DISTRIBUTION MAPS OF RECENT DINOFLAGELLATE CYSTS IN BOTTOM SEDIMENTS FROM THE NORTH ATLANTIC OCEAN AND ADJACENT SEAS

by REX HARLAND

ABSTRACT. Distribution maps have been drawn for forty-two extant species of dinoflagellate cysts recovered from bottom sediments in the North Atlantic Ocean and adjacent seas. Data have been compiled from published and unpublished work for a total of one hundred and forty-two sample stations. The maps clearly show the influence of the North Atlantic circulation pattern, and areas of convergence, on the patterns of dinoflagellate cyst distribution. Areas of concentrations of cyst species are noted and discussed, as are the differing distribution patterns of several cysts that have at some time been referable to a single thecate species. The differences of distribution between neritic and oceanic cyst assemblages is clearly demarcated. Finally a tentative broad ecological classification of cyst types is attempted. *Impagidinium aculeatum* (Wall) and *I. sphaericum* (Wall) are proposed as new combinations.

THE analysis of dinoflagellate cysts in Quaternary and Recent sediments from the offshore region of the British Isles has been underway at the Institute of Geological Sciences (IGS) for several years. The work has concentrated upon the areas of the North Sea and offshore western Scotland and England, where the IGS has drilled several boreholes and taken many vibrocores that have yielded good sequences of marine Quaternary sediments. The overall intention was to eludicate the Quaternary history, as recorded in these marine sediments, and to relate the various biostratigraphical events to the commonly understood climatic patterns. Indeed over the past few years several such sequences have been analysed and a number of climatic events recognized. These events are usually characterized, in the dinoflagellate cyst record, by a series of 'favourable' and 'unfavourable' units, in terms of productivity and diversity, within sediments that would, under normal circumstances, be expected to yield consistently good dinoflagellate cyst assemblages. This work has been related to foraminiferal analyses of the same strata and some of the results are published (Harland 1973, 1974, 1977, 1978; Binns *et al.* 1974; Hughes *et al.* 1977; Gregory *et al.* 1978; Harland *et al.* 1978; Gregory and Harland 1978). The Quaternary climatic history as recorded in marine continental shelf sediments is beginning to emerge and work in this area is still underway.

It has, however, been somewhat worrying that the ability to interpret the Quaternary record has been hampered by a lack of knowledge concerning the distributions of modern dinoflagellate cysts in bottom sediments in the North Atlantic area, i.e. the dinoflagellate cyst thanatocoenosis. Indeed there is also a lack of knowledge of the synecology of living dinoflagellate cysts and their relationships to natural phytoplankton populations. Research by such workers as Anderson and Wall (1978), Dale (1976, 1977, 1978), and Reid (1975, 1977, 1978) has assisted in the understanding of the ecology of living cysts, and that of Dodge (1977), Dodge and Hart-Jones (1974, 1977), Holligan (1979, 1981), and Holligan *et al.* (1980), has been of value in understanding the ecology of phytoplankton populations particularly in British waters, but nevertheless much more data need collecting and analysis.

In the course of the work at IGS it became clear that one of the areas where more information was urgently required was the nature of the dinoflagellate cysts thanatocoenosis in the North Atlantic Ocean, and more particularly in the northern part of the North Atlantic. Although a number of

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works on dinoflagellate cyst distributions had been published there are no maps available showing the percentage distributions of the various dinoflagellate cyst species. Such maps are commonly published for other organisms, including planktonic and benthonic foraminiferans, diatoms, and radiolarians, for the North Atlantic region and other oceans of the world. This appeared to be a fact that could be rectified and one which had direct application to the interpretation of the Quaternary dinoflagellate cyst record, since it is clear that in the fossil record a thanatocoenosis is all the information available. This study and compilation is hopefully a step in linking the fossil record to the modern thanatocoenosis thence to the biocoenosis and finally to a full understanding of the ecology of dinoflagellates and their cysts.

HISTORY OF STUDY

The study of the modern dinoflagellate cyst thanatocoenosis in the North Atlantic began with the pioneering thesis of Williams (1965), the results of which were published in 1971. He used principal component analysis on data from thirty-five sites in the North Atlantic and recognized a number of 'facies' which could be related to such surface conditions as water mass configurations and current distributions. Also recognized was the fact that certain species appeared to be concentrated in particular areas. Graham and Bronikowsky (1944) had also noted a link between the distribution of the thecate dinoflagellate species and water mass configurations.

Reid (1972*a*) followed this work in a thesis which described the distribution of dinoflagellate cyst species in Recent intertidal sediments around the British Isles. Cluster analysis was used on some sixty-eight samples and again close relationships were seen between the dinoflagellate cyst thanatocoenosis and the various water masses around the British Isles. This work was subsequently published in a series of papers (Reid 1972*b*, 1974, 1975, 1977).

In 1976 Dale published on some of the primary factors that influence the composition of cyst assemblages in bottom sediments. His study compared the integrated phytoplankton records in the Trondheimsfjord area of Norway with the assemblages preserved in the sediments. These observations are discussed more fully later in relation to the results of the present study, as they indicate a number of constraints that must be understood and taken into account in the interpretation of this kind of data and research.

A little later Morzadec-Kerfourn (1977) recognized, in a series of offshore sediment samples from Brittany, an onshore-offshore differentiation. An oceanic realm characterized by such cysts as *Impagidinium aculeatum* (Wall) and *Spiniferites bulloideus* (Deflandre and Cookson), a coastal realm with *S. bentori* (Rossignol) and an estuarine realm with *Lingulodinium machaerophorum* (Deflandre and Cookson) were noted.

In the same year Reid and Harland attempted a summary of current knowledge on the distribution of dinoflagellate cysts in the North Atlantic. They concluded that the cyst thanatocoenosis is dependent upon a number of interrelated factors that include: (1) latitude—encompassing factors of solar radiation, temperature, and climate, so in essence giving rise to a series of latitudinal biogeographical zones; (2) water depth—as exemplified by the onshore-offshore differentiation; (3) water mass—including interaction of water masses, e.g. convergence, upwelling, bathymetry, current distribution, all at many differing scales of occurrence; and (4) sedimentary factors—selective concentration etc.

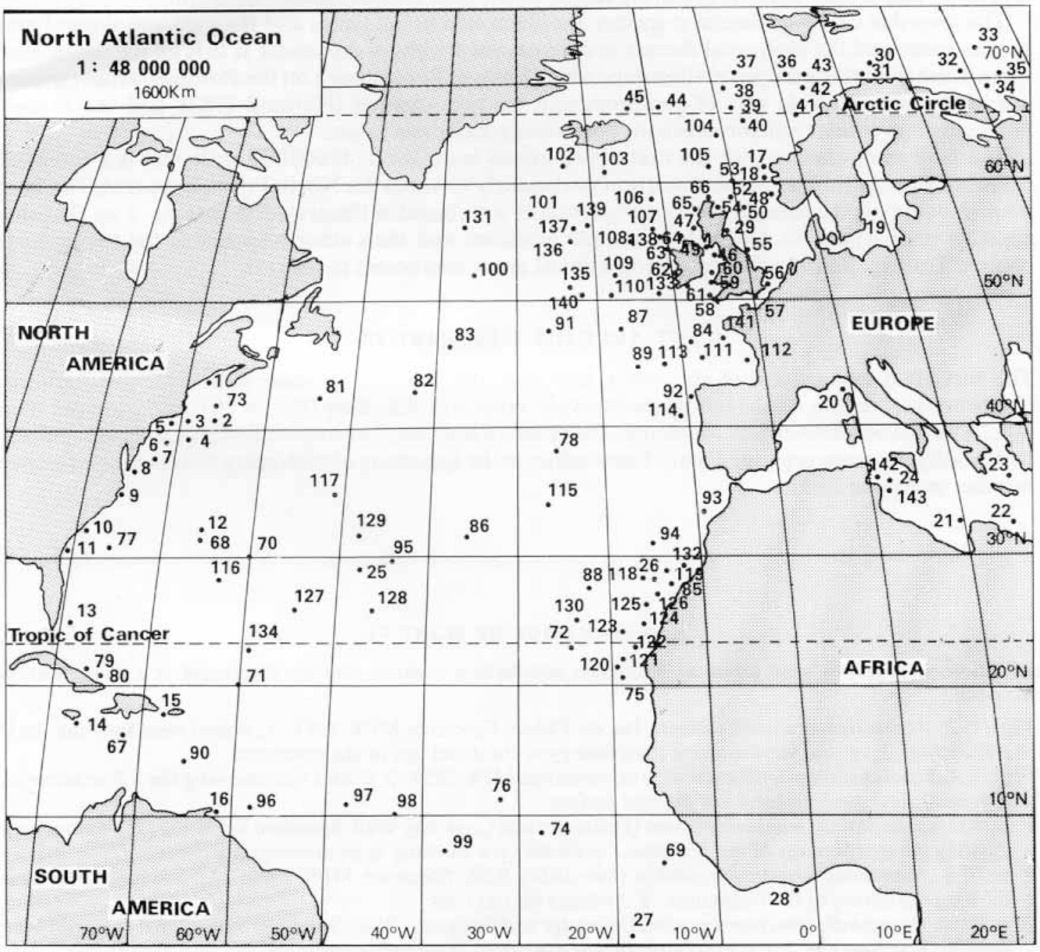
At much the same time Wall *et al.* (1977) published a major piece of work that analysed the cyst thanatocoenosis of one hundred and sixty-eight samples in the North and South Atlantic and Pacific Oceans. Using Q-mode factor analysis, cluster analysis, and a species diversity index they also recognized onshore to offshore and latitudinal variations in distributions involving both individual taxa, and associations of species. This largely confirmed the conclusions of Reid and Harland (1977) but Wall *et al.* (1977) also proposed an ecological classification for the extant cyst species and suggested that the genesis of such ecological species groups in nature can be interpreted by use of stability-predictability concepts where surface water masses are taken to be unique hydrographic niches with their own stability and predictability characteristics.

Most recently Turon (1980) has studied Recent dinoflagellate cysts in the north-east Atlantic and related their distributions to environmental factors such as temperature and the hydrographic structure of the water.

It is clear from this review that although the major factors appear to have been identified, the distribution of individual species is not documented nor has the thanatocoenosis been linked to the biocoenosis except perhaps, in part, by the work of Reid (1978) and Dale (in press).

MATERIALS AND METHODS

The present study has involved the compilation of data from the doctoral theses of D. B. Williams (1965) and P. C. Reid (1972*a*), with their permission and helpful assistance; from the published work of Wall *et al.* (1977), Morzadec-Kerfourn (1977, 1979), and Turon (1980), who have also been most helpful in supplying some of the original data; and the incorporation of some of my own records



TEXT-FIG. 1. North Atlantic Ocean at a 1 : 48 000 000 scale drawn on a modified cylindrical projection showing the approximate location of the one hundred and forty-two samples.

held at the Institute of Geological Sciences (IGS), Leeds. In addition the British Museum (Natural History) supplied many more samples to assist in filling some of the more obvious gaps. In total the assemblages from one hundred and forty-two samples have been utilized of which forty-nine are attributable directly to me. Appendix I lists the samples, their localities, authors responsible for the data, and the various registered catalogue numbers. Those registered in the IGS collections can be examined at the IGS, Leeds.

All the samples have undergone standard palynological preparation techniques although those processed at Leeds have not been given any oxidation, to avoid the loss of peridiniacean cysts (Dale 1976). In general therefore there is some bias toward the gonyaulacacean cysts, and no attempt has been made to isolate calcareous cysts. This is comparable to techniques employed in our studies on Quaternary sediments and hopefully makes the results compatible.

The data are expressed in terms of percentage, the common factor in all the data sets, and in most cases are based upon a count of over 100 specimens and in many cases over 250 specimens. The complete data set on which this study is based is held by the Palaeontology Unit, IGS, Leeds where it is open to inspection. Persons requiring copies of the data should contact the author.

The recorded dinoflagellate cyst species are illustrated in the plates and the palaeontological cyst species name and the biological thecate species names are given. Appendix II lists all the considered species and their thecate cyst relationships where known. Recent work on the *Protoperidinium* species has indicated a possible way of compromising the two schemes (Harland 1982), and this is used herein, but no similar scheme exists for gonyaulacacean cysts as yet.

The base map used to plot the cyst distributions is on the 1:48000000 scale and is a modified cylindrical projection, so some distortion particularly towards the North Pole is apparent. The base map showing all the sample stations sequentially numbered is illustrated in text-fig. 1 so that this together with Appendix I will show sample positions and the author responsible for the original counts. Text-fig. 2 shows the main geographical areas mentioned in the text.

CYST SPECIES DISTRIBUTIONS

The forty-two cyst species of this study have had maps drawn of their individual distributions. Contours were drawn on the following intervals: up to and including 10%; > 10 to 50%; greater than 50%. The distributions reflect, of course, the scope of the sampling and no doubt additional samples will modify the maps presented here. The number at the beginning of each entry refers to the reference number in Appendix II.

EXPLANATION OF PLATE 43

All photomicrographs were taken by Nomarski interference contrast and are illustrated at a magnification of × 500.

Figs. 1, 2. *Achomosphaera andalousiense* Jan du Chêne, Specimen MPK 1213. 1, dorsal view showing the P archeopyle. 2, ventral view showing morphology of the distal tips of the processes.

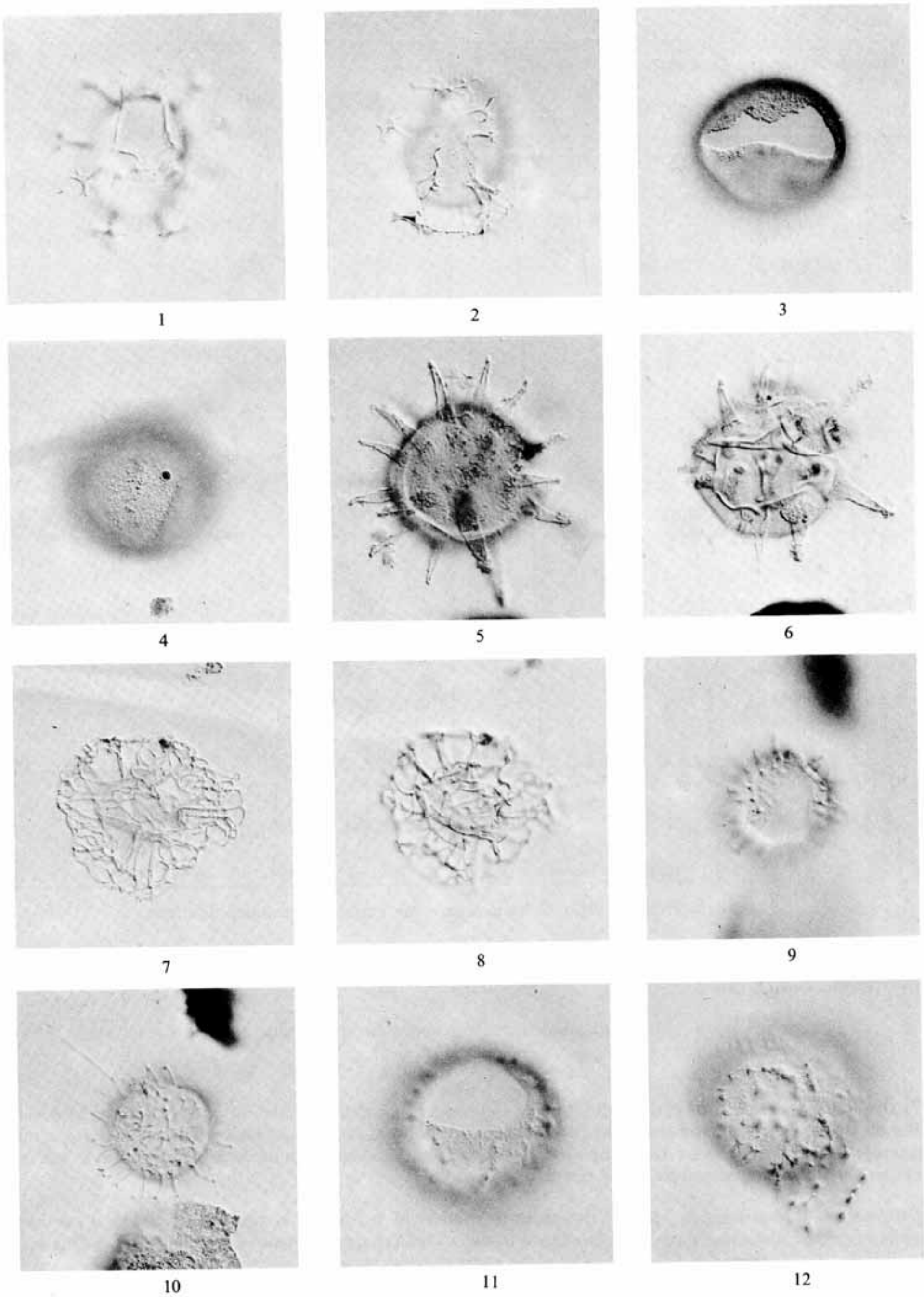
Figs. 3, 4. *Bitectatodinium tepikiense* Wilson, Specimen MPK 2959. 3, dorsal view showing the 2 P archeopyle. 4, ventral view showing nature of the cyst surface.

Figs. 5, 6. *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall, Specimen MPK 1225. 5, ventral view showing the morphology of the processes. 6, dorsal view showing some archeopyle sutures.

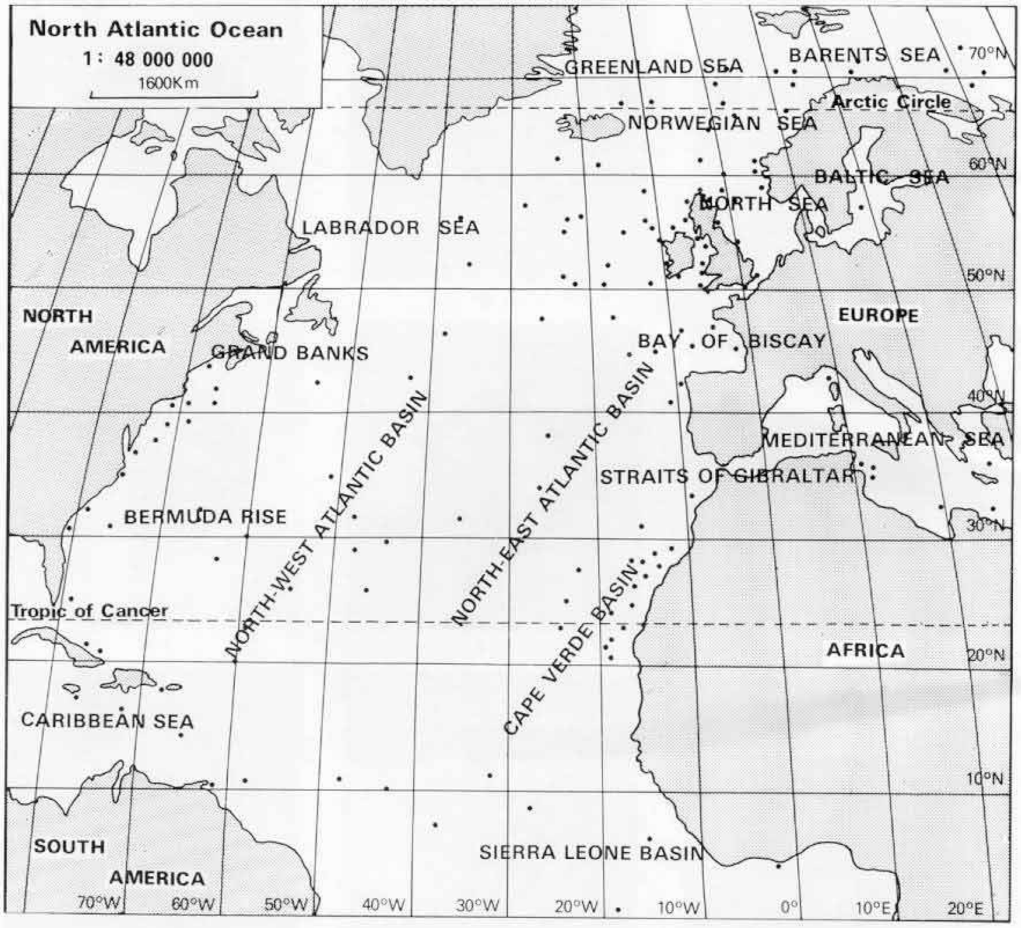
Figs. 7, 8. *Nematosphaeropsis labyrinthea* (Ostenfeld) Reid, Specimen MPK 2963. 7, ?oblique dorsal view showing the nature of the trabeculae. 8, ?oblique ventral view.

Figs. 9, 10. *Operculodinium centrocarpum* (Deflandre and Cookson) Wall, Specimen MPK 2962. 9, dorsal view showing P archeopyle. 10, ventral view showing the process morphology.

Figs. 11, 12. *O. israelianum* (Rossignol) Wall, Specimen MPK 3117. 11, dorsal view showing a broad P archeopyle. 12, ventral view showing the operculum and process morphology.



HARLAND, Recent dinoflagellates



TEXT-FIG. 2. North Atlantic Ocean showing major geographical features.

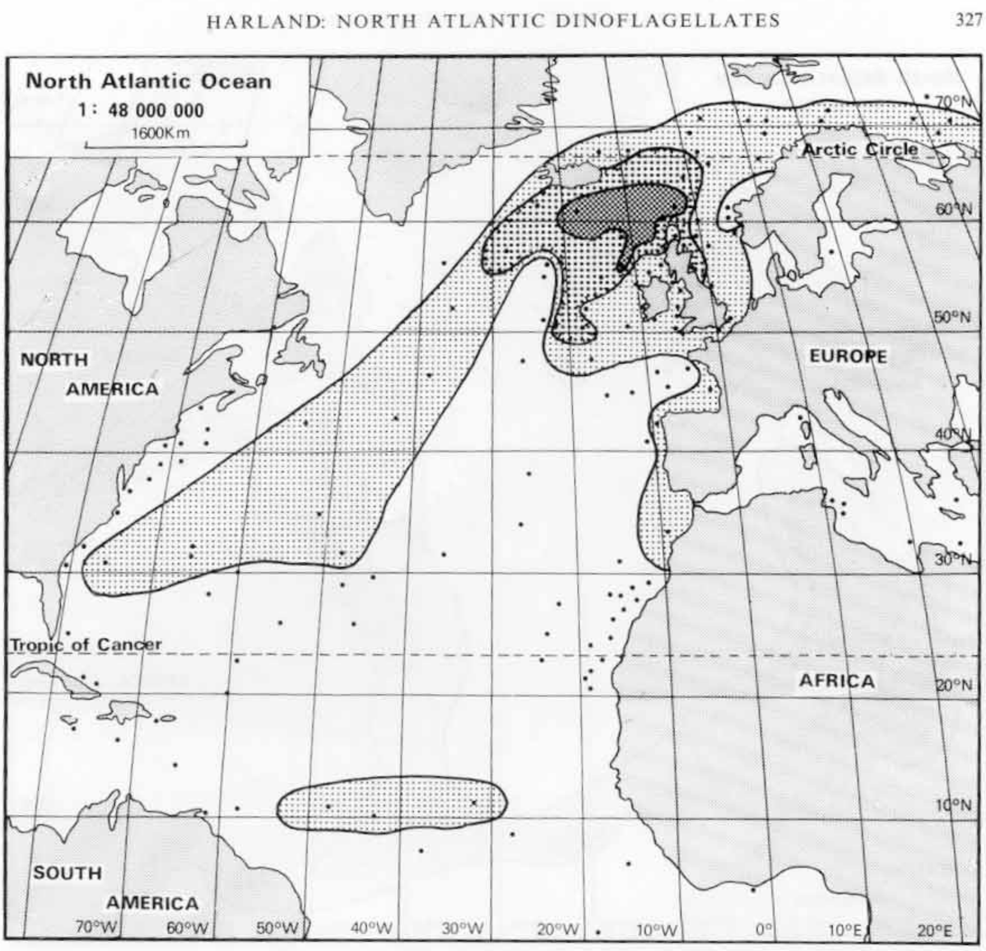
Gonyaulacacean Cysts

1 *Achomosphaera andalousiense* Jan du Chêne 1977

Plate 43, figs. 1, 2

Taxonomic Comments. This cyst, attributable to *Gonyaulax* sp. indet., was first described from the Miocene by Jan du Chêne (1977). It was also described by Harland (1977) as *Spiniferites septentrionalis* sp. nov., a junior synonym. The attribution to *Achomosphaera* Evitt is arbitrary, based upon the lack of parasutures, and in my opinion is artificial serving little useful purpose.

Distribution. In one sample, 133, off the south-west coast of Ireland. It is possibly a reworked occurrence as its restricted distribution and its abundance in older Quaternary sediments would suggest. In Quaternary sequences it may indicate a pre-Flandrian or even possibly a pre-Ipswichian age, but further study is required.



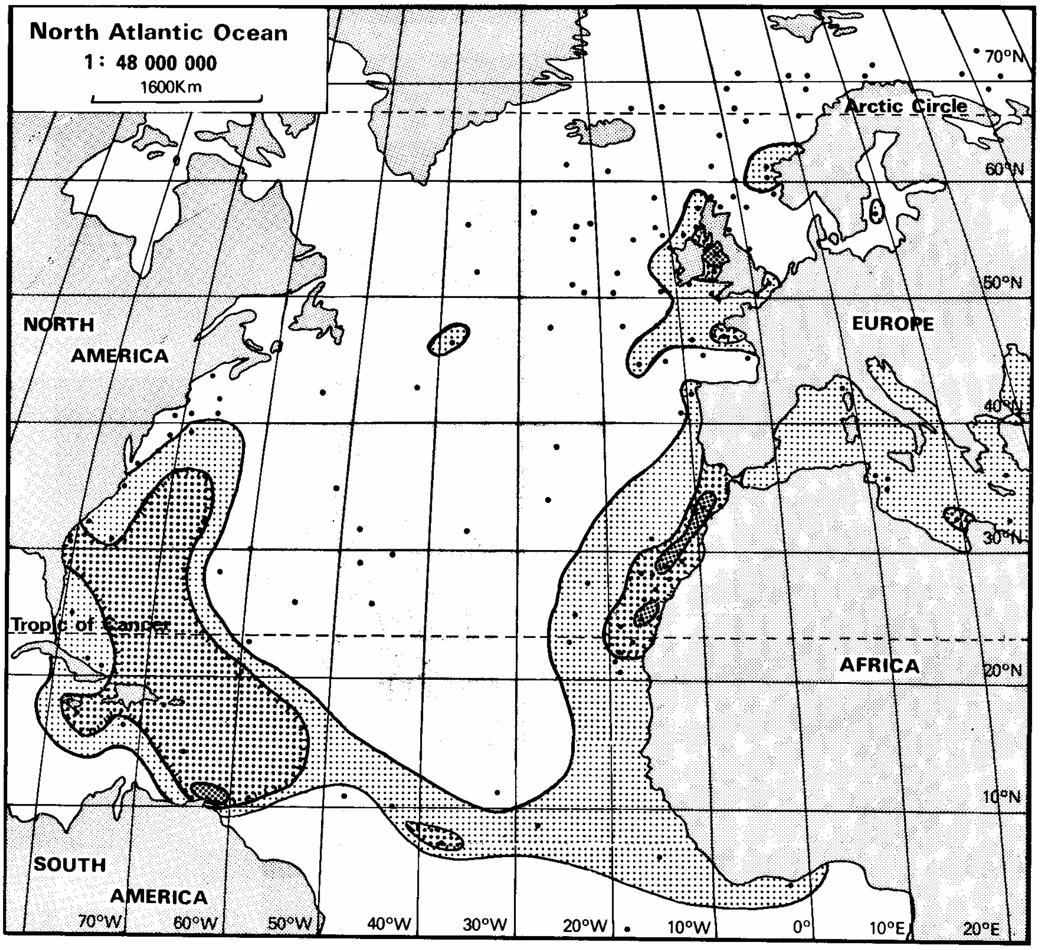
TEXT-FIG. 3. Distribution of *Bitectatodinium tepikiense* Wilson. Light stipple indicates up to and including 10% occurrence, medium stipple > 10% to 50% occurrence and coarse stipple greater than 50% occurrence.

2 *Bitectatodinium tepikiense* Wilson 1973

Text-fig. 3; Plate 43, figs. 3, 4

Taxonomic Comments. A well-known form and one of the many cyst types attributable to *Gonyaulax spinifera* (Claparède and Lachmann) Diesing. It is very similar to the cyst species *Tectatodinium pellitum* Wall but is distinguished by the possession of a 2P archeopyle.

