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Scaled chrysophytes in Middle Eocene lake sediments from Northwestern Canada, including descriptions of six new species

by

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with 4 figures

Abstract: Although chrysophyte stomatocysts have a fossil record that likely extends to the lower Cretaceous, to date neither scales nor bristles of the scaled chrysophyte genera older than Holocene have been reported. This leaves the origin of this important group of freshwater algae a mystery. We discovered abundant and diverse scaled chrysophyte microfossils in ca. 47 Ma sediments (Middle Eocene, Lutetian) deposited as the post-eruptive infill of a crater formed during intrusion of the Giraffe Pipe kimberlite, in the Northwest Territories of Canada. The microfossils are exceptionally well preserved and represent at least eleven different scaled chrysophyte taxa, including 7 species of *Mallomonas*, 1 of *Synura*, 2 of *Spiniferomonas* and 1 of *Chrysosphaerella*. Six of these are herein described as new species. Although some taxa do not appear to have modern analogs, others can be readily traced to, or are morphologically identical with, extant species. Our findings prove definitively that the most common genera of scaled chrysophytes found in freshwater habitats worldwide today were well established by the middle Eocene, and that these organisms are most likely much older than 47 Ma. Simple as well as highly complex scale morphologies are equally represented among Eocene chrysophytes. Furthermore, our observations lead us to hypothesize that bristles and domes associated with *Mallomonas* evolved well after the genus had become an established component of lake phytoplankton.

NB: 47 Ma = 47 million years

Key words: *Chrysosphaerella*, *Eocene*, Giraffe Pipe, fossils, *Mallomonas*, new species, scaled chrysophytes, *Spiniferomonas*, *Synura*

Introduction

Members of the Class Chrysophyceae with siliceous cell coverings and those in the Class Synurophyceae, collectively referred to as scaled chrysophytes, are common components of most freshwater habitats, including ponds, lakes, bogs, wetlands, streams and rivers (Siver

2003; Nicholls & Wujek 2002). All members of the scaled chrysophytes produce flat, plate-like siliceous structures, called scales, that overlap each other on the cell membrane to form a continuous siliceous cell covering except for a pore from which the flagellum(a) emerges. Most, but not all, members of the genus *Mallomonas* form a second type of siliceous structure called a bristle, a long slender rod with a bent proximal end that fits under the anterior part of the scale. The anterior ends of most *Mallomonas* scales associated with bristles are molded into a more or less spherical structure, or dome, under which the proximal end of the bristle fits. Such scales are referred to as domed scales. No other scaled chrysophyte genera form bristles.

Scaled chrysophytes can often dominate plankton assemblages and are important components of metalimnetic strata in lacustrine habitats (Siver 2003). As a group, scaled chrysophytes often flourish under poorly buffered, slightly acidic conditions, low in dissolved salts and nutrients, and with moderate amounts of humic substances. Despite this generalization, at the species level, scaled chrysophytes can be found over a wide range of environmental conditions and their remains have been extremely useful in reconstructing recent (hundreds of years) paleoenvironments (e.g. Smol 1995).

Although the origin and age of the diatoms remains controversial (Witkowski & Sieminska 2000), their fossil record appears to extend to the lower Jurassic (180–190 Ma; Harwood & Nikolaev 1995). By the latest Cretaceous, diatoms had clearly colonized freshwater habitats (Chacón-Baca et al. 2002), and by the middle Eocene they were abundant in lakes of western North America (Krebs 1994). In contrast, chrysophyte stomatocysts have no fossil record older than Lower Cretaceous, with only sporadic occurrences in marine sediments of Aptian-Albian age (~110 Ma, Harwood & Gersonde 1990). Stomatocysts do not appear abundantly in freshwater deposits of western North America until the Miocene (e.g. Williams 1985), although this may in part reflect a paucity of studies. These examples serve to illustrate that the early fossil records of both diatoms and stomatocysts are rather cryptic. However, by comparison to the scaled chrysophytes, for which there are no reports of scales or bristles older than Holocene (Whitehead et al. 1989), the fossil records of diatoms and stomatocysts are comparatively rich! As a consequence, the age and evolutionary history of the scaled chrysophytes, as well as the timing of their appearance in freshwater habitats, remain unknown. The purpose of this paper is to report new finds of well-preserved scales and bristles representing at least 11 different organisms from the genera *Mallomonas*, *Synura*, *Chryso-sphaerella* and *Spiniferomonas*, all recovered from Middle Eocene (ca. 47 Ma = 47 million years old) lake sediments in the Northwest Territories, Canada.

Study site and sample preparation

This investigation is based on two samples (95.6 m and 127.6 m; all depths are from the ground surface) from a drill core obtained at the Giraffe Pipe kimberlite locality in the Lac de Gras field, Northwest Territories, Canada (64°44'N, 109°45'W). The core was initially obtained by BHP Diamonds Canada Inc. for diamond exploration. When the core was found to be largely comprised of sedimentary strata (i.e., 50–163 m), it was archived at the Geological Survey of Canada in Calgary, where pollen and organic geochemical investigations have been initiated (Hamblin et al. 2003). The core contains 57 m of lacustrine sediment (106–163 m), primarily mudstone and shale, that are overlain by another 56 m of highly organic peaty sediment with abundant plant macrofossils (50–106 m). Thus, the investigated samples include both the lacustrine (127.6 m) and wetland (95.6 m) paleoenvironments.

