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Mallomonas gigantica sp. nov., an Eocene synurophyte possessing the largest known siliceous scales

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Abstract: A new fossil species representing the genus *Mallomonas*, *M. gigantica*, is described from the Giraffe Pipe Eocene maar lake locality situated near the Arctic Circle in northern Canada. The new species possesses rolled bristles and two basic types of scales that lack V–ribs, body scales and specialized apical scales. *Mallomonas gigantica* possesses the largest body scales reported for the genus, including for both fossil and contemporary taxa. Scales reached 12 µm in length and with a surface area near 100 µm^2. Body scales are large, square–shaped, with a narrow posterior rim, large and thick anterior submarginal ribs, and a shallow dome with a curved margin that aids in securing the bristle. Base plate pores are small, and closely spaced over the scale surface except under the anterior submarginal ribs and dome. Specialized apical scales are smaller, more circular, asymmetric, and with a forward–projecting spine. The craspedodont bristles, have an open slit running the length of the shaft, an expanded and flat foot, and a row of small teeth lining the apex of the shaft. Although the scale structure is distinctly different, some features of the scales and bristles are most closely related to the fossil species *M. schumachii*, another taxon with large scales described from the same fossil locality. Given the lack of a V–rib, *M. gigantica* may represent a stem taxon of section *Planae*, but similarities with species in the modern section *Punctiferae* lineage are also discussed. The large, robust and heavy nature of the scales may have posed disadvantageous to the cell by making a slow swimmer more prone to sinking.

Keywords: Eocene, extinct, *Mallomonas*, new species, *Planae*, *Punctiferae*, synurophytes

INTRODUCTION

Mallomonas Perty is the largest and most diverse genus within the order Synurales, a monophyletic clade of heterokont algae bearing siliceous scales within the class Chrysophyceae (Kristiansen 2005; Škaloud et al. 2013; Siver et al. 2015; Jadrná et al. 2021). The genus is almost exclusively freshwater and consists of unicellular flagellates with an organized covering of overlapping scales and commonly found as a member of the planktic community in all types of environments, including wetlands, ponds, lakes and slower moving streams and rivers (Siver 2015). According to AlgaeBase (Guiry & Guiry 2007; searched Dec. 28, 2023), a total of 432 species and subspecific forms have been described. Of these, a fair number have been combined over time. In addition, because other taxa originally described with only light microscopy remain unstudied with newer techniques, including electron microscopy and molecular gene sequencing, their status relative to other well–defined species remains unclear. Given these limitations, the number of *Mallomonas* species that are well studied and identifiable based on current methods is likely closer to 250. The species are divided into approximately 19 sections, some of which contain only one or two species while others are species rich and further subdivided into different series (Kristiansen 2002; Siver et al. 2015).

The siliceous scales can range from having a simple design to a highly complex one with elaborate designs (Siver 2015 and numerous references therein). Because each scale on a cell has the same design, scale morphology has served as a primary means of delineating between species, and is an effective means to better examine extinct fossil forms. Although the basic design is common for all scales, the shapes of scales differ depending on where on the cell the scales are placed. The majority of scales covering the main body of the cell are called body scales. Specialized–shaped scales surround a pore on the apical end of the cell from which the flagella(um) emerges, and typically the posterior–most scales are smaller to better conform to covering the cell, and on some species the posterior scales each have a spine that projects outwards from the cell (Siver 1991; Kristiansen 2002). Practically all species of *Mallomonas* have a second type of siliceous structure called a bristle. Bristles are elongate structures with one end modified to fit under the apical end of a scale, and a long shaft that radiates outwards from the cell covering. When the cell swims, the bristles usually rotate and become streamlined pointing towards the posterior of the cell, a position that would reduce the drag on the swimming cell.

The flat portion of the scale is referred to as the base plate, and all scale types on all species have an upturned posterior rim where the scale perimeter bends up and curls over the base plate (Siver 1991; Kristiansen 2002). The base plate is usually perforated with pores, and the size, spacing and location of these pores can serve as a diagnostic character. Most species have additional structures positioned on top of the base plate, including for example, ribs, papillae, a V–rib, and a dome, and some features such as a wing or spine, that protrude up or out from the base plate. The V–rib, a thick v–shaped rib positioned on the base plate with the open part facing the anterior end of the scale, is used to help position and orientate the scales on the cell covering (Siver & Glew 1990). The dome is a raised portion of the anterior end of the base plate into which the end of the bristle, or foot, is situated and held in place. Additional ribs and papillae can be used to form an endless number of specific designs.

