwater heterokonts commonly found in the plankton of lakes, ponds, sluggish rivers and wetlands globally (Siver 2003; Kristiansen 2005). The cell is surrounded by a series of overlapping, flat, siliceous structures called scales, with designs that are taxonomically diagnostic at the species level. Synurophytes are ubiquitous in freshwater habitats (Siver 2003; Kristiansen 2005) and often form a significant component of phytoplankton communities, with the richest floras recorded from habitats that are slightly acidic, dilute, weakly buffered, with low to moderate concentrations

of nutrients and humic substances (Siver 1995). Since numerous species are restricted to specific environmental conditions, coupled with the species-specific siliceous scales that remain in aquatic sediments, synurophytes are valuable bioindicators, especially for reconstructing paleoenvironments (Smol 1995; Kristiansen 2005). There are over 220 known living species and subspecific taxa within the Class Synurophyceae (Kristiansen & Preisig 2007; Kim & Kim 2008; Nemcova et al. 2011), with the vast majority represented by the genus *Mallomonas*. As a group, synurophytes are closely related to organisms within the Class Chrysophyceae, and in fact may represent a clade within the latter class (Grant et al. 2009).

All synurophyte scales consist of a base plate with a posterior upturned rim (Fig. 1). On the majority of species, the base plate is partially or fully perforated with small pores, and the upturned rim usually encircles about one-half of the perimeter (Siver 1991). Scales of many species contain additional structures, including ribs, reticulations, papillae, anterior submarginal ribs and V-ribs. These features are collectively known as secondary structures (Wee 1982; Siver 1991) because they are deposited on top of the base plate. As the name implies, the V-rib is a prominent V-shaped ridge of silica with a base in the proximal region of the scale and arms that extend to about the middle of the scale (Fig. 1). Often, two additional siliceous ridges, called the anterior submarginal ribs, originate near the ends of the V-rib arms, run parallel to the distal margins of the scale and terminate near the apex. Collectively, the V-rib and anterior submarginal ribs are referred to as the submarginal rib complex (Siver 1991). The V-rib is believed to be involved in spacing and aligning the scales on the cell coat (Siver & Glew 1990), and it is of phylogenetic significance (Jo et al. 2011). The area of the scale bounded by the submarginal rib complex is referred to as the shield, and the area outside of this complex as the flange. On many species, a portion of the distal margin is elevated or raised above the base plate, forming a hollow cavity called the dome (Fig. 1).

The cell covering of most *Mallomonas* species contains a second siliceous structure, the bristle. Bristles are elongated structures each composed of a flat basal portion called the foot, and a long slender shaft. The foot is tucked under the distal margin of the scale such that the shaft radiates outward from the cell (Siver 1991). For species with domed scales, the foot is fitted within the cavity of the dome, like a ball-and-socket joint, and the shaft emerges from an inverted U-shaped opening allowing for the bristle to rotate relative to the swimming axis. Like the scale, the structure and distribution of bristles on the cell are of taxonomic significance.

The evolutionary history of synurophytes based on the geologic record is poorly known. The majority of fossil records are of the siliceous resting stage, or cyst, with the oldest known deposit from the Aptian-Albian of the Lower Cretaceous (ca. 110 Ma, Harwood & Gersonde 1990). Since members of the Class Chrysophyceae also produce siliceous cysts (Nicholls & Wujek 2003), it is unknown if the Aptian-Albian specimens include members of the synurophytes. In western North America, cysts are largely not found in abundance until much later in the Miocene (Williams 1985; Siver & Wolfe 2005a), yielding a large gap in the geologic record. In addition to the scant reports of chrysophyte cysts, until recently, there was no geologic record of synurophyte

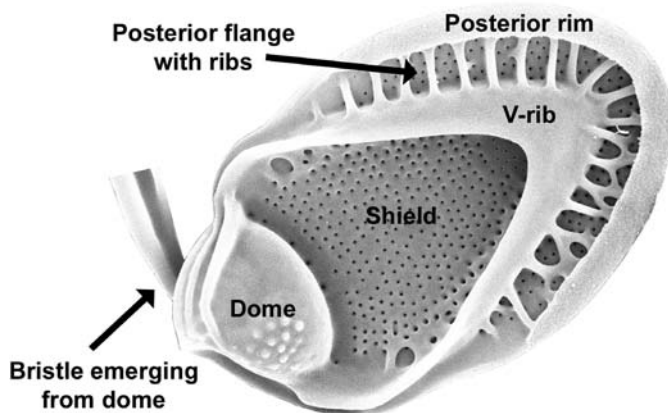


Fig. 1. Modern scale of *Mallomonas muskokana* (Nicholls) Siver & Wolfe illustrating the major parts of a scale, including the dome, shield, V-rib, posterior rim, posterior flange and emergence of the bristle from the dome.

scales or bristles. This has changed with the discovery of a vast array of specimens in an extensive core taken from an Eocene kimberlite maar lake known as Giraffe Pipe (Siver & Wolfe 2005a, b; Siver et al. 2009; Wolfe & Siver 2009). Among the wealth of microfossils uncovered from the Giraffe core are synuophyte scales and bristles representing numerous species, including ones that are surprisingly similar in structure to modern taxa (e.g. Siver & Wolfe 2005a; Siver et al. 2009), and others with unique morphological characters that are presumed to be extinct (Siver & Wolfe 2010). The purpose of this paper is to describe a suite of three taxa with scales that contain well defined dome structures that are unique in that they are recessed from the distal scale margin unlike any modern living forms.

