

Re-study of some dinoflagellate cysts from the Oligocene and Miocene of Germany

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ABSTRACT—The type material of six dinoflagellate cyst species from the Late Oligocene to Middle Miocene of northwest Germany, described originally by Gerlach (1961), is reillustrated and redescribed. It is shown to include representatives of nine species. *Areosphaeridium* (ex: *Baltisphaeridium*) *pectiniforme* is found to be a senior synonym of *Areosphaeridium multicornutum* Eaton. *Systematophora placacantha* is considered to be a senior synonym of *Cleistosphaeridium* (ex: *Baltisphaeridium*) *panniforme* (Gerlach). The new combination *Rhynchodiniopsis tenuitabulata* (Gerlach) is proposed. Revised diagnoses for these three species and for *Leptodinium membranigerum* (Gerlach), *Achomosphaera triangulata* (Gerlach) and *Lejeunecysta hyalina* (Gerlach) are proposed. The morphology of a form described here for the first time, and tentatively attributed to *Phthanoperidinium*, is considered perhaps to imply a separate origin for the Phthanoperidiniaceae: for that reason familial, rather than tribal, rank is preferred for that group. The stratigraphical ranges of the nine species here recognised and of two others of Gerlach's species redescribed in earlier papers are detailed; elimination of misattributed forms means that these ranges are shorter than the published literature suggests.

INTRODUCTION

The history of early studies of Oligocene and Miocene dinoflagellate cysts has been summarised in an earlier paper (Sarjeant, 1983). Whilst Dorothea Maier was completing her studies of cysts from borehole cores and outcrops in the Niederrheingebiet, Nordrhein-Westfalen, Schleswig-Holstein and Jutland (Denmark) at the University of Kiel, Ellen Gerlach was examining assemblages from two boreholes through sediments of similar age in the Emsland region of northwest Germany at the University of Tübingen. Maier found extreme difficulty in dealing with the diverse morphologies with which she found herself confronted and her research supervisor, Walter Wetzel, had too poor a comprehension of these microfossils (as his own papers make evident; see Wetzel, 1952, 1955) to give her the guidance she needed. In contrast, though Ellen Gerlach's research supervisor, Otto Schindewolf, was not himself a micropalaeontologist, she had the great advantage of being able to consult Alfred Eisenack for advice when in difficulties. In consequence, whilst Maier's work (1959) was to occasion confusion among other palynologists and to be the focus for much criticism, Gerlach's single paper (1961) was of higher quality and has proved of greater utility.

Four new genera were proposed by Gerlach. One of these, *Pentadinium*, has come to be regarded as of great importance in Tertiary stratigraphy (see Benedek, Gocht & Sarjeant, 1982 and Edwards, 1982, for recent interpretations). Another, *Lejeunia*, proved to be the

junior homonym of a modern liverwort (see Artzner & Dörhöfer, 1978). However, under the substitute name *Lejeunecysta* Gerlach's genus remains one that is widely recognised; its type species is reillustrated, and its distribution discussed, herein. Her third genus, *Membrano-phoridium*, fell into disuse but has been effectively reinstated by Stover & Evitt (1978), under a revised definition. A misunderstanding concerning the morphology of her fourth genus, *Emslandia*, caused it to be formally abandoned for a while; however, recently it has been likewise reinstated under a revised definition (Benedek & Sarjeant, 1981).

In contrast, the species assigned by Gerlach to genera already proposed before 1961 have fallen largely into disuse; only one of them, *Spiniferites* (ex: *Hystrichosphaera*) *cornutus* (Gerlach, 1961) Sarjeant, 1970, has been regularly reported. There are three reasons for this: first, because the advances in knowledge of dinoflagellate cysts since 1961 mean that her diagnoses can be no longer considered adequate for confident identification of those taxa; second, because her illustrations were produced at too small a magnification; and third, because her holotypes and paratypes are, in some instances, markedly dissimilar in morphology.

My work on Gerlach's holotypes was undertaken during visits to the University of Tübingen in 1979 and 1981. During those visits, I received continuous and courteous co-operation from Dr. Hans Gocht, many of whose perceptive comments are reflected in the pages that follow. Six of Gerlach's species are reillustrated,

and five of them redescribed, herein; nine taxa are recognised among them. I hope to complete work on her other types during a future visit to Tübingen.

The seventeen samples from which Gerlach's assemblages were obtained stemmed from two shallow borings,

Emsbüren 7 (mapsheet Lohne 3509, R = 2586100/H = 54812830) and Emsbüren 9 (mapsheet Lohne 3509, R = 2588090/H = 5808343), put down through the Oligocene and Miocene sediments of Hannover in the triangle of land bounded by Nordhorn, Lingen and

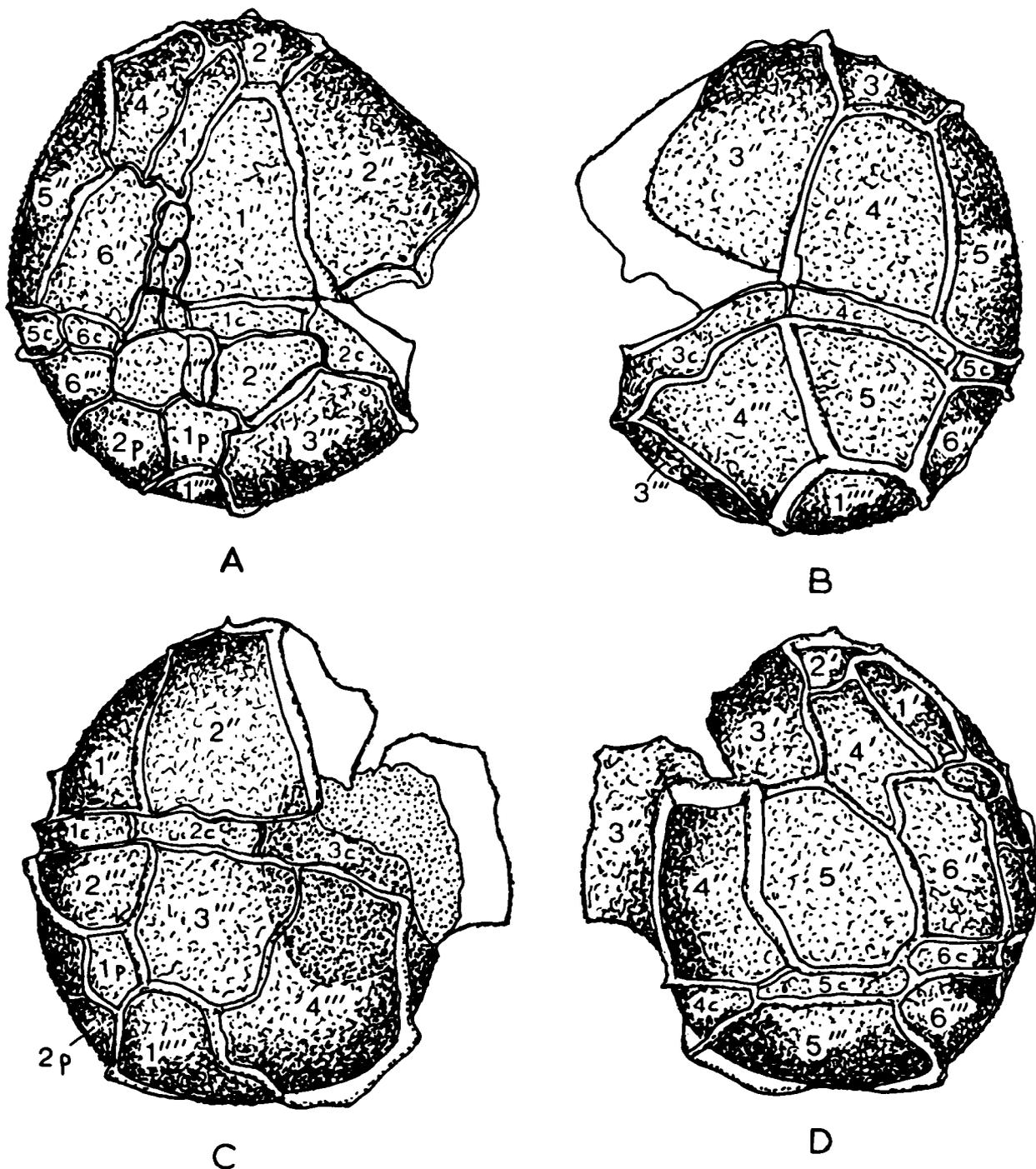


Fig. 1. *Leptodinium membranigerum* Gerlach, 1961, emend. nov. A, B. The lectotype: A, In oblique ventral view; B, In oblique dorsal view. C, D. The paratype: C, In left lateral view; D, In right lateral view. ($\times 1,000$).

Rheine. Full details of the petrography of the samples and of the method of preparation are given by Gerlach (1961, pp. 146–149).

All described specimens are lodged in the Gerlach collection, Institut für Paläontologie, University of Tübingen. Their present condition is highly variable. Some remain in as good order as when Gerlach described them, but others have split open or suffered in varying degree from bacterial or fungal attack, and two could not be located on the slide supposed to contain them. Details are given in the ensuing pages and lectotypes designated when necessary.

SYSTEMATIC DESCRIPTIONS

Kingdom Plantae

Division Pyrrhophyta Pascher

Class Dinophyceae Fritsch

Suborder Gonyaulacystineae Norris, 1978

Family Gonyaulacystaceae Sarjeant & Downie, 1966, emend. Sarjeant, 1982

Genus *Leptodinium* Klement, 1960, emend. Sarjeant, 1982

Leptodinium membranigerum Gerlach, 1961, emend. nov.

(Pl. 1, figs. 1, 3; Pl. 2, figs. 1, 2; Pl. 3, fig. 3; Pl. 4, fig. 6; Fig. 1)

1961 *Leptodinium membranigerum* Gerlach, 162–164, pl. 26, figs. 1–4, 7, text-figs. 4–5.

1964 *Leptodinium membranigerum* Gerlach; Eisenack & Klement, 495–596.

1964 *Leptodinium membranigerum* Gerlach; Downie & Sarjeant, 126.

1967 *Leptodinium membranigerum* Gerlach; Sarjeant, tab. II (p. 328).

1973 *Leptodinium membranigerum* Gerlach; Lentin & Williams, 87.

1975 *Leptodinium membranigerum* Gerlach; Harker & Sarjeant, chart 17 (p. 250).

1977 *Leptodinium membranigerum* Gerlach; Lentin & Williams, 98.

1978 *Impagidinium? membranigerum* (Gerlach); Stover & Evitt, 166.

1981 *Impagidinium? membranigerum* (Gerlach); Lentin & Williams, 154.

Original Diagnosis. “A species of the genus *Leptodinium* with oval theca. Tabulation formula as given in the generic diagnosis; 4', 6'', 5''', 1p and 1'''. Epitheca larger and more elongate than the rounded hypotheca. Girdle furrow spiral, formed of six plates. Offset of its ends somewhat more than a furrow breadth. Longitudinal furrow wholly undifferentiated. Sutures of plates marked by low hyaline crests, shell membrane appearing to bear a thornlike point at the position of convergence of two crests. Plates finely granulate, membrane relatively thin” (Gerlach, 1961, p. 162–163, new transl.).

