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## A review of rare and less well known extant marine organic-walled dinoflagellate cyst taxa of the orders Gonyaulacales and Suessiales from the Northern Hemisphere

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### Abstract :

Dinoflagellate resting cysts with rare exception produce the only discrete link between the biology of extant dinoflagellate species and their fossil record. The geological preservability of such cysts allows them to be used for quantitative paleoecological reconstructions, especially in the Quaternary, and for biostratigraphy and the calibration of molecular clocks with the geological record. This contribution reviews and updates the taxonomy of 27 uncommon dinoflagellate cyst species and morphotypes belonging to the orders Gonyaulacales and Suessiales with occurrences in upper Quaternary marine sediments of the Northern Hemisphere. Comparative descriptions and illustrations are provided along with the biological affinity of each taxon where known and lowest stratigraphic occurrence.

### Highlights

► 25 rare or endemic extant dinoflagellate cyst species and two morphotypes are briefly described and illustrated. ► 23 belong to the Gonyaulacales and 4 to the Suessiales. ► Their stratigraphic ranges are provided.

**Keywords :** Dinoflagellate cysts, Gonyaulacales, Suessiales, Marine sediment, Quaternary

## Introduction

Organic-walled dinoflagellate cysts are a common component of the marine sedimentary fraction in both coastal and oceanic settings and represent a specific stage (presumably a resting stage formed following sexual fusion) in the life cycle. Of the more than 2000 free-living species that have been documented in the marine realm (Gómez, 2012), around 12–15%, as a conservative estimate, produce a geologically preservable organic-walled resting cyst (Head, 1996). In contrast to the cells formed during the active life stages of dinoflagellates, these cysts when occurring in the fossil record represent a crucial link to the living dinoflagellate populations and, thus, their contemporary environment. Consequently, cyst assemblages recovered from sedimentary deposits are widely used in the fields of paleoceanography, paleoclimatology, and biostratigraphy. Whereas assemblages tend to be dominated by a number of frequent and fairly widely occurring species, less common species can add valuable information because of their often restricted ecological constraints and/or stratigraphic ranges.

This review gives a short illustrated description and the lowest stratigraphic occurrence of 22 dinoflagellate cyst species and one informal cyst morphotype belonging to the order Gonyaulacales, and three dinoflagellate cyst species and one informal cyst morphotype belonging to the order Suessiales, with an occasional to rare occurrence or poorly known record in Upper Pleistocene to recent marine sediments of the Northern Hemisphere. The list of taxa illustrated here represents those species present at fewer than 40 locations in the new “n = 1968” modern surface sediment dataset of de Vernal et al. (this issue). Taxa with equally rare occurrences but belonging to the orders Gymnodiniales and Peridiniales are discussed by Mertens et al. (this issue), and species belonging to the orders Gonyaulacales and Suessiales with endemic occurrence in the Black Sea Corridor are discussed by Mudie et al. (2017). The reader is referred to Van Nieuwenhove et al. (this issue) regarding the understanding of the concept of “rare species” as used here, while endemism among dinoflagellate cyst species is elaborated by Marret et al. (this issue). A review of extant freshwater dinoflagellate cysts is given by Mertens et al. (2012).

This contribution uses Kofoid labeling to describe plate tabulation, and dual nomenclature where available to link the separate taxonomies that have evolved for non-fossil and fossil dinoflagellates (Head et al., 2016).

## Systematic part

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

Class DINOPHYCEAE Pascher, 1914

Subclass PERIDINIPHYCIDAE Fensome et al., 1993

Order GONYAULACALES Taylor, 1980

Suborder GONIODOMINEAE Fensome et al., 1993

Family PYROPHACACEAE Lindemann, 1928

**Comments.** The Goniodomataceae Lindemann, 1928 (as Goniodomaceae in Fensome et al., 1993) is a rejected name (Prud'homme van Reine, 2017) following a recommendation by Elbrächter and Gottschling (2015). The Pyrophacaceae is here considered an acceptable substitute.

Subfamily PYRODINIOIDEAE Fensome et al., 1993

**Genus *Capisocysta* Warny and Wrenn, 1997 emend. Head, 1998a**

***Capisocysta lata* Head, 1998a**

Plate 1, figs. 1–3

**Distinguishing characters.** Spheroidal proximate species with a thin inner wall that has a smooth to granulate outer surface and a loosely attached delicate translucent outer layer. The outer layer is often lost in dissociated specimens. When lost, the outer layer can occasionally be replaced by small pustules on the surface of the inner wall. Tabulation expressed only on the hypocyst, and the individual hypocystal plates are often dissociated as they are all involved in the formation of the hypotractal archeopyle (i.e., an archeopyle that involves the loss of the hypocyst; Head, 1998a). Based on Head (1998a).

**Dimensions.** Central body diameter 40–56  $\mu\text{m}$  (Head, 1998a).

**Remarks.** This species is characterized by its rare archeopyle style (both hypotractal and hypocystal sensu Head, 1998a) in which all of the hypocystal plates may be lost. When this happens, the remaining hemispheric epicyst can be recognized as such by the hyposulcal tab, i.e. the combined right and left sulcal plates and first postcingular plate, that generally remains attached to the epicyst. The derivation of the name *Capisocysta* indeed reflects this distinctive epicystal morphology (Warny and Wrenn, 1997). This species is distinguished from *Capisocysta lyellii* Head, 1998a, which is presently known only from the Pliocene, by the presence of a single antapical plate (two in *Capisocysta lyellii*) and less strongly ornamented wall.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence.** Lower Pliocene (Head, 1998a).

Subfamily Helgolandinioideae Fensome et al., 1993

**Genus *Desotodinium* De Schepper et al., 2004**

***Desotodinium wrennii* De Schepper et al., 2004**

Plate 1, figs. 4–6

**Distinguishing characters.** A large, thin-walled proximate species with smooth to shagreenate or scabrate wall surface, and circular to subcircular outline in polar view. Diaphanous equatorial flange with irregular margin may be present. Hypocystal archeopyle comprising three postcingular plates and two antapical plates; otherwise only weak expression of tabulation on hypocyst, and none on epicyst. Based on De Schepper et al. (2004).

**Dimensions.** Central body maximum diameter 47–67  $\mu\text{m}$  based on Pliocene specimens from Belgium (De Schepper et al., 2004).

**Remarks.** *Desotodinium wrennii* was described from the Pliocene of Belgium (De Schepper et al., 2004). *Tuberculodinium vancamptoeae* differs in having large barrel-shaped processes that separate the two central body wall layers, and in *Capisocysta lata* nearly all hypocystal plates are involved in archeopyle formation.

**Biological affinity.** Probably the cyst of *Pyrophacus horologium* Stein, 1883 as described by Wall and Dale (1971), according to De Schepper et al. (2004).

**Stratigraphic range and distribution.** Lower Pliocene through Upper Pleistocene of the Gulf of Mexico (as Forma D in Wrenn and Kokinos, 1986) and modern sediments of Lima, Peru (as cysts of *Pyrophacus horologium* in Wall and Dale, 1971). To our knowledge, neither *Desotodinium wrennii* nor the cysts of *Pyrophacus horologium* have otherwise been reported from modern sediments.

Suborder GONYAULACINEAE autonym

Family GONYAULACACEAE Lindemann, 1928

Subfamily CRIBROPERIDINIOIDEAE Fensome et al., 1993

**Genus *Lingulodinium* Wall, 1967 emend. Dodge, 1985**

***Lingulodinium hemicystum* McMinn, 1991**

Plate 2, figs. 1–9

**Distinguishing characters.** Large transparent to light yellow species with spherical to subspherical central body bearing numerous (up to 30) blade-shaped processes. Archeopyle epittractal (all epicystal plates involved in archeopyle formation; Head, 1998a). Processes have a smooth surface, are nontabular, hollow, distally tapered, each with a circular  $\sim 3\text{--}5\ \mu\text{m}$  diameter base. Processes can become bulbous towards their base. The cyst wall reportedly has a  $\sim 1\ \mu\text{m}$  thick inner layer with a psilate to finely granulate surface, and a thinner, psilate outer layer. The epittractal archeopyle is formed by a splitting of the cyst into two equal halves, which are therefore both found. Tabulation is not otherwise expressed, and only a small sulcal notch or sulcal tab can be seen on better-preserved unfolded specimens. Based on McMinn (1991).

**Dimensions.** Central body diameter 50–65  $\mu\text{m}$ , average process length 5–13  $\mu\text{m}$  (McMinn, 1991).

**Remarks.** *Lingulodinium hemicystum* is morphologically very similar to *Lingulodinium machaerophorum* with which it could be confused during routine counts. *Lingulodinium machaerophorum* differs in having between one and five precingular plates individually released during archeopyle formation (Wall, 1967). Small spinules or grana on the distal ends of the process, that are typical for *Lingulodinium machaerophorum*, are not observed on *Lingulodinium hemicystum*. *Lingulodinium brevispinosum* Matsuoka and Bujak, 1988 has processes that are shorter and with rounded process tips. No mention is made of striations on the process bases for the type material (McMinn, 1991), but observations from South Korea and the South China Sea suggest faint striations

on the process bases of some specimens (see, for instance, the specimen illustrated by McMinn, 1992, his plate 2, fig. 15).

**Biological affinity.** Unknown, but presumably related to *Lingulodinium polyedrum* given the close similarity of *Lingulodinium hemicystum* with *Lingulodinium machaerophorum*.

**Lowest stratigraphic occurrence and distribution.** Neogene. *Lingulodinium hemicystum* was described from recent material collected in estuaries of New South Wales, Australia (McMinn, 1991), and reported in late Quaternary (last glacial) sediments from coastal waters of southeastern Australia (McMinn, 1992). Zegarra and Helenes (2011) listed a single occurrence of this species in the Eastern Equatorial Pacific during the Neogene. *Lingulodinium hemicystum* was also reported from a sediment trap in the western North Pacific and from Holocene samples from the South China Sea (Li et al., 2017, 2018), as well as from estuarine surface sediments of southern South Korea (Pospelova and Kim, 2010, where *Lingulodinium hemicystum* was grouped together with *Lingulodinium machaerophorum*). In the Atlantic, *Lingulodinium hemicystum* was identified only by Paredes et al. (2015) in Miocene (and possibly Oligocene) deposits from the Golfo San Jorge Basin of eastern Patagonia. *Lingulodinium hemicystum* therefore appears to have a shorter stratigraphic range (Oligocene or Miocene to Holocene) than *Lingulodinium machaerophorum* (Paleocene–Holocene), as also remarked by L.E. Edwards in Head (1994a, p. 216).

