

# *Mallomonas aperturae* sp. nov. (Synurophyceae) reveals that the complex cell architecture observed on modern synurophytes was well established by the middle Eocene

PETER A. SIVER\*

*Department of Botany, Connecticut College, New London, CT 06320, USA*

**ABSTRACT:** *Mallomonas*, the largest genus within the class Synurophyceae, consists of unicellular, flagellated, heterokont organisms each with an external cell covering comprised of species-specific overlapping siliceous scales. Most species also possess bristles, which are elongated needle-like siliceous structures that radiate out from the scale coat. A new fossil species, *Mallomonas aperturae*, is described from the middle Eocene Giraffe Pipe locality situated near the Arctic Circle in northern Canada. The new species possesses uniquely sculptured tripartite scales, each possessing a well-developed V-rib, dome and anterior wing-like extensions. The most unique feature is a large and elongated opening along the posterior side of the dome, a structure known only on scales of the modern species, *Mallomonas paludosa* (Synurophyceae). It is proposed that the opening on the dome may provide a means for securing bristles to the scales and aiding in bristle rotation. Remarkably, remains of cells with scales still in position were recovered from Giraffe Pipe mudstones, allowing for examination of the alignment and overlapping nature of scales making up the cell covering. The V-rib and anterior wing structures on the scale surface were used to precisely space and orient the scales, indicating that the ability to produce a highly structured cell covering, a hallmark of synurophyte algae, was well established by the middle Eocene. This evidence further supports the hypothesis that fossil species bearing scales with well-developed V-ribs can be used as a marker for the ability of the organism to build a highly organised cell covering.

**KEY WORDS:** Eocene, Extinct, Fossil, Giraffe Pipe, *Mallomonas*, New species, Synurophyceae, Synurophytes, V-rib

## INTRODUCTION

The Synurophyceae is a clade of ecologically successful heterokont algae characterised by distinctive siliceous scales that form a highly organised covering around the cell (Kristiansen 2005; Siver 2015a). Synurophytes are unicellular or colonial, motile organisms with one or two emergent flagella. Cells are completely covered with overlapping scales except for the opening from which the one or two flagella emerge. Scale design is diagnostic at the species level, and, coupled with the fact that many species grow best under specific environmental conditions, scale remains in sediments can serve as bioindicators of past environments (Stevenson & Smol 2015; Arseneau *et al.* 2016). Most species have different types or shapes of scales at each end of the cell relative to those known as body scales that cover the main portion of the cell. In addition to scales, most species of the large genus *Mallomonas* possess a second type of siliceous structure, the bristle. Bristles are thin, elongate structures with one end tucked under the apical end of a scale such that they radiate outwards from the cell.

All scales possess a base plate that is perforated with pores and an upturned rim, known as the posterior rim, that bends up and over the base plate along the proximal margin (Siver 1991; Kristiansen 2005). Many species have scales with additional features, including secondary layers of silica deposited onto the base plate that form distinct designs, and spines or wings extending past the base plate (Fig. 1).

Unique to some species of *Mallomonas* are scale structures that produce highly organised cell coverings, including the V-rib and dome. The V-rib is a prominent V-shaped ridge of silica positioned on the base plate, forming the boundary between the shield and the posterior flange. The dome is a raised cavity along the distal end of the scale into which the proximal end of the bristle, or foot, is attached. The bristle shaft emerges from an inverted U-shaped opening along the distal margin of the dome. Scales that have a dome and V-rib are termed tripartite scales (Harris 1953), as they have three main regions: dome, shield and posterior flange. Siver and Glew (1990) described the manner in which scales overlap on the cell covering (Fig. 2) and further hypothesised that the V-rib structure served as a means to precisely align the scales.

Although recent studies differ as to whether Synurophyceae form a distinct class of heterokonts (Yang *et al.* 2012) or a clade nested within Chrysophyceae (Synurales; Škaloud *et al.* 2013), all concur that synurophytes are monophyletic. There are currently just over 220 species or subspecific taxa recognised within the class Synurophyceae based on characteristics of the siliceous components as observed with electron microscopy (EM) and largely confirmed with more recent molecular analyses (Jo *et al.* 2013, 2016; Siver *et al.* 2015). Additional species have been described based on light microscope (LM) observations, but not linked to taxa described with EM (Kristiansen 2002). Some of the species based on LM may indeed be different from those known with EM; whereas, others may overlap, and these differences may never be resolved.

The evolutionary history of the synurophytes is poorly understood due in large part to a meager fossil record. Until the recent discovery of the Giraffe Pipe locality in the

\* Corresponding author (pasiv@conncoll.edu).

