

GEONETTIA WALTONENSIS, A NEW GONIODOMACEAN DINOFLAGELLATE FROM THE PLIOCENE OF THE NORTH ATLANTIC REGION, AND ITS EVOLUTIONARY IMPLICATIONS

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ABSTRACT—A new species of the unusual dinoflagellate cyst genus *Geonettia* de Verteuil and Norris, 1996a is here described from the Pliocene of the western North Atlantic and eastern England. *Geonettia waltonensis* new species is only the second species to be formally described for this genus, whose type, *G. clineae* de Verteuil and Norris, 1996a, has a range of Miocene through Pliocene. *Geonettia* is a gonyaulacalean, goniodomacean genus of the subfamily Pyrodinioideae and is closely related to *Eocladopyxis* Morgenroth, 1966 and *Capisocysta* Warny and Wrenn, 1997, also found in the Cenozoic. However, *Geonettia* is the only known dinoflagellate cyst genus to have plates that dissociate extensively on both epi- and hypocyst during excystment. *Geonettia waltonensis* has this style of excystment, but its hypocystal tabulation is more akin to *Capisocysta lata* Head, 1998a than to *G. clineae*. Comparison of tabulation and other morphological features suggests that during the late Miocene, *Capisocysta lata* evolved from *Geonettia waltonensis* or a closely related species through failure of its epicystal plates to dissociate. *Geonettia waltonensis* probably did not evolve directly from *G. clineae* but may represent a separate lineage within *Geonettia* that arose during the Miocene.

INTRODUCTION

EXCYSTMENT IN most modern and fossil dinoflagellate cyst species is facilitated by displacement of one to four plates on the epicyst. One notable exception is the Neogene dinoflagellate cyst *Geonettia* de Verteuil and Norris, 1996a, whose plates dissociate extensively along pre-formed lines of weakness on both epicyst and hypocyst. During excystment, the cyst wall literally falls to pieces (de Verteuil and Norris, 1996a), the term holocystal archeopyle being coined for this feature (Head, 1998a). Only one other genus, *Eocladopyxis* Morgenroth, 1966, from the Paleogene, has a similar style of archeopyle formation, but fragmentation tends to be less complete, and, unlike *Geonettia*, cysts of that genus bear processes. *Capisocysta* Warny and Wrenn, 1997 emend. Head, 1998a, a late Miocene and Pliocene genus, differs from *Geonettia* in that only the hypocystal plates dissociate. On the basis of tabulation, archeopyle style, and stratigraphic distribution, *Eocladopyxis*, *Geonettia*, and *Capisocysta* appear to be closely related within the subfamily Pyrodinioideae.

The Pyrodinioideae is represented today by a single theca-based genus, *Pyrodinium* Plate, 1906, which contains probably just one living species, *Pyrodinium bahamense* Plate, 1906 (Balch, 1985; Taylor and Fukuyo, 1989). Living pyrodinioidean cysts are assigned to just two cyst-based species: *Polysphaeridium zoharyi* (Rossignol, 1962) Bujak et al., 1980, which in fact is produced by *Pyrodinium bahamense* (see Head, 1996); and *Capisocysta lata* Head, 1998a whose thecate stage has yet to be identified (Head, 1998a). Nevertheless, the Pyrodinioideae are well known: *Pyrodinium bahamense* is a familiar bioluminescent dinoflagellate, and a western Pacific strain is responsible for paralytic shellfish poisoning in humans. The fossil history of *Pyrodinium bahamense* extends back to the early Eocene (Stover et al., 1996). Other fossil pyrodinioidean genera, of which there are at least eight, extend the range of this subfamily back to the Cretaceous (Fensome et al., 1993).

The present study describes a new species of *Geonettia*, only the second to be formally described for this genus. *Geonettia waltonensis* n. sp. has been found in two samples from the upper upper Pliocene of Deep Sea Drilling Project (DSDP) Site 603, New Jersey lower continental rise; and at two Pliocene localities in eastern England: Rockhall Wood in Suffolk, and Walton-on-the-Naze in Essex (Fig. 1). At Rockhall Wood, *G. waltonensis*

occurs in both the Ramsholt (middle lower or upper lower Pliocene) and Sudbourne (lower upper Pliocene) members of the Coralline Crag Formation (Head, 1997). At Walton-on-the-Naze, deposits known as the Walton Crag are somewhat younger than the Coralline Crag Formation but still lie within the lower upper Pliocene (Head, 1998c). Here, *G. waltonensis* has been found in two samples. Detailed information on these localities is given in the Appendix. *Geonettia waltonensis* is rare (less than 1 percent) in all samples examined.

Geonettia waltonensis has only a thin and featureless wall, yet the extensive plate dissociation in this species exposes its tabulation with clarity. The present study elucidates this tabulation (Fig. 2) and compares *G. waltonensis* with other members of the *Eocladopyxis*–*Geonettia*–*Capisocysta* complex (Figs. 3, 4). From this work it has been possible to place *G. waltonensis* within a phylogenetic context (Fig. 5), and explore particularly the evolutionary relationship between *Geonettia* and *Capisocysta*.

Geonettia sp. represents another new species of the genus,

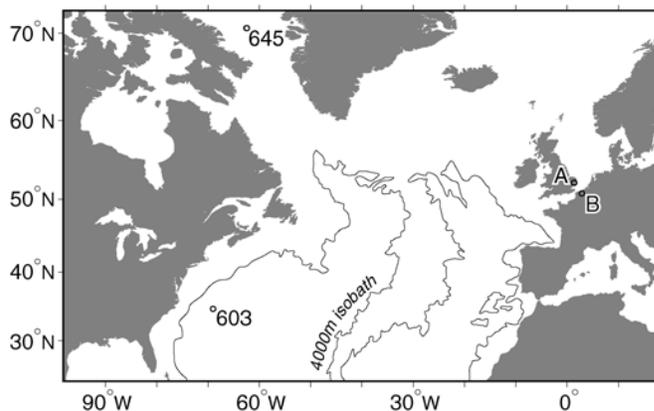


FIGURE 1—Location of sites where *Geonettia waltonensis* n. sp. and *Geonettia* sp. have been found. *Geonettia waltonensis* n. sp. is reported from the Pliocene of: DSDP Site 603, lower continental rise off New Jersey; Walton-on-the-Naze and Rockhall Wood, eastern England (A); and the Kalmthout Borehole of Belgium (B). *Geonettia* sp. is reported from the upper Miocene of both DSDP Site 603 and ODP Site 645, Baffin Bay.

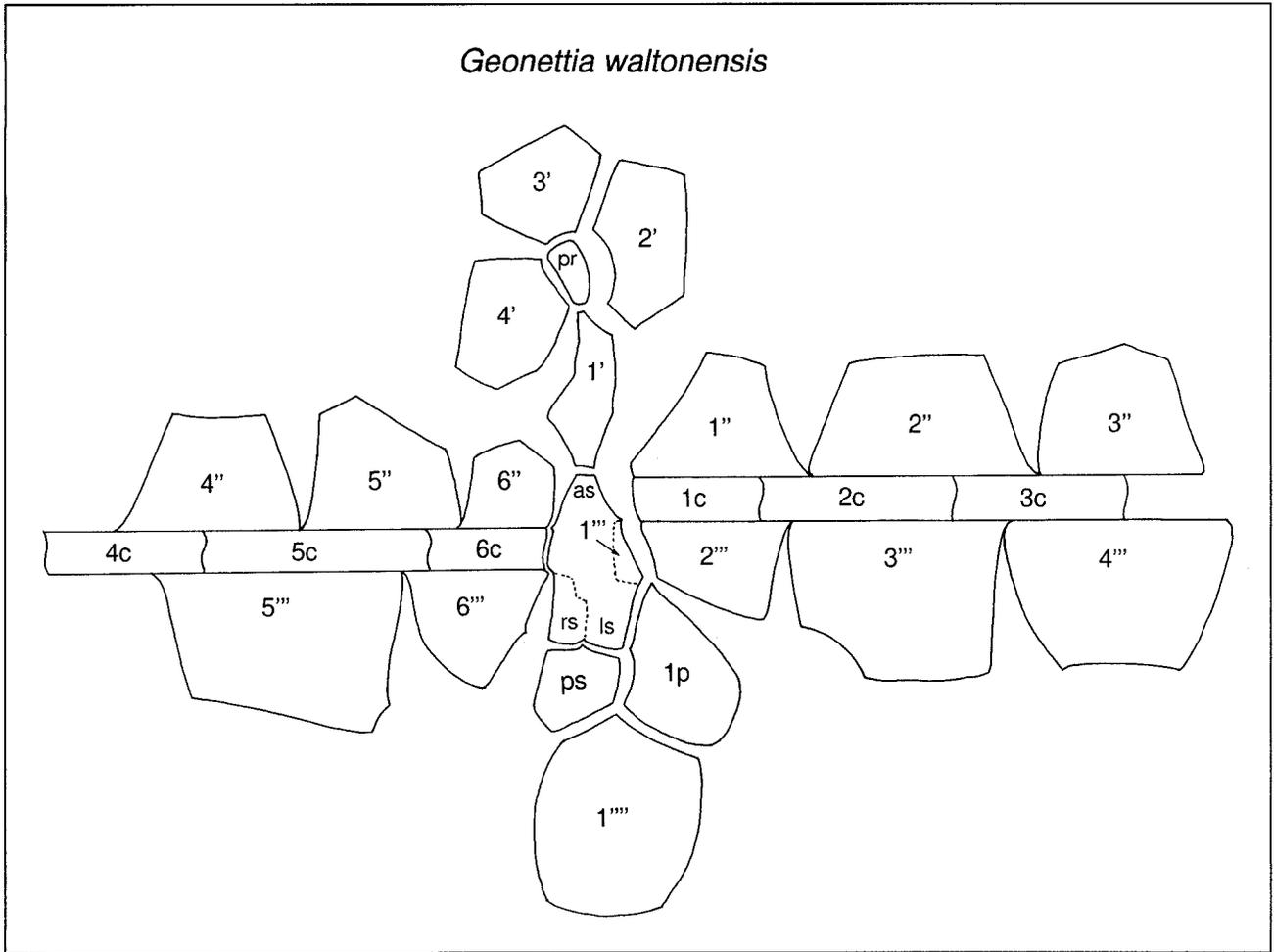


FIGURE 2—Exploded view showing the tabulation in *Geonettia waltonensis* n. sp. Notation: pr = preapical; 1'-4' = apical series, 1''-6'' = precingular series; 1c-6c = cingular series; spc = sulcal plate complex (which includes as = anterior sulcal plate, rs = right sulcal plate, ls = left sulcal plate, and usually 1''' = first postcingular plate); ps = posterior sulcal plate; 1p = posterior intercalary plate; 2'''-6''' = second to sixth postcingular plates; and 1'''' = antapical plate. Dashed lines indicate plate boundaries that do not usually lead to plate separation.

