



A review of past and recent research on Cretaceous silicoflagellates

KEVIN McCARTNEY¹

¹ Department of Environmental Studies, University of Maine at Presque Isle, Presque Isle, ME 04769, USA
Email: kevin.mccartney@umpi.edu (corresponding author)

Abstract

Previous knowledge of Cretaceous silicoflagellates has come primarily from scattered Maastrichtian or late Campanian localities. Silicoflagellates from the earlier Upper Cretaceous have been observed from the southern shore of the Baltic Sea and eastern slope of the northern Ural Mountains, and Lower Cretaceous from the Weddell Sea near Antarctica are also known. Much of the previous work, including type specimens for genera and species, have been illustrated with few and simple line drawings. Taxonomic distinctions and evolutionary lineages have often been speculative.

Recent studies of Santonian and lower Campanian marine sediments from several sites in the northern Canada Arctic Margin and Archipelago substantially increase our knowledge of Cretaceous silicoflagellate morphology, biostratigraphy, and early evolutionary history. This work, which develops from previous diatom studies, provides new information on the enigmatic genera *Cornua* and *Variramus*, describes new genera and species, and presents new information on the timing of silicoflagellate evolutionary events. Seven new biostratigraphic zones replace the previously applied single biostratigraphic unit for the Cretaceous.

This article reviews recent silicoflagellate discoveries in the context of previous work to provide a current general knowledge of the subject that includes important taxa.

Introduction

Silicoflagellates are single-celled heterokont algae with certain haptophyte affinities (Daugbjerg & Henriksen 2001). They are photosynthetic, exclusively marine, and in life are generally restricted to the euphotic zone. Silicoflagellates are well understood and are used biostratigraphically in the Neogene though general utility is less than that of diatoms or radiolarians due to sparser evolutionary events. Their skeletons are composed of opal-A material that becomes unstable upon deeper burial (Littke *et al.* 1991), which reduces preservation potential in Paleogene and Cretaceous sediments.

Silicoflagellates have an extensive and fairly well studied Cenozoic record with high and low-latitude zonations for most of the era (see Perch-Nielsen 1985). Cenozoic skeletons consistently have a basal ring of generally polygonal shape and constructed of more or less linear sides, that meet to form corners. Most also have an apical structure built upon struts that attach one to each basal side. The apical structure and basal ring give a general hemispherical shape to the skeleton. There are typically spines at the corners of the basal ring and each side has a pike that points away from the apical structure (abapically).

The known silicoflagellate record begins in the Cretaceous, but the early history has not been well understood. Until recently, this record consisted of six genera, one of which was problematic, and a single formally described biostratigraphic zone. That zone and most known Cretaceous silicoflagellate taxa are from the latest Campanian to Maastrichtian. Rare and isolated occurrences of older silicoflagellates were separated by extensive time intervals where silicoflagellates had not been observed or studied.

Recently studied sediments have provided silicoflagellates within these previous gaps and new interpretations of Cretaceous evolutionary history. These discoveries include new taxa and an improved understanding of the history and diversity for all six previously known and two new genera. The number of

biostratigraphic zones has increased to seven. These provide an opportunity to reexamine the known Cretaceous record in light of the new observations.

Initial studies of Cretaceous silicoflagellates

Silicoflagellates were first described by C. G. Ehrenberg in the late 1830s. Ehrenberg wrote some 20 papers on them, for which he erected the genus *Dictyocha* Ehrenberg (1837: 61). Among the various species was *Dictyocha triacantha* (Ehrenberg 1844: 80), which had three basal sides. The first to recognize the silicoflagellates as a separate group was Lemmermann (1901), who described many new varieties of *D. triacantha* that are now recognized as separate species. Lemmerman's two pages of figures consisted of simple line drawings with usually one illustration per new variety.

