

FOSSIL MICROPLANKTON IN DEEP-SEA CORES FROM THE CARIBBEAN SEA

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ABSTRACT. Quaternary fossil microplankton is described from three piston cores taken in the Caribbean Sea. Two cores were from the abyssal plain of the Yucatan Basin in the western Caribbean and the third from the Cariaco Trench, a deep-water depression lying within the continental shelf off Venezuela. This microplankton includes five new genera and eighteen new or reclassified species of dinoflagellates. Its stratigraphic distribution is outlined and its origin and ecology is discussed.

INVESTIGATION of the organic microplankton in Quaternary marine deposits was neglected for decades while research into Palaeozoic, Mesozoic, and Tertiary microplankton progressed. The belief that hystrichospheres were extinct arose because the apparent absence of living forms from modern plankton was accentuated by the difficulties involved in sampling Holocene or Pleistocene marine deposits. Similarly, the phylogenetic relationships between fossil dinoflagellates and living dinoflagellates remained unknown partly because the Quaternary constituted a palaeontological hiatus for microplankton.

Recently, certain problems concerning the nature and distribution of living and fossil microplankton throughout the Quaternary were examined with encouraging results. Evitt and Davidson (1964) and Wall (1965) demonstrated that microplankton (including 'hystrichospheres') with archeopyles were the resting spores (cysts) of dinoflagellates, thus unounding the 'extinction hypothesis' and removing a major objection against recognition of the valid existence of Quaternary microplankton. In the fields of systematics and stratigraphy, Rossignol's pioneer work (Rossignol 1961, 1962, 1964) on the Quaternary of Southern Israel and the Nile Delta demonstrated the abundance of microplankton in these deposits and exemplified its value in subsurface correlations. Similarly, West (1961) also encountered numerous microplankton in his study of the marine Early Pleistocene in Norfolk, England.

This paper represents an initial extension of microplankton studies into the realm of marine geology. It describes microplankton from three Kullenberg piston cores taken in the Caribbean Sea during R/V *Atlantis* cruises A-240 in 1957 and A-254 in 1960. Two of these cores (A254/330 and A254/327) came from the abyssal plain of the Yucatan Basin situated south of Cuba and the third (A240/18) came from the Cariaco Trench, a deep-water trench located within the limits of the continental shelf north of the Venezuelan coast (Table 1; text-fig. 1).

The general topography of the Caribbean Sea floor including its northernmost basin, the Yucatan Basin, was described by Wust (1963, p. 166). Core A254/330 was taken in the centre of the Yucatan abyssal plain and core A254/327 along its north-easterly extension towards the continental rise south of the Isla de Pinos and Gulf of Batabano. The geology of the Cariaco Trench was described by Athearn (1965) and its hydrography and stagnation discussed by Richards and Vacarro (1956) and Heezen,

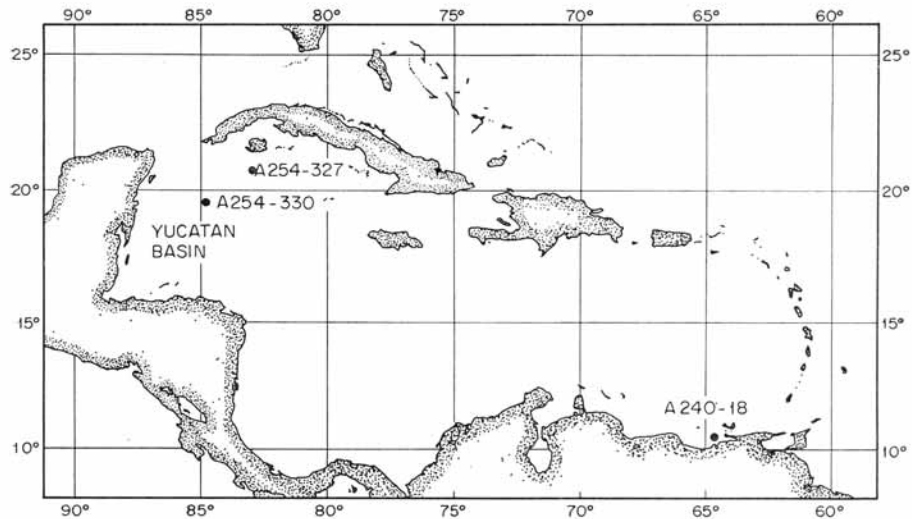
Menzies, Broecker, and Ewing (1958) respectively. Core A240/18 was taken in the eastern deep-water basin of the trench.

LITHOLOGICAL DESCRIPTIONS OF THE CORES

Core A254/330. This core comprises a light grey (N7) lutite from 34.5 cm. to its base at 605 cm. Above there are thin (1–8 cm.) alternating bands of yellowish grey (5Y 7/2),

TABLE I. Locations, depths, and lengths of cores.

Core	Latitude	Longitude	Depth in metres	Length in centimetres
A254/330	19° 35' N.	84° 51' W.	4,430	605
A254/327	20° 45' N.	83° 00' W.	4,355	499
A240/18	10° 30.8' N.	64° 40' W.	1,344	952



TEXT-FIG. 1. Location of cores.

light olive grey (5Y 6/1), and grey (N3, N5) lutites. Foraminifera are only abundant above 34.5 cm. and the sediments are extremely fine-grained in their absence. The basal grey lutite is highly calcareous (60–70% CaCO_3) and contains calcitic dust, some foraminifera and microforaminifera, rhabdoliths, coccoliths, and discoasters, the latter in a poor state of preservation. Samples: 4, 10, 18, 27, 40, 150, 180, 240, 355, 455, and 600 cm.

Core A254/327. From the surface to 397 cm. excepting a thin light brown (5YR 6/4) lutite band between 9 and 16 cm., this core comprises a loosely compacted, light grey, coarse globigerina-pteropod ooze almost entirely composed of foraminifera and pteropods with fine shell debris including gasteropods and lamellibranch sprat, rare ostracods and, near the base in particular, frequent pieces of carbonized wood. From 397 cm. to the base at 499 cm., there is a series of lutite bands. These are greenish grey (5GY 7/1)

down to 439 cm. and light yellowish grey (5Y 7/1) below. They are silty between 450 and 477 cm. Other fine silt laminae occur at 402, 407–10, and 424 cm. Samples: 2, 11, 16, 40, 125, 180, 250, 350, 390, 400, 411, 420, 434, 443, 459 cm.

Core A240/18. This core is a greyish olive silt and clay succession, mostly unlaminated but with restricted zones containing laminated bands, each only a few centimetres thick, at over twenty levels. Foraminifera were abundant only at 195 cm. This and other cores from the Cariaco Trench were described by Athearn (1965, figs. 4–6). Samples: 25, 80, 175, 275, and 380 cm.

The numerical colour code is from the Geological Society of America Rock Colour Chart.

CYST-THECA RELATIONSHIPS AND TAXONOMY

Fossil dinoflagellates are studied to trace the phylogeny of the group and facilitate its stratigraphic applications. In my opinion both purposes are served best by retaining the existing taxonomic system for the fossils even though the possibility of combining certain fossil and modern categories has arisen recently. The fossil taxonomy cannot be abandoned for practical reasons (Deflandre 1964, p. 5029; Evitt and Davidson 1964, p. 10) but it can be improved by more precise morphological observations. They will increase the value of stratigraphic and phylogenetic studies.

If, for practical reasons, two systems of classification must coexist their mutual relationships need to be understood. Eventually most Pleistocene and some late Tertiary cysts will be correlated with their parental thecae; how then will the two systems compare? Initial indications are that the scope of a fossil genus (e.g. *Hystrichosphaera*) will be coincident with that of a subgeneric thecate group (e.g. the 'Spinifera' group of *Gonyaulax*). If this applies to other groups as seems probable from research on modern cysts, then the scope of a fossil genus is narrower than the thecate genus which in this sense is polyphyletic. The phylogeny of a thecate subgeneric group will be traced through the fossil record by the history of a cyst genus with its constituent species. Conversely, prior knowledge of a cyst–theca relationship could aid in formulation of a fossil genus. Perhaps eventually the scope of modern dinoflagellate genera can be revised to coincide more precisely with the fossil scheme. Cysts of modern dinoflagellates are seldom common in plankton, but they are not so rare as once believed; over fifty types with archeopyles have now been isolated from Woods Hole plankton.

One serious hazard to successful correlation of the two systems is the case where a fossil genus envelops a wide morphological range of species with variable archeopyles, potentially belonging to several different thecate genera or species-groups. The two largest microplankton genera, *Hystrichosphaeridium* (Deflandre 1937) Eisenack 1958 and *Baltisphaeridium* (Eisenack 1958) Downie and Sarjeant 1963, are heterogeneous in this context. They were established before the taxonomic value of the archeopyle and other dinoflagellate cyst characters was realized. Now they need to be restricted as their species are re-interpreted and reclassified. For example, *Baltisphaeridium* (type species: *B. longispinosum* Eis., a Lower Palaeozoic species with a circular pylome) is a genus for acanthomorphitid acritarchs (Downie, Evitt, and Sarjeant 1963, p. 7) and should not include dinoflagellate cysts. Again, *Hystrichosphaeridium* should be restricted to include

only species with tubular, plate-centred processes and apical archeopyles comparable with the type species, *H. tubiferum* (Ehrenberg 1838) Deflandre 1937. To rectify this situation necessitates the creation of new genera: the disadvantage is more names to manipulate, but the advantage of an increased understanding of the chronological, phylogenetic, and ecological distribution of microplankton is considerable. This taxonomic trend is clearly foreshadowed by Evitt's (1961, 1963) reviews. Consequently, three new genera are created for species previously allocated to *Baltisphaeridium* and *Hystrichosphaeridium*. They are diagnosed with particular reference to their archeopyles, spine structure, and arrangement.

TABULATION PATTERNS AND TAXONOMY

Detailed tabulation patterns were determined for all Caribbean species with sutural septa. The constant similarity of their plate-area patterns was surprising. Species belonging to different genera (*Hystrichosphaera*, *Leptodinium*, or *Gonyaulacysta*) according to pre-existing criteria had identical plate patterns (text-fig. 2). The formula was always gonyaulacid, 3-4', Oa, 6", 6g, 5-6"', 1p, 1'''. While tabulation is a useful and often diagnostic character, obviously in this case ornamentation must assume a role of equal importance if these genera are to remain separated.

LEPTODINIUM KLEMENT VERSUS GONYAULACYSTA DEFLANDRE

There is no basic difference between the tabulation patterns of *Hystrichosphaera*, *Gonyaulacysta*, or *Leptodinium*. Allowing for the fact that we are dealing with cysts reflecting the tabulation of their parental thecae in differing degrees of perfection (especially in the ventral area), members of all three genera exhibit orthodox gonyaulacid tabulation. But ornamentation can serve as a basis for separation if *Leptodinium* is reserved for species possessing only low, narrow sutural septa of more or less equal height but lacking either the plate-cornered spines of *Hystrichosphaera* or the more elaborate crispate or otherwise serrated septa of *Gonyaulacysta*. There is a case for combining *Leptodinium* and *Gonyaulacysta*, but for the reasons expressed above, phylogeny and stratigraphy may benefit by their continued separation. For example, only species of *Leptodinium* as defined here (and not *Gonyaulacysta*) occur in the Quaternary which emphasizes the comparatively distant relationship between *Gonyaulacysta* and extant *Gonyaulax*. In fact, *Gonyaulacysta* as currently defined (Deflandre 1964, p. 5030) includes only extinct species represented by their cysts. The same argument applies to use of the broader diagnoses of *Baltisphaeridium* and *Hystrichosphaeridium* when dealing with Quaternary microplankton. Use of these names implies that species comparable with their respective species exist as living or post-Tertiary organisms which to the extent of existing knowledge is incorrect.