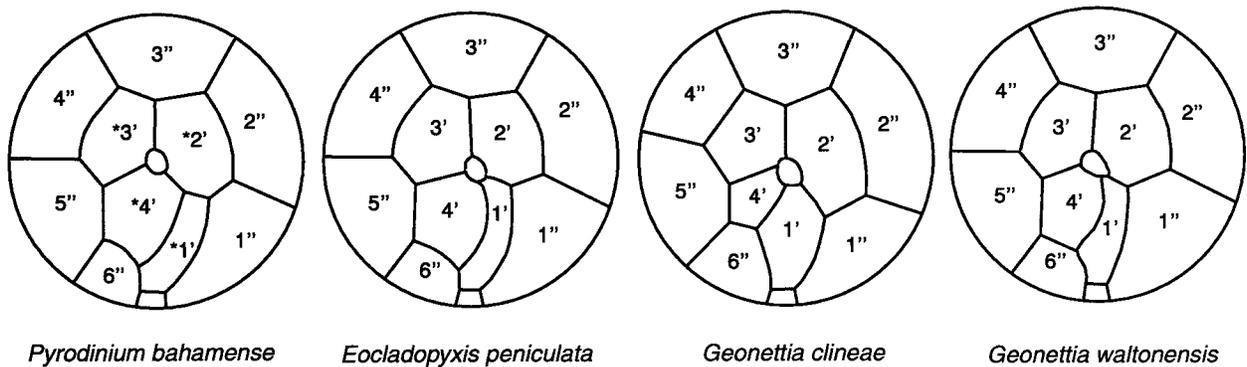


FIGURE 3—Schematic drawings of epitabulation in *Pyrodinium bahamense* Plate, 1906, *Eocladopyxis peniculata* Morgenroth, 1966, *Geonettia clineae* de Verteuil and Norris, 1996a, and *Geonettia waltonensis* n. sp. Adapted in part from de Verteuil and Norris, 1996a, text-fig. 3. See Figure 2 for plate notation, additionally, *1'-*4' = first to fourth apical homologues.

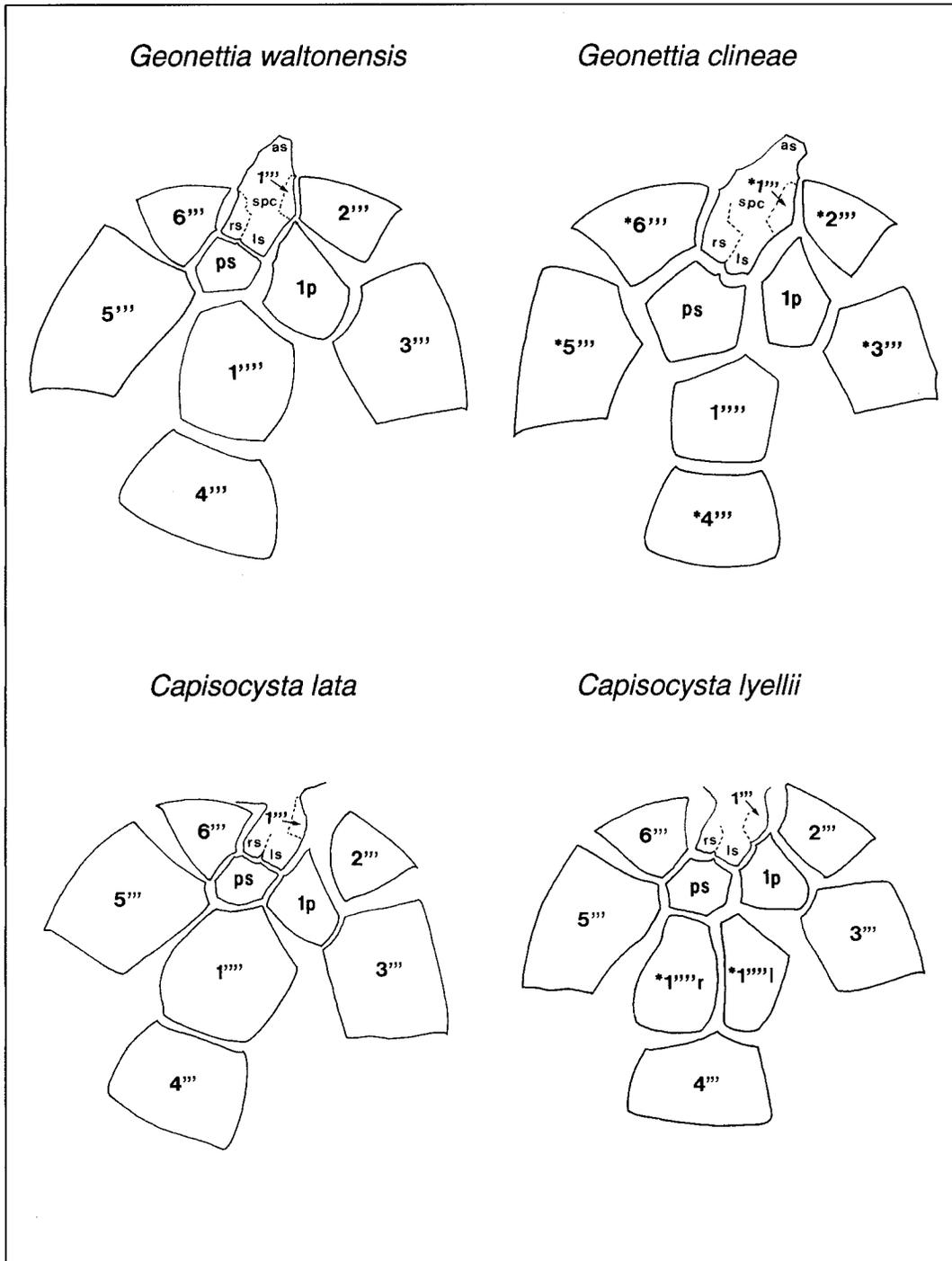


FIGURE 4—Comparison of hypotabulation in *Geonettia waltonensis* n. sp., *Geonettia clineae* de Verteuil and Norris, 1996a, *Capisocysta lata* Head, 1998a, and *Capisocysta lyellii* Head, 1998a. Note striking similarities between *Geonettia waltonensis* and *Capisocysta lata* which include a small, narrow posterior sulcal (ps), compared with a much larger ps in *Geonettia clineae*. See Figure 2 for plate notation; additionally, *1'''–*6''' = first to sixth postcingular homologues; *1'''l = left first antapical homologue; *1'''r = right first antapical homologue. Drawings of *C. lata* and *C. lyellii* are from Head (1998a, fig. 1), and that of *G. clineae* has been constructed from various illustrations in de Verteuil and Norris (1996a).

and is herein described informally from two incomplete specimens. One specimen is from the upper Miocene of Ocean Drilling Program (ODP) Site 645, Baffin Bay, and the other from the upper Miocene of DSDP Site 603, New Jersey lower continental rise.

MATERIALS AND METHODS

Materials.—*Geonettia waltonensis* n. sp. has been examined in the present study from eleven samples. DSDP samples, 603C-7-2, 85–87 cm and 603C-8-5, 100–102 cm are both dark green-

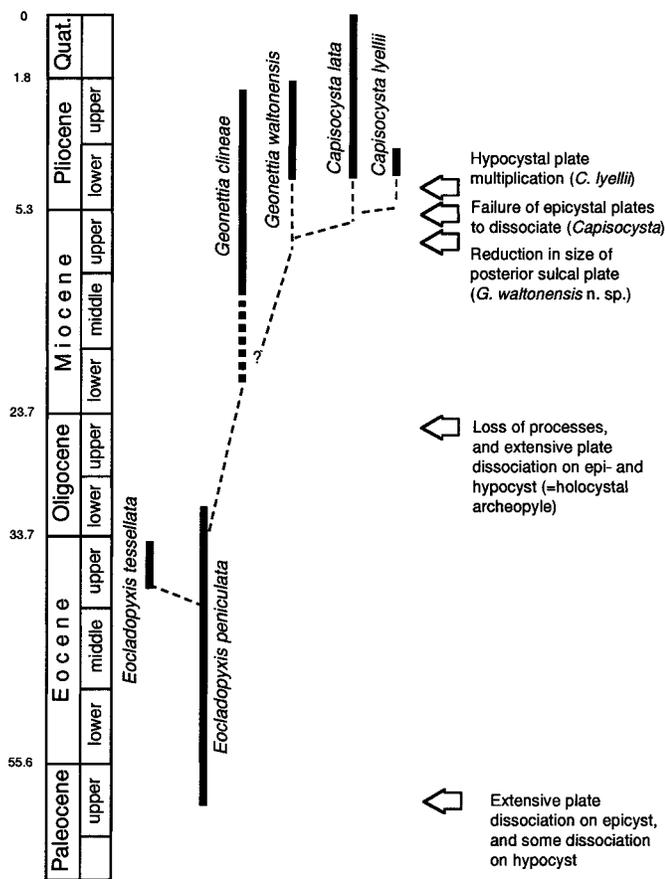


FIGURE 5—Proposed phylogeny in the *Eocladopyxis*–*Geonettia*–*Capisocysta* complex. A broad solid line indicates known stratigraphic occurrence, a broad dashed line indicates a questionable range, and a narrow dashed line indicates suggested evolutionary relationship. Stratigraphic ranges are conservative and expected to be extended by future studies. Note the close relationship between *G. waltonensis* n. sp. and *Capisocysta lata* Head, 1998a, and further note that *G. waltonensis* may not be directly descended from *Geonettia clineae* de Verteuil and Norris, 1996a. See text for discussion. The stratigraphic column is not drawn to scale.

ish gray clays (Site 603 report, in van Hinte et al., 1987). Rockhall Wood samples NQ2 through NQ4 are from the Ramsholt Member, NQ2 through NQ3 being silty carbonate sands, and NQ4 a limestone concretion from the same level as NQ3. Rockhall Wood samples CCS1 through CCS4 are from silty layers occurring within the cross-stratified shelly sands of the overlying Sudbourne Member (Head, 1997). Walton-on-the-Naze sample WC2 is an unoxidized shelly sand from the lowest 5 cm of the basal horizon of the Walton Crag, and sample WC4 is from a thin, ferruginous, silty layer occurring within overlying cross-bedded shelly sands and 2 m above the base of the Walton Crag (Head, 1998c).

Geonettia sp. has been examined in two samples: ODP sample 645E-7R, CC, a gray clayey sand (Site 645 report, in Srivastava et al., 1987); and DSDP sample 603C-37-5, 20–22 cm, a dark gray nannofossil bearing claystone (Site 603 report, in van Hinte et al., 1987).

Sample processing.—Processing techniques for the Rockhall Wood and Walton-on-the-Naze samples are given in Head (1997, 1998c) respectively. Samples from DSDP Hole 603C

(each about 10 ccs) were processed using standard demineralization techniques (HF, HCl), after which the residues were stained with safrannin-o, sieved at 10 μ m, and strew mounted on microscope slides using Cellosize and Elvacite (details are given in Kolev, 1993). A similar procedure, but with mild oxidation, was used for the sample from ODP Hole 645E (see Anstey, 1992). With the exception of this sample, no oxidation or alkali treatment was employed during the processing of any samples used in the present study, since this treatment is known to damage certain cysts.

Examination of specimens.—A total of 54 complete and fragmented specimens of *Geonettia waltonensis* n. sp. was observed in all the samples. The thin cyst wall, extensive plate dissociation, and common crumpling and fragmentation of specimens all complicated the analysis. Color photographic prints, using a microscope with phase contrast optics, were made for routine study and often proved more convenient than direct observation under the microscope.

