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Tracing lineages of scale–bearing Chrysophyceae over geologic time

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Abstract: Until the discovery of a massive number of fossil specimens in the early Eocene locality known as Giraffe Pipe, little was known about Chrysophyceae that bear siliceous scales from the geologic record. More recently, remains of chrysophyte scales have been reported from another Eocene site known as Horsefly, and uncovered from a Late Cretaceous site known as the Wombat locality. The aims of this investigation were to add the additional records from the Eocene and Cretaceous sites and to trace the known distributions of lineages, both with and without modern congeners, over the last 83 Ma. Twenty–nine scale types, referred to herein as lineages, have now been documented from the fossil record. Although the majority of the records document lineages within the order Synurales, specifically in the genera *Mallomonas* and *Synura*, species of the non–synurophyte genera *Chrysosphaerella*, *Paraphysomonas*, *Lepidochromonas*, and *Spiniferomonas* are also recorded, and the occurrences of stem lineages noted.

Key words: Chrysophyceae, Cretaceous, Eocene, fossil, Giraffe Pipe, Horsefly, lineage, Synurales, Wombat

INTRODUCTION

Historically, heterokont algae with siliceous scale coverings were classified within the class Chrysophyceae (Pascher 1914; Bourrelly 1957). These scale–bearing taxa were also commonly separated into two groups, those such as *Mallomonas* Perty and *Synura* Ehrenberg with bilaterally symmetric scales that form an organized cell covering, and taxa such as *Paraphysomonas* DeSaedeleer and *Chrysosphaerella* Lauterborn with more radially symmetric scales that are less organized on the cell. Based on a broad suite of characters, including pigmentation, arrangement of flagellar basal bodies and roots, organization of the siliceous scales, basal contractile vacuoles, and lack of an eyespot, Andersen (1987) removed the genera with bilaterally symmetric scales from the Chrysophyceae and placed them into a new class, the Synurophyceae. However, using SSU rDNA and rbcL gene data Škaloud et al. (2013) found that the synurophyte clade was resolved as a distinct monophyletic clade, but was nested within the Chrysophyceae clade, and best classified as an order, the Synurales. Subsequent studies support placement of the synurophytes as a monophyletic order within the Chrysophyceae (Škaloud et al. 2020; Jadrná et al. 2021).

Jo et al. (2016) proposed that the order Synurales be divided into three families: the Mallomonadaceae, Synuraceae, and Neotessellaceae, represented by the type genera *Mallomonas*, *Synura,* and *Neotessella* Jo, Kim, Shin, Škaloud et Siver, respectively. Taxa in the Neotessellaceae differ from the other synurophytes by possessing radially symmetric scales that surround a colony of cells and not each individual cell. Other non–Synurales genera within the Chrysophyceae that form radially symmetric scales include *Paraphysomonas*, *Spiniferomonas* Takahashi, and *Lepidochromonas* Kristiansen in the order Paraphysomonadales (Cavalier–Smith et al. 1996), and *Chrysosphaerella* in the order Chromulinales (Škaloudová et al. 2013).

The species–rich genera *Mallomonas* and *Synura* that comprise the majority of species within the Synurales were originally divided into sections and series based primarily on the morphology of siliceous structures, a system largely supported by molecular works. Kristiansen (2002) divided the genus *Mallomonas* into 19 sections. As noted by Siver et al. (2015), nine of the sections are rare and contain only one or two species each, while the remaining 10 sections are more speciose, each with between five and over 40 taxa. Based on molecular data, Siver et al. (2015) further proposed that section Heterospinae be moved to a series within section Planae. Species within the genus *Synura* are now classified in three sections, section Synura, section Curtispinae, and section Petersenianae (Škaloud et al. 2020).

Fossil records of Chrysophyceae are based primarily on remains of siliceous cysts, scales, and bristles (Siver et al. 2015). The oldest known records are of cysts from a freshwater deposit in China that dates to the Late Triassic at ~230 Ma (Zhang et al. 2016). Because all members of class Chrysophyceae can produce cysts, it is not certain which groups within the class produced the structures uncovered in China. Further, since no scales were uncovered by Zhang et al. (2016), it is likely that the cysts were produced by non–scale bearing species. Fossil locations containing evidence of scales and bristles are much younger, and fewer in number. Siver & Wolfe (2005a) published the first records of scale and bristle remains older than Holocene from a 48 Ma early Eocene locality known as Giraffe Pipe located near the Arctic Circle in northern Canada. Numerous studies based on material from the Giraffe Pipe locality followed, including information on, for example, new species (e.g., Siver 2015a; 2018b), evolutionary stasis of some scale types (Siver et al. 2013b), giant scale types (Siver 2022), modes of bristle attachment (Siver & Lott 2012), arrangement of scales on the cell coat (Siver 2018b), and biogeography considerations (Siver & Wolfe 2009). Specimens from an additional and slightly older (~52 Ma) fossil site, the Horsefly locality, addressed the concept of paleoendemic species (Siver et al. 2019a). Another much older fossil locality from the Late Cretaceous (83 Ma) named Wombat, and also situated near the Arctic Circle in northern Canada, is now known to contain numerous remains of scales, bristles, and cysts of Chrysophyceae (Siver et al. 2013a; Siver 2022).

More recently, additional records have been uncovered from the Giraffe Pipe, Horsefly, and Wombat localities. The objective of this study is to provide a preliminary report on these new findings, summarize all previous fossil records of scales and bristles relative to geologic time, and develop a time line for all known scale types.

