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New insights into skeletal morphology of the oldest known silicoflagellates : *Variramus*, *Cornua* and *Gleserocha* gen. nov.

Nouvelles connaissances sur la morphologie du squelette des plus anciennes silicoflagellés connus : *Variramus*, cornes et *Gleserocha* gen. nov.

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Mots clés: Silicoflagellé fossile, Crétacé, Antarctique, Site 693 ODP, Arctique, Îles Devon

Abstract

Two of the oldest known silicoflagellate-bearing sediments, lower Albian at Ocean Drilling Program Site 693 in the Weddell Sea of Antarctica and Santonian in the Devon Island sequence of the Canadian Archipelago, are re-examined with a focus on silicoflagellate genera *Variramus*, *Cornua*, and *Gleserocha* that lack basal rings, a feature appearing during late Santonian/early Campanian time within the genus *Corbisema*. The extraordinary variability of *Variramus aculeifera* is studied, and a new genus *Gleserocha* is proposed for taxa with apical structures made of three struts, but without pikes. This new genus includes previously described *Variramus wisei* and *Cornua tapiae* and new species *G. harrisonii*, and is here proposed as a genus transitional between *Variramus* and *Cornua*. Two unusual new species of *Cornua*, *C. deflandrei* and *C. witkowskiana*, are also described and a revised terminology is proposed for the skeletal components of *Cornua* and closely related genera.

Résumé

Les plus anciens silicoflagellés provenant des sédiments de l'Albien inférieur du Site 693 de l'Ocean Drilling Program (ODP) dans la mer de Weddell en Antarctique et des sédiments du Santonien des îles Devon de l'archipel arctique canadien sont revus, afin de mieux comprendre les genres *Variramus*, *Cornua* et *Gleserocha* qui ne possèdent pas d'anneau basal. Cette caractéristique est apparue au Santonien supérieur/Campanien inférieur en même temps que le genre *Corbisema*. Les variations étonnantes de *Variramus aculeifera* sont analysées et un nouveau genre, *Gleserocha*, est décrit, qui regroupe les espèces ayant une structure apicale sans épine et composée de trois entretoises. Ce nouveau genre incluant deux espèces déjà décrites comme étant *Variramus wisei* et *Cornua tapiae* et de la nouvelle espèce *G. harrisonnii*, est proposé pour constituer la forme de transition qui relie *Variramus* et *Cornua*. Deux nouvelles espèces inédites de *Cornua*, soient *C. deflandrei* et *C. witkowskiana*, sont aussi décrites et nous proposons une nouvelle terminologie pour décrire l'endosquelette de *Cornua* et des genres similaires.

1. Introduction

Silicoflagellates are unicellular, marine planktonic algae that produce siliceous skeletons composed of hollow rods that connect to form skeletal latticeworks. Although their fossil record extends back to early Albian time (Early Cretaceous, ~115 million years ago), they are best known from the Eocene to Recent. Data on Late Cretaceous and Paleocene silicoflagellate evolution are relatively sparse. Recent descriptions of diverse, previously unknown silicoflagellate skeletal morphologies from Cretaceous sediments (McCartney

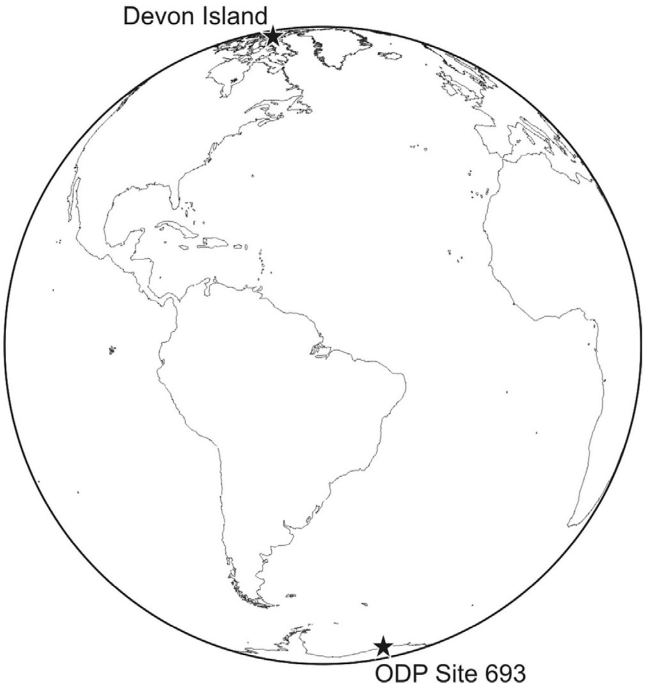

Figure 1. Locations of study sites. Base map generated using Ocean Drilling Statigraphic Network application (www.odsn.de).

et al., 2010, McCartney et al., 2011a and McCartney et al., 2011b) highlight the need to fill the ~35 m.y. gap that separates the two oldest known silicoflagellate occurrences at Ocean Drilling Program (ODP) Site 693, Weddell Sea, Antarctica (early Albian), and at Devon Island, Canadian High Arctic (Santonian) (Fig. 1 and Fig. 2).

McCartney et al. (1990) described silicoflagellate assemblages from ODP Site 693 (Fig. 2), and rediscovered a highly variable group of morphologies that lack a closed basal ring (*Variramus*), previously known only from few line drawings (Deflandre, 1940, Deflandre, 1944, Deflandre, 1950, Gleser, 1959 and Gleser, 1966). McCartney et al. (2011b) documented silicoflagellates in Santonian sediments from Devon Island (Fig. 2), describing new morphological structures in other genera that also lack basal rings. All silicoflagellate skeletal morphologies that lack basal rings (e.g., *Variramus*, *Schulzyocha*, *Umpiocha*, *Cornua*, *Lyramula*) became extinct at or before the K-Pg boundary (Harwood, 1988 and McCartney et al., 2010) (Fig. 2). However, taxa that possess basal rings and apical structures resembling Cenozoic skeletal morphologies (*Corbisema* and *Arctyocha*) appear by Campanian-Maastrichtian time in successions around the world, with only *Corbisema* continuing across the K-Pg boundary as the progenitor of all Cenozoic silicoflagellates.

Snapshots of early silicoflagellate history reviewed herein will illustrate: (1) low diversity of non-basal ring forms in the Albian (*Variramus*, *Schulzyocha*); (2) high diversity of basal ring lacking forms in the Santonian (*Variramus*, *Schulzyocha*, *Umpiocha*, *Cornua*); and (3) divergence of basal ring bearing lineage from the non-basal ring group (i.e., the evolution of *Corbisema* from *Cornua*) near the Santonian-Campanian boundary (Gleser, 1962 and McCartney et al., 2011b). In order to provide a better understanding of silicoflagellate evolution prior to the rise of the basal ring, we explore the possible evolutionary links between *Variramus* and *Cornua*, and propose the new genus *Gleserocha* for a group of transitional morphologies. In addition, a revised terminology is presented for the skeletal components of early silicoflagellates that were the likely progenitors of extant silicoflagellates, all of which bear a basal ring.

2. Materials and methods

ODP Site 693 samples re-examined here (113-693B-19X-4, 77–78 cm and 113-693B-19X-4, 103–104 cm) are from original samples used by Gersonde and Harwood (1990), Harwood and Gersonde (1990) and McCartney et al. (1990); these papers should be consulted for details about sample preparation.

Early Cretaceous siliceous microfossils from ODP Site 693 (Hole 693A, Core 44R-1; and Hole 693B, Core 19X-4) were originally assigned a broad Aptian/Albian age. However, siliceous microfossil-bearing sediments from Unit VI (radiolarian diatomite) of ODP Holes 693A and 693B are actually early to mid-Albian in age based on biostratigraphic ranges of associated calcareous nannofossils, foraminifera, dinoflagellates, radiolarians, and diatoms. This interval is bracketed below by well-dated uppermost Aptian microfossils and sediment. Mutterlose and Wise (1990) assigned the ~70 m-thick Cretaceous section (including Unit VI and the underlying claystone of Unit VII) to the calcareous nannofossil *Rhagodiscus angustus* Zone (late Aptian-early Albian in age). This zone is also represented at Deep Sea Drilling Project (DSDP) Site 511 on the Falkland Plateau, and serves as the basis for correlating many sections across the Aptian/Albian boundary interval, which Mutterlose et al. (2008) imply occurs at ~453 mbsf in Hole 693A (~45 m below the silicoflagellate-bearing interval). An important occurrence in support of this age assignment is the calcareous nannofossil *Eprolithus apertior* in the base of Core-section 693A-49R-1, which first occurs in the upper Aptian where it marks the base of the *Rhagodiscus angustus* Zone.

Similarly, Leckie (1990) reported the presence of late Aptian planktonic foraminifera in underlying Cores 693A-47R and -48R that are known from the *Hedbergella trocoidea* Zone and uppermost Aptian *Paraticinella eubejaouarnsis* Zone. Specifically, Leckie reported the presence of *Hedbergella excela* and *Hedbergella infracretacea* group [note: the names listed above follow the synon-

