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The cyst-theca relationship of *Protoperidinium americanum* (Gran & Braarud) Balech

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ABSTRACT–The cyst-theca relationship of *Protoperidinium americanum* (Gran & Braarud) Balech was investigated using single cyst germination techniques. This *Protoperidinium* has an unusual theca with four intercalary plates (plate formula 4', 4a, 7'', 4c, 7s, 5''', 2''''). It has a distinctive brown capsulate cyst which has an apical archeopyle. The position of this species in the genus *Protoperidinium* is discussed. The distribution of the cyst on the west coast of Scotland is described.

INTRODUCTION

The formation of cysts by dinoflagellates is now well documented (Dale, 1983 and references therein). Investigations of cyst-theca relationships have been carried out over some twenty years (Wall & Dale, 1968a, b; 1969, 1971; Fukuyo *et al.*, 1977; Matsuoka *et al.*, 1982; Lewis *et al.*, 1984). There still remain, however, a large number of relationships to be determined; of 170 cyst morphotypes in Recent sediments, only about 50 have been correlated with their dinoflagellate motile stages (Dale, 1983). Besides scientific curiosity, there are two reasons for such investigations. The first is the improvement in taxonomic understanding that can be achieved (Dale, 1978) and the second is to allow interpretation of the cyst content of the sediment. This sedimentary record is a valuable one as the occurrence of certain dinoflagellate species in the plankton can be short-lived and in low numbers (see for example Braarud *et al.*, 1958). Their presence, however, can more easily be detected from the sediments (Dale, 1976 & 1983; Lewis *et al.*, 1985). Investigations into the ecology and taxonomy of dinoflagellates in Scottish sea-lochs, therefore, include studies of cyst -theca relationships.

The motile cell of *Protoperidinium americanum* (Gran & Braarud) Balech was originally described from the Gulf of Maine and in the same work was reported from the west coast of Ireland (Gran & Braarud, 1935). It has also been reported from the North West of Spain (Gaarder, 1954). A comprehensive description of the species is given by Borgese de Mayer (1983) from South Atlantic ocean specimens. The cyst of the species was informally described by Reid in his thesis (1972) and has been found in Trondheimsfjord, Norway (Dale, 1976, fig. 16) and Japan (Fukuyo, pers. comm.).

METHODS

For the distribution study, sediments were collected from the Scottish west coast using a Craib corer, during the summers of 1982 and 1983. Sampling sites are shown in Fig. 1. For the most part the top 5 cm of sediment was taken and kept at 4°C for later study. For microscopy a small amount of sediment (0.5–0.75 g) was sonicated gently in sea water for 1 minute and then passed through 63 μm and retained on 38 μm sieves using standard amounts of filtered sea water. The material collected on the 38 μm sieve was then washed off into a small amount of filtered sea water and poured into a gridded petri dish for examination under a Wild binocular microscope using $\times 80$ magnification. The distribution of the cysts down a core taken in September 1986 from Loch Creran was also investigated. The core was taken, extruded and sectioned into 1 cm portions which were kept at 4°C for later study. For cyst counting, a small sub-sample (approximately 0.5 g) of sediment was sonicated for two minutes. It was then sieved through a 75 μm sieve and retained on a 20 μm sieve. Material retained on the 20 μm sieve was then washed off into approximately 25 cm^3 of seawater and allowed to settle into exactly 10 cm^3 of seawater. This was thoroughly mixed and two 1 cm^3 aliquots of this suspension were counted in a 1 cm^3 Sedgewick Rafter Chamber using an Olympus model BHS binocular microscope at $\times 100$ magnification. Cyst numbers were converted to a dry weight basis by using a volume correction, the wet/dry weight ratio of the sediment sample and the weight of the mud sub-sample to calculate the number of cysts per gram dry weight of sediment.

Cysts for germination were normally collected in April (i.e. over-wintered) from Loch Creran. Incubation and SEM techniques are as described in Lewis