Materials and Methods

Fossil localities. Remains of chrysophytes from three fossil sites were used and/or summarized in this study: the Giraffe Pipe, Horsefly, and Wombat localities. Descriptions of each fossil locality have been published previously and are briefly summarized herein. The Giraffe Pipe locality is a kimberlite diatreme that was emplaced into the Slave Craton near the Arctic Circle in the Northwest Territories of Canada approximately 47.8 million years at the transition between the Ypresian and Lutetian (Siver & Wolfe 2005a; Wolfe et al. 2006). The resulting diatreme crater filled with water, becoming a maar lake, and subsequently infilled with lacustrine remains, followed by an extensive deposit of paludal sediments, and eventually the crater was capped by glacial till. 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 and terrestrial remains. The mudstones represent a continuous history of the Eocene maar lake spanning hundreds of thousands of years (Siver et al. 2019b) and contain a rich and diverse assemblage of extraordinarily preserved siliceous microfossils, including specimens of freshwater chrysophytes and synurophytes, as well as diatoms, testate amoebae, heliozoans, phytoliths, and sponge spicules (e.g., Wolfe & Siver 2009; Siver et al. 2010; Siver et al. 2019b). Like the Giraffe Pipe locality, the Wombat locality is another diatreme crater formed by phreatomagmatic volcanism (Grande et al. 2022), that eventually filled with lacustrine and later terrestrial sediments. An extensive drill core taken by BHP Billiton Diamonds Inc. in 1993 recovered 160 m of laminated aquatic sediments, of which a 24–meter section and another five–meter section are especially rich with well–preserved siliceous microfossils (e.g., Siver et al. 2016). Recent high–resolution analyses using MC–LA–ICP–MS U–Pb zircon geochronology from two distal rhyolitic tephra beds yielded an age of 82.97±0.60 Ma, corresponding to the Late Cretaceous (Grande et al. 2022).

The Horsefly fossil locality is located in east–central British Columbia. Horsefly represents an ancient, warm, monomictic or possibly meromictic, softwater lake that existed between 44–52 Ma (Wilson 1977; Wilson & Barton 1996; Wolfe & Edlund 2005) in a region that experienced a warm and wet climate and lacked freezing conditions in winter (Greenwood et al. 2005; Archibald et al. 2014). This places Horsefly in the early to middle Eocene, with a maximum age slightly older than the emplacement of the Giraffe locality. For this study, small subsamples from a 767–year long sequence (H2 sequence) collected by Wilson & Barton (1996) and archived at the University of Alberta, Canada, were examined for chrysophyte microfossils. Each subsample is estimated to represent approximately 30 years of deposition along the H2 sequence. Horsefly is also the type locality for the early Aulacoseiraceae genus, *Eoseira* (Wolfe & Edlund 2005).

Sample Preparation. Mudstone fragments (~100 mg) from each core section examined were oxidized using 30% H_2O_2 under low heat for 1–2 hr, rinsed with distilled water, and the resulting slurries were stored in glass vials at 4 ºC. This mild oxidation procedure resulted in separation of numerous siliceous microfossils from the rock matrix as well as small remaining fragments for most samples from the Giraffe Pipe core. For most rocks from the Horsefly and Wombat cores, this procedure resulted in the fossil rock fragmenting into smaller pieces (flakes), which were studied for fossil remains. Aliquots of each sample were air–dried onto a piece of heavy–duty aluminum foil. The aluminum foil samples were trimmed and attached to aluminum stubs with Apiezon® wax. All 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 FESEM or a FEI Nova NanoSEM 450 field emission scanning electron microscope (SEM).

Definitions. For this study, "lineage" is used to define the closest modern species or group of species to which a fossil taxon shares a common scale structure. In some cases, the scale characters of the fossil specimens are very similar to, and even hard to distinguish from, their modern counterparts. In other situations, there are sufficient features to link the fossil taxa to specific modern congeners. In both of these cases, if the fossil specimens have not already been officially described, then the modern names are used to identify the fossil specimens as was done in Siver et al. (2015). Fossil organisms with a species name of "GP#" or "W#" are as given in Siver et al. (2015) and Siver (2022), respectively. Stem organisms represent extinct fossil taxa with unique scale designs that can't be linked directly to any specific modern species. Most stem taxa can still be associated with broader clades of modern organisms, such as those with species that either possess a V–rib or not for *Mallomonas*, or species that have scales with either forward–projecting spines or a keel in the case of *Synura*.

Table 1. Twenty–nine modern or stem lineages to which fossil chrysophytes are assigned, and the current known distribution of each taxon in the geologic record. The taxon numbers correspond to those on Figure 1. Key: M–E–C = the lineage is documented from modern through the Eocene to the Cretaceous; M–E = the lineage is documented from modern through the Eocene; E–C = the lineage is represented from the Eocene to the Cretaceous, but not known from modern collections; E = these lineages are only known from the Eocene and ; C = species representing these lineages are only known from the Cretaceous. Section and series designations are according to Kristiansen (2002), Siver et al. (2015), and Škaloud et al. (2020).

Taxon #	Taxon(a)	Lineage	Fossil category	References
1	*Mallomonas asmundiae*	section Striatae, *Mallomonas asmundiae*	M–E	Siver et al. 2009
2	*Mallomonas bangladeschica*	section Planae, series Matvienkoanae, *M. bangladeschica*	M–E	Siver et al. 2015
3	*Mallomonas multiunca* v. *pocosinensis*; *M. bakeri*; *M. skogstadii*	section Heterospinae	M–E	Siver et al. 2015; Siver 2018a
4	*Mallomonas pleuriforamen*	section Planae, series Matvienkoanae	M–E	Jo et al. 2013
5	*Mallomonas* GP4	section Punctiferae, series Punctifera	M–E	Siver et al. 2015
6	*Mallomonas oviformis*	section Planae, series Matvienkoanae	M–E	Siver et al. 2015
7	*Chrysosphaerella* spp.	class Chrysophyceae, order Chromulinales	M–E	Siver & Wolfe 2005; this paper
8	*Spiniferomonas* sp.	class Chrysophyceae, order Paraphysomonadales	M–E	Siver & Wolfe 2005
9	*Synura macracantha*	section Petersenianae	M–E	Siver et al. 2013
10	*Synura nygaardii*	section Curtispinae	M–E	Siver et al. 2013
11	*Synura recurvata*	section Synura	M–E	Siver & Wolfe 2005; Siver et al. 2013
12	*Mallomonas giraffensis*	section Pseudocoronatae, series Lelymenae	M–E	Siver & Wolfe 2005
13	*Mallomonas dispar*, *M. lancea*, *M.* GP11	section Mallomonas, series Tonsuratae, Intermediae and Alpina	M–E	Siver et al. 2009; Siver et al. 2015
14	*Mallomonas intermedia*	section Mallomonas, series Intermediae	M–E	Siver et al. 2019
15	*Mallomonas pseudocaudata*, *M. caudata*	section Planae, series Caudata	M–E–C	Siver & Wolfe 2005; this paper
16	*Mallomonas insignis*	section Insignis	M–E–C	Siver et al. 2013; this paper
17	*Mallomonas lychenensis* and related species	section Quadratae, series Allorgei	M–E–C	Siver et al. 2015; this paper
18	*Mallomonas aperturae*	section Leboimianae, *M. paludosa*	M–E–C	Siver 2018b
19	*Synura petersenii* related taxa	section Petersenianae	M–E–C	Siver et al. 2013; this paper
20	*Paraphysomonas* spp. and *Clathramonas* spp	class Chrysophyceae, order Paraphysomonadales	M–E–C	this paper

Table 1 Cont.