Distribution. A north-temperate to arctic distribution across the North Atlantic with an area of concentration between Iceland and Scotland. It also occurs to the west of the Iberian Peninsula and toward the equator along latitude 10° N. between 50° and 30° W. Wall *et al.* (1977) recorded this species from an estuarine environment which led them to classify it with that environment. *B. tepikiense* is a common component in Quaternary sequences about the area of the British Isles. Its distribution appears to be particularly associated with the North Atlantic Current and the Iceland–Faeroes–Scotland ridge. The disparate occurrence off South America may indicate the presence of a separate taxonomic entity.



TEXT-FIG. 4. Distribution of *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall. Ornament as before.

3 *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall 1967

Text-fig. 4; Plate 43, figs. 5, 6

Taxonomic Comments. This, the well-known cyst of *Gonyaulax polyedra* Stein, is a variable form especially in relation to archeopyle development and the ratio of the length of processes to the cyst diameter (Harland 1977).

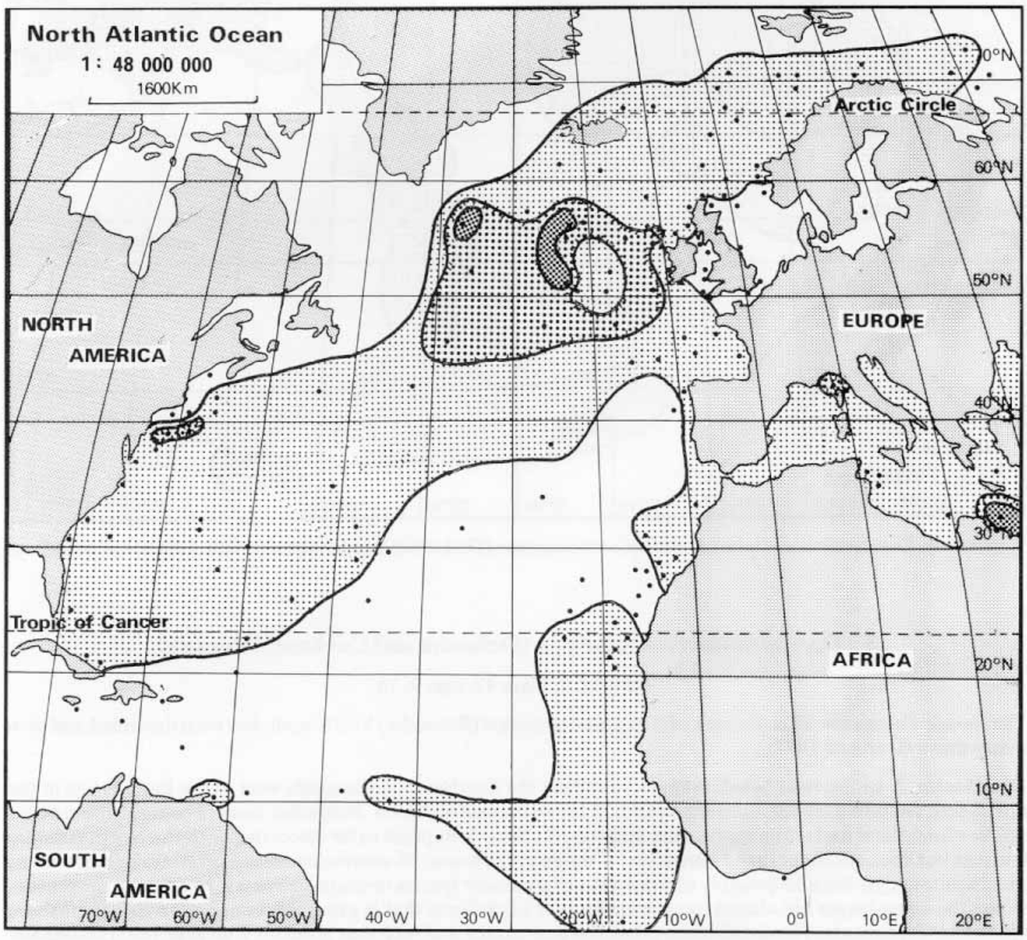
Distribution. This cyst appears to have a distribution in the southern part of the North Atlantic, Caribbean, off the west coast of Africa, Mediterranean, and off the west coast of the British Isles. Areas of concentration include the Caribbean, off the north-west African coast, and in the Irish Sea. It appears to be associated with the South Equatorial Current. It is often associated with estuarine low-salinity environments (Wall *et al.* 1977) as portrayed here in the Irish Sea but it also seems associated with highly saline waters, e.g. off the west coast of Africa. The species may be, therefore, tolerant of marine salinities both less and greater than normal. Williams (1971) had already pointed out the facies associated with the Straits of Gibralter and north-west Africa. Wall *et al.* (1977) also note that the possession of differences in archeopyle morphology are not evenly distributed such that there may be some ecophenotypic variations. *L. machaerophorum* occurs rarely in offshore Quaternary sediments except in the Irish Sea where it appears to have been established sometime in the middle Flandrian.

4 *Nematosphaeropsis labyrinthea* (Ostenfeld) Reid 1974

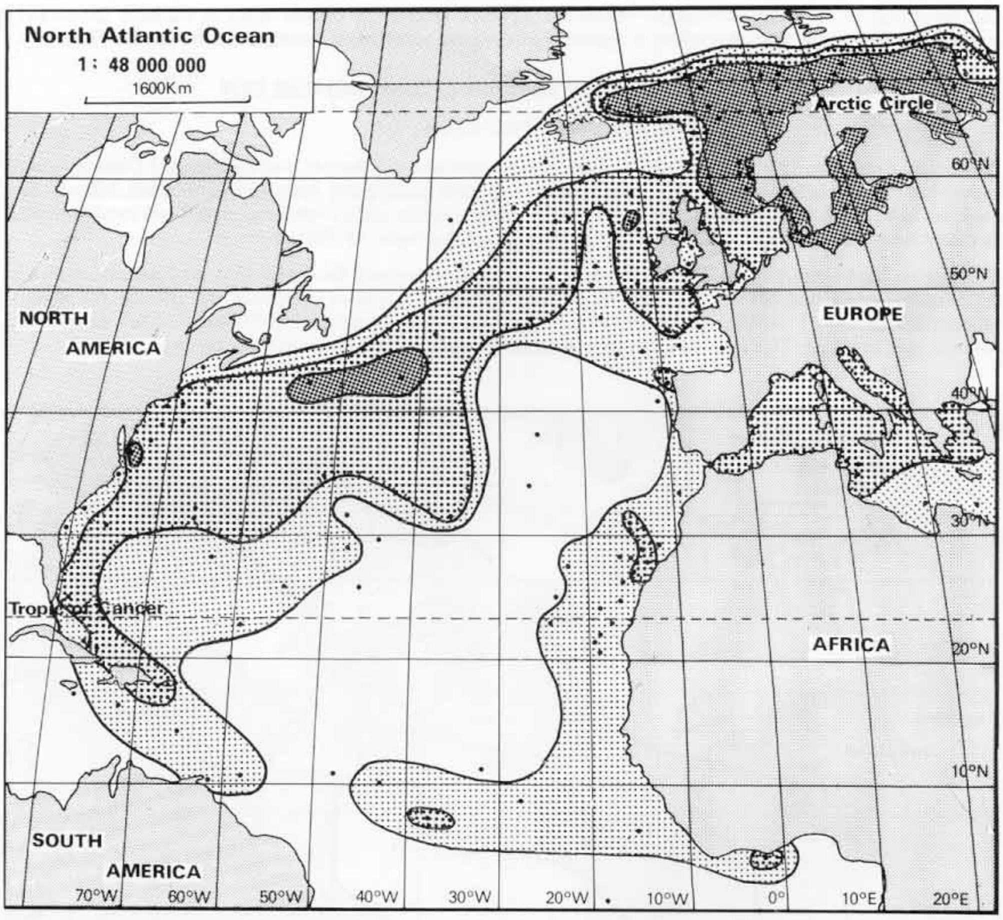
Text-fig. 5; Plate 43, figs. 7, 8

Taxonomic Comments. This cyst, another of *Gonyaulax spinifera* (Claparède and Lachmann) Diesing, is well known but unfortunately usually appears somewhat distorted making any detailed examination difficult. The specimen in Plate 43, fig. 7 clearly shows some double trabeculae but often even these are difficult to observe and therefore may indicate an assignment to the genus *Cannosphaeropsis* O. Wetzel.

Distribution. Widespread in the North Atlantic especially associated with the North Atlantic Current but also in the Mediterranean and off parts of the west coast of Africa. Areas of concentration include the eastern Mediterranean and off the west coast of Ireland at about the region where the North Atlantic Current and East Atlantic gyre separate. This cyst is more rarely seen in offshore British Quaternary sequences.



TEXT-FIG. 5. Distribution of *Nematosphaeropsis labyrinthea* (Ostenfeld) Reid. Ornament as before.



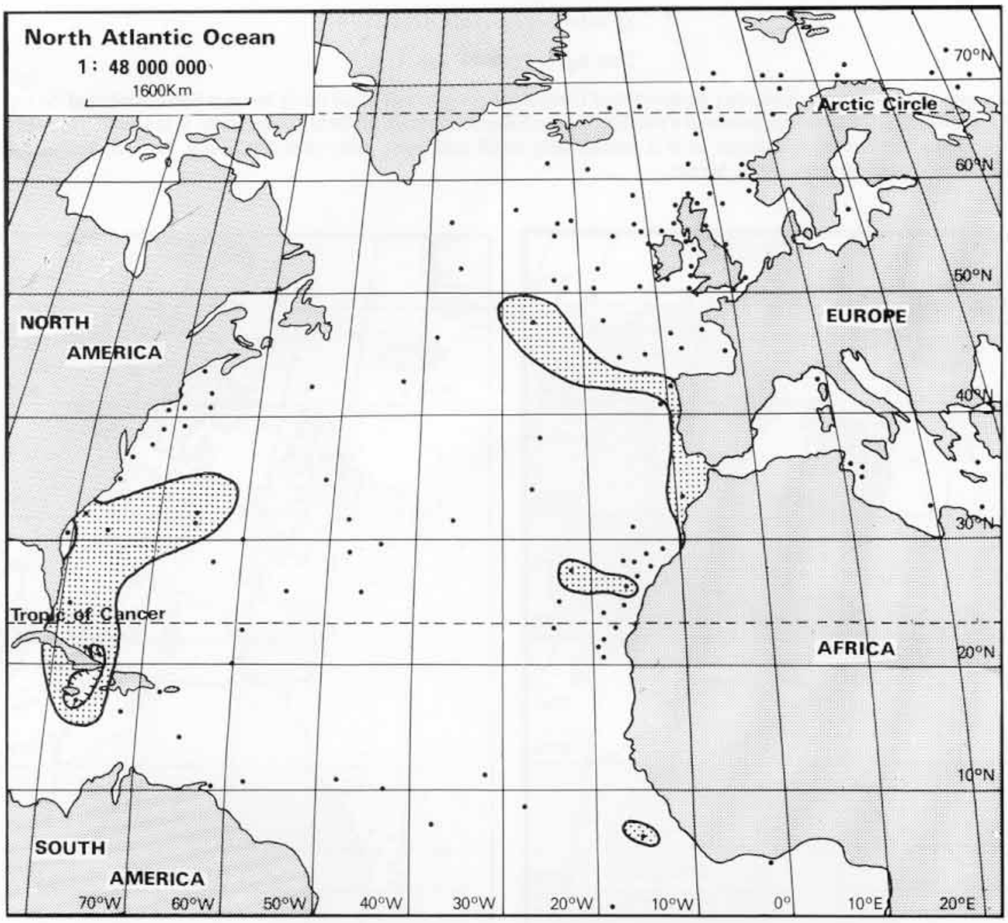
TEXT-FIG. 6. Distribution of *Operculodinium centrocarpum* (Deflandre and Cookson) Wall. Ornament as before.

5 *Operculodinium centrocarpum* (Deflandre and Cookson) Wall 1967

Text-fig. 6; Plate 43, figs. 9, 10

Taxonomic Comments. This, the cyst of *Gonyaulax grindleyi* (Reinecke) Von Stosch, has been described and seen many times (Harland 1977).

Distribution. A widespread North Atlantic cyst from the Caribbean in the south-west to the Barents Sea in the north-east, including the Mediterranean and off the west coast of Africa. Particular areas of concentration occur off Newfoundland and in the Norwegian and Barents Seas. It appears to be associated with the North Atlantic Current but does not occur in the central-eastern side of the ocean. *O. centrocarpum* can certainly be regarded as an ubiquitous cyst but also possibly as somewhat of a pioneer species in north-temperate to arctic environments where the assemblages are almost monospecific. It is a cyst form that is extremely common in British offshore Quaternary sediments. The distribution presented here agrees well with that given by Wall *et al.* (1977) especially in terms of its disposition in the outer neritic region.



TEXT-FIG. 7. Distribution of *Operculodinium israelianum* (Rossignol) Wall. Ornament as before.

6 *Operculodinium israelianum* (Rossignol) Wall 1967

Text-fig. 7; Plate 43, figs. 11, 12

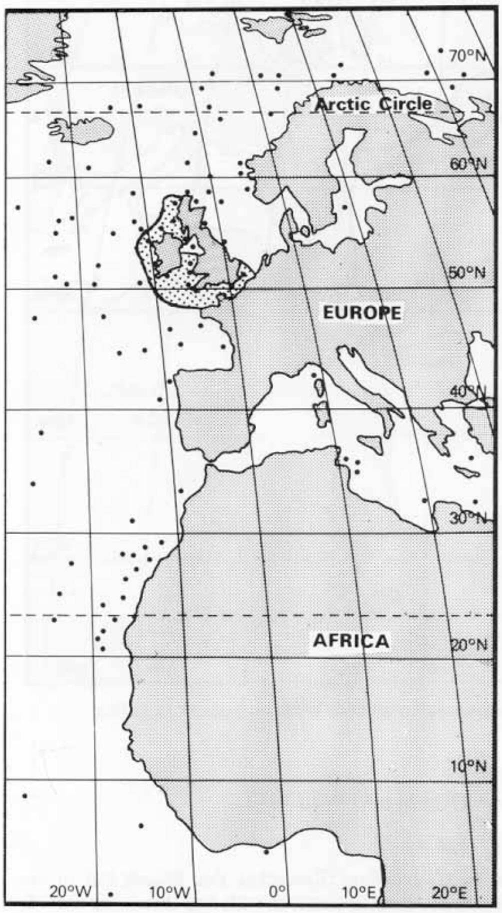
Taxonomic Comments. This cyst may also be produced by *G. grindleyi* (Reinecke) Von Stosch but to my knowledge no incubation studies have been carried out to establish a relationship with any thecate species. It differs from *O. centrocarpum* in size, being larger, and in having a much broader P archaeopyle and shorter, squat processes.

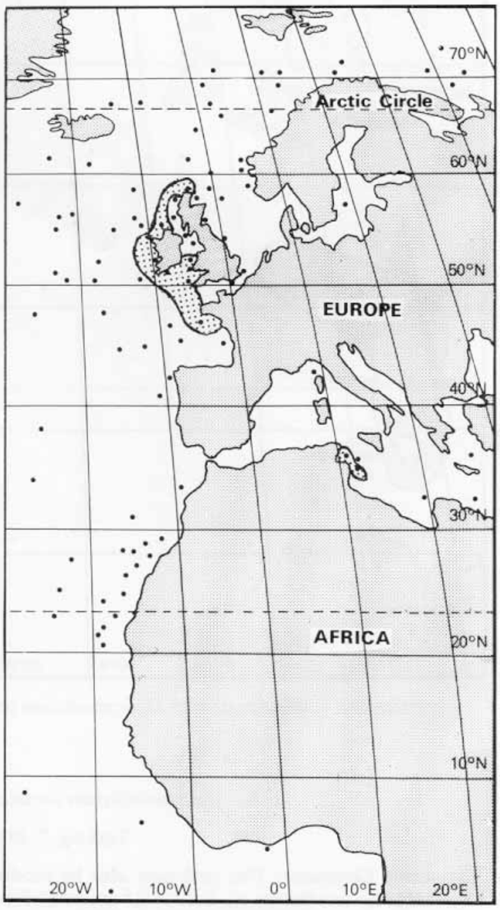
Distribution. O. israelianum has a much more restricted distribution than *O. centrocarpum* being confined to the Caribbean, off the Iberian Peninsular and off the west coast of Africa. Its major centre of concentration appears to be the Caribbean. This species is of particular interest in that the early Pleistocene marine sediments of the British Isles contain *O. israelianum* in abundance at a time when the environmental evidence was suggestive of a 'glacial' climate (Wall and Dale 1968*a*). This is in marked contrast to what is known of its present distribution and further study is needed to explain the discrepancy.

7 *Spiniferites belerius* Reid 1974

Text-fig. 8; Plate 44, figs. 1, 2

Taxonomic Comments. This may be the cyst of *Gonyaulax scrippsae* Kofoid but it has not been incubated, to my knowledge, so that the suggestion of a relationship to a thecate form is probably premature. It is a form not easily recognized in Recent sediments as it is particularly small and may, more often than not, be included in the category *Spiniferites* sp. indet. herein.





TEXT-FIG. 8 (*left*). Distribution of *Spiniferites belerius* Reid. Ornament as before.

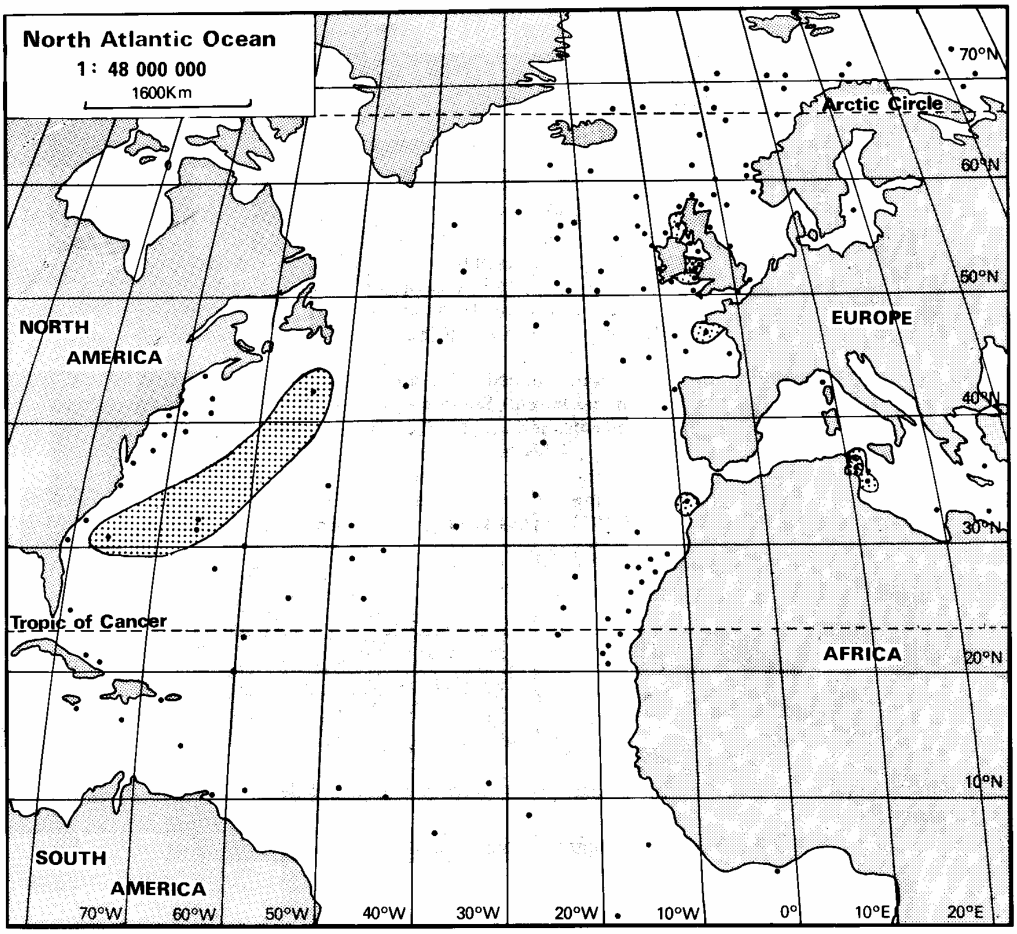
TEXT-FIG. 9 (*right*). Distribution of *Spiniferites delicatus* Reid. Ornament as before.

Distribution. Restricted distribution around the western side of the British Isles excluding the Irish Sea. It is not a species that has been recognized elsewhere, but it does occur in Quaternary sequences although its identification can be difficult. Its restricted distribution pattern may be largely as a result of these identification difficulties.

8 *Spiniferites bentori* (Rossignol) Wall and Dale 1970

Text-fig. 10; Plate 44, figs. 3, 4

Taxonomic Comments. This cyst of *Gonyaulax digitalis* (Pouchet) Kofoid is fairly distinctive, but is a species of some intraspecific variability especially in relation to the length of the processes, and includes a form sometimes referred to as *Spiniferites nodosus* Wall.



TEXT-FIG. 10. Distribution of *Spiniferites bentori* (Rossignol) Wall and Dale. Ornament as before.

Distribution. Restricted to the offshore area of the eastern seaboard of the United States, the western side of the British Isles, plus one or two isolated occurrences. Wall *et al.* (1977) recognized two morphotypes within this species which probably account for the disparate distribution between the United States and European occurrences. Reid (1972*b*) regarded *S. bentori* as being prominent in enclosed bays with rather localized temperature and salinity conditions. It has been seen as an early component in sediments associated with the Flandrian marine transgression in the Irish Sea area (Pantin 1978).

9 *Spiniferites delicatus* Reid 1974

Text-fig. 9; Plate 44, figs. 5, 6

Taxonomic Comments. This the cyst of a *Gonyaulax* sp. indet. is fairly readily distinguished by its process morphology, petaloid distal tips, and high granular membranous parasutural membranes. It is not a cyst that is commonly recognized.

Distribution. Restricted to the western side of the British Isles, but its distribution may reflect a failure to identify it. It was first identified in British intertidal sediments and described by Reid (1974). It has only rarely been seen in offshore marine Quaternary sequences.

10 *Spiniferites elongatus* Reid 1974

Text-fig. 11; Plate 44, figs. 7–10

Taxonomic Comments. This cyst species is attributable to *Gonvaulax spinifera* (Claparède and Lachmann) Diesing. There is, however, some evidence to suggest that the *Spiniferites* cysts may not all belong to *G. spinifera sensu stricto* but to another related type. It was first recognized as a distinct morphotype by Wall and Dale (1968*b*) and by Harland and Downie (1969). *S. elongatus* in the present study also includes those forms named *S. frigidus* in Harland *et al.* (1980) (Plate 44, figs. 9, 10) and a description of the variation within these species in north-temperate and arctic waters is in preparation by Harland and Sharp. The importance of elongate *Spiniferites* species in northern waters has already been noted (Harland 1982*b*).

Distribution. A somewhat restricted distribution, confined to the north-eastern seaboards of the United States and around the British Isles and Norwegian and Barents Sea. Some isolated occurrences in the Mediterranean and off the west coast of Africa. Areas of concentration occur in the western Atlantic and in the Norwegian and Barents Sea, the latter mostly formed by the *S. frigidus* morphotype.

This cyst is often found in offshore marine Quaternary sediments albeit in small percentages. Its distribution suggests that it may be quite useful in recognizing colder north-temperate to arctic environments, but it does not appear to be an estuarine type (Wall *et al.* 1977) as has been suggested, on the present evidence.

EXPLANATION OF PLATE 44

All photomicrographs were taken with Nomarski interference contrast, unless otherwise stated, and are illustrated at a magnification of × 500.

Figs. 1, 2. *Spiniferites belerius* Reid, photomicrographs kindly supplied by P. C. Reid. 1, dorsal view showing the archeopyle. 2, median view showing somewhat atypically developed antapical membrane. Photographed in plain light.

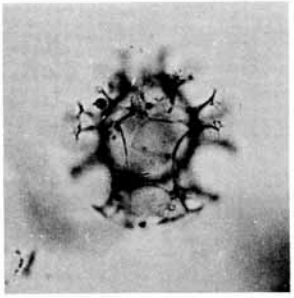
Figs. 3, 4. *S. bentori* (Rossignol) Wall and Dale, Specimen MPK 1216. 3, median view showing apical horn and nature of the processes. 4, ventral view showing well-developed narrow, rectangular 1′′′ paraplate.

Figs. 5, 6. *S. delicatus* Reid, Specimen MPK 1222. 5, oblique dorsal view showing the archeopyle. 6, high dorsal view showing the distinctive nature of the process tips.

Figs. 7, and 8. *S. elongatus* Reid, Specimen MPK 2579. 7, oblique dorsal view showing the archeopyle. 8, ventral view showing the sulcus and sulcal paratabulation.

Figs. 9, 10. *S. frigidus* Harland and Reid, Specimen MPK 2424. 9, dorsal view showing the archeopyle. 10, ventral view showing the 1′ and 4′ apical paraplates. This species is included in the *S. elongatus* counts as it is regarded as a part of the variation for the species.

Figs. 11, 12. *S. lazus* Reid, Specimen MPK 1204. 11, oblique dorsal view showing the archeopyle. 12, oblique ventral view.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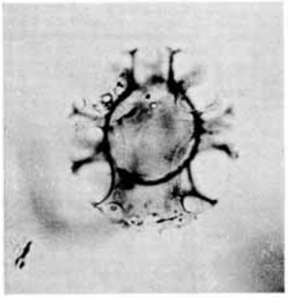
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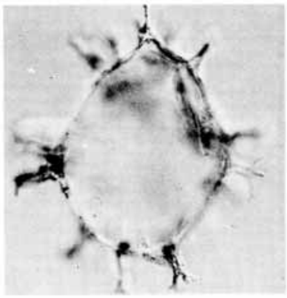
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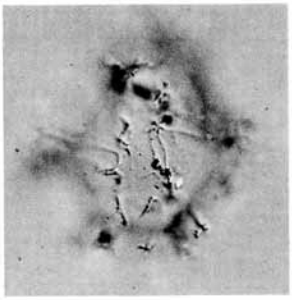
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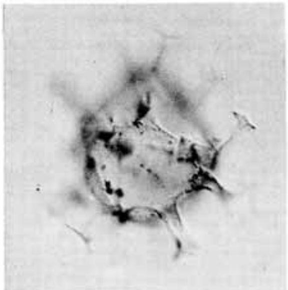
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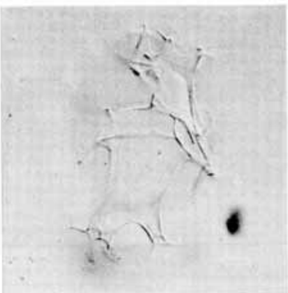
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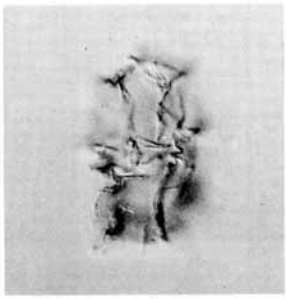
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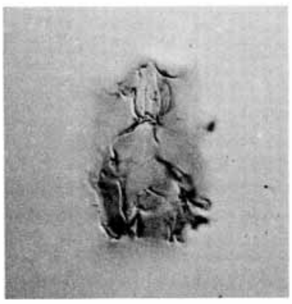
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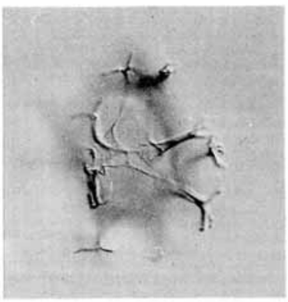
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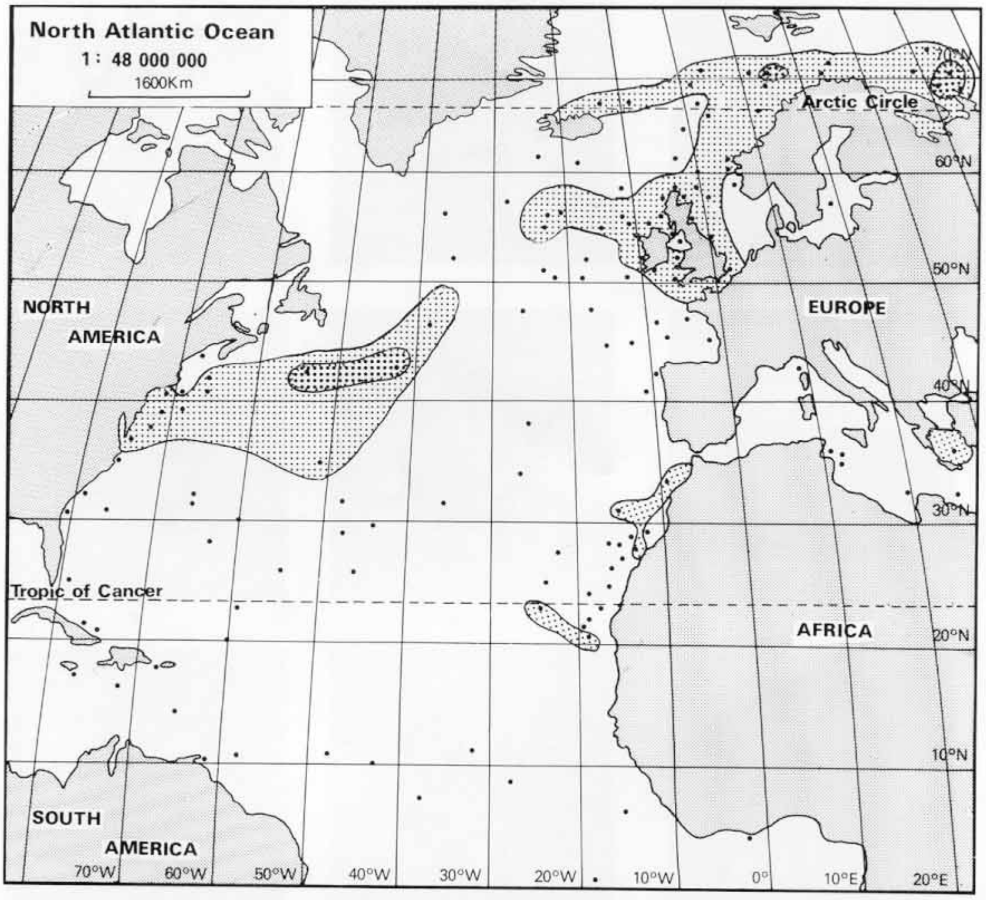
12

HARLAND, Recent dinoflagellates



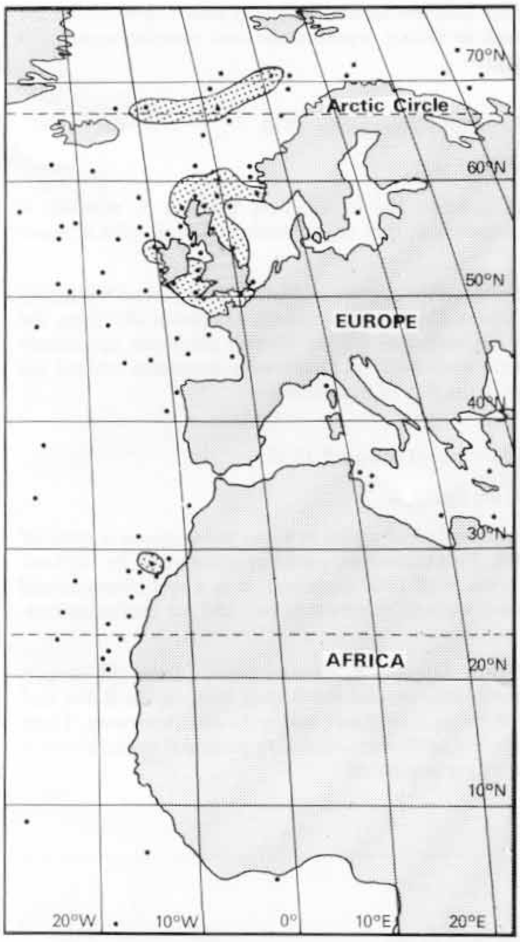
TEXT-FIG. 11. Distribution of *Spiniferites elongatus* Reid. Ornament as before.

