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NEW GONIODOMACEAN DINOFLAGELLATES WITH A COMPOUND HYPOTRACTAL ARCHEOPYLE FROM THE LATE CENOZOIC: *CAPISOCYSTA* WARNY AND WRENN, EMEND

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ABSTRACT—Two new species of dinoflagellate are described from the upper Cenozoic of the North Atlantic region. They are assigned to the goniodomacean genus *Capisocysta* Warny and Wrenn, 1997 emend., whose archeopyle uniquely forms by the extensive and exclusive dissociation of hypocystal plates. *Capisocysta lata* new species is recorded from the upper lower Pliocene Coralline Crag Formation of eastern England, the lower and upper Pliocene of the subsurface Great Bahama Bank, and as a living cyst from Phosphorescence Bay, Puerto Rico. *Capisocysta lyellii* new species is reported from the Coralline Crag Formation of eastern England. *Capisocysta* provides the only unambiguous example of a hypocystal archeopyle in the order Gonyaulacales and the only example of a hypotractal archeopyle in the division Dinoflagellata.

The spherical, proximate cysts have pre-formed lines of weakness that occur exclusively on the hypocyst, where they follow plate boundaries. Upon excystment, these sutures facilitate the separate release of plates 2–6''', ps, 1p, and 1'''. Sulcal plates ls and rs and postcingular plate 1''' typically remain attached to the epicyst, forming a distinctive hyposulcal tab. The single antapical plate in *C. lata* is represented in *C. lyellii* by two plates (left and right first antapical homologues) that are released separately.

Capisocysta has a tropical to warm temperate distribution today. It thrived and perhaps formed blooms in tropical carbonate platform environments of the Bahamas during the Pliocene, and might prove to be a useful indicator of very warm intervals within the Pliocene of higher latitude regions including the southern North Sea basin.

To facilitate discussion of *Capisocysta*, several morphological terms have been modified or newly introduced. These terms more precisely describe archeopyle position and extent in dinoflagellates.

INTRODUCTION

GONIODOMACEANS ARE photosynthetic dinoflagellates whose principal life-cycle stage comprises the motile cell. Goniodomaceans are widespread in warm to cold temperate marine environments, and have a fossil record extending from at least Early Cretaceous to the present (e.g., Fensome et al., 1993). Some living species produce blooms, including the tropical–subtropical *Pyrodinium bahamense*, a well known bioluminescent dinoflagellate that causes paralytic shellfish poisoning in the Pacific. Some fossil species are also inferred to have formed blooms, including *Geonettia clineae* de Verteuil and Norris, 1996a and species of the *Homotryblium* complex (de Verteuil and Norris, 1996a).

Goniodomaceans have a distinctive hypotabulation that includes a quinqueform (five sided) first antapical homologue (Fensome et al., 1993). Some goniodomaceans also show a tendency towards increase in plate numbers [e.g., *Fragilidium heterolobum* and *Tuberculodinium vancampoae* (Rossignol, 1962) Wall, 1967] and extensive plate dissociation during archeopyle formation (e.g., *Polysphaeridium* Davey and Williams, 1966, *Eocladopyxis* Morgenroth, 1966, and *Geonettia* de Verteuil and Norris, 1996a). *Capisocysta* Warny and Wrenn, 1997 emend. exhibits a typical goniodomacean hypocystal tabulation—although in the case of one species an increase in plate number—and extensive plate dissociation during archeopyle formation. But uniquely among all known goniodomaceans, or indeed any other dinoflagellates within the order Gonyaulacales, *Capisocysta* has an archeopyle restricted unambiguously to the hypocyst.

Capisocysta was erected monospecifically by Warny and Wrenn (1997) for goniodomaceans whose archeopyles are formed by dissociation of the hypocyst, leaving the epicyst and some attached hyposulcal plates intact. Its type species, *C. wallii*, was described from the upper Miocene and Pliocene of Morocco. The holotype, however, is an isolated epicyst and details of the hypotabulation are unknown.

Capisocysta lata new species is here reported from the Pliocene of both eastern England and the Great Bahama Bank, and from modern sediments of Puerto Rico. It has a well-developed

hypotractal archeopyle, most of whose constituent plates (2–6''', ps, 1p, 1''', Fig. 1) dissociate extensively along pre-formed lines of weakness. No such lines occur on the epicyst, which consequently remains intact. The left and right sulcal plates and first postcingular plate are all attached to the epicyst. This results in a distinctive hyposulcal tab that is reminiscent of the episulcal tab found only on *Polysphaeridium* and other goniodomaceans with epitactal archeopyles. This style of archeopyle—compound, hypotractal, with hyposulcal tab—is known only for the genus *Capisocysta*.

The epitabulation of *Capisocysta* is not expressed on the cyst. However, the well expressed hypotabulation in *C. lata* allows it to be classified as a goniodomacean within the subfamily Pyrodinioideae.

The most significant difference between *Capisocysta lyellii* new species, here recorded from the Pliocene of eastern England, and *C. lata* is in the antapical region, where the first antapical plate (1''') of *C. lata* is represented by two plates in *C. lyellii*. These two plates (labelled left and right first antapical homologues) together are apparently homologous with the single antapical plate in other pyrodinioideans. Such reasoning is based on the otherwise close similarities between *C. lata* and *C. lyellii*, on the documented tendency within the Goniodomaceae towards plate multiplication, and on comparison with *Geonettia* and the general tabulation model for the *Homotryblium* complex, exemplified by *Eocladopyxis*.

The common presence of *C. lata* in the tropical Pliocene of the Bahamas, its occurrence in the warm-temperate mid-Pliocene of the southern North Sea, and its presence in the tropical and warm-temperate environments of Puerto Rico and Portugal today, are all consistent with the warm marine ecological affinities that characterize the Pyrodinioideae (Fensome et al., 1993; de Verteuil and Norris, 1996a).

SIGNIFICANCE OF HYPOCYSTAL AND EPICYSTAL ARCHEOPYLES

Of the 260 living dinoflagellate species that produce a resting cyst (Head, 1996), only the cysts of *Pyrophacus steinii* (known

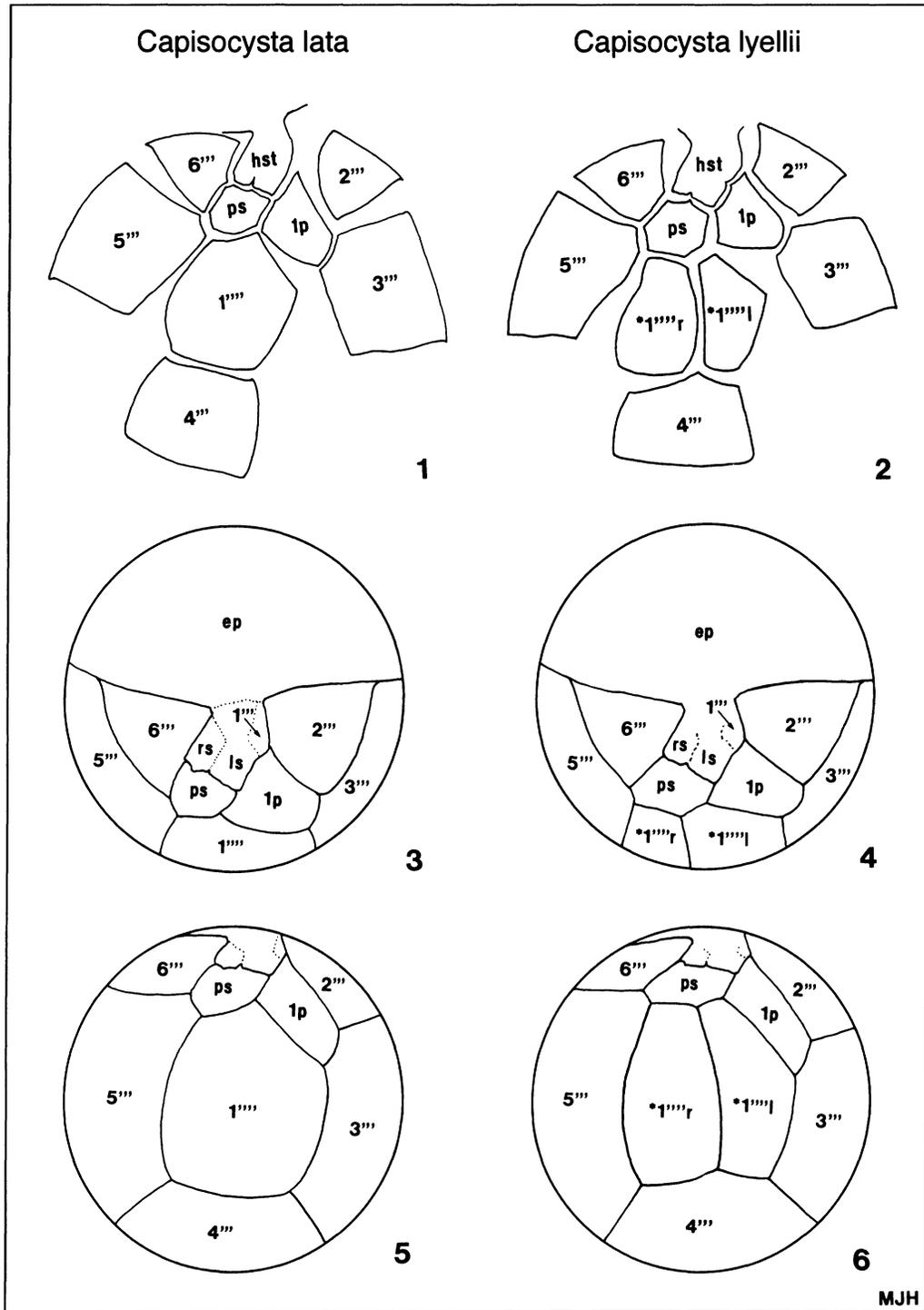


FIGURE 1—Comparison of tabulation in *Capisocysta lata* and *Capisocysta lyellii*. Note particularly the pair of antapical plates (*1'''l and *1'''r) in *C. lyellii* compared to the single plate (1''') in *C. lata*, and the respective differences between both the posterior sulcal plate (ps) and fourth postcingular plate (4''') in these two species. 1, 2, exploded diagrams showing external view of hypocystals plates in 1, *Capisocysta lata* based on tracing of the holotype (see Fig. 2.1, 2.2), with 6''' reconstructed; and 2, *Capisocysta lyellii* based on tracing of the holotype (Fig. 5.3, 5.4), with 2''' reconstructed from paratype (Fig. 5.1, 5.2). 3–6, schematic drawing of tabulation as represented on a sphere and using Kofoed labels; 3, 4 ventral views and 5, 6 antapical views of *C. lata* and *C. lyellii* respectively. Notation: ep = epicyst; hst = hyposulcal tab; rs = right sulcal plate; ls = left sulcal plate; ps = posterior sulcal plate; 1–6''' = first to sixth postcingular plates; 1p = posterior intercalary plate; 1''' = first antapical plate; *1'''l = left first antapical homologue; *1'''r = right first antapical homologue.

as *Tuberculodinium vancampoae*) and of *Pyrophacus horologium* (see Wall and Dale, 1971) have archeopyles that may be hypocystal (see below).