21	*Mallomonas* GP1, *M.* GP2, other related species	section Torquatae, series Eoae, series Mangoferae, *M. mangofera*	M–E–C	Siver et al. 2015; this paper
22	*Mallomonas porifera*	proposed stem species of section Planae	E–C	Siver & Wolfe 2010; this paper
23	*Mallomonas elephantus* and related taxon	proposed stem species of section Planae	E–C	Siver & Wolfe 2016; this paper
24	*Mallomonas schumachii*	proposed stem species of section Planae	E–C	Siver 2015a; this paper
25	*Synura cronbergiae*	? stem taxon of section Curtispinae	E–C	Siver 2013
26	*Mallomonas media*	proposed stem species of section Planae	E	Siver & Lott 2012
27	*Mallomonas* GP13	proposed stem species of section Planae	E	Siver et al. 2015; Siver 2022
28	*Mallomonas* W1	proposed stem species of section Planae	C	Siver 2022; this paper
29	New genus (to be described)	proposed stem species before split of the genera *Mallomonas* and *Synura*	C	this paper

Results and Discussion

Evidence for 29 lineages of scale–bearing chrysophytes has now been documented from the fossil record, with the oldest specimens dating to the Late Cretaceous at 83 Ma (Table 1; Fig. 1). Specimens representing many of the 29 lineages have been published previously (Table 1). Records will be added for some lineages, and others will be published for the first time with this communication. The majority of the records document lineages within the order Synurales and specifically those within the genera *Mallomonas* and *Synura*. Specimens of the non–synurophyte genera *Chrysosphaerella*, *Paraphysomonas*, *Lepidochromonas*, and *Spiniferomonas* are also reported in this communication.

The 29 lineages can be divided into five groups depending on the portion of the geologic record over which specimens have been uncovered: a) those present today and known in Eocene deposits (n = 14; M–E group); b) ones present today and known back to the Cretaceous (n = 7; M–E–C group); c) lineages that span the Eocene to Cretaceous period, but are not known today (n = 4; E–C group); d) taxa only known from the Eocene (n = 2; E group); and e) those only documented in Cretaceous rocks (n = 2; C group).

M–E Lineages

Of the 14 lineages containing taxa known as far back as the Eocene and with definite links to modern organisms, 12 represent synurophytes and two other scale–bearing chrysophyte genera (Table 1; Fig. 1). The scale structures of six of the lineages, represented by *Mallomonas asmundiae* (Wujek et Van der Veer) Nicholls, *M. bangladeshica* (Takahashi et Hayakawa) Wujek et Timpano, *M. oviformis* Nygaard, *M. intermedia* Kisselev emend. Péterfi et Momeu, *Synura nygaardii* (Petersen et Hansen) Kristiansen, and *S. macracantha* (Petersen et Hansen) Asmund, are virtually identical when comparing fossil specimens with modern congeners (Siver et al. 2013a; 2015; 2019a). These represent excellent examples of evolutionary stasis with respect to scale morphology over geologic time extending to at least the early Eocene. *Mallomonas bangladeshica* and *M. oviformis* represent two lineages within section Planae. Because of their highly ornate structure, the similarity between modern and fossil scales of *M. bangladeshica* is especially impressive.

Mallomonas intermedia represents one lineage within the highly diverse and species–rich section *Mallomonas*, and *M. asmundiae* a heavily ribbed species in the section Striatae, and both of these taxa possess tripartite scales believed to be a more derived group within the *Mallomonas* clade (Kristiansen 2002; Siver et al. 2015). Records containing remains of *M. intermedia* are slightly older because it has been uncovered at the Horsefly locality (Siver et al. 2019a). Multiple molecular–based studies (Siver et al. 2015; Škaloud et al. 2020) suggest that *Synura macracantha* holds a basal position within the section Petersenianae clade, and fossils of specimens virtually identical with *S. nygaardii* indicate this scale type was also well developed by the Eocene.

Another group of organisms from Eocene rocks possesses scales that differ from related modern congeners, but can be linked to them. Three species extracted from Giraffe Pipe mudstones, *Mallomonas bakeri* Siver, *M. skogstadii* Siver (Siver 2018a), and *M. multiunca* v. *pocosinensis* Siver (Siver et al. 2015) represent Eocene members of section Heterospinae, a lineage within the section Planae clade (Siver et al. 2015). *Mallomonas pleuriforamen* Siver et al. represents another lineage within the Planae clade that includes *M. matvienkoae* Asmund et Kristiansen and its relatives (Jo et al. 2013). Scales and bristles belonging to *Mallomonas* GP4 (Siver et al. 2015) and scales of *Synura recurvata* Siver et Wolfe (Siver & Wolfe 2005b) are clearly linked to modern species in section Punctiferae and the modern species *S. uvella* Ehrenberg, respectively. *Mallomonas dispar* Siver, Lott et Wolfe, *M. lancea* Siver, Lott et Wolfe and *M.* GP11 represent three additional fossil species possibly linked to *M. galeiformis* Nicholls, *M. corcontica* (Kalina) Péterfi et Momeu, and *M. alpina* Pascher et Ruttner emend. Asmund et Kristiansen, respectively, within the highly diverse section *Mallomonas* (Siver et al. 2009, 2015). Lastly, scales of *Mallomonas giraffensis* Siver et Wolfe are large, tripartite, and with substantial anterior wings, and represent an Eocene member of the lineage containing *M. lelymene* Harris et Bradley (Siver & Wolfe 2005b).

