

Diversity of calcareous dinoflagellate cysts in surface sediments of Gullmar Fjord, Sweden – an unrecognized gene pool of the Thoracosphaeraceae (peridinean dinoflagellates)

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Abstract An unexpectedly diverse and unusual association of calcareous dinoflagellate cysts (Thoracosphaeraceae) is reported from surface sediments of Gullmar Fjord, Sweden. The association is interpreted to be extant and comprises eight taxa, five of which have not been previously reported from this area. The taxa are *Calcigonellum elongatum*, *Caracomia arctica*, *Leonella granifera*, *Praecalacigonellum schizosaeptum*, *Scrippsiella acuminata*, *S. lachrymosa*, *S. rotunda*, and *Scrippsiella* sp. aff. *S. trifida*. The association is unique, as it combines pelagic and neritic taxa previously not found together, which might be explained by the highly seasonal environmental conditions of Gullmar Fjord. The recovered cysts reveal a variety of new morphological and ultrastructural details: *P. schizosaeptum* has a radial ultrastructure and most likely a Type A archaeopyle; wall-forming crystals of *C. elongatum* and *S. lachrymosa* show a compound ultrastructure, while those of *P. schizosaeptum* and *S. rotunda* grow epitaxially. Such differences in the ultrastructure of the wall forming crystallites suggest the possibility of fundamentally different biomineralisation mechanisms in calcareous dinoflagellates. At least two distinct species are currently united in *S. rotunda*, with cysts described from the Gulf of Naples, Norway and the China Sea being different to those of the type locality and Gullmar Fjord. Among the taxa recovered from Gullmar Fjord are rare species with an uncommon combination of morphological features, and include species whose molecular data is currently unavailable. An inclusion of their molecular data, particularly that of *C. arctica* and *P. schizosaeptum*, into phylogenetic reconstructions would be crucial to further elucidate the ongoing discussion on the systematic significance of the various cyst characters, such as archaeopyle-, ultrastructure-, and tabulation-type.

Keywords calcareous dinoflagellate cysts, Thoracosphaeraceae, Gullmar Fjord, *Caracomia*, *Praecalacigonellum*, ultrastructure.

1. Introduction

All dinoflagellates forming cysts enforced by or made of calcium carbonate belong to the monophyletic peridinean family Thoracosphaeraceae (Elbrächter *et al.*, 2008), a taxon that has been shown to also include many non-calcifying taxa, such as the microcarnivorous *Pfesteria*, as well as endosymbiotic forms (e.g. Gottschling *et al.*, 2012; Gottschling & Söhner, 2013). At present, about 38 modern species are known to form calcareous cysts and molecular data are available for 21 of these taxa (Gottschling *et al.*, 2005a, b; Attaran-Fariman & Bolch, 2007; Zinssmeister *et al.*, 2012; Gu *et al.*, 2013; Craveiro *et al.*, 2013).

The systematics of calcareous dinoflagellates is notoriously problematic, as two parallel and originally independent taxonomic systems are applied to the group: a ‘neontological’ system, mainly based on the morphology of the theca, and a ‘paleontological’ system, based on characters of the calcareous cysts. Both systems are currently not readily compatible. Cysts of extant calcareous dinoflagellates show a much wider morphological variety than the observed thecae, which have a highly conserved

plate tabulation pattern. Initially, only three theca-types were distinguished, reflected in the ‘neontologically’ described genera *Enciculifera*, *Pentapharsodinium* and *Scrippsiella*, genera now also known to include species with organic walled cysts. This is opposed by currently 20 extant and about 260 fossil genera whose descriptions are based on, or emphasize, cyst morphology (Streng *et al.*, 2004a; Elbrächter *et al.*, 2008; Gottschling & Soehner, 2013). Taxonomic complications arose when germination experiments with cysts of the cyst-based genera generated motile stages fitting the diagnoses of either *Scrippsiella*, *Pentapharsodinium* or *Enciculifera* (e.g. Janofske & Karwath, 2000; Montresor *et al.*, 2003).

Key characters for distinguishing calcareous dinoflagellate motile cells are the number and shape of epithecal, hypothecal, cingular and sulcal plates, and the presence or absence of a spine on the first cingular plate C1 (also referred to as the T-plate), although the motile cell of *Thoracosphaera* is described as an athecate dinoflagellate (Tangen *et al.*, 1982; Inouye & Pienaar, 1983; Karwath, 2000). Diagnostic cyst characters comprise archaeopyle

morphology, tabulation (if present), cyst wall ultrastructure (including crystallography), and shape (e.g. Streng *et al.*, 2004a, 2009; Meier *et al.*, 2009).

The crystallographic orientation of the c-axes of the calcite crystals constituting the cyst wall was first considered taxonomically important by Keupp (1981). He distinguished three wall types (radial, oblique, and pithonelloid) that formed the basis for his calcareous dinoflagellate classification and taxonomy (Keupp, 1987, 1991). Streng *et al.* (2002, 2004a) challenged this classification scheme and considered archaeopyle characteristics to be more indicative when considering high-rank phylogenetic relationships.

The first molecular studies using nuclear ITS and LSU rRNA sequence data were performed to resolve the discrepancy between the ‘neontological’ and the ‘palaeontological’ system. They confirmed the monophyly of calcareous dinoflagellates as a group of calcifying and non-calcifying taxa (D’Onofrio *et al.*, 1999; Montresor *et al.*, 2003; Gottschling *et al.*, 2005a; Kremp *et al.*, 2005), i.e., the family Thoracosphaeraceae. Three monophyletic groups are segregated within the family, namely, the E/Pe clade (species of *Ensiculifera* and *Pentapharsodinium*); the heterogeneous T/Pf clade (including species of *Thoracosphaera*, *Pfisteria*, *Leonella*, and *Posoniella*); and *Scrippsiella sensu lato* (including cyst-based taxa such as *Calciodinellum*, *Calcigonellum*, and *Pernambugia*). *Scrippsiella s.l.* appears to be closely related to the T/Pf-clade. The validity of the three clades was confirmed by subsequent molecular studies, which included additional calcareous taxa (e.g. Zinssmeister *et al.*, 2012; Gu *et al.*, 2013).

Molecular data helps to identify character polarity and to reconsider morphological concepts in taxonomy. The phylogenetic hypothesis of increasing complexity in archaeopyle formation already put forward by Keupp and Versteegh (1989), and further reinforced by Streng *et al.* (2004a), is supported by the retrieved molecular trees (e.g. Gottschling *et al.*, 2005a; Zinssmeister *et al.*, 2012; Gu *et al.*, 2013), showing extant taxa with a simple archaeopyle are paraphyletic (clades E/Pe and T/Pf), while representatives with a combination archaeopyle are monophyletic (i.e. *Scrippsiella s.l.*). In contrast, molecular data did not support cyst wall ultrastructure as a significant character when considering high-rank systematics. The oblique wall type is found in the E/Pe clade, while the tangential wall type is putatively dominant in *Scrippsiella s.l.* However, the radial, tangential and oblique wall types are found in the T/Pf clade.

Although molecular data is available for almost two thirds of known extant calcareous dinoflagellate taxa, the resulting molecular phylogenetic reconstructions still must be considered biased. The majority of the sequenced taxa have cysts with a combination archaeopyle (mesoepicystal or epitrectal) and a tangential ultrastructure, whereas taxa representing other combinations of archaeopyle type and

ultrastructure are underrepresented or not represented at all. Hence, to fully assess the significance of cyst characters for phylogenetic reconstructions, these taxa should also be included. Key taxa here would be *Caracomia arctica* (Gilbert & Clark, 1983) Streng *et al.*, 2002, the only extant species known combining a combination archaeopyle with a radial ultrastructure; *Praecalacigonellum schizosaeptum* Versteegh, 1993, one of only two known extant species with a simple apical archaeopyle and a radial ultrastructure; or *Calciperidinium asymmetricum* Versteegh, 1993, the only species with a presumed intercalary archaeopyle. However, accessibility of these taxa is hampered by their rareness and/or occurrences in remote places. Herein, we report a diverse extant association of calcareous dinoflagellate cysts from surface sediments of the easily accessible Gullmar Fjord of the Swedish west coast, an association that includes two of the key taxa, *C. arctica* and *P. schizosaeptum*. In addition, the association includes *Calciodinellum elongatum* (Hildebrand-Habel *et al.*, 1999) Meier *et al.*, 2002 *ex* Streng *et al.*, 2006 and *Scrippsiella rotunda* Lewis, 1991 *ex* Head, 1996 whose molecular data are also still unknown.