#### **Genus *Operculodinium* Wall, 1967 emend. Matsuoka et al., 1997**

##### ***Operculodinium aguinawense* Marret and Kim, 2009**

Plate 3, figs. 1–6

**Distinguishing characters.** Subspherical to ovoid central body having a thin wall with a fibroreticulate outer surface and irregularly spaced processes. Process distribution shows some alignment (e.g. Marret and Kim, 2009, pl. 3, figs. 1, 4) and is presumably intratabular. The processes are cylindrical, solid with fibrous or perforated conical bases and about 1/3 of the cyst diameter in length. Process tips are minutely pectinate/multifurcate. Archeopyle is formed by loss of precingular plate 3'. Archeopyle angles relatively well defined.

**Dimensions.** Central body diameter 37–69  $\mu\text{m}$ , process length 8–17  $\mu\text{m}$  (Marret and Kim, 2009).

**Remarks.** *Operculodinium aguinawense* differs from *Operculodinium centrocarpum* sensu Wall and Dale, 1966 by its broader cylindrical processes that have fibrous bases. It differs from *Operculodinium israelianum* Rossignol, 1962 by its smaller size and longer but less numerous processes.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence.** From at least Marine Isotope Stage (MIS) 5e (Late Pleistocene; Marret and Kim, 2009).

##### ***Operculodinium crassum* Harland, 1979**

Plate 3, figs. 7–9

**Distinguishing characters.** Spherical central body with a relatively thick wall that has a fibroreticulate, “spongy” periphragm and numerous irregularly spaced processes that are probably intratabular in distribution. The processes are conical with minutely expanded distal tips, relatively short (about 1/5 to 1/8 of cyst diameter) and are fibrous. Archeopyle formed by loss of precingular plate 3′′. Archeopyle angles are rounded.

**Dimensions.** Central body maximum diameter 54–74  $\mu\text{m}$ , process length 8–17  $\mu\text{m}$  (Harland, 1979).

**Remarks.** Harland in Head and Wrenn (1992, p. 20) considered *Operculodinium crassum* a taxonomic junior synonym of *Operculodinium israelianum*, but both were retained as distinctive species by Head (1996) pending further study of both species. A restudy of topotype material by MJH indicates that the wall thickness of *Operculodinium crassum* is generally  $\sim 1.5\text{--}2.0\ \mu\text{m}$  rather than the  $2.0\text{--}4.0\ \mu\text{m}$  reported by Harland (1979). The range of wall thickness in *Operculodinium israelianum* is not known. Whereas *Operculodinium israelianum* is known from modern sediments (e.g. Limoges et al., 2013), no occurrences postdating the Pleistocene have been reported for *Operculodinium crassum*. However, its modern-day existence cannot be excluded considering its close morphological similarity with the extant species *Operculodinium israelianum*.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence.** Upper Miocene of ODP Site 400, Bay of Biscay (Harland, 1979) and Lower Miocene of ODP Sites 642 and 643, Norwegian Sea (Manum et al., 1989).

#### ***Operculodinium giganteum* Wall, 1967**

Plate 4, figs. 1–3

**Distinguishing characters.** Large species with a rounded-polyhedral body that has a spongy/fibroreticulate periphragm. The numerous processes are short with a conical base and minutely expanded distal ends. Tabulation is intratabular, and alignment of processes can be observed that partially reflects gonyaulacoid tabulation. Archeopyle formed by loss of precingular plate 3′′.

**Dimensions.** Central body diameter 74–86  $\mu\text{m}$ , process length 2–4  $\mu\text{m}$  (Wall, 1967).

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** Eocene of India (Sarkar and Singh, 1988). Observed in Holocene sediment of the Caribbean Sea (e.g., Wall, 1967). *Operculodinium giganteum* was also observed in modern marine sediments of Lake Inkerman, New Brunswick, Canada (I. Aguilar, personal communication).

#### ***Operculodinium? longispinigerum* Matsuoka, 1983**

Plate 4, figs. 4–7

**Distinguishing characters.** Small species having a spherical to subspherical central body with a finely and faintly to moderately granulate surface and sparsely distributed nontabular processes. The processes are nonfibrous, solid, and slender, and long compared to the central body size. Shafts are smooth but may become granulate distally. Processes taper to fine or blunt points, often becoming sinuous distally, or may branch into two or three (rarely four) delicate distal terminations. Different process terminations may occur on the same specimen. Archeopyle precingular, presumably caused by loss of plate 3'' (Matsuoka, 1983; Head and Westphal, 1999).

**Dimensions.** Central body maximum diameter 29–42  $\mu\text{m}$ , process length 5–14  $\mu\text{m}$  (Matsuoka, 1983; Head and Westphal, 1999).

**Remarks.** Head and Westphal (1999) questionably assigned this species to the genus *Operculodinium* on account of its nonfibrous processes and finely granulate rather than fibroreticulate central body surface. In addition, it differs from *Operculodinium centrocarpum* sensu Wall and Dale (1966) by its relatively longer and fewer processes that have acuminate or multifurcate, rather than minutely expanded, distal ends.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** Lower Miocene of the Norwegian Sea and France (see Head and Westphal, 1999) and Upper Miocene of Japan (Matsuoka, 1983). *Operculodinium? longispinigerum* was observed in modern sediments of the Gulf of Mexico (Limoges et al., 2013).

Subfamily GONYAULACOIDEAE (Autonym)

### Genus *Achomosphaera* Evitt, 1963

*Achomosphaera andalusiensis* Jan du Chêne, 1977 emend. Jan du Chêne and Londeix, 1988  
subsp. *andalusiensis* (Autonym)

Plate 4, figs. 8–10

**Distinguishing characters.** Spiniferate cyst with an ovoidal central body that has a thin wall with a smooth to shagreenate surface. Processes are exclusively gonal, and often hollow with a smooth or shagreenate shaft surface. They may have claustra at their base, and terminate distally in characteristic fenestrate platforms. Fenestrations result from branchlets of the bifurcate tips connecting to those of the neighboring bifurcation on the same process. Septa on the central body are lacking, and tabulation is expressed only by process distribution and the precingular archeopyle, formed by loss of plate 3''.

**Dimensions.** Central body width 34–44  $\mu\text{m}$ , central body length 40–50  $\mu\text{m}$ , process length 14–26  $\mu\text{m}$  (Jan du Chêne and Londeix, 1988).

**Remarks.** *Achomosphaera andalusiensis* was considered a taxonomic senior synonym of *Spiniferites septentrionalis* Harland, 1977 by Harland (1983). However, this synonymy was questioned by Head and Wrenn (1992), and not followed by Londeix et al. (2009, p. 67–68; 2018, p. 54) and herein. For comparison with *Spiniferites septentrionalis*, see remarks thereunder.

**Intraspecific morphotypes.** *Achomosphaera andalusiensis* subsp. *suttonensis* Head, 1997, described from the Lower Pliocene of eastern England (Head, 1997), has more fenestrations in the distal platforms of the processes, resulting in a perforate appearance. *Achomosphaera andalusiensis* subsp. *suttonensis* is not known to range outside of the Pliocene (Louwye et al., 2004).

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** Ambiguity in distinguishing *Achomosphaera andalusiensis* subsp. *andalusiensis* from *Spiniferites septentrionalis* makes it difficult to track the exact stratigraphic record of *Achomosphaera andalusiensis andalusiensis* from the literature, especially when illustrations are lacking. Following Londeix (2018), the lowest occurrence datum of *Achomosphaera andalusiensis andalusiensis* appears to be the upper Langhian (Middle Miocene), based on records by Powell (1986) and McCarthy and Mudie (1996) while the *Achomosphaera andalusiensis* dinozone (Piasecki, 1980), which spans nearly the entire Upper Miocene, indicates its common abundance during the Late Miocene. The subspecies has its highest common occurrence in the uppermost Pliocene (Head, 1997; Londeix, 2018) but is only rarely observed in modern sediments.

#### **Genus *Ataxiodinium* Reid, 1974**

##### ***Ataxiodinium* cf. *zevenboomii* Head, 1997**

Plate 5, figs. 1–6

**Distinguishing characters.** Ovoid cavate species with a smooth endoblast and a smooth to faintly granulate periblast. The periblast connects with the endoblast via numerous funnel-shaped invaginations which are unevenly distributed over the cyst surface. Precingular archeopyle.

**Dimensions.** Endoblast length 32–31  $\mu\text{m}$ , endoblast equatorial diameter 27–34  $\mu\text{m}$ , periblast length 34–46  $\mu\text{m}$ , periblast equatorial diameter 31–38  $\mu\text{m}$ , ratio of endoblast length/equatorial diameter 1.1–1.2 (based on new measurements by AL on seven specimens from the Baltic Sea).

**Remarks.** The modern specimens illustrated here are ovoidal only and lack the strongly elongate shape of the holotype and topotype specimens of *Ataxiodinium zevenboomii* from the mid-Pliocene of eastern England (Head, 1997).

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** *Ataxiodinium* cf. *zevenboomii* has only been recorded from surface sediments of the Baltic Sea (unpublished observation by AL).

#### **Genus *Dalella* McMinn and Sun, 1994 emend. Zevenboom and Santarelli in Zevenboom, 1995**

##### ***Dalella chathamensis* McMinn and Sun, 1994**

Plate 5, figs. 7–12

**Distinguishing characters.** Spherical to subspherical central body with a finely granulate surface and conspicuous trabeculae that are connected to the central body at the apex, archeopyle margin, the sulcus, and to the hypocyst in the ventral area only. The trabeculae consist of flat, ribbon-like threads with a thickened central ridge. Archeopyle precingular formed by loss of plate 3''.

**Dimensions.** Central body diameter 18–35  $\mu\text{m}$ , total diameter 46–78  $\mu\text{m}$  (McMinn and Sun, 1994).