The Eocene Giraffe Pipe locality has also yielded scales representing the non–synurophyte genera *Chrysosphaerella* and *Spiniferomonas*. Plate and spine scales, that most closely resemble those of the modern *C. brevispina* Korshikov, and ones more similar to *C. longispina* Lauterborn (Siver 1993), were well formed by the Eocene. Scales related to *C. brevispina* (Figs 2–3) were especially common throughout a large portion of

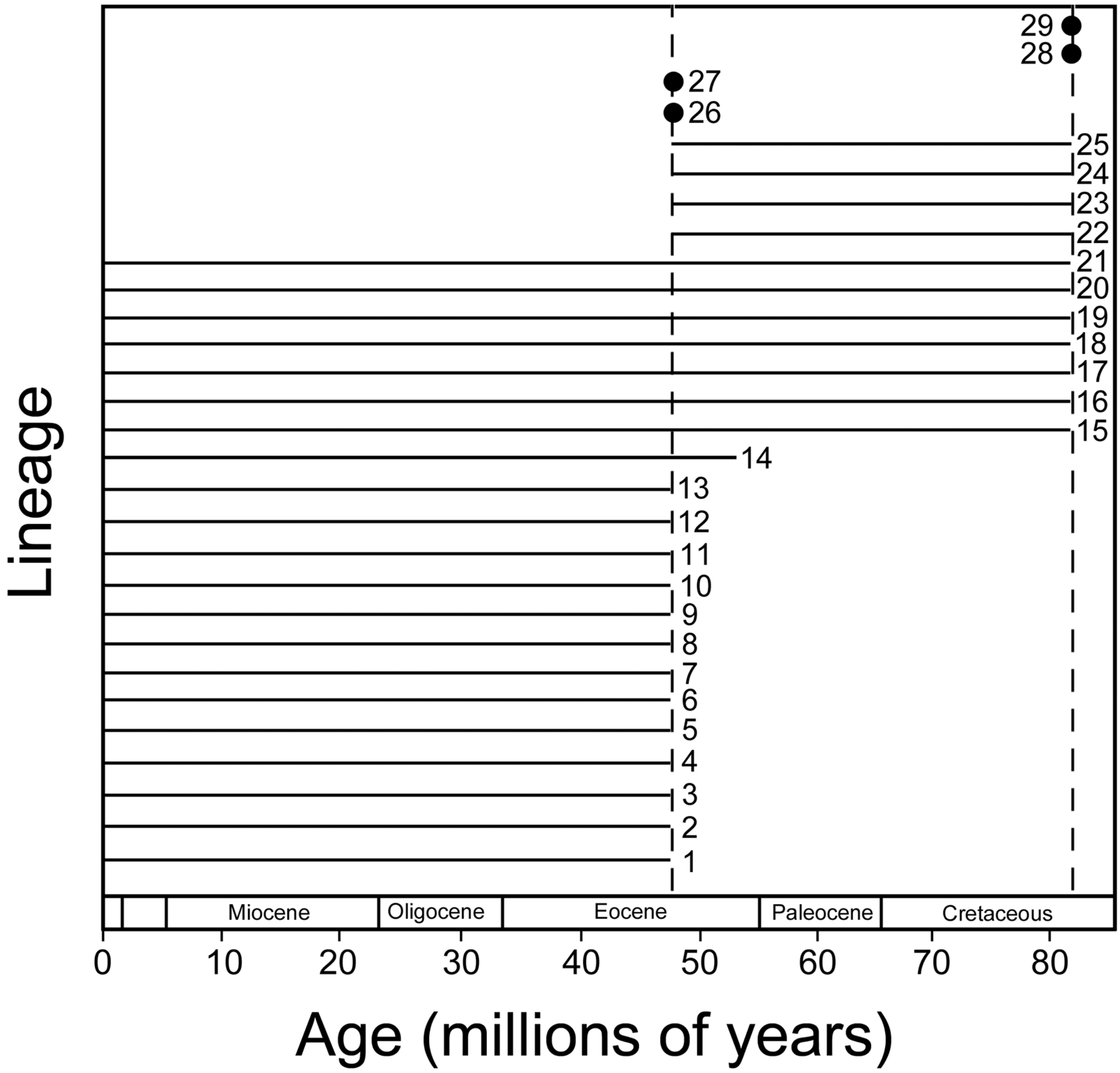
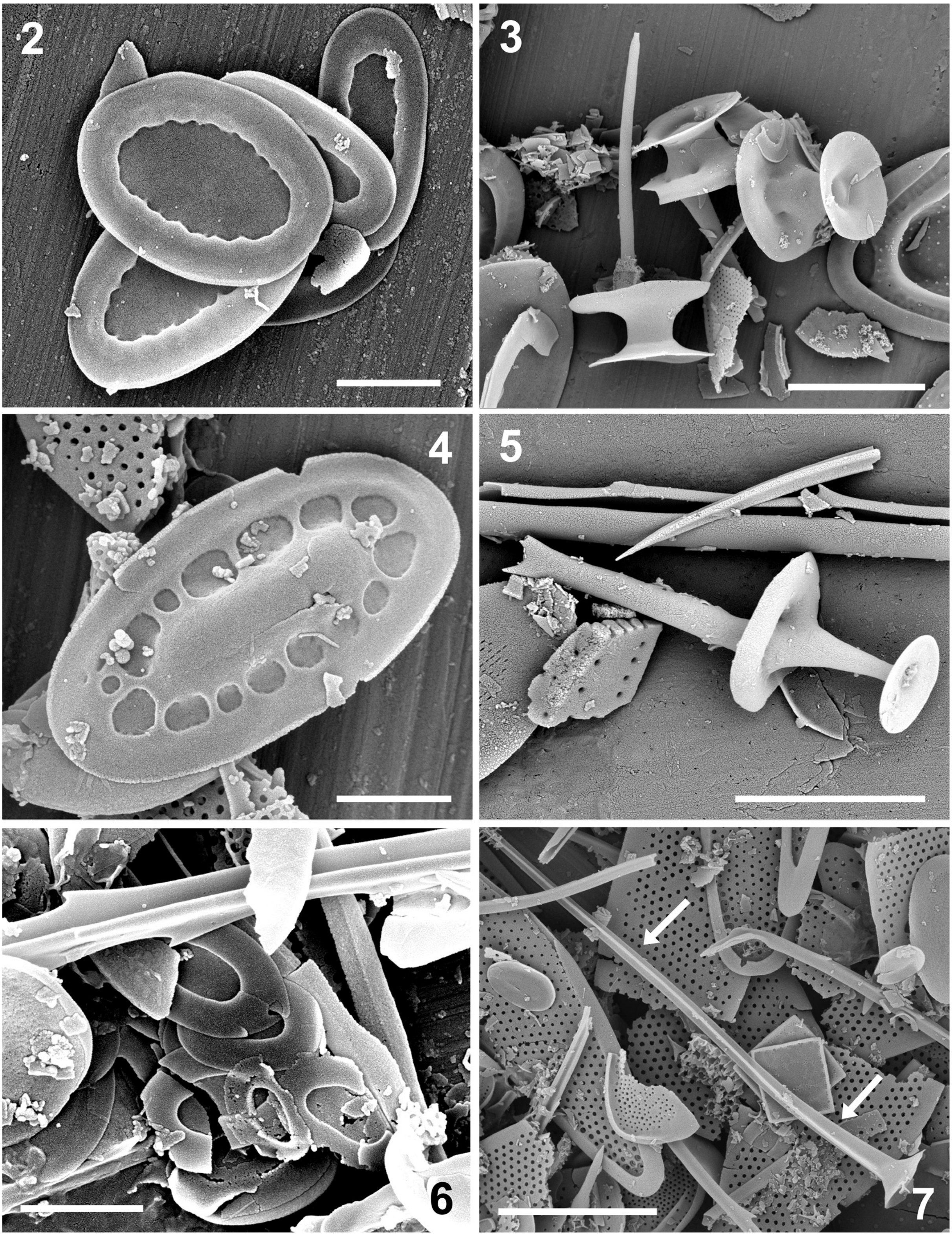