Among the more than 550 fossil dinoflagellate cyst genera described (Lentin and Williams, 1993) only *Capisocysta* Warny and Wrenn, 1997 emend., *Caligodinium* Drugg, 1970, and possibly *Tuberculodinium* Wall, 1967 have hypocystal archeopyles. *Caligodinium* (Santonian through Miocene) is now considered a peridiniacean genus and has a convincing hypocystal archeopyle (Manum and Williams, 1995). The archeopyle in the goniodominean genus *Tuberculodinium* (Eocene or Oligocene through Recent) is variously considered precingular (e.g., Drugg 1970, Wrenn and Damassa, 1989) or hypocystal (e.g., Wall and Dale, 1971; Evitt, 1985) and appears not to involve more than one series of plates. Forma D of Wrenn and Kokinos (1986), reported from the Pliocene and Pleistocene of the Gulf of Mexico, has an archeopyle they interpreted to be hypocystal. This form was considered by Head (1996) to be possibly the cyst of *Pyrophacus horologium*.

Two fossil cyst genera, *Eocladopyxis* (Paleogene) and *Geonettia* (Neogene), have a propensity to dissociate extensively along epicystal and hypocystal plate boundaries upon excystment, but these are not hypocystal archeopyles since epicystal plates are also involved—indeed primarily so in *Eocladopyxis*. The siliceous dinoflagellate *Peridinites* Lefèvre, 1933 ecdyses by the loss of hypothecal plates, but this fossil dinoflagellate represents a mineralized theca and not a resting cyst (Harding and Lewis, 1995).

Hypocystal archeopyles are thus exceptionally rare in dinoflagellate evolution. Why are archeopyles almost exclusively situated on the epicyst? Perhaps there is a link with swimming direction, since living motile dinoflagellates typically swim forward relative to their overall morphology (Levandowski and Kaneta, 1987): the archeopyle, too, being positioned forward on the cyst relative to its overall morphology. The connection is not obviously functional because, in living dinoflagellates, the protoplast exits the cyst by amoeboid movement, not by flagellar propulsion (although flagella may be formed on the protoplast prior to excystment; Dale, 1983 and references therein). The absence of the archeopyle from the hypocyst may account for the evolutionary stability of hypothecal tabulation that has been so effective in deducing dinoflagellate phylogeny (e.g., Fensome et al., 1993). If this is the case, it could explain the variability in the hypothecal tabulation of *Capisocysta*. In *Capisocysta* there is no clear suggestion from cyst morphology that the motile stage swam any direction other than forward or that the cyst was anteriorly attached to the substrate. The significance of archeopyle position in *Capisocysta* therefore remains unresolved.

PHYLOGENY IN THE *EOCLADOPYXIS-GEONETTIA-CAPISOCYSTA* COMPLEX

The tendency for hypocystal plates to dissociate extensively is demonstrated only in the goniodomacean genera *Eocladopyxis*, *Geonettia*, and *Capisocysta*. These three genera have similar quinqueform hypocystal tabulations, and *Eocladopyxis* and *Geonettia* have similar epitabulation patterns (this being unknown for *Capisocysta*). It thus appears that they are phylogenetically related. The stratigraphic record, based on McLean (1976), Liengjarern et al. (1980), de Verteuil and Norris (1996a), Warny and Wrenn (1997), and herein, suggests a simplistic but possible sequence of events: 1) development of extensive plate dissociation but with (epitactal) archeopyle retained in the proximochorate to marginally chorate *Eocladopyxis* (Paleocene–Oligocene); 2) loss of processes and more extensive plate dissociation whereby entire cyst disintegrates, in *Geonettia* (early Miocene–Pliocene); and 3) fusion of epicystal plates thereby restricting

archeopyle formation to the hypocyst, in *Capisocysta* (late Miocene–present). *Capisocysta lyellii* may have evolved from *Capisocysta lata* since it has an antapical plate pair apparently derived from a single ancestral plate found, for example, in *C. lata* (Fig. 1). However, the stratigraphic ranges of these two species are too imprecisely known yet to provide firm support for this idea.

The tendency for an increase in the number of plates in *Capisocysta*, here placed in the Pyrodinioideae, is seen also in forms placed by Fensome et al. (1993) in the Helgolandinoideae (e.g., *Tuberculodinium*). The Pyrodinioideae is known from the Paleogene (based on *Eocladopyxis*) and so too is the Helgolandinoideae (based on *Tuberculodinium*), so these two lineages would appear to have been separate since at least this time. If so, an increase in plate numbers in *Capisocysta* represents convergent evolution with respect to the Helgolandinoideae.

MATERIALS AND METHODS

Materials.—These are 1) samples from the Pliocene Coralline Crag Formation of eastern England, which was then part of the southern North Sea; 2) single-specimen mounts of *C. lata* from modern sediments of Puerto Rico; and 3) samples from selected lower and upper Pliocene intervals of the Clino borehole, Bahamas.

Samples from eastern England were reported in an earlier study of the dinoflagellates by Head (1997; in press), although *Capisocysta* was not then recognized owing to the mostly incomplete nature of specimens and their scarcity. The four samples (labelled NQ1 through NQ4) are silty carbonate sands from the Ramsholt Member (upper lower Pliocene) of the Coralline Crag Formation, Rockhall Wood, Suffolk (52°02'N, 1°22'E), deposited in warm-temperate seas at a minimum water depth of 50 m (see Hodgson and Funnell, 1987 and Head, 1997 for details).

Two single-specimen mounts of *C. lata* were supplied by D. Wall and are from surface sediment of Phosphorescence Bay, Puerto Rico (17°58.5'N, 67°0.9'W). They had been picked from sample 103 of Wall et al. (1977) collected in a water depth of 3 m. The sample was demineralized with HCl and weak HF, and individual cysts, with their protoplasts unexpectedly still surviving, were extracted and dissected to determine their plate configuration. This cyst type was found to be very rare and was not incubated. The motile stage is therefore unknown (D. Wall, personal commun.).

The Pliocene Bahamas samples are from a larger project involving the palynology of the Clino borehole in progress by the present author and H. Westphal (e.g., Westphal et al., in press). This borehole (24°36'07"N, 79°10'41"W) was drilled on the western margin of the Great Bahama Bank as part of the Bahamas Drilling Project, and penetrated more than 600 m of Quaternary and Neogene carbonates (Eberli et al., 1997). Two separate intervals of the Clino borehole were examined: six samples from the upper lower Pliocene, 494.39–476.40 m (1622.00–1563.00 ft) below mud pit (mbmp), represent a lower slope environment; and eight samples from the upper upper Pliocene, 262.18–220.48 mbmp (860.17–723.38 ft), represent an upper slope environment. Details of the chronostratigraphy and paleoenvironment are given in Eberli et al. (1997), Westphal (1997), and Westphal et al. (in press). Illustrated specimens are from upper Pliocene samples CUS-K11 (234.12 m below mud pit, 768.13 fbmp) and CUS-M7 (232.71 mbmp, 763.50 fbmp).

Methods.—Coralline Crag and Bahamas samples were processed by first demineralizing in HCl and HF. Neither oxidative nor alkali treatments were used but the Bahamas residues required ultrasound for about 45 secs. Residues were stained with safranin o and sieved at 7 µm (Coralline Crag residues) or 10

μm (Bahamas residues) using Nitex nylon screens. Remaining residue, where available, was sieved at 20 μm to concentrate the larger dinoflagellates. Residues were strew mounted on microscope slides using Cellosize and Elvacite.

The two modern specimens of *C. lata* from Puerto Rico had been mounted on individual microscope slides using glycerine jelly and sealed with bees wax. The slides, made a number of years ago, were workable but had suffered some desiccation making photography difficult.

Photography.—Specimens are illustrated with a vario-orthomat 2 camera attached to a Leitz Dialux microscope. Images are all true, i.e., not reversed. An England Finder reference follows the sample (and slide) number for each specimen illustrated.

Repository.—Microscope slides containing holotypes, paratypes, and some other figured material are housed in the Invertebrate Section of the Department of Palaeobiology, Royal Ontario Museum, Toronto, Ontario, under the catalog numbers ROM 52493 (NQ2 slide 1), ROM 53301 (NQ4 slide 3), ROM 53302 (NQ4 slide 4), ROM 53303 (CUS-K11 slide 2), ROM 53304 (CUS-K11 slide 3), and ROM 53305 (CUS-M7 slide 3).

Time scale.—This paper uses the time scale of Berggren et al. (1995) and, where necessary, ages cited from the literature have been adjusted accordingly.

TERMINOLOGY

The new terms *episulcal tab* and *hyposulcal tab* are introduced as modifications of the term *sulcal tab* to discriminate between such projections occurring on the epicyst (e.g., *Homotryblium* Davey and Williams, 1966 and *Polysphaeridium*) and hypocyst (*Capisocysta*). *Episulcal tab* here replaces the term *sulcal tab* which is defined as follows: "In pyrodinioidean cysts [with an epicystal archeopyle], the projection on the archeopyle margin formed by the anterior sulcal plate" (Fensome et al., 1993, p. 262). The term *hyposulcal tab* is here defined as follows: In pyrodinioidean cysts with a hypocystal archeopyle, the projection on the archeopyle margin formed by one or more plates within the sulcal region lying posterior to the cingulum. The *hyposulcal tab* typically comprises the left and right sulcal plates and first postcingular plate (or its homologue, the left accessory sulcal plate).

