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Mallomonas skogstadii sp. nov. and *M. bakeri* sp. nov.: Two new fossil species from the middle Eocene representing extinct members of the section Heterospinae?

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Abstract – Two new fossil species of the synurophyte genus *Mallomonas*, *M. skogstadii* and *M. bakeri*, are described from Giraffe Pipe, an Eocene locality situated near the Arctic Circle in northern Canada. Scales of both new species share a suite of characters, including an oval-shaped rib encircling approximately half of the base plate and most of the dome, a series of thick ribs on the posterior flange, but lacking on the shield, a thin posterior rim, and a flat and shallow dome. In addition, both species possess two types of scales, body scales and apical scales. Apical scales of *M. bakeri* form a unique forward-projecting dome, and those of *M. skogstadii* are significantly different in shape than the body scales. Scales of *M. skogstadii* are significantly larger and have a different base plate pore pattern than those of *M. bakeri*, and remains of both taxa were uncovered in strata deposited hundreds of years apart. Based on comparison made with modern species, *M. bakeri*, and to a lesser extent *M. skogstadii*, are placed into, and likely represent basal representatives of section Heterospinae. The floras associated with each species reflect acidic environments, probably high in dissolved humic content.

INTRODUCTION

Mallomonas Perty, the largest genus within the heterokont Class Synurophyceae, is a common component of plankton communities in lakes, ponds, bogs, wetlands and slow moving lentic systems (Siver, 2015a). The genus consists exclusively of motile unicells possessing 1-2 emergent flagella, and a unique cell covering consisting of species-specific siliceous scales precisely arranged on the cell membrane. The vast majority of species possess a second type of siliceous structure, the bristle, needle-like structures that attach to the anterior ends of the scales and radiate outward from the cell surface (Siver, 1991; Kristiansen, 2002). The structures of scales and bristles are important characters for distinguishing between species, a concept well supported by molecular works (e.g. Jo *et al.,*, 2013; Škaloud *et al.,*, 2012; 2014).

Kristiansen (2002) listed 172 taxa of *Mallomonas* classified into 19 sections, delimited largely by features of the scales and bristles determined with electron microscopy. Although an exhaustive list has not been published since 2002, additional species have been described (e.g. Kristiansen & Preisig 2007; Němcová *et al.,*, 2008; 2012; 2015; Jo *et al.,*, 2013; Kim *et al.,*, 2014; Gusev, 2015; Gusev *et al.,*,

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2016; 2017; Gusev & Siver, 2017; Siver & Lott, 2016). There are also many species validly described with light microscopy, but lack the resolution of detail attained with electron microscopy. Only a portion of these species have been successfully linked with taxa known from electron microscopy (Kristiansen, 2005).

Details of scale ultrastructure are well known and described in detail by Wee (1982), Siver (1991) and Kristiansen (2002). Briefly, scales of all species consist of a base plate partially or wholly perforated with pores, and an upturned posterior rim that on most species encircles approximately half of the scale perimeter. Scales of most species contain additional structures on the external surface referred to as secondary features. These include various arrangements of ribs, papillae, and on many scale types a prominent ridge generally in the form of a V and appropriately named the V-rib. The bottom of the V-rib is positioned on the base plate in the proximal region, and the arms extend forward towards the distal end of the scale. The distal end on many scale types is raised with a hollow undersurface, or cavity, into which the base of the bristle fits. This structure, termed the dome, can take many shapes and designs. On some species, the scales lack domes, but still have the bristle tucked under the distal scale margin.

Based on gene sequence data, the genus *Mallomonas* is divided into two major clades differentiated on the presence or absence of a V-rib on the scale and bristle morphology (Jo *et al.,* 2011; 2013; Siver *et al.*, 2013b; 2015). Divergence of the two clades is estimated to have occurred during the Early Cretaceous approximately 124 Ma ago (Siver *et al.*, 2015). The clade lacking the V-rib structure is composed of taxa classified by Kristiansen (2002) belonging to the section Planae, which includes four series, Caudata, Matvienkoae, Teilingianae, and Peronoides. Results of the molecular studies showed that *Mallomonas heterospina* in the sectio Heterospinae also belonged in the clade lacking a V-rib, prompting Jo *et al.,* (2011; 2013) to recommend section Heterospinae be transferred to section Planae and included as a fifth series. To date, although the transfer is well supported by molecular and morphological data, it has not officially been proposed. Since only one member of section Heterospinae has been sequenced and included in the molecular phylogeny, it is perhaps wise to delay the official transfer until additional species can be included in future analysis.

With the exception of two localities, Giraffe Pipe (Siver and Wolfe, 2005; 2009) and Wombat Pipe (Siver *et al.*, 2013a), there is no fossil record of synurophyte scales and bristles. The waterbody represented in the maar crater at the Giraffe locality holds a wealth of fossil scales and bristles that have been used to trace aspects of the evolutionary history of synurophytes (Siver *et al.,* 2015). To date, 14 fossil species of *Mallomonas* have been described from the middle Eocene Giraffe Pipe locality (Table 1). The purpose of this paper is to describe two additional species with unique scale structures and tentatively placed in section Heterospinae.

SITE DESCRIPTION

The Giraffe Pipe locality (64º44’ N, 109º45’ W) represents 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 crater subsequently partially filled with water forming a maar lake. Over time, the crater slowly infilled with a sequence of

Table 1. Fossil species of *Mallomonas* described from the Eocene Giraffe Pipe locality in northern Canada, including the range in size of body scales.