Fig. 1. The known distributions of 29 lineages of scaled chrysophytes, including synurophyte and non–synurophyte taxa, in the fossil record spanning the Late Cretaceous to modern day. The numbers refer to those referred to in Table 1.



Figs 2–7. SEM images of fossil synurophyte scales from the early Eocene Giraffe Pipe locality: (2) plate and (3) spine scales of a taxon linked to *Chrysosphaerella brevispina*; (4) plate and (5) spine scales of a taxon linked to *Chrysosphaerella longispina*; (6) plate and (7) spine scales of a taxon linked to *Spiniferomonas trioralis*. Scale bars 1 µm (10–11, 13) and 2 µm (8–9, 12).

the Giraffe core, while those closer to *C. longispina* (Figs 4–5) were less common, but clearly present. Although spine scales with moderate–length shafts were found, those with longer shafts typical of *C. longispina* were not observed. It is possible that this is due to breakage of the longer spine shafts. Specimens representing scales of *Spiniferomonas* were also uncovered in Giraffe rocks, including three–ribbed spine scales (Fig. 7) and plate scales with one large lacunae (Fig. 6) similar to those of *S. trioralis* Takahashi. Plate scales of *Spiniferomonas* species with more complex morphologies were not found.

M–E–C Lineages

Specimens from seven modern lineages, represented by *Mallomonas caudata* Iwanoff emend. Krieger, *M. insignis* Penard, *M. lychenensis* Conrad, *M. paludosa* Fott, *M. mangofera* Harris et Bradley, *Synura petersenii* sensu lato, and the paraphysomonads, are reported here from the 83 Ma Wombat fossil locality (Figs 1, 8–16). Each of these organisms is well represented in contemporary freshwater environments (Siver 1991; Kristiansen 2002; 2005; Siver et al. 2013b; Scoble & Cavalier–Smith 2014; Siver 2015b; Škaloud et al. 2020).

Mallomonas caudata (Siver 1991; Kristiansen 2005) and species in the section Peterseniane of *Synura* (Škaloud et al. 2020) are among the most widespread and commonly reported synurophytes known today (Siver 2015b). Scales and bristles clearly linked to modern specimens of *M. caudata* were found in multiple strata within the Wombat core (Figs 8–9). The single elongated pore found close to the posterior rim on *M. caudata* scales and the tiny teeth commonly noted on the serrated portion of the bristle were present on the Cretaceous specimens affirming the presence of this organism at 83 Ma. *Mallomonas caudata* was found to be a younger and more derived species within the section Planae diverging from the clade containing *Mallomonas matvienkoae* ~55Ma (Siver et al. 2015). The presence of this taxon in much older Cretaceous rocks implies that other members of the section Planae are therefore much older than presently reported.

Both Siver et al. (2015) and Škaloud et al. (2020) found *Synura macracantha* at the base of the section Petersenianae, diverging from the remaining species in this clade between 65 Ma and 88 Ma, respectively. Although numerous specimens of this species have been reported from the Eocene Giraffe core (Siver et al. 2013a), it has not been found at older fossil sites. However, specimens representing other species within section Petersenianae, with scales more closely aligned to species that are believed to be more recently evolved than *S. macracantha*, are reported here from 83 Ma (Fig. 10). The scales are small and possess a broad keel supported on the base plate by a series of short struts. Given these findings, current age estimates for section Petersenianae are likely underestimated.