The depositional model is that explosive kimberlite emplacement produced a small (ca. 200–400 m diameter) but deep (> 115 m) crater that was sufficiently deep and stable to accu-

multate these facies, which broadly represent progressive shallowing and eventual terrestrialization of the limnic environment. The model Rb-Sr age for emplacement is 47.8 ± 1.4 Ma, based on results from kimberlitic phlogopite (Creaser et al. 2003). Pollen assemblages from throughout the sequence (i.e., *Pistillipollenites*, *Platycarya*, *Metasequoia*, *Glyptostrobus*, *Quercoidites*, and *Alnus* spp.) are also diagnostic of a middle Eocene age, and indicate that subaqueous sedimentation began immediately after kimberlite emplacement (Hamblin et al. 2003). Likely owing to its steep-sided morphometry, the crater was not scoured during Pleistocene glaciations.

Samples were processed by oxidation in 30% H_2O_2 , followed by repeated centrifugation and rinsing. Aliquots of each resulting clean slurry were air dried onto pieces of heavy duty aluminum foil. The aluminum foil samples were trimmed, attached to aluminum stubs with Apiezon[®] wax, coated with a mixture of gold and palladium for 1 min with a Polaron Model E sputter coater and observed with a Leo 982 field emission SEM.

Observations

Siliceous remains from 11 different scaled chrysophytes were recovered from the Giraffe Pipe samples, including 7 species of *Mallomonas*, 1 of *Synura*, 2 of *Spiniferomonas* and 1 of *Chrysosphaerella*. Several scales of unknown taxonomic identity were also found and are illustrated below. Of the 11 scaled chrysophyte taxa, six are described as new species. The remaining forms appear to be morphologically identical to modern species.

Mallomonas giraffensis Siver & Wolfe nov. sp. (Figs 1A–C)

Latin diagnosis: Squamae magnae, $8-11 \times 5-6.5$ μm , lateraliter incurvatae, et costis submargina-libus in alas secundum latera cupulae extendentibus. Crista v-formis ampla, ramis extendentibus et cum alis ad cupulam confundentibus. Lamina basalis poris minutis fortuito spatio perforata, saepe in seriebus transversis dispositis. Series costarum brevium, parallelum, et secundum marginem posteriorem dense dispositarum. Limbus posterior glaber, sine orna-mentis. Latus sinistrum cupulae area rimarum parallelum et nonnumquam seriei pororum rotundorum. Structura setarum ignota.

Dimensions of scales: $8-11 \times 5-6.5$ μm ($n = 20$)

Type: Figure 1B

Type locality: 95.6 meters in the Giraffe Pipe core from the Lac de Gras kimberlite field, Northwest Territories, Canada ($64^\circ 44' \text{N}$, $109^\circ 45' \text{W}$).

The epithet is based on the informal name of the deposit.

Scales of this species are large, have a well developed V-rib, a large and prominent dome, lateral incurvings, and the anterior submarginal ribs are extended into wings along the sides of the dome (Figs 1A–C). The hood of the V-rib is broad and rounded, and the arms of the V-rib extend and fuse to the margins of the wings at the level of the dome. The base plate on the shield is perforated with small randomly spaced pores that may be arranged in transverse rows (Fig. 1A, C). A series of short, closely-spaced struts align the posterior margin, presumably under an upturned rim. The posterior flange between the struts and the base of the V-rib is smooth and unornamented. The left side of the dome has a patch of parallel slits and often, but not always, a series of circular pores each with a larger diameter than the base plate pores (Fig. 1C). A few scales, believed to represent anterior scales surrounding the flagellar opening, have an even broader dome with a wide opening for the bristle, but reduced development of the lateral wings (Fig. 1C).

Mallomonas giraffensis clearly belongs in the Series Lelymenae (Kristiansen 2002) and is closely related to the modern species *Mallomonas lelymene* Harris & Bradley. The overall size of the scales, the large and prominent dome and the structure of the wings are very similar between the two taxa. The primary difference is that scales of *M. lelymene* have a secondary layer on the shield consisting of a reticulation of ribs (Harris & Bradley 1960). In addition, the series of struts under the posterior rim on scales of *M. lelymene* are more developed and extend farther onto the posterior flange.

Bristles of *M. lelymene* are short (10–16 µm), robust, slightly curved, with a series of longitudinal ribs and a unilateral serration of small teeth (Kristiansen 2002). Scales of *M. giraffensis* were relatively abundant in the sample from 95.6 meters. Assuming that each scale possessed one bristle, we found a similar bristle type to that of *M. lelymene* with roughly the same density as *M. giraffensis* scales (Figs. 1F–G). The bristles were 20–25 µm, stout, rolled and hollow, and possessed both a series of longitudinal striations and a series of evenly-spaced thickened bands of silica that encircled the bristle. We found a second type of bristle that was slightly longer, hollow and with two rows of serrated teeth (Figs. 1H–I), but this bristle type had a different density than that of *M. giraffensis* scales. We can not be certain if either of these bristle types are associated with *M. giraffensis*.

***Mallomonas convallis* Siver & Wolfe nov. sp. (Fig. 1E)**

Latin diagnosis: Squamae ovales, 5–6 × 4–4.5 µm, margine anteriore ample rotundato, crista v-formi, margine posteriore excavato et incluso, et limbo posteriore humile. Scutum serie nodulorum rotundorum exigue elevatorum, amplorum plusminusve aequidistantium. Crista v-formis ampla, non in cucullum expansa, ramis curvatis et ad marginem extensis.

Margo posterior in tubum cavum inclusum expansus. Structura setarum ignota.