SYSTEMATIC DESCRIPTIONS

Class DINOPHYCEAE

Order PERIDINIALES

Family GONYAULACACEAE Lindemann

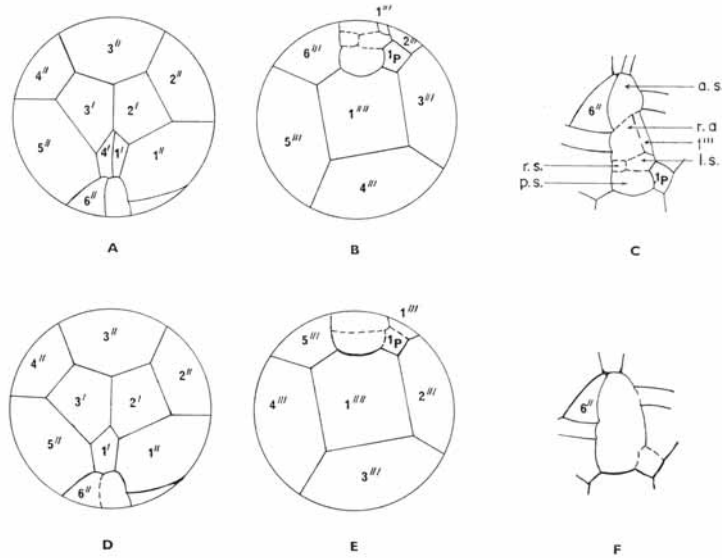
Genus HYSTRICHOSPHAERA (O. Wetzel) Deflandre 1937

Revised diagnosis. Ovoid to circular dinoflagellate cysts with sutural septa and spines developed from the outer of a two-layered cell wall reflecting a tabulation of 3-4', Oa, 6'', 6g, 5-6'', 1p, 1'''. Archeopyle dorsal and precingular (3''), precingular plate-area 6'' triangular. Spines not extensively united distally.

Hystrichosphaera furcata (Ehr.) O. Wetzel 1932

Plate 14, figs. 1, 2; text-fig. 2

Description. The test is ovoid with broadly rounded apices; circular in polar view. The girdle is narrow, descending and displaced by slightly more than its width ventrally;



TEXT-FIG. 2. Tabulation model for Quaternary species of *Hystrichosphaera* and *Leptodinium*. A, B, C, Complete development as seen in *H. bentori*, *H. membranacea* sp. nov., *H. tertiaria* var. *obliqua* nov., *L. paradoxum* sp. nov., and *L. sphaericum* sp. nov. in apical, antapical, and ventral projections. D, E, F, Incomplete development as seen in *H. furcata*, *H. hyperacantha*, *H. bulloidea*, *H. mirabilis*, *H. scabrata* sp. nov., *Nematosphaeropsis balcombiana*, and some specimens of *L. paradoxum*. a.s., anterior sulcal; r.a., right accessory; r.s., right sulcal; l.s., left sulcal; p.s., posterior sulcal.

the longitudinal furrow is weakly inclined, narrow anteriorly, only extending on to the epitheca for a short distance but broadening posteriorly. The tabulation (3-4', Oa, 6'', 6g, 5-6'', 1p, 1''') reflected primarily by very low sutural septa which are no more than traces between spine bases. In the apical series there are two pentagonal dorsal plate-areas and two smaller, linear ventral areas; the septum separating the latter is small and variously developed. The precingular areas are subrectangular except for plate-area 6'' which is triangular. The archeopyle is developed from plate-area 3''. The postcingular plates are also subrectangular apart from the first which, when visible, lies to the left of the furrow and is a weak linear structure comparable with that found in extant *Gonyaulax*. The

posterior intercalary area is small, anterior to the large, subrectangular antapical area. Spines are the dominant ornamentation and are situated at the corners of plates in most instances but can occur in between along the sutures. Septa are not usually well developed. The most complex spines, which are initially trifurcate and secondarily bifurcate, are found along the girdle, at the head of the furrow, around the posterior intercalary plate and at the dorsal antapical points. In these positions, two parallel branchlets of a spine may be directed along the course of a suture-trace. Intratabular areas are more or less smooth.

Dimensions. Maximum test size 43–62 μ .

Remarks. This is a conspicuous member of almost every core sample examined, and there can be little doubt that this long-ranging species not only survived into but proliferated during the Pleistocene.

Hystrichosphaera hyperacantha Deflandre and Cookson 1955

Plate 14, fig. 3; text-fig. 2

Remarks. The distinction between this species and *H. furcata* concerns the stronger development of two spines inserted along the longitudinal sutural traces between plate-area corners and the weaker tabulation pattern seen in *H. hyperacantha*. Every transitional stage between the restriction of spines to plate-area corners and a maximal development of two 'intercalary' spines (with a minute bifurcation beyond the main bifurcation) along the longitudinal suture-traces has been observed in specimens of *Hystrichosphaera* from the Yucatan Basin. Thus it is debatable whether *H. hyperacantha* is not a robust variety of *H. furcata* rather than a separate species. For statistical purposes at least, this species was grouped with *H. furcata* until further studies have been possible.

Hystrichosphaera bulloidea Deflandre and Cookson 1955

Text-fig. 2

Remarks. This species is extremely common in the marine Quaternary of the Caribbean. It is similar to *H. furcata* but is smaller, its test rarely exceeding 40 μ . It is a variable species with respect to the length of its spines and the development of septa. A culture of

EXPLANATION OF PLATE 14

- Figs. 1–16. *Hystrichosphaera* spp. 1–2, *H. furcata* (Ehr.) Wetzel, A254/330, depth 600 cm. 1, dorsal. 2, ventral; test only 48 μ . 3, *H. hyperacantha* Defl. and Cooks., A254/330, depth 455 cm.; test only 50 μ . 4, *H. bentori* Rossignol, A254/327, depth 408 cm.; ventral; test only 55 μ . 5, 6, *H. mirabilis* Rossignol. 5, A254/330, depth 600 cm.; test 58 μ . 6, A254/327, depth 420 cm., test 53 μ . 7–9, *H. nodosa* sp. nov., Holotype, A240/18, depth 25 cm.; test 57 μ . 7, dorsal. 8, apical. 9, ventral. 10–13, *H. scabrata* sp. nov., Holotype, A254/330, depth 150 cm.; test 55 μ . 10, dorsal. 11, ventral. 12, apical. 13, antapical. 14, 15, *H. membranacea* Rossignol comb. nov. A254/330, depth 180 cm., test 56 μ . 14, antero-ventral. 15, postero-ventral. 16, *H. tertiaria* Eis. and Gocht var. *obliqua* var. nov., type specimen, A254/327, depth 400 cm.; test 44 μ .
- Fig. 17. *Nematosphaeropsis balcombiana* Defl. and Cooks., A254/330, depth 240 cm.; test 42 μ .
- Figs. 18, 19. *Leptodinium aculeatum* sp. nov. 18, Holotype, A254/327, depth 459 cm.; test 36 μ . 19, A254/330, depth 27 cm., apical; test 36 μ .
- Fig. 20. *Leptodinium patulum* sp. nov., Holotype, A254/330, depth 355 cm.; test 59 μ ; dorsal.

Gonyaulax scrippsae Kofoid was started from a specimen of *H. bulloidea* suggesting this theca-cyst relationship, but confirmation by repetition has not been demonstrated.

Hystrichosphaera bentori Rossignol 1962

Plate 14, fig. 4; text-fig. 2

1961 *Hystrichosphaera bentori* Rossignol, pl. 1, figs. 7, 8.

1962 *Hystrichosphaera bentori* Rossignol, p. 132.

1963 *Hystrichosphaera bentori*; Rossignol, pl. 1, figs. 13-15, text-fig. 17.

1964 *Hystrichosphaera bentori*; Rossignol, p. 84, pl. 1, figs. 3, 7, 8, pl. 3, figs. 2, 3; text-fig. A-F.

Remarks. This species, which has been shown to be the cyst of *Gonyaulax digitale* (Pouchet) Kofoid by Evitt and Davidson (1964, p. 5) and Wall (1965, p. 312), has a reflected tabulation typical of the genus *Hystrichosphaera*. It is relatively infrequent in Caribbean deep-sea cores.

Hystrichosphaera mirabilis Rossignol 1962

Plate 14, figs. 5, 6; text-fig. 2

1962 *Hystrichosphaera mirabilis* Rossignol, p. 162.

1963 *Hystrichosphaera mirabilis* Ross.; Rossignol, pl. 2, figs. 16-21.

1964 *Hystrichosphaera mirabilis* Ross.; Rossignol, p. 86, pl. 2, figs. 1-3, pl. 3, figs. 4, 5.

Remarks. This is a common species in the marine Quarternary of the Caribbean cores examined. The spines are densely set along the sutures and are briefly bifurcate or trifurcate distally. There is a conspicuous sutural flange bordering the margins of the antapical area. The tabulation is 3-4', Oa, 6", 6g, 5-6", 1p, 1"', and the archeopyle is precingular (3"). Its shape is similar to the archeopyle of *H. furcata* but it is easily deformed. Several specimens from the Cariaco Trench were observed possessing an inner capsule whose wall was composed of a refractive, yellowish substance; they were comparable with specimens previously described by Rossignol (1963), but the inner capsule was thinner.

Hystrichosphaera nodosa sp. nov.

Plate 14, figs. 7-9; text-fig. 2

Holotype. Plate 14, figs. 7-9; test $57 \times 48 \mu$, specimen 39/5, Core A240/18, depth 25 cm., Cariaco Trench (10° 30' 8" N. 64° 40' W.).

Diagnosis. A species of *Hystrichosphaera* with much reduced spines forming small sclerotia at the plate-area angles.

Dimensions. Test $31 \times 28 \mu$ to $62 \times 52 \mu$. 20 specimens.

Occurrence. Yucatan Basin and Cariaco Trench, uncommon.

Description. The test is ovoid with weakly truncated apices. The plate-areas are defined by distinct but low (1μ or less) sutural septa and are typical in number and arrangement for the genus. The characteristic processes are restricted to the corners of plate-areas. They are small, either bifurcate or trifurcate and recurve strongly towards their

own bases or lie along the test surface so that there appears to be a small pad or sclerotium of tissue at each junction. Only rarely do the spines project more than a few microns above the test wall. The species forms a typical 3" archeopyle and has a weakly inclined furrow.

Remarks. This species gives the impression that as a cyst it was closely pressed against its parental thecal covering and that the spines were unable to develop fully, but it is not necessarily an immature form.

Hystrichosphaera scabrata sp. nov.

Plate 14, figs. 10–13; text-fig. 2

Holotype. Plate 14, figs. 10–13; test $55 \times 50 \mu$, spines 12.5μ , specimen 17/4, Core A254/330, depth 150 cm., Yucatan Basin ($19^{\circ} 35' N. 84^{\circ} 51' W.$).

Diagnosis. A species of *Hystrichosphaera* with microgranular sutural septa, membranous processes and a broad posterior ventral area.

Dimensions. Test $48\text{--}55 \mu$, processes $10\text{--}17 \mu$. Numerous examples.

Occurrence. Common in Cores A254/330 and A254/327, rarer in the Cariaco Trench.

Description. The theca is ovoid with broadly rounded apices and divided into epithecal and hypothecal hemispheres by a narrow descending girdle displaced by its own width ventrally. The test wall is thin, its outer layer forming microgranular sutural septa. Their outline in optical section is undulate and their height equivalent to one-third of the test diameter. These septa unite at the corners of plate-areas to form spine-like processes with trifurcate or further subdivided tips with strongly divergent angles. Its tabulation is typical for the genus, 3–4', Oa, 6", 6g, 5–6", 1p, and 1"', and the plate pattern as for *H. furcata* and *H. bentori*. A complex process occurs at the head of the longitudinal furrow, above which, the two ventral apical plate areas (1', 4') are situated; they may be incompletely separated. The furrow is weakly inclined and has at least four constituent platelet-areas. Usually, however, only the posterior sulcal platelet is obvious. In the postero-ventral area the posterior intercalary plate-area is well developed and almost as broad as the furrow itself at this point. The archeopyle is typical (3") and weakly rounded.

