

## Paleontological Society

---

Palynology and Paleoenvironments of a Pliocene Carbonate Platform: The Clino Core, Bahamas

Author(s): Martin J. Head and Hildegard Westphal

Source: *Journal of Paleontology*, Vol. 73, No. 1 (Jan., 1999), pp. 1-25

Published by: Paleontological Society

Stable URL: <http://www.jstor.org/stable/1306740>

Accessed: 06/07/2010 16:17

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://dv1litvip.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=sepm> and <http://www.jstor.org/action/showPublisher?publisherCode=paleo>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



*Paleontological Society* and *SEPM Society for Sedimentary Geology* are collaborating with JSTOR to digitize, preserve and extend access to *Journal of Paleontology*.

<http://dv1litvip.jstor.org>

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

MARTIN J. HEAD AND HILDEGARD WESTPHAL

Department of Geology, Earth Sciences Centre, University of Toronto, Ontario, Canada, M5S 3B1, and  
GEOMAR Forschungszentrum für marine Geowissenschaften, Wischhofstr. 1–3, D-24148 Kiel, Germany;  
present address: RSMAS, University of Miami, 4600 Rickenbacker Causeway, Miami FL 33149-1098

**ABSTRACT**—Neritic dinoflagellates from periplatform (slope) carbonates of the Clino borehole, located on the western, leeward margin of the Great Bahama Bank, record environmental fluctuations on the platform top. A lower Pliocene interval (3.6–4.2 Ma) contains platform-top sediments shed onto the lower slope when the platform was open and ramplike. Despite this open topography, abundant *Polysphaeridium zoharyi* indicate the presence of restricted marine environments on the platform top. Terrestrial palynomorphs are rare throughout this interval and imply a mostly or fully submergent platform top.

By late Pliocene times (about 2.1–2.3 Ma) the platform had become flat-topped and steep-sided, with the Clino site located on its upper slope. 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 infer 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? megranum* Head new species, and *Spiniferites rhizophorus* Head new species.

## 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 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 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 morphology in the early Pliocene to a steep-sided platform in the late Pliocene. The name of this borehole refers to the cliniform slope deposits that characterize much of the hole. Slopes are important in understanding the development of a carbonate platform because they accumulate sediment that originated on the platform top, yet, unlike the platform top, their record is less punctuated by sea-level drop and emergence (Schlager et al., 1994). Furthermore, because of their proximity to the open ocean, they are easier to date biostratigraphically than the platform top where biostratigraphic markers are typically rare or absent owing to unfavorable environmental conditions (Droxler and Schlager, 1985; Schlager et al., 1994). Seismic geometries (Fig. 2) indicate that westward transport of sediment by far dominated, strongly reducing the influence of mainland Florida.

The present study is limited to two intervals of the Clino core,

a lower Pliocene section (476.40–494.39 meters below mud pit = mbmp) representing the lower-slope environment of a distally steepened, ramplike topography, and an upper Pliocene section (220.48–262.18 mbmp) representing the upper slope of a steep-sided, flat-topped platform (Eberli and Ginsburg, 1987, 1989; Eberli et al., 1997; Fig. 2). These two intervals are the focus of a larger sedimentary and diagenetic study, whose objectives are to identify sea-level fluctuations in the order of 100 ka in periplatform carbonates and to assess the effects of changes in platform topography (ramplike vs. steep sided) on the composition and nature of periplatform slope carbonates (Westphal, 1997; Westphal et al., in press). Previous studies on the platform interior (Beach, 1982) and basinal sediments (Reijmer et al., 1992) have already shown an overall shift in composition from lower to upper Pliocene that has been attributed to the morphologic evolution of the platform. Palynology has been integrated into this larger study to gain further insights into the marine environment (dinoflagellates) and to assess evidence of emergence of the platform top (spores and pollen).

The dinoflagellates have been given detailed taxonomic treatment because their low-latitude record in the Pliocene is poorly known. In the low-latitude western North Atlantic, detailed studies are known only for a deep water site in the Gulf of Mexico (Wrenn and Kokinos, 1986), and there are no previous detailed reports of Pliocene dinoflagellates from a tropical carbonate platform.

This paper follows the time scale of Berggren et al. (1995) and, where necessary, ages cited from the literature have been adjusted accordingly.

## 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 nannofossil datums.

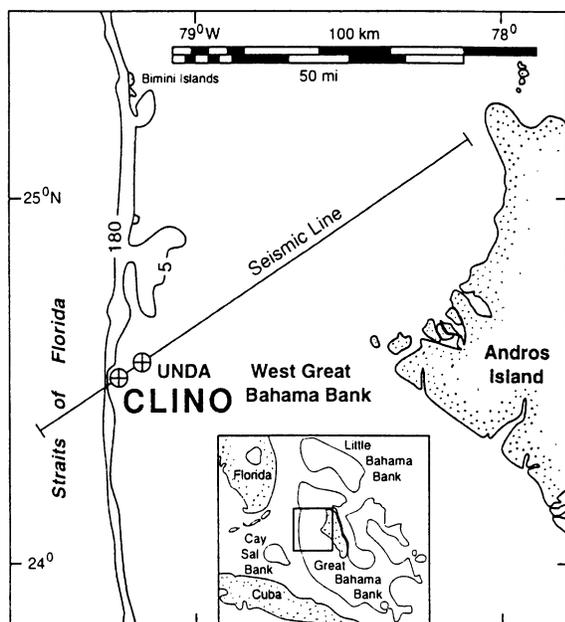


FIGURE 1—Location of the Clino and Unda boreholes. Contours are in meters. Note the large areal extent and low relief of the Great Bahama Bank, which is mostly covered by shallow water. The seismic line is that of the profile shown in Fig. 2. From Lidz and McNeill (1995, fig. 1).

**Lower Pliocene interval (476.40–494.39 mbmp; 1563.00–1622.00 fbmp).**—This interval occurs within a reversely magnetized section that the integrated age model assigns to Chron C2Ar (3.580–4.180 Ma; late early Pliocene). Our interval is calculated to cover a time span of about 140 ka (Lidz and McNeill, 1995).

**Upper Pliocene interval (220.48–262.18 mbmp; 723.38–860.17 fbmp).**—The Olduvai subchron has its base at 146.0 m (1.95 Ma) and thus postdates the studied interval. The top of our interval coincides approximately with a normal event tentatively recognized as the Reunion at about 221 mbmp (725 fbmp; 2.14–2.15 Ma). Below this normal event, the reversed subchron C2r2r (base at 2.581 Ma) extends down to 378 mbmp (1240 fbmp). According to the integrated age model for the Clino core, our interval was deposited during extremely rapid sedimentation and is dated between about 2.1 and 2.3 Ma (late late Pliocene, early Gelasian). It is calculated to cover a time span of about 75 ka (Lidz and McNeill, 1995).

#### MATERIALS AND METHODS

Fourteen carbonate samples were processed in Toronto, six (prefixed “CLS”) from the lower Pliocene interval and eight (prefixed “CUS” or “CGS”) from the upper Pliocene interval.

**Sample processing.**—Already lithified and dry, the samples were first weighed (2.1 to 18.6 g; Fig. 3). Between one and three *Lycopodium clavatum* spore tablets were added to each sample to enable estimation of absolute palynomorph abundances, and samples were then demineralized in cold HCl and HF. Oxidants, alkalis, and hot acids were not used since these can damage certain organic-walled microfossils, especially cysts of heterotrophic dinoflagellates. Residues were first sieved at  $>10\ \mu\text{m}$  and a microscope slide was made for each sample. Remaining residues were then sonicated for about 30–45 secs, to concentrate the palynomorphs, and stained with safranin-O. After sieving again at  $>10\ \mu\text{m}$ , slides were made to study the dinoflagellate cysts and pollen quantitatively, and to search for acritarchs. Remaining residue, where available, was re-sieved at 20

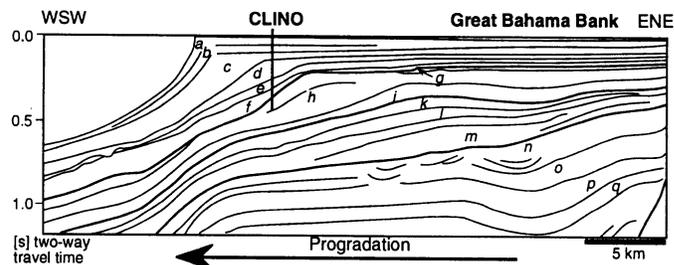


FIGURE 2—Seismic profile (see Fig. 1) of the western part of the Great Bahama Bank, showing progradation of the bank and steepening of the slope with time. Seismic sequences are lettered, with a–c representing Pleistocene and uppermost Pliocene, and parts of d and f corresponding respectively to the upper and lower Pliocene intervals of the present study. The Clino borehole terminated in the upper Miocene. Adapted from Eberli et al. (1997, fig. 3).

$\mu\text{m}$  to concentrate the larger dinoflagellates and determine whether any rare species were present—a necessary consideration in these low diversity assemblages. Examination of the  $>20\ \mu\text{m}$  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 Cellosize 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  $25\times$  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).

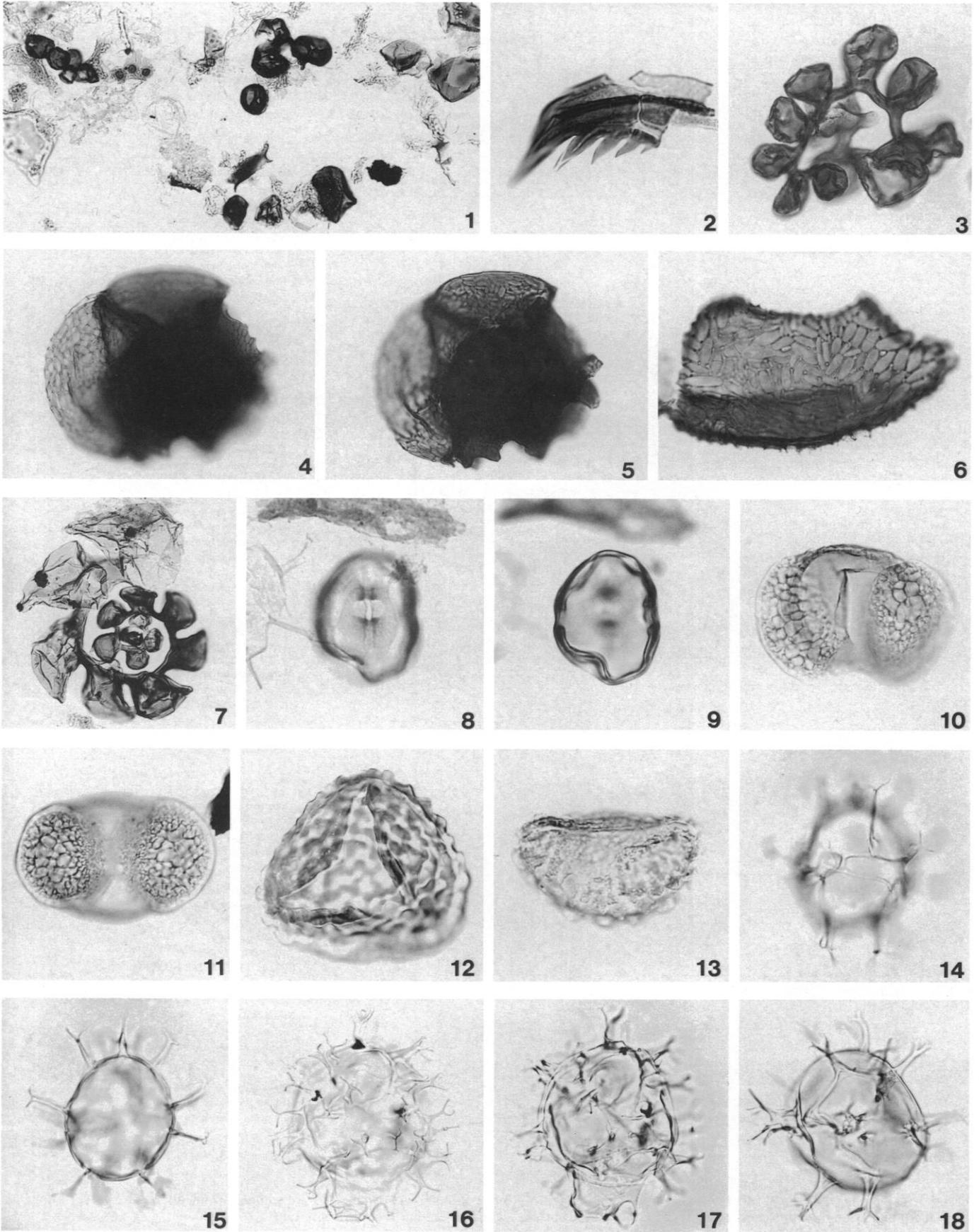
**Limitations to counts.**—Microforaminiferal linings are very abundant in most assemblages but were difficult to quantify owing to their mostly fragmented state, often occurring as single chambers (see Fig. 4.1). Traverse and Ginsburg (1966) noted a similar phenomenon for modern Bahamian assemblages. 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  $25\times$  objective. It was therefore decided not to include counts for *Kallosphaeridium* sp. or the leiospheres, but simply to record their presence in each sample (Fig. 3). Reliable counting of *Kallosphaeridium* sp. in these samples would require using a  $100\times$  objective.