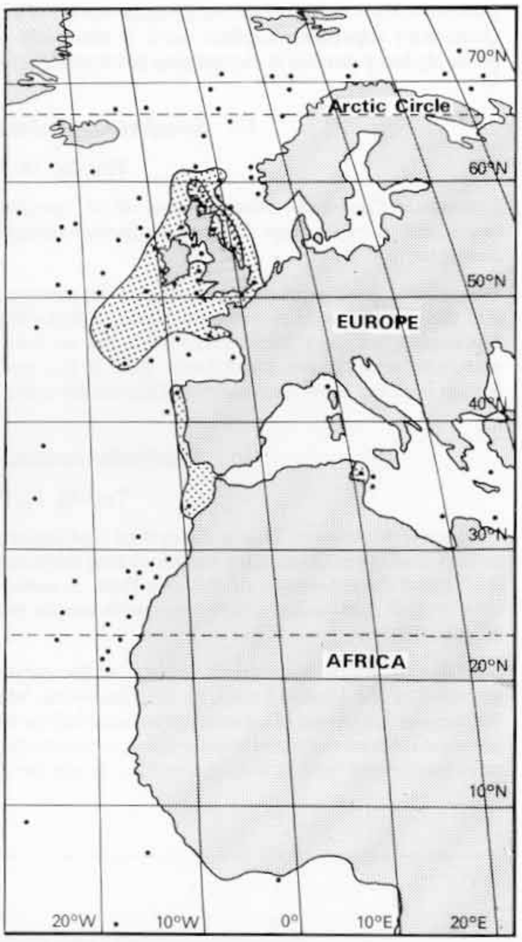
11 *Spiniferites lazus* Reid 1974

Text-fig. 12; Plate 44, figs. 11, 12

Taxonomic Comments. A well-known cyst in sediments around the United Kingdom, it is attributable to *Gonyaulax* sp. indet. as no incubation experiments have been carried out to relate it to a thecate species. This cyst is morphologically characterized by the perforate 'lace-like' periphragm at the bases of the processes, and its rather asymmetrical appearance.

Distribution. Restricted to offshore British Isles, the Norwegian Sea, and an isolated occurrence off the north-west coast of Africa. In no case was it recorded in percentages above 10%. This cyst is interesting, however, in that in some Quaternary sequences it has been recorded up to 50% of the assemblage. It appears, in general, to be a north-temperate cyst species and of possible particular environmental significance.





TEXT-FIG. 12 (*left*). Distribution of *Spiniferites lazus* Reid. Ornament as before.

TEXT-FIG. 13 (*right*). Distribution of *Spiniferites membranaceus* (Rossignol) Sarjeant. Ornament as before.

12 *Spiniferites membranaceus* (Rossignol) Sargeant 1970

Text-fig. 13; Plate 45, figs. 3, 4

Taxonomic Comments. Another well-known cyst type of *Gonyaulax spinifera* (Claparède and Lachmann) Diesing. It is characterized by membranous processes particularly at the antapical and paracingulum regions. Wall *et al.* (1977) drew attention to their belief that the *S. membranaceus* as described by Reid (1974) and herein is not conspecific with that of Rossignol (1964). This probably explains the rather restricted distribution recorded here, in temperate waters, and the isolated occurrences in more tropical waters (samples 67 and 117 not shown on the map) may in fact be the other morphotype. *S. membranaceus sensu* Reid is the only form known to the author. It is also a very variable cyst species.

Distribution. Restricted to areas around the British Isles, into the eastern Atlantic, and off the Iberian peninsula. Isolated occurrences were also recorded in the Caribbean, western Atlantic, and Mediterranean. A centre of concentration is noted off the north-eastern coast of England. This species is occasionally seen in offshore marine Quaternary sequences. Further work is obviously needed to clearly separate the two morphotypes, as it probably has potential in recognizing particular enviroments.

13 *Spiniferites mirabilis* (Rossignol) Sargeant 1970

Text-fig. 14; Plate 45, figs. 1, 2

Taxonomic Comments. Another cyst of *G. spinifera* (Claparède and Lachmann) Diesing, *S. mirabilis* is characterized by its large size and distinctive antapical membrane. It is occasionally confused with *S. membranaceus.*

Distribution. A widespread distribution in the western Atlantic off the eastern seaboard of the United States and into the Caribbean, in the eastern Atlantic off the British Isles, Iberia and the north-west coast of Africa, the Norwegian Sea, and Mediterranean. It has an area of concentration off the Iberian peninsula apparently associated with the eastern Atlantic gyre. It is a cyst seen occasionally in Quaternary sequences around the British Isles but more commonly in Quaternary sediments in the Bay of Biscay area.

14 *Spiniferites ramosus* (Ehrenberg) Mantell 1854

Text-fig. 15; Plate 45, figs. 5, 6

Taxonomic Comments. This is the cyst of *Gonyaulax scrippsae* Kofoid which in some publications is referred to as *S. bulloideus* (Deflandre and Cookson) Sarjeant 1970. This taxonomic problem is discussed by Harland (1977) and the separation of this cyst from *S. ramosus sensu* Wall 1965 explained. It is a cyst characterized by a typical *Spiniferites* morphology with simple processes without membranes etc. and no particular outstanding feature.

Distribution. Fairly widespread but not in the central North Atlantic. *S. ramosus* occurs down the eastern seaboard of the United States, in the Caribbean, Mediterranean, around the British Isles, in the Baltic and Norwegian Sea. Areas of concentration occur off the United States, Caribbean, and in the Mediterranean. There are some isolated occurrences off north-east South America and north-west Africa. In general it appears to be a more neritic cyst type. It is fairly common in marine Quaternary sequences.

EXPLANATION OF PLATE 45

All photomicrographs were taken using Nomarski interference contrast, unless otherwise stated, and are illustrated at a magnification of × 500.

Figs. 1, 2. *Spiniferites mirabilis* (Rossignol) Sarjeant, Specimen MPK 1626. 1, dorsal view showing the archeopyle. 2, median view showing the large antapical membrane.

Figs. 3, 4. *S. membranaceus* (Rossignol) Sarjeant, Specimen MPK 1208. 3, dorsal view showing the archeopyle. 4, median view showing the nature of the antapical membrane.

Figs. 5, 6. *S. ramosus* (Ehrenberg) Loeblich and Loeblich, Specimen MPK 1205. 5, dorsal view showing the archeopyle. 6, ventral view. Photographed in plain light.

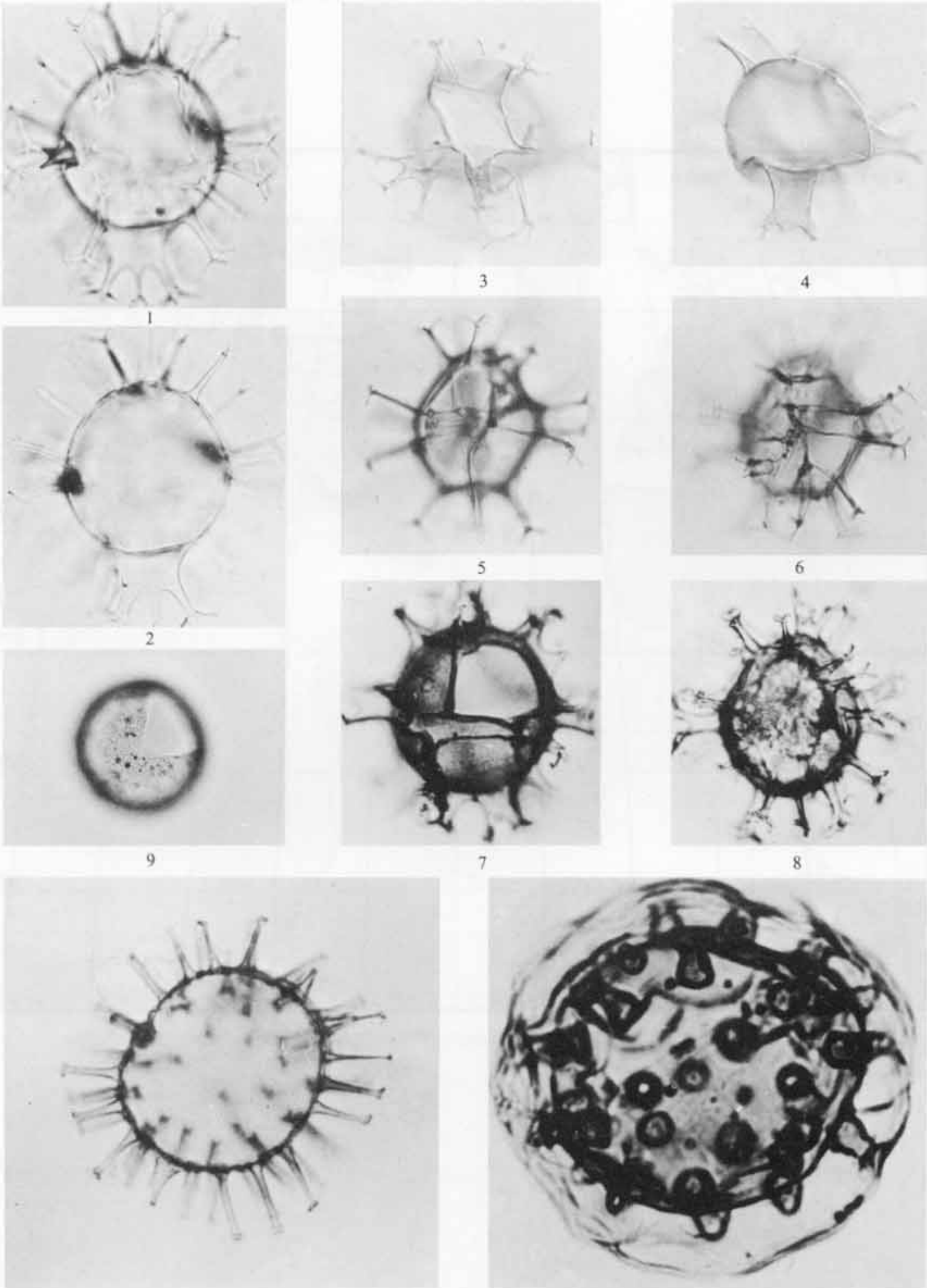
Fig. 7. *S. scabratus* Wall. Photograph kindly supplied by D. Wall, oblique dorsal view. Photographed in plain light.

Fig. 8. *S. ramosus sensu* Wall. Photograph kindly supplied by D. Wall, median view showing the nature of the processes. Photographed in plain light.

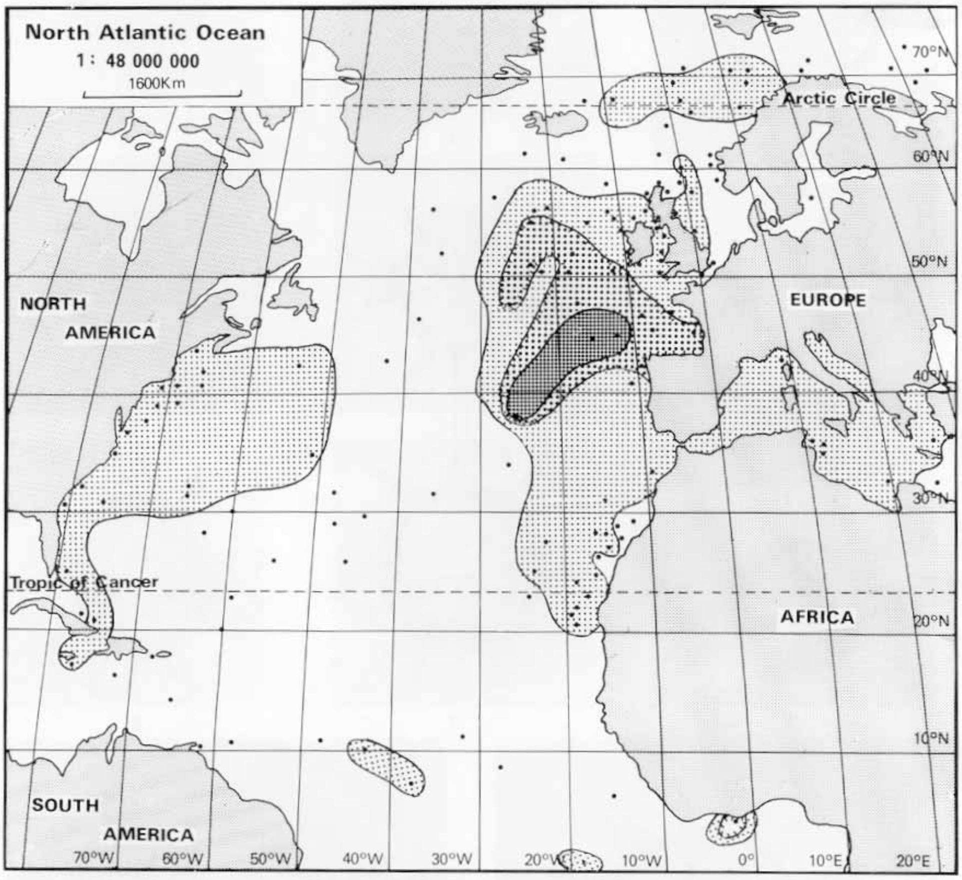
Fig. 9. *Tectatodinium pellitum* Wall, Specimen MPK 1628, oblique dorsal view showing the archeopyle.

Fig. 10. *Polysphaeridium zoharyi* (Rossignol) Bujak *et al.* Photograph kindly supplied by D. Wall, polar view. Photographed in plain light.

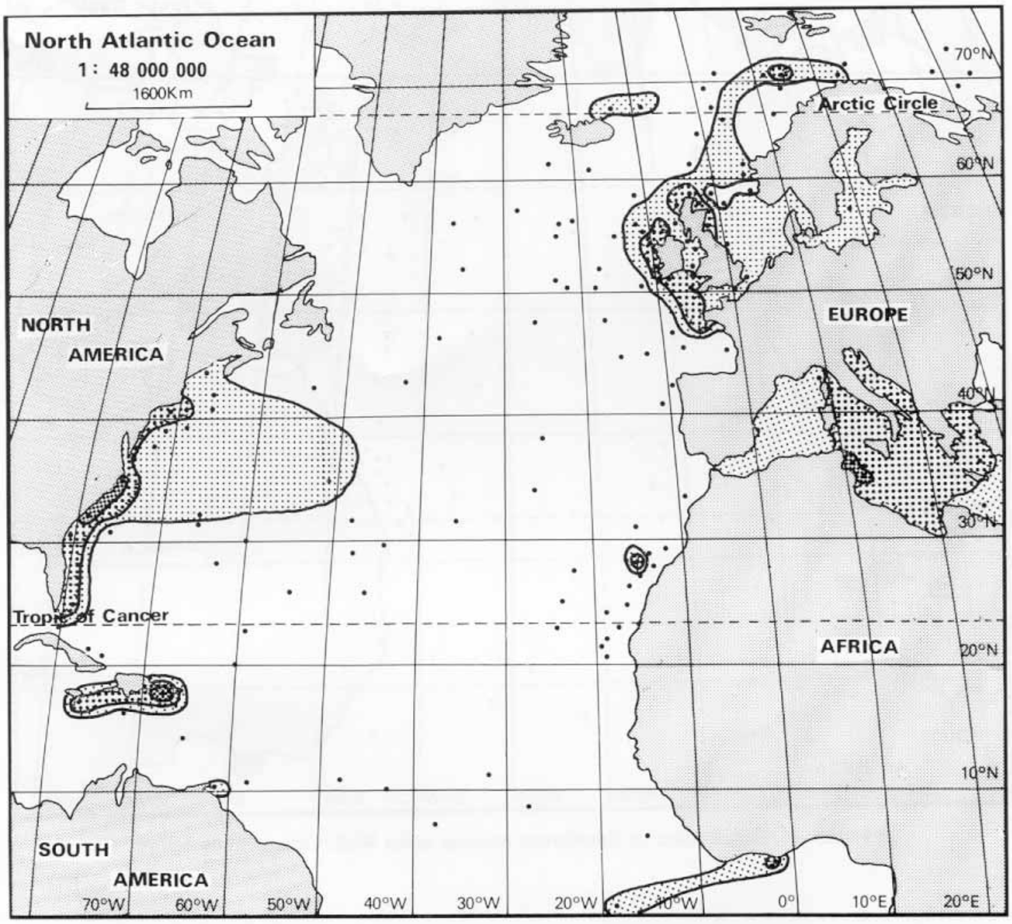
Fig. 11. *Tuberculodinium vancampoae* (Rossignol) Wall. Photograph kindly supplied by D. Wall, antapical view showing the archeopyle. Photographed in plain light.



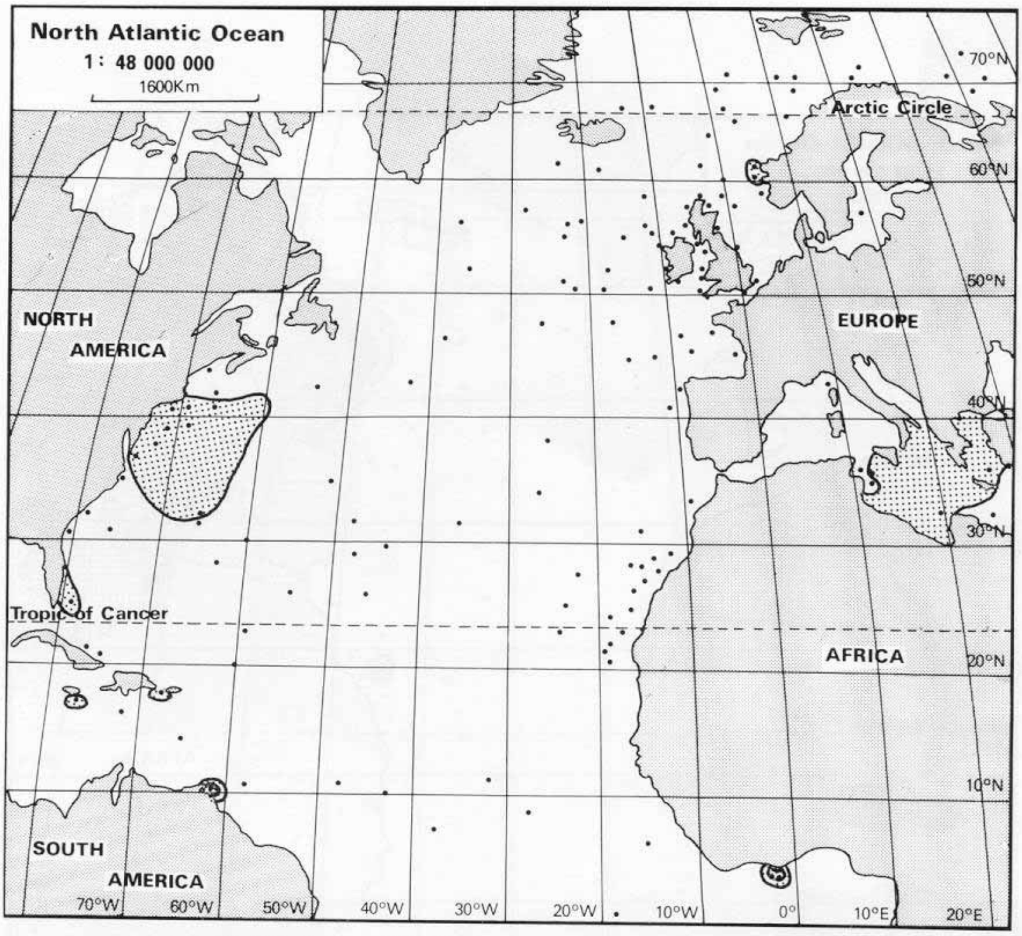
HARLAND, Recent dinoflagellates



TEXT-FIG. 14. Distribution of *Spiniferites mirabilis* (Rossignol) Sarjeant. Ornament as before.



TEXT-FIG. 15. Distribution of *Spiniferites ramosus* (Ehrenberg) Mantell. Ornament as before.



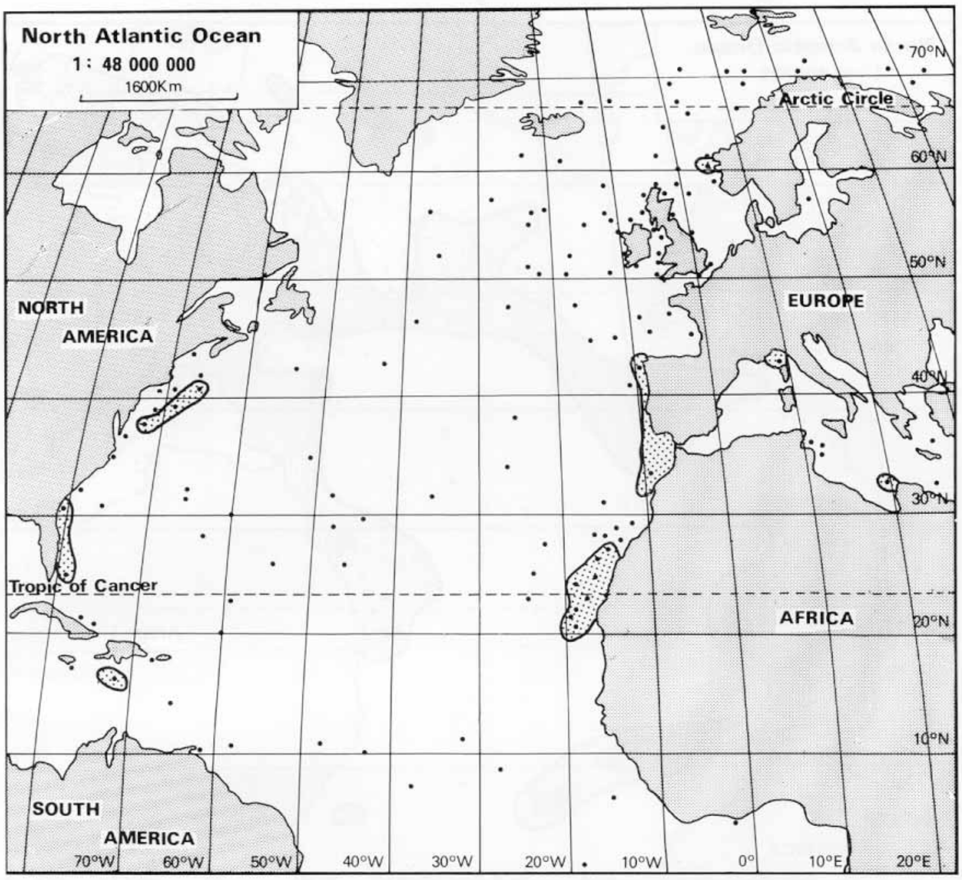
TEXT-FIG. 16. Distribution of *Spiniferites ramosus sensu* Wall. Ornament as before.

15 *Spiniferites ramosus sensu* Wall 1965

Text-fig. 16; Plate 45, fig. 8

Taxonomic Comments. This cyst of *Gonyaulax spinifera* (Claparède and Lachmann) Diesing has been confused with *S. ramosus* and *S. bulloideus*; see Harland (1977) for discussion.

Distribution. Restricted occurrences off the eastern seaboard of the United States and in the Mediterranean. Isolated occurrences are observed in the Caribbean, off Africa and off Norway. The latter may be a misidentification given the taxonomic uncertainty of the species, but certainly it has not been seen around the coasts of the British Isles, nor has it been seen in Quaternary sequences in marine offshore deposits near the United Kingdom.



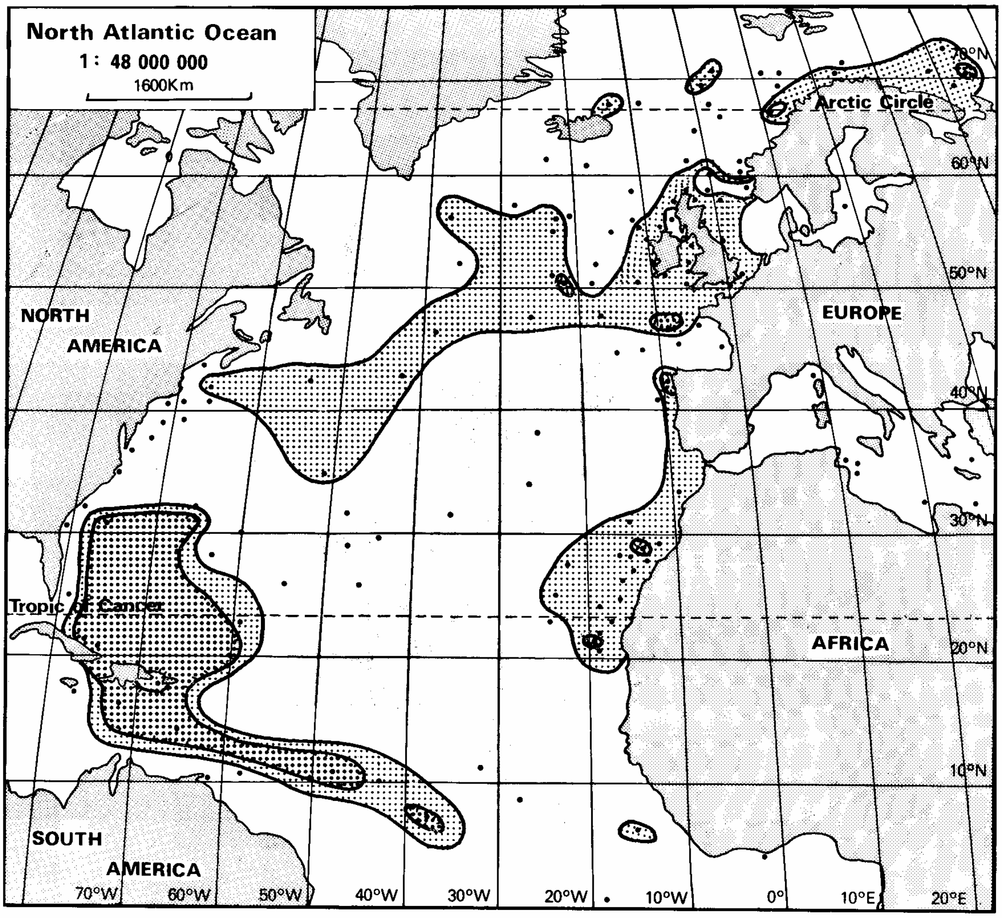
TEXT-FIG. 17. Distribution of *Spiniferites scabratus* Wall. Ornament as before.

