

PALAEOPERIDINIUM CRETACEUM: A BRACKISH-WATER PERIDINIINEAN DINOFLAGELLATE FROM THE EARLY CRETACEOUS

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ABSTRACT. New SEM observations of topotype material of *Palaeoperidinium cretaceum* from the early Cretaceous of Alberta, Canada have allowed a complete description of this poorly known morphotype, including tabulation and plate overlap patterns. The features displayed by *P. cretaceum* show that, unlike other members of the genus, this morphotype cannot be interpreted as an extrathecal 'exophragm'. The life-cycle stage represented by *P. cretaceum* is discussed in relation to the life-cycle of modern dinoflagellates. It is suggested that *P. cretaceum* may represent a hitherto unknown fossilizable zygotic stage in the dinoflagellate life-cycle.

THIS paper details the unusual morphology displayed by *Palaeoperidinium cretaceum* Pocock (1962) as revealed by the scanning electron microscope (SEM). This morphology is interpreted in the light of recent discoveries regarding this genus and our present knowledge of the dinoflagellate life-cycle.

The genus *Palaeoperidinium* was created by Deflandre (1935, p. 227) to accommodate those dinoflagellate fossils which displayed a similar morphology to that of the modern dinoflagellate genus *Peridinium* (now *Protooperidinium*), but whose tabulation was insufficiently known to allow allocation to an existing genus. No type species was designated and the genus became a 'waiting genus' for incompletely known morphotypes (Sarjeant 1967, p. 242).

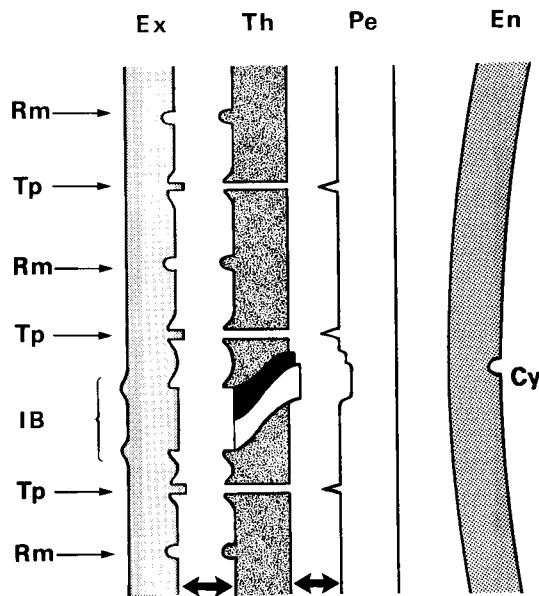
Palaeoperidinium pyrophorum, originally described by Ehrenberg (1838) and allocated to the modern genus *Peridinium*, was selected as the type species of the genus when it was formally emended by Sarjeant (1967).

Interest in the genus *Palaeoperidinium* has been stimulated by the meticulous study of late Cretaceous *P. pyrophorum* (Gocht and Netzel 1976). Utilizing the superior resolution capabilities of the SEM, Gocht and Netzel showed that the prominent sculptural elements of *P. pyrophorum* are located on the internal surface of the fossil and not the external surface as in other known fossil peridiniineans. Previous observations had shown that the dinoflagellate fossil record consisted of intrathecal cysts. Furthermore, tabulation patterns are known to occur on the internal surfaces of modern dinocyst wall layers (cf. *Peridinium limbatum* Evitt and Wall (1968), which led Gocht and Netzel to explain cyst formation and morphology in *P. pyrophorum* in terms of genetic control by the cell protoplast.

However, whereas it does seem reasonable to explain the endocystical tabulation of *Peridinium limbatum* in terms of genetic control (the possibility of the theca acting as a 'template' being precluded), it is unlikely that such a mechanism can be invoked for *P. pyrophorum*. Evitt (1985 pp. 205–207) reasoned that *P. pyrophorum* is unlikely to represent a conventional intrathecal cyst because its single wall layer often contains a two-walled internal body which itself could be interpreted as an intrathecal cyst. He also argued that phenetic influences on the ontogeny of an individual mature theca (represented by pandasutural areas) were unlikely to be found on a body wall independent of the theca. In the case of *P. pyrophorum*, the most elegant interpretation of the negative relief patterns on the internal cyst surface is that they were formed by direct contact with the external surface of the parent theca.

Thus, *P. pyrophorum* was taken to represent a resistant (sporopollenin?) extrathecal structure

(Evitt 1985, p. 206), subsequently termed an 'exophragm' (Evitt *et al.* 1987). The presumed relationships of exophragm, thecal and cyst wall layers can be seen in text-fig. 1. Evitt *et al.* (1987) have subsequently examined *P. basilum* and two as yet undescribed early Cretaceous species and concluded that they too seem to be exophragms. Modern dinoflagellates are not known to produce fossilizable extrathecal wall layers, but some species do form a gelatinous extrathecal sheath (Evitt 1985, p. 206) indicating a mechanism whereby such a layer might be deposited.



TEXT-FIG. 1. Cross-sectional wall layer relationships in a hypothetical dinoflagellate. Ex = 'exophragm', Th = thecal plate, Pm = periphragm, En = endophragm. The first three wall layers are formed closely appressed to one another. The following features are represented in various guises on several of the wall layers: Rm = reticular murus, Tp = trichocyst pore, IB = intercalary growth band, Cy = cell cytoplasm. This cross-section is a composite reconstruction, the 'exophragm' (Ex) is based on that of *Palaeoperidinium pyrophorum*, the thecal plates (Th) on modern *Peridinium*, the periphragm (Pe) on *Subtilisphaera terrula* and the endophragm (En) on modern *Peridinium limbatum* (note parasutural groove on internal surface of endophragm). The plasmalemma, vesicular membranes and pellicle are omitted. N.B., all wall layers shown would not be present at one time.

Palaeoperidinium cretaceum was first described by Pocock (1962) from the Quartz Sand Member of the early Cretaceous Lower Mannville Formation (Imperial McMurray Testhole 6, Alberta, Canada). Davey (1970) made *P. cretaceum* the type species of his new genus *Astrocyta* after studying Albian specimens from the International Yarbo No. 17 borehole, east of Regina, Saskatchewan. Subsequent authors have treated *Astrocyta* as a junior synonym of *Palaeoperidinium* (Lentin and Williams 1976), but Bujak and Davies (1983, p. 134) suggest the retention of *Astrocyta* to accommodate conventional intrathecal cysts presently allocated to *Palaeoperidinium*. More recently the type specimen of *P. cretaceum* has been re-examined by Jansonius (1986).

