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PALYNOLOGY AND PALEOENVIRONMENTS OF A PLIOCENE CARBONATE PLATFORM: THE CLINO CORE, BAHAMAS

MARTIN J. HEAD AND HILDEGARD WESTPHAL

INTRODUCTION

The Clino borehole (24°36′07″N, 79°10′41″W) was drilled in 1990 on the northwestern margin of the Great Bahama Bank as part of the Bahamas Drilling Project (Fig. 1). Along with the nearby Unda borehole, situated 10 km to the east northeast, it forms the platform-top-to-slope record of a transect that ended with the drilling of deeper water sites of the Ocean Drilling Program (ODP) Leg 166 in the Straits of Florida (Eberli et al., 1997). Objectives of drilling the Great Bahama Bank were to investigate sea-level changes during the late Cenozoic and to learn more about the history of carbonate sedimentation and diagenesis on a major carbonate platform and slope.

The Clino borehole was continuously cored in a water depth of 7.60 m, penetrating over 600 m of Pleistocene, Pliocene and upper Miocene carbonates. The Clino site is located just inward of the platform margin on a seismic profile that reveals prograding geometries (Fig. 2). The depositional environment of this site has changed from lower slope during the late Miocene of 7.60 m, penetrating over 600 m of Pleistocene, Pliocene and early Pliocene, to upper slope in the late Pliocene, and margin-reef and platform in the latest Pliocene through present. At the same time, the platform evolved from a ramplike morphologic form to upper slope in the late Pliocene, and margin-reef and platform in the latest Pliocene through present. The name of this borehole refers to the clinoform slope deposits that characterize much of the hole. Samples characteristic of sea-level highstands and lowstands were selected for analysis. Polysphaeridium zoharyi is abundant only in lowstand samples and may have thrived in proximity to terrestrial vegetation. In highstand samples Lingulodinium machaerophorum replaces P. zoharyi, perhaps in response to less restricted marine environments on the platform top. This change in assemblages, along with apparent variations in cyst influx, reflects a fluctuating history of currents and salinities over the platform top in the late Pliocene. Upper Pliocene lowstand samples contain anomalously high proportions of terrestrial palynomorphs, allowing the identification of two phases of emergence and vegetation of the platform top. Palynology therefore appears to be a sensitive indicator of short-term (4th-order) sea-level change on carbonate platforms.

Dinoflagellate concentrations correlate positively with carbonate compaction and, in turn, that compacted layers have undergone dissolution of their metastable constituents. Dinoflagellate concentrations therefore can be useful in the often difficult task of assessing compaction and dissolution in fine-grained limestones where other indicators are absent. The following dinoflagellate species are formally proposed: Operculodinium bahamense Head new species, Operculodinium? megaplanum Head new species, and Spiniferites rhizophorae Head new species.

AGE CONTROL FOR INTERVALS EXAMINED

Our two studied intervals are constrained by an integrated age model for the Clino core (Eberli et al., 1997; McNeill et al., in press) which is based on magnetostratigraphic and strontium isotope data along with planktonic foraminiferal and some calcareous nanofossil datums.
Lycopodium clavatum spore tablets were added to each sample tarchs. Remaining residue, where available, was re-sieved at 20 \mu m to concentrate the larger dinoflagellates and determine whether any rare species were present—a necessary consideration in these low diversity assemblages. Examination of the \textgreater 20\mu m slides showed they had lost some Lycopodium clavatum spores, as judged by the apparent abundance of Polysphaeridium zoharyi, rendering them unreliable for determination of absolute abundance.

Nitex nylon screens were used throughout for sieving, and residues were strew mounted onto microscope slides using Cellsize and Elvacite.

**Counting.**—All major palynomorph groups were counted, and absolute abundances per gram dry weight of rock were then estimated for dinoflagellates and terrestrial palynomorphs (Fig. 3). Dinoflagellate and acritarch taxa were individually identified and counted, although no attempt was made to identify spores and pollen to generic or specific level. Specimens were counted using a 25X objective until 250 dinoflagellates had been registered, except for samples CGS-1 and CGS-2 where only 100 dinoflagellates were counted owing to their sparsity. Abundance and error calculations follow the method of Stockmarr (1971) but are adjusted for the use of L. clavatum tablets batch #710961 (supplied by Lund University) for which the sum (X) = 69556, standard deviation (s) = \pm 1541, and coefficient of variation (V) = 2.2\%, based on groups of five tablets. Hence for one tablet, X = 13,911, s = \pm 689, and V = 4.95\% (see Maher, 1981, p. 158-159).

**Limitations to counts.**—Microforaminiferal linings are very abundant in most assemblages but were difficult to quantify owing to their mostly fragmented state, often occurring as single chambers (see Fig. 4.1). Traverse and Ginsburg (1966) noted a similar phenomenon for modern Bahamanian assemblages. Following these authors, only foraminiferal linings with six or more chambers were counted (Fig. 3). Hence these linings are greatly underrepresented in the overall counts.

Although most dinoflagellates were easily recognized and identified during counting, specimens of Kallosphaeridium sp. (Fig. 8.13-8.17) could often not be distinguished from leiospheres (Fig. 14.18, 14.19), and leiospheres themselves could not always be distinguished from other debris under the 25X objective. It was therefore decided not to include counts for Kallosphaeridium sp. or the leiospheres, but simply to record "spiny acritarchs" (Fig. 14.16, 14.17). Although the sum of these
### Upper Lower Pliocene (3.6 – 4.1 Ma)

<table>
<thead>
<tr>
<th>Sample</th>
<th>Age</th>
<th>Depth (feet below mud pit)</th>
<th>Depth (meters below mud pit)</th>
<th>Sample number</th>
</tr>
</thead>
<tbody>
<tr>
<td>C2Ar (Upper Gilbert)</td>
<td>1622.00</td>
<td>1621.50</td>
<td>1567.50</td>
<td>CUS-M1</td>
</tr>
<tr>
<td>C2r (Lower Matuyama)</td>
<td>494.39</td>
<td>494.23</td>
<td>477.77</td>
<td>CUS-K6</td>
</tr>
</tbody>
</table>

**Depositional environment**
- Sea-level lowstand (shaded) / inferred compaction (C)

**Dinoflagellates (raw counts)**
- Impagidinium sp. A
- Operculodinium janduchenei
- Hystrichokolpoma rigaudiae
- Operculodinium? megagranum
- Operculodinium paradoxum
- Lejeunecysta marieae
- Nematopharopsis rigidia
- Protoperidinioid cyst sp. A
- Bitectatodinium cf. reedwadi
- Operculodinium pulitanum
- Bitectatodinium reedwadi
- Seleneplexus septiores
- Seleneplexus quinta
- Tabulocystus vacanpooe
- Axistoxium zevenboomii

**Marine algae incertae sedis (raw counts)**
- Incertae sedis sp. A
- Incertae sedis sp. B

**Other marine palynomorphs (raw counts)**
- Trochosporal microforaminiferal lining B
- Copepod fragments

**Terrestrial palynomorphs (raw counts)**
- Fungal spores and hyphae
- Fern and lepidophyte spores
- Bisaccate pollen
- Angiosperm pollen

**Palynomorphs per gram dry weight (concentrations)**
- Estimated total dinoflagellates
- Estimated total terrestrial palynomorphs

**Sample data**
- Sample dry weight (in grams)
- Quantity of Lycopodium clavatum tablets
- Quantity of Lycopodium clavatum spores counted

**Palynomorphs per gram dry weight (concentrations)**
- Estimated total dinoflagellates
- Estimated total terrestrial palynomorphs

**Figure 3**—Dinoflagellates and other palynomorphs recovered in the present study. Also indicated are samples from inferred sea-level lowstands (shaded) and strongly compacted samples (C). A “+” indicates a taxon present but recorded only outside of the count (i.e., rare), whereas “*” indicates qualitatively the presence of a taxon not specifically counted during analyses.
acanthomorph acritarchs is considered accurate, their differentiation under the 25X objective is approximate owing to their small size.

**Photography.**—Specimens were photographed using a vario-orthomat 2 camera attached to a Leitz Dialux microscope. Images are all true, i.e., not reversed. An England Finder reference follows the sample (and slide) number for each specimen illustrated.