16 *Spiniferites scabratus* Wall 1967

Text-fig. 17; Plate 45, fig. 7

Taxonomic Comments. S. scabratus is the cyst of an unknown *Gonyaulax* sp. and was first described by Wall (1967). It has, however, not been seen by me in my studies around the British Isles.

Distribution. Restricted occurrences off the eastern seaboard of the United States, Caribbean, Iberian peninsula, north-west Africa, and some isolated occurrences in the Mediterranean and Norway. The map certainly is suggestive that the cyst prefers neritic tropical to sub-tropical environments; its record off Norway is probably a misidentification or possibly a case of reworking. It has not been seen by me in offshore marine Quaternary sequences.



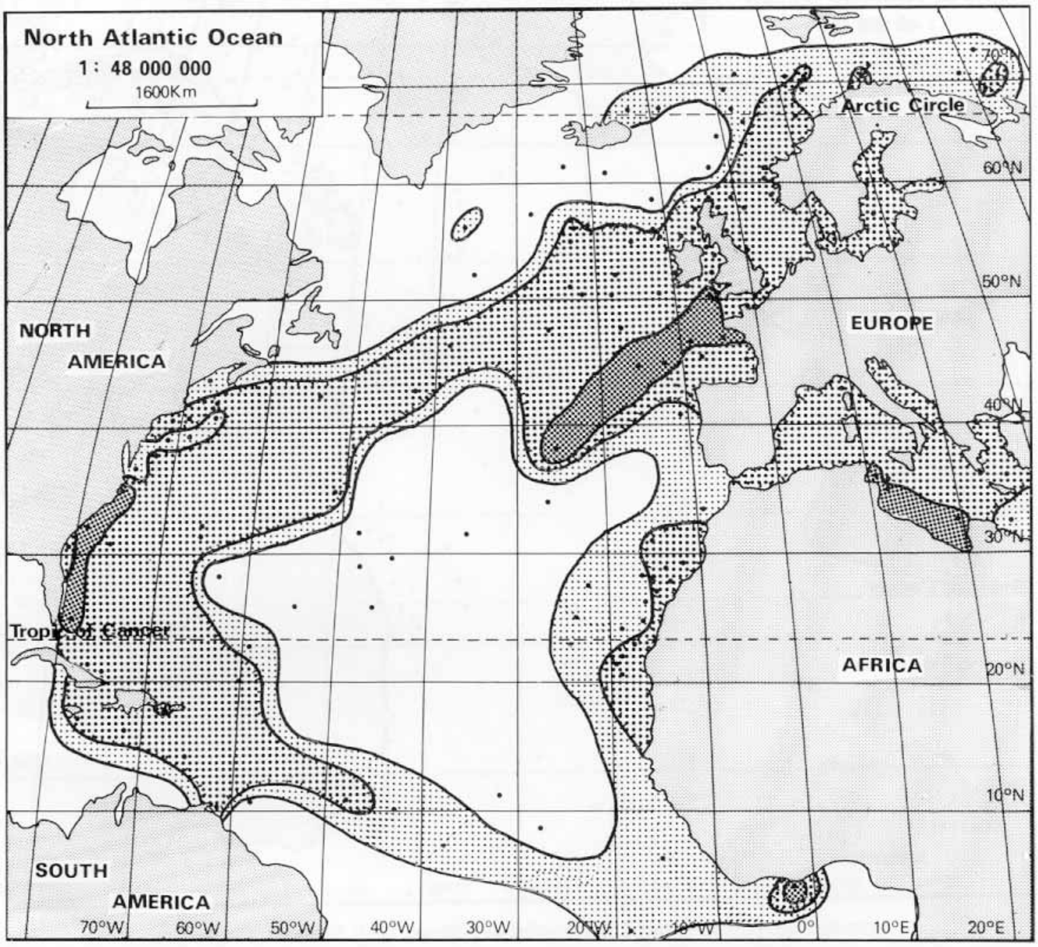
TEXT-FIG. 18. Distribution of *Spiniferites* spp. indet. Ornament as before.

17 *Spiniferites* spp. indet.

Text-fig. 18

Taxonomic Comments. This category combines all the records of *Spiniferites* cysts that have not been positively identified. Many may be badly orientated or broken whereas others may be new species not yet studied in detail.

Distribution. North Atlantic from the New England coast to the British Isles and into the Barents Sea, the Caribbean, and off the north-west coast of Africa. A major concentration in the Caribbean area is evident but further comment is not justified because of the nature of the record.

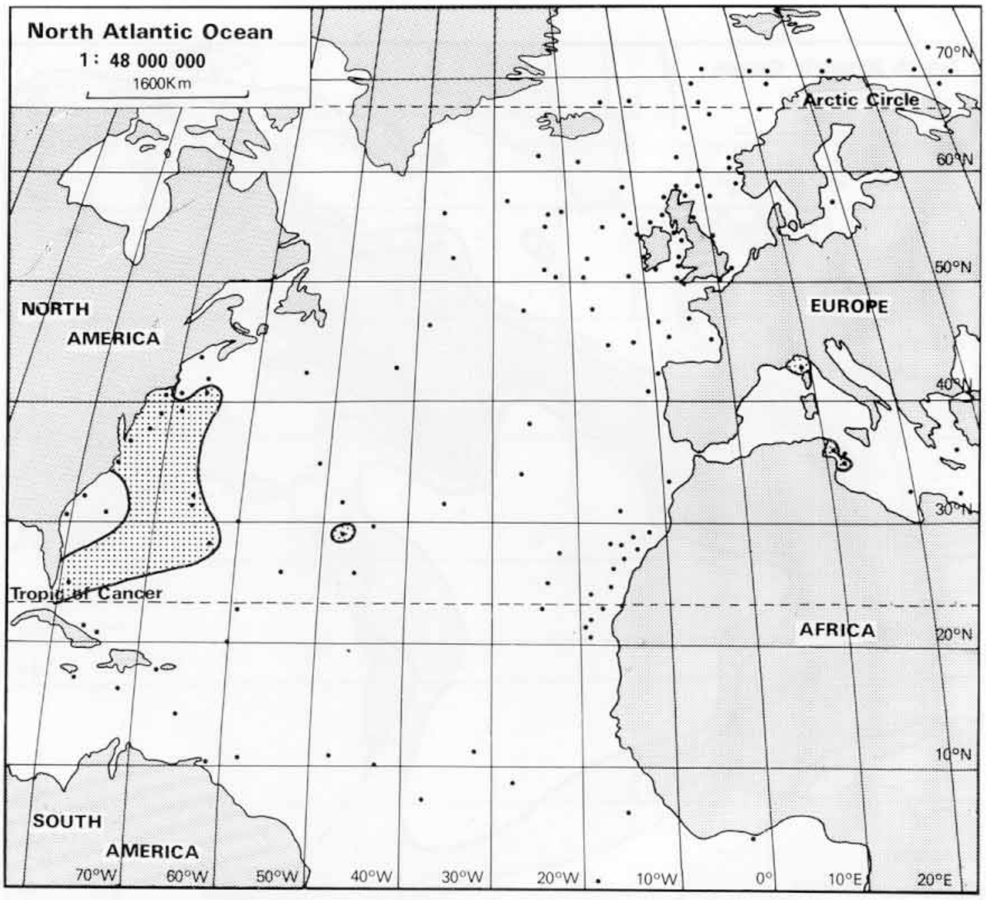


TEXT-FIG. 19. Distribution of total *Spiniferites* species. Ornament as before.

18 Total *Spiniferites* spp.

Text-fig. 19

General Comments. A widespread distribution with centres off the eastern seaboard of the United States, the eastern Atlantic, off the Iberian peninsular, the southern Mediterranean, and off the west coast of Africa. The pattern reflects the North Atlantic circulation pattern with the central Atlantic devoid of *Spiniferites* cysts. This may be accounted for in terms of distribution by current systems of a group of cysts that basically enjoy a neritic environment.



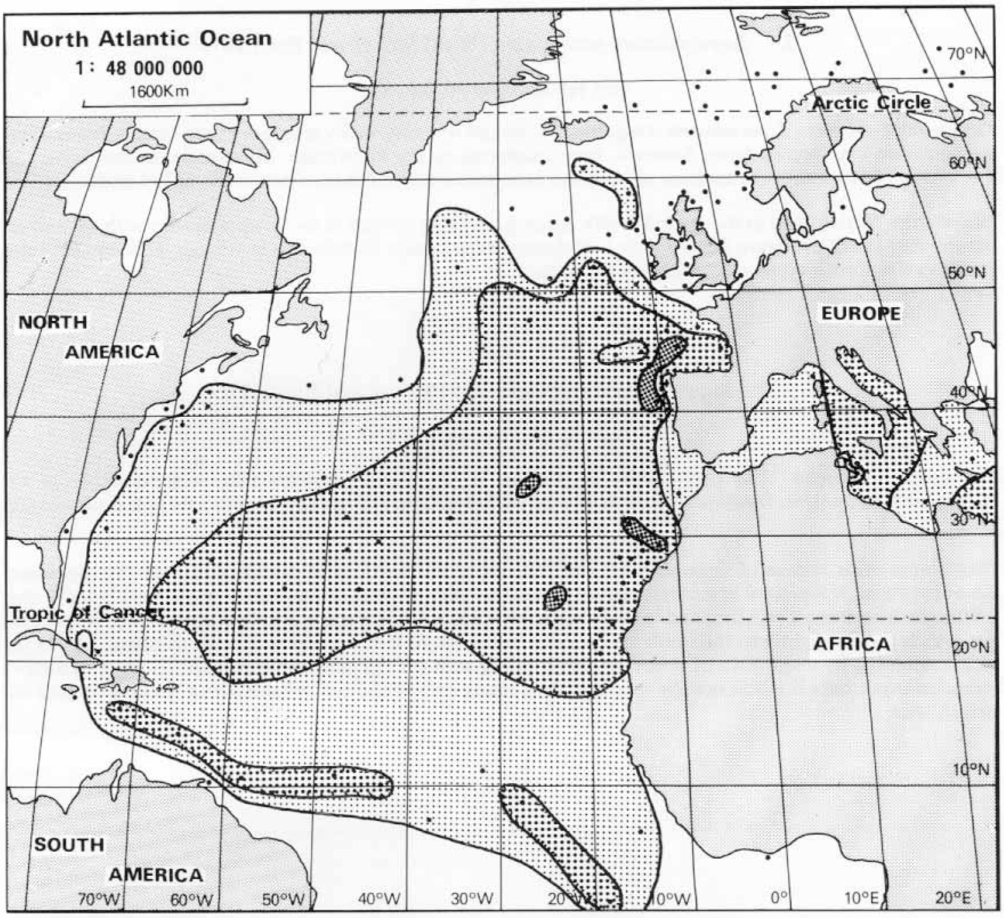
TEXT-FIG. 20. Distribution of *Tectatodinium pellitum* Wall. Ornament as before.

19 *Tectatodinium pellitum* Wall 1967

Text-fig. 20; Plate 45, fig. 9

Taxonomic Comments. T. pellitum is the cyst of an unidentified *Gonyaulax* species and is easily confused with *Bitectatodinium tepikiense* Wilson. It is distinguished by possession of a single paraplate precingular archeopyle. The distribution maps of *B. tepikiense* and *T. pellitum* are quite different.

Distribution. This cyst is known only from the south-eastern seaboard of the United States and from isolated occurrences in the Mediterranean. It is obviously a neritic cyst but is of especial interest in that it, like *Operculodinium israelianum* (Rossignol), makes up large percentages of early Pleistocene dinoflagellate cyst assemblages from southern England. This kind of occurrence in Pleistocene sequences is in marked contrast to its occurrence in Recent sediments and needs explanation, especially in relation to the 'cold' environment of the early Pleistocene in contrast to its present south-temperate to sub-tropical distribution.



TEXT-FIG. 21. Distribution of *Impagidinium aculeatum* (Wall) comb. nov. Ornament as before.

20 *Impagidinium aculeatum* (Wall) comb. nov.

Text-fig. 21; Plate 46, figs. 1–3

Taxonomic Comments. Stover and Evitt (1978) failed to transfer *Leptodinium aculeatum* Wall to their new genus *Impagidinium*. This is done here: *I. aculeatum* (Wall) comb. nov. = *L. aculeatum* Wall 1967, pp. 104–105, pl. 14, figs. 18, 19, text-figs. 3C, 3D. This form is a cyst type of one of the *Gonyaulax spinifera* group. It is a particularly characteristic morphotype characterized by the form of the parasutural membranes.

Distribution. Widespread in the central North Atlantic and Mediterranean with centres of concentration toward the eastern Atlantic particularly off the Iberian peninsula and north-west Africa. Its pattern of distribution is much more oceanic in aspect than any of those species previously discussed. Records of this species in Quaternary sediments are confined to very rare occurrences off the British Isles.

21 *Impagidinium paradoxum* (Wall) Stover and Evitt 1978

Text-fig. 22; Plate 46, figs. 4, 5

Taxonomic Comments. I. paradoxum is regarded as the cyst of a *Gonyaulax spinifera* group species. None of the *Impagidinium* cyst species have, however, been incubated to my knowledge. This species is somewhat like *I. aculeatum* but without the aculeate parasutural membranes and it does not possess an apical boss.

Distribution. Widespread in the central North Atlantic and also present in the Mediterranean with an isolated occurrence in the Norwegian Sea. As with *I. aculeatum* its pattern of distribution is oceanic. This species is also rarely seen in British offshore Quaternary deposits.

22 *Impagidinium patulum* (Wall) Stover and Evitt 1978

Text-fig. 23; Plate 46, figs. 6, 7

Taxonomic Comments. The cyst species *I. patulum* is yet another species that is attributable to the *G. spinifera* group. It is, however, characterized by its size and paratabulation particularly in the parasutural area.

Distribution. This species of *Impagidinium* is a little more restricted in its distribution than the previously described forms. It is present in the west-central part of the Atlantic off the eastern seaboard of the United States, off the north-west coast of Africa and in the Mediterranean Sea. It also occurs in isolated areas in the Norwegian Sea and in a strip slightly to the south and parallel to the 50 °N. latitude line and in the southern part of the North Atlantic. Its major area of concentration is in the west-central part of the Atlantic. In spite of a more restricted occurrence it is still oceanic in aspect. It is rarely seen in Quaternary offshore sequences around the British Isles.

EXPLANATION OF PLATE 46

All photomicrographs were taken by Nomarski interference contrast and are illustrated at a magnification of × 500.

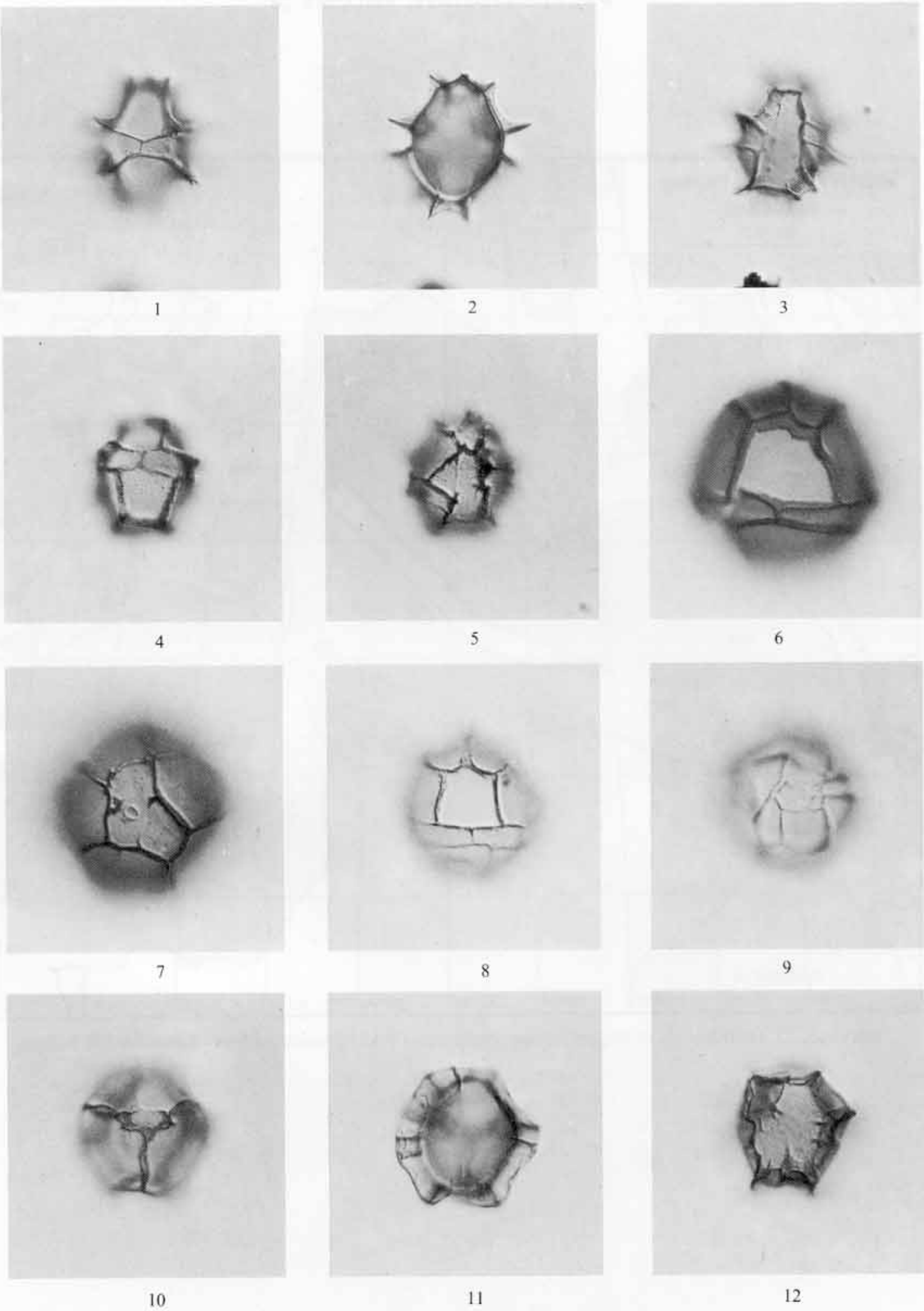
Figs. 1–3. *Impagidinium aculeatum* (Wall) comb. nov., Specimen MPK 3118. 1, dorsal view showing P archeopyle. 2, median view showing characteristic parasutural membranes and gonal processes. 3, ventral view showing broad sulcal area.

Figs. 4, 5. *I. paradoxum* (Wall) Stover and Evitt, Specimen MPK 3119. 4, dorsal view showing P archeopyle. 5, ventral view showing sulcus together with the triangular 6″ paraplate and small elongate 1″ paraplate.

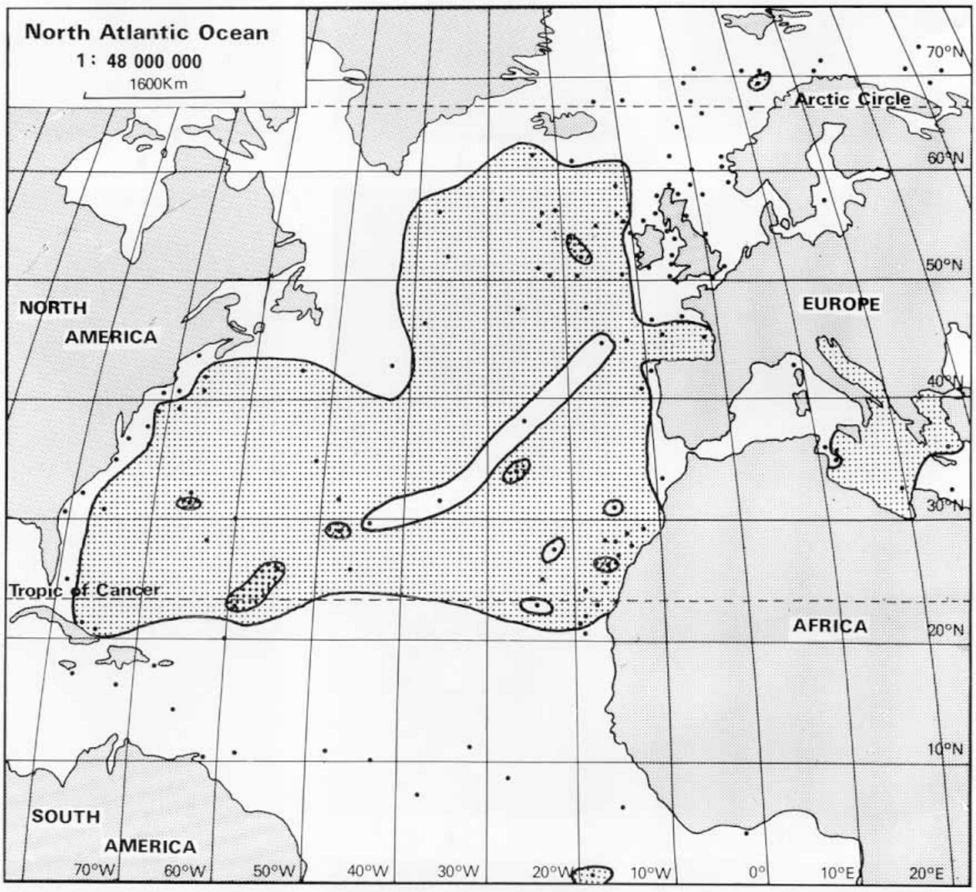
Figs. 6, 7. *I. patulum* (Wall) Stover and Evitt, Specimen MPK 3120. 6, dorsal view showing P archeopyle and apical paraplates 2′ and 3′. 7, ventral view showing antapical part of sulcus with the posterior intercalary paraplate and posterior and median sulcal paraplates.

Figs. 8, 9. *I. sphaericum* (Wall) comb. nov., Specimen MPK 3121. 8, dorsal view showing the P archeopyle and apical paraplates 2′ and 3′. 9, ventral view showing the antapical part of the sulcus with the posterior intercalary paraplate and the posterior, right, left and right accessory sulcal paraplates.

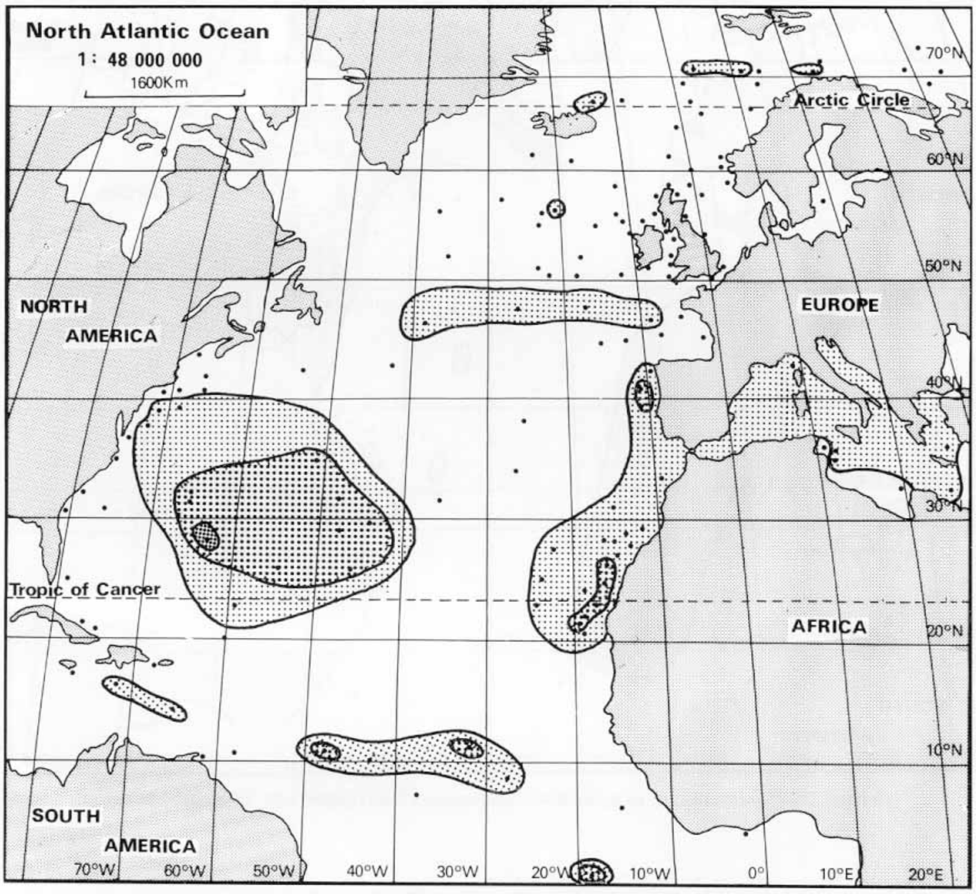
Figs. 10–12. *I. strialatum* (Wall) Stover and Evitt, Specimen MPK 3122. 10, dorsal view showing the P archeopyle. 11, median view showing the parasutural membranes. 12, ventral view.



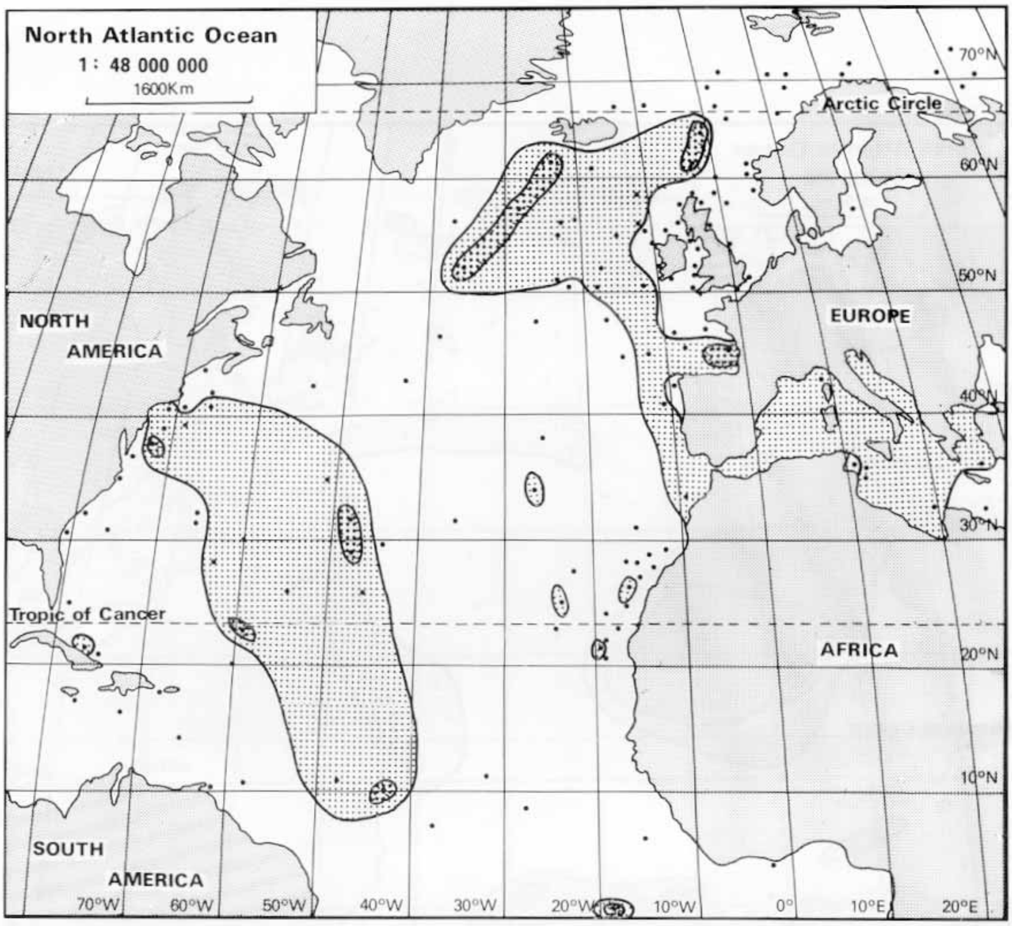
HARLAND, Recent dinoflagellates



TEXT-FIG. 22. Distribution of *Impagidinium paradoxum* (Wall) Stover and Evitt. Ornament as before.