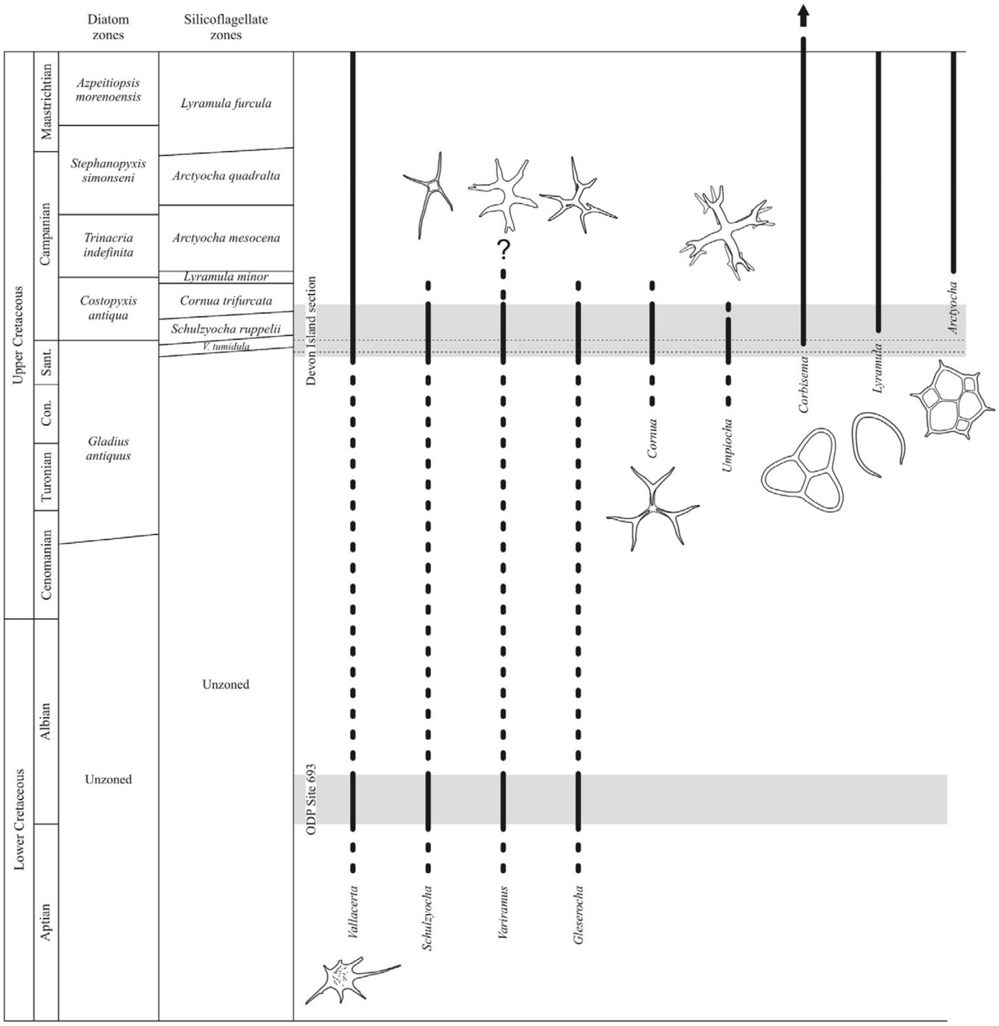

Figure 2. Stratigraphic ranges and schematic representations of Cretaceous silicoflagellate genera versus the diatom and silicoflagellate biostratigraphic zonations of Tapia and Harwood (2002), and McCartney et al. (2011b), respectively. Shaded areas represent the approximate stratigraphic intervals spanned by the study sections. Dashed lines indicate the approximate interval of the Devon Island section examined here, equivalent to *Vallacerta tumidula* Zone. Sketches of silicoflagellate skeletal morphologies are not to scale. Abbreviations: Con.: Coniacian; Sant.: Santonian.

ymy for Leckie's (1990) taxa, as presented in the more recent paper of Huber and Leckie, 2011]. Mohr (1990) reported rich, and well preserved dinoflagellate assemblages from Cores 693A-44R and -45R, of which *Codoniella campanulata* and *Hapsocysta peridictya* suggest an Albian age for Core 693A-44. Ling and Lazarus (1990) suggested a broad Albian to Santonian age for radiolarians in Cores 693A-44R and -43R, but described them as of low diversity and lacking mid- to low-latitude zonal taxa, which limited their ability to give a clear age to the siliceous microfossil-rich sediments and constrain an upper age for this interval. Although diatom biostratigraphy is presently not well developed for the mid-Cretaceous, the rich diatom assemblages described from Core-section 693A-44R-1 by Gersonde and Harwood (1990) and Harwood and Gersonde (1990) must be considerably older than the latest Albian to earliest Cenomanian diatoms preserved in amber from southwestern France (Girard et al., 2008 and Girard et al., 2009), which show a considerably higher level of evolutionary development, and include different taxa than the ODP Site 693 assemblage. This suggests the diatom and silicoflagellate assemblages from ODP Site 693 are more likely to be of early to mid-Albian age (~107 to 113 Ma), predating the appearance of several diatom genera (e.g., *Costopyxis* and *Hemiaulus*, among others), and allowing for sufficient time to explain the considerable morphological advancement and diversification evident in the above mentioned amber samples of Late Albian age.

We also re-examined sample EF0401 collected from Devon Island by Chin et al. (2008). Details of the preparation procedure can be found in Witkowski et al. (2011). Sample EF0401 from Devon Island was collected from the uppermost Santonian (to possibly lowest Campanian) interval of the Kanguk Formation (see stratigraphic section in Chin et al., 2008 and Witkowski et al., 2011), and assigned to the diatom *Gladius antiquus* Zone of Tapia and Harwood (2002), based on the flora described in Witkowski et al. (2011), including the presence of the nominative taxon. This sample is also assigned to the silicoflagellate *Vallacerta tumidula* Zone of McCartney et al. (2011b), defined as the interval between the first occurrence of *Vallacerta tumidula* up to the first occurrence of *Schulzyocha ruppelii*.

In order to obtain the best light microscope (LM) effects, a random settling technique was used to prepare new slides from both localities for this study. For each sample, multiple cover slips were stuck to the bottom of a Petri dish, which was then filled with deionized water. Several drops of the chemically treated residue were then pipetted into the water. Petri dishes were left at room temperature until all liquid evaporated. Dry cover slips were mounted onto slides using Naphrax diatom mountant. Silicoflagellate skeletons, when enabled to settle freely onto the cover slip, were found to be positioned horizontally more often than when residues on the coverslips were heated on a hot plate. The improved slides enabled higher quality microphotography.

The complex, three-dimensional structure of the silicoflagellate skeletons presented here also required use of a stacking technique in LM photography; compiling multiple overlain focal levels into a single image ('stacking') also permitted us to avoid showing multiple focal levels on individual photomicrographs. Stacking was performed using the freeware application Picolay by Heribert Cypionka (www.picolay.de).

Specimens were selected for scanning electron microscope (SEM) examination using a mechanical micromanipulator (Narishige MN-151). Picked specimens were placed on a previously sputtered double-sided Scotch tape following the method outlined by Nikolaev (1982).

3. Terminology

Cenozoic silicoflagellates have a closed basal ring, usually of polygonal shape, comprised of linear sides and angular corners. Terminology for *Corbisema*, which is a representative example of Cenozoic silicoflagellates, is shown in Fig. 3(1) for comparison with Cretaceous skeletons. Struts in *Corbisema* attach to the basal ring and support the apical structure. The term "element" is here used only for components of the basal or apical structure (e.g., strut) that connect at each end to other portions of the silicoflagellate skeleton. Elements differ from spines and pikes, which terminate at one end. Elements and spines almost always meet at triple junctions with obtuse angles close to 120° (McCartney and Loper, 1989 and McCartney and Wise, 1990).

Spines and pikes appear to be distinctly different structures that serve separate functions. Spines are consistently linear, connect to two elements of either the basal or apical structure and are oriented radially from the apparent middle of the cell. Basal spines in Cenozoic morphologies and Cretaceous *Arctyocha* (e.g., Plate 9.1 in Bukry, 1985; Plate 1 in McCartney et al., 2011a), *Corbisema* (e.g., Fig. 3(1)) and *Vallacerta* (see Fig. 6A–G in McCartney et al., 2010) usually occur in a plane, termed the "basal plane" (McCartney et al., 2010). Pikes are generally shorter, connect to the basal structure, point abapically and often curve or point towards a common point beneath the middle of the apical structure. The location of the pike varies and may occur beneath the strut attachment, or may rarely connect to the strut. Where the pike meets two basal elements, the angles between the pike and two elements may not be similar, contrary to basal spines. Pikes apparently serve to help hold the two sibling members of a double skeleton together (Moestrup and Thomsen, 1990). While the term "apical pike" has been used in the literature (Bukry, 1974 and Malinverno, 2010), our use is restricted to the basal structure.

Cenozoic terminology is applied to the Cretaceous silicoflagellate skeletons where possible (Fig. 3), with the terms strut, strut attachment, apex, bridge, spine and pike applied as appropriate with some modification. In *Cornua* (Fig. 3(2)) and *Schulzyocha* (Plate 7 in McCartney et al., 2011b), apical structures are the same as in *Corbisema* and Cenozoic forms of *Dictyocha*, respectively, with struts that connect to an apex or bridge on one end and basal components on the other. But in the new genus *Gleserocha* described here (Fig. 3(4–5)), the basal end of the strut can connect to another element or a series of elements, which are here called "substruts". Together, struts and substruts form a "limb". In *Variramus* the terms bridge, strut and substrut are used in a more general sense and are not associated with limbs (Fig. 3(3)). Thus, while struts always attach to the basal ring on Cenozoic silicoflagellates (Fig. 3(1)), in some Cretaceous morphologies there are additional elements between struts and basal components.

McCartney et al. (2011b) defined the sabaton and pike-and-spine for some Cretaceous skeletal morphologies. A sabaton is present where an element connects with a short pike and longer spine, e.g., in *Gleserocha wisei* nov. comb. (Fig. 3(4)) and *Schulzyocha*. A pike-and-spine is generally a linear structure pointed at both ends, located at the end of a substrut, and occurs in *Gleserocha tapiae* nov. comb. (Fig. 3(5)). Sabatons are generally aligned with the substrut and occur in the plane of the limb, whereas pike-and-spines occur as a linear component oriented transversely to the substrut. The "spine" of the sabaton and pike-and-spine is straight