DOI: 10.2216/17-112.1

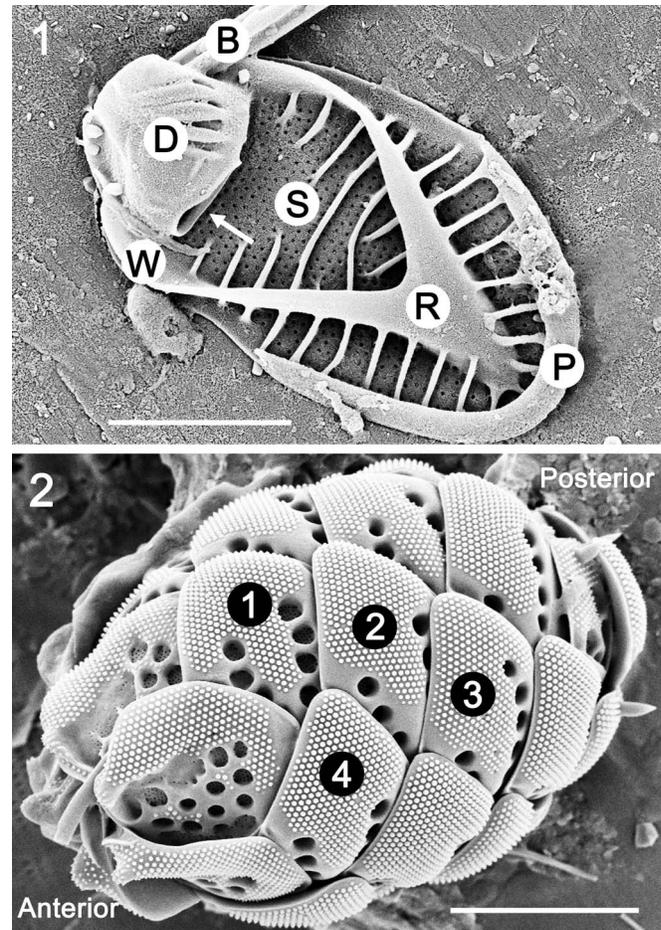
© 2018 International Phycological Society

Canadian Arctic dating to the middle Eocene, there was no geologic record of synurophyte scales or bristles older than Holocene (Siver & Wolfe 2005; Siver *et al.* 2015). The wealth of well-preserved specimens from the Giraffe Pipe locality confirms that the group was well established in freshwater ecosystems by the middle Eocene, and subsequent findings have yielded preliminary insights into how scales, bristles and cells have evolved over time (Siver *et al.* 2009; Siver & Wolfe 2010; Siver & Lott 2012). Three additional observations are noteworthy with respect to the current study. First, relaxed molecular clock methods calibrated with Giraffe Pipe microfossils show that the synurophytes originated approximately 156 Ma, with the primary genera *Mallomonas* and *Synura* diverging during the lower Cretaceous at 130 Ma (Siver *et al.* 2015). Second, the V-rib is an important character in the evolutionary history of the Synurophyceae. Jo *et al.* (2013) and Siver *et al.* (2015) showed that *Mallomonas* diverged into two major clades in the Cretaceous, one clade containing species with scales lacking a V-rib and the other with scales possessing a V-rib. Third, one out of every three scale types uncovered from the Giraffe Pipe locality has modern analogs. This supports the concept of prolonged morphological stasis (Siver *et al.* 2009, 2013); whereas, most extinct species lacking modern counterparts had significantly larger scales and surface areas over four times the mean for modern species (Siver 2015b). The purpose of this paper is to describe a new fossil species of *Mallomonas* from the Giraffe Pipe core, formally referred to as *Mallomonas* GP 17 (Siver *et al.* 2015), that is closely aligned with the modern species, *Mallomonas paludosa* Fott. Remarkably, remains of cells of the fossil species reveal the original arrangement and organisation of scales on the cell, allowing for a direct comparison of the form of the cell covering between modern and Eocene synurophytes, and yield support for the hypothesis that the V-rib spaces and orientates the scales on the scale covering.

## MATERIAL AND METHODS

The Giraffe Pipe core was sectioned and stored in core boxes (Wolfe *et al.* 2006). Samples from the core are identified with a three-part number (Siver 2015b). The first number represents the core box. The larger the core box number, the deeper the section is within the core. Core box 11 represents the top and end of the lacustrine phase within the core sequence. 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 is the measurement in centimeters down from the top of a core length. For example, sample 13-1-130 represents a sample taken from 130 cm down along the core length positioned in channel 1 from box 13. This study includes samples from sections 13-1-130, 13-2-120, 14-1-40, 14-1-60, 14-2-32, 15-1-15 and 16-2-22, representing 10.92 m of core length estimated to cover several tens of thousands of years.

Mudstone fragments (50–100 mg) from each section of the Giraffe Pipe core examined were oxidised using 30% H<sub>2</sub>O<sub>2</sub> under low heat for a minimum of an hour and rinsed with



**Figs 1, 2.** SEM images.

**Fig. 1.** Tripartite siliceous scale with emerging bristle from the modern taxon, *Mallomonas paludosa*. The parts include dome (D), shield (S), V-rib (R), posterior rim (P), anterior wings (W) and bristle (B). White arrow indicates opening at base of dome. Scale bar = 2  $\mu$ m.

