

## A first account of *Mallomonas* specimens representing section Torquatae from the fossil record: descriptions of two species from the Eocene

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**Abstract:** *Mallomonas* Perty is a genus of photosynthetic and heterokont algae belonging to the order Synurales, within the class Chrysophyceae. It is the most speciose genus within the Synurales, and consists of motile unicells with a cell covering composed of highly sculptured and precisely arranged siliceous scales and bristles. The genus is a common and often important element of planktic habitats with species found in numerous types of aquatic environments. *Mallomonas* is divided into 19 sections, many of which are further divided into multiple series. The section Torquatae is one of the larger sections of the genus comprised of species with a distinctive arrangement of siliceous components and a unique forward projecting apical end, the collar. With the exception of a few localities, very little is known about the evolutionary history of the Synurales, including *Mallomonas*. In this study, we describe two new species belonging to section Torquatae from the early Eocene, which represent the first taxa for this section known from the fossil record. Because the general characteristics of all siliceous components are similar to those on modern species, it is clear that this section of the *Mallomonas* lineage was well-evolved by the Eocene.

**Key words:** Eocene, Giraffe Pipe, *Mallomonas*, new species, section Torquatae, Synurales

## INTRODUCTION

*Mallomonas* Perty is a genus of photosynthetic and heterokont algae in the order Synurales, a monophyletic clade of siliceous scale-bearing organisms contained within the class Chrysophyceae (KRISTIANSEN 2005; ŠKALOUD et al. 2013; SIVER 2015a). Species consist of motile unicells that inhabit numerous types of aquatic environments, including wetlands, ponds, and lakes, worldwide (SIVER 2015a). The genus is almost exclusively freshwater and can form an important component of the planktic community especially in waterbodies that are slightly acidic, dilute, and with moderate concentrations of nutrient and dissolved humic substances.

*Mallomonas* cells are covered by flat siliceous scales that are precisely arranged to form an organized cell covering (SIVER & GLEW 1990; KRISTIANSEN 2002). The structure and ornamentation of the scales are unique to each species, and most species produce differently-shaped scales to precisely fit over specific locations on the cell. Scales covering the main portion of the cell, referred to as body scales, will differ in shape from those covering the posterior end of the cell, and those that surround the emergent flagella(um). Regardless of

where the scales fit within the cell covering, the basic design and characteristics are similar and diagnostic at the species level. Practically all species of *Mallomonas* produce a second type of siliceous structure, the bristle. Bristles are elongate structures with one end, the foot, modified to fit under the apical end of a scale, and a long shaft that radiates outwards from the cell covering.

The flat portion of the scale is referred to as the base plate, and on all scale types, the proximal margin bends up and over the base plate forming the posterior rim. For most species, at least part of the base plate, if not the entire surface, is perforated with small pores (SIVER 1991; KRISTIANSEN 2002). Most species have scales with additional layers and structures of silica deposited onto the base plate, resulting in a wide variety of distinctive designs. These can include, for example, papillae, ribs, a V-rib, and a dome, as well as structures that protrude from the base plate such as a wing or spine. The V-rib is a v (or u)-shaped ridge of silica positioned on the base plate closer to the posterior end, with the arms stretching towards the anterior end and often fusing with ribs near the margins, the anterior ribs. The area between the V-rib and the posterior rim is called the posterior flange, the region between the anterior ribs and the margin the anterior flange, and

the area contained by the V-rib and anterior ribs the shield. The dome is a raised structure on the distal end of the scale into which the bristle foot is tucked, and from which the shaft radiates from the cell surface.

*Mallomonas* is a large genus divided into approximately 19 sections based largely on the structure of the siliceous components (KRISTIANSEN 2002; SIVER et al. 2015). According to SIVER et al. (2015), nine of the sections are rare and contain only one or two species each, while the remaining sections are more species-rich, and many are divided further into multiple series. Section Torquatae Momeu et Péterfi is one of the larger sections within the genus consisting of species with a very distinctive arrangement of scales and bristles. Cells have a unique forward-protruding apical end known as the collar that consists of a ring of specialized scales, the collar scales, from which the flagellum emerges. Collar scales are dome-bearing, asymmetric, with a broad posterior and a narrower anterior end. The majority of the cell covering consists of symmetric, rhomboidal-shaped scales that lack a dome and are generally positioned at a right angle relative to the collar. Posterior-most scales are smaller, asymmetric, and often with an apical protuberance or spine. Bristles are usually short, curved, and restricted to collar scales.

Until recently, remains of *Mallomonas* in the fossil record were not known older than the Holocene (SIVER & WOLFE 2005; SIVER et al. 2015). Fossils of species representing multiple sections in the genus are now known from the Eocene (SIVER et al. 2015) and Cretaceous (SIVER 2022). Although fossil species specifically from section Torquatae were first noted by SIVER et al. (2015), no formal descriptions have been proposed. The objective of this paper is to describe the first species known from the fossil record belonging to section Torquatae, and to discuss their relationships to modern species.

## MATERIALS AND METHODS

**Site description.** The fossils examined in this study were subsampled from a long core taken from the Giraffe Pipe locality, a kimberlite diatreme that emplaced into the Slave Craton in the Northwest Territories of Canada (64°44' N, 109°45' W) approximately 47.8 million years ago during the middle Eocene (SIVER & WOLFE 2005; WOLFE et al. 2006). Detailed descriptions of the Giraffe Pipe locality are given in WOLFE et al. (2006) and WOLFE et al. (2017), and are only briefly discussed herein. Subsequent to emplacement, the diatreme crater became an aquatic environment and slowly infilled with a sequence of lacustrine sediments, then paludal remains, and eventually capped by Neogene glacial deposits (SIVER & WOLFE 2005; WOLFE et al. 2006). A 163 m long drilled core was uncovered from the Giraffe maar in 1999 by BHP Billiton Inc. (WOLFE et al. 2006), of which 68.3 m represent lacustrine mudstones.