Hystrichosphaera membranacea Rossignol comb. nov.

Plate 14, figs. 14, 15; text-fig. 2

1964 *Hystrichosphaera furcata* var. *membranacea* Rossignol, p. 86, pl. 1, figs. 4, 9, 10; pl. 3, figs. 11, 12.

Holotype. Rossignol 1964, p. 86, pl. 1, fig. 4, Ashkelon, Israel; Recent. Test $57 \times 50 \mu$.

Description. The test is circular, ovoid, or weakly elongated (broader than high). Its surface is scabrate to microgranular and ornamented by membranous sutural septa which are stronger where they fuse at the corners of plate-areas. Distal projections arising from the septa are trifurcate or more complex at plate corners but bifurcate in between. There is a strong antapical dorsal and lateral flange around plate-area 1'" that is equal in height to one-third of the test diameter. The tabulation and plate pattern is typical for

the genus. The archeopyle is dorsal and precingular ($3''$) and the furrow is weakly inclined and broader posteriorly. It is possible to recognize anterior, right accessory, right and left and posterior sulcal platelet-areas within the furrow; of these, the right sulcal is very small.

Remarks. This uncommon species differs from *Hystrichosphaera mirabilis* by lacking strong rows of spines over its test; instead its processes are weak and membranous. It differs from *H. scabrata* sp. nov. by possessing a strong antapical flange. This appears to be a distinctive form which ranges back into the Miocene and worthy of elevation to specific status. Some small Tertiary specimens resemble *H. bulloidea* but lack two dorsal antapical spines seen in that species.

Hystrichosphaera tertiaria Eisenack and Gocht 1960 var. *obliqua* var. nov.

Plate 14, fig. 16; text-fig. 2

Type specimen. Plate 14, fig. 16; test $44 \times 40 \mu$, spines *c.* 12μ , specimen 17B/1, Core A254/327, depth 400 cm., $20^{\circ} 45' N.$, $83^{\circ} 00' W.$

Description. The test is ovoid, sometimes with a rudimentary apical boss, has a smooth to weakly microgranular wall, and is divided by an equatorial, narrow, descending girdle. Its tabulation is 4', Oa, 6'', 6g, 6''', 1p, 1''' and the arrangement of plate-areas is identical with that seen in *H. furcata* and *H. bentori*. The longitudinal furrow is narrow anteriorly but widens posteriorly and is oblique, while the girdle is quite strongly displaced about it. The spines are characteristic: the most complex closely resemble those of *H. tertiaria* as figured by Eisenack (1954, pl. 9, figs. 1–4, text-fig. 3) under the synonym *H. cf. furcata*. They are trifurcate with secondary branchlets which tend to remain parallel and often are connected by delicate membranes as they flare. Such spines are restricted to plate-area corners but bifurcate spines occasionally ornament longitudinal septa. The two dorsal antapical spines are particularly prominent as an aid to identification.

Dimensions. Test only 40–50 μ , spines 10–12 μ . 6 specimens measured.

Occurrence. Relatively uncommon, Core A254/327, Yucatan Basin.

Remarks. This variety differs from the typical form of *H. tertiaria* Eisenack and Gocht in being smaller (less than 50 μ), but has the characteristic spines and general appearance of the former. (The plate-pattern of *H. tertiaria* is considered to be gonyaulacid (text-fig. 2A, B) and not as originally stated by Eisenack and Gocht (1960, p. 515): this reinterpretation is based upon the original illustrations and examples from cores A254/330 and A254/327.) *Hystrichosphaera bentori* is closely related but can be distinguished by its stronger apical boss and more numerous processes.

Genus NEMATOSPHAEROPSIS Deflandre and Cookson 1955

Nematosphaeropsis balcombiana Deflandre and Cookson 1955

Plate 14, fig. 17

Remarks. This is a persistent but relatively infrequent species in the Caribbean marine Quaternary from the Yucatan Basin and Cariaco Trench. It is recognizable by its outer

trabeculum of parallel strands suspended above sutural septal traces by spines at the corners of plate-areas. Its tabulation and archeopyle are similar to those of *Hystrichosphaera furcata*. There may be two varieties in the Pleistocene: one form possesses a relatively small, globular central body, whose diameter is around $25\ \mu$ and whose spines are equal to a radius; the other is more robust and has an ovoid central body with a maximum length around $40\ \mu$ and has spines equivalent to one-third of this dimension. Both range from the Miocene or earlier into the Holocene.

Genus LEPTODINIUM Klement 1960 emend.

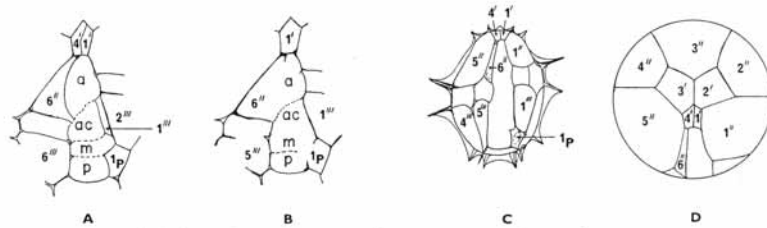
Revised diagnosis. Ovoid, spherical, or polyhedral tests ornamented with more or less level, low sutural septa (but not with spines), developed from the outer of a two-layered wall, reflecting a tabulation of 3-4', Oa, 6'', 6g, 5-6'', 1p, 1'''. Girdle spiral, ventral sulcus only just extending on to the epitheca and in contact with 1'. Archeopyle dorsal and precingular (3''). Apical or antapical projections essentially absent.

Remarks. Development of a linear, gonyaulacid first postcingular plate-area in cysts is variable and unreliable as a criterion for separating *Leptodinium* from *Gonyaulacysta*, but the characteristic sutural septa and lack of apical structures in *Leptodinium* are distinctive.

Leptodinium aculeatum sp. nov.

Plate 14, figs. 18, 19; text-figs. 3c, d

Holotype. Plate 14, fig. 18; test $36 \times 29\ \mu$, specimen 7/8, Core A254/327, depth 459 cm., Yucatan Basin ($20^{\circ} 45' N. 83^{\circ} 00' W.$).



TEXT-FIG. 3. Tabulation schema for *Leptodinium* spp. A, B, *L. paradoxum* sp. nov., ventral variation C, D, *L. aculeatum* sp. nov., ventral and apical. a, anterior; ac, accessory; m, median; p, posterior ventral platelet areas.

Diagnosis. A relatively small, ovoid species with a relatively wide girdle zone and extensive ventral area; test hyaline with sutural septa most strongly developed in the posterior intercalary area; precingular plate-area 6'' very narrow.

Dimensions. Test only $28-38\ \mu$ long; septa up to $9.5\ \mu$ high. Over 100 specimens.

Occurrence. Yucatan Basin; Pleistocene, and Holocene.

Description. The test is ovoid and divided into more or less equal epithecal and hypothecal regions by a relatively wide, weakly descending girdle, displaced by its own width ventrally. It is ornamented by hyaline, sutural septa whose maximum elevation (equiva-

lent to one-quarter of the diameter) is found at the corners of plate-areas and along the left margin of the ventral area, especially near the posterior intercalary area; in between the septa are lower. At the equator the septa are inclined so that the girdle plate-areas widen distally. The tabulation is 3-4', Oa, 6'', 6g, 5''', 1p, 1'''. There are two pentagonal dorsal apical plate-areas (2', 3') and two minute median ventral areas (1', 4'). Precingular areas 1'' to 5'' are subrectangular, the sixth is linear and narrow; plate-area 3'' forms a trapezoidal archeopyle. There are five subrectangular postcingular areas, 1''' and 5''' being smaller than the others; the adjacent posterior intercalary plate-area is small and the outer test wall may be completely separated from the inner at this point. There is a single small, subquadrangular antapical area. The longitudinal furrow occupies almost the entire length of the ventral area, extending well into the epitheca. It occupies approximately one-third of the equatorial diameter and widens slightly posteriorly.

Leptodinium patulum sp. nov.

Plate 14, fig. 20; Plate 15, figs. 1-4; text-fig. 4

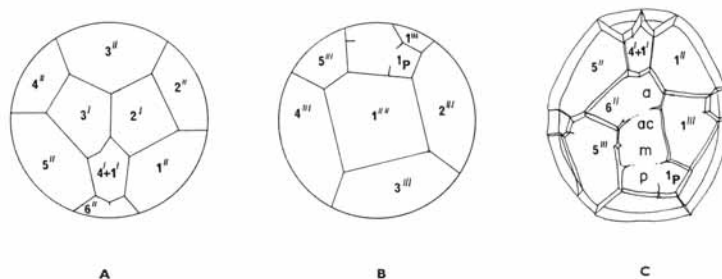
Holotype. Plate 15, figs. 1, 2; text 50 × 55 μ, specimen 10/8, Core A254/330, depth 355 cm., Yucatan Basin (19° 35' N. 84° 51' W.).

Diagnosis. An ovoid species of *Leptodinium* ornamented with low, level sutural septa forming a plate-area pattern characteristically reduced on the ventral surface. Test rarely less than 40 μ.

Dimensions. Test only 38-62 μ long, 34-55 μ broad; septa 2.5 to 7 μ high. Over 50 specimens.

Occurrence. Yucatan Basin, relatively infrequent; known from the Middle Miocene to Holocene.

Description. The test appears weakly ovoid in lateral view and circular in polar view. Its surface is smooth to weakly microgranular and bears a pronounced reflected tabulation defined by low, level sutural septa approximately equivalent to one-tenth of the test diameter in height. The formula is 4', Oa, 6'', 6g, 5''', 1p, 1'''. The test is divided into



TEXT-FIG. 4. Tabulation of *Leptodinium patulum* sp. nov. A, apical; B, antapical; C, ventral.

epithecal and hypothecal regions by a relatively narrow, weakly descending girdle; dorsally the girdle plate-areas are complete, but only the uppermost of the delimiting septa are present along two cingular plate-areas on the ventral surface adjacent to the furrow. The epitheca lacks intercalary plate-areas. The apical series comprises two large pentagonal dorsal plate-areas (2' and 3') and a smaller, median ventral, compound

plate-area representing 1' and 4'; here there is no complete division into two plate-areas but there is a significant re-entrant angle in the septum separating this areas from 3'. There are five discrete, subrectangular precingular plate-areas; 3" forms a conspicuous dorsal archeopyle with its borders slightly within the septa. The sixth precingular plate-area is not differentiated from the anterior sulcal platelet-area with which it forms a compound area in the mid-ventral equatorial region. The remainder of the furrow extends posteriorly and is almost entire; median and posterior platelet-areas are only indicated by rudimentary septal ingrowths. Similarly, the septum separating the relatively larger posterior intercalary plate-area from the furrow may be developed only partially. The remainder of the hypotheca comprises five large, subrectangular plate-areas and one quadrangular antapical (1").

Remarks. The characteristic tabulation of this species differentiates it clearly from any previously described.

Leptodinium paradoxum sp. nov.

Plate 15, figs. 5-8; text-figs. 2, 3A, B

Holotype. Plate 15, fig. 5; test only $31 \times 26 \mu$, specimen 8/6, Core A254/330, depth 40 cm., Yucatan Basin ($19^{\circ} 35' N.$, $84^{\circ} 51' W.$).

Diagnosis. A very small ovoid species with a tabulation 3-4', Oa, 6", 6g, 5-6"', 1p, 1"', defined by low sutural septa which are sometimes reduced in the ventral area. Test not exceeding 40μ .

Dimensions. Test only 29-38 μ ; septa around 3 μ . Over 50 specimens.

Occurrence. Yucatan Basin; known range of Middle Miocene to Holocene.