Materials and methods

Mudstone chips (50–100 mg) from multiple zones of the Giraffe core (Table 1) were oxidized using 30% H₂O₂ under low heat for a minimum of an hour, rinsed with distilled water, and the resulting slurries stored in glass vials. This procedure results in separation of many siliceous microfossils from the mudstone matrix as well as small remaining fragments each containing numerous embedded specimens. Aliquots of each clean slurry were air dried onto pieces of heavy duty aluminum foil. The aluminum foil samples were trimmed, attached to aluminum stubs with Apiezon® wax, and coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater. Samples were examined with a Leo 982 field emission scanning electron microscope. A minimum of 20 specimens for each species were used for morphometric analysis.

Each sample from the Giraffe core is identified with a three-part number (Table 1). The first number represents the core box. Deeper sections of the core correspond to larger box numbers. Each box contains three 1.5 m core lengths, identified as channels 1, 2 and 3. The second number represents the channel. The third number represents the length in cm measured down from the top of a core length. Thus, sample 18-3-31 represents a sample taken from 31 cm down along the core length positioned in channel 3 from box 18.

Table 1. Samples within the Giraffe Pipe core containing the new *Mallomonas* species. The vertical depth within the core and the estimated depth within the maar lake are given.

Species	Core Box #	Depth in Core (m)	Depth in lake (m)
<i>M. media</i>	13-1-15	78.47	8.89
	13-1-33	78.6	9.02
	14-2-32	80.78	11.2
	14-1-60	82.09	12.51
<i>M. preisigii</i>	13-2-120	78.14	8.56
	13-1-33	78.6	9.02
	13-1-80	78.94	9.36
	13-1-144	79.41	9.83
	14-3-20	79.6	10.02
<i>M. ampla</i>	13-1-144	79.41	9.83
	14-3-20	79.6	10.02
	17-3-125	90.24	20.66
	17-2-25	90.61	21.03
	17-2-94	91.11	21.53
	19-1-100	98.83	29.25
	20-2-25	100.48	30.9
	20-1-40	101.69	32.11
	20-1-60	101.83	32.25
	20-1-95	102.09	32.51

Site description

The Giraffe Pipe locality (64°44'N, 109°45'W) is a kimberlite diatreme that was emplaced into the Slave Craton in the Northwest Territories of Canada approximately 47.8 million years ago during the Middle Eocene (Siver & Wolfe 2005a; Wolfe et al. 2006). The diatreme crater subsequently filled with water, becoming a maar lake and slowly infilled with a sequence of lacustrine, then paludal sediments, and was later capped by Neogene glacial deposits (Siver & Wolfe 2005a; Wolfe et al. 2006). The Giraffe Pipe is one of many kimberlites in the Lac de Gras field, most of which have Cretaceous or Paleogene emplacement ages (Heaman et al. 2004). A 163 m long drilled core was uncovered from the kimberlite maar in 1999 by BHP Billiton Inc. (Siver & Wolfe 2009). A total of 113.1 m of the core contained well preserved stratified organic sediment, including 68.3 m of lacustrine lake sediments, overlain with 44.8 m of peaty material. An air-fall tephra bed located near the transition between lake

and terrestrial sediments was dated at 40 million years using fission tracking (Doria 2011), indicating that all of the lake sediments are Eocene in nature. We envisage that, after phreatomagmatic kimberlite emplacement, a waterbody formed within the deep crater that persisted for about 7 to 8 million years before transition to a terrestrial environment. The current investigation is based on 19 samples from between the 78 to 102 m section of the core (Table 1). This interval broadly corresponds to lake depths between 8 and 33 m deep.

Results

***Mallomonas media* sp. nov.** Siver & Lott

Scales are large, broadly ovate with a posterior rim, a thick secondary layer that aligns the front half of the scale and a distinctly recessed dome (Figs 2A–F). Scales range in size from about 8–11 μm \times 5–6.5 μm . The posterior rim encircles about half of the scale perimeter and is supported by a series of short parallel ribs (Fig. 2D, arrow). Base plate pores are restricted to the posterior region of the scale, but are lacking under the posterior rim. The thick secondary layer aligning the anterior scale perimeter consists of a honeycomb-like series of chambers covered with a thin layer of silica. The secondary layer overlaps the terminal ends of the posterior rim, and is widest along the distal portion of the scale. The dome, positioned on the scale just behind the thick secondary layer, is oval, approximately 2 μm in length and aligned roughly perpendicular with the scale axis. On most specimens, the dome is set back at least 2 μm from the distal margin.

HOLOTYPE: Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, CANA85742.

