Mallomonas elephantus sp. nov. (Synurophyceae), an Extinct Fossil Lineage Bearing Unique Scales from the Eocene

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With 5 figures

Abstract: A new fossil species of *Mallomonas*, *M. elephantus* sp. nov., is described from an Eocene maar lake situated near the Arctic Circle in northern Canada. The new species has three distinctly different types of scales, craspedodont bristles, and is believed to represent a stem taxon of the section *Planae*. Body scales are large, oval to square-shaped, with a shallow U-shaped transverse rib centrally positioned on the base plate, large rimmed pores at the base of the posterior rim, and large widely-spaced papillae. The anterior margin of a second, and smaller, scale type bends sharply 90° to the right forming a unique type of extension and resulting in a highly asymmetrical shape. The size of the asymmetric scales is highly variable, and this scale type likely covered the posterior end of the cell. The third scale type has a triangular-shape caused by a short projecting spine. The variation in size of the triangular scales is small and these scales are believed to have formed a ring around the flagellar pore. Bristles are long with smooth, rolled shafts, and a broad flat foot. The surface area of body scales is about three times the size of the mean for modern species, supporting the hypothesis that many extinct synurophyte species had gigantic scales. Based on a model relating scale length to cell length, the size of *M. elephantus* cells is estimated to have been twice as large as the mean for modern species.

Key words: Eocene, extinct, fossil, *Mallomonas*, new species, synurophytes, Synurophyceae.

Introduction

Mallomonas Perty, the largest genus within the heterokont Synurophyceae clade, consists of motile, unicellular, freshwater organisms commonly found in the plankton of lakes, ponds, bogs and wetlands (Kristiansen 2005, Siver 2015a). The most diverse floras of synurophytes are commonly observed from habitats that are slightly acidic,

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dilute, poorly buffered, with low to moderate concentrations of nutrients and humic substances (Siver 1995). The *Mallomonas* cell consists of a series of relatively flat, siliceous structures, or scales, that are organized into a covering surrounding the entire plasma membrane with the exception of a small pore from which the flagellum emerges. Practically all species of *Mallomonas* possess a second type of siliceous component known as the bristle. Bristles are long, needle-like structures composed of a foot and shaft (Siver 1991, Kristiansen 2002). The foot is flattened, bent at an angle relative to the shaft, and tucked under the apical end of a scale, allowing the shaft to radiate outwards from the cell. The ultrastructural details of the scales and bristles are of taxonomic significance at the species level, a concept well supported by molecular phylogenetic studies (Jo et al. 2011, 2013, Škaloud et al. 2012; 2014).

In his monograph on *Mallomonas*, Kristiansen (2002) recognized 172 taxa that could be distinguished on the basis of examination of the siliceous components with electron microscopy. Other species have since been described using EM (e.g. Kristiansen & Preisig 2007, Němcová et al. 2012, 2015). In addition to species known well with EM, there are numerous taxa that were originally described with light microscopy (LM), but where the ultrastructural details of the siliceous components remain unknown (Kristiansen 2002, 2005). This has resulted in a discrepancy between the two different methods, and it is unlikely that the identity of many of the species described with LM will ever be known.

All *Mallomonas* scales consist of a base plate with an upturned rim along the posterior margin. The base plate is usually partially or fully perforated with pores, and the upturned rim usually encircles about one-half of the scale perimeter (Siver 1991). Scales of many species contain additional structures on the external surface, including ribs, reticulations, papillae, anterior submarginal ribs and V-ribs, collectively referred to as secondary structures (Wee 1982, Siver 1991, Kristiansen 2002). The V-rib is a prominent ridge of silica with a base in the proximal region of the scale, and arms that extend to about the middle of the scale. The V-rib is involved in spacing and aligning the scales on the cell coat (Siver & Glew 1990), and is of significance in the evolutionary history of the genus (Jo et al. 2011, Siver et al. 2015). The overall design of the base plate and secondary structures is unique at the species level, and therefore of taxonomic significance.

Recently, Siver et al. (2015) used a combination of morphometric, molecular and paleobiological methods to summarize what is known on the evolutionary history of synurophytes. The study included morphometric data on 100 modern taxa and 27 fossil species, and molecular data on 40 modern species. Siver et al. (2015) found that *Mallomonas* diverged from other synurophytes during the Early Cretaceous at 130 Ma, and soon thereafter the genus further split into two major subclades, signaling the evolution of the V-rib. These authors further noted that the group of extinct fossil species lacking modern counterparts had gigantic scales, significantly larger than those found on modern taxa, and that the large scale size may have played a role in their demise. The purpose of this paper is to describe a new species of extinct *Mallomonas* from an ancient Eocene Arctic lake with large scales featuring a unique suite of features.