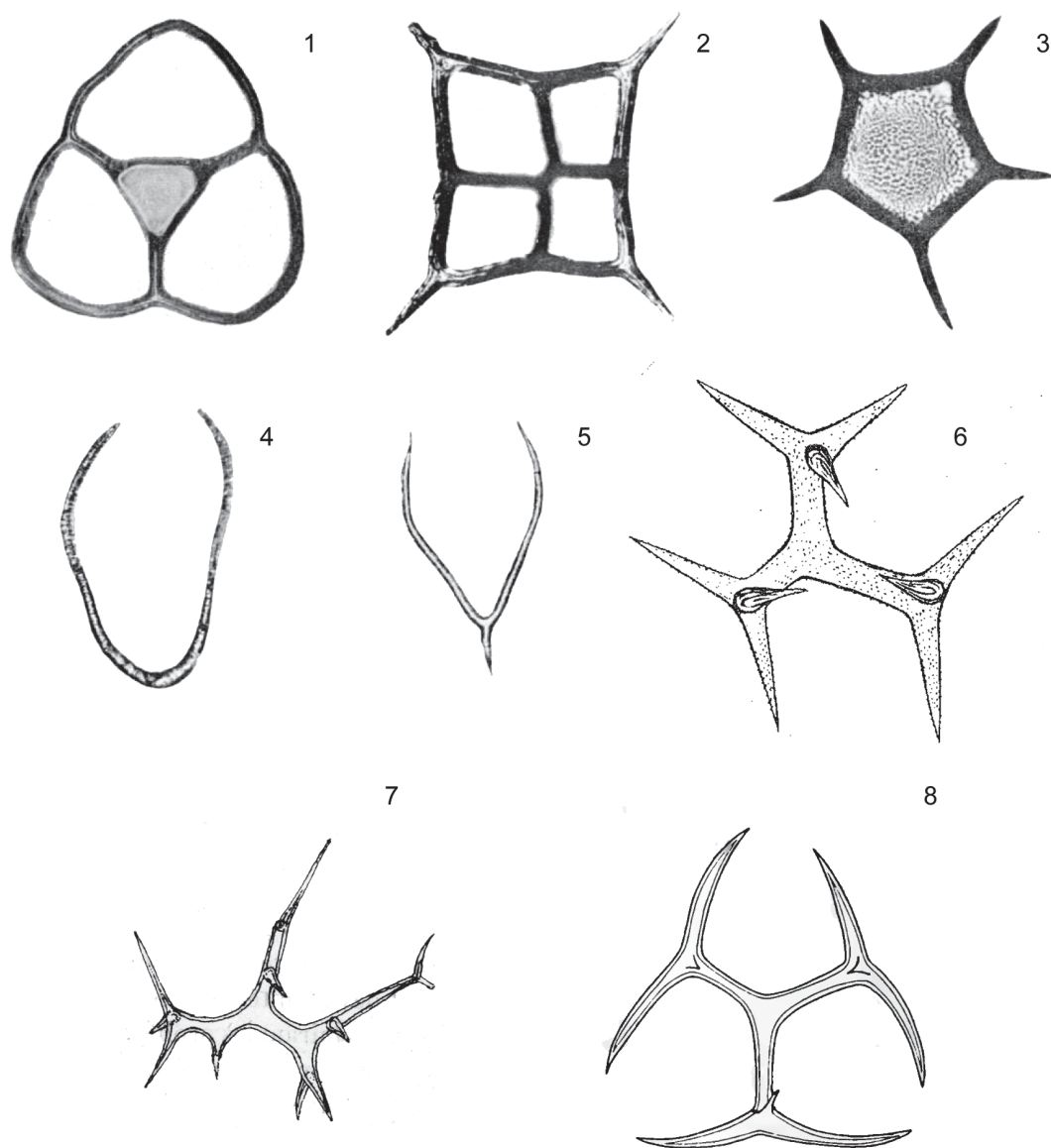
Cretaceous silicoflagellates were not discovered until 1928, when both Hanna and Schulz published landmark papers. Hanna (1928) observed diverse silicoflagellates from the Moreno Shale of southern California. He placed the three-sided skeletons into the new genus *Corbisema* Hanna (1928: 261), and described the new species *C. geometrica* Hanna (1928: 261)(Fig. 1), which usually had an apical plate. This genus, including *C. geometrica*, is also important in the Paleogene, which accounts for their previous illustration by Ehrenberg and Lemmermann from Cenozoic sediments.

In addition to *Corbisema*, Hanna (1928) described a four-sided silicoflagellate skeleton as *Dictyocha quadrata* Hanna (1928: 261)(Fig. 2), and the genera *Vallacerta* Hanna (1928: 262)(Fig. 3) and *Lynamula* Hanna (1928: 262)(Figs. 4-5), neither of which had been previously illustrated. The genus *Vallacerta* has an apical dome that is connected directly to the basal ring without the occurrence of struts. Illustrated specimens of *V. hortonii* Hanna (1928: 262) had five basal sides. *Lynamula* has a simple 'Y,' 'V,' or 'U'-shaped skeleton made of two curved limbs that meet at an angle, perhaps with a spine.

Schulz (1928) was published a few months after Hanna's paper and without prior knowledge of this work. Schulz examined sponge "mummies" that wash out of a cliff on the then-German coast near what is now Gdynia in Poland, and observed well-preserved silicoflagellates. The mummies were deposited as glacial outwash and their geographic origin is unknown. Schulz observed both *Corbisema* and *Vallacerta*, which he retained in the genus *Dictyocha*, but described the new genus and species *Cornua trifurcata* Schulz (1928: 285), which has three struts whose terminations bifurcate into basal elements that do not connect to form a basal ring (Fig. 6). Schulz illustrated three skeletons of *Cornua* from abapical and oblique view that show linear basal elements and prominent pikes.