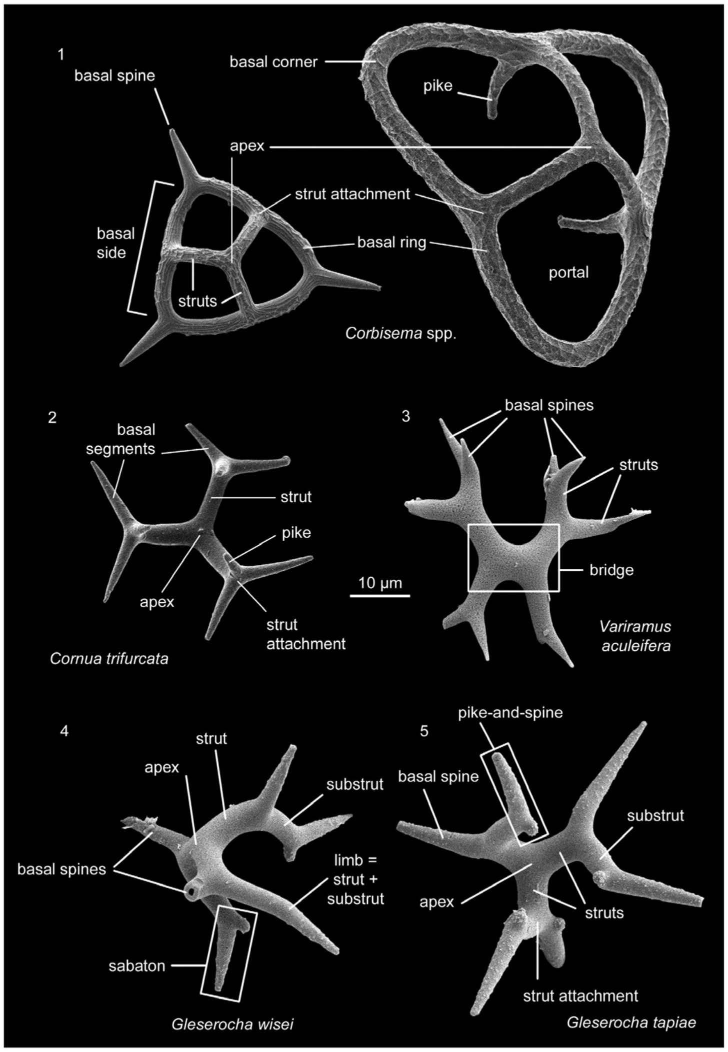

Figure 3. Descriptive terminology for silicoflagellate skeletal morphology. 1. *Corbisema* Hanna, specimen on left: Miocene, Hata Formation, Japan, apical view. Specimen on right: Late Cretaceous, Ural Mountains, oblique apical view. 2. *Cornua trifurcata* Schulz, Late Cretaceous, Ural Mountains, abapical view. 3. *Variramus aculeifera* (Deflandre), Early Cretaceous, sample 113-693B-19X-4, 77–78 cm, view undefined. 4. *Gleserocha wisei* (McCartney, Witkowski and Harwood) nov. comb., Early Cretaceous, sample 113-693B-19X-4, 77–78 cm, oblique apical view. 5. *Gleserocha tapiae* (McCartney, Witkowski and Harwood) nov. comb., Early Cretaceous, sample 113-693B-19X-4, 77–78 cm, abapical view.

and oriented radially with respect to the center of the cell. Thus, the orientation of these spines is equivalent to those of Cenozoic skeletal morphologies, although not connected to two elements.

In *Cornua* (Fig. 3(2)), the strut generally attaches to two basal components that each terminate distally. These components occur commonly within the basal plane. However, they are not oriented radially, and in some species curve in the direction of the next strut attachment (e.g., Fig. 1c in Gleser, 1962; pl. 6, Figs. 3 and 6 in McCartney et al., 2011b). Neither the term "element," which connects at both ends, or "spine" is appropriate for what we hereafter refer to as basal "segments" (Fig. 3(2)).

4. Occurrence and skeletal morphology of the oldest silicoflagellates

4.1. Previous interpretations of Variramus and Cornua

Deflandre, 1940, Deflandre, 1944 and Deflandre, 1950 published three illustrations of *Cornua aculeifera*, with varied morphologies. This species was placed subsequently in *Variramus* by McCartney et al. (1990). McCartney et al. (2011b) reported three new species of the variramid group in Santonian sediments from Devon Island; *Variramus gleseri* and *Variramus tozeri* are rare, but *Variramus wisei* (transferred to *Gleserocha* in this study) is abundant. *Variramus wisei* is also abundant at ODP Site 693, although most specimens are fragmentary; it is also known from multiple sites in the Ural

Mountains and from the Horton River section, in the Canadian Arctic (McCartney et al., 2011a).

Two species of *Cornua* were described by Schulz (1928) and Gleser (1959) from upper Santonian or lower Campanian sediments in central Europe and the Ural Mountains, respectively, and illustrated by simple line drawings. *Cornua*'s occurrence in Canadian Arctic sediments (McCartney et al., 2010 and McCartney et al., 2011a) showed that the distribution of *Cornua* was much broader than previously thought. *Cornua* exhibits especially variable morphology in the Santonian portion of the Devon Island sequence, where some of its morphotypes are associated with the oldest known *Corbisema* (McCartney et al., 2011b), supporting the interpretation of *Cornua* as an immediate ancestor to *Corbisema*.

4.2. Interpretation of G. tapiae and G. wisei

The *Vallacerta tumidula* Zone (Fig. 2) on Devon Island contains examples of two unusual species that were described by McCartney et al. (2011b) as *Cornua tapiae* and *V. wisei*. The former was placed in *Cornua* based on a flattened morphology that includes an apex and three struts. Each strut, however, attaches to dissimilar components: a spine and a substrut that terminates in a linear pike-and-spine. *Variramus wisei* was included within *Variramus aculeifera* by McCartney et al. (1990), as in the Albian of ODP Site 693 it occurred most commonly as fragments. Since then, *G. tapiae* and *G. wisei* were identified as distinct and consistent morphologies also in other Cretaceous deposits with no intergradation between one another, which corroborates the view that they represent separate species, and not aberrant variants of a single taxon or other taxa. Whereas their superficial similarities to *Variramus* and *Cornua* are apparent, SEM examination of complete specimens shows that *G. tapiae* and *G. wisei* have a similar structure that is distinct from both *Variramus* and *Cornua*. *Gleserocha* gen. nov. is proposed here to comprise this group of silicoflagellate skeletal morphologies.

Gleserocha wisei nov. comb. has a consistent form of three limbs that meet at an apex similar to that of *Cornua* and *Corbisema*. Using the apex as a point of reference, the skeleton is here interpreted to have three struts that attach to a spine and a substrut (Fig. 3(4), Plate 6, Figs. 1–6). The substrut can connect to an additional spine and substrut, but more often ends directly in a sabaton. The strut and substrut form a limb that generally lies in a plane. The spines are aligned with the center of the skeletal structure and have a slight offset, usually to the dextral side of the limb (McCartney et al., 2010, Fig. 5B). The three limbs form a roughly spherical design. *Gleserocha tapiae* nov. comb. has a similar general structure with an apex and three struts (Fig. 3(5), Plate 5, Figs. 7–9), but the overall design is more flattened. The struts are rotated sinistrally and the spines are oriented to occur more closely within a plane.

Similar skeletal structures of *G. tapiae* and *G. wisei* warrant their placement in this new genus, which is distinct from *Variramus* and *Cornua*. Both species display considerable variability, but have greater consistency of form than *V. aculeifera*, of which Deflandre (1950) observed that no two specimens appear alike. Having examined several hundred specimens of *V. aculeifera*, we concur with this statement. Separation of these *Gleserocha* species from *Cornua* is warranted by the attachment of the strut to a spine and substrut, which is unlike any known species of *Cornua*. The radial position of the spines is different from the segments of *Cornua*, and also shows a slight dextral offset not observed in *Cornua* or *Corbisema*. Also, while the short ends of the sabaton of *G. wisei* and pike-and-spine of *G. tapiae* are probably related to the pike of *Cornua*, the latter is more pronounced and not directly associated with the radially-oriented spine-like components.

Gleserocha offers an evolutionary link between *Variramus*, an important silicoflagellate genus of the early Albian, and *Cornua* of Santonian and early Campanian age. This evolutionary trend is from extreme variability in the early Albian to a narrower range of morphological variability in the Santonian-early Campanian. Similar to *Umpiocha*, *Gleserocha* is characterized by an apical structure made of limbs composed of multiple elements, whereas *Cornua* has only struts that generally attach to three pairs of segments that lie in a basal plane (Fig. 2). This latter skeletal design gave rise to *Corbisema*, and thus also to the broad diversity of the Cenozoic silicoflagellate form.

5. Discussion

The phylogeny of Early Cretaceous silicoflagellates presented by McCartney et al. (2010) was based on direct observation of specimens from the Santonian through Maastrichtian, but was speculative for the time interval between the early Albian and Santonian, where no specimens have been observed. Four lineages were interpreted in the interval between the early Albian and late Santonian: (1) *Vallacerta*, believed to have descended from *Schulzyocha*; (2) *Schulzyocha*; (3) *C. tapiae*, which evolved into *Umpiocha*, *Cornua* and *Corbisema*; and (4) *Variramus*, which included *V. wisei* that led to *Lyramula*. Observations from the present study generally support this interpretation, but shed more light on relationships that were insufficiently understood. Interpretations for *Vallacerta* and *Schulzyocha* remain largely as presented by McCartney et al. (2010), but our description of *Gleserocha* changes the interpretation of both the *Cornua* and *Variramus* lineages.

We show *Gleserocha* to be a long-lived genus that ranged from Albian to at least early Campanian in age. Given its tri-radial skeletal morphology, *Gleserocha* is probably ancestral to *Cornua* and *Corbisema*, but the evolutionary transition remains uncertain. *Cornua* is sufficiently diverse in the Devon Island succession to suggest a long evolutionary history prior to the Santonian. The limbs of *Gleserocha*, which include offset spines and terminal sabatons, are similar to those of *Umpiocha umpiana*. *Umpiocha*, however, has a quadrate structure and elongated limbs that curve beneath the apical structure, and disappears without descendants prior to the early Campanian. Thus, *Gleserocha* is suggested here as the likely progenitor of *Umpiocha*, *Cornua* and ultimately *Corbisema*, and therefore represents an ancestor to all modern silicoflagellates.

This paper describes three new species, all of which are unusual in comparison to other members of their respective genera. *Gleserocha harrisonii* occurs in several deposits, and despite considerable morphological variability, always displays the same skeletal pattern. The skeletal morphology lacks obvious pikes and has a generally spherical shape, which places it in *Gleserocha*, but lacks radial spines, substruts, sabatons or pike-and-spines present in other members of the genus. *Cornua deflandrei* is unique among *Cornua* in possessing segments that do not lie within a plane. Finally, *C. witkowskiana* is unusual in possessing only one basal segment per strut, and has an unusual pike structure. The presence of these unusual morphologies in the Santonian suggests that a number of key events in silicoflagellate evolution took place between the Albian and the Santonian. Unfortunately, no siliceous microfossil-bearing sedimentary successions of this age are available for study.

The origin of *Lyramula* is an open question. McCartney et al. (2010) considered *Lyramula* to have evolved from *Variramus*, and illustrated *V. wisei* (here transferred to *Gleserocha*) as the transitional taxon in their phenogram. *Lyramula*, however, has a simple skeletal morphology that is usually formed of two limbs that lack pikes, meeting at an angle, and associated with an apex spine. Apex spines are unusual among silicoflagellates. Some specimens of *Schulzyocha loperi*, which is the simplest of the early skeletal morphologies, bear apical spines (McCartney et al., 2010, Fig. 5D). Therefore, *S. loperi* may be the most reasonable ancestor to *Lyramula*. Alternatively, the ancestors of *Lyramula* may remain to be discovered, or the genus could have developed from a naked silicoflagellate ancestor that does not have an earlier fossil record.

