Palynology
2022, Volume 46, Issue 1, Pages 1934908 (17p.)
https://doi.org/10.1080/01916122.2021.1934908
https://archimer.ifremer.fr/doc/00696/80835/

A morphological comparison of two cladopyxidacean dinoflagellates: the extant *Micracanthodinium setiferum* and the fossil *Cladopyxidinium saeptum* (Dinophyceae, Gonyaulacales)

Mertens Kenneth [1, *], Carbonell-Moore M. Consuelo [2], Gardner Kristina [3]

[1] Ifremer, LITTORAL, F-29900 Concarneau, France
[2] Oregon State University, Department of Botany and Plant Pathology, College of Agricultural Sciences, 2082 Cordley Hall, Corvallis, OR 97331-2902, U.S.A.
[3] Department of Earth Sciences, University of Delaware, DGS Building, 257 Academy Street Newark, DE 19716-7501, U.S.A

* Corresponding author : Kenneth Mertens, email address : kenneth.mertens@ifremer.fr

Abstract :

Among dinoflagellates, extant cladopyxidaceans may provide a missing link to better understand the first evolutionary transformations from ancestral configurations towards the more abundant and more derived patterns in Gonyaulacales and Peridiniales. A restudy of the extant, motile-defined Micracanthodinium setiferum from plankton samples from the Indian and Atlantic Oceans and Mediterranean Sea demonstrates that the correct plate formula is Po Pt X 3′+*4′ 4a 7″ 7C 4S? 6‴ 0p 2⁗. A ventral pore is found between 1′, 3′ and *4′. A restudy of the extinct, fossil-defined Cladopyxidium saeptum from the upper Paleocene of Delaware (U.S.A), demonstrated the presence of an identical tabulation. A ventral pore (=porichnion) was positioned between *1′ and 7″. Cladopyxidium is morphologically closer to Micracanthodinium than to Cladopyxis. However, since Cladopyxidium has been extinct since the middle Eocene it is unlikely that Micracanthodinium and Cladopyxidium will have a direct biological link; the close morphological link between both does suggest an important phylogenetic relationship between both in the evolution of cladopyxidaceans.

Keywords : Dinoflagellates, partiform, Kofoidian, porichnion, Paleocene, Eocene

1. Introduction

The Cladopyxidaceae is a family of dinoflagellates within the order Gonyaulacales Taylor, which combines extant, photosynthetic, warm marine (specifically oceanic) genera with fossil genera occurring in marine strata of Early Jurassic to Neogene age; no undisputable fossils are known from the Quaternary (Fensome et al. 1993, 1996a; Medlin and Fensome 2013; Goodman 2017). Extant cladopyxidaceans may provide a missing link to better understand the first evolutionary transformations from ancestral configurations towards the more abundant and more derived patterns in Gonyaulacales and Peridiniales (Below 1987; Edwards 1990; Fensome et al. 1996, 1999; Medlin and Fensome 2013). There are five extant genera: *Acanthodinium* Kofoid, *Cladopyxis* Stein, *Micracanthodinium* Deflandre emend. Dodge, *Palaeophalacroma* Schiller (=*Epiperidinium* Gaarder), ?*Sinodinium* Nie and 16 fossil genera: ?*Beyrichodinium* Below, *Cladopyxidium* McLean, *Chlonoviella* Lebedeva, *Druggidium* Habib, *Enneadocysta* Stover & Williams, *Fibradinium* Morgenroth, *Freboldinium* Below, ?*Gillinia* Cookson & Eisenack, *Glyphanodinium* Drugg, *Histiocysta* Davey, *Microdinium* Cookson & Eisenack, *Mikrocysta* Bjaerke, *Praussia* Williams et al. (=*Hyalosphaera* Prauss), *Subtilidinium* Morgenroth, ?*Walvisia* Miles, *Wervekodinium* Below.

Micracanthodinium is an extant cladopyxidacean genus created by Deflandre (1937) for a *Cladopyxis* species described by Lohmann (1903). Its type species, *M. setiferum* (Lohmann) Deflandre, is a small cell with thin, unbranched extensions, particularly present along the cingulum. Deflandre also transferred *Cladopyxis bacillifera* Schiller to *M. bacilliferum* (Schiller) Deflandre. It is of interest to point out that Deflandre (1937) did not study any material and the reason to create a new genus was that both *Cladopyxis* species, *C.*

setifera and *C. bacillifera*, did not seem to bear plates in contrast with others (*C. brachiolata* and *C. caryophylla*), hence they were placed in a separate genus, *Micracanthodinium*. Later, Dodge (1982) transferred *Cladopyxis claytonii* to the third species, *Micracanthodinium claytonii* (R.W. Holmes) Dodge. Dodge (1995) reported a tabulation for *M. setiferum* from the NE Atlantic, as Po, 4′, 7″, 7c, ?s, 6‴, 2⁗ (Figure 1).

McLean (1972) described the fossil cladopyxidacean genus *Cladopyxidium* with type species *Cladopyxidium septatum* from the Aquia Formation (late Paleocene) of the Virginia-Maryland Coastal Plain (U.S.A.). He documented the plate formula ?′, 4a, 7″, 6c+t, ?s, 5‴, 1p, 1⁗, with the archeopyle corresponding to plates 2′ and 3′ (Figure 2). In the comparison section of his paper, McLean related *C. septatum* to the extant *Cladopyxis hemibrachiata* Balech, suggesting they had a similar plate tabulation pattern (Figure 3). Later, Stover and Evitt (1978, p. 29–30) emended the genus based on observations of numerous well-preserved specimens and reexamination of the type specimens. The authors reinterpreted the tabulation as 4′, 3–4a, 7″, 6c, 5s, 6‴, 1p, 1⁗, and considered *C. septatum* synonymous to *Microdinium saeptum* Morgenroth 1968 and *Microdinium robustum* Davey 1969, making *Cladopyxidium saeptum* (Morgenroth) Stover and Evitt 1978 the senior name, although the nomenclatural type of the genus *Cladopyxidium* remained the holotype of *Cladopyxidium septatum*. Below (1987, p. 32–33) further emended the genus and proposed the plate formula: 4′, 4a, 7″, 7c, 5s, 6‴, 2⁗. In addition, Below described a porichnion between plates 1′ and 4′ for the species *Cladopyxidium septocrispum* and *Cladopyxidium velatum* of which he also described the overlapping plate pattern, which allowed him to infer that there are four apical homologues instead of five anterior intercalary plates. More recently, Goodman (2017) provided detailed tabulations for two unnamed *Cladopyxidium* species, species A and B, comparing them to the closely related fossil genera *Histiocysta* Davey and *Microdinium* Cookson & Eisenack.

Here, a morphological study of dinoflagellates resembling the fossil *Cladopyxidium septatum* and the extant *Cladopyxis hemibrachiata* showed that McLean was not correct in his assertion. In addition, the epitypification of another cladopyxidacean *Micracanthodinium setifera* (Lohmann) Deflandre emend. Dodge reveals a closer resemblance to *C. septatum* than to *C. hemibrachiata*.

2. Material and Methods

2.1. Study of Micracanthodinium setifera

Cells of *Cladopyxis hemibrachiata* and *Micracanthodinium setifera* found in samples from the Indian and Atlantic Oceans and Mediterranean Sea were studied using scanning electron microscopy (SEM) as expressed in Carbonell-Moore (2017) (Figure 4). Samples from the North Atlantic were collected by during the NAAMES 3 campaign as part of the phytoplankton visual analysis by continued pumped surface seawater filtration using the protocol followed in Carbonell-Moore (2018, p. 52). The original Coral Sea sample was taken during the Sp 16/80 cruise detailed in Hallegraeff & Jeffrey (1984) and a subsample was given by Prof. Hallegraeff to MCC-M.

The epitype of *Micracanthodinium* was chosen among seventy-two cells of *Micracanthodinium* (see Table 1). Cells were observed with scanning electron microscopy. Samples were treated in similar fashion to the protocol described in Carbonell-Moore (2017, p. 58) and observed with the same instrument expressed therein. Digital images were edited in Adobe-Photoshop 2020 to remove the filter background without altering the pictured cell. Due to sample manipulation and preparation for SEM, setae were broken in specimens with long setae. Dodge (1995, p.308, 310) reported a similar finding. Plate tabulation nomenclature follows Kofoid (1909, 1911), Balech (1980) and Carbonell-Moore & Mertens (2019). For the apical pore complex we follow Carbonell-Moore (1994, p.76).

2.2. Study of fossil **Cladopyxidium saeptum**

Several cores were drilled during a groundwater monitoring project in Southern New Castle – Northern Kent Countries, Delaware, U.S. (Andres et al. 2018). Sample 110292 and L110302 were subsampled from a core respectively at depth 449.0–449.1 ft and 463.9–464.0 ft from Woodland Beach, Kent Co., Delaware (lat. 39.313583, long. -75.509516, alt. 12 ft). Sample L110740 was subsampled from a core at depth 328.4–328.6 ft from Smyra, Kent Co., Delaware (lat. 39.296225, long. -75.612136, alt. 52 ft). All samples underwent palynological processing using a method derived from a mixture of the standard procedure used at the Delaware Geological Survey (DGS) labs and some of the acid free methods in place at Morehead State University. First, samples were dried at 60 °C, then weighed and separated into bottles. A hemocytometer was utilized to count-calibrate the amount of 25µ polystyrene beads present in one millimeter of fluid. One milliliter of fluid, containing 144,333 25µ Polystyrene beads, was added to each sample, following which sediments were immersed in distilled water, centrifuged, and decanted. Carbonate mineral matter removal, using 37% hydrochloric acid (HCl), was conducted following which samples were rinsed with distilled water until neutralized. Sand was removed via swirling and the decanted muddy solution containing palynomorphs was retained in beakers for further processing. Sand was dried and retained in labeled envelopes for storage in the DGS building. After palynomorphs settled, beakers were decanted and samples immersed in 48% hydrofluoric acid (HF) for siliciclastic matter removal. After HF, samples were treated with 20% HCl. After being rinsed to neutrality, samples were transferred to 50 ml tubes. Approximately 20ml of saturated calgon solution was added to each 50 ml tube for silt disbursement, following which they were thoroughly mixed by vortexing periodically for no less than 24 hours to manually disaggregate cohesive material. Rinsing with deionized (DI) water and decanting took place

until water was no longer opaque. Samples underwent sieving via 10µm pluriStrainer® filters. Where fine heavy material was abundant enough in the residue to interfere with grain identification, samples were subjected to heavy density floatation with the following procedure. A 2% HCl wash, zinc chloride (ZnCl) liquid, with a heavy density of 2.0, was added and samples were vortexed. Once separation had occurred, organic material was collected from the top of the liquid using a 5 ml pipette and transferred to 15 ml tubes before another 2% HCl wash and neutralization.

Residues were stained with Safranin and set with 25% ethanol. Glass slides were made for all 50 samples using polyvinyl acetate (PVA) and Norland optical adhesive 6.5 prior to sealing via ultraviolet light treatment. Acetolysis was not involved.

For scanning electron microscopy (SEM), single specimens were isolated from the plankton samples using a micropipette on a IX70 (Olympus) inverted microscope. The cells were deposited on polycarbonate membrane filters (GTTP Isopore, 0.22 µm pore size; Millipore, Billerica, MA, USA), which were rinsed with distilled water. The filters were processed following the methods described in Chomérat and Couté (2008). They were dehydrated in a graded series of ethanol baths (15%–100%), critical point dried, stuck to a stub using double-sided adhesive tape and coated with gold. The cells on the stubs examined at the Station of Marine Biology in Concarneau using a Sigma 300 Gemini (Carl Zeiss Inc., Oberkochen, Germany) field-emission SEM equipped with both a conventional Everhart-Thornley and in-lens secondary electron detectors at 1.5 kV. The sulcal plate labelling follows Balech (1980).

