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Mallomonas lottii sp. nov., a new fossil species in section Papillosae from the Eocene that forms hexagonal patterns on its scales

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Abstract
A new fossil species in section Papillosae of the genus *Mallomonas* is described from the Giraffe Pipe maar lake located near the Arctic Circle in northern Canada. The new species, *Mallomonas lottii*, has scales with papillae arranged in regular hexagonal patterns on the base plate, a prominent V-rib, a shallow and recessed dome, an unornamented posterior flange, and lacks base plate pores and anterior submarginal ribs. A survey revealed that formation of hexagon patterns is a common feature of *Mallomonas* species in sections Papillosae, Quadratae and series Mangofera of section Torquatae. The underreporting of the honeycomb pattern is likely due to it being overlooked on specimens where papillae are densely spaced, and if there is a papilla in the geometric center of each hexagon. *Mallomonas korshikovii* is the closest modern congener to *M. lottii*, with both species sharing multiple scale traits. The primary difference is that scales of *M. lottii* lack a papilla at the geometric center of each hexagon.

Keywords
Eocene; Extinct; *Mallomonas*; New species; Papillosae; Synurophytes

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Introduction

Mallomonas Perty belongs to the Synurales, a monophyletic order of heterokont algae within the class Chrysophyceae that form a cell covering composed of taxonomically significant siliceous scales (Siver *et al*., 2015; Škaloud *et al*., 2013). All *Mallomonas* species are unicellular flagellates commonly found in the plankton of freshwater environments, including ponds, lakes, wetland pools and slow-moving rivers (Kristiansen, 2005; Siver, 2015).

Today, species descriptions are based largely on the ultrastructure of the siliceous scales, and when possible, coupled with molecular sequence data (Gusev *et al*., 2018; Gusev *et al*., 2024; Jo *et al*., 2013). According to AlgaeBase (Guiry & Guiry, 2020), a total of 468 species and subspecific forms of *Mallomonas* have been described over the last approximately 175 years. Many of these entities, especially the subgeneric taxa, have been combined over time. Because of the limits of resolution of a light microscope, it has not been possible to link the original descriptions of many species to observations made with an electron microscope. As noted by Kristiansen under the description of *Mallomonas* on AlgaeBase (Guiry & Guiry, 2020), "many species described before EM cannot be recognized because their scale structure is unknown, but in several cases it has been possible to harmonize microscopically described species with EM based taxonomy". This means that an unknown number of new descriptions using high-resolution EM are undoubtedly duplicates of earlier ones made with light microscopy. Given these limitations, Siver (2024) estimated the number of *Mallomonas* species that are well studied and identifiable based on current methods is likely closer to 250. The species are grouped into subgeneric sections and series based in large part on similarities in scale and bristle ultrastructure (Kristiansen, 2002; Siver *et al*., 2015).

The basic design of a *Mallomonas* scale consists of a flat base plate and an upturned posterior margin, referred to as the posterior rim (Kristiansen, 2005; Si-

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ver, 1991). The base plate is perforated with pores on most species, and the spacing and positions of pores can serve as stable taxonomic characters. From this basic design, additional structures can be added to base plate, including papillae, ribs, spines, wings, a V-rib, and a dome, resulting in a wide diversity of scale types. The V-rib is a thick "v" or "u"-shaped rib situated on the base plate with the base closer to the posterior margin, and the two arms extending towards the anterior margin of the scale. The V-rib aids in orienting and spacing the scales on the cell covering (Siver & Glew, 1990). The dome is a raised portion of the anterior end of the scale, forming a cavity from which the base of a second siliceous structure, the bristle, is secured. The long and slender part of the bristle, the shaft, exits from the dome and extends outward from the scale covering. Scales with domes, referred to as dome scales, may cover the cell, or be restricted to a specific part of the cell, depending on the species. The base of the bristle secured in the dome can rotate, resulting in a shifting in the direction of the radiating shaft. The region of the scale between the V-rib and the dome is referred to as the shield, and between the V-rib and posterior rim, the posterior flange. The anterior flanges are positioned along the margins between the ends of the V-rib arms and anterior end of the scale. Additional structures, including papillae, ribs and pores, can be placed onto the shield and flanges, resulting in many species-specific designs.