**Repository.**—All microscope slides containing holotypes and paratypes are housed in the Invertebrate Section of the Department of Palaeobiology, Royal Ontario Museum, Toronto, under the catalog numbers ROM 53304 (CUS-K11/3), and ROM 53427–53434 (CLS-K4/4, 5, CLS-K6/3, CUS-K10/2, CUS-M8/2, 3, CUS-M8/4, CUS-M9/4).

**PALynomorph Assemblages**

Abundances of the major palynomorph groups and dinoflagellate taxa are shown in Fig. 3. Limitations of the counting method are discussed under Materials and Methods. Assemblages typically contain abundant pale membranous material (Fig. 4.1), which is assumed to be mostly of marine algal origin. Microforaminiferal linings are also common in most samples, although often fragmented and therefore underestimated in counts. Except in samples CGS-1 and CGS-2, spores and pollen and palynodebris of clearly terrestrial origin are rare. Spores and pollen are represented mostly by bisaccate pollen (mainly *Pinus*).

Dinoflagellates are abundant and generally well preserved, with little indication of reworking if judging from the stratigraphic ranges of taxa present. A total of 30 taxa were recorded and nearly all are neritic. Compared with (mostly oceanic) higher-latitude records, this represents a relatively low species richness (average of 15 taxa per sample) and is explained at least partly by the near absence of oceanic taxa and by the poor representation of protoperidinioid species.

**DINOflagellate Biostratigraphy**

Dinoflagellates from our lower Pliocene interval (476.40–494.39 mbmp) are consistent with a Pliocene age. *Bitectatodinium raedwaldii* has not been reported from deposits older than Pliocene (Head, 1997) but its stratigraphic range is not well known. *Spiniferites rhizophorus* Head, n. sp. is of unknown stratigraphic significance, but *H. rigaudiae* ranges above the uppermost Pliocene (Head, 1997). *Kallosphaeridium* *sp.* is not known from the literature, but the genus itself appears to range no higher than Pliocene. Stratigraphic ranges of taxa mentioned above are treated in detail in the Systematic Paleontology section.

**DINOflagellate Concentration and Carbonate Diagenesis**

To determine whether dinoflagellate concentrations have been enriched passively during carbonate compaction, we chose alternating compacted and uncompacted fine-grained samples for study throughout the lower and upper Pliocene intervals. Estimated palynomorph concentrations are shown in Fig. 3, and the degree of inferred compaction of samples is based on ultrafacies and other studies (Westphal, 1997). Samples coded with the letter “M” (e.g., CLS-M3 and CUS-M8) are inferred to have been strongly compacted, whereas adjacent samples coded with the letter “K” (e.g., CLS-K6 and CUS-K12) are less compacted or uncompacted. In our lower Pliocene interval, dinoflagellate concentrations are clearly greater in the “M” samples (10571–14977 per gram dry weight vs. 1933–5945 for the “K” samples). In the sedimentologically more diverse upper Pliocene interval, the pattern is still present but less pronounced, with “M” samples having concentrations of 2446 to 13511 per gram dry weight and “K” samples having concentrations of 1796 to 3208.

Hence, the data show a strong positive correlation between dinoflagellate concentration and compaction of the sediment. This is particularly true for the lower Pliocene interval where an absence of taxonomic trends in the composition of the dinoflagellate assemblages suggests that the source environment has not varied sufficiently to strongly influence cyst productivity. Variations in concentration also correlate with the deformation of the dinoflagellates themselves as seen in SEM bulk samples and with other compaction indicators (Westphal and Munnecke, 1997). Since compaction alone has no bearing on dinoflagellate concentration (per gram of dry sediment), the increase in concentration is thought to represent secondary, diagenetic enrichment by dissolution of the carbonate's metastable constituents. This mainly accounts for the lower Pliocene samples with their
rather uniform sedimentological and palynological compositions. The upper Pliocene dinoflagellate concentrations show a less strong positive correlation with compaction, and variations are not explained by diagenetic enrichment alone. Samples from this interval are sedimentologically more variable and so additional factors should be considered, including shifts in cyst productivity and influx due to sea-level fluctuations.

In conclusion, examination of dinoflagellate concentrations along with the composition of the assemblages can be useful in quantitatively assessing the compaction and partial dissolution of fine-grained carbonates, especially where other indicators (e.g., clay enrichment) are absent.

**PALEOENVIRONMENT BASED ON DINOFLAGELATES AND SPOROMORPHS**

During carbonate platform submergence, slope deposition largely comprises fine-grained sediment transported from the platform top, with open marine biota forming a minor contribution. Periplatform slope deposits may therefore preserve a good record of platform top environments. The following section summarizes environmental interpretations based on the palynology, although detailed discussions for individual dinoflagellate taxa are given in the Systematic Paleontology section.

**Lower Pliocene interval (476.40–494.39 mbmp).**—This interval represents the lower slope of a ramp-like carbonate platform, as determined by the seismic profile (Fig. 2). It was deposited in a water depth of 300 to 400 m, and at a distance of about 16 km west of the shallow waters of high carbonate production (the “carbonate factory”) according to Eberli et al. (1997). The ben- thic foraminifers are not diagnostic of any specific environment but normal-salinity lagoons, hypersaline lagoons, and normal-salinity open shelves are all possible sources, and contributions may have come from several facies belts on the platform (Westphal, 1997; Westphal et al., in press).

Dinoflagellate assemblages are dominated by neritic taxa, particularly *Polysohaeriidium zoharyi* (13–64 percent) and *Achomosphaera/Spiniferites* spp. (17–70 percent), with lesser amounts of *Lingulodinium machaerophorum* (2–13 percent) and *Operculodinium* spp. including *O. israelianum* (4–17 percent). Modern assemblages from the Great Bahama Bank (Wall et al., 1977) are characterized by high abundances of *Spiniferites* spp. (53–55 percent), *Operculodinium* spp. (14–27 percent), *P. zoharyi* (9–20 percent), and *L. machaerophorum* (8–12 percent). The Clino assemblages are therefore broadly similar but may have higher values of *P. zoharyi*. This species is particularly significant, having a tropical to subtropical modern distribution and favoring shallow, restricted marine environments with variable but often high salinities. The lower Pliocene Clino assemblages therefore largely reflect transport from the carbonate platform top, where tropical–subtropical, restricted marine conditions evidently persisted throughout the interval. Such conditions persisted despite the ramp-like morphology and relatively open circulation of the platform in the early Pliocene (Beach and Ginsburg, 1980; Eberli et al., 1997; Westphal et al., in press).

Other extant thermophilic species include *Lingulodinium machaerophorum*, *Capisocysta lata*, and *Tuberculodinium vancompoae*, there being no cool-water species unequivocally present in this interval of the Clino core. Heterotrophic dinoflagellates are represented in low numbers by *Selenopemphix nephroides*, *S. quanta*, and round brown cysts, this overall scarcity indicating nutrient levels that were not excessively high. Oceanic and outer neritic taxa are extremely rare and are restricted to a few specimens of *Impagidinium* spp. in sample CLS-K4. The almost total exclusion of oceanic species in both studied intervals of the Clino core is surprising since the skeletal composition of sediments, especially in the lower Pliocene interval, has a persistent open-ocean derived component including planktonic foraminifers, as might be expected for slope environments (Westphal, 1997; Westphal et al., in press).

The dinoflagellate assemblages are fairly similar in all samples from the lower Pliocene interval, and this same low variability is seen also in the sedimentology for this interval. It may be yet another expression of how a ramp-like topography can buffer the effects of small sea-level fluctuations on a carbonate platform (Burchette and Wright, 1992; Westphal, 1997; Westphal et al., in press).

Terrestrial palynomorphs and debris in the lower Pliocene interval are consistently rare. This rarity indicates the absence of a terrestrial vegetation source in the vicinity and is consistent with a deep-water setting and a mostly or fully submerged platform top. The sedimentology shows no evidence of emergence on the platform.