Dimensions of scales: 5–6 × 4–4.5 µm (n = 10)

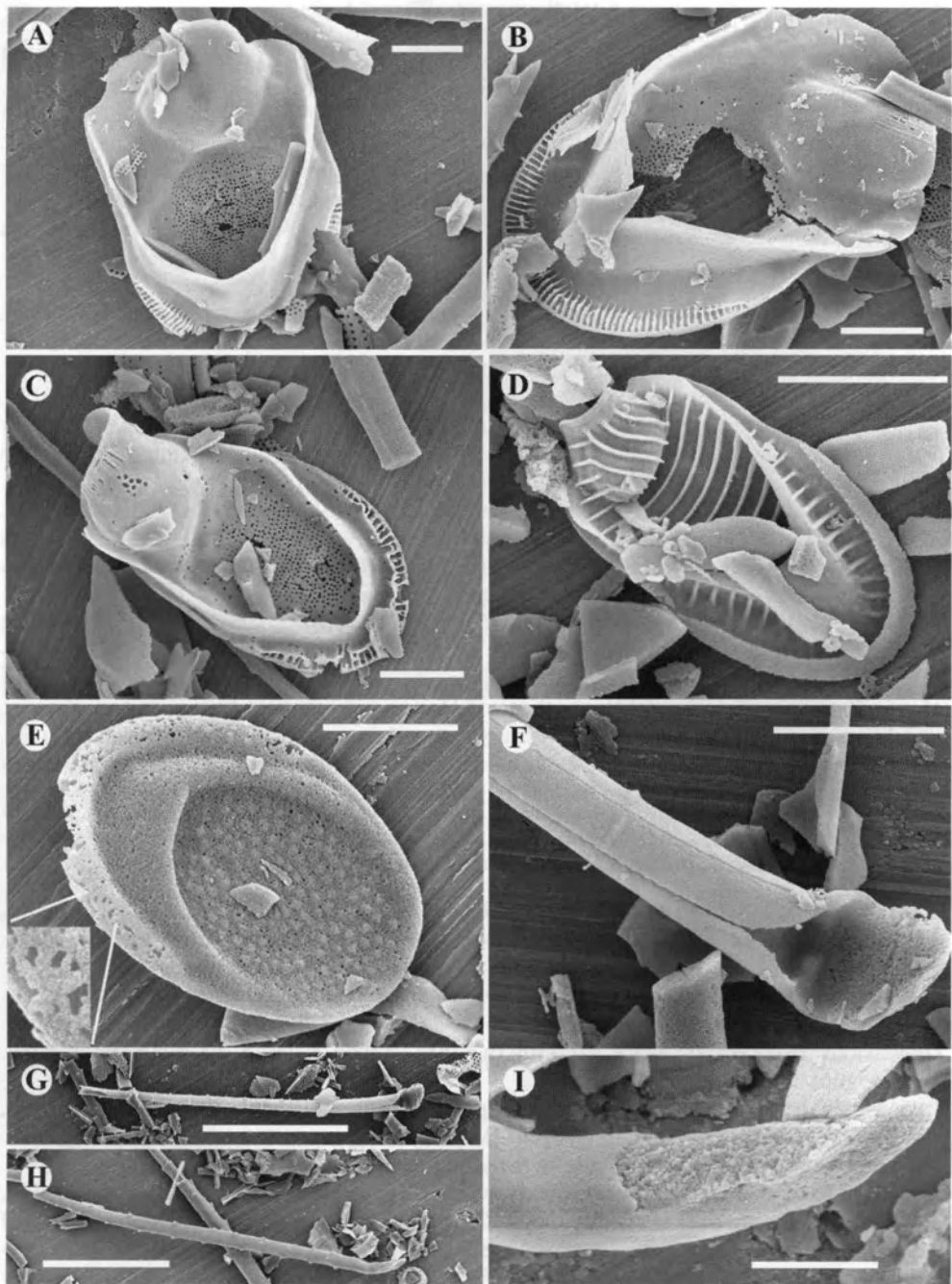
Type: Figure 1E

Type locality: 95.6 meters in the Giraffe Pipe core from the Lac de Gras kimberlite field, Northwest Territories, Canada (64° 44' N, 109° 45' W).

The epithet is based on the tubular nature of the enclosed posterior rim.

Scales are oval with a broadly rounded anterior margin, a V-rib and a hollow enclosed posterior margin (Fig. 1E and insert). The shield consists of a series of circular, slightly raised, broad and more or less evenly-spaced siliceous nodules. The V-rib is broad with curved arms that extend to the margin of the scale and the posterior flange is shallow. The most interesting feature of the scales of *Mallomonas convallis* is the enclosed and tubular nature of the posterior margin. On modern taxa the posterior margin of the scale bends up and over the base of the scale, forming what is called a posterior rim (Siver 1991). If the posterior rim on a modern species were to bend completely over and fuse with the posterior flange it would enclose a space analogous to what is found on scales of *M. convallis*. In addition to differences in the posterior rim, the V-rib of *M. convallis* scales does not become extended to form a hood as is common on most scales of modern species.

Fig. 1. *Mallomonas* scales and bristles from 95.6 m in Giraffe Pipe sediments. **A–C:** Body (A–B) and apical (C) scales of *Mallomonas giraffensis* sp. nov. Note the large dome and V-rib, lack of secondary structures on the shield, and ribs along the posterior margin. Scale bars are 2 µm. **D:** Scale of *Mallomonas pseudocratis*. Scale bar is 2 µm. **E:** Scale of *Mallomonas convallis* sp. nov. Note the pattern of blunt siliceous nodules on the shield, shallow V-rib, and enclosed nature of the posterior margin (insert). Scale bar is 2 µm. **F–I:** Remains of two types of bristles, rolled (F–G) and enclosed (H–I). Scale bars are 10 µm for G–H, 2 µm for F, and 1 µm for I.



Mallomonas porifera Siver & Wolfe nov. sp. (Figs 2A–C)

Latin diagnosis: Squamae corporis magnae, sine cupula $6-7 \times 4.5-5.5 \mu\text{m}$, cupuliferae $7-10 \times 6-6.5 \mu\text{m}$, ovales ad subcirculares, exigue asymmetricae et limbo posteriore exiguo. Squamae anteriores triangulares, asymmetricae, cupula ampla hyalina. Lamina basalis poris minutis rotundis aequidistantibus oblecta. Poris nullis circum ambitum squamae. Porus solus major rotundus plusminusve centraliter in squama locatus. Area circum hunc porum hyalina et poris minoribus carens. Structura setarum ignota.