Because scale and bristle designs are specific for each species, and because these structures can be uncovered in the fossil record, they serve as an effective means for examining evolutionary history of the genus (Čertnerová *et al*., 2019; Siver, 2023). The oldest known synurophytes, including *Mallomonas* species, date to the Cretaceous, with many more species having been uncovered in Eocene remains (Siver, 2023). A new fossil species that arranges papillae in regular hexagonal patterns has been uncovered in an Eocene locality. The objectives of this paper are to describe this species, which is the first fossil taxon representing the section Papillosae, and to examine the extent to which hexagon structures are formed within the genus.

Material and Methods

Mudstone chips (50–100 mg) from different sections of the extensive Giraffe Pipe core were oxidized using 30% H_2O_2 under low heat for 2 hours, rinsed a minimum of five times with distilled water, and the slurries were stored in glass vials at 4 °C. This procedure successfully extracted siliceous microfossils from the mudstone and removed most of the organic matter from the sample. Aliquots of the clean material were air-dried onto flat pieces of heavy-duty aluminum foil, trimmed, attached to aluminum stubs with Apiezon wax, coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater, and examined with either a Leo 982 field emission SEM or a FEI Nova NanoSEM 450 field emission SEM. Morphometric measurements were made directly from SEM images, and the area of a regular hexagon was calculated using the formula:

$$A = [(3 \times \sqrt{3})/2] \times a^2$$

where A = area; a = length of a side.

Location and identification of samples from the Giraffe core are given in Siver & Lott (2012). The core was cut into 1.5 m sections and placed into premade core boxes containing channels for three cut sections (4.5 m total). Each sample is identified with a three-part number. The first number represents the core box. Deeper sections of the core correspond to larger box numbers. The channels in each box are marked 1, 2 and 3. The second number represents the channel number. The third number is the length in cm measured from the top of a core length. Thus, sample 12-3-140 represents a sample taken from 140 cm down along the core length positioned in channel 3 from box 12.

Type material for *Mallomonas lottii* has been archived at the Canadian Museum of Nature, Ottawa, Canada. Numerous publications, including Takahashi (1978), Siver (1991), and Kristiansen (2002), were used to identify *Mallomonas* taxa that arrange shield papillae in regular hexagon patterns.

Site description: The Giraffe Pipe locality (64°43'48" N, 109°45' W) is a kimberlite diatreme that was emplaced into the Slave Craton in the Northwest Territories of Canada approximately 48 million years ago during the Eocene (Creaser *et al*., 2004; Siver & Wolfe, 2005). The diatreme crater filled with water to varying depths at different points in time, becoming a maar waterbody. Over time, the crater slowly infilled with a sequence of lacustrine, then paludal sediments, and finally Neogene glacial deposits (Siver & Wolfe, 2005; Wolfe *et al*., 2006). The emplacement age, based on a Rb-Sr model from kimberlitic phlogopite, provides a maximum approximate age estimate for the maar lacustrine sediments (Creaser *et al*., 2004). The Giraffe Pipe is one of many kimberlites in the Lac de Gras field with emplacement ages ranging from Cretaceous to Paleogene (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). The core contained well-preserved stratified organic sediment, including 68.3 m of lacustrine mudstones, overlain with 44.8 m of peaty material. Several air-fall tephra beds were used to help establish age estimates of the lacustrine remains. 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. A single zircon grain from a tephra layer in the lowermost lacustrine sediments was dated to 48.72 ± 0.29|0.30 Ma (Buryak *et al*., 2024). Based on the emplacement and tephra ages 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 examination of 93 samples taken from between 134 and 100 m along the core, only two of which contained ample remains of the newly described species.