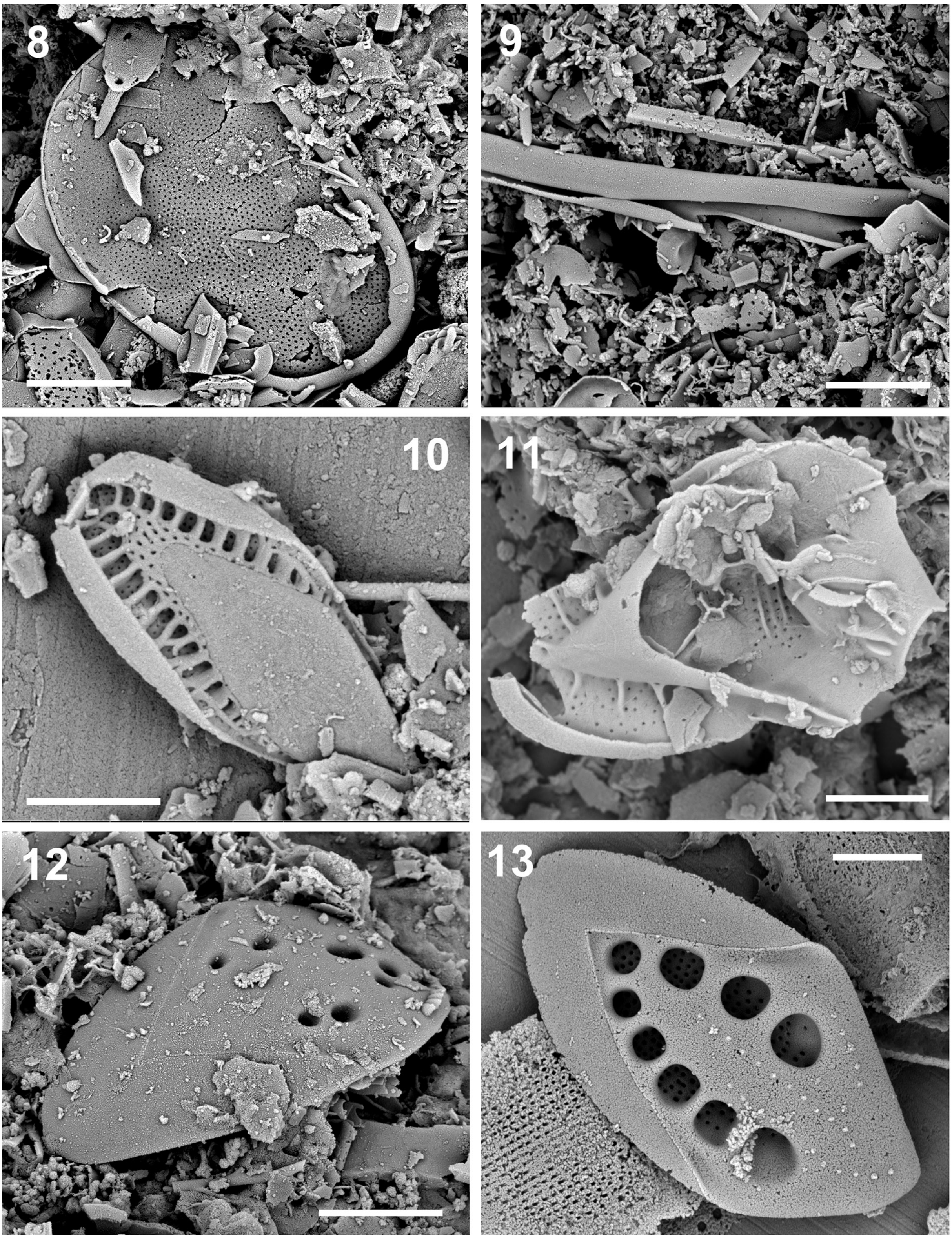
Mallomonas aperturae Siver, reported from the Eocene Giraffe Pipe locality, represents an ancient congener of the modern species, *M. paludosa* (Siver 2018b). Both species have tripartite scales with large V–ribs and domes, transverse and parallel ribs across the shield, and large posterior flanges with parallel struts. Both species also possess a distinctive opening along the posterior border of the dome, an unusual and unique structure that clearly links these taxa. Scales of a third species, referred to as *Mallomonas* W2, also possessing the unique opening on the dome, have now been found in Cretaceous rocks (Fig. 11). By comparing scale features over time in this lineage, the extent of the V–rib hood and anterior wings have become less prominent, while the development of rib patterns has been enhanced.

Fossil scale representatives of the section Quadratae, including ones that are morphologically related to *M. lychenensis* (Figs 12–13), section Insignes that are similar to those of *M. insignis* (Fig. 14), and specimens belonging to section Torquatae, series Mangoferae (Figs 15–16) are reported here from Late Cretaceous material. Multiple scale types from the Giraffe Pipe core belonging to species within the section Quadratae were first reported by Siver et al. (2015, their Figs 6H, 7A–B). Specimens of scales matching one of these morphotypes, and clearly related to the modern species *M. lychenensis*, have now been found in Cretaceous rocks from the Wombat locality (Fig. 12). Similarly, massive numbers of scales from Eocene rocks that are morphologically equivalent to *Mallomonas insignis* were previously reported by Siver et al. (2013b), and are now recorded from the Late Cretaceous (Fig. 14). Specimens from the section Torquatae lineage were reported previously by Siver et al. (2015, their Figs 7C–D), and are now also recorded from Cretaceous mudstones (Fig. 15–16), indicating that this lineage was well advanced by this time period.

Up until now, remains of paraphysomonads are not known from the fossil record, perhaps due, in part, to being overlooked because of their small size. Paraphysomonads, which are widespread and often numerous in modern aquatic ecosystems (Nicholls & Wujek 2003), are primarily represented by the two heterotrophic genera, *Paraphysomonas* and *Lepidochromonas* (Scoble & Cavalier–Smith 2014). Close examination of fractured rocks from both Eocene and Cretaceous fossil localities has revealed numerous scale types belonging to these genera (Figs 17–19) and clearly signaling that both genera were well developed by the Late Cretaceous. Although work is underway to thoroughly describe this trove of species, it is interesting to note that even intricate 3–D scale types found among some *Lepidochromonas* species (Scoble & Cavalier–Smith 2014) are evident in Cretaceous rocks (Fig. 19).