Samples from the Giraffe core are identified using a three-part number (SIVER 2015b). The first number represents

the core box assigned at the time the core was taken. The larger the number, the deeper the section is within the core. The lacustrine sediments are contained between boxes 27 (oldest) and 11 (end of the lacustrine phase). 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 distance in cm down from the top of a core length. Thus, sample 13–1–50 represents a sample taken 50 cm along the core length positioned in channel 1 from box 13. The current study examined samples from sections 13–1–15, 13–1–33, 13–1–50, and 15–1–15.

**Sample preparation and examination.** Mudstone fragments (~100 mg) from each core section were oxidized using 30% H<sub>2</sub>O<sub>2</sub> under low heat for 1–2 hr, rinsed a minimum of four times with distilled water, and the resulting slurries stored in glass vials at 4 °C. This mild oxidation procedure resulted in separation of numerous siliceous microfossils from the rock matrix as well as small remaining fragments for most samples from the Giraffe Pipe core. Subsamples from each slurry were diluted ~1:10 with distilled water and air-dried onto a piece of heavy-duty aluminum foil. The aluminum foil samples were trimmed, attached to aluminum stubs with Apiezon® wax, coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater, and examined with a Leo (Zeiss) 982 FESEM or a FEI Nova NanoSEM 450 field emission scanning electron microscope (SEM).

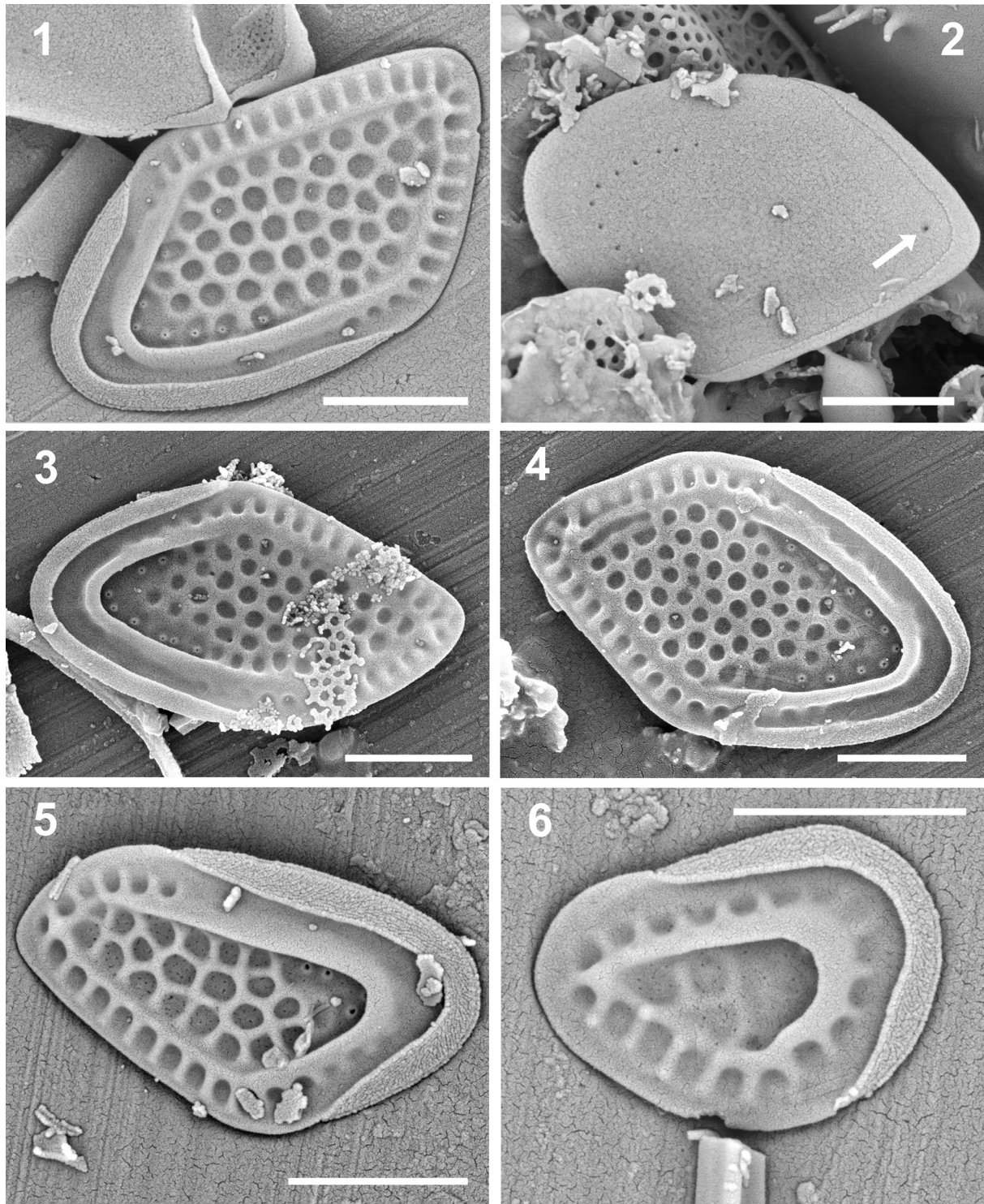
## RESULTS

A limited number of fossil specimens representing species of *Mallomonas* in section Torquatae were previously reported from the Giraffe Pipe core. Continued exploration of the core uncovered specific sections containing many more specimens, and a sufficient number to be able to formally describe two of the Eocene species.

### *Mallomonas caverna* sp. nov. Siver et Lott (Figs 1–12)

**Description:** Body scales are rhomboidal-shaped, with a bilateral symmetry, a broadly rounded posterior end, and a slightly more acute anterior end (Figs 1–4). Body scales range in size from 3.1–3.6×1.7–2.3 µm, with a mean of 3.4×2.1 µm (n=15). The scales lack a dome and have a shallow posterior rim with a mean width of 0.16 µm that encircles approximately half of the perimeter. The V-rib is U-shaped, possesses a shallow hood, and is positioned close to the posterior margin. The arms of the V-rib curve and become continuous with the anterior submarginal ribs. A linear row of rimmed pores aligns the inside margin at the base of the V-rib and typically extends at least half-way up the V-rib (Figs 3–4). Most scales have at least eight rimmed pores, and up to 14 have been observed on some scales. Except for the rimmed pores, the base plate lacks additional pores. The posterior flange is smooth and lacks secondary structure. The anterior flange consists of a series of short, well-developed, and evenly-spaced ribs extending from the anterior submarginal ribs to the anterior perimeter. The shield consists of a well-developed