Deflandre (1940, 1944, 1950) obtained a sample from Hanna labeled as "Diatomite de Panoche Hills, Fresno County, Cal. (Etage de Moreno)," that included a variable group of silicoflagellate skeletons that lacked basal rings, which he described as *Cornua aculeifera* Deflandre (1944: 464)(Fig. 7) and illustrated with three line drawings. Deflandre emphasized that the skeletons were remarkably plastic, and that it was difficult to find two specimens that were alike. Also described was *Vallacerta hannai* Deflandre (1944: 463), which had small skeletons with seven basal sides and pikes that occurred on struts at some distance from the base of an apical plate.

José (1949, 1951) and Gleser (1959) observed Cretaceous silicoflagellates at various localities on the eastern slope of the northern Ural Mountains. The silicoflagellates observed by José are probably from the early Campanian; those of Gleser are probably older and may age into the Santonian. Gleser (1959) identified *Cornua aculeifera*, *C. trifurcata* and described the new species *C. poretzkajae* Gleser (1959: 110)(Fig. 8), illustrating each with a single line drawing, though a few more illustrations were provided in Gleser (1966), translated into English in 1970. *C. poretzkajae* has basal elements that bend towards the basal element of the next adjacent strut and takes the general appearance of a *Corbisema* that is missing the corners. Gleser (1959) also described *Vallacerta tumidula* Gleser (1959: 107), whose apical dome has a central area separated from the rest of the dome by an incised trench.



FIGURES 1–8: Original illustrations for important silicoflagellate taxa to 1959. Fig. 1. *Corbisema geometrica*, Hanna (1928). Fig. 2. *Dictyocha quadralta* Hanna (1928); placed in *Arctyocha* by Bukry (1985). Fig. 3. *Vallacerta hortonii* Hanna (1928); now usually called *V. hortonii*. Fig. 4. *Lyramula simplex* Hanna (1928). Fig. 5. *Lyramula furcula* Hanna (1928). Fig. 6. *Cornua trifurcata* Schulz (1928). Fig. 7. *Cornua aculeifera* Deflandre (1944); placed in *Variramus* by McCartney et al. (1990). Fig. 8. *Cornua poretzkajae* Glezer (1959).

The Cretaceous silicoflagellate literature summarized to this point represents the initial articles on the subject, which describe four genera – *Corbisema*, *Lyramula*, *Vallacerta* and *Cornua*. Except for Hanna (1928), all the silicoflagellates presented to here were illustrated with simple line drawings. Mandra (1960, 1968), Tsumura (1962), Ling (1972) and Cornell (1974) further examined silicoflagellates from the Moreno formation of California and have separated *Corbisema* into various species, often elevating to species level the varieties originally described by Lemmermann (1901).

More recent silicoflagellate study during the remainder of the 20th century can be quickly presented, as there are few significant papers that introduce important new taxa. Bukry (1985) noted that skeletons of *Dictyocha quadralta* Hanna (1928: 261) lack basal pikes and are not evolutionarily related to Cenozoic *Dictyocha* and placed this taxon in the new genus *Arctyocha* Bukry (1985: 130). This skeletal morphology had also been observed in the Moreno Shale (Mandra 1960, 1968), Deep Sea Drilling Project (DSDP) Leg 29 Site 275 of the Southwest Pacific (Perch-Nielsen, 1975) and the CESAR-6 core from the Arctic Ocean (Ling et al. 1973, Bukry 1981, Dell’Agnese & Clark 1994).

Silicoflagellates from the Lower Cretaceous were observed by McCartney et al. (1990), who describe a Lower Cretaceous, Albian age, flora that occur in a short interval of Ocean Drilling Program (ODP) Leg 113 Site 693 of the Weddell Sea near Antarctica. The silicoflagellate flora consisted of small seven-sided *Vallacerta hannai* very similar to those of Deflandre (1944) and an extremely variable group similar to *Cornua aculeifera* illustrated in the same paper. The new genus *Variramus* McCartney, Wise, Harwood & Gersonde (1990: 432) included most of the morphological variation into *V. aculeifera* (Deflandre) McCartney, Wise, Harwood & Gersonde (1990: 432), with quadrate skeletons placed in the new species *V. loperi* McCartney, Wise, Harwood & Gersonde (1990: 432).

