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F. J. R. TAYLOR

DINOFLAGELLATES FROM THE INTERNATIONAL INDIAN OCEAN EXPEDITION

A REPORT ON MATERIAL COLLECTED BY THE R. V. "ANTON BRUUN" 1963–1964

WITH PLATES 1–46, 6 FIGURES, 5 CHARTS AND 5 TABLES IN THE TEXT
AND AS APPENDIX

STUTTGART 1976
E. SCHWEIZERBART'SCHE VERLAGSBUCHHANDLUNG
(NÄGELE u. OBERMILLER)

Dinoflagellates from the International Indian Ocean Expedition

A report on material collected by the R. V. "Anton Bruun" 1963-1964

By

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With plates 1–46, 6 figures, 5 charts and 5 tables in the text
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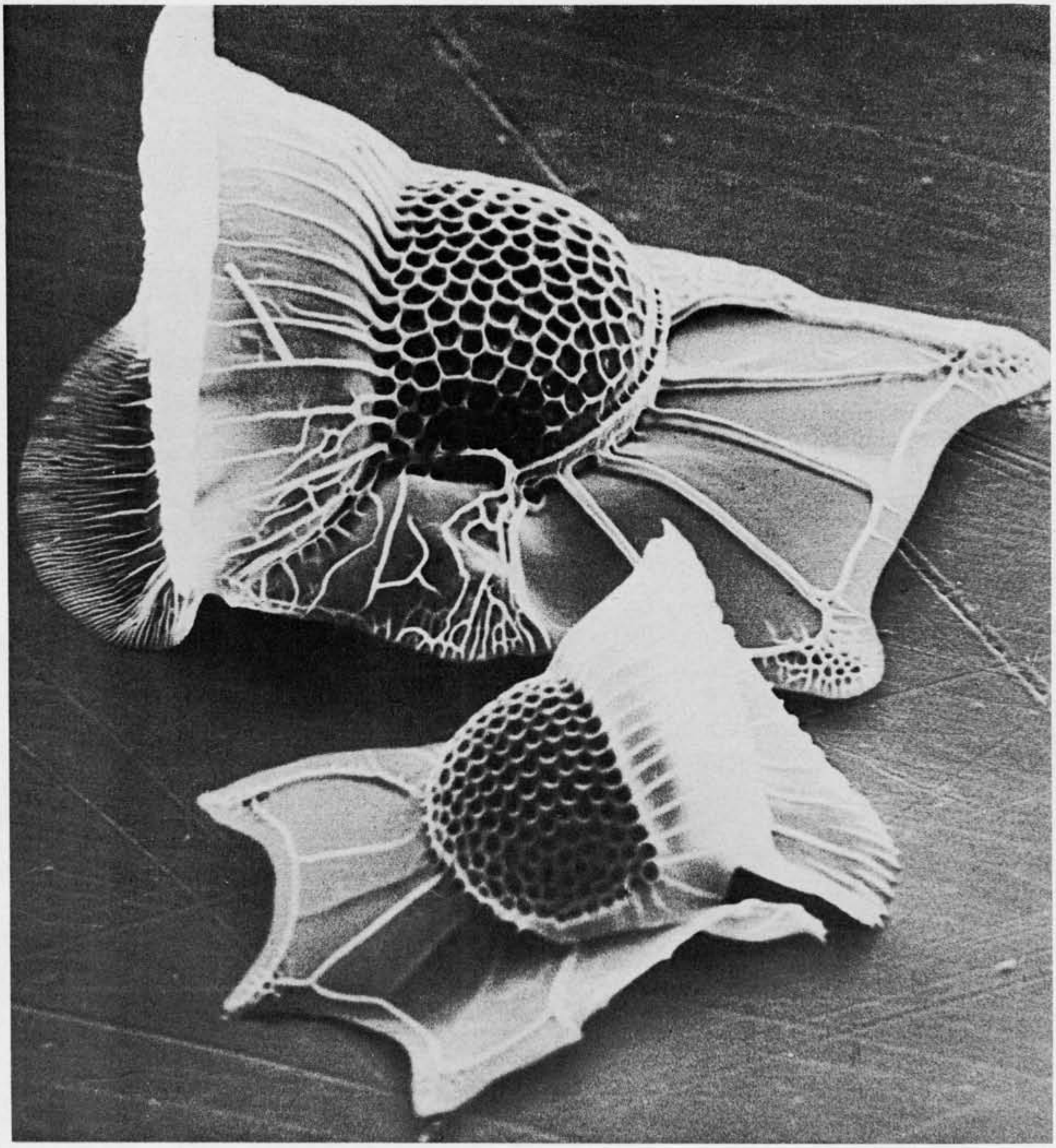
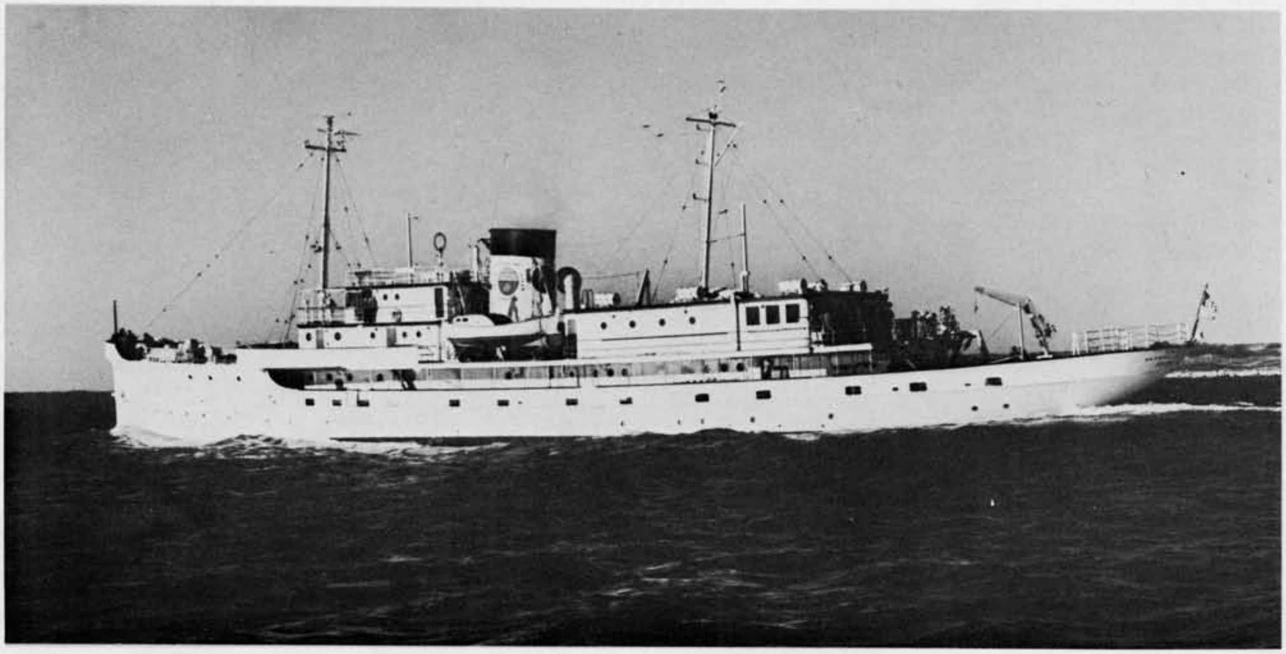


Scanning electron micrograph of two common members of the Indian Ocean dinoflagellate community; *Ornithocercus magnificus* STEIN (foreground) and *Ornithocercus quadratus* SCHÜTT. Magnification: 1035x.



The R.V. "ANTON BRUUN" photographed during the International Indian Ocean Expedition cruises (photograph courtesy of Dr. John H. RYTHER and the Woods Hole Oceanographic Institution).

Abstract

This report deals with the dinoflagellates observed in 213 samples collected in the Indian Ocean during nine cruises of the R.V. "Anton Bruun" from March, 1963 to November, 1964. The cruises were part of the United States contribution to the International Indian Ocean Expedition. 291 species attributed to 45 genera were recorded, of which 9 are new species and 3 are new infraspecific taxa. 77 are new records for the Indian Ocean. There are 50 = 50 nomenclatural revisions proposed. Two early genera: ***Pyrigidium*** STEIN under a substituted name, *Corythodinium* LOEBL. et LOEBL., and *Berghiella* KOF. et MICHENER, have been revived. Two new families are proposed as botanical equivalents for two zoological subfamilies.

All species are illustrated by line drawings and, in some cases, by scanning electron microscopy. There are 530 figures of taxa. An attempt has been made to provide all references to each species in which a figure occurs subsequent to the compilation by SCHILLER (1931–1937). There is comparative descriptive information, taxonomic comment, and distributional data for each species.

The Introduction includes a discussion of the asexual species concept, as applied to dinoflagellates, and in the final section there is a discussion of the general types of distributions found. The majority of species are thermophilic, decreasing sharply south of 32 °S except in the south-west where the Agulhas Current extends tropical distributions southwards. There are probably no species whose range is entirely limited to the Indian Ocean, endemicism being restricted to a few taxa whose distributions are centered on the waters of the Indo-Malaysian Archipelago. The majority occur in all warmer waters (tropicopolitan). Some southern stations entered the Subtropical Convergence Region and a few sub-Antarctic species were found. Due to sampling from 200 m there was a relatively large number of rare species known to occur in sub-euphotic layers (e.g. within the genera *Citharistes, Histioneis, Heterodinium* and the subgenus *Archaeceratium* of *Ceratium).*

Introduction

This report is the result of the microscopic analysis of 213 samples collected during nine of eleven cruises by the R.V. "Anton Bruun" in the Indian Ocean from March, 1963 to November, 1964. These cruises were carried out as part of the United States Program in Biology during the international oceanographic undertaking referred to as the International Indian Ocean Expedition. The ship was operated by the National Science Foundation of the United States.

The position of the stations from which dinoflagellate material was obtained is illustrated in charts 1 and 2. The dates of collection, depth of sampling, and environmental data pertinent to the samples are contained in a series of manuscript reports produced by the Woods Hole Oceanographic Institution (RYTHER & CHIN, 1964–1965) and will not be included here.

In view of the great wealth of species present in the material, a departure has been made from the usual procedure in reports on material of this type in that at least one figure of each taxon has been included to increase the potential usefulness of the work. To further this end the line-drawings have, wherever feasible, been drawn to the same scale within each genus.

As it is often difficult to locate works on dinoflagellates which have been published subsequent to the major compilations by authors such as SCHILLER (1931–1937), more recent references to the taxa have been made as complete as possible. Notes to facilitate intercomparison are included, as well as comment on the systematic position of the taxa where this may be contentious. Lengthy station lists have been omitted in favour of citation of the stations from which the individual taxa were encountered.

After the routine floristic analysis had been completed the use of a Cambridge Mark II A Scanning Electron Microscope (SEM) became possible. Samples with interesting microflora were selected for reexamination using a high-power stereoscopic light microscope and individuals were isolated by micropipette, washed by transfer through distilled water, dried on aluminium specimen holders, coated under vacuum with evaporated gold/palladium wire, and examined with SEM, usually at accelerating voltages of 10 to 20 kV. (See discussion of the application of the instrument to tropical material by TAYLOR, 1972b. A more detailed description will be included in a UNESCO publication on the preservation of zooplankton, edited by H.G. STEEDMANN, in preparation).

It would have been a pleasure, both taxonomically and aesthetically, to illustrate this work almost entirely with SEM micrographs. One of their greatest assets from the point of view of the taxonomist of microplankton is that it is relatively easy to relate SEM micrographs of whole specimens with light microscope images, and the topological formation of delicate transparent lists such as those surrounding the posterior part of the sulcus of *Peridinium*, is particularly difficult to see with the light microscope unless related to a SEM micrograph. Cost and time have precluded their extensive use here although six plates of the most interesting micrographs have been included and the line-drawings were checked for accuracy where possible.

Acknowledgements

The author is deeply indebted to MARIAN E.W. SLATER for her assistance at all stages of preparation of this work. In addition to work on the text Mrs. SLATER also traced many of the final line drawings from the author's originals, excluding the figures on plates 9 and 10.

The material for the study was provided through the kind offices of Dr. H.A. FEHLMANN, Director, and E.G. MENEZ of the Smithsonian Oceanographic Sorting Center, Washington, D.C.. Collection of the material was funded by the National Science Foundation of the United States, and the author received support during the analyses from the National Research Council of Canada. Parts of the manuscript were written at the Station Zoologique, Villefranche-sur-Mer, during the tenure of a Canadian/French scientific exchange fellowship.

The Material

The material subjected to microscopic analysis consisted of samples of mixed phytoplankton forwarded to the author by the Smithsonian Oceanographic Sorting Center, Washington, D.C. All had been originally obtained as part of the basic programme by means of vertical hauls from 200 m to the surface (depth permitting) with a microplankton net of 50 cm mouth diameter and No. 25 mesh (American system). They were all preserved in formalin neutralised with hexamine. Thecate dinoflagellates appeared to be reasonably well preserved although non-thecate species were predominantly absent and were presumably destroyed. Other groups, such as the diatoms, appeared to be in rather battered condition and most chain formers were dissociated.

The positions and numbers of the stations are indicated on charts 1 and 2. Table 1 summarises the relationship between the cruises, stations, dates, and provides an indication of the regions involved.

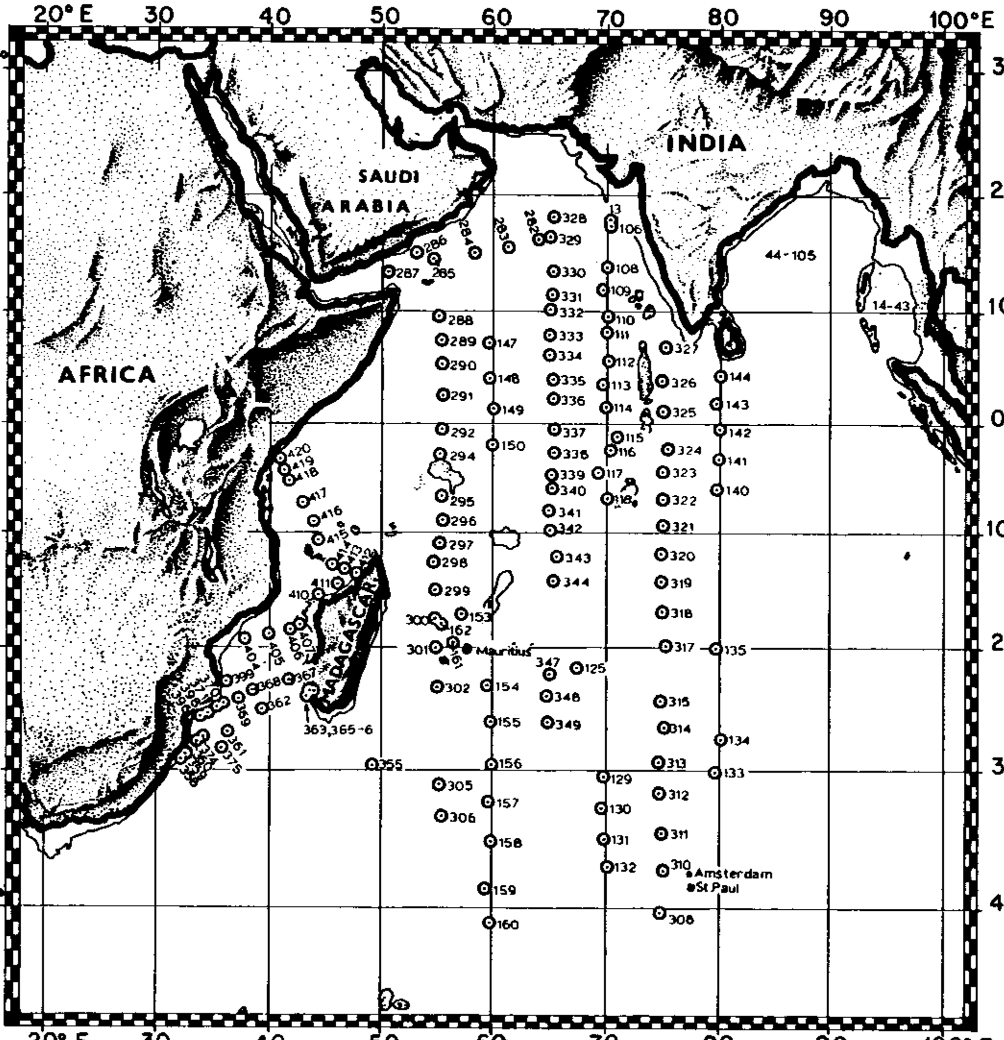


Chart 1. Stations from which dinoflagellate material was collected by the R.V. "Anton Bruun" during the International Indian Ocean Expedition, 1963–1964. For details of the Bay of Bengal/Andaman Sea area please refer to Chart 2. The periods during which groups of samples were taken are indicated in Table 1.

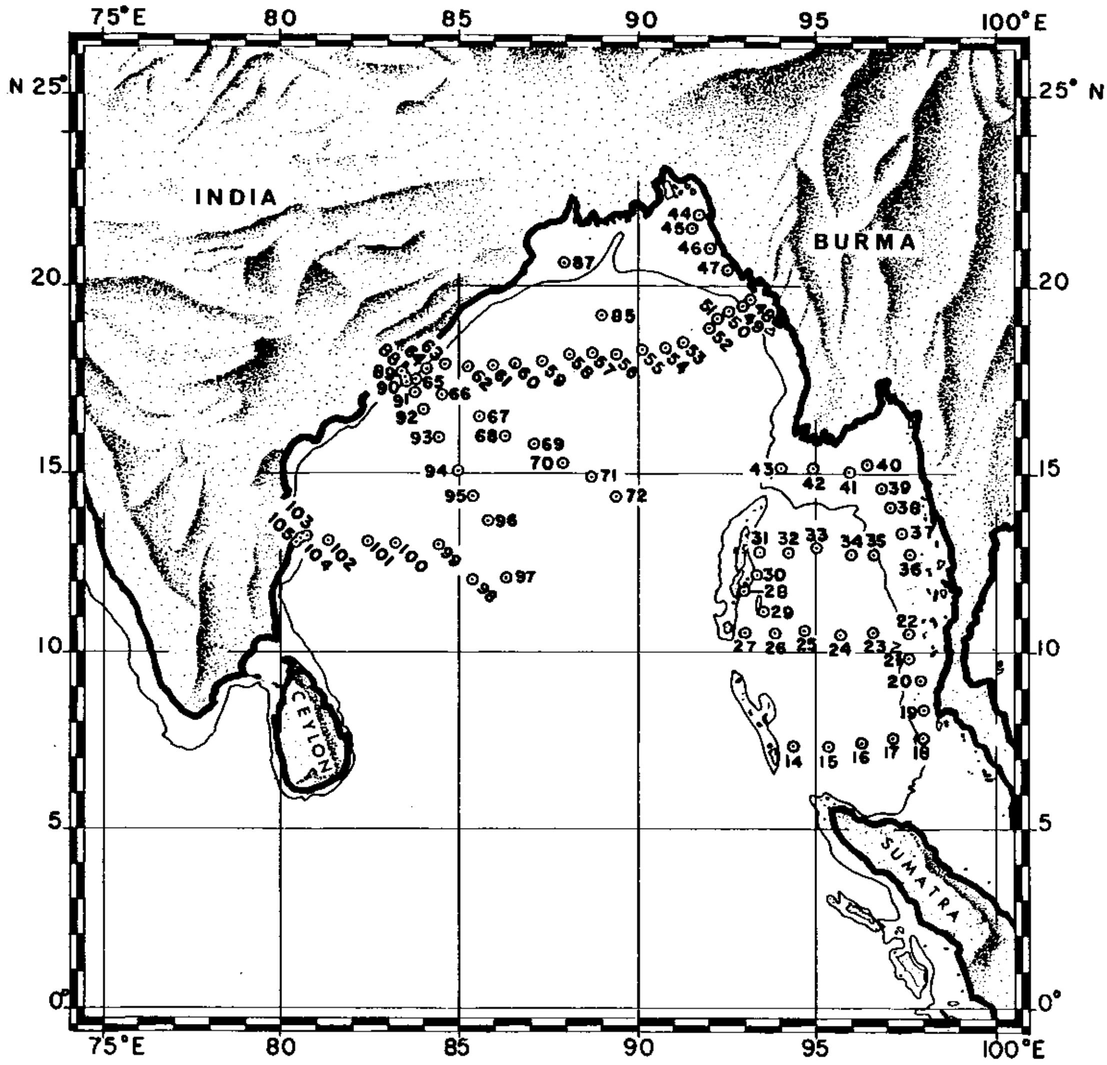


Chart 2. The station positions within the Bay of Bengal and the Andaman Sea. All these stations were occupied during cruise I (March – May, 1963).

In addition to the basic programme of routine physico-chemical analyses and plankton sampling, each cruise was related to the purposes of various interest groups who performed their studies usually within the overall aim of meridional sampling, with stations spaced between two and five degrees of latitude apart. Briefly stated the main objectives of the cruises involved here, together with the personnel who undertook studies of related interest to this dinoflagellate study, were:

Cruise I – predominantly interested in bottom trawling and dredging in the Andaman Sea and Bay of Bengal. The stations were concentrated in the eastern region in the hope of observing any effects following the North East Monsoon. R. NORRIS on board this and the following cruise made observations on living dinoflagellate material, including the taking of colour micrographs. Two publications have resulted from his work (1966, 1967).

Cruise II – undertaken during the period of the South West Monsoon, using long-line fishing methods to study the distribution of large pelagic fishes and sharks. In addition to the work of R. NORRIS, S. McDOWELL Jr. examined tintinnids.*

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* An abstract of his results, to the generic level, was presented to the Second International Conference on Protozoology, London, 1965.

Table 1. Summarised cruise, station and date information (cruise appellation as employed in the data reports of the Woods Hole Oceanographic Institution).

Cruise	Station Numbers	Monsoon	Dates	No. of Samples	Locality
A	13	Inter.	4 III 63	1	W. coast of India
I	14–105	Inter.	19 III–3 V 63	79	Andaman Sea, Bay of Bengal
II	106–144	S. W.	23 V–17 VII 63	25	70° and 80 °E meridians
III	147–160	S. W.	16 VIII–12 IX 63	12	60 °E meridian
IVa	161–162	Inter.	25, 26 X 63	2	N. of Mauritius
V	282–327	N. E.– Inter.	29 I–30 IV 64	40	Arabian Sea, and 55 °E, 75 °E meridians
VI	328–355	S. W.	17 V–12 VII 64	21	65 °E meridian
VII	358–375	S. W.	30 VII–24 VIII 64	15	Southern end of Mozambique Channel
VIII	396–420	Inter.	28 IX–5 XI 64	18	Durban to Mombassa through the Mozambique Channel

Cruise III – concerned with deep mid-water trawling for bathypelagic organisms. A.W.H. BÉ studied foraminifera, and J. FELL studied the occurrence and distribution of pelagic yeasts (FELL 1967).

Cruise IVa – the only cruise particularly concerned with microplankton and chemical aspects of primary productivity. The personnel, chiefly from the Woods Hole Oceanographic Institution, and headed by J.H. RYTHER, included numerous productivity and nutrient chemistry specialists. (Most unfortunately, only two samples were available for study here). Some preliminary results were published (RYTHER & MENZEL, 1965).

Cruise V – a seasonally-contrasted continuation of Cruise II, consisting of a very extensive series of samples, several of which were obtained during the North East Monsoon. M.B. ALLEN carried out observations on nannoplankton cells.

Cruise VI – continued the work of Cruise III.

Cruise VII – began two cruises in the western Indian Ocean by carrying out a principally benthic sampling programme to the south of the Mozambique Channel. O. BANDY, cruise leader, investigated the benthic foraminifera.

Cruise VIII – the last cruise on which plankton samples were routinely collected, passing northwards through the Mozambique Channel from Durban to Mombassa. A. SOURNIA investigated the diel variability of primary productivity during this cruise (1967b) and also examined blue-green algae (1968c). He used dinoflagellate material for his semi-monographic study on the genus *Ceratium* (1968a).

Later RYTHER et al. (1966) described the general features of primary productivity observed on all the cruises on which the fixation of ^{14}C was measured. Two papers were published on particulate organic matter (MULLIN 1965a, b) and one on nitrogen fixation associated with masses of the plankton blue-green algae *Trichodesmium* in the Arabian Sea (DUGDALE, GOERING & RYTHER 1964). GRICE & HULSEMANN (1967) reported on bathypelagic calanoid copepods collected on cruises II and VI.

Finally, although this report contains the full results of the dinoflagellate work by this author, three short papers on particular aspects of the material have been published previously (TAYLOR 1969, 1971, 1972b), a summary of general aspects of the study has been published (1973b) and the material has been used for supplemental reference in four papers (TAYLOR 1968, TAYLOR & CATTELL 1969, TAYLOR 1972a, 1973a).

Earlier Indian Ocean dinoflagellate studies

Until the advent of the International Indian Ocean Expedition, the Indian Ocean could claim to be one of the least studied bodies of water in the world, a dubious distinction which has now passed to the South Pacific Ocean. This was as true, or more so, for the study of dinoflagellates as for any other aspect.

The "Challenger" Expedition, 1873–1876, passed through the Indian Ocean but, unlike the diatoms, the dinoflagellates were not given monographic treatment in the reports, the only references being those of MURRAY (1876, 1885) on *Pyrocystis*, a common genus in the Indian Ocean but, as no localities were given, these references cannot be claimed for the area.

It was the eminent Swedish planktologist, P.T. CLEVE, who published the first figures of Indian Ocean dinoflagellates. In 1900 he published two papers (1900a, b) containing notes on a variety of organisms he observed in material collected in the southern Indian Ocean by the Dutch frigate "Tromp", and in miscellaneous samples from the Red Sea. Later he published a more extensive paper (1901) on plankton from the northern Indian Ocean and Malaysian waters, listing sixty-nine dinoflagellate species with localities although unfortunately illustrating none. His final work on the Indian Ocean was published in 1904 on a series of Arabian Sea samples collected by Thorild WULFF on a cruise to and from Bombay (via the Suez Canal). He listed sixty species of which two were new.

The Danes OSTENFELD & SCHMIDT published an early, taxonomically important work on microplankton from the Red Sea and the Gulf of Aden (1901) which included figures and the descriptions of eight new taxa and one new combination. Several of their taxa are distinctive members of the Indian Ocean community.

Other early short papers on northern Indian Ocean material were published by SCHRÖDER (1906 – in which he compared the microfloras of different tropical regions) and CZAPEK (1909 – including comments on dinoflagellate-produced bioluminescence).

In 1906 and 1907 KARSTEN published the first major reports on extensive material from the Indian Ocean, his having been collected by SCHIMPER on the German "Valdivia Expedition" around the world. Although the 1906 volume was primarily concerned with Atlantic Ocean material it also included observations on a short cruise along the southern African coast from Cape Town to Port Elizabeth and return. The 1907 volume dealt exclusively with Indian Ocean material drawn chiefly from the central Indian Ocean as the "Valdivia" passed from Antarctic waters to the East Indies. KARSTEN's numerous figures, although strongly stylized during the lithographic process, form an indispensable basis for the study of Indian Ocean microplankton. The latter part of the volume included one of the earliest lengthy discussions of general aspects of oceanic microplankton ecology including distribution with depth and possible influence of the environment on the form of plankton species, his observations supplementing the classic studies of SCHÜTT (1893, 1895), on tropical Atlantic Ocean material.

BÖHM published four papers of significance to the Indian Ocean. The first (1931a) was a short paper on dinoflagellates from the Persian Gulf, based on material collected by V. PIETSCHMANN in October, 1910, a contribution which has been largely overlooked by later workers including WOOD (1963a) in his checklist. He listed fifty taxa, illustrating sixteen of them. Several were new species. Although his larger work on the distribution and biometrical aspects of variation in *Ceratium* (1931b) primarily concerned Asian coastal waters it contained an appendix dealing with ceratia from the southern Bay of Bengal. His third work (1931c) dealt with members of the genera *Histioneis* and *Parahistioneis* found in the northern Indian Ocean. In 1935 he published an interesting study of morphological variability in two species of *Dinophysis*, *D. miles* and *D. caudata*, occurring in the Indian Ocean.

A major work on Indian Ocean dinoflagellates was published by MATZENAUER in 1933. Although he omitted the genus *Ceratium* he provided more than one hundred illustrations of other taxa, mostly of species of *Peridinium*. His material was independently collected by MOLISCH and RUTTNER in the 1920's during cruises in the northern Indian Ocean from the East Indies to the Suez Canal. MATZENAUER attempted to distinguish regional differences from his limited material and also included some biometrical data on some highly variable species of *Dinophysis*.

The former's omission of *Ceratium* was fully compensated for by the studies of STEEMAN NIELSEN on the ceratia collected by the "Dana" during a circum-global cruise from 1928 to 1930, first with a southern Pacific Ocean study (1934, which included most of the illustrations of taxa) and then one on east Asian waters and the Indian Ocean (1939a). He discussed distributional features and attempted to assign the species to three categories according to their apparent depth preferences. Oligophotic species, occurring predominantly below 100 m were recognised. (A third paper by him, 1939b, dealt solely with this aspect. It was later given largely supportive data by GRAHAM & BRONIKOVSKY 1944, although not with the use of Indian Ocean material.)

Following these studies there was a period in which dinoflagellates received only scant attention. This hiatus was broken by the inclusion of west Australian coastal species in WOOD's large work (1954) on dinoflagellates from Australasian waters. The usefulness of this major work, and of its two supplements (1963b, c), was seriously reduced by the sketchy nature of the illustrations and, in the case of the first publication, their excessivly reduced printed size.

SILVA (1956a, 1960) produced two works on the dinoflagellates, diatoms and tintinnids from Mozambique waters, illustrating a moderate number of species. Her publications were not cited by WOOD in his checklist (1963a) of Indian Ocean dinoflagellate species. BALLANTINE (1961) supplemented these observations with a study on a few samples from the vicinity of Zanzibar, recording 34 species and illustrating more than half of them, including a new species of *Gymnodinium*. TRAVERS & TRAVERS (1965) produced a preliminary list of phytoplankton and zooplankton species found at Tuléar, Madagascar. Further mention of dinoflagellate species from the Mozambique Channel is found in the works of ANGOT (1965, 1970) and ANGOT & GERARD (1967). The most extensive work in the west central Indian Ocean, particularly with reference to the Mozambique Channel, has been carried out by SOURNIA. In addition to various works on aspects of primary productivity (including a review on seasonal variation in tropical primary productivity: 1969) his publications of 1966a, b, 1967a, 1968a, b, d, 1970 and 1973 either include descriptions or provide lists of dinoflagellates from the area. One of them (1968a) is an extensive monograph on the genus *Ceratium* and another (1966b) dealt with morphological variability within the same genus.

In the south western Indian Ocean there have been a number of publications dealing with dinoflagellates of that region. The "red tide" studies of GRINDLEY & TAYLOR (1962, 1964, 1971, plus TAYLOR 1962) are marginal to the area, chiefly concerning False Bay which, although it is east of Cape Point, is west of Cape Agulhas, the latter making a more realistic western boundary to the Indian Ocean than the former. TAYLOR (1963, 1967) published further studies on the region, the first paper describing a new genus, and the second including a list of 142 dinoflagellate species (plus diatoms and other phytoplankton groups) found in the International Indian Ocean Expedition material collected by the S.A.S. "Natal." The Agulhas Current was shown to carry tropical species below 30 °S off the coast of southern Africa although the majority were not present by the time the current reached its south-western extremity below Cape Agulhas. Use of "Anton Bruun" material has been made previously by TAYLOR either incidentally (1969b, 1972a) or as the chief topic (1969a, 1972b, 1973b). The last cited work consists of a summary of the main distributional features descovered during the present analysis.

Further records of dinoflagellates from the south-western region are to be found in the works of THORRINGTON-SMITH (1969) and NEL (1968). REINECKE (1971, 1973a, b) in addition to papers on red water from the west (Atlantic) coast of South Africa, has published several parts of a monograph on *Ceratium* utilising material from the Agulhas Current region during the International Geophysical Year. Finally, GRINDLEY & HEYDORN (1970) have published a study on red-water caused by *Noctiluca* in the St. Lucia estuary system in northern Natal.

The north-western Indian Ocean is usually taken to include the Red Sea. Relatively little study on the dinoflagellates of that area (not investigated here, either) has been made. HALIM (1969a) has reviewed the knowledge of the phytoplankton of the Red Sea, including the names of the principal dinoflagellate species. DOWIDAR (1971, 1972) has described form variation in *Ceratium egyptiacum* as it appears throughout its restricted range from the eastern Mediterranean Sea, through the Suez Canal, to the Red Sea. KIMOR (1972) has made a comparison of the microplankton communities in the same area (using the Gulf of Aquaba as an index for the Red Sea) in an attempt to observe the influence of the Suez Canal on distributions, a question also considered by HALIM (1970).

HASSAN & SAIFULLAH (1972a, b) have begun a series of papers on dinoflagellates of the northern Arabian Sea off the coast of Pakistan, providing illustrations and some autecological notes.

A great many short papers which mention a few dinoflagellate species as part of unillustrated descriptions of phytoplankton composition off both the east and west coasts of India have been published in Indian journals since the 1920's (for example, those of GONZALVES 1947, and CHACKO 1950). Many of these have been cited by SOURNIA (1969) in his review on seasonal variability in tropical phytoplankton. SUBRAHMANYAN (1954, 1958, 1966, 1968) has published the only taxonomic works from this area concentrating principally on the phytoplankton off the west coast of India. In a check-list of species found in a five-year study in that area he recorded 109 species of dinoflagellates (1958), these being repeated with seasonal data by SUBRAHMANYAN & SARMA (1960). His most important dinoflagellate work is a monograph on the genus *Ceratium* (see further comments under the latter). "Red tides" caused by dinoflagellates in Indian waters have been described by AIYAR (1936), BHIMICHAR & GEORGE (1950), PRASAD (1953), and PRAKASH & SARMA (1964). SUBRAHMANYAN & SARMA (1967) found that dinoflagellates comprised a significant portion of the nannoplankton not retained by nets.

There have been no detailed taxonomic studies on the dinoflagellates of the Bay of Bengal or the Andaman Sea subsequent to the early studies of CLEVE and KARSTEN mentioned previously. General features of the phytoplankton of these regions have been described by DURAIRATNAM (1963, Ceylon), ZERNOVA (1962, 1967) and ZERNOVA & IVANOV

(1964, Andaman Sea) and NORRIS (1966, 1967) has photographically illustrated living dinoflagellates collected during cruises I and II of the "Anton Bruun."

In the open northern and central Indian Oceans SUKHANOVA (1962a, b, 1964) has described quantitative aspects and some features of the dinoflagellate communities. DURAIRATNAM (1964) described the depth preferences for 52 species found in the vicinity of Cocos-Keeling Island. THORRINGTON-SMITH (1971) has provided the results of an attempt to recognise tropical Indian Ocean communities and their relationship to "phytohydrographic" regions by various types of cluster analysis. The latter author found that only 38 of 237 phytoplankton species retained on membrane filters were dinoflagellates.

TSURUTA's large work on the plankton distributions of oceanic fishing grounds (1963), lists a total of 43 species of dinoflagellates from four Indian Ocean localities: south of the Greater Sunda Islands (Sumatra, Java, etc.), the north-central Indian Ocean, the south-eastern Arabian Sea, and the eastern Indian Ocean. Unfortunately only the diatoms were recorded from Bay of Bengal samples. These samples were collected by the Shunkotsu-maru between 1953 and 1958. Earlier short papers on the same subject by him, in Japanese, are summarised in this work.

Four papers deal with dinoflagellates of the eastern Indian Ocean. There are those of WOOD (1954, 1963b, c) mentioned earlier, plus a checklist of the species found in the Indian Ocean (WOOD, 1963a) and some papers on communities of phytoplankton in Australian waters (WOOD, 1964). DESROSIÈRES (1965) has given a description of the surface phytoplankton populations collected with a Hardy Plankton Recorder along 110 °E during two cruises of the Australian contribution to the International Indian Ocean Expedition.

The tropical and warm-temperate, oceanic dinoflagellates are so cosmopolitan that the preceding notes are really of limited historical or biogeographical interest. For example, no study on Indian Ocean members of this group could ignore studies from contiguous and confluent waters such as the East Indian observations of WEBER-VAN BOSSE (1901), FORTI (1901), SCHMIDT (1901), OSTENFELD (1915) and BÖHM (1931b, 1936). For that matter, all the classic works on the warmer regions of the Atlantic Ocean, Mediterranean Sea and Pacific Ocean are of direct relevance, as are the growing number of studies since 1940 by authors such as ABÉ, BALECH, GRAHAM, the LOEBLICHS, STEIDINGER, WALL and WOOD, all cited as comprehensively as possible in the reference list.

Some general taxonomic considerations

Before discussing the "Anton Bruun" material it is unfortunately necessary to digress here in order to clarify the conceptual and factual basis used in making nomenclatural decisions. Not only has there been disagreement among those few authors who have expressed their views on this subject, but in many cases one can only guess as to the manner in which many have interpreted concepts such as subspecies, variety and form. For example in SCHILLER's major work (1931–1937) he did not indicate the manner in which he used variety, leading PAULSEN (1949) to conclude that "one gets the impression that a small deviation from the specific characters is called a *varietas* and a smaller deviation is called a *forma* – quite subjectively." In fact this is not all that strange an approach (see the Infraspecific Taxa subsection which follows).

In dinoflagellates these difficulties with infraspecific concepts are undoubtedly an extension of problems in the concept of species. This in turn stems largely from the infrequently observed sexuality in the majority of members of the group and the consequent inapplicability of the generally used (and misnamed) "biological species concept" with its basis on reproductive isolation among sexually reproducing populations (see MAYR 1957, SONNEBORN 1957, PRINGSHEIM 1970).

In planktonic protists sexuality is sometimes cryptic. For example, although "auxospores" have been frequently observed in marine planktonic diatoms, it has only been relatively recently that their probable zygotic nature has been realised (LEWIN & GUILLARD 1963). Consequently caution seems advisable in claiming an absence or rarity of sexuality in other little known groups. Despite this, it is still evident from cultured species that asexual fission can continue through countless generations in the dinoflagellates, cryptomonads and euglenoids without the "senescence" and/or death known to occur in the absence of sexuality in groups which possess sexual reproduction (see reviews by JENNINGS 1929, PREER 1969).

In wholly asexual organisms all individuals are genetically isolated from each other (perpetual apomyxis). Genetic novelties which arise in individuals, if viable, are transmitted to all succeeding generations from that parent until further changed or until the generational radiation is extinguished. Mutations can be considered the primary, although not the sole, source of variability in such organisms. The haploid condition that is probably present in at least some dinoflagellates (DODGE 1963, 1966) increases the likelihood of the novelty being patently expressed, rather than remaining latent, and may be a highly adaptive condition. On the other hand, many dinoflagellates may be polygenomic ("polyenergid") as suggested by their great numbers of chromosomes (also known in ciliates, amoebae and radiolaria). Fortunately a new level of sophistication is being introduced to the understanding of dinoflagellate nuclear characteristics with the application of electron microscopy (e.g. KUBAI & RIS 1969, SOYER & HAAPALA 1974), DNA renaturation kinetics (ALLEN et al. 1975) and other analyses beyond the level of light microscopy.

With haploid species the daughter cells should have identical nuclear genomes. However they can still be genetically different as a consequence of an unequal sharing of "cytoplasmic" genes (mitochondrial, chloroplastic, other?) as well as being physiologically different due to chemical gradients in the dividing mother cell. Polygenomic parent cells can produce small genetic differences in their daughter cells (assuming some "heterozygosity") during simple asexual fission. In a sense they can have unlike alleles at the same loci on different homologous chromosomes, potentially perhaps tens or hundreds. Single compound chromosomes containing the entire haploid genome may be present, although ALLEN et al.'s (1975) results show that this is not so for *Crypthecodinium cohnii.* A variant mechanism has been proposed by SONNEBORN (1957, p. 300) operating by "the possession of multiple gene loci for alternative and mutually exclusive traits which are readily transformed one into another in response to different environmental conditions." The latter mechanism (hypothetical) would be equally useful for diploid organisms and would not require cell division to create new phenotypes.

With species in which sexual reproduction is present but infrequent (excluding monoecious inbreeding) one encounters a situation where longterm genetic isolation is interrupted periodically by participation in a gene pool. Thus new variations are contributed to the pool where they can be potentially shared by those other than the immediate progeny of the mutant although to a much more reduced extent per number of generations than in wholly or alternately sexually reproducing species. The life-cycle studies of VON STOSCH (1964, 1965, 1967, summarised 1972, 1973) have revealed cryptic sexuality in each of six species studied to that date.

It is possible that several types may be present in dinoflagellates, including different types of nuclear division. Unequal nuclear division has been observed. SILVA (1969, 1971) found that dwarf cells can arise from smaller nuclear moieties in some species, this suggesting a gene dosage effect.

In view of the considerations outlined above one might expect a greater presence of gradual gradients of variability in wholly or primarily asexually reproducing species than in those in which the frequency of sexual reproduction is high. As variability is largely the product of point- and chromosomal mutations the rate of speciation (in this case, disjunctive variance) might be expected to be low. The tendency of such organisms to occur in relatively constant environments probably reflects the limitations on distribution imposed by their reduced flexibility to major environmental changes, although in the case of some internal symbionts it is more probably due to loss of sexual abilities. On the other hand there has been no assessment of the efficiency of dino-mitosis and the rate of chromosomal mutation (or its equivalent) might be higher than in conventional, spindle-mediated mitosis.

There are indications from micropaleontology that in marine dinoflagellates the rate of morphological change has been relatively slow. One of the commonest species in tropical and subtropical oceanic regions is *Heteraulacus polyedricus* (POUCHET) DRUGG et LOEBLICH [= *Goniodoma polyedricum* (POUCHET) JÖRGENSEN]. MORGENROTH (1966) has reported and illustrated specimens (presumably cysts) from a Lower Eocene deposit in northern Germany which he referred to this species. A very similar form has also been found by DRUGG & LOEBLICH (1967) from a North American, Middle Eocene deposit which, because of the poor formation of some plate-equivalents, they designated as a new genus (*Heteraulacacysta*) These findings suggest that there has been remarkably little morphological change over a period of approximately 50 million years in the lineage of one of the most cosmopolitan and "successful" marine species. Other lineages, particularly among those cysts referred to the fossil genera *Leptodinium* and *Spiniferites,* may be older (c.f. WALL 1970, SARJEANT 1974, TAYLOR 1976).

The asexual species concept

In permanently asexual organisms the biological species concept ceases to exist because its most attractive feature, a good operative definition ("can the subject potentially interbreed with others or not? "), cannot operate at all. Even if sexuality is eventually demonstrated in nearly all dinoflagellates, the manner in which "asexual species" is conceptually formulated is still important in its bearing on primarily asexually-reproducing species. In this context SONNEBORN's (1957) chapter dealing principally with ciliate genetics in the work edited by MAYR (1957), and to a lesser extent, the chapters by MAYR in the same publication, deserve close examination for they represent the only extensive, relatively recent discussions of the asexual species problem.

SONNEBORN considered that part of the problem involved in arriving at a satisfactory, all embracing definition for both sexual and asexual species was the insistence by most earlier authors that a species be the unit of evolution as well as the customary unit of identification. From previous work on ciliate mating types he had included several genetically different subgroups within single species. At first he termed these subgroups "varieties" but later, in his 1957 paper, proposed the term "syngens" for them, defining one syngen as a group characterised by "minimal irreversible evolutionary divergence" (1957, p. 289) and considering it to be the evolutionary unit within the ciliates he studied. Effectively these units seem to correspond with "sibling species" (MAYR 1948) and with the older term "biotype" (see JENNINGS 1929). Syngens do not usually correspond with morphologically-defined species, and this was one reason SONNEBORN preferred to distinguish between the two, using "species" only for the latter.

He attempted to extrapolate the concept of syngens from sexual to asexual protists, arguing that, although they could not be measured in the same manner, homologous units did exist in asexual organisms. Unfortunately, although he intended to produce a concept which emphasised the functional equivalence of syngens in sexual and asexual organisms, his arguments appear to be rather circular. He stressed that asexual syngens could only be delimited by extensive experiments involving as many comparative factors as possible. "The discontinuity and the complexity of its genetic basis are the essential features of the difference between closely related syngens" (1957, p. 290). This then was a quasi-quantitative genetic distinction requiring no "gene pool" equivalent. However he then maintained that only syngens could "potentially contribute to the further evolution of the group" (1957, p. 291), thereby returning to the old problem posed by permanently asexual species: only single individuals can genetically contribute to the future evolution of their descendants. Furthermore, because of asexuality they can be considered to have diverged irreversibly in an evolutionary sense. Perhaps he maintained this potential for reversibility (only implicit in his writing) because of his agreement with the view that probably all asexuality in protists is secondarily derived. With dinoflagellates and euglenoids it would be difficult to dismiss their asexuality as secondary because it is in these groups that one finds several features suggestive of a very primitive nuclear condition, especially in dinoflagellates. Features such as the lack of a fully dispersed chromosomal phase (except in *Noctiluca* and a few other genera), minimal histone penetration of the chromosomes, and apparent participation of the nuclear membrane (which does not break down) in genophore separation, are all somewhat similar to the prokaryotic condition, leading DODGE (1965) to suggest the term "mesokaryotic" for them. These features were unknown at the time of SONNEBORN's article.

Despite the difficulties in producing an unequivocal concept of the "asexual syngen" SONNEBORN did produce a good operational guideline for the recognition of asexual species:

> "the genetic difference between species in asexual organisms should be as nearly as possible of the same kind and magnitude as in sexual organisms" (1957, p. 284).

Although the information to assess this is lacking at present it can be weighed in the future, and it also strikes at the arguments for species distinctions based on single, apparently genetically small, differences in asexual species (see following section).

This definition of a species is essentially an analogue of the biological species concept. It is based on quantitative genetic discontinuity and not on the mechanism by which it is expressed. DNA hybridisation studies may prove to be a useful tool for testing this genetic divergence in predominantly asexual species. None have been performed on dinoflagellates at the time of writing.

By largely ignoring such conceptual subtleties plankton taxonomists have successfully established thousands of asexual morphological species; "successfully" in the sense that the system they have produced by observation, trial and much continuing error, does work most of the time as a means of communication. The reason for this modest success would seem to be that asexual planktonic systematics has dealt with a structured morphological range containing fairly readily establishable morphological discontinuities. MAYR's explanation for such structure in asexually reproducing organisms (instead of the presence of large, vaguely-defined continua) was:

> "existing types are the survivors among a great number of produced forms, [that] the surviving types are clustered around a limited number of adaptive peaks, and [that] ecological factors have given the former continuum a taxonomic structure. Each adaptive peak is occupied by a different 'kind' of organism, and it is legitimate to call each of these clusters of biotypes a species" (1957, p. 382).

His version of the asexual species was similar to SONNEBORN's except that it excluded criteria other than morphological:

> "Those asexual individuals are included in a single species that display no more morphological difference from each other than do conspecific individuals in related sexual species." (1957, p. 381).

MAYR's definition might serve as a useful short-term operational guide although contemporary views undoubtedly support SONNEBORN's quantitative genetic difference approach as a means to a long-term goal. SIMPSON (in SIMPSON & BECK 1965) has provided an evolutionary species definition which applies equally to uni- and biparental organisms. It is not useful for present empirical applications, however.

Infraspecific taxa

Dinoflagellate taxonomic literature is full of references to infraspecific taxa, usually subspecies, varieties and forms. Treatment of such taxa has often been highly casual, with forms and varieties being interchanged without explanation (for example in the major works of JÖRGENSEN 1911, 1920 and LOPEZ 1955, 1966). Author accreditation has also been given in ranks other than those in which the authors concerned created their combinations. LOEBLICH Jr. & LOEBLICH III (1966, 1968, 1969, 1970a, b) have tried to establish the priorities for authors at ranks above species, but below the species level this tedious (but necessary) task continues piecemeal (e.g. SOURNIA's, 1968a, monograph on *Ceratium*).

There are those who have argued that asexual organisms that differ constantly from each other in however slight a way should be considered as different species (e.g. PAULSEN 1949) so that infraspecific genetic differences can be ruled out. SONNEBORN has answered this approach effectively:

> "Species differences in sexual organisms are based upon complex, not simple, genetic differences. To reduce species differences to a single trait dependent on a single gene difference is to equate species differences in asexual organisms to the level of individual differences in sexual organisms." (1957, p. 286).

Variability within morphologically-defined species of protists is often considerable and of many different kinds JENNINGS (1929) recognised more than a dozen causes of variability such as age following division, pathology, etc. He subdivided these into short term phenotypic (genecological) responses (although he did not use these terms for them), longer term phenotypic responses involving several or many generations but reversible on return to environmental conditions similar to those prevailing originally, and genotypic differences. Many of these could appear within a clone (a "pure line") derived from a single parent cell. It is not necessary to detail all those possible sources of variability within a species or clone at this stage. Here we can deal with those of particular consequence to the field taxonomist and ecologist.

Morphological continua

Perhaps the most troublesome, common problem in handling dinoflagellate taxa is what to do with species which show large, sometimes multidirectional, morphological continua. The genus *Ceratium* has several of these problem species (e.g. *C. tripos, C. breve, C. concilians* and *C. horridum*). Although some of this variation may be attributed to phenotypic plasticity (see below under Genecological variants) much of it resembles the type of small scale, genetically-based variability found in ciliates and testaceans by JENNINGS (review, 1929) referred to earlier.

Several of the variants had been considered separate species until shown to be connected to others by continuous variation. A classic example of this is the demonstration of the link between *C. pulchellum* and *C. tripos* by LOPEZ (1955), using visual and biometric data. Such treatment is consistent with SONNEBORN's views discussed earlier.

These variants have been given both formal and parasystematic designations and are discussed further later (see Formal recognition of infraspecific taxa).

Life-cycle polymorphism

One of the greatest degrees of morphological variability observed in dinoflagellates results from life-cycle transformations. These involve both unigenerational and multigenerational transformations. Cyst formation is the most obvious unigenerational change and has been most involved in the process of equating the observations of micropaleontologists (dealing largely with cysts) with those of neontologists. The discovery that hystrichosphaerids were virtually all dinoflagellate cysts was a comparable discovery to that relating the planktonic "Zoea" larva with the adult crab and the "Leptocephalus" larva with the eel (see reviews on dinoflagellate life cycles by WALL 1970, 1971a and remarks under *Gonyaulax* here). Members of the Noctilucales also pass through striking maturational changes (see CACHON & CACHON 1967, 1969a) which have been given names such as "sporont" (small, freshly reproduced individual) and "trophont" (large, mature individual). These variants could all perhaps be classed as "Ontogenophenes." Multigenerational changes involving planktonic cysts and shortlived motile stages are a principal feature of the Pyrocystaceae (see later) and parasitic species. APSTEIN (1909) proposed the term "generatio" for the distinct life-cycle stages of *Pyrocystis* although this has not been adopted by later authors and the various stages are not recognised formally in the taxonomy of the group.

A recent practical problem which has arisen in dinoflagellate taxonomy is the occurrence of sexual dimorphism in sexually-reproducing species of *Ceratium*. Although suspected since the turn of the century it was only clearly established by VON STOSCH (1964) in *C. horridum*. It also appears to be likely in *C. tripos*. Not only have the smaller male gametes been termed separate species, but they have also been assigned to a different subgenus (*Ceratium* vs. *Tripoceratium*) due to their antapical horn arrangement. The present dilemma involves questions such as: Are all marine *Ceratium* species sexually reproductive? If so, how many exhibit sexual polymorphism? Also, are there small members of *Ceratium* which are genuine species and yet appear identical to the gametes of other species? In what other genera do similar phenomena appear, and with what frequency? At present there is not sufficient information to resolve any of these important questions. At least, thanks to their recognition as separate species it will be possible to reconstitute the distributional data with ease when such questions are finally answered.

Genecological variants

The degree of morphological plasticity which can be expressed by members with a similar genetic constitution due to differing environmental influences ("ecophenes") is a problem which has concerned, and still does concern, those studying natural communities. It has drastic effects on morphological taxonomy, and is important in understanding the degree of short-term "physiological adaptation" which each species is capable of.

Horn length and robustness in species of *Ceratium* has been one of the most discussed aspects of this type. It has been observed that the horns of many *Ceratium* species were longer and more delicately developed in warmer (KARSTEN 1907), oligotrophic waters (as expressed by phosphate values) and shorter and more robust in colder, relatively eutrophic waters (PETERS 1932, STEEMANN NIELSEN 1934). The distance from land (oceanic or neritic) was thought to have an influence on horn length in a similar manner to that indicated by phosphate levels (STEEMANN NIELSEN 1934). Body size appears to also be related to temperature, being widest in cold temperature and narrowest in warmer waters. Implicit in the writing of these authors is the view that the responses are forms of phenotypic plasticity. LOPEZ (1966) found that this size/temperature variation had a seasonal expression in the western Mediterranean Sea with greatest girdle diameters relative to horn length occurring in winter, the period in which the species were also most abundant. However,he considered the seasonally-appearing states were different genotypes, rather than physiological responses of the same genotype.

The view that many species of *Ceratium* occur summer and winter temperature-regulated variants was taken further by SOURNIA (1966b, 1968a). He identified the psychrophilic (cold-loving) and thermophilic variants of eleven species. A comparison of the ranks used by LOPEZ and SOURNIA in discussing these variants is indicative of the confusion which can arise. LOPEZ (1966), probably not intending to imply rank designation, refers in his text to the variants in some places as varieties, and in other parts of the text as forms. However, when he lists the taxa in a formal way or assigns figures to them he invariably uses the subspecies naming convention, e.g. *C. candelabrum dilatatum*, without using the term subspecies at all. This lack of clarity in rank designation is very unfortunate, but it is an example of the casualness with which these taxa have often been treated.

SOURNIA (1966b, 1968a) used the varietal rank for the main temperature/seasonal taxa in *Ceratium*, proposing the term "forma" for other variants apparently not regulated by temperature. He did not assert that the former were genotypic variants, as claimed by LOPEZ, but his use of "variety," if used according to custom, implies it. However it is not then clear that he thinks all other variants are phenotypic only. Instead he draws attention to our continuing ignorance about such matters despite the few culture studies which have been undertaken.

A striking type of variability in *Ceratium*, apparently related to the factor (-s?) in the water regulating horn length, is the phenomenon of autotomy. This term, the same as that used for the regulated loss of appendages in invertebrates or the tails of lizards, for example, was used first in dinoflagellates by KOFOID (1908) for the abscission of horns. Various stages of the phenomenon can be seen here in figs. 173, 190–192, 201, 212, 220, 222 and possibly 205, 206 and 208. After abscission of the horns regrowth can, and probably does occur. Regrowth is often evident by an abrupt change in the thickness of the wall material at the points close to the body where abscission occurs (figs. 212, 220). It can sometimes be strikingly out of alignment with the usual horn shape (fig. 220). In *C. vultur* the latter is so common that this state is recognised as a forma (f. *recurvum*). Autotomy would appear to be a good example of a genecological response, although the precise factors regulating it are unknown (nutritional? water density? light?).

There are many other cases known where such phenomena may occur in dinoflagellates. As one further example the reader can refer to the notes on *Dinophysis miles* var. *schroeteri* here (or in TAYLOR 1973b), limited in its distribution to the waters of south-eastern Asia. One possibility is that its peculiar condition arises from a local environmental effect although the apparent (not certain because of depth of sampling) co-occurrence with another morph suggests a genotypic difference.

Physiological strains

Marked physiological differences have been observed within some morphologically-based dinoflagellate species. *Noctiluca scintillans* is known to occur both in a strongly bioluminescent state and also from the North East Pacific Ocean in a condition lacking in bioluminescence (ECKERT & FINDLAY 1962, and personal observation). Strains of *Gonyaulax acatenella* with strongly pigmented chloroplasts as well as strains that are colourless are known, the former producing paralytic shellfish toxin, the latter reportedly not (PRAKASH & TAYLOR 1966). Sand dinoflagellates commonly exhibit colourless or pigmented appearances within apparently the same species (personal observations). It is clearly important to determine if such colour differences are the result of bleaching due to nutrient or physical effects (chlorosis), or due to a total lack of chloroplasts. Also, the degree to which such effects are genetically versus environmentally controlled is important in applying such non-morphological differences to the delimitation of species. As indicated earlier, it is probably premature to use such data as a primary means of species distinction. However all such data will be ultimately important in defining Sonnebornian "asexual species."

These physiological variants have not been accorded formal infraspecific nomenclatural recognition, the term "strain" being useful in this context although in its strictest sense it can only be used for clonal descendants determined under culture conditions.

Teratological individuals

Before describing an unusual-looking cell as a new species it is necessary to note the marked aberrations which have been known to occur in the development of some species. Supernumery horns are quite commonly found in members of *Ceratium* (eg. SOUZA 1950, HASLE & NORDLI 1951). Another type of aberration seems to be exhibited by the specimen shown here in fig. 139 in which the left antapical horn of a cell which in all other respects greatly resembles a member of *C. symmetricum*, arises in an unusual manner, the basal region of the body also showing a large bump not present in normal cells. BURSA (1962) has described further types of aberrants which can develop in both thecate and non-thecate species due to osmotic stress, feeding, damage, etc.

In field material such teratological individuals can be partially recognised because of their individuality in populations showing a more regular appearance.

Formal recognition of infraspecific taxa

Having accepted the existence of many different types of variants within dinoflagellate species it is necessary to decide which, if any, should be formally recognised in their systematics, why, and by which names. It could well be argued that the categories subspecies, variety and forma have been used so ambiguously that they are sources of confusion and should be abandoned. Others, such as HUXLEY (1940), considered such distinctions, other than subspecies, were not important enough to warrant formal taxonomic recognition, a view now incorporated into the Zoological Code (1961 version). The following is a personal view of the problem from a chiefly pragmatic standpoint:

One obvious value of the formal naming of a taxon is that, once established in the identificatory literature, it will appear in non-taxonomic, community or species level ecological studies as a label for a category. If it does not appear in the identification guides used by ecologists, it will not be recorded by them and a great deal of potentially valuable environmental data will be lost. One quasi-infraspecific taxon for which this is most serious is the "later-to-be-raised-to-species-level" variant. The act of subsequent raising of the variant to the species level immediately casts doubt on the distributional and other environmental data previously assigned to the category that included it in all cases where figures or descriptions are not available. Also, environmental data for the new species must be obtained de novo. If the raised taxon was recognised previously as a formal infraspecific rank it is a simple matter to sort out relevant data for both it and its former partner, data which may extend back more than fifty years and involve several major oceanographic expeditions. From the ecologist's viewpoint "splitting," however much of an irritation if may be, should be greatly preferable to "lumping." The latter, if wrong, is rendered useless; the former is remediable.

Apart from the above, there are undoubtedly some genuinely infraspecific categories which deserve recognition among the range of variants known. Which of these should be recognised is determined largely by the questions one wishes to ask although it might be assumed that some are of broad enough interest for almost all taxonomists, geneticists and ecologists. SONNEBORN's species definition admits of genotypic variation within the asexual species. Such genetic variability can be of a gradual clinal type from one extreme to another, or it may be in the form of a few major variants with very rare intermediates. It is the existence of intermediates, however rare, which unites them operationally into a species. These differences in structural distribution are an important feature of the make-up of the species and could be recognised formally within existing terminology.

The Botanical Code allows for the formal treatment of the following infraspecific taxa: Subspecies, Variety, Subvariety, Form and Subform (ICBN, Art. 4). However, the Zoological Code excludes all infraspecific taxa except for subspecies (ICZN, Arts. 1, 45 c, e) in accordance with the view expressed by HUXLEY (1940). It is evident from the preceding that the Botanical Code at present offers a greater flexibility in handling the infraspecific variation of protists.

Subspecies: Recognition of this taxon poses a problem largely because the concept of a subspecies has often been associated with distinct distributional groups (i.e. Turessonian "ecotypes"). Thus HUXLEY (1940, p. 36 et seq.) indicated that a definable geographical range was an essential part of the concept. Providing that the concept is not limited in this way it seems to have useful potential for microplankton species as a term for the recognition of major genetic variants where these are few and the morphological distribution falls heavily within these few types, intermediates being rare. Although thus amenable to definition it is difficult to apply at present without adequate biometrical data. In fact none of the taxa dealt with in this work is known well enough to fit this concept well. The closest would appear to be the major summer and winter variants of some species of *Ceratium* (SOURNIA 1966b, 1968a). The biometrical studies of LOPEZ (1955, 1966) have indicated numerous intermediates between the major conglomerates of morphs ("clusters"). At some future date it might be possible to agree on a measure of quantitative taxonomy which would indicate whether selection of the taxon subspecies or variety was preferable. In other words the procedure advocated here ist the use of variety until the clinical distribution of genotypic variation has been clearly elaborated and some agreement has been reached as to the degree of clumping of features necessary for subspecies recognition.

Variety: This concept is used here in rather the same way as it has been used for diatoms by FRIEDRICH HUSTEDT, i.e. as end-points for clinal, genetically produced, variational ranges: „die Varietäten sollen hier die Endglieder von Formenreihen bezeichnen. Eine Benennung von (selbstverständlichen) Zwischenformen ist überflüssig und nachteilig, weil sie die Nomenklatur ins Uferlose führen muß, ohne irgend etwas Neues zu bringen." (1930, p. 648). However one essential variety to be recognised is that represented by the original specimen (or figure) on which the species is based (the nominate variety). This may not be an endpoint, in which case this is an exceptional recognition of an intermediate condition. This nominate variety, as with nominate taxa at other levels, is given the same epithet as the species but without the citation of an author for it. It is also to be understood that variability can occur in more than one direction, and several end-point varieties may be recognisable. In passing it can be noted that HUXLEY (1940) proposed the term "paramorph" to replace variety because he thought it had become too muddled in its usage.

Form: Forms are here considered to be purely phenotypic variants in the sense proposed by SALISBURY (1940). This is also the most common manner in which the term has been used for microplankton organisms (in the few cases where it has been defined, e.g. PAULSEN 1949). Potentially such plasticity could be related to external environmental influences ("ecophenes") or to a developmental or life cycle modification ("ontogenophenes" or sexual dimorphism – see earlier sub section on life cycle polymorphism). Ecologists and perhaps evolutionists concerned with adaptiveness would be more interested in the former usage, whereas general biologists might be more interested in the latter. For the present any of these could be incorporated under this term although the demands of precise scientific communication are not well served as a result. Instead it is used here only to denote presumed ecophenes and it should be indicated as to which environmental parameter is thought to produce the response.

All other infraspecific variants have to be dealt with informally by the use of terms such as "strains" (= stocks, clonally-derived lines of descent), "phases" or "stages" (for life-cycle variants) etc. "Ecotype" has usually been used in a different sense to ecophene. It has been taken to signify groups which are genetically different because of ecological effects. In one sense this could simply be a direct product of natural selection (e.g. selection caused by hot springs, hypersaline lakes, etc.), and this in turn might correspond to geographic subspecies.

Finally, how can intermediates be handled in the nomenclature? HUSTEDT's view of variety (above) considered any such names superfluous, as have many other authors. HUXLEY (1940), however, did propose a parasystematic notation to indicate the intermediates of a cline by the use of hyphens connecting the "subspecies" at the ends of the cline preceded by "cl". SOURNIA (1966b, 1968a) proposed a similar method, although he was concerned with the naming of individuals rather than populations. Individuals are not usually considered of sufficient significance in taxonomy (other than types) to warrant names although it could be argued that in asexual species they assume a greater potential importance. SOURNIA's system is most useful in the naming of illustrated specimens. If the individual is approximately mid-way between two variants it is indicated by a hyphenated combination of their names, eg. *Ceratium fusus* var. *fusus-seta* (the first name of the linked pair being that which has priority in the rules of nomenclature). He also proposed use of the signs ">" and "<", indicating greater affinity to one end or the other of the cline.

Application of the Codes of Nomenclature

Dinoflagellates can be handled systematically by application of either the International Code of Botanical Nomenclature (ICBN – STAFLEU 1972) or the International Code of Zoological Nomenclature (ICZN – STOLL 1961; minor modifications of no consequence here were made in 1964). LOEBLICH & TAPPAN (1966) have provided a useful summary of the difficulties inherent in such a situation and JEFFREY (1973) has summarised the application of both codes for the non-specialist. Some points deserve repeating for the situation at present is highly unsatisfactory in several respects.

Firstly, those who study the taxonomy of microplankton have usually been relatively isolated from other taxonomists (often being more ecologically than taxonomically inclined) and have often been very casual in following the recommendations of either Code. Unfortunately this can only lead to confusion for, even if they do not see the value of following a standard practise, others that do will feel compelled to revise and rename their taxa as they are legally entitled to do so, compounding the confusion by adding further names to the literature. There seems to be little doubt that the short time required to become familiar with one of the Codes is well repaid by the authority and clarity of the presentation of new taxa. Recently much-needed revisions have been undertaken by LOEBLICH & LOEBLICH III (1966, 1968, 1969, 1970a, b, 1971) and SOURNIA (1968b), making use of the ICBN.

Which Code is used probably depends on whether one considers oneself a zoologist or botanist, and the nature of the publication to be used. The ICBN has been used here not so much because this author feels more a botanist than a zoologist (he considers himself to be a protistologist) but particularly because the ICBN makes more specific provision for the treatment of lower organisms (algae or "microscopic plants," e.g. Arts. 39, 44, 45), and the greater number of infraspecific taxa recognised by the ICBN allows the greater flexibility needed for the formal handling of asexual species (see earlier remarks). The practice of citing all the authors involved in the formation of a combination, rather than simply the first author of the species, seems a more useful aspect of the ICBN. It is more stringent, but is also perhaps a bit more complex because of the multitude of limiting dates used. The neccessity for Latin diagnoses and reference notes appears to this author to be less and less valuable as the years go by. Specialists in fossil dinoflagellates have agreed to use only the ICBN.

At present, one author using the ICZN can use a homonym in the ICBN as a name for a different taxon providing that it is published in accord with the former rules, and vice versa. Thus one author can adamantly insist upon, and legally use, a name which another author is equally legally forbidden to use. This appears to have disturbingly confusing consequences for those studying dinoflagellates or any of the other groups claimed by both zoologists and botanists (eg. euglenoids, cryptomonads, chrysomonads). As an example, refer to the text on *Diplopsalis* BERGH in the systematic section which follows. To zoologists the name is pre-occupied by *Diplopsalis* SCLATER, a subgenus of birds, because genera and subgenera are considered to be in the same rank ("genus group") for nomenclatural purposes, but botanists can disregard this due to the allowance for inter-kingdom homonymy and the fact that subgenera are considered as being in a different rank than genera. This type of problem will arise repeatedly unless those dealing with such "overlap" groups agree among themselves to not accept preoccupation in either Code for new taxa of micro-organisms. BALECH (1967a), for example, has not recognised the pre-occupation of *Murrayella* KOFOID because the earlier name occurs within the plant kingdom. Fortunately this problem has fallen away with the recognition of the earlier genus *Pyrgidium* STEIN here (as its substituted name *Corythodinium* LOEBLICH et LOEBLICH III).

Various other differences, such as the acceptance of tautonomy (repetition of the genus name as the species name) by the ICZN but not by the ICBN, only serve to emphasise the need for a common code to deal with organisms which have much closer affinities to one another than they do to either animals or plants. Bacteria and viruses have already been accorded such recognition but the confusion continues because blue-green prokaryotes are still dealt with under the ICBN. Either there must be agreement to follow only one of the existing codes, or a new code should be created for the flagellates.

The outer layers of dinoflagellates

Throughout this work the terms "theca" (thecate, athecate), and "amphiesma" are used. As there have been differences among recent authors in the manner in which these terms have been used it is necessary to clarify their usage here.

With the advent of electron microscopy it became clear that the generally accepted concept of "naked" (lacking a cell wall, see eg. KOFOID & SWEZY 1921) and "armoured" (with a cell wall consisting of cellulosic plates) as the only two alternative states for dinoflagellates other than when encysted was a considerable oversimplification. Thin sections demonstrated that the delicate polygonal patterns observed on some "naked" species, especially with the use of silver impregnation (e.g. BIECHELER 1934, 1952), appeared to correspond to membrane-lined cavities (vesicles) within the outer layers of the cells. The cellulose (or glucan) plates which constitute the wall in most "armoured" species occur within these flattened vesicles (c.f. reviews by DODGE & CRAWFORD 1970, DODGE 1971, LOEBLICH III 1970 and the papers of KALLEY & BISALPUTRA 1970, 1971). These plates can be heavily-developed and obvious with the light microscope, or may be very delicate and difficult to see (as in *Woloszynskia*). They are usually fully penetrated by pores, often (always?) associated with trichocysts, and both these and the sutures between the plates are consequently lined by the vesicle membranes. Also, in many genera they are empty although they may still impart a rigidity to the outer layers by their "honey-comb"-like structure in a manner similar to the pellicle of ciliates. In another similarity with ciliates there may also be a deeper, strengthened layer which can maintain the cell's integrity following the shedding of the outer layers ("ecdysis" – only in some genera). Newly formed thecal units may lack most of their sutures initially (KALLEY & BISALPUTRA 1970) sutures presumably arising by digestion of the plate material and invasion by infolding of the vesicular membranes. DODGE (1971) has doubted this process.

Difficulties have arisen in the manner in which the term theca is used. LUND (1962) had maintained that, because of the possibility of cryptic plates being present, the distinction between thecate and nonthecate species was difficult and should be abandoned. This view was supported by LEADBEATER & DODGE (1966) and DODGE & CRAWFORD (1970). They used the term theca in a strikingly different way to its conventional use (for the cellulose-plated structure only) by applying it to the entire outer complex of the dinoflagellate cell. Having thus totally redefined the term, they then declared the earlier distinction between thecate and athecate cells invalid. TAYLOR & CATTELL (1969) preferred to use the term "periplastic reticulum" for the outer region of species lacking cellulosic plates within their vesicles although that name is now unnecessary with LOEBLICH III's exhumation of an early term by SCHÜTT, the "amphiesma." DODGE and his co-workers have continued to use the "theca" in its widest sense.

The following view is advocated here: Firstly, a distinction can still be made, if desired, between those dinoflagellates with vesicles containing deposited wall units (thecal plates) and those with empty vesicles. These two categories correspond to the traditional terms thecate and athecate respectively, the only change being the recognition of cryptic thecae by modern staining or electron microscopy techniques. Complications may be introduced if distinctions between different types of deposited wall materials are made. The above terms are necessary to avoid confusion when dealing with old and new observations. The concept of the whole peripheral complex as a unit, as proposed by DODGE, is biologically attractive and can be maintained by using SCHÜTT's term "amphiesma" (as in LOEBLICH III 1970, TAYLOR 1973a, 1976), thus avoiding the possibility of confusion as a result of the redefinition of a widely used term.

The position of the plasmalemma (conventionally considered to be the outer-most cell membrane) was briefly problematic. KALLEY & BISALPUTRA (1971) maintained that in *Peridinium trochoideum* the plasmalemma is not the outermost membrane because the whole outer layer of the cell, including its plates, is shed during ecdysis, and they advocated the recognition of the outermost permanent membrane as the plasmalemma. The difficulty with the latter view is that in dinoflagellates it is only the outer-most membrane which surrounds the flagella and this membrane is consequently homologous with that termed the plasmalemma in all other flagellates. Evidently the plasmalemma and most of the amphiesma is shed in such species, requiring the differentiation of a new plasmalemma from underlying units each time ecdysis occurs.

LOEBLICH III (1970) has recognised the term "pellicle" for the semi-rigid layer which surrounds such a cell after ecdysis. The term also has attractiveness for application to the flexible, thick outer layers of members of the Ptychodiscaceae which resemble thecae but are not made up of plates. They are entirely dissolved by sodium hypochlorite (GAARDER 1954, on *Ptychodiscus*). This usage can only be considered provisional until the ultrastructural relationships of the layer (s) and its chemical composition are established.

A great variety of cyst walls are known which need not be detailed here (see reviews by WALL 1971, SARJEANT 1974 and TAYLOR 1976). Some are cellulosic, whereas others may have mineral impregnations.

The majority of species observed in the "Anton Bruun" material were either thecate cells or cysts. This is assumed to be a product of the method of preservation, commercial formaldehyde causing athecate species to burst if used in concentrations above 5 % (possibly in turn due to the presence of methyl alcohol as an additive). The exceptions here (shown chiefly on plates 37 and 39) consist either of those which apparently possess a pellicular wall (*Berghiella, Ptychodiscus*), strong peripheral vesiculation (*Balechina*), or preserve reasonably well for unknown reasons (e.g. *Kofoidinium*).

Problems in the derivation and interpretation of plate formulae

One of the most useful devices in the description of thecate dinoflagellates has been the plate formula, a listing of the constituent plates of the theca in a sequence representing the total number of plates within recognised regional "series." For the sake of brevity a type of shorthand notation is used to designate the series. The most widely used notation in the description of the peridinoid dinoflagellate is that developed by KOFOID (1907c, 1909a) except that the superscript ^{a} has replaced $^{\circ}$ in denoting anterior intercalary plates. Thus, for example, the plate formula of the genus *Pyrodinium* PLATE can be given as consisting of four apical plates, no anterior intercalaries, six precingulars, six girdle plates (cingulars), five or six sulcal plates, six postcingulars, two posterior intercalaries and one antapical plate; or 4′, 0a, 6″, 6C, 5–6S, 6‴, 2p, 1⁗.

Although this formula describes the quantitative plate composition it does not indicate much qualitative information other than the total number of plates per series. Furthermore the allocation of certain plates to different series could radically alter the formula. Thus, the same organism could also reasonably be described by the formula 3′, 0a, 7″, 7C, 5S, 5‴, 0p, 3⁗ or several other variations. The changes in the example involve the transference of an apical plate to the precingular series, alterations in the plates considered as sulcal, girdle or postcingular plates, and the substitution of antapical plates for posterior intercalaries. This type of difficulty has been stressed recently by STEIDINGER (1971).

Clearly facile comparisons of plate formulae are not sufficient in the comparison of taxa. Agreement must be reached on the criteria used in the recognition of "series." The latter is not a simple matter for the series are only rarely sharply demarcated from each other by strong structural features. It seems much more important to attempt to recognise homologous plates than to use simplistic criteria in assigning them to series. For example, apical plates are recognised by the fact that they have some point of contact with the apex (or apical closing platelet). If one or more of these is displaced by even the smallest degree, and does not touch the girdle on the other end, it could at present be termed an anterior intercalary plate. This seems to be unfortunate for, once so termed, it introduces exaggerated differences into the plate formula. It would seem to be much better to refer to it as a "displaced" apical plate.

TAYLOR (1976) has made an attempt to recognise "basic patterns" of plate development from which probably plate homologies can be worked out. Depending on the response to the models used for this purpose it might be possible to produce a new system of tabular notation which would recognise displacements and subdivisions of plate homologues.

In the interim one modification has been introduced here (see *Pyrodinium*) in which the so-called first apical plate of gonyaulacoids (suggested to be a precingular homologue by TAYLOR 1976) is designated separately from the others (as "+ 1") when it fails to contact the apical closing platelet.

General systematic arrangement

The general systematic arrangement employed for the presentation of the information on the taxa contains several modifications which reflect criticisms and structural relations published by several authors in recent years. It is similar to that employed by LOEBLICH III (1970), differing from that of BALLANTINE & PARKE (in PARKE & DIXON 1964, 1968) in that *Protoceratium* has been included under the Gonyaulacaceae, instead of remaining in a separate family and similarly *Diplopsalis* has been transferred to the Peridiniaceae. *Pyrophacus* has been returned to the family Pyrophacaceae erected by LINDEMANN (1928) for this genus. To a large extent these revisions have been motivated by comments made by PAULSEN (1949) regarding these genera and their classification and reasons for these modifications are given under the genera concerned. *Paleophalacroma* has been transferred from the order Dinophysiales, to which it would be assigned if SCHILLER's (1931) structural interpretation of the genus was still valid, and placed under the family Cladopyxidaceae of the Peridiniales in view of BALECH's (1967b) analysis of the full tabulation. *Pyrocystis* and *Dissodinium* are left within a distinct family characterised by the great predominance of a cyst stage in their life cycles (TAYLOR 1972a, SWIFT & WALL 1972) although the similarity of their cysts is probably from parallel origins rather than a close, common one (TAYLOR 1976). At the ordinal level the distinction of the Prorocentrales, Dinophysiales and Peridiniales as principal orders (the Dinophysiales being considered as intermediate between the other two) seems reasonable and workable, the recognition of the orders of parasitic dinoflagellates (e.g. Blastodiniales, Coccidiniales) being more questionable. SCHILLER's (1935) treatment of parasitic genera, employing the "Schwärmertypus" as a means of establishing interrelationships (as suggested by CHATTON 1920), is probably a reasonably sound approach, although his collection of all parasitic forms under the order Blastodiniales seems superficial and has not been followed here. The inclusion of all under the Peridiniales would be subject to the same criticism. The parasitic genus *Amoebophrya* encountered in the "Anton Bruun" material is placed in a separate family, the Amoebophryaceae, proposed by LOEBLICH III (1970), but not in the order Coccidiniales as advocated by him, its position seeming to be uncertain at present.

The Noctilucales seem to form a good ordinal group united by the usually large vacuolated bodies with frequently reduced girdle or sulcus. This is one of the groups which deviate from the usual dinokaryotic nuclear condition (ZINGMARK 1970a). A case could perhaps be made for the ordinal recognition of the Amphilothales and Kolkwitziellales (both orders proposed by LINDEMANN 1928) on the basis of their unusual skeletal and wall structures, but this has not been used here. LOEBLICH III (1970) omits the Amphilothaceae and Ptychodiscaceae. Both are recognised here.

At present the large number of families recognised reflects the slight investigation of probable inter-generic relationship that has been undertaken so far. The recognition of lineages within the orders (e.g. peridinoid, gonyaulacoid and gymnodinoid within the Peridiniales – WALL & DALE 1968a: TAYLOR 1976) may lead to a greater gathering of genera into larger units, perhaps into sub-orders or fewer families.

The families are arranged alphabetically under the orders although the orders themselves are in the sequence in which they are usually arranged systematically. The genera and species are listed alphabetically under the families. Where taxa are not identified to particular specific epithets they are listed last under each genus. In the case of a few large genera, such as *Ceratium* and *Peridinium*, the use of subgenera and sections has been retained to aid in reference to their constituent species.

The arrangement in which the orders, families and genera appear in the text can be determined from the Table of Contents.

Literature and author citation

Although taxonomists are familiar with the procedures observed in the citation of references, synonyms and authors, a brief description of that used here may be of assistance to those wishing to use this publication as a source reference and simple aid in identification.

By convention the citation that precedes a description is a highly condensed, formal presentation. Although not obviously so, this citation should usually be in Latin. Effectively this produces little visible change other than the Latinised spelling of authors' names, the use of et instead of and for combining two authors, the abbreviation t. for plate (tabulum), and the appearance of Latin comments (often abbreviated), such as **non**, **nec** (not, nor), **auct. nonnul.** (of some authors), **vix** (doubtful, questionable), **ex** (the description or discovery of one author formally proposed and published by another author), **sensu** (in the sense of), **sub** (under the name of), **pro parte** (in part), etc. Proposed taxonomic innovations are indicated by: **gen. n.** – new genus, **sp. n.** – new species, **comb. n.** – new combination (often combined with **stat. n.** – a change in the rank of the taxon) or **emend.** – a major change in the characterisation of a taxon.

This convention has been followed here, with one major modification: publications are referred to solely by author and date, as they are in the text, rather than by the now cumbersome early practice of abbreviating the title of the paper. The chief danger lies in the possibility of confusion between several papers by the same author in one year. SCHILLER (1933–1936) adopted this modification and ran into difficulties, particularly with KOFOID's numerous papers.

One of the principal aims of this publication is to serve as a guide to relevant taxonomic literature that has appeared subsequent to SCHILLER's major compilation. Taken together with the major taxa listings (not below genus) by LOEBLICH & LOEBLICH III (1966, 1968, 1969, 1970a, b 1971) and the compilation of species described since SCHILLER's work by SOURNIA (1974), it should be possible to locate a great deal of the post-Schillerian literature. Accordingly an attempt has been made here to include every taxonomic reference after SCHILLER which includes a figure of the species in question as well as those of earlier authors missed by SCHILLER such as MARTIN (1928, 1929) and CANDEIAS (1930). The work of MARUKAWA (1921) in Japanese, cited by KATO (1957) was omitted by SCHILLER and could not be obtained for reference here, and several Russian works (KISSELEV 1940, GAIL 1950, KUSJMINA 1960, and PROSHKINA-LAVRENKO & MAKAROVA 1968) were not seen before going to press*. It apparently was a type of identificatory atlas. Undoubtedly some have been missed, but it is hoped that no major reference has been omitted. To include references already cited by SCHILLER would have been to involve needless duplication. Consequently in most cases references to publications which appeared between the original description and its inclusion in SCHILLER's monograph have been omitted except where a major earlier monograph contains much more information than SCHILLER's work (e.g. KOFOID & SKOGSBERG 1928, KOFOID & ADAMSON (1933). If the citation is complete the original reference will appear after – (indicating a repeat of the author's name) below the name of the taxon, and it will be immediately followed by other references, if any.

Similarly, synonymies are restricted for the most part to changes which are now proposed or have been made subsequent to SCHILLER's monograph. Where new combinations are made the basionym (the original combination from which the new combination has been made) has been indicated in order to conform with Article 33 of the International Code of Botanical Nomenclature (STAFLEU 1972).

References are as complete as possible to 1974, with only a few from 1975 and 1976. It should be noted that they are cumulative to the species level; in other words, the citations beneath each species are the sum of all references both to the species and to its subordinate taxa (varieties, forms). The latter are not cited separately in the references although the criteria for their recognition are usually discussed and their distributions are presented separately in the eventuality that they may be of ecological interest, or in case one or more of them are later raised to the species level.

In the citations the sign – – – indicates a repetition of the author (s) in the reference immediately preceding it. The sign . . . in the synonymy indicates where the citation is incomplete, the missing citations occurring in SCHILLER (1931–1937) or in other good monographic treatments referred to.

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* SUBRAHMANYAN'S second volume on Indian Ocean dinoflagellates (1971) only became available to the author this work was in proof stage.

THE TAXA

Class Dinophyceae FRITSCH

This class, considered by most authors to contain the most primitive representatives of the dinoflagellates, was created for those few genera in which the flagella arise in an apical position. Both nonthecate and thecate genera are included within it. While the anterior insertion of the flagella is undoubtedly distinctive, the separation of these members at the level of class would be more appropriate if there were other features by which they differed from the bulk of dinoflagellates bearing laterally-inserted flagella. Their thecate members (Order Prorocentrales) possess fewer thecal plates (approximately ten) than other dinoflagellates. There are, however, resemblances to the thecal arrangement of the dinophysoid genera, with the notable exception of a girdle series, present only in the latter.

To date electron microscopy has been restricted to the thecate members of this class. From such studies it is evident that in most respects (other than those above), they are similar to members of the other principal class (Dinophyceae), possessing the same flagellar dimorphism, dinokaryotic nucleus, trichocysts, pusules and other typically dinoflagellate appertinances (DODGE & BIBBY, 1973).

Until non-thecate members of the class are examined, and in particular those that appear to possess flagella which are similar to each other (e.g. *Desmomastix, Pleromonas*), the question of the appropriate level cannot be satisfactorily resolved, but it seems probable that a lower hierarchical level will be more suitable for the distinction of the anteriorly flagellated dinoflagellates.

Order Prorocentrales LEMMERMANN

Family Prorocentraceae BUTSCHLI

Genus *Prorocentrum* EHRENBERG

Syn.: *Exuviaella* CIENKOWSKI

Earlier this genus was maintained as distinct from *Exuviaella* CIENKOWSKI by the presence of a more or less apical spine adjacent to the flagellar opening (-s) as a principle distinguishing feature of *Prorocentrum*, lacking in *Exuviaella* although small apical spinelets were known in some members of the latter (e.g. PAULSEN 1908, LEBOUR 1925, SCHILLER 1931). Secondarily *Prorocentrum* was considered to be more compressed than *Exuviaella*, and also in general, more acute in antapical contour. In practice a great deal of confusion has arisen due to variability within the species, minimal descriptions, and the presence of several species which are borderline cases.

For example, a detailed examination of a culture (Plymouth no. 18) isolated from Plymouth Sound in 1949, led PARKE & BALLANTINE (1957) to conclude that it was the same species as figured by LEBOUR (1925) as *Exuviaella apora* SCHILLER. PARKE & BALLANTINE concluded that it was not SCHILLER's species and named the culture *Exuviaella mariae-lebourae*. BURSA (1959) also studied Plymouth no. 18 and, apparently unaware of PARKE & BALLANTINE's paper, described it as a new species – *Prorocentrum cordiformis*, pointing out that it was apparently intermediate between the two genera. BURSA's individuals from the same original culture were much smaller than PARKE & BALLANTINE's, being completely beyond the size range reported by the latter, and were subtriangular in shape rather than oval to sphaeroidal.

Thus in this case, assuming that no contamination had occurred, the same source culture led the authors involved not only to different generic designations, but also to descriptions which differ in both size and shape, with no overlap between them. HULBERT (1965) subsequently reduced *E. mariae-lebourae* to varietal status due to studies of variability in populations of *E. minima* PAVILLARD.

Electron microscope studies of the theca, such as those of BRAARUD et al. (1958) and DODGE (1965), suggest that porulation types may be an important means of delimiting the taxa once degrees of clonal variability are known, but in field samples it is often difficult to see the porulation clearly except when the plates are separated.

The variability of shape and apical spine development observed by BRAARUD & ROSSAVIK (1951) and BURSA (1959, 196~~0~~2) in cultures of *P. micans* EHRENBERG (the type species of the genus) and the variations in field populations observed by HULBERT (1965) indicate that both body shape and spine development are doubtful criteria on which to separate the genera and the species recognition should also allow for such variability. ABÉ (1967a) advocated abandoning any attempt to separate the genera, all taxa concerned thus becoming assigned to *Prorocentrum* EHRENBERG in view of its priority.

In the same study ABÉ illustrated what he assumed to be a single periflagellar plate (bearing the spine) in two species, one of which is the type of *Prorocentrum* (*P. micans*). LOEBLICH III (1970) combined this information together with an early electron microscope study of DODGE (1965) in which the flagella of three species of *Exuviaella* were found to simply pass between the anterior margins of the valves, and proposed an emendation which would permit continued separation of the genera; namely that in *Prorocentrum* the flagella emerge via pores (with or without a pore plate) whereas in *Exuviaella* they emerge from a gap between the valves, having only two plates.

None of these authors was apparently aware of an unillustrated contribution by NIE (1947) in which he claimed to have observed four small platelets in the flagellar region in some Prorocentroids. He thought that three of these platelets contributed to the flagellar pores, and the fourth to the spine. BIECHELER (1952) illustrated seven or eight small platelets in *P. micans* without comment. BALECH (1971a) illustrated eight in *P. compressum*. DODGE & BIBBY (1973) rediscovered some of these cryptic plates in several species. Unaware of earlier observations, they concluded that approximately four to six small plates are located in the periflagellar region. FAUST (1974) has shown seven or possibly eight small platelets surrounding the flagellar pores of *P. minimum* var. *mariae-lebourae* and VON STOSCH (1974) has reported up to 14 in P. *micans*.

A further structure which has escaped comment can be seen in various figures and also in two cases in the Indian Ocean material. This is the apparent existence of a double-layered wall in some species, possibly only during part of their life-cycle. For example, in ABÉ's figures (1967a, fig. 2 c–e) a secondary wall structure can be seen internal to the outer theca, tubular pores apparently passing from the inner to the outer wall. In *Prorocentrum magnum* (GAARDER) a similar structure is apparent in both the original figures and the specimen figured here (pl. 1, fig. 10), the inner and the outer walls being connected around the flagellar pore region. It is possible that this appearance in broad lateral view is produced by an inwardly-directed flange in the seam region. However, some published figures show that the feature is visible in other views of the theca (ABÉ 1967a, fig. 2 c, d). DODGE & BIBBY (1973) have sectioned some thecae and make no mention of an inner wall, and in one of their figures illustrating a section of the seam region there appears to be an indication of an inward flange on each valve. Possibly this structure is related to megacytic growth.

Prorocentrum compressum (BAILEY) ABÉ Plate 1, Figs. 8, 9

– 1976:110, f. 2 F, 4 H, I, t. 4, f. E, F; ABÉ, 1967a: 372 – non descr. nec f. 2 c–e (a, b? ex DODGE);
STEIDINGER et WILLIAMS 1970:60, t. 37, f. 133.
Syn.: . . . . *Exuviaella compressa* (BAILEY) OSTENFELD. . . . SCHILLER 1931: 17, f. 11 a–d; RAMPI 1940:248, t. 1, f. 2; KISSELEV 1950:58, f. 75 a–c, GAARDER 1954:23, f. 25; WOOD 1954:178, f. 2; SILVA 1955:111, t. 1, f. 1, CURL 1959, f. 109; HALIM 1960a, t. 1, f. 10; BALECH 1962b:121, t. 16, f. 203; YAMAJI 1966:66, t. 31, f. 12; HADA 1967:9, f. 11 a, b; WOOD 1968:55, f. 137.

ABÉ did not provide a basionym, the combination being validated by DODGE. ABÉ's figures show features which are inconsistent with earlier descriptions of this species, most notably the flagellar pore structure. PARKE & BALLANTINE (1957) concluded that *P. compressum* possesses only one flagellar pore, but DODGE (1976) has illustrated double pores close together. It is possible that ABÉ's figs. 2a and 2b are this species, 2a being unusual in having three apical spinelets, but this can not be determined with certainty. His other figures are apparently of *P. lenticulatum* (MATZENAUER).

The specimen shown in pl. 1, fig. 8 is slightly larger (length 50 µm) than the range reported by SCHILLER (1931, length 34–46 µm). The smaller specimen also figured here (pl. 1, fig. 9) shows a superficial resemblance to *P. lebourae*

SCHILLER, but differs from the latter in that the pores are not regularly arranged in rows. *P. lebourae* is in many respects similar to this species, DODGE (1976) concluding that the former is simply a rounded form of *P. compressum*.

A species also closely related to these is *P. obtusum* OSTENFELD which has many similarities with the smaller specimen illustrated, but the original figure is too poor to be of much value.

Stations: 15, 29, 30 51, 53, 57, 60, 91, 100, 103, 112–114, 116, 129, 130, 140, 148, 153, 156, 157, 286, 288, 293, 294, 301, 310, 312, 322, 341, 342, 347.

This was the most commonly encountered member of this genus in the material. It occurred in small numbers at scattered stations throughout the entire area at all seasons. It is listed as a temperate and tropical cosmopolitan species by MARGALEF (1961c), a distribution type exemplified here by its occurrence in regions such as the Andaman Sea, western Arabian Sea and also at the southernmost stations approaching the subtropical convergence (Islands of St. Paul and Amsterdam). The six Indian Ocean records listed by WOOD (1963a) require amplification by those of BÖHM (1931a), SILVA (1956a, 1960), SUBRAHMANYAN & SARMA (1967), NEL (1968) and SOURNIA (1970).

Prorocentrum cordatum (OSTENFELD) DODGE Plate 1, Figs. 14, 15
– 1976:118, f. 2 H, I, t. 4C.
Syn.: ... *Exuviaella cordata* OSTENFELD 1901:134, f. 4; SCHILLER 1931:23, f. 18c–f; MARGALEF & DURÁN 1953:20, f. 2 j.

In shape the Indian Ocean specimens agreed very well with this species, although they were larger (length 30–34 µm as opposed to 24 µm, valve width 21–28 µm as opposed to 18–20 µm). They possessed a very distinctive porulation pattern type shared by *P. ovale* (GOURRET) SCHILLER (not previously observed) in which the larger, most obvious pores were lacking from a central zone which passed from the flagella pore region approximately two thirds of the distance to the antapical end. Delicate ground markings were also visible in some specimens, these possibly being thin areas in the valve rather than true pores (apertures).

Two variations in cell shape were observed in the material. Heart-shaped specimens similar to those originally described were seen. In addition more bluntly oval specimens were found which have an identical pore pattern. MARGALEF & DURÁN (1953) have figured a specimen similar to this second type. This elongate variant also shows resemblances to *P. oblongum* (SCHILLER), the latter thought to be a variant of *P. compressum* by DODGE (1976).

Stations: 56, 131, 149, 285, 288.

Found only occasionally at scattered stations. The furthest south it occurred was at station 131 (35° S), suggesting a tolerance for cooler waters. It has been observed previously in the Black and Caspian Seas and on the northwest coast of Spain. This is a new record for the Indian Ocean.

Prorocentrum gracile SCHÜTT Plate 1, Fig. 2
SCHILLER 1931:37, f. 39 a, b; BÖHM 1936:13, f. 3c 1–3; WAILES 1939:11, f. 26; SILVA 1960:39, t. 23, f. 2; WOOD 1963c:3, f. 3; – 1968:122, f. 376; STEIDINGER et WILLIAMS 1970:61, t. 37, f. 134 a–c; DODGE 1976:114, f. 3 B, t. 2 D, 3 E.

From published figures it appears that this species achieves maximum size in tropical waters. In the cold temperate waters off British Columbia, where it is the most commonly-occurring representative of the genus, its length rarely exceeds 46 µm (WAILES, 1939 and orig. observ.), whereas the present specimen was 52 µm in length (spine lacking), a size consistent with SILVA's (1960) observations on specimens from Inhaca, Mozambique. SILVA also reported an exceptionally large specimen, 99 µm long excluding the spine and figured a specimen from Dakar (1956b, pl. 3, f. 1) which is almost certainly this species (under "*Prorocentrum micans* EHRENBERG? "). BÖHM (1936) found that western Pacific specimens varied in length from 48 to 66 µm.

This species is very similar to, if not conspecific with, *P. sigmoides* BÖHM, the latter possibly reflecting shape deformation associated with large size. *P. sigmoides* differs from the "typical" *P. gracile* in being concavely depressed along one seam margin, and in having an apical depression, as well as by its large size (BÖHM, 1933 – length 72 to 77 µm; TAFALL, 1942 – length 68 to 82 µm). However, the specimen figured by TAFALL from the tropical eastern Pacific appears to be intermediate between *P. sigmoides* and *P. gracile* in general shape. The structural differentiation between regular pores and larger trichocyst pores figured by TAFALL (1942, pl. 35, f. 18, 19) can also be seen in the specimen referred to as *P. gracile* herein. The only feature thus not shared by SCHÜTT's and BÖHM's species is the apical depression in *P. sigmoides*. It is possible that the unusually large specimen referred to by SILVA above was of the *sigmoides* type, but in the absence of a figure this cannot be ascertained. DODGE (1976) considers *P. sigmoides* to be synonymous with *P. gracile*.

Stations: 374, 405.

Two specimens encountered in the Mozambique Channel region. This is the same area from which SILVA (1960) and SOURNIA (1968b, 1970) have recorded the species. Other records of the species from the Indian Ocean are those of OSTENFELD & SCHMIDT (1901 – Red Sea), SCHRÖDER (1906 – Arabian Sea), and BÖHM (1931a – Persian Gulf). It has been recorded from the Coral Sea by WOOD (1963c).

Prorocentrum lenticulatum (MATZENAUER) comb. n. Plate 1, Figs. 11, 12

Basionym: *Exuviaella lenticulata* MATZENAUER 1933:438, f. 1 a,b; BÖHM 1936:12, f. 2 (sub *E. lenticula*, lapsus pennae); SCHILLER 1931:514, f. 596; TAFALL 1942:436, t. 34, f. 1, 2, 7 (sub *E. lenticula*); ABÉ 1967a: f. 2 c–e (sub *P. compressum*).

The specimen in figure 12 shows an unusual surface development which might be secondary material deposited on the thecal surface, a process incomplete in the specimen figured. Also apparent in the specimen is the inner wall structure referred to in preliminary comments on this genus. The species can be distinguished from *P. compressum* (BAILEY) ABÉ by its heavy porulation, subequal length and diameter (30–39 µm), and angularly lenticular shape in seam view although DODGE (1976) considers it to be "a rather short form" of *P. compressum*. The individual figured by SILVA (1955, pl. 1, f. 12) under *P. rotundatum* SCHILLER may be the same taxon as the present specimens.

Stations: 32, 36, 150, 295, 298, 336, 341, 370, 399.

This species was first described from the Indian Ocean (MATZENAUER 1933) and later recorded from Tuléar, Madagascar by TRAVERS & TRAVERS (1965) and SOURNIA (1968b). It has also been recorded from the eastern and western Pacific Ocean. It was here encountered in small numbers in the Andaman Sea, the Mauritius/Seychelles region and the Mozambique Channel.

Prorocentrum magnum (GAARDER) DODGE Plate 1, Fig. 10

– 1976:111, f. 2 G.
Syn.: *Exuviaella magna* GAARDER 1954:23, f. 26.

This is an exceptionally large and distinctive species. The size range reported by GAARDER (1954; length) was 72–92 µm. Specimens seen in the "Anton Bruun" material ranged in length from 86–94 µm. In the specimen illustrated the paired flagellar pores were clearly visible in broad lateral view, as well as the double wall structure previously referred to in the notes under the genus herein. In size this species is rivalled only by *P. gracile* SCHÜTT (and *P. sigmoides* BÖHM, if a distinct species – see notes under *P. gracile*).

Stations: 33, 142, 319, 334.

Single specimens were found at several equatorial stations. This is the first record of the species in the Indian Ocean. It has only been previously encountered in the tropical Altantic Ocean.

Prorocentrum micans EHRENBERG Plate 1, Fig. 1

MARTIN 1928:11, t. 3, f. 10–13, t. 7, f. 4, t. 8, f. 3; SCHILLER 1931:35, f. 37 a–f; WANG et NIE 1932:311, f. 22; RAMPI 1940:251, f. 9; MARGALEF 1946:92, f. 1/1; SILVA et PINTO 1948:162, t. 2, f. 1; MASSUTI et MARGALEF 1950, f. 25, 44; KISSELEV 1950:62, f. 85 a–c; BRAARUD et ROSSAVIK 1951:5, f. 2–5; BIECHELER 1952:20, f. 3/1–3, f. 55–57; MARGALEF et DURÁN 1953:20, f. 2 i; SILVA 1953:80, f. 1, 2; – 1955:113, t. 1, f. 3–10; – 1956c:8, t. 2, f. 1, 2; WOOD 1954:179, f. 5; MARGALEF 1957a:45, f. 1 a; BURSA 1959:1 et seq., f. 1–29, 36–41, 48–66, 71–74, 79–94; HALIM 1960a:189, t. 1, f. 1–5; DE ANGELIS 1961, f. 1, 8; MARGALEF 1961a:76, f. 25 c; DODGE 1965:608, f. 1, t. 1, f. 1–4; YAMAJI 1966:67, t. 31, f. 13; ABÉ 1967a:371, f. 1 a–g; HADA 1967:8, f. 9 A; WOOD 1968:123, f. 380; STEIDINGER et WILLIAMS 1970:61, t. 38, f. 136 a, b; HASSAN & SAIFULLAH 1972a:63, f. 1; DODGE 1976:112, f. 3 A, E, t. 2 A–C, E. F; Vix SOBRINO 1918, t. 4, f. 1 d omitted by (SCHILLER praetermissavit).

One of the specimens here referred to this species (illustrated) is unusual in form, and its identification must be considered tentative. The apical spine is weakly developed and the antapical region is more rounded than the majority of figures of this species. In size and shape it resembled *P. mexicanum* TAFALL (1942:440, pl. 34, f. 3, 8) and the specimens of *P. maximum* (GOURRET) SCHILLER of BÖHM (1936:12, f. 3 a, 1, 2). TAFALL has suggested that BÖHM's specimens may be representatives of his species. They differ most obviously from *P. micans* in that the apical spine arises on the lower profile of the apical end of the cell when seen in broad lateral view. The specimen in question differs from the latter in its apical spine position, and is referred to *P. micans* in view of the variability reported for this species by

BRAARUD & ROSSAVIK (1951) and BURSA (1959), and in particular, the general arrangement and types of pores present on the theca. The trichocyst pores are marginally arranged, sloping in an oblique plane with reference to the valves, and often in parallel rows, features which agree well with the electron microscope observations of DODGE (1965). However, STEIDINGER & WILLIAMS (1970) provide a phase-contrast picture of *P. gracile* which also exhibits these features. The other specimen encountered agreed well with the specimens of ABÉ (1967a).

Stations: 60, 112.

Single individuals were found in the Bay of Bengal and off the Maldive Islands. It has been frequently encountered by other authors in Indian Ocean material (see list in WOOD 1963a and also BÖHM 1931a, SILVA 1956a, PRAKASH & SARMA 1964, SUBRAHMANYAN & SARMA 1960, 1967, TAYLOR 1967, LEWIS 1967, SOURNIA 1968b, 1970, GRINDLEY & SAPEIKA 1969, and HASSAN & SAIFULLAH 1972a). It shows a peculiar tendency towards being a codominant in outbreaks of "red water" caused by several other dinoflagellates, particularly of the genus *Gonyaulax*.

Prorocentrum minimum (PAVILLARD) SCHILLER Plate 1, Fig. 17

– 1931:32, f. 33 a, b; HULBERT 1965:95, t.1, f. 1–6, t. 2; DODGE 1976:117, f. 4 E–G, t. 3 A–D.

Syn.: *Exuviaella minima* PAVILLARD, 1916:11, t. 1, f. 1 a, b.
Prorocentrum triangulatum MARTIN 1929:556, f. 1, 2 a–c, 3 a, b.
Exuviaella mariae-lebourae PARKE et BALLANTINE 1957:643, f. 1–18; DODGE 1965:609, f. 3, t. 2, f. 5–8; BIRNHAK et FARROW 1965:1, f. 1–3. [= *E. mariae-lebouriae* auct. mult.]
Prorocentrum cordiformis BURSA 1959:17, f. 104–107.
P. mariae-lebouriae (PARKE et BALL.) LOEBLICH III 1970: 906

The conspecificity of *E. mariae-lebourae* with *P. cordiformis*, indicated by DODGE (1965), and of both with *P. minimum* (proposed by HULBERT 1965), has already been discussed here under the general comments on the genus *Prorocentrum*. HULBERT retained recognition of the taxa *triangulatum* (MARTIN) and *mariae-lebouriae* (PARKE et BALLANTINE) at the varietal level. Only one specimen, referred here to the latter variety, was observed in the material. It agreed well with the shape of the specimens observed by the original authors, by DODGE (1965) and BIRNHAK & FARROW (1965). The double flagellar pore structure was also present. The fine spines covering the valve shown by electron microscope study could not be seen, but the arrangement of the pores agrees well with that observed by DODGE. The specimen differed from previous descriptions principally in size, being 23 µm in length and 20 µm in valve width (usual size range: length 14–17 µm, valve width 11–15 µm). It is not, however, as large as *P. aporum* (SCHILLER) DODGE whose length is reported as 30–32 µm and valve width 21–26 µm. A further difference observed was that many of the pores, especially in the vicinity of the valve margin, appeared to be sloped obliquely as in *P. micans*, a characteristic whose taxonomic significance is not as yet clear.

Station: 310.

One specimen was found in the vicinity of the Islands of Amsterdam and St. Paul (close to the Subtropical Convergence region). It has not apparently been previously recorded from the southern hemisphere, records being restricted to the tropical and north Atlantic Ocean.

Prorocentrum oblongum (SCHILLER) comb. n. Plate 1, Fig. 7

Basionym: *Exuviaella oblonga* SCHILLER 1928:50, f. 6 a–c; – 1931:22, f. 17 a–c; HALIM 1960a:191, t. 1, f. 12; WOOD 1968:56, f. 140.
Syn.: *Prorocentrum ovalis* RAMPI sensu SILVA 1952b:600, t. 6, f. 2.

The specimen figured herein differs from the type description in the sharply excavated region adjacent to the flagellar pores. According to SCHILLER the right valve bears a pore (-plate?), the left valve simply being scooped out apically. In size it is almost identical to the Adriatic specimens: length 30 µm, valve width 22 µm. The species is somewhat similar to *P. compressum* (BAILEY) ABÉ ex DODGE* and *P. ovalis* RAMPI [non *P. ovale* (GOURRET) SCHILLER] but is smaller, longer in relation to diameter, and lacking apical spines around the flagellar pore although the latter could have become detached from the specimen. SCHILLER (1931) has also indicated that it possesses an oblique flagellar canal, a feature which could not be resolved in the illustrated specimen. The latter also shows superficial similarities to *Prorocentrum lima* (EHRENBERG) DODGE, being similar in size and in possessing an apical excavation. However, *P. lima* is broadly excavated, the thecal apical regions rising in sharp points on either side of the apical depression (see DODGE 1965:611, f. 6, pl. 3, f. 10, 11) and lacks a flagellar pore. Other specimens encountered were similar in form to that illustrated.

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* DODGE (1976) considers this to be synonymous with *P. oblongum*.

Stations: 289, 396, 417, 420.

Single specimens found in the western Indian Ocean from the Mozambique Channel to the Arabian Sea. It has previously been reported from the Mediterranean Sea and the Straits of Florida.

Prorocentrum ovale (GOURRET) SCHILLER Plate 1, Fig. 16

SCHILLER 1931:42, f. 45 a; WOOD 1968:123, f. 383. – Non *P. ovalis* RAMPI 1940.

Due to the minimal original description and figure which does not provide information as to porulation, and the observation of only one valve, lacking a pore plate or spine, in the present material, this identification must remain tentative. The valve is assigned to this species on the basis of its distinctive shape, not apparently shared with any other described species.* The porulation on the valve consisted of many large pores, slightly closer together around the margin, and a distinctive aporulate zone leading from the flagellar region approximately three quarters of the length towards the antapical end. GOURRET did not provide precise size data, although SCHILLER's tentative magnification of his figure suggests a length of approximately 37 µm. WOOD (1968) states the length is 25 µm. The present specimen had a length of 44 µm and a valve width of 25 µm.

The species usually has a small spine, presumably arising from a pore plate, on the lower side of the flagellar aperture.

Station: 56.

Apparently it has only been previously recorded from the Mediterranean. In the Indian Ocean it was present at one station in the Bay of Bengal.

Prorocentrum pyriforme (SCHILLER) HASLE** Plate 1, Fig. 13

– 1969:153; STEIDINGER et WILLIAMS 1970:61, t. 38, f. 137.

Basionym: *Exuviaella pyriformis* SCHILLER 1928:50, f. 5; – 1931:23, f. 19.

The specimen referred here to this species (one dissociated valve, right side) differs from SCHILLER's original description in being larger (length 28 µm, valve diameter 26 µm as compared with 20–24 µm and 18–20 µm respectively) and in having a noticeable anterior excavation of the valve margin assumed here to correspond to missing pore plates. The latter are not mentioned by SCHILLER, although it is possible that they might have been missed if the valves were not separated. He does refer to the flagellar pore being laterally displaced, a situation which might be expected to produce an excavation of the right valve. The only other described species to which this specimen might be referred is *P. cornutum* SCHILLER. However, the latter species is even smaller (length 16 µm, valve diameter 14 µm). DODGE (1976) has made *P. pyriforme* synonymous with *P. cordatum* without comment.

Station: 288.

At one locality in the western Arabian Sea. Not previously recorded from the Indian Ocean. It was originally described from the Adriatic and has been found in the Gulf of Mexico.

Prorocentrum triestinum SCHILLER Plate 1, Figs. 3, (4, 5?)

SCHILLER 1931:40, f. 43 a–f; SILVA 1953:80, f. 3 (sub *Prorocentrum* sp.); – 1955:114, t. 1, f. 11; BURSA 1959, f. 117; HALIM 1960a:190, t. 1, f. 8; DODGE 1965:609, f. 2; – 1976:112, f. 2 A–C, t. 1 E.

In size the three specimens agree well with the type description. However, each varies somewhat from SCHILLER's description. None bore the small spine usually found in this species which DODGE (1965) found to be an extension of one valve margin rather than being produced from a pore plate. Although the specimen in fig. 3 has the sharply pointed, slightly curved antapical end characteristic of the species, its apical end, in addition to lacking a spine, shows a symmetrical development of the "shoulders," whereas in all extant figures these are shown to slope. Those in figs. 4 and 5 both show antapical bluntness with no marked lateral curvature and R. MARGALEF (pers. comm.) believes that they may belong to a separate species. It may be noted that the specimens in figs. 3 and 4 are from the same sample (st. 374). The assignment of these specimens to *P. triestinum* SCHILLER is based on the agreement in size and the simplicity of thecal structure (a feature emphasized by DODGE, 1965), bearing in mind the morphological plasticity demonstrated for *P. micans* EHRENBERG by BRAARUD & ROSSAVIK (1951) and BURSA (1959). The latter author has asserted that cubic "paramylum" (presumably starch, as paramylum has never been definitely found in this group) grains within the cells are also distinctive of this species. It was not possible to discern these in the present specimens, possibly due to poor preservation.

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* DODGE (1976) has combined this with *P. maximum* (GOURRET) SCHILLER, *P. obtusum* OSTENFELD, *P. mexicanum* TAFALL, *P. proximum* MAKAROVA and *P. rampii* SOURNIA.

** HASLE (1969) did not make this combination validly as she omitted full reference to the basionym. It is validated herein.

DODGE (1976) considers *P. redfeldii* BURSA and *P. pyrenoideum* BURSA to be synonymous with this species.

Stations.: 15, 374.

Found in the southern Andaman Sea and off the coast of Mozambique (all specimens illustrated). It has only been previously recorded from the Indian Ocean by SILVA (1960). It is known from the Mediterranean, English Channel, and the western Pacific Ocean (see HALIM (1960a).

Prorocentrum veloi TAFALL Plate 1, Figs. 6a, b
– 1942:437, t. 34, f. 4–6.

In the absence of any descriptions other than TAFALL's to provide indications of variability, this identification is made on the basis of "nearest fit." The specimens observed (two) agreed with *P. veloi* in length and in general shape, having a similar angular lateral expansion of the valves (when observed in broad girdle view) and angular prolongation of one apical "shoulder." They differed from TAFALL's description in that the lateral expansion was closer to the antapical end instead of being almost central in position, in possessing central valve indentations when seen in seam view instead of being flat, and in the ratio of length to valve width (1.9–2.1 instead of 2.7).

P. veloi TAFALL is closest to *P. obtusidens* SCHILLER, the chief distinction lying in the lateral expansions of the former, and it is possible that these taxa may be conspecific. *P. dentatum* STEIN also lacks the lateral expansions; the anterior prolongation is sharply pointed and so is the antapical end. DODGE (1976) has made these three conspecific, and has added *P. monacense* KUFFERATH (1957) to the synonymy.

An interesting feature observed in the Indian Ocean specimens was the narrowing of the seam zone in a position corresponding to one of the lateral expansions (fig. 6 b). It was not present on the other lateral expansion.

Stations: 15, 335.

It was recorded here from the Andaman Sea and the southern Arabian Sea. It is only previously known from the type locality (tropical eastern Pacific Ocean).

Prorocentrum species 1 Plate 1, Figs. 18 a, b

This small species was represented by only one specimen whose valve structure was clearly perceived. When seen in valve view the cell was almost spherical in shape, the walls being distinctively thickened immediately adjacent to the single flagellar pore. The surfaces of the valves were sparsely marked with delicate porulae or pseudoporulae (thin areas in the valve, not apertures). In seam view the valves were seen to be smoothly convex. The seam was surrounded by a faint zone differentiated from the rest of the valves. The cell observed was surrounded by a gelatinous matrix.

Attempts to refer it to described species proved unsatisfactory although it did show affinities with several. It agreed in size and general shape with *Prorocentrum balticum* (LOHMANN) LOEBLICH III and *Prorocentrum minimum* var. *mariae-lebourae* (PARKE & BALLANTINE) HULBERT but differed from them in appearing to possess only one flagellar pore. Other species supposedly possessing only one flagellar pore are *P. aporum* (SCHILLER) DODGE and *P. pusillum* (SCHILLER) DODGE & BIBBY, but these differ in size and shape. PARKE & BALLANTINE (1957) refer MARTIN's (1929, pl. 3, f. 1–4) specimens of *P. aporum* to *P. mariae-lebourae* [= *P. minimum*]. These specimens of MARTIN bear a close resemblance to the present specimen, as do those of SILVA (1956c, p. 2, f. 4, 5) causing "red water" in Angolan waters.

In view of this confused situation it is considered best to leave this specimen unassigned to any described species. HADA (1967, p. 9, f. 11 B) similarly does not name a small specimen which may also be this species.

Station: 147.

A single specimen (illustrated) was recorded from the southern Arabian Sea.

Class Desmophyceae SMITH

Dinoflagellates in which the flagella are inserted laterally

Order Dinophysiales LINDEMANN

The subdivision of this order into two principal families by KOFOID & SKOGSBERG (1928) has received further support from the detailed morphological studies of ABÉ (see ABÉ, 1967a). The latter author has shown that the genera *Amphisolenia* and *Triposolenia* differ from other members of the order in the arrangement of the smaller ventral hypothecal plates. In these genera the plates lie side-by-side, whereas in the other genera the left ventral hypothecal plate is more apically situated than the right ventral hypothecal plate, reaching an extreme situation in the "*Dinophysis-Citharistes* group" in which they apparently lie one directly above the other.

A confusing situation exists at present in which three systems of tabular notation have been proposed. TAI & SKOGSBERG (1934) proposed a system based essentially on a subdivision of the series into left and right components, those of the left side being denoted by capitalised letters, and those of the right side by small case letters. Both the system of BALECH (1967a) and ABÉ (1967a) number the series continuously from left to right as is the practice in the Peridiniales, BALECH's representing a modification of TAI & SKOGSBERG's system, and ABÉ's a modification of the system widely used for the Peridiniales. In order to facilitate intercomparison of these systems Table 2 below provides the equivalent notations in each.

Table 2. Notational equivalents in three Dinophysoid tabulation systems.

Plates (L = left, R = right)	TAI & SKOGSBERG	BALECH	ABÉ
L ventral epithecal	E_2	E_1	1'
L dorsal epithecal	E_1	E_2	2'
R dorsal epithecal	e_1	E_3	3'
R ventral epithecal	e_2	E_4	4'
Pore plate	P	P_0	–
Apical plate (s)	–	A_1*A_2	–
L ventral girdle plate	G_2	C_1	1g
L dorsal girdle plate	G_1	C_2	2g
R dorsal girdle plate	g_1	C_3	3g
R ventral girdle plate	g_2	C_4	4g
L ventral hypothecal	H_2	H_1	1"
L dorsal hypothecal	H_1	H_2	2"
R dorsal hypothecal	h_1	H_3	3"
R ventral hypothecal	h_2	H_4	4"
Anterior sulcal plate	S_1	S.a.	a
Left sulcal plate	S_2	S.s.	1
Right sulcal plate	s_1	S.d.	r
Posterior sulcal plate	s_2	S.p.	p

* NORRIS & BERNER (1970) termed this small, usually overlooked plate, as the "pore platelet", designated as Ppl.

From the table it can be seen that there is a greater possibility of confusion between the systems of TAI & SKOGSBERG and BALECH. For example, the plates signified by E_1 and E_2 are reversed in the two systems, and similarly H_1 and

H_2 are reversed. It is questionable, in view of the fundamental separation of the cells into left and right sides, whether it is desirable to follow the Peridinoid practice of numbering the series from left to right around the cells. In a future search for plate homologies these later systems may prove of value. However, if this is the aim, then ABÉ's system may prove deceptive in employing the same tabular notation for both groups. For example, in the Peridinoid genera the superscript " indicates precingular plates, whereas in the Dinophysoid genera the same superscript would be applied to plates that are postcingular in position. The a and p used in ABÉ's sulcal plate notation should not be confused with the notation for the anterior and posterior intercalary plates found in some Peridinoid genera.

In summary, none of the systems seems wholly satisfactory to this author but, rather than adding to the confusion by proposing modifications, it would seem best in the future to choose one and clearly specify the system used, taking care to avoid errors if either BALECH's or TAI & SKOGSBERG's systems are preferred.

Since the detailed study of TAI & SKOGSBERG (1934) it has been assumed that the thecae of all members of this order consisted of 17 plates. However, a small additional plate has been found near the apical pore by BALECH (1971 a, b) and NORRIS & BERNER (1970).

TAYLOR (1971, 1973a) has illustrated the detailed thecal morphology of members of the genus *Ornithocercus*, including cell division processes, using the scanning electron microscope.

Family Amphisoleniaceae LINDEMANN

Genus *Amphisolenia* STEIN

Amphisolenia astragalus KOFOID et MICHENER Plate 2, Fig. 24; Plate 3, Fig. 24 b

KOFOID et SKOGSBERG 1928:380, f. 49/6, t. 10, f. 1, 6, 8, 10; SCHILLER 1931:170, f. 157; WOOD 1963b:9, f. 20.

Characterized by the well-developed, rounded heel on the foot, lacking a heel spine and possessing only one antapical spine. It is not readily confused with other species.

Stations: 33, 60.

Found in small numbers at only two stations, one in the Andaman Sea, the other in the Bay of Bengal. Described from the tropical Pacific Ocean. Only previously recorded from the Indian Ocean by NEL (1968 – southwestern sector).

Amphisolenia asymmetrica KOFOID Plate 2, Fig. 30; Plate 3, Fig. 30 b

KOFOID et SKOGSBERG 1928:429, f. 54/6, 56/5, t. 11, f. 5, 6, 7, 13; SCHILLER 1931:181, f. 173.

The single specimen here referred to this rare species differs from the type description in being shorter (length 720 µm as opposed to 1080–1207 µm), the head being only five times longer than wide instead of seven to eight. Also, the sharp heel spine arises some distance antapically from the flexure of the foot, instead of immediately at the flexure. KOFOID & SKOGSBERG also figured the foot of a specimen lacking a heel.

Despite the above variations this author is satisfied that the present specimen is a variant of *A. asymmetrica*, being similar in general form to earlier descriptions and with very similar antapical spine arrangement at the end of the foot. The foot of the present specimen was not bent at an angle to one side in addition to the ventral flexure. Variation in this type of lateral torsion appears to be fairly common among species with a differentiated foot region. For example, it is also apparently variable in *A. thrinax* SCHÜTT.

Station: 102.

A single specimen (illustrated) found at one station in the Bay of Bengal. Previously recorded only from the eastern tropical Pacific Ocean.

Amphisolenia bidentata SCHRÖDER Plate 2, Fig. 21, 22; Plate 3, Fig. 21 b, 22 b

KOFOID et SKOGSBERG 1928:409, f. 54/1–4, f. 56/1; SCHILLER 1931:178, f. 169 a–e; BÖHM 1936:26, f. 10a 1, 2; RAMPI 1940:264, f. 44; MASSUTI et MARGALEF 1950, f. 72; WOOD 1954:205, f. 55; SILVA 1955:124, t. 2, f. 1–4; HALIM 1965:378, f. 1/10, 11 a–c; YAMAJI 1966: 72, t. 33, f. 11; ABÉ 1967c:111, f. 42 a–k; HALIM 1967:704, t. 1, f. 1, 2, t. 2, f. 15; WOOD 1968:18, f. 19; STEIDINGER et WILLIAMS 1970: 43; t. 2, f. 5 a–c; SAIFULLAH et HASSAN 1973b:150, f. 1 A, B.

KOFOID & SKOGSBERG (1928) considered it possible that *A. palmata* STEIN may represent a more mature state of the same taxon, having three antapical spinulae (one on the right valve) instead of only two. *A. bidentata* is distinguished from *A. lemmermanni* KOFOID, also similar, in being longer (length 700–900 μm), with a narrower width of the mid-body in proportion to total length (see comments under *Amphisolenia* species 1). *A. taylorii* SAIFULLAH et HASSAN may be a close relative in which the foot is doubled, but it seems closer to *A. rectangulata*. It was the most commonly encountered species of *Amphisolenia*.

Stations: 15, 16, 28, 33, 36, 37, 39, 53, 55, 56, 59, 60, 62–64, 68–71, 98–103, 106, 112, 113, 125, 130, 134, 135, 140, 142, 148, 150, 153, 155, 285, 287, 288, 291, 294, 295, 297, 299, 301, 302, 319, 321, 322, 325, 326, 332–334, 336, 341, 398, 412, 413, 415, 417–419.

Common over the greater part of the area studied, although never in large numbers at any one station. In the south central Indian Ocean it was usually limited to stations north of 25 °S, the record at station 130 being exceptional. In the western part of the Indian Ocean it occurs further south, having been recorded by TAYLOR (1967) from the southwestern Indian Ocean. WOOD (1963a) lists many prior records to this species in the Indian Ocean, to which should be added those by SILVA (1956a), SUKHANOVA (1962a, b), TSURUTA (1963), DURAIRATNAM (1964), SOURNIA (1967a, 1970), TAYLOR (1967), THORRINGTON-SMITH (1969) and SAIFULLAH & HASSAN (1973 b).

Amphisolenia globifera STEIN Plate 2, Figs. 26, 27; Plate 3, Figs. 26 b, 27 b

KOFOID et SKOGSBERG 1928:388, f. 49/9, 50/1–5, t. 8, f. 1, 2, 4, 8; SCHILLER 1931:174, f. 161 a–e; SILVA 1958:23, t. 1, f. 7–9; HALIM 1960a:190; t. 2, f. 10; BALECH 1962b:134, t. 18, f. 272; WOOD 1963b:10, f. 24; – 1968:19, f. 25; LÉGER 1971a:30, f. 13.

A distinctive, small species (length 150–200 μm), characterized by a partial to strong swelling of the antapical end of the cell on which spines are either absent or two in number. It differs from both *A. quadrispina* KOFOID and *A. schauinslandii* LEMMERMANN in being smaller and in having two antapical spines instead of four. A constriction often delimits the apical side of the antapical swelling (f. 27 b), although this is not a constant feature (f. 26 b). In ventral or dorsal view the antapical swelling is globular in appearance, but it may be flattened so that it is not of this appearance in lateral view.

Stations: 68, 85, 98

Single individuals were seen at three stations in the Bay of Bengal. It has been recorded by several authors in Indian Ocean waters (see WOOD 1963a – to which should be added SOURNIA 1967a, 1970 and TAYLOR 1967). It is a tropical cosmopolitan species but has also been found in the cold Benguela Current off South-West Africa (WOOD 1968).

Amphisolenia palaeotheroides KOFOID Plate 2, Fig. 31; Table 3, Fig. 31 b

KOFOID et SKOGSBERG 1928:427, f. 56/4, t. 11, f. 2, 3, 4; SCHILLER 1931:181, f. 172, BALECH 1962b:134, t. 18, f. 269, 270; WOOD 1963b: 10, f. 26; – 1968:20, f. 28; LÉGER 1973a:18, f. 4.

In common with *A. asymmetrica* KOFOID and *A. palmata* STEIN this species possesses a differentiated foot with heel spine and three antapical spines. It differs from the former in that the head is not narrowly elongated (nor is the foot to the same extent), and from the latter most simply in that the length of the region from the antapical end of the midbody to the tip of the foot is less than the length of the remaining parts of the cell.

Stations: 294, 302.

Single individuals were encountered at two stations in the Mauritius/Seychelles region. The species has only been previously recorded from the Indian Ocean by WOOD (1962 – see WOOD 1963a) and TRAVERS & TRAVERS (1965). It is known from the tropical Pacific Ocean and from the Caribbean.

Amphisolenia schauinslandii LEMMERMANN Plate 2, Figs. 28, 29; Plate 3, Fig. 28 b; Plate 41, Fig. 495

KOFOID et SKOGSBERG 1928:374, f. 49/4, t. 7, f. 1–8; SCHILLER 1931:169, f. 155; BALLANTINE 1961:218, f. 10–12; WOOD 1963b:10; f. 28; – 1968:21, f. 31.

A distinctive species. It resembles *A. rectangulata* KOFOID in possessing four antapical spines on the straight antapical end, but can be readily distinguished from it by the shape and position of the mid-body, characteristically widest nearer its antapical end. The relative width of the mid-body is quite variable (see figs.). In the "Anton Bruun" material the specimens showed a slight inflation at the antapical end, but according to KOFOID & SKOGSBERG (1928:376) this is a variable feature.

Stations: 68, 101, 288.

Found in small numbers at stations in the Bay of Bengal and the Arabian Sea. WOOD (1963a) listed several Indian Ocean records of this species, to which that of SOURNIA (1967a, 1970) from the Mozambique Channel should be added. It is also known from the tropical Pacific Ocean and the Caribbean Sea region.

Amphisolenia schroederi KOFOID Plate 2, Fig. 32; Plate 3, Fig. 32 b

KOFOID et SKOGSBERG 1928:400, f. 49/15, t. 10, f. 2–4; SCHILLER 1931:176, f. 165; BALECH 1962b:132, t. 18, f. 271; WOOD 1963b:11, f. 29.

Some of the specimens, such as that illustrated, possessed secondary projections on the antapical end in addition to the two antapical spines characteristic of this species, thus giving the appearance of three or four antapical spines (BALECH's figure also shows this feature). In consequence this may lead to confusion with *A. rectangulata* KOFOID. However, the latter possesses a body much more clearly differentiated from the rest of the cell. In *A. schroederi* the body merges gradually with the rest of the cell in a similar manner, although not to as great an extent as in *A. complanata* KOFOID.

Stations: 57, 102, 109, 111, 125.

Single specimens were recorded from stations in the Bay of Bengal, eastern Arabian Sea, and the central Indian Ocean. It has been previously recorded from the eastern Indian Ocean by WOOD (1962 – see 1963a) and in the southwestern Indian Ocean by TAYLOR (1967).

Amphisolenia spinulosa KOFOID Plate 2, Fig. 25; Plate 3, Fig. 25 b

KOFOID et SKOGSBERG 1928:362; SCHILLER 1931:171, f. 158 a–c; SILVA 1955:127, t. 2, f. 15–17; WOOD 1968:21, f. 32.

A rare, rather poorly defined species not subject to detailed scrutiny by KOFOID & SKOGSBERG (1928). Its chief characteristics are its elongate, curved antapical region, lacking a differentiated foot, truncated at the end, and with three small antapical spines. In some respects it resembles *A. sigma* HALIM (and the possibly synonymous species *A. mozambica* SOURNIA), but differs from it principally in the presence of antapical spines. The un-named specimens illustrated and described by SILVA (1958:24, t. 1, f. 13–18) are somewhat like *A. sigma* HALIM, also lacking antapical spines.

Station: 102.

A single specimen was found at one station in the western Bay of Bengal. It has been previously recorded from the Indian Ocean by NEL (1968), and is known from the tropical Pacific (type) and the tropical Atlantic Ocean (GAARDER 1954, WOOD 1968).

Amphisolenia thrinax SCHÜTT Plate 2, Fig. 20

KOFOID et SKOGSBERG 1928:438, f. 54/7–9, 56/8, t. 12, f. 2, 6; SCHILLER 1931:183, f. 176; WOOD 1954:206, f. 57a, b; BALECH 1962b: 135, t. 18, f. 266; YAMAJI 1966:72, t. 33, f. 12; ABÉ 1967c:114, f. 44 a–f; WOOD 1968:21, f. 33.

A distinctive species whose principal distinguishing characteristic consists of two lateral antapical branches arising from the main antapical stem, usually in a plane almost at right angles to the deflection of the anterior head. It differs from *A. bifurcata* MURRAY et WHITTING, *A. projecta* KOFOID, *A. quadricauda* KOFOID et MICHENER and *A. quinquecauda* KOFOID in the number of antapical branches and the manner of their arrangement. It has been the most commonly encountered member of this group of species (the Bifurcata group of KOFOID & SKOGSBERG 1928).

The specimen illustrated here differs from the description of KOFOID & SKOGSBERG (1928:438) in that the length of the neck is shorter in proportion to its thickness, being four times its width in length, instead of six to eight. The relative lengths of the antapical branches is known to vary, and also the degree of inflation.

Stations: 31, 33, 35, 57, 59, 62, 66, 68, 69, 85, 87, 99, 100, 140, 294, 301, 326, 333, 334, 415.

It was common in the Bay of Bengal, also occuring at other stations in the northern Indian Ocean. It was only recorded from two stations (294, 301) south of the equator, one north of the Seychelle Islands, the other in the vicinity of Mauritius. WOOD (1963a) listed several previous Indian Ocean records, to which should be added that of SOURNIA (1967a, 1970) from the Mozambique Channel, and SUKHANOVA (1962a, b) TSURUTA (1963) and DURAIRATNAM (1964) from the northern Indian Ocean.

Amphisolenia sp. Plate 2, Fig. 23; Plate 3, Fig. 23 b

Individuals referred to this category bqre a close resemblance to *A. bidentata* SCHRÖDER and *A. lemmermannii* KOFOID but differed from both in being shorter (length 420–480 µm, in this respect being closer to *A. lemmermannii*) and in the gradual fusion of the mid-body into the antapical process, the mid-body being relatively more slender than in either of the above taxa. There is some doubt as to the distinction of *A. lemmermannii* from *A. bidentata* (see KOFOID

& SKOGSBERG, 1928:412), although BÖHM (1936:27) could apparently recognise the two as distinct in the tropical Pacific. Further comments of BÖHM's, however, suggest that there is little purpose in distinguishing the two, as he noted that the antapex of the short form was bent ventrally, this supposedly being a characteristic of *A. bidentata* (used to distinguish it from *A. lemmermannii* by KOFOID & SKOGSBERG). He also described the antapical spines as being present on the right valve only, whereas KOFOID & SKOGSBERG referred these spines to the left valve. The latter confusion probably arose from optical reversal, a common error in dinoflagellate literature that is particularly difficult to avoid in *Amphisolenia.*

In view of the above it may be said that this *Amphisolenia* species most closely resembled *A. lemmermannii* but showed deviations from both it and *A. bidentata.* There also appears to be a strong possibility that all three are variants of *A. bidentata.*

Stations: 27, 52, 57, 60, 99, 100, 108, 134.

It was found in small numbers chiefly in the Bay of Bengal. However, it was also present at a station off the east coast of India, and at one station in the south central region of the Indian Ocean.

Genus *Triposolenia* KOFOID

Triposolenia bicornis KOFOID Plate 3, Fig. 33

KOFOID et SKOGSBERG 1928:473, f. 66; SCHILLER 1931:188, f. 182 a–c; ABÉ 1967c:114, f. 45; WOOD 1968:128, f. 400; LÉGER 1971b: 27, f. 9.

For the most part the specimen illustrated was similar to the specimens described by KOFOID & SKOGSBERG. However, in common with the specimens figured by ABÉ and LÉGER (although not commented upon by them) it did not have a notably subspherical head, the epitheca being only slightly convex. The mid-body of the illustrated specimen had more convex contours than the type specimen, but KOFOID & SKOGSBERG and WOOD have figured specimens showing great convexity.

T. bicornis, although a relatively rare species (as are all members of this genus), is apparently the most commonly encountered species of the genus. It is distinguished from *T. depressa* KOFOID in having a relatively narrower neck and in being larger in overall size. It also resembles *T. intermedia* KOFOID et SKOGSBERG but differs in that the neck is not as curved as in the latter and the antapicals are bent in a more angular fashion with maximum flexure further from the mid-body.

Station: 57.

A single specimen was found at one station in the Bay of Bengal. It has been previously recorded from the Indian Ocean by SOURNIA (1967 a, 1970). The species was the commonest representative of *Triposolenia* in the eastern tropical Pacific material of KOFOID & SKOGSBERG (1928) and was also found to be widespread throughout the Mediterranean by JÖRGENSEN (1923).

Family Dinophysiaceae (BERGH) BÜTSCHLI

Genus *Citharistes* STEIN

This rare genus, together with *Histioneis,* exhibits some of the most elaborate and complex differentiation of the cell wall to be found among the protists. *Citharistes* represents an unusual modification of the dinophysoid structural type in which the cell body is deeply excavated upon its dorsal side. It seems possible that such an arrangement could be arrived at by a shifting of the epitheca onto the ventral side of ancestral individuals similar to *Histioneis highleyi* MURRAY et WHITTING, with re-arrangement of the girdle lists to create the so-called "phaeosome chamber," lined on its inner surfaces by the dorsal girdle plates (2g and 3g, using ABÉ's 1967a notation) – see fig. 98 b. Numerous coccoid blue-green algae occur in one species (below) but may be absent from the only other species described: *C. regius* (NORRIS, in SUBBA RAO 1973).

Citharistes apsteini SCHÜTT Plate 10, Figs. 98 a, b; Plate 41, Fig. 496

KOFOID et SKOGSBERG 1928:712, f. 102/1–5; SCHILLER 1932:257, f. 253 a, b; BALECH 1962b:140, t. 17, f. 255; WOOD 1963b:22, f. 67; – 1968:43, f. 98; BALECH 1971b:23, t. 1, f. 1, 2, 5, 6, 10; TAYLOR 1973b, f. 4 g; SUBBA RAO 1973:89, f. 1.

This species is most readily distinguished from *C. regius* STEIN in that the phaeosome chamber is much larger, resulting in a thinner posterior portion of the cell body than in *C. regius*. *C. apsteini* exhibits a range of form from individuals in which the cell body is formed in a fairly smoothly curved C-shape of subequal thickness throughout (e.g. WOOD, 1968) to individuals such as the one illustrated here in which the postero-ventral region of the cell body has a marked ventral swelling. These variants (varieties?) are linked by individuals exhibiting continuous intergradation and are undoubtedly only one species. The individual illustrated, by comparison with published figures, apparently represents an extreme development of the postero-ventral swelling.

Some other minor features of interest shown by the present specimen were that, contrary to KOFOID & SKOGSBERG's (1928) description the pores on the thecal wall were for the most part situated between the areolae except for those within the row of areolae immediately beneath the apical portion of the posterior cingular list. The structure resembling a right sulcal list extends the full distance to the postero-ventral swelling, rather than terminating shortly after the fission rib. A curious feature noted on dislocating the thecal plates was that the apparent right sulcal list separated at the fission rib in consort with the left sulcal list, being apparently closely appressed to the latter.

Station: 71.

Several specimens were found at a station in the Bay of Bengal. It is known from tropical and subtropical Atlantic and Pacific Ocean waters, and has been recorded from the eastern Indian Ocean by WOOD (1962, in WOOD 1963a) and SUBBA RAO (1973 – also from the Bay of Bengal). The latter author considered it to be a deep water species.

Genus *Dinophysis* EHRENBERG

Until recently this genus has been maintained as distinct from *Phalacroma* STEIN, principally on the basis of differing degrees of epithecal elevation. For example, KOFOID & SKOGSBERG (1928, p. 207, 210) used a ratio of 0.86 for the distance between the lower girdle list and the upper margin of the epitheca in comparison with the distance from the lower girdle list to the antapex of the cell as the demarcation between *Dinophysis* and *Phalacroma*. All species of the former have a ratio less than or equal to the figure given above, those of the latter having a ratio greater than 0.86. They also pointed out that in general the anterior cingular list was directed anteriorly in *Dinophysis*, the epitheca being only very visible above the anterior margin of the anterior cingular list. However, in the same work (1928:59) they emphasised the difficulty in application of these criteria: "It should be remembered, however, that these two genera merge into each other, and that their separation is almost arbitrary."

TAI & SKOGSBERG (1934, p. 414), after a detailed examination of the full tabulation of species of these genera could find no fundamental basis for their separation: "It is far from impossible that future investigators will decide upon the union of all these forms under a single genus, *Dinophysis*." This has, in fact, been the case, with both ABÉ (1967b) and BALECH (1967a) independently making the proposal within the same month (May) of the same year. ABÉ made new combinations only for the taxa he encountered in Japanese waters, whereas BALECH published a complete list of new combinations for all described taxa formerly referred to *Phalacroma*. As precise dates of publication have not been determined as yet, this author has followed the middle course of assigning the combinations of the few taxa dealt with by ABÉ to him, and the remainder to BALECH. This course has also been followed by PARKE & DIXON (1968). It is not clear at present whether any purpose would be served by retaining *Phalacroma* at a subgeneric level.

The unification of these genera also serves to alleviate the nomenclatural difficulty involved with the preoccupation of the name *Phalacorma* by a trilobite genus, as indicated by BALECH (1944). BALECH's new name for *Phalacroma* STEIN – *Prodinophysis*, has only been reinforced by LOEBLICH III (1965 and 1967), being neglected by other authors.

An interesting feature of some importance in the taxonomy of the genus is the apparent existence of two size forms in some species. This was first observed by JÖRGENSEN (1923) in connection with *D. schuettii* MURRAY et WHITTING and in this publication is also shown to occur in *D. swezyae* KOFOID et SKOGSBERG.

Dinophysis acutoides BALECH? Plate 4, Fig. 44

– 1967a:84.

Syn.: *Phalacroma acutum* (SCHÜTT) PAVILLARD .... JÖRGENSEN 1923:10, f. 8; SCHILLER 1931:87, f. 79a; MARGALEF et DURÁN 1953:22, f. 2 m; MARGALEF, HERRERA, RODRIGUEZ-RODA et LARRAÑETA 1954:88, f. 1 b; MARGALEF, MUÑOZ et HERRERA 1957:5, f. 1b; ABÉ 1967b:70, f. 22 a–1, sub *Dinophysis acutum* (SCHÜTT) PAVILLARD, lapsus pennae, non *D. acuta* EHRENBERG.

The taxon here tentatively referred to this name proved problematic to deal with. This was of particular concern as it is fairly well represented in the Indian Ocean. Many of the specimens exhibited a dorso-posterior concavity such as the specimen illustrated, in this manner superficially resembling *D. cuneus* (SCHÜTT) ABÉ. However, there was a gradient in body shape through this to forms in which the dorsal surface, when seen in side view, was smoothly convex and thus were similar to the type illustration (SCHÜTT 1895: plate 4, fig. 17/1). The illustrated specimen is also somewhat broader in comparison to length than most of the specimens observed, many of the others resembling the specimen in fig. 22 of ABÉ (1967b). One character by which they all deviated from other figures of this species was the markedly greater length of the third left sulcal rib (R 3) in comparison with R 2. In SCHÜTT's original figures these appear to be subequal in length. It is chiefly for this reason that the identification here is tentative.

Stations: 13, 17, 33–35, 37, 43, 55, 57, 69–71, 94, 96–98, 100, 101, 103, 113, 114, 116, 140–143, 317, 323–325.

Found in small numbers at stations in the Andaman Sea, the central and western Bay of Bengal, the eastern Arabian Sea, and in the central Indian Ocean region to the south of India. In view of the tentative nature of the identification there is little purpose in describing the distributional characteristics of the species or previous Indian Ocean records.

Dinophysis apicata (KOFOID et SKOGSBERG) ABÉ Plate 4, Fig. 36
– 1967b:73, f. 23 c–g.

Syn.: *Phalacroma apicatum* KOFOID et SKOGSBERG 1928:111, f. 10/1–5; SCHILLER 1931:76, f. 68 a–c; WOOD 1954:184, f. 10; MARGALEF 1969a, f. 3 A; STEIDINGER et WILLIAMS 1970:59, t. 35, f. 120.
Phalacroma operculatum auct. non STEIN . . . . MARGALEF et MORALES 1960:5, f. 2 c.

This large species is very closely related to *D. argus* (STEIN) ABÉ, from which it is separated solely on the grounds of its more sharply conical epitheca. The faint ground reticulation of the theca is not shown in the specimen illustrated, although it is usually apparent in most specimens, being identical to that of *D. argus.* It is likely that further study will indicate that this taxon should be considered as an infraspecific variant of *D. argus.*

An interesting feature of the specimen illustrated (which is slightly tilted, the subconical epitheca being not quite as obvious as in full side view) is that, instead of a third left sulcal rib (R 3) there was a distinct gap in the same position.

Stations: 23, 26, 38, 55, 59, 60, 71, 93, 99, 101, 103, 113, 135, 153, 318, 323.

Found in small numbers predominantly in the Bay of Bengal and Andaman Sea, but also encountered to the south of India and once in the vicinity of the Seychelles. It has been previously recorded from the Indian Ocean by TRAVERS & TRAVERS (1965) and SOURNIA (1968b – Madagascar). It is known from the tropical Pacific Ocean.

Dinophysis argus (STEIN) ABÉ Plate 4, Fig. 35
– 1967b:71, f. 23 a, b; HERMOSILLA 1973a:28, t. 1, f. 19, 21.

Syn.: *Phalacroma argus* STEIN 1883, t. 18, f. 15 (?), 16, 17; . . . . KOFOID et SKOGSBERG 1928:104, f. 8/1, 2, 9; CANDEIAS 1930:15, t. 1, f. 18; SCHILLER 1931:74, f. 67 a; RAMPI 1940:255, f. 17; MARGALEF 1948b:45, f. 1 h; SILVA 1949:334, t. 4, f. 7; MASSUTI et MARGALEF 1950, f. 63 a, b; WOOD 1954:186, f. 16 a, b; STEIDINGER et WILLIAMS 1970:59, t. 35, f. 121.

A large, distinctive species closely related to *P. apicata* (KOFOID et SKOGSBERG) BALECH – see comparative comments under the latter. The specimen illustrated differed from others previously described, and others observed in this material, in lacking the third rib of the left sulcal list.

Stations: 32, 57, 62–64, 103, 109, 116, 130, 143, 144, 161, 289, 302, 341, 362, 366, 414, 419.

Present in small numbers at stations scattered throughout the area studied but more commonly in the northern parts. It was found furthest south (st. 130) in June. Recorded by several authors from the Indian Ocean (WOOD 1963a plus SILVA 1956a, TRAVERS & TRAVERS 1965, SOURNIA 1968b and THORRINGTON-SMITH 1969).

Dinophysis brevisulcus TAI et SKOGSBERG Plate 4, Fig. 34
– 1934:430, text f. 3 A–K.

When this specimen was first seen it was assumed to be a specimen of *D. rotundata*. The third rib(R3) of the left sulcal list was not developed, but this was assumed to be a transient maturational state. Dr. E. Balech kindly drew the author's attention to another distinction which can be readily used to separate this taxon from *D. rotundata*: the right sulcal list is much shorter in *D. brevisulcus,* only extending approximately level to R2 of the left sulcal list, whereas in

D. rotundata it reaches R3. Both species have been described and figured by TAI & SKOGSBERG (1934). In one of ABÉ's (1967b) figures of *D. rotundata* he has drawn a specimen which possesses a strong R3 but has a short right sulcal list (his fig. 15 b). If this is not an error it may indicate that either *D. brevisulcus* can develop an R3 (TAI & SKOGSBERG doubted it because of the mature appearance of the list on their specimens), or that perhaps the two species are linked by intermediates. The present specimen was smaller than the type material, being only 38 µm in length (type specimens 51–53 µm long).

Stations: 32.

Only a single specimen from the Andaman Sea was observed. This is a new record for the Indian Ocean. The type locality is Monterey Bay, California. Other records for the species are not known to this author.

Dinophysis caudata SAVILLE-KENT Plate 6, Fig. 59

KOFOID et SKOGSBERG 1928:314, f. 44/1–8; MARTIN 1929:21, t. 4, f. 14; SCHILLER 1931:153, f. 145 a–o; WANG et NIE 1932:309, f. 21; TAI et SKOGSBERG 1934:453, f. 9 A–K, f. 10 D–F; BÖHM 1935:277, f. 4 a–i; – 1936:20, f. 7 a–e, f. 8 a/1–12, b/1–3, f. 9 a–j; RAMPI 1940:263, f. 41; BALECH 1951a:1, f. 1–76; MARGALEF 1946:92, f. 1/3; SILVA et PINTO 1948:162, t. 2, f. 3; SILVA 1949:338, t. 8, f. 8; MASSUTI et MARGALEF 1950, f. 59; MARGALEF et DURÁN 1953:22, f. 3 n; WOOD 1954:201, f. 49 a–e, 50 a–g, MARGALEF 1957a:45, f. 1 d, e, f; CURL 1959:305, f. 110; HALIM 1960a, t. 2, f. 2; BALLANTINE 1961:218, f. 8; MARGALEF 1961a:76, f. 25 d; – 1961b:140, f. 2/3; KLEMENT 1964:358, t. 2, f. 5; ABÉ 1967b:56, f. 14 a–d; HALIM 1967:726, t. 4, f. 48; HADA 1967:10, f. 14 A; WOOD 1968:47, f. 112; STEIDINGER et WILLIAMS 1970:48, t. 17, f. 46, 47; HASSAN et SAIFULLAH 1972a:67, f. 4; HERMOSILLA 1973a:27, t. 1, f. 14, 27.

This species is highly variable in form, having led many authors to recognise a host of distinct taxa within the assemblage considered by KOFOID & SKOGSBERG (1928) as constituent of this species. BÖHM (1936) suggested that his material from the western Pacific Ocean and the Mediterranean Sea could be viewed as three genetically different varieties of the same species. Of these, if they are recognised, the variety *allieri* JÖRGENSEN should be termed the variety *caudata* in view of the designation of JÖRGENSEN's (1923) fig. 30 as conforming to the type description of SAVILLE-KENT by KOFOID & SKOGSBERG (1928:320). The great majority of specimens encountered in the Indian Ocean corresponded to the variety *pedunculata* SCHRÖDER as described by BÖHM (1935, 1936), others tending towards or conforming with the variety *abbreviata* JÖRGENSEN, also described by BÖHM.

The closest relatives to *D. caudata* are *D. tripos* GOURRET, from which it is distinguished by virtue of the latter's additional dorso-posterior projection (although it may possibly be conspecific), and *D. miles* CLEVE in which the dorso-posterior region is greatly elongated to a length subequal to or much longer than the posterior process (see f. 57, 58). These species are all commonly observed in joined pairs, triplets, or quadruplets resulting from incomplete separation after fission.

Stations: 15, 21, 26, 40, 45, 50, 88, 398.

Found in moderate numbers in the Andaman Sea, Bay of Bengal, and at one station at the southern end of the Mozambique Channel. All stations were in close proximity to land, a feature observed by this author previously in southwestern Indian Ocean material (TAYLOR ms., 1964). It is apparently a predominantly neritic species found in tropical to warm temperate waters throughout the world. It has been recorded by many authors from the Indian Ocean, the list provided by WOOD (1963a) being supplemented by the records of BÖHM (1931a) from the Persian Gulf (as f. *persica*), SILVA (1960) from Inhaca, Mozambique, SUBRAHMANYAN & SARMA (1960) from the west coast of India, TSURUTA (1963) from the north-central region, ANGOT (1965) from Madagascar, TAYLOR (1967) from inshore waters off the coast of South Africa, NEL (1968) also from the southwestern Indian Ocean, SOURNIA (1968b, 1970) and ANGOT (1970) from Madagascar, and HASSAN & SAIFULLAH (1972a) from the Arabian Sea.

Dinophysis circumsuta (KARSTEN) BALECH Plate 4, Fig. 43

– 1967a:82; NORRIS et BERNER 1970:158, f. 2–8.

Basionym: *Phalacroma circumsutum* KARSTEN 1907:421, t. 53, f. 8 . . . . KOFOID et SKOGSBERG 1928:182, f. 23/6; SCHILLER 1931:100, f. 92; SILVA 1958:20, t. 1, f. 3; WOOD 1963b:5, f. 6; LÉGER 1972b:25, f. 10.
Non BALLANTINE 1961:218, f. 6, 7.
Phalacroma doryphorum auct. non STEIN – HALIM 1960a, t. 1, f. 27.

A distinctive species, distinguished from *D. doryphorum* (STEIN) ABÉ by virtue of the strong, single spine supporting the posterior list projection, the spine being directed postero-ventrally. The posterior projection is confluent with the left sulcal list, whereas it is separate in *D. doryphorum*. In general, but not always, the main supporting rib of the left sulcal list (R 3) is longer, extending the list out further. The specimen illustrated by HALIM (1960a) from Villefranche-sur-Mer in the Mediterranean under the name of *Phalacroma doryphorum* STEIN has a shorter R 3, similar in length to *D. dory-*

phorum, but the presence and orientation of the antapical spine is here taken to be the most distinctive characteristic of *D. circumsuta*. NORRIS & BERNER (1970) have also attributed his figure to this species.

Stations: 54, 59, 67, 71, 72, 100, 102, 103, 149, 287, 294, 404.

Single specimens were encountered in the Bay of Bengal, Arabian Sea, and the Mozambique Channel, generally at oceanic stations. Originally described from the Indian Ocean, this species has also been recorded from this region by MATZENAUER (1933), SOURNIA (1966a, 1968b, 1970) and NEL (1968). It is known from the tropical Pacific Ocean, the Gulf of Mexico, and the Mediterranean Sea.

Dinophysis cuneus (SCHÜTT) ABÉ Plate 5, Figs. 46, 47

– 1967a:68, f. 21 a–h.

Syn.: *Phalacroma cuneus* SCHÜTT .... KOFOID et SKOGSBERG 1928:124, f. 12/1–3; SCHILLER 1931:84, f. 76 a–d; RAMPI 1940:256, f. 22; SILVA 1949:334, t. 4, f. 6; MASSUTI et MARGALEF 1950, f. 67; WOOD 1954:187, f. 20 a, b; BALECH 1962b:129, t. 17, f. 238–242, 247; YAMAJI 1966:67, t. 31, f. 16; STEIDINGER et WILLIAMS 1970:59, t. 35, f. 122.
Phalacroma blackmani MURRAY et WHITTING 1899:130, t. 31, f. 4 a, b.

A well defined species, cuneiform in ventral view, most closely related to *D. gigantea* (KOFOID et MICHENER) BALECH, from which it differs only in being smaller in size (maximum length 88 µm as opposed to 148 µm in *D. gigantea*). *D. striata* (KOFOID) BALECH differs in that the left sulcal list is very wide posteriorly, projecting as far as the posterior margin of the hypotheca. *D. triangularis* (WOOD) BALECH may represent a malformation of *D. cuneus* in which the greatest depth of the body is dorsal to the central axis, instead of ventral. The specimen of *D. cuneus* figured by HALIM (1960a, pl. 1, f. 26 as *P. cuneus*) from the Mediterranean is unusual in having an epitheca raised much higher than in extant figures of *D. cuneus*. Indeed, the specimen looks almost intermediate between this species and *D. argus* (STEIN) ABÉ.

The conspecificity of *Phalacroma blackmani* MURRAY et WHITTING with this species was first indicated by JÖRGENSEN (1923) who listed it without comment as a synonym. SCHILLER (1931) agreed with JÖRGENSEN, dismissing the differences raised by KOFOID & SKOGSBERG (1928): "Allein die dafür vorgebrachten Gründe sind nebensächlich." In support of this somewhat arbitrary statement a comparison of figures 46 and 47 here shows that the curvature of the supporting ribs of the left sulcal list may curve either anteriorly or ventrally. Figure 46 closely resembles the figure of MURRAY & WHITTING but lies within the size range of *D. cuneus*. KOFOID & SKOGSBERG (1928:128) drew attention to the presence of a marked "parasagittal list" in *P. blackmanni*, this referring to the hyaline listlike projection arising from the posterior surface of the hypotheca, greatest in width at the antapex of the cell. Present observations indicate that this structure is not a constant feature in this taxon, but is developed in association with fission and remains for an apparently short period after fission. It is probably homologous with the "dorsal megacytic bridge" described in *Ornithocercus* by TAYLOR (1973a). The specimen in figure 47 possesses one half of the theca with fully developed reticulation, and the other half only with porulae, a situation indicative of recent fission. This specimen also exhibits the greatest development of the dorsal megacytic bridge. This structure is also probably homologous with similar structures observed and illustrated in *D. caudata* (fig. 59), where it serves as a link between the daughter cells, *D. miles* (figs. 57, 58) and *D. swezyae* (fig. 64). It should be emphasised, however, that these are not parasagittal lists such as those which exist in several species, e.g. *D. limbata* (KOFOID et MICHENER) BALECH. True parasagittal lists extend ridge-like over much of the cell profile, including the epitheca.

Stations: 13–15, 17, 19, 23, 24, 28, 29, 32, 34–36, 38, 52, 56, 63, 65, 66, 68–71, 91, 94–100, 102, 103, 113, 114, 118, 134, 135, 141, 142, 147, 149, 154, 162, 282, 289, 291, 294, 295, 305, 317, 320, 325, 327, 329, 331, 336, 339, 341, 344, 413.

One of the commonest species in the material, encountered in 28.5 % of the samples. It occurred sporadically over most of the area studied, but was not found in samples south of 32 °S in the central Indian Ocean. The other area where it was poorly represented was the Mozambique Channel. It has, however, been found further south by this author in a previous study (TAYLOR, ms. 1964, 1967) off the east coast of South Africa in October, 1962. WOOD (1963a) has listed several records of the species from the Indian Ocean, to which the records of SILVA (1956a), TAYLOR (1967), and NEL (1968), and SOURNIA (1968b, 1970) should be added. The species is widespread throughout tropical and subtropical waters.

Dinophysis doryphorum (STEIN) ABÉ Plate 4, Figs. 41, 42

– 1967b:77, f. 26; NORRIS et BERNER 1970:161, f. 23–45; LÉGER 1973b:21, f. 10.

Syn.: *Phalacroma doryphorum* STEIN .... KOFOID et SKOGSBERG 1928:175, f. 23/1–5; CANDEIAS 1930:16, t. 1, f. 20; SCHILLER 1931: 99, f. 91 a, b; MATZENAUER 1933:444; RAMPI 1940:257, f. 27; MARGALEF 1948b:45, f. 1i; SILVA 1949:335, t. 4, f. 9; MASSUTI et MARGALEF 1950, f. 69; WOOD 1954:191, f. 30 a, b; RICARD 1970, t. 2, f. j.
Non HALIM 1960a, t. 1, f. 7.

This species can be readily distinguished from *D. circumsuta* (KARSTEN) BALECH, its nearest relative, on the basis of the strong spine supporting the antapical list projection present in the latter. In *D. doryphorum* this antapical list frequently exhibits thickening at the distal end and around edges (c. f. fig. 42), and the shape of the list may vary from clavate to acute. As may be seen from a comparison of figs. 41 and 42, if the specific assignment of the specimen in fig. 41 is correct, the length and thickness of the third rib on the left sulcal list may vary. In the specimen in fig. 41 the antapical list is apparently in a stage of reformation following cell division. The species differs from *D. paulsenii* (SCHILLER) BALECH (= *Phalacroma mucronatum* KOFOID et SKOGSBERG) in the rounded shape of the latter when seen in lateral view, the higher epitheca in the former, and the smaller size of *D. paulsenii* (maximum length 45.4 µm).

Stations: 14, 21, 23–26, 29, 30, 32, 34–39, 41, 54, 58, 60, 62–64, 66, 68–72, 92, 97–99, 102–104, 106, 113, 114, 116, 129, 130, 133–135, 141, 143, 148, 149, 150, 156, 311, 326, 334, 417.

It was common but not abundant in the Andaman Sea, Bay of Bengal, and the Arabian Sea. It was also present at scattered stations in the south central region, found furthest south at station 311 near the Islands of Amsterdam and St. Paul in April, 1964. It was only recorded from one station in the western region, off the coast of east Africa.

Although generally described as present in tropical to warm temperate waters it was here absent from the most equatorial waters. WOOD (1963a) listed several previous Indian Ocean records, to which those of SILVA (1956a), SOURNIA (1966a, 1968b, 1970), TAYLOR (1967), NEL (1968), and ANGOT (1970) should be added.

Dinophysis exigua KOFOID et SKOGSBERG Plate 4, Fig. 37
– 1928:239, f. 30/1–3; SCHILLER 1931:111, f. 102 a, b; WOOD 1963b:6, f. 12 a (non b); BALECH 1967a:86, t. 1, f. 4–12; WOOD 1968:48, f. 113.

This small species has been subjected to a detailed plate analysis by BALECH (1967a). His specimens possessed an exceptionally large and distinctive apical pore. This feature could serve to distinguish it from *D. rotundata* CLAPARÈDE & LACHMANN and *D. parvula* (SCHÜTT) BALECH which have some similarities with it. The illustrated specimen differs from previous descriptions in that the girdle lists do not project as much anteriorly and it possesses distinct, closely-set porulation. The shape of the type specimens, seen in side view, was shown to vary, particularly in the dorsal profile, by KOFOID & SKOGSBERG (1928), the figured specimen corresponding to their more narrowly elongate form (their fig. 30/2). BALECH (pers. comm.) doubts that the figured specimen is conspecific with the species he examined in the Gulf of Mexico. Others seen in the "Anton Bruun" material showed the more typical girdle list inclination.

Stations: 69, 294, 359.

Single individuals were encountered in the Bay of Bengal, the Seychelle Islands region, and off the southeast coast of southern Africa. It has been recorded previously from the Indian Ocean by WOOD (1962 – see WOOD, 1963a) and from the tropical Atlantic (Gulf of Mexico) and tropical Pacific Oceans.

Dinophysis expulsa KOFOID et MICHENER Plate 6, Figs. 62 a, b
Syn.: *Phalacroma expulsum* (KOFOID et MICHENER) KOFOID et SKOGSBERG 1928:157, t. 5, f. 1, f. 20/1–5; MUÑOZ, HERRERA & MARGALEF 1956:76, f. 1 c, d; HALIM 1960a, t. 1, f. 24 a, b.
Phalacroma stenopterygium JÖRGENSEN 1923:11, f. 10.

A rare, distinctive species recognised most readily in ventral view. In this view the body appears wedge-shaped with a marked depression one quarter to one third the distance from the lower girdle list to the antapex. In lateral view most specimens exhibit a sloping of the longitudinal axis of the body from 5° to 15°. The most closely related species is *D. protuberans* (KOFOID et SKOGSBERG) BALECH which possesses a lateral swelling in place of the depression of *D. expulsa*, as well as other differing features.

Stations: 30, 62.

Single individuals were found in the western regions of the Andaman Sea and the Bay of Bengal. It has been previously recorded from the eastern tropical Pacific and the Mediterranean, but not from the Indian Ocean.

Dinophysis favus (KOFOID et MICHENER) BALECH Plate 5, Figs. 50, 51
– 1967a:82.
Syn.: *Phalacroma favus* KOFOID et MICHENER .... KOFOID et SKOGSBERG 1928:146, t. 2, f. 7, f. 14/4, 5; CANDEIAS 1930:15, t. 1, f. 19; SCHILLER 1931:91, f. 83; RAMPI 1940:257, f. 26; SILVA 1949:335, t. 4, f. 8; WOOD 1954:189, f. 27; HALIM 1960a, t. 1, f. 25.

The species differs from *D. rapa* (STEIN) ABÉ principally in the constricted, projecting antapex of this species, differing from *D. hindmarchii* (MURRAY et WHITTING) BALECH which also has a projecting antapex by having a much lower epitheca. The specimens illustrated here give an idea of some of the variability inherent in this species, e.g. variations in the length of the third rib (R 3) of the left sulcal list, and variations in the degree of constriction of the antapex.

Stations: 23–25, 113, 140, 143, 312.

The species was found in small numbers at three stations in the Andaman Sea, three stations to the south and west of India, and at one station south of 30 °S in the central region in April, 1964. It is known from the tropical and subtropical waters of the three major oceans, and also from the Mediterranean. Recorded from the Indian Ocean only by MATZENAUER (1933), WOOD (1962 – listed 1963a), and NEL (1968).

Dinophysis hastata STEIN   Plate 5, Figs. 52–55

KOFOID et SKOGSBERG 1928:261, f. 32/1–17, f. 33/1–3; SCHILLER 1931:138, f. 131 a–n; BÖHM 1936:17, f. 6 a–h; RAMPI 1940:262, f. 40; WOOD 1954:199, f. 47 a (b?); GAARDER 1954:19, f. 19 a, b; MARGALEF, DURÁN et SAIZ 1955:95, f. 5 c; MARGALEF, MUÑOZ et HERRERA 1957:5, f. 1 a; HALIM 1960a, t. 2, f. 4; YAMAJI 1966:71, t. 32, f. 17; ABÉ 1967b:76, f. 25; WOOD 1968:49, f. 115; MARGALEF 1969a, f. 3 C; STEIDINGER et WILLIAMS 1970:49, t. 17, f. 48; NORRIS et BERNER 1970:165, f. 46–59.

Syn.: *D. uracantha* auct. non STEIN - - - SILVA 1956b:356, t. 3, f. 5.
Phalacroma hastatum PAVILLARD 1909?
Phalacroma odiosum (PAV.) PAVILLARD 1930.
Dinophysis odiosa (PAV.) TAI & SKOGSBERG (c.f. LÉGER, 1973a).

One of the commonest representatives of *Dinophysis* in the area studied. Variability in field material has been the subject of reasonably intensive study by KOFOID & SKOGSBERG (1928) and BÖHM (1936). NORRIS & BERNER (1970) have stressed that this may be a collective species. The specimens illustrated here show two of the commonest appearances within the Indian Ocean material (figs. 52, 54) and fission stages associated with them in which the lower part of the left sulcal list (posterior to the fission rib) and the antapical fin are missing. Whilst assignment of the latter specimens (figs. 53, 55) to this species must remain tentative, observation of specimens in all stages of reformation of the right side of theca, with its associated structures (which includes the posterior part of the left sulcal list) in the present material leaves little doubt that this assignment is correct. The specimen in fig. 54 corresponds to the variety *uracanthides* JÖRGENSEN which, according to KOFOID & SKOGSBERG (1928), may represent an intermediate stage between this species and *D. uracantha* STEIN.

At present the nearest related species, *D. uracantha*, is distinguished from *D. hastata* principally on the basis of the dorso-antapical insertion of the antapical fin, instead of ventro-antapical in *D. hastata*. LÉGER (1973a) has maintained the distinction of *D. odiosa* (PAV.) TAI et SKOGSBERG (erroneously creating a new combination), chiefly on the basis of left sulcal list features, although admitting that the sole character which is not overlapped by *D. hastata* is the distance between the first and third ribs (R 1 and R 3), being 0.03 of a cell length less in *D. odiosa*.

Stations: 15, 26, 29–31, 36, 51, 53, 54, 57, 59, 61, 64–66, 69, 71, 91, 95–98, 102, 103, 116, 301, 335, 396.

It was common in the Andaman Sea and the Bay of Bengal and was also found in small numbers in the southern Arabian Sea region, once near Mauritius, and once at a station close to Lourenco Marques at the southern end of the Mozambique Channel. The species has been recorded from the Indian Ocean by several previous authors including SOURNIA (1966a, 1968b, 1970) from Mauritius and Tulear (southwest Madagascar) and NEL (1968) from the southwestern Indian Ocean, these records being additional to those listed by WOOD (1963a).

Dinophysis infundibula SCHILLER   Plate 6, Fig. 61

– 1928:76, f. 38; – 1931:112, f. 104.

Syn.: *D. parva* SCHILLER 1928:77, f. 39; – 1931:111, f. 103; RAMPI 1940:258, f. 30; GAARDER 1954:20, f. 21; HALIM 1960a, t. 1, f. 30 (sub. *D. punctata* SCHILLER – sic), t. 1, f. 31; WOOD 1963b:7, f. 15; – 1968:50, f. 121.
Non WAILES 1939:25, f. 71.

The species, and the one considered conspecific, were both described by SCHILLER from the same locality (the Adriatic) in the same work. Although SCHILLER did not draw attention to their specific distinction, from the descriptions it can be assumed that this was based chiefly on the width of girdle lists, the relative intensity of chloroplast pigmentation, and differences in the inclination of the apical/antapical axis. From an examination of existing figures, and from material from the coastal waters of British Columbia (unpublished), it is here concluded that PARKE, BALLANTINE & GAARDER (in PARKE & DIXON, 1968) are correct in making them conspecific, the above characters showing variation not conducive to their specific separation.

The characteristics by which this species may be distinguished from others are: the small size (maximum length 30 µm, usually 21–26 µm) combined with a greatest width in lateral view which is median to post-median, apex more acute than antapex, a relatively short dorso-ventral length of the upper girdle list where it arises from the epithecal border (exemplified particularly by the type specimen and that illustrated here), and termination of the left sulcal list in an approximately median position. The latter serves to distinguish it from its closest relative, *D. recurva* KOFOID & SKOGSBERG, which is also larger and more elongate in shape. The upper girdle list suture is often inclined at an angle to the lower girdle list suture when seen in lateral view, the dorsal end being more anterior than the ventral end (see esp. GAARDER's, 1954, figure).

ABÉ (1967b) has listed *D. parva* SCHILLER as a synonym for *D. ovum* SCHÜTT without comment. However, if the criteria for recognition of the taxon listed above are satisfactory this designation is highly doubtful, the taxa being readily separable. For example, *D. ovum* has a flattened epitheca which immediately serves to distinguish it from *D. infundibula.*

Other closely related species, which may eventually prove to be conspecific, are *D. dentata* SCHILLER and *D. umbosa* SCHILLER. In form *D. sphaerica* STEIN bears a close resemblance, but it is larger (length 43–47 µm).

Station: 326.

A single individual (illustrated) was observed at this station in the northwestern sector, west of the Maldive Islands, in April 1964. The species has only been recorded previously from the Indian Ocean (eastern sector) by WOOD (1962 – listed 1963a).

Dinophysis miles CLEVE Plate 6, Figs. 57, 58

KOFOID et SKOGSBERG 1928:227; SCHILLER 1931:160, f. 147 a–d, 148 a, b, 149 a, b; MATZENAUER 1933:445, f. 10 (+ fig. in SCHILLER); BÖHM 1935:272, f. 2 a–c; – 1936:26; SILVA 1956a:55, t. 9, f. 4, 5; BALLANTINE 1961:218, f. 9; TAYLOR 1967, t. 4 (91), f. 35; – 1973b, f. 5 b; HASSAN & SAIFULLAH 1972a:68, f. 5 a, b.

This species represents one of the most extreme body modifications of the genus, and can be looked upon as an extension of a developmental series from *D. caudata* SAVILLE-KENT, through *D. tripos* GOURRET to this species in which the dorsal process achieves maximum development (c.f. TAYLOR, 1976).

The specimens illustrated represent two infraspecific taxa which have been recognised in the literature – the variety *schroeteri* (FORTI) BÖHM [= *Heteroceras schroeteri* FORTI, 1901, p. 6, f. 1, 2; *D. miles schroeteri* (FORTI) OSTENFELD, 1915, p. 6] inadvertently misnamed *"schröderi"* by MATZENAUER (1933), exemplified by the specimen in fig. 57, and the variety *indica* BÖHM (1935) of which the specimen in fig. 58 is a fair example. A third type, the variety *miles* (formerly incorrectly named *maris rubri*, but representing the type variety and form of the species i.e. CLEVE 1900b, fig. 1a), was not present in the material. The reader is referred to the detailed study of BÖHM (1935) for descriptions of these three varieties.* In brief, the variety *miles* has the shortest, most posteriorly inclined dorsal process, the variety *schroeteri* the longest and least posteriorly inclined dorsal process, with the variety *indica* intermediate (but demarcated by discontinuity) between the two. SCHILLER (1931) included individuals consistent with the var. *schroeteri* within the var. *indica*, but BÖHM's arguments in favour of their separation are convincing to this author. The specimen of var. *schroeteri* illustrated here is interesting in that it appears to be an extreme example, the length of the dorsal process (147 µm from mid-line of the body) exceeding the size data given by BÖHM and greater than those illustrated by SCHILLER (1931 – calculated from the magnifications given).

Previous authors have interchanged *varietas* and *forma* in regard to the above infraspecific taxa with complete disregard for taxonomic convention (or conceptual distinction), altering the infraspecific designation (even within the same publication) whilst retaining the author designation for the original taxon, irrespective of whichever one was used. For this reason BÖHM (1935) is here given authorship of the var. *schroeteri* and var. *indica* as he was apparently the first to employ *varietas* for these taxa, even though throughout the text (with the exception of the text to fig. 2) he also employed *formae.*

The reason why *varietas* is here preferred to *forma* in reference to these taxa is that the two types found in this material can be found apparently co-existent in the same samples (see the introductory comments under Infraspecific taxa). For this reason, and because of interesting distributional features, the data below has been kept separate.

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* MATZENAUER (1933) proposed two forms (f. *triposoidea* and f. *arabica* which can be considered within the range of the var. *miles.* SCHRÖDER's f. *maris ionii* is a further variant within the latter variety.

Stations: var. *indica* – 23, 34, 36–38, 42, 43, 47–49, 65, 87, 287, 412.
var. *schroeteri* – 15, 21, 23–25, 29, 31, 32, 34, 36–39, 41–43, 46, 47, 49–51.

Both taxa were found in small numbers predominantly in the Andaman Sea and Bay of Bengal at neritic stations (all stations within the Andaman Sea are here considered to be under neritic influence). However, the var. *schroeteri* was restricted to the eastern side of the Bay of Bengal, whereas the var. *indica* was also present on the western side, as well as being recorded from one station in the Gulf of Aden.

The species is apparently known only from the Indo-West Pacific region, with occasional records in the Mediterranean considered by BÖHM (1935) to be indicative of migration through the Suez canal. Of particular interest are the distributional characteristics of the varieties described by BÖHM(1935) and partially confirmed here. The variety *miles* appears to be largely confined to the Red Sea (the type locality) and the Persian Gulf (BÖHM 1931a). The variety *schroeteri* is highly characteristic of the Andaman Sea – East Indies region, whilst the variety *indica* is found widely distributed over the area between the two localities. It has been recorded from the Red Sea by SUKHANOVA (1969) and from the Gulf of Tonkin by KUSJMINA (1971). It is also the variety encountered in the southern parts of the Indian Ocean as indicated by the figures of SILVA (1956a from Mozambique) and the record of "forma" *indica* from the southwestern region where it had a neritic distribution (TAYLOR, ms. 1964, 1967). Other southern records (SILVA 1960, ANGOT & GÉRARD 1967, SOURNIA 1968b, NEL 1968, ANGOT 1970) do not specify the infraspecific type in the lists involved.

This situation, based on readily recognisable morphotypes, appears to warrant further detailed investigation as it has interest with regard to the species problem in dinoflagellates. Further studies are necessary to determine if the distributions of the infraspecific taxa are as localised as they appear to be, to observe seasonal influences, to determine if there are microdistributional differences between the apparently sympatric varieties, to see if there truly are disjunctions in the size characteristics of the varieties, and to determine if environmental factors such as salinity or land-derived substances may not play a phenodeterminant role.

The list of Indian Ocean records given by WOOD (1963a) requires amplifying by those of BÖHM (1931a, 1935) SCHILLER (1931 – excluding those from MATZENAUER's manuscript that were published by the latter author at a later date – 1933), plus the more recent southern records mentioned above, and SUKHANOVA (1962 a, b), ZERNOVA (1962), TSURUTA (1963), DURAIRATNAM (1964), ANGOT (1965), SOURNIA (1970), and HASSAN & SAIFULLAH (1972a).

Dinophysis mitra (SCHÜTT) ABÉ Plate 5, Fig. 49
– 1967b:63, f. 18 a–q.
Syn.:*Phalacroma mitra* SCHÜTT .... KOFOID et SKOGSBERG 1928:143, 144; SCHILLER 1931:90, f. 82 a–c; RAMPI 1940:257, f. 25;
YAMAJI 1966:67, t. 31. f. 19.
Vix WOOD 1954:189, f. 26.

This species is closely related to, if not conspecific with, *D. rapa* (STEIN) ABÉ. KOFOID & SKOGSBERG (1928) drew attention to two features which they considered of value in distinguishing the species – the greater angularity of the ventral margin of the cell when seen in side view and a greater degree of concavity betwenn the antapex and the end of the left sulcal list (R 3) in *D. rapa*. SCHILLER (1931) used only the latter characteristic to distinguish the two species. ABÉ (1967b) later showing that this criterion could not be applied as it is apparently related to the degree of megacytic (expansion in volume prior to cell division) growth. ABÉ's course of action is perplexing as it appears to be self-contradictory. On page 63 he united *Phalacroma mitra* SCHÜTT with *Phalacroma rapa* STEIN, presumably because SCHILLER's selected criterion cannot be applied, but he used *Dinophysis mitra* (SCHÜTT) as the final combination, even though the specific epithet *rapa* has priority by twelve years. On page 66 he then described *Dinophysis rapa* (STEIN) as a separate taxon, his starting reference under the synonym being that of JÖRGENSEN (1923) whose figure does not show the criteria which ABÉ then used as the chief characteristics of *D. rapa.*

In essence the situation seems to be the following – *D. mitra* may be distinguished from *D. rapa* solely on the first criterion drawn attention to by KOFOID & SKOGSBERG (1928), namely the angular projection of the region of the cell adjacent to the R 3 end of the left sulcal list in *D. rapa*, the same region in *D. mitra* being gently, convexly rounded. As a result of this angularly-protruding region the sulcal region of *D. rapa* is straight to concave in outline when seen in lateral view, whereas it is convex in *D. mitra.* ABÉ (1967b) also considered it significant that the left side of the sulcal region projected further than the right side in *D. rapa.* However, it is difficult to determine as it depends on viewing the cell precisely in full side view (for example, the present illustrated specimen of *D. mitra* – pl. 5, f. 49, is slightly tilted, producing a similar appearance of the sulcal region as that attributed by ABÉ to *D. rapa*).

D. mitra and *D. rapa* are also closely related to *D. favus* (KOFOID et MICHENER) BALECH (see comparative notes under the latter), and form a complex analagous to the *D. caudata* – *D. tripos* – *D. miles* complex referred to in this report.

Stations: 17, 19, 29, 30, 35, 37, 38, 62, 66, 68–70, 92, 108, 109, 110, 129, 131, 134, 305, 313.

The species occured in small numbers in the Andaman Sea, the western Bay of Bengal, off the west coast of India, and on several different cruises at stations in the southern central regions below 30 °S. It is apparently widespread, having been recorded from tropical and and warm temperate regions throughout the world, but the confused systematic position renders many of these records unreliable. As it has not been illustrated by those authors recording it previously from the Indian Ocean (see WOOD 1963a, plus NEL 1968) the validity of these records cannot be checked.

Dinophysis parvula (SCHÜTT) BALECH* Plate 4, Figs. 38, 39
– 1967a:83.
Syn.: . . . . *Phalacroma parvulum* (SCHÜTT) JÖRGENSEN 1923:7, f. 4; KOFOID et SKOGSBERG 1928:85, f. 3/4–6; SCHILLER 1931:63, f. 57 a–c (d?); BÖHM 1936:15, f. 5 b/1, 2; RAMPI 1940:252, f. 14; MARGALEF 1948b:47, f. 1 f; MASSUTI et MARGALEF 1950, f. 64 a, b; HALIM 1960a, t. 1, f. 22; MARGALEF et DURÁN 1953:20; BALECH 1962b:125, t. 17, f. 251; WOOD 1963b:6, f. 10: BALECH 1971a:71, t. 10. f. 144–153.

The majority of the specimens referred here to this species had a wide left sulcal list, corresponding to forms originally described as *P. lativelatum*. However, the width was found to vary in a manner not conducive to the separation of that species from *P. parvulum*. This is also suggested by the figures of HALIM (1960a) and BALECH (1962b). The possibility that the two are conspecific was pointed out by KOFOID & SKOGSBERG (1928) who used the left sulcal fin-width as the sole character used for separation of the two.

A distinctive feature of the Indian Ocean specimens was the greater convexity of the dorsal surface in comparison with the ventral surface, a feature shared with *D. modesta* (BÖHM) BALECH, whose left sulcal list is, however, relatively narrow. In size they more closely approximated the specimens of JÖRGENSEN (1923) from the Mediterranean than those of KOFOID & SKOGSBERG (1928) from the eastern tropical Pacific Ocean.

As may be seen from plate 4, this species is closely similar to *D. exigua* KOFOID et SKOGSBERG. The latter may possibly represent a small form of *D. parvula*, although KOFOID & SKOGSBERG's specimens of the latter were within the same size range. (See also the notes under *D. exigua*).

Stations: 52, 66, 70, 95, 96, 100, 102, 103, 106, 129, 312.

The species was widespread but not abundant in the Bay of Bengal. It was also found at two stations south of 30 °S at two different times of the year. It has been previously recorded from the Indian Ocean by several authors (see WOOD 1963a) plus TRAVERS & TRAVERS (1965) and is known from the Mediterranean Sea, and the Atlantic and Pacific Oceans.

Dinophysis porodictyum (STEIN) ABÉ Plate 4, Fig. 45
sensu ABÉ, 1967b:61, f. 17 a–f.

The specimens encountered in this material showed a close agreement with those illustrated and described by ABÉ (1967b). However, as indicated by him there are some marked differences between these specimens and others which have been referred to this taxon (under the name *Phalacroma porodictyum* STEIN). For example, those of KOFOID & SKOGSBERG (1928:98, f. 6/1–5), RAMPI (1940:254, f. 24), HALIM (1960a, t. 1, f. 28), and BALECH (1962b, t. 16, f. 214) all possess epithecae which are considerably more raised than the present specimens (and also more than the type specimen) and bear a strong resemblance to *D. argus* (STEIN) ABÉ. The present specimens and those of ABÉ, on the other hand, bear a closer resemblance to *D. acutoides* BALECH and *D. amygdala* BALECH (= *Phalacroma ovum* SCHÜTT) in the way in which some authors, such as BALECH (1962b), have interpreted the latter.

As STEIN's original figures are somewhat equivocal it appears necessary to decide at some future data which interpretation of them will be accepted, and to erect a new name for the other form which has also been given this name.

Station: 312.

Several specimens were observed at one station in the south central region in April. This form has only been previously recorded from Japanese waters (although the other type referred to above has a widespread tropical to warm temperate distribution).

Dinophysis rapa (STEIN) ABÉ Plate 5, Figs. 48 a, b; Plate 41, Fig. 488
– 1967b:66, f. 19.
Syn.: *Phalacroma rapa* STEIN . . . . KOFOID et SKOGSBERG 1928:139, f. 16/1–5; SCHILLER 1931:88, f. 80 a–d; MARGALEF 1948b:45, f. 1. j, k; MASSUTI et MARGALEF 1950, f. 68; MARGALEF et DURÁN 1953:22, f. 2n; SILVA 1956b:335, t. 3, f. 4; STEIDINGER et WILLIAMS 1970:59, t. 35, f. 123.
Non WOOD 1954, f. 24 a, b.
Vix RAMPI 1940:256, f. 23.
Phalacroma dolichopterygium auct. non MURRAY et WHITTING – SILVA 1956a:54, t. 9, f. 1.

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* Care should be taken to not confuse this taxon nomenclaturally with *D. parva* SCHILLER, here considered to be conspecific with *D. infundibula* SCHILLER.

Under this taxon ABÉ (1967b) provided a reference to "KOFOID & SKOGSBERG 1931, partim, p. 139, Fig. 89 a, b, d (c is questionable)," in addition to a reference to a page and figures by KOFOID & SKOGSBERG (1928). Unfortunately, as his publication is part of an intended continuing series the full literature citation was not provided and this author cannot find any publication by the above authors in 1931. Consequently, it has not been possible to verify ABÉ's reference but it is apparently an error, partly confused with the figures reproduced by SCHILLER (1931).

For relationships and criteria used for demarcating this taxon, please refer to the comments under *D. mitra* (SCHÜTT) ABÉ.

Stations: 24, 91, 94, 100, 102, 140, 143, 144, 294, 319, 322, 324, 325.

The species was recorded in small numbers from stations in the Andaman Sea, western Bay of Bengal, on two cruises to the south of India, and once from the vicinity of the Seychelle Islands. It is similar in world distribution to *D. mitra*, but the records are subject to the same error as in the latter species (for Indian Ocean records see WOOD 1963a, plus those of SILVA 1956a, SOURNIA 1966a, 1968b, 1970 and ANGOT 1970).

Dinophysis ruudii (BRAARUD) BALECH Plate 1, Figs. 19 a, b, c
– 1967a:84.
Syn.:*Phalacroma ruudii* BRAARUD 1935:112, f. 32; GAARDER 1938:80, f. 10; HASLE 1960:32, f. 24 a, b.

This small species exhibits one of the simplest thecal structures among the Dinophysiales. The structural features shown in the figures given here were all clearly visible in the specimen which, if not an immature stage, represents a reduction in the thecal plate number typical of the Dinophysiales, appearing to lack the small ventrally situated plates associated with the epitheca and hypotheca. Furthermore, a left sulcal list was lacking in the specimen.

The species appears to be most closely related to *D. braarudii* (NORDLI) BALECH and, to a lesser extent, *D. pulchella* (LEBOUR) BALECH. It differs from *D. braarudii* principally in having a higher epitheca, and both it and *D. braarudii* differ from *D. pulchella* in being distinctly left-handed in girdle displacement, the latter having no apparent girdle displacement. *D. pulchella* is the broadest member of the group, both in lateral and ventral views, and it also has the most completely developed left sulcal list.

Station: 147.

A single specimen (illustrated) was found in the southern Arabian Sea in August, 1963. It has been recorded previously from widely differing localities – in the North Atlantic from polar waters to the west African coast, and in the equatorial Pacific Ocean (see HASLE 1960). This is the first record of this species in the Indian Ocean.

Dinophysis schuettii MURRAY et WHITTING Plate 6, Figs. 65, 66
KOFOID et SKOGSBERG 1928:296, f. 40/1–7; SCHILLER 1931:147, f. 140 a–e; RAMPI 1940:263, f. 39; MARGALEF 1951:54, f. 2c; SILVA 1956a:55, t. 9, f. 3; WOOD 1963b:7, f. 17a, b; YAMAJI 1966:71, t. 32, f. 18; HALIM 1967:728, t. 9, f. 135; TAYLOR 1967, t. 4 (91), f. 36; – 1973b, f. 6 a, b; WOOD 1968:52, f. 126; MARGALEF 1969a, f. 3 B; NORRIS et BERNER 1970:179, f. 92–112; LÉGER 1971b:27, f. 12; – 1973b:18, f. 7.
Vix MORALES 1952:77, f. 4.

A distinctive species most closely related to *D. swezyae* KOFOID et SKOGSBERG, from which it differs in lacking the accessory lobe present on left sulcal list below R 3 (see figs. 63–66).

Of interest here is the feature, first indicated by JÖRGENSEN (1923) and confirmed by KOFOID & SKOGSBERG (1928), that this species exists in two distinct size classes. The latter authors could not find any other consistent morphological difference between the two classes. The present material confirmed the size distinction, examples of each being illustrated (the distal break present on R 2 in the smaller specimen is not a constant feature) and also a similar phenomenon was observed in *D. swezyae* for the first time. The significance of this phenomenon is not as yet understood. This author agrees with previous authors that both size classes are conspecific, suspecting that they will be subsequently demonstrated to be life-cycle stages perhaps related to the "small form" phenomenon described by SILVA (1971). However, NORRIS & BERNER (1970) report the occurrence of intermediates. The specimens figured by WOOD (1963b) appear to both be aberrant, showing marked peculiarities of the upper girdle list development.

Stations: Large size class – 14, 66, 71, 94, 95, 99, 103, 116, 135.
Small size class – 30, 62, 63, 66, 69, 93, 100.

The species was found predominantly in the Andaman Sea and in the central and western Bay of Bengal. The smaller size class was restricted to these localities, in one case (st. 66) co-occurring with the large size class. The latter was also found at a station to the south of India and one near 20 °S in the central Indian Ocean. The species is widely distributed in tropical and warm temperate waters, and has been previously recorded from the Indian Ocean by six authors (see WOOD 1963a plus SILVA 1956a; TAYLOR 1967; NEL 1968; ANGOT 1970; and SOURNIA 1970).

*Dinophysis swezyae** KOFOID et SKOGSBERG Plate 6, Figs. 63, 64
– 1928:289, f. 39/1–3, t. 5, f. 9; SCHILLER 1931:146, f. 138; NORRIS et BERNER, 1970:183, f. 113–120.

This is a very rare species, most closely related to *D. schuettii* MURRAY et WHITTING (see comments under the preceeding taxon). As mentioned previously this species apparently exhibits two distinct modes of size in a similar manner to *D. schuettii*. Judging by the ten specimens observed (8 of the large, 2 of the small) the size disjunction in length is situated between 40 and 45 µm. KOFOID & SKOGSBERG did not find any specimens less than 47 µm in length. NORRIS & BERNER's (1970) specimen was also of the larger type.

In the smaller specimen illustrated fine ground reticulation was present on the theca, although it has been omitted from the drawing for the sake of clarity.

Stations: Large size: 374. – Small size: 57.

Large specimens were found at one station at the southern end of the Mozambique Channel, the smaller specimens at a station in the northern Bay of Bengal. This appears to be the first record of this species from the Indian Ocean. It is known only from the eastern tropical Pacific Ocean (the type locality) and the Gulf of Mexico.

Dinophysis urceola KOFOID et SKOGSBERG? Plate 6, Figs. 60 a, b
– 1928:281, f. 37/1; SCHILLER 1931:144, f. 135.

This rare species, apparently known only from one cell observed by the original authors, is the closest category to which the present specimen (only one observed – illustrated) could be very tentatively assigned. The dimensions of this specimen (length of cell body 82 µm, maximum width 68 µm, maximum width in ventral view 38 µm) are much greater than the type specimen (length 48.5 µm, maximum width 43.0 µm) and its closest relatives: *D. monacantha* KOFOID et SKOGSBERG, *D. trapezia* KOFOID et SKOGSBERG, and *D. collaris* KOFOID et MICHENER. The assignment is here based primarily upon the body shape in lateral view (no information is available concerning the appearance of the ventral side of the type) and particularly the marked narrowing of the upper part of the body a short distance below the lower girdle list together with general list arrangement.

On the other hand, the detailed characteristics of the left sulcal list, with the exception of the absence of an accessory lobe, are very similar to *D. trapezia*, particularly in the inclination and length of R 3 and the posterior "sail". Proportionally the length of the sail is greater than either *D. urceola* and *D. trapezia* and it arises in a mid-ventral position rather than ventro-dorsally. A further distinction of lesser magnitude is the termination of the right sulcal list approximately half way between R 2 and R 3 rather than close to R 2.

In summary, if the presence of an accessory lobe is significant (as it has been considered, for example in the distinction of *D. schuettii* from *D. swezyae*) this taxon appears to be intermediate between *D. urceola* and *D. trapezia*, particularly as the posterior sail is part of the same unit as the left sulcal list. All the similar species referred to above are relatively rare, with little information available regarding variability. This situation together with the apparent intermediate position of the specimen and the observation of only a single specimen, argues against recognition of a separate species at this time. The large size of the present specimen may also be used as an argument for specific distinction, but the bimodal size characteristics referred to in several places in this text with regard to other *Dinophysis* species suggests caution in this respect.

Station: 109.

A single specimen was observed west of the Maldive Islands in the Arabian Sea. If considered to be *D. urceola*, this is the first record of the taxon subsequent to its original description from the tropical eastern Pacific Ocean.

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* The ending of the specific epithet has been feminised in accordance with the procedure of recognising the gender of the person honoured in the name, in this case Olive Swezy.

Dinophysis species 1 Plate 4, Fig. 40

It is strongly suspected that this represents an unusual form of *D. amygdala* BALECH (= *Phalacroma ovum* SCHÜTT). Its unique features were the marked flattening of both the apex and the antapex in a manner not referrable to any known description.

Station: 36.
Found at one station in the Andaman Sea close to the Burmese coast.

Dinophysis species 2 Plate 5, Fig. 56

One small cell, apparently in a state following fission (lacking the lower part of the left sulcal list an with lack of ornamentation or supporting spines for the girdle on the right side), bore a superficial resemblance to *D. lachmannii* PAULSEN (see SOLUM, 1962) in size and general shape. However, its incomplete development prohibited accurate identification. In general shape, although not in size, it also bore a resemblance to *D. hastata* STEIN. While this size discrepancy would usually be considered too great to seriously entertain such a relationship, the bimodal size characteristics of *D. schuettii* MURRAY et WHITTING and *D. swezyae* KOFOID et SKOGSBERG suggest such a possibility.

Station: 62.
Recorded from one station in the western Bay of Bengal.

Genus *Histioneis* STEIN

All members of this genus are rare tropical to warm temperate species and in consequence little is known of their degrees of variability, their detailed morphology, or their distribution. They may occur preferentially in deeper layers than most dinoflagellates (RAMPI 1947). As their mode of fission is essentially similar to other members of the Dinophysiales (c.f. TAYLOR 1973a) the same considerations must be taken with regard to immature individuals as in other genera of this order. For example, it appears likely that *H. fragilis* BÖHM et SCHILLER is based on an immature individual lacking that part of the left sulcal list posterior to the fission rib.

In determining the affinities of the Indian Ocean specimens the following characteristics were considered of chief importance: shape of the body, size, features of the hypothecal wall, primary ribs of the left sulcal list (particularly the features of the fission region), type of secondary reticulation of the left sulcal list and girdle list features (lateral pouch development, inclination of the upper girdle list). Allowance has been made for varying degrees of secondary reticulation on the lists, as this may be simply an expression of maturation following fission.

With the exception of *H. biremis* STEIN and *H. highleyi* MURRAY et WHITTING all other members encountered in this material lacked areolation on the hypothecal walls and could be subdivided into two main groups: A) those with a reniform body and two main radiating ribs from the body plus an oblique supporting rib submarginal on the upper part of the left sulcal list (figs. 90, 91, 92), and B) those with a more slipper-shaped body, the posterior component of the fission rib reflected in a loop to connect with the posterior main rib (sometimes termed R 3), and lacking a clearly developed oblique rib on the upper part of the left sulcal list (figs. 93–97). This major split is reflected in the key to the species provided by KOFOID & SKOGSBERG (1928) but not in a formal manner as yet.

Of particular interest in this study was the discovery of vestigial right sulcal lists in all the species. Because of their reduced size, transparency, and lack of rib support (except for *H. dolon* and its related species in group A above) they have been missed by previous authors. In species of group B the right sulcal list consists of a small flap projecting a short distance out from the cell body. In group A the right sulcal list is larger although very delicate, and is supported by a rib which has been interpreted as one of the left sulcal ribs in the past (see figs. 90–92, 485). In all cases a plate, thought to be the posterior sulcal plate or the smaller right hypothecal component, could be seen from a right lateral view of the specimens, and in all cases it appeared to extend to the junction of the fission rib with the body.

This genus has particularly suffered from the over-stylisation or sketchiness of many of the published figures, a situation whose unfortunateness is increased by the inadequacy of verbal descriptions in coping with the structural complexity of its members. Its taxonomy and, in particular, the status of more recently described taxa and the delimitation of sections within the genus appear to be in serious need of revision. The scanning electron microscope should be of great assistance in understanding the spatial relationships of the complex list structures.

Histioneis biremis STEIN Plate 9, Fig. 89
KOFOID et SKOGSBERG 1928:669, f. 95/11, f. 97/1–3; SCHILLER 1931:254, f. 250; BALECH 1962b:139, t. 17, f. 253; TAYLOR 1973b, f. 6 e.

A distinctive species which can be readily distinguished from *H. bighleyi* MURRAY et WHITTING, its nearest known relative, by a posterodorsal prolongation of the body rather than centroposterior, by the more concave girdle surface and by the more inclined fission rib of the latter species. BALECH's (1962b) specimen was apparently immature, with a malformed anterior moiety of the left sulcal list. It appears to be continuous with the right side of the lower girdle list, an anomaly which is probably a structural misinterpretation. In the specimen illustrated here (fig. 89) an irregular, list-like outgrowth was present in a position where it might be considered homologous with the right sulcal list and its presence has been confirmed by scanning electron microscopy (TAYLOR 1973b).

Stations: 58, 62.

Several specimens were found in stations in the northwestern Bay of Bengal. The species has been previously recorded from the tropical Atlantic and Pacific Oceans, but not from the Indian Ocean.

Histioneis depressa SCHILLER Plate 10, Fig. 94
– 1931:237, f. 230; RAMPI 1941c:119, f. 1; – 1947:12, f. 14; WOOD 1954:213, f. 69; – 1963b:14, f. 45 a, b (?); BALECH 1971b:21, t. 1, f. 14–17, t. 2, f. 18.

This identification is based on a similarity in size, shape of the body, and general characteristics of the left sulcal list. However, there are discrepancies whose significance cannot be assessed in view of the sketchy detailing of the left sulcal list structures by most of the authors cited above. The figures of SCHILLER, RAMPI, and WOOD (1963b), omit any sign of a fission rib or fission region. The figure of WOOD (1954) does suggest a fission rib, but its distal inclination is towards the dorsal side. BALECH's (1971b) figures, however, show a posteriorly-directed fission region. In the present specimen a fission region was present which was directed in a posterior direction in a similar manner to the larger species, *H. mitchellana* MURRAY et WHITTING (fig. 97). In fact the specimen in many respects resembled a very small *H. mitchellana* in which the reticulation is reduced in complexity, and if this individual is *H. depressa* the species should be undoubtedly assigned to the same subgroup as the former, instead of to the "Longicollis Group" as SCHILLER has done. With regard to the resemblance to *H. mitchellana,* the possibility that the present taxon is a "small form" of the latter (see SILVA 1971) should be noted.

A further difference present was the shape of the "loop" connecting the fission rib connecting the posterior component of the fission rib with the posterior rib. In the present specimen this was approximately quadrangular in shape, whereas in SCHILLER's, RAMPI's, and WOOD's figures this is shown to be more elongated. The specimen also showed similarities to that figured in later papers by RAMPI (1948) and BALECH (1971a) under the name *H. cymbalaria* STEIN. Unfortunately the size data accompanying RAMPI's figure is so confused (in the text the total length is given as 100 μm, but the magnification given for the figure gives a total length of approximately 4570 μm!) that it is not possible to make a reasonable assessment of his specimen. BALECH's specimen from Argentinian waters is very similar in size. His allocation of the individual to STEIN's description was not certain. Similarities are also evident between the present specimen, *H. cleaveri* RAMPI, *H. rampii* HALIM, and *H. detonii* RAMPI. The latter appears to be a less complexly ribbed variant with a narrower body than *H. depressum.*

Station: 103.

A single specimen was found at a station in the vicinity of Madras in the Bay of Bengal. *H. depressa* has only been recorded from the Mediterranean, from the east coast of Australia, the Coral Sea, and the tropical Atlantic. If BALECH's (1971a) specimen is the same taxon, then it also occurs in the south Atlantic Ocean.

Histioneis dolon MURRAY et WHITTING Plate 9, Fig. 90; Plate 40, Fig. 485; Plate 41, Fig. 493
KOFOID et SKOGSBERG 1928:698, f. 96/6; SCHILLER 1931:250, f. 245 a, b; WOOD 1954:215, f. 72; BALECH 1962b:138, t. 18, f. 261; NORRIS (D.R.) 1969a:185, f. 25; TAYLOR 1972b, t. 1, f. 5.
Vix WOOD 1963b:14, f. 46.

Although rare, this species is one of the more commonly encountered members of the genus. It can be recognised by its reniform cell body, large dorsal extension of the left sulcal list beyond the posterior supporting rib, the numerous rows of secondary thickening running parallel to the margin of the posterior part of the left sulcal list, and the development of large lateral pouches on the lower girdle list. According to KOFOID & SKOGSBERG (1928) size is fairly constant in this species but NORRIS (1969a) has found somewhat smaller specimens in the Gulf of Mexico. It is very similar, if not conspecific with *H. megalocopa* STEIN, the chief differences, allowing for the stylisation of the type of figure of the latter, being the more posterior inclination of the fission rib in *H. megalocopa.* Omission of list extensions perpendicular to the lateral view are common in early figures and are not considered significant here. (See also the comparisons under *H. hippoperoides* KOFOID et MICHENER.)

WOOD (1963b) has illustrated a very unusual individual referred to this species in which the left sulcal list is continued in a broad sheet around the dorsal side up to the upper rim of the lower girdle list. The posterior part of the list appears to be in an immature state. The specimen has a cell body which lacks the depression on its upper surface characteristic of *H. dolon* and its related species. If the drawing is accurate its assignation to *H. dolon,* due to the latter characteristic, is highly doubtful. Furthermore, if it is *H. dolon,* the figure being sketchy, then there seems little purpose in recognising *H. aequatorialis* WOOD, which shares the dorsal extension of the left sulcal list, except that it differs in having a cell body shape similar to *H. longicollis* KOFOID, a character which would justify separation.

Some of the specimens of this species that were encountered could be partially dissected, and it was by this means that the existence of the delicate hyaline right sulcal list, almost invisible except under phase contrast, was discovered, and later confirmed with scanning electron microscopy. It is supported by a rib arising from the hypotheca midway between the fission rib and the posterior supporting rib (see fig. 485). This rib can be seen in the figure by BALECH (1962b), and it is also present in other species of group A (figs. 91, 92).

Stations: 135, 315, 320.

A total of ten individuals were observed, the species being recorded from three stations all situated in the central Indian Ocean region between 10° and 20 °S. The species is known from the tropical Atlantic and Pacific Oceans, and has been recorded from the Indian Ocean by KARSTEN (1907), WOOD (1962 – see WOOD 1963a), TRAVERS & TRAVERS (1965) and SOURNIA (1968b).

*Histioneis highleyi** MURRAY et WHITTING Plate 41, Figs. 491, 492

KOFOID et SKOGSBERG 1928:673, f. 95/14, 98/1–4; SCHILLER 1931:255, f. 251 a, b; WOOD 1963b:16, f. 49; YAMAJI 1966:71, t. 32, f. 20 (sub. *highlei*); BALECH 1971b:23, t. 1, f. 11, 12.

This species most closely resembles *H. biremis* STEIN in possessing an areolated cell body with a posteriorly-directed lobe. It differs from that species in that the posterior lobe arises from the mid-antapical portion of the body, the fission rib is inclined at approximately 45° to the long axis (instead of being almost in line with it) and the girdle chamber excavates the dorsal surface of the cell body more deeply.

Stations: 58, 101, 325.

Single individuals were found at two stations in the Bay of Bengal. The species is rare and limited to tropical waters. It has not been previously recorded from the Indian Ocean although WOOD (1963b) has found it in the adjacent Coral Sea.

Histioneis hippoperoides KOFOID et MICHENER ? Plate 9, Figs. 91, 92

KOFOID et SKOGSBERG 1928:701, f. 96/5, t. 23. f. 1, 3; SCHILLER 1931:251, f. 247; ABÉ 1967c:98, f. 37 a–c; NORRIS (D.R.) 1969a:185, f. 26.

Vix WOOD 1954, f. 70

At present a very confused situation exists in the distinction between this species, *H. milneri* MURRAY et WHITTING, *H. helenae* MURRAY et WHITTING, and to a lesser extent, *H. dolon* MURRAY et WHITTING. The difficulty appears to be largely due to uncertainty regarding the degrees of variability in cell size and in girdle and list characteristics (phenotypic plasticity) and in particular, those changes accompanying increased maturity of the list structures.

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* Also variously cited as *highlei* – originally *highleii.* However, as the name is derived from P. HIGHLEY, illustrator, the above form is correct (ICBN, Rec. 73c).

ABÉ (1967c) considered that the chief characteristic by means of which *H. hippoperoides* could be distinguished from *H. helenae* and *H. milneri* was the presence of strongly developed lateral pouches on the lower girdle list of the former. On this basis the specimen in fig. 92 can be referred to *H. hippoperoides*, although it differs from the type specimen in having a fission rib which is sharply bent in its distal region like *H. dolon*, and in having an upper girdle list which flares more greatly than the type. The specimen in fig. 91 agrees well with the type in the features of the upper girdle list, but it has only slightly developed lateral pouches. It does, however, have an unbent fission rib. Both specimens are here suspected to be in immature states with reduced reticulation on the left sulcal list. The situation is further complicated by the resemblance of the specimen named *H. helenae* by WOOD (1963b, f. 48a) to an intermediate between *H. dolon* and *H. helenae*, although the figure lacks detailed precision.

It is strongly suspected that in future *H. helenae* and *H. hippoperoides* will become synonyms of *H. milneri* MURRAY et WHITTING, and that they might even be demonstrated to be smaller, less complex forms of *H. dolon* and its possible conspecies – *H. megalocopa* STEIN.

In view of the lack of certainty regarding the identity of the two individuals referred to this category, their relative localities are kept separate below.

Stations: (fig. 91) 58. – (fig. 92) 63, 342.

Both types were found in the Bay of Bengal. The form with the wide lateral pouches was also found once in the central Indian Ocean region. No authors have recorded specimens under this name from the Indian Ocean. However, WOOD (1962 – see WOOD 1963a) has recorded both *H. helenae* and *H. milneri* (also WOOD 1963c) from the Indian Ocean. In general all the species referred to above are known from tropical and subtropical waters. GAARDER (1954) found that the distributions of *H. helenae* and *H. milneri* were similar in the Atlantic Ocean.

Histioneis hyalina KOFOID et MICHENER Plate 10, Fig. 93

KOFOID et SKOGSBERG 1928:679, f. 95/5, t. 20, f. 4; SCHILLER 1931:238, f. 231a (b?); BALECH 1971b:19, t. 2, f. 26. 29, 31. Vix WOOD 1963b:17, f. 50 a, b.

H. longicollis auct. non KOFOID – SCHILLER 1931:234, f. 226b.

This species differs principally from *H. longicollis* KOFOID and *H. kofoidii* FORTI et ISSEL by the greater dorso-ventral length of the body relative to its depth, and from *H. pacifica* KOFOID et SKOGSBERG by a greater length of the "stalk" of the upper girdle list, lack of a well-developed posterior reticulation on the left sulcal list and a generally more elongate appearance.

SCHILLER's specimen referred to above is in fact somewhat intermediate between this taxon and *H. longicollis*, casting doubt on their separation.

Station: 417.

One specimen (illustrated) was identified from a station in equatorial waters mid-way between Madagascar and Kenya. Originally described from the tropical Pacific Ocean, it has subsequently been recorded from the Indian Ocean only by SCHILLER (1931). BALECH (1971b) found specimens in the equatorial Atlantic Ocean.

Histioneis mitchellana MURRAY et WHITTING Plate 10, Fig. 97; Plate 41, Figs. 494, 497, 498

KOFOID et SKOGSBERG 1928:690, f. 96/4, t. 21, f. 2; SCHILLER 1931:245, f. 239 a, b; ABÉ 1967c:100, f. 39 a–c; TAYLOR 1972b, t. 1, f. 6; – 1973b, f. 4 e. Vix WOOD 1963b:19, f. 62.

Syn.: *H. schilleri* BÖHM et SCHILLER 1931:244, f. 238 a, b; BÖHM 1936:31, f. 12c; WOOD 1963b:19, f. 62.

Both SCHILLER (1931) and BÖHM (1936) maintained the distinction of *H. schilleri* from *H. mitchellana* on the grounds of the angular projection of the left sulcal list opposite the cell body, and the less flaring upper girdle list of the former. The specimen illustrated is very similar to the type, particularly as shown in the more detailed figures of KOFOID & SKOGSBERG (1928), except that it combines a widely flaring upper girdle list with an angular left sulcal list and thus appears to be intermediate between the two species mentioned. Consequently, they are here considered to be conspecific.

In ABÉ's recent (1967c) work he suggested that *H. pulchra* KOFOID is also conspecific with *H. mitchellana* (the latter having priority). This suggestion is not, however, followed here for the reasons outlined under *H. pulchra*.

Stations: 33, 57, 67.

Single specimens were found at a station in the northern Andaman Sea, and at two stations in the Bay of Bengal. The species has been formerly recorded from the Indian Ocean by SCHRÖDER (1906) and WOOD (1963b – as *H. schilleri*). It is known from both tropical Atlantic and Pacific Ocean waters.

Histioneis panda KOFOID et MICHENER Plate 10, Fig. 96
KOFOID et SKOGSBERG 1928:964, f. 85/1; f. 95/9; SCHILLER 1931:248, f. 242; NORRIS (D.R.) 1969a:188, f. 31–33.
Vix WOOD 1963c:7, f. 18.

The illustrated specimen agreed well with the type in virtually all respects except for a wider anterior opening of the lower girdle list. In the latter it more closely resembled *H. pietschmannii* BÖHM ex SCHILLER. As BALECH (1962b) has indicated, these two species are very similar to one another and it is strongly suspected that they are conspecific in view of the intermediacy of the present specimen. One major distinction which could be pointed to is the reference in the type description to a well-developed right sulcal list in *H. pietschmannii.* However, both BALECH (1962b) and ABÉ (1967c),in assigning specimens to latter species, ignored this aspect of the type description, action which may be justified by a lack of confidence in the accuracy of observation and critical attitude of the original authors (SCHILLER omitted any mention of the great degree of similarity between *H. panda* and *H. pietschmannii,* instead, comparing it with *H. pulchra* KOFOID, from which it differs greatly). ABÉ succeeded in demonstrating secondary fins running dorso-ventrally from the main posterior rib to the fission rib, a feature which might also be used for distinguishing the species, although these structures are easily missed and may also be present only in the most mature specimens. They are suggested but not clearly shown in the figures of NORRIS (1969a).

H. panda is superfically similar to *H. panaria* KOFOID et SKOGSBERG, but the latter apparently lacks the recurved extension of the posterior component of the fission rib.

Stations: 58, 71, 101.

Single specimens were observed at each of the above stations, all within the Bay of Bengal. The species has not been previously recorded from the Indian Ocean, although the type locality of *H. pietschmannii* is within this region (and it has been subsequently recorded from the Indian Ocean by WOOD, 1963b). The only other known localities for *H. panda* are the eastern tropical Pacific Ocean and Gulf of Mexico.

Histioneis pulchra KOFOID Plate 10, Fig. 95
KOFOID et SKOGSBERG 1928:686, f. 96/2, t. 21, f. 4, 7, t. 23, f. 2; SCHILLER 1931:243, f. 237 a, b.
Vix WOOD 1963b, f. 61.

This species differs from *H. mitchellana* MURRAY et WHITTING, its nearest relative, in several respects, but the most significant distinction is here considered to be the inclination of the fission line on the left sulcal list (compare figs. 95, 497). In *H. mitchellana* this is directed in an almost exactly posterior direction, whereas in *H. pulchra* it has a gentle sigmoid curvature and is inclined postero-ventrally. Although this distinction has not been drawn attention to in previous works it is clearly evident from published figures, and furthermore this author considers the characteristics of the fission region on the left sulcal list to be of great value in distinguishing the species within this genus. Secondary features which may also be used to distinguish the two species are the strength of the reticulation in *H. pulchra,* the larger and ventrally distorted area enclosed by the recurved posterior component of the fission rib, and in general, the less narrow body of *H. pulchra.*

Station: 28.

Two specimens were observed in a sample from the western Andaman Sea (in a depth of less than 75 metres). The species has only been previously recorded from the Indian Ocean by TRAVERS & TRAVERS (1965) and SOURNIA (1968b – list). It was originally described, and has been subsequently recorded several times, from the tropical Pacific Ocean, and has been found once in the Atlantic Ocean (GAARDER 1954).

Genus *Ornithocercus* STEIN

Members of this genus, together with those of *Dinophysis* formerly designated as *Phalacroma*, are the commonest representatives of the Dinophysiales in tropical and subtropical waters, appearing to play a somewhat similar role in these waters to the other members of *Dinophysis* which are common in cold temperate waters. Recently ABÉ (1967c) and D.R. NORRIS (1969a) have subjected a number of the commonest species of *Ornithocercus* to detailed morphological analysis, supplementing the first detailed morphological study by NIE (1943) on *O. thumii* (A. SCHMIDT) KOFOID et SKOGSBERG. TAYLOR (1971) has illustrated the principal features of six species from the "Anton Bruun" material as seen under the scanning electron microscope and in a later paper (1973a) has illustrated the process of thecal division and the effect this has on morphology. Two aberrant types of division were included. The possible adaptive value of the thecal features has also been discussed (TAYLOR 1971).

Despite doubts as to the constancy of the list features, these still appear to be among the most useful criteria involved in species delimitation with due caution for maturational influences. Apart from the left sulcal list features which are the most obvious, the size and shape of the right sulcal list and the number of ribs of the upper girdle lists are of use in special recognition. Where reference is made to ribs on the left sulcal list they are designated as "a, b" etc., beginning from the dorsal side, following the system of KOFOID & SKOGSBERG (1928). TAYLOR (1971) has shown that the side of the left sulcal list on which the "c" rib arises is a useful taxonomic feature, combined with the region of widening of the plate giving rise to the posterior moiety of the left sulcal list (ABÉ 1967c).

Ornithocercus formosus KOFOID et MICHENER Plate 7, Fig. 75
KOFOID et SKOGSBERG 1928:577, f. 91/1, 2, t. 17, f. 4, 5; SCHILLER 1931:207, f. 197 a–d; WOOD 1963b:11, f. 30.
Vix WOOD 1954, f. 58c sub *O. heteroporus* KOFOID.

This is a rarely encountered, highly distinctive, medium-sized species. It differs from the other species by its combination of a strongly developed dorsal accessory moiety of the left sulcal list, demarcated by a dorsal suture in the position of the "a" rib, (not unique to this species but more strongly developed) with a lack of distinct, regularly placed equivalents to the "b", "c", and "d" ribs of the other species. Strong reticulation on the left and right sulcal lists and the posterior girdle list is common.

Stations: 67, 103.

Only five specimens were found at two stations in the western Bay of Bengal.

This appears to be the first record of the species from the Indian Ocean, all previous records being restricted to the tropical and subtropical Pacific Ocean.

Ornithocercus francescae (G. MURRAY) BALECH Plate 8, Fig. 84; Plate 42, Figs. 502, 503
BALECH 1962b:136, t. 18, f. 259; ABÉ 1967c:95, f. 36 a, b.
Syn.: *Histioneis francescae* G. MURRAY in MURRAY et WHITTING, 1899:333, t. 32, f. 3.
Parahistioneis francescae KOFOID et SKOGSBERG 1928:590; SCHILLER 1931:210, f. 198.
Ornithocercus carolinae KOFOID 1907a:205, t. 15, f. 92; JÖRGENSEN 1923:38, f. 53; KOFOID et SKOGSBERG 1928:572, f. 89/1–7, t. 17, f. 1, 6; MANGIN 1930:74, f. 17/6; WOOD 1954:210, f. 64; BALECH 1962b:135, f. 260; YAMAJI 1966:72, t. 33, f. 8 (sub *calolinae*); D.R. NORRIS 1969a, f. 18.

JÖRGENSEN (1923) suggested that the taxon *francescae* G. MURRAY should be referred to the genus *Ornithocercus*, and that *O. carolinae* is connected by a range of intermediate forms to *O. francescae* (also shown by KOFOID & SKOGSBERG 1928). The degree of reticulation on the lower girdle list is undoubtedly variable, depending on ontogenetic differentiation but in the *carolinae* type it apparently remains relatively less reticulate. The body shape of the latter type is also narrower (fig. 503). The specimen illustrated by line drawing here (fig. 84) shows the lobing characteristic of *O. carolinae*, but the cell body shape is of the *O. francescae* type (see BALECH 1962b and fig. 502 here). BALECH's recognition of both *O. francescae* and *O. carolinae* at the species level does not appear to be tenable due to the presence of such intermediates. It may be possible to recognise the end points of the cline as varieties, or, due to the rarity of intermediates, as subspecies (see the introductory section on infraspecific taxa) but too few specimens have been observed to date. The species appears to be most closely related to *O. formosus* from which it can be readily distinguished by having a central convexity of the posterior margin of the left sulcal list, rather than a marked concavity.

Stations: 99, 108, 320, 412.

It was rare, occurring in the Bay of Bengal and at one station in the central Indian Ocean.

The species has only been previously recorded from the Indian Ocean by TAYLOR (1967, as *O. carolinae* – southwestern sector). Other records note its presence in the Atlantic and Pacific Oceans, and in the Mediterranean Sea.

Ornithocercus heteroporus KOFOID Plate 8, Fig. 83
KOFOID et SKOGSBERG 1928:517, f. 75/1–5, t. 18, f. 1, 3; SCHILLER 1931:195, f. 187 a–d; RAMPI 1940:265, f. 53; MARGALEF, HERRERA, RODRIGUEZ-RODA et LARRAÑETA 1954:89, f. 1 f; WOOD 1954:207, f. 58 a, b (non c); SILVA 1956a:56, t. 9, f. 6; YAMAJI 1966:72, t. 33, f. 9; ABÉ 1967c:81, f. 28 a, b; D.R. NORRIS 1969a, f. 19; TAYLOR 1971, t. 4, f. 27, 28.
Syn.: *O. biclavatus* WOOD 1954:211, f. 66.

This "dainty sub-tropical species" (JÖRGENSEN 1923, p. 38) is readily distinguishable in being small, with relatively small girdle lists and a bilobed left sulcal list whose posterior margin is usually concave and which extends only as far as the antapex of the cell body or ventral to it. The name is somewhat deceptive as the pores and areolae are no different from species such as *O. quadratus* and *O. magnificus*. In *O. splendidus* SCHÜTT the left sulcal list never extends to the antapex of the cell and lacks the strong antapical supporting rib of *O. heteroporus*. The extensive, usually highly reticulate girdle lists of *O. splendidus* also serve to readily separate the species. Finally, the body wall of *O. splendidus* is never areolated as it is in *O. heteroporus*. Pores are much fewer than areolae.

The means of distinguishing *O. heteroporus* from *O. bilobatus* RAMPI (1950a:3, f. 12), *O. biclavatus* WOOD (1954, cited above), *O. triclavatus* WOOD (1954:210, f. 65) and *O. heteroporoides* ABÉ (1967c:83, f. 29a–c) is less clear. As indicated above, and in agreement with ABÉ (1967c), *O. biclavatus* WOOD is considered synonymous with *O. heteroporus*, differing in no distinctive way other than the presence of rugose reticular masses occupying the lobes of the left sulcal list (much the same as in the specimen of *O. quadratus* in fig. 81). These masses are not considered to represent a significant species character here.

At first glance *O. bilobatus* RAMPI appears very similar to *O. biclavatus* WOOD. It can be distinguished from *O. heteroporus* in that the left sulcal list extends onto the dorsal surface of the hypotheca as with *O. heteroporoides* ABÉ and *O. triclavatus* WOOD. In fact *O. bilobatus* RAMPI and *O. heteroporoides* ABÉ appear to be synonymous (that of RAMPI having priority). *O. triclavatus* WOOD appears to be a teratological form of *O. heteroporus* similar to those observed in *O. thumii* by this author.

Stations: 35, 37, 325.

Single specimens were found at stations on the eastern side of the Andaman Sea, in March, 1963 and south of India, in April, 1964. The species is widely distributed, but not common, in subtropical waters. WOOD's (1963a) Indian Ocean list requires augmentation by the references of HANDEL-MAZZETTI (1910, south Arabian coast, cited by JÖRGENSEN 1923) SILVA (1956a), TRAVERS & TRAVERS (1965) and SOURNIA (1968b).

Ornithocercus magnificus STEIN emend. SCHÜTT Frontispiece; Plate 7, Figs. 67, 68, 69; Plate 42, Figs. 505 a, b

KOFOID et SKOGSBERG 1928:529, f. 79/1–9, t. 16, f. 3; CANDEIAS 1930:17, t. 1, f. 25, SCHILLER 1931:198, f. 190 a, b; RAMPI 1940:265, f. 54; MASSUTI et MARGALEF 1950, f. 70 a, b; WOOD 1954:203, f. 60 a, b; – 1963b:11, f. 32; SILVA 1949:339, t. 4, f. 17; – 1955:131, t. 3, f. 5; MARGALEF 1957b:90; HALIM 1960a, t. 2, f. 12; BALLANTINE 1961:218, f. 13; MARGALEF 1961b:140, f. 3/1, 2; YAMAJI 1966:72, t. 33, f. 5; TAYLOR 1967, t. 91 (4), f. 37; ABÉ 1967c:88, f. 32; D.R. NORRIS 1969a:178, f. 2–15; STEIDINGER et WILLIAMS 1970:54, t. 25, f. 79 a, b; TAYLOR 1971, t. 2, f. 9–12; – 1973a, t. 2, f. 9–12; t. 3, f. 15, 16, 18.
Vix MARGALEF et DURÁN 1953:24, f. 13 1.

A small-bodied species which superficially resembles *O. thumii* in the manner in which the left sulcal list is lobed. However, as demonstrated by TAYLOR (1971) the species has more fundamental affinities with *O. quadratus*. In particular they share the same median flexure of the left sulcal list associated with a local widening of the hypothecal plate from which it arises, the "c" rib passing over the right face of the list instead of the left face as is the case in the majority of species of *Ornithocercus*. Other features have been described in detail by D.R. NORRIS (1969a).

Two characters usually useful in recognising the species are the shape of the right sulcal list (sloping sharply up from near the fission rib, with no posterior lobing), a character also exhibited often by *O. skogsbergii* (which differs in many other respects, however) and the distal termination of the "c" rib in a position usually distinctly dorsal to the central lobe (the specimens figured by TAYLOR 1967 and STEIDINGER & WILLIAMS 1970 are atypical in this respect). Some variants are strongly areolated, the whole surface being deeply pitted (as in the frontispiece specimen), whereas in other apparently mature specimens the thecal surface is only gently indented.

Stations: 13, 15, 17, 19, 24, 26, 29, 31, 32, 34, 35, 37, 38, 41, 50, 52–63, 66–71, 90, 93–96, 98–102, 106, 108, 109, 113, 114, 134, 135, 140, 147, 149, 160, 294, 295, 325, 412.

The species was very widespread in the central Bay of Bengal waters in April..Otherwise it was of sporadic occurrence. It was recorded from one station (160) south of 40 °S and was particularly sparse from April to July 1964, in the open Indian Ocean waters. This species was the commonest in the "Meteor" South Atlantic material (KÄSLER 1938). It has been recorded from the Indian Ocean by many authors (WOOD 1963a). The following records should be added to those previously listed: BÖHM (1931a – Persian Gulf), SILVA (1956a), TSURUTA (1963), PRAKASH & SARMA (1964), SOURNIA (1966a, 1967a, 1968b, 1970), TAYLOR (1967), LEWIS (1967), NEL (1968) and ANGOT (1970). LEWIS recorded a maximum concentration of 117,500 cells per litre at 10 m depth in association with a bloom of *Gonyaulax polygramma* in the Arabian Sea, and SUBRAHMANYAN (1958) has also noted it as being associated with "red water" off the west coast of India.

Ornithocercus quadratus SCHÜTT Frontispiece; Plate 8, Figs. 77–82; Plate 42, Figs. 499–501.

KOFOID et SKOGSBERG 1928:561, t. 17, f. 2, f. 85/5, f. 86/1–14, f. 87/1–20; SCHILLER 1931:204, f. 194 a–f, 195 a–d; RAMPI 1940:265, f. 55; SILVA 1949:340, t. 4, f. 19; – 1956a:57, t. 9, f. 7, 8; WOOD 1954:209, f. 63 a–c; MARGALEF 1961b:140, f. 3/3; SOURNIA 1967a:424, t. 1, f. 1; ABÉ 1967c:89, f. 33 a, b; D.R. NORRIS 1969a, f. 20; TAYLOR 1971, t. 1, f. 1–4, t. 2, f. 5–8, t. 5, f. 29–33; – 1972b, t. 1, f. 1; – 1973a, t. 1, f. 1–6, t. 2, f. 7, 8, 13, t. 3, f. 17, t. 4, f. 19–25; – 1973b, f. 5 c.
Vix RAMPI 1939b:459, f. 11; – 1940, f. 56.
Syn.: *O. assimilis* JÖRGENSEN 1923:37, f. 51; BÖHM 1936:29, f. 11c.
O. galea (POUCHET) ABÉ 1967c:83, f. 30 a–c.
O. steinii auct. non SCHÜTT . . . YAMAJI 1966, t. 12, f. 6.

A major characteristic by which this species is distinguished from others within the genus is usually taken to be the bi-angular shape of the posterior margin of the left sulcal list (in other words, lacking any median posterior lobes, the posterior margin being approximately parallel to the girdle inclination). The species encompasses a great deal of variability. KOFOID & SKOGSBERG (1928) recognised five variants (termed formae by them) within the species distinguished by size, shape of the girdle region when seen in lateral view, and left sulcal list features.

From this author's experience the initial impression during analysis of field material results in a conviction that at least two separate species are involved (*O. assimilis* JÖRGENSEN and *O. quadratus*). However, this conviction fades as more and more individuals are encountered which exhibit intermediate characteristics. The scanning electron microscope has proved an invaluable aid in making the comparative observations here.

Specimens corresponding to all five of KOFOID & SKOGSBERG's "forms" were found in the material. As there is no indication at present that the two clinal end-point phenotypes result from plasticity effects, they are recognised here as varieties in accordance with the views expressed in the introductory section on infraspecific taxa. Intermediate variants are recognised as forms although there may be little purpose in their recognition. Only four of these taxa are separated here and two (corresponding to the formae *assimilis* and *simplex*) required revision.

Because of this slightly confused situation the taxa as recognised here should be clearly defined. They are:

O. quadratus var. *quadratus*: – the type variety (based on the type specimen designated by KOFOID & SKOGSBERG 1928, i.e. SCHÜTT 1900, fig. 4), recognisable by its large size with a body usually strongly ovoid in the dorso-ventral dimension (60 µm or greater), lacking areolation over the dorsal quarter of the hypotheca. The dorsal side of the girdle is concave. The areolae correspond approximately to the pores, most areolae having one pore within them. The margin of the left sulcal list, when fully developed, bears numerous reticulae to the exterior of the marginal rib. The list ribs are relatively smooth. The fission rib region of the left sulcal list often projects out angularly (e.g. fig. 80). The right sulcal list has a strong posterior lobe. In the specimen in fig. 80 the cell body is unusually high for this variant.

O. quadratus var. *quadratus* forma *schuettii* KOFOID et SKOGSBERG: – recognised as an intermediately-sized variant in which the body is not as wide dorso-ventrally (45–60 µm) as in the var. *quadratus* forma *quadratus* and the area bare of areolae is less extensive but still apparent in side view. When mature, such individuals exhibit only slight ribbing external to the marginal rib. The main sulcal ribs lack side branches (except for the "a" rib). The dorsal region of the girdle is concave, as in the forma *quadratus*. Areolae are relatively small with pores only one third to one quarter as numerous as the areolae.

O. quadratus var. *quadratus* forma *simplex* KOFOID et SKOGSBERG: – this form consists of medium to small-sized cells in which the dorso-ventral cell-body dimension does not usually exceed 45 µm. The cell-body shape is rounded to oval (in the apical-antapical plane), and the dorsal profile of the girdle is flattened. The girdle lists do not extend more than a short distance beyond the body. The area of the hypotheca free of areolae is restricted to a narrow dorsal band, hard to see in lateral view. The right sulcal list is narrow and has only a slight posterior lobe. Areolae are far more numerous than pores. The sulcal list ribs usually lack lateral branches although not always (fig. 81). The upper girdle lists lack reticulation between the ribs, this being one of the simplest means of separating the taxon from the var. *assimilis* below.

O. quadratus var. *assimilis* (JÖRGENSEN) stat. et comb. nov. [basionym = *O. assimilis* JÖRGENSEN 1923, p. 37, f. 51]: It only requires a comparison of JÖRGENSEN's type figure (1923, fig. 51) with that of *O. quadratus* in his work (his fig. 50), conveniently drawn to the same scale, to see that *O. assimilis* as conceived by him was undoubtedly a small taxon, and not intermediate in size as indicated by KOFOID et SKOGSBERG for their forma *assimilis*. Indeed, the specimen illustrated by KOFOID & SKOGSBERG as one of the examples of their forma *simplex*, (their fig. 87/13) is almost identical in general characteristics to the type illustration of *O. assimilis* JÖRGENSEN. This taxon can be distinguished from the other taxa more readily than they can be separated from each other although very rare intermediates have been seen by this author. It could perhaps, be deserving of subspecific status.

The cell body is small (dorso-ventral distance rarely reaching 50 µm and usually less than 45 µm) and the dorsal side is usually distinctly flatter than in the other varieties, a feature remarked on by BÖHM (1936) (exception in fig. 82). Effectively the whole hypotheca is covered by numerous small areolae, often deeply pitted, with few pores, no barren area being visible from the side. Most distinctively, the upper left side of the girdle list is reticulated in its central region (never on the right side). The upper moiety of the left sulcal list is usually incompletely developed. Unlike the other varieties it is the "b" rib which is usually situated on the right side of the list, instead of the "c" rib (c.f. fig. 499). The sulcal ribs often bear numerous delicate or strong side branches (fig. 79) which may unite into a proximal meshwork (fig. 82). The forma *intermedia* KOFOID et SKOGSBERG could not be distinguished from the var. *assimilis* and so has not been recognised here.

TAYLOR (1971) has shown that ABÉ's (1967c) attempt to distinguish this species on the basis of the local expansion of the h_1 plate (employing TAI & SKOGSBERG's, 1934, system) in the mid-antapical region is not of exclusive value as it has been found also in *O. magnificus* (and possibly *O. heteroporus*). In *O. splendidus* and *O. thumii* the widening is more dorsal and is not as angular. Associated with this local widening of the plate is the displacement of the "c" rib to the right side of the list, instead of lying on the left side of the list as do all the other supportive ribs other than the submarginal rib. Also, ABÉ's recognition of *Dinophysis galea* POUCHET as a taxon of *Ornithocercus* is unfortunate. KOFOID & SKOGSBERG (1928, p. 185 and 548) have summarised the difficulties in recognising the latter, recommending that the second of the four disparate organisms illustrated by POUCHET (1883, fig. G) be considered the type (in which case it is probably synonymous with *Dinophysis circumsuta*). Apparently unaware of this, ABÉ (loc. cit.) suggested the fourth figure (an *Ornithocercus*) as the type. These specimens of POUCHET and ABÉ correspond to the var. *assimilis* recognised here.

In passing, attention can be drawn to fig. 501 which illustrates the plates in the vicinity of the apical pore, including the recently discovered "A" plate, known for other dinophysoid genera but not for *Ornithocercus*. There is a possibility of still further, faintly demarcated plates, being present.

Stations: var. *quadratus* – 296, 335, 342, 418.
f. *schuettii* – 14, 15, 20, 21, 24–26, 29–31, 34, 37, 62, 64, 66, 91, 92, 95, 96, 100–104, 108, 109, 110, 113, 115, 116, 125 129, 130, 133–135, 140–144, 147, 148, 150, 153, 154, 156, 161, 162, 285, 296, 299, 301, 302, 317, 320–322, 324, 340, 347, 358, 365, 370, 399, 405.
f. *simplex* – 66, 68–70, 91, 96, 99, 110, 150.
var. *assimilis* – 14, 16, 23, 25, 26, 29, 30, 34, 35, 53, 55, 56, 58, 59, 61–63, 65–71, 94–101, 103, 114, 140, 141, 143, 144, 153, 297, 300, 314, 318–320, 328, 329, 339, 347, 371.

The species was present at 46.5 % (99) of the stations sampled, making it one of the commonest dinoflagellates encountered (as was the case in the "Michael Sars" Atlantic material examined by GAARDER 1954). The var. *schuettii* was widespread over the area sampled, but within the Bay of Bengal it tended to be replaced in the north-central stations by individuals of the var. *assimilis*. The var. *simplex* was found at oceanic stations in the Bay of Bengal and at two stations in the northwestern Indian Ocean. The species was apparently absent from stations within the low salinity influence of the Ganges-Brahmaputra and Irrawaddy deltas, from the most southerly stations (furthest southward extension in June/July, 1963), and from a series of stations north of the Seychelle Island group. TAYLOR (ms., 1964) found it to be of sporadic occurrence in the southwestern Indian Ocean, being most widely spread in January.

As might be expected, the species has been frequently recorded from the Indian Ocean, and also from other tropical to temperate waters. The list provided by WOOD (1963a) should be augmented by the following Indian Ocean records: SILVA (1956a), SOURNIA (1966a, 1967a, 1968b, 1970), and TAYLOR (1967).

Ornithocercus skogsbergii ABÉ Plate 7, Fig. 70

– 1967c:85, f. 31 a–k (vix f. e)
Ornithocercus sp. sensu KOFOID et SKOGSBERG 1928, f. 92/3.

This species resembles *O. steinii* and *O. thumii* very closely in general form, particularly the former with regard to the location of the distal end of the "b" rib within the dorso-posterior lobe of the left sulcal list. ABÉ did not make comparisons between his specimens and other species, and so it is difficult to know which features he considered most useful in making the specific distinction. The species is strikingly smaller than *O. steinii*, the maximum body dimension not exceeding 50 µm. Consequently, it resembles *O. magnificus* and *O. heteroporus* in general dimensions but is readily distinguishable from them in its other features. The posterior margin usually has only three lobes, the "d" rib being lacking, but specimens are known with a fully developed "d" rib, resulting in four posterior lobes. A second, distinctive feature is the wider angle between the "b" and "c" ribs resulting from a slight ventral inclination of the "c" rib and the usual straightness of the "b" rib. The angle between the "b" and "c" ribs is always greater than 40° and is most striking at its greatest (ABÉ's figs. a, d), when it may exceed 60°. In *O. steinii* the angle is usually less than 40° (commonly approximating 35°). The number of ribs on the upper girdle lists is somewhat variable in *O. skogsbergii*. Most commonly there are six ribs (including the marginal fission ribs) but seven have also been observed here.

Taken together, these features plus others given by ABÉ suggest a valid separation from other species. However, some large specimens were observed in this material which resembled *O. steinii* in size, rib development, and lobing but which exhibited the ventrally-deflected "c" rib with a consequent "b" and "c" angle of greater than 40°. As ABÉ's descriptions were only published after the main analysis of the "Anton Bruun" material was completed and it was not possible to relocate large specimens of this type for more detailed examination, it is not known if these large specimens should have been assigned to *O. skogsbergii* (in which case the overlap with *O. steinii* would be considerable), or simply indicate the need for caution in applying the criteria of rib angles.

Stations: 108, 294.

The common presence of specimens at these two stations was only recognised on re-examination of selected samples for scanning electron microscopy after the publication of ABÉ's description. It is likely that their presence was much wider than indicated, their records being inadvertently combined with *O. steinii*. The stations were in the eastern Arabian Sea and north of the Seychelle Islands. ABÉ's specimens were from Sagami Bay in Japan and, on the basis of earlier illustrated specimens by various authors, ABÉ believed the species also occurred in the tropical Atlantic Ocean.

The species has not yet been recorded from the Indian Ocean by other authors.

Ornithocercus splendidus SCHÜTT Plate 8, Figs. 85, 86; Plate 40, Fig. 486; Plate 42, Fig. 504

KOFOID et SKOGSBERG 1928:521, f. 77/1–11, f. 85/3, t. 16, f. 2, 4, t. 17, f. 3; SCHILLER 1931:196, f. 189 a–f; MASSUTI et MARGALEF 1950, f. 34; WOOD 1954:207, f. 59; SILVA 1955:128, t. 3, f. 1–4; YAMAJI 1966:72, t. 33, f. 10; ABÉ 1967c:81, f. 27a–c; HALIM 1967:732, t. 5, f. 62–64; D.R. NORRIS 1969a, f. 21; TAYLOR 1971, t. 3, f. 13–18; – 1972b, t. 1, f. 2.

The species differs strikingly from the only other species with which it might possibly be confused, *O. heteroporus* KOFOID, the great extension of the girdle lists, the delicate and strongly bilobed nature of the left sulcal list (usually with reticular masses in each lobe), size, and the lack of reticulation on the thecal wall. The latter is sparsely and fairly regularly penetrated by pores. The epitheca is relatively distinctive in that it is more widely covered with pores than other species of *Ornithocercus*. Reticulation is strongest on the lower girdle list but is also present on the upper girdle list.

Stations: 13, 17, 30, 33, 55, 97, 99, 100, 102, 103, 106, 108, 114, 116, 135, 141, 143, 144, 149, 150, 153, 154, 288, 298, 301, 302, 318, 319, 320, 322, 335, 347, 358, 369, 405, 413, 419.

The species was widespread and sporadic in occurrence. It was absent from the stations in the vicinity of deltas in the Bay of Bengal and Andaman Sea, from south of 25 °S on all cruises except in the Agulhas Current region of the southwestern sector, and from all stations on the 65 °E meridian occupied in May to July, 1964. The latter phenomenon is most difficult to account for in view of the occurrence of the species at several stations occupied during a comparable period in 1963 (stations 106–144 on the 70° and 80 °E meridians). In the "Michael Sars" Atlantic Ocean material GAARDER (1954) found it to be restricted to the warmest water encountered. It was found to occur only below 100 m in the Atlantic Ocean (KÄSLER 1938).

It has been recorded occasionally from the Indian Ocean (WOOD 1963a plus SILVA 1956a; TSURUTA 1963; TAYLOR 1967; SOURNIA 1967a, 1968b, 1970; and NEL 1968 as *O. splendens* SCHÜTT).

Ornithocercus steinii SCHÜTT emend. KOFOID et SKOGSBERG Plate 7, Figs. 72, 73

KOFOID et SKOGSBERG 1928:551, f. 83/1–12, t. 16, f. 1. t. 17, f. 9; SCHILLER 1931:202, f. 192a–f; BÖHM 1936:27, f. 11a; GAARDER 1954:35, f. 41; WOOD 1954:203, f. 62; MARGALEF 1961b:140, f. 3/4; YAMAJI 1966:72, t. 33, f. 6, non t. 12, f. 6; HALIM 1967:731, t. 5, f. 65; SOURNIA 1967a:426, t. 1, f. 3, 4; ABÉ 1967c:94, f. 34 a, b (vix c); D.R. NORRIS 1969a, f. 22; STEIDINGER et WILLIAMS 1970:54, t. 25, f. 80; TAYLOR 1971, t. 4, f. 20–22, 25; HASSAN et SAIFULLAH 1972a:68, f. 6.

Non SILVA 1949, t. 4, f. 18 (*O. thumii*), vix SILVA 1955, (non t. 3, f. 6).

Syn.; *O. serratus* KOFOID 1907a:206, t. 15, f. 93.

O. orbiculatus KOFOID et MICHENER 1911:300; KOFOID et SKOGSBERG 1928:559, t. 17, f. 7; SCHILLER 1931:203, f. 193.

This species is most closely related to *O. thumii* (c.f. TAYLOR 1971) from which it is most readily distinguished by the termination of the distal end of the "b" rib within the dorsal lobe of the left sulcal list. It shares this feature with *O. skogsbergii* which is, however, markedly smaller (see comments here under *O. skogsbergii*).

In general *O. steinii* has a greater number of primary ribs supporting the upper girdle list components than *O. thumii* (TAYLOR 1971). However, there is an overlap in this feature and care must also be taken to allow for incomplete maturational states. The range for *O. steinii* (including the marginal ribs adjacent to the ventral plate moieties) is: left list 6–10 (most commonly 9), right list 5–9 (9). For *O. thumii* the range is: left list 6–8 (6), right list 5–7 (5). The range is much greater in *O. steinii* than in *O. thumii. O. skogsbergii* has a similar number of ribs on the upper girdle list to *O. thumii.*

In *O. steinii* there is commonly a left sulcal list lobe associated with the "d" rib whereas in *O. thumii* the "d" rib does not usually end in a distinct lobe. In *O. skogsbergii* the "d" rib is usually absent, but when present it is not associated with a strong lobe.

Stations: 13, 16, 17, 19, 21, 24, 28, 29, 32, 34, 37, 38, 39, 53, 56, 57, 62, 63, 91, 99, 103, 109, 114, 115, 125, 129, 130, 135, 142, 143, 144, 154, 161, 162, 282, 287, 294, 312, 315, 317, 329, 331, 414.

This is a very sporadic distribution, only widespread in the Andaman Sea. The species was sparse in equatorial waters and was not found south of 34 °S. Records of *O. skogsbergii* are probably included among these stations (see comments under that species).

O. steinii has been commonly recorded from subtropical waters. WOOD's (1963a) list should be augmented by the reference of SILVA (1956a), TSURUTA (1963), DURAIRATNAM (1964), SOURNIA (1966a, 1967a, 1968b), TAYLOR (1967), NEL (1968), THORRINGTON-SMITH (1969), and HASSAN & SAIFULLAH (1972a).

Ornithocercus thumii (A. SCHMIDT) KOFOID et SKOGSBERG Plate 7, Figs. 71, 72, 74
– 1928:540, f. 81/1–11, t. 18, f. 4–6 (sub *thurni* – lapsus oculi); SCHILLER 1931:200, f. 191 a–h; BÖHM 1936:28, f. 11b; NIE 1943:23, f. 1–11; SILVA 1949, t. 4, f. 18 (sub *O. steinii* SCHÜTT); WOOD 1954:208, f. 61 a–c; BALLANTINE 1961:218, f. 14; ESTABLIER et MARGALEF 1964:28, f. 7c; SOURNIA 1967a:426, t. 1, f. 2; ABÉ 1967c:90, f. 34 a–i; D.R. NORRIS 1969a, f. 23; STEIDINGER et WILLIAMS 1970:54, t. 25, f. 81; TAYLOR 1971, t. 3, f. 19, t. 4, f. 23, 24, 26; – 1973a, t. 3, f. 14.
[*O. thurnii* auct. nonnull.]

In the systematic history of this species there are two curious errors. Originally it was considered to be a diatom and named by A. SCHMIDT after an early collector of marine diatoms, E. THUM. KOFOID & SKOGSBERG (1928), in correctly assigning it to the dinoflagellates and transferring it to this genus apparently misread *"thumi"*, using the variant *"thurni"* consistently throughout their text. All subsequent dinoflagellate systematists until SOURNIA (1967a) perpetuated this error, presumably also misreading it by suggestion if they referred to the original description.

Detailed aspects of its morphology have been described by NIE (1943), ABÉ (1967c – apparently unaware of NIE's earlier work) and TAYLOR (1971). The species is here distinguished from its closest relative, *O. steinii* SCHÜTT, principally in the manner selected by KOFOID & SKOGSBERG (1928), namely that the "b" rib of the left sulcal list in *O. thumii* terminates distally in a position distinctly ventral to the dorsal lobe of the list, whereas in *O. steinii* the "b" rib terminates within the dorsal lobe. *O. thumii* also usually has fewer ribs supporting the upper girdle list than *O. steinii* (see comments under the latter).

Among the teratological forms observed in the material (usually consisting of a disorganisation of the supportive ribs of the left sulcal list into a reticular network) individuals were also seen which had large, projecting reticular masses at the angles of the left sulcal list.

Stations: 17, 21, 23, 25, 30–32, 35, 36, 39, 55, 57–60, 62, 64–66, 68–72, 91–104, 106, 108–111, 113–116, 129, 135, 140–143, 148, 153, 154, 283–285, 287, 291, 294, 296, 313, 317–319, 320, 325, 328, 329, 332, 334, 338, 344, 370, 375, 405, 413, 414, 419.

This was one of the commonest species in the region, present in 82 of the 213 samples. The only area where it was not recorded was from south of 32 °S in the central region. It was most abundant, but not dominant, in one of a group of very rich samples off the east coast of India (st. 100). The species is widely distributed in warm waters, both oceanic and neritic, and has been recorded previously from the Indian Ocean by several authors (see WOOD 1963a, plus SOURNIA 1967a, 1968b, 1970, NEL 1968, and THORRINGTON-SMITH 1969).

Genus *Parahistioneis* KOFOID et SKOGSBERG

This genus appears to occupy a position intermediate between the genera *Ornithocercus* STEIN and *Histioneis* STEIN. BALECH (1971b) has considered *Parahistioneis* to be congeneric with *Histioneis.*

Parahistioneis para MURRAY et WHITTING Plate 9, Figs. 87, 88; Plate 41, Fig. 490
KOFOID et SKOGSBERG 1928:601, f. 85/6; SCHILLER 1931:215, f. 205 a, b; BALECH 1962b:137, t. 17, f. 254.
Syn.: *P. conica* BÖHM ex SCHILLER 1931:210, f. 199; TAYLOR 1972b, t. 1, f. 3.

Seven specimens of this species were observed, three of which have been illustrated here to indicate the variability which can occur within this species. In addition it was possible in all cases, upon careful examination, to discern a right sulcal list. The latter structure is similar to that present in *P. rotundata* (KOFOID et MICHENER) KOFOID et SKOGSBERG, ending close to the insertion of the fission rib of the left sulcal list. The specimen in fig. 87 also had an additional reticulated structure bridging across from the right ventral side of the hypotheca to the upper supporting rib of the left sulcal list (a similar structure is occasionally present in members of *Ornithocercus*). In general all the specimens agreed well in size and body shape; however, the left sulcal list structures were seen to vary considerably (compare figs. 87, 88). In view of the variability observed the distinct status of *P. paraformia* KOFOID et SKOGSBERG is highly doubtful. *P. conica* BÖHM ex SCHILLER and *P. acuta* BÖHM ex SCHILLER are both invalid (ICBN Art. 34) because of their tentative form of original proposal but in any case, the former seems to be synonymous with *P. para*.

Stations: 56, 58, 61, 67, 70

The species occurred singly at stations in the central part of the Bay of Bengal. It has not been previously recorded from the Indian Ocean although this is the type locality of both of BÖHM's species mentioned above. It is known from the tropical Atlantic and Pacific Oceans.

Order Peridiniales HAECKEL

All members of this order are thecate, bearing cellulosic plates within multiple peripheral vesicles of the amphiesma (cf. DODGE & CRAWFORD 1970; KALLEY & BISALPUTRA 1970; LOEBLICH III 1970). DODGE has used the term theca to refer to the outer membraneous layers of the cell as well as, or in the absence of, plates (see Introductory section on the outer layers of dinoflagellates).

Unlike the *Prorocentrales* and *Dinophysiales* the arrangement of the plates in the *Peridiniales* is considered to be primarily in concentric "latitudinal series" (apicals, precingulars, cingulars/girdle plates, postcingulars, antapicals). Exceptions are the sulcal plates and miscellaneously positioned plates termed intercalaries. Cell division can involve the oblique sharing of the mother theca, each daughter cell forming complimentary thecal elements after division. Alternatively the cell may shed the old theca ("ecdysis"), cell division occurring in a naked or encysted state. Various types of cysts are known. In one family, the *Pyrocystaceae*, a cyst stage is dominant in the life cycle.

Family Amphitholaceae LINDEMANN [= Amphilothaceae auct. nonnul.]

Non-thecate species possessing an internal skeleton not obviously composed of two separated parts.

Genus *Dicroerisma* TAYLOR et CATTELL

Syn.: *Discroerisma* lapsus calami

The description of this genus was based in part on an individual in the present material. Due to postal delays the proof of the manuscript was not corrected and numerous typographical errors exist in the paper, of which the most unfortunate is the misspelling of the genus name both in the title to the paper and in the same manner at several points in the text. The correct name is *Dicroerisma* meaning "forked support", referring to the structure of the endoskeleton. Article 73 of the International Code of Botanical Nomenclature allows for the correction of typographic and orthographic errors, as does Article 32 of the Zoological Code. The correct spelling of the name did appear in the original paper in addition to the erroneous spelling. *Dicroerisma* has also been used as the correct form by LOEBLICH & LOEBLICH (1971). Consequently, for all these reasons it is maintained here.

Only one species is known in this genus at present.

Dicroerisma psilonereiella TAYLOR et CATTELL Plate 37, Fig. 432
– 1969:169, t. 1, f. 1 a–d.

This small species is highly distinctive despite its lack of a theca and consequent ease of deformation due to poor preservation. It can be readily recognised by the slender internal skeleton in the form of an inverted Y with ends which bifurcate still further. No other dinoflagellate taxon is known which has this type of skeleton. In other members of the order the skeleton is basket-like and peripheral. In fact, in some respects the skeleton resembles that of an Ebriid, a feature which may be of phylogenetic interest although the chemical nature of the endoskeleton is as yet unknown.

The individual found in the "Anton Bruun" material was surprisingly well preserved and could be readily recognised as similar to specimens from the Pacific Ocean. The terminal points of the endoskeleton were more blunt than in the Pacific specimens. The species apparently lacks chloroplasts.

Station: 21.

This station was located in the Andaman Sea. The only other known locality is the coastal waters of British Columbia, Canada. This indicates strong thermotolerance. The species is probably neritic, but this distribution is too sparse for any conclusions to be drawn.

Family Ceratiaceae LINDEMANN

At present this includes only one large genus, *Ceratium*.

Genus *Ceratium* SCHRANK

This genus contains by far the majority of species encountered in oceanic waters, particularly in the tropics. Many of the species are considered to live subeuphotically (c.f. STEEMANN NIELSEN 1934, 1939 a, b and GRAHAM & BRONIKOVSKY 1944), particularly members of the subgenus *Archaeceratium*.

Marine members of the genus differ most evidently from fresh water species in that the plates of the ventral region are greatly reduced in thickness. STEIDINGER & WILLIAMS (1970) have illustrated ventral plates from the marine species *C. hexacanthum* and *C. massiliense* although these are not visible without dissection or by the use of a scanning electron microscopy on glutaraldehyde-fixed material. D.R. NORRIS (1969) has shown apparent phagotrophy occurring in the ventral region of *C. lunula*, implying that these plates must disarticulate in some manner.

The taxonomy of the genus has been complicated by the imprecision of the observation of early authors, the variability of some species, especially within the subgenus *Ceratium* (= *Biceratium*), and the inadequate understanding of sexuality within the genus (see VON STOSCH, 1964, 1965, 1967). In addition to the early, invaluable studies by JÖRGENSEN (1911, 1920), PETERS (1932), STEEMANN NIELSEN (1934, 1939a) and GRAHAM & BRONIKOVSKY (1944) some progress has been made toward the precise delimination of variability by culture studies (HASLE & NORDLI 1951; NIELSEN 1956; NORDLI 1957) and by the use of biometrical techniques although the latter has been confined to populations from only restricted areas (e.g. LOPEZ 1955, 1966; YARRANTON 1967; DOWIDAR 1972; REINECKE 1973 a, b). LOPEZ (1966) and DOWIDAR (1972) found differences between summer and winter forms of the same species within the western Mediterranean Sea and the Suez Canal region, respectively. The summer forms had relatively small bodies in comparison with the winter. This seems to be related chiefly with temperature, salinity perhaps augmenting the effect.

Recently two semi-monographic publications on members of the genus in the Indian Ocean have appeared: those of SUBRAHMANYAN (1968) and SOURNIA (1968a), the latter being an extensive exposition in addition to his earlier (1966b) paper on variability within the genus. Of the two large works, that of SUBRAHMANYAN is more extensive in descriptions, SOURNIA's work omitting certain taxa and not providing formal, complete descriptions. SUBRAHMANYAN has drawn many of his figures from previous works, and its chief value is as an English language version of the section on *Ceratium* in SCHILLER (1936). Unfortunately some of the errors in SCHILLER have also been continued by SUBRAHMANYAN (e.g. the omission of *C. obesum* PAVILLARD) and his neglect of many infraspecific variants (following the views of GRAHAM & BRONIKOVSKY 1944) seems to be unfortunate. He has not observed formal taxonomic procedure with nominate taxa. SOURNIA's work, although incomplete, has two main contributions to make: firstly, the literature citations in connection with each taxon attempt to be exhaustive; and secondly, he has maintained a critical attitude to earlier decisions, rectifying many of the irregularities referred to above in accordance with the International Code of Botanical Nomenclature.

REINECKE (1971, 1973 a, b) has begun a monographic series on *Ceratium* also using Indian Ocean material, the first of which includes a useful general introduction to the biology of the genus. She has adopted YARRANTON's (1967) method of using polar co-ordinate graph paper to express the curvature of horns numerically (super-imposing camera-lucida drawings on it). Polynomial regression calculations could be applied to the data. Unlike him she found that intraspecific variability rendered the technique of little taxonomic use.

Observations on polymorphism in chains of *C. tripos* (see LOHMANN 1908, KOFOID 1909b, and others given by VON STOSCH 1964 and REINECKE 1971) and *C. trichoceros* (STEIDINGER & WILLIAMS 1970) raise the possibility that several taxa conventionally assigned to some subgenera may be maturational stages in the division cycle of members assigned to other subgenera. It is the anterior-most daughter cell that, for a short time after division, lacks the characteristically outwardly-directed antapical horns, the posterior-most lacking the anterior horn (illustrated in detail by VON STOSCH 1967 and TORIUMI 1968, 1971). Thus anterior moieties of members of *Tripoceratium* may temporarily resemble members of the subgenus *Ceratium* in their immature state.

The problem of sexual dimorphism is a serious one in our present state of highly inadequate knowledge. It is definitely established in *C. horridum* and is probable in *C. tripos* (VON STOSCH 1964), the male conjugants being small, with small antapical horns and are probably derived from anterior daughter cells by a persistence of the immature state. They thus pose the same difficulties to field taxonomists as that described in the preceding paragraph (see also the introductory section on Some Taxonomic Considerations which uses *Ceratium* as the example for several variability problems). There is also the possibility that other species of *Ceratium* have conjugation involving iso-conjugants. For example, as early as 1885 POUCHET figured cells of *C. fusus* (and perhaps *C. longirostrum*) joined in pairs and there are other such figures. The difficulty with the early observations on preserved material is to know whether the authors were observing cells during aberrant division, or cells which had joined together.

As with the other large genus in this report, *Peridinium*, the use of subgenera and sections can be useful in arranging the taxa for ready identification. In *Ceratium* the following subgenera are used here (in the sequence they appear:

s. g. *Archaeceratium* JÖRGENSEN
s. g. *Ceratium* [= *Biceratium* (VANHÖFFEN) JÖRGENSEN]
s. g. *Amphiceratium* (VANHÖFFEN) OSTENFELD
s. g. *Tripoceratium* KOFOID [= *Euceratium* (GRAN) OSTENFELD,
Orthoceratium SOURNIA]

. Although all have been subdivided into sections, use has only been made of sections for the largest of these subgenera: *Tripoceratium.*

The features of each group are given where appropriate in the text.

Subgenus *Archaeceratium* JÖRGENSEN
[Includes *Poroceratium* (VANHÖFFEN) KOFOID]

The members of this subgenus are all distinctive in appearance, with a flattened epitheca and lacking an apical horn. Several possess a so-called ring pore on the mid-ventral surface of the epitheca. Scanning electron microscopy of these (TAYLOR, unpublished) has revealed this to be a distinct plate closing an aperture in the theca. They tend to be stenothermal species, being restricted to the warmest regions of the oceans, and there is evidence that they are umbriphilic (shade-loving), preferring depths below 50 m and often below 100 m (STEEMANN NIELSEN 1934, 1939a; GRAHAM & BRONIKOVSKY 1944). The leaf-like flattening of the epitheca is presumably an adaptive character (see discussion section dealing with shade species).

The number of species in this subgenus is less than ten, five of which are included here. Most of these species have been reported as containing chloroplasts (e.g. SCHÜTT 1895).

Treatment of species belonging to the section Digitata (*C. digitatum* SCHÜTT, *C. schroeteri* B. SCHRÖDER etc.) has varied in the past. Early workers such as JÖRGENSEN (1911) placed them under the subgenus *Ceratium* (= *Biceratium*). Here they are included under *Archaeceratium* in view of their lack of a distinct apical horn.

Ceratium cephalotum (LEMMERMANN) JÖRGENSEN Plate 11, Fig. 106

STEEMANN NIELSEN 1934:7, f. 2; SCHILLER 1936:356, f. 388; GRAHAM et BRONIKOVSKY 1944:15, f. 2 A–C; WOOD 1954:271, f. 185; YAMAJI 1966:91, t. 44, f. 2; SOURNIA 1968a:388, t. 1, f. 2; SUBRAHMANYAN 1968:14, f. 7.

Most similar in size and appearance to *C. praelongum* but easily distinguished from it by the marked lateral expansion of the epitheca, the latter being distinctly wider than its height above the girdle. Also, the epitheca is more rounded on the left margin than on the right. The apical pore is strongly displaced to the right side.

Stations: 30, 103, 135, 340, 369.

It was scattered in small numbers at a few northern Indian Ocean stations, at 20 °S in the Central region, and further south (st. 369) in the Mozambique Channel, where it was possibly transported by currents.

This species is considered to be very thermophilic, only occurring in the warmest waters of the Atlantic and Pacific Oceans (PETERS 1932; STEEMANN NIELSEN 1934; GRAHAM & BRONIKOVSKY 1944). KARSTEN (1907), BÖHM (1931b), and STEEMANN NIELSEN (1939a) found it only in the most equatorial waters of the Indian Ocean. However TAYLOR (ms. 1964, 1967) and NEL (1968) have found it in the southwestern sector off South Africa. TAYLOR found it in the Agulhas Current which represents a southerly extension of warm water in that sector. Other references not included in the list of WOOD (1963a) are those of DURAIRATNAM (1964), SOURNIA (1968 a, b, 1970) and SUBRAHMANYAN (1968).

Ceratium digitatum SCHÜTT Plate 11, Fig. 105

STEEMANN NIELSEN 1934:8, f. 5; SCHILLER 1936:358, f. 392; RAMPI 1939a:302, f. 3; GRAHAM et BRONIKOVSKY 1944:16, f. 5 A–E; GAARDER 1954:11, f. 12; WOOD 1963b:39, f. 144; YAMAJI 1966:93, t. 44, f. 19; SUBRAHMANYAN 1968:16, f. 13–15; WOOD 1968:27, f. 52.

An unusual, readily recognisable species in which the epitheca and the left antapical horn are strongly reflected towards the dorsal side. The epitheca is also markedly concave on its ventral face. The apical pore arises from a short projection at the apex. The left antapical horn bears rows of strong spines. The right horn is short and pointed, directed posteriorly. The closest relative is probably *C. schroeteri* B. SCHRÖDER, which shows less extreme modifications of the *Archaeceratium* plan (both are customarily placed in the section Digitata JÖRGENSEN). *C. tasmaniae* WOOD (1963b) differs from these species in that the epitheca is bent ventrally instead of dorsally.

Stations: 19, 64, 103, 325.

Single individuals were found at neritic stations in the Andaman Sea, western Bay of Bengal, and at one station south of India.

This species was considered to be very rare by GRAHAM & BRONIKOVSKY (1944), but STEEMANN NIELSEN (1939a) indicated that it was more common in the Indian than in the Pacific or Atlantic Oceans. It is apparently distinctly umbriphilic and stenothermal. Its presence at such coastal stations as those of the present study might be interpreted as being indicative of upwelling. TAYLOR (ms. 1964, 1967) found it off Durban in the southwestern Indian Ocean, this record and that of SUBRAHMANYAN (1968) being additional to those few provided by WOOD (1963a).

Ceratium gravidum GOURRET Plate 11, Figs. 99, 100, 101 a, b

PETERS 1932:28, t. 2, f. 12g; STEEMANN NIELSEN 1934:8, f. 3, 4; SCHILLER 1936:357, f. 389; RAMPI 1939a:301, f. 1; GRAHAM et BRONIKOVSKY 1944:15, f. 3 A–C, 4 P–U; WOOD 1954:272, f. 186a + 186 a, b (errat.); – 1963b:40, f. 146; SILVA 1955:49, t. 7, f. 1; KATO 1957:11, t. 3, f. 1; HALIM 1960a, t. 4, f. 21; MARGALEF 1961b:142, f. 2/12; – 1964, f. 2 E; TORIUMI 1964b:24, t. 3, f. 10; YAMAJI 1966:91, t. 44, f. 3, 4, 5; HALIM 1967:719, t. 1, f. 9, 10; SOURNIA 1968a:388, t. 1, f. 3; SUBRAHMANYAN 1968:14, f. 10, 11; WOOD 1968:31, f. 62; TAYLOR 1973b, f. 4 f.

A large, striking species exhibiting the strong leaf-like flattening (see fig. 101 b) of the epitheca found also in *C. cephalotum* and *C. praelongum*. It differs from the latter species in being much larger, with relatively more slender antapical horns. The species exists in a wide range of forms which were not considered to be a direct environmental response by GRAHAM & BRONIKOVSKY (1944). Due to the continuous variability observed they disregarded JÖRGENSEN's (1911, 1920) varieties, being followed in this by SOURNIA (1968a) and SUBRAHMANYAN (1968) although, in view of the considerations given in the introductory section, they could still be recognised as such. WOOD (1963b) added a variety. The figures given here (plate 11) embrace the extremes of variability known in this species.

Stations: 13, 31, 58, 60, 68, 69, 71, 92, 95, 101, 135, 294, 321, 324, 325, 412.

The species was present in small numbers at scattered stations. The most southerly station was st. 135 (20 °S). The distribution of varieties showed no particular pattern. This is a tropical, interoceanic, oligophotic species (STEEMANN NIELSEN 1939a). HALIM (1967) found it associated with upwelling in the vicinity of Caribbean trenches. The Indian Ocean references of SUKHANOVA (1962b), TAYLOR (1967), SOURNIA (1968a, b, 1970) and SUBRAHMANYAN (1968) should be added to those of WOOD (1963a).

Ceratium praelongum (LEMMERMANN) KOFOID ex JÖRGENSEN Plate 11, Figs. 102, 103
BÖHM 1931b:43, f. 37a; STEEMANN NIELSEN 1934:7, f. 1; SCHILLER 1936:356, f. 387; GRAHAM et BRONIKOVSKY 1944:14, f. 1 A–D; SILVA 1958:32, t. 3, f. 4; WOOD 1963b:40, f. 148; YAMAJI 1966:91, t. 44, f. 1; HALIM 1967:723, t. 3, f. 43; SOURNIA 1968a:386, t. 1, f. 1; SUBRAHMANYAN 1968:14, f. 8, 9; WOOD 1968:38, f. 83.

Although superficially resembling a slender variety of *C. gravidum* this species is in a considerably different size range, being only two thirds or less the length of the latter. It appears closest to *C. cephalotum*, lacking the lateral epithecal expansion of the latter. Indeed, the range of variation within *C. gravidum* encompasses a spectrum as wide as these two species put together, leading one to suspect the conspecificity of *C. praelongum* with *C. cephalotum*. However, intermediate forms between the latter similar to those in the case of *C. gravidum* have not been reported. Variations in the proportionate length of the epitheca are known (SUBRAHMANYAN 1968). Fig. 103 illustrates a common type of variant in which the left antapical horn is deflected to the left and slightly towards the dorsal side. More slender specimens than that illustrated have been observed (width 60 μm). The early reference of BÖHM (1931b) is included above because it is omitted by SCHILLER (1936) and SOURNIA (1968a).

Stations: 13, 15, 16, 57, 62, 63, 66, 71, 89, 99–103, 109, 110, 135, 153, 287, 321, 331, 340, 342, 369, 371, 412, 413, 417, 418.

This was the most commonly encountered member of *Archaeceratium*. There are scattered records of its occurrence on all cruises. The most southerly records were from st. 135 and the stations in the Mozambique Channel, but it is known from the Agulhas Current further south. This is also considered to be a shade species although STEEMANN NIELSEN (1939 a, b) listed it as "mesophotic" rather than "oligophotic". The Indian Ocean records of TAYLOR (1967), SOURNIA (1968 a, b, 1970), and SUBRAHMANYAN (1968) should be added to those listed by WOOD (1963a).

Ceratium schroeteri B. SCHRÖDER Plate 11, Fig. 104
SCHILLER 1936:358, f. 391; SILVA 1956a:67, t. 12, f. 1–3; WOOD 1963b:42, f. 150; YAMAJI 1966:92, t. 44, f. 7; SUBRAHMANYAN 1968:16, f. 12; STEIDINGER et WILLIAMS 1970:47, t. 41, f. 154; LÉGER 1972a:27, f. 9, 10.

The specimen figured here is unusual in that the epitheca slopes slightly towards the dorsal side, rather than gently towards the ventral side. Usually the species can be recognised in side view because the ventral profile presents a gentle sigmoid appearance. The species appears to be intermediate between *C. digitatum* SCHÜTT and *C. tasmaniae* WOOD.

Stations: 68, 100, 103.

Single individuals were found at a few stations in the western Bay of Bengal. This species is very rarely encountered. It is an Indo-Pacific, tropical species. It was apparently not present in the extensive collections of STEEMANN NIELSEN (1934, 1939a) nor in the "Carnegie" material of GRAHAM & BRONIKOVSKY (1944). It has only been recorded from the Indian Ocean by SCHRÖDER (1906), SILVA (1956a), TAYLOR (1967), and SUBRAHMANYAN (1968).

Subgenus *Ceratium*

Syn.: s. g. *Biceratium* (VANHÖFFEN) JÖRGENSEN

Members of this subgenus possess a distinct apical horn, with short or moderately long, unequal antapical horns which are directed posteriorly. Several of the species are highly variable and difficult to handle systematically, such as *C. candelabrum*, *C. furca*, and *C. pentagonum* (see SOURNIA 1966b, 1968a).

SOURNIA (1968a) pointed out that, as this subgenus probably contains the type species, the name *Biceratium* is incorrect according to modern taxonomic practice (Article 22, International Code of Botanical Nomenclature).

As indicated under the genus, several of the taxa usually included here may be male conjugants or immature anterior daughter cells of members of the subgenus *Tripoceratium*.

Ceratium belone CLEVE Plate 12, Fig. 119
CANDEIAS 1930:30, t. 3, f. 60, 60 A; PETERS 1932:29, t. 3, f. 14d; STEEMANN NIELSEN 1934:10, f. 10; SCHILLER 1936:369, f. 407a; RAMPI 1942:222, f. 2; GRAHAM et BRONIKOVSKY 1944:19, f. 8 A–I; MARGALEF 1948b:49, f. 2 f; SILVA 1949:354, t. 6, f. 20; HALIM 1960a:191, t. 4, f. 6; YAMAJI 1966:92, t. 44; f. 9; SOURNIA 1968a:399, f. 22; SUBRAHMANYAN 1968:21, f. 31; WOOD 1968:24, f. 40; STEIDINGER et WILLIAMS 1970:44, t. 4, f. 10.

A highly distinctive, elongate species. Most variability within the species involves the length of the body anterior to the girdle (see GRAHAM & BRONIKOVSKY, loc. cit.), but the apical part may also exhibit slight, varying degrees of curvature. It differs markedly from *C. incisum*, the only species with which it could be confused. It is usually much longer, with a narrower, more tapering epitheca, and a squared-off posterior portion of the body (the accessory fin in this area does, however, slope down to the cell's left).

Stations: 17, 39, 41, 58, 93, 294, 344, 414.

With the exception of station 344, and to a lesser extent, 93, these are all in close proximity to land and within the tropics. The first three are in the eastern Andaman Sea, stations 39 and 41 being close to the delta of the Irrawaddy River. This distribution is in accordance with earlier observations that it is a high stenothermal species, also favouring more eutrophic waters. Indian Ocean records additional to those provided by WOOD (1963a) are: SILVA (1956a), TSURUTA (1963) and SOURNIA (1966a, 1968b, 1970).

Ceratium boehmii GRAHAM et BRONIKOVSKY Plate 12, Figs. 122, 123

– 1944:22, f. 12 A–C [BÖHM 1931b, f. 9 c, e, f sub *C. kofoidii* JÖRGENSEN].

A small, long-horned species very close to, if not conspecific with, *C. kofoidii* JÖRGENSEN (both SOURNIA 1968a, and SUBRAHMANYAN 1968, considered it conspecific). The specimens here were designated as *C. boehmii* on the basis of the following criteria: the girdle diameter was less than 25 µm; the cell body relatively long (circa 45 µm); the antapical horns were long, especially the left one and, in the present case, were not divergent (actually convergent in fig. 122). In size (contrary to the claim of GRAHAM & BRONIKOVSKY 1944) this species is very similar to *C. kofoidii* (see JÖRGENSEN 1911). It is principally the longer, parallel horns which distinguish it from *C. kofoidii*. In the future it may be found more appropriate to recognise *C. boehmii* at the varietal level.

Stations: 38, 43, 54, 66, 89, 91, 105, 288, 289, 290, 338, 369.

It occurred in small numbers at predominantly neritic stations in the Andaman Sea and western Bay of Bengal, but it was also present at a few oceanic stations in the northwestern Indian Ocean and at one station at the southern end of the Mozambique Channel. The species has only been recorded from the tropical Pacific Ocean, although, if it is conspecific with *C. kofoidii*, then Indian Ocean records are not uncommon (see WOOD 1963a plus SILVA 1956a; – 1960; TAYLOR 1967; SOURNIA 1968 a, b; SUBRAHMANYAN 1968).

Ceratium candelabrum (EHRENBERG) STEIN Plate 12, Figs. 124, 125, 126

STEEMANN NIELSEN 1934:8, f. 6, 7; SCHILLER 1936:364, f. 401 a, b, 402 a–c, 403; NIE 1936:30, f. 1 A–C; f. 2; RAMPI 1939a:302, f. 4, 5, 7; GRAHAM et BRONIKOVSKY 1944:17, f. 6 A–K; MARGALEF 1948b:49, f. 2 c; SILVA 1949:354, t. 9, f. 1; MARGALEF et DURÁN 1953:35, f f. 10 d–e; WOOD 1954:273, f. 187 a, b; KATO 1957:12, t. 3, f. 2, 3; HALIM 1963:496, f. 1; TORIUMI 1964b:24, t. 3, f. 13; LOPEZ 1966:333, f. 3, 4, t. 1, f. 1, 2, f. 52, 56–58, et p. 411, f. 88 I–III, 89; YAMAJI 1966:93, t. 45, f. 1, 2; SOURNIA 1968a:390, f. 14–17, t. 2, f. 6; SUBRAHMANYAN 1968:17, f. 16–20; WOOD 1968:25, f. 44; STEIDINGER et WILLIAMS 1970:44, t. 41, f. 153; HERMOSILLA 1973a:24, t. 2, f. 8, 9.

The systematic history of this species contains a great deal of confusion, mostly concerning the infraspecific taxa. It has been conveniently summarised by SOURNIA (1968a). SOURNIA recognises only two main varieties: the var. *candelabrum* and the var. *depressum* (POUCHET) JÖRGENSEN; with one form: f. *subrotundum* (PAVILLARD) SOURNIA represented by individuals having undergone extreme autotomy. An error was introduced by JÖRGENSEN (1920) when he illegally designated the type form as "*α-curvatulum*, " at the same time attributing to it characters more correctly referrable to the var. *depressum*. This error was perpetuated by SCHILLER (1936).

It is now possible to recognise the var. *candelabrum* by its relatively short horns (left antapical horn subequal to, or less than the width of the cell at the girdle), the antapicals of which project straight posteriorly. This variety also usually has heavier markings. The var. *depressum* (= *α-curvatulum*) has much longer horns, the apicals and antapicals of which (termed "anticals and posticals" respectively by JÖRGENSEN, 1920) are often distinctly curved. The central body is wider but with proportionately less depth. The forma *subrotundum*, as mentioned above, is represented by autotomised specimens.

Stations: var. *candelabrum*: 32, 49, 54, 284, 320, 359, 371, 405.
var. *depressum*: 16, 24, 30, 32, 34, 50, 57, 59, 62–64, 68, 69, 71, 93, 95, 96, 98, 100, 102, 103, 109, 114, 134, 147, 148, 150, 153, 155, 161, 283, 294, 298, 300, 323, 325, 326, 341, 347, 360, 362, 370, 371, 398, 413, 415, 420.
f. *subrotundum*: 147.

As is obvious from the above, the var. *depressum* was that most commonly found, a situation similar to that found by STEEMANN NIELSEN (1934, 1939a) in the Pacific and Indian Oceans, GRAHAM & BRONIKOVSKY (1944) in the Pacific, and TAYLOR (ms., 1964) in the southwestern Indian Ocean. There was no clear distributional separation between the varieties in the present material. There are many references to the species from the Indian Ocean listed in WOOD (1963a) to which the following should be added: SILVA (1956a), SUKHA-

NOVA (1962b), TSURUTA (1963), SOURNIA (1966a, 1968a, b, 1970), TAYLOR (1967 – as the forms listed in SCHILLER 1936), NEL (1968), and ANGOT (1969).

Ceratium ehrenbergii KOFOID Plate 12, Fig. 116

KOFOID 1907b:171, t. 2, f. 16; JÖRGENSEN 1911, t. 4, f. 80; NIE 1936:38, f. 9.
Syn.: *C. tripos* forma *brevicorne* (LEMMERMANN) ex parte; JÖRGENSEN 1920, f. 47, 52, vix 53.

This is an exceptionally rare species, apparently only seen previously by LEMMERMANN, KOFOID, NIE, JÖRGENSEN, and the present author. Although the horns of the present specimen are more slender than the original, and the apical horn is displaced towards the right side of the cell (as in JÖRGENSEN 1920, fig. 47), the original description fits the specimen extremely well, even to size. A feature not drawn attention to by previous authors lends further support to the recognition of this as a valid, distinct species and not a variant of *C. tripos* (JÖRGENSEN 1911) or *C. pentagonum* (SOURNIA 1968a). It is undoubtedly closely related to the latter. The original description is reproduced here: "a small species of the *C. lineatum* group with rotund midbody and short horns. Midbody with convex margins and very convex dorsal face, excavated ventrally. Girdle somewhat anteriorly placed, with prominent lists. Apical horn short. Antapicals short, pointed, slightly divergent. Surface with linear striae. Length, 90–110 µm; transdiameter, 50 µm." To this may be added the variations shown by the present specimen (those mentioned above and the less anteriorly displaced girdle). Most importantly however, the species exhibits a very characteristically steep slope of the antapical profile with relation to the girdle plane. The angle this profile subtends with the girdle plane (designated δ by JÖRGENSEN 1911) is 38°–40°. With the exception of *C. incisum* (where the antapical profile blends steeply into the left antapical horn) this is one of the largest angles subtending the girdle plane found in the subgenus.

The recent observations of dimorphism in *C. trichoceros* (subgenus *Tripoceratium*) by STEIDINGER & WILLIAMS (1970) suggests the possibility that *C. ehrenbergii* may be a form produced by a similar process, but there is no way of knowing this at present.

Station: 104.

A single specimen was observed in the vicinity of Madras. The species has been found previously in the Atlantic and Pacific Oceans.

Ceratium furca (EHRENBERG) CLAPARÈDE et LACHMANN Plate 12, Figs. 107, 108, 109

WAILES 1928, t. 1, f. 8, t. 2, f. 10; – 1939:44, f. 131; CANDEIAS 1930:29, t. 3, f. 57–59; PETERS 1932, t. 2, f. 11a, t. 3, f. 14c, 15e, t. 4, f. 17c; WANG et NIE 1932:297, f. 10, 11; STEEMANN NIELSEN 1934:9, f. 8, 9; SCHILLER 1936:368, f. 404a (vix b, non c), 405a: NIE 1936:32, f. 3 A, B, 4 A, B; RAMPI 1939a: 302, f. 8; GRAHAM et BRONIKOVSKY 1944:18, f. 7 A–H; MARGALEF 1948b:49, f. 2 d; SILVA et PINTO 1948:171, t. 2, f. 10; HASLE et NORDLI 1951, f. 5a; MARGALEF et DURÁN 1953:35, f. 9 d–m; WOOD 1954:274, f. 189 b, c, (vix a); KATO 1957:12, t. 3, f. 4 a, b; MARGALEF 1957a:91, f. 1 g, h, i; CURL 1959:305, f. 115; HALIM 1960a:186, t. 4, f. 7; – 1963, f. 2; CASSIE 1961, t. 7, f. 15; MARGALEF 1961a:79, f. 26 b–d; – 1961b:140, f. 2/8–11; YAMAJI 1966:92, t. 44, f. 10, 11; LOPEZ 1966:355, f. 6, 7, t. 1, f. 5, 6, et p. 417, f. 68, 72, 92; HADA 1967:20, f. 31 B; SILVA 1968, t. 5, f. 3; SOURNIA 1968a:395, f. 18–20; SUBRAHMANYAN 1968:20, f. 21–29; WOOD 1968:29, f. 57; MARGALEF 1969a, f. 4 E–H; STEIDINGER et WILLIAMS 1970:45, t. 7, f. 20 a, b; RICARD 1970, t. 2, f. h; HERMOSILLA 1973a:17, t. 2, f. 1; – 1973b:63, t. 33, f. 1–2, 7–8. [SOBRINO 1918, T. 4, f. b and CUESTA 1919, t. 52 (f. 1), D omitted by SCHILLER 1936].

The taxonomic situation in this species is essentially similar to that in *C. candelabrum* in that infraspecific variability and the parataxonomic treatment of early authors has led to confusion (summarised by SOURNIA, 1968a). Treating the situation in the same manner one can readily recognise two varieties which represent terminal types in the range of variation: the type variety: var. *furca* (incorrectly named var. *berghii* LEMMERMANN) which has much longer horns than the short-horned variety: var. *eugrammum* (EHRENBERG) SCHILLER. In addition, *C. hircus* SCHRÖDER may represent a rotund form with curving antapicals. BÖHM (1931b) found a disjunctive size range within the short variant in his western Pacific material. This has not, however, been substantiated by later authors using material from the same and different localities (e.g. STEEMANN NIELSEN 1934, 1939a; GRAHAM & BRONIKOVSKY 1944). LOPEZ (1966) could demonstrate a discontinuous size range in his Spanish Mediterranean material, his two groups corresponding roughly with the two varieties recognised here (not the two groups within var. *eugrammum* seen by BÖHM 1931b). GRAHAM & BRONIKOVSKY (1944) in fact concluded that there were probably not just two, but "many varieties or races" involved, but that they were almost impossible to separate on the basis of size only. MARGALEF & DURÁN (1953) have also presented size data for two varieties. For the time being this author has adopted the same path as SOURNIA (1968a), formally recognising two principal varieties.

C. furca is very similar in shape to *C. boehmii* GRAHAM et BRONIKOVSKY but, as can be readily seen from plate 12, the former is much larger with a girdle diameter not usually less than 30 µm, whereas the latter is usually close to 20 µm. In fact JÖRGENSEN's (1920) *C. furca* f. *nannofurca*, a problematic form much smaller than other members of *C. furca*, is well within the size range of *C. boehmii* (see comments under the latter species) and should perhaps be considered as distinct from *C. furca*. It is difficult to see how it might be considered transitional between var. *furca* and var. *eugrammum* as indicated by SOURNIA (1968a).

Stations: var. *furca*: 34, 37, 38, 41, 42, 43, 51, 53, 58, 66, 71, 87, 114, 288, 326.
var. *eugrammum*: 20, 36, 38, 39, 41–45, 47, 53, 88, 89, 100, 103, 104, 291, 299, 326, 331, 341, 410.

It is evident that both varieties can co-exist within the same water-column, a point already made by several authors. However, only the var. *furca* is known to extend into temperate waters. Most authors have considered the species to be neritic although, as pointed out by GRAHAM & BRONIKOVSKY (1944), some of STEEMANN NIELSEN's (1934) Pacific data indicates otherwise. STEEMANN NIELSEN considered this to be probably the result of island proximities or upwelling. PETERS (1932) found a predominantly neritic distribution in the South Atlantic. He also noted that the species appeared to favour river run-off areas and upwelling regions.

In the light of the above it is interesting that the species exhibited one of the most distinctly neritic distributions in the "Anton Bruun" material, particularly in the Andaman Sea/Bay of Bengal region. Also confirming PETER's (1932) observations, it seemed to be one of the few species favouring stations in the Ganges, Brahmaputra, and Irrawady River influences (stations 38–43, 45–47). Some of the few stations from which it was recorded in the open ocean were clearly near islands (e.g. station 326 near the Maldive Islands). Others were not, but these were very few (291, 299, 331, 341). TAYLOR (ms., 1964) found the var. *eugrammum* at neritic stations in the southwestern Indian Ocean, occurring in moderate abundance in the vicinity of Port Elizabeth in January.

Indian Ocean records: In WOOD (1963a) plus TSURUTA (1963), ANGOT (1965), ANGOT & GÉRARD (1967), TAYLOR (ms., 1964, 1967), NEL (1968), SOURNIA (1968 a, b, 1970), SUBRAHMANYAN (1968), and ANGOT (1970).

Ceratium incisum (KARSTEN) JÖRGENSEN Plate 12, Fig. 118

STEEMANN NIELSEN 1934:10, f. 11; SCHILLER 1936:370, f. 407b; GRAHAM et BRONIKOVSKY 1944:19, f. 9 A–E; WOOD 1954:275, f. 190; SILVA 1955:50, t. 7, f. 2; YAMAJI 1966:92, t. 44, f. 8; SOURNIA 1968a:400, f. 21; SUBRAHMANYAN 1968:21, f. 31; WOOD 1968: 32, f. 67.

This rare species is easily recognised by the manner in which the left antapical horn blends smoothly with the hypotheca, leading to a smooth, curving profile from the inner edge of the right antapical horn to the tip of the left antapical horn. This knife-like, or tooth-like, form led to the name of the species. The epitheca is also characteristically shaped. The species is superficially similar to *C. belone* (see comments under that species) and also to *C. brunellii* RAMPI (1942). The latter seems to lack the incurved acuteness of the left antapical horn and the fin on the posterior margin.

Stations: 21, 38, 58, 62, 98, 117, 374, 418, 420.

It occurred at scattered stations, somewhat similarly to *C. belone* (predominantly neritic). The most southerly station here was station 374 in the Agulhas Current south of Lourenco Marques (Mozambique). It has been recorded previously from the Indian Ocean by DURAIRATNAM (1964), TAYLOR (ms., 1964, 1967), SOURNIA (1968 a, b, 1970), and SUBRAHMANYAN (1968) plus the few authors listed by WOOD (1963a).

Ceratium lineatum (EHRENBERG) CLEVE Plate 12, Fig. 121

WAILES 1928, t. 2, f. 9; – 1939:43, f. 130; WANG 1936:152, f. 24; SCHILLER 1936:372, f. 410; BALECH 1944:424, t. 1, f. 2, 3; GRAHAM et BRONIKOVSKY 1944:22, f. 11 E–G; SILVA et PINTO 1948:171, t. 2, f. 12; WOOD 1954:277, vix f. 192 a, b; CASSIE 1961, t. 7, f. 8; – 1963, t. 1, f. e; YAMAJI 1966:93, t. 44, f. 16; HADA 1967:20, f. 31 C; SOURNIA 1968a:404, f. 25, 26; SUBRAHMANYAN 1968:24, f. 36; MARGALEF 1969a: f. 4 I; HERMOSILLA 1973b:61, t. 32, f. 1–3, 7, 9.
Non WOOD 1968:34, f. 72.
Syn.: *Ceratium* sp. KATO 1957:13, t. 3, f. 8 a, b.

This species is one of several small species of *Ceratium* which are difficult to tell apart and may in some instances be conspecific. The others are *C. boehmii* GRAHAM et BRONIKOVSKY, *C. kofoidii* JÖRGENSEN, and *C. minutum* JÖRGENSEN. It is here recognised by the characters drawn attention to in the first major monograph on the Ceratia: that by JÖRGENSEN (1911); namely that it is relatively larger than the others (girdle diameter 25–47 µm, body length without horns much greater than the breadth, i.e. 40–60 µm), with distinctly divergent antapical horns in which the right horn is between one third and two thirds the length of the left antapical horn. The specimen figured here seems to be a good representative of the species.

Stations: 340, 365, 417.

Rare, at a few stations in the west central Indian Ocean (two oceanic, one inshore near Tuléar, Madagascar). Early authors considered it a northern, temperate species and JÖRGENSEN (1920) did not find it in the Mediterranean. However its author, CLEVE (1899) did find it in the Indian Ocean and tropical Atlantic. SOURNIA (1968a) attributed this contradictory distribution to confusion of the species with *C. pentagonum* by some authors, although the difference in size makes this difficult to do.

Indian Ocean references: In WOOD (1963a), TSURUTA (1963), ANGOT (1965), plus ANGOT & GÉRARD (1967), TAYLOR (1967), NEL (1968), SOURNIA (1968a), SUBRAHMANYAN (1968), and ANGOT (1970).

Ceratium minutum JÖRGENSEN Plate 12, Fig. 120

MARTIN 1928:30, vix t. 2, f. 17–19, t. 5, f. 13–14; SCHILLER 1936:374, f. 413 a–c; RAMPI 1942:223, f. 6; MARGALEF et DURÁN 1953: 37, f. 9 a–c; WOOD 1954:279, vix. f. 196; HALIM 1960a, t. 4, f. 9; SOURNIA 1968a:406, f. 27; SUBRAHMANYAN 1968:27, f. 39, 40; WOOD 1968:36, f. 79.

The smallest of the group of species referred to in the comments under *C. lineatum*, the girdle diameter usually being within 25–30 µm. The cell body is relatively shorter than *C. kofoidii*, which in turn is shorter than the others (WOOD's 1968 interpretation of *C. lineatum* and *C. kofoidii* seems reversed). In the original description JÖRGENSEN (1920) described the side-walls of the body as being relatively flattened (i.e. little convexity). However, the specimens illustrated by LEBOUR (1925) and MARTIN (1928) were decidedly convex, and the specimen figured here also had a tendency to a rounding of the cell body shape. The very small right antapical horn is also diagnostic of this species. The left horn is usually less elongate and thin than the specimen figured here.

Stations: 298, 313.

Rare in the material although its presence in nets, in view of its size, can only be considered fortuitous. Single specimens were found at two oceanic stations, one of which (st. 313) was close to 30 °S. It has only been definitely recorded from the Indian Ocean by SOURNIA (1968a, 1970) and SUBRAHMANYAN (1968), WOOD's (1954) Australian record being in doubt due to his figure.

Ceratium pentagonum GOURRET Plate 12, Figs. 111, 112, 113

CANDEIAS 1930:30, t. 3, f. 61; PETERS 1932:29, t. 1 a–c, t. 3, f. 15 a, t. 4, f. 18; STEEMAN NIELSEN 1934:11, f. 12; SCHILLER 1936:370, f. 408 a–c (f. a non f. *robustum*); WAILES 1939:43, f. 129; RAMPI 1939a:303, f. 17, 20; GRAHAM et BRONIKOVSKY 1944:20, f. 10 D, H–N; MARGALEF 1946:93, f. II 1, 2; MARGALEF et DURÁN 1953:37, f. 10 f; GAARDER 1954:15, f. 14; WOOD 1954:276, f. 191 a–f; SILVA 1955:51, t. 7, f. 3, 4; KATO 1957:13, t. 4. f. 9; CURL 1959:306, f. 120; HALIM 1960a, t. 4, f. 8; – 1963:496, f. 3, 4; BALLANTINE 1961:228, f. 48; CASSIE 1961, t. 7, f. 7, 10; BALECH 1962b:179, f. 379–384; TORIUMI 1964b:24, t. 3, f. 12; KLEMENT 1964:354, t. 2, f. 6; LOPEZ 1966:344, f. 5, t. 1, f. 3, 4, f. 59, 63, et p. 413, f. 90 I–III; YAMAJI 1966:92, t. 44, f. 14; SOURNIA 1968a:400, f. 23, 24; SUBRAHMANYAN 1968:23, f. 32, 33; WOOD 1968: 37, f. 82; MARGALEF 1969a, f. 4 J; STEIDINGER et WILLIAMS 1970:47, t. 12, f. 31; RICARD 1970, t. 2, f. g; HERMOSILLA 1973b:62, t. 32, f. 4–6, 8.

Syn.: . . . . *C. subrobustum* (JÖRGENSEN) STEEMANN NIELSEN 1934:11, f. 13; GRAHAM et BRONIKOVSKY 1944:20, f. 10 A, B, E–G.
C. balticum (MÖBIUS) BALECH 1944:425, t. 1, f. 1, 5.
Ceratium sp. MEYER, 1966, f. 48 vix f. 49.

The situation in this species parallels that found in the species *C. candelabrum* and *C. furca* already described. Longer horned, more robust specimens inhabit the coldest part of the range, but are also found occasionally in the warmest parts. The infraspecific variants are treated the same way here, with the extremes being recognised in the nomenclature. However, there is difficulty in determining the var. *pentagonum* (as in the other two species early authors designated no var. *pentagonum*). SOURNIA (1968a) who recognised var. *candelabrum* and var. *furca* in the other two species, curiously made no attempt to do so in this species. He recognised LOPEZ's (1966) forma *pentagonum*; however, one of the varieties he mentions must include the type and consequently became the var. *pentagonum*. This is not as easy as it might appear as GOURRET's (1883) type specimen was evidently a teratological individual in which the apical horn was vestigial. It more closely resembles the var. *tenerum* JÖRGENSEN than the var. *subrobustum* JÖRGENSEN or the var. *robustum* (CLEVE) JÖRGENSEN and consequently it may be considered more appropriate in future to replace the former variety with var. *pentagonum*.

In SOURNIA's work the species is distinguished from other similar species [*C. setaceum* JÖRGENSEN, *C. lineatum* (EHRENBERG) CLEVE] by the character drawn attention to by JÖRGENSEN (1920): the left and right antapical horns are much less dissimilar in length. In addition the size and shape of the cell body are distinctive.

Treatments of the infraspecific variants have varied among earlier authors. Here the following varieties are recognised:

var. *tenerum* JÖRGENSEN, recognised by its short antapical horns and moderate size (f. 112);
var. *longisetum* (OSTENFELD et J. SCHMIDT) JÖRGENSEN, similar to var. *tenerum* but with a very long, very slender apical horn (f. 113);
var. *subrobustum* JÖRGENSEN, the warm-water, large form (diameter to 90 µm as in the specimen illustrated here), with longer antapical horns than the two former varieties, diverging only slightly, and with little or no fin on the antapical profile of the cell body (f. 111);
var. *robustum* (CLEVE) JÖRGENSEN, the polar variety, like var. *subrobustum* but with even longer, more divergent horns and a continuous fin running the length of the antapical, cell body profile between the horns [= *C. balticum* (MÖBIUS) BALECH].

GRAHAM & BRONIKOVSKY's (1944) subspecies *pacificum* appears to be ill-defined and heterogeneous, requiring further study. *C. ehrenbergii* KOFOID is here considered a separate species (see comments under that taxon).

Stations: var. *tenerum* – 13, 17, 19, 25, 32, 34, 37, 38, 51, 53, 56, 57, 60, 62, 67–72, 91, 92, 94, 96–100, 102–104, 112, 113, 125, 129, 134, 135, 147, 149, 153, 156, 159, 288, 294, 298, 302, 305, 306, 314, 315, 318, 320, 327, 341, 344, 355, 358, 359, 369, 371, 374, 375, 398, 404, 412, 413, 417, 420.
var. *longisetum* – 15, 293, 319, 320, 322, 325, 338.
var. *subrobustum* – 104, 162, 298, 369, 371, 411, 420.

The var. *tenerum* was the commonest representative of the subgenus *Ceratium* in the material, being widely scattered on all cruises. In the Bay of Bengal it closely paralleled the distribution of *Ornithocercus magnificus*, absent from coastal stations and particularly the low salinity river-plume areas. It extended to almost 40 °S, more in the west than in the east. The var. *longisetum* was found at only a few stations, none further south than 12 °S (March, 1964). The var. *subrobustum* occurred, with the exception of station 104 (Bay of Bengal) only in the western area in the Mozambique Channel and between Mauritius and the Seychelle Islands.

C. pentagonum has been recorded from the Indian Ocean by numerous authors (see WOOD 1963a plus SILVA 1960; SUKHANOVA 1962b; TSURUTA 1963; DURAIRATNAM 1964; SOURNIA 1966a, 1968 a, b, 1970; TAYLOR 1967; NEL 1968, SUBRAHMANYAN 1968; THORRINGTON-SMITH 1969; and ANGOT 1970.

Ceratium setaceum JÖRGENSEN Plate 12, Figs. 114, 115

PETERS 1932:33, vix. t. 3, f. 15 b; c; SCHILLER 1936:373, f. 411; RAMPI 1942:223, f. 8; GRAHAM et BRONIKOVSKY 1944:22, f. 11 A; WOOD 1954:278, vix f. 194a (non b); SUBRAHMANYAN 1968:26, f. 37, 38; WOOD 1968:39, f. 88
Non STEEMANN NIELSEN 1934:12, f. 16.

This rare species resembles a small *C. pentagonum* var. *longisetum* or a large *C. kofoidii*, being intermediate between them in size. However, as JÖRGENSEN (1920) pointed out, in can be readily distinguished from *C. pentagonum* in that the left antapical horn is always twice or more the length of the right antapical horn. The large girdle diameter (35–45 µm) makes it clearly distinguishable from the small species, and also the angularity of the right profile of the hypotheca, in this way resembling *C. pentagonum*.

Stations: 53, 54, 62, 63, 69, 91, 92, 94, 104, 327.

It was only found in small numbers at stations (chiefly near the coast) in the Bay of Bengal and one station off the southwest tip of India. Distributional data on the species is scanty as a result of its rarity, but it seems to occur chiefly in tropical and subtropical waters.

Indian Ocean records: In WOOD (1963a) plus ANGOT (1965) TAYLOR (1967), NEL (1968), SUBRAHMANYAN (1968), THORRINGTON-SMITH (1969), and ANGOT (1970).

Ceratium teres KOFOID Plate 12, Fig. 110; Plate 40, F. 484

PETERS 1932:32, t. 3, f. 14e; STEEMANN NIELSEN 1934:11, vix. f. 14; SCHILLER 1936:372, f. 409 a, b; NIE 1936:36, f. 7 A, B; GRAHAM et BRONIKOVSKY 1944:21, f. 11 B–D; MARGALEF 1948b:49; f. 2 e; SILVA 1949:355, t. 6, vix f. 21; WOOD 1954:277, f. 193 a, b; MARGALEF, HERRERA, RODRIGUEZ-RODA et LARRAÑETA 1954:92, f. 3a; HALIM 1960a, t. 4, f. 10; – 1963:493, vix f. 5; CASSIE 1961, t. 7, f. 11; LOPEZ 1966:352, f. 8, t. 1, f. 7, 64, et p. 415, f. 64, 91; YAMAJI 1966:93, t. 44, f. 17 (sub *terres*); SOURNIA 1968a:405, f. 28; SUBRAHMANYAN 1968:24, f. 34, 35; WOOD 1968:40, f. 90; STEIDINGER et WILLIAMS 1970:47, t. 13, f. 35 a, b.

This small species is reasonably distinctive in view of its rounded, porulate body (with flat posterior profile) and short, more or less divergent antapical horns, the right being more turned out than the left. The left antapical horn, on close inspection, is usually slightly constricted at the base near the body, but this is often omitted from earlier figures. It is superficially similar to *C. setaceum* and the small forms of *C. pentagonum* (see comments under those species).

Stations: 32, 35, 37, 53, 56–60, 62, 65, 66, 69–72, 92, 93, 99, 102, 103, 104, 106, 114, 115, 150, 155, 290, 294, 301, 310, 312, 325, 326, 335, 358, 406.

It was fairly common but not abundant at stations in the northern Andaman Sea, central and western Bay of Bengal, and in the open Indian Ocean. It occurred in both oceanic and neritic provinces. An interesting distributional feature was its presence on one occasion relatively far south in the vicinity of the Islands of Amsterdam and St. Paul (st. 310, 37 °S), one of the few tropical species to extend this far south. GRAHAM & BRONIKOVSKY (1944) also found that although it occurred predominantly in warm water it did occur rarely at colder stations (40 °S: surface temperature 15.0 °C).

Indian Ocean records: In WOOD (1963a) plus SILVA (1956a, 1960), SOURNIA (1966a; 1968 a, b, 1970), TAYLOR (1967), SUBRAHMANYAN & SARMA (1967), SUBRAHMANYAN (1968), NEL (1968), and THORRINGTON-SMITH (1969).

Subgenus *Amphiceratium* (VANHÖFFEN) OSTENFELD

Species in which the cell is very elongated. Both antapical horns are directed posteriorly. The right horn is greatly reduced and the left horn is often very extended.

Ceratium biceps CLAPARÈDE et LACHMANN Plate 13, Figs. 127, 128
1859:400, t. 19, f. 8; KOFOID 1908a:370, f. 21–24; – 1908b:389.
Syn.: . . . . *C. extensum* (GOURRET) CLEVE . . . . CANDEIAS 1930:31, t. 3, f. 63; PETERS 1932:39, t. 3, f. 14f, vix t. 2, f. 10 d; STEEMANN NIELSEN 1934:14, f. 24; SCHILLER 1936:380, f. 419; NIE 1936:41, f. 11 A–C; RAMPI 1939a:304, f. 11; GRAHAM et BRONIKOVSKY 1944:24, f. 11 BB–DD; SILVA 1949:356, t. 6, f. 22; MARGALEF et DURÁN 1953:40, f. 10 a; WOOD 1954:283, f. 203; KATO 1957:14, t. 4, f. 10 a–c; HALIM 1960a:230, t. 4, f. 3; – 1963:497, f. 9; YAMAJI 1966:94, t. 45, f. 8; SUBRAHMANYAN 1968:32, f. 56, 57; WOOD 1968:28, f. 54; STEIDINGER et WILLIAMS 1970:45, t. 7, f. 19.
? *Ceratium* sp. KATO 1957:15, t. 4, f. 11 a, b (teratol.?) antapical

This species is by far the longest of the subgenus (compare the figures in plate 13). It exists in two morphological conditions. In one the cell body lacks a right apical horn and the hypotheca (including horn) is considerably larger than the epitheca (KATO 1957, apparently reversed this relationship). The other is more rare. It has a relatively strongly-developed right antapical horn and the cell body is centrally situated, the epitheca and hypotheca, plus horns, being subequal in length. This was termed *C. extensum* forma *strictum* (OKAMURA et NISHIKAWA) SCHILLER (erroneously attributed to STEEMANN NIELSEN, 1934, who did not apparently make the combination). It is the form illustrated by WOOD (1968).

STEEMANN NIELSEN (1934), SCHILLER (1936), and GRAHAM & BRONIKOVSKY (1944) used the presence or absence of a right antapical horn as the sole criterion for distinguishing them as forms, but recent authors have tended to ignore the distinction, citing variability as the reason for omission. All ignored KOFOID's (1908b) early claim that this variability was simply due to cell division and his revival of CLAPARÈDE & LACHMANN's name. The differential in epi- and hypothecal proportions appears to be usually associated with the other horn characteristics, and is consistent with KOFOID's interpretation. In cell division plate-sharing between daughter cells is of the normal oblique peridinoid type, as KOFOID (1908a) illustrated. Thus the right daughter cell receives only the short right antapical horn, having to reform both the apical and left antapical horns. The length of the latter two should consequently be approximately equal when first forming. On the other hand the left daughter cell should reflect the mature state of the anterior and left antapical horns, the left antapical horn tending to grow longer than the apical horn. The difficulty in this interpretation is that it does not explain how, in those cells with a short right antapical horn, the apical horn is longer than in the form which presumably retains the mature apical horn. As these forms may be directly related to cell division there does not seem to be any point in their formal nomenclatural recognition. Their distributional data are kept separate below to check further for any ecophenological effects.

Stations: no right horn: 29, 35, 55, 57, 61, 101, 116, 291, 294, 313, 315, 318, 343, 360, 361, 367, 405, 407, 420.
right horn: 50, 66, 67, 91, 97, 113, 283, 284, 287, 288, 302, 315, 320, 358, 360, 361, 414, 415.

Both occurred in small numbers at scattered stations throughout the area. They were coexistent at stations 315, 360, and 361. The right-horned state was seen in the Arabian Sea, but not the other. In this material both occurred with approximately the same frequency.

In the southwestern Indian Ocean TAYLOR (ms., 1964) found the species to be common and widely distributed in summer and autumn, and it occurred relatively abundantly at three oceanic stations in April (two close to 40 °S in the Agulhas Current). It has been considered a relatively eurythermal species which prefers warmer waters by earlier authors (e.g. GRAHAM & BRONIKOVSKY 1944). The list of Indian Ocean records in WOOD (1963a) requires amplification with the following: SILVA (1956a, 1960), SUKHANOVA 1962b), TSURUTA (1963),

DURAIRATNAM (1964), ANGOT (1965), SOURNIA (1966a, 1968b, 1970), TAYLOR (1967), NEL (1968), SUBRAHMANYAN (1968), THORRINGTON-SMITH (1969), and ANGOT (1970).

Ceratium bigelowii KOFOID Plate 13, Figs. 134, 135

STEEMANN NIELSEN 1934:13, f. 18; SCHILLER 1936:376, f. 414 b; GRAHAM et BRONIKOVSKY 1944:22, f. 11, I, K–M; BALECH 1962b: 181, t. 25, f. 388–392; WOOD 1963b:39, f. 143; SUBRAHMANYAN 1968:28, f. 46, 47; STEIDINGER et WILLIAMS 1970:44, t. 4, f. 11 a, b.

This is one of the most distinctive species of the subgenus. The epitheca is greatly expanded laterally, widening abruptly above the level of the precingulars. The right antapical horn is very short and usually slightly divergent. The slender apical horn turns slightly to the right distally, the left antapical horn bent more strongly to the right a varying distance from the cell body.

Stations: 27, 38–40, 71, 125, 343.

It occurred singly at stations in the Andaman Sea and at two stations in the west central Indian Ocean.

The species is considered to be very rare, being highly stenothermal and oceanic (GRAHAM & BRONIKOVSKY 1944). It is found chiefly in the tropical Indo-Pacific region, the only record from the Atlantic Ocean being that of STEIDINGER & WILLIAMS (1970) in the Gulf of Mexico. The Indian Ocean records for this species are those of STEEMANN NIELSEN (1939a), WOOD (1962 – in 1963a), SUKHANOVA (1962b), TSURUTA (1963), TRAVERS & TRAVERS (1965), SOURNIA (1968b), and SUBRAHMANYAN (1968).

Ceratium falcatiforme JÖRGENSEN Plate 13, Figs. 138, 139

STEEMANN NIELSEN 1934:14, f. 23; SCHILLER 1936:378, f. 417 b; WOOD 1954:282, f. 201; HALIM 1960a:191, t. 4, f. 5; BALECH 1962b: 181, t. 25, f. 387; SOURNIA 1968a:414, f. 39; SUBRAHMANYAN 1968:31, f. 54; LÉGER 1973a:23, f. 8.

This is the smallest member of the "*falcatum*-complex" (see remarks under *C. falcatum*). In the present material the total length of the species never exceeded 320 µm and was usually below 250 µm (but LÉGER 1973a has found a specimen of 360 µm in length). On a reduced scale the epitheca plus horn resembles the shape of *C. falcatum* but the hypotheca is more gradually bent than in *C. falcatum*, being more like *C. longirostrum* or *C. fusus*. Although SUBRAHMANYAN (1968) considered it variable and difficult to recognise, in this material it was one of the more readily distinguishable species of *Amphiceratium*.

Stations: 40, 41, 99, 305, 306, 308, 310, 313, 370.

It occurred at stations in the Andaman Sea near the Irrawaddy Delta, in the western Bay of Bengal and at scattered open ocean stations. Most interestingly, it occurred at four stations below 30 °S, two of which (stations 308, 310) are close to the Islands of Amsterdam and St. Paul.In fact station 308, where the species was moderately abundant, was below 40 °S with a surface temperature of 15.03 °C. From surface temperature characteristics it appears that both stations 308 and 310 can be considered as being situated within the Subtropical Convergence Region (DÉFANT 1938, FUKASE 1962, DELÉPINE 1963).This was also suggested by the presence of subantarctic diatoms in the samples (e.g. *Rhizosolenia alata* f, *inermis*, *Corethron criophilum* var. *criophilum*).

As previous authors have regarded the distribution of this species as similar to others of the "*falcatum*-complex", and it did occur in the equatorial high-temperature regions, it may be presumed that its presence within the convergence region was due to lateral mixing.

Indian Ocean records: In WOOD (1963a) plus TAYLOR (1967), SOURNIA (1968 a, b), NEL (1968), and SUBRAHMANYAN (1968).

Ceratium falcatum (KOFOID) JÖRGENSEN Plate 13, Fig. 133

STEEMANN NIELSEN 1934:14, f. 22; SCHILLER 1936:377, f. 417a; RAMPI 1939a:303, f. 14; GRAHAM et BRONIKOVSKY 1944:24, f. 11 W–AA; WOOD 1954:281, f. 400; SILVA 1955:57, t. 7, f. 11; BALLANTINE 1961:244, f. 49; HALIM 1963:496, f. 7; SOURNIA 1968a:414, f. 38; SUBRAHMANYAN 1968:30, f. 53; WOOD 1968:29, f. 56.

This relatively small species of *Amphiceratium* is one of four closely related taxa (*C. falcatum*, *C. falcatiforme*, *C. inflatum*, and *C. longirostrum*) which are frequently difficult to separate, leading some authors to "sink" all or most of them into one species (e.g. PETERS 1932). STEEMAN NIELSEN (1934) considered that they constituted a "formenkreis" although he maintained their separation. His application of the term is curious as he pointed out himself that they exhibit a very similar inter-oceanic, high stenothermal distribution. Although difficulty was also experienced with this "species complex" (as it could loosely be termed) in the present work, the distinctions as summarised by JÖRGENSEN (1920, p.35) and SOURNIA (1968a, p. 414, table 1) have been applied for the present. STEEMANN NIELSEN (loc. cit.) has indicated that, if it is subsequently considered appropriate to sink the species into one, PETERS' (1932) practise of referring them to *C. inflatum* was incorrect. However, his suggestion to rescussitate *C. pennatum* KOFOID was equally incorrect as it appears that *C. longirostrum* GOURRET has priority (see JÖRGENSEN 1920, p. 37).

C. falcatum is recognised by its size, relative inequality in the length of the epitheca (plus horn) versus the hypotheca (plus horn), the relative straightness of the apical horn with an apparent junction between the elongate epitheca and its apical horn, and the sharp distal bend of the left antapical horn.

Stations: 162, 312.

It was only found in small numbers at two stations, one south of 30 °S and the other near Mauritius. This rarity is at odds with the observations of previous authors who found this to be the commonest member of the group. It has been recorded previously from the Indian Ocean (see WOOD 1963a plus SUKHANOVA 1962b, TAYLOR ms. 1964, 1967, TRAVERS & TRAVERS 1965, NEL 1968, and SUBRAHMANYAN 1968).

Ceratium fusus (EHRENBERG) DUJARDIN Plate 13, Figs. 129, 130, 136? 137?

WAILES 1928, t. 1, f. 5, 6; – 1939:42, f. 127; MARTIN 1928:30, t. 6, f. 7; CANDEIAS 1930:31, t. 3, f. 64, 64a; PETERS 1932:37, t. 3, f. 14a, t. 4, f. 17e; STEEMAN NIELSEN 1934:14, f. 25, 26; SCHILLER 1936:378, f. 418 a, b, c; NIE 1936:41, f. 12 A–D, f. 13; RAMPI 1939a:303, f. 12, 13; GRAHAM et BRONIKOVSKY 1944:25, f. 11 EE, 13 A–D; BALECH 1944:426, t. 1, f. 4, 6; SILVA et PINTO 1948:171, t. 2, f. 11; HASLE et NORDLI 1951, f. 1 a–h, 2 a–h, 5 b, c, 6 a–f, 7 a–h; WOOD 1954:282, f. 202; KATO 1957:13, t. 3, f. 5 a–c, 6 a, b; MARGALEF 1957a:47, f. 1j; – 1961a:81, f. 26 e–g; CURL 1959:306, f. 116; BALLANTINE 1961:224, f. 50; CASSIE 1961, t. 7, f. 9; BRUNEL 1962:176, t. 51, f. 1, 3; YAMAJI 1966:93, t. 45, f. 3, 4, 5; HADA 1967:20, f. 31 A; SOURNIA 1968a:408, f. 32–35; SUBRAHMANYAN 1968:31, f. 55, t. 1, f. 3–6; WOOD 1968:29, f. 58; STEIDINGER et WILLIAMS 1970:45, t. 8, f. 21 a, b; AVARIA 1970, t. 3, f. 4; HERMOSILLA 1973a:19, t. 2, f. 2–7.

[SOBRINO 1918, t. 4, f. 1 a omitted by SCHILLER].

Vix WANG 1936:153, f. 25 (sub var. *schuetti* LEMMERMANN)

Syn.: .... *C. seta* (EHRENBERG) KOFOID .... WANG et NIE 1932:299, f. 12.

Ceratium sp., MEYER 1966, f. 47.

A medium-sized species. The epitheca tapers very gradually into an apical horn which is fairly straight or gently curved towards the dorsal side. The hypotheca and left antapical horn are usually longer than the epitheca/apical horn. The left antapical horn varies from almost straight to strongly curved towards the dorsal side. The right antapical horn is reduced or absent. Two main varieties have been recognised: var. *fusus*, with stronger horns and usually with a small right antapical horn; and var. *seta* (EHRENBERG) SCHILLER, a warmer water (Indo-Pacific) form with more slender horns, shorter, with a more marked dissimilarity in the length of the hypotheca in comparison with the epitheca and usually lacking the right antapical horn. Some authors have also recognised var. *schuetti* LEMMERMANN, a variant with a very swollen epitheca (still tapering into the apical horn as in the type) and lacking a right antapical spine. Some very small specimens (length 245–350 µm) have been referred to the latter by WANG (1936, p. 153, f. 25). They correspond to specimens like that figured here on plate 13, fig. 136. These are so much smaller than the dimensions provided by JÖRGENSEN (1911, p. 29, length 470–630 µm) that this allocation is highly doubtful. Also, the epitheca/apical horn transition is more abrupt than in earlier figures. At present it is not clear what to do with this small form. It may perhaps be more appropriately referred to *C. inflatum*.

The presence or absense of a right antapical horn, together with the disproportion of the epi- and hypothecal lengths, seems to parallel the situation in *C. biceps* and may thus be related to cell division, removing the need for formal nomenclatural recognition of the var. *seta*. However, this requires confirmation.

HASLE & NORDLI (1951) have described many aberrants from a culture of this species. Most aberrations involved supernumery horns. The reason for the aberrations was not discovered.

Stations: var. *fusus*: 57
var. *seta*: 38, 40, 42, 44, 46, 47, 57, 89–92, 99–101, 103, 159, 285, 302, 310, 318, 321, 325, 326, 341, 358, 360–362, 367, 369, 398, 412, 416, 420.
var. *schuettii* (? sensu WANG) 45.

BALLANTINE (1961) found the var. *seta* to be one of the most abundant dinoflagellates in the vicinity of Zanzibar in February/March, 1956. The species has been frequently found in the Indian Ocean by previous authors (see WOOD 1963a plus the records of DURAIRATNAM 1964, SILVA 1956a, 1960; TSURUTA 1963; ANGOT 1965; ANGOT & GERARD 1967; TAYLOR 1967; SOURNIA 1968 a, b, 1970; SUBRAHMANYAN 1968; THORRINGTON-SMITH 1969; and ANGOT 1970).

Ceratium geniculatum (LEMMERMANN) CLEVE Plate 13, Figs. 140 a, b

STEEMANN NIELSEN 1934:13, f. 17; SCHILLER 1936:375, f. 414; GRAHAM et BRONIKOVSKY 1944:22, f. 11 J; SILVA 1949:355, t. 9, f. 2;

WOOD 1954:279, f. 197; – 1963b:40, f. 45; YAMAJI 1966:92, t. 44, f. 12; SOURNIA 1968a:407, f. 30, 31; SUBRAHMANYAN 1968:28, f. 43–45; WOOD 1968:30, f. 60.

A distinctive small species, easily recognisable from other small *Amphiceratium*, such as *C. falcatiforme*, by means of the sigmoid flexure of the epitheca when seen in ventral view (usually less than in the specimen illustrated) and the three fin-like body folds also present on the epitheca. *C. pacificum* WOOD (non SCHRÖDER 1906) is almost identical, differing only in the distal inward bend of the left antapical horn. As indicated, his name is also invalid.

Stations: 36, 47, 56, 66, 91, 92, 103, 108, 302, 420.

The species was rare, occurring at scattered stations in the Andaman Sea, at one station in the eastern Arabian Sea, one station south of Réunion, and at one close to Mombassa. It is known from the tropical waters of the three major oceans. The Indian Ocean records comprise those of KARSTEN (1907), STEEMANN NIELSEN (1939a), WOOD (1962 – in 1963a), TAYLOR (1967), SOURNIA (1968 a, b, 1970), NEL (1968), and SUBRAHMANYAN (1968).

Ceratium inflatum (KOFOID) JÖRGENSEN Plate 13, Fig. 132

STEEMANN NIELSEN 1934:13, f. 20; SCHILLER 1936:376, f. 415; RAMPI 1939a:303, f. 15; GRAHAM et BRONIKOVSKY 1944:23, f. 11 O–S; WOOD 1954:281, f. 198; SILVA 1955:56, t. 7, f. 9; YAMAJI 1966:93, t. 45, f. 6; SOURNIA 1968a:412, f. 36; SUBRAHMANYAN 1968:29, f. 48, 49; STEIDINGER et WILLIAMS 1970:46, t. 10, f. 25.

Syn.: . . . . *C. nipponicum* OKAMURA 1912:8, t. 3, f. 44 a–e.
C. pennatum KOFOID . . . . NIE 1936:39, f. 10 A–E; KATO 1957:14, t. 3, f. 7.

This is one of the group of closely similar species discussed under *C. falcatum*. JÖRGENSEN (1920, p. 35) has drawn attention to two forms of this species: one in which the epitheca is somewhat bulbous in appearance immediately above the girdle and with a smoothly-curving left antapical horn (figs. 45, 46 in his 1911 monograph); and a second in which the expanded portion of the epitheca blends more gradually into the apical horn and the left antapical horn bends abruptly in the distal part (fig. 48a in JÖRGENSEN 1911, under the name of *C. pennatum* KOFOID, reproduced as *C. inflatum* in his 1920 paper, fig. 25, and also illustrated by KATO 1957). The latter form has not been formally recognised in the nomenclature. It contains individuals which closely approach the appearance of *C. falcatum* (see plate 13, fig. 132 here) but which can still be distinguished by the inequality of epi- and hypothecal lengths.

OKAMURA (1912) attempted to distinguish *C. nipponicum* from *C. inflatum* on the basis that the former was flattened in one plane, the original description by KOFOID making no mention of this feature. However, all later authors have observed this feature in specimens referrable to *C. inflatum*. *C. nipponicum* OKAMURA was, incidentally, omitted by SCHILLER (1936) and from both the monographs on *Ceratium* by SOURNIA (1968a) and SUBRAHMANYAN (1968).

Station: 318.

Only one specimen (illustrated) is referred here to the species. It occurred at an equatorial station to the south of India. The species is described as "a rare, intolerant tropical species confined entirely to warm water" by GRAHAM & BRONIKOVSKY (1944).

Indian Ocean records: WOOD (1963a) plus SILVA (1960), SUKHANOVA (1962b), TSURUTA (1963), ANGOT (1965), ANGOT & GÉRARD (1967), TAYLOR (ms. 1964, 1967), SOURNIA (1968 a, b, 1970), NEL (1968), SUBRAHMANYAN (1968), THORRINGTON-SMITH (1969), and ANGOT (1970).

Ceratium longirostrum GOURRET Plate 13, Figs. 131 a, b

CANDEIAS 1930:31, t. 3, f. 62, 62 a, b; STEEMANN NIELSEN 1934:13, f. 21; SCHILLER 1936:376, f. 416; RAMPI 1939a:303, f. 9; GRAHAM et BRONIKOVSKY 1944:24, f. 11 T–V; MARGALEF 1948b:49, f. 2 g; MARGALEF et DURÁN 1953:40, f. 10 b–c; WOOD 1954:281, f. 199; SILVA 1955:57, t. 7, f. 10; HALIM 1960a, t. 4, f. 4; – 1963:496, f. 6; SOURNIA 1968a:413, f. 37; SUBRAHMANYAN 1968:30, f. 50–52; STEIDINGER et WILLIAMS 1970:46, t. 10, f. 27; RICARD 1970, t. 2, f. i.

Another member of the "*falcatum*-complex", within the same size range, but quite readily recognisable by its distinctly longer epitheca (plus horn) than hypotheca (plus horn), the smooth, gradual curvature of the horns, and the gradual blending of the epitheca with its horn. It most closely resembles the "second form" of *C. inflatum* referred to under the latter species. *C. falcatum* also has a longer epitheca than hypotheca, but the hypothecal (left antapical) horn is sharply bent. Generally the latter species is smaller, but this was not noticeable in this material.

Stations: 32, 41, 42, 56, 67, 362, 367.

It was found in small numbers at clusters of stations in the Andaman Sea, Bay of Bengal, and the Mozambique Channel. The distribution of this species has been considered by previous authors as indistinguishable from *C. inflatum* (rare, high stenothermal). In the "Anton Bruun" material *C. longirostrum* was apparently less rare, although evidently also showing a preference for water of high temperature. Additional Indian Ocean records to those in WOOD (1963a) are SUKHANOVA (1962b), SOURNIA (1966b, 1968 a, b, 1970) TAYLOR (ms. 1964, 1967) NEL (1968), and SUBRAHMANYAN (1968).

Subgenus *Tripoceratium* KOFOID

Syn.: s.g. *Euceratium* (GRAN) OSTENFELD; s.g. *Orthoceratium* SOURNIA. [Includes *Macroceratium* KOFOID]

SOURNIA (1968a) proposed the name *Orthoceratium* to replace that originated by GRAN. Article 21 of the International Code of Botanical Nomenclature forbids the use of the prefix *Eu-*, combined with the name of the genus, for the creation of a subgenus or section. However, KOFOID's (1909b) name has priority within the same rank, even though it was used originally in a more restricted sense, excluding the section Macroceras which he raised to subgeneric status (*Macroceratium*).

This is a large subgenus, used here to encompass all members of *Ceratium* which exhibit the classical "anchor" shape in which both antapical horns usually proceed laterally after leaving the body. They are often recurved towards the anterior of the cell. Because of its size the use of sections in this subgenus is helpful. The following (fewer than are recognised by most recent authors) are used here, based primarily on antapical horn features:

Section *Densa* JÖRGENSEN – The left horn is much shorter than the right horn and is bluntly pointed.

Section *Macroceras* OSTENFELD – The posterior profile of the cell is moderately or strongly indented due to one or both antapical horns being directed posteriorly for a short distance before curving out laterally. The ends of the horns are usually narrow but truncated. The name of the section is commonly mis-spelled Macroceros.

Section *Palmata* (PAVILLARD) JÖRGENSEN – Similar to the section Tripos but with the ends of the horns subdivided in a digitate manner.

Section *Platycornia* JÖRGENSEN – Horns as for section Tripos but flattened strongly in their distal regions.

Section *Reflexa* JÖRGENSEN – The left horn is bent strongly towards the posterior and is short.

Section *Tripos* – Horns arise laterally from the cell body with little indentation of the posterior profile. The tips of the horns are simple and acute.

Their arrangement is alphabetical for convenience although they are usually arranged "systematically", reflecting presumed relationships. Some, such as the sections Platycornia, Palmata, and Densa, are based on very superficial features.

Section Densa JÖRGENSEN

This section includes only one species at present.

Ceratium dens OSTENFELD et SCHMIDT Plate 17, Fig. 172

STEEMANN NIELSEN 1934:15, f. 27; SCHILLER 1936:381, f. 420 a, b; NIE 1936:44, f. 14 A, B; WOOD 1954:284, f. 204; YAMAJI 1966:105, t. 51, f. 3; SOURNIA 1968a:457, f. 80; SUBRAHMANYAN 1968:34, f. 58, t. 3, f. 16.
Vix STEIDINGER et WILLIAMS 1970: *Ceratium* sp., t. 15, f. 40.

This is a large distinctive species, readily recognisable due to the very short, bluntly acute left antapical horn. The body and right antapical horn are somewhat similar to *C. humile* in shape. The apical horn is straight and tilted to the left. The right antapical horn can exhibit autotomy in some specimens.

The species was thought to occur in two varieties, the var. *dens* in which the left horn projects laterally, and the var. *reflexa* J. SCHMIDT in which the horn projects more posteriorly. However, BÖHM (1931b) has observed heteromorphic chains in which both types occurred (his figure is repeated in SCHILLER 1936). In view of the structural resemblances to *C. humile* it is interesting that they are also similar in distribution. Because of the distributional features below, STEIDINGER & WILLIAMS' (1970) tentative attribution of their specimen to this taxon (which seems possible) is of great interest.

Stations: 14, 16, 20, 21, 28, 29, 34, 36, 38, 39, 42, 43, 47, 49, 50, 87, 283, 284, 287.

Although considered rare it occurred relatively frequently in the eastern Bay of Bengal -- Andaman Sea area and at three stations in the Arabian Sea.

This appears to be an Indo-Pacific species, not having been recorded from the Atlantic Ocean or the Mediterranean Sea. If STEIDINGER & WILLIAMS' (1970) specimen is this taxon it would be a first record for the Atlantic Ocean. It has a high stenothermal, neritic distribution but the above distribution indicates more flexibility in its salinity response. SUKHANOVA's (1962b), SOURNIA's (1968a, 1970), SUBRAHMANYAN's (1968) and ANGOT's (1970) records need to be added to those listed by WOOD (1963a). Although not recorded in the literature from the eastern Pacific Ocean BALECH has found the species to be abundant on the coast of southern California (pers. comm. to A. SOURNIA).

Section Macroceras OSTENFELD

Ceratium carriense GOURRET Plate 20, Fig. 200

CANDEIAS 1930:37, t. 3, f. 77; PETERS 1932:50, t. 2, f. 10h; STEEMANN NIELSEN 1934:26, f. 64; SCHILLER 1936:425, f. 464 a, b, 465, 466 b vix a; NIE 1936:65, f. 30 A–C; RAMPI 1939a:310, f. 35, 37; GRAHAM et BRONIKOVSKY 1944:39, f. 22 A; MARGALEF 1948a:21, f. 3, 7, 8, 9; MARGALEF et DURÁN 1953:42, f. 12 1; WOOD 1954:308, f. 236 a, b; SILVA 1955:172, t. 9, f. 5–8; TRÉGOUBOFF et ROSE 1957:116, t. 26, f. 16; HALIM 1960a, t. 5, f. 11; – 1963:499; TAYLOR 1967:102, t. 49, f. 12, 13, t. 50, f. 1; SOURNIA 1968a:469; SUBRAHMANYAN 1968:77, f. 143, 144, t. 7, f. 36; WOOD 1968:25, f. 46; STEIDINGER et WILLIAMS 1970:44, t. 5, f. 13 a, b, 14 a, b.

This species is very similar to *C. massiliense* and may, in fact, be conspecific although most previous authors have kept them separate. (REINECKE 1973b has reduced *C. carriense* to varietal status on the basis of polar co-ordinate data regarding the horns.) It has been separated by the widely spread antapical horns, greater than 60° from apical horn. In the var. *volans* (CLEVE) JÖRGENSEN the antapical horns are very slender, long, and the angle with the apical horn approaches 90°. Generally the posterior profile of the cell body appears more indented than in *C. massiliense* because of a short posterior deflection of the proximal region of the left antapical horn (in addition to the posteriorly-deflected base of the right antapical horn) but, as evident on plate 20, this character, although constant for *C. carriense,* is not always a reliable distinction. Similarly, distinctions based on cell body shape are not reliable.

Only the var. *carriense* was recognised in the "Anton Bruun" material although many tended towards the var. *volans.*

Stations: 42, 64, 87, 95, 96, 99, 114, 115, 117, 125, 129, 134, 150, 153, 154, 294, 313, 315, 325, 326, 335, 341, 347, 358, 370, 399, 415, 417.

This distribution is intriguing in that, with the exception of a few stations in the Bay of Bengal, the species occurred predominantly in two latitudinal belts, one between 5 °S to 5 °N and the other between 20° and 30 °S. This pattern suggests that it was largely absent from the westward-flowing South Equatorial Current but was present in its eastward-flowing returns. The southern limit of approximately 30 °S in the central area accords with other authors' observations that the species is less thermotolerant than *C. massiliense.* However, like it, *C. carriense* appears to be an inter-oceanic, surface species (STEEMANN NIELSEN 1934, GRAHAM et BRONIKOVSKY 1944). It has been recorded from the Indian Ocean quite frequently (cf. WOOD 1963a plus the references of SILVA 1956a, SUKHANOVA 1962 a, b, TSURUTA 1963, DURAIRATNAM 1964, SOURNIA 1966a, 1968 a, b, 1970, TAYLOR 1967, NEL 1968, SUBRAHMANYAN 1968, THORRINGTON-SMITH 1969, and REINECKE 1973b).

Ceratium contrarium (GOURRET) PAVILLARD Plate 21, Fig. 213

CANDEIAS 1930:37, t. 4, f. 78; PETERS 1932:50, t. 2, f. 10c; STEEMANN NIELSEN 1934:77, f. 67; GRAHAM et BRONIKOVSKY 1944:40, f. 22 E, 24 A, B; MARGALEF 1948b:49, f. 2h; SILVA 1949:361, t. 9, f. 12; MARGALEF 1957a:47, f. 3f; TRÉGOUBOFF et ROSE 1957:116, t. 26, f. 18; HALIM 1960a, t. 5, f. 14; HALIM 1963:499, f. 30; SOURNIA 1968a:473, f. 90; WOOD 1968:26, f. 49; HERMOSILLA 1973a:26, t. 2, f. 17.

Syn.: . . . . *C. tricboceros* var. *contrarium* (GOURRET) SCHILLER 1936:431, f. 471, (et f. 470 sub *C. tricboceros*); WOOD 1954:311, f. 239c (non b); SUBRAHMANYAN 1968:82, f. 148 (et f. 147 sub *C. tricboceros*); REINECKE 1973b:365, f. 22 G–K, f. 24 A–E.

Several authors have followed SCHILLER's (1936) proposal that this taxon should be united with *C. tricboceros* (EHRENBERG) KOFOID. However, others (most recently SOURNIA 1968a), have kept them distinct. The distinction is based primarily on the antapical horn arrangement. In *C. contrarium* the proximal parts of the antapical horns and particularly the left horn, are directed more posteriorly than in *C. tricboceros* and the distal regions proceed in a constantly divergent manner after they bend anteriorly. In *C. tricboceros* the distal horn regions run subparallel to each other. REINECKE (1973b) indicated that the girdle transdiameter of the latter is less than 45 µm. In both taxa the antapical horns commonly exhibit undulations. In addition, SOURNIA has drawn attention to the larger cell body and the continuation of the proximal part of the left horn in the same plane as the posterior profile of the cell body. He found that the flexure of the right horn occurred nearer the cell body than the left horn. Unfortunately the specimens illustrated here (pl. 21, fig. 210, 213) do not support SOURNIA's observations other than the presence of a larger cell body in *C. contrarium,* demonstrating that intermediates between the two species may exist in cell body features and REINECKE's data also suggests the varietal separation is probably more appropriate.

Stations: 39, 41, 42, 46, 65, 72, 87, 287, 288, 293, 311.

It occurred at scattered stations in both the northern and southern regions. Although it was moderately abundant at st. 41 near the Irrawaddy delta it also occurred at 35 °S (cruise V, April 1963) on one occasion. This occurrence at a cool southerly station agrees with GRAHAM et BRONIKOVSKY's (1944) observations in the Pacific Ocean where the species, although thermophilic, tolerated lower tempertures than in the Atlantic Ocean. It is considered to be a surface species (above 50 m).

Records are probably confused due to the resemblance of the species to *C. trichoceros* but as indicated above, this may not matter. Indian Ocean records other than those listed by WOOD (1963a) are: SILVA (1956a, 1960), SUKHANOVA (1962 a, b – var. *contrarium*), TSURUTA (1963 as the synonymous *C. inflexum*), DURAIRATNAM (1964 – var. *contrarium*), SOURNIA (1966a – var. *contrarium*, 1968a, b, 1970), SUBRAHMANYAN (1968), and REINECKE (1973b).

Ceratium deflexum (KOFOID) JÖRGENSEN Plate 20, Fig. 197

STEEMANN NIELSEN 1934:25, f. 63; SCHILLER 1936:428, f. 467 a non b; NIE 1936:63, f. 29 A, B; GRAHAM et BRONIKOVSKY 1944:39, f. 22 C, D; WOOD 1954:310, f. 237; KATO 1957:19, t. 7, f. 25; TORIUMI 1964:25, t. 3, f. 14; YAMAJI 1966:101, t. 49, f. 3; SOURNIA 1968a: 464, f. 86; SUBRAHMANYAN 1968:78, f. 145 non 146; WOOD 1968:27, f. 51; RICARD 1970, t. 2, f. a; REINECKE 1973b:303, f. 7 A–L, f. 8 A, B, f. 12 I, L, f. 14 C.

This is usually distinctive, with antapical horns which are directed first posteriorly and then both curving ventrally. KOFOID (1907a) and PETERS (1932) have included the species with *C. macroceros* and *C. massiliense* respectively, because of resemblance of the proximal portions of the horns and body shape, but the strong ventral bend of the horns is usually sufficient to separate the species, REINECKE (1973b) considers that some specimens formerly assigned to *C. macroceros* may be members of this species with weak ventral deflection of the antapical horns (e.g. that of OSTENFELD & SCHMIDT 1901). In ventral view the antapical horns may appear to diverge or to run parallel. BÖHM (1931a) has figured a continuous variability between these two conditions, REINECKE (1973b) recognising forms on this basis, the divergent condition being termed the f. *deflectomassum* REINECKE.

Stations: 14, 28, 29, 39, 47, 53, 65, 69, 71, 88, 90, 92, 93, 99, 100, 102, 112, 113, 116, 147, 290, 293, 313, 314, 317, 320, 406, 411, 412, 416,

The species was present at a few stations, all north of 30 °S. It was only fairly widespread during cruise V. It is a rare, warm, interoceanic species and appears to be relatively stenothermal. It has been found to be a surface species (GRAHAM & BRONIKOVSKY 1944). There are relatively few Indian Ocean records. In addition to those listed by WOOD (1963a) there are those of SUKHANOVA (1962 a, b), TSURUTA (1963), DURAIRATNAM (1964), SOURNIA (1968a, 1970), SUBRAHMANYAN (1968), and REINECKE (1973b).

Ceratium hexacanthum GOURRET Plate 22, Figs. 214, 215, 219

CANDEIAS 1930:39, t. 4, f. 82; PETERS 1932:54, t. 2, f. 10a, 11b; STEEMANN NIELSEN 1934:29, f. 73; SCHILLER 1936:421, f. 462 a–c; RAMPI 1939a:308, f. 44; – 1939c:111, f. 13; – 1942:227, f. 7, 10, 11, 12; GRAHAM et BRONIKOVSKY 1944:44, f. 27 F, G; MARGALEF 1946:94, f. III 3–6; SILVA 1949:362, t. 7, f. 9, 10, t. 9, f. 14; KISSELEV 1950:254, f. 438; MARGALEF et DURÁN 1953:42, f. 10u; WOOD 1954:306, f. 234 a, b; TRÉGOUBOFF et ROSE 1957:116, t. 26, f. 13, 14; HALIM 1960a, t. 4, f. 17; – 1963:499, f. 35; KLEMENT 1964:357, t. 3, f. 6; MARGALEF et HERRERA 1964:62; DAVIS 1965:1, f. I–IV; SOURNIA 1968a:484, f. 98; SUBRAHMANYAN 1968:72, f. 140–142; WOOD 1968:31, f. 63; STEIDINGER et WILLIAMS 1970:45, t. 9, f. 23 a–c.

This species is striking in appearance. It is most similar to *C. obesum* PAVILLARD but it has different horn dispositions (see notes under the latter species) and the cell body is usually strongly reticulated.

The var. *hexacanthum* forma *hexacanthum* is characterised by a left antapical horn which is directed anteriorly, not curled proximally into a spiral, not directed ventrally for any great distance, and therefore not appearing to cross in front of the apical horn when seen from the ventral side. Here the variety is illustrated by an autotomised form (fig. 214; similar to that figured by PETERS 1932, f. 11b).

The forma *spirale* (KOFOID) SCHILLER is a modification of the preceeding taxon in which the distal region of the left antapical horn is coiled spirally (fig. 215). GRAHAM & BRONIKOVSKY (1944) saw no value in recognising such forms but their recurrent characteristic development suggests that this phenomenon may have value as an indicator of some as yet unknown internal or external factor.

Another variant which can be recognised is the var. *contortum* LEMMERMANN, in which the antapical horns are long but not coiled, the right horn passing to the left side, well to the dorsal side of the cell, and the left horn directed strongly towards the ventral side and to the right (f. 219). GRAHAM & BRONIKOVSKY (1944) have illustrated a chain of such individuals. JÖRGENSEN (1920) has excluded KARSTEN's (1906) specimens from this variety. The forma *hiemale* (PAVILLARD)

JÖRGENSEN is a winter form of the var. *contortum*, the horns being much shorter and set closer to the body. It was not found in the "Anton Bruun" material.

The var. *aestuarium* (SCHRÖDER) JÖRGENSEN has subparallel, apically-directed antapical horns, with reduced reticulation on the body.

Other infraspecific taxa recognised are the var. *karstenii* PAVILLARD and the forma *pavillardii* (RAMPI) SOURNIA (= *C. aestuarium* var. *pavillardii* RAMPI 1939a).

REINECKE (1973a) believes that this taxon is sufficiently distinct from others of the section Macroceras to warrant recognition within the separate section Reticulata (JÖRG.) BÖHM.

Stations: var. *hexacanthum* forma *hexacanthum*: 17, 52, 56, 57, 99, 361, 375.
var. *hexacanthum* forma *spirale*: 43.
var. *contortum*: 59, 71, 97, 130, 135, 144, 287, 294.

The species was very widely scattered but not common, ranging from lower salinity Andaman Sea waters to high salinity Gulf of Aden waters. The occurrence was too sporadic to draw conclusions other than its apparent preference for higher temperatures. It occurred furthest south at st. 130 (34 °S) during cruise II.

It has usually been considered an inter-oceanic thermophilic species found in water above 20 °C but it is sometimes tolerant of colder conditions in the North Atlantic Ocean (GRAHAM & BRONIKOVSKY 1944). STEEMANN NIELSEN (1934) found that it occurred closer to the surface in samples rich in plankton (upwelling?) but was deeper, below 100 m, at stations poorer in plankton. GRAHAM & BRONIKOVSKY (1944) could not confirm this observation with the "Carnegie" material.

Many references require being added to those listed by WOOD (1963a): SILVA (1956a, 1960); SUKHANOVA (1962b), TSURUTA (1963, as *C. reticulatum*), DURAIRATNAM (1964, both as the species and its synonym *C. reticulatum*), SOURNIA (1966a, 1968a, b, 1970) TAYLOR (1967), NEL (1968), and SUBRAHMANYAN (1968).

Ceratium horridum (CLEVE) GRAN Plate 20, Fig. 202, Plate 21, Figs. 203–208, 211, 212

CANDEIAS 1930:38, t. 4, f. 79–81 a; SCHILLER 1936:413, f. 455 a–c; GRAHAM et BRONIKOVSKY 1944:42, f. 23 I–L, 24 C–I, 25 A–G; MARGALEF 1948b:49, f. 2 i; SILVA 1949:362, t. 7, f. 5, 6, 7, 8, t. 9, f. 19; KISSELEV 1950:253, f. 50, 430; MARGALEF et DURÁN 1953:42, f. 12 g–k; WOOD 1954:300, f. 230 a, b; HERRERA, MUÑOZ et MARGALEF 1955:18, f. 1 K; KATO 1957:17, t. 5, f. 14; HALIM 1960a, t. 5, f. 10; – 1963:499, f. 32; TAYLOR 1967, t. 93, f. 54; SOURNIA 1968a:474, f. 91–95; SUBRAHMANYAN 1968:63, f. 113, 115–122, vix 114 (SCHILLER emend.); WOOD 1968:32, f. 65; MARGALEF 1969a, f. 5 D.

Vix WAILES 1928, t. 1, f. 1; – 1939:45, f. 136.

Syn.: .... *C. buceros* ZACHARIAS .... SCHILLER 1936:415, f. 456 a–e, 457 a–c; MARGALEF, HERRERA, RODRIGUEZ-RODA et LARRAÑETA 1954:92, f. 3 b; HERRERA, MUÑOZ et MARGALEF 1955:18, f. 1 H, I, J; WOOD 1968:24, f. 43; MARGALEF 1969a, f. 5 C; STEIDINGER et WILLIAMS 1970:44, t. 4, f. 12.
C. claviger KOFOID .... STEEMANN NIELSEN 1934:28, f. 70; YAMAJI 1966:104, t. 50, f. 9.
C. intermedium (JÖRGENSEN) JÖRGENSEN .... WANG et NIE 1932:300, f. 13; WANG 1936:163, f. 31; SILVA et PINTO 1948:172, t. 2, f. 14; YAMAJI 1966:104, t. 50, f. 8.
C. mollis KOFOID .... STEEMANN NIELSEN 1934:28, f. 71, WANG 1936:162, f. 30 (sub *C. molle*); YAMAJI 1966:104, t. 50, f. 10.
C. tenue OSTENFELD et SCHMIDT .... STEEMANN NIELSEN 1934:28, f. 69; NIE 1936:71, f. 34; GRAHAM et BRONIKOVSKY 1944: 43, f. 26 C–D; YAMAJI 1966:103, t. 50, f. 4, 5, 6; REINECKE 1973b:342, f. 18 A–H, 19 A–K, 20 A–F.

This small species encompasses a great deal of variability. It was first fully assembled and sorted out by JÖRGENSEN (1920) and its taxonomic history is summarised by SOURNIA (1968a). VON STOSCH (1964) has observed an instance of sexual conjugation involving anisogametes in this species, the male conjugant resembling a small member of the subgenus *Ceratium*. The following are the main infraspecific taxa, treated as varieties in a similar manner to GRAHAM & BRONIKOVSKY (1944, who, however, recognised *C. tenue* as a separate species):

The var. *horridum*, so-named because it includes the type specimen, is relatively robust with antapical horns only moderately divergent or subparallel. The horns are shorter than in the other varieties.

The var. *claviger* (KOFOID) GRAHAM et BRONIKOVSKY is distinctive because of the small terminal inflated regions present on elongate, subparallel antapical horns (SOURNIA has termed this a *forma*, implying a solely phenotypic modification). Very small terminal inflations have also been seen in the var. *tenue* and var. *denticulatum*.

The var. *molle* (KOFOID) GRAHAM et BRONIKOVSKY is very similar to the preceding variety and perhaps should not be distinguished from it except at the level of a forma. It lacks the terminal inflations, possibly due to autotomy.

The var. *inclinatum* (KOFOID) stat. et comb. n. [= *C. inclinatum* KOFOID, *C. tenue* f. *inclinatum*] is a long-horned, delicate variety with a distinctive antapical horn configuration. They bend outwards at first and then bend somewhat abruptly to become subparallel in the apical plane, this change of direction occurring well above the cell body.

The var. *tenue* (OSTENFELD et SCHMIDT) stat. nov. is a slender, long-horned variety, similar to the preceding but lacking the angular mid-bends of the antapical horns. Perhaps the taxon *inclinatum* could be considered a form of this variety but the necessary information for this decision is lacking. BÖHM (1931b) interpreted the var. *inclinatum* quite differently, basing it on body features, his specimens having short horns. If the taxon *tenue* is regarded as a separate species (e.g. REINECKE 1973b) it has priority over *C. buceros* although most earlier authors have not recognised this fact.

The var. *patentissimum* (OSTENFELD et SCHMIDT) stat. et comb. nov. [basionym *C. patentissimum* OSTENFELD et SCHMIDT 1901:168, f. 22; also = *C. tenuissimum* KOFOID] has the antapical horn very widespread, almost at 90 ° to the apical horn, and thus resembles *C. carriense* from which it is distinguished by being smaller, lacking a proximal ventrally-directed region on the right antapical horn, and having a small spine arising at the base of the left horn (as do other members of *C. horridum*).

Finally, the var. *denticulatum* JÖRGENSEN can be recognised by its moderately widespread antapical horns with moderately extensive denticulations on the under sides of the flexure of the horns (fig. 202). In many respects it resembles a small *C. carriense*, emphasised by its position on plate 20.

Stations: var. *horridum*: 16, 19, 20, 27, 30, 32, 35, 36, 38, 42, 44, 53, 54, 56, 60, 63, 64, 67, 70, 71, 91, 92, 97, 99, 100–103, 109, 112–114, 147, 150, 286, 297, 308, 324, 327.
var. *claviger*: 63, 282, 298, 370, 417.
var. *molle*: 60, 67, 70–72, 93, 99, 100, 103, 104, 142, 324.
var. *inclinatum*: 327.
var. *tenue*: 16, 50, 63, 72, 89, 93, 96, 98, 101, 108, 129, 131, 132, 134, 153, 160, 291, 294, 296, 310, 312, 323, 325–327.
var. *patentissimum*: 113, 147, 150, 298, 301, 302, 305, 318, 328, 342.
var. *denticulatum*: 91, 101, 113, 294, 312–314, 319, 320, 324–326, 334, 341, 360, 374, 396, 410, 411, 412, 414.

The var. *horridum* had a predominantly northern distribution, only one occurrence being south of 12 °S and that at an extreme southern station (308). It was abundant at st. 99 in the southern Bay of Bengal.

The second most abundant variety, the var. *tenue*, was more widespread, six stations being south of 30 °S in the central area. The var. *molle* and the var. *claviger* occurred at scattered stations. The var. *claviger* was the only representative of the species to occur west of Madagascar. The latter pair of varieties did not co-occur at any stations.

The var. *denticulatum* was also fairly common, mostly in the central Indian Ocean on cruise V and at near-shore localities off the east coast of Africa and the west coast of Madagascar.

The var. *patentissimum* occurred at scattered stations in the central Indian Ocean from 20 °N to 30 °S. It did not co-occur with the var. *tenue*.

The var. *inclinatum* was found at only one station to the south of India.

Both the var. *horridum* and the var. *tenue* have been reported as relatively oligophotic, preferentially occurring at deeper levels to 100 m or more (GRAHAM & BRONIKOVSKY 1944). The species is considered to be inter-oceanic and tropical to subtropical although the var. *horridum* is considered to be more thermotolerant (SOURNIA 1968a).

The following Indian Ocean records (including synonymous records) should be added to those listed by WOOD (1963a): SILVA (1956a, 1960), SUKHANOVA (1962b), TSURUTA (1963), DURAIRATNAM (1964), SOURNIA (1966a, 1968 a, b, 1970), TAYLOR (1967), NEL (1968), SUBRAHMANYAN (1968), THORRINGTON-SMITH (1969), and REINECKE (1973b).

Ceratium macroceros (EHRENBERG) VANHÖFFEN Plate 20, Figs. 198, 199; Plate 22, Fig. 218

CANDEIAS 1930:35, t. 4, f. 75; WANG 1932, f. 29; PETERS 1932:47, t. 4, f. 17b; STEEMANN NIELSEN 1934:25, f. 59; SCHILLER 1936:428, f. 468 a–d; NIE 1936:62, f. 28 A, B; WAILES 1939:45, f. 137; WANG 1936:160, f. 29; RAMPI 1939a:310, f. 42; GRAHAM et BRONIKOVSKY 1944:37, f. 21 B–F; SILVA 1949:360, t. 7, f. 2, t. 9, f. 11; – 1952b, t. 6, f. 11; KISSELEV 1950:254, f. 63 e.p. 422; MARGALEF 1951:57, f. 2 e, f; MARGALEF et DURÁN 1953:42, f. 12 a–f; WOOD 1954:310, f. 238 a, b; TRÉGOUBOFF et ROSE 1957, t. 26, f. 17; KATO 1957:18, t. 7, f. 23; HALIM 1960, t. 4, f. 6, t. 5, f. 7; – 1963:498, f. 27; BALLANTINE 1961:225, f. 56; KLEMENT 1964:357, t. 3, f. 1; YAMAJI 1966:100, t. 48, f. 12, 13; SOURNIA 1968a:460, f. 83–85; SUBRAHMANYAN 1968:79, f. 149–151; WOOD 1968:36, f. 77; STEIDINGER et WILLIAMS 1970:46, t. 11, f. 29 a, b; RICARD 1970, t. 2, f. c; REINECKE 1973b:281, f. 1 A–F, f. 2 A–E, f. 3 A–F, f. 12 M.
[CUESTA 1919, t. 52 (f. 1), A–C, SCHILLER 1936 praetermissavit.]
Non CURL 1959:306, f. 118 (= *C. horridum*).
Syn.: *C. gallicum* KOFOID . . . . WOOD 1968:59, f. 59.

Although several of the species in the section Macroceras have a right antapical horn which is strongly directed towards the posterior for a distance of nearly a body length before curving anteriorly, only *D. deflexum* also has the left antapical horn similarly directed and in the latter case it is easily distinguished by both antapical horns also being strongly ventral in their deflection. REINECKE (1973b) has provided a more detailed account of the distinction of the species.

The species is recognised in two main varieties which also tend to have geographic distinction (see distribution below): the var. *macroceros* is a robust variety with a heavily developed theca of large size (girdle diameter exceeding 60 µm and occasionally 100 µm) and less abrupt antapical horn flexure (f. 218); and the var. *gallicum* (KOFOID) SOURNIA [= subsp. *gallicum* (KOFOID) JÖRGENSEN] which is much more delicate with a smaller body size, slender horns abruptly curved, and often a somewhat angular left body profile (f. 199). A posterior accessory list is often well developed in association with the base of the left antapical horn. The designation of variety was used before SOURNIA by both PETERS (1932) and SCHILLER (1936). However, both of the latter attributed the variety incorrectly to others.

Autonomy is common in this species. PETERS (in SCHILLER 1936, and KISSELEV 1950) has found heteromorphic chains, some anterior members of which have very short antapical horns with no reflexed portions (thus resembling the section *Biceratium*). Incomplete girdle development has also been seen (f. 199).

Stations: var. *macroceros*: 302, 306, 311, 323.
var. *gallicum*: 15, 17, 21, 34, 50, 51, 58–60, 62, 63, 65, 66, 69, 70, 88, 89, 91–95, 98–100, 102, 104, 108, 109, 114, 125, 129, 130, 132, 134, 135, 141, 142, 150, 154, 157, 161, 162, 285, 287, 293–295, 298, 299, 301, 302, 312–315, 317–319, 322, 325, 327, 342, 347, 348, 355, 358, 360, 362, 370, 371, 416, 419.

In accord with authors such as PETERS (1932), STEEMANN NIELSEN (1934, 1939a), and GRAHAM & BRONIKOVSKY (1944) who have studied large areas of the major oceans it was found that the var. *gallicum* not only predominated over the var. *macroceros* but was also one of the commonest taxa in the material from tropical and subtropical areas. Together with *C. euarcuatum, C. contortum, C. paradoxides,* and others it could be used as a general indication of the southern limit of moderately eurythermal species in the Indian Ocean. Also in common with many it was notably absent from most of the Mozambique Channel stations, occurring only to the north and south of the Channel.

The var. *macroceros* had a much more limited distribution. Two of the four stations were below the warm temperature boundary indicated by the var. *gallicum*, but two other records (including the specimen illustrated) were from stations further north. In fact, station 323 is not far from the equator. This distribution partially confirms views that the variety is a cooler water representative but it may also co-occur with the var. *gallicum* (as at st. 302). The species has been found by other authors (STEEMANN NIELSEN 1934, GRAHAM & BRONIKOVSKY 1944) to occur predominantly above 100 m depth. REINECKE (1973b) has discussed the correlation of phenotypes with environmental conditions.

Indian Ocean records: Many listed by WOOD (1963a) plus those of SILVA (1956a, 1960), TSURUTA (1963), DURAIRATNAM (1964), ANGOT (1965), SOURNIA (1966a, 1968 a, b, 1970), TAYLOR (1967), NEL (1968), SUBRAHMANYAN (1968), THORRINGTON-SMITH (1969), and REINECKE (1973b).

Ceratium massiliense (GOURRET) KARSTEN Plate 20, Figs. 193–196.

CANDEIAS 1930:36, t. 3, f. 76; PETERS 1932:50, t. 1, f. 2 a, b, t. 2, f. 10 f, t. 3, f. 16 a; WANG et NIE 1932:301, f. 14; STEEMANN NIELSEN 1934:25, f. 60–62; SCHILLER 1936:422, f. 463 a–d; RAMPI 1939a:308, f. 32, 33, 40; GRAHAM et BRONIKOVSKY 1944:38, f. 22 F, I–L (vix G, non H); MARGALEF 1946, f. III 2; SILVA 1949:361, t. 7, f. 3; MARGALEF et DURÁN 1953:42, f. 12 m–r; WOOD 1954:306, f. 235 a–c; MARGALEF 1957a:48, f. 3 g; TRÉGOUBOFF et ROSE 1957:116, t. 26, f. 15; KATO 1957:18, t. 6, f. 18, 20; CURL 1959:306, f. 117; HALIM 1960a, t. 5, f. 15; – 1963:498, f. 28, 29; MARGALEF 1961a:81, f. 26 h; KLEMENT 1964:357, t. 3, f. 2; YAMAJI 1966:104, t. 50, f. 11, 12, 13; TAYLOR 1967, t. 91, f. 39; SOURNIA 1968a:465, f. 87, 88; SUBRAHMANYAN 1968:74, t. 4, f. 23, t. 7, f. 34, 35; TORIUMI 1968:3, f. 5, 8, 9; WOOD 1968:36, f. 78; STEIDINGER et WILLIAMS 1970:46, t. 11, f. 30 a, b, t. 12, f. 30 c–e; AVARIA 1970, t. 3, f. 6; HERMOSILLA 1973b:64, t. 33, f. 3, 4; TAYLOR 1973b, f. 4 b; REINECKE 1973a, f. 6 E; – 1973b:315, f. 12 A–H, J, K, f. 13 D, E, f. 14 A, B, f. 15 A–E, vix f. 13 F–H, non fig. 16 A–G.

The confusion concerning the correct name for this common warm-water taxon has been outlined by JÖRGENSEN (1920) and REINECKE (1973b). SOURNIA (1968a) considered JÖRGENSEN's (1911) combination as the first legal establishment of *C. massiliense* but REINECKE has convincingly argued in favour of attributing it to KARSTEN (1906), this also avoiding some difficulties of priority which would otherwise go to SCHRÖDER's (1906) species names.

The species shows resemblances to *C. horridum* (which is much smaller), *C. deflexum* (in which the left antapical horn is strongly posteriorly directed in its proximal region like *C. macroceros*), and *C. carriense* (see comments under that taxon), the latter having been combined with it by REINECKE (1973b, as a variety).

Three main infraspecific taxa were recognised by SOURNIA but only two are used here:

The var. *massiliense* [= var. α *macroceroides* (KARSTEN) JÖRGENSEN] has relatively slender horns and, apart from the occasional presence of small fins near the base of the apical horn and small spines on the posterior proximal regions of the antapical horns, it is not strongly ornamented. The proximal region of the left antapical horn usually curves slightly to the posterior before bending anteriorly (f. 196), but not always (f. 194).

The var. *armatum* (KARSTEN) JÖRGENSEN, including the var. *protuberans* (KARSTEN) JÖRGENSEN, has more robust horns and cell body. Fins are usually (f. 193), but not invariably (f. 195) developed on the proximal contours of the apical horn and can also be present on the upper curves of the antapical horns. The antapical spinulae on the horns are somewhat stronger. The proximal region of the left antapical horn is only slightly bent to the posterior after leaving the cell body before curving anteriorly. The cell body is usually more convex than in the var. *massiliense.*

The var. *protuberans* has been recognised in the past as being smaller and lacking fins on the apical horn and upper antapical horn profiles. These horn features agree with the specimen illustrated here as fig. 195. However, this specimen was not notably smaller than the other varieties. Furthermore, the var. *protuberans* is presumed to have longer horns than the var. *armatum,* whereas this specimen did not (compare to f. 193). Because of the contradictions posed by this and other specimens, the taxon is not recognised here.

SOURNIA (1968a) relegated the var. *armatum* to a forma, using JÖRGENSEN's (1920) combination. This may be a reasonable action in view of the apparent cooler temperature preference of the taxon.

Stations: var. *massiliense*: 18, 20, 21, 23, 28, 30, 37–39, 41, 42, 47, 48, 50, 51, 53, 59, 60, 62, 63, 68, 69, 85, 91, 95, 98–101, 103, 106, 112, 116, 125, 140, 144, 150, 153, 161, 284, 287, 291, 293, 294, 298, 301, 302, 305, 306, 312–315, 318, 320, 325, 327, 362, 371, 406, 413, 415, 418, 419.
var. *armatum*: 87, 131, 134, 147, 310.

The var. *massiliense* was one of the most widely spread taxa in the material. The limits of its southern distribution closely resembled those of *C. tricboceros,* exhibiting large north-south fluctuations.

The var. *armatum* was less common and, from the above stations, appeared to occur in both warm and colder waters. However, if a distinction is made between specimens with the outward deflected antapical horn with fins (f. 193) versus those with an incurving antapical horn (f. 195) an interesting distribution emerges. The former, which could be designated a warm-water form, occurred at a few scattered stations (87, 134, 147) not south of 28 °S. The latter was confined to two extreme southern stations (131, 310) near the Subtropical Convergence Region.

Both varieties are considered inter-oceanic and the var. *massiliense* is one of the commonest taxa in tropical and subtropical waters. TAYLOR (ms. 1964, 1967) found it to be the commonest representative of *Ceratium* in the southwest Indian Ocean. The var. *armatum* has been found in cold temperate waters by several authors (JÖRGENSEN 1911, PETERS 1932, etc.). The species is considered to have a surface distribution (GRAHAM & BRONIKOVSKY 1944).

The species has been recorded from the Indian Ocean by many authors, usually as the var. *massiliense* (var. *macroceroides*). The following should be added to those listed by WOOD (1963a): SILVA (1956a, 1960), SUKHANOVA (1962 a, b), ZERNOVA (1962), TSURUTA (1963), DURAIRATNAM (1963, 1964), ZERNOVA & IVANOV (1964), ANGOT (1965), SOURNIA (1966a, 1968 a, b, 1970), TAYLOR (1967), SUBRAHMANYAN (1968), NEL (1968), ANGOT (1970), and REINECKE (1973b).

Ceratium obesum PAVILLARD   Plate 22, Figs. 216, 217

– 1930:10, f. 11; – 1931:95, t. 3, f. 11 A, B.

This rare species has apparently not been seen previously other than by its discoverer, and it was omitted from the works of SCHILLER, and SUBRAHMANYAN (1968). It resembles *C. bexacanthum* (to which it was appended by SOURNIA 1968a) but it has a robust body lacking any surface reticulation and the apical horn is strongly deflected towards the ventral side. PAVILLARD's figures show a slender body shape which results partly from distortion arising from the angle at which the species usually rests on the slide, the ventral flexure of the apical horn making that structure look shorter than it is. These spatial relationships, including the ventrally-curved left horn, are illustrated by the multiple views given here.

Station: 294.

Several specimens were found at only one station immediately to the north of the Seychelles Bank.

The only previous records of the species are from the vicinity of the Azores in the North Atlantic and Monaco in the Mediterranean.

Ceratium recurvatum SCHRÖDER   Plate 21, Fig. 209

– 1906:367, f. 40.

Syn.: *C. deflexum* var. *recurvatum* (SCHRÖDER) JÖRGENSEN 1911:65, f. 139; SCHILLER 1936:428, f. 467b; SUBRAHMANYAN 1968, f. 146.

The "Anton Bruun" specimens of this very rare species did not resemble *C. deflexum* at all, although JÖRGENSEN (1911) assigned this species to *C. deflexum* at the varietal level (after a re-examination of SCHRÖDER's samples). In fact, as can be seen from fig. 209, there was a marked resemblance in the body shape and the formation of the right antapical horn to *C. trichoceros* and *C. contrarium*. Perhaps this taxon is a conglomerate of several species exhibiting a particular type of horn aberration. All the "Anton Bruun" specimens resembled fig. 209. It is distinctive in being the only taxon in the section Macroceros in which the left antapical horn proceeds posteriorly (and ventrally), and then turns to the right distally.

All the figures by other authors are reproductions of SCHRÖDER's original figure.

Stations: 338, 342, 413, 414, 417.

Single specimens were found at two equatorial stations on cruise VI and at three stations near northern Madagascar. This clustered distribution tends to negate the view that these are aberrant forms of one or more species.

The species was first described from the Arabian Sea (one cell) and does not appear to have been seen again, other than perhaps mistakenly by JÖRGENSEN (1911) from the same sample. KARSTEN (1907) referred to it but had not apparently seen it. This applies also to SUBRAHMANYAN (1968).

Ceratium trichoceros (EHRENBERG) KOFOID Plate 12, Fig. 117; Plate 21, Fig. 210

WANG et NIE 1932:303, f. 15; PETERS 1932:51, t. 1, f. 3 a–c, t. 2, f. 17a; STEEMANN NIELSEN 1934:27, f. 68; SCHILLER 1936:430 non f. 470 nec 471; NIE 1936:70, f. 33 A–C; RAMPI 1939a:310, f. 38, 39; GRAHAM et BRONIKOVSKY 1944:40, f. 22B; SILVA 1949:361, t. 7, f. 4 (sub *tricoceros*); WOOD 1954:311, f. 239 a, b, c (sub *C. macroceros* var. *contrarium*); KATO 1957:19, t. 6, f. a, b; CURL 1959:306, f. 122; HALIM 1960a, t. 5, f. 18; – 1963:499, f. 31; BALLANTINE 1961:225, f. 57; MARGALEF 1961a:81, f. 26i; KLEMENT 1964:358, t. 3, f. 8; TORIUMI 1964a:43, t. 2, f. 8; DAVIS et STEIDINGER 1966:1, f. 1–4; YAMAJI 1966:103, t. 50, f. 2; STEIDINGER, DAVIS et WILLIAMS 1967, t. 6, f. c; SOURNIA 1968a:472, vix f. 89 (= *C. ramakrishnii* SUBRAHMANYAN?); SUBRAHMANYAN 1968:81, t. 7, f. 37, non f. 147 nec 148; WOOD 1968:40, f. 91; MARGALEF 1969a, f. 5E; STEIDINGER et WILLIAMS 1970:47, t. 14, f. 36 a–d; REINECKE 1973b:353, f. 13 A–C, f. 22 A–F, f. 24 F–L (non 22 G–K, 24 A–E); TAYLOR 1973b, f. 4 a.
Vix MARGALEF et DURÁN 1953, f. 12f (sub *C. macroceros*); RICARD 1970, t. 2, f. b (*C. contrarium*?).

This large species resembles *C. contrarium* and the two may be conspecific variants as suggested by SCHILLER (1936) and REINECKE (1973b). The distinctions have been discussed here under *C. contrarium*. As indicated, SOURNIA's figure resembles the recently described *C. ramakrishnii* SUBRAHMANYAN (1968) with its domed, convex body shape contracted towards the base of the hypotheca. The type specimens had more inwardly curved horns but SUBRAHMANYAN's species is otherwise very similar to *C. trichoceros*.

STEIDINGER & WILLIAMS (1970) have observed a strong dimorphism in living cells, an anterior daughter cell resembling a member of the section Ceratium in having its slender, short antapical horns projecting directly backwards (their fig. 36c; here fig. 117). This form is very similar to *C. ehrenbergii* (pl. 12, f. 116) but the angle of the posterior cell body profile to the girdle plane is not as great. MARGALEF & DURÁN's (1953, f. 12f) specimen may also correspond to this form.

The formal recognition of the short-horned variant with both antapical horns directed posteriorly accords with the principles by which formae are here recognised (see Introductory section) and consequently it is named the forma *crypticum* f. nov.

In view of VON STOSCH's (1964) observations on sexuality in *C. horridum* it seems possible that this form may also be a "male" gamete prior to sexual conjugation, resembling the heteromorphism in *C. tripos* (which may also be associated with sexuality, VON STOSCH 1964).

Stations: forma *trichoceros*: 28, 31, 37–39, 41, 46, 48, 49, 56, 59, 62–64, 67–69, 71, 88, 90, 98–103, 115–117, 140, 284, 287, 294, 299, 301, 305, 306, 314, 315, 317–319, 324–326, 328, 331, 332, 342, 361, 362, 396, 405, 412, 413, 420.
forma *crypticum*: 47.

The distribution of this species is interesting not only in that it is one of more widely spread tropical species in the material but also because it achieved maximum numbers at the southern edge of the south equatorial current region (st. 318). A preference for equatorial waters has been commented on by GRAHAM & BRONIKOVSKY (1944) and SUKHANOVA (1962 a, b; see also TAYLOR 1973b). Its depth distribution is not clear. The species was strikingly absent from the central regions in the material from cruise III (August–September, 1963). On the other hand it was one of the few species of *Ceratium* present within the Mozambique Channel on cruise VIII (September–October, 1964), most species only occurring at stations at either end of the Channel. It also occurred at two southern stations (305, 306) below 30 °S.

Due to probable confusion with *C. contrarium*, records of this species are of doubtful value. The following authors have recorded it from the Indian Ocean (excluding those referring to *C. trichoceros* var. *contrarium*, although both are often listed together) other than those listed by WOOD (1963a): SILVA (1956a, 1960), ZERNOVA (1962), SUKHANOVA (1962 a, b) TSURUTA (1963), DURAIRATNAM

(1963, 1964), ZERNOVA & IVANOV (1964), ANGOT (1965), ANGOT & GÉRARD (1967), SOURNIA (1966a, 1968 a, b, 1970) TAYLOR (1967), SUBRAHMANYAN (1968), NEL (1968), THORRINGTON-SMITH (1969), ANGOT (1970), and REINECKE (1973b).

Ceratium vultur CLEVE Plate 20, Fig. 201? ; Plate 22, Figs. 220–224; Plate 40, Fig. 483, Plate 43, Fig. 511
PETERS 1932:54, t. 1, f. 7 a, b; STEEMANN NIELSEN 1934:27, f. 65, 66; SCHILLER 1936:418, f. 459, a, b, 460 a–c; GRAHAM et BRONIKOVSKY 1944:41, f. 23 A–H (vix C, G); WOOD 1954:304, f. 233 a; BALLANTINE 1961:225, f. 55; WOOD 1963c:16, f. 53; KLEMENT 1964:356, t. 2, f. 4; YAMAJI 1966:101, t. 49, f. 4–7; SOURNIA 1968a:480, f. 96, 97; SUBRAHMANYAN 1968:68, f. 131–133, t. 5, f. 27, 28, t. 6, f. 31 non f. 134; WOOD 1968:41, f. 94; STEIDINGER et WILLIAMS 1970:47, t. 15, f. 39, t. 41, f. 155; RICARD 1970, t. 2, f. d; REINECKE 1973a:58, f. 5 A–N, f. 6 A–D, F–H, L–R, f. 7 A–F, f. 8 A–E, f. 14 D.
Non WOOD 1963c:16, f. 53 (= *C. reflexum* CLEVE?).
Syn.: . . . . *C. sumatranum* (KARSTEN) JÖRGENSEN . . . . NIE 1936:68, f. 31, 32; YAMAJI 1966:102, t. 49, f. 8, 9.
C. recurvum (JÖRGENSEN) REINECKE 1973a:75, f. 6, J, f. 7 G.

Ceratium vultur is highly variable in form but is nevertheless recognisable in most of its variations. The apical horn of subapical members of chains is usually very short. SOURNIA (1968a) recognised four principal variations as formae. REINECKE (1973a) has provided a detailed description of the species, including many earlier figures. She has recognised two varieties and five forms. She has raised the f. *recurvum* to specific status, a practice not followed here, and considered *C. pavillardii* JÖRGENSEN to be a variety, following GRAHAM & BRONIKOVSKY (1944). The treatment here is based on simpler criteria than hers, the polar co-ordinate technique not being used at the time the analyses were made.

The var. *vultur* has a very short, antapically-directed basal portion of the left antapical horn before it is sharply bent towards the anterior. Forms within this variety are the forma *vultur*, with robust, long horns (not found in this material); the forma *sumatranum* (KARSTEN) SOURNIA in which the right antapical horn is directed almost laterally from the body (fig. 224, 201?) and which seems to intergrade with the f. *valdiviae* REINECKE; the forma *angulatum* (JÖRGENSEN) comb. nov. [basionym *C. sumatranum* forma *angulatum* JÖRGENSEN 1911, p. 74, f. 155] in which both the left and right horns turn abruptly towards the anterior shortly after leaving the body and the girdle ends are inclined at an angle to each other because of a dorsal flexure (fig. 222); and the forma *recurvum* (JÖRGENSEN) SCHILLER in which regrowth after autotomy is out of line with the original curve of the horns, bending sharply laterally (fig. 220).

The var. *japonicum* (SCHRÖDER) JÖRGENSEN has a left antapical horn which extends posteriorly for more than 0.5 of the girdle width before being bent sharply towards the anterior. It occurs in both robust (fig. 223, 483) and delicate (fig. 221) forms, not previously recognised at an infraspecific level. The robust form corresponds to that described as *C. robustum* by OSTENFELD et SCHMIDT (1901, p. 166, fig. 17) and so is here termed *C. vultur* var. *japonicum* forma *robustum* stat. nov. (basionym given above), the delicate form being the forma *japonicum*. REINECKE (1973a) has distinguished a f. *neglectum* from the latter on the basis of a differing curvature of the left antapical horn.

Stations: var. *vultur* – f. *sumatranum*: 15, 16, 19, 21, 29, 35, 41, 43, 50, 57, 59, 61, 92, 97, 100, 102, 103, 106, 112, 113, 294, 325, 327.
– f. *angulatum*: 52–54, 57, 59, 62, 64–66, 70, 87–91, 95, 98, 99.
– f. *recurvum*: 24, 47, 91, 101, 103, 116, 418.
var. *japonicum* – f. *robustum*: 13, 14, 23, 39, 41, 50, 109, 125, 134, 135, 147, 285, 288, 301, 334, 413.
– f. *japonicum*: 56, 91.

The species as a whole was widespread, but it was notably absent from the open ocean in the equatorial current regions (5 °S to almost 20 °S). The f. *angulatum* was entirely restricted to the Bay of Bengal, the f. *sumatranum* having a similar but wider distribution including a few open northern Indian Ocean stations.

It was the robust form of var. *japonicum* (and to a much lesser extent var. *vultur*) which represented the species in the wider oceanic areas, being absent from the equatorial current. No representative was found south of 30 °S although it has been found in the southwestern Indian Ocean by TAYLOR (1967) and NEL (1968).

This pattern corresponds with the view that the species is an intolerant thermophile (PETERS 1932; GRAHAM et BRONIKOVSKY 1944). It has been found to prefer deeper levels although it also occurs in surface water. There are many Indian Ocean records (WOOD 1963a) to which those of SUKHANOVA (1962b), TSURUTA (1963), DURAIRATNAM (1964), ANGOT (1965), SOURNIA (1966a, 1968a, b, 1970), TAYLOR (1967), NEL (1968), SUBRAHMANYAN (1968), and REINECKE (1973a) can be added.

Section Palmata (PAVILLARD) JÖRGENSEN

Ceratium ranipes CLEVE Plate 19, Figs. 189–192

CANDEIAS 1930:35, t. 4, f. 74; PETERS 1932:47, t. 2, f. 12 d, e; STEEMANN NIELSEN 1934:24, f. 58; SCHILLER 1936:409, f. 451 a, b; RAMPI 1939a:307, f. 2; GRAHAM et BRONIKOVSKY 1944:37, f. 19 I–K, 20, 21 A; WOOD 1954:299, f. 227; SILVA 1955:168, t. 9, f. 1; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 10; HALIM 1960a, t. 4, f. 16; – 1963:498, f. 26; KLEMENT 1964:356, t. 3, f. 3; LOPEZ 1966, f. 19, 20; SOURNIA 1968a:459, f. 81, 82; SUBRAHMANYAN 1968:60, f. 110; WOOD 1968:38, f. 84; STEIDINGER et WILLIAMS 1970:47, t. 13, f. 33.

Syn.: .... *C. palmatum* var. *ramipes* [sic].... NIE 1936:61, f. 27.

This species is highly distinctive, having unusual finger-like extensions which radiate from the ends of the antapical horns. GRAHAM & BRONIKOVSKY indicated that the number of fingers, when present, may range from three to twenty-one and can be unequal on the left versus right horn. The length of the fingers and the antapical horns is also variable. The presence of numerous chloroplasts within these extensions supports the view expressed by STEEMANN NIELSEN (1934) that these structures represent adaptations to shade conditions (see Discussion section).

Autotomy, by which the distal portions of the horns are cut off, was observed frequently in the "Anton Bruun" material (figs. 190–192), as were signs of regrowth (fig. 191). At such times there is a superficial resemblance to *C. platycorne* (see comments under the latter). Autotomised specimens have been recognised as the var. *furcellatum* (LEMMERMANN) BÖHM although, if recognised, the designation of forma would be more appropriate [*C. ranipes* var. *palmatum* (SCHRÖDER) CLEVE forma *furcellatum* (LEMMERMANN) stat. nov.; basionym *C. tripos* var. *furcellata* LEMMERMANN 1900:363].

Although variability is consequently considerable there still appear to be two distinguishable varieties which are, in a sense, analogous of the variants observed in members of the section Tripos such as *C. gibberum*. In the var. *ranipes* the horns are strongly incurved towards the body, the right horn in particular being also directed dorsally (e.g. fig. 192, BÖHM 1931b, f. 30 f, g; GRAHAM & BRONIKOVSKY 1944, figs. 19 I–K). In the var. *palmatum* (SCHRÖDER) CLEVE the horns are open and subparallel, both sloping towards the cell's left in contrast to the apical horn which slopes strongly to the right in both varieties. Distinctions based on the number of fingers have not been found to be useful and consequently the distinction of the var. *palmatum* here is on an emended feature, having been formerly based on the small number of fingers. There is a general tendency for the longer-horned specimens to have fewer fingers but short-horned individuals with only a few fingers have also been seen.

Stations: var. *ranipes*: 32, 65, 103.
var. *palmatum*: 13, 17, 22, 31, 32, 58, 62, 69, 117, 129, 140, 144, 155, 282, 319, 370, 416, 419.

The species was occasional, being widespread throughout most of the area sampled. It did not occur further south than 31 °S in the central region but other studies (see below) have recorded it from the southwestern Indian Ocean.

It is usually considered an inter-oceanic tropical species. It appears to be a consistent shade species, usually occurring below 50 m in earlier studies (STEEMANN NIELSEN 1934; GRAHAM & BRONIKOVSKY 1944). In addition to the records listed by WOOD (1963a) the species has been found in the Indian Ocean by SILVA (1960), SUKHANOVA (1962b), TSURUTA (1963), TAYLOR (1967), SOURNIA (1968 a, b, 1970), NEL (1968), SUBRAHMANYAN (1968), and THORRINGTON-SMITH (1969).

Section Platycornia JÖRGENSEN

Ceratium platycorne VON DADAY Plate 19, Figs. 185, 188

PETERS 1932:47, t. 2, f. 12b; STEEMANN NIELSEN 1934:24, f. 56, 57; SCHILLER 1936:408, f. 450 a, b; CANDEIAS 1938:249, f. 10; RAMPI 1942:223, f. 3, 4; GRAHAM et BRONIKOVSKY 1944:36, f. 19 C–H; SILVA et PINTO 1948:173, t. 2, f. 15; KISSELEV 1950:252, f. 426; MARGALEF et DURÁN 1953:42, f. 11 a–d; WOOD 1954:297, f. 226; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 8, 9; KATO 1957:17, t. 5, f. 16 a b; HALIM 1960a, t. 4, f. 12; LOPEZ 1966, f. 17, 18; YAMAJI 1966:99, t. 48, f. 6, 7; SOURNIA 1968a:453, f. 78, 79; SUBRAHMANYAN 1968:58, f. 108, 109; LÉGER 1971b:27, f. 11.

Syn.: .... *C. compressum* GRAN .... SCHILLER 1936:390, f. 427b; KISSELEV 1950:248, f. 424, WOOD 1954:312, f. 240; YAMAJI 1966: 99, t. 48, f. 3.
? *Ceratium* sp. SILVA 1949:357, t. 6, f. 23, t. 9, f. 3.

The body of this species, allowing for size variation, is fairly regular, but the antapical horns exhibit strong, characteristic variability. At one extreme the horns are tapering, like other members of the section, this occurring in the cold-water variety *compressum* (GRAN) JÖRGENSEN. The apical horn tapers gradually into the epitheca. In the var. *dilatatum*

(KARSTEN) JÖRGENSEN (= *C. lamellicorne* KOFOID) the antapical horns are tubular for most of their length, extending beyond the base of the apical horn before becoming irregularly flattened distally (fig. 188). The apical horn arises more abruptly than in the preceding or following varieties. The var. *platycorne* has a body similar to the var. *compressum* but the horns are laterally compressed into flattened "paddles" shortly after leaving the body, being obviously flattened at the girdle plane. The ends of the "paddles" may be truncated or more or less irregularly cleft. Specimens exhibiting the greatest lateral extension of the paddles used to be referred to the var. *cuneatum* (JÖRGENSEN) GRAHAM et BRONIKOVSKY (e.g. fig. 185) in which the width of the "paddle" approximates the girdle width and the ends are usually fairly flat. However, GRAHAM & BRONIKOVSKY (1944) stated that it blended fully into the central variety. The forma *incisum* JÖRGENSEN refers to deeply cleft ends to the antapical horns of the var. *platycorne*. In the var. *platycorne* the paddle walls are greatly thinned except for the outer margin. Chloroplasts are densely packed into the paddle regions.

The differences between the above varieties are so great as to suggest to many earlier authors that they should be kept separate at the species level. In the "Anton Bruun" material specimens of the var. *compressum* did not occur. Also intergrades between the other varieties were not seen. However, they have been reported by other authors such as JÖRGENSEN (1920) and GRAHAM & BRONIKOVSKY (1944) and consequently they have been retained here at the varietal level.

The body of this species resembles *C. ranipes* CLEVE, particularly in the row of finned spines along the post-margin. After autotomy of the distal portions of the antapical horns (which are extremely distinctive) the species can still be readily distinguished by the strongly sloping apical horn, the widely set antapical horns, and less rounded cell body (in ventral view) than *C. ranipes*.

Stations: var. *platycorne*: 32, 103, 133, 302, 418.
var. *dilatatum*: 320.

The species was rare, occurring only at scattered warm-water stations throughout the area. The single station at which the var. *dilatatum* occurred was near 11 °S in the central region. It can be considered as an inter-oceanic, high stenothermal species.

Both STEEMANN NIELSEN (1934) and GRAHAM & BRONIKOVSKY (1944) found a marked preference for deeper levels, below 50 m and often below 100 m.

The list of Indian Ocean records given by WOOD (1963a) requires augmentation by those of TAYLOR (1967), SOURNIA (1968a, b, 1970), SUBRAHMANYAN (1968) and THORRINGTON-SMITH (1969). NEL (1968) has recorded *C. compressum* from the southwestern Indian Ocean.

Section Reflexa JÖRGENSEN

Ceratium reflexum CLEVE Plate 17, Fig. 173

STEEMANN NIELSEN 1934:29, f. 74; SCHILLER 1936:420, f. 461; GRAHAM et BRONIKOVSKY 1944:45, f. 27H; WOOD 1963b:40, f. 149; YAMAJI 1966:106, t. 51, f. 5; SOURNIA 1968a:485, f. 99, t. 3, f. 13; SUBRAHMANYAN 1968:70, f. 135–139; WOOD 1968:38, f. 85; REINECKE 1973a:77, f. 6 S, f. 7 H.
Non SILVA 1955:172, t. 9, f. 9.

Although often poorly illustrated the species is readily recognisable by the posteriorly-directed left antapical horn. Proximally it diverges very slightly from the cell body and then bends abruptly towards the posterior in a plane approximately parallel with the apical horn. However, in some instances the distal portion has been bent at right angles to the apical axis. The posterior cell body margin is strongly sloped in relation to the girdle plane. Autotomy has been observed (fig. 173).

Stations: 63, 100, 116, 129, 144.

The species was rare in the material, occurring only at a few Bay of Bengal and central Indian Ocean stations. It was found furthest south at station 129.

It has been observed infrequently in the Indian, Pacific, and tropical North Atlantic Oceans. It is apparently a high stenothermal, oceanic species (e.g. DESROSIÈRES 1969 in the Pacific Ocean) and was considered probably shade-loving by GRAHAM & BRONIKOVSKY (1944) although the records are too few to be conclusive as yet. The records of SOURNIA (1966a, 1968a, 1970), SUBRAHMANYAN (1968), and REINECKE (1973a) should by added to those listed by WOOD (1963a).

Section Tripos

Ceratium arietinum CLEVE Plate 16, Figs. 162, 165

PETERS 1932:41, t. 4, f. 22 a–c; STEEMANN NIELSEN 1934:21, f. 45; SCHILLER 1936:403, f. 414 a–c; RAMPI 1939a:307, f. 28; GRAHAM et BRONIKOVSKY 1944:31, f. 16 A–K (vix G); SILVA 1949:359, t. 9, f. 7; KISSELEV 1950:252, f. 420 a, b; MARGALEF et DURAN 1953:42,

f. 11 h, i, j, k; WOOD 1954:294, f. 221 a–e; GAARDER 1954:9, f. 10; KATO 1957:16, t. 6, f. 21; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 4; HALIM 1960a, t. 4, f. 4; – 1963:497, f. 10; TORIUMI 1964a:43, t. 1, f. 3; SOURNIA 1968a:429, f. 51–54; LOPEZ 1966, f. 27; YAMAJI 1966:97, t. 47, f. 7 (sub *C. arieticum*); SUBRAHMANYAN 1968:54, f. 95–97; WOOD 1968:23, f. 37; HERMOSILLA 1973a:22, t. 1, f. 15, t. 3, f. 20.
Syn.: . . . . *C. bucephalum* (CLEVE) CLEVE . . . . MARTIN 1928:29, t. 6, f. 6, t. 8, f. 8; CANDEIAS 1930:33, t. 3, f. 69; SCHILLER 1936:392, f. 430; SILVA 1949:358, t. 9, f. 6; KISSELEV 1950:248, f. 421 a, b, 423, 429; WOOD 1954:288, vix f. 210 a–c; KATO 1957:16, t. 6, f. 22; TORIUMI 1964a:43, t. 1, f. 2; YAMAJI 1966:97, t. 47, f. 8, 9; TORIUMI 1968:3, f. 4.

C. arietinum is a distinctive, medium-sized species. It is distinguished from *C. declinatum* (KARSTEN) JÖRGENSEN, perhaps the most similar species to it, in the shape of the body, the latter being more elongate and having a less convex left profile to the body combined with an apical horn arising further to the left. The latter is also generally smaller but there is an overlap between the smallest variants of *C. arietinum* and the largest of *C. declinatum*. The right side parts of the girdle are reduced in *C. arietinum* but much more so in *C. declinatum*.

As early as 1911 JÖRGENSEN indicated the great similarity of *C. bucephalum* to this species. GRAHAM & BRONIKOVSKY (1944) were the first to "sink" *C. bucephalum* into *C. arietinum* although they made it a subspecies of the latter. SOURNIA's (1966b, 1968) designation of the taxon as a variety is more compatible with the treatment of infraspecific taxa here. The var. *bucephalum* represents the most widely separated antapical horn state.

Other varieties have been named, the value of which is not clear. They are: the var. *arietinum* (= f. *detortum* and f. *valens*) in which the cells are relatively large with a short to medium-length apical horn and a strongly incurved right antapical horn; and the var. *gracilentum* (JÖRGENSEN) SOURNIA which is more slender with a long apical horn.

Stations: var. *arietinum*: 294, 325, 362, 366, 371, 416.
var. *gracilentum*: 135, 153, 313.

The former occurred at two open Indian Ocean stations and several in the Mozambique Channel region. The latter was found only at several southern Indian Ocean stations. This species was one of the very few which were not found in either the Bay of Bengal or the Arabian Sea. STEEMANN NIELSEN (1934) considered it a deep species as it often occured below 50 m. Both varieties are warm water taxa but the latter seems to be a more strictly tropical oceanic variety. WOOD's (1963a) Indian Ocean records require augmentation by those of SILVA (1956a), DURAIRATNAM (1964), TAYLOR (1967), SOURNIA (1966b; 1968 a, b, 1970), and NEL (1968).

Ceratium axiale KOFOID Plate 15, Fig. 158

PETERS 1932:41, t. 2, f. 12h; STEEMANN NIELSEN 1934:20, vix f. 42; SCHILLER 1936:402, f. 442; GRAHAM et BRONIKOVSKY 1944:30, f. 15 D, E; WOOD 1954:293, vix f. 219; – 1968:23, f. 39 (errat. f. 38); SUBRAHMANYAN 1968:52, f. 93.

This is a distinctive species similar in body form and left antapical horn to *C. euarcuatum* but with a closely-set right horn with a sharp flexure approximately half way along its length. The apical horn curves to the right. *C. symmetricum* var. *coarctatum* sometimes mimics *C. axiale* in right antapical horn features but can be recognised easily by the cell body size and shape.

Stations: 32, 92, 98, 129.

Rare, at three stations within the Bay of Bengal/Andaman Sea and one southern central station (30 °S). It is a rare warm-water, interoceanic species. It has been recorded previously from the Indian Ocean by STEEMANN NIELSEN (1939), WOOD (1954), TRAVERS & TRAVERS (1965), SOURNIA (1968b), NEL (1968), and SUBRAHMANYAN (1968).

Ceratium azoricum CLEVE Plate 15, Fig. 160

WAILES 1928, t. 1, f. 3; CANDEIAS 1930:34, t. 3, f. 70; PETERS 1932:43, t. 3, f. 14h; STEEMANN NIELSEN 1934:20, f. 43; SCHILLER 1936:406, f. 447; RAMPI 1939a:307, f. 25; WAILES 1939:44, f. 132; GRAHAM et BRONIKOVSKY 1944:30, f. 16 M–P; KISSELEV 1950:252, f. 413 a, b; MARGALEF et DURÁN 1953:11, f. e–g; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 6; HALIM 1960a, t. 4, f. 13; BALECH 1962b, f. 398, 399; TORIUMI 1964b:24, t. 3, f. 11; LOPEZ 1966, f. 26; YAMAJI 1966:98, t. 48, f. 1; SOURNIA 1968a:435, f. 58, 62, 63; SUBRAHMANYAN 1968:56, f. 102; HERMOSILLA 1973a:23, t. 2, f. 10; – 1973b:67, t. 36, f. 1–4.
Vix SILVA 1949:358, t. 6, f. 24; WOOD 1954:295, f. 222 a, b; – 1968:23, f. 38 non f. 39 (errat); HALIM 1960a, t. 4, f. 13.

This is a small species (diameter of body 38–51 µm) very similar to, if not conspecific with *C. petersii* STEEMANN NIELSEN. It is here kept seperate, recognition being based on the features indicated by STEEMANN NIELSEN. These are a wider body diameter (50–57 µm), more widely spread horns and the occurrence of lists on the base of the apical horn of *C. petersii*. Here, in addition, the body of *C. azoricum* seemed narrower at the top than *C. petersii* but the figures of BALECH (1962b) from the Pacific Ocean indicate that this is not reliable. The difference in antapical horn spread is chiefly due to the degree of divergence of the right antapical horn, being least in *C. azoricum*.

In the specimens seen here the girdle was almost totally undeveloped. WOOD's records are cited as doubtful above because the drawings do not permit a clear distinction between *C. azoricum* and *C. petersii*. Also, the presence of lists on the Atlantic Ocean specimens (1968) strongly suggests that they were, in fact, *C. petersii*.

Stations: 17, 103.

The species was observed at only two stations, one in the southern Andaman Sea and the other off Madras in the Bay of Bengal. This conforms to the view that it is essentially a tropical to subtropical species. It appears to prefer relatively eutrophic waters, occurring in the tropical Pacific Ocean most abundantly in the vicinity of the Galapagos Islands (DESROSIÈRES 1969). There are several records from colder temperate waters (e.g. WAILES 1928, British Columbia) but some of these may refer to *C. petersii*.

The references of TSURUTA (1963), ANGOT (1965), SOURNIA (1968 a, b, 1970), NEL (1968), SUBRAHMANYAN (1968) and ANGOT (1970) should be added to the Indian Ocean records listed by WOOD (1963a).

Ceratium breve (OSTENFELD et. J. SCHMIDT) B. SCHRÖDER Plate 14, Figs. 141–146

WANG et NIE 1932:306, f. 19; PETERS 1932:39, t. 3, f. 13d; STEEMANN NIELSEN 1934:18, f. 36 non f. 35; SCHILLER 1936:391, f. 429 a, b; NIE 1936:50, f. 18 A–C, 19 A, B (sub *C. brave*); GRAHAM et BRONIKOVSKY 1944:27, f. 14 G–J, L, O, P (vix K, M, n); SILVA 1949:357, t. 9, f. 4; WOOD 1954:288, non f. 209 a, b; SILVA 1958, f. 5; BALLANTINE 1961:225, f. 53; KLEMENT 1964:355, t. 3, f. 4; BARTH et OSORIO 1965, f. 1d (sub *C. tripos*); YAMAJI 1966:95, t. 46, f. 1, 2, 3; SOURNIA 1968a:426, f. 47–50, t. 2, f. 7; SUBRAHMANYAN 1968:40, f. 62. 63. t. 3, f. 13–15; MARGALEF 1969a, f. 5 F.

Syn.: . . . . *C. schmidtii* JÖRGENSEN . . . . WANG et NIE 1932:308, f. 20; STEEMANN NIELSEN 1934:18, f. 37; NIE 1936:54, f. 22 A–D; SCHILLER 1936:400, f. 440; WOOD 1954:291, f. 216 a (non b); HALIM 1963:498, f. 20, 21; LOPEZ 1966:419, f. 22; YAMAJI 1966:95, t.46, f. 6; SUBRAHMANYAN 1968:49, f. 88 [sic 38, errat.].

A large-bodied distinctive species in which variability (other than the usual length of the apical horn) involves the curvature of posterior horns and the degrees of ventral concavity of the body. Four varieties are recognised: the var. *breve* in which the right posterior horn curves moderately inward towards the body (figs. 141, 142); the var. *parallelum* (J. SCHMIDT) JÖRGENSEN in which the right posterior horn opens away from the body and the left posterior horn also opens wider from the body (f. 146); the var. *curvulum* JÖRGENSEN in which the right posterior horn is tightly curved in towards the body (f. 143) and which can probably be included in the var. *schmidtii*; and the var. *schmidtii* (JÖRGENSEN) SOURNIA in which the body is distinctly concave ventrally, the posterior horns also thus directed ventrally (f. 144, 145).

The species is closest to *C. humile* JÖRGENSEN, from which it is readily separated by its body shape, the latter having a straighter posterior margin and much less convex right upper profile. The horns of the latter are larger and relatively more slender in appearance with the left antapical horn unusually long.

Stations: var. *breve*: 15–17, 19, 20, 23, 49, 110, 144, 148–150, 153, 288, 294, 297, 325, 420.
var. *parallelum*: 13, 14, 19, 21, 28, 34, 36–39, 41, 44, 47, 50, 62, 64, 65, 71, 87, 91, 99, 100, 102–106, 108–110, 113, 115, 116, 142, 147, 288, 295, 296, 299, 314, 327, 331, 334, 341, 374, 414, 418.
var. *schmidtii*: 23, 30, 42, 67, 88, 89, 91, 96, 99–101, 103, 104, 106, 109, 110, 113, 115, 140, 142, 294.

The most widespread and abundant variety was the var. *parallelum* which was common throughout the northern Indian Ocean and the neritic waters of the Bay of Bengal and Andaman Sea. It was most abundant at station 105 near Madras. The var. *breve* occurred at scattered stations in the Andaman Sea and over the northwestern Indian Ocean. The var. *schmidtii* was found at a few northern stations, particularly in the eastern Arabian Sea on cruise II. These stations were all not far from islands.

SOURNIA (1968a) examined Mozambique Channel material from this expedition. He commented (p. 428) that it was not possible to discern latitudinal or other ecological distinctions between the varieties (he did not recognise var. *breve*) with regard to their distribution.

However, the distribution of the var. *schmidtii* in the present material conformed to STEEMANN NIELSEN's (1939a) observation of a neritically-biased distribution in the Indian Ocean.

The Indian Ocean references of WOOD (1963a) require augmentation by those of MENON (1931, 1945), HORNELL & NAYUDU (1923), SUKHANOVA (1962b, *breve* and *schmidtii*), TSURUTA (1963), DURAIRATNAM (1964, *breve* and *schmidtii*), TAYLOR (1967, *breve* and *schmidtii*), SOURNIA (1968 a, b, 1970, *breve* and *schmidtii*), NEL (1968), SUBRAHMANYAN (1968), and THORRINGTON-SMITH (1969).

The species is characterised as an inter-oceanic warm-water form of sporadic occurrence.

Ceratium carnegiei GRAHAM et BRONIKOVSKY Plate 17, Fig. 174

– 1944:34, f. 18 A–C; GAARDER 1954:10, f. 11; SOURNIA 1968a:452, f. 77, t. 3, f. 11; SUBRAHMANYAN 1968:91, f. 162–164.

This is a distinctive, rare species. It is large and robust, being somewhat similar to *C. lunula* and *C. longipes* f. *ventricosum* (SOURNIA 1968a, has indicated that fig. 18 A of GRAHAM & BRONIKOVSKY may be the latter). Its most distinctive feature is the relatively large volume of the epitheca. It is markedly higher than its nearest relatives and is sometimes wider near the apical horn than near the girdle.

Station: 420.

Several individuals were observed at this station close to the east African coast. SOURNIA (1968a, 1970) the only other author to encounter the species in the Indian Ocean, found his specimen near the Comoro Islands (Comores) also in the west central Indian Ocean. It was originally described from the Pacific Ocean and has also been found in the North Atlantic Ocean.

Ceratium concilians JÖRGENSEN Plate 19, Fig. 186
PETERS 1932:44, t. 2, f. 8; STEEMANN NIELSEN 1934:22, f. 49; SCHILLER 1936:396, f. 435; RAMPI 1939a:306, f. 36; GRAHAM et BRONIKOVSKY 1944:33, f. 17 H, I; MARGALEF 1948a:20, f. 3, 4; WOOD 1954:290, f. 213; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 2; HALIM 1960a, t. 4, f. 20; – 1963:497, f. 11; LOPEZ 1966, f. 28; SUBRAHMANYAN 1968:45, f. 74, 75; WOOD 1968:26, vix f. 47; STEIDINGER et WILLIAMS 1970:44, t. 6, f. 15.

This species resembles the distorted right horn form of *C. gibberum* GOURRET and some authors have suggested that they may be linked by transitional forms (BÖHM 1931b; WOOD 1954; SOURNIA 1968a – no figures given) although this has not been established. In the present material *C. concilians* could always be recognised by its smaller body, being rounder in profile (especially the epitheca which is much more convex). The apical horn bends strongly to the right and there is a lack of ridge ornamentation on the theca. The figures on plate 19 illustrate these distinctions well. In both taxa the girdle plane is strongly bent in the centre.

WOOD's (1968) figure is curious in that it shows the right antapical horn passing ventrally in front of the cell instead of dorsally. This is presumably an error as he makes no comment on what would otherwise be considered a major variation and he refers to dorsal flexure in the description.

Stations: 37, 63, 65, 91, 101, 118, 140, 142, 153–155, 294, 341.

Found at scattered northern Indian Ocean stations, often close to land. This confirms STEEMANN NIELSEN's (1934) contention that this is a neritic species which extends into the oceanic region fairly frequently. It is an inter-oceanic warm-water species. In addition to the records listed by WOOD (1963a) it has been found in the Indian Ocean by TRAVERS & TRAVERS (1965), SOURNIA (1966a, 1968 a, b), TAYLOR (1967), NEL (1968), SUBRAHMANYAN (1968), and ANGOT (1970).

Ceratium contortum (GOURRET) CLEVE Plate 18, Figs. 179–181, 184
PETERS 1932:46, t. 2, f. 10g, 12a; STEEMANN NIELSEN 1934:23, f. 52, 53; SCHILLER 1936:395, f. 433, 434; NIE 1936:58, f. 25 A, B, 26; GRAHAM et BRONIKOVSKY 1944:34, f. 18 D–H, J, M, N, vix I, J non L, K; SILVA 1952b:604, t. 6, f. 10; WOOD 1954:289, f. 212 a–c; SILVA 1955:167, t. 8, f. 2; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 1; BARTH et OSORIO 1965, f. 1 b, c, h (sub *C. tripos*); YAMAJI 1966: 96, t. 46, f. 10, 11; WOOD 1968:26, f. 48; SOURNIA 1968a:441, f. 67–70, 72 vix 71 t. 2, f. 9; SUBRAHMANYAN 1968:44, f. 69–71; STEIDINGER et WILLIAMS 1970:44, t. 6, f. 16 a, b, 17 a, b; RICARD 1970, t. 2, f. e.
Syn.: *C. arcuatum* CLEVE .... PETERS 1932:44, t. 2, f. 9 (*C. arcuatum longinum*), 10e, non 11c; SILVA 1949:357, t. 9, f. 5; YAMAJI 1966:98, t. 47, f. 10.
Non *C. arcuatum* VANHÖFFEN nec *C. tripos* var. *arcuatum* GOURRET.
C. karstenii PAVILLARD .... STEEMANN NIELSEN 1934:23, f. 51; SCHILLER 1936:393, f. 431b vix a, non f. 432a vix b; RAMPI 1939a: 306, f. 18; KISSELEV 1950:249, f. 463, 512; MARGALEF et DURÁN 1953:40, f. 10 r; WOOD 1954:289, f. 211a non b; SILVA 1955:162, t. 8, f. 1; TRÉGOUBOFF et ROSE 1957:116, t. 25, f. 16; HALIM 1960a, t. 5, f. 5; – 1963:498, f. 19; BALLANTINE 1961:225, f. 54; MARGALEF 1961b:142, f. 3/8; KLEMENT 1964:355, t. 2, f. 8; LOPEZ 1966, f. 37; YAMAJI 1966:96, t. 46, f. 12, 13; SUBRAHMANYAN 1968:42, f. 67, 68.
Vix WOOD 1968:33, f. 68.
C. longinum KARSTEN .... SCHILLER 1936:398, f. 438; NIE 1936:57, f. 24 A, B; KISSELEV 1950:250, f. 439; WOOD 1954:297 vix f. 225 (f. 211b sub *C. karstenii*); – 1968:34, f. 73; YAMAJI 1966:98, t. 46, f. 14; SUBRAHMANYAN 1968:48, f. 79–81.

There is a strong similarity between *C. contortum* and *C. longinum* KARSTEN, *C. karstenii* PAVILLARD and, in the case of the largest specimens of both species, *C. lunula* (SCHIMPER ex KARSTEN) JÖRGENSEN. SOURNIA (1968a) has "lumped" the first three as *C. contortum*, whereas SUBRAHMANYAN (1968) has kept them distinct. SOURNIA's action conformed with observations of GRAHAM & BRONIKOVSKY (1944, p. 35: "In the Carnegie collections every possible intergrade was found between *C. contortum*; *C. longinum*, and *C. karstenii* . . ."). In the "Anton Bruun" material there were indeed many variants exhibiting intergrades, four of which are shown on plate 18. However, specimens corresponding to SCHILLER's interpretation of *C. karstenii* could always be distinguished quite readily from the others (see comments under that taxon). Among the others it was found that nearly all of the specimens could be assigned to one of four varieties, suggesting that their recognition as morphological "clusters" seem realistic. The four varieties used here were:

C. contortum var. *contortum*, recognised by its slender form with a compound bend of the right horn, the sharpest flexure occurring distally;

C. contortum var. *saltans* (SCHRÖDER) JÖRGENSEN, in which the right horn is strongly bent in the proximal portion;

C. contortum var. *karstenii* (PAVILLARD) SOURNIA emend.; large-bodied (transdiameter 90 to 100 µm) with the antapical horns forming a smooth arc, the right horn sometimes bent in the distal region if the horn is long;

C. contortum var. *subcontortum* (SCHRÖDER) stat. nov. [basionym: *C. subcontortum* SCHRÖDER 1906 = *C. contortum* f. *subcontortum* (SCHRÖDER) STEEMANN NIELSEN 1934, p. 23], in which the right horn is bent only moderately and lacks an additional proximal or distal bend.

To these might be added the var. *longinum* (KARSTEN) SOURNIA, resembling the latter but with the left horn bent abruptly towards the interior close to the body. The latter variety was not found in this material.

SOURNIA (1968a) considered that the var. *saltans* could not be satisfactorily distinguished from the var. *contortum*, although here it has been used to see if there are biogeographic differences.

SOURNIA's derivations of his var. *karstenii* and var. *robustum* are confusing for he seems to interpret them oppositely to their designation by JÖRGENSEN (cf. 1920, p. 76, 77 under *C. arcuatum* CLEVE). However, the difficulty lies in the recognition of the var. *robustum* for JÖRGENSEN's original figure (1911, f. 118) shows only the dorsal side. SCHILLER's (1936, f. 432a) specimen, shown in ventral view, may be a separate taxon (see here under *C. schrankii* KOFOID). For present purposes the var. *karstenii* is emended to include individuals SOURNIA would consider being in the var. *robustum* and to exclude those conforming with *C. schrankii* KOFOID.

The var. *karstenii* recognised here is best exemplified by the figures of JÖRGENSEN (1911, pl. 6, f. 117; 1920, f. 71). The taxon was considered by PAVILLARD (1907) to be best illustrated by KARSTEN's (1907) plate 20, figure 13 b.

Stations: var. *contortum*: 13, 35, 71, 100, 102, 104, 106, 108, 112, 118, 134, 135, 147, 318, 347, 375, 399, 413, 414.
var. *saltans*: 85, 89, 94, 97, 282, 283, 290, 294, 299, 322, 323, 325.
var. *subcontortum*: 13, 62, 65, 91, 99, 100, 102, 318, 320.
var. *karstenii*: 13, 17, 21, 26, 31, 33, 38, 59, 61–63, 65, 70, 71, 98, 101, 103, 104, 106, 109, 110, 112, 129–131, 135, 142, 150, 155, 161, 162, 287, 288, 300, 311, 313, 325, 329, 337, 340, 360, 371, 374.

The species as a whole was widespread throughout the warmer waters of the Indian Ocean. The most widespread variety, the var. *robustum*, was absent between 5° and 15 °S and below 36 °S. The var. *contortum* had a similar but more sparse distribution and did not occur as far south. The var. *saltans* occurred only north of 16 °S. The var. *subcontortum* was limited to a few stations in the western Bay of Bengal and a few south of India.

The species is an inter-oceanic warm-water species. JÖRGENSEN (1911) reported the var. *saltans* as being abundant in the Red Sea and near Zanzibar. STEEMANN NIELSEN (1934) has suggested that the var. *subcontortum* is a shade form, the other varieties being surface forms.

In addition to the Indian Ocean records listed by WOOD (1963a) there are those of SILVA (1956a), SUKHANOVA (1962b), TSURUTA (1963), DURAIRATNAM (1964), SOURNIA (1966a, 1968 a, b, 1970), SUBRAHMANYAN (1968), THORRINGTON-SMITH (1969), and ANGOT (1970). Unlike other tropical species it does not seem to extend far southwards in the Agulhas Current.

Ceratium declinatum (KARSTEN) JÖRGENSEN Plate 16, Figs. 163, 164, 166, 167

PETERS 1932:43, t. 4, f. 23 a–c; STEEMANN NIELSEN 1934:22, f. 46, 47; SCHILLER 1936:404, f. 445 a–d; NIE 1936:52, f. 20 A, B; RAMPI 1939a:307, f. 26, 29; GRAHAM et BRONIKOVSKY 1944:32, f. 16 Q–T, 17 A–C; KISSELEV 1950:249, f. 425; RAMPI 1952b:121, f. 8; MARGALEF et DURÁN 1953:42, f. 10 o, p; WOOD 1954:293, f. 218 a–c; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 5; HALIM 1960a: 185, t. 4, f. 22–26; – 1963:497, f. 12; BARTH et OSORIO 1965, f. le (sub *C. tripos*); LOPEZ 1966, f. 32; YAMAJI 1966:98, t. 47, f. 11; STEIDINGER, DAVIS et WILLIAMS 1967; t. 6, f. b; SOURNIA 1968a:438, f. 66, t. 2, f. 8; SUBRAHMANYAN 1968:54, f. 98–101, t. 4, f. 20; WOOD 1968:27, f. 50; STEIDINGER et WILLIAMS 1970:45, t. 7, f. 18; HERMOSILLA 1973a:25, t. 2, f. 11–16; – 1973b:66, t. 34, f. 1–3.

This is a small, distinctive species (body length 40–60 µm) more closely resembling *C. arietinum*. The cell body is narrow, the apical horn arising close to the left side of the body and the left side of the body is less convex than *C. arietinum*. The girdle is not fully developed around the body. As with the latter species there is a range of variation which has been recognised, various infraspecific epithets being used (JÖRGENSEN's formae and varieties, and the subspecies of PETERS and STEEMANN NIELSEN). The var. *declinatum* (=f. *debile* JÖRGENSEN) is represented by individuals in which the right horn curves outwards distally (PETERS 1932, f. 23a; STEEMANN NIELSEN 1934, f. 46; GRAHAM & BRONIKOVSKY 1944, f. 16 R; and f. 166 here). In the var. *normale* (JÖRGENSEN) stat. nov. the right horn is straight in its distal part. The var. *angusticornum* (PETERS) stat. nov. is one of the smallest variants, being distinguished rather dubiously from the var. *laticornum* (PETERS) GRAHAM et BRONIKOVSKY by a more incurved right antapical horn than the latter. It projects up almost straight as in the var. *normale*. The var. *majus* JÖRGENSEN is the most robust variant, the antapical horns not curving inward and being relatively short.

GRAHAM & BRONIKOVSKY (1944) and SUBRAHMANYAN (1968) considered that there was little value in the recognition of these infraspecific taxa. SOURNIA (1968a) recognised three formae: f. *normale* JÖRGENSEN, f. *declinatum*, and f. *brachiatum* JÖRGENSEN (with which he considered the subspecies *angusticornum* and *laticornum* might be included) and the var. *majus* JÖRGENSEN. His use of formae here was based on the observations of HALIM (1960a) in the Mediterranean where it appeared that at least some variation may be attributable to seasonal environmental changes. This phenotypic plasticity would accord with the concept of formae used here also. However, as the factors regulating these phenotypes are still not established the use of varieties for all variants is preferred here.

Stations: var. *declinatum*: 16, 17, 19, 20, 28, 34, 55, 56, 59, 65, 68, 71, 72, 85, 91, 94, 98, 100, 102–105, 108, 112, 113, 314, 323, 325, 326.
var. *angusticornum*: 62, 64, 68, 69, 71, 72, 93, 95, 99, 158, 294.
var. *majus*: 14, 150, 159.

The var. *declinatum* was by far the most common variant found. It was widespread throughout the Andaman Sea and Bay of Bengal and was also present at several stations to the west and south of India. It occurred furthest south at station 314 (24 °S). The smallest variety (*angusticornum*) was found in the central and western Bay of Bengal, at one station north of the Seychelle Islands, and at one far southern station (158, 35 °S). The var. *majus* was rare at three stations, one of which (159, 38 °S) was the most southerly record for the species in the Indian Ocean.

The species is inter-oceanic, ranging from tropical to temperate waters. GRAHAM & BRONIKOVSKY (1944) considered that cold water records of the species (they found it at one cold station in the Atlantic in addition to many warm water records), were the result of displacement from its normal tropical distribution. The following records are additional to those listed by WOOD (1963a): ANGOT (1965), SOURNIA (1966a, 1968 a, b, 1970), TAYLOR (1967), NEL (1968), SUBRAHMANYAN (1968), and ANGOT (1970).

Ceratium euarcuatum JÖRGENSEN Plate 15, Figs. 155, 157, 159

PETERS 1932:40, t. 1, f. 4 a–c; STEEMANN NIELSEN 1934:18, f. 38; SCHILLER 1936:402, f. 443; RAMPI 1939a:306, f. 30; GRAHAM et BRONIKOVSKY 1944:28, f. 15 N, M; WOOD 1954:294, f. 220; HALIM 1960a:185, t. 5, f. 2, 3; MARGALEF 1961b:140, f. 3/7; HALIM 1963: 497, f. 13 (sub *euarcuatum*); SOURNIA 1968a:436, f. 64, 65; SUBRAHMANYAN 1968:53, f. 94; WOOD 1968:28, f. 53; MARGALEF 1969a, f. 5 A, B.

A distinctive species, somewhat similar to *C. symmetricum*, from which it can be readily recognised by its much more steeply angled posterior profile (in relation to the plane of the girdle). Slender horned specimens tend to have a larger apical horn than the more robustly horned specimens (see JÖRGENSEN 1920; SOURNIA 1968a). *C. axiale* KOFOID is also very similar to this species when the cell body characteristics are examined (see comments under that species), and the three species may eventually be united.

Fig. 159 illustrates an unusual specimen interpreted here to be a malformation of the left antapical horn in *C. euarcuatum* rather than a new taxon, this being based on the observations on aberrant specimens of other species of *Ceratium* by NIELSEN (1956) and HASLE & NORDLI (1951, cf. their fig. 8a).

SUBRAHMANYAN (1968) has relegated *C. filicorne* STEEMANN NIELSEN to synonymy with this species. The former has very widespread posterior horns. The original figure (1934, f. 39) resembled a variant of *C. euarcuatum* but the figures of GRAHAM & BRONIKOVSKY (1944, f. 15 B, C) resemble *C. symmetricum* more closely.

Stations: 15, 16, 37, 60, 63–66, 89, 99, 101, 103, 108–110, 125, 129, 130, 134, 135, 153–155, 159, 161, 162, 282, 292, 294, 298, 300–302, 306, 312–315, 317–322, 331, 341, 342, 347, 359, 361, 371, 374, 412, 417–420.

GRAHAM & BRONIKOVSKY (1944) considered this species to be "one of the best indicators of warm tropical water". They did, however, find it occasionally in tropical upwelling regions. In the Indian Ocean material here it had a most interesting distribution, being widely distributed in the southern Indian Ocean and strikingly absent (or in very low numbers) from stations near the equator other than 292 and 294. Also it showed a curious anomaly with regard to the Mozambique Channel, being found at both northern and southern ends but not within it. These features seem to suggest a factor other than temperature as governing the distribution of this species over much of the Indian Ocean. It is clearly oceanic.

The records of DURAIRATNAM (1964), SOURNIA (1966a, 1968 a, b, 1970), NEL (1968), and SUBRAHMANYAN (1968) need to be added to the Indian Ocean records listed by WOOD (1963a).

Ceratium gibberum GOURRET Plate 19, Fig. 187

CANDEIAS 1930:34, t. 3, f. 71–73; PETERS 1932:44, t. 3, f. 13c; STEEMANN NIELSEN 1934:22, f. 48; SCHILLER 1936:397, f. 436 a, b, 437; NIE 1936:54, f. 21; WANG 1936:158, f. 28; RAMPI 1939a:306, f. 24; GRAHAM et BRONIKOVSKY 1944:33, f. 17 D–G; SILVA 1949: 359, t. 9, f. 8, 9; KISSELEV 1950:250, f. 437; MARGALEF et DURÁN 1953:42, f. 10 s–t; WOOD 1954:290, f. 214 a–c; KATO 1957:16, t. 5, f. 17; CURL 1959:306, f. 117; HALIM 1960a, t. 4, f. 19; – 1963:498, f. 14; KLEMENT 1964:356, t. 2, f. 7; TORIUMI 1964a:43, t. 1, f. 1; LOPEZ 1966, f. 23, 24; YAMAJI 1966:95, t. 46, f. 4, 5; HADA 1967:20, f. 32; SOURNIA 1968a:446, f. 73, 74; SUBRAHMANYAN 1968:46, f. 76–78; TORUMI 1968:3, f. 6, 7; WOOD 1968:30, f. 61; STEIDINGER et WILLIAMS 1970:45, t. 8, f. 22 a, b; TORIUMI 1971:65, f. 1 a, b, 2, 3 a, b, 4 a, b, 7, 8; HERMOSILLA 1973a:21, t. 3, f. 19

This species closely resembles *C. concilians* but differs from it in that the cell body is larger, the epitheca is flattened with an angular right precingular junction, a more sharply convex postmargin, and a straighter apical horn. Linear and reticular ridges have not been observed on thecae of *C. concilians* but are common on *C. gibberum*. In the original description GOURRET (1883) recognised the type and two varieties, the var. *contortum* (subsequently raised to specific status) and the var. *sinistrum*.

It is still possible to recognise two varieties of this species, the var. *gibberum* (= var. *subaequale* JÖRGENSEN) in which the right horn is only slightly curved in, and the var. *dispar* (POUCHET) SOURNIA (= var. *sinistrum* GOURRET) in which the right horn is strongly bent inwards, passing over the dorsal side of the cell body. POUCHET's varietal epithet has priority over that of GOURRET. Intermediates between the two varieties exist but are rare.

Only the var. *dispar* was observed in this material.

Stations: 13, 14, 33, 34, 37, 38, 47, 50, 62, 64, 66, 87, 100, 102, 108, 110, 143, 144, 147, 153, 162, 282, 297, 320, 323, 330, 341, 362, 371, 414, 416, 418, 419.

This variety was relatively common, but never occurred in large numbers. It was restricted to waters north of 20 °S except in the west where, in common with other tropical species, its distribution extended further south. Although described as purely oceanic (STEEMANN NIELSEN 1934) it often occurred near land masses.

Many of the apparently oceanic stations are not far from island groups. It has been found to occur chiefly within the upper 50 m. (GRAHAM & BRONIKOVSKY 1944).

The species has been commonly recorded from the Indian Ocean. The records provided by WOOD (1963a) require augmentation by those of SILVA (1956a, 1960) DURAIRATNAM (1964), ANGOT (1965), SOURNIA (1966a, 1968 a, b, 1970), TAYLOR (1967), NEL (1968), SUBRAHMANYAN (1968), and ANGOT (1970).

Ceratium humile JÖRGENSEN Plate 14, Fig. 148

STEEMANN NIELSEN 1934:17, f. 34; SCHILLER 1936:390, f. 428; GRAHAM et BRONIKOVSKY 1944:27, f. 14 A; WOOD 1954:287, vix f. 208; YAMAJI 1966:97, t. 47, f. 6; SUBRAHMANYAN 1968:38, f. 64, 65; WOOD 1968:32, f. 66.

A large-bodied species resembling *C. breve* and *C. tripos*, from which it is distinguished by its long right antapical horn. low epitheca with an angular anterior profile, and flattened posterior profile, sloping strongly in relation to the girdle plane. *C. egyptiacum* HALIM is also very similar and in most respects it resembles a variant in which the left antapical horn is short, slender, and bent almost at a right angle towards the ventral side. The left antapical horn of *C. humile* may be slightly divergent or, more commonly, parallel to convergent with the cell body. Some figures show a more curved posterior profile although this may be due to tilting of the specimens. The illustrated specimen had a right antapical horn which was less divergent than usual. More often the angle is very similar to that in *C. dens* and often the cell body shape is also similar to *C. dens*.

Stations: 39, 40, 47, 58, 63, 67, 70, 71, 85, 89.

Present in moderate numbers at three coastal stations on the eastern side of the Bay of Bengal/Andaman Sea, and over a wider area in the western half of the Bay of Bengal, all during the post-N. E. Monsoon period. NEL (1968) has recorded the species from the south-western Indian Ocean, but other Indian Ocean records (in WOOD 1963a) are for the northern Indian Ocean.

According to SUBRAHMANYAN (1968) this is a neritic, warm-water Indo-Pacific species. Its type locality is in Japanese coastal waters. GRAHAM & BRONIKOVSKY (1944) reported one cell from the tropical Atlantic Ocean and STEIDINGER & WILLIAMS (1970) and WOOD

(1968) have also found it in the Atlantic Ocean. However, the species seems to occur most frequently in southern Asian waters. It has not been observed off the west coast of North America as yet.

Ceratium limulus (GOURRET ex POUCHET) GOURRET Plate 18, Fig. 182
PETERS 1932:46, t. 1, f. 6; STEEMANN NIELSEN 1934:24, f. 54; SCHILLER 1936:407, f. 448; RAMPI 1939a:307, f. 19; GRAHAM et BRONIKOVSKY 1944:35, f. 19 A; SILVA 1949:360, t. 9, f. 10; WOOD 1954:296, f. 223 a, b; KATO 1957:17, t. 5, f. 15; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 7; HALIM 1960a, t. 4, f. 14; HERRERA, MUÑOZ et MARGALEF 1955:20, f. 1, F, G; LOPEZ 1966, f. 21; YAMAJI 1966:99, t. 48, f. 4; SOURNIA 1968a:458, t. 1, f. 5; SUBRAHMANYAN 1968:56, f. 103–105; WOOD 1968:34, f. 71; RICARD 1970, t. 1, f. f.

This is a highly distinctive, flattened, short-horned species, easily separated from *C. paradoxides* CLEVE by the shape of the epitheca with two humps or strong angularities on either side of the base of the apical horn, combined with a lack of reticulation covering the body. The left antapical horn is usually outcurving or straight distally, whereas it is usually incurving in *C. paradoxides.*

Stations: 37, 52, 92, 102, 130, 134, 288.

In accordance with STEEMANN NIELSEN's (1934, 1939a) observations the species was rare, occurring in both eutrophic (Bay of Bengal) and oligotrophic oceanic waters. It occurred at one station in the south central region below 32 °S. It has not been found to be particularly shade-loving in other studies.

The references of DURAIRATNAM (1964), TAYLOR (1967), SOURNIA (1968a, b, 1970), SUBRAHMANYAN (1968), NEL (1968), THORRINGTON-SMITH (1969), and ANGOT (1970) should be added to those provided by WOOD (1963a).

Ceratium longissimum (SCHRÖDER) KOFOID Plate 17, Fig. 175
SCHILLER 1936:413, f. 454 a, b; RAMPI 1939c:111, f. 12; – 1942:225, f. 14; GRAHAM et BRONIKOVSKY 1944:43, f. 26 A, B; WOOD 1954:299, f. 228; SILVA 1955:171, t. 9, f. 2, 3; MARGALEF 1957b:92, f. 2 e; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 11; HALIM 1960a, t. 5, f. 9; YAMAJI 1966:106, t. 51, f. 6; SUBRAHMANYAN 1968:63, f. 111, 112.

Curiously, and inappropriately, previous authors have assigned this rare species to the section Macroceros PAVILLARD despite its fundamental similarity to *C. schrankii* and other members of the section Tripos. For example, it completely lacks the posterior proximal deflection of the antapical horns (leading to an indented appearance of the posterior margin). JÖRGENSEN (1920) noted this similarity to the section Tripos but did not transfer it and even recent authors such as SUBRAHMANYAN (1968) have not questioned the traditional allocation. Admittedly the distinction is somewhat artificial. *C. horridum* can exhibit both types of appearance. Nevertheless allocation to the section Tripos seems most appropriate.

This species resembles *C. schrankii* but is much smaller with very long antapical horns sloping to the right and subparallel with the apical horn. JÖRGENSEN (1920) illustrated a form in which the antapical horns were strongly divergent (f. *subdivaricatum*) but this was not observed in the present material. GRAHAM & BRONIKOVSKY (1944) found that in the var. *longissimum* the horns of the Pacific strain seemed to diverge somewhat more than the Atlantic strain (or that found here), confirmed by the figure of WOOD (1954).

It also resembles *C. contortum* var. *longinum* but the latter does not have particularly long antapical horns and the left horn of the latter turns more abruptly in an apical direction shortly after leaving the body instead of curving in a smooth arc. *C. longissimum* also usually has a cell body smaller than *C. contortum.*

Stations: 31, 108, 117, 294, 319, 321.

Present at a few scattered stations in the north central Indian Ocean and one Andaman Sea station. It is known from the Mediterranean Sea, the equatorial Atlantic Ocean, Pacific Ocean, and has been found previously in the Indian Ocean by STEEMANN NIELSEN (1939a), SUKHANOVA (1962b), and SUBRAHMANYAN (1968). The former termed it a tropical, truly oceanic shade species. GRAHAM & BRONIKOVSKY (1944) found it to be "one of the most pronounced shade species encountered". It seems to occur most frequently between 200 and 100 m.

Ceratium lunula (SCHIMPER ex KARSTEN) JÖRGENSEN Plate 16, Fig. 171; Plate 18, Fig. 183
WANG et NIE 1932:305, f. 18; PETERS 1932:44, t. 2, f. 12c; STEEMANN NIELSEN 1934:23, f. 50; NIE 1936:56, f. 23 (sub *C. lunulae*); SCHILLER 1936:399, f. 439; GRAHAM et BRONIKOVSKY 1944:33, f. 17 J–N; WOOD 1954:291, f. 215 a, b; SILVA 1955:167, t. 8, f. 3–5; MARGALEF 1961b:142, f. 3/9; YAMAJI 1966:96, t. 46, f. 7, 8, 9; SOURNIA 1968a:450, f. 75, 76; SUBRAHMANYAN 1968:49, f. 82–87, t. 7, f. 33, non t. 3, f. 19 (*C. contortum*); WOOD 1968:35, f. 76; D. R. NORRIS 1969:448, f. 1, 2; STEIDINGER et WILLIAMS 1970:46, t. 10, f. 28.

The shape of the cell body is distinctive, with a sub-triangular epitheca due to only slight (or no) convexity of the upper surfaces. This, combined with the central position of the apical horn, and the widely spreading antapical horns which do not form a smoothly arcing profile with the posterior part of the cell body, serves to distinguish the species in both its delicate and robust forms from *C. karstenii* and *C. contortum.*

SOURNIA (1968a) has explained why the taxon cannot be ascribed solely to SCHIMPER. D. R. NORRIS (1969b) has observed the apparent phagocytosis of a species of *Peridinium* by this species.

JÖRGENSEN (1911) recognised two forms: the f. *megaceros* ("*magaceros*" in GRAHAM & BRONIKOVSKY 1944) with a long apical horn, and the f. *brachyceros* with a short apical horn. As these conditions probably reflect only the position in a chain, the long-horned individuals being the anterior-most, these forms do not seem worth recognising. On the other hand in the "Anton Bruun" material there was a striking difference in appearance between the slender individuals and larger, more robust individuals. The latter, in fact, could be confused with robust specimens of *C. contortum* if the shape was not clearly perceived. This point is emphasised by the placement of the figures on the plates. Furthermore, although the body of the robust form is larger than the other, its horns are frequently more slender. In view of these striking differences the two taxa are here given varietal status.

C. lunula var. *lunula* (f. 171) is the smaller-bodied form with a girdle transdiameter of less than 90 µm, usually closer to 80 µm. The antapical horns are long, relatively strongly built, and are broadly divergent.

C. lunula var. *robustum* var. nov. (f. 183). This differs from the var. *lunula* in that the body is larger, usually exceeding 100 µm in girdle transdiameter. The upper epithecal surfaces are more convex. The antapical horns taper more strongly. They are often less divergent than the var. *lunula* but not always. The surface of the theca bears irregularly longitudinal ridges and strongly developed lists arise from the base of the apical horn and on the upper proximal edges of the antapical horns.

Stations: var. *lunula*: 38, 57, 62.
var. *robustum*: 31, 37, 94, 129, 134, 149, 153, 282, 287, 290, 311, 323, 325, 329, 334, 365, 398, 404, 418, 419.

The var. *lunula* was rare, occurring at only three stations, one in the Andaman Sea and two in the northern Bay of Bengal. The var. *robustum* was more common. GRAHAM & BRONIKOVSKY (1944) found the species to have a similar distribution to *C. breve* but it was more thermophilic and it has usually not been found further south than 20 °S. In the "Anton Bruun" material however, while predominantly occurring in high temperature waters, the species was also found at three stations near 30 °S (one at 35 °S). TAYLOR (1967) and NEL (1968) have also found it south of 30 °S in the southwestern sector.

It is a tropical to subtropical inter-oceanic species. In addition to those Indian Ocean records listed by WOOD (1963a) there are the following: SILVA (1956b, 1960), SUKHANOVA (1962b), TSURUTA (1963), DURAIRATNAM (1964), TAYLOR (1967), NEL (1968), SOURNIA (1968 a, b, 1970), and SUBRAHMANYAN (1968).

Ceratium paradoxides CLEVE Plate 18, Fig. 178; Plate 43, Fig. 509

STEEMANN NIELSEN 1934:24, f. 55; SCHILLER 1936:408, f. 449; GRAHAM et BRONIKOVSKY 1944:36, f. 19 B; SILVA 1955:168, t. 8, f. 6; WOOD 1963b:40, f. 147; YAMAJI 1966:99, t. 48, f. 5; TAYLOR 1967, t. 93, f. 54 (sub *horridum* GRAN); SOURNIA 1968a:458, t. 1, f. 4; SUBRAHMANYAN 1968:57, f. 106, 107; WOOD 1968:37, f. 80.

This species is similar to *C. limulus* but differs by the features listed under that taxon here. In addition *C. paradoxides* is somewhat larger, the girdle diameter ranging from 70 to 80 µm. All horns show smooth curvature to the right.

The misnamed figure provided by TAYLOR (1967) was due to a typographical error.

Stations: 14, 18, 26, 35, 61–63, 65, 99, 103, 112, 113, 125, 129, 135, 143, 144, 150, 154, 157, 161, 294, 297, 321, 326, 334, 366, 370.

Although considered a rare species it occurred fairly commonly but never in large numbers in the samples. It occurred predominantly in the western Bay of Bengal (a common pattern for "shade species") and over a wide area of the Indian Ocean.

It has been considered a "shade species" by STEEMANN NIELSEN (1934) and GRAHAM & BRONIKOVSKY (1944). It is inter-oceanic and subtropical to tropical in distribution. The references of TSURUTA (1963), TAYLOR (1967), SOURNIA (1968a, 1970), NEL (1968), and SUBRAHMANYAN (1968) should be added to those listed by WOOD (1963a) for the Indian Ocean.

Ceratium petersii STEEMANN NIELSEN Plate 15, Fig. 161

– 1934:20, f. 44; SCHILLER 1936:406, f. 446; GRAHAM et BRONIKOVSKY 1944:31, f. 16 L; WOOD 1954:296, f. 224 a, b; BALECH 1962b: 183, t. 26, f. 395–397; LOPEZ 1966, f. 25; SOURNIA 1968a:436, f. 59–61; SUBRAHMANYAN 1968:91, f. 165.

As indicated under *C. azoricum* this species may well be an extreme variant of the former. The means of distinction is also indicated under *C. azoricum* here. The specimen figured on plate 15 has less divergent horns than this species often exhibits. Like *C. azoricum* the girdle seems to be very poorly developed.

Stations: 159, 160.

These two stations were among the most southerly stations sampled. Station 160 was below 40 °S, further south than the distribution of warmer water species such as *C. declinatum* and *C. euarcuatum*.

GRAHAM & BRONIKOVSKY (1944) suggested that it might be considered as a "subpolar" species except for occasional anomalous warmer incursions off the west coast of South America. They doubted that PETERS' (1932) specimens from the South Atlantic were the same as those seen by STEEMANN NIELSEN off New Zealand.

This is a first record for the species in the Indian Ocean. It is probably circumpolar in the Southern Ocean.

Ceratium schrankii KOFOID Plate 17, Figs. 176, 177

Syn.: *C. arcuatum* auct. non CLEVE sensu PETERS 1932, t. 2, f. 11c.
C. karstenii auct. non PAVILLARD sensu SCHILLER 1936, f. 431 a. Vix. SUBRAHMANYAN 1968, f. 67, 68.
C. karstenii var. *robustum* sensu SCHILLER 1936, f. 432a; SUBRAHMANYAN 1968, f. 72.
C. contortum CLEVE sensu GRAHAM et BRONIKOVSKY 1944 e.p. f. 18 L vix K.
C. contortum var. *karstenii* sensu SOURNIA 1968a, f. 71, t. 3, f. 10 (vide *C. contortum*, infra).

This name has been revived [it was formerly relegated to being a synonym of *C. arcuatum* CLEVE = *C. karstenii* PAVILLARD, now = *C. contortum* (GOURRET) CLEVE] to refer to a taxon which may or may not be considered as distinct from *C. contortum* (see comments under the latter). On the basis of published figures it appears highly probable that it intergrades with *C. contortum*. For example, JÖRGENSEN's (1920) figure of his form "*α Karstenii*" might be considered at first sight to be an intermediate. However, this is due mostly to the appearance of the horns which are somewhat heavier than is usual for *C. contortum*. A close scrutiny shows that in body shape it is very similar to fig. 184 here of *C. contortum* var. *karstenii*. It was found during the analysis of the "Anton Bruun" material, that individuals conforming to *C. schrankii* could always be readily separated from other forms assigned here to *C. contortum*. On this basis it seemed best to retain the distinction, the taxa being readily combined if found appropriate by future study.

KOFOID (1907a) considered that the features which distinguished his species from *C. arcuatum* were its subequal antapical horns (a distinction which is not particularly reliable as indicated by figures of *C. contortum* here), a wider arc of the horns, and a narrower epitheca. In addition he noted that the apical horn was not bent to the left initially as much as in *C. arcuatum*. Although he commented that the apical horn was usually short in the "Anton Bruun" material the reverse was true. This character is notoriously variable in the section Tripos and consequently this difference is not considered important. Also KOFOID persistently referred to the smoothly curving nature of the posterior margin, an expression which actually masks one of the most distinctive features of this taxon: a distinct flattening of the mid-posterior margin, subtle but quite definite in comparison with the strong convexity of *C. contortum*. His figures show this feature quite plainly.

In summary, then, this taxon seems to be recognisable in comparison with *C. contortum* by a combination of relatively robust antapical horns, usually subequal or with the right horn only slightly longer, narrow cell body (compared with *C. contortum* var. *karstenii*) and apical horn arising from the centre or to the left of the epitheca and bending immediately to the right rather than proceeding first to the left and then the right.

In antapical horn features it is really more like some varieties of *C. tripos*.

Stations: 32, 34, 37, 38, 42, 67, 93, 118, 125, 149, 154, 155, 161, 294, 301, 312, 313, 317, 360–362, 369, 405, 416, 420.

This distribution (N. Andaman Sea, W. Bay of Bengal, warm water areas of the Indian Ocean but absent from the 10 ° S region) is similar to that shown by *C. contortum* var. *karstenii* (emend.) which suggests a close affinity but at the same time argues against differences in appearance due to environmental influences on the phenotype (formae). In fact this distribution is also similar to *C. lunula*.

Because of confusion regarding identities former records are doubtful. The specimens illustrated by the authors cited in the references here were found in the eastern tropical Pacific Ocean, the Atlantic Ocean (equatorial current and southern region), and the Mozambique Channel. SCHILLER (1936) did not give localities for his specimens.

This is officially a new record from the Indian Ocean although SOURNIA (1968a) has illustrated a similar specimen under *C. contortum*. SUBRAHMANYAN's (1968) figures of *C. karstenii* might refer to this taxon but have more curved posterior margins.

Ceratium symmetricum PAVILLARD Plate 15, Figs. 152–154, 156

STEEMANN NIELSEN 1934:19, f. 40, 41; SCHILLER 1936:401, f. 441 a–d; RAMPI 1939a:306, f. 27; GRAHAM et BRONIKOVSKY 1944:29, f. 15 H–L; RAMPI 1952b:120, f. 6; MARGALEF et DURÁN 1953:42, f. 10q; WOOD 1954:292, f. 217 a–c; TRÉGOUBOFF et ROSE 1957:115, t. 26, f. 3; HALIM 1960a, t. 5, f. 1; MARGALEF 1961b:142, f. 3/10; HALIM 1963:498, f. 24, 25; LOPEZ 1966, f. 29, 30; SOURNIA 1968a: 432, f. 55–57 (sub *symetricum*); SUBRAHMANYAN 1968:51, f. 89–92; STEIDINGER et WILLIAMS 1970:47, t. 149, f. 34.
Non WOOD 1968:40, f. 89 (*C. azoricum*?)

Syn.:. . . . *C. gracile* (JÖRGENSEN) GOURRET . . . . PETERS 1932:41, t. 4, f. 21 b, c non a vix d; SILVA et PINTO 1948:173, t. 6, f. 22; YAMAJI 1966:98, t. 47, f. 12, 13.

The name *C. gracile* (GOURRET) JÖRGENSEN for this taxon was rejected by PAULSEN (1930) because of differences in interpretation by earlier authors, and more convincingly, by GRAHAM & BRONIKOVSKY (1944) because they considered it impossible to identify the original figure precisely (GOURRET 1883, pl. 1, f. 1). The latter's argument seems reasonable and has been followed by recent monographers. At the species level *C. symmetricum* PAVILLARD has priority of *C. gracile*, the latter epithet being originally proposed at the varietal level.

GRAHAM & BRONIKOVSKY (1944) recognised three principal varieties in contradiction to STEEMANN NIELSEN's (1934) view that they blended too much to warrant recognition. These varieties are: the var. *symmetricum* (f. 154) with a relatively short apical horn and widely spread antapical horns; the var. *orthoceras* (JÖRGENSEN) GRAHAM et BRONIKOVSKY (f. 152) with closely set antapical horns and relatively short apical horn); and the var. *coarctatum* (PAVILLARD) GRAHAM et BRONIKOVSKY (f. 153, 156).

The species is closest to *C. euarcuatum* and *C. filicorne* STEEMANN NIELSEN. It differs from the former in its more symmetrical posterior profile and in the smaller, relatively shorter cell body. The latter is similar in cell body shape, particularly in comparison with the var. *coarctatum*. However, the posterior horns are very widespread and relatively slender in *C. filicorne*. To date it appears to have only been found in the Pacific Ocean.

Stations: var. *symmetricum*: 112, 113, 297, 323.
var. *orthoceras*: 117, 321.
var. *coarctatum*: 17, 60, 99, 102, 113, 300, 313, 374.

The species was largely limited to the northern Indian Ocean but the var. *coarctatum*, which was the more widespread variety, also occurred at the southern end of the Mozambique Channel and in the mid-southern region near 30 °S. It is a warm-water, inter-oceanic species. GRAHAM & BRONIKOVSKY (1944) considered it to be "a pronounced shade species", occurring consistently in deeper samples.

The Indian Ocean references of WOOD (1963a) require augmentation by those of SILVA (1956a), TSURUTA (1963, as *C. gracile* var. *symmetricum*), DURAIRATNAM (1964), SOURNIA (1966a, 1968 a, b, 1970), TAYLOR (1967), NEL (1968), and SUBRAHMANYAN (1968).

Ceratium tripos (O. F. MÜLLER) NITZSCH Plate 14, Figs. 147, 149–151; Plate 16, Figs. 168–170

WAILES 1928, t. 3, f. 1; MARTIN 1929:30, t. 7, f. 7; WANG et NIE 1932:304, f. 16, 17; WANG 1936:157, f. 27; SCHILLER 1936:384, f. 321a; NIE 1936:48, f. 17 A, B; WAILES 1939:44, f. 133; MARGALEF 1946, f. III 1; SILVA et PINTO 1948:172, t. 6, f. 23; KISSELEV 1950:246–248, f. 36 *a*–в, 49, 51, 62, 428, 431 *a*, б, 432 *a*, 432, 440, 441, 442; HASLE et NORDLI 1951, f. 3 a–k, 4 a–c, 7i, 8 a–f; MARGALEF et DURÁN 1953:40, f. 10 g–n; WOOD 1954:285, f. 205 a, b, c; LOPEZ 1955:156, f. 6; KATO 1957:15, t. 4, f. 12 a, b, 13 a, b; TRÉGOUBOFF et ROSE 1957:116, t. 25, f. 14; CURL 1959:306, f. 123; HALIM 1960a, t. 4, f. 15; CASSIE 1961, t. 7, f. 6; MARGALEF 1961a:81, f. 26j; BARTH et OSORIO 1965, f. 1 a, f, g, vix i, non b, c, d, e, h; LOPEZ 1966:330, f. 33–36, t. ("Foto") 2/1–3; YAMAJI 1966:97, t. 47, f. 1–5; HADA 1967:20; STEIDINGER et WILLIAMS 1970:47, t. 14, f. 37 a, b, t. 15, f. 38 a, b; TORIUMI 1971:65, f. 5 a, b, 6; HERMOSILLA 1973b:65, t. 33, f. 5.

Syn.:. . . . *C. pulchellum* SCHRÖDER . . . . CANDEIAS 1930:32, t. 3, f. 65–68; WANG 1936:155, f. 26; NIE 1936:45, f. 15 A, B; RAMPI 1939a:304, f. 21–23; SILVA et PINTO 1948:172, t. 2, f. 13; WOOD 1954:286, f. 206 a, b, c; SILVA 1956a:68, t. 12, f. 4; TRÉGOUBOFF et ROSE 1957:116, t. 25, f. 15; CURL 1959:306, f. 121; HALIM 1960a, t. 4, f. 15, 18; – 1963:498, f. 22, 23; BALLANTINE 1961:225, f. 51, 52; KLEMENT 1964:355, t. 2, f. 3; YAMAJI 1966:99, t. 48, f. 2.
C. schroederi NIE 1936:47, f. 16 A, B.

The early confusion in the recognition of this species arose from widely differing interpretations of the taxon, MÜLLER's original description not being sufficient to delimit the species precisely. Most early authors have drawn (accurately?) specimens in which the right antapical horn does not lie in a smooth arc with the posterior profile and left antapical horn, instead being bent outwards from the base (e.g. EHRENBERG 1836). The var. *balticum* SCHÜTT (and also the forma *subsalsum* OSTENFELD) is probably closest to the type variety (JÖRGENSEN 1911) and consequently that taxon should now become the var. *tripos*.

The taxonomic confusion and the infraspecific variability has been summarised by SOURNIA (1968a; see also HASLE & NORDLI 1951, and LOPEZ 1955). In brief, recent work has indicated that there is a continuum of variation linking the var. *pulchellum* (B. SCHRÖDER) LOPEZ with the var. *atlanticum* (OSTENFELD) PAULSEN (i.e. from those small specimens with a greatly reduced right antapical horn, to those larger cells with well developed, widely placed antapical horns). In addition there is a group of other varieties and forms, mostly occurring in colder or brackish waters (see JÖRGENSEN 1911, 1920 and SOURNIA 1968a). Variability in individuals forming chains, and also in cultures, has been described (summarised by HASLE & NORDLI 1951).

The following infraspecific taxa have been recognised in the present material:

C. tripos var. *atlanticum* (OSTENFELD) PAULSEN as above. The transdiameter of the cells ranges from approximately 65–90 µm.

C. tripos var. *indicum* (BÖHM) comb. nov. (basionym = *C. pulchellum* var. *indicum* BÖHM 1931b:420, f. 38 a, b), omitted by SOURNIA (1968a) although it corresponds to his fig. 43 and the present figs. 168, 169. The transdiameter of the body is relatively narrow, below 60 µm and the posterior profile is flatter than the other variants. The degree of slope with relation to the girdle plane varies greatly.

C. tripos var. *pulchellum* (B. SCHRÖDER) LOPEZ, as above, ranging from forms with a greatly reduced right horn – f. *pulchellum* (f. 147), to those with smoothly-curving antapical horns fairly widespread – f. *semipulchellum* JÖRGENSEN (f. 150).

Variants with greatly reduced horns, especially the antapical horns, are known to occur clonally and are thus not recognised formally here.

Stations: var. *atlanticum*: 30, 31, 34, 38–45, 54, 56, 60, 70, 100, 101, 103, 108, 135, 144, 147, 153, 162, 283, 284, 286–290, 302, 320, 326, 371, 420
var. *indicum*: 13, 16–20, 23, 27, 31, 32, 34, 35, 37, 38, 41, 50, 54, 60, 65, 69–72, 87, 88, 90, 91, 93, 96, 99–103, 108–110, 112, 114–118, 134, 149, 150, 153, 162, 285–287, 290, 291, 294, 302, 315, 325, 327–329, 332, 334, 336, 341, 360–363, 365, 368, 370, 371, 375, 396, 419
var. *pulchellum* f. *pulchellum*: 99, 103, 129, 134, 294, 299, 312, 320, 323, 326
var. *pulchellum* f. *semipulchellum*: 287, 295, 341, 359, 362, 371, 413, 419

The var. *indicum* was the most widespread representative of the species, occurring in the Andaman Sea, Bay of Bengal, the Arabian Sea and at a cluster of stations at the southern end of the Mozambique Channel. It was sporadic in the central Indian Ocean, extending to 28 °S only.

The var. *atlanticum* occurred in patches, notably in the northern Andaman Sea and Bay of Bengal (both regions under river influence), and near the Gulf of Aden. Other occurrences were more scattered.

The var. *pulchellum* occurred only rarely in the northern parts of the ocean, being sporadically widespread in the western and southern regions. The f. *pulchellum* extended to 32 °S. The f. *semipulchellum* was found chiefly to the north and south of the Mozambique Channel where the other form was absent.

There have been many earlier records of the species in the Indian Ocean, WOOD's (1963a) list requiring the addition of the records of SILVA (1956a, 1960), TSURUTA (1963), DURAIRATNAM (1963), ANGOT (1965), ANGOT & GÉRARD (1966), SOURNIA (1966, 1968 a, b, 1970), TAYLOR (1967), NEL (1968), SUBRAHMANYAN (1968), THORRINGTON-SMITH (1969), and ANGOT (1970).

Family Ceratocoryaceae LINDEMANN

Members of this family all belong to one genus, typically bearing multiple strong spines limited to the hypotheca.

Genus *Ceratocorys* STEIN

This genus was the subject of a detailed study by GRAHAM (1942). In addition, the most common species, *C. horrida* STEIN was further dissected into its component plates by BALECH (1949b). GRAHAM subdivided the genus into two subgenera, both sharing the same plate formula but differing in whether or not the first postcingular plate is distinguishable from the sulcal area or not. He recognised seven species, omitting one (*C. magna*) which is recognised here. *C. alleni* TAFALL (1942), additional to those included by GRAHAM, is in all probability based on a left daughter cell of *C. gourretii* shortly after division, the antapical spines being totally lacking.

The plate formula of the genus was given by KOFOID (1910) as P, 3′, 1^a, 5″, 8c, 6‴, 1p, 1⁗. Although excessive in the number of girdle plates this formula seems better than that given by GRAHAM (1942). Despite the latter's extensive analysis of the plates he interpreted the apical plates in a peculiar manner, giving them as (P) 2′, 2^a. . . . . From an examination of his and other published figures, plus the "Anton Bruun" material (chiefly with the scanning electron microscope for this purpose, e.g. fig. 529) it is concluded here that the apical arrangement can be considered as either P, 3 + 1′, or P, 3′, 1^a, depending on whether one interprets a small quadrangular plate at the junction of the right quadrants as an intercalary plate or a displaced apical plate. Occasionally it touches the pore plate.

BALECH's (1949b) detailed analysis was marred by unusual plate terminology. The only plate he termed as an apical plate was the apical pore plate (P here) and he reversed KOFOID's notation for those plates customarily considered to be apical plates with that for the precingular plates. LOEBLICH III (1970) has interpreted BALECH's analysis as revealing a pattern with the following formula: P, 3', 1a, 5'', 6c, 10s, 4''', 1''''. In this action he differed from KOFOID's interpretation chiefly by lumping two small plates with the sulcals, considered by KOFOID (and here) to be postcingulars (see also GRAHAM's, 1942 discussion of the position of the small plate apparently homologous with the first postcingular plate of KOFOID), and he did not acknowledge the existence of a plate homologous to 1^p (see text fig. 1, p. 97 comparing *Heteraulacus* with the gonyaulacoid plate pattern).

Here the formula for the genus is interpreted as: P, 3' (+ 1' or 1^a), 5'', 6c, 7s (8?), 6''', 1^p, 1''''.

Ceratocorys armata (SCHÜTT) KOFOID Plate 26, Figs. 269 a, b, 272, 273

SCHILLER 1936:444, f. 486 a–e; GRAHAM 1942:40, f. 53 A–E, f. 54 A–E; MARGALEF, HERRERA, RODRIGUEZ-RODA, et LARRAÑETA 1954:92, f. 3 e, f; YAMAJI 1966:71, t. 33, f. 3; STEIDINGER, DAVIS, et WILLIAMS 1967, t. 7, f. c; STEIDINGER et WILLIAMS 1970:48, t. 15, f. 41 a, b.
Vix WOOD 1954:314, f. 243 a, b; – 1968:42, f. 95.
Non HALIM 1960a, t. 3, f. 19.

This species differs from *C. magna* chiefly in size (see latter), being much smaller. It also has much less elaborate thecal ornamentation than either *C. magna* or *C. reticulata* GRAHAM. Spines are restricted to the antapical region. There are three or four well-developed spines associated with the antapical plate. Additional small spines are associated with the ridged edges of the plates. *C. aultii* GRAHAM is also similar, sharing a similar number of antapical spines (although the latter seem to be more slender) and also in having the first postcingular plate strongly demarcated outside the sulcal groove. In *C. aultii* the sulcal region seems to be wider posteriorly and slightly curving, but GRAHAM (1942) only illustrated a megacytic specimen and so shape distinctions are difficult to make. *C. skogsbergii* GRAHAM differs chiefly in that the first postcingular is incorporated into the sulcal area (only one small quadrangular plate, the second postcingular, being visible at the junction of the left girdle end and the sulcus, instead of two). There are other differences as well.

In fig. 273 a specimen is shown in lateral view which is much more apico-antapically compressed than usual.

Stations: 29, 68, 72, 94, 97, 103, 133, 144, 283, 294, 326, 330, 331, 348, 371.
(compressed form: 23, 294)

It occurred at scattered stations over a wide area, the most southerly being station 133 at 30 °S.

The species is an inter-oceanic tropical to subtropical species with a distribution similar to *C. horrida*, only it is rarer and is supposedly less thermotolerant (GRAHAM 1942). In addition to the Indian Ocean references provided by WOOD (1963a) there are those of SOURNIA (1966a, 1967a, 1968b, 1970), and TAYLOR (1967).

Ceratocorys bipes (CLEVE) KOFOID Plate 26, Figs. 271, 276; Plate 43, Figs. 514

SCHILLER 1936:445, f. 448 A; GRAHAM 1942:43, f. 57 A–F; GAARDER 1954:16, f. 15; WOOD 1963c:16, f. 56; YAMAJI 1966:32, t. 33, f. 4; TAYLOR 1972b, t. 2, f. 12.

This small species is readily recognisable by the presence of the two bulbous posterior projections of the cell body each bearing a spine with delicate fins. Both spines arise from the antapical plate. GAARDER (1954) observed a specimen, apparently of this species, which lacked the posterior spines. Her figure, a ventral view, agrees well with other figures of this species other than the lack of spines.

Stations: 13, 20, 63, 103, 143, 150, 283.

It occurred in small numbers in the northern Indian Ocean (both the Arabian Sea and Bay of Bengal), not occurring further south than station 150 (3 °S).

This seems to be one of the most highly stenothermal members of the genus (see also *C. gourretii*), only occurring in warm temperate waters when it is carried there by intrusions of currents originating in tropical waters (e.g. the Kurosiwo off Japan). It has not as yet been found in the southern Indian Ocean. WOOD (1963a) has provided a few (three) Indian Ocean records of the species, to which his own (1963c) should be added. It is known from the Pacific Ocean in the vicinity of Japan.

Ceratocorys gourretii PAULSEN Plate 26, Figs. 274, 277

SCHILLER 1936:446, f. 488 B; GRAHAM 1942:44, f. 59 A–H; WOOD 1954:314, f. 244 a, b; SILVA 1956a:69, t. 11, f. 13; TRÉGOUBOFF et ROSE 1957:117, t. 27, f. 5; BALLANTINE 1961, f. 61 (sub *C. horrida*); WOOD 1968:42, f. 96; MARGALEF 1969b:346, f. 1 A, B; LÉGER 1972a:28, f. 13.

Vix RAMPI 1950c:246, t. 4, f. 17.
Syn.: . . . . *C. alleni* TAFALL 1942:443, t. 36, f. 20, 22, 23, 26. *C. jourdanii* KOFOID 1910 . . . . YAMAJI 1966:71, t. 33, f. 2; non GOURRET, 1883, (*Dinophysis jourdanii*) nec SILVA 1949:363, t. 9, f. 15.

This small species resembles *C. horrida.* It can, however, be easily distinguished by its usually smaller, rotund (but laterally flattened) body. Its length is 38–62 µm as opposed to a range of 38–97 µm for *C. horrida* (GRAHAM's size data). It possesses similar dorsal and ventral spines to *C. horrida,* except that they are never as extensive as in the latter, particularly with regard to the dorsal and ventral spines. Also it has only three antapical spines instead of the four in the latter species. As with *C. skogsbergii* the first postcingular plate is hidden within the sulcal region. The confused systematic history of *C. gourretii* has been summarised by GRAHAM (1942).* *C. alleni* TAFALL is almost certainly a left daughter cell of this species shortly after division. RAMPI (1950c) has figured a specimen purported to be *C. gourretii* but which has four antapical spines.

In one of the specimens illustrated here (fig. 274) the dorsal spine is subdivided into two spinelets. This is unusual but has been observed previously (e.g. GRAHAM 1942, f. 59 F). The other specimen is apparently a new daughter cell (left moiety), which resembles *C. kofoidii* PAULSEN (probably synonymous).

Stations: 57, 58, 61, 63, 64, 71, 98–100, 103, 108, 154.

Like *C. bipes* this is a relatively rare, high stenothermal species. In the material it occurred mostly within the northern Indian Ocean, with one record near Mauritius (st. 154). GRAHAM (1942) found that it was apparently absent from water below 22 °C. TAYLOR (ms., 1964) found it at a few stations in the southwestern Indian Ocean, apparently carried south by the Agulhas Current, and it has also been found in that locality by NEL (1968). Indian Ocean references additional to those listed by WOOD (1963a) and above are: SILVA (1956a, 1960), SOURNIA (1967a, 1968b, and 1970), and TAYLOR (1967).

Ceratocorys horrida STEIN Plate 26, Figs. 265–268, Plate 46, Fig. 529

CANDEIAS 1930:39, t. 2, f. 55 (sub *Caratocorys*); SCHILLER 1936:443, f. 485 a–c; GRAHAM 1942:38, f. 1 B, f. 47 A–E, 48 A–H, 49 A–K, 50 A–C; MARGALEF 1948b:49, f. 3c; BALECH 1949b:166, f. 1–29; RAMPI 1950c:246, t. 4, f. 20; GAARDER 1954:16, f. 16 a, b; WOOD 1954:313, f. 242 a, b; SILVA 1955:173, t. 10, f. 1–4; TRÉGOUBOFF et ROSE 1957:117, t. 27, f. 4; BALLANTINE 1961:225, f. 62 non 61; HALIM 1967, t. 1, f. 14; STEIDINGER, DAVIS et WILLIAMS 1967, t. 7, f. a, b; WOOD 1968:42, f. 97; STEIDINGER et WILLIAMS 1970:48, t. 16, f. 42 a, b; HERMOSILLA 1973a:29, t. 3, f. 1–5; TAYLOR 1973b, f. 4 c (opt. rev.).

C. horrida is one of the most common members of the tropical and subtropical dinoflagellate community. It is also highly distinctive in appearance. The only other species of *Ceratocorys* which possesses strongly extended spines on the upper part of the hypotheca is *C. gourretii* PAULSEN (see previous species for comparisons and also the comments under the genus). It has long been known that the species undergoes a drastic change in appearance as a result of cell division comparable to that found in the dinophysoid dinoflagellates. The left daughter cell receives the two large dorsal and ventral spines and has to reform the four antapical spines (fig. 266), whereas the right daughter cell has to reform the two large upper spines, initially possessing only the four antapical spines (fig. 268). GRAHAM (1942) has reported specimens which were apparently reforming all the spines, although none of this stage were observed in the "Anton Bruun" material. GAARDER (1954) has illustrated an aberrant fission product with one mature antapical spine.

Apart from the effects of division there is a great deal of variation in the length of spines. The var. *horrida* (including var. *longicornis* LEMMERMANN) has a relatively stout body with moderately long spines approximating 60–90 µm in length whereas the var. *extensa* PAVILLARD has a relatively smaller body with extremely long, divergent spines reaching more than 130 µm in length (fig. 267). KARSTEN's (1907) multiple-spined var. *africana* was probably teratological.

Stations: var. *horrida*: 13, 14, 17, 19, 21, 23, 26, 28–32, 35–38, 43, 51, 53, 56, 59–72, 85, 91–96, 98–100, 102, 103, 106, 109, 110, 113–116, 125, 135, 140–143, 150, 153, 154, 161, 282, 287, 294, 297, 301, 302, 315, 317, 322–324, 326, 327, 329, 334–336, 340, 342, 370, 413.
var. *extensa*: 64, 66.

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* In contradiction to GRAHAM, but in agreement with PAULSEN (1930), *C. jourdanii* (GOURRET) KOFOID is not believed to be a synonym of *C. gourretii.* GOURRET's figure (1883, pl. 3, f. 55, as *Dinophysis jourdanii*) shows an angular, elongate body with wide girdle lists and long spines. The presence of only three, instead of four antapical spines therefore appears to be teratological, possibly due to damage, the cell being attributable to *C. horrida.* The specimens figured by SCHÜTT (1895, pl. 4, f. 20, 1–20, 4) are *C. gourretii,* as is the figure of MURRAY & WHITTING (1899, pl. 30, f. 5 a). KOFOID (1910) gave the first detailed description of the present taxon.

The var. *horrida* was very common and widespread in the northern Indian Ocean, particularly in the Bay of Bengal and Andaman Sea. It was relatively abundant at station 100. It only occurred south of 20 °S to the west and south of Madagascar. TAYLOR (ms., 1964) found it in October and January in Agulhas Current water, occurring furthest south in the former month. NEL (1968) has also found it in the southwestern Indian Ocean.

GRAHAM (1942) considered this species to be a valuable indicator of tropical and subtropical water, especially as it is common (although not usually abundant) and inter-oceanic. It does not apparently tolerate water below 19 °C. It is not as stenothermal as *C. bipes* or *C. gourretii*, whose values as indicators are, however, limited by their rarity.

In addition to the Indian Ocean records mentioned above and those listed by WOOD (1963a) there are those of SILVA (1956a), TSURUTA (1963), SOURNIA (1966a, 1967a, 1968b, 1970), TAYLOR (1967), NEL (1968), THORRINGTON-SMITH (1969), and ANGOT (1970).

Ceratocorys magna KOFOID Plate 26, Fig. 270
SCHILLER 1936:445, f. 487.
Syn.: *Ceratocorys spinifera* MURRAY et WHITTING, pro parte, t. 30, f. 6d.
C. reticulata auct. non GRAHAM ... TAYLOR 1973b, f. 6 c.

This rare species is very similar to *C. armata* but it is much larger in size, the diameter (excluding girdle lists) exceeding 125 µm whereas the same dimension in *C. armata* usually does not exceed 93 µm (more commonly near 70 µm). KOFOID (1910) created the species for one figure (an apical view only) erroneously included by MURRAY & WHITTING with figures of the taxon now known as *Gonyaulax ceratocoroides* KOFOID. GRAHAM did not find such large specimens and consequently considered that MURRAY & WHITTING may have made an error, omitting the species from his treatment of the genus.

In the "Anton Bruun" material there were quite a large number of specimens agreeing in size with *C. magna*, and there is consequently no doubt that they exist. Whether or not they deserve distinction from *C. armata* is another question which cannot be resolved as yet. The species has strong resemblances to *C. reticulata* GRAHAM, which is also large, reaching 114 µm in diameter but the latter is not as heavily marked and the antapex of the latter is not as wide as in *C. magna*, leading to a sharper angle subtended by the sides of the hypotheca to each other.

In its strongest development of thecal ornamentation, *C. magna* bears ridges which appear almost vermiform and the plates bear broad intercalary flanges which may cover much of the face of some of the plates (cf. TAYLOR 1973b, f. 6 c).

Stations: 13, 31, 32, 38, 49, 52–54, 57, 62, 66, 68, 69, 71, 87, 91, 92, 97, 100, 101, 103.

Considering the scarcity of records by other authors the species was surprisingly common in the Bay of Bengal/Andaman Sea area. It must be noted that, as *C. reticulata* was only distinguished from *C. magna* after the primary analysis was complete, some of these records may refer to *C. reticulata*.

The species was first described from the North Atlantic Ocean and has since been recorded apparently only by TRAVERS & TRAVERS (1965) and SOURNIA (1968b) from Tuléar in the Indian Ocean.

Ceratocorys reticulata GRAHAM Plate 26, Fig. 275; Plate 43, Fig. 510
– 1942:42, f. 55 A–D.
Vix SILVA 1955:174, t. 10, f. 5–7.
Non TAYLOR 1973b, f. 6 c [= *C. magna*].

This is a large species, rivalling *C. magna* in size (and possibly being confused with it at times). It can, however, be recognised as a separate species for the present on the basis of its size (length without spines 84–98 µm, diameter without lists 86–114 µm), its very regular, close reticulation (not quite as angular as shown by GRAHAM 1942) and the narrowness of the antapex which results in the walls of the hypotheca subtending a sharper angle to each other than in *C. magna*. It is similar in its plate arrangement to *C. armata*. There are three antapical spines although SILVA (1955) reported four antapical spines, her figure being difficult to assign to this species because of lack of detail.

Station: 51.

A single specimen was found in the northern Bay of Bengal.

GRAHAM (1942) found it in both the Atlantic and Pacific Oceans in water above 20 °C. SILVA's (1955) record from Angolan waters is doubtful. She has also (1956a) recorded it from the Mozambique coast.

Family Cladopyxidaceae LINDEMANN

BALECH (1964c, 1967b) has redefined the zoological equivalent of this family (Cladopyxidae KOFOID), so that it now includes three genera: *Cladopyxis, Palaeophalacroma* and *Sinodinium*. The formula for the group is 3–4', 3–4^{a}, 7'', 6c, 5–6s, 6''', 2''''. The absence of girdle lists and the left-handed displacement are features which also unite the family. The genus *Micracanthodinium* DEFLANDRE has appendages similar to those of *Cladopyxis* but they are unbranched. It might also be assigned to this family. However the tabulation of its members has not been established as yet.

Genus *Cladopyxis* STEIN

Unlike the other members of this family *Cladopyxis* usually has three apical plates instead of four, and its most distinctive feature is the possession of elongate appendages, usually branched distally. *Micracanthodinium* DEFLANDRE is distinguished by the possession of very slender, simple appendages, lacking terminal branching. Several of the species listed under *Cladopyxis* by SCHILLER (1936) belong to DEFLANDRE's genus [e.g. *M. setiferum* (LOHMANN) DEFLANDRE (1937), *C. bacillifera* SCHILLER and probably *C. claytonii* HOLMES]. *C. quadrispina* PAVILLARD appears to be quite different, lacking a well-defined girdle and with only four spines in a sub-parallel arrangement. The latter species is of enigmatic systematic position.

A distinctive feature of the type species of *Cladopyxis* is the peculiar arrangement of the appendages, all of which arise in a single plane which lies at an angle to the girdle plane, highest on the dorsal side and lowest on the ventral side (see especially fig. 506). It might be possible to re-arrange the genera taking this feature into account, in which case KOFOID's rejected genus *Acanthodinium* might be recognised for those species in which the spines arise both dorsally and ventrally on the epi- and hypothecae. This is the case for one of the two species he originally described: *A. spinosum* KOFOID, but the other, described first, *A. caryophyllum* KOFOID, does not have this feature and is probably synonymous with *C. brachiolata*.

A curious feature of *C. claytonii* HOLMES is that the whole theca dissolves rapidly in a sodium hypochlorite solution, suggesting a possibility of further generic distinction based on the nature of the theca.

Cladopyxis brachiolata STEIN Plate 25, Figs. 255–259 a, b; Plate 43, Figs. 506–508

SCHILLER 1936:471, f. 541 a, b; RAMPI 1950c:246, f. 22; MARGALEF et DURÁN 1953:44, f. 13 k; GAARDER 1954:17, f. 17 a–j (vix b); TRÉGOUBOFF et ROSE 1957:118, t. 27, f. 14; HALIM 1960a, t. 2, f. 13; BALECH 1962b:166, t. 23, f. 364; – 1964c:28, f. 1–10; WOOD 1968:43, f. 100.

Syn.: *C. steinii* ZACHARIAS 1906:567, f. 20.
? . . . *C. caryophyllum* (KOFOID) PAVILLARD . . . . SCHILLER 1936:470, f. 540; WOOD 1968:44, vix f. 101.
Cladopyxis sp., MARGALEF, HERRERA, RODRIGUEZ-RODA et LARRAÑETA 1954:92, f. 2 h.

This, the type species of the genus, has been described in detail by BALECH (1964c). GAARDER (1954) asserted that the degree of branching should not be a specific character in view of variability seen by her in North Atlantic material. Thus she believed that *C. caryophyllum*, in which the terminations of the processes are usually quadripartite, with fine "webbing" between the points, is synonymous with *C. brachiolata* in which the terminations undergo repeated branching. It had already been established by earlier authors that the tablature of both taxa is the same. Cell division can undoubtedly influence the appearance of the cells, and probably accounts for the observation of individuals with less than five appendages, or possibly, those with less than ten. Also, in some cases one finds cells with spines in differing states of maturity (e.g. fig. 257). The small protuberance in fig. 259a may represent a new appendage beginning to develop. Fig. 256 illustrates a cell of the *C. caryophillum* type. It can be seen that the whole cell is more robust than in the more-branched cells. The only cells observed with the scanning electron microscope were of this type.

When seen in side-view it can sometimes be seen that the postero-dorsal region protrudes from the rest of the cell body, being demarcated by a broad intercalary band (cf. BALECH 1964c, and figs. 506, 507 here).

GAARDER (1954) also included *C. spinosa* (KOFOID) SCHILLER in the synonymy of this species. However, as indicated in the introductory remarks to this genus, it was shown by KOFOID to have spines arising from precingulars 2'' and 7'', instead of being limited to 3''–6'' on the dorsal side of the cell. It also appears to have spines on the dorsal side of the hypotheca, instead of only on the ventral side as in *C. brachiolata*.

Her suggestion probably arose from the observation of individuals similar to that in fig. 258 here. However, the latter are clearly different from *C. spinosa* and are probably immature forms of *C. brachiolata* in which all, instead of some of the spines are incompletely developed.

BALECH (1964c) has distinguished a species which is very similar to the small-bodied (length of body 26.5–35 µm), five-spined members of *C. brachiolata*, but has four small anterior intercalary plates instead of two very large ones and one smaller one. He called this species *C. hemibrachiata*. In a personal communication he has suggested that all five-spined individuals may belong to this taxon, but the few details of the tablature of such specimens seen in this material do not seem to support this view.

The specimen figured here as fig. 255 had unusual tabulation, having several small supernumery plates, one of which, to the right of the first apical plate, corresponds with one of the anterior intercalary plates of BALECH's species, leading to some doubt as to the permanence of these features.

Stations: 66, 70, 71, 99, 103, 109, 142, 299, 302, 305, 306, 312–315, 317, 318, 320, 332, 334.

GAARDER (1954) found that her specimens occurred only in the warmest parts of the North Atlantic Ocean. However, in the South Pacific Ocean BALECH (1962b, 1964c) found the species between 25 °S and 35 °S. In the "Anton Bruun" material, although it occurred at a few stations both in the Bay of Bengal and the Arabian Sea, it was widespread and common between 10 and 33 °S during cruise V (chiefly in March), the only period at which it occurred south of the equator. Its maximum abundance was at station 313, close to 30 °S, being one of only a few species which increased in abundance near the Subtropical Convergence Region.

The robust specimens corresponding to *C. caryophyllum* were restricted to the southern stations on the 75 °E meridian, co-occurring with the slender, more-branched forms. The smallest cells occurred at warmer stations.

Genus *Palaeophalacroma* SCHILLER

The detailed thecal study of *P. unicinctum* by BALECH (1967b) has revealed that its plate structure shows considerable affinities with the genus *Cladopyxis*, its name being misleading with regard to its systematic position. The plates of the smaller members attributed to the genus have not been determined as yet. The upper girdle edge is more prominently developed than the lower edge, the latter being poorly defined in two of the species. This is very similar to the subgenus *Sphaerodinium* of *Heterodinium*. BALECH has indicated that *Peridinium herbaceum* SCHÜTT is probably a member of *Palaeophalacroma*, making the appropriate combination.

Palaeophalacroma sphaericum sp. n. Plate 25, Figs. 261 a, b

The cells are small and approximately isodiametric (length 20 µm, transdiameter 18 µm), the surface of the theca being marked by only a few prominent ridges and scattered poroids. The girdle is demarcated only by an upper ridge showing distinct left-handed displacement at the flagellar pore site. The first apical plate and the apical pore are defined by ridges, more strongly developed on the right than on the left side. The ventral area is also bounded by ridges on both sides. It extends two thirds of the distance from the girdle to the antapex. It is narrow throughout its length.

Other plate details could not be determined. However these features are sufficient to indicate a similarity to *P. verrucosum* SCHILLER (fig. 260) and at the same time, permit distinction of the two taxa on the grounds of the more rounded shape and greater development of ridges associated with the apical plate and ventral in *P. sphaericum*. Some of the smaller cells attributed to *P. unicinctum* by SCHILLER (1931) may have been this taxon, his species now being interpreted in a distinctly different manner by BALECH (1967b; see below).

Type locality: Station 161, west of the island of Mauritius (two specimens).

Palaeophalacroma verrucosum SCHILLER Plate 25, Figs. 260 a, b

SCHILLER 1931:48, f. 49 c.

This species, not seen previously except by SCHILLER, is small, being similar in size to *P. sphaericum* sp. n. (length 18–28 µm, transdiameter 16–22 µm) but it is more ovoid in shape. The specimen observed here had a flattened antapex although this feature was not included in the original description. A further distinction between the two species is that in *P. verrucosum*, although the upper girdle ridge is clearly developed, the ridges associated with the first apical plate (apparently very narrow) are difficult to see, and on the hypotheca there is only a single ridge passing towards the antapex to the left of the flagellar pore.

In both species the only other visible thecal structures are scattered poroids, thought by SCHILLER to project as small bumps in the case of *P. verrucosum.*

Station: 156.

A few specimens were found near 30 °S in the southern Indian Ocean. The species was originally found in the Adriatic Sea and SCHILLER states that it was also found by HENTSCHEL in tropical waters of the Atlantic Ocean. There are no previous Indian Ocean records of the species.

Palaeophalacroma? sp. Plate 25, Figs. 262 a–c

A puzzling specimen was found which appears to be intermediate between *Cladopyxis* and *Palaeophalacroma* in several respects. BALECH (1967b) has shown that, in addition to the possession of processes, *Cladopyxis* also differs from *Palaeophalacroma* in the number, size and shape of certain plates. The present specimen has a plate arrangement more similar to that of *Cladopyxis* than *Palaeophalacroma* although its lack of processes precludes inclusion of it in the former genus, and its large body (length 45 µm, transdiameter 36 µm) exceeds that found in members of *Cladopyxis.* It has a superficial resemblance to *Palaeophalacroma unicinctum* SCHILLER (= *Heterodinium detonii* RAMPI 1943b, and possibly *Epiperidinium michaelsarsii* GAARDER 1954). However, in addition to being larger, the first apical plate was broader, there were only three apical plates (not all shown in the figure) instead of four, the right sulcal plate is short in the apical axis, and the posterior sulcal plate is large and posteriorly pointed, cell features resembling *Cladopyxis.*

Station: 155.

One specimen was found to the south of Mauritius.

Family Gonyaulacaceae LINDEMANN

Genus *Alexandrium* HALIM

This genus was proposed for a small species, *A. minutum,* producing red water near Alexandria, Egypt (HALIM 1960b). At the time of description it was not distinguishable from *Pyrodinium* on the basis of primary plate pattern, although HALIM compared it only to *Glenodinium.* As with earlier authors dealing with *Pyrodinium,* HALIM did not recognise the essential homology of the small plate next to the sulcus, termed by him a ventral accessory plate, with the small, so-called first precingular plate of *Gonyaulax.* HALIM's analysis of the sulcal plates differs from *Pyrodinium* and *Gonyaulax,* but apparently through incomplete dissection (see text fig. 1).

In fact this species has a primary plate pattern very similar to *Gonyaulax monilata* HOWELL, the plate corresponding to the gonyaulacoid first apical plate not reaching the apical closing platelet (the arrangement provisionally designated as 3 + 1' here).

It is suggested that both of these, plus another species, be transferred to the genus *Pyrodinium* (see under the latter for the resulting new combinations).

Much of the confusion that surrounds these taxa arises from a lack of recognition of plate homologies within the gonyaulacoid genera. A possible basic thecal pattern from which various genera may have developed has been presented elsewhere (TAYLOR 1976). Text figure 1 illustrates the similarities in basic pattern between *Heteraulacus, Alexandrium, Pyrodinium* and *Gonyaulax.*

Genus *Amphidoma* STEIN

The hypotheca of members of this genus is identical to that of *Gonyaulax,* possessing an asymmetrically placed posterior intercalary plate. However the epitheca is unlike any other member of the family. It has six apical plates and no anterior intercalary plates. The first apical plate is slender. BALECH (1971b) could find only three sulcal plates in *A. nucula* (below).

The only previous record of a member of this genus in the Indian Ocean is SOURNIA's (1972a) discovery of *A. acuminata* STEIN.

Amphidoma nucula STEIN Plate 25, Fig. 263
SCHILLER 1935:316, f. 332 a–d; SILVA 1955:154, t. 6, f. 1, 2; BALECH 1971b:35, t. 9, f. 168–174.
Syn.:*Murrayella spinosa* KOFOID 1907b:192, t. 9, f. 57.
Amphidoma spinosa (KOFOID) KOFOID et MICHENER 1911:275; SCHILLER 1935:316, f. 333.
Gonyaulax rouchii RAMPI 1948:4, f. 4.

This species has recently been subjected to detailed thecal analysis by BALECH (1971b). Its biconical shape is somewhat variable, the hypothecal pole sometimes appearing smoothly confluent with the central part of the cell, at other times (as here), more abruptly formed. The antapex can bear a small spinelet. The length varies from 30 to 50 µm.

A. steinii SCHILLER is very similar to this species but possesses linearly arranged pores and lacks any distinct antapical projection. In *A. acuminata* STEIN and *A. elongata* KOFOID et MICHENER the antapex is more drawn out, although one of the specimens included under *A. nucula* by BALECH approaches them in its hypothecal extension. *A. caudata* HALLDAL is distinctly different, with a conical epitheca, shallow, rounded hypotheca, and a well-developed antapical caudate process. In the absence of original or contemporary figures of the several other species described by KOFOID & MICHENER (1911), further comparisons are difficult.

Station: 327.
Only one cell was observed in a sample from near the southern tip of India. The species is known from the warmer waters of the Atlantic Ocean and the Southern Ocean. It has not been previously recorded from the Indian Ocean.

Amphidoma sp. Plate 25, Fig. 264

BALECH (1971b) has emphasised the variability in shape of *A. nucula* STEIN and, taking his comments into consideration, the illustrated specimen may correspond to a form in which the hypothecal projection blends smoothly with the broadest part of the cell. It shows a resemblance to STEIN's type figures, but the latter are too stylised to permit a detailed comparison. The specimen did not possess an antapical spinelet. The surface markings were fainter than in the specimen in fig. 263. It is smaller (length 24 µm, transdiameter 15 µm) than the size range usually given for *A. nucula*, being similar in size to *A. obtusa* KOFOID et MICHENER. The apical plate features for the latter do not agree with the present specimen, the precingular plates being described as shorter than the apical plates other than apical 1'. The specimen figured by WOOD (1963b, f. 135) may be this taxon, being similar in shape, but no size data or ventral details were provided by him.

Station: 374.
A single specimen was found near the southern African coast south of the Mozambique Channel.

Genus *Gonyaulax* DIESING
[*Goniaulax* auct. nonnull.]

Syn.:*Acanthogonyaulax* GRAHAM 1942:52.
Amylax MEUNIER 1910:51.
Roulea GOURRET 1883:63, 86.
Steiniella SCHÜTT 1895:151.
Spiniferites MANTELL 1850:191; 1854, text figs. 77–79.
Hystrichosphaera WETZELL 1933:136 (nom. nud.).

Although many of the species of this ecologically important genus are well characterised, the limits of the genus itself are more difficult to set. As can be seen from Table 3 there are several genera recognised at present which have plate formulae similar to that of *Gonyaulax*.

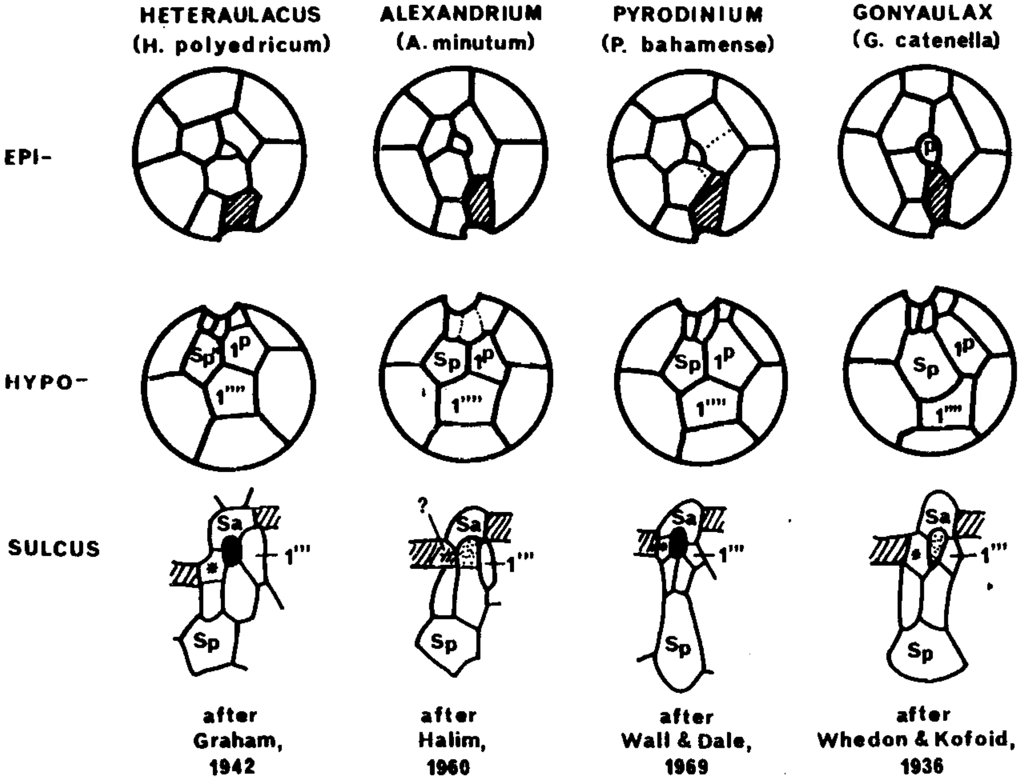
The usual, primary character of a left-handed (descending) displaced girdle is a useful criterion when combined with the plate formula. Furthermore, another feature associated with most species of *Gonyaulax* is a pronounced asymmetry in the development of the various posterior plates (Text fig. 1), probably related to the girdle distortion. Thus it appears that the plate customarily designated as the posterior sulcal plate (Sp), which is usually strongly developed in *Gonyaulax*, may be a homologue of a plate usually termed an antapical plate (as in *Heteraulacus*, which was considered to have three antapical plates by most authors until recently). From Text fig. 1 it can be seen that there seems to be a gradual transition between the Sp, 1P, 1'''' arrangement and that formerly designated as 3''''(cf. TAYLOR 1976 for a more detailed account).

Table 3. The plate formula of *Gonyaulax* and related genera (contemporary, uniform interpretation).

Gonyaulax	P	3–4'	0–4^a	6''	6C	5–10S	5–6'''	1P	1''''
Protoceratium	P	3'	1^a	6''	6C+t	9S	5'''	1P	1''''
Alexandrium	P	3+1'	0^a	6''	6C(+t)	5– 7S	6'''	1–2P	1''''
*Fragilidium***	P	4'(+1'?)	0^a	9''(8''?)	12C	8S	7'''	1P	1''''
Spiraulax	P	4'	1^a	6''	6C	6S	6'''	1P	1''''
Pyrodinium	P	3+1'	0^a	6''	6C	6S	6'''	1P	1''''
*Peridiniella**	P	4'	3^a	7''	6C	?	6(5?)'''	1P	1''''
Heteraulacus	P	3'	0^a	7''	6C	5S	6'''	1P	1''''
Ceratocorys	P	3'	1^a	5''	6C	5–10S?	4–6'''	1P?	1''''
Pacbydinium	P	3'	0^a	5''	?	3S	5'''	0P	3''''
Ampbidoma	P	6'	0^a	6''	6C	3S?	6'''	1P	1''''

* This genus was not figured by its originators (KOFOID & MICHENER 1911) and has not apparently been seen by others since its description. The number of postcingular plates was tentatively given for the type species. In another species to be described from the Andaman Sea elsewhere by this author only five postcingular plates are present.

** In comparing this genus with *Gonyaulax* it seems evident that BALECH's 2'''' is a homologue of the Sp, 1'''' corresponds to the usual 1P, and p is the 1'''' of *Gonyaulax*. Furthermore, his 7''' seems to correspond to a right sulcal plate. His twelfth girdle plate could also be considered a sulcal plate corresponding to that asterisked in text fig. 1, but here it is left as a girdle plate.



Text fig. 1. Plate patterns of three gonyaulacoid taxa and a possible relative (plate designations homologised).

* There are at least two or three further small sulcal plates in the vicinity of the flagellar pore. The plate asterisked has been termed a "transitional plate" but, comparing it to the plates of *Peridinium*, it evidently corresponds to the "right accessory sulcal plate" of GRAHAM (1942).

The recognition of various parasystematic "series" within the genus has persisted since first introduced by KOFOID (1911a). The clusters of species should be either accorded the formal status of subgenera, or be raised to the level of genera. The former course seems wiser until more species have had their plate structure more fully elaborated and until their life-cycles are better known. Cyst types may prove to be useful in group recognition. At present these are known to embrace several distinctive types including smooth-walled cysts, cysts with low ridges, cysts with numerous short spines, and "hystrichosphaerid" cysts with a fixed number of long, branched projections corresponding to the plate arrangement of the parent theca (see WALL 1970, 1971a for a review of these types and the fossil genera they correspond to). Archeopylar (excystment pore) position and features may also be useful. For example, WALL & DALE (1969) have advocated the continued distinction of *Pyrodinium* from *Gonyaulax* partly on archeopylar features. WALL (1970) has suggested that the genus may have to be subdivided in view of the dissimilar cyst types present.

At present it appears that the generic name *Gonyaulax* DIESING (1866) may not have strict priority, as it is known that the genus *Spiniferites* MANTELL (1850, 1854) was created for fossil forms, some of which are known to be cyst stages of members of *Gonyaulax*. If it could be established that the type of *Spiniferites* [designated as *S. ramosus* (EHRENBERG) MANTELL by LOEBLICH & LOEBLICH, 1966] corresponded to the resting stage of a species of *Gonyaulax* then the former genus would have priority. However, it is apparently extinct and such evidence, other than by inference from living species, is not likely to be forthcoming. It should not be difficult to make a case for the conservation of *Gonyaulax* DIESING against *Spiniferites* MANTELL under the circumstances, although an attempt by SARJEANT (1964) to conserve *Hystrichosphaera* against the latter has been opposed (LOEBLICH & TAPPAN 1967) and rejected (SARJEANT 1970).

In the genus *Pyrocystis*, as recently emended (TAYLOR 1972a), the cyst stages form the dominant phase of the life-cycle, gonyaulacoid motile cells existing for less than a day (SWIFT & WALL 1972). This genus is at present united with *Dissodinium* in a separate family, the Pyrocystaceae, but the latter is probably at least diphyletic, and should be discarded.

The first authors to study the ventral area in detail appear to be GRAHAM (1942) and NIE (1947), but the latter's paper was only an abstract. He reported finding six sulcal plates in *C. diegensis*, *C. digitale*, *G. spinifera*, and *G. monacantha* but he did not illustrate their formation. Unlike *Peridinium*, *Gonyaulax* appears to be rather variable in the number and arrangement of sulcal plates although the large, curved anterior sulcal plate and the large posterior plate appear to be fairly constant.

Gonyaulax areolata KOFOID et MICHENER Plate 35, Fig. 408
– 1911:270; SCHILLER 1935:278.

The recognition of this species is difficult in view of the lack of a figure accompanying the original description. SCHILLER merely translated KOFOID & MICHENER's diagnosis into German. He did, however add a distributional detail (see below).

The present designation is based on visual reconstructions of KOFOID & MICHENER's descriptions (see also *G. minuta*, *G. pavillardii*, and *G. subulata* here). In this case the fit appears to be reasonably good. The specimen here was a bit smaller (length 34 μm instead of 40 μm). The apical horn was here opened, apparently due to ecdysis. One possible distinction between this specimen and that of KOFOID & MICHENER is the suspected presence of an anterior intercalary plate on the right ventral surface of the epitheca. However, this could not be clearly determined in the present specimen and could thus perhaps have been overlooked by KOFOID & MICHENER if indeed, it is a separate plate from the apicals. Ribs were not evident on the girdle lists. The antapical spines were not strongly developed here. They are apparently outgrowths from the margin of the ventral area. The girdle displacement is approximately one girdle width and the ends do not overhang one another. The surface of the plates is densely covered with small areolae (reticulae?).

Station: 365.

A single specimen was found in the vicinity of Tuléar, southern Madagascar. SCHILLER (1935) has recorded the species from the Indian Ocean but he did not provide any details other than "Indik". This record was omitted by WOOD (1963a). There do not seem to be any further records other than the original description from the equatorial Pacific Ocean.

Gonyaulax brevisulcatum DANGEARD Plate 36, Figs. 411–413
– 1927b:338, f. 5 a, b; SCHILLER 1935:279, f. 282 a, b.
Syn.: *Gonyaulax* spec. PAULSEN 1930:39, f. 24.
G. paulsenii GAARDER 1954:25, f. 28 a–d.
Vix *G. borealis* NORDLI 1951a:53, f. 6 a–f.

A fairly large (diameter 58–78 μm), distinctive shperical species which has, however, caused confusion, due to an apparent tendency towards plate pattern variability. Also, early figures of the species were poorly drawn. In fact, in this interpretation it is assumed that DANGEARD's (1927b) iconotype is optically reversed as, although he assigned it to *Gonyaulax* [which is characterised by left-handed (descending) displacement] he figured it as having a right-handed displacement. Optical reversals are common in the work of earlier authors and the danger is still prevalent, usually resulting from focussing through the specimen.

The species is worthy of note, for its epitheca is rather peridinoid in plate arrangement, with its three symmetrically arranged anterior intercalary plates (not shown here; see GAARDER 1954), but the hypothecal plates are typically asymmetrical in the manner distinctive for *Gonyaulax*. The greatest variability, if the interpretation here is correct, involves the sutures which normally attach on either side of the first apical plate (between the apicals and precingulars). Although these usually insert approximately mid-way between the girdle and the apex, in one specimen found here these were entirely lacking (fig. 413). GAARDER (1954) has given the plate formula of *G. paulseni* as (P), $4'$, 3^{a}, $7''$, (? C, ? S), $6'''$, 1^{p}, $1''''$.

A further distinctive feature is the horse-shoe-shaped ridge, open to the ventral side, which surrounds the apex of the cell. It is difficult to see a distinct apical closing platelet in the area endorsed by the ridge. This ridge may serve as a convenient identification aid.

The species nearest to *G. brevisulcatum* seems to be *G. sphaeroidea* KOFOID. The latter is smaller (diameter approximately 30 μm), lacks the apical ridge, and has unusually expanded antapical portions of the sulcal lists, similar to those in *Diplopsalis*. A narrow plate which lies along the right margin of the apical plate is unusual and might be considered either another apical plate or an anterior intercalary plate (see BALECH 1962b). It is also strongly porulated, the porulae being fairly evenly spaced apart. In *G. brevisulcatum* the pores are delicate, close-set, and difficult to see under routine conditions. GAARDER's (1954) specimen described as *G. sphaeroidea* may have been *G. brevisulcatum* as it was 65 μm in diameter and had an apical eminence. She did not show epithecal plates other than the first apical plate.

NORDLI (1951a) figured a peculiarly-shaped cyst within the cells he termed *G. borealis*. The cysts resembled *Peridinium trochoideum* in general shape. A cyst was observed within one of the cells here although it did not have a peridinoid shape. It was much smaller than the mother cell. The chief distinction of the mature *G. borealis* theca seems to be its much smaller size (diameter 22–28 μm). Its plate pattern is almost identical to that given by GAARDER (1954) for *G. paulseni*. It occurs in colder waters. It may be a boreal infraspecific variant.

This taxon also shows a very strong resemblance to *Peridinium globosum* DANGEARD (1927a, commented on also by GAARDER 1954). The latter differs apparently in lacking girdle displacement and the apical ridge. The specimen figured here as fig. 412 particularly resembles the latter, but it has a displacement of approximately one girdle width. It has the apical ridge but because this is shifted more towards the ventral side it is not obvious in ventral view. The antapical view given by DANGEARD apparently shows two antapical plates unequal in size. However, such a figure, if incomplete, could be reconciled with NORDLI's gonyaulacoid hypotheca. A further difference is that although these anterior intercalary plates are present in both, they are displaced to the left side in *P. globosum*. The most difficult feature to account for is that one author would create two taxa in different genera for the same species.

In summary, the variability shown by the "Anton Bruun" specimens suggests the possibility that several taxa previously thought to be distinct may in fact, be the same, even including one assigned to *Peridinium*.

Stations: 94, 96, 98, 301.

Found at three closely-situated stations in the Bay of Bengal and one station near Mauritius. Only a few cells were seen in each sample. DANGEARD found both *G. brevisulcatum* and *P. globosum* in the eastern tropical Atlantic Ocean. MATZENAUER (1933) has recorded *G. sphaeroidea* from the Indian Ocean, but the present taxon does not appear to have been recorded from the Indian Ocean in any of its guises. However, THORRINGTON-SMITH (1969) has recorded *P. globosum* from the vicinity of Durban. It is probably a tropical, inter-oceanic species.

Gonyaulax bruunii sp. n. Plate 35, Figs. 409 a–d
BALECH 1971b:27, t. 7, f. 125–129 sub "*G. monacantha minor* PAVILLARD? "
Vix PAVILLARD 1916:22, t. 1, f. 8.

A small, rotund species with well-developed apical horn and strong, slender, single antapical spine arising from the right posterior margin of the posterior sulcal plate. Girdle displaced from one to two girdle widths; left-handed (descend-

ing). Plates marked only by pores. Thecal component occupying the usual first apical plate position divided into two plates by a median suture passing from the girdle to the apex. Sixth precingular plate is triangular. First post-cingular plate is small, narrowly rectangular. Posterior intercalary plate not extending as far towards the antapex as the posterior sulcal plate. Girdle and sulcal regions demarcated by strong ridges, other sutures weakly marked.
Length (without spine): 30–36 µm; diameter 20–26 µm (includes BALECH's 1971b size data).
Plate formula: 4', 6'', 6C, 5(?)S, 6''', 1P, 1''''.
Iconotype: Plate 35, fig. 409 a–d.
Type locality: Station 404. Western Mozambique Channel, Indian Ocean.

Named for Anton Bruun and similarly for the vessel which made the cruise during which the species was discovered.

This is undoubtedly the same organism that was recently figured and described by BALECH (1971b) from the equatorial Atlantic Ocean. He also found that the plate usually considered as the first apical plate was divided into two moieties and BALECH's observations can be used to augment those given here. However, the specimens are so alike as to provide little information on variability. This agreement in appearance, combined with being apparently the only species of *Gonyaulax* to possess a divided "first apical plate", seems to be more than sufficient for the creation of a new species. There are resemblances to *G. monacantha* PAVILLARD (not present in the material) which is probably closely related, and also to *G. subulata* KOFOID et MICHENER (see comments under that species here).

The suture observed to subdivide the first apical plate is also reminiscent of the appearance of *Ensiculifera mexicana* BALECH (1967a) in which it was discovered, however, to be due to the presence of a long, delicate spine projecting from a plate in the ventral area. *Ensiculifera* seems to have a strongly peridinoid plate arrangement, including symmetrically developed antapical plates. The type species, *E. mexicana,* lacks an antapical spine.

Station: 404.

Two specimens were observed in material from a single station off the coast of Mozambique in the western Mozambique Channel region. BALECH (1971b), as indicated, found his specimens in equatorial Atlantic Ocean waters.

Gonyaulax ceratocoroides (MURRAY et WHITTING) KOFOID Plate 35, Fig. 410; Plate 44, Figs. 515, 516
SCHILLER 1935:309, f. 321 a–c; WOOD 1963c:13, f. 47; – 1968:57, f. 144.
Syn.: *Ceratocorys spinifera* MURRAY et WHITTING 1899:329, t. 30, f. 6 a, b, e non c vix d.
Acanthogonyaulax spinifera (MURRAY et WHITTING) GRAHAM 1942:53, f. 64 A–E; 65; BALECH 1962b:163, t. 22, f. 357, 358.

In the introductory comments to *Gonyaulax* it was indicated that, as a result of scanning electron microscopy, GRAHAM's (1942) claim that the taxon has 9 precingular plates is doubted. Thus the chief grounds for recognising the taxon as a separate genus fall away. Some of the results of scanning microscopy are given here on plate 44.

The species is highly distinctive in view of its well-developed fins and spines arising from the margins of the hypothecal plates. In these respects it mimics the genus *Ceratocorys* but it does not have a similar plate pattern. The scoop-like ventral-antapical opening of the sulcus is also unusual, resulting from the strong growth of the fins.

Stations: 16, 17, 52, 58, 60, 64, 99, 100, 103, 417.

Common at scattered stations in the Andaman Sea and Bay of Bengal. It was also present at one station off the east coast of Africa.

As it was not particularly rare in the Bay of Bengal material it is strange that the only previous Indian Ocean record is that of TAYLOR (1967). It is known from the type locality: the tropical Atlantic Ocean (also from the Mediterranean Sea), and from the Pacific Ocean. It is probably limited to warm-temperate to tropical waters.

Gonyaulax diegensis KOFOID Plate 35, Fig. 400
SCHILLER 1935:281, f. 285 a–i; WANG 1936:148, f. 21; RAMPI 1943a:319, f. 1; SILVA 1949:342, t. 5, f. 4; – 1952a, t. 2, f. 10; KISSELEV 1950:220, f. 389 a–d; MARGALEF et DURÁN 1953:33, f. 8 a–e; WOOD 1954:259, f. 164; – 1968:58, f. 148; HADA 1967:16, f. 27 B.

This is a distinctive, common species in many parts of the world, most similar to *G. digitale* KOFOID. It can be recognised by its more rotund shape, especially of the body of the epitheca and by the apparently invariable presence of non-reticulated margins to the plates. These are apparently not intercalary zones. The latter may be present in addition to the marginal zones. KOFOID (1911a) considered that a further distinction was a small fourth apical plate (in *G. digitale* there are only three apical plates). A small plate was seen in the position of 4′ in the present specimens, confirming the possibility of using this distinguishing feature.

Station: 35.

Found at only one station in the Andaman Sea.

It is, however, one of the more eurythermal species of the genus, being more common in temperate than in tropical waters. It has been recorded previously from the Indian Ocean by WOOD (1954, 1962 in 1963a), SUBRAHMANYAN (1958), SILVA (1956a, 1960) and TAYLOR (1967).

Gonyaulax fragilis (SCHÜTT) KOFOID Plate 36, Fig. 420

SCHILLER 1935:305, f. 316 a–h vix i; KISSELEV 1950:225, f. 394a–z; WOOD 1954:260, f. 166; – 1968:58, f. 150. Vix RAMPI 1943a:325, f. 13 (*G. hyalina*?); MARGALEF et DURÁN 1953:35, f. 8 n (*G. hyalina*?); SILVA 1956a:66, t. 11, f. 10 (*G. hyalina*?); BALECH 1962b:159, t. 22, f. 351 (*G. hyalina*?).

This species is very similar to *G. inflata* and *G. hyalina* and has probably been confused with the latter on several occasions. Seen in full ventral view the shape is distinctive, being oval with a rounded convex antapical profile (the specimen figured here is seen somewhat apically, the sulcal depression producing a bilobed antapical appearance). Although ostensibly this species could be distinguished from *G. inflata* in having three plates instead of one this distinction is doubted (see also under *G. inflata*). In fact it appears that *G. fragilis* and *G. inflata* have very similar apical plates. The first apical plate is very narrow and lies in a mid-ventral groove. Apicals two and three are situated rather symmetrically to the left and right of the elongate, well developed apical closing platelet which extends well into the dorsal surface, whereas in *G. hyalina* there is a narrow plate extending down the right side of the first apical plate, making an additional fourth apical plate.

The surface markings on *G. fragilis* and *G. inflata* are very similar, with strongly developed reticulation bearing short spines at the reticular junctions on most plates. On the apical plates this is apparently reducted to short, disjunct ridges arranged in semiparallel or radiating rows. The latter structure may, however, be an immature developmental state. This author has not seen regularly parallel ridges such as those figured by SCHILLER (1935, f. 316 i), RAMPI (1943a, fig. 13), SILVA (1956a, fig. 10), or BALECH (1962b) on any specimens. Indeed, such markings, combined with a relatively broader shape, might be considered one of the distinguishing features of *G. hyalina* from *G. fragilis*. The iconotype of SCHÜTT did not show any parallel ridges on *G. fragilis*. If the above authors are correct in their inclusion of linearly marked specimens, then fig. 420 here may be a small specimen of *G. inflata*. These species are evidently too imperfectly known to permit a sound decision at present, but these assignments seem the most reasonable to this author.

Stations: 301, 311, 313.

Found at only three stations; one near Mauritius and the others in the south-central region.

If SILVA's (1956a) record from Mozambique is transferred to *G. hyalina* then this species has only been previously recorded from the Indian Ocean by WOOD (1962, in 1963a). The world distribution of this species is uncertain because of possible confusion with *G. hyalina*. However, it is probably an inter-oceanic species and is restricted to tropical or warm temperate waters.

Gonyaulax fratercula BALECH Plate 35, Fig. 392

– 1964b:31, t. 4, f. 47–58; TAYLOR 1975:114, f. 8 a–e.
Vix *G. catenella*? sensu KLEMENT 1964:352, t. 2, f. 2.

This species is one of a group of closely similar chain-forming members of *Gonyaulax* (others are *G. catenella* WHEDON et KOFOID, *G. cohorticula* BALECH, *G. conjuncta* WOOD) or non-chain-formers [*G. acatenella* WHEDON et KOFOID, *G. tamarensis* LEBOUR which are nevertheless frequently found in pairs or fours. All appear to have identical plate formulae: P, 4′, 0^a, 6″, 6C, 7S+t, 6‴, 1^p, 1⁗ and differ in the size and shape of particular plates (see also comments here under *Alexandrium* for other species also very similar but which have a 3 + 1′ arrangement). The distinction of these species has been extensively discussed by BALECH (1964b, 1967a, 1971b), STEIDINGER (1971) and TAYLOR (1975).

G. fratercula is intermediate in size, with a length of 32–49 µm and a diameter of 29–47 µm. It is smaller in length than *G. cohorticula* (48–55 µm) although there is an overlap in the diameters of the cells (41–47 µm). In ventral view they can be most readily distinguished by the shape of the anterior sulcal plate. In *G. fratercula*, as with many others of this group, the upper (apical) surface of the anterior sulcal plate curves in a smooth arc, indenting the epitheca with a concave notch. In *G. cohorticula* the anterior sulcal plate deeply and rectangularly indents the epitheca, lacking the curving profile of *G. fratercula*. "Curtain-fin" development (closing the girdle), shown in *G. fratercula* by BALECH, is known to be a variable phenomenon (TAYLOR 1975).

Gonyaulax catenella is similar in size but is usually flattened rather than isodiametric. It is for this reason (combined with size data) that KLEMENT's specimens from the Gulf of California are tentatively attributed to *G. fratercula* although plate information on his specimens is lacking.

G. conjuncta WOOD is problematic because little information regarding the plate pattern was provided in the original description, and no indication whatever of size. In a later work (WOOD 1968) he gave the cell length as 25 μ. BALLANTINE (1961) figured and described specimens which she attributed to *G. conjuncta* but her specimens from Zanzibar were 50–63 μm in length (equal to breadth). In view of this confusion WOOD's taxon is difficult to assess.

G. acatenella is also similar to *G. fratercula*. However, in addition to differences in the apical plates (especially 3' and 4') the epitheca is higher than the hypotheca in *G. acatenella*. The latter has been found to produce paralytic shellfish poison and to vary in the degree of development of pigmentation (PRAKASH & TAYLOR 1966).

It is possible that HALIM's (1967) specimens of *G. tamarensis* var. *excavata* from the coast of Venezuela were, in fact, *G. fratercula*, but insufficient information is available to determine this.

Stations: 16, 29, 36, 38.

A few short chains were observed at four stations, all within the Andaman Sea.

The species was originally described from the Mar del Plata in the western South Atlantic Ocean. It does not appear to have been recorded from elsewhere as yet.

Gonyaulax fusiformis GRAHAM Plate 36, Figs. 421, 422
– 1942:50, f. 63 A–G.

This is a rare tropical species, readily identifiable by reference to GRAHAM's detailed plate description. At first sight it might be confused with *Spiraulax jolliffei*, as it is similar in its biconical, fusiform shape. It is, however, more slender. Like *S. jolliffei* there is a large rectangular anterior intercalary plate on the right ventral face of the epitheca. However, there are two intercalary plates in *G. fusiformis* due to an extension of the dorsally-situated second apical plate which surrounds the right side of the apical closing platelet, thus isolating it from plates on the right side near the apex. The easiest means of recognition however, is the presence of a long, narrow, bent first apical plate in *G. fusiformis* in the customary position, the genus *Spiraulax* being recognisable by the absence of a plate in this position. *G. birostris* has much more drawn out apical and antapical horns than *G. fusiformis*.

There is a strong resemblance between *G. acuta* KOFOID et MICHENER and *G. fusiformis*. They are very similar in size and shape, girdle and sulcal features. However, as with the other species of *Gonyaulax* described by KOFOID & MICHENER (1911) a figure of their species is lacking. Consequently, their statement that there are three apical plates and no anterior intercalary plates can only be taken literally. These features can then, theoretically, serve to distinguish the species.

Stations: 33, 62, 67, 68, 103.

Found in small numbers at one station in the northern Andaman Sea and four in the western Bay of Bengal.

This species does not seem to have been found previously in the Indian Ocean. It is known from the tropical Atlantic and Pacific Oceans and appears to be relatively stenothermal and tolerant of low phosphate values (GRAHAM 1942).

Gonyaulax glyptorhynchus MURRAY et WHITTING Plate 35, Fig. 404
SCHILLER 1935:301, f. 310 a–c.
Vix WOOD 1954:260, f. 167.

This is an extremely rarely observed species although it is possible that it has been confused with the closely similar species, *G. highlei* MURRAY et WHITTING and *G. birostris* STEIN which have been found more frequently. It is similar to *G. highlei* in size but can be distinguished, according to the original descriptions, by the lack of girdle reticulae in *G. glyptorhynchus* and the smoothly spinous nature of the antapical horn in *G. highlei*. The antapical horn is hirsute in *G. glyptorhynchus*.

The main distinction between *G. birostris* and this species is the considerable difference in size. The cell body length (excluding processess) is 32–40 µm, the diameter being 23–30 µm (a combination of MURRAY & WHITTING's size information and that found here), whereas *G. birostris* is usually described as almost twice the size. For this reason WOOD's figure (above) is questioned. No size was given by him and his figure lacks a magnification. However, it is drawn almost identical in size to a figure labelled as *G. birostris*. His figures do not illustrate any clear distinction between the specimens. In a later publication (WOOD 1968) he suggested a possible synonymy between *G. birostris, G. highlei,* and *G. glyptorhynchus.*

From KOFOID & MICHENER's (1911) description (no figure, but see below) *G. subulata* is also similar to *G. glyptorhynchus.* It differs most obviously in that the antapical spine is short and subulate (narrow, sharply-pointed) and the apical horn is shorter in relation to the body. Its body dimensions are similar to those of *G. glyptorhynchus.*

As with many other of MURRAY & WHITTING's figures the iconotypes are upside down. This can be readily determined by the position of the oval ventral area. Also, the apical plates were shown apparently after ecdysis as they are here. Future studies should further elucidate the relationships with *G. highlei* and *G. birostris.* RAMPI (1952b) has provided a reasonably detailed analysis of the latter.

BALECH (1962b) considered that *G. glyptorhynchus* was synonymous with *G. birostris* but on the basis of size they have been maintained as distinct here. His description corresponds to *G. birostris* STEIN.

Stations: 51, 130.

Only two specimens were seen: one in the northeastern Bay of Bengal and the other in the south-central Indian Ocean below 30 °S. It has been previously recorded from the Indian Ocean by WOOD (1962, in 1963a), TAYLOR (1967), and SOURNIA (1968b, 1970). It is apparently a very rare inter-oceanic species, recorded relatively recently from the Atlantic Ocean by GAARDER (1954).

Gonyaulax hyalina OSTENFELD et J. SCHMIDT Plate 36, Figs. 415, 416, 418, 419
SCHILLER 1935:306, f. 318 a–c; WOOD 1954:264, f. 177.
[*G. fragilis* auct. nonnull.?]

This species, originally described from the Gulf of Aden, is similar to *G. fragilis* and *G. inflata* (see also comments under both latter species). It is readily distinguishable from them by its less narrow first apical plate, the presence of a slender fourth apical plate on the right ventral surface, and the strong, parallel longitudinal ridges passing over an otherwise delicately marked theca (secondary markings consist of delicate side ridges projecting at right angles to the primary ridges and pores). It usually has a broader shape, the specimen in fig. 415 being an exception. An apical view of a dissociated, delicately developed epitheca is shown in fig. 419. The fourth apical plate can be seen as a narrow rectangle, lacking markings other than peripheral ridges. From the original figures it appears that there may be an anterior intercalary plate situated on the right ventral side, but it may be obscured by the surface markings and could not be unequivocably demonstrated here. Its presence remains a possibility, however. As noted under *Oxytoxum, O. gigas* KOFOID shows some surprising resemblances to this species in its plate structure, and it may in future be transferred to the genus *Gonyaulax* if the arrangement of plates is in agreement with the latter.

Secondary spines projecting out from the margins of the postcingular plates were quite commonly observed (fig. 418). A further distinctive feature appears to be the lack of strong ridges on the large posterior intercalary plate as well as the sulcal plates, although this may vary developmentally.

The specimen in fig. 415 has a slender shape, also seen in smaller specimens. Individuals down to 44 µm in length have been found, the large cells exceeding 75 µm.

Stations: 29, 30, 33, 35, 37, 38, 43, 51, 54, 57, 60, 62, 71, 93, 100, 102, 114, 118, 142, 150, 315, 322, 328, 329, 412, 417.

This was one of the more widespread dinoflagellates in the material, particularly in the northern Indian Ocean and at all seasons. It has been previously recorded from the Indian Ocean by MATZENAUER (1933) and WOOD (1962, in 1963a).

SCHILLER's (1935) error, perpetuated by WOOD (1954), indicated a northern Atlantic Ocean distribution for this species. In fact, although it has been recorded from the Pacific as well as the Indian Ocean, it does not appear to have been found yet in the Atlantic Ocean. However, it is possible that some of the Atlantic Ocean (Gulf Stream) or Mediterranean Sea records of *G. fragilis* may refer to *G. hyalina,* in which case it is an inter-oceanic, warm water species.

Gonyaulax inflata (KOFOID) KOFOID Plate 36, Fig. 417
SCHILLER 1935:308, f. 319; RAMPI 1950a:7, f. 2; MUÑOZ, HERRERA et MARGALEF 1956:76, f. 1 m, n (sub *Gonyaulax* c.f. *inflata*);
BALECH 1962b:157, t. 22, f. 343–348.

Syn.: *G. pavillardii* DANGEARD 1927b:340, f. 6 b, c.
Non *G. pavillardii* KOFOID et MICHENER 1911.
G. dangeardii (DANGEARD) SCHILLER 1935:281, f. 284; WOOD 1968:57, f. 146.
G. sp. A. MARGALEF et DURÁN 1953:35, f. 8 t–v, x, y.

This is a large, tropical species. The specimens here assigned to this species were quite similar to those figured by KOFOID and BALECH but were broader antapically. KOFOID did not provide much on which to base comparisons but BALECH has given a detailed description. The identification here is based chiefly on its large size (length 80–165 µm), and conical epitheca, combined with a hypotheca with a flattened base usually, but not always, sloping more to the left. The surface of the plates is intensely reticulated with short spines on the hypotheca, the epitheca showing only short, parallel ridges in radiating patterns in the Indian Ocean specimens. An unusual specimen is figured here. It possessed a large bulge on the left side of unknown significance. Only one specimen was seen in this state. DANGEARD's (1927b) figure did not show the first postcingular plate or posterior intercalary plate. However, it is thought that these plates, so distinctive of *Gonyaulax*, were missed due to tilting of the specimen. Also, according to KOFOID (1911a) the species is supposed to have only one apical plate. However, it is here thought that four apical plates exist, an extremely reduced first apical plate lying within the narrow mid-ventral furrow, two symmetrically arranged large apicals lying to the left and the right of the apical closing platelet and a smaller dorsal closing plate. BALECH (1962b) also found four apical plates plus the apical closing platelets.

From supplementary observations made here an affinity with *G. fragilis* and *G. hyalina* becomes evident. The surface markings are similar, and the extremely narrow first apical plate, demarcated by strong ridges is common to both. So also is the narrow, slit-like apical closing platelet extending well onto the ventral side, and the symmetrical appearance of the second and third apical plates (see comments here under *G. fragilis*).

Station: 286.
Three specimens were observed at one station near the Gulf of Aden.
This is a new record for the Indian Ocean under any of the names listed above. The species is known from the Atlantic Ocean, the Spanish coast, and the Pacific Ocean. It is probably an inter-oceanic, warm water species.

Gonyaulax kofoidii PAVILLARD Plate 35, Figs. 393, 394
SCHILLER 1935:285, f. 288; RAMPI 1943a:320, f. 4; SILVA 1949:343, t. 5, f. 8, 9; WOOD 1954:260, f. 168 a–c; – 1968:59, f. 151.

Although observed fairly often, this species has been only rarely illustrated. The occurrence of apical ecdysis is evidently common, thecae with apical plates gaping apart being often observed (as here, fig. 393, the specimen being almost identical to that of KOFOID 1911a, pl. 14, f. 30).

The species is perhaps most similar to *G. pacifica* (fig. 395) but it can be readily distinguished by its much smaller size (length without spine 90–110 µm, – 150? WOOD 1968), the more tapering shape of its hypotheca, a smaller degree of dorso-ventral flattening (considerable in *G. pacifica*), and closer set pores. There are numerous other differences, especially in the ventral region.

Due to a few instances when individuals were seen forming ecdysal cysts, and the co-occurrence of individuals of one cyst type in a sample with numerous cells of *G. kofoidii*, it was possible to describe the cysts formed by this species (fig. 394). The cyst wall is smooth with an apical projection and a slight trace of a girdle depression but no structure corresponding to the antapical spine (as is present on the cyst of *G. pacifica*, fig. 397).

Stations: 15, 41, 43, 54, 64 (cysts only at 37, 38, 47, 56).
Fairly common at stations in the Bay of Bengal (also at one station in the Andaman Sea).
The species has been previously recorded from the Indian Ocean by WOOD (1954, 1962 in 1963a), SILVA (1956a), SOURNIA (1966a, 1968b, 1970), and ANGOT (1970). It is a cool-temperate to tropical inter-oceanic species.

Gonyaulax milneri (MURRAY et WHITTING) KOFOID Plate 35, Fig. 401; Plate 44, Figs. 517 a–c
SCHILLER 1936:522, f. 612 a–c; RAMPI 1952a:108, f. 11; WOOD 1963b:37, f. 133; – 1968:59, f. 152.

The species has apparently only been originally illustrated four times before, once in the type description (as *Goniodoma milneri* MURRAY et WHITTING 1899), once by RAMPI and twice by WOOD. For this reason it is figured here both as a line drawing and in scanning electron micrographs.

It is highly distinctive and unlikely to be confused with any other species of *Gonyaulax*. At first sight it does resemble a member of *Heteraulacus* (= *Goniodoma*) but the tabulation on the epitheca is like that of many *Gonyaulax* species. The theca is strongly developed, with numerous close-set pores and with ridges, lists, and spines marking the plate sutures. Neither MURRAY & WHITTING nor RAMPI illustrated the termination of the first apical plate short of the girdle, but this feature has been confirmed here several times.

Ecdysis for this species is unusual for the genus *Gonyaulax* in that it is probably lateral rather than apical (observations of MURRAY & WHITTING and original).

Stations: 101, 116, 294, 302, 332.

Found in small numbers at a few scattered stations including the Bay of Bengal, Arabian Sea, equatorial waters, and one station south of Mauritius.

The species has only been recorded from the Indian Ocean by WOOD 1962, in 1963a). It is known from the tropical Atlantic and Pacific Oceans and also from the Mediterranean Sea.

Gonyaulax minuta KOFOID et MICHENER Plate 35, Fig. 402
– 1911:271; SCHILLER 1935:287; WOOD 1968:59, f. 154.
Syn.: *G. minima* MATZENAUER 1933:450, f. 17; vix SCHILLER 1935:287, f. 291 a, b, vix 292 c–e; KISSELEV 1950:221, f. 383 a, b, vix c–e; WOOD 1954:264, f. 179; – 1968:59, f. 153.

The original description, as with others in the same work, lacks an illustration. Consequently its recognition is subjectively interpretive although in this case WOOD (1968) has provided a figure.

It is a very small species of the "polygramma group" (length 14–30 µm). It bears resemblances to *G. polygramma*, *G. pavillardii*, and *G. turbynei* but is smaller. Markings other than weak linear ridges are difficult to see. MATZENAUER (1933) figured only pores in addition to the faint longitudinal ridges and WOOD's specimen apparently only had pores. There is a slight apical eminence. WOOD's specimens apparently had a well-developed apical horn although this was not evident in the present specimens.

Details of the plate pattern are as yet lacking. MATZENAUER's original figures did not clearly distinguish between linear ridges and sutures and WOOD's figure is only a ventral view. The present material was not suitable for detailed analysis.

WOOD (1968) has distinguished between *G. minima* and *G. minuta* and his figures do, indeed, suggest a difference not evident in his, or the original descriptions. The antapex of his figure of *G. minima* is flattened and slopes strongly to the left, whereas *G. minuta* is figured with an evenly rounded antapex. Furthermore, the sulcus is shown to flare posteriorly in the former taxon. Future study is required to affirm these differences.

Station: 411.

A few specimens were found at one station in the Mozambique Channel.

The species has only been recorded once since its initial description (from the eastern tropical Pacific Ocean) by WOOD (1968, from the Straits of Florida). However, *G. minima* was first described from the Indian Ocean (MATZENAUER found it to be an abundant nanoplankton species) and subsequent Indian Ocean records of the latter comprise those of WOOD (1954, 1962 in 1963a), DURAIRATNAM (1964), and SUBRAHMANYAN & SARMA (1967).

Gonyaulax ovalis SCHILLER Plate 35, Fig. 405
.... SCHILLER 1935:289, f. 296 a–d.

The specimen illustrated agreed closely with SCHILLER's description and figures although it is somewhat smaller (length 30 µm) than the length (48–52 µm) given. SCHILLER has indicated that MATZENAUER's (1933) *G. ovata* from the Indian Ocean may be synonymous. However, *G. ovata* was not shown to possess an apical horn whereas *G. ovalis* has a distinct, short, abruptly attached horn resembling the "affixed" type in *Peridinium*. The theca of *G. ovalis* is distinctively thick in appearance.

Station: 405.

Found only at one station in mid-Mozambique Channel. It has apparently been observed previously in the Mediterranean Sea and in the southern sector of the Pacific Ocean (HASLE 1969) although, if MATZENAUER's taxon is synonymous, then it has also been observed in the Indian Ocean.

Gonyaulax pacifica KOFOID Plate 35, Figs. 395, 397; Plate 40, Fig. 482
SCHILLER 1935:290, f. 297; GRAHAM 1942:48, f. 62 A–L; RAMPI 1943a:321, f. 3; SILVA 1949:343, t. 5, f. 7; MARGALEF, HERRERA, RODRIGUEZ-RODA, et LARRAÑETA 1954:91, f. 3d; WOOD 1954:261, f. 170 a, b; TAYLOR 1969:165, t. 1, f. 1, 2.
Syn.: *Steiniella cornuta* KARSTEN 1907:348, t. 53, f. 7.
Murrayella briani RAMPI 1941a:60, t. 2, f. 1.

A distinctive, very large (for the genus), highly flattened species. The flattening is asymmetrically dorso-ventral. It is somewhat similar to *G. kofoidii* but the latter does not exceed 110 µm, whereas *G. pacifica* ranges in length (without spine) from 115 to 167 µm. Furthermore, in *G. pacifica* the porulation is more delicately developed and widely spaced. Broad intercalary bands are usually present between the apical and precingular plates. GRAHAM (1942) has carried out a detailed dissection of the theca.

During the examination of the "Anton Bruun" material the observation of unusual delicate internal plates surrounding the nucleus prior to and during cyst formation was considered of sufficient interest to warrant separate publication (TAYLOR 1969). A cyst is also shown here (figs. 397, 482). It differs from that of *G. kofoidii* in being longer and bearing a distinct antapical projection, as well as by internal details.

Stations: 18, 31, 32, 36, 37, 57, 62–66, 71, 94, 95, 99, 100, 102, 103, 108, 112, 117, 131, 161, 294, 300, 315, 322, 326.

This was the commonest member of *Gonyaulax* in the material, particularly in the western Bay of Bengal. It was scattered throughout the oceanic region, occurring as fas south as 35 °S. The species has been previously recorded from the Indian Ocean by KARSTEN (1907), WOOD (1954, 1962 in 1963a), SILVA (1956a), DURAIRATNAM (1964), TAYLOR (1967), and SOURNIA (1966a, 1968b, 1970). It is known also from the Pacific and Atlantic Oceans and the Mediterranean Sea. It is a warm-temperate to tropical inter-oceanic species.

Gonyaulax pavillardii KOFOID et MICHENER Plate 35, Fig. 403
– 1911:271; SCHILLER 1935:290.
Non *G. pavillardii* DANGEARD 1927b.

As with *G. areolata* and *C. minuta* this identification is based on a reconstruction from KOFOID & MICHENER's description due to the lack of an iconotype. This identification is more tentative because the present specimen measured only 31 µm x 30 µm whereas the original description was based on larger material (48 µm x 44 µm). Other features were, however, quite similar.

The predominantly linear markings are common to most members of the "polygramma group" (KOFOID 1911a) and in fact, it is doubtful if *G. pavillardii* can be satisfactorily separated from *G. turbynei* into which it may blend. It shares the same roundly oval posterior plate with *G. turbynei.* The latter species has a fairly distinctive arrangement of the first apical plate but the description of *C. pavillardii* is not detailed enough to make comparisons, simply stating that it is narrow and widened posteriorly.

Stations: 26, 371.

Found at one Andaman Sea station and one off the coast of Mozambique.

This species has not been previously recorded from anywhere other than the type locality (eastern tropical Pacific Ocean) although, if it is indeed distinct, it has probably been confused with *G. turbynei.*

Gonyaulax polyedra STEIN Plate 35, Fig. 396
SCHILLER 1935:291, f. 299 a–f [+ SOBRINO 1918, f. 1, 2, t. 2, f. 1–4 (t. 3, f. 1, 2), CONRAD 1926:94, t. 2, f. 37]; RAMPI 1943a:321, f. 14; KISSELEV 1950:222, f. 386; NORDLI 1951b:207, f. 1 a–f; MARGALEF et DURÁN 1953:33, f. 8 f–i; WOOD 1954:261, f. 171 a, b; EVITT 1964, f. 2 (sub. *polydrea*); WALL 1967, f. 6 A; WALL et DALE 1967, t. 1, f. N, O; WALL, GUILLARD et DALE 1967, f. 1, 2; WALL et DALE 1968b:271, t. 1, f. 17, 18, t. 3, f. 3–6; WOOD 1968:60, f. 156; WALL 1971a, t. 2, f. 7, 8, 9.
Vix MARGALEF, DURÁN et SAIZ 1955:97, f. 5 n.
[*G. polyhedra* auct. nonnul.]

A distinctive, angularly-shaped species. It resembles *G. milneri* in possessing a flat antapex, but other resemblances between the two species are minor. The surface of the theca is evenly and strongly porulated with faint reticulation also present. A peculiar epithecal tabulation has been figured by WALL (1967) in which two intercalary plates are produced as a result of being pushed away from the epex.

One type of cyst is spherical with numerous fairly short spines (NORDLI 1951b) and resembles *Lingulodinium machaerophorum* (DEFLANDRE et COOKSON) WALL (1967, WALL, GUILLARD & DALE 1967). However, it can also produce a cyst with a smaller body and longer, fewer spines.

The species is usually strongly luminescent. Aspects of its physiological periodicity have been examined by SWEENEY (1969). Ultrastructural features have been described by SWEENEY & BOUCK (1966), and SCHMITTER (1971). Its association with "red water" blooms, fish kills, and toxicity has been discussed by KOFOID (1911a), NIGHTINGALE (1936), and SCHRADIE & BLISS (1962), amongst others. Its potential as a food source has been described by PATTON et al. (1967).

Station: 109.

Only a single specimen was seen in the "Anton Bruun" material, occurring in the southeastern Arabian Sea. It is apparently of rare occurrence in the Indian Ocean, having been observed previously from this area only be MATZENAUER (1933) and WOOD (1962, in 1963a). On the other hand it is a common summer species off the California coast where it also shows a markedly neritic distribution. It commonly occurs in the latter region in summer in sufficient numbers to cause "red water" with occasionally associated outbreaks of marine fauna mortality. Although recorded several times from the Atlantic Ocean and the Mediterranean Sea it does not seem to occur in abundance there. It can be considered an inter-oceanic, warm-temperate to tropical species with a preference for neritic waters.

Gonyaulax polygramma STEIN Plate 35, Fig. 398

SCHILLER 1935:292, f. 300 a–j, 301 g, h (+ WAILES 1928:3, t. 3, f. 26–28); WAILES 1939:28, f. 74, 81; RAMPI 1943a:323, f. 8; MARGALEF 1948b:47, f. 11; SILVA 1949:342, t. 5, f. 5; 6; KISSELEV 1950:222, f. 391 a–e; WOOD 1954:261, f. 172 a–c; MARGALEF et DURÁN 1953: 33; f. 8j; MARGALEF 1957a:47, f. lm; STEIDINGER 1968:1, f. 1 a–c, 2–6, 8, 9, 10 a–c, 11–13, 14 a–c; WOOD 1968:60, f. 157; RICARD 1970, t. 2, f. n; HERMOSILLA 1973b:58, t. 31, f. 12–16.

Vix TAYLOR 1962:237, t. 1, f. 1–5; GRINDLEY et TAYLOR 1964:111, f. A. (? = *G. reticulata* KOFOID et MICHENER).

In its maturely developed state this species is distinctive with a stout apical horn, strongly developed subparallel, linear ridges, a strongly areolated theca and very slight overlap of the ends of the girdle. The posterior plate of the ventral area is shallowly depressed and widest at its antapical end. One to several spinelets, sometimes bearing a small list, are usually present along the antapical edge of the posterior plate. TAYLOR (1962) has indicated that there is an apparent progression in size and complexity of thecal development among members of the genus assigned by KOFOID (1911a) to the parasystematic "polygramma group". However, the main species to cause distinction problems are *G. minima* MATZENAUER and *G. turbynei* MURRAY et WHITTING, because of the possibility of confusion with immature cells of *G. polygramma*, and *G. reticulata* KOFOID et MICHENER (which was never illustrated). The other species of the group, *G. kofoidii*, *G. pacifica*, and *G. scrippsae* are not particularly similar to *G. polygramma*. *G. rostrata* DANGEARD is based on an inverted individual which was evidently involved in ecdysis. The ventral area plates appear to be distorted, causing judgement difficulties (see comments here under *G. minuta* KOFOID et MICHENER).

STEIDINGER (1968) has indicated that the specimens from a "red water" bloom figured by TAYLOR (1962) and GRINDLEY & TAYLOR (1964) are different from the usual concept of *G. polygramma*, a well-developed apical horn being absent. Also, the reticulation of the theca was very pronounced. She suggested that these specimens probably corresponded to the description of *G. reticulata*, an opinion with which this author concurs. Although no figures of the latter are available it seems that the figures of TAYLOR (1962) and GRINDLEY & TAYLOR (1964) may serve as illustrations of it. On the other hand, this does not resolve the problem of whether *G. reticulata* deserves separate recognition from *G. polygramma*. It appears to represent an extreme variant in a cluster of somewhat similar taxa which may or may not be distinguished at the species level. Smooth-walled cysts with an apical protuberance and slight depressions corresponding to the girdle and sulcus are produced by apical ecdysis.

Stations: 24, 34, 35, 37, 38, 52, 69, 72, 96, 103, 104, 130, 153, 154, 291, 294, 305, 341, 344.

This was the second most common representative of the genus in the material (after *G. pacifica*). It occurred at scattered stations over most of the area although, like *G. pacifica*, it was apparently absent in the Mozambique Channel region during the period of sampling (cruises VII and VIII). It was never abundant although, like *G. polyedra*, it has occasionally formed blooms dense enough to produce "red water" and marine fauna mortalities (NISHIKAWA 1901; PRAKASH & SARMA 1964; LEWIS 1967; but probably not the blooms reported by GRINDLEY & TAYLOR 1962, 1964 – see above). It does not seem to produce a specific toxin of the mussel-poison type. Blooms require temperatures above 17–20 °C.

Indian Ocean records of the species are frequent (see WOOD 1963a plus KARSTEN 1907; SILVA 1956a, 1960; DURAIRATNAM 1964; PRAKASH & SARMA 1964; TRAVERS & TRAVERS 1965; SOURNIA 1966a, 1968b; LEWIS 1967 and TAYLOR 1967). It is an inter-oceanic temperate to tropical species.

Gonyaulax subulata KOFOID et MICHENER Plate 35, Fig. 407

– 1911:270; SCHILLER 1935:303.

Syn.: *G.* sp. B. MARGALEF et DURÁN 1953:35, f. 81; DURÁN, SAIZ, LOPEZ-BENITO, et MARGALEF 1956:69, f. 2b.

G. buxus BALECH 1967a:106, t. 6, f. 100–107; SILVA 1968:38, t. 7, f. 14–17.

This is another case (see *G. areolata*, *G. minuta*, and *G. pavillardii*) where one of the "Anton Bruun" taxa showed resemblances to an unillustrated description of KOFOID & MICHENER. Here the general thecal details corresponded well with the original description, including the size (length including spine 51–58 µm, 47 µm in original; diameter 25–28 µm, 27 µm in original) the girdle being displaced approximately 1–1.5 girdle widths with none or slight overlap of the ends. The apical horn resembles that of *G. glyptorhynchus* but it is not as long. It was approximately 10 µm in length, the plates gaping apart, presumably due to ecdysis. In the figures by the other authors cited the apical horn is shown with closed plates. BALECH (1967a) has given a detailed description of the species while under the understandable impression that he was creating a new species.

The antapex of the cell can be symmetrically conical, the subulate (narrow, awl-shaped) spine being central in location (MARGALEF & DURÁN 1953), or it can arise more from the right side of the antapex (other figures, including that here). It seems most closely related to *G. bruunii* sp. n. and *G. glyptorhynchus*.

The plate boundaries are hard to see. The first apical plate is somewhat displaced towards the left side. The sixth precingular plate is quadrangular. The plates are covered with fine, irregularly reniform markings and pores.

Station: 162.

Only a few specimens were found in the vicinity of Mauritius.

The species has been found in the Gulf of Mexico and on the Spanish coast, in addition to its discovery by KOFOID & MICHENER in eastern tropical Pacific Ocean material. Consequently it is probably an inter-oceanic, warm-temperate to tropical species. It has not been found previously in the Indian Ocean.

Gonyaulax turbynei MURRAY et WHITTING Plate 35, Fig. 399

SCHILLER 1935:299, f. 307 a, b; RAMPI 1943a:324, f. 12; KISSELEV 1950:224, f. 388 a–d; WOOD 1954:263, f. 175; – 1968:61, f. 161; SILVA 1955:153, t. 6, f. 14, 15; BALECH 1971a:164, t. 35, f. 689–691, t. 36, f. 692–694.
Vix MARGALEF et DURÁN 1953:35, f. 8s; MARGALEF 1969a, f. 3G.

SCHILLER's specimen (1935, f. 307b), like a surprising number of other figures of *Gonyaulax* in his monograph, is upside down. The species differs from *G. polygramma* in being smaller (not exceeding 50 µm in length), lacking an apical horn, and having less pronounced ridges. A reticular meshwork may or may not be strongly developed. The specimen illustrated here is very similar in development to the iconotype. Specimens less than 32 µm in length (if any) are likely to be confused with the smaller members of the "polygramma group" such as *G. minima* MATZENAUER. *G. scrippsae* is also similar but possesses a distinct overlap of the displaced ends of the girdle, one result of which is that the sixth precingular plate is triangular instead of quadrangular in shape.

TAYLOR (1962) and STEIDINGER (1968) have discussed the problem of distinguishing between immature members of *G. polygramma* and *G. turbynei*. So has KOFOID (1911a). He suggested that STEIN's (1883, t. 4, f. 19) small, highly striated specimen may be an immature form of *G. turbynei* and proposed the name *G. turbynei* forma *longistriata* for it. BALECH (1971a) has provided some details of the plate formation of the species.

Stations: 63, 374.

Rare, at two stations, one off the east coast of India and the other off the east coast of Africa. It has been previously recorded from the Indian Ocean by SCHRÖDER (1906), MATZENAUER (1933), WOOD (1954), and TAYLOR (1967). It is known from the tropical and southern Atlantic Oceans, the Mediterranean Sea, and the equatorial, eastern and western Pacific Ocean. It does not usually occur in large numbers.

Genus *Protoceratium* BERGH

Due to the strongly developed reticulation on the thecae of all members of this genus it has been difficult to determine plate patterns. This can only be effectively achieved by the dissection of the theca. The formula for the genus given by SCHILLER (1936) is $1-3', 0^a, 6'', 6''', 0-1^P, 1-3''''$. He stated that an apical pore was absent although it is obviously present in one of the figures he included (his fig. 339 a) and it is definitely present in *P. spinulosum* observed here (pl. 36, fig. 414). An apical plate was mentioned by KOFOID & MICHENER (1911). WALL & DALE (1968a) found at least two different types of cysts in *P. reticulatum* which resemble fossils ascribed to the genus *Operculodinium*. Both types are spiny.

It is difficult to know whether the detailed pattern of *Protoceratium reticulatum* (CLAPARÈDE et LACHMANN) BÜTSCHLI (the type species) has been determined or not. Recently REINECKE (1967) has described what she considered to be a new species of *Gonyaulax, G. grindleyi,* providing full details of the tabulation. The plate pattern is unquestionably compatible with the genus *Gonyaulax* (P, 3', 1^a, 6", 6C+t, 9S, 6''', 1P, 1''''). However, there are also very strong resemblances to *P. reticulatum* (a resemblance also noted by LOEBLICH III 1970 who referred to REINECKE's taxon only under the latter name) and the cysts she found are identical with one type observed by WALL & DALE (1968). Transferral of the type species to another genus places other members of *Protoceratium* in a taxonomically nebulous position which will have to be resolved in the future.

Precise observational techniques make it possible to assign a species more readily to a recent, precisely defined taxon, than to an older, more equivocally described taxon. Unless the step is taken to recognise an old taxon in its presumed newly detailed guise, the result of this process is the disappearance of many species from the literature with the loss of the literature which was applied to them. Whether or not such a process is desirable is an entirely subjective problem. It would certainly be alleviated if type specimens rather than type figures (iconotypes) were available, although dissection requirements still could not be met. VON STOSCH (1969) has described features of a culture of *G. grindleyi.*

This author agrees with LOEBLICH III (1970) that *G. grindleyi* is probably the same taxon that some authors have called *P. reticulatum.* However, whether this was true for the original description can never be absolutely resolved. The lack of future records of *P. reticulatum* by authors applying critical plate criteria would be strongly supportive of their union, considering that the latter has been commonly recorded from temperate waters. BALECH (1971a) has accepted REINECKE's species without reference to a resemblance to *Protoceratium.*

Only one specimen of another species was found in the "Anton Bruun" material. A few of the sutures on the ventral surface were visible, but the remainder were masked by the heavy thecal ornamentation and an attempt to dissect it was unsuccessful.

Protoceratium spinulosum (MURRAY et WHITTING) SCHILLER Plate 36, Fig. 414
– 1936:326, f. 340.
Vix HALIM 1960a, t. 3, f. 20 (sub *Prorocentrum,* lapsus pennae).

The present observations appear to be the first since the specimen was examined by MURRAY & WHITTING (1899). It can be distinguished from all other members of the genus by the very strong, knob-like spines which project out from virtually all intersections of the strong network of ridges covering the theca. The height of the ridges is approximately 6 µm. In addition to the spines and ridges there are delicate hyaline lists which stretch arc-like between adjacent spines. The girdle lists are formed in a similar fashion. The girdle is closer to the anterior end of the cell than the posterior end. Fine pores are present in the thin "areolae" of the theca.

This specimen resembled the type specimen very closely. The size range known at present is (type specimen in brackets): length 78 (58) – 56 µm, diameter 80 – (50) µm. HALIM's (1960a) drawing from Villefranche-sur-Mer in the Mediterranean does not contain sufficient detail to be certain if it represents this species or not. The strength of spine development is not indicated clearly. It was close in size to the type specimen (length 58.5 µm, diameter 50.7 µm).

Stations: 34, 101, 117, 133.

Single individuals were observed at stations in the Andaman Sea, the Bay of Bengal, and at 30 °S in the southern central Indian Ocean. The species has only been definitely recorded from the northern Atlantic Ocean (28 °N) although if HALIM's (1960a) designation is correct it also occurs within the Mediterranean Sea.

Genus *Pyrodinium* PLATE

This genus was first thought to differ from *Gonyaulax* by the presence of 5 instead of 6 postcingular plates (e.g. by SCHILLER 1935), but a subsequent study of the type species, *P. bahamense,* by WALL & DALE (1969) found that it had the usual small gonyaulacoid first post-cingular plate. The latter study, plus that of BUCHANAN (1968) have shown that *P. bahamense* has an essentially similar plate pattern to some members of *Gonyaulax* but differs in the nature of cyst archeopyle (a complex "2A + 6P" type instead of a simple precingular archeopyle), and by the so-called first apical plate not reaching the apical closing platelet. This plate pattern seems to be intermediate between that of *Heteraulacus* and *Gonyaulax* (see text fig. 1 here, and TAYLOR 1976).

In fact, two species which have been assigned to *Gonyaulax* (*G. monilata, G. balechii*) and the single species of HALIM's (1960b) genus *Alexandrium*, also share this condition in which the plate corresponding to the gonyaulacoid first apical plate does not reach the apex, being indistinguishable in plate pattern from *Pyrodinium* at generic level detail. Details of the cysts of these species are unknown at present, and the sulcal plate details seem incompletely determined in *A. minutum*, but it is this author's opinion that the three taxa above (plus the genus *Gessnerium* which has been shown to be based on the optically reversed theca of *Gonyaulax monilata*) should be transferred to *Pyrodinium*. Cyst features, when determined, will test this conclusion.

At present the plate pattern for *Pyrodinium* can be given as P, 3–4 + 1', 0^2, 6'', 6c, 5s, 6''', 1^P, 1''''. New combinations proposed here are:

Pyrodinium monilatum (HOWELL) comb. nov.
Basionym: *Gonyaulax monilata* HOWELL 1953:153, f. 1–5.
Syn.: *Gessnerium mochimaensis* HALIM 1967 ex HALIM 1969b:619.
Gessnerium monilata (HALIM) LOEBLICH III 1970:903 (892).

Pyrodinium balechii (STEIDINGER) comb. nov.
Basionym: *Gonyaulax balechii* STEIDINGER 1971:183, f. 1 A–D.

Pyrodinium minutum (HALIM) comb. nov.
Basionym: *Alexandrium minutum* HALIM 1960b:102, f. 1 a–j.

The genus appears to have a close affinity to some of the thin-walled *Gonyaulax* species possessing minimal girdle displacement, e.g. *G. catenella* WHEDON et KOFOID, *G. acatenella* WHEDON et KOFOID and *G. tamarensis* LEBOUR and others attributed to the parasystematic "catanella" (STEIDINGER 1971) or "tamarensis" groups (TAYLOR 1975), and it is interesting that paralytic shellfish poison production is found in some members of both.

Pyrodinium schilleri (MATZENAUER) SCHILLER Plate 35, Fig. 406
– 1935:314, f. 330 a–e; TAFALL 1942:442, t. 36, f. 21, 24, 25, 27, 28.
Syn.: *Gonyaulax schilleri* MATZENAUER 1933:449, f. 16 a–e.

This species was first described by BÖHM (1931a) from the Persian Gulf. It apparently differs from *P. bahamense* in lacking the large lateral lists extending from the girdle lists to the antapical spine (on both sides, closing the antapex completely). Also it was originally thought to have five apical plates instead of the 3 + 1' of *P. bahamense.* As a result of the observations of TAFALL (1942) and here, the species is known to usually occur with a 4 + 1' configuration. As in the latter species the left antapical spine (associated actually with the sulcal list) is much longer than the right spine. Cell division can create temporarily short-horned specimens such as that figured by MATZENAUER (1933) in ventral view. The original specimens were noticeably flattened apico-antapically, but the "Anton Bruun" specimens did not exhibit such strong flattening and neither did those of TAFALL from the eastern tropical Pacific Ocean.*

Station: 18.
Two specimens were observed in a sample from the Andaman Sea near Phuket, Thailand.
The species is also known from the Persian Gulf and the Red Sea as well as the eastern Pacific Ocean.

Pyrodinium sp. ? Plate 36, Figs. 423 a–d

At first sight the individual illustrated resembles *P. balechii.* However, closer examination reveals differences which, combined with the poor resolution of ventral plates, do not permit such an identification.

The chief differences are: the presence of weak ridges on the epitheca as well as the hypotheca; the large sixth precingular plate (more like *P. minutum*); the narrow, vertically elongate first postcingular plate (also like *P. minutum*); the peculiarly situated fourth postcingular plate, surrounded by the third and fifth precingulars which have a common suture beneath it (rather like *Amphidiniopsis* WOLOSZYNSKA), the possibility of two posterior intercalary plates (or one elongate

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* STEIDINGER et al. (1967) say that some cells have characters of both *P. schilleri* and *P. bahamense*, but do not specify which *P. bahamense* has been reported to produce shellfish poison in New Guinea (MACLEAN 1973).

plate reaching as far dorsally as the antapical plate) and the flattened antapex. Also, the epitheca is not as large as the hypotheca.

The cell's dimensions were: length 31 µm; diameter 28 µm.

Station: 365.

Found at an inshore station near Tuléar, Madagascar. Only one specimen was seen.

Genus *Spiraulax* KOFOID

Syn.: *Spiraulaxina* LOEBLICH III 1970:904 (892)

Although the plate formula of this genus falls within the compass of *Gonyaulax* DIESING, KOFOID (1911b) and GRAHAM (1942) considered that the absence of a plate homologous to the peridinoid and gonyaulacoid first apical plate (usually extending mid-ventrally from girdle to apex) was sufficient to distinguish it from other fusiform gonyaulacoid taxa with a single antapical horn and "scooplike" ventral area (e.g. *G. fusiformis* GRAHAM). The presence of a large anterior intercalary plate situated on the right ventral face of the epitheca, instead of the dorsal face, is unusual but is also present in *Gonyaulax fusiformis* GRAHAM, and possibly in *G. hyalina* OSTENFELD et SCHMIDT.

A confused nomenclatural situation has arisen over the interpretation of early descriptions, leading to the proposal of three generic names and two species names, for possibly only one, or at the most two taxa. Consequently an explanation is necessary.

MURRAY & WHITTING (1899) figured a new species which they called *Gonyaulax jolliffei*. It was fusiform in shape, illustrated upside down (as were all their figures of fusiform *Gonyaulax* species, a feature curiously uncorrected by SCHILLER 1935), and their figure was evidently of a theca that had undergone apical ecdysis, the apical plates gaping apart similar to fig. 424 here. Their figures showed no first apical extending from the apex to the girdle, thus corresponding to *Spiraulax*. However, they also showed no signs of an anterior intercalary plate.

KOFOID (1911b) assumed that the anterior intercalary plate had been overlooked by MURRAY & WHITTING (1899), a not unreasonable assumption in view of numerous other omissions and stylistic interpretations by them. However, he should not, perhaps, have been as certain as his treatment suggested. His generic description was based on a detailed analysis of his own material and also corresponded to an earlier figure by ENTZ (1905). In accordance with his view that his taxon and that observed by MURRAY & WHITTING (1899) were the same he used *Gonyaulax jolliffei* as a basionym (although not terming it such), creating the new combination *Spiraulax jolliffei* (MURRAY et WHITTING) KOFOID.

GRAHAM (1942) disagreed with KOFOID's conclusion, considering that the forms observed by MURRAY & WHITTING were a different taxon to that described by KOFOID. He did not, however, have evidence for this other than MURRAY & WHITTING's figures, having only observed specimens corresponding to KOFOID's material. Consequently his creation of a new name, *Spiraulax kofoidii* GRAHAM, for KOFOID's material and his own (thus making this the type of the genus) was precipitate. As no author has yet found specimens corresponding to MURRAY & WHITTING's illustration his action seems inappropriate.

The situation has been further complicated by LOEBLICH III (1970) who, on the basis of GRAHAM's opinion, has created a new genus, *Spiraulaxina* LOEBLICH III, for the taxon observed by GRAHAM (1942) and KOFOID (1911b). The only reason given for this action is: "As noted by GRAHAM 1942, p. 54, *Spiraulax kofoidii* is not congeneric with *Spiraulax jolliffei* (MURRAY & WHITTING) KOFOID, 1911, hence *Spiraulaxina* gen. nov. is proposed for GRAHAM's species."

To summarise the situation: KOFOID created a new genus, *Spiraulax*, as the result of observations on material which may or may not be conspecific with *G. jolliffei* MURRAY et WHITTING. The description of the genus provided by KOFOID in fact excludes MURRAY & WHITTING's material if their figures are taken literally in that a dextro-ventrally situated anterior intercalary plate (1^a) is considered one of the generic criteria. If, with modern observational techniques, the existence of a taxon corresponding precisely to MURRAY & WHITTING's description can be demonstrated, then *S. jolliffei* KOFOID is not synonymous with *G. jolliffei* MURRAY et WHITTING. This has not occurred as yet and in the opinion of this author, is unlikely to. However, should such an eventuality arise, and only then, the problem can be solved either by use of GRAHAM's new name (*Spiraulax kofoidii*) or by careful stress of authorship of names, as above.

The creation of a further new genus, the type of which is *Spiraulaxina kofoidii*, seems unwarranted and confusing for it embraces the material and figures essential to the description of *Spiraulax* by KOFOID (1911b).

Until such time as specimens corresponding to MURRAY & WHITTING's figures are convincingly demonstrated to exist, especially with regard to the absence of an anterior intercalary plate on the right ventral side, this author recommends provisional acceptance of KOFOID's judgement and its consequences (see treatment of *Spiraulax jolliffei* below). The absence of a mid-ventral apical plate extending from the apex to the ventral area, together with the single, right anterior intercalary plate, seem sufficiently distinctive to warrant the separation of *Spiraulax* KOFOID from *Gonyaulax* DIESING.

If specimens corresponding to MURRAY & WHITTING's figures are discovered it would seem best to adopt GRAHAM's new name: *Spiraulax kofoidii*, for the type of the genus *Spiraulax*.

Spiraulax jolliffei KOFOID Plate 36, Fig. 424

[? *Spiraulax jolliffei* (MURRAY et WHITTING) KOFOID] .... SCHILLER 1935:312, f. 328 a–e; RAMPI 1943a:326, f. 16; MARGALEF 1948b: 47, f. 1m; WOOD 1954:265, f. 181; HALIM 1967:751, t. 7, f. 100; WOOD 1968:128, f. 399.

Syn.: ? *Gonyaulax jolliffei* MURRAY et WHITTING 1899:324, t. 28, f. 1 a, b.
Spiraulax kofoidii GRAHAM 1942:55, f. 66 A–G.
Spiraulaxina kofoidii (GRAHAM) LOEBLICH III, 1970:904.
[Orthographic variants: *jollifei* (SCHRÖDER 1906; SCHILLER 1935; HALIM 1967), *joliffei* (KARSTEN 1907)]

The criteria for the recognition of this commonly observed tropical species, together with its confused systematic history have been extensively discussed in the comments under the genus here. The genus is monospecific to date.

Stations: 53, 54, 61, 95, 98, 100, 103, 108, 161, 302, 326, 405, 420.

Common but not abundant at scattered stations in the Bay of Bengal, the eastern Arabian Sea and the west-central Indian Ocean. The majority of the stations were oceanic rather than neritic.

GRAHAM (1942) has indicated that the Indian Ocean records of SCHRÖDER (1906) and KARSTEN (1907), both referring to *Gonyaulax jolliffei* although providing no figures, should not be accepted. On the other hand he did accept MATZENAUER's (1933) Indian Ocean record. Other Indian Ocean records are those of WOOD (1962, in 1963a), SILVA (1956a), and SOURNIA (1966a as *S. jolliffei*, and 1967a, 1968b as *S. kofoidii*). The species is also known from the tropical oceanic areas of the Atlantic and Pacific Oceans.

Family Gymnodiniaceae LEMMERMANN

Members of this family all lack a theca composed of obvious plates, have ventrally inserted flagella, and lack ocelli, tentacles or cnidocysts. The degree of torsion or displacement of the girdle (left-handed) is variable.

Genus *Amphidinium* CLAPARÈDE et LACHMANN

This genus is distinguished arbitrarily from *Gymnodinium* by the location of the girdle within the anterior third of the body. The majority of members of the genus are benthic and/or sandloving, usually exhibiting either dorso-ventral or lateral flattening. The less well-known planktonic species seem to usually lack flattening (subgenus *Rotundinium* KOFOID et SWEZY).

Amphidinium sp. Plate 37, Fig. 434

This species could not be identified with certainty due to the lack of structural detail remaining from preservation. It most closely resembles several small species of LOHMANN's in size, e.g. *A. crassum* and *A. longum*, but the former has an acute epicone and a rounded hypocone, and the latter, although it has a similar hypocone to the present species, has a much smaller, acute epicone. The cell's length was 23 µm and its diameter 13 µm.

Station: 287.

It was found in the Gulf of Aden.

Genus *Balechina* LOEBLICH et LOEBLICH

The genus name was proposed by the above authors (1966) as a replacement for the subgenus *Pachydinium* PAVILLARD on raising it to generic status. At the latter level it became a junior homonym for the genus *Pachydinium* PAVILLARD. Recognition of *Balechina* as distinct from *Gymnodinium* is followed here in view of the thick, semi-rigid amphiesma possessed by the former. The amphiesmal vesicles are easily distinguishable with the light microscope in the former genus, but are only seen with difficulty in the latter. The thick amphiesma apparently allows members of *Balechina* to be more adequately preserved with routine commercial formalin than *Gymnodinium*.

The semi-rigidity of the amphiesma of *Balechina* may be due to the deposition of a flexible or fibrous material but none have been examined with the electron microscope as yet. Unlike members of the Ptychodiscaceae there is no distinct envelope ("pellicle") penetrated by a single large flagellar aperture. Instead the two flagella arise from widely separated entry points (the latter being visible even when the flagella have been shed). The transverse flagellum arises within the sulcus from its customary origin near the proximal left end of the girdle, the longitudinal flagellum arising from a point further down the sulcus, directly over the nucleus in the two species observed here.

The apparent strength of the amphiesma of *Balechina* is also of interest with regard to the existence of fossilised *Gymnodinium*-like species with a thick, ridged covering. These have been referred to the genus *Dinogymnium* EVITT and have been assumed to be cysts.

Balechina coerulea (DOGIEL) comb. nov. Plate 37, Fig. 443, Plate 40, Fig. 481

Basionym: *Gymnodinium coeruleum* DOGIEL 1906:35, t. 2, f. 46, 47; KOFOID et SWEZY 1921:197, f. Z 4; KOFOID 1931:10, t. 1, f. 5; SCHILLER 1932:344, f. 349 a, b; STEIDINGER et WILLIAMS 1970:51, t. 22, f. 68 a, b.

A large (length usually more than 200 µm), distinctive species. DOGIEL (1906) figured two shapes, one with a much more conical epicone than the other. KOFOID & SWEZY (1921) selected the more rounded figure for their treatise. Later KOFOID (1931) and STEIDINGER & WILLIAMS (1970) have shown that in living cells the epicone is distinctly conical. A roundly conical shape has been seen by this author (unpublished) in living cells from Villefranche-sur-Mer, in the Mediterranean Sea. Living cells are not usually as acutely pointed as that figured here. The most distinctive feature of the species, the strong blue peripheral pigmentation located in granules, is not a constant feature, brownish pink or green cells being commonly mixed with blue individuals. The blue is rapidly bleached in formalin preservation. The large nucleus is situated in the hypocone. The specimen observed had ingested diatoms.

The species resembles *G. gracile* (which has a larger hypocone in relation to the epicone) and *G. costatum* (which has a length exceeding 150 µm). The descending girdle is shared by many large species of this genus and there is a strong possibility that several of them are conspecific.

Station: 59.

One cell was found in the north-central Bay of Bengal. This is the first record of the species from the Indian Ocean. It has been observed previously in the Mediterranean Sea, Japan and the Gulf of Mexico.

Balechina marianae sp. n. Plate 37, Fig. 442, Plate 40, Fig. 480

Syn.: ? *Gymnodinium* J. STEIDINGER et WILLIAMS 1970:52, t. 23, f. 72.

This taxon, not previously named, can be readily distinguished from all other members of the genus by the presence of a strong, apically-situated mamilla or boss. The amphiesma resembles that present in *B. coerulea* being strongly vesiculated with linear ribs superimposed upon the vesicular reticulation. The length is 115–120 µm, and the transdiameter 70–76 µ. The apical region lacks strong reticulation. The girdle is deeply impressed and displaced left-handedly by one-fifth to one-quarter of the transdiameter. The heights of the epi- and hypocone may be subequal but can be altered by cell division. For example, in the specimen of STEIDINGER & WILLIAMS the hypocone was longer than the epicone, probably being a posterior daughter cell shortly after division. Their specimen had a narrower anterior epicone than that observed in the "Anton Bruun" material. The nucleus is situated in the hypocone. Various accumulation bodies are present. The species is probably phagocytic.

The species is named in recognition of tireless assistance provided during the author's researches by MARIAN E.W. SLATER.

Station: 55.

Two cells were found in the north-central Bay of Bengal, not far from the locality for *B. coerulea* in the material.

STEIDINGER & WILLIAMS' (1970) specimen was from the eastern Gulf of Mexico during the "Hourglass" cruises. Other specimens have been observed by this author in Mediterranean Sea material collected from Villefranche-sur-Mer in September, 1972, co-occurring with *B. coerulea* (unpubl. obs.).

Genus *Gymnodinium* STEIN

Under *Balechina* it has been indicated that members with a thickened outer region exhibiting delicate areolation, and often ridges, have been recently elevated from subgeneric (*Pachydinium*) to separate generic rank. Such cells tend to preserve considerably better with formalin than those with thinner outer layers assigned to the genus *Gymnodinium*, and consequently it is not surprising that only one cell of the latter type was found in the "Anton Bruun" samples. There is clearly a great need for a future study of living material from tropical waters to augment the preliminary study of NORRIS (1966), in order to get a better idea of the representation of this and other fragile genera.

Gymnodinium sp. Plate 37, Fig. 435.

This medium sized cell, length 58 µm, diameter 35 µm, lacking appreciable flattening, was very similar to *G. herbaceum* KOFOID in KOFOID & SWEZY (1921, p. 220, f. Y, 17, pl. 4, f. 44). It had a similar ovoid body and was very similar in size to that of the original material (length 55 µm) from Naples in the Mediterranean Sea. The main difference was that the striations, reported for the surface of the hypocone only, could not be seen.

A large accumulation body was located at the anterior end. KOFOID & SWEZY (1921) reported that this species and its close relatives, e.g. *G. ravescens*, all possess chloroplasts but ingest small cells.

Station: 296.

It was found south of the Seychelle Islands during cruise V.

Family Heteraulacaceae LOEBLICH et DRUGG

[Syn.: Goniodomaceae LINDEMANN; Heteraulaceae LOEBL. et DRUGG]

A new family name was necessary when it was discovered that the name of the type genus, *Goniodoma* STEIN, was invalid (DRUGG & LOEBLICH 1967; LOEBLICH & DRUGG 1968a, b).

In the introductory comments to the Gonyaulacaceae attention was drawn to the ease with which the gonyaulacoid plate pattern and the pattern of *Heteraulacus* could be compared and possibly derived from one or other (most probably the gonyaulacoid from the heteraulacoid, the latter possessing little distortion from a radially symmetrical arrangement).

To this author the two families appear to be very closely related, and could, perhaps, be united.

Only one genus of this family was found in the material. The other, *Goniodinium* P. DANGEARD, is of doubtful systematic position, one of its two species probably being referrable to *Centrodinium* (see later).

Genus *Heteraulacus* DRUGG et LOEBLICH

Syn.: *Goniodoma* STEIN non ZELLER

Of the seven species given by SCHILLER (1936) under this genus, only two: *H. polyedricus* (POUCHET) DRUGG et LOEBLICH and *H. sphaericus* (MURRAY et WHITTING) LOEBLICH III, can be readily recognised. Two, described by KOFOID & MICHENER (1911), have never been illustrated and have not been identified by subsequent authors. It is possible that this may occur in the future, as has been done for several of their *Gonyaulax* species here. *Goniodoma ostenfeldii* PAULSEN was later (1949) transferred by its author to *Gonyaulax*, but the plate pattern given by him in the latter work differs markedly from that in the original figures. *Goniodoma striatum* MANGIN lacks a clear diagnosis and there was no figure of a full ventral view and so, despite its linear markings, it cannot be rocognised with certainty. *Goniodoma lacustre* LINDEMANN, for which no figure was given in SCHILLER, was suggested to be a species of *Glenodinium* but appears to be closer to *Fragilidium*. *Goniodoma depressum* GAARDER (1954) may be a good species, but *G. concavum* GAARDER is a life-cycle stage of *Pyrocystis noctiluca*. SILVA (1956b, 1969) has partially determined the plates of two further species of the genus.

Heteraulacus polyedricus (POUCHET) DRUGG et LOEBLICH Plate 28, Figs. 291–294; Plate 43, Fig. 513
– 1967:183.
Syn.: *Goniodoma polyedricum* (POUCHET) JÖRGENSEN . . . CANDEIAS 1930:19, t. 1, f. 28, 29; SCHILLER 1936:438, f. 479 a–e; GRAHAM 1942:46, f. 60; NIE and WANG 1942:65, f. 1 A–K, f. 2 A–D; MARGALEF 1948a:21, f. 2, 3, 4; SILVA 1949:341, t. 5, f. 1; KISSELEV 1950:256, f. 446; RAMPI 1950c:245, f. 10; MARGALEF et DURÁN 1953:44, f. 13 a; WOOD 1954:313, f. 241 a–c; TRÉGOUBOFF et ROSE 1957:117, t. 27, f. 2; HALIM 1960a, t. 3, f. 14; – 1967:729, t. 4, f. 53, 54; BALLANTINE 1961:225, f. 58–60; WOOD 1963b: 42, f. 154; STEIDINGER, DAVIS et WILLIAMS 1967, t. 9, f. a; WOOD 1968:62, f. 163.
G. acuminatum STEIN et auct. nonnul. . . . WANG et NIE 1932:295, f. 7, 8.
Heteraulacus acuminatus (EHRENBERG) DIESING . . . STEIDINGER et WILLIAMS 1970:53, f. 76 a–f.

This is a very common tropical species, and as indicated in the introduction, it may have a long geological history. GRAHAM and NIE & WANG (1942) have provided detailed plate analyses of the species. It is characterised by its angular shape, with a flattened antapex.

Megacytic growth produces wide pore-free bands, modifying the shape of some plates, and, as can be seen in the antapical view shown in figure 294 b, the fins usually accompanying the sutures may not coincide with all the plates after megacytic growth.

Stations: 13–15, 17–19, 25, 26, 28, 30–35, 37, 38, 42, 43, 49, 51, 52, 54–58, 60–63, 65, 66, 68–71, 90–92, 96–98, 100, 101, 103, 106, 109–111, 114–116, 125, 129, 130, 133–135, 141, 144, 147, 148, 150, 154, 161, 162, 286, 287, 290, 291, 294, 295, 299, 305, 314, 315, 317, 320, 337, 339, 344, 374, 419.

The earliest fossil record of this species is the Lower Eocene of Northern Germany (MORGENROTH 1966). It is a cosmopolitan tropical to subtropical species.

The records of SILVA (1956a, 1960), TAYLOR (1967), SOURNIA (1968b), and NEL (1968) can be added to those listed by WOOD (1963a) for the Indian Ocean.

Heteraulacus sphaericus (MURRAY et WHITTING) LOEBLICH III Plate 28, Fig. 290
– 1970:904.
Basionym: *Goniodoma sphaericum* MURRAY et WHITTING 1899:325, t. 27, f. 3 . . . . SCHILLER 1936:439, f. 480 a–d; NIE et WANG 1942:66, f. 3 A–D; RAMPI 1950c:245, f. 18; MARGALEF et DURÁN 1953:44, f. 13 d–g; SILVA 1956a:68, t. 11, f. 12; TRÉGOUBOFF et ROSE 1957:117, t. 27, f. 3; HALIM 1960a, t. 3, f. 13 a, b, c; WOOD 1968:62, f. 164; HADA 1970:18, f. 16.

This species is readily distinguished from *H. polyedricus* by its rounded shape, lacking the angularity of suture junctions found in the latter. It is usually smaller (diameter 35–52 µm), but there is an overlap in the size range of the two species. There is a displacement of the first precingular plate so that it reaches further apically than the seventh precingular plate beside it, and it is triangular in shape instead of rectangular. The latter can also be found in megacytic specimens of *H. polyedricus*, however,(cf. plate 28, f. 293). A ventral pore may be present on the epitheca, but it could not be seen in the specimen figured here.

Stations: 35, 36, 39, 59, 60, 68, 93, 95, 97, 100, 103.

It is a rare inter-oceanic species. WOOD (1963a) lists three Indian Ocean records of the species, to which should be added those of SILVA (1956a, 1960).

Family Heterodiniaceae LINDEMANN

Genus *Heterodinium* KOFOID

This is a distinctive, rarely encountered genus limited chiefly to tropical waters. A few species (e.g. *H. rigdenae, H. blackmanii*) extend into warm temperate regions. BALECH (1962b) modified KOFOID & ADAMSON's (1933) plate formula by reducing the number of postcingular plates to $6'''$ from $7'''$ so that it is at present characterised by a plate formula of P, $3'$, 1^{a}, $6''$, 6C (? S), $6'''$, $3''''$.

In addition a ventral pore plate is present. The ventral pore, usually situated in the mid-ventral face of the epitheca, is surrounded by a ridge which often forms a query-like shape.

A feature of this genus of ecological interest is the predominance of records of occurrence below 100 m or deeper (see KOFOID & ADAMSON 1933; GAARDER 1954). This may explain its apparent rarity in the material of other expeditions where sampling has not extended deeper than 100 m. The predominance of records in the western half of the Bay of Bengal in January, the western Arabian Sea and north of the Seychelles may be related to vertical movement of water (see general discussion of the distribution of "umbriphilic" species).

Heterodinium agassizii KOFOID Plate 23, Fig. 229

KOFOID et ADAMSON 1933:86, t. 10, f. 4–8, t. 16, f. 27; SCHILLER 1936:342, f. 369; HALIM 1967:730, t. 4, f. 55–57.

This is one of the highly reticulated members of the flattened subgenus *Platydinium*. It appears closest to *H. fides* KOFOID but differs in that the profile of the epitheca in ventral (or dorsal) view is smoothly rounded with only slight concavity above the girdle. HALIM's (1967) specimen is equivocal in this respect but does exhibit other features (below) similar to *H. agassizii*. Also the antapical horns are relatively longer and less divergent. Most of the surface areolae have a single prominent pore near the centre in both species. Both also have distinctly serrate marginal fins surrounding the hypotheca.

Station: 103.

Only one specimen of this species was found in the Bay of Bengal. This is a new record from the Indian Ocean. It has been found previously in the tropical Pacific and Atlantic Oceans, and the Mediterranean and Caribbean Seas. Like most other species of the genus it has been considered a deep euphotic or subeuphotic species (KOFOID & ADAMSON 1933). In GAARDER's (1954) Atlantic samples it was present in hauls from 200–100 m and 200–0 m.

Heterodinium blackmanii (MURRAY et WHITTING) KOFOID Plate 23, Fig. 225

KOFOID et ADAMSON 1933:74, t. 9, f. 1–4, 7, t. 15, f. 25; SCHILLER 1936:340, f. 367 non 366; BALECH 1962b:154, t. 21, f. 341, 342. Non WOOD 1954:267, f. 184 a, b (= *H. curvatum* KOFOID)

One of the largest species (length usually greater than 200 µm) of the subgenus *Heterodinium* (elongate, tapering epitheca; antapical horns well developed). It is most closely related to, if not conspecific with (SCHILLER's suggestion) *H. curvatum* KOFOID. BALECH (1962b) has discussed the distinction of these two taxa at length. The simplest means of recognising them: the more curved epitheca (sinistral), narrower, more acute antapical horns, and reduced reticulation of the latter were consistent in the present material, lending to the continued distinction of the taxa in this report (although *H. curvatum* was not observed).

Stations: 109, 134.

Found singly at a station off the west coast of India and in the south central Indian Ocean close to 27 °S.

The species has been recorded previously from the Indian Ocean by SCHRÖDER (1906) and KARSTEN (1907). The latter found it between 5 °N and 30 °S. Although rare, this species is one of the commonest members of the genus. KOFOID & ADAMSON's (1933) data suggested a preference for deeper waters but KARSTEN's records were from the upper 15 m (except for one haul from 200 to 0 m). The species is inter-oceanic and may not be as obligately stenothermal as many of the warm temperature species.

Heterodinium doma (MURRAY et WHITTING) KOFOID ? Plate 23, Fig. 236

KOFOID et ADAMSON 1933:30, t. 1, f. 8, 9, t. 15, f. 3; SCHILLER 1936:331, f. 346; RAMPI 1941a:56 vix t. 1, f. 6; BALECH 1962b:150, t. 20, f. 329.

One of the more elaborately reticulated members of the sphaerodally-shaped subgenus *Sphaerodinium*, this taxon resembles other species which lack antapical spines or horns and in particular *H. schilleri* PAVILLARD and *H. sphaeroideum* KOFOID. The former is much smaller (length 20 µm) and the latter has a distinctly larger hypotheca than epitheca with little or no displacement of the girdle.

The specimen illustrated here in some respects appears intermediate between *H. doma* and *H. sphaeroideum.* It is the same size as the former and has a larger epitheca than hypotheca. However, the girdle displacement is less than that shown by other authors, and the right proximal region of the girdle is not as overhung by the epitheca. BALECH's (1962b) specimen has an unusual concave antapical end.

Station: 65.

Found at one station close to the continental shelf in the western Bay of Bengal.

The species has been previously recorded from the Indian Ocean by WOOD (1954, 1962 in 1963a). It is known from the tropical Pacific and Atlantic Oceans.

Heterodinium fides KOFOID Plate 23, Fig. 228

KOFOID et ADAMSON 1933:90, t. 11, f. 2, 4, 6, t. 16, f. 28, t. 19, f. 56–58; SCHILLER 1936:343, f. 370 a, b.

This species closely resembles *H. agassizii* KOFOID (see comments under the latter, here). In addition to shape distinctions it also tends to be smaller. Little further information can be added. The specimen observed here was very similar to the type specimen.

Station: 109.

A single specimen was observed at this station off the west coast of India from which *H. blackmannii* was also recorded.

A further new record for the Indian Ocean. KOFOID & ADAMSON (1933) considered this species as stenothermal and subeuphotic in distribution in the eastern tropical Pacific Ocean.

Heterodinium globosum KOFOID Plate 23, Fig. 231

KOFOID et ADAMSON 1933:45, t. 4, f. 1–4, t. 15, f. 10; SCHILLER 1936:333, f. 353; RAMPI 1941a:58, t. 1, f. 2, 5; – 1969b:324, t. 4, f. 2; BALECH 1962b:152, t. 20, f. 331, 332.

Syn.: ? *H. gracile* BÖHM 1936:33, f. 12 d/1–3.

? *H. leiorhynchum* sensu RAMPI 1939b:463, f. 1; – 1941a:59, t. 1, f. 7, 8; – 1952b:116, f. 2; TRÉGOUBOFF et ROSE 1957:114, t. 24, f. 14; HALIM 1960a:191, t. 2, f. 25.

This medium-sized, spherical species is relatively distinctive with its rotund body, short apical horn gradually tapered from the epitheca and unequal antapical horns. Reticulation is usually irregularly and somewhat sparsely developed. Broad intercalary bands are usually present. Curiously KOFOID & ADAMSON's description referred to the right horn being "a bit shorter". All their figures of this species however, show the right horn is considerably shorter than the left; in fact, more so than the specimen illustrated here.

There is difficulty in treating descriptions of Mediterranean specimens attributed to *H. leiorhynchum* (MURRAY & WHITTING) KOFOID. Those of RAMPI (1939b, 1941a and 1952b) and HALIM (1960) resemble *H. globosum* although are not quite as spherical in body shape. This interpretation seems to originate from a comment of PAVILLARD's (pers. comm. to RAMPI) that the original figures by MURRAY & WHITTING (1899) are undoubtedly somewhat stylised. KOFOID & ADAMSON (1933) recognised both taxa although their figure of *H. leiorhynchum* lacks the detail of their other analyses. They considered the presence of distinct antapical spines as indispensible for the recognition of the latter. To this author the taxon which most resembles *H. leiorhynchum* in shape is *H. spiniferum* KOFOID et MICHENER. However, it lacks the antapical spines and instead possesses a spinous fin between the bases of the antapical horns. The specimens termed *H. leiorhynchum* by RAMPI and HALIM also lack these antapical spines. As these Mediterranean specimens therefore differ from *H. leiorhynchum* and seem to correspond to *H. gracile* BÖHM (1936) the latter name may be the most appropriate if distinction from *H. globosum* is maintained.

The present specimens closely resemble the type specimen of *H. globosum* and consequently that is the name applied here.

Stations: 56, 64, 289.

Observed at two stations in the northern Bay of Bengal and one near the Gulf of Aden. This is a further new record for the Indian Ocean. The species is known from both the tropical Atlantic and Pacific Oceans and probably occurs in the Mediterranean Sea.

Heterodinium inaequale KOFOID Plate 23, Fig. 233
KOFOID et ADAMSON 1933, t. 16, f. 32; SCHILLER 1936:344, f. 372 a, b non c; RAMPI 1950a:9, f. 6.
Syn.: *H. laticinctum* KOFOID . . . . KOFOID et ADAMSON 1933:95, t. 10, f. 3, t. 16, f. 30, t. 18, f. 52–55.

This member of the subgenus *Platydinium* is recognisable by its rounded epitheca, lack of reticulation, sharp, unequal incurved antapical horns and serrated antapical fin. There seems to be little doubt that, as suggested by SCHILLER (1936), *H. laticinctum* KOFOID & ADAMSON is a large, robust form (total length 145 μm) of *H. inaequale*. SCHILLER also considered *H. pavillardi* (PAVILLARD) KOFOID & ADAMSON as synonymous. The latter is smaller, with antapical horns which are less incurved. However, if this is considered as synonymous then it seems unreasonable to maintain the identity of *H. asymmetricum* KOFOID & ADAMSON which also has a less incurved left antapical horn and has, in addition, a right horn which is reduced almost to a vestige. At present the best course seems to be to retain the specific distinction of *H. pavillardii* and *H. asymmetricum* until intermediate forms are demonstrated. *H. laeve* KOFOID & MICHENER is also similar but has long, curved antapical horns, the left still somewhat longer than the right horn.

Station: 412.

Only one specimen was observed from Nosy-Bé (Madagascar). The species has not been previously recorded from the Indian Ocean although WOOD (1954) has recorded *H. asymmetricum* from the Southern Ocean. It is known from the Pacific and Atlantic Oceans and the Mediterranean Sea.

Heterodinium mediocre (KOFOID) KOFOID et ADAMSON Plate 23, Fig. 234
– 1933:102, t. 16, f. 36, t. 19, f. 59–65, t. 21, f. 74; SCHILLER 1936:345, f. 375 a–c non 376.
Syn.: *H. gesticulatum* forma *mediocris* KOFOID.

In many respects the specimen illustrated here is intermediate between *H. mediocre* and *H. gesticulatum* KOFOID. It is designated as the former because the epitheca is roundly symmetrical, the antapical horns are widely divergent, and the sinistral lobe (bulge on the left side of the hypotheca) is less marked than in typical members of *H. gesticulatum*. On the other hand it differs from the variability described by KOFOID & ADAMSON by the presence of a "bald" apical plate (1′) and wide intercalary bands (both features of *H. gesticulatum* but probably variable), and lack of denticles along the antapical margin. The type specimen of *H. gesticulatum* exhibited a sloping of the epitheca towards the left which was not evident in the specimens in this material.

The recognition of *H. mediocre* forma *sinistrum* (KOFOID & ADAMSON) as an infraspecific variant by SCHILLER does not seem consistent with his recognition of *H. deformatum* (KOFOID) KOFOID & ADAMSON at the specific level (see comparative comments under *H. sinistrum* here). Probably both should be considered as infraspecific variants, but then *H. mediocre* may prove to be more appropriately considered as an infraspecific variant of *H. gesticulatum* as KOFOID suggested originally. For the present the specific recognition of each taxon seems to be the wisest path.

Station: 287.

A single specimen was observed at the entrance to the Gulf of Aden.

H. mediocre has not been recorded from the Indian Ocean previously although TAYLOR (1967) recognised *H. gesticulatum* in the southwestern Indian Ocean. It was originally described from the eastern tropical Pacific Ocean.

Heterodinium milneri (MURRAY et WHITTING) KOFOID Plate 23, Fig. 232
KOFOID et ADAMSON 1933:41, t. 3, f. 1, 2, 4–6, t. 15, f. 8; SCHILLER 1936:333, f. 351 a, b; HERRERA, MUÑOZ, et MARGALEF 1955:18, f. 1 E; BALECH 1962b:151, t. 20, f. 330; – 1971a:160, t. 32, f. 668, 669.
Vix RAMPI 1939b:463, f. 3; – 1941a:57, t. 1, f. 10; TRÉGOUBOFF et ROSE 1957:114, t. 24, f. 16; WOOD 1963b:39, f. 142.
Syn.: *Peridinium milneri* MURRAY et WHITTING 1899:327, t. 29, f. 3 a, b.
Non *Goniodoma milneri* MURRAY et WHITTING 1899:325, t. 27, f. 2 a, b, c, d.

This is a small spheroidal species, only 50 to 87 μm in length. SCHILLER provides a length of 130 μm, but this appears to be an error not agreeing with the dimensions of KOFOID & ADAMSON (1933), RAMPI (1941a), BALECH (1962b) or the present specimens. The species differs from *H. murrayi* KOFOID by its shorter apical horn, shorter antapical spines (4 instead of 3 although only 3 are obvious), and reduced reticulation. In both species there is a greatly displaced girdle and the body of the epitheca is shorter than the hypotheca.

In this species the ventral pore is very inconspicuous and is situated close to the apex. Also, the plate pattern on the ventral face of the epitheca is anomalous, presumably due to the girdle displacement although other species with strong displacement, *H. murrayi* and *H. obesum* KOFOID maintain the conventional arrangement of precingulars, apical plates, and ventral pore (plate).

SCHILLER (1936) erroneously cited *Goniodoma milneri* as the original binomial. In MURRAY & WHITTING (1899) both *Peridinium milneri* and *Goniodoma milneri* are described as distinct taxa. The former was transferred to *Heterodinium* by KOFOID and the latter to *Gonyaulax*, also by KOFOID (see here under *Gonyaulax* for details).

Station: 101.

A single specimen was observed at this station off the east coast of India.

The species is known from the tropical Atlantic and Pacific Oceans and the Mediterranean Sea. It was the commonest species of *Heterodinium* found by GAARDER (1954) in "Michael Sars" Atlantic Ocean material. It has not apparently been observed previously in the Indian Ocean.

Heterodinium rigdenae KOFOID Plate 23, Figs. 227, 230

KOFOID et ADAMSON 1933:78, t. 5, f. 4, t. 15, f. 16, t. 17, f. 42–47; SCHILLER 1936:337, f. 360 a–d; BALECH 1962b:153, t. 21, f. 336–338; WOOD 1963c:15, f. 49.

In its most reticulated state this species is readily recognisable. It is most close to, if not conspecific with, *H. crassipes* SCHILLER. The latter's only obvious difference is the large fin which extends between the antapical horns (noted by KOFOID & ADAMSON). An extreme variant, thought to be this species, is shown in fig. 230. It totally lacked surface reticulation and the antapical horns were more divergent than the variability previously known. It was present in the same sample as the other specimen illustrated.

Stations: 35, 71, 100, 116, 142, 294.

Although by no means common this was the most highly represented member of *Heterodinium* in the material. It occurred at scattered stations in the Bay of Bengal, Andaman Sea, and at three stations in the northern Indian Ocean (cruises I, II, and V).

It has been previously recorded from the Indian Ocean by KARSTEN (1907) and WOOD (1962, in 1963a). It is one of the most eurythermal members of the genus, occurring in warm-temperate as well as tropical waters. It was the commonest species in "Albatross" Pacific Ocean material examined by KOFOID & ADAMSON (1933).

Heterodinium sinistrum KOFOID et ADAMSON Plate 23, Fig. 235

– 1933:105, t. 16, f. 34, t. 21, f. 78.

Syn.: *H. mediocre* forma *sinistrum* (KOFOID et ADAMSON) SCHILLER 1936:346, f. 376.

In the comments under *H. mediocre* the alternative treatments of this taxon (infraspecific or specific) and others closely similar (*H. gesticulatum, H. deformatum*) have been discussed. *H. sinistrum* represents a variant in which the left antapical region of the hypotheca has become elongated and the epitheca slopes towards the right. *H. deformatum* represents the other extreme, with great reduction of the left side.

Station: 313.

Observed at one station in the south central Indian Ocean near 30 °S.

This taxon has only been previously recorded from the eastern tropical Pacific Ocean.

Heterodinium whittingae KOFOID Plate 23, Fig. 226

KOFOID et ADAMSON 1933:92, t. 16, f. 29; SCHILLER 1936:343, f. 371; GAARDER 1954:32, f. 35 a, b; MARGALEF 1969a, f. 4 A–C; RAMPI 1969b:326, t. 4, f. 1; LÉGER 1973a:20, f. 6.

A distinctive, large, flattened species with large well-developed reticulations and sharp, inwardly-curved antapical horns. It is not likely to be confused with other species. Its closest resemblance (superficial) is with *H. scrippsii*, from which it is readily distinguished by being much more flattened, and in the shape of its antapical horns which curve outwards in *H. scrippsii.*

Station: 334.

Found at only one station in the northern Indian Ocean (southern Arabian Sea). This is a first record for the Indian Ocean. The species is relatively eurythermal, being found in warm temperate as well as tropical waters in the Pacific and Atlantic Oceans.

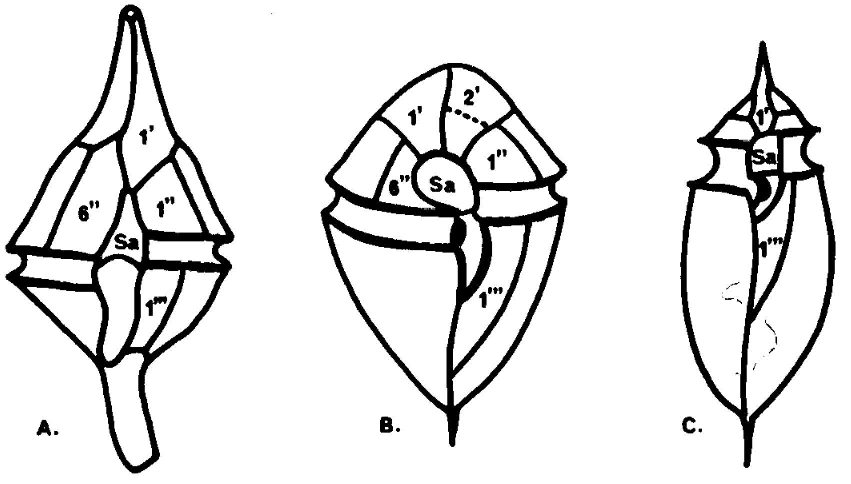
Family Oxytoxaceae LINDEMANN

Conventionally this family has been regarded as consisting of two genera, *Oxytoxum* STEIN and *Pavillardinium* (KOFOID) DE TONI (=*Murrayella* KOFOID). They have been separated almost solely by the position of the girdle (whether it is anterior or submedian in position respectively). Plate information on many of the taxa has been lacking or incomplete due to their rarity and/or small size. The rare psammophilic genus *Adenoides* BALECH, also apparently a member of the family, has a tabulation of 1', 4", 5c, 5s, 5''', 5P, 1'''' (BALECH 1956).

Recently it has become evident that a) the genus *Centrodinium* KOFOID shows strong resemblances to some members assigned to *Pavillardinium* ("Group A"); b) *Pavillardinium* has grown to include two rather dissimilar groups, one of which resembles *Centrodinium* ("Group A") and the other, some members of *Oxytoxum* ("Group B"); and c) *Oxytoxum* has come to include at least two dissimilar groups, one of which (originally described as the genus *Pyrgidium* STEIN) shows resemblances to the "Group B" of *Pavillardinium* above, and the other is more distinctively separate.

In other words, as information on the above genera has increased, and further species have been added, the generic limits as originally proposed have become increasingly inappropriate. Here attention is drawn to new criteria which can be readily observed and applied to recognise three generic groupings which seem to be more realistic to this author. In the process it has been found that the revised schema requires the reinstatement of STEIN's (1883) genus *Pyrgidium*, although with the epithet substituted by *Corythodinium* LOEBLICH et LOEBLICH III, and the dismantling of *Pavillardinium*.

Details are given below under each genus. Text figure 2 illustrates the chief features by which each can be recognised in ventral view. All members of this family share a tendency towards left-handed displacement of the girdle with accompanying torsion effects. Torsion and displacement is least in *Oxytoxum*, moderate and involving the hypotheca mostly in *Centrodinium*, and strongest, effecting both the epi- and hypotheca, in *Corythodinium*. In all three genera the sulcus notches the hypotheca strongly (strongest in *Centrodinium* and least in *Oxytoxum*) and in two the anterior sulcal plates invade the epitheca strongly. In *Centrodinium* the anterior sulcal plate is subtriangular and in *Corythodinium* it is large and obovate.



CENTRODINIUM CORYTHODINIUM OXYTOXUM

Text fig. 2. Ventral views of the three principal genera of the Oxytoxaceae recognised here. Note the differences in the form of the ventral area (not all plates are shown) and the anterior sulcal plate (Sa).

Genus *Centrodinium* KOFOID

Syn.: *Murrayella* KOFOID pro parte; *Pavillardinium* KOFOID pro parte.

When this genus was first described KOFOID (1907b) indicated its probable affinity with *Ceratium*. This allocation has become increasingly doubtful with time. KOFOID's figures indicated only a few plate sutures on the left side and only one ventral view was given, illustrating the considerable lateral flattening of the genus and the presence of an elongate sulcal furrow, but showing none of the plates on the ventral side. Nevertheless, KOFOID provided numbers of plates for each series [2(– 4'?), 6'', 5''', 1^p, 4''''].

Unfortunately he referred to "five precingulars" on the hypotheca, undoubtedly intending to refer to postcingulars judging from the context in which the error appeared (he had already given the number of plates on the epithecal series, and an intercalary plate on the hypotheca was termed a "dorsal intercalary". This led SCHILLER (1936) to give the number of precingular plates as 5''. WOOD (1954) later suggested the possible presence of an anterior intercalary plate ("1^a? ") although he gave no reason for this. His figure is too imprecise to clearly determine the plate formulation and is probably inverted.

BALECH (1962b) also considered the question of plates. On the basis of both left and right-side observations on four species from the Pacific Ocean he concluded that the plate formula ought to be altered to 2', 3^a, 7'', 5C? , 5''', 1^p, 1''''; a drastic revision but not too surprising in view of the difficulty in observing the plates. Unfortunately, he did not detail the appearance of any of the plates as seen in ventral view.

A more serious complication became evident in one of BALECH's later (1967a) studies although there were earlier indications of the problem. He noted a strong resemblance to *Centrodinium* in his detailed analysis of the plates of a new species, *Murrayella mimetica*. However, he considered that the difference in plate formula (3', 1^a, 6'', 6C, 5''', 2^p, 1''''), combined with a smaller size and strongly-developed thecal markings with pores covering the whole surface of the theca, was sufficient to warrant separation from *Centrodinium*. The plate formula was similar to that which he had established for other species of *Pavillardinium* (although this did not include the type species of the latter).

Under *Corythodinium* the problem of the recognition of the genus *Pavillardinium* (=*Murrayella*) has been discussed in detail. The type species of the latter has been included in *Corythodinium*. Here some other members formerly assigned to *Pavillardinium* (and which now are in a nebulous systematic position because of the removal of the type and their own inability to conform to the criteria of *Corythodinium*) are believed to correspond closely to *Centrodinium* and are consequently transferred to it. If desired two subgenera (one exhibiting lateral flattening and posterior torsion, and the other not) could be recognised although there does not seem to be much to be gained from this at present.

As now proposed the genus *Centrodinium* can exist as either strongly or only moderately flattened (laterally) species. All have girdles exhibiting left-handed displacement, the displacement usually not being more than one girdle width. The anterior sulcal plate is distinctively shaped, being fairly narrow and subtriangular with one apex pointing towards the anterior of the cell. The sixth precingular plate is often long and narrow, often being acute at its apical end. The posterior sulcal region is always displaced towards the right side at its lower end and in those members most similar to the type species (*C. elongatum* KOFOID) the antapex of the cell is drawn out and has obvious torsion. It is also often distally bent towards the cell's left.

In addition to those species usually assigned to the genus the following taxa have been transferred:

Centrodinium biconicum	(MURRAY et WHITTING) comb. nov. [basionym = *Ceratium biconicum* MURRAY et WHITTING 1899:323, t. 27, f. 4 a–c; Syn. *Murrayella biconica* (MURRAY et WHITTING) PAVILLARD 1931:98, t. 3, f. 15; *Pavillardinium biconicum* RAMPI 1948:937, f. 8]
Centrodinium pavillardii	nom. nov. [basionym = *Murrayella intermedium* PAVILLARD 1916:44, t. 2, f. 5; a new combination is prevented by *C. intermedium* PAVILLARD 1930]
Centrodinium mimeticum	(BALECH) comb. nov. [basionym = *Murrayella mimetica* BALECH 1967a:117, pl. 8, fig. 129–132, pl. 9, f. 133–135]
Centrodinium pacificum	(RAMPI) comb. nov. [basionym = *Pavillardinium pacificum* RAMPI 1950a:10, f. 15]
Centrodinium punctatum	(CLEVE) comb. nov. [basionym = *Steiniella punctata* CLEVE 1900c:18, pl. 8, fig. 4 cf. BALECH 1971b:34, pl. 8, fig. 154–158, pl. 9, f. 159–167 = *M. punctata* (CLEVE) KOFOID, ? *M splendida* RAMPI 1941a, *Pavillardinium splendidum* (RAMPI) RAMPI 1950a]

In addition the following taxa are also probably referrable to *Centrodinium*:

Murrayella ovalis PAVILLARD 1930:12, f. 16; – 1931:98, pl. 3, f. 16 (insufficient detail).
Murrayella sp. BALECH 1962b:187, pl. 24, f. 374.
Unidentified sp. BALECH 1962b:188, pl. 23, f. 365.
? *Goniodinium spiniferum* P. DANGEARD 1927b:337, f. 3 a–c (anterior sulcal detail not shown).

Centrodinium sp. Plate 24, Figs. 237 a–c

[? *Centrodinium mimeticum* (BALECH) comb. nov.]

The specimen shows many resemblances to *Centrodinium mimeticum* (BALECH) comb. nov. and also strengthens the proposed ties of taxa of the latter type to *Centrodinium.* It exhibits strong lateral flattening, with a broader epitheca than hypotheca, the poorly-demarcated plates being recognisable more by their pore-free intercalary zones than by sutures. There is a long, narrow sulcus with delicate fins, and an elongated posterior end drawn out into a horn exhibiting a twisted (descending) appearance. A few of the sutures are associated with strong ridges. The plate pattern could not be fully established on the right side and so only those details shown in the figures here are known. The plate details show many resemblances to *C. mimeticum*, especially in the arrangement of the plates on the ventral side of the epitheca although BALECH did not observe distinct torsion in the posterior part of the cell. Also, there are some other puzzling anomalies (perhaps arising from erroneous observations here). The most striking is that in the "Anton Bruun" specimen there was a median dorsal longitudinal suture (associated with a girdle suture) on the hypotheca, whereas BALECH found a plate (3‴) to be centrally situated in that position. The size here is compatible with the range given by BALECH (length 93–127.5 µm; transdiameter 37.5–50 µm).

Station: 103.
A single specimen was observed from the Bay of Bengal in the vicinity of Madras. BALECH's specimens were from the Gulf of Mexico.

Genus *Corythodinium* LOEBLICH et LOEBLICH III emend. nov.

Syn.: *Pyrgidium* STEIN 1883; *Murrayella* KOFOID 1907b; *Pavillardinum* DE TONI 1936; *Oxytoxum* STEIN pro parte.

This genus was created by STEIN (1883, p. 20 as *Pyrgidium*) for five species considered by him to be similar to *Oxytoxum.* These were *P. constrictum, P. mitra, P. reticulatum, P. sceptrum,* and *P. tesselatum.* His description, as in the case of *Oxytoxum*, was based on inverted specimens (so that his references to the epi- and hypothecae were reversed) and his depiction of the thecal plates was relatively incomplete although excellent for the time. LOEBLICH & LOEBLICH (1966) have designated *P. tesselatum* STEIN as the type of the genus, also providing the name used here in view of preoccupation of STEIN's epithet by a genus of gastropods and of lichens. Of the five original species included by STEIN, *P. mitra* and *P. sceptrum* are now excluded as a result of the emendation below.

As generic characters STEIN drew attention to the presence of five plates on the "Vorderleib" (now known to be five postcingulars on the hypotheca) of which that associated with the sulcus (the "Mundbasal") was shorter and narrower than the others. An antapical spine was present ("Frontstachel"). The hypotheca was strongly indented below the flagellar pores, forming a well-defined sulcus. He considered that the epitheca consisted of five precingulars and one apical plate. Three of these species were large, relatively broad, with low, wide epithecae, lacking apical spines (*P. constrictum, P. reticulatum,* and *P. tesselatum*) whereas the other two had apical spines (long in *P. sceptrum*, very small in *P. mitra*). *P. reticulatum* was figured only from the dorsal side. One of the species he assigned to *Oxytoxum*, *O. diploconus* showed strong resemblances to the group of three species above but was figured only in side view, and he made no comment as to this resemblance. The side view was sufficient to show that it had a descending, displaced girdle (one girdle width).

As the genus had been formulated by STEIN it intergraded completely with *Oxytoxum*, due to the common possession of an anteriorly displaced girdle and the deep notch in the hypotheca associated with the sulcus. Due to the inclusion of *P. mitra* and *P. sceptrum* in the genus there was also a complete morphological gradiant towards the small rounded members of *Oxytoxum* and towards the elongate members with terminal spines such as *O. scolopax.* Consequently it seemed quite reasonable for later authors to "sink" *Pyrgidium* into *Oxytoxum*, PAULSEN (1908) considering it to be a subgenus, and SCHÜTT (1896) and SCHILLER (1936) referring to it as a section of *Oxytoxum*.

KOFOID (1907b) created a new genus *Murrayella* (pre-occupied by a genus of the red algae: *Murrayella* SCHMITZ) the type of which (*M. globosum* KOFOID) was very similar to the "group of three" in STEIN' work but it had the girdle submedian in position.

Of the other species assigned by him to this genus *M. spinosa* KOFOID was shown later to be synonymous with the type species of *Amphidoma* (BALECH 1971b), and *M. punctata* (CLEVE) KOFOID is here transferred to *Centrodinium*, leaving only *M. rotundata* KOFOID, which because of the lack of a ventral view, cannot be properly treated here.

Pavillardinium (as *Murrayella* was renamed by DE TONI) has continued to be recognised by either of its names, with species being added to it periodically. In the process it has become evident that there are two rather dissimilar units within *Pavillardinium*, one resembling the type species and the other resembling *Centrodinium* (see comments under the latter for further details of those members now transferred to it). Action has been taken here to hopefully clarify this situation, and make it more realistic, by down-grading the very arbitrary criterion of girdle position and focussing on a hitherto neglected feature of the theca, easily visible, which seems to this author to be an important character. As a result the genus *Pyrgidium* sensu lato has been resurrected, including three of its original species, one of which is the type (*P. tesselatum* STEIN) and the genus *Pavillardinium* DE TONI (= *Murrayella* KOFOID) sensu stricto has been "sunk" into *Corythodinium*.

The characters now considered to be important in the delimitation of *Corythodinium* emend. are:

Relatively robust species, rounded or broadly elongated, lacking "affixed" apical spines (although the epitheca may rise to a pointed cone) but usually possessing an antapical spine. The epitheca often shows signs of dextral torsion, with the plates displaced accordingly. In a few species the epitheca may be laterally flattened and raised into a crest. The girdle is strongly developed, lacking lists, with right-handed (descending) displacement of one or more girdle widths. The proximal ends of the girdle may overlap slightly. Both the epitheca and the hypotheca are strongly notched by the sulcus. The anterior sulcal plate is unusually large and usually obovate (sometimes pentangular) with the narrower end closer to the flagellar pore(s). The thecal plates are usually strongly reticulated and poroid, and intercalary bands may develop.

The plate formula of the type species is $3'$, 2^a, $6''$, 5C, ? S, $5'''$, $1''''$ but the range of variation within the genus cannot be established clearly as yet. *C. belgica* (MEUNIER) comb. nov. has four apical plates, no intercalary plate and only five precingular plates. *C. globosum* (KOFOID) comb. nov. has an anterior intercalary plate on the ventral side. As emended the genus includes the following taxa (with references to recent detailed descriptions, if available, and basionyms where new combinations are involved):

C. belgicae (MEUNIER) comb. nov. [basionym = *Oxytoxum belgicae* MEUNIER 1910, pl. 16, f. 38–41; cf. BALECH 1971a:167, pl. 36, f. 695–703]

C. biconicum (KOFOID) comb. nov. [basionym = *Amphidoma biconica* KOFOID 1907a:311, pl. 32, f. 50–52, = *Murrayella* KOFOID; GAARDER 1954:34, f. 40 a–e]

C. carinatum (GAARDER) comb. nov. [basionym = *O. carinatum* GAARDER 1954:35, f. 42 a, b]

C. compressum (KOFOID) comb. nov. [see below]

C. constrictum (STEIN) comb. nov. [basionym = *Pyrgidium constrictum* STEIN 1883, t. 5, f. 15–18]

C. cristatum (KOFOID) comb. nov. [basionym = *O. cristatum* KOFOID 1907b:188, p. 10, f. 64, cf. BALECH 1962b:170, pl. 19, f. 290, 291]

C. curvicaudatum (KOFOID) comb. nov. [basionym = *O. curvicaudatum* KOFOID 1907b:189, pl. 10, f. 61]

C. diploconus (STEIN) comb. nov. [basionym = *Oxytoxum diploconus* STEIN 1883, pl. 5, f. 5; cf. BALECH 1971a:166, pl. 36, f. 704]

C. elegans (PAVILLARD) comb. nov. [basionym = *Oxytoxum elegans* PAVILLARD 1916:43, pl. 2, f. 4; cf. BALECH 1971b: 31, pl. 8, f. 138–141]

C. frenguellii (RAMPI) comb. nov. [basionym = *O. frenguellii* RAMPI 1941a (1943?):65, pl. 2, f. 2; note that MARGALEF's 1969a, fig. 3J is optically reversed]

C. globosum (KOFOID) comb. nov. [see below]

C. latum (GAARDER) comb. nov. [basionym = *O. latum* GAARDER 1954:36, f. 43; BALECH 1962b:170, t. 19, f. 292–294, 297–301]

C. michaelsarsii (GAARDER) comb. nov. [basionym = *O. michaelsarsi* GAARDER 1954:37, f. 44; figure incomplete; determination by GAARDER's comparisons to *O. tesselatum* and *O. elegans*]

C. recurvum (KOFOID et MICHENER) comb. nov. [basionym = *O. recurvum* KOFOID et MICHENER 1911:288 – no figures; determination by comparison with *O. cristatum*]

C. reticulatum (STEIN) comb. nov. [basionym = *Pyrgidium reticulatum* STEIN 1883, t. 5, f. 14; cf. BALECH 1971b:31, pl. 7, f. 135–137]

C. tesselatum (STEIN) LOEBLICH et LOEBLICH III 1966:23. [type, cf. BALECH 1971b:30, pl. 70, f. 130–134]

Not all the taxa above necessarily deserve separate recognition, some no doubt being synonymous. The following indeterminate taxa are probably also assignable to *Corythodinium*: *M. rotundatum* KOFOID (1907b), *O. brunellii* RAMPI (1939b), and *O. areolatum* RAMPI (1941a, also in HERRERA, MUÑOZ & MARGALEF 1955, f. 1 L), *Oxytoxum* sp. BALECH (1971a, pl. 36, f. 708–713).

Pyrgidium mitra STEIN and *P. sceptrum* STEIN are excluded from the genus, remaining within the genus to which they are now assigned (*Oxytoxum* STEIN). *Murrayella australica* WOOD is probably a species of *Amphidoma*.

Corythodinium compressum (KOFOID) comb. nov. Plate 24, Fig. 254
Basionym: *Oxytoxum compressum* KOFOID 1907b:188, t. 10, f. 63; . . . . SCHILLER 1936:461, f. 522; WOOD 1963b:44, vix f. 162 a, b.

This species resembles *C. carinatum* (GAARDER) comb. nov. so closely that they are probably synonymous although GAARDER (1954) found both species in her material. The name, *C. carinatum*, refers to a strong lateral flattening of the epitheca into a crest whereas this is not mentioned for *O. compressum*. However, it should be noted that this would not be evident when the cells are seen from the side or three-quarter view as shown here or in KOFOID's original figure. In size the taxa are similar with a total length of 90 to 115 µm including a strong, sharply-pointed antapical spine, curving ventrally, 12 to 16 µm in length. *C. cristatum* (KOFOID) is also similar in size and shape although the epitheca is relatively larger. It is flattened laterally, as in *C. carinatum*, but is curved over in a hook apico-dorsally.

The constriction on the hypotheca of *C. constrictum* (STEIN) comb. nov. serves to distinguish it from *C. compressum* and it is also smaller (total length approximately 75 µm).

Station: 53.

Only one specimen was observed. The station was in the northern Bay of Bengal. This is a rare species which has only been previously recorded from the Indian Ocean by WOOD (1962, in 1963a) and SOURNIA (1968b). It was originally described from the eastern tropical Pacific Ocean.

Corythodinium globosum (KOFOID) comb. nov. Plate 24, Figs. 238 a, b
Basionym: *Murrayella globosa* KOFOID 1907b:191, t. 9. f. 56.
Syn.: *Pavillardinium globosum* (KOFOID) DE TONI .... RAMPI 1950a:9, f. 21.

This is a distinctive, rarely observed species. It is readily identifiable by the presence of an unusual anterior intercalary plate which is situated on the ventral epithecal surface in such a way that it intrudes between the first apical plate (displaced to the right upper quadrant of the epitheca as in other members of this genus) and the very large anterior sulcal plate, almost cutting off contact. Intercalary bands seem to be commonly developed in this species, making the precise position of the sutures difficult to locate although the plates themselves are very evident, with strong reticulation.

It is not yet known if any other members of *Corythodinium* also possess the ventrally situated anterior intercalary plate.

Station: 61.

Only one specimen was found. It occurred in the northwestern Bay of Bengal. The species was originally described from the eastern tropical Pacific Ocean. It has not apparently been previously recorded from the Indian Ocean.

Genus *Oxytoxum* STEIN

Some of the early confusion regarding this taxon has been explained in the comments under *Corythodinium*. Although STEIN created the latter as a separate genus two of the five species originally assigned to it exhibited intermediate features, leading later authors to include *Corythodinium* (using STEIN's epithet: *Pyrgidium*) under *Oxytoxum*. As now reinstated the genus *Corythodinium* can be recognised from *Oxytoxum* by the possession of a large obovate or pentangular anterior sulcal plate which invades the epitheca strongly, and also by the strong left-handed girdle displacement. In *Oxytoxum* the anterior sulcal plate (often bounded by thickened edges) only indents the epitheca slightly, if at all, and the girdle shows only slight signs of displacement. All members of *Oxytoxum* have an anteriorly situated girdle with a relatively small epitheca, whereas the epitheca is relatively larger in *Corythodinium* (broader across its base) and the girdle may be either median or anterior in position. It should be noted that *O. gigas* KOFOID is not a member of *Oxytoxum* but instead belongs to *Gonyaulax*. It is highly probable that it is synonymous with *G. mitra*.

As indicated earlier, *Oxytoxum* exhibits the least signs of torsion in the family, and the sulcus notches the hypotheca only slightly. The plate pattern is very poorly known, existing formulae having been derived from the larger members now transferred to *Corythodinium*. Recently BALECH (1971a) has partially dissected the epithecal plates of *O. scolopax*. In the present work some superficial details of the flagellar pore region of the same species have been illustrated with the aid of the scanning electron microscope (fig. 512). The presence of what appears to be a vestigial list to the right of the flagellar pore is interesting in the light of the description of a new species here in which a list (perhaps its homologue) is clearly developed (*O. lativelatum* sp. n.).

The resemblance of the genus to *Oxyphysis*, discussed by KOFOID (1926), appears to be superficial as the latter is apparently a good dinophysoid genus.

Two species of *Oxytoxum* described recently by RAMPI (1969a), *O. tonollii* and *O. margalefii*, do not conform with the proposed criteria for the recognition of the genus. It is suspected that they may be inverted members of *Amphidoma* (see comments under the latter).

Oxytoxum crassum SCHILLER Plate 24, Fig. 242
– 1936:459, f. 518 a, b; WOOD 1968:88, f. 251.

This identification is somewhat tentative because the present specimen (only one seen) had an acute rather than ovally rounded antapex. Small apical and antapical spines are present, although the latter are only faintly shown in one of SCHILLER's figures and not in the other. They are, however, mentioned in his text.

The sutures are very strongly marked by ridges, especially on the epitheca. SCHILLER stated that five apical and five precingular plates are present although only four apical plates could clearly be seen here (a figure which fits other members of the genus). The flagellar pore is very evident.

This species resembles *O. mitra* STEIN but is apparently much smaller. STEIN (1883) did not give a size in his original description but from his magnification data (given as ranging from 450 to 690 X) the length can be presumed to be between 70 and 110 μm.

Station: 319.

Found at a central Indian Ocean station on cruise V. This is a new record for the Indian Ocean. The species was first described from the Adriatic Sea and has since been recorded from the Straits of Florida.

Oxytoxum globosum SCHILLER Plate 24, Fig. 247
– 1936:458, f. 515 a, b; RAMPI 1969b:327, t. 4, f. 4.
Non WOOD 1963c:17, f. 59.

This is a very small, rotund species. The Indian Ocean specimens were only 12–14 μm in length. RAMPI (1969b) reported a length of 15 μm and SCHILLER's original figure calculates to 17 μm. A small apical papillum is present and SCHILLER also described a small antapical spine although the latter could not be observed in the Indian Ocean material. *O. ovum* GAARDER is similar in general appearance but it is much larger (40 μm in length).

Station: 315.

Only two specimens were observed at a southern central Indian Ocean station on cruise V. Although WOOD (1963c) has recorded the species from the eastern Indian Ocean his figure cannot be referred to this species, possessing a subglobular epitheca with a diameter of approximately half that of the hypotheca instead of approximately two thirds. Consequently, this appears to be a new record for the Indian Ocean. It was originally described from the Adriatic Sea.

Oxytoxum laticeps SCHILLER Plate 24, Fig. 249
– 1936:461, f. 523; WOOD 1954:46, f. 170; – 1963b:46, vix f. 170; HASLE 1960:37, f. 31; WOOD 1968:90, f. 260.

SCHILLER's original figure only showed the dorsal side with no details of thecal surface structure. Consequently, HASLE's identification was based only on shape and size. The epitheca is broad, low and evenly convex. In the original description and in the present specimens an apical spine was lacking, although HASLE has figured a small apical spine. HASLE's specimens had a fairly strongly displaced girdle (left-handed, descending) but this was not as great in the present material and is not shown at all in WOOD's figures. The size range, as presently known, is: length 15–25 μm; diameter 9–15 μm.

The species differs from *O. mediterraneum* SCHILLER in possessing a posterior spine and lacking strong, linearly arranged pores. It is also similar to *O. viride* SCHILLER which has (according to the interpretation here) a different ventral area construction (see fig. 248). *O. punctulatum* RAMPI (1952a) also lacks a posterior spine, has a wide sulcal region, and has closely set rows of punctae similar to *O. mediterraneum*. It has a wider epitheca than *O. pachyderme.*

Station: 374.

Only a few specimens were observed at a station off the southern African coast. It was originally described from the Adriatic Sea and has been found in the Coral Sea, the eastern tropical Pacific Ocean, the Indian Ocean (WOOD 1963b), and the tropical Atlantic Ocean. It is apparently a surface species.

Oxytoxum lativelatum sp. n. Plate 24, Figs. 240 a, b

A small rotund species; the epitheca much smaller than the hypotheca, subglobular with small crenulations marking the upper girdle ridge. Girdle diameter approximately one quarter of the maximum diameter; height approximately one-fifth to one-quarter of the total cell length. The hypotheca is roundly lenticular with an acutely pointed antapex. The broadest region is near the mid-point of the cell. Its surface is finely reticulated. Its walls appear to be thicker than the remaining theca. The plate pattern is not known as yet. The first postcingular plate is narrow, only reaching halfway to the antapex.

A strongly developed but transparent fin arises from the right side of the flagellar pore. It extends slightly onto the epitheca. There is also an internally projecting spine (into the cell body) which arises near the flagellar pore.

Length: 28 μm; maximum diameter 18 μm.

Iconotype: Plate 24, fig. 240 a, b.

Type locality: Southern Indian Ocean; 31° 58'S, 59° 51'E.

No species of *Oxytoxum* have as yet been described bearing a fin of the type depicted here (see *O. semicollatum* sp. n. for a different type) although it is possible that such structures may have been missed due to their transparency. As indicated under *O. scolopax* the latter has a vestigial structure of similar type and position and this may be relatively common in the genus. The inwardly-projecting curved spine associated with the flagellar pore is also unusual.

This species has resemblances to two species described by RAMPI but differs from them in the presence of the flagellar fin and spine. In fact, the figure of *O. minutum* RAMPI (1948, fig. 5) from the subtropical Pacific Ocean shows a structure which may be a fin although no mention of it was made in the text. In any case his species is easily distinguishable due to its broad epitheca and antapically rounded hypotheca. In shape *O. lativelatum* is very similar to *O. spinosum* RAMPI (1941a, fig. 15; HALIM 1960a, pl. 3, fig. 24) and it is possible that RAMPI missed the fin. He only illustrated the species in ventral view. His type material was somewhat smaller (length 20 μm) than *P. lativelatum.*

There are also strong resemblances in shape to *O. sphaeroideum* STEIN var. *sphaeroideum* but the latter lacks the antapical spine in addition to the fin and internal spine (cf. SCHILLER 1936, p. 452, fig. 498).

Station: 157.

Three specimens, all similar in size and shape, were found at this single southern Indian Ocean station.

Oxytoxum nanum HALLDAL Plate 24, Figs. 245, 246
– 1953:56, f. 20.

This species is similar to *O. variabile* SCHILLER but differs from it by its broader girdle, and by the epitheca being displaced slightly to the left. It is not as variable as the latter, the "Anton Bruun" specimens all being relatively similar in size (total length ranges from 20–26 μm). The body is curved, being ventrally concave in its posterior part. The sulcus distinctly notches the hypotheca.

Stations: 156, 289, 291, 305, 310, 358, 365, 366, 370, 371, 374, 404, 407.

As with other small *Oxytoxum* species, the use of nets for sampling probably results in severe under-representation. In the present case the distribution exhibited is nevertheless interesting. With the exception of a few northern and southern (to 38 °S) open ocean stations, mostly on cruise V, it was recorded frequently from a cluster of closely set stations in the southern half of the Mozambique Channel and also a bit further south. These latter stations were predominantly close to either the African or Mascarene coasts.

It was originally described from Weather Ship M (66 °N) in the North Atlantic Ocean where it was common and at times achieved a concentration of 8500 cells per litre. It does not appear to have been observed since then although it has possibly been confused with *O. variabile*. It must be strongly eurythermal, and is a surface species in the North Atlantic.

Oxytoxum pachyderme SCHILLER [valid. nov.] Plate 24, Fig. 250
Basionym: *O. pachyderme* SCHILLER 1936:460, f. 519 "ad interd." WOOD 1963b:48, vix. f. 168.

SCHILLER's description of this taxon is invalid by the International Code of Botanical Nomenclature (Art. 34) because of the temporary status which he gave to it. Rather than create an unnecessary new name SCHILLER's description is here formally established.

The species is small (length 18–30 µm; upper limit derived from WOOD). SCHILLER did not give a size in the text but his magnification for the figure indicates a length of 24 µm. It is relatively rotund with a low, convex epitheca and a relatively wide girdle. There is a small antapical spine and a less conspicuous apical spine. The specific epithet refers to the thick appearance of the wall. There are, however, several other species with equally thick walls. WOOD (1963b) made no reference to, nor illustrated the thick nature of the wall.

The present specimen is not as broad as that of SCHILLER, and the epitheca was slightly wider.

Station: 312.

Two specimens were observed in a single sample from a southern central Indian Ocean station (32 °S). It was originally described from the Adriatic Sea and WOOD found it in the Coral Sea. It has not been recorded previously from the Indian Ocean.

Oxytoxum parvum SCHILLER Plate 24, Fig. 239
– 1936:464, f. 531; WOOD 1963b:48, f. 177; – 1968:92, f. 267; HERRERA et MARGALEF 1963:78, f. 24q; RAMPI 1969b:328, t. 4, f. 3.
Syn.: ? *O. tenuistriatum* RAMPI 1941a:63, t. 2, f. 14.

The specimen illustrated here is essentially intermediate in features between the description of SCHILLER and that of RAMPI's taxon above. It was 43 µm in length (*parvum*: 36 µm; *tenuistriatum*: 52 µm) with a short-spined, somewhat globose epitheca. *O. parvum* was originally shown to have a slightly more developed apical spine than this specimen whereas *O. tenuistriatum* has a slightly shorter spine. The theca (of both) is marked by longitudinal costae as well as finer rows of pores. An interesting feature exhibited by both SCHILLER's specimen and the present one was a prominant round inclusion in the posterior part of the cell. They probably are accumulation bodies.

In the indentation of the epitheca by the sulcus the specimen also resembled *O. longiceps* SCHILLER which is also similar to *O. parvum* but is larger (length 66 µm). GAARDER (1954) found specimens which bridged the size range of *O. parvum* with *O. longiceps* (length of her specimens 45–65 µm) although indentation of the epitheca by the sulcus was lacking. Perhaps this taxon will also be shown to be synonymous (*O. parvum* having priority) in the future.

Station: 18.

A single specimen was found at a station in the southern Andaman Sea near Phuket Island. The species is known from the Mediterranean Sea, the tropical Atlantic Ocean, the western Pacific Ocean, and WOOD (1962, in 1963a) has recorded it from the eastern Indian Ocean.

Oxytoxum scolopax STEIN Plate 24, Figs. 252, 253; Plate 43, Fig. 512
SCHILLER 1936:453, f. 502 a–c; RAMPI 1939b:465, f. 16; – 1941a:63, t. 2, f. 9; KISSELEV 1950:259, f. 449; RAMPI 1952a:113, f. 1; WOOD 1954:315, f. 245; SILVA 1956a:69, t. 11, f. 14; TRÉGOUBOFF et ROSE 1957:118, t. 27, f. 8 A, B; SILVA 1958:32, t. 3, f. 7; CURL 1959:306, f. 124; HALIM 1960a, t. 3, f. 26; HERRERA et MARGALEF 1963:78, f. 24 r; YAMAJI 1966:107, t. 51, f. 16; STEIDINGER, DAVIES, et WILLIAMS 1967, t. 6, f. f; TAYLOR 1967, t. 91, f. 38; WOOD 1968:93, f. 270; STEIDINGER et WILLIAMS 1970:54, t. 27, f. 87; BALECH 1971a:166, t. 36, f. 705–707; SOURNIA 1972a:155, f. 10.

This is one of the commonest members of the genus. With its elongate shape (length 70–120 µm), sharp, prominent spines on both the apex and antapex, and bladder-like swelling at the base of the antapical spine it is distinctive. *O. sceptrum* (STEIN) SCHRÖDER is not as slender and lacks the posterior swelling.

From the accompanying electron micrographs it can be seen that there is a slightly developed fin on the right side of the flagellar pore. It is probably this fin which is developed much further in *O. lativelatum* sp. n. The micrographs also give a good visualisation of the surface structure of the theca. Some details of the epithecal and girdle plates have been elucidated by BALECH (1971a). The sheath-like structure found associated with one of the cells (fig. 253) could have been produced either by the cell or by an organism which had ingested and then egested it.

Specimens from the cold southern station (308) were more robust than those in warmer waters.

Stations: 71, 98, 99, 108, 308, 315.

Although not common this species was very widely distributed, being one of the few to be found south of 40 °S in the Subtropical Convergence region near the Islands of Amsterdam and St. Paul.

The species is inter-oceanic. Although it appears to prefer warmer waters it can also apparently tolerate cold-temperate conditions. GAARDER (1954) found the species to be scattered throughout the "Michael Sars" Atlantic Ocean material she examined.

In addition to the records listed by WOOD (1963a) the species has been recorded previously from the Indian Ocean by SILVA (1956a), ZERNOVA (1962), TSURUTA (1963), TAYLOR (1967), SUBRAHMANYAN & SARMA (1967), NEL (1968), and SOURNIA (1968b, 1970, 1972a) and ANGOT (1970).

Oxytoxum semicollatum sp. n. Plate 24, Fig. 241

Cells small with a reduced epitheca one fifth of the total length; girdle relatively wide, one quarter total length; hypotheca widest just below the girdle, antapex acute. Thecal surface porulate. Plate pattern not yet resolved. The species is distinguished by a delicate lower girdle list projecting anteriorly, not outwards, higher on the right side than on the left side. Sulcal area indents hypotheca but not epitheca.

Length: 19–20 µm; maximum diameter 12 µm (2 specimens).
Iconotype: Plate 24, fig. 241.
Type locality: Coast of Mozambique; 24° 42'S, 35° 23'E.

O. lativelatum sp. n. is the only member of the genus *Oxytoxum*, other than this species, which possesses a well developed list and in addition to considerable differences in cell body features, the lists are organised completely differently. In the case of *O. lativelatum* it is situated perpendicularly adjacent to the flagellar pore whereas it can be considered a homologue of a girdle list in this case.

When dealing with such delicate structures there is always the possibility that they are in fact parts of previously described species which have been missed by previous authors. The present species shows strong resemblances in shape to *O. sphaeroideum* STEIN var. *steinii* OSTENFELD et PAULSEN but is apparently considerably smaller (judging from STEIN's magnifications as no size is given by SCHILLER 1936). MARGALEF & DURÁN (1953, f. 2 X) have figured a small specimen which may be the present species as it possesses an upwardly-directed "spine" arising from the left side of the lower girdle rim. This is the opposite side to the fin reported here, but this may be the result of optical reversal or variability in the feature.

Station: 371.

After extensive searching of the material only two specimens could be found in one sample from the coast of Mozambique (August, 1964).

Oxytoxum subulatum KOFOID Plate 24, Figs. 251 a, b

SCHILLER 1936:465, f. 535; WOOD 1954:316, f. 250; MARGALEF 1961b:142, f. 3/11.
Vix BALECH 1962b:168, t. 19, f. 295, 296.
Syn.: *O. milneri* auct. non MURRAY et WHITTING .... RAMPI 1941a:68, t. 2, f. 4; – 1952a:112, t. 1, f. 3; KISSELEV 1950:260, f. 453; TRÉGOUBOFF et ROSE 1957:118, t. 27, f. 13; HALIM 1960a, t. 3, f. 23; BALECH 1962b:169, t. 19, f. 284, 285; YAMAJI 1966:107, t. 51, f. 15; LÉGER 1971a:30, f. 12.
Vix WOOD 1963b:46, f. 173.

This is a large species. It most closely resembles *O. challengeroides* KOFOID (which is shorter, not exceeding 80 µm, largely due to the lack of a long apical process, but also differing by a less tapered antapex), and also apparently, *O. milneri* MURRAY et WHITTING. The latter could be synonymous but on the other hand, it probably belongs to a separate genus (*Corythodinium*).

The species are similar in size (length, *O. m.* 110–131 µm, *O. s.* 124–142 µm), and shape. The chief superficial distinction seems to be the canula-like, truncated tip to the epitheca of *O. subulatum*, that in *O. milneri* being sharply pointed, the epitheca also being more smoothly conical. The narrow portion of the epitheca is shifted towards the ventral side in *O. subulatum*. Much of the difficulty in making a decision arises from the fact that MURRAY & WHITTING (1899) only illustrated their specimen from the dorsal side, and KOFOID (1907b) only illustrated *O. subulatum* from the right side. Here BALECH's (1971b) interpretation of MURRAY & WHITTING's species is used for its recognition. As a result it has been assigned to the genus *Corythodinium* due to the presence of the large anterior sulcal plate indenting the epitheca. HASLE's (1960) specimen appears to have been the same taxon as BALECH's, but she did not illustrate the ventral details of her specimen.

Station: 99.

It was only found at one station in the southwestern Bay of Bengal. The species has only been found in the Indian Ocean once before (see WOOD 1963a). It was originally described from the eastern tropical Pacific Ocean and has been found by WOOD (1954) in the western Pacific Ocean and by MARGALEF (1961b) in the Atlantic Ocean off the coast of northwestern Africa.

Oxytoxum variabile SCHILLER Plate 24, Figs. 243, 244
– 1936:455, f. 505 a, b; HASLE 1960:38, f. 34 b–d vix a; WOOD 1963b:49, f. 183; RAMPI 1969b:330, t. 3, f. 8, 9.
Syn.:*O. gracile* SCHILLER 1936:455, f. 506.

This small species exhibits a strong degree of variation, particularly in size, its reported dimensions (combined from the above sources) being: length 14–26 µm (30 µm in WOOD 1963b), diameter 5.5–12 µm. HASLE (1960) considered that its variability may also include *O. gracile* SCHILLER (which has a less convex lower girdle surface and more concave sides to its epitheca). On the basis of observations on the "Anton Bruun" material this synonymy appears to be reasonable. Delicate reticulation has been seen on the theca of some specimens.

O. nanum HALLDAL is also similar but is retained as separate here on the basis of the relatively broader, less excavated girdle, asymmetrically placed epitheca (displaced to the left), and strong linear markings (figs. 245, 246).

Stations: 157, 327, 336, 365, 374, 404, 407.

Recorded in small numbers from scattered central and western Indian Ocean stations, including the Mozambique Channel. It was apparently absent from the Bay of Bengal although, due to its small size, it is quite possible for it to not be retained by nets. Using closing bottles HASLE (1960) found that it achieved numbers up to 4000 cells per litre in equatorial Pacific Ocean samples, and was common at all depths to 300 or 400 m. It is clearly an important tropical species requiring sedimentation or centrifugation techniques to fully assess its abundance and distribution. It has been previously recorded from the Indian Ocean by WOOD (1962, in 1963a). Other records include the Mediterranean Sea, the tropical Pacific Ocean, and the Tasman Sea.

Oxytoxum viride SCHILLER Plate 24, Fig. 248
– 1936:456, f. 510 b; WOOD 1968:94, f. 276.

A small (length 17–20 µm) species with rounded epi- and hypotheca. The epitheca is relatively well-developed being approximately one-fifth to one-quarter of the cell length. There is a small spinule at the tip of the hypotheca and (in the present material only) an inconspicuous apical projection may also be present. The most striking feature, visible even in formalin-preserved material several months after collection, is the presence of numerous small, bright-green chloroplasts (yellow-green in formalin). In ventral view, shown here for the first time, the girdle appears to be interrupted at the flagellar pore.

Station: 335.

A single specimen was observed at a station in the southern Arabian Sea.

The species has only been seen previously by SCHILLER (Adriatic Sea), GAARDER (1954, eastern tropical Atlantic Ocean), and WOOD (Strait of Florida).

Family Peridiniaceae EHRENBERG

This family is here represented by the genera *Diplopsalis* BERGH, *Peridiniopsis* LEMMERMANN, *Peridinium* EHRENBERG and *Zygabikodinium* LOEBLICH et LOEBLICH III.

Genus *Diplopsalis* BERGH

Syn.:*Dissodium* ABÉ, partim.

This is the earliest described member of a group of spheroid to lenticular genera similar to *Peridinium*, but having for the most part, only three apical plates instead of four (see Table 4). In several, including *Diplopsalis* sensu stricto, there is only one antapical plate, instead of two as in *Peridinium*. The genus *Entzia* LEBOUR has four apical plates but has only one antapical plate. Nevertheless most authors have included it with *Peridinium*.

The history of this group is extremely confused, largely due to the fact that the earliest figures lacked tabulation (being difficult to see when the cell contents are present), and tabulational details are the chief means by which they are presently separated. Also, the effects of individual variability are still not well understood.

The genera can only be handled in the manner followed by the consensus of modern authors, building on the detailed studies of PAVILLARD (1913), LEBOUR (1922) and NIE (1943). The latter authors have summarised the historical confusion surrounding the genera.

A recent major development has been the proposal by BOURRELLY (1968a, b) to discard the genus *Glenodinium* because of the impossibility of defining its type species and the very differing interpretation which it has been given by many authors. This has partly arisen from the tendency to use *Glenodinium* as a convenient label for species whose tabulation was not elaborated fully or, in some instances, not at all. BOURRELLY has put all of the members with only one anterior intercalary plate into the genus *Peridiniopsis* in view of an analysis of the type species of the latter genus (BOURRELLY 1968b). This seems to be a sound suggestion to the present author, provided that *Peridiniopsis* is limited to those taxa with two antapical plates, thus already separating it from *Diplopsalis* (see below). Steps should be taken to have *Glenodinium* EHRENBERG declared a nomen confusum or nomen ambiguum (Botanical Code, articles 69, 70) and to allocate the species to other readily definable genera.

Further confusion has arisen due to differences between the Botanical and Zoological Codes (see Introduction). LOEBLICH III had asserted (1970, p. 905) that the genus *Diplopsalis* BERGH is pre-occupied by SCLATER's subgenus of birds, a view which is acceptable to the zoologist but not to botanists. If the principal is accepted that only names valid according to both codes may be used for dinoflagellates, ABÉ's name *Dissodium* should be used. This is unfortunate due to the possibility of confusion with *Dissodinium* PASCHER. LOEBLICH III (1970) has indicated that members of *Diplopsalis* have two antapical plates. This reflects NIE's (1943) broader interpretation of the genus. Here the majority of these taxa would be considered to belong to the genus *Peridiniopsis*.

The subdivision in the table is logical and reflects the strictest recent interpretation of the genera. *Diplopsalis* is here limited to those species with only one antapical plate, as stressed by BALECH (1967a). However, how meaningful it is after variability is taken into account is unknown.

The large dorsal anterior intercalary plate of *Diplopsalis* can touch the apical pore in some cases (e.g. Pl. 28, fig. 298), thus theoretically altering the epithecal plates from 3', 1^a, 6'' to 4', 0^a, 6''. Allowance for such minor variability must clearly be made before creating new taxa. NIE (1943) considered that the anterior intercalary plates and the antapical plates were liable to variability, whereas the apical, precingular, post-cingular, cingular and sulcal plates were more conservative. Thus he did not distinguish *Peridiniopsis* from *Diplopsalis*.

Another point to be stressed is that there should not be a great inconsistency in the criteria used for generic recognition here and in *Peridinium*. In the latter a difference in the number of anterior intercalary plates is of subgeneric rather than generic significance, if no other differences are also present. While this is chiefly an arbitrary matter, the use of differing magnitudes of distinction among such closely related taxa does not seem logical.

From the table it can be seen that *Diplopsalis* and *Peridiniopsis* share the peculiarity of having only six precingular plates (the rest having seven) but differ in the presence of only one antapical plate in the former as well as in the number of cingular plates. *Zygabikodinium* and *Diplopsalopsis* have a combination of 3', 7'', differing only in the number of antapical plates. *Entzia* and *Peridinium* both have a 4', 7'' combination, also differing primarily in their antapical plate number.

Diplopsalis lenticula BERGH Plate 28, Figs. 298, 299

LEBOUR 1922:795, f. 1–5; – 1925:99, t. 15, f. 1 a–e; NIE 1943:10, f. 9–13; WOOD 1954:222, f. 86 a–c; TRÉGOUBOFF et ROSE 1957: 109; t. 23, f. 6 A, B; MARGALEF et MORALES 1960:5, f. 2 d; YAMAJI 1966:79, t. 37, f. 1; WALL et DALE 1968a:279, f. 7, t. 4, f. 19; STEIDINGER et WILLIAMS 1970:49, t. 18, f. 51.

Vix MARTIN 1928:23, f. 11–13 (*D. lebourae?*); HADA 1967:16, f. 26; WOOD 1968:54, f. 132.
Non WANG et NIE 1932:296, f. 9; SILVA 1952a:35, t. 3, f. 1, 2 vix 3.
Syn.: *Glenodinium lenticula* (BERGH) SCHILLER 1935:103, f. 95 a–h; KISSELEV 1950:136, f. 217 *а–г*, 220 *а–в*, non 218 *а–в*, nec 219 *а–в*.
Dissodium lenticulum (BERGH) LOEBLICH III 1970:905.

This is the type species of the genus, and although tabulation was not indicated in the original figures it is now accepted as having three apical plates, one large, symmetrical, dorsal anterior intercalary plate, six precingular plates (early figures, such as that of PAVILLARD 1913, often showed five, the mid-dorsal suture being omitted), five post-cingular plates and only one antapical plate. The cells are lenticular in shape, varying in transdiameter from 32–68 µm (usually less than 55 µm). KISSELEV (1935) created a forma *globularis* for those with a more spherical shape, later transferring it along with the f. *lenticula* to *Glenodinium*.

Fig. 298 shows an unusual epitheca in that it is more dorso-ventrally compressed than usual, and because of a dorsal shift of the apical pore, it looks as if it has four apical plates rather than three plus an intercalary plate. LEBOUR (1922) also found such variants occasionally.

WALL & DALE (1968a) have found that the cysts are spherical, with a smooth surface and a large apical archeopyle.

D. lebourae (NIE) BALECH is similar, being initially described as a variety of the above, but has been separated because of its spherical shape, sometimes even longer than broad, shape, large size (usually greater than 57 µm, but there is overlap with the above) and particularly prominent left sulcal list.

Stations: 94, 95, 101, 103, 104, 105.

The species was found only at a few stations in the west-central Bay of Bengal. However it was abundant at two of these (94, 101). Only two of the stations coincided with the distribution of the morphologically similar taxon, *Peridiniopsis asymmetrica*.

WOOD's (1963a) list of Indian Ocean records includes references to *Peridiniopsis asymmetrica* which should not be combined with *D. lenticula* (e.g. BALLANTINE 1961). Nevertheless there are still numerous records of the species from the Indian Ocean, SILVA's (1956a) and TAYLOR's (1967) references being additional to those listed by WOOD. It is evidently thermotolerant, being found in both cold-temperate and tropical waters. LEBOUR (1922) considered it to be a neritic species.

Table 4. Plate formulae of *Diplopsalis* BERGH and related genera.

Diplopsalis s. str. (= *Dissodium* ABÉ)	3′	1^{a}	6″	3C	6S	5‴	1⁗
*Peridiniopsis/Oblea** (= *Diplopelta, Glenodinium partim*)	3′	$1-2^{a}$	6″	3–6C	6S	5‴	2⁗
Zygabikodinium (= *Diplopeltopsis*)	3′	$1-2^{a}$	7″	3C	4S	5‴	1⁗
Diplopsalopsis	3′	2^{a}	7″	?	?	5‴	2‴
Entzia	4′	2^{a}	6–7″	3C	?	5‴	1⁗
Peridinium	4′	$2-4^{a}$	7″	3–6C	4–7S	5‴	2⁗

**Oblea* BALECH (1964b) has a similar formula to *Peridiniopsis* but has been distinguished from it in view of the strongly lateral displacement of the principal (largest) anterior intercalary plate.

Genus *Peridiniopsis* LEMMERMANN

Syn.: *Diplopelta* JÖRGENSEN; *Glenodinium* partim; *Dissodium* ABÉ partim.

This genus is very similar to *Diplopsalis*, differing by its possession of two antapical plates instead of one. The type species, *P. borgei* has six cingular plates, but the marine species seem to have only three (NIE 1943), an interesting parallelism to the marine and freshwater species of *Peridinium*. NIE (1943) did not distinguish between members with two antapical plates and those with one and consequently many of the species he described belong, in actuality, to *Peridiniopsis*. The following are here transferred:

Peridiniopsis hainanensis (NIE) comb. nov. [basionym: *Diplopsalis hainanensis* NIE 1943:13, f. 20–25]
Peridiniopsis pingii (NIE) comb. nov. [basionym: *Diplopsalis pingii* NIE 1943:16, f. 26–31]

Peridiniopsis excentrica (NIE) comb. nov. [basionym: *Diplopsalis excentrica* NIE 1943:17, f. 32–36]

LOEBLICH III (1970) followed NIE's broader interpretation, but transferred them all to *Dissodium* ABÉ in view of his assertion that *Diplopsalis* is pre-occupied.

In Table 4 it has been indicated that the genus *Oblea* shares the same tabulation but the single anterior intercalary plate is displaced very strongly to the left side of the epitheca [e.g. *O. rotunda* (LEBOUR) BALECH]. For further comments, see the discussion under *Diplopsalis.*

Peridiniopsis asymmetrica MANGIN Plate 28, Figs. 296 a, b; Plate 45, Figs. 520 a–c

LEBOUR 1922:798, f. 6–10; – 1925:101, t. 15, f. 3 a–e; WAILES 1928, t. 3, f. 9–12; – 1939:29, f. 83 A–D; BALLANTINE 1961:219, f. 18–20.

Syn.:. . . *Glenodinium lenticulum* forma *asymmetrica* (MANGIN) SCHILLER 1935:105, f. 97 a–e (non f, g, vix h); KISSELEV 1950:136, f. 219 a–β.

Diplopsalis lenticula forma *asymmetrica* (MANGIN) STEIDINGER, DAVIS et WILLIAMS 1967, t. 6, f. d; STEIDINGER et WILLIAMS 1970: 49, t. 18, f. 52.

Diplopsalis asymmetrica (MANGIN) LINDEMANN 1928:91; NIE 1943:14, f. 1–8; SILVA 1958:29, t. 2, f. 8–10; MARGALEF 1964, f. 2B; YAMAJI 1966:79, t. 37, f. 2.

Dissodium asymmetricum (MANGIN) LOEBLICH III, 1970:905.

Diplopelta asymmetrica (MANGIN) BALECH 1964b:22.

As NIE (1943) has remarked, this is probably the largest, most widely distributed and best known member of the *Diplopsalis/Peridiniopsis/Zygabikodinium* group. Its tabulation is that usual for the genus. The first anterior intercalary plate is small, rhomboid, and displaced to the left side, the second anterior intercalary being much larger and almost mid-dorsal. The body shape varies from lenticular to round, and the transdiameter can reach 95 µm. Typically the girdle lists lack supportive spines.

P. bainanense is perhaps the closest species to it, having only one anterior intercalary plate instead of two. In *P. excentrica* the apical plates are reduced in size, the second anterior intercalary plate being very large and covering most of the epitheca. *P. pingii* is much smaller, having a transdiameter of 40–45 µm.

Stations: 15, 17–19, 21, 24, 25, 28, 30, 32, 34, 35, 39, 40, 42, 48, 49, 51, 52, 62, 64, 65, 69, 71, 72, 87, 90, 92, 95–98, 105, 129, 130, 133, 144, 147, 148, 156, 285–287, 291, 310, 312, 359, 362, 366, 369, 371, 375, 415, 418, 420.

This was the commonest of the lenticular taxa, and was also one of the commonest species in the material. Although found as far south as 38 °S it was generally absent from the central Indian Ocean and also, with the exception of the Gulf of Aden, from the Arabian Sea. In the Bay of Bengal it occurred chiefly at neritic stations (except those of lowest salinity), and it was widespread throughout the Andaman Sea. It was common both north and south of the Mozambique Channel, but was not found in the central channel at the time of cruise VIII (October).

The species is cosmopolitan, tolerating both cold-temperate and tropical conditions. It has been found on several occasions previously in the Indian Ocean, although WOOD (1963a) listed the records under *Diplopsalis lenticula* and erroneously included MATZENAUER's (1933) and SUBRAHMANYAN's (1958) records under *"Diplopsalis minor."*

Genus *Peridinium* EHRENBERG

This is one of the largest genera of thecate dinoflagellates and various attempts have been made to subdivide it into subgroupings or other genera. For example, one of the earliest attempts was that of PAULSEN (1908) who recognised two subgenera: *Protoperidinium* (BERGH) OSTENFELD in which the girdle displacement is right-handed and antapical horns are lacking; and *Euperidinium* GRAN, with left-handed girdle displacement and often with antapical horns. This simple subdivision was soon seen to be insufficient to handle the ever-increasing number of species, and JÖRGENSEN (1913) produced a new system which was based on the shape of the first apical plate, (four-sided: *Orthoperidinium;* five-sided: *Metaperidinium;* six-sided: *Paraperidinium*), three groups being subdivided further into various sections. Although his major groups are not used, many of his sections are still recognised, and his emphasis on the first apical plate was incorporated by later authors (principally PAVILLARD 1916, PETERS 1928, PAULSEN 1930, SCHILLER 1935, ABÉ 1936a and PAULSEN 1949) into a system using a combination of the features of the first apical plate plus the second (mid-dorsal) anterior intercalary plate, expressed in abbreviated jargon such as "ortho-quadra", "meta-penta" etc. (see text fig. 3), together with more general features such as the shape of the body, girdle displacement, presence or absence of antapical horns and spines, etc.

For those members with only two anterior intercalary plates, this convention could not be used. LEBOUR (1922) proposed that the latter be recognised as a subgenus: *Archaeperidinium* (JÖRGENSEN), those with three anterior intercalary plates remaining in the subgenus *Peridinium*. This subdivision is followed here.

Other subgenera have also been proposed. The majority of freshwater members lack an apical pore, and LEFÈVRE (1932) proposed the subgenus *Cleistoperidinium* (LEMMERMANN) LEFÈVRE for the latter, *Poroperidinium* (LEMMERMANN) LEFÈVRE including all those with an apical pore (now restricted to fresh-water species). As *Cleistoperidinium* includes the type species of the genus it has to be referred to as the subgenus *Peridinium* (Botanical Code, Article 22).

At present, using a broad definition for the genus, it can be recognised from its nearest relatives (*Diplopsalis* and other similar genera) by its possession of four apical plates, two or more anterior intercalary plates (up to four), and two antapical plates, the latter being fairly evenly developed.

Thus the plate formula for *Peridinium* can be written:

$$4', 2\text{–}3(4)^{a}, 7'', 5''', 2''''$$

excluding the cingular and sulcal plates for the moment.

The girdle (cingular) and ventral area (sulcal) plates have assumed considerable significance in the taxonomy of *Peridinium*, although for differing purposes. The cingular plates (designated by a capital C) have become important in distinguishing subgenera (or according to some authors, genera) and the shape, size and configuration of the sulcal plates have provided valuable accessory information in the recognition of species. Text fig. 3 illustrates the cingular and sulcal plate terminology of members of the subgenus *Protoperidinium* (BERGH) OSTENFELD.

KOFOID (1909a) was the first to depict the sutures of the sulcal plates of a member of the genus (*P. steinii*), although he did not dissociate them for a complete examination and consequently saw only the gross features of the four principal platelets. He called them the anterior, median, sinistral and posterior ventral plates (see table 5 for his notation and that used by later authors).

BARROWS (1918), in his study on plate variability in the genus, experienced great difficulty in seeing the sulcal plates, incorrectly predicting that they would prove too variable to be of value.

FAURÉ-FREMIET & PUIGAUDEAU (1922) figured ventral sutures in a few species of *Peridinium* but, as GRAHAM (1942, p. 12) put it: "These must have been drawn from the authors' imagination, as they bear no relation whatever to the actual tabulation of these species."

It was ABÉ (1936 a, b) who placed considerable emphasis on the sulcal plates, having found that they were remarkably conservative, his observations agreeing with KOFOID's except for slight modification. In addition he discovered an interesting platelet which, because of its location at the left proximal end of the girdle but protruding into the sulcal region, could be considered either a cingular or a sulcal plate. It is much smaller than the regular cingular plates. He termed it the transitional plate. He used the terms anterior, posterior, left and right to designate the sulcal plates. His very clear figures showed that, with the exception of the longitudinal lists bordering the ventral area (usually more strongly developed on the left side), the main fin near the flagellar pore (the right accessory sulcal list) arises from the inner (pore side) posterior edge of the right sulcal plate. From his figures it is also evident that the large posterior flagellar pore is formed chiefly as an excavation of the left sulcal plate.

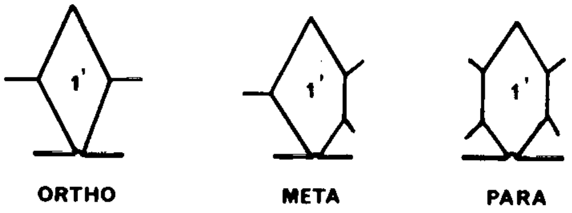
Table 5. Notational equivalents used for the sulcal plates of *Peridinium*.

	KOFOID 1909a	ABÉ 1936b	NIE 1939	GRAHAM 1944	BALECH after 1964
Transitional	–	t	LA	lg	T
Anterior	a. pl.	a	RA	as	Sa
Right	m. pl.	d	RF	rs	Sd
R. accessory	–	–	–	ras*	
Left	s. pl.	s	LF	Ls	Ss**
Median (internal)	–	–	conn.	ris	Sm
P. accessory	–	–	?	pas	Spa
Posterior	p. pl.	p	post.	ps	Sp

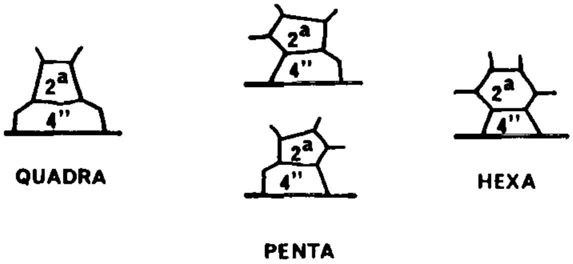
* Only observed in *P. pallidum*, occurring at the distal end of the girdle.

** In his earlier papers, noted as S. i. (e.g. BALECH 1949a).

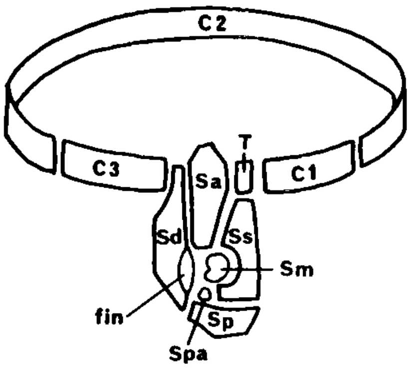
The first apical plate:



The second (mid-dorsal) intercalary plate:



The girdle and sulcal plate designations:



Text fig. 3. Conventional nomenclature for important plates in the description of *Peridinium*.

NIE (1939) also focussed his attention on the sulcal plates of several species, obtaining similar results to ABÉ although he used a different terminology. In addition he discovered a small plate in the flagellar pore region which he called the connecting plate (conn.). He treated the transitional plate as a sulcal plate.

GRAHAM (1942) recognised the four main sulcal plates (anterior, posterior, left and right) as conservative elements which varied in size and shape only. However he recognised three other plates of varying occurrence: a right accessory sulcal plate (in 1 species only), a small posterior accessory plate forming the posterior end of the flagellar pore, and a right internal sulcal plate lying internally to the flagellar pore. PAULSEN (1949) considered that the laboriousness involved in resolving these plates detracted from the usefulness in the analysis of field material, and he also doubted if some of the distinctions drawn by ABÉ were as great as he claimed.

Despite such reservations BALECH has, in an extensive series of papers over the last twenty years, undertaken to dissect the ventral plates of many species, with great success and has contributed to the understanding of the structure of the ventral region in a fundamental way. His notation for the sulcal plates now seems to be gaining acceptance.

There is little doubt that when new species are described in this and related genera, all efforts should be made to elucidate the ventral plates. However, in view of the rarity of species distinguished at present solely by sulcal plate differences, and faced with the floristic analysis of hundreds of samples, sulcal plate dissection does not seem to be feasible except in isolated cases.

DIWALD's (1939) study of variability in primary plate patterns in 16 species has been unjustifiably ignored.

The first genus to be separated from *Peridinium* purely on the grounds of the cingular plates was *Scrippsiella* (BALECH 1959a). *S. sweenyae*, the type species, was found to have five cingular plates plus a "transitional plate" and 4 sulcal plates. LOEBLICH III (1968) added a second genus, *Cachonina*, which has a similar number of cingular plates (six, fully developed) but differs from *Scrippsiella* in having more plates in its apical and precingular series. BALECH (1967a) created *Ensiculifera*, which possesses four cingular plates plus a transitional plate (the latter possessing a long, anteriorly-directed, internal spine).

BALECH (1963b) and LOEBLICH III (1968) raised an interesting and taxonomically disturbing point. The marine species of *Peridinium* were all found to possess three cingular plates plus a transitional plate. However it appeared that the freshwater species, including the type: *P. cinctum* (MÜLLER) EHRENBERG, may have more cingular plates. Consequently, as they had made the number of cingular plates a criterion for generic distinction, it appeared that the many species of marine peridinia might all have to be renamed, being attributed to the next available generic name. LOEBLICH III (1968) first suggested this to be *Archaeperidinium* JÖRGENSEN, but then later (1970) realised that *Protoperidinium* BERGH was the earliest genus which specifically included members with three cingular plates, its type being *P. pellucidum.*

BOURRELLY (1968a) investigated the cingular plates of twelve freshwater species of *Peridinium.* He found that the type species and three other members of the subgenus *Peridinium*, all of which lack an apical pore plate, possess five cingular plates, the sutures corresponding with the postcingular series. In addition two members of the subgenus *Poroperidinium* (fresh-water species possessing an apical pore) also have five cingular plates. The remaining five members of *Poroperidinium* examined and one member of *Cleistoperidinium* all have six cingular plates. He concluded that as the freshwater peridinia varied in cingular plate number, and that this variance did not correspond with the presence or absence of an apical pore, it was not appropriate to use cingular plate number as a generic criterion. BOLTOVSKOY (1973 a, b) has made similar plate observations, and also concluded that apical pore development may be variable in fresh water species.

Apart from any consideration as to the quantitative taxonomic significance of the number of cingular plates (as opposed to any other thecal criteria) the procedural situation seems to be clear. If the sole means of recognising *Scrippsiella* and *Ensiculifera* as distinct from *Peridinium* at the generic level is the number of cingular plates then all the marine species of *Peridinium* (more than 200) have to be renamed, as well as many freshwater species, a step clearly contrary to the avowed conservationary aim of the International Codes of Nomenclature. BOURRELLY (1968a) considered such changes as of little value.

One solution out of this dilemma would be to accept cingular plate number as a subgeneric character where appropriate, the marine peridinia retaining their combinations at the cost of reducing *Scrippsiella* and *Ensiculifera* to subgeneric status. The existence of similar cingular plate numbers (five or six) in the freshwater members of the subgenus *Peridinium* also argues against their separate generic status. *Cachonina* seems to warrant generic separation in view of its large number of apical plates (five), the first apical plate not reaching the sulcus, and the numerous (eight) precingular plates. Its hypothetical tabulation resembles that of *Peridinium.* If it were reduced to a subgenus of *Peridinium* it would also be necessary to sink several other long established genera separated from *Peridinium* on apical or antapical plate differences.

However, another solution can be offered which retains *Scrippsiella* and *Ensiculifera* at the generic level: an additional distinction can be made between them and *Peridinium*: the production of calcified cysts. *Peridinium trochoideum* (STEIN) LEMMERMANN is the only member of *Peridinium* known to produce calcitic cysts like those of the above genera, and has been considered closely related to them by WALL et al. (1970). In fact, if cyst characters are considered of major importance *P. trochoideum* should probably be transferred to *Scrippsiella.* This would accord with the views of TAYLOR (1972a) and SWIFT & WALL (1972), as well as micropaleontological practice.

It is hoped that this action may stave off the creation of a great many new combinations, all of which, even if not accepted, will have to be cited in any formal taxonomic treatment which may follow. However this hope is a meagre one. LOEBLICH III (1970) has already transferred two of the species considered to *Protoperidinium* BERGH.*

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* The hope of fore-stalling the creation of large numbers of new combinations, resulting from the recognition of the genus *Protoperidinium*, by the above proposals, has been negated by the appearance, after the submission of this manuscript to the publisher, of two additional papers on *Protoperidinium* by BALECH (1973, 1974). In the second of these he has created 231 new combinations for marine peridinia transferred to *Protoperidinium* (including all the species referred to *Peridinium* here, but not those referrable to *Scippsiella*).

Key to the subgenera of *Peridinium*, and some related genera, recognised here

1. Apical pore always lacking, usually with 5 cingular plates . . . . . *Peridinium* [= *Cleistoperidinium* LEFÈVRE]
   Apical pore present . . . . 2.
2. Three cingular plates + transitional plate . . . . 3.
   More than three cingular plates . . . . 5.
3. Two anterior intercalary plates . . . . *Archaeperidinium*
   Three anterior intercalary plates . . . . 4.
4. Six precingular plates . . . . *Minusculum*
   Seven precingular plates . . . . *Protoperidinium*
5. Four cingular plates (+ transitional plate) . . . . *Ensiculifera* (Genus)
   Five cingular plates (+ transitional plate) . . . . *Scrippsiella* (Genus)
   Six cingular plates . . . . *Poroperidinium*

Four of these, *Archaeperidinium*, *Minusculum*, *Protoperidinium* and the genus *Scrippsiella*, were present in the "Anton Bruun" material.

The subgenera *Archaeperidinium* and *Protoperidinium* are usually dealt with as one unit, sharing the same number of cingular plates. The key below follows this convention.

Key to the sections of the subgenera *Archaeperidinium* JÖRGENSEN and *Protoperidinium* (BERGH) OSTENFELD

1. Two anterior intercalary plates . . . . 2 (Subgenus *Archaeperidinium*)
   Three anterior intercalary plates . . . . 4 (Subgenus *Protoperidinium*)
2. Anterior intercalary plates equal in size 3
   Ant. intercalary plates very unequal in size . . . . Sect. *Excentrica* PAULSEN
3. Girdle left-handed (descending) . . . . Sect. *Avellana* PAULSEN
   Girdle not displaced . . . . Sect. *Archaeperidinium*
4. Lacking antapical spines or horns . . . . Sect. *Tabulata* JÖRGENSEN
   Lacking hollow antapical horns but with antapical spines . . . . . 5.
   With hollow antapical horns . . . . 6.
5. First apical plate: Meta . . . . Sect. *Humili-Piriformia* PAULSEN
   First apical plate: Para . . . . Sect. *Protoperidinium*
6. First apical plate: Meta . . . . Sect. *Divergentia* JÖRGENSEN
   First apical plate: Ortho . . . . 7.
7. Antapical horns blunt, short, 2^a usually hexa . . . . Sect. *Conica* JÖRGENSEN
   Antapical horns more drawn out, 2^a usually quadra . . . . Sect. *Oceanica* JÖRGENSEN

Subgenus *Archaeperidinium* (JÖRGENSEN) LEBOUR

Members of this subgenus differ from those of the subgenus *Protoperidinium* by the possession of only two anterior intercalary plates. In other respects, such as the possession of an apical pore and number of cingular plates, they appear to be similar to the latter. They all have an "ortho" first apical plate.

Three sections have been recognised within this subgenus: *Avellana* PAULSEN, in which the girdle is left-handed and the anterior intercalaries are symmetrical; *Archaeperidinium* (= *Monovela* ABÉ) in which the girdle has no displacement; and *Excentrica* PAULSEN in which the anterior intercalary plates are very unequal in size (see PAULSEN 1949 for further details). As so few species are involved in the present work the sections have not been employed.

Peridinium abei PAULSEN Plate 33, Figs. 363, 366

SCHILLER 1935:138, f. 136 a–h; ABÉ 1936a:667, f. 52–61; KISSELEV 1950:157, f. 250; WOOD 1954:229, f. 91; SILVA 1956a:60, t. 10, f. 4–6; MARGALEF 1957a:45, f. 3a; YAMAJI 1966:86, t. 41, f. 10; HALIM 1967:734, t. 5, f. 68, 69; WOOD 1968:97, f. 283; STEIDINGER et WILLIAMS 1970:55, t. 27, f. 90 a–c; HASSAN et SAIFULLAH 1972b:160, f. 1 a, b.

Syn.: *P. biconicum* ABÉ . . . BÖHM 1931a:194, f. 14; MATZENAUER 1933:454, f. 26 a–d; NIE 1939, f. 4. Non *P. biconicum* DANGEARD.

This species exhibits quite a large variation in its shape. Although always biconical, it can be elongated due to the extension of the apical and antapical (right side only) horns. BÖHM (1931a) termed this the forma *elegans* (of *P. biconicum*: it was transferred to *P. abei* by ABÉ 1936a) and it is equivalent to the f. *elongata* of MATZENAUER (1933). At the other extreme it can be broad and short with no apical or antapical prolongations, this being termed the *f. rotundata* by ABÉ (1936a). The var. (forma) *abei* is between these two extremes. Although the antapex is usually noticeably asymmetrical, the right side being larger than the left (fig. 363); one can also find cells in which the antapex is perfectly conical (fig. 366). The latter are usually megacytic (with intercalary bands well developed). The above variants are considered as varieties in accordance with the principles outlined in the introduction:

P. abei PAULSEN var. *elegans* (BÖHM) stat. nov. [Basionym: *P. biconicum* forma *elegans* BÖHM 1931a:194 = *P. abei* f. *elegans* ABÉ].

P. abei PAULSEN var. *rotundata* (ABÉ) stat. nov. [Basionym: *P. abei* forma *rotundata* ABÉ 1936a:667].

P. abei is in most respects very similar to *P. ventricum* ABÉ, the chief distinction being that in the former the epi- and hypotheca are subequal in length, whereas in the latter the epitheca is smaller than the hypotheca. As can be seen from fig. 521a, this is not always easy to judge. *P. abei* is larger (length 70–105 µm) than *P. ventricum* (length 51–54 µm).

Stations: 46, 104, 363, 369.

The species occurred in the Bay of Bengal and at the southern end of the Mozambique Channel. It is evidently thermophilic, and is evidently tolerant of high salinities in view of its occurrence in the Persian Gulf (BÖHM 1936 – record omitted by WOOD 1963a). It is interoceanic, and has been found in the Indian Ocean also by MATZENAUER (1933), WOOD (1954), SILVA (1956a), and HASSAN & SAIFULLAH (1972b).

Peridinium minutum KOFOID Plate 33, Fig. 372

WAILES 1928:4, t. 3, f. 42, 43; SCHILLER 1935:141, f. 140 a–d; ABÉ 1936a:671; NIE 1939, f. 12 A–E; KISSELEV 1950:158, f. 239; SILVA 1955:135, t. 4, f. 7, 8; MARGALEF, DURÁN et SAIZ 1955:95, f. 5 i, j; BALECH 1964a:180, t. 1, f. 1–10; HALIM 1967:741, t. 9, f. 125, 126; WOOD 1968:104, f. 311; WALL et DALE 1968a, t. 4, f. 6, 7.

Syn.: *P. monospinum* PAULSEN ... WAILES 1928:3, t. 3, f. 34–36; – 1939:32, f. 93; ABÉ 1936a:670; SILVA 1949:344, t. 5, f. 12, 13.

This is a distinctive rotund species with a small, smoothly attached apical horn and lacking girdle excavation. The two anterior intercalary plates are asymmetrically or symmetrically developed. BALECH (1964a) has provided a detailed plate analysis.

PAULSEN (1930, 1949) agreed with the conspecificity of his species with that of KOFOID. Originally he had asserted that it differed in being larger (length 48–60 µm instead of 23–43 µm). BALECH (1964 a, b) revised the size data of *P. minutum* (to length 46–56 µm, partly to distinguish it from *P. aspidotum* BALECH (length 35–39 µm) which also exhibits greater dorso-ventral flattening, asymmetrical development of 1″ and 7″ and postcingulars and subequal anterior intercalaries. *P. constrictum* ABÉ is large (length 55–64 µm) and supposedly has a shorter sulcus.

WALL & DALE (1968a) have studied the species during encystment, finding that it produces a cyst with numerous blunt processes.

Station: 53.

Found in small numbers at only one station situated in the northern Bay of Bengal. The species is known from both cold temperate and tropical waters in the three major oceans but not from the Mediterranean Sea, suggesting an exclusion from high salinity areas. It has been recorded from the southern Arabian Sea by SUBRAHMANYAN (1958) and SUBRAHMANYAN & SARMA (1967) and from the southwest Indian Ocean by SILVA (1956a, 1960) and TAYLOR (1967).

Peridinium ventricum ABÉ Plate 45, Fig. 521 a–c

SCHILLER 1935:143, f. 144 a–e; NIE 1939, f. 9 A–E; KISSELEV 1950:210, f. 345; WOOD 1954:229 vix f. 93 a, b.

As indicated under *P. abei* this species is very similar to it, the chief distinction being the smaller size of *P. ventricum* (length 51–54 µm) and the short epitheca in comparison with the hypotheca. Both exhibit the curious, slit-like apical plate (fig. 521 b) found also in some other members of the subgenus. Also, in both, the right posterior part of the hypotheca usually protrudes beyond the left part. *P. thorianum* PAULSEN, as interpreted by some authors (e.g. NIE 1939), also looks very similar to *P. ventricum*, showing a similar curved first apical plate (also in *P. abei*). However other authors (e.g. WAILES 1939) have interpreted *P. thorianum* quite differently, showing a more conventionally-shaped "ortho" plate.

Station: 420.

Only one specimen was found in the vicinity of Mombassa. The species appears to be thermophilic, like *P. abei*, but is rarer than it. It is known only from Far Eastern waters and from the Indian Ocean (one record: WOOD 1962 in WOOD 1963a).

Subgenus *Protoperidinium* (BERGH) OSTENFELD

This subgenus contains the bulk of the marine species of *Peridinium;* that is, those with an apical pore, three girdle plates plus a transitional plate, and three anterior intercalary plates. It has been subdivided into numerous sections (see the key appearing before the subgenus *Archaeperidinium*) and they are useful in handling the species here. The criteria used for recognising the sections are the nature of the first apical plate, the second (mid) anterior intercalary plate and, to a lesser extent, the girdle displacement and possession or absence of hollow antapical projections.

Section *Conica* JÖRGENSEN

Members of this section have an "ortho" (four-sided) first apical plate. The second anterior intercalary plate is usually "hexa", but "quadra" and "penta" configurations occasionally occur. Girdle displacement is either negligible or left-handed. The epitheca of most specimens is conical, having fairly straight sides. Antapical projections consist of slight, hollow projections, angular, often tipped with short spines but never having long, slender antapical spines.

As in the section *Divergentia* problems in recognition can arise as a result of the strong development of intercalary bands ("megacytic" cells).

Peridinium achromaticum LEVANDER Plate 33, Figs. 371 a, b

SCHILLER 1935:229, f. 225 a–h (vix g); WAILES 1939:34, f. 103; NIE 1939, f. 16; KISSELEV 1950:195, f. 330; SILVA 1952b:601, t. 6, f. 5, 6; WOOD 1954:250 vix f. 144; HALIM 1960a, t. 3, f. 12 a, b; BALECH 1963b:112, f. 1–10.
Vix BIECHELER 1952:67, f. 39/1–5.

This is an interesting species because of its usual association with brackish water (see distributional comments below). It is recognisable by its almost rhomboidal shape with convexly rounded antapices, negligible girdle displacement, and the presence of small spines on the antapices. It is not dorso-ventrally flattened. It most closely resembles *P. conicoides* PAULSEN with which it may have been confused at times, the latter having a more smoothly rounded epitheca and antapices, which have an angular shape.

There are several interpretational problems associated with this species. Firstly, in the brackish water Baltic specimens, such as those illustrated by WOLOSZYNSKA (reproduced in SCHILLER 1935), the edge of the sulcus is lined with low but strong sulcal lists and it is the profiles of these which give the appearance of antapical spines. However in the figures of SILVA (1952b), HALIM (1960a) and particularly in the detailed analysis by BALECH (1963b), the spines appear to arise independently at the termination of rather angular antapices, like those of *P. conicoides.* Also in their specimens the sides of the epithecae are smoothly convex rather than angular. *P. conicoides* is apparently larger (length 48–60 µm in comparison with values of 24–48 µm usually given for *P. achromaticum*). However the megacytic cell illustrated here, which seems to fit *P. achromaticum* in other respects, was very large (length 64 µm, transdiameter 59 µm).

Another unusual feature of the specimen illustrated is the longitudinal rather than cross-striation of the intercalary bands. This is rare in marine species (but see fig. 306 b) but it is not uncommon in fresh-water species.

Station: 45.

The occurrence of this species at a station close to the delta of the Ganges River in the northern Bay of Bengal accords with its common occurrence in brackish or even fresh-water. The surface salinity at this station was 19.82 ‰, and at 10 metres 31.74 ‰. MATZENAUER (1933) apparently found specimens (not illustrated) near Ceylon, this being the only previous record of the species from the Indian Ocean. In other oceans it is usually found in cold-temperate to tropical coastal waters with low salinity, such as the Baltic Sea, Argentinian lagoons, and in the Pacific Ocean, low salinity waters off British Columbia and Port Hacking harbour (New South Wales). A notable exception to this pattern is HALIM's (1960a) discovery of the species at Villefranche-sur-Mer in the Mediterranean Sea where the salinity only drops below 37 ‰ in very localised parts after strong rainfall.

Peridinium biconicum P. DANGEARD [non ABÉ] Plate 33, Fig. 365

MATZENAUER 1933:458, f. 33; SCHILLER 1935:230, f. 227 a–e; NIE 1939, f. 4; STEIDINGER et WILLIAMS 1970:55, t. 28, f. 91 a, b.
Non SILVA 1956a:64, t. 11, f. 1–3 [= *P. symmetricum* HALIM].
Syn.: ? *Peridinium* sp., WANG et NIE 1932:294, f. 5.

A moderately sized (length 75–100 μm) rounded species with slight dorso-ventral flattening. The shapes of the epi- and hypotheca are rather similar but the latter is slightly more rounded. It is not particularly like any of the other members of the section, most of which have a mid-ventrally indented hypotheca. However *P. symmetricum* HALIM (1967) is very similar, differing in that the sides of the epi- and hypotheca are straight or concave and the apices, especially the antapex, are acute.

Stations: 71, 88, 95.

Found only at three stations in the central and western Bay of Bengal. The species is rare. It is known from temperate and tropical regions of the Atlantic Ocean, the Mediterranean Sea, and has been found previously in the Indian Ocean by MATZENAUER (1933; – SILVA's 1956a record is discounted). There do not seem to be any Pacific Ocean records of the species as yet.

Peridinium conicum (GRAN) OSTENFELD et SCHMIDT Plate 33, Figs. 361, 362

SCHILLER 1935:233, f. 229 a–j, 230 a–c, 231 a–d; 232; DIWALD 1939:178, f. 3 a, b; WAILES 1939:34, f. 100; SILVA et PINTO 1948:168, t. 6, f. 10, 11; BALECH 1949a:405, t. 6, f. 131–142; KISSELEV 1950:195, f. 326, 327; RAMPI 1950b:235, t. 1, f. 3; MARGALEF et DURÁN 1953:29, f. 6 m–p; WOOD 1954:250, f. 146 a, b; MARGALEF, DURÁN & SAIZ 1955, f. 5 h; MARGALEF 1957a:45, f. 2d; TRÉGOUBOFF et ROSE 1957:111, t. 23, f. 18; HALIM 1960a, t. 3, f. 11; BRUNEL 1962:189, t. 56, f. 1–4, t. 57, f. 1–3; KLEMENT 1964:351, t. 1, f. 6; YAMAJI 1966:87, t. 42, f. 5; TORIUMI 1966a:3, t. 3, f. 6; DEFLANDRE 1966, t. 1, f. 1–6; HADA 1967:18, f. 28 F; HALIM 1967:736, t. 6, f. 74; WOOD 1968:99, f. 292; STEIDINGER et WILLIAMS 1970:55, t. 29, f. 94 a, b; HERMOSILLA 1973b:32, t. 14, f. 1–20.
Vix WANG 1936:132, f. 9.
Non GRAN et BRAARUD 1935:380, f. 57 (= *P. laticeps* GRÖNTVED, cf. GAARDER 1954).

Syn.: . . . *P. matzenaueri* GAARDER 1954:46, f. 60 a–c non BÖHM 1936 = *P. aliferum* GAARDER in PARKE et DIXON 1968:803; vix BALECH 1971a:87 (t. 14, f. 218–227 sub *P. vulgare*?).
P. leonis auct. non PAVILLARD; BALECH 1949a, f. 91; MARGALEF et DURÁN 1953, f. 7 b.

This species is distinctive but is somewhat polymorphic, particularly with regard to the size and shape of the hypotheca, leading to the recognition of various varieties and forms. Its length has been reported to vary from 52–105 μm. It is easily distinguishable from *P. pentagonum* and *P. latissimum* by its lack of dorso-ventral flattening, and from others such as *P. leonis* by the triangular shape of its first and seventh precingular plates.

The "Anton Bruun" specimens corresponded with two varieties: the var. *concavum* MATZENAUER, and the var. *asamushi* (ABÉ) stat nov. [Basionym *P. conicum* forma *asamushi* ABÉ 1927, f. 25].

The first of these was distinguished by MATZENAUER (1933) on the basis of the concave sides of its epi- and hypotheca, rather than convex as in the var. *conicum*. GAARDER (1954) considered such cells sufficiently different to warrant the recognition of a separate species, naming it *P. matzenaueri*, not knowing the name was pre-occupied by a species of BÖHM's (cf. PARKE & DIXON 1968). She corrected this in a checklist in 1968 by renaming it *P. aliferum*. An additional feature she added for the distinction of the taxon as a species was a slight right-handedness in the girdles of her specimens. However, none of the "Anton Bruun" specimens exhibited any appreciable displacement while agreeing in all other respects with MATZENAUER's description. Furthermore, the var. *asamushi* also has concave sides to its hypotheca and, although it was originally found to have slightly convex epithecal sides, here it was seen to occasionally be slightly concave (fig. 362).

It seems best to keep both taxa with *P. conicum* for the present until their position is further studied. Both varieties have larger antapical projections than the var. *conicum*, but in the var. *asamushi* they are particularly large, appearing as blunty pointed lobes. ABÉ found four anterior intercalary plates in his type material, but here all had only three and the "four" condition seems to be a teratological subdivision of the central plate.

The forma *guardafuiana* MATZENAUER appears to be a megacytic form of one of these two varieties. DEFLANDRE (1966) has provided photographs of an apparent specimen of this species present in a flint deposit approximately 80 million years old! DIWALD's (1939) specimens illustrate plate aberrations.

Stations: var. *conicum*: 23, 25, 38.
var. *asamushi*: 51, 105.

Both varieties were found only in the Andaman Sea and the Bay of Bengal. As HALIM (1967) has indicated, the species as a whole appears to be cosmopolitan, very eurythermal and halotolerant, although the above varieties occur predominantly in tropical waters. There are numerous records of the species in the Indian Ocean, those listed by WOOD (1963a) requiring augmentation by those of SILVA (1956a, 1960), SOURNIA (1968b, 1970), and NEL (1968).

Peridinium divaricatum MEUNIER Plate 33, Fig. 370

SCHILLER 1935:235, f. 233 a–e; SILVA 1952b:603, t. 6, f. 7, 8; WOOD 1954:251, f. 147; – 1968:101, f. 297.

This brackish water species is similar to *P. leonis* and *P. conicoides* in shape and in the shape of the first and seventh precingulars (quadrangular rather than triangular). It differs from both in the possession of hollow, divergent antapices, not as well-developed here as in European coastal waters. The original size data indicated that the length was subequal to the transdiameter, in the vicinity of 50 µm. Cells here reached 62 µm (illustrated).

Stations: 44, 45, 49.

The occurrence of this species only along the northern coast of Burma, particularly near the delta region at the head of the Bay of Bengal, accords with its designation as a low-salinity species. It has not been previously recorded from the Indian Ocean, but is known from brackish coastal water off Belgium, England, eastern Australia, and from the Strait of Florida (high salinity?).

Peridinium latissimum KOFOID Plate 33, Fig. 360

MATZENAUER 1933:456, f. 30 a, c, e (vix b non d); MARGALEF 1957a:45, f. 2 c; WALL et DALE 1968a:274, t. 2, f. 6, 7, t. 3, f. 14; WALL 1971a, t. 2, f. 14.

Syn.: *P. pentagonum* GRAN var. *latissimum* (KOFOID) SCHILLER 1935:242, f. 243 a–j (vix b, non d); WOOD 1954:253, f. 150 b, c; KLEMENT 1964:352, t. 1, f. 8; STEIDINGER et WILLIAMS 1970:57, t. 34, f. 113; WALL et DALE 1967, t. 1, f. Q; vix BALLANTINE 1961:222, f. 26, 27.

P. pentagonum GRAN forma/var. *depressum* ABÉ. . . HALIM 1967:745, t. 6, f. 82, 83, t. 7, f. 86 (as forma); YAMAJI 1966:88, vix t. 42, f. 8 (as forma).

P. pentagonum auct. non GRAN; NIE 1939, f. 2 A–E; vix SILVA et PINTO 1948:170, t. 6, f. 19; BALECH 1949a:401, t. 5, f. 92–110; MARGALEF et DURÁN 1953:29, f. 6 1, q–x (partim); WOOD 1968:107, f. 321.

? *P. pentagonides* BALECH 1949a:403, t. 5, f. 111–113, t. 6, f. 114–130; SILVA 1956b:356, t. 3, f. 7, 8.

? *P. exiquipes* MANGIN . . . SCHILLER 1935:265, f. 263; HALIM 1967:739, t. 6, f. 76, 77. [et HALIM 1965:376, f. 1/1–3 sub *P. pentagonum* var. *depressum*].

? *P. parapentagonum* WANG 1936:136, f. 11, 12.

For a taxon which at first sight appears to be readily recognisable, there has been a great deal of confusion and complication. Although many authors have followed SCHILLER's decision to relegate this taxon to varietal status under *P. pentagonum* GRAN, which it does resemble very closely, WALL & DALE (1968a), for example, have maintained its distinction as a species largely on two grounds: firstly, that the first apical plate is "para" instead of "ortho", and secondly, because its cyst is smooth-walled with very reduced antapical projections instead of being covered by small spinules and possessing large antapical projections. Their first assertion is questionable, even though much has been made of the position of the sutures to either side of the first apical plate by several other authors above (for example *P. pentagonides* BALECH is given as having a "meta" first apical plate). In KOFOID's original figures the condition can barely be described as "para". Instead the sutures all come together very close to one another. That was also the case in the "Anton Bruun" material but cells were found in which the sutures on either side were either barely anterior to, posterior to, or coincident with the first apical plate sutures arising from the girdle. The result, theoretically, is that "ortho", "meta" and "para" conditions were seen, the differences arising from the shifting of sutures by only a few microns. It would seem to be much better to maintain that in *P. latissimum* the lateral sutures are very close to or anterior to the junction, whereas in *P. pentagonum* both sutures are situated antapically from the junction.

The difference in cysts is not minor, and to this distinction could be added the earlier means of distinguishing the taxa, namely: the cells are much flattened dorso-ventrally, that dimension usually being half or less than half of the transdiameter. The transdiameter is usually greater than in *P. pentagonum* (usually more than 105 µm and reaching 124 µm) although there is overlap; and the antapical depression is relatively flat, broad and angular.

P. pentagonides BALECH was distinguished not only by its "meta" first apical plate but also by its relatively small size (transdiameter 87–95 µm) and the less-curved appearance of its girdle when seen in ventral view.

P. exiquipes MANGIN (= *P. parapentagonum* WANG) is distinguished from *P. latissimum* chiefly by its girdle displacement (left-handed) of approximately one girdle width. HALIM (1967) has discussed their separation at length. *P. exiquipes* shares the great flattening of *P. latissimum* but is more angular in apical view, having a V-shape rather than a narrowly reniform shape. Thus a distinction between the two is possible although at which level remains in doubt.

KLEMENT (1964) and HALIM (1967) have both commented on the asymmetry of the left and right sides of the cells when seen from above, but whereas the former indicates that the left side is larger than the right, HALIM claims the reverse. This difference could be real, significant or insignificant, or could be due to optical reversal.

All the specimens in the "Anton Bruun" material were similar to that illustrated here in being flattened, very wide, lacking girdle displacement (although with a sinuous curve when seen in ventral view), and with the suture junctions very close to one another. It is possible, however, under routine analytical conditions, that a few cells of one taxon may have been confused with another.

Stations: 43, 45, 103.

A few cells were seen, only in Bay of Bengal samples close to the coast. Judging from the records of the "var. *latissima*" listed in WOOD (1963a) they have been moderately frequent in the Indian Ocean. To these should be added the records of TAYLOR (1967) and WALL & DALE (1968b), the latter discovering cysts in western Arabian Sea sediments. The species appears to be an inter-oceanic, tropical form.

Peridinium latistriatum BALECH? Plate 33, Figs. 373 a–c
– 1958:86, t. 4, f. 66–80.
Syn.: *P. subinerme* auct. non PAULSEN; PETERS 1928:52, f. 15 c, g.

One large cell (length 102 µm, transdiameter 84 µm) with extremely wide intercalary bands was observed. It most closely resembled BALECH's taxon although it seems inadvisable to recognise a "species" known only in its megacytic state. It is suspected that this organism may be the megacytic condition of one of *P. subinerme*'s relatives, possibly *P. rosaceum* BALECH (not *P. roseum* PAULSEN!), the latter having a similar shape with a flattened antapex and high, conical epitheca.

An unusual feature of the present cell was either a shifting of the first apical plate to the right side of the cell, or the subdivision of the existing first apical plate into two unequal components. The former seems more likely.

Station: 99.

It was found in the south-western Bay of Bengal. Neither of the above species has been recorded previously from the Indian Ocean. The species was originally described from the Antarctic Ocean, making the tropical Indian Ocean locality an unusual discovery.

Peridinium leonis PAVILLARD Plate 33, Fig. 369
SCHILLER 1935:236, f. 236 a–m (non k), 237 a–d; DIWALD 1939:177, f. 23 a–e; SILVA et PINTO 1948:165, t. 6, f. 3; KISSELEV 1950:196, f. 333, 334; RAMPI 1950b:235, f. 14; MARGALEF et DURÁN 1953:31, f. 6 j, k, 7 c (non b); WOOD 1954:251, f. 148 a (vix b, c); TRÉGOUBOFF et ROSE 1957:111, t. 23, f. 19; HALIM 1960a, t. 3, f. 10; WOOD 1968:104, f. 310.
Vix KISSELEV 1950:198, f. 335 (var. *concavilaterale*). Non MATZENAUER 1933:456, f. 29 b, c (vix a): WANG 1936:134, f. 10 (= *P. striatum* BÖHM); BALECH 1949a, t. 4, f. 91 (= *P. conicum*); KLEMENT 1964:351, t. 1, f. 7, 9; STEIDINGER et WILLIAMS 1970:56, t. 32, f. 105, (= *P. striatum* BÖHM); HERMOSILLA 1973b:34, t. 16, f. 1–21.

Like *P. subinerme* this species can be readily distinguished from *P. conicum* and its relatives by the quadrangular instead of triangular shape of the first and seventh precingular plates (a constant feature of *P. conicum* whereas it is variable in *P. persicum*). It can be distinguished from *P. subinerme* by the straighter sides of its epitheca and the narrower angle which they subtend at the apex. Small antapical spines are usually present. Most of the "Anton Bruun" specimens corresponded with the taxon referred to as the f. *gainii*, which has the most widely set apart antapices, the posterior margin being only shallowly indented (similar to *P. subinerme*).

P. divaricatum MEUNIER is very similar to *P. leonis*, being distinguished primarily by the greater development of the cell antapices into small, acute, strongly-divergent horns.

In the reference citation here specimens with a striated epithecal surface resembling *P. striatum* BÖHM, sometimes with a more convex epitheca, and with closely set antapices, have been excluded as they are not here considered to be the same species. BÖHM's name cannot be used for such specimens, however, as it is preoccupied by one created by OSTENFELD & SCHMIDT (1901), and if recognised as distinct, will require a new name.

Stations: 39, 41, 45, 142.

The first three stations listed above are fairly near large river deltas (the Irrawaddy and the Ganges) within the Andaman Sea and the Bay of Bengal, the last station being south of India. This would seem to suggest a preference for lower salinity or a land-derived nutrient, but Mediterranean records (where it has been found to be plentiful) negate this idea, Mediterranean salinity being high (circa 38 ‰) except in the vicinity of the major river outflows. The species is known from cold-temperate to tropical waters, and has been found in all the major oceans. There are several previous Indian Ocean records (excluding some, at least, of MATZENAUER's) and those of SILVA (1956a, 1960) and TAYLOR (1967) can be added to the list given by WOOD (1963a).

Peridinium persicum SCHILLER Plate 33, Figs. 368 a, b
– 1935:272.
Syn.: *P. schilleri* BÖHM 1931a:193, f. 9, non *P. schilleri* PAULSEN.
P. punctulatum forma *asymmetrica* MATZENAUER 1933:458, f. 32.
P. matzenaueri BÖHM 1936:44, f. 19 b; HALIM 1967:741, t. 7, f. 89.
P. margalefii SILVA 1956a:64, t. 11, f. 4–7.
? *P. subinerme* forma *asymmetrica* MATZENAUER 1933:458, f. 31.

This is a distinctive member of the section Conica. Although like many, it has an "ortho-hexa" tabulation, it can be recognised by the asymmetrical development of the antapices, the left being distinctly larger than the right. Theoretically it might be possible to distinguish *P. persicum* from *P. matzenaueri* on the basis of two quadrangular precingulars (1'' and 7'' in the former, and triangular precingulars in the latter), but the existence of specimens such as the present one or that of SILVA (1956a) in which one is quadrangular and the other is triangular makes the distinction of dubious value. HALIM 1967, has previously suggested their synonymy, although not also with *P. margalefii* SILVA. There seem to be no sound distinctions between the latter, and SILVA (1956a) may not have been aware of the earlier taxa as she makes no reference to any similarity of her taxon with them. The girdle may be slightly left-handed or not displaced.

Because of tilting, the specimen illustrated here appears to have a greater antapical indentation than is usual for the species. However, in reality the posterior indentation is only moderate and it is the deeply excavated sulcus which produces the deeply indented appearance.

The size range for the species is: length 72–82 µm, transdiameter 75–91 µm. Dorso-ventral flattening is slight.

Although the species was based only on MATZENAUER's form of *P. punctulatum* by BÖHM, it seems likely that MATZENAUER's asymmetrical form of *P. subinerme* is also the same taxon, the only difference being that the antapical indentation is minimal.

P. obtusum KARSTEN, as originally figured by him (1906, pl. 13, f. 12) has resemblances to *P. matzenaueri* and the left antapical horn does appear to be slightly larger than the right. However as he figured it only in three-quarter apicoventral view it is difficult to make a good comparison. Most later authors have interpreted his taxon as having equally developed antapical horns. The surface striations of *P. obtusum* (resembling *P. striatum* BÖHM) are apparently not present in *P. matzenaueri*.

Station: 144.

A single cell was found to the south of Ceylon. The species appears to be an inter-oceanic warm-water form as it has been recorded form the Caribbean Sea, the Indian Ocean, including the Persian Gulf (by BÖHM 1931a, MATZENAUER 1933 and SILVA 1956a, 1960) and the tropical western Pacific Ocean.

Peridinium subinerme PAULSEN Plate 33, Figs. 364, 367 a, b
SCHILLER 1935:243, f. 244 a–o (non 245 a–c); BÖHM 1936:44, f. 16 a 1–4; DIWALD 1939:175, f. 22 a–d; SILVA 1949:345, t. 5, f. 15–17; MARGALEF et DURÁN 1953:29, f. 6 e (vix d); WOOD 1954:254, f. 151; SILVA 1955:142, t. 5, f. 4, 5; YAMAJI 1966:87, t. 42, f. 3; HALIM 1967:748, t. 6, f. 84, t. 7, f. 85; WOOD 1968:109, f. 330.
Vix KISSELEV 1950:200, f. 338, 342; RAMPI 1950b:235, f. 10; GAARDER 1954:49, f. 64 a–c (f. *excavatum* GAARDER); MUÑOZ, HERRERA et MARGALEF 1956, f. 1 i–k; BALECH 1971a:91, t. 15, f. 249–252.
Non STEIDINGER et WILLIAMS 1970:58, t. 34, f. 115 (= *P. obtusum* KARSTEN?).

The body of this species varies considerably in length, from broader than long, to longer than broad. It is distinguished from other members of the section by its greater convexity, particularly in the broad angle subtended to each other by the sides of the epitheca as they approach the apex. The antapices are broadly rounded or slightly pointed. Many of the specimens illustrated are megacytic, leading one to suspect that the taxon may consist partially of megacytic members of another species of the section. However, in the "Anton Bruun" material a very small cell (fig. 364) was found which exhibited the same features without megacytism. The second dorsal intercalary plate is "hexa" in non-megacytic specimens, but may or may not become "quadra" with the development of intercalary bands (in fig. 367 the "hexa" formation was retained).

GAARDER (1954) has recognised a "forma" *excavatum*, distinguished by a strong indentation of the posterior part of the sulcus (not affecting the post-margin, however). One specimen had a very peculiar epithecal tabulation, the anterior intercalary plates being discontinuous because of the third apical plate contacting the precingular series directly on the dorsal side. However other specimens were "ortho-hexa".

P. punctulatum PAULSEN has a similar shape, but the plates may be finely rugose due to numerous small spines. It usually has a "penta" rather than a "hexa" second anterior intercalary plate, but not always. Another supposed distinction is that the epitheca is not as high as in *P. subinerme* but the specimens here plainly contradict this distinction (cf. PAULSEN 1949 for further discussion). Indeed it is suspected that the specimen in fig. 367 may correspond to *P. punctulatum*, having puncta, but it did not possess spinulae. The distinction of these two species remains troublesome, expecially in tropical waters.

HALIM (1967) considered that *P. subinerme* is smaller than *P. punctulatum*. While the specimen in fig. 364 is indeed small, the other megacytic specimen had a length exceeding 90 µm, nearly twice the normal length for the species.

Stations: 38, 105.

Specimens were found only at a station in the eastern Andaman Sea and at one close to Madras in the Bay of Bengal. SILVA's (1956a and 1960) records should be added to the few listed for the Indian Ocean by WOOD (1963a).

Section *Divergentia* JÖRGENSEN
[= Divergens auct. nonnul.; Metaperidinium; incl. Paradivergentia]

Members are characterised by a meta/quadra (rarely hexa) plate combination and by the presence of an antapex more or less divided into antapical horns. Girdle displacement is variable, being none, left-handed or right-handed. Left-handed species, or those with no displacement, show affinities with the section Oceanica (*P. venustum*, ortho/quadra, is very similar to *P. elegans*) whereas those with right-handed displacement tend more towards the section Protoperidinium (e.g. *P. solidicorne*).

This section is very commonly represented in tropical waters, especially by members of the "Divergens Complex". The latter is particularly troublesome to deal with as it embraces considerable multidirectional variation. More than ten taxa have been recognised at the species level. Where some have been combined with others (e.g. *P. curtipes* with *P. crassipes*) there has been inconsistency in treating others which differ by equally small or even lesser differences.

Text figure 4 below provides a view of the variation within the "Divergens Complex" as indicated by simplified outline figures (to scale).

All the taxa shown in the diagram, with the exception of *P. curtipes* forma *asymmetrica* MATZENAUER, *P. tregouboffii* HALIM and *P. anguipes* BALECH, were present in the "Anton Bruun" material. The outlines are derived from scanning electron micrographs in which the specimens could be oriented in a similar manner. In water mounts, they tend to lie tilted with the ventral apical surface showing the most (see figs. on the plates). Comparison of the outline drawings should obviate lengthy descriptive comments.

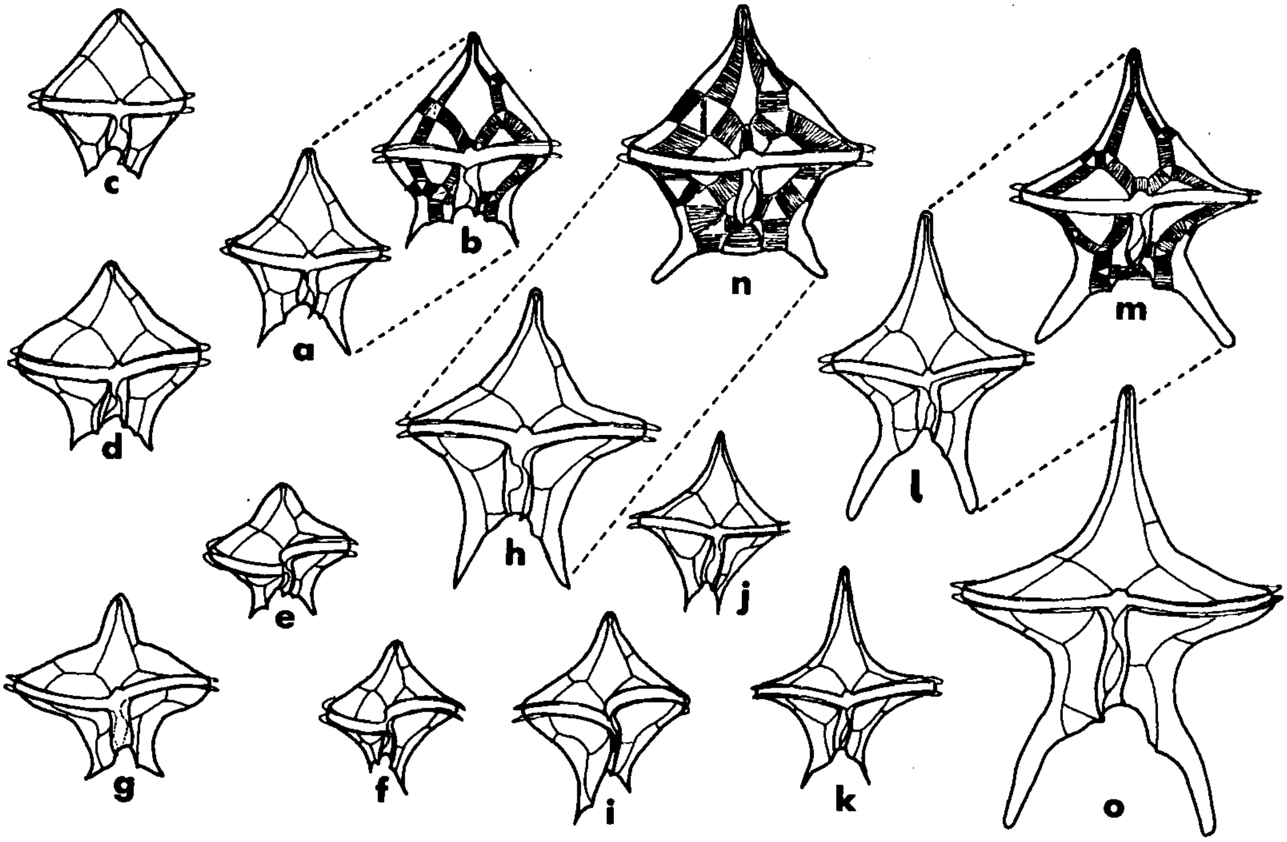
P. remotum KARSTEN and *P. fatulipes* KOFOID are considered to be parallel maturational states of *P. divergens* and *P. elegans* respectively and not as species. *P. tumidum* may be the corresponding state of *P. grande* but has been kept separate pending further examination. The lateral displacement of the antapical horns (by which they were recognised) is the result of the development of intercalary bands, a feature which has apparently escaped previous authors other than HALIM (1967 – for *P. fatulipes*). An interesting feature of intercalary band development in *Peridinium* is that, like the development of the megacytic zone in the Dinophysiales, it is greatest in the posterior region of the cell and least at the anterior end. This is most marked in *P. elegans* in the *"fatulipes"* stage where the great width of the band passing between the antapical horns (i.e. between the antapical plates), gives the appearance of a "bridge" between the bases of the horns.

A glance at the text figure below is sufficient to show that, with the possible exception of some as yet undiscovered sulcal plate distinctions, many of the taxa differ by less than in other species of *Peridinium* and, in another section, they might be considered infraspecific variants. Key questions in this problem are whether or not intermediates exist, what their frequency is, and whether or not such variation is genetically based. At present there is very little of such information. Also, information is lacking on the details of the ventral area for most species.

P. curtipes has been commonly combined with *P. crassipes* because of supposed intermediates, although, due to differing orientations of the figures, it is difficult to assess many of the existing figures. In the "Anton Bruun" material the girdle-displacement of the former could always be used to distinguish the two (see other comments under the species) provided the cells were oriented in full ventral view.

It is not possible at present to decide which members of the complex deserve specific, subspecific, varietal or other distinction. Although it undoubtedly is excessive "splitting" to distinguish most of the primary variants (with the exception of *"remotum"*, *"fatulipes"*, and possibly *P. tregouboffii*) at the species level, this practice is followed here as an interim measure except where new taxa would have to be created (see *P. elegans* f. *granulatum*).

One feature not shown in the figure which also exhibits trends is the shape of the cell equator seen from the apex. In the closest members to *P. divergens* it is round or broadly oval. In *P. grande* the ventral side becomes flattened so that the shape is almost hemispherical. This suppression of the ventro-median portion, with increased development of the ventrolateral parts, results in an almost V-shaped profile both in *P. brachypus* and in *P. elegans*.



Text fig. 4. Members of the "Divergens Complex" of *Peridinium* section *Divergentia* (originals except for figures f, g and j).

a. *P. divergens* EHR. – b. Megacytic *P. divergens* EHR. [= *P. remotum* KARST.] – c. *P. acutipes* P. DANG. – d. *P. crassipes* KOF. – e. *P. curtipes* JORG. – f. *P. curtipes* f. *asymmetrica* (redrawn from MATZENAUER 1933) – g. *P. anguipes* BAL. (redrawn from BALECH 1967a) – h. *P. grande* KOF. – i. *P. asymmetricum* KARST. – j. *P. tregouboffii* HAL. (redrawn from HALIM 1955) – k. *P. brachypus* SCHILL. – l. *P. elegans* CLEVE – m. Megacytic *P. elegans* [= *P. fatulipes* KOF.] – n. *P. tumidum* OKAM. [? = megacytic *P. grande* KOF.] – o. *P. elegans* f. *granulatum* (KARST.) MATZ.

Here *P. elegans, P. brachypus,* and *P. remotum* (as a synonym of *P. divergens*) are included in this section, rather than in the section Oceanicum where they were placed confusingly by SCHILLER (1935). SCHILLER's action was based on the observation of an "ortho" tabulation in a specimen resembling *P. elegans*. Such a feature has not apparently been seen by any other authors, and all the numerous "Anton Bruun" specimens had "meta" tablature. He did not figure the tablature of *P. brachypus* but said it had an epitheca like *P. elegans* forma *granulatum,* thus mislocating it by association.

A further confusing element is that some of the figures of MANGIN (1928) seem to be optically reversed. Thus *P. obtusipes* MANGIN is almost certainly a short-horned variant of *P. elegans* or *P. grande.*

Peridinium acutipes P. DANGEARD Text Fig. 4 C; Plate 31, Figs. 317, 318, 321, 325
MATZENAUER 1933:469, f. 54.
Syn.: *P. divergens* forma *acutipes* (DANGEARD) SCHILLER 1935:227, f. 223 a–d.
P. quadratum MATZENAUER 1933:469, f. 55.
P. brochii auct. non KOFOID et SWEZY; BALECH 1951b:320, t. 6, f. 88–114.

There is undoubtedly a strong resemblance between this taxon and *P. divergens* on the one hand, and *P. brochii* on the other. It is kept separate here for the reasons outlined in the introduction to this section although it will probably be combined with *P. divergens* again when more information is available. It differs from *P. divergens* in the flattened or almost convex sides of the epitheca and the more closely-set antapical prominences, each of which has only a small acute projection rather than the longer, conical points in *P. divergens.* The original length given was 110–120 µm, but in this material some cells as short as 88 µm were seen. Megacytic specimens (fig. 321) resemble those of *P. divergens. P. quadratum* MATZENAUER appears to represent the minimum divergence of the antapical projections of *P. acutipes.*

Stations: 17, 33–35, 37, 38, 40, 43, 50, 57, 59–64, 66–71, 87, 89–103, 105, 106, 108, 113, 141, 143, 150, 284, 287, 288, 294, 297, 313, 318, 323, 341, 358, 374, 399, 404, 405, 410, 413, 418.

This was the commonest representative of *Peridinium* in the material. In examining the record above it must be remembered that it must have undoubtedly been confused with *P. divergens* in some samples as the distinction is difficult to make consistently under routine conditions.

It occurred at only a few scattered stations on the eastern side of the Bay of Bengal/Andaman Sea, but was very evenly distributed at nearly all stations in the western half of the Bay of Bengal. On cruise II (S.W. Monsoon) it was only present at northern stations (only one being south of the equator). On cruise III it occurred at only one station near the equator. During the N.E. Monsoon (cruise V) it was more widespread but scattered, occurring as far south as 29 °S in the central region. With the return of the S.W. Monsoon it was present at one station near 8 °S (cruise VI). It also occurred at various stations in the Mozambique Channel region during the late S.W. Monsoon and the intermonsoon period following it.

Thus the general picture is one of a distribution chiefly limited to the northern and western regions during the S.W. Monsoon, but spreading into the south central regions during the N.E. Monsoon while remaining very common in the western Bay of Bengal at such times.

Because of confusion and combination with *P. divergens,* it is difficult to assess this taxon's distribution independently. MATZENAUER (1933) recorded *P. acutipes* from the northern Indian Ocean (and also the synonymous *P. quadratum*), and the species was originally described from the "Sylvana" cruise in the tropical Atlantic Ocean.

Peridinium angustum P. DANGEARD Plate 31, Figs. 333, 334
– 1927b:362, f. 29 a, b; SCHILLER 1935:228, f. 224 d, e (sub *P. wiesneri* SCHILLER); NIE 1939, f. 15 (sub *P. wiesneri*).

SCHILLER (1935) included DANGEARD's species tentatively under his *P. wiesneri.* Although they are closely similar *P. angustum* is much broader relative to its length, *P. wiesneri* being round or narrowly oval like *P. pellucidum.* Also *P. angustum* has much less right-handed girdle displacement (approximately 0.5) than *P. wiesneri* (in the latter it exceeds one girdle width). Finally, the antapical horns of *P. angustum* are very short and subequal in length, whereas they are longer, closely set, divergent and unequal in length in *P. wiesneri.* BALECH (1971b) has given a detailed analysis of the latter species, concluding that SCHILLER's action in combining the two was unjustified.

Stations: 65, 114, 290.

A few cells were found at three stations in the northern Indian Ocean: two in the southern Arabian Sea and one in the western Bay of Bengal. This is the first record of the species in the Indian Ocean. It was originally described from the tropical Atlantic Ocean, and NIE has figured a mis-identified specimen from Japanese waters.

Peridinium asymmetricum KARSTEN Text Fig. 4 i; Plate 31, Fig. 326
– 1907:418, t. 53, f. 2; MATZENAUER 1933:467, f. 51; BÖHM 1936:41, f. 17 a 1, 2; KISSELEV 1950:208, f. 351, 358 (sub *asymmetrica,* sic).
Non *P. asymmetricum* (MANGIN) OSTENFELD.

KARSTEN's original figure is rather poor, probably leading to the neglect of the species by SCHILLER (1935 – listed only) and it is due to MATZENAUER's figure of a dorsal view that the species is clearly recognisable. The cells show a very strong asymmetry of the antapical horns, with the right antapical horn much longer than the left horn. This is the reverse of that found in the var. *asymmetricum* of *P. curtipes*. The asymmetry is also expressed on the epitheca due to the strongly raised curve of the left side of the girdle, the proximal end being displaced similarly to *P. curtipes*. The original illustration does not show these features as strongly as those of MATZENAUER, BÖHM and the present author. Spines on the antapical horns were not strongly developed in many of the specimens observed although they have been reported by KARSTEN and MATZENAUER. The posterior ends of the horns bear linear striations (ridges) similar to those in *P. divergens*.

Stations: 16, 17, 32, 57, 67, 70, 103, 143, 318.

Observed in small numbers in the higher salinity regions of the Andaman Sea/Bay of Bengal area, to the south of India, and at one central station (17 °S). It has only been previously recorded from the northern Indian Ocean by KARSTEN (1907) and MATZENAUER (1933), these being omitted from WOOD (1963a).

Peridinium brachypus SCHILLER Text Fig. 4 k, Plate 30, Figs. 313 a, b
– 1935:248, f. 249.
Syn.: ? *P. tregouboffii* HALIM 1955:1, t. 1, f. 1–6, t. 2, f. 1–7; –1960:197, t. 2, f. 31.

This is a distinctive, relatively small species, described originally from the Indian Ocean and only seen since in the Mediterranean Sea. Unfortunately SCHILLER included the species under the section Oceanica, implying the presence of an "ortho" first apical plate although this assignment was due to a resemblance to *P. elegans* (which usually has "meta"). His figure showed no plates at all. It is similar to *P. acutipes* in possessing closely-set, non-divergent antapical horns (acutely pointed), but its epitheca and equatorial profile are more like *P. grande* and *P. elegans*. SCHILLER illustrated a specimen with a longer apical horn than most of the specimens observed here, and such individuals could be considered as representing the var. *brachypus*. On the other hand, individuals corresponding to *P. tregouboffii* have the shortest apical horn, not much greater than *P. depressum*. Some specimens of *P. tregouboffii* resemble intermediates between *P. depressum* and *P. brachypus*.

The epitheca of the species is similar to *P. elegans* and the strong dorso-ventral distortion resembles *P. granulatum*. However it differs strikingly in size (length 94–130 µm, diameter 86–110 µm). The second anterior intercalary plate is narrow, being much higher than wide.

Stations: 26, 27, 28, 34, 54, 60, 65, 66, 95, 97–101, 103, 130, 140, 141, 142, 144.

Common in samples from the western Bay of Bengal, but also to a lesser extent in the Andaman Sea. The remaining records were from a group of stations to the south of India. In view of this distribution the record from station 130, below 32 °S, is suspect. A re-examination of the sample did not reveal further specimens.

The species is known only from its type locality: the Indian Ocean near Sumatra (SCHILLER 1935), and, if conspecific with *P. tregouboffii*, from Villefranche-sur-Mer in the Mediterranean. HALIM (1960a) considered the latter to be a rare, umbriphilic ("sciaphile") species.

Peridinium brochii KOFOID et SWEZY Plate 31, Figs. 332, 335
SCHILLER 1935:221, f. 218 a–g (non h, i = *P. acutipes* DANGEARD); BÖHM 1936:41, f. 16 d; NIE 1939, f. 18 A–D; KISSELEV 1950:192, f. 322 *β–e* (non *a*, *б*); RAMPI 1950b:235, f. 9; MARGALEF et DURÁN 1953:27, f. 4 w, y; WOOD 1954:247, f. 136; TRÉGOUBOFF et ROSE 1957:111, t. 23, f. 15; HALIM 1967:734, t. 6, f. 72, 73; HERMOSILLA 1973a:30, t. 1, f. 1–6, t. 3, f. 6–13.
Vix WOOD 1968:98, f. 288; STEIDINGER et WILLIAMS 1970:55, t. 28, f. 92 (= ? *P. acutipes* DANGEARD).
Non BALECH 1951b:320, t. 6, f. 88–114 (= *P. acutipes* DANGEARD); HALIM 1960a, t. 3, f. 1 (= *P. divergens* EHRENBERG).
Syn.: *P. adriaticum* BROCH non SCHMARDA . . . HADA 1967:17, f. 28 c.
Non TORIUMI 1966a:3, t. 3, f. 7 (= ? *P. divergens* EHRENBERG).
P. divergens var. *adriaticum* (BROCH) SCHILLER 1929:407, f. 23, 24.

This problematic species is similar to *P. acutipes* DANGEARD, *P. inflatum* OKAMURA (which was made a form of it by SCHILLER 1935) and *P. angustum* DANGEARD. It differs from the first-named by having roundly concave-convex sides to the epitheca (instead of almost flat) and the posterior projections are more widely set. However it should be mentioned here that all the specimens which resembled *P. brochii* in this material were more or less megacytic. As has been pointed out in the introduction to this section, the shape distortion which results from growth of the intercalary bands has not been taken into account by former authors and, for example, with the exception of the more narrowly conical apex, *P. brochii* could very easily be the megacytic form of *P. angustum* or *P. wiesneri* SCHILLER, the latter having closely-set antapical projections. *P. inflatum* can be recognised as distinct here by the presence of small antapical spines, but this feature derives more from MATZENAUER's (1933) interpretation of the latter and not the original figures. All three are obviously very similar. *P. retiferum* MATZENAUER has rather coarse reticulation, similar to the specimen in fig. 334 here, and could be considered synonymous with this taxon, or *P. inflatum* as indicated by SCHILLER (1935).

Japanese authors, no doubt using the early works of ABÉ, have tended to continue using the pre-occupied epithet of BROCH's (*P. adriaticum*).

Stations: 22, 24, 25, 28, 29, 31, 34, 36, 68, 69, 94, 102, 103, 105, 110, 118, 150.

It occurred in small numbers in the central Andaman Sea, a few stations in the western Bay of Bengal, two northern stations on cruise II, and another equatorial station on cruise III (both latter cruises being undertaken during the S.W. Monsoon period).

It has been recorded most commonly from tropical and warm-temperate waters, the coldest areas being those in which GAARDER (1954) found it to the north of Ireland (presumably under the influence of the Gulf Stream). It has been recorded fairly commonly from the Indian Ocean (as listed in WOOD 1963a, plus NEL 1968 and SOURNIA 1968b, 1970).

Peridinium crassipes KOFOID Text Fig. 4 d, Plate 31, Figs. 327, 331

SCHILLER 1935:223, f. 220 a–i, l–p (non j, k); WANG 1936:141, f. 14; DIWALD 1939:173, f. 8 d, e, 21 a, vix b; WAILES 1939:38, f. 15; SILVA et PINTO 1948:167, t. 6, f. 7, 8; KISSELEV 1950:192, f. 328 *а, в, з*; RAMPI 1950b:235, f. 17; WOOD 1954:247, f. 137 a–d; MARGALEF 1957a:45, f. 2 e; TRÉGOUBOFF et ROSE 1957:111, t. 23, f. 16; HALIM 1960a, t. 2, f. 32; BRUNEL 1962:192, t. 58, f. 1–5; WOOD 1968:99, f. 293; STEIDINGER et WILLIAMS 1970:55, t. 29, f. 95 a, b; BALECH 1971a:146, t. 28, f. 530–534, t. 29, f. 535–537.

Vix MARGALEF 1948a:19, f. 2/5, 2/6; KISSELEV 1950, f. 323 *а–в*, 328 *д, е*; HALIM 1967:736, t. 6, f. 75.

Non MATZENAUER 1933:467, f. 50 a–d (incl. forma *asymmetrica* MATZENAUER); BÖHM 1936:41, f. 16 c; GRAHAM 1942:27, f. 37 A–G; KISSELEV 1950, f. 328 *б, ж*; YAMAJI 1966:89, t. 43, f. 5.

Syn.: *P. curtipes* auct. non JÖRGENSEN . . . . MARGALEF et DURÁN 1953:29, f. 5 i–n (*P. crassipes curtipes*).

This is a large, distinctive species, distinguishable from *P. divergens* in being much wider relative to its length, with the hypotheca usually narrowing rapidly until approximately one-half to two-thirds of the distance from the girdle to the antapex. The apex usually tapers smoothly, but if *P. amplum* MATZENAUER (1933, p. 468, f. 53 a, b) is synonymous, it it may also abruptly become sharply conical at the apical-precingular junction. *P. anguipes* BALECH, is also similar [text fig. 4g], bearing an abruptly conical epitheca, but is very narrow in the hypocone as well, resulting in a greatly flattened appearance. If *P. amplum* MATZENAUER is included, the transdiameter of this species can reach 137 µm.

The distinction of *P. crassipes* from *P. curtipes* has caused difficulties from the beginning, and SCHILLER (1935) followed PETERS (1928) in uniting them. In this author's opinion much of the difficulty may arise from the fact that the most clear distinction, the girdle displacement, is not evident when the cells are lying in their normal position under the coverslip (as are most of the specimens on plate 31). In the "Anton Bruun" material it was possible to distinguish two quite distinct taxa, provided the cells were seen in full ventral view, as shown in the outlines in the text figure here.

In *P. crassipes* girdle displacement is lacking, the proximal ends meeting more or less symmetrically at the sulcus, the latter being relatively shallowly depressed. In *P. curtipes*, as recognised here, the left proximal region of the girdle rises up at an angle to the plane of the girdle and the right proximal region curves sharply into the deep, narrow sulcus at a generally lower level. PAULSEN (1949) and WOOD (1954) also kept the species distinct, although the comments of the latter on the criteria used do not fit the original concept of *P. curtipes.* DANGEARD (1927b) and MATZENAUER (1933) made a similar distinction, but reversed the criteria, their *curtipes* corresponding to *crassipes* and *vice versa.* BALECH (1971a) considered that the specimens of PETERS (1928) were not the same taxon as those of KOFOID.

In the introductory comments to this section it was pointed out that, while many of these taxa could, and probably should, be united at infraspecific levels, the difficulty in handling them all in a consistent manner makes this perhaps premature at present. Data arising from excessive "splitting" can always be recombined whereas the discovery of excessive "lumping" leads to an inevitable doubt of existing data for both of the "lumped" taxa.

Here *P. crassipes* and *P. curtipes* have been kept as distinct. In what is probably an exercise in futility, the recent literature pertaining to them has also been segregated although in some cases it is difficult to determine which taxon was involved.

As a matter of historical curiosity, the unnamed specimen figured by MICHAELIS (1830) on which EHRENBERG based *P. michaelis* strongly resembles *P. crassipes* in shape. However, it could conceivably belong to several different species and most recent authors have neglected the species.

Stations: 38, 45, 95, 110, 133, 135, 141.

Cells of this species were positively identified from only a few stations in the Bay of Bengal/Andaman Sea region (including rather low salinity stations) and on cruise II from scattered stations extending to 30 °S. It is strongly suspected that this distribution is minimal because of the inadvertent attribution of smaller specimens to *P. curtipes* when full ventral views were not obtainable.

Records of this widely distributed tropical to temperate species are frequent from the Indian Ocean (see WOOD 1963a plus SILVA 1956a, 1960; PRAKASH & SARMA 1964; SOURNIA 1968b, 1970; NEL 1968 and ANGOT 1970) but due to the lack of illustrations in many cases, the true representation of the species cannot be judged at present. As noted above, MATZENAUER's (1933) record is incorrect, but he did record this species as *P. curtipes*.

Peridinium curtipes JÖRGENSEN sensu stricto Text Fig. 4 e, Plate 31, Figs. 322, 323
– 1913, Bericht 8.
Vix WOOD 1954:248, f. 138.
Non MATZENAUER 1933:468, f. 52 a, b, vix c.

Syn.: *P. crassipes* auct. non KOFOID . . . . DANGEARD 1927b:365, f. 32 c; SCHILLER 1935, f. 220 j, k; BÖHM 1936:41, f. 16 c; GRAHAM 1942:27, f. 37 A–G; KISSELEV 1950, f. 528 σ; YAMAJI 1966:89, t. 43, f. 5. *P. crassipes* subsp. *curtipes* (JÖRGENSEN). . . MARGALEF 1957a:45, f. 2 e.

The difficulties in distinguishing this taxon from *P. crassipes* have been discussed extensively under the latter. Here *P. curtipes* is thought to be distinguishable principally by the torsion of the girdle exhibited near the sulcus, the left proximal part rising up at an angle, the right proximal part lower, projecting more ventrally before curving in to the narrow, deep sulcus. In the "Anton Bruun" material most of the cells were less than 80 µm in transdiameter (one, illustrated in fig. 323, being less than 50 µm), whereas those corresponding to *P. crassipes* were usually more than 90 µm and sometimes exceeded 110 µm in transdiameter.

Stations: 16, 19, 21, 24–26, 28, 31, 32, 36, 37, 40, 41, 45, 53, 57–59, 65, 67, 69, 87, 91, 92, 100, 101, 103, 105, 106, 108–110, 114–118, 129, 135, 140–142.

This distribution was similar to that of *P. crassipes* (the taxa co-occurring at 4 stations) although *P. curtipes* was more common. It was patchy in the Bay of Bengal and Andaman Sea, and like *P. crassipes*, was recorded from the remaining Indian Ocean only during cruise II (S.W. Monsoon), also reaching 30 °S. It was particularly well represented in the South Equatorial Current, and in the returning Monsoon Current off the west coast of India.

As with *P. crassipes* the world distribution is difficult to determine, other than that it is probably inter-oceanic. JÖRGENSEN (1913) thought that it was a northern species with a colder distribution than *P. crassipes*, but that is not borne out here. DANGEARD (1927b) also found it to be common in warmer waters, but his confused conception of the species in this case casts doubt on such supportive data.

It has been recorded from the Indian Ocean by KARSTEN (1907), MATZENAUER (1933, with *crassipes* and *curtipes* reversed), and SILVA (1956a, 1960), and by WOOD (1954) from the Antarctic sector.

Peridinium divergens EHRENBERG sensu PAULSEN Text Fig. 4 a, b; Plate 31, Figs. 319, 320, 324; Plate 46, Fig. 530
SCHILLER 1935:226, f. 222 d–g (non a – *P. acutipes*, b, c – *P. grande*); DIWALD 1939:171, f. 6 a–c, 7, 8 f–h, 11 c, 19 a–c, vix 20 a, b; WAILES 1939:38, f. 114; SILVA et PINTO 1948:165, t. 2, f. 9; KISSELEV 1950:194, f. 234 non 329, vix 7, 16; RAMPI 1950b:235, f. 11; MARGALEF et DURÁN 1953:27, f. 5 a–c; WOOD 1954:248, vix. f. 139; MARGALEF 1957a:45, f. 3 d; TRÉGOUBOFF et ROSE 1957:111, t. 23, f. 17; YAMAJI 1966:89, t. 43, f. 6; STEIDINGER, DAVIS et WILLIAMS 1967, t. 8, f. c, d; WOOD 1968:101 vix f. 298; STEIDINGER et WILLIAMS 1970:56, t. 30, f. 98 a, b; TAYLOR 1972b, t. 1, f. 4.
Syn.: . . . . *P. remotum* KARSTEN sensu MATZENAUER 1933:473, f. 61 a, b (non WOOD 1954:249, f. 140).

As indicated by both JÖRGENSEN (1913) and LEBOUR (1925) the taxon most frequently referred to as *P. divergens* may not correspond with the original description. However it is impossible to be sure in view of the resemblance of *P. divergens* to several other species in shape although very different in tablature (e.g. *P. depressum*).

The interpretation here follows that of PAULSEN (1907, 1908) who tried to base his on a figure by Joseph MÜLLER referred to by EHRENBERG. LEBOUR (1925), SCHILLER (1935) and KISSELEV (1950) erroneously included figures from STEIN (1883, pl. 10) which correspond with *P. grande*, bearing large, hollow acute antapical horns. SCHÜTT (1895) figured a multitude of different taxa (as we now recognise them) under the name. PAULSEN's figures seem to provide the best critical starting point for the species.

The taxon is apparently solely distinguished from other members of the "Divergens Complex" which have sharp, thick, divergent antapical spines and no girdle displacement (e.g. *P. crassipes, P. grande*) by its size and shape. This is best seen in the text figure and its surface structure is evident from the scanning electron micrograph (fig. 530). It can be noted that *P. crassipes*, which can be similar in size, is much broader in girdle transdiameter relative to its length. *P. grande* is much larger (see notes under that taxon), with relatively larger, more obviously hollow, antapical horns.

P. acutipes DANGEARD was considered to be a form of *P. divergens* by SCHILLER (1935) Here it and others of the "Divergens Complex" are, for the most part, kept distinct because it seems premature to determine the levels at which the members should be combined (see comments under each taxon and under the sectional introduction). It differs by having short, more closely set posterior horns and a finer reticulation than *P. divergens.*

It seems evident that *"P. remotum"*, as interpreted by MATZENAUER (1933), is only the appearance of *P. divergens* when intercalary bands are fully developed, and consequently does not deserve formal recognition. SCHILLER (1935) held this opinion, but repeated a type of inconsistency which appears several times in his monograph: on the one hand he made *P. remotum* KARSTEN a synonym of *P. divergens* and yet, on the other, recognised it on page 262 as a distinct species.

P. asymmetricum KARSTEN, also kept separate here, differs from *P. divergens* in that the right antapical horn is markedly longer than the left horn and, furthermore, the girdle shows strong left-handed displacement (the latter being similar to *P. curtipes*).

Superficially *P. divergens* also resembles *P. depressum.* However they can be immediately separated by the "ortho" tablature of the latter, larger posterior horns, and left-handed girdle displacement.

Stations: 24, 29, 33–35, 40–43, 48, 51, 52, 54, 58, 59, 62, 63, 65, 88–92, 101, 103, 105, 113, 130, 144, 147, 162.

This was a fairly common species of *Peridinium* in the material, but it was largely confined to the Bay of Bengal and the Andaman Sea. It had a maximum abundance at station 43 near the Irrawaddy delta and it probably prefers neritic conditions. It has been found in all the major oceans. In addition to the Indian Ocean records cited by WOOD (1963a) it has also been recorded by SILVA (1956a, 1960), TAYLOR (1967), SOURNIA (1968b, 1970) and NEL (1968).

Peridinium elegans CLEVE Text Fig. 4 l, m, o, Plate 30, Figs. 308, 309, 311, 312, 314, 315; Plate 46, Fig. 528

SCHILLER 1935:254, f. 252 a–e, (vix f), 253 a–d (vix e, f), KISSELEV 1950:203, f. 345; MARGALEF 1961a, f. 3/5, 6; – 1961b:140, f. 2/6; 3/5, 6; KLEMENT 1964:350, t. 1, f. 3, 5; STEIDINGER et WILLIAMS 1970:56, t. 30, f. 99, 100 a, b; TAYLOR 1973b, f. 6 d.

Vix WOOD 1954:249, f. 141.

Syn.: *P. annulatum* KOFOID et MICHENER 1911:280.

P. fatulipes KOFOID . . . . SCHILLER 1935:256, f. 254 a, b, e, f (non c, d, g, h); WOOD 1963b:36, vix f. 131; YAMAJI 1966:90, t. 43, f. 9 (*P. faltipes*, sic); HALIM 1967:740, t. 9, f. 127; WOOD 1968:101, f. 300 ("ortho"!); non STEIDINGER et WILLIAMS 1970:56, t. 31, f. 102 a, b (= *P. tumidum* OKAMURA).

P. grande auct. non KOFOID . . . . YAMAJI 1966, t. 43, f. 7.

This large (length usually between 150 and 220 μm), slender species is quite distinctive, particularly due to its hollow, elongate, non-acute antapical processes, usually bearing small lateral spinulae resulting from increased development of the surface reticulation. Nevertheless it has been confused on occasions with *P. grande* KOFOID, a species with shorter apical and antapical horns and a relatively more robust appearance, possessing acute antapices drawn out like *P. divergens.* PAVILLARD (1931, p. 65) has discussed some of the difficulties but SCHILLER's (1935) treatment is confused, and several other authors, including WOOD (1954) give the form of the first apical plate as "ortho."

It has been pointed out in the introductory comments to this section that the divergent antapical horns which were the only means of distinguishing *P. fatulipes* from *P. elegans* are solely the result of intercalary band development, a view first put forward by HALIM (1967) and confirmed here by the examination of numerous scanning electron micrographs of individuals corresponding to that taxon. Consequently it may not be formally recognised, being only a life-cycle stage. It corresponds with the forma *divergens* of MATZENAUER (1933). *P. tumidum* OKAMURA is larger with a fuller body and shorter antapical horns. It is kept separate here, possibly being the megacytic stage of *P. grande.*

P. annulatum KOFOID et MICHENER was never officially illustrated. However from original drawings by Josephine MICHENER in the author's possession, plus hindsight in reading their description, it is evident that it is the same as *P. elegans,* the annulations being the reticulation which is variably developed on the antapical (and to a lesser extent, the apical) horns of *P. elegans.* BALECH (pers. comm.) has concurred with this conclusion.

P. truncatum GRAHAM was distinguished primarily on the basis of the narrowness of the second precingular plate (in contrast to SCHILLER's wholly atypical specimen illustrated by him as f. 253 d). As all specimens in the Indian Ocean material examined here had a narrow second precingular plate (not necessarily narrowest distally, but varying slightly) there was the choice of assigning all the specimens to GRAHAM's well-described and elegantly illustrated taxon or to the early taxon of CLEVE's. The latter course seemed the most reasonable.

Recognition of the most appropriate position for *P.* (*divergens*) *granulatum* KARSTEN (1907) is particularly difficult. It is easy to recognise, being very large, the transdiameter approaching or exceeding 200 µm for cells 220 to 240 µm in length (instead of having a transdiameter less than 165 µm as is usual in *P. elegans*), with elongate antapical processes either moderately divergent and straight, or bent distally as in fig. 309 here. A spiny fin may be developed between the bases of the antapical horns, but only occasionally. MATZENAUER (1933) relegated it to a form of *P. elegans*, which it undoubtedly closely resembles. In view of the principle outlined in the introductory remarks to this section this should, perhaps, be raised to specific status. However, temporarily MATZENAUER's taxon has been retained. It should also be noted that it does not apparently correspond with this author's concept of a forma (see comments in the Introductory section on Infraspecific Taxa, p. 15), there being no indication of its form being due to environmental influence.

P. obtusipes MANGIN resembles a very short-horned variant of *P. elegans* (allowing for the evident optical reversal), but it is premature to make a decision concerning it. The specimen allocated to *"fatulipes"* by HALIM (1967) also appears to have had short antapical horns.

Stations: forma *elegans*: 13, 38, 65, 68–70, 94, 99–103, 108, 110, 130, 141, 142, 284, 286, 287, 297, 320, 325.
"forma" *granulatum*: 24, 38, 52, 60, 70, 71, 91, 92, 101, 106, 144, 344.

The species occurred chiefly in the western Bay of Bengal, the Gulf of Aden and at stations to the south of India. The forma *granulatum* occurred in general in more northern Bay of Bengal samples than the forma *elegans*. The most southerly station for the species was an isolated record at st. 130, south of 32 °S. WOOD (1954) considered it to be a tropical inter-oceanic species. Indian Ocean records additional to those of WOOD (1963a) are: KARSTEN (1907); SUKHANOVA (1962b); TRAVERS & TRAVERS (1965), TAYLOR (1967), SOURNIA (1968b) and NEL (1968). The records from the S.W. Indian Ocean suggest that it is carried south-westward by the Agulhas Current.

Peridinium grande KOFOID Text Fig. 4 h; Plate 30, Fig. 310 a, b

SCHILLER 1935:259, f. 255 a–e; WANG 1936:142, f. 15 (non 16); BÖHM 1936:41, f. 18 a 1–4; KISSELEV 1950:204, f. 355; RAMPI 1950b:236, f. 16; WOOD 1954:249, f. 142; SILVA 1955:145, t. 5, f. 8, 9; HALIM 1967:741, t. 6, f. 78–80; WOOD 1968:102, f. 303; STEIDINGER et WILLIAMS 1970:56, t. 31, f. 104.
Non YAMAJI 1966:90, t. 43, f. 7 (= *P. elegans* CLEVE).
Syn.: *P. divergens* auct. non EHRENBERG . . . . SCHILLER 1935, f. 222 b, c (ex STEIN 1883); KISSELEV 1950, f. 329.
P. tumidum OKAMURA?

This is a large, robust species, distinguishable from *P. elegans*, which rivals it in size, by the relatively rotund body, with shorter antapical processes shaped as acutely-pointed horns. It resembles *P. divergens* in the latter aspect but the horns are relatively longer in *P. grande* and the whole cell is much bigger, the transdiameter of the former not exceeding 100 µm, whereas *P. grande* is over 130 µm and usually near 150 µm in transdiameter. KOFOID gave 195 µm as the maximum transdiameter, but cells as large as this were not seen in the "Anton Bruun" material. All specimens had a "meta" first apical plate, as did those of PAVILLARD (1931), MATZENAUER (1933) and HALIM (1967). Only SCHILLER (1935) appears to have seen "ortho" tablature (as he also did for *P. elegans*, another "meta" species).

P. knipowitschii USSATCHEV is rather similar in shape, but it is only approximately half the size and has very acute and slender antapices (see KISSELEV 1950, p. 203, f. 341).

As pointed out elsewhere *P. tumidum* may represent a megacytic stage of this species but has been kept temporarily separate here.

Stations: 14–16, 21, 23, 25–28, 30–32, 34, 37–39, 47, 51, 53–56, 64, 66–71, 103, 109, 111, 113, 115, 118, 125, 140, 141, 144, 148, 282, 283, 287, 291, 294, 325, 327, 332, 334, 340, 399, 419, 420.

This was very commonly represented over the whole northern Indian Ocean in a manner similar to *P. acutipes*. However unlike the latter it was common in the southern Andaman Sea and the north-eastern parts of the Bay of Bengal, suggesting a greater salinity tolerance. It did not exhibit a southern spread in the N.E. Monsoon, perhaps being less thermotolerant.

It is apparently a strictly tropical, inter-oceanic species. In addition to the Indian Ocean records listed by WOOD (1963a) it has been recorded by SILVA (1956a), SUKHANOVA (1962b), TRAVERS & TRAVERS (1965), SOURNIA (1968b), NEL (1968) and ANGOT (1970).

Peridinium granii OSTENFELD ex PAULSEN Plate 32, Fig. 341

SCHILLER 1935:189, f. 188 g–z (non a–f = *P. petersii*); WAILES 1939:38, f. 112; KISSELEV 1950:182, f. 301, 307, 308; NORDLI 1951a: 52, f. 4; WOOD 1954:238, f. 116 a–c, 117 a–c; YAMAJI 1966:89, t. 43, f. 1 (ex PAULSEN); WOOD 1968:103, f. 304; BALECH 1971a:138, t. 27, f. 514–519.
Vix RAMPI 1950b:233, f. 8, 26; SILVA 1955:136, t. 4, f. 11, 12; TRÉGOUBOFF et ROSE 1957:110, t. 23, f. 10.
Non GRAN et BRAARUD 1935:383, f. 60 (? = *P. mastophorum* BALECH); GAARDER 1954:44, f. 54 a b, f. 55 a–c; f. 56 [= *P. garderae* BALECH et *P. spirale* (GAARDER) BALECH]; TORIUMI 1966a:3, t. 2, f. 4 a, b; HERMOSILLA 1973b:22, t. 6, f. 1–17.
Syn.: *P. breve* auct. non PAULSEN . . . SCHILLER 1935, f. 194 e–i; MARGALEF 1957a:45, f. 3 c.

This species has here been assigned to this section because of its resemblance to *P. solidicorne* although it has probably the least developed antapical horns of any member of the group. The shape of the cell is distinctive (PAULSEN 1907, called it "almost cordate"), two outwardly-directed antapical spines representing prolongations of the antapical protuberances. The sulcal-fin profiles may also appear as spines marking the inner edges of the antapical horns. Some authors have shown the species as "para", but most seem to have found a "meta" condition (as here). PAULSEN's original figures are equivocal on this point. The second anterior intercalary is "penta" (five-sided). In BALECH's (1971a) figures the antapical spines project directly backwards, rather than outwards.

NORDLI (1951a) has illustrated a thick-walled, ovoid resting spore within a cell of this species.

P. mite PAVILLARD has been recognised as a distinct species (e.g. by LEBOUR 1925), supposedly having solid as opposed to hollow antapical spines more widely set apart than in *P. granii.* It is highly unlikely that any of the spines in this group are truly solid, virtually all being subulate extentions of the larger antapical horns. However, from the detailed figures of BALECH (1971a) it can be seen that the antapical spines do not arise from horns, as in *P. granii,* and so the species are here kept separate.

P. petersii BALECH is a large, cold-water species which is similar but which has only antapical spines, showing no evidence of a mid-antapical depression with consequent antapical projections of the body and is consequently more similar to *P. mite* than to *P. granii.*

P. garderae BALECH differs principally in having a strongly ascendant (right-handed) girdle displacement.

Stations: 53, 55.

The species was rare, occurring only at two stations in the north-eastern Bay of Bengal. It appears to be thermotolerant, known from cold-temperate to tropical waters in all the major oceans. Records are common from the Indian Ocean (see WOOD 1963 a plus SILVA 1956a, 1960; PRAKASH & SARMA 1964; ANGOT 1965, 1970; TAYLOR 1967 and NEL 1968) and it is possible that some of the records to *P. mite* (excluding that of MATZENAUER 1933 which, according to BALECH 1971a, is *P. mastophorum*) may apply to *P. granii* or vice-versa.

Peridinium inflatum OKAMURA Plate 31, Figs. 328, 330

MATZENAUER 1933:466, f. 48 a–d; MARGALEF 1961b:140, f. 2/5; MARGALEF et DURÁN 1953:29, f. 5 d–h.
Syn.:*P. brochii* forma *inflatum* (OKAMURA) SCHILLER 1935:222, f. 219 a–f; GAARDER 1954:39, f. 47.

This species has usually been considered to be a variant of *P. brochii* and is very similar to it. MATZENAUER (1933) had drawn attention to the small short spines arising from its antapical projections, these arising abruptly rather than as smoothly continuous projections of conical antapical horns. Also, the hypocone is relatively larger than in *P. brochii.*

In the original, very incomplete figures of this species no girdle displacement was indicated. In most of the "Anton Bruun" specimens referred to this taxon there was a slight right-handed displacement and in one specimen tentatively assigned to this taxon (fig. 330) the right-handed displacement was marked, being more than one girdle width. GAARDER's (1954) specimen also showed this anomaly.

As with *P. brochii,* the only specimens seen here were all megacytic and this undoubtedly influences the appearance of the cells. The status of the species is thus very unsatisfactory at present.

Stations: 25, 65, 87, 103.

A few cells were found scattered through the Andaman Sea and the Bay of Bengal. The species has been found in Japanese waters, in the warmer parts of the Atlantic Ocean, and in Pacific coastal waters of Australia, as well as being recorded from the Indian Ocean by MATZENAUER (1933) and DURAIRATNAM (1964).

Peridinium solidicorne MANGIN Plate 32, Figs. 338, 339

SCHILLER 1935:218, f. 215 a–l; BÖHM 1936:39, f. 15 b 1–5; DIWALD 1939:169, f. 8 a–c, 10 a–f; KISSELEV 1950:190, f. 317, 321; RAMPI 1950b:234, f. 25; WOOD 1954:247, f. 135; SILVA 1955:146, t. 5, f. 10, 11; MARGALEF 1957a:47, f. 3 b; MARGALEF, MUÑOZ et HERRERA 1957:6, f. 1 c; BALECH 1971b:25, t. 6, f. 105–111.
Vix WOOD 1968, f. 328 ("ortho").
Syn.:*P. spiniferum* SCHILLER 1935 (non CLAPARÈDE et LACHMANN):218, f. 214 A–E; KISSELEV 1950:190, f. 320; STEIDINGER et WILLIAMS 1970:50, t. 34, f. 114 a, b.
Peridinium sp., MEYER 1966 vix f. 48.

This is a medium-sized (length 70 to 120 μm) species, most readily distinguished by the strong short spines, often finned, protruding from the outer corners of the short antapical horns. Girdle displacement can be slightly right-handed. Although the original figure showed a "meta" first apical plate most other authors have found the plate to be "para" (it was this configuration which contributed to recognition of the section Para-divergentia, now discontinued). In the "Anton Bruun" material many examples of "meta" configurations were found (illustrated) as well as "para", the latter arising from a small shift in the suture on the right side between apical four and its corresponding precingular plate. There is also evidently variability in the shape of the second anterior intercalary plate, both "quadra" and "hexa" configuration having been reported (cf. DIWALD 1939).

MATZENAUER (1933) and SCHILLER (1929) referred to three varieties based on antapical horn plus spine shapes. These were: the var. *mikronyx* SCHILLER in which the spines are slender and more or less straight; the var. *makronyx* SCHILLER with short, conical antapical horns and thick, solid-looking, divergent spines (fig. 339 here), and the var. *bradynyx* MATZENAUER in which the depression between the antapical horns (associated with the sulcus) is deeply hollowed out, the ends of the antapical horns are "squared-off" and the spines are moderately divergent (fig. 338 here). It is not known if there is much point in recognising these taxa. SCHILLER (1935) did not discuss them in his monograph. As this author is in agreement with DIWALD (1939) and PAULSEN (1949) that *P. spiniferum* SCHILLER is a variant of *P.solidicorne*, it can be added that in this variant the antapical horns are sharply conical, the spines blending almost imperceptibly with the horns. The strongly developed puncta are often stronger on the hypotheca than on the epitheca. "Para-hexa" combinations are most common in the latter taxon. It is here proposed as the var. *spiniferum* stat. et comb. nov. [basionym *P. spiniferum* SCHILLER 1935:218, f. 214 A–E].

Specimens corresponding to the latter taxon have been examined with the scanning electron microscope and it has been observed that there are narrow furrows running down the inner side of each antapical horn from the sulcus, partly hollowing the antapical spines.

BALECH (1971b) has carried out a plate dissection of specimens corresponding to the var. *mikronyx.*

Stations: 13, 15, 18, 19, 25–27, 30, 32, 34, 37, 47–49, 51, 52, 59, 62, 65, 67–69, 87, 91, 95, 96, 98, 100, 101, 313, 318, 325–327, 337, 358, 361, 362, 371, 396, 398, 399, 413.

The varieties were not distinguished from each other at the time of the analysis. The species was one of the commonest members of the genus, but in certain seasons only. It was widespread in the Bay of Bengal/Andaman Sea following the N.E. Monsoon and was also present off the west coast of India at this time. However it was not found at any stations on cruises II, III or IV, only re-appearing during the N.E. Monsoon at scattered stations extending as far south as 29 °S on cruise V (only on the 75 °E meridian line). In the western regions it was common at the southern end of the Mozambique Channel during the S.W. Monsoon (S.E. Trades at that locality). This distribution is somewhat similar to *P. acutipes* but is more restricted than it.

In addition to the Indian Ocean records listed by WOOD (1963a; only two) it has been recorded by SILVA (1956a, 1960), TRAVERS & TRAVERS (1965), TAYLOR (1967), SOURNIA (1968b), NEL (1968) and THORRINGTON-SMITH (1969). The species is an inter-oceanic tropical to temperate species. If *P. areolatum* PETERS is conspecific, as considered by SCHILLER (1935), then it also occurs in Antarctic waters.

Peridinium tumidum OKAMURA Text Fig. 4 n; Plate 30, Fig. 316

MATZENAUER 1933:472, f. 60 a, b;
YAMAJI 1966:90, t. 43, f. 8.
Syn.: *P. tesselatum* KARSTEN 1907, t. 50, f. 11 a, b.
P. fatulipes auct. non KOFOID . . . SCHILLER 1935, f. 254 c, d, g, h; STEIDINGER et WILLIAMS 1970:56, t. 31, f. 100 a, b.

SCHILLER (1935) considered this species to be synonymous with *P. fatulipes.* However, as indicated elsewhere in this section, it is more probable that it is a megacytic stage of *P. gracile.* It can be rocognised by the greatly swollen cell body, the "bar" spanning the bases of the antapical horns (produced by the mid-dorsal intercalary band) being strongly evident and sometimes producing a convexity in this region (see MATZENAUER's 1933, figures and those of PAVILLARD 1931, pl. 2, f. 14 B, C). The bar appears to be differentiated from the intercalary band as a distinct structure, judging by various drawings, but it has not been possible to confirm this with the scanning electron microscope. The antapical horns are shorter than in the megacytic stage of *P. elegans.*

It is difficult to know whether *P. tesselatum* KARSTEN or *P. tumidum* OKAMURA has priority, as both appeared in the same year (1907). Previous authors have given priority to OKAMURA.

Stations: 67, 90, 102, 143, 284, 315.

Specimens corresponding to this taxon were found at a few scattered stations in the Northern Indian Ocean and at one southern Indian Ocean station (315) during the S.W. Monsoon. This distribution is compatible with the view that the taxon is a stage of *P. grande*, most of the stations being in proximity to those from which *P. grande* was recorded (co-occurring at one of them).

Specimens have been observed from the western Pacific Ocean, the Mediterranean Sea and the tropical Atlantic Ocean, and in the Indian Ocean by MATZENAUER (1933).

Section *Humili - Piriformia* (JÖRGENSEN) PAULSEN
[Incl. sect. *Humilia* JÖRGENSEN and *Piriformia* JÖRGENSEN]

This represents a synthesis of two earlier sections of JÖRGENSEN by PAULSEN (1949). All members have a "meta" first apical plate, the second anterior intercalary plate being either "quadra" (Humilia) or "penta". "Hexa" conformations of the second anterior intercalary plate have rarely been reported (see *P. dakariense* here, for example). Within one species variability of the anterior intercalary plates may occur (e.g. *P. ovatum* STEIN, as described in LEBOUR 1925, p. 110) and it was chiefly for this reason that PAULSEN combined the sections.

All members exhibit right-handed girdle displacement, sometimes greatly "over-hanging" due to torsion. The posterior margins of the sulcus may or may not be extended by spines. Large posterior spines may also be present, but only in some members.

As little information is available on phenotypic plasticity within members of this section (in particular on the relatives of *P. globulus* STEIN which evidently can exhibit great plasticity in cell shape and in the configuration of certain plates), the taxonomy of these taxa is unsatisfactory.

Here the same attitude has been adopted as in the case of the "Divergens Complex" within the section Divergentia, namely: to recognise small variants at the specific level for later ease in combining data on the taxa at any appropriate level.

Peridinium cerasus PAULSEN Plate 29, Figs. 302, 303
– 1907:12, f. 12 a–g. . . SILVA 1949:350, t. 6, f. 3, 4; WOOD 1954:237, f. 113 a, b; YAMAJI 1966:82, t. 39, f. 7 (ex PAULSEN); HALIM 1967:735, t. 9, f. 122.
Vix LEBOUR 1925:130, t. 27, f. 1 a–e; WAILES 1939:40, f. 119; RAMPI 1950b:232, f. 22; MARGALEF et DURÁN 1953:26, f. 4 f, g; MARGALEF DURÁN et SAIZ 1955:95, f. 5 g. Non DIWALD 1939:163, f. 14 a–c (= *P. subpyriforme*).
Syn.: ? *P. quarnerense* (SCHRÖDER) BROCH auct. nonnul.

This species was one of the earliest spherical species to be distinguished from *P. globulus.* In the original figures and description the most distinctive features were its more strongly developed apical horn and moderately well-developed antapical spines set wider apart than the main sulcal width. The cells were spherical and the girdle was only slightly right-handed, lacking the distortion commonly found in *P. globulus.* The tabulation was first shown as "ortho-quadra." Later PAULSEN (1930) asserted that a "meta" first apical plate was the usual condition. The species is small, the transdiameter usually being in the vicinity of 35 to 40 µm but reaching 61 µm in Antarctic material. The cells found here were between 42 and 56 µm. The illustrated specimen is atypical in having the second anterior intercalary plate "penta" rather than "quadra." BALECH (pers. comm.) has examined Atlantic material of *P. cerasus* and found it to have a "quadra" plate and a tapering apical horn instead of "affixed." Other specimens resembled those of PAULSEN (1930).

P. quarnerense (SCHRÖDER) BROCH is most probably the same species, possessing a usually spherical shape and well-developed antapical spines. The apical horn is not usually shown to be as well-developed as in the "typical" *P. cerasus.* In the majority of extant figures it appears as if the antapical spines are part of the sulcal lists (as in *P. subpyriforme* DANGEARD), not separate, as in *P. cerasus.* It is suspected that the majority of specimens attributed to *P. quarnerense* are either *P. subpyriforme*, a few being *P. cerasus* or small individuals of *P. globulus*, but it is not possible to be sure in most cases because of lack of details in the drawings. In the event of synonymy, *P. cerasus* PAULSEN has priority over *P. quarnerense* (SCHRÖDER) BROCH, at the species level. *P. subpyriforme* DANGEARD is here considered to be distinct in view of the antapical spines being integral parts of the left and right sulcal lists near the posterior flagellar pore rather than being set wide apart more posteriorly. DIWALD (1939) followed SCHILLER (1935), combining *P. quarnerense* with *P. globulus.*

P. bellulum BALECH (1971a) is also very similar to *P. cerasus*, differing mainly in being ovoid in shape. It can be smaller than the latter, some cells being only 30 µm in transdiameter, but there is overlap in the size ranges of the two species.

Stations: 17, 53, 289.

Only a few cells were seen, these being found at stations in the Andaman Sea, the Bay of Bengal and the southwestern Arabian Sea. The species appears to be very thermotolerant, being known from the Weddell Sea in the Antarctic (PETERS 1928) as well as from temperate and tropical waters. WOOD (1963a) lists two previous Indian Ocean records, to which those of SILVA (1956a, 1960) and NEL (1968) should be added.

Peridinium corniculum KOFOID et MICHENER Plate 32, Fig. 342
– 1911:281.

This species is one of many which KOFOID & MICHENER described but did not illustrate. In view of the difficulty experienced by most authors in attempting to visualise the appearance of these species it is not surprising that no further reference to the species has been made, other than SCHILLER's (1935, p. 273) comment that the diagnoses without illustrations are worthless.

The author has been assisted in making the identification by possession of the original pencil drawings of *Peridinium* made by Josephine MICHENER, presumably of the type material. The dates on the drawings (1907, 1908) predate the published descriptions (see also *P. pacificum* here). If possible these originals will be published separately at a later date.

A pair of the figures, marked tentatively as a variant of *P. globulus,* show the dorsal and ventral views of *P. corniculum* as it was later described. What is not evident in the description (as it predated JÖRGENSEN's system of plate nomenclature) is that the species is "meta-penta". It is quite similar to *P. tubum* especially with its rotund body and flaring apical horn. However it is much bigger. The transdiameter ranges from 48 µm (here) to 55 µm (type), the length without apical or antapical horns from 48 µm (here) to 51 µm (type). The apical horn is approximately 10 µm long. Girdle displacement is about one girdle width.

One difference between the present specimen and the type is the well developed right sulcal fin, projecting between the two antapical spines. This was presumably missed by MICHENER.

Stations: 59, 64, 99.

One specimen was found at each of several stations in the western Bay of Bengal. The species was originally described from the eastern tropical Pacific Ocean ("Albatross Expedition"), and does not appear to have been seen until now.

Peridinium dakariense P. DANGEARD Plate 29, Figs. 306 a, b
SCHILLER 1935:181, f. 184 a, b.
Non WOOD 1954:235, f. 109.
Syn.:*P. gibbosum* MATZENAUER 1933:461, f. 41 a, b; SCHILLER 1935:182, f. 181 c, d; BALECH 1971a:92, t. 16, f. 258–268.
P. parvispinum GAARDER 1954:48, f. 61 a, b; BALECH 1959b:22, t. 1, f. 25–35.

The shape of this species is distinctive, the epitheca smoothly hemispherical the hypotheca being indented posteriorly to form two rounded antapical lobes. It is slightly flattened dorso-ventrally. The apical pore is slightly raised and may be directed towards the ventral side, as here. On the inner surfaces of the posterior depression (or nearly at the apices of the posterior lobes) there are two short, acute spines. In the original specimen (only one was seen by DANGEARD) the girdle had virtually no displacement and the spines projected almost straight back. However in the specimens of MATZENAUER (1933), GAARDER (1954), and BALECH (1959b), and particularly here, right-handed girdle displacement is evident. BALECH's drawings do not exhibit the characteristic shape very clearly, perhaps due to lateral tilting.

An unusual feature of this species is its combination of a "meta-hexa" arrangement. This is most similar to the species figured on the same plate, *P. paradoxum* sp. n. (figs. 307 a, b) which also had a similar shape (while being megacytic) but which exhibited strong girdle torsion, and had a large, ventrally placed posterior flagellar pore. The longitudinal striations on some intercalary bands are also unusual in *P. dakariense,* being reminiscent of some fresh water and brackish water species (e.g. *P. achromaticum* here). BALECH (1971a) illustrated a specimen, designated as *P. gibbosum,* which had a "penta" second anterior intercalary plate and relatively little girdle displacement.

It could be argued that *P. dakariense* could be separated from the others (which are almost certainly synonymous) by its lack of girdle displacement and differently-directed, slightly larger antapical spines. This would be possible (in which case the present material would be attributed to *P. gibbosum*), but there seems to be a complete gradation of girdle displacement exhibited by the existing figures, with DANGEARD's specimens at one extreme and the present one and that of BALECH (1959b) at the other.

GAARDER's length data (53–87 µm excluding spines) embraces that reported by others.

Station: 148.

Only one specimen, as illustrated, was observed. The species is known from the tropical and temperate North Atlantic Ocean, and was recorded from the Indian Ocean by MATZENAUER (1933).

Peridinium globulus STEIN Plate 29, Figs. 301 a–d

SCHILLER 1935:182, f. 185 a–c, g, h, k–r, f. 187 a–i (non f. 185 d–f, i, j, f. 186 a–z); DIWALD 1939:159, f. 3e, 4 a–e, 11b, 13 a–c, vix f. 13 d–i; NIE 1939, f. 1; KISSELEV 1950:180, f. 299, f. 306 (non f. 298, f. 300); RAMPI 1950b:232, f. 20, 23 (non 21); WOOD 1954:236, f. 110 a, b; TRÉGOUBOFF et ROSE 1957:110, t. 23, f. 9.
Vix SILVA 1949:350, t. 6, f. 1, 2 ("ortho"); HERRERA, MUÑOZ et MARGALEF 1955, f. 1 C, D; WOOD 1968, f. 302 ("ortho").
Non SILVA 1952b:603, t. 6, f. 9 (= *P. subpyriforme* DANGEARD).
Syn.:. . . *P. ovatum* (POUCHET) SCHÜTT . . . SILVA et PINTO 1948:166, t. 6, f. 5, 6; WOOD 1954:236, f. 112 a–d; BRUNEL 1968:198, t. 61, f. 1–5, t. 62, f. 1–4; WOOD 1968:106, f. 316; BALECH 1971a:112, t. 21, f. 384–386, t. 22, f. 387–391; HASSAN et SAIFULLAH 1972b:160, f. 2.
? *P. majus* DANGEARD 1927b:359, f. 25 c; YAMAJI 1966:82, t. 39, f. 6.
? *P. spheroides* DANGEARD 1927a:5, f. 3 A–D.

The precise delimitation of this species is very difficult. Before 1907 nearly all spherical individuals of *Peridinium* were probably referred to this species but since then many others have been described. Ovoid or lenticular members of *Peridinium* were usually attributed to *P. ovatum* (POUCHET) SCHÜTT. *P. quarnerense* (SCHRÖDER) SCHRÖDER later became separated, largely on the basis of the presence of two antapical spines, the cells usually being shown as spherical. The degree of girdle displacement was illustrated as varying from almost none to considerable right-handedness with overlap of the proximal parts of the girdle in both *P. globulus* and *P. ovatum.* Although most authors illustrated a "meta" (pentagonal) first apical plate there were differences in the shape of the second anterior intercalary plate, the latter being found to vary from "quadra" (four-sided) to "penta" (five sided) by MARSHALL and LEBOUR (in LEBOUR, 1925 including reference to material from India), and the original figure of *P. globulus* showed a "hexa" (six-sided) second anterior intercalary plate.

MATZENAUER (1933) asserted, on the basis of Indian Ocean material, that smaller cells are rounder and larger cells become more ovoid in shape, this removing much of the justification for recognising *P. ovatum* as a distinct species. *P. quarnerense* (SCHRÖDER) BROCH is almost certainly synonymous with *P. cerasus* PAULSEN, the latter having priority at the species level (for further discussion, see under the latter taxon here).

P. majus DANGEARD was created for cells resembling *P. ovatum* but which, according to DANGEARD (1927b), differed by their larger size (transdiameter 120 µm), lack of antapical spines (fins?), lack of supporting spines on the girdle lists, and a "penta" second anterior intercalary plate. He raised them to the species level from an earlier (1927a) treatment at the varietal level. The plate pattern he figured is similar to that seen here on a smaller cell which also possessed girdle-list spines (fig. 301). The status of this species is uncertain at present.

In this muddled state it has been considered best, for the present, to exclude *P. cerasus* from *P. globulus* but to include *P. ovatum*. *P. simulum* PAULSEN, which is similar to the latter, has been kept separate here (see comments under that species). The specimen illustrated here (fig. 301, had an epitheca like *P. majus,* but did not have the other features associated with that species.

The other specimens found at the stations below varied in shape from spherical to lenticular, but all had strong girdle displacement. It was not determined whether the "quadra" or the "penta" variant was more common. In most, the sulcal lists projected to a greater or lesser extent below the posterior margin, but not more than that shown in fig. 301.

Stations: 13, 15, 17, 25–27, 29, 31, 32, 34, 46, 47, 49–51, 53, 55, 56, 58, 61, 65, 68–71, 85, 88, 90–93, 98, 99, 105, 108–110, 148, 282, 291, 325, 367, 370, 413.

The species was particularly common in the Bay of Bengal where it was one of the few to be common in the north-eastern part. It also occurred in the central and southern Andaman Sea, and was more rare in the Arabian Sea. It was recorded at three stations in the Mozambique Channel region. It was not found at any central Indian Ocean station south of the equator. This pattern suggests that it is stenothermal but fairly halotolerant, perhaps also with a neritic preference. The distribution in the Indian Ocean is very similar to that recorded here for *P. subpyriforme* (very similar to *P. quarnerense*), making one doubtful of their specific separation.

It has been found in the tropical Atlantic Ocean, the Mediterranean Sea, the western Pacific Ocean, and in the Indian Ocean by many authors, a number of whom, however, referred to the "var. *quarnerense*" (e.g. TAYLOR 1967; SOURNIA 1968b, 1970). WOOD's (1963a) lists require augmentation by the records of SILVA (1956a, 1960), NEL (1968), and HASSAN & SAIFULLAH (1972b).

Peridinium latispinum MANGIN Plate 32, Fig. 336; Plate 44, Fig. 519

SCHILLER 1935:193, f. 190 A a–d; NIE 1939, f. 17 A–F; WOOD 1954:240, vix. f. 119; TAYLOR 1973b, f. f a.
Syn.: *P. africanoides* P. DANGEARD 1927b:357, f. 22 c; MATZENAUER 1933:460, f. 39 a, b; BÖHM 1936:41, f. 16 b 1, 2.
? *P. sylvanae* P. DANGEARD 1927a:2, f. 1 A–C; – 1927b:357, f. 22 a, b; SILVA 1958:30, t. 2, f. 11, 12.

This is a medium to large species, 80 to 100 µm in length excluding the antapical spines. Neither MANGIN nor DANGEARD observed the "meta" first apical plate and it was NIE (1939) who first determined the full tabulation of the species. The second anterior intercalary plate is "penta" and is displaced towards the left side. Typically the cells have a pyriform shape, the apex tapering smoothly to form the apical horn. Occasionally, particularly in megacytic cells, the horn may have an abrupt "affixed" appearance. The apical horn is often finned at the plate sutures.

With the scanning electron microscope it has been possible to examine the unusual lists and fins of this species (cf. fig. 519). The most distinctive feature of the species is the more ventral projection of the left antapical spine in comparison with the right. The left sulcal list is much more strongly developed than the right throughout its length, only the posterior part of the right sulcal list becoming appreciably extensive as it extends onto the antapical spine. As BÖHM (1936) first observed, each spine bears three fins, one being an extension of the sulcal list, the other two being laterally directed. The edges of these fins are distinctively serrated in appearance. The accessory list close to the right margin of the posterior flagellar pore is quite large and lies much closer to the left than the right sulcal list.

P. africanoides DANGEARD is undoubtedly the same species. *P. sylvanae* DANGEARD is probably the same, but as originally figured it has a rounder shape with shorter antapical spines, an "affixed"-looking apical horn, and a "hexa" second anterior intercalary plate. Only the latter offers a good reason for separation, but "penta" to "hexa" variation is quite common in this section of *Peridinium*.

Recently BALECH (1971a) has described *P. joergensii* (based on *P. pedunculatum* of JÖRGENSEN). It strongly resembles *P. latispinum* but is somewhat smaller, the cell body not exceeding 74 µm, with a rather angular shape. The spines are long and are not apparently as displaced with regard to each other as in *P. latispinum*.

It is noted elsewhere that the *P. pyrum* BALECH (see fig. 337 here) may well be a small variant of *P. latispinum*.

Stations: 16, 20, 23, 24, 30, 32, 37, 38, 41, 46, 47, 51, 91, 101, 106, 144, 323, 358, 362, 370, 398.

This species exhibited an interestingly idiosyncratic distribution. The great majority of stations were near land, and it was absent from the many central and southern Indian Ocean stations. It was scattered throughout the Andaman Sea, was not as common and more neritic in the Bay of Bengal, occurred at two stations off the south and west coasts of India, and at one (323) further south from India not far from the Chagos Archipelago. It was also present at a cluster of stations at the southern end of the Mozambique Channel.

This distribution is suggestive of a stenothermal tropical species with a strong neritic preference. It was originally described from the tropical Atlantic Ocean. In the western tropical Pacific Ocean BÖHM (1936) found it to be one of the commonest species of *Peridinium*. It has been previously recorded from the Indian Ocean by MATZENAUER (1933) and SILVA (1956a, 1960) under the name of *P. africanoides*, and by TAYLOR (1967).

Peridinium longicollum PAVILLARD Plate 32, Fig. 346.
– 1916, t. 2, f. 3; SILVA 1949:348, t. 5, f. 24.
Non DANGEARD 1927b:358, f. 329 a–c (= *P. tenuissimum* KOFOID).
Syn.: *P. mediterraneum* (KOFOID) BALECH 1964a:184, t. 2, f. 26–35.
P. steinii mediterraneum KOFOID 1909a:40, t. 2, f. 1–7.
P. steinii var. *mediterraneum* (KOFOID) SCHILLER 1935:198, f. 193 a, c (non d–f); RAMPI 1950b:233, f. 7; WOOD 1954:241, f. 120 b; TRÉGOUBOFF et ROSE 1957:110, t. 23, f. 11.
? *P. pedunculatum* SCHÜTT . . . MARGALEF 1964, f. 2 c.

This taxon, recognised at the species level by some, and at an infraspecific level by others, is very similar to *P. steinii* JÖRGENSEN from which it has been separated chiefly by its more rounded body with a longer, more abruptly tapered apical horn, and much longer antapical spines. The cell body plus horn, but excluding spines, attains a length of 60 µm. *P. tenuissimum* KOFOID is similar in size and shape, but has a "para" first apical plate.

In asserting its difference from *P. steinii*, BALECH (1964a) raised *P. steinii mediterraneum* KOFOID to the level of species. However that rank was pre-occupied by PAVILLARD's taxon, considered by BALECH, SCHILLER and others, to be synonymous. Consequently PAVILLARD's name should be used when referring to this taxon at the species level.

This taxon was the first member of *Peridinium* to be subjected to detailed structural study (by KOFOID 1909a).

MARGALEF (1964) has interpreted *P. pedunculatum* SCHÜTT in the same manner as this species. Unfortunately SCHÜTT (1895) gave no tabulation for his species, leading to a varied interpretation by later authors. In his figures the apical horn was more abruptly "affixed" than here.

Station: 113.

A few cells were found at one station near the Maldive Islands, southwest of India. The species has not been recorded as such from the Indian Ocean, but as a variety of *P. steinii* it has been recorded by SOURNIA (1968b). It is known from the Mediterranean Sea, and the coasts of Portugal, Australia and California.

Peridinium orientale MATZENAUER Plate 32, Fig. 347
– 1933:460, f. 368; SCHILLER 1935:271, f. 275.

This species, first described from the Indian Ocean, most closely resembles another very small member of this section, *P. sourniai* nom. nov., from which it can be distinguished by its slightly larger size (length 30–40 µm without spines), much shorter antapical spines, and more roundly pyriform shape. An examination of one of the "Anton Bruun" specimens revealed a "hexa" dorsal intercalary plate, a feature which, if constant, could also serve to distinguish them. The girdle has right-handed displacement.

Station: 153.

Only two specimens could be found in a sample from north of Mauritius. MATZENAUER (1933) observed it in the Red Sea, the southern Bay of Bengal, and the East Indies. It has not apparently been observed by other authors.

Peridinium pacificum KOFOID et MICHENER Plate 32, Fig. 343
– 1911:283.
Syn.: *P. pellucidum* auct. non SCHÜTT . . . MATZENAUER 1933:461, f. 42 a–c; MARGALEF 1951:56, f. 2, g.
? *P. capdevillei* BALECH 1959b:25, t. 2, f. 46–52; – 1971a:150, t. 30, f. 578–588, t. 31, f. 589–593.

This, like *P. corniculum*, is another species not illustrated in the original publication but identified here with the aid of unpublished drawings by Josephine MICHENER. In this case the figure (dated March, 1908) is named so that there can be no doubt as to its association with the published description. The only anomaly noticed is that the antapical horns are approximately one girdle-width in length, instead of 1.5 as in the description. Not evident in the description is the fact that the species has a "meta" first apical plate. From a rough sketch the second anterior intercalary plate appears to be "quadra" but this may be unreliable as there is an obvious error involving the first apical plate in the sketch.

The species is similar to *P. pellucidum* and its numerous, troublesome relatives except that the "meta" first apical plate, combined with the girdle displacement (1–2 girdle-widths, ascending) can be used to easily recognise it. The length, without spines, varies from 40–62 µm and the transdiameter from 50–70 µm. From MATZENAUER's description and figures it is evident that he found *P. pacificum* in the Indian Ocean (SCHILLER 1935 included MATZENAUER's specimens with *P. pellucidum*).

There is also a resemblance to *P. granii* which has, however, more widely placed antapical spines. *P. mediocre* BALECH has less girdle-displacement and no evident left antapical projection of the cell body. *P. patagonicum* BALECH and *P. capdevillei* BALECH are also similar. BALECH (1971a) has shown a displacement of approximately one girdle width for the latter and it is possible that it is synonymous with *P. pacificum*. It has a "quadra" second anterior intercalary plate.

Stations: 56, 85, 142.

It was found at two stations in close proximity to each other in the northern Bay of Bengal and at one station to the south of India. MATZENAUER's records may not all be applicable to this taxon as some may have referred to true *P. pellucidum*. However it is evident that he did find the present taxon at least once in the northern Indian Ocean.

Peridinium paradoxum sp. n. Plate 29, Figs. 307 a, b

This taxon is very distinctive, bearing several unusual features. It could not be attributed to any species known to the author. Its principal distinguishing features are: its unusual shape (very similar to *P. dakariense*), rounded with an indented posterior margin, very strong right-handed girdle displacement with torsion resulting in the ends of the girdle overlapping ("overhang"), a very short sulcus with the posterior flagellar pore (its margins much thickened) displaced towards the ventral side. The plate arrangement is "meta-hexa", another similarity with *P. dakariense*. Very small sulcal fins can give the appearance of two small antapical spinelets if the cells are tilted. A short, tubular apical pore is present.

It is largely the girdle torsion (with accompanying distortion of the epithecal plates) and the position of the posterior flagellar pore, which distinguishes this species from *P. dakariense*, its most apparent close relative. However, there are also strong resemblances between this species and the taxon GAARDER called *P. globulus* var. *quarnerense* f. *spirale*, the latter having a similar distorted girdle. GAARDER (1954) mentioned that the second anterior intercalary of the latter could vary from "penta" to "hexa".

Length: 82–94 µm (without spines).
Transdiameter: 76–82 µm.
Type locality: Andaman Sea (station 25).

Stations: 25, 35.

Three cells, all megacytic, were observed in samples from two stations, both in the Andaman Sea.

Peridinium pyrum BALECH Plate 32, Fig. 337
– 1959b:24, t. 2, f. 38–42; – 1971a:93, t. 16, f. 269–276, t. 17, f. 277–283.

This species is very like a small variant of *P. latispinum*. It has much the same pyriform shape and, most significantly, has the same displaced antapical spines, the left spine being much more ventrally placed than the right horn. The antapical spines are smaller, and also tend to be more dissimilar in length, than in *P. latispinum* (bearing in mind that in ventral view the left antapical spine looks shorter in any case, due to its angle to the viewer). The fins are very delicate and were not shown in the original figures, although BALECH figured them in his later, more detailed study (1971a). Like *P. latispinum* they have serrated edges. The length of the cells, excluding the spines, is 37–59 µm, the transdiameter being 31–48 µm. The tabulation is "meta-penta".

P. unipes BALECH (1962a) is fairly similar in size and shape, but it has a relatively longer apical horn and the fin-less antapical spines are apparently not displaced in relation to each other. *P. joergensii* BALECH (1971a) is also similar, but has longer antapical spines, being even more like *P. latispinum*.

Stations: 43, 55, 70, 100, 101.

All of the stations were in the Bay of Bengal, being a little further offshore than those at which *P. latispinum* was found. They co-occurred at station 101.

Previous records of the species are limited to the temperate and subantarctic South Atlantic Ocean. The species appears to be thermotolerant.

Peridinium simulum PAULSEN Plate 29, Fig. 304
– 1930:58, f. 30 A, B; BALECH 1959b:21, t. 1, f. 11–19; HALIM 1960a, t. 2, f. 28; HERMOSILLA 1973b:21, t. 5, f. 1–17.
Syn.: *P. ovatum* auct. non SCHÜTT . . . SILVA 1949:348, t. 5, f. 25, 26.
P. globulus auct. non STEIN . . . KISSELEV 1950, f. 298 *a* (ex BROCH).

This species can be distinguished from *P. globulus*, according to PAULSEN, by its size (diameter 80–94 µm, apico-antapical height 46–67 µm: smallest values from this material) and its more compressed, lenticular shape. It is evidently very closely related and the specimens referred to this species by PAULSEN had all been assigned to *P. globulus* by previous authors. The narrow, strongly-curved sulcus seems to also be a distinctive feature separating it from *P. ovatum* (POUCHET) SCHÜTT, which also lacks girdle distortion, having only moderate right-handed displacement.

P. cepa BALECH is somewhat similar in shape, but lacks the strongly curving sulcus and has long fins/spines associated with the lower part of the sulcus.

As indicated by PAULSEN (1930) *P. majus* DANGEARD is also very similar, differing by its possession of a pentagonal second anterior intercalary plate. It has a larger transdiameter, exceeding 100 µm, and it does not have the distorted "overhanging" girdle of *P. simulum*.

Stations: 367, 369.

It was found at only two stations, both situated at the southern end of the Mozambique Channel. It has not been formally recorded from the Indian Ocean. The specimens referred to this taxon by PAULSEN (1930) were from the Mediterranean Sea, and SILVA's (1949) record under another name was from the coast of Portugal.

Peridinium sourniai nom. n. Plate 32, Fig. 356; Plate 33, Fig. 375?
Syn.: *P. bimucronatum* SCHILLER 1935:266, f. 265 a, b.
P. bispinum SCHILLER 1935:266, f. 266 a, b; BALECH 1971a:108, t. 20, f. 358–364.

This minute species (body length 22–30 µm, transdiameter 20–23 µm) is readily distinguishable by its small size combined with a pyriform body with two medium-length, straight antapical spines. Its tabulation (meta/penta) was determined by BALECH. The "penta" dorsal intercalary plate and the length of the spines serve to distinguish it from *P. orientale* MATZENAUER which has shorter spines, is somewhat larger, and appears to have a "hexa" second anterior intercalary plate (see notes under that species here). Both have right-handed girdle displacement. *P. birobis* ABÉ is of the same size, but has longer spines and a "hexa" second anterior intercalary plate.

SCHILLER's original descriptions of both the above species are invalid according to the ICBN (Art. 34) because they were only tentatively proposed ("ad interdum"). He suspected that they were both the same taxon. A new name is here proposed for the unified taxon. It is named after Alain SOURNIA in recognition of his contributions to tropical phytoplankton biology, and to the knowledge of Indian Ocean dinoflagellates in particular.

The specimen shown in fig. 375 differs in its shape, being broader in the epitheca, and has very short horns. It seems to be similar to the *Peridinium* sp. in BALECH (1971a, pl. 20, f. 365–367). No plates could be determined on the present specimen.

Stations: 298, 327, 374.

A few cells were found at one station south of India, one north of Mauritius, and one near the African coast at the southern end of the Mozambique Channel. It would not be expected to be efficiently retained by the nets used due to its small size.

The species was originally described from the Adriatic Sea, and BALECH (1971a) found it off the coast of Argentina. It has not apparently been observed previously in the Indian Ocean.

Peridinium steinii JÖRGENSEN Plate 32, Figs. 349 a, b

SCHILLER 1935:196, f. 192 a–h; SILVA 1949:347, t. 5, f. 22, 23; KISSELEV 1950:184, f. 304; RAMPI 1950b:233, t. 7, f. 28; MARGALEF et DURÁN 1953:26, f. 4 j–1; WOOD 1954:240, f. 120 a; MARGALEF 1957a:47, f. 2 f; HALIM 1960a, t. 3, f. 8; BALLANTINE 1961:219, f. 21, 22; WOOD 1968:109, f. 329; MARGALEF 1969a, f. 3 E; HERMOSILLA 1973b:40, t. 19, f. 1–12.
Vix MARGALEF 1957a:47, f. 2 f.

This is a medium-sized, pyriform species superficially resembling members of the section *Protoperidinium*, such as *P. pallidum*, but it is readily distinguished from them by its "meta-penta" configuration, this apparently not being subject to much variation. *P. pyriforme* PAULSEN is fairly similar in body shape, with a "meta-penta" tabulation, but it has much shorter antapical spines. The most similar taxon is *P. longicollum* PAVILLARD (see comments under that species here). The latter is considered to be a distinct species chiefly because of its much longer antapical spines, its body being generally rounder with a more abrupt and longer apical horn than *P. steinii*.

The dimensions of this species are usually given as: length (without spines) 47–58 µm, transdiameter 21–39 µm (MARGALEF & DURÁN 1953). However, gross cell enlargement accompanies infection by a parasitic dinoflagellate, *Amoebophrya ceratii* (fig. 349 b). The infected cell was 80 µm in length (excluding spines) and 58 µm in transdiameter. Such gigantism accompanying infection, with no dislocation of the plates, was reported earlier for cells of *Gonyaulax catenella* by TAYLOR (1968).

Station: 67.

Only one cell was found in a station in the north-western Bay of Bengal. There have been numerous references to the presence of the species in the Indian Ocean (cf. WOOD 1963a plus SILVA 1956a; DURAIRATNAM 1964; PRAKASH & SARMA 1964; TAYLOR 1967; SOURNIA 1968b, 1970; and NEL 1968), but it is not clear if all these records exclude or include *P. longicollum*. The species has been found in all oceans in temperate as well as tropical waters.

Peridinium subpyriforme P. DANGEARD Plate 29, Figs. 305 a–d, Plate 32, Figs. 348 a, b?

– 1927b:358, f. 21; ABÉ 1936b:40, f. 30–37; SILVA 1949:349, t. 5, f. 31, 32; KISSELEV 1950:212, f. 374.
Syn.: *P. globulus* var. *quarnerense* auct. nonnull. .... SILVA 1952b:603, t. 6, f. 9.

This medium-sized globular species (length 40–67 µm) has been described in detail by ABÉ (1936b), and the specimens observed here are very similar to his description. The species is very similar to *P. quarnerense* (SCHRÖDER) BROCH and was included with it (as *P. globulus* var. *quarnerense* SCHRÖDER) by SCHILLER (1935). The difficulties in recognising *P. quarnerense* are discussed here under *P. cerasus* PAULSEN, the latter also being very similar but distinguished by its well-developed apical horn and antapical spines, the latter not being spines of the main part of the sulcal lists but instead being set further apart, more posteriorly.

P. patens DANGEARD is similar to *P. subpyriforme*, differing only in the possession of a "hexa" second interior intercalary plate instead of a "penta" plate. As this depends on only a very slight difference in the position of sutures, this separation is of doubtful value.

Stations: 14, 16, 46, 54, 55, 57, 59, 60, 64, 66, 69, 71, 91, 94, 96, 103, 105, 144, 147, 148, 287, 301, 325, 329, 358, 365, 366, 370, 374, 415, 419, 420.

The species (probably here including cells conforming to *P. quarnerense*) was fairly common only in the northern and western Indian Ocean. It was found both to the north and south of the Mozambique Channel but not in it at the time of the cruise there (cruise VIII, September, 1964). It is probably a stenothermal species, preferring high tropical temperatures. It has been found in the tropical Atlantic Ocean, Japanese coastal waters, and in the northern Indian Ocean by MATZENAUER (1933). Probably some of the records listed by WOOD (1963a) for *P. quarnerense* also apply to this taxon.

Peridinium tubum SCHILLER Plate 32, Fig. 344

– 1935:272, f. 280 a–c; WOOD 1968:110, f. 334.
Vix STEIDINGER et WILLIAMS 1970:58, t. 34, f. 118.

This small species (transdiameter 15–27 µm) has apparently only been seen three times (it is listed but not figured by HERRERA & MARGALEF 1963, who do, however, give a size for their specimen). The specimen illustrated by STEIDINGER & WILLIAMS (1970) was 31 µm long, which is a little large for this species. Also, although it is difficult to see, it appears that in their specimen the apical horn is wider at its base than at its tip, this being one of the features which distinguishes *P. sinaicum* MATZENAUER from *P. tubum*. Girdle displacement is little or none in *P. tubum*.

Like previous authors this author was unable to make out the thecal plates and consequently the systematic position of this taxon remains uncertain. Because of superficial resemblances to members of the section Humili-piriformia it is here placed in that section although it is quite possible that it is a member of the section *Protoperidinium* (with a six-sided, "para", first apical plate instead of a five-sided "meta" plate).

Station: 417.

Only one specimen, as illustrated, was found, the locality being off the east-African coast, north of the Mozambique Channel. The species was originally found abundantly at 100 m in the Adriatic Sea. In addition to the Mediterranean Sea it is also known from the Straits of Florida. It has not been found previously in the Indian Ocean.

Section *Oceanica* JÖRGENSEN

The members of this section all have an "ortho-quadra" tabulation (rarely "penta" or "hexa"), and have well-developed hollow antapical horns. An apical horn may or may not also be well developed. Girdle displacement, if present, is left-handed.

SCHILLER's (1935) treatment of this section included all the long-horned members with a "meta" first apical plate (e.g. *P. grande, P. elegans*), leading to a very confused situation in which there was no clear distinction between this section and the section *Divergentia*. Here all such species with elongate antapical horns and a "meta-quadra" tabulation (the "Divergens Complex") have been put into the section Divergentia, where they form a more homogenous and logical grouping.

As a result of the above transferral the section *Oceanica* narrows down to just *P. oceanicum* and its closest relatives: *P. claudicans, P. depressum, P. murrayi*, these forming a difficult "species complex" due to considerable morphological variability.

It can be noted in passing that the fossil genus *Deflandrea* EISENACK probably refers to cysts of members of this section (see WALL 1965; WALL & DALE 1966; WALL & DALE 1968a for the cysts of living members of the section).

Peridinium depressum BAILEY Plate 34, Fig. 383; Plate 45, Fig. 526

CANDEIAS 1934:1, f. 1 a, b, 2 a–f, 4; SCHILLER 1935:250, f. 251 a–r; BÖHM 1936:45, f. 17 b 1, 2; DIWALD 1939:179, f. 1 a, b; NIE 1939, f. 8 A–E; WAILES 1939:35, f. 105 A–C; GRAHAM 1942:18, f. 4 A, f. 14–19, 21–28; SILVA et PINTO 1948:164, t. 2, f. 7, 8; MARGALEF 1948b:47, f. 2 a; PAULSEN 1949:59, f. 24 A–C, I–K; BALECH 1949a:390, t. 1, f. 1–11, t. 2, f. 12–40 (sub. *Peridinium* cf. *depressum*); KISSELEV 1950:203, f. 31–33, 340, 344; RAMPI 1950b:236, t. 1, f. 1, 2; MARGALEF et DURÁN 1953:31, f. 7 c–g; WOOD 1954:255, f. 155 a, b; TRÉGOUBOFF et ROSE 1957:111, t. 23, f. 20; SILVA 1958, vix t. 8, f. 1, 2; CURL 1959:305, f. 113; BALLANTINE 1961:222, f. 29–31; MARGALEF 1961a:79, f. 25 e; BRUNEL 1962:196, t. 59, f. 1–4, t. 60, f. 1–11; YAMAJI 1966:89, t. 43, f. 4; WOOD 1968:100, f. 295 a, b; STEIDINGER et WILLIAMS 1970:56, t. 29, f. 96 a, b; HERMOSILLA 1973b:27, t. 10, f. 1–18.

Vix TORIUMI 1966a:3, t. 2, f. 5 a, b; HADA 1967:18, f. 29 A.
Syn.: . . . *P. saltans* MEUNIER . . . PAULSEN 1949:61, f. 24 D–H; non WAILES 1939:35, f. 106 [= *P. paulsenii* PAVILL.? *P. knipowitschii* Ussatschev?].
P. venustum KARSTEN . . . BALLANTINE 1961:222, f. 35–37.
P. obliqueforme SCHILLER 1935:270, f. 273.
P. claudicanoides GRAHAM 1942:24, f. 29 A–H.
? *Peridinium* sp. MEYER 1966:45.
P. oceanicum auct. non VANHOFFEN . . . GRAHAM 1942, f. 34 A–E (f. *spiniferum* GRAHAM), 35 A, B (f. *bisintercalares* GRAHAM), 36 A, B (f. *tricornutum* GRAHAM).

In the early literature there was much confusion between this species and *P. divergens* EHRENBERG, the latter being very similar in size and shape. Tabulation was not shown in either original description. Later it became accepted that *P. depressum* has an "ortho" first apical plate, whereas *P. divergens* has a "meta" first apical plate. Early studies on variability in the species were undertaken by PETERS (1928) and CANDEIAS (1934).

GRAHAM (1942) has also provided a detailed analysis of this species, including study of shape variability, a plate dissection (supplemented by BALECH 1949a) and a historical outline. In his treatment he excluded from the species most members with thick, cuneate antapical horns, forming a new species for them: *P. claudicanoides.* He recognised a multitude of varieties and forms, one of which (his var. *rectius*) corresponds, effectively, to *P. venustum* MATZENAUER, with straight or slightly concave sides to the hypotheca between the girdle and the antapical horns, instead of convex. It also forms an intermediate condition between the slender antapical horned specimens (*P. depressum* sensu stricto) and the broader horns of his other species, thus weakening his arguments for its separate recognition.

It appears that in tropical or warm temperate waters, such as the Indian Ocean or the Mediterranean Sea, the majority of specimens correspond to the broadly cuneate antapical horn types, whereas in the temperate and polar water forms the antapical horns are much more slender. Thus the majority of tropical and warm temperate specimens correspond either to the var. *claudicanoides* (GRAHAM) stat. et comb. n. [basionym: *P. claudicanoides* GRAHAM 1942:24, fig. 29 A–H], with a rapidly tapering hypotheca and broad antapical horns, or the var. *rectius* GRAHAM (= *P. venustum* MATZENAUER), also with broad antapical horns but tapering less gradually below the girdle. One further warm water variant is exemplified by NIE's (1939) figures. In this variant (not given a name here) the broadly cuneate antapical horns are widely set apart, girdle distortion is greatest, and the posterior rim of the fin passing around the antapico-dorsal side of the sulcus is serrated.

All these warm-water varieties have distinctly left-handed girdle displacement and, when seen in full ventral view, the left proximal side of the girdle describes an arc, curving upwards from the sulcus. In temperate and cold-water specimens this feature is much less evident. Indeed, in many figures of such specimens (e.g. LEBOUR 1925; PETERS 1928) no displacement can be seen although this may be partly due to tilting of the specimens.

Additions to the synonymy of the species given by SCHILLER (1935) are *P. saltans* MEUNIER (in view of the observations of PAULSEN 1949 and the earlier opinion of DANGEARD 1927b, who made it a form of *P. depressum*); *P. venustum* KARSTEN, which corresponds to one of GRAHAM's varieties as indicated above (and is much narrower than most members, having a transdiameter of only 50–80 µm instead of up to 173 µm); *P. obliqueforme* SCHILLER, based on an undoubtedly optically-reversed figure of MANGIN's (1928 – some of his figures in this paper were reversed, such as that of *P. obtusipes*); and *P. claudicanoides* GRAHAM as indicated above.

Stations: 44, 45, 90, 103.

Specimens were found in small numbers in samples from the Bay of Bengal, including two near the Ganges River delta. As indicated by GRAHAM (1942) the species seems to be cosmopolitan, being both thermo- and halotolerant. It has been recorded frequently from the Indian Ocean, the records of SILVA (1956a, 1960), PRAKASH & SARMA (1964), ANGOT (1965, 1970), ANGOT & GERARD (1967), DURAIRATNAM (1964), TAYLOR (1967), NEL (1968) and SOURNIA (1968b, 1970) being additional to those listed by WOOD (1963a).

Peridinium murrayi KOFOID Plate 34, Figs. 379, 380; Plate 45, Figs. 522 a, b, 523

MATZENAUER 1933:464, f. 46 a, b; SCHILLER 1935:259, f. 256 a–e; BÖHM 1936:49, f. 18 b 1, 2; MARGALEF 1948b:47, f. 1 n–p; KISSELEV 1950:204, f. 356; WOOD 1954:256 non f. 156; KLEMENT 1964:350, t. 1, f. 4; WOOD 1968:105, f. 312; LÉGER 1973b:19, f. 8, 9.
Syn.: *P. oceanicum* auct. non VANHÖFFEN, GRAHAM 1942, f. 30 A–D, 32 A–C, 33; WOOD 1954, f. 197a.

This large species most closely resembles *P. oceanicum*, being distinguished from it chiefly by its more elongate apical horn which arises more abruptly from the epitheca than in the latter species. The antapical horns can be more divergent than in *P. oceanicum* although the specimens found here corresponded to the less divergent-horned variants observed by PAVILLARD and MATZENAUER. MATZENAUER (1933) attempted to distinguish three varieties: the var. *murrayi* (not named as such by him) in which the antapical horns diverge by 53–57°, his var. *orientalis* in which they diverge by 34–44°, and the var. *occidentalis* PAVILLARD with horn divergence of 31–32°. It is not clear yet if there is any value in distinguishing these varieties. MATZENAUER's variety is so similar to that of PAVILLARD that they should probably be combined under the latter's name referring to the specimens with slight antapical horn divergence. All the specimens in the "Anton Bruun" material were of the latter type.

WOOD (1968) erroneously states that SCHILLER considered this species as synonymous with *P. oceanicum*. However, one must admit some doubts oneself when seeing how similar BÖHM's (1936) specimens, which he referred to as *P. oceanicum* var. *typicum* BROCH (= var. *oceanicum*), are to broad specimens of *P. murrayi*. One might add the additional criterion that in *P. murrayi* the girdle is clearly at the widest point of the cell, whereas in *P. oceanicum* the sides of the epitheca are as wide or wider. GRAHAM (1942) included the slender varieties of *P. murrayi* in *P. oceanicum* but they are kept with *P. murrayi* here.

Stations: 28, 37, 38, 106, 131, 144, 147, 148, 153, 156, 282, 363, 371, 398.

The species was fairly common, being found at three stations in the Andaman Sea, several in the Arabian Sea, several in the central and southern Indian Ocean (reaching 36 °S at station 131), and three at the southern end of the Mozambique Channel. In view of the great number of species of *Peridinium* found in the Bay of Bengal its apparent absence from that region is rather striking. It has only been recorded three times previously from the Indian Ocean (cf. WOOD 1963a).

Peridinium oceanicum VANHÖFFEN Plate 34, Figs. 381, 382

SCHILLER 1935:260, f. 257 a–f, h, j, k (non g, g 1, g 2, i); BÖHM 1936:49, f. 21 a–d (vix e, f); DIWALD 1939:178, f. 11 d, e; SILVA et PINTO 1948: 169, t. 6, f. 17, 18; KISSELEV 1950:204, f. 346; RAMPI 1950b:236, t. 1, f. 5; BALECH 1951b:306, t. 1, f. 1–8, t. 2, f. 9–32; MARGALEF et DURÁN 1953: 31, f. 7 j, k; WOOD 1954:256, f. 157 b (non a); MARGALEF 1957a:47, f. 3e; MARGALEF, MUÑOZ et HERRERA 1957:6, f. 1 d; HALIM 1960a, t. 2, f. 29; BALLANTINE 1961:222, f. 32. 34 (vix 33); MARGALEF 1961a:79, f. 25 h (vix i, j); KLEMENT 1964:350, t. 1, f. 1, 2; TORIUMI 1966a:3, t. 3, f. 8 a, b; YAMAJI 1966:86, t. 41, f. 14; HALIM 1967:742, t. 7, f. 87; WOOD 1968:105, f. 313; AVARIA 1970, t. 3, f. 5; HERMOSILLA 1973b:26, t. 9, f. 1–15.

Non GRAHAM 1942:24, f. 30–36.

Syn.: . . . *P. oceanicum* var. *oblongum* auct. non AURIVILLIUS, YAMAJI 1966:87, t. 42, f. 1 (partim); HALIM 1967:742, t. 7, f. 88.
P. oblongum auct. non CLEVE . . . STEIDINGER et WILLIAMS 1970:57, t. 32, f. 107 a–d.
Peridinium sp. MEYER 1966, f. 4.

This large species is distinguished from *P. murrayi* chiefly by the presence of a shorter, less-abruptly arising apical horn combined with a larger body. The antapical horns are also relatively shorter. As indicated under *P. murrayi* there are specimens which appear to exhibit intermediate features and their allocation becomes arbitrary. More difficult still is the recognition of *P. oblongum* (AURIVILLIUS) CLEVE as a distinct species from *P. oceanicum*. The majority of authors since SCHILLER have tried to maintain the distinction (e.g. BÖHM 1936; RAMPI 1951b; WOOD 1954; MARGALEF 1961a, etc.), a few (BALECH 1951b; YAMAJI 1966; HALIM 1967) putting them together. The principal attempted distinction appears to be that *P. oblongum* lacks any apical horn and the antapical horns are not as slender as in *P. oceanicum* (it thus having a shape more like *P. claudicans* but being much larger). WALL & DALE (1968a) asserted that *P. oblongum* is smaller than *P. oceanicum* but much of their comments are based on the observations of GRAHAM (1942). The latter's treatment of *P. oceanicum* seems very peculiar to this author as none of the many specimens illustrated correspond with the conventional interpretation of *P. oceanicum*, including specimens similar to the slender variants of *P. murrayi* and others which seem much more similar to *P. depressum* than to *P. oceanicum*. Nevertheless other authors also consider *P. oblongum* to be smaller, with a length less than 170 µm.

None of the "Anton Bruun" specimens accorded with the earlier concepts of *P. oblongum* (e.g. LEBOUR's 1925, plate 1, fig. 1 a reproduced by SCHILLER). Clearly, like several other muddled, difficult-to-handle species complexes, this situation has to be further resolved. References to *P. oblongum* have been excluded from the literature citation above.

BÖHM (1936) added a var. *crassum* to the var. *oceanicum* (= var. *typicum* BROCH), distinguished by its broader than long body, shorter apical horn and minimally divergent antapical horns. None as wide as this were found in the material, the widest cells (e.g. fig. 382) with transdiameters greater than 110 µm, also being long.

Stations: 13, 19, 23, 39, 41, 43, 46, 87, 89, 144, 148, 282, 286, 287, 358, 361, 374, 396, 399, 413, 420.

The species was fairly common, but showed a marked distributional preference for land, only station 148 being far from the coast. This accords with GAARDER's (1954) finding that in the North Atlantic the species was very common "along the coastal banks of south-western Europe and north-west Africa", being only scattered elsewhere. BÖHM (1936) found it to be more common in the northern parts of the western Pacific Ocean than in the vicinity of the East Indies.

Thus the species appears to be a thermotolerant temperate to tropical neritic species. It has been frequently found in the Indian Ocean (see list in WOOD 1963a plus the records of SILVA 1956a, 1960; TAYLOR 1967; NEL 1968; SOURNIA 1968b, 1970; and THORRINGTON-SMITH 1969).

Section *Protoperidinium*

[= Sect. *Pellucidum* JÖRGENSEN]

As this section contains the type species of the subgenus: *P. pellucidum* (BERGH) SCHÜTT, the name of the section has been changed to repeat the subgeneric epithet in accordance with Art. 22 of the ICBN.

Members of this section are characterised by a "para-hexa" plate combination. They are lacking antapical horns, although antapical spines are common, and all have right-handed (ascending) girdle displacement. "Ortho" (first apical) and "penta" and "quadra" (second anterior intercalary) plate configurations have been reported aberrantly in some species.

Peridinium diabolus CLEVE Plate 32, Fig. 354; Plate 45, Fig. 525

SCHILLER 1935:204, f. 198 a–h; SILVA et PINTO 1948:167, t. 6, f. 9; KISSELEV 1950:187, f. 319; RAMPI 1950b:233, f. 12; MARGALEF et DURÁN 1953:26, f. 4 p–u; WOOD 1954:243, f. 125; TRÉGOUBOFF et ROSE 1957:110, t. 23, f. 13; HALIM 1960a, t. 3, f. 3; – 1967:739, t. 8, f. 116, 117; NORRIS 1966, f. 2; STEIDINGER, DAVIS et WILLIAMS 1967, t. 8, f. f; WOOD 1968:100, f. 296.

Syn.: *P. formosum* PAVILLARD 1909:279, f. 2 B.

P. longipes KARSTEN . . . . RAMPI 1950b:234, f. 13; SILVA 1956a:65, t. 11, f. 8, 9; – 1958:31, t. 3, f. 3; BALECH 1964a:189, t. 3, f. 48–55; YAMAJI 1966:86, t. 41, f. 13; STEIDINGER et WILLIAMS 1970:57, t. 30, f. 97.

Non BALECH 1959b:28, t. 3, f. 86–95 (= *P. acanthophorum* BALECH 1962a).

This is a large, highly distinctive species recognisable, particularly in tropical waters, by its greatly extended antapical spines. The left sulcal list projects posteriorly beyond the body, forming a "scoop-like" structure, almost tubular, being continuous with the accessory list on the right side of the flagellar pore. The cell transdiameter varies from 35 to 75 µm. A large specimen is illustrated here. The antapical spines occur chiefly in warmer waters, whereas shorter, less divergent-horned specimens are found in temperate waters.

It is debatable whether such variants deserve formal recognition and at which rank. There is some confusion in the systematic history of the species (the synonym above is only one of several listed by SCHILLER, although his listing of *P. longicollum* PAVILLARD seems wrong, the species being a legitimate member of the section *Humili-piriformia*). CLEVE (1900c) based his species on an earlier figure by MURRAY & WHITTING (1889, pl. 29, f. 4 b), providing two rather dissimilar original figures. His fig. 20 is similar to that of MURRAY & WHITTING, with long posterior horns (only slightly divergent). This figure can be taken to represent the var. *diabolus*. CLEVE's other figure (f. 19) showed a much shorter-spined form also with a less drawn-out apex. PAVILLARD (1909) named this as a separate species, *P. formosum*, and it is here proposed that it be recognised at the varietal level: *P. diabolus* var. *formosum* (PAVILLARD) stat. et comb. nov. [Basionym: *P. formosum* PAVILLARD 1909:279, f. 2 B].

P. longipes KARSTEN is similar to the var. *diabolus* but, like most tropical specimens, has a very long, narrow apical horn, a rather angular body, and long, strongly divergent horns. Here this is not considered to be a separate species, but is considered to be an extreme infraspecific variant. It is proposed as *P. diabolus* var. *longipes* (KARSTEN) stat. et comb. nov. [Basionym: *P. longipes* KARSTEN 1907:418, pl. 3, f. 6 a, b].

All the specimens seen here corresponded to the latter variety. In the Mediterranean Sea most specimens resemble the var. *diabolus*. The var. *formosum* is a more temperate form.

Stations: 18, 21, 31, 49, 59, 91, 104, 148, 358, 366, 369, 417–419.

It occurred at scattered stations in the Andaman Sea and Bay of Bengal (usually near the coast), one southern Arabian Sea station, and at several in the Mozambique Channel and to the north of it. It has been recorded from the Indian Ocean by numerous authors (see WOOD 1963a plus SILVA 1956a, SUKHANOVA 1962b, NORRIS 1966, TAYLOR 1967, SOURNIA 1968b, 1970, and NEL 1968). The species is interoceanic, its varieties extending from temperate to tropical waters. It seems to have a fairly strong neritic preference.

Peridinium heteracanthum P. DANGEARD Plate 32, Figs. 352, 353 a, b, 357
– 1927a:6, f. 4 A–D; – 1927b:371, f. 38; MATZENAUER 1933:480, f. 72; SCHILLER 1935:206, f. 199 a, b; SILVA 1960:40, t. 23, f. 7–9.

This spherical-bodied species is recognisable by its asymmetrically developed sulcal lists (the left one extends as a curving projection beyond the right one) and "para-hexa" tabulation. Both features distinguish it from the otherwise similar species *P. sphaericum* OKAMURA. The majority of globose species belong predominantly to the section Humilipiriformia, possessing a "meta-penta" or "meta-quadra" tabulation. Unfortunately the plates are often very difficult to see, leading one to rely on the left sulcal list features for routine identification. DANGEARD (1927a) observed no girdle displacement but MATZENAUER (1933) figured right-handed displacement.

The apical horn is very small and in some cases (e.g. fig. 352) almost invisible. Most cells have a transdiameter of 60–65 µm, but occasionally larger (70 µm) and smaller (45 µm) cells may be seen.

Stations: 21, 85, 87, 103, 105, 108, 144, 149, 294, 363, 398, 420.
It was found at one station in the Andaman Sea, two in the northern-most Bay of Bengal, one near Bombay, several stations to the south and west of India, at a western Indian Ocean station off East Africa, and at the southern end of the Mozambique Channel.
It is undoubtedly a tropical species, described originally from the tropical Atlantic Ocean. MATZENAUER (1933) and SILVA (1960) have found it previously in the Indian Ocean. This author is not aware of any Pacific Ocean records as yet.

Peridinium inclinatum BALECH Plate 32, Fig. 351
– 1964a:187, t. 2, f. 36–40, t. 3, f. 41–47.
Syn.: *P. sphaericum* OKAMURA non MURRAY et WHITTING . . . . SCHILLER 1935:214, f. 210 a–f; KISSELEV 1950:213, f. 375; SILVA 1960:41, t. 23, f. 10; Vix BALLANTINE 1961:222, f. 23, 25 (non 24); Non WOOD 1968:109, f. 328 (= *P. ovum* SCHILLER).
P. sphaeroidea ABÉ 1927:397, f. 17; MATZENAUER 1933:479, f. 71 a–c (incl. var. *gracilis* MATZENAUER); SILVA 1949:352, t. 6, f. 13, 14; non DANGEARD 1927b:372, f. 39 e, f (= *P. nipponicum* ABÉ?)
P. nipponicum auct. non ABÉ; BÖHM 1936:37, f. 13 c.

A medium-sized (transdiameter 54–66 µm), spherical-shaped species, readily recognisable from other species it resembles (such as *P. ovum* SCHILLER) by the "stepped" appearance of its girdle when seen in ventral view, resulting from an angular down-sloping of the right end of the girdle as it approaches the sulcus, and by the well-developed, divergent antapical spines. The latter can be seen to possess fins.

Stations: 31, 95, 398.
A rare species, occurring only at one station each in the Bay of Bengal, Andaman Sea, and the Mozambique Channel. It has been recorded from the Indian Ocean by MATZENAUER (1933 as *P. sphaeroidea*), SILVA (1960), BALLANTINE (1961), TAYLOR (1967), SOURNIA (1968b), and ANGOT (1970), the latter authors referring to it under OKAMURA's name.

Peridinium nipponicum ABÉ Plate 32, Fig. 359
SCHILLER 1935:207, f. 202 a–d (non e, f); KISSELEV 1950:213, f. 369.
Vix STEIDINGER et WILLIAMS 1970:57, t. 32, f. 106.
Non MATZENAUER 1933:480, f. 73 a, b (= *P. ovum* SCHILLER); BÖHM 1936:37, f. 13 c (= *P. inclinatum* BALECH); HADA 1967:18, f. 28 D (= *P. ovum* SCHILLER).
Syn.: *P. sphaeroidea* auct. non ABÉ; DANGEARD 1927b:372, f. 39 e, f.

This medium to small ovoid species can be distinguished from *P. ovum* SCHILLER, which it greatly resembles, by a difference in antapical spine development. According to its discoverer it possesses four antapical spines of different lengths. Interpreting this in the light of more recent knowledge it might be asserted that there are two fairly long antapical spines with fins (somewhat longer than in *P. ovum*), with well developed spiny fins between. These fins projecting down between the large spines give the impression of two additional short spines. One may be a sulcal list projection and the other part of a lateral fin on the left antapical spine (as it appeared to be here), or both may be parts of the sulcal lists. It is necessary to resolve these questions and to decide if it is reasonable to separate *P. nipponicum* from *P. ovum*.

The specimen illustrated here is unusually narrowly oval for the species, others being more similar to *P. ovum* in shape.

Stations: 32, 64.
It occurred at one station in the Andaman Sea (at which *P. ovum* also occurred) and at one station near the east coast of India. It was originally described from Japanese waters. Subsequent records are suspect (MATZENAUER's 1933, Indian Ocean record being rejected). It has only been recorded from the Indian Ocean by WOOD (1962, in 1963a) and TAYLOR 1967).

Peridinium ovum SCHILLER Plate 32, Fig. 350

SCHILLER 1935:208, f. 205 A–h; DIWALD 1939:167, f. 5 a–c, 11 f, g; RAMPI 1950b:234, t. 2, f. 29; WOOD 1954:244, f. 128 a (vix b); – 1968:106, f. 317; STEIDINGER et WILLIAMS 1970:57, t. 33, f. 108; BALECH 1971a:158, t. 34, f. 658–666.

Syn.: *P. sphaericum* auct. non OKAMURA; WOOD 1954, f. 132 a; BALLANTINE 1961, f. 24; YAMAJI 1966, t. 40, f. 10; WOOD 1968:109, f. 328.
P. nipponicum auct. non ABÉ; MATZENAUER 1933:480, f. 73 a, b; HADA 1967:18, f. 28 D.
P. rectum auct. non KOFOID .... SILVA 1949:351, t. 6, f. 5, 6.

This is a medium-sized (length without spines 40–62 μm), ovoid species, most similar to *P. ellipsoides* DANGEARD (1927b = *P. ellipsoideum* DANGEARD 1927a). SCHILLER (1935) considered the two species to be synonymous. As BALECH (1971a) has pointed out, the latter has much shorter antapical spines but in other respects it is very similar.

P. rectum KOFOID and *P. oviforme* DANGEARD are similar in shape but have "meta-penta" tabulation, belonging to the section *Humili-piriformia* (KOFOID originally showed no tabulation for *P. rectum*, the "meta" plate being a later interpretation).

P. nipponicum ABÉ is another "para-hexa" species which is very similar to *P. ovum*. It supposedly differs in the nature of the antapical spines and sulcal lists (see comments here under that taxon).

Stations: 27, 30, 32, 35, 44, 95.

Found only at stations in the Andaman Sea and the Bay of Bengal. The species is a tropical to subtropical interoceanic taxon but has been found previously in the Indian Ocean only by MATZENAUER (1933 – as *P. nipponicum*), BALLANTINE (1961 – as *P. sphaericum*) and TAYLOR (1967).

Peridinium pallidum OSTENFELD Plate 32, Fig. 345

SCHILLER 1935:209, f. 206 a–m; DIWALD 1939:168, f. 17 a–d; WAILES 1939:40, f. 122; GRAHAM 1942:32, f. 42 A–H, 43 A–D; SILVA 1949:351, t. 6, f. 7, 8; KISSELEV 1950:188, f. 314; RAMPI 1950b:234, f. 18; WOOD 1954:244, f. 129 b (vix a); SILVA 1955:141, t. 4, f. 16–18; HALIM 1960a, t. 3, f. 2; BRUNEL 1962:199, t. 64, f. 4; WOOD 1968:106, vix f. 318; MARGALEF 1969a, f. 3 F; STEIDINGER et WILLIAMS 1970:57, t. 33, f. 109.

This species has a pyriform body with "para-hexa" tabulation. It is very similar to *P. pellucidum* (BERGH) SCHÜTT, the only distinctions being that *P. pallidum* is usually flattened dorso-ventrally, the width being approximately two-thirds the transdiameter, whereas *P. pellucidum* is circular in cross-section. Although the size ranges overlap, *P. pallidum* is larger (length without spines 53–107 μm, as opposed to 40–68 μm for *P. pellucidum*). GRAHAM (1942) doubted that such a distinction could be made. He also provided a detailed plate analysis of the species. *P. pallidum* contains numerous chloroplasts, whereas *P. pellucidum* lacks them.

The specimens observed here all exhibited flattening to a greater or lesser extent.

P. schilleri PAULSEN was united with *P. pallidum* (as a variety) by SCHILLER (1935). It is here considered as a separate taxon due to its rotund shape, lacking dorso-ventral flattening, combined with a strongly developed, ventrally projecting accessory lobe of the left sulcal list (see further comments under that taxon.

Stations: 19, 46, 62–66, 87, 99, 100, 102, 133, 134.

It occurred at stations in the Andaman Sea, Bay of Bengal, and at two southern Indian Ocean stations near 30 °S. The species is known from cold-temperate to tropical waters in all oceans. LEBOUR (1925) considered it to be more oceanic in distribution than *P. pellucidum*. Records are rare from the Indian Ocean (see WOOD 1963a plus NEL 1968).

Peridinium schilleri PAULSEN Plate 32, Fig. 340; Plate 46, Figs. 527 a, b

– 1930:56, f. 27.

Non *P. schilleri* BÖHM 1931a:193, f. 9 (= *P. margalefii* SILVA).

Syn.: *P. pallidum* OSTENFELD var. *schilleri* (PAULSEN) SCHILLER 1935:211, f. 207 A–C; RAMPI 1950b:234, f. 19; MARGALEF et DURÁN 1953:27, f. 4 n, o (subsp.); vix STEIDINGER et WILLIAMS 1970:57, t. 33, f. 110.
P. tristylum auct. non STEIN .... BALECH 1951b:325, t. 7, f. 115–137; SILVA 1955:141, t. 5, f. 1, 2.

As indicated under *P. pallidum* this species is here considered distinct from the latter because of its rounded body, lacking dorso-ventral flattening (see fig. 527 b) and because of the presence of a much larger, ventrally-projecting, posterior left sulcal list. The areolation observed on the specimens here was relatively coarse. In her material GAARDER (1954) observed one instance of a "meta-hexa" combination.

P. schilleri BÖHM is a completely different species and the name is preoccupied by that of PAULSEN.

Stations: 55, 64, 103, 153, 161.

Found only at a few stations in the northern Bay of Bengal and at one station near Mauritius. The taxon has not been recorded previously from the Indian Ocean (either as a species or as a variety). It is known from the North and South Atlantic Ocean (where GAARDER 1954 found it to have quite a similar distribution to *P. pallidum* in her "Michael Sars" material) and the Mediterranean Sea.

Peridinium tenuissimum KOFOID Plate 32, Fig. 355

MATZENAUER 1933:477, f. 68; SCHILLER 1935:215, f. 211 a–c; WOOD 1954:246, f. 133; – 1968:109, f. 331.

Syn.: ? *P. acanthophorum* BALECH 1962a:34, t. 3, f. 78–83.

P. longipes auct. non KARSTEN; BALECH 1959c:28, t. 3, f. 86–95.

This species resembles a much smaller version of *P. diabulus* CLEVE, but it is not only smaller (length without spines 45–60 μm, transdiameter 25–34 μm) but also has a rounder body, lacking the concave posterior profile of *P. diabolus.* The construction of its spines and its sulcal fins appears to be very similar to the latter.

This author finds *P. acanthophorum* BALECH difficult to separate from *P. tenuissimum.* BALECH did not compare the taxa when he created his species. The main difference in his description is that his specimens were broader than those described here and in earlier works, having a transdiameter of 40–50 μm, thus overlapping in this dimension with *P. diabolus.* This will require further examination in order to clarify the situation.

Stations: 71, 88, 95.

Specimens were found only at three Bay of Bengal stations. However several other authors have recorded the species from the Indian Ocean (see WOOD 1963a plus SOURNIA 1966a, TAYLOR 1967, and NEL 1968). It is a rare, tropical, inter-oceanic species.

Peridinium tristylum STEIN Plate 32, Figs. 348 a, b

SCHILLER 1935:216, f. 212 a–d; WOOD 1968:110, vix f. 332. Non BALECH 1951b:325, t. 7, f. 115–137; SILVA 1955:141, t. 5, f. 1–3; HERMOSILLA 1973b:47, t. 23, f. 10–16.

This is a rare species, evidently closely related to *P. schilleri* PAULSEN with which it was confused by BALECH (1951b, as indicated also by MARGALEF & DURÁN 1953) and SILVA (1955). The original figures of STEIN (1883, pl. 9, f. 15–17) are peculiar in that the cells are shown to be very elongated. A "para-quadra" combination was shown. No one else seems to have seen precisely the same shape and this might perhaps be due to distortion in the original figures. Instead, the few figures which can be affirmed as the same taxon found here all correspond to the var. *ovata* SCHRÖDER, the latter not being nearly as elongate as the original specimens.

It has been possible to examine both *P. schilleri* and *P. tristylum* with the scanning electron microscope (cf. pl. 46, fig. 527 a, b for the former) although cost has prohibited publishing all these figures. *P. tristylum,* in addition to having three much longer posterior spines (the centre one of which is in fact a profile of a greatly extended "scoop-shaped" right sulcal list, the left sulcal list also being posteriorly extended but not as thick in profile), has a different body shape. In *P. schilleri* the epitheca has relatively straight sides with almost no apical horn region whereas the specimens observed here had an apex drawn out into a short apical horn which blends smoothly with the epitheca. More distinctively the hypotheca of *P. schilleri* is much fuller and hemispherical, whereas it narrows rapidly (although still convex), after the girdle in *P. tristylum.* The markings on the surface are more strongly developed in *P. schilleri* than in *P. tristylum.* Both are reticulated and both seem to be "para-hexa" most commonly, and are thus also similar to *P. pallidum* (see discussion under that species here). *P. okamurai* ABÉ is also similar, having a shape resembling STEIN's figures, but it apparently lacks posterior extensions of the sulcal lists.

Stations: 103, 155, 286, 324, 420.

A few cells were found at each of several stations scattered over the Bay of Bengal, Arabian Sea, the central Indian Ocean and close to Mombassa in East Africa.

Earlier records are in doubt because of possible confusion with *P. schilleri.* However it does seem to have been found in the Mediterranean Sea and in the tropical Atlantic Ocean. WOOD (1963a) has listed the few Indian Ocean records ostensibly of this species to which those of TAYLOR (1967) and SILVA (1960) should be added.

Section *Tabulata* JÖRGENSEN

Members of this section all lack antapical spines of any appreciable size and do not have antapical horns, the majority being globose in shape. They have an "ortho" first apical plate, and have three anterior intercalary plates, the latter feature distinguishing them from some similar members of the subgenus *Archaeperidinium*, with only two anterior intercalary plates. The second anterior intercalary plate can be "quadra," "penta" or "hexa." Girdle displacement, if present, is left-handed. The genus *Scrippsiella* resembles members of this section, and some members of the section Conica could almost be assigned here (e.g. *P. achromaticum*) if the antapical lists and spines were a bit more reduced, this indicating the strong arbitrariness still inherent in the system.

Peridinium trochoideum (STEIN) LEMMERMANN Plate 33, Figs. 374 a–d
SCHILLER 1935:137, f. 134 c–e (vix a, b, non f, g); WAILES 1939:34, vix. f. 102; KISSELEV 1950:157, f. 244; SILVA 1952a:36, t. 3, f. 4–6; BIECHELER 1952:71, f. 4 A, B, 41/1–3 (vix f. 4); MARGALEF et DURÁN 1953:26, f. 4, a; YAMAJI 1966:83, t. 40, f. 2; WOOD 1968: 110, f. 333; STEIDINGER et WILLIAMS 1970:58, t. 34, f. 117 a, b; HERMOSILLA 1973b:41, t. 19, f. 13–18.
Syn.: . . . *P. faeroense* PAULSEN 1905:5, f. 5; – 1908:64, f. 85; LEBOUR 1925:113, t. 19, f. 2 a–d.
Scrippsiella faeroense (PAULSEN) BALECH et SOARES 1966:106, f. 11–20.

This is a small, ovoid species (length 15–42 μm). FINE & LOEBLICH (1974) had difficulty in distinguishing a culture attributed to this species from one supposedly representing *Scrippsiella sweenyae*. Although fairly similar in shape *P. trochoideum* does not appear to have the straight epithecal sides of *S. sweenyae* and should differ in cingular plates. DICKENSHEETS & COX (1971) could not distinguish between cultures of *P. trochoideum* and *P. faeroense* (= *S. faeroense*), despite detailed examination, leading to the conclusion that earlier authors (e.g. SCHILLER 1935) were correct in considering them synonymous, and this strongly indicates that *Scrippsiella* is probably the most appropriate location for *P. trochoideum*. Although plate dissections are difficult among these small species it is usually possible to determine if there are more than three girdle plates by examining the dorsal side of the thecae. If girdle-plate sutures are visible on the dorsal side the cells are almost certainly not members of the subgenera *Archaeperidinium* or *Protoperidinium* (see, e.g., fig. 377 b in comparison with 374 b). Thus in *P. trochoideum*, in addition to moderate convexity of the epithecal sides, no girdle sutures are usually visible on the dorsal surface. [For other differences between *S. sweenyae* and *P. trochoideum* see BALECH 1959a.] *P. nudum* MEUNIER is more rounded than *P. trochoideum* but is otherwise very similar to it.

The specimen illustrated here is somewhat different from the usual appearance of the species in that the first apical plate is narrower, the precingular sutures being set quite high.

Station: 20.

A few cells were found near the coast in the eastern Andaman Sea. The species is often found in reduced salinity regions and is very rare away from the coast, HULBURT's (1965) Gulf Stream record being anomalous. It appears to be thermotolerant. It has only been recorded from the Indian Ocean by SUBRAHMANYAN (1958), SUBRAHMANYAN & SARMA (1967, both references as *Glenodinium*) and SILVA (1956a, 1960).

Subgen. *Minusculum* (LEBOUR) BALECH

LEBOUR (1925, p. 137) created a new genus for a species (below) differing from other members of *Peridinium* in the possession of one less precingular plate (six instead of seven). In other respects it resembles the marine species of *Peridinium* (its cingular and sulcal plates have not been examined in detail as yet). *P. adulterum* BALECH (1971a, p. 125) also belongs to this subgenus sharing not only the same number of precingular plates, but also the unusually large size of the sixth precingular plate and also the curvature of the first apical plate. *P. defectum* BALECH is another member, possibly conspecific with *P. minusculum* (see below).

Peridinium minusculum PAVILLARD Plate 32, Fig. 358
SCHILLER 1935:194, f. 190 B a–e; KISSELEV 1950:183, f. 302; MARGALEF et DURÁN 1953:27, f. 5 o.
Syn.: *Glenodinium bipes* PAULSEN 1904:21, f. 3, 4.
Minuscula bipes LEBOUR 1925:138, t. 29, f. 3; WAILES 1939:41, f. 124.
? *Peridinium defectum* BALECH in BALECH et EL-SAYED 1965:118, t. 3, f. 42–50.

This very small species has a very distinctive shape and tabulation. The first apical plate is set towards the left side and is strongly curved. The sixth precingular plate is very large. As indicated above there is no seventh precingular plate. Three anterior intercalary plates are present according to PAVILLARD (1917), who carried out the first detailed plate analysis (SCHILLER did not use his excellent figures), and LEBOUR (1925).

P. defectum is very similar in shape and is also small. It has the unusual first apical plate, the large sixth precingular plate, and lacks a seventh precingular plate. It differs in that it appears to have only two anterior intercalary plates. Also, although, like PAVILLARD, BALECH reported the presence of five postcingular plates, he included in this a plate which PAVILLARD assigned to the ventral area. *P. minusculum* has a length (excluding spines) of 20–35 μm, that of *P. defectum* being given as 30–42 μm.

P. adulterum is also small, but has a very rotund shape.

Stations: 48, 374.

Being very small such cells might not be expected to be retained by the nets used here. Nevertheless several cells were found at a station in the Bay of Bengal close to the Burmese coast, and in the south-west Indian Ocean off the coast of Southern Africa. The species is evidently thermotolerant, occurring in both cold temperate and tropical waters. *P. defectum* BALECH is an Antarctic taxon, found first in the Weddell Sea. *P. minusculum* has been found in the Indian Ocean only by TRAVERS & TRAVERS (1965), TAYLOR (1967) and SOURNIA (1968b), these records antedating WOOD's (1963a) checklist.

Scrippsiella BALECH ex LOEBLICH III

In the introductory comments on the genus given here it was explained that in order to avoid the creation of more than two hundred new combinations for the majority of the marine species of *Peridinium* (transferring them to *Protoperidinium* BERGH) one must recognise this genus not only by the number of girdle plates (five plus "transitional" plate) but also the nature of the cyst (calcitic).

LOEBLICH III (1965) provided Latin diagnoses for the genus and its type species, stating that BALECH used botanical classification and that both were invalid without Latin. Examination of BALECH's paper reveals that the foundation for LOEBLICH's conclusion (unusual in the light of BALECH's habitual use of the zoological conventions) is BALECH's statement: "The general characteristics of this organism place it in the Peridiniaceae" (his italics, p. 199). This use of a botanical family name requires that LOEBLICH III's validation be recognised in formal usage.

WALL & DALE (1968b) and WALL (1971a) have indicated that the cysts of the type species (*S. sweenyae*) have an outer calcareous wall with a "microgranular" texture. The archeopyle is apical.

At the time of writting only three species have been assigned to this subgenus: *S. sweenyae* BALECH, *S. saladense* BALECH and *S. faroense* (PAULSEN) BALECH, the latter being probably synonymous with *Peridinium trochoideum* (DICKENSHEETS & COX 1971) and the latter probably should be placed here.* The existence of girdle sutures visible on the dorsal side of the theca of *P. bangoei* SCHILLER in positions corresponding with those of members of this subgenus, suggests that it has more than three cingular plates and may also belong here. This also applies to the unidentified species below.

Scrippsiella? sp. Plate 33, Figs. 377 a, b

This very small taxon resembled *S. sweenyae* but was much smaller (length 15–16 μm, transdiameter 12 μm) than the figures for the latter given by BALECH (1959a: length 24–32.5 μm, transdiameter 19–24 μm). Also the epitheca was more convex, being shaped more like *P. trochoideum.* The apical horn was small, and there appeared to be a small apiculus at the antapical end. The girdle was slightly left-handed. The tabulation was "ortho-hexa", three anterior intercalary plates being present.

As it may simply be a variant of *S. sweenyae,* and as only two specimens were seen, a new species has not been created.

Stations: 298, 342.

The illustrated specimens were found at a station north of Mauritius and at one further east.

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* Subsequent to forwarding this to the publisher STEIDINGER & BALECH (Phycologia, in press) have transferred *P. trochoideum* to *Scrippsiella,* and have also added *P. subsalsum* OSTENFELD to this genus as a result of the analysis of detailed plate analyses. This in turn raises the possibility that *P. sociale* (HENNEGUY ex LABBÉ) BIECHELER and *P. gregarium* LOMBARD & CAPON, both of which closely resemble *S. subsalsa,* may also be eventually shown to be closer to *Scrippsiella* than *Peridinium.*

Genus *Zygabikodinium* LOEBLICH et LOEBLICH III

Syn.: *Diplopeltopsis* PAVILLARD

As PAVILLARD's generic name is pre-occupied by that of a lichen it has been renamed by LOEBLICH & LOEBLICH (1970a). Although theoretically zoologists can continue to use PAVILLARD's name it has been stressed at several places in this text that this type of confusion can most readily be avoided if dinoflagellate specialists do not accept homonymy in either the plant or animal kingdoms.

LOEBLICH and LOEBLICH III (1970a) have designated *Z. lenticulatum* (MANGIN) LOEBL. et LOEBL. III as the type.

Zygabikodinium lenticulatum (MANGIN) LOEBLICH et LOEBLICH III Plate 28, Figs. 295, 297, 300
– 1970a:541.
Syn.:. . . . *Peridinium lenticulatum* MANGIN 1911:30, f. iii, iv.
Diplopsalis lenticula forma *minor* PAULSEN 1907:9, f. 9 . . . . WOOD 1954:222, f. 87 a, b; STEIDINGER et WILLIAMS 1970:49, t. 18, f. 53.
Diplopeltopsis minor (PAULSEN) PAVILLARD 1913:7; LEBOUR 1922:801, f. 11–15; – 1925:102, t. 15, f. 2 a–e; WAILES 1928, t. 3, f. 17–19, t. 11, f. 11; – 1939:29, f. 84 A–C, 85 B; BALECH 1959b:20, t. 1, f. 10; WALL et DALE 1968a:280, f. 7, t. 4, f. 21, 22; WALL 1971a, t. 2, f. 19, 20; vix CANDEIAS 1938:242, f. 4; HADA 1970:17, f. 15.
Glenodinium lenticulum forma *minor* (PAULSEN) SCHILLER 1935:105, f. 96 a–e; KISSELEV 1950:136, f. 218.
Diplopsalis minor (PAULSEN) SILVA 1955:132, t. 4, f. 1–4; WOOD 1968:54, f. 133.
? *Diplopeltopsis minor* var. *occidentalis* WAILES 1928:7, t. 11, f. 12; – 1939:29, f. 85 A.
Non MARGALEF et MORALES 1960:5, f. 2 d (opt. rev.?).

Although the taxon has been best known under the name *Diplopeltopsis minor*, LOEBLICH & LOEBLICH III (1970a) have correctly indicated that not only the generic name must be changed but also the specific epithet, because that of MANGIN (1911) has priority at that level. SCHILLER (1935) recognised the synonymy but did not give correct priority. The only unfortunate aspect of these changes is the increased possibility of nomenclatural confusion with *Diplopsalis lenticula* BERGH.

This species has a transdiameter ranging from 28–66 µm, the largest specimens being in warmer waters. In colder waters the size is usually between 40 and 55 µm. Its epithecal tablature is rather similar to *Peridiniopsis asymmetrica*, having the same arrangement of one large and one small anterior intercalary plate. However, it can be readily recognised by its seven precingular plates (instead of six), combined with a single antapical plate. The left sulcal list is well developed, being keel-like in shape. The cells are usually lenticular.

BALECH has recognised two other species whose thecal surfaces are more strongly marked with granulations or small bumps. WAILES (1928) has recognised a var. *occidentalis* which has only one anterior intercalary plate, large, and symmetrically positioned.

WALL & DALE (1968a) have found that the resting spores of this species are small, oblate, and split open along the upper margin of the girdle.

Stations: 44, 102.

The species was found only at two stations, both in the Bay of Bengal. These warm-water records are atypical in view of previous distributional data.

In comparison with *Diplopsalis lenticula* and *Peridiniopsis asymmetrica*, this species has a strong preference for colder waters, both in the northern and southern hemispheres. BALECH (1957) reported it from the Antarctic, from near Argentina and off Adélie Land. WOOD (1954 and in 1963a) has also found it in the Antarctic and in the Indian Ocean off the west coast of Australia. The other Indian Ocean records listed by him do not refer to this taxon.

Family Podolampadaceae LINDEMANN [= Podolampaceae]

The outstanding feature of members of this peridinoid family is their lack of a girdle. Nevertheless authors detailing the plates of members of this group recognise both pre- and postcingular series of plates (in the broad sense) based on apparent homologies. BALECH (1963a) has discussed the apparent relationships of this family to others close to it.

Genus *Blepharocysta* EHRENBERG

Syn.: *Lissodinium* MATZENAUER

This genus has been subjected to detailed examination by NIE (1939), GAARDER (1954), BALECH (1963a) and ABÉ (1966).

Blepharocysta okamurai ABÉ Plate 28, Fig. 289
– 1966:144, f. 33–38.
Syn.: *B. splendor-maris* auct. non EHRENBERG: – SCHÜTT 1895 pro parte: t. 20, f. 61/15; OKAMURA 1907:127, t. 5, f. 34 a–d; LINDEMANN 1928:101, f. 88 a, b; RAMPI 1943:148, f. 8, 9; BALECH 1963a pro parte: 16, f. 34, 35, 38–44.

ABÉ separated this species from *B. splendor-maris* EHRENBERG, the type species, by the former's smaller, more oval shape, the approximately median position of the suture between the precingular and postcingular plates and the consequent relative narrowness of the latter in relation to the former. Further, he considered the central member of the posterior-most plates (termed "hypothecals" by him in addition to two antapical plates, other authors terming them all antapicals) to be smallest in *B. okamurai* and *B. paulseni* SCHILLER. The latter species is very similar to *B. okamurai* but may be distinguished from it by its lack of an anterior intercalary plate (unless this was omitted by SCHILLER) and more anterior position of the suture between the precingular and postcingular plates.

Unfortunately under routine analytical conditions these distinctions are sometimes difficult to make, rendering distributional data less valuable and it is possible that some of the specimens included here were of *B. splendor-maris.*

Stations: 58, 66–70, 85, 100, 105, 113, 143.
Rare, occurring at a few central Bay of Bengal stations and at two stations south of India during cruise II (May, July, 1963). This species has not been recorded from the Indian Ocean previously.

Genus *Podolampas* STEIN

Previous authors have generally neglected mention of the synonymy of this genus with *Parrocelia* GOURRET. As both were described in the same year, 1883, it becomes a matter of detailed publication date to determine priority of these and also another major contribution which appeared in 1883, that of POUCHET. From private communications of C.A. KOFOID in the author's possession the month of STEIN's publication can be determined as November, but it has not as yet been possible to determine that of GOURRET's publication. As it was the last part of the journal issued for the year it is likely that it was issued late in the year. Furthermore, GOURRET referred it to the appearance of POUCHET's (1883) article which seems to have been the first of the three to appear. This matter should be resolved, if possible, as it involves the priority of several of GOURRET's taxa. The practice has been to assign priority to POUCHET and then to STEIN.

Relatively recently this genus has been examined in detail by BALECH (1963a) and ABÉ (1966). Both of these authors apparently missed the earlier study by NIE (1942).

Podolampas antarctica BALECH Plate 27, Fig. 283
in BALECH et EL-SAYED 1965:121, t. 4, f. 56–64.

This species is very similar to *P. spinifera* as is evident from a comparison of the figures on plate 27. It has a similar body shape and is the only other species which possesses a small apical spine. It is distinguishable most readily by the presence of three antapical spines rather than one as in *P. spinifera.* The supernumery spines occur on the outer edge of the right antapical list and in the centre between the central list moieties of the left and right antapical spines. The right antapical spine of the illustrated specimen was less developed than that of the type. Also list areolation was less strongly developed. It may later prove necessary to unite the two taxa although their distributions (see below) also indicate a separation.

Station: 306.
In view of the original description of this species from the Weddell Sea, its occurrence at one of the most southerly stations in the material suggests that it may prove a useful indicator species, provided it is not confused with *P. spinifera.* It has not been recorded previously from the Indian Ocean.

Podolampas bipes STEIN Plate 27, Figs. 287, 288; Plate 45, Fig. 524

SCHILLER 1936:474, f. 544 a, b; RAMPI 1941b:146, f. 2, 5; NIE 1942:56, t. 1, f. 1–14; SILVA 1949:363, t. 6, f. 17; MASSUTI et MARGALEF 1950, f. 75; KISSELEV 1950:260, f. 434; TRÉGOUBOFF et ROSE 1957:119, t. 27, f. 16; HALIM 1960a, t. 3, f. 32; BALLANTINE 1961:225, f. 63; BALECH 1963a:9, t. 1, f. 8–14; ABÉ 1966:150, f. 55–68; YAMAJI 1966:107, t. 51, f. 19; STEIDINGER, DAVIS et WILLIAMS 1967, t. 4, f. a; STEIDINGER et WILLIAMS 1970:60, t. 36, f. 125.

Syn.:*Parrocelia ovalis* GOURRET 1883:81, t. 3, f. 48, 48a.

Podolampas reticulata KOFOID 1907b:187, t. 2, f. 11; BALECH 1963a:11, t. 2, f. 15–19; STEIDINGER et WILLIAMS 1970:60, t. 36, f. 126 a, b.

Podolampas bipes forma *reticulata* (KOFOID) SCHILLER 1936:474, f. 545; WOOD 1954:317, f. 251b.

Generally this species exists in two highly distinctive states arising chiefly from differences in the structure of the antapical spines and their associated fins. Some authors have considered them separate species but here, in view of ABÉ's (1966) claim of discovering intermediates, they are included together. They could be considered as formae as SCHILLER has done, but, as formae are here restricted to phenotypic responses to specific local environmental conditions (see the general section) they have been termed varieties.

P. bipes var. *bipes* is recognised by relatively strong antapical spines with accessory lists which have smooth margins. Reticulation is usually absent on the lists or is very faint and restricted to a small distal portion of the lists. The large precingular plates have a basic reticulation on them which is only faintly developed.

P. bipes var. *reticulata* (KOFOID) stat. nov. (basionym = *P. reticulata* KOFOID) is very similar to the var. *bipes* in thecal features although the ground reticulation is more strongly developed on the precingular plates. The antapical spines are usually shorter than the var. *bipes* and the margins of the lists associated with them are irregularly serrated. The lists are usually reticulated over most of their distal portions.

The species is distinctive in its large size, with much broader dimensions than any other species. The precingular plates, in particular, are large and covered with pores sloped to the surface so that they present an echinulate appearance.

Stations: *P. bipes* var. *bipes*: 13, 17, 19, 29, 35, 38, 42, 49, 51, 52, 54, 58, 59, 62, 63, 68, 69, 71, 92, 95, 99–103, 109, 116, 142, 148, 153, 157, 420.
P. bipes var. *reticulata*: 35, 37, 43, 51, 52, 68, 71, 418.

The var. *bipes* was the commonest representative of *Podolampas* in the material. It occurred sporadically at widespread stations north of 33 °S but was absent from the cruise V samples (Jan.–April). The var. *reticulata* was relatively rare, five of its eight recorded stations being the same as those from which the var. *bipes* was recorded, arguing against the taxa being environmentally induced variants. With the exception of station 418 near Mombassa the var. *reticulata* was found only in the Bay of Bengal and Andaman Sea.

The Indian Ocean records provided by WOOD (1963a) require augmentation by those of ZERNOVA (1962), TAYLOR (1967), SOURNIA (1967a, 1968b, 1970), NEL (1968), and ANGOT (1970).

Podolampas elegans SCHÜTT Plate 27, Figs. 280, 281

SCHILLER 1936:475, f. 546; RAMPI 1941b:146, f. 1, 4; KISSELEV 1950, f. 435*б* (sub. *P. palmipes*); GAARDER 1954:55, f. 73 a–e; SILVA 1958:33, t. 3, f. 10; TRÉGOUBOFF et ROSE 1957:119, t. 27, f. 17; CURL 1959:306, f. 125; WOOD 1963b:50, f. 186; BALECH 1963a:6, t. 1, f. 1–7; ABÉ 1966:149, f. 52–54; STEIDINGER et WILLIAMS 1970:60, t. 36, f. 127.

A medium-sized, relatively broad species recognisable form *P. palmipes* by its two equally developed, long antapical spines, widely spaced apart. The inner flanges of the antapical lists are relatively narrow, that associated with the left antapical spine possessing a distinctive lobe situated below the flagellar pore. Both the narrowness of the antapical lists and the shape of the lobe distinguish this species from the specimen in fig. 282 whose identity is unknown.

Stations: 54, 55, 62, 66, 71, 97.

Recorded from a few stations in the central Bay of Bengal during Cruise I. This restricted distribution was unusual as the species has been recorded by several authors not only from the northern Indian Ocean (see WOOD 1963a) but also from the Mozambique Channel region (SOURNIA 1967a, 1968b, 1970) and further south off South Africa by TAYLOR (1967).

In the "Michael Sars" N. Atlantic material GAARDER (1954) found *P. elegans* to be the most common representative of the genus.

Podolampas palmipes STEIN Plate 27, Figs. 278, 279 (286?)

SCHILLER 1936:475, f. 547 a, b; RAMPI 1941b:147, f. 3, 6; MARGALEF 1948b:50, f. 3d; KISSELEV 1950:262, f. 435 *а* (non *б*); SILVA 1952a:40, t. 3, f. 17; GAARDER 1954:57, f. 74 a, b; WOOD 1954:317, f. 252 a, b (253?); TRÉGOUBOFF et ROSE 1957:119, t. 27, f. 19;

VIVES et LOPEZ-BENITO 1957:52, f. 1 n; BALECH 1963a:12, t. 2, f. 20–27; ABÉ 1966:147, f. 45–51; YAMAJI 1966:18, t. 51, f. 18; STEIDINGER et WILLIAMS 1970:60, t. 36, f. 128 a, b.
Vix NIE 1942:57, f. 15, 16.

This medium-sized species is relatively more slender than *P. bipes* and *P. elegans* but more broadly pear-shaped than *P. spinifera*. Because of flattening in these species care must be taken that the cells are seen in full ventral view when making such a discrimination. There are two antapical spines with associated lists, the left spine being markedly longer and more strongly developed than the right spine. Allowance for redevelopment of the spines after fission must be made as this can markedly alter their relative lengths. The specimen in fig. 279 was apparently in a monospinous condition immediately following fission. NIE (1942) is the only author to show both antapical spines as approximately equal in length and for this reason his identification is questioned above. His illustrated specimen was similar to that in fig. 282 here. The figures of WOOD (1954) are optically reversed.

The specimen in fig. 286 has a distinctly disjunct apical horn rather than the smoothly formed epithecal curve of *P. palmipes*. The suggestion of a girdle-like structure, apparently internal, is interesting in view of the assumption that such a region corresponds to an absent girdle, the thecal plates being termed precingulars and postcingulars in all species of *Podolampas* even though a girdle has not been seen in any species. The size and inequality of the antapical spines suggest an affinity with *P. palmipes* but the identification is tentative.

Stations: 28, 30, 35, 59, 62, 64, 71, 102, 103, 105, 327, 405, 412. (Fig. 286; 321).

Like other species of the genus this species occurred at sporadic stations in the central Bay of Bengal. However the other Indian Ocean stations off southern India and in the Mozambique Channel correllate with GAARDER's (1954) observation that the species is more common near land. It has been recorded frequently from the Indian Ocean (WOOD 1963a plus ZERNOVA 1962; SOURNIA 1966a, 1967a, 1968b, 1970; TAYLOR 1967; NEL 1968; and ANGOT 1970).

Podolampas spinifera OKAMURA Plate 27, Figs. 284, 285.

SCHILLER 1936:476, f. 548; RAMPI 1939b:468, f. 17; – 1941b:148, f. 10; MARGALEF 1948b:50, f. 3e; TRÉGOUBOFF et ROSE 1957:119, t. 27, f. 18; WOOD 1963b:50, vix. f. 187; BALECH 1963a:14, t. 2, f. 28–33; ABÉ 1966:145, f. 39–44; YAMAJI 1966:107, t. 51, f. 17; STEIDINGER, DAVIS et WILLIAMS 1967, t. 4, f. b; STEIDINGER et WILLIAMS 1970:60, t. 36, f. 129. (*P. spinifer* auct. nonnull.).

A slender species recognisable from all other members of *Podolampas* by the possession of a single posterior spine and also a small, curved apical spine (otherwise known only from *P. antarctica* BALECH). The posterior fin associated with the spine is apparently tripartite and curved in a scoop-like shape. Its edges may be thickened so that they may appear as secondary, marginal spines. WOOD (1963b) has referred to intergrade forms between this species and *P. palmipes* although he did not provide details. The specimen figured by him lacked an apical spine.

Stations: 32, 33, 54, 58, 94, 98, 99, 104, 116, 326.

This species has a similar general distribution to *P. bipes* (and for that matter, most other species of *Podolampas* which are inter-oceanic, warm-water forms) in that it occurred most commonly at central Bay of Bengal stations and a few stations to the south of India. Although rarely recorded from the Indian Ocean prior to WOOD (1963a), it has subsequently been identified by SOURNIA (1966a, 1967a, 1968b, 1970) from the Madagascar region and TAYLOR (1967) from the South West Indian Ocean.

Podolampas sp. Plate 27, Fig. 282

Vix NIE 1942, f. 15, 16 (sub *P. palmipes* STEIN)

This specimen, as indicated under *P. elegans*, resembles the latter in the characteristics of antapical spines but not in the details of the lists associated with them. Between the two spines the lists are broadly developed and the lobe of that associated with the left antapical spine has a straight margin adjacent to its neighbouring list. The narrow appearance of the cell is a result of its rotation towards the right side. The specimen of NIE referred to above resembled this specimen in antapical list development but NIE's figure was apparently a mid-ventral view.

Station: 51a.

A single specimen was observed at a station near the coast of Burma.

Family Ptychodiscaceae LEMMERMANN

Although LINDEMANN (1928) recognised only the genus *Ptychodiscus* within this family, his grounds for recognising other similarly constructed dinoflagellates in another separate family, the Kolkwitziellaceae (ovoid in shape rather than apico-antapically flattened) seem to be superficial, particularly in view of the considerable shape plasticity known to occur in *Ptychodiscus* (see BOALCH 1969 and below). LOEBLICH III (1970) has transferred one of the group of general involved, *Lophodinium,* to a new family for species bearing multiple cryptic, delicate plates, partly on the assumption that the ridged, non-plated type specimen was a cyst.

Here at least three genera are considered to belong within this familial group, all possessing a flexible, tough outer region not apparently subdivided into plates although it may or may not bear reticular markings and ridges. It is not clear if this structure is the homologue of a theca, of a cyst wall, or of an entirely different structure (perhaps like the "pellicle" referred to by LOEBLICH III 1970). Here it is conceived of as a type of strengthened deposition within the outer layer of the amphiesma. The flagella exit through a single large aperture, this latter feature serving to distinguish members of this family from those of the Gymnodiniales in which the outer regions also are semi-rigid (e.g. *Balechina* – see section on the outer layers of dinoflagellates in the introduction). GAARDER (1954) found that the wall of *Ptychodiscus* could be entirely dissolved by sodium hypochlorite, and this is probably also the case with *Berghiella* although it was not tried. The genera represented in the material are *Berghiella* and *Ptychodiscus. Kolkwitziella* LINDEMANN is also probably a member of this family. *Lophodinium* LINDEMANN is possibly also a member, although the genus is poorly defined.

Genus *Berghiella* KOFOID et MICHENER

To this author's knowledge no one has either observed the type species or assigned any other species to this genus since it was first described by KOFOID & MICHENER (1911). Undoubtedly this lack of records results not only from the rarity but also from the lack of illustrations in the original publication. Elsewhere in the present work (e.g. *Gonyaulax*) taxa from the same work have been recognised as the result of close resemblance between the descriptions of KOFOID & MICHENER and members of the "Anton Bruun" material. The recognition of *Berghiella* here is a similar case.

Because the genus is obscure and the diagnosis is brief and highly relevant it is quoted in full here: "With the form of a spheroidal *Gonyaulax* with very abruptly differentiated low cylindrical apical horn with truncate apex. Girdle with hyaline lists, descending, displaced less than a girdle width, not impressed. Ventral area not delimited posteriorly. Absolutely no trace of subdivision of theca into plates or regions. Type species *B. perplexa.*" (KOFOID & MICHENER 1911, p. 301).

By comparison with the specimen here assigned to this genus (fig. 441) one notes two departures from the generic diagnosis. Firstly, the girdle is not displaced; and secondly, it is impressed. They are not considered significant here because of the slightness of displacement in the type species (only 0.33 of a girdle width) and the flexibility of the theca. There are other similarities in the description of the type species. For example, mention is made of a narrow "crease" running forward from the ventral area towards the cell apex. This is also present in the present species.

Berghiella josephinae sp. n. Plate 37, Fig. 441

This is a distinctly formed species possessing a thick, flexible, pellicle-like wall bearing very fine reticulae over its surface. The sub-spherical body possesses a short, truncated apical horn and a well-defined, impressed median girdle, not displaced. The girdle is delimited by thick ridges produced by folding of the wall. In the type specimen the upper limit of the left side of the girdle lacked the ridge for one-third of the distance around the girdle. However it is not known if this is teratological or not. In addition to the very fine reticulae, closely-set linear markings are visible in the vicinity of the girdle. A thin fold or ridge passes from the apex of the ventral area (indenting the epicone) towards the apex of the cell. A small flap-like structure is located near the flagellar aperture (single). Chloroplasts are not obvious in preserved material. Length 70 μm, breadth 70 μm.

The species is named in honour of Josephine Rigden MICHENER, co-author of the genus, and the originator of much of the early careful observation used by C.A. KOFOID in his dinoflagellate studies.

It differs from *B. perplexa* by lacking girdle displacement, by having an impressed girdle (variable?) and by the girdle lists being stout ridges bearing markings instead of being thin, hyaline structures.

Station: 32.

The type locality is a station in the northern Indian Ocean. Only one specimen was observed (normally a new species would not be created for a single species but the distinctiveness of this taxon seems to transcend customary limitations).

Genus *Ptychodiscus* STEIN

BOALCH (1969) has recently reviewed this genus which is one of several which possess a flexible, thick pellicle not apparently divided into component plates. With the light microscope no surface markings are visible in this genus, apart from ridging within the girdle, this being one feature which distinguishes it from *Berghiella*, a second being the presence of a keel-like carina. From the position of the single large flagellar aperture it can be concluded that the carina is situated on the apical, and not the antapical end. Only one species is known from this genus if the recommendations of BOALCH are accepted, the variety of appearances recorded so far being attributed by him to varying degrees of swelling and shrinkage before, or as a result of, fixation.

Ptychodiscus noctiluca STEIN Plate 37, Figs. 438–440; Plate 40, Fig. 487

SCHILLER 1935:75, f. 60 d, e non a–c; BALECH 1967a:78, t. 1, f. 1–3; BOALCH 1969:781, t. 1, f. A–Q; STEIDINGER et WILLIAMS 1970: 62, t. 39, f. 141.

Syn.: *Diplocystis antarctica* CLEVE 1900a:924, f. a–d.
Ptychodiscus carinatus KOFOID 1907b:168, t. 1, f. 8, 9; PAVILLARD 1916:12; SCHILLER 1935:77, f. 61 a, b.
Ptychodiscus inflatus PAVILLARD . . . . SCHILLER 1935:77, f. 62 a, b; RAMPI 1950a:6, f. 22; GAARDER 1954:58, f. 75; MARGALEF 1957b:90, f. 2 c; TRÉGOUBOFF et ROSE 1957:108, t. 23, f. 3. ? BALECH 1962b:141, t. 19, f. 277–280.

BOALCH (1969), as indicated above, has included all the known species of *Ptychodiscus* in this one taxon (although excluding MURRAY & WHITTING's, 1899, specimens, which he did not consider as belonging to this genus). The apical/antapical variation exhibited by the species, ranging from great flattening (*P. carinatus* KOFOID) to a swollen appearance (*P. inflatus* PAVILLARD), was attributed by him to fixation and preservation artifacts. The more flattened state is exhibited when the cells are alive.

Numerous small chloroplasts are present. Sometimes these are more ovoid (f. 487), somewhat resembling blue-green algae.

Stations: 13, 21, 30, 37, 301.

Most of the cells were found in the Andaman Sea, the only exception being a station near Mauritius.

The species appears to be relatively eurythermal, tolerating a range from the tropical regions of the three major oceans to cold water such as that off the Faroe Islands or the subantarctic sector of the Pacific.

Family Pyrocystaceae (SCHÜTT) APSTEIN

This family consists of members in which planktonic cyst stage (– s) of the life cycle have become predominant, the motile gymnodinoid or gonyaulacoid swarmers having a highly ephemeral existence. Some are parasitic. Many are dominant members of the tropical plankton. Two genera are at present assigned to the family – *Dissodinium* PASCHER and *Pyrocystis* J. MURRAY ex SCHÜTT. In view of the strong likelihood of diphyletism this family should probably be abandoned.

Genus *Dissodinium* PASCHER

Syn.: *Diplodinium* KLEBS non *Diplodinium* FIORENTINI

This genus consists essentially of gymnodinoid dinoflagellates in which one or two consecutive cyst stages, usually planktonic, are predominant in the life cycle. The most commonly observed cysts are crescentic (lunate) in shape but spherical cysts are known for some species as well. TAYLOR (1972a) recently emended the genus to clarify its distinction from *Pyrocystis* (the latter has strongly thecate motile cells with *Gonyaulax*-like tabulation). Although it was stated that two consecutive cyst stages are present it appears that in some members of the genus direct development of motile cells from a single cyst is possible (e.g. BOUQUAHEUX 1972). The report by SWIFT & REMSEN (1970) of delicate thecal plates in the motile stage of *D. pseudolunula* was due to the presence of a contaminant (SWIFT 1973).

It is possible that other species with crescentic cysts, at present assigned to *Pyrocystis*, may also prove to have gymnodinoid motile cells. At present two species, *D. pseudocalani* (GÖNNERT) DREBES (1969, 1972), and *D. pseudolunula* SWIFT (1973), have parasitic stages confirming VON STOSCH's (1967) earlier suggestion of this likelihood. It is these species that show two successive cyst stages most clearly and it may be necessary later to draw a generic distinction between them and other members of *Dissodinium* (see discussion of the problem by SWIFT 1973 and DREBES 1974).*

SCHILLER, in his monograph (1937), doubted the species distinction of many of the crescentic (lunate) cysts on the basis of size because, if the length of the outer convex surface was measured instead of the greatest linear dimension, the distinctions claimed by the original authors seemed less convincing. However it has been found that the use of the maximum linear dimension, being a function of both the curved length and the degree of curvature, has permitted the same distinctions to be drawn between crescentic cysts as those made by the original authors (notably PAVILLARD 1931, 1935), and consequently they have been retained. As it is potentially confusing care should be taken in distinguishing between curved length and the maximum linear dimension in describing the crescentic cysts. BOUQUAHEUX (1972) has used a multidimensional approach to describe the cysts of *D. elegans.* A further discussion of this problem is given here under the genus *Pyrocystis.*

Dissodinium bicorne (KOFOID et SWEZY) comb. n. Plate 38, Fig. 453

Basionym: *Gymnodinium bicorne* KOFOID et SWEZY 1921:191, f. BB 10, t. 2, f. 14. [Non *Pyrocystis bicornis* BLACKMAN ex MURRAY et WHITTING 1899:338, nomen nudum]
WAILES 1928, t. 1, f. 55 (sub *Gymnodinium lunula* SCHÜTT), t. 2, f. 13, non t. 1, f. 51, vix t. 1, f. 54; – 1939:18, f. 44.

This rarely recorded species has crescentic cysts similar to *D. lunula* but they were described as more curved than *D. lunula* by the original authors. They are within the smallest size range of the latter taxon, ranging from 50 to 100 µm in maximum linear dimension. The crescentic cysts give rise to single, relatively large motile cells resembling *Gyrodinium*, the girdle displacement being about two girdle widths. Although the crescentic cysts are more curved than *D. lunula* and smaller than those of *Pyrocystis robusta* they might be confused with *D. pseudolunula*, the latter having a similar curvature and size. However it gives rise to quite different gymnodinoid motile cells and the cysts have pigmented chloroplasts (see comments under *D. lunula*). The specimen figured by WOLOSZYNSKA (1929, pl. 15, fig. 3) may correspond to this taxon but no size information was given by her. One of SCHÜTT's (1895) miscellaneous crescentic cysts labelled *D. lunula*, his fig. 80.8, may correspond to this taxon but the swarmer is not shown in ventral view. It is possible that *D. bicorne* may prove to be an aberrant form of *D. lunula.* SCHILLER (1937) made them synonymous, but made no mention of the differences noted above.

Stations: 63, 64, 99, 103.

Rare, at a few stations in the Bay of Bengal. Known previously from the Pacific coast of North America, but not recorded from the Indian Ocean.

Dissodinium elegans (PAVILLARD) MATZENAUER Plate 38, Figs. 458, 459
– 1933:441. (454. . . .457?)

Syn.: *Pyrocystis elegans* PAVILLARD 1931:38, t. 1, f. 21 A, B; SCHILLER 1937:493, f. 569; MARGALEF 1948b:45, f. 1 c; MASSUTI et MARGALEF 1950, f. 39; RAMPI 1950c:247, f. 13; SILVA 1956:70, t. 12, f. 6; TRÉGOUBOFF et ROSE 1957:124, t. 28, f. 15; BOUQUAHEUX 1972:4, f. 2 A–F, f. 3, t. 2, f. a–f.

MATZENAUER's combination has been accepted here in view of BOUQUAHEUX's (1972) description of gymnodinoid motile cells (one or two) arising in cysts of this type. The cysts are lunate although she observed strong variability in the smaller cysts. The cysts range in size from 200 to 370 µm (greatest dimension). The largest ones are more curved than *Dis-*

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* G. DREBES and M. ELBRÄCHTER (pers. comm.) favour restriction of *Dissodinium* to include only parasitic species, although it could also be emended to exclude such species. If this distinction is made formally, it will have to include a redesignation of types bearing in mind that the type of *Dissodinium* (*D. lunula*) was based on mixed material (cf. p. 176–177).

sodinium gerbaultii, which they resemble but which are slightly larger again. They can be distinguished from *D. lunula* in that they are usually larger in maximum linear dimension than the primary (spherical) cysts of that species. There appears to be a size cluster near 200 µm and another near 300 µm and the distributional data for these has been separated below. Cysts corresponding to extreme variants observed by BOUQUAHEUX have also been observed here (figs. 454–456), the smallest (length 85 µm) being asymmetrically fusiform.

Stations: (Large form) 24, 34, 50, 53, 62, 102, 108, 153, 288, 292, 294, 320, 329, 334, 340, 417, 418, 420.
(Small form) 14, 33, 36, 37, 57, 60, 62, 68, 69, 91, 100, 102.

The larger form was found scattered throughout the area studied north of 20 °S but the small form was limited to the Bay of Bengal/Andaman Sea region. The species is known from the Mediterranean and warmer Atlantic and Pacific waters and has been recorded from the Indian Ocean by MATZENAUER (1933), SILVA (1956a, 1960) WOOD (1962, cited in 1963a), TRAVERS & TRAVERS (1965), and SOURNIA (1968b). It has not been found further south than Mozambique as yet.

Dissodinium gerbaultii (PAVILLARD) comb. n. Plate 38, Figs. 444, 445
Basionym: *Pyrocystis gerbaultii* PAVILLARD 1935:4, f. 2; SCHILLER 1937:493, f. 570; SOURNIA 1967b:430, f. 5.
Vix YAMAJI 1962:36.

This rare tropical species is known only in its crescentic secondary cyst stage, but SOURNIA (1967b) has observed a pair of apparently gymnodinoid daughter cells within one of the cysts. The latter observation has led to the proposed new combination. The crescentic cysts are the longest of that type which have been described so far, measuring 480 to 550 µm in maximum linear dimension. They are also less curved than the next longest crescentic cysts, those of *D. elegans.* All the secondary cysts of *D. gerbaultii* in the "Anton Bruun" material had small, sharply pointed, apical papillae, a feature not referred to in earlier descriptions.

Stations: 13, 14, 18, 52, 53, 56, 62, 63, 92, 101, 103, 114, 116, 135, 142, 153, 287.

Present in small numbers at scattered stations north of 20 °S. TRAVERS & TRAVERS (1965) and SOURNIA (1967b, 1968b, 1970) have recorded it from the Mozambique Channel region, these being the only records of the species other than the type description from material collected by the yachtsman Alain GERBAULT between the Galapagos and Marquesas Islands during his solo circumnavigation of the world.

Dissodinium lunula (SCHÜTT) PASCHER Plate 38, Figs. 451 (452?)
Syn.: *Gymnodinium lunula* SCHÜTT 1895, t. 25, f. 80.3, 80.4. Non DOGIEL 1906, t. 1, f. 1–25; KOFOID et SWEZY 1921:221, f. I, t. 5, f. 55; LEBOUR 1925:36, t. 4, f. 1 a–g; et auct. nonnull.
Pyrocystis lunula (SCHÜTT) SCHÜTT . . . . SWIFT et DURBIN 1971, f. 1, 2, 27, 28, vix 31, 32, non 7–9, 26, 29, 30; DREBES 1974:1, f. a–c.
Non SCHILLER 1937:488, f. 599/1–11; KISSELEV 1950, f. 35/1–11; et auct. nonnull.

Recently it has been suggested that two species have been confused under the above name due to similarity in the external morphology of their crescentic cysts (both less than 180 µm in length from tip to tip, sharply pointed and not markedly swollen in the central region). SWIFT (1973) has proposed a new species: *D. pseudolunula,* apparently parasitic at some stage during its life-cycle, whose crescentic stage can be distinguished from that of *D. lunula* by the lack of obviously pigmented chloroplasts (pigmentation only developing in the motile cells)*, the cytoplasm retracting rapidly from the cyst apices (not leaving four horn-like extensions of cytoplasm as in *D. lunula*). It may be added that the latter may also be more strongly curved than *D. lunula* if the type figures are restricted as suggested here (see below).

Unfortunately it is now difficult to determine which earlier references apply to which taxon as the above features are often not shown. Some of the figures selected by SWIFT from SCHÜTT's (1895) monograph to act as types for *D. lunula,* largely on the basis of apparently uniflagellate swarmers, are possibly other species (e.g. SCHÜTT's figs. 80.6 and 80.7 are of a strongly curved cyst 294 µm in maximum linear dimension, probably corresponding to *D. elegans,* and his fig. 80.8 may be referrable to *D. bicorne*). His figs. 80.3 and 80.4 seem best suited to act as the iconotypes for this species, being of the right size (length 176 µm) and moderate curvature, possessing chloroplasts.

It appears that most of the early detailed life-cycle studies (by KOFOID & SWEZY 1921, LEBOUR 1925, etc.) and some more recent culture observations have been based on *D. pseudolunula* (e.g. the cyst-wall structural study of SWIFT

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* M. ELBRÄCHTER informs me that a few easily overlooked chloroplasts are present in the primary cyst.

& REMSEN 1970; bioluminescence observations by SWIFT & TAYLOR 1967, and SWIFT & REYNOLDS 1968; and some of the developmental observations of DREBES 1970 and SWIFT & DURBIN (1972). Consequently caution must be used in applying this earlier data and the records of authors such as WAILES (1928, 1939), SILVA (1949, 1968), MASSUTI & MARGALEF (1950), WOOD (1954), MARGALEF, DURÁN & SAIZ (1955), TRÉGOUBOFF & ROSE (1957), YAMAJI (1966), HADA (1967), and SOURNIA (1967b) need evaluation to determine to which species they refer.

SWIFT (1973) has questioned the existence of spherical primary cysts in *D. lunula*, although he allows the possibility in view of observations of such a stage in *D. elegans*. In the "Anton Bruun" material spherical cysts of compatible size were seen (fig. 452). Unfortunately, due to the decolourising effect of formalin it was not possible to determine if these round cysts were pigmented.

Distinctions between *D. lunula* and other species with crescentic stages can be made by external morphological features (see comments under *D. bicorne, D. elegans, Pyrocystis robusta* and *P. obtusa*). The spherical primary cyst of *D. lunula*, if it exists (as postulated here: fig. 452), is much smaller than that of *P. noctiluca*, being less than 200 µm in diameter.

Stations: 62, 63, 70, 72, 87, 95, 99, 101, 102, 298, 333, 340, 348.

Found in small numbers at scattered stations in the central and western Bay of Bengal and in the west central Indian Ocean. There is a possibility of confusion between the primary cyst of this species and the secondary cysts of *P. noctiluca*. For example MATZENAUER (1933) referred to a small globose form with a tight ("straffe") wall under the latter species. This may have been *D. lunula*. Other Indian Ocean records listed by WOOD (1963a), plus SUKHANOVA (1962b), TAYLOR (1967), SOURNIA (1968b, 1970 – tentative) and NEL (1968) are subject to the limitations discussed above.

The type locality of the species is the tropical Atlantic Ocean. SWIFT (1973) believes that *D. lunula* is a warm, oceanic species, not growing below 25 ‰, the numerous cold temperate records referring in fact to *D. pseudolunula*.

Genus *Pyrocystis* J. MURRAY ex SCHÜTT*

The taxonomic difficulties involved in the treatment of this genus, ecologically important in tropical oceanic waters, have been recently discussed by TAYLOR (1972a) and SWIFT & WALL (1972). The presence of thecate cells with a tabulation resembling *Gonyaulax*, sometimes arising in pairs within planktonic secondary cysts of *P. noctiluca* and *P. fusiformis* (the type species), required emendation of the generic diagnosis (TAYLOR 1972a) so as to clearly distinguish it from *Dissodinium* PASCHER and *Gonyaulax* DIESING (see comments here under *Dissodinium*). The former has cysts of very similar morphology to those of *Pyrocystis* but has gymnodinoid motile cells whose thecal plates, if present, are too delicate for observation with the light microscope without special preparation. The recognition of *Pyrocystis* as distinct from *Gonyaulax* in view of the predominance and particular morphology of the cysts in the former is in accord with the recommendations of WALL & DALE (1968b). The latter authors have called for the recognition of cyst types in generic distinctions in order to unify the work on fossil forms (mostly cysts) with that on recent species. Although it is too soon to be certain it appears likely that fusiform cysts are limited to this genus, and lunate (crescentic) cysts to *Dissodinium*. Spherical cysts can occur in both genera.

At present only *P. noctiluca, P. fusiformis* and *P. acuta* have been shown to possess strongly thecate motile cells. In the case of the first- and last-named species the tabulation on the motile cell is that of *Gonyaulax*. In the case of *P. fusiformis* the tabulation observed by KOFOID & MICHENER differed from *Gonyaulax* in having reduced tabulation on the hypotheca and a girdle which is only slightly displaced. V. MEUNIER and E. SWIFT (1976 – Phycologia, in press) have observed *Gonyaulax*–like thecae resembling those of *P. noctiluca* in a culture attributed to *P. fusiformis*. The reason for the discrepancy between their observations and those of KOFOID & MICHENER is not clear.

Some species still included under *Pyrocystis* here produce crescentic cysts very similar to those of *Dissodinium*, e.g. *P. hamulus* and *P. robusta*, and, should they be shown in future to have gymnodinoid motile cells, it will be necessary to transfer them to *Dissodinium*.

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* R. ROSS of the British Museum has kindly assisted the author in unravelling the applications of the Botanical Code to this genus. The first appearance of a generic diagnosis, and hence valid publication of the genus, is in SCHÜTT (1896), being lacking from MURRAY's earlier notes (1876, 1885). As two species were described in the initial publication Art. 42 does not apply. Unfortunately, by recognising the later data as the valid beginning of the genus, it then antedates a genus of echinoderms.

There are other unsatisfactory aspects of the taxonomy of the species which need to be resolved in future. SWIFT & WALL (1972) questioned the inclusion of two cyst stages in the generic emendation as they have obtained an apparently complete life cycle in *P. acuta* which alternated solely between short-lived thecate motile cells and a single, rapidly expanding cyst stage. TAYLOR (1972a – unaware of their observations) referred to the two cyst stages because of the observations of MURRAY (1885) showing globular cysts forming within larger cysts in *P. noctiluca*, and also because of the observation here that most cysts in the field often seem to fall into two size categories. Secondary cysts have not been observed in any of the fusiform taxa. Certainly it is now evident that secondary cysts are not obligate in cultural strains. However MURRAY's observations are yet to be explained. Furthermore, although two successive cyst stages have been well documented in *D. pseudolunula*, BOUQUAHEUX (1972) observed a similar phenomenon in *D. elegans* to that observed by SWIFT & WALL (1972), only one cyst stage alternating with the motile cells although the number of motile cells (one or two) corresponding with slightly different cyst morphologies. Although thecate cells form in *Pyrocystis*, naked aplanospores are more common in culture.

There also seems to be a possibility of several species sharing morphologically similar cysts. This may be one reason for the apparently wide distribution of *P. noctiluca*. Size has been used as an important criterion in the past (see comments here under *Dissodinium* for SCHILLER's criticism) and still seems to corroborate the existence of certain cyst morphotypes within restricted size ranges. However, the cysts of other species, most notably *P. fusiformis*, seem to vary in size through a considerable range. The observation of species in culture should help to resolve these problems.

Distributional aspects of this genus are discussed later in the section on general distribution in the Indian Ocean.

Pyrocystis apiculatus sp. n. Plate 39, Fig. 474

Cysts 370 to 420 µm in length, broadly ellipsoid in shape with an evident apiculus at one pole. Numerous chloroplasts and oil droplets are usually present. Other life cycle stages are unknown.
Iconotype: Plate 39, Fig. 474.
Type locality: Station 418 off the east coast of Africa near Zanzibar.

This species most closely resembles *P. fusiformis* forma *biconica* KOFOID from which it differs by its larger size and the presence of an apiculus. It is likely that several of the early references to the former may actually refer to this species and it may be conspecific with *Pyrocystis ellipsoides* (HAECKEL) LEMMERMANN (see also MATZENAUER 1933, p. 440, f. 4) although this is impossible to determine. The latter taxon, based on *Photocystis ellipsoides* HAECKEL (1890, p. 30 footnote), is so vaguely founded (ellipsoid cells) that it would perhaps be best to consider it a nomen nudum together with *Nectocystis murrayana* HAECKEL. SCHILLER (1937) omitted any mention of them or LEMMERMANN's (1900) combinations.

Stations: 116, 418, 420.

It occurred in small numbers at one station near the Chagos Archipelago in the north central Indian Ocean, and at two stations off the east coast of Africa.

Pyrocystis fusiformis WYVILLE-THOMSON ex BLACKMANN[*] Plate 39, Figs. 466–468, 471–473.
SCHILLER 1937:486, f. 557 a, b, d, e, non c; RAMPI 1950c:247, f. 12; MASSUTI et MARGALEF 1950, f. 37; MARGALEF et DURÁN 1953:24, f. 2 r–t; WOOD 1954:318, f. 256 a, b; SILVA 1956a:70, t. 12, f. 5; – 1958:34, t. 3, f. 1; TRÉGOUBOFF et ROSE 1957:124, t. 28, f. 14; MARGALEF 1961b:142, f. 3/12; YAMAJI 1962:116, f. 6; – 1966:73, t. 34, f. 5; SOURNIA 1967b:430, f. 4; STEIDINGER et WILLIAMS 1970: 62, t. 39, f. 142 non 144; SWIFT et DURBIN 1971, f. 3, 4, 10–12, 16, 17–21; BOUQUAHEUX 1972:2, t. 1 a–f; TAYLOR 1972a:49, f. 2, 6–9.
Syn.:*P. lanceolata* SCHRÖDER . . . . FORTI 1922:26, t. 1, f. 5; MATZENAUER 1933:441, f. 6; SCHILLER 1937:490, f. 562; RAMPI 1950c: 247, f. 11; YAMAJI 1966:73, t. 34, f. 6.
Non GAARDER 1954:59, f. 76 (= *P. acuta* KOFOID).

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[*] The first appearance of the species name is in J. MURRAY (1876) in which the latter attributed it to WYVILLE-THOMSON by the letters "Wy.-T.," without further comment. Neither this publication, nor MURRAY's later (1885) figures of the species, makes the species legitimate, as the genus was not validly published until SCHÜTT (1896). Thus, although validly published in 1876 (since the Code's special provisions for microscopic algae allows for a named figure to be sufficient for early publications: Art. 44, Note), the name only became legitimate after 1896. BLACKMANN (1902) was the first to use the name after the generic diagnosis had been provided. LOEBLICH & LOEBLICH's (1970b) attribution of the name to "J. MURRAY in THOMPSON [sic] and MURRAY 1885" is incorrect, and this reference should not have been used in designating *P. fusiformis* as the type of the genus.

The f. *fusiformis* can achieve considerable size. It has been reported to range from below 600 to 1600 µm in length. PAVILLARD (1931) referred to cysts smaller than 600 µm although these were possibly confused with *P. rhomboides*. However SOURNIA's (1967a) specimen, 420 µm in length, seems to be *P. fusiformis* and the figures of KOFOID and MICHENER in TAYLOR (1972a) indicate a cyst-length of 563 µm or less. In fact, in initial development after thecal ecdysis the cysts may be only 150 µm in length (BOUAUAHEUX 1972). In all the specimens observed here one end of the cyst was sharply tipped and the other more rounded. Deformations due to cover-slip pressure or fixation are common and this can produce transverse surface ridges (not cross-walls as MATZENAUER 1933, thought) or shape changes.

In the f. *biconica* KOFOID the cysts are much smaller, usually less than 300 µm in length with both ends rounded. TAYLOR (1972 a) has illustrated thecate cells in this form, but plate details were not determined.* KOFOID and MICHENER (in TAYLOR 1972a) and this author have observed thecate stages arising in cysts 500 to 600 µm in length. The thecate cells of the f. *fusiformis* have a tablature similar to *Gonyaulax* but with fewer plates on the hypotheca. SCHÜTT (1895), OKAMURA (1907) and PAVILLARD (1931) reported that the daughter cells which arise in cysts of the f. *biconica* appear to be non-thecate but these observations were apparently based on immature daughter cells in view of TAYLOR's (1972a) demonstration of a theca in this form. This may also explain BOUQUAHEUX's (1972) omission of a thecate stage in her material.

The forma *detruncata* MATZENAUER appears to warrant recognition as cells very similar to those seen by MATZENAUER (1933) were also found in the "Anton Bruun" material. They are more slender (70–95 µm in diameter) with narrowly rounded ends which are both alike. They vary in length from 730 to 1120 µm. The forma *lanceolata* (SCHRÖDER) stat. et comb. nov. [Basionym – *Pyrocystis lanceolata* SCHRÖDER 1900, p. 13, pl. 1, f. 11] has cysts with acute apices. The terminal portions may or may not be slightly contracted before expanding as moderate terminal inflations with acute apices. BOUQUAHEUX (1972) observed cells of this type in her material of *P. fusiformis*. The length/breadth ratio of this form seems to be surprisingly constant, usually being 10:1. It is the latter form which most closely resembles the related species *P. acuta* KOFOID. In this taxon the cysts are very slender over most of their length and usually slightly curved, often with subapical swellings. The thecate stage is very similar in tabulation to that of *P. fusiformis*, apparently differing in having one less postcingular plate and the presence of a large posterior intercalary plate (see SWIFT & WALL 1972 for a description of the life cycle of the species in culture). There is also a difference in girdle plate 6C.

A new species has been recognised here which resembles the f. *biconica* but which is larger and possesses a distinctive apiculus (*P. apiculata* sp. n.).

Stations: forma *fusiformis*: 13, 15, 49, 50, 53, 60, 65, 66, 69, 70, 85, 89, 98–100, 103, 106, 108, 109, 111, 112, 114, 118, 142, 150, 162, 282, 284, 286–288, 290, 294, 315, 323, 325, 332, 336, 342, 359, 371, 405, 413, 419, 420.
forma *biconica*: 98–101, 113, 116, 294, 295, 323.
forma *detruncata*: 100, 101, 116, 117, 134, 140, 154.
forma *lanceolata*: 327.

The f. *fusiformis* was a common but not abundant taxon in the material, the other forms being less frequent. The lack of records from the Andaman Sea (other than station 15) and from the northern Bay of Bengal stations suggests that it is possibly more stenohaline than *P. noctiluca*. However, recent unpublished observations by this author have recorded the variety from Phuket Island in the south-eastern Andaman Sea in late May. The forma *detruncata* occurred further south than the f. *fusiformis* but the records are too few to characterise the distribution broadly. The f. *biconica* had a similar distribution to the f. *fusiformis* but was less common. The forma *lanceolata* was observed at one station south of India.

The species has been commonly recorded from tropical and subtropical waters. The Indian Ocean records listed by WOOD (1963a) require amplification by those of SILVA (1956a), SUKHANOVA (1962a, b), ZERNOVA (1962), TSURUTA (1963), ZERNOVA & IVANOV (1964), SOURNIA (1966a, 1967a, 1968b, 1970) and TAYLOR (1967, 1972a, 1973b).

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* V. MEUNIER and E. SWIFT (1976 – Phycologia, in press) report that cysts resembling this form occur occasionally in cultures of *P. noctiluca* (containing thecate cells) and this form may simply be a shape distortion of the latter's primary cysts, explaining its size distribution.

Pyrocystis hamulus CLEVE Plate 38, Figs. 446–450

SCHILLER 1937:490, f. 563 a, b, 564, 565; WOOD 1954:320, f. 259 a–c; SILVA 1955:115, t. 1, f. 14; – 1956a:71, t. 15, f. 8; YAMAJI 1962: 36, 116 (2); – 1966:74, t. 34, f. 7, 8; HALIM 1967:750, t. 10, f. 150.

This is a rare, distinctive tropical species. The cysts are narrow along most of their length with a lenticular swelling in the mid-body. The closest species seems to be *P. acuta* KOFOID from which *P. hamulus* differs by its more tapering shape. The species often occurs in pairs, the cysts connected by crossing over near the tips, and several varieties have been recognised on the basis of the curvature of the cysts.

The variety *inaequalis* SCHRÖDER was originally distinguished by the cysts being strongly bent on either side of the central swelling. However the type specimen of the species was of this form, albeit single, and so this should constitute the var. *hamulus* whether it occurs singly or in pairs. One of the arms of a cyst may be curved while the other is straight. In the variety *semicircularis* SCHRÖDER the curvature is rounded so that the pair circumscribe a circular or broadly oval space.

The specimen in fig. 447 exhibited an unusual variation in having the "arms" of the cyst strongly reflexed. As this seems to constitute a major new variant it has been named here the variety *reflexus* var. n. It differs from the var. *hamulus* in having the arms of the cyst initially inclined from the central body in the usual manner but then arcuately reflexed over most of their length. Iconotype: Plate 38, fig. 447. Location: Arabian Sea, St. 13.

Many of the cells of *P. hamulus* have indentations at intervals along the length of the cyst walls. The presence of these is variable and the reason for them not understood. Possibly they are related to the excystment process.

Stations: var. *hamulus*: 13–16, 18, 20, 23, 25, 29, 30, 33, 47, 53, 59, 60, 62–66, 89, 91, 99, 100, 103, 104, 108, 117, 140, 142, 143, 282, 284, 294, 301, 318, 323, 328, 329, 331, 349.
var. *semicircularis*: 99, 107, 131.
var. *reflexus*: 13.

As is evident above, the var. *hamulus* was much more commonly found than the other varieties. At station 100 in the southern Bay of Bengal it was abundant. The presence of the species in both the high (Arabian Sea) and low salinity (Andaman Sea) regions suggests that it is more halotolerant than *P. fusiformis* but it is not as widespread as *P. noctiluca.*

Indian Ocean records: Those listed in WOOD (1963a) plus KARSTEN (1907), SILVA (1956), SUKHANOVA (1962b), TRAVERS & TRAVERS (1965), TSURUTA (1963), SOURNIA (1968b) and NEL (1968).

Pyrocystis noctiluca J. MURRAY ex SCHÜTT[*] Plate 38, Figs. 461–465

YAMAJI 1962:30, 36, 87, 116, t. 4, f. 10; – 1966:73, t. 34, f. 3; SWIFT et DURBIN 1971, f. 5, 6, 13–15, 22–25.

Syn.: *P. pseudonoctiluca* WYVILLE-THOMSON in J. MURRAY .... SCHILLER 1937:485, f. 556 a–c; KISSELEV 1950:266, f. 456 a–c; WOOD 1954:318, f. 255; TRÉGOUBOFF et ROSE 1957:124, t. 28, f. 12 A–C; R.E. NORRIS 1966:127, f. 10; SOURNIA 1967b:431, f. 7; STEIDINGER et WILLIAMS 1970:62, t. 39, f. 143 (144 sub *P. pseudonoctiluca f. biconica,* sic); TAYLOR 1972a:48, f. 1, 3–5; 9; – 1973b, f. 4 d; SUKHANOVA et RUDYKOV 1973, f. 1, 2.
Goniodoma concavum GAARDER 1954:27, f. 32.
Gonyaulax concava (GAARDER) BALECH 1967a:108, t. 6, f. 108–116.
Peridinium spec. KARSTEN 1907, t. 54, f. 7.
Vix *Peridinium* sp. MUÑOZ, HERRERA et MARGALEF 1956:76, f. h.

This species exists in at least two globose stages, one of which may form within the other as shown in early figures by MURRAY (1885) and has a motile state which is thecate and corresponds in plate tabulation to the genus *Gonyaulax* (see BALECH 1967a, TAYLOR 1972a and figs. 463, 464 here). The largest globose cysts are from 350 to 800 µm in dia-

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[*] TAYLOR (1972a) claimed that the name *P. pseudonoctiluca* WY. T. in J. MURRAY (1876) could be used because Art. 68 of the Botanical Code states that a species name is not illegitimate simply because the generic name is illegitimate. This is however, at first sight, at odds with Art. 43 of the Botanical Code: "A name of a taxon below the rank of genus is not validly published unless the name of the genus or species to which it is assigned is validly published at the same time or was validly published previously." R. ROSS (an editor of the Code at the time of writing) has pointed out that Article 68 must be read in conjunction with Art. 6, especially Note 1. In the light of the latter Art. 68 evidently applies to generic names which are validly published but are not legitimate for some other reason, whereas Art. 43 applies when the generic name does not fulfil the requirements for valid publication. It would seem that the Code could be made less liable to misinterpretation by an appropriate admonishment on the use of Art. 68 or, as ROSS has suggested (pers. comm.), by improving the logicality of the order of the Articles of the Code. MURRAY changed the epithet from *pseudonoctiluca* WY. T. (1876) to *noctiluca* MURRAY (1885), and SCHÜTT (1896) unfortunately used the latter name in conjunction with his validation of the genus.

meter, the smaller stage which forms in pairs within the large primary cysts being 150 to 200 μm in diameter. The motile cells (= *Gonyaulax concava*) are approximately 60 to 80 μm in diameter. TAYLOR (1972a) has provided early unpublished figures by KOFOID and MICHENER which depict these stages, and they were also seen unwittingly in Indian Ocean material by KARSTEN (1907). Naked aplanospores occur more frequently in cultures than thecate motile cells. The species is considered to be one of the commonest causes of bioluminescence in tropical oceanic waters.

The large globose cysts can be readily distinguished from those of *Dissodinium lunula* by size, but there is a danger of confusing the smallest cysts of *P. noctiluca* from the largest of the former as the size ranges overlap very slightly.

Stations: 13–17, 20, 21, 23–28, 30, 31, 33–37, 39, 42–44, 47, 49–51, 53–63, 65–71, 87, 89–103, 106, 108–114, 116–118, 125, 129, 130, 133–135, 140–144, 147–150, 153, 282, 284, 286, 291, 292, 294, 295, 297, 299, 302, 313, 314, 317, 318, 320, 321, 323–326, 331, 340, 344, 406.

This was the commonest species in the material. It was abundant at stations 62, 91, 99, and 100, all within the Bay of Bengal. With the exception of the south-western region the species was generally limited to stations north of 30 °S. As the species is so widespread and occasionally abundant in the Indian Ocean its distribution was illustrated and discussed by TAYLOR (1973b), and is referred to again in the latter section on general distributional features (chart 3, p. 193). In addition to being moderately thermotolerant the species must also be relatively halotolerant, causing bioluminiscence in temporary brack-water pools in the south of India (NAIR et al., 1967).

WOOD's (1963a) Indian Ocean records should be amplified by those of SENÔ (1962), SUKHANOVA (1962 a, b), ZERNOVA (1962, 1967), TSURUTA (1963), ZERNOVA & IVANOV (1964), DESROSIÈRES (1965), NAIR et al. (1967), TAYLOR (1967), SOURNIA (1967b, 1970), NEL (1968, as *P. noctiluca*), and THORRINGTON-SMITH (1969).

Pyrocystis rhomboides MATZENAUER Plate 39, Figs. 469, 470
– 1933:441, f. 5; SCHILLER 1937:489, f. 560.

A rarely observed small species resembling *P. fusiformis* f. *biconica* in size and less so in shape. It is distinguished by its regularly rhomboidal shape with relatively straight sides and acute apices. It does not usually exceed 300 μm in size and is consequently much smaller than *P. fusiformis* f. *fusiformis*. These figures are apparently the only ones other than the type figure. A two-celled stage has been seen (here, and also by MATZENAUER) but motile stages are unknown and, although thecae were not seen, the specimens seen here were considered too immature to warrant removal from the genus *Pyrocystis*.

Stations: 37, 53, 60, 62, 66, 87, 94, 100, 140, 150, 153, 286, 319, 322, 326, 334.

Present in small numbers at scattered stations north of 20 °S. It was originally described from the Arabian Sea and has been subsequently recorded from the south-western Indian Ocean (TAYLOR 1967) and the tropical western Pacific (RAMPI 1952d, BALECH 1962).

Pyrocystis robusta KOFOID Plate 38, Fig. 460
SCHILLER 1937:492, f. 568; SILVA 1949:332, t. 4, f. 1; RAMPI 1950c:247, f. 14; MARGALEF et DURÁN 1953:24, f. 2 u (sub *P. obtusa*); WOOD 1954:320, f. 260 a, b; MARGALEF HERRERA, RODRIGUEZ-RODA et LARRAÑETA 1954:90, f. 2 d; MARGALEF 1961b:142, f. 3/13; SOURNIA 1967a:431, f. 8. Vix BALLANTINE 1961:228, f. 64, 65.

A fairly small species producing strongly crescentic cysts. The central part of the cyst is relatively broad and slightly swollen, the apices being sharply pointed (by which means it is distinguished from *P. obtusa* PAVILLARD) and bent over considerably. While the larger cysts (maximum linear dimension 150 to 250 μm) are easily distinguishable the smaller cysts below 100 μm may be confused with *Dissodinium bicorne* (as may be the case in the present text). KOFOID (1907b) recorded specimens as small as 77 μm. No motile stage is known and it may be necessary to assign the taxon later to *Dissodinium*. BALLANTINE (1961) has illustrated lunate cysts formed within a spherical cyst which she tentatively assigned to this species. The diameter of the spherical cysts was much greater (400–500 μm) than the lunate stage of *P. robusta*, being closer to *Dissodinium gerbaultii* in size, but too little morphology of the lunate cysts is shown to make a reasonable judgement on the matter.

Stations: 28, 32, 48, 62, 63, 99, 100, 134, 140, 284, 324, 327, 340.

Present at scattered stations, chiefly neritic in the Andaman Sea and Bay of Bengal but also at mid-Indian Ocean stations. Although not found in the south-west in this material it has been recorded from the Mozambique Channel region by SILVA (1956a), SOURNIA (1967b, 1968b, 1970), and ANGOT (1970) and further south by NEL (1968). WOOD (1963a) has provided the few other Indian Ocean records known.

Family Pyrophacaceae LINDEMANN

This family consists of only one genus.

Genus *Pyrophacus* STEIN (emend. STEIDINGER et DAVIS 1967; emend. WALL et DALE 1971)

As indicated this genus has recently undergone examination and revision by STEIDINGER & DAVIS (1967), STEIDINGER, DAVIS & WILLIAMS (1967) and WALL & DALE (1971). As stressed by the former (and by WANG 1936) this genus is remarkable among the peridinoid genera in the degree of variability in the numbers of plates involved in each series and the formation of various intercalary plates. The latter may be formed in an asymmetrical manner on both the epi- and hypotheca although most particularly on the latter. WALL & DALE (1971) have indicated, however, that the variability falls within quantitatively definable clusters so that at present three taxa (all represented here) may be recognised at the specific level, instead of the genus being considered monotypic. Also noteworthy was the recognition by the latter of the common identity of the unusual cyst of one of the species with the fossil taxon *Tuberculodinium vancampoae* (ROSSIGNOL) WALL. As this is the type of the latter genus *Tuberculodinium* WALL must now be considered a synonym of *Pyrophacus.*

As presently conceived, the total plate variability of *Pyrophacus* can be encompassed by the formula 5–9', 0–8a, 7–15", 9–16c, 8–17"', 0–9p, 3–7"" (LOEBLICH III 1970 gives the formula derived from STEIDINGER & DAVIS 1967). The appearance in preserved plankton samples is unusual in that the thecae are only rarely observed with cell contents, at which times the cells are lenticular in shape (see plate 34, f. 384). Most commonly entire, completely flat epi- or hypothecae are found. It seems doubtful that this is a simple response to preservation although its significance is unknown at present. Several authors, such as OKAMURA (1912), SILVA (1949), WOOD (1954) and BALLANTINE (1961) have figured the phenomenon. Coccoid cells have been observed in cultures of *P. vancampoae* but these arose as products of germination from cysts. WALL & DALE (1971) report signs that motile cells may form within them. "Spores" observed by STEIN (1883, pl. 24, figs. 11–13) apparently were division pairs within cysts retained within the parent theca, a similar phenomenon also being illustrated by MARGALEF & DURÁN (1953, fig. 13 i) and STEIDINGER & DAVIS (1967).

WALL & DALE (1971) believe that the closest generic affinities are with *Fragilidium* BALECH ex LOEBLICH III and *Helgolandinium* and support recognition of the family *Pyrophacaceae* LINDEMANN as emended. LOEBLICH III (1971) considered *Helgolandinium* to be a variation within *Fragilidium.*

Pyrophacus horologium STEIN emend. WALL et DALE Plate 34, Figs. 387, 388, 390
SCHILLER 1935:87, f. 73 a–c (vix d, e); SILVA 1949:353, t. 6, vix f. 15 non f. 16; – 1956a:59, t. 10, f. 1; KISSELEV 1950:127, f. 205 a–c; RAMPI 1950c:243, f. 7; MARGALEF et DURÁN 1953:24, f. 13 h, i; STEIDINGER et DAVIS 1967:2, f. 1–9; STEIDINGER et WILLIAMS 1970: 62, t. 39, f. 146 A, B; WALL et DALE 1971:230 (234), f. 1 A, D, f. 4 D–G, f. 9, f. 31–37; HERMOSILLA 1973b:55, t. 29, f. 8–10.
Non *P. horologium* sensu WANG 1936.

This species can, according to WALL & DALE (1971), be distinguished from both other species so far described in its possession of fewer plates (5–6', 0–1a, 7–10", 9c, (6s?), 8–10"', 0–1p, 3–5"") on both the epi- and hypotheca. Its commonest individual plate formula is 5', 0a, 9", 9c, 9"', 1p, 3"". It is usually smaller than the other species (transdiameter 35–136 µm) although there is overlap with the smallest specimens of the other species and one hypotheca in the present material exceeded the largest transdiameter recorded for any species (fig. 390). It measured 275 µm in lateral diameter with a dorso-ventral dimension of 225 µm. There is usually only a single posterior antapical plate (3""), this plate in particular undergoing extensive subdivision in the other species. The surface markings consist of densely scattered microgranules. The cysts are simple, oblate-reniform, surrounded by gelatinous material.

The name *horologicum* [sic] is an error originated by SCHILLER. SOURNIA (1967b) appears to have misread STEIN'S epithet, stating that it should be "*horlogium*". The latter does not appear at all in this author's copy of STEIN'S work.

Stations: 13, 19, 21, 27, 28, 39, 40, 43, 44, 70, 71, 87, 115, 116, 140.

Present in small numbers at stations in the eastern Arabian Sea and Bay of Bengal, usually near the coast. Less common and abundant than *P. steinii.* The species has been frequently recorded from the Indian Ocean although in several cases it is not clear whether it is *P. horologium* sensu lato or *P. steinii* sensu lato. The references listed by WOOD (1963a) require augmentation by those of SUKHANOVA (1962b), ANGOT (1965, 1970), TAYLOR (1967), SOURNIA (1967a, 1968b, 1970) and NEL (1968).

Pyrophacus steinii (J. SCHILLER) WALL et DALE Plate 34, Figs. 384, 385, 386, 389; Plate 44, Fig. 518
– 1971:234, f. 1 B, 26–30.

Syn.: *P. horologicum* var. *steinii* J. SCHILLER 1935:87, f. 74 a, b (non c, d); KISSELEV 1950:127, f. 206 *а*, *б* non *в*; RAMPI 1950c:243, f. 8; WOOD 1954:221, f. 84 b vix c; SILVA 1956a:59, t. 10, f. 2, 3; BALLANTINE 1961:218, f. 16, 17; STEIDINGER et DAVIS 1967:4, f. 6–9 a, b; STEIDINGER et WILLIAMS 1970:62, t. 40, f. 147; LÉGER 1973a:19, f. 5 (*horlogium* sic).
P. horologium STEIN sensu WANG 1936:150, f. 22, 23; SILVA 1949:353, t. 6, f. 16; MARGALEF et DURÁN 1953:24, f. 13 b, i; YAMAJI 1966:79, t. 37, f. 6; HADA 1967:15, f. 25 (sub *horolongicum*).

This taxon can be distinguished from *P. horologium* by the characters referred to under the latter. An additional diagnostic feature of *P. steinii* is the presence of marginal striations on the precingular plates in addition to thecal granules and pores. These striations presumably led to the specific epithet of the type species with which this taxon was initially combined. There is a possibility, as indicated by WALL & DALE, of a few cells exhibiting intermediate features (with regard to plate pattern) between it and *P. vancampoae*. SILVA (1956a) indicated that some of her Portuguese specimens (1949) were of the type species, and others of this species (as the variety). The hypotheca figured in her 1949 paper is clearly of *P. steinii*, showing the common arrangement of three posterior antapical plates in addition to the coupling antapical plate and left antapical plate. WALL & DALE (1971) provide a plate formula of 6–7′, 0a, 11–13″, 12c, (? s), 11–14‴, 1–2p, 4–6⁗. The commonest individual formula they found was 7′, 0a, 12″, 12c, (? s), 12‴, 1p, 5⁗. Cyst features are as yet unknown.

Stations: 13, 39, 44, 47, 50–53, 65, 68, 69, 71, 89, 91–95, 99–101, 104–106, 108, 109, 113, 294, 295, 297, 314, 320, 325, 326, 335, 342, 370, 398, 412, 414, 420.

This was the most commonly occurring member of the genus in the Indian Ocean. It was also one of the more widespread taxa in the material being found at chiefly oceanic stations throughout the Bay of Bengal, eastern Arabian Sea, central Indian Ocean and northern Mozambique Channel. In the south central regions it did not occur further south than 27 °S.

It is probable that most of the Indian Ocean references to *P. horologium* (as *P. horologicum*) refer to this taxon in addition to those listed as var. *steinii*. More recent references not included by WOOD (1963a) are those of SILVA (1956a), DURAIRATNAM (1964) and TAYLOR (1967). It has been commonly recorded from Atlantic Ocean localities.

Pyrophacus vancampoae (ROSSIGNOL) WALL et DALE Plate 34, Fig. 391
– 1971:(231)234, f. 1 C, E, 2 A–E, 3, 4 A–C, 6–8, 10–25.

Syn.: *Pterospermopsis? Van Campoae* ROSSIGNOL 1961:134, t. 2, f. 1.
Pterospermopsis vancampoae ROSSIGNOL 1964:90, t. 2, f. 17, 18, t. 3, f. 15.
Tuberculodinium vancampoae (ROSSIGNOL) WALL 1967:114, t. 16, f. 16, 17.
Pyrophacus Form B_1 STEIDINGER et DAVIS 1967:5, f. 10–15 a, b, 16 c, d; STEIDINGER, DAVIS et WILLIAMS 1967, f. 5; STEIDINGER et WILLIAMS 1970:62, t. 40, f. 148.
P. horologium STEIN 1883, pro parte: t. 24, f. 3; MARGALEF 1948a:21, f. 1, 2; MASSUTI et MARGALEF 1950, f. 53 a, b, vix c.
P. horologium var. *steinii* sensu KISSELEV 1950, f. 206 *в* (non *а*, *б*) – icon ex STEIN 1883.

This species has the greatest number of thecal plates and also the greatest diversity in plate pattern. Its most obvious feature in this respect, if present, is the group of up to 9 posterior intercalary plates which appear as a discontinuous series between the postcingular series and the posterior antapical plates. Anterior intercalary plates are also commonly present. The plate formula as provided by WALL & DALE (1971) is: 7–9′, 0–9a, 13–15″, 12–16c, (8s?), 12–17‴, 1–9p, 5–7⁗. The commonest formula is 8′, 0a, 14″, 14c, (8s?), 14‴, 1p, 6⁗. The surface markings consist of both grana and pores. The cyst is highly distinctive, oblately discoidal in shape with 29–36 short tubercles between two wall layers.

Stations: 44, 116, 117, 129, 135, 153, 162, 294.

The Bay of Bengal station was in close proximity to the Ganges River delta but the other scattered records are for stations throughout the Indian Ocean. Several of these are near island groups, but others are not. Little can be concluded from this distribution pattern.

This is a first record of the species from the Indian Ocean. WALL & DALE (1971) have listed the following localities for recent specimens: Caribbean Sea, Bermuda, and Abidjan (Ivory Coast). It has a fossil history dating back to the Lower Miocene. To these may be added the specimens of MARGALEF (1948a) described from the Mediterranean coast of Spain.

Order Noctilucales HAECKEL

Most of the recent work on members of this order, largely on neglected genera by CACHON & CACHON (1964, 1966, 1967, 1969a), on the ultrastructure of *Noctiluca* by SOYER (1968a, b, 1969 a, b, c, 1970 a, b, c) and on nuclear organisation (AFZELIUS 1963; AFZELIUS & HALYARSON 1964; ZINGMARK 1970) supports the view that this group differs quite markedly from the Peridiniales. Most members exhibit rather elaborate ontogeny, the mature stage often being highly vacuolated and large. Contractile, muscle-like fibrils permit shape changes and the movement of tentacular structures. The unusual nuclear features exhibited by *Noctiluca* (the chromosomes undergo a relatively dispersed phase, like many euglenoids, and the nuclear membrane possesses pouch-like "blebs" at certain stages of its development) are characteristic of the trophont, and not of the spores. ZINGMARK (1970) has coined the term "nocticaryotic" for the nuclear type found in *Noctiluca*. It also occurs in several parasitic genera (J. & M. CACHON, pers. comm.).

CACHON & CACHON (1967, 1969a) recognised three subgroups within this order (although they informally termed them subfamilies within one zoological family). They are here recognised as families within one order:

A. Family Kofoidiniaceae fam. nov. (= zool. subfamily Kofoidininae J. et M. CACHON), in which the mature stage is strongly flattened laterally, the girdle running along the anterior margin, and the sulcus greatly extended, running along the posterior margin of the cell, reaching the dorsal side. Three genera are assigned here: *Kofoidinium, Pomatodinium*, and *Spatulodinium*.

B. Family Leptodiscaceae fam. nov. (= zool. subfamily Leptodiscinae J. et M. CACHON), in which strong flattening is antero-posterior. There are wing-like extensions (the velum), but they are not associated with the girdle or sulcus. The latter may be greatly reduced. The transverse flagellum is usually free distally. In *Cymbodinium* only one flagellum is present. In *Leptodiscus* and *Craspedotella* the cell may undergo rhythmic, medusa-like contractions. Other genera assigned here are: *Abedinium* (= *Leptophyllus*), *Petalodinium*, and *Scaphodinium*.

C. Family Noctilucaceae KENT, emended to omit the genera listed above and including only *Noctiluca* and *Pronoctiluca*. In this family the sulcus is well developed but the girdle is greatly reduced.

With the exception of *Noctiluca* these genera are predominantly tropical to warm-temperate in distribution. Some, e.g. *Kofoidinium*, may occur deep within or beyond the euphotic zone. Only *Kofoidinium, Noctiluca*, and *Pronoctiluca* were observed in the "Anton Bruun" material. Most do not preserve well with commercial formalin and may be easily damaged by nets.

Family Kofoidiniaceae fam. nov.

Genus *Kofoidinium* PAVILLARD

Members of this genus undergo an exceptional morphological transformation during their developmental cycle. CACHON & CACHON (1967), as a result of studies on living material, have recognised six stages, labelled "a" to "f", in three species. Features of particular interest are: the shell ("coque") which, unlike a theca, is held by only a few specialised points of contact (hooks) to the cell body (not apparently within the cell membrane); the considerable lateral flattening in the mature sporont, producing a large keel-like velum; the raising of the left side of the girdle to form an apical crest; the extension of the longitudinal sulcus in a furrow along the edge of the velum onto the dorsal surface; the existence of pigmented and non-pigmented stages, and the presence of individuals at 1200 m in the Mediterranean (FENAUX 1958).

The genus appears to be most closely related to *Pomatodinium* CACHON et CACHON and *Spatulodinium* CACHON et CACHON (not found in the material). Their classification in the Noctilucales seems well founded.

The distributions which follow are certainly under-representative as the cells are hard to recognise in rich net samples in view of their delicate and unusual shape. It is interesting that, although non-thecate, they were often found to be surprisingly well preserved. Many loose shells were observed in the samples but not recorded because of this author's ignorance of their true nature at the time of analysis (cruise I material was examined last). Because of their great delicacy they resemble almost structureless hoops, the central portion being almost invisible under low magnification. It is strongly suspected that *K. velleloides* PAVILLARD, the type species (commonly mispelled "*velelloides*"), is present in the Indian Ocean, but was not recognised early enough in the analysis to be recorded. One species, *K. arcticum* BURSA (1964) has been found in the Atlantic Ocean. The single specimen was evidently deformed due to preservation.

Kofoidinium lebourae (PAVILLARD) comb. nov. Plate 39, Fig. 477

Basionym: *Gymnodinium lebourii* PAVILLARD 1921:868, f. 1–6; LEBOUR 1925:43, t. 5, f. 3; SCHILLER 1932:376, f. 385 a, b.

Syn.: *Gymnodinium pseudonoctiluca* POUCHET pro parte, POUCHET 1885, t. 4, f. 34, 36, vix 35 non 37; – 1892, f. 1, 7–10; LEBOUR 1917: 188, f. 3.
Gymnodinium fulgens KOFOID et SWEZY 1921:209, f. X 30.
Kofoidinium pavillardi CACHON et CACHON 1967:429, f. 1–3, t. 1, f. 1–5, t. 2, f. 1–4, t. 3, f. 1, 2, t. 4, f. 1–5, t. 5, f. 1, 2, 4–6 (7, 8?).
Vix FENAUX 1958, f. 2–5, sub *K. velelloides* (sic, nôn. f. 1); STEIDINGER et WILLIAMS 1970:54, t. 25, f. 78 a, b.

Due to the highly detailed study of CACHON & CACHON (1967) it has been possible to recognise the probable conspecifity of this species as described in its immature state (their stages "b" to "d") with the mature "sporont". Although they were aware of this likelihood they did not select the first available name, and instead created a new taxon. This was probably due to the lack of distinct chloroplasts in the stages corresponding to the *Gymnodinium* species, those described by PAVILLARD and others supposedly having chloroplasts. However, as the appearance of chloroplasts can be variable, as indicated for *Polykrikos lebourae* by HERDMAN (1924), *Gonyaulax acatenella* by PRAKASH & TAYLOR (1966), and observed in many sand dinoflagellates (where it may be due to chlorosis – TAYLOR and K.D. BAILLIE, unpublished observations) this apparent lack cannot be accepted with certainty.

The new combination proposed above is a product of these considerations.

The mature sporont (illustrated) apparently reaches 700 μm in diameter although in the "Anton Bruun" material the largest found was 620 μm. This large size distinguished the species from *K. splendens* which does not usually exceed 400 μm in diameter. There are also differences in the shape of the left girdle crest (smoothly-rounded instead of angled when seen in side view), the ribbing within the girdle and sulcus, the type of hooks holding the shell and the shell structure itself. In *K. lebourae* the shell is delicately areolated, the areolate being approximately 10 to 12 μm in diameter.

Stations: 50, 51, 53, 54, 57, 58, 59, 61–65, 87, 92, 94, 95, 96, 99, 102, 103, 294.

It was very common and widespread in the western Bay of Bengal during the late N.E. Monsoon period (cruise I), and was found also at one station north of the Seychelle Islands. In view of the occurrence of this species below 300 to 600 metres (FENAUX 1958, CACHON & CACHON 1967) this is an interesting addition to the other deep-occurring species also found in the western Bay of Bengal at this time (see the section on possible "shade flora" in TAYLOR 1973b). SOURNIA (1972a) has recorded this species from the vicinity of Nosy-Bé (Madagascar). The first described species, *K. velelloides* PAVILLARD, is known from the Mediterranean, the Pacific and Atlantic Oceans. It is possible that some of the records lacking figures (e.g. RAMPI 1952d; BALECH 1962b) may refer to species described later. The figures of STEIDINGER & WILLIAMS (1970) of specimens of *Kofoidinium* from the Gulf of Mexico do not seem to be this taxon, but it is hard to be certain from their photographs. BALECH (1971b) has listed the species as being present in tropical Atlantic Ocean waters.

Kofoidinium splendens CACHON et CACHON Plate 39, Figs. 475, 476

– 1967:437, f. 6 a, t. 4, f. 6–8.

Syn.: ? *Gymnodinium pyrocystis* JÖRGENSEN 1912:10; KOFOID et SWEZY 1921:246; LEBOUR 1925:45.

A few specimens of this recently described species were seen, all lacking their shells. They could, however, be identified on the size and shape of the sporont. The velum is usually less than 400 μm in diameter. The periphery of the velum close to the longitudinal sulcus is marked by irregular ridges which run concentrically with it. A lenticular body is present near the ventral margin. The left girdle margin of the epicone (the upper profile when seen in the usual side view) is markedly angular. The ventral margin of the velum is smoothly rounded.

Precise distinctions between this species and *K. velleloides* PAVILLARD are difficult to make because of the incompleteness of the original description and the distorted condition of the type specimens of the latter. The identification here was based on close agreement with the description of *K. splendens* by CACHON & CACHON (1967) rather than by differences with *K. velleloides*. CACHON & CACHON (1967) have provided a more recent interpretation of the latter which includes distinctions not apparent in the type description, such as an abrupt angularity in the ventral margin of the velum. The lack of a lenticular body may also be a useful distinction. The Indian Ocean specimens harboured several zooxanthella-like bodies per cell, a feature also observed in the type material and not known from *K. velleloides* sensu lato.

A juvenile stage, corresponding to stage "b" of CACHON & CACHON (1967) has been tentatively assigned here to *K. splendens* in view of the very close similarity, despite fixation deformation, to the specimen in their figure 6 on plate 4. It is this stage which suggested a possible conspecificity with *Gymnodinium pyrocystis* JÖRGENSEN. Although the latter is almost certainly a stage "b" of a species of *Kofoidinium* the lack of a figure in any of the descriptions makes it almost impossible to decide which species it corresponds to. *K. splendens* seems the closest but the early descriptions may have also included specimens of several species. It has been considered best not to make a new combination in this case.

Stations: 95, 97, 370 (juvenile).

This species was much rarer than the former, being found in small numbers at two western Bay of Bengal stations, the juvenile specimen (stage "b") being recorded from the vicinity of the Mozambique coast. These are the first records for this species in the Indian Ocean. It was originally described from the Mediterranean Sea.

Family Noctilucaceae KENT

Genus *Noctiluca* SURIRAY ex LAMARCK

The first time this name appeared in the form of a Latin binomial was in LAMARCK's "Animaux sans vertebres" (1816). In this work LAMARCK accredited the genus name to SURIRAY. The latter author had proposed the genus in a manuscript presented to the French Academy of Science in 1810, but he did not publish the work until much later. Early authors, familiar with each other's manuscripts, usually accredited the genus to SURIRAY but the form given above is in accord with the International Codes of Botanical and Zoological Nomenclature (the ICZN does not distinguish between ex and in). In fact *Noctiluca* SURIRAY ex LAMARCK is a junior homonym, but the senior homonym, *Noctiluca* HOUTTUYN has been rejected from the zoological literature. At some future date it might be desirable to formally conserve *Noctiluca* SURIRAY ex LAMARCK.

At the time of writing the genus consists of apparently only one species (below). Apart from general floristic studies it has been subjected to detailed examination in three unrelated aspects: its role in causing "red water" phenomena (e.g. AIYAR 1936; BHIMICHAR & GEORGE 1950; GRINDLEY & HEYDORN 1970; GRINDLEY & TAYLOR 1971), its bioluminescence (NICOL 1958; ECKERT 1966), and the unusual nature of its ultrastructure (see references in the introductory comments to the order). The species can regulate its density so that it may occur distributed over wide depths (generally within the upper 50 m) or it may become buoyant, occurring directly at the surface. From unpublished observations on cells in culture it appears that, when at the surface *Noctiluca* may be a neuston-feeder, using its tentacle to "wipe-off" bacteria and small cells from the surface film (orig. obs.).

Noctiluca scintillans (MACARTNEY) EHRENBERG Plate 39, Figs. 478, 479

. . . . KOFOID et SWEZY 1921:407, f. KK 1–6; LEBOUR 1925:69, f. 17 a–d; WANG et NIE 1932:312, f. 24; WAILES 1939:15, f. 34; MASSUTI et MARGALEF 1950, f. 36 b, c; SILVA 1952b:600, t. 6, f. 4; MARGALEF, DURÁN et SAIZ 1955:95, f. 5 d; YAMAJI 1966:73, t. 34, f. 2.

Syn.: . . . . *N. miliaris* SURIRAY ex LAMARCK . . . . FORTI 1922:23, t. 1, f. 1 (2); SCHILLER 1933:553, f. 582 a–e; WOOD 1954:220, f. 83 a (vix b); SUBRAHMANYAN 1954, f. 2 (3); TRÉGOUBOFF et ROSE 1957:107, t. 22, f. 17 A, B (*miliaria*); QUAYLE 1969, f. 6; SWEENEY 1971:54, f. 1 A.

Although this species is common and widespread it has only been illustrated rarely, possibly due to difficulties in its depiction. Its very large, sac-like form and tentacle make it easily recognisable. In its more juvenile stages it might be confused with *Spatulodinium* although the highly modified form of the latter renders this doubtful. In the present work both a juvenile and medium-sized individual have been illustrated, both from the apical side, a feature most readily determined by the prominent apical trough. The ventral indentation is hidden from view. The formation of multiple, large feeding sacs, shown in fig. 479, is quite common in *N. scintillans.* There have been several reports of the presence of green flagellate symbionts within the main cell vacuole, particularly from populations near the East Indies (see e.g. SUBRAHMANYAN 1954; SWEENEY 1971) but none were seen in this material.

Many authors have used the name *N. miliaris* although MACARTNEY's specific epithet has clear priority. Perhaps a case could be made in zoological nomenclature for considering *N. scintillans* as a *nomen oblitum* (SOURNIA, pers. comm., cf. ICZN Art. 23b) in view of the lengthy period of disuse between EHRENBERG's combination and its revival by KOFOID & SWEZY (1921). Apart from the absence of this practise in the ICBN, it also seems best to adopt the simplest policy; namely, that of accepting the priority of *scintillans*, particularly as it has been used in two major authoritative works in this century: KOFOID & SWEZY (1921) and LEBOUR (1925), as well as in many of the other works in this century:

Stations: 22, 23, 29, 30, 31, 33, 35–43, 47, 48, 49, 51, 54, 68, 88, 94, 95, 104, 105, 155, 322, 340, 412.

The species was most commonly present at stations in the eastern Andaman Sea. It achieved large numbers at stations 39, 41, 42, and 43 near the Irrawaddy delta where it bloomed in association with a small, unrecognisably preserved flagellate on which it was feeding. It is tempting to suspect that it was a similar situation to that reported off Calicut by SUBRAHMANYAN (1954) but there is little to substantiate this other than the very small size of the flagellate. Although *N. scintillans* is essentially neritic, it can occur at extreme oceanic stations such as 322 and 340, both in equatorial waters. It has been known to bloom extensively off both the east (AIYAR 1936) and west coasts of India where it has been implicated in fishery decline (BHIMICHAR & GEORGE 1950). Blooms have been reported from many areas including St. Lucia estuary on the east coast of southern Africa; (GRINDLEY & HEYDORN 1970), the Cape of Good Hope (GRINDLEY & TAYLOR 1971), the English Channel (LEFÈVRE & GRALL 1970), the western Mediterranean (LOPEZ & ARTE 1971), and British Columbia coastal waters (QUAYLE 1969).

Genus *Pronoctiluca* FABRE-DOMERGUE

This non-photosynthetic genus is of more enigmatic systematic position than other members of the Noctilucales, showing certain resemblances, particularly in the reduction of the flagellar apparatus, including grooves, to *Entomosigma* SCHILLER and *Oxyrrhis* DUJARDIN. The flagella are anteriorly inserted in *Pronoctiluca* (PAVILLARD 1917) and *Entomosigma* whereas they are posterior in *Oxyrrhis*. Members of *Pronoctiluca* have a flexible cell wall, often granular in appearance. Delicate cyst walls are produced exterior to the wall. Large accumulation bodies are often present, usually in the posterior portion of the cell. The tentacle can be flexed considerably, appearing at various angles in preserved material. Shape changes accompany ontogeny in the type species (*P. pelagicum* FABRÉ-DOMERGUE).

The genus is here retained within the Noctilucaceae largely on the basis of the observations of CACHON & CACHON (1966), authors whose experience with members of the order is considerable. They have indicated that some early figures attributed to this genus are in reality developmental stages of *Kofoidinium*. KOFOID & SWEZY (1921) doubted that *Pronoctiluca* was a dinoflagellate genus.

Pronoctiluca pelagica FABRÉ-DOMERGUE Plate 37, Figs. 426–428, 430, 431

SCHILLER 1932:268, f. 258 a–i; KISSELEV 1950:82, f. 133; CHATTON in GRASSÉ 1952:343, f. 248 A–C; WOOD 1954:216, f. 74; SILVA 1955:115, t. 1, f. 13; TRÉGOUBOFF et ROSE 1957:106, t. 22, f. 15; TAYLOR 1967, t. 6 (93), f. 57.

This species together with others in the genus, although not exceptionally rare in tropical waters, has only been illustrated rarely. Apart from the small figures of WOOD (1954), and the photograph of TAYLOR (1967), all the references cited above reproduce figures by PAVILLARD (1917). The latter illustrated the transition of the species from a fusiform shape to a more rounded pyriform stage with flattened antapex which produces multiple delicate "cyst" walls external to it. The tentacle projects through all the walls produced. The initial cyst wall remains attached antapically to the secondary wall so that it resembles a hyaline cup enclosing the posterior part of the cell. This process may be repeated more than once. Extremely small cells (length 16 µm excluding tentacle) were also found (fig. 430). It could not be determined if these were a developmental stage of *P. pelagica* or not.

P. pelagica differs from *P. spinifera* in lacking the antapical projection characteristic of the latter. They are similar in size when mature (25 to 35 µm in length, excluding the tentacle and cyst walls).

Stations: 17, 96, 155, 282, 283, 289, 297, 298, 301, 313, 315, 322, 327, 341, 365, 369, 371, 374, 405, 411, 412, 414, 416, 417, 420.
Small form: 135, 284, 323.

It was widely distributed (in small numbers) occurring chiefly at oceanic stations. It was most common in the Mozambique Channel region and off the coast of east Africa (August to November).

The species has been found in the Indian Ocean only by WOOD (1962 in 1963a) and TAYLOR (ms. 1964, 1967). It is known from the North Atlantic, and the Baltic and Mediterranean Seas. MARSHALL (1933) found it present in small numbers throughout the year in the Great Barrier Reef lagoon.

Pronoctiluca rostrata sp. n. Plate 37, Fig. 425

Several individuals and a discarded "sheath" of a large, distinctive species of *Pronoctiluca* were found. The cells are spindle-shaped consisting of three main external components. A short, cylindrical apical region is surmounted by a relatively slender tentacle and has a distinct sulcal groove passing down most of its length. The mid-body is large, containing most of the cell contents. It is broadest in the centre, tapering equally at both ends where it attaches to the apical piece and the rostrate antapical projection. The latter appears to arise rather abruptly from the mid-body and the wall in this region appeared slightly thicker in some specimens. The tip is acutely pointed and the region of the junction may appear slightly swollen.

The surface of the wall exhibits the same finely granular appearance observed in other species of *Pronoctiluca*. Two large, unusual-looking bodies, presumed to correspond to accumulation bodies, occupied much of the mid-body in the specimens observed. No chloroplasts are evident.

Total length including tentacle: 115–128 µm
Length of mid-body: 74– 78 µm
Width of mid-body: 16– 20 µm
Length of rostrate process: 25– 28 µm
Type locality: Station 327, southwest of India. It was also found in the central Bay of Bengal (st. 17).
Comparisons: This species is larger than *P. acuta* (LOHMANN) SCHILLER (maximum length 60 µm) and differs also in that the rostrate process arises abruptly from the mid-body rather than being a gradual extension of it. The apical region appears to be very similar, however. Some of LOHMANN's figures look suspiciously like *Prorocentrum gracile*!

Pronoctiluca spinifera (LOHMANN) SCHILLER Plate 37, Fig. 429
SCHILLER 1932:270, f. 259 a–c (vix d); CHATTON in GRASSÉ 1952, f. 248 D; WOOD 1954:217, f. 75; HERRERA et MARGALEF 1963:76, f. 24m; YAMAJI 1966:73, t. 34, f. 1; TAYLOR 1967, t. 6 (93), f. 58; RAMPI 1969b:322, t. 1, f. 7; SOURNIA 1972a:156, f. 14.
Syn.: *Cystodinium* sp., BALECH 1971a:168, t. 38, f. 747.

This species is rarer than *P. pelagica*, and cyst-formation is unknown. A peculiar type of pairing has been figured by HERRERA & MARGALEF (1963). It is recognisable most readily by its antapical process which may be relatively blunt (fig. 429) or more acute (HERRERA & MARGALEF 1963; TAYLOR 1967). It differs from *P. rostrata* in being smaller and in the smoothness of the transition from the mid-body to the antapical process.

The specimen illustrated here was apparently in a stage immediately prior to ejection of the accumulation body, a phenomenon observed previously in *P. pelagica* by PAVILLARD (1917).

Stations: 108, 150.

Single individuals were observed at a station in the eastern Arabian Sea and north of the Seychelle Islands.

This species has only been recorded from the Indian Ocean by WOOD (1962, in 1963a), TAYLOR (ms. 1964, 1967), and SOURNIA (1972a). It was found at only one station over the Agulhas Bank in the southwestern Indian Ocean and at Nosy-Bé (Madagascar). It is known from the three major oceans and the Mediterranean Sea. BALECH (1971a) found cells corresponding to this taxon abundant near the Rio de la Plata in the South Atlantic Ocean.

Incertae Sedis

Family Amoebophryaceae LOEBLICH III

[= Amoebophryidae J. CACHON, zool. fam. = Coelomastigina CHATTON et BIECHELER]

This family consists of only one genus at present.

Genus *Amoebophyra* KÖPPEN

Syn.: *Hyalosaccus* KÖPPEN

All members of this genus are intracellular parasites, their hosts consisting of dinoflagellates, tintinnids, or radiolarians. The feeding state (trophont) forms a distinctive bee-hive-shaped cavity, the "mastigocoele," so named because it is lined with rows of flagella belonging to incipient daughter cells of the parasite. It is by the presence of this cavity that they can be most readily recognised within their hosts. Extrusion from the host involves a complex inversion of the parasite. It emerges in a polynucleated state which is very elongated and is termed the vermiform stage. After further nuclear divisions biflagellated spores are liberated. They are the infective stage. Ultrastructural features of members of the genus have been illustrated by CACHON & CACHON (1969b, 1970).

Amoebophyra ceratii (KÖPPEN) J. CACHON Plate 32, Fig. 349 b
– 1964:70, t. 1, f. 6, t. 2, f. 7–10, t. 13, f. 12–16, non t. 2, f. 11; TAYLOR 1968:2241, f. 1–10; BALECH 1971a:145, t. 30, f. 566, 567.
Syn.: *Hyalosaccus ceratii* KÖPPEN pro parte. . . . CHATTON et BIECHELER 1935:505, f. 1–8; GRASSÉ 1952:1020, f. 819 A–H.
[Un-named figures in CUESTA 1919, t. 52 (f. 1) B, t. 53 (f. 2 A–K); LEBOUR 1925, f. 3 a–c; BALECH 1963a, f. 37].

Under routine conditions this species is only detectable within its hosts in an advanced developmental state. It parasitises both thecate and non-thecate dinoflagellates. In the latter it develops initially in the peripheral cytoplasm whereas in thecate hosts (of the genera *Prorocentrum, Blepharocysta, Diplopsalis, Peridinium, Gonyaulax, Ceratium*) it appears to preferentially digest the host nucleus first. CACHON (1964) has described and illustrated cytological features of the development of the species, CUESTA (1919) having unwittingly also illustrated various stages, and TAYLOR (1968) has photographically illustrated its appearance within the chain-forming, toxin-producer *Gonyaulax catenella* (suggesting the possibility of a future use as a biological control agent to regulate sources of paralytic shellfish poison).

Closely related species (*A. grassei* J. CACHON and *A. leptodiscii* J. CACHON) are distinguished chiefly by their hosts (*Oodinium* and *Leptodiscus* respectively) and the appearance of their vermiform or motile stage (cf. CACHON 1964). Three other species are found in non-dinoflagellate hosts.

Stations: 29 – in *Diplopsalis* sp.
67 – in *Peridinium steinii*
29, 327 – in unidentified cysts.

Found in various dinoflagellate hosts in the Andaman Sea, the Bay of Bengal, and off the southern tip of India.

These are the first records of any member of this group from the Indian Ocean. Until recently the genus was virtually unknown outside the Mediterranean and North Seas. TAYLOR (1968) has recorded it from the North East Pacific and BALECH (1971a) has observed it in the South Atlantic Ocean. Like many parasites it is probably relatively cosmopolitan.

Family?

Genus *Bernardinium* CHODAT?

This is a very enigmatic, poorly known genus represented by only one very small fresh-water alpine species, *B. bernardiense* CHODAT. The cells are not known to have tabulation. A girdle groove passes only half-way around the body equatorially, and SCHILLER (1935) suspected that it may, in fact, have been based on poorly observed members of *Hemidinium*. The latter does, however, have very definite tabulation, the incomplete girdle forming a descending spiral rather than a level semi-circle. No sulcus was known for the type species.

The genus is here resurrected tentatively as the only appropriate designation for a large, curious taxon found in the "Anton Bruun" samples (below).

Bernardinium sp.? Plate 37, Figs. 436 a, b

Although the organism referred to here could not be identified it nevertheless had several distinctive features. It was 56 µm long with a transdiameter of 50 µm and a dorso-ventral width of 42 µm. In ventral view it was rectangular with rounded corners. The cingular groove was most unusual. It depressed the cell sharply, but not broadly, only over the ventral surface and a small part of each lateral surface. In ventral view it could be seen to undulate strongly on the right half of the cell, plunging down to an acute point assumed to be the flagellar origin. The left side of the girdle was shorter, less undulate, and slightly lower than the right. No sign of a sulcus was seen.

The cell was enclosed in a strong wall, fairly thick, but not apparently made of plates. Beneath the wall was a broad hyaline zone. The cell contents were not strongly pigmented, but this may have been due to bleaching of the chlorophyll by formalin. The most striking intracellular feature was a very prominent spherical capsule, thought to be a pyrenoid sheathed with starch, although it could have been, more improbably, a capsule surrounding the nucleus as a nucleus was not observed elesewhere in the cell.

There is a strong possibility that this may have been a cyst rather than an actively swimming cell.

Station: 322.

It was found in the central Indian Ocean to the south of India.

Family Gloeodiniaceae SCHILLER

Species possessing a palmelloid, gelatinous state, possibly also filamentous.

Genus *Gloeodinium* KLEBS

Gloeodinium marinum BOUQUAHEUX Plate 40, Fig. 486
– 1971:314, f. 1–4, t. 40, f. 4 a–c; t. 41, f. a–c, t. 42, f. a–c.
[SCHÜTT 1895, t. 26, f. 91; MARGALEF, HERRERA, RODRIGUEZ-RODA et LARRAÑETA 1954:94, f. 1 a (sub *Pelagocystis?*); GAARDER 1954:60, f. 77 a, b.]

The cysts have a very characteristic morphology, each containing a prominent nucleus with the granular interphasic appearance of the dinokaryon. Staining with aceto-carmine displays the nuclei very strongly. BOUQUAHEUX (1971) has described the ultrastructure of the cells. They are roundly oval, approximately 20–38 µm in diameter, deeply embedded in phase-transparent mucilage. They often occur in pairs within the mass, being a product of synchronous division, daughter cells becoming more widely separated with the subsequent production of further mucilage. In the "Anton Bruun" material the number of cysts per mass was observed to vary from four to thirty-two (fig. 48 b). BOUQUAHEUX (1971) found that there were two types of cycle; one in which motile cells (gymnodinoid) occurred after the 16-celled stage, and another which occurred after a 64-celled stage. The cysts are pigmented. At several stations they were quite abundant (see below).

GAARDER's illustrations of cysts are identical to those observed here insofar as the limited morphology permits identification. She speculated that they may arise from prorocentroid cells such as *Prorocentrum compressum*. MARGALEF et al. (1954, above) thought the cysts belonged to a member of the Xanthophyceae. BOUQUAHEUX (1971) described the motile cells as gymnodinoid, but did not illustrate them. Customarily this genus is thought to have *Hemidinium*-like motile cells (LOEBLICH III 1970). Consequently several genera may later be distinguished by their motile cells in a similar way to the *Dissodinium/Pyrocystis* distinction.

Stations: 13, 15, 21, 33, 37, 62, 142, 299, 313, 317, 318, 321, 327.

They occurred at several stations in the Andaman Sea, one in the eastern Bay of Bengal, and were scattered over the central Indian Ocean. They were moderately abundant at stations 142 (south of India) and 299 (north of Mauritius). GAARDER (1954) found them at one station in the Atlantic Ocean and MARGALEF et al. (1954) observed the cysts in the western Mediterranean Sea, as did BOUQUAHEUX (1971 – Villefranche Bay).

General Features

This aspect has served as the basis for a separate contribution (TAYLOR 1973b) and so only the major points have been abstracted here, with the addition of a few observations not made in the previous publication.

The present report can deal only with qualitative aspects in view of the sampling techniques used aboard the "Anton Bruun". However, some preliminary remarks may assist the reader in seeing the dinoflagellates of the Indian Ocean in a general ecological perspective.

From other Indian Ocean studies it is known that for coastal localities diatoms far exceed the dinoflagellates in number in samples obtained by nets (e.g. SUBRAHMANYAN & SARMA 1960) or bottles (SOURNIA 1968d), and this may apply to a lesser extent in certain oceanic areas (TAYLOR 1967; NEL 1968; THORRINGTON-SMITH 1971). However there are three circumstances in which the dinoflagellates assume a major importance. The most obvious of these is the outbreak of "red water" caused by almost monospecific blooms of dinoflagellates. The only sign of such an event during the "Anton Bruun" cruises was the presence of large numbers of *Noctiluca scintillans* (MAC.) EHR. near the Irrawaddy delta in the northern Andaman Sea. RYTHER & MENZEL (1965) and RYTHER et al. (1966) found exceptionally high primary productivity to the south of Arabia during the "Anton Bruun" cruises. In the cruise V material from the area there were large numbers of an unrecognisable flagellate, as well as large amounts of detritus, but it was not apparently due to either diatoms or dinoflagellates. Other accounts of "red water" caused by dinoflagellates are provided in the introductory section on Earlier Indian Ocean Dinoflagellate Studies.

SUBRAHMANYAN & SARMA (1965) found that nearly half of the small cells not retained by nets off the south west coast of India were dinoflagellates, raising the possibility that they are at least occasionally major constituents of the nanoplankton. Furthermore, in oceanic areas dinoflagellates, although sparse, may not be as reduced in number as the diatoms, thus increasing their relative importance (KARSTEN 1907; DESROSIÈRES 1965). In the Caribbean Sea ZERNOVA (1970) has found a similar pattern, dinoflagellates constituting the predominant oceanic biomass. It must be born in mind that, as a group, the dinoflagellates play a complex role nutritionally because of the presence of totally photosynthetic, nonphotosynthetic and phagocytic-plus-photosynthetic ("myxotrophic") members.

TAYLOR (1973b) has discussed the evidence for shade-loving dinoflagellates occurring habitually below 50 or 100 m. Such species include most of the members of the subgenus *Archaeceratium* of *Ceratium*, with their flattened, leaf-like epitheca; the *Ceratium* species with "finger-" or "paddle-like" antapical horns (*C. ranipes, C. platycorne*), many of the morphologically elaborate dinophysoid species (e.g. *Histioneis* spp., *Ornithocercus splendidus*), the genus *Heterodinium* and some noctilucoids: e.g. *Kofoidinium*. The ceratia involved all seem to possess morphological adaptations for permitting the maximum amount of light to reach their chloroplasts (GRAHAM 1941). HALIM (1967) has used the presence of such species in surface waters as being indicative of upwelling. In the "Anton Bruun" material, although the samples integrated the material from the surface to 200 m, nevertheless they showed a horizontal distribution of such species associated with areas where an upward movement of water was expected (TAYLOR 1973b).

Species Composition

The sampling and preservation methods used during the expedition introduced considerable bias in the determination of the species present. It can be expected that non-thecate species and those with a maximum dimension of less than 60 microns were greatly under-represented. On the other hand, the practice of sampling from 200 m to the surface significantly increased the representation of "shade-loving" genera such as *Histioneis* or *Heterodinium*. For example, no representatives of either genus were found by TAYLOR (1967) in a series of samples taken from the south-western Indian Ocean by similar methods but operating only to a depth of 100 m.

A relatively large number of species (286) were found, of which 36 % were first records for the Indian Ocean. Only five of these can be thought of as usually allochthonous to the Indian Ocean. Two were brackish water species occurring near the plume of the Ganges River: *Peridinium achromaticum* LEVANDER and *Peridinium divaricatum* MEUNIER. The remainder were southern subpolar species found at one station in the Subtropical Convergence Region near 40 °S: *Ceratium petersii* STEEMANN NIELSEN, *Peridinium latistriatum* BALECH and *Podolampas antarctica* BALECH.

The richness of the species representation is evidently due largely to the great area of the Indian Ocean covered by the "Anton Bruun" even though many of the species have wide distributions. For example, SUBRAHMANYAN (1958) found only 109 species present in coastal waters off the west coast of India during a five year survey, and in a more restricted locality SOURNIA (1968d) recorded 57 species, his sampling also being limited to shallow depths.

Ceratium was the most represented genus (58 species). It is in the tropics that one encounters the full range of morphological variability within the genus, from the enlarged and flattened epithecae of the members of the subgenus *Archaeceratium*, to the elongate, rod-like members of *Amphiceratium*, to the antapical horn elaborations found among some members of *Tripoceratium*. Only 10 of the marine species included by SCHILLER in his monograph (1936) are not present here.

Peridinium had almost as many species (56), but these were much less widespread in most cases. The genus as a whole tends to be more neritic than *Ceratium*. *Gonyaulax* also was represented by a moderate number of species but, although several of them can be abundant enough to cause "red water" (e.g. *G. polygramma* STEIN, *G. polyedra* STEIN), they were not particularly abundant at any station.

One of the characteristics of the tropics is the relatively large number of dinophysoid species. In the "Anton Bruun" material *Dinophysis* was represented by 24 species, although it can be noted that those formerly attributed to *Phalacroma* are here included within it. It is in the tropics that one encounters the most morphologically elaborate, bizarre members of this group, particularly in the exclusively tropical genera *Ornithocercus*, *Parahistioneis*, *Histioneis* and *Citharistes*. Here also there is a parallelism to the elongate members of *Ceratium* found in the tropical genus *Amphisolenia*. Symbiotic associations with coccoid blue-green algae are also found in the more elaborate dinophysoid genera and they may exhibit morphological adaptations to these associations although this has not been established. The nutritional inter-relationships between the symbionts, if any, are also unknown and individuals lacking the symbionts can be found.

Distributional, Regional, and Seasonal Aspects

The photosynthetic dinoflagellates seem, in general, to be able to tolerate lower inorganic nutrient levels than the diatoms, possibly due to their ability to migrate through the water column, and this makes their distribution in the tropics not as clearly associated with nutrient levels as that of other photosynthetic groups. Temperature is evidently a major factor for many species, with salinity in the middle ranges playing a more minor role (GRAHAM & BRONIKOVSKY 1944). The same species able to tolerate brackish conditions may also be found in hypersaline lagoons (KIMOR & BERDUGO 1969).

There are probably no species which are limited exclusively to the Indian Ocean. Restricted distributions are to be found among a few Indo-West-Pacific taxa and, as might be expected, these are usually neritic species. For example, *Peridinium compressum* (ABÉ) NIE is known from coastal localities on the south-east coast of South Africa, the Gulf of Aden, and Japan. *Dinophysis miles* var. *schroeteri* (FORTI) BÖHM is much more restricted in its distribution although it is more common. It occurs only in the Andaman Sea/East Indies region, an area where the presence of strong inter-oceanic currents suggests that either the taxon dies out when displaced from the region or that it represents a type of phenotypic response to an environmental factor peculiar to the region. This question is discussed more fully under the taxon earlier, and has also had attention drawn to it in a separate publication (TAYLOR 1973b). *Ceratium egyptiacum* HALIM exhibits a similar narrow distribution, occurring only near the Suez Canal. It may represent a modification of *C. humile* JÖRGENSEN which was thought, until recently, to also be an exclusively Indo-West Pacific species but is now known to occur also in the tropical Atlantic Ocean (see earlier notes). *C. dens* OSTENFELD et SCHMIDT is a similar example, with a centre of distribution from the Bay of Bengal to South China Sea, extending occasionally into the Arabian Sea and into the eastern Pacific Ocean. There is only one tentative record of *C. dens* from the tropical Atlantic Ocean (STEIDINGER & WILLIAMS 1970). *Gonyaulax hyalina* OSTENFELD et SCHMIDT is a more widely distributed Indo-West Pacific species, occurring over most of the northern Indian Ocean in the present material. Unlike the previous species *G. hyalina* is not noticeably neritic.

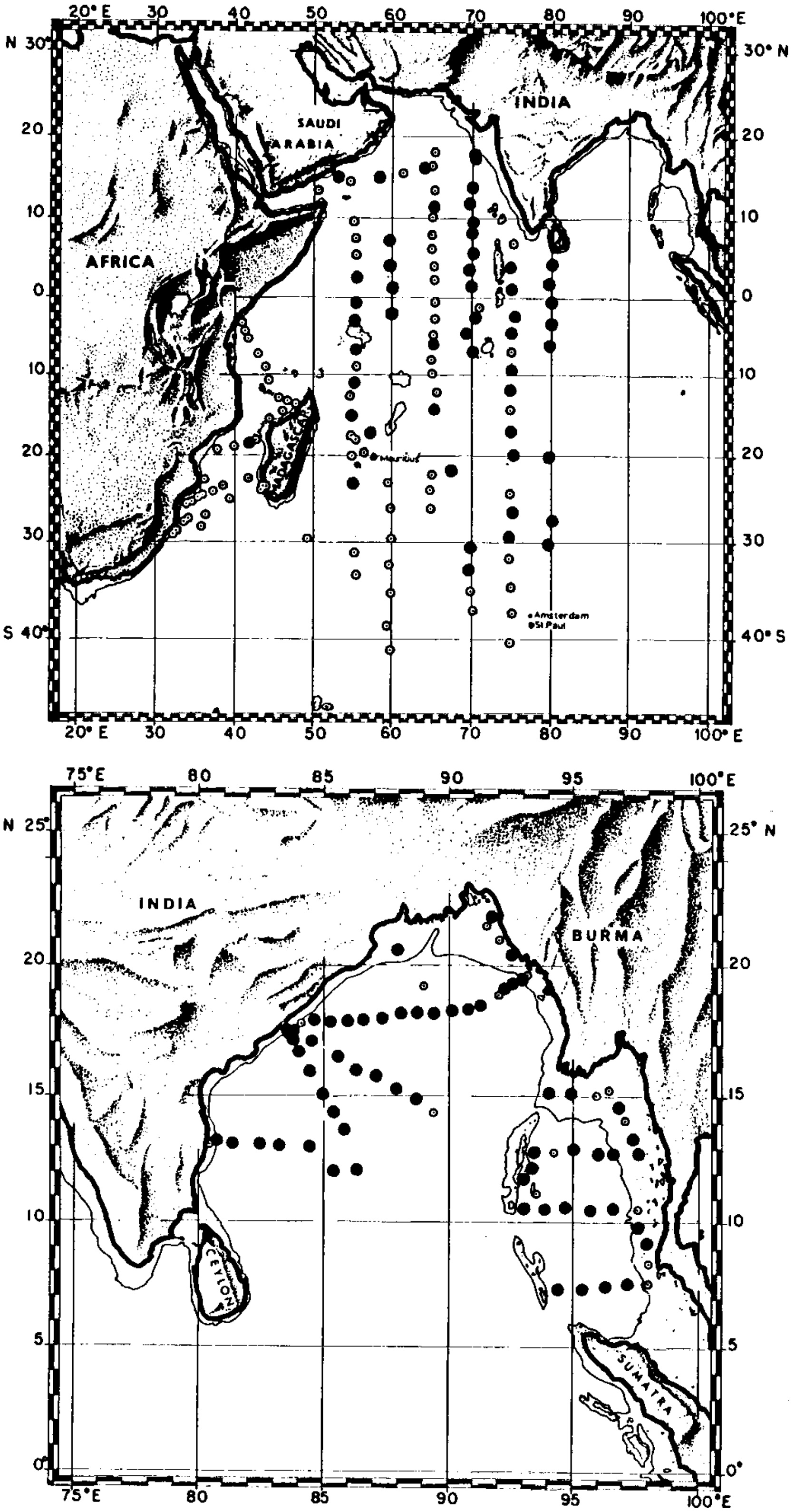

Chart 3. The Distribution of *Pyrocystis noctiluca*.

The majority of species in the material exhibited a northern and central Indian Ocean preference. The most obligate thermophiles, such as *Ceratocorys bipes, Amphisolenia thrinax, Ceratium inflatum, Gonyaulax fusiformis, Peridinium tenuissimum* and *Pyrocystis hamulus,* are found north of 20 °S, whereas the most common and widespread species tend to have a central southern limit nearer 30 °S. The latter is exemplified by *Pyrocystis noctiluca* (chart 3), one of the members of SUKHANOVA's (1962a, b) "basic tropical complex." Other members thought to compose this tropical group are *Ceratium carriense, C. massiliense* and *C. trichoceros.* DESROSIÈRES (1965) and TAYLOR (1973b) have commented on this grouping, pointing out that it includes dissimilar elements, some being thought to be relatively stenothermal (*C. trichoceros, C. carriense*) while the others are more thermotolerant. There are several other species which could be appropriately added to this grouping in view of their common and widespread occurrence in tropical and subtropical waters. For example *Ceratocorys horrida* is a common high-temperature species, *Heteraulacus polyedricus* and *Pyrophacus steinii* being more thermotolerant.

GRAHAM & BRONIKOVSKY (1944) referred to *Ceratium euarcuatum* as "one of the best indicators of warm tropical water" in their material from the Atlantic and Pacific Oceans. In the "Anton Bruun" samples it had an interesting distribution (chart 4). It was more widespread, especially in the southern central region, than one might expect from GRAHAM & BRONIKOVSKY's description, reaching 38 °S in September on cruise III. The large hiatus between 5 °S and 10 °N suggests an absence from the equatorial currents. *C. carriense,* on the other hand, although mostly absent from the South Equatorial Current, was present in the northern, eastwardflowing currents. The lack of records of both from the mid-Mozambique Channel (although found at both ends of it) is seen in the distribution of many other species.

It is evident from the studies of SOURNIA (e.g. 1968d) that relatively poor dinoflagellate populations are present at inshore locations in the Mozambique Channel region for most of the year. At Nosy-Bé, Madagascar, maximum numbers occur in winter (May to September). During "Anton Bruun" cruises VII and VIII (September, October) the open Channel stations were relatively poor in dinoflagellates. The distribution of several other species of *Ceratium,* found commonly both north and south of the Channel, showed a striking absence in the central stations. Examples of these were *C. macroceros* (EHR.) VANH., *C. gibberum* GOURRET, *C. tripos* var. *indicum* (BÖHM) comb. nov., and *Peridiniopsis asymmetrica* MANGIN. The most widespread species in the material, *Pyrocystis noctiluca* MURRAY, was found at only one station west of Madagascar, although it has been found in the Channel and to the south at other times by several authors (SOURNIA 1967b, 1970; TAYLOR 1967 and NEL 1968). The period when the samples were taken in the Mozambique Channel was prior to the summer rains, and the water was relatively cool with a high salinity. MENACHE (1963) found that during one October-November period the dynamic topography in the Mozambique Channel, plotted relative to the 1000 decibar level, indicated that an anticyclonic gyre was present instead of a smooth southward flow through the Channel, and it may be this type of circulation which contributes to the sparseness of the dinoflagellates.

It must be borne in mind that samples taken inshore in less than 25 m of water may not be indicative of the fluctuations of dinoflagellates only a short distance further out from the coast. Unpublished observations by this author in the vicinity of Phuket Island, Andaman Sea, showed that dinoflagellates were very sparse from inshore samples where the depth was less than 25 m. Only a few miles further offshore in 30 to 80 m of water, the number and variety was greatly increased.

The majority of species found here occurred at one or more stations within the Andaman Sea or the Bay of Bengal. It appears that the period following the North East Monsoon (cruise I, March to May) is one of great richness in dinoflagellates in the offshore waters of this region. This applied particularly to samples from the Andaman Sea and the central east coast of India. Indicative of this was the recognition of 88 dinoflagellate taxa from one sample (station 103). ZERNOVA & IVANOV (1964) found large numbers of dinoflagellates in the Andaman Sea during the N.E. Monsoon, with lower numbers in the Bay of Bengal.

By contrast, the Arabian Sea samples were disappointingly sparse. There were no samples from the south coast of Arabia during cruise IVa when extremely high productivity was measured (RYTHER & MENZEL 1965), apparently associated with the eastward-flowing Somali Current. However RYTHER et al. (1966) found that productivity was still high during cruise V in the same area. An examination of the samples from that area (284–287) showed that thecate dinoflagellates did not contribute greatly to this high productivity, although there were the poorly-preserved remains of a small flagellate, coccolithophorids, and large amounts of detritus. Cruise II was undertaken off the west coast of India during the S.W. Monsoon, but the stations were further offshore than the coastal areas of upwelling and high productivity known to occur at such times (cf. BANSE 1968). Diatoms have been found to be a major constituent of such blooms. Increases in the number of species of dinoflagellates were found here near the island chains of the Laccadives and Maldives.

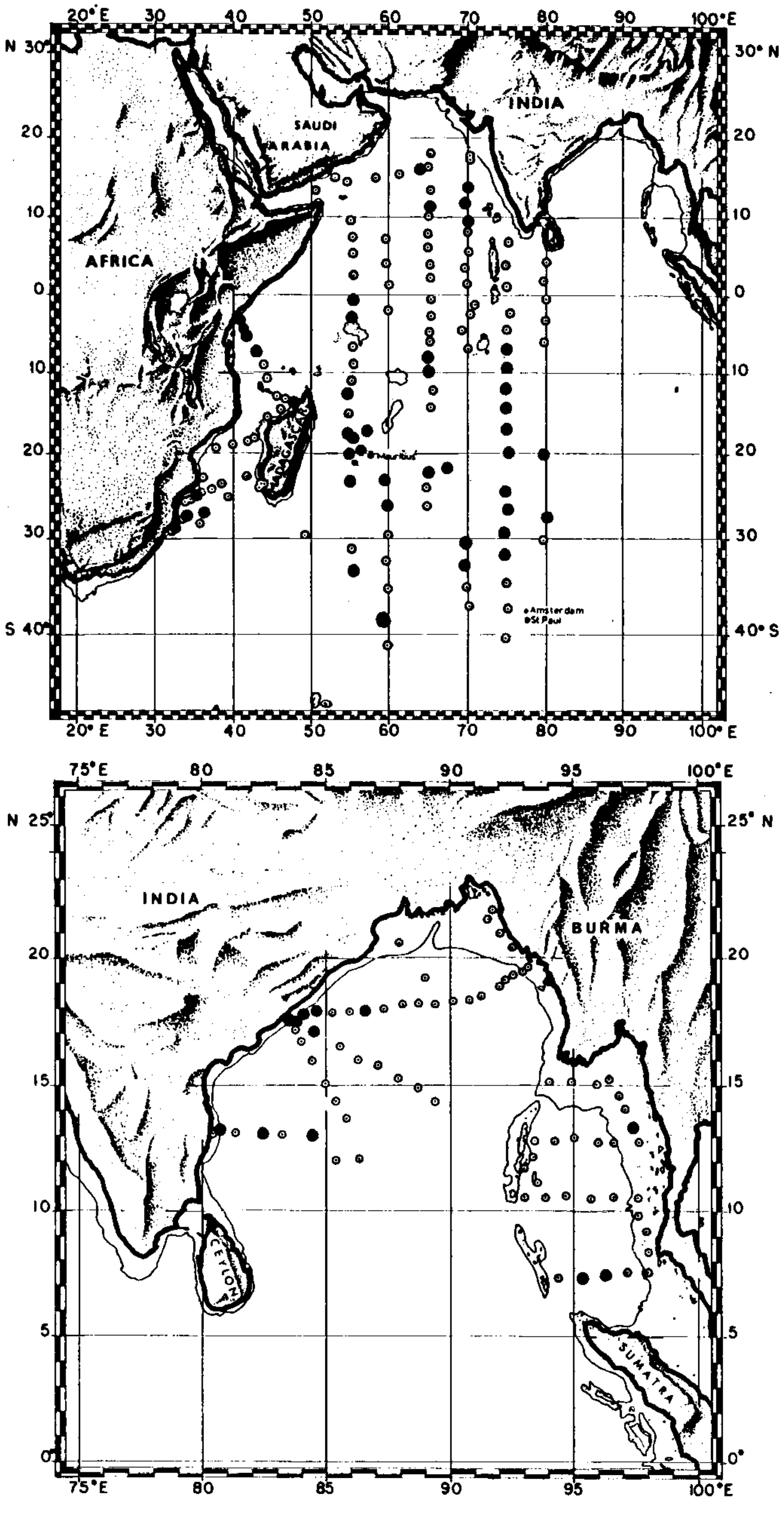

Chart 4. The Distribution of *Ceratium euarcuatum*.

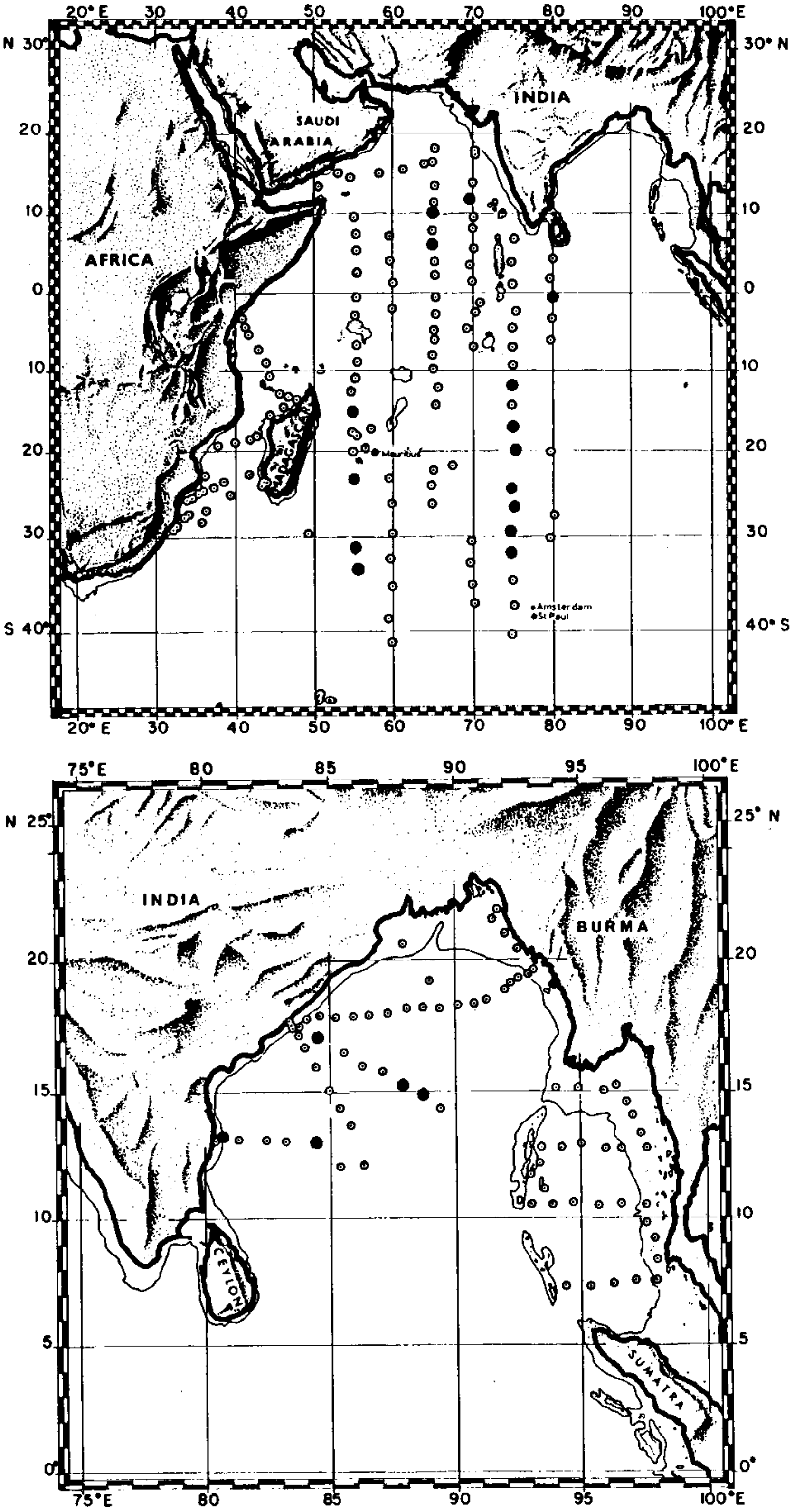

Chart 5. The Distribution of *Cladopyxis brachiolata.*

Increases in the dinoflagellates were evident at stations near the equatorial current shear zones and particularly near the equator. ZERNOVA (1962) found an increase in the dinoflagellates collected by the "Vityaz" at the equator, with a reduction in the South Equatorial Current and a moderate increase south of it. SUKHANOVA (1962b) also found an increase in the members of her "basic tropical complex" at stations situated between the South Equatorial Current and the Equatorial Counter Current. This region is termed the South Equatorial Divergence, and is situated between 3 °S and 8 °S, depending on the season (BEZRUKOV 1963; ZERNOVA 1967).

Another rich area for dinoflagellates was immediately to the north of the Seychelle Islands Platform. The Equatorial Counter Current was flowing close to the north of it when large numbers were found at station 294.

In the southern central Indian Ocean below 30 °S samples were poor in dinoflagellates. Only when the Subtropical Convergence Region is reached near 40 °S is there a slight increase in dinoflagellates, diatoms showing a greater increase. A few species, notably *Cladopyxis brachiolata* (Chart 5) and *Ceratium falcatiforme,* although also occurring in warmer waters, showed marked increases near the islands of Amsterdam and St. Paul within this region. Many species of *Oxytoxum* seem to have a preference for the cooler oceanic waters north of the Subtropical Convergence Region.

Samples were not taken from the south west Indian Ocean or the eastern Indian Ocean during these cruises. However it is known from other studies that there is a relatively rich dinoflagellate flora off the east coast of South Africa, including many tropical species borne south-westwards by the warm Agulhas Current (TAYLOR 1967; NEL 1968; THORRINGTON-SMITH 1969).

By comparison the eastern Indian Ocean is very poor in phytoplankton due to low nutrient levels, except for seasonal (August-September) upwelling south of Java, Timor, and off the north-west coast of Australia. TSURUTA (1963) and DESROSIÈRES (1965) found relatively few species in this area.

In brief, then, endemicism is rare and is restricted to the waters of the Indo-Malayan Archipelago. The greatest number of species occurred in the Andaman Sea and Bay of Bengal. Increases were found near oceanic divergences. The eastern and southern central Indian Ocean are known to be very impoverished in dinoflagelattes. In the south west Indian Ocean the Agulhas Current extends the distribution of tropical species well south of their general latitudinal limits.

TAYLOR (1973b) has indicated that seasonal northern and southern shifts in the surface temperature structure and species distribution are not restricted to the northern Indian Ocean (where they are obviously associated with monsoonal reversals), but also extend into the southern Indian Ocean. This is apparently related, not only to the shifting positions of major currents, but also to the seasonal breakdown of the thermocline in the open southern Indian Ocean (TAYLOR 1967). It is evident that seasonal effects must be taken into account when discussing the distribution of any planktonic organisms in these waters.

Appendix

Latin diagnoses for new taxa

Below are the Latin diagnoses for new taxa described elsewhere in the text. They were kindly prepared for the author by Dr. HANNAH CROASDALE.

New Families

Leptodiscaceae fam. nov.

Cellulae Noctilucoideae, anterio-postice valde applanatae. Extensiones aliformes veli nec cingulo nec sulco consociatae; sulcus saepe reductus. [= Leptodiscinae J. et M. CACHON, subfamilia zoologica]

Kofoidiniaceae fam. nov.

Cellulae Noctilucoideae, maturae valde applanatae. Cingulum marginem anteriorem cellulae circumscripsit, sulco secundum marginem posteriorem extendente, latus dorsale attingente. [= Kofoidininae J. et M. CACHON, subfamilia zoologica]

New Species

Palaeophalacroma sphaericum sp. nov.

Cellulae parvae, subsphaericae; cingulum aliquantulum premedium, solum crista superiore evoluta. Areola ventralis per cristam tenuem circumdata, antapicem non attingens. Cristae apicem cingulo medio-ventraliter coniungunt. Superficies thecalis poroideis sparsis tecta. Species a *P. verrucoso* differt ut forma plus rotundata atque cristae plus evolutae. Longitudo 20 μm; transdiameter 18 μm. Iconotypus: Tab. 25, figs. 261 a, b. Locus typi: Oceanicus Indicus occidento-centralis.

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Gonyaulax bruunii sp. nov.

Cellulae parvae, rotundatae, cornu apicali bene evoluto. Cingulum par latitudinem unius vel douroum cingulorum dispositum. Una spina antapicalis prominens tenuis adest, e margine dextro posteriore areolae ventralis enascens, pinnis lateralibus nullis. Laminae thecales solum poris signatae. Epitheca medio-ventralis e duabus, non uno, laminis apicalibus tenuibus constat. Sexta lamina precingularis triangularis. Prima lamina postcingularis parva et anguste rectangularis. Lamina intercalaris posterior tam longe quam lamina sulcalis posterior non antapicaliter extendit. Suturae delicatae nisi cristae validae cinguli atque margines areolarum ventralium. Longitudo (sine spines) 30–36 μm; transdiameter 20–26 μm. Formula laminarum 4', 0^a, 6'', 6C, 5(?)S, 6''', 1^p, 1''''. Iconotypus: Tab. 35, figs. 409 a–d. Locus typi: Locus Mozambique Channel dictus.

Balechina marianae sp. nov.

Cellulae gymnodinoideae. Amphiesma incrassatum, valde vesiculatum, costis linearibus praeditum. Mamilla prominens lata apicaliter sita. Cingulum profunde impressum, per quintum quartumve transdiametrum sinustrosus dispositum. Epitheca hypothecaque cellularum maturarum longitudine subaequae. Forma interdum modice varians. Chloroplasti nulli. Nucleus in hypocono iacet. Longitudo cellularum 115–120 μm; transdiameter 70–76 μm. Cellulae non manifeste applanatae.

Nomen huius speciei Marian E.W. SLATER, auctori adiutricem, honorat. Iconotypus: Tab. 37, fig. 442, Tab. 40, f. 480. Locus typi: Locus Bay of Bengal dictus.

Oxytoxum lativelatum sp. nov.

Species parva rotundataque; hypotheca multo maior quam epitheca; cingulum latum, quasi a quarta ad quintam partem longitudinis cellulae. Epitheca convexa, sine papilla apicali, margine inferiore aliquantulum crenulato. Hypothece lenticularis, antapicem acutum praebens. Cellula latissima prope medio-longitudinem. Superficies thecalis subtiliter reticulata. Pinna hyalina delicatula in latere dorsali regionis pori flagellaris eminet, ab epitheca ad hypothecam extendens. Spina brevis in cellulam infra porum flagellarem eminet. Longitudo 28 µm; transdiameter 18 µm. Iconotypus: Tab. 24, figs. 240 a, b. Locus typi: Oceanus Indicus Australis.

Oxytoxum semicollatum sp. nov.

Cellulae minimae, epitheca longitudine quinta pars longitudinis totae, rotunde conica. Cingulum latum, latitudine quarta pars longitudinis totae. Hypotheca ad cingulum latissima; antapex acutus. Signa superficia porulis sparsis delicata. Collare cinguli inferioris delicatum antice, non extrorsus, eminet, altius dextra quam sinistra, aegre visum. Sulcus hypothecam paululum incidit. Iconotypus: Tab. 24, fig. 241. Locus typi: Ora Mozambique.

Peridinium paradoxum sp. nov.

Cellulae mediocres rotundatae, antapice paululum inciso, dorso-ventraliter satis compresso. Porus apicalis tubularis parvus adest. Prima lamina apicalis pentagonalis; secunda lamina intercalaris anterior hexagona. Cingulum per latitudinem trium cingulorum dextrorsus (ascendenter) dispositum, extremitatibus ob torsionem sulci superpositis. Porus flagellaris posterioris ventraliter positus, ora incrassata praeditus. Spinae antapicales nullae aut minimae. Longitudo 82–94 µm; transdiameter 76–82 µm. Iconotypus: Tab. 29, figs. 307 a, b. Locus: Mare Andaman.

Berghiella josephinae sp. nov.

Cellulae mediocres; corpus rotundatus, cornu apicale breve ex epicono leviter enascens habens, ad apicem truncatum. Membrana flexibilis, in laminis non divisa, reticulata. Cingulum, latere supetiore sinistro excepto, cristis cinguliaribus superpendentibus impressum; sine amotione. Signa linearia in cingulo et huic contigua. Apertura flagellaris magna, singularis. Areola ventralis et epiconum et hypoconum breviter incidit. Longitudo 70 µm, transdiameter 70 µm.

Nomen huius speciei mortuam Josephine Rigden Michener, co-auctorem generis, honorat. Iconotypus: Tab. 37, fig. 441. Locus typi: Oceanus Indicus Borealis.

Pyrocystis apiculata sp. nov.

Cystes late ellipsoideae; 370–420 µm longitudine, apiculo membranam crassiorem habente in una extremitate praeditae. Multi chloroplasti et guttulae olei adsunt. Cyclus vitae ignotus. Iconotypus: Tab. 39, fig. 474. Locus typi: Prope Zanzibar.

Pronoctiluca rostrata sp. nov.

Cellulae fusiformes, apicibus acutis dissimilaribusque. Regio apicalis brevis cylindrica tentaculum gracilem fert atque canaliculum sulcalem habet. Medio-corpus magnum, ad utram extremitatem attenuatum. Antapex acutus, rostratus, e medio-corpore abrupte enascens. Membrana aspectu tenuis granulosaque. Chloroplasti nulli. Corpora accumulationis magna interdum adsunt. Longitudo cum tentacula 115–128 µm; longitudo medio-corporis 74–78 µm; longitudo processus rostrati 25–28 µm. Iconotypus: Tab. 37, fig. 425. Locus typi: versus meridiem et occidentatem a India.

New Infraspecific Taxa

Ceratium lunula (SCHIMPER ex KARSTEN) JÖRGENSEN var. *robustum* var. nov.

— Varietas a var. *lunula* differens ut corpus maius et superficies epithecales superiores convexiores, et cornua antapicalia magis attenuata. Collaria valida in partibus superioribus proximalibus cornum antapicalium reperta. Theca cristas longitudinales validas habet. Transdiameter cinguli maior quam 100 µm. Iconotypus: Tab. 18, fig. 183. Locus typus: Mare Arabicum.

Ceratium trichoceros (EHRENBERG) KOFOID forma *crypticum* f. nov.

— Forma a f. *trichocerote* differens possessione duorum cornuum antapicalium brevium tenuiorum, paululum divergentium, numquam, autem, apicem versus reflexorum. Facies obliqua posterioris corporis ad planum cinguli tantum modice inclinata. Cornu apicale rectum. Iconotypus: Tab. 12, fig. 117. Locus typi: Sinus Bengalensis.

Pyrocystis hamulus CLEVE var. *reflexus* var. nov.

— Varietas a varietate *hamulo* differens ut utrumque brachium cystis ex adverse reflexum, curvans, post e corpore ad angulum solitum primum emergens. Iconotypus: Tab. 38, fig. 447. Locus typi: Mare Arabicum.

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Explanation of Plates 1–46

Plate 1. *Prorocentrum, Dinophysis*

1. *Prorocentrum micans* EHRENBERG. An atypically shaped individual. St. 112. – 2. *P. gracile* SCHÜTT. St. 405. – 3 (4? 5?). *P. triestinum* SCHILLER. (3) St. 374, (4) St. 374, (5) St. 15. – 6. *P. veloi* TAFALL; a) broad lateral view, b) seam view. St. 15. – 7. *P. oblongum* (SCHILLER) comb. n. St. 396. – 8, 9. *P. compressum* (BAILEY) ABÉ; (8) St. 15, (9) St. 341. – 10. *P. magnum* (GAARDER) DODGE St. 344. – 11, 12. *P. lenticulatum* (MATZENAUER) comb. n. (11) St. 336, (12) St. 370.– 13. *P. pyriforme* (SCHILLER) HASLE. St. 288. – 14. *P. cordatum* (OSTENFELD) comb. n.; an elongate form. St. 56. – 15. *P. cordatum* (OSTENFELD) DODGE; the more usual form. St. 288. – 16 *P. ovale* (GOURRET) SCHILLER; a single valve lacking the pore plate and spine. St. 56. – 17. *P. minimum* (PAVILLARD) SCHILLER var. *mariae-lebourae* (PARKE et BALLANTINE) HULBURT. St. 310. – 18. *P.* species 1; cell enclosed with a delicate mucilagenous sheath; a) valve view, b) seam view. St. 147. – 19. *Dinophysis ruudii* (BRAARUD) BALECH; a) ventral view, b) left lateral view, c) apical view. St. 147.

Plate 2. *Amphisolenia*

20. *Amphisolenia thrinax* SCHÜTT. St. 333. – 21. *A. bidentata* SCHRÖDER. St. 398. – 22. *A. bidentata* SCHRÖDER. St. 333. – 23. *A.* sp. St. 108. – 24. *A. astragalus* KOFOID et MICHENER. St. 33. – 25. *A. spinulosa* KOFOID. St. 102. – 26. *A. globifera* STEIN. St. 35. – 27. *A. globifera* STEIN. St. 68. – 28. *A. schauinslandii* LEMMERMANN. St. 288. – 29. *A. schauinslandii* LEMMERMANN. St. 68. – 30. *A. asymmetrica* KOFOID. St. 102. – 31. *A. palaeotheroides* KOFOID. St. 294. – 32. *A. schroederi* KOFOID. St. 109.

Plate 3. *Amphisolenia*-details, *Triposolenia*

21b. *A. bidentata* SCHRÖDER; antapex. St. 398. – 22b. *A. bidentata* SCHRÖDER. St. 333. – 23b. *A.* sp. St. 108. – 24b. *A. astragalus* KOF. et MICHENER; antapex. St. 33. – 25b. *A. spinulosa* KOFOID (ventral view). St. 102. – 26b. *A. globifera* STEIN (left side). St. 35. – 27b. *A. globifera* STEIN (right side). St. 68. – 28b. *A. schauinslandii* LEMMERMANN; antapex. St. 288. – 30b. *A. asymmetrica* KOFOID. St. 102. – 31b. *A. palaeotheroides* KOFOID; antapex. St. 294. – 32b. *A. schroederi* KOFOID (ventral view). St. 109. – 33. *Triposolenia bicornis* KOFOID. St. 57.

Plate 4. *Dinophysis*

34. *D. brevisulcus* TAI et SKOGSBERG. St. 32. – 35. *D. argus* (STEIN) ABÉ. St. 341. – 36. *D. apicata* (KOF. et SKOGSB.) ABÉ. St. 323. – 37. *D. exigua* KOF. et SKOGSBERG. St. 359. – 38. *D. parvula* (SCHÜTT) BALECH. St. 52. – 39. *D. parvula* (SCHÜTT) BALECH. St. 106. – 40. *D.* sp. 1. St. 36. – 41. *D. doryphorum* (STEIN) ABÉ. St. 334. – 42. *D. doryphorum* (STEIN) ABÉ. St. 326. – 43. *D. circumsutum* (KARSTEN) BALECH. St. 404. – 44. *D. acutoides* BALECH? St. 325. – 45. *D. porodictyum* (STEIN) BALECH. St. 312.

Plate 5. *Dinophysis*

46. *D. cuneus* (SCHÜTT) ABÉ. St. 341. – 47. *D. cuneus* (SCHÜTT) ABÉ; right half immature; megacytic bridge remnant present. St. 289. – 48. *D. rapa* (STEIN) ABÉ; a) right side, b) ventral view. St. 294. – 49. *D. mitra* (SCHÜTT) ABÉ. St. 305. – 50. *D. favus* (KOF. et MICH.) BALECH. St. 312. – 51. *D. favus* (KOF. et MICH.) BALECH. St. 112. – 52. *D. hastata* STEIN; a mature individual. St. 15. – 53. *D. hastata* STEIN; newly-divided left daughter cell. St. 24. – 54. *D. hastata* STEIN (var. *uracanthides* JÖRG.); a variant with a less ventrally placed antapical fin. St. 16. – 55. *D. hastata* STEIN; a recently divided left daughter cell. St. 116. – 56. *D.* sp. 2; an immature left daughter cell. St. 62.

Plate 6. *Dinophysis*

57. *D. miles* CLEVE var. *schroeteri* (FORTI) BÖHM. St. 15. – 58. *D. miles* CLEVE var. *indica* BÖHM. St. 287. – 59. *D. caudata* SAVILLE-KENT. St. 45. – 60. *D. urceola* KOF. et SKOGSBERG? a) left side, b) right ventral view. St. 109. – 61. *D. infundibula* SCHILLER. St. 326. –

62. *D. expulsa* KOF. et MICHENER; a) ventral view, b) right side. St. 30. – 63. *D. swezyae* KOF. et SKOGSBERG; small size class. St. 57. – 64. *D. swezyae* KOF. et SKOGSBERG; large size class. St. 374. – 65. *D. schuettii* MURR. et WHITTING; large size class. St. 116. – 66. *D. schuettii* MURR. et WHITTING; small size class. St. 30.

Plate 7. *Ornithocercus*

67. *Ornithocercus magnificus* STEIN; a newly divided right daughter cell. St. 412. – 68. *O. magnificus* STEIN. St. 294. – 69. *O. magnificus* STEIN; a fully mature specimen. St. 147. – 70. *O. skogsbergii* ABÉ. St. 108. – 71. *O. thumii* (A. SCHMIDT) KOF. et SKOGSB; a recently divided left daughter cell. St. 296. – 72. *O. thumii* (A. SCHMIDT) KOF. et SKOGSB. St. 344. – 73. *O. steinii* SCHÜTT. St. 331. – 74. *O. thumii* (A. SCHMIDT) KOF. et SKOGSB. St. 328. – 75. *O. formosus* KOF. et MICHENER. St. 67. – 76. *O.* sp.; an immature specimen in which the posterior moiety of the left sulcal list is undergoing redevelopment. St. 338.

Plate 8. *Ornithocercus*

77. *O. quadratus* SCHÜTT var. *schuettii* (KOF. et SKOGSB.) stat. n. St. 14. – 78. Apical view of *O. quadratus* var. *quadratus*. St. 296. – 79. *O. quadratus* SCHÜTT var. *assimilis* (JÖRGENSEN) comb. n. St. 412. – 80. *O. quadratus* SCHÜTT var. *quadratus* – with an unusual dorsal projection of the left sulcal list. St. 342. – 81. *O. quadratus* SCHÜTT var. *simplex* (KOF. et SKOGSBERG.) stat. n. An immature right daughter cell soon after fission. St. 300. – 82. *O. quadratus* SCHÜTT var. *assimilis* (JÖRGENSEN) comb. nov. St. 150. – 83. *O. heteroporus* KOFOID. St. 35. – 84. *O. francescae* (G. MURRAY) BALECH. St. 320. – 85. *O. splendidus* SCHÜTT. St. 405. – 86. *O. splendidus* SCHÜTT; the left dorsal hypothecal plate and right ventral hypothecal plate, with attached lists. St. 322.

Plate 9. *Parahistioneis, Histioneis*

87. *Parahistioneis para* MURR. et WHITTING. St. 56. – 88. *P. para* MURR. et WHITTING. St. 67. – 89. *Histioneis biremis* STEIN. St. 62. – 90. *H. dolon* MURR. et WHITTING. St. 361. – 91. *H. hippoperoides* KOF. et MICH. St. 58. – 92. *H. hippoperoides* KOF. et MICH.? St. 63.

Plate 10. *Histioneis, Citharistes*

93. *Histioneis hyalina* KOF. et MICH. St. 417. – 94. *H. depressa* SCHILLER. St. 103. – 95. *H. pulchra* KOFOID. St. 28. – 96. *H. panda* KOF. et MICH. St. 58. – 97. *H. mitchellana* MURR. et WHITT. St. 33. – 98. *Citharistes apsteinii* SCHÜTT; a) right side, b) dissociated right dorsal girdle plate. St. 71.

Plate 11. *Ceratium*, Subgenus *Archaeceratium*

99. *C. gravidum* GOURRET. St. 324. – 100. *C. gravidum* GOURRET; the most extreme variety with regard to epithecal expansion, being greater than var. *latum* JÖRG. St. 31. – 101. *C. gravidum* GOURRET; more elongate than "var. *angustum*" JÖRG., corresponding with the "var *elongatum*" of WOOD (1963b); a) ventral view, b) left lateral view. St. 325. – 102. *C. praelongum* (LEMM.) KOF. ex Jörg., st. 15. – 103. *C. praelongum* (LEMM.) KOF. ex JÖRG.; hypotheca only, showing a variation of the left antapical horn. St. 417. – 104. *C. schroeteri* B. SCHRÖDER. St. 68. – 105. *C. digitatum* SCHÜTT. St. 19. – 106. *C. cephalotum* (LEMM.) JÖRG. St. 340.

Plate 12. *Ceratium*, Subgenera *Ceratium* and *Tripoceratium*

107, 108. *C. furca* (EHRENB.) CLAP. et LACHM. var. *eugrammum* (EHRENB.) SCHILLER; limited to tropical waters. (107) St. 331, (108), St. 36. – 109. *C. furca* (EHRENB.) CLAP. et LACHM. var. *furca* [= var. *berghii* (LEMM.)]; occurring in both tropical and temperate waters. St. 288. – 110. *C. teres* KOFOID. St. 358. – 111. *C. pentagonum* GOURRET var. *subrobustum* JÖRG. St. 411. – 112. *C. pentagonum* GOURRET var. *tenerum* JÖRG. St. 344. – 113. *C. pentagonum* GOURRET var. *longisetum* (OST. et J. SCHM.) JÖRG. St. 15. – 114. *C. setaceum* JÖRG. St. 69. – 115. *C. setaceum* JÖRG. St. 327. – 116. *C. ehrenbergii* KOFOID. St. 104. – 117. *C. trichoceros* (EHRENBERG) KOFOID f. *crypticum* f. nov. St. 47. – 118. *C. incisum* (KARSTEN) JÖRG. St. 418. – 119. *C. belone* CLEVE. St. 17. – 120. *C. minutum* JÖRG. St. 313. – 121. *C. lineatum* (EHRENB.) CLEVE. St. 340. – 122. *C. boehmii* GRAHAM et BRON. (= *C. kofoidii* JÖRG.?). St. 338. – 123. *C. boehmii* GRAHAM et BRON. St. 38. – 124. *C. candelabrum* (EHRENB.) STEIN var. *candelabrum*. St. 359. – 125. *C. candelabrum* (EHRENB.) STEIN var. *depressum* (POUCHET) JÖRG. St. 298. – 126. *C. candelabrum* (EHRENB.) STEIN forma *subrotundum* (PAVILLARD) SOURNIA. This form represents specimens which have undergone autotomy. St. 147.

Plate 13. *Ceratium*, Subgenus *Amphiceratium*

127. *C. biceps* CLAP. et LACHM. [= *C. extensum* (GOURRET) CLEVE]. St. 343. – 128. *C. biceps* CLAP. et LACHM. St. 360. – 129. *C. fusus* (EHRENBERG) DUJARDIN var. *fusus*. St. 47. – 130. *C. fusus* (EHR.) DUJ. var. *seta* (EHR.) SCHILLER. St. 341. – 131. *C. longirostrum* GOURRET; a) left ventral view, b) dorsal view. St. 362. – 132. *C. inflatum* (KOF.) JÖRG. St. 318. – 133. *C. falcatum* (KOF.) JÖRG. St. 312. – 134. *C. bigelowii* KOFOID. St. 27. – 135. *C. bigelowii* KOFOID. A dissociated epitheca. St. 125. – 136. *C. fusus* (EHR.) DUJ. var. *schuettii* LEMM.? A very small specimen (see text). St. 45. – 137. *C. fusus* (EHR.) DUJ. var. *schuettii* LEMM.? Lateral view. St. 370. – 138. *C. falcatiforme* JÖRG. St. 310. – 139. *C. falcatiforme* JÖRG. St. 306. – 140. *C. geniculatum* (LEMM.) CLEVE. [Two scales, one to facilitate comparison with the other figures on the plate, the other to illustrate detail] St. 302.

Plate 14. *Ceratium*, Subgenus *Tripoceratium*, Section *Tripos*

141. *C. breve* var. *parallelum* (J. SCHMIDT) JÖRG., tending towards the var. *breve*. An anterior terminal cell from a chain. St. 108. – 142. *C. breve* var. *breve*, with moderately in-curving antapical horns. St. 420. – 143–145. *C. breve* var. *schmidtii* (JÖRG.) SOURNIA. The degree of ventral concavity, shown in fig. 145, is variable, sometimes being greater than shown. (143) St. 88, (144) St. 106, (145) St. 107. – 146. *C. breve* var. *parallelum* (J. SCHMIDT) JÖRG. St. 331. – 147. *C. tripos* var. *pulchellum* (SCHRÖDER) LOPEZ forma *pulchellum*, showing extreme reduction of the right antapical horn. St. 294. – 148. *C. humile* JÖRG.; a short apical-horned individual probably from a chain. St. 39. – 149. *C. tripos* var. *atlanticum* (OST.) PAULSEN; resembling the probably synonymous *C. tripodioides* JÖRG. St. 285. – 150. *C. tripos* var. *pulchellum* (SCHRÖDER) LOPEZ forma *semipulchellum* JÖRG. St. 341. – 151. *C. tripos* var. *atlanticum* (OSTENFELD) PAULSEN. St. 420.

Plate 15. *Ceratium*, Subgenus *Tripoceratium*, Section *Tripos*

152. *C. symmetricum* PAVILLARD var. *orthoceras* (JÖRG.) GRAHAM et BRONIKOVSKY. St. 321. – 153. *C. symmetricum* PAV. var. *coarctatum* (PAV.) GRAHAM et BRON., St. 16. – 154. *C. symmetricum* PAV. var. *symmetricum*. St. 323. – 155. *C. euarcuatum* JÖRG.; slender-horned form. St. 15. – 156. *C. symmetricum* PAV. var. *coarctatum* (PAV.) GRAHAM et BRON.; short horned, unequal length form. St. 313. – 157. *C. euarcuatum* JÖRG.; robust-horned form. St. 306. – 158. *C. axiale* KOFOID. St. 129. – 159. *C. euarcuatum* JÖRG.? with a highly aberrant left horn. St. 158. – 160. *C. azoricum* CLEVE. St. 17. – 161. *C. petersii* STEEMANN NIELSEN. St. 159.

Plate 16. *Ceratium*, Subgenus *Tripoceratium*, Section *Tripos*

162. *C. arietinum* CLEVE var. *arietinum*. St. 362. – 163. *C. declinatum* var. *majus* JÖRG. St. 159. – 164. *C. declinatum* var. *angusticornum* JÖRG. St. 62. – 165. *C. arietinum* var. *gracilentum* (JÖRG.) SOURNIA. St. 313. – 166. *C. declinatum* var. *declinatum*. St. 326. – 167. *C. declinatum* var. *angusticornum* JÖRG., tending towards var. *brachiatum* (JÖRG.) stat. n. St. 294. – 168. *C. tripos* var. *indicum* (BÖHM) comb. n. St. 371. – 169. *C. tripos* var. *indicum* (BÖHM) comb. n. St. 419. – 170. *C. tripos* var. *pulchellum* (SCHRÖDER) LOPEZ forma *semipulchellum* JÖRG.; superficially resembling *C. declinatum* but markedly larger. St. 366. – 171. *Ceratium lunula* (SCHIMP. ex KARST.) JÖRG. var. *lunula*. St. 38.

Plate 17. *Ceratium*, Subgenus *Tripoceratium*, Sections *Densa*, *Tripos*, *Reflexa*

172. *C. dens* OSTENFELD et SCHMIDT. St. 287. – 173. *C. reflexum* CLEVE; an autotomised specimen. St. 116. – 174. *C. carnegei* GRAHAM et BRONIKOVSKY. St. 420. – 175. *C. longissimum* (SCHRÖDER) KOFOID. St. 294. – 176, 177. *C. schrankii* KOFOID. (176) St. 125, (177) St. 360.

Plate 18. *Ceratium*, Subgenus *Tripoceratium*, Sections *Limulus*, *Tripos*

178. *C. paradoxides* CLEVE. St. 334. – 179. *C. contortum* (GOURRET) CLEVE var. *subcontortum* (SCHRÖDER) stat. n. St. 320. – 180. *C. contortum* (GOURRET) CLEVE var. *contortum*. St. 347. – 181. *C. contortum* (GOURRET) CLEVE var. *saltans* (SCHRÖDER) JÖRG. St. 294. – 182. *C. limulus* (GOURRET ex POUCHET) GOURRET. St. 288. – 183. *C. lunula* (SCHIMPER ex KARSTEN) JÖRG. var. *robustum* var. n. The apical horn length is variable and may also bend towards the cell's left. St. 329. – 184. *C. contortum* (GOURRET) CLEVE var. *karstenii* (PAVILLARD) SOURNIA. Usually individuals of this variety have a longer right antapical horn than this specimen and the horn often has a distal twist. St. 340.

Plate 19. *Ceratium*, Subgenus *Tripoceratium*, Sections *Tripos*, *Palmata*

185. *C. platycorne* VON DADAY var. *platycorne* (= var. *cuneatum* JÖRG.) St. 418. – 186. *C. concilians* JÖRG. St. 341. – 187. *C. gibberum* GOURRET var. *dispar* (POUCHET) SOURNIA. St. 330. – 188. *C. platycorne* DADAY var. *dilatatum* (KARSTEN) JÖRG. St. 320. – 189. *C. ranipes* CLEVE var. *palmatum* (SCHRÖDER) CLEVE. St. 416. – 190. *C. ranipes* CLEVE var. *palmatum* f. *furcellatum* (LEMMERMANN) stat. n. St. 419. – 191. *C. ranipes* var. *palmatum* f. *furcellatum* (LEMMERMANN) stat. n. Regrowth of the autotomised parts appears to have begun. St. 155. – 192. *C. ranipes* CLEVE var. *ranipes*; an autotomised specimen. St. 32.

Plate 20. *Ceratium*, Subgenus *Tripoceratium*, Section *Macroceros*

193. *C. massiliense* (GOURRET) KARSTEN var. *armatum* (KARSTEN) JÖRG. (warm water form). St. 147. – 194. *C. massiliense* (GOURRET) KARST. var. *massiliense*. St. 329. – 195. *C. massiliense* (GOURRET) KARST. var. *armatum* (KARSTEN) JÖRG. (cold water form). St. 310. – 196. *C. massiliense* (GOURRET) KARST. var. *massiliense*. St. 313. – 197. *C. deflexum* (KOFOID) JÖRG. St. 406. – 198. *C. macroceros* (EHRENB.) CLEVE var. *gallicum* (KOFOID) SOURNIA. St. 348. – 199. *C. macroceros* (EHRENB.) CLEVE var. *gallicum* (KOFOID) SOURNIA. St. 347. – 200. *C. carriense* GOURRET var. *carriense*. St. 335. – 201. *C. vultur*? An autotomised specimen which resembles *C. carriense*. St. 317. – 202. *C. horridum* GRAN var. *denticulatum* JÖRG. St. 335.

Plate 21. *Ceratium*, Subgenus *Tripoceratium*, Section *Macroceros*

203. *C. horridum* GRAN var. *inclinatum* (KOF.) stat. n. St. 327. – 204. *C. horridum* GRAN var. *tenue* (OST. et SCHMIDT) stat. n. St. 294. – 205. *C. horridum* GRAN; an autotomised small specimen, perhaps of var. *tenue*, or possibly a male gamete. St. 327. – 206. *C. horridum* GRAN; possibly a male gamete or an autotomised var. *molle*. St. 415. – 207. *C. horridum* GRAN var. *horridum*. St. 324. – 208. *C. horridum* GRAN var. *molle* (KOF.) GRAHAM et BRON. St. 324. – 209. *C. recurvatum* SCHRÖDER. St. 342. – 210. *C. trichoceros* (EHRENB.) KOFOID. St. 348. – 211. *C. horridum* GRAN var. *claviger* (KOF.) GRAHAM et BRON. St. 298. – 212. *C. horridum* GRAN var. *patentissimum* (OST. et SCHMIDT) stat. et comb. n. [= *C. tenue* f. *tenuissimum* (KOF.) JÖRG.]. St. 318. – 213. *C. contrarium* (GOURRET) PAVILLARD. St. 287.

Plate 22. *Ceratium*, Subgenus *Tripoceratium*, Section *Macroceros*

214. *C. hexacanthum* GOURRET var. *hexacanthum*: an autotomised form. St. 361. – 215. *C. hexacanthum* GOURRET var. *hexacanthum* forma *spirale* (KOF.) SCHILLER. St. 43. – 216. *C. obesum* PAVILLARD. Ventral view. St. 294. – 217. *C. obesum* PAVILLARD. Apical view showing the ventral deflection of the apical horn. St. 294. – 218. *C. macroceros* (EHRENB.) CLEVE var. *macroceros*. St. 323. – 219. *C. hexacanthum* GOURRET var. *contortum* LEMM. St. 294. – 220. *C. vultur* CLEVE var. *vultur* forma *recurvum* (JÖRG.) SCHILLER. St. 418. – 221. *C. vultur* CLEVE var. *japonicum* (SCHRÖDER) JÖRGENSEN forma *japonicum*; delicate form close to the f. *neglectum* REINECKE. St. 56. – 222. *C. vultur* CLEVE var. *vultur* forma *angulatum* (JÖRG.) comb. n. St. 52. – 223. *C. vultur* CLEVE var. *japonicum* (SCHRÖDER) JÖRGENSEN forma *robustum* (OST. et SCHMIDT) stat. n. St. 344. – 224. *C. vultur* CLEVE var. *vultur* forma *sumatranum* (KARSTEN) SOURNIA. St. 294.

Plate 23. *Heterodinium*

225. *Heterodinium blackmanii* (MURR. et WHITT.) KOF. St. 109. – 226. *H. whittingae* KOFOID. St. 334. – 227. *H. rigdenae* KOFOID; St. 294. – 228. *H. fides* KOFOID. St. 109. – 229. *H. agassizii* KOFOID (dorsal view). St. 103. – 230. *H. rigdenae* KOF.? ; an immature specimen with unusually divergent antapical horns. St. 294. – 231. *H. globosum* KOFOID. St. 289. – 232. *H. milneri* (MURR. et WHITT.) KOF. St. 101. – 233. *H. inaequale* KOFOID. St. 412. – 234. *H. mediocre* (KOF.) KOF. et ADAMSON. St. 287. – 235. *H. sinistrum* KOF. et ADAMSON. St. 313. – 236. *H. doma* (MURR. et WHITT.) KOF.?; a specimen tending towards *H. sphaeroideum* KOF. St. 65.

Plate 24. *Centrodinium*, *Corythodinium*, *Oxytoxum*

237. *Centrodinium* sp. [= *Murayella mimetica* BALECH?]; a) ventral, b) left, and c) dorsal views. St. 103. – 238 a, b. *Corythodinium globosum* (KOFOID) comb. n. St. 61. – 239. *Oxytoxum parvum* SCHILLER. The globular posterior structure is probably an accumulation body. St. 18. – 240. *O. lativelatum* sp. n.; a) ventral view, b) right lateral view. St. 157. – 241. *O. semicollatum* sp. n. St. 371. – 242. *O. crassum* SCHILLER? The antapex is more pointed than in the original figure. St. 319. – 243. *O. variabile* SCHILLER. St. 336. – 244. *O. variabile* SCHILLER. St. 327. – 245. *O. nanum* HALLDAL. St. 404. – 246. *O. nanum* HALLDAL. Three-quarter left side view. St. 370. – 247. *O. globosum* SCHILLER; a specimen with a flatter epitheca than usual. St. 315. – 248. *O. viride* SCHILLER. St. 335. – 249. *O. laticeps* SCHILLER. St. 374. – 250. *O. pachyderme* SCHILLER ex TAYLOR. St. 312. – 251. *O. subulatum* KOFOID; a) ventral view, b) left side view. St. 99. – 252. *O. scolopax* STEIN. St. 308 (south of 40 °S). – 253. *O. scolopax* STEIN; a specimen surrounded by a delicate mucilagenous sheath. St. 315. – 254. *Corythodinium compressum* (KOFOID) comb. nov. Three-quarter left side view. St. 53.

Plate 25. *Cladopyxis, Palaeophalacroma, Amphidoma*

255. *Cladopyxis brachiolata* STEIN; tilted ventral view normally presented by the cells under the light microscope. St. 305. – 256. *C. brachiolata* STEIN; bearing peripheral fins; this type originally termed *C. caryophyllum* KOFOID. St. 299. – 257. *C. brachiolata* STEIN; a specimen with two processes more juvenile than the other four. St. 334. – 258. *C. brachiolata* STEIN. St. 66. – 259 a, b. *C. brachiolata* STEIN; two views of a specimen with four (epithecal?) processes. St. 320. – 260 a, b. *Palaeophalacroma verrucosum* SCHILLER; ventral and left-side views. St. 156. – 261 a, b. *P. sphaericum* sp. n; ventral and slightly right-side views. St. 161. – 262 a, b, c. *Palaeophalacroma* sp.; ventral, left side and apico-ventral details. St. 155. – 263. *Amphidoma nucula* STEIN. St. 327. – 264. *Amphidoma* sp. St. 374.

Plate 26. *Ceratocorys*

265. *C. horrida* STEIN; right lateral view. St. 14. – 266. *C. horrida* STEIN; recently divided, with juvenile antapical processes. St. 14. – 267. *C. horrida* STEIN var. *extensa* PAVILL. St. 64. – 268. *C. horrida* STEIN; recently divided, lacking the anterior processes. St. 340. – 269 a, b. *C. armata* (SCHÜTT) KOF.; right lateral and apical views. St. 348. – 270. *C. magna* KOF.; ventral view. St. 101. – 271. *C. bipes* (CLEVE) KOF.; right lateral view; St. 13. – 272. *C. armata* (SCHÜTT) KOF.; ventral view. St. 315. – 273. *C. armata* (SCHÜTT) KOF.; right lateral view. St. 294. – 274. *C. gourretii* PAULSEN; right lateral view. St. 154. – 275. *C. reticulata* GRAHAM; ventral view. St. 59. – 276. *C. bipes* (CLEVE) KOF.; antapical view. St. 150. – 277. *C. gourretii* PAULSEN; recently divided, lacking the anterior spines. St. 63.

Plate 27. *Podolampas*

278. *Podolampas palmipes* STEIN. St. 327. – 279. *P. palmipes* STEIN. An immature specimen, shortly after fission. St. 412. – 280. *P. elegans* SCHÜTT; three-quarter left side view. St. 54. – 281. *P. elegans* SCHÜTT. St. 55. – 282. *P.* sp. Possibly *P. elegans* but differing in the development of the lists between the antapical spines. Three quarter left side view. St. 51. – 283. *P. antarctica* BALECH. Very similar to *P. spinifera* but possessing three antapical spines. St. 306. – 284, 285. *P. spinifera* OKAMURA. (f. 284 three-quarter left side view). (284) St. 320, (285) St. 326. – 286. *P. palmipes* STEIN? The right antapical spine is unusually curved. The "girdle"-like appearance may be due to intercalary development or is associated with an internal cyst. St. 321. – 287. *P. bipes* STEIN var. *reticulata* stat. n. St. 418. – 288. *P. bipes* STEIN var. *bipes*. St. 420.

Plate 28. *Blepharocysta, Heteraulacus, Diplopsalis, Peridiniopsis, Zygabikodinium*

289. *Blepharocysta okamurai* ABÉ. St. 113. – 290. *Heteraulacus sphaericus* (MURRAY et WHITTING) LOEBLICH III. St. 35. – 291. *H. polyedricus* (STEIN) DRUGG et LOEBL.; ventral view. St. 419. – 292 a, b. *H. polyedricus* (STEIN) DRUGG et LOEBL.; apical and antapical views. St. 15. – 293. *H. polyedricus* (STEIN) DRUGG et LOEBL.; a megacytic cell. St. 344. – 294 a, b. *H. polyedricus* (STEIN) DRUGG et LOEBL.; apical and antapical views of a megacytic cell. St. 14. – 295. *Zygabikodinium lenticulatum* (MANGIN) LOEBL. et LOEBL. III; ventral view. St. 101. – 296 a, b. *Peridiniopsis asymmetrica* MANGIN; apical and antapical views. St. 18. – 297. *Zygabikodinium lenticulatum* (MANGIN) LOEBL. et LOEBL. III; right lateral view. St. 101. – 298. *Diplopsalis lenticula* BERGH; apical view. St. 101. – 299. *Diplopsalis lenticula* BERGH; antapical view. St. 101. – 300. *Zygabikodinium lenticulatum* (MANGIN) LOEBL. et LOEBL. III; apical view. St. 102.

Plate 29. *Peridinium*, Subgenus *Protoperidinium*, Sect. *Humili-Piriformia*

301 a–d. *P. globulum* STEIN; ovate form corresponding to *P. ovatum* (POUCHET) SCHÜTT. St. 15. – 302. *P. cerasus* PAULSEN?; ventral view showing atypical intercalary arrangement (asymmetrical) and abruptly "affixed" apical horn. – 303. *P. cerasus* PAULSEN?; same specimen, dorsal view. St. 17. – 304. *P. simulum* PAULSEN. St. 367. – 305 a–d. *P. subpyriforme* DANGEARD. St. 15. – 306 a, b. *P. dakariense* DANGEARD. St. 148. – 307 a, b. *Peridinium paradoxum* sp. n. St. 25.

Plate 30. *Peridinium*, Subgenus *Protoperidinium*, Sect. *Divergentia*

308. *P. elegans* CLEVE forma *elegans*. St. 141. – 309. *P. elegans* CLEVE forma *granulatum* (KARSTEN) MATZENAUER. St. 344. – 310. *P. grande* KOFOID; a) ventral view; b) dorsal view. St. 282. – 311. *P. elegans* CLEVE; specimen slightly tilted laterally. St. 287. – 312. *P. elegans* CLEVE; dorsal view of a detached epitheca. St. 286. – 313. *P. brachypus* SCHILLER; a) low ventral view, b) apical view. St. 130. – 314. *P. elegans* CLEVE; megacytic stage (= *P. fatulipes* KOFOID); ventral view. St. 284. – 315. *P. elegans* CLEVE; dorsal view of another megacytic cell. St. 284. – 316. *P. tumidum* OKAMURA (= *P. elegans* CLEVE?); megacytic cell. St. 315.

Plate 31. *Peridinium*, Subgenus *Protoperidinium*, Section *Divergentia*

317. *P. acutipes.*P. DANGEARD. St. 341. – 318. *P. acutipes* P. DANGEARD; smaller cell. St. 17. – 319. *P. divergens* EHRENBERG. St. 24. – 320. *P. divergens* EHRENBERG. St. 162. – 321. *P. acutipes* P. DANGEARD; megacytic form. St. 34. – 322. *P. curtipes* JÖRGENSEN. St. 410. – 323. *P. curtipes* JÖRGENSEN; a very small individual. St. 418. – 324. *P. divergens* EHRENBERG; megacytic form (= *P. remotum* KARSTEN). St. 35. – 325. *P. acutipes* P. DANGEARD. St. 63. – 326. *P. asymmetricum* KARSTEN. St. 118. – 327. *P. crassipes* KOFOID. St. 110. – 328. *P. inflatum* OKAMURA. St. 25. – 329. *P. divergens* EHRENBERG. St. 103. – 330. *P. inflatum* OKAMURA? A specimen with strongly right-handed displacement. St. 87. – 331. *P. crassipes* KOFOID; epitheca of large specimen. St. 291. – 332. *P. brochii* KOF. et SWEZY; megacytic form with coarse reticulation. St. 150. – 333. *P. angustum* DANGEARD; somewhat resembling *P. wiesneri* SCHILLER. St. 290. – 334. *P. angustum* DANGEARD; similar to f. 333 but with more closely-set antapical spines. St. 114. – 335. *P. brochii* KOF. et SWEZY; megacytic form with fine reticulation. St. 118.

Plate 32. *Peridinium*, Subgenus *Protoperidinium*, Sections *Divergentia*, *Humili-Piriformia* and *Protoperidinium*. Also Subgenus *Minuscula*

336. *P. latispinum* MANGIN. St. 362. – 337. *P. pyrum* BALECH; possibly a small variant of *P. latispinum*. St. 43. – 338. *P. solidicorne* MANGIN var. *bradynyx* MATZENAUER. St. 371. – 339. *P. solidicorne* MANGIN var. *makronyx* SCHILLER. St. 18. – 340. *P. schilleri* PAULSEN. St. 161. – 341. *P. granii* OSTENFELD ex PAULSEN. St. 53. – 342. *P. corniculum* KOFOID et MICHENER. St. 59. – 343. *P. pacificum* KOFOID et MICHENER. St. 56. – 344. *P. tubum* SCHILLER. St. 417. – 345. *P. pallidum* OSTENFELD. St. 133. – 346. *P. longicollum* PAVILLARD. St. 113. – 347. *P. orientale* MATZENAUER. St. 153. – 348. *P. tristylum* STEIN; dorsal and ventral views of two different specimens. St. 420. – 349 a, b. *P. steinii* JÖRGENSEN; an enlarged cell infected by the dinoflagellate *Amoebophrya ceratii* (KÜPPEN) CACHON. St. 67. – 350. *P. ovum* SCHILLER. St. 30. – 351. *P. inclinatum* BALECH. St. 398. – 352. *P. heteracanthum* P. DANGEARD; a large individual with reduced apical horn. St. 363. – 353 a, b. *P. heteracanthum* P. DANGEARD; ventral and right side views. St. 105. – 354. *P. diabolus* CLEVE var. *longipes* (KARSTEN) stat. et comb. nov. St. 14. – 355. *P. tenuissimum* KOFOID. St. 71. – 356. *P. sourniai* nom. nov. (= *P. bispinum* SCHILLER). St. 374. – 357. *P. heteracanthum* DANGEARD; a small individual. St. 85. – 358. *P.* [*Minuscula*] *minusculum* PAVILLARD. St. 374. – 359. *P. nipponicum* ABÉ. St. 32.

Plate 33. *Peridinium* Subgenera *Archaeperidinium*, *Protoperidinium* [section *Conica*] and *Scrippsiella*

360. *P. latissimum* KOFOID. St. 41. – 361. *P. conicum* (GRAN) OSTENFELD et SCHMIDT var. *conicum* MATZENAUER. St. 23. – 362. *P. conicum* (GRAN) OSTENFELD et SCHMIDT var. *asamushi* (ABÉ) stat. nov. St. 51. – 363. *P. abei* PAULSEN var. *abei*; a specimen with the usual antapical asymmetry. St. 46. – 364. *P. subinerme* PAULSEN; a small specimen. St. 38. – 365. *P. biconicum* DANGEARD. St. 88. – 366. *P. abei* PAULSEN var. *abei*; a specimen with no antapical asymmetry. St. 363. – 367 a, b. *P. subinerme* PAULSEN; a large megacytic specimen seen in ventral and dorsal views; resembling *P. punctulatum* PAULSEN in its possession of puncta. St. 105. – 368 a, b. *P. persicum* SCHILLER; a cell in three-quarter apico-ventral and apico-dorsal views. St. 144. – 369. *P. leonis* PAVILLARD forma *gainii* (P. DANGEARD) SCHILLER. St. 39. – 370. *P. divaricatum* MEUNIER. St. 44. – 371 a, b. *P. achromaticum* LEVANDER; ventral and dorsal views of an unusually large specimen. St. 45. – 372. *P. minutum* KOFOID; a specimen near the maximum size range. St. 53. – 373 a–c. *P. latistriatum* BALECH? A grossly megacytic cell seen in ventral, left three-quarter apical and dorsal views. St. 99. – 374. *P. trochoideum* (STEIN) LEMMERMANN; ventral, dorsal, apical and antapical views. St. 20. – 375. *Peridinium* sp. A (cf. *P. sourniai* nom. nov.); plates not seen. St. 327. – 376. *Peridinium* sp. B; plates not fully established; not discussed in the text. St. 337. – 377. *Scrippsiella*? sp.; ventral and dorsal views of two different specimens. St. 342 and St. 298 respectively. – 378. *Peridinium* sp. C.; plates not fully established; not discussed in the text. St. 337.

Plate 34. *Peridinium*, Subgenus *Protoperidinium*, Section *Oceanica*, and *Pyrophacus* STEIN

379. *Peridinium murrayi* KOFOID; a slender specimen. St. 363. – 380. *Per. murrayi* KOFOID; a broader specimen. St. 106. – 381. *Per. oceanicum* VANHÖFFEN. St. 396. – 382. *Per. oceanicum* VANHÖFFEN. St. 399. – 383. *Per. depressum* BAILEY var. *rectius* GRAHAM. St. 44. – 384. *Pyrophacus steinii* (SCHILLER) WALL et DALE; an intact cell in ventral view. St. 104. – 385. *Pyr. steinii* (SCHILLER) WALL et DALE; a rounded cell with a typically dissociated theca. St. 418. – 386. *Pyr. steinii* (SCHILLER) WALL et DALE; epitheca. St. 349. – 387. *Pyr. horologium* STEIN; a small hypotheca. St. 417. – 388. *Pyr. horologium* STEIN; an epitheca. St. 115. – 389. *Pyr. steinii* (SCHILLER) WALL et DALE; a hypotheca. St. 335. – 390. *Pyr. horologium* STEIN; a very large hypotheca. St. 39. – 391. *Pyr. vancampoae* (ROSSIGNOL) WALL et DALE; a hypotheca. St. 162.

Plate 35. *Gonyaulax*, *Pyrodinium*

392. *G. fratercula* BALECH: a pair joined in their normal fashion. St. 16. – 393. *G. kofoidii* PAVILLARD; theca after apical ecdysis. St. 15. – 394. *G. kofoidii* PAVILLARD; cyst. St. 37. – 395. *G. pacifica* KOFOID. St. 295. – 396. *G. polyedra* STEIN. St. 109. – 397. *G. pacifica* KOFOID; cyst, showing perinuclear plates (cf. Pl. 40, fig. 482). St. 21. – 398. *G. polygramma* STEIN. St. 294. – 399. *G. turbynei* MURR.

et WHITT. St. 63. – 400. *G. diegensis* KOFOID..St. 35. – 401. *G. milneri* (MURR. et WHITT.) KOF. St. 332. – 402. *G. minuta* KOF. et MICHENER. St. 411. – 403. *G. pavillardii* KOF. et MICHENER? A small cell. St. 371. – 404. *G. glyptorhynchus* MURR. et WHITT. The apical plates have separated, presumably due to ecdysis. St. 51. – 405. *G. ovalis* SCHILLER. St. 405. – 406. *Pyrodinium schilleri* (MATZENAUER) SCHILLER. St. 18. – 407. *Gonyaulax subulata* KOF. et MICH. St. 162. – 408. *G. areolata* KOF. et MICH. New iconotype. St. 365. – 409. *G. bruunii* sp. n. a) ventral, b) dorsal, c) right side views, and d) ventral detail not to scale. St. 404. – 410. *G. ceratocoroides* (MURR. et WHITT.) KOF. St. 417.

Plate 36. *Gonyaulax, Protoceratium, Pyrodinium, Spiraulax*

411. *G. brevisulcatum* DANGEARD. St. 98. – 412. *G. brevisulcatum* DANGEARD; with supernumery plate. St. 301. – 413. *G. brevisulcatum* DANGEARD; with aberrant ventral epithecal pattern. St. 94. – 414. *Protoceratium spinulosum* (MURR. et WHITT.) SCHILLER. St. 117. – 415. *G. hyalina* OST. et SCHMIDT; a large atypically-shaped individual. St. 150. – 416. *G. hyalina* OST. et SCHMIDT. St. 328. – 417. *G. inflata* (KOF.) KOFOID. The left lateral swelling is aberrant. St. 286. – 418. *G. hyalina* OST. et SCHMIDT; a small individual with spines. St. 29. – 419. *G. hyalina* OST. et SCHMIDT; apical view. St. 93. – 420. *G. fragilis* (SCHÜTT) KOFOID. St. 315. – 421. *G. fusiformis* GRAHAM. St. 33. – 422. *G. fusiformis* GRAHAM. St. 67. – 423. *Pyrodinium* sp.?; a, b) ventral views, c) left, d) antapico-dorsal views. St. 365. – 424. *Spiraulax jollifei* KOFOID; ventral view. The apical plates are gaping apart, due to ecdysis. St. 405.

Plate 37. Various genera, mostly non-thecate

425. *Pronoctiluca rostrata* sp. n. St. 327. – 426. *Pronoctiluca pelagica* FABRE-DOMERGUE. St. 289. – 427. *P. pelagica* FABRE-DOMERGUE. St. 374. – 428. *P. pelagica* FABRE-DOMERGUE. St. 369. – 429. *Pronoctiluca spinifera* (LOHMANN) SCHILLER. St. 150. – 430. *Pronoctiluca pelagica* FABR.-DOM. St. 323. – 431. *P. pelagica* FABR.-DOM. St. 322. – 432. *Dicroerisma psilonereiella* TAYLOR et CATTELL. St. 21. – 433. Unknown, non-thecate dinoflagellate, apparently non-photosynthetic; not discussed in the text. St. 374. – 434. *Amphidinium* sp. St. 287. – 435. *Gymnodinium* sp. (*herbaceum* KOFOID?); with large anterior accumulation body. St. 296. – 436. *Bernadinium* sp.? Side and ventral views. St. 322. – 437. Unidentified, minute thecate species, plates not resolved; not discussed in the text. St. 15. – 438. *Ptychodiscus noctiluca* STEIN; the swollen state formerly termed *Pt. inflatus* PAVILL. St. 21. – 439. *Pt. noctiluca* STEIN; a small cell. St. 301. – 440. *Pt. noctiluca* STEIN; a flattened specimen corresponding to those formerly known as *Pt. carinatus*. St. 13. – 441. *Berghiella josephinae* sp. n. St. 32. – 442. *Balechina marianae* sp. n. St. 55. – 443. *Balechina coerulea* (DOGIEL) comb. n. St. 59.

Plate 38. *Pyrocystis, Dissodinium*

444. *Dissodinium gerbaultii* (PAVILLARD) comb. n.; contents in the cornuate vegetative state. St. 287. – 445. *D. gerbaultii* (PAVILL.) comb. n.; contents beginning to form motile cells. St. 114. – 446. *Pyrocystis hamulus* CLEVE. St. 294. – 447. *P. hamulus* CLEVE var. *reflexus* var. n. St. 13. – 448. *P. hamulus* CLEVE var. *semicircularis* SCHRÖDER. St. 131. – 449. *P. hamulus* CLEVE var. *semicircularis* SCHRÖDER. St. 97. – 450. *P. hamulus* CLEVE var. *hamulus*, showing the pairing commonly observed in all the varieties. St. 18. – 451. *D. lunula* (SCHÜTT) PASCHER. St. 348. – 452. *D. lunula* (SCHÜTT) PASCHER. St. 63. – 453. *D. bicorne* (KOFOID et SWEZY) comb. n. St. 63. – 454–457. Immature cysts corresponding to early stages in the transformation of motile cells after ecdysis (cf. BOUQUAHEUX, 1972), perhaps including *D. elegans* (PAVILLARD) MATZENAUER (454) St. 72, (455) St. 334, (456) St. 62, (457) St. 57. – 458. *D. elegans* (PAVILLARD) MATZENAUER. St. 340. – 459. *D. elegans* (PAVILLARD) MATZENAUER. St. 57. – 460. *P. robusta* KOFOID. St. 340. – 461. *P. noctiluca* J. MURRAY ex SCHÜTT; small cyst. St. 340. – 462. *P. noctiluca* J. MURRAY ex SCHÜTT; early formation of two motile cells. St. 125. – 463. *P. noctiluca* J. MURRAY ex SCHÜTT; thecate motile cells, characteristically at an angle to each other. St. 294. – 464. *P. noctiluca* J. MURRAY ex SCHÜTT; the thecate stage, a) ventral, b) dorsal view. St. 341. – 465. *P. noctiluca* J. MURRAY ex SCHÜTT. A large cyst. St. 286.

Plate 39. *Pyrocystis, Kofoidinium, Noctiluca*

466. *Pyrocystis fusiformis* WY. T. ex BLACKMAN f. *fusiformis*. St. 342. – 467. *P. fusiformis* f. *lanceolata* (SCHRÖDER) stat. et comb. n. St. 327. – 468. *P. fusiformis* f. *detruncata* MATZ. St. 154. – 469. *P. rhomboides* MATZ. St. 286. – 470. *P. rhomboides* MATZ. St. 340. – 471. *P. fusiformis* f. *biconica* KOF. St. 116. – 472. *P. fusiformis* f. *biconica* KOF. St. 98. – 473. *P. fusiformis* WY. T. ex J. MURRAY; a deformation producing strongly dissimilar apices. St. 98. – 474. *P. apiculatus* sp. n. St. 418. – 475. *Kofoidinium splendens* CACHON et CACHON; sporont lacking its shell. St. 96. – 476. *K. splendens* CACHON et CACHON; juvenile (stage "b"). St. 370. – 477. *K. lebourae* (PAVILL.) comb. n.; sporont. St. 50. – 478. *Noctiluca scintillans* (MAC.) EHRENB.; juvenile. St. 38. – 479. *N. scintillans* (MAC.) EHRENB.; young individual forming two feeding vacuoles. St. 42.

Plate 40. Bright field and phase contrast photomicrographs

480. *Balechina marianae* sp. n.; median focus. St. 55. – 481. *Balechina coerulea* (DOGIEL) comb. n. St. 59. – 482. A cyst of *Gonyaulax pacifica*, with the perinuclear plates seen in optical section (cf. pl. 35, f. 397). St. 37. – 483. *Ceratium vultur* var. *japonicum* (SCHRÖDER)

JÖRG. f. *robustum* (OST. et SCHMIDT) stat. n.; anterior pair from a chain. St. 133. – 484. *Ceratium teres* KOFOID; chromosomes clearly visible. St. 325. – 485. *Histioneis dolon* MURR. et WHITT.; the posterior moiety of the left sulcal list displaced to reveal the right sulcal list (rib arrowed). St. 135. – 486. *Gloeodinium marinum* BOUQUAHEUX; typical gelatinous colony. St. 33. – 487. *Ptychodiscus noctiluca* STEIN; apical view showing the numerous small chloroplasts. St. 13.

Plate 41. Scanning Electron Micrographs

488. *Dinophysis rapa* (STEIN) ABÉ. St. 58. X 1,110. – 489. Detail of the ventral region of a megacytic, unidentified species of *Dinophysis*, illustrating the apical pore (to the viewer's right near the upper girdle list). St. 325. X 2,430. – 490. *Parahistioneis para* MURR. et WHITT. (from TAYLOR, 1973b). St. 325. X 1,155. – 491. *Histioneis highleyi* MURR. et WHITT. St. 325. X 980. – 492. *H. highleyi* MURR. et WHITT.; antapical view. St. 101. X 1,235. – 493. *H. dolon* MURR. et WHITT.; the lower girdle list partly torn. St. 135. X 750. – 494. *H. mitchellana* MURR. et WHITT; the lower girdle list partly torn. St. 58. X 1,215. – 495. *Amphisolenia schauinslandii* LEMM. Detail of the antapex. St. 325. X 11, 645. – 496. *Citharistes apsteinii* SCHÜTT. St. 58. X 1,120. – 497. *Histioneis mitchellana* MURR. et WHITT.; ventral view. St. 58. X 980. – 498. *H. mitchellana* MURR. et WHITT.; detail of the vestigial right sulcal list. St. 325. X 5, 665.

Plate 42. Scanning Electron Micrographs (*Ornithocercus*)

499. *Ornithocercus quadratus* var. *assimilis* (JÖRG.) stat. et comb. n. Note the presence of the "b" rib on the right side of the left sulcal list. St. 412. X 1,555. – 500. *O. quadratus* SCHÜTT var. *quadratus*; antapical view. St. 325. X 2, 130. – 501. *O. quadratus* SCHÜTT; detail of the apico-ventral region, showing the apical pore and adjacent platelets. St. 100. X 7,515. – 502. *O. francescae* (G. MURRAY) BALECH; the more typical *francescae* form. St. 100. X 1,420. – 503. *O. francescae* (G. MURRAY) BALECH; an individual corresponding to the variant formerly termed *O. carolinae* KOF. St. 108. X 1,340. – 504. *O. splendidus* SCHÜTT; ventral view. St. 315. X 865. – 505. *O. magnificus* STEIN; a) dorsal, b) ventral views of the cell body. St. 37. a) X 2,335. b) X 2,510.

Plate 43. Scanning Electron Micrographs

506. *Cladopyxis brachiolata* STEIN; right side view. St. 313. X 1,285. – 507. *Cl. brachiolata* STEIN; three-quarter right side view of individual with an elongated body. St. 313. X 2,195. – 508. *Cl. brachiolata* STEIN; apico-ventral view. St. 313. X 1,295. – 509. *Ceratium paradoxides* CLEVE; detail of the left dorsal girdle region. St. 148. X 2,660. – 510. *Ceratocorys reticulata* GRAHAM; dorsal view. St. 59. X 695. – 511. *Ceratium vultur* CLEVE var. *vultur*; detail of the method of connection of cells within a chain. St. 103. X 1,155. – 512. *Oxytoxum scolopax* STEIN; detail of the ventral area, illustrating the small fin to the right of the flagellar pore. St. 294. X 10,500. – 513. *Heteraulacus polyedricus* (POUCHET) DRUGG et LOEBL. St. 56. X 1,620. – 514. *Ceratocorys bipes* (CLEVE) KOF.; ventral view. St. 63. X 1,235.

Plate 44. Scanning Electron Micrographs

515. *Gonyaulax ceratocoroides* (MURR. et WHITT.) KOF. St. 58. X 2,240. – 516. *G. ceratocoroides* (MURR. et WHITT.) KOF.; antapico-ventral view into the posterior sulcal aperture. St. 325. X 2,255. – 517. *G. milneri* (MURR. et WHITT.) KOF.; a) ventral, b) apical, c) right antapical views. St. 116. a) X 1,175. b) X 1,385. c) X 1,375. – 518. *Pyrophacus steinii* (SCHILLER) WALL et DALE; detail of the hypotheca in the vicinity of the sulcus. St. 420. X 2,430. – 519. *Peridinium latispinum* MANGIN. St. 47. X 1,385.

Plate 45. Scanning Electron Micrographs

520. *Peridiniopsis asymmetrica* MANGIN; a) ventral view, b) apical pore, c) apical view. St. 18. a) X 1,340. b) X 7,165. c) X 1,385. – 521. *Peridinium ventricum* ABÉ; a) ventral view, b) apical pore, c) apical view. St. 420. a) X 1,125. b) X 7,285. c) X 1,445. – 522. *Peridinium murrayi* KOFOID; a) detail of sulcus and b) three-quarter ventral view. St. 325. a) X 2,545. b) X 605. – 523. *Peridinium murrayi* KOFOID; three-quarter dorsal view showing the oblique plane of the girdle. St. 325. X 555. – 524. *Podolampas bipes* STEIN var. *bipes*; antapical view (dorsal side uppermost). St. 103. X 1,500. – 525. *Peridinium diabolus* CLEVE; detail of ventral area. St. 102. X 2,695. – 526. *Peridinium depressum* BAILEY var. *claudicanoides* (GRAHAM) stat. et comb. n. St. 420. X 655.

Plate 46. Scanning Electron Micrographs

527. *Peridinium schilleri* PAULSEN; a) ventral and b) antapical views. St. 420. a) X 2,625. b) X 1,550. – 528. *Peridinium elegans* CLEVE f. *granulatum* (KARSTEN) MATZENAUER; antapico-dorsal view. St. 92. X 680. – 529. *Ceratocorys horrida* STEIN; three-quarter ventral view. Sr. 93. X 970. – 530. *Peridinium divergens* EHRENBERG. St. 420. X 1,100.

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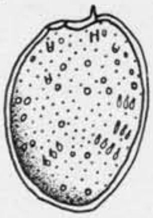

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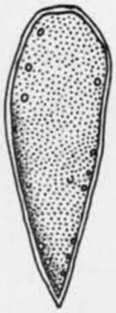

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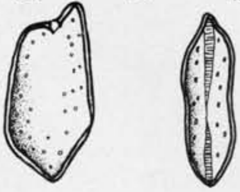

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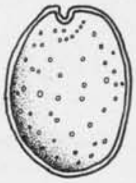

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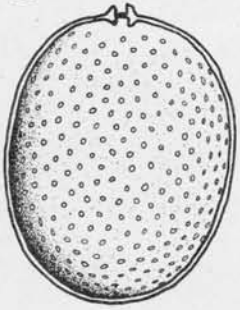

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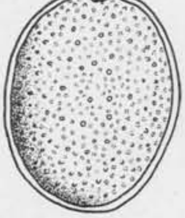

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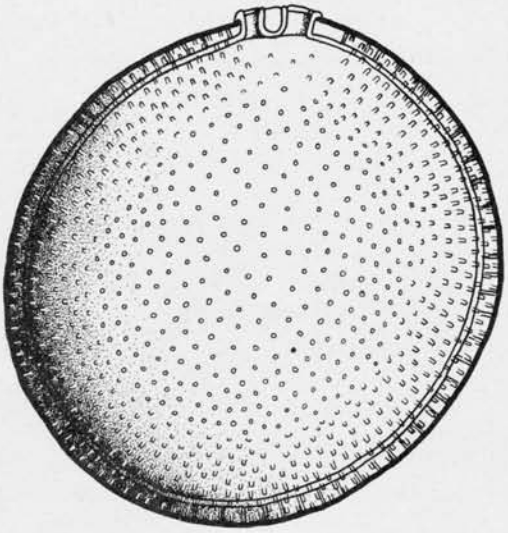

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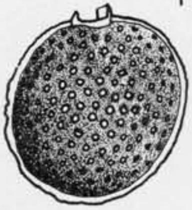

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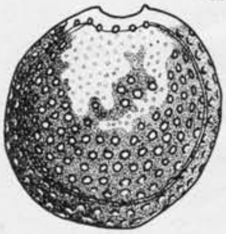

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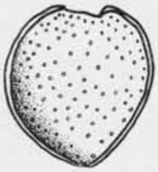

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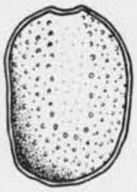

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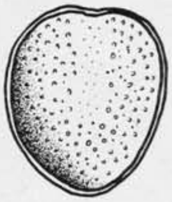

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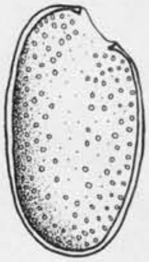

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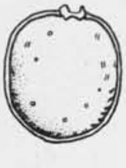

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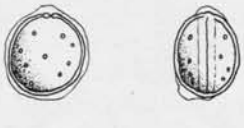

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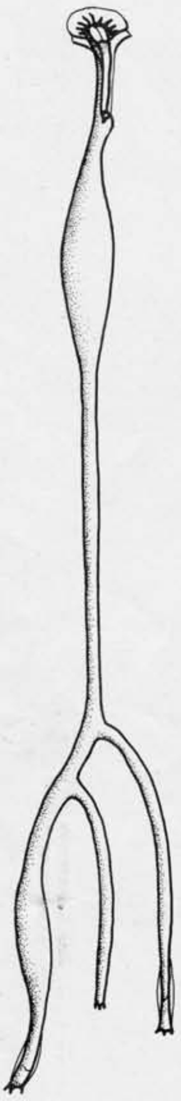

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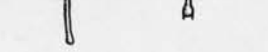

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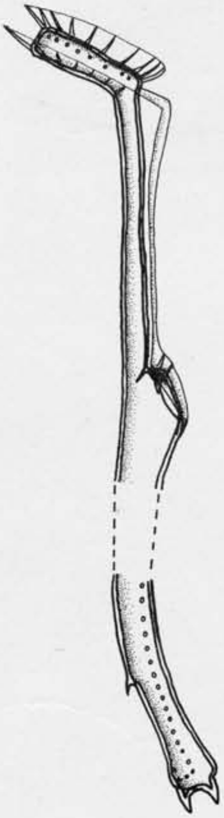

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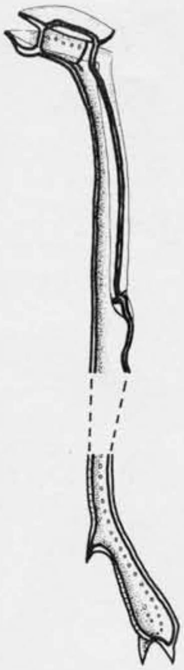

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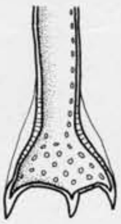

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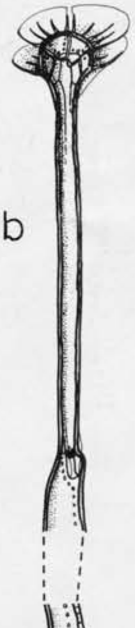

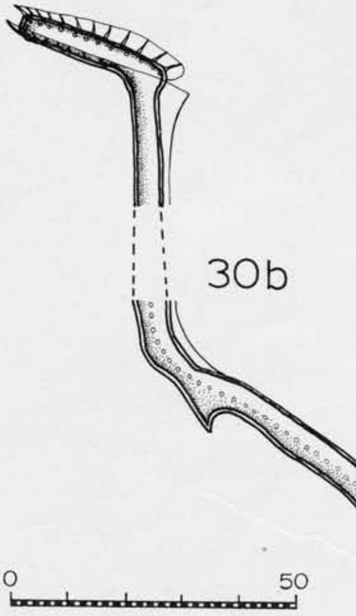

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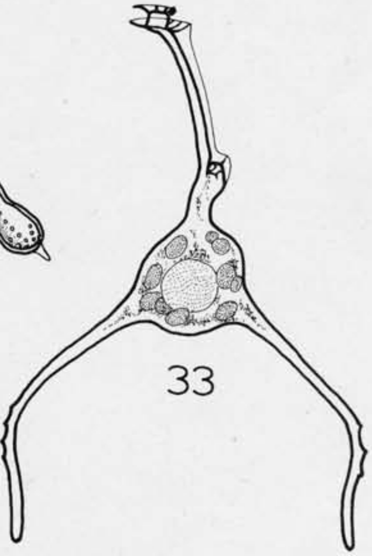

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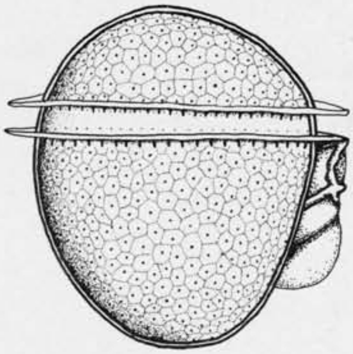

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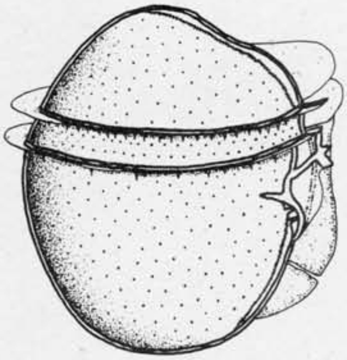

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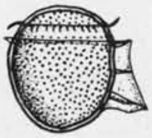

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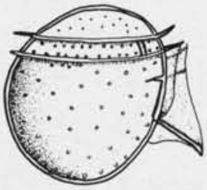

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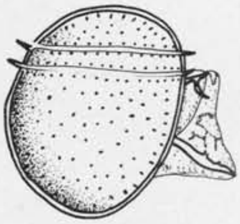

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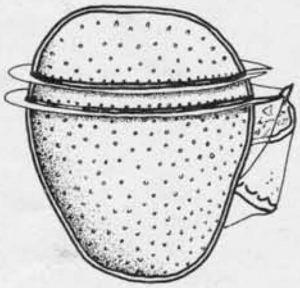

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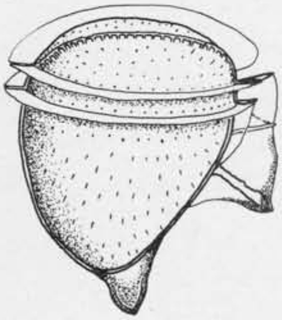

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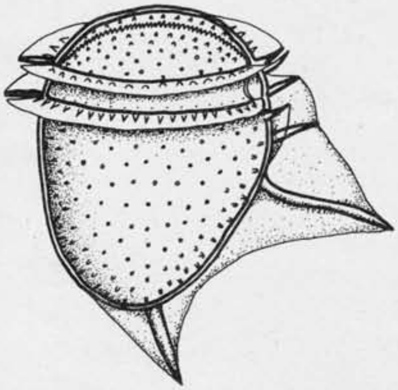

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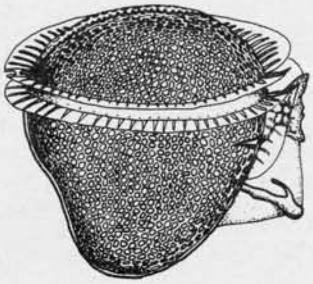

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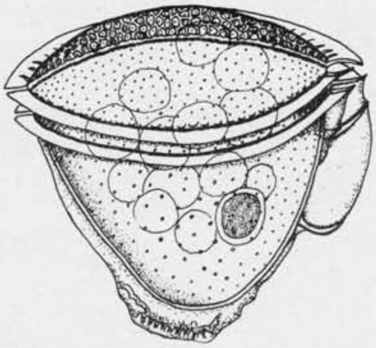

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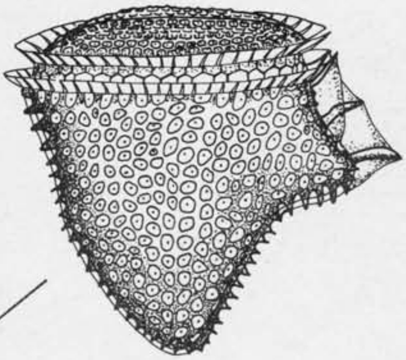

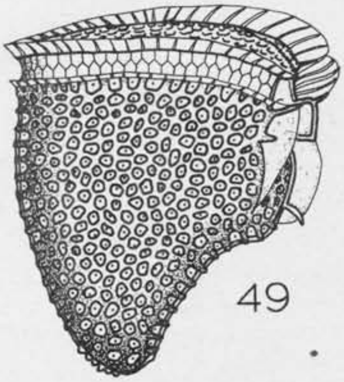

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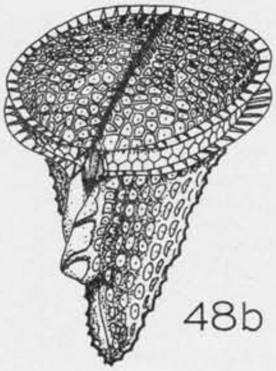

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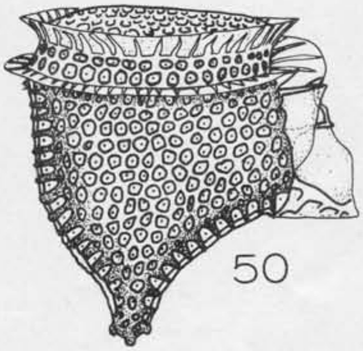

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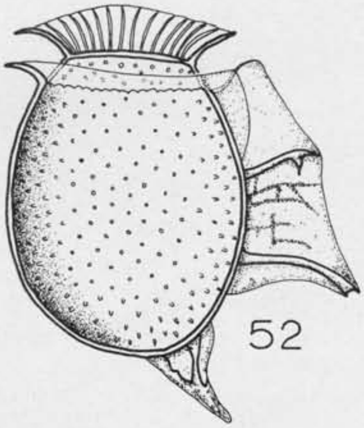

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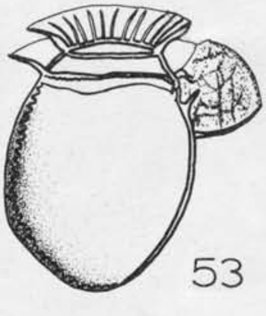

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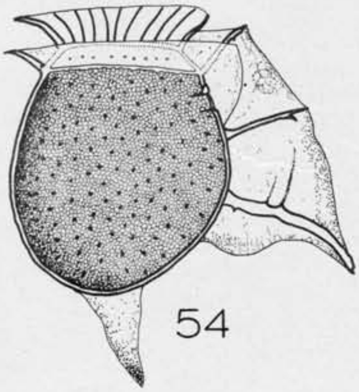

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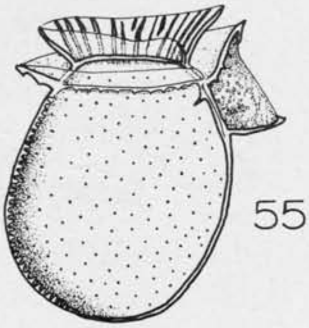

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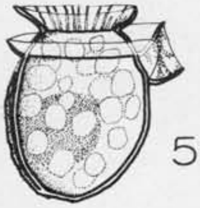

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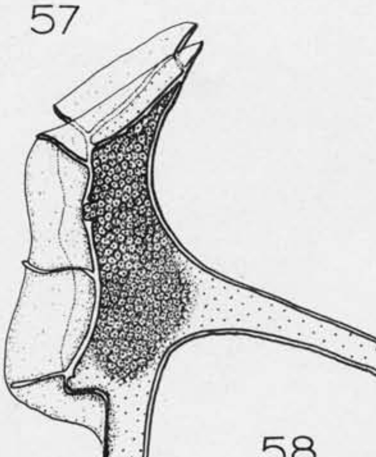

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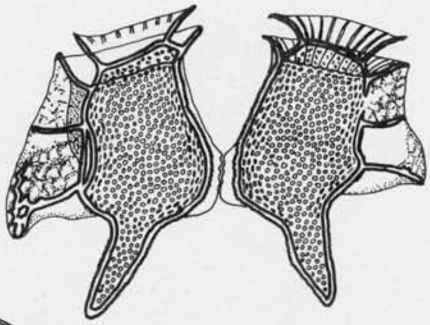

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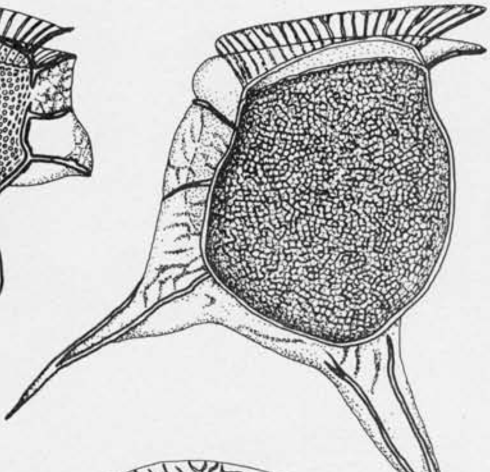

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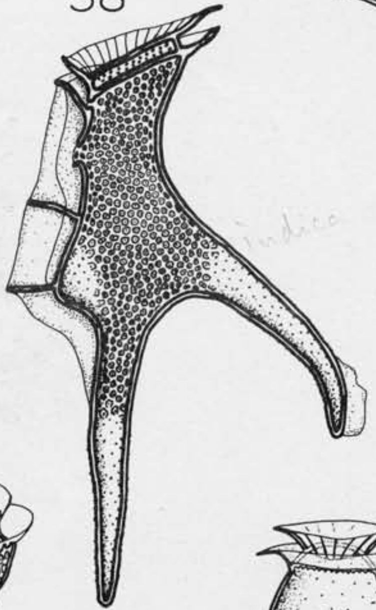

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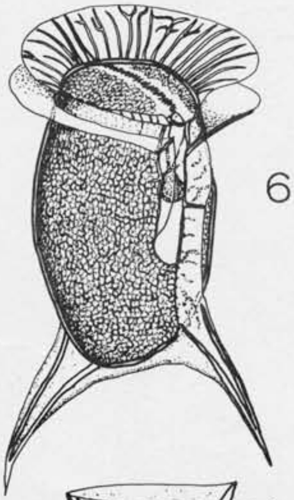

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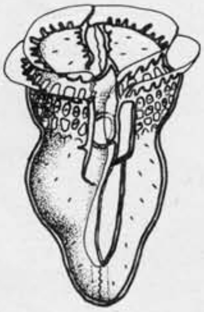

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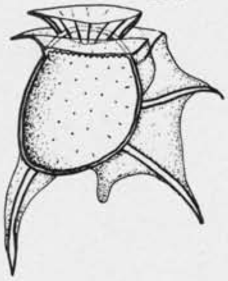

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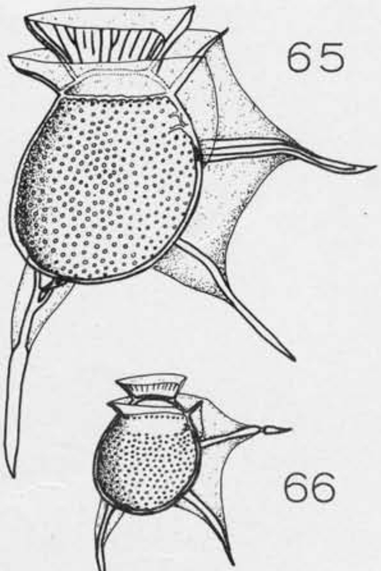

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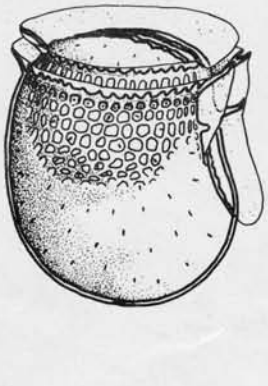

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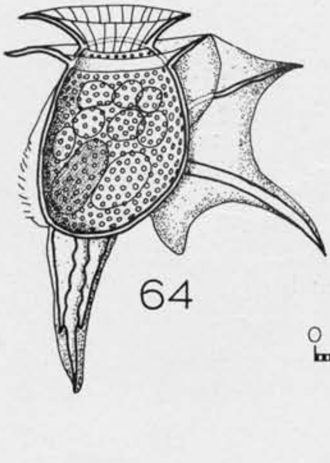

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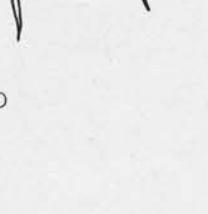

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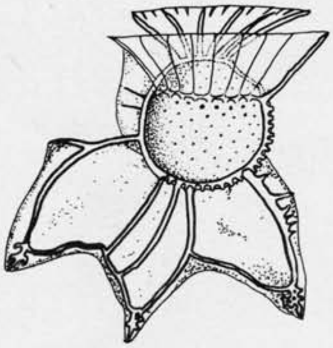

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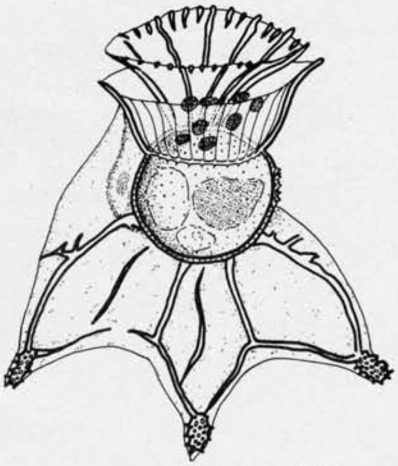

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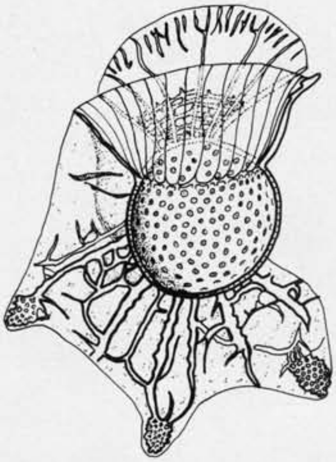

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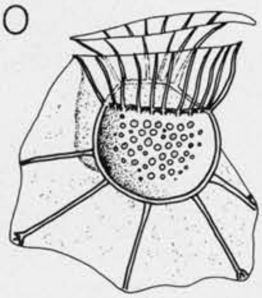

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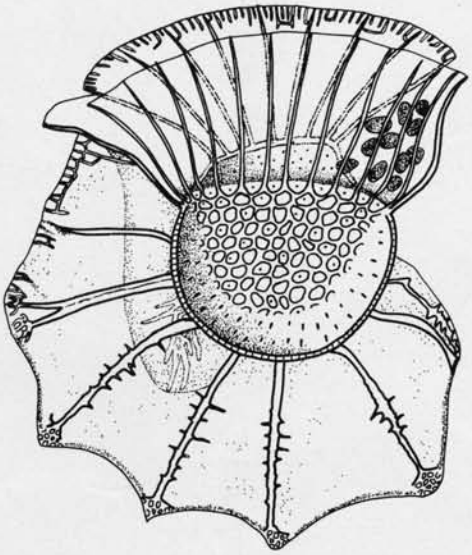

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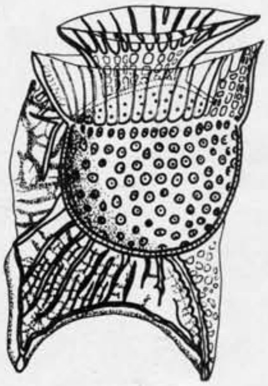

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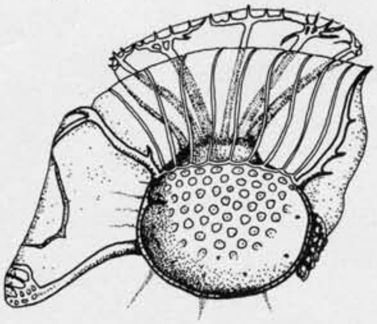

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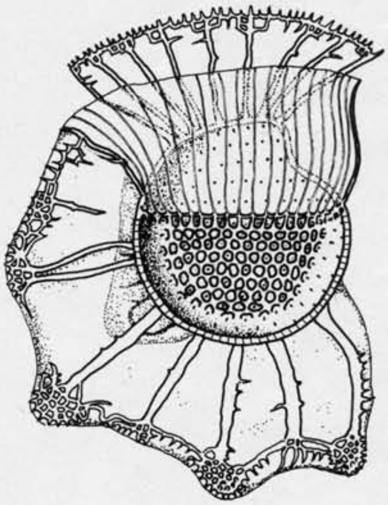

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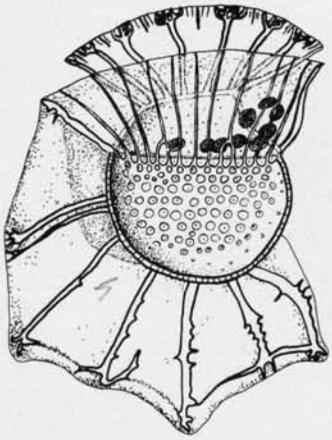

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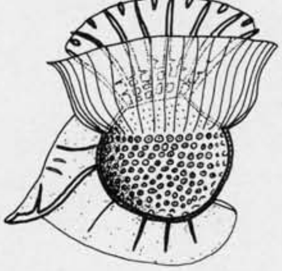

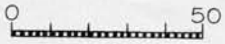

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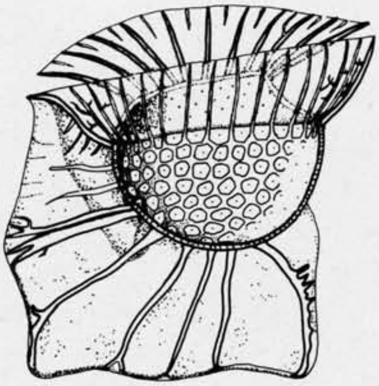

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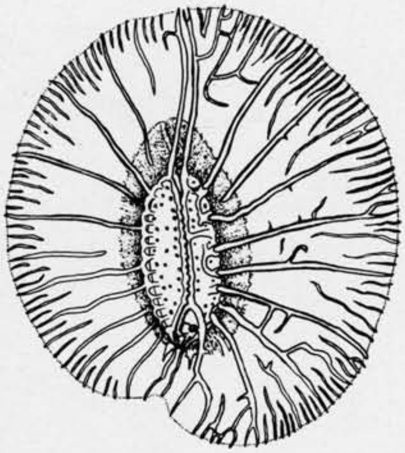

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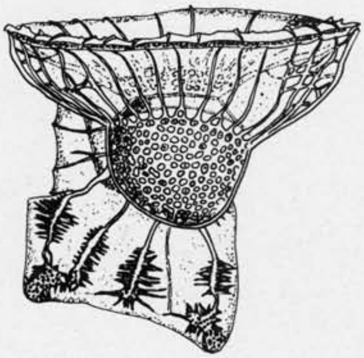

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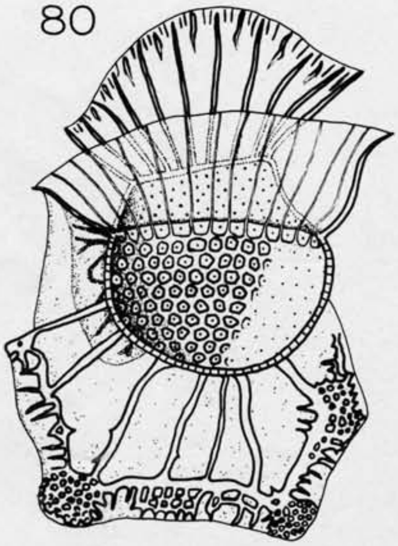

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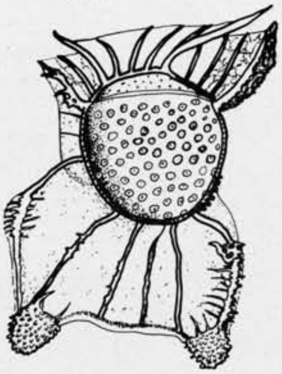

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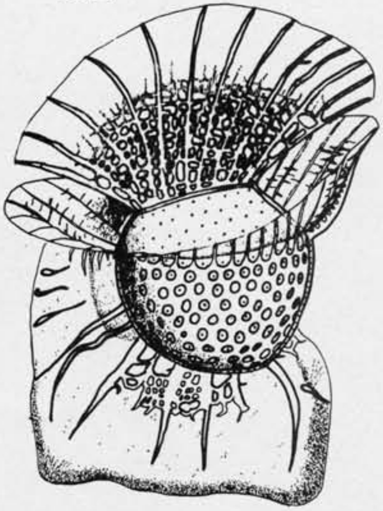

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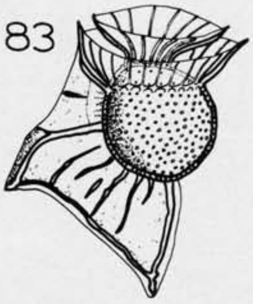

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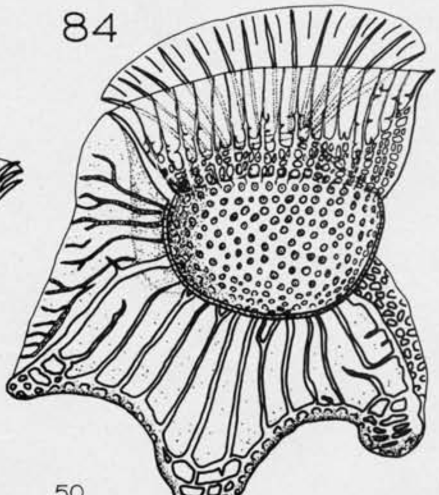

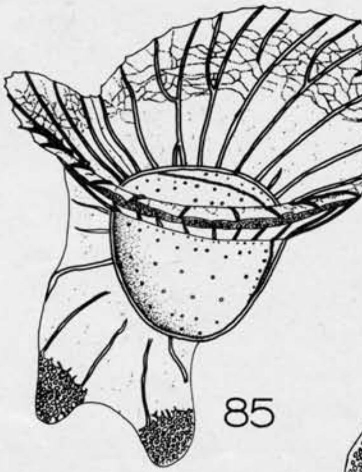

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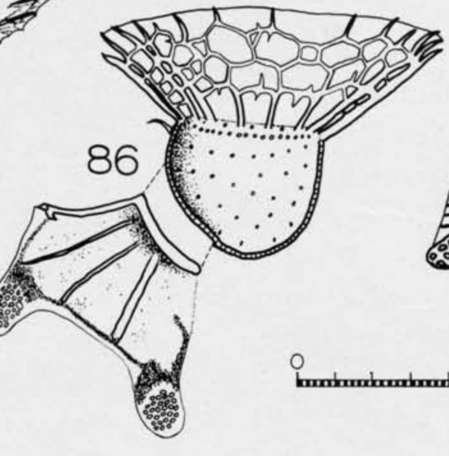

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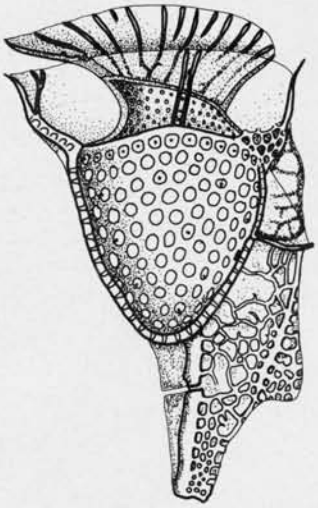

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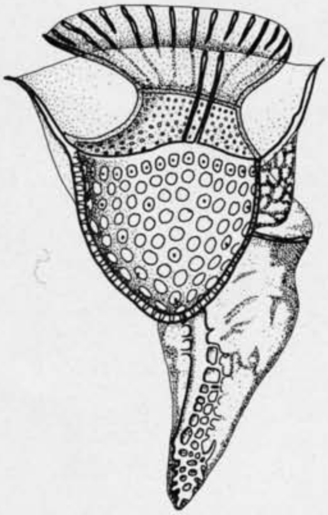

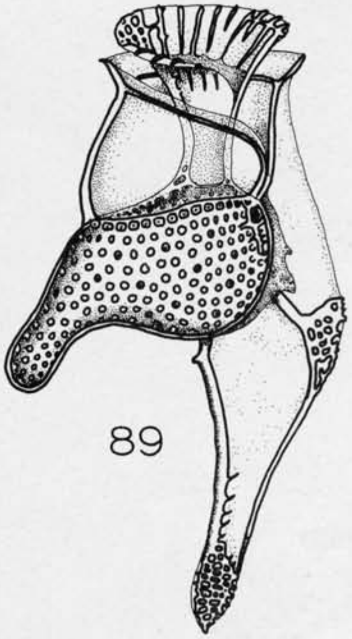

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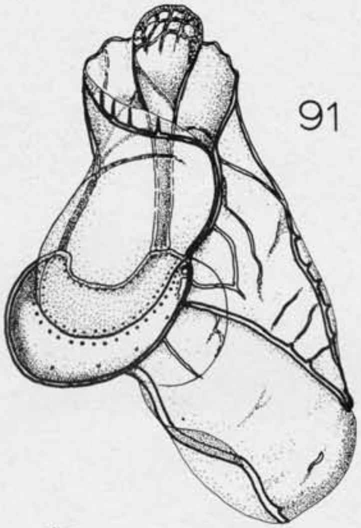

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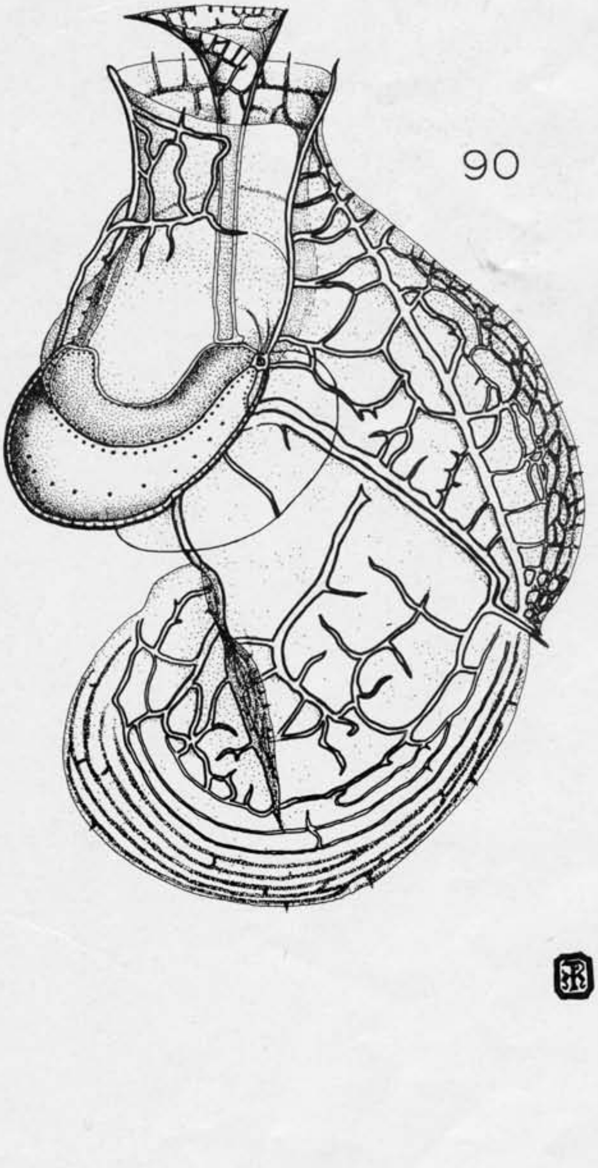

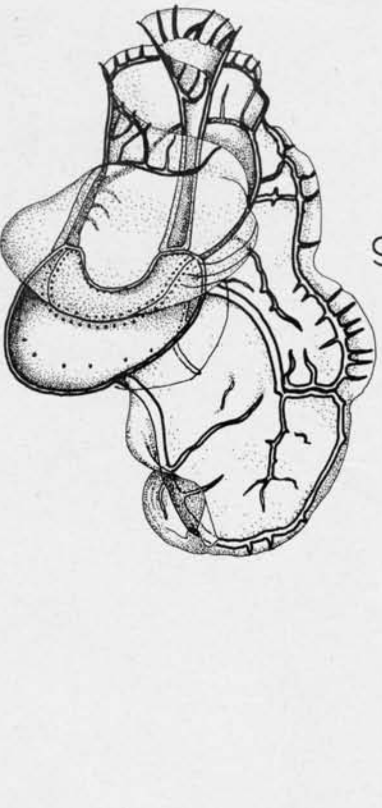

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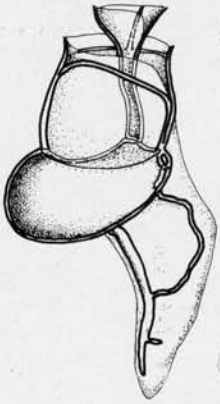

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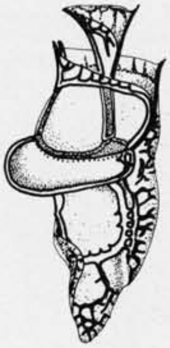

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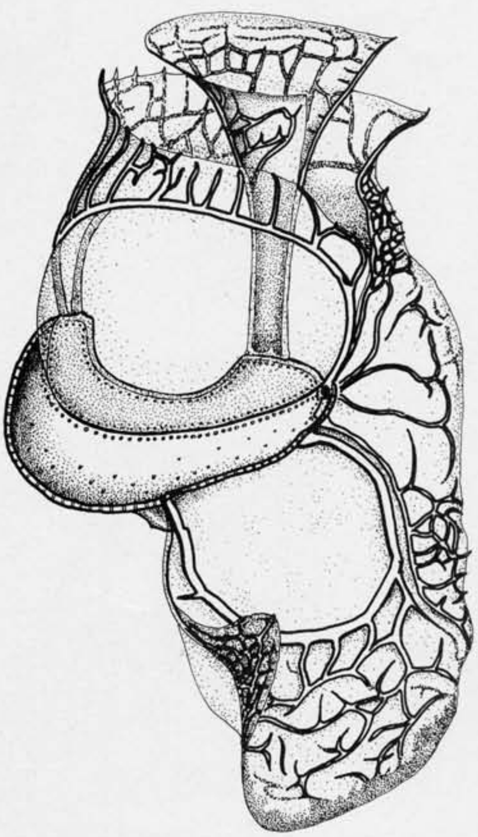

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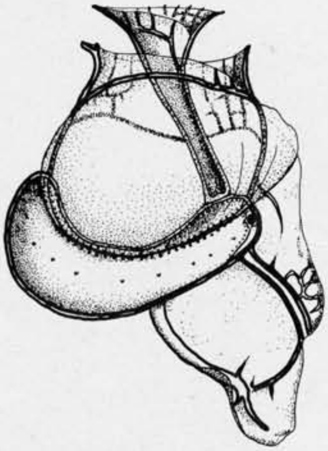

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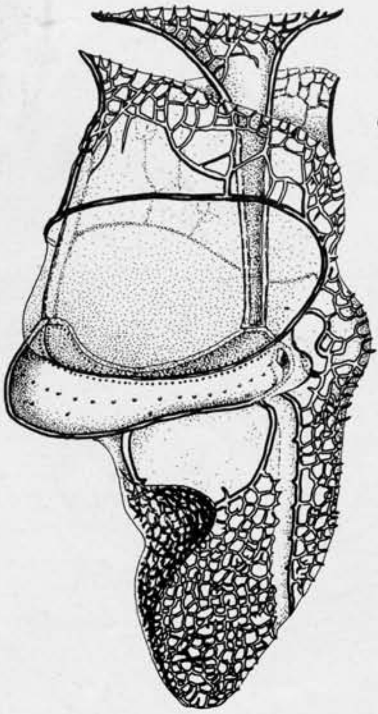

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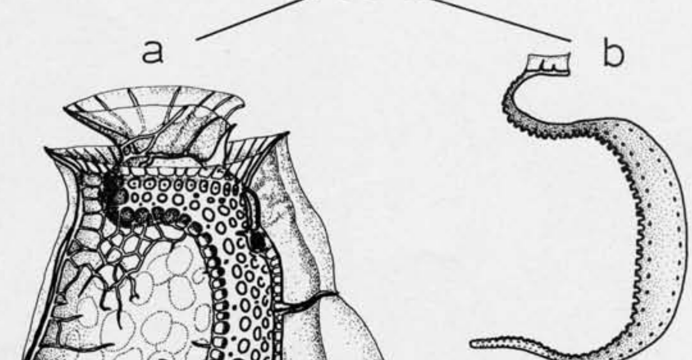

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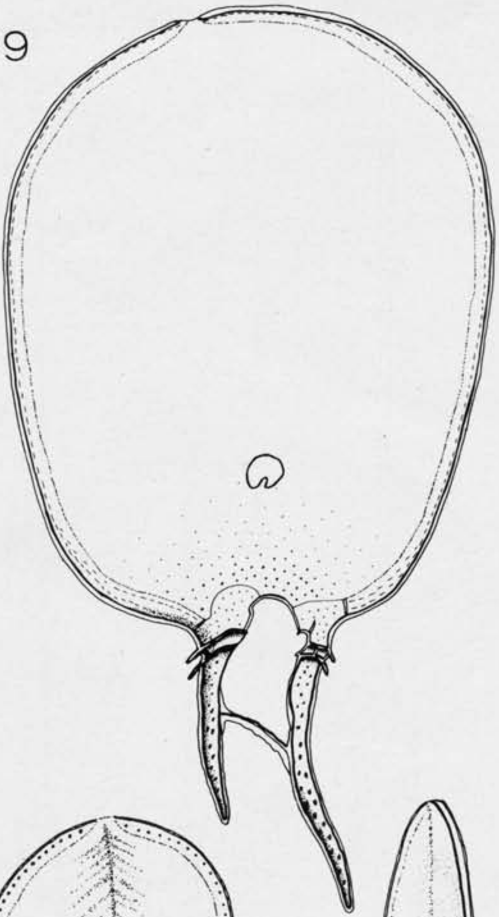

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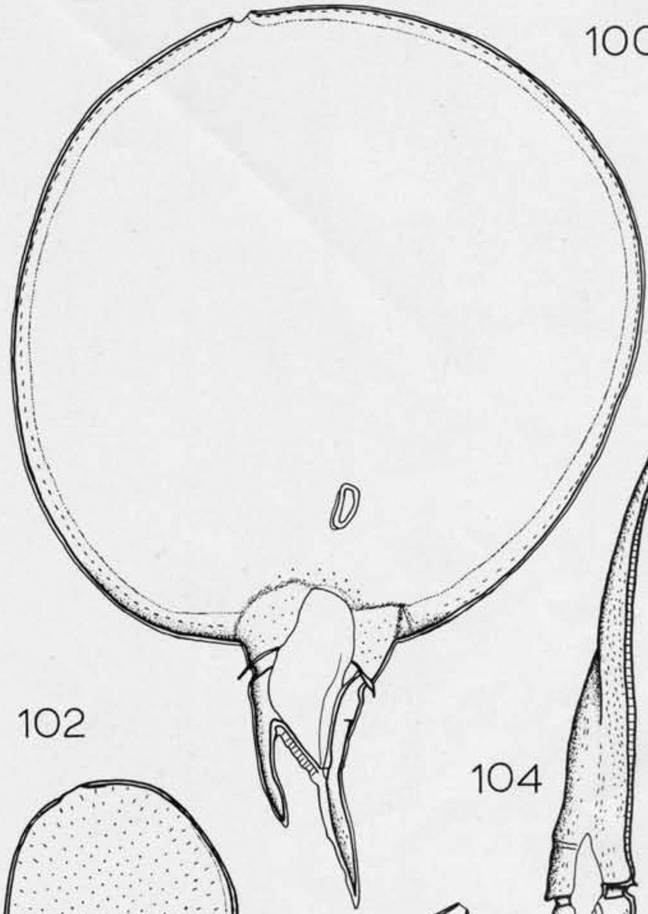

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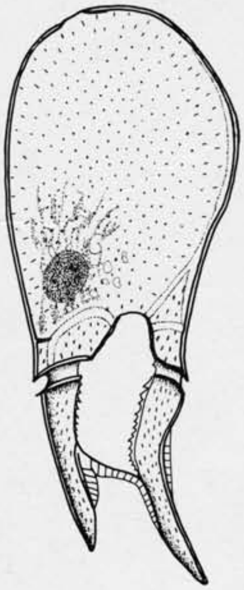

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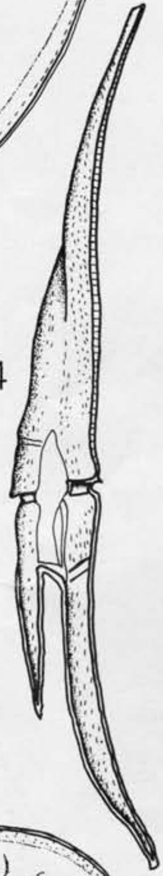

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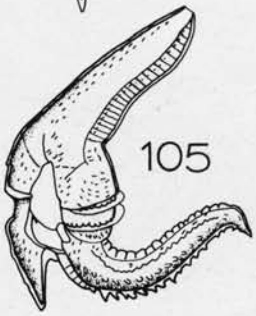

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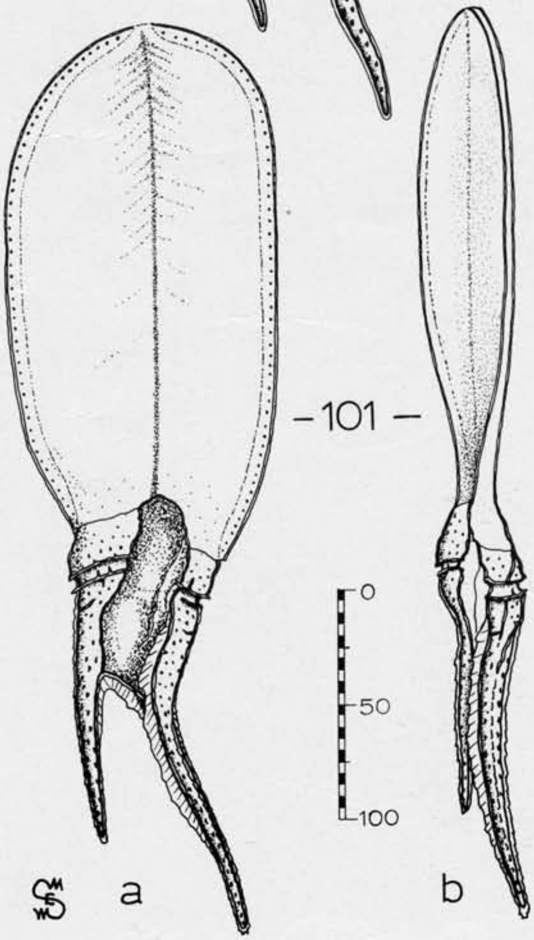

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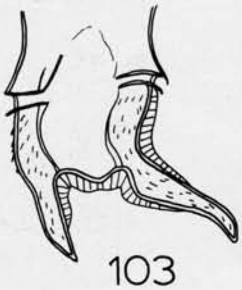

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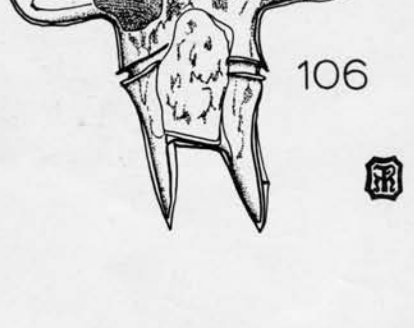

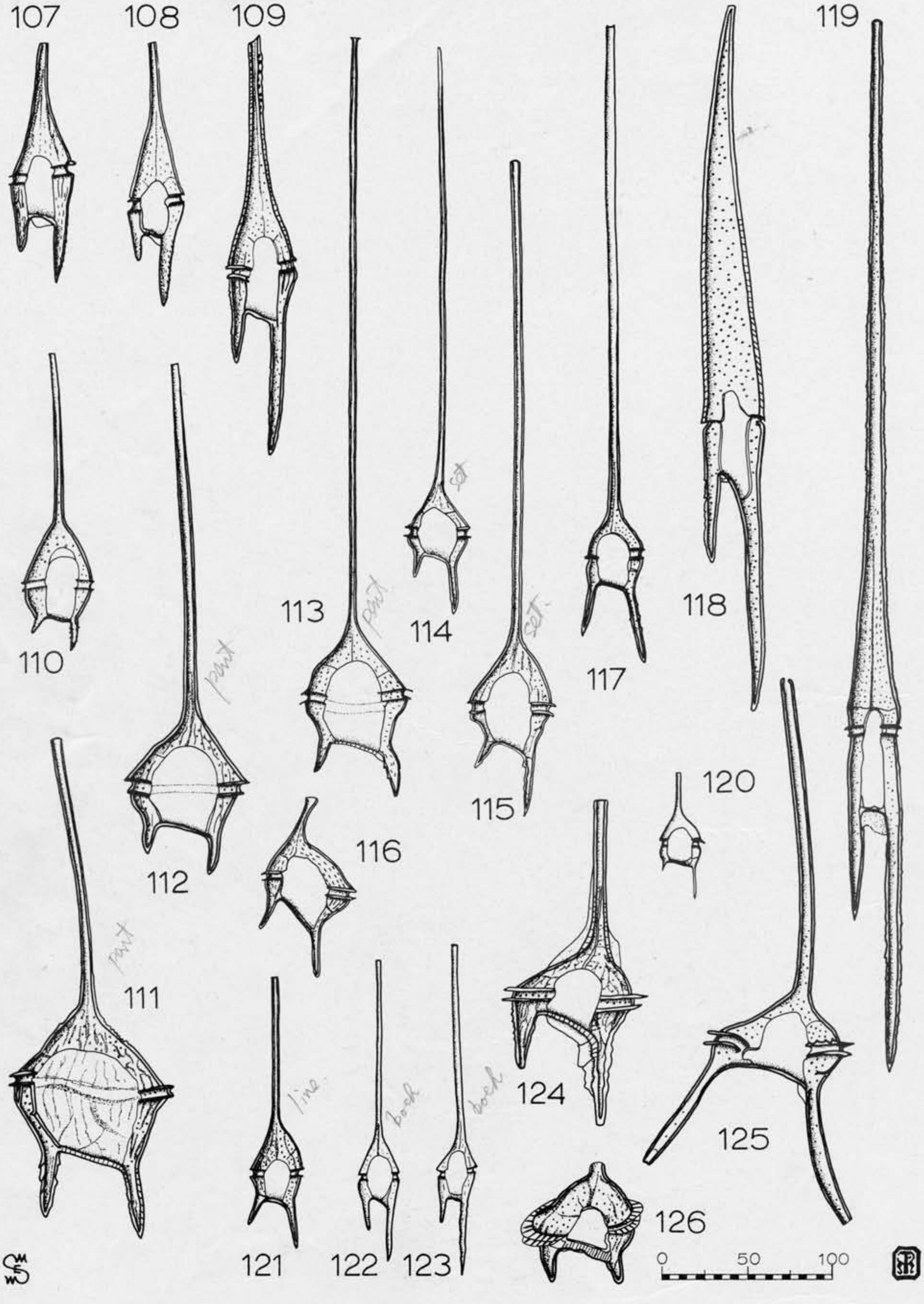
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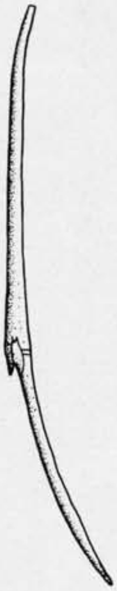

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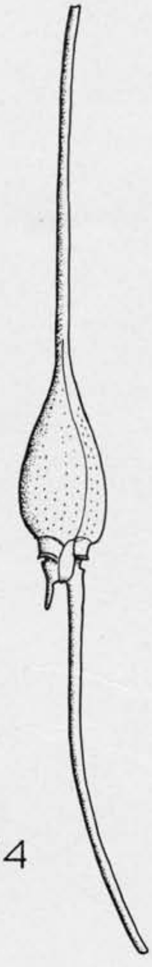

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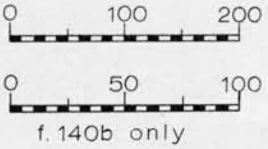

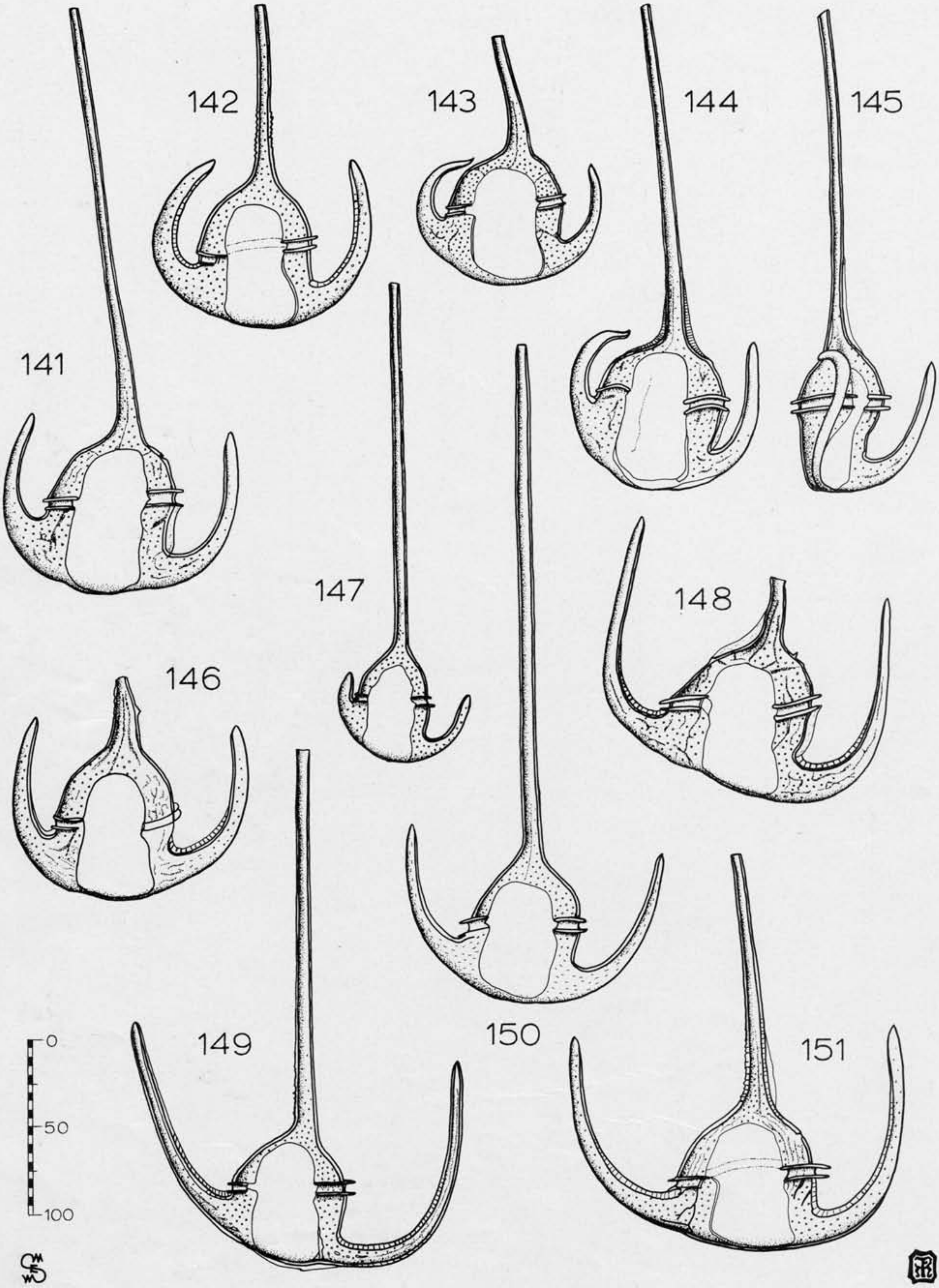
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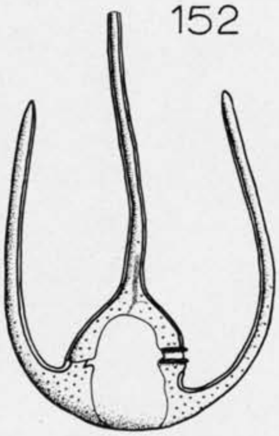
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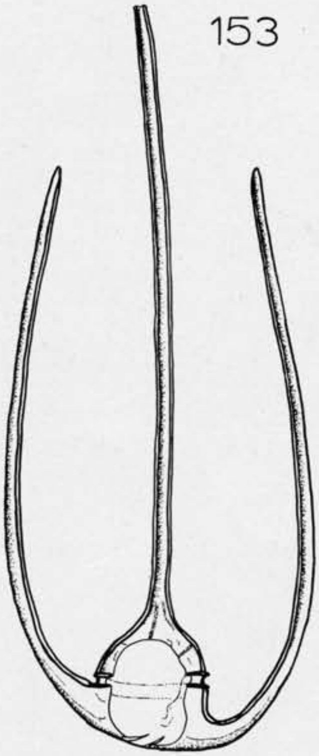
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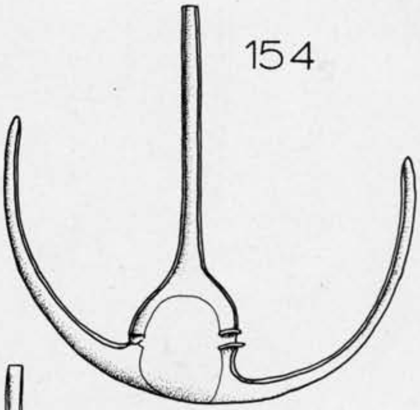
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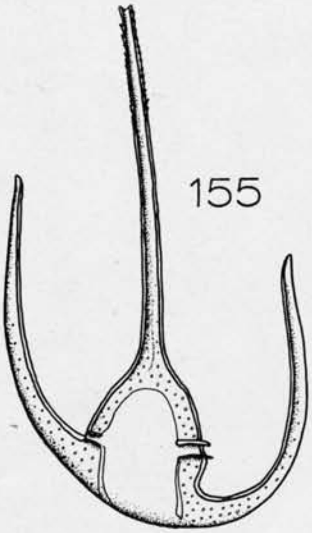
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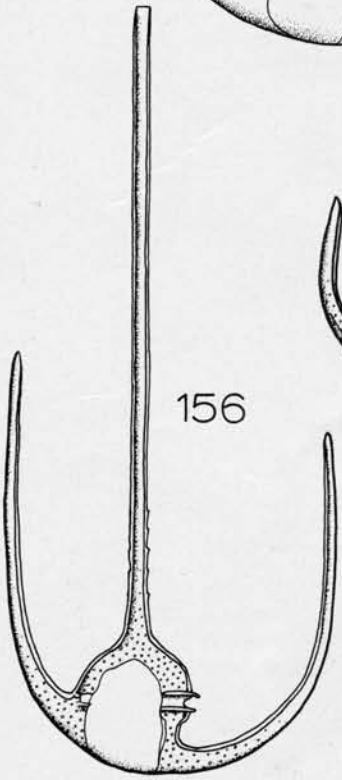
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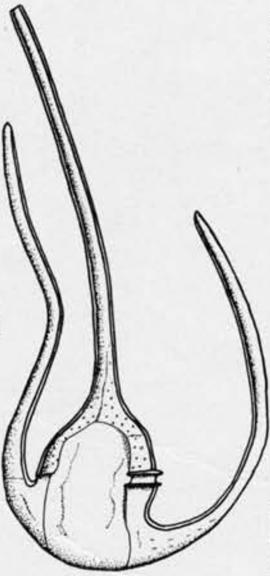
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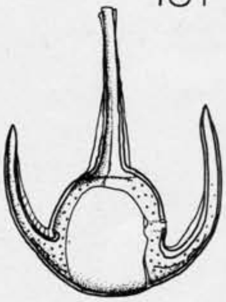
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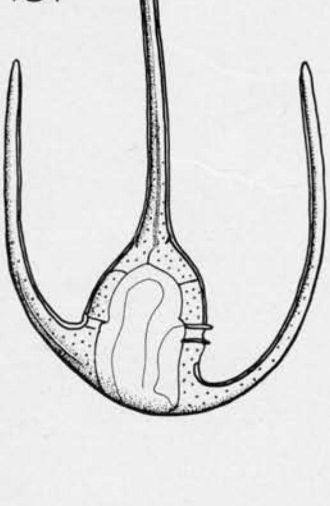
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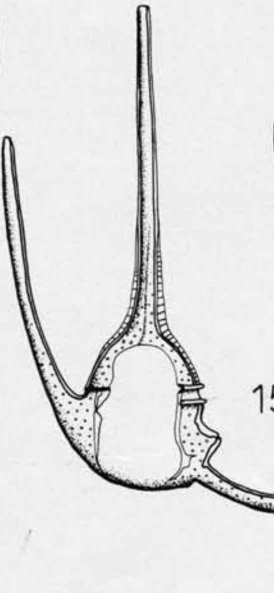
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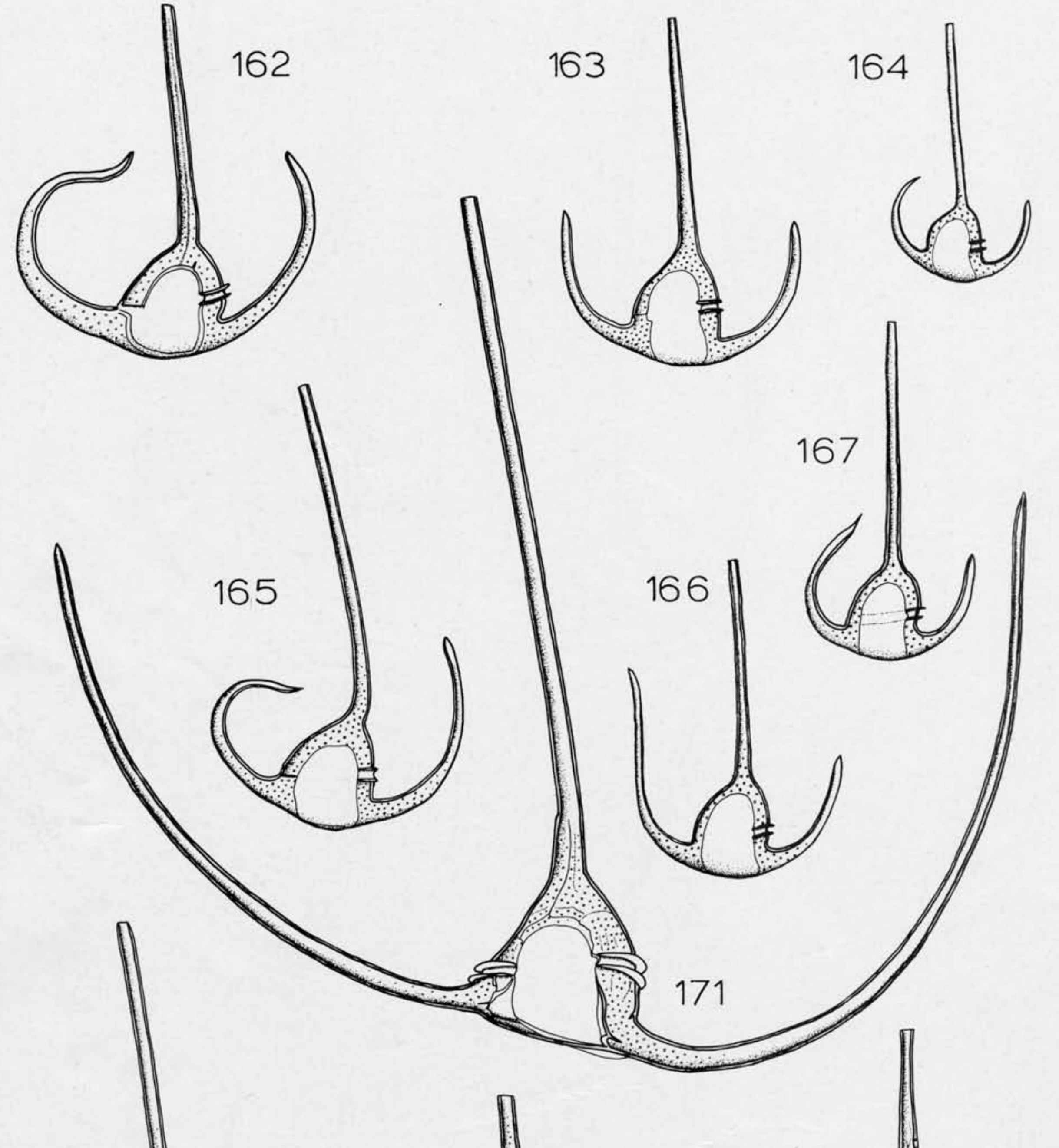
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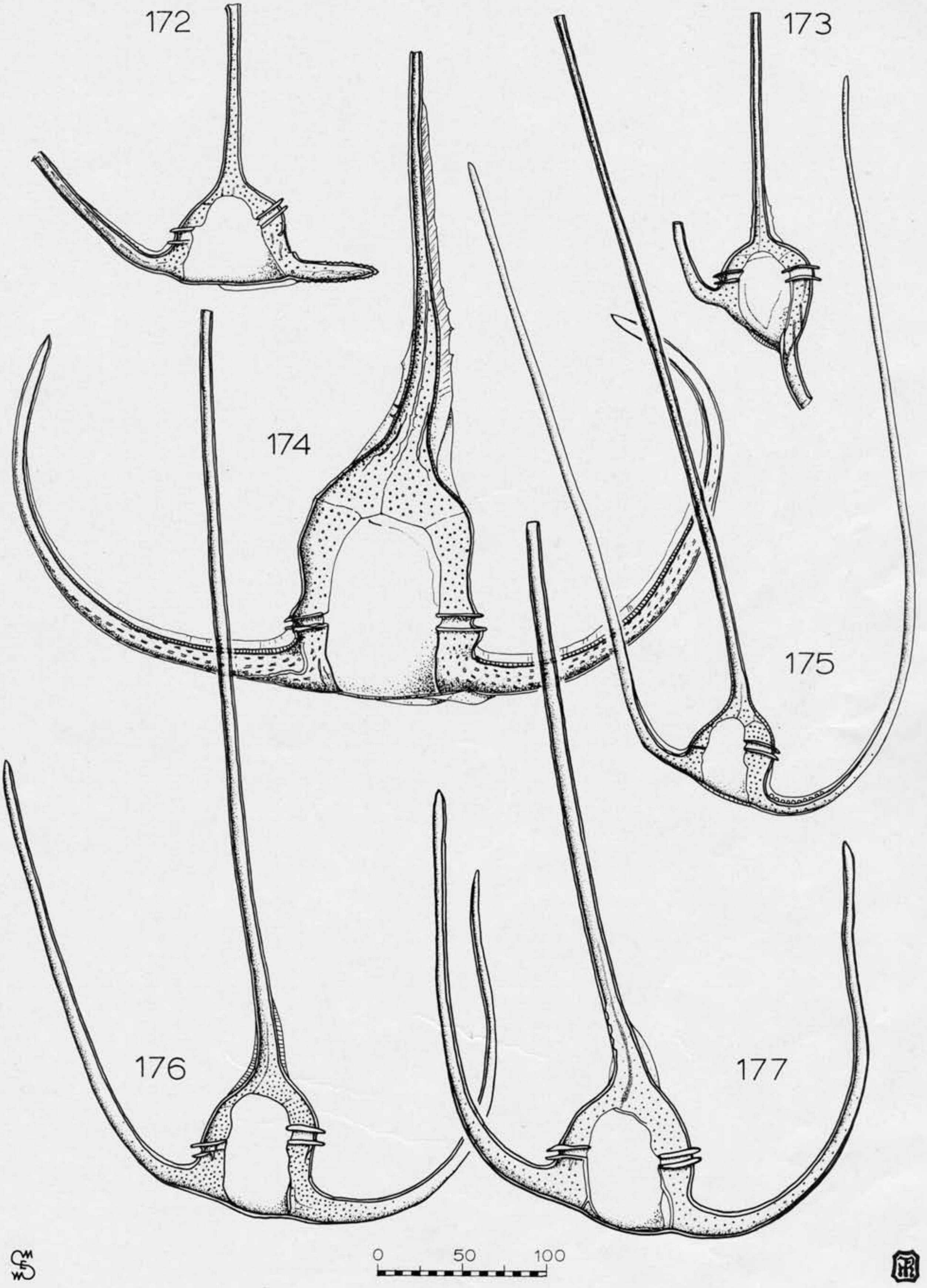
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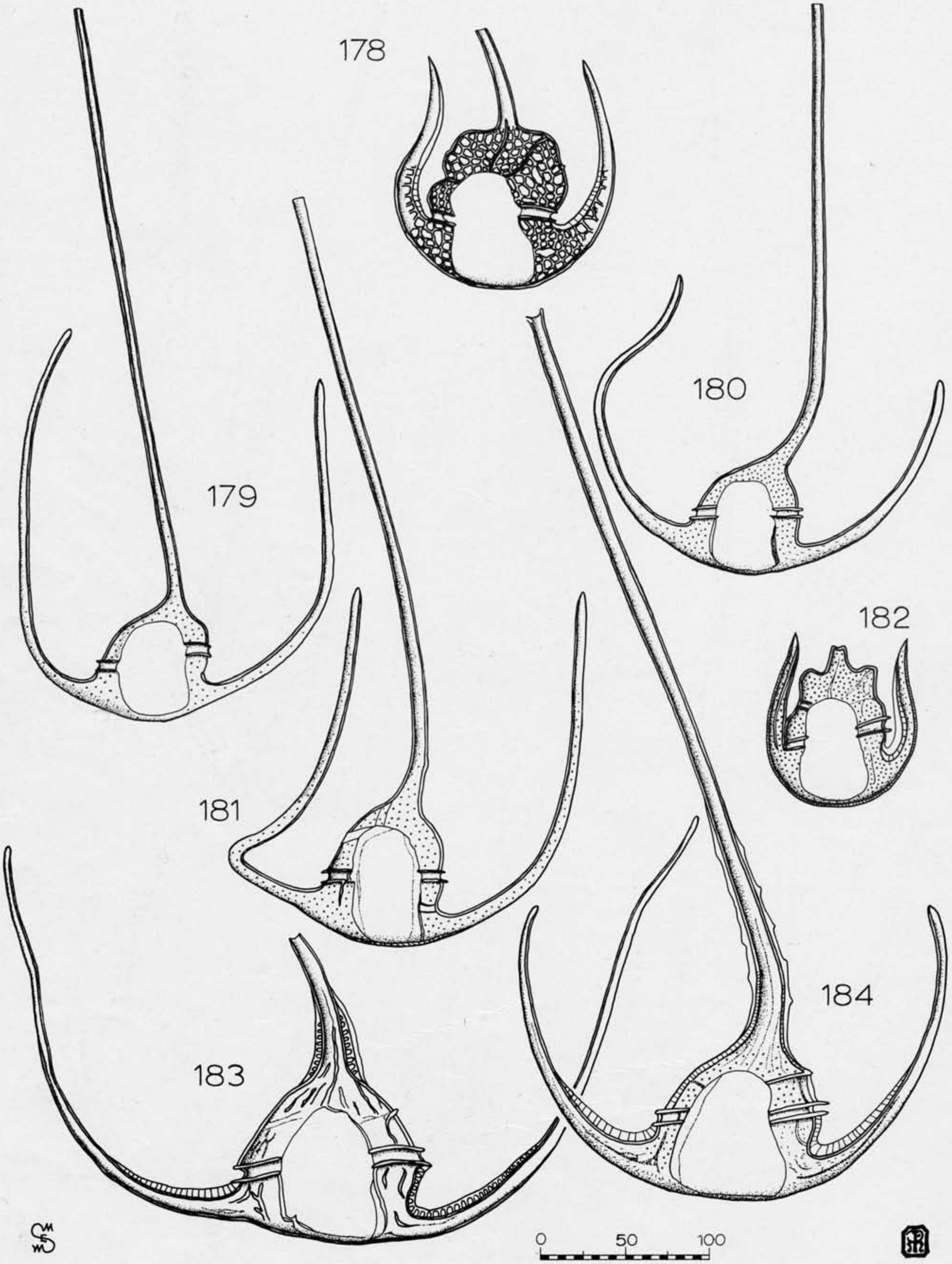
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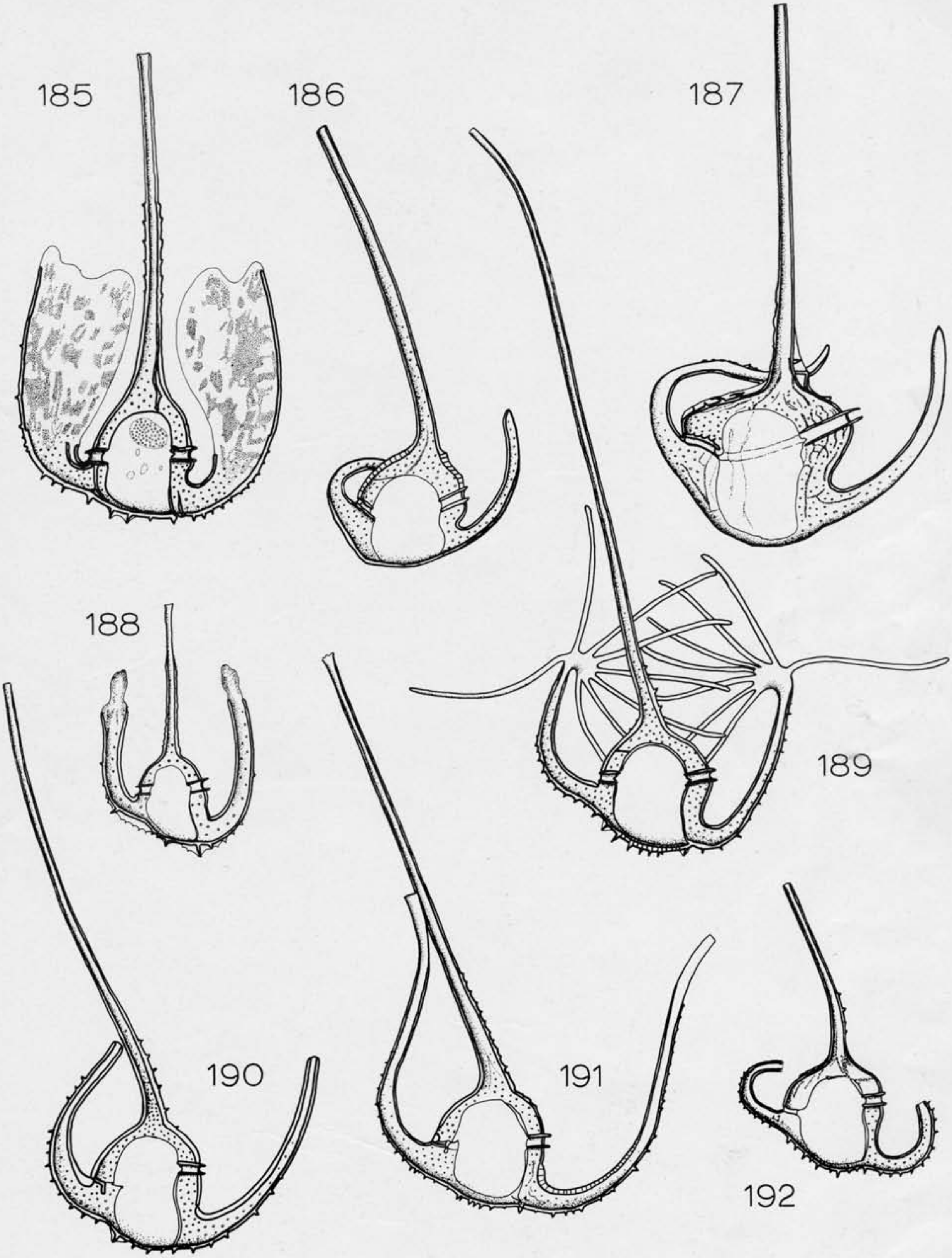
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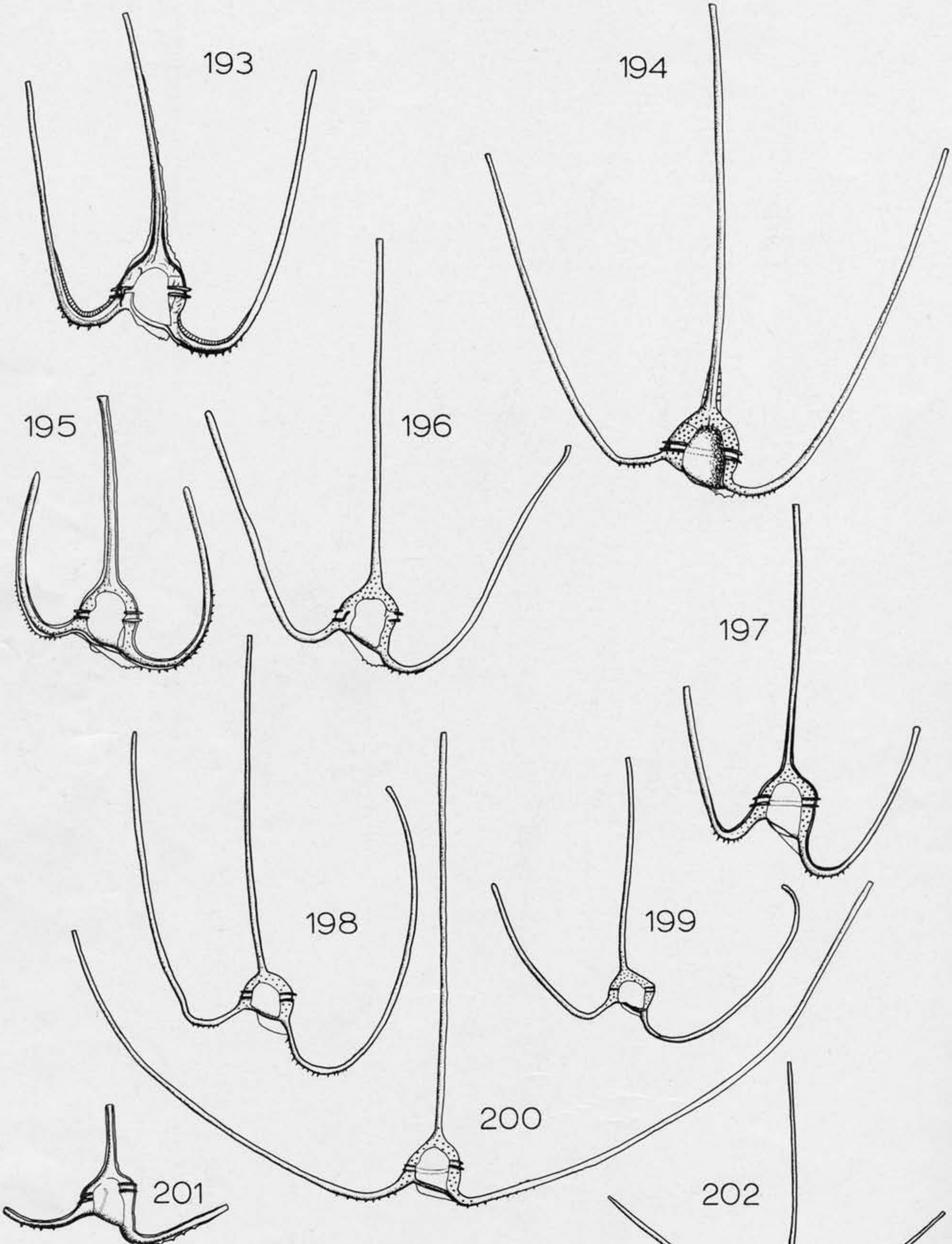
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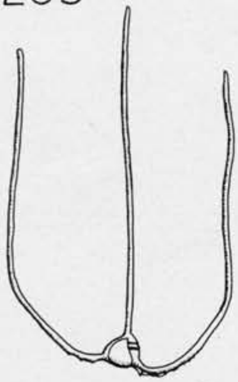

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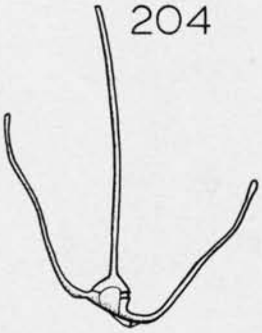

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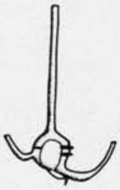

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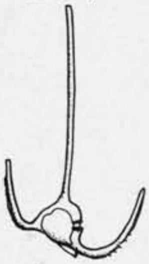

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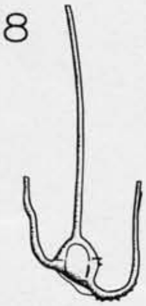

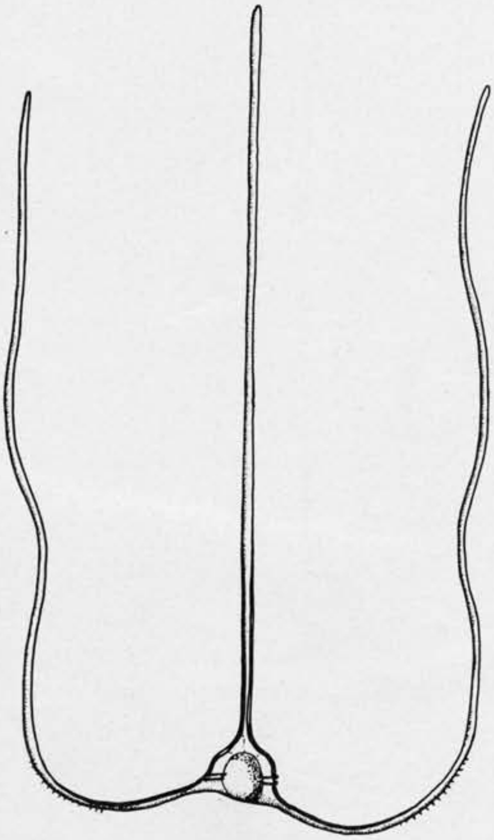

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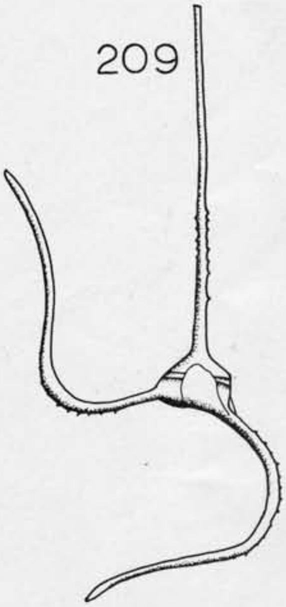

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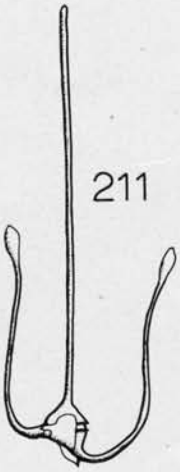

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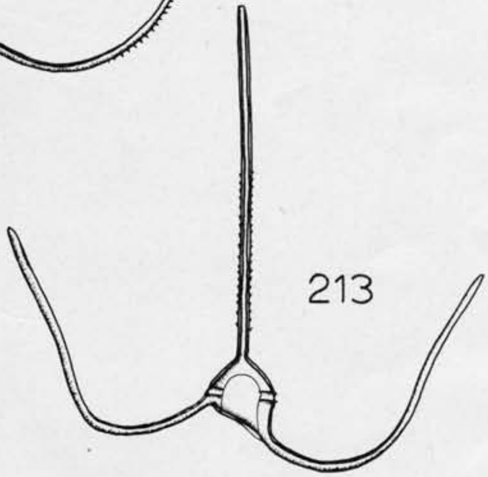

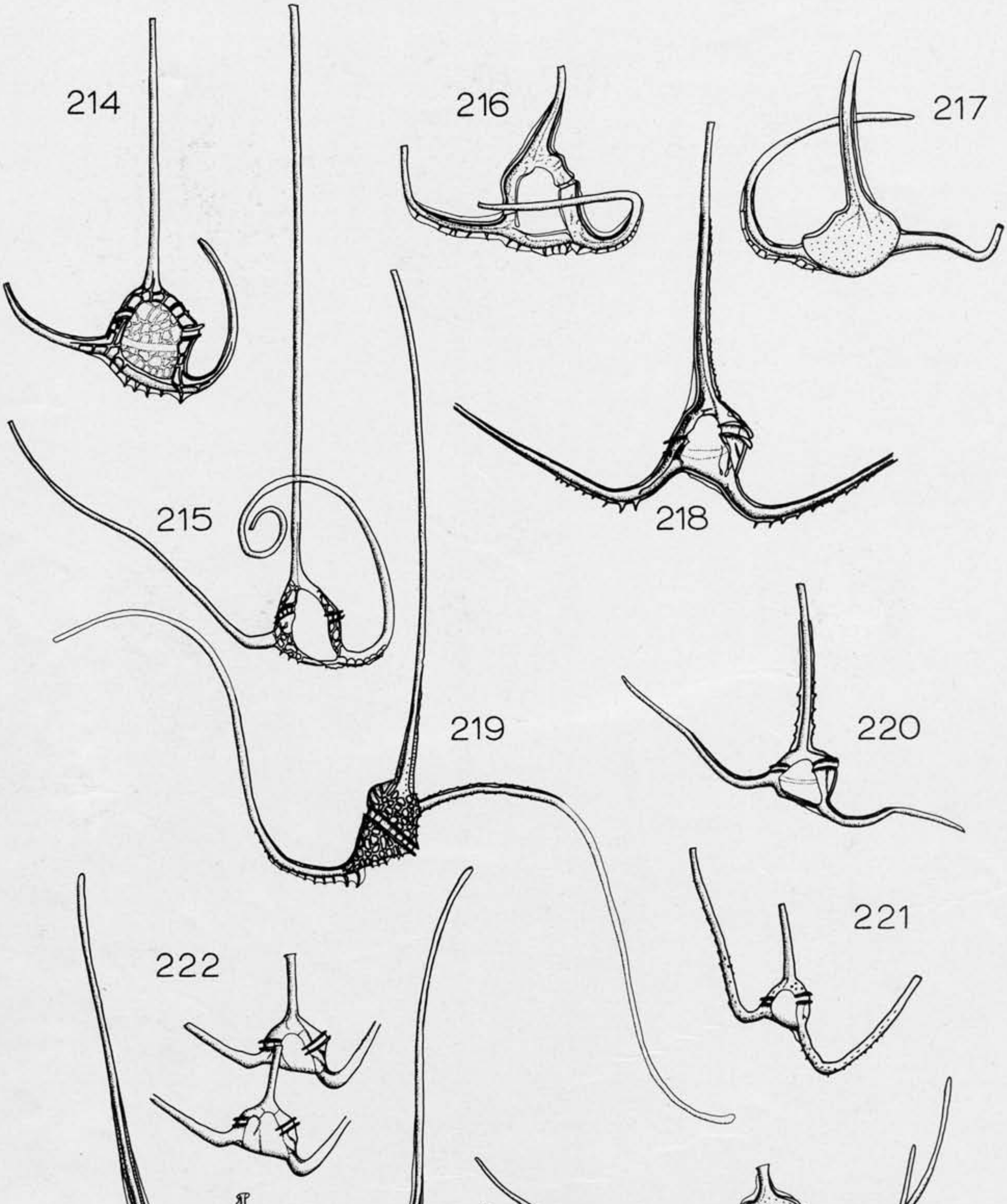
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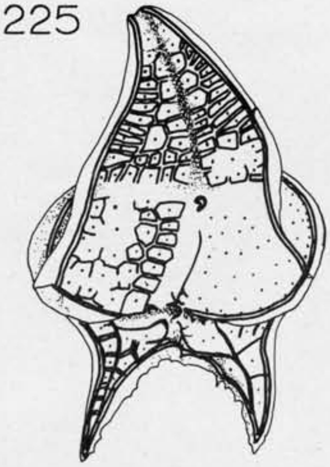

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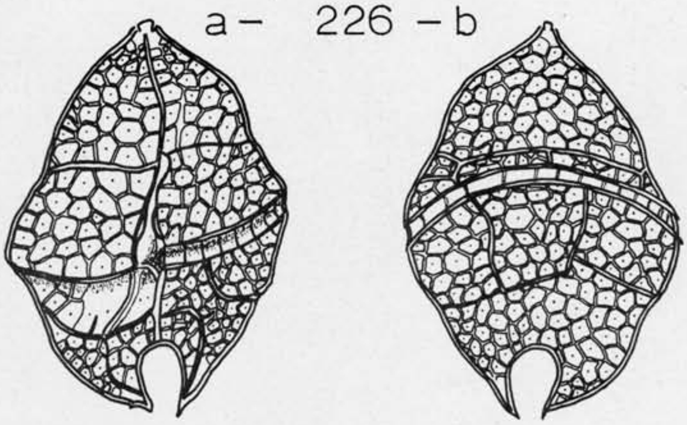

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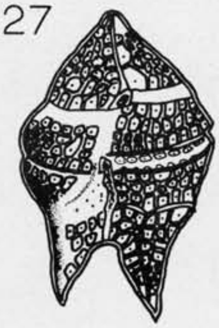

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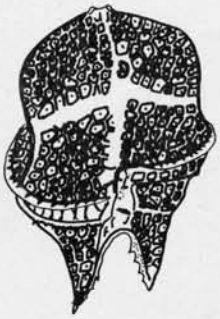

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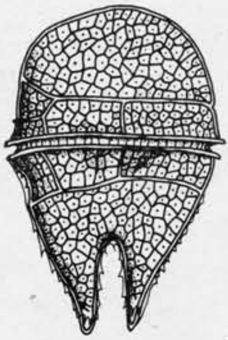

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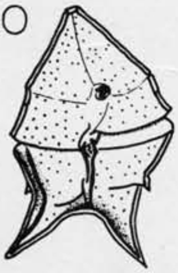

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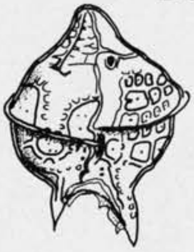

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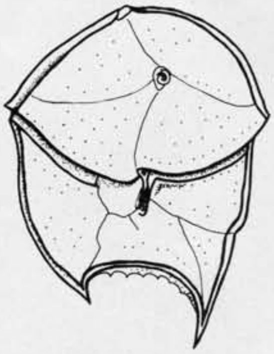

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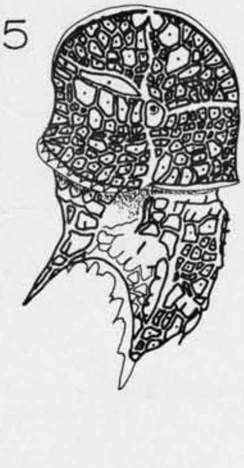

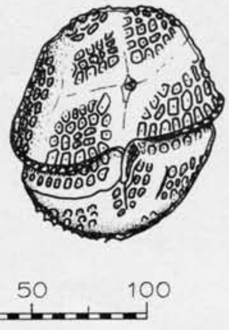

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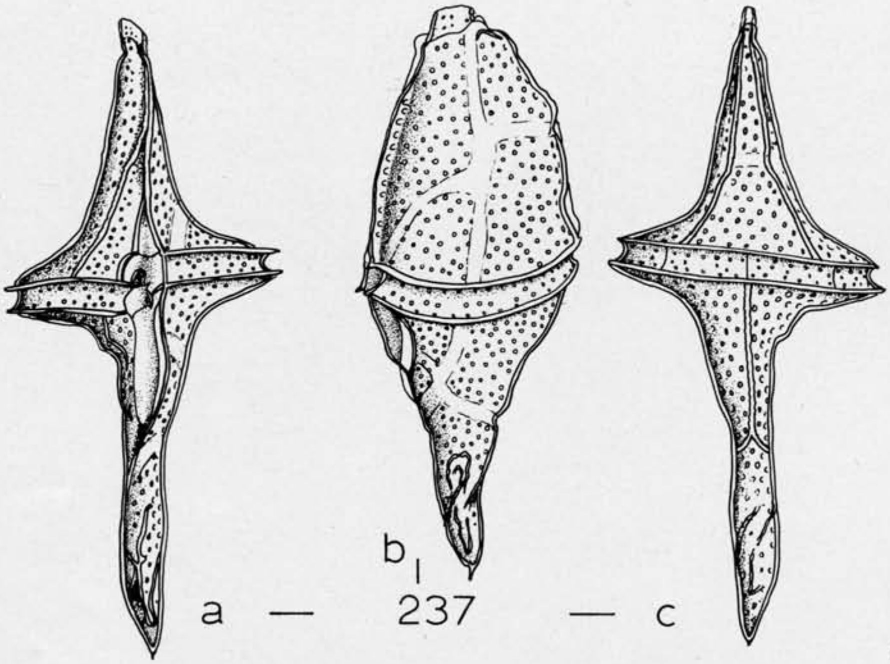

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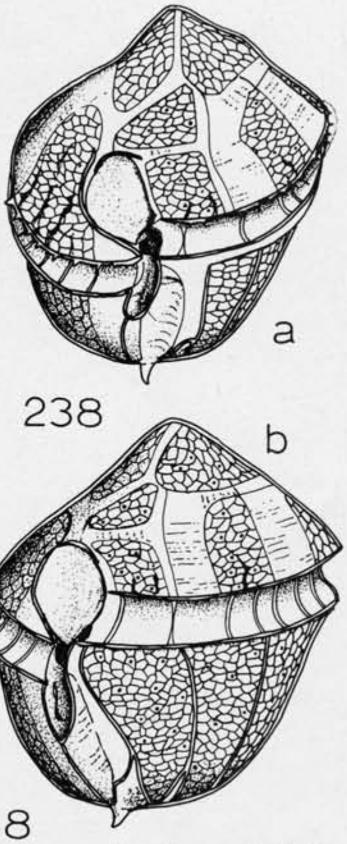

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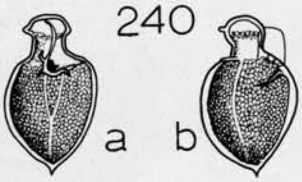

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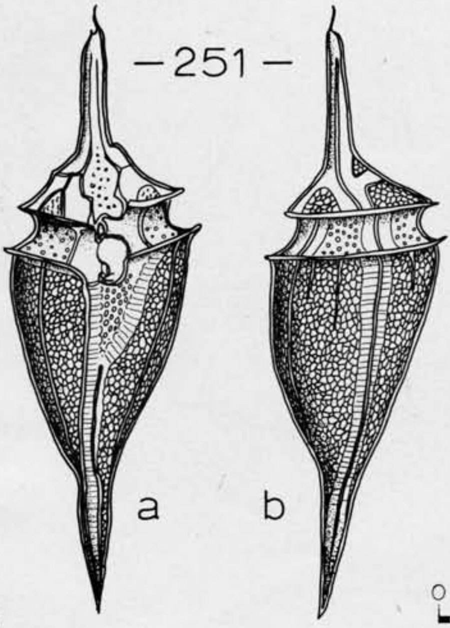

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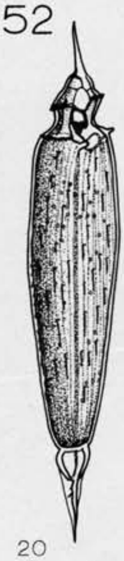

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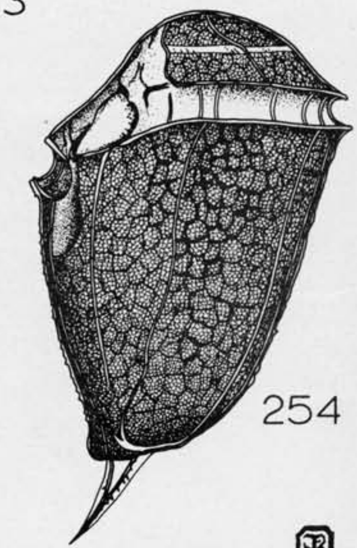

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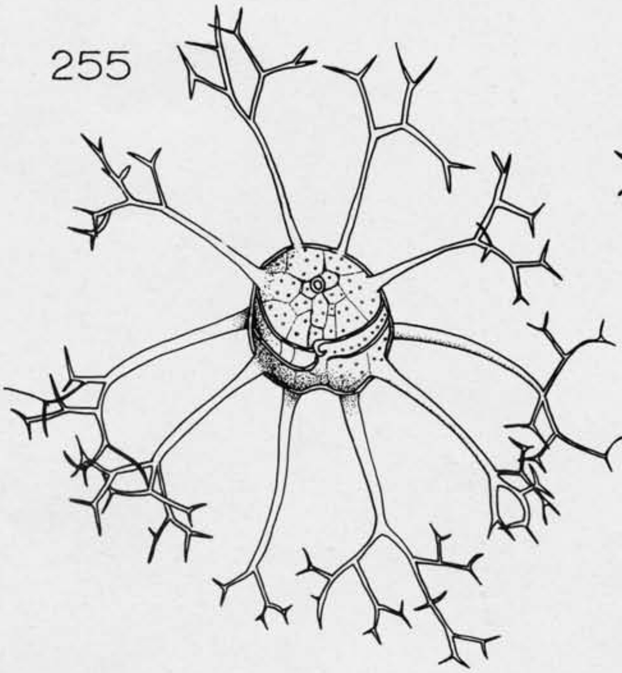

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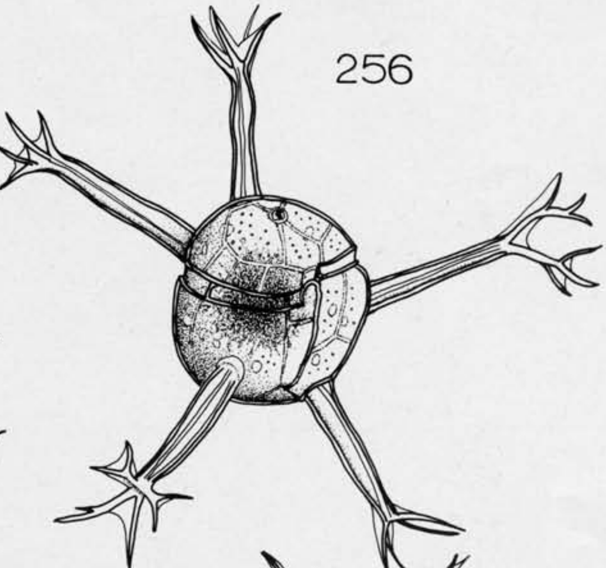

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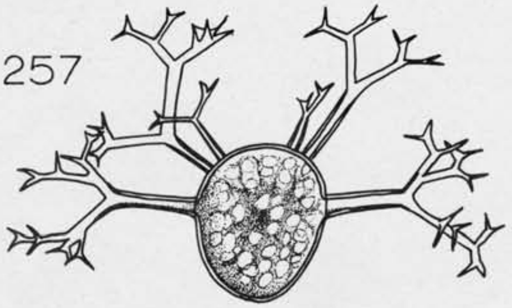

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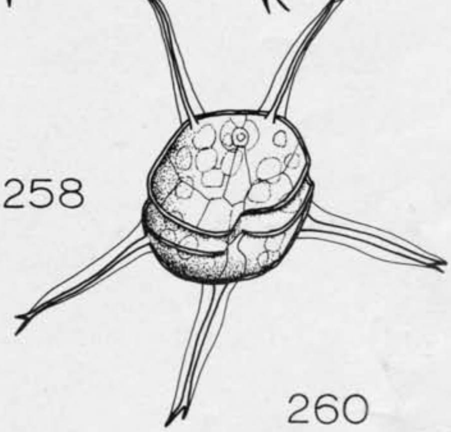

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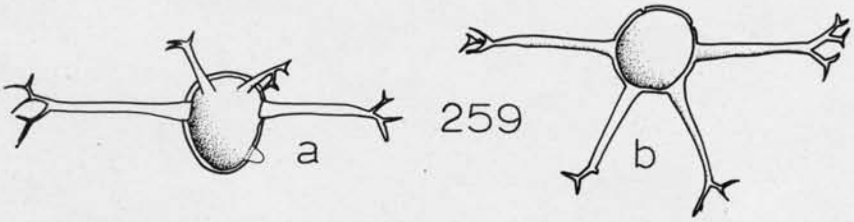

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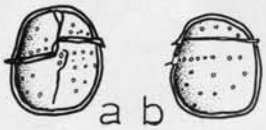

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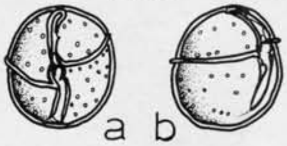

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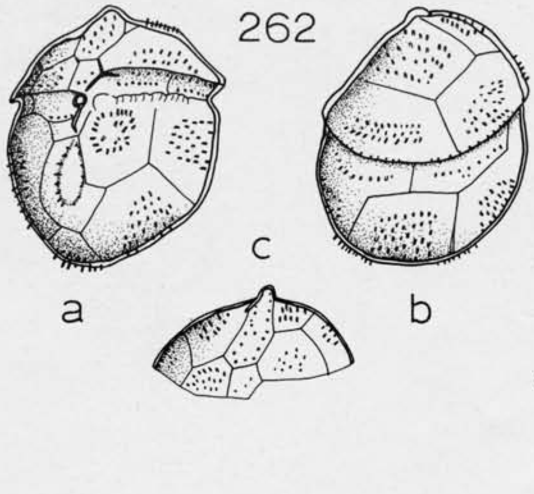

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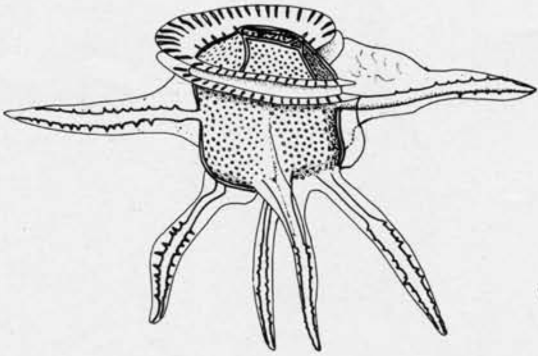

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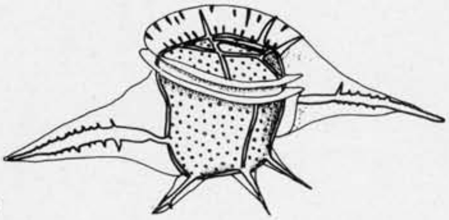

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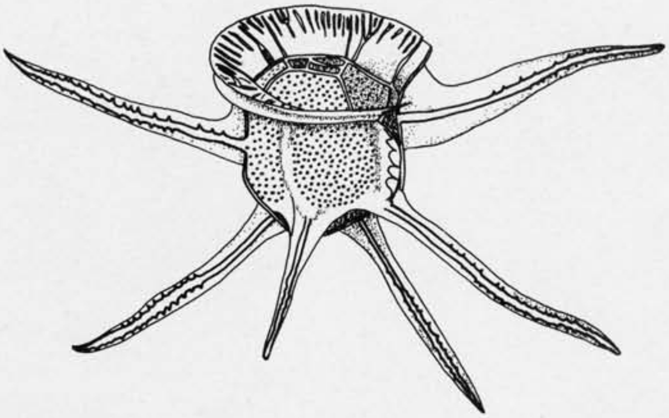

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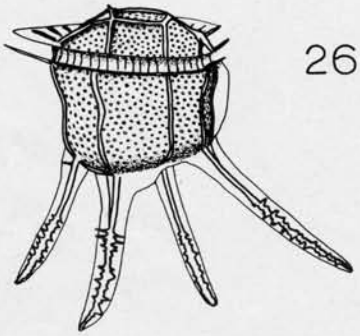

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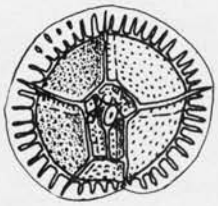

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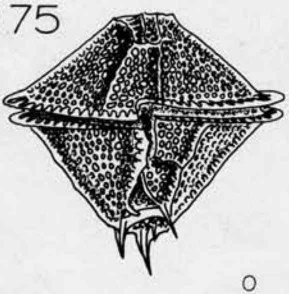

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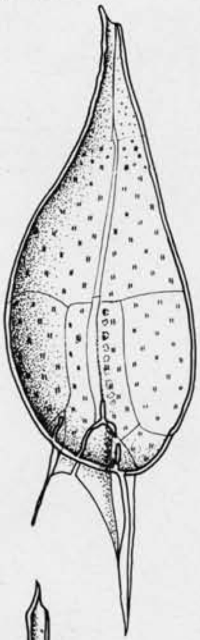

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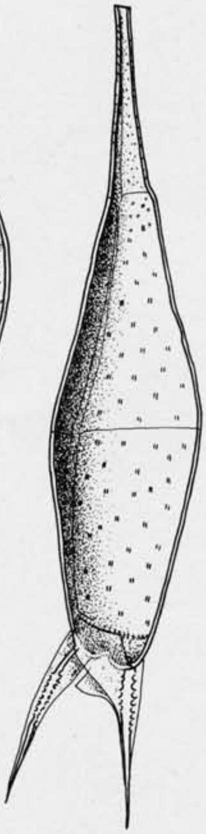

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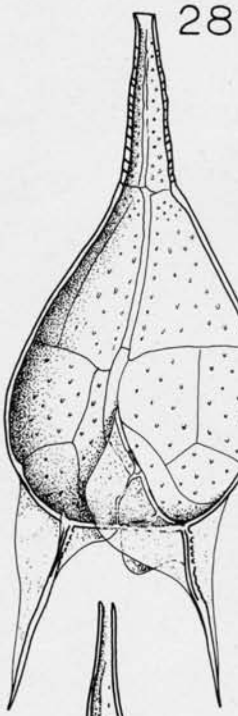

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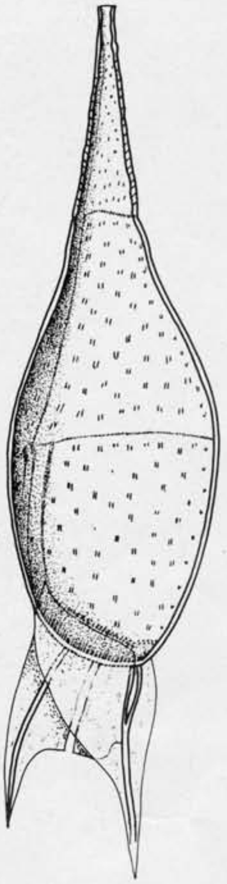

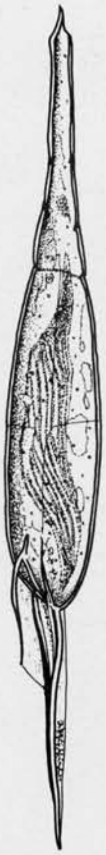

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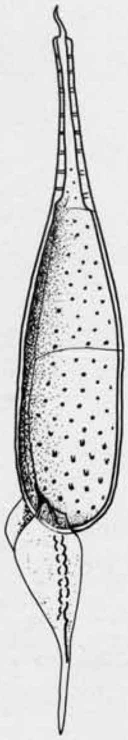

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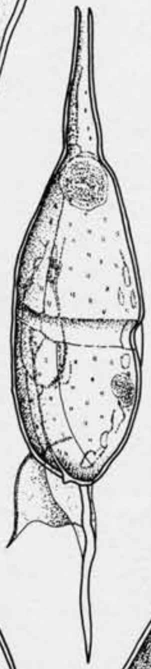

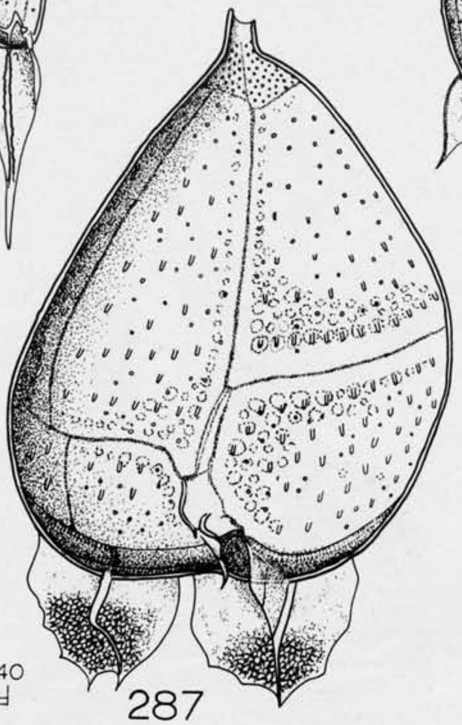

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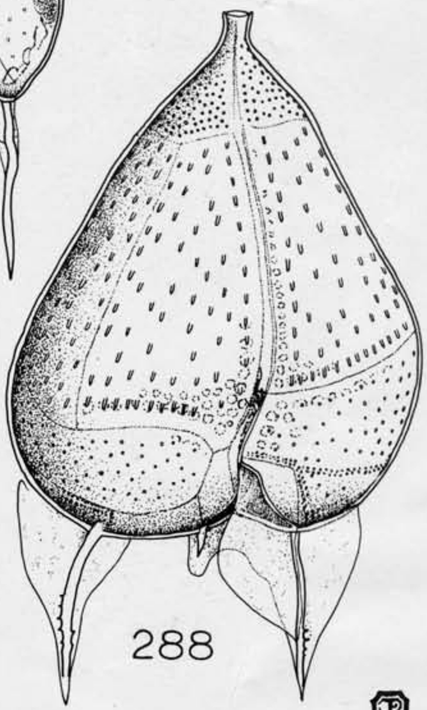

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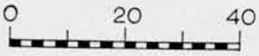

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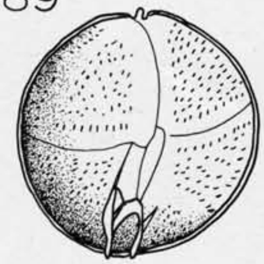

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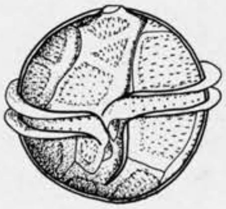

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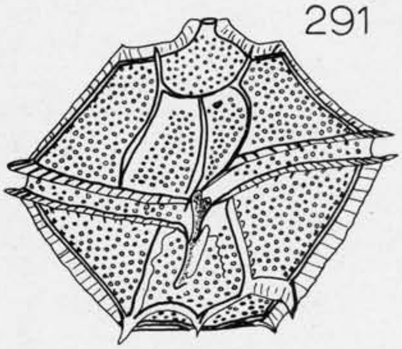

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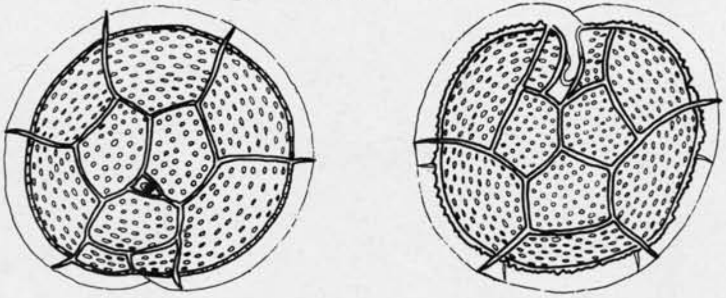

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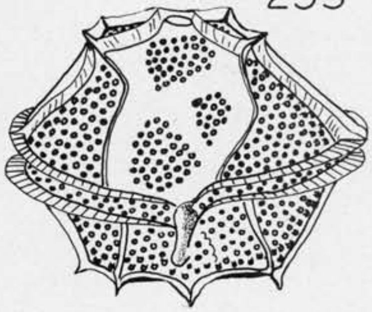

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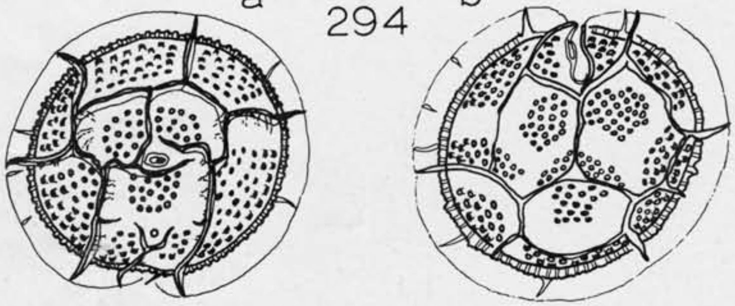

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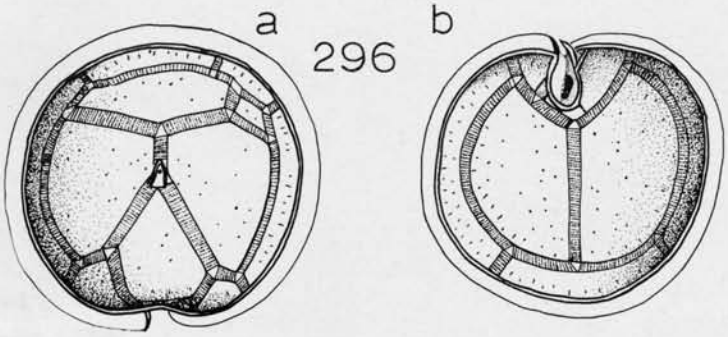

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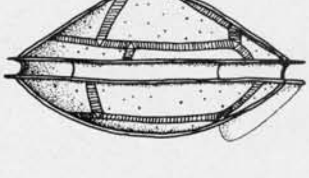

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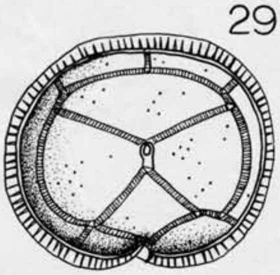

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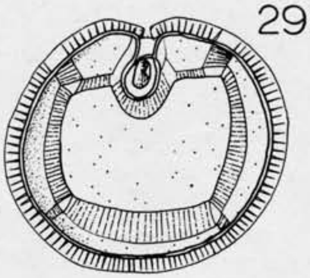

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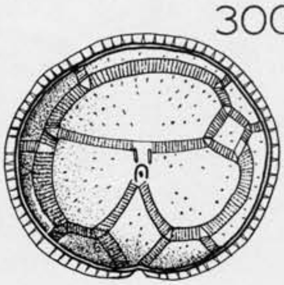

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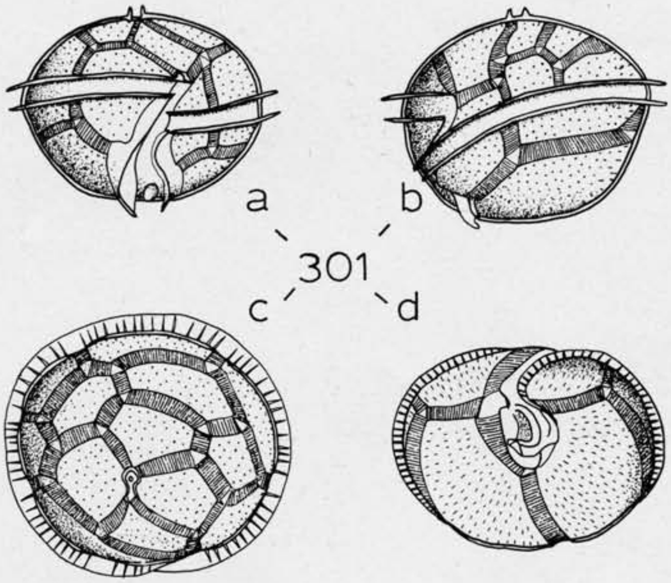
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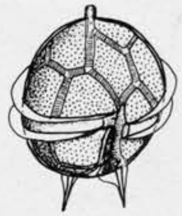
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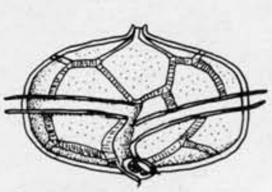
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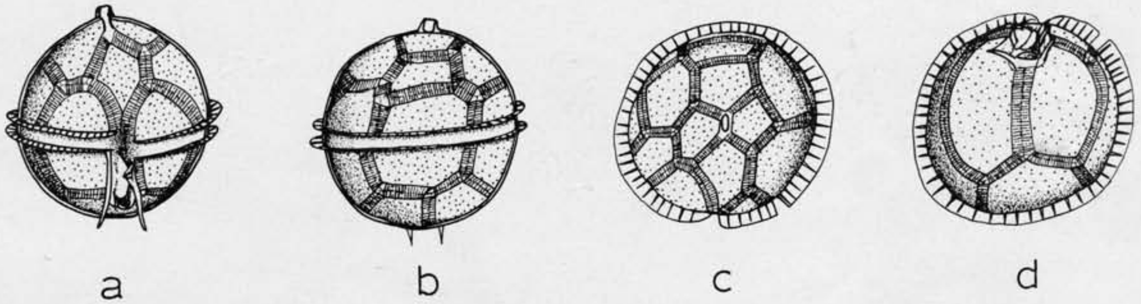

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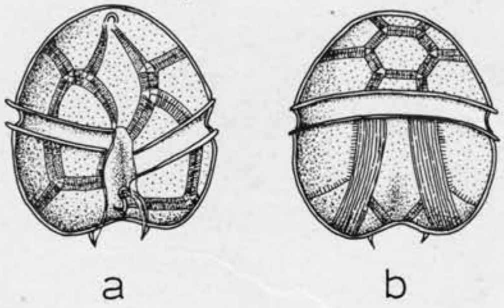

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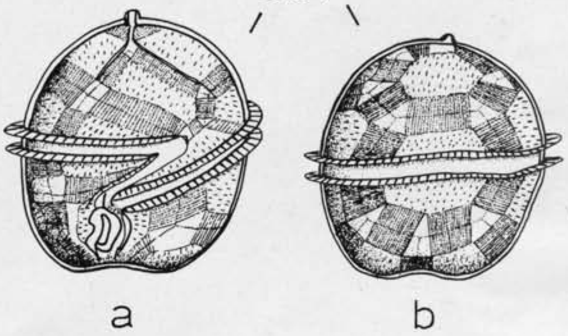

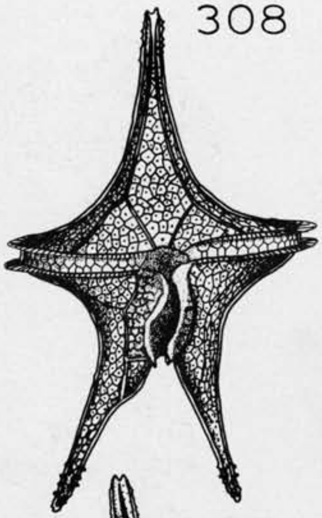

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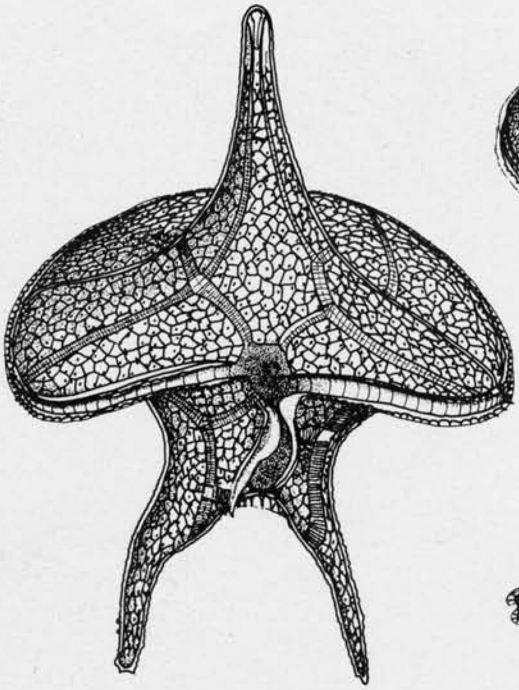

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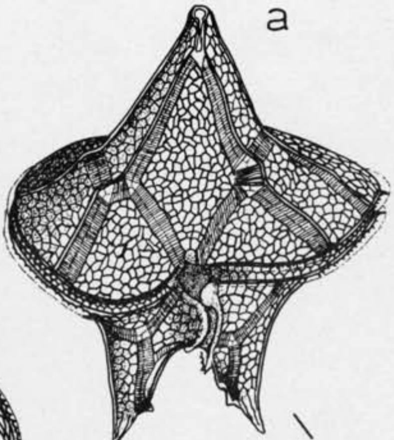

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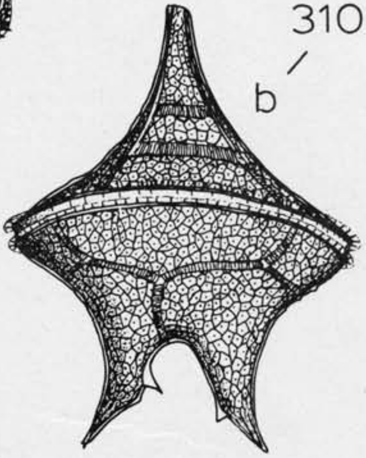

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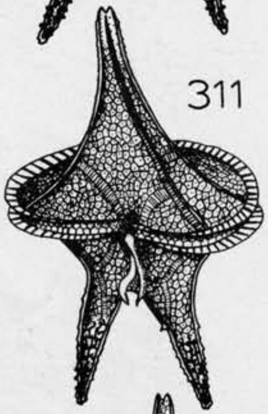

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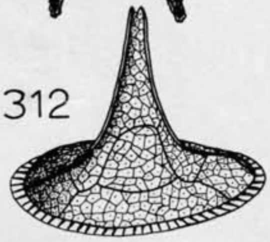

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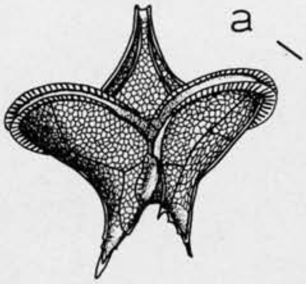

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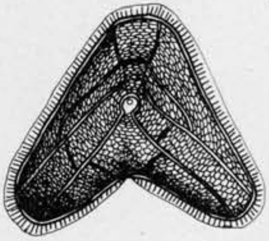

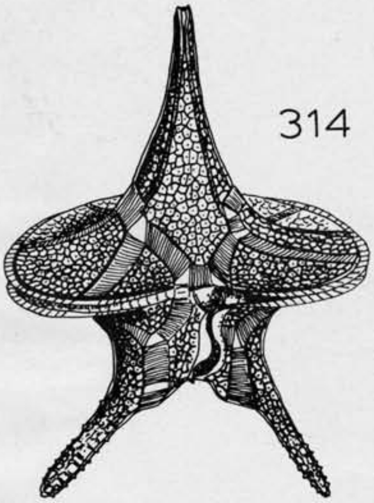

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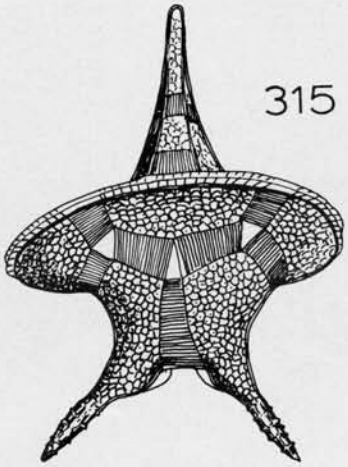

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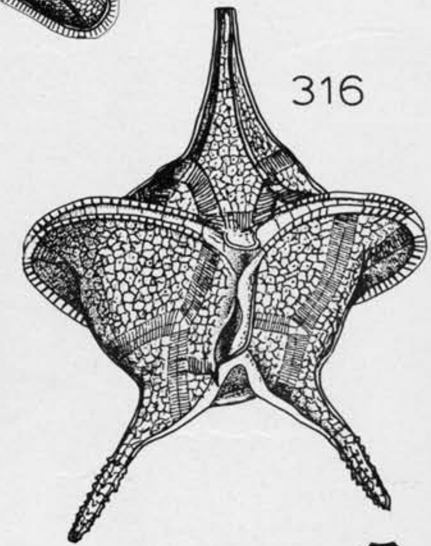

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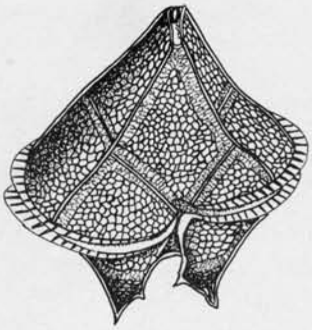

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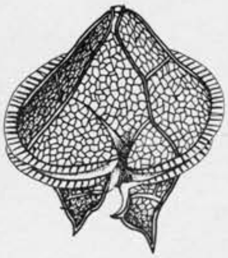

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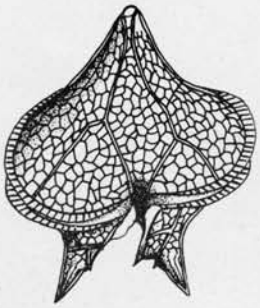

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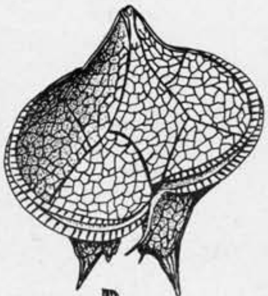

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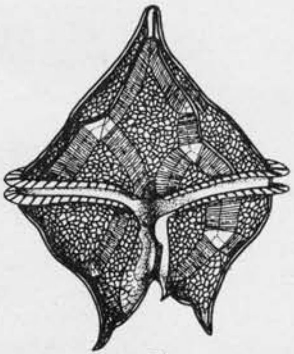

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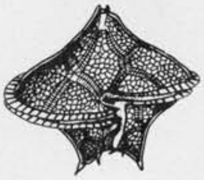

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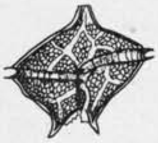

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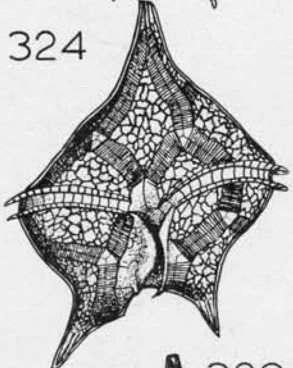

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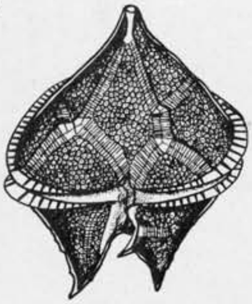

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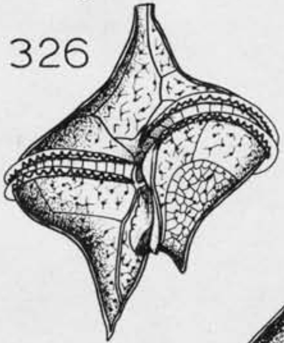

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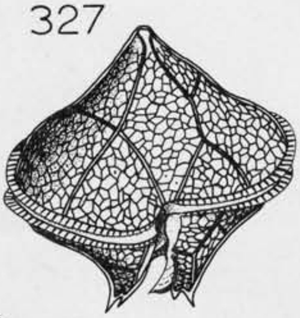

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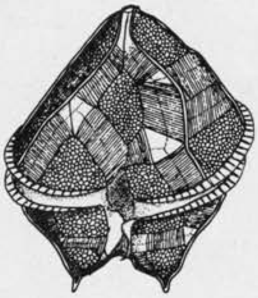

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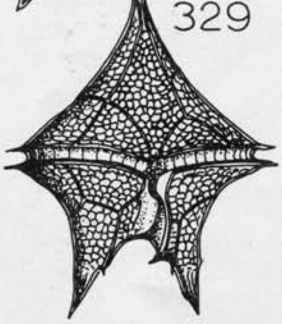

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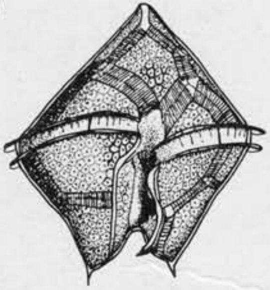

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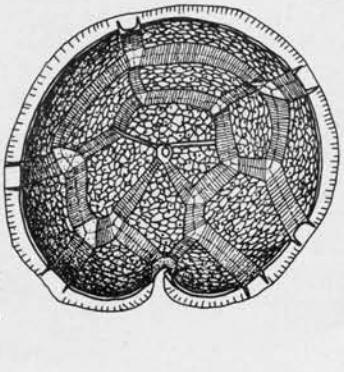

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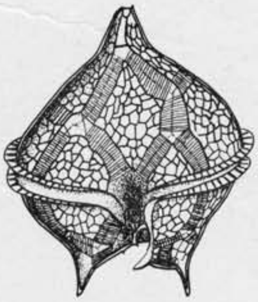

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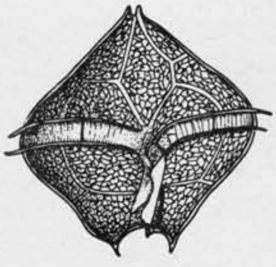

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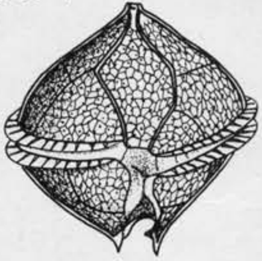

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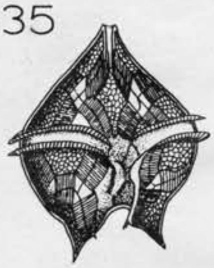

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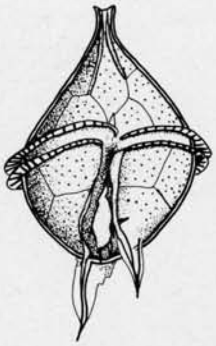

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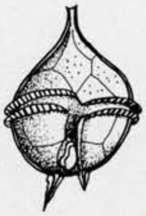

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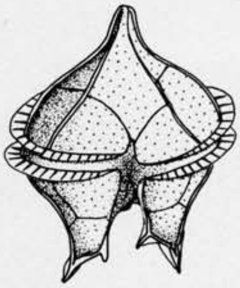

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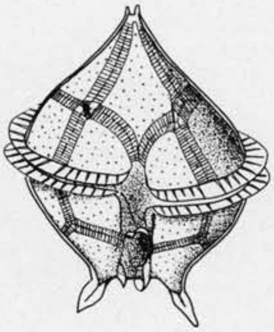

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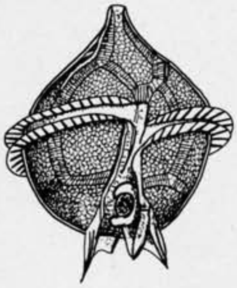

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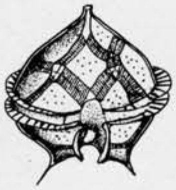

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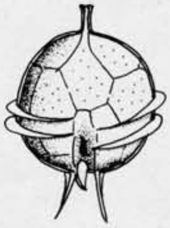

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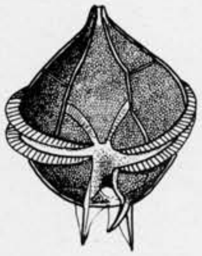

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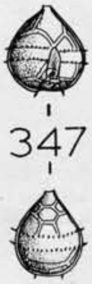

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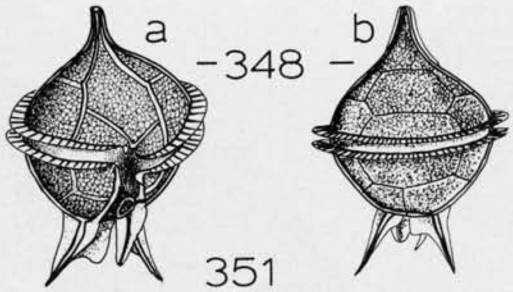

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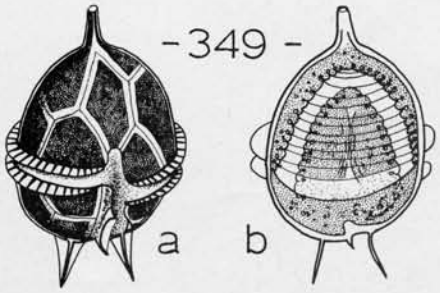

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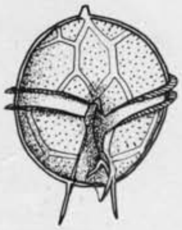

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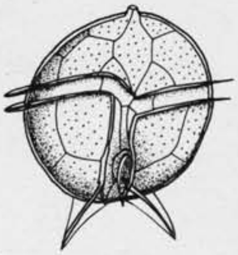

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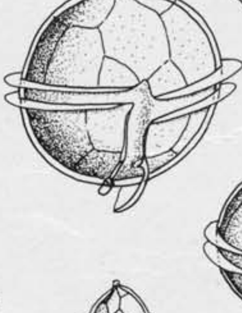

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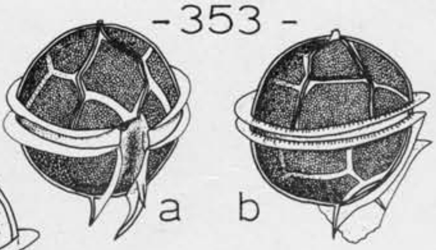

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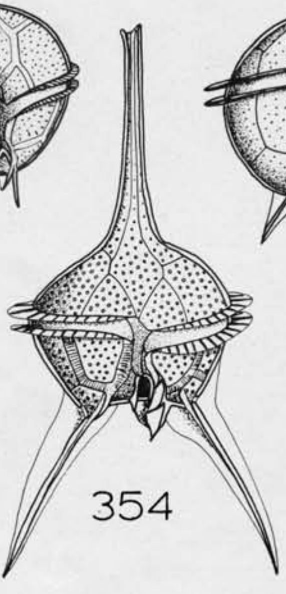

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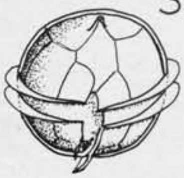

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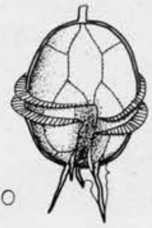

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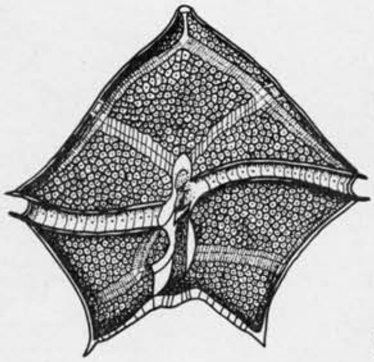

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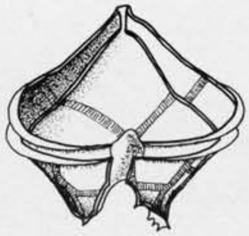

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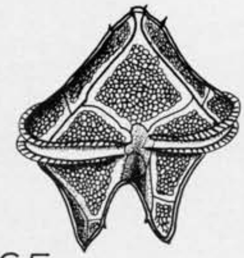

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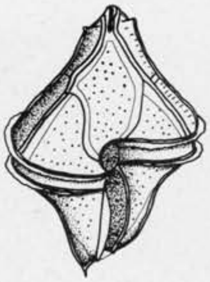

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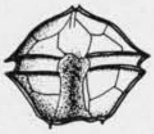

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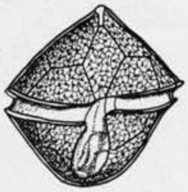

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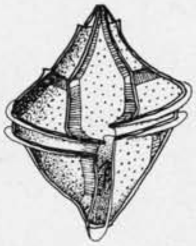

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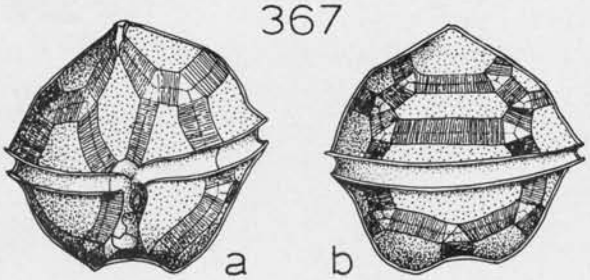

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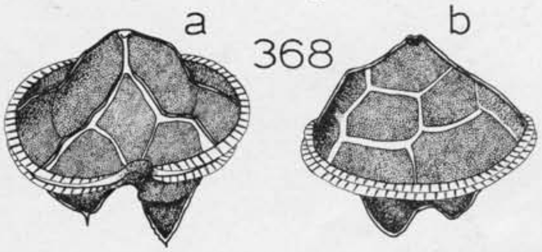

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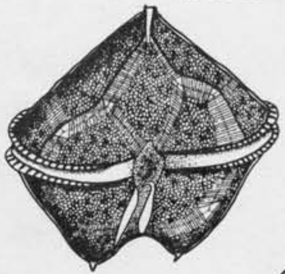

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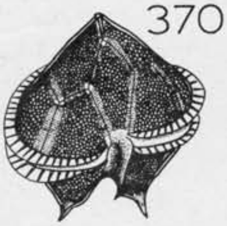

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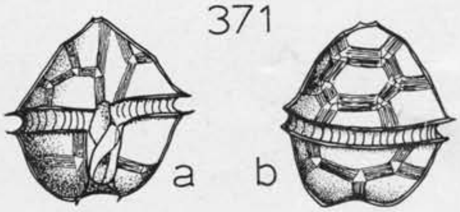

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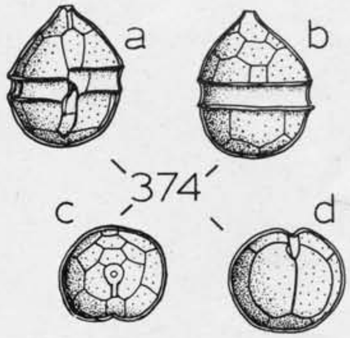

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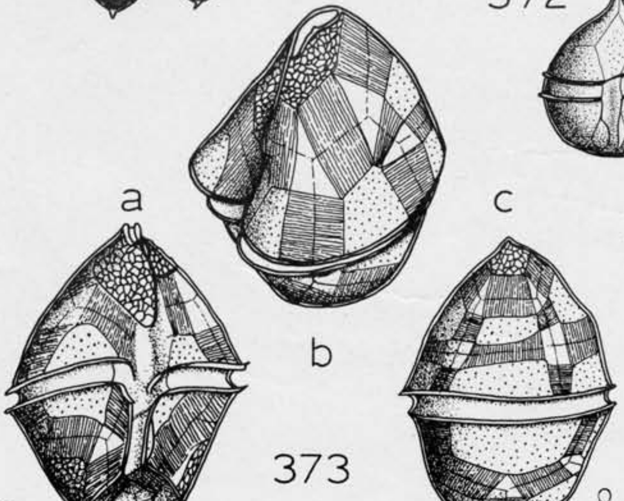

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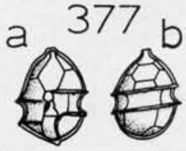

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