

Morphological variation of pike structures in *Corbisema* (Silicoflagellata) from the Early and Middle Eocene

Kevin McCartney*

Department of Environmental Studies & Sustainability, University of Maine at Presque Isle, Presque Isle, ME 04769, USA; *kevin.mccartney@maine.edu

Kenta Abe

Graduate School of Science & Engineering, Yamagata University, 1-4-12 Kojirakawa-machi, Yamagata 990-8560, Japan

Richard W. Jordan

Department of Earth & Environmental Sciences, Faculty of Science, Yamagata University, 1-4-12 Kojirakawa-machi, Yamagata 990-8560, Japan

Jakub Witkowski

Geology & Palaeogeography Unit, Faculty of Geosciences, University of Szczecin, ul. Mickiewicza 18, 70-383 Szczecin, Poland

Manuscript received 27th March, 2015; revised manuscript accepted 3rd September, 2015

Abstract Early to Middle Eocene silicoflagellates from three localities (Denmark, Russia and the Arctic Ocean) exhibit a wide range of morphological diversity in their pikes, including unusual distal terminations that have not been previously reported. Some of the *Corbisema* possess pikes that are rotated consistently in the same direction. Other specimens show a sharp distal change of direction, generally away from the centre of the cell, or a distal termination similar to a sabaton. In some cases, the skeletal morphology and presence or lack of pikes provides information to suggest the double skeleton configuration of the species.

Keywords silicoflagellates, morphology, *Corbisema*, Eocene, Denmark, Russia, Arctic Ocean

1. Introduction

Corbisema is of special importance among silicoflagellates as the only genus to survive the Cretaceous-Palaeogene transition, and thus is the ancestor of all Cenozoic silicoflagellates (McCartney *et al.*, 2010a). *Corbisema* has a skeletal morphology comprising a basal ring of three sides and corners, with a simple apical structure made up of three struts that meet at an apex (Figure 1). Despite a generally simple skeletal design, there is considerable morphological diversity. For some species, the basal sides are more-or-less linear and meet at sharp corners, where a basal spine completes a triple junction. Other skeletons have rounded corners that lack spines. There is also considerable diversity in skeleton size, or presence/absence of basal pikes or apical plate/ring.

Silicoflagellates are most commonly photographed in apical view (Figure 1a), which obscures the pikes that are best observed in abapical view (Figure 1b). Pikes are an important and understudied aspect of *Corbisema*, and silicoflagellate skeletal design in general. Terms such as ‘ancillary spines’ (Martini, 1977), ‘accessory spines’ (Mandra, 1960) and ‘support spines’ (Gleser, 1959) have been used in older literature. The term ‘pike’ was first used by Bukry (1976), and is here restricted to basal structures.

Spines and pikes are quite distinct. Spines, which often occur at the corners of the basal ring and may be present on the apical structure, are oriented radially, with respect to the centre of the silicoflagellate cell. Spines are linear, or nearly so, and in non-aberrant skeletons are always of similar design on a given specimen.

Pikes attach to the abbasal or interior surfaces of the basal sides and point in some abapical direction. Pikes on an individual specimen are often similar, but may differ, and terminations are generally rounded, rather than pointed, as on the distal ends of spines. Spines and pikes also appear to serve separate functions. The purpose of the spines is uncertain; van Tol *et al.* (2012) suggested that they protect against predation, but Sargeant *et al.* (1987; see also McCartney *et al.*, 2010a) suggested that spines might retard settling out of the photic zone. Takahashi *et al.* (2009) observed that the spine length can vary with environmental factors. Pikes, on the other hand, appear to hold together two members of a double skeleton (also known as doublets; Moestrup & Thomsen, 1990; McCartney *et al.*, 2014a, 2015a).

Although pikes occur in most silicoflagellate genera, a number of species in each genus lack pikes. We believe the paired skeletons of a doublet that lacks pikes would