Of the six Cretaceous genera presented thus far, *Cornua* was particularly enigmatic as the few illustrations provided little detail and information was scanty. While *Cornua* had been reported in a few studies (Bukry 1974, Quinterno et al. 1994, Desikachary & Prema 1996) since the work of Gleser, these were present in very low numbers and not accompanied by good photographs; it is uncertain that any of these later occurrences are actually *Cornua*. Lipps (1970), in a review article, believed that the illustrated *Cornua* might be sponge spicules while McCartney (1987) thought that they could be teratoid *Corbisema*.

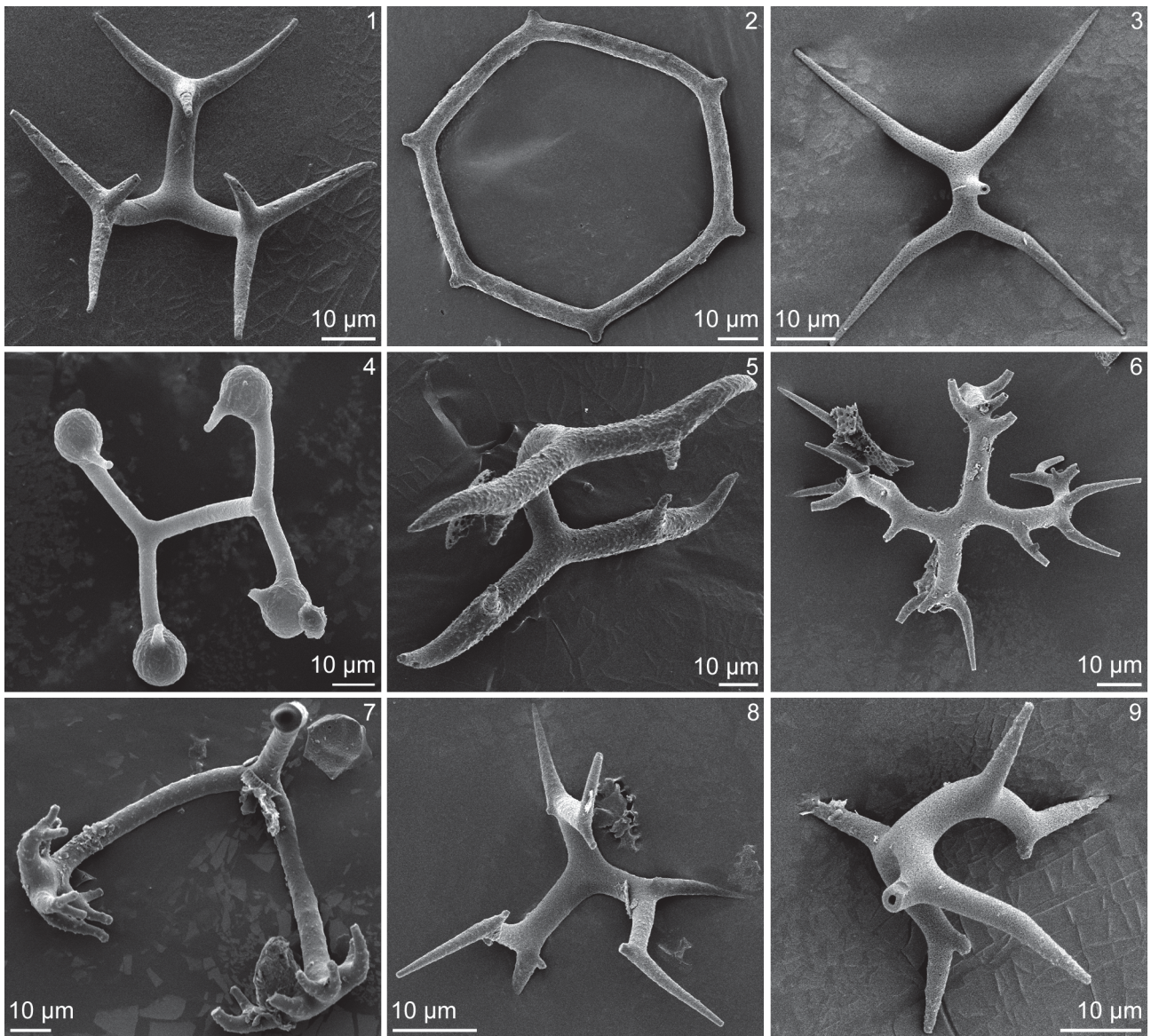
The three periods of time where silicoflagellates had been observed and studied – the Maastrichtian, Santonian/early Campanian and Aptian – are separated by two lengthy time intervals. The youngest of these intervals includes most of the Campanian. While the precise stratigraphic position of the Schulz (1928) and Gleser (1959) studies are unknown, these probably straddle the Santonian and earliest Campanian. Some of the later Cretaceous studies, especially those where *Arctyochoa* are present, include the latest Campanian. Most of the Campanian, which spanned about 13 myr, had not been examined for silicoflagellates. The second and more lengthy gap in the known silicoflagellate record extends from the Albian to Santonian, or about 25 myr.