The term *epittractal archeopyle* is used in the sense of Fensome et al. (1993, p. 253) for: "An archeopyle involving the loss of the epittract [=epicyst], with the archeopyle suture lying immediately anterior to the cingulum." The term *epicystal archeopyle* is here newly defined as follows: An archeopyle restricted to the loss of one or more plates on the epicyst, although cingular plates may be additionally involved. The terms *epittractal archeopyle* and *epicystal archeopyle* have long been treated as synonyms (Williams et al., 1978). However, the definitions used in the present paper recognize the need to distinguish between archeopyles that comprise the entire epicyst (*epittractal archeopyles*) and those located on the epicyst but perhaps only involve part of it (*epicystal archeopyles*). Hence, an *epittractal archeopyle* is a particular kind of *epicystal archeopyle*. A parallel need arises with the hypocyst, and so the following terms are newly defined. A *hypottractal archeopyle* is an archeopyle involving the loss of the hypocyst (=hypottract), with the archeopyle suture lying immediately posterior to the cingulum. This style is presently known only for *Capisocysta*. A *hypocystal archeopyle* is an archeopyle restricted to the loss of one or more plates on the hypocyst. This style is represented by *Capisocysta*, *Caligodinium*, and possibly *Tuberculodinium*. The new term *holocystal archeopyle* is defined as an archeopyle involving extensive plate dissociation on both the epicyst and hypocyst. This

style is represented by *Geonettia* and to some extent *Eoclodopyxis*. For completeness, an *ambicystal archeopyle* is defined as an archeopyle involving one or more plates on *both* the epicyst and hypocyst. A *holocystal archeopyle* is therefore a particular kind of *ambicystal archeopyle*.

The paraterminology of Evitt et al. (1977) has been avoided for reasons given in Fensome et al. (1996, p. 125). The terminologies of Evitt (1985), Fensome et al. (1993, 1996) and de Verteuil and Norris (1996a and b) are otherwise selectively applied to *Capisocysta*, and Kofoid plate notation (slightly modified below) is used for reasons given in de Verteuil and Norris (1996a and b).

The first postcingular plate (1''') is small and tapers towards the cingulum. It is not certain whether this plate actually contacts the cingular series, but for the purpose of plate labeling it is assumed to do so. If it does not, the term left accessory sulcal plate (las) would then be more appropriate in strict Kofoid plate labelling. In any case, the first postcingular plate in *Capisocysta* is 1) an integral part of the hyposulcal tab and only rarely separates from it, and 2) is clearly homologous with the left anterior [sic] sulcal plate of *Geonettia* which does not contact the cingular series (de Verteuil and Norris, 1996a, pls. 2 and 4).

The posterior sulcal plate (ps) in *Capisocysta* is so labelled because its small size and position suggest that it represents part of the sulcus, although, as de Verteuil and Norris (1996a) have noted, the precise boundaries of a reflected sulcus are somewhat arbitrary on a cyst where no actual depression occurs. The posterior sulcal plate in *Capisocysta* is inferred to be homologous with the second posterior intercalary (2p) in *Geonettia*.

The Kofoid antapical plate (1''') in *C. lata* is represented in *C. lyellii* by two plates. However, the strict application of Kofoid terminology (as 1'''' and 2''') is avoided for this gonyaulacalean species whose antapical plates are assumed to be derived from one ancestral antapical plate. Accordingly, the new terms *left first antapical homologue* (*1''''l) and *right first antapical homologue* (*1''''r) are used for these plates.

SYSTEMATIC PALEONTOLOGY

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

Subdivision DINOKARYOTA 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 GONIODOMACEAE Lindemann, 1928

Subfamily PYRODINIOIDEAE Fensome et al., 1993

CAPISOCYSTA Warny and Wrenn, 1997 emend.

Type specimen.—The holotype of *Capisocysta wallii* Warny and Wrenn, 1997, pl. 8, fig. 7, 10.

Original diagnosis.—Autocysts characterized by a hypocystal archeopyle (Type H (6HP) 1HA, the opercular pieces generally disarticulate upon excystment) and a one piece epicyst that incorporates the paracingular area. A parasulcal tab projects posteriorly from the ventral margin of the epicyst. (Warny and Wrenn, 1997, p. 297.)

Emended diagnosis.—Proximate goniodomacean cysts whose archeopyle is compound and hypottractal. The hypocyst, except usually for parts of the sulcus, dissociates into constituent plates but the epicyst remains as one piece.

Discussion.—The emended diagnosis is broadened to acknowledge the demonstrated and potential variability in the number of hypocystal plates for this genus, and to allow for the presence of an outer wall layer. It also restricts this genus to species with low surface relief.

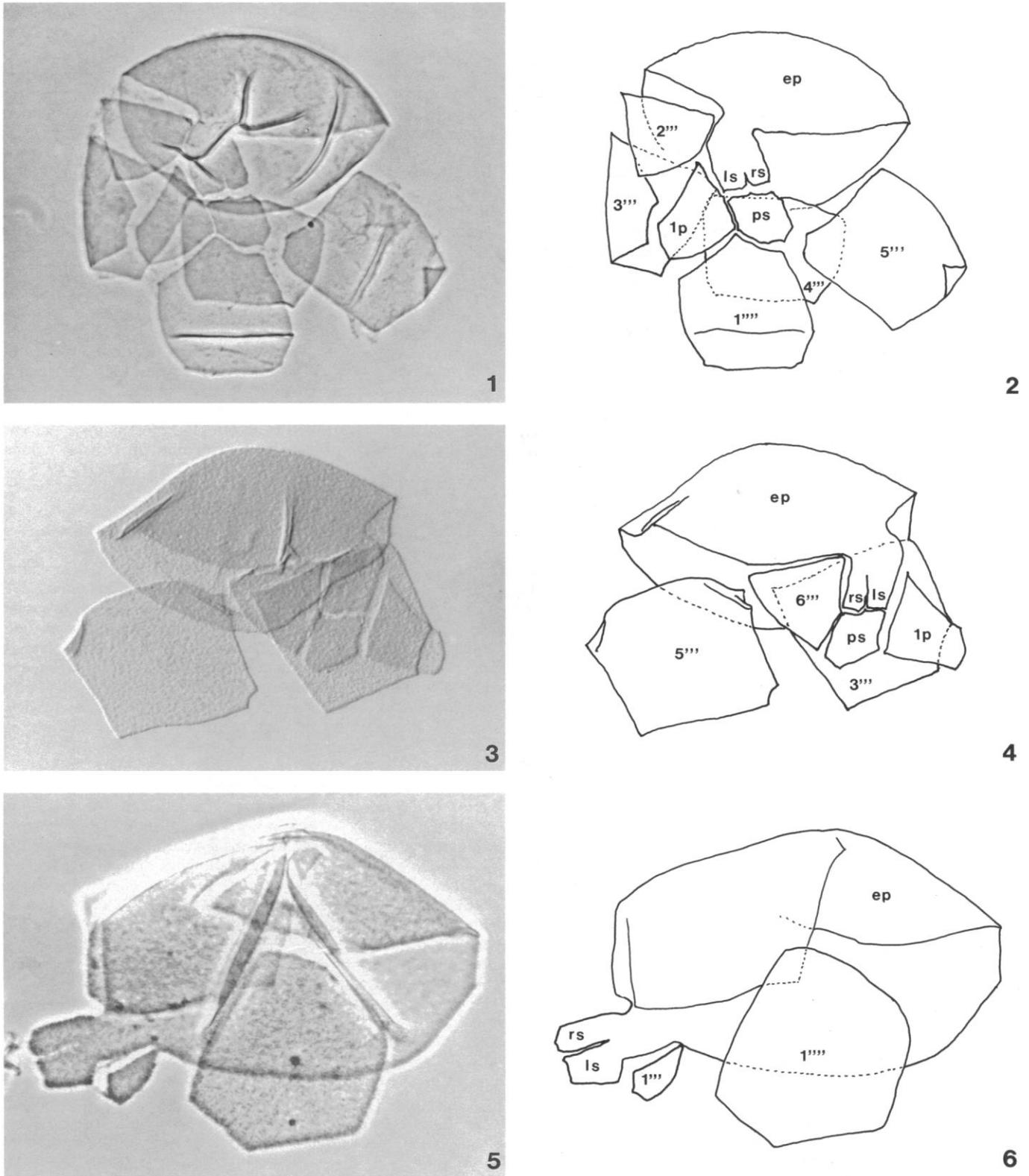


FIGURE 2—*Capisocysta lata* new species from the Great Bahama Bank. Photomicrographs are phase contrast (1, 5) or interference contrast (2) images. Various magnifications. Tracings are shown to right of photomicrographs; dashed lines do not necessarily indicate real order of overlap; see Figure 1 for plate notation. 1, 2, Holotype, showing nearly smooth wall surface with some adherent remnants of the diaphanous outer layer; all plates present except 6'''; sample CUS-K11 (Clino borehole), slide 3, M19/0; maximum diameter of epicyst, 41 μm . 3, 4, sample CUS-K11 (Clino borehole), slide 3, P14/1; maximum diameter of epicyst, 53 μm . 5, 6, specimen showing epicyst with nearly detached 1'''; sample CUS-K11 (Clino borehole), slide 3, V33/0; maximum diameter of epicyst (excluding hyposulcal tab), 47 μm .

Tabulation is expressed on the hypocyst by pre-formed lines of weakness that follow plate sutures and may be visible on undehisced specimens. The cyst wall consists of a thicker inner wall, which is unstratified under light microscopy and has a smooth or ornamented surface, and this may be accompanied by a loose outer diaphanous layer. The outer layer is often not preserved but is more likely to be seen in undehisced specimens.

The hyposulcal tab (comprising rs, ls, and 1''') is a distinctive feature. However, since specimens occasionally lose this tab in archeopyle formation, its significance at the generic level is uncertain.

Comparison.—*Capisocysta* is unique among dinoflagellate cysts in possessing an archeopyle formed by the extensive and exclusive loss of hypocystal plates, including those of the postcingular series, so that upon excystment only the epicyst, some sulcal plates, and the first precingular plate usually remain fully intact. *Geonettia* differs in the extensive loss of both epicystal and hypocystal plates during excystment. *Geonettia lineae* has a larger posterior sulcal plate than *Capisocysta*, although this may not be a significant feature at the generic level: an undescribed species of *Geonettia* from the Pliocene of eastern England (Fig. 6) has a nearly identical posterior sulcal plate to *C. lata*. Related genera *Eocladopyxis*, *Polysphaeridium*, and *Homotryblium* differ from *Capisocysta* in bearing processes and having archeopyles that involve epicystal plates, although some dissociation of hypocystal plates may occur in *Eocladopyxis*.