3. Results

3.1. Systematic paleontology

Division DINOFLAGELLATA (Bütschli, 1885) Fensome et al. 1993

Class DINOPHYCEAE Pascher 1914

Subclass PERIDINIPHYCIDAE Fensome et al. 1993

Order GONYAULACALES Taylor 1980

Suborder CLADOPYXIINEAE Fensome et al. 1993

Family CLADOPYXIDACEAE Kofoid 1907

Micracanthodinium Deflandre 1937, p. 114.

Type species. *Micracanthodinium setiferum* (Lohmann) Deflandre 1937, p. 114.

Other species in this genus. *Micracanthodinium bacilliferum* (Schiller) Deflandre and *Micracanthodinium claytonii* (R.W.Holmes) J.D.Dodge.

Remarks. In general, specimens studied here belonging to the genus *Micracanthodinium* were of two types: some had thin, slender processes or setae, arranged as described by Lohmann (1903) and Schiller (1937) while others were devoid of such processes. As there were no differences in plate tabulation pattern between both types, only one description is presented here as it applies to both. Most of the cells observed in the present study presented a shape more like that seen in Lohmann's holotype so we consider that our cells must be identified as *Micracanthodinium setiferum*, which concurs with the distribution reported by Dodge (1995, p. 310). Total number of *Micracanthodinium* cells observed with SEM: 72. Total number of cells identified as *Micracanthodinium setiferum*: 63. Total number of cells without spines: 33. Total number of cell with spines: 30. Total number of other species: 9, two of which have great resemblance to the cell identified by Dodge (1995, fig. 2) as *Micracanthodinium setiferum.*

Micracanthodinium setiferum (Lohmann) Deflandre 1937, p. 114 emend. nov.

Plates 1–4; Figures 5–10.

Synonymy.

Cladopyxis setifera Lohmann (1903), p. 64, pl. I, his fig. 15 (basionym).

Micracanthodinium setiferum Dodge (1995), p. 311, his figs. 1–7.

Iconotype. Lohmann (1903), p. 64, his pl. I, fig. 15.

Epitypes. Plate 1, figures 5 and 6.

Emended Diagnosis. Small size, round to oval in shape, plate surface covered with equally spaced short barbs arranged in almost perfectly straight lines. May or may not bear long setae, rarely more than one setae per plate. Eight climactal plates and two fundital plates. Hyposome partiform, taller than the episome; cingulum displaced about one-third width, no overhang. Four anterior intercalary plates of dissimilar size. Second and third apical homologues much larger than the first and fourth apical homologues. A ventral pore is located between 1′, 3′ and *4′.

Dimensions. Length, 8.0 (12.0) 17.0 µm (SD=1.98, n=33); width 8.0 (11.5) 16.0 µm (SD= 1.8, n=28), depth 10.0 (11.0) 13.0 µm (SD= 1.3, n=8).

Description. Small sized cell (Plate 1, figure 3), ellipsoid, episome shorter than the hyposome (e.g. Plate 1, figures 2, 4), apex may be obtuse (e.g. Plate 1, figure 2, Supplementary

Information Plate 1, figure 1) or flattened (e.g. Plate 1, figure 5, Supplementary Information Plate 1, figures 2, 3). Apical pore complex (APC) formed by three plates: a cover plate (P_t) which has a tubular structure that resembles a folded lamina (Plate 1, figures 6, 7), a pore plate (P_o) (Plate 1, figures 6, 7), which is smooth and has no pores and a canal plate (X), which has two concave sides connecting with the ends of P_o and three straight sides which contact the apical plates (Plate 1, figure 6, Plate 2, figures 1, 2). First apical is triangular anteriorly and connects with the APC (Plate 2, figures 1–3). Apical plates 2′ and 3′ are very large, of convex sides, occupying about one third of the episome (e.g. Plate 2, figures 1–7, Plate 3; Figure 5). The fourth apical homologue (*4′) has five sides, four of which of similar size while the fifth is very short, abutting anteriorly with the fourth anterior intercalary plate (Plate 2, figure 2; Figure 5). A ventral pore is located between 1′, 3′ and *4′. There are four anterior intercalary plates of dissimilar size, the 3a being the smallest and the 4a the largest and boomerang shaped (Figures 5, 7; Supplementary Information Plate 1, figures 6, 7). Both series, the apical and the intercalary plates possess only one pore on each plate whose location is always the same in any given cell (e.g., Plate 2, figures 1, 4, 7; Figure 5). Each pore is lined by a raised crown of small spine buds. There are seven Kofoidean precingular plates, 1″ through 6″ of similar size, while 7″ is much smaller (Plate 1, figure 2; Figure 5). Each plate bears two pores with the exception of plates 2″ and 3″ that bear only one pore. In the case of cells with long setae only one seta emerged from one of the two pores (e.g. Plate 1, figure 1; Supplementary Information Plate 1, figures 4, 5). These epithecal plates overhang the wide, cavozone cingulum (e.g. Plate 1, figures 1, 2; Figures 7, 9; Supplementary Information Plate 1, figures 2, 3). There are seven cingular plates, of which the largest is the first one (C_1) and the smallest the seventh one (C_7) (Figures 7, 9). There are also two pores on each plate, but no setae emerge from the cingular plates. The sulcus is short and is composed of at least four plates: Sa, Sd, Spa and Spp (Figure 7, 10). Its anterior part is formed by the anterior sulcal

plate (Sa), which overhangs the flagellar pore (Plate 2, figure 3; Figure 7, 10). The right side of the sulcus is represented by the Sd plate with a wide list covering the anterior flagellar pore (Plate 3, figures 1, 2 (white arrow); Figure 10). There is also a list surrounding the posterior flagellar pore attached to the Spa plate that extends to the left of the sulcus (Plate 3, figures 3, 4 (black arrow); Figure 10); a large pore can be seen on the left of this plate (Plate 3, figures 2, 3 (dashed circle); Figure 10) and is hidden behind the overhang of the first postcingular plate (Plate 3, figure 4). The hyposome is formed by the large posterior sulcal plate (Sp or Z) which is anterior to the first antapical plate (or X plate), therefore resulting in a partiform hyposome (Fensome et al. 1993, p. 65, their text-fig. 64A) and by five large postcingular plates and one smaller one (1‴) (Fig. 2; Plate 3; Figure 9). The second antapical plate occupies the cell′s antapex (Figures 6, 7). Most plates (including the cingular plates) display the same kind of ornamentation: short barbs equally distributed forming parallel straight lines. The posterior sulcal plate has a small anterior area that is devoid of barbs (Supplementary Information Plate 1, figures 3, 4). Plates in the hyposome also have two pores, which are always found in the same position on any particular plate. When the cell has long setae, they also emerge from one of these pores (Supplementary Information Plate 1, figure 4). As mentioned by Dodge (1995, p. 310) the setae emerge not only from the precingular and postcingular plates, but also from the apex and antapex (Supplementary Information Plate 1, figures 4, 5). Plate formula: Po Pt X 3′+*4′ 4a 7″ 7C 4S? 6‴ 0p 2⁗.

In older cells, growth bands may be found, making in some cases, difficult to discern the sutures (Plate 2, figures 1, 4, 8). In other cases, these bands actually enclose the plate in a nicely fashion (Plate 4, figures 1, 2). These bands are ornamented as seen in gonyaulacoids. The plate overlap was not discernable. Two forma are described below to denote specimens respectively with or without setae.

Forma.

M. setiferum* f. *spinosa Mertens & Carbonell-Moore *forma nov.* (Plate 1, figure 1) with setae (= *Micracanthodinium setiferum* sensu Dodge (1995), his fig. 6).

M. setiferum* f. *anacantha Mertens & Carbonell-Moore *forma nov.* (Plate 1, figure 2) without setae.

Remarks. There were other species of *Micracanthodinium* found in the samples along with *M. setiferum*. However, the specimens were not suitable for a positive identification as the heavy ornamentation prevented to elucidate the sutures. An example is shown in Plate 4 figure 3, and Supplementary Information Plate 2, figure 1–5, which is the same taxon displayed in Dodge (1995, figure 5).

Cladopyxidium McLean, 1972, p. 862

Type: McLean, 1972, pl. 1, figs. 5–8, as *Cladopyxidium septatum*.

Cladopyxidium saeptum (Morgenroth) Stover and Evitt 1978 emend. herein

Plate 5, figures 1–7; Plate 6, figures 1–4; Figure 11–14.

Synonymy.

Microdinium saeptum Morgenroth (1968), p. 536-537

Microdinium robustum Davey (1969), p. 6, pl. 1, fig. 3; pl. 2, fig. 2.

Cladopyxidium septatum McLean (1972), p. 862–863, pl. 1, figs. 1–3, 5–8, 10–12.

Holotype. Morgenroth, 1968, p. 536–537, pl. 41, figs. 7–9; pl. 42, fig. 1.

Emended Diagnosis. Proximate cysts with paratabulation Po, Pt, X, 3′+*4′, 4a, 7″, 6c, ?4s, 6‴, 2⁗. The first apical is insert and the hypocyst is partiform. The wall is relatively thick (~1μm), and smooth on the outer and inner surface. The ends of the descending cingulum are displaced by ~0.2 widths. The archeopyle corresponds to the APC and the two apical plates 2′+3′; it has a smooth margin with rounded angles. The operculum is free.

Dimensions. Length, 18.6 (24.7) 30.6 μm (SD=3.1, n=42); width 15.0 (20.0) 26.0 μm (SD= 2.3, n=41), depth 17.8 (19.0) 20.0 μm (n=4). Height of septa 0.6 (1.0) 1.4 μm (SD=0.2, n=33)

Description. The proximate, elongate cysts have polyhedral shape (Plate 5, figure 2) and a typical partiform gonyaulacoid tabulation (sensu Fensome et al., 1993, text-Fig. 64A). The epicyst is shorter in length than the hypocyst. The wall is relatively thick (~1μm), with a smooth inner and outer surface. Externally, sutures are marked by lines formed of small spherical granules, in between the elevated crests of the adjacent plates. Internally, these sutures are marked by openings in the wall.

The apical pore complex (APC) consists of a cover plate (Pt) surrounded by a pore plate (P_o) and a small X plate which was rarely visible (Plate 5, figure 6). There are three apical plates and one apical homologue. The first apical plate (1′) is elongated and heptagonal and insert (sensu Fensome et al., 1993, text-Fig. 62A), whereas the second apical plate (2′) is heptagonal (Plate 5, figure 3–4, 6). The third apical plate (3′) is hexagonal. The fourth apical homolog (*4′) is pentagonal and is the only apical homologue that does not contact the APC (Plate 5, figure 6). There is a large ventral pore (porichnion) located between *1′ and 7″ (Plate 5, figure 7). The precingular series consists of seven large plates, where 2″ is the largest, and 6″ is the smallest. Plate 1″ is quadrangular, 3″, 4″, 5″, 6″ and 7″ are pentagonal, 2″ is hexagonal (Plate 5, figures 1–4). The paracingulum is slightly left-handed (descending), lined with narrow lists,

and comprises six cingular plates. The ends of the cingulum do not overhang, and are displaced by ~0.2 widths (Plate 5, figure 2).

The parasulcus is narrow anteriorly and widens posteriorly. It consists of at least four plates (Plate 5, figures 2, 7). The anterior sulcal plate (Sa) is relatively large and anteriorly intruded between plates 1″ and 7″ and has a broad contact with 1′ (Plate 5, figure 7). There is a left sulcal plate that contacts the first and seventh cingular plate, the posterior sulcal plate and the first postcingular plate. The flagellar pores (FPs) seems surrounded by several small plates which were rarely expressed and difficult to visualize. Finally, there is the large posterior sulcal (Sp), which is omegaform (Plate 5, figure 2, 5).

The hypocyst is partiform (Plate 5, figure 5). There are six postcingular plates. Plate 1‴ is the smallest in the series. All other postcingular plates are large, though 6‴ is relatively smaller; in addition, they are trapezoidal and four-sided (Plates 5, figure 1–6). There are two antapical plates that are respectively four- and six-sided (Plate 5, figure 5).

The archeopyle is moderately wide and reflects the APC plus the surrounding two apical plates 2′+3′, whereas the operculum is released as a single piece, and has rounded angles (Plate 5, figure 6).