**Upper Pliocene interval (220.48–262.18 mbmp).**—By late Pliocene times, the Clino site was an upper slope of a steep-sided, flat-topped platform (Fig. 2). The sediments were deposited in a water depth of about 200 m and a distance of about 8.5 km from the platform margin (Eberli et al., 1997). The deposits are mostly fine grained (the six CUS-prefixed samples) and represent sea-level highstands, but two horizons are coarse grained (the two CGS-prefixed samples) and are thought to have been deposited under lowstand conditions (Westphal, 1997; Westphal et al., in press). All samples from our upper Pliocene interval are dominated by neritic dinoflagellates, with oceanic and outer neritic species being rare or absent. However, the assemblage composition differs significantly between highstand and lowstand samples.

**Upper Pliocene highstand samples.**—These fine-grained carbonates are dominated by aragonite needles transported from the interior of the platform top, with foraminifers predominantly indicating hypersaline lagoons (Westphal, 1997; Westphal et al., in press). The dinoflagellates differ from those of our lower Pliocene interval in showing a strong decline in *P. zoharyi* (less than 2 percent) and a corresponding increase in *L. machaerophorum* (10–31 percent). A similar negative correlation between *P. zoharyi* and *L. machaerophorum* has also been noted for modern distribution patterns in the Persian Gulf (Bradford and Wall, 1984) and Quaternary and lower Tertiary deposits of Israel and the Caribbean (Wall and Dale, 1969). It appears to indicate a change to less restricted conditions and perhaps reduced salinities, although evidently still higher than normal judging from the foraminifers in these samples. *Lingulodinium machaerophorum* is a well-known euryhaline species and its presence does not contradict this interpretation. Increased abundance of *L. machaerophorum* may also indicate a slight elevation in nutrient levels caused for example by diffuse upwelling (Dale, 1996), but not a strong elevation since heterotrophic dinoflagellates remain poorly represented. It is also possible that reduced numbers of the tropical to subtropical *P. zoharyi* reflect slight cooling in the late Pliocene, although the dinoflagellate assemblage in general indicates conditions no cooler than warm temperate.

The rarity of terrestrial palynomorphs and debris in these highstand samples again indicates the absence of a nearby terrestrial vegetation source and is consistent with a mostly or fully submerged platform top.

Of the highstand samples, CUS-M8 is somewhat unusual in being the only one containing *Nematosphaeropsis rigida* and in having the highest value of *L. machaerophorum* (31 percent). The reason for this difference is not clear.

**Upper Pliocene lowstand samples.**—The sedimentology of these two samples identifies the platform rim or upper slope as
their predominant source, with transportation to the Clino site via episodic mass flows. Under such conditions the platform top would have been emergent, terminating the large-scale production and transport of fine sediment to the slope (the "highstand shedding" of Droste and Schlager, 1985; Schlager et al., 1994). Foraminifers indicate that normal-salinity marine lagoons were present on the platform top (Westphal, 1997; Westphal et al., in press). The low overall palynomorph concentrations of these two samples (Fig. 3) reflect their coarse grain, but the ratio of terrestrial palynomorphs to dinoflagellates (0.36 to 0.97) is an order of magnitude higher than for the highstand samples (0.004 to 0.020). This provides strong supporting evidence for two episodes of emergence of the platform top and colonization by plants during this interval of the late Pliocene. Evidence of late Pliocene emergence also comes from deposits on the platform top itself (Beach and Ginsburg, 1980). Palynology therefore corroborates the view that coarse-grained deposits are formed when a drop in sea level exposes the platform top, causing fine-grained sediment production and its export to the slope to diminish. Owing to the high sedimentation rate in the upper Pliocene of the Clino core (Eberli et al., 1997), 4th-order sea-level cycles (in the order of 100ka; Vail et al., 1991) can be discriminated by palynology.

These lowstand samples, in contrast to the highstand samples, show a return to abundant P. zoharyi (27–44 percent) and a marked reduction in L. machaerophorum (2–7 percent). This indicates a temporary return of restricted marine conditions that presumably occurred in some embayments of the exposed platform top. There is a strong association today between P. zoharyi and mangrove vegetation. Perhaps during lowstands P. zoharyi thrived in proximity to terrestrial vegetation on the platform top. It is unclear whether P. zoharyi also points to hypersaline conditions. If so, the dinoflagellates and foraminifers are sourced from different environments on the platform.

Comparison of intervals.—Variability between palynological assemblages is greater for the upper Pliocene than lower Pliocene interval. This seems partly to reflect the changing position of the Clino site from lower slope in the lower Pliocene to upper slope in the upper Pliocene. But it mainly reflects the stronger expression of sea-level fluctuations (conceivably as little as a few meters) on the steep-sided, flat-topped platform in the upper Pliocene than on the more open, ramplike lower Pliocene platform. Perhaps increased variability in the upper Pliocene interval, observed both in the sedimentology and palynology, is also linked to the intensification of climatic fluctuations and resulting higher amplitude sea-level fluctuations that began at about 2.6 Ma in the North Atlantic.

**SYSTEMATIC PALEONTOLOGY**
(by M. J. Head)

Division DINOFLAGELLATA (Bütschli, 1885)
Fensome et al., 1993
Class DINOPHYCEAE Pascher, 1914
Subclass PERIDINIPHYCIDAE Fensome et al., 1993
Order GONYAULACALES Taylor, 1980
Family GONYAULACEAE Lindemann, 1928

**ACHOMOSPHAERA/SPINIFERITES spp.**
Figures 4.14–4.18, 6.1–6.6

Discussion.—This group was not systematically studied and during counts was treated as a single category. However, the presence or absence of certain distinctive or paleoecologically useful species was noted. In particular, Spiniferites mirabilis (Rossignol, 1964) Sarjeant, 1970 (Fig. 4.16, 4.17) and Spiniferites rhizophor us Head, n. sp. (Figs. 4.18, 6.1–6.6, and see below under Spiniferites) both occur in most samples but are infrequent. Neither Achomosphaera andaloussiensis nor Spiniferites elongatus were seen.

**Achomosphaera and Spiniferites** are cosmopolitan neritic genera, and together constitute between 23 and 84.5 percent of coastal assemblages in the Bahamas today (Wall et al., 1977).

**GENUS ATAXIODINIUM** Reid, 1974

**Ataxiodinium zevenboomii** Head, 1997

**Figures 5, 6.7–6.12**

**Ataxiodinium zevenboomii** Head, 1997, p. 171–172, figs. 5, 6.4–6.16, 18.5, 18.6 (See for synonymy.)

**Dimensions.**—Endoblast length, 29(35.5)43 μm, standard deviation, 3.8; endoblast equatorial diameter, 22(29.1)38 μm, standard deviation, 4.3; periblast length, 32(39.0)48 μm, standard deviation, 4.3; periblast equatorial diameter, 26(32.0)38 μm, standard deviation, 3.6; maximum wall separation at ambitus, (1.2–4.5) μm; ratio of endoblast length/equatorial diameter, 0.9(1.2)1.6, standard deviation, 0.19. Fourteen specimens measured. See also Fig. 5.

**Paleoecology.**—Present records indicate a neritic distribution and a warm-temperate to tropical climatic range.

**Previous records.**—Upper Miocene and lower Pliocene of The Netherlands (as "Ataxiodinium elongatum" ms name in Zevenboom, 1995), mid Pliocene of eastern England (Head, 1997), and Pliocene or lower Pleistocene of Australia (as Ataxiodinium sp. in McMin, 1992b).

**Discussion.**—Clino specimens are generally broader and less elongate than those reported from the type area by Head (1997), but there is overlap (see Fig. 5) and cysts seem otherwise identical with the type material.

**GENUS BITECTATODINIUM** Wilson, 1973

**Bitemeitatodinium raedwaldii** Head, 1997

**Figure 6.13–6.16**

**Bitemeitatodinium raedwaldii** Head, 1997, p. 175, figs 7.7–7.20, 15.15–15.17, 16.1–16.3. (See for synonymy.)

**Dimensions.**—Maximum diameter (including luxuria), 42(47.2)51 μm, standard deviation, 3.1; wall thickness, ca. 0.9–2.5 μm. Fourteen specimens measured.

**Paleoecology.**—A thermophilic species (Head, 1997) with a temperate to tropical climatic range, and known from inner neritic to oceanic sediments.
Previous records.—Mid Pliocene of eastern England (Head, 1997), upper Pliocene of the Norwegian Sea (as “cf. Biectatodinium sp.” in Head in Head and Wrenn, 1992), and uppermost Pliocene of southwestern England (as “Genus et species indeterminate” in Head, 1993).