Emended Diagnosis. Cyst proximate, holotabulate, and acavate; relatively thin but composed of two closely appressed wall layers. Ambitus broadly ovoidal, with epitract markedly larger than hypotract. Low crests, undulate to irregularly scalloped or echinate distally, define the paratabulation 4', 6'', 6c, 6''', 2p, 1''', ?6s. Paraplate 4' is quite large and asymmetrically pentagonal, having a fairly long boundary with a quadrate 6''; this boundary intersects that of 1' in a position anterior to that of 1' with the sulcus. All precingular paraplates are larger than their postcingular equivalents. The right boundary of the small, elongate paraplate 1''' is poorly marked; for this reason the sulcus, which broadens posteriorly, may appear to have the form of an inverted, broad-hafted axe with its blade to the right. Faint lines divide the sulcus into one anterior, at least four median and one (or two?) posterior paraplates. Two posterior intercalary paraplates of similar size separate the sulcus from the rather small antapical paraplate. The cingulum is of moderate breadth, forming a feeble laevorotatory spiral such that its two ends differ in anteroposterior position only by the cingulum's breadth. Surface of phragma uniformly granulate.

Archaeopyle single-plate precingular (type P) formed by the opening or loss of paraplate 3'''.

Holotype. Preparation 1170/14(676), illustrated by Gerlach, 1961, pl. 26, figs. 1–3, lodged in the Gerlach collection, University of Tübingen [Not found: believed to have disintegrated]. **Lectotype.** Preparation 1170/23, illustrated by Gerlach, 1961, pl. 26, fig. 7; text-fig. 5 and herein, pl. 1, figs. 1, 3; Figs. 1A–B; same depository. **Paratype.** Preparation 1170/16 (670; illustrated herein, pl. 2, figs. 1–2; Figs. 1C–D).

Type Horizon and Locality. Upper Oligocene, depth 151 m, Emsbüren boring no. 7, northwest Germany.

Dimensions. Holotype (in lateral view): length 55 μm, breadth 47 μm. Lectotype (in slightly oblique dorsoventral view and slightly flattened): length 74 μm, breadth 66 μm. Paratype (in lateral view): length 63 μm, breadth 53 μm. Range of dimensions: length 55–74 μm, breadth 47–63 μm (near 51 μm). Material: 10 specimens. [Note: Gerlach's original, lower measurement of the lectotype width is used here].

Remarks. The holotype was not found, the presence of what appears to be the collapsed and decayed residue of a cyst suggesting that it has disintegrated. Of the two paratypes cited by Gerlach, one (Pr. 1170/15) could not be identified with certainty: three examples of *L. membranigerum*, all in poor state, were present on this slide but none of the three could be identified with Gerlach's illustration (1961, pl. 26, fig. 4). The other paratype was located and is here reillustrated, but it has

collapsed and is in lateral view (Pl. 2, figs. 1–2, Fig. 1C-D). Moreover, it contains the detached operculum of another dinoflagellate cyst with dissimilar ornament (see Pl. 3, fig. 3). For these reasons, it was considered unsuitable to serve as lectotype. Instead, another specimen figured, but not named as a paratype, by Gerlach (1961, pl. 26, fig. 7) was chosen. It is in dorso-ventral view and, though split open at the left side, remains as well preserved as when she illustrated it.

This species was allocated tentatively to *Impagidinium* by Stover & Evitt (1978); but the relative size and the shapes of paraplates 4' and 6'', and their relation to paraplate 1', do not accord with the diagnosis of that genus. Yet the occurrence of a species of *Leptodinium* in sediments as young as the Late Oligocene is surprising. Since *L. membranigerum* has not yet been reported from Tertiary sediments elsewhere, the possibility that these specimens were reworked from more ancient strata cannot be ruled out. However, since this species has not been reported from earlier stratigraphic levels and since no other reworked species are present, there is as yet no good reason to doubt that it is indigenous.

Genus *Rhynchodiniopsis* Deflandre, 1935, emend. Sarjeant, 1982

Rhynchodiniopsis tenuitabulata (Gerlach, 1961) comb. nov., emend.

(Pl. 2, fig. 3; Pl. 4, fig. 3; Fig. 2)

- (pars) 1961 *Gonyaulax tenuitabulata* Gerlach, 159–161, pl. 25, figs. 10, 11, text-figs. 1–3.
 ?1963 *Gonyaulax* cf. *G. tenuitabulatum* (sic) Gerlach; Brosius, 37, pl. 1, fig. 5.
 1964 *Gonyaulax tenuitabulata* Gerlach; Eisenack & Klement, 407–408.
 1964 *Gonyaulax tenuitabulata* Gerlach; Downie & Sarjeant, 115.
 1967 *Gonyaulacysta tenuitabulata* (Gerlach); Sarjeant, tab. II (p. 328), *nomen nudum*.
 1968 *Gonyaulacysta tenuitabulata* (Gerlach); De Coninck, 23 (taxonomic change only).
 1969 *Gonyaulacysta tenuitabulata* (Gerlach); Sarjeant in Davey *et al.*, 11.
 1973 *Gonyaulacysta tenuitabulata* (Gerlach); Lentin & Williams, 64.

- 1975 *Gonyaulacysta tenuitabulata* (Gerlach); Harker & Sarjeant, chart 17 (p. 250).
 1977 *Gonyaulacysta tenuitabulata* (Gerlach); Lentin & Williams, 10.
 1978 *Millioudodinium tenuitabulatum* (Gerlach); Stover & Evitt, 174.
 ?1979 *Gonyaulacysta tenuitabulata* (Gerlach); Barss, Bujak & Williams, 42.
 1981 *Millioudodinium tenuitabulatum* (Gerlach); Lentin & Williams, 191.
 non 1968 *Gonyaulacysta tenuitabulata* (Gerlach); De Coninck, 23, pl. 5 figs. 9, 10, 13–16.
 non 1975 *Gonyaulacysta tenuitabulata* (Gerlach); De Coninck, 21, 25.
 non 1975 ?*Gonyaulacysta tenuitabulata* (Gerlach); De Coninck, 18, 72.
 non 1976 *Gonyaulacysta tenuitabulata* (Gerlach); Eaton, 226, pl. 8, fig. 9, text-figs. 14a, b.
 non 1983 *Millioudodinium tenuitabulatum* (Gerlach); Matsuoka, 106, pl. 1, figs. 6a, b.

Original Diagnosis. “Shell thin-walled, broadly spheroidal, with short, blunt apical horn. Tabulation pattern: 4', 6'', 6''', lp, lpv, 1'''”. Plates enclosed by low, narrow crests. Girdle furrow spiral, with an offset of about 1 1/2 furrow widths. Membrane finely granulate.” (Gerlach, 1961, p. 160, new transl.).

Emended Diagnosis. Cyst proximate, holotabulate, apically cornucavate (monocornucavate). Ambitus spheroidal to broadly rounded-subpolygonal, with epittract and hypottract of almost equal shape and relative size. Apical horn short, tapering and blunt. Low, narrow crests, entire to undulate distally, delimit the paraplates: the crests on the horn may impart to it a trifid appearance. Paratabulation 2pr, 4', 6'', 6c, 6''', lp, 1''', ?8s. Paraplate 4' is quite large and asymmetrically quadrate, having a long boundary with an almost rectangular 6''; their mutual boundary intersects that of paraplate 1' just anterior to the junction of the latter paraplate with the sulcus. Paraplate 1' broadens considerably in its posterior portion. Paraplate 3'' is unusually small, whereas paraplates 2' and 3' are somewhat larger than usual. Paraplate 1''' is reduced and elongate and 2''' reduced

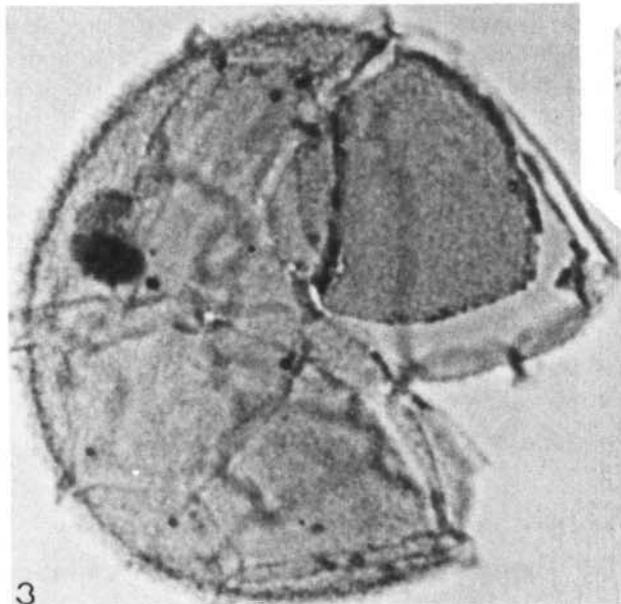
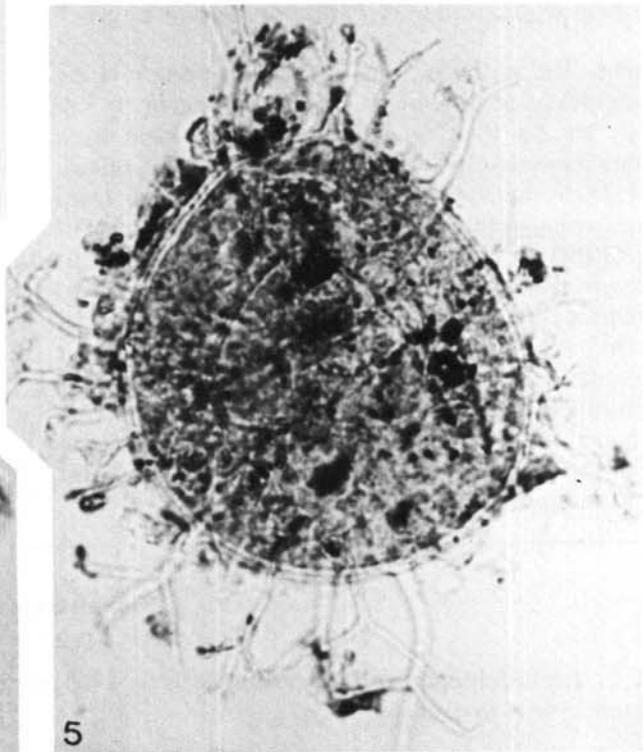
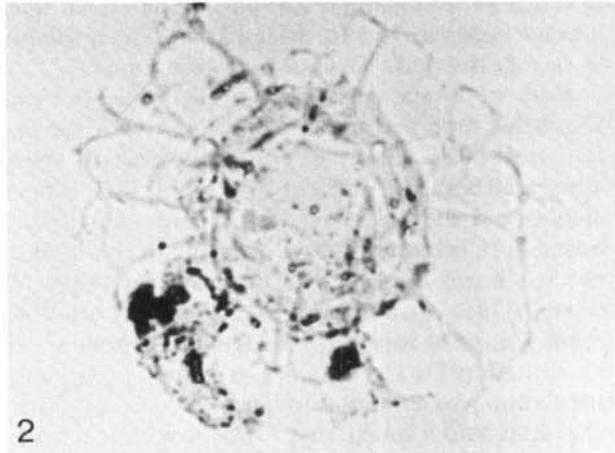
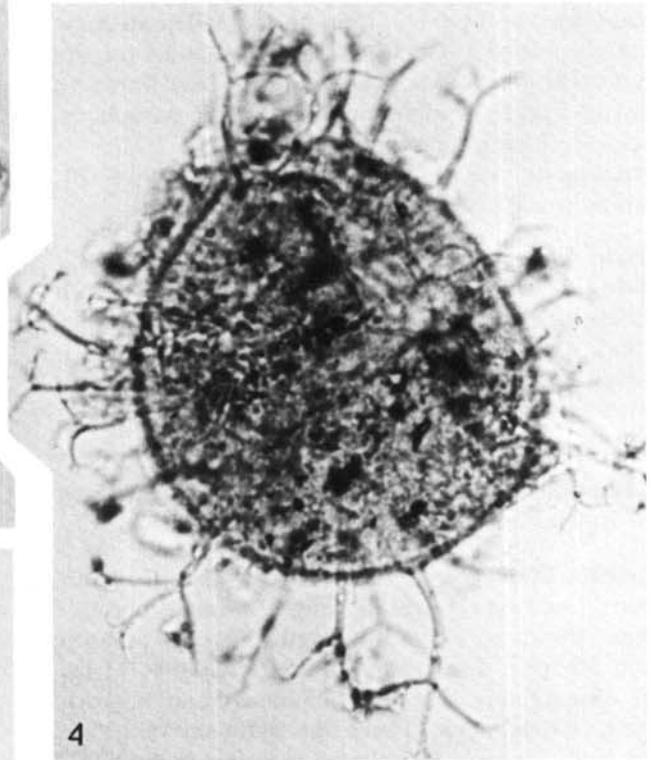
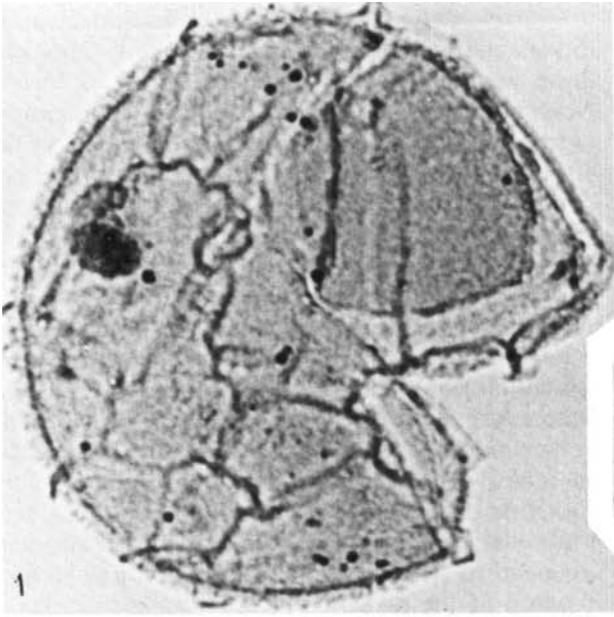
Explanation of Plate 1

