



Research paper

Silicoflagellate double skeletons in the geologic record



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ABSTRACT

Modern silicoflagellates are known to produce double skeletons, which are considered as pre-division stages; members of modern doublets are aligned at basal corners, using either pikes or organic material between the abbasal surfaces of the basal rings to hold together. In contrast, fossil doublets from the Cretaceous and Paleogene often have the corners of each skeleton oriented between those of the paired member in what is known as the Star-of-David configuration. Until recently, however, virtually nothing was known about the fine structure of fossil double skeletons. As a follow-up to our recent study on extant silicoflagellate doublets, we present a compilation of data on the fossil record of silicoflagellate double skeletons, with particular focus on the Cretaceous and Paleogene.

Fossil silicoflagellate double skeleton specimens are extremely rare, with the oldest being from the late Santonian–early Campanian. In order to test whether silicoflagellates may have produced doublets prior to that time, we have constructed three-dimensional computer models of silicoflagellate double skeleton morphologies. Our findings indicate that doublet formation was part of the silicoflagellate reproductive cycle already since early in the evolutionary history of the group, before the development of the basal ring. Two distinct double skeleton configurations developed at some point in this evolution, with the Star-of-David group likely becoming extinct in the Oligocene, and the corner-aligned group represented by the Neogene and modern silicoflagellates. At present, the doublet configuration in fossil silicoflagellates can only be determined confidently with paired skeletons, but the occurrence, position and orientation of pikes may offer useful clues to interpret the doublet configuration from single skeletons. Unusual pike morphologies of some silicoflagellates from the Eocene strongly suggest a Star-of-David configuration. Silicoflagellate skeletal morphologies with pikes appear to be less abundant in the fossil record as double skeletons, and may disassociate more readily than morphologies that lack pikes and are instead held together by organic material between the basal rings.

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1. Introduction

Silicoflagellates (Class Dictyochophyceae P.C. Silva, 1980) are marine unicellular heterokonts that during a portion of their life cycle possess an opaline siliceous skeleton composed of hollow rods and ranging in size from ~10 to ~100 μm. Cenozoic skeletons generally include a basal ring of geometric shape and an apical structure that consists of elements interconnecting at triple junctions. Silicoflagellate biology is not well understood, but studies of natural and cultured populations show multiple life cycle stages, the majority of which are non-skeleton-bearing cells (Moestrup and Thomsen, 1990; Daugbjerg and Henriksen, 2001). For most of their history of study (Loeblich et al., 1968), biologists and micropaleontologists

identified only skeleton-bearing silicoflagellates, and thus their taxonomy is based entirely on skeletal morphology.

An understudied aspect of silicoflagellate biology and paleontology is the double skeleton (also known as a doublet or paired skeleton), where the second (daughter) skeleton is formed prior to mitotic division. In a recent paper, McCartney et al. (2014c) provided the first detailed examination of double skeleton fine structure in all modern silicoflagellate genera and noted two distinct basal ring morphologies that may relate to separate strategies for holding the paired skeletons together prior to division. Modern *Dictyocha* Ehrenberg and *Stephanocha* McCartney and Jordan (previously known as *Distephanus* Stöhr; see Jordan and McCartney, 2015) are held together by a zig-zag basal ring structure that projects pikes into the cellular domain of the paired skeleton (Moestrup and Thomsen, 1990), which is a possible adaptation to allow easy separation of the two skeletons after cellular division (McCartney et al., 2014c). Skeletons that lack pikes, such as the

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modern genus *Octactis* Schiller, do not show a zig-zag pattern in the basal ring and may be held together in a doublet by a strong organic adhesive (most likely of polysaccharide nature as seen in haptophytes and diatoms; e.g., Hirokawa et al., 2013 and Wustman et al., 1997, respectively) at abbasal surfaces beneath the basal corners.