The present study was prompted by the discovery of abundant specimens of *P. cretaceum*, from 130 ft (39.62 m) in the IGS (now British Geological Survey) Hunstanton Borehole in Norfolk. These specimens were observed during an SEM-based biostratigraphical project on the dinocysts of the western European Barremian (Harding in press). Topotype material of both *P. cretaceum* and '*Astrocyta cretacea*' have been made available to enable an SEM study of this morphotype.

MATERIAL AND METHODS

The topotype material was supplied as a wet residue, prepared following standard palynological techniques, but without oxidation or alkali treatment, in order to keep degradation of this thin-walled taxon to a minimum. Little obscuring amorphous organic matter was present. Other samples mentioned in this paper have been oxidized. For SEM observation, specimens were either strewn-mounted or individually picked via micropipette from an aqueous solution on to squares of X-ray film. This minimizes the loss of morphological definition experienced with standard SEM preparation techniques (e.g. Hughes *et al.* 1979). The specimens were found to adhere well to the moistened emulsion, with no sinking of palynomorphs into the mounting medium. The film squares, most bearing scribed reference grids, were cemented on to aluminium pin-stubs with

cyanoacrylate adhesive, and sputter-coated with gold. Observations were made using a Philips 501B SEM; permanent micrographic records were made on 70 mm Ilford FP4 film.

Residues were stained using Saffranin O, but specimens of *P. cretaceum* showed no coloration. This negative staining reaction has been observed in many types of thin-walled dinocysts, raising the question as to whether they are of the same composition as other 'sporopollenin' dinocysts. Lentin (pers. comm.) suggested that *P. cretaceum* might have a wall composed of chitinous material (*n*-acetylglucosamine). In order to test this possibility a chitin-specific stain was added to the residue. This stain consisted of iodine, potassium iodide and hydrated calcium chloride in distilled water, a positive test turning chitin red-violet (Lillie 1965, p. 503). The test proved negative. This result is perhaps unsurprising, given that hot hydrochloric acid is used in the processing of a palynological residue and that chitinous arthropod exoskeletal cuticle will dissolve in such a medium. The precise composition of the wall of *P. cretaceum* therefore remains unclear.

The following descriptions are based on the examination of the topotype material and use conventional dinocyst terminology (see Evit 1985), although the prefix 'para-' is not used (Norris 1978). Illustrated specimens are held in the Sedgwick Museum, Cambridge, England.

PALAEONTOLOGY AND AGE OF THE SAMPLES

In Hunstanton borehole sample HUN 130 was unique amongst the European samples in yielding abundant specimens of *P. cretaceum*. No more than ten specimens were recorded in total from all of the other localities studied: Speeton (Yorks.), Alford (Lincs.), Warlingham (Surrey) and Gott (West Germany) (Harding in press). The microfungal assemblages isolated from HUN 130 suggested that this sample represents a much nearer-shore environment than the other samples in which *P. cretaceum* only rarely occurred. After a light microscope (LM) count of 200 palynomorphs (slide X413/3) the microfungal composition of the sample was found to be as follows (%): saccate gymnosperm pollen, 39; *Classopollis*, < 1; *Eucommuidites*, 1; large trilete fern spores, 10; small trilete fern spores, 18; angiosperm pollen (*Afropollis*), 2; *P. cretaceum*, 3; other dinocysts, 10; foram. linings, 1; fungal bodies, 2; unidentified 'simple sacs', 13.

The single species of angiosperm pollen present in this sample represents a new species of the genus *Afropollis* (Penny 1989). Twenty-six dinocyst taxa were identified in the sample, most of a very low numerical abundance. The limited dinocyst assemblage and the abundance of terrestrial palynomorphs suggest a strong terrestrial input into a marginal area of deposition – probably a brackish-water environment. The sample is of late Barremian age.

In contrast, the microfungal assemblage in the topotype sample (LM slide JANSONIUS 640/4) gave the following composition after a count of 200 palynomorphs (%): saccate gymnosperm pollen, 14; large trilete fern spores, 2; small trilete fern spores, 6; angiosperm pollen, < 1; *P. cretaceum*, 6; other dinocysts, 7; unidentified 'simple sacs', 64.

This sample has a low-diversity dinocyst flora in which ten taxa have been identified at least to generic level. The dinocysts are dominated by *P. cretaceum* with ceratioids, some similar to those described by Bint (1986), forming the next largest group. The large percentage of unidentified 'simple sacs' precludes making accurate environmental statements. However, the remaining microflora and especially the nature of the dinocyst assemblage (see Bint 1986) suggest a low-salinity (at most brackish) origin for the deposition of this sample. This sample was originally dated as Cretaceous by Pocock (1962), but a more precise estimate of Aptian or Albian age was given by Jansonius (1986). The latter age is favoured here from the presence of tricolpate angiosperm pollen with bimodal luminal sizes and by the ceratioid dinocysts.

The sample from the International Yarbo borehole No. 17 (count of 200 palynomorphs from slide CH238/3) yielded a microfungal assemblage as follows (%): saccate gymnosperm pollen, 4; small trilete fern spores, 7; '*Astrocysta*' *cretacea*, 6; *Ovoidinium ostium*, 16; other dinocysts, 17; unidentified palynomorphs, 50 (poorly preserved).

Ten species of dinocyst have so far been recorded. Identified terrestrial palynomorphs are rare, with a far greater percentage of dinocysts present in the assemblage. This leads to the conclusion that this sample was deposited in an environment in which a more normal marine salinity prevailed than in those discussed above. However, as will be seen later, the dinoflagellate from this sample

which Davey (1970) described under the new genus *Astrocysta*, is not the same morphotype as that from the type sample of *P. cretaceum*. Thus, environmental interpretations derived from the International Yarbo sample are not of significance in assessing the life environment of *P. cretaceum*. The age of the sample is late Albian (Davey 1970).

From the analyses of the first two study samples it appears that *P. cretaceum* occurs in residues isolated from samples deposited in restricted salinity environments. The distribution of this morphotype in samples from restricted environments is also corroborated by some samples from offshore Canada where this species comprises 100% of the dinocyst flora (Lentin pers. comm.). It is perhaps unwise to suggest that *P. cretaceum* was a freshwater species. It does seem reasonable, however, to interpret *P. cretaceum* as being formed by a dinoflagellate which was found in low-salinity marginal environments. The presence of marine dinocysts alongside *P. cretaceum* may be due to taphonomic transport of *P. cretaceum* into these areas (i.e. they are allochthonous), or that the morphotype was euryhaline.