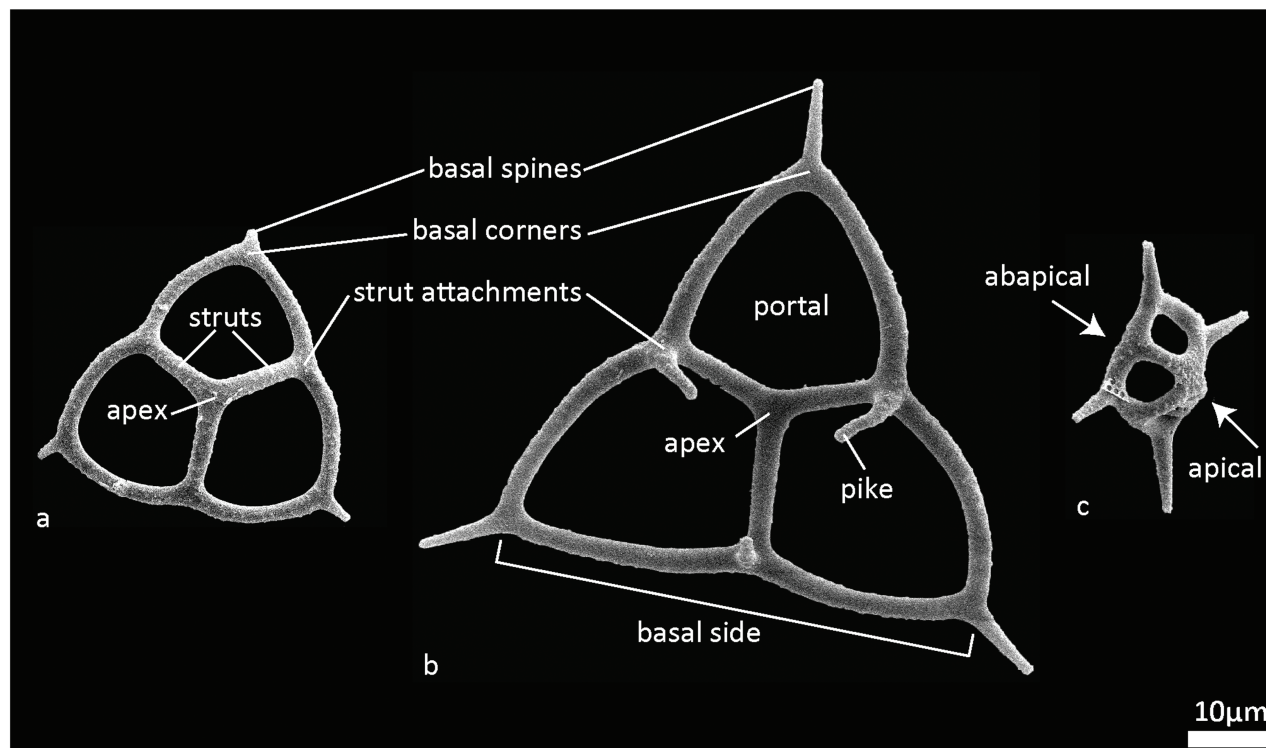


Figure 1: Descriptive terminology for silicoflagellate skeletal morphology: (a) *Corbisema apiculata* (Lemmermann) in apical view, (b) *C. apiculata* (Lemmermann) in abapical view, (c) *Dictyocha* sp. with four basal sides in oblique apical view

be connected at the abbasal surfaces of basal elements and spines, and held together by organic material; such a doublet is known as the corner-aligned configuration (McCartney *et al.*, 2015a, b). A *Corbisema* doublet without pikes and with corners aligned was illustrated by Bachmann (1970, pl.1, fig.17). Modern *Dictyocha* and *Stephanocha* (previously known as *Distephanus*, see Jordan & McCartney, 2015) are also corner-aligned, but have pikes that are rotated away from the strut attachments, and proceed into the centre of the opposing skeleton in fairly close proximity to the strut of the paired skeleton (McCartney *et al.*, 2014a).

Recent documentation of *Corbisema* double skeletons in the Cretaceous (McCartney *et al.*, 2010b) and Eocene (McCartney *et al.*, 2015a, b) shows two distinct configurations of doublets in the fossil record. Most known fossil doublets, and all of the modern examples, have basal corners and spines of paired skeletons aligned. The known fossil skeletons of *Corbisema hastata* (Lemmermann) Frenguelli have one of the paired skeletons rotated 180° on the long axis, so that corners are aligned with the opposite basal sides of the other, in a Star-of-David configuration (McCartney *et al.*, 2010b, 2015a, b).

Both double skeleton configurations, the corner-

aligned and Star-of-David, are known among Palaeogene silicoflagellates. The corner-aligned configuration has not been observed in the Cretaceous, with the only known *Corbisema* double skeleton of this age being in the Star-of-David configuration (McCartney *et al.*, 2010b). In the Cenozoic, *Corbisema* of the Star-of-David configuration has been reported by McCartney *et al.* (2015a - Paleocene and Eocene; 2015b - Eocene), and corner-aligned double skeletons of this genus have been observed by Bachmann (1970 - Oligocene), Bukry (1987 - Eocene), Dumitrică (1974 - Miocene) and McCartney *et al.* (2015a - Eocene). Little is known about silicoflagellate doublets and there is inadequate information to enable identification of the doublet configuration through examination of an individual skeleton. In this study, we suggest that the shape and orientation of the pike may be helpful in such determinations.