Description. The test is ovoid to polyhedral and divided equatorially into epithecal and hypothecal regions by a relatively wide, descending girdle displaced by its own width ventrally. The longitudinal furrow broadens on to the hypotheca and is weakly inclined. The sutural septa are hyaline and very low (equivalent to approximately one-tenth of a diameter); the test varies from smooth to microgranular. The apical plate series comprises two pentagonal dorsal areas and a linear, median compound ventral area which may be

EXPLANATION OF PLATE 15

- Figs. 1-4. *Leptodinium patulum* sp. nov. 1, 2, Holotype, A254/330, depth 355 cm.; test 59 μ , apical and postero-ventral. 3, A254/330, depth 27 cm.; test 58 μ , ventral. 4, A254/330, depth 150 cm., test 60 μ , antero-ventral.
- Figs. 5-8. *Leptodinium paradoxum* sp. nov. 5, Holotype, A254/330, depth 40 cm.; test 31 μ , antapical. 6, A254/330, depth 240 cm.; test 30 μ , apical. 7, 8, Upper Miocene, near Guadalupe Island, both tests 36 μ and ventral views showing complete and incomplete plate-patterns.
- Figs. 9, 10. *Leptodinium striatum* sp. nov. 9, Holotype, A254/330, depth 355 cm.; test 36 μ . 10, A254/330, depth 180 cm.; test 36 μ , ventral.
- Figs. 11-15. *Leptodinium sphaericum* sp. nov. 11, 12, Holotype, A254/330, depth 10 cm.; test 50 μ , dorsal and apical. 13-15, A254/330, depth 240 cm.; test 55 μ , dorsal, antero- and postero-ventral.
- Figs. 16, 17. *Lingulodinium machaerophorum* Defl. and Cooks., comb. nov., 16, A254/327, depth 434 cm.; test only 44 μ . 17, A254/330, depth 600 cm.; test 40 μ .
- Figs. 18-20. *Hemicystodinium zoharyi* Rossignol comb. nov., A254/330, depth 600 cm.; test only 65 μ . Optical, polar, and lateral views.

divided longitudinally to form two areas (1' and 4'). Precingular areas 1'' to 5'' are sub-rectangular, 3'' being an archeopyle; 6'' is triangular and either incompletely separated from the furrow or possessing a concave outer margin. The furrow may be divided into three platelet-areas by very reduced septa. The girdle plate-areas are rectangular; sections of the septa outlining 5g and 6g may be missing. There are usually five postcingular areas but in some specimens there are six due to the additional presence of a small linear first post-cingular area, 1'''. There is a small posterior intercalary area and a quadrangular antapical area.

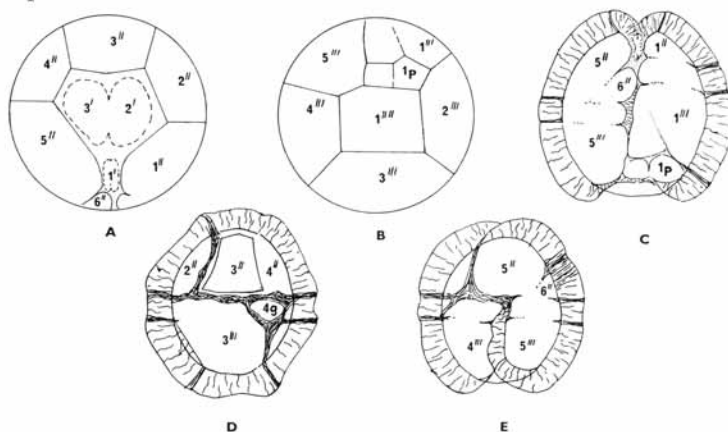
Remarks. *L. paradoxum* sp. nov. recalls *L. patulum* sp. nov. in some details of its tabulation but is smaller. It differs from *L. aculeatum* sp. nov. in outline and in configuration of the sixth precingular area.

Leptodinium strialatum sp. nov.

Plate 15, figs. 9, 10; text-fig. 5

Holotype. Plate 15, fig. 9; test only $36 \times 29 \mu$, specimen 11/1, Core A254/330, depth 355 cm., Yucatan Basin ($19^{\circ} 35' N.$, $84^{\circ} 51' W.$).

Diagnosis. A small species of *Leptodinium* with relatively broad, weakly radially striate sutural septa reduced in the ventral area.



TEXT-FIG. 5. Tabulation of *Leptodinium strialatum* sp. nov. A, apical; B, antapical; C, ventral; D, dorsal; E, right lateral.

Dimensions. Test only $26-38 \mu$, septa $5-10 \mu$. Over 50 specimens.

Occurrence. Yucatan Basin; known range from Middle Miocene to Holocene.

Description. The test is ovoid with broadly rounded apices and smooth to weakly microgranular. It is ornamented by relatively broad sutural septa (equivalent to between one-fifth and a quarter of the equatorial diameter) with weak radial striations. These indicate a tabulation of 3-4', Oa, 6'', 6g, 5'', 1p, 1''', whose basic pattern follows that of *Leptodinium aculeatum* sp. nov. and *L. paradoxum* sp. nov., but in *L. strialatum* the septa are

so reduced in several places that there are large, open compound areas on the test. These include two conspicuous longitudinal ventral areas where the cingular plates 6g and 1g are so reduced that the girdle is scarcely recognizable between the pre- and post-cingular series. The cingular areas on the dorsal surface also are reduced, only area 4g being complete and visible below the precingular archeopyle (3"). There is no longitudinal septum between the archeopyle and the fourth precingular area.

The structure of the ventral region is not easily discernible but there appear to be one or two minute ventral apical plates (1' and 4'), a small anterior sulcal platelet, and a reduced sixth precingular plate-area. In this region the girdle appears to be displaced by its own width. The longitudinal furrow, too, is poorly defined; its left margin is very weakly developed in particular, but posteriorly there is a conspicuous posterior sulcal platelet-area and a posterior intercalary area. Below these there is a square antapical area.

Remarks. *Pentadinium laticinctum* Gerlach 1961 is similar in overall appearance but is considerably larger and different in details of tabulation.

Leptodinium sphaericum sp. nov.

Plate 15, figs. 11-15; text-fig. 2a-c

Holotype. Plate 15, figs. 11, 12; test only $50 \times 43 \mu$, specimen 29/2, Core A254/330 depth 10 cm., Yucatan Basin (19° 35' N., 84° 15' W.).

Diagnosis. A spherical to polyhedral species with very low sutural septa defining a tabulation 4', Oa, 6", 6g, 6"', 1p, 1'''; test with a small apical boss. Size approximately 40-58 μ .

Dimensions. Test 43-58 μ including apical boss; septa around 3 μ . 9 specimens.

Occurrence. Yucatan Basin; Pleistocene and Holocene.

Description. The test is spherical to polyhedral and has a small blunt apical boss. Its surface is weakly microgranular and ornamented by very low sutural septa, only a few microns high. Its tabulation is 4', Oa, 6", 6g, 6"', 1p, 1'''. The girdle is narrow, descending, composed of rectangular plate-areas and divides the test equatorially into equal epithecal and hypothecal regions; ventrally the girdle is displaced by slightly more than its own width. The longitudinal furrow is quite strongly inclined and comprises five platelet-areas, namely, anterior, right accessory, right and left sulcal, and posterior sulcal; of these, the right sulcal is very small while the posterior sulcal is large. There are two pentagonal dorsal apical areas and two linear median anterior ventral areas in the apical series. The precingular series comprises six areas, of which the third forms an archeopyle and the sixth is triangular with a concave left margin. There are six post-cingular areas, 1'' being a small linear structure on the left margin of the sulcus; the other areas are subrectangular. The posterior intercalary area is relatively large and anterior to a quadrangular antapical area (1''').

Remarks. An identical cyst was isolated from a plankton haul in the North Atlantic (40° 00' N., 71° 15' W.) in July 1963 at a depth not greater than 100 metres. It had colourless cell contents and no archeopyle but otherwise was identical with fossil specimens from the Yucatan Basin. The shape of polyhedral varieties superficially resembles that of *Gonyaulax polyedra* Stein but in other details these species are quite different.

Genus LINGULODINIUM gen. nov.

Type species. Lingulodinium machaerophorum Deflandre and Cookson 1955 comb. nov.

Diagnosis. Spherical to ovoid dinoflagellate cysts which, after dehiscence, possess a large, compound epithecal archeopyle representing the loss of either four or five precingular plate-areas. The remainder of the epitheca forms an elongate angular projection or lingula; this corresponds to several (apical, intercalary, and one precingular) plate-areas. The test wall is microgranular to microreticulate and ornamented with numerous intratabular spines.

Lingulodinium machaerophorum Deflandre and Cookson 1955 comb. nov.

Plate 15, figs. 16, 17; text-fig. 6

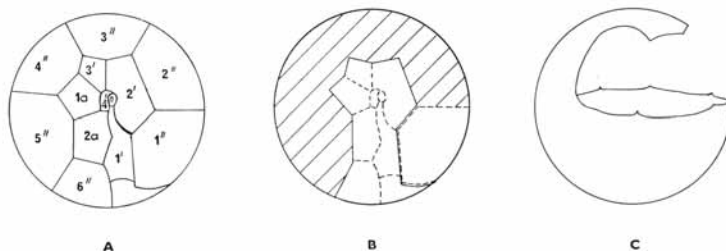
1955 *Hystrichosphaeridium machaerophorum* Deflandre and Cookson, p. 274, pl. 9, figs. 4, 8.

1961 *Hystrichosphaeridium ashdodense* Rossignol, pl. 1, fig. 9.

1962 *Hystrichosphaeridium ashdodense* Ross.; Rossignol, p. 132, pl. 2, fig. 2.

1964 *Baltisphaeridium machaerophorum* Defl. and Cooks.; Rossignol, p. 90, pl. 2, fig. 14, pl. 3, figs. 20, 21.

Description. The test is spherical but rarely found whole. Upon dehiscence it develops a large compound precingular archeopyle, so all that remains of the epitheca is a narrow, elongated, angular projection, attached to the hypotheca ventrally. The archeopyle, in its



TEXT-FIG. 6. Comparison of *Gonyaulax polyedra* Stein with *Lingulodinium machaerophorum* Defl. and Cooks., comb. nov. A, epithec tabulation of *G. polyedra*, Woods Hole, August 1965; B, plate equivalence of the archeopyle (shaded) in *L. machaerophorum*; C, lateral view of *L. machaerophorum* (spines omitted).

most entire form, represents the loss of five precingular plate-areas (1'' to 5'') but it may represent only four plates (2'' to 5'') or very rarely, only the dorsal precingular plate 3''. The test is microgranular and bears numerous (15 to 20 in optical section), flexuous, hollow spines of variable length. Their bases are circular and minutely striated; their distal extremities are flexuous, closed, and bear spinules. There is a tendency towards flattening of the spines. Size. Test 36 to 50 μ .

Remarks. This fossil species is almost certainly the cyst of *Gonyaulax polyedra* Stein, since it compares closely with the cysts described by Erdtman (1954, fig. 3B) and Evitt and Davidson (1964, p. 4, pl. 1, fig. 13). The archeopyles of the fossils have been interpreted on this assumption. In its early stages of development, the archeopyle may appear

as a simple 3" structure (see Rossignol 1964, pl. 3, fig. 21) which is comparable with that found in other cysts of *Gonyaulax*. *L. machaerophorum* is a common species both in the Yucatan Basin and Cariaco Trench cores and appears to attain its acme in the Quaternary. It certainly occurs in the Miocene, but apparently less abundantly. Records of older occurrences should be re-evaluated with particular attention to spines and archeopylar structure before the first appearance of this species is established. These structures should serve to distinguish this from other species such as *Baltisphaeridium hirsutum* Ehr.

Family INCERTAE SEDIS

Genus HEMICYSTODINIUM gen. nov.

Type species. *Hemicystodinium zoharyi* Rossignol 1962.