Double skeletons of fossil silicoflagellates are very rare, most likely resulting from disassociation *in vivo*, separation during settling and burial, or due to aggressive sample preparation techniques. A list of fossil double skeletons known prior to this study is included in Table 1. From these reports we note that all known fossil double skeletons of *Dictyocha*, *Distephanopsis* Dumitrică, *Stephanocha*, and *Naviculopsis* Frenguelli, as well as all Neogene *Corbisema* Hanna, are configured with basal polygons superimposed in a “corner-aligned configuration” (McCartney et al., 2014c), as illustrated in Fig. 1A. In contrast, some Eocene *Corbisema* and all known doublets from the Cretaceous align basal corners with the middle of basal sides of the paired skeleton, in what is known as the “Star-of-David configuration” (Schulz, 1928; McCartney et al., 2010a,b, 2014a,d), as illustrated in Fig. 1B.

In the present paper we (1) present new light- and scanning electron microscope observations (LM and SEM, respectively) of fossil double skeletons from the Paleogene, (2) use physical and computer models of some Cretaceous taxa to interpret their as yet unknown double skeletons, and (3) argue that double skeleton configurations have important phylogenetic implications for silicoflagellate evolution in general, and the relationships and systematics of *Corbisema* in particular.

2. Materials and methods

2.1. Sources and numbers of specimens

Single-skeleton specimens of silicoflagellate taxa from the Albian to Santonian that were the basis for construction of computer models (Figs. 2–4) come from:

- a) Ocean Drilling Program (ODP) sample 113-693B-19X-4, 77–78 cm (Fig. 2A; of early to mid-Albian age) from Weddell Sea, Southern Ocean. For details of stratigraphy see Gersonde and Harwood

(1990) and McCartney et al. (2014b). The silicoflagellates in this sample were documented previously by McCartney et al. (1990, 2014b).

- b) Samples EF0401 (Figs. 2G, 3A, H; of presumed Santonian age), EF0102 (Fig. 4A) and EF0103 (Fig. 4F; of early Campanian age) from Eidsbotn Graben, Colin Archer Peninsula, Devon Island, Nunavut, Arctic Canada. For details of stratigraphy consult Chin et al. (2008) and Witkowski et al. (2011). Silicoflagellates in these samples were documented previously by McCartney et al. (2010b, 2014b).

A total of 19 double skeletons of fossil silicoflagellates from Paleogene successions are examined in this study, including twelve in SEM and seven in LM. Only skeletons of three- and four-sided taxa were available for study. These came from the following materials:

- a) Early Eocene material labeled as Mors, Denmark (Figs. 5A–O; 6A–B, E–K; 7B–C, E–G; 10A–D, F–J), currently curated in the Friedrich Hustedt Diatom Study Centre at the Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung (AWI), Bremerhaven, Germany (accession number: E1758). Exact sampling site and level are not available; however, diatom and silicoflagellate assemblages strongly suggest that this sample comes from one of the Fur Formation outcrops of northern Denmark (Homann, 1991; Fenner, 1994; Pedersen, 2008).
- b) Middle Eocene sediments from the Lomonosov Ridge in the central Arctic Ocean (Figs. 6C–D; 8A–H; 10E) cored by the Integrated Ocean Drilling Program (IODP) Expedition 302 (commonly referred to as ACEX – Arctic Coring Expedition). These include samples 302-M0002A-54X-1, 2–3 cm (depth: 230.02 meters below sea floor [mbsf]), 302-M0004A-9X-1, 2–3 cm (287.32 mbsf), and 302-M0004A-11X-3, 3–4 cm (300.34 mbsf). Silicoflagellates from these samples were documented previously by Onodera and Takahashi (2009).
- c) Middle Eocene double skeleton of *Dictyocha* (Fig. 7A) from Falkland Plateau of southwest Atlantic Ocean, Deep Sea Drilling Project (DSDP) Sample 71-512-14-3, 49–51 cm (55.0 mbsf), assigned to the middle Eocene silicoflagellate *Dictyocha grandis* Range Zone of

Table 1
A listing of all previously illustrated fossil silicoflagellate double skeletons. The Dumitrică (1967) illustrations are also listed in Dumitrică (1974), and all Dumitrică illustrations are included in Dumitrică (2014), which includes line drawings of other specimens that are listed in this table. Those marked by “*” are in the Star-of-David configuration.