Suprageneric assignment.—This is based on a quinqueform antapical plate (two plates in *C. lyellii*), presence of two fundital plates (1p and 1''''', the latter as two plates in *C. lyellii*), six postcingular plates, and the fact that the posterior sulcal plate (ps) is small and apparently within the sulcus. The epitabulation in *Capisocysta* is indeterminable. The propensity for plates to dissociate extensively during excystment is a characteristic feature of many pyrodinioideans including *Polysphaeridium zoharyi* (the cyst of *Pyrodinium bahamense*).

Status of the type species.—*Capisocysta wallii* Warny and Wrenn, 1997 was described from the Neogene of Morocco, its holotype being of Messinian (late Miocene) age. The illustrated type material consists of isolated epicysts bearing the hyposulcal tab distinctive of this genus. The holotype itself is an isolated epicyst bearing only the hyposulcal tab. Hence details of the hypocystal tabulation for *C. wallii* are largely unknown, and for the holotype will never be known except perhaps by inference.

Warny and Wrenn (1997, fig. 3) did present a hypocystal tabulation scheme for *C. wallii*. However, this was based on modern specimens from Puerto Rico (interpreted by D. Wall, personal commun. in Warny and Wrenn, 1997) and presented on the assumption that these modern specimens are conspecific with the type material from Morocco. This assumption is now shown to be untenable because at least two species of *Capisocysta* exist in the fossil record (*C. lata* and *C. lyellii*, of the present paper)

and these are distinguished entirely on hypocystal details that are unknown for *C. wallii*. Of course it remains to be seen whether more than one species of *Capisocysta* is present, or conceivably present, in the Moroccan type material. Meanwhile, in the interests of taxonomic precision, the present paper restricts the name *C. wallii* to the holotype and identifies the modern specimens from Puerto Rico as belonging to *C. lata*.

Occurrence.—Upper Miocene (Tortonian) through lower Pliocene of Morocco (as *C. wallii* in Warny and Wrenn, 1997), lower through upper Pliocene of the Bahamas (*C. lata*, this paper), lower Pliocene of the southern North Sea (*C. lata* and *C. lyellii*, this paper), Holocene of Deep Sea Drilling Project, Site 502, western Caribbean Sea (as *C. wallii* in Warny and Wrenn, 1997), and extant in Puerto Rico and Portugal (*C. lata*, this paper).

Stratigraphic range.—Upper Miocene (Tortonian) through present day.

Paleoecology.—The fossil and modern distribution of *Capisocysta* suggests neritic, warm-water affinities for this genus, which is consistent with the ecological classification of the pyrodinioideans given by Fensome et al. (1993). The absence of dark wall coloration suggests autotrophy; most living heterotrophic dinoflagellates produce cysts with a brown, densely colored wall.

CAPISOCYSTA LATA new species

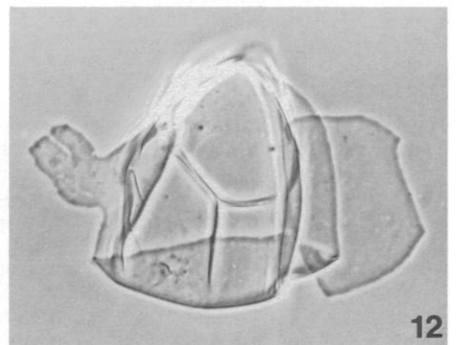
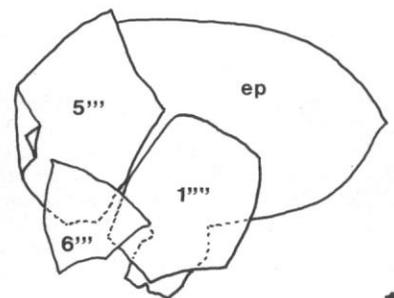
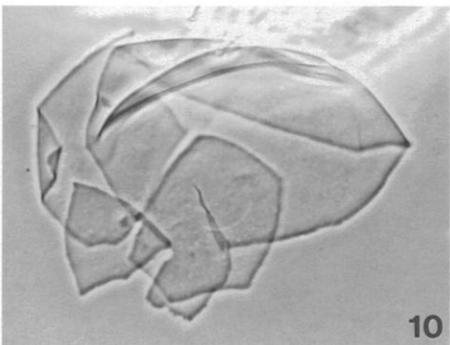
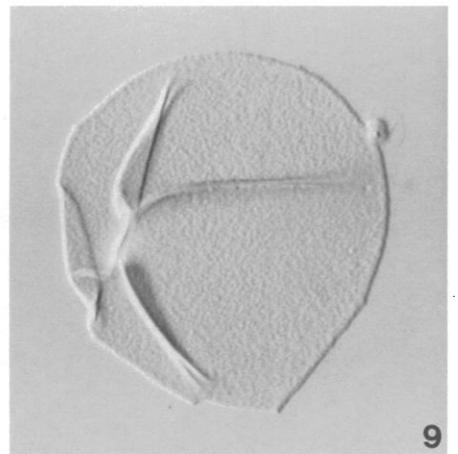
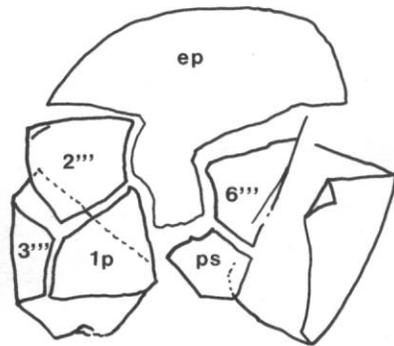
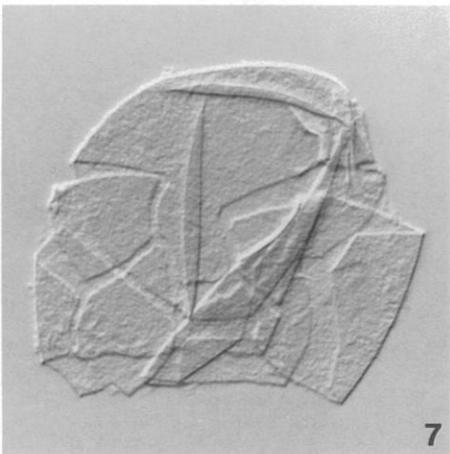
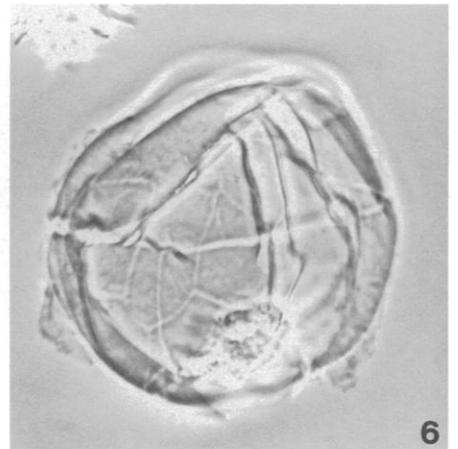
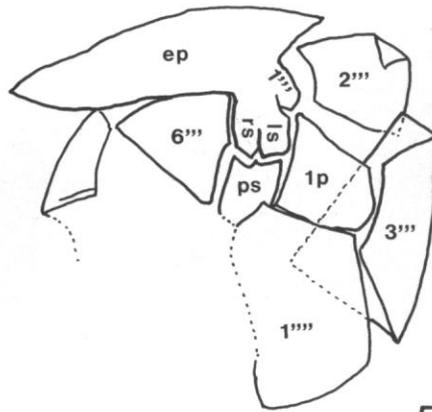
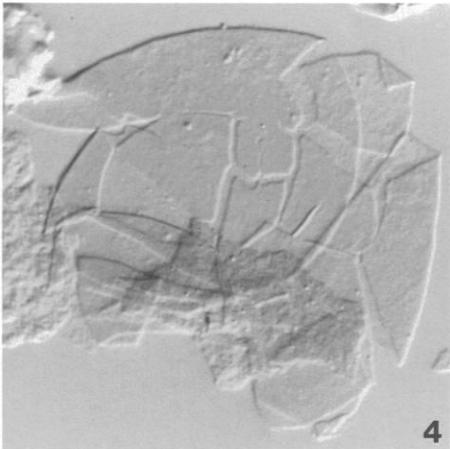
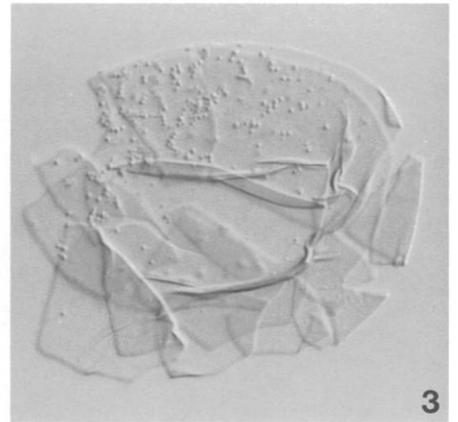
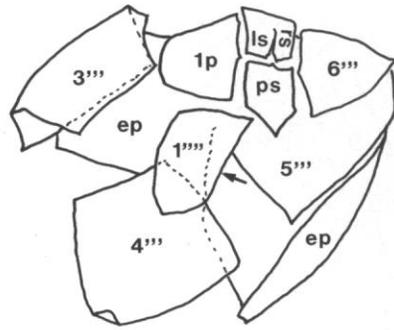
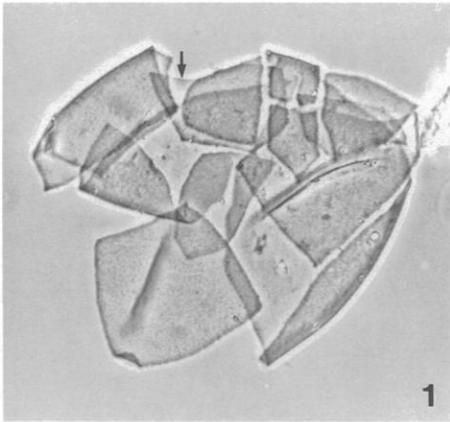
Figures 1.1, 1.3, 1.5, 2–4

Capisocysta lata Head. HEAD, in press, pl. 4, fig. 3.