Diagnosis. Spherical to ovoid dinoflagellate cysts which dehisce equatorially to form hemispheres; rims of the hemispheres with a small projection or indentation and slight displacement at the mid-ventral point. Ornamentation variable, from microreticulate to spinose; spines, when present, variable in length and predominantly simple. Elements of ornamentation randomly disposed or intratabular.

Hemicystodinium zoharyi Rossignol 1962 comb. nov.

Plate 15, figs. 18–20

1962 *Hystrichosphaeridium zoharyi* Rossignol, p. 132, pl. 2, fig. 10.

1964 *Hystrichosphaeridium zoharyi* Rossignol 1962; p. 88, pl. 2, figs. 4, 9, 10, 11.

Description. Test hemispherical, the mid-ventral point marked by a small subrectangular projection and displacement of the rim. Test smooth to microreticulate, spine bases weakly striate. Spines numerous, length variable, all but a few simple and capitate, the others bifurcate.

Remarks. The parallel alignment of spines in the equatorial region reflects the position of a girdle and the mid-ventral projection or sulcal notch probably indicates the former position of the anterior limit of the longitudinal furrow. This is a common species in the Yucatan Basin and Cariaco Trench where both varieties described by Rossignol (1964, p. 88) are represented abundantly.

Genus OPERCULODINIUM gen. nov.

Type species. *Operculodinium centrocarpum* Deflandre and Cookson 1955 comb. nov.

Diagnosis. Spherical to ovoid cysts possessing simple, dorsal precingular archeopyles (reflecting plate 3"), and lacking polar structures. A weakly defined girdle and ventral sulcal depression often present. Cell wall double, the inner thin and the outer thicker and microgranular or microreticulate. Elements of ornamentation variable, from small cones to long spines but all with circular, minutely striated bases and often capitate extremities. Spine arrangement intratabular with several spines to each plate-area, commonly arranged immediately within the reflected plate-area margins.

Remarks. Members of this genus differ from species of *Apteodinium* Eisenack 1958 and

Trichodinium Eisenack and Cookson 1960 by lacking polar projections and possessing spines. Several members were allocated previously to the acritarch genus *Baltisphaeridium* but this is inadmissible for forms possessing archeopyles and other dinoflagellate cyst characteristics.

Operculodinium centrocarpum Deflandre and Cookson 1955 comb. nov.

Plate 16, figs. 1, 2, 5

- 1953 *Hystrichosphaeridium* sp. a Cookson, p. 115, pl. 2, figs. 26, 27.
 1953 *Hystrichosphaeridium* sp. b Cookson, p. 115, pl. 2, fig. 28.
 1955 *Hystrichosphaeridium centrocarpum* Deflandre and Cookson, p. 272, pl. 8, figs. 3, 4.
 1959 *Hystrichosphaeridium centrocarpum* Defl. and Cooks.; Maier, p. 314, pl. 28, fig. 9.
 1961 *Baltisphaeridium centrocarpum* Defl. and Cooks.; Gerlach, p. 192, pl. 28, fig. 9.
 1963 *Baltisphaeridium centrocarpum* Defl. and Cooks.; Brosius, p. 44, pl. 6, fig. 6, text-fig. 8a, b.

Description. The test is almost spherical and densely ornamented with slender radiating spines whose length (8–16 μ) varies between approximately one-fifth and one-quarter of the cell diameter. The dorsal precingular archeopyle is large and subtrapezoidal. The outer cell wall is microgranular and the immediate spine bases are conical with minute striations. The spine tips bear small hooklets which are visible only at high magnifications. The spines are aligned in the girdle region but there is no distinct ventral sulcus. The spine arrangement is intratabular, most spines lying alongside the sutural lines.

Dimensions. Caribbean specimens vary from 40 to 56 μ for the test alone. Miocene specimens may be much larger, with diameters approaching 90 μ .

Operculodinium israelianum Rossignol 1962 comb. nov.

Plate 16, figs. 3, 4

- 1962 *Hystrichosphaeridium israelianum* Rossignol, p. 132, pl. 2, fig. 3.
 1964 *Baltisphaeridium israelianum* Ross.; Rossignol, p. 91, pl. 2, fig. 12, pl. 3, figs. 13, 14.

Remarks. Specimens similar to those described by Rossignol are common in the Yucatan Basin and Cariaco Trench cores. Their spines vary from three to six microns and are equivalent to approximately one-tenth or less of the test diameter which ranges from 40 to 65 μ . A narrow girdle and small mid-ventral depression are visible sometimes. The dorsal archeopyle is trapezoidal and precingular. Caribbean and Mediterranean specimens examined consistently have very short spines with weakly capitate tips and in these respects differ from the description given by Rossignol (1964, p. 91). *O. israelianum* is fundamentally similar to *O. centrocarpum* according to these observations and only distinguishable by its smaller spines relative to the test size but this is a consistent feature.

Operculodinium psilatatum sp. nov.

Plate 16, figs. 6–8

Holotype. Plate 16, figs. 6–8; test 58 \times 56 μ , spines 2 μ , specimen 23/4, Core A240/18, depth 175 cm., Cariaco Trench, (10° 30' 8" N., 64° 40' W.).

Description. The test is ovoid and without polar structures. The wall is smooth, with a tectate appearance and has sparse, extremely small and delicate spines which are scarcely

visible at low magnifications except as darker spots on the test wall. There is a very well defined, narrow equatorial girdle, which is displaced slightly at the mid-ventral point. Below it there is a smaller sulcal depression with an ellipsoidal scar. The archeopyle is trapezoidal, precingular, and dorsal.

Dimensions. Test dimensions 50–60 μ maximum. Numerous examples.

Occurrence. Particularly abundant in the Cariaco Trench core A240/18, less abundant in the Yucatan Basin cores.

Remarks. The minute spines and well-developed girdle distinguish this species from *O. israelianum*.

Operculodinium giganteum sp. nov.

Plate 16, figs. 9, 10

Holotype. Plate 16, figs. 9, 10; test 84 \times 72 μ , spines 3 μ , specimen 55/1, Core A254/327, depth 420 cm. Yucatan Basin (20° 45' N., 83° 00' W.).

Diagnosis. A very large, polyhedral species bearing numerous short capitate spines and possessing traces of tabulation.

Dimensions. Test only 74–86 μ , maximum dimensions, spines 2–4 μ . 10 specimens.

Occurrence. Yucatan Basin, Core A254/327, relatively rare.

Description. The test is polyhedral with broadly truncated extremities. The wall is microreticulate or microgranular and bears numerous tiny spines. Some of these are aligned either side of suture-like lines on the test and appear to reflect a gonyaulacid tabulation where there is a small posterior intercalary plate-area and a subrectangular 6" plate-area. Full details were not determined. The girdle is equatorial, narrow, and descending and the furrow is also very narrow and marked by two parallel rows of spines. The archeopyle is dorsal and precingular (3"). The spines have conical bases and capitate tips.

Genus TECTATODINIUM gen. nov.

Type species. *Tectatodinium pellitum* sp. nov.

EXPLANATION OF PLATE 16

- Figs. 1, 2, 5. *Operculodinium centrocarpum* Defl. and Cooks., comb. nov., A254/330, depth 180 cm.; test only 54 μ .
 Figs. 3, 4. *Operculodinium israelianum* Rossignol comb. nov., A254/330, depth 180 cm.; test 53 μ .
 Figs. 6–8. *Operculodinium psilatatum* sp. nov. Holotype, A240/18, depth 175 cm.; test 58 μ ; dorsal, lateral, and ventral views.
 Figs. 9, 10. *Operculodinium giganteum* sp. nov., Holotype, A254/327, depth 420 cm.; test 84 μ ; lateral and ventral.
 Figs. 11, 12. *Tectatodinium pellitum* gen. et sp. nov. 11, Middle Miocene, near Guadalupe Island, test 50 μ . 12, Holotype, outer continental shelf near Beirut, Lebanon; test 52 μ .
 Figs. 13, 14. *Chytroisphaeridia cariacensis* sp. nov., A240/18, depth 380 cm. 13, Paratype, test 40 μ . 14, Holotype, test 52 μ .
 Figs. 15, 16. *Tuberculodinium vancampoeae* Rossignol comb. nov. 15, A254/327, depth 459 cm., over-all 101 μ . 16. A254/330, depth 600 cm., over-all 95 μ .

Diagnosis. Spherical to ovoid dinoflagellate cysts without apical, antapical, or any other form of projections. Test wall double (resembling tectate pollen), the outer layer being thicker and less compact or homogeneous than the inner. Test penetrated by a large dorsal precingular archeopyle representing the loss of one plate. A girdle or ventral sulcus rarely present.

Remarks. This genus is intended for smooth-walled microplankton resembling leiospheres but differing by possessing simple, dorsal precingular archeopyles which denote dinoflagellate affinities. It differs from *Operculodinium* gen. nov. in the absence of spinose ornamentation and from *Pyxidiella* Cookson and Eisenack 1958 by being less elongate and possessing a precingular archeopyle.

Tectatodinium pellitum sp. nov.

Plate 16, figs. 11, 12

Holotype. Plate 16, fig. 12; test $52 \times 50 \mu$, wall 5μ thick, specimen 23A/4, $33^{\circ} 34.5' N.$, $35^{\circ} 12' E.$

Description. The test is ovoid and thick-walled. The latter is double-layered, the inner being thin and homogeneous, the outer thicker and spongy; apparently it is formed by numerous, finely interwoven fibrils so that in optical section the focus is indistinct. In surface view the test appears microgranular. There is a large, dorsal, trapezoidal archeopyle but no girdle or ventral sulcus.

Dimensions. Test $40-55 \mu$, wall thickness $3-7 \mu$. Numerous examples.

Occurrence. Relatively uncommon, Yucatan Basin and Cariaco Trench; known range of Miocene to Holocene.

Remarks. Rossignol (1964, p. 92) invalidly classified Pleistocene forms which apparently belong to this species as *Leiosphaeridia scrobiculata* Deflandre and Cookson 1955. The latter species had been transferred previously to *Pyxidiella* by Cookson and Eisenack (1958, p. 52) while the genus *Pyxidiella* had been placed with the Dinophyceae by Downie, Evitt, and Sarjeant (1963, p. 13). Live specimens from the Woods Hole region have been induced to excyst and although the parental dinoflagellate has not been identified, the dinophycean affinities of this cyst seem beyond doubt.

Family PERIDINIACEAE Lindemann
Genus CHYTROEISPHAERIDIA Sarjeant 1962

Chytroeisphaeridia cariaeoensis sp. nov.

Plate 16, figs. 13, 14

Holotype. Plate 16, fig. 14; test 52μ , archeopyle $20 \times 28 \mu$, specimen 41/3, Core A420/18, depth 380 cm., $10^{\circ} 30.8' N.$, $64^{\circ} 40' W.$

Diagnosis. A spherical dinoflagellate cyst with a large elongate hexagonal dorsal intercalary archeopyle.

Dimensions. Test $36-55 \mu$ diameter. Numerous examples.

Occurrence. Abundant in the Cariaco Trench, relatively rare in the Yucatan Basin.

Description. The test is spherical, often with sharp secondary folds bordering depressions, and penetrated by a hexagonal dorsal, intercalary archeopyle. This is elongated equatorially, its width being almost equal to twice its height, while its size (around $16 \times 28 \mu$) and shape are constant. Other splits occur in the test but do not reflect a tabulation. The wall is thin and may enclose an inner capsule with either a minutely thin, hyaline wall or a waxy yellow refractive wall. There are often small, granular inclusions within the cell lumen. Unmacerated cysts are characteristically brown but they become paler after oxidation.

Comparison. *Chytroeisphaeridia simplicia* Wall 1965 differs by having an asymmetrical, hexagonal archeopyle with a length: breadth ratio of 1:1. The natural affinities of both species lie with *Peridinium*, and the archeopyle represents the loss of a dorsal intercalary plate.

Family INCERTAE SEDIS

Genus TUBERCULODINIUM gen. nov.