Results

Mallomonas lottii sp. nov. **Siver (Figs 1a–f)**

Description: Scales are oval, range in size from 3.9–4.5 × 2.5–3 µm (mean = 4.2 × 2.7 µm), and are tripartite, possessing a V-rib and dome (Fig. 1). The base plate lacks pores (Fig. 1d). The V-rib is prominent, positioned

slightly below the center of the base plate, with straight to slightly curved arms that terminate close to the margin. Anterior submarginal ribs are lacking. The notch of the V-rib is U-shaped and lies approximately 1.5 µm from the posterior margin. The posterior flange is wide and unornamented. The posterior rim is ~0.45 µm wide and encircles approximately ½ of the scale perimeter. The dome cavity is shallow, slightly recessed from the margin, elongated, and spans approximately half of the scale diameter (Fig. 1d). The surface of the dome is covered with scattered papillae. The shield is covered with papillae arranged in regular hexagons, each with a mean area of 0.057 µm^2, and that are tesselate forming a honeycomb pattern. A single papilla is positioned at each vertex of the hexagon, and adjacent vertices are sometimes connected by a thin rib (Figs 1a–b, e). The ribs can be more prominent along the V-rib arms. A papilla is lacking from the geometric center of each hexagon, and the long diagonals range in length from 0.27–0.3 µm. A row of marginal papillae is found on the anterior half of the scale, surrounding the dome and terminating at the ends of the V-rib arms. Bristle and cyst structure is unknown.

Holotype: Here designated the collection of specimens on SEM stub deposited at the Canadian Museum of Nature, Ottawa, Canada. CANA 1343194.
Type material: Material from section 12-3-140 of the Giraffe Pipe core collected by P. A. Siver.
Iconotype: Fig. 1a, uncovered from section 12-3-140 of the Giraffe Pipe core.
Etymology: The name is in honor of Anne Marie Lott, long-time colleague, friend, and chrysophyte expert.
Distribution: The type material from section 12-3-140 was dominated with chrysophytes, testate amoebae, and especially heliozoans. In addition to numerous chrysophyte cysts, this section of the core had abundant numbers of *Chrysosphaerella* sp., *Mallomonas insignis* Penard, and *Synura recurvata* Siver *et* Wolfe scales. Testate amoebae scales belonging to both *Euglypha* spp. and *Scutyglypha* sp. were common, and the most abundant numbers of microfossil scales were heliozoans belonging to the genera *Choanocystis*, *Acanthocystis,* and *Pterocystis*. In addition to 12-3-140, scales of *Mallomonas lottii* were also found at stratum 19-2-100 of the Giraffe Pipe core.

Mallomonas species with structures arranged in regular hexagons

A survey of the literature revealed that arrangement of shield papillae in distinct hexagonal shapes is widespread among the genus, especially for taxa in section Papillosae (Table 1). In addition to *M. lottii*, honeycomb patterns are also observed on scales of *M. korshikovii* Gusev*, M. binocularis* Siver, *M. delanciana* Siver, *M. kalinae* Řezáčová, *M. papillosa* Harris *et* Bradley, *M. rasilis* Dürrschmidt, *M. furtiva* Gusev, Čertnerová, Škaloudová *et* Škaloud, *M. guttata* Wujek, *M. paxillata* (Bradley) Péterfi *et* Momeu, *M. skvortsovii* Gusev, Doan-Nhu, Ngoc *et* Kapustin, *M. distinguenda* Gusev, Doan-Nhu, Nguyen *et* Kapustin, *M. calceolus* Bradley, *M. tropica* Dürrschmidt *et* Cronberg, *M. parvula* Dürrschmidt, *M. ouradion* Harris *et* Bradley, and *M. cronbergiae* Piatek. Except for the fossil taxon, *M. lottii*, all include a papilla in the geometric center of each hexagon. One species, *M. distinguenda*, forms a honeycomb shield pattern by connecting the vertices with ribs, making it slightly different from the other taxa in the section. In addition to hexagonal shield designs, practically all of the species in section Papillosae also form scales that lack base plate pores, have smooth posterior flanges without secondary structures, a relatively small dome, and the majority of species also lack anterior submarginal ribs (Table 1). Most species also have short and smooth bristles with either a pointed or a bifurcate, fishtail-like, apex.