Materials and methods

Samples from the Giraffe core are identified with a three-part number (Siver 2015b). The first number represents the core box. The larger the number, the deeper the section is within the core. Box 11 represents the top and end of the lacustrine phase within the 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 cm 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 13-1-130, 14-1-40, 14-1-60 and 15-1-15.

Mudstone fragments (50–100 mg) from each section of the Giraffe core examined were oxidized using 30% H_2O_2 under low heat for a minimum of an hour, rinsed with distilled water, and the slurries stored in glass vials at 4°C. This mild oxidation procedure results in separation of many siliceous microfossils from the mudstone matrix as well as small remaining fragments. 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 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 Polaron Model E sputter coater. Samples were examined with a Leo (Zeiss) 982 FESEM or a FEI Nova NanoSEM 450 field emission scanning electron microscope (SEM).

Measurements of scales were made directly from electron micrographs. The length and width estimates for the asymmetric scales do not include the right-sided extension of the margin. Three measurements are given for the triangular-shaped scales: the width including the apical spine; the length from the base of the posterior rim to the opposing margin and; the width between the opposing ends of the posterior rim.

SITE DESCRIPTION: The Giraffe Pipe locality (64°44'N, 109°45'W) is a kimberlite diatreme that was emplaced into the Slave Craton in the Northwest Territories of Canada approximately 47.8 million years ago during the middle Eocene (Siver & Wolfe 2005, Wolfe et al. 2006). The diatreme crater filled with water, becoming a maar lake, and slowly infilled 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 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. An air-fall tephra bed located near the end of the aquatic phase was dated at approximately 40 million years using fission tracking (Doria et al. 2011), indicating that the lake sediments were deposited during the Eocene. We envisage that, after phreatomagmatic kimberlite emplacement, a waterbody formed within the crater that persisted for hundreds of thousands of years, varying in depth and physical attributes over time, slowly infilling, and eventually transitioning to a terrestrial environment.