Figs 1–6. Scanning electron micrographs of *Mallomonas caverna* sp. nov. (1–4) Body scales; note the symmetric shape, the reticulum of ribs on the shield forming the circular and evenly-spaced depressions, the linear array of small pores aligning the base of the V-rib, the row of short ribs on the anterior margins, and the smooth posterior flange; (1) the holotype; (2) the undersurface of the scale; note the linear row of pores, the single distal pore (arrow), and the rim aligning the anterior half of the cell. (5–6) Posterior scales; note the smaller size and extended right side of the scale resulting in the asymmetry. Scale bars 1 µm.

reticulum of connected ribs that encircle a series of large, circular, and evenly-spaced depressions, or wells (Figs 1, 3–4). In the middle of the shield, the depressions range in diameter from 0.12–0.21 µm, with a mean of 0.16 µm (n=40). The linear row of rimmed pores

penetrate the base plate and are easily observed from the scale undersurface (Fig. 2). An additional single pore situated close to the anterior end of the scale, is clearly visible from the undersurface, but is not observed from the scale surface (Fig. 2, arrow). On the bottom of the

scale, the anterior perimeter is lined with a shallow rim along the undersurface (Fig. 2). This rim commences near the middle of the scale, approximately at the point where the posterior rim on the surface terminates, and is approximately the same width as the posterior rim. Posterior scales are small, asymmetric, and often with a reduced number of pores (Figs 5–6).

Collar scales are tripartite, highly asymmetric, with a broad rounded posterior end, a narrow anterior end (Figs 7–9), and range in size from  $3\text{--}4 \times 1.9\text{--}2.6\text{ }\mu\text{m}$  (width taken at the broad posterior end,  $n=10$ ). The ventral and dorsal margins are distinctly concave and convex, respectively. Ornamentations of the posterior rim, posterior flange, and shield are similar to that found on the body scales. The anterior submarginal ribs continue around the margin of the dome, with the left rib extended into a short spine (Figs 7–8). Although the linear row of rimmed pores is clearly evident on the collar scales, the single anterior pore is lacking (Fig. 9). The concave ventral margin, and the base of the dome except for the opening from which the bristle emerges, are reinforced with a thick rib (Fig. 9). A distinct patch of small pores is found near the dome opening. Bristles are short, curved, similar in length, range in length from  $5.8\text{--}6.4\text{ }\mu\text{m}$ , with several wide grooves on the shaft, and an expanded and flat foot (Figs 10–12).

**Holotype:** Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, CANA 169566. The holotype is represented here by Fig. 1.

**Type material:** Rock specimen sub-sampled from section 13–1–50 of the Giraffe Pipe core, Lac de Gras kimberlite field region, Northwest Territories, Canada.

**Etymology:** The species epithet, *caverna*, refers to a cave or cavern in Latin, and represents the prominent wells on the shield.

**Comments:** *Mallomonas caverna* was common in rocks spanning 35 cm of the Giraffe Pipe core, including ample populations in samples 13–1–50, 13–1–33, and 13–1–15. This section of the core is dominated by another synurophyte, *Synura cronbergiae* Siver, and a number of diatom species belonging to *Eunotia* Ehrenberg. Other notable organisms uncovered in this section of the core include *Mallomonas media* Siver, *M. preisigii* Siver, *M. ampla* Siver et Lott, multiple species of paraphysomonads and euglyphids, and an undescribed species of *Mallomonas* that belongs in section Punctiferae.

***Mallomonas deserta* sp. nov. Siver et Lott (Figs 13–22)**

**Description:** Body scales are rhomboidal-shaped, with a bilateral symmetry, rounded posterior and anterior ends, and range in size from  $2.1\text{--}3.3 \times 1.9\text{--}2.6\text{ }\mu\text{m}$  with a mean of  $2.9 \times 2.2\text{ }\mu\text{m}$  ( $n=12$ ) (Figs 13–16). The posterior rim is narrow, with a mean width of  $0.16\text{ }\mu\text{m}$ , and encircles approximately half of the perimeter, terminating close to the widest portion of the scale. The V-rib is U-shaped, narrow, positioned close to the posterior margin, and

terminates at the ends of the posterior margin. The arms of the V-rib curve are continuous with the anterior submarginal ribs. The anterior submarginal ribs are thick, rounded, positioned close to the scale margin, and connect at the distal apex often with a small spine or protrusion (Figs 13–15, arrow on Fig. 15). A linear row of tiny papillae align the top of each anterior submarginal rib (Figs 13–16). There is a linear row of large and evenly-spaced pores, numbering approximately 6.8 per micron, on the narrow anterior flange. The row of pores is continuous around the distal apex and terminates at the ends of the posterior rim. On some specimens, many of the large pores are rimmed (e.g., Fig. 14), but the rims can be obscured on more silicified specimens. Another set of large pores is found along the inside base of the anterior submarginal rim and often continues along the base of the V-rib arms (Figs 15–16). These pores are also with thickened rims, often unevenly spaced in a row, and sometimes reduced in number to a few. A small and narrow window can be found at the base of the posterior rim (Fig. 15), but often hard to discern. The posterior flange is narrow, smooth, and lacks secondary structure. The shield also lacks secondary structure and possesses very small and widely-spaced pores.

Posterior scales are small, highly asymmetric, with features similar to those found on body scales (Figs 17–18). The posterior rim and arm of the V-rib are extended further along the right side of the scale, both terminating close to the distal apex. The spine is more prominent (Fig. 18), but still less than  $\sim 300\text{ nm}$ . Collar scales are approximately  $4.7 \times 1.8\text{ }\mu\text{m}$  (including the spine), are tripartite, highly asymmetric, with a broad rounded posterior end, a small rounded dome, and a forward-projecting apical end extending well past the dome (Figs 19–20). The shield is smooth and unornamented. Three to four small rimmed pores are randomly spaced in a row along the base of the V-rib. The arms of the anterior submarginal rib extend well past the dome, with the ventral arm passing over the dome, and connect to form a sharp spine (Figs 19–20). The extended ventral arm forms an elongated groove with the scale margin (Fig. 20, arrows). Bristles are short, range in length from  $6.2\text{--}7.0\text{ }\mu\text{m}$ , ribbed and tapered to a sharp point (Figs 21–22). The proximal foot is flat and angled towards the dorsal side.