Hexagonal shield patterns were not limited to section Papillosae. Most, if not all species in section Quadratae, including *Mallomonas lychenensis* Conrad, *M. parana* Vigna *et* Kristiansen, and *M. pseudobronchartiana* Gusev, Siver *et* Shin, arrange shield papillae in tesselate hexagons designs. Likewise, most species in series Mangoferae of section Torquatae also arrange shield papillae into hexagonal designs, including *M. mangofera* Harris *et* Bradley, *M. minuscula*, *M. fragariformis,* and *M. spinosa* (considered here as belonging to series Mangoferae). In addition, the pores and pits on scales of *M. hexagonis* Nicholls and *M. lemuriocellata* P. Hansen, respectively, are arranged in hexagonal patterns. One species in series Mangofera, *M. liturata* Nicholls, formed shield papillae in squares instead of hexagons. *Mallomonas annulata* (Bradley) Harris and *M. multisetigera* Dürrschmidt, in sections Annulatae and Multisetigerae, respectively, have shield papillae arranged in hexagons, but the pattern can become disorganized on some scales. Some species in section Heterospinae, including *M. hamata* Asmund, *M. americana* Dürrschmidt, *M. harrisae* Takahashi, *M. canina* Kristiansen, and *M. pugio* Bradley, arrange the base plate pores, not papillae, into hexagon patterns. The holes (pores) on the surface of the secondary covering on scales in the *M. matvienkoae* complex (series Matvienkoae in section Planae) are sometimes arranged in a hexagon pattern. In contrast, species in other sections, including sections Mallomonas, Striatae, and Punctiferae, were not found to form hexagonal structures.

Discussion

Mallomonas korshikovii is the closest modern congener to *M. lottii*, with both species sharing multiple scale traits. Scales of both taxa are oval, have a prominent V-rib placed close to the center of the scale, lack or have weakly developed anterior submarginal ribs, and possess a shallow and broad dome that is slightly recessed from the scale margin (Gusev, 2013). The V-rib is broad and grades into an unornamented posterior flange, and the posterior rim encircles half of the scale perimeter on both species. Of note, scales of both taxa also lack base plate