With the first appearances of *Corbisema* and *Lyramula* near the Santonian/Campanian boundary (McCartney et al., 2011b), silicoflagellates changed rapidly to the assemblage of taxa that are well known from the Campanian and Maastrichtian. *Schulzyocha* and *Umpiocha* are rare in the early Campanian, and neither *Cornua* nor *Gleserocha* appear to range above the lower Campanian (Fig. 2). While there is a well-established taxonomy for the four surviving genera that persisted into the Maastrichtian, variability makes consistent identification difficult. Yet, recent studies show that silicoflagellates have a high potential as zonal indicators for the high-latitude Cretaceous sequences, and also as paleoenvironmental proxies for the Paleogene. Revision of old taxonomic concepts, more precise morphological definitions, and the development of a consistent system of classification is essential for continued improvement of this group for biostratigraphy and paleoenvironmental reconstruction of Cretaceous and Paleogene sedimentary sequences.

6. Conclusions

The interpretation of early silicoflagellate evolution presents considerable challenges in working with often fragmentary material, of great morphological variability, and with little external context to facilitate a better understanding. This is compounded by the 35 m.y. gap between the two oldest silicoflagellate-bearing deposits, each including an assemblage characterized by great morphological variability. Yet, considerable advances in understanding the silicoflagellate fossil record have been made over the past 25 years since the discovery of ODP Site 693 Albian silicoflagellates, in part by interpretation of a more or less continuous record from the Santonian to the Maastrichtian.

In this paper, we re-examine the *Variramus* group of the original ODP Site 693 assemblage and from the Santonian interval of the Devon Island succession. Each of these snapshots provided some perspective for a better understanding of the other. *Variramus wisei*, which formed a significant portion of the diversity at ODP Site 693, is found to be quite similar to *C. tapiae*, a major species in the Santonian, hence these are here combined into the new genus *Gleserocha*. Both taxa occur in both deposits, and help to bridge the considerable time gap separating them. By Santonian time, however, variramids occur in greatly reduced numbers and are replaced by a wide range of new taxa that – in our interpretation - developed from *Gleserocha*. The variramid group diversified into five genera: *Variramus*, *Schulzyocha*, *Umpiocha*, *Gleserocha*, and *Cornua*. Transitions in silicoflagellates from the early Albian to Santonian show trends toward: (1) less extreme variability, (2) the development of an apical structure that rises above the basal plane, often with spines directed away from the cell center, and (3) pikes that point abapically. This diversification declined rapidly with the evolution and ascendance of *Corbisema* near the Santonian-Campanian transition. The timing and nature of the silicoflagellate radiation prior to Santonian remains unknown and unknowable until new geologic sections are found to fill the gap.

7. Systematic paleontology

Division: OCHROPHYTA Cavalier-Smith, 1995
Class: DICTYOCHOPHYCEAE P.C. Silva, 1980
Order: DICTYOCHALES Haeckel, 1894
Family: DICTYOCHACEAE Lemmermann, 1901

Genus ***Cornua*** Schulz, 1928
Type species: *Cornua trifurcata* Schulz, 1928, p. 285–286, Fig. 83A–C.

Discussion: With the placement of *C. tapiae* into the new genus *Gleserocha*, the oldest currently known occurrence of *Cornua* is in the Santonian interval of the Devon Island succession (McCartney et al., 2011b).

Cornua engelii McCartney et al., 2011b
Plate 1, Figs. 8–9; Plate 4, Figs. 1–3
2010. *Cornua engelii* McCartney et al., Fig. 5J
2011b. *Cornua engelii* McCartney et al., p. 48, pl. 1, Figs. 4–8, pl. 6, Figs. 1 and 2

Discussion: This species is characterized by relatively long linear struts with short basal segments of equal length. The pikes occur on the abapical surfaces of the struts and curve towards the apical axis. They are generally long and often bifurcate. The location of the pike along the strut varies but is typically half to two-thirds the distance from apex to strut attachment. Struts of a representative specimen are 45 μm long and 6 μm wide near the apex, but taper to 4 μm near the strut attachment.

Cornua deflandrei McCartney, Witkowski & Harwood, nov. sp.
Plate 1, Figs. 4–7; Plate 4, Figs. 4–6
2010. *pro parte*, *Cornua trifurcata* Schulz; McCartney et al., Figs. 5G–H
2011b. *pro parte*, *Cornua trifurcata* Schulz; McCartney et al., pl. 1, Figs. 2 and 3?, 10

Material: Ten specimens observed in six microscope slides.

Description: The basal segments are rotated and differentiated. Seen from apical view, the sinistral segment is longer and thicker than the dextral segment, referred to as ‘dominant’, vs. ‘lesser’, respectively. Using the basal plane as a reference, the dominant segment moves apically away from this plane while the lesser segment moves abapically. The shape of the pikes is variable; pikes can be digitated or have other unusual shapes. Location of the pike is also variable and can occur at the abapical surface of the strut attachment or nearby on any of the three skeletal components. Pike location can vary even on an individual specimen. Struts are typically robust, 4–6 μm wide, and shorter than either of the basal segments.

Discussion: Some specimens of this taxon are similar to large specimens of *C. trifurcata* also observed in the EF0401 sample, thus we believe that the two taxa are closely related. Those specimens of *C. deflandrei* that are morphologically similar to *C. trifurcata* (McCartney et al., 2011b, pl. 1, Fig. 3) usually have basal segments of more equant size that are rotated to a lesser degree than in smaller specimens. Both the large *C. trifurcata* and *C. deflandrei* can have wedged terminations at the distal ends of the segments, but these terminations are not as pronounced or consistent as in *C. witkowskiana* described below. Measured specimens have dominant segments of 30–42 μm and lesser segments of 20–25 μm.

Type specimen: Holotype on slide #NUPB 198 (Plate 1, Fig. 7). Reposited for the Nunavut Government in the Canadian Museum of Nature. Struts are about 20 μm from apex to basal triple junction. Sinistral (from apical view) basal segments are of variable length, 35 to 40 μm; dextral segments about 25 μm. Type specimen is in abapical view.

Type locality: Eidsbotn Graben, Devon Island, sample EF0401.

Derivation of name: The species is named after Georges Deflandre (1897–1973; see Caulet, 2013) to honor his detailed examination of silicoflagellate variability.

Occurrence: This species is present in the late Santonian *Vallacerta tumidula* Zone and the early Campanian *Schulzyocha ruppelii* Zone in the Devon Island succession (Fig. 1).

Cornua trifurcata Schulz, 1928
Plate 2, Figs. 1–2; Plate 4, Figs. 7–9
2010. *Cornua trifurcata* Schulz; McCartney et al., Fig. 5I
2011a. *Cornua trifurcata* Schulz; McCartney et al., p. 72–74, pl. 6, Figs. 1–5, 7–10, 14
2011b. *Cornua trifurcata* Schulz; McCartney et al., p. 49–50, pl. 1, Figs. 1 and 3?

Discussion: Specimens are typically larger than those from younger deposits at Horton River (McCartney et al., 2011a). Basal segments (40–60 μm) are commonly

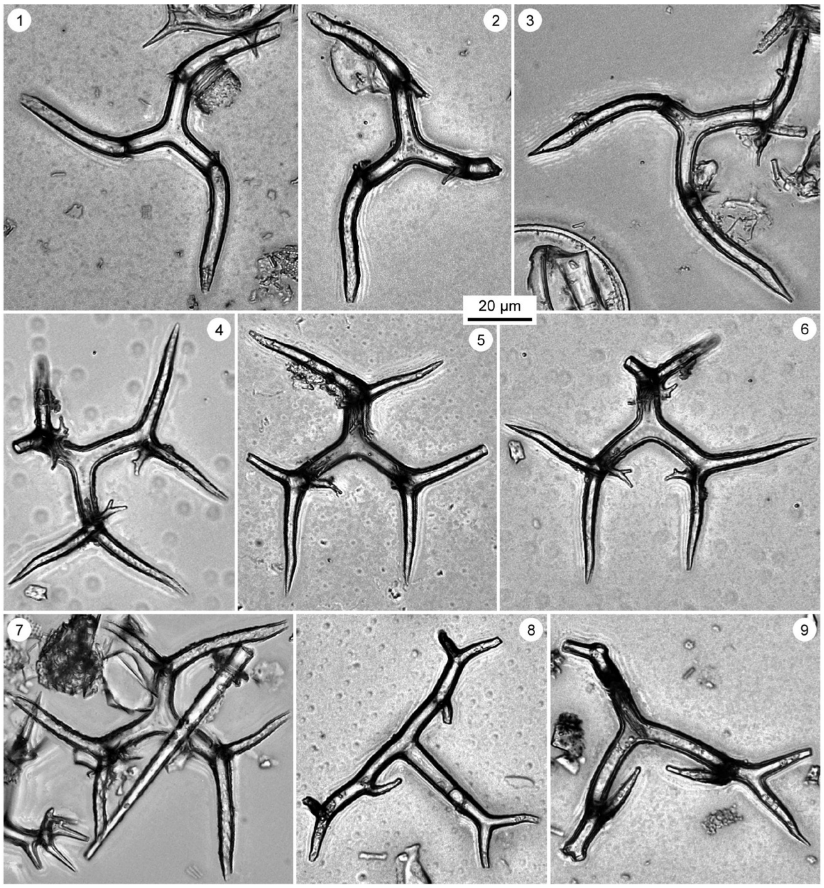

Plate 1. LM photomicrographs of *Cornua* from Devon Island, sample EF0401. Figs. 1–3. *Cornua witkowskiana* nov. sp. McCartney and Harwood; 1: abapical view, holotype, slide NUPB 190, Figs. 2 and 3: apical view. Figs. 4–7. *Cornua deflandrei* nov. sp. McCartney, Witkowski and Harwood; Figs. 4–6: apical view, Fig. 7: holotype, abapical view, slide NUPB 198. Figs. 8 and 9. *Cornua engelii* McCartney, Witkowski and Harwood; Fig. 8: abapical view of tilted specimen, with the lower right corner of the specimen tilted upwards, Fig. 9: apical view of specimen, with upper left corner of specimen tilted downwards.

longer than struts and usually linear, although terminations may curve towards the next strut. The width of the strut does not vary significantly along the length. Pikes usually connect at the strut attachments but may be located near the strut attachment on the abapical surface of the strut or a basal segment. Pikes generally have a single termination, but may be bifurcated or (rarely) digitated. The length of the pike may exceed half the length of the strut. The pikes point toward a common center in abapical space.