**Remarks.** Species of the genus *Nematosphaeropsis* differ from *Dalella chathamensis* in having parallel pairs of trabeculate that connect adjacent gonol/intergonal processes distally and do not contact the central body.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** Isolated rare occurrences in the Upper Pliocene of DSDP Site 610, eastern North Atlantic Ocean (De Schepper and Healy, 2009), and occasionally observed in the Holocene (e.g., McMinn and Sun, 1994). *Dalella chathamensis* was originally described from, and is more common in, modern sediments of the Southern Hemisphere (McMinn and Sun, 1994; Prebble et al., 2013) but has since also been reported occasionally from modern sediments of the Northern Hemisphere (Pospelova et al., 2008; Cornet et al., 2012).

#### **Genus *Gonyaulax* Diesing, 1866**

**Comments.** A genus defined by its motile stage.

#### **Cyst of *Gonyaulax baltica* Ellegaard et al., 2002**

Plate 6, figs. 1–6

**Distinguishing characters.** Spiniferate cyst having a spherical to ovoidal central body with a thin, smooth to slightly granular outer wall. Processes are gonol and occasionally intergonal, but can also be lacking over much of the cyst. When fully developed, they are hollow and trifold with bifurcate distal tips. Shorter processes often end bluntly. Septa are low, but higher septa joining the antapical processes are common. Archeopyle precingular formed by loss of plate 3'', rarely also 4''.

**Dimensions.** Central body length 35–49  $\mu\text{m}$ , central body width 31–44  $\mu\text{m}$ , process length 2–5  $\mu\text{m}$  (Ellegaard et al., 2002).

**Remarks.** The type locality is the Kattegat off the Swedish west coast (southeastern Baltic Sea). Ellegaard et al. (2002) designated a cyst as the holotype, with motile cells belonging to the same strain as the holotype and serving as isotypes also being figured. The diagnosis is based on both motile stage and cyst characters.

Because of their wide morphological variability, some cysts of *Gonyaulax baltica* may resemble *Spiniferites belerius* or *Spiniferites bulloideus* sensu Wall, 1965. Cysts of *Gonyaulax baltica* generally differ from *Spiniferites belerius* in lacking a trumpet-shaped antapical process, and from *Spiniferites bulloideus* sensu Wall, 1965 in having somewhat more robust processes.

**Remarks on biological affinity.** Incubation experiments and molecular analyses of cysts identified as *Impagidinium caspiense* Marret et al., 2004 from the Caspian Sea showed that these cysts produce

motile cells that genetically relate to *Gonyaulax baltica* (Mertens et al., 2017). It may be that *Gonyaulax baltica* can produce cysts assignable to two different cyst-based genera, *Spiniferites* and *Impagidinium*, likely in response to differing environmental factors, in particular salinity (Mertens et al., 2017). The complete disappearance of processes as observed on the cysts in the Caspian Sea (i.e., *Impagidinium caspiense*) thus would appear to be the extreme end of a morphological gradation that was partly observed in the Baltic Sea, too, where *Gonyaulax baltica* including its cyst was first described (Ellegaard et al., 2002).

**Lowest stratigraphic occurrence and distribution.** Reported from the Upper Holocene (Ellegaard et al., 2002; Mertens et al., 2017; unpublished observations from the Baltic Sea by NVN); with a lowest occurrence in the Upper Pleistocene of the Baltic (Head, 2007).

**Genus *Impagidinium* Stover and Evitt, 1978**

***Impagidinium japonicum* Matsuoka, 1983**

Plate 7, figs. 1–6

**Distinguishing characters.** Chorate species with a spherical to ellipsoidal central body and a finely granulate surface. The tabulation is reflected by well developed, finely granulate septa of uniform height. The bases of septa are not cavate. The cingulum is displaced two or three times its own width. Archeopyle precingular formed by loss of plate 3''.

**Dimensions.** Central body length 38–55  $\mu\text{m}$ , central body width 34–53  $\mu\text{m}$ , septa height 7.0–13.7  $\mu\text{m}$  (Matsuoka, 1983).

**Remarks.** *Impagidinium japonicum* has similarly high septa as *Impagidinium striatum* but differs in being larger and having finely granulate septa without striations.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** Pliocene to Lower Pleistocene of central Japan (Matsuoka, 1983) and the Circum-Arctic (de Vernal and Mudie, 1989). This species was also documented in modern sediments of the North Atlantic Ocean (Bonnet et al., 2012).

***Impagidinium velorum* Bujak, 1984**

Plate 7, figs. 7–9

**Distinguishing characters.** Pale, proximochorate species with an ovoidal central body and smooth to shagrinose surface. The tabulation is reflected by high membranous sutural septa with smooth distal margins. The cingulum is represented by a single septum, and septa border the sulcus. The septa are solid and of uniform height approximating the diameter of the central body, but the septa are often flattened against the central body, obscuring details of tabulation. Archeopyle precingular formed by loss of plate 3''. Based on Bujak (1984) and unpublished observations.

**Dimensions.** Central body length 17–33  $\mu\text{m}$ , central body width 17–28  $\mu\text{m}$ , septa height 19–25  $\mu\text{m}$  (Bujak, 1984).

**Remarks.** *Impagidinium velorum* differs from *Impagidinium pallidum* by its smaller central body and much higher sutural septa, and by the cingulum being marked by a single septum only.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** Middle or Upper Eocene of the North Pacific (Bujak, 1984) and ODP Site 643, Norwegian Sea (Manum et al., 1989). This species was also documented in modern sediments of the North Atlantic Ocean (Bonnet et al., 2012).

### Genus *Nematosphaeropsis* Deflandre and Cookson, 1955 emend. Wrenn, 1988

#### *Nematosphaeropsis rigida* Wrenn, 1988

Plate 8, figs. 1–3

**Distinguishing characters.** Chorate to proximochorate species having an egg-shaped to slightly elongate central body. The wall is thin ( $<1\ \mu\text{m}$ ) and its surface is smooth to scabrate. Specimens occasionally show isolated and widely spaced intratabular grana. The central body bears solid gonial and (?) intergonial processes that are connected distally by pairs of penitabular trabeculae. The trabecular structure creates a subspherical concentric shell around the central body. The bases of the processes are usually perforate and may be proximally connected by low ridges. In cross-section, the processes are subrounded to subtriangular, while the trabeculae appear rounded. Archeopyle precingular formed by loss of precingular plate 3''. Based on Wrenn (1988).

**Dimensions.** Central body length 33–41  $\mu\text{m}$ , central body width 29–39  $\mu\text{m}$ , overall length 49–72  $\mu\text{m}$ , overall width 46–73  $\mu\text{m}$ , process length 2–7  $\mu\text{m}$  (Wrenn, 1988).

**Remarks.** *Nematosphaeropsis rigida* is distinguished from others of the genus by the combination of solid processes and distinctively robust trabeculae of rounded cross-section. Additionally, the process bases are usually perforate and the plates are generally well defined. The superficially similar *Nematosphaeropsis labyrinthus* has a more spherical central body, hollow and relatively longer processes, and trabeculae that are flattened in cross-section and ribbon-like.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** Miocene (Wrenn, 1988). *Nematosphaeropsis rigida* has been observed in modern sediments off Massachusetts, USA (as *Nematosphaeropsis balcombiana* in Wall and Dale, 1967) and in the Gulf of Mexico (e.g., Limoges et al., 2013).

### Genus *Spiniferites* Mantell, 1850, emend. Sarjeant, 1970

#### *Spiniferites hainanensis* Sun and Song, 1992

Plate 8, figs. 4–7

**Distinguishing characters.** Central body subspherical to ellipsoidal with a smooth to finely granulate surface. Processes are gonial and intergonial, tapering, and the distally furcate tips may be additionally bifurcate. The processes are fenestrate notably at their base and connected by densely fenestrate moderately high septa. Archeopyle precingular formed by loss of plate 3''.

**Dimensions.** Central body width 35–42  $\mu\text{m}$ , central body length 43–49  $\mu\text{m}$ , process length ca. 10.5  $\mu\text{m}$  (Sun and Song, 1992).

**Remarks.** *Spiniferites hyperacanthus* differs by its solid rather than perforated sutural septa. *Spiniferites multisphaerus* differs by its apical protuberance and vesicular central body and processes.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** Pleistocene (Sun and Song, 1992). *Spiniferites hainanensis* was observed in modern sediments from the Gulf of California (Cuellar-Martinez et al., 2018).

#### ***Spiniferites multisphaerus* Price and Pospelova, 2014**

Plate 8, figs. 8–12

**Distinguishing characters.** Central body ovoidal to pear-shaped. An apical boss is usually present. The thick wall is vesicular, constructed of bubble-like elements that continue in the septa and process shafts and give the surface a pitted or reticulate appearance. Processes are gonial and occasionally intergonial, with stubby furcate distal ends. Archeopyle precingular formed by loss of plate 3''.

**Dimensions.** Central body width 36–51  $\mu\text{m}$ , central body length (including apical boss), 41–66.5  $\mu\text{m}$ , process length 1.5–8  $\mu\text{m}$  (Price and Pospelova, 2014; Londeix et al., 2018).

**Remarks.** Londeix et al. (2018) placed this species in the genus *Hafniasphaera* Hansen, 1977, as *Hafniasphaera multisphaera*, based on the thickness and structure of the vesicular wall, but the species is retained in *Spiniferites* by Mertens et al. (2018c), Limoges et al. (2018) and herein because of the occurrence of specimens with a wall texture intermediate between *Hafniasphaera* and *Spiniferites*.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence.** Upper Pleistocene of the Gulf of California (Price and Pospelova, 2014).

#### ***Spiniferites ristingensis* Head, 2007**

Plate 9, figs. 1–12

**Distinguishing characters.** Central body ovoidal with or without apical boss. The central body surface has a minutely bubbly appearance caused by densely distributed blisters and hollow undulations in

the outer layer of the two-layered cyst wall. The processes are membranous and granulate, and are either truncated or form irregularly polygonal platforms at the distal ends. They are gonal only and joined by sutural crests with a granulate surface. Membranes forming the sutural crests and processes are distinctly bilayered. Archeopyle precingular formed by loss of plate 3''.