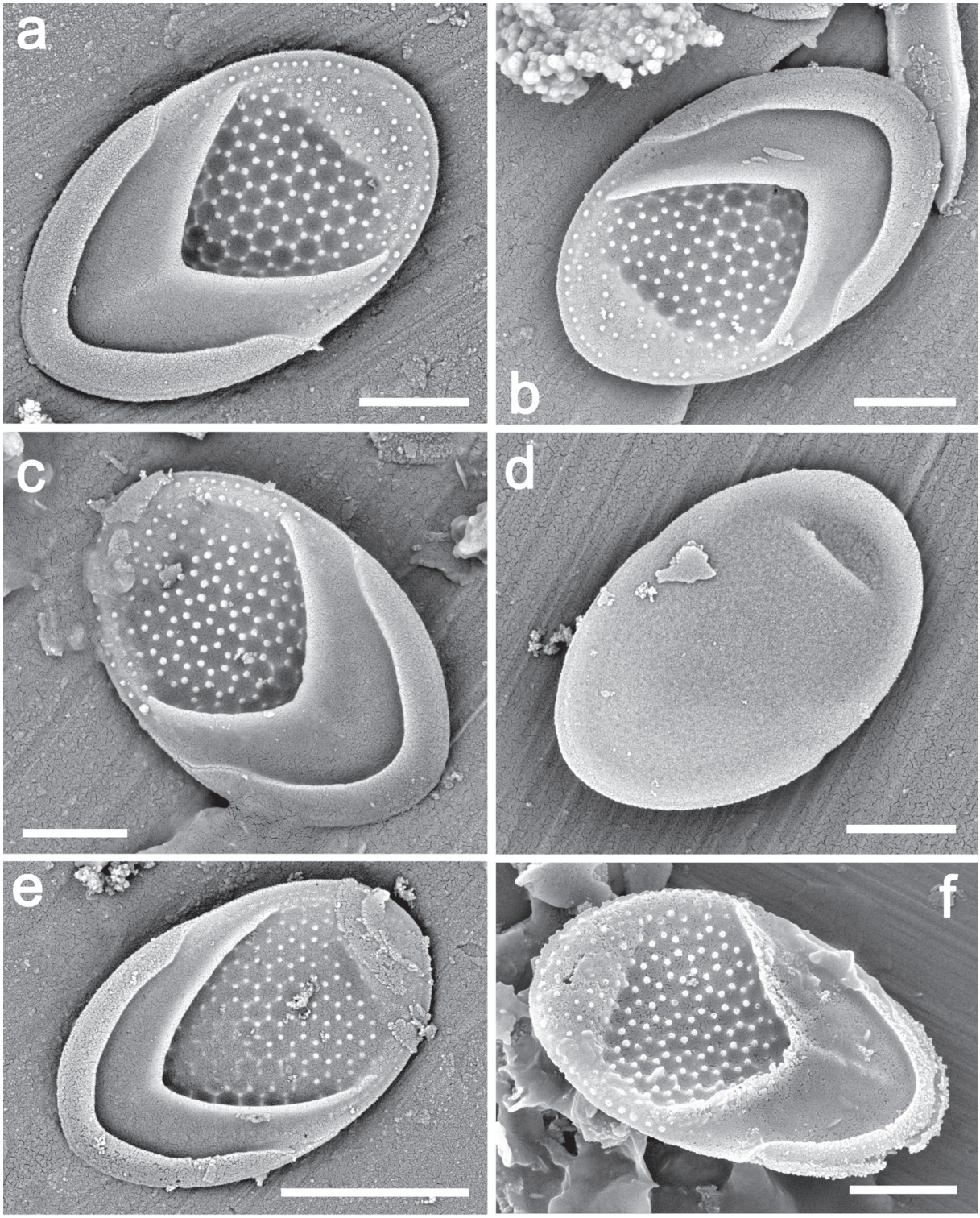


Fig. 1. Siliceous scales of the Eocene fossil species, *Mallomonas lottii*. Note the distinctive arrangements of papillae into hexagonal patterns; the elongated, shallow and recessed dome **(d)**; the prominent V-rib and the lack of base plate pores **(d)**. All scales are from the type material taken from section 12-3-140 of the Giraffe Pipe core, except for the specimen in **(f),** which was from section 19-2-100. Scale bars 1 µm (a–d, f) and 2 µm (e).

pores. *Mallomonas korshikovii* was placed in section Papillosae when it was originally described (Gusev, 2013). Because of the close similarity in scale structure, *M. lottii* is also placed in section Papillosae. However, it is noted that both of these species have a dome structure that differs from other species in section Papillosae and may represent a separate lineage.

Even though *M. lottii* and *M. korshikovii* scales share similarities, there are also differences in their structures. The angle of the V-rib base is less acute and more

Table 1. Scale characteristics for 17 species in series Papillosa or series Ouradiotae under section Papillosae* of the genus *Mallomonas* that arrange shield papillae or ribs into regular hexagonal patterns.

Mallomonas species	Shield papillae form hexagons?	Base plate pores	Dome	V-rib	Posterior flange	Anterior submarginal ribs	Bristles
series Papillosa							
M. lottii	+, missing central papilla	Lacking	Shallow, wide, slightly recessed, scattered papillae	Wide hood, prominent, U-shaped angle	Shallow, unornamented	Lacking	not known
M. korshikovii	+, central papilla less developed	Lacking	Variable shapes, shallow, slightly recessed, scattered papillae	Wide hood, prominent, U-shaped angle	Shallow, unornamented	Lacking or weakly developed	Short, smooth shaft, bifurcate apex
M. kalinae	+, central papilla	Lacking, 1-few pores at base of V-rib	Small, lack papillae	Narrow hood, more acute angle	Shallow, unornamented	+, continuous with V-rib arms	Short, smooth and slightly curved shaft, pointed apex
M. binocularis	+, central papilla may be missing	Lacking, two pores at base of V-rib	Small, slightly recessed, few papillae	Narrow hood, U-shaped angle	Shallow, unornamented	Lacking	Short, smooth and slightly curved shaft, pointed apex
M. delanciana	+, papillae widely spaced, central papilla often missing	Lacking	Small, slightly recessed, few papillae	Narrow hood, more acute angle	Shallow, unornamented	Lacking, parallel struts on flange	Short, ribbed shaft, bifurcate apex
M. rasilis	+, central papilla	Lacking, one pore at base of V-rib	Small, lack papillae, some reports of papillae	Narrow hood, more acute angle	Shallow, unornamented	Lacking	Short, unilaterally serrated, pointed apex
M. furtiva	+, central papilla	Lacking, one pore at base of V-rib	Small, often with papillae	Narrow hood, rounded	Shallow, unornamented	+, continuous with V-rib arms	Serrated, pointed apex
M. papillosa	+, central papilla	Lacking, one pore at base of V-rib	Small, can have papillae	Narrow hood, rounded	Shallow, unornamented	Lacking, parallel struts on flange	Short, unilaterally serrated, pointed apex
M. paxillata	+, central papilla	Lacking	Small, can have papillae	Narrow hood, rounded	Shallow, unornamented	+, continuous with V-rib arms, left ASMR extends as spine	Short, smooth shaft, bifurcate apex
M. guttata	+, central papilla, multiple large depressions	Lacking	Small, can have papillae	Narrow hood, U-shaped angle	Shallow, unornamented	Lacking, papillae cover flange	Short, smooth shaft, pointed apex
M. distinguenda	-, ribs form regular hexagons with weakly formed central papilla	Lacking, 2–3 pore at base of V-rib	Small dome	Narrow hood, V to U-shaped angle	Shallow, unornamented	Lacking	Unknown
M. skvortsovii	+, central papilla	Lacking, one pore at base of V-rib	Dome moderate size with parallel ribs	Relatively wide, struts underneath	Shallow, unornamented	Lacking, papillae cover flange	Unknown
M. calceolus	+, central papilla, widely spaced	Lacking	Small dome	Narrow hood, U-shaped angle	Shallow, unornamented	+, continuous with V-rib arms, weakly developed	Short, smooth shaft, bifurcate apex