All figures are ×1000.

Figs. 1, 3. *Leptodinium membranigerum* Gerlach, 1961, emend. nov. The lectotype: fig. 1, oblique ventral view; fig. 3, oblique dorsal view, by transparency.

Fig. 2. *Areosphaeridium pectiniforme* (Gerlach, 1961) Stover & Evitt, 1978, emend. nov. The holotype, in polar view.

Figs. 4, 5. *Achomosphaera triangulata* (Gerlach, 1961) Davey & Williams Davey *et al.*, 1979, emend. nov. The holotype: fig. 4, ventral view, by transparency; fig. 5, dorsal view.



and quadrate, both paraplates being separated from the antapex by paraplate lp. Cingulum of moderate breadth and degree of spirality, its two ends differing in antero-posterior position by 1 1/2 times its width. The sulcus is moderately broad, extending from mid-point on the epitract to the antapex; it is subdivided by faint lines into at least six, perhaps eight or more, small paraplates. Surface of phragma granulate.

Archaeopyle single-plate precingular (type P), formed by loss of paraplate 3": operculum free.

Holotype. Preparation 1170/10 (269), illustrated by Gerlach, 1961, pl. 25, figs. 10, 11; lodged in the Gerlach collection, University of Tübingen. [Not found; see later remarks]. **Lectotype.** Preparation 1170/11 (283), illustrated herein, pl. 2 fig. 3, pl. 4 fig. 3, Fig. 2; same depository. **Paratype.** Specimen 1170/12 (280); same depository [not found].

Type Horizon and Locality. Middle Oligocene, depth 179 m. Emsburen boring no. 7, northwest Germany.

Dimensions. Holotype: overall length 84 μm , breadth 74.5 μm . Lectotype: overall length 88 μm , breadth 79.7 μm . Paratype: overall length 84 μm , breadth 77.8 μm . Range of dimensions: overall length 84–93 μm (mean 88 μm), breadth 74.5–95 μm (mean 82 μm). **Material:** 10 specimens. (These figures for size range are quoted from Gerlach, but almost certainly include the forms here distinguished as *Phthanoperidinium* sp.).

Remarks. The holotype was not found; however, the slide supposed to contain it included a specimen sufficiently similar to it in general form, to have been probably considered referable to this species by Gerlach. It is of closely similar size and shape, but lacks any trace of the archaeopyle so prominently seen in Gerlach's figure (1961, pl 25, fig. 11). It is here redescribed as *Phthanoperidinium* sp. In consequence, there are two possibilities First, that the holotype is contained in that slide, but has either disintegrated to unrecognisability or was simply missed in traversing. Second, that the slide was mislabelled, the specimen here illustrated (Pl. 3 figs. 4–5) being mistaken for the holotype at some stage of Gerlach's work. Whatever the reason, the holotype must be considered lost and a lectotype selected.

Gerlach designated two paratypes (*ibid.*, p. 159), though neither of them was illustrated. Only one of these was found; it is here designated as lectotype. Nevertheless, it is far from being ideal, containing dark organic material and showing some evidences of fungal attack, as well as being slightly folded at left. In consequence, the paratabulation could not be determined with complete confidence, the form and relative size of paraplates 2" and lp and the exact number and shape of the midventral sulcal paraplatelets remaining uncertain, as is indicated by the broken lines in my diagram (Fig. 2).

Fortunately, the anterior ventral and dorsal paratabulation could be confidently elucidated. Unusual features are the relatively small size of 3" (lost in archaeoformation) and, as a result, the proportionate enlargement of 2' and 3' (see Pl. 4, fig. 3). An unusually broad paraplate 1' and a long, quite broad sulcus furnish additional distinguishing characters. The diagnosis is emended to stress these characteristics and to include mention of the presence of preapical paraplates. The anterior ventral paratabulation demonstrates that this species belongs, not in the genus *Millioudodinium* as presently defined, but in *Rhynchodiniopsis*.

None of the specimens attributed to this species since Gerlach's time accords beyond doubt with the revised diagnosis. The German Upper Oligocene specimen compared with this species by Brosius (1963) is the most similar, but the ambitus is rather more angular and the apical horn broader. The record from the early Miocene of the Grand Banks, offshore eastern Canada (Barss *et al.*, 1979) is unsubstantiated by an illustration. Other records must be rejected. The Belgian Eocene specimen illustrated by De Coninck (1968) has an indistinct paratabulation, an ambitus and apical horn of dissimilar character and a much larger archaeopyle; it cannot be referable to this species. De Coninck's later record (1975) must, in consequence, also be rejected. Eaton's English Eocene specimen (1976), illustrated in oblique ventral view, has a shorter apical horn, a small posterior ventral paraplate, a much larger paraplate 3" (lost in archaeopyle formation) and, in consequence, smaller dorsal apical paraplates. The specimens from the Early to Middle Miocene of Japan described by Matsuoka (1983) are too elongate, and have too dissimilar a ventral paratabulation, for retention in this species.

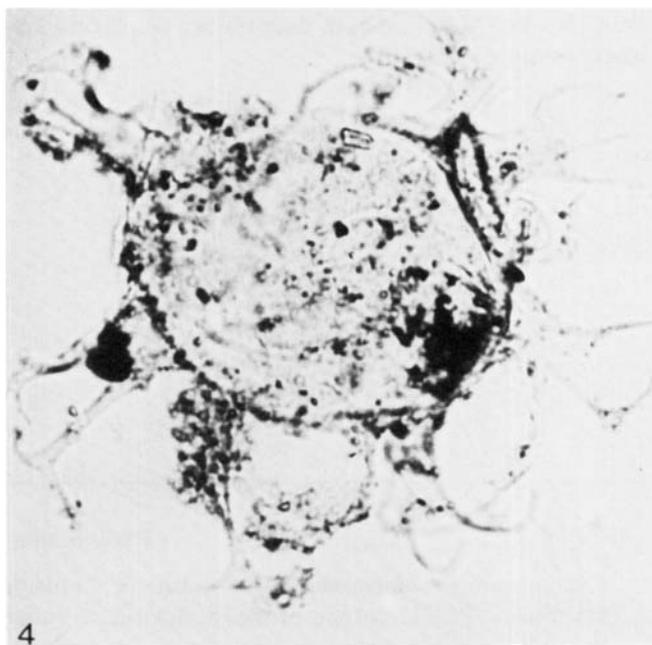
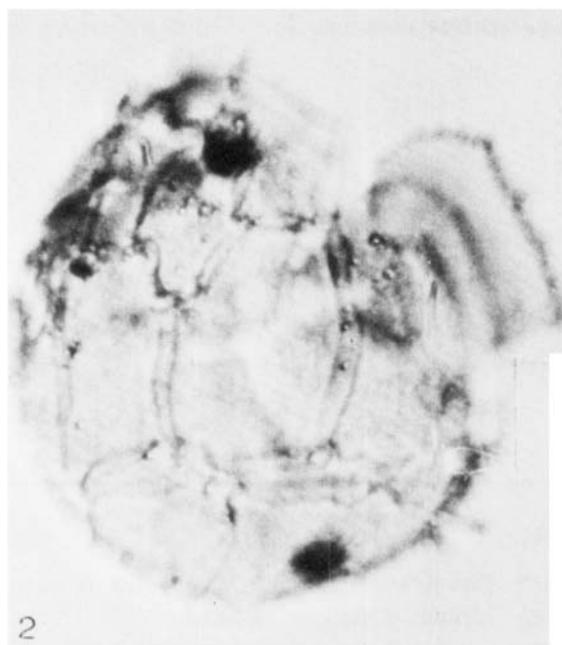
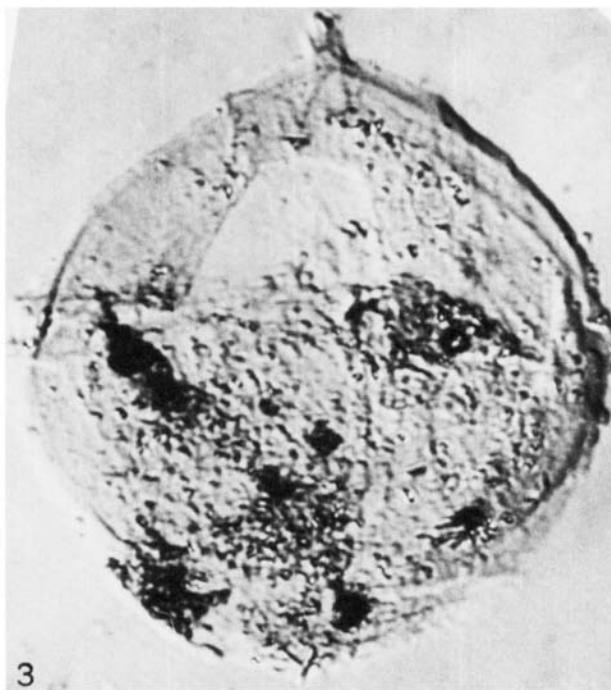
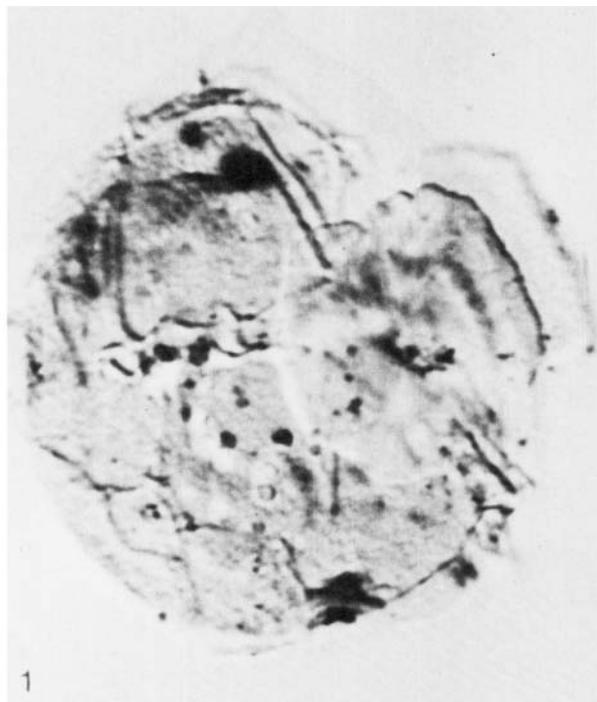
Explanation of Plate 2

All figures are $\times 1000$.