Plate formula: Po Pt X? 3′+*4′ 4a 7″ 7C 4S? 6‴ 0p 2⁗.

The plate overlap could not be observed.

Remarks. The interval where the sample was taken is upper Paleocene. Samples from the Vincentown/Aquia interval in the same stratigraphic interval in the region (Dover AFB, Delaware; Millville, New Jersey; South Dover Bridge, Maryland) have nannofossils indicating this sample is probably from the lower part of zone NP9a or NP8.

4. Discussion

4.1. Comparison of **Micracanthodinium** *to type material and related taxa*

Micracanthodinium was created by Deflandre without studying any physical material. He did so because he considered that *Cladopyxis* showed plates (Deflandre mentioned Pavillard's findings of plates on *Cladopyxis quadraspina* Pavillard), in contrast with both *Cladopyxis* listed by Schiller (1937), i.e., *C. setifera* and *C. bacillifera*. Deflandre thus concluded that both species deserved a separate genus. Although species of *Micracanthodinium* have been reported several times in the literature (Dodge 1995, p. 310), the only plate tabulation pattern study has been that of Dodge (1995) resulting in emendation of the genus. It is very likely that Dodge saw several different species as can be observed in his photomicrographs figs 2–7. Only one of his cells (his fig. 6) agrees very well with what is epitypified here (Plate 1, figure 1). While Dodge did not document any anterior intercalary plates - they are not easily observed - we counted four (Plate 2, figures 2, 5; Figures 8, 9). One of the remarkable features of *M. setifera* in our study is the perfect alignment of the short barbs which cover most thecal plates. This feature is only observed in Dodge's fig. 6, which corresponds to a cell from the Eastern Equatorial Atlantic, as shown by the distribution map shown in his fig. 8. In all his other cells the barbs are randomly located. We have also observed this kind of ornamentation in our study, though we consider that these cells correspond to different species of *Micracanthodinium* (Plate 4, figure 3; Supplementary Information Plate 2, figure 1–5). This is supported but the fact that these cells have a different kind of cover plate in the apical pore complex-it is ornamented (Supplementary Information Plate 2, figure 3) as well as different plate ornamentation and pore distribution. These cells have numerous pores on each plate (Supplementary Information Plate 2, figure 4), and they seem to be distributed more towards the margin of the plates as observed in *Cladopyxis*. Lastly, the shape of the Sp plate is not the same as the posterior suture with plate 2′′′′ is much shorter in *M. setiferum* (Supplementary Information Plate 1, figure 3, Supplementary Information Plate 2, figure 4). In the cells

similar to Dodge's is practically impossible to see the anterior intercalary plates (Plate 2, figure 2; Supplementary Information Plate 2, figure 5).

While Dodge (1995, p. 310) found two flagellar pores in *Micracanthodinium*, we were not able to confirm this. Supplementary Information Plate 2, figures 3 and 4 show two different inside views of the sulcus: one has two openings while the other cell has one long opening. However, Plate 3, figures 3 and 4 of another cell, show the external sulcal view, and seems to show two openings.

Micracanthodinium is easily differentiated from *Cladopyxis* in: 1) the absence of robust extensions; 2) having four anterior intercalary plates instead of three (Figures 5, 15); 3) having very large 2′ and 3′ plates while in *Cladopyxis* these plates are small (Figures 5, 15) and 4) the presence of three strict apical plates and one homologue in *Micracanthodinium*, while in *Cladopyxis* there are four strict apical plates (Figures 5, 15). In addition, the precingular plates are larger in *Cladopyxis* than in *Micracanthodinium.* The plate ornamentation is also different. In *Micracanthodinium* species there are barbs of equal or similar length equally distributed or not and it has few pores, while *Cladopyxis* has small bumps instead of barbs and a line of many pores may be seen. Finally, the pore plate in *Micracanthodinium* is smooth (Plate 1, figures 6, 7), while in *Cladopyxis* it has a ring of pores (Figure 15, small arrow).

4.2. Comparison of Cladopyxidium saeptum *to type material and related taxa*

C. saeptum as described by Morgenroth (1966, as *Microdinium saeptum*) has a length of 15–22 µm and a width of 14–20 µm, and a height of the septa of 1–2 µm. McLean (1972, as *C. septatum*) reported a length of 25–37 µm and width of 22–32 µm, and a septum height up to 2 µm. Marheinecke (1992, as *C. septum*) reported lengths of 22–25 µm, width of 20–23 µm, and height of septa 2–3 µm Our specimens, with their length of 18.6–30.6 µm, width of 15.0–

26.0 µm, and height of septa 0.6–1.4 µm, largely overlap in size with the specimens documented by these authors.

Morgenroth (1966, as *M. saeptum*) did not report any anterior intercalaries for the type of *C. saeptum*, but he probably was unable to study the plate pattern carefully. Later, McLean (1972, as *C. septatum*) reported four anterior intercalary plates, although he counted what we called the apical homologue as an anterior intercalary plate, and therefore the resulting number of anterior intercalary plates is less than one than in our study. The photographs in Morgenroth (1966) and McLean (1972) do not allow to verify their reported tabulations. Below (1987) considered to be four anterior intercalary plates in the genus *Cladopyxidium*, although he did not study any *C. saeptum*, and therefore, emended the genus to only encompass this tabulation. Marheinecke (1992) did record such a tabulation for *C. saeptum*, and more recently Goodman (2017) recorded a similar tabulation for *Cladopyxidium* sp. A. In conclusion, our study demonstrates a tabulation of *C. saeptum* similar to the one recorded for the genus *Cladopyxidium* by Below (1987) and for *C. saeptum* by Marheinecke (1992). It is not clear whether specimens with three intercalaries suggested by McLean (1972) really exist or whether McLean (1972) made a mistake in his interpretation of the tabulation. Either way, *C. svalbardella* has clearly only three intercalary plates which makes three to four anterior intercalary plates acceptable within the genus *Cladopyxidium*, as proposed by Stover and Evitt (1978).

Another difference is the interpretation of the sulcal plates. Our interpretation is in line with that proposed by Below (1987). However, what in our study is recorded as the seventh cingular plate, has been interpreted as the right accessory plate (r.a.s.) by Goodman (2017). The left sulcal plate (Ss) has also been interpreted as a merging of the right and left sulcal by Goodman (2017). The discovery of many small plates around flagellar pores, suggests that the interpretation might be more complicated.

The porichnion was observed between 1′ and 7″ in our specimens of *C. saeptum*, which was not observed by either McLean (1972) or Morgenroth (1966). Below (1987) however, described a porichnion between plates 1′ and 4′ for the species *Cladopyxidium septocrispum* and *Cladopyxidium velatum*, but his photograph does not allow to verify this. Therefore, it is unclear whether the presence of the porichnion varies on species level or not.

C. saeptum can be differentiated from other species of *Cladopyxidium. C. exilimuratum* Schumacker-Lambry is thinner, has a larger archeopyle, a lower height of the septa (max. 1 µm) and a weak expression of the paratabulation (Schumacker-Lambry 1978, p. 37). *C. foveolatum* has a foveolate autophragm (McMinn 1988, p. 148–150). *C. globosum* has a spherical form with an angular archeopyle (Marheinecke 1992, p. 104–105). *C.? halembayense* does not show a paratabulation (Slimani 1994, p. 10–11). *C. marheineckei* has pronounced septa on the hypocyst (Marheinecke 1992, p. 104, as *C. velatum*). *C. paucireticulatum* has irregular septa and granules forming an intratabular reticulum (Slimani 1994, p. 11–12). *C. septocrispum* has a perforate wall and thick septa, beset with granules (Below 1987, p. 33–34). *C. svalbardense* has only three apical intercalary plates (Below 1987, p. 60, as *Cladopyxis svalbardensis*). *C. velatum* has a pronounced development of distal septa (Below 1987, p. 34–36). *C. verrucosum* has intratabular protuberances of the wall (Marheinecke, 1992, p. 103).

4.3. Comparison between Micracanthodinium, Cladopyxidium *and* Cladopyxis

There is a ventral pore (porichnion) in *Cladopyxidium* (Plate 5, figures 2, 3, 7 (arrowhead) which is located more anteriorly in *Micracanthodinium* (Plate 2, figure 3; Supplementary Information Plate 1, figure 1 (arrowhead); Figure 5 (arrowhead)); in *Cladopyxis* it is absent (Figure 15). *Micracanthodinium* and *Cladopyxidium* have four anterior intercalary plates, a partiform hyposome and in general, the same plate (para)tabulation formula, whilst

Cladopyxis has only three anterior intercalaries when using the apical homologue. The round archeopyle of *Cladopyxidium* agrees well with the shape of the large 2′ and 3′ apical plates of *Micracanthodinium*, in *Cladopyxis* both plates are much smaller. The cingulum is slightly displaced in *Cladopyxidium* as well as in *Micracanthodinium* and *Cladopyxis* (e.g. Plate 5, figure 2; Plate 1, figure 2; Figure 15). *Cladopyxidium* and *Micracanthodinium* have a wide and excavated cingulum. (Figures 13, 14, 8, 9), whilst there is nearly no excavation in *Cladopyxis* (cf. Balech 1964, fig. 11). On the other hand, the suture of the last cingular plate (C_7) with plate Sp in *Cladopyxidium* (Plate 5, figures 2, 5) does not exist in *Micracanthodinium* (e.g. Plate 1, figures 1, 2; Figure 8), neither in *Cladopyxis* (cf. Balech 1964, fig. 1).

4.4. Distribution and ecology of Micracanthodinium

Micracanthodinium was commonly found in surface samples using small mesh nets 25 µm while filtering for long periods of time (ca. 6 hours). It was frequently observed in the samples from the Western Indian Ocean and in the North Atlantic (NAAMES 3). Dodge (1995, p.310) lists the sightings of *Micracanthodinium* in the literature. In the present study it was observed also in the Equatorial Atlantic (Equalant I) and in the Mediterranean Sea.

Having analyzed a different assortment of plankton samples provides the unique opportunity of analyzing the dinoflagellate flora accompanying *Micracanthodinium.* Due to its small size, in routine plankton examinations is in, all likelihood, overlooked. In our case, all analyses have been carried out using scanning electron microscopy. Hence the large number of *Micracanthodinium* cells studied: 72. The great majority are from the Western Indian Ocean, a body of water with an incredible diversity of dinoflagellates (Taylor 1976).

There is no coincidence that the most frequent accompanying *Micracanthodinium* were cells also very small. In this group the small-sized *Oxytoxum* spp. (~ 15–20 µm) such as

O. crassum Schiller, *O. mediterraneum* Schiller, *O. sphaeroideum* Stein were present with *Micracanthodinium*. Larger species, such as *O. scolopax* Stein, *O. diploconus* Stein, *O. turbo* Kofoid, *O. tessellatum* (Stein) Schütt were also present though in fewer numbers. In the small- sized group the species of *Amphidoma* Stein and *Azadinium* Elbrächter & Tillmann were notoriously present with *Micracanthodinium.* Other genera present in this group were *Alexandrium* Halim (undescribed species), *Gonyaulax* spp. (e.g. *G. minima* Matzenauer). Within the Dinophysiales, the most common genera were *Histioneis* Stein, *Parahistioneis* Kofoid & Skogsberg and *Citharistes* Stein. Interestingly, all other cladopyxidaceans, were also present, especially C. *hemibrachiata* Balech and *Palaeophalacroma*.

The Coral Sea species were similar to those above. The Atlantic flora was less diverse, and no group was particularly more frequent than another. The North Atlantic (NAAMES 3) included species such as *O. scolopax, Cladopyxis hemibrachiata, Peridiniella* (Kofoid & Michener) Balech spp., *Protoceratium reticulatum* (Claparède & Lachmann), *Lissodinium schilleri* (Matzenauer) Carbonell-Moore, *Azadinium* sp. and *Protoperidinium* Bergh spp. (e.g. *P. steinii* (Jørgensen) Balech).