2. Material and methods

Surface sediments of the outer Gullmar Fjord have been analyzed for calcareous dinoflagellate cysts. The samples were retrieved during January 2005 by carefully sampling the sediment surface of two boxcorers taken at two nearby sites: sample 1 at 58.2692°N, 11.4809°E (water depth 47m), and sample 2 at 58.2668°N, 11.4840°E (water depth 38m) (Figure 1). The obtained sediments were refrigerated at 5°C until processing in the laboratory one week after sampling. The samples were washed through 90 and 20 micron sieves and the obtained fractions were dried in an oven at 40°C. The 20–90µm fractions were checked under a binocular microscope for their content of cysts as well as associated microorganisms. Due to the relatively high organic and siliciclastic content of the samples, cysts were relatively rare in the fractions and time-consuming to pick. For this reason, cysts were concentrated by gently swirling the fractions in an evaporating dish with some water. This helps to separate the light organic material from heavier “clastic” content. The thus separated clastic material had a significantly higher cyst content than the initial homogeneous fraction and has been picked preferentially. This, however, means that the retrieved cyst association may differ from the natural percental composition of the association. About 100 cysts have been picked from the two samples and analyzed for this study.

Cysts and associated material were mounted on aluminum stubs with adhesive carbon tape, sputter-coated with a gold-palladium alloy, and photographed using a field emission scanning electron microscope (Zeiss Supra35VP) at the Evolutionary Biology Center (Microscopy Unit) of Uppsala University. All material is deposited

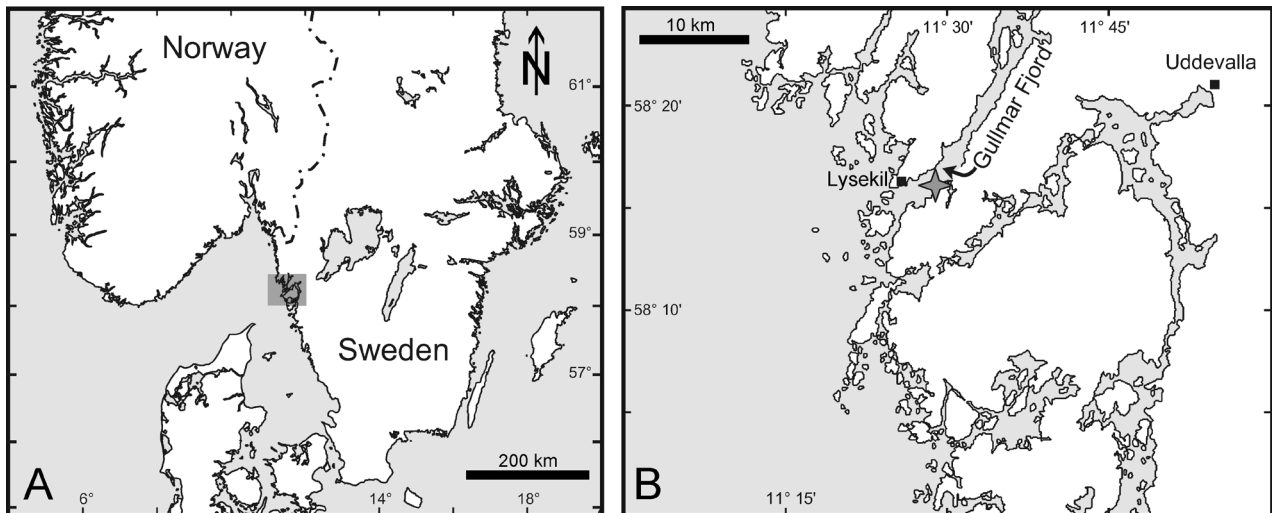


Figure 1: A. Map of southern Scandinavia with area shown in B indicated. B. Detail map of the Swedish west coast showing sample site (star) in Gullmar Fjord

at the Museum of Evolution, Uppsala University, under the collection number PMU 29987.

3. Results

The analyzed samples from Gullmar Fjord yielded an unexpectedly high number of calcareous dinoflagellate taxa contrasting previous phytoplankton studies from the same area (e.g. Persson *et al.*, 2000; Godhe *et al.*, 2001; McQuoid, 2005). The recovered associations include at least eight different morphotypes, which can be assigned to seven species, i.e., *Calciodinellum elongatum*, *Caracomia arctica*, *Leonella granifera*, *Praecalcionellum schizosaepum*, *Scrippsiella acuminata*, *S. lachrymosa*, and *S. rotunda*. Only *S. acuminata*, *S. lachrymosa*, and potentially *C. elongatum* had previously been described from Gullmar Fjord (Godhe *et al.*, 2001, see below). The eighth morphotype is described under open nomenclature as *Scrippsiella* sp. aff. *S. trifida*. Cysts of *Scrippsiella trifida* reported by Godhe *et al.* (2001) from sediment traps in Gullmar Fjord have not been observed.

Caracomia arctica (Gilbert & Clark, 1983)

Streng *et al.*, 2002

Caracomia arctica f. *arctica* Autonym

Plate 1

Description: Cysts of *Caracomia arctica* f. *arctica* from Gullmar Fjord ($n = 25$) match previous reports in cyst shape, spherical to ovaloidal, and in the habitus of the wall-forming crystals. Maximum diameter of recovered cysts ranges from 28.7–47.7 μm (mean 39.8 μm , $n = 17$), with 2.5–3.9 μm thick cyst walls (c. 8% of cyst diameter, $n = 6$). An approximately 0.2 μm thick, inner organic wall has been observed in all hatched cysts. Hatched cysts normally show the typical, bilaterally symmetrical outline of the mesoepticyst archaeopyle (Pl. 1, figs A, B), but irregular archaeopyle(?) outlines have been observed

as well (Pl. 1, fig. E). Distal terminations of wall-forming crystals are trigonal with a polylobate outline, occasionally affected by dissolution, resulting in flattened crystal tips and revealing an axial canal homologous to the one observed in *C. arctica* f. *rossensis* (Streng *et al.*, 2011).