Results

Mallomonas elephantus sp. nov. Siver & Wolfe

Cells of *Mallomonas elephantus* possess three types of scales, body scales, scales with a large, trunk-like extension along one margin, and triangular-shaped scales (Figs 1–4). Body scales are large, range in size from 6.7–9.6 × 4.4–6.1 μm, and possess a broadly rounded posterior margin, and a square-shaped anterior end (Figs 1; 4A–B; 5). The mean size of body scales is 7.8 × 5.3 μm. The posterior rim is shallow and encircles approximately half of the scale perimeter. A shallow, U-shaped rib crosses the scale
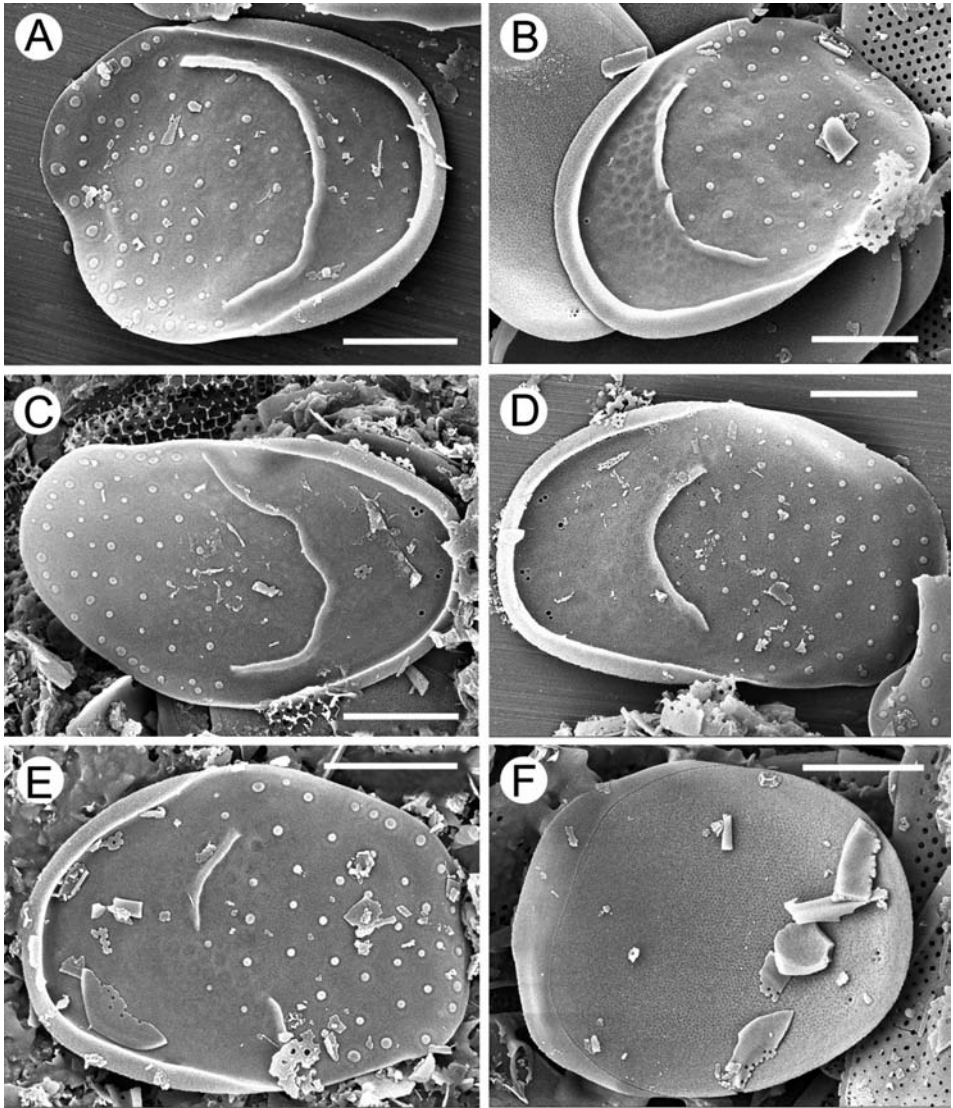
Fig. 1. Body scales of *Mallomonas elephantus*. Note the square (A–B, E–F) to oval (C–D) shape, position of the U-shaped transverse rib, the posterior rib encircling approximately 1/2 the scale perimeter, and the widely-spaced surface papillae. The size, arrangement and distribution of base plate pores is shown on the undersurface of the scale (F). The variability of the transverse rib ranges from wide (A), to shallow (D), to interrupted (B), to irregular (C), to incomplete (E). Note the positions of isolated (A–B) and small groups (C–D, F) of rimmed pores in the posterior region of the scale. Scale bars = 2 μm.