TYPE MATERIAL: Slurry prepared from section 14-1-60 of the Giraffe Pipe core by P.A.Siver and deposited at the Canadian Museum of Nature, CANA85742.

ICONOTYPUS: Figure 2B, uncovered from section 14-1-60 of the Giraffe Pipe core.

The epithet refers to the location of the dome, being closer to the center of the scale. *Mallomonas media* was found in four closely-spaced sections of the core, corresponding to water depths ranging from ca. 9 to 12.5 m (Table 1).

***Mallomonas preisigii* sp. nov.** Siver

Scales are either domed (Figs 3A–D) or domeless (Figs 3E–F). Scales are broadly oval, range in size from 3.5–4 \times 2–2.2 μm , and possess a posterior rim, a V-rib with arms that are continuous with the anterior submarginal ribs and a wide posterior flange. The base plate is devoid of pores and the shield and posterior flange are unornamented. The dome is shallow, laterally expanded and recessed from the distal margin. The base of the V-rib is broad and U-shaped, and the anterior submarginal ribs terminate on the sides of the dome. The posterior rim encircles half, or slightly less than half, of the perimeter and often extends further along one side of the scale.

HOLOTYPE: Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, CANA 85743.

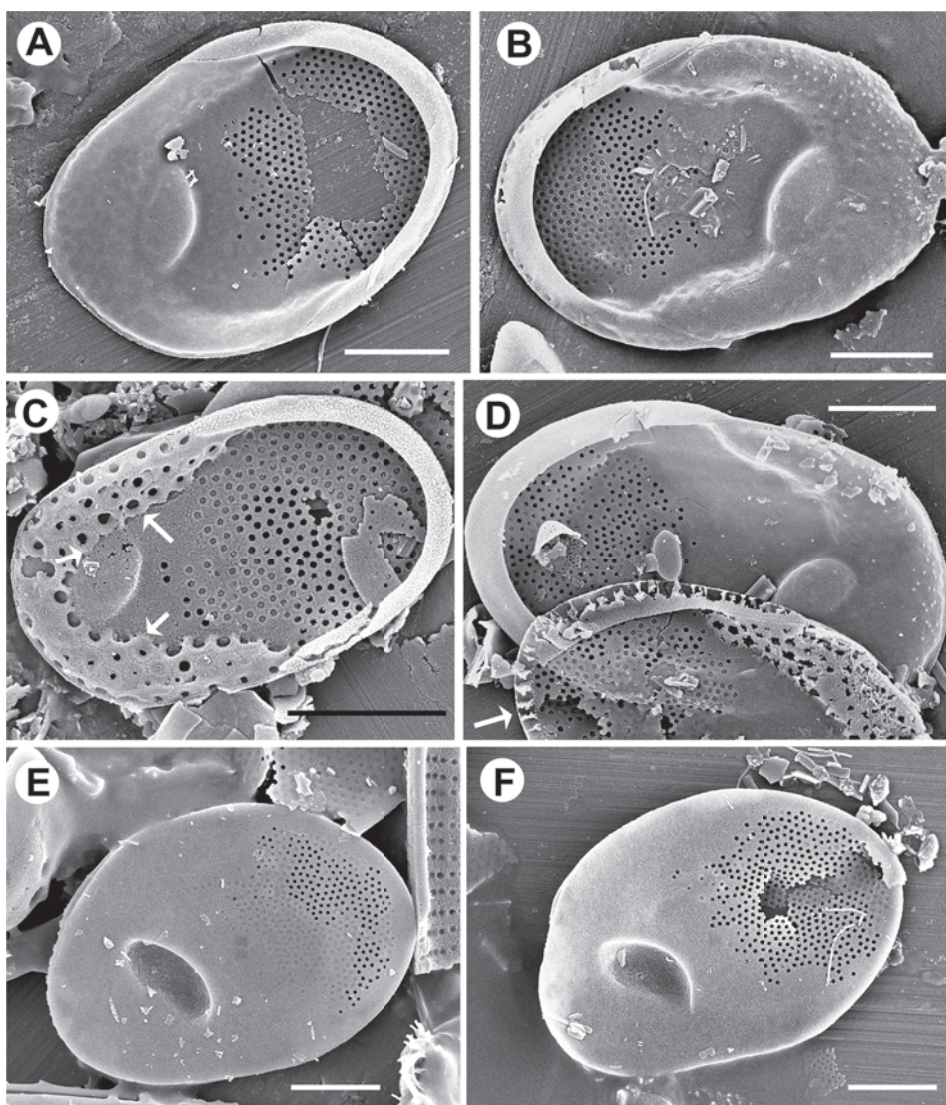


Fig. 2. Scales of *Mallomonas media*. A–B. Specimens denoting the posterior rim, thick secondary layer aligning the anterior margin, base plate pores and recessed dome. C. Note the reticulated nature and boundary (arrows) of the anterior secondary layer. D. An intact (top) and a partially degraded (bottom) scale. Note the ribs underlying the posterior rim (arrow) on the degraded scale. E–F. Undersurface of scales illustrating the shallow nature of the dome and position of the base plate pores. All scale bars = 2 μ m.