Discussion.—Specimens, although often crumpled, show the distal fusion of pili that is a defining feature of this species.

B. raedwaldii Head, 1997

Description.—Proximate, approximately spherical cysts having a precingular (2P) archeopyle. Wall consists of a solid peduncle of even thickness (less than 0.3 μm) surmounted by a luxuria of dense, erect, apparently free-standing pili. Pili have a diameter of about 0.3 μm at their base, with separation of about 0.5 μm or less between adjacent pili.

Discussion.—Four crumpled specimens were seen. They differ from other specimens here assigned to B. raedwaldii in having somewhat coarser ornament and there being no clear indication of extensive distal fusion between adjacent pili.

B. tepikiense Wilson, 1973 sensu stricto

Description.—Luxuria arises as mostly discrete, rodlike elements finer than type material (see Head, 1994, p. 302, 304, text-fig. 3) but otherwise similar. Two specimens found.

Palaeoecology.—The type material from the middle Pleistocene of New Zealand is associated with a mild to warm climate (Wilson, 1973). In contrast, records of B. tepikiense from the modern North Atlantic show a north-temperate or cold-temperate distribution (Head, 1996a and references therein; Dale, 1996), but these specimens often have a vermiculate wall pattern unlike that reported for the type material, and conceivably have somewhat different environmental tolerances.

Stratigraphic range.—Uncertain owing to taxonomic difficulties.

Genus Dapsilidinium Bujak et al., 1980

Dapsilidinium pseudocolligerum (Stover, 1977)

Bujak et al., 1980

Figures 7, 8.1–8.6

Polysphaeridium pseudocolligerum STOVER, 1977

p. 74–75, pl. 1, figs. 14–19.

Dapsilidinium pseudocolligerum (Stover, 1977) Bujak et al., 1980, p. 28.

Description.—Central body surface is finely granulate, and solid low coni of about 1.0 μm or less in diameter are sparsely distributed on surface of some specimens. Processes have finely granulate surface, granules more conspicuous towards distal ends. Process bases usually have elongate claustra similar to those seen under SEM (de Verteuil and Norris, 1996, pl. 11, fig. 4, pl. 18, fig. 8). Most processes fairly evenly spaced over cyst surface, but specimens always have at least one pair of processes, and sometimes as many as four pairs, fused together for most of their length.

Dimensions.—Average diameter of central body, 37(42.3)49 μm; average process length, 10(13.6)17 μm. Diameter of process bases, 2.5–5.0 μm. Thirty specimens measured. See also Fig. 7.

Previous records.—Numerous reports from the lower Oligocene through upper Miocene of the North Atlantic and adjacent areas (see Head et al., 1989a, p. 435 and de Verteuil and Norris, 1996, p. 36 for discussion), both as D. pseudocolligerum and D. pastielsii. I follow de Verteuil and Norris (1996, p. 36) in not differentiating these two species in the Neogene literature. This species has a highest occurrence in the upper upper Miocene of Maryland and Virginia (de Verteuil and Norris, 1996), yet has been found in the lower Pliocene of east-central Florida (Weedman et al., 1995) and probable lower Pliocene of southwestern Florida (Edwards et al., 1998). It is also locally abundant in the upper Pliocene of the Gulf of Mexico (as Dapsilidinium sp. A in Wrenn and Kokinos, 1986; see correlations of Aubry, 1993). The absence of higher latitude Pliocene records may reflect a response to cooling of the North Atlantic during the latest Miocene and evolution of the cold Labrador Current. Cooling has also been implicated in the middle Miocene disappearance of D. pseudocolligerum from the Northwestern Pacific by Bujak and Matsuoka (1986, as D. pastielsii). Significantly, this species occurs persistently through the upper Pliocene (a single Pleistocene occurrence may be reworked) of the tropical Indian Ocean (as D. pastielsii in McMinn, 1992a) and has a highest occurrence in the upper Pliocene of the northeast Australian margin (McMinn, 1993a). The present study establishes the presence of
D. pseudocolligerum in the upper upper Pliocene of the tropical North Atlantic.

Stratigraphic range.—Lower Oligocene of the western North Atlantic (Stover, 1977) though upper Pliocene of the Gulf of Mexico (as Dapsilidinium sp. A in Wrenn and Kokinos, 1986) and upper upper Pliocene of the present study.

Paleoecology.—The present study and previous records indicate a tropical to warm-temperate climatic range, and a distribution in neritic and oceanic sediments.

Genus Hystrichokolpoma Klumpp, 1953, emend. Williams and Downie, 1966

Hystrichokolpoma rigaudiae Defflandre and Cookson, 1955

Figure 8.7, 8.8

Hystrichokolpoma rigaudiae Defflandre and Cookson, 1955, p. 279–281, pl. 6, figs. 6, 10, text-fig. 42.

Previous records.—Lower Eocene of England (e.g., Islam, 1984) through Pleistocene of the Mediterranean (Rossignol, 1962, 1964) and possibly Pleistocene and possibly middle Pleistocene of the Gulf of Mexico (Wrenn and Kokinos, 1986; de Vernal et al., 1992). Occurs widely in the Miocene of the North Atlantic region, locally and often sporadically in the Pliocene (e.g., Habib, 1971; Versteegh and Zonneveld, 1994; Weedman et al., 1995; McCarthy and Mudie, 1996; Versteegh, 1997; Head, 1997), and only in lower latitudes does it extend into the lower Pleistocene and possibly middle Pleistocene (de Vernal et al., 1992).

Paleoecology.—A thermophilic species judging from the present study and previous records; indeed Bujak and Matsuoka (1986) linked its disappearance from northern Japan at the end of the early Pleistocene to Northern Hemisphere cooling. In contrast, it appears to be associated with cooler isotopic intervals in the upper Pliocene of southern Italy (Versteegh and Zonneveld, 1994), suggesting environmental responses that are not well understood.

Discussion.—Occurs rarely but persistently throughout the lower interval of the Clino core, although it is absent from the upper interval.

Genus Impagidinium Stover and Evitt, 1978

Impagidinium paradoxum (Wall, 1967) Stover and Evitt, 1978

Figure 8.9, 8.10

Leptodinium paradoxum Wall, 1967, p. 106–107, pl. 15, figs. 5–8; text-figs. 2–3A, B.


Discussion.—Five specimens were recorded, having a central body length of 25 to 32 μm and a crest height of 2.5 to 3.5 μm. Specimens have a faintly granulate surface, a weakly expressed sulcal tabulation, and lack an apical boss.

Genus Impagidinium Stover and Evitt, 1978

Impagidinium paradoxum (Wall, 1967) Stover and Evitt, 1978

Figure 8.9, 8.10

Leptodinium paradoxum Wall, 1967, p. 106–107, pl. 15, figs. 5–8; text-figs. 2–3A, B.


Discussion.—Five specimens were recorded, having a central body length of 25 to 32 μm and a crest height of 2.5 to 3.5 μm. Specimens have a faintly granulate surface, a weakly expressed sulcal tabulation, and lack an apical boss.
abundant and specimens comprise at least 16 percent of dinoflagellates in sample CGS-2.

Genus Lingulodinium Wall, 1967, emend. Wall and Dale in Wall et al., 1973

Lingulodinium machaerophorum (Deflandre and Cookson, 1955) Wall, 1967

Figure 8.18, 8.19

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


Paleoecology.—A well-known extant euryhaline species with a temperate to tropical distribution. Edwards and Andrle (1992) have shown that in modern sediments of the North Atlantic, percentages are highest (more than about 10 percent) where winter sea-surface temperatures are above 15°C and summer sea-surface temperatures are above 27°C.

It is a well-known indicator of elevated nutrient levels and has an affinity for estuarine environments (Dale, 1996; see also references in Head, 1997). However, it is also well represented in modern sediments of the North Atlantic, percentages are highest (more than about 10 percent) where winter sea-surface temperatures are above 15°C and summer sea-surface temperatures are above 27°C.