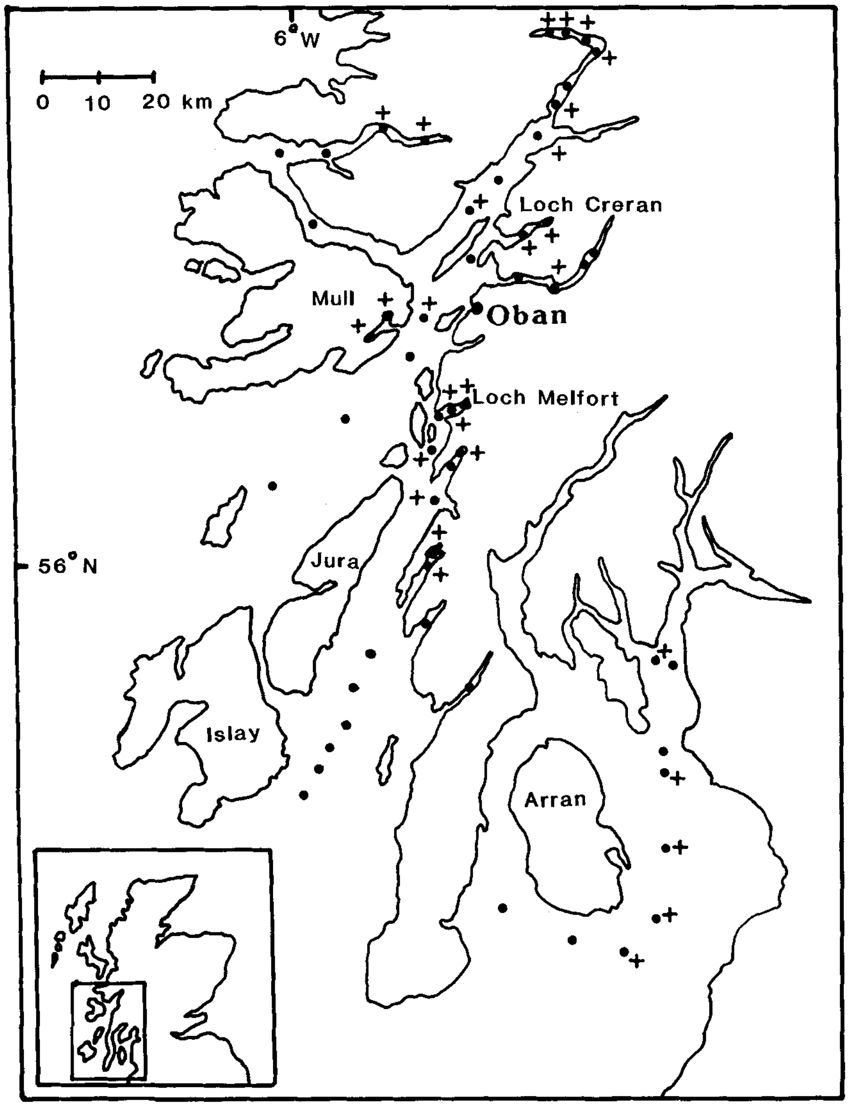

Fig. 1. Map of the west coast of Scotland showing the distribution of *Protoperidinium americanum*. Circles denote stations sampled, + indicates the presence of *P. americanum* in sediment sample.

et al. (1984) with the additional use of a Cambridge S100 and S410 scanning electron microscopes.

OBSERVATIONS

Some people have argued that a separate nomenclature should be retained for dinoflagellate cysts (see for example, Reid, 1974 and Bradford, 1975). It is our feeling that this is unnecessarily complicated and artificial for dinoflagellate cysts belonging to extant species, where sufficient information is available to link stages of the life-cycle (see also Dale, 1978). Although this cyst species was informally described by Reid (unpub. thesis, 1972) as "*Epidinium shagrinum*", it is proposed to describe it here under the name of its motile stage.

Division Pyrrophyta Pascher, 1914
Class Dinophyceae Fritsch, 1929
Order Peridiniales Haeckel, 1894
Family Peridiniaceae Ehrenberg, 1832
Genus *Protoperidinium* Bergh, emend. Balech, 1974
Protoperidinium americanum (Gran & Braarud) Balech
(Pl. 1, figs. 1–8; Pl. 2, figs. 1–6; Fig. 2a–e)

Dimensions. Theca: 30–40 μm long, 28–38 μm wide; 7 specimens measured. Cyst: 35–52 μm across; 20 specimens measured.

Description of cysts. Cysts of this species are very easily recognised. They are capsulate and pale brown in colour. Before excystment they have the typical *Protoperidinium* contents of numerous pale droplets (Pl. 1, fig. 1). The endocyst is spherical. The thick-walled endophragm is composed of two parts, the inner layer is smooth and is overlain by the granular outer layer (Pl. 1, figs. 6, 8). The periphragm is thin, smooth and clear and it fits loosely around the endocyst, in places being pressed close to the endophragm and in others gently folded away (Pl. 1, fig. 5). The folds are not related to any paratabulation, indeed, aside from the archeopyle no paratabulation was evident in the general morphology of the cyst.

The archeopyle is unusual for the genus and is different in the endocyst and the pericyst. The endoarcheopyle is compound polyplacoid (Pl. 1, fig. 4) being composed of three opercular pieces which appear to represent the loss of the second, third and fourth apical paraplates (Fig. 2c). These opercular pieces may remain protuding outwards shortly after excystment (Pl. 1, fig. 3) but they are quickly lost thereafter. In some cases these opercular pieces were seen to have fallen into the cyst. In some specimens that had not excysted but where the contents had decomposed, the principal and accessory archeopyle sutures surrounding each opercular piece were clear. The periarcheopyle is somewhat variable. This, however, may be a secondary effect caused by the thinness of the periphragm which makes it prone to splitting and tearing after excystment. In several specimens, a clear three-way split has been found (Pl. 1, fig. 7) and this possibly is the true archeopyle. This split may represent the parasutures between the apical paraplates, 2', 3', and 4' but in the specimens where this was observed it was not possible to check the orientation of the splits with the endoarcheopyle. Following Evitt (1985), the archeopyle formula is $?/3A_{2-4'}$.