Cornua witkowskiana McCartney & Harwood, nov. sp.

Plate 1, Figs. 1–3

Material: Five specimens observed on six microscope slides.

Description: Skeleton consists of three struts that appear linear when seen from apical view, and are each attached to a basal segment that curves sinistrally over more than 45°, with most of the curve being near the strut attachment, just distal of the pike. A pike, which may be a simple termination or more complicated structure, occurs at the strut attachment and points abapically and in a dextral direction. All three basal segments occur within a plane and have a similar curve that produces a three-armed spiral configuration, like a 3-armed swastika. The basal segments have a wedge-shaped termination, with the point being on the outside of the curve. The flat face of the wedge occurs on the inside of the curved segment and is aligned with the center of the cell.

Discussion: No specimens of this rare species were available for SEM examination; only five skeletons were examined in LM. Despite a limited number of specimens, there was consistency in both the shape and size of skeletons. Length of the combined strut and basal segment, measured as a straight line from apex to tip, ranged from 54 to 60 µm, with length of the strut being slightly less than a third the total distance. Struts have a width of about 5 µm, and the wedge surface is about 12 µm. Basal segment curvature is consistently sinistral when seen from apical view (note that the type specimen (Plate 1, Fig. 1) is seen from abapical view). Where the strut attaches to the basal segment there is usually a pike, but the size and shape are variable. Where present, pikes point dextrally.

Placement of this unusual skeletal morphology in *Cornua* is tentative. The few known specimens assigned to this taxon consistently have only one basal segment, while all other *Cornua* species have two segments. *Cornua witkowskiana* also has unusual pike structures, although these are also observed on some specimens of *C. deflandrei*, to which *C. witkowskiana* may be closely related.

Derivation of name: This species is named after Dr. Andrzej Witkowski, diatomist at the Palaeoceanology Unit, Faculty of Earth Geosciences, University of Szczecin.

Type specimen: Holotype on Slide #NUPB 190 (Plate 1, Fig. 1). Struts are 16–18 µm long, and basal segments 38–40 µm long (linear distance from pike to termination). The wedge termination of the most complete basal spine (bottom of photograph) is 8 µm long. Reposited in the Canadian Museum of Nature for the Nunavut Government.

Type locality: Eidsbotn Graben, Devon Island, sample EF0401.

Occurrence: This species occurs in the Santonian interval of the Devon Island succession within the *Vallacerta tumidula* Zone.

Genus ***Gleserocha*** McCartney, Witkowski & Harwood, nov. gen.

Generitype: *Gleserocha wisei* (McCartney, Witkowski & Harwood) McCartney, Witkowski & Harwood, nov. comb.

Description: Skeletons consist of an apical structure made of three struts that meet at an apex. Each of the struts attach to two other components that are generally different from one another. There is no pike near the strut attachment.

Differentiation: This genus differs from *Cornua* in that the two abapical components that meet at the strut attachment are generally dissimilar. In *Cornua* the strut attaches to two similar basal segments with a pike near the strut attachment, and lacks a substrut. *Umpiocha* differs from *Gleserocha* in having a quadrate structure based on four struts and limbs that curve abapically beneath the apical structure.

Discussion: *Gleserocha* is thought to be an evolutionary link between *Variramus* and *Cornua*, and as such includes a species transferred from each of the two genera. *Gleserocha wisei* was previously known largely from fragments and placed in *Variramus*, whereas *G. tapiae* was placed in *Cornua* due to its flattened structure and tri-radial symmetry. *Gleserocha* is also the likely ancestor of *U. umpiana*, as suggested by the presence of sabatons and pike-and-spines in both genera.

Derivation of name: *Gleserocha* is named after Zoya I. Gleser, a pioneer in the identification and interpretation of Cretaceous silicoflagellates (Gleser, 1959 and Gleser, 1966). A reexamination of samples from the Ural Federal District in Russia that Gleser likely examined shows that she may have observed specimens of all three species now included in this genus.

Gleserocha harrisonii McCartney, Witkowski & Harwood nov. sp.

Plate 3, Figs. 13–15; Plate 5, Figs. 1–5

Material: Six specimens observed in six microscope slides.

Description: Skeleton consists of three struts that radiate from an apex and attach to two diverging segments. Each pair of segments is often curved but occurs in a general plane that is at approximate right angles to segments associated with each of the other two struts. The segments generally have the appearance of curving around a spherical surface. The length and curvature of the segments, even those attached to a single strut, can vary and one or more of the segments may be more linear than curved. Pikes, sabatons, or pike-and-spines, are absent.

Differentiation: This taxon differs from all other species of *Gleserocha* or *Cornua* in the variability of the basal segments, even on an individual specimen. The two segments associated with the same strut may be of different shape and/or length. Despite this variability, the general morphology is more consistent than in *Variramus*. Thus, the number of struts and the lack of pikes place this taxon in *Gleserocha*. *Gleserocha harrisonii*, however, does not have spines radially aligned with the center of the cell.

Discussion: Specimens of *G. harrisonii* were considered to be aberrant by McCartney et al. (2011b). Similar specimens have, however, been more recently observed in a number of localities from the Ural Federal District of Russia. This indicates that this skeletal morphology is

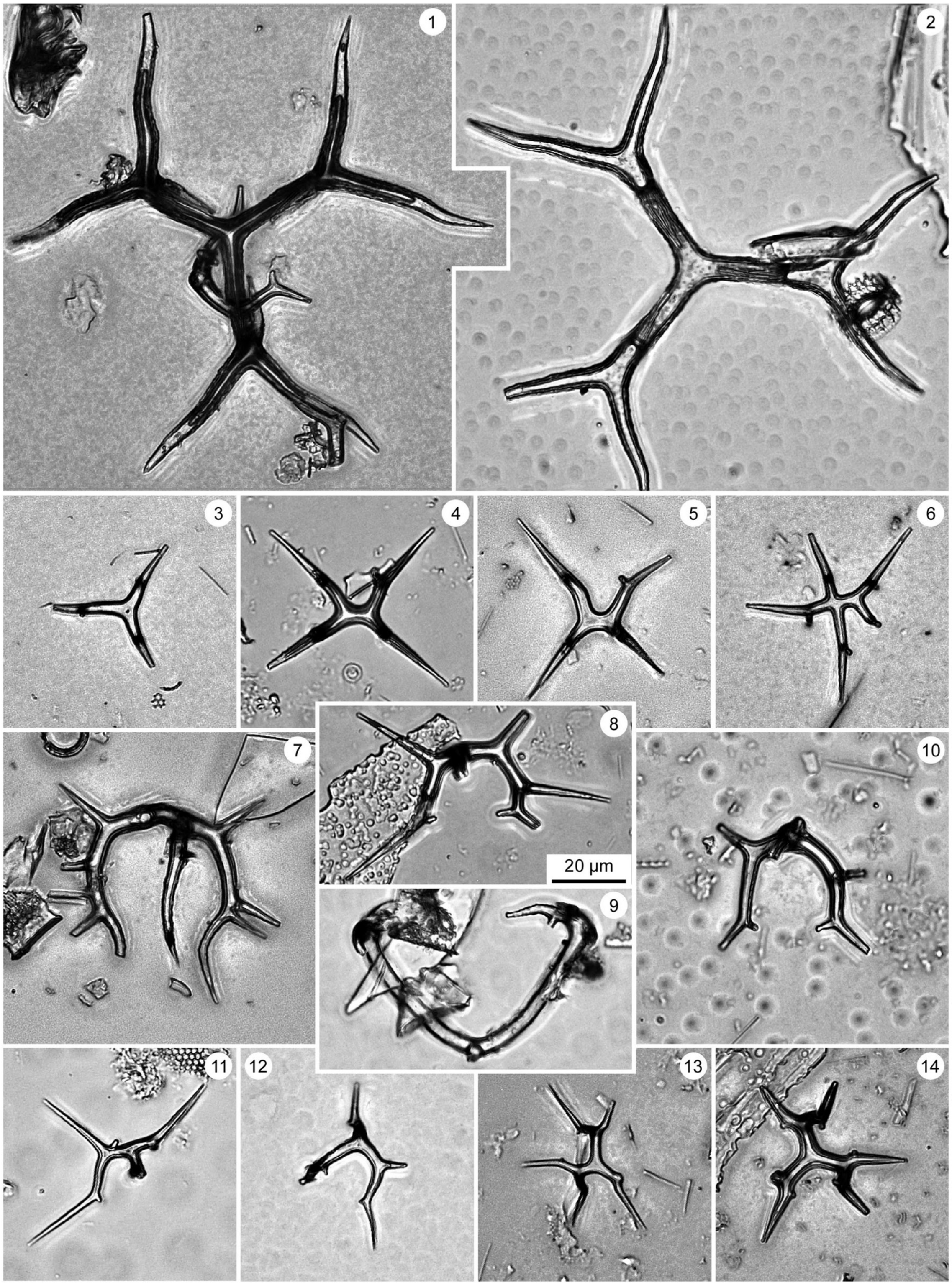

Plate 2. LM photomicrographs of Albian and Santonian silicoflagellates. Figs. 1 and 2. *Cornua trifurcata* Schulz; Devon Island sample EF0401, apical view. Figs. 3–6. *Schulzyocha loperi* (McCartney, Wise, Harwood and Gersonde) McCartney, Witkowski and Harwood, sample 113-693B-19X-4, 77–78 cm, all specimens in apical view. Figs. 7, 8, 10–12. *Gleserocha wisei* nov. comb. (McCartney, Witkowski and Harwood) McCartney, Witkowski and Harwood; Fig. 7: Devon Island sample EF0401, lateral view, Figs. 8 and 10: sample 113-693B-19X-4, 77–78 cm, lateral view, Figs. 11 and 12: sample 113-693B-19X-4, 77–78 cm, views undefined. Fig. 9. *Umpiocha jeletzkyi* McCartney, Witkowski and Harwood, Devon Island sample EF0401, apical view. Figs. 13 and 14. *Gleserocha tapiae* nov. comb. (McCartney, Witkowski and Harwood) McCartney, Witkowski and Harwood, sample 113-693B-19X-4, 77–78 cm.; Fig. 13: abapical view, substrut rotated dextrally, Fig. 14: abapical view, substrut rotated sinistrally.