Dimensions: Domeless scales: $6-7 \times 4.5-5.5 \mu\text{m}$ ($n = 20$); Domed scales: $7-10 \times 6-6.5 \mu\text{m}$ ($n = 10$).

Type: Figure 2A

Type locality: 95.6 meters in the Giraffe Pipe core from the Lac de Gras kimberlite field, Northwest Territories, Canada ($64^\circ 44' \text{N}$, $109^\circ 45' \text{W}$).

The epithet is based on the nature of the large single pore found on the shield.

Scales are of two types, domeless body scales (Figs. 2A–B) and domed anterior scales (Fig. 2C). Body scales are large, oval to subcircular, slightly asymmetric and with a small posterior rim. Anterior scales are triangular-shaped, asymmetric, with a broad hyaline dome and an opening on the right side from which the bristle most likely emerges. The base plate is covered with evenly spaced, small, circular pores except around the perimeter of the scale (Fig. 2B). A single large circular pore is present more or less in the center of each scale. The region immediately surrounding the large pore is usually hyaline and devoid of smaller pores. Secondary structures are lacking. Bristle structure is unknown.

The relationship of *Mallomonas porifera* to modern species is unclear. The large base plate pore is structurally similar to one found on *M. matvienkoae* (Matvienko) Asmund & Kristiansen, but scales of this taxon have a secondary layer and lack a dome. The body scales of *M. porifera* share some similarities to those of *Mallomonas caudata* Ivanov emend. Krieger, which are also planar, lack secondary structures and possess a single large pore. Like *M. matvienkoae*, *Mallomonas caudata* lacks domed scales and the structure of the large pore on scales of *M. caudata* differs from that on *M. porifera*.

Mallomonas pseudohamata Siver & Wolfe nov. sp. (Figs 2D–E)

Latin diagnosis: Squamae corporis minutae ($2-3 \times 2-2.5 \mu\text{m}$, cupuliferae $4-5 \times 3-3.5 \mu\text{m}$), ovales ad subcirculares, sine cupula et margine exiguo dimidiam partem ambitu circumdanti.

Lamina basalis poris aequidistantibus magnis rotundis oblecta. Structurae secundariae absunt. Structura setarum ignota.

Dimensions: Body scales: $2-3 \times 2-2.5 \mu\text{m}$ ($n = 20$); Domed scales: $4-5 \times 3-3.5 \mu\text{m}$ ($n = 10$).

Type: Figure 2D

Type locality: 95.6 meters in the Giraffe Pipe core from the Lac de Gras kimberlite field, Northwest Territories, Canada ($64^\circ 44' \text{N}$, $109^\circ 45' \text{W}$).

The epithet is based on the similarity of the scales to those of *Mallomonas hamata*.

Scales are of two types, domeless body scales (Fig. 2E) and domed anterior scales (Fig. 2D). Body scales are oval to subcircular, with a small posterior rim that encircles about half the perimeter of the scale. Anterior scales are triangular-shaped, with a broadly rounded posterior end and an elongated hyaline dome (Fig. 2D). The base plate is covered with evenly spaced, large, circular pores (Fig. 2E). Secondary structures are lacking. Bristle structure is unknown.

Both scale types of *Mallomonas pseudohamata* are similar to those of *M. porifera* and both taxa were found in the same sample. However, scales of *M. pseudohamata* are significantly

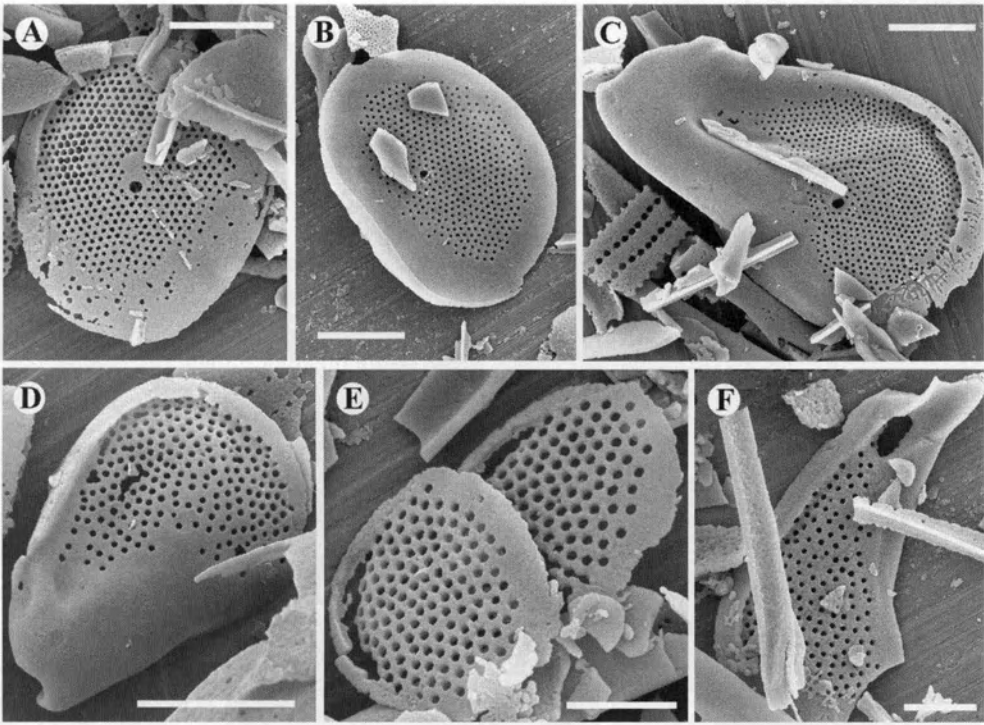


Fig. 2. *Mallomonas* scales from 95.6 m in Giraffe Pipe sediments. **A–C:** Top (**A**) and bottom (**B**) views of body scales, and an apical (**C**) scale of *Mallomonas porifera* sp. nov. Scales are simple with closely spaced base plate pores, a shallow posterior rim, and a large, single, centrally positioned pore. Scale bars are 2 μ m. **D–E:** Apical (**D**) and body (**E**) scales of *Mallomonas pseudohamata* sp. nov. Scales are small, simple, and with relatively large base plate pores. Scale bars are 2 μ m (**D**) and 1 μ m (**E**). **F:** Collar scale from an undescribed species. Scale bar is 1 μ m.