MORPHOLOGY OF *PALAEOPERIDINIUM CRETACEUM*

The most striking feature of *P. cretaceum* is its diaphanous nature. The body wall is only $\approx 0.2 \mu\text{m}$ thick and does not absorb staining compounds. Specimens show strong primary dorso-ventral compression and a distinctive peridinioid ambitus (Pl. 1, fig. 1). The apical region is drawn out into a broad-based, tapering, truncated, apical horn (Pl. 2, fig. 7). The antapical region bears two asymmetrical horns, that on the left being the more pronounced (Pl. 2, fig. 9). The cyst consists of a single thin wall layer, the antapical horns are solid and the apical horn is thickened distally.

Surface features

The majority of specimens do not display well developed tabulation – indeed the surface features of many are negligible or extremely indistinct. Tabulation, when discernible, is more distinct on the ventral surface and the dorsal hypocyst, specimens with clearly expressed dorsal epicystal tabulation being rare. This may be interpreted as indicating that tabulation was originally less well expressed on the dorsal epicyst. However, as so many specimens entirely lack definite surface features, it may be that the dorsal epicyst is more prone to post-mortem degradation than the rest of the cyst. Fortunately, the abundance of *P. cretaceum* in the study sample has allowed a reconstruction of the tabulation of this morphotype.

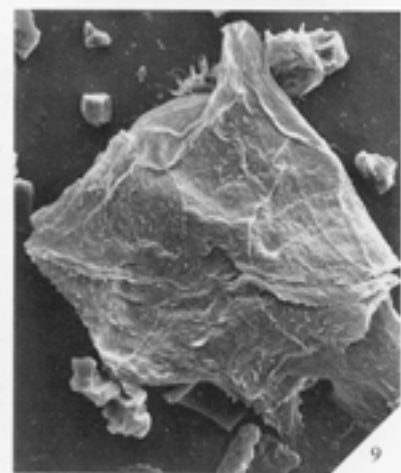
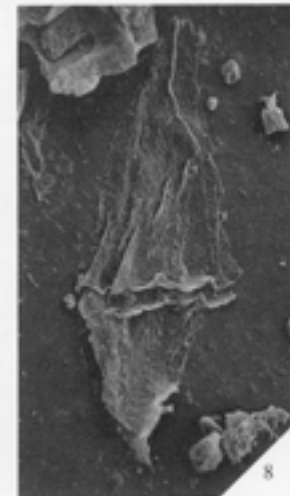
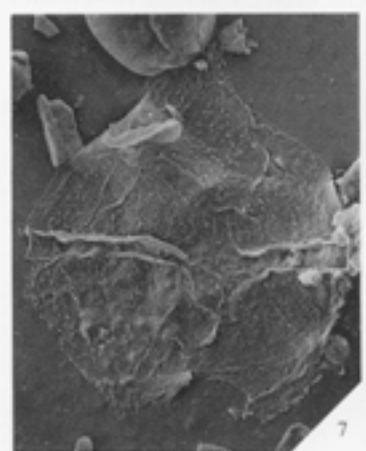
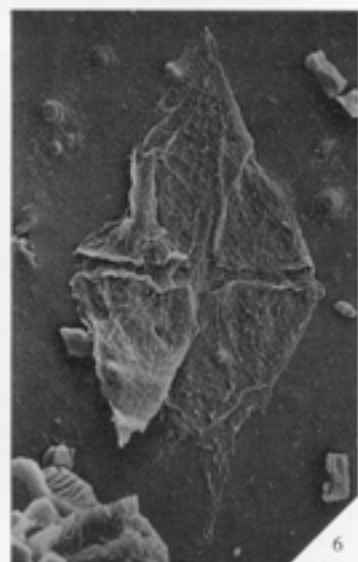
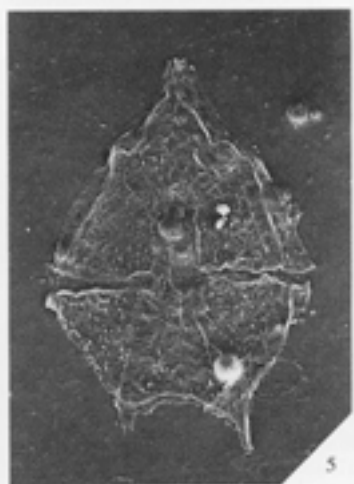
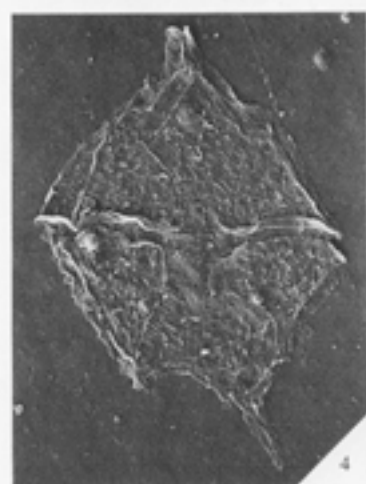
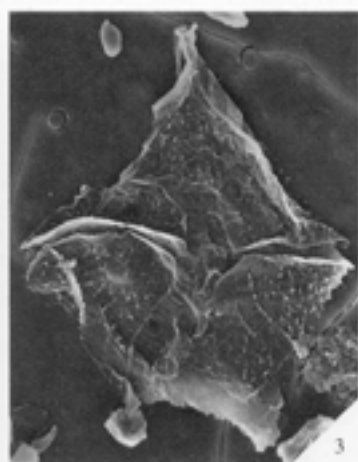
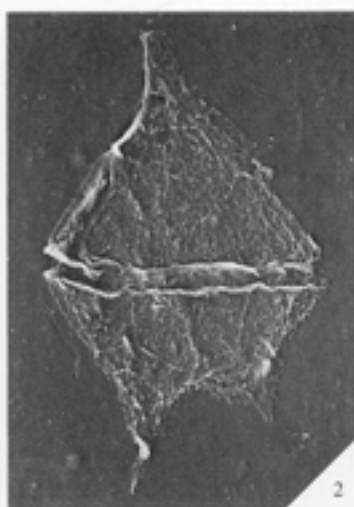
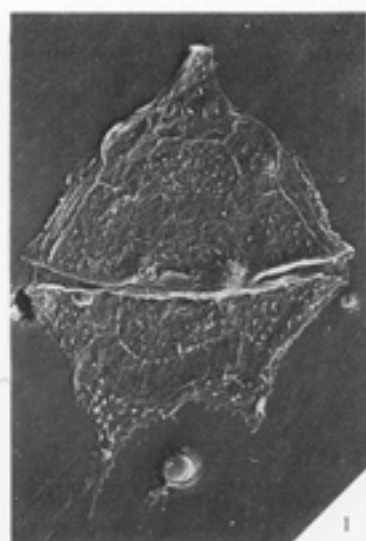
Tabulation is standard ortho-hexa peridinioid type (text-fig. 2), no variation from this pattern having been observed (unlike the aberrant ortho-penta organization found on occasional specimens of *Subtilisphaera terrula* – Harding 1988). The 2a plate is iso-deltaform (Δ , as defined by Bujak and Davies 1985, p. 25).