2. Materials and methods

Specimens examined in this study came from the following sources:

(1) Lower Eocene material from Mors, Denmark, curated in the Friedrich Hustedt Collection at the Alfred Wegener Institut für Polar- und Meeresforschung, Bremerhaven, Germany (accession number E1758). No exact sampling

site or level are available for this sample, however, the diatom and silicoflagellate assemblages strongly suggest that it comes from one of the Fur Formation outcrops of northern Denmark (*e.g.* Pedersen, 2008);

(2) Kamichev or Kamischev, presumed to be Kamyshlov, Sverdlovsk District, Russia, Lower Eocene (Oreshkina *et al.*, 2004). A small subsample of this material was received from the Natural History Museum, London. It represents part of the original materials from this locality distributed in Europe during the early 20th Century (see *e.g.* Ross & Sims, 1985);

(3) Lomonosov Ridge in the central Arctic Ocean was drilled during Integrated Ocean Drilling Program (IODP) Leg 302 (also known as the Arctic Coring Expedition - ACEX). The sample examined here (IODP 302-4A-11X-2W, 63-64cm) is from the Middle Eocene (Stickley *et al.*, 2008; Onodera & Takahashi, 2009).

The precise localities for the Mors and Kamyshlov samples are unknown, and detailed studies of the silicoflagellates are not available (but see Perch-Nielsen, 1976, for the Fur Formation, and Locker & Martini, 1987, for Kamyshlov). Because these are isolated samples that have not been studied in sufficient detail to enable confident determination of species, and since the emphasis of this paper is on pike diversity rather than taxonomy, species identification is tentative.

3. Pikes of Eocene *Corbisema*

Pikes of *Corbisema* from the Lower Eocene Mors material show considerable variability. Several taxa present, including two-, three- and four-sided specimens, lack pikes. *Corbisema* without pikes are generally of small size, but have long basal spines (Pl.1, figs 1, 2). *Corbisema* and several *Dictyocha* doublets, observed from the Mors sample (McCartney *et al.*, 2015a), and known *Naviculopsis* specimens (see McCartney *et al.*, 2015a), suggest these taxa formed corner-aligned double skeletons.

Only some of the *Corbisema* possess pikes, but these display considerable diversity, and sometimes vary even on one individual. Pikes may be linear in shape and point laterally or abapically towards the centre of the cell (Pl.1, fig.3), may be oriented perpendicular to the basal plane (Pl.1, figs 4-6), or may curve in various directions (Pl.1, figs 6, 7). Pike size also varies considerably, from small (Pl.1, figs 3, 9, 10) to quite prominent (Pl.1, fig.11). Distal terminations are rounded and may be slightly bulbous.

In some specimens, one or more sides bear a small pike, whereas other sides lack a pike.

Pikes in most *Corbisema* specimens are located abapically, below the strut attachment, but may be rotated from that position. In any discussion of a rotation direction with respect to the basal corners, we present the rotation from an apical view perspective. For those pikes that are rotated from the position of the strut attachment, nearly all observed in this study show a dextral rotation (Pl.1, figs 9, 10; Pl.2, figs 3, 8, 12 (right specimen)). Rotation may be slight or pronounced, and not necessarily consistent from one pike attachment to the next. Some specimens show both rotated and unrotated pikes (Pl.2, fig.1). Perch-Nielsen (1975, pl.2, fig.16) illustrated a similar specimen from the Cretaceous.

Many *Corbisema* skeletons observed from abapical view have pikes that trend abapically in a position that would likely interfere with pikes where the paired skeletons are corner-aligned (Pl.1, figs 3-5; Pl.2, figs 2-4). A single double skeleton of *Corbisema* in the Star-of-David configuration was observed in the ACEX material (McCartney *et al.*, 2015b) that has prominent pikes that curve into the area of the apical portal of the opposing skeleton. Doublets of *Corbisema* with similar prominent pikes are most likely also of the Star-of-David configuration (see McCartney *et al.*, 2010b, 2015a, b for photographs of double skeletons).