**Dimensions.** Central body length 39–49  $\mu\text{m}$ , maximum process length 11–17  $\mu\text{m}$  (Head, 2007).

**Remarks.** *Spiniferites delicatus* Reid, 1974 has similar processes but higher sutural crests, a reduced archeopyle, and a central body surface that appears more delicately microgranular to microreticulate rather than coarse and bubbly. *Spiniferites alaskensis* differs in lacking undulations on the surface (for further details, see Marret and Mertens, 2018).

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** Recorded from sediments spanning the Miocene–Pliocene boundary (Popescu et al., 2015) and MIS 5e (Late Pleistocene) (Head et al., 2005, as *Spiniferites* sp. 1; Head, 2007). *Spiniferites ristingensis* is locally abundant in modern sediments off Southwestern Portugal (Mertens et al., 2018c). Possibly recorded from the Upper Holocene of the Baltic Sea (NVN, unpublished observations).

#### ***Spiniferites septentrionalis* Harland, 1977**

Plate 10, figs. 1–3

**Distinguishing characters.** Central body ovoidal with a relatively thick wall and a scabrate to microgranulate surface. Processes are gonal only, long and slender, with fenestrate or petaloid distal ends. Tabulation expressed by faint ridges and low septa, notably around the archeopyle. Archeopyle precingular formed by loss of plate 3''.

**Dimensions.** Central body width 29–38  $\mu\text{m}$ , central body length 34–48  $\mu\text{m}$ , process length 10–16  $\mu\text{m}$  (Harland, 1977).

**Remarks.** *Spiniferites septentrionalis* resembles *Achomosphaera andalousiensis* subsp. *andalousiensis* but differs by its thicker and more granular wall, the presence of ridges and septa, and less well developed fenestrate process tips.

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** The subtleties in distinguishing *Spiniferites septentrionalis* from *Achomosphaera andalousiensis* subsp. *andalousiensis* make it difficult to assess records from the literature, especially when illustrations are lacking. Londeix (2018) accepted a lowest occurrence datum of upper Tortonian or Messinian (Upper Miocene) based on records by Harland (1979), and the species is present in upper Quaternary sediments (Harland, 1977). *Spiniferites septentrionalis* disappears in the Middle Pleistocene just before the onset of MIS 5e in the North Atlantic Bay of Biscay (Penaud et al., 2008) and just before the onset of the Holocene in the Mediterranean Sea (Turon and Londeix, 1988). Its presence in modern sediments is likely but unconfirmed.

**Genus *Tectatodinium* Wall, 1967 emend. Head, 1994*****Tectatodinium pellitum* Wall, 1967 emend. Head, 1994**

Plate 10, figs. 4–9

**Distinguishing characters.** Subspherical to broadly ovoidal cyst with a thick wall consisting of a thin solid inner layer (pedium) and a thick spongy outer layer (luxuria) of interconnecting, irregular lamellae that rise from a vesicular base and do not fuse or join distally (i.e. a distally open luxuria). The cyst wall appears densely granulo-fibrous under the light microscope. A small apical protuberance is usually present. Archeopyle precingular formed by loss of plate 3'', and typically has well defined angles and an irregular margin.

**Dimensions.** Maximum diameter 32–54  $\mu\text{m}$ , wall thickness 1.6–5.7  $\mu\text{m}$ . (Head, 1994; Head and Nøhr-Hansen, 1999).

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence.** Lower Paleocene (Hansen, 1977, as *Tectatodinium rugulatum*; Head and Nøhr-Hansen, 1999). Pre-Paleocene records of the species are considered questionable (Head and Nøhr-Hansen, 1999).

Subfamily UNCERTAIN

**Genus *Melitasphaeridium* Harland and Hill, 1979*****Melitasphaeridium angustum* Matsuoka, 1983**

Plate 11, figs. 1–3

**Distinguishing characters.** Small proximochorate subspherical species with a coarsely granular surface and somewhat fibrous, slender and hollow intratabular processes with closed acuminate distal tips. Archeopyle precingular formed by loss of plate 3''.

**Dimensions.** Central body length 33–42  $\mu\text{m}$ , central body width 30–37  $\mu\text{m}$ , process length 9.5–13  $\mu\text{m}$  (Matsuoka, 1983).

**Remarks.** According to Matsuoka (1983), *Melitasphaeridium angustum* is distinguished from *Melitasphaeridium choanophorum* (Deflandre and Cookson, 1955) Harland and Hill, 1979 by its more granular surface and in having hollow acuminate processes.

**Biological affinity.** Unknown

**Lowest stratigraphic occurrence.** Middle Miocene to Pliocene of eastern Japan. As with *Melitasphaeridium choanophorum* (see below), *Melitasphaeridium angustum* may also occur in upper Quaternary sediments in specific areas, but records are unconfirmed owing to low abundances and close morphological similarity with *Melitasphaeridium choanophorum*.

***Melitasphaeridium choanophorum* (Deflandre and Cookson, 1955) Harland and Hill, 1979**

Plate 11, figs. 4–11

**Distinguishing characters.** Spherical central body with a finely granulate surface and rigid to slightly flexuous, hollow tubular processes. The distal tips of the processes are typically flared to form circular platforms with serrated margins, although process tips vary even on the same specimen, with some platforms being significantly reduced in diameter. Archeopyle precingular formed by loss of plate 3''.

**Dimensions.** Central body 28.0–42.0  $\mu\text{m}$ , process length 14.0–21.0  $\mu\text{m}$  (Harland and Hill, 1979). Smaller specimens were recorded by Price et al. (2017): central body 24.6–37.8  $\mu\text{m}$ , process length 9.0–14.8  $\mu\text{m}$ .

**Biological affinity.** Unknown.

**Lowest stratigraphic occurrence and distribution.** *Melitasphaeridium choanophorum* was originally described from post-Upper Miocene sediments of Australia (Deflandre and Cookson, 1955) and has since been recorded in the Northern Hemisphere from the Oligocene of Germany (Benedek, 1972), the Lower Miocene and Pliocene of offshore eastern Canada (Williams, 1975; Williams and Bujak, 1977) and the Lower to Middle Miocene of the offshore Norwegian-Greenland Sea (Manum, 1976). Late Quaternary records are restricted to the Cariaco Basin (Mertens et al., 2009; Bringué et al., 2019), the Gulf of Mexico (Limoges et al., 2014) and the South China Sea (Li et al., 2017). *Melitasphaeridium choanophorum* has been observed in modern sediment from the Gulf of Mexico (Limoges et al., 2013; Price et al., 2017).

Family UNCERTAIN

**Genus *Pentapladodinium* Mertens, Carbonell-Moore, Pospelova and Head in Mertens et al., 2018a**

**Comments.** A genus defined by its motile stage.

**Cyst of *Pentapladodinium saltonense* Mertens, Carbonell-Moore, Pospelova and Head in Mertens et al., 2018a**

Plate 12, figs. 1–9

**Distinguishing characters.** Spherical central body with a thick wall consisting of a thin smooth pedium and a thicker spongy-fibrous luxuria appearing loosely granular in surface view. The numerous processes are irregularly spaced suggesting intratabular distribution, except for occasional alignment along the cingular margins. They are solid and fibrous along their entire length with an expanded base and usually minutely expanded, but sometimes tapering distal ends. Closely spaced processes can be joined at the base, and shorter and thinner processes can be interspersed between the dominating longer processes. The archeopyle is relatively wide and reflects the precingular thecal plate \*(3''+4'') or both plates 2'' and \*(3''+4'').

**Dimensions.** Central body diameter 46–71  $\mu\text{m}$ , process length 1.0–5.7  $\mu\text{m}$ , wall thickness 0.9–2.4  $\mu\text{m}$  (Mertens et al., 2018a).

**Remarks.** *Operculodinium israelianum* has a narrower archeopyle and may have longer processes than the cyst of *Pentaplagodinium saltonense*. *Operculodinium centrocarpum* sensu Wall and Dale, 1966 (= the cyst of *Protoceratium reticulatum* (Claparède and Lachmann, 1859) Bütschli, 1885) has a smaller central body, a narrower archeopyle, lacks a thick spongy-fibrous luxuria, and its processes have more pronounced distal expansions.

**Biological affinity.** Germination experiments link this cyst to the motile stage of *Pentaplagodinium saltonense* (Mertens et al., 2018a). *Ceratocorys mariaavidiorum* Salgado et al., 2018 is a junior synonym of the dinoflagellate *Pentaplagodinium saltonense* (see Mertens et al., 2018b). Mertens et al. (2018a) and Salgado et al. (2018) show that *Pentaplagodinium saltonense* had until then erroneously been identified as *Protoceratium reticulatum* (Claparède and Lachmann, 1859) Bütschli, 1885 (al. *Gonyaulax grindleyi* Reinecke, 1967).

**Lowest stratigraphic occurrence.** Upper Cenozoic (Mertens et al., 2018a).

Suborder UNCERTAIN

Family UNCERTAIN

#### **Genus *Dapsilidinium* Bujak et al., 1980**

##### ***Dapsilidinium pastielsii* (Davey and Williams, 1956) Bujak et al., 1980**

Plate 12, figs. 10–12

**Distinguishing characters.** Large chorate species with a spheroidal central body and finely granulate surface. The intratabular, fairly evenly spaced hollow processes with a granulate surface taper distally to a narrow neck before expanding minutely to an opening with a serrated or irregular margin. Two or three processes may be fused along most of their length. Process bases usually have elongate claustra that may be more pronounced where processes are fused. Archeopyle formed by loss of the four apical plates, operculum free.

**Dimensions.** Central body diameter 37–56  $\mu\text{m}$ , process length 8.5–18.0  $\mu\text{m}$  (this study).

**Remarks.** *Dapsilidinium pseudocolligerum* (Stover, 1977) Bujak et al., 1980 described from the Oligocene of the eastern United States shelf, was formerly differentiated from *Dapsilidinium pastielsii* by its longer and more widely spaced processes with narrower bases (Stover, 1977), but additional measurements by Mertens et al. (2014, their supplemental figure DR2) reveal that these parameters do not distinguish these species unambiguously. Hence, Mertens et al. (2014) considered *Dapsilidinium pseudocolligerum* a junior synonym of *Dapsilidinium pastielsii*, a judgement followed here.

**Biological affinity.** Undescribed dinoflagellate closely related to the hystrichokolpomoid lineage and placed within the subfamily Cribroperidinioideae (Mertens et al., 2014).