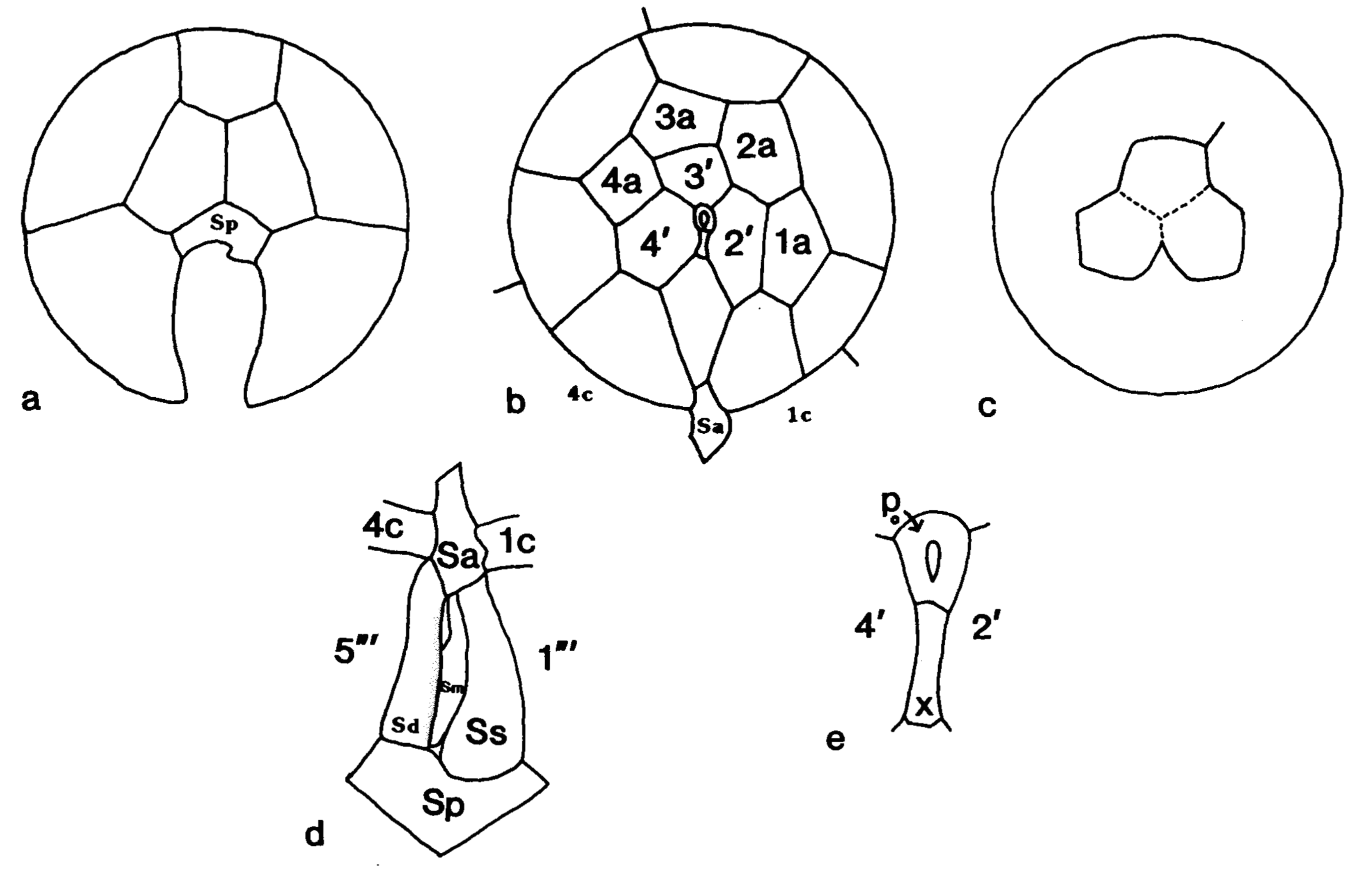

Fig. 2. Line drawings of *Protoperidinium americanum*, those of thecate cell taken from scanning micrographs of seven specimens, that of the cyst taken from light micrographs of eight specimens.

a) Hypothecal tabulation.
b) Epithecal tabulation.
c) Endocyst depicting archeopyle (apical view). Dotted lines denote accessory archeopyle sutures separating the opercular pieces.
d) Sulcal tabulation. Shading represents sulcal wing situated between the Sd and Sm plates. The small unmarked plate at the base of the Sm plate is the Spa plate, that at the top of the plate is the Sdi plate.
e) Apical tabulation.

Like many *Protoperidinium* cysts, that of *Protoperidinium americanum* is not robust and empty specimens from the sediments were frequently found to be flattened. Occasional specimens were noted without the periphragm.