Acanthomorph acritarchs were subdivided into two groups, *Nannobarbophora walldalei* (Fig. 14.10–14.15) and “small spiny acritarchs” (Fig. 14.16, 14.17). Although the sum of these

UPPER LOWER PLIOCENE (3.6–4.1 Ma)						UPPER UPPER PLIOCENE (ca. 2.1–2.3 Ma)								Age
C2Ar (upper Gilbert)						C2r (lower Matuyama)								Chron
lower slope						upper slope								Depositional environment
c	c	c				c		c	c					Sea-level lowstand (shaded) / inferred compaction (c)
1622.00	1621.50	1567.50	1565.08	1563.67	1563.00	860.17	858.50	842.50	839.50	768.13	763.50	741.50	723.38	Depth (feet below mud pit)
494.39	494.23	477.77	477.04	476.61	476.40	262.18	261.67	256.79	255.88	234.12	232.71	226.01	220.48	Depth (meters below mud pit)
CLS-M3	CLS-K6	CLS-M2	CLS-K5	CLS-M1	CLS-K4	CUS-M9	CUS-K12	CGS-2	CUS-M8	CUS-K11	CUS-M7	CUS-K10	CGS-1	Sample number
														<b>Dinoflagellates (raw counts)</b>
														Impagidinium sp. A
														Operculodinium janduchenei
														Hystrichokolpoma rigaudiae
														Operculodinium? longispinigerum
														Bitectatodinium tepikiense s.s.
														Impagidinium paradoxum
														Operculodinium? megagranum Head n. sp.
														Lejeuncysta marieae
														Nematosphaeropsis rigida
														Protoperidinioid cyst sp. A
														Bitectatodinium cf. raedwaldii
														Operculodinium psilatium
														Bitectatodinium raedwaldii
														Selenopemphix nephroides
														Selenopemphix quanta
														Tuberculodinium vancampoeae
														Ataxiodinium zevenboomii
														Melitasphaeridium choanophorum
														Achomosphaera / Spiniferites spp. (total)
														Capisocysta lata
														Dapsilidinium pseudocolligerum
														Kallosphaeridium sp.
														Lingulodinium machaerophorum
														Operculodinium bahamense Head n. sp.
														Operculodinium spp. including O. israelianum
														Polysphaeridium zoharyi
														Round brown cysts
														Spiniferites mirabilis
														Spiniferites rhizophorus Head n. sp.
														Lejeuncysta sp. cf. L. marieae
														TOTAL IN-SITU DINOFLAGELLATES
														<b>Marine algae incertae sedis (raw counts)</b>
														Incertae sedis sp. A
														Incertae sedis sp. B
														Leiospheres
														Nannoborbophora walldalei
														Small spiny acritarchs
														Acritarch sp. 1
														Cyclopsiella sp.
														<b>Other marine palynomorphs (raw counts)</b>
														Trochospiral microforaminiferal lining B
														Copepod fragments
														Foraminiferal linings (6 or more chambers)
														Scolecodonts
														<b>Terrestrial palynomorphs (raw counts)</b>
														Fungal spores and hyphae
														Fern and bryophyte spores
														Bisaccate pollen
														Angiosperm pollen
														TOTAL TERRESTRIAL PALYNOFORMS
														<b>Terrestrial palynomorphs / dinoflagellates</b>
														<b>Sample data</b>
														Sample dry weight (in grams)
														Quantity of Lycopodium clavatum tablets
														Quantity of Lycopodium clavatum spores counted
														<b>Palynomorphs per gram dry weight (concentrations)</b>
														Estimated total dinoflagellates
														(estimated standard error)
														Estimated total terrestrial palynomorphs
														(estimated standard error)

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 25× 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 utility as there are no previous reports in the literature. *Hystrichokolpoma rigaudiae* and *Operculodinium? longispinigerum* are persistent throughout the interval yet are absent from the upper Pliocene interval. They possibly have local biostratigraphic significance, but *H. rigaudiae* ranges above the upper Pliocene elsewhere in the North Atlantic (de Vernal et al., 1992) and *O.? longispinigerum* has an uncertain range in the North Atlantic but extends into the Pleistocene in the Australian region (McMinn, 1993b).

Dinoflagellates from the upper Pliocene interval (220.48–262.18 mbmp) are more helpful. They appear to indicate an age no younger than late Pliocene, this being consistent with the integrated age model for the Clino core (Eberli et al., 1997). *Dapsilidinium pseudocolligerum* has a highest common occurrence in the upper Pliocene of the Gulf of Mexico (as *Dapsilidinium* sp. A in Wrenn and Kokinos, 1986; Aubry, 1993), sporadic higher occurrences there conceivably representing reworking. Elsewhere *D. pseudocolligerum* occurs no higher than Pliocene. The following three species may be useful but their range tops are not presently well constrained: *Ataxiodinium zeeboomii* is not known higher than upper Pliocene or possibly lower Pleistocene (Head, 1997), *Bitectatodinium raedwaldii* is not known above uppermost Pliocene (Head, 1997), and *Lejeunecysta marieae* has a highest known occurrence of upper Pliocene (Head, 1996a). *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 uncompact 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 uncompact. 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

←  
 FIGURE 4—Photomicrographs are all bright field images. Various magnifications. Max. dia. = maximum diameter. 1, Typical palynofacies, after brief sonication and sieving at 10 μm, showing abundant fragmented microforaminiferal linings as darker subspherical objects, and lighter membranous debris of presumed algal origin; note the absence or near absence of terrigenous material; length of field of view 330 μm; CUS-K10(2), H24/4. 2, Invertebrate remains, probable scolecodont; length 51 μm; CLS-M2(2), U42/0. 3, Trochospiral microforaminiferal lining A; max. dia. 74 μm; CLS-K4(4), R10/4. 4–6, Trochospiral microforaminiferal lining B; 4, 5, showing 4 upper focus and 5 mid focus, max. dia. 86 μm, CLS-K4(4), C36/2; 6, fragment showing distinctive reticulation, length 81 μm, CLS-K4(4), B32/4. 7, Trochospiral microforaminiferal lining C; max. dia. 128 μm, CLS-K4(5), Q46/3. 8, 9, Tetracolporate angiosperm pollen; 8 upper focus, 9 mid focus, polar diameter 27 μm, CGS-2(2), R8/3. 10, 11, Bisaccate pollen of *Pinus*; 10, length 49 μm, CGS-1(2), Q23/0; 11, length 48 μm, CGS-1(2), R44/3. 12, Trilete fern spore; max. dia. 59 μm, CUS-M8(3), N26/0. 13, Monolete fern spore; length 46 μm, CGS-2(2), R32/1. 14, 15, *Spiniferites ramosus*; ventral view of 14 dorsal surface, 15 mid focus, central body length 34 μm, CGS-1(2), K29/3. 16, 17, *Spiniferites mirabilis*; ventral view of 16 ventral surface, 17 mid focus, central body length 49 μm, CUS-K11(3), V37/4. 18, *Spiniferites rhizophorus* Head, n. sp.; dorsal view of dorsal surface, central body length 48 μm, CLS-K4(4), E42/4.

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 DINOFLAGELLATES 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 ramplike 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 benthic 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 *Polysphaeridium 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 ramplike 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 vancampoeae*, 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 ramplike 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 Droxler 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 GONYAULACACEAE Lindemann, 1928

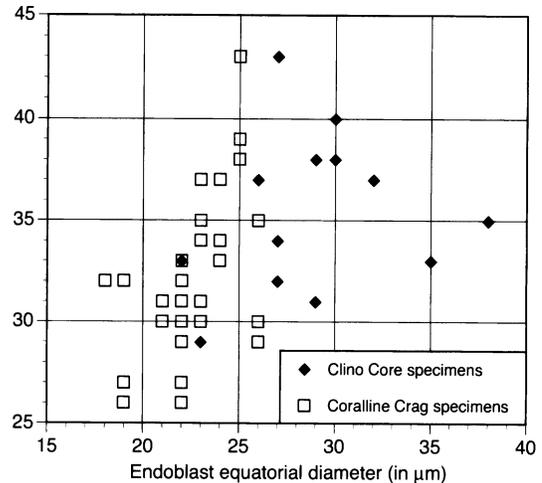
Genera ACHOMOSPHAERA Evitt, 1963 and

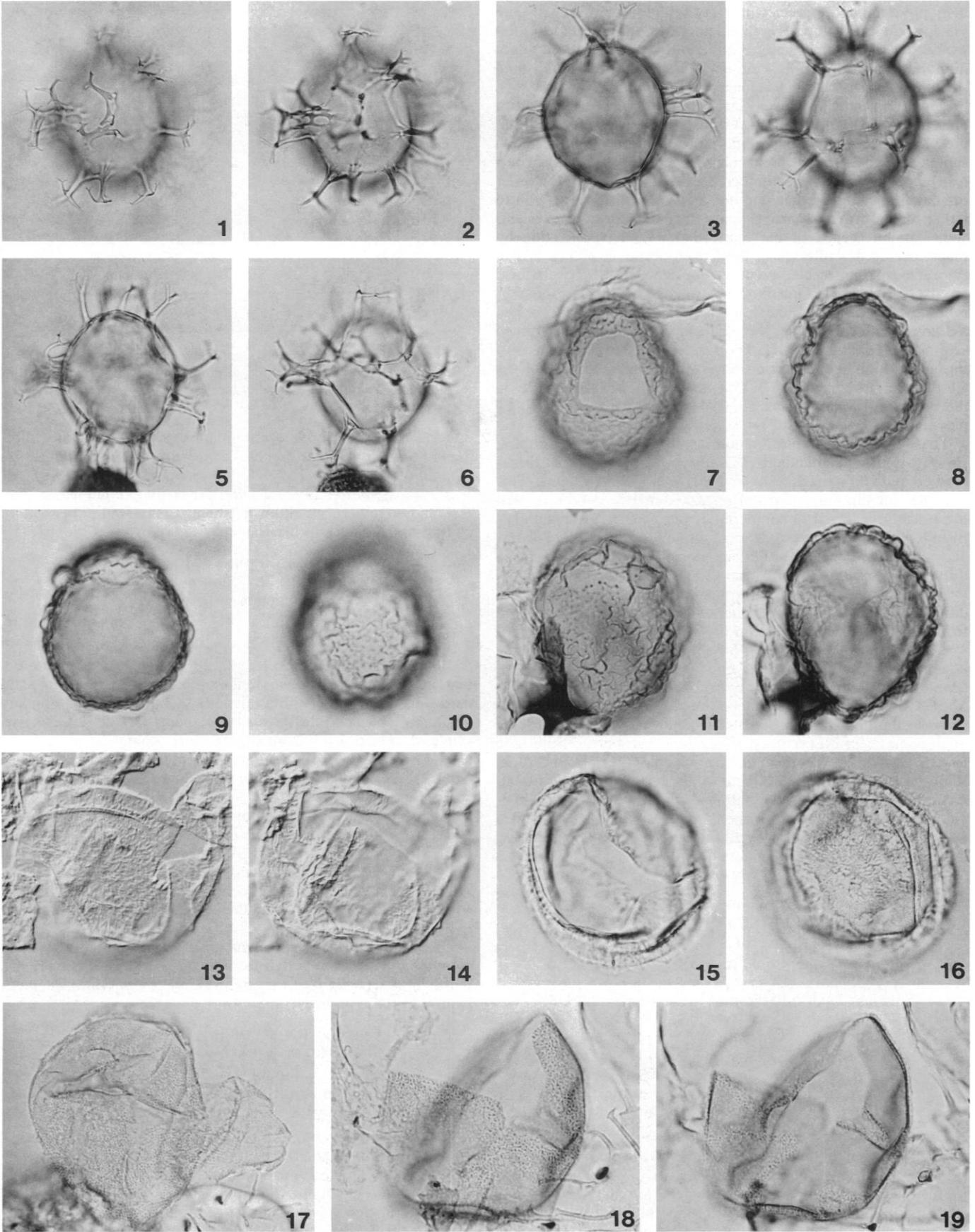
SPINIFERITES Mantell, 1850, emend. Sarjeant, 1970

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 rhizophorus* Head, n. sp. (Figs. 4.18, 6.1–6.6, and see below





*Previous records.*—Mid Pliocene of eastern England (Head, 1997), upper Pliocene of the Norwegian Sea (as “cf. *Bitectatodinium* 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.

*BITECTATODINIUM* sp. cf. *B. RAEDWALDII* Head, 1997

Figure 6.17

*Description.*—Proximate, approximately spherical cysts having a precingular (2P) archeopyle. Wall consists of a solid pedium of even thickness (less than 0.3  $\mu\text{m}$ ) surmounted by a luxuria of dense, erect, apparently free-standing pili. Pili have a diameter of about 0.3  $\mu\text{m}$  at their base, with separation of about 0.5  $\mu\text{m}$  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.

*BITECTATODINIUM* TEPIKIENSE Wilson, 1973 sensu stricto

Figure 6.18–6.19

*Bitectatodinium tepikiense* WILSON, 1973, p. 351–353, fig. 2, nos. 1–12.

*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.