Figs. 1, 2. *Leptodinium membranigerum* Gerlach, 1961, emend. nov. The paratype: fig. 1, left lateral view; fig. 2, right lateral view, by transparency.

Fig. 3. *Rhynchodiniopsis tenuitabulata* (Gerlach, 1961) comb. nov., emend. The lectotype, in dorsal view.

Fig. 4. *Chiropteridium galea* (Maier, 1959) emend. Sarjeant, 1983. Specimen in oblique ventral view. [A former paratype of *Baltisphaeridium panniforme* Gerlach, 1961].



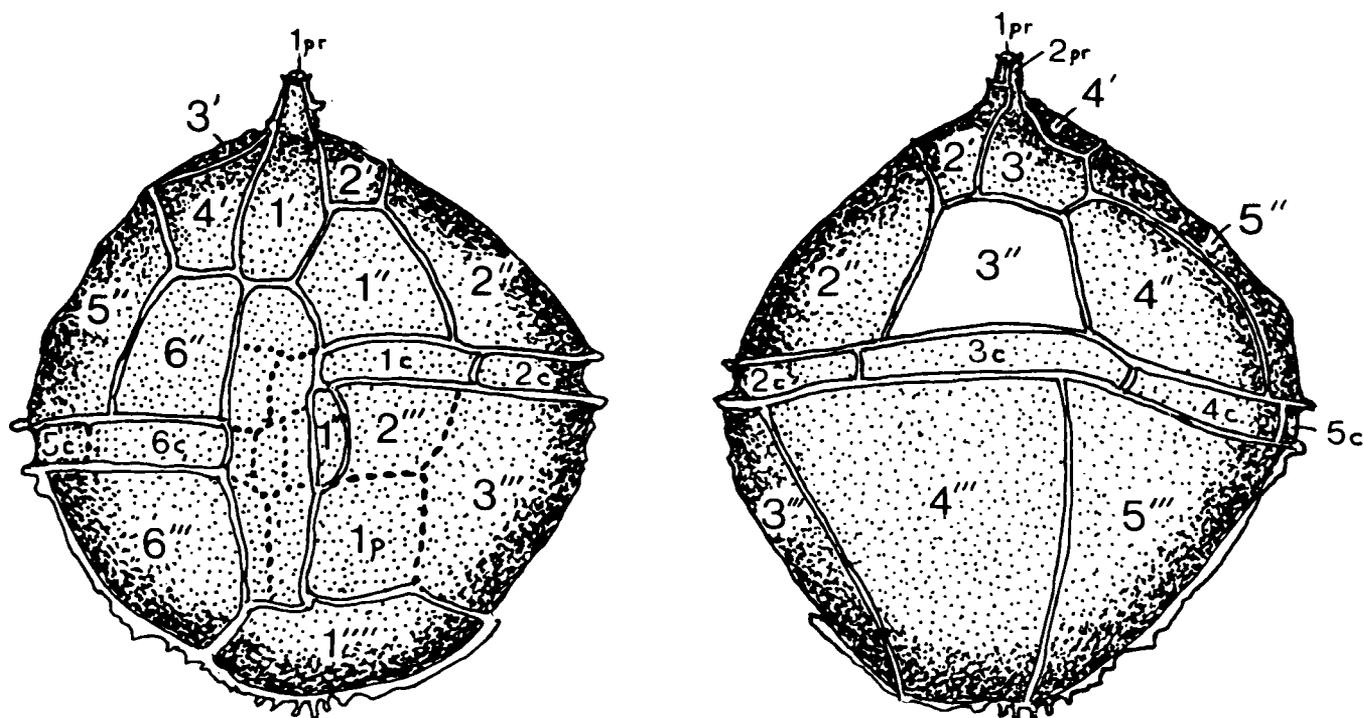
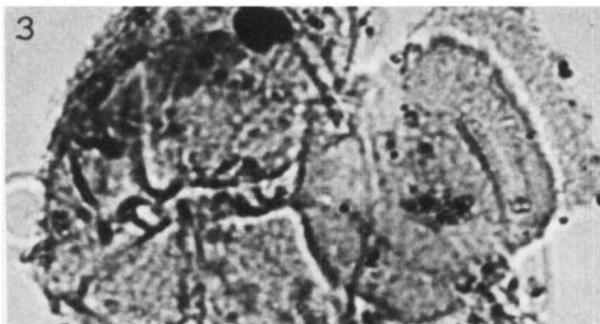
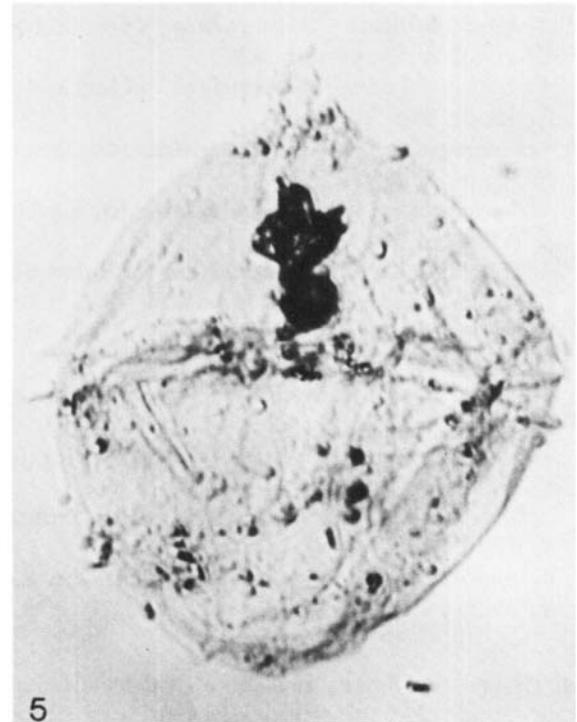
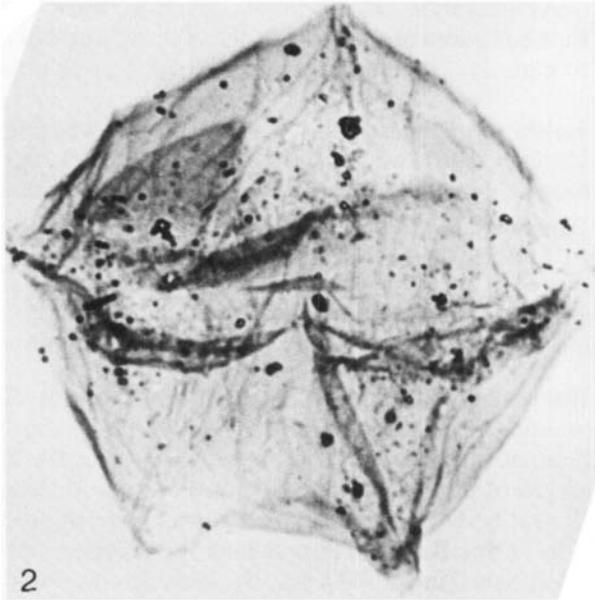
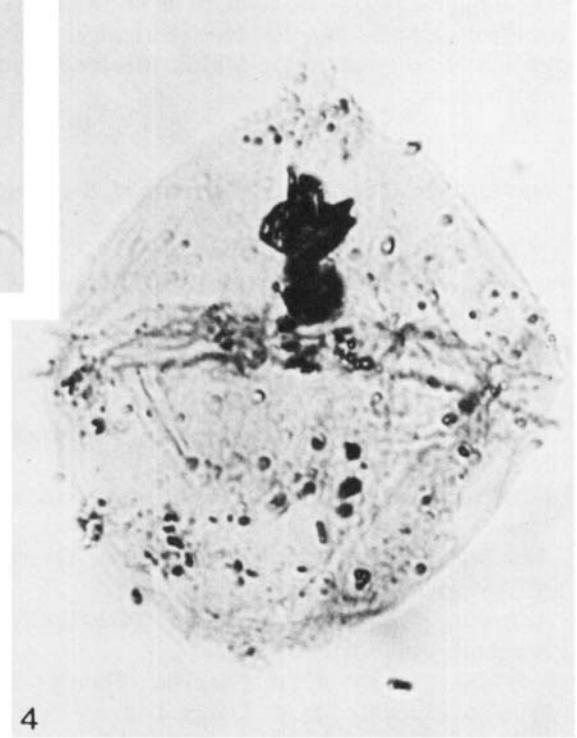
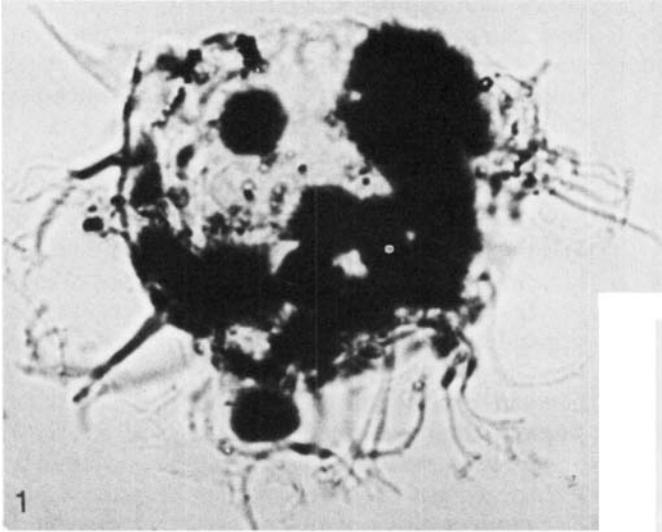


Fig. 2. *Rhynchodiniopsis tenuitabulata* (Gerlach, 1961) comb. nov., emend. Left: in ventral view. Right: in dorsal view. Broken lines indicate uncertainty concerning exact parasuture position: dotted lines indicate a tentative interpretation ($\times 1,000$).