Type species. *Tuberculodinium vancampoeae* Rossignol 1962 comb. nov.

Diagnosis. Test discoidal, with two cell wall layers, the outer supported above the inner by numerous short, stout, tuberculate projections. Dorsal surface with a large compound archeopyle which probably corresponds to a combination of precingular and intercalary plates.

Tuberculodinium vancampoeae Rossignol 1962 comb. nov.

Plate 16, figs. 15, 16

1962 *Pterospermopsis van campoeae* Rossignol, p. 134, pl. 2, fig. 1.

1964 *Pterospermopsis van campoeae* Ross.; Rossignol, p. 90, pl. 2, figs. 17, 18; pl. 3, fig. 15.

Holotype. Rossignol 1964, p. 90, pl. 2, fig. 17; Pleistocene, Ashdod, Israel.

Description. The test is discoidal with two cell wall layers, the outer separated from the inner by numerous short, stout, hollow, tuberculate processes. These are circular in surface view, but in lateral views their shapes vary from spherical to figure-of-eight-shaped while the distal extremity of a process may flare and merge with the outer wall layer. The archeopyle is large and polyhedral; it has one long straight side and approximately eight shorter sides roughly arranged about an arc. It probably represents both dorsal precingular and intercalary plates, in which case the whole test is flattened dorso-ventrally. There are sometimes weak traces of a girdle, longitudinal furrow, and a slight posteroventral sulcal depression on the surface opposite to the archeopylar opening, which support this interpretation. Over-all variations observed in the structure of this species include loss or partial detachment of the outer layer and the presence of an inner capsule with a refractive, yellowish wall.

Occurrence. Relatively uncommon but persistent, Yucatan Basin and Cariaco Trench.

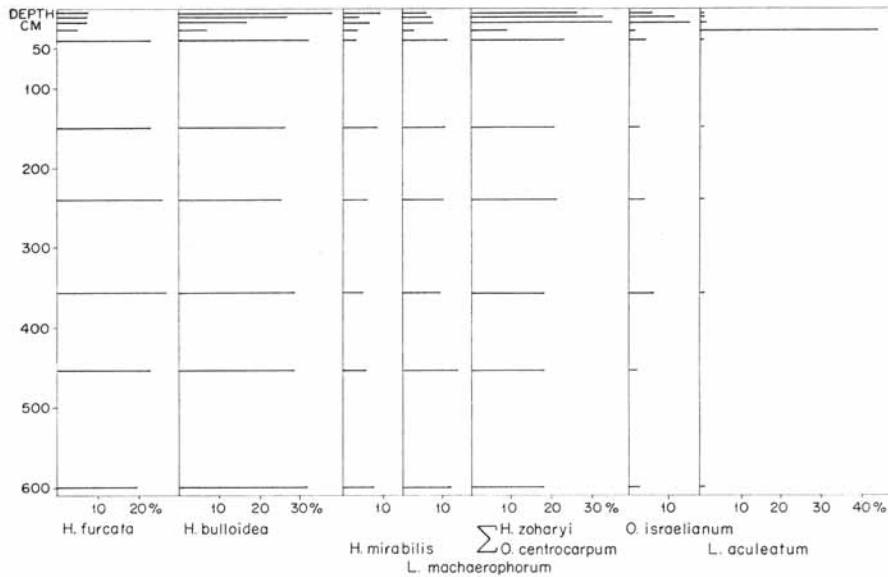
Dimensions. Over-all size from 62 to 113 μ , maximum dimensions.

Discussion. This species does not have the structure of *Pterospermopsis* and, in consideration of the presence of an archeopyle, must be regarded as a dinoflagellate cyst:

therefore it is removed from *Pterospermopsis* to a new genus. As a dinoflagellate cyst it possesses an unusual appearance and its natural affinities remain quite obscure. Its known stratigraphic range is from Miocene to Holocene.

STRATIGRAPHIC DISTRIBUTION OF MICROFOSSILS

Core A254/330. (Text-fig. 7.) Over thirty species were found in this core; sixteen occurred at every horizon examined and the remainder were distributed sporadically throughout.



TEXT-FIG. 7. Relative frequency distribution of common microplankton species in core A254/330.

Microplankton was most abundant at 240 cm. and had a minimum at 27 cm. judging by the numbers counted in approximately equal samples. In the thick grey lutite sequence below 34.5 cm. the composition of the assemblages was relatively constant; *Hystrichosphaera* species (in particular *H. furcata* and *H. bulloidea*) accounted for 59 to 64%, *Lingulodinium* gen. nov. for 9 to 14%, species of *Leptodinium* for less than 3%, and species of *Hemicystodinium* and *Operculodinium* together for 22 to 28% of the assemblages. Above 34.5 cm., the composition of assemblages varied as lithology became variable. At 27 cm. *Leptodinium aculeatum* sp. nov. formed 44%; here there was a decline in other genera rather than any overwhelming increase in *Leptodinium*. From 18 cm. to the surface there was a gradual restoration to abundance of *Hystrichosphaera*, *Hemicystodinium* gen. nov., *Lingulodinium*, and *Operculodinium* gen. nov.

Foraminifera indicate that the whole sequence in this core is Pleistocene. *Globobulimina hexagona* Natland and *G. conglomerata* Schwager are sporadic throughout, while the former associates with a relative abundance of *Globorotalia menardii menardii*

SPECIES	Core A254 - 330										Core A254 - 327										Core A240 - 18								
	4	10	18	27	40	150	240	355	455	600	2	11	16	40	125	180	250	350	390	400	408	411	420	434	443	459	25	80	175
<i>Hydrichthys furcata</i>	46	39	12	6	128	124	296	197	175	122	2	22	2	1	1	2	...	19	27	17	14	54	46	85	8	5	11
<i>H. hypercontha</i>	240	147	31	9	176	141	282	214	222	199	8	115	8	4	2	5	9	2	10	80	67	39	122	86	133	292	9	21	13
<i>H. bullidea</i>	1	1	4	1	2	...	2	
<i>H. bentoni</i>	
<i>H. mirabilis</i>	57	24	13	4	18	44	73	40	45	52	1	7	1	...	1	3	10	3	7	1	11	24	65	4	10
<i>H. noboa</i>	1	2	2	...	4	5	1	8	7	5	
<i>H. scabrata</i>	12	16	4	1	...	19	54	17	36	18	...	18	...	1	...	2	1	...	2	6	4	...	7	1	3	27
<i>H. membranacea</i>	2	1	
<i>H. ferraria</i> var. <i>obliqua</i>	1	2	7	17	3	
<i>Nematospheeropsis baicombiana</i>	5	1	1	1	1	...	2	2	...	2	1	1	...	1	1
<i>Leptodinium oculatum</i>	4	4	2	52	2	4	11	7	1	4	...	13	1	1	7	4	19	8	3	7	7
<i>L. patulum</i>	1	5	3	6	1	2	6	8	3	2	...	1	1	3	
<i>L. paradoxum</i>	3	3	1	7	1	4	2	1	1	3	...	2	1	2	...	1	3	1	2	...	4	
<i>L. striatum</i>	3	1	1	8	2	9	9	3	2	1	...	4	...	1	...	1	2	1	...	5	2	3	
<i>L. sphaericum</i>	...	4	1		
<i>Lingulodinium machaerophanum</i>	40	38	13	3	64	58	109	70	104	71	1	4	2	3	2	...	1	3	11	28	12	32	29	20	56	11	28	20	
<i>Hemicystodinium zabaryi</i>	166	192	64	11	125	113	240	133	136	111	23	28	9	19	7	10	4	12	8	19	40	20	31	46	38	94	13	10	15
<i>Operculodinium centrocarpum</i>	37	65	27	1	20	13	45	43	17	19	2	1	1	1	1	4	8	1	4	2	11	29	36	14	53
<i>O. israelianum</i>	1	1	4	1	2	...	11	
<i>O. giganteum</i>	
<i>O. patulum</i>	2	6	1	1	...	2	2	...	2	1	1	1	...	
<i>Tectodinium pellitum</i>	3	23	1	...	0	2	5	5	3	4	...	1	1	6	3	8	
<i>Chytriosphaeridia ouliscensis</i>	
<i>Chytriosphaeridia</i> sp. <i>indet.</i>	2	...	1	2	5	5	...	2	3	4	...	2	3	
<i>Tuberculodinium vancampoe</i>	3	2	2	1	3	4	1	1	1	1	2	2	2	1	5	2	1	2	
Others	11	4	5	8	9	3	5	6	5	8	1	70	2	4	1	4	3	2	3	16	18	12	37	7	16	35	19	24	27
Total	630	574	181	118	554	543	1142	744	757	616	41	290	25	36	24	32	21	21	36	187	239	142	281	239	289	672	219	188	212

Table 2. Distribution of Microplankton in Caribbean piston cores A254-330, A254-327 and A240-18.

and small numbers of *G. menardii flexuosa* in the upper 34.5 cm. According to data by Ericson, Ewing, Wollin, and Heezen (1961, pp. 260, 268) and Ericson, Ewing, and Wollin (1964), these foraminifera indicate that the entire core is older than the main Wisconsin (Wurm) Glaciation (LG1 2-3). Possibly the upper 20 cm. represent the Wisconsin (Wurm) Interstadial (LG1 1/2), from c. 20 cm. to 34.5 cm. represents the early Wisconsin Glaciation (LG1 1) and the thick grey lutite below is a Sangamon (Riss-Wurm) Interglacial deposit. This assumes that the diagnostic foraminifera are *in situ*. There is evidence of some reworking at most levels; redeposited Pliocene foraminifera (*Globigerinoides fistulosa* Schubert and *Globigerina digitata*) occur at depths of 27, 10, and 4 cm., although as extremely rare forms, and a few scattered Pliocene discoasters including *D. challengerii*, *D. pentaradiatus*, and *D. brouweri* occur at all levels. All these forms cited as reworked Pliocene species are extinct in the Pleistocene according to Ericson, Ewing, and Wollin (1963).

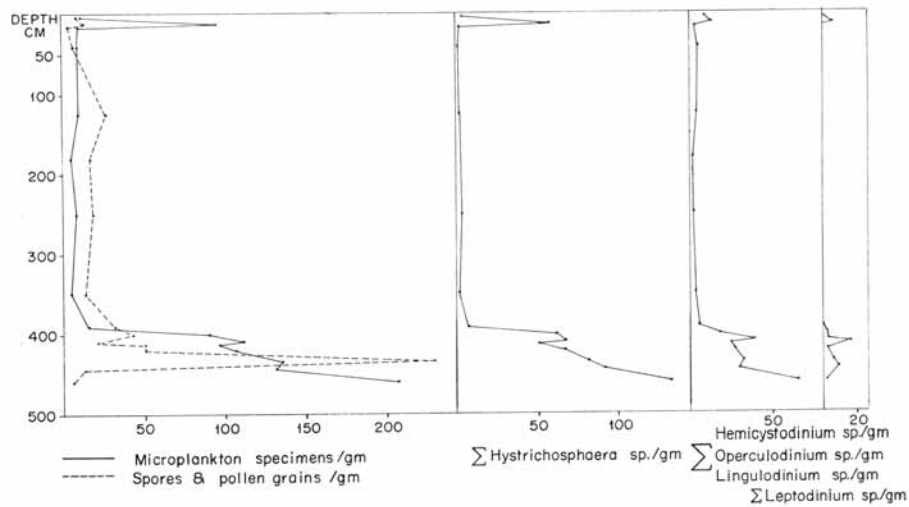
Core A254/327. (Text-fig. 8.) This core contains the same species as core A254/330. They also are continuously distributed throughout the column but there are fewer species and specimens in the coarse, thick globigerina-pteropod ooze that comprises most of the core than in the basal lutite sequence. Microplankton decreases from 208 specimens/gm. to 91/gm. at progressively younger horizons within the basal lutites. The globigerina-pteropod ooze above has a maximum of 16/gm. although a lutite band within it at 9 to 16 cm. has 91/gm. There is a pollen and spore maximum at 434 cm. with 232 grains/gm. due to an abundance of bisaccate pollen and fern spores. The proportional composition of microplankton in the samples from the basal lutites is more or less constant. *Hystrichosphaera* species comprise 54 to 68%, *Lingulodinium* comprises 6 to 11%, and *Hemicystodinium* and *Operculodinium* together comprise a minimum of 12 to 20% of the assemblages. *Leptodinium* is abundant only at one level (411 cm.) where it forms 18% of the assemblage. The relative paucity of microplankton in the globigerina-pteropod ooze makes percentage determinations unreliable.