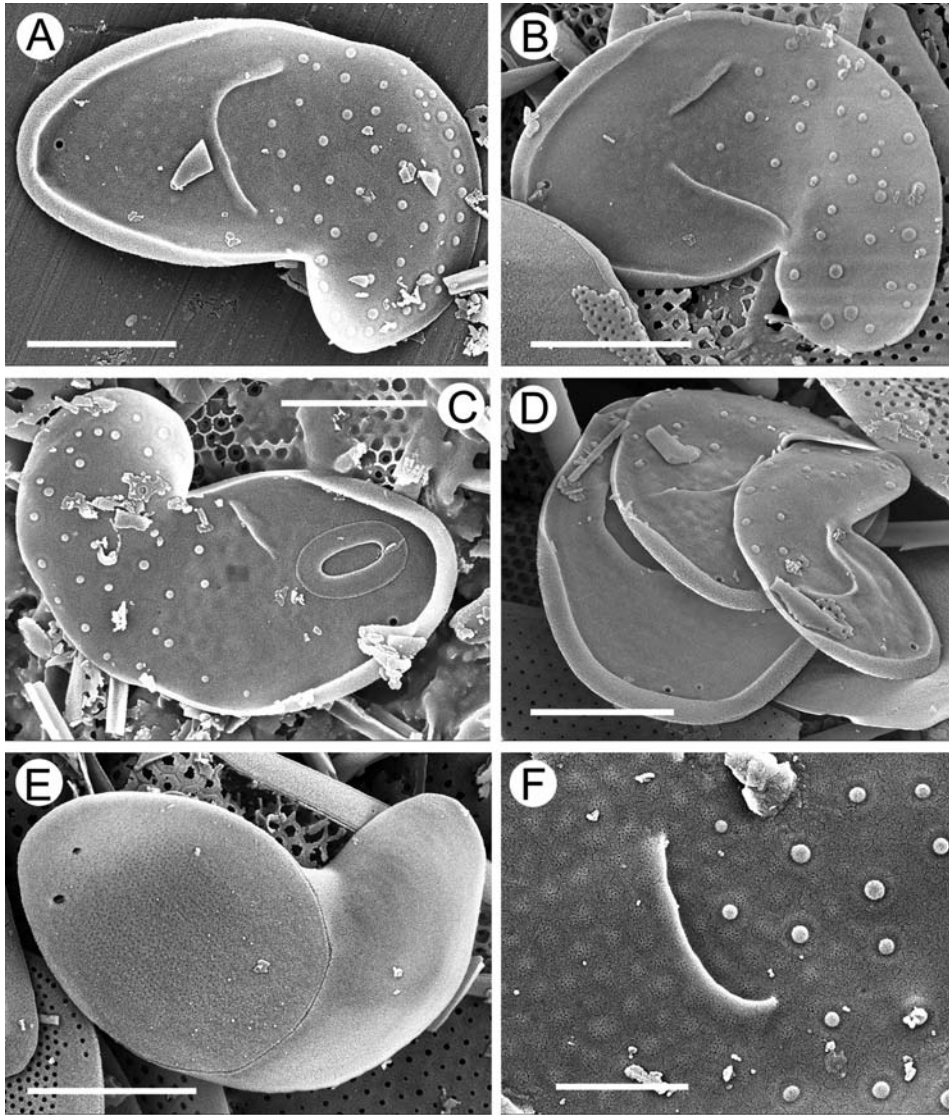
Fig. 2. Asymmetric scales of *Mallomonas elephantus* with the anterior margin bending 90° to the right side forming a trunk-like extension (A–E). Note the arrangement of large papillae on the anterior half of the scale, the distribution of large rimmed pores, and position of the posterior rim. The shape of the transverse rib ranges from complete (A, D), to interrupted (B), to incomplete (C). E) Undersurface of a scale denoting the base plate pores and delineation of the trunk-like extension. F) Close-up of the central region denoting a small transverse rib, the relative arrangement of surface papillae, and groups of surface pores. Scale bars = 1 μm (F) and 2 μm (A–E).
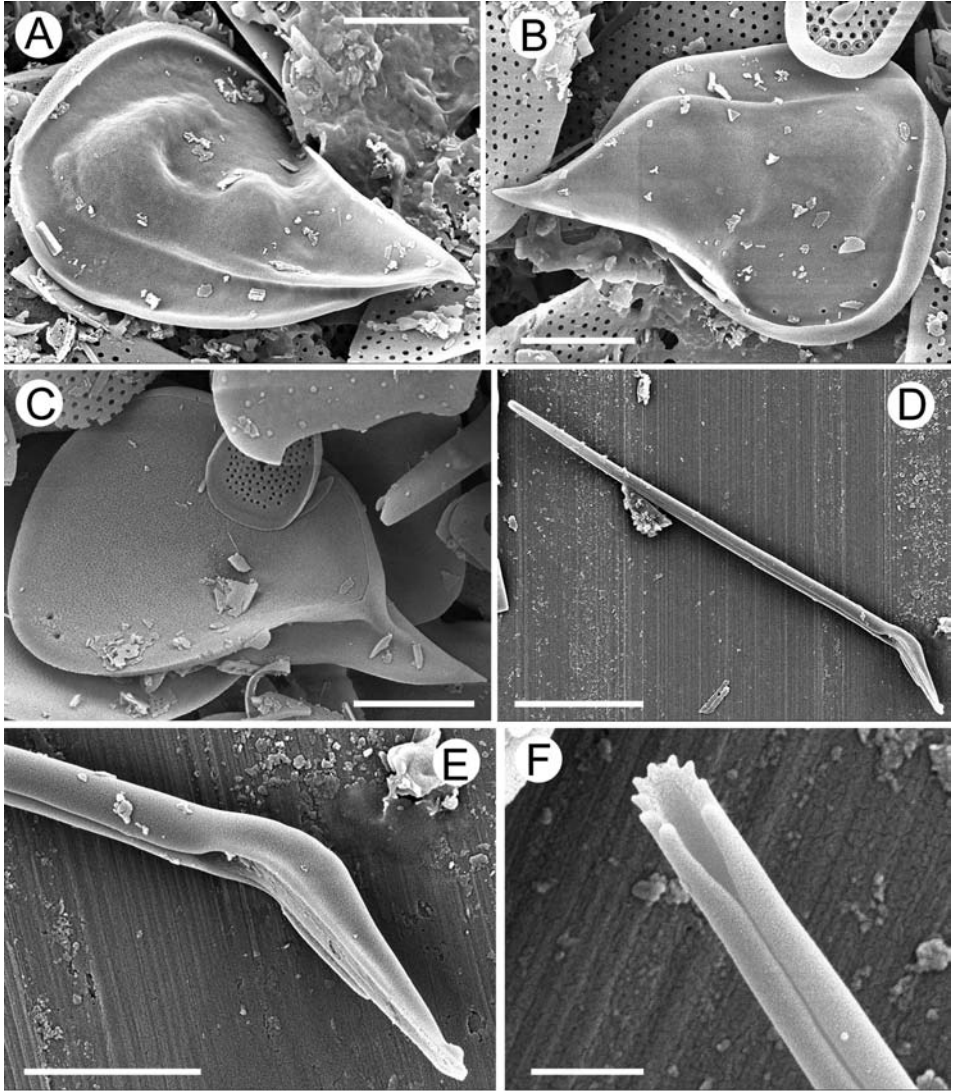
Fig. 3. Triangular-shaped scales (A–C) and bristles (D–F) of *Mallomonas elephantus*. A–C) Note the extention of the spine to the left side of the scale relative to the posterior rim, and the irregularly raised portion of the base plate on the triangular-shaped scales. D) Whole bristle depicting the large foot, smooth and rolled shaft, and toothed distal apex. E–F) Close-ups of the foot and distal apex of the bristle in "D." Scale bars = 500 nm (F), 2 μm (A–C, E) and 5 μm (D).