Explanation of Plate 3

- Fig. 1. *Systematophora placacantha* (Deflandre & Cookson, 1955) Davey 1969, emend. May, 1980. A specimen in ventral view. [The lectotype of *Baltisphaeridium panniforme* Gerlach, 1961] ($\times 1,000$).
- Fig. 2. *Lejeunecysta hyalina* (Gerlach, 1961) Artzner & Dörhöfer, 1978, emend. nov. The holotype, in dorsal view. (The archaeopyle can be seen by transparency, as a lighter area) ($\times 750$).
- Fig. 3. *Leptodinium membranigerum* Gerlach, 1961, emend. nov. The lectotype in median focus, showing the extraneous operculum that has become lodged within the split-open cyst ($\times 1,000$).
- Figs. 4, 5. ?*Phthanoperidinium* sp. Specimen in preparation 1170/10: fig. 4, dorsal view; fig. 5, ventral view, by transparency ($\times 1,000$).



For the moment, *Rhynchodiniopsis tenuitabulata* can be considered, in view of the fact that two morphological types were assigned to it by Gerlach, to be known confidently only from the Middle Oligocene (with a questionable extension of range up to the Middle Miocene) and only from Germany.

Family Spiniferitaceae Sarjeant, 1970, emend. Sarjeant & Downie, 1974

Genus *Achomosphaera* Evitt, 1963

Achomosphaera triangulata (Gerlach, 1961) Davey & Williams in Davey *et al.*, 1969, emend. nov.
(Pl. 1, figs. 4, 5)

- 1961 *Baltisphaeridium triangulatum* Gerlach, 194–195, pl. 29, fig. 1.
1963 *Baltisphaeridium triangulatum* Gerlach; Downie & Sarjeant, 92.
1964 *Baltisphaeridium triangulatum* Gerlach; Downie & Sarjeant, 97.
1966 *Achomosphaera triangulata* (Gerlach); Davey & Williams, 52, *nomen nudum*.
1967 *Achomosphaera triangulata* (Gerlach); Sarjeant, tab. 8 (p. 334).
1969 *Achomosphaera* cf. *A. sagena* Davey & Williams; Gocht, 36, pl. 7, figs. 1–2.
1969 *Achomosphaera triangulata* (Gerlach); Davey & Williams in Davey *et al.*, 4.
1971 *Achomosphaera triangulata* (Gerlach); Eisenack & Kjellström, 83.
1972 *Achomosphaera triangulata* (Gerlach); Benedek, tab. 3.
?1972 *Achomosphaera* aff. *A. triangulata* (Gerlach); p. 22, pl. 5, figs. 3a, b.
1973 *Achomosphaera triangulata* (Gerlach); Lentin & Williams, 10.
1974 *Achomosphaera* cf. *A. ramulifera* (Deflandre); Cookson & Eisenack, 54 (*pars*), pl. 23, fig. 14.
1975 *Achomosphaera* sp. Williams & Brideaux, pl. 17, fig. 9.
1975 *Achomosphaera triangulata* (Gerlach); Harker & Sarjeant, chart 18 (p. 251).
1977 *Achomosphaera triangulata* (Gerlach); Lentin & Williams, 2.
1978 *Achomosphaera triangulata* (Gerlach); Stover & Evitt, 139.
1981 *Achomosphaera triangulata* (Gerlach); Lentin & Williams, 4.

Original Diagnosis. “Theca in outline oval to circular. Processes numerous, massive, divided into three branches, which bear at their ends two hooklets. Processes two- and three-rooted [lit. “footed”]. Pylome trapezoidal. Membrane granulate.” (Gerlach, 1961, p. 194, new transl.).

Emended Diagnosis. Proximochorate, spiniferate cysts, hercotabulate. Ambitus ovoidal, with epitract somewhat larger than hypotract. Epitract in the form of a broad hemiellipsoid, hypotract almost hemispheroidal. Processes gonial and intergonial in situation, varying in length according to position on the cyst from about 25% to 28% of the cyst breadth, sometimes appearing longer because of distortions in the orientation of their branches. Gonial processes slender, arising from broad bases but of very constant thickness between the base and the position of branching; trifurcate, their branches long and directed almost parallel (or at only a low angle) to the phragma surface, with bifid terminations, the branchlets typically recurved. Intergonal processes present in situations corresponding to the sutures between precingular and between postcingular plates; slimmer than the gonial processes and bifurcate, with extremely slender branches that may be simple or bifid. Paratabulation not directly indicated. Surface of phragma coarsely granulate to shagreenate or verrucate.

Archaeopyle single-plate precingular (type P), formed by loss of a portion of the cyst wall corresponding to plate 3". Operculum shield-shaped, free or attached.

Holotype. Preparation 1170/50(409), illustrated by Gerlach, 1961, pl. 29, fig. 1, and herein, pl. 1, figs. 3–4 lodged in the Gerlach collection, University of Tübingen.

Paratypes. A. Preparation 1170/51(437). B. Preparation 1170/52(397); same depository.

Type Horizon and Locality. Middle Miocene, depth 85 m, Emsbüren borehole no. 9, northwest Germany.

Dimensions. Holotype: length of central body 58 μm , breadth 53 μm , length of processes c. 12–15 μm . Paratype A: length of central body 60 μm , breadth 48 μm , length of processes c. 12–14 μm . Paratype B: length of central body 53 μm , breadth 42 μm , length of processes c. 9–11 μm . Range of dimensions: length of central body 36–60 μm (mean 53 μm), breadth 33–48 μm (mean 44 μm). 12 specimens measured (material 36 specimens). [Note: Gerlach quotes unrealistically high lengths for the processes, up to 22 μm . No specimens seen had processes of such high proportionate length].

Remarks. The *Spiniferites/Achomosphaera/Nematosphaeropsis* group of dinoflagellate cysts is a particularly long-ranging one and known to be especially prone to intraspecific variation; this was recognised by Lejeune-Carpentier (1937a, b), in her restudies of Ehrenberg's type material of *Spiniferites ramosus* (then *Hystrichosphaera ramosa*) and given emphasis by Davey & Williams' work on two of those genera (1966). Nevertheless, a plethora of new species names continue to be proposed and the task of sorting out this taxonomic mess grows ever more formidable. It seems likely that future

studies of variation in *Achomosphaera ramulifera* (Deflandre, 1937) Evitt, 1963 may show *A. triangulata* to merit merely subspecific or varietal status. For the moment, however, it is retained as a separate species and distinguished from *A. ramulifera* by the slimness of its spines and the length of their branches.

Although not reported as such from other localities since its first description, *A. triangulata* may be recognised under different names in illustrations by some other authors. Gocht's form from the Late Eocene of Germany (1969) is illustrated in polar view, but seems to correspond with *A. triangulata* in all particulars. Benedek's single specimen from the Middle Oligocene of Germany, described as *A. aff. triangulata*, is stated to have only two process branches ('hooklets'); however, in all other respects it is closely comparable and may well prove, on restudy, to have trifurcate gonial processes. One of the forms from the Late Eocene of Victoria, Australia, illustrated by Cookson & Eisenack (1974) seems, though crushed, to accord with this taxon, as does that from the Cenozoic of the Grand Banks, offshore eastern Canada, illustrated by Williams & Brideaux (1975). On these bases, *A. triangulata* is seen to have a wide geographic range and a stratigraphic range from Late Eocene to Middle Miocene. (Gerlach's records include Middle Oligocene representatives).

Suborder Hystrichosphaeridiineae Norris, 1978

Family Hystrichosphaeridiaceae Evitt, 1963, emend.
Sarjeant & Downie, 1974

Genus *Areosphaeridium* Eaton, 1971

Areosphaeridium pectiniforme (Gerlach, 1961) Stover
& Evitt, 1978, emend. nov.
(Pl. 2, fig. 2; Pl. 4, fig. 2)

- (pars) 1961 *Baltisphaeridium pectiniforme* Gerlach,
195–196, pl. 28, fig. 14; text-fig. 18.
1963 *Baltisphaeridium pectiniforme* Gerlach;
Brosius, 43–44, pl. 1, fig. 7; text-fig. 2,
nos. 9a-b.
1963 *Baltisphaeridium pectiniforme* Gerlach;
Downie & Sarjeant, 92.
1963 *Baltisphaeridium pectiniforme* Gerlach;
Downie & Sarjeant, 94.
(pars) 1965 *Cordosphaeridium capricornum*
Cookson & Eisenack, pl. 15, fig. 3
(only).
1966 *Baltisphaeridium pectiniforme* Gerlach;
Davey, Downie, Sarjeant & Williams, 17.
1966 *Cleistosphaeridium pectiniforme*
(Gerlach); Davey, Downie, Sarjeant &
Williams, 170.
1967 *Cleistosphaeridium pectiniforme*
(Gerlach); Sarjeant, tab. 5 (p. 331),
nomen nudum.

- 1969 *Cleistosphaeridium pectiniforme*
(Gerlach); Davey, Downie, Sarjeant &
Williams, 16.
1971 *Areosphaeridium multicornutum* Eaton,
363–364, pl. 4, figs. 1–7; text-fig. 6.
1973 *Cleistosphaeridium pectiniforme*
(Gerlach); Lentin & Williams, 29.
1973 *Areosphaeridium multicornutum* Eaton;
Lentin & Williams, 16.
1975 *Areosphaeridium multicornutum* Eaton;
Auffret & Gruas-Cavagnetto, 647, 650.
1975 *Areosphaeridium multicornutum* Eaton;
Eisenack & Kjellström, 31–32 (96c-d).
1975 *Cleistosphaeridium pectiniforme*
(Gerlach); Harker & Sarjeant, chart 20
(p. 25).
1975 *Areosphaeridium multicornutum* Eaton;
Harker & Sarjeant, chart 22 (p. 255).
1976 *Areosphaeridium multicornutum* Eaton;
Costa, Downie & Eaton, tab. I.
1976 *Areosphaeridium multicornutum* Eaton;
Bujak, 107, pl. 2, figs. 1–8; text-figs. A.
1976 *Areosphaeridium multicornutum* Eaton;
Eaton, 250, pl. 6, fig. 3; text-fig. 30.
1977 *Cleistosphaeridium pectiniforme*
(Gerlach); Lentin & Williams, 29.
1977 *Areosphaeridium multicornutum* Eaton;
Lentin & Williams, 12.
1978 *Areosphaeridium? pectiniforme*
(Gerlach); Stover & Evitt, 20.
1978 *Areosphaeridium multicornutum* Eaton;
Stover & Evitt, 20.
1979 *Areosphaeridium multicornutum* Eaton;
Barss, Bujak & Williams, 49, 51, 52, 57,
58, 81, 86, 94.
? 1979 *Areosphaeridium cf. A. multicornutum*
Eaton; Barss, Bujak & Williams, 90.
1980 *Areosphaeridium multicornutum* Eaton;
Liengjarern, Costa & Downie, tab. 1.
1980 ?*Areosphaeridium pectiniforme*
(Gerlach); Weiler in Doebel *et al.*, 58,
tab. 4.
1980 *Areosphaeridium multicornutum* Eaton;
Bujak, Downie, Eaton & Williams, 23,
tab. 7c (p. 20).
1981 *Cleistosphaeridium pectiniforme*
(Gerlach); Eisenack & Kjellström, 105
(214a).
1981 *Areosphaeridium? pectiniforme*
(Gerlach); Lentin & Williams, 21.
1981 *Areosphaeridium multicornutum* Eaton;
Lentin & Williams, 20.

Original Diagnosis. "A species of the genus *Baltisphaeridium* with slender solid processes, which are widely extended on both sides [of the tip] and set with

numerous small hooklets. Form of capsule circular to oval. Membrane granulate." (Gerlach, 1961, p. 195, new transl.).