smaller, have larger base plate pores, and lack the characteristic large pore found on scales of *M. porifera*. Scales of *M. pseudohamata*, especially the shape, bear a resemblance to those of *M. hamata*.

***Mallomonas pseudocaudata* Siver & Wolfe nov. sp. (Figs. 3F–G)**

Latin diagnosis: Squamae magnae, 5–6 \times 4–5 μ m, rotundae ad ovaes, margine posteriore 2/3 ambitu circumdanti. Pars posterior squamae poris minutis fortuitis intervallis perforata, pars anterior glaber, hyalina et sine ornamentis. Sine structuris secundariis. Structura setarum ignota.

Dimensions of scales: 5–6 \times 4–5 μ m (n = 20)

Type: Figure 3F

Type locality: 127.6 meters in the Giraffe Pipe core from the Lac de Gras kimberlite field, Northwest Territories, Canada (64° 44' N, 109° 45' W).

The epithet is based on the similarity of the scales to those of *Mallomonas caudata*.

Scales are large, circular to oval with a posterior rim that encircles approximately 2/3 of the perimeter (Figs. 3F–G). The posterior half of the scale is perforated with small, randomly

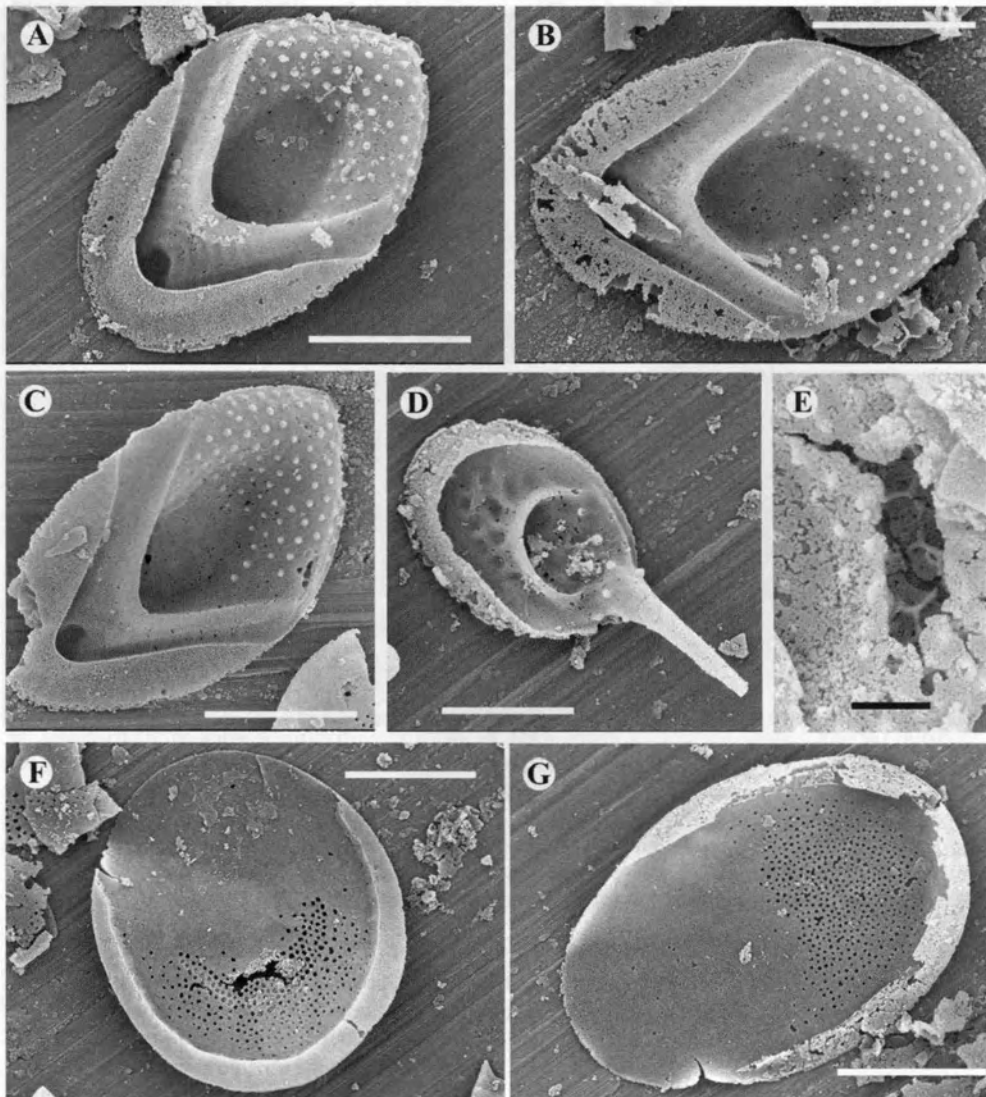


Fig. 3. A–E: *Mallomonas insignis* from 127.6 m in Giraffe Pipe sediments, illustrating body (A–C, E) and caudal (D) scales. Body scales are large with a well developed V-rib, posterior rim, and secondary structures along the anterior end. The internal reticulation of ribs is depicted on the broken scale in E. Caudal scales are smaller and possess a spine, reduced semicircular V-rib, and a secondary reticulation of ribs. Scale bars are 2 μm (A–C), 1 μm (D), and 0.5 μm (E). F–G: Scales of *Mallomonas pseudocaudata* sp. nov. from 127.6 m in Giraffe Pipe sediments. Note that base plate pores are restricted to the posterior part of the scale, and that the posterior rim encircles about two thirds of the perimeter. Scale bars are 2 μm .

spaced pores and the anterior end is smooth, hyaline and unornamented. Secondary structures are lacking. Bristle structure is unknown.

