



Research paper

Fine structure of silicoflagellate double skeletons



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ABSTRACT

Silicoflagellate double skeletons are commonly considered to be pre-division stages, even though their life cycle is only partially resolved, especially with respect to reproduction. Double skeletons of the modern silicoflagellate genera *Dictyocha* Ehrenberg, *Distephanus* Stöhr, and *Octactis* Schiller are for the first time examined in detail by scanning electron microscopy in order to improve our understanding of how skeletal morphology relates to paired skeletons. A number of genus-specific mechanisms enable sibling skeletons to be held together at their abbasal surfaces, including a zig-zag design of the basal ring achieved via apical structure, strut attachment and pike rotation (in *Distephanus* and *Dictyocha*), and the presence of organic material binding the generally planar basal rings (in *Octactis*). Contrary to what is generally understood, the siblings are not mirror images of one another. Instead, the triple junctions formed by the skeletal elements of each apical structure are transposed across the middle of the dividing cell to produce a copy with the same rotation. Thus, two dome-shaped skeletons represent halves of a more spherical design, which suggests that the role of the silicoflagellate basal ring is to enable double skeleton formation, but the full implications of this have yet to be explored. Although the purpose of double skeleton formation in silicoflagellates remains unclear, observations from the fossil record indicate that differences in the relative alignment of doublet members can have a high significance for phylogeny. Differences in the doublet structure of living silicoflagellates call for a combined biological and geological perspective of the utility of maintaining *Dictyocha*, *Distephanus* and *Octactis* as separate genera.

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1. Introduction

Silicoflagellates (Class Dictyochophyceae P.C. Silva) are marine unicellular pigmented heterokonts (Daugbjerg and Henriksen, 2001) that have a fossil record extending to at least 115 million years (myr) ago, i.e., to the Early Cretaceous (McCartney et al., 1990, 2010b, 2014b). The group has a wide biogeographic distribution, but their biology is poorly understood mainly because their life cycle has been resolved

only partially (Henriksen et al., 1993). Multiple life cycle stages have been identified in natural and cultured populations, only one of them being skeleton-bearing (Henriksen et al., 1993), but it is unknown which is the prevalent form. Furthermore, the naked and skeleton-bearing stages have been linked relatively recently (Jochem and Babenerd, 1989; Moestrup and Thomsen, 1990), and therefore the ecological importance of silicoflagellates in marine ecosystems may be underestimated.

An intriguing and largely overlooked aspect of silicoflagellate biology is the formation of double skeletons (also termed doublets or paired skeletons) that are widely regarded as pre-division stages (Boney, 1981; Moestrup and Thomsen, 1990). These are usually presented as chance discoveries without in-depth discussion, although they have been used as productivity indicators by Takahashi and Blackwelder (1992)

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and Takahashi et al. (2009). Both the purpose and mechanisms underlying double skeleton formation have received little attention in studies on natural and cultured populations, and the few published illustrations (listed in Table 1) provide insufficient details. Therefore, this study aims to provide the first detailed examination of double skeleton structure for all modern silicoflagellate genera. In addition, we review the silicoflagellate skeletal morphology with a particular focus on double skeleton structure, expecting that an improved understanding of silicoflagellate biology and skeletal morphology will help increase their utility in various fields of Earth sciences.

2. Taxonomy

The general morphology of siliceous skeletons (Figs. 1A–E and 2A–D) has been the basis for silicoflagellate taxonomy with genera commonly distinguished by the presence or absence and/or complexity of the apical structure. This paleontological approach has been criticized (Van Valkenburg and Norris, 1970), but given the lack of data on naked stages in most of the living taxa, skeletal morphology-based taxonomy remains the only plausible method of species identification. The skeleton-bearing life cycle stages of extant silicoflagellates are characterized either by an apical bridge (*Dictyocha* Ehrenberg) or apical ring (*Distephanus* Stöhr and *Octactis* Schiller).

There are, however, significant differences in the taxonomic interpretation of the group by biologists and paleontologists. Biologists generally recognize three modern species often combined into the genus *Dictyocha* (Moestrup and Thomsen, 1990; Henriksen et al., 1993), while paleontologists and oceanographers typically see a larger diversity of both genera and species in the Holocene (Poelchau, 1976).

Biologists generally place skeletons with apical rings in *Dictyocha*, based in part on nomenclatural grounds, as the name *Distephanus* Stöhr 1880 is a junior homonym of *Distephanus* Cassini 1817, a terrestrial plant (Moestrup and Thomsen, 1990). Silicoflagellates with apical bridges (*Dictyocha*) and apical rings (*Distephanus*), however, have long and distinct geologic histories dating back at least to the Eocene (~56–34 myr ago). Therefore, paleontologists interpret these morphologies as belonging to separate genera and thus have continued to use '*Distephanus*' despite the taxonomic invalidity (e.g., Malinverno, 2010; Rigual-Hernández et al., 2010). *Distephanopsis* Dumitrică (1978) has come into some recent use in place of *Distephanus* (e.g. Desikachary and Prema, 1996; Dumitrică, 2014), although it is currently illegitimate, and besides there has not been a new combination offered for *Distephanus speculum*. In this paper, we use *Distephanus*, but a potential

taxonomic alternative will be presented in the near future in a separate communication.