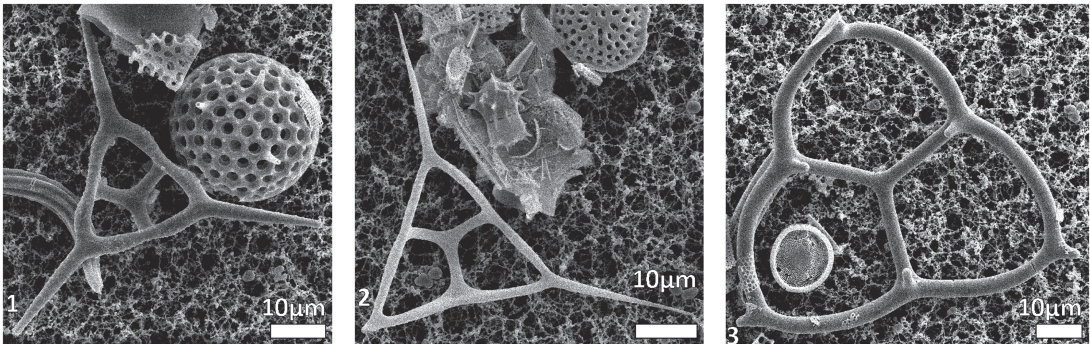
4. Pikes with unusual terminations

We observed specimens with pikes of unusual L- or T-shaped terminations, abundant in the Mors material, but also present in the ACEX and Kamyshlov samples, and illustrate these in Plate 2. These terminations are fragile and seldom preserved on all pikes, so we are unable to determine whether the occurrence is consistent. Usually, these pikes are $\sim 10\mu\text{m}$ long and narrow, and trend in a direction perpendicular to the basal plane. Pikes with L-shaped terminations (Pl.2, figs 3-11, 13) turn at nearly right-angles away from the cell centre. The distal portion of the pike appears to be generally parallel to the associated strut, if seen in apical or abapical view.

Pikes with T-shaped terminations (Pl.2, figs 14, 15) intersect a more-or-less perpendicular component that proceeds laterally in both directions. As with the L-shaped terminations, the distal portion is aligned with the associated strut. In some cases, the distal component is foot-shaped,

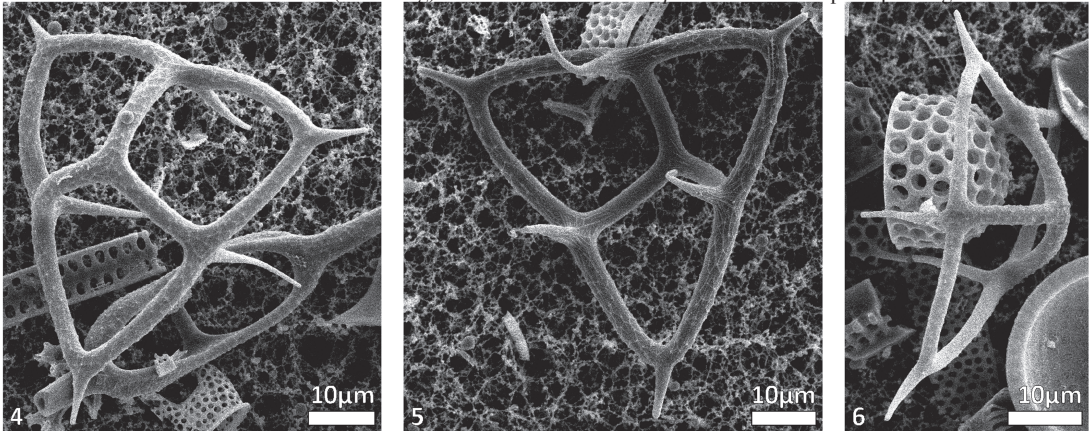
Plate 1

SEM images of *Corbisema* showing basal structures in abapical view, except 4 (apical view) and 6 (lateral view)
All specimens from Mors