Diagnosis.—Spherical cysts with loose outer diaphanous layer and thicker inner wall whose outer surface is smooth to granulate. Tabulation expressed extensively on hypocyst, with individual loss of plates 2–6''', 1p, ps, and 1'''''. Sulcal plates ls and rs and postcingular plate 1''' usually remain attached to epicyst forming a hyposulcal tab. Width of posterior sulcal plate (ps) does not exceed that of left and right sulcal plates combined. Plate 4'''' has a monothigmate, rectilinear posterior margin that contacts an undivided antapical plate (1''''').

Description.—Cysts are spherical and proximate, and have a thin (less than 0.3 μm) inner wall layer whose outer surface varies from smooth to granulate. Undehisced specimens are nearly always covered with a loose, diaphanous layer which is often absent in dehisced specimens (but remnants are present on the holotype, Fig. 2.1). Occasionally, the diaphanous layer is replaced by small, preservational? pustules scattered over the surface (Fig. 3.3). Undehisced specimens usually contain an accumulation body ("omphalos" of Dörhöfer and Davies, 1980) variably positioned within the cyst (Fig. 3.6). Tabulation is expressed only by pre-formed lines of weakness, these being visible as pale, narrow lines on undehisced specimens (Fig. 3.6) and which control the discrete separation of plates in dehisced

FIGURE 3—*Capisocysta lata* new species from eastern England (1, 2) and the Great Bahama Bank (3–12). Photomicrographs are phase contrast (1, 6, 10, 12) or interference contrast (3, 4, 7, 9) images. Various magnifications. Tracings are shown to right of photomicrographs; dashed lines do not necessarily indicate real order of overlap; see Figure 1 for plate notation. 1, 2, specimen showing 1'''' torn in two, with the dorsal part in the center of the cyst (arrow indicates torn margin) and the remaining fragment (its geniculate ventral margin facing down, and its torn margin arrowed in 1) beneath 1p; sample NQ2, slide 1, D45/0; maximum dimension of cyst, 61 μm . 3, showing small preservational pustules on epicyst surface; sample CUS-K11 (Clino borehole), slide 3, U34/2; maximum dimension of cyst, 54 μm . 4, 5, sample CUS-M7 (Clino borehole), slide 3, O48/0; maximum dimension of cyst, 65 μm . 6, undehisced specimen showing ventral surface with plate sutures, loose diaphanous outer layer, and omphalos; sample CUS-K11 (Clino borehole), slide 3, P34/2; maximum diameter of cyst (excluding diaphanous layer), 43 μm . 7, 8, sample CUS-K11 (Clino borehole), slide 3, E49/0; maximum diameter of epicyst, 46 μm . 9, epicyst with detached hyposulcal tab; sample CUS-K11 (Clino borehole), slide 3, O24/1; maximum diameter, 47 μm . 10, 11, sample CUS-K11 (Clino borehole), slide 3, G19/4; maximum diameter of epicyst, 45 μm . 12, specimen showing attached 4'''' and partial separation of ls and rs on the hyposulcal tab; sample CUS-K11 (Clino borehole), slide 3, S44/0; total length including attached plate, 67 μm .



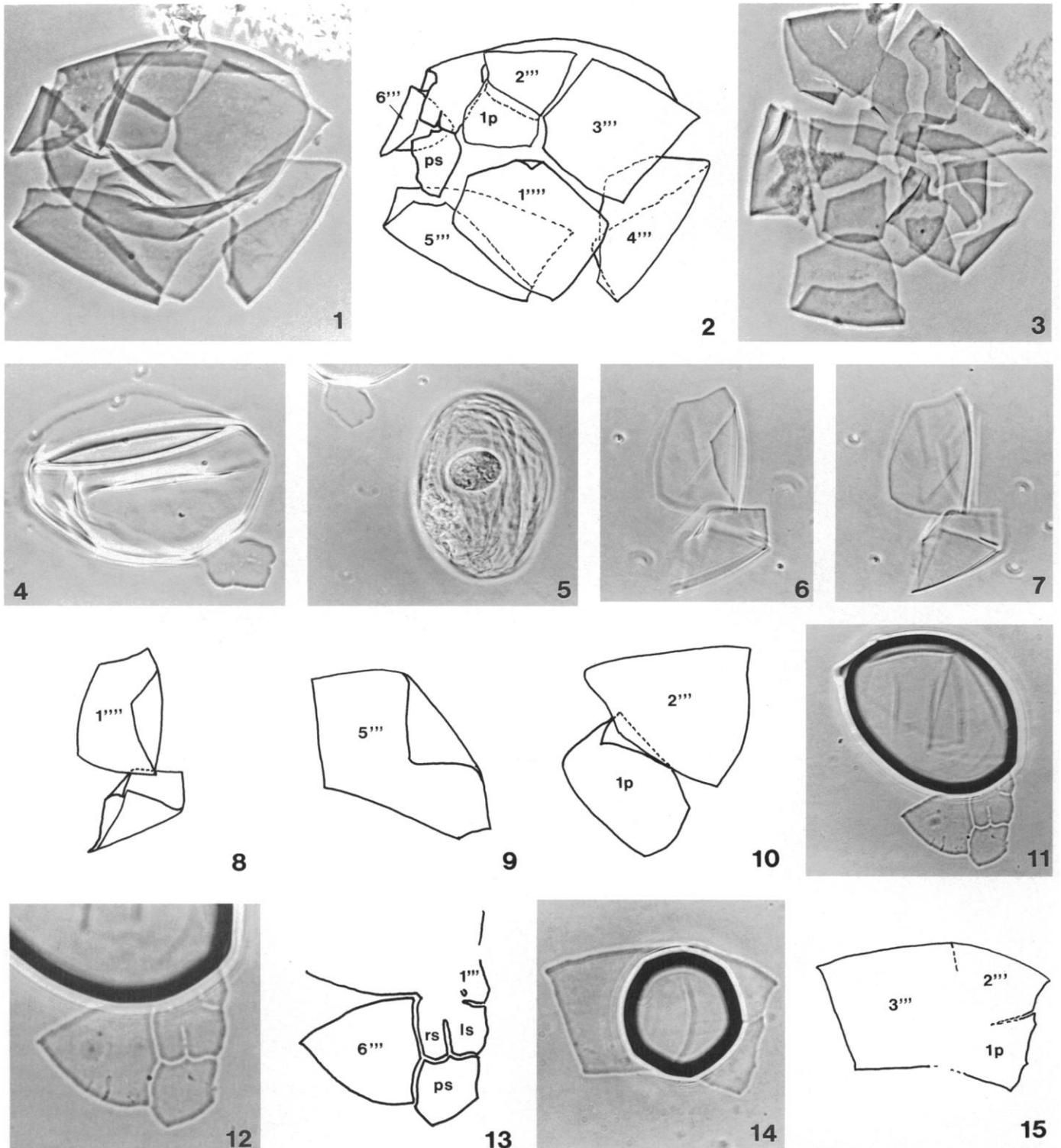


FIGURE 4—*Cypisocysta lata* new species from the Great Bahama Bank (1–3) and modern sediments of Phosphorescence Bay, Puerto Rico (4–15). Photomicrographs are phase contrast images. Tracings are shown to right of, or immediately following, photomicrographs; dashed lines do not necessarily indicate real order of overlap; see Figure 1 for plate notation. 1, 2, sample CUS-K11 (Clino borehole), slide 2, V51/2; maximum diameter of epicyst, 49 μm . 3, sample CUS-K11 (Clino borehole), slide 2, W46/1; maximum dimension of cyst, 59 μm . 4–10, fragments of a single specimen (M102/1) after HCl and weak HF treatment, manually broken apart to release the following components. 4, maximum diameter of epicyst, 56 μm , R39/3; 5, the surviving protoplast, maximum diameter, 58 μm , R39/3; 6–8, external view of plate 1'''' with possible 4''' below, with 6 low focus, 7 high focus, maximum dimension of 1'''', 35 μm , S39/1; 9, camera lucida drawing of 5''' in external view, maximum dimension, 43 μm , S39/0; 10, camera lucida drawing of 1p and 2''' in external view, maximum dimension of 2''', 23 μm , S39/1. 11–15, fragments of a single specimen (M102/2) after HCl and weak HF treatment, manually broken apart to release the following components. 11–13, epicyst with hyposulcal tab and attached ps and 6''' with the epicyst margin obscured by a blob of glycerine jelly, epicyst maximum diameter, 55 μm , O33/4; 14, 15, internal view of plates 1p, 2''' and 3''' with the contact between these plates obscured by a central blob of glycerine jelly, maximum dimension of plate cluster, 50 μm , P33/0.