Table 1 Cont.

***Mallomonas* species**	**Shield papillae form hexagons?**	**Base plate pores**	**Domes**	**V-rib**	**Posterior flange**	**Anterior submarginal ribs**	**Bristles**
M. tropica	+, central papilla	Lacking, one pore at base of V-rib	Small, rounded, with papillae	Narrow hood, V to U-shaped angle	Shallow, unornamented	+, weakly developed	Long, unilaterally serrated, pointed apex
series Ouradiotae*							
M. parvula	+, central papilla	Lacking	Lacks a dome	Narrow hood, straight arms, extend to margin	Shallow, unornamented	Lacking	Short, smooth shaft, bifurcate apex
M. ouradion	+, central papilla, less obvious on some scales	Lacking	?, dome may be shallow, elongate and recessed	Narrow hood, V to U-shaped angle	Shallow, unornamented	Lacking	Short, smooth shaft, bifurcate apex
M. cronbergiae	+, central papilla, papillae large and closely spaced	Lacking on the shield, 3–7 pores ar posterior rim	Lacks a dome	Well-developed, narrow hood	Shallow, unornamented	Lacking, papillae cover flange	Short, smooth shaft, bifurcate apex

* series Ouradiotae is currently described under section Papillosae (Kristiansen, 2002; Kristiansen & Preisig, 2007). By definition, scales of species in section Papillosae possess domes. However, species in series Oudadiotae are described as lacking domes on their scales, in contrast to the section description. Given this and other differences between species in series Ouradiotae and series Papillosa, the former series will likely be raised to the section level.

rounded, and the V-rib arms curve slightly on *M. lottii* scales compared to those on *M. korshikovii*. *Mallomonas lottii* scales are also larger than *M. korshivovii* scales. The most notable difference is in the design of the hexagonal arrangement of papillae on the shield. In both cases, the papillae are arranged as regular hexagons, that in turn are fitted together to produce a virtually perfect honeycomb pattern. Thus, each hexagon has six equal sides and six equal angles of 120°, and collectively the hexagons are tesselate, fitting together without gaps. Interestingly, the papillae found on the dome in each taxon are not arranged as hexagons. The main difference between the two species is that there is an additional papilla placed in the geometric center of each hexagon on *M. korshikovii* scales (Gusev, 2013), that is lacking on *M. lottii* scales. This means that if a long diagonal (one connecting opposing vertices of a hexagon that passes through the geometric center) is traced from one polygon to the next, there is a difference in the spacing of papillae between both taxa. The papillae are spaced equidistant along any long diagonal connecting adjoining hexagons on *M. korshikovii* scales. In contrast, the distances between papillae on a long diagonal of a *M. lottii* scale alternate between X and ½ X. This type of precision in the placement of papillae on scales forming within the silica deposition vesicle is impressive for a unicellular organism, and likely reflects a difference in the blueprint pattern used to construct the scale. Lastly, it is of interest that Gusev *et al.* (2022) later illustrated a scale (fig. 3D) of *M. korshikovii* that appears to lack the central papilla (not reported in the original description), yielding a scale structure even more similar to its fossil counterpart.