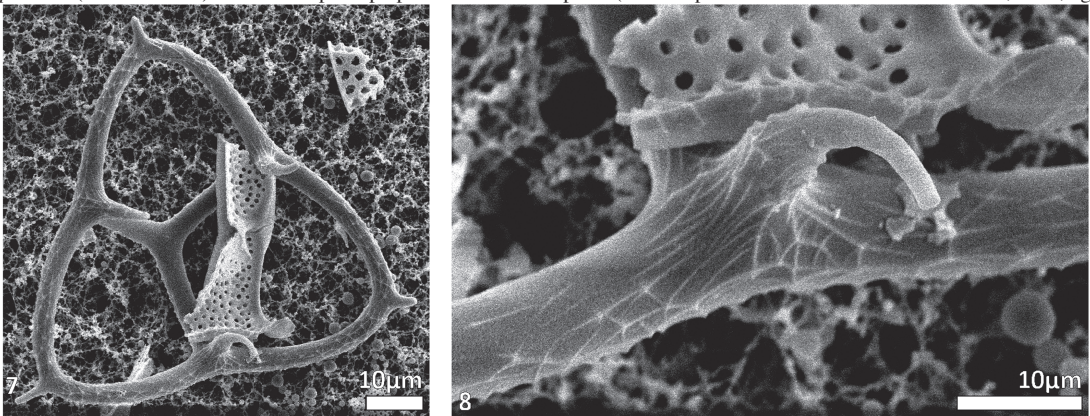


C. triacantha (Ehrenberg) Hanna

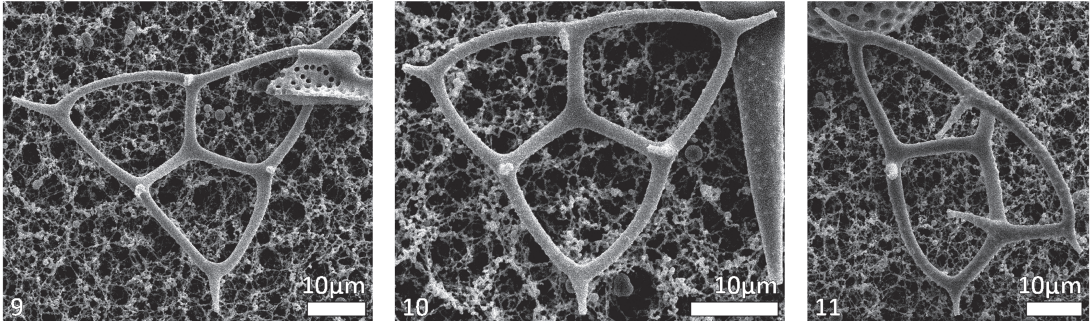
C. apiculata with short pikes pointing to centre of cell



C. apiculata (Lemmermann) Hanna with pikes perpendicular to basal plane (similar specimen illustrated in Lemmermann, 1901, fig.20)



C. apiculata with two pikes curved away from centre of cell (8 = detail of pike and surface ornamentation illustrated in 7)



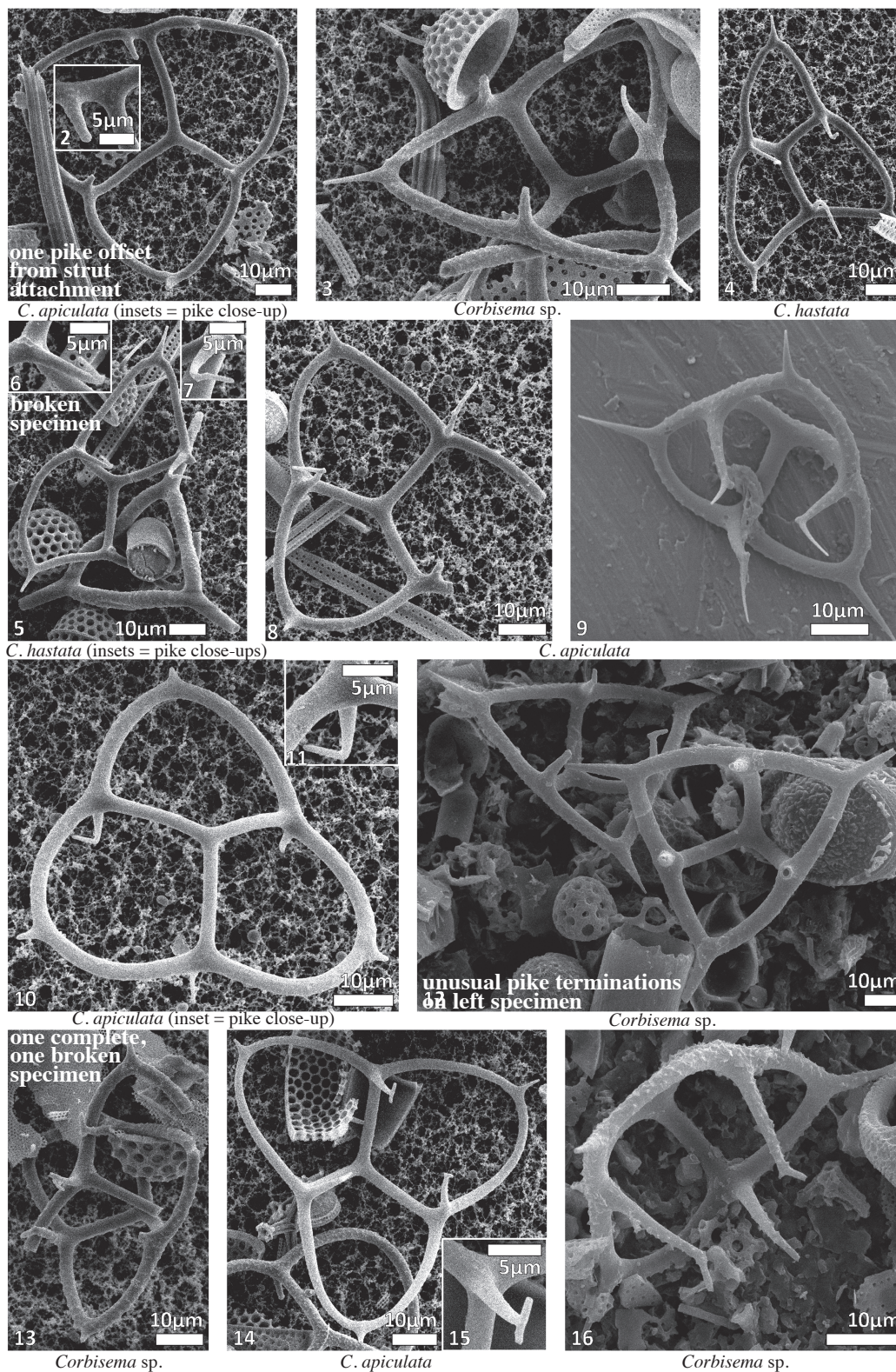
Corbisema sp. with pikes slightly rotated