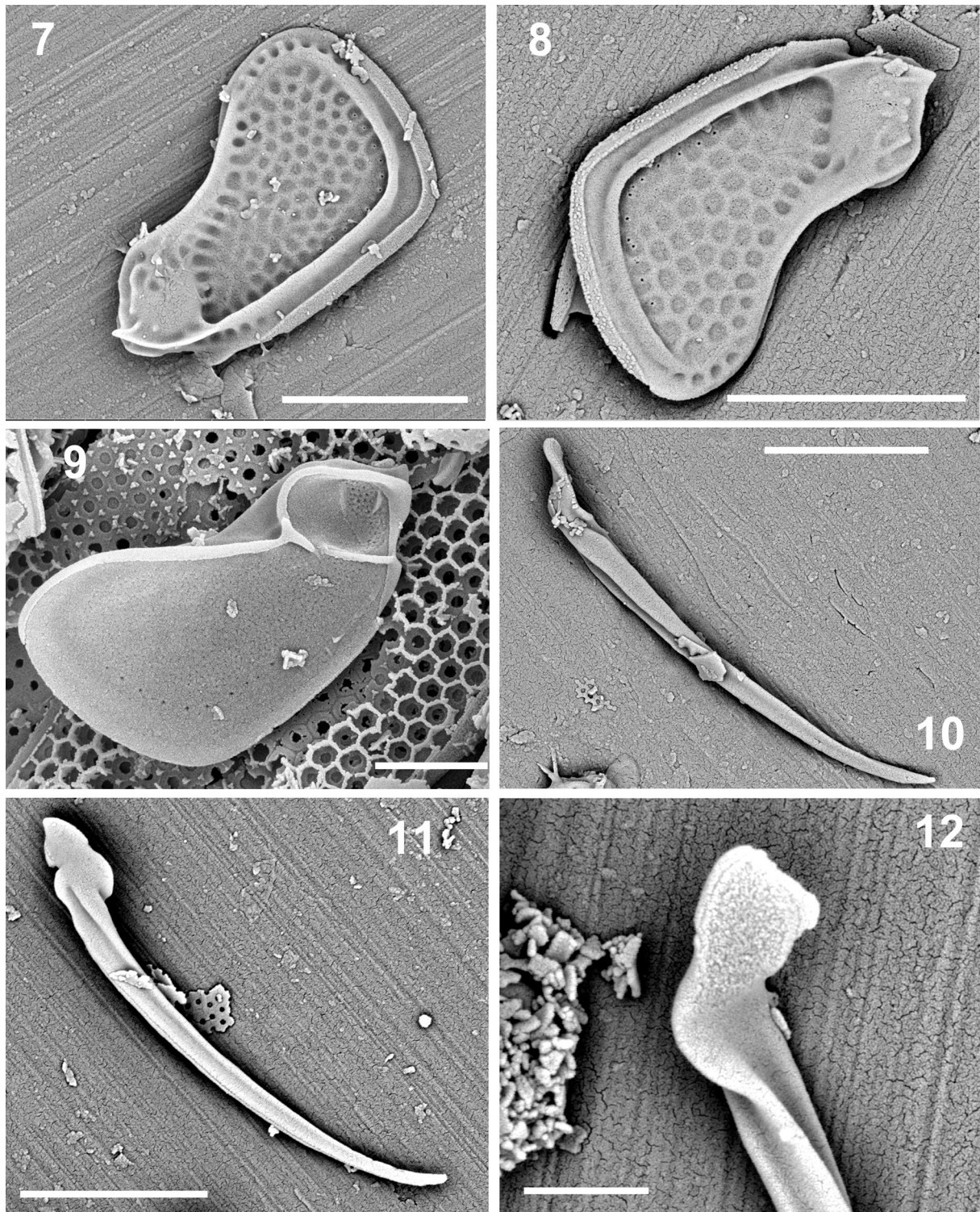
**Holotype:** Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, CANA 129567. The holotype is represented here by Fig. 15.

**Type material:** Rock specimen subsampled from section 15–1–15 of the Giraffe Pipe core, Lac de Gras kimberlite field region, Northwest Territories, Canada.

**Etymology:** The epithet, *deserta*, is taken from the Latin word for deserted, and represents the expansive shield lacking secondary structure.