TEXT-FIG. 23. Distribution of *Impagidinium patulum* (Wall) Stover and Evitt. Ornament as before.



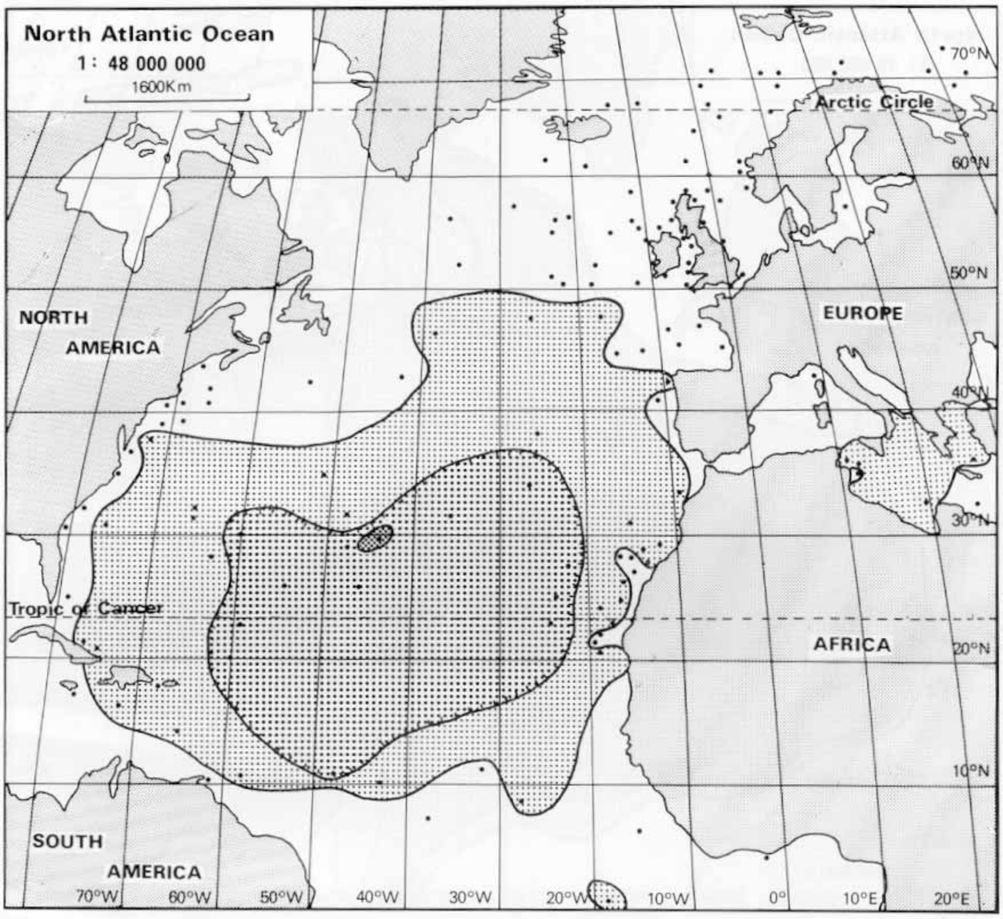
TEXT-FIG. 24. Distribution of *Impagidinium sphaericum* (Wall) comb. nov. Ornament as before.

23 *Impagidinium sphaericum* (Wall) comb. nov.

Text-fig. 24; Plate 46, figs. 8, 9

Taxonomic Comments. As with *I. aculeatum*, Stover and Evitt (1978) failed to transfer *L. sphaericum* Wall into the genus *Impagidinium*. It is therefore done here: *I. sphaericum* (Wall) comb. nov. = *Leptodinium sphaericum* Wall 1967, pp. 108, pl. 15, figs. 11–15, text-figs. 2A–C. This cyst form is also regarded as belonging to the *G. spinifera* group. It is characterized by its size, paratabulation details and apical boss.

Distribution. Its distribution, like that of *I. patulum*, centres off the eastern seaboard of the United States and north-west South America, also the Mediterranean and off the west coast of the British Isles and Iberian peninsula. There are some isolated occurrences off the north-west coast of Africa. This cyst, nevertheless, reveals an oceanic aspect in its distribution. It is very rarely seen in offshore Quaternary sequences in the British Isles area.



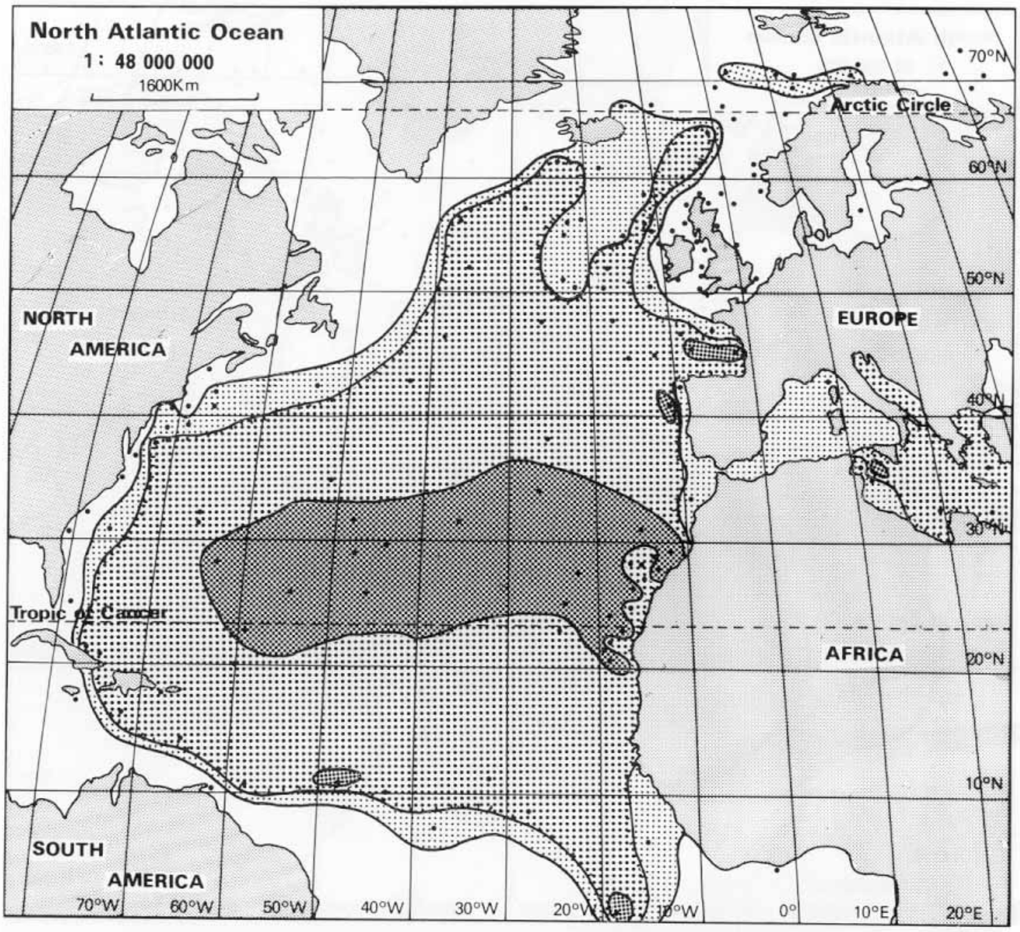
TEXT-FIG. 25. Distribution of *Impagidinium strialatum* (Wall) Stover and Evitt. Ornament as before.

24 *Impagidinium strialatum* (Wall) Stover and Evitt 1978

Text-fig. 25; Plate 46, figs. 10–12

Taxonomic Comments. Another cyst type related to the *G. spinifera* group. It is characterized by high parasutural membranes that are often striated, together with a distinctive parasulcal tabulation.

Distribution. It is distributed in the central North Atlantic but also in the Mediterranean with one isolated occurrence at the equator. This pattern is obviously oceanic, and the cyst is rarely seen in offshore Quaternary sequences around the British Isles.

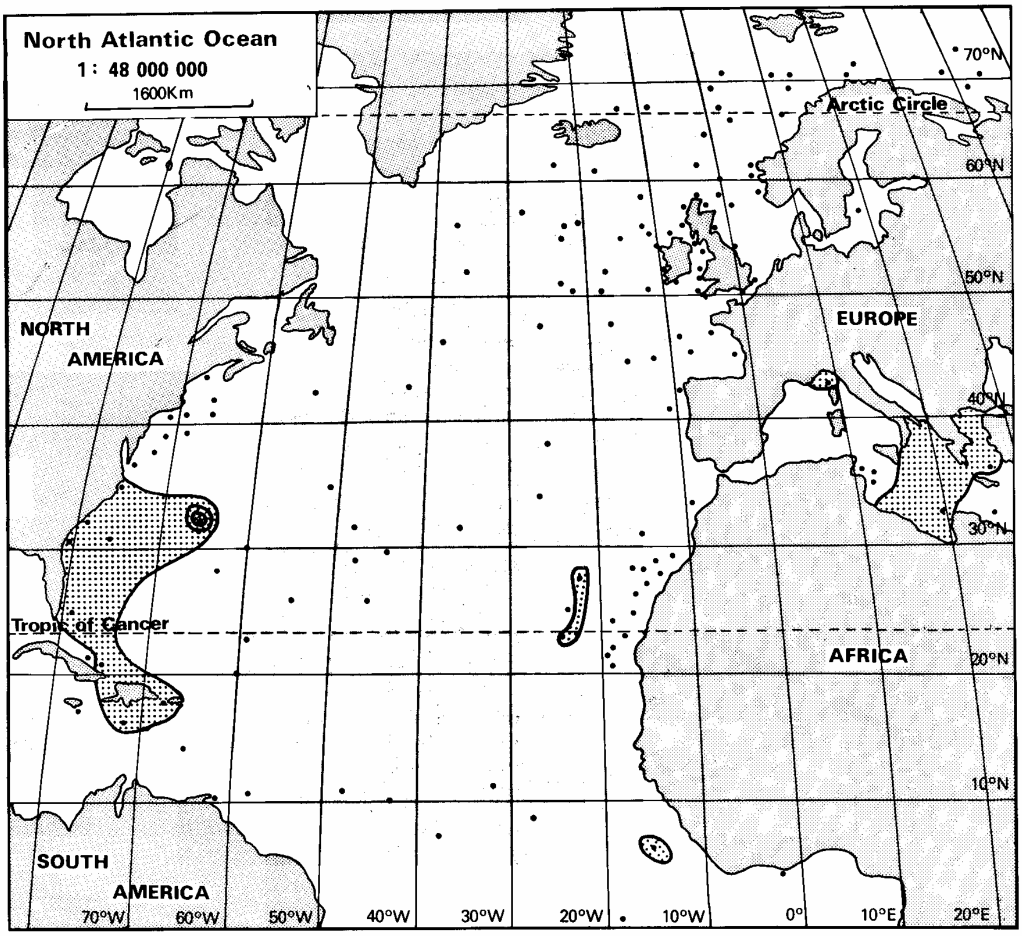


TEXT-FIG. 26. Distribution of total *Impagidinium* species. Ornament as before.

25 Total *Impagidinium* spp.

Text-fig. 26

General Comments. The total distribution pattern for *Impagidinium* species clearly shows a widespread North Atlantic distribution centred on the oceanic realm.



TEXT-FIG. 27. Distribution of *Polysphaeridium zoharyi* (Rossignol) Bujak *et al.* Ornament as before.

26 *Polysphaeridium zoharyi* (Rossignol) Bujak *et al.* 1980

Text-fig. 27; Plate 45, fig. 10

Taxonomic Comments. This morphospecies is the cyst of *Pyrodinium bahamense* Plate and is characterized by its large size and particularly its epicystal archeopyle. It is also better known as *Hemicystodinium zoharyi* (Rossignol) Wall but since the type species of *Polysphaeridium* has recently been discovered to have an epicystal archeopyle the genus *Hemicystodinium* Wall 1967 becomes a junior synonym of *Polysphaeridium*. Bujak *et al.* (1980) formally transferred *zoharyi* to *Polysphaeridium*.

Distribution. The occurrence of *P. zoharyi* appears restricted to the Caribbean, Bermuda and south-eastern seaboard of the United States, and to the Mediterranean with a couple of isolated occurrences off north-west Africa. A centre of concentration occurs at Bermuda. Its distribution points to a tropical-sub-tropical environmental preference. It has not been seen in marine offshore Quaternary deposits from the area of the British Isles. Occasional mentions in the literature from this area are without doubt the misidentification of *O. centrocarpum* (e.g. Harland 1968, Downie and Singh 1969).

Pyrophacacean Cysts

27 *Tuberculodinium vancampoae* (Rossignol) Wall 1967

Text-fig. 28; Plate 45, fig. 11

Taxonomic Comments. This large and distinctive species with an antapical archeopyle is the cyst of *Pyrophacus* Form B1 of Steidinger and Davis (1967).

Distribution. Restricted to the south-eastern seaboard of the United States, the Mediterranean and isolated occurrences including the west-central coast of Africa. As with *P. zoharyi* its restricted distribution pattern indicates a tropical-sub-tropical preference. It has not been seen in offshore Quaternary sediments in the British Isles area.

Peridiniacean Cysts

Following the recent review by Harland (1982), the names used in this section are those using the combined thecate and cyst taxonomies. Appendix I lists both the cyst names and the thecate names. No new cyst names are therefore proposed as the various species are all adequately covered by the combined approach of Harland (1982). Williams (1965, 1971) failed to distinguish the various species of *Protoperidinium* hence the record from his data may be somewhat incomplete.

28 *Protoperidinium* (*Protoperidinium* sect. *Asymmetropedinium*) *punctulatum* (Paulsen) Balech 1974

Plate 47, fig. 1

Taxonomic Comments. This spherical brown cyst of *P. punctulatum* is characterized by its asymmetrical archeopyle. However unless orientated advantageously it can be confused with other brown spherical *Protoperidinium* cysts. It has no palaeontological name but would be regarded as a new species of *Brigantedinium*.

Distribution. This species has not been unequivocally recognized in bottom sediments from the North Atlantic, hence the failure to publish a distribution map, but Wall and Dale (1968*b*) recorded these cysts from Woods Hole, U.S.A. It is, however, more than likely to have been included in counts of both *P. avellana* and total *Protoperidinium* spp.

EXPLANATION OF PLATE 47

All photomicrographs were taken by Nomarski interference contrast and are illustrated at a magnification of × 500.

Fig. 1. *Protoperidinium* (*Protoperidinium* sect. *Asymmetropedinium*) *punctulatum* (Paulsen) Balech, Specimen MPK 2953, showing the asymmetrical operculum.

Figs. 2, 3. *P.* (*Protoperidinium* sect. *Brigantedinium*) *conicoides* (Paulsen) Balech, Specimen MPK 1232. 1, dorsal view showing the archeopyle. 2, ventral view showing flagellar scars.

Fig. 4. *P.* (*Archaeperidinium* sect. *Fuscusasphaeridium*) *avellana* (Meunier) Balech, Specimen MPK 1236, showing symmetrical operculum in place at the archeopyle.

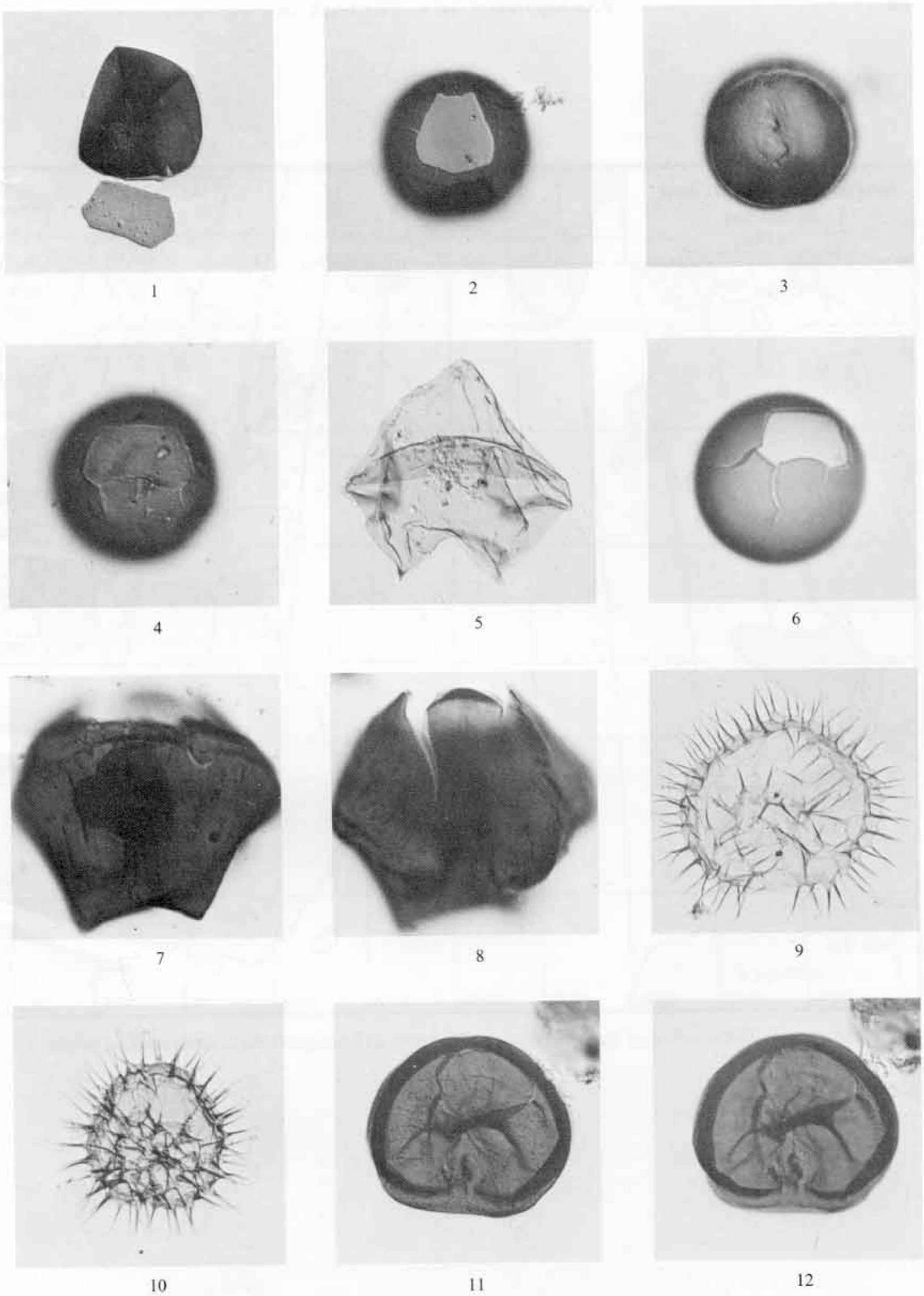
Fig. 5. *Protoperidinium* sp. indet., *Lejeunia paratenella* Benedek, Specimen MPK 1247, dorsal view showing attenuated hexa archeopyle with operculum in place.

Fig. 6. *P.* (*Archaeperidinium* sect. *Fuscusasphaeridium*) *denticulatum* (Gran and Braarud) Balech, photograph kindly supplied by D. Wall. Oblique dorsal view photographed in plain light.

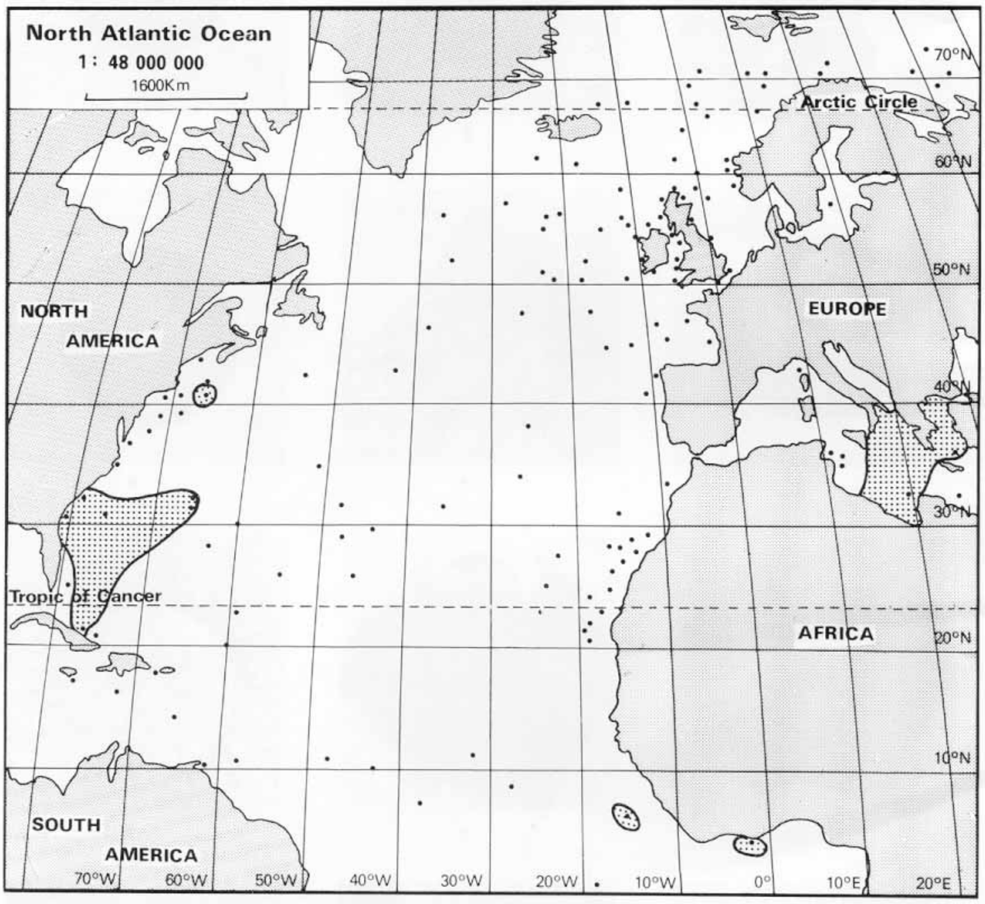
Figs. 7, 8. *P.* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech, Specimen MPK 1230. 7, dorsal view showing the archeopyle and operculum. 8, ventral view showing the deeply indented parasulcus.

Figs. 9, 10. *P.* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech. 9, Specimen MPK 2772. 10, Specimen MPK 2949. The two specimens show some of the range of variation in size.

Figs. 11, 12. *P.* (*Protoperidinium* sect. *Selenopemphix*) *subinerme* (Paulsen) Loeblich III, Specimen MPK 3151. 11, apical view showing offset archeopyle with the operculum in place. 12, antapical view.



HARLAND, Recent dinoflagellates



TEXT-FIG. 28. Distribution of *Tuberculodinium vancampoae* (Rossignol) Wall. Ornament as before.

29 *Protoperidinium* (*Protoperidinium* sect. *Brigantedinium*) *conicoides* (Paulsen) Balech 1974

Text-fig. 29; Plate 47, figs. 2, 3

Taxonomic Comments. This is another brown spherical cyst but with a distinctive large intercalary archeopyle that may or may not be composed of one or two intercalary paraplates. It has been described under the palaeontological name of *B. simplex* (Wall) Reid.

Distribution. Only seen in nearshore sediments around parts of the British Isles particularly in the Irish Sea, Sea of the Hebrides, and Forth Approaches, although Wall and Dale (1968*b*) recorded it at Woods Hole, U.S.A., and Dale (1976) from Trondheimsfjord, Norway. The distribution is undoubtedly affected by identification difficulties if poorly orientated specimens are recovered. Some occurrences will have been included in the total *Protoperidinium* count.

30 *Protoperidinium* (*Archaeperidinium* sect. *Fuscusasphaeridium*) *avellana* (Meunier) Balech 1974

Plate 47, fig. 4

Taxonomic Comments. Yet another brown spheroidal cyst with a distinctive archeopyle which is laterally elongate but symmetrical. It has been described with the palaeontological name of *B. cariacoense* (Wall) Reid.

Distribution. Only recorded in bottom sediments in the Forth Approaches, sample number 29, but also seen by Wall and Dale (1968*b*) in the Woods Hole region and as a cf. by Dale (1976) in Trondheimsfjord, Norway. Again difficulties in identification of badly preserved or poorly orientated material may well have biased the record and many occurrences will have been included in the total *Protoperidinium* count.

31 *Protoperidinium* (*Archaeperidinium* sect. *Fuscusasphaeridium*) *denticulatum* (Gran and Braarud) Balech 1974

Plate 47, fig. 6

Taxonomic Comments. This cyst, another spheroidal brown species, is uniquely characterized by its laterally elongate symmetrical archeopyle (see Harland 1982, text-fig. 7). In palaeontological taxonomy it would perhaps be regarded as a new species of *Brigantedinium*. The photograph kindly supplied by D. Wall depicts a form more closely similar to *P. avellana* in terms of archeopyle than the drawing (Plate 3, fig. 30) published in Wall and Dale (1968*b*). Difficulties in positively identifying this cyst are immediately apparent.

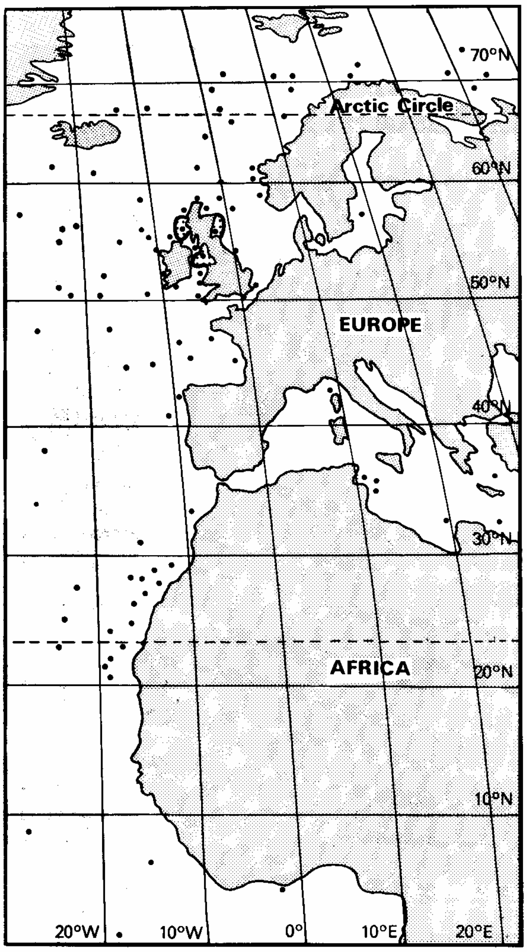
Distribution. Recorded from only one bottom sample, number 46, in the present study in the Irish Sea but Wall and Dale (1968*b*) have recorded it from the Woods Hole region, U.S.A. and Dale (1976) from Trondheimsfjord, Norway although both query the specific identification. Difficulties in identification suggest that this cyst may have been more commonly included in the total *Protoperidinium* counts.

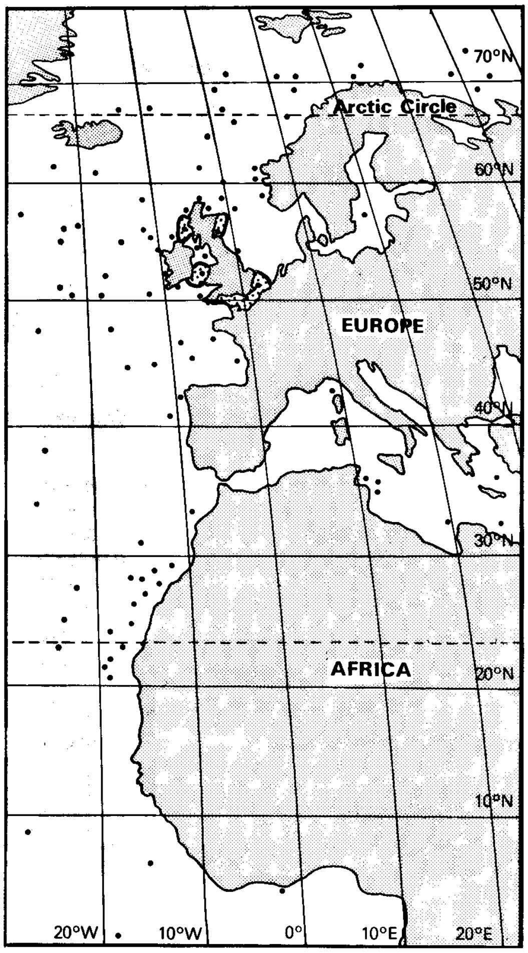
32 *Protoperidinium* sp. indet.