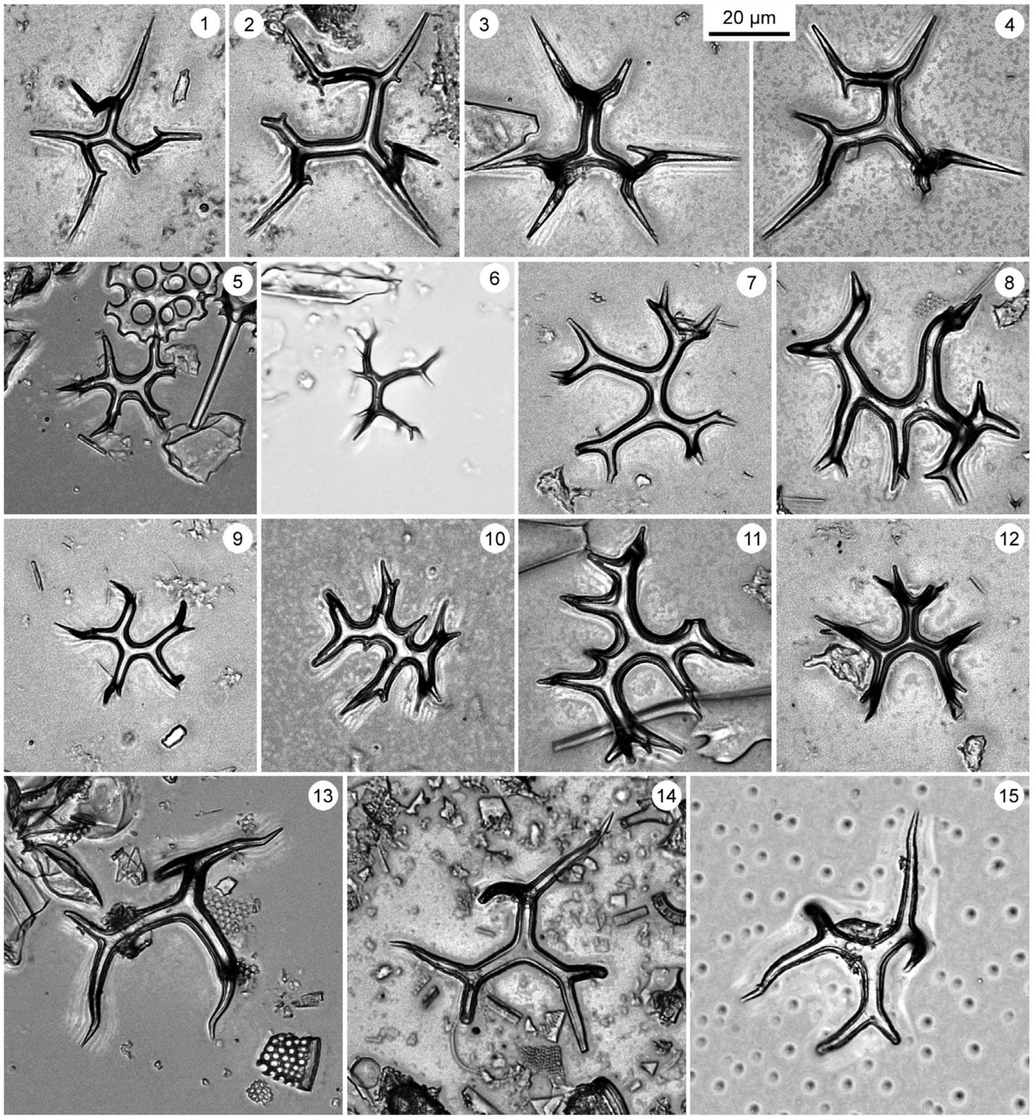

Plate 3. LM photomicrographs of Albian and Santonian silicoflagellates. Figs. 1–4. *Gleserocha tapiae* nov. comb. (McCartney, Witkowski and Harwood) McCartney, Witkowski and Harwood, sample 113-693B-19X-4, 77–78 cm, all specimens in apical views. Figs. 5–12. *Variramus aculeifera* (Deflandre) McCartney, Wise, Harwood and Gersonde; Figs. 5 and 6: Devon Island sample EF0401, Figs. 7–12: sample 113-693B-19X-4, 77–78 cm. Figs. 13–15. *Gleserocha harrisonii* nov. sp. McCartney, Witkowski and Harwood, Devon Island sample EF0401, all specimens in apical views, Fig. 15: holotype, slide NUPB 199.

consistent over a wide geographic area, and is therefore recognized as a new species with potential biostratigraphic value.

While *G. harrisonii* lacks the substruts that occur in *G. tapiae* and *G. wisei*, the segments are differentiated. The two segments associated with each strut are often rotated with respect to one another, so that each pair lies more or less in a plane perpendicular to the other two pairs, in such a way that the components would wrap loosely around a sphere. Thus, these segments do not lie in or close to what could be interpreted as a basal plane, as occurs in *Cornua*. However, one or more of these components may point linearly away from the spherical shape created by the other skeletal components (Plate 3, Fig. 15; Plate 5, Figs. 4, 5). As with the other two *Gleserocha* species, from apical view the dextral component is generally diminished in length and thickness compared to the sinistral component (Plate 3, Fig. 13; Plate 5, Figs. 3–5), although exceptions occur.

Derivation of name: This species is named after Michael Harrison, a graduate student at the University of Nebraska–Lincoln, who has assisted in the construction of physical models being used in the study of silicoflagellate double skeletons.

Type specimen: Holotype on slide #NUPB 199 (Plate 3, Fig. 15). Struts 10–14 µm in length, basal spine that is in plane of focus (upper right of the photograph) is

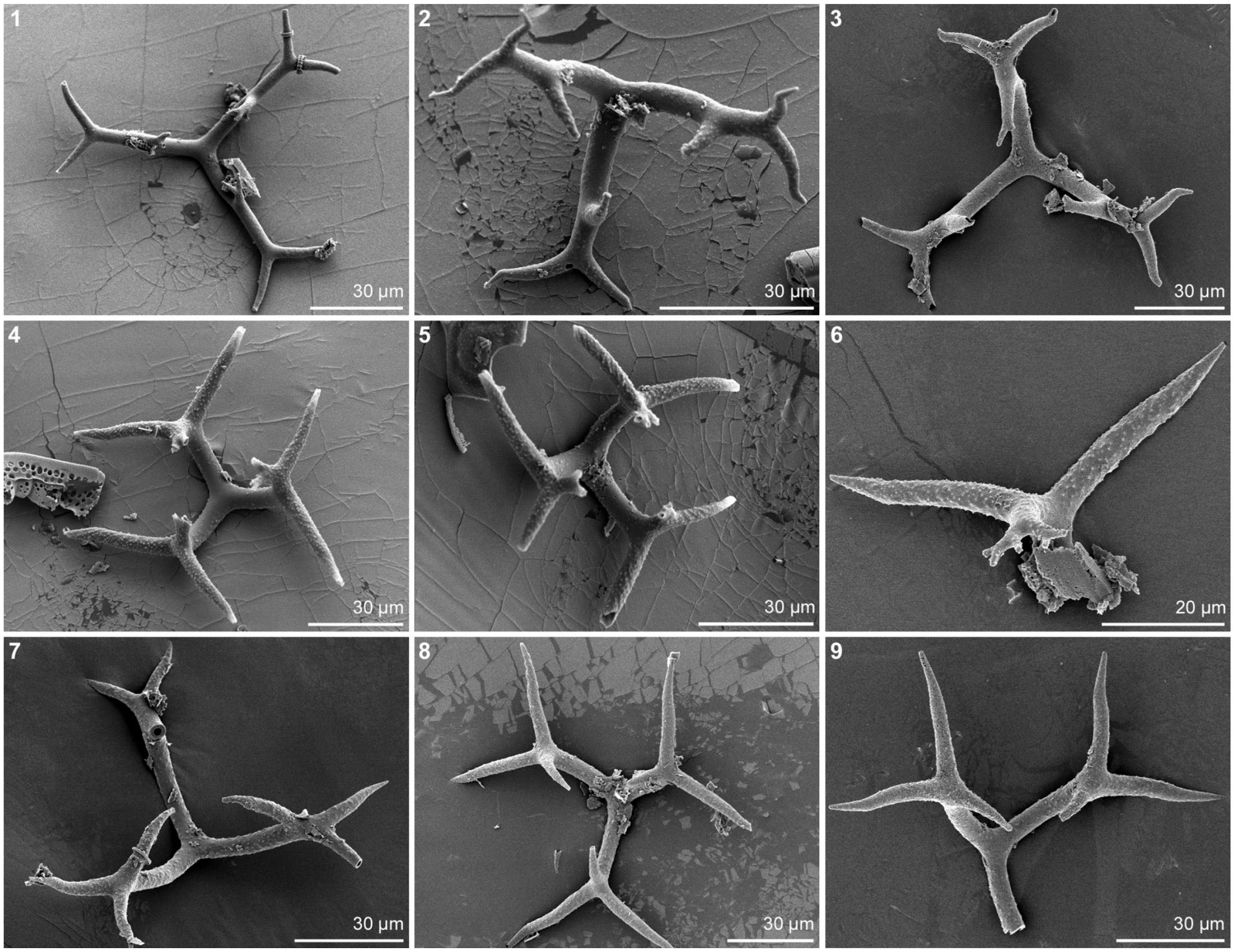

Plate 4. SEM photomicrographs of *Cornua* from Devon Island sample EF0401. Figs. 1–3. *Cornua engelii* McCartney, Witkowski and Harwood; Fig. 1: abapical view, Figs. 2 and 3: oblique abapical view. Figs. 4–6. *Cornua deflandrei* nov. sp. McCartney, Witkowski and Harwood; Fig. 4: abapical view, Fig. 5: oblique abapical view, Fig. 6: abapical view of fragment with multi-digitate pike. Figs. 7–9. *Cornua trifurcata* Schulz; Figs. 7 and 8: oblique abapical view, Fig. 9: abapical view of fragment showing pikes.

30 µm long. Reposited in the Canadian Museum of Nature for the Nunavut Government.

Type locality: Eidsbotn Graben, Devon Island, sample EF0401.

Occurrence: This species is present in the late Santonian *Vallacerta tumidula* Zone and the early Campanian *Schulzyocha ruppelii* Zone in the Devon Island succession. It was also recorded in samples from Belaya Rechka and Leplya rivers, Ural Federal District, Russia, that tentatively correlate with upper and lower *Schulzyocha ruppelii* Zone.