C. hastata (Lemmermann) Frenguelli

Plate 2

SEM images of *Corbisema* showing pikes with unusual terminations (e.g. L-shaped in 13; T-shaped in 14, 15; sabaton-like in 16) in abapical view, except 9, 16 (oblique abapical) and 10, 11 (apical view)

1-8, 10, 11, 13-15 from Mors; 9 from Kamyshlov; 12, 16 from ACEX



with a shorter heel and longer foot. Observed specimens with foot-shaped termination consistently show the longer portion pointing away from the cell centre (Pl.2, figs 9, 12, 13). Distal pikes on specimens from ACEX material may have sabaton-like terminations (see McCartney *et al.*, 2011a, b, 2014b). These terminations occur at the ends of long and linear pikes, with the termination pointing abapically (Pl.2, fig.16).

5. Discussion

In this study, specimens of *Corbisema* with basal rings of small diameter generally lack pikes and have a flat basal ring and long basal spines. Such a flat abbasal plane would increase the surface contacts between paired skeletons in a corner-aligned configuration. Double skeleton specimens of four-sided *Dictyocha* have been observed in the Mors material, in the corner-aligned configuration (McCartney *et al.*, 2015a). These have a planar abbasal surface, and the presence of long spines strengthens the hypothesis that *Corbisema* without pikes likely formed double skeletons of the corner-aligned configuration. A double skeleton of *Corbisema* that is believed to lack pikes has been observed by McCartney *et al.* (2015a) and is similar to a specimen illustrated by Bachmann (1970).

McCartney *et al.* (2015b) illustrated a *Corbisema* doublet from ACEX in the Star-of-David configuration that has prominent pikes that curve towards the middle of the apical portals. This specimen is documented with 14 SEM photographs in the supplemental materials included in McCartney *et al.* (2015a). Similarity in size and shape of the Mors and ACEX specimens presented here to this ACEX doublet specimen suggests that these skeletons are probably also associated with Star-of-David doublets (see McCartney *et al.*, 2015a).

Corbisema skeletons with slightly rotated pikes generally have a medium-sized ($\sim 40\mu\text{m}$; see Pl.1, figs 9, 10), flat basal ring; the spines are also of medium size. Consistent rotation in a dextral direction, when seen in apical view, could provide a means for two identical skeletons to form a corner-aligned doublet, without the pikes interfering with one another. While the dextrally rotated pikes, and the occurrence of a flat basal plane, may suggest a corner-aligned double skeleton, the evidence is not sufficient to make a strong prediction.