Description of thecae. Some 25 thecate motile cells have been obtained from successful incubations. They frequently rounded off after excystment and did not properly form their theca (Pl. 1, fig. 2). Cells lacked chloroplasts but contained some pale green bodies. The cells are nearly spherical, being slightly longer than wide. The theca is very delicate making plate determination difficult. Plates are smooth with slight undulations which are most noticeable on the hypotheca (Pl. 2, fig. 3). The trichocyst pores are simple holes with an inset 'canon'-like structure (Pl. 2, fig. 7); they are scattered over the plates and were often found in rows along the plate margins (Pl. 2, figs. 4, 5). The girdle is median, very slightly offset and excavated with no list and, apart from the trichocysts, there is no girdle ornament (Pl. 2, fig. 1). It consists of four cingular plates.

The apical pore structure consists of a cover plate (p_0) with a ridge surrounding a tiny pore plate (Pl. 2, fig. 6; Fig. 2e). In most specimens this tiny pore plate had been lost (Pl. 2, figs. 2, 7). A near rectangular canal plate joins the pore plate to the somewhat asymmetrical first apical plates (Pl. 2, figs. 6, 7). The most striking feature of the plate structure of this organism are the four intercalary plates (Pl. 2, Figs. 2, 4). The sulcus is large and indented, reaching the antapex of the cell (Pl. 2, fig. 5). The Sp plate is larger than is usual in *Protoperidinium* species (Pl. 2, fig. 3; Fig. 2b). There is a small sulcal wing situated between the Sd and Sm plate (Fig. 2d). Aside from the intercalary plates, the plate formula was as for a typical *Protoperidinium:* – 4', 4a, 7'', 4c, 7s, 5''', 2''''.

In all respects this description, made with the aid of scanning electron microscopy, tallies with the detailed one given by Borgese de Mayer (1983).

Distribution. The cyst was found in core samples marked in Fig. 1. The highest cyst numbers were found in Lochs Creran and Melfort but these lochs were the most extensively studied (for further details see Lewis, 1985). In addition to the sampling sites shown in Fig. 1, three more northerly lochs were sampled, Lochs Nevis, Hourn, and Torridon. Cysts were found to be present in Loch Torridon. Counts of the sectioned core from Creran showed an increase in total cyst numbers (empty and full cysts) from the top of the core to the bottom (from 1,376 cysts per gram dry weight of sediment in the top 1 cm to 2,175 cysts per gram dry weight of sediment in the 14 cm section).

The thecate cell was never noted in phytoplankton samples from the sites of the distribution study or in Loch Creran during a two year seasonal study of the dinoflagellates.

DISCUSSION

Reid (1972), in his investigation of dinoflagellate cysts around the British Isles, found *P. americanum* most commonly on the west coast of Scotland. It was also present on the east coast of Scotland and around Ireland but was absent from the English Channel and the Bristol Channel. In this study the *P. americanum* cyst was found in most of the sea-lochs sampled and its

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Explanation of Plate 1

Cyst of *Protoperidinium americanum*

Fig. 1. Light micrograph of whole cyst from 14 cm section of Loch Creran depth distribution sampled, Z287. 36 μm across.

Fig. 2. Light micrograph of germinated cyst, in this case the 'gymnodinioid' cell did not survive but rounded off, the cell 30 μm long, cyst from Loch Creran sediment sample, Z68.

Fig. 3. Light micrograph of excysted cyst showing three separate opercular pieces. Cyst 52 μm across, from Loch Creran sediment sample, Z154.

