

Two unusual silicoflagellate double skeletons

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Abstract A study of silicoflagellate double skeletons revealed two unusual doublets that are illustrated and discussed here. One of these comprises two ten-sided *Octactis* skeletons that appear to form a doublet, but both in the same (apical) orientation. The other specimen is a double skeleton of *Dictyocha* that is slightly disarticulated, with a third, less robust skeleton in between. These unusual double skeletons suggest that there is much more to be learned about the formation of silicoflagellate skeletons and the reproductive processes in this protist group.

Keywords Silicoflagellate, double skeletons, teratoid

1. Introduction

Silicoflagellate double skeletons (also called doublets or paired skeletons) are commonly observed in modern water samples (see Boney, 1981), although there has been little recent study on the subject. Hovasse (1932) was the first worker to propose that double skeletons were formed during a stage of reproduction prior to division, and witnessed and described the growth of the daughter skeleton. While there have been modern studies of silicoflagellate clonal cultures (Van Valkenburg, 1971; Moestrup & Thomsen, 1990; Henriksen *et al.*, 1993), the detailed process of formation and separation of the double skeletons is not well understood.

Current paleontologic and biologic interpretations of silicoflagellate taxonomy differ vastly, with biologists placing all modern skeletal morphologies into *Dictyocha*, while paleontologists still use *Distephanus* (see, for example, Malinverno, 2010). In this paper, we apply the three genera commonly interpreted in the fossil record: four-sided *Dictyocha*, six-sided *Distephanus* and eight-sided *Octactis*. Figure 1 shows a typical six-sided *Distephanus* double skeleton with skeletal terminology. Sibling skeletons are connected along abapical surfaces of the basal rings and aligned at the basal corners with superimposed spines, although in some specimens the spines are slightly separated through disarticulation. In *Dictyocha* and *Distephanus*, the pikes for each skeleton extend abapically into the region of the other, and serve to help hold the skeletons together (Moestrup & Thomsen, 1990). *Octactis* has no pikes and the skeletons are presumably held together exclusively by organic material.

Silicoflagellate skeletons are well known for their extremely broad limits of morphological variation (see McCartney & Wise, 1990, for a discussion of silicoflagellate skeletal variability), including common teratoid specimens (Martini, 1977). Also, members of a doublet

sometimes show considerable morphological plasticity: the daughter skeleton may have thinner elements (Schulz, 1928), and the two skeletons may separate before the development of the daughter is complete (Hovasse, 1932). Boney (1981) reported that about 5% of double skeletons had one skeleton that was dissimilar to the other. Gemeinhardt (1930, fig. 5), Bukry & Foster (1973, Pl. 7, figs 2-4), Boney (1976) and Takahashi *et al.* (2009, Pl. 2, fig. 5) illustrated double skeletons of six-sided *Distephanus*, where one of the sibling skeletons had a divided window, and Malinverno (2010) also noted variant morphologies of *Distephanus speculum* within doublets. Bukry (1976, Pl. 8, figs. 8-9) showed a pair with different variants of the “pseudofibula plexus” (McCartney & Wise, 1990).

During a recent collection and study of silicoflagellate double skeletons, two specimens displayed unusual teratoid morphologies that have not previously been illus-

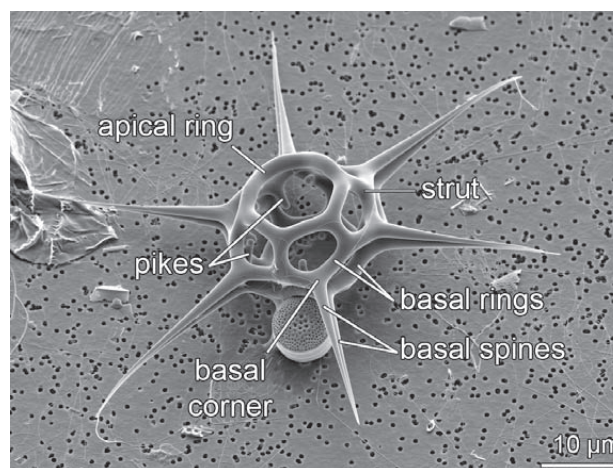


Fig 1. Scanning electron micrograph of *Distephanus speculum* double skeleton with descriptive morphological terminology. Specimen was collected by C. Findlay in the Southern Ocean, cruise WOCE 7, CTD54 10m, 61°S 140°E

trated. Both specimens were chance discoveries; these are presented and discussed here to make other researchers aware of the need to photograph double skeletons when encountered during scanning electron microscope examination of plankton samples. This study aims also to show that more can be learned of the formation and division of silicoflagellate double skeletons.