Mallomonas pseudocaudata is best placed in the Sectio Planae and is most similar to *M. caudata* Ivanov emend. Krieger. Scales of *M. pseudocaudata* differ from those of *M. caudata* in lacking ornamentation on a broader portion of the anterior end, and in lacking the large elongated pore found on scales of *M. caudata*.

***Synura recurvata* Siver & Wolfe nov. sp. (Figs. 4A–G)**

Latin diagnosis: Lamina squamae poris minutissimis et fortuitis intervallis perforata. Margo squamam praeter tertiam partem anteriorem circumdans. Spina crassa. Stratum secundarium partem anteriorem squamae tegens. Series costarum brevium a strato secundario ad marginem extendit. Spina tubulosa, super porum amplum posita, basi crassa et apice obtusa, corollam apicalem dentium recurvatarum gerens. Spina cum serie linearum longitudinalium, saepe secundum axim torquentium et ad basim conjugentium. Series costarum saepe in lamina basale incipit et cum parte inferiore spinae secundum latus anterius conjungit.

Dimensions: Scales: 6–7 × 4–5 μm (n = 20); Spines: 2.2–3.3 μm (n = 20)

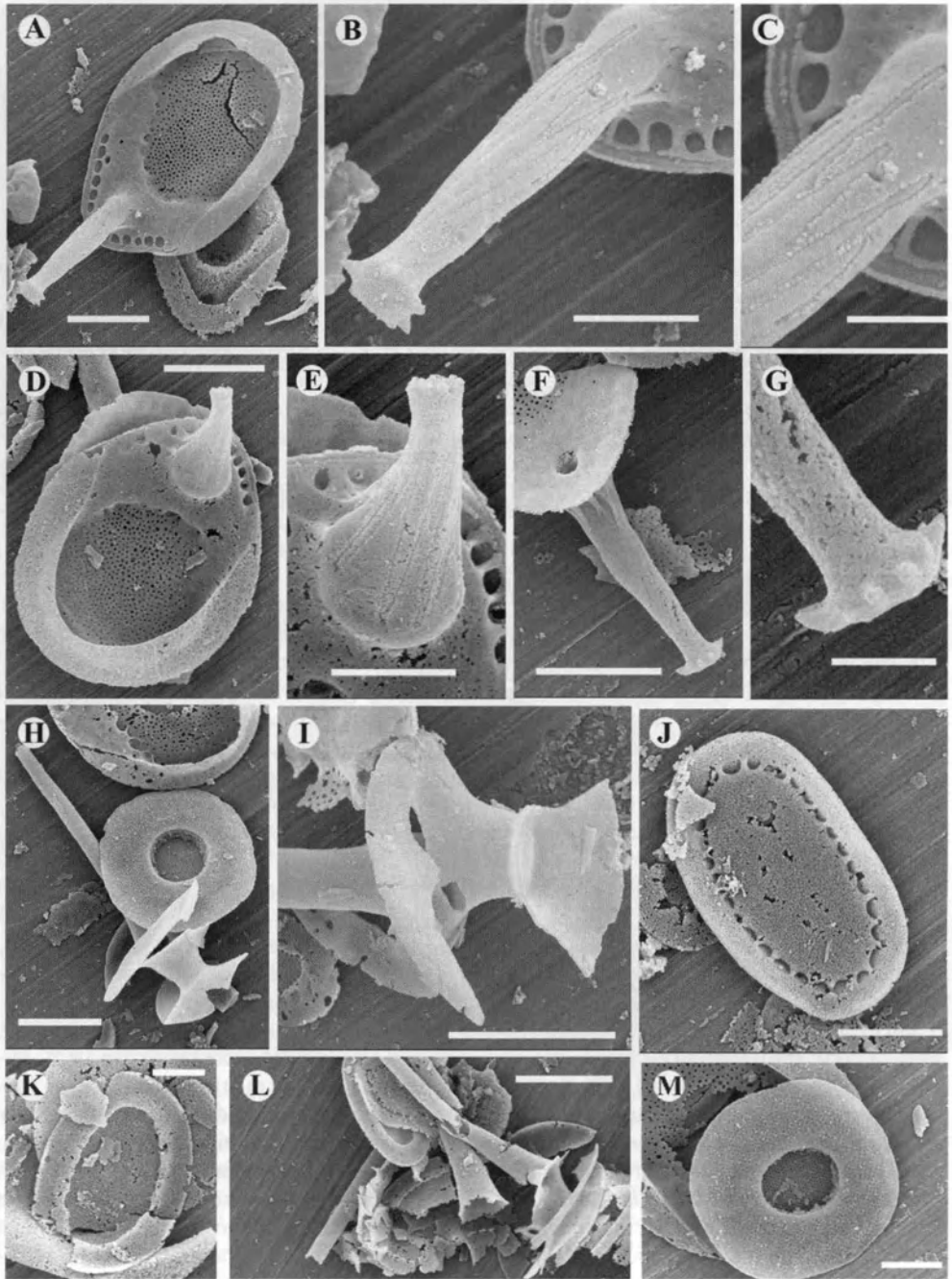
Type: Figure 4A

Type locality: 127.6 meters in the Giraffe Pipe core from the Lac de Gras kimberlite field, Northwest Territories, Canada (64° 44' N, 109° 45' W).