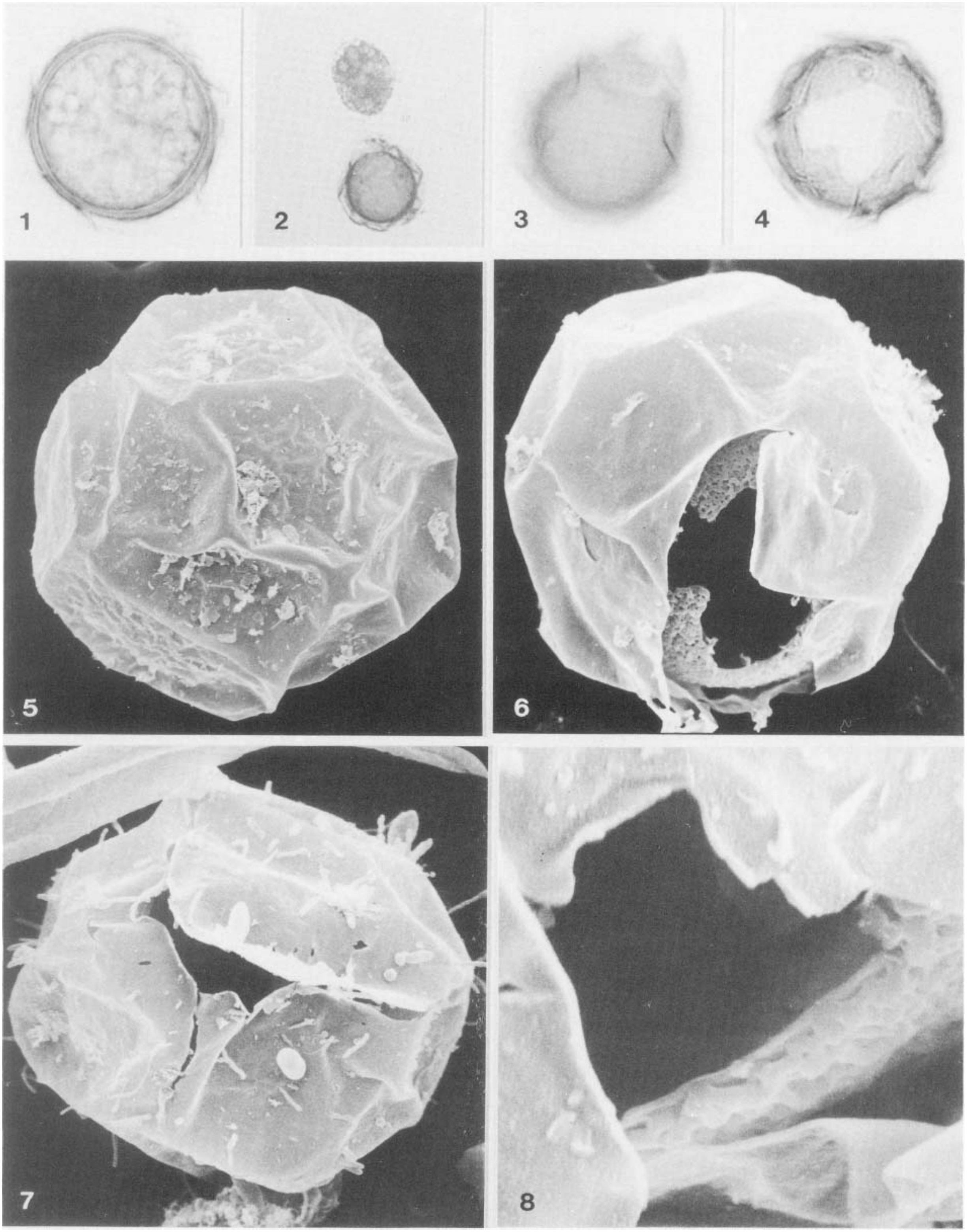
Fig. 4. Light micrograph of empty cyst showing archeopyle of the inner wall, cyst 40 μm across from Loch Creran sediment sample, Z283.

Fig. 5. SEM of whole cyst from Loch Creran sediment sample, cyst 37 μm across.

Fig. 6. Empty cyst showing split in outer wall layer and the archeopyle of the inner layer, cyst 37 μm across.

Fig. 7. Empty cyst showing three way split in the outer wall. Cyst from Loch Creran sediment sample, 38 μm across.

Fig. 8. Empty cyst, showing two layer structure of the inner wall. Cyst from Loch Creran sediment sample ($\times$ 10,000).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absence in other samples is most likely due to the general paucity of cysts in those samples (for example, samples from the Sound of Jura). From the other scattered reports of the thecate stage and the cyst, this species would appear to have a fairly widespread coastal distribution although it is rarely seen in the plankton (Gran & Braarud, 1935; Gaarder, 1954; Borgese de Mayer, 1983; Dale, 1976). Despite extensive counting of the thecate dinoflagellates from water samples from the west coast of Scotland, this species has never been noted (Lewis, 1985). This is possibly becuase of confusion with other species or could be due to its rarity in the water column. The distribution of *Protoperidinium americanum* is clearly most easily discerned by examining bottom sediments. This species does not appear to have been described from the fossil record but as it is fairly delicate, it would probably not preserve well. However, it is perhaps surprising that it was not noted in Harland's distribution survey of Recent dinoflagellate cysts which did record many other *Protoperidinium* species (Harland, 1983).

The structure of this cyst is somewhat atypical of the Recent marine *Protoperidinium* cysts thus far known, none of which are capsulate or have apical archeopyles. The most similar marine cyst is *Dubridinium caperatum* Reid which was established as the cyst of *Diplopeltopsis minor* (Paulsen) Pavillard [= *Zygabikodinium lenticulatum* (Paulsen) Loeblich & Loeblich III] by Wall & Dale (1968a). In *D. caperatum*, however, the wall layers are closely associated, the archeopyle is epicystal and there is also some paratabulation. There are, however, a number of Recent capsulate freshwater cysts, for example *Peridinium limbatum* (Stokes) Lemmermann, investigated by Evitt & Wall (1968) and *Peridinium wisconsinense* Eddy, investigated by Wall & Dale (1968a) but these differ from *Protoperidinium americanum* in having apical and antapical horns, in the presence of paratabulation and in their archeopyles. The archeopyle of *P. wisconsinense* is the most similar, being apical and representing the loss of 2', 3', 4', and part of 1'. It does, however, remain attached ventrally and the paraplates do not separate. The archeopyle of *P. limbatum* is transapical (Wall & Dale, 1968a; Evitt & Wall, 1968). Perhaps the most similar of these freshwater cysts is cyst type D of Norris & McAndrews (1970), it being more rounded than the previous two. Other freshwater *Peridinium* cysts appear to have three walls, for example *Peridinium cinctum f. ovoplanum* Lindemann (Pfeister, 1975) and *Perdinium willei* Huitfield-Kass (Pfeister, 1976). The *P. americanum* cyst would seem to be most closely related to the two-walled freshwater cysts.