The oldest known fossil scales and bristles date to the late Cretaceous, with the vast number of fossil species described from Eocene mudstones (Siver 2023). Some of the fossil species have scales that are surprisingly similar to those of modern forms, while others present very different designs and structures, representing extinct lineages. Some of the extinct species possessed large scales, and are estimated to also have had significantly larger cells (Siver 2022). The objective of this paper is to describe a new and unique fossil species from an Eocene deposit in northern Canada that has the largest scales known to date for species of *Mallomonas.*

Materials and Methods

Mudstone chips (50–100 mg) from each stratum of the Giraffe core (Table 1) examined in this study were oxidized using 30% H_2O_2 under low heat for 1–2 hours, rinsed a minimum of five times with distilled water, and the resulting slurries stored in glass vials at 4 ºC. This procedure resulted in separation of siliceous microfossils from the mudstone matrix. One–ml aliquots of the clean slurries were air dried onto flat pieces of heavy–duty aluminum foil, trimmed and attached to aluminum stubs with Apiezon wax. Samples were coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater, and examined with either a Leo 982 field emission SEM, or a FEI Nova NanoSEM 450 field emission SEM.

Morphometric measurements of body scales (n=24), anterior scales (n=8) and bristles (n=12) were made from SEM images. The length of the triangular–shaped scales includes the spine, and in all cases the width was measured at the widest point. Surface area was estimated assuming an ellipse shape using the formula: SA = (a*b*π), where a = radius of the major axis, b = radius of the minor axis, and π = 3.14.

Location and identification of samples from the Giraffe

Table 1. Strata in the Giraffe Pipe core containing remains of *Mallomonas gigantica*. The depth in the core measured from the ground surface and a summary of the most important co-inhabiting organisms are given for each statum. The percentage of the total number of microfossils uncovered is listed in parentheses for each organism.

Stratum	Depth in core (m)	Major co-inhabiting taxa
14–3–140	109.9	Chrysophyte cysts (6), *Mallomonas lychenensis* (48), *M. porifera* (26), *M. skogstadii* (4), other *Mallomonas* spp. (7), *Synura cronbergiae* (5), eunotioid diatoms (2), *Paraphysomonas* spp. (1), *Chrysosphaerella brevispina* (1)
14–3–130	110.1	Chrysophyte cysts (10), *Mallomonas lychenensis* (66), *M. porifera* (13), *M. skogstadii* (4), other *Mallomonas* spp. (3), *Synura cronbergiae* (2), eunotioid diatoms (1), *Chrysosphaerella brevispina* (1)
14–1–60	112.2	Chrysophyte cysts (9), *Mallomonas lychenensis* (16), *M. porifera* (21), *M. media* (3), *M. schumachii* (28), *Synura cronbergiae* (6), eunotioid diatoms (14)
15–3–41	113.6	Chrysophyte cysts (40), *Mallomonas lychenensis* (33), *M. porifera* (15), other *Mallomonas* spp. (3), eunotioid diatoms (10)
15–3–75	113.9	Chrysophyte cysts (45), *Mallomonas lychenensis* (1), *M. porifera* (1), other *Mallomonas* spp. (14), *Synura cronbergiae* (7), eunotioid diatoms (20)

core are given in Siver & Lott (2012). Each section of the core was immediately cut and placed into a core box. Each sample 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, stored in three channels marked 1, 2 and 3. The second number of the sample number represents the channel. The third number is the length in cm measured from the top of a core length. Thus, sample 15–3–75 represents a sample taken from 75 cm down along the core length positioned in channel 3 from box 15.