*Paleoecology.*—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  $\mu\text{m}$  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

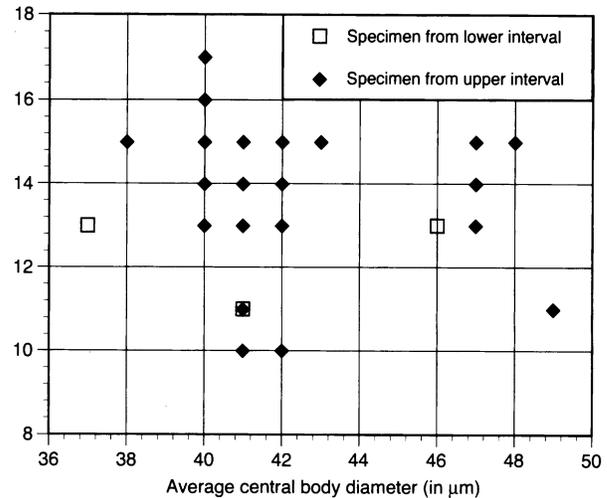


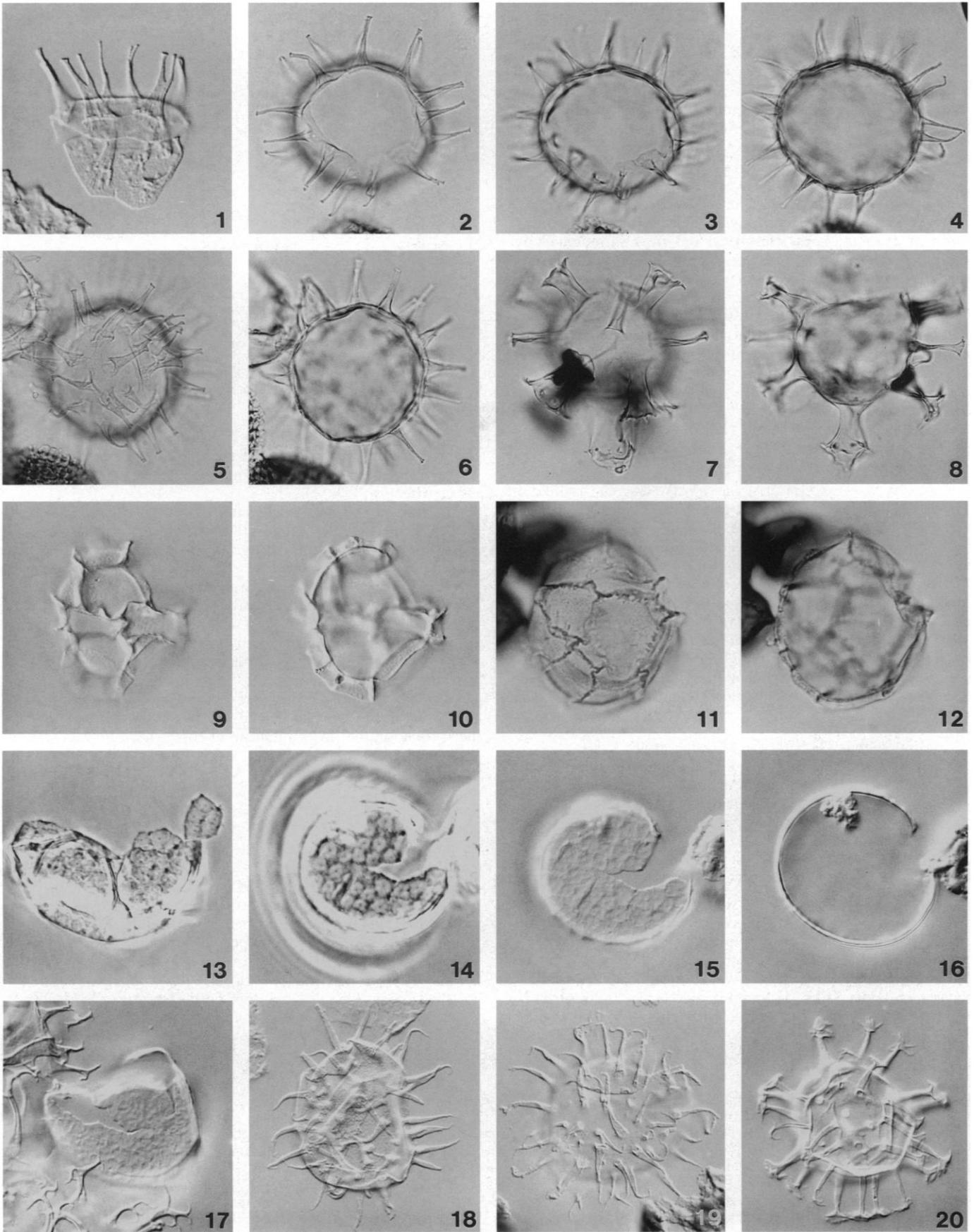
FIGURE 7—*Dapsilidinium pseudocolligerum* showing central body diameter vs. process length for specimens from the lower Pliocene and upper Pliocene intervals.

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  $\mu\text{m}$ ; average process length, 10(13.6)17  $\mu\text{m}$ . Diameter of process bases, 2.5–5.0  $\mu\text{m}$ . 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

FIGURE 6—Photomicrographs are interference contrast (13–15) or bright field images. Various magnifications. Max. dia. = maximum diameter. 1–6, *Spiniferites rhizophorus* Head, n. sp.; 1–4, holotype, ventral view of 1 ventral surface, 2 lower focus, 3 mid focus, 4 dorsal surface, central body length 50  $\mu\text{m}$ , CLS-K4(5), T10/4; 5, 6, dorsal view of 5 mid focus, 6 dorsal surface, central body length 46  $\mu\text{m}$ , CLS-K6(3), F14/3. 7–12, *Ataxiodinium zevenboomii*; 7–10, dorsal view of 7 dorsal surface, 8 lower focus, 9 mid focus, 10 ventral surface, endoblast length 32  $\mu\text{m}$ , CGS-2(2), F14/3; 11, 12, ventral view of 11 ventral surface, 12 dorsal surface, endoblast length 34  $\mu\text{m}$ , CUS-K12(3), V40/1. 13–16, *Bitectatodinium raedwaldii*; 13, 14, upper and lower foci respectively, max. dia. (including luxuria) 47  $\mu\text{m}$ , CUS-M7(3), Q27/2; 15, 16, ventral view of 15 dorsal surface, 16 ventral surface, max. dia. (including luxuria) 48  $\mu\text{m}$ , CUS-M8(4), V17/0. 17, *Bitectatodinium* sp. cf. *B. raedwaldii*; ventral view of ventral surface, max. dia. (including torn fragment) 58  $\mu\text{m}$ , CUS-K11(3), G14/3. 18, 19, *Bitectatodinium tepikiense* sensu stricto; dorsal view of 18 dorsal surface, 19 mid focus, max. dia. (including luxuria) 53  $\mu\text{m}$ , CLS-K4(4), Q23/2.



*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 Deflandre and Cookson, 1955  
Figure 8.7, 8.8

*Hystrichokolpoma rigaudiae* DEFLANDRE 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 lower 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.

*Impagidinium paradoxum* (Wall, 1967) STOVER AND EVITT, 1978, p. 166.

*Discussion*.—Five specimens were recorded, having a central body length of 25 to 32  $\mu\text{m}$  and a crest height of 2.5 to 3.5  $\mu\text{m}$ . Specimens have a faintly granulate surface, a weakly expressed sulcal tabulation, and lack an apical boss.

IMPAGIDINIUM SP. A

Figure 8.11, 8.12

? *Impagidinium* sp. E; WRENN AND KOKINOS, 1986, pl. 1, figs. 4–6, pl. 16, fig. 5.

*Description*.—Central body broadly ovoidal (length, 34  $\mu\text{m}$ , equatorial diameter, 30  $\mu\text{m}$ ) lacking apical horn, with a thin, finely but conspicuously granulate wall; gonyaulacoidean tabulation indicated by crests of low (2.0  $\mu\text{m}$ ), even height. Crests themselves have finely granulate surface; their bases have closely-spaced, solid rodlike elements that fuse with central body surface. Ventral surface not clearly visible but tabulation appears relatively well expressed. Single specimen found.

*Discussion*.—This specimen is most similar to *Impagidinium* sp. E of Wrenn and Kokinos (1986), recorded from the upper Pliocene and Pleistocene of the Gulf of Mexico, but is somewhat smaller (central body length, 34  $\mu\text{m}$ ; cf. about 37–47  $\mu\text{m}$  for *Impagidinium* sp. E, as measured from illustrations) and has more pronounced rodlike elements at the crest bases.

*Impagidinium* sp. A differs from *Impagidinium plicatum* Versteegh and Zevenboom, 1995, described from the Pliocene of the Mediterranean, in having rather shorter and less membranous crests that are not so conspicuously crenulated, and rodlike elements at the crest bases. *Impagidinium plicatum* has reduced expression of tabulation in the sulcal area, whereas this is probably not true of *Impagidinium* sp. A.

Genus KALLOSPHAERIDIUM de Coninck, 1969, emend. Jan du Chêne et al., 1985

KALLOSPHAERIDIUM SP.

Figure 8.13–8.17

*Description*.—Small spherical cysts with thin wall; surface faintly ornamented either with small granules or combination of small granules and low ridges that may form a partial irregular reticulum with lumina ca. 1–3  $\mu\text{m}$  across. Archeopyle apical and adnate; principal archeopyle suture strongly angular. Accessory archeopyle sutures generally do not extend onto operculum and may or may not be expressed elsewhere on epicyst. No other indication of tabulation.

*Dimensions*.—Maximum diameter, 31(32.8)37  $\mu\text{m}$ . Ten specimens measured.

*Previous records*.—A record of *Kallosphaeridium* sp. by Emslie et al. (1996, table 7, unillustrated) from the upper Pliocene of Florida is the only post-Miocene occurrence previously known for this genus.

*Discussion*.—Specimens are present in all samples but were not included in counts owing to difficulty in recognizing undehisced specimens as dinoflagellates. Even under the 100 $\times$  objective it was difficult to distinguish such specimens from leiospheres (see below), owing to the often faint and variable wall ornamentation. However, *Kallosphaeridium* sp. may be quite

FIGURE 8—Photomicrographs are interference contrast (1, 9, 10, 15–20), bright field (2–8, 11, 12), or phase contrast (13, 14) images. Various magnifications. Max. dia. = maximum diameter. 1–6, *Dapsilidinium pseudocolligerum*; 1, external view of operculum, width 29  $\mu\text{m}$ , CUS-M7(2), W12/0; 2–4, apical view of 2 apical surface, 3 slightly lower focus, 4 mid focus, central body maximum diameter, 43  $\mu\text{m}$ , CUS-K11(3), N24/3; 5, 6, antapical view of 5 antapical surface, 6 mid focus, central body maximum diameter, 43  $\mu\text{m}$ , CUS-K11(3), V19/2. 7, 8, *Hystrichokolpoma rigaudiae*; 7, lateral view of upper surface, central body width 49  $\mu\text{m}$ , CLS-K6(3), P25/3; 8, lateral view at mid focus, central body width 50  $\mu\text{m}$ , CLS-K6(3), D25/3. 9, 10, *Impagidinium paradoxum*; left lateral view of 9 left lateral surface, 10 mid focus, central body length 32  $\mu\text{m}$ , CLS-K4(4), W26/0. 11, 12, *Impagidinium* sp. A; left lateral view of 11 left lateral surface, 12 mid focus, central body length 34  $\mu\text{m}$ , CLS-M2(3), J12/3. 13–17, *Kallosphaeridium* sp.; 13, lateral view at mid focus, max. dia. (including operculum) 48  $\mu\text{m}$ , CLS-K4(2), R42/4; 14–16, apical view of 14 and 15 apical surface, 16 mid focus, max. dia. 32  $\mu\text{m}$ , CLS-M2(3), M21/3; 17, apical view of apical surface, max. dia. 32  $\mu\text{m}$ , CUS-K11(3), N18/0. 18, 19, *Lingulodinium machaerophorum*; 18, lateral view of upper surface, central body max. dia. 45  $\mu\text{m}$ , CUS-K11(2), W9/4; 19, lateral view of upper surface, central body max. dia. 46  $\mu\text{m}$ , CLS-K4(4), S35/1. 20, *Melitasphaeridium choanophorum*; specimen bearing both *choanophorum*-like and *pseudorecurvatum*-like process terminations, left lateral view of left lateral surface, central body max. dia. 31  $\mu\text{m}$ , CUS-K11(2), W6/2.

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.

*Lingulodinium machaerophorum* (Deflandre and Cookson, 1955) WALL, 1967, p. 109; Head, 1997, p. 179, figs. 9.1–9.4 (see references therein for synonymy).

**Paleoecology.**—A well-known extant euryhaline species with a temperate to tropical distribution. Edwards and Andrieu (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 continental slope and rise sediments of the Mediterranean and Caribbean seas (Wall et al., 1977) and is concentrated in more open waters of the Persian Gulf and adjacent areas (Bradford and Wall, 1984). Dominance of *L. machaerophorum* away from estuarine environments may be a signal for diffuse (but not strong) coastal upwelling resulting in limited nutrient enrichment (Dale, 1996): high values in the Clino core may similarly be explained by diffuse coastal upwelling.

**Stratigraphic range.**—Upper Paleocene through Recent (Head, 1996a).

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

Genus MELITASPHAERIDIUM Harland and Hill, 1979

MELITASPHAERIDIUM CHOANOPHORUM (Deflandre and Cookson, 1955) Harland and Hill, 1979, emend. Harland and Hill, 1979

Figures 8.20, 9.1, 9.2

*Hystrichosphaeridium choanophorum* DEFLANDRE AND COOKSON, 1955, p. 271, 272, text figs. 23–29.

*Melitasphaeridium choanophorum* (Deflandre and Cookson, 1955) HARLAND AND HILL, 1979, p. 39; emend. HARLAND AND HILL, 1979, p. 39–41.

*Melitasphaeridium aequabile* 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 Kokinos, 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  
emend. 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* sp. 2. MANUM, BOULTER, GUNNARSDOTTIR, RANGNES, AND SCHOLZE, 1989, pl. 14, figs. 10, 11.

?*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

*Operculodinium* sp. 3. MANUM, BOULTER, GUNNARSDOTTIR, RANGNES, AND SCHOLZE, 1989, pl. 13, figs. 5, 6.

*Diagnosis*.—A large species of *Operculodinium* with long, sparsely distributed processes; tabulation relatively completely expressed by low sutural 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 luxuria. Gonyaulacacean tabulation indicated by low (ca. 1  $\mu\text{m}$  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 aculeate platforms, each with up to eight or more aculeae. Process distribution sparse and nontabular, with process bases sometimes crossing sutural ridges. Process length variable on individual specimens, some processes being up to 32  $\mu\text{m}$  in length. Archeopyle precingular Type 1P (3"), enlarged, has rounded angles. Operculum free.