It is worth to emphasize that all of these samples were oceanic phytoplankton samples, mostly from the surface, and filtered through a 20 µm – mesh-opening, up to six hours at a time. This also means that most of the species are photosynthetic and not subject to environmental changes except for climatological ones.

5. Conclusions

Although *Cladopyxidium* is closer in morphology to *Micracanthodinium* than to *Cladopyxis*, some differences between both taxa remain. However, the first occurrence of *Cladopyxidium* in the lower Jurassic (Below 1987, as *C. svalbardense*) and a last occurrence in the middle Eocene (Kothe et al. 1988, as *Cladopyxidium* sp.), suggest that this genus

became extinct a long time ago, and it is therefore unlikely that *Micracanthodinium* and *Cladopyxidium* will have a direct biological link; the close morphological link between both does suggest an important link between both in the evolution of cladopyxidaceans. Molecular sequences should be obtained of extant cladopyxidaceans to better understand their phylogenetic relations. However, our multiple efforts to sequence *Cladopyxis* to-date have been unsuccessful.

Acknowledgements

The Regional Council of Brittany, the General Council of Finistère and the urban community of Concarneau-Cornouaille-Agglomération are acknowledged for the funding of the Sigma 300 FE-SEM of the station of Marine Biology in Concarneau. MCC-M would like to thank Prof. Balech for the Equalant I sample which he kindly sent her many years ago for studies on Podolampadaceans. The samples from the Coral Sea was kindly supplied by Prof. Gustaaf Hallegraeff also many years ago for the same purpose. MCC-M also would like to thank Bethan Jones and Brian Verwey for taking the samples during the NAAMES 1 and NAAMES 3 campaigns respectively. Marta Torres (Oregon State University) is thanked for sampling in the Mediterranean Sea for MCC-M. Lucy Edwards is greatly acknowledged for interesting discussions and providing samples. Two anonymous reviewers and the editor are thanked for constructive remarks that improved the manuscript.

Funding

M.C.C-M thanks the Oregon State University Research Incentive Program for funding scanning electron microscopy. NAAMES was supported by a NASA-Grant-NNX15AF30G to Dr. Michael J. Behrenfeld.

Biography

Kenneth Neil Mertens is a researcher at Ifremer, LER BO, Concarneau, France. He received his Ph.D. in 2009 from Ghent University. His research interests are the taxonomy, evolution, phylogeny and biogeography of dinoflagellates, and the palaeoceanographical application of dinoflagellate cysts, particularly in the Quaternary and Neogene.

Consuelo Carbonell-Moore is a retired oceanographer, researching the morphology of tropical dinoflagellates at Oregon State University, in Corvallis, Oregon, U.S.A. She has described several new genera and species of dinoflagellates. Her main focus is the study of the family Podolampadaceae Lindemann as well as rare dinoflagellates found in deep waters (shade species) in different tropical areas of the world's oceans.

Kristina Gardner is a Master's student with a Bachelor in Science in Geology from Morehead state university where her undergraduate thesis was on fungal palynomorphs from the PETM in Texas. Currently she is pursuing a Master's degree at the University of Delaware using dinocysts and pollen and spores extracted from samples from the Paleocene-Eocene boundary in the central Delaware coastal plain. The aim is an environmental reconstruction of the nearshore to offshore transition to clarify the stratigraphy at the truncation of the Rancocoas aquifer in Kent County, Delaware.

References

Andres AS, Coppa ZJ, He C, McKenna TE. 2018. Southern New Castle-Northern Kent Countries Groundwater Monitoring Project: Results of Subsurface Exploration and Hydrogeological Studies. Report of Investigations, No. 82. Newark, DE: Delaware Geological Survey, University of Delaware.

Balech E. 1980. On thecal morphology of dinoflagellates with special emphasis on cingular and sulcal plates. Universidad Nacional Autónoma de México, Centro de Ciencias del Mar y Limnología, Anales 7, 57–68.

Below R. 1987. Evolution und Systematik von Dinoflagellaten-Zysten aus der Ordnung Peridiniales. II: Cladopyxiaceae und Valvaeodiniaceae. Palaeontographica Abteilung B 206:1–115.

Carbonell-Moore MC. 1994. On the taxonomy of the family Podolampadaceae Lindemann (Dinophyceae) with descriptions of three new genera. Review of Palaeobotany and Palynology 84:73–99.

Carbonell-Moore MC. 2017. The rediscovery of *Archaeosphaerodiniopsis* Rampi (Dinophyceae). European Journal of Phycology 53:52–57.

Carbonell-Moore MC. 2018. Further observations of *Archaeosphaerodiniopsis verrucosa* Rampi (Dinophyceae). European Journal of Phycology 52:57–63.

Carbonell-Moore MC, Mertens KN. 2019. Should *Gonyaulax hyalina* and *Gonyaulax fragilis* (Dinophyceae) remain two different taxa? Phycologia 58:685–689.

Chomérat N, Couté A. 2008. *Protoperidinium bolmonense* sp. nov. (Peridiniales, Dinophyceae), a small dinoflagellate from a brackish hypereutrophic lagoon (south of France). Phycologia 47:392–403.

Davey RJ. 1969. Some dinoflagellate cysts from the Upper Cretaceous of northern Natal, South Africa. Palaeontologia Africana 12:1–23.

Deflandre G. 1937. *Phanerodinium*, genre nouveau de Dinoflagellé fossile des silex. Bulletin de la Société française de Microscopie 6:109–115.

Dodge JD. 1982. Marine dinoflagellates of the British Isles. London: Her Majesty's Stationery Office; p. 1–303.

Dodge JD. 1995. Thecal structure, taxonomy, and distribution of the planktonic dinoflagellate *Micracanthodinium setiferum* (Gonyaulacales, Dinophyceae). Phycologia 34:307–312.

Edwards LE. 1990. Peridinialean dinoflagellate plate patterns, labels and homologies. Review of Palaeobotany and Palynology 65:293–303.

Fensome RA, Taylor FJR, Norris G, Sarjeant WAS, Wharton DI, Williams, GL. 1993. A classification of living and fossil dinoflagellates. Micropaleontology Special Publication Number 7:1–245.

Fensome RA, Riding JB, Taylor FJR. 1996. Chapter 6. Dinoflagellates. In: Jansonius J, McGregor DC., editors. Palynology: principles and applications 1. American Association of Stratigraphic Palynologists Foundation, Dallas, p. 107–169.

Fensome RA, Saldarriaga JF, Taylor FJR. 1999. Dinoflagellate phylogeny revisited: Reconciling morphological and molecular based phylogenies. Grana 38:66–80.

Goodman, DK. 2017. Tabulation patterns in some fossil representatives of the dinoflagellate family Cladopyxiaceae Stein 1883. Palynology 41:290–308.

Hallegraeff, G.M., Jeffrey, S.W. 1984. Tropical phytoplankton species and pigments of continental shelf waters of North and North-West Australia. Marine Ecology Progress Series 20: 59–74.

Holmes RW. 1956. The annual cycle of phytoplankton in the Labrador Sea, 1950–51. Bulletin Bingham Oceanographic College. 16:1–74.

Kofoid CA. 1909. On *Peridinium steini* Jörgensen, with a note on the nomenclature of the skeleton of the Peridinidae. *Archiv für Protistenkunde* 16:25–47.

Kofoid C.A., 1911. Dinoflagellata of the San Diego region. IV. The genus *Gonyaulax*, with notes on its skeletal morphology and a discussion of its generic and specific characters. University of California Publications in Zoology 8:187–286.

Köthe A, Khan AM, Ashraf, M. 1988. Biostratigraphy of the Surghar Range, Salt Range, Sulaiman Range and the Kohat area, Pakistan, according to Jurassic through

Paleogene calcareous nannofossils and Paleogene dinoflagellates. Geologisches Jahrbuch Reihe B 71P:3–87.

Lohmann H. 1903. Neue Untersuchungen über den Reichthum des Meeres an Plankton und über die Brauchbarkeit der verschiedenen Fangmethoden. Zugleich auch ein Beitrag zur Kenntnis des Mittelmeerauftriebs. Wissenschaftliche Meeresuntersuchungen, Abteilung Kiel, Neue Folge 7:1–87.

Marheinecke U. 1992. Monographie der Dinozysten, Acritarcha und Chlorophyta des Maastrichtium von Hemmoor (Niedersachsen). Palaeontographica, Abteilung B 227:1–173.

McLean DM. 1972. *Cladopyxidium septatum*, n. gen., n. sp., possible Tertiary ancestor of the modern dinoflagellate *Cladopyxis hemibrachiata* Balech, 1964. Journal of Paleontology 46:861–863.

McMinn A. 1988. Outline of a Late Cretaceous dinoflagellate zonation of northwestern Australia. Alcheringa 12:137–156.

Medlin LK, Fensome RA. 2013. Dinoflagellate macroevolution: Some considerations based on an integration of molecular, morphological and fossil evidence. In: Lewis JM, Marret F, Bradley L., editors. Biological and geological perspectives of dinoflagellates. Geological Society, London; p. 263–274

Morgenroth P. 1968. Zur Kenntnis der Dinoflagellaten und Hystrichosphaeridien des Danien. Geologisches Jahrbuch, Hannover, 86, 533–578.

Schiller J. 1937. Dritte Abteilung. Dinoflagellatae (Peridineae) in monographischer Behandlung, 2. Teil. In: Kolkwitz R., editor. Zehnter Band, Flagellatae. In: Dr. L. Rabenhorst's Kryptogamen–Flora von Deutschland, Österreich und der Schweiz. Akademische Verlagsgesellschaft, Leipzig, p. ivii, 1–590. [Lieferung (= instalment) 1: 1–160 was effectively published in 1935a. Lieferung 2: 161–320 was published in

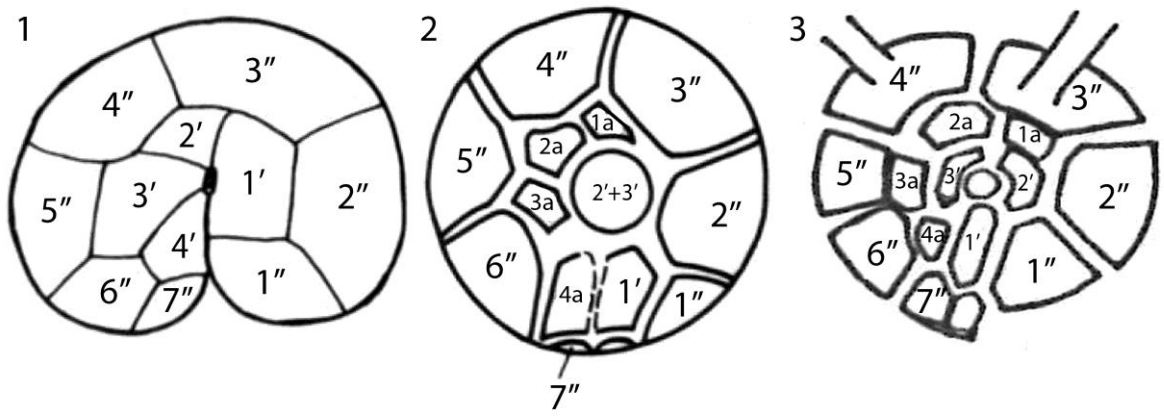
1935b. Lieferung 3: 312–480 was published in 1936, Lieferung 4: 481–590 was published in 1937, when the four instalments were bound as 2. Teil (= Part 2). Both parts were reprinted in 1971 by Strauss & Cramer, Leutershausen, and by Johnson Reprint Co., New York, undated.]

Schumacker-Lambry J. 1978. Palynologie du Landenien inférieur (Paléocène) à Gelinden-Overbroek/Belgique. Relations entre les microfossiles et le sédiment. 157 p., 18 pl.; Université de Liège, Laboratoire de Paléobotanique et de Paléopalynologie, Liège, Belgium.

Slimani H. 1994. Les dinokystes des craies du Campanien au Danien à Halembaye, Turnhout (Belgique) et à Beutenaken (Pays-Bas). Mémoires pour servir à l'explication des cartes géologiques et minières de la Belgique 37:1–173.