The ventral epicyst displays a large rhomboidal first apical plate (1', Pl. 2, fig. 7), the anterior margins (1'/2' and 1'/4') of which are delineated by low septa up to $1 \mu\text{m}$ high (arrowed in Pl. 2, fig. 7). Anterior to the first apical plate, the septa run parallel along the lateral margins of a small, axially elongated plate, identified as the canal plate of Dodge and Hermes (1981) (Pl. 3, fig. 5). The distal extremity of the apical horn is encircled by a collar formed by the fusion of the lateral septa. This collar, which often possesses subdued denticulation, surrounds a solid cylindrical or conical projection (Pl. 3, fig. 5).

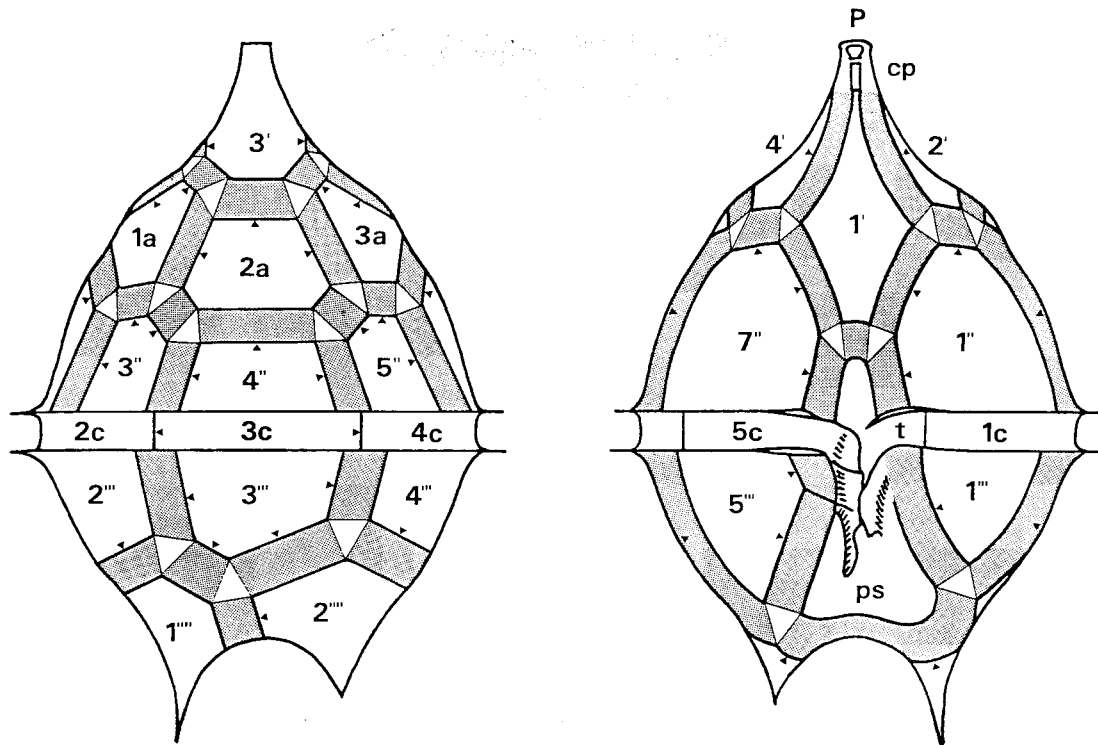
EXPLANATION OF PLATE 1

All figures are from a depth of 640 ft in the Imperial McMurray Testhole 6, Alberta, Canada and preparation JANSONIUS, unless otherwise stated. Also given are the SEM stub numbers (IC-), a 6-figure stub grid reference or specimen number, and film and frame number.

Figs. 1–9. *Palaeoperidinium cretaceum*. Fig. 1, IC517, specimen 1, 3002/72 b. Dorsal view, showing tabulation, $\times 640$. 2, IC517, specimen 2, 3004/72 b. Dorsal view, showing tabulation, $\times 640$. 3, IC447, specimen 1, 3035/73. Ventral view, showing prominent sulcal rostrum, $\times 800$. 4, IC517, specimen 4, 3006/72 b. Ventral view, $\times 640$. 5, IC517, specimen 3, 3008/72 b. Ventral view, $\times 640$. 6, IC458, 133/078, 3013/74. Oblique ventral view, note elongate left antapical horn, $\times 800$. 7, IC456, 114/054, 3027/75. Ventral view, $\times 800$. 8, IC456, 124/064, 3032/75. Left lateral view, $\times 800$. 9, IC448, specimen 14, 3041/73. Ventral view, $\times 800$.