It is a well-known indicator of elevated nutrient levels and has an affinity for estuarine environments (Dale, 1996; see also references in Head, 1997). However, it is also well represented in modern sediments of the North Atlantic, percentages are highest (more than about 10 percent) where winter sea-surface temperatures are above 15°C and summer sea-surface temperatures are above 27°C.

Discussion.—Common in most Clino samples with values up to 31 percent.

Genus Melitasphaeridium Harland and Hill, 1979


Figures 8.20, 9.1, 9.2


Melitasphaeridium aqueabile Matsuoka, 1983, p. 114, 115, pl. 3, figs. 7–9, pl. 4, fig. 3, text fig. 9.

Dimensions.—Central body maximum diameter, 25(31.2)40 μm, standard deviation, 3.62; average process length (excluding distal platforms), 8(9.6)13 μm, standard deviation, 1.16. Nineteen specimens measured.

Previous records.—Widely distributed throughout the North Atlantic region during the Miocene and, to a lesser extent, Pliocene (e.g., see Head et al., 1989c; Head, 1997), with Quaternary records mostly for lower latitudes, e.g., lowermost Pleistocene of the Iberia Abyssal Plain (McCarthy and Mudie, 1996) and upper Pleistocene and Holocene of the Gulf of Mexico (Wrenn and Mudie, 1986; de Vernal et al., 1992).

Stratigraphic range.—Melitasphaeridium choanophorum sensu stricto ranges from lower Oligocene through Holocene (Head et al., 1989a; de Vernal et al., 1992).

Paleoecology.—Melitasphaeridium choanophorum is a well-known extinct thermophilic species (Head et al., 1989a; Head, 1997) of shelf environments, and appears to have inner neritic associations in the Pliocene of the Mediterranean (as M. pseudorecurvatum in Versteegh and Zonneveld, 1994).

Discussion.—Neogene and Quaternary records of Melitasphaeridium choanophorum and M. pseudorecurvatum (e.g., Wrenn and Kokinos, 1986, pl. 20, fig. 3) are not discriminated in the present study since process terminations are highly variable in the late Cenozoic, even on individual specimens, as noted in Head and Wrenn (1992), Strauss and Lund (1992), and Head (1997). Clino specimens are mostly assignable to Melitasphaeridium choanophorum var. “reductum” Strauss and Lund 1992, although the variability of process terminations seen is comparable to that recorded by Strauss and Lund (1992, fig. 2, a–g) for Miocene specimens from Germany and includes process terminations typical of M. choanophorum and M. pseudorecurvatum. The varietal name Melitasphaeridium choanophorum var. “reductum” was not validly published in Strauss and Lund (1992) since the institution where the type material is conserved was not specified (ICBN Art. 37.5).

Genus Nematosphaeropsis Deflandre and Cookson, 1955

Nematosphaeropsis rigida Wrenn, 1988

Nematosphaeropsis rigida Wrenn, 1988

Figure 9.3–9.8

Nematosphaeropsis rigida Wrenn, 1988, p. 144, 146, 148, pl. 2, figs. 1–6, pl. 3, fig. 4, pl. 4, figs. 1–5, pl. 6, figs. 3, 4. (see for synonymy).

Nematosphaeropsis sp. 1. Head, Norris, and Mudie, 1989a, p. 438, pl. 6, figs. 12–14.


?Nematosphaeropsis balcombiana Deflandre and Cookson, 1955, p. 268, 269, pl. 8, fig. 5.

Previous records.—Middle and upper Miocene and lower Pliocene of the Norwegian Sea (as Nematosphaeropsis sp. 2 in Manum et al., 1989; Poulsen et al., 1996), upper Miocene through Holocene of the Gulf of Mexico (Wrenn, 1988; and as Nematosphaeropsis sp. B in Wrenn and Kokinos, 1986; Aubry, 1993), Miocene through Holocene of the Caribbean Sea (as Nematosphaeropsis balcombiana in Wall, 1967, pl. 14, fig. 17), upper Miocene of the Labrador Sea (as Nematosphaeropsis sp. 1 in Head et al., 1989a), upper Pliocene of the central North Atlantic (Versteegh, 1997), and upper Pliocene through Holocene of the Mediterranean (Versteegh and Zonneveld, 1994; Zonneveld, 1995).

Paleoecology.—An extant cyst (as “Nematosphaeropsis balcombiana”) that has been incubated to produce the motile form Gonyaulax spinifera (Wall and Dale, 1967, 1968; Wall, 1971). It appears to have a tropical to mild-temperate climatic range and an inner neritic to oceanic? distribution, based on its fossil record (see above) and presence in modern coastal sediments of Woods Hole, Massachusetts (Wall and Dale, 1967; 1968; Wall, 1971). It is linked to warmer isotopic intervals of the late Pliocene in southern Italy (Versteegh and Zonneveld, 1994).

Discussion.—Present in a single sample (CUS-M8) where represented by numerous well preserved specimens.

Nematosphaeropsis balcombiana, described from the middle Miocene of Australia (Deflandre and Cookson 1955), resembles Nematosphaeropsis rigida Wrenn 1988 superficially. Deflandre and Cookson illustrated the holotype of N. balcombiana with a single photograph that has since been interpreted in different ways (compare Wrenn, 1988, pl. 7, fig. 3 with Mudie in Head and Wrenn, 1992, p. 16). The holotype clearly should be re-examined if possible.

Genus Operculodinium Wall, 1967

Operculodinium bahamense Head, new species

Figures 9.9–9.14, 10.1–10.5

**Diagnosis.**—A large species of *Operculodinium* with long, sparsely distributed processes; tabulation relatively completely expressed by low sutch ridges that appear as dark narrow lines on surface.

**Description.**—Central body broadly egg-shaped to nearly spherical, the wall consisting of thin, solid pedium, and thicker, distally open, spongy-fibrous to fibro-microreticulate luxuriae. Gonyaulacacean tabulation indicated by low (ca. 1 μm or less) sutural ridges composed of coalesced fibers or granules, appearing as dark narrow lines on surface. Cingulum narrow, equatorial, and descending with displacement of about one width. A flagellar scar may be indicated by elongate indentation in mid-sulcal area. Processes are slender and solid, with fibrous, expanded bases; and terminate distally in small aculate platforms, each with up to eight or more aculeae. Process distribution sparse and nontubular, with process bases sometimes crossing sutural ridges. Process length variable on individual specimens, some processes being up to 32 μm in length. Archeopyle precingular Type 1P (3°), enlarged, has rounded angles. Operculum free.

**Dimensions.**—Holotype: length (excluding process), 81 μm; process length, 6-11 μm; wall thickness, ca. 1.7 μm. Range: Maximum diameter (excluding process), 80(89.7)106 μm; average process length, 7(15.0)24 μm. Wall thickness, ca. 0.6(1.11.7) μm. Thirty specimens measured.

**Eymology.**—Named with reference to the Great Bahama Bank, type locality of this species.

**Holotype.**—Fig. 9.9-9.12. Sample CUS-K11, slide 3; England Finder reference G18/2. ROM 53304. Clino core, 234.12 m (768.13 ft) below mud pit; upper upper Pliocene.

**Comparison.**—*Operculodinium giganteum* Wall, 1967 may also have sutural lines, but processes are shorter (2-4 μm) and more densely distributed. *Operculodinium wallii* Matsuoka, 1983 lacks sutural lines or ridges. *Operculodinium floridium* Head et al., 1989b, emend. Head, 1997 (see Head in Head and Wrenn, 1992), Accepted records are: lower Miocene of the Norwegian Sea (Head in Head and Wrenn, 1992), lower Miocene of the Indian Ocean (Head and Wrenn, 1992), lower and lower middle Miocene of the eastern U.S.A. (de Verteuil and Norris, 1996), middle Miocene through upper Pleistocene of the northeastern Australian margin (McMinn, 1993a, 1993b), upper Miocene through Quaternary of the Indian Ocean (McMinn, 1992a), Pliocene of Japan (Matsuoka, 1983), and Quaternary of southern Australia (McMinn and Wells, 1997).