TYPE MATERIAL: Slurry prepared from section 13-1-80 of the Giraffe Pipe core collected by P.A.Siver and deposited at the Canadian Museum of Nature, CANA85743.

ICONOTYPUS: Figure 3A, uncovered from section 13-1-80 of the Giraffe Pipe core.

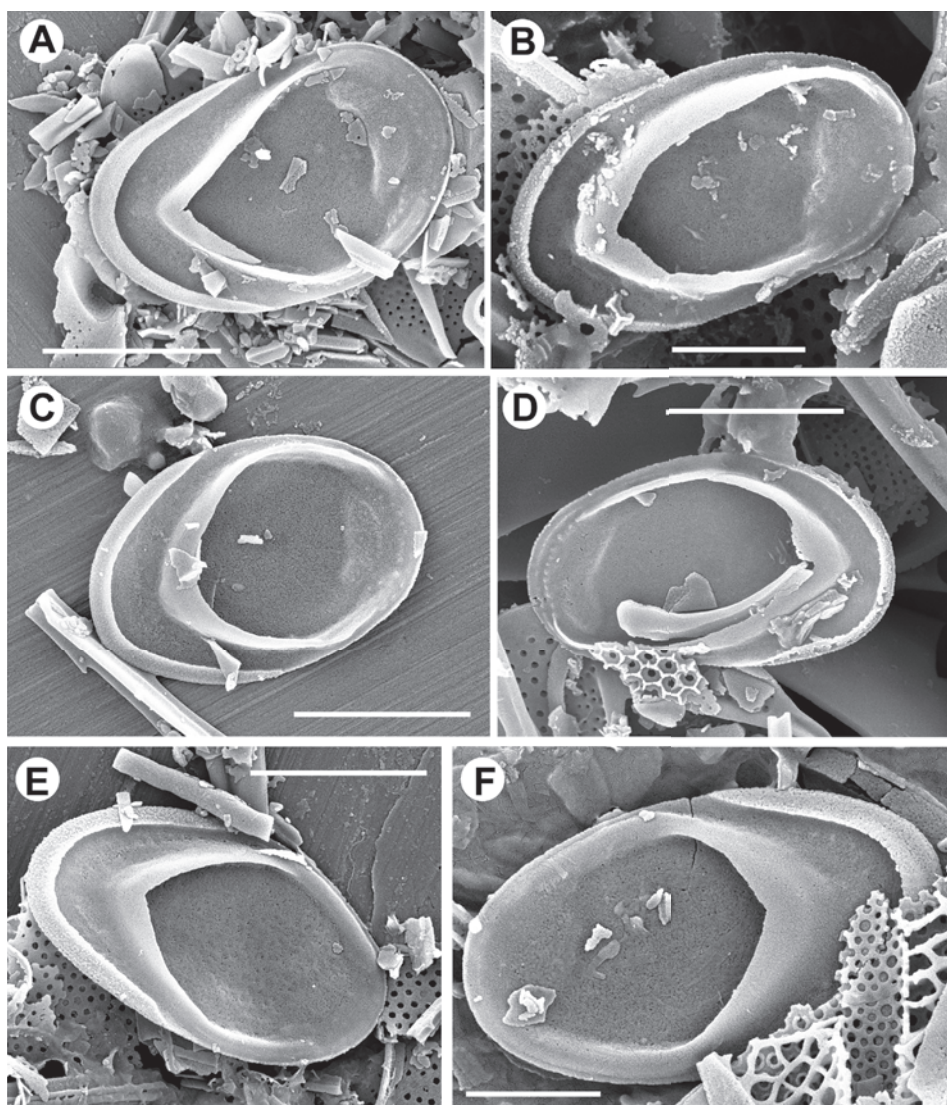


Fig. 3. Domed (A–D) and domeless (E–F) scales of *Mallomonas preisigii*. Note the short posterior flange, the lack of pores and ornamentation on the base plate, the broad V-rib, and the shallow and recessed dome. Scale bars are = 1 μ m (B, F) or 2 μ m (A, C–E).

The epithet is in honor of the chrysophyte expert Hans R. Preisig. *Mallomonas preisigii* was uncovered in five sections of the core, corresponding to water depths ranging from 8.5 to 10 m (Table 1).