HARDING, *Palaeoperidinium*



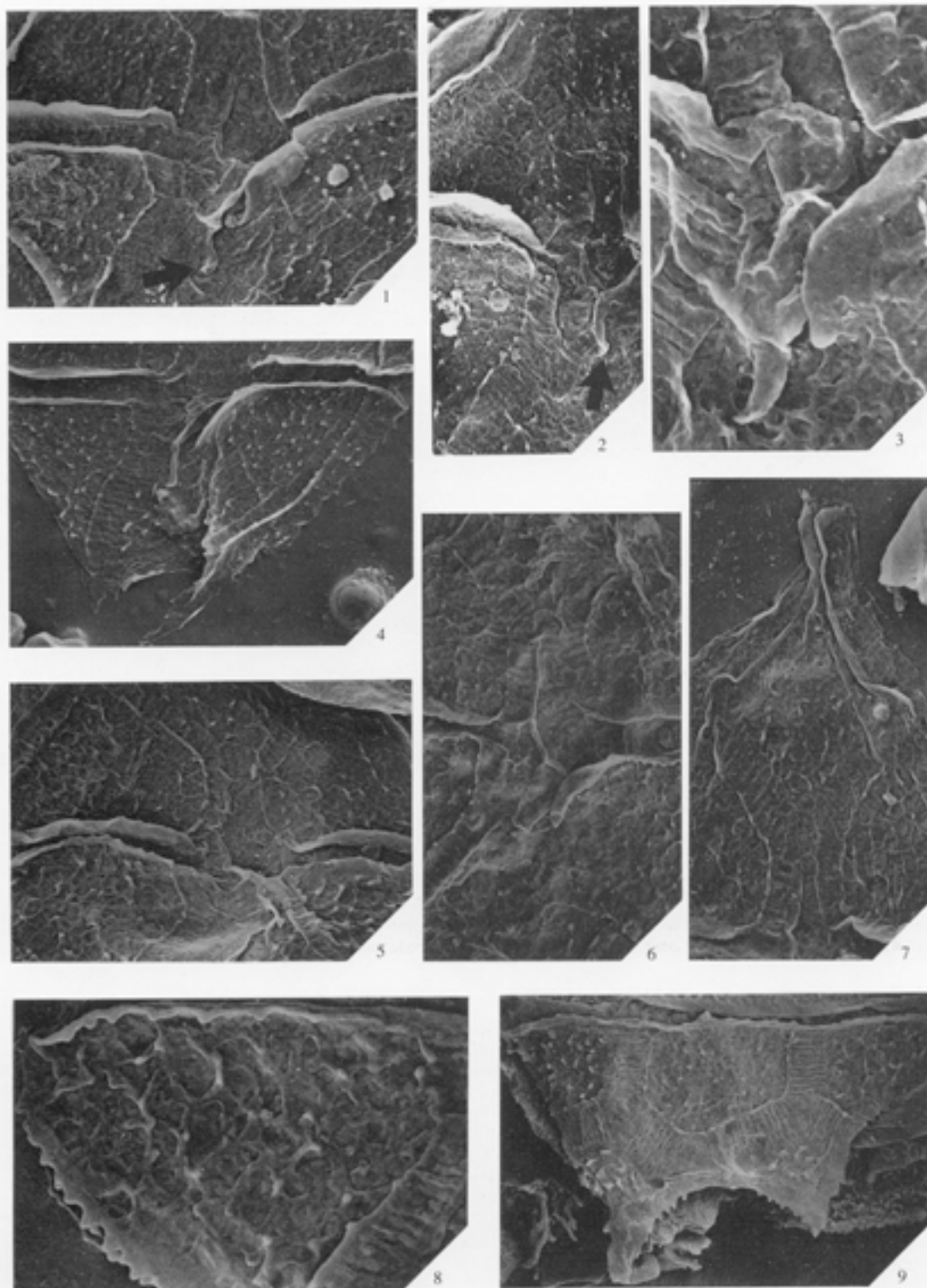
TEXT-FIG. 2. Idealized reconstruction of the tabulation of *Palaeoperidinium cretaceum*, left = dorsal view, right = ventral view. Intercalary bands are stippled. Direction of plate overlap in the thecate organism is shown by the arrowheads, which also indicate the side of the intercalary band which bears the more pronounced bounding ridge. P = apical projection, t = transitional cingular/sulcal plate, cp = canal plate, rostrum indicated by solid arrow, left sulcal list indicated by open arrow.

The planar cingulum is a prominent depression bordered by distally denticulate septa on both posterior and anterior margins, the septa having a maximum height of $\approx 4 \mu\text{m}$ (Pl. 2, figs. 1 and 4). The septa at the right-hand and anterior left-hand terminations of the cingulum decrease in height as they approach the sulcus. However, the posterior left-hand septum is directed antapically into the sulcus, forming what neontologists would call a 'sulcal list' (Pl. 2, figs. 1-6). There is also a similar structure developed on the left-hand margin of the right sulcal plate, this 'list' being extended onto the posterior sulcal plate in the form of a rostrum (Pl. 2, figs. 1-6). This latter 'list' in particular is convex and arches over the left sulcal plate.

The sculpture of the plate area is subdued and reticulate (often very poorly preserved), the junctions of the reticulum (in particular) often bear distal outgrowths of a lobate or conical nature (Pl. 2, fig. 8). These distal

EXPLANATION OF PLATE 2

Figs. 1-9. *Palaeoperidinium cretaceum* Fig. 1, IC449, specimen 1, 3040/73. Ventral view, detail showing high cingular lists, left sulcal list and rostrum (arrowed), $\times 1600$. 2, IC457, 105/031, 3037/75. Ventral view, detail of sulcal area, left sulcal list is well shown (arrow), $\times 1600$. 3, IC447, specimen 1, 3036/73. Ventral view, detail of sulcal area, left sulcal list and rostrum well developed, $\times 3000$. 4, IC449, specimen 7, 3044/73. Ventral view, detail of hypocyst, lists prominent, $\times 1600$. 5, IC456, 168/044, 3024/75. Ventral view, detail of sulcal area, note plate reticulation and cingular lists, $\times 1600$. 6, IC515, specimen 4, 3026/72a. Ventral view, detail of sulcal area, $\times 1600$. 7, IC457, 133/054, 3040/75. Ventral view, detail of rhomboidal 1' plate and apical horn, $\times 1600$. 8, IC458, 127/054, 3017/74. Detail of plate 5''', showing reticulation, $\times 3000$. 9, IC456, 120/050, 3028/75. Dorsal view, showing tabulation, striate intercalary bands and hypocystal ambital denticulation, $\times 1360$.



HARDING, *Palaeoperidinium*

outgrowths give a denticulate outline to the hypocyst ambitus, especially pronounced on the antapical horns (Pl. 3, fig. 2 – this feature is not seen on the epicyst as the ambitus here is occupied by plate-bounding septa).

All specimens displaying tabulation possess intercalary ('pandasutural') bands. These bands are prominent, plate-bounding areas $\approx 4 \mu\text{m}$ in width with strongly developed cross-striations (Pl. 2, fig. 9) except at the triangular junctions between adjacent intercalary bands (Pl. 3, fig. 6). There is no evidence of a feature reflecting a suture-plane between adjacent plates. The two lateral margins of an individual intercalary band are dissimilar. One margin is bordered by a low ridge, often distally denticulate especially on the hypocyst (Pl. 2, fig. 9). This ridge is developed into the lateral septa found on the ventral epicyst. The opposite margin has a less distinct boundary, but in some instances may appear to be folded over the adjacent plate area. This differential development of intercalary band margins clearly reflects the mode of thecal plate overlap. Netzel (1982) showed that one of the methods for analysing the direction of plate overlap was to recognize an overlapping plate margin by the development of crests or ridges of differing heights. In the case of *P. cretaceum*, the margin of the intercalary band bearing the denticulate ridge can be identified as the overlapping plate, allowing the reconstruction of the overlap pattern (text-fig. 2). This reconstruction shows that the keystone (Evitt 1985) or ridge-tile (Netzel 1982) plates are 4" and 3", the conventional arrangement for modern peridinioid dinoflagellates. This contrasts with the arrangement determined for the early Cretaceous dinocyst *Subtilisphaera terrula* (Harding 1988), in which the 3" and 3" plates were involved.