**Comments:** Large numbers of *Mallomonas deserta* specimens were uncovered in the type material from



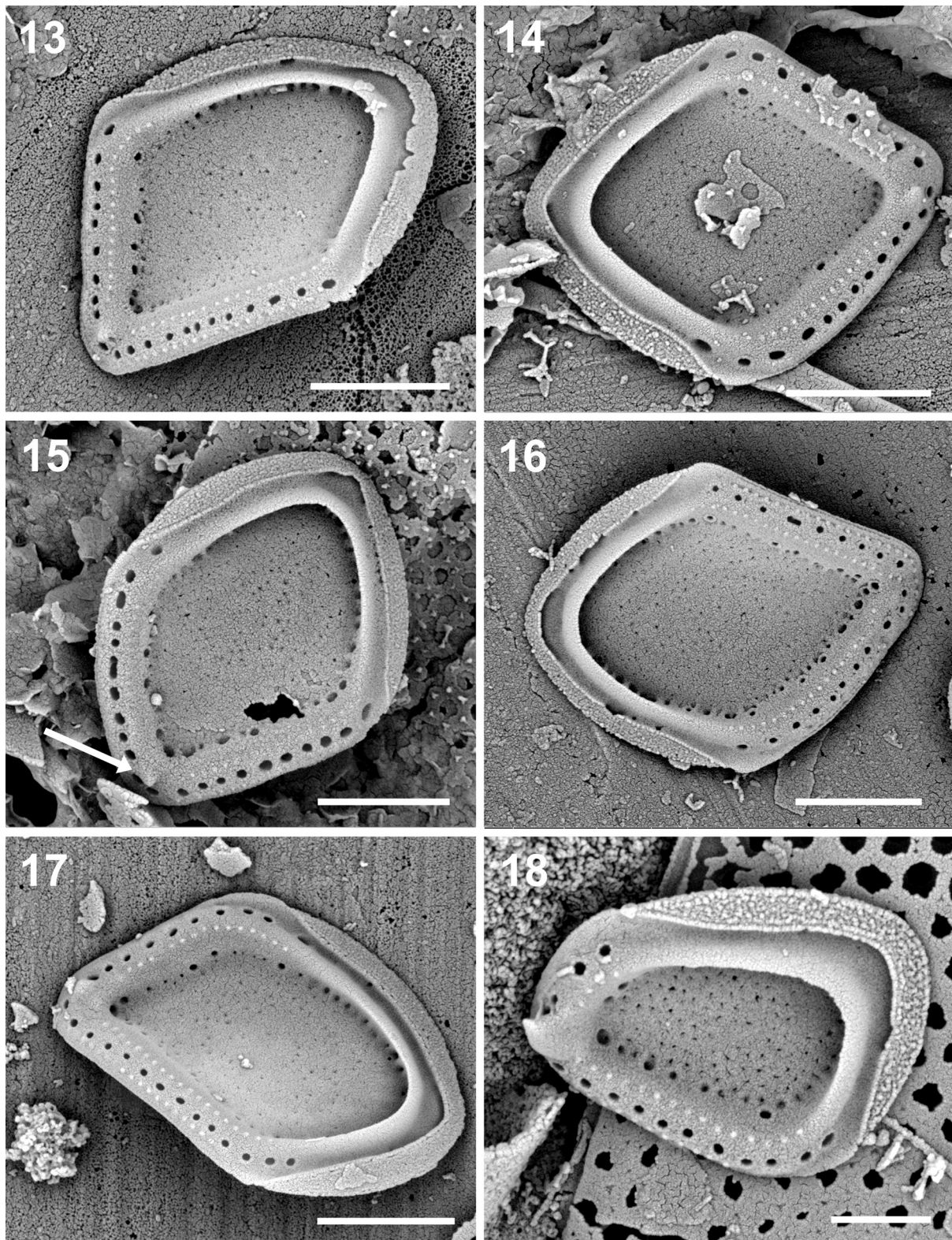


Figs 7–12. Scanning electron micrographs of *Mallomonas caverna* sp. nov. (7–9) Collar scales; note the asymmetry of the scale, the dome with forward projecting short spine, and the broad posterior end; (9) the undersurface; as on the body scales, other than the linear array of pores at the base of the V-rib, base plate pores are not obvious; note the patch of pores within the dome and the thickened border along the ventral margin and surrounding the dome except where the bristle emerges. (10–11) Whole bristles and (12) a close up of the proximal foot; note the short, ribbed, and curved nature of the shaft, and the flat and expanded foot. Scale bars 500 nm (12), 1  $\mu$ m (9), 2  $\mu$ m (7–8, 11), and 3  $\mu$ m (10).

section 15–1–15. This section of rock was dominated by a collection of undescribed taxa closely related to *M. lychenensis*, a species of *Chrysosphaerella* similar to the modern taxon *C. brevispina*, eunotioid diatoms, and testate

euglyphid plates. Other less abundant species included *Mallomonas dispar* Siver, Lott et Wolfe, *M. schumachii* Siver, *M. elephantus* Siver et Wolfe, *M. porifera* Siver et Wolfe, and *Synura cronbergiae* Siver.





Figs 13–18. Scanning electron micrographs of *Mallomonas deserta* sp. nov. (13–16) Body scales; note the symmetric shape, the lack of secondary structure on the shield, the rows of pores on each side of the anterior submarginal ribs, the smooth posterior flange, and the small apical protuberance (arrow on fig. 15); the scale in Fig. 15 represents the holotype. (17) A scale with a slight asymmetry, and a shape in between a body and posterior scale. (18) Posterior scale; note the smaller size, the extended right side of the scale resulting in the asymmetry, and the slightly longer spine. Scale bars 500 nm (18) and 1  $\mu$ m (13–17).



## DISCUSSION

There is no doubt that *Mallomonas caverna* and *M. deserta* belong in Sectio Torquatae as originally described by MOMEU & PÉTERFI (1979), and later by KRISTIANSEN (2002). The presence of highly asymmetric tripartite collar scales, rhomboidal and domeless body scales, smaller and subcircular posterior scales, and short and distinctively curved bristles found on the two new species match those used to define section Torquatae. In addition, scales of species contained in section Torquatae have both a thin posterior rim and posterior flange, and V-rib arms that are continuous with the anterior submarginal ribs (SIVER 1991). Species in this section of the genus also have cells with a distinctly forward-projected apical end, or collar, formed by a ring of collar scales. The body scales are precisely arranged in spiral rows and usually orientated at 90° to the long axis of the cell (SIVER & GLEW 1990; SIVER 1991). Although we were not able to uncover whole cells, given the close match of scale types between modern species in section Torquatae and both *M. caverna* and *M. deserta*, and the fact that the arrangement pattern of scales forming the cell covering on other contemporary species in *Mallomonas* has been documented for other fossil Eocene species (SIVER 2018), it is highly likely that cells of *M. caverna* and *M. deserta* had the same architecture as modern species.