2. An unusual *Octactis* double skeleton

Figure 2 depicts a specimen of *Octactis pulchra* Schiller 1925 that was collected from the Arabian Sea surface waters during the cruise M74/1 B of the R/V Meteor (site 947, 23 September 2007, see Bohrmann, *et al.* 2010). *Octactis* skeletons typically have eight sides, although the number of sides can vary. The apical structure consists of struts that thin apically with fragile apical ring elements. The struts attach to the middle of the nearly linear basal sides, which lack pikes (Ling & Takahashi, 1985). The two skeletons of the unusual specimen presented here have ten basal sides. Skeletons are aligned at the corners, with the near sibling composed of elements and spines that are somewhat less robust than the far skeleton. The far sibling is more completely formed, with well-formed struts that appear to have supported a complete apical ring that was subsequently removed through breakage. The presence of the struts shows that the skeleton is in apical view.

All known silicoflagellate double skeletons consist of two apical structures that are directed away from one another, with the abapical surfaces of the basal rings adjoining. However, the specimen presented here has a more completely formed distal skeleton in apical view, with the sibling skeleton being proximal (*i.e.*, on top of the distal skeleton), and also appears to be apically

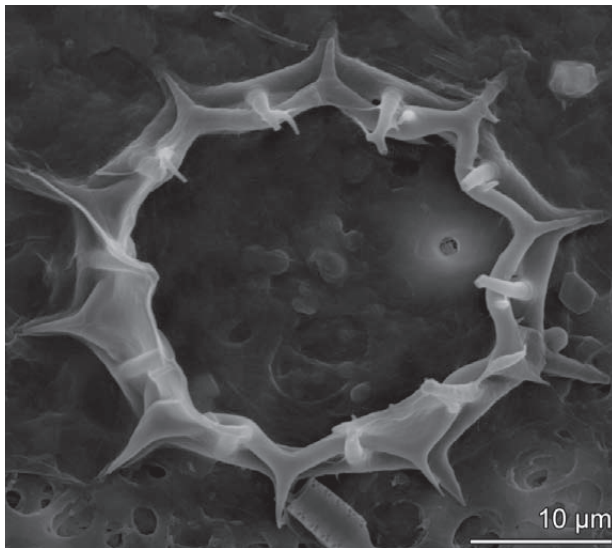


Fig 2. Scanning electron micrograph of two *Octactis* skeletons, both in apical view. The distal skeleton is more robust and believed to be the mother skeleton, with the proximal basal ring being the daughter. The struts of the distal skeleton are better developed, and probably supported an apical ring now lost to breakage. The struts of the proximal skeleton are less well formed and terminate without supporting a ring. Struts of both skeletons trend towards the observer, which places them in apical orientation.

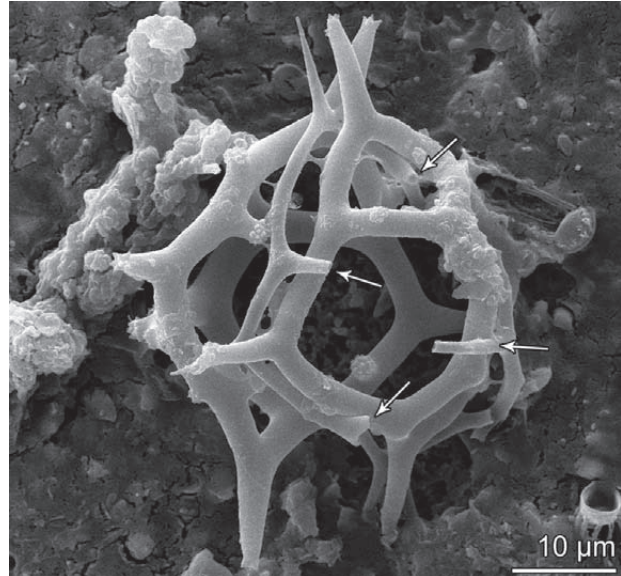


Fig 3. Scanning electron micrograph of three *Dictyochoa* skeletons interpreted as representing a triple skeleton. The skeletons to the right and left with similar size and robust structure are interpreted as a somewhat disarticulated doublet. The less robust skeleton in between has four struts (marked with arrows) directed to the right, showing it to be paired with the sinistral skeleton.

oriented. Thus, the distal skeleton occurs beneath the proximal skeleton, with both skeletons in apical orientation.