**Fig. 2.** Whole cell of *Mallomonas lichenensis* illustrating precise organisation of cell covering and overlapping pattern of scales found on most species within the genus. Anterior end where flagellum emerges and posterior end are indicated. Scales marked 1, 2 and 3 are positioned in the same spiral row, with scale 1 abutting the scale that terminates at the flagellar pore. Scale 2 is overlapped by the scale behind it in the same row (scale 3) and by scale 4 situated in the spiral row above it. Scale bar = 5  $\mu$ m.

distilled water, and the slurries were stored in glass vials at 4°C. This mild oxidation procedure resulted in separation of many siliceous microfossils from the mudstone matrix, as well as small remaining fragments often containing numerous microfossils. An aliquot of each slurry was air-dried onto a piece of heavy-duty aluminum foil. The aluminum foil samples were trimmed and attached to aluminum stubs with Apiezon wax. In addition, fragments of rocks were mounted directly onto scanning electron microscope (SEM) stubs using double-sided carbon tape. Silver paint was used to connect the base of each rock fragment to the stub to reduce charging. All samples were coated with a mixture of gold and palladium for 2 min with a Model E sputter coater (Polaron, Hertfordshire, UK). Samples were examined with a Leo 982 FESEM (Zeiss, Jena, Germany) or an FEI Nova NanoSEM

450 FESEM (FEI Corporation, New York, New York USA). Measurements of scales were taken directly from electron micrographs.

Detailed descriptions of the Giraffe Pipe locality are given in Siver *et al.* (2015) and Wolfe *et al.* (2017) and are only briefly discussed herein. The Giraffe Pipe locality (64°44'N, 109°45'W) represents a kimberlite diatreme that was emplaced into the Slave Craton in the Northwest Territories of Canada approximately 47.8 Ma during the middle Eocene (Siver & Wolfe 2005; Wolfe *et al.* 2006). Subsequent to emplacement, the diatreme crater became an aquatic environment and slowly in-filled with a sequence of lacustrine and later paludal sediments. The sediment strata were capped by Neogene glacial deposits (Siver & Wolfe 2005; 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, collared at a 47° angle, was uncovered from the Giraffe Pipe maar in 1999 by BHP Billiton Inc. (Siver & Wolfe 2009). A total of 113.1 m of the core contain well preserved stratified organic sediment, including 68.3 m of lacustrine mudstones, overlain with 44.8 m of peaty and terrestrial remains. The lake sediments were all deposited during the middle Eocene. The water body formed within the crater persisted for hundreds of thousands of years, varying in depth and physical attributes over time, slowly in-filling, and eventually transitioning to a terrestrial environment.

## RESULTS

### *Mallomonas aperturae* Siver *sp. nov.*

Figs 3–14

**DESCRIPTION:** Scales were large, broadly ovate with a posterior rim, V-rib, anterior wings, dome, lateral incurvings, and additional secondary structures (Figs 3–8). Scales ranged in size from 5.9–8.8  $\mu\text{m} \times 3\text{--}4.3 \mu\text{m}$  ( $n = 16$ ), with mean values of 6.7  $\mu\text{m}$  and 3.8  $\mu\text{m}$ . The base plate was covered with more or less evenly spaced pores that became aligned in transverse rows on the shield. The posterior rim slightly overarched the base plate, encircled about half of the scale perimeter and terminated at the lateral incurvings. The V-rib was large and consisted of an extensive hood and arms that extended to the scale perimeter near the lateral incurvings, then curved slightly and terminated along the base of the anterior wings (Figs 3–8). The anterior flanges extended to form wings that were elevated above the base plate and terminated along the sides of the dome. The dome was large with a well-formed inverted U-shaped opening on the right side from which the bristle emerged (Figs 5, 6). On some scales one to two (sometimes three) parallel ribs obliquely crossed the dome and terminated on the left side of the U-shaped opening (Figs 4–6). Transverse dome ribs were lacking on some scales (Fig. 3). The dome had a patch of tiny pores on the left side, opposite the bristle opening (arrow, Fig. 9). The most unique feature of the dome was a large, elongate, reinforced opening situated at the base along the shield (arrows, Figs 3, 4). The dome opening spanned the length of the dome. The posterior flange was large, covered with six to eight rows of pores that had a similar diameter to those on the shield, and a series of parallel and more or less equally spaced ribs that attached to the V-rib and extended to the posterior rim (Figs 3–8). Some ribs were forked or branched. On most scales there was a series of transverse ribs on the distal portion of the shield behind the dome (Figs 4–6, 8). The transverse shield ribs were equally spaced with two rows of base plate pores between each pair. On some scales, the transverse ribs extended farther down the shield yet on others were

lacking altogether.

Bristle structure was unknown. Cysts were spherical to slightly oval and approximately 17  $\mu\text{m}$  in diameter, were covered with small evenly spaced siliceous bumps (scabrae) and had a simple pore with a shallow and slightly raised collar (Figs 12–14). Scales were well organised in spiral rows on the cell covering such that the domes were equally spaced over the cell (Fig. 12). The right anterior wing aligned with and rested atop the left side of the V-rib hood on the scale in front of it within the same spiral row. The left anterior wing aligned with and rested atop the right side of the V-rib hood on a scale in the neighbouring spiral row. This alignment spaced the domes and therefore the emergent bristles approximately 4–5  $\mu\text{m}$  apart in each direction.