Text-fig. 30; Plate 47, fig. 5.

Taxonomic Comments. This cyst, undoubtedly of *Protoperidinium* affinity, is better known by its palaeontological species name *Lejeunia paratenella* Benedek. It is hoped that in the future living specimens of this species might be incubated to determine its specific affinity.

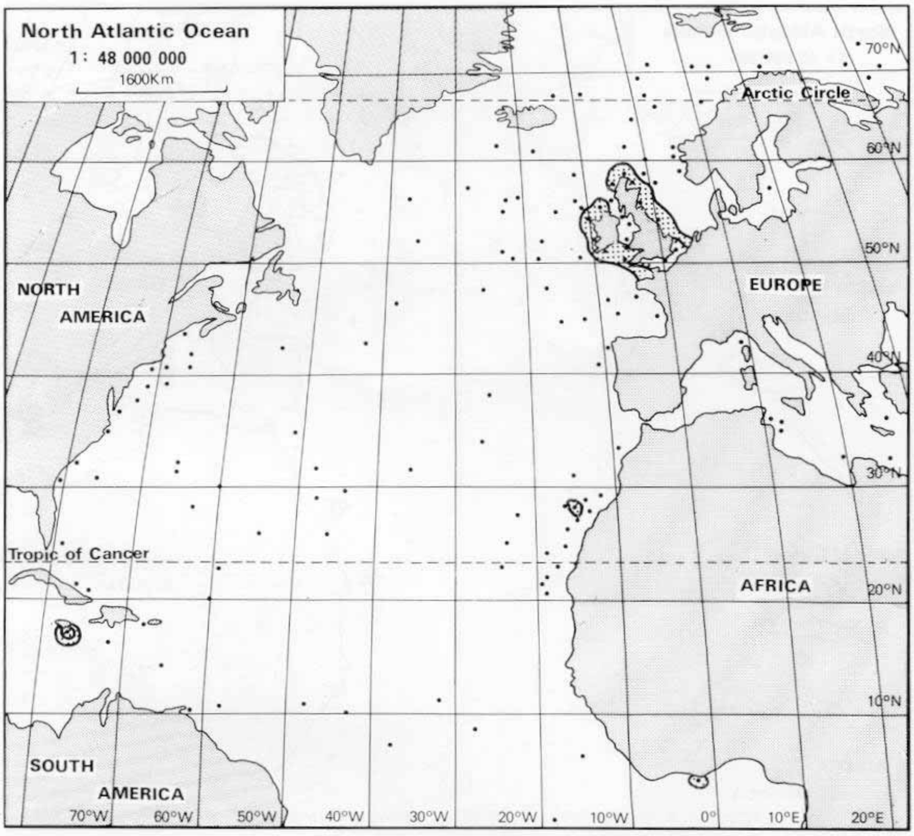
Distribution. Seen in nearshore sediments around the British Isles particularly in the Sea of the Hebrides, Cardigan Bay, English Channel, and Forth Approaches. It is thought to be indigenous to the assemblages although it and several related species occur in Tertiary marine sediments. It is on occasions prolific in certain assemblages e.g. Quaternary sequences in the Firth of Clyde (Harland 1973).





TEXT-FIG. 29 (*left*). Distribution of *Protoperidinium* (*Protoperidinium* sect. *Brigantedinium*) *conicoides* (Paulsen) Balech. Ornament as before.

TEXT-FIG. 30 (*right*). Distribution of *Protoperidinium* sp. indet. (*Lejeunia paratenella* Benedek). Ornament as before.



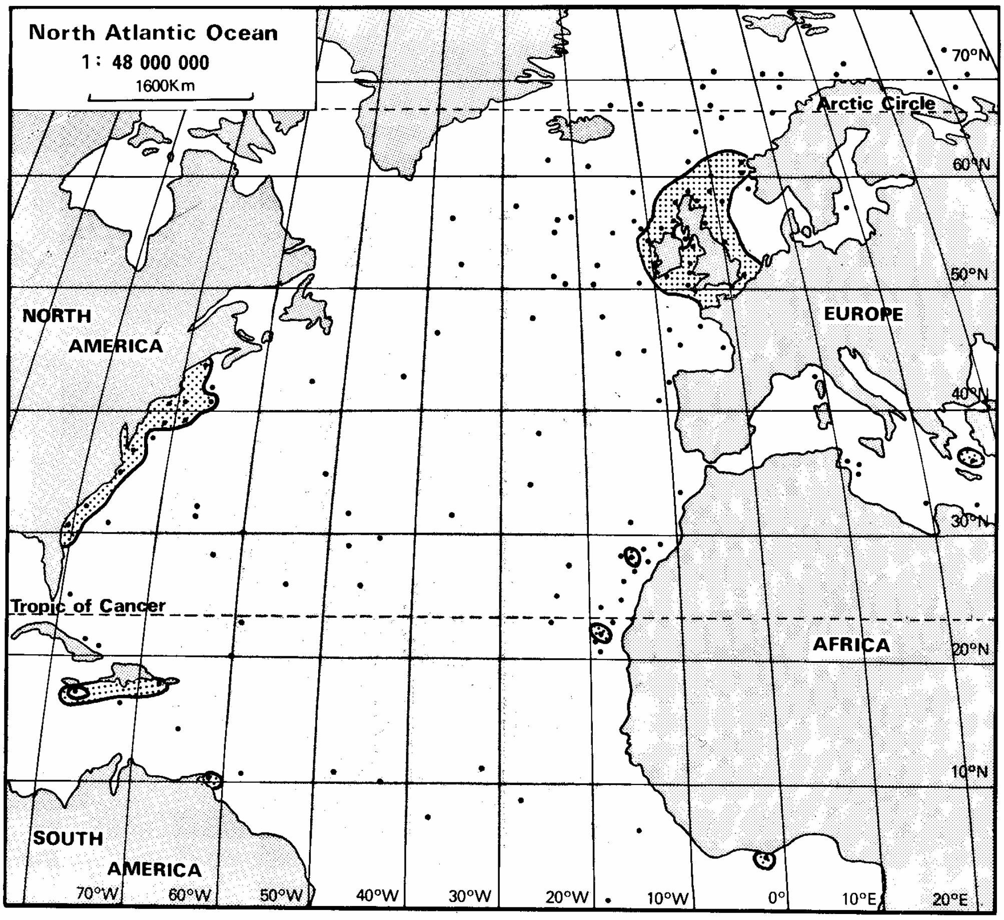
TEXT-FIG. 31. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech. Ornament as before.

33 *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech 1974

Text-fig. 31; Plate 47, figs. 7, 8

Taxonomic Comments. This brown peridinioid cyst has also been described under the palaeontological names *Trinovantedinium concretum* Reid and *Quinquecuspis concretum* (Reid) Harland. It is the cyst of *P. leonis* but there are some complications in the recognition of various 'species' having much the same morphology as this species (Harland 1982). Recognition of bona fide species within this group may lead to further precision in the understanding of the distribution of this and the other related species. Species not positively identified as *P. leonis* are included in the total *Protoperidinium* count.

Distribution. Restricted to the coastal areas around the British Isles and to some isolated occurrences in the Caribbean and off the west coast of Africa. This species has also been recorded by Wall and Dale (1968*b*) in the Woods Hole region of the U.S.A. It occasionally occurs in offshore marine Quaternary sequences.



TEXT-FIG. 32. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech. Ornament as before.

34 *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *conicum* (Gran) Balech 1974

Text-fig. 32; Plate 47, figs. 9, 10

Taxonomic Comments. This characteristic and well-known species is typically apically/antapically compressed, spinose and possesses an offset intercalary archeopyle. Variation in size has been noted (Bradford 1975) and this is illustrated in the photomicrographs presented here. In palaeontological literature it has been referred to as *Multispinula quanta* Bradford.

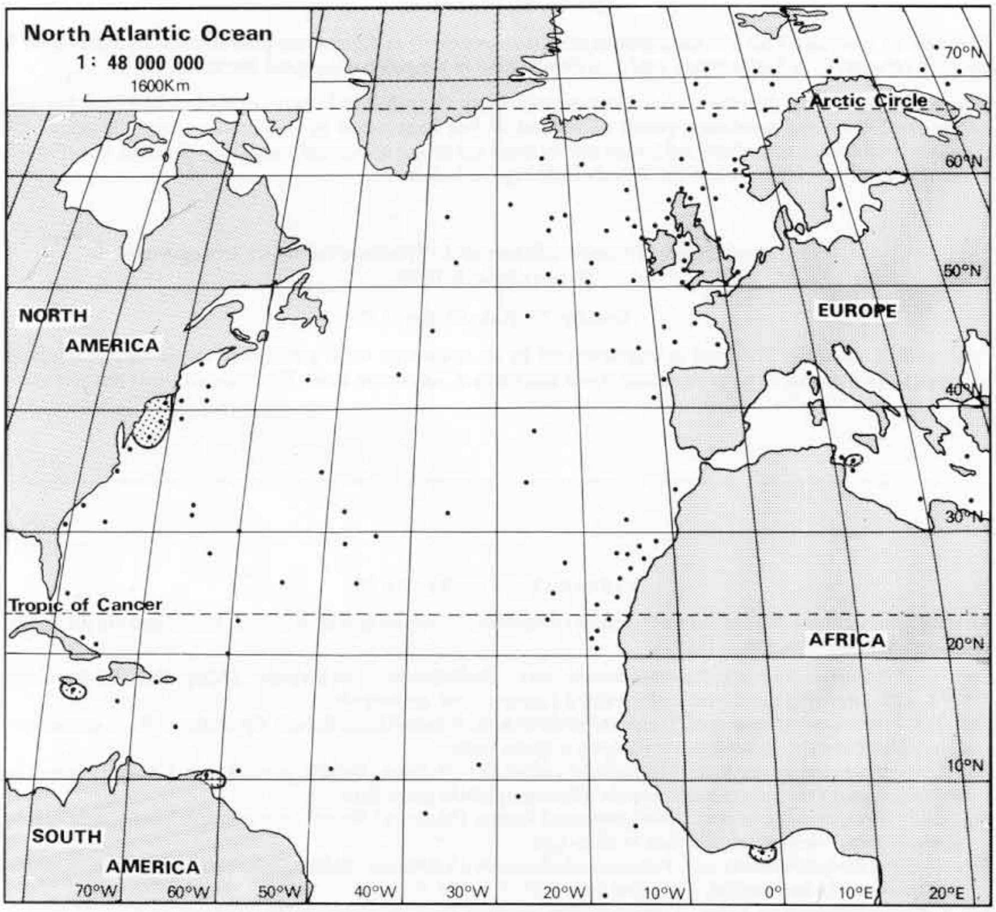
Distribution. Restricted to the coastal sediments around the British Isles and along the eastern seaboard of the United States. There appear to be some isolated occurrences in the Caribbean, off the north-east coast of South America, the Mediterranean, and off the west coast of Africa. This cyst is well known in Quaternary sequences from the offshore region of the British Isles, and may have the potential of identifying specific environmental conditions.

35 *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *nudum* (Meunier) Balech 1974

Plate 48, fig. 5

Taxonomic Comments. This cyst form is very similar to that of *P. conicum* but is smaller, and carries relatively longer spines. Some reservation is expressed in the assignation of these cysts (Wall and Dale 1968*b*) to the parental theca. In the present study difficulty was experienced in positively identifying this species given the intraspecific variability of *P. conicum* and the presence of other similar cysts such as *M. minuta* Harland and Reid and Cyst B of Harland (1977). Further work is clearly desirable on this group of species.

Distribution. Isolated occurrences in the North Sea, sample 53, and Barents Sea, sample 31, but has also been recorded by Wall and Dale (1968*b*) from the eastern seaboard of the United States. Other occurrences may be included, because of taxonomic and identification difficulties, in the maps for Cyst B of Harland (1977) or in the total *Protoperidinium* counts.



TEXT-FIG. 33. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *subinerme* (Paulsen) Loeblich III. Ornament as before.

36 *Protoperidinium* (*Protoperidinium* sect. *Selenopemphix*) *subinerme* (Paulsen) Loeblich III

Text-fig. 33; Plate 47, figs. 11, 12

Taxonomic Comments. An apically/antapically compressed cyst with an offset archeopyle but no spines. It has been described in the palaeontological literature as *Selenopemphix nephroides* Benedek.

Distribution. Isolated occurrences off the eastern seaboard of the United States, the Caribbean, the Mediterranean and off the west coast of Africa. It can be an important species in some Quaternary sequences especially in the Biscay area (work in preparation).

37 *Protoperidinium* (*Archaeperidinium* sect. *Stelladinium*) *compressum* (Abé) Balech 1974

Text-fig. 34; Plate 48, fig. 1

Taxonomic Comments. This cyst has a unique stellate morphology and a two paraplate intercalary archeopyle. It has been referred to as *Stelladinium stellatum* (Wall) Reid in the palaeontological literature.

Distribution. Restricted distribution in nearshore sediments of the British Isles particularly to the Irish Sea, and off the north-west and south-east coasts of Ireland. It has been noted in Quaternary sequences across the Pleistocene/Holocene boundary and it may signify some particular ecological condition. Wall and Dale (1968*b*) found it in local plankton around the Woods Hole region, U.S.A.

38 *Protoperidinium* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum* (Gran) Balech 1974

Text-fig. 35; Plate 48, figs. 2, 3

Taxonomic Comments. This cyst is characterized by its colourless wall, peridinioid shape and broad hexa archeopyle. In palaeontological literature it was known as *T. capitatum* Reid. The assignation of the cyst to the

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EXPLANATION OF PLATE 48

All photomicrographs were taken by Nomarski interference contrast unless otherwise stated and are illustrated at a magnification of × 500.

Fig. 1. ***Protoperidinium* (*Archaeoperidinium* sect. *Stelladinium*) *compressum*** (Abé) Balech, Specimen MPK 1256, showing the dorsal surface and 2 I symmetrical archeopyle.

Figs. 2, 3. ***P.* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum*** (Gran) Balech, Specimen 1240. 2, dorsal view showing archeopyle. 3, median view showing apical boss.

Fig. 4. ***P.* (*Protoperidinium* sect. *Votadinium*) *claudicans*** (Paulsen) Balech, photograph kindly supplied by D. Wall, dorsal view showing archeopyle. Photographed in plain light.

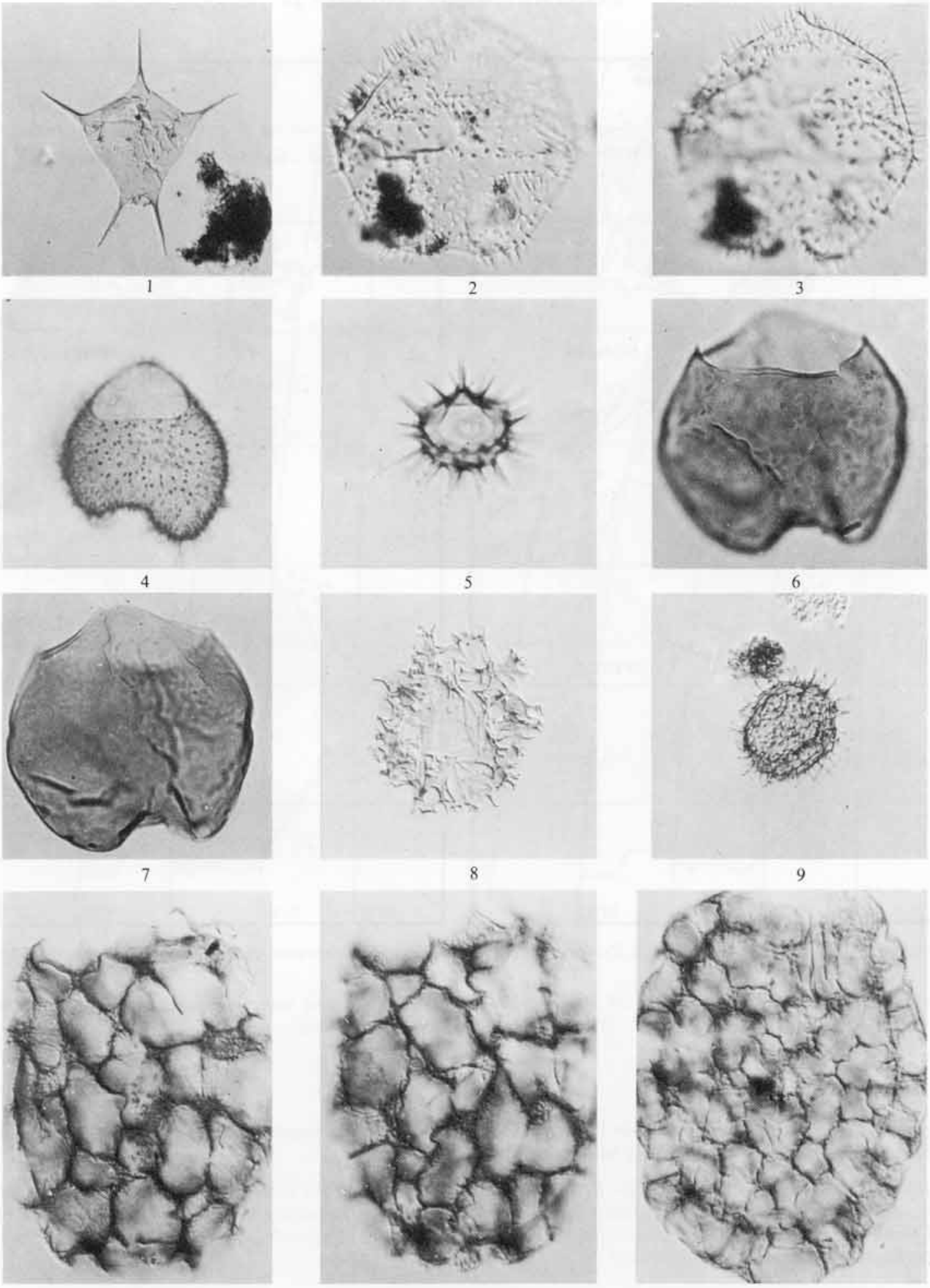
Fig. 5. ***P.* (*Protoperidinium* sect. *Selenopemphix*) *nudum*** (Meunier) Balech, photograph kindly supplied by D. Wall, dorsal view. Photographed in plain light.

Figs. 6, 7. ***P.* (*Protoperidinium* sect. *Votadinium*) *oblongum*** (Aurivillius) Balech, Specimen MPK 2778. 6, dorsal view showing the archeopyle. 7, ventral view.

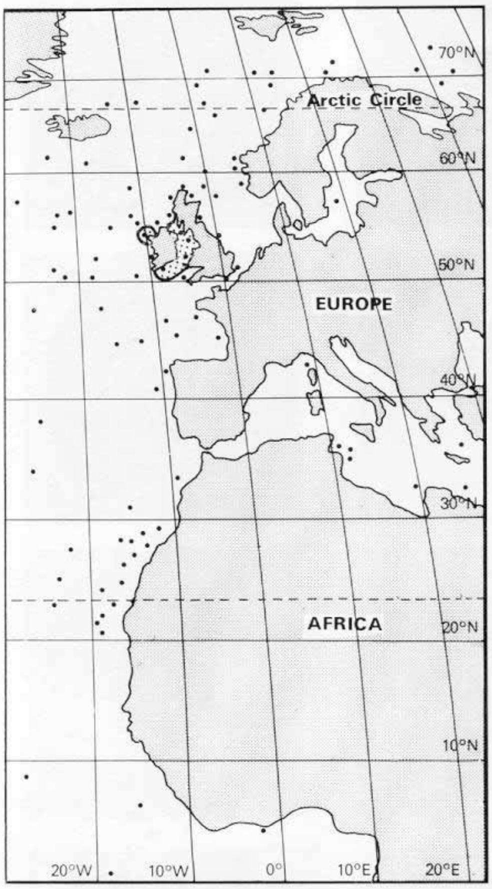
Fig. 8. ***Protoperidinium*** sp. indet., ***Xandarodinium xanthum*** Reid, Specimen MPK 2773.

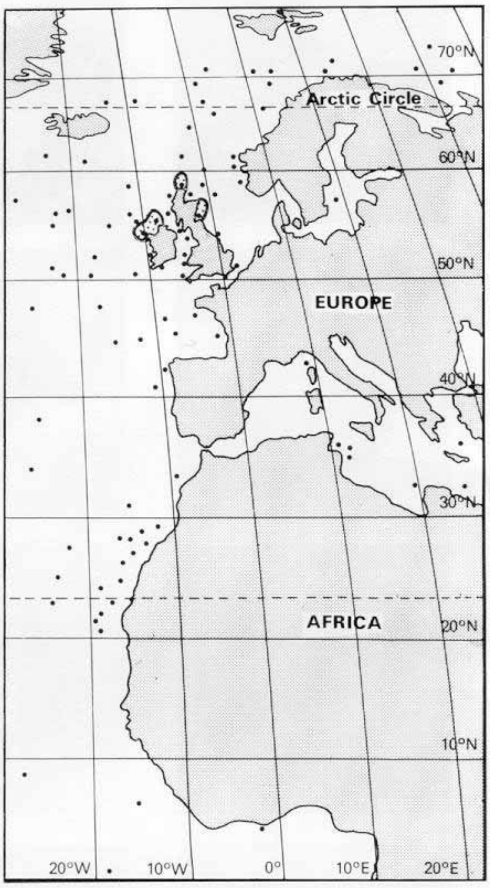
Fig. 9. ***Protoperidinium*** sp. indet., Cyst-type B of Harland (1977), Specimen MPK 1251.

Figs. 10–12. ***Polykrikos schwartzii*** Bütschli, Specimens MPK 2600 and 2605.



HARLAND, Recent dinoflagellates



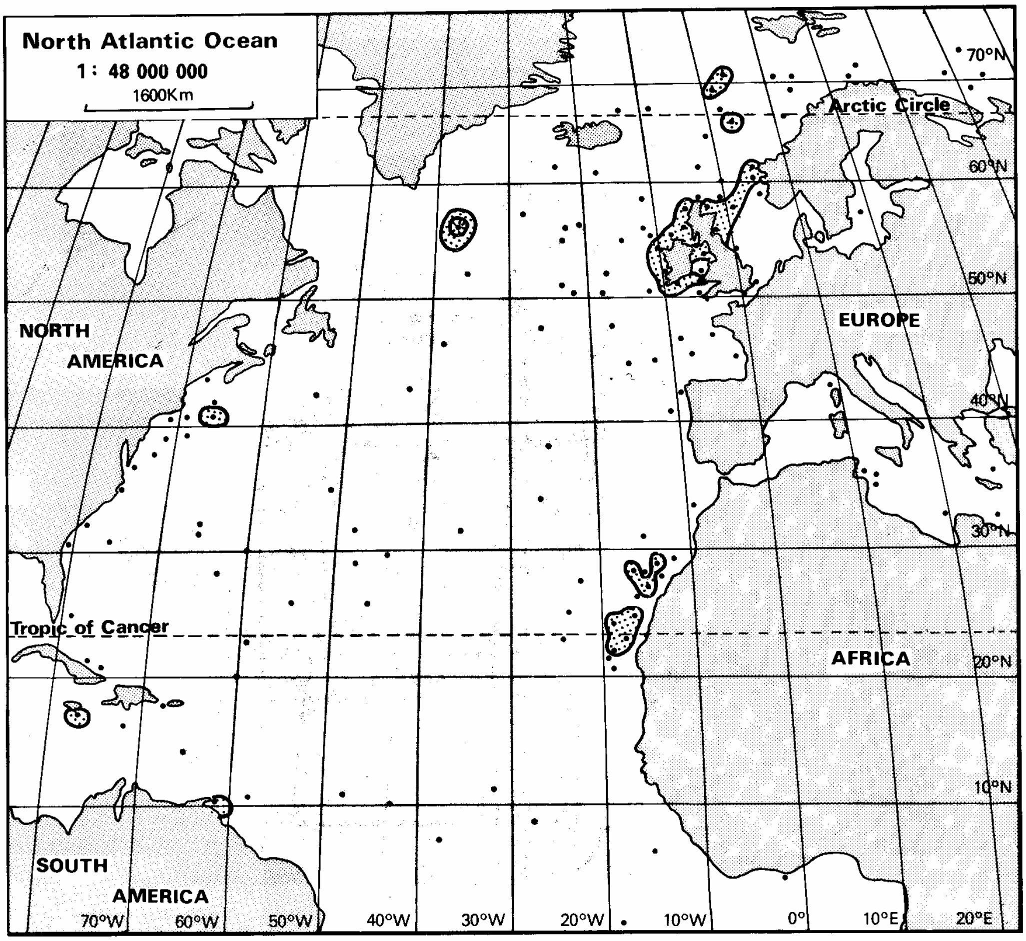


TEXT-FIG. 34 (*left*). Distribution of *Protoperidinium* (*Archaeoperidinium* sect. *Stelladinium*) *compressum* (Abé) Balech. Ornament as before.

TEXT-FIG. 35 (*right*). Distribution of *Protoperidinium* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum* (Gran.) Balech. Ornament as before.

parent theca is known (Wall and Dale 1968*b*), but similar cysts have produced thecae with minor differences such that several species or varieties may be involved.

Distribution. Around the coast of the British Isles, the North Sea, off the north-west coast of Africa and some isolated occurrences in the Norwegian Sea, Atlantic, off the eastern seaboard of the United States and the Caribbean. It is occasionally found in marine offshore Quaternary sequences. Its occurrence may have some particular environmental significance.



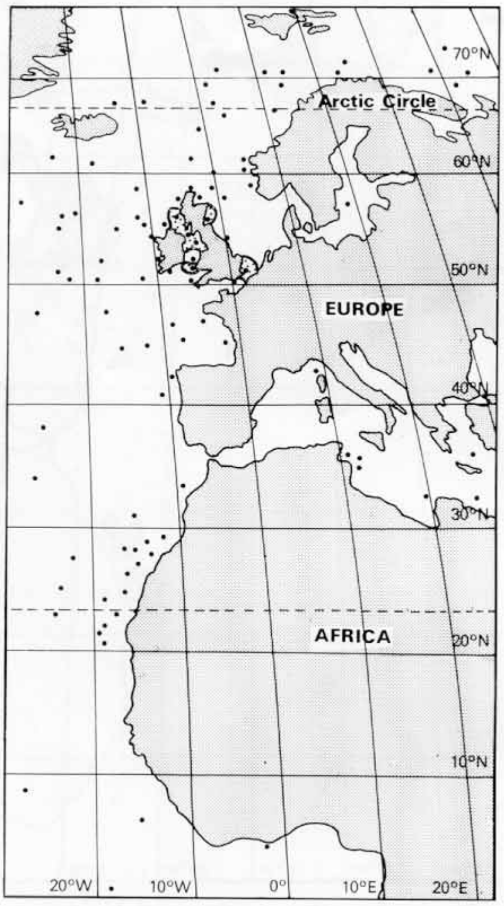
TEXT-FIG. 36. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *claudicans* (Paulsen) Balech. Ornament as before.

39 *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *claudicans* (Paulsen) Balech 1974

Text-fig. 36; Plate 48, fig. 4

Taxonomic Comments. This cyst is characterized by its chordate shape and archeopyle that truncates the apex. It has, in the past, been referred to as *Votadinium spinosum* Reid in palaeontological literature.

Distribution. Restricted to the nearshore sediments around the British Isles in particular off northern Scotland and Ireland and in the Forth Approaches. Wall and Dale (1968*b*) also recorded it from Bermuda and from local plankton in the Woods Hole region of the U.S.A. It is a cyst that I have never seen in offshore Quaternary sequences, and only rarely in Recent bottom sediments.