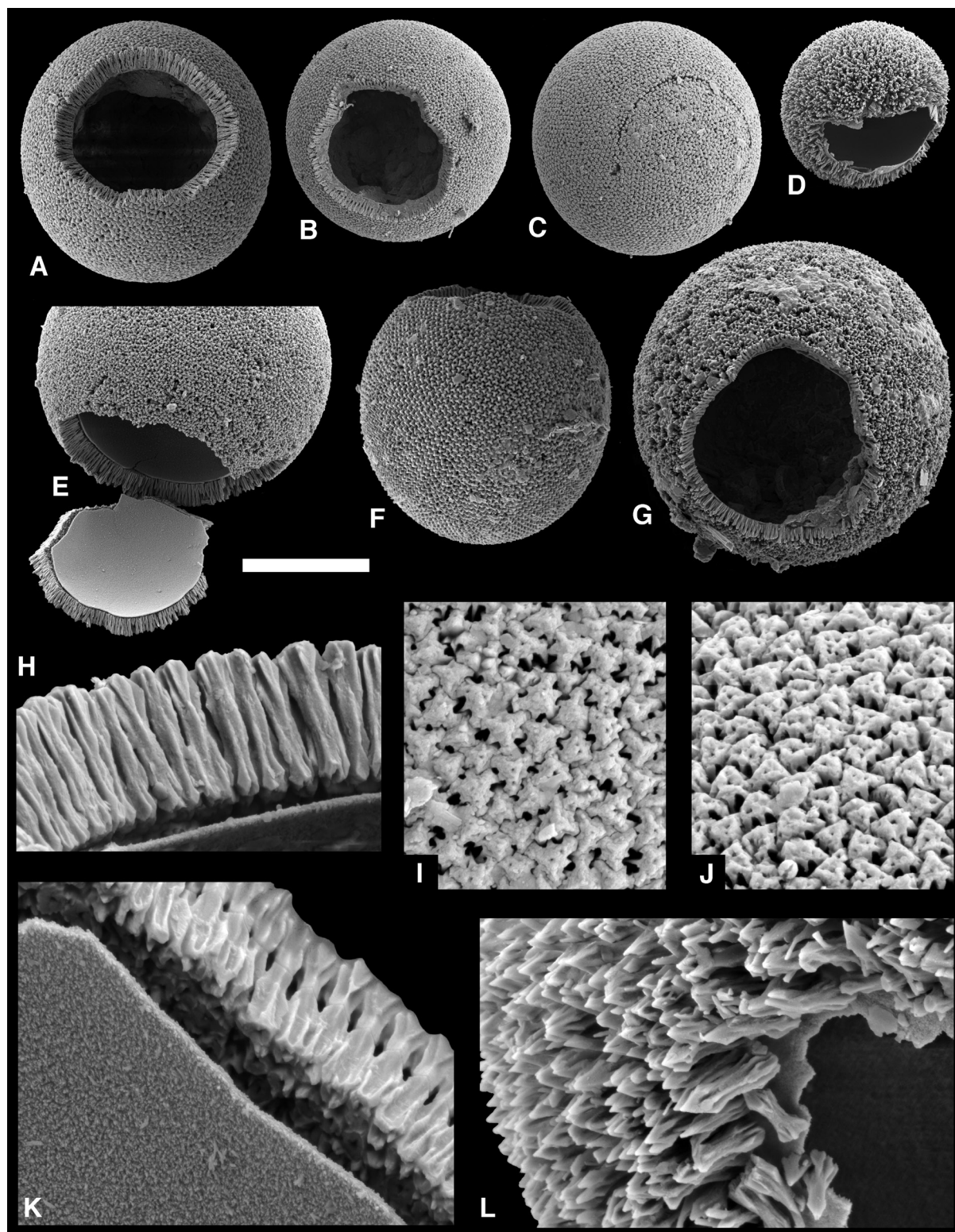
Remarks: The species *Caracomia arctica* currently includes five *formae* (see Streng *et al.*, 2009; 2011), distinguished by differences in the habitus of the wall-forming crystals. Cysts from Gullmar Fjord are best compared with the type and paratypes of *Caracomia arctica* as originally described by Gilbert & Clark (1983) from the central Arctic Ocean. The same taxon has later been reported from the South Atlantic Ocean, the southern Indian Ocean and the Ross Sea, Antarctica (Streng *et al.*, 2002, 2011; Vink, 2004). The Gullmar Fjord cysts are, however, significantly smaller than the 65–105 μm type series (Gilbert & Clark, 1983), but match specimens from the Kerguelen Plateau (Streng *et al.*, 2002).

Praecalcionellum schizosaepum Versteegh, 1993

Plate 2

Description: Eight cysts show the typical tabulation pattern of *P. schizosaepum*. A flattened, convex, cryptotabulate epicyst with a rounded, pentagonal outline is separated by a ridge from an oligotabulate hypocyst. The epicyst bears a central pentagonal to subcircular archaeopyle, interpreted to represent plate 3'. The hypocyst bears a small, triangular sulcal zone and five postcingular plates. The two antapical plates are fused to form the angled antapical ridge, the vertex of which points ventrally (Pl. 2, fig. C; Figure 2). The cyst walls are built of radially arranged, rod-like crystals with triradiate symmetry. Proximally, crystals emerge from a narrow base with an equilateral, triangular outline with side lengths ranging from about 0.21–0.25 μm . The width of crystals increases rapidly and reaches a more or less constant width after 0.4–0.6 μm (Pl. 2, fig. F). Distally,

Plate 1. *Caracomia arctica* f. *arctica*



Cysts of *Caracomia arctica* f. *arctica* Autonym from Gullmar Fjord. Scale bar equals 20 μm for cysts (A–G) and 2.5 μm for close-ups (H–L). **A, B:** Hatched cysts showing typical mesoepicystal archaeopyle (specimens mic04-b09 and mic03-d18). **C:** Complete cyst with archaeopyle suture partly visible (mic03-e08). **D:** Relatively small cyst with irregular opening (archaeopyle?) (mic03-d23). **E:** Cyst with irregular archaeopyle and corresponding operculum (mic04-a08). **F:** Slightly ovoidal cyst in lateral view (mic02-i04). **G:** Relatively large open cyst (mic02-a02). **H, I:** Wall cross-section and outer cyst surface of another cyst (mic03-h15). **J:** Cyst surface of 'C'. **K:** Wall cross-section with inner organic layer of 'E'. **L:** Wall-forming crystals of cyst seen in 'D'.

the triradiate crystals are $0.35\text{--}0.5\mu\text{m}$ wide in intratabulate areas, but can become broader when forming sutural ridges. The length of crystals also varies, reaching around $1.5\mu\text{m}$ in intratabulate areas and up to $6.9\mu\text{m}$ as part of sutural ridges (Pl. 2, fig. E). Occasionally, wall-forming crystals show faint inclined lines on their lateral faces, indicative of a potential epitaxial crystal growth. The morphological long-axis of the wall forming crystals corresponds with the crystallographic c-axis. Remains of a thin inner organic layer are occasionally observed (Pl. 2, fig. E).

Remarks: Interpretation of the archaeopyle of *P. schizosaeptum* is not straight forward, as relatively large, circular archaeopyles have been described from the type material (Versteegh 1993). Furthermore, the configuration of the epicyst of *P. schizosaeptum* appears very similar to *Juergenella*, for which a mesoepicystal archaeopyle has been shown (see discussion in Streng *et al.*, 2009). However, some of the cysts from Gullmar Fjord show a clear pentagonal outline of the archaeopyle (Pl. 2, fig. B) indicative of plate 3' only, confirming the original interpretation by Versteegh (1993).

For the first time, the crystallographic ultrastructure has been analyzed for *P. schizosaeptum* by examining a