**Discussion.**—Only acuminate and bifurcate process terminations were reported for the upper Miocene through lower Pleistocene type material of Japan (Matsuoka, 1983), whereas the Clino specimens often have some processes bearing three (and occasionally more) distal terminations. Specimens from the Neogene of the Indian Ocean have been reported only with acuminate processes (McMinn, 1992a), but specimens from the Miocene of the eastern U.S.A. may have fine bifid or trifid distal terminations (de Verteuil and Norris, 1996a). This species is assigned questionably to the genus *Operculodium* because, in contrast to the type species *O. centrocarpum*, it has processes that are not fibrous, even at their base, and a central body surface that is finely and faintly granulate instead of fibroreticulate.

**Operculodinium? longispinigerum** Matsuoka, 1983

**Figure 10.6-10.13**

**Operculodinium longispinigerum** Matsuoka, 1983, p. 125, pl. 9, figs. 5-9; Head and Wrenn, 1992, p. 22, 24, pl. 5, figs. 4, 8, 11; McMinn, 1992a, p. 435, pl. 2, figs. 3, 6, 8, 9; McMinn, 1992b, p. 158, pl. 3, figs. 7, 9-15; McMinn, 1993a, pl. 2, fig. 13; de Verteuil and Norris, 1996, pl. 8, figs. 13-15.

**Description.**—Cysts approximately spherical with finely and faintly to moderately granular surface. Processes appear to be nontubular, are solid and nonfibrous, often becoming sinuous distally. Surface of processes may become granular distally. Processes taper to fine or blunt points or may have two or three (occasionally four or more?) fine distal terminations. Individual specimens often have variety of process terminations, but usually carry some furcate processes. Archeopyle precingular, probably Type 1P, but Type 2P possible in some specimens; operculum free. No other indications of tabulation.

**Dimensions.**—Central body maximum diameter, 27(33.6)42 μm, standard deviation, 3.50; process length (excluding distal furcations), 5(6.8)9 μm, standard deviation, 1.10. Twenty-six specimens measured.

**Previous records.**—The stratigraphic range is not well established in the North Atlantic, this species having been confused with the superficially similar *Operculodinium eirikianum* Head et al., 1989b, emend. Head, 1997 (see Head in Head and Wrenn, 1992; Head, 1997). Accepted records are: lower Miocene of the Norwegian Sea (Head in Head and Wrenn, 1992), lower Miocene of the Indian Ocean (Head and Wrenn, 1992), lower and lower middle Miocene of the eastern U.S.A. (de Verteuil and Norris, 1996, p. 29, 30) and therein for discussion of other records), upper lower and lower middle Miocene of the offshore eastern U.S.A. (de Verteuil, 1996), middle Miocene through upper Pleistocene of the northeastern Australian margin (McMinn, 1993a, 1993b), upper Miocene through Quaternary of the Indian Ocean (McMinn, 1992a), Pliocene of Japan (Matsuoka, 1983), and Quaternary of southern Australia (McMinn and Wells, 1997).

**Operculodinium? megagarum** Head, new species

**Figures 10.14, 10.15, 12.1-12.9**

*Operculodinium* sp. A. Wrenn and Kokinos, 1986, pl. 10, fig. 6-7, pl. 20, fig. 1.

*Operculodinium* sp. C. Jan du Chêne, 1977, p. 112, text-fig. 4.9, pl. 1, fig. 12.

**Diagnosis.**—Egg-shaped gonnyaulacacean cyst with small, rounded apical protuberance. Wall consists of pedium whose surface has a dense cover of small granules along with sparse, irregular distribution of larger elements represented by grana, blunt spines, and bacula. Archeopyle precingular Type 1P (3°) with smooth margins and well-developed angles; operculum free. No other indications of tabulation.

**Description.**—Apical protuberance varies between 0.5 and 3.0 μm in height. Pedium moderately thick (ca. 0.5 μm or less), surface bearing dense cover of small (less than 0.5 μm) granules along with sparse, irregular distribution of larger elements consisting of grana, blunt spines, and bacula. These larger elements...
Figure 9—Photomicrographs are interference contrast (1, 2) or bright field images. Various magnifications. Max. dia. = maximum diameter. 1, 2, Melitasphaeridium choanophorum; 1, uncertain view of upper surface showing choanophorum-like process terminations, central body max. dia. 31 μm, CUS-K11(3), R23/2; 2, ventral view of ventral surface showing "reductum"-like process terminations, central body length 31 μm, CUS-K11(3), H27/0. 3-8, Nematosphaeropsis rigida; 3, ventral? view of ventral? surface, central body max. dia. 43 μm, CUS-M8(4), L22/3; 4, 5, uncertain view of 4 upper surface and 5 slightly lower focus, central body length 38 μm, CUS-M8(4), Q32/0; 6-8, ventral
(up to ca. 3 µm high) often have irregular shapes, may appear to be composed of aggregations of granules, and often have constricted bases. They may be evenly distributed over entire cyst, but are often larger and more concentrated on ventral and antapical surfaces.

**Dimensions.**—Holotype: length, 49 µm; thickness, 47 µm. Range: maximum diameter, 47(52.4)59 µm, standard deviation 3.12. Twenty-one specimens measured.

**Etymology.**—Named with reference to the large, irregular granules that occur on the surface of this species.

**Holotype.**—Fig. 12.1–12.3. Sample CUS M8, slide 4; England Finder reference S31/3. ROM 53433. Clino core, 255.88 m (839.5 ft) below mud pit; upper upper Pliocene.

**Comparison.**—Cf. Pyxidiella sp. of Jan du Chêne (1977) is similar but a pronounced apical protuberance is not indicated.

**Previous records.**—Upper Miocene through upper lower Pleistocene (ca. 0.8–0.9 Ma; as Operculodinium sp. A in Wrenn and Kokinos, 1986; Aubry, 1993). Possibly recorded from the upper Miocene of Spain (as cf. Pyxidiella sp. in Jan du Chêne, 1977).

**Discussion.**—The generic assignation is tentative owing to the lack of fibrous processes, presence of a nonfibrous wall, angular archeopyle margin, and apical protuberance. Operculodinium centrocarpum, the type of the genus, differs in all these features.

**Operculodinium psilatum** Wall, 1967

Figure 12.10


**Discussion.**—Specimens are rare in the Clino core. This species has been recorded in deposits from lower Pleistocene through Holocene of the North Atlantic region (Head, 1996a).

**Operculodinium spp. including O. ISRAELIANUM** (Rossignol, 1962) Wall, 1967

Figures 11, 12.11–12.16

**Hystrichosphaeridium israelianum** Rossignol, 1962, p. 132, pl. 2, fig. 3.

**Operculodinium israelianum** (Rossignol, 1962) WALL, 1967, p. 111;

**LENTIN AND WILLIAMS, 1993, p. 467–468 (see for nomenclatural history).

**Description.**—Luxuria fibro-micoreticulate, becoming spongy in thicker walled specimens. Processes have fibrous bases and usually bear minute distal platforms or aculeae. A heterogeneous group showing variation in size, process length and form, density of process distribution, density of luxuria, and wall thickness. Typical morphotypes are illustrated in Fig. 12.11–12.16.

**Dimensions.**—Maximum central body diameter, 38(52.7)69 µm, standard deviation, 7.3; process length, 4(9.4)17, standard deviation 2.54. Ratio of central body diameter/process length, 3.1(6.2)16.3, standard deviation 2.35. One hundred specimens were measured from the lower interval. See also Fig. 11.

**Comparison.**—Most specimens (e.g., Fig. 12.11–12.13) fall within the morphological range given for O. israelianum (holotype: central body diameter 40 µm, process length up to about 6 µm, judging from the illustration in Rossignol, 1962; range: central body diameter 45–65 µm, process length 6–10 µm, Rossignol, 1964). But many specimens have relatively longer processes, and some larger specimens overlap with O. centrocarpum (holotype: central body maximum diameter 75 µm, process length about 17 µm, Matsuoka et al., 1997; other type specimens: central body diameter 54–80 µm, process length 13–18 µm, Deflandre and Cookson, 1955). Occasional specimens with thick, spongy luxuria resemble O. crassum, a thick-walled morphotype now included within O. israelianum (Head and Wrenn, 1992).