Gleserocha tapiae (McCartney, Witkowski & Harwood) McCartney, Witkowski & Harwood, nov. comb.

Plate 2, Figs. 13–14; Plate 3, Figs. 1–4; Plate 5, Figs. 6–9

1990. *pro parte*, *Variramus aculeifera* (Deflandre) McCartney et al., p. 432, pl. 1, Figs. 2, 8, pl. 6, Fig. 5.

2010. *Cornua tapiae* McCartney et al., Fig. 5E–F

2011b. *Cornua tapiae* McCartney et al., p. 49, pl. 2, Figs. 1–5, pl. 6, Figs. 7–12

Discussion: General morphology of the skeleton is flatter than *G. wisei*, which accounts for the occurrence of more complete skeletons. Apical structure consists of three struts that meet at an apex. Struts attach abapically to a spine and a substrut. The spine points away from the center of the skeleton and is offset slightly. The substrut is directed abapically and terminates in a pike-and-spine. Pike-and-spines of the three struts are oriented radially, and the pike end points to a location beneath the apex. Viewed apically, the substrut is generally sinistral, but dextral substruts occur in about 20% of the specimens from Site 693, and rarely in those from Devon Island.

Gleserocha wisei (McCartney, Witkowski & Harwood)

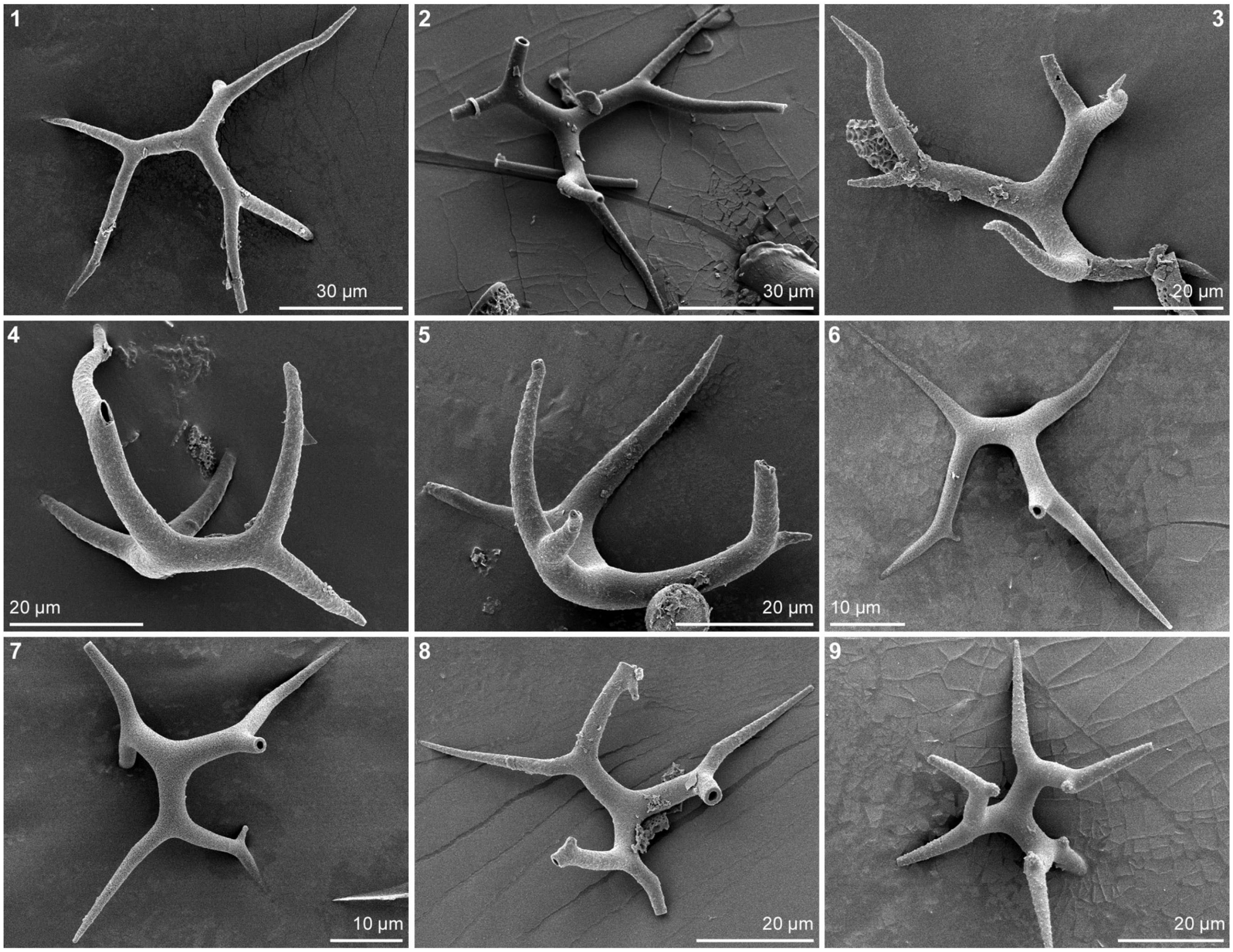

Plate 5. SEM photomicrographs of *Gleserocha*. Figs. 1–5. *Gleserocha harrisonii* nov. sp. McCartney, Witkowski and Harwood, all specimens from Devon Island sample EF0401; Figs. 1 and 2: apical view, Fig. 3: abapical view, Figs. 4 and 5: lateral view. Figs. 6–9. *Gleserocha tapiae* nov. comb. (McCartney, Witkowski and Harwood) McCartney, Witkowski and Harwood; Figs. 6 and 7: sample 113-693B-19X-4, 77–78 cm, apical view, Fig. 8: Devon Island sample EF0401, abapical view, Fig. 9: sample 113-693B-19X-4, 77–78 cm, abapical view.

McCartney, Witkowski & Harwood, nov. comb.

Plate 2, Figs. 7–8, 10–12; Plate 6, Figs. 1–6

1990. *pro parte, Variramus aculeifera* (Deflandre) McCartney et al., pl. 1, Fig. 11; pl. 4, Fig. 6

2010. *Variramus wisei* McCartney et al., Fig. 5B–C2011a. *Variramus* sp. A of McCartney et al., pl. 6, Figs. 11–13

2011b. *Variramus wisei* McCartney et al., p. 55–56, pl. 3,Figs. 1–9, pl. 9, Figs. 4–6

Discussion: Skeleton consists of three struts that meet at anapex and attach to a spine and a substrut. The spine is usuallyoffset on the dextral side of the limb (Plate 6, Figs. 2–5, andFig. 5B of McCartney et al., 2011b), although an offset to thesinistral side occurs uncommonly (Plate 6, Fig. 1). The spineangles away from the center of the cell. Substrut may terminatein a sabaton or connect to another substrut, or a series of spinesand substruts. The strut and one or more substruts make up alimb that curves around the cell, with the sabaton aligned withthe limb. The spine portion of the sabaton is aligned with thecenter of the cell.

The three-dimensional skeletal shape made of slenderhollow rods probably accounts for common breakage dueto taphonomic processes, and during sample treatment andpreparation of microscope slides. Incomplete specimens occurat many orientations, which made the original interpretationof skeletal morphology difficult and increased the apparentvariability. However, intact skeletons of *G. wisei* displayconsiderable variability, and it is possible that this group ofskeletal morphologies includes several species. The specimensobserved from ODP Site 693 materials have relatively simpleskeletons with three struts that each attach to a spine and asubstrut that terminates in a sabaton. Speci-

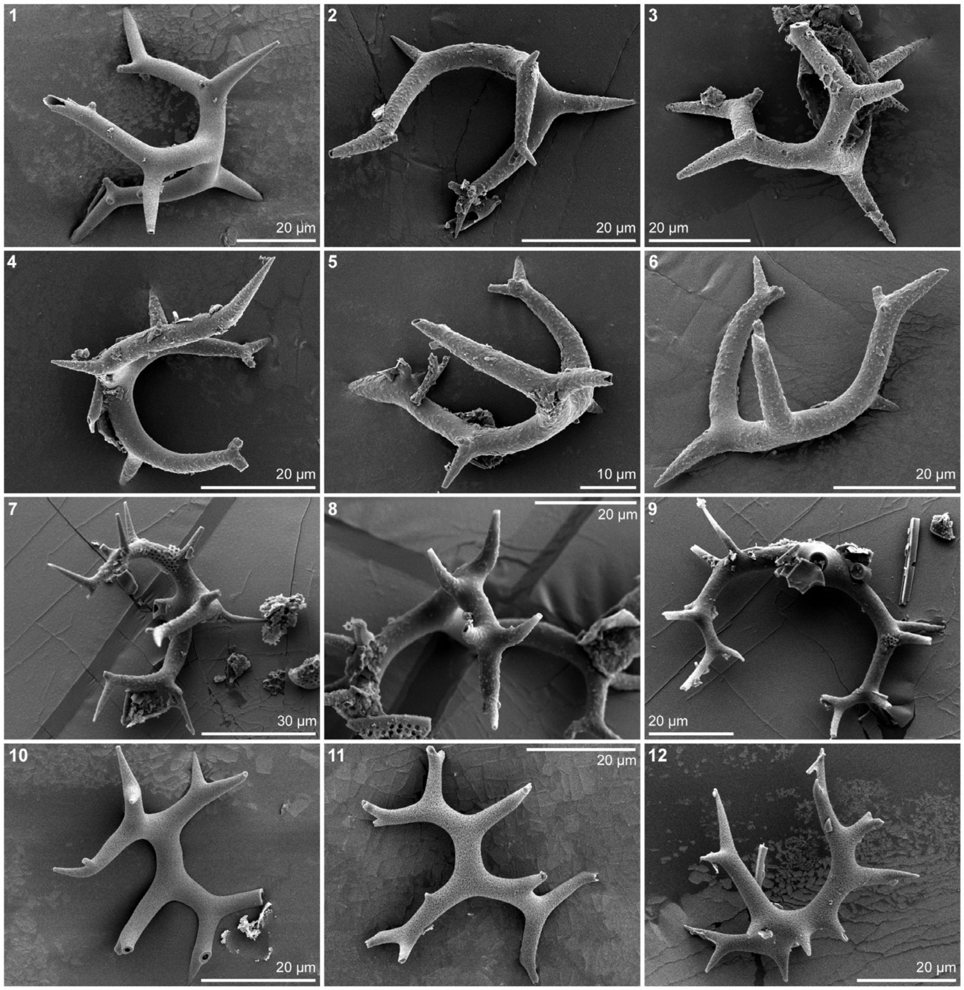

Plate 6. SEM photomicrographs of Albian and Santonian silicoflagellates. Figs. 1–6. *Gleserocha wisei* nov. comb. (McCartney, Witkowski and Harwood) McCartney, Witkowski and Harwood; Fig. 1: sample 113-693B-19X-4, 77–78 cm, lateral view, Figs. 2–6: Devon Island sample EF0401, lateral view. Figs. 7–9. *Umpiocha umpiana* McCartney, Witkowski and Harwood, sample 113-693B-19X-4, 77–78 cm, lateral view. Figs. 10–12. *Variramus aculeifera* (Deflandre) McCartney, Wise, Harwood and Gersonde, views unspecified; Figs. 10 and 11: sample 113-693B-19X-4, 77–78 cm, Fig. 12: sample 113-693B-19X-4, 103–104 cm.