The archaeopyle

A low percentage of specimens (10% of 200 specimens observed in LM) have been discovered which display an archaeopyle, but this may be due in part to the nature of the opening. Jansonius (1986) described the archaeopyle found on the holotype of *P. cretaceum* as being A313Pa (3', 1–3a, 3–5"). This is a transapical archaeopyle (Bujak and Davies 1983, p. 21). This definition shows that the dorsal epicystal plates remain attached, as a compound operculum, via the cingulum to the rest of the cyst after release of the cell contents. Thus, theoretically, the presence of an archaeopyle can only be recognized when this operculum is laterally displaced (as in the holotype) or is removed mechanically. However, those specimens illustrated in Pl. 3, figs. 5, 6, 11, show no sign of a mechanical removal of the operculum, a conventional suture accounting for the loss of the operculum. Furthermore, specimens have been found which appear to show the initiation of the archaeopyle suture along the precingular–cingular junction (Pl. 3, fig. 4). It may be inferred from this that the archaeopyle type in *P. cretaceum* is A313P, hemiepicystal rather than transapical, the operculum sometimes remaining adnate along the cingulum (*sensu* Evitt 1985).

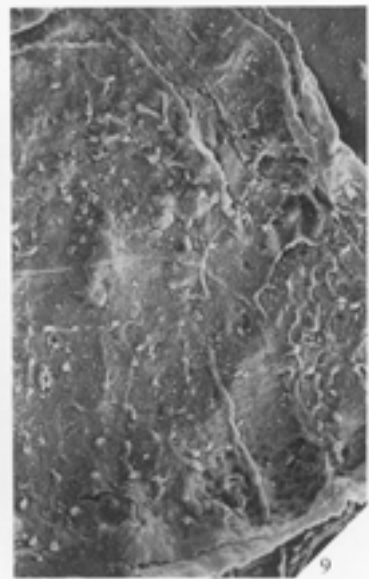
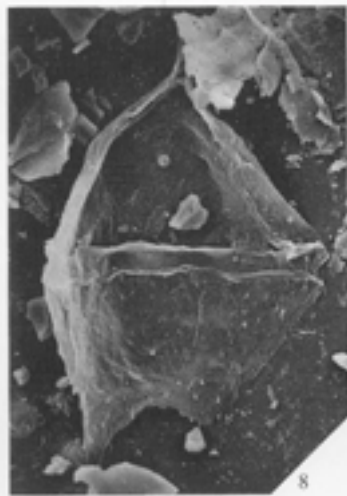
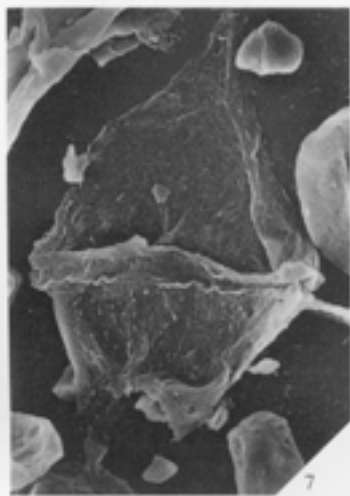
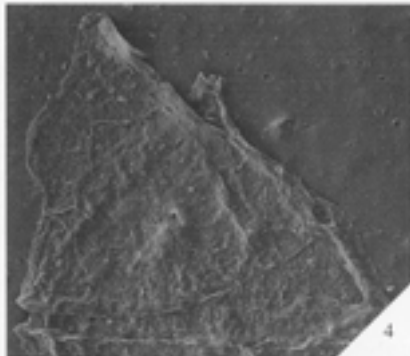
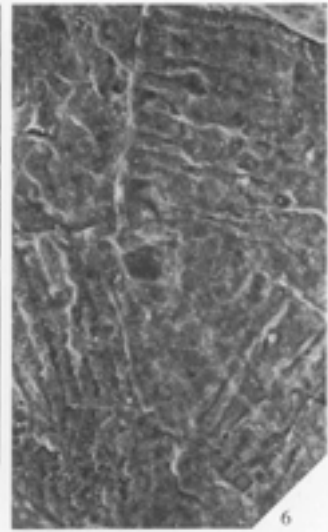
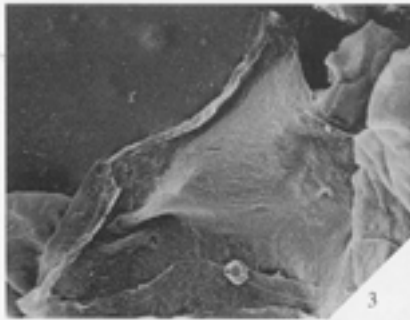
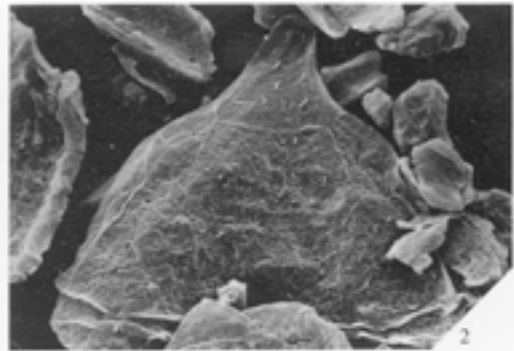
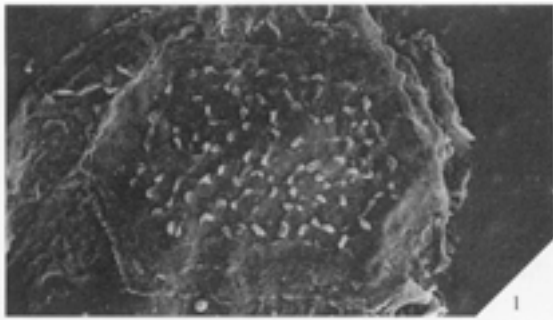
It should be noted at this point that on specimens from which the operculum has been lost, the inner surface of the body wall can be examined. In all instances the inner surface has been found to be devoid of sculpture, even when tabulation is expressed on the external surface of the body wall (Pl. 3, figs. 3, 7, 8).

AFFINITIES

Palaeoperidinium cretaceum, based on the morphology described above, belongs to the tribe Palaeoperidinioideae of Bujak and Davies (1983). Further elucidation of its affinities can be made by determining the number of cingular plates developed. Boltovskoy (1979) showed a strong

EXPLANATION OF PLATE 3

Figs. 1–9. *Palaeoperidinium cretaceum*. Fig. 1, IC456, 106/035, 3026/75. Dorsal view, detail of deltaform 2a plate, intratabular reticulum subdued although distal outgrowths from this reticulum are prominent, $\times 2400$. 2, IC456, 146/007, 3001/74. Dorsal view, detail of epicyst, note 2a plate, $\times 1040$. 3, IC475, 146/077, 3001/74. Dorsal view, detail of epicyst showing archaeopyle, note lack of ornamentation on the interior of the epicyst, $\times 1200$. 4, IC515, specimen 5, 3027/72a. Dorsal epicystal detail showing operculum detached along the cingulum, $\times 880$. 5, IC457, 124/037, 3038/75. Ventral view of apical horn showing canal plate and apical projection, $\times 3000$. 6, IC517, specimen 5, 3009/72 b. Detail of triple junction between adjacent striate intercalary bands, $\times 3000$. 7, IC457, 104/076, 3035/75. Dorsal view, archaeopyle well displayed, $\times 800$. 8, IC457, 117/059, 3036/75. Dorsal view, archaeopyle well displayed, $\times 800$. 9, topotype specimen of '*Astrocysta*' *cretacea*. IC513, specimen 3, 3028/72a. Detail of dorsal epicystal intercalary bands, note lack of striation, $\times 1600$.