Foraminiferal analyses indicate that the upper 16 cm. including the thin brown lutite band are post-glacial sediments with an abundance of *Globigerinoides rubra*, some specimens of *Globorotalia menardii* and *G. menardii tumida*. Below this to its base at 397 cm. the underlying globigerina-pteropod ooze contains colder water foraminifera (*G. truncatulinoides*, *G. crassiformis*, *G. dutertrei*) and comparatively few warmer water species and can be considered as Wisconsin (Wurm) in age. The presence of abundant displaced terrestrial and shallow water neritic organisms in this layer can be correlated with glacial lowering of sea level over the Gulf of Batabano platform (see Bandy 1964, p. 1672) during this time. The basal lutites do not contain sufficient foraminifera for dating but on the basis of their high microplankton content they can be regarded provisionally as warmer water deposits representing the Wisconsin Interstadial (LG1 1/2).

Core A240/18. Fifteen species were observed in five spot samples from this core. Microplankton was abundant but always accompanied by large quantities of kerogenic material. Between 413 and 630 specimens per gramme were recorded in the upper three samples (25, 80, 175 cm.), excluding some very small forms. The common species were *Chytroei-sphaeridia cariacensis* sp. nov., *Hystrichosphaera mirabilis*, *H. bulloidea*, *Operculodinium israelianum*, and *O. psilatatum* sp. nov. In contrast with Yucatan Basin cores, *Leptodinium* was absent. All the samples are post-glacial in age.

CONCLUSIONS

Piston cores from the ocean floors can provide valuable information concerning Quaternary microplankton. This preliminary study describes the microplankton from two piston cores taken in the Yucatan Basin abyssal plain and one from the Cariaco Trench in the Caribbean Sea. It differs from earlier Quaternary studies (listed in Downie and Sarjeant 1964, pp. 73, 74), which were confined mostly to deltaic or lagoonal environments, by examining a totally marine succession, but it supplements them in demonstrating how widespread and abundant microplankton is in the Quaternary.



TEXT-FIG. 8. Microplankton distribution in core A254/327.

The species content of Quaternary assemblages from widely separated geographical provinces may be very similar as illustrated by comparison of Caribbean and Mediterranean analyses. The minimum of 25 species recorded from the Caribbean includes 11 of the 14 species described by Rossignol (1964) from the Mediterranean. Moreover, *Leptodinium aculeatum* sp. nov., *L. patulum* sp. nov., *L. sphaericum* sp. nov., *Hystrichosphaera bulloidea*, and species of *Chytroisphaeridia* were found recently in samples dredged from the outer continental shelf near Lebanon (R/V *Chain* Cruise 43, Station 78 at 33° 24.5' N., 35° 12' E.). This new record of these species occurring in the Mediterranean makes agreement between species lists representing the two provinces complete excepting only a few rare varieties.

The cumulative results of all the currently available analyses indicate that the following microplankton are characteristic of the Quaternary.

1. Tabulated spiny cysts belonging to *Hystrichosphaera* and *Nematosphaeropsis*.
2. Tabulated cysts with level sutural septa and without spines or polar projections, allocated to *Leptodinium*.

3. Non-tabulated cysts with precingular archeopyles; these may have a simple archeopyle (3") and possess radial spines (*Operculodinium* gen. nov.) or lack spines (*Tectatodinium* gen. nov.) or alternatively they may have a compound archeopyle representing the loss of several precingular plates and have radial spines (*Lingulodinium* gen. nov.).

4. Non-tabulated, smooth-walled dark brown cysts of *Peridinium* varying in shape from spherical to peridinioid and possessing dorsal intercalary (sub-apical or apical) archeopyles which are basically hexagonal in shape: the spherical fossil forms have been allocated to *Chytroeisphaeridia* while the peridinioid forms are without names at present, but are most closely comparable with *Deflandrea*.

5. Unclassified small, unornamented cysts around 30 μ in size with apical archeopyles; these are extremely common in some Pleistocene samples but have not been formally described at present.

6. Strongly tuberculate forms with compound archeopyles, called *Tuberculodinium* gen. nov.

7. *Hystrichokolpoma*.

8. A few species of the acritarch genus *Cymatiosphaera*.

9. The problematical form *Concentricystes*, which is quite common in deep-sea sediments as well as in neritic or epicontinental deposits.

Members of the first five groups commonly dominate Pleistocene assemblages; representatives of the other groups are less common. *Hystrichokolpoma* is the only genus with restricted stratigraphic occurrence; it has not been found in deposits younger than early Sicilien.

Stratigraphic comparison with late Tertiary microplankton recorded from the Miocene and Oligocene of Germany by Eisenack (1954), Maier (1959), Gerlach (1961), and Brosius (1963) and from the Miocene of Australia by Deflandre and Cookson (1955), reveals that many Tertiary species do not survive into the Pleistocene. These include *Gonyaulacysta tenuitabulata* Gerlach, *Hystrichosphaera cornuta* Gerlach, *Cordosphaeridium inodes* (Klumpp) Eisenack, *C. diktyoplokus* (Klumpp) Eisenack, *C. divergens* Eisenack, *C. floripes* (Deflandre and Cookson) Eisenack, *C. microtriaina* (Klumpp) Eisenack, *Hystrichosphaeridium alcicornu* Eisenack, *H. asperum* Maier, *H. grallaeforme* Brosius, *H. leptodermum* Maier, *H. salpingophorum* Deflandre, *H. simplex* (White) Deflandre, *H. stellatum* Maier, *H. tubiferum* (Ehrenberg) Wetzell, *H. xipheum* (Maier) Sarjeant, *Tenua hystrix* Eisenack, *Rottnestia borussica* (Eisenack) Cookson and Eisenack, *Thalassiphora pelagica* (Eisenack) Eisenack and Gocht, *Pentadinium laticinctum* Gerlach, and *Palmickia lobifera* Eisenack, in addition to older Tertiary genera with numerous species such as *Deflandrea* (*s.s.*) and *Wetzeliella*. However, most species found in the Pleistocene also occur in Miocene or older strata: at present only the following Pleistocene species have not been found in older strata: *Hystrichosphaera bentori* Rossignol, *Leptodinium aculeatum* sp. nov., *L. sphaericum* sp. nov., *Hemicystodinium zoharyi* Rossignol, *Operculodinium psilatium* gen. et. sp. nov., *O. giganteum* gen. et sp. nov. All the other Quaternary species described here occur in Miocene strata in the Caribbean region. Unfortunately, very little is known about Pliocene microplankton that would permit any worthwhile comparisons with either the Miocene or Pleistocene.

DISCUSSION

Morphological and biological studies (Evitt and Davidson 1964; Wall 1965) demonstrate that Quaternary microplankton assemblages almost entirely comprise the resting spores (cysts) of thecate dinoflagellates. For example, *Hystrichosphaera bentori*, *H. furcata*, *H. mirabilis*, *H. bulloidea*, *Nematosphaeropsis balcombiana*, *Lingulodinium machaerophorum* nov. comb., *Operculodinium centrocarpum* nov. comb., *Tectatodinium pellitum* n. gen. et sp., and a number of *Chytroisphaeridia* species all have been isolated from Atlantic marine plankton in the Woods Hole region. The study of living material is a new concept in hystrichosphere research which is relevant especially to Quaternary ecology, but as yet undeveloped. Nevertheless, the elemental origin of the thanatocoenose from a phytoplanktonic community is established in principle and the biological function of microplankton becomes a little clearer. Species of *Gonyaulax*, *Peridinium*, and *Protoceratium* emerge as the prime cyst-producers and factors influencing their spore production and marine distribution account for the presence or absence of a fossil cyst-species in the Quaternary sediments of a region in the first instance. Beyond these, factors concerning productivity, sedimentation, and fossilization determine the abundance of microplankton, as they do for other pelagic microfossils.

A few palaeoecological observations based upon fossil sequences are possible. Neritic and epicontinental assemblages in the Quaternary appear liable to considerable and rapid fluctuations in composition involving a small number of common species, especially where there are non-marine intercalations. Individual assemblages are often poor in species. Conversely, known deep-sea assemblages are comparatively stable in composition but richer in species. Isolated species are not restricted to either neritic or open oceanic environments but many appear to be incapable of survival in brackish or fresh water. Thus in the eastern Mediterranean epicontinental province, Rossignol (1962) envisaged two main associations alternating throughout the lower Pleistocene; these also were recognizable in samples dredged from the outer continental shelf off Lebanon. One association was dominated by *Hystrichosphaera furcata*, *H. bentori*, and *Lingulodinium machaerophorum* (synonym: *Hystrichosphaeridium ashdodense* Ross.) and the other by *Hemicystodinium zoharyi* (synonym: *Hystrichosphaeridium zoharyi* Ross.). Also in the Caribbean Cariaco Trench, the few assemblages examined were dominated by different species, namely, *Hystrichosphaera mirabilis*, *Chytroisphaeridia cariacensis* sp. nov., and *Operculodinium israelianum* comb. nov. In contrast, Yucatan Basin abyssal lutite assemblages frequently were dominated by *Hystrichosphaera bulloidea* with *H. furcata* a common associate and the proportional representation of these and other species remained constant within narrow limits throughout the observed sequences. The only exception was an increase of *Leptodinium aculeatum* sp. nov. in thin bands within both cores.

Of the parameters influencing the distribution of microplankton, salinity, temperature, and light variations are probably most significant, but the extent of their influence is not well known. Rossignol (1962) suggested that subnormal salinities caused by increased freshwater run-off favoured the development of a *Hemicystodium zoharyi* association in the Mediterranean Pleistocene and that the alternating *Hystrichosphaera furcata*, *H. bentori*, *Lingulodinium machaerophorum* association accumulated under conditions of normal salinity for the area and time. Temperature-induced fluctuations have not

been identified positively, but judging by Yucatan Basin cores there are two methods of approach which merit further investigation. First, the maximal absolute abundances of microplankton expressed in terms of specimens per gramme of lutite may indicate the warmer climatic intervals, and secondly, an increase of *Leptodinium aculeatum* sp. nov. may be indicative of climatic change. Useful knowledge of the present-day distribution of dinoflagellate cysts for comparison with layers in cores is almost non-existent and should be acquired. Again, the possibly disturbing influence of turbidity currents on the composition of microplankton assemblages in the deep-sea also requires further investigation.

The presence of microplankton in the deep-sea raises several problems. Judging by the amount of known reworking as indicated by displaced foraminifera and discoasters, less than 5% of the microplankton in the Yucatan Basin lutites are redeposited (this is not true for the coarse globigerinapteropod ooze in core A254/327 which shows excessive quantities of terrigenous and neritic material probably displaced from the Gulf of Batabano platform). Also, diagnostic Miocene or older Tertiary species are absent from these lutites and it appears that most of the cysts accumulated by settling from the euphotic zone. Yet it is difficult to envisage survival of an excysted protoplast at such depths (over 4,000 m.), especially since excystment may be regulated in part by seasonal temperature fluctuations. Settling of cysts to these depths apparently constitutes a loss to the organism, but it is estimated provisionally from fossil analyses plus sedimentation data available for the Caribbean area (Van Andel, Postma and Kruit 1954; Muller 1959; Ericson, *et al.* 1961) that at least ten times and up to a thousand times more cysts accumulate upon shelf structures than in the deep-sea plains, so that the loss is small. Special flotation aids, for example longer spines, may be a feature of oceanic cysts; short-spined varieties of *Hystrichosphaera bentori* appear most frequently close to shore, in the harbour at Woods Hole for instance. These problems require further investigation.