Site Description. The Giraffe Pipe locality (64.73° N, 109.75° W) is a kimberlite diatreme that was emplaced into the Slave Craton in the Northwest Territories of Canada approximately 47.8 ± 1.4 million years ago during the Eocene (Creaser et al. 2004; Siver & Wolfe 2005; 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 2005; Wolfe et al. 2006). The emplacement age estimate, based on a Rb–Sr model from kimberlitic phlogopite, provides a maximum age estimate for maar lake sedimentation (Creaser et al. 2004). 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 47º angle, 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 mudstones, overlain with 44.8 m of peaty material. Multiple air–fall tephra beds found within the core were used to further provide age estimates of the maar infill. Based on CA–ID–TIMS tephra zircon U–Pb dating of the tephra layers, a Bayesian model age of 47.995 ± 0.082|0.087 Ma (Ypresian) was established for the upper portion of the lacustrine sediments, while a single zircon grain from tephra in the lowermost lacustrine sediments had an age of 48.72 ± 0.29|0.30 Ma (Buryak et al. 2024). Based on the age estimates, the hypothesis is that shortly after phreatomagmatic kimberlite emplacement, a waterbody formed within the crater that varied in depth over time and persisted for thousands of years before transition to a terrestrial environment. The current investigation is based on five samples taken from between 109.9 and 113.9 m along the core (Table 1).

Results

***Mallomonas gigantica* sp. nov. Siver (Figs 1–3)**

Description: Body scales are large, ovate to square–shaped, with a posterior rim, large and thickened anterior submarginal ribs that terminate near the apical end, and a shallow rudimentary dome (Figs 1a–b, e–f; Figs 2a–b). Body scales range in size from 9.6–12.2 µm × 7.5–10.4 µm, have a mean size of 10.8 µm × 8.6 µm, and a mean surface area of 73 µm^2. Except for the thickened areas of the scale, the base plate is covered with very small and relatively evenly spaced pores (Fig. 2b), and this region of the scale lacks any additional secondary structure. The posterior rim is shallow, extends around approximately half of the scale perimeter, and slightly further along the left side of the scale (Figs 1b, e–f). Typically, the posterior rim is wider along the sides of the scale, and narrower around the posterior end. The thickened anterior submarginal ribs are elevated above the base plate approximately equal to, or slightly higher than, the posterior rim (Figs 1a–b, e–f). The dome is shallow, only slightly raised above the base plate, and with an opening for emergence of the bristle on the right side (Figs 2a–b). The left side of the margin of the dome is curved inward to help secure the bristle (Figs 2a–b). Smaller scales, presumably found closer to the posterior end of the cell, have the same overall structure except that the anterior submarginal ribs are thinner and not as robust, and they lack a developed dome (Figs 1c–d).

Apical scales are oval to circular, asymmetric, and with a triangular–shaped, forward–projecting spine and a mean diameter (long axis) of 6.3 µm (Figs 2c–d). The posterior rim continues around the scale perimeter on the left side, and connects to the spine that is approximately 1.6 µm long (Fig 1c). However, the posterior rim is not extended around the right side of the scale, resulting in a distinct asymmetry. The margin is raised only slightly on the right side of the projecting spine. The anterior submarginal rib is lacking on the left side along the extended posterior rim, but is present and reduced along the right side (Fig. 2c). As found on body scales, base plate pores cover the scale except under the region covered by the anterior submarginal rib (Fig. 2d).

Bristles are of the rolled or craspedodont type with a wide groove or slit running the length of the shaft (Figs 3a–d). They are slightly curved, range in length from 22–33 µm, smooth along the lower portion and with small teeth lining the apical end (Fig. 3b). The foot is flat, bent at approximately a 45º angle with the shaft, and often with a slight groove along the bottom portion opposite of the shaft slit (Figs 3e–f).