An additional reason for the application of *Dictyocha* as the only extant silicoflagellate genus by phycologists is due to the results of early culturing experiments. Van Valkenburg and Norris (1970) concluded that clonal cultures of *Dictyocha fibula* Ehrenberg produced skeletal morphologies of three genera (*Dictyocha*, *Distephanus* and *Cannopilus* Haeckel) as used by paleontologists. Most of the skeletons illustrated in Van Valkenburg (1970), however, appear teratoid and often lack the essential symmetries of silicoflagellates commonly observed in the fossil record or in living natural populations. General taxonomic conclusions should not be based on obviously aberrant morphologies.

In addition to skeletal morphology, Chang et al. (2012) provided preliminary molecular data which suggested that silicoflagellates with an apical bridge (*Dictyocha*) and apical ring (*Distephanus*) may indeed represent distinct genera of the Dictyochales. The molecular phylogeny in Chang et al. (2012) indicated that *Distephanus speculum* (*Dictyocha speculum* in Chang et al., 2012) and *Octactis pulchra* (*Dictyocha octonaria* in Chang et al., 2012; Chang, pers. comm., 2014) are more closely related, and may be classified within a single genus (Chang, pers. comm., 2014; see also Ling and Takahashi, 1985). Despite this, we treat *Octactis* Schiller as a separate genus, as there are significant morphological differences between skeletons of this taxon and *Distephanus*, which include the placement of the strut attachments and the absence of pikes as will be presented below.

3. The silicoflagellate skeleton

Although out of necessity the skeleton serves as the basis for the taxonomy of extant silicoflagellates, few studies on its formation are available (Preisig, 1994). The few transmission electron microscope (TEM) studies of *Distephanus speculum* have not addressed skeleton formation to any extent (e.g., Moestrup and Thomsen, 1990). TEM photographs of *D. fibula* (Van Valkenburg, 1970, 1980) suggest skeleton secretion to be internal, as sectioned cells revealed four large vacuoles with thick walls. As a consequence, it was speculated that these were skeleton-forming vacuoles (Van Valkenburg, 1970, 1980). By contrast Moestrup and Thomsen (1990) concluded that the *Distephanus* skeleton is external. McCartney and Loper (1989, 1992), based on optimization models of the skeletal morphologies of three silicoflagellate genera, interpreted the skeleton as supporting the cell boundary to a shape that might reduce surface tensional forces.

Studies on silicoflagellate skeletons lack a consistent terminology. The terminology used here (Fig. 2) incorporates terms proposed by

Table 1
Previously published illustrations of silicoflagellate double skeletons.

Author (year)	Illustration	Genus	Illustration
Haeckel (1887)	pl. 101, fig. 12	<i>Dictyocha</i>	line drawing
Möbius (1887)	pl. 8, figs. 50, 52	<i>Distephanus</i> , <i>Dictyocha</i>	line drawings
Gemeinhardt (1930)	fig. 53e	<i>Distephanus</i>	line drawing
Hovasse (1932)	fig. 3	<i>Distephanus</i>	line drawing
Hovasse (1946)	figs. 1a, 4a, 4b, 4c	<i>Dictyocha</i> , <i>Distephanus</i>	line drawings
Deflandre (1950)	figs. 18–24, 40–41	<i>Distephanus</i> , <i>Mesocena</i> ?	line drawings
O'Kane (1970)	fig. 11	<i>Distephanus</i>	line drawing
Tampieri (1972)	pl. 2, figs. 1, 3; pl. 3, fig. 1	<i>Dictyocha</i>	SEMs
Boney (1976)	fig. 1d–f	<i>Distephanus</i>	line drawings
Poelchau (1976)	pl. 5, fig. b	<i>Dictyocha</i>	LM
Haq (1978)	fig. 3	<i>Distephanus</i>	SEM
Ling and Takahashi (1985)	pl. 1, fig. 5; pl. 2, figs. 1, 2, 4	<i>Octactis</i>	SEMs
Moestrup and Thomsen (1990)	pl. 7, figs. 30–33; pl. 9, fig. 39	<i>Distephanus</i>	LMS
Takahashi and Blackwelder (1992)	figs. 3-2, 3-3, 3-5	<i>Distephanus</i> , <i>Octactis</i>	LMS
Hallegraeff (2005)	fig. 4.2d	<i>Distephanus</i>	SEM
Takahashi et al. (2009)	pl. 2, figs. 3, 5, 14	<i>Distephanus</i>	LMS
Davidson et al. (2010)	fig. 4f	<i>Distephanus</i>	SEM
Cefarelli et al. (2011)	fig. 4o	<i>Distephanus</i>	SEM
Onodera and Takahashi (2012)	fig. 5	<i>Distephanus</i>	LMS

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