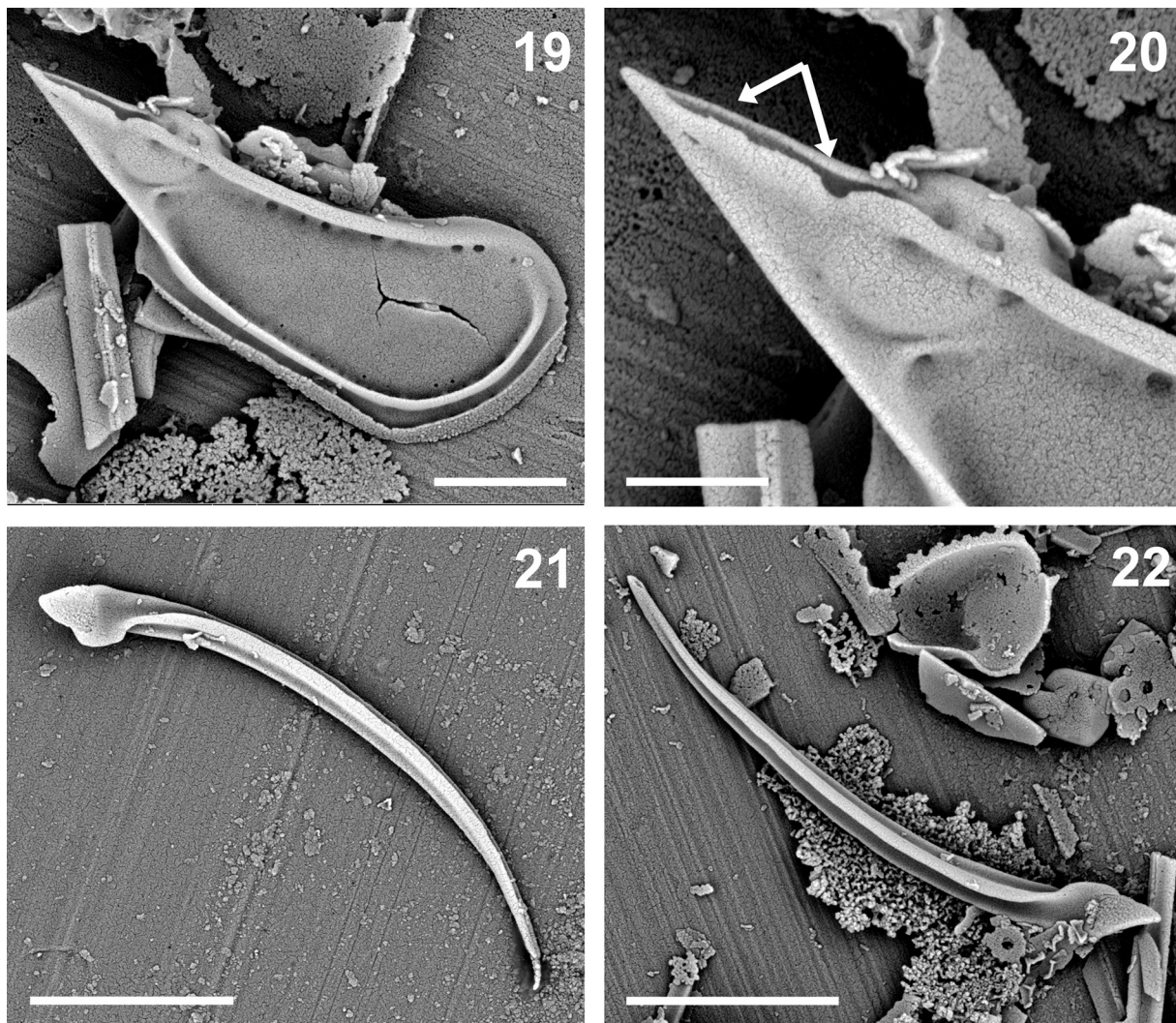
Although not formally described, specimens representing a taxon that would be classified in the series Mangoferae of section Torquatae were reported from Cretaceous mudstones estimated to be 83 Ma (SIVER 2023). The description of *Mallomonas caverna* and *M. deserta* from the younger Giraffe Pipe locality confirms that taxa belonging to section Torquatae had evolved at least 48 Ma ago in the Eocene. Given the close association of fossil specimens representing section Torquatae from both the Eocene and the Cretaceous with modern species, it seems probable that the defining characteristics of this lineage were well developed by the early Cenozoic, if not well before this time period. In addition, it is also clear that the age of the section Torquatae lineage is significantly older than the 43 Ma estimate proposed by SIVER et al. (2015).

*Mallomonas caverna* is most closely aligned with the modern species *M. serrata* Nicholls (NICHOLLS 1984), and to a lesser extent *M. prora* Dürschmidt (DÜRRSCHMIDT 1982), both in series Eoae. The shields of body scales of *M. serrata* and *M. caverna* are covered with similarly-shaped and large depressions formed by fusion of a reticulation of secondary ribs. In addition, body scales of both taxa have narrow and smooth posterior flanges, and a series of evenly spaced short ribs radiating from the anterior submarginal ribs onto the anterior flanges. A key feature also shared by both species is the combination of possessing a linear array of tiny pores on the shield along the base of the V-rib, coupled with a single pore centrally placed close to the

distal margin. However, scales of the two species differ in several key characteristics. First, body and collar scales of *M. caverna* are smaller in overall size and with narrower posterior rims. Second, the linear array of tiny pores on *M. caverna* scales are rimmed and are not situated within a “window” as is the case with scales of *M. serrata*. Third, the bristles of *M. caverna* are significantly smaller, and we have never observed spines on posterior scales. Lastly, scales of *M. caverna* lack serrated distal margins that are characteristic of *M. serrata* (NICHOLLS 1984).

Although scales of *M. caverna* have less in common with another species in series Eoae, *Mallomonas prora*, they do share a few similarities. Scales of both taxa have a pattern of circular pits on the shield, smooth posterior flanges, and evenly-spaced ribs on the anterior flanges. *Mallomonas prora* also has some scales, presumably those approaching the posterior end of the cell that are highly asymmetric, similarly to *M. caverna*. However, the shield pits are significantly smaller on scales of *M. prora*, they lack the linear row of tiny pores and the single distal pore, and have posterior scales with short spines. It is not known if collar scales of either *M. serrata* or *M. prora* possess the thickened margin on the undersurface of the scale that aligns the ventral margin and base of the dome, and the patch of small pores on the dorsal side of the dome that are prominent on *M. caverna* scales.