Although molecular data aids in determining differences between species of *Mallomonas* (Čertnerová *et al*. 2019; Jo *et al*., 2013), taxonomic descriptions are primarily based on morphological differences in the siliceous structures produced, especially the scales. This represents a morphological species concept (Pecina & Vďačný, 2020; Siver, 2015), and the same concept that would form the basis for species determinations in the fossil record. If the scales of a fossil taxon and a modern species were identical, which is not the case for *M. lottii* and *M. korshikovii*, would they represent the same species? Most available evidence supports the idea that a 48 Ma-year-old organism would not be the same species as a modern congener. Hedges *et al.* (2015) estimated the mean times-to-speciation for a wide variety of plants and animals to be ~ 2 Ma. Evidence of speciation times for protists is rare, but multiple studies have proposed times similar to or <2 Ma (Finlay, 2002; Škaloud *et al*., 2019, 2024; Theriot *et al*., 2006). Although further study is needed to determine speciation rates in protist lineages more precisely, the available evidence supports the concept that a 48 Ma taxon would not be the same species as a modern congener given random mutations and genetic drift (Hedges *et al*., 2015).

Although rarely reported, arrangement of shield

papillae into regular hexagons is a common feature of species in section Papillosae (Table 1), as well as in several additional lineages within the genus. One reason for being underreported is that the honeycomb pattern may not be as obvious at first glance on scales where the papillae are closely and densely-spaced. For example, Řezáčová (2006) noted that the shield papillae on *M. kalinae* were regularly spaced in different rows, but the pattern was not described as a honeycomb of tesselate hexagons. Likewise, in the description of *M. binocularis*, Siver (2002) wrote: "The shield is covered with evenly spaced papillae that are aligned in rows as observed from several angles". Both of these species clearly arrange shield papillae in regular hexagonal patterns, and despite descriptions noting the equal spacing of papillae along different diagonals, the hexagonal patterning was not identified. The pattern is much more obvious if the central papilla is of a different size as on *M. korshikovii* scales, or lacking altogether, as is the case for the fossil *M. lottii*. The papillae in the geometric centers of hexagon arrangements formed on scales of *M. binocularis* and *M. delanciana* are usually present, but can be missing in some hexagons on the same scale. When the central papilla is missing, the hexagonal pattern is quite distinctive (e.g., fig. 1 in Siver, 2002).

Scales produced by most species in section Papillosae with papillae arranged in hexagonal patterns share a number of other distinctive features, including a shallow or small dome, a smooth posterior flange lacking secondary structures, and the lack of base plate pores (Table 1). Two additional species in series Ouradiotae of section Papillosae, *M. parvula* and *M. ouradion*, share all of these features, but lack domes. The lack of base plate pores within this lineage, other than the one to a few isolated pores on the shield at the base of the V-rib found on some taxa, is especially interesting given that base plate pores are produced by most *Mallomonas* species. The majority of species also lack anterior submarginal ribs, and have a V-rib with arms that terminate on the base plate close to the scale margin. The notable exceptions are *M. furtiva*, *M. kalinae* and *M. paxillata* that have anterior submarginal ribs that are continuous with the V-rib arms (Table 1). The wide and prominent V-rib found on *M. lottii* and *M. korshikovii* is unique among species in the section Papillosae lineage. Most of the taxa in section Papillosae also have short bristles that have an unornamented shaft and terminate with a sharp point or a bifurcate (fishtail-like) apex. In summary, the collection of characters common to most members of the section Papillosae lineage, including the hexagonally arranged papillae on the shield, lack of base plate pores, and the lack of structures on the posterior flange, evolved by at least the early Eocene.