The archeopyle is interesting as it differs considerably from the intercalary archeopyles typical of other *Protoperidinium* species. It does not fit in with any of the peridinioid archeopyle types surveyed by Evitt (1985). A 3A archeopyle is, however, figured for a non-peridinioid cyst (fig. 6.9 H) so this type is not unique. The difference in archeopyle in the endophragm and the periphragm indicates that the two walls are structurally independent, fitting into the scheme described by Eaton (1984) for fossil cavate cysts.

The arrangement of the plates of the epitheca and the cingulum are also somewhat atypical for the genus. In *Protoperidinium*, there are normally two or three intercalary plates. The fourth intercalary plate appears to be unique to this species. The first intercalary (1a) could perhaps be regarded as the extra one with respect to the rest of the genus (Fig. 2a). It is unusual in that it touches the first precingular plate (1''), an arrangement found within the genus *Peridinium* (*Peridinium aciculiferum* (Lemmermann) Lemmermann in Bourrelly, 1970) but not *Protoperidinium*. The genus *Peridinium*, however, does seem to have much less conservative epithecal plate arrangements. The cingular plates, although the same in number as other members of the genus, are different in arrangement. The first cingular

Explanation of Plate 2

SEM illustrations of excysted thecate cells of *Protoperidinium americanum*

Fig. 1. Ventral view, cell approximately 35 μm across.

Fig. 2. Apical view of cell in fig. 1, cell approximately 35 μm across.

Fig. 3. Antapical view, cell approximately 35 μm across.

Fig. 4. Ventral/apical view showing first intercalary plate, cell approximately 30 μm across.

Fig. 5. View of sulcus ($\times$ 4,000).

Fig. 6. Apical pore showing tiny pore plate in the centre ($\times$ 9,900).

Fig. 7. Detail of apical pore and trichocyst pores. The outer cell membrane (normally stripped away during SEM processing) is still present in the bottom left hand corner of the picture ($\times$ 11,500).

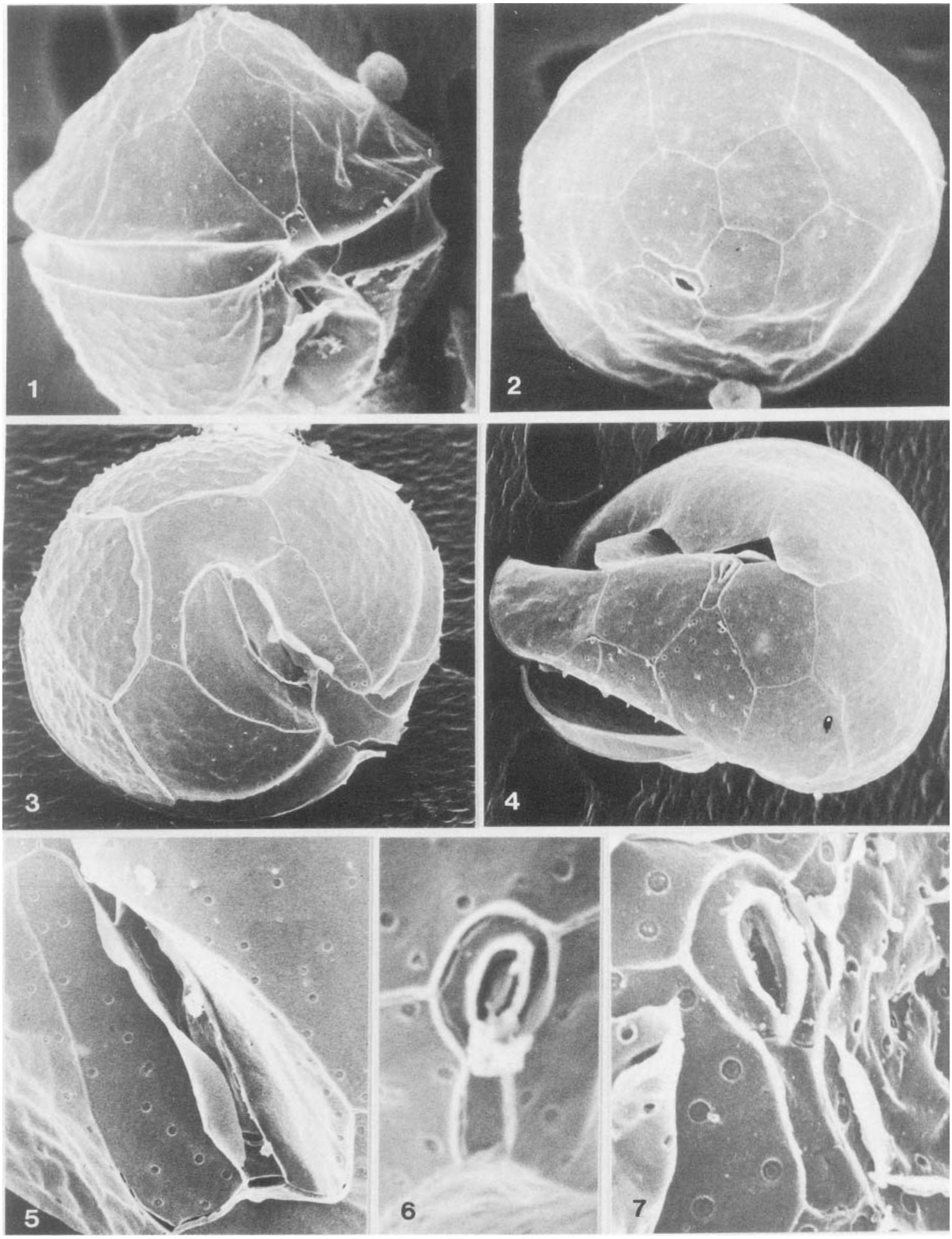
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plate (1c or the T plate of some authors, e.g. Balech, 1974) is much longer than is usual, running from the sulcus, past the first precingular (1″) plate and part way into the second precingular (2″) plate (Fig. 2b). In other *Protoperidinium* species, this area is usually occupied by the first two cingular plates. Consequently, the very large third cingular plate (3c) of other *Protoperidinium* species is replaced by the second and third cingulars in this species; an arrangement analagous to that found in *Peridinium*.