approximately 2/3 the distance from the anterior margin with the ends becoming aligned with the ends of the posterior rim (Figs 1A–D). The transverse rib is highly variable, ranging from small (Fig. 1D), to large (Fig. 1A), to interrupted and incomplete (Figs 1B,
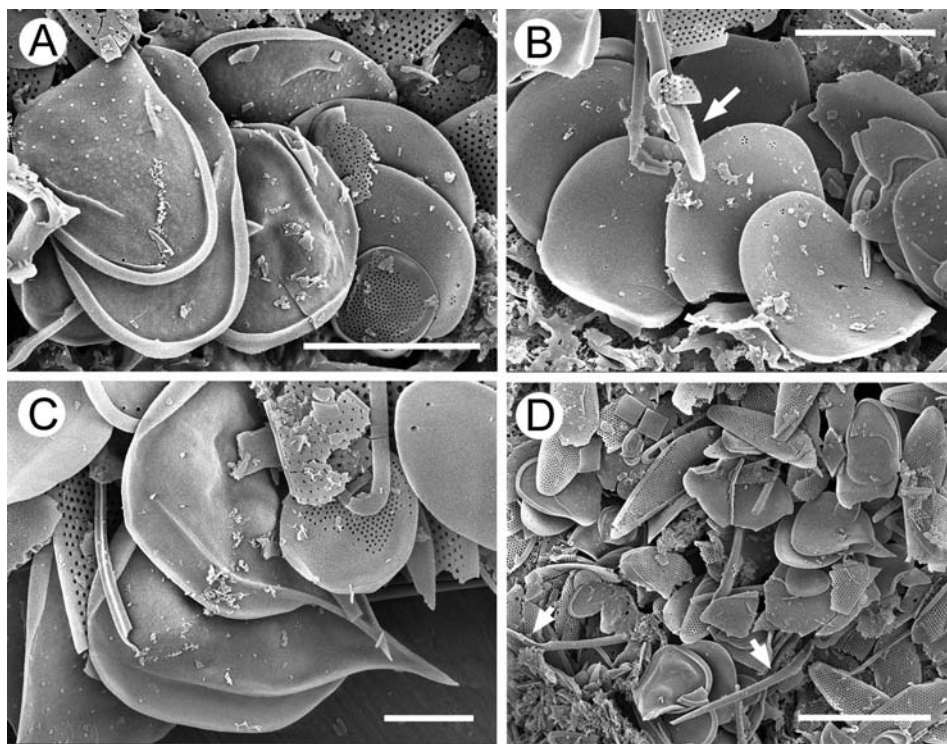
Fig. 4. Micrographs of fractured mudstone surfaces containing numerous scales, especially representing *Mallomonas elephantus* and *Synura cronbergiae*. A–B) Groups of body scales of *M. elephantus* showing the surface and undersurface of the scales. The arrow in (B) denotes the foot of a bristle. C) Several triangular-shaped scales of *M. elephantus* possibly still overlapped in their original positions. D) Rock surface showing all three types of scales and bristles of *M. elephantus*, and remains of *S. cronbergiae* scales. The arrows denote the foot portions of bristles. Scale bars = 2 μm (C), 5 μm (A–B) and 10 μm (D).