The proximal skeleton has basal ring elements bent around the struts of the distal more complete sibling which indicates it to be daughter to the distal mother skeleton. The proximal skeleton has incompletely formed struts, which further supports the conclusion that this is a later and less completely formed skeleton. What makes this pair of skeletons most unusual, and unique in the context of the current literature, is that these appear to compose a double skeleton with both siblings in apical view, since all struts develop towards the observer.

3. An unusual *Dictyochoa* double skeleton

Figure 3 shows a specimen of *Dictyochoa* sp. that was collected at a Long Term Ecological Research coastal site in the North Adriatic Sea, Eastern Mediterranean (Cabrini *et al.*, 2010) on February 5, 2010 at 10 m water depth. The group appears to comprise two robust members of a somewhat disarticulated double skeleton. The two robust skeletons are of similar size and shape, and have basal corner spines with similar distal terminations. However, interposed between these is a third skeleton of similar size but composed of thinner skeletal elements. This skeleton is broken but three of the basal spines are roughly aligned with the spines of the dextral robust skeleton in a double skeleton position but with both skeletons in apical orientation. The result is an apparent triple skeleton.

There may be several possible explanations for this unusual assemblage. The group may represent unrelated skeletons that were combined during the collection or processing of the sample, with either the middle skeleton inserted between a doublet or all three skeletons

being unrelated. The two robust skeletons, however, have enough in common to strongly suggest that they do represent a double skeleton pair. We believe it unlikely that the third more fragile skeleton of similar size and type could be inter-positioned between two members of a double skeleton by chance.

Therefore we can hypothesize that the two robust skeletons became partially separated during an incomplete division and that a third skeleton was formed prior to the death of the cell, forming a triple skeleton. We interpret the skeletal components, marked with arrows in Figure 3, as being struts, although the apical bridge has been lost through breakage. This would place the middle skeleton as the daughter of the left-hand skeleton. Once the original doublet separated (the left and right skeletons), the middle skeleton formed as a daughter to the left skeleton and later separated from the mother but remained connected, through the struts, to the right skeleton. There is not enough information to be able to adequately explain the assemblage, but the triplet suggests that double skeletons can have complicated histories.

4. Discussion

The only prior discussion of aberrant silicoflagellate skeletal morphologies in the context of doublets dealt with siblings that had slightly different apical skeletal designs or possessed one basal ring that was incomplete or had bifurcated spines (Boney, 1976; 1981). However, while individual skeletons may be aberrant or two sibling skeletons may have normal but different morphologies, the two partners of the doublet appear to be associated in a non-aberrant divisional process. Hovasse (1932) called this 'partner abnormality' and we suggest that this term be applied to such situations, with teratoid (or aberrant) used for doublets such as the two described in this paper that appear to result from an unusual divisional process.

Of the two specimens presented in this paper, the *Dictyocha* triplet appears to be the less unusual, as two skeletons are similar and the third skeleton can perhaps be explained by secondary growth after an incomplete divisional process; this triplet could also be a chance assemblage of unrelated skeletons. The *Octactis*, however, is extremely unusual. Unlike the triplet, there is little question that this is some type of double skeleton, but the position of the daughter skeleton upon the apical surfaces of the mother-skeleton's basal ring is not known to have been observed previously. Until more skeletons in this configuration are observed, our best explanation is as a true "freak of nature."

McCartney and Wise (1990) have provided a review of environmental factors that have been hypothesized to influence silicoflagellate skeletal variability and teratoidism. Salinity appears to be an important factor, as unusual skeletal morphologies (e.g., Shitanaka, 1983) can be abundant in coastal environments. The optimal salinity of silicoflagellate growth in culture was observed to be 24 by Van Valkenburg and Norris (1970) and 20-25 by Henriksen *et al.* (1993). The *Dictyocha* specimen was collected at a salinity of 38.31, with salinity range from

34.21 to 38.48 during the year of observation, while the *Octactis* specimen was associated with a salinity of 36.2. More detailed studies of silicoflagellate skeletal variability in relation to salinity are needed to clarify whether the findings reported here may be salinity induced.

5. Conclusions

The two specimens illustrated in this paper show that unusual teratoid forms occur not only among single skeletons, but also in double skeleton morphologies. Additional specimens showing double skeletons in general and teratoid morphologies in particular should be sought for further study. Should additional specimens be observed, multiple photographs from various views are needed in order to better resolve the details of the double skeleton morphology. Such analysis may provide further insight into controls on morphogenesis of the double skeletons and the separation during cellular division.

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