**HOLOTYPE SPECIMEN:** Portion of a single gathering of cells on the SEM stub deposited at the Canadian Museum of Nature, CANA 126426. Material from section 16-2-22 of the Giraffe Pipe core sampled and collected by P.A. Siver. Figs 3–8 are representative specimens from the gathering.

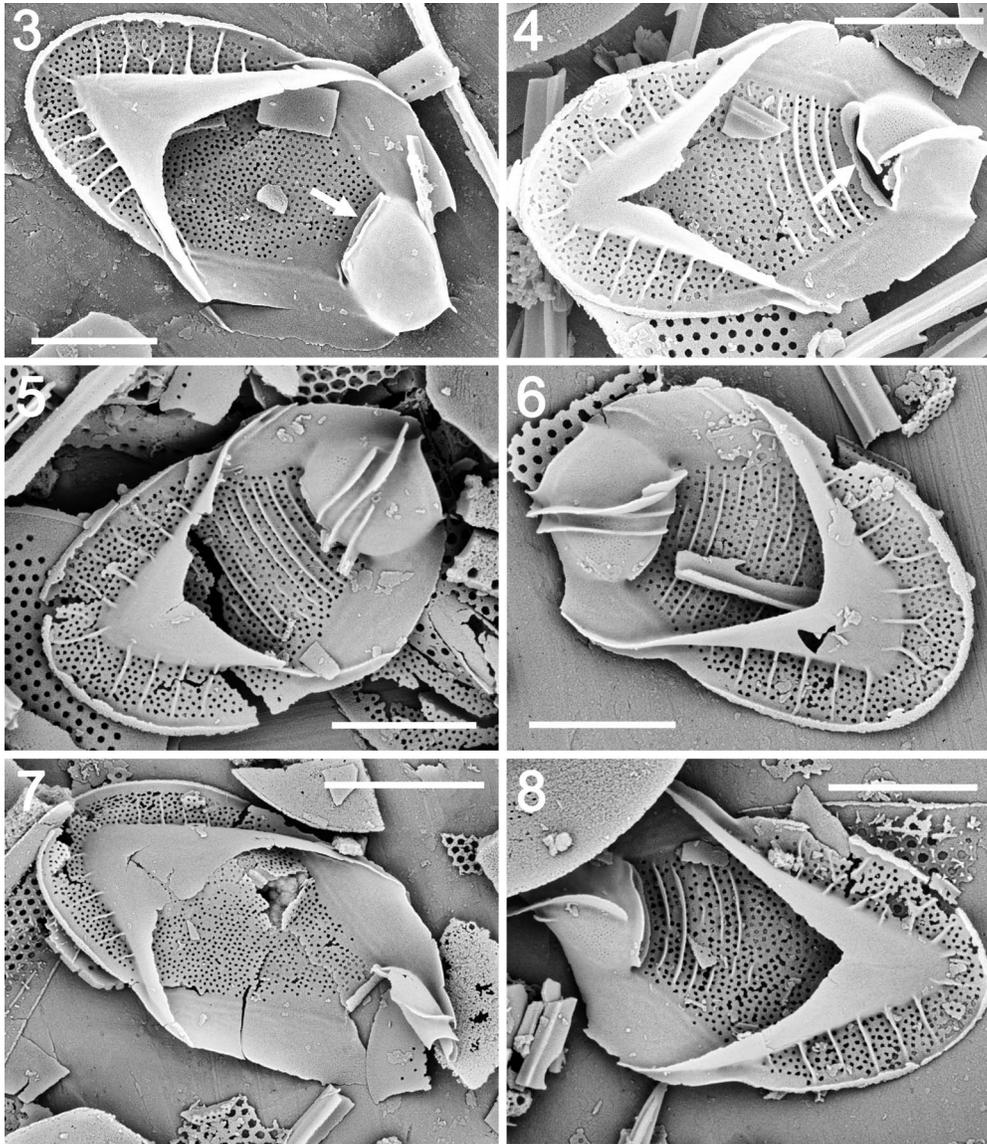
**ETYMOLOGY:** *Aperturæ* (Latin = opening or aperture) refers to the large opening or aperture at the base of the dome.

### Distribution and co-occurring taxa

In addition to section 16-2-22 of the Giraffe Pipe core that represents the holotype, *M. aperturae* was also found in 13-1-130, 13-2-120, 14-1-40, 14-1-60, 14-2-32 and 15-1-15. All seven samples were dominated with synurophyte microfossils, with lesser numbers of diatoms representing *Eunotia* spp.; *Oxyneis apporrecta* Siver, Wolfe & Edlund; and *Nupela mutabilis* Siver, Wolfe & Edlund. Other common to abundant synurophytes included *Mallomonas lichenensis* Conrad; *M. porifera* Siver & Wolfe; *M. lancea* Siver, Lott & Wolfe; *M. GP18* (Siver *et al.* 2015); *M. multiunca* v. *pocosinensis* Siver; *Synura cronbergiae* Siver; and *Synura macracantha* (Petersen & Hansen) Asmund. All samples also contained multiple euglyphid species, sponge spicules and numerous chrysophyte cysts.