Photography.—Specimens are illustrated with a vario-orthomat 2 camera attached to a Leitz Dialux microscope with phase contrast optics (Figs. 7–12). Images are all true, i.e., not reversed. Line drawings of photographed specimens were made by tracing color photographic prints taken at several focal planes for each specimen. An England Finder reference follows the sample (and slide) number for each specimen illustrated, and slides were examined with the labels to the right, except where noted in the plate caption.

Repository.—Microscope slides containing the holotype and all other figured material are housed in the Invertebrate Section of the Department of Palaeobiology, Royal Ontario Museum, Toronto, Ontario, under the catalog numbers ROM 52488 (CCS1 slide 1), ROM 52494 (NQ3 slide 1), ROM 52495 (NQ4 slide 1), ROM 53652 (CCS2 slide 1), ROM 53653 (WC2 slide 2), ROM 53654 (DSDP sample 603C-8-5, 100–102 cm, slide 1), and ROM 53655 (ODP sample 645E-7R, CC).

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 AND PLATE LABELLING

Morphological terminology in this study follows Head (1998a) who introduced some new terms, redefined others, and outlined general preferences (see Fensome et al., 1993, 1996; de Verteuil and Norris, 1996b) including an adherence to Kofoidian labelling.

First postcingular plate (1^{'''}) and homologue (*1^{'''}).—Plates have been labelled as far as possible according to the standard gonyaulacalean model (Fensome et al., 1993, text-fig. 13), which includes six postcingular plates (1^{'''}–6^{'''}). In *Geonettia waltonensis* n. sp. the first postcingular plate (1^{'''}) is very reduced and is included within the sulcal region. It seldom detaches or shows any demarcation from neighboring sulcal plates, but in one specimen (Fig. 9.5, 9.6) it either actually or nearly touches the first cingular plate. For the purpose of plate labelling, it is assumed indeed to contact the cingular series and is therefore designated as a postcingular plate (1^{'''}) in the strict Kofoidian sense. Subsequent plates of the postcingular series are accordingly labeled as second (2^{'''}) to sixth (6^{'''}) postcingular plates.

The homologous plate in *Geonettia clineae* is labelled by de Verteuil and Norris (1996a) as the left accessory sulcal plate (1as). De Verteuil and Norris' photographs and tracings (de Verteuil and Norris, 1996a, pl. 2, fig. 2b, 3b, and pl. 4, figs. 3b and 4b, but compare with their text-fig. 2) indeed show this to be a sulcal plate because, by strict Kofoidian application, it does not touch the cingular series. However, it is labelled in the present

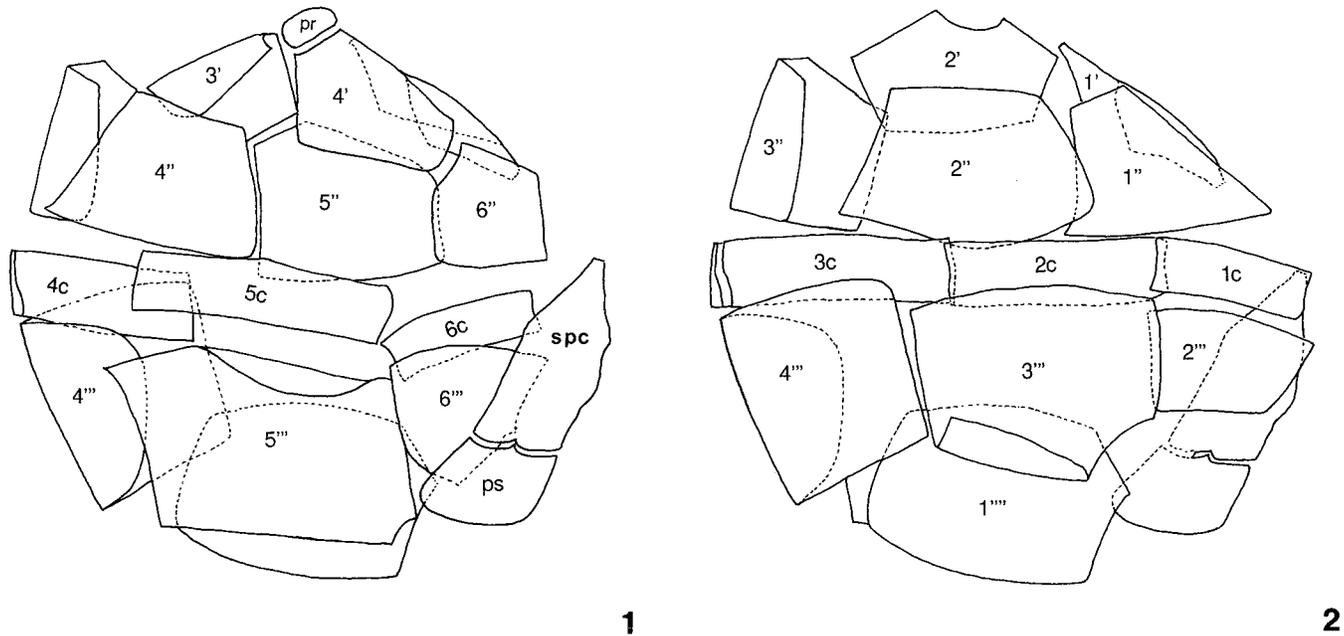


FIGURE 6—Holotype of *Geonettia waltonensis* n. sp. from DSDP Hole 603C. Tracings are based on the specimen illustrated in Figure 7.1–7.3. Dashed lines do not necessarily indicate real order of overlap. See Figure 2 for plate notation. 1, 2, right lateral view of 1, right lateral surface and 2, left lateral surface. The posterior intercalary plate (1p) is apparently present on this specimen but crumpled, and is not included in the tracings. Sample DSDP-603C-8-5, 100–102 cm, slide 1, R37/3; length of cyst, 50 μ m.

paper as the first postcingular homologue (*1'') to facilitate comparison with the standard gonyaulacalean model, and particularly with *Geonettia waltonensis* and the pyrodinioidean genus *Capisocysta*, each of whose first postcingular plate (1'') appears to touch the cingular series (Head, 1998a). Hence, the first postcingular plate (1'') in *Geonettia waltonensis*, the first postcingular plate (1'') in *Capisocysta*, and the first postcingular homologue (*1'') in *Geonettia clineae* (=left accessory sulcal plate in de Verteuil and Norris, 1996a) are all considered homologous.

It should be noted that while the topology of the first postcingular homologue is important for plate labelling, too much taxonomic significance should not be attached to whether it actually touches the cingular series. In *Pyrodinium bahamense*, the type of *Pyrodinium* and hence of the Pyrodinioideae, the first postcingular plate may or may not touch the cingular series depending on the individual specimen (see illustrations in Balech, 1985). Indeed, Balech (1985, p. 20) has observed that the first postcingular plate in *Pyrodinium bahamense* is notably intermediate in development between the sulcal and the postcingular series, thus showing the conversion of a hypocystal plate into a sulcal one. This feature seems to be generally true in the Pyrodinioideae.

Sulcal plate complex (spc).—This term is introduced to indicate a discrete, separately-released opercular piece that represents more than one sulcal plate. In *Geonettia waltonensis* it usually represents the anterior sulcal plate (as), right accessory sulcal plate (ras), right sulcal plate (rs), left sulcal plate (ls), and first postcingular plate (1'''); but never the posterior sulcal plate (ps) since this plate is always released separately.

Posterior sulcal plate (ps).—The second posterior intercalary plate (2p) of *Geonettia clineae*, as labelled by de Verteuil and Norris (1996a), is inferred to be homologous with posterior sulcal plate (ps) in *Capisocysta*, so labelled because its geometry indeed suggests it to be an extension of the sulcus (Head, 1998a). The corresponding plate in *Geonettia waltonensis* appears similarly to occur within the sulcus and, as with *Capisocysta*, is labelled the posterior sulcal plate (ps). To make comparison between these taxa easier, the present paper relabels the

second posterior intercalary (2p) in *Geonettia clineae* as its posterior sulcal plate (ps). This does not affect the labelling of the first posterior intercalary (1p), which remains the same for all considered species.

COMPARATIVE MORPHOLOGY OF GEONETTIA WALTONENSIS

Geonettia waltonensis n. sp. and the type of the genus, *G. clineae* are both proximate spherical cysts with broadly similar tabulation patterns, yet *G. waltonensis* differs from *G. clineae* in many details: presence of a thin, unornamented wall; an apical pore complex consisting of a single, unornamented, oval plate; absence of Q plates; a long narrow first apical plate having a long, concave contact with 4' a small posterior sulcal plate whose margins with 6''' and 1p are parallel; a sixth postcingular plate (6''') that is triangular in shape; a short contact between 5''' and ps; and a lesser dissociation of sulcal plates (see Table 1).

In significant contrast to *Geonettia clineae*, the hypocystal tabulation in *G. waltonensis* is almost identical to that of *Capisocysta lata* (Table 1), although plate dissociation does not occur on the epicyst of *C. lata*, making it easy to separate these two species. Even with damaged specimens, the presence of cingular plates readily distinguishes *Geonettia waltonensis* from *Capisocysta lata*.

Geonettia sp. (Figs. 11, 12) from the upper Miocene of ODP Hole 645E, Baffin Bay (as *Dinocyst* sp. 1 in Anstey, 1992) and uppermost Miocene of DSDP Hole 603C, New Jersey lower continental rise (personal observation), differs from *G. waltonensis* in having a conspicuously granulate wall surface, although some details of its hypotabulation are not fully known (Table 1).

EVOLUTION IN THE PYRODINIOIDEAE

The order Gonyaulacales has been subdivided into five suborders, of which the Goniodomineae is characterized by a distinctive hypotabulation that includes a quinqueform (five-sided)