Recent discoveries

Recent work on sediments from northern Canada provides information from these previously unstudied intervals. These discoveries develop from two Masters theses that investigated diatom history during the Santonian and Campanian. Tapia (1996) and Tapia & Harwood (2002) examined sediments from the Horton River near the northern coast of Canada and several islands of the Canadian Archipelago, while Witkowski (2008), Chin et al. (2008) and Witkowski et al. (2011) studied sediments from Devon Island in the Canadian High Arctic. These sediments have extraordinarily well preserved silicoflagellates of unusual skeletal morphologies, and include the first *Cornua trifurcata* to be photographed (Fig. 9).

The Horton River site spans nearly the entire Campanian. The highest portion of this sequence contains a flora consistent with the *Lynamula furcula* Zone described by Bukry & Foster (1974), which was previously the only silicoflagellate zone of the Cretaceous. Near the bottom of this sequence are sediments that contain abundant *Cornua trifurcata*, which are used to define the *C. trifurcata* Partial Range Zone (McCartney et al. 2011a). The top of this zone is defined as the last abundant—and probable extinction—of the nominative taxon. Immediately above the *C. trifurcata* Zone is a depauperate interval that lacks *Cornua*, described as the *Lynamula minor* Interval Zone, characterized by a predominance of *Lynamula minor* (Deflandre) Deflandre (1950: 62). The general small size of the silicoflagellates and unusual morphologies of both *Lynamula* and *Corbisema* suggest that this zone may represent an environmentally stressed interval of time that followed the extinction of much of the previous silicoflagellate flora (McCartney et al. 2011a).

Above the *Lynamula minor* Interval Zone are two zones named after species of *Arctyochoa*. The oldest of these is the *Arctyochoa mesocena* Range Zone, which has abundant specimens of two new *Arctyochoa* species: *A. balkwillii* McCartney, Witkowski & Harwood (2011a: 68) has basal rings with six to twelve or more sides and a wide range of apical designs while *A. mesocena* McCartney, Witkowski & Harwood (2011a: 69) lacks an apical structure (Fig. 10). Above this zone is the *A. quadralta* Range Zone; the other Late Cretaceous occurrences that have common *A. quadralta*, in California, the CESAR-6 core and DSDP Site 275, may correlate with this interval.



FIGURES 9–16: Recently discovered or photographed Cretaceous silicoflagellates. Fig. 9. Modern photograph of *Cornua trifurcata*, Til'tim XI locality (see Witkowski *et al.*, 2012). Fig. 10. *Arctyochoa mesocena*, sample C-8606, Horton River, Canada. Fig. 11. *Schulzyocha loperi*, ODP 113-693B-19X-4, 77–78 cm. Fig. 12. *Schulzyocha ruppelii*, EF0103, Devon Island, Canada. Fig. 13. *Schulzyocha lurveyi*, EF0102, Devon Island, Canada. Fig. 14. *Umpiocha umpiana*, EF0401, Devon Island, Canada. Fig. 15. *Umpiocha jeletzkyi* EF0401, Devon Island, Canada. Fig. 16. *Umpiocha jeletzkyi*, EF0401, Devon Island, Canada. Fig. 17. *Cornua tapiae*, EF0401, Devon Island, Canada. *Variramus wisei*, ODP 113-693B-19X-4, 77–78 cm.

The *Arctyochoa mesocena* Zone also shows an evolutionary transition for *Corbisema lateradiata* (Schulz) Perch-Nielsen (1975: 686) through *C. geometrica* Hanna (1928: 261) to *C. parallela* Hajós & Stradner (1975: 938), which is a trend to larger and rounder basal rings and apical plates. These skeletal morphologies were previously known in the Maastrichtian, without knowledge as to which was the more primitive. Deflandre (1940) thought that *C. geometrica* was as long-lived species that through expansion of the apical plates had given rise to *Vallacerta*. The Horton interval showed that *C. geometrica* was a later development from a more trigonal basal ring with pointed corners. All three corbisemid morphologies continue into the Paleogene.

The Devon Island interval is interpreted as Santonian to early Campanian in age and contains well preserved silicoflagellates of three assemblages, each described as a zone (McCartney *et al.* 2011b). The youngest of these is the *Cornua trifurcata* Zone described in McCartney *et al.* (2011a). Below this zone are two assemblages of very unusual and previously undescribed silicoflagellates. These are the *Schulzyocha ruppelii* Range Zone and below that the *Vallacerta tumidula* Partial Range Zone.