E), to sometimes missing altogether. Large widely-spaced papillae cover the anterior half of the scale, but are lacking in the posterior region behind the transverse rib (Figs 1A–E). Three types of pores are found on body scales. The posterior two-thirds of the base plate has small, evenly-spaced pores easily observed on the undersurface of the scale (Fig. 1F). However, the base plate pores are not visible on the scale surface. A second, much larger type of pore with a reinforced rim penetrates the base plate along the posterior rim. The number and spacing of the large pores is highly variable. Many scales have one or two isolated pores, while others have multiple clusters of one to four (or more) pores each. Lastly, distinct groups of roughly 10 to 15 very small pores cover the majority of the scale surface (Fig. 2F), however, these pores are only observed from the surface of the scale and can't be detected from the undersurface (Fig. 2E).

The second type of scale is significantly smaller and more oval-shaped than the body scales, but highly asymmetrical caused by the anterior end bending 90º to the right

side, forming a trunk-like extension (Figs 2A–E). The asymmetric scales are highly variable in dimensions, range in size from 3.8–6.5 × 1.6–4.0 µm (Fig. 5), and the wing can extend up to 2 µm past the perimeter. Most of these scales have either a shallow, or more often incomplete, transverse rib. The majority of asymmetric scales have one or two large posterior rimmed pores (Figs 2A–E), and all possess the large surface papillae and groups of very small surface pores. As viewed from the underside, the wing portion lacks base plate pores and is clearly delineated from the remainder of the scale (Fig. 2E).

The shape of the base plate on the third type of scale is more circular, but takes an overall triangular-shape as a result of a forward projecting spine (Figs 3A–C; 4C–D). These scales lack the transverse rib, the groups of small surface pores, and rarely possess surface papillae. Scales range in size from 6.7–8.3 µm (with the spine) × 5.1–5.4 µm × 4.5–5.3 µm (Fig. 5). From one to four large rimmed pores are found at the base of the posterior rim, and the anterior margin is reinforced with a thick rib. The center of the scale is irregularly raised relative to the base plate (Figs 3A–B), forming a shallow cavity (Fig. 3C).

Bristles of *M. elephantus* range in length from about 20 to 38 µm, are craspedodont with rolled shafts that are smooth and hollow, and a broad, flat foot that can reach 3 to 4 µm in length (Figs 3D–F). The apical tip is often lined with small teeth (Fig. 3F).

Numerous fractured rock surfaces containing rich assemblages of in-situ scales, especially of *M. elephantus* and *Synura cronbergiae* Siver, were examined in an attempt to determine the arrangement of scales and bristles on the cell (Fig. 4). Although this task proved to be difficult, several observations are noteworthy. Groups of scales apparently still in relative position to one another were observed. Within these remains, the smaller asymmetric scales with trunk-like extensions were often found to one side of the larger body scales (Fig. 4B). In addition, groups of triangular-shaped scales, some still overlapped, were commonly observed (Fig. 3C). The remains of bristles (arrows, Figs 4B, D) were often broken and no longer associated with the scales. However, the number of bristles was roughly equivalent to the number of apical scales.

HOLOTYPE: Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, CANA 110,023. Material from section 13-1-130 of the Giraffe Pipe core collected by P.A. Siver.

ICONOTYPUS: Figure 1A, uncovered from section 13-1-130 of the Giraffe Pipe core.

EPITHET: *Mallomonas elephantus* is taken from the Latin word for elephant and refers to the trunk-like extension found on the asymmetric scales.

Remains of *Mallomonas elephantus* were uncovered in the 4 sections of the Giraffe core examined in the study, with massive numbers of specimens contained in mudstones from section 13-1-130. This region of the core is dominated by *Synura cronbergiae*, and also contains significant numbers of chrysophyte cysts. Other notable taxa found with *M. elephantus* include remains of *Spiniferomonas*, *Mallomonas pleuriforamen* Siver, Lott, Jo, Shin, Kim & Andersen and an undescribed species of *Mallomonas* that belongs in section *Punctiferae*. In previous publications (e.g. Siver et al. 2015) *M. elephantus* was referred to as *Mallomonas* GP 9.