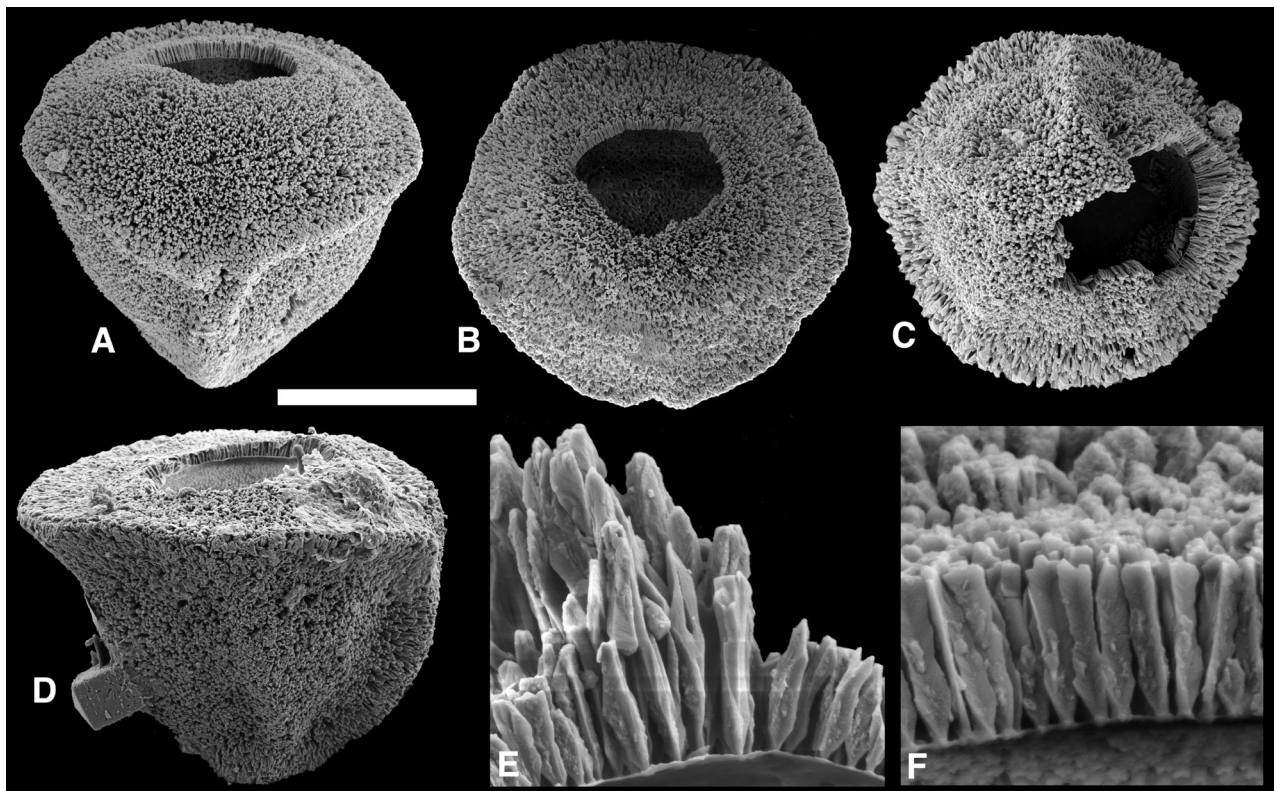
complete cyst under the light microscope. Under polarized light and with the gypsum plate employed, the cyst showed identical interference colors as *Leonella granifera*, with yellow colors in quadrant I and III, and blue colors in quadrant II and IV (compare, e.g., Meier *et al.*, 2009: fig. 5E). This arrangement is characteristic for cysts with a radial crystallographic ultrastructure, i.e., the c-axes of the wall forming crystals are radially arranged.

Leonella granifera (Fütterer, 1977) Janofske & Karwath in Karwath, 2000

Pl. 3, figs F–K

Description: Cysts of *L. granifera* ($n = 24$) are spherical in shape and measure $23.5\text{--}32.2\mu\text{m}$ in diameter (mean $26.9\mu\text{m}$, $n = 23$). Most cysts are complete and show a distinctly delineated, circular operculum. Hatched cysts accordingly show a circular archaeopyle and an about $1.5\text{--}2.0\mu\text{m}$ thick wall. No organic inner wall has been observed. The appearance of the outer cyst surface is quite variable, ranging from smooth without distinguishable terminations of wall forming crystals, to evenly textured surfaces with tri-radiate crystal terminations resembling three-bladed propellers, to irregular

Plate 2. *Praecalzigonellum schizosaeptum*



Cysts of *Praecalzigonellum schizosaeptum* Versteegh, 1993 from Gullmar Fjord. Scale bar equals $20\mu\text{m}$ for cysts (A–D), $4\mu\text{m}$ (E), and $2\mu\text{m}$ (F). **A, B:** Hatched cyst in sulcal and apical view (mic03-g20). **C:** Cyst in antapical view (mic04-g04); sulcus points upwards. **D:** Hatched cyst in lateral view (mic03-d14). **E:** Cross-section of cyst wall showing increased lengths of wall-forming crystals when forming sutural ridges (mic04-g03). **F:** Cross-section of cyst wall showing morphology of wall forming crystals; detail of 'A'.

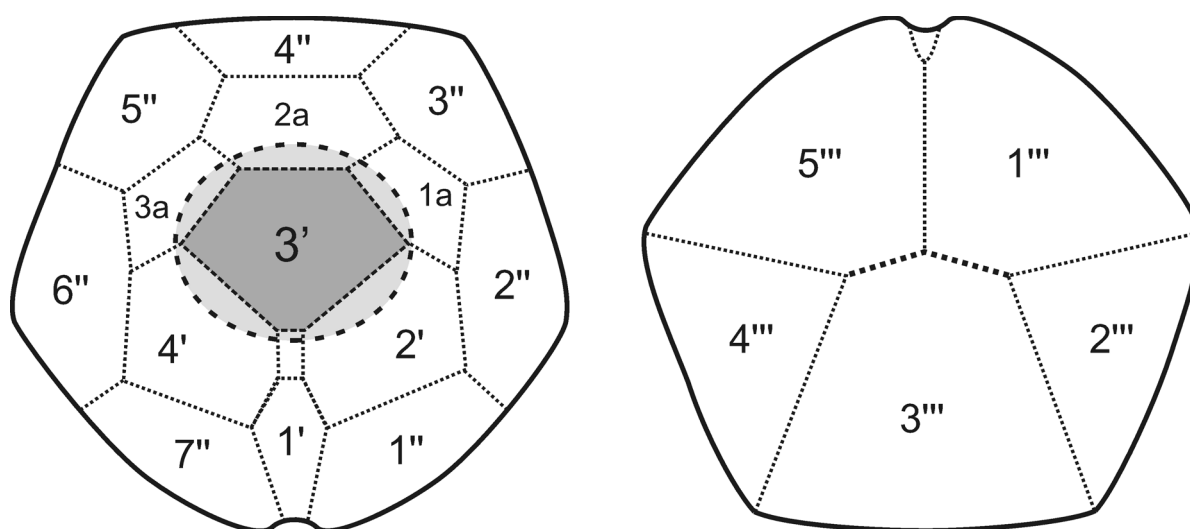


Figure 2: Reconstruction of cyst tabulation of *Praecalcionellum schizosaeptum* Versteegh, 1993 in apical (left) and antapical view (right) with a Type A archaeopyle

surfaces affected by early diagenetic (?) crystal growth (Pl. 3, figs F–J).

Remarks: The variability of the cyst surfaces observed in *L. granifera* from Gullmar Fjord suggests that cysts of this species are easily affected by early diagenesis. Bison *et al.* (2007, pl. 1, fig. 5, 7) illustrated cysts of *L. granifera* from the Pliocene of Cyprus showing a similar phenomenon. One of the specimens (Bison *et al.*, 2007 p. 1, fig. 7), with its secondarily enlarged crystals on the outer surface, resembles cysts of *Fuetererella deflandrei* (Kamptner 1956). In fact, cysts described as *F. deflandrei* by Streng *et al.* (2004a, b) from the Miocene might rather represent *L. granifera*.

Calciadinellum elongatum (Hildebrand-Habel *et al.*, 1999) Meier *et al.*, 2002 *ex* Streng *et al.*, 2006
Pl. 3, figs A–E

Description. Five cysts have been assigned to *Calciadinellum elongatum*, all of which are somewhat elongate ovoidal in shape. Three cysts are complete and two cysts represent collapsed cysts revealing an inner organic layer. The complete cysts measure 31.2–31.5 μm in length and 26.4–27.7 μm in width (length-width ratio 1.13–1.18, $n = 3$). Cyst walls are about 2.2 μm thick and built of a single layer of rhombohedral crystals, which can have a skeletal appearance (Pl. 3, Fig. E). Complete cysts show an irregular, round archaeopyle suture delineating a c. 20 μm wide operculum. Apical position, shape and size of the operculum (measuring about 2/3 of cyst diameter) indicate a mesoepicystal archaeopyle. Wall-forming crystals show an internal ultrastructure of minute nanocrystals that are arranged in a regular, three-dimensional fabric to form a rhombohedral element. This may indicate a compound structure.