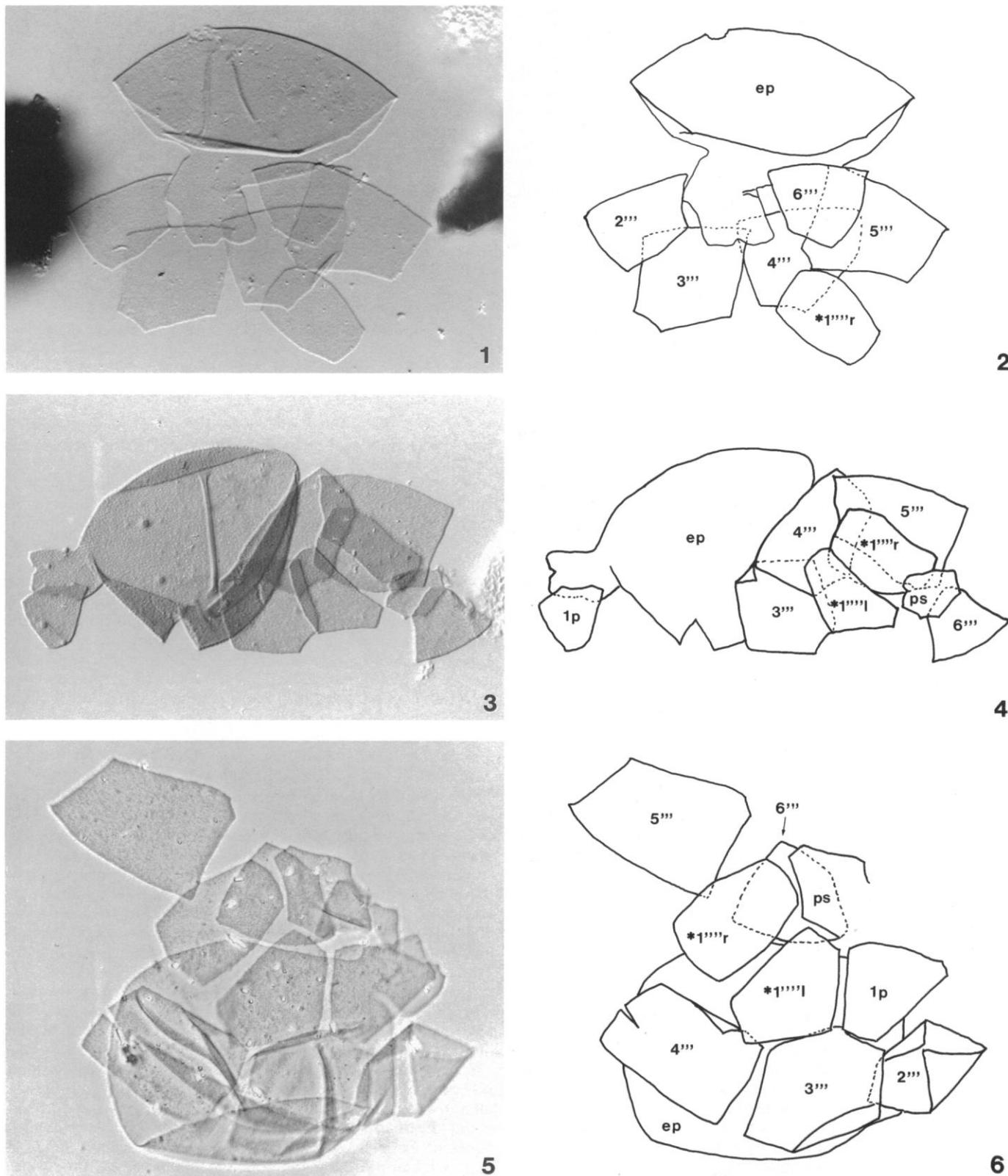


FIGURE 5—*Capisocysta lyellii* new species from eastern England. Photomicrographs are interference contrast (1, 3) or phase contrast (5) images. Various magnifications. Tracings are shown to right of photomicrographs; dashed lines do not necessarily indicate real order of overlap; see Figure 1 for plate notation. 1, 2, sample NQ4, slide 4, O30/3; maximum diameter of epicyst, 66 μm . 3, 4, Holotype, showing irregularly microreticulate wall surface and having all plates present except 2'''; sample NQ4, slide 3, H13/0; maximum diameter of epicyst (excluding hyposulcal tab), 55 μm , total length including all plates, 113 μm . 5, 6, sample NQ4, slide 3, S47/0; maximum diameter of epicyst (excluding hyposulcal tab), 50 μm , total length including all plates, 83 μm .

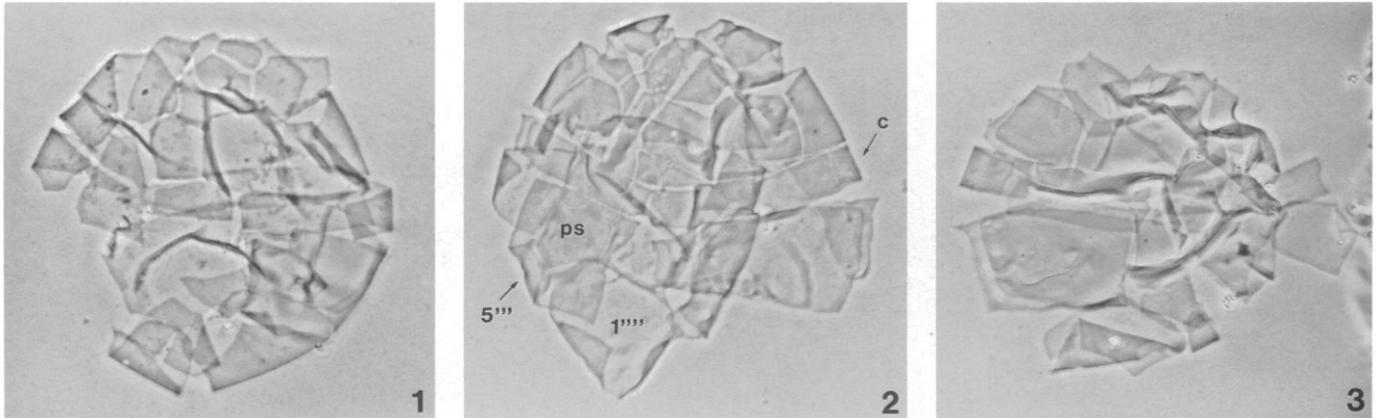


FIGURE 6—*Geonettia* sp. of Head, 1997 from the Coralline Crag of eastern England, shown for comparison with *Capisocysta*. Photomicrographs are phase contrast images. Various magnifications. See Figure 1 for plate notation; c = cingular series. 1, sample CCS1, slide 1, N25/4; length, 46 μm . 2, sample CCS2, slide 1, O43/3; note small, narrow ps and large single 1'''' as in *Capisocysta lata*; length, 55 μm . 3, sample CCS2, slide 1, V17/0; length, 43 μm .

specimens. These lines are absent from the epicyst, are weakly and incompletely developed on the sulcus, and are fully developed elsewhere on the hypocyst, facilitating complete dissociation into constituent plates as follows: five postcingular (2–6'''), one posterior sulcal (ps), one posterior intercalary (1p), and one antapical (1'''). These plates form a compound hypotractal archepyle, with no apparent preferential order of plate loss.

The right and left sulcal plates (rs and ls) and first postcingular plate (1''') nearly always remain attached to the epicyst as a hyposulcal tab. Only rarely does the tab separate from the epicyst (Fig. 3.9), leaving a shallow, arcuate recess in the epicyst margin which perhaps demarcates the anterior margin of the left (and right?) sulcal plate. Plates of the hyposulcal tab are usually completely fused, but an angular notch on the posterior margin of the hyposulcal tab, always to the right of center, delimits the shared contact of left and right sulcal plates and corresponds to a projection on the contacting margin of the posterior sulcal plate (which fully detaches). The left and right sulcal plates are occasionally partly delimited by lines of weakness. Rarely, the first postcingular plate is nearly fully separated (Fig. 2.5, 2.6). It tapers anteriorly to a truncated point but it is uncertain whether this contacts the cingulum. The sulcus is quite strongly inclined to the right on the hypocyst. The posterior sulcal plate (ps), which anteriorly abuts the hyposulcal tab, is the same width as the ls and rs combined. Its posterior margin is geniculate and dithigmate, contacting 1'''' on the longer side and 5''' on the shorter side: it is the smallest of those plates released routinely during dehiscence.

There are six postcingular plates of which 2''' and 6''' are relatively small, 6''' being approximately triangular. Plates 3''', 4''', and 5''' are larger and approximately rectangular. Plate 4''' has a monothigmate rectilinear posterior margin and is mid-dorsally positioned. Plates 3''' and 5''' are similar in size and both are camerate, having characteristic arcuate indentations at their posteroventral corners where they contact plates 1p and ps respectively. Plate 5''' always has a smaller indentation than 3'''. The posterior intercalary (1p) is relatively small and comparable in size to 2''' and 6'''. The antapical plate (1''') is quinqueform and large although somewhat smaller than 3''' or 5'''.

The cingulum is slightly laevorotatory. It is indicated only by the shared margin of the postcingular series and the epicyst. Slight angularities on the epicyst margin correspond to junctions of the postcingular series.

Some plate corners on the hypocyst are extended into minute,

acute projections that intercalate with minutely rounded corners on adjacent plates. Although difficult to interpret for all plates, acute projections on the anterior margins of those in the postcingular series consistently point towards the dorsal surface so that the corresponding angles of adjacent plates are always minutely rounded. The anterior margin of the dorsally located 4''' is minutely rounded at both angles (e.g., Figs. 2.1, 2.2, 3.1, 3.2).

Comparison.—*Geonettia clineae*, described from the Miocene of Maryland (de Verteuil and Norris, 1996a), differs in having a much larger posterior sulcal plate (labelled 2p in de Verteuil and Norris), plates that dissociate on the epicyst as well as the hypocyst, and a reflected apical pore complex. In *G. clineae* the wall surface is fibrillar, and a diaphanous outer layer has not been reported. *Capisocysta lyellii* has a plate pair instead of a single plate at the antapex, and the posterior margin of 4''' is geniculate and dithigmate, not rectilinear and monothigmate as in *C. lata*. See also under Comparison for *C. lyellii*.

Etymology.—*Lata*, Latin, broad, wide; with reference to the single, relatively wide antapical plate that differentiates this species from *C. lyellii*.

Holotype.—Figure 2.1, 2.2. Sample CUS-K11, slide 3, England Finder reference M19/0. ROM 53304.

Measurements.—Holotype: maximum diameter of epicyst, 41 μm . Range based on Bahamas sample CUS-K11: maximum diameter of undehisced cysts (excluding diaphanous outer layer) 40(43.0)46 μm , $n = 12$; maximum diameter of epicyst (excluding hyposulcal tab) in dehisced cysts, 41(47.9)56 μm , $n = 21$. Thirty-three specimens were measured.

Type stratum and locality.—Upper Pliocene at a depth of 234.12 m (768.13 ft) below mud pit in the Clino borehole (24°36'07"N, 79°10'41"W), about 75 km west of Andros Island, on the west margin of the Great Bahama Bank.

Occurrence.—In the Clino borehole, Bahamas, present in all six samples from the lower Pliocene interval (494.39–476.40 mbmp) which is assignable to chron C2Ar (3.58–4.18 Ma) and is thus late early Pliocene (Eberli et al., 1997). Also present in all eight samples from the upper Pliocene interval (262.18–220.48 mbmp) of the Clino borehole, comprising 0.4 to 14 percent of the dinoflagellate assemblages. This interval is estimated to be about 2.1–2.3 Ma and occurs within chron C2r2r (late late Pliocene) according to the integrated age model of Eberli et al. (1997).

In the Coralline Crag Formation, eastern England, occurs rarely (e.g., Fig. 3.1, 3.2) in all four samples (NQ1–NQ4) of the

Ramsholt Member (ca. 3.8–3.6 Ma; late early Pliocene; see Head, 1997). Specimens were not observed in the overlying Sudbourne Member, which is also of Pliocene age.