HARDING, *Palaeoperidinium*

correlation between the number of cingular plates and the nature of the intercalary bands found in the adcingular plate series amongst modern dinoflagellates. From the six broad intercalary bands of *P. pyrophorum* (then still believed to be a cyst), Boltovskoy inferred the presence of six cingular plates. Bujak and Davies (1983) later reinterpreted this cingular tabulation as being one transitional cingular/sulcal and five cingular plates. According to the method outlined by Boltovskoy (1979), *P. cretaceum* should also have five cingulars and a transitional plate. However, Taylor (1987, p. 52) has pointed out that Boltovskoy's method is fallible, as some modern species of *Protooperidinium* have only three cingulars but produce six broad intercalary bands. Hence, Boltovskoy's method is an unreliable way of determining the number of cingular plates in modern dinoflagellates and it seems unwise to apply it to fossil cysts as suggested by Bujak and Davies (1983, p. 35). Greater use of SEM observation is likely to allow the number of cingular plates in fossil dinocysts to be determined with more certainty. This study shows that the cingular tabulation of *P. cretaceum* is the same as that represented on the exophragm of *P. pyrophorum*.

P. cretaceum, therefore, is a peridiniinean characterized by an ortho-hexa style of tabulation, a linteloid second anterior intercalary plate and an epicystal tabulation displaying symmetry about the dorsal midline. These features clearly show that *P. cretaceum* is morphologically more closely related to the modern freshwater genus *Peridinium sensu stricto* than to the marine genus *Protooperidinium* (which has only three cingular plates). The dorsal epicystal symmetry narrows this attribution further to the bipesioid group of *Peridinium sensu stricto*, the cinctioid group having no such symmetry (Bujak and Davies 1983). *P. cretaceum* is the oldest peridiniinean dinoflagellate fossil described from sediments deposited in environments of less than normal marine salinity. Peridiniinean dinocysts have not previously been *conclusively* identified in such sediments prior to the Oligocene, although other groups of dinocysts have now been reported from reduced salinity environments of the early Cretaceous of southern England (Hughes and Harding 1985; Batten 1985; Lister and Batten 1988), the USA (Bint 1986) and China (Lentin *et al.* 1988).

SYSTEMATIC PALAEOLOGY

Genus PALAEOPERIDINIUM Deflandre (1935) emend. Sarjeant (1967)

Palaeoperidinium cretaceum Pocock (1962)

- 1962 *Palaeoperidinium cretaceum* Pocock, p. 80, pl. 14, fig. 219.
 1970 *Astrocysta cretacea* (Pocock); Davey, p. 359.
 1986 *Palaeoperidinium cretaceum* Pocock; Jansonius, p. 214, pl. 5, fig. 6.

Emended diagnosis. Shape. Typically pentagonal peridinioid ambitus. Prominent broad-based apical horn, two antapical horns of which the left-hand is the more pronounced. Epicyst usually longer than hypocyst. Greatest width across cingulum. Strong primary dorso-ventral compression. *Phragma.* Autophragm, very thin ($\approx 0.2 \mu\text{m}$ thick), when well preserved shows corrugated intercalary bands delineating tabulation. Septa developed bordering cingulum, sulcus, ventral apical region. Plate areas have subdued reticulate sculpture. *Tabulation.* Ortho-hexa peridinioid type, 4', 3a, 7'', 5c, 5''', 4s. Iso-deltaform second anterior intercalary. Apical structure indicates an apical pore plate and a small ventral canal plate. A cingular/sulcal transitional plate also present. *Archaeopyle.* Type (A313P), hemiepicystal, operculum often remains adherent along the cingulum. *Cingulum.* Planar, with five plates and one transitional. Bordered by distally denticulate septa. *Sulcus.* Consists of four plates; right sulcal plate bears a convex sulcal 'list' which is prolonged onto the posterior sulcal in the form of a rostrum. Less prominent 'list' is found on the left sulcal.

Dimensions. Length = (68) 80 (101) μm . Number of specimens measured = 30.

Remarks. The description of this species is revised following the examination of topotype material. Although the type species of the genus has been shown to be a fossil of extrathecal origin, *P. cretaceum*, is retained in the same genus. Bujak and Davies (1983) suggested that the genus

Astrocysta Davey be retained for those species of *Palaeoperidinium* which were shown not to be extrathecal structures. This practice is unnecessary as there is an obvious phylogenetic relationship between the taxa. Such a practice would lead to the same problems of dual nomenclature presently experienced with modern motile dinoflagellates and their corresponding cyst stages.

The morphotype described by Davey (1970) as the type of his new genus *Astrocysta* is not synonymized with *P. cretaceum* in this work. Unfortunately, the poor preservation of the Saskatchewan topotype specimens does not suit them to SEM analysis, but the resulting micrographs do show that the morphotype is a conventional intrathecal cyst and not an 'exophragm' (Pl. 3, fig. 9). The morphology of the cyst does reveal that '*Astrocysta*' is a junior synonym of *Palaeoperidinium* (as envisaged above). Measurement of twenty-two specimens of '*A. cretacea*' has resulted in the following: length = (90) 112.5 (135) μm . The minimum and maximum dimensions comply with those given by Davey (1970), but the mean of Davey's measurements is 10 μm less than that determined here from a greater number of specimens. Thus, the average specimen from Davey's material is a full 30 μm (37.5%) longer than the average specimen of *P. cretaceum*. Whilst this could indicate an evolutionary increase in the size of the organism through Albian time, it is felt more likely that the morphotype described by Davey (1970) is referable to a separate taxon, albeit within the genus *Palaeoperidinium*. Judging from the associated palynoflora, '*Astrocysta cretacea*' appears to have occupied a more saline environment than *P. cretaceum*.