Holotype: Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, CANA 131273.
Type material: Material from section 15–3–75 of the Giraffe Pipe core collected by P.A. Siver.
Iconotype: Figure 1b, uncovered from section 15–3–75 of the Giraffe Pipe core.
Epithet: The name refers to the large size of the scales.
Distribution: *Mallomonas gigantica* was found in five strata over a four–meter sequence in the Giraffe Pipe core (Table 1). This section of the extensive core was dominated with chrysophytes, including *Mallomonas lychenensis* Conrad, *M. porifera* Siver et Wolfe, *Synura cronbergiae* Siver, and cysts which accounted for 33%, 15%, 4% and 22% of the microfossils, respectively. Eunotioid diatoms, mostly species in *Eunotia* Ehrenberg, were also common in this section of the core. Several additional *Mallomonas* species with exceptionally large scales, *Mallomonas schumachii* Siver, *M. media* Siver et Lott, and *M. skogstadtii* Siver, were also found in these strata. *Mallomonas gigantica* was most abundant

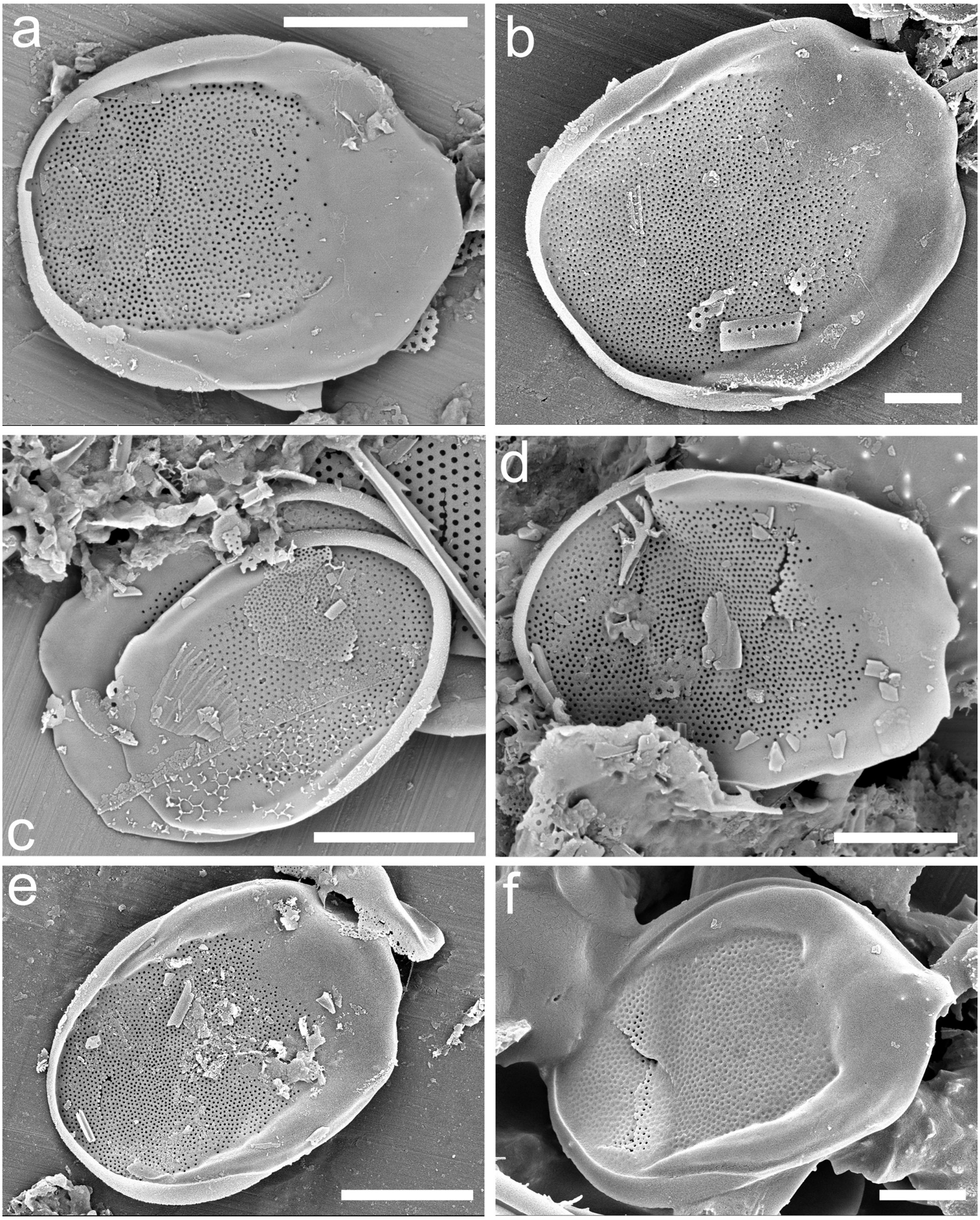

Fig. 1. Scanning electron microscope images of *Mallomonas gigantica* body scales: (a–f) note the square–shape, the robust and thickened anterior submarginal ribs, shallow dome and narrow posterior rim; the base plate consists of small and closely–spaced pores, and lacks additional secondary structure; scales in (a–e) are from the collection of specimens representing the type; the scale in (b) is the largest one recorded from stratum 15–3–75; scales in (c–d) are smaller in size and assumed to be located in the posterior region of the cell; these specimens have thin and less developed anterior submarginal ribs than those found on larger body scales; scales on specimen (c) lack a developed dome; the curled margin of the dome is best seen on (f). Scale bars 2 µm (b, d, f), 3 µm (c) and 4 µm (a, e).