## DISCUSSION

*Mallomonas aperturae* was first reported by Siver *et al.* (2015) as *Mallomonas* GP17. Since that publication, numerous additional specimens have been studied, including cysts containing attached scales, allowing for examination of the original scale covering. This taxon belongs in the section *Leboimianae* and is clearly most closely aligned with the modern species, *M. paludosa*. Both species have tripartite scales with large V-ribs and domes, transverse and parallel ribs across the shield, large posterior flanges with parallel struts and, most important, the distinctive opening along the posterior border of the dome. In fact, the large opening found on the domes of these two species is unique within the genus. *Mallomonas aperturae* scales are slightly larger (14%) than those of *M. paludosa* reported from Connecticut populations (Siver 1991) but within the range given by Kristiansen (2002) and in both cases yielding similar length:width ratios. Scales of *M. aperturae* differ from its modern counterpart in seven important ways. First, the transverse shield ribs are fewer in number, restricted to the anterior portion of the shield, and are more closely spaced and separated by two (instead of usually three) rows of pores. Second, the hood on the V-rib is much larger and



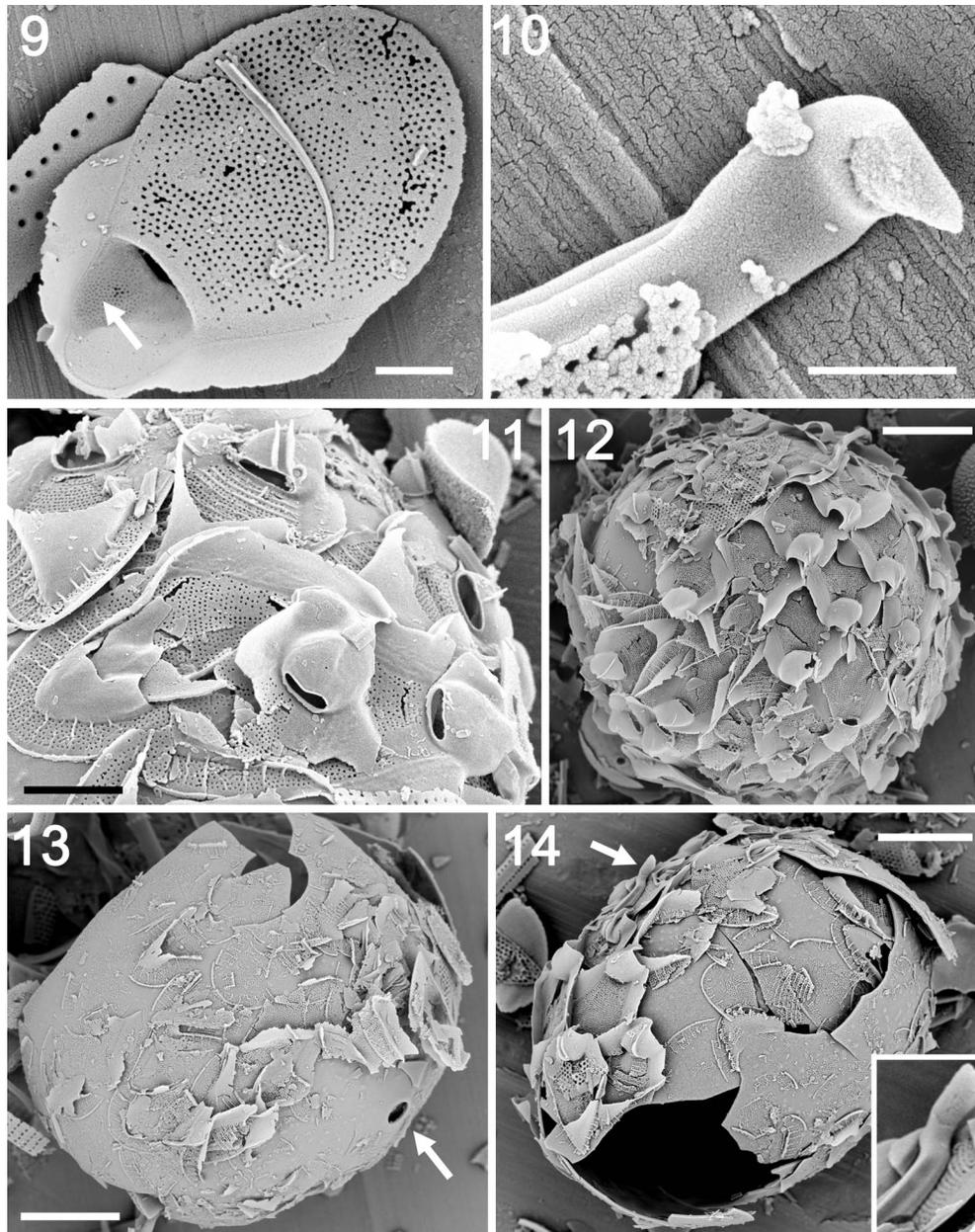
**Figs 3–8.** Diversity of scale types representing fossil species *Mallomonas aperturae*, observed with SEM. All scales are from the Holotype specimen. Each specimen illustrates the large dome and V-rib, shallow posterior rim, parallel ribs on posterior flange and extensive anterior wings. Specimens in Figs 4–6 and 8 possess ribs on the shield and dome; whereas, they are lacking on specimens in Figs 3, 7. Note the distribution of pores on the base plate and wide posterior flange. The large opening on the base of the dome is best seen in Figs 3, 4 (white arrows). Scale bars = 2  $\mu$ m (Figs 3–6, 8) or 3  $\mu$ m (Fig. 7).