mens from the DevonIsland succession show greater variability, with the substrutsometimes rotated at the attachment (Plate 6, Fig. 1), and insome complete specimens the relative size of the substrut,sabaton and basal spines varies from one limb to another (Plate6, Figs. 2 and 6). While most specimens have a single substrut, specimens with two or more spines and substruts on each limboccur (Plate 6, Fig. 6; see also McCartney et al., 2011a, pl. 9,Fig. 3).Genus ***Schulzyocha*** McCartney et al., 2011bType species. *Schulzyocha loperi* (McCartney et al.) McCartney et al., 2011b.*Schulzyocha loperi* (McCartney et al.) McCartney et al.,2011bPlate 2, Figs. 3–61990. *Variramus loperi* McCartney et al., p. 432–433, pl. 4,Figs. 3, 4, pl. 8, Figs. 4–92010. *Variramus loperi* McCartney et al., Fig. 5D2011a. *Variramus loperi* McCartney et al., p. 80, pl. 6, Fig. 62011b. *Schulzyocha loperi* McCartney et al., p. 51, pl. 4, Fig. 6

Genus ***Schulzyocha*** McCartney et al., 2011b

Type species. *Schulzyocha loperi* (McCartney et al.) McCartney et al., 2011b.

Schulzyocha loperi (McCartney et al.) McCartney et al., 2011b

Plate 2, Figs. 3–6

1990. *Variramus loperi* McCartney et al., p. 432–433, pl. 4,Figs. 3, 4, pl. 8, Figs. 4–9

2010. *Variramus loperi* McCartney et al., Fig. 5D

2011a. *Variramus loperi* McCartney et al., p. 80, pl. 6, Fig. 6

2011b. *Schulzyocha loperi* McCartney et al., p. 51, pl. 4, Fig. 6

Discussion: This species typically has four struts that has four struts that connect to a single-element bridge, although five-strutted forms with a more complicated and expanded bridge structure also occur. The struts end with a sabaton consisting of a small pike and a long spine that is slightly deflected at this juncture. In most specimens, the skeleton is relatively flat, with the bridge (Plate 2, Fig. 4) near to the plane of focus of the spines. Bridge lengths vary but are usually similar to the struts, with spines typically being longer. The four strut and spine combinations are generally similar, with the locations of the pikes positioned as with the corners of a rectangle, although one limb may be twisted out of the general plane of the others. In some cases, the bridge is more highly arched and an apical spine occurs at the bridge midpoint. Forms with two diverging spines on the bridge were also observed. Position of the pikes in the basal plane reflect well-ordered and symmetrical pentagonal or rectangular shaped space, with the pikes representing the corner points (McCartney et al., 1990, pl. 8, figs. 4–7).

Five-strutted forms generally have the extra strut connected to the bridge at a triple junction which forms a bridge with two elements. Such forms can be bilaterally symmetrical with the fifth strut connected to the bridge midpoint, or the strut-bridge connection can be off-center (Plate 2, Fig. 5). In some cases where there is a simple bridge, one of the four struts bifurcates so that there are five pikes and spines. The bridge may also be expanded and flattened (McCartney et al., 1990, pl. 8, figs. 4–7). Five-sided forms can have the general appearance of *V. aculeifera*, but are easily identified by the consistent positions of pikes.

Other variants also occur, e.g. morphologies where one of the struts go directly to a spine without a pike (Plate 2, Fig. 4). These morphologies are placed in *S. loperi* when all the elements and spines that connect to the bridge occur in a symmetrical pattern. A few skeletons (Plate 2, Fig. 3) with three struts that meet at an apex are here placed in *S. loperi* as variants or teratoid morphologies.

Specimens of *S. loperi* are relatively abundant at Site 693, but are less common in the Santonian and early Campanian of the Arctic. Only eight specimens were counted in the original Devon Island study, and it was not observed at Horton River or in a recent reexamination of samples from the Ural Federal District.

Genus ***Umpiocha*** McCartney et al., 2011b.

Type species: *Umpiocha umpiana* McCartney et al., 2011b.

Umpiocha jeletzkyi McCartney et al., 2011b

Plate 2, Fig. 9

2011b. *Umpiocha jeletzkyi* McCartney et al., pl. 2, Figs. 16; pl. 8, Figs. 6–10

Discussion: Only a single specimen of this rare species was observed in LM in this study (Plate 2, Fig. 9). This specimen has only two limbs preserved, seen in lateral view looking down the bridge axis. The two limbs span 65 µm across and extend 40 µm beneath the point where the struts connect to the bridge; this size range is consistent with the skeletons observed previously.

Umpiocha umpiana McCartney et al., 2011b

Plate 6, Figs. 7–9

2011b. *Umpiocha umpiana* McCartney et al., pl. 2, Figs. 6, 9, 14–15, 18; pl. 8, Figs. 1–5

Discussion: *Umpiocha* is characterized by a short apical bridge and four long limbs that curve and come close to meeting again beneath the apical structure. Limbs are separated into many short substruts by two rows of spines similar to those of *G. tapiae*. Some spines may terminate in pike-and-spine devices, the pattern and nature of which is poorly understood as few specimens have been available for SEM examination. It is extremely difficult to resolve the skeletons' complex structure in LM. Some specimens (McCartney et al., 2011b) have limbs composed of many substruts that curve completely beneath the apical bridge with terminal spines that come close to touching, while others have less well-developed limbs (Plate 6, Figs. 7 and 8). This unusual species warrants the collection of more specimens and further study, particularly with the SEM.

Genus ***Variramus*** McCartney et al. ex McCartney et al., 2011b

Type species: *Variramus aculeifera* (Deflandre, 1944) McCartney et al., 1990.

Variramus aculeifera (Deflandre) McCartney et al., 1990

Plate 3, Figs. 5–12; Plate 6, Figs. 10–12
1940. "Forme cornuoide de *Dictyocha* spec. ind.", Deflandre, p. 509, Fig. 11
1944. *Cornua aculeifera* Deflandre, p. 464, Figs. 8–9
1950. *Cornua aculeifera* Deflandre, p. 60, Fig. 160–162
1990. *Variramus aculeifera* (Deflandre) McCartney et al., pl. 1, Figs. 7, 9; pl. 2, Figs. 1, 5, 10; pl. 3, Fig. 6
2011b. *Variramus aculeifera* (Deflandre) McCartney et al., pl. 3, Figs. 10–15

Discussion: This species is characterized by extreme variability. Skeleton has a flattened shape with a central area considered as part of an apical structure that comprises a bridge made of at least three elements. Intersections where bridge elements connect are triple junctions, with the third member being an element or a spine. Elements may bifurcate into additional elements, but usually terminate into small spines that can have various orientations. Connected to the bridge are additional elements analogous to the struts of more modern silicoflagellate morphologies. The struts are generally oriented in radial directions away from the bridge, and together with the bridge elements form patterns similar to the Neogene "*pseudofibula* plexus" group of morphologies (see McCartney and Wise, 1990), and include pseudofibulid (Plate 3, Figs. 9, 10), notabilid (Plate 3, Figs. 5, 7, 9) and varianid (Plate 3, Fig. 12) forms.

Struts and other elements may bear small spines at various locations and angles, but are often unornamented. Struts may bifurcate into additional elements (Plate 3, Figs. 7, 11), but more often end in two small terminal spines. Terminal spines may both occur in the general plane of the skeleton, or may be rotated with respect to that plane, and may or may not be of similar size. The type of terminations varies from one element to another, and they occur in no apparent order or sequence, although similar terminations may be present on most or all of the struts. The overall skeleton has no specific symmetry, although it is usually slightly elongated in the direction of the bridge.

Variramus aculeifera is distinguished from *S. loperi* by the small terminal spines, lack of consistent pikes, and a more general lack of symmetry. While both taxa show considerable variability, *V. aculeifera* is more variable in the number and distribution of the struts and the variety of terminations. *S. loperi* usually has four or five struts with pikes that have locations positioned as with the corners of a rectangle or pentagon, while *V. aculeifera* generally has five, six or more struts of varying length, which also tend to bifurcate more readily. Four-strutted skeletons of *V. aculeifera* occur, and resemble Deflandre's (1944, fig. 8) illustration. However, the other two specimens illustrated by Deflandre (1944, fig. 9 and 1940, fig. 11), which have a less organized arrangement of skeletal elements and spines are more common.

A few fragmentary specimens were observed in LM to have elements that rise above the general structure of the skeleton. In some cases, these vertical elements appear to establish a higher level – a "second story" – and in a few cases had sabaton or pike-and-spine structures. However, such fragments were few, inconsistent, and not observed in SEM. The *V. aculeifera* group of morphologies requires further study.

This taxon is more abundant in ODP Site 693 samples than those from Devon Island. Specimens from the former locality also tend to be larger in size, as shown in Plate 3.

Variramus gleseri McCartney et al., 2011b

1959. *Cornua aculeifera* Deflandre; Gleser, p. 109, Fig. 11

1990. *pro parte, Variramus aculeifera* (Deflandre) McCartney et al., pl. 4, Fig. 7

2011b. *Variramus gleseri* McCartney et al., pl. 2, Figs. 12 and 13

Discussion: A skeleton of this configuration was the only illustrated specimen (Gleser, 1959) between the original description of *C. aculeifera* by Deflandre, 1940, Deflandre, 1944 and Deflandre, 1950 and the study by McCartney et al. (1990). McCartney et al. (2011b) recognized this morphology as a separate species, but it is rarely observed in the Devon Island succession. Specimens generally bear small spines of no particular orientation on the skeletal elements, and a short simple bridge.

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