Emended Diagnosis. Proximate, skolochorate cysts, intratabulate and acavate. Central body subspherical to subovoidal or subpolygonal; phragma thin, two layered. Processes ranging in length between about 35% to 45% of the cyst breadth. Each process is distally expanded and bifurcate (licrate); the attitude of the bifurcations ranges from patulate to recurved. The two branches are of variable relative and absolute length; they vary in breadth from slender, with a denticulate distal margin, to broad, with a denticulate or irregular distal margin and with some development of fenestration. Paratabulation 4', 6", 7c, 6'", lp, 5pa, 1''''. The paraplates, however, are not always fully represented; the processes equivalent to 6" and lp, and up to three of the cingular processes, may be lacking and the preantapical processes are often very incompletely developed (as few as one may be present in some specimens). The antapex, with its single process, is typically offset to the right of the midventral line. Surface of phragma laevigate to finely or more coarsely granulate.

Archaeopyle apical (type tA): operculum (or opercular pieces?) free.

Holotype. Preparation 1170/53(290), illustrated by Gerlach, 1961, pl. 28, fig. 14, text-fig. 18, and herein, pl. 1, fig. 2; pl. 4, fig. 2; lodged in the Gerlach collection, University of Tübingen.

Type Horizon and Locality. Middle Oligocene, depth 179m, Emsburen borehole no. 7, northwest Germany.

Dimensions. Holotype (in apical view): diameter of central body 32 μm , length of processes c. 13 μm .

Remarks. Even when Eaton first proposed his species *Areosphaeridium multicornutum*, he was aware that it might prove to be a junior synonym of Gerlach's *Baltisphaeridium pectiniforme*, for he commented: "*B. pectiniforme* has been recorded by two writers, GERLACH (1961) from the Middle Oligocene of Germany, and BROSIUS (1963) from the Upper Oligocene of Germany. The specimens figured by these two writers have processes which are identical to those of *A. [reosphaeridium] arcuatum* [now *A. dictyostilum* (Menéndez, 1965) emend. Sarjeant, 1981] and *A. multicornutum*. It is possible that one of the species described from the Bracklesham Beds may be identical to *B. pectiniforme*, but the precise relationship between the English and the German forms cannot be determined until the number and distribution of the processes in *B. pectiniforme* is known" (Eaton, 1971, p. 364).

In the ensuing thirteen years, though the two species recognised by Eaton have been widely reported, Gerlach's material has remained unstudied. My examination of it shows Eaton's hesitancy to have been fully justified, since the two specimens reported by Gerlach represent, not one, but both species! The holotype, a thin-walled specimen in apical view and having numerous, very slender processes, corresponds in all particulars with Eaton's *Areosphaeridium multicornutum*. In consequence, the latter name must be regarded as a subjective junior synonym of *Areosphaeridium pectiniforme* and its use abandoned.

The paratype, in contrast, is thicker-walled, with more massive processes that are broader at base and tip than those of the holotype and are much less numerous. It is reattributed below to *A. dictyostilum*.

Areosphaeridium pectiniforme has a known range from middle Eocene to late Oligocene; specimens found in Miocene sediments by Barss *et al.* (1979) were considered to be reworked. It has been reported from

Explanation of Plate 4

All figures are $\times 1000$.

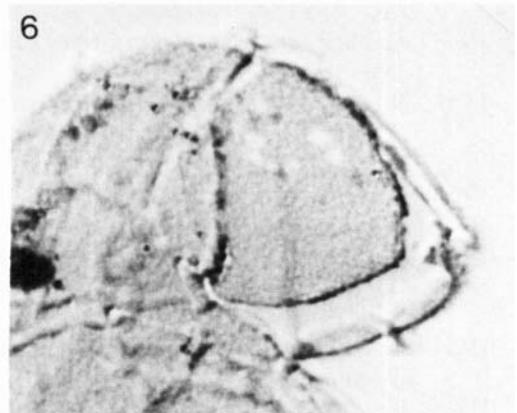
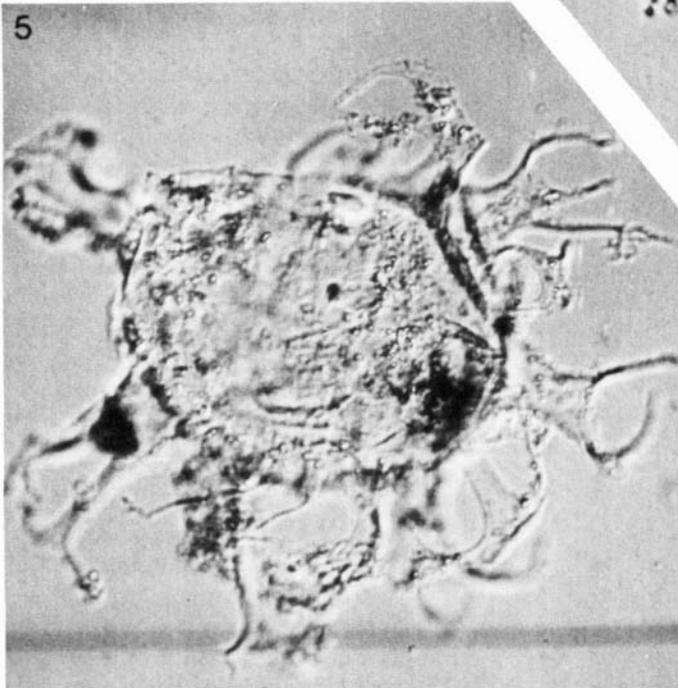
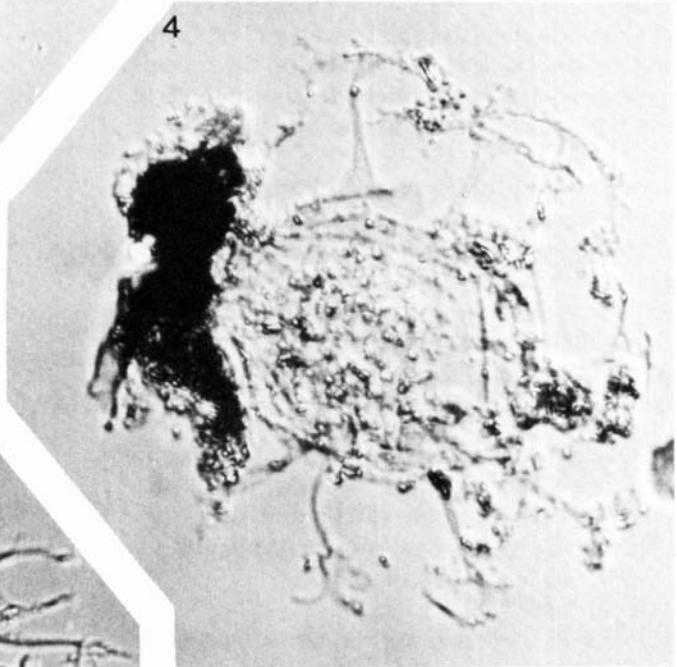
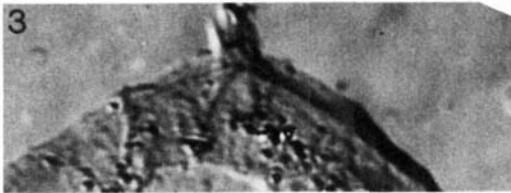
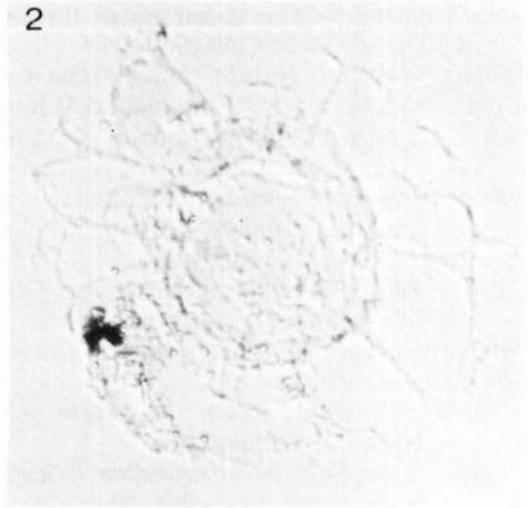
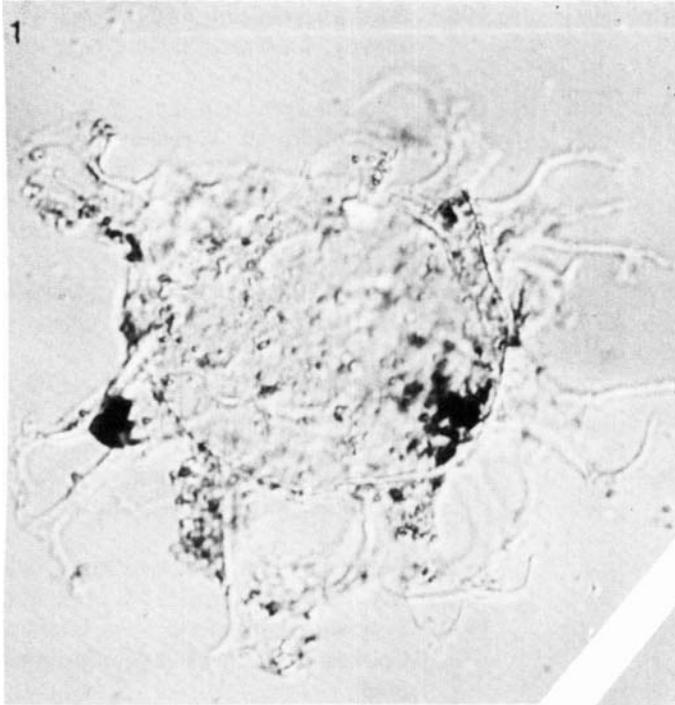
Figs. 1, 5. *Chiropteridium galea* (Maier, 1959) emend. Sarjeant, 1983: fig. 1, oblique ventral view; fig. 2, oblique dorsal view, by transparency. [A former paratype of *Baltisphaeridium panniforme* Gerlach, 1961]. Phase-contrast microphotographs.

Fig. 2. *Areosphaeridium pectiniforme* Gerlach, 1961, emend. nov. The holotype, in polar view. Phase-contrast microphotograph.

Fig. 3. *Rhynchodiniopsis tenuitabulata* (Gerlach, 1961) comb. nov., emend. The holotype: detail of apex, showing the dorsal apical paraplates.

Fig. 4. *Areosphaeridium dictyostilum* (Menéndez, 1965) emend. Sarjeant, 1981. Damaged specimen in (?) polar view. [The former paratype of *Baltisphaeridium pectiniforme* Gerlach, 1961].

Fig. 6. *Leptodinium membranigerum* Gerlach, 1961, emend. nov. The lectotype: details of the still-attached operculum, by transparency.



Germany, England, marine sediments of the English Channel (Auffret & Gruas-Cavagnetto, 1975) and the Grand Banks, offshore eastern Canada (Barss *et al.*, 1979). It has also been tentatively identified from the Labrador Shelf, offshore eastern Canada (*ibid.*, p. 90).

Areosphaeridium dictyostilum (Menéndez, 1965)
emend. Sarjeant, 1981.

(Pl. 4, fig. 4)

(pars) 1961 *Baltisphaeridium pectiniforme* Gerlach,
195–196. [Not illustrated].

[A full synonymy for this species to 1980 is given
by Sarjeant, 1981, p. 115].