E–C Lineages

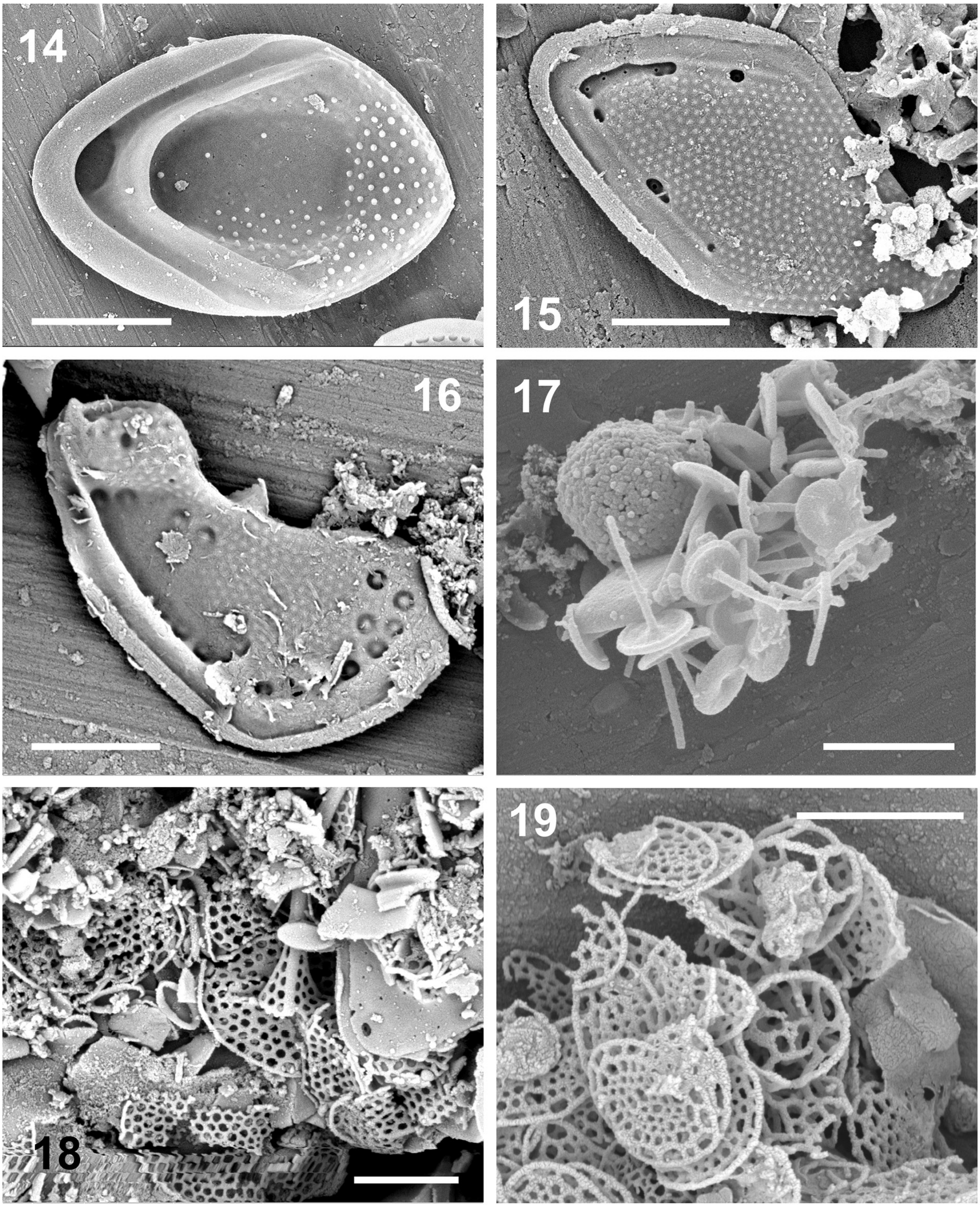
Four lineages of synurophytes found in both Eocene and Cretaceous rocks, but lacking in modern ecosystems, are represented by *Mallomonas porifera* Siver et Wolfe, *M. elephantus* Siver et Wolfe, *M. schumachii* Siver and *Synura cronbergiae* Siver (Fig. 1). Representatives of all four lineages have been described from the Giraffe Pipe locality (Siver 2013, 2015a; Siver & Wolfe 2010, 2016), but are now reported from the older Cretaceous rocks. Abundant populations of *Mallomonas porifera* and *Synura cronbergiae*, often in the same samples, are found over wide sections of the Giraffe core. Interestingly, both species are also common to abundant in the same rocks from the Wombat locality,



Figs 8–13. SEM images of fossil synurophyte scales from either the early Eocene Giraffe Pipe (13) or the Late Cretaceous Wombat (8–12) locality: (8) scale of a taxon linked to *Mallomonas caudata*; (9) close–up of the distal end of a bristle from a species linked to *M. caudata*; (10) scale of a taxon linked to *Synura petersenii* clade; (11) *Mallomonas* W4, possibly linked to the *M. elephantus* lineage; (12–13) scales of two different species related to the *Mallomonas lychenensis* lineage. Scale bars 1 µm (2, 4, and 6), 3 µm (3 and 5), and 4 µm (7).

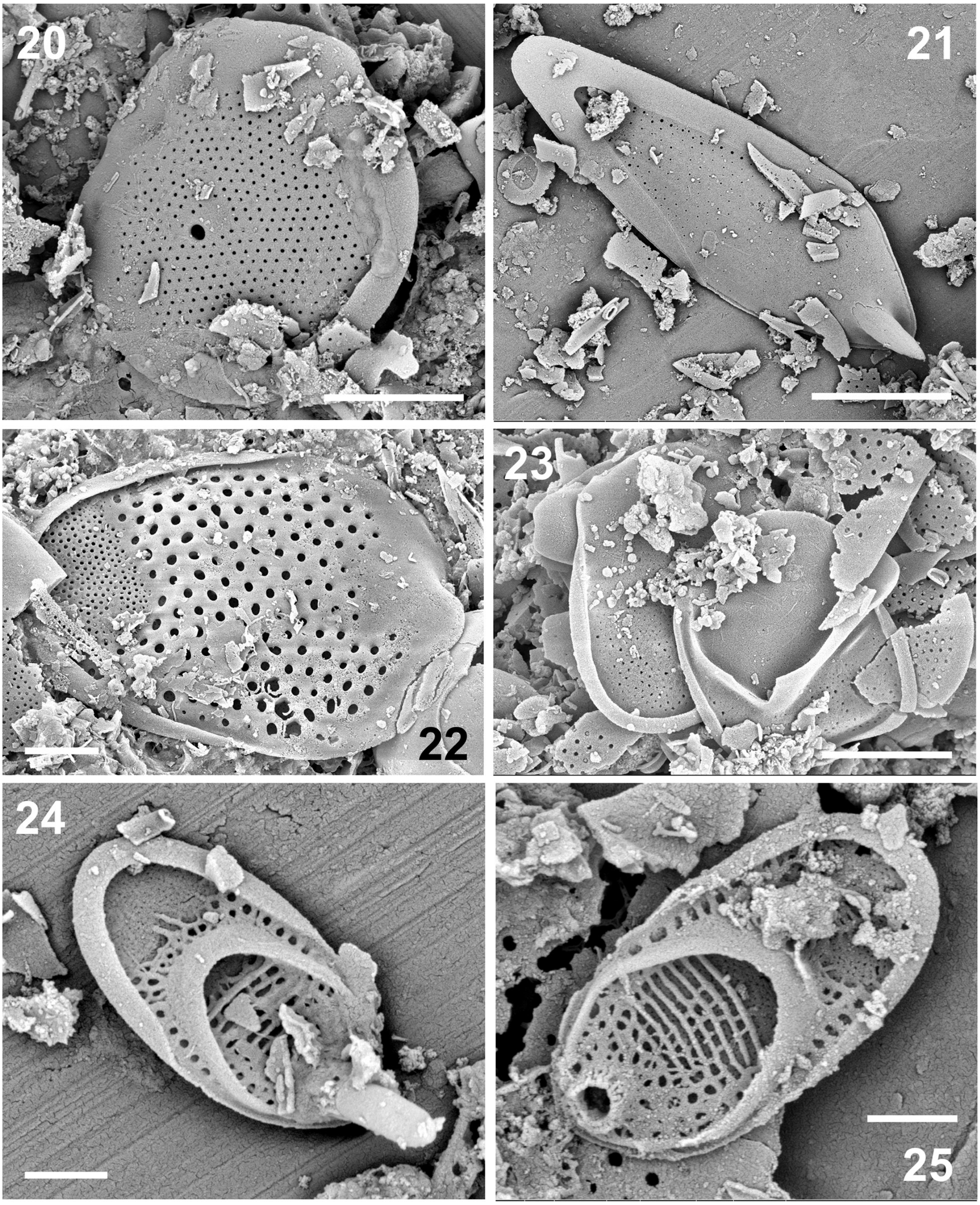
implying that both thrived under similar environmental conditions over an extensive period of time. Details of the *M. porifera* (Fig. 20) and *S. cronbergiae* (Fig. 21) scales from the Wombat core are virtually identical to those in the younger Eocene rocks.