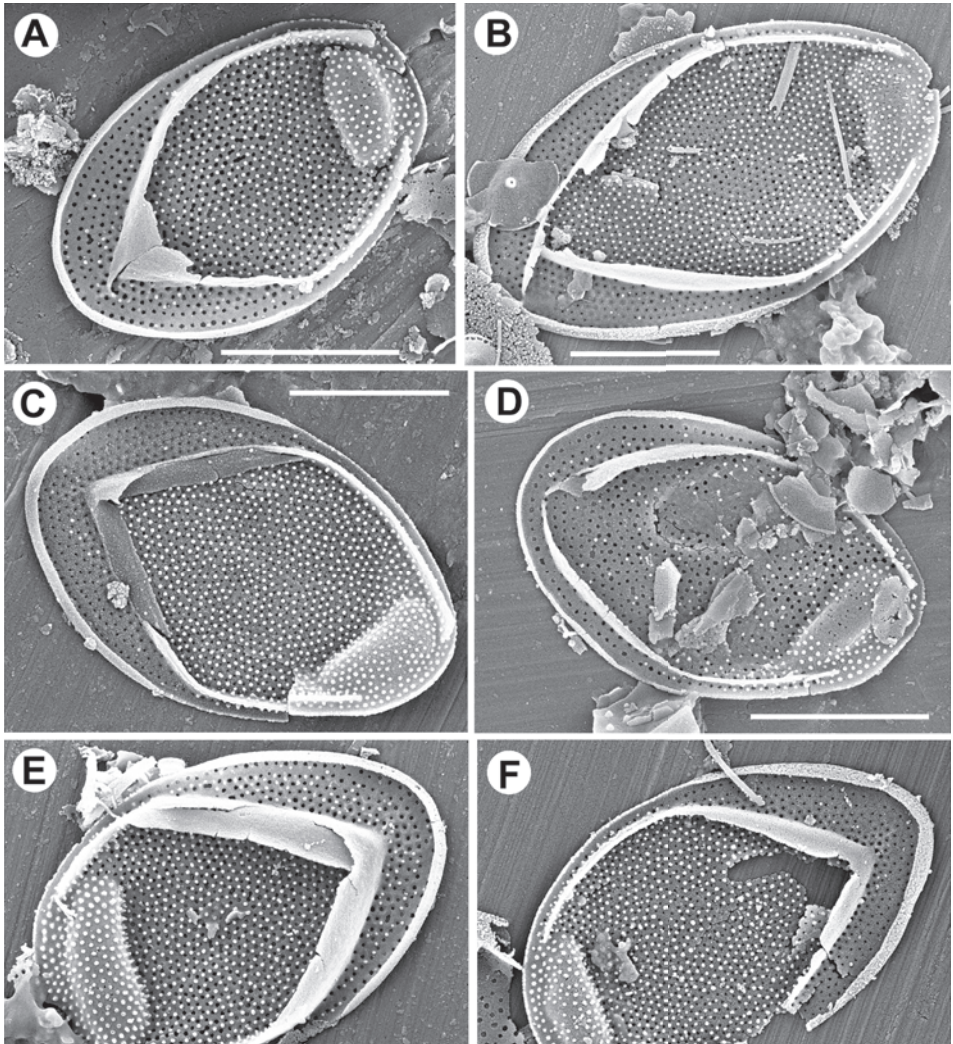


Fig. 4. Scales of *Mallomonas ampla*. Scales of this species have a thin posterior rim, evenly-spaced pores covering the base plate, a V-rib with arms that are continuous with the anterior submarginal ribs, small papillae covering the shield, and a laterally expanded and recessed dome. All scale bars = 2 μm .

***Mallomonas ampla* sp. nov.** Siver & Lott

Scales are large, oval with a perforated base plate, posterior rim, V-rib and a shallow dome structure (Figs 4A–F). Scales range in size from $4.7\text{--}6.7 \times 3.1\text{--}4.1 \mu\text{m}$. The posterior rim is thin, encircles approximately half of the scale perimeter and can be asymmetric, extending further along one side of the scale. The base plate pores extend across the scale and are more or less evenly spaced (Figs 5G–H). The base of the V-rib