Species & Authority	*Range in Size Body Scales (µm)*	*Reference*
M. giraffensis Siver & Wolfe	8-11 x 5-6.5	Siver & Wolfe, 2005
M. convallis Siver & Wolfe	5-6 x 4-4.5	Siver & Wolfe, 2005
M. porifera Siver & Wolfe	6-7 x 4.5-5.5	Siver & Wolfe, 2005
M. pseudohamata Siver & Wolfe	2-3 x 2-2.5	Siver & Wolfe, 2005
M. pseudocaudata Siver & Wolfe	5-6 x 4-5	Siver & Wolfe, 2005
M. dispar Siver, Lott & Wolfe	3-3.9 x 2.4-2.6	Siver et al., 2009
M. lancea Siver, Lott & Wolfe	5.4-7.3 x 3.1-4.2	Siver et al., 2009
M. media Siver & Lott	8-11 x 5-6.5	Siver & Lott, 2012
M. preisigii Siver	3.5-4 x 2-2.2	Siver & Lott, 2012
M. ampla Siver & Lott	4.7-6.7 x 3.1-4.1	Siver & Lott, 2012
M. pleuriforamen Siver, Lott, Jo, Shin, Kim & Andersen	6.8-7.4 x 5.6-6.3	Jo et al., 2013
M. schumachii Siver	7.2-9.9 x 6.2-8.7	Siver, 2015b
M. elephantus Siver & Wolfe	6.7-9.6 x 4.4-6.1	Siver & Wolfe, 2016
M. aperturae Siver	5.9-8.8 x 3-4.3	Siver, 2018
M. skogstadii Siver	7.6-9.8 x 3.2-5.3	This paper
M. bakeri Siver	3.6-4.8 x 2.5-3.3	This paper

lacustrine, then paludal sediments, and was eventually capped by Neogene glacial deposits (Siver & Wolfe, 2005; Wolfe *et al.,* 2006). Giraffe Pipe is one of numerous kimberlites in the Lac de Gras field, most of which have Cretaceous or Paleogene emplacement ages (Heaman *et al.,* 2004; Sarkar *et al.*, 2015). A 163 m long drilled core, collared at a 47º 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, terrestrial and paludal remains. The waterbody within the crater persisted for hundreds of thousands of years, varying in depth and physical attributes over time, slowly infilling, and eventually transitioning to a terrestrial environment. The entire sequence was formed during the middle Eocene.

MATERIALS AND METHODS

Sections of 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 end of the lacustrine phase within the sequence. Each box contains three 1.5 m core lengths, identified as channels 1, 2 and 3, accounting for 4.5 m of mudstone per core box. The second number represents the channel. The third number is the measurement in cm down from the top of a core length. For example, 16-2-22 represents a sample taken from 22 cm down along the core length positioned in channel 2 from box 16. Over 150 sections from the Giraffe Pipe core have been examined to date for synurophyte remains. Samples from six sections, all from core boxes 14 or 16, contained numerous specimens of one, but not both, of the new species described in this paper (Table 2). Samples containing the new species from boxes 14 and 16 span 52 cm and 20 cm of vertical core length, respectively. Although the precise number of years represented by the two core lengths is not known, each is estimated to cover hundreds of years (Siver & Wolfe, 2009). The approximately 7 m between the two core lengths most likely accounts for several thousand years.

Mudstone fragments (0.5 g) from each section of the Giraffe core examined were oxidized using 30 % H_2O_2 under low heat for a minimum of an hour and rinsed five times with repeated centrifugation. The resulting slurries were stored in glass vials at 4 ºC. This mild oxidation procedure resulted in separation of numerous siliceous microfossils from the mudstone matrix, as well as small fragments still containing collections of microfossils. An aliquot from each slurry was air dried onto a piece 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 a Leo (Zeiss) 982 field emission scanning electron microscope (FESEM), or an FEI Nova NanoSEM 450 FESEM. Measurements of scales were made directly from electron micrographs. When appropriate, the length measurements include the extended dome structures.

Table 2. Locations of strata from the Giraffe Pipe core harboring *Mallomonas skogstadii* and *M. bakeri*. Vertical depths within the core, and common taxa found in each sample, are given.

Taxon	*Core sample*	*Corrected vertical depth (m)*	*Common associated taxa*
M. skogstadii	16-2-22	87.29	*M. lychenensis*, *M. porifera*, *M. multiunca* var. *pocosenensis*, *M. aperturae*, *M. dispar*, *Synura cronbergiae*, *Eunotia* spp., *Oxyneis apporrecta*
	16-2-49	87.49	*M. lychenensis*, *M. porifera*, *M. multiunca* var. *pocosenensis*, *M. aperturae*, *M. dispar*, *Synura cronbergiae*, *Eunotia* spp., *Oxyneis apporrecta*
M. bakeri	14-3-100	80.19	*M. lychenensis*, *M. porifera*, *M. multiunca* var. *pocosenensis*, *Actinella* spp., *Eunotia* spp.
	14-3-130	80.41	*M. lychenensis*, *M. porifera*, *M. multiunca* var. *pocosenensis*, *Chrysosphaerella* sp., *Synura cronbergiae*, *Eunotia* spp.
	14-3-140	80.48	*M. lychenensis*, *M. porifera*, *M. multiunca* var. *pocosenensis*, *M. schumachii*, *Chrysosphaerella* sp., *Synura cronbergiae*, *Actinella* sp., *Eunotia* spp., *Oxyneis apporrecta*
	14-2-22	80.71	*M. lychenensis*, *M. porifera*, *M. multiunca* var. *pocosenensis*, *M. pseudohamata*, *M. media*, *M.* spp., *Synura cronbergiae*, *Actinella* sp., *Eunotia* spp., *Oxyneis apporrecta*