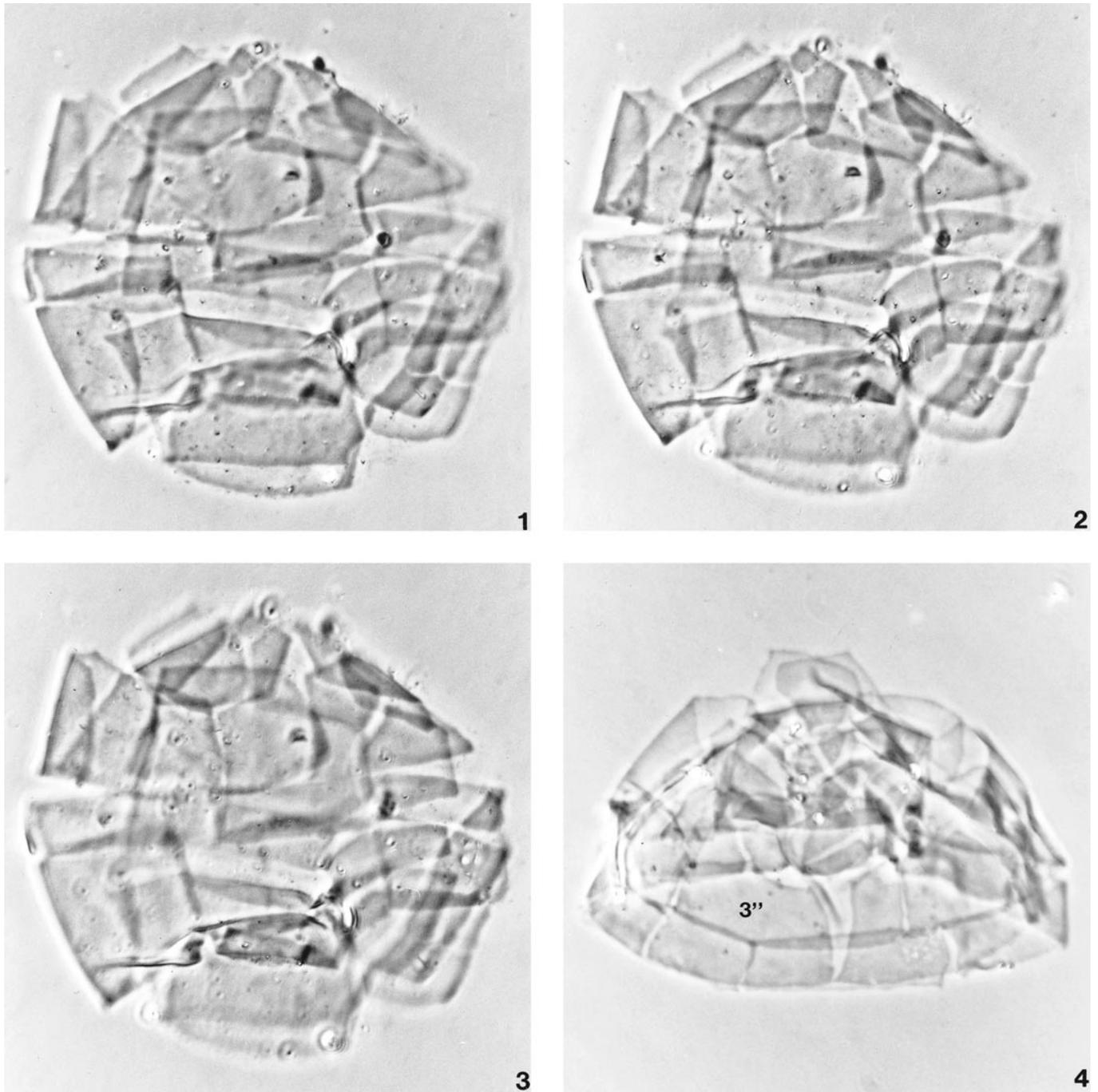


FIGURE 7—*Geonettia waltonensis* n. sp. Photomicrographs are in phase contrast. Various magnifications. 1–3, holotype of *Geonettia waltonensis* from DSDP Hole 603C. Right lateral views at high through low focus. See Figure 6 for tracings and interpretation. Sample DSDP-603C-8-5, 100–102 cm, slide 1, R37/3; length of cyst, 50 μm . 4, ventral? view of a detached epicyst with adherent cingular plates, from the Coralline Crag Formation, Rockhall Wood, Suffolk. Sample CCS2, slide 1, T47/2; equatorial diameter, 48 μm .

antapical homologue (Fensome et al., 1993, 1996). The Goniodomineae is divided into two families, the Pyrocystaceae which is represented by a single genus with no known cyst record, and the Goniodomaceae represented by four subfamilies including the Pyrodinioideae. The family Goniodomaceae is represented by fossils of Early Cretaceous to Holocene age, the subfamily Pyrodinioideae also having fossil representatives in the Cretaceous (Fensome et al., 1993).

Pyrodinioideans are distinguished from other members of the family Goniodomaceae in having the right sulcal (rs) and posterior sulcal (ps) homologues both contained within the sulcus (Fensome et al., 1993), although this definition requires subjective judgement for cysts whose sulcus is not demarcated by an actual depression (de Verteuil and Norris, 1996a, p. 268). The topology of the first apical plate may be metasert (e.g., *Pyrodinium* and *Homotryblium* Davey and Williams, 1966) or insert

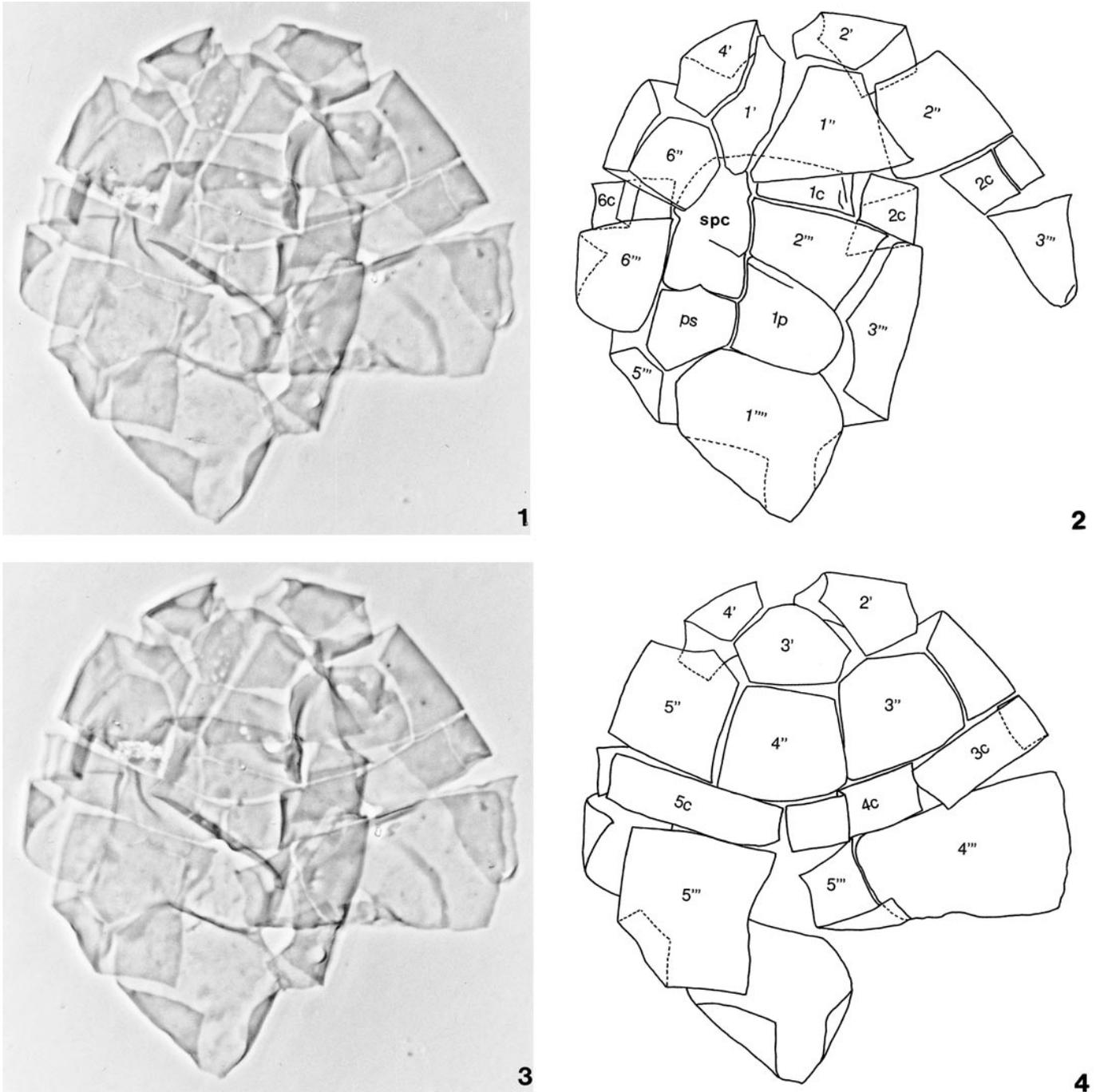


FIGURE 8—*Geonettia waltonensis* n. sp. from the Coralline Crag Formation, Rockhall Wood, Suffolk. Photomicrographs are in phase contrast. 2 and 4 are tracings of the specimen in 1 and 3. Dashed lines on 2 and 4 do not necessarily indicate real order of overlap. See Figure 2 for plate notation. 1–4, ventral views of 1, 2, ventral surface, and 3, 4, dorsal surface. The hypocyst is torn and folded inwards, and plates 2c, 3''', and 5''' are each torn into two pieces. Sample CCS2, slide 1, O43/3; equatorial diameter, 56 μm .

(e.g., *Eocladopyxis*, *Geonettia*, and *Hystrichosphaeridium* Deflandre, 1937) and seems to be of value in determining phylogenetic relationships within the Pyrodinioideae. A particularly useful attribute of pyrodinioidean cysts is the propensity for plates to separate quite extensively during excystment. So extensive is this plate dissociation in *Geonettia* and related genera that tabulation patterns, and hence phylogenetic relationships, can be elucidated in unusual detail.

Eocladopyxis, *Capisocysta*, and *Geonettia* differ from all other pyrodinioideans in having plate dissociation on the hypocyst. From similarities in epitabulation (not known for *Capisocysta*) and archeopyle style for these genera, it has been suggested that they are all closely related within the Pyrodinioideae (Head, 1998a). From the available stratigraphic evidence, Head (1998a, p. 799) postulated the following sequence of events: 1) development of extensive plate dissociation but with epitracial

archoeopyle retained, in the proximochorate to chorate *Eocladopyxis* (Paleocene–Oligocene); 2) loss of processes and more extensive plate dissociation, whereby the entire cyst disintegrates, in *Geonettia* (early Miocene–Pliocene); and 3) failure of epicystral plates to dissociate, thereby restricting archoeopyle formation to the hypocyst, in *Capisocysta* (late Miocene–present), and 4) a tendency towards plate multiplication, as seen in *Capisocysta lyellii*, which may have evolved from *Capisocysta lata* (late Miocene?–early Pliocene). This sequence of events, shown in Figure 5, is based on stratigraphic occurrences in: McLean (1976), Liengjareern et al. (1980), Anstey (1992), de Verteuil (1996, 1997), de Verteuil and Norris (1996a, 1996c), Warny and Wrenn (1997), and Head (1998a). It should be noted that upper Miocene range top given for *Geonettia clineae* by de Verteuil and Norris (1996a) can now be extended into the Pliocene: this species occurs as high as the lowermost Pliocene (Subchron C3n4n) of DSDP Hole 603C on the New Jersey lower continental rise (personal observation) and upper Pliocene of ODP Hole 645E, Baffin Bay (personal observation). The range base for *Geonettia clineae* is at least as low as upper middle Miocene (de Verteuil and Norris, 1996a), and specimens bearing some resemblance to *G. clineae* have been reported from the upper lower Miocene of the eastern U.S.A. (de Verteuil and Norris, 1996c, table 3; and L. de Verteuil, personal communication).