In his study of Quaternary dinoflagellates from the Caribbean Sea, Wall (1967) separated O. centrocarpum from O. israelianum exclusively on relative process length: ranging between one-fifth and one-quarter of the central body diameter in O. centrocarpum, and one-tenth or less of the central body diameter in O. israelianum. This distinction was not possible for the Clino specimens, whose process length show a continuous range between one-sixteenth and one-third of the central body diameter (see Fig. 11).

**Ecology.**—Operculodinium israelianum is a tropical and subtropical estuarine species today (Wall et al., 1977) although its ecological range does extend into warm temperate regions (Dale, 1983; Head and Wrenn, 1992) and its climatic tolerance was evidently broader in the past. Notably, it flourished during the late Pliocene in certain cool-temperate or subarctic shallow environments of the southern North Sea (Wall et al., 1977, Head, 1996a, 1998a).

**Genus** *Spiniferites* Mantell, 1850, emend. Sarjeant, 1970

**Spiniferites rhizophorus** Head, new species

Figures 4.18, 6.1–6.6

**Diagnosis.**—Central body broadly ovoidal, with unstratified wall having nearly smooth surface. Processes gonal, some branched proximally to form numerous still-like columns. Sutures may be indicated by faint lines, or by low, solid ridges linking process bases. Archeopyle precingular Type P (3°); operculum free.

**Description.**—Central body broadly ovoidal, with finely and faintly punctate/granulate surface appearing nearly smooth. Wall between processes unstratified under light microscopy. Processes gonal and trifurcate, usually with secondary bifid terminations. Process shafts solid, some arising from unbranched bases, others branched proximally so process is supported by numerous still-like columns. Sutures may be indicated by faint lines on surface of central body, or by low, solid ridges linking process bases, and may be expressed between closely adjacent process bases by adjoining trabeculae, often supported by stilt-like columns.

**Dimensions.**—Holotype: central body length, 50 µm; average process length, 16 µm. Range: central body length, 38(46.0)51 µm, standard deviation, 3.96; average process length, 9(14.0)17 µm, standard deviation, 2.46. Twenty specimens measured.

**Etymology.**—Named with reference to the stilt-like branching of process bases that recalls the aerial roots of the mangrove genus *Rhizophora*.

**Holotype.**—Fig. 6.1–6.4. Sample CLS-K4, slide 5; England Finder reference T10/4. ROM 53428. Clino core, 476.4 m (1563 ft) below mud pit; upper upper Pliocene.

**Discussion.**—This species is distinguished by pronounced proximal branching of some process stems, although most specimens have some processes that are unbranched. In some areas of the cyst, particularly in lateral and ventral areas, closely adjacent process stems may be replaced by a single complex of columns or subvertical strands, which may be interlinked to...
Figure 10—Photomicrographs are all bright field images. Various magnifications. Max. dia. = maximum diameter. 1–5, Operculodinium bahamense Head, n. sp.; 1, ventral view of dorsal surface, length (excluding processes) 86 μm, CUS-K10(2), W20/2 (see also Fig. 9.13, 9.14); 2, 3, left antapical view of 2 left antapical surface, 3 slightly lower focus, length (excluding processes) 91 μm, CUS-M9(4), L41/1; 4, 5, internal view of detached operculum, length 49 μm, CUS-K10(2), N38/1. 6, 7, Operculodinium janduchenei; ventral view of 6 dorsal surface, 7 slightly higher focus, length (excluding processes) 30 μm, CUS-M2(3), ×260. 8–13, Operculodinium? longispinigerum; note finely and faintly granulate wall surface, solid process stems and unbranched or finely furcate process terminations; 8, 9, left lateral view of 8 left lateral surface, 9 slightly lower focus, central body length 34 μm, CUS-M2(4), R23/1; 10, uncertain view of upper surface, central body max. dia. 38 μm, CUS-M1(5), U29/3;
form an irregular latticework. No other species of *Spiniferites* is known to have such development of process bases.

Although infrequent, this species occurs in most samples of the Clino core. There are no known previous records.

Family *Goniomataceae* Lindemann, 1928

Subfamily *Helgolandinioideae* Fensome et al., 1993

Genus *Tuberculodinium* Wall, 1967

*Tuberculodinium* *vancampoae* (Rossignol, 1962) Wall, 1967

Figure 12.17

*Pterospermopsis? Van Campoae* Rossignol, 1962, p. 134, pl. 2, fig. 1


**Paleoecology.**—This extant species has a tropical through temperate climatic range (Wall et al., 1977; Dale, 1996; Head, 1996a and references therein). It rarely exceeds 10 percent of modern assemblages where it is relatively abundant in tropical estuaries (Wall et al., 1973), but is also relatively common away from shore in the Persian Gulf (Bradford and Wall, 1984). In contrast to *Polysphaeridium zoharyi*, it appears to be more abundant in low salinities (Wall et al., 1977).

**Stratigraphic range.**—Upper Oligocene (Costa and Downie, 1979) or Eocene (see Head et al., 1989a) through Recent (Head, 1996b).

**Discussion.**—A rare component representing less than two percent of the Clino assemblages, but consistently present in the lower interval and sporadic in the upper interval.

Subfamily *Pyrodioidae* Fensome et al., 1993


*Capisocysta lata* Head, 1998b

Figure 12.18


**Discussion.**—A tropical to warm-temperate neritic species, reported as a living cyst from Puerto Rico and Portugal (Head, 1998b) and known also from the middle and upper Pliocene of eastern Guinea (Head, 1998a, 1998b, 1998c). *Capisocysta wallii* Warny and Wrenn, 1997, the type species, is similar but its hypocystal tabulation is largely undetermined, this preventing detailed comparison. *Capisocysta wallii* is known from the upper Miocene and lower Pliocene of the Atlantic coast of Morocco (Warny and Wrenn, 1997).

Genus *Polysphaeridium* Davey and Williams, 1966, emend.

Bujak et al., 1980

*Polysphaeridium zoharyi* (Rossignol, 1962)

Bujak et al., 1980

Figure 12.19, 12.20

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

*Polysphaeridium zoharyi* (Rossignol, 1962) Bujak et al., 1980, p. 34.

**Description.**—Central body surface varies from nearly smooth to faintly granulate. Nearly all specimens have relatively long processes (see Dimensions) and are therefore assignable to *P. zoharyi* subsp. *zoharyi* (autonym), but short-processed specimens referred to *P. zoharyi* subsp. *ktana* (Rossignol, 1964) Lentin and Williams, 1981 were seen occasionally.

**Dimensions.**—Average central body diameter, 43(51.6)58 μm, standard deviation, 3.3; average process length, 11(15.5)21 μm, standard deviation, 1.87; ratio of central body diameter to process length, 2.8(3.4)4.5, standard deviation, 0.3. Thirty specimens measured.

**Ecology.**—An inner neritic tropical and subtropical extant species favoring saline estuarine and lagoonal environments, with highest abundances (greater than 20 percent) where depths are less than 22 m, winter sea-surface temperatures are above 16°C, and summer sea-surface temperatures are above 25°C (Wall and Dale, 1969; Wall et al., 1977; Edwards and Andrle, 1992, text fig. 18). It is locally common today (up to 20 percent) in shallow restricted lagoons of the Bahama Islands, where sea-surface temperatures have an annual range of 20 to 31°C and salinities are very high, ranging between 37 and 42 per mill (Wall et al., 1977). Furthermore, *P. zoharyi* is abundant (greater than 45 percent) and fairly evenly distributed over much of the Persian Gulf, where salinities in this restricted water body are mostly in excess of 40 per mill and sea-surface temperatures have an annual range of 17 to 32°C (Bradford and Wall, 1984). Here, *P. zoharyi* shows a negative correlation with more open marine conditions and, as with the Clino core, has a strong negative correlation to *L. machaerophorum* which seems to prefer less restricted conditions. A similar negative correlation with *L. machaerophorum* has also been noted in lower Tertiary and Quaternary deposits of the Caribbean and Israel (Wall and Dale, 1969).

High salinities are not the only factor controlling distribution, however, because *P. zoharyi* is also associated with low and fluctuating salinities in Florida (Brewster-Wingard et al., 1996), and percentages reaching 98 percent have been recorded from sheltered bays in Bermuda whose salinities are about 34 to 37 per mill (Wall et al., 1977). In Florida Bay (Edwards and Weedman, 1996) and elsewhere (Wall and Dale, 1969) both *P. zoharyi*...
and its thecate stage may increase in abundance with proximity to vegetation such as mangrove (see also below) and sea grass.