There is also a similarity of *M. caverna* scales with those of *M. favosa* Nicholls, *M. hexagonis* Nicholls, and *M. lusca* Gusev et Kezlya in series Mangoferae (KRISTIANSEN 2002). The original description of *M. favosa*, based on transmission electron microscopy, depicts the shield of body scales consisting of a reticulation of ribs that form a series of polygonal-shaped meshes (NICHOLLS 1984). In a latter publication, DÜRRSCHMIDT & CROOME (1985) showed that the mesh reticulation was covered with an additional layer of silica with small papillae on the surface. This means that the polygonal reticulation of meshes is internal, situated on top of the base plate, but below the surface layer. DÜRRSCHMIDT & CROOME (1985) further described *M. favosa* forma *gemina* with a similar internal scale structure. Based on the view held by DÜRRSCHMIDT & CROOME (1985) and followed by other authors (e.g., SIVER 1991), the scales of *M. favosa* are quite different from those of *M. caverna*, and the former species belongs in series Mangoferae and not series Eoae. Scales of *M. hexagonis* present a similar situation as those of *M. favosa*. In addition, scales of *M. hexagonis* differ from those of *M. caverna* in having meshes with a hexagonal outline, and the scales lack the row of rimmed pores. Although scales of *M. lusca* have a similar reticulation of meshes on the shield that appears to also be covered with a thin outer siliceous layer, the number and position of the rimmed pores on *M. caverna* scales, along with the lack of the large pit found at the base of the V-rib on *M. lusca* scales (GUSEV & KEZLYA 2021) clearly separate these two species.



Figs 19–22. Scanning electron micrographs of *Mallomonas deserta* sp. nov. (19–20) Collar scale; note the shield devoid of secondary structure, and the long forward-projecting spine formed by extension and fusion of the anterior submarginal ribs; (20) a close-up of the spine showing the groove along the ventral margin. (21–22) Whole bristles depicting the short, ribbed, and curved nature of the shaft, and the flat and expanded foot. Scale bars 500 nm (20), 1  $\mu$ m (19), and 2  $\mu$ m (21–22).

Scales of *M. deserta* share features with a number of modern species in section *Torquatae*, including *Mallomonas newfoundlandicus* Siver (SIVER & LOTT 2017), *M. papuensis* Kapustin, Gusev et Kulikovskiy (KAPUSTIN et al. 2019), *M. inornata* Nicholls (NICHOLLS 1989) and *M. torquata* f. *simplex* Nicholls (NICHOLLS 1988a). All five species have scales with similarly shaped posterior rims and V-ribs, smooth and largely unornamented shields, unornamented posterior flanges, and lack well-formed base plate pores. In addition, all of the species, except *M. inornata*, have a row of holes on the anterior flanges. The forward-projecting spines on the collar scales of all four modern species are longer than those on other modern species, but the exceptionally long spines on *M. newfoundlandicus* (SIVER & LOTT 2017) and *M. papuensis* (KAPUSTIN et al. 2019) are a much closer match to those found on *M. deserta*. All four modern taxa, especially *M. newfoundlandicus*, *M. torquata* f. *simplex*, and *M. papuensis*, have poste-

rior scales with spines that are considerably longer than the small protrusion found on *M. deserta* scales.

A few additional features serve to distinguish the fossil *M. deserta* from modern species. Body scales of *M. newfoundlandicus* are similar in size to those of *M. deserta*, but the collar scales on the former species are larger and with longer forward-projecting spines. Body scales of *M. papuensis* are significantly smaller than those of *M. deserta*, plus the collar scales have a distinct discontinuity (interruption) between the arm of the V-rib and the ventral anterior submarginal rib. Cells of *M. inornata* have exceptionally small scales compared to those of *M. deserta*. Body scales of *M. torquata* f. *simplex* are larger than those of *M. deserta*, and they can have additional secondary ornamentation on the shield close to the V-rib and anterior submarginal ribs.

Although placement of *M. caverna* into series *Eoae* seems clear because of a close match in scale characteristics, aligning *M. deserta* into a specific series



is not clear. Given the smooth and unornamented shields on *M. deserta* scales, it does not fit into any of the four recognized series, series Pumilio, Eoae, Mangoferae, and Doignonianae (KRISTIANSEN 2002). Each of the four series was originally described largely based on differences in secondary features on the scales, especially of the patterns formed by ribs on the shield. Because the shield on *M. inornata* scales is unpatterned and lacks regularly-spaced meshes formed by a reticulation of thick ribs, it is not clear why KRISTIANSEN (2002) placed this species into series Eoae. Likewise, scales of *M. papuensis* also have smooth unornamented shields and in our opinion do not fit the characters used to define series Eoae, as was done by KAPUSTIN et al. (2019). Given the number of new species described in section Torquatae since the KRISTIANSEN (2002) publication, a reassessment of the existing series may be in order.

The functions of several structural features observed on *M. caverna* scales, as well as on other species in section Torquatae are not known. For example, what is the purpose of the linear array of tiny pores at the base of the V-rib, as well as the isolated pore on the distal end of the scale? Similar linear arrays of small pores along the V-rib are found in other species in section Torquatae, such as *M. mangofera* f. *foveata* Dürschmidt (DÜRRSCHMIDT 1983), *M. madagascariensis* Hansen et Kristiansen (HANSEN & KRISTIANSEN 1995), and *M. roscida* Dürschmidt (DÜRRSCHMIDT 1986). Other species possess a single distinctive pore at the base of the V-rib, including *M. favosa* Nicholls (NICHOLLS 1984), *M. liturata* Nicholls (NICHOLLS 1988b), and *M. palaestrica* Hansen, Johansen et Skovgaard (HANSEN et al. 1993). Our belief is that these specialized pores are strategically placed and used to aid in holding the scales together in precise locations on the cell coat by secreting an organic “glue.” Species in other sections of the genus also have isolated pores or patches of pores at the base of the V-rib, such as *Mallomonas papillosa* Harris et Bradley (SIVER 1991) and *M. binocularis* Siver (SIVER 2002), or in a similar position on the scale for some taxa that lack a V-rib, such as species on the *M. matvienkoae* Asmund et Kristiansen complex (Jo et al. 2013) and the elongated pore found on scales of *M. caudata* Iwanoff (SIVER 1991). It is of further interest that many species that have these specialized pores often lack or have reduced base plate pores. Perhaps this provides a means to glue the scales together at specific points associated with the overlapping pattern of the scales on the cell coat. In a similar fashion, perhaps the patch of pores found on the dorsal side of the dome is involved in helping to hold the bristle in place.