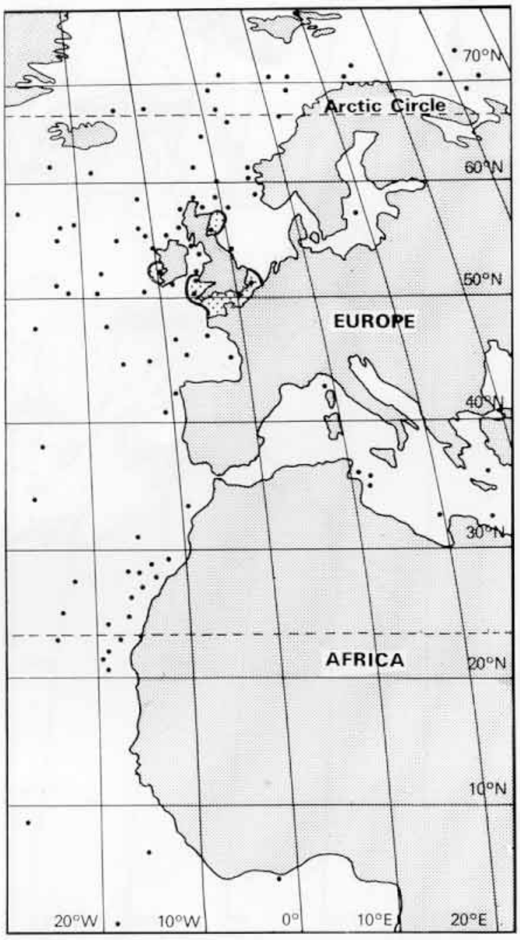
TEXT-FIG. 37. Distribution of *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *oblongum* (Aurivillius) Balech. Ornament as before.

40 *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *oblongum* (Aurivillius) Balech 1974

Text-fig. 37; Plate 48, figs. 6, 7

Taxonomic Comments. Like *P. claudicans* this cyst is characterized by its chordate shape and characteristic archeopyle but it is brown and does not possess spines. Reid (1977) referred to this cyst as *Votadinium calvum* Reid.

Distribution. Restricted to nearshore sediments around the British Isles particularly the Irish Sea, Sea of the Hebrides, Forth Approaches, and eastern English Channel. It has also been noted in the local plankton at Woods Hole, U.S.A. (Wall and Dale 1968*b*). It is very rarely seen in offshore Quaternary sequences.



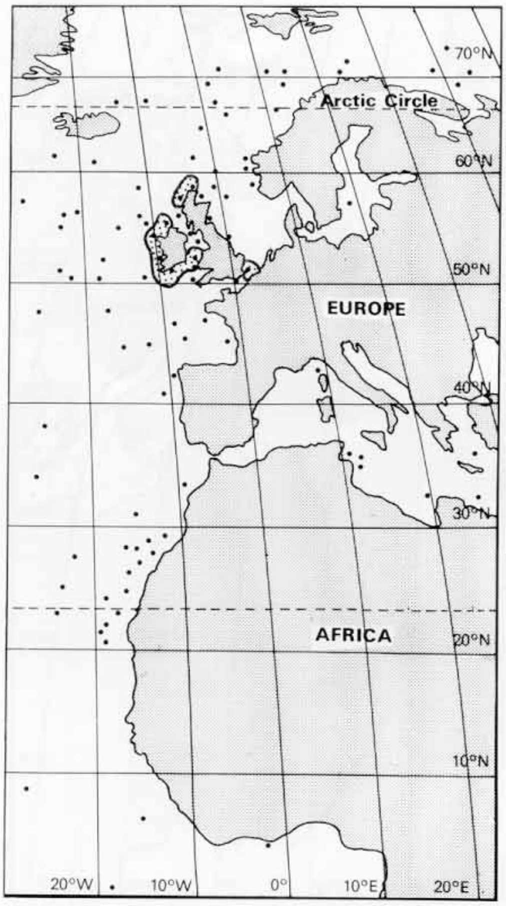
TEXT-FIG. 38. Distribution of *Protoperidinium* sp. indet. (*Xandarodinium xanthum* Reid). Ornament as before.

41 ?*Protoperidinium* sp. indet.

Text-fig. 38; Plate 48, fig. 8

Taxonomic Comments. This cyst, known as *Xandarodinium xanthum* Reid in palaeontological literature is thought to be a cyst of a *Protoperidinium* sp. but to date no incubation experiments have confirmed or denied this hypothesis. The cyst has a unique morphology with hollow processes carrying distal furcate and bifid solid tips and an often reniform ambitus suggestive of an apical/antapical compression. It is a cyst type in need of further study.

Distribution. Restricted to the southern and south-western coast of England, the Forth Approaches, and off the west coast of Ireland. It is extremely rare in offshore Quaternary sequences.



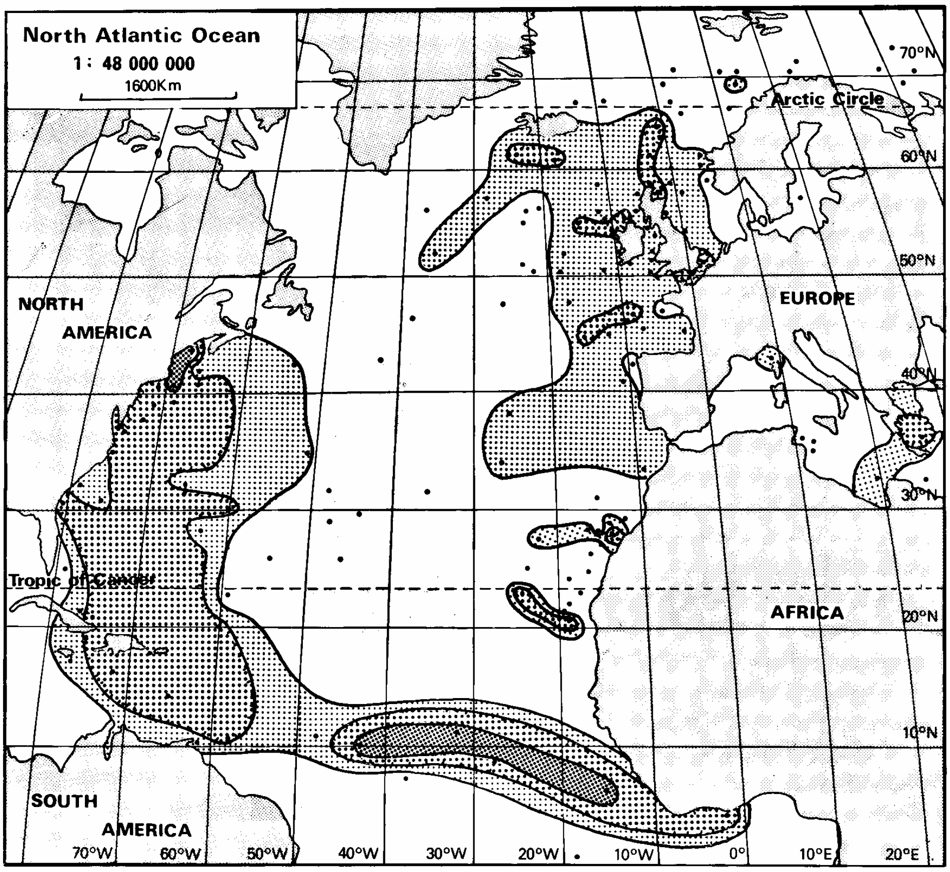
TEXT-FIG. 39. Distribution of ?*Protoperidinium* sp. indet. (Cyst type B of Harland 1977). Ornament as before.

42 Cyst-type B of Harland (1977)

Text-fig. 39; Plate 48, fig. 9

Taxonomic Comments. A spheroidal cyst that carries numerous processes up to ⅕th the cyst diameter in length. Each process has a number of small backward facing distal spinules. The affinities of this cyst are not known as no paratabulation or archeopyle have been observed. It is possibly a *Protoperidinium* cyst or a cyst of a gymnodinialean dinoflagellate.

Distribution. Restricted around the coast of the British Isles particularly off north-west Scotland, south and west coasts of Ireland, Cardigan Bay, and the eastern English Channel. It is rarely seen in offshore Quaternary sequences but may have been confused with *Multispinula minuta* Harland and Reid which differs in having aciculate processes.



TEXT-FIG. 40. Distribution of *Protoperidinium* spp. indet. Ornament as before.

43 *Protoperidinium* spp. indet.

Text-fig. 40

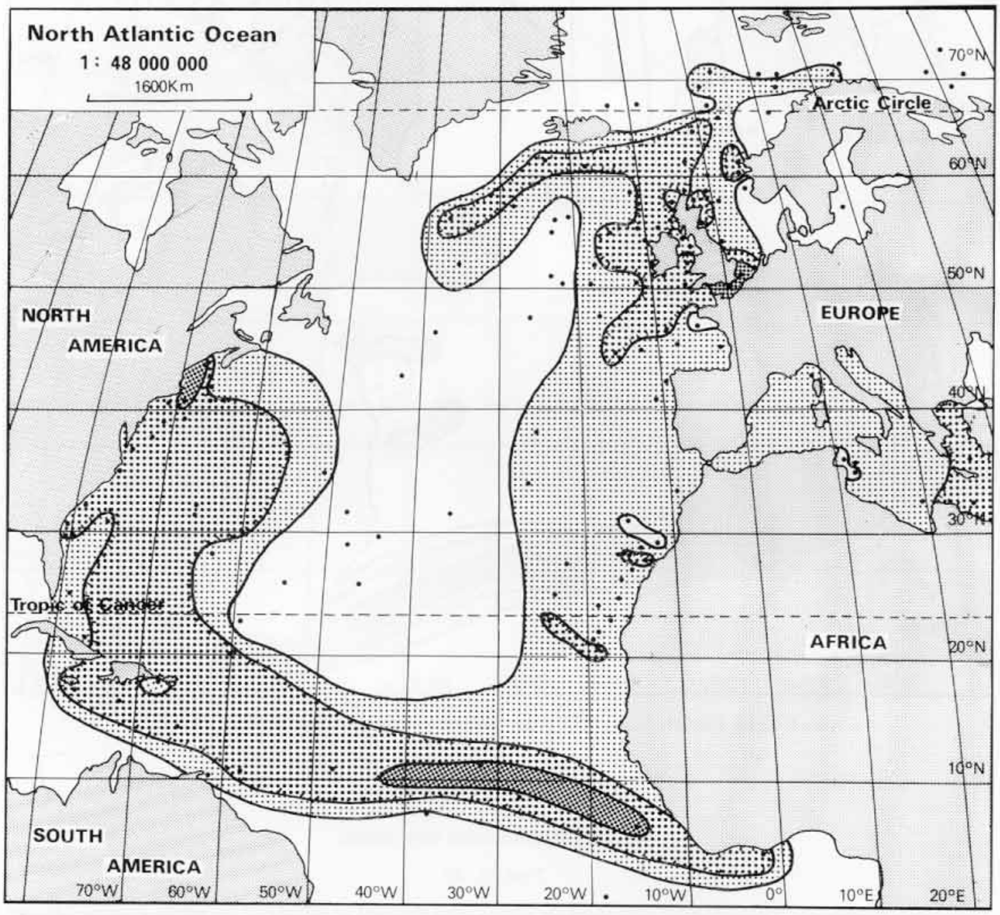
Taxonomic Comments. This category puts together all the cysts thought to belong to the genus *Protoperidinium*. A large proportion of these cysts consists of unidentified brown spheroidal forms not orientated to allow positive identification or badly preserved.

Distribution. Widespread in the north-eastern Atlantic around the British Isles and Iberian peninsula and also off the eastern seaboard of the United States, into the Caribbean and along latitude 10°N. to the west coast of Africa. Also present off the north-west coast of Africa and in the Mediterranean. Major areas of concentration occur off the eastern seaboard of the United States and along latitude 10°N. Unidentifiable *Protoperidinium* cysts are nearly always present in offshore marine Quaternary sequences.

44 Total *Protoperidinium* spp.

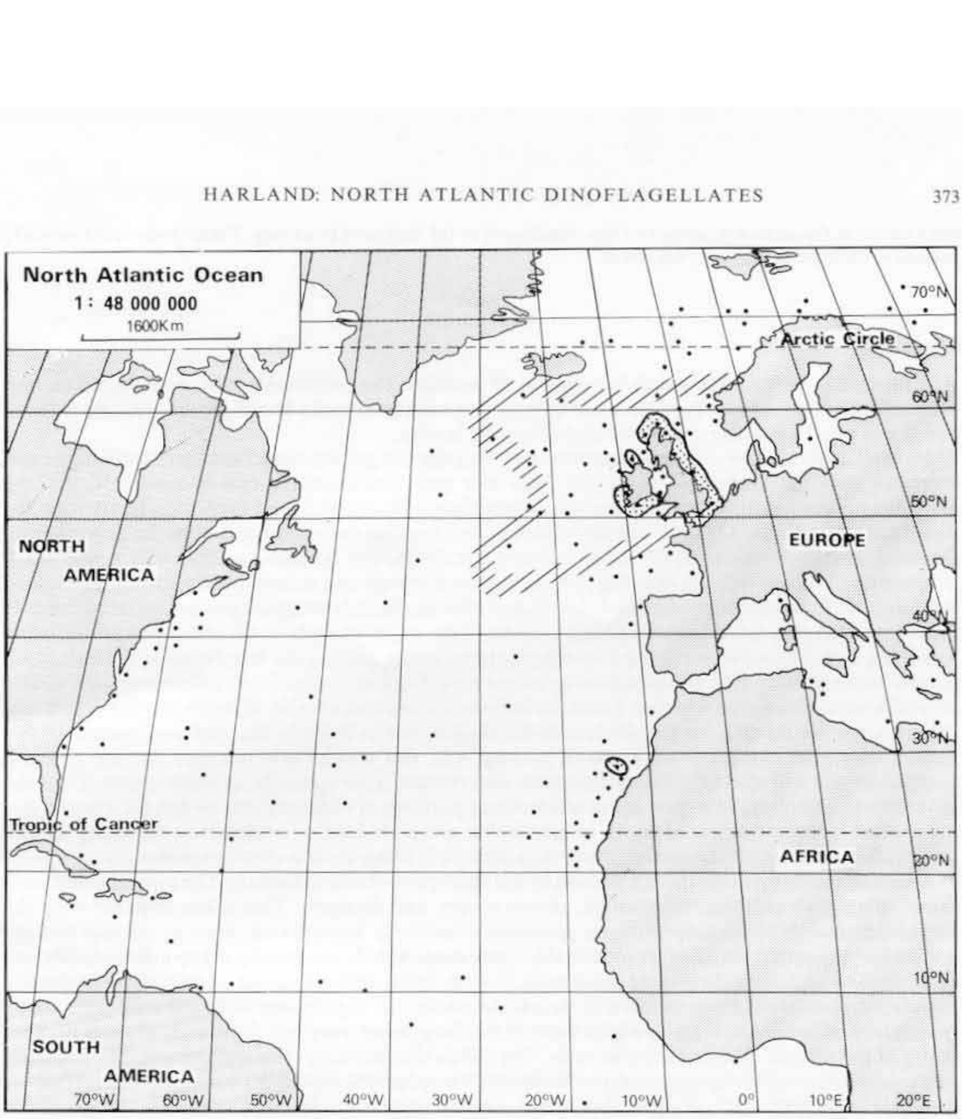
Text-fig. 41

General Comments. The distribution map for total *Protoperidinium* is extremely like that presented for the unidentified *Protoperidinium* cysts and in essence outlines the fact that much of the peridiniacean assemblage is not identified to specific level. The scope for future research in this area is therefore great and no doubt much



TEXT-FIG. 41. Distribution of the total *Protoperidinium* spp. Ornament as before.

more is to be learned from more precise identifications of peridiniacean material. Areas of major concentrations of *Protoperidinium* cysts are close to the Bay of Fundy area off the eastern seaboard of North America, along 10°N. latitude between longitude 40°W. and 15°W. and also in the English Channel. *Protoperidinium* cysts are often seen in offshore marine Quaternary sequences sometimes in great profusion.



TEXT-FIG. 42. Distribution of *Polykrikos schwartzii* Bütschli. Ornament as before. Hachured boundary indicates approximate distribution as given in Harland (1981).

Polykrikacacean Cysts

45 *Polykrikos schwartzii* Bütschli 1873

Text-fig. 42; Plate 48, figs. 10–12

Taxonomic Comments. These cysts are morphologically unique and have recently been described in detail (Harland 1981). Particularly interesting is the wide range of variation seen within this one species.

Distribution. The distribution portrayed in text-fig. 42 is somewhat misleading in that it appears to be restricted along the coasts of the British Isles particularly the north-eastern coast of Scotland and the southern coast of England, and off the northern, southern and south-western coasts of Ireland. Harland (1981) collated additional data from Reid (1978), Dale (1976) and from Professor John Dodge (pers. comm.) to show a much broader distribution in the eastern Atlantic and this is indicated by the hachured boundary. These cysts are occasionally present in offshore Quaternary sequences.

RESULTS

Constraints

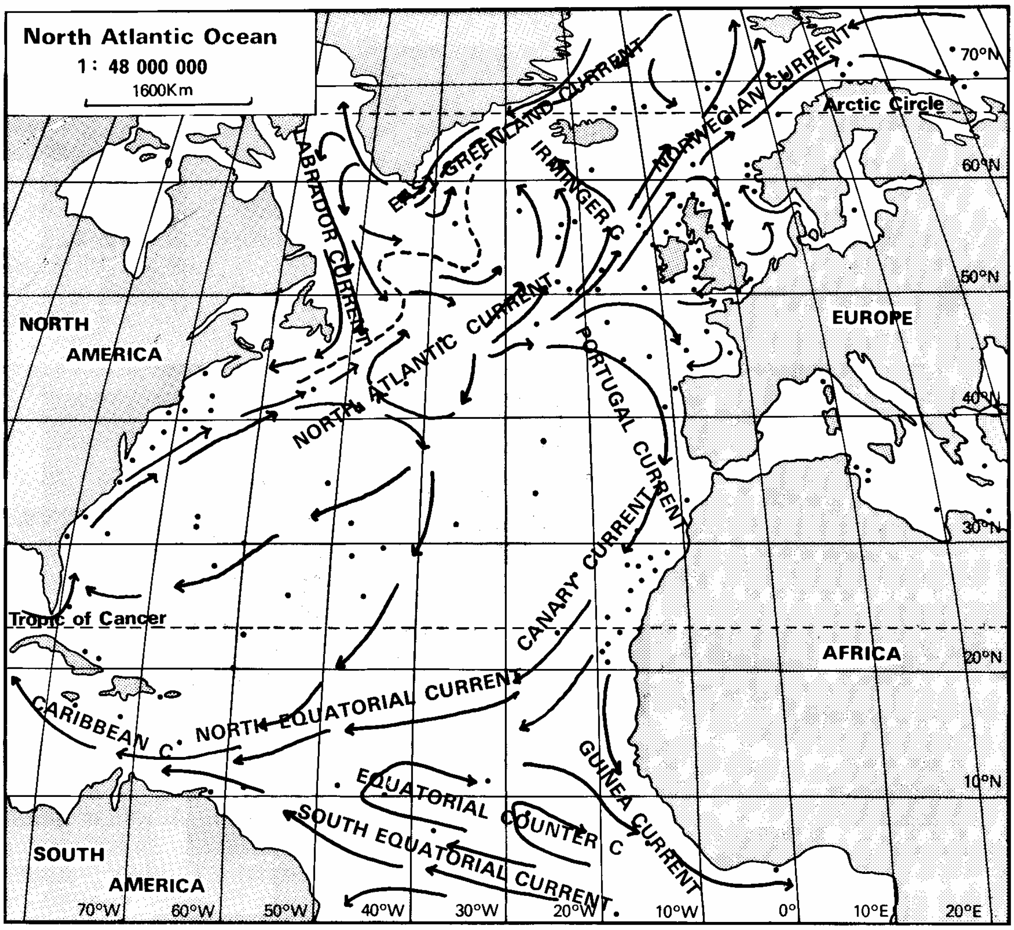
It is necessary, before discussing the results, to mention the constraints that must be taken into account with work of this kind. It is too easy and attractive to make broad generalizations without bearing in mind a number of factors that affect the results.

The first and most obvious constraint is that the assemblages examined are thanatocoenoses and therefore may be somewhat removed from the real dinoflagellate cyst biocoenosis. All the assemblages will have contained unknown proportions of living and dead dinocysts. In addition the dinoflagellate cyst assemblages, whether alive or dead, are also removed again from the living thecate dinoflagellate populations of the area. Indeed Dale (1976) has pointed out that only a very small proportion of the total living dinoflagellate population in a given area will produce cysts and indeed only some of these will be preserved as fossils and survive the palynological processing techniques. It is now realized that not all dinoflagellate cysts have the same inherent structural potential for being fossilized, a vital factor in surviving palynological processing techniques. It is therefore difficult, if not almost impossible, to give any conclusions concerning the total living dinoflagellate population. It is also difficult to determine whether, given the knowledge from incubation experiments that a cyst and thecate stage are related, the motile/thecate dinoflagellate was living in the overlying waters. In this respect transport along current systems (text-fig. 43), and sorting according to particle size and specific density will affect the thanatocoenosis and remove it, to a greater or lesser degree, from the biocoenosis. Dinoflagellate cysts act as sedimentary particles of variously clay or fine silt size and this may affect concentrations of cysts in particular areas. Indeed a comparison of many of the distribution charts with the surface current patterns will often show a close correspondence.

A second factor involves the integration of the record in bottom sediments. The samples used were taken using grab samples, vibrocorers, piston corers, and dredgers. This taken together with the knowledge that bottom sediments are generally extensively bioturbated, even in oceanic bottom sediments means that the samples used in this study are probably integrating many hundreds of years of deposition and possibly several thousands. It is probably more accurate to refer them to the late Flandrian, than to call them modern or Recent. In addition it is probable that shelf sediments are an integration of hundreds of years whilst those in the deep ocean integrate thousands of years because of major differences in sedimentation rates. The distinction between shelf and oceanic dinoflagellate cyst assemblages will be accentuated by this factor. These factors should be considered in any study of fossil dinoflagellate cyst assemblages when similar aged samples from differing geographical localities are being compared.

A third important factor that seriously affects the interpretation of this study and indeed any quantitative work on Quaternary or older sequences is the overrepresentation of some species. It has been reported (Dale 1976) that in plankton counts at Woods Hole, the ratio of cysts to thecae for *Gonyaulax grindleyi* was about 1 : 2 whereas for *Protoperidinium oblongum* is was 1 : 120 and for *G. digitalis* 1 : 500. In terms of the record here and in the analysis of Quaternary sequences small changes in the living plankton population would give large changes in the resultant cyst assemblages.

Other factors include the danger of including material reworked from older sediments, a possibility that experience can go some way to eliminating especially in the case of Tertiary or older sediments. Whereas the spectre of reworking from older Quaternary sediments is one that cannot be eliminated, it is hoped that it is negligible in the present study. It is also possible that some of the bottom sediments are considerably older because of scour effects etc., and contain dinoflagellate cyst assemblages not in ecological equilibrium with the present oceanographical conditions. This factor is especially important if on comparison of these results with those taken from living cyst populations discrepancies are noticed. This work assumes that, given the integration effect, these assemblages are in ecological equilibrium until proved otherwise.



TEXT-FIG. 43. North Atlantic surface currents (compiled from various sources).

The data is mapped as percentage counts and therefore in interpreting the maps it must be realized that any change of one species will obviously alter the proportions of all the other species. Equal emphasis should be placed upon those species that only appear as a tiny proportion of the cyst assemblage, but may indeed reveal interesting information concerning the environment.

The present data set is naturally subject to the particular biases of the various authors that have contributed data, including myself. This is manifest in the different processing techniques that were undoubtedly used, in the identification procedures, and the state of taxonomy at the time the work was done. D. B. Williams (1965, 1971), for instance, recognized very few *Protoperidinium* spp. but saw plenty of brown spherical objects, totalled with the *Protoperidinium* spp. indet. category here, and only a few people have consistently recognized the various *Spiniferites* species erected by Reid (1974).

Finally, this study is based upon a limited number of samples and further work should be done to improve the coverage. Of particular interest are the areas of the Labrador Sea (see Mudie 1981*a* and *b*), the region between latitudes 10 °N. and 20 °N. and better coverage in the Mediterranean.

Results

The maps show that the distribution of many species is closely linked with the patterns of currents in the North Atlantic and that many areas of concentration occur associated with areas of convergence and/or divergence, e.g. *B. tepikiense* (text-fig. 3) on the Iceland-Faroes Ridge, *S. mirabilis* (text-fig. 14) in the Portugal Current, i.e. East Atlantic gyre. This agrees well with the earlier findings of Williams (1971) and subsequent workers.

The species concerned can now, however, be categorized using these maps into a broad ecological classification similar to that compiled by Wall *et al.* (1977). This classification is presented in Table 1 and is a broader based scheme than that of Wall *et al.* (1977). It may, however, be a better basis because of this for the interpretation of Quaternary sequences as no doubt the constraints discussed earlier are directly at work here in smudging some of these rather arbitrary ecological divisions. It should be possible to place any Quaternary assemblage into this scheme by virtue of its contained species, but there is an obvious need to refine and subdivide each of the areas depicted here, especially in the light of comments made concerning the identifications of particular species. The addition of data from living cyst work will no doubt improve this kind of classification and identify areas where the smudging is great and can be discounted.

Also apparent is the correspondence between the diversity, i.e. number of species/assemblage, and distribution, as depicted in text-fig. 44 and Table 1. The greatest species diversity occurs in the temperate neritic realm followed by the tropical neritic and arctic neritic.

The separation of the neritic and oceanic realms is also clearly demonstrable (compare the distribution maps of the *Impagidinium* and *Spiniferites*/*Protoperidinium* spp.) in the present study. This factor was discussed by Wall *et al.* (1977) and earlier by Williams (1971) but there does seem to be a fundamental division in terms of the cyst thanatocoenosis even given all our constraints especially those of the problems of the integration of the record. Recent work (Dale in prep.) confirms this but also reveals significant differences between the flux of dinoflagellates into deep ocean sediment and assemblages similar to those described here. There is much to be learnt in terms of thanatocoenosis vs. biocoenosis but it may nevertheless be speculated that oceanic dinoflagellates have a somewhat different life cycle to those living in neritic waters and do not have benthonic cysts but ones that adopt a planktonic life style only dropping into bottom sediments after their function is complete.

A final result that comes out of this work substantiates remarks made by Reid and Harland (1977) on the separate distributions of various cysts all attributed to a single thecate species. In this respect it is worth comparing the distributions of *Bitectatodinium tepikiense* (text-fig. 3), *Nematosphaeropsis labyrinthea* (text-fig. 5), *Spiniferites elongatus* (text-fig. 11), *S. membranaceus* (text-fig. 13), *S. mirabilis* (text-fig. 14), and *S. ramosus* (text-fig. 15) all of which have been incubated to produce thecae attributable to *G. spinifera* and the *Impagidinium* spp. which are supposed, because of reasons based upon their paratabulation to also be referable to the *G. spinifera* group. This disparity in the geographical ranges of the various *Gonyaulax spinifera* cysts may indicate either different ecophenotypes expressed in the cyst morphology or the presence of a number of related species that are difficult to separate using the criteria currently employed. A further study of *G. spinifera* and its several cyst types is obviously required.

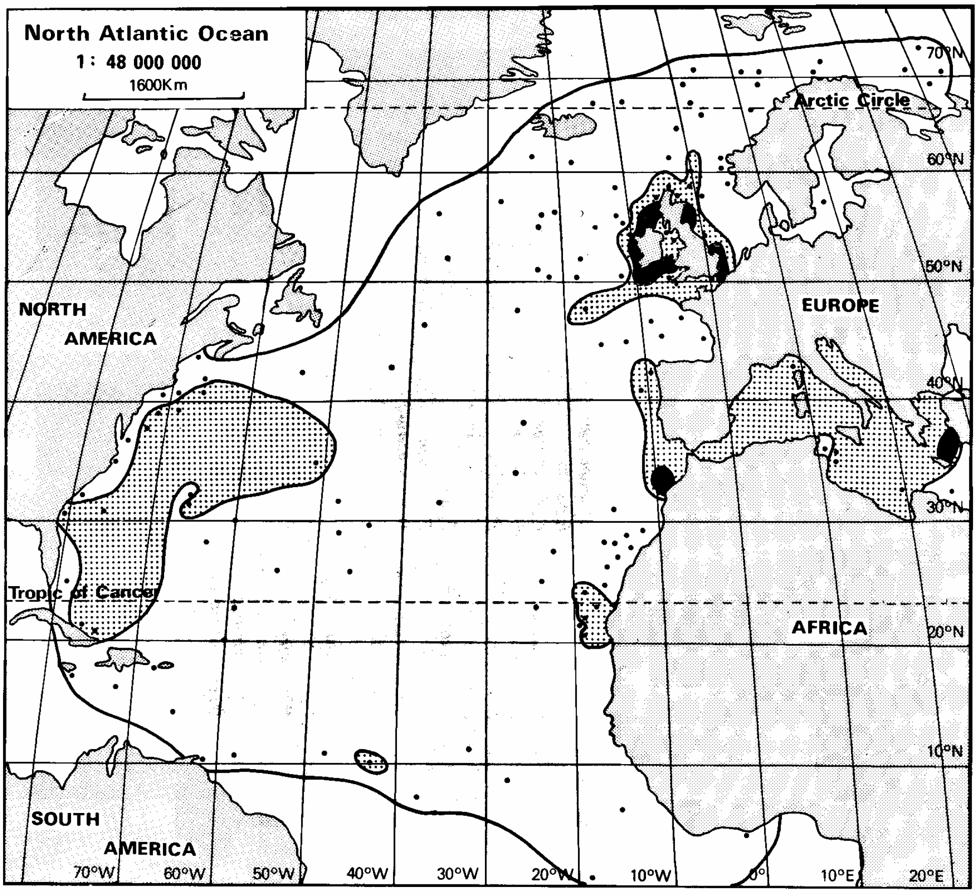
DISCUSSION

The main purpose of this study was to provide a series of maps showing the distribution of various dinoflagellate cyst species in bottom sediments throughout the North Atlantic area. The data were culled from various sources and some of the constraints and results have already been commented upon. The information is limited and should not be over-interpreted, if for no other reason than that we are not dealing with living material. It is, however, probably worthwhile to make some comparisons with the work of Wall *et al.* (1977) which is the most up to date account of dinoflagellate cyst distributions, and the factors that control the distributions.