RESULTS

Mallomonas skogstadii Siver sp. nov. **Figs 1-6**

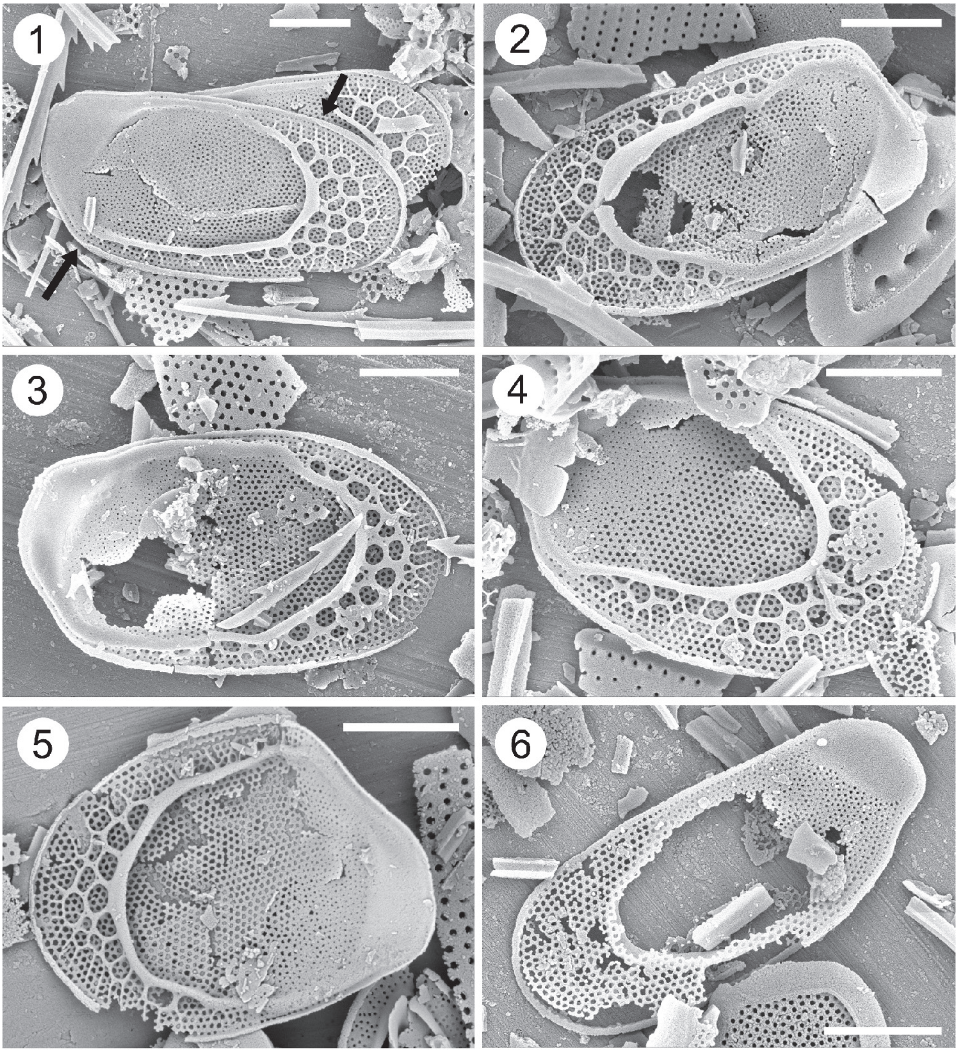
Description: Cells of *Mallomonas skogstadii* possess two types of scales, an elongate-oval body scale (Figs 1-4, 6), and a slightly shorter and broader type of scale (Fig. 5). Body scales are large, range in size from7.6-9.8 ξ 3.2-5.3 µm (n=12) with a mean of 8.5-4.5 µm (Fig. 7), possess a posterior rim, and a roughly oval-shaped rib structure that connects to a forward projecting dome. The base plate is perforated with numerous, evenly-spaced pores. Pores on the flange are much larger in diameter and found immediately juxtaposed to the scale margin where they form precisely-spaced concentric rows (Figs 1-4, 6). Progressing onto the shield, the spacing and size of the pores remains similar to that on the flange, but form a quincunx pattern. The size of the pores reduces abruptly on the anterior 1/3 portion of the shield. The ratio in diameter between posterior and anterior base plate pores is approximately 5:1. The oval-shaped rib is positioned on the posterior end of the scale approximately 2 µm from the posterior rim. The structure extends along both margins, is closer to the right margin, and terminates along the sides of, or continues around, the dome. The oval-rib is often thickest along the posterior end of the scale, but it lacks a defined hood-like structure. A reticulation of ribs extends from the oval structure onto the wide posterior flange and along the left anterior flange (Figs 1-4). The ribs form a series of circular-shaped, secondary structures, each encircling approximately 8-12 large base plate pores. There are two to three layers of circular ribs on the posterior flange, but typically only one along the left anterior flange. No secondary ribs were observed on the shield side of the oval rib. The posterior upturned rib is very thin, approximately 0.2 µm wide, and extends further along the left margin (arrows, Fig. 1). The dome is shallow, flat, devoid of pores or ribs, raised above the base plate, extends 1-2 µm past the base plate on most scales, and is often positioned slightly to the right side, resulting in an asymmetric scale shape. This structure is presumably equivalent to a dome, however, presence of bristles were not confirmed. The second scale type is similar in all aspects to the body scales, but are wider and with a smaller length to width ratio (Fig. 5). This scale type ranged in size from 7.0-7.4 ξ 5.6-6.0 µm (n=5), with a mean of 7.2 ξ 5.8 (Fig. 7), and is believed to represent an apical scale that surrounds the flagellar pore.

Holotype: Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, CANA # 127978. All specimens illustrated are from the Holotype.

Holotype Material: Mudstone collected by P.A. Siver from section 16-2-22 of the Giraffe Pipe core and deposited at the Canadian Museum of Nature, CANA # 127978.

Epithet: *Mallomonas skogstadii* is named in honor of my colleague, friend and synurophyte expert, Dr. Asbjorn Skogstad, Oslo, Norway.