*Dimensions*.—Holotype: length (excluding process), 81  $\mu\text{m}$ ; process length, 6–11  $\mu\text{m}$ ; wall thickness, ca. 1.7  $\mu\text{m}$ . Range: Maximum diameter (excluding process), 80(89.7)106  $\mu\text{m}$ ; average process length, 7(15.0)24  $\mu\text{m}$ . Wall thickness, ca. 0.6(1.1)1.7  $\mu\text{m}$ . Thirty specimens measured.

*Etymology*.—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  $\mu\text{m}$ ) and more densely distributed. *Operculodinium wallii* Matsuoka, 1983 lacks sutural lines or ridges. *Operculodinium floridium* Warny and Wrenn, 1997 has shorter (2–10  $\mu\text{m}$ ) processes whose distribution is dense and distinctly intratabular, and lacks sutural lines or ridges.

*Previous records*.—Upper middle and upper Miocene of the Norwegian Sea (as *Operculodinium* sp. 3 in Manum et al., 1989).

OPERCULODINIUM JANDUCHENEI Head, Norris, and Mudie,  
1989b

Figure 10.6, 10.7

*Operculodinium janduchenei* Head, Norris, and Mudie, 1989b, p. 459,  
pl. 4, figs. 7–8, 12.

*Previous records*.—Middle Miocene through Quaternary of the Indian Ocean (McMinn, 1992a), middle and upper Miocene of the northern North Atlantic (Engel, 1992), upper Miocene of the eastern U.S.A. (de Verteuil and Norris, 1996), upper Miocene through Pleistocene of the northeast Australian margin (McMinn, 1993a), and modern sediments of southern Australia (McMinn and Wells, 1997). Previous North Atlantic upper Miocene and Pliocene records have been discussed by Head et al. (1989a, b).

*Discussion*.—A single well-preserved specimen was found, having a strongly granulate body surface and length (excluding processes) of 30  $\mu\text{m}$ . Processes are conical, mostly distally-closed, and about 3.0  $\mu\text{m}$  long.

OPERCULODINIUM? LONGISPINIGERUM Matsuoka, 1983  
Figure 10.8–10.13

*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 nontabular, 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  $\mu\text{m}$ , standard deviation, 3.50; process length (excluding distal furcations), 5(6.8)9  $\mu\text{m}$ , 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 (Aquitainian and Burdigalian) of France (Head in 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 northeast 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 *Operculodinium* 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? MEGAGRANUM 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.

? cf. *Pyxidiella* sp. JAN DU CHÈNE, 1977, p. 112, text-fig. 4.9, pl. 1, fig.  
12.

*Diagnosis*.—Egg-shaped gonyaulacacean 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  $\mu\text{m}$  in height. Pedium moderately thick (ca. 0.5  $\mu\text{m}$  or less), surface bearing dense cover of small (less than 0.5  $\mu\text{m}$ ) granules along with sparse, irregular distribution of larger elements consisting of grana, blunt spines, and bacula. These larger elements

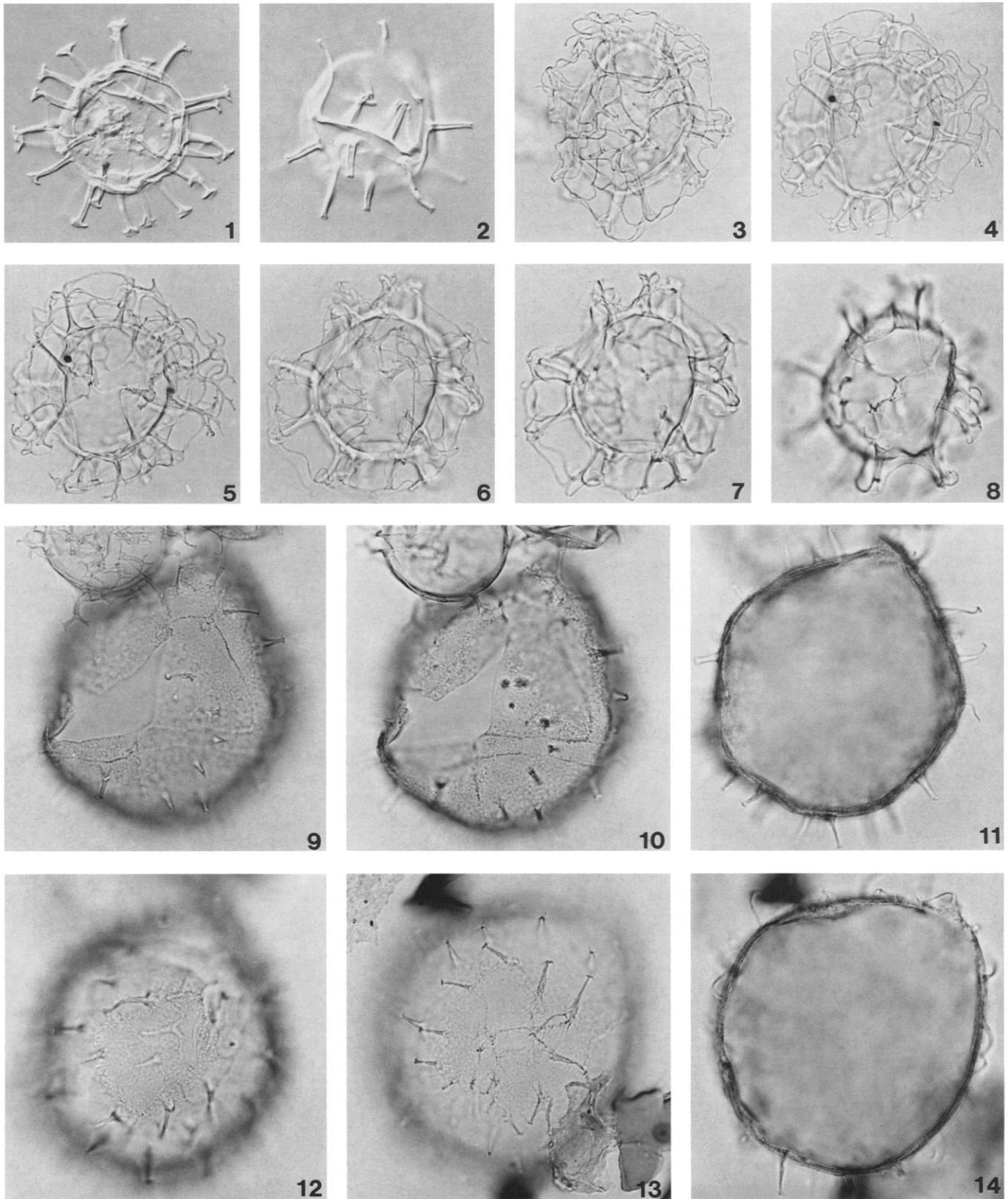


FIGURE 9—Photomicrographs are interference contrast (1, 2) or bright field images. Various magnifications. Max. dia. = maximum diameter. 1, 2, *Melitasphaeridium choanophorum*; 1, uncertain view of upper surface showing *choanophorum*-like process terminations, central body max. dia. 31  $\mu\text{m}$ , CUS-K11(3), R23/2; 2, ventral view of ventral surface showing “*reductum*”-like process terminations, central body length 31  $\mu\text{m}$ , CUS-K11(3), H27/0. 3–8, *Nematospaeropsis rigida*; 3, ventral? view of ventral? surface, central body max. dia. 43  $\mu\text{m}$ , CUS-M8(4), L22/3; 4, 5, uncertain view of 4 upper surface and 5 slightly lower focus, central body length 38  $\mu\text{m}$ , CUS-M8(4), Q32/0; 6–8, ventral

(up to ca. 3  $\mu\text{m}$  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  $\mu\text{m}$ ; thickness, 47  $\mu\text{m}$ . Range: maximum diameter, 47(52.4)59  $\mu\text{m}$ , standard deviation 3.12. Twenty-one specimens measured.

*Etymology.*—Named with reference to the large, irregular grana 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

*Operculodinium psilatum* WALL, 1967, p. 111, 112, pl. 16, figs. 6–8.

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

OPERCULODINIUM spp. including *O. ISRAELIANUM* (Rossignol, 1962) Wall, 1967  
Figures 11, 12.11–12.16

*Hystichosphaeridium 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-microreticulate, 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  $\mu\text{m}$ , 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  $\mu\text{m}$ , process length up to about 6  $\mu\text{m}$ , judging from the illustration in Rossignol, 1962; range: central body diameter 45–65  $\mu\text{m}$ , process length 6–10  $\mu\text{m}$ , Rossignol, 1964). But many specimens have relatively longer processes, and some larger specimens overlap with *O. centrocarpum* (holotype: central body maximum diameter 75  $\mu\text{m}$ , process

length about 17  $\mu\text{m}$ , Matsuoka et al., 1997; other type specimens: central body diameter 54–80  $\mu\text{m}$ , process length 13–18  $\mu\text{m}$ , 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 gonial, some branched proximally to form numerous stilt-like columns. Sutures may be indicated by faint lines, or by low, solid ridges linking process bases. Archeopyle precingular Type P (3<sup>o</sup>); 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 gonial and trifurcate, usually with secondary bifid terminations. Process shafts solid, some arising from unbranched bases, others branched proximally so process is supported by numerous stilt-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  $\mu\text{m}$ ; average process length, 16  $\mu\text{m}$ . Range: central body length, 38(46.0)51  $\mu\text{m}$ , standard deviation, 3.96; average process length, 9(14.0)17  $\mu\text{m}$ , 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 lower 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

←  
view of 6 ventral surface, 7 mid focus, 8 dorsal surface, central body length 34  $\mu\text{m}$ , CUS-M8(4), L35/1. 9–14, *Operculodinium bahamense* Head, n. sp.; 9–12, holotype, right latero-dorsal view of 9 dorsal surface, 10 slightly lower focus, 11 mid focus, 12 ventral surface, length (excluding processes) 81  $\mu\text{m}$ , CUS-K11(3), G18/2; 13, 14, ventral view of 13 ventral surface, 14 mid focus, length (excluding processes) 86  $\mu\text{m}$ , CUS-K10(2), W20/2 (see also Fig. 10.1).

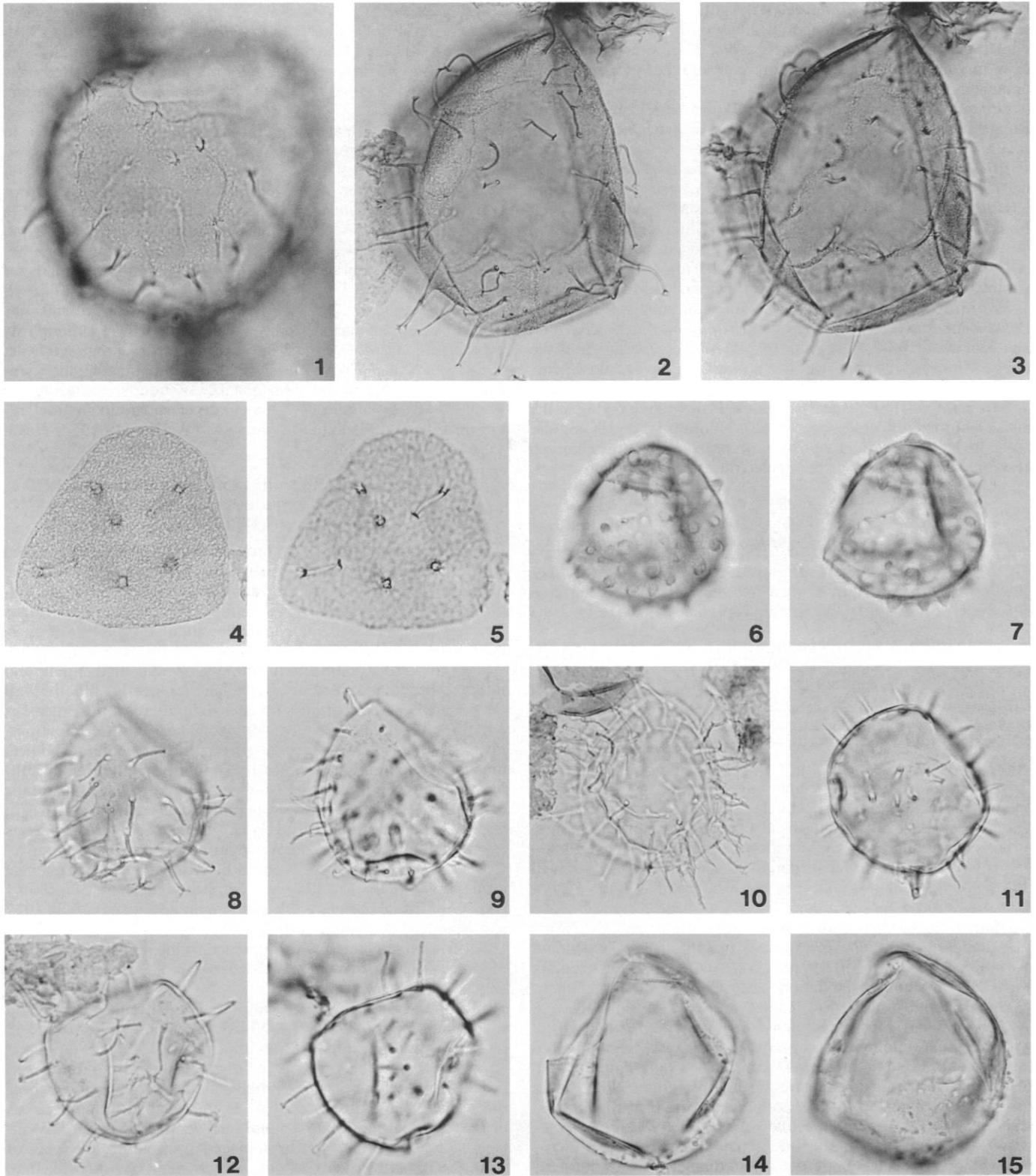


FIGURE 10—Photomicrographs are all bright field images. Various magnifications. Max. dia. = maximum diameter. 1–5, *Operculodinium bahamense* Head, n. sp.; 1, ventral view of dorsal surface, length (excluding processes) 86  $\mu\text{m}$ , CUS-K10(2), W20/2 (see also Fig. 9.13, 9.14); 2, 3, left antapical view of 2 left antapical surface, 3 slightly lower focus, length (excluding processes) 91  $\mu\text{m}$ , CUS-M9(4), L41/1; 4, 5, internal view of detached operculum, length 49  $\mu\text{m}$ , CUS-K10(2), N38/1. 6, 7, *Operculodinium janduchenei*; ventral view of 6 dorsal surface, 7 slightly higher focus, length (excluding processes) 30  $\mu\text{m}$ , CLS-M2(3),  $\times 26/0$ . 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  $\mu\text{m}$ , CLS-M2(4), R23/1; 10, uncertain view of upper surface, central body max. dia. 38  $\mu\text{m}$ , CLS-M1(5), U29/3; 14–15, *Operculodinium? longispinigerum*; 14, left lateral view, central body length 34  $\mu\text{m}$ , CLS-M2(4), R23/1; 15, left lateral view, central body length 34  $\mu\text{m}$ , CLS-M2(4), R23/1.