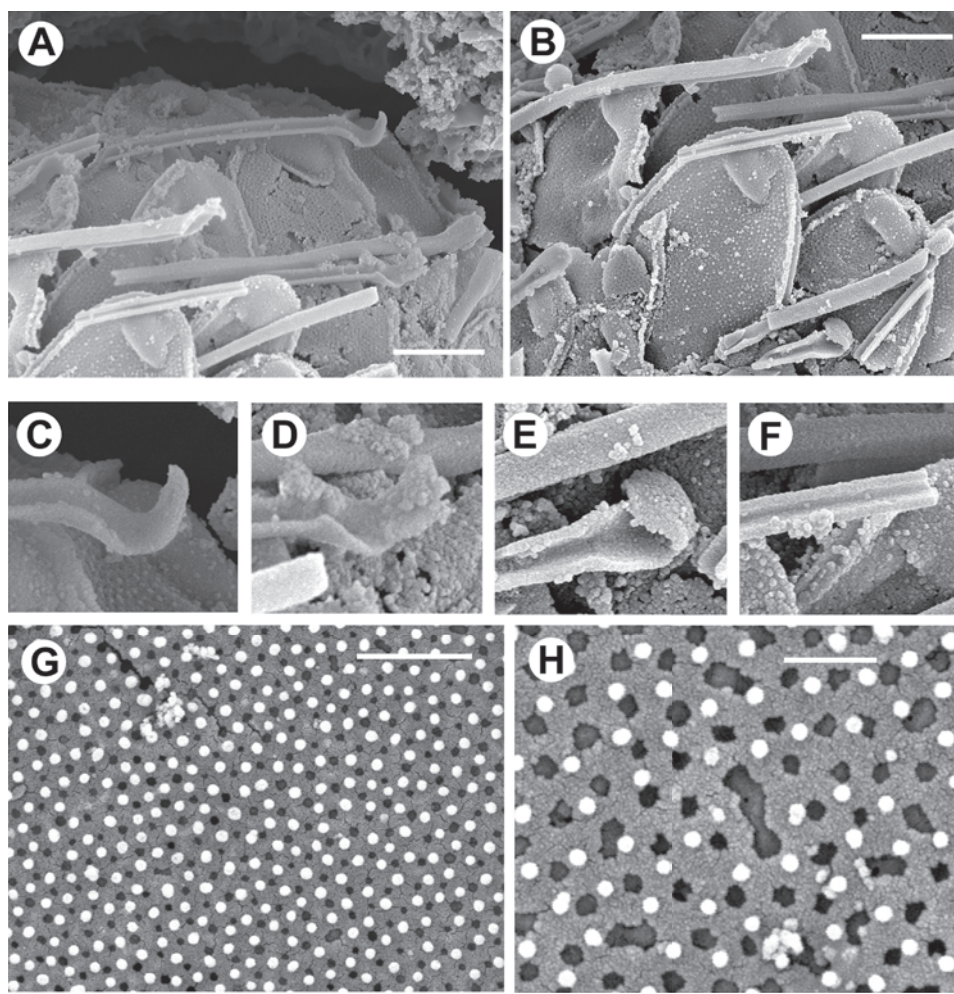


Fig. 5. Scales and bristles of *Mallomonas ampla*. A–B. A portion of an intact cell showing the overlapping nature of the scales and remains of bristles. C–F. Close-up images of specimens in A–B denoting the flattened and hooked nature of the bristle foot (C–E), and the rolled nature of the shaft (F). G–H. High magnification of the shield region of two scales illustrating the spacing of pores and papillae. Scale bars are 200 nm (H), 500 nm (G) and 2 μ m (A–B). C–F are magnified 250% relative to A and B.

is strongly hooded, but the arms of this structure are thin, curve and become continuous with the anterior submarginal ribs. The anterior submarginal ribs extend up to or partially around the dome. On scales with broader domes the anterior submarginal ribs are often extended into short wing-like structures. The domes are shallow, distinctly set back from the anterior margin, and vary in shape from circular, to oval to broadly oval (Fig. 4). The dome can be asymmetrically positioned (Fig. 4E). The shield, dome and sometimes the posterior flange are ornamented with small, evenly spaced papillae (Figs 5G–H).

The few intact bristles observed were short and ranged in length from 6–14 μm . The margins of the bristles are rolled to form an open groove yielding a U-shaped design in cross section (Figs 5A–B, F). The foot of the bristle is distinctly hooked and the lower portion of the shaft flattened (Figs 5C–E). The distal tip is slightly bifurcate.

Based on the remains of an intact scale coat (Figs 5A–B), the scales of *Mallomonas ampla* are arranged in overlapping spiral rows where each scale is overlapped by the scale positioned behind it within the same row and by scales in the spiral row below.

HOLOTYPE: Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, CANA 85744.

TYPE MATERIAL: Slurry prepared from section 17-2-94 of the Giraffe Pipe core by P.A.Siver and deposited at the Canadian Museum of Nature, CANA85744.

ICONOTYPUS: Figure 4A, uncovered from section 17-2-94 of the Giraffe Pipe core.

The epithet refers to the wide and broad nature of the dome. Remains of *Mallomonas ampla* were widespread and uncovered in ten sections of the core, corresponding to water depths ranging from 9.8 to 32.5 m.

Discussion

All contemporary *Mallomonas* species possessing a dome use this structure to secure one or more bristles to the scale covering (Siver 1991; Kristiansen 2002). The foot of the bristle is modified, usually flattened and bent at an angle, to fit under the dome such as to allow it to rotate as the organism swims, and to minimize contact with other scales. On most species, there is an inverted U-shaped opening along the margin of the dome from which the bristle emerges. Typically, when actively swimming, the bristles of *Mallomonas* species are rotated such that they are angled backwards, more or less parallel with the swimming axis, becoming streamlined with the longitudinal cell axis (Siver 1991; Kristiansen 2002). When the cell slows or stops, the bristles can rotate outward from the cell, often even pointing forward, perhaps acting as a flotation aid to maintain buoyancy. If the dome is recessed from the distal scale perimeter, as in the three Eocene species described above, rotational flexibility would be decreased since part of the shaft would underlie a portion of the scale. Thus, assuming it is more beneficial for the cell to have flexibility in bristle rotation, it is not surprising that these earlier dome structures became extinct and replaced with ones where the dome was positioned on the scale perimeter. In addition to the three species described here, we have seen other scale morphotypes in the Giraffe core with recessed domes. Unfortunately, although we know these addition scale types exist in the core, they are rare and we have not yet been able to find enough specimens to provide full descriptions. What we can say is that scales with recessed domes were common in the Eocene.