Stover LE, Evitt WR. 1978. Analyses of pre-Pleistocene organic-walled dinoflagellates. Stanford University Publications, Geological Sciences 15, 300 p.

Taylor FJR 1976. Dinoflagellates from the International Indian Ocean1976. Expedition. Bibliotheca Botanica 132:1–234.



Figures 1–3. Line drawing of apical views of species discussed here. 1. *Micracanthodinium setiferum*, redrawn after Dodge (1995, his fig. 1C). 2. *Cladopyxidium saeptum*, redrawn after McLean (1972, his fig. 10). 3. *Cladopyxis hemibrachiata*, redrawn after Balech (1964, his fig. 13).

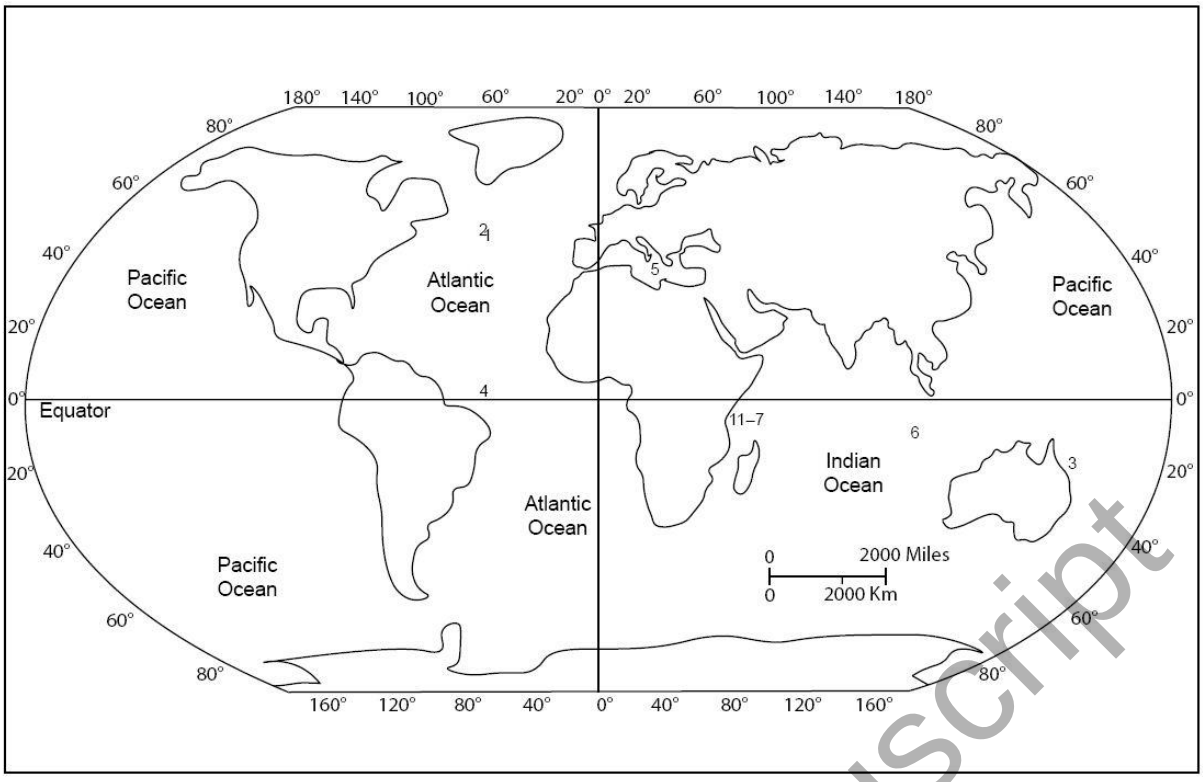
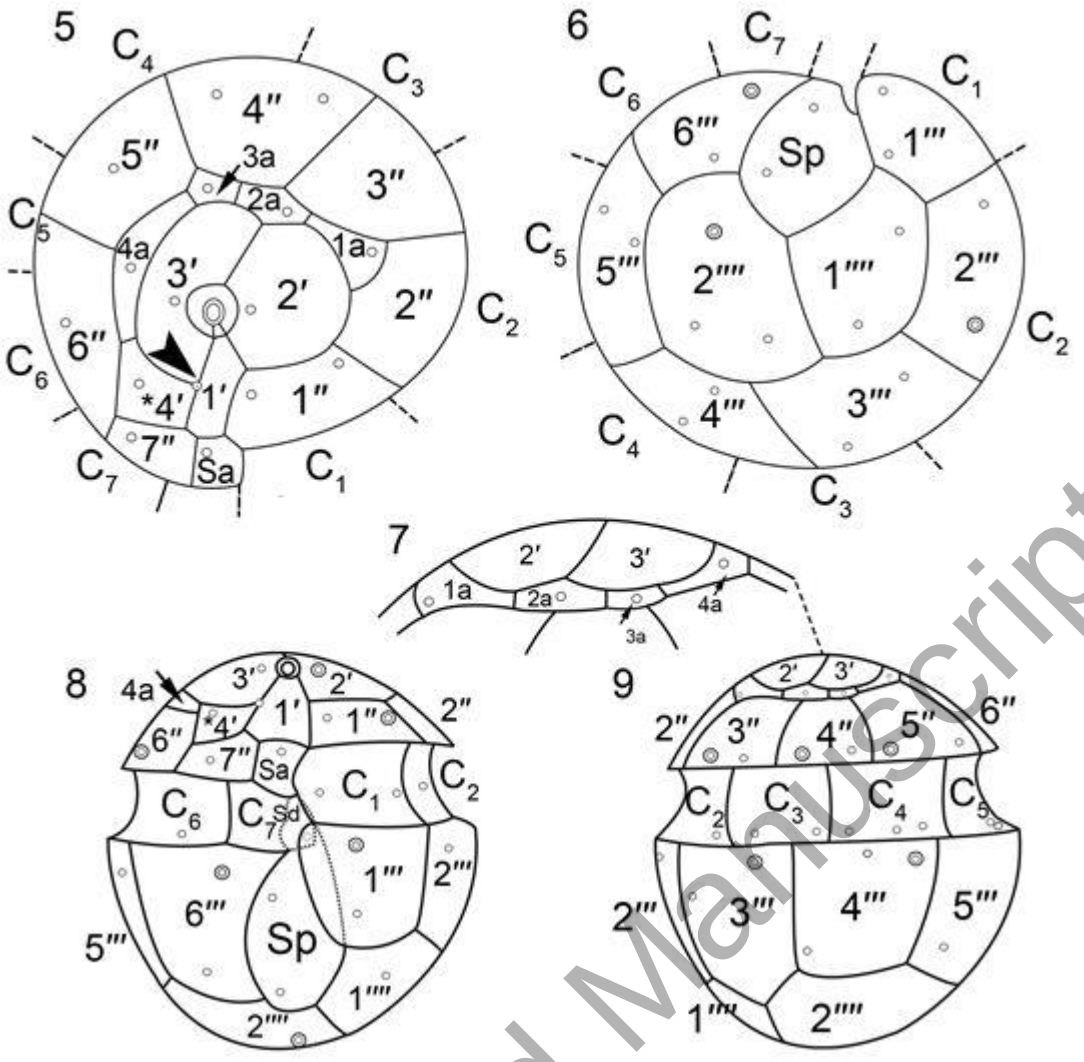


Figure 4. Map of sample locations mentioned in Table 1 used for SEM study of *Micracanthodinium* species.



Figures 5–9. Line drawings of *Micracanthodinium setiferum*. 5. Apical view. 6. Antapical view. 7. Ventral view. 8. Configuration of anterior intercalary plates. 9. Dorsal view. Double circles indicate pores where setae may emerge from. Single circles indicate pores without setae.

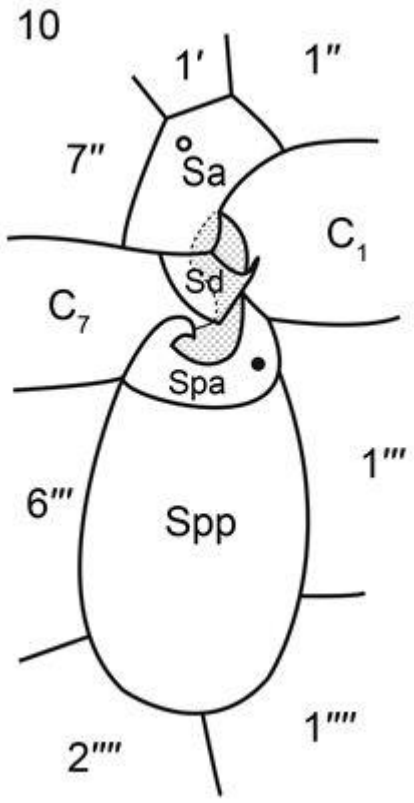
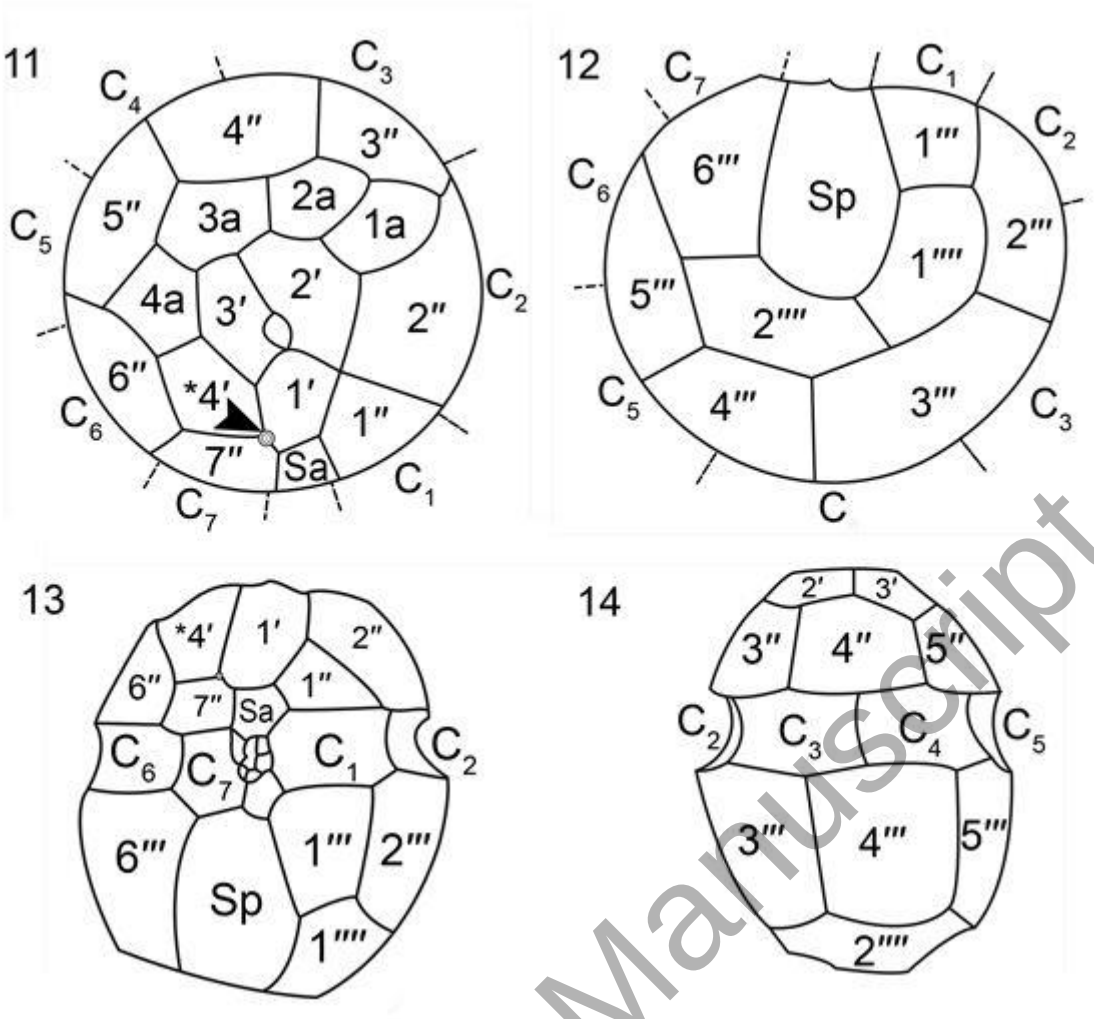
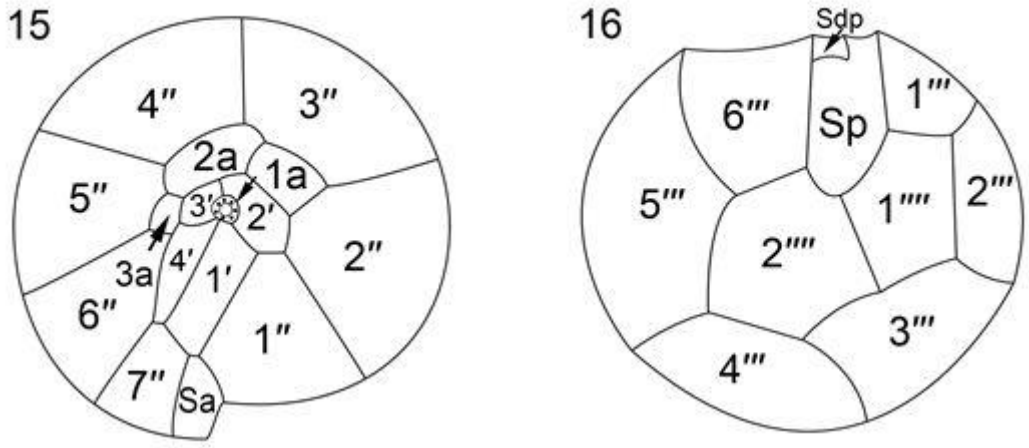