Remarks: In modern environments, *C. elongatum* was so far only known from open marine settings of the

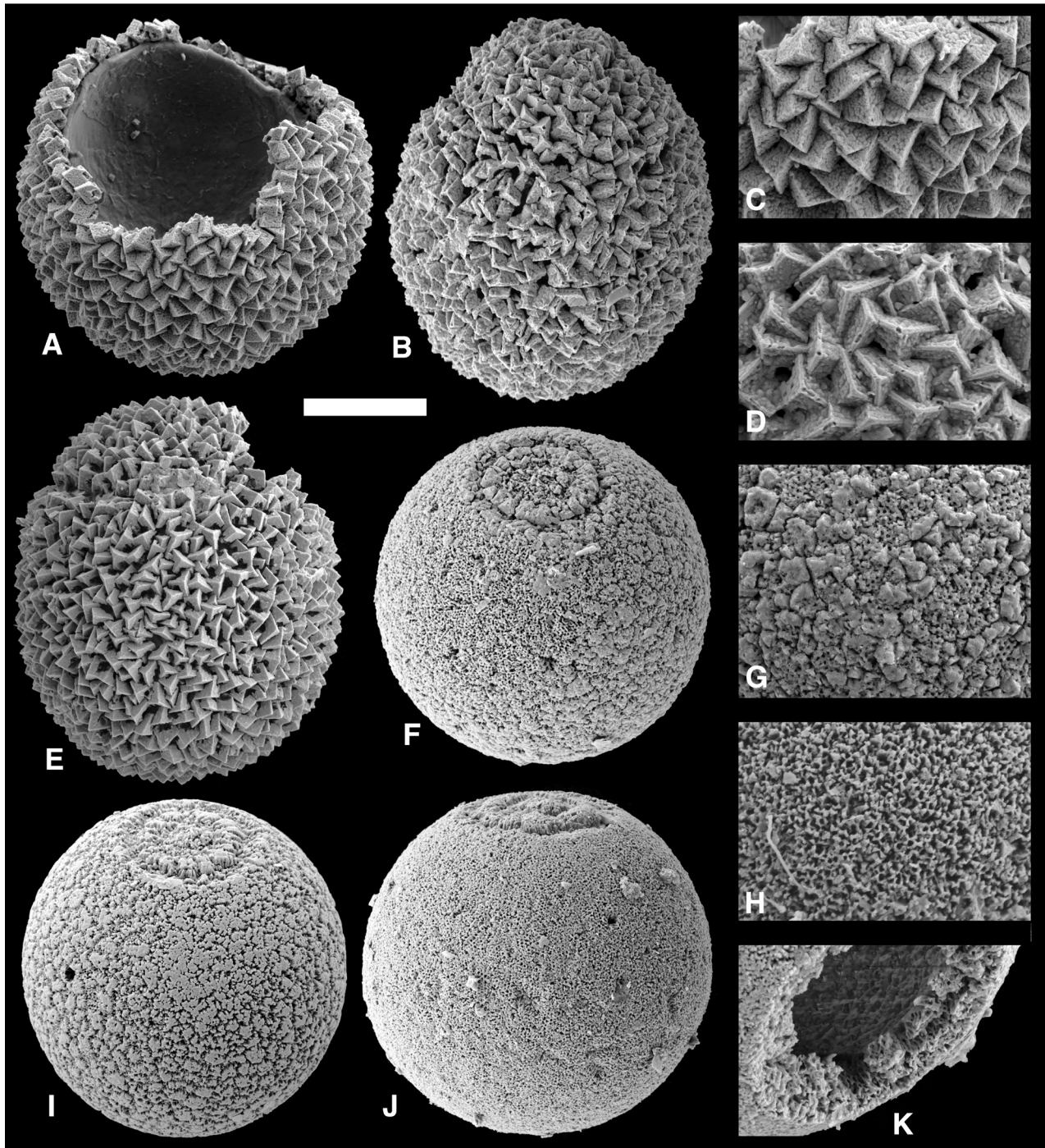
Mediterranean Sea and potentially the central Pacific (see Meier *et al.*, 2002 for details). This is the first report of *C. elongatum* from a more restricted marine environment.

Cysts of *C. elongatum* are distinguished from similar cysts of *C. levantinum* by their ovaloidal shape. Cyst of *Scrippsiella crystallina* Lewis, 1991 *ex* Head, 1996 are like *C. elongatum*, ovaloidal in shape, having a mesoepicystal archaeopyle and a single-layered wall made of rhombohedral crystals, suggesting a tangential ultrastructure. Cysts of both taxa are distinguished by the more elongate shape of *S. crystallina* (length-width ratio 1.33–1.42, as measured from illustration in Lewis, 1991), as well as their bigger wall-forming crystals. Specimens previously reported as *S. crystallina* from Gullmar Fjord (Godhe *et al.*, 2001) are likely to be co-specific with the specimens of *C. elongatum*.

Scrippsiella lachrymosa Lewis, 1991 *ex* Head, 1996
Pl. 4, figs A–C

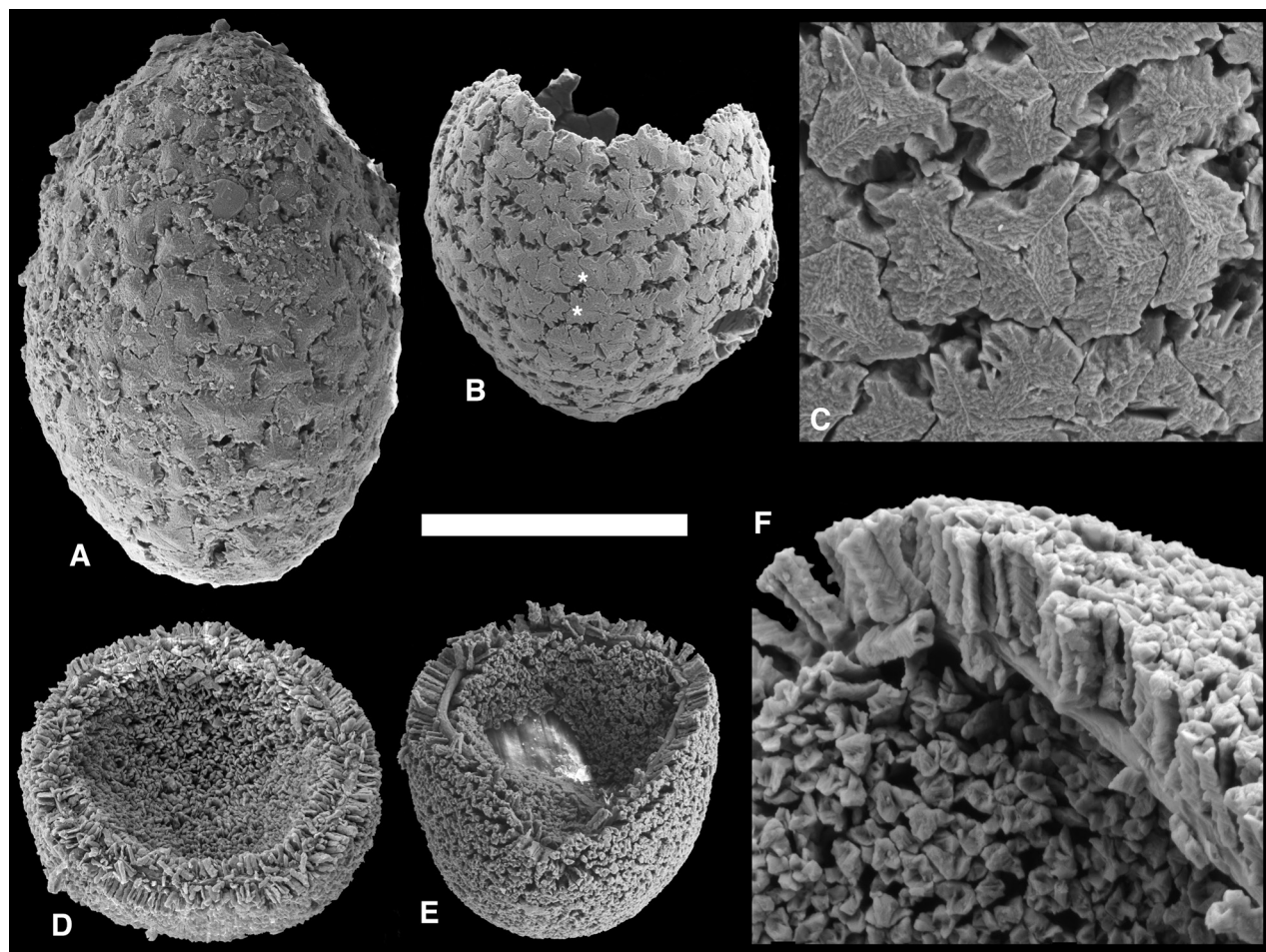
Description: Only two cysts of *S. lachrymosa* were recovered, a complete cyst and an imperfect hatched cyst (Pl. 4, figs A, B). The imperfect cyst measures 26.1 μm in width; the complete cyst is 28.6 μm wide and 41.8 μm long. The cyst wall is about 1.2 μm thick and consists of a single layer of flattened crystals with irregular outline measuring 1.5–2.8 μm in diameter. Distally, crystals display three faint faces representing the tip of a very flattened rhombohedron. A fine canal penetrates the crystals centrally and three faint sutures representing the edges of the rhombohedron radiate from it. A similar tri-radiate pattern is observed on the proximal crystal faces forming the interior surface of the cyst. An internal ultrastructure of minute nanocrystals forming each crystal can be seen (Pl. 4, fig. C). Wall forming crystals are irregularly arranged except for the equatorial area of the cysts. Here, two parallel rows of crystals are visible