The core samples containing specimens of *Mallomonas skogstadii* had an exceptionally large and diverse array of microfossils. Both samples exhibited a very similar flora, especially dominated by *Mallomonas lychenensis* and *M. porifera*, along with abundant specimens of the diatom genera *Eunotia* and *Actinella*. In addition, specimens of the synurophyte species *M. multiunca* var. *pocosenensis* Siver, *M. aperturae*, *M. dispar* and *Synura cronbergiae*, along with those of the diatom *Oxyneis apporrecta* Siver, Wolfe & Edlund, were common (Table 2). Both samples also contained an array of chrysophyte cysts, euglyphid plates and sponge



Figs 1-6. SEM images of the fossil species, *Mallomonas skogstadii*. **1-4.** Surface views of body scales depicting the oval-shaped rib, different sized base plate pores, thin posterior rim, large posterior flange with reticulation of ribs, and broad and shallow dome. Arrows on Fig. 1 depict the asymmetric position of the posterior rim. **5.** Scale believed to be an apical scale positioned close to, or encircling, the flagellar pore. **6.** Undersurface of a broken body scale missing most of the shield region. Note the flat dome and different sizes of the base plate pores. Scale bars = 2 µm.

spicules. Scales of *M. skogstadii* were previously referred to as *Mallomonas* GP18 in Siver *et al.,* (2015).

Mallomonas bakeri Siver sp. nov. **Figs 8-17**

Description: Cells of *Mallomonas bakeri* possess two types of scales, a circular to oval body scale (Figs 8-13), and a similar sized scale type that is oval and with a large, forward projecting dome-like structure (Figs 14-17). Body scales range in size from 3.6-4.8 ξ 2.5-3.3 µm (n=20) with a mean of 4.3-2.9 µm (Fig. 7), have a posterior rim, a wide posterior flange, and a circular to oval-shaped rib structure that originates near the center of the scale and encircles the shield and dome. The base plate is perforated with large-diameter and evenly-spaced pores that form concentric rows along the posterior margin, and a quincunx pattern in the center of the scale (Figs 8-9). On most scales, the proximal end of the circular to oval rib is positioned near the center of the scale, broadly U-shaped, and continues around the dome. There is a small sharp spine protruding from the oval rib near the center, or slightly to the right side, of the dome (arrows, Figs 8-10, 13). The position of the oval rib results in an overly wide posterior flange, and combined with the anterior flanges account for approximately ½ the total surface area. The oval-rib is often thickest along the posterior end of the scale, but it lacks a defined hood-like structure. A reticulation of smaller ribs extends from the circular oval rib onto the posterior and anterior flanges, but not onto the shield (Figs 8-13). The ribs form one, and sometimes two, rows of large, circular meshes, each enclosing 6-13 base plate pores. The posterior upturned rib is very thin, approximately 0.15-0.2 µm wide, and extends slightly further along the left side of the scale. The dome is broad, shallow, flat, devoid of pores or ribs, raised only slightly above the base plate, and extends approximately 1 µm past the base plate. The proximal end of the dome usually forms a straight transverse edge on the shield. A single row of pores, often alternating with short struts, is situated along each side of the dome. The second type of scale, thought to represent an apical scale, differs from the body scales in four characters.