Of the three taxa described, *Mallomonas ampla* can be directly linked to a modern living species, *Mallomonas multisetigera* Dürschmidt. The body scales of both taxa are similarly shaped, have narrow posterior rims, base plate pores over the entire scale, surface papillae, and shallow, variable-shaped domes. In addition, on both taxa surface papillae are noticeably fewer on the posterior flange. As the name implies, scales of

Mallomonas multisetigera with broad domes can secure multiple bristles. Although we lack direct evidence, the equally broad nature of the domes on *M. ampla* were probably used to secure more than one bristle to the cell covering.

Mallomonas ampla differs from its modern congener in five respects. First, scales of *Mallomonas ampla* are significantly larger. Kristiansen (2002) gives a range in scale size for *M. multisetigera* of $2.5\text{--}5 \times 1.8\text{--}2.8\text{ }\mu\text{m}$, whereas most scales of *M. ampla* are larger than these upper limits. Second, the V-rib on modern specimens of *M. multisetigera* is, on average, more extensive than on *M. ampla* scales. Third, the base plate pores of *M. multisetigera* are noticeably larger on the posterior flange, a feature not obvious on *M. ampla*. Fourth, the domes of *M. ampla* scales are fully recessed from, and do not abut, the anterior scale margin. Fifth, bristles of *M. multisetigera* are completely rolled, have expanded distal tips, and lack the recurved hook-like foot found on *M. ampla* specimens. Overall, we view these differences as slight modifications in structure and it is clear that the *Mallomonas multisetigera* lineage, given section status by Asmund & Kristiansen (1986), is ancient, extending to at least the Eocene. Given the similarities in scale morphology and arrangement on the cell covering between *M. multisetigera* and *M. ampla*, it is likely that this lineage extends further back into the Cenozoic and possibly even into the Cretaceous.

Unlike *Mallomonas ampla*, the relationship of *M. media* to modern taxa is less clear. Scales of *Mallomonas media* possess a dome and a reinforced distal margin, but lack a submarginal rib complex. This combination of characters, especially with the highly recessed nature of the dome, is unique within the genus. There are only a few modern species of *Mallomonas*, for example *Mallomonas hamata* Asmund in the Sectio Heterospinae, that lack a submarginal rib complex, but have distinct domes (Siver 1991). However, other features of *M. media*, such as the secondary reticulation along the anterior margin, posterior rim struts and large size, suggests that it is probably not closely related to taxa within the Sectio Heterospinae. Except for the presence of the dome, scales of *M. media* share features with taxa in the Sectio Planae (Kristiansen 2002). Although there are distinct differences, the concentration of base plate pores in the posterior portion of the scale, coupled with a secondary layer on the distal end of the scale, found on *M. media* scales is slightly similar to *M. matvienkoe* (Matvienko) Asmund & Kristiansen. Perhaps, *M. media* represents an ancient taxon from the lineage that derived *M. hamata*, but it is equally likely that it represents a species within the Sectio Planae experimenting with formation of the dome. Lastly, the thick distal secondary reticulation found on *M. media* scales is strikingly similar to the one found on *Mallomonas insignis* Penard, but scales of the latter species have definite V-ribs and lack domes.

Like *Mallomonas media*, the relationship of *Mallomonas preisigii* relative to modern taxa is also unclear. Several characters, including the tripartite nature of the scale, shallow depth of the dome, distinct lack of base plate pores and the short posterior rim, resemble species within the Sectio Papillosa. Superficially, the scales of *M. preisigii* resemble those of *Mallomonas calceolus* Bradley and it may be that the two species are related. If, over geologic time, the dome shifted to the distal margin, it could have resulted in a taxon similar to *Mallomonas calceolus*.

Whether these three fossil species with recessed domes represent failed evolutionary experiments with domes, or are the ancient precursors to the numerous domed species found globally today, is unclear. Given the extensive nature of the Giraffe core and the exquisitely preserved wealth of microfossils it holds, coupled with remains from other geologically older kimberlite maar lakes also under investigation (e.g. the Wombat pipe), we are hopeful that additional scale types will be uncovered that will help piece together the evolutionary history of scaled chrysophytes.