The *Schulzyocha ruppelii* Range Zone is characterized by the occurrence of several species of the new genus *Schulzyocha* (McCartney *et al.* 2011b: 50). The type species of this genus is *S. loperi* (McCartney, Wise, Harwood & Gersonde) McCartney, Witkowski & Harwood (2011b: 51)(Fig. 11), described by McCartney *et al.* (1990) as a species of *Variramus*. The nominative species of the zone is *Schulzyocha ruppelii* McCartney, Witkowski & Harwood (2011b: 52), an extremely unusual silicoflagellate with bulbs (Fig. 12) at the ends of the struts. The zone includes five new species of this genus, including *S. lurveyi* McCartney, Witkowski & Harwood (2011b: 51)(Fig. 13), which has very unusual basal elements. All of the new *Schulzyocha* species are restricted to the *Schulzyocha ruppelii* Zone. The *Schulzyocha ruppelii* Zone also has in its bottommost sample the oldest known occurrence of *Lyrāmula*, which does not occur in the underlying zone.

The *Vallacerta tumidula* Partial Range Zone includes a variety of especially unusual taxa, even by the standards established by the *Schulzyocha ruppelii* Zone. The most unusual of these is the new genus *Umpiocha* McCartney, Witkowski & Harwood (2011b: 52), which is characterized by long limbs that curve beneath the apical structure, with terminations that come near to touching. The four curved limbs are not connected to an obvious basal plane, with a general shape that is more spherical than all known silicoflagellates except the Neogene *Cannopilus* Haeckel (1887: 1567). Two species have been placed in *Umpiocha*; *U. umpiana* McCartney, Witkowski & Harwood (2011b: 53)(Fig. 14) has two rows of spines on the limbs while *U. jeletskyi* McCartney, Witkowski & Harwood (2011b: 53)(Fig. 15) lacks spines but has digitated terminations to the limbs.

The *Vallacerta tumidula* Partial Range Zone also includes an unusual new species of *Cornua*. The struts of *C. tapiae* McCartney, Witkowski & Harwood (2011b: 49)(Fig. 16) terminate in basal elements that are twisted and do not occur in a planar surface as do the basal elements of previously described *Cornua*. A similar twist is repeated at the end of each strut, producing a “pinwheel” effect. The *Cornua* have considerable variability and has been observed during recent reexamination of the ODP Site 693 material (McCartney *et al.* 2011a), making this and *Variramus wisei* McCartney, Witkowski & Harwood (2011b: 55)(Fig. 17) especially long-lived Cretaceous silicoflagellate species.

Discussion

The silicoflagellate literature is briefly summarized in Table 1. Both the Horton River and Devon Island floras provide a broader context for interpreting silicoflagellates of the Cretaceous. The base of the Horton River section provides the first *Cornua trifurcata* assemblage observed in half a century, and the first ever to be extensively documented photographically. This, combined with the older flora of Devon Island and ODP Site 693, represents an archaic group of silicoflagellates of which only *Vallacerta* has a basal ring. The other archaic genera are *Variramus*, *Cornua*, *Schulzyocha* and *Umpiocha*, all of which lack a basal ring.

With the exception of *Vallacerta*, this archaic silicoflagellate flora either becomes extinct or very much less abundant at the top of the *C. trifurcata* Zone, in the early Campanian. The overlying *Lyrāmula minor* Zone has a depauperate flora dominated by small and unusual *Lyrāmula*. If this zone does represent recovery following a silicoflagellate mass extinction, the recovery was rapid as the zone occurs in only a single sample in the Horton River section. Rapid diversification followed with the evolution of *Arctyochoa* and appearance of plated *Corbisema* in the next higher zone.

Arctyochoa and *Corbisema*, combined with *Lyrāmula* and *Vallacerta*, form the late Campanian/Maastrichtian flora that has been the subject of most of Cretaceous silicoflagellate literature. The previous literature, however, does not discuss the many-sided *Arctyochoa* and the diverse morphologies that lack an apical structure observed in the Horton River section. This record shows a trend for *Arctyochoa* towards fewer basal sides and less complex apical structures as the Campanian proceeds. Four-sided *Arctyochoa* morphologies are most typical near the Campanian/Maastrichtian boundary. It is uncertain if and for how long the genus persists into the Maastrichtian, but it is generally not present in exclusively Maastrichtian sections.