Within this proposed development of the *Eocladopyxis*–*Geonettia*–*Capisocysta* complex, *Geonettia waltonensis* seems to occupy a key position, for three reasons: 1) its entire cyst wall dissociates fully into constituent plates, resulting in a holocystical archoeopyle that is also characteristic of *Geonettia clineae*; 2) its first apical plate is dissimilar in shape to *Geonettia clineae*; and 3) its hypocystal tabulation is almost identical with that of *Capisocysta lata*. In many respects *Geonettia waltonensis* is more similar to *Capisocysta lata* than to *Geonettia clineae*. Indeed, the shared features of *Geonettia waltonensis* and *Capisocysta lata*—shape and small size of the posterior sulcal plate, triangular shape of the sixth postcingular plate, smooth, thin wall in *G. waltonensis* and in some specimens of *C. lata*—almost overshadow the important difference that only the hypocyst dissociates into plates in *Capisocysta*. It is therefore suggested, given that the holocystical archoeopyle is a relatively early-derived feature within the *Eocladopyxis*–*Geonettia*–*Capisocysta* complex (early Miocene at latest), that *Capisocysta lata* is descended either directly from *G. waltonensis* or from a close relative. This predicts that *Capisocysta lata* represents the early stages of a new (*Capisocysta*) lineage. The proposition can be tested in two ways: 1) *G. waltonensis*, or a close relative, will need to be found in deposits older than *Capisocysta* (*Capisocysta* has been found in deposits as old as late Miocene; Warny and Wrenn, 1997; Head, 1998a); and 2) the episomal tabulation of *Capisocysta lata* should be similar to that of *G. waltonensis*, particularly regarding the shape and insert topology of the first apical plate. Although these aspects are not determinable from the cyst, *Capisocysta lata* is an extant species and so details of its thecal epitabulation should enable this to be determined, once its thecal stage becomes known. It should be noted that, whereas a diaphanous outer wall layer is present on some specimens of *Capisocysta lata*, this feature has not been observed in *G. waltonensis*. It must also be emphasized that the holocystical archoeopyle in the Pyrodinioideae is here assumed to have evolved only once, but it remains to be tested whether in fact the holocystical archoeopyle could have reappeared in a lineage characterized by a hypotractal archoeopyle (e.g., *Capisocysta*).

In assessing the relationship between *G. waltonensis* and *G. clineae*, the numerous small differences in tabulation and wall ornamentation must be considered along side the shared features

of a holocystical archoeopyle and absence of processes. While *Geonettia waltonensis* is therefore thought not to have evolved directly from *G. clineae*, they presumably share a common ancestor. *Geonettia waltonensis* may be more closely related to the late Miocene *Geonettia* sp. (Figs. 11, 12) than to *G. clineae*, although some details of the hypocystal tabulation in *Geonettia* sp. are presently undetermined. It is accordingly possible that *Geonettia waltonensis* represents a separate lineage within *Geonettia* that arose during the Miocene.

Finally, the shape and topology of the first apical plate in *Geonettia* and related species deserve particular attention. Metastert versus insert topologies are significant and unlikely to be overlooked, but the width and geometry of the contact between plates 1' and 4' (concave with respect to 1' for *G. waltonensis* and *Geonettia* sp.) may also be important. Judging from the thecal morphology of *Pyrodinium bahamense* (see Balech, 1985; Taylor and Fukuyo, 1989), this contact might be influenced by the position in the thecal stage of the ventral pore on the left margin of plate 4', and therefore be a functionally or metabolically active region of the epitheca. With this in mind, the first apical plate in *G. clineae* is omegaform, a shape not known in any related species here considered. The discovery of new *Geonettia* species (and perhaps also of *Eocladopyxis*) may ultimately shed light on the evolutionary and taxonomic significance of an omegaform first apical plate.

SYSTEMATIC PALEONTOLOGY

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

Subdivision DINOKARYOTA Fensome et al., 1993

Class DINOPHYCEAE Pascher, 1914

Subclass PERIDINIPHYCIDAE Fensome et al., 1993

Order GONYAULACAE Taylor, 1980

Suborder GONIODOMINEAE Fensome et al., 1993

Family GONIODOMACEAE Lindemann, 1928

Subfamily PYRODINIOIDEAE Fensome et al., 1993

GEONETTIA de Verteuil and Norris, 1996a

GEONETTIA WALTONENSIS new species

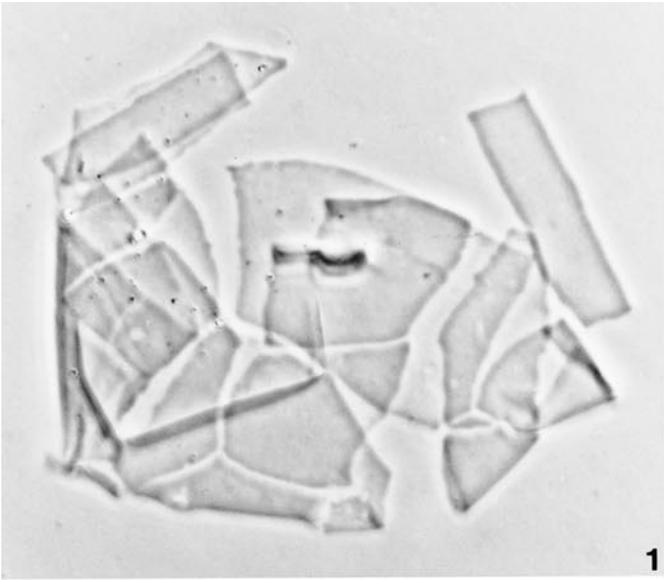
Figures 2–10; Table 1

Geonettia? sp. HEAD, 1997, p. 185, 189, figs. 12.17–12.19, 13.1–13.4; LOUWYE AND LAGA, 1998, tab. 1.

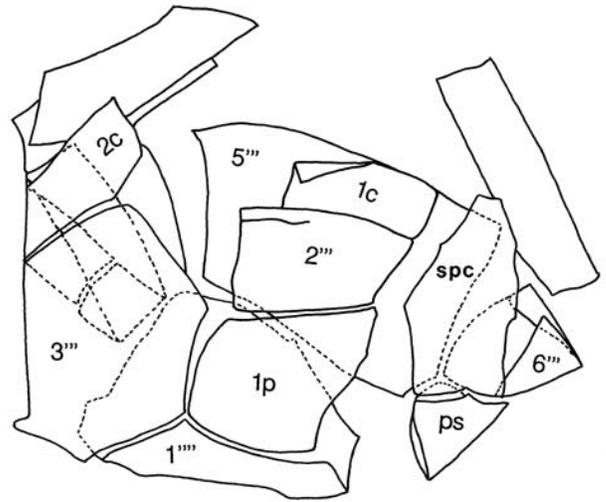
Geonettia sp. of HEAD, 1997. HEAD, 1998a, fig. 6.1–6.3; HEAD, 1998b, pl. 2, fig. 4; HEAD, 1998c, p. 816, fig. 4d.

Diagnosis.—A species of *Geonettia* characterized by a thin, smooth wall, a single unsculptured ovoidal preapical plate, a narrow first apical plate (1') whose contact with 4' is concave and whose contact is broadest with plates 1'' and 4', and a posterior sulcal plate (ps) that is smaller than either fundital (1p or 1''') and whose margins with 6''' and 1p are approximately parallel. The posterior margin of ps is dithigmate geniculate, having a longer contact with 1''' than 5'''.

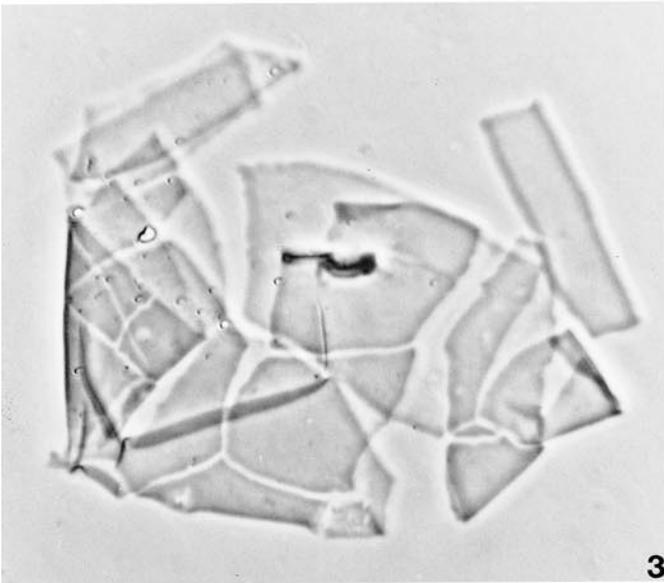
Description.—Cysts proximate and spherical to subspherical, having a thin (less than 0.3 μm) wall, smooth surface, and no visible stratification under light microscopy. Tabulation expressed only by pre-formed lines of weakness, these being visible as pale narrow lines on undehisced specimens, which control the discrete separation of plates in dehisced specimens. These lines of weakness are incompletely developed on the sulcus but are otherwise fully developed on both epicyst and hypocyst. They facilitate an almost complete dissociation of the cyst into constituent plates, as follows: 1pr, 1'–4', 1''–6'', 1c–6c, 2'''–6''', ps, 1p, 1''', and a single plate (spc) representing the remaining sulcal plates (presumably: as, ras, rs, ls, and 1''') from which 1''' occasionally shows some separation. These plates form