Discussion

The combination of characteristics of the three scale types of *Mallomonas elephantus* is unlike that found on any known modern species within the genus, leading to the conclusion that this Eocene taxon is extinct. Jo et al. (2011) and Siver et al. (2015) documented that the genus *Mallomonas* split into two major clades in the Early Cretaceous around 130 Ma ago. One clade contains species that have scales with a true V-rib and ribbed bristles often bearing teeth along the shaft. The other major clade, containing the large section *Planae*, has species with scales that lack a V-rib and commonly possess craspedodont bristles. This type of bristle forms when an elongated siliceous sheet folds to produce a hollow shaft with a seam where the margins of the sheet meet (Kristiansen 2002, Siver et al. 2015). Given the lack of a true V-rib, coupled with craspedodont bristles, *Mallomonas elephantus* represents a stem taxon within the clade lacking this former structure. Although the position of *M. elephantus* within the clade is difficult to determine, this species does share some features with taxa in the Series *Peronoides* of the section *Planae*. Series *Peronoides* diverged at 111 Ma, at the base of the large clade with species lacking a V-rib. Like *M. elephantus*, taxa in series *Peronoides* have specialized triangular-shaped apical scales with a forward projecting spine, and body scales with a central thickened rib. However, other features of *M. elephantus*, such as the scales with trunk-like extensions, are unique. As additional fossil species are uncovered, a better understanding of the placement of *M. elephantus* within the phylogeny can be made.

A possible hypothesis regarding the arrangement of scale types on the cell covering of *M. elephantus* is that the triangular-shaped scales surrounded the anterior flagellar pore, the body scales were arranged along the majority of the cell surface, and the smaller asymmetrical scales were localized in the posterior region. Triangular-shaped scales similar in structure to those on *M. elephantus* are commonly found arranged in a ring around the flagellar pore with the spines directed outward from the cell (Kristiansen 2002). For example, similar shaped scales surrounding the flagellar pore are found on some species within the section *Planae*, including *M. peronoides* (Harris) Momeu & Péterfi and *M. bangladeshica* (Takahashi & Hayakawa) Wujek & Timpano, and on species within the section *Punctiferae*. This scale type has also been noted on fossil species, such as *Mallomonas schumachii* Siver (Siver 2015b). In addition, scales that surround the flagellum pore typically have a small range in size (Kristiansen 2002), probably because these scales need to fit precisely within the ring surrounding the emergent flagellum. It is most reasonable to assume that the triangular scales of *M. elephantus*, which have a narrow size range (Fig. 5), served a similar function in encircling and forming the flagellar pore.

Unlike the triangular-shaped scales, the position of the highly asymmetric scales on the cell covering, as well as the function of the 90° extension from the anterior margin, are less clear. In fact, there are no known species, modern or fossil, that have this type of structure. There are several modern species, for example *Mallomonas vannigera* Asmund, *M. pseudocoronata* Prescott and *M. duerrschmidtiae* Siver, with wing-like extensions. However, the structures on these modern species all originate from submarginal ribs and extend upward from the base plate away from the cell. On
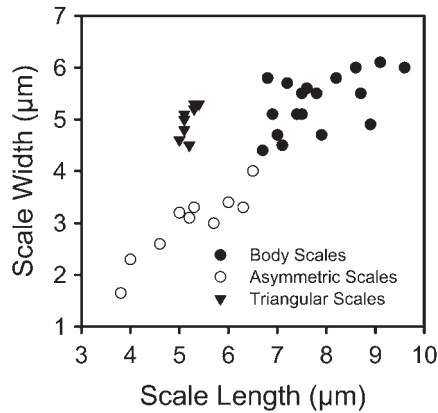
Fig. 5. Scatter plot of scale length versus scale width for body, asymmetric and triangular-shaped spine scales of *Mallomonas elephantus*.

M. elephantus scales the extension is a continuation of the margin and is more or less on the same plane as the base plate. One possible role of this structure was to aid in attaching bristles. However, it is not known if bristles were even associated with this scale type, and there is no evidence that the extension wrapped around the shaft or formed a cavity to accommodate the bristle foot. *Mallomonas* species with large body scales, as is the case for *M. elephantus*, often produce smaller scales with modified designs to more efficiently bend around and cover the posterior end. Furthermore, specialized posterior scales often have a larger range in size since they typically become progressively smaller closer to the caudal end of the cell. Given their smaller size and high degree of size variability, the asymmetric scales were likely found on the posterior end of the cell. If this is true, the extensions could have offered a more proficient means by which the organism formed a complete scale covering around the posterior end of the cell.