Skeletons of *Corbisema* with unusual terminations are enigmatic. Several explanations for these terminal features

are plausible. In general, the length and position of the centrally-located pikes often suggest that a Star-of-David doublet is probable, since the paired pikes of a corner-aligned double skeleton would appear to occupy the same space. If the doublet is in the Star-of-David configuration, the pikes may extend into the region of the large portals on the adjacent skeleton, and thus might help support the cell boundary in that portion of the apical cell-surface. Alternatively, the long pikes and cross-components may provide attachment points for organic material that would hold the paired skeletons together. A third explanation could be that sabaton-like terminations, which are typical of some Cretaceous species that lack a basal ring, may be the result of a reversion to ancestral skeletal morphologies during times of environmental stress, as proposed by Guex (2006) and discussed by McCartney *et al.* (2010a).

6. Conclusions

Pikes have been overlooked features of silicoflagellate skeletons. Several new observations on *Corbisema* pike structure are made: 1) some small skeletons may possess flat basal rings and lack pikes; 2) some skeletons have prominent curved pikes; 3) pikes may rotate slightly in a dextral direction, if seen in apical view, although the pike location may not be consistent on all basal sides; 4) pikes may deviate from the general trend to form a sharp angle in the distal direction; and 5) pikes may bear sabaton-like terminations.

Pikes of *Corbisema* show considerable diversity of shape and size in a number of Eocene samples. Some pikes can show a consistent rotation away from the strut attachment, or have unusual distal terminations. The shape and placement of the pikes on individual skeletons may have potential use in determining doublet configuration.

Acknowledgements

We thank the Integrated Ocean Drilling Program for supplying the ACEX material, Friedel Hinz (the Hustedt Collection, Bremerhaven) for sending the Mors material, and Patricia Sims (the Natural History Museum, London) for kindly sharing a small subsample of the Kamyshev material. We are also grateful to Elisa Malinverno and David M. Harwood, who reviewed the manuscript and made useful comments.

References

- Bachmann, A. 1970. Silicoflagellaten aus dem oberösterreichischen Egerien (Oberoligozän). *Verhandlungen der Ge-*