The epithet is based on the backward bent nature of the teeth on the tip of the spine.

Scales with a base plate perforated with very small and randomly-spaced pores, a posterior rim around the proximal two-thirds of the scale, a well developed and thick spine, and a secondary layer over the anterior 1/3 of the scale (Figs. 4A, D). A series of short ribs extend from the secondary layer to the anterior margin (Figs. 4B, E). These short ribs often fuse with another rib running parallel with the margin forming what appear as a series of large openings. The spine is hollow, with a stout base, and a flared, flat apex lined with a ring of small teeth that most often are bent slightly backwards (Figs. 4B, E–G). Spines have a series of longitudinal striations that often spiral or twist along the shaft and become connected in pairs at the base (Figs. 4C, E). The spine is subtended by a large pore (Fig. 4F). A series of ribs originating on the base plate and fusing with the lower portion of the spine is present, especially on the anterior side (Fig. 4F).

Several structural features of the scales serve to separate this taxon from all known species. First, compared to modern *Synura* species with extended spines, the base plate pores of *Synura recurvata* are very small and more randomly spaced. The base plate pores of *S. spinosa*, *S. curtispina*, *S. sphagnicola*, *S. echinulata* and *S. uvella* are significantly larger in diameter, more orderly arranged and often rimmed with a thickened layer of silica (Takahashi 1978; Nicholls & Gerrath 1985; Siver 1987). Second, the pattern of teeth at the tip of the spine, a characteristic used to aid in separating taxa at the species level (Petersen & Hansen 1958; Siver 1987), differs on scales of *S. recurvata* from all known species. Despite these minor differences, scales of *S. recurvata* are structurally very similar to modern spine-bearing species, especially *S. spinosa* and *S. uvella*. Like *S. recurvata*, scales of *S. uvella* and *S. spinosa* can both have ribs adjoining the base of the spine to the base plate. Both *S. spinosa* and *S. uvella* have multiple teeth on the spine apex, but they are not in a peripheral ring and do not bend backwards as they do in *S. recurvata*. In addition, Siver (unpub. obs.) has observed a similar pattern of longitudinal striations on *S. uvella* spines as are found on those of *S. recurvata*.



Additional taxa observed

The remains of seven additional organisms were found in the Giraffe Pipe samples, five of which appear to represent extant scaled chrysophytes (Figs. 1D, 3A–E, 4H–L). A few scales that are identical in structure to those of *Mallomonas pseudocratis* Dürschmidt were found in the sample from 95.6 m (Fig. 1D). The pattern of ribs on the dome, shield and posterior flange, as well as the overall dimensions and shape of the scales found in the Giraffe Pipe sample, match nicely those of *M. pseudocratis* (Siver 1991; Kristiansen 2002). The remains of four additional scaled chrysophyte taxa that, from a morphological standpoint, are essentially equivalent to modern species were found in the 127.6 m sample. Scales of *Mallomonas insignis* Penard (Figs. 3A–E) were common at 127.6 m. These scales have a well developed V-rib, a large depression at the base of the V-rib, a posterior rim underlain with a series of struts, a thin and smooth central shield, and an anterior end consisting of a honeycomb reticulation covered with an outer layer covered with papillae. The honeycomb reticulation was best observed on scales where the siliceous top layer was damaged (Fig. 3E). Smaller scales, equivalent to caudal scales of *M. insignis*, with spines, a rounded reduced V-rib, and a well developed reticulation on the posterior flange were also found in the 127.6 m sample (Fig. 3D).

Additionally, we found what appear to be the remains of *Chrysophaerella brevispina* (Figs. 4H–J), *Spiniferomonas* sp. (Fig. 4K) and *Spiniferomonas coronacircumspina* (Fig. 4L) from the 127.6 m sample. Spine-bearing scales that are identical to those of *C. brevispina* (Fig. 4H–I) and *S. coronacircumspina* (Fig. 4L) were rare, but well-preserved, in this sample. Isolated spineless scales of *C. brevispina* and *S. coronacircumspina* both have an oval arrangement of scalloped ridges and can be difficult to distinguish (Nicholls 1984; Siver 1993). In general, the scalloped ridges of scales from *C. brevispina* tend to be better developed compared to those of *S. coronacircumspina*, leading us to believe that the scale in Fig. 4J belongs to the former taxon. Isolated scales with a single lacuna and lacking scalloped ridges (Fig. 4K), presumably from another species of *Spiniferomonas*, were also observed.

Scales representing two additional organisms, one from 95.6 m (Fig. 2F) and another from 127.6 m (Figs 4H, M), were found. The scale in Fig. 2F may represent a collar scale belonging within *Mallomonas* Sectio Torquatae, but it was rare and we were unable to link it to body scales. We do not know the taxonomic affinity of the circular scales illustrated in Figs. 4H and M, although it is possible that they represent either a heliozoan or a further representative of *Paraphysomonas*. Although not the focus of this study, we did find a few structures that we believe to be chrysophyte stomatocysts at both 95.6 m and 127.6 m. The majority of the stomatocysts were smooth and unornamented.