1981 *Areosphaeridium arcuatum* Eaton;
Lentin & Williams, 20.

1981 *Areosphaeridium dictyostilum* (Menéndez);
emend. Sarjeant, 1981, 115–116.

Remarks. As noted above, the “paratype” of Gerlach’s *Baltisphaeridium pectiniforme* proved to be a specimen of *Areosphaeridium dictyostilum*. It is in oblique polar view and is somewhat crushed and obscured (see Pl. 4 fig. 4).

This species has been reported hitherto only from the late Eocene (see Sarjeant, 1981, p. 116). Its occurrence in the Middle Oligocene may represent an extension of its range or (since only a single, poor specimen is present) may be a consequence of reworking. Certainly the record should be distrusted until further middle Oligocene specimens are reported.

Family Systematophoraceae Sarjeant & Downie, 1974

Genus *Systematophora* Klement, 1960

Systematophora placacantha (Deflandre & Cookson,
1955) Davey, Downie, Sarjeant & Williams, 1969,
emend. May, 1980.

(Pl. 3, fig. 1)

1955 *Hystrichosphaeridium placacanthum*
Deflandre & Cookson, 276–277, pl. 9,
figs. 1–3.

(pars) 1961 *Baltisphaeridium panniforme* Gerlach,
196–198, pl. 28, fig. 13.

1963 *Baltisphaeridium placacanthum*
(Deflandre & Cookson); Downie &
Sarjeant, 92.

1963 *Baltisphaeridium panniforme* Gerlach;
Downie & Sarjeant, 92.

1964 *Baltisphaeridium placacanthum*
(Deflandre & Cookson); Downie and
Sarjeant, 94.

1964 *Baltisphaeridium panniforme* Gerlach;
Downie & Sarjeant, 94.

1966 *Systematophora placacantha* (Deflandre
& Cookson); Davey, Downie, Sarjeant
& Williams, 173, *nomen nudum*.

1966 *Baltisphaeridium panniforme* Gerlach;
Davey, Downie, Sarjeant & Williams,
174.

1966 *Impletosphaeridium placacanthum*
(Deflandre & Cookson); Morgenroth,
35–36, pl. 9, figs. 10–11.

1966 *Impletosphaeridium panniforme*
(Gerlach); Morgenroth, 35 [taxonomic
change only].

?1967 *Baltisphaeridium* cf. *B. placacanthum*
(Deflandre & Cookson); De Coninck,
217, 226.

1969 *Systematophora placacantha* (Deflandre
& Cookson); Davey, Downie, Sarjeant
& Williams, 17.

1970 *Adnatosphaeridium caulleryi* (Deflandre);
Heisecke, 250, 252, pl. 9, fig. 4; pl. 10 figs.
1–2.

1970 *Systematophora placacantha* (Deflandre
& Cookson); Verdier, 13, pl. 9, figs. 1–2.

1971 *Systematophora placacantha* (Deflandre &
Cookson); Eisenack & Kjellström, 1007–
1008.

1972 *Impletosphaeridium placacanthum*
(Deflandre & Cookson); Gruas-
Cavagnetto, 72, pl. 3, fig. 1.

1973 *Systematophora placacantha* (Deflandre
& Cookson); Lentin & Williams, 133.

1973 *Impletosphaeridium panniforme*
(Gerlach); Lentin & Williams, 82.

1975 *Systematophora placacantha* (Deflandre
& Cookson); Haskell & Wilson, pl. 3,
fig. 7.

1975 *Systematophora placacantha* (Deflandre
& Cookson); Benedek, 45.

1975 *Systematophora placacantha* (Deflandre
& Cookson); Williams & Brideaux, pl.
27, fig. 1; text-figs. 7, 8, 12, 14.

1975 *Systematophora placacantha* (Deflandre
& Cookson); Harker & Sarjeant, chart
23 (p. 256); chart 54 (p. 287).

1975 *Impletosphaeridium panniforme*
(Gerlach); Harker & Sarjeant, chart 21
(p. 254).

1976 *Systematophora placacantha* (Deflandre
& Cookson); Benson, 228, pl. 14, figs.
8–9.

1977 *Systematophora placacantha* (Deflandre
& Cookson); Ioannides and Colin, fig. 2.

1977 *Systematophora placacantha* (Deflandre
& Cookson); Stover, text-fig. 2.

1977 *Systematophora placacantha* (Deflandre
& Cookson); Lentin & Williams, 159.

1977 *Impletosphaeridium panniforme*
(Gerlach); Lentin & Williams, 88.

- 1978 *Systematophora placacantha* (Deflandre & Cookson); Stover & Evitt, 84.
 1978 *Cleistosphaeridium panniforme* (Gerlach); Stover & Evitt, 31.
 1979 *Systematophora placacantha* (Deflandre & Cookson); Barss, Bujak & Williams, 15, 44, 52, 55, 56, 58, 62, 67, 76, 83, 86.
 1979 *Systematophora placacantha* (Deflandre & Cookson); Piasecki, pl. 3, fig. 8; text-figs. 4, 5.
 1980 *Systematophora placacantha* (Deflandre & Cookson); Bujak, 88, pl. 21, figs. 11, 12.
 1980 *Systematophora placacantha* (Deflandre & Cookson); emend. May, 68, pl. 7, figs. 8–11.
 1981 *Systematophora placacantha* (Deflandre & Cookson); Lentin & Williams, 273.
 1981 *Cleistosphaeridium panniforme* (Gerlach); Lentin & Williams, 50.
 1983 *Systematophora placacantha* (Deflandre & Cookson); Goodman & Ford, 866, pl. 8, figs. 6–7; text-fig. 3.
non 1966 *Impletosphaeridium panniforme* (Gerlach); Morgenroth, 35, pl. 9, figs. 8–9.

Original Diagnosis of *Baltisphaeridium panniforme*

Gerlach: "Central bodies ellipsoidal to spheroidal, almost exclusively without apical caps. Upper and lower sides and margin of the theca set with numerous long, slender, solid processes, which may be simple or divided, commonly with adjacent processes grown together in fanshaped pattern and distally branched into several points. Shell membrane delicate, finely reticulate". (Gerlach, 1961, p. 197, new transl.).

Remarks. The holotype of *Baltisphaeridium panniforme*, as originally illustrated (preparation 1170/55(315); Gerlach, 1961, pl. 28, fig. 13) was far from being an ideal specimen; it was badly obscured by adherent material and contained black pyritic inclusions. In the intervening years, it has deteriorated into unrecognisability and its exact character can no longer be determined. Two paratypes were named, though neither was illustrated. One of these, preparation 1170/56(585), though in the morphological range included in Gerlach's diagnosis, differs too markedly from the holotype to serve as a suitable lectotype (see Pl. 2., fig. 4; Pl. 4, figs. 1, 5, herein); it is discussed later. The other paratype, preparation 1170/56(624), though much obscured internally and externally by pyrite crystals, corresponds much more closely to the holotype. This is reillustrated here (Pl. 3 fig. 1) and selected as lectotype.

The morphology of this specimen cannot be fully determined. Nevertheless, the nature of its processes and their arrangement into groups shows it to be a *Systematophora*; moreover, it is sufficiently similar in morphology to *S. placacantha* (Deflandre & Cookson) to be regarded as referable to that species. Accordingly, *Cleistosphaeridium* (ex: *Baltisphaeridium*) *panniforme* is here regarded as a subjective junior synonym of *Systematophora placacantha* and abandoned.

May (1980) has proposed a revised diagnosis for *S. placacantha* which has tightened its definition considerably. This revision was based, not on the Australian Miocene type material, but on latest Cretaceous (Maastrichtian) specimens from New Jersey. Whether all the specimens attributed to this species (the type material included!) accord with the emended diagnosis, remains to be determined.

The German Lower Eocene specimens allocated to *Impletosphaeridium panniforme* by Morgenroth (1966) have a circular opening and processes of a very different nature; they cannot be included into *S. placacantha*. If all other records listed in the synonymy prove acceptable on rescrutiny, then this species has a stratigraphic range from latest Cretaceous to late Miocene. Its geographic range is wide; it has been reported from Germany (Gerlach, 1961; Benedek, 1975), doubtfully from Belgium (De Coninck, 1967), more positively from France (Gruas-Cavagnetto, 1972), England (Bujak, 1980), Denmark (Piasecki, 1980), Maryland and New Jersey, U.S.A. (Benson, 1976; May, 1980), Argentina (Heisecke, 1970) and Australia (Deflandre & Cookson, 1953; Verdier, 1970). In addition, it has been recorded from submarine sediments in the North Atlantic Ocean (Ioannides & Colin, 1977), the Grand Banks and Scotian Shelf, offshore eastern Canada (Williams & Brideaux, 1975; Barss *et al.*, 1979), offshore from the southeastern United States (Stover, 1977), in the southwestern Atlantic Ocean (Goodman & Ford, 1983) and from the Tasman Sea off Tasmania (Haskell & Wilson, 1975). All records appear to come from sediments laid down in cool to warm temperate marine waters; it has yet to be reported from polar or tropical marine sediments.

Family Areoligeraceae Evitt, 1963, emend. Sarjeant & Downie, 1966

Genus *Chiropteridium* Gocht, 1960

Chiropteridium galea (Maier, 1959) emend. Sarjeant, 1983

(Pl. 2, fig. 4; Pl. 5, figs. 1, 5)

(*pars*) 1961 *Baltisphaeridium panniforme* Gerlach, 196–198.

[A full synonymy for this species is given in Sarjeant, 1983, pp. 108–109].

Paraplate 1'' is elongate and narrow, having an oblique boundary with elongate and relatively narrow 1p, which also separates the quadrate paraplate 2'' from the antapex. Paraplate 6'' is relatively small, whereas 4'' is the largest of all the paraplates. The two antapical paraplates are both comparatively small, their mutual boundary poorly seen in this specimen. Sulcus broad, extending from apex to antapex and undivided. Archaeopyle not developed.

Figured Specimen. Preparaton 1170/10, illustrated herein, Pl. 3, figs. 4–5; text-fig. 3. Lodged in the Gerlach collection, University of Tübingen.

Horizon and Locality. Middle Oligocene, depth 179 m, Emsbüren borehole no. 7, northwest Germany.

Dimensions. Figured specimen: overall length 83 μm, length of apical horn 10 μm, breadth 70.5 μm. Unique.

Remarks. This specimen is present in the preparation labelled by Gerlach as containing the holotype of *Rhynchodiniopsis* (ex: *Gonyaulax*) *tenuitabulata*. Though it is similar in size and ambitus to the holotype (as illustrated by Gerlach, 1961, pl. 25, figs. 10, 11) it is certainly not that specimen, since it has no archaeopyle and is conspicuously different in paratabulation. However, it appears certain that Gerlach attributed this specimen to *R. tenuitabulata* and quite probable that, at some stage, the preparations containing it and the holotype came to be inadvertently transposed.

The typical paratabulation pattern of *Phthanoperidinium*, both according to the emendations of Edwards & Bebout (1981) and the more recent emendation of Islam (1982), contains only five postcingulars and no posterior intercalary paraplate. However, this difference is not so great as may appear at first sight. Some species of *Phthanoperidinium*, for example *P. brooksii* Edwards & Bebout 1981 (see especially their text-fig. 3) show an inbend to the left of the sulcal margin of paraplate 1'' equivalent of paraplate 1''' of this specimen); moreover, that paraplate does not impinge upon the antapex, being separated from it by a space comparable to that occupied by paraplate 1p in the German specimen. It seems, therefore, that the two left ventral paraplates seen in this specimen have been lost in later species of *Phthanoperidinium*.