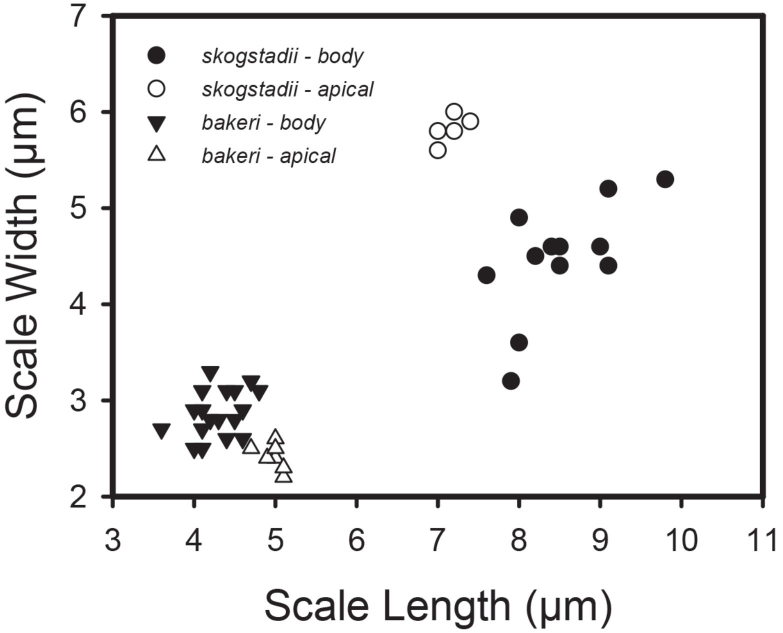
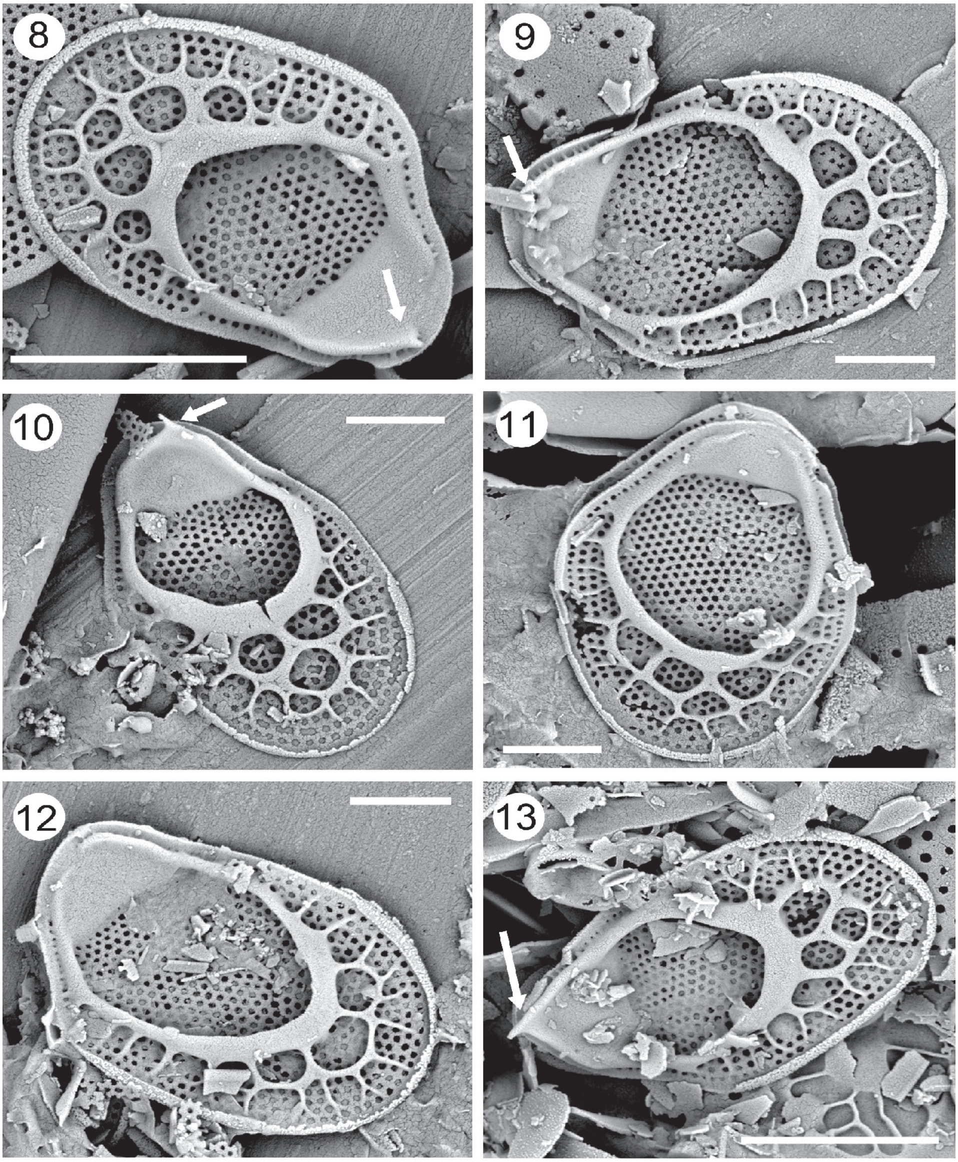
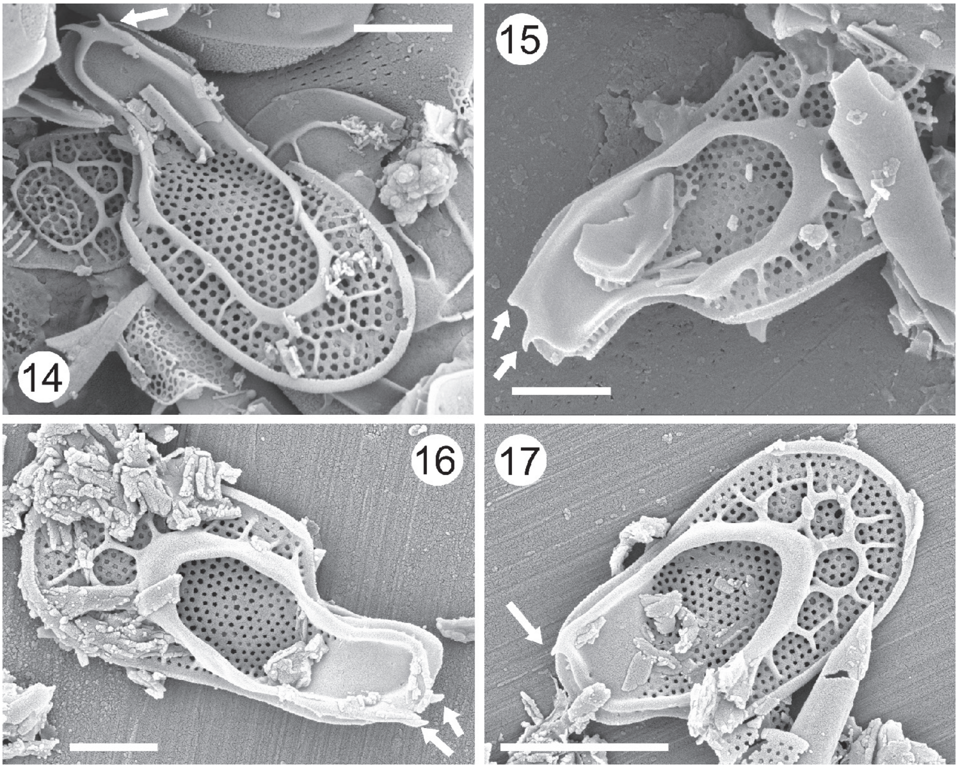


Fig. 7. Plot of length versus width of body and apical scales for *Mallomonas skogstadii* and *M. bakeri*.



Figs 8-13. SEM images of body scales from the fossil species, *Mallomonas bakeri*. Note the large base plate pores, well-defined oval shaped rib, thin posterior rim, large posterior flange with reticulation of ribs, and broad and hyaline dome. Arrows indicate the short spines on the oval rib. Scale bars = 1 µm (Figs 9, 10, 12) and 2 µm (Figs 8, 11, 13).