Hexagonal patterns are common in nature, forming a wide variety of structures, including honeycombs formed by bees, insect eye facets, turtle shells, aggregates of soap bubbles, and many crystal forms of snowflakes. Such designs are often reported to provide strength and they optimize space. With respect to the siliceous scales of *Mallomonas*, the most intriguing examples of hexagon patterns come from the closely related protist group, the diatoms (Bobeth *et al*., 2020; Lansky *et al*., 2024; Round *et al*., 1990; Sumper, 2002). Like synurophytes, diatoms also produce a cell covering composed of highly sculptured siliceous components collectively referred to as the frustule (Round *et al*., 1990). In addition, both synurophyte scales and diatom frustule components are produced within a specialized vesicle, the silica deposition vesicle (SDV), in the cell. Examples of hexagonal designs produced by diatoms include arrangements of pores and papillae on *Stephanopyxis* (Lansky *et al*., 2024), the areolae chambers of *Coscinodiscus* valves (Sumper, 2002), and areola coverings found on many species (Round *et al*., 1990).

Given the similarities between synurophytes and diatoms, especially involvement of a SDV, it would not be surprising if the mechanism that forms structures with hexagonal patterns found on diatom valves and on scales produced by *Mallomonas* species was the same. Multiple mechanisms for the production of complex siliceous structures, including formation of hexagonal features in diatoms, have been proposed. One model is based on the diffusion-limited precipitation of silica along leading edges of components within the SDV (Gordon & Drum, 1994). Sumper (2002) and later Bobeth *et al*. (2020) proposed another model where a phase separation of a complex of organic molecules served as a template for the deposition of silica. Recently, a third model put forth by Lansky *et al*. (2024) specifically addressed formation of hexagonal patterns on *Stephanopyxis* valves. The Lansky *et al*. (2024) model involved a two-step process where silica is first deposited to form equally-spaced rods, known as elongation rods. Second, a series of smaller rods then forms between and connect adjoining elongation rods enclosing individual pores. Differences in the arrangement and spacing of the smaller rods formed on each side of an elongation rod determined whether the pores ultimately formed a hexagonal or a square pattern. Although the mechanism coordinating formation of the siliceous rods to form the precise patterns is not fully known, the process is highly controlled and precise within these single-celled protists. Likewise, the function of the shield papillae on *Mallomonas* scales is not known. Although Knotek & Škaloud (2023) found that transverse shield ribs did not provide additional strength to scales, it would be interesting to test if shield papillae arranged in hexagons do increase scale strength.

Siver & Lott (2023) provided a detailed history of the ontogeny of the Giraffe Pipe maar waterbody, and identified five major transitions based on the fossil remains. The stratum containing the type material for *M. lottii*, 12-3-140, was situated between the end of the Heterotrophic Zone and beginning of the Terminal Lake Zone. This region of the core was characterized by elevated concentrations of heterotrophic protist remains, including euglyphids and especially heliozoans, and in-

dicated a shallow pond or wetland with elevated nutrients. Although scale remains of *M. lottii* can be found within the numerous microfossils in 12-3-140, their concentration relative to other taxa was low. The closest modern congener to *M. lottii*, *M. korshikovii*, has been reported from five sites in tropical Viet Nam, including two coastal mangrove pools (Gusev, 2013), and three waterbodies (a swamp, a reservoir and a lake) situated on coastal islands (Gusev *et al*., 2022). In general, the sites ranged in pH from 5 to 7, had elevated mineral concentrations, and water temperatures >30 °C at the time of collection. Although the localities harboring the modern congener are quite varied, the pH range and shallow nature of some of the sites do overlap with the reconstructed conditions of the Giraffe Pipe waterbody. In addition, although the fossil locality was situated near the Arctic Circle in Canada, the climate was significantly warmer than today (Wolfe *et al*., 2017), and interestingly the site harbored tropical aquatic organisms (Siver & Wolfe, 2009; Pisera *et al*., 2013) and the surrounding landscape included palm trees (Siver *et al*., 2025).

In summary, *M. lottii* was discovered from an Eocene locality situated close to the Arctic Circle in Canada, and is the first taxon representing section Papillosae in the fossil record. The species produces scales with papillae arranged in distinctive hexagonal designs, a character noted to be shared by members of section Papillae as well as with species in a few other lineages of the genus. *Mallomonas korshikovii* is a modern congener known only from a few sites in tropical Viet Nam that forms scales similar to those of *M. lottii*. Formation of hexagonal shapes is common in nature, but the advantage or benefit to arranging papillae in such shapes on synurophyte scales remains a mystery.

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