in stratum 15–3–75 where it accounted for 11% of the microfossils, and accounted for 2% or less in the other four strata. Despite the lower abundances relative to other microfossils, specimens of *M. gigantica* were not difficult to find given the large numbers of microfossils extracted from the rocks.

DISCUSSION

There are no known modern or fossil species of *Mallomonas* that possess a suite of characters that matches that of *M. gigantica*. There is also no known counterpart to the large and thickened type of anterior submarginal rib found on *M. gigantica* scales, leading to the conclusion that this Eocene species is extinct. Given the lack of a definitive V–rib, this species may be a stem taxon related to section *Planae*. However, an argument could also be made that *M. gigantica* represents a stem species of the section *Punctiferae* lineage. *Mallomonas gigantica* scales share some similarities with modern species in section *Punctiferae*, namely *M. punctifera* Korshikov and *M. transsylvanica* Péterfi et Momeu (Siver 1991; Kristiansen 2002). Body scales of both of these modern species have elongated submarginal ribs that run from the dome to near the posterior end of the scale, a shallow dome with a curved margin that helps secure the bristle, a thin and shallow posterior rim, and small–diameter base plate pores. Like *M. gigantica*, section *Punctiferae* species also lack a true V–rib and possess similar asymmetric and triangular–shaped apical scales. It is also of note that based on molecular gene data, the section *Punctiferae* lineage diverges early from the large clade containing species with a true and distinctive V–rib (Siver et al. 2015; Škaloud et al. unpublished data). Given these characteristics, perhaps *M. gigantica* actually represents an ancient stem taxon of the modern section *Punctiferae* lineage. Although the thick submarginal ribs found on *M. gigantica* scales are quite different than those on section *Punctiferae* species, the thinner ones found on the smaller posterior scales are quite similar. However,