If this interpretation is correct, then it is possible that *Phthanoperidinium* was not a product of the Deflandroid lineage, but was instead a "parallel evolution", derived directly from the Gonyaulacoids. This might account for the fact, remarked on by Bujak & Davies (1983, p. 134), that its paratabulation is so unusually clear; and it calls into question the intrafamilial hierarchy proposed by those authors to include this genus. For that

reason, I prefer to continue to treat the Phthanoperidiniaceae as a separate family, rather than reducing them to the rank of a tribe within the Subfamily Palaeoperidinioideae, as advocated by Bujak & Davies.

Since only a single specimen was available for study, however (and in particular because its style of archaeopyle is unknown), no new generic or specific name is proposed for it.

- Family Protoperidiniaceae Bujak & Davies, 1983
 Subfamily Protoperidinioideae Bujak & Davies, 1983
 Genus *Lejeunecysta* Artzner & Dörhöfer, 1978
Lejeunecysta hyalina (Gerlach, 1961) Artzner & Dörhöfer 1978, emend. nov.
 (Pl. 3, fig. 2)
- 1961 *Lejeunia hyalina* Gerlach, 1961, 169–171, pl. 26, figs. 10–11.
 1964 *Lejeunia hyalina* Gerlach; Eisenack & Klement, 485–486.
 1964 *Lejeunia hyalina* Gerlach; Downie & Sarjeant, 125.
 1967 *Lejeunia hyalina* Gerlach; Vozzhennikova, 105–106 [English transl., 1971, 161–162].
 1967 *Lejeunia hyalina* Gerlach; Sarjeant, tab. IV (p. 330).
 1968 *Lejeunia hyalina* Gerlach; De Coninck, 19, pl. 1, figs. 28–29; pl. 2, figs. 6–7.
 1972 *Lejeunia hyalina* Gerlach; emend. Kjellström, 469 [taxonomic change only].
 1973 *Lejeunia hyalina* Gerlach; Lentin & Williams, 85.
 1975 *Lejeunia hyalina* Gerlach; De Coninck, 15, 21, 59.
 1975 *Lejeunia hyalina* Gerlach; Auffret & Gruas-Cavagnetto, 650.
 1975 *Lejeunia hyalina* Gerlach; Harker & Sarjeant, chart 18 (p. 251).
 1976 *Lejeunia hyalina* Gerlach; Lentin & Williams, 68, 69, 71, pl. 10, fig. 145.
 1977 *Lejeunia hyalina* Gerlach; Lentin & Williams, 1976.
 1977 *Lejeunia hyalina* Gerlach; De Coninck, encl. 1.
 1978 *Lejeunecysta hyalina* (Gerlach); Artzner & Dörhöfer, 1381.
 1978 *Lejeunia hyalina* Gerlach; Stover & Evitt, 112.
 1979 *Lejeunecysta hyalina* (Gerlach); Artzner *et al.*, fig. 244 (p. 109).
 1980 *Lejeunia hyalina* Gerlach; Liengjareern, Costa & Downie, tab. 1.
 1980 *Lejeunia hyalina* Gerlach; Bujak, Downie, Eaton & Williams, tab. 7B (p. 19).
 1981 *Lejeunecysta hyalina* (Gerlach); Lentin & Williams, 170.

- 1983 *Lejeunia hyalina* Gerlach; De Coninck, Geets & Willems, 89.
- non 1972 *Lejeunia hyalina* Gerlach; Kjellström, figs. 1–2.
- non 1976 *Lejeunia hyalina* Gerlach; Lentin & Williams, pl. 10, fig. 153 [Kjellström's specimen].
- non 1978 *Lejeunia hyalina* Gerlach; Wilson, 152–153, pl. 12, fig. 8.
- non 1983 *Lejeunecysta hyalina* (Gerlach); Matsuoka 106, pl. 15, figs. 5–6.

Original Diagnosis. “Typical species of the genus *Lejeunia*. Apical horn and antapical horns more or less widely splayed out. Membrane thin, striped by vertically directed foldlets. Girdle furrow narrow, only slightly sunken, with distance of offset of 1/2 to 1 furrow breadth. Longitudinal furrow indicated”. (Gerlach, 1961, p. 169, new transl.).

Emended Diagnosis. Proximate, cingulotabulate peridinioid cysts, acavate, apparently formed of autophragm only. Ambitus broadly rounded-subpentagonal, prolonged into a single, very short apical horn and two larger antapical horns, set widely apart. Overall length and overall breadth typically equal. Epitract almost hemispheroidal, surmounted by a broad-based, nipple-like apical horn; hypotract in the form of a slightly obliquely truncated cone, the horns arising from the angles. Left antapical horn slightly longer and somewhat more acute than right. Cingulum extremely narrow and bordered by raised ridges that form acute angles on the left and right flanks, imparting pentagonality to the ambitus; only slightly laevorotatory, its two ends scarcely differing in anteroposterior position. Sulcus marked by the gap between the ends of the cingulum and by an inbulge of the ventral surface that is more marked posteriorly than anteriorly. Surface of phragma laevigate or very finely granulate, marked by irregular longitudinal lines running from anterior to posterior across both surfaces of the cyst. Adjacent lines may be parallel or may converge or diverge.

Archaeopyle single-plate intercalary, type I, symmetrically positioned on the dorsal surface and formed by loss of a portion of the cyst wall equivalent to a linteoid anterior intercalary paraplate (2a) in which sides H₂ and H₄ are of similar size and the whole outline closely comparable to text-fig. 3A of Bujak & Davies (1983).

Holotype. Preparation 1170/23(677), figured by Gerlach, 1961, pl. 26, figs. 10–11, and herein, pl. 3, fig. 2. Lodged in the Gerlach collections, University of Tübingen. **Paratypes** A. Preparation 1170/24 (670). B. Preparation 1170/25(679). Same depository.

Type Horizon and Locality. Upper Oligocene, depth 151 m, Emsbüren borehole no. 7, northwest Germany.

Dimensions. Holotype: length 93 μm, breadth 93 μm. Paratype A: length 84 μm, breadth 74 μm (slightly obliquely positioned). Paratype B: length 92 μm, breadth 92 μm. Range of dimensions: length 61–93 μm (mean 85 μm), breadth 61–93 μm (mean 81 μm). Measured specimens: 5.

Remarks. The longitudinal surficial lines that characterise this species are difficult to interpret. They are too narrow, and too uniform, to seem a likely product of post-mortem shrinkage. These lines are absent from the hollow between the two antapical horns, nor do they seem to traverse the cingulum. It is likely that they include, or mask, traces of a paratabulation and it is possible that they reflect growth stages of the motile theca.

The style of archaeopyle formation in *L. hyalina* remained long a source for controversy. Had Gerlach's illustrations been reproduced at larger scale, this might have been avoided, for an intercalary archaeopyle is present in the lower (dorsal) surface of the holotype itself (see Pl. 3 fig. 2).

The Swedish Upper Cretaceous specimen attributed to *Lejeunecysta* (then *Lejeunia*) *hyalina* by Kjellström (1972) has a very much larger intercalary archaeopyle and appears to be tricornucavate. I consider it referable to *Phelodinium magnificum* (Stanley, 1965) Stover & Evitt, 1978. The Late Cretaceous specimen figured by Wilson (1978) also corresponds better with *Phelodinium magnificum*. The Japanese Miocene forms described by Matsuoka (1983) are too elongate, and have antapical horns that are too short, for retention in *L. hyalina*; in ambitus they are perhaps closest to *L. beninensis* Biffi & Grignani, 1983, but they lack the tiny antapical hornlets which characterise that species. It is likely that Matsuoka's specimens should be placed into a new species of *Lejeunecysta*. Vozzhennikova's record (1967) is unaccompanied by illustrations and must be distrusted accordingly. The Norwegian/Greenland Sea forms of Middle Oligocene to Early Miocene date reported by Manum (1976) are, from his illustration, too dissimilar in morphology to be retained in this species.

Lejeunecysta hyalina has a known range from Early Eocene (Ypresian) to Late Oligocene. It is recorded from Germany, Belgium (De Coninck, 1968, 1975; De Coninck *et al.*, 1983), England (Liengjaren *et al.*, 1980; Bujak *et al.*, 1980), the Netherlands (De Coninck, 1977) and submarine sediments of the English Channel (Auffret and Gruas-Cavagnetto, 1975). This species is absent from the rich Oligocene *Lejeunecysta/Phelodinium* assemblage described by Biffi & Grignani (1983); and, indeed, no extra-European records have yet been published.

STRATIGRAPHICAL RESULTS

In Table 1 is given a list of species described originally by Gerlach and redescribed in this paper or earlier ones by Benedek & Sarjeant (1981) and Benedek, Gocht & Sarjeant (1982). For simplicity of reference, the arrangement adopted is alphabetical. (The justifications for the ranges quoted are set forth above or in the earlier papers). Species in Gerlach's assemblage that have not yet been re-examined are omitted from this Table.

Two species, *Leptodinium membranigerum* and *Rhynchodiniopsis tenuitabulata*, and the form here styled *?Phthanoperidinium* sp. are known as yet only from Gerlach's assemblage. One species, *Systematophora placacantha*, is long-ranging and another, *Achomosphaera triangulata*, potentially so. All other species appear to be of stratigraphical utility in the identification of middle to late Palaeogene strata at outcrop or in subsurface.

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Table 1. Present and original names and stratigraphical distribution of re-examined species in the Gerlach Collection, University of Tübingen.

PRESENT SPECIES NAME	ORIGINAL NAME (GERLACH, 1961)	KNOWN STRATIGRAPHIC RANGE
<i>Achomosphaera triangulata</i> (Gerlach)	<i>Baltisphaeridium triangulatum</i>	Late Eocene-Middle Miocene
<i>Areosphaeridium dictyostilum</i> (Menéndez)	<i>Baltisphaeridium pectiniforme</i> (pars)	Late Eocene-?Middle Oligocene
<i>Areosphaeridium pectiniforme</i> (Gerlach)	<i>Baltisphaeridium pectiniforme</i> (pars)	Middle Eocene-Late Oligocene
<i>Chiropteridium galea</i> (Maier)	<i>Baltisphaeridium panniforme</i> (pars)	Early Oligocene-Middle Miocene
<i>Emslandia emslandensis</i> Gerlach	<i>Emslandia emslandensis</i>	Middle Oligocene-Middle Miocene
<i>Lejeunecysta hyalina</i> (Gerlach)	<i>Lejeunia hyalina</i>	Early Eocene-Late Oligocene
<i>Leptodinium membranigerum</i> Gerlach	<i>Leptodinium membranigerum</i>	Late Oligocene
<i>Pentadinium laticinctum</i> Gerlach	<i>Pentadinium laticinctum</i> <i>Pentadinium taeniagerum</i>	Late Eocene-Middle Miocene
<i>?Phthanoperidinium</i> sp.	<i>Gonyaulax tenuitabulata</i> (pars)	Middle Oligocene
<i>Rhynchodiniopsis tenuitabulata</i> (Gerlach)	<i>Gonyaulax tenuitabulata</i> (pars)	Late Oligocene-?Middle Miocene
<i>Systematophora placacantha</i> (Deflandre & Cookson)	<i>Baltisphaeridium panniforme</i> (pars)	Latest Cretaceous-Late Miocene

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