Figure 10. Line drawings of *Micracanthodinium setiferum*. Sulcus. Sa= anterior sulcal plate. Sd= right sulcal plate. Spa=left-anterior posterior sulcal plate. Spp= Posterior posterior sulcal plate.



Figures 11–14. Line drawings of *Cladopyxidium saeptum*. 11. Apical view. 12. Antapical view. 13. Ventral view. 14. Dorsal view.



Figures 15–16. Line drawings of *Cladopyxis hemibrachiata.* 15. Apical view. 16. Antapical view.

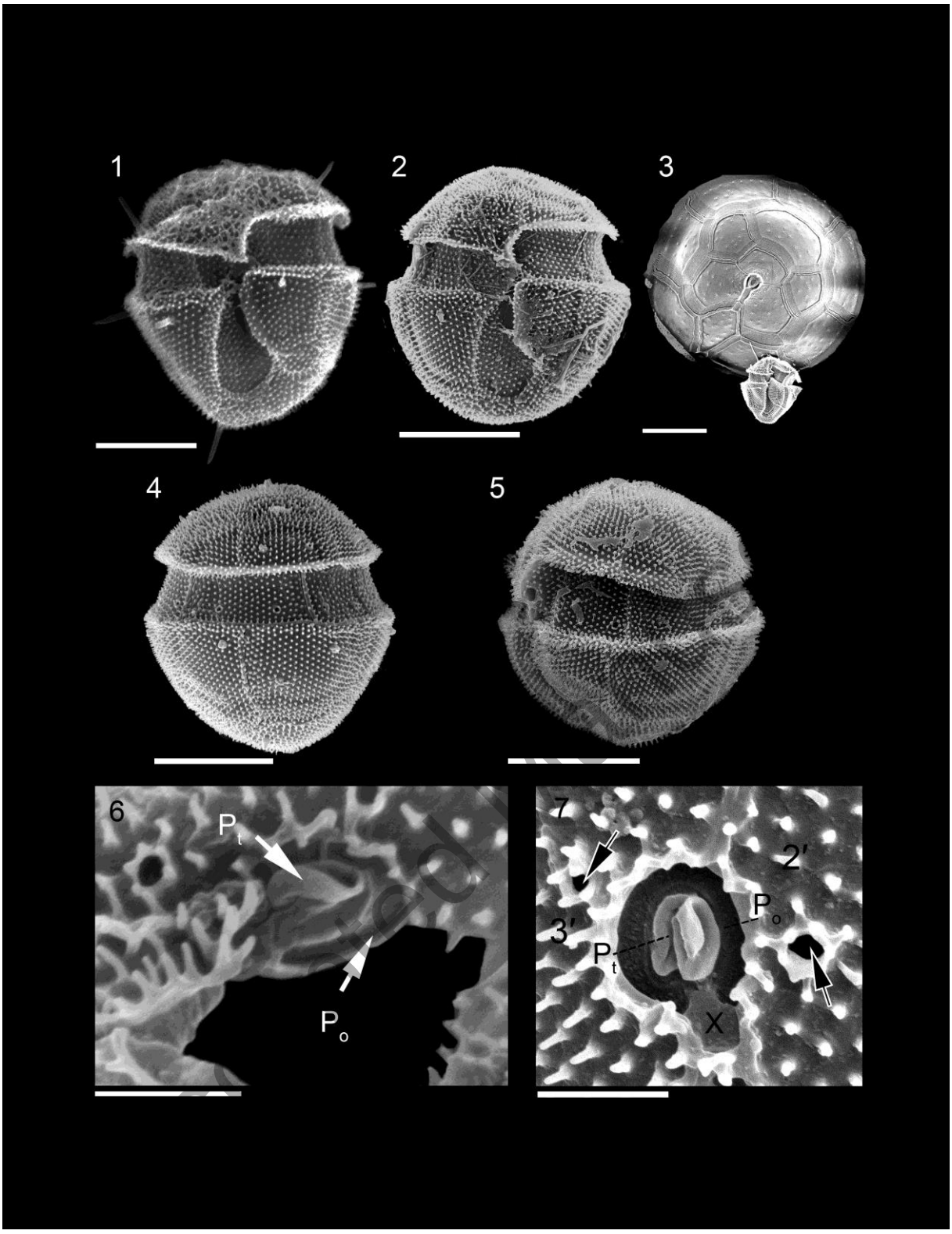

1
2
3
4
5
6
P_t
P_o
7
2′
3′
P_o
P_t
X

Plate 1. Scanning electron photomicrographs (SEM) of *Micracanthodinium setiferum*. 1. Ventral view of *M. setiferum* f. *spinosa* Mertens & Carbonell-Moore *forma nov.* (with setae), specimen from the Indian Ocean 2. Ventral view of *M. setiferum* f. *anacantha* (without setae), specimen from the Indian Ocean. 3. Comparison of the small size of *M. setiferum* with an average peridinioid. Cell from the Indian Ocean. 4. Dorsal view of *M. setiferum* f. *anacantha*, specimen from the Indian Ocean. 5. Left side view of *M. setiferum* f. *anacantha* from the Indian Ocean. 6. Apical pore complex (APC) of *M. setiferum* f. *anacantha* from the Indian Ocean, showing pore plate (P_o) and cover plate (P_t). 7. Apical pore complex (APC) of *M. setiferum* f. *anacantha* from the Coral Sea showing pore plate (P_o), cover plate (P_t), X plate (X). Single pore plates are indicated by black arrows. Scale bars = 1: 4 µm; 2, 4–5: 5 µm; 3: 10 µm; 6–7: 1 µm.

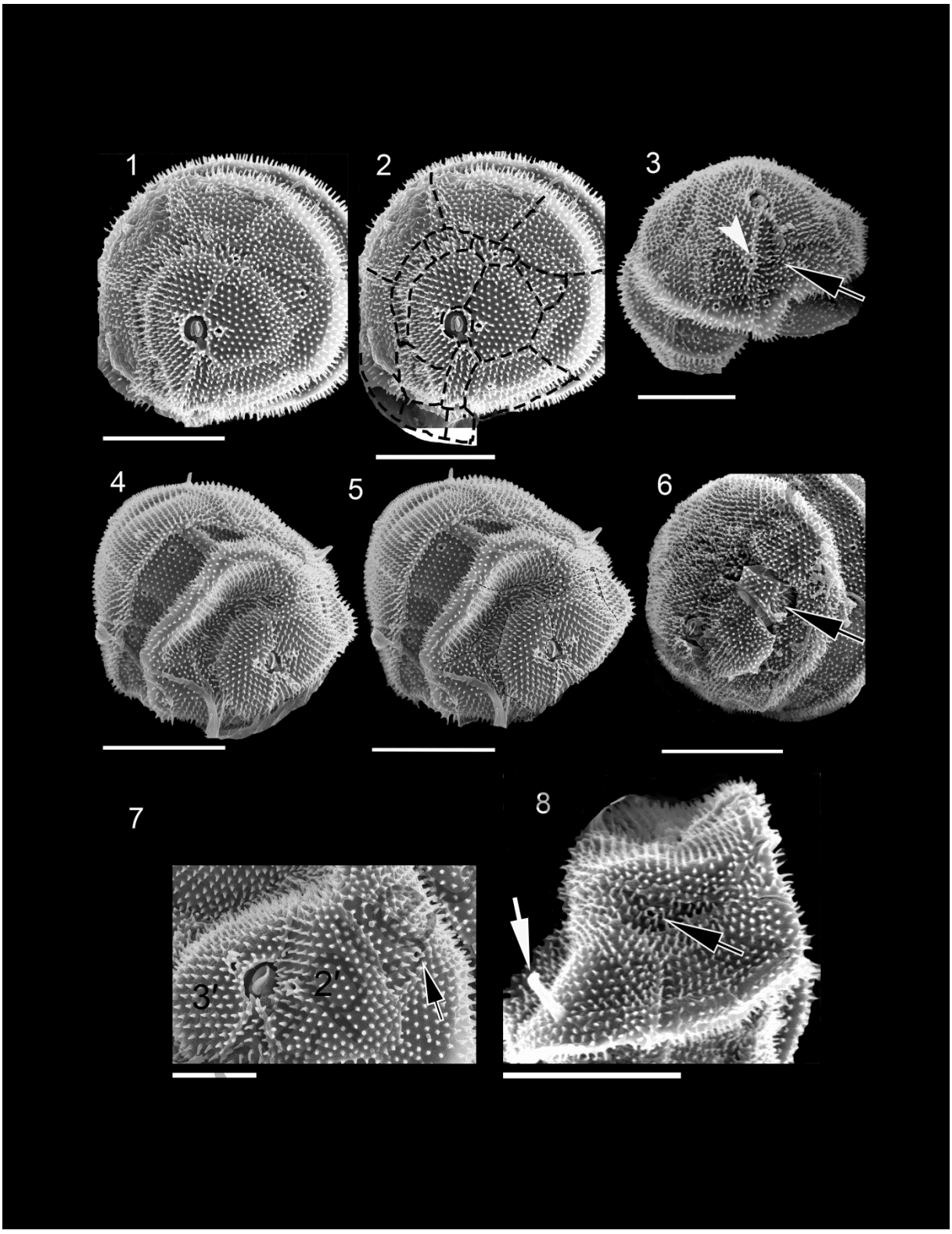

1
2
3
4
5
6
7
3'
2'
8

Plate 2. Scanning electron photomicrographs (SEM) of *M. setiferum.* Notice the similitude in appaerance of cells from different locations. f. *anacantha*. 1–2. Apical view, interpreted tabulation is shown in 2. Cell from the Coral Sea. 3. Ventro-apical view showing first apical plate and anterior sulcal plate. Cell from the Equatorial Atlantic. f. *spinifera.* 4–5. Dorso-apical view, interpreted tabulation is shown in 5. Cell from the Indian Ocean. f. *anacantha*. 6. Apical-left view. Arrow points to the first anterior intercalary plate. Cell from the Indian Ocean. f. *spinifera.*7. Detail of the epitheca of cell shown in 4 and 5. Notice the large size of second and third apicals. Arrow points to the pore on the left of the first anterior intercalary plate. f. *spinifera.* 8. Different cell. Right side of the epitheca. White arrow points to a broken seta. Black arrow points to the fourth anterior intercalary plate, with one pore in the middle. Specimen from the Indian Ocean. Scale bars = 1–2, 4–6: 5 µm; 3,8: 4 µm; 3: 10 µm; 7: 2 µm.