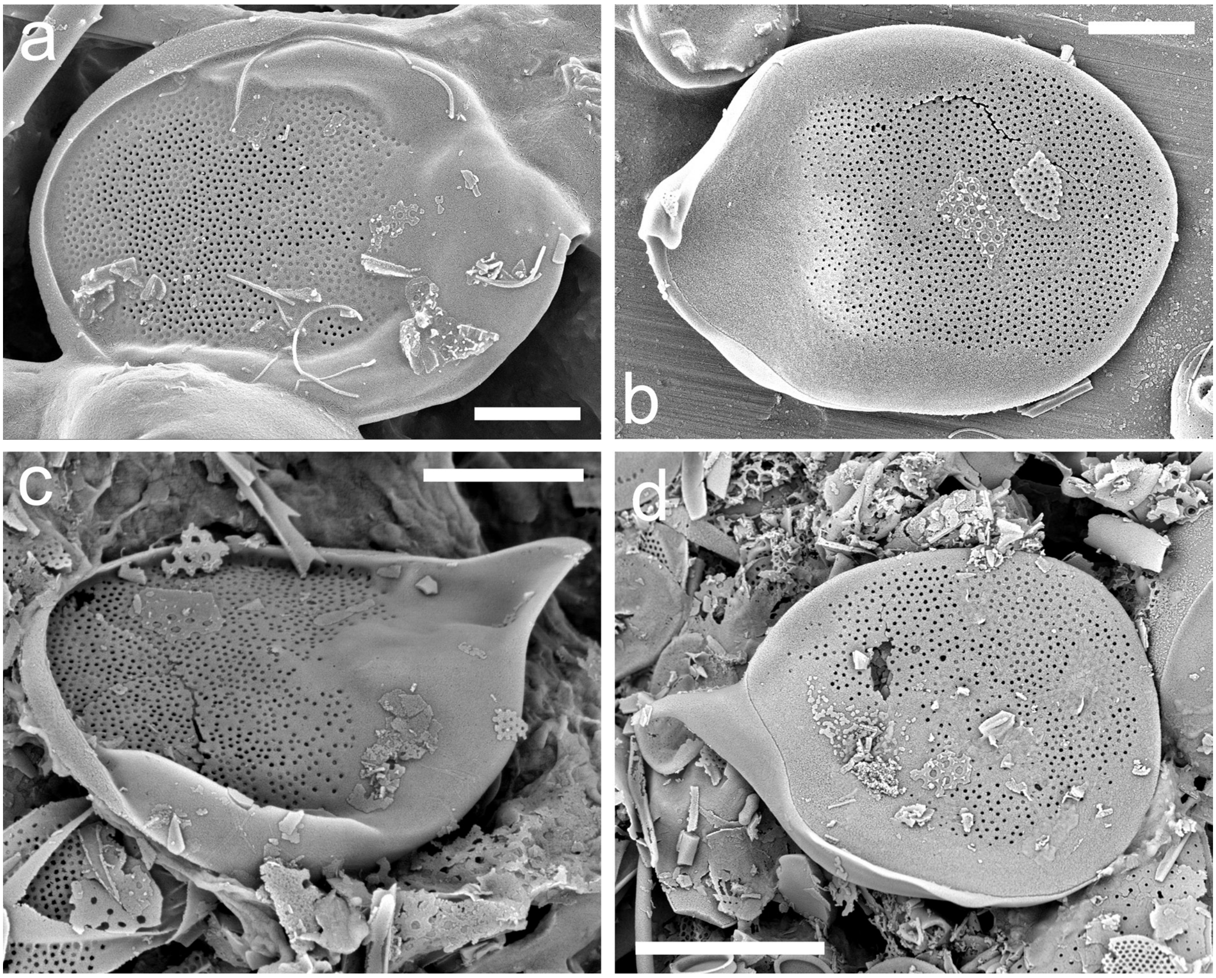

Fig. 2. Scanning electron microscope images of body scales (a–b) and apical scales (c–d) of *Mallomonas gigantica*: (a) typical body scale depicting the base plate pores, narrow posterior rim, thickened anterior submarginal ribs, shallow dome, and recurved dome margin; (b) undersurface of a body scale showing the closely spaced base plate pores and recurved dome margin used to help secure the bristle; note the base plate pores are lacking under the dome and submarginal ribs; (c–d) surface and undersurface views of the asymmetric and triangular–shaped apical scales; note the well–formed anterior submarginal rib on the right side, but lacking on the left side. Scale bars 2 µm (a–c) and 3 µm (d).