- ologischen Bundesanstalt, **2**: 275-305.
- Bukry, D. 1976. Silicoflagellate and coccolith stratigraphy, southeastern Pacific Ocean, Deep Sea Drilling Project Leg 34. *Initial Reports of the DSDP, Scientific Results*, **34**: 715-735.
- Bukry, D. 1987. Eocene siliceous and calcareous phytoplankton, Deep Sea Drilling Project Leg 95. *Initial Reports of the DSDP, Scientific Results*, **95**: 395-415.
- Dumitrică, P. 1974. *Silicoflagelatele Miocene din Romania*. Teza de doctorat, Universitatea din Bucuresti, Facultatea de Geologie-Geografie, Bucuresti: 224pp.
- Gleser, Z.I. 1959. Nekotorye novye dannye o semeistve Vallacertaceae Deflandre (Silicoflagellatae) [Some new data on the Family Vallacertaceae Deflandre (Silicoflagellatae)]. *Informatsionnyi Sbornik*, **10**: 103-113.
- Guex, J. 2006. Reinitialization of evolutionary clocks during sublethal environmental stress in some invertebrates. *Earth and Planetary Science Letters*, **242**: 240-253.
- Jordan, R.W. & McCartney, K. 2015. *Stephanocha* nom. nov., a replacement name for the illegitimate silicoflagellate genus *Distephanus* Stöhr. *Phytotaxa*, **201**: 177-187.
- Lemmermann, E. 1901. Silicoflagellatae. *Deutsche Botanische Gesellschaft*, **19**: 247-271.
- Locker, S. & Martini, E. 1987. Silicoflagellaten aus einigen russischen Paläogen-Vorkommen. *Senckenbergiana Lethaea*, **68**: 21-67.
- Mandra, Y.T. 1960. Fossil silicoflagellates from California, U.S.A. *International Geological Congress, XXI Session, Norden, 1960, Report*, **Pt.6**: 77-89.
- Martini, E. 1977. Systematics, distribution and stratigraphical application of silicoflagellates. In: A.T.S.C. Ramsey (Ed.). *Oceanic Micropaleontology, Volume 2*. Academic Press, London: 1327-1343.
- McCartney, K., Abe, K., Harrison, M.A., Witkowski, J., Harwood, D.M., Jordan, R.W. & Kano, H. 2015a. Silicoflagellate double skeletons in the fossil record. *Marine Micropaleontology*, **117**: 65-79.
- McCartney K., Abe, K., Witkowski, J. & Jordan, R.W. 2015b. Two rare silicoflagellate double skeletons of the Star-of-David configuration from the Eocene. *Journal of Micropaleontology*, **34**: 97-99.
- McCartney, K., Harwood, D.M. & Witkowski, J. 2010b. A rare double skeleton of the silicoflagellate *Corbisema*. *Journal of Micropaleontology*, **29**: 185-186.
- McCartney, K., Witkowski, J. & Harwood, D.M. 2010a. Early evolution of the Silicoflagellates during the Cretaceous. *Marine Micropaleontology*, **77**: 83-100.
- McCartney, K., Witkowski, J. & Harwood, D.M. 2011a. Late Cretaceous silicoflagellate taxonomy and biostratigraphy of the Arctic Margin, Northwest Territories, Canada. *Micropaleontology*, **57**: 61-86.
- McCartney, K., Witkowski, J. & Harwood, D.M. 2011b. Unusual early assemblages of Late Cretaceous silicoflagellates from the Canadian Archipelago. *Revue de Micropaléontologie*, **54**: 31-58.
- McCartney, K., Witkowski, J. & Harwood, D.M. 2014b. New insights into skeletal morphology of the oldest known silicoflagellates: *Variramus*, *Cornua* and *Gleserocha* gen. nov. *Revue de Micropaléontologie*, **57**: 75-91.
- McCartney, K., Witkowski, J., Jordan, R.W., Daughbjerg, N., Malinverno, E., van Wezel, R., Kano, H., Abe, K., Scott, F., Schweizer, M., Hallegraeff, G.M. & Shiozawa, A. 2014a. Fine structure of silicoflagellate double skeletons. *Marine Micropaleontology*, **57**: 75-91.
- Moestrup, Ø. & Thomsen, H.A. 1990. *Dictyocha speculum* (Silicoflagellata, Dictyochyaceae), studies on armoured and unarmoured stages. *Biologiske Skrifter*, **37**: 1-22.
- Onodera, J. & Takahashi, K. 2009. Taxonomy and biostratigraphy of middle Eocene silicoflagellates in the central Arctic Basin. *Micropaleontology*, **55**(2-3): 209-248.
- Oreshkina, T.V., Aleksandrova, G.N. & Kozlova, G.E. 2004. Early Eocene marine planktonic record of the East Urals margin (Sverdlovsk region): biostratigraphy and paleoenvironments. *Neues Jahrbuch für Geologie und Paleontologie*, **234**: 201-222.
- Pedersen, S.A.S. 2008. Palaeogene diatomite deposits in Denmark: geological investigations and applied aspects. *Geological Survey of Denmark and Greenland Bulletin*, **15**: 21-24.
- Perch-Nielsen, K. 1975. Late Cretaceous to Pleistocene silicoflagellates from the southern southwest Pacific, DSDP Leg 29. *Initial Reports of the DSDP*, **29**: 677-721.
- Perch-Nielsen, K. 1976. New silicoflagellates and a silicoflagellate zonation in north European Palaeocene and Eocene diatomites. *Bulletin of the Geological Society of Denmark*, **25**: 27-40.
- Ross, R. & Sims, P.A. 1985. Some genera of the Biddulphiaceae (diatoms) with interlocking linking spines. *Bulletin of the British Museum (Natural History), Botany Series*, **13**(3): 277-381.
- Sarjeant, W.A.S., Lacalli, T. & Gaines, G. 1987. The cysts and skeletal elements of dinoflagellates: speculations on the ecological causes for their morphology and development. *Micropaleontology*, **33**: 1-36.
- Stickley, C.E., Koç, N., Brumsack, H.-J., Jordan, R.W. & Suto, I. 2008. A siliceous microfossil view of middle Eocene Arctic environments: A window of biosilica production and preservation. *Paleoceanography*, **23**: PA1S14, doi: 10.1029/2007PA001485.
- Takahashi, K., Onodera, J. & Katsuki, K. 2009. Significant populations of seven-sided *Distephanus* (Silicoflagellata) in the sea-ice covered environment of the central Arctic Ocean, summer 2004. *Micropaleontology*, **55**: 313-325.

- van Tol, H.M., Irwin, A.J. & Finkel, Z.V. 2012. Macroevolutionary trends in silicoflagellate skeletal morphology: the costs and benefits of silicification. *Paleobiology*, **38**(3): 391-402.