**Plate 3. *Calciadinellum elongatum* (A–E) and
Leonella granifera (F–K)**



Calciadinellum elongatum (Hildebrand-Habel *et al.*, 1999) Meier *et al.*, 2002 *ex* Streng *et al.*, 2006 (A–E) and *Leonella granifera* (Fütterer, 1977) Janofske & Karwath *in* Karwath, 2000 (F–K) from Gullmar Fjord. Scale bar equals 10 μ m for cysts (A, B, E, F, I, J) and 5 μ m for close-ups (C, D, G, H, K). **A:** Incomplete cyst with collapsed inner organic layer (mic04-b19). **B:** Complete cyst with archaeopyle suture visible (mic04-f09). **C:** Detail of cyst surfaces of 'A'. **D:** Cyst surface of a complete cyst (mic04-c12). **E:** Complete cyst with skeletal wall-forming crystals (mic04-c18). **F, I, J:** Three different complete cysts with outer cyst surfaces showing different textures (mic04-d18, mic04-f15, and mic03-f12). **G:** Cyst surface of specimen mic04-d12. **H:** Cyst surface of specimen mic03-h01. **K:** Archaeopyle and cross section of cyst wall (mic04-e04).

Plate 4. *Scrippsiella lachrymosa* (A–C) and *Scrippsiella* cf. *rotunda* (D–F)



Scrippsiella lachrymosa Lewis, 1991 ex Head, 1996 (A–C) and *Scrippsiella* cf. *rotunda* Lewis, 1991 ex Head, 1996 (D–F) from Gullmar Fjord. Scale bar equals 20 μm for cysts (A, B, D, E) and 5 μm for close-ups (C, F). A: Complete cyst in lateral view (mic04-e01). B: Incomplete cyst with cingulum indicated by equatorial double-row of crystals (mic03-f18) (rows marked by asterisks). C: Detail of 'B' showing cyst surface with tri-radiate crystals. D, E: Two collapsed complete cysts (mic04-f02 and mic04-d15). F: Detail of 'E' showing organic inner layer and epitaxially grown wall-forming crystals.

in one specimen denoting the cingulum (Pl. 4, fig. B; see also Lewis, 1991: fig. 30).

Remarks: Wall-forming crystals with a flat proximal surface and a general tri-radiate pattern are also observed in *S. acuminata*, *S. trifida*, *S. regalis*, and *S. triquetracapitata*, whereas other species of *Scrippsiella* show rhombohedral crystals (e.g. *S. kirschiae* and *S. bicarinata*; see Zinssmeister *et al.*, 2012). In phylogenetic analyses the rhombohedral taxa are distinct from *S. acuminata* (Zinssmeister *et al.*, 2012), suggesting that crystal types might be indicative of certain clades. However, cysts of *S. kirschiae* and *S. bicarinata* also differ from the "tri-radiate" taxa in being tabulated, pointing towards the importance of tabulation in distinguishing clades and taxa. As no molecular data of *S. trifida*, *S. regalis*, or *S. triquetracapitata* is currently available, neither hypothesis can be corroborated.

Scrippsiella rotunda Lewis, 1991 ex Head, 1996
Pl. 4, figs D–F

Description. Three cysts are assigned to *Scrippsiella rotunda*, all of which are collapsed revealing an organic layer below the calcareous layer (Pl. 4, figs E, F). Originally, the cysts appeared to have been spherical to ovaloidal in shape with estimated maximum diameters of 25–30 μm . Measured diameters of two of the cysts are 23.6 and 27.1 μm , respectively. The calcareous layer is built of 1.8 to 2.0 μm long, rod-like crystals characterized by a compressed, diamond-shaped cross section, measuring 0.3 and 0.7 μm in diameter, respectively. Individual crystals seem to have grown epitaxially as indicated by the fine lines visible on the lateral faces of the crystals. All cysts are complete and no archaeopyle suture has been observed. The collapsed state of the cysts indicates a weak coalescence between the individual wall forming crystals.

Remarks. The cysts from Gullmar Fjord match the original description and illustration of *S. rotunda* from the west coast of Scotland, including the poor stability of the cysts (Lewis 1991). The only character that could not be confirmed in the Swedish material is the presence of a mesoepicystal archaeopyle. Although the epitaxial growth of the wall forming crystals has not been mentioned by Lewis (1991), it is visible in the illustration of the cyst wall (Lewis, 1991: fig. 51). Curiously, subsequent illustrations of the species from the Gulf of Naples (D'Onofrio *et al.*, 1999; Nuzzo & Montresor, 1999) and the China Sea (Gu *et al.*, 2011) show cysts that differ from the type material, although the cysts are of equal dimensions. Cysts assigned to *S. rotunda* from the Gulf of Naples have smooth cyst surfaces and seemingly larger and flat distal tips of the wall forming crystals. Additional details of the wall forming crystals have neither been described nor illustrated. It is likely that these cysts might, in fact, represent a new species. Accordingly, the molecular data also available for *S. rotunda*, based on specimens from the Gulf of Naples, the eastern North Atlantic (Gottschling *et al.*, 2005a, b) and the China Sea (Gu *et al.*, 2011), would be of the undescribed species. Extant cysts described by Ishikawa & Taniguchi (1993) as *S. rotunda* from the Onagawa Bay, Japan might be close to the type material, but the illustrations and description do not allow a detailed comparison.

The crystallographic ultrastructure of *S. rotunda* is unknown, however, the epitaxial growth of the crystals might indicate a radial orientation of the c-axes, analogous to *Caracomia stella* (Streng *et al.*, 2002) and *P. schizosaepum* (see above). This would further mean that *Scrippsiella rotunda* would be the first known species with a typical *Scrippsiella*-type motile stage, but having a cyst with a mesoepicystal archaeopyle and a radial, rather than a tangential, ultrastructure. The latter two characters are diagnostic for the cyst-based taxon *Caracomia* (Streng *et al.*, 2002). Due to the lack of sufficient material, a radial ultrastructure could not be determined by light microscopy.

Scrippsiella acuminata (Ehrenberg, 1836)

Kretschmann *et al.*, 2015

Pl. 5, figs A–J

Description: Cysts assigned to *Scrippsiella acuminata* are most common among the specimens recovered ($n = 35$). They are ovoidal to spherical in shape, measuring 29.2–40.4 μm in equatorial diameter and 29.5–49.1 μm in length, including spines. This corresponds to diameters of 24.6–33.1 μm and lengths of 23.8–40.4 μm without spines ($n = 10$). Accordingly, spine lengths of up to 4.5 μm have been measured. The cyst wall is built of a single layer of thumbtack-shaped calcareous crystals, characterized by a 2.6–3.7 μm broad basal plate with an irregular, tri-radiate outline and a central spine. Cross-sections of spines are generally triangular in outline, but are often polygonal as spines display more than three

edges. The distal surface of the basal plate is ornamented by regular or irregular radiating ridges, whereas the base of the spine, i.e. the transition between basal plate and spine, typically shows fine pits. Spines can be pointed or blunt or weakly capitate. An inner organic layer is generally present and can be seen in collapsed cysts or through gaps between individual wall forming crystals.