Details of three different scale types and bristles



Figs 14–19. SEM images of fossil synurophyte scales from the early Eocene Giraffe Pipe locality (14, 17, and 19), or the Late Cretaceous Wombat locality (15–16 and 18); (14) *Mallomonas insignis*; (15–16) *Mallomonas* W3, a taxon linked to taxa in the series Mangoferae of the section Torquatae; (17) *Paraphysomonas* sp.; (18) *Lepidochromonas* sp.; (19) *Lepidochromonas* sp. Scale bars 1 µm (15–19) and 2 µm (14).

of *Mallomonas schumachii* were well documented from the Eocene (Siver 2015a), and this species possesses some of the largest scales known for the synurophytes (Siver 2022). The same scale types, especially the large body scales (Fig. 22), are now reported from the Late Cretaceous (Fig. 1). However, this taxon, nor any with remotely similar features, is known in modern waterbodies and the organism is considered to represent a stem lineage of section Planae. *Mallomonas elephantus* is another extinct species originally described from the Eocene (Siver & Wolfe 2016). This organism has distinctly shaped and unique scales that are also among the largest



Figs 20–25. SEM images of fossil synurophyte scales from the Late Cretaceous Wombat locality: (20) *Mallomonas porifera*; (21) *Synura cronbergiae*; (22) *Mallomonas schumachii*; (23) *Mallomonas* W4; (24–25) scales of an organism representing an undescribed genus, possibly a stem taxon to both the *Mallomonas* and *Synura* clades. Scale bars 500 nm (24–25), 2 µm (20, 22–23) and 3 µm (21).

known within the genus. Oddly shaped scales representing an undescribed species of *Mallomonas* (Fig. 23), referred to here as *M*. W4 and with some similarities to *M. elephantus*, have been found in Cretaceous rock samples. Although these two taxa are clearly different, they appear to represent the same stem lineage.

E and C Lineages

Four additional organisms, known only from either the Eocene (n = 2; E group) or Cretaceous (n = 2; C group), represent additional extinct lineages within the synurophyte clade (Fig. 1). *Mallomonas media* Siver et Lott (Siver & Lott 2012) and a second species originally reported as *M.* GP13 (Siver et al. 2015, Fig. 9D) represent stem lineages only known from Eocene rocks. Both of these taxa have uniquely sculptured scales that are among the largest known for the synurophytes. In fact, the mean size of a body scale of *M.* GP13 is 10×8 µm and it has a surface area close to 80 µm, making it the largest known scale type (Siver 2022). Nothing close to or matching these massive and robust scales has been found in any other fossil material to date. The large and uniquely featured scales of *M. media* possess small domes that are significantly recessed from the anterior margin and apparently represent a rudimentary means of attaching the bristles (Siver & Lott 2012). Other than the Eocene rocks in which *M. media* was originally uncovered, this type of scale has not been observed in any other material and represents another ancient lineage within the section Planae.

Remains of two particularly interesting extinct organisms have been uncovered only in the Late Cretaceous material from the Wombat locality. Both species will be officially described fully in a future publication. One of these organisms, referred to as *Mallomonas* W1 in Siver (2022), possesses gigantic and square–shaped scales best described as a stem organism within section Planae. The second taxon (Figs 24–25) represents what will likely be a new genus and initial thinking is that it may represent an organism that is basal to both the *Mallomonas* and *Synura* clades. Scales of this taxon are small and have forward projecting spines associated with a large pore observed on the undersurface of the base plate, a characteristic feature of the section Curtispinae of *Synura*. On the other hand, the prominent U–shaped feature found on the base plate is not found on scales from any known *Synura* and is more aligned with a V–rub structure found on many *Mallomonas* taxa. Given these scale characters, coupled with the fact that it has only been found in the oldest rocks, it likely represents a stem lineage common to both the *Mallomonas* and the *Synura* clades.

In summary, although much remains to be discovered concerning the evolutionary history of the chrysophyte clade through examination of ancient rock deposits, much progress has been made over the last 17 years. Prior to the findings of Siver & Wolfe (2005a), no chrysophyte scales or bristles had been reported older that the Holocene. The discovery of a treasure trove of specimens distributed in over 70 m of rock from the Giraffe Pipe locality, in addition to specimens from the Horsefly fossil locality, has provided a rich amount of evolutionary information for the chrysophyte clade. The many species uncovered and recorded from these Eocene rocks display a flora containing a suite of organisms easily traced to modern lineages and, in fact, display various levels of evolutionary stasis. Another suite of taxa, some massively abundant in the rock remains, have no modern counterparts. Of these more ancient taxa, many have now been recorded in rocks that are ~35 Ma older in the Late Cretaceous, and the oldest records are those from the Wombat locality that are 83 Ma. Several fossil species with unique scale designs are known only from the Cretaceous rocks and some may represent ancient stem lineages that existed prior to the evolution of the separate clades representing *Mallomonas* and *Synura*. The totality of information now available from the fossil record will provide additional age constraints for use in molecular phylogenetic analyses and can be used to trace changes in the siliceous structures produced by these important organisms over geologic time. Future work needs to be directed towards a continued search for additional fossil sites, both younger and older, than the rocks represented in this investigation.

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