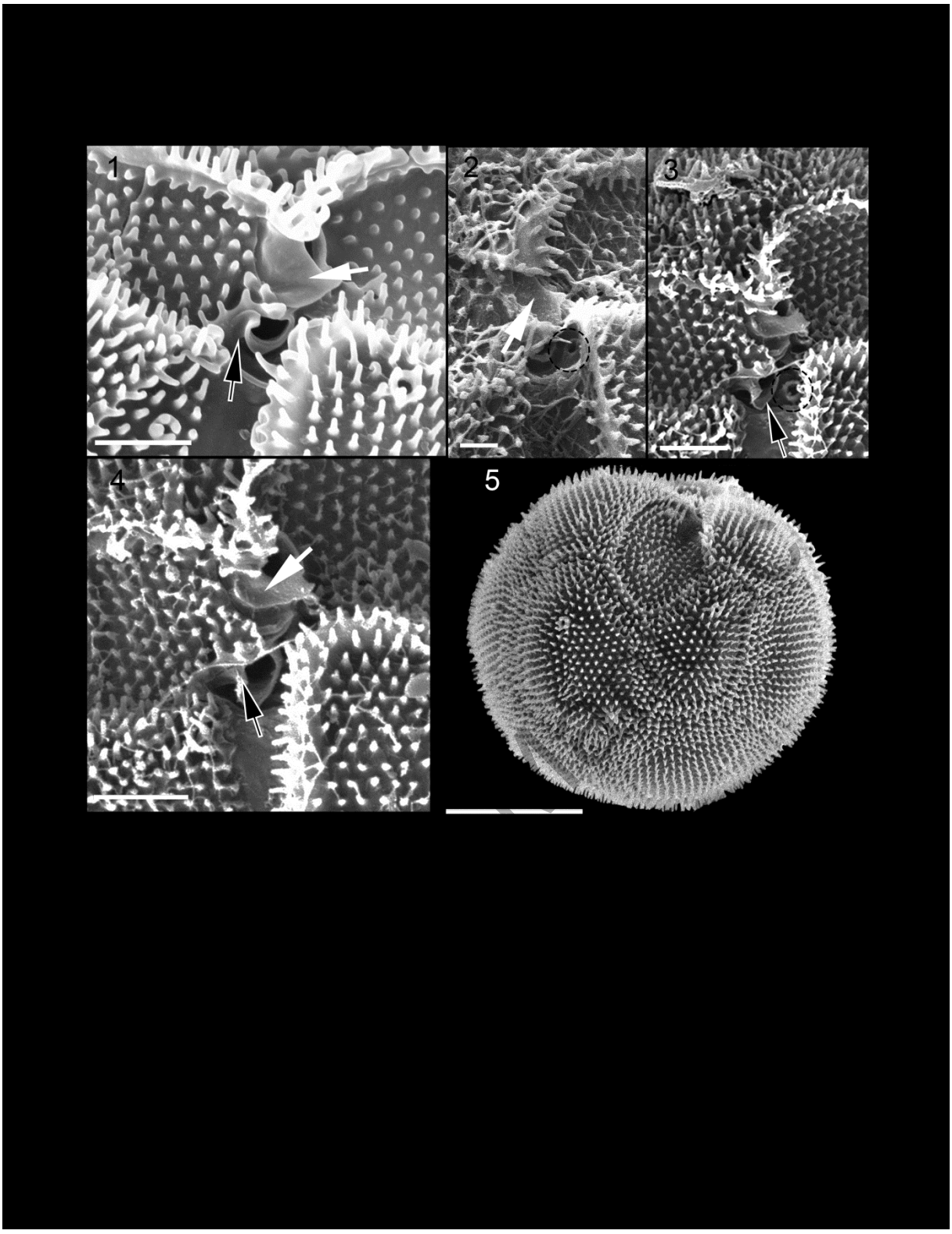

1
2
3
4
5

Plate 3. Scanning electron photomicrographs (SEM) of *M. setiferum. M. setiferum* f. *anacantha.*1–4. External views of sulcus showing external features. 1. Cell from the North Atlantic. White arrow indicates the flange of the right anterior sulcal plate (Sd). Black arrow the anterior posterior sulcal. 2. Cell from the Indian Ocean. Dashed circle encircles the pore on the Spa plate. 3–4 Different cell from the Indian Ocean. Dashed circle shows the same pore. Note that the pore is not visible in 4. Black arrows points to the flange of the Spa plate 5. Antapical view of cell shown in 1. Partiform hypotheca. Scale bars = 1– 4: 1 µm; 5: 4 µm.

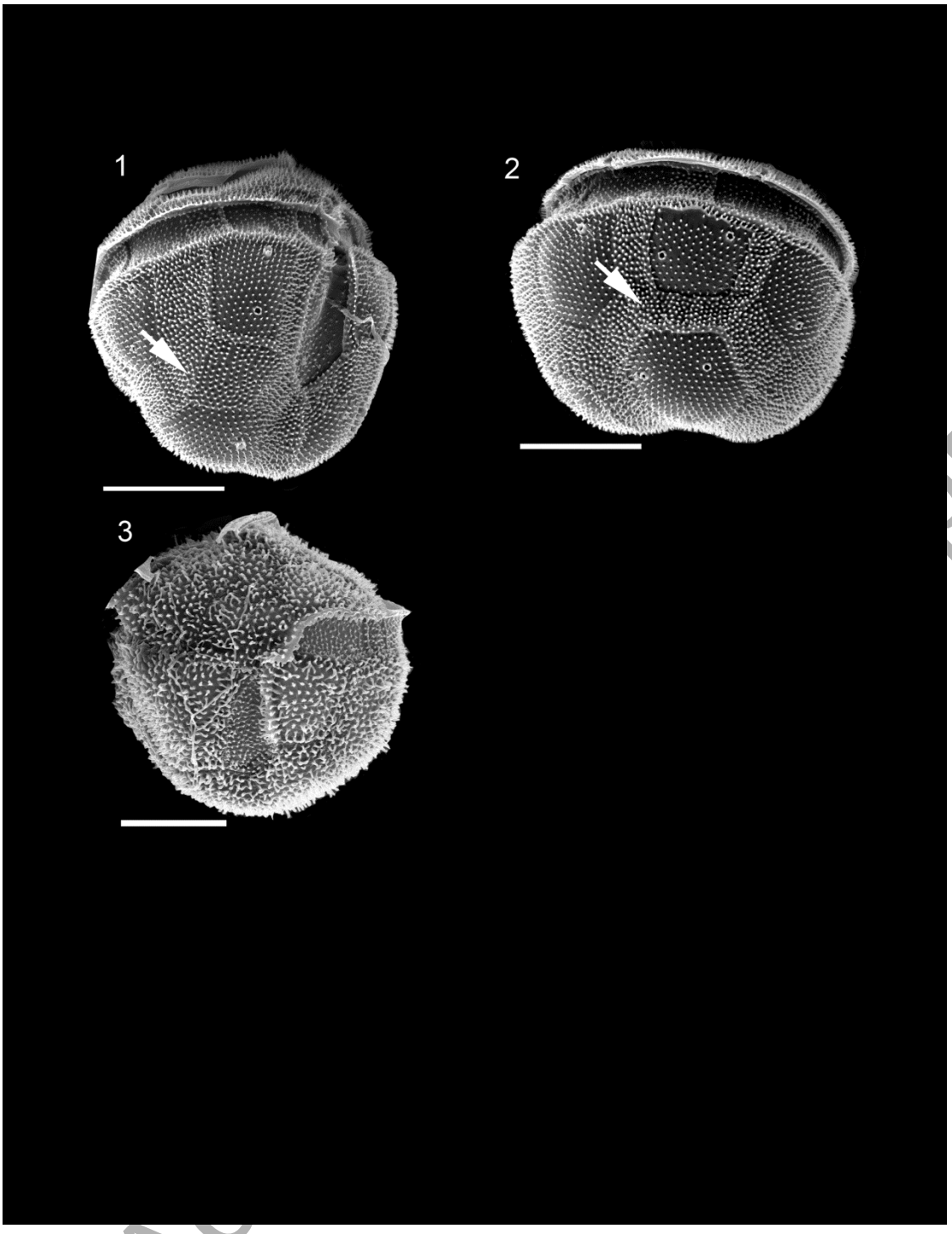


Plate 4. 1–2. Scanning electron photomicrographs (SEM) of *M. setiferum* f. *anacantha*. Different growth bands. Different specimen from the Indian Ocean. 3. *Micracanthodinium* sp. Cell from the North Atlantic, similar to Dodge (1995) figure 2. All scale bars = 5 µm.

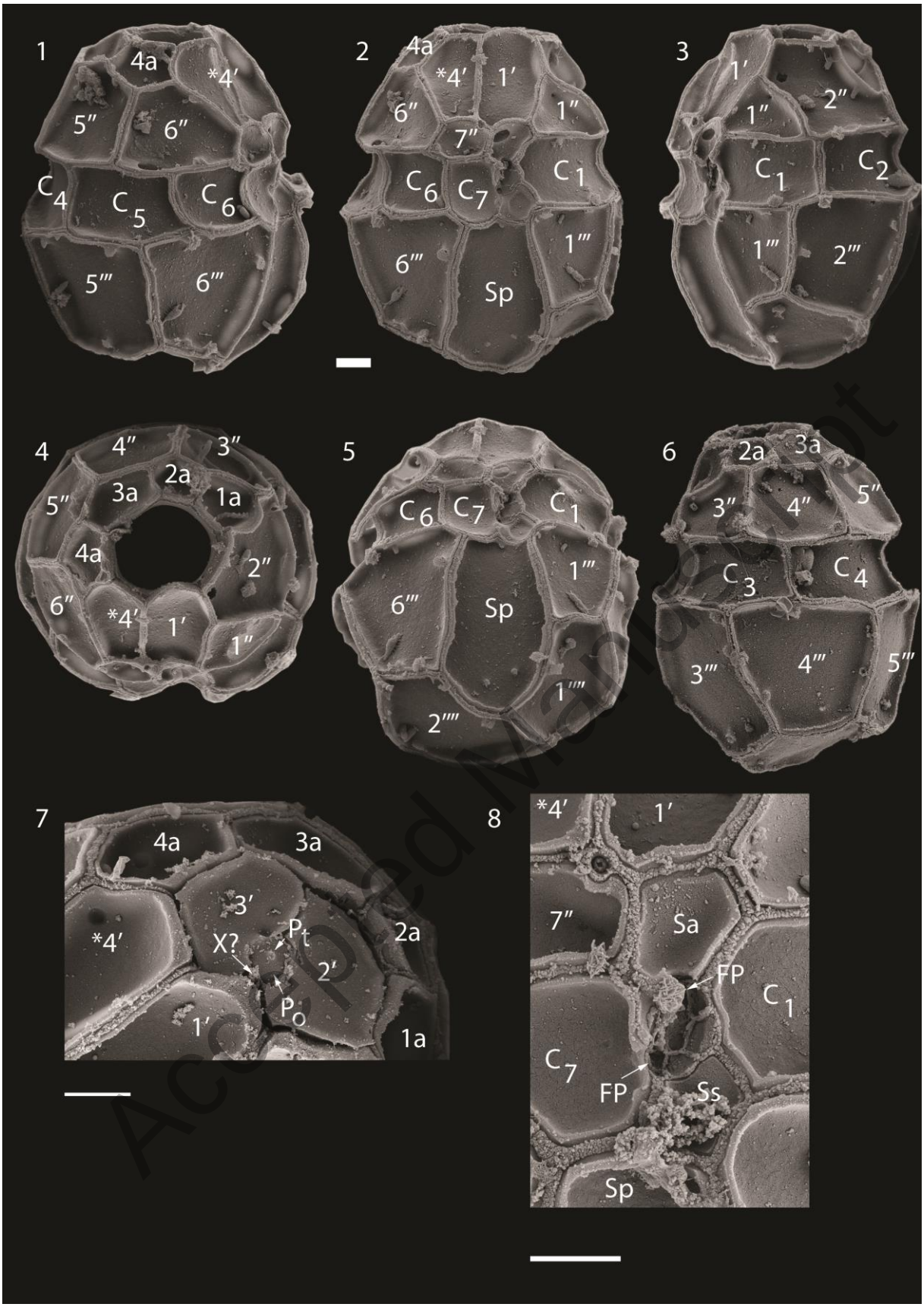


Plate 5. Scanning electron photomicrographs (SEM) of *Cladopyxidium saeptum.* 1. Ventro-lateral view. 2. Ventral view. 3. Ventro-lateral view. 4. Apical view. 5. Ventro-antapical view. 6. Dorsal view. 7. Focus of apical plates. 8. Sulcal plates and ventral pore (=porichnion) located between *4′, 1′ and 7″. All scale bars = 10 μm.