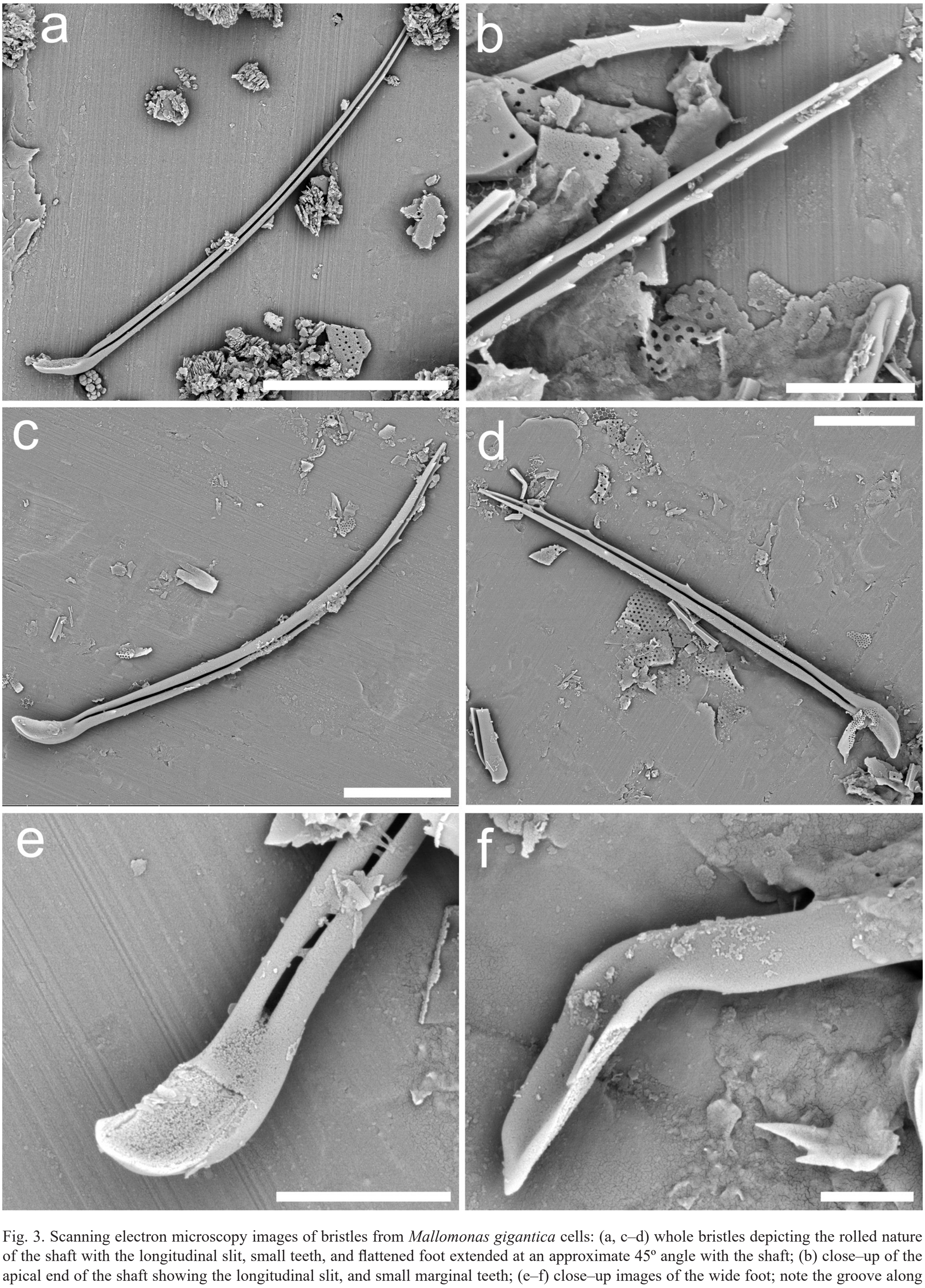

Fig. 3. Scanning electron microscopy images of bristles from *Mallomonas gigantica* cells: (a, c–d) whole bristles depicting the rolled nature of the shaft with the longitudinal slit, small teeth, and flattened foot extended at an approximate 45º angle with the shaft; (b) close–up of the apical end of the shaft showing the longitudinal slit, and small marginal teeth; (e–f) close–up images of the wide foot; note the groove along the undersurface of the foot on (f). Scale bars 1 µm (f), 2 µm (b, e), 5 µm (c–d) and 10 µm (a).

the character of the bristles differs between the fossil and modern taxa. The rolled nature of the bristles on *M. gigantica* scales with an open slit differs from the ribbed type of bristle shaft found on Section *Punctiferae* species today. Bristle differences do not preclude a possible link between these organisms as modifications to the bristle structure may have evolved later.