At about the time that *Arctyochoa* diminishes in abundance, more complex *Lyrāmula* morphologies with three to many limbs and less symmetrical skeletons occur. Complex *Lyrāmula* skeletons were illustrated by Deflandre (1940, 1950) and also observed in section 2–5 of DSDP Site 275 (Bukry 1975) and the CESAR-6 core (Bukry 1981). Unusual *Arctyochoa* morphologies that have struts that support an apical window have also been observed in the late Campanian (Harwood 1988, McCartney *et al.* 2010b). A detailed examination of the California and Site 275 sections is needed to determine if these transitions are correlated with other evidence of environmental stress.

Despite the many papers that include observations of silicoflagellates in the Maastrichtian, few generalizations can be made about the nature of that record. No near complete record of Maastrichtian silicoflagellate history is available, as can be observed at Horton River for the Campanian. Except for the section at Seymour Island (Harwood 1988), little information is available about the impact of the terminal Cretaceous extinction event on the silicoflagellates. If any of the Cretaceous silicoflagellate genera except *Corbisema* survived the K/Pg boundary, they did not persist for long. All Cenozoic silicoflagellates evolved from *Corbisema*.

TABLE 1: List of all Cretaceous silicoflagellate literature, with age and geographic region. "X?" indicates where the taxon was identified but the authors of the reference maintain some level of uncertainty as to its identification, "?" indicates where the authors think this taxon may occur.

Reference	Age	Geographic Region	<i>Arctyochoa</i>	<i>Corbisema</i>	<i>Cornua</i>	<i>Lyrāmula</i>	<i>Vallacerta</i>	<i>Variramus</i>	<i>Schulzychoa</i>	<i>Umpiocha</i>
Bukry, 1974	Maastrichtian	DSDP Site 216, E Indian Ocean		X	X?	X	X			
Bukry, 1975	late Campanian—Maas.	DSDP Site 275, SW Pacific Ocean	X	X	X?	X	X	?		
Bukry, 1981, 1985	late Campanian—Maas.	Alpha Ridge, Arctic Ocean	X	X	?	X	X	?	?	
Cornell, 1974	Maastrichtian	California, USA		X						
Dell'Agnesse and Clark, 1994	late Campanian—Maas.	Alpha Ridge, Arctic Ocean	X	X		X	X			
Gresham, 1985	Maastrichtian	DSDP Site 216, E Indian Ocean	X?	X		X				
Gleser, 1959, 1966	Santonian to early Camp.	Ural Mountains, Russia		X	X	X	X			
Jouse, 1949, 1951		Ural Mountains, Russia		X		X	X			
Hajos and Stradner, 1975	late Campanian—Maas.	DSDP Site 275, SW Pacific Ocean	X	X		X	X			
Hanna, 1928	Maastrichtian	California, USA	X	X		X	X			
Harwood, 1988	Maastrichtian	Seymour Is., Antarctica	X	X		X	X			
Ling, 1972	Maastrichtian	California, USA		X		X	X			
Ling <i>et al.</i> , 1973	late Campanian—Maas.	Canadian Arctic	X			X	X			
Mandra, 1960, 1968	Maastrichtian	California, USA		X		X	X			
Martinez Macciavello, 1987	late Campanian—Maas.	Seymour Is., Antarctica		X		X				
McCartney <i>et al.</i> , 1990	Albian	ODP Site 693, Weddell Sea					X	X	X	
McCartney <i>et al.</i> 2011a	Campanian	Canadian Arctic	X	X	X	X	X	X		
McCartney <i>et al.</i> 2011b	Santonian to early Camp.	Canadian Arctic		X	X	X	X	X	X	X
Moshkovitz <i>et al.</i> , 1983	Maastrichtian	Israel				X				
Quinterno <i>et al.</i> , 1994	late Campanian—Maas.?	Tonga Trench, Pacific		X	X	X	X	X?		
Perch-Nielsen, 1975	late Campanian—Maas.	DSDP Site 275, SW Pacific Ocean	X	X		X	X			
Sawamua and Otowa, 1979	uncertain	Japan			X	X				
Schulz, 1928	early Campanian	Baltic Sea, Poland		X	X					
Tsumura, 1963	Maastrichtian	California, USA	X?				X	X?		

Priorities for future study

The recent discoveries provide a new context for the interpretation of Cretaceous silicoflagellate history. Many of the localities studied in past decades now require new and more detailed examination. Among these is the Moreno formation of California, which has seen little study since Cornell (1974). None of the previous studies were systematic examinations of stratigraphic sections with a high resolution sample interval. The Horton River zonation suggests that the *Arctyochoa* of California may be of latest Campanian age, and not Maastrichtian as generally stated in the Californian silicoflagellate studies.