Acknowledgements

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References

- ASMUND, B. & J. KRISTIANSEN 1986: The genus *Mallomonas* (Chrysophyceae). A taxonomic survey based on the ultrastructure of silica scales and bristles. – *Opera Botanica* **85**: 1–128.
- DORIA, G., D.L. ROYER, A.P. WOLFE, A. FOX, J.A. WESTGATE & D.J. BEERLING 2011: Declining atmospheric CO₂ during the late middle Eocene climate transition. – *Amer. J. Sci.* **311**: 63–75.
- GRANT, J., Y.I. TEKLE, O.R. ANDERSEN, D.J. PATTERSON & L.A. KATZ 2009: Multigene evidence for the placement of a heterotrophic amoeboid lineage *Leukarachnion* sp. among photosynthetic stramenopiles. – *Protist* **160**: 376–38.
- HARWOOD, D.M. & R. GERSONDE 1990: Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Wendell Sea). Part 2: Resting spores, Chrysophycean cysts, and endoskeletal dinoflagellate, and notes on the origin of diatoms. – *Proc. of the Ocean Drilling Program, Science Results, Leg 113, College Station, TX*, p. 403–426.
- HEAMAN, L.M., B.A. KJARSGAARD & R. CREASER 2004: The temporal evolution of North American kimberlites. – *Lithos* **76**: 377–398.
- JO, B.Y., W. SHIN, S.M. BOO, H.S. KIM & P.A. SIVER 2011: Studies on ultrastructure and three-gene phylogeny of the genus *Mallomonas* (Synurophyceae). – *Journal of Phycology* **47**: 415–425.
- KIM, H.S. & J.H. KIM 2008: *Mallomonas koreana* sp. nov. (Synurophyceae), a new species from South Korea. – *Nova Hedwigia* **86**: 469–476.
- KRISTIANSEN, J. 2002: The genus *Mallomonas* (Synurophyceae) – A taxonomic survey based on the ultrastructure of silica scales and bristles. – *Opera Botanica* **139**: 1–218.
- KRISTIANSEN, J. 2005: *Golden Algae: A Biology of Chrysophytes*. – A.R.G. Gantner Verlag K.G.
- KRISTIANSEN, J. & H.R. PREISIG 2007: *Chrysophyte and haptophyte algae*, pt. 2: Synurophyceae, Süßwasserflora von Mitteleuropa: vol. 1/2, (Ed. A. PASCHER) Spektrum Akademischer Verlag, Germany.
- NĚMCOVÁ, Y., P. BULANT & J. KRISTIANSEN 2011: *Mallomonas solea-ferrea* and *Mallomonas siveri* (Chrysophyceae/Synurophyceae): two new taxa from the Western Cape (South Africa). – *Nova Hedwigia* **93**: 375–384.
- NICHOLLS, K.H. & D.E. WUJEK 2003: Chrysophycean Algae. – In: WEHR, J.D. & R.G. SHEATH (eds.), *Freshwater Algae of North America*. – Academic Press. Pages 471–509.

- SIVER, P.A. 1991: The Biology of *Mallomonas*. Morphology, Taxonomy and Ecology. – Kluwer Academic Publishers. Dordrecht, The Netherlands.
- SIVER, P.A. 1995: The distribution of chrysophytes along environmental gradients: Their use as biological indicators. – In: SANDGREN, C., J. SMOL & J. KRISTIANSEN (eds.), Chrysophyte Algae: Ecology, Phylogeny and Development. – Cambridge Press, Pages 232–268.
- SIVER, P.A. 2003: The Synurophyceae. – In: WEHR, J.D. & R.G. SHEATH (eds.), Freshwater Algae of North America. – Academic Press, Pages 523–558.
- SIVER, P.A. & J.R. GLEW 1990: The arrangement of scales and bristles on *Mallomonas*: A proposed mechanism for the formation of the cell covering. – Can. J. Bot. **68**: 374–380.
- SIVER, P.A. & A.P. WOLFE 2005a: Eocene scaled chrysophytes with pronounced modern affinities. – Int. J. Plant Sci. **166**(3): 533–536.
- SIVER, P.A. & A.P. WOLFE 2005b: Scaled chrysophytes in Middle Eocene lake sediments from Northwestern Canada, including descriptions of six new species. – Nova Hedwigia, Beiheft **128**: 295–308.
- SIVER, P.A., A.M. LOTT & A.P. WOLFE 2009: Taxonomic significance of asymmetrical helmet and lance bristles in the genus *Mallomonas* (Synurophyceae) and their discovery in Eocene lake sediments. – European Journal of Phycology **44**(4): 447–460.
- SIVER, P.A. & A.P. WOLFE 2010: A whole-cell reconstruction of *Mallomonas porifera* Siver & Wolfe from the Eocene: Implications for the evolution of chrysophyte cell architecture. – Nova Hedwigia, Beiheft **136**: 117–126.
- SMOL, J.P. 1995: Application of chrysophytes to problems in paleoecology. – In: SANDGREN, C.D., J.P. SMOL & J. KRISTIANSEN (eds). Chrysophyte algae: Ecology, phylogeny and development. Cambridge University Press, Pages 232–250.
- WEE, J.L. 1982: Studies on the Synuraceae (Chrysophyceae) of Iowa. – Bibliotheca Phycologica, Band 62. J. Cramer Verlag, Braunschweig, West Germany.
- WILLIAMS, J.L. 1985: Miocene chrysophyte cysts from a lacustrine deposit in Northern Idaho. – In: SMILEY, C.J. (Ed.), Late Cenozoic history of the Pacific Northwest. – Allen Press, Lawrence, KS, Pages 61–66.
- WOLFE, A.P., M.B. EDLUND, A.R. SWEET & S. CREIGHTON 2006: A first account of organelle preservation in Eocene nonmarine diatoms: observations and paleobiological implications. – Palaios **21**: 298–304.
- WOLFE, A.P. & P.A. SIVER 2009: Three extant genera of freshwater thalassiosiroid diatoms from Middle Eocene sediments in northern Canada. – Am. J. Bot. **96**: 487–497.

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