more pronounced on the fossil species. Third, the arms of the V-rib terminate at the scale margin on *M. aperturae* and are not continuous with the anterior submarginal ribs. Fourth, the wings on the fossil taxon are considerably larger. Fifth, *M. aperturae* has fewer ribs on the dome. Sixth, the lateral incurvings are more pronounced on the fossil species. Lastly, the opening on the posterior of the dome on the fossil form is, on average, longer and often spans the length of the dome. Despite the differences, both taxa are clearly closely related.

*Mallomonas aperturae* also bears some resemblance to the other modern species within section Leboimeanae, *Mallomonas leboimeae* Bourrelly. However, a distinctive opening at the base of the dome has not been reported for *M. leboimeae*, and it is unclear from published micrographs if this structure is present. In addition, compared to *M. leboimeae* scales, the

V-rib hood and anterior wings are much more extensive on scales of *M. aperturae*, and scales of the latter taxon are significantly smaller and have a different secondary structure on the shield.

Uncovered remains of whole cells where the scales remain largely intact are rarely, if ever, observed in paleolimnological studies using sediments that are hundreds to thousands of years old. Normally, the scale coat disarticulates upon either cyst formation or with death of the cell. This makes the specimens uncovered from the Giraffe Pipe mudstones surprising and unique. Furthermore, intact scale coats are observed only on cells that had formed cysts. Apparently, the internal siliceous cyst provided the mould onto which the scales were pressed and ultimately fused together during formation of the mudstone matrix. Scales



**Figs 9–14.** Specimens of fossil species *Mallomonas aperturae*, observed with SEM.

**Fig. 9.** Undersurface of scale showing distribution of base plate pores, delineation of anterior wings and patch of small pores (white arrow) on dome in relation to large opening. Scale bar = 1  $\mu\text{m}$ .

**Fig. 10.** Foot of bristle with upturned end believed to be from this species. Scale bar = 500 nm.

**Fig. 11.** Group of scales fused onto a cyst with large openings on domes. Scale bar = 2  $\mu\text{m}$ .

**Fig. 12.** Cyst with attached scales arranged in original overlapping pattern found on cell surface. Note that anterior wings of scales rest atop V-ribs of neighboring scales. Scale bar = 5  $\mu\text{m}$ .

**Fig. 13.** Cyst with a few attached scales. Note slightly raised collar (arrow) and small widely spaced bumps on cyst wall. Scale bar = 5  $\mu\text{m}$ .

**Fig. 14.** Cyst with attached scales arranged in original overlapping pattern found on cell surface. Broken piece of bristle with angled foot (arrow) enlarged in insert may belong to this taxon. Scale bar = 5  $\mu\text{m}$ .

remain attached even after treatment with acids used to remove organic compounds. The environment within the crater containing the Giraffe Pipe water body likely resulted in an anoxic and essentially undisturbed hypolimnion, aiding the cell components to remain intact. Indeed, remains of whole cells of other synurophytes, such as *Mallomonas porifera* (Siver & Wolfe 2010), and euglyphid tests complete

with numerous siliceous plates (Barber *et al.* 2013) have been reported from Giraffe Pipe mudstones. However, this is the first report of the scales not only remaining together but also retaining their original positions and orientations on the cell covering.

More importantly, the intact specimens allow for examination and comparison of the cell covering design between

the fossil and modern forms. The most common pattern of scale overlap on modern *Mallomonas* species is the arrangement of the scales in spiral rows around the cell with their longitudinal axes positioned such that the distal end (i.e. the end with the dome) faces between 45° and 90° (perpendicular) with respect to the long axis of the cell as measured from the flagellar end (Siver & Glew 1990; Siver 1991). A very few species (e.g. *Mallomonas retrorsa* Siver and *M. baskettei* Siver & Lott) reverse this pattern whereby the posterior rim side of the scale faces the flagellar end of the cell (Siver 1988; Siver & Lott 2016). Each scale is typically overlapped by the scale positioned behind it in the same spiral row and by scales situated in the spiral row above it. That is, the spiral rows overlap from the flagellar to posterior ends of the cell. For example, the scale marked #2 on the whole cell illustrated in Fig. 2 is overlapped by scale #3 behind it in the same spiral row and by scale #4 in the spiral row above it. Scale #2, in turn, overlaps the scale in front of it in the same spiral row, scale #1. Furthermore, the V-rib structure is believed to aid in the precise spacing of the scales and therefore also the bristles (Siver 1991; Siver *et al.* 2015).