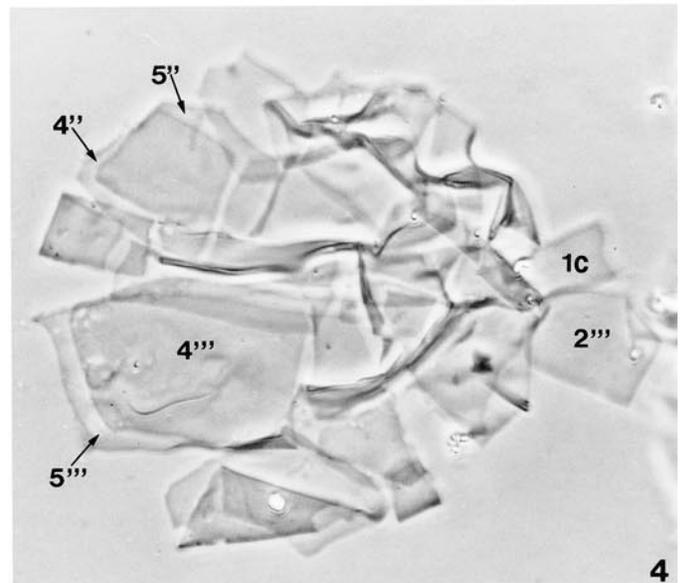
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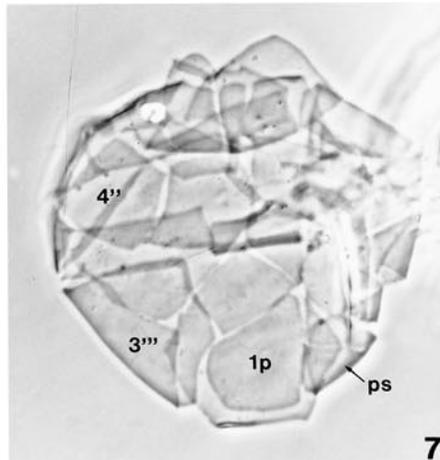
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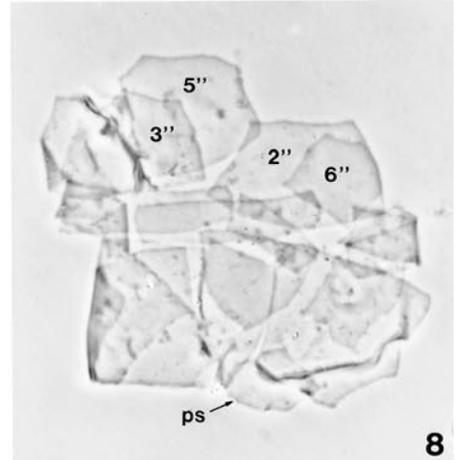
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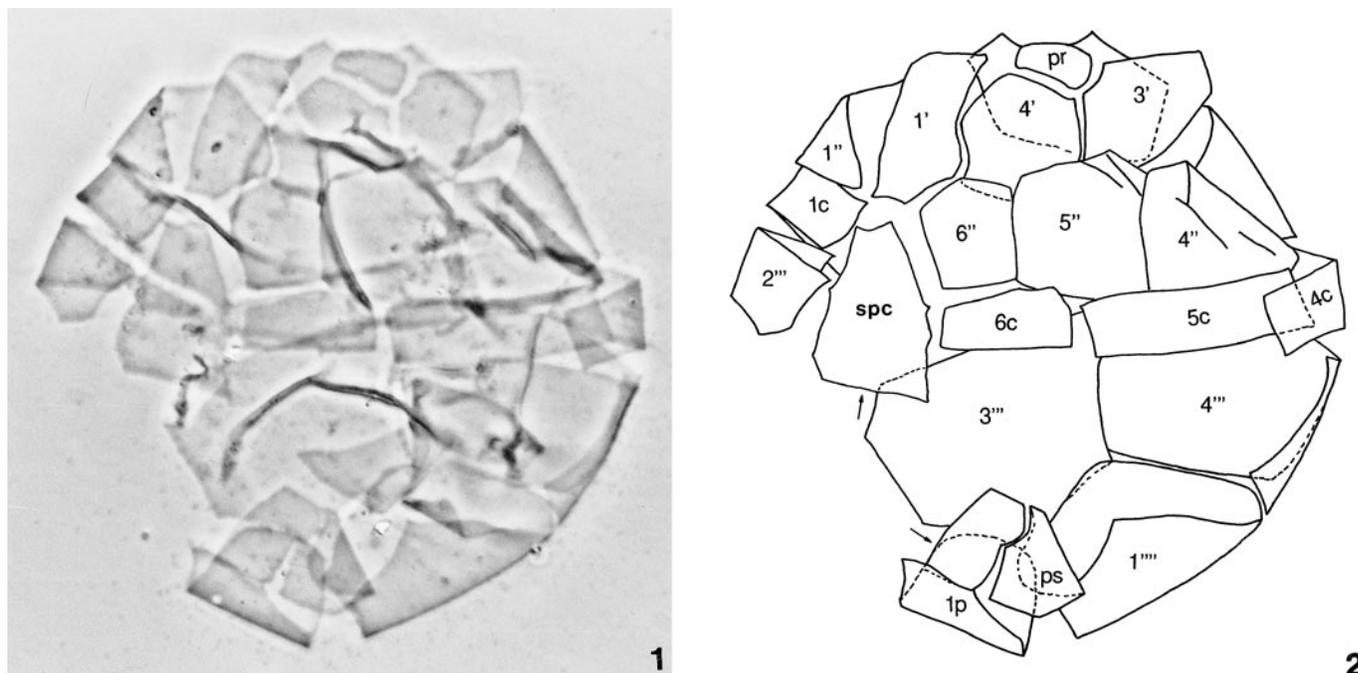


FIGURE 10—*Geonettia waltonensis* n. sp. from the Coralline Crag Formation, Rockhall Wood, Suffolk. 1 is a phase contrast photomicrograph, and 2 is a tracing of the specimen in 1. Dashed lines on 2 do not necessarily indicate real order of overlap. See Figure 2 for plate notation. 1, 2, left dorso-lateral view showing right ventro-lateral surface of epicyst and part of the left dorso-lateral surface of the hypocyst. The hypocyst is torn and incomplete, and the sulcal plate complex (spc) is torn into two pieces (the torn margins are each marked with an arrow). Sample CCS1, slide 1, N25/4; equatorial diameter, 47 μm .

a holocystal archeopyle, with no apparent preferential order of plate loss.

The apical pore complex is represented by a single ovoidal preapical plate (pr) which is smooth and has no apparent markings. The first apical plate (1') is insert, narrowly contacting the preapical plate. It also narrowly contacts the sulcal series. A characteristic feature of the first apical plate (1') is its broad contacts with 4' and 1'' and particularly its concave and slightly angular contact with 4'. Apical plates 2', 3', and 4' are of approximately equal size, and 2' and 4' make the longest contact with the preapical plate.

Of the precingular series, 6'' is notably the smallest, the others being of somewhat similar size. Plates 3'' and 6'' have dithigmate geniculate anterior margins and are relatively symmetrical, whereas 5'' is dithigmate geniculate and strongly asymmetrical owing to a long contact with 4' and short contact with 3'. Plates 1'', 2'' and 4'' have rectilinear monothigmate anterior margins, and 1'' is triangular owing to broad, strongly converging margins that contact 1' and 2''. Plate 3'' is approximately mid-dorsal in position. The posterior (adcingular), dorsally-directed angles of

plates 1'', 2'', 4'', 5'' and 6'' are drawn into minute acute projections, the corresponding ventrally-directed angles of these plates being minutely rounded. Both posterior angles in plate 3'' are minutely rounded. The adcingular margins of precingular plates are generally straight, but subtly expressed obtuse points may occur at the contact with boundaries between cingular plates.

The cingulum has a width of about 4.5–5.5 μm and is laevorotatory, with about one cingular width of displacement. The cingular plates, of which there are 6, have a rectangular shape that may be modified slightly in two ways: 1) plate boundaries separating 1c/2c, 3c/4c and 4c/5c and 5c/6c are weakly reverse-sigmoidal, whereas that separating 2c/3c is uncertain but may be nearly straight (see Fig. 8); and 2) anterior and posterior margins may show subtly expressed obtuse points where they contact plate junctions of the precingular and postcingular series, although this feature is often not visible.

The sulcus separates into two units, the posterior sulcal plate (ps) and the sulcal plate complex (spc). The sulcal plate complex consists of the anterior sulcal plate (as), right accessory sulcal plate (ras), right sulcal plate (rs), left sulcal plate (ls), and first

FIGURE 9—*Geonettia waltonensis* n. sp. Photomicrographs are in phase contrast. Dashed lines on 2 do not necessarily indicate real order of overlap. See Figure 2 for plate notation. 1–3, dorsal views of the partially separated plates of a detached hypocyst, with 1 at slightly higher focus than 3, and 2 a tracing of the specimen shown in 1 and 3. Walton-on-the-Naze, Essex, sample WC2, slide 2, L27/3; width of plate cluster, 48 μm (also illustrated in Head, 1998c, fig. 4d). 4, equatorial view of a fairly complete but folded specimen. Coralline Crag Formation, Rockhall Wood, Suffolk; sample CCS2, slide 1, V17/0; maximum equatorial diameter (including 2''), 56 μm . 5, 6, external view of sulcal plate complex and posterior sulcal plate, showing rare partial separation of rs, ls, and 1''. 6, tracing of the specimen illustrated in 5, with dashed lines indicating what are interpreted to be lines of thinning that demarcate plate boundaries. Coralline Crag Formation, Rockhall Wood, Suffolk; sample CCS2, slide 1, K36/2; length of sulcal plate complex (excluding ps), 18 μm . 7, dorsal view at mid focus, with selected plates labelled. Coralline Crag Formation, Rockhall Wood, Suffolk; sample NQ3, slide 1, H27/0; maximum width, 41 μm . 8, equatorial view of incomplete specimen, with selected plates labelled. Coralline Crag Formation, Rockhall Wood, Suffolk; sample NQ4, slide 1, G24/0; maximum diameter of plate cluster, 50 μm .

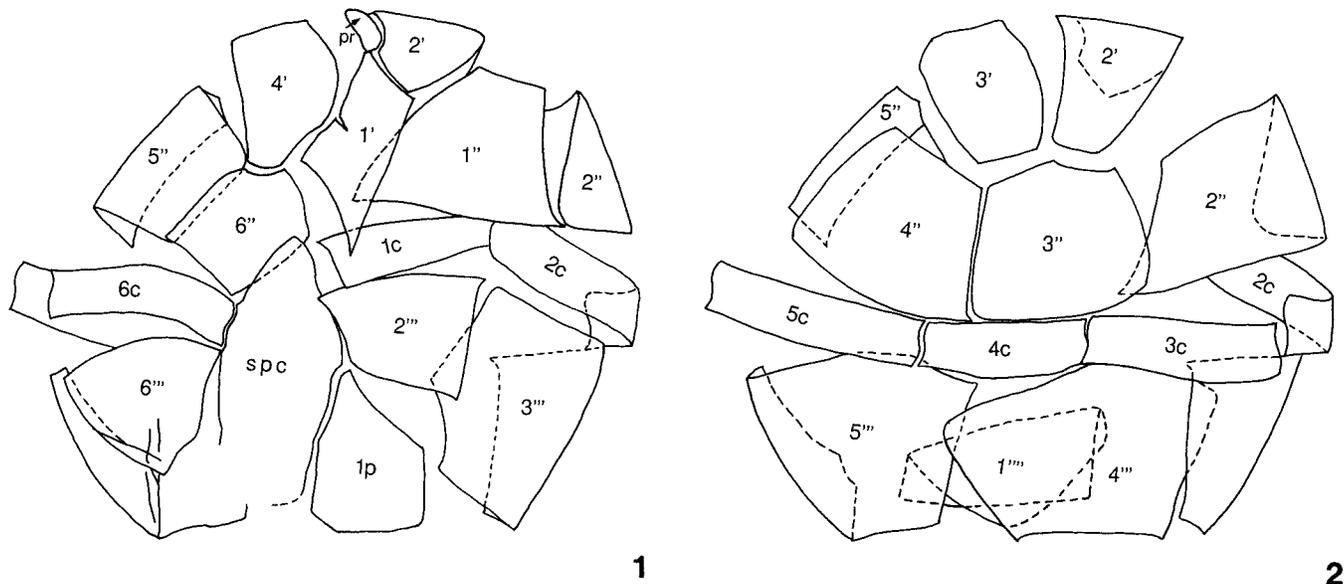


FIGURE 11—*Geonettia* sp. from the upper Miocene of ODP Hole 645E, Baffin Bay. Tracings are based on the specimen illustrated in Figure 12. Dashed lines do not necessarily indicate real order of overlap. See Figure 2 for plate notation. 1, 2, Ventral views of 1, ventral surface and 2, dorsal surface. Note that the separation of 1' from the sulcal plate complex (spc) may have been modified by tearing. The posterior margin of the spc is uncertain, and the posterior sulcal plate (ps) is missing. Sample ODP 645E-7R, CC, slide 1 (oxidized #1), Q37/3 (label to left); maximum width of cyst, 54 μ m.

postcingular plate (1'''). These plates are usually completely fused, but the first postcingular plate (1''') was seen on a few specimens to be partially separated, revealing a narrow, anteriorly tapering, subrectangular plate that just touches the first cingular plate (1''' and 1c apparently share a triple junction in the one specimen where the anterior margin of 1''' was clearly discernible, Fig. 9.5, 9.6, and see Fig. 2 for reconstruction). An angular notch on the posterior margin of the sulcal plate complex, always to the right of center, delimits the shared contact of the 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. The posterior sulcal plate (ps), which anteriorly abuts the sulcal plate complex, is the same width as the ls and rs combined; its lateral margins (with 1p and 6''') run parallel. Its posterior margin is geniculate and dithigmate, contacting 1''' on the longer side and 5''' on the shorter side: it is the smallest individual plate routinely released from the hypocyst during dehiscence. The sulcus is posteriorly inclined to the right on the hypocyst.