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 GONIODOMACEAE 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  
*Tuberculodinium vancampoae* (ROSSIGNOL, 1962) WALL, 1967, p. 114–115.

**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 PYRODINIOIDEAE Fensome et al., 1993

Genus CAPISOCYSTA Warny and Wrenn 1997, emend. Head, 1998b

CAPISOCYSTA LATA Head, 1998b

Figure 12.18

*Capisocysta lata* HEAD, 1998b, p. 802–807, figs. 1.1, 1.3, 1.5, 2–4.

**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 England (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  $\mu\text{m}$ , standard deviation, 3.3; average process length, 11(15.5)21

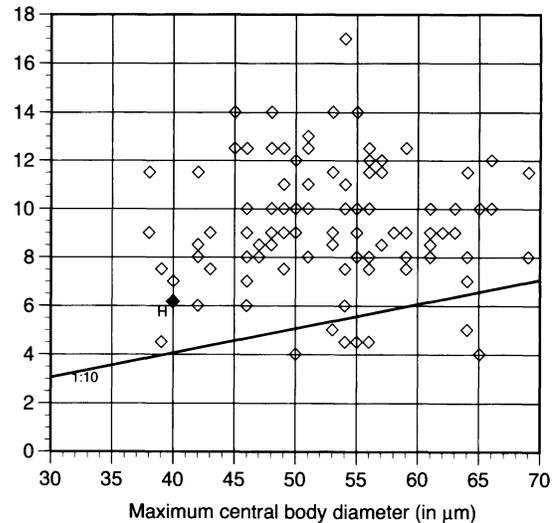


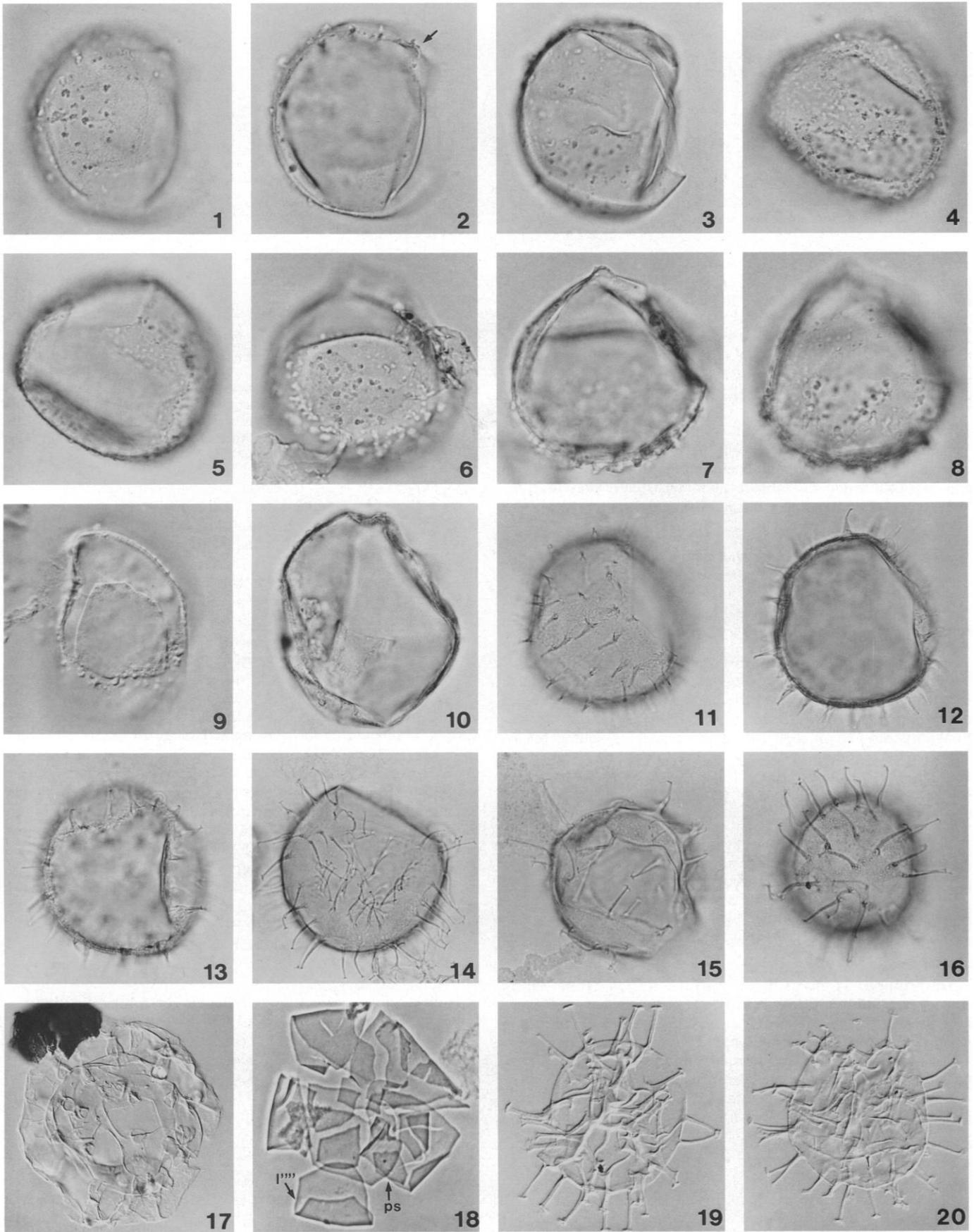
FIGURE 11—*Operculodinium* spp. including *O. israelianum* showing central body diameter vs. process length for specimens from the lower Pliocene interval. A line indicates the ratio 10:1 for central body diameter vs. process length. ♦ = the holotype (H) of *O. israelianum*, as measured from ROSSIGNOL (1962, pl. 2, fig. 3).

$\mu\text{m}$ , 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 Andrie, 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*

11, ventral view of dorsal surface, central body max. dia. 33  $\mu\text{m}$ , CLS-M2(4), O28/0; 12, 13, antapical? view of 12 upper surface, 13 lower surface, central body max. dia. 27  $\mu\text{m}$ , CLS-K4(4), J12/3. 14, 15, *Operculodinium?* *megagranum* Head, n. sp.; right lateral view of 14 mid focus, 15 left lateral surface, length (excluding ornament) 51  $\mu\text{m}$ , CUS-M8(4), W16/0.



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. commun.). 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

Genus LEJEUNECYSTA Artzner and Dörhöfer, 1978 emend.  
Lentin and Williams, 1976

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

LEJEUNECYSTA MARIEAE (Harland in Harland et al., 1991)  
Lentin and Williams, 1993  
Figure 14.1

*Protoperidinium* (*Protoperidinium* sect. *Lejeunecysta*) *mariea* (sic)  
HARLAND in Harland, Bonny, Hughes, and Morigi, 1991, p. 653, fig. 4j–4l.

*Lejeunecysta mariae* (sic) (Harland in Harland et al., 1991) LENTIN AND WILLIAMS, 1993, p. 383.

*Lejeunecysta mariea* (sic) Harland in Harland et al., 1991; HEAD, 1993, p. 31, fig. 19.16–19.21, 21.1, 26.14, 26.15.

*Lejeunecysta marieae* (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  $\mu\text{m}$ -long, solid pointed tips, convex margins on epicyst, and faintly granular wall surface. The Clino specimen (length, 49  $\mu\text{m}$ ) is somewhat larger than usually reported: e.g., a range in length of 34–50  $\mu\text{m}$  for the type locality of eastern England (Harland in Harland et al., 1991) and 27–47  $\mu\text{m}$  for the upper upper Pliocene of southwestern England (Head, 1993).

LEJEUNECYSTA sp. cf. *L. MARIEAE* (Harland in Harland et al., 1991) Lentin and Williams, 1993  
Figure 14.2

*Discussion.*—Specimens are comparable with *L. marieae* but have a smooth wall surface. This contrasts with the faint but optically discernible surface texture usually seen on specimens of *L. marieae* (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, pl. 11, figs. 1–3, 7–9; HEAD, 1993, p. 36, 37, 39, figs. 20.16–20.22, 21.8, 21.9, 21.12 (see for full synonymy).

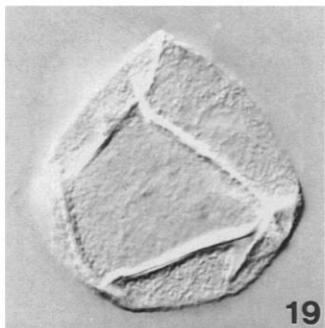
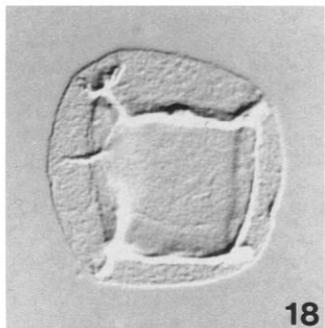
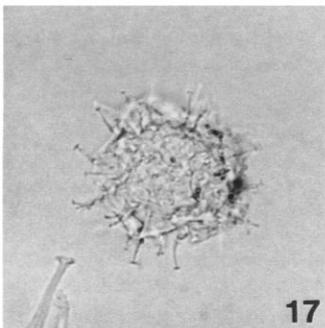
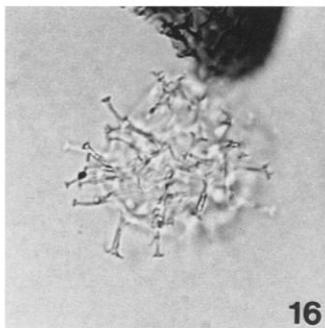
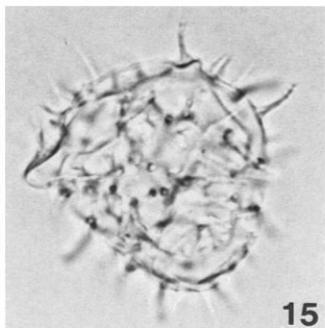
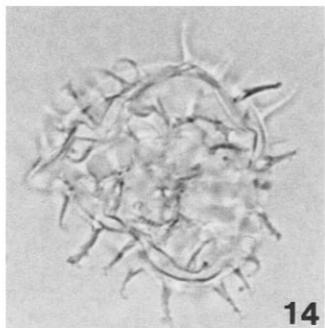
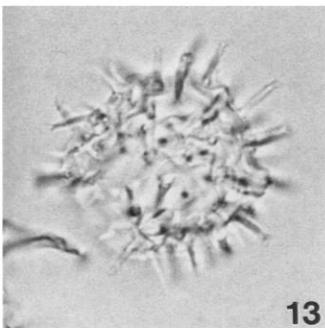
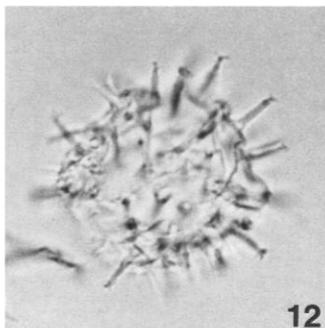
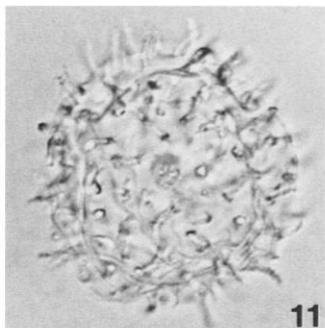
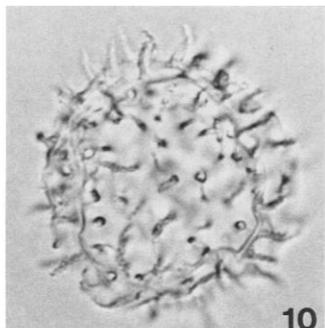
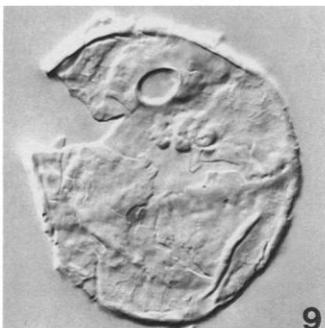
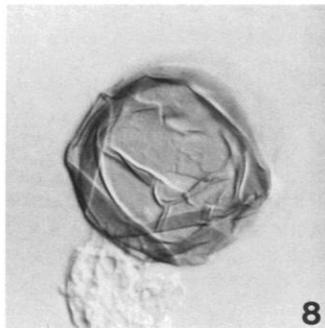
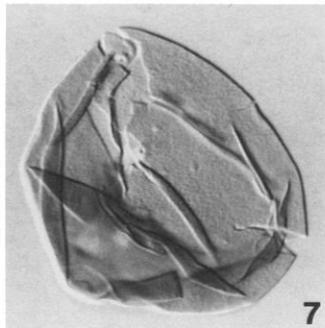
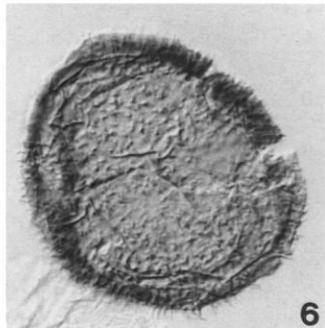
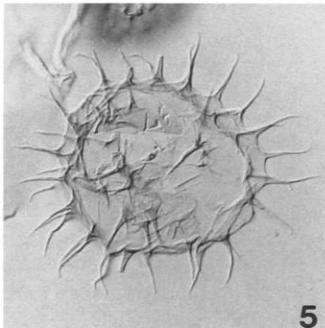
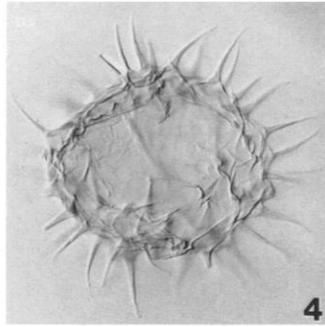
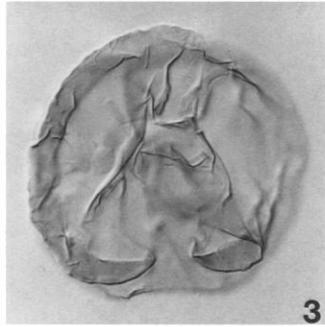
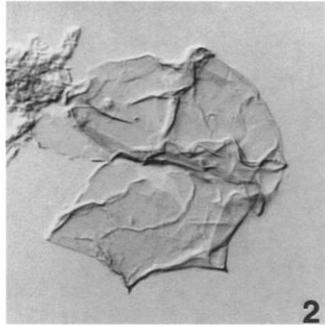
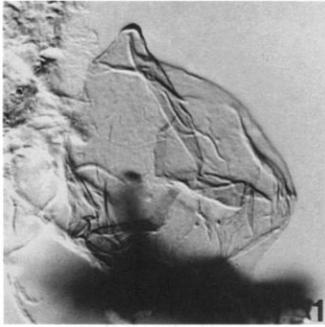
*Dimensions.*—Width of central body, 32(46.1)61  $\mu\text{m}$ ; standard deviation, 7.22; average process length, 8(10.9)15  $\mu\text{m}$ , standard deviation, 1.75. Thirty-eight specimens were measured (see also Fig. 13).