The spacing of scales on the cell covering of *M. apertureae*, as revealed from the Eocene specimens, shows a highly organised pattern with precise alignment where each wing of the scale rests atop an arm of the V-rib on a neighbouring scale. The alignment supports the concept that the function of the V-rib is indeed to align and space both the scales and the bristles on the cell. The arrangement further provides evidence that for some species the anterior wings are also intricately involved in organizing the cell covering. Given these findings, it is concluded that fossil species with scales that feature a well formed V-rib also had a well-organised cell covering.

The pattern by which scales were overlapped on *M. apertureae* is similar to that expressed by modern species. However, it is difficult to determine in which direction the individual scales were oriented within each row since the position of the flagellar pore is not known. Often, specialised scales surround the flagellar pore, but no such scales are obvious for *M. apertureae*. As already noted, each scale is overlapped by the scale positioned behind it in the same row and by a scale in the adjoining spiral row towards the flagellar end of the cell (Siver 1991; Gusev *et al.* 2017). That is, the spiral rows overlap each other from the flagellar end of the cell to the posterior end. If this pattern was the same for the fossil *M. apertureae*, then the anterior ends of the scales were facing towards the posterior of the cell. Given the pattern observed on specimens of *M. apertureae*, in order for the dome end of the scales to be oriented towards the flagellar end of the cell, the spiral rows were overlapped in an opposite manner, from the posterior end of the cell to the anterior end. Regardless, the organised cell covering that is a hallmark of the synurophytes was highly evolved by the middle Eocene.

The function of the large elliptical opening on the dome remains unclear. It is proposed that this structure served to either help secure the bristle to the dome structure or allow the bristle to rotate more freely. An upturned end or angled foot of the bristle could fit into the opening and help secure the bristle in place. This could be especially useful if the U-shaped opening of the dome faced the posterior of the cell.

Although it was not possible to definitively determine the type of bristle belonging to *M. apertureae*, specimens with upturned (Fig. 10) and angled (arrow, Fig. 14) feet were present in the samples.

The function of bristles for *Mallomonas* species is unclear, but they have been proposed as a deterrent to predation (Kristiansen 2005) or as a means to enhance flotation (Siver 2015a). That all scales on *M. apertureae* possessed a dome and the scales were equally spaced on the cell covering, means that bristles extended outward from the cell in all directions. Extended bristles would increase the cell's ratio of surface area to volume and effectively increase buoyancy of the cell. Extended bristles would likewise increase the effective size of the cell, making it more difficult to be eaten by zooplankton.

In summary, *M. apertureae* possessed tripartite scales with well-formed wings, V-ribs and domes, which formed a highly organised covering around the cell. The V-rib and anterior wings were integral in spacing the scales on the cell and therefore also in spacing of the radiating bristles. This finding supports the hypothesis that extinct species with scales possessing a V-rib had well-organised cell coverings. The description of *M. apertureae* further demonstrates that synurophyte algae were well established by the middle Eocene and clearly evolved prior to this geologic period.

## ACKNOWLEDGEMENTS

This work was funded with support to PAS from the US National Science Foundation (NSF) (DEB-1144098; EAR-1725265) and by an NSF equipment grant (NSF#1126100) to Marie Cantino (University of Connecticut). The work was performed, in part, at the Biosciences Electron Microscopy Facility of the University of Connecticut. The author thanks Anne Lott for help with sample preparation and James Romanow and Xuanhao Sun for assistance with the SEM facilities.

## REFERENCES

- ARSENEAU K.M.A., DRISCOLL C.T., CUMMINGS C.M., POPE G. & CUMMING B.F. 2016. Adirondack (NY, USA) reference lakes show a pronounced shift in chrysophyte species composition since ca. 1900. *Journal of Paleolimnology* 56: 349–364.
- BARBER A., SIVER P.A. & KARIS W. 2013. Euglyphid testate amoebae (Rhizaria: Euglyphida) from an Arctic Eocene waterbody: evidence of evolutionary stasis in plate morphology for over 40 million years. *Protist* 164: 541–555.
- GUSEV E.S., SIVER P.A. & SHIN W. 2017. *Mallomonas bronchartiana* Compere revisited: two new species described from Asia. *Cryptogamie, Algologie* 38: 3–16.
- HARRIS K. 1953. A contribution to our knowledge of *Mallomonas*. *Botanical Journal of the Linnean Society* 55: 88–102.
- HEAMAN L.M., KJARSGAARD B.A. & CREASER R.A. 2004. The temporal evolution of North American kimberlites. *Lithos* 76: 377–397.
- JO B.Y., SHIN W., KIM H.S., SIVER P.A. & ANDERSEN R.A. 2013. Phylogeny of the genus *Mallomonas* (Synurophyceae) and descriptions of five new species on the basis of morphological evidence. *Phycologia* 52: 266–278.
- JO B.Y., KIM J.I., ŠKALOUD P., SIVER P.A. & SHIN W. 2016. Multigene phylogeny of *Synura* (Synurophyceae) and descrip-