P. americanum clearly has some affinities with *Peridinium* but differs in the number of cingular plates and the lack of chloroplasts. Nevertheless, it is a unique member of the genus *Protoperidinium*. The cyst is atypical in both the archeopyle and general morphology and with the difference in thecal plate tabulation, this raises the question of the position of this species in the genus. However, as at present only one species of this type is known, we feel that any taxonomic revisions should wait for further examples.

An additional problem is that of dual nomenclature. While with fossil species there is a clear need for a separate nomenclature, the case for such a dual nomenclature for Recent cysts is not so clear cut. However, with *P. americanum* the link between the cyst and the thecate stage has been clearly established and each completely described. As Dale (1978, p. 192) concluded, "New cyst-based nomenclature should not be created just to 'artificially' maintain dual classification" and Reid (1974, p. 587) also suggested that the "thecate stage should take precedence for nomenclatural purposes". In conclusion, we feel this cyst should be known as the "cyst of *P. americanum*" as is the case for some other Recent cysts (for example *P. limbatum* and *P. wisconsinense*; Evitt, 1985).

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REFERENCES

Balech, E. 1974. El genero "*Protoperidinium*" Bergh, 1881 ("*Peridinium*" Ehrenberg, 1831, Partim). *Rev. Mus. Cienc. natur., Hidrobiol.*, **IV**, (1), 1–79, figs. I–XXXI.

Borgese de Mayer, M. B. 1983. Un *Protoperidinium* de tabulacion atipica y neuvo para el hemisferio sur (Dinoflagellata). Subsecretaria de estado de ciencia y tecnologia consejo nacional de investigaciones cientificas y tecnicas centro nacional, Peurto Madryn Chubut, **71**, 1–8, figs. 1–17.

Bourrelly, P. 1970 *Les algues d'eau douce*. Intitiation à la systématiques. Collection "faunes et flores actuelles" Tome III: Les Algues bleues et rouges Les Eugléniens, Péridiniens et Crytomonadines. 512pp. Boubée, Paris.

Braarud, T., Føyn, B. & Hasle, G. R. 1958. The marine and fresh-water phytoplankton of the Dramsfjord and the adjacent part of the Oslofjord, March–December 1951. *Hvalråd. Skr.*, Oslo, **43**, 3–102.

Bradford, M. R. 1975. New dinoflagellate cyst genera from the recent sediments of the Persian Gulf. *Can. J. Bot.*, Ottawa, **53**, 3064–3074, figs. 2–28.

Dale, B. 1978. Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in Recent sediments from Trondheimsfjord, Norway. *Rev. Palaeobot. Palynol.*, Amsterdam, **22**, 39–60, figs. 1–3, 1 pl.

Dale, B. 1978. Acritarchous cysts of *Peridinium faeroense* Paulsen: Implications for dinoflagellate systematics. *Palynology*, Dallas, **2**, 187–193, figs. 1–2.