**Lowest stratigraphic occurrence and distribution.** Lower Paleocene (Brinkhuis and Schiøler, 1996), possibly Campanian or Maastrichtian (e.g., Marheinecke, 1992), and thought to have become extinct in the Early Pleistocene (Head and Westphal, 1999) until living cysts were recorded by Mertens et al. (2014) in surface sediments of the western central Pacific Ocean.

Order SUESSIALES Fensome et al., 1993

Family SUESSIACEAE Fensome et al., 1993

**Genus *Biecheleria* Moestrup et al., 2009**

**Comments.** A genus defined by its motile stage.

**Cyst of *Biecheleria baltica* Moestrup et al., 2009**

Plate 12, figs. 1–7

**Distinguishing characters.** Spherical cyst with a hyaline wall covered by densely and evenly spaced processes. Process length varies from very short verticillate-like protrusions to simple rods a few  $\mu\text{m}$  long. The nature of the archeopyle is unknown, but specimens illustrated here superficially suggest an epittractal archeopyle.

**Dimensions.** Central body diameter 20–30  $\mu\text{m}$  (Kremp et al., 2005).

**Remarks.** The motile cells that produce these cysts were originally identified from Baltic Sea material by Kremp et al. (2005) as *Gymnodinium halophilum* Biecheler, 1952 which they then transferred to the genus *Woloszynskia* Thompson, 1951 as *Woloszynskia halophila* (Biecheler, 1952) Kremp et al., 2005. However, Moestrup et al. (2009) considered the Baltic specimens described by Kremp et al. (2005) as distinct from *Gymnodinium halophilum*, and assigned them to a new species *Biecheleria baltica*, while transferring Biecheler's *Gymnodinium halophilum* to *Biecheleria halophila*.

**Lowest stratigraphic occurrence.** At least the Upper Holocene of the Baltic Sea (unpublished observations by NVN).

**Cyst of cf. *Biecheleria baltica* Moestrup et al., 2009**

Plate 12, figs. 8–11

**Remarks.** Cysts appearing very similar to *Biecheleria baltica* have been found in Holocene sediments and sediment trap samples from numerous Arctic and temperate regions (Price and Pospelova, 2011; Bringué et al., 2013; Heikkilä et al., 2014, 2016; Limoges et al., 2018; unpublished observations by AR in the Beaufort Sea and Canadian Arctic Archipelago). These authors noted a central body diameter between 8 and 30  $\mu\text{m}$  and a process length between 0.5 and 3  $\mu\text{m}$  for these (sub)arctic specimens. They are identified in the literature as "cyst of cf. *Biecheleria baltica*" or "cyst of cf.

*Biecheleria* sp.", and here referred to as cf. *Biecheleria baltica* pending more information on the cyst–theca relationship for these arctic specimens.

#### **Cyst of *Biecheleria cincta* (Siano et al., 2009) Balzano et al., 2012**

See Siano et al. (2009) and Luo et al. (2013) for rare illustrations of this cyst.

**Distinguishing characters.** Small spherical cyst with a brown to dark wall covered with small grains and numerous short (0.5–1.0  $\mu\text{m}$ ) columnar spines. Some spines can be distally capitate. A faint tabulation pattern probably reflecting the position of the amphiesmal vesicles of the vegetative cell is present on the surface of the cyst. The archeopyle is small and circular.

**Dimensions.** Central body diameter 10–17  $\mu\text{m}$  (Siano et al., 2009; Luo et al., 2013).

**Remarks.** The cyst has presently been observed only in cultures established from surface seawater (Siano et al., 2009) and coastal surface sediment samples (Luo et al., 2013). The full stratigraphic range of the cyst is undocumented.

#### **Genus *Polarella* Montresor et al., 1999**

**Comments.** A genus defined by its motile stage.

#### **Cyst of *Polarella glacialis* Montresor et al., 1999**

Plate 12, figs. 12–19

**Distinguishing characters.** Small spiny cylindrical cyst with an elongated, rounded-cylindrical to characteristically "peanut-shaped" head; the body wall is smooth, but faint lines can sometimes be observed reflecting plate boundaries. Intratabular, plate-centered acicular processes reflect the tabulation except in the cingulum, where processes are absent. Processes are needle-shaped (acicular), each tapering with a wide base and a straight to slightly concave shaft ending in a pointed distal tip. The nature of the archeopyle is unknown.

**Dimensions.** Central body width 8–15  $\mu\text{m}$ , central body length 12–17  $\mu\text{m}$ , process length 2.7–4.2  $\mu\text{m}$  (Montresor et al., 1999).

**Lowest stratigraphic occurrence.** At least MIS 3 (Upper Pleistocene) (unpublished observations by AL and NVN; Stijn De Schepper, personal communication November 2018).

#### **Acknowledgements**

We are most grateful to Marianne Ellegaard, Sofia Ribeiro, Fabienne Marret, Jan A.I. Hennissen, Aurélie Penaud and Frédérique Eynaud for providing pictures or palynological slides. AL, MJH and VP acknowledge financial support from their respective Natural Sciences and Engineering Research Council of Canada Discovery Grants. Editor-in-chief Richard Jordan and two anonymous reviewers are thanked for their valuable comments and suggestions.

## Plate Captions

**Plate 1** 1–3. *Capisocysta lata*, the holotype from the Pliocene of eastern England (Head, 1998) in (1) bright field, (2) interference contrast and (3) phase contrast. 4–6. *Desotodinium wrennii*, specimen from the Pleistocene (Olduvai Subchron) of the western North Atlantic (DSDP Hole 603C). High to low focus, apical view, showing the ps plate at the top, the two antapical plates below, and three postcingular plates below these. All images by MJH. All scale bars = 10  $\mu\text{m}$ .

**Plate 2** 1–9. *Lingulodinium hemicystum*. 1–2. High and low focus of specimen from the Pacific Ocean. 3, 6. High and low focus of specimen from surface sediments offshore Qingdao (China). 4. High focus of another specimen from Omura Bay (Japan) surface sediments. 5. Optical section of specimen with cell content from the same locality. 7–9. High to low focus at slightly different orientations of specimen from the same locality. Images 1–2 by VP, 3–9 by KNM. All scale bars = 10  $\mu\text{m}$ .

**Plate 3** 1–6. *Operculodinium aguinawense*. 1–3. High to low focus, apical view, of a topotype from the Gulf of Guinea. 4–6. High to low focus, antapical view, of another topotype from the Gulf of Guinea. 7–9. *Operculodinium crassum*, topotype from the Bay of Biscaya (DSDP Leg 48, Hole 400A), seen in (7) high focus and (8–9) optical section at two slightly different focal depths. Images 1–6 by NVN (slide provided by Fabienne Marret, 7–9 by MJH. All scale bars = 10  $\mu\text{m}$ .

**Plate 4** 1–3. *Operculodinium giganteum*, high to low focus of specimen from Inkerman Lake, Pokemouche River estuary (New Brunswick, Canada) surface sediments. 4–7. *Operculodinium longispinigerum*. 4–5. Specimen from the Gulf of Mexico. 6–7. High focus and optical section of a different specimen from the Gulf of Mexico. 8–10. *Achnosphaera andalousiensis* subsp. *andalousiensis* from the Gulf of Mexico (ODP Leg 160, Site 625b). 8. High focus on fenestrate distal ends of processes. 9. Lower focus on the dorsal surface of the cyst. 10. Optical section. Image 1–3 by AR, 4–7 by AL, 8–10 by KNM.

**Plate 5** 1–6. *Ataxiodinium* cf. *zevenbooni*, two specimens at high to low focus from the Baltic Sea. 7–12. *Dalella chathamensis*. 7–9. High to low focus on specimen from MIS 5e at the Challenger Plateau, off New Zealand (DSDP Site 593). 10. Specimen from the South Indian Ocean (core MD12-3396). 11–12. Different focal depths of a different specimen from the same locality. Image 1–3 by NVN, 4–6 by AL, 7–9 by Fabienne Marret, 10–12 by Frédérique Eynaud. All scale bars = 10  $\mu\text{m}$ .

**Plate 6** 1–6. Cyst of *Gonyaxilax baltica*. 1–3. High to low focus, dorsal view, of specimen from Limfjord (Denmark). 4–6. High to low focus of specimen with cell content from Langden Station, Tvärminne (Gulf of Finland) surface sediments. All images by KNM. All scale bars = 10  $\mu\text{m}$ .

**Plate 7** 1–6. *Impagidinium japonicum*. 1–6. New micrographs of the holotype (Matsuoka, 1983). High to low focus, dorsal view. 7–9. *Impagidinium velorum*, specimen from the latest Pliocene of the central North Atlantic Ocean (IODP Hole U1313C; from Hennissen, 2013). 7. Focus on the microgranulate wall of the central body. 8. Optical section. 9. Focus on the sutural crests. 1–6 by MJH, 7–9 by Jan A.I. Hennissen. All scale bars = 10  $\mu\text{m}$ .

**Plate 8** 1–3. *Nematosphaeropsis rigida*. 1–2. Optical section and low focus on specimen from the Gulf of Mexico (Limoges et al., 2013). 3. Optical section of a different specimen from the same locality. 4–7. *Spiniferites hainanensis* from Southern China surface sediments. 4–6. Increasing focal depth, dorsal view. 7. Oblique dorso-lateral view of the hypocyst. 8–12. *Spiniferites multisphaerus*. 8–9. Optical section and low focus on specimen from the Pacific Ocean. 10–12. Different focal depths of a different specimen from the Pacific Ocean. Image 1–3 by AL, 4–7 by KNM, 8–12 by VP. All scale bars = 10  $\mu\text{m}$ .

**Plate 9** 1–12. *Spiniferites ristingensis*, specimens from (sub)surface sediments off Portugal (core PO287-39B, Ribeiro et al., 2016). 1–3. High to low focus, apical view. 4–6. High to low focus, dorsal view. 7–8. High and mid-focus, dorso-lateral view. 9–12. High to low focus, oblique antapical view. All images by KNM. All scale bars = 10 µm.