*Polysphaeridium zoharyi* is the cyst of the thecate, bloom-forming dinoflagellate *Pyrodinium bahamense*, the Pacific variety of which today is a well-known producer of toxic red tides. A common feature of all sites of red tides in the western Pacific has been the presence of mangroves in the general vicinity (Maclean, 1989), although the reason for this remains unknown (F.J.R. Taylor, pers. comm.). Wind-driven upwelling seems to initiate red tides, raising both cysts and nutrients into the water column (Maclean, 1989). The association of dominant *P. zoharyi* with massive seabird and fish kills in upper Pliocene deposits of Florida has been taken as evidence for toxic red tides in the fossil record (Emslie et al., 1996).

*Previous records.—*Numerous records for the Neogene of the North Atlantic, particularly in lower latitudes. Present in Florida, sometimes dominant, since at least the late Eocene (Weedman et al., 1995) and occurring abundantly throughout the upper Miocene, Pliocene, and Pleistocene of the Gulf of Mexico (Wrenn and Kokinos, 1986).

**Discussion.—**-*Polysphaeridium zoharyi* was described from the subsurface lower Pleistocene of Israel (Rossignol, 1962, 1964). Although modern cysts are identical in most respects with fossil specimens, including those of the present study, they often have relatively shorter processes.

Order *Peridiniales* Haeckel, 1894
Family *Congruentidiaceae* Schiller, 1935
Lentin and Williams, 1976

**Discussion.—**See Head (1993, p. 30, 31) for discussion of this genus and its emendation.

*Lejeunecysta mariae* (Harland in Harland et al., 1991) Lentin and Williams, 1993

Figure 14.1


*Lejeunecysta mariae* (Harland in Harland et al., 1991) Lentin and Williams, 1993; HEAD, 1996a, p. 563, fig. 15.9, 15.10.

**Stratigraphic range.—**Middle Miocene of the western North Atlantic (de Verteuil, 1996) through upper upper Pliocene (ca. 1.9–2.1 Ma) of southwestern England (Head, 1993) and upper upper Pliocene of the present study. Additional records from the middle Miocene through Pliocene of the North Atlantic region are given in Harland in Harland et al. (1991) and Head (1996a).

**Discussion.—**A single specimen recorded having features characteristic of this species (see Harland in Harland et al., 1991; Head, 1993) including a solid apical horn tip, strongly divergent antapical horns with 3.5 μm-long, solid pointed tips, convex margins on epicyst, and faintly granular wall surface. The Clino specimen (length, 49 μm) is somewhat larger than usually reported: e.g., a range in length of 34–50 μm for the type locality of eastern England (Harland in Harland et al., 1991) and 27–47 μm for the upper upper Pliocene of southwestern England (Head, 1993).


Figure 14.2

**Discussion.—**Specimens are comparable with *L. mariaeae* but have a smooth wall surface. This contrasts with the faint but optically discernible surface texture usually seen on specimens of *L. mariaeae* (Head, 1993), including those near the type locality (Head, 1996a).

**Genus Selenopemphix** Benedek, 1972, emend. Head, 1993
**Selenopemphix nephroides** Benedek, 1972 emend. Bujak in Bujak et al., 1980

Figure 14.3

**Selenopemphix nephroides** BENEDEK, 1972; p. 47–48, pl. 11, fig. 13; pl. 16, figs. 1–4; tab. 2; emend. Bujak in Bujak, Downie, Eaton, and Williams, 1980, p. 84; HEAD, 1993, p. 36, figs. 20.2–20.15, 21.4–21.6 (see for discussion of synonymy).

**Discussion.—**Specimens were seen occasionally. This species is widespread in Cenozoic deposits (Head, 1993).

**Selenopemphix quanta** (Bradford, 1975) Matsuoka 1985

Figure 13, 14.4, 14.5

**Multispinula quanta** BRADFORD, 1975, p. 3067–3070, figs. 5–6, non 7.

**Selenopemphix quanta** (Bradford, 1975) MATSUOKA, 1985, p. 51–52, standard deviation, 7.22; average process length, 8(10.9)15 μm, standard deviation, 1.75. Thirty-eight specimens were measured (see also Fig. 13).

**Dimensions.—**Width of central body, 32(46.1)61 μm; standard deviation, 7.22; average process length, 8(10.9)15 μm, standard deviation, 1.75. Thirty-eight specimens were measured (see for discussion of synonymy).

**Ecology.—**Modern distributions span a wide range of sea-surface temperatures but highest relative abundances are in shallow, tropical and subtropical areas at depths less than 40 m (Edwards and Andrei, 1992). It has a ubiquitous distribution in the Persian Gulf region (Bradford and Wall, 1984).

**Discussion.—**Specimens compare with cysts produced by the
living dinoflagellate Protoperidinium conicum, rather than those of Protoperidinium nudum which are smaller with fewer and relatively longer processes (Head, 1996b). However, in modern sediments, cysts assignable to S. quanta show wide morphological variation, sometimes exhibiting continuous gradation between larger and smaller morphotypes (see Head, 1993, p. 37 for discussion). Fossil occurrences of S. quanta have been reviewed in Head (1993).

**Undetermined genera**

**Protoperidinioid cyst A**

**Figure 14.6**

**Discussion.**—A single specimen was recorded having a subspherical ambitus (45 × 38 µm), possible polar compression, and a brown pigmented wall. The surface is densely covered with hairlike processes up to 2 µm long which arise from broad bases and taper to sharp or blunt points. Between the densely spaced process bases, the wall surface is more or less smooth. No evidence of tabulation was seen.

Round brown cysts

**Figure 14.7, 14.8**

**Dimensions.**—Maximum diameter, 31(40.3)49 µm. Twenty-six specimens measured.

**Discussion.**—Specimens are mostly crumpled and have a smooth to finely and faintly granulate surface. Some specimens might be assignable to the genus Brigantedinium Reid, 1977 although an archeopyle was usually not visible or was obscured by crumpling.

**Genus CYCLOPSIELLA**

**CYCLOPSIELLA sp.**

**Figure 14.9**

**CyclopsIELLA sp. cf. C. elliptica**

**NannobARbOPHORA WALLDALEI**

**Figure 14.10-14.15**

**Nannobarboxphora walldalei**—Upper Miocene through lower Pliocene of Atlantic coast of Morocco (as Impletosphaeridium acropora in Warny and Wrenn 1997), and lower Pliocene through lower Pleistocene of the North Atlantic region (Head, 1996a, 1998a).

**Paleoecology.**—A neritic species whose oceanic records perhaps represent long distance transport. Its climatic range is tropical through mild- or warm-temperate, judging from previous records and the present study. It appears to occur only in warmer intervals of the upper Pliocene in the North Sea (Head, 1998a) and is related to warmer isotopic intervals of the upper Pliocene in the Mediterranean (as Acritarch sp. B in Versteegh and Zonneveld, 1994).

**Discussion.**—Impletosphaeridium acropora Warny and Wrenn, 1997, documented with excellent SEM illustrations by its authors, is here judged to be conspecific with and junior to N. walldalei. Warny and Wrenn (1997) placed their species simultaneously under the group Acritarcha and the dinoflagellate order Gonyaulacales. Owing to its small size and absence of tabulation, N. walldalei is not considered a dinoflagellate but a marine alga of unknown affinity (following Head, 1996a).

Small spiny acritarchs

**Figure 14.16, 14.17**

**Description.**—Small cysts? with spherical central body, having thin wall and smooth or nearly smooth surface. Processes
numeros, usually with smooth, hollow process shafts that end distally as minute platforms or bifid and trifid terminations. Some specimens may have slender, solid processes. No signs of tabulation or excystment aperture seen.

**Dimensions.**—Central body diameter, 19(22.8)26 μm; process length, 4(5.5)7 μm. Thirteen specimens measured.

**Discussion.**—Typical specimens are illustrated in Fig. 14.16, 14.1. However, because of the relatively low magnification used during counting, some specimens of *N. walldalei* have likely been included in this category.

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