First, the scales are more elongate and with a larger length to width ratio (Figs 7, 14-17). Second, the dome is greatly extended forward, forming a wing-like structure and positioned to the right side of the scale. Third, the oval rib is much more prominent on the dome. Fourth, there are often two prominent spines on the anterior



Figs 14-17. SEM images of apical scales from the fossil species, *Mallomonas bakeri*, characterized by the large forward-projecting dome. Note the large base plate pores, well-defined oval shaped rib that surrounds most of the dome, and thin posterior rim. Arrows denote the short spines on the oval rib. Scale bars = 1 µm (Figs 14-16) and 2 µm (Fig. 17).

end of the oval rib. Including the wing, this scale type ranges in size from 4.7-5.1 ξ 2.2-2.6 µm (n=7) with a mean of 5.0 ξ 2.4 µm. The wing extends forward between 1-2 µm. Bristle structure is not known.

Holotype: Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, CANA #127979. All specimens illustrated are from the Holotype.

Holotype Material: Mudstone collected by P.A. Siver from section 14-3-130 of the Giraffe Pipe core and deposited at the Canadian Museum of Nature, CANA #127979.

Epithet: *Mallomonas bakeri* is named in honor of Professor Alan Baker, University of New Hampshire, U.S.A., phycologist, limnologist, mentor and friend.

Similar to sections containing *M. skogstadii*, samples containing specimens of *Mallomonas bakeri* also had a large and diverse number of microfossil remains, and strikingly similar floras (Table 2). Like those harboring *M. skogstadii*, ones with *M. bakeri* were also dominated by *M. lychenensis*, *M. porifera*, *Eunotia* spp. and *Actinella* spp. Additional taxa in the samples with *M. bakeri* included *M. schumachii*, *M. pseudohamata*, *M. media*, and *Chrysosphaerella sp*., along with chrysophyte cysts and euglyphid remains.

DISCUSSION

In many respects, scales of *Mallomonas skogstadii*, and especially *M. bakeri*, most closely resemble those found on species belonging to section Heterospinae, and it is highly likely that both fossil taxa represent extinct lineages within this section of the genus. Like the two new fossil taxa, most extant species of section Heterospinae have an oval-shaped rib structure from which other secondary ribs originate, and a similar shaped, shallow, and forward projecting dome on the body scales. Most taxa in section Heterospinae also have thin and relatively inconspicuous posterior rims, base plates covered with regularly-spaced pores, and secondary ribbing forming wide circular structures encircling groups of base plate pores (Kristiensen, 2002), similar to both new fossil species. This collection of features is especially evident on scales belonging to *M. heterospina*, *M. harrisiae*, *M. pugio*, *M. canina* and *M. hindonii* (Siver, 1991; Kristiansen, 2002; Kristiansen & Preisig, 2007), supporting association of the fossil species with section Heterospinae.

A few features of *M. skogstadii* scales differ from contemporary members of section Heterospinae. For example, scales of *M. skogstadii* are significantly larger, with a surface area close to 3 times that for modern species. In addition, the reduction in pore diameter on the anterior of the scale differs from contemporary species which possess largely similar-sized pores across the scale. Perhaps *M. skogstadii* is an older and more basal lineage within the section. In contrast, body scales of *M. bakeri* have a pore pattern and overall size similar to modern species making placement of this taxon in section Heterospinae less problematic. That said, the long forward-projecting dome found on the second scale type for *M. bakeri* has no modern analog. These unique scales are most likely anterior scales, forming a ring around the flagellar pore. Although the extension on these fossil scales is extreme, anterior scales with forward-projecting components are common within the genus, including on some members of section Heterospinae. Anterior scales with extended domes are especially notable on *M. harrisiae* and *M. hindonii*, and in the latter case there is often a bifurcated spine on the oval rib structure (Kristiansen, 2002).

Numerous remains of bristles, especially broken pieces, were present in all samples containing *M. skogstadii* and *M. bakeri*, but most have been assigned to other species of *Mallomonas* and those potentially belonging to either fossil species have not been confirmed at this time. Presumably, bristles were anchored underneath of the flat and shallow dome structures on body scales, as well as associated with scales possessing forward projecting domes. The samples did harbor bristles with thin shafts and hooked apices, a common form for members of section Heterospinae, but examination of rock fragments containing groups of scales and brisles representing whole cell remains indicated this bristle type was associated with *M. multiunca* var. *pocosenensis*. Although numerous scales of both fossil species were contained in the fragment samples, whole cell remains were not observed.

Mallomonas skogstadii is another synurophyte joining a growing list of extinct species that possessed significantly larger scales than the vast majority of contemporary taxa (Siver, 2015b, 2018; Siver & Wolfe, 2016). This list includes *M. elephantus*, *M. schumachii*, *M. aperaturae*, *M. porifera* and *M. media*. According to Siver *et al.,* (2015b), the mean size of body scales of modern species is 4.3 ξ 2.8 µm, yielding an approximate surface area of 12 µm^2, versus 8.7 ξ 4.2 µm and 35 µm^2 for extinct species that lack direct modern analogs. The mean size of body scales for *M. skogstadii* is virtually identical to that of the group of extinct species with large scales. In addition, Siver *et al.,* (2015) proposed a model relating cell size to scale length where species with larger scales had significantly larger cells. Based on this model, cells of *M. skogstadii* were approximately twice as large as the average for modern species. It is possible that large cells, coupled with large and heavy scales, made the cells swim slower and be more prone to predation and sinking out of the euphotic zone. One feature of *M. skogstadii* scales that may provide supporting evidence for this idea is the fact that the large and thin shield lacking secondary ribs could have been an evolutionary attempt to reduce the overall weight of the cell. A potential downside is that the thin shield was more prone to breakage. The vast majority of the fossil specimens had broken shields, often totally missing, compared to the posterior flange that is fortified with secondary ribbing.