The V-rib structure found on many species of *Mallomonas* is proposed as a mechanism to evenly space and align scales and bristles into a highly organized arrangement on the cell surface (Siver & Glew 1990, Siver 1991). In a recent study of the evolutionary history of the synurophytes, Siver et al. (2015) noted that a few species in the clade lacking a V-rib, such as *Mallomonas bangladeschica* and *M. heterospina* Lund, evolved different types of rib designs that probably function like, but are analogous to, a true V-rib. The transverse rib found on *M. elephantus* scales falls into this category and likely evolved to serve a similar role in aligning scales on the cell. However, given the large degree of variability in the structure it was probably less efficient than a well formed V-rib.

Based on rough estimates of the ratio of scales to bristles made from fractured rock surfaces, it is clear that not all scales were associated with bristles. Rather, the number of bristles was similar to the number of triangular-shaped scales, and it is possible that only these scales had bristles. However, the possibility that bristles

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were associated instead with the asymmetric scales, or both scale types, can't be ruled out. The craspedodont bristles of *M. elephantus* are stout and wide structures with a relatively large and flat foot compared to modern forms (Siver et al. 2015). Other fossil species from the Eocene that are within the section *Planae*, including *M. porifera* (Siver & Wolfe 2010) and *M. schumachii* (Siver 2015b), also have thick, hollow bristles with more complex foot structures as compared to modern species. This suggests that the evolutionary trend for the craspedodont bristle type has been a reduction in width, size and complexity of the foot, likely coincident with a reduction in overall scale size.

The formation of pores in the posterior region of the scale that are greater in diameter than base plate pores is not unique to *M. elephantus*. Rather, isolated or groups of such pores are quite common within the genus, and found in both of the major clades identified by Siver et al. (2015). One or two isolated pores are found in diverse taxa such as *Mallomonas matvienkoae* (Matvienko) Asmund & Kristiansen, *M. rasilis* Dürrschmidt and *M. binocularis* Siver, while linear arrays are present in *M. maculata* Bradley, *M. favosa* Nicholls and *M. mangofera* Harris & Bradley. Groups of closely spaced large pores most similar to those found in *M. elephantus* are present on scales of *M. matvienkoae* var. *myakkana* Siver and var. *grandis* Dürrschmidt & Cronberg, and on the fossil species, *M. pleuriforamen*. Differences in the structure and distribution of pores can be an effective character used to distinguish between species (Kristiansen 2002, Siver 2002, Jo et al. 2013). The function of these large pores is unknown. Perhaps these pores are involved in distributing adhesives used to help hold scales in position, especially in species lacking other pores that penetrate the base plate.

Based on an in-depth analysis of the differences in scale size between fossil and modern species of *Mallomonas*, Siver et al. (2015) reported that extinct species have significantly larger scales than modern taxa. In that study, body scales of modern species had a mean size of 4.3 × 2.8 μm as compared to 8.7 × 4.2 μm for extinct taxa lacking modern analogs. On average, the surface area of extinct species was 3 times greater than modern forms. With a mean size of 7.8 × 5.3 μm, body scales of *M. elephantus* are also significantly larger than the average body scale found on modern species. Siver et al. (2015) further established a significant relationship between scale length and cell length for modern species. Assuming this relationship is valid for fossil taxa, cells of *M. elephantus* are estimated to have been approximately 40 μm long as compared to the mean of 22 μm for modern species. Thus, as hypothesized by Siver et al. (2015) for other extinct species of *Mallomonas*, the gigantic and heavy scales found on *M. elephantus*, coupled with potentially large cells, may have proved disadvantageous for survival during the warm greenhouse climates of the middle Eocene, eventually resulting in its demise. Perhaps large and heavy cells were cumbersome, more difficult to propel through the water, and subject to increased sinking rates given the lower densities associated with warmer water. Lastly, scale size and surface area for this species is comparable to the means for other extinct forms, including *Mallomonas porifera* Siver & Wolfe (Siver & Wolfe, 2010) and *M. media* Siver & Lott (Siver & Lott 2012), supporting the hypothesis that the size of scales has declined over recent geologic time.

Acknowledgements

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