There are five additional postcingular plates of which 2''' and 6''' are relatively small, 6''' being approximately triangular. Plates 3''', 4''', and 5''' are larger. Plate 4''' has a monothigmate rectilinear posterior margin and is middorsally positioned. Plates 3''' and 5''' are similar in size and both have dithigmate geniculate posterior margins with characteristic arcuate indentations at their posteroventral corners where they contact plates 1p and ps respectively. Plate 5''' always has a smaller indentation than 3'''. As with the precingular series, plates of the postcingular series have dorsally-directed angles drawn into minute acute projections along their anterior (adcingular) margins, with the corresponding ventrally-directed angles of these plates being minutely rounded. This feature occurs on 2''', 3''', 5''' and 6''', with both anterior angles in plate 4''' being minutely rounded. The adcingular margins of postcingular plates are generally straight, but subtly expressed obtuse points may occur at the contact with boundaries between cingular plates.

There are two fundital plates, 1p and 1'''. The posterior intercalary (1p) is relatively small and comparable in size to 2''' and 6'''. The antapical plate (1''') is quinqueform and larger than 1p.

Etymology.—Named after Walton-on-the-Naze, Essex, eastern England, from where an important specimen (Head, 1998c, fig. 4d; Fig. 9.1–9.3) gave critical insights into the ventral tabulation of this species.

Type.—Holotype, Figures 6.1, 6.2, 7.1–7.3. DSDP Hole 603C, New Jersey lower continental rise. Sample 603C-8-5, 100–102 cm, slide 1, England Finder reference R37/3. ROM 53654.

Other material examined.—DSDP samples, 603C-7-2, 85–87 cm and 603C-8-5, 100–102 cm (Site 603 report, in van Hinte et al., 1987); Rockhall Wood samples CCS1–CCS4 and NQ2–NQ4 (Head, 1997); and Walton-on-the-Naze samples WC2 and WC4 (Head, 1998c).

Measurements.—Holotype: cyst length 50 μ m; cyst equatorial diameter 51 μ m; width of cingulum 5.0–5.5 μ m. Range: cyst length 41(46.9)57 μ m; cyst equatorial diameter 41(48.4)56 μ m; width of cingulum 4.5–5.5 μ m. Ten specimens were measured.

Comparison.—*Geonettia clineae*, the type species, differs from *G. waltonensis* in having a fibroreticulate luxuria, a more complexly structured apical pore complex, the presence of one or two Q plates, and in the geometries of several plates. In particular, the first apical plate is shorter, wider, and omegaform, and cingular plates have generally less straight and less parallel anterior and posterior margins. On the hypocyst, the posterior sulcal plate is much larger, widening posteriorly so that it is similar in size to the two funditals 1p and 1''' (see Table 1).

Geonettia sp. (Figs. 11, 12; Table 1) from the upper Miocene differs from both *G. waltonensis* and *G. clineae* in having a granular surface; although its first apical plate, which is insert, appears closer in shape to *G. waltonensis* than to *G. clineae*. This species has other similarities with *G. waltonensis* (Table 1) but requires further study to allow detailed comparison.

Capisocysta lata has a hypocystal tabulation virtually identical to that of *G. waltonensis*, and the cyst may have a smooth

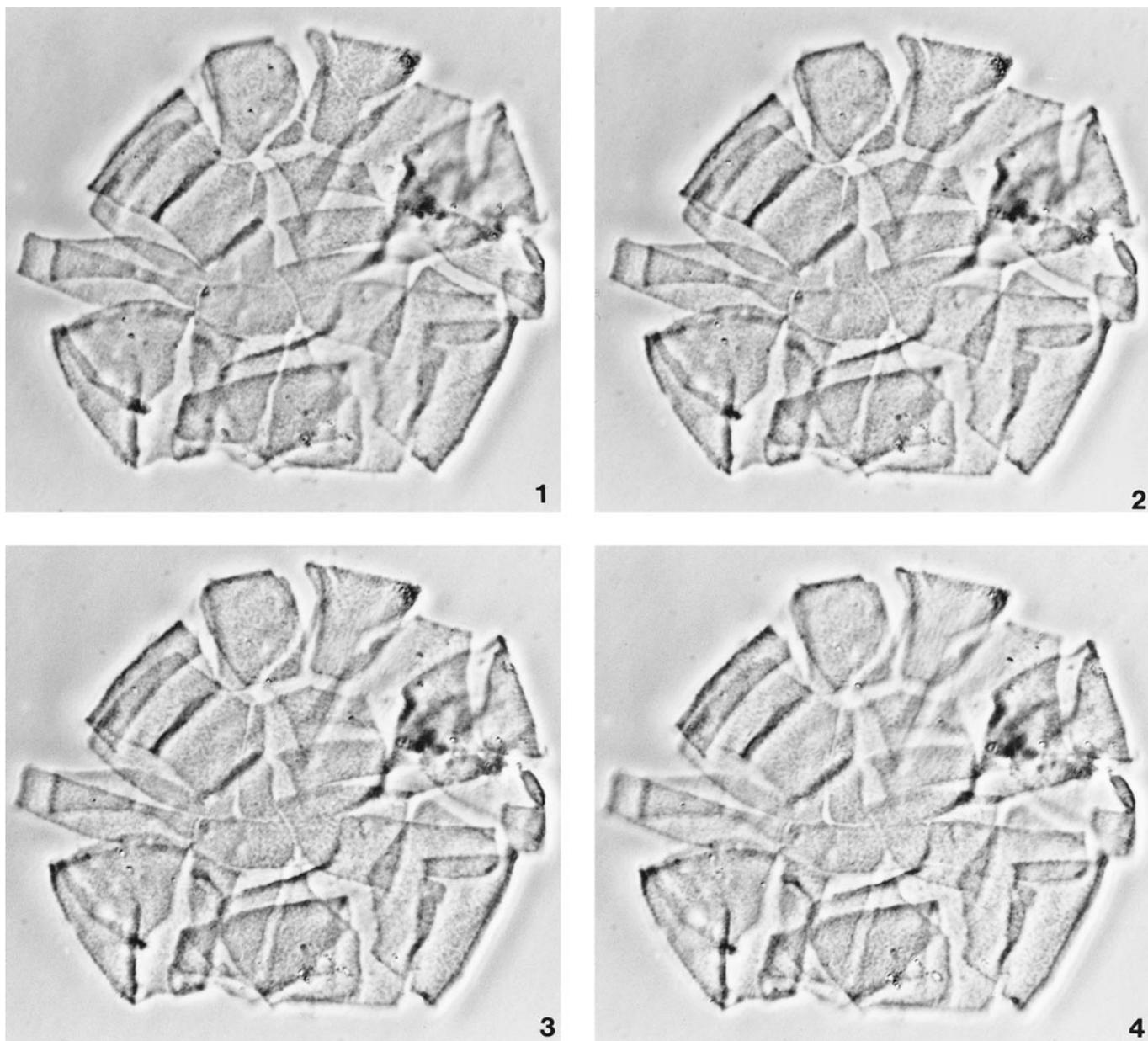


FIGURE 12—*Geonettia* sp. from the upper Miocene of ODP Hole 645E, Baffin Bay. Photomicrographs are in phase contrast. 1–4, Ventral views of 1 ventral surface; 2–4 progressively lower foci to dorsal surface. See Figure 11 for tracings and interpretation. Sample ODP 645E-7R, CC, slide 1 (oxidized #1), Q37/3 (label to left); maximum width of cyst, 54 μ m. This specimen was illustrated as *Dinocyst* sp. 1 in Anstey (1992, pl. 10, figs. 1 and 3).

wall. However, plates in *Capisocysta lata* only dissociate on the hypocyst (Table 1).

Type stratum and locality.—Upper upper Pliocene, Chron C2r (=2.58–1.95 Ma), 66.42 m below sea floor, DSDP Hole 603C, New Jersey lower continental rise.

Occurrence.—In DSDP Hole 603C, restricted to samples 603C-7-2, 85–87 cm and 603C-8-5, 100–102 cm, which occur in the upper upper Pliocene Chron C2r. The estimated age of Sample 603C-7-2, 85–87 cm is 2.1 Ma, and that of Sample 603C-8-5, 100–102 cm is 2.3 Ma. *Geonettia waltonensis* comprises less than 0.5 percent of the total dinoflagellates in these two samples. At Rockhall Wood in eastern England, it occurs in all but one of 8 samples taken from the Ramsholt and Sudbourne

members of the Coralline Crag Formation, but does not exceed 1 percent of the total dinoflagellates in these samples (Head, 1997). The Ramsholt Member is middle lower or upper lower Pliocene, being tentatively dated at 3.8–3.6 Ma using nannofossils and no older than 4.6 Ma based on foraminifers (see discussions in Head, 1997; 1998b). The Sudbourne Member is probably lower upper Pliocene (Head, 1997; 1998b). At Walton-on-the-Naze, *Geonettia waltonensis* occurs in one of three samples analyzed from the basal horizon of the Walton Crag and in a sample from 2 m above the base. It comprises less than 1 percent of the total dinoflagellates in each of these two samples (Head, 1998c). The Walton Crag is lower upper Pliocene, between 3.0 Ma and a little older than 2.6 Ma, and younger than

TABLE 1—Comparison of morphological features in species of the pyrodinioidean genera *Geonettia* and *Capisocysta*.

Character	<i>Geonettia clineae</i> fibroreticulate	<i>Geonettia waltonensis</i> smooth	<i>Geonettia</i> sp. granulate	<i>Capisocysta lata</i> smooth to granulate; di- aphanous outer layer sometime present	<i>Capisocysta lyellii</i> granulate to irregularly microgranulate
Archeopyle	holocystal	holocystal	holocystal	compound hypotractal	compound hypotractal
Cingular series detaches from cyst	yes	yes	yes	no	no
Internal surface of apical pore complex	sculptured	smooth	smooth?	smooth	smooth
Q plates	one or possibly two	none	apparently none	unknown	unknown
4'-1' contact longer than 2'-1' contact	slightly	considerably	moderately	unknown	unknown
4'-1' contact relative to 1'	nearly straight	concave	concave	unknown	unknown
Dissociation of anterior sulcal, right anterior sul- cal, and transition plates	yes	no	no	no	no
ps much smaller than *1''''	no	yes	unknown	yes	yes
Contacts of ps with 6''' and 1p	strongly divergent	parallel	unknown	parallel	moderately divergent
Contact of ps with 5''' very short	no	yes	yes	yes	yes
Shape of 6'''	trapezoidal	triangular	triangular	triangular	triangular
Multiplication of first an- tropical homologue	no	no	no	no	two plates

the Coralline Crag Formation (Head, 1998c). In Belgium, *Geonettia waltonensis* is known from a single specimen reported in the Lillo Formation (middle or upper Pliocene) of the Kalmthout Borehole (as *Geonettia?* sp. Head 1997 in Louwe and Laga, 1998).

Stratigraphic range.—Lower Pliocene of eastern England (tentatively dated at 3.8–3.6 Ma, and no older than 4.6 Ma) through upper upper Pliocene (ca. 2.1 Ma, just below the Olduvai subchron) in DSDP Hole 603C, New Jersey lower continental rise, western North Atlantic.