*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 Andrieu, 1992). It has a ubiquitous distribution in the Persian Gulf region (Bradford and Wall, 1984).

*Discussion.*—Specimens compare with cysts produced by the

FIGURE 12—Photomicrographs are bright field (1–8, 10–16), interference contrast (9, 17, 19, 20), or phase contrast (18) images. Various magnifications. Max. dia. = maximum diameter. 1–9, *Operculodinium? megagranum* Head, n. sp.; 1–3, holotype, left lateral view of 1 left lateral surface, 2 slightly lower focus showing apical protuberance (arrowed), 3 mid focus, length (excluding ornament) 49  $\mu\text{m}$ , CUS-M8(4), S31/3; 4, 5, ventral view of 4 ventral surface, 5 dorsal surface, width (excluding ornament) 50  $\mu\text{m}$ , CUS-M8(4), M38/4; 6–8, left lateral view of 6 left lateral surface, 7 mid focus showing apical protuberance, 8 right lateral surface, length (excluding ornament) 51  $\mu\text{m}$ , CUS-M8(3), P36/0; 9, right lateral view of upper surface showing operculum within the cyst, length (excluding ornament) 56  $\mu\text{m}$ , CUS-M8(2), P40/0. 10, *Operculodinium psilatium*; dorsal view of dorsal surface, length (excluding processes) 64  $\mu\text{m}$ , CLS-K6(3), W31/4. 11–13, *Operculodinium israelianum*; 11, 12, left lateral? view of 11 left lateral? surface, 12 mid focus, central body max. dia. 61  $\mu\text{m}$ , CLS-K6(3), L18/0; 13, ventral view of ventral surface, central body max. dia. 61  $\mu\text{m}$ , CLS-K6(3), J45/3. 14, *Operculodinium centroparpum*; antapical view of antapical surface, central body max. dia. 56  $\mu\text{m}$ , CUS-K11(3), R23/2. 15, 16, *Operculodinium* sp.; 15, lateral view of lateral surface, central body max. dia. 48  $\mu\text{m}$ , CLS-M2(3), H48/0; 16, ventral view of ventral surface, central body max. dia. 45  $\mu\text{m}$ , CLS-K6(3), L35/1. 17, *Tuberculodinium vancampoae*; antapertural view of antapertural surface, max. dia. 105  $\mu\text{m}$ , CLS-K4(4), E28/3. 18, *Capisocysta lata*; dorsoventral view at mid focus showing posterior sulcal plate (ps) and single antapical plate (1<sup>st</sup>), max. dia. of cyst 59  $\mu\text{m}$ , CUS-K11(2), W46/1. 19, 20, *Polysphaeridium zoharyi*; 19, antapical? view of upper surface, central body max. dia. 50  $\mu\text{m}$ , CLS-K4(4), W22/0; 20, antapical? view of upper surface, central body max. dia. 58  $\mu\text{m}$ , CLS-K4(2), O25/2.





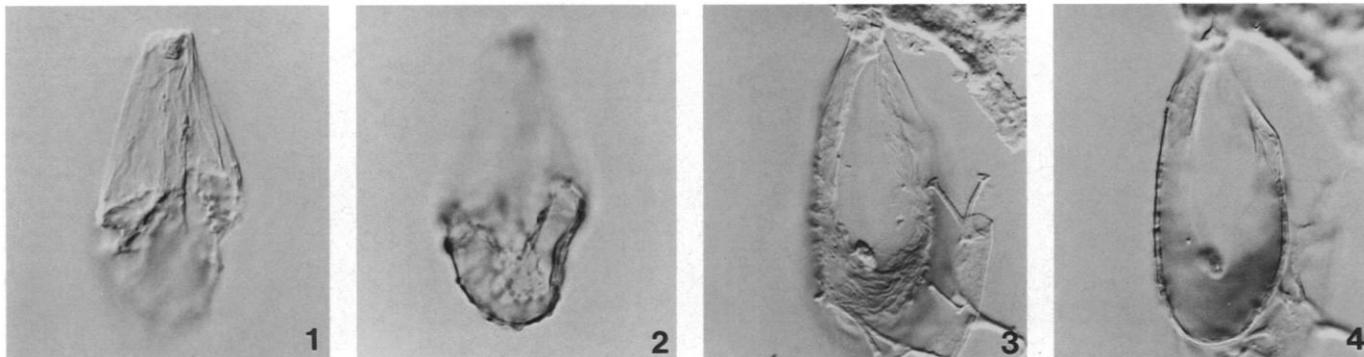


FIGURE 15—Photomicrographs are interference contrast (1, 3, 4) or bright field (2) images. Various magnifications. Max. dia. = maximum diameter. 1, 2, Incertae sedis A; showing 1 upper surface and 2 mid focus, length 57  $\mu\text{m}$ , CLS-K5(4), V17/0. 3, 4, Incertae sedis B; showing 3 upper surface and 4 mid focus, length 66  $\mu\text{m}$ , CLS-K4(4), T29/0.

numerous, 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  $\mu\text{m}$ ; process length, 4(5.5)7  $\mu\text{m}$ . 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.

Leiospheres  
Figure 14.18, 14.19

**Discussion.**—These are small to moderate in size, have a thin wall with a smooth or finely granulate surface, and tend not to take up stain. There is no discernible pylome. Preservation is variable, and thinner walled specimens could not always be distinguished from *Kallosphaeridium* sp. under the relatively low magnification used during counting.

Acritarch sp. 1  
Figure 14.20

**Discussion.**—Specimens are spherical, about 17 to 32  $\mu\text{m}$  in diameter, with a bilayered wall, the outer layer being raised into pronounced wrinkles and folds. A pylome was usually not seen. Specimens are fairly common in some samples (e.g., CUS-K10) but were not counted owing to their variable preservation.

Incertae sedis A  
Figure 15.1, 15.2

**Discussion.**—Two elongate specimens seen, both having a length of 57  $\mu\text{m}$ , with an ornamented, round-ended lower half, and an unornamented, thin-walled tapering upper half. Ornament consists of low rounded verrucae up to 2.0  $\mu\text{m}$  high that coalesce to form lineations and intersecting ridges. The upper half is smooth and there appears to be an indentation, or perhaps even a separation into two parts, running along the length.

Incertae sedis B  
Figure 15.3, 15.4

**Discussion.**—An elongate crescent-shaped specimen with an ornamented, round-ended lower half, and upper half drawn into two tapering projections that become progressively thinner-walled and less ornamented. Ornamentation on the lower half consists of low (less than 0.5  $\mu\text{m}$  high), subparallel anastomosing ridges. A single specimen was seen, having a length of 66  $\mu\text{m}$ .

ACKNOWLEDGMENTS

We thank R. N. Ginsburg and G. P. Eberli (University of Miami) for the opportunity to study material from the Clino core. M. J. H. is grateful to G. Norris (University of Toronto) for support from his Natural Sciences and Engineering Research Council of Canada operating grant. H. W. thanks C. Dullo and J. J. G. Reijmer (GEOMAR, Kiel, Germany) for support and helpful discussions. The research was supported by a grant from the German Science Foundation (RE 1051/3) to J. J. G. Reijmer. The Clino core was collected with funding from the United States National Science Foundation under Grants OCE 891-7295 and OCE 910-4294, from the Industrial Associates of the Comparative Sedimentology Laboratory of the Rosenstiel School of Marine and Atmospheric Sciences, and from the Swiss National Science Foundation. Our appreciation goes to L. E. Edwards (U.S. Geological Survey, Reston, Virginia), J. J. G. Reijmer, and G. L. Williams (Geological Survey of Canada—Atlantic, Halifax, Nova Scotia) for their very helpful reviews of the manuscript.

REFERENCES

- ARTZNER, D. G., AND G. DÖRHÖFER. 1978. Taxonomic note: *Lejeuncysta* nom. nov. pro *Lejeunia* Gerlach 1961 emend. Lentin and Williams 1976—dinoflagellate cyst genus. Canadian Journal of Botany, 56:1381–1382.
- AUBRY, M.-P. 1993. Neogene allostratigraphy and depositional history of the De Soto Canyon area, northern Gulf of Mexico. Micropaleontology, 39:327–366.
- BEACH, D. K. 1982. Depositional and diagenetic history of Pliocene–Pleistocene carbonates of northwestern Great Bahama Bank; evolution of a carbonate platform. Unpublished M.Sc. thesis, University of Miami, 447 p.
- , AND R. N. GINSBURG. 1980. Facies succession of Pliocene–Pleistocene carbonates, Northwestern Great Bahama Bank. AAPG Bulletin, 64:1634–1642.
- BENEDEK, P. N. 1972. Phytoplanktonen aus dem Mittel- und Oberoligozän von Tönisberg (Niederrheingebiet). Palaeontographica, Abteilung B, 137:1–71.
- BERGGREN, W. A., D. V. KENT, C. C. SWISHER, III, AND M.-P. AUBRY. 1995. A revised Cenozoic geochronology and chronostratigraphy, p. 129–212. In W. A. Berggren, D. V. Kent, and J. Hardenbol (eds.), Geochronology, Time Scales and Global Stratigraphic Correlation. Special Publication, 54. SEPM (Society for Sedimentary Geology), Tulsa, Oklahoma.
- BRADFORD, M. R. 1975. New dinoflagellate cyst genera from the recent sediments of the Persian Gulf. Canadian Journal of Botany, 53:3064–3074.
- , AND D. A. WALL. 1984. The distribution of Recent organic-walled