Based on gene sequence data, section Heterospinae belongs to the clade containing species that lack true V-ribs (Jo *et al.,* 2011, 2013; Siver *et al.,* 2015), the prominent structure that aids in spacing and aligning scales on the cell covering (Siver & Glew, 1990; Siver, 2018). Despite the lack of a true V-rib, some species in this clade have evolved structures that are analogous to, and likely serve a similar role, as a V-rib. Examples of such analogous structures are found on extant species such as *M. bangladeschica* and *M. heterospina* (Siver *et al.,*, 2015), and a rudimentary example is found on the extinct species *M. elephantus* (Siver & Wolfe, 2016). As is the case for *M. heterospina* and other members of the section Heterospinae, the oval rib structure on scales found on both fossil species falls into this category

Although the size, spacing and distribution of base plate pores has been used in species descriptions for decades (Kristiansen, 2002), closer detailed analyses of such characters have recently been shown to be very useful, especially in distinguishing between closely related cryptic taxa of synurophytes (Jo *et al.,* 2013; Skaloud *et al.,* 2014). Pore diameter can vary greatly between species, including ones where pores are barely visible or occluded by thin siliceous coverings, species with large-diameter pores, ones with varying-sized pores, and taxa with additional specialized groups of pores each of which is often fortified with a thickened rim. Although numerous synurophytes have base plate pores of one size, many also have patterns displaying pores of different diameters, spatially arranged in distinct patterns. *Mallomonas skogstadii* represents a species with a distinct and highly organized pattern of pores, with respect to size, spacing and arrangement into rows, suggesting that highly organized pore patterns is an ancient character, dating at least to the Eocene, and further supports use of this character in delimiting species.

At first glance scales of both new fossil species could be mistakenly assigned to the same species, given the similar ribbing pattern, large posterior flange, and thin posterior rim. Indeed, scales of both taxa were initially lumped together. However, multiple avenues of evidence support separate species diagnoses. First, the size of scales is significantly different between the two species, and there is no overlap in size of body scales. Second, the pore patterns are distinctly different. Third, the pronounced forward-projecting domes on *M. bakeri* scales are not found on *M. skogstadii*. Fourth, the species were present in different sections of the core, separated by hundreds of years. Thus, all evidence firmly supports the presence of two distinct species.

The section of core containing both new species is part of a longer sequence believed to represent an acidic phase for the maar lake (Siver & Wolfe, 2009). This hypothesis is supported by the abundance of acid-loving synurophytes and diatoms dominating this portion of lake history. Each of the three diatom genera abundant throughout this section, *Eunotia* spp., *Actinella* spp. and *Oxyneis* spp., are well known to thrive in acidic environments (Round *et al.*, 1990; Camburn & Charles, 2000; Siver & Hamilton, 2012). Likewise is true for *M. multiunca* var. *pocosenensis*, restricted to very acidic and humic-stained ponds along the southern part of the Atlantic Coastal Plain (Siver, 2003), and *M. paludosa*, the modern congener of *M. aperturae* (Siver, 2018). Abundant remains of the fossil species *M. porifera* are also most often associated with acidic-loving organisms. An acidobiontic or acidophilic classification for both new species is further supported if they are indeed related to members of section Heterospinae. Many species from this section, including *M. canina*, *M. pugio*, *M. hindonii*, *M. harrisae*, *M. multiunca* var. *pocosenensis* and *M. heterospina*, are primarily distributed in acidic habitats, many times below pH 5, that are often rich in dissolved humic substances (Takahashi, 1978; Kristiansen, 1982; Siver & Hamer, 1989; Siver, 1991; Eloranta, 1995; and numerous references therein).

In summary, the Eocene maar lake nestled within the Giraffe crater harbored a treasure trove of well preserved synurophyte specimens that collectively have enriched our understanding of evolutionary history. The two new species, *M. skogstadii* and *M. bakeri*, significantly add to this rich and developing history and will ultimately enhance efforts for reconstructing ancient environmental conditions.

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REFERENCES

CAMBURN, K.E. & CHARLES, D.F., 2000 — *Diatoms of low-alkalinity lakes in the Northeastern United States*. Special Publication 18, Academy of Natural Sciences of Philadelphia. Philadelphia, Pa, Scientific Publications,

ELORANTA P., 1995 — Biogeography of chrysophytes in Finnish lakes. *In*: Sandgren, CD., Smol JP & Kristiansen J (eds), *Chrysophyte Algae: Ecology, phylogeny and development*. Cambridge, Cambridge University Press, pp. 214-231.

GUSEV E.S., 2015 — A new species of the genus *Mallomonas* (Synurales, Chrysophyceae), *Mallomonas fimbriata* sp. nov. *Phytotaxa* 195: 291-296.

GUSEV, E.S., DOAN-NHU, H., NGUYEN-NGOC, L., KAPUSTIN, D. A. 2016. Two new species of the genus *Mallomonas* from the Cat Tien National Park (Viet Nam): *Mallomonas distinguenda* and *Mallomonas skvortsovii*. *Phytotaxa* 273: 59-64.

GUSEV E.S. & SIVER, P.A., 2017— *Mallomonas neoampla* sp. nov. from Vietnam, a new species that bridges the gap between fossil and modern taxa. *Nova Hedwigia* 104: 521-528.

GUSEV E.S., SIVER, P.A., & SHIN, W., 2017 – *Mallomonas bronchartiana* Compere revisited: Two new species described from Asia. *Cryptogamie, Algologie* 38: 3-16.

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., BOO S.M., KIM H.S. & SIVER P.A., 2011 — Studies on ultrastructure and three-gene phylogeny of the genus *Mallomonas* (Synurophyceae). *Journal of phycology* 47: 415-425.