Autecology.—Precise interpretation of the ecology of *Geonettia waltonensis* is hindered by its scarcity in the samples examined. Occurring always with a frequency of less than 1 percent, *Geonettia waltonensis* might be near the limits of its environmental tolerance, particularly given that some pyrodinioideans form blooms in favorable circumstances.

Notwithstanding these limitations, the pattern of occurrence of *Geonettia waltonensis* in eastern England suggests an intolerance of cold, inequable conditions. It inhabited the North Sea when conditions were warm temperate (Coralline Crag) to mild temperate (Walton Crag), and its apparent absence from younger Pliocene deposits in eastern England may be in response to cooling at 2.54 Ma and possible increased seasonality thereafter.

DSDP Site 603 is oceanic in setting but contains abundant neritic dinoflagellates transported from the shelf. Specimens of *Geonettia waltonensis* may have a similar neritic origin. *Geonettia waltonensis* co-occurs in sample 603C-7-2, 85–87 cm with the temperate to cool-water taxa *Bitectatodinium tepikiense* (5 percent), *Filisphaera* spp. (12 percent), and *Habibacysta tectata* (4 percent); and the warm-water taxa *Lingulodinium machaerophorum* (5 percent), *Polysphaeridium zoharyi* (2 percent) and *Tectatodinium pellitum* (1 percent). In sample 603C-8-5, 100–102 cm, *Geonettia waltonensis* occurs with the temperate to cool-water taxa *Bitectatodinium tepikiense* (4 percent), *Filisphaera* spp. (12 percent), and *Habibacysta tectata* (0.5 percent); and the warm-water taxa *Lingulodinium machaerophorum* (1 percent), *Polysphaeridium zoharyi* (12 percent) and *Tectatodinium pellitum* (3 percent). On face value, these associations imply temperate climatic conditions, although it is not certain that the dinoflagellates all come from the same climatic zone: they may well have been mixed by long distance transport to Site 603, thereby complicating their ecological interpretation.

During a palynological study of Pliocene carbonate periplatform deposits from the Bahamas (Head and Westphal, 1999), specimens of *Geonettia waltonensis* were looked for. None were found, despite abundance of the other pyrodinioideans, *Polysphaeridium zoharyi* and *Capisocysta lata*. This absence allows conjecture that *Geonettia waltonensis* is not primarily a tropical/subtropical species, at least of carbonate periplatform environments.

In summary, *Geonettia waltonensis* occurs in temperate, neritic environments and seems to be intolerant of cold, perhaps inequable conditions. It is possibly a temperate rather than a tropical/subtropical species, but more records are needed to confirm this assessment. The evidence nevertheless seems consistent with the general observation that pyrodinioideans are warm-water dinoflagellates (Fensome et al., 1993; Head, 1998a).

Discussion.—Regarding the morphology of *Geonettia waltonensis*, the presence of acute projections on the adcingular, dorsally-directed angles of plates in both precingular and postcingular series follows the expected imbrication style for gonyaulacaleans (Fensome et al., 1993, 1996; de Verteuil and Norris, 1996a; Head, 1998a), with plates 3'' and 4'' lacking these projections and so identified as keystones. An analogous situation occurs within the cingular series, the sutures that separate these plates being reverse-sigmoidal, except possibly the 2c/3c boundary which seems to be nearly straight on at least some specimens (e.g., Fig. 8). This reverse-sigmoidal configuration presumably corresponds in some way to plate overlap on the cingular series.

The generic assignment of *Geonettia waltonensis* requires discussion because this species differs from the type, *Geonettia clineae*, in several details of epi- and hypotabulation (see Comparative Morphology of *Geonettia waltonensis*). In particular, Q plates (one or two) described for *Geonettia clineae* are not seen either in *Geonettia waltonensis* or in *Geonettia* sp. These Q plates are notable in *Geonettia clineae* because they are otherwise more or less restricted to the sexiform dinoflagellates, Suborder Gonyaulacineae (de Verteuil and Norris, 1996a).

On the other hand, the hypotabulation in *Geonettia waltonensis* is almost identical to that of *Capisocysta lata*, raising the question as to whether *Geonettia waltonensis* should be placed in *Capisocysta*. However, the archeopyle in *Capisocysta* is restricted to the hypocyst, and its epitabulation is not yet known. Furthermore, the hypotabulation of the type, *Capisocysta wallii*,

is not known in detail (see Head, 1998a). Hence it would be premature at this stage to assign *Geonettia waltonensis* to *Capisocysta* solely because its hypotabulation is similar to that of *Capisocysta lata*.

GEONETTIA sp.

Figures 11–12; Table 1

Dinocyst sp. 1. ANSTEY, 1992, p. 156–158, pl. 10, figs. 1 and 3, text-fig. 12.

Material examined.—Two specimens, one from ODP sample 645E-7R, CC (Site 645 report, in Srivastava et al., 1987); and the other from DSDP sample 603C-37-5, 20–22 cm (Site 603 report, in van Hinte et al., 1987).

Occurrence.—Upper Miocene of ODP Site 645, Baffin Bay (as *Dinocyst* sp. 1 in Anstey, 1992), and uppermost Miocene (upper Messinian) of DSDP Site 603, New Jersey lower continental rise (personal observation).

Discussion.—Two specimens were examined, of which one is illustrated (Figs. 11, 12). This specimen is nearly complete but missing the posterior sulcal plate. A granulate wall surface readily distinguishes *Geonettia* sp. from *Geonettia clineae*, which has a fibroreticulate surface, and *G. waltonensis* which is smooth. The apical pore complex in *Geonettia* sp. is represented by a single ovoidal preapical plate (pr) which has no apparent internal sculpturing. Q plates were not seen. The first apical plate (1') is more similar in shape to *G. waltonensis* than to *G. clineae*, having a concave and moderately long contact with 4'. The separation of 1' from the sulcal plate complex (spc) appears to be a tear rather than a plate boundary, judging from the nature of this contact in other species of *Geonettia*. The cingular plate boundaries are weakly reverse-sigmoidal, as with *G. waltonensis* and to a lesser extent *G. clineae*. The sulcal plate complex (spc) is only observed clearly in the illustrated specimen and gives no indication of the dissociation of constituent plates, although the first postcingular plate (or homologue) is certainly included, forming part of the outline of the spc. The first postcingular plate (1'') is so labelled (rather than its homologue *1'') for ease of comparison with *G. waltonensis*, and subsequent plates are labelled accordingly. The posterior margin of the sulcal plate complex in *Geonettia* sp. could not be resolved with certainty, and the posterior sulcal plate (ps) is apparently missing in the illustrated specimen (Figs. 11, 12). However, there appears to be a small arcuate indentation at one of the corners of 5''' (Fig. 11.2) which would indicate a very short contact with ps. This feature, along with the triangular shape of 6''', suggests a hypotabulation more similar to *G. waltonensis* (and to *Capisocysta lata* and *C. yellii*) than to *Geonettia clineae*.

ACKNOWLEDGMENTS

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APPENDIX: LOCALITY INFORMATION

DSDP Leg 93, Hole 603C.—This hole was drilled at 35°29.78'N; 70°01.86'W in a water depth of 4643 m on the lower slope of the New Jersey continental rise, western North Atlantic (Site 603 report, in van Hinte et al., 1987). Hole 603C has an essentially complete uppermost Miocene through lowermost Pleistocene sequence, represented by about 366 m of hemipelagic, nannofossil-bearing clay/claystone assigned to the Blake Ridge Formation (Haggerty et al., 1987). Age control is based on biostratigraphy, including planktonic foraminifers (Ma'alouleh and Moullade, 1987) and other microfossils (Moullade, 1987), and on magnetostratigraphy (Canninga et al., 1987). A total of 57 samples from this Pliocene-lowermost Pleistocene interval has been analyzed in detail for dinoflagellates (Kolev, 1993; Head and Norris, 1996; Head, unpublished). *Geonettia waltonensis* n. sp. occurs in just two samples, 603C-7-2, 85–87 cm and 603C-8-5, 100–102 cm, from the upper upper Pliocene. Sample 603C-7-2, 85–87 cm is assigned to planktonic foraminiferal Zone PL6 and to the upper part of Chron C2r (just below the Olduvai subchron), and therefore can be dated at about 2.1 Ma. Sample 603C-8-5, 100–102 cm is close to the boundary between planktonic foraminiferal zones PL6 and PL5 and to the middle part of Chron C2r, and can be dated at about 2.3 Ma. *Geonettia* sp. occurs in the single sample 603C-37-5, 20–22 cm, which is assigned to planktonic foraminiferal Zone PL1a, calcareous nannofossil zone CN9b (Muza et al., 1987), and Chron C3r, and therefore can be dated at about 5.3–5.6 Ma (upper Messinian).

ODP Leg 105, Hole 645E.—Drilled at 70°27.48'N; 64°39.30'W in a water depth of 2066 m on the western margin of Baffin Bay (Site 645 report, in Srivastava et al., 1987), Hole 645E was terminated in the lower Miocene with the recovery of a more or less complete ca. 700 m-thick Miocene section. Age control is based mostly on dinoflagellate cysts (Head et al., 1989; Anstey, 1992).

Rockhall Wood, Suffolk, eastern England.—This is the site (52°02'N, 1°22'E) of a classic exposure of the Coralline Crag Formation, subdivided into the Ramsholt and Sudbourne members at this locality. The Ramsholt Member is late early Pliocene in age and is tentatively dated at between 3.8 and 3.6 Ma (latest early Pliocene) based on nannofossils

(see discussion in Head, 1997, 1998b). It consists of silty carbonate sands deposited in warm-temperate seas at a minimum water depth of 50 m (see Hodgson and Funnell, 1987 and Head, 1997 for details). The overlying Sudbourne Member consists of cross-stratified shelly sands with occasional interbedded silty layers. This member is not much younger than the Ramsholt Member and is considered to be early late Pliocene in age (Head, 1997, 1998b). Dinoflagellates have been reported from Rockhall Wood by Head (1997) who examined eight samples: four (labelled NQ1 through NQ4) from the Ramsholt Member, and four (labelled CCS1 through CCS4) from the Sudbourne Member. Rare specimens of *Geonettia waltonensis* occur in all but one of the eight samples examined (Head, 1997, as *Geonettia?* sp.).

Walton-on-the-Naze, Essex, eastern England.—Sea cliffs (51°51'N,

1°17'E) near Walton-on-the-Naze expose marine Pliocene deposits known as the Walton Crag, which have been designated as the Walton Crag Bed of the Red Crag Member and Formation (Funnell and West, 1977). They are assigned to the Reuverian B pollen stage (between 3.0 Ma and a little older than 2.6 Ma) and are therefore early late Pliocene in age (Head, 1998c). The deposits comprise a discontinuous basal horizon of shelly sands overlain by cross-bedded shelly sands that were deposited in up to 20–30 m of water. Head (1998c) reported dinoflagellates in three samples from the basal horizon (samples WC1–WC3) and one sample from a thin, silty layer within the cross-bedded shelly sands (sample WC4). *Geonettia waltonensis* is present in just two samples (WC2 and WC4) where it occurs rarely (Head, 1998c, as “*Geonettia* sp. of Head, 1997”).