- tions of four new species based on morphological and DNA evidence. *European Journal of Phycology* 51: 413–430.
- 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*. Koeltz Scientific Books, Königstein, Germany. 167 pp.
- SIVER P.A. 1988. *Mallomonas retrorsa* sp. nov., a new species of scaled-Chrysophyceae with backwards orientated scales. *Nordic Journal of Botany* 8: 319–323.
- SIVER P.A. 1991. *The biology of Mallomonas: morphology, taxonomy and ecology*. Kluwer Academic Publishers, Dordrecht, Netherlands. 230 pp.
- SIVER P.A. 2015a. The Synurophyceae. In: *Freshwater algae of North America: ecology and classification* (Ed. by J.D. Wehr, R.G. Sheath & J.P. Kociolek), pp. 605–650. Academic Press, San Diego, California.
- SIVER P.A. 2015b. *Mallomonas schumachii* sp. nov., a fossil synurophyte bearing large scales described from an Eocene maar lake in Northern Canada. *Nova Hedwigia* 101: 285–298.
- SIVER P.A. & GLEW J.R. 1990. The arrangement of scales and bristles on *Mallomonas* (Chrysophyceae) – a proposed mechanism for the formation of the cell covering. *Canadian Journal of Botany* 68: 374–380.
- SIVER P.A. & LOTT A.M. 2012. Fossil species of *Mallomonas* from an Eocene Maar lake with recessed dome structures: early attempts at securing bristles to the cell covering? *Nova Hedwigia* 95: 517–529.
- SIVER P.A. & LOTT A.M. 2016. Descriptions of two new species of Synurophyceae from a bog in Newfoundland, Canada: *Mallomonas baskettii* sp. nov. and *Synura kristiansenii* sp. nov. *Nova Hedwigia* 102: 501–511.
- SIVER P.A. & WOLFE A.P. 2005. Eocene scaled chrysophytes with pronounced modern affinities. *International Journal of Plant Sciences* 166: 533–536.
- SIVER P.A. & WOLFE A.P. 2009. Tropical ochrophyte algae from the Eocene of Northern Canada: a biogeographic response to past global warming. *Palaios* 24: 192–198.
- SIVER P.A. & WOLFE A.P. 2010. A whole-cell reconstruction of *Mallomonas porifera* Siver and Wolfe from the Eocene: implications for the evolution of chrysophyte cell architecture. *Nova Hedwigia, Beiheft* 136: 117–127.
- SIVER P.A., LOTT A.M. & WOLFE A.P. 2009. Taxonomic significance of asymmetrical helmet and lance bristles in the genus *Mallomonas* and their discovery in Eocene lake sediments. *European Journal of Phycology* 44: 447–460.
- SIVER P.A., WOLFE A.P., ROHLF J., SHIN W. & JO B.Y. 2013. Combining geometric morphometrics, molecular phylogeny, and micropaleontology to assess evolutionary patterns in *Mallomonas* (Synurophyceae, Heterokontophyta). *Geobiology* 11: 127–138.
- SIVER P.A., JO B.Y., KIM J.I., SHIN W., LOTT A.M. & WOLFE A.P. 2015. Assessing the evolutionary history of the class Synurophyceae (Heterokonta) using molecular, morphometric, and paleobiological approaches. *American Journal of Botany* 102: 921–941.
- ŠKALOUD P., KRISTIANSEN J. & ŠKALOUDOVÁ M. 2013. Developments in the taxonomy of silica-scaled chrysophytes – from morphological and ultrastructural to molecular approaches. *Nordic Journal of Botany* 31: 385–402.
- STEVENSON R.J. & SMOL J.P. 2015. Use of algae in ecological assessments. In: *Freshwater algae of North America: ecology and classification* (Ed. by J.D. Wehr, R.G. Sheath & J.P. Kociolek), pp. 921–962. Academic Press, San Diego, California.
- WOLFE A.P., EDLUND M.B., SWEET A.R. & CREIGHTON S. 2006. A first account of organelle preservation in Eocene nonmarine diatoms: observations and paleobiological implications. *Palaios* 21: 298–304.
- WOLFE A.P., REYES A.V., ROYER D.L., GREENWOOD D.R., DORIA G., GAGEN M., SIVER P.A. & WESTGATE J.A. 2017. Concurrent paleoclimate and CO<sub>2</sub> reconstruction from the sedimentary fill (latest middle Eocene) of a subarctic kimberlitic maar crater. *Geology* 45: 619–622.
- YANG E.C., BOO G.H., KIM H.J., BOO S.M., ANDERSEN R.A. & YOON H.S. 2012. Supermatrix data highlight the phylogenetic relationships of photosynthetic stramenopiles. *Protist* 163: 217–231.

Received 11 October 2017; accepted 25 November 2017