Wall *et al.* (1977) set out to provide an environmental-climatic analysis of extant cyst-based

TABLE 1. An ecological classification of extant dinoflagellate cysts

	Inner Neritic		Outer Neritic		Oceanic	
Arctic	*O. centrocarpum* *S. elongatus*		*B. tepikiense* *N. labyrinthea* *O. centrocarpum* *S. elongatus*	*S. lazus* *S. mirabilis* *S. ramosus*	*B. tepikiense* *N. labyrinthea* *O. centrocarpum* *S. elongatus*	*I. patulum*
Temperate	*L. machaerophorum* *O. centrocarpum* *O. israelianum* *S. belerius* *S. bentori* *S. delicatus* *S. elongatus* *S. lazus* *S. membranaceus* *S. mirabilis* *S. ramosus* *S. ramosus s. Wall* *S. scabratus* *T. pellitum* *P. zoharyi*	*T. vancampoae* *P. conicoides* *P. avellana* *P. denticulatum* *L. paratenella* *P. leonis* *P. conicum* *P. subinerme* *P. compressum* *P. pentagonum* *P. claudicans* *P. oblongum* *X. xanthum* *P. schwartzii*	*A. andalousiense* *B. tepikiense* *L. machaerophorum* *N. labyrinthea* *O. centrocarpum* *O. israelianum* *S. belerius* *S. bentori* *S. delicatus* *S. elongatus* *S. lazus* *S. membranaceus* *S. mirabilis* *S. ramosus* *S. ramosus s. Wall*	*S. scabratus* *T. pellitum* *I. aculeatum* *I. paradoxum* *I. patulum* *I. sphaericum* *I. strialatum* *P. zoharyi* *T. vancampoae* *P. leonis* *P. conicum* *P. pentagonum* *P. schwartzii*	*B. tepikiense* *L. machaerophorum* *N. labyrinthea* *O. centrocarpum* *S. elongatus* *S. mirabilis* *I. aculeatum* *I. paradoxum* *I. patulum* *I. sphaericum* *I. strialatum*	
Tropical	*L. machaerophorum* *O. centrocarpum* *O. israelianum* *S. ramosus* *S. ramosus s. Wall* *P. zoharyi* *T. vancampoae* *P. leonis*	*P. conicum*	*B. tepikiense* *L. machaerophorum* *N. labyrinthea* *O. centrocarpum* *O. israelianum* *S. ramosus* *I. aculeatum* *I. sphaericum*	*I. strialatum* *P. zoharyi* *T. vancampoae* *P. leonis* *P. conicum*	*B. tepikiense* *L. machaerophorum* *N. labyrinthea* *O. centrocarpum* *I. aculeatum* *I. patulum* *I. sphaericum* *I. strialatum*	



TEXT-FIG. 44. North Atlantic showing the areas of different species diversity; blank areas 1–10 species, stippled areas 11–15 species, black areas 16–20 species.

dinoflagellate species, to develop an ecological/environmental classification, to determine the factors that influence distributions and to put forward a theoretical model to explain dinoflagellate cyst distributions. There are no great discrepancies between that and the present study and both the climatic and environmental trends are clearly visible in the maps herein and are summarized in Table 1, and this is also true for the inshore-offshore trend. Some differences are apparent in the species diversity distributions and unlike the study of Wall *et al.* (1977) this work does not show a consistent increase in diversity seaward but shows, for instance (text-fig. 44) an increase offshore in the eastern seaboard of North America but an increase towards the shore around the British Isles. This no doubt reflects the greater number of known cyst species around the British Isles due to the detailed work of Reid (1974, 1977).

The notion of specific species-water type relationships also appears to be borne out by the maps produced here as some close similarities are apparent between current patterns and cyst distributions.

High concentrations of particular cyst species also seem related to hydrographical effects, although particular cause-effect relationships are not dealt with here. There is then an intimate relationship between individual and grouped cyst species, water types, and hydrography. Further studies using cluster analysis and multidimensional scaling techniques are under way. Preliminary results show that reasonably sensible groups do occur and that they are linked to the hydrography of the area. The possibility of understanding the individual effects of latitude and hydrography upon the cyst distributions is real.

The comparison between the present work and that of Wall *et al.* (1977) can also be carried out on an individual species basis. This is done here for species where discrepancies are worth noting and where the data are particularly useful in interpreting the Quaternary dinoflagellate record.

(a) *Bitectatodinium tepikiense* Wilson—this species is categorized as an estuarine temperate species by Wall *et al.* (1977) based upon its occurrence in their samples but only to a maximum of 11% in one of their assemblages. The map published herein indicates maximum concentrations of over 50% in the area between Iceland and Scotland suggesting that it is more properly associated with a north-temperate oceanic to outer neritic environment. This also better compares with its rich occurrences in offshore Quaternary marine sediments.

(b) *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall—the map presented here suggests a wider environmental niche than the cosmopolitan estuarine of Wall *et al.* (1977). It is probably a species that is tolerant of wide environmental fluctuations and can withstand both reductions and increases in salinity better than most. Alternatively its great specific variability *in toto* suggests the distinct possibility that several morphotypes, with ?differing ecological requirements, may be encompassed within the present diagnosis of the species.

(c) *Nematosphaeropsis labyrinthea* (Ostenfeld) Reid—the map herein largely supports the ecological grouping as given in Wall *et al.* (1977) but does highlight a major concentration of the cysts in the mid-Atlantic off Ireland, possibly associated with the eastern Atlantic gyre or the submarine topography of the area.

(d) *Operculodinium centrocarpum* (Deflandre and Cookson) Wall—the association with the North Atlantic Current is obvious together with the general cosmopolitanism of this cyst species. The high concentrations in arctic waters may be somewhat false in that it is probably an artificial effect due to the general reduction of other cyst species or alternatively it may indicate a possible real ecological preference for that habitat.

(e) *O. israelianum* (Rossignol) Wall—the map produced supports the tropical-subtropical estuarine or nearshore categorization of this cyst type (Wall *et al.* 1977) but its occurrence off the Iberian peninsula may be significant in relation to its presence in early Pleistocene assemblages in East Anglia and in offshore areas.

(f) *Spiniferites* spp.—although the *Spiniferites* group shows a preference for a cosmopolitan neritic environment many individual species appear linked to specific conditions, e.g. *S. bentori* (Rossignol) Wall and Dale, *S. lazus* Reid and *S. membranaceus* (Rossignol) Sarjeant. In contrast *S. elongatus* Reid appears to be a mainly north-temperate to arctic neritic to oceanic species whose potential for the interpretation of Quaternary sequences is good, and *S. mirabilis* (Rossignol) Sarjeant shows a centre of concentration in the eastern Atlantic with potential for the interpretation of Quaternary sequences from that area. Unfortunately the nature of the detailed ecological requirements of these species is still not known.

(g) *Tectatodinium pellitum* Wall—the map herein tends to show a rather more restricted distribution than the ecological classification of Wall *et al.* (1977) suggests. Its widespread occurrence in early Pleistocene sediments in East Anglia and offshore the British Isles at times of interpreted climatic deterioration (Wall and Dale 1968*a*) certainly needs some explanation.

(h) *Impagidinium* spp.—these species identify as tropical to temperate oceanic forms. However, their individual distributions show differences that are probably most significant and certainly in some Quaternary sequences the high percentages of particular species points to specific environmental conditions.

(i) *Polysphaeridium zoharyi* (Rossignol) Bujak *et al.*—the ecological classification of this species (Wall *et al.* 1977) is supported by the map published herein.

(j) *Tuberculodinium vancampoae* (Rossignol)—the map published herein supports the position of this species in terms of the ecological classification of Wall *et al.* (1977).

(k) *Protoperidinium* spp.—these species generally show a fairly cosmopolitan temperate to tropical, coastal to outer neritic/oceanic distribution. There is, however, much to be learned about individual species as this group is often not well speciated. In particular knowledge of the ecological requirements of *P. compressum* (Abé) Balech, *P. conicum* (Gran) Balech, and *P. subinerme* (Paulsen) Loeblich III would be most useful as these species regularly turn up in many offshore Quaternary sequences. Indeed many of the currently recognized species may in fact encompass several varieties or species and this is also an area in need of more investigation.

CONCLUSIONS

The series of maps produced have shown the distributions of forty-two extant dinoflagellate cyst species in the North Atlantic area based upon both published and unpublished data. The maps clearly show both the latitudinal–climatic and onshore–offshore trends already identified by Wall *et al.* (1977) and Reid and Harland (1977) and the influence of the oceanic current systems. It is obvious that much more is to be learnt concerning the ecological requirements of species but it is hoped that these maps may constitute some sort of basis to which other pieces of information can be added. Particular emphasis has been placed upon these species that turn up with some frequency in offshore marine Quaternary sequences as the potential in their use in interpreting the Quaternary history of climate and oceanography is great. Finally it must be stressed that the need to understand the living dinoflagellate in its natural habitat is paramount in understanding both the implications of this kind of work and in utilizing all the potential of this group in understanding past oceanographic realms.

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APPENDICES

I SAMPLE LOCALITY DATA

The samples studied, their localities, sources of data, and the authors responsible for the original percentage counts of the contained dinoflagellate cyst assemblages are listed below. The Institute of Geological Sciences registered numbers and the British Museum (Natural History) catalogue numbers are also included where applicable. Latitude and longitude are quoted to the nearest minute.

Sample No.	*Locality*	*Author*	*IGS Reg. No.*	*B.M. (N.H.) Cat. No.*
1	44° 01′ N.; 68° 30′ W.	Wall *et al.* (1977)	—	—
2	40° 18′ N.; 67° 00′ W.	,, ,,	—	—
3	40° 28′ N.; 69° 31′ W.	,, ,,	—	—
4	39° 08′ N.; 69° 28′ W.	,, ,,	—	—
5	40° 54′ N.; 70° 45′ W.	,, ,,	—	—
6	38° 59′ N.; 70° 29′ W.	,, ,,	—	—
7	38° 14′ N.; 72° 16′ W.	,, ,,	—	—
8	37° 02′ N.; 75° 54′ W.	,, ,,	—	—

Sample No.	*Locality*	*Author*	*IGS Reg. No.*	*B.M. (N.H.) Cat. No.*
9	35° 24′ N.; 75° 42′ W.	Wall *et al.* (1977)	—	—
10	33° 02′ N.; 79° 33′ W.	,, ,,	—	—
11	31° 14′ N.; 81° 14′ W.	,, ,,	—	—
12	32° 15′ N.; 64° 50′ W.	,, ,,	—	—
13	24° 13′ N.; 78° 09′ W.	,, ,,	—	—
14	17° 57′ N.; 76° 44′ W.	,, ,,	—	—
15	18° 01′ N.; 67° 12′ W.	,, ,,	—	—
16	10° 21′ N.; 61° 48′ W.	,, ,,	—	—
17	62° 10′ N.; 05° 59′ E.	,, ,,	—	—
18	60° 11′ N.; 05° 13′ E.	,, ,,	—	—
19	57° 04′ N.; 17° 37′ E.	,, ,,	—	—
20	42° 16′ N.; 07° 11′ E.	,, ,,	—	—
21	33° 56′ N.; 19° 39′ E.	,, ,,	—	—
22	32° 33′ N.; 25° 15′ E.	,, ,,	—	—
23	35° 45′ N.; 25° 15′ E.	,, ,,	—	—
24	34° 47′ N.; 13° 09′ E.	,, ,,	—	—
25	29° 00′ N.; 47° 28′ W.	,, ,,	—	—
26	28° 09′ N.; 15° 25′ E.	,, ,,	—	—
27	01° 29′ N.; 19° 43′ W.	,, ,,	—	—
28	05° 00′ N.; 03° 34′ W.	,, ,,	—	—
29	56° 03′ N.; 03° 30′ W.	Harland (1981)	CSB 2066–2085 2266–2285	—
30	73° 20′ N.; 25° 29′ E.	,, (1982*b*)	2305	1957, 328(3)
31	71° 15′ N.; 27° 54′ E.	,, ,,	2306	1957, 328(6)
32	71° 28′ N.; 38° 20′ E.	,, ,,	2308	1957, 328(16)
33	73° 28′ N.; 41° 19′ E.	,, ,,	2310	1957, 328(23)
34	69° 28′ N.; 41° 27′ E.	,, ,,	2311	1957, 328(30)
35	70° 28′ N.; 43° 28′ E.	,, ,,	2312	1957, 328(31)
36	70° 31′ N.; 10° 46′ E.	,, (unpubl.)	2314	1957, 328(52)
37	70° 29′ N.; 04° 30′ E.	,, ,,	2315	1957, 328(54)
38	69° 30′ N.; 01° 18′ E.	,, ,,	2316	1957, 328(56)
39	69° 29′ N.; 01° 24′ E.	,, ,,	2317	1957, 328(57)
40	66° 31′ N.; 03° 28′ E.	,, ,,	2318	1957, 328(58)
41	66° 30′ N.; 11° 00′ E.	,, ,,	2319	1957, 328(72)
42	69° 29′ N.; 13° 12′ E.	,, ,,	2320	1957, 328(81)
43	71° 28′ N.; 13° 37′ E.	,, ,,	2321	1957, 328(90)
44	67° 36′ N.; 10° 33′ W.	,, ,,	2322	1962, 160(10)
45	67° 19′ N.; 13° 25′ W.	,, ,,	2323	1962, 160(13)
46	54° 00′ N.; 04° 00′ W.	,, (1977)	CSA 96–150	—
47	57° 00′ N.; 07° 00′ W.	,, ,,	composite	—
48	59° 23′ N.; 03° 29′ E.	,, (unpubl.)	CSA 1332, 1292	—
49	55° 22′ N.; 05° 30′ W.	,, (1977)	composite	—
50	58° 04′ N.; 00° 34′ E.	,, ,,	CSA 1533	—
51	Sample of reworked older material; removed from data			—
52	58° 30′ N.; 00° 20′ E.	Harland (unpubl.)	composite	—
53	60° 00′ N.; 00° 00′ E.	,, ,,	composite	—
54	58° 07′ N.; 03° 40′ W.	Reid (1972*b*, 1974, 1975, 1977)	—	—
55	54° 17′ N.; 00° 24′ W.	,, ,,	—	—
56	51° 20′ N.; 01° 25′ E.	,, ,,	—	—
57	50° 47′ N.; 00° 03′ E.	,, ,,	—	—
58	50° 10′ N.; 05° 20′ W.	,, ,,	—	—
59	51° 42′ N.; 04° 56′ W.	,, ,,	—	—
60	52° 43′ N.; 04° 03′ W.	,, ,,	—	—
61	51° 55′ N.; 08° 16′ W.	,, ,,	—	—
62	52° 35′ N.; 09° 30′ W.	,, ,,	—	—
63	54° 20′ N.; 09° 35′ W.	,, ,,	—	—

Sample No.	*Locality*	*Author*	*IGS Reg. No.*	*B.M. (N.H.) Cat. No.*
64	55° 12′ N.; 07° 52′ W.	Reid (1972*b*, 1974, 1975, 1977)	—	—
65	57° 40′ N.; 06° 50′ W.	,, ,,	—	—
66	58° 25′ N.; 04° 30′ W.	,, ,,	—	—
67	16° 19′ N.; 70° 29′ W.	Williams (1965)	—	D9.38
68	32° 06′ N.; 64° 30′ W.	,, ,,	—	D15.4
69	06° 03′ N.; 15° 08′ W.	,, ,,	—	D21.12
70	30° 00′ N.; 59° 58′ W.	,, ,,	—	D23.16
71	20° 00′ N.; 60° 02′ W.	,, ,,	—	D23.22
72	Data not available: position taken from thesis figure	,, ,,	—	M25
73	″ ″ ″	,, ,,	—	M69
74	09° 29′ N.; 27° 59′ W.	,, ,,	—	M4630
75	20° 14′ N.; 19° 22′ W.	,, ,,	—	M4751
76	10° 18′ N.; 30° 19′ W.	,, ,,	—	M4632
77	31° 15′ N.; 75° 08′ W.	,, ,,	—	M7380
78	38° 53′ N.; 25° 09′ W.	,, ,,	—	M9036
79	21° 00′ N.; 75° 05′ W.	,, ,,	—	M9070
80	21° 05′ N.; 74° 56′ W.	,, ,,	—	M9071
81	43° 21′ N.; 52° 24′ W.	,, ,,	—	M9110
82	42° 56′ N.; 40° 19′ W.	,, ,,	—	M9113
83	45° 53′ N.; 39° 26′ W.	,, ,,	—	M9114
84	45° 26′ N.; 09° 20′ W.	,, ,,	—	M9711
85	28° 08′ N.; 13° 35′ W.	,, ,,	—	M9722
86	31° 20′ N.; 35° 07′ W.	,, ,,	—	M9728
87	47° 32′ N.; 16° 38′ W.	,, ,,	—	M9737
88	Data not available: position taken from thesis figure	,, ,,	—	SM 231
89	40° 07′ N.; 25° 22′ W.	,, ,,	—	SM 876
90	14° 01′ N.; 64° 31′ W.	,, ,,	—	1938, 1290(5)
91	47° 44′ N.; 25° 26′ W.	,, ,,	—	1954, 40(6)
92	41° 49′ N.; 09° 34′ W.	,, ,,	—	1956, 389(22)
93	33° 27′ N.; 09° 21′ W.	,, ,,	—	1957, 648(57)
94	30° 30′ N.; 14° 11′ W.	,, ,,	—	1957, 648(63)
95	30° 03′ N.; 42° 16′ W.	,, ,,	—	1962, 333
96	10° 07′ N.; 58° 32′ W.	,, ,,	—	1962, 338
97	10° 00′ N.; 46° 53′ W.	,, ,,	—	1962, 345
98	09° 58′ N.; 42° 50′ W.	,, ,,	—	1962, 346
99	07° 58′ N.; 36° 19′ W.	,, ,,	—	1962, 347
100	52° 42′ N.; 36° 05′ W.	Turon (1980)	—	—
101	57° 56′ N.; 29° 08′ W.	,, ,,	—	—
102	62° 01′ N.; 24° 29′ W.	,, ,,	—	—
103	61° 20′ N.; 18° 26′ W.	,, ,,	—	—
104	63° 01′ N.; 01° 59′ W.	,, ,,	—	—
105	61° 59′ N.; 02° 30′ W.	,, ,,	—	—
106	58° 05′ N.; 10° 43′ W.	,, ,,	—	—
107	56° 19′ N.; 11° 33′ W.	,, ,,	—	—
108	55° 36′ N.; 14° 29′ W.	,, ,,	—	—
109	51° 28′ N.; 17° 41′ W.	,, ,,	—	—
110	50° 09′ N.; 17° 22′ W.	,, ,,	—	—
111	46° 46′ N.; 08° 41′ W.	,, ,,	—	—
112	45° 05′ N.; 02° 57′ W.	,, ,,	—	—
113	45° 28′ N.; 13° 31′ W.	,, ,,	—	—
114	40° 55′ N.; 10° 35′ W.	,, ,,	—	—
115	34° 49′ N.; 26° 12′ W.	,, ,,	—	—

Sample No.	*Locality*	*Author*	*IGS Reg. No.*	*B.M. (N.H.) Cat. No.*
116	27°29′N.; 64°59′W.	Harland (unpubl.)	CSB 3267	M49
117	35°35′N.; 50°27′W.	,, ,,	CSB 3268	M86
118	28°17′N.; 15°06′W.	,, ,,	CSB 3269	M3608
119	28°25′N.; 14°46′W.	,, ,,	CSB 3270	M3609
120	20°20′N.; 19°35′W.	,, ,,	CSB 3271	M4752
121	21°07′N.; 18°49′W.	,, ,,	CSB 3272	M4756
122	22°38′N.; 18°30′W.	,, ,,	CSB 3273	M4762
123	23°46′N.; 18°09′W.	,, ,,	CSB 3274	M4766
124	25°10′N.; 16°58′W.	,, ,,	CSB 3275	M4770
125	26°11′N.; 16°25′W.	,, ,,	CSB 3276	M4777
126	26°27′N.; 15°15′W.	,, ,,	CSB 3277	M4782
127	25°31′N.; 54°40′W.	,, ,,	CSB 3279	M7337
128	26°32′N.; 56°45′W.	,, ,,	CSB 3280	M7338
129	32°43′N.; 47°30′W.	,, ,,	CSB 3281	M7393
130	24°56′N.; 24°46′W.	,, ,,	CSB 3282	M7397
131	56°11′N.; 37°41′W.	,, ,,	CSB 3283	M8777
132	28°08′N.; 13°35′W.	,, ,,	CSB 3284	M9722
133	50°22′N.; 11°44′W.	,, ,,	CSB 3285	M9739
134	23°20′N.; 59°58′W.	,, ,,	CSB 3286	D23.20
135	51°55′N.; 23°03′W.	,, ,,	CSB 3288	1953,164(6)
136	55°03′N.; 23°59′W.	,, ,,	CSB 3289	1953,164(7)
137	55°13′N.; 22°37′W.	,, ,,	CSB 3290	1954,40(5)
138	55°19′N.; 11°02′W.	,, ,,	CSB 3291	1954,41(3)
139	56°24′N.; 20°07′W.	,, ,,	CSB 3292	1954,41(4)
140	50°06′N.; 21°54′W.	,, ,,	CSB 3293	1954,41(8)
141	47°43′N.; 04°55′W.	Morzadec-Kerfourn (1977)	—	—
142	35°59′N.; 11°51′E.	,, ,, (1979)	—	—
143	34°45′N.; 13°04′E.	,, ,, ,,	—	—

II DINOFLAGELLATE TAXA

The dinoflagellate taxa included in this study, their thecal equivalence and the relevant plate and figures in this publication are listed below.

DIVISION Pyrrhophyta Pascher 1914
CLASS Dinophyceae Fritsch 1929
ORDER Peridiniales Haeckel 1894

Family Gonyaulacaceae Lindemann 1928

Reference No	Cyst Name	Thecate Name	Figure
1	*Achomosphaera andalousiense* Jan du Chêne	?*Gonyaulax* sp. indet.	Pl. 43, figs. 1,2
2	*Bitectatodinium tepikiense* Wilson	*G. spinifera* (Claparède & Lachmann) Diesing	Pl. 43, figs. 3,4
3	*Lingulodinium machaerophorum* (Deflandre and Cookson) Wall	*G. polyedra* Stein	Pl. 43, figs. 5,6
4	*Nematosphaeropsis labyrinthea* (Ostenfeld) Reid	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 43, figs. 7,8
5	*Operculodinium centrocarpum* (Deflandre and Cookson) Wall	*G. grindleyi* (Reinecke) Von Stosch	Pl. 43, figs. 9,10
6	*O. israelianum* (Rossignol) Wall	*G.* sp. indet? *grindleyi* (Reinecke) Von Stosch	Pl. 43, figs. 11,12
7	*Spiniferites belerius* Reid	?*G. scrippsae* Kofoid	Pl. 44, figs. 1,2
8	*S. bentori* (Rossignol) Wall and Dale	*G. digitalis* (Pouchet) Kofoid	Pl. 44, figs. 3,4
9	*S. delicatus* Reid	*Gonyaulax* sp. indet.	Pl. 44, figs. 5,6
10	*S. elongatus* Reid [incl. *S. frigidus* Harland and Reid]	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 44, figs. 7–10
11	*S. lazus*	*Gonyaulax* sp. indet.	Pl. 44, figs. 11,12
12	*S. membranaceus* (Rossignol) Sarjeant	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 45, figs. 3,4
13	*S. mirabilis* (Rossignol) Sarjeant	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 45, figs. 1,2
14	*S. ramosus* (Ehrenberg) Mantell	*G. scrippsae* Kofoid	Pl. 45, figs. 5,6
15	*S. ramosus* (Ehrenberg) Mantell *sensu* Wall	*G. spinifera* (Claparède and Lachmann) Diesing	Pl. 45, fig. 8
16	*S. scabratus* Wall	*Gonyaulax* sp. indet.	Pl. 45, fig. 7
17	*Spiniferites* spp. indet.	*Gonyaulax* spp. indet.	
19	*Tectatodinium pellitum*	*Gonyaulax* sp. indet.	Pl. 45, fig. 9
20	*Impagidinium aculeatum* (Wall) comb. nov.	*Gonyaulax* sp. indet.	Pl. 46, figs. 1–3
21	*I. paradoxum* (Wall) Stover and Evitt	*Gonyaulax* sp. indet.	Pl. 46, figs. 4,5
22	*I. patulum* (Wall) Stover and Evitt	*Gonyaulax* sp. indet.	Pl. 46, figs. 6,7
23	*I. sphaericum* (Wall) comb. nov.	*Gonyaulax* sp. indet.	Pl. 46, figs. 8,9
24	*I. strialatum* (Wall) Stover and Evitt	*Gonyaulax* sp. indet.	Pl. 46, figs. 10–12
26	*Polysphaeridium zoharyi* (Rossignol) Bujak *et al.*	*Pyrodinium bahamense* Plate	Pl. 46, fig. 10

		Family Pyrophacaceae Lindemann 1928	
27	*Tuberculodinium vancampoae* (Rossignol) Wall	*Pyrophacus* Form B1, Steidinger and Davis	Pl. 45, fig. 11
		Family Peridiniaceae Ehrenberg 1832	
28	*Brigantedinium* sp. nov.	*Protoperidinium* (*Protoperidinium*) *punctulatum* (Paulsen) Balech	Pl. 47, fig. 1
29	*B. simplex* (Wall) Reid	*P.* (*Protoperidinium*) *conicoides* (Paulsen) Balech	Pl. 47, figs. 2, 3
30	*B. cariacoense* (Wall) Reid	*P.* (*Archaeperidinium*) *avellana* (Meunier) Balech	Pl. 47, fig. 4
31	*Brigantedinium* sp. nov.	*P.* (*Archaeperidinium*) *denticulatum* (Gran and Braarud) Balech	Pl. 47, fig. 6
32	*Lejeunia paratenella* Benedek	*Protoperidinium* sp. indet.	Pl. 47, fig. 5
33	*Quinquecuspis concretum* (Reid) Harland	*P.* (*Protoperidinium*) *leonis* (Pavillard) Balech	Pl. 47, figs. 7, 8
34	*Selenopemphix quanta* (Bradford) comb. nov.	*P.* (*Protoperidinium*) *conicum* (Gran) Balech	Pl. 47, figs. 9, 10
35	*Selenopemphix* sp. nov.	*P.* (*Protoperidinium*) *nudum* (Meunier) Balech	Pl. 48, fig. 5
36	*S. nephroides* Benedek	*P.* (*Protoperidinium*) *subinerme* (Paulsen) Loeblich III	Pl. 48, fig. 11, 12
37	*Stelladinium stellatum* (Wall) Reid	*P.* (*Archaeperidinium*) *compressum* (Abé) Balech	Pl. 48, fig. 1
38	*Trinovantedinium capitatum* Reid	*P.* (*Protoperidinium*) *pentagonum* (Gran) Balech	Pl. 48, figs. 2, 3
39	*Votadinium spinosum* Reid	*P.* (*Protoperidinium*) *claudicans* (Paulsen) Balech	Pl. 48, fig. 4
40	*Votadinium calvum* Reid	*P.* (*Protoperidinium*) *oblongum* (Aurivillius) Balech	Pl. 48, figs. 6, 7
41	*Xandarodinium xanthum* Reid	?*Protoperidinium* sp. indet.	Pl. 48, fig. 8
42	Cyst-type B of Harland	*Protoperidinium* sp. indet.	Pl. 48, fig. 9
		ORDER Gymnodiniales Lemmermann 1910	
		Family Polykrikaceae Kofoid and Swezy 1921	
45	Cyst nov.	*Polykrikos schwartzii* Bütschli	Pl. 48, figs. 10–12