**Plate 10** 1–3. *Spiniferites septentrionalis*, three specimens from MIS 6 in the Bay of Biscay (core MD03-2692, Penaud et al., 2008). 4–9. *Tectatodinium pellitum* from the eastern Mediterranean Sea. 4–6. High to low focus, ventro-lateral view. 7–8. High focus and optical section of a different specimen. 9. Optical section of another specimen. Image 1–3 by Aurélie Penaud, 4–9 by KNM. All scale bars = 10 µm.

**Plate 11** 1–3. *Melitasphaeridium angustum*, new micrographs of the holotype (Matsuoka, 1983). Apical view in (1) high focus and (2–3) optical section at two slightly different focal depths. 4–11. *Melitasphaeridium choanophorum* from the Gulf of Mexico. 4–6. High to low focus. 7, 11. Different focal depths of different specimen. 8–10. High to low focus of another specimen. Image 1–3 by KNM, 4–11 by AL. All scale bars = 10 µm.

**Plate 12** 1–9. Cyst of *Pentapladodinium saltonense* from Salton Sea (California, USA) surface sediments. 1–3. High to low focus, dorsal view. 4–5. High focus and optical section of a different specimen. 6, 9. High focus and optical section of a different specimen. 7–8. High focus and optical section of another specimen. 10–12. *Dapsilidinium pastielsii*, three different specimens from the Philippines. All images by KNM. All scale bars = 10 µm.

**Plate 13** 1–7. Cyst of *Biecheleria baltica* from the Baltic Sea (core KSK12-01D). 1–2. Optical section and low focus of specimen with cell content. 3–4. High focus showing the (?) archeopyle, and low focus, of a different specimen. 5–7. High to low focal view of another specimen suggesting an epicystal archeopyle. 8–11. Cyst of cf. *Biecheleria baltica*. 8–9. High focus and optical section of specimen with cell content from the Arctic. 10–11. High focus and optical section of specimen with cell content from NE Greenland. 12–15. Cyst of *Polarella glacialis*. 12. Optical section of specimen from the Arctic. 13–15. High to low focus of specimen from northern Baffin Bay. 16–17. Different focal depths of a specimen with cell content from northern Baffin Bay. 18–19. Different focal depths of specimen with cell content from the Wandel Sea. Image 1–7, 13–17 by NVN, 8–9, 12 by VP, 10–11, 18–19 by AL. All scale bars = 10 µm.

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## Highlights

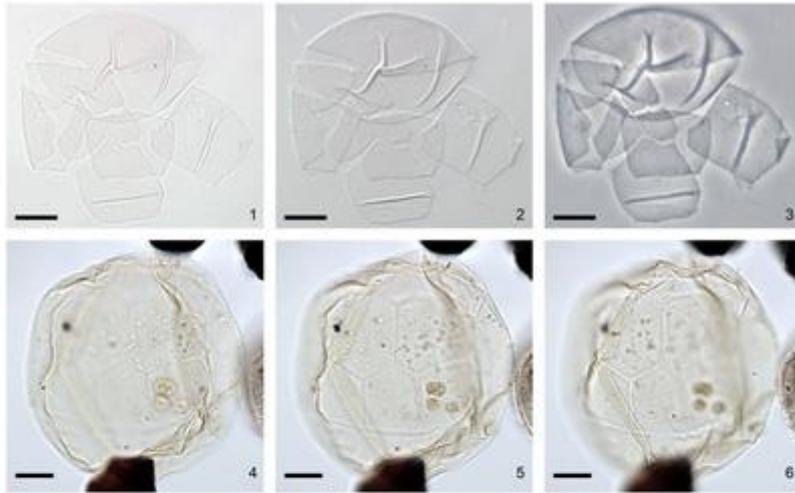
- 25 rare or endemic extant dinoflagellate cyst species and two morphotypes are briefly described and illustrated
- 23 belong to the Gonyaulcales and 4 to the Suessiales
- their stratigraphic ranges are provided

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**Declaration of Interest**

This revised version of our manuscript was approved by all authors and we collectively have no conflict of interest to declare.

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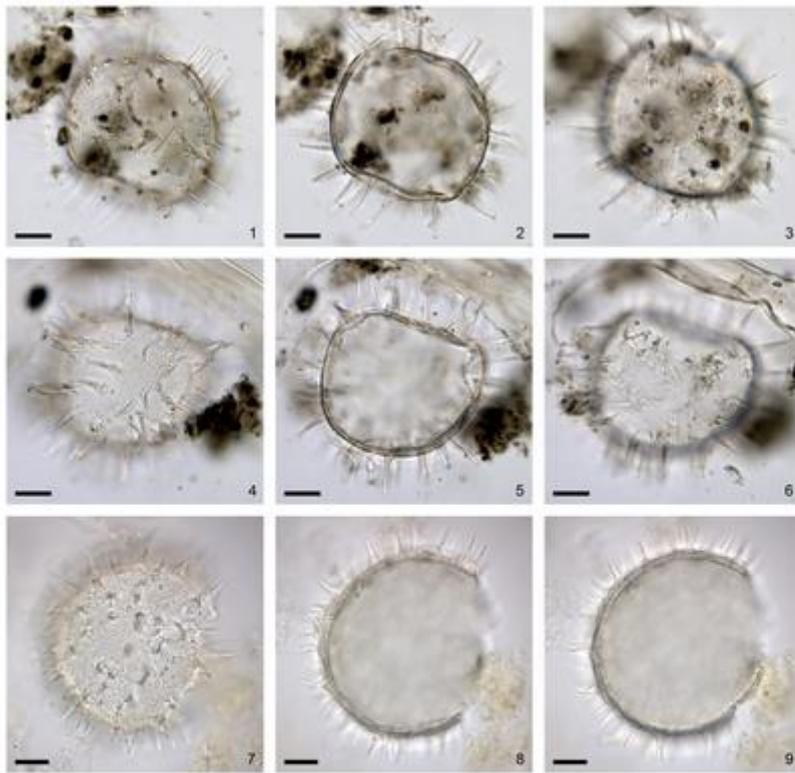
Plate 1. 1–3. *Capisocysta lata*, the holotype from the Pliocene of eastern England (Head, 1998a, Head, 1998b) in (1) bright field, (2) interference contrast and (3) phase contrast. 4–6. *Desotodinium wrennii*, specimen from the Pleistocene (Olduvai Subchron) of the western North Atlantic (DSDP Hole 603C). High to low focus, apical view, showing the ps plate at the top, the two antapical plates below, and three postcingular plates below these. All images by MJH. All scale bars = 10  $\mu\text{m}$ .



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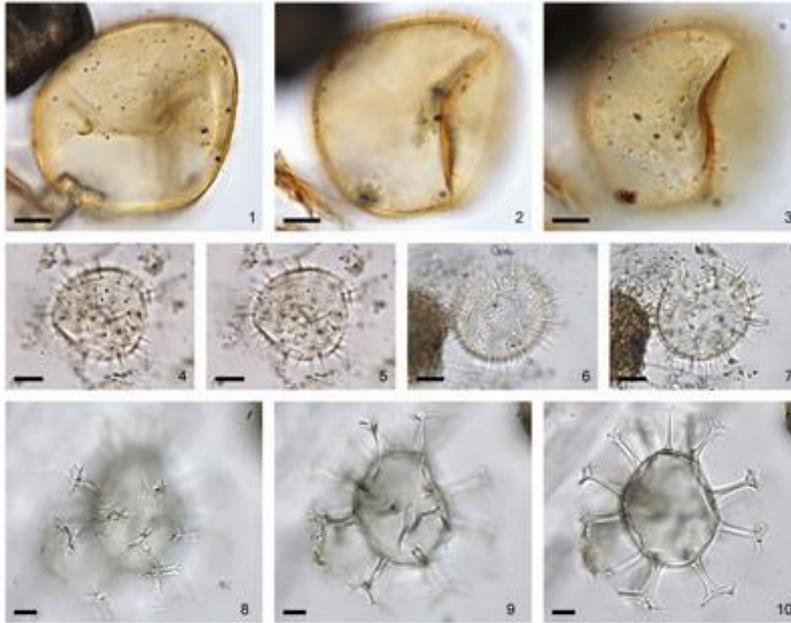
Plate 2. 1–9. *Lingulodinium hemicystum*. 1–2. High and low focus of specimen from the Pacific Ocean. 3, 6. High and low focus of specimen from surface sediments offshore Qingdao (China). 4. High focus of another specimen from Omura Bay (Japan) surface sediments. 5. Optical section of specimen with cell content from the same locality. 7–9. High to low focus at slightly different orientations of specimen from the same locality. Images 1–2 by VP, 3–9 by KNM. All scale bars = 10  $\mu$ m.



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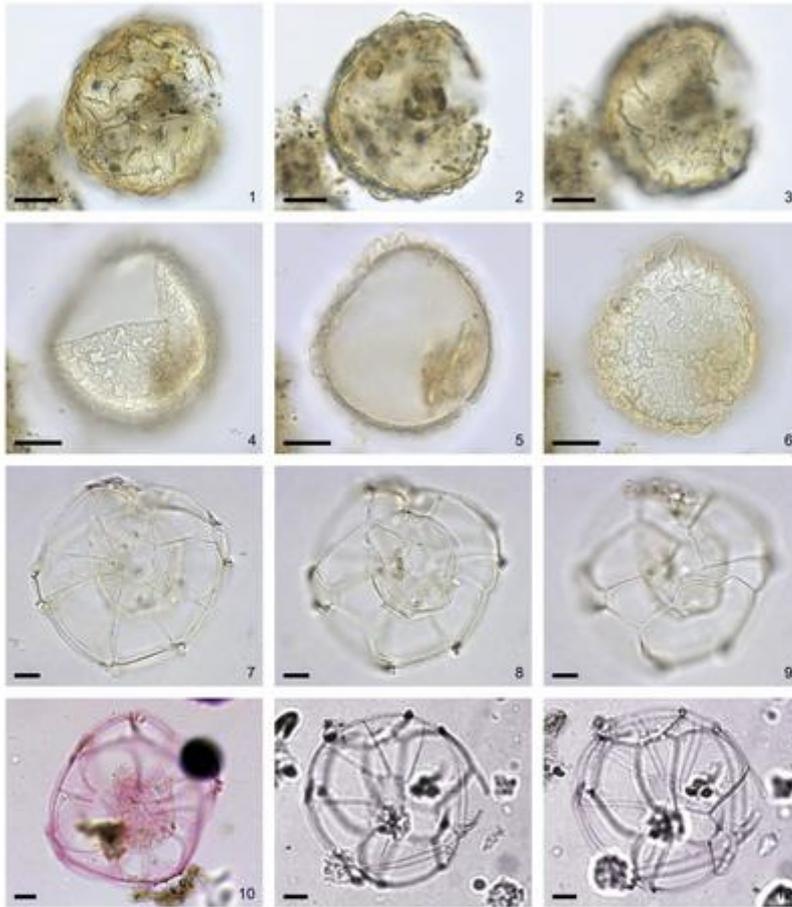
Plate 3. 1–6. *Operculodinium aguinawense*. 1–3. High to low focus, apical view, of a toptype from the Gulf of Guinea. 4–6. High to low focus, antapical view, of another toptype from the Gulf of Guinea. 7–9. *Operculodinium crassum*, toptype from the Bay of Biscay (DSDP Leg 48, Hole 400A), seen in (7) high focus and (8–9) optical section at two slightly different focal depths. Images 1–6 by NVN (slide provided by Fabienne Marret, 7–9 by MJH). All scale bars = 10  $\mu\text{m}$ .