NATURE OF THE FOSSIL

The general morphology of *P. cretaceum* presents an aspect unlike that of most cyst-types, in that it appears to be outwardly similar to the motile, thecate stage of many modern peridiniinean dinoflagellates. This raises the question: which stage in the dinoflagellate life cycle does *P. cretaceum* represent?

SEM examination reveals that sculptural elements on the body wall of *P. cretaceum* are located on the external surface, the internal surface being laevigate (e.g. Pl. 3, fig. 3). In this respect it is unlike other recently studied species currently placed in this genus (Gocht and Netzel 1976; Evitt *et al.* 1987). *P. pyrophorum* is also known with internal bodies which have been interpreted as conventional intrathecal hypnozygotic cysts (Evitt 1985). Pocock (1962; p. 80) mentioned that occasional specimens of *P. cretaceum* contained 'spherical cysts' but an LM study of 200 specimens for this study has not revealed any such structures. It would therefore appear that *P. cretaceum* is not an extrathecal mould or exophragm.

The striking morphology of *P. cretaceum* allows comparison with the motile thecate stages of modern dinoflagellates, in the same manner as Evitt (1985, pp. 267–268) likened fossil *Dinogymnium* and modern *Gymnodinium*. There is a strong resemblance between the *P. cretaceum* and modern peridiniinean thecae. Evitt (1985) stated that for the two gymnodinioid genera previously mentioned, there is 'complete compatibility between the form of the depressions here considered to be flagellar furrows and actual occupation of the depression by flagella of design and function typical for dinoflagellates'. However, the presence of an archaeopyle in *P. cretaceum* would argue against interpretation as a vegetative theca. In this case, the 'archaeopyle' may be interpreted as an ecdysial opening formed in the vegetative theca to allow release of the cell contents in response to vegetative reproduction (eleutheroschisis) or adverse conditions. Boltovskoy (1973) detailed ecdysial openings (which he erroneously referred to as 'archaeopyles') in several modern *Peridinium* species. A strong correlation exists between the plates involved in thecal ecdysial openings and those involved in archaeopyle formation.

Against interpretation of *P. cretaceum* as a vegetative motile stage are the facts that the theca would have to have been impregnated with sporopollenin or a similar resistant organic compound, a feature unknown amongst modern thecae, and that pore-structures representing trichocyst pores, apical pore complexes and flagellar pores were not detected on the fossil. The first condition may not be a difficulty given that 'diversity is the hallmark of dinoflagellates' (Evitt 1985, p. 268) and that other types of sporopollenin-impregnated membranes occur in the palaeoperidinioid lineage.

More serious is the presence of a cylindrical projection at the end of the apical horn, where a pore might be expected. This projection is similar to the first preapical (P) plate of cribopteridinioid dinocysts which has been interpreted as a plug-like infilling of the apical pore (Evitt 1985, p. 75). The lack of trichocyst pores and flagellar pores is similarly disquieting. Also, if *P. cretaceum* were a thecate organism, the thecal plates would have dissociated when subjected to Javelle water (discounting the unknown effects of diagenesis or sporopollenin impregnation). This is not the case. Thus, it seems unlikely that *P. cretaceum* represents a fossilized vegetative theca.

If not a vegetative thecate stage, is it possible that *P. cretaceum* might represent an individual, resistant component of the dinoflagellate amphiesma (as defined by Loeblich 1970)? The pellicle is the only component of the amphiesma in modern dinoflagellates with any likelihood of being fossilized. The pellicular layer is found in modern thecate dinoflagellates lying inside the vesicular layer, which encloses the thecal plates (Loeblich 1970, see also text-fig. 1). Pellicles are possessed by most thecate dinoflagellates and many are acid-resistant (Morrill and Loeblich 1981). Modern species, especially of *Peridinium*, have acetolysis-resistant pellicles with a presumed sporopollenin component in their fibrous wall-structure (Morrill and Loeblich 1981).

The pellicle and the inner vesicular membrane form the outer wall of ecdysial cysts (also referred to as temporary, vegetative and pellicular cysts) after the shedding of the theca (see Dürr and Netzel 1974 and the 'spheroplasts' of Adamich and Sweeney 1976). The pellicular layer has fossilization potential, but lacks prominent sculptural features other than subdued ridges and pore openings. The simple sac-like morphology of modern dinoflagellate pellicles argues against *P. cretaceum* being a fossilized pellicular layer or an ecdysial cyst.

From the discussion above, interpretation of *P. cretaceum* as a stage in the vegetative part of the dinoflagellate lifecycle cannot be accepted. Thus it must represent part of the sexual phase: the planozygotic theca, the hypnozygotic theca or the hypnozygotic cyst. Corroboration of the involvement of the sexual phase is given by the broad intercalary bands of *P. cretaceum*. Studies by Pfeister and Skvarla (1979, 1980) of the vegetative and sexual theca of species of modern *Peridinium* have shown that, at most, vegetative thecae produce only very narrow intercalary bands. It is the plano- and hypnozygotic thecae that display extremely broad intercalary bands, indicating plate growth to accommodate the growing cell protoplasm.

It seems improbable that the fossil can be identified as a conventional hypnozygotic cyst as the surface features are incompatible with the wall layer having been deposited beneath the amphiesmal vesicles. The cyst of *Subtilisphaera terrula* clearly shows evidence of having been formed adpressed to the inside of the thecate organism (Harding 1988), but the thin, delicate cingular and sulcal 'lists' of *P. cretaceum* are entirely compatible with their having been functional and thus external features.

P. cretaceum appears to represent a resting stage, presumably formed after sexual reproduction, but its morphological features argue against it being viewed as a conventional subthecal hypnocyst. Given our relative lack of knowledge regarding present-day zygotic cysts, it is suggested that *P. cretaceum* may be a hitherto unknown fossilizable zygotic stage in the dinoflagellate life-cycle. Given the structural innovations already known within the lineage containing *P. cretaceum*, and the morphological experimentation (especially with archaeopyle types – Bujak and Davies 1983) amongst early Cretaceous Peridiniineae, this conclusion may not be an entirely untenable notion.

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This manuscript was submitted before the recent presentation on *Palaeoperidinium* given by Evitt *et al.* (1989) at the DINO4 conference at Woods Hole, Massachusetts. This elegant presentation used sophisticated microcasting and SEM image-processing techniques to reveal the details of the internal surface of specimens referred to *Palaeoperidinium pyrophorum*. The internal surface of *P. cretaceum*, studied using scanning electron microscopy, has not revealed any similar features to those displayed by the material illustrated at DINO4. Further investigation has failed to identify any internal membrane/conventional cyst wall addressed to the internal surface of the wall of *P. cretaceum* which could obscure such features. The evidence presented is that *P. cretaceum* represents a dinoflagellate fossil of a different organizational nature to those described by Evitt *et al.* (1989).

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