Remarks: Kretschmann *et al.* (2015) recently demonstrated that *S. acuminata* is the senior synonym of *S. trochoidea* (von Stein, 1883) Loeblich III, 1976.

Scrippsiella sp. aff. *S. trifida* Lewis, 1991 ex Head, 1996

Pl. 5, figs K–N

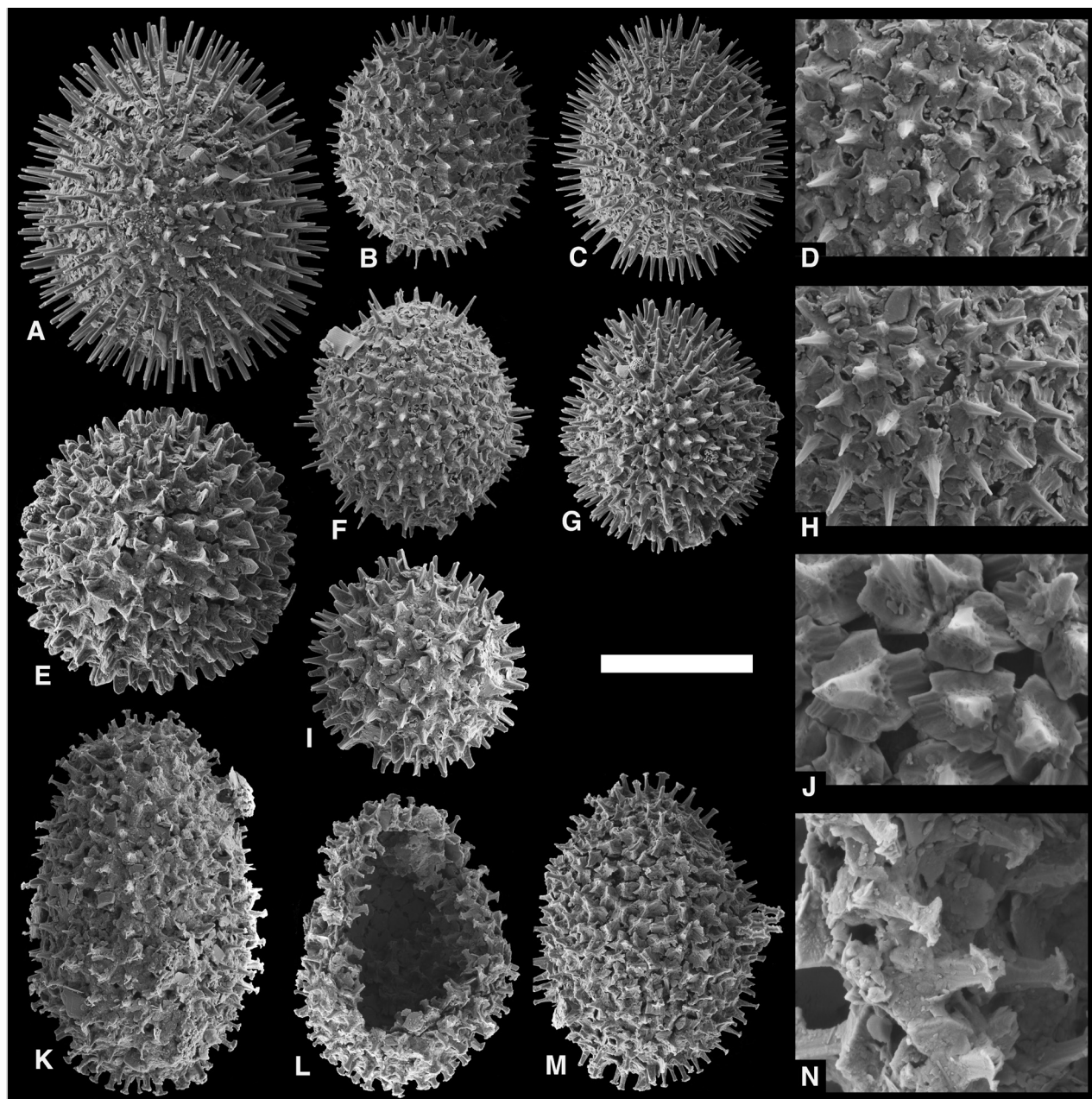
Description: Five elongated cysts with capitate spines appear to be distinct from the majority of other spiny cysts described as *S. acuminata* above. The cysts are ovoidal to elongate ovoidal in shape measuring 39.0–50.7 μm in length and 26.8–32.4 μm in width (including spines). The cyst wall is built of a single layer of spine-like, triradiate crystals, characterized by a 2.5–3.0 μm wide basal plate with irregular outline from whose center a capitate spine arises. Spines are triangular in cross-section and are less than 2.5 μm long. Distally, spines flare out and form a triangular head. A central fine canal appears to penetrate the wall forming crystals, running from the midpoint of the flat proximal side of the basal plate to the distal tip of the spines. No clear archaeopyles or archaeopyle sutures have been observed.

Remarks: Cysts of *S. trifida*, as originally described by Lewis (1991) and later by Head *et al.* (2006), are characterized by relatively large wall-forming crystals with trifurcate, recurving or blunt spines. Spines are enclosed between an inner and outer organic wall layer, both of which are most likely made of dinosporin (Head *et al.*, 2006), which makes them resistant to taphonomic processes. Despite common observations of organic layers in other cysts from Gullmar Fjord (*C. arctica*, *S. cf. rotunda*, *C. elongatum*, *P. schizosaepum*), none of the five cysts described as *Scrippsiella* sp. aff. *S. trifida* has any organic layer preserved. Furthermore, the wall-forming crystals of the Swedish specimens appear to be too small and the spines are not recurving to be readily compared with *S. trifida*. Similar cysts with capitate spines have previously been described by, e.g., Montresor *et al.* (1994: fig. 12a) and Joyce (2004: fig. 10), as *Scrippsiella trochoidea* (= *S. acuminata*), although neither capitate spines were mentioned in the re-description of *S. trochoidea* by Janofske (2000) nor from the type area of *S. acuminata* (Kretschmann *et al.*, 2015).

Associated micro-fauna and -flora

When searching for calcareous dinoflagellate cysts under a binocular microscope, objects of a similar size have also been picked, which did not turn out as calcareous cysts. Thus, a variety of other taxa have been observed, which include 1) organic-walled dinoflagellate cysts and

**Plate 5. *Scrippsiella acuminata* (A–J) and
Scrippsiella sp. aff. *S. trifida* (K–N)**



Scrippsiella acuminata (Ehrenberg, 1836) Kretschmann, *et al.*, 2015 (A–J) and *Scrippsiella* sp. aff. *S. trifida* Lewis, 1991 ex Head, 1996 (K–N) from Gullmar Fjord. Scale bar equals 20 μm for cysts (A–C, E–G, I, K–M), 8 μm (D, H) and 4 μm (J, N) for close-ups. A–C, E–G, I: Ovoid to spherical cysts illustrating morphological variability of morphotypes assigned to *S. acuminata* (A, mic04-d10; B, mic03-g13; C, mic04-d14; E, mic04-d08; F, mic03-g01; G, mic04-f10; I, mic03-h19). D, H, J: Close-ups of outer cyst surfaces; D: detail of 'F'; H: detail of 'C'; J: detail of 'G'. K–M: Elongate ovoid to ovoid cysts of *Scrippsiella* sp. cf. *S. trifida* (K, mic04-d01; L, mic03-g05; M, mic03-f05). N: Detail of 'L' showing capitate wall-forming crystals.

other cyst like objects, e.g. *Bitectatodinium tepikiense* Wilson and *Spiniferites*-like cysts; 2) tests of agglutinating tintinnids, i.e. *Stenosemella nivalis* (Meunier), *S. ventricosa* (Claparède & Lachmann) and *S. punctata* (Wailes); 3) tests of benthic foraminifera, e.g., common *Bulimina marginata* d'Orbigny, *Buliminella borealis*

Haynes, *Lagena* spp. and early growth stages of various other taxa; and 4) individual spherical sponge spicules, i.e. *Geodia*-like sterrasters. Few coccoliths of, e.g., *Coccolithus pelagicus* (Wallich) Schiller or *Emiliania huxleyi* (Lohmann) Hay & Mohler, have been observed as tintinnid test constituents.