This preliminary study can only outline a few taxonomic and distributional aspects concerning microplankton in the Quaternary. The fields of research suddenly opened by the discovery of living and submarine fossil specimens remain essentially unexplored.

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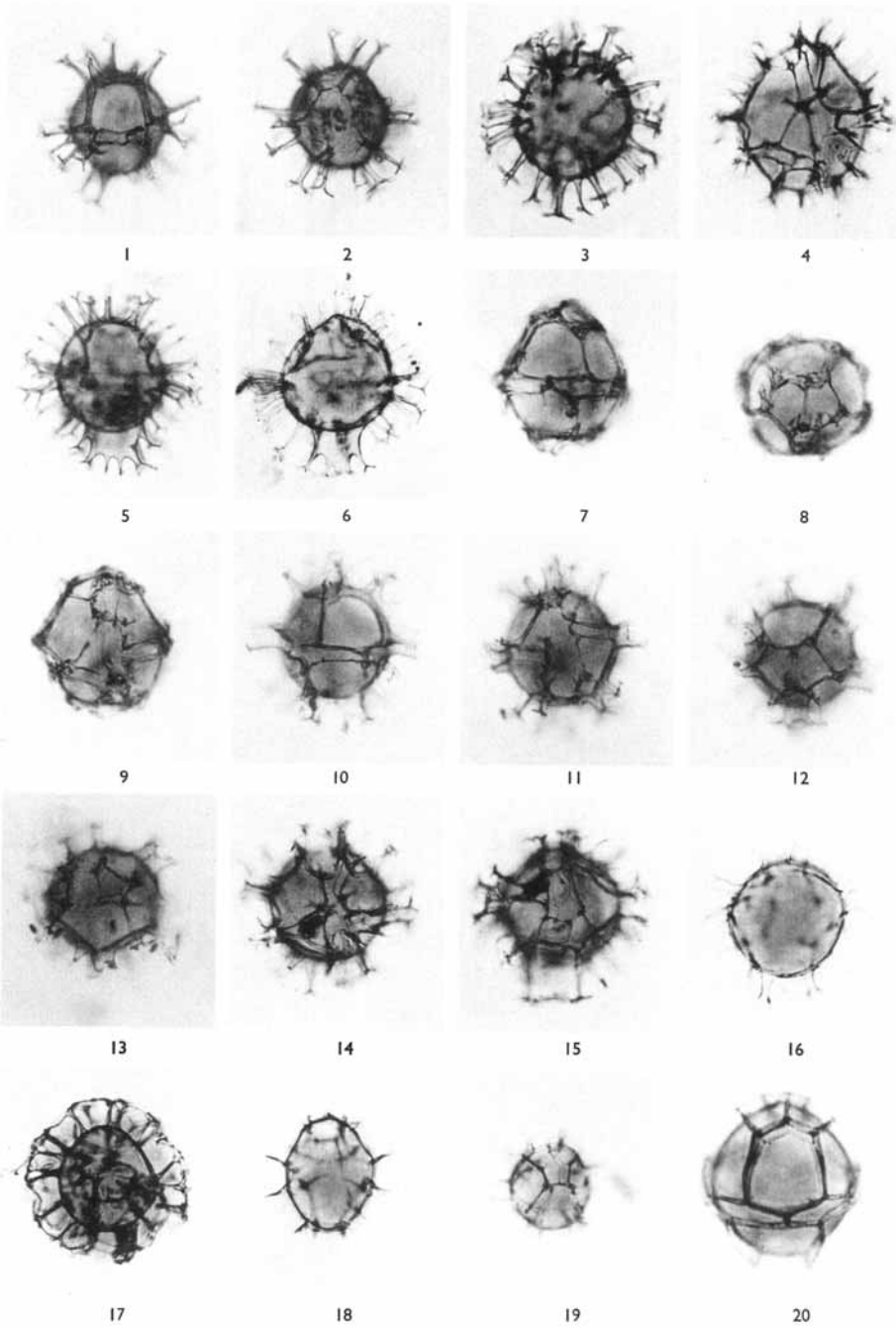
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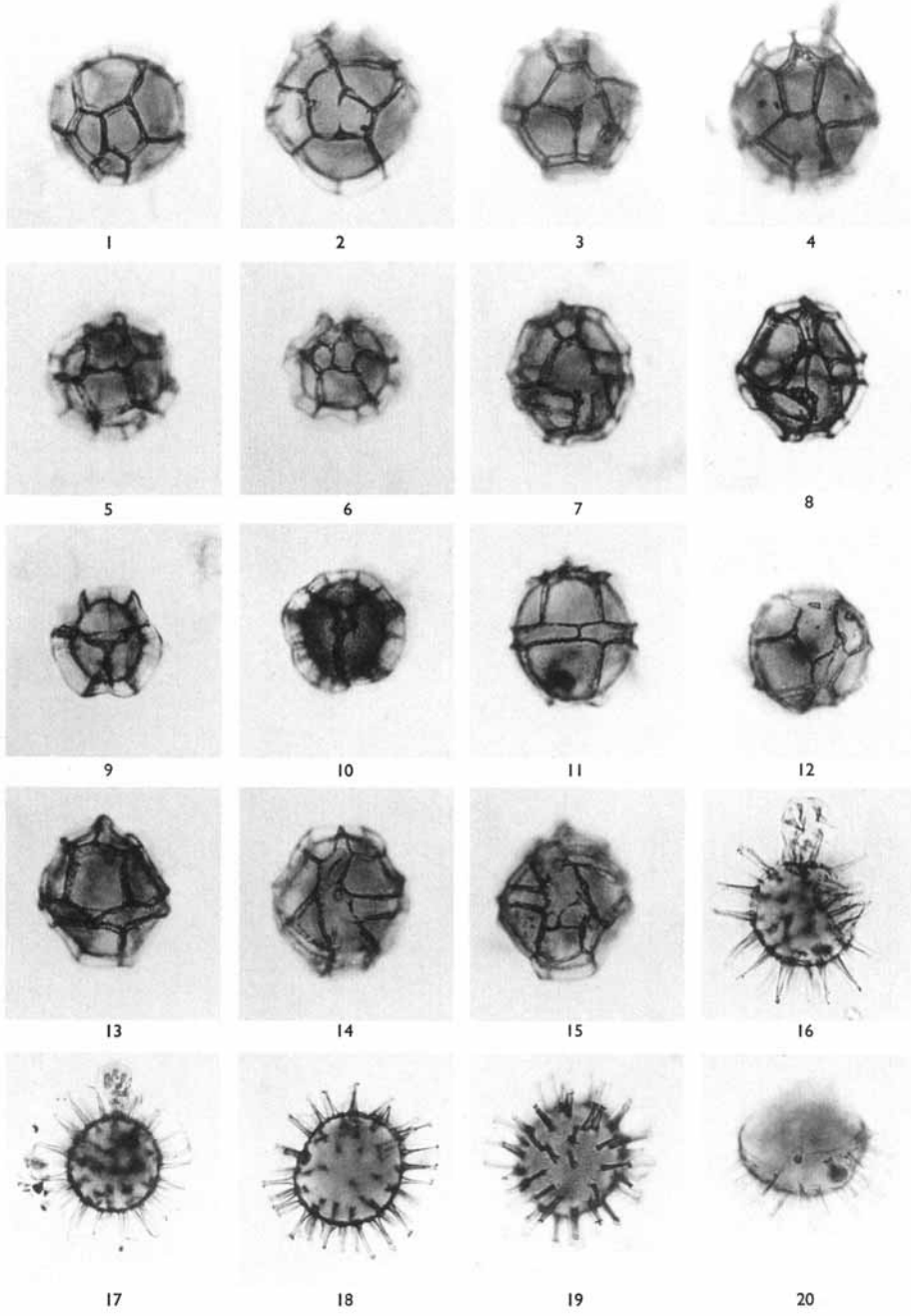
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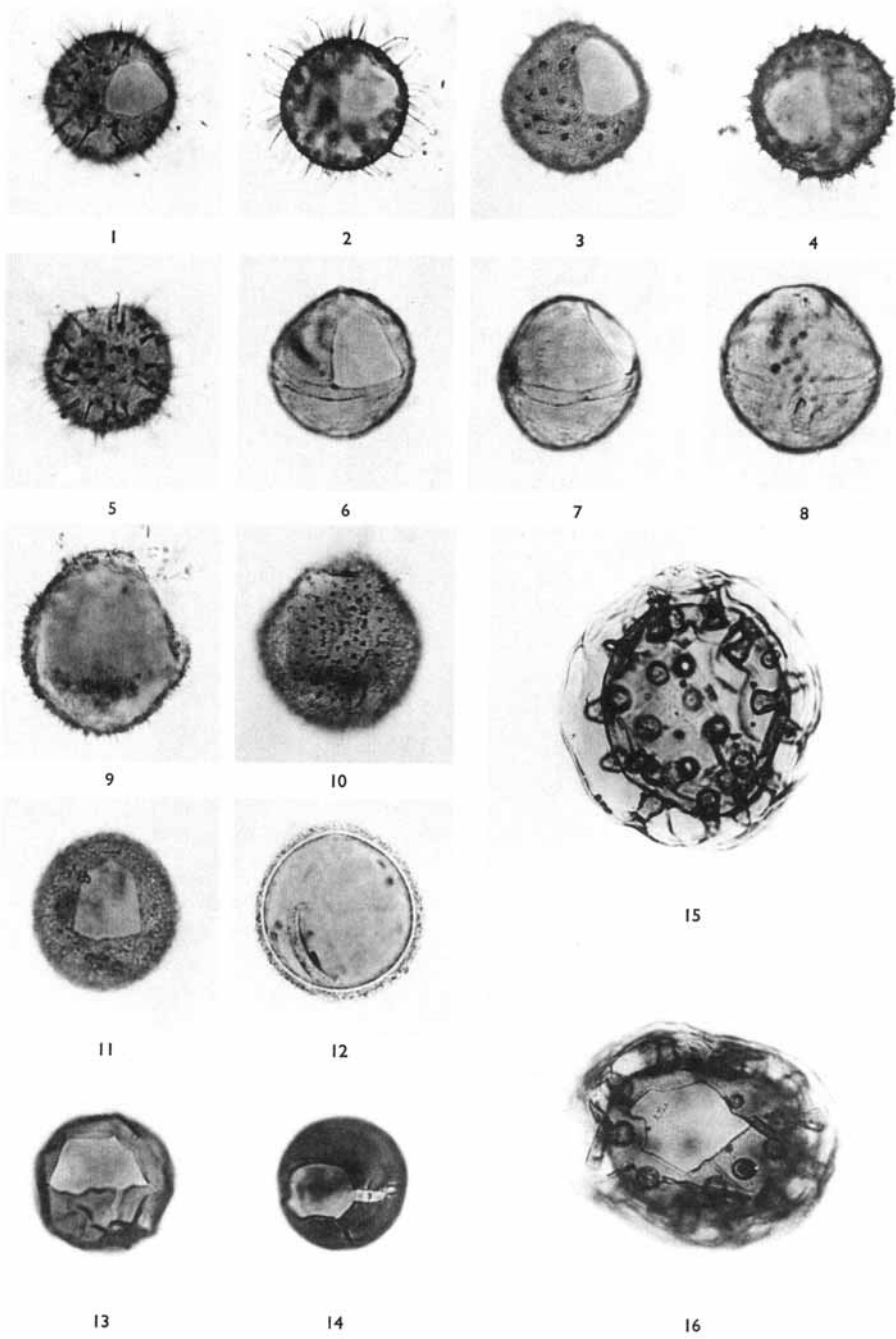
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