In summary, scale structure characteristic of species belonging to section Torquatae was well evolved by the early Eocene, and most likely earlier by the Late Cretaceous. *Mallomonas caverna* and *M. deserta* represent the first taxa in this lineage to be formally described from the fossil record. The

extensive Giraffe Pipe fossil locality has produced a wealth of new species and evolutionary history for synurophyte algae, as well as other organisms such as diatoms and euglyphid testate amoebae. Additional fossil specimens from other localities in the Eocene and earlier time periods will undoubtedly yield further clues on the origin and evolutionary history of these ecologically important siliceous organisms.

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#### REFERENCES

- DÜRRSCHMIDT, M. (1982): Studies on the Chrysophyceae from southern Chilean inland waters by means of scanning and transmission microscopy, II. – Arch. Hydrobiol. Suppl. 63: 121–63.
- DÜRRSCHMIDT, M. (1983): A taxonomic study of the *Mallomonas mangofera* group (Synuraceae, Chrysophyceae) including the description of four new taxa. – Pl. Syst. Evol. 143: 175–196.
- DÜRRSCHMIDT, M. (1986): New species of the genus *Mallomonas* (Mallomonadaceae, Chrysophyceae) from New Zealand. – In: KRISTIANSEN, J. & ANDERSEN, R.A. (eds.): Chrysophytes: Aspects and problems. – pp. 87–106, Cambridge University Press, Cambridge.
- DÜRRSCHMIDT, M. & CROOME, R. (1985): Mallomonadaceae (Chrysophyceae) from Malaysia and Australia. – Nord. J. Bot. 5: 285–298.
- GUSEV, E. & KEZLYA, E. (2021): *Mallomonas lusca* sp. nov. (Synurales, Chrysophyceae) – a rare species from Southeast Asia. – Phytotaxa 529: 105–112.
- HANSEN, P.; JOHANSEN, J.E.; SKOVGAARD, A. & KRISTIANSEN, J. (1993): *Mallomonas palaestrica* sp. nov. (Synurophyceae), a new member of sect. Torquatae from Denmark. – Nord. J. Bot. 13: 107–110.
- HANSEN, P. & KRISTIANSEN, J. (1995): *Mallomonas madagascariensis*, *M. lemuriocellata* and *M. crocodilorum* (Synurophyceae), three new species from Madagascar. – Nord. J. Bot. 15: 215–223.
- 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.
- KAPUSTIN, D.A.; GUSEV, E.S. & KULIKOVSKIY, M.S. (2019): *Mallomonas papuensis* sp. nov. (Chrysophyceae, Synurales), a new species from the high mountain bog pool in Papua province, Indonesia. – Phytotaxa 402: 281–287.
- KRISTIANSEN, J. (2002): The genus *Mallomonas* (Synurophyceae) – A taxonomic survey based on the ultrastructure of silica scales and bristles. – Opera Bot. 139: 1–218.
- KRISTIANSEN, J. (2005): Golden algae: a biology of chrysophytes. – 167 pp., Koeltz Scientific Books, Königstein, Germany.

- MOMEU, L. & PÉTERFI, L.S. (1979): Taxonomy of *Mallomonas* based on the fine structure of scales and bristles. – Contr. Bot. Cluj-Napoca: 1979: 13–20.
- NICHOLLS, K.H. (1984): Four new *Mallomonas* species of the Torquatae series. – Can. J. Bot. 62: 1583–1591.
- NICHOLLS, K.H. (1988a): The identification of some *Mallomonas* species of the *M. doignonii* group (Chrysophyceae). – Nord. J. Bot. 8: 109–116.
- NICHOLLS, K.H. (1988b): Descriptions of three new species of *Mallomonas* (Chrysophyceae): *M. hexagonis* sp. nov., *M. liturata* sp. nov., and *M. galeiformis* sp. nov. – Br. Phycol. J. 23: 159–66.
- NICHOLLS, K.H. (1989): Description of four new *Mallomonas* taxa (Mallomonadaceae, Chrysophyceae). – J. Phycol. 25: 292–300.
- SIVER, P.A. (1991): The biology of *Mallomonas*: morphology, taxonomy and ecology. – 230 pp., Kluwer Academic Publishers, Dordrecht.
- SIVER, P.A. (2002): Two new taxa in the Section Papillosae of the genus *Mallomonas* from the Ocala National Forest, Florida, U.S.A. – Nord. J. Bot. 22: 123–128.
- SIVER, P.A. (2015a): The Synurophyceae. – In: WEHR, J.D.; SHEATH, R.G. & KOCIOLEK, J.P. (eds): Freshwater algae of North America: ecology and classification (2<sup>nd</sup> ed.). – pp. 605–650, Academic Press, San Diego.
- 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. (2018): *Mallomonas aperturae* sp. nov. (Synurophyceae) reveals that the complex cell architecture observed on modern synurophytes was well established by the middle Eocene. – Phycologia 57: 273–279.
- SIVER, P.A. (2022): Downsizing: The demise of large scales and large cells in the genus *Mallomonas* (Synurales, Chrysophyceae). – Nature Special Reports 12: 4896.
- SIVER, P.A. (2023): Tracing lineages of scale-bearing Chrysophyceae over geologic time. – Fottea 23: 164–176.
- SIVER, P.A. & GLEW, J.R. (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. & LOTT, A.M. (2017): The scaled chrysophyte flora in freshwater ponds and lakes from Newfoundland, Canada, and their relationship to environmental variables. – Cryptogam. Algol. 38: 325–347.
- SIVER, P.A. & WOLFE, A.P. (2005): Eocene scaled chrysophytes with pronounced modern affinities. – Int. J. Plant Sci. 166: 533–536.
- 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. – Am. J. Bot. 102: 1–21.
- ŠKALOUD, P.; KRISTIANSEN, J. & ŠKALOUDOVÁ, M. (2013): Developments in the taxonomy of silica-scaled chrysophytes – from morphological and ultrastructural to molecular approaches. – Nord. J. Bot. 31: 385–402.
- 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.H.; SIVER, P.A. & WESTGATE, J.A. (2017): Middle Eocene CO<sub>2</sub> and climate reconstructed from the sediment fill of a subarctic kimberlite maar. – Geology 45: 619–622.