In Phosphorescence Bay, Puerto Rico, recorded rarely (Fig. 4.4–4.15) from a single surface-sediment sample. The cysts were recently living, as shown by the presence of protoplasts (Fig. 4.5). Living cysts have also been found in Óbidos Lagoon (39°25'N, 9°12'W) on the western coast of Portugal (D. Wall, personal commun.).

Stratigraphic range.—Upper lower Pliocene of eastern England and the Bahamas, through present day.

Autecology.—*Capisocysta lata* is rare to common in tropical periplatform carbonates in the Pliocene in the Clino borehole, Bahamas. These sediments accumulated on the platform slope but predominantly originate from the platform top where *C. lata* probably lived. Details of the sedimentology and dinoflagellates for the Clino borehole are given in Westphal et al. (in press). In eastern England, *C. lata* is consistently present, but not common, in silty, carbonate-rich sands that comprise the Ramsholt Member of the Coralline Crag Formation. This member is considered broadly warm temperate and was deposited at a minimum water depth of 50 m (see Head, 1997). *Capisocysta lata* is known as a living cyst in Phosphorescent Bay, Puerto Rico, where rare specimens have been found in sediment at a water depth of 3 m. The climate here is tropical, the sediments are rich in carbonates, and salinities average 36 parts per thousand (Wall et al., 1977). Living cysts reported from Óbidos Lagoon, Portugal (D. Wall, pers. commun.) show that the ecological range of this species extends into warm-temperate environments today.

Therefore *C. lata* has a known paleoecological range of tropical through warm temperate. It clearly thrived in carbonate-rich environments, probably on the inner to middle shelf and on the tops of carbonate platforms. Temperature and other requirements of *C. lata* appear rather similar to those of *G. clineae* (de Verteuil and Norris, 1996a) and, like *G. clineae* and its living relative *P. zoharyi*, *C. lata* may have formed blooms.

Discussion.—The presence and direction of acute projections on the anterior margins of the postcingular series are comparable to those found on *C. lyellii* and *Geonettia*. This pattern follows the expected imbrication style for gonyaulacaleans (Fensome et al., 1993, 1996; de Verteuil and Norris, 1996a), with plate 4''' as a keystone, assuming that the corresponding plate overlap on the theca opposes the direction of acute projections on the cyst.

CAPISOCYSTA LYELLII new species

Figures 1.2, 1.4, 1.6, 5

Capisocysta lyellii Head. HEAD, in press, pl. 4, figs. 1, 2.

Diagnosis.—Spherical cysts with granulate to irregularly microreticulate outer surface. Tabulation expressed extensively on hypocyst, with individual loss of plates 2–6''', 1p, ps, and a plate pair representing 1'''. Sulcal plates ls and rs and first postcingular plate usually remain attached to epicyst forming a hyposulcal tab. Posterior sulcal plate (ps) widens posteriorly from its contact with left and right sulcal plates. Plate 4''' has a dithigmate geniculate posterior margin and the antapical region has a plate pair whose left plate (*1''''l) is pentagonal and right plate (*1''''r) is stenoplate.

Description.—Cysts are spherical and proximate, and have a thin (less than 0.5 μm) wall whose outer surface varies from irregularly microreticulate (as on the holotype) to granulate. Preformed lines of weakness are absent from the epicyst, weakly and incompletely developed on the sulcus, and fully developed elsewhere on the hypocyst, causing complete dissociation into constituent plates as follows: five postcingular (2–6'''), one posterior sulcal (ps), one posterior intercalary (1p), and a pair of

antapical homologues (*1''''l and *1''''r). Together these plates form a hypotractal compound archeopyle, with no apparent preferential order of plate loss.

The right and left sulcal plates (rs and ls) and first postcingular plate (1''') always remain attached to the epicyst as a hyposulcal tab. Plates of the hyposulcal tab are usually completely fused, but an angular notch on the posterior margin of the hyposulcal tab, always to the right of center, delimits the shared contact of left and right sulcal plates and corresponds to a projection on the contacting margin of the posterior sulcal plate (which fully detaches). The right and left sulcal plates are occasionally partly delimited by lines of weakness. The sulcus is quite strongly inclined to the right on the hypocyst. The posterior sulcal plate (ps), which anteriorly abuts the hyposulcal tab, widens away from the tab and posteriorly contacts 5''' (on the shortest side), *1''''l, and *1''''r.

There are five postcingular plates of which 5''' is wider than 3''', resulting in 4''' being offset to the left. Plate 4''' is large and has a dithigmate geniculate posterior margin. Plates 3''' and 5''' are both camerate, having characteristic arcuate indentations at their posteroventral corners where they contact plates 1p and ps respectively. Plate 5''' always has a smaller indentation than 3'''. The posterior intercalary (1p) is relatively small and comparable in size to 6'''. Two plates, here labelled left and right first antapical homologues (*1''''l and *1''''r), occur at the antapex. Plate *1''''l is pentagonal, its narrowest margin contacting ps. Plate *1''''r is stenoplate whose convex narrower margins contact ps and 4'''. The dorsal margins of these antapical plates contact the geniculate, dithigmate posterior margin of 4'''. These two plates can be viewed as a single, broadly quinqueform (five-sided) first antapical plate surrounded by five other plates.

Specimens otherwise closely resemble *C. lata* including the position of minute acute projections on the anterior margins of the postcingular series. No undehisced specimens were observed, and it was not possible to determine if specimens originally bore a loose, diaphanous outer layer as in *C. lata*.

Comparison.—*C. lata* has a single antapical plate (1''') whereas *C. lyellii* has an antapical plate pair (*1''''l and *1''''r). Both of the antapicals in *C. lyellii* contact 4''', which is slightly offset to the left and has a posterior margin that is geniculate and dithigmate, in contrast to the mid-dorsal position and rectilinear monothigmate posterior margin of 4''' in *C. lata*. The ps in *C. lyellii* is somewhat larger than in *C. lata* and widens posteriorly. Ornament varies from smooth to granulate in *C. lata* and is nearly smooth to granulate or irregularly microreticulate in *C. lyellii*.

Etymology.—Named for Sir Charles Lyell (1797–1875), the first and most celebrated geologist to describe the Rockhall Wood site (Lyell, 1839), which is now the type locality of this species.

Holotype.—Figure 5.3, 5.4. Sample NQ4, slide 3; England Finder reference H13/0, ROM 53301.

Measurements.—Holotype: maximum diameter of epicyst (excluding hypocyst tab), 55 μm. Range: maximum diameter of epicyst (excluding hypocyst tab) in dehisced cysts, 49(54.5)66 μm. Six specimens were measured.

Type stratum and locality.—Ramsholt Member, about 6.4 m above the base of the Coralline Crag Formation, Rockhall Wood, Suffolk, eastern England (see Head, 1997).

Occurrence.—Recorded only from eastern England (this study) where it occurs rarely in samples NQ1 and NQ4 of Head (1997) from the Ramsholt Member (ca. 3.8–3.6 Ma; late early Pliocene), Coralline Crag Formation.

Stratigraphic range.—Upper lower Pliocene of eastern England.

Autecology.—This species lived in the warm-temperate, neritic waters of the southern North Sea during the late early Pliocene. The Ramsholt Member of the Coralline Crag Formation is a carbonate silty sand deposited at a water depth of at least 50 m (Hodgson and Funnell, 1987). It is not known whether the dinoflagellates lived in waters this deep or if the cysts were transported from shallower areas.

Discussion.—*C. lyellii* is regarded as a species distinct from *C. lata* because 1) it differs in the presence of two antapical plates in place of one; 2) this difference has a subtle but pervasive effect on the geometry and topology of other hypocystal plates; and 3) *C. lyellii* was not seen in the Pliocene of the Clino borehole, Bahamas, despite the identification of numerous specimens of *C. lata*.