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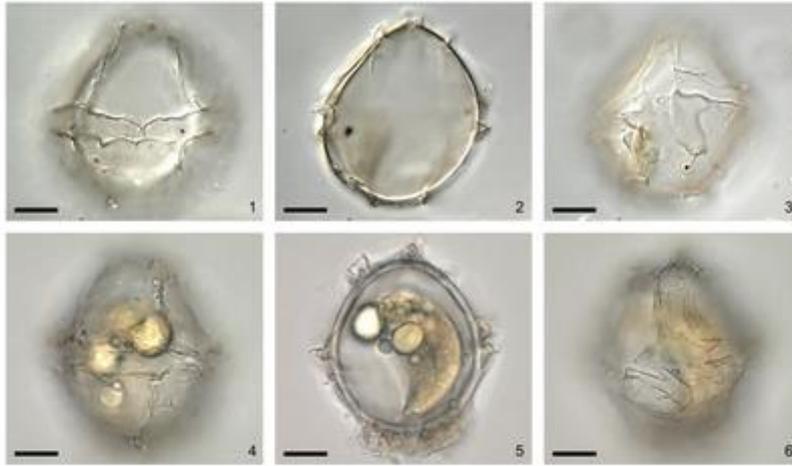
Plate 4. 1–3. *Operculodinium giganteum*, high to low focus of specimen from Inkerman Lake, Pokemouche River estuary (New Brunswick, Canada) surface sediments. 4–7. *Operculodinium longispinigerum*. 4–5. Specimen from the Gulf of Mexico. 6–7. High focus and optical section of a different specimen from the Gulf of Mexico. 8–10. *Achomosphaera andalouisiensis* subsp. *andalouisiensis* from the Gulf of Mexico (ODP Leg 100, Site 625b). 8. High focus on fenestrate distal ends of processes. 9. Lower focus on the dorsal surface of the cyst. 10. Optical section. Image 1–3 by AR, 4–7 by AL, 8–10 by KNM.



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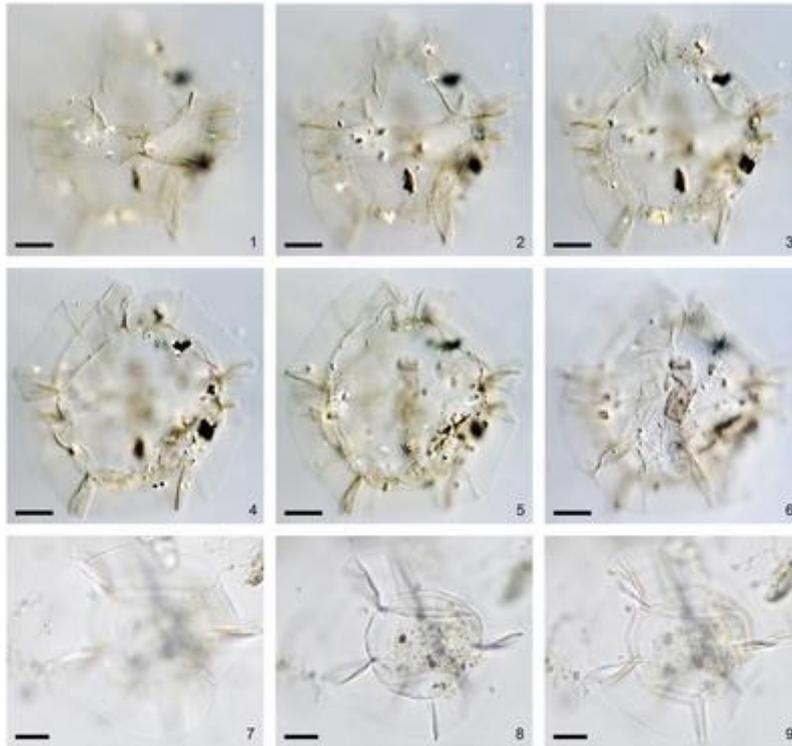
Plate 5. 1–6. *Ataxiodinium* cf. *zevenboomii*, two specimens at high to low focus from the Baltic Sea. 7–12. *Dalella chathamensis*. 7–9. High to low focus on specimen from MIS 5e at the Challenger Plateau, off New Zealand (DSDP Site 593). 10. Specimen from the South Indian Ocean (core MD12–3396). 11–12. Different focal depths of a different specimen from the same locality. Image 1–3 by NVN, 4–6 by AL, 7–9 by Fabienne Marret, 10–12 by Frédérique Eynaud. All scale bars = 10  $\mu$ m.



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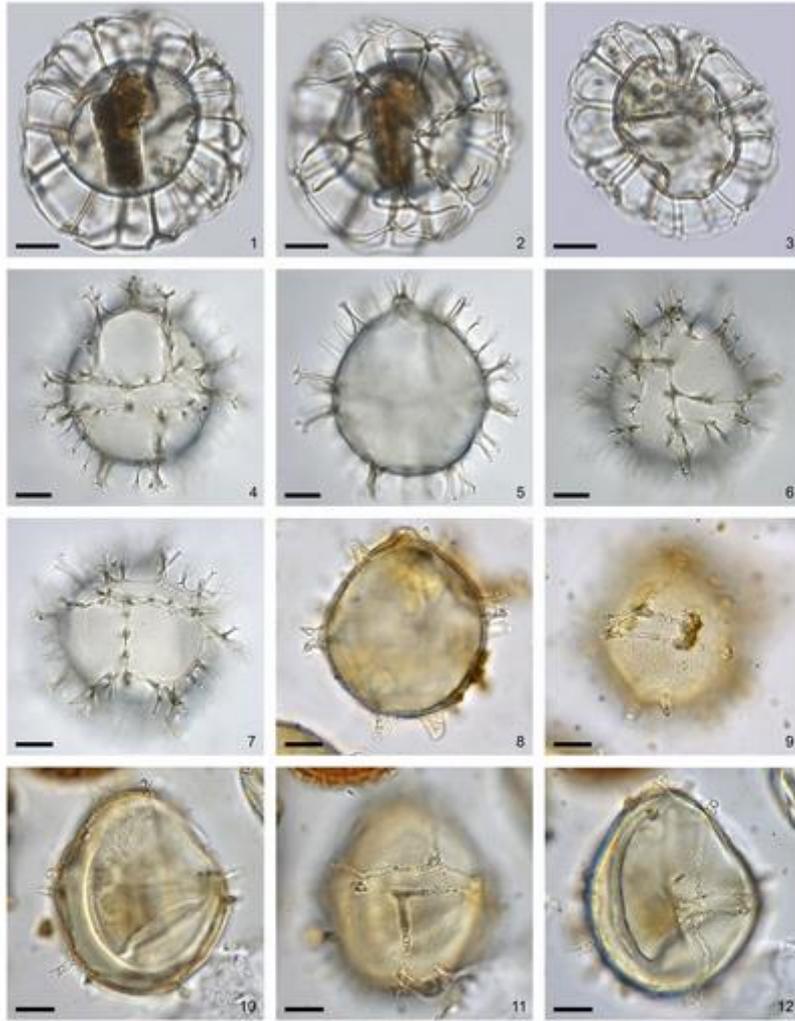
Plate 6. 1–6. Cyst of *Gonyaulax baltica*. 1–3. High to low focus, dorsal view, of specimen from Limfjord (Denmark). 4–6. High to low focus of specimen with cell content from Langden Station, Tvärminne (Gulf of Finland) surface sediments. All images by KNM. All scale bars = 10  $\mu\text{m}$ .