4. Discussion

The recovered cysts originate from surface sediments, hence it is reasonable to assume that they are extant rather than representing sub-Recent or Holocene fossils. This is supported by the presence of an inner organic layer in specimens of almost all species, except for *L. granifera* and *S. lachrymosa*. Typically, inner organic layers of calcareous cysts are not preserved in the fossil record, but some exceptions exist (e.g. Monnet, 1993). Of the species found in Gullmar Fjord, only *C. arctica* is known to have a durable inner organic layer that can withstand fossilization (Gilbert & Clark, 1983; Streng *et al.*, 2002, 2009). Furthermore, many cysts display signs of potential recent excystment. Hatched cysts often have their endocoel void of any sedimentary infill (Pl. 1, fig. E; Pl. 2, fig. B) likely to indicate recent hatching of the motile stage. Gullmar Fjord is also known for relatively high sedimentation rates, particularly in its deeper part, with up to several millimeters per year (e.g. Filipsson & Nordberg, 2010; Polovodova *et al.*, 2011). This further strengthens the interpretation of the recovered cysts being extant, although the sample locations are in shallower water, further to the mouth of the fjord for which no sedimentation rates are available.

However, the Swedish west coast is still in the process of glacio-isostatic uplift with the study area, rising by 2–3 mm per year (Pässe & Andersson, 2005; Cossellu & Nordberg, 2010). With this uplift, post-Pleistocene sediments of the fjord could become exposed and reworked along the coast and subsequently re-deposited within deeper parts of the fjord, potentially contaminating surface sediments with fossil specimens. We are not aware of any study that would suggest such a scenario for the investigated area.

Modern associations of calcareous dinoflagellate cysts comprising eight different morphotypes, as recovered in Gullmar Fjord, are not unusual. Pelagic and off-shore (water depths > 200 m) associations obtained from surface sediments comprise, e.g., up to 12 morphotypes in the Mediterranean Sea (e.g. Meier *et al.*, 2002), seven to nine morphotypes in the South Atlantic Ocean (e.g. Vink, 2004), and eight morphotypes in the South China Sea (Gu *et al.*, 2011). Associations from near shore and shallower environments, comparable to the conditions at the sample site in Gullmar Fjord, are typically less diverse (Lewis, 1991; Ishikawa & Taniguchi, 1993; Gu *et al.*, 2011; Soehner *et al.*, 2012), but associations with eight to nine morphotypes have been described from the Gulf of Naples and the Gulf of Salerno (Montresor *et al.*, 1994; Soehner *et al.*, 2012). Although the relatively high diversity of the Gullmar Fjord association is noteworthy, the really remarkable aspect is its composition. The recovered association is dominated by three taxa: *S. acuminata* (c. 33%), *C. arctica* (c. 23%) and *L. granifera* (c. 22%). This assemblage is also characterized by a unique combination of

typical neritic species (*Scrippsiella* spp. and *P. schizosaeptum*) and species previously only known from open oceanic settings (*C. arctica* and *L. granifera*). *Caracomia arctica* is the only cold water calcareous dinoflagellate species (Streng *et al.*, 2002) and since the Pleistocene the taxon is almost exclusively known from monospecific associations at high latitudes (Gilbert & Clark, 1983; Streng *et al.*, 2002, 2004b, 2011). Only Vink (2004) reported *C. arctica* in association with other calcareous cysts in surface sediments from offshore Argentina, where its occurrence is connected to the cold Falkland Current. Surprisingly, the environmental parameters that correlate with occurrences of *C. arctica* and *L. granifera* are quite opposite (Vink, 2004, tab. 4) and the two species have not been previously found in association. High abundances of *L. granifera* are characteristic for areas with substantial river input and nutrient enrichment (Vink, 2004). The high seasonality of the outer Gullmar Fjord with respect to surface water temperature, primary production, salinity, as well as stratification (Lindahl *et al.*, 1998, 2009) might be able to explain the seemingly heterogeneous association and the absence of certain taxa in the sediment study of Godhe *et al.* (2001), which only covered the period May–June. Hence, it is likely that vegetative cells of certain taxa, such as *C. arctica* or *L. granifera*, are only a seasonal part of the plankton assemblage and stay encysted during the environmentally unfavorable part of the year. With, e.g., water surface temperatures of the outer Gullmar Fjord fluctuating between c. 0°C in winter and over 20°C in summer, it is reasonable to assume that a coldwater species as *C. arctica* would avoid the warm months. Long-term sediment trap studies lasting at least one year are needed to resolve and investigate potential seasonality in calcareous cyst production.

5. Conclusions

- The diversity of calcareous dinoflagellate cysts in Gullmar Fjord is higher than previously documented and comprises at least nine different taxa or morphotypes: *C. arctica*, *P. schizosaeptum*, *C. elongatum* (= *S. crystallina* of Godhe *et al.*, 2001), *L. granifera*, *S. lachrymosa*, *S. rotunda*, *S. acuminata*, *S. sp. aff. S. trifida*, and *S. trifida*. Of these taxa, *C. arctica*, *P. schizosaeptum*, *L. granifera*, *S. rotunda*, and *S. sp. aff. S. trifida* have not been previously documented from this area.
- The recovered association is unique, combining pelagic and neritic taxa, as well as taxa with rather different environmental preferences. The strongly seasonal environmental conditions in the outer Gullmar Fjord might be able to explain the diverse and seemingly heterogeneous association.
- *C. arctica* and *C. elongatum* are reported for the first time to occur in a more restricted marine environment. Furthermore, the occurrence of *C. arctica* is the first report of this species from a modern, non-arctic environment.

- Cysts of *P. schizosaeptum* are demonstrated to have a radial ultrastructure and most likely a Type A archaeopyle.
- The occurrence of *S. rotunda* in Gullmar Fjord is probably only the second record of this species beside the type area. Other reported occurrences and the published molecular data are likely to belong to a new and undescribed taxon.
- Observed and described cyst characters of *S. rotunda* suggest reference to *Caracomia*, but ultrastructural details have to be verified first.
- Among the taxa reported from Gullmar Fjord are the following species whose molecular data is currently unavailable: *C. arctica*, *P. schizosaeptum*, *C. elongatum*, and *S. rotunda* sensu Lewis 1991. An inclusion of these molecular data, particularly of *C. arctica* and *P. schizosaeptum*, into phylogenetic reconstructions would be crucial to further elucidate the ongoing discussion on the systematic significance of the various cyst characters, such as archaeopyle-, ultrastructure-, and tabulation-type. The cysts of the two species display a combination of characters currently not represented by any sequenced calcareous dinoflagellate species and would add critical morphological diversity. Cryptotabulate cysts with a mesoepicystal archaeopyle and radial ultrastructure are characteristic for *C. arctica*, while and oligotabulate cysts with a simple apical archaeopyle and a radial ultrastructure are characteristic for *P. schizosaeptum*.
- Many of the studied cysts from Gullmar Fjord show ultrastructural details in the wall-forming crystals that have not been recognized before. Epitaxial growth in *S. rotunda* and *P. schizosaeptum* vs. the compound structures of *S. lachrymosa* and *C. elongatum* suggest the possibility of fundamentally different biomineralisation mechanisms in calcareous dinoflagellates.

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