Author	Year	Illustration	Genus	Age	Illustration
Ehrenberg	1854	pl. 22, fig. 42	<i>Dictyocha</i>	Miocene	Line drawing
Stöhr	1880	pl. 7, fig. 9	<i>Stephanocha</i> [as <i>Distephanus</i>]	Miocene	Line drawing
Schulz	1928	figs. 19, 27, 65e, 75	<i>Corbisema</i> *, <i>Naviculopsis</i> , <i>Cannopilus</i>	Eocene Miocene	Line drawings
Bachmann and Ichikawa	1962	pl. 2, figs. 16, 28	<i>Dictyocha</i> , <i>Stephanocha</i> [as <i>Distephanus</i>]	Miocene	Line drawings
Jerković	1963	fig. 15	<i>Deflandryocha</i>	Miocene	Line drawing
Bachmann	1964	pl. 2, fig. 11	<i>Stephanocha</i> [as <i>Distephanus</i>]	Miocene	Line drawing
Dumitrică	1967	pl. 1, fig. 4; pl. 2, fig. 11	<i>Stephanocha</i> [as <i>Distephanus</i>]	Miocene	Line drawings
Bachmann	1970	pl. 1, fig. 17	<i>Corbisema</i>	Oligocene	Line drawing
Dumitrică	1973	pl. 4, fig. 8	<i>Dictyocha</i>	Miocene	Line drawing
Dumitrică	1974	pl. 4, figs. 2–6; pl. 5, figs. 11, 16; pl. 6, figs. 11; pl. 7, fig. 11; pl. 9, fig. 14; pl. 25, fig. 18; pl. 26, fig. 15; pl. 33, fig. 3 pl. 50, figs. 1, 4, 10, 13	<i>Cannopilus</i> , <i>Corbisema</i> <i>Dictyocha</i> <i>Stephanocha</i> [as <i>Distephanus</i>]	Miocene	Line drawings
Bukry and Foster	1973	pl. 7, figs. 2–4	<i>Stephanocha</i> [as <i>Distephanus</i>]	Pliocene	LMS
Perch-Nielsen	1975	pl. 3, fig. 21	<i>Corbisema</i> *	Oligocene	LM
Bukry	1976	pl. 8, figs. 8–9	<i>Stephanocha</i> [as <i>Distephanus</i>]	Miocene	LMS
Bukry	1978	pl. 4, figs. 6, 8	<i>Naviculopsis</i>	Paleocene	LMS
Bukry	1987	pl. 4, fig. 4	<i>Corbisema</i>	Eocene	LM
Frydas	2004	pl. 3, figs. 8, 14	<i>Dictyocha</i> , <i>Stephanocha</i> [as <i>Distephanus</i>]	Miocene	SEMS
McCartney et al.	2010a	fig. 1a	<i>Corbisema</i> *	Cretaceous	LM
McCartney et al.	2010b	fig. 7b, c, h	<i>Vallacerta</i> *	Cretaceous	LMS
McCartney et al.	2011b	pl. 2, fig. 17	<i>Schulzyocha</i> *	Cretaceous	LM
McCartney et al.	2014a	fig. 1a, b	<i>Corbisema</i> *	Eocene	LM, SEM
McCartney et al.	2014d	pl. 3, figs. 4–5	<i>Vallacerta</i> *	Cretaceous	LMS
Dumitrică	2014	figs. 4.1–10, 4.13; 5.1–8, 5–9; 9.2–5.	<i>Cannopilus</i> , <i>Corbisema</i> , <i>Dictyocha</i> , <i>Stephanocha</i> [as <i>Distephanus</i>]	Miocene	Line drawings

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