Dale, B. 1983. Dinoflagellate resting cysts: "benthic plankton". *In Fryxell, G. A. (Ed.), Survival strategies of the algae*, 69–136, figs. 1–46, Cambridge University Press.

Eaton, G. L. 1984. Structure and encystment in some fossil cavate dinoflagellate cysts. *J. micropalaeontol.*, London, **3**, 53–64, figs. 1–5, pls. 1–2.

Evitt, W. R. (1985). *Sporopollenin Dinoflagellate cysts, their morphology and interpretation*, xv + 333pp. Amer. Assoc. Strat. Palynol. Found.

Evitt, W. R. & Wall, D. 1968. Dinoflagellate studies IV. Theca and cyst of Recent freshwater *Peridinium limbatum* (Stokes) Lemmermann. *Stanford Univ. Publs., Geol. Sci.*, Palo Alto, **XII**, (2), 1–15, pls. 1–4.

Fukuyo, Y., Kittaka, J. & Hirano, R. 1977. Studies on the cysts of marine dinoflagellates I. *Protoperidinium minutum* (Kofoid) Loeblich. *Bull. Plankton Soc. Japan*, **24**, 11–18, In Japanese with English abstract.

Gaarder, K. R. 1954. Dinoflagellatae from the "Michael Sars" North Atlantic Deep Sea Expedition, 1910. *Rept. Sci. results of the Michael Sars North Atlantic Deep sea exped. 1910*, Bergen, **II** (3), 77 figs.

Gran, H. H. & Braarud, T. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity). *J. Biol. Bd. Can.*, **1**, 279–467.

Harland, R. 1983. Distribution maps of recent dinoflagellate cysts in bottom sediments from the North Atlantic ocean and adjacent seas. *Palaeontology*, London, **26**, 321–397, figs. 1–44, pls. 43–48.

Lewis, J. M. 1985. *The ecology and taxonomy of marine dinoflagellates in Scottish sea-lochs*. Unpub. PhD thesis, University of London.

Lewis, J., Dodge, J. D. & Tett, P. 1984. Cyst-theca relationships in *Protoperidinium* species (Peridiniales) from Scottish sea lochs. *J. micropalaeontol.*, London, **3**, 25–34, figs. 1–2, pls. 1–2.

Lewis, J., Tett, P. & Dodge, J. D. 1985. The cyst-theca cycle of *Gonyaulax polyedra (Lingulodinium machaerophorum)* in Creran, a Scottish west coast seas-loch. *In* Anderson, D. M., White, A. W. & Baden, D. (Eds.), *Toxic dinoflagellates*, 85–90, Elsevier Science Publishing Co., Inc.

Matsuoka, K., Kobayashi, S. & Iizuka, S. 1982. Cysts of *Protoperidinium divaricatum* (Meunier) Parke et Dodge 1976 from surface sediments of Omura Bay, West Japan. *Rev, Palaebot. Palynol.*, Amsterdam, **38**, 109–118, figs. 1–2, pls. 1–2.

Norris, G. & McAndrews, J. H. 1970. Dinoflagellate cysts from post-glacial lake muds, Minnesota (U.S.A.). *Rev. Palaeobot. Palynol.* Amsterdam, **10**, 131–156, figs. 1–5, pls. 1–3.

Pfeister, L. A. 1975. Sexual reproduction of *Peridinium cinctum f. ovoplanum* (Dinophyceae). *J. Phycol.*, Lawrence, Kansas, **11**, 259–265, figs. 1–3.

Pfeister, L. A. 1976. Sexual reproduction of *Peridinium willei* (dinophyceae). *J. Phycol.*, Lawrence, Kansas, **12**, 234–238, figs. 1–13.

Reid, P. C. 1972. *The distribution of dinoflagellate cysts, pollen and spores in Recent marine sediments from the British Isles*. Unpub. PhD. thesis, University of Sheffield.

Reid, P. C. 1974. Gonyaulacacean dinoflagellate cysts from the British Isles. *Nova Hedwigia*, Stuttgart, **XXV**, 579–637, figs. 1–4, pls. 1–4.

Wall, D. & Dale, B. 1968a. Modern dinoflagellate cysts and evolution of the Peridiniales. *Micropaleontology*, New York, **14**, 265–304, figs. 1–7, pls. 1–4.

Wall, D. & Dale, B. 1968b. Quaternary calcareous dinoflagellates (Calciodinellideae) and their natural affinities. *J. Paleontology*, Tulsa, **42**, 1395–1408, figs. 1–3, pl. 172.

Wall, D. & Dale, B. 1969. The "hystrichosphaerid" resting spore of the dinoflagellate *Pyrodinium bahamense*, Plate, 1906. *J. Phycol.*, Lawrence, Kansas, **5**, 140–149, figs. 1–34.

Wall, D. & Dale, B. 1971. A reconsideration of living and fossil *Pyrophacus* Stein, 1883 (Dinophyceae). *J. Phycol.*, Lawrence, Kansas, **7**, 221–235, figs. 1–40.