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.

KIM H.S., KIM J.H., SHIN W.N., JO B.Y., 2014 — *Mallomonas elevata* sp. nov. (Synurophyceae), a new scaled Chrysophyte from Jeju Island, South Korea. *Nova Hedwigia* 98: 89-102.

KRISTIANSEN J., 1982 — *Mallomonas canina* sp. nov. (Chrysophyceae). *Nordic journal of botany* 2: 293-296.

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*. Koenigstein, Gantner Verlag.

KRISTIANSEN J. & PREISIG H.R., 2007 — *Chrysophyte and Haptophyte algae*. 2. Teil/Part 2: Synurophyceae. *In* B. Büdel, G. Gärtner, L. Krienitz, H. R. Preisig & M. Schagerl (Eds), *Süsswasserflora von Mitteleuropa* (p. 252). Berlin, Heidelberg: Spektrum Akademischer Verlag.

NĚMCOVÁ Y., NOVÁKOVÁ S. & ŘEZÁČOVÁ -ŠKALOUDOVÁ M., 2008 — *Synura obesa* sp. nov. (Synurophyceae) and other silica-scaled chrysophytes from Abisko (Swedish Lapland). *Nova Hedwigia* 86(1-2): 243-254.

NĚMCOVÁ Y., KREIDLOVÁ J., KOSOVÁ A., & NEUSTUPA J., 2012 — Lakes and pools of Aquitaine region (France) -a biodiversity hotspot of Synurales in Europe. *Nova Hedwigia* 95: 1-24.

NĚMCOVÁ, Y., PICHRTOVÁ, M. & ZEISEK, V., 2015 — *Mallomonas alpestrina sp. nov*. (Synurales, Chrysophyceae, Stramenopiles) and its spineless relatives—*Mallomonas alata* group. *Phytotaxa* 222:111-120.

ROUND F.E., CRAWFORD, R.M. & MANN, D.G., 1990 — *The Diatoms - morphology and biology of the genera*. Cambridge University Press, Cambridge, 747 p.

SARKAR, C., HEAMAN, L.M. & PEARSON, D.G., 2015 — Duration and periodicity of kimberlite volcanic activity in the Lac de Gras kimberlite field, Canada and some recommendations for kimberlite geochronology. *Lithos* 218-219: 155-166.

SIVER P.A. & HAMER J.S., 1989 — Multivariate statistical analysis of the factors controlling the distribution of scaled Chrysophytes. *Limnology and oceanography* 34(2): 368-381.

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. *Canadian journal of botany* 68: 374-80.

SIVER P.A., 1991 — *The biology of Mallomonas: morphology, taxonomy, and ecology*. Dordrecht, Kluwer Academic Publishers, 228 p.

SIVER P.A., 2003 — *Mallomonas multiunca* var. *pocosinensis* var. nov. (Synurophyceae) from freshwater localities along coastal sections of North Carolina, U.S.A. *Nova Hedwigia* 76: 147-156.

SIVER, P.A. & WOLFE A.P., 2005 — Scaled Chrysophytes in Middle Eocene Lake Sediments From Northwestern Canada, Including Descriptions of Six New Species. *Proceedings of the Sixth International Chrysophyte Symposium*: 295-308.

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., LOTT A.M. & WOLFE A.P., 2009 — Taxonomic significance of asymmetrical helmet and lance bristles in the genus *Mallomonas* (Synurophyceae) and their discovery in Eocene lake sediments. *European journal of phycology* 44(4): 447-460.

SIVER, P.A. & HAMILTON P.B., 2011— *Diatoms of North America: The Freshwater Flora of the Atlantic Coastal Plain*. *Iconographia diatomologica* 22: 1-920.

SIVER P.A., LOTT A.M. & WOLFE A.P., 2013a — A summary of Synura taxa in early Cenozoic deposits from Northern Canada. *Nova Hedwigia, Beiheft* 142: 181-190.

SIVER P.A., WOLFE A.P., ROHLF J., SHIN W. & JO B.Y., 2013b — Combining geometric morphometrics, molecular phylogeny, and micropaleontology to assess evolutionary patterns in *Mallomonas* (Synurophyceae, Heterokontophyta). *Geobiology* 11: 127-138.

SIVER P.A., 2015a — Synurophyte Algae. *In*: Wehr, JD., Sheath, RG., Kociolek, JP. (eds) *Freshwater Algae of North America: Ecology and Classification*, *2nd edition*. Boston, MA, Academic Press, pp. 607-651.

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., 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.

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(3/4): 501-511.

SIVER, P.A. & WOLFE A.P., 2016 — *Mallomonas elephantus* sp. nov. (Synurophyceae), an extinct fossil lineage bearing unique scales from the Eocene. *Nova Hedwigia* 103: 221-223.

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.

ŠKALOUD P., KYNČLOVÁ A., BENADA O., KOFROŇOVÁ O. & ŠKALOUDOVÁ M., 2012 — Toward a revision of the genus *Synura*, section Petersenianae (Synurophyceae, Heterokontophyta): morphological characterization of six pseudo-cryptic species. *Phycologia* 51: 303-329.

ŠKALOUD P., ŠKALOUDOVÁ M., PROCHÁZKOVÁ A. & NĚMCOVÁ Y., 2014 — Morphological delineation and distribution patterns of four newly described species within the *Synura petersenii* species complex (Chrysophyceae, Stramenopiles). *European journal of phycology* 49: 213-229.

TAKAHASHI E., 1978 — *Electron microscopical studies of the Synuraceae (Chrysophyceae) in Japan, taxonomy and ecology*. Tokyo, Tokai University Press.

WEE JL.1982 — *Studies on the Synuraceae (Chrysophyceae) of Iowa*. 62: 1-183.

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.