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REFERENCES

- BERGGREN, W. A., D. V. KENT, C. C. SWISHER, III, AND M.-P. AUBRY. 1995. A revised Cenozoic geochronology and chronostratigraphy, p. 129–212. In W. A. Berggren, D. V. Kent, and J. Hardenbol (eds.), *Geochronology, Time Scales and Global Stratigraphic Correlation*. SEPM Special Publication, 54. SEPM (Society for Sedimentary Geology), Tulsa, Oklahoma.
- BÜTSCHLI, O. 1885. Erster Band. Protozoa, p. 865–1088. In Dr. H. G. Bronn's *Klassen und Ordnungen des Thier-Reiches, wissenschaftlich dargestellt in Wort und Bild*. C. F. Winter'sche Verlagshandlung, Leipzig und Heidelberg.
- DALE, B. 1983. Dinoflagellate resting cysts: benthic plankton, p. 69–136. In G. A. Fryxell (ed.), *Survival Strategies of the Algae*. Cambridge University Press, Cambridge, U.K.
- DAVEY, R. J., AND G. L. WILLIAMS. 1966. The genus *Hystriochsphaeridium* and its allies, p. 53–106. In R. J. Davey, C. Downie, W. A. S. Sarjeant, and G. L. Williams, *Studies on Mesozoic and Cainozoic Dinoflagellate Cysts*. Bulletin of the British Museum (Natural History) Geology, Supplement 3.
- DE VERTEUIL, L., AND G. NORRIS. 1996a. Middle to upper Miocene *Geonettia clineae*, an opportunistic coastal embayment dinoflagellate of the *Homotryblium* Complex. *Micropaleontology*, 42:263–284.
- , AND —. 1996b. Part II. Homology and structure in dinoflagellate cyst terminology, p. 83–172. In L. de Verteuil, L. and G. Norris, *Miocene Dinoflagellate Stratigraphy and Systematics of Maryland and Virginia*. *Micropaleontology*, 42 (supplement).
- DÖRHÖFER, G., AND E. H. DAVIES. 1980. Evolution of archeopyle and tabulation in rhaetogonyaulacinean dinoflagellate cysts. *Life Sciences Miscellaneous Publications*, Royal Ontario Museum, 91 p.
- DRUGG, W. S. 1970. Some new genera, species, and combinations of phytoplankton from the Lower Tertiary of the Gulf Coast, U.S.A. North American Paleontological Convention, Chicago, September 1969, Proceedings, Part G:809–843.
- EBERLI, G. P., P. K. SWART, D. F. MCNEILL, J. A. M. KENTER, F. S. ANSELMETTI, L. A. MELIM, AND R. N. GINSBURG. 1997. A synopsis of the Bahamas Drilling Project: results from two deep core borings drilled on the Great Bahama Bank, p. 23–41. In G. P. Eberli, P. K. Swart, M. J. Malone, et al., *Proceedings of the Ocean Drilling Program, Initial Reports*, 166. Ocean Drilling Program, College Station, Texas.
- EVITT, W. R. 1985. Sporopollenin Dinoflagellate Cysts: Their Morphology and Interpretation. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas, 333 p.
- , J. K. LENTIN, M. E. MILLIQUOD, L. E. STOVER, AND G. L. WILLIAMS. 1977. Dinoflagellate cyst terminology. Geological Survey of Canada, Paper, 76-24:1–11.
- FENSOME, R. A., J. B. RIDING, AND F. J. R. TAYLOR. 1996. Dinoflagellates, p. 107–169. In J. Jansonius and D. C. McGregor (eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, College Station, Texas, volume 1.
- , F. J. R. TAYLOR, G. NORRIS, W. A. S. SARJEANT, D. I. WHARTON, AND G. L. WILLIAMS. 1993. A Classification of Living and Fossil Dinoflagellates. *Micropaleontology Special Publication Number 7*, 351 p.
- HARDING, I. C., AND J. LEWIS. 1995. Siliceous dinoflagellate thecal fossils from the Eocene of Barbados. *Palaeontology*, 37:825–840.
- HEAD, M. J. 1996. Modern Dinoflagellate cysts and their biological affinities, p. 1197–1248. In J. Jansonius and D. C. McGregor (eds.), *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, College Station, Texas, volume 3.
- , 1997. Thermophilic dinoflagellate assemblages from the mid Pliocene of eastern England. *Journal of Paleontology*, 71:165–193.
- , In press. Marine environmental change in the Pliocene and lower Pleistocene of eastern England: the dinoflagellate evidence reviewed. In T. Van Kolfshoten and P. Gibbard (eds.), *The Dawn of the Quaternary*. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, 63.
- HODGSON, G. E., AND B. M. FUNNELL. 1987. Foraminiferal biofacies of the early Pliocene Coralline Crag, p. 44–73. In M. B. Hart (ed.), *Micropalaeontology of Carbonate Environments*. British Micropalaeontological Society Series. Ellis Horwood Ltd., Chichester, U.K.
- LEFÈVRE, M. 1933. Recherches sur les péridiniens fossiles des Barbades. *Bulletin, Muséum d'histoire naturelle, Paris, serie 2*, 5:415–418.
- LENTIN, J. K., AND G. L. WILLIAMS. 1993. Fossil dinoflagellates: index to genera and species, 1993 edition. American Association of Stratigraphic Palynologists Contributions Series, 28, 856 p.
- LEVANDOWSKY, M., AND P. J. KANETA. 1987. Behaviour in dinoflagellates, p. 360–397. In F. J. R. Taylor (ed.), *The Biology of Dinoflagellates*. Botanical Monographs Volume 21, Blackwell Scientific, Oxford, U.K.
- LIENGJARERN, M., L. COSTA, AND C. DOWNIE. 1980. Dinoflagellate cysts from the Upper Eocene–Lower Oligocene of the Isle of Wight. *Palaeontology*, 23:475–499.
- LINDEMANN, E. 1928. Abteilung Peridineae (Dinoflagellatae), p. 3–104. In A. Engler and K. Prantl (eds.), *Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere den Nutzpflanzen*. Zweite stark vermehrte und verbesserte Auflage herausgegeben von A. Engler. 2 Band. Wilhelm Engelmann, Leipzig.
- LYELL, C. 1839. On the relative ages of the Tertiary deposits commonly called "Crag" in the counties of Norfolk and Suffolk. *Proceedings of the Geological Society of London*, 3:126–130.
- MANUM, S. B., AND G. L. WILLIAMS. 1995. Hypocystal archeopyles in the dinoflagellate cyst genus *Caligodinium* Drugg. *Palynology*, 19: 183–190.
- MCLEAN, D. M. 1976. *Eocladopyxis peniculatum* Morgenroth, 1966, Early Tertiary ancestor of the modern dinoflagellate *Pyrodinium bahamense* Plate, 1906. *Micropaleontology*, 22, p. 347–351.
- MORGENROTH, P. 1966. Mikrofossilien und Konkretionen des nordwest-europäischen Untereozäns. *Palaeontographica, Abteilung B*, 119:1–53.
- PASCHER, A. 1914. Über Flagellaten und Algen. *Berichte der Deutschen Botanischen Gesellschaft*, 36:136–160.
- ROSSIGNOL, M. 1962. Analyse pollinique de sédiments marins Quaternaires en Israël. II. Sédiments pléistocènes. *Pollen et Spores*, 4:121–148.
- TAYLOR, F. J. R. 1980. On dinoflagellate evolution. *BioSystems*, 13:65–108.
- WALL, D. 1967. Fossil microplankton in deep-sea cores from the Caribbean Sea. *Palaeontology*, 10:95–123.

- , AND B. DALE. 1971. A reconsideration of living and fossil *Pyrrophacus* Stein, 1883 (Dinophyceae). *Journal of Phycology*, 7:221–235.
- , —, G. P. LOHMAN, AND W. K. SMITH. 1977. The environmental and climatic distribution of dinoflagellate cysts in modern marine sediments from regions in the North and South Atlantic oceans and adjacent seas. *Marine Micropaleontology*, 2:121–200.
- WARNY, S. A., AND J. H. WRENN. 1997. New species of dinoflagellate cysts from the Bou Regreg Core: a Miocene-Pliocene boundary section on the Atlantic coast of Morocco. Review of Palaeobotany and Palynology, 96:281–304.
- WESTPHAL, H. 1997. Sediment input and diagenesis of periplatform carbonates on a leeward slope of Great Bahama Bank. Unpublished Ph.D. dissertation, Christian-Albrechts-Universität zu Kiel, Germany, 163 p., plus 9 appendices.
- , J. J. G. REIJMER, AND M. J. HEAD. In press. Input and diagenesis on a carbonate slope (Bahamas): response to morphologic evolution and sea-level fluctuations. In P. M. Harris, A. H. Saller, T. Simo, and R. Handford (eds.), *Advances in Carbonate Sequence Stratigraphy—Application to Reservoirs, Outcrops and Models*. SEPM Special Publications.
- WILLIAMS, G. L., W. A. S. SARJEANT, AND E. J. KIDSON. 1978. A glossary of the terminology applied to dinoflagellate amphiesmae and cysts and acritarchs: 1978 edition. American Association of Stratigraphic Palynologists, Contributions Series, 2A, 121 p.
- WRENN, J. H., AND S. P. DAMASSA. 1989. *Tuberculodinium vancampoeae*: a curious reflection of its former self. *Palynology*, 13:289 (Abstract).
- , AND J. P. KOKINOS. 1986. Preliminary comments on Miocene through Pleistocene dinoflagellate cysts from De Soto Canyon, Gulf of Mexico, p. 169–225. In J. H. Wrenn, S. L. Duffield, and J. A. Stein (eds.), *Papers from the First Symposium on Neogene Dinoflagellate Cyst Biostratigraphy*. American Association of Stratigraphic Palynologists Contributions Series, 17.

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IMPLICATIONS OF INTRACOLONIAL VARIATION IN A PALEOZOIC BRYOZOAN

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ABSTRACT—Relative differences between environmentally controlled variation and genetically controlled variation are important when investigating morphologic variation in general, especially when establishing species concepts. The colonial nature of bryozoans provides a means for distinguishing between the two sources; variation can be partitioned into within-colony (microenvironmental) and among-colony (environmental + genetic) components. For the Paleozoic order Cryptostomata, biologically and taxonomically significant morphologic characters are well defined and methods for recognizing morphotaxa are well established.

The importance of within-colony variation to the morphometric treatment of fenestrate species was assessed after the discovery of a large specimen of *Hemitrypa* sp. Variation within the colony was compared to variation among and within two congeneric species. The distribution of study segments across the colony allowed assessment of variation both along the growth axis and laterally between segments of approximately equivalent generational age. Repeatability of methods was assessed using data measured independently from identical segments by three workers.

Variation within the large colony is less than variation among congeneric species, indicating that genetic differences among species exceed variation resulting from combined phenotypic and genotypic sources within species. Neither astogenetic nor ontogenetic morphologic gradients are recognized. Variation between data collected from identical segments by pairs of workers falls within the range of variation for the entire colony. Thus, multiple workers can reproduce data to the finest level of meaningful resolution. Cryptostome morphospecies concepts are validated.

The potential for partitioning genotypic versus environmental variation in reduced, multidimensional morphospace is reinforced. Studies of microevolution and speciation may be designed that account for these factors.

INTRODUCTION

DISTINGUISHING BETWEEN environmental and genetic components of variation is an elusive goal in paleontological research but one that is critical to establishing meaningful species concepts in fossils. Sound species concepts, in turn, form the basis for paleoecological and evolutionary analyses. Colonial organisms, with colonies comprised of individual units sharing a single genotype, provide a means for comparing within-colony (microenvironmental) variation versus among-colony (environmental + genetic) variation (e.g., Schopf, 1976; Brande and Bretsky, 1982). The relationship between the two is essential, especially when interpreting morphologic variation among statistical populations derived from a limited number of specimens. Furthermore, a connection has been established between among-colony variation and genetic heritability (Cheetham et al., 1993, 1994, 1995).

For bryozoan colonies, several sources of within-colony variation have been identified: 1) subcolonial organization (cormidia of Anstey et al., 1976); 2) ontogeny; 3) polymorphy; 4) microenvironment; and 5) astogeny (latter four sources after Boardman et al., 1983). Of these, astogeny (systematic, related to generational position within a colony) is the least uniformly accepted in terms of process (see e.g., Pachut et al., 1991). Astogenetic variation, however, has been recognized as a potential problem for species concepts, especially among Paleozoic stenolaemates (Anstey and Perry, 1970). For fenestrates (suborder Fenestellina), studies of astogenetic variation within individual characters have addressed this concern (e.g., Elias, 1964; Stratton and Horowitz, 1977; McKinney, 1980; McKinney and Stedman, 1981, Stedman, 1982); the present research assesses fenestrate astogenetic variation using a multivariate approach.

Development of suitable character lists for analysis has relied

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References

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