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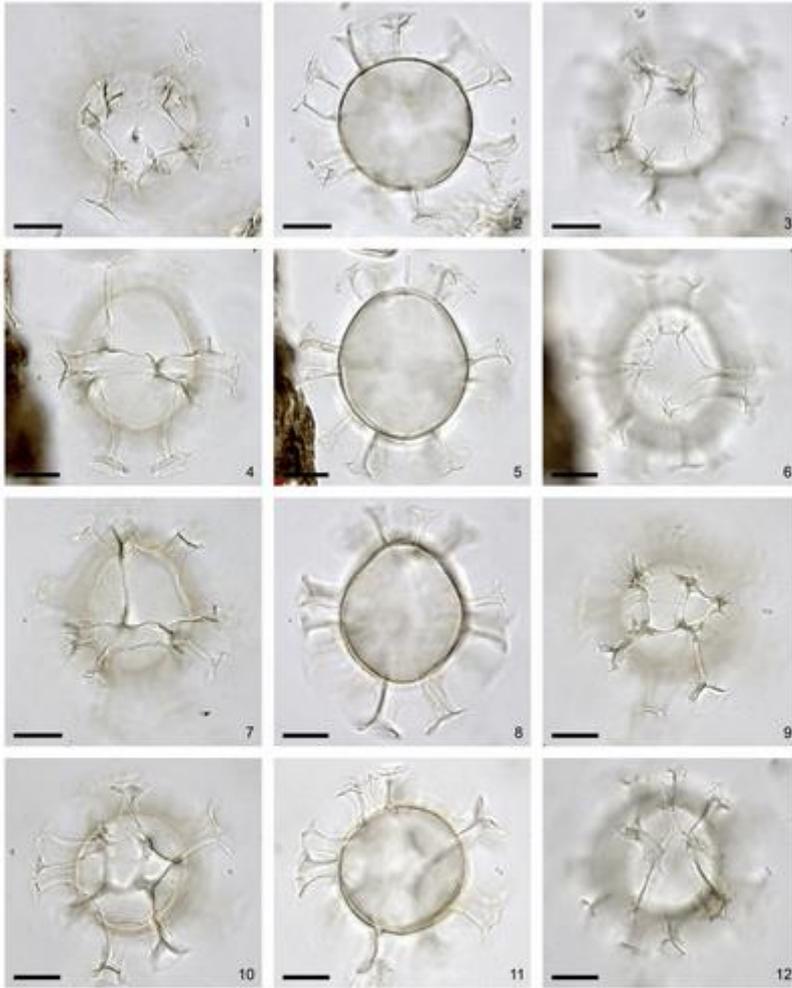
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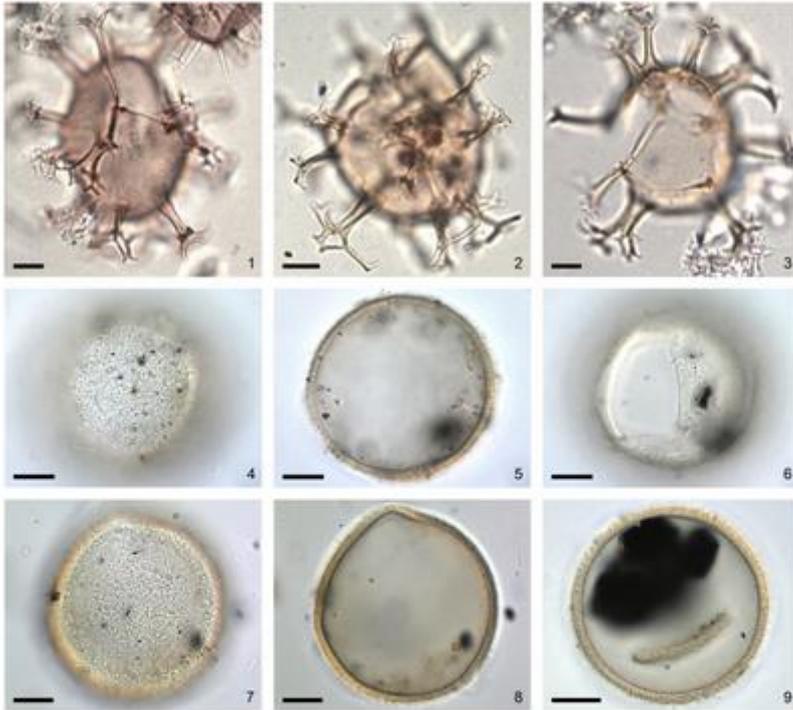
Plate 8. 1–3. *Nematospaeropsis rigida*. 1–2. Optical section and low focus on specimen from the Gulf of Mexico (Limoges et al., 2013). 3. Optical section of a different specimen from the same locality. 4–7. *Spiniferites hainanensis* from Southern China surface sediments. 4–6. Increasing focal depth, dorsal view. 7. Oblique dorso-lateral view of the hypocyst. 8–12. *Spiniferites multisphaerus*. 8–9. Optical section and low focus on specimen from the Pacific Ocean. 10–12. Different focal depths of a different specimen from the Pacific Ocean. Image 1–3 by AL, 4–7 by KNM, 8–12 by VP. All scale bars = 10  $\mu$ m.



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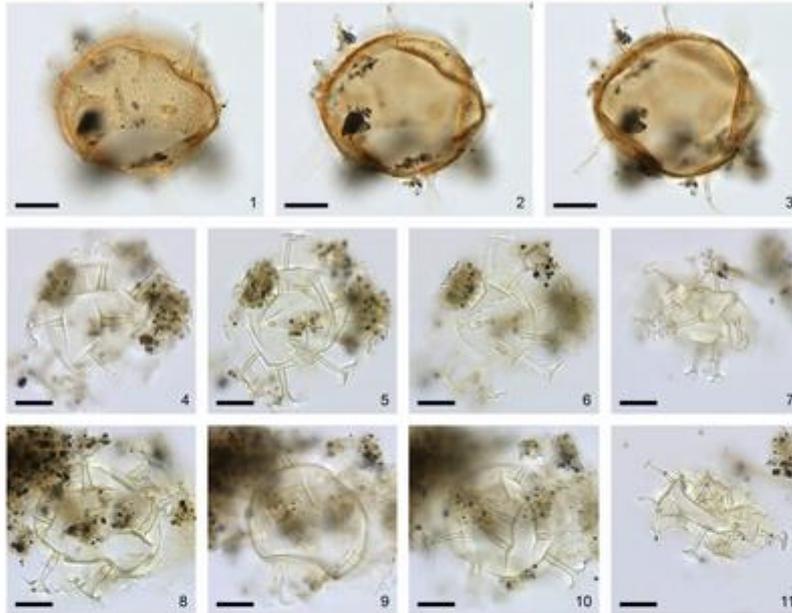
Plate 9. 1–12. *Spiniferites ristingensis*, specimens from (sub)surface sediments off Portugal (core PO287-39B, [Ribeiro et al., 2016](#)). 1–3. High to low focus, apical view. 4–6. High to low focus, dorsal view. 7–8. High and mid-focus, dorso-lateral view. 9–12. High to low focus, oblique antapical view. All images by KNM. All scale bars = 10  $\mu\text{m}$ .



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Plate 10. 1–3. *Spiniferites septentrionalis*, three specimens from MIS 6 in the Bay of Biscay (core MD03–2692, [Penaud et al., 2008](#)). 4–9. *Tectatodinium pellitum* from the eastern Mediterranean Sea. 4–6. High to low focus, ventro-lateral view. 7–8. High focus and optical section of a different specimen. 9. Optical section of another specimen. Image 1–3 by Aurélie Penaud, 4–9 by KNM. All scale bars = 10  $\mu$ m.



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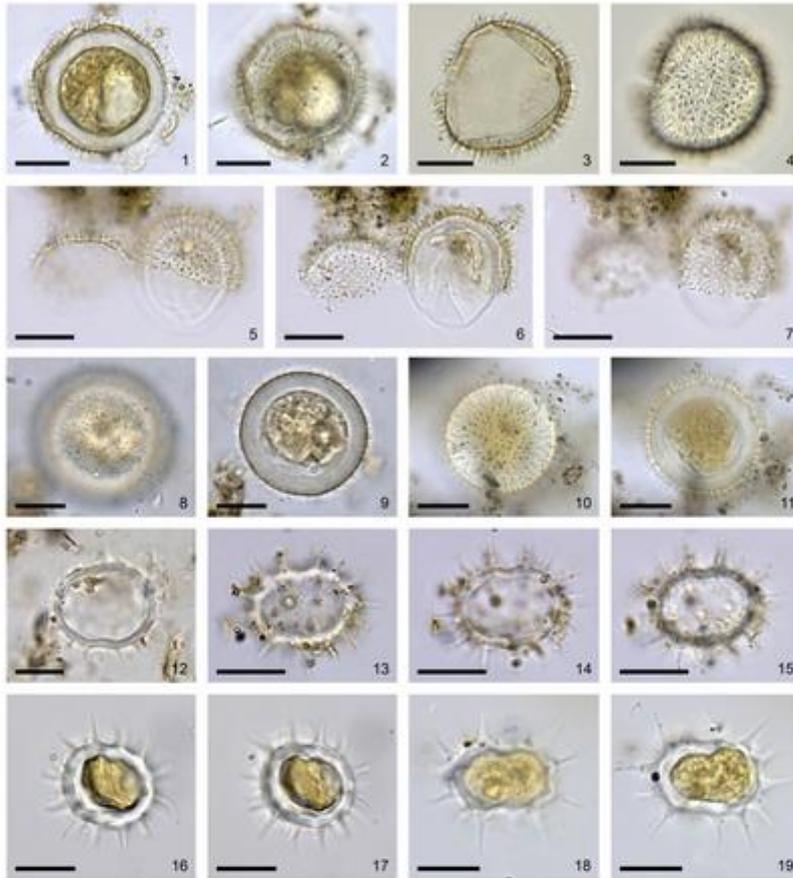
Plate 11. 1–3. *Melitasphaeridium angustum*, new micrographs of the holotype (Matsuoka, 1983). Apical view in (1) high focus and (2–3) optical section at two slightly different focal depths. 4–11. *Melitasphaeridium choanophorum* from the Gulf of Mexico. 4–6. High to low focus. 7, 11. Different focal depths of different specimen. 8–10. High to low focus of another specimen. Image 1–3 by KNM, 4–11 by AL. All scale bars = 10  $\mu\text{m}$ .



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Plate 12. 1–9. Cyst of *Pentaplecodinium saltonense* from Salton Sea (California, USA) surface sediments. 1–3. High to low focus, dorsal view. 4–5. High focus and optical section of a different specimen. 6, 9. High focus and optical section of a different specimen. 7–8. High focus and optical section of another specimen. 10–12. *Dapsilidinium pastielsii*, three different specimens from the Philippines. All images by KNM. All scale bars = 10 µm.



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Plate 13. 1–7. Cyst of *Biecheleria baltica* from the Baltic Sea (core KSK12-01D). 1–2. Optical section and low focus of specimen with cell content. 3–4. High focus showing the (?) archeopyle, and low focus, of a different specimen. 5–7. High to low focal view of another specimen suggesting an epicystal archeopyle. 8–11. Cyst of cf. *Biecheleria baltica*. 8–9. High focus and optical section of specimen with cell content from the Arctic. 10–11. High focus and optical section of specimen with cell content from NE Greenland. 12–19. Cyst of *Polarella glacialis*. 12. Optical section of specimen from the Arctic. 13–15. High to low focus of specimen from northern Baffin Bay. 16–17. Different focal depths of a specimen with cell content from northern Baffin Bay. 18–19. Different focal depths of specimen with cell content from the Wandel Sea. Image 1–7, 13–17 by NVN, 8–9, 12 by VP, 10–11, 18–19 by AL. All scale bars = 10  $\mu\text{m}$ .