The presence of unusual *Arctyochoa* and *Lyracula* near the bottom of core 2 at DSDP Site 275 also needs further study. The Initial Scientific Results for that leg include three silicoflagellates studies (Bukry 1975, Hajós & Stradner 1975, Perch-Nielsen 1975) which have different species interpretations. *Corbisema geometrica* v. *apiculata* Jousé (1951: 78) of Hajós & Stradner (1975) is equivalent to *C. lateradiata* (Perch-Nielsen 1975) and *C. geometrica lateradiata* (Schulz) Bukry (1975: 853). Such disparities of *Corbisema* interpretation occur throughout the Maastrichtian literature. There are also differences in the interpretation of *Corbisema* taxa (*C. apiculata* Frenguelli (1940: 62), *C. inermis* (Lemmermann) Bukry (1975: 854), *C. archangelskiana* (Schulz) Frenguelli (1940: 62)) between the Maastrichtian and Paleogene literature (e.g., McCartney *et al.* 2011b, for a discussion of *C. inermis*). *Corbisema* requires a thorough study to develop a more consistent species interpretation.

The Devon Island section also deserves much more detailed analysis. The original samples were collected during an exploratory search for fossil vertebrates, so a systematic sampling for microfossil study was not made. The three zones interpreted by McCartney *et al.* (2011b) were made on the basis of eight samples (three samples for each of the higher two zones, two samples in the lowest zone). Another expedition to this island to obtain more samples would provide a better understanding of the early evolution of *Corbisema*, as well as the diversification and variability of *Cornua* and *Schulzyocha*.

The Devon Island section also provides a better knowledge of *Variramus*, with three new species which considerably narrow the interpretation of *V. aculeifera* as presented by McCartney *et al.* (1990). The Albian section of ODP Site 693 needs to be restudied. A reexamination of Site 693 materials has observed *Cornua tapiae* in the Albian. With the reclassification of *V. loperi* to *Schulzyocha*, the known Albian diversity has increased from two *Variramus* and one *Vallacerta* species to four genera – *Variramus*, *Vallacerta*, *Schulzyocha* and *Cornua* – the first of these now having several species.

Work is also needed to determine the provenance of the original sample studied by Deflandre (1940, 1944) from which *Vallacerta hannai* and what was then called *Cornua aculeifera* were described. Deflandre obtained this sample from Hanna, who labeled it as Maastrichtian in age, and from a Panoche Hills section of the Moreno formation. Deflandre however described a flora that is very similar to the Albian ODP Site 693 occurrence. If, as appears likely, the locality information was either mislabeled by Hanna or Deflandre, then *Where did it come from?* Could an unknown Lower Cretaceous silicoflagellate-bearing unit of strata be present in California or elsewhere?

Finally, more work needs to be done on any basic differences between the Cretaceous and Cenozoic silicoflagellate flora. A rare double skeleton of *Corbisema* was found in the Horton River section and illustrated by McCartney *et al.* (2010a). This specimen shows each skeleton of the pair rotated with respect to the other, in a “star-of-David” configuration. Double skeleton specimens of *Vallacerta* and *Schulzyocha* also show this rotated pattern (McCartney *et al.* 2010b, 2011b). Thus far, all observed double skeletons from the Cretaceous show rotated double skeletons while Cenozoic double skeletons have the basal corners and spines aligned with each other. Why would Cretaceous and Cenozoic double skeletons be so different? There is still a great deal to learn about the Cretaceous and early Cenozoic silicoflagellate record.

Conclusions

During the past century, a variety of workers have observed and illustrated silicoflagellate skeletal morphologies from the Cretaceous. This body of work started with Lemmermann, who in 1901 described Paleogene taxa that are now commonly used for Cretaceous species of *Corbisema*. Hanna and Schulz in 1928 formally described three additional Cretaceous genera, and illustrated the Cretaceous morphology now known as *Arctyochoa*. Subsequent work through the 1980s have added to the knowledge of these genera through the description of new species and extending their known geographic distributions.

The geologic record of Cretaceous silicoflagellates, however, was not appreciably extended by the subsequent work, as the geologic age of known silicoflagellates continued to be latest Campanian through Maastrichtian, and a relatively brief interval in the Santonian to earliest Campanian. In 1990, the discovery of an assemblage of early and variable silicoflagellates from the Albian extended the known silicoflagellate record considerably, but did not clarify the evolutionary relationships among the previously known genera.

More recent research in the Canadian Arctic provides a better understanding of early silicoflagellates. *Cornua* is now known to be an important and long-lived genus. The transition from *Cornua* to *Corbisema* can now be better placed temporally, and may involve two lineages. An evolutionary lineage is now available for the *Corbisema* with apical plates. Dates of first appearance are now known for *Lyrarmula* and *Arctyochoa*, and unusual new silicoflagellates have been described in the Santonian. This information provides a larger context and new perspective for interpretation of the previously known taxa.

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