Mallomonas gigantica cells possess the largest body scales known within the genus with respect to surface area (Siver 2022). Scales of this species are also among the largest known with respect to length and width, with the largest scale measured at 12.2 µm × 10.4 µm and yielding a surface area close to 100 µm^2. Other fossil *Mallomonas* taxa with large body scales include Eocene species *M. schumachii* Siver, *M. giraffensis* Siver et Wolfe, *M. media* Siver et Lott, and an undescribed Cretaceous species referred to as *Mallomonas* W1 (Siver 2022). These fossil scales have a surface area over six times larger than the mean valve for contemporary species (Siver 2022). Of the numerous modern species included in the Siver (2022) study, *Mallomonas bronchartiana* had the largest body scales with a surface area of 37–44 µm^2, approximately 38% and 50% smaller than the mean and largest *M. gigantica* scales, respectively. Other contemporary species with large scales, but smaller than those of *M. bronchartiana*, include *M. caudata* Ivanov, *M. pseudobronchartiana* Gusev, Siver et Shin, *M. velari* Gusev, Siver et Shin, *M. vietnamica* Gusev, Kezlya et Trans, *M. gusakovii* Gusev et al., and *M. leboimei* Bourrelly (Kristiansen 2002; Gusev et al. 2017, 2019, 2021). The totality of evidence supports the hypothesis put forth by Siver (2022) that fossil *Mallomonas* cells produced significantly larger and gigantic scales relative to contemporary species.

Given the size of *M. gigantica* scales reported here, coupled with previous findings, the concept that fossil species formed larger body scales than modern taxa can be modified with respect to scale type. Six of the largest known fossil scale types, both in terms of length and surface area, are ones that lack a V–rib and are best classified within the genus under section *Planae*. Of these and assuming it is related to section *Planae*, *M. gigantica* produces the largest body scales. This implies that the evolutionary downsizing of scales over geologic time described by Siver (2022) is especially apparent within the lineages of taxa that lack a V–rib.

What is perhaps interesting is that most diatomists often overlook synurophyte scales in their clean preparations because of their small size. However, single scales of *M. gigantica*, and a few of its Eocene relatives, are actually larger than some diatom frustules, including for example those of some *Discostella* Houk et Klee, *Achnanthidium* Kützing and *Oxyneis* Round species (Houk & Klee 2004; Siver & Hamilton 2011). For example, *M. gigantica* scales are larger than most specimens of the common and widespread species *Discostella stelligera* (Cleve et Grunow) Houk et Klee, and almost twice as large as *Cyclotella atomus* Hustedt frustules (Hustedt 1937). Even smaller species of other common genera such as *Eunotia* are of similar length (Siver & Hamilton 2011). These types of size comparisons help illustrate the degree to which *Mallomonas* scales have declined in size over the Cenozoic (Siver 2022).

Although the vast majority of *M. gigantica* scales are large with a mean size of 10.8 µm × 8.6 µm, smaller scales with the same basic morphology were also uncovered within the rock strata among the many large ones. The smallest of these scales was 5.2 µm × 4.4 µm. The assumption is that the smaller scales were produced and used to form the scale covering surrounding the posterior end of the cell (Siver & Glew 1990; Siver 1991). Smaller, rather than larger, scales can better fit around the curved posterior end that encloses the cell, compared to the larger body scales covering the middle sections of the cell. The thickened anterior submarginal ribs were possibly used to aid in spacing and orientating the scales within the cell covering, in a similar fashion to the role of the V–rib (Siver & Glew 1990). This may have been especially important given the small and narrow nature of the posterior rim which would not aid in spacing the scales.

Based on the models developed by Siver (2022) using scale surface area to predict cell length, and scale length to predict cell width for fossil taxa, the mean cell dimensions for *M. gigantica* would have been 80 × 22 µm, with the largest cell estimated to have been 100 µm × 26 µm. The mean estimated size of *M. gigantica* cells is approximately four times larger than the mean for modern species and twice as large compared to the mean value for all known fossil species (Siver 2022). The largest cells estimated for *M. gigantica* are 60% larger than any known modern species. According to Siver (2022), the large cells of fossil species, coupled with large heavy scales, may have been slow swimmers and more prone to predation, and would have had to expend more energy to maintain their position in the water column.

In summary, *M. gigantica* produced the largest known scales known for the genus, and it is estimated to have had large, probably slower, swimming cells. This adds yet another fossil species from the early Cenozoic with large scales and supports the hypothesis that scale size for lineages that lacked a V–rib has declined over recent geologic time. *Mallomonas gigantica* was probably a stem lineage of either section *Planae* or section *Punctiferae*.

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