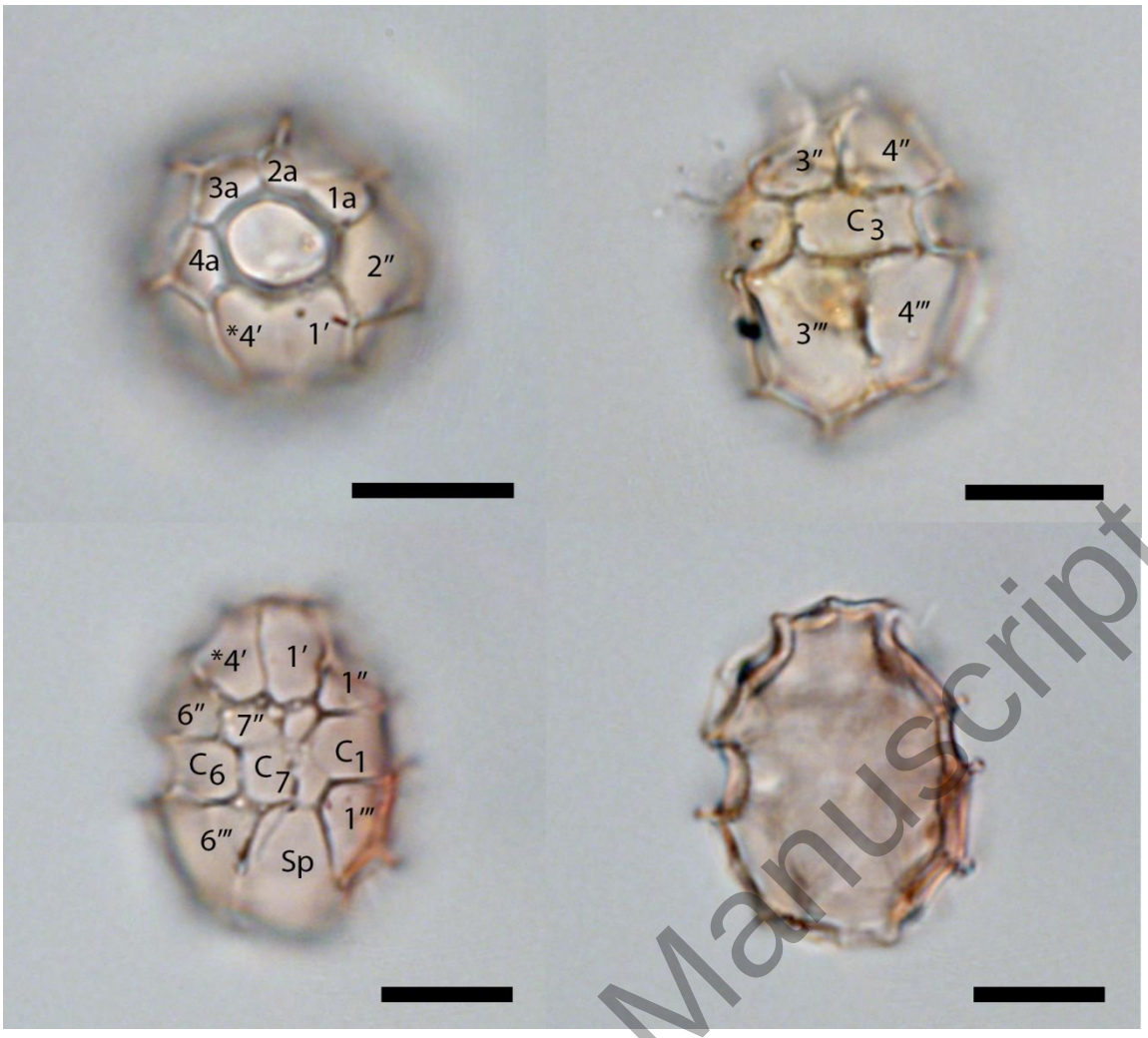


Plate 6. Light micrographs of *Cladopyxidium saeptum* (sample L110302). 1. Apical view. 2. Dorsal view. 3. Ventral view. 4. Mid-focus of cyst shown in 3. All scale bars = 10 μm.

Table 1. Detailed location and measurements of cells of *Micracanthodinium* referred to in this study.

SEM ID	FIGURE THIS STUDY	CAMPAIGN NAME	STATION NR.	Number on map	LATITUDE		LONGITUDE		STUB ID	Length (µm)	Dorso-Ventral (µm)	Width (µm)	SEM ID
1487	Plate 1 Figure 1	WOCE I-2 (Indian Ocean)	1233	7	5.0413°	S	45.2797°	E	Stub 1109	11	-99	10	1487
6091	Plate 1 Figure 2	WOCE I-2 (Indian Ocean)	1238	9	4.4638°	S	42.1112°	E	Stub 07-Mar 24, 2017	11	-99	11	6091
5462	Plate 1 Figure 3	WOCE I-2 (Indian Ocean)	1238	9	4.4638°	S	42.1112°	E	Stub 02-Feb 05, 2017	-99	30	33	5462
5389	Plate 1 Figure 4	WOCE I-2 (Indian Ocean)	1239	10	4.3605°	S	41.537°	E	Stub 09-Mar 24, 2017	11	-99	11	5389
2102	Plate 1 Figure 5	WOCE I-2 (Indian Ocean)	1233	7	5.0413°	S	45.2797°	E	Stub 1108	-99	-99	-99	2102
5099	Plate 1 Figure 6	WOCE I-2 (Indian Ocean)	1238	9	4.4638°	S	42.1112°	E	Stub 02-Feb 05, 2017	-99	-99	-99	5099
4679	Plate 1 Figure 7	Coral Sea Sp 16/80	8	3	19.3°	S	151.5°	E	Stub 04-June 17, 2016	9	10	11	4679
4679	Plate 2 Figure 1	Coral Sea Sp 16/80	8	3	19.3°	S	151.5°	E	Stub 04-June 17, 2016	9	10	11	4679
4679	Plate 2 Figure 2	Coral Sea Sp 16/80	8	3	19.3°	S	151.5°	E	Stub 04-June 17, 2016	9	10	11	4679
4658	Plate 2 Figure 3	EQUALANT 1	67	4	2 °	N	37.42°	W	Stub 01-June 17, 2016	11	-99	11	4658
4001	Plate 2 Figure 4	WOCE I-2 (Indian Ocean)	1243 to 1244	11	4.1055°	S	40.1167°	E	Stub 1243-1244-Jun 2011	11	-99	11	4001
4001	Plate 2 Figure 5	WOCE I-2 (Indian Ocean)	1243 to 1244	11	4.1055°	S	40.1167°	E	Stub 1243-1244-Jun 2011	11	-99	11	4001
3058	Plate 2 Figure 6	WOCE I-2 (Indian Ocean)	1239	10	4.3605°	S	41.537°	E	Stub 01-May 14, 2013	12	-99	12	3058
4001	Plate 2 Figure 7	WOCE I-2 (Indian Ocean)	1243 to 1244	11	4.1055°	S	40.1167°	E	Stub 1243-1244-Jun 2011	11	-99	11	4001
5126	Plate 2 Figure 8	WOCE I-2 (Indian Ocean)	1238	9	4.4638°	S	42.1112°	E	Stub 01-Feb 05, 2017	13	-99	-99	5126
5594	Plate 3 Figure 1	NAAMES 3	3	1	47.083°	N	40.08°	W	Stub 10-Jan 26, 2018	11	10	11	5594
3848	Plate 3 Figure 2	WOCE I-1 (Indian Ocean)	1090	6	7.9992°	S	98°	E	Stub 08-May 01, 2014	10	8	11	3848
3044	Plate 3 Figure 3	WOCE I-2 (Indian Ocean)	1239	10	4.3605°	S	41.537°	E	Stub 01-May 14, 2013	16	13	15	3044
3044	Plate 3 Figure 4	WOCE I-2 (Indian Ocean)	1239	10	4.3605°	S	41.537	E	Stub 01-May 14, 2013	16	13	15	3044
5594	Plate 3 Figure 5	NAAMES 3	3	1	47.083°	N	40.08°	W	Stub 10-Jan 26, 2018	11	10	11	5594
5289	Plate 4 Figure 1	WOCE I-2 (Indian Ocean)	1235	8	4.7917°	S	43.925°	E	Stub 06-Mar 24, 2017	15	-99	11	5289
5289	Plate 4 Figure 2	WOCE I-2 (Indian Ocean)	1235	8	4.7917°	S	43.925°	E	Stub 06-Mar 24, 2017	15	-99	11	5289
5753	Plate 4 Figure 3	NAAMES 3	5	2	51.6548°	N	39.4879°	W	Stub 04-Feb 22, 2018	15	19	16	5753
4658	Suppl. Infor. Plate 1, Figure 1	EQUALANT 1	67	4	2 °	N	37.42°	W	Stub 01-June 17, 2016	11	-99	11	4658
2102	Suppl. Infor. Plate 1, Figure 2	WOCE I-2 (Indian Ocean)	1233	7	5.0413°	S	45.2797°	E	Stub 1108	-99	-99	-99	2102
3848	Suppl. Infor. Plate 1, Figure 3	WOCE I-1 (Indian Ocean)	1090	6	7.9992°	S	98°	E	Stub 08-May 01,2014	10	8	11	3848
4162	Suppl. Infor. Plate 1, Figure 4	R/V Meteor MED 112	214	5	37.4762°	N	17.1438°	E	Stub 03-Jan 19, 2015	14	11	15	4162
1487	Suppl. Infor. Plate 1, Figure 5	WOCE I-2 (Indian Ocean)	1233	7	5.0413°	S	45.2797°	E	Stub 1109	11	-99	10	1487
3050	Suppl. Infor. Plate 1, Figure 6	WOCE I-2 (Indian Ocean)	1239	10	4.3605°	S	41.537°	E	Stub 01-May 14, 2013	11	-99	11	3050
3056	Suppl. Infor. Plate 1, Figure 7	WOCE I-2 (Indian Ocean)	1239	10	4.3605°	S	41.537°	E	Stub 01-May 14, 2013	11	-99	10	3056
5753	Suppl. Infor. Plate 2, Figure 1	NAAMES 3	5	2	51.6548°	N	39.4879°	W	Stub 04-Feb 22, 2018	15	19	16	5753
5753	Suppl. Infor. Plate 2, Figure 2	NAAMES 3	5	2	51.6548°	N	39.4879°	W	Stub 04-Feb 22, 2018	15	19	16	5753
4693	Suppl. Infor. Plate 2, Figure 3	Coral Sea Sp 16/80	8	3	19.3°	S	151.5°	E	Stub 04-June 17, 2016	17	15	14	4693
4693	Suppl. Infor. Plate 2, Figure 4	Coral Sea Sp 16/80	8	3	19.3°	S	151.5°	E	Stub 04-June 17, 2016	17	15	14	4693
5753	Suppl. Infor. Plate 2, Figure 5	NAAMES 3	5	2	51.6548°	N	39.4879°	W	Stub 04-Feb 22, 2018	15	19	16	5753