Fig. 4. Additional chrysophyte scales from 127.6 m in Giraffe Pipe sediments. **A–G:** Scales of *Synura recurvata* sp. nov. illustrating the posterior rim, the extent of secondary structures on the anterior end, and the nature of the spine. **B–C** are magnified images of the scale in **A**, depicting the arrangement of teeth on the spine tip, and patterning of ribs along the shaft. The spine in **(E)** is a magnification of the scale in **(D)**, showing the ribbed structure and the twisting tendency of spines. Note the large base plate pore subtending the spine **(F)**, and recurvate nature of the teeth on the apex **(G)**. Scale bars are 2 μm (**A**, **D**, **F**), 1 μm (**B**, **E**), and 0.5 μm (**C**, **G**). **H–J:** Spine (**H–I**) and spineless (**J**) scales of *Chrysophaerella brevispina*. Note the double-plate nature of the base of the spine scales and the oval scalloped ridge of the spineless scales. The circular scale in **(H)** is of unknown taxonomic affinity. Scale bars are 2 μm (**H–I**), and 1 μm (**J**). **K:** Spineless scale of an unidentified *Spiniferomonas* species. Scale bar is 0.5 μm . **L:** Spine-less and spined scales of *Spiniferomonas coronacircumspina*. Scale bar is 2 μm . **M:** Siliceous scale of unknown taxonomic affinity. Scale bar is 1 μm .

Discussion and Conclusions

Stomatocysts are hollow siliceous structures formed through either asexual or sexual reproduction by all species of chrysophytes, including numerous non scale-bearing genera, as well as those with scales (Kristiansen & Preisig 2001). Stomatocysts appear to have a longer fossil record than scaled chrysophytes, as to our knowledge, there are no prior records of the siliceous cell coverings (scales or bristles) of scaled chrysophytes older than Holocene. As a result, the fossil record provides nothing concerning the origin and ontogeny of scaled chrysophytes. Our findings from lake sediments in the Giraffe Pipe crater not only demonstrate that scaled chrysophytes were well established by the middle Eocene, but that simple as well as complex scale morphologies were present by this time, resulting in assemblages that ultimately differ little from modern counterparts. Structures such as base plate pores, posterior rims, V-ribs, domes, spines and secondary siliceous features are well illustrated by scales from the Giraffe Pipe. Based on these observations, the origin of scaled chrysophytes certainly predates the middle Eocene.

Our study also confirms that the common and important genera *Mallomonas*, *Synura*, *Chrysophaerella* and *Spiniferomonas* had evolved by ca. 47 Ma. Some of the scale types found in the Giraffe Pipe samples, including those of *M. convallis* and *M. porifera*, are indeed quite different from known extant species. Others have distinct differences in their scale patterns, but can be easily linked to modern species flocks. For example, scales of *M. giraffensis* are very similar to *M. lelymene*, whereas those of *S. recurvata* have affinities to both *S. uvella* and *S. spinosa*. Still, because other forms present in the Giraffe Pipe material formed scales that appear to be morphologically identical to those of modern species, we have no reason to doubt that these represent ancient species that have survived to the present, e.g., *Chrysophaerella brevispina*, *Mallomonas insignis*, and *M. pseudocratis*.

In addition to scale patterns, characteristics of the bristles found in Giraffe Pipe specimens also share similarities with modern bristles. Bristles are divided into two regions, the shaft and the foot (Siver 1991). The shaft is usually slightly curved, smooth or ribbed, and often marked with teeth. Some species have bristles that are essentially rolled up sheets of thin silica with an open slit along the axis of the shaft where the folded margins meet (Siver 1991; Kristiansen 2002). Other bristle types are not rolled or folded. The foot of the bristle that fits under the anterior end of the scale, generally under the dome, is most often flat and bent at an angle relative to the shaft. We found copious bristles in the 95.6 m sample, but none in the deeper 127.6 m sample. Both rolled (Figs. 1F–G) and enclosed (Figs. 1H–I) bristles were present at 95.6 m, and in all cases one end was flattened and angled from the shaft, forming a foot. Bristles with teeth along the margins of the shaft, as well as bristles with longitudinal ridges, were also commonly observed. The rings of silica found on the shafts of the bristles in Figs 1 F–G do not have any known modern analogs.

We found it most interesting that among the many scaled chrysophyte fossils found at 127.6 m no bristles were found. Very few species of *Mallomonas* lack bristles (Kristiansen 2002), a notable exception being *M. insignis*, which additionally differs from other *Mallomonas* species by possessing spine-bearing scales on both ends of the cell. Scales that appear morphologically identical to *M. insignis* (Figs. 3A–E) are abundant at 127.6 m in the Giraffe Pipe, whereas dome-bearing scales are absent from this sample, but abundant at 95.6 m. Our observations thus offer preliminary support to the hypothesis of Lavau et al. (1997) that the absence of a dome is a primitive state. Although more speculative, our findings may also suggest that bristles are derived traits that developed subsequent to the evolution of scales.

Finally, of all the scaled chrysophyte microfossils observed in the Giraffe Pipe material, none is present in both samples, which we believe reflects the markedly different habitats they represent (lake *versus* wetland). Based on what is known about the ecology of modern scaled

chrysophytes, both environments were probably characterized by soft waters that were at least slightly acidic. *Mallomonas lelymene*, which is closely related to *M. giraffensis*, has been found in bogs (Péterfi & Momeu 1976), as well as in acidic, humic waters (Kling & Kristiansen 1983; Hartmann & Steinberg 1989). Given the 95.6 m sample likely represents a shallow marshy environment, we envisage that *M. giraffensis* and *M. lelymene* are ecologically similar taxa. *Mallomonas insignis*, abundant at 127.6 m, has been reported from nutrient enriched sites most often during colder seasons of the year (Harris 1958; Péterfi & Momeu 1976; Gutowski 1989). *Chrysosphaerella brevispina*, also found at 127.6 m, is a cold water taxon most often found in winter and spring months with a weighted mean less than 10 °C (Siver 1993 and references therein). These elements of morphological and ecological similarity imply that, with additional study, it may become possible to apply scaled chrysophytes towards more detailed paleoenvironmental reconstructions of Eocene lacustrine environments. To a large extent, this possibility is borne out of the astonishing apparent similarities between middle Eocene and extant scaled chrysophytes.

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