- dinoflagellate cysts in the Persian Gulf, Gulf of Oman, and North-western Arabian Sea. *Palaeontographica*, Abteilung B, 192:16–84.
- BREWSTER-WINGARD, G. L., S. E. ISHMAN, L. E. EDWARDS, AND D. A. WILLARD. 1996. Preliminary report on the distribution of modern fauna and flora at selected sites in north-central and north-eastern Florida Bay. U.S. Geological Survey Open-File Report 96-732, 34 p.
- BUJAK, J. P. 1980. Dinoflagellate cysts and acritarchs from the Eocene Barton Beds of southern England, p. 36–91. *In* J. P. Bujak, C. Downie, G. L. Eaton, and G. L. Williams, *Dinoflagellate cysts and acritarchs from the Eocene of southern England*. The Palaeontological Association, Special Papers in Palaeontology, 24.
- , AND K. MATSUOKA. 1986. Late Cenozoic dinoflagellate cyst zonation in the Western and Northern Pacific, p. 7–25. *In* J. H. Wrenn, S. L. Duffield, and J. A. Stein (eds.), *Papers from the First Symposium on Neogene Dinoflagellate Cyst Biostratigraphy*. American Association of Stratigraphic Palynologists Contributions Series, 17.
- , C. DOWNIE, G. L. EATON, AND G. L. WILLIAMS. 1980. Taxonomy of some Eocene dinoflagellate cyst species from southern England, p. 26–36. *In* J. P. Bujak, C. Downie, G. L. Eaton, and G. L. Williams, *Dinoflagellate Cysts and Acritarchs from the Eocene of Southern England*. The Palaeontological Association, Special Papers in Palaeontology, Number 24.
- BURCHETTE, T. P., AND V. P. WRIGHT. 1992. Carbonate ramp depositional systems. *Sedimentary Geology*, 79:3–57.
- BÜTSCHLI, O. 1885. Erster Band. Protozoa, p. 865–1088. *In* Dr. H. G. Bronn's Klassen und Ordnungen des Thier-Reiches, wissenschaftlich dargestellt in Wort und Bild. C. F. Winter'sche Verlagshandlung, Leipzig and Heidelberg.
- COSTA, L. I., AND C. DOWNIE. 1979. Cenozoic dinocyst stratigraphy of Sites 403 to 406 (Rockall Plateau), IPOD, Leg 48, p. 513–529. *In* L. Montadert, D. G. Roberts, et al., *Initial Reports of the Deep Sea Drilling Project*, 48. U.S. Government Printing Office, Washington, D.C.
- DALE, B. 1983. Dinoflagellate resting cysts: "Benthic Plankton," p. 69–136. *In* G. A. Fryxell, (ed.), *Survival Strategies of the Algae*. Cambridge University Press, Cambridge.
- , 1996. Dinoflagellate cyst ecology: modelling and geological applications, p. 1249–1275. *In* J. Jansonius and D. C. McGregor (eds.), *Palynology: Principles and Applications*. Volume 3. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas.
- DAVEY, R. J., AND G. L. WILLIAMS. 1966. The genus *Hystrichosphaeridium* and its allies, p. 53–106. *In* R. J. Davey, C. Downie, W. A. S. Sarjeant, and G. L. Williams, *Studies on Mesozoic and Cainozoic dinoflagellate cysts*. Bulletin of the British Museum (Natural History) Geology, Supplement 3.
- DE CONINCK, J. 1969. Dinophyceae et Acritarcha de l'Yprésien du Soudage de Kallo. Institut royal des sciences naturelles de Belgique, Mémoire 161, p. 1–67.
- DE VERNAL, A., L. LONDEIX, P. J. MUDIE, R. HARLAND, M. T. MORZADÉ-KERFOURN, J.-L. TURON, AND J. H. WRENN. 1992. Quaternary organic-walled dinoflagellate cysts of the North Atlantic Ocean and adjacent seas: ecostratigraphy and biostratigraphy, p. 289–328. *In* M. J. Head and J. H. Wrenn (eds.), *Neogene and Quaternary Dinoflagellate Cysts and Acritarchs*. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas.
- DE VERTEUIL, L. 1996. Data report: Upper Cenozoic dinoflagellate cysts from the continental slope and rise off New Jersey, p. 439–454. *In* G. S. Mountain, K. G. Miller, P. Blum, et al. (eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*, 150. Ocean Drilling Program, College Station, Texas.
- , AND G. NORRIS. 1996. Miocene dinoflagellate stratigraphy and systematics of Maryland and Virginia. *Micropaleontology*, 42 (supplement):1–172.
- , K. CUNNINGHAM, G. NORRIS, AND D. MCNEILL. 1996. Palynological evidence for the age and depositional environment of Upper Neogene siliciclastics in southernmost Florida, p. 31. Ninth International Palynological Congress, Houston, Texas, Program and Abstracts.
- DEFLANDRE, G., AND I. C. COOKSON. 1955. Fossil microplankton from Australian Late Mesozoic and Tertiary sediments. *Australian Journal of Marine and Freshwater Research*, 6:242–313.
- DROXLER, A. W., AND W. SCHLAGER. 1985. Glacial versus interglacial sedimentation rates and turbidite frequency in the Bahamas. *Geology*, 13:799–802.
- DRUGG, W. S., AND A. R. LOEBLICH, JR. 1967. Some Eocene and Oligocene phytoplankton from the Gulf Coast, U.S.A. *Tulane Studies in Geology*, 5:181–194.
- EBERLI, G. P., AND R. N. GINSBERG. 1987. Segmentation and coalescence of Cenozoic carbonate platforms, northwestern Great Bahama Bank. *Geology*, 15:75–79.
- , AND —. 1989. Cenozoic progradation of northwestern Great Bahama Bank, a record of lateral platform growth and sea-level fluctuations, p. 339–351. *In* P. D. Crevello, J. L. Wilson, J. F. Sarg, and J. F. Read (eds.), *Controls on Carbonate Platform and Basin Development*. Special Publication, 44. SEPM (Society of Economic Paleontologists and Mineralogists), Tulsa, Oklahoma.
- EBERLI, G. P., P. K. SWART, D. F. MCNEILL, J. A. M. KENTER, F. S. ANSELMETTI, L. A. MELIM, AND R. N. GINSBURG. 1997. A synopsis of the Bahamas Drilling Project: results from two deep core borings drilled on the Great Bahama Bank, p. 23–41. *In* G. P. Eberli, P. K. Swart, M. J. Malone, et al., *Proceedings of the Ocean Drilling Program, Initial Reports*, 166. Ocean Drilling Program, College Station, Texas.
- EDWARDS, L. E., AND V. A. S. ANDRLE. 1992. Distribution of selected dinoflagellate cysts in modern marine sediments, p. 259–288. *In* M. J. Head and J. H. Wrenn (eds.), *Neogene and Quaternary Dinoflagellate Cysts and Acritarchs*. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas.
- , AND S. D. WEEDMAN. 1996. Dinocysts in the shallow subsurface, southern Florida: Hydrology, biostratigraphy, and ecosystems studies. Ninth International Palynological Congress, Houston, Texas, Program and Abstracts, p. 37–38.
- , —, K. R. SIMMONS, T. M. SCOTT, G. L. BREWSTER-WINGARD, S. E. ISHMAN, AND N. M. CARLIN. 1998. Lithostratigraphy, petrography, biostratigraphy, and strontium-isotope stratigraphy of the surficial aquifer system of western Collier County, Florida. U.S. Geological Survey Open-File Report 98-205, 79 p.
- EMSLIE, S. D., W. D. ALLMON, F. J. RICH, J. H. WRENN, AND S. D. DE FRANCE. 1996. Integrated taphonomy of an avian death assemblage in marine sediments from the late Pliocene of Florida. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 124:107–136.
- ENGEL, E. R. 1992. Palynologische Evidenz klimarelevanter Ereignisse in miozänen Sedimenten des Nordatlantiks. *Geologisches Jahrbuch, Series A*, 125:3–139.
- EVITT, W. R. 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs, I. *Proceedings of the National Academy of Sciences*, Washington, 49:158–164.
- FENSOME, R. A., F. J. R. TAYLOR, G. NORRIS, W. A. S. SARJEANT, D. I. WHARTON, AND G. L. WILLIAMS. 1993. A classification of living and fossil dinoflagellates. *Micropaleontology Special Publication Number 7*, 351 p.
- HABIB, D. 1971. Dinoflagellate stratigraphy across the Miocene–Pliocene boundary, Tabiano stratotype section. *In* A. Farinacci (ed.), *Proceedings of the Second Planktonic Conference, Rome 1970*, (Edizioni Tecnoscienza, Roma), 1:591–598.
- , AND S. D. KNAPP. 1982. Stratigraphic utility of Cretaceous small acritarchs. *Micropaleontology*, 28:335–371.
- HAECKEL, E. 1894. Entwurf eines natürlichen Systems der Organismen auf Grund ihrer Stammesgeschichte, Erster Teil: Systematische Phylogenie der Protisten und Pflanzen. Georg Reimer, Berlin, 400 p.
- HALL, C. A., JR. 1964. Shallow-water marine climates and molluscan provinces. *Ecology*, 45:226–234.
- HARLAND, R., AND J. HILL. 1979. A reappraisal of the Cainozoic dinoflagellate cyst "*Hystrichosphaeridium*" *choanophorum* Deflandre et Cookson 1955. *Review of Palaeobotany and Palynology*, 28:37–45.
- , A. P. BONNY, M. J. HUGHES, AND A. N. MORIGI. 1991. The lower Pleistocene stratigraphy of the Ormesby Borehole, Norfolk, England. *Geological Magazine*, 128:647–660.
- HEAD, M. J. 1993. Dinoflagellate cysts, sporomorphs, and other palynomorphs from the upper Pliocene St. Erth Beds of Cornwall, southwestern England. *Paleontological Society Memoir 31* (Journal of Paleontology, 67[3]Supplement), 62 p.
- , 1994. Morphology and paleoenvironmental significance of the Cenozoic dinoflagellate genera *Habibacysta* and *Tectatodinium*. *Micropaleontology*, 40:289–321.
- , 1996a. Paleocological and taxonomic revision of late Cenozoic dinoflagellates from the Royal Society borehole at Ludham, eastern England. *Journal of Paleontology*, 70:543–570.

- . 1996b. Modern dinoflagellate cysts and their biological affinities, p. 1197–1248. In J. Jansoni, and D. C. McGregor (eds.), *Palynology: principles and applications*, vol. 3. American Association of Stratigraphic Palynologists Foundation, College Station, Texas.
- . 1997. Thermophilic dinoflagellate assemblages from the mid Pliocene of eastern England. *Journal of Paleontology* 71:165–193.
- . 1998a. Marine environmental change in the Pliocene and early Pleistocene of eastern England: the dinoflagellate evidence reviewed. In T. Van Kolfschoten, and P. Gibbard (eds.), *The Dawn of the Quaternary*. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, 60:119–225.
- . 1998b. New goniodomeacean dinoflagellates with a compound hypotractal archeopyle from the late Cenozoic: *Capisocysta* Warny and Wrenn, emend. *Journal of Paleontology*, 72:797–809.
- . 1998c. Pollen and dinoflagellates from the Red Crag at Walton-on-the-Naze, Essex: evidence for a mild climatic phase during the early Late Pliocene of eastern England. *Geological Magazine*, 135:803–817.
- , AND J. H. WRENN (eds.). 1992. A forum on Neogene and Quaternary dinoflagellate cysts: The edited transcript of a round table discussion held at the Second Workshop on Neogene Dinoflagellates, p. 1–31. In M. J. Head and J. H. Wrenn (eds.), *Neogene and Quaternary Dinoflagellate Cysts and Acritarchs*. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas.
- , G. NORRIS, AND P. J. MUDIE. 1989a. Palynology and dinocyst stratigraphy of the upper Miocene and lowermost Pliocene, ODP Leg 105, Site 646, Labrador Sea, p. 423–451. In S. P. Srivastava, M. A. Arthur, B. Clement, et al., *Proceedings of the Ocean Drilling Program, Scientific Results, 105*. Ocean Drilling Program, College Station, Texas.
- , —, AND —. 1989b. New species of dinocysts and a new species of acritarch from the upper Miocene and lowermost Pliocene, ODP Leg 105, Site 646, Labrador Sea, p. 453–466. In S. P. Srivastava, M. A. Arthur, B. Clement, et al., *Proceedings of the Ocean Drilling Program, Scientific Results, 105*. Ocean Drilling Program, College Station, Texas.
- , —, AND —. 1989c. Palynology and dinocyst stratigraphy of the Miocene in ODP Leg 105, Hole 645E, Baffin Bay, p. 467–514. In S. P. Srivastava, M. A. Arthur, B. Clement, et al., *Proceedings of the Ocean Drilling Program, Scientific Results, 105*. Ocean Drilling Program, College Station, Texas.
- ISLAM, M. A. 1984. A study of Early Eocene palaeoenvironments in the Isle of Sheppey as determined from microplankton assemblage composition. *Tertiary Research* 6:11–21.
- JAN DU CHÈNE, R. 1977. Étude palynologique du Miocène supérieur Andalou (Espagne). *Revista Española de Micropaleontología*, 9:97–114.
- , L. E. STOVER, AND J. DE CONINCK. 1985. New observations on the dinoflagellate cyst genus *Kalosphæroidium* De Coninck 1969. *Cahiers de Micropaléontologie*, Centre national de la Recherche Scientifique, 4:1–18.
- KLUMPP, B. 1953. Beitrag zur Kenntnis der Mikrofossilien des mittleren und oberen Eozän. *Palaeontographica*, Abteilung A, 103:377–406.
- LENTIN, J. K., AND G. L. WILLIAMS. 1976. A monograph of fossil peridinioid dinoflagellate cysts. *Bedford Institute of Oceanography Report Series, BI-R-75-16*, 237 p.
- , AND G. L. WILLIAMS. 1981. Fossil dinoflagellates: index to genera and species, 1981 edition. *Bedford Institute of Oceanography Report Series, BI-R-81-12*, 345 p.
- , AND —. 1993. Fossil dinoflagellates: index to genera and species, 1993 edition. *American Association of Stratigraphic Palynologists Contributions Series*, 28, 856 p.
- LIDZ, B. H., AND T. J. BRALOWER. 1994. Microfossil biostratigraphy of prograding Neogene platform-margin carbonates, Bahamas: Age constraints and alternatives. *Marine Micropaleontology*, 23:265–344.
- , AND D. F. MCNEILL. 1995. Deep-sea biostratigraphy of prograding platform margins (Neogene, Bahamas): key evidence linked to depositional rhythm. *Marine Micropaleontology*, 25:87–125.
- LINDEMANN, E. 1928. Abteilung Peridineae (Dinoflagellatae), p. 3–104. In A. Engler and K. Prantl (eds.), *Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere den Nutzpflanzen*. Zweite stark vermehrte und verbesserte Auflage herausgegeben von A. Engler. 2 Band. Wilhelm Engelmann, Leipzig.
- MACLEAN, J. L. 1989. An overview of *Pyrodinium* red tides in the Western Pacific, p. 1–7. In G. M. Hallegraeff and J. L. Maclean (eds.), *Biology, epidemiology and management of Pyrodinium red tides*. ICLARM Conference Proceedings 21. International Center for Living Aquatic Resources Management, Manila, Philippines.
- MAHER, L. J. 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Review of Palaeobotany and Palynology*, 32:153–191.
- MANTELL, G. A. 1850. A pictorial atlas of fossil remains, consisting of coloured illustrations selected from Parkinson's "Organic remains of a former world," and Artis's "Antediluvian phytology." Henry G. Bohn, London, 207 p.
- MANUM, S. B., M. C. BOULTER, H. GUNNARSDOTTIR, K. RANGNES, AND A. SCHOLZE. 1989. Eocene to Miocene palynology of the Norwegian Sea (ODP Leg 104), p. 611–662. In O. Eldholm, J. Thiede, E. Taylor, et al., *Proceedings of the Ocean Drilling Program, Scientific Results, 104*. Ocean Drilling Program, College Station, Texas.
- MATSUOKA, K. 1983. Late Cenozoic dinoflagellates and acritarchs in the Niigata District, central Japan. *Palaeontographica*, Abteilung B, 187: 89–154.
- . 1985. Organic-walled dinoflagellate cysts from surface sediments of Nagasaki Bay and Senzaki Bay, West Japan. *Bulletin of the Faculty of Liberal Arts, Nagasaki University, Natural Science*, 25(2):21–115.
- , A. MCMINN, AND J. H. WRENN. 1997. Restudy of the holotype of *Operculodinium centrocarpum* (Deflandre & Cookson) Wall (Dinophyceae) from the Miocene of Australia, and the taxonomy of related species. *Palynology*, 21:19–33.
- MCCARTHY, F. M. G., AND P. J. MUDIE. 1996. Palynology and dinoflagellate biostratigraphy of Upper Cenozoic sediments from Sites 898 and 900, Iberia Abyssal Plain, p. 241–265. In R. B. Whitmarsh, D. S. Sawyer, A. Klaus, and D. G. Masson, (eds.), *Proceedings of the Ocean Drilling Program, Scientific Results, 149*. Ocean Drilling Program, College Station, Texas.
- MCMINN, A. 1992a. Neogene dinoflagellate distribution in the eastern Indian Ocean from Leg 123, Site 765, p. 429–441. In F. M. Gradstein, J. N. Ludden, A. C. Adamson, et al., *Proceedings of the Ocean Drilling Program, Scientific Results, 123*. Ocean Drilling Program, College Station, Texas.
- . 1992b. Pliocene through Holocene dinoflagellate cyst biostratigraphy of the Gippsland Basin, Australia, p. 147–161. In M. J. Head and J. H. Wrenn (eds.), *Neogene and Quaternary Dinoflagellate Cysts and Acritarchs*. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas.
- . 1992c. Recent and late Quaternary dinoflagellate cyst distribution on the continental shelf and slope of southeastern Australia. *Palynology*, 16:13–24.
- . 1993a. Neogene dinoflagellate cyst biostratigraphy from sites 815 and 823, Leg 133, northeastern Australian margin, p. 97–105. In J. A. McKenzie, P. J. Davies, A. Palmer-Julson, et al., *Proceedings of the Ocean Drilling Program, Scientific Results, 123*. Ocean Drilling Program, College Station, Texas.
- . 1993b. Quaternary dinoflagellate cyst distribution at Sites 820, Great Barrier Reef, p. 93–95. In J. A. McKenzie, P. J. Davies, A. Palmer-Julson, et al., *Proceedings of the Ocean Drilling Program, Scientific Results, 123*. Ocean Drilling Program, College Station, Texas.
- , AND P. WELLS. 1997. Use of dinoflagellate cysts to determine changing Quaternary sea-surface temperature in southern Australia. *Marine Micropaleontology*, 29:407–422.
- MCNEILL, D. F., G. P. EBERLI, B. H. LIDZ, P. K. SWART, AND J. A. M. KENTER. In press. Chronostratigraphy of prograding carbonate platform margins: a record of dynamic slope sedimentation, Western Great Bahama Bank. In R. N. Ginsburg (ed.), *Contributions in Sedimentology*. SEPM (Society for Sedimentary Geology), Tulsa, Oklahoma.
- PASCHER, A. 1914. Über Flagellaten und Algen. *Berichte der Deutschen Botanischen Gesellschaft*, 36:136–160.
- POULSEN, N. E., S. B. MANUM, G. L. WILLIAMS, AND M. ELLEGAARD. 1996. Tertiary dinoflagellate biostratigraphy of Sites 907, 908, and 909 in the Norwegian–Greenland Sea, p. 255–287. In J. Thiede, A. M. Myhre, J. V. Firth, et al. (eds.), *Proceedings of the Ocean Drilling Program, Scientific Results, 151*. Ocean Drilling Program, College Station, Texas.
- REID, P. C. 1974. Gonyaulacacean dinoflagellate cysts from the British Isles. *Nova Hedwigia*, 25:579–637.
- . 1977. Peridiniacean and Glenodiniacean dinoflagellate cysts from the British Isles. *Nova Hedwigia*, 29:429–463.
- REIJMER, J. J. G., W. SCHLAGER, H. BOSSCHER, C. J. BEETS, AND D. F.

- MCNEILL. 1992. Pliocene/Pleistocene platform facies transition recorded in calciturbidites (Exuma Sound, Bahamas). *Sedimentary Geology*, 78:171–179.
- ROSSIGNOL, M. 1962. Analyse pollinique de sédiments marins Quaternaires en Israël. II. Sédiments Pléistocènes. *Pollen et Spores*, 4:121–148.
- . 1964. Hystrichosphères du Quaternaire en Méditerranée orientale, dans les sédiments Pléistocènes et les boues marines actuelles. *Revue de Micropaléontologie*, 7:83–99.
- SARJEANT, W. A. S. 1970. The genus *Spiniferites* Mantell, 1850 (Dinophyceae). *Grana*, 10:74–78.
- SCHILLER, J. 1935. Dinoflagellatae (Peridineae) in monographischer Behandlung. 2. Teil, Lieferung 2, p. 161–320. In R. Kolkwitz (ed.), *Zehnter Band, Flagellatae*. In Dr. L. Rabenhorst's *Kryptogamen-Flora von Deutschland, Österreich und der Schweiz*. Akademische Verlagsgesellschaft, Leipzig.
- SCHLAGER, W., J. J. G. REIJMER, AND A. W. DROXLER. 1994. Highstand shedding of carbonate platforms. *Journal of Sedimentary Petrology*, B64:270–281.
- STOCKMARR, J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores*, 13:615–621.
- STOVER, L. E. 1977. Oligocene and Early Miocene dinoflagellates from Atlantic Corehole 5/5B, Blake Plateau. *American Association of Stratigraphic Palynologists, Contributions Series*, 5A:66–89.
- , AND W. R. EVITT. 1978. Analyses of pre-Pleistocene organic-walled dinoflagellates. *Stanford University Publications Geological Sciences*, 15:1–300.
- STRAUSS, C., AND J. J. LUND. 1992. A Middle Miocene dinoflagellate cyst microflora from Papendorf near Hamburg, Germany. *Geologisch-Paläontologisches Institut und Museum, University of Hamburg, Mitteilungen*, 73:159–189.
- TAYLOR, F. J. R. 1980. On dinoflagellate evolution. *BioSystems*, 13:65–108.
- TRAVERSE, A., AND R. N. GINSBURG. 1966. Palynology of the surface sediments of Great Bahama Bank, as related to water movement and sedimentation. *Marine Geology*, 4:417–459.
- VAIL, P. R., F. AUDEMARD, S. A. BOWMAN, P. N. EISNER, AND C. PEREZ-CRUZ. 1991. The stratigraphic signatures of tectonics, eustacy, and sedimentology—an overview, p. 617–659. In G. Einsele, W. Ricken, and A. Seilacher (eds.), *Cycles and Events in Stratigraphy*. Springer, Berlin-Heidelberg-New York.
- VERSTEEGH, G. J. M. 1994. Recognition of cyclic and non-cyclic environmental changes in the Mediterranean Pliocene: A palynological approach. *Marine Micropaleontology*, 23:147–183.
- . 1997. The onset of major Northern Hemisphere glaciations and their impact on dinoflagellate cysts and acritarchs from the Singa section, Calabria (southern Italy) and DSDP Holes 607/607A (North Atlantic). *Marine Micropaleontology*, 30:319–343.
- , AND D. ZEVENBOOM. 1995. New genera and species of dinoflagellate cysts from the Mediterranean Neogene. *Review of Palaeobotany and Palynology*, 85:213–229.
- , AND K. A. F. ZONNEVELD. 1994. Determination of (palaeo-)ecological preferences of dinoflagellates by applying detrended and canonical correspondence analysis to Late Pliocene dinoflagellate cyst assemblages of the south Italian Singa section. *Review of Palaeobotany and Palynology*, 84:181–199.
- WALL, D. 1967. Fossil microplankton in deep-sea cores from the Caribbean Sea. *Palaeontology*, 10:95–123.
- . 1971. Biological problems concerning fossilizable dinoflagellates. *Geoscience and Man*, 3:1–15.
- , AND B. DALE. 1967. The resting cysts of modern marine dinoflagellates and their paleontological significance. *Review of Paleobotany and Palynology*, 2:349–354.
- , AND —. 1968. Modern dinoflagellate cysts and evolution of the Peridinales. *Micropaleontology*, 14:265–304.
- , AND —. 1969. The 'hystrichosphaerid' resting spore of the dinoflagellate *Pyrodictinium bahamense* Plate 1906. *Journal of Phycology*, 5:140–149.
- , —, AND K. HARADA. 1973. Descriptions of new fossil dinoflagellates from the Late Quaternary of the Black Sea. *Micropaleontology*, 19:18–31.
- , —, G. P. LOHMAN, AND W. K. SMITH. 1977. The environmental and climatic distribution of dinoflagellate cysts in modern marine sediments from regions in the North and South Atlantic oceans and adjacent seas. *Marine Micropaleontology*, 2:121–200.
- WARNY, S. A., AND J. H. WRENN. 1997. New species of dinoflagellate cysts from the Bou Regreg Core: a Miocene–Pliocene boundary section on the Atlantic Coast of Morocco. *Review of Palaeobotany and Palynology*, 96:281–304.
- WEEDMAN, S. D., T. M. SCOTT, L. E. EDWARDS, G. L. BREWSTER-WINGARD, AND J. C. LIBARKIN. 1995. Preliminary analysis of integrated stratigraphic data from the Phred #1 corehole, Indian River County, Florida. U.S. Geological Survey Open-File Report 95-824, 63 p.
- WESTPHAL, H. 1998. Carbonate platform slopes—a record of changing conditions. *Lecture Notes in Earth Sciences, Volume 75*. Springer Verlag, Berlin, Heidelberg, New York, 179 p.
- , AND A. MUNNECKE. 1997. Mechanical compaction versus early cementation in fine-grained limestones: differentiation by the preservation of organic microfossils. *Sedimentary Geology*, 112:33–42.
- , J. J. G. REIJMER, AND M. J. HEAD. In press. Input and diagenesis on a carbonate slope (Bahamas): response to morphologic evolution and sea-level fluctuations. In P. M. Harris, A. H. Saller, T. Simo, and R. Handford (eds.), *Advances in Carbonate Sequence Stratigraphy—Application to Reservoirs, Outcrops and Models*. Special Publication. SEPM (Society for Sedimentary Geology), Tulsa, Oklahoma.
- WILLIAMS, G. L., AND C. DOWNIE. 1966. The genus *Hystrichokolpoma*. In R. J. Davey, C. Downie, W. A. S. Sarjeant, and G. L. Williams, *Studies on Mesozoic and Cainozoic dinoflagellate cysts*. *Bulletin of the British Museum (Natural History) Geology, Supplement* 3:176–181.
- , L. E. STOVER, AND E. J. KIDSON. 1993. Morphology and stratigraphic ranges of selected Mesozoic–Cenozoic dinoflagellate taxa in the Northern Hemisphere. *Geological Survey of Canada Paper* 92-10, 137 p.
- WILSON, G. J. 1973. Palynology of the middle Pleistocene Te Piki bed, Cape Runaway, New Zealand. *New Zealand Journal of Geology and Geophysics*, 16:345–354.
- WRENN, J. H. 1988. Differentiating species of the dinoflagellate cyst genus *Nematosphaeropsis* Deflandre and Cookson, 1955. *Palynology*, 12:129–150.
- , AND J. P. KOKINOS. 1986. Preliminary comments on Miocene through Pleistocene dinoflagellate cysts from De Soto Canyon, Gulf of Mexico, p. 169–225. In J. H. Wrenn, S. L. Duffield, and J. A. Stein (eds.), *Papers from the First Symposium on Neogene Dinoflagellate Cyst Biostratigraphy*. *American Association of Stratigraphic Palynologists Contributions Series*, 17.
- ZEVENBOOM, D. 1995. *Dinoflagellate Cysts from the Mediterranean Late Oligocene and Miocene*. CIP-Gegevens Koninklijke Bibliotheek, Den Haag, 221 p. (Published Ph.D. thesis, State University of Utrecht)
- ZONNEVELD, K. A. F. 1995. Palaeoclimatic and palaeo-ecological changes during the last deglaciation in the Eastern Mediterranean—implications for dinoflagellate ecology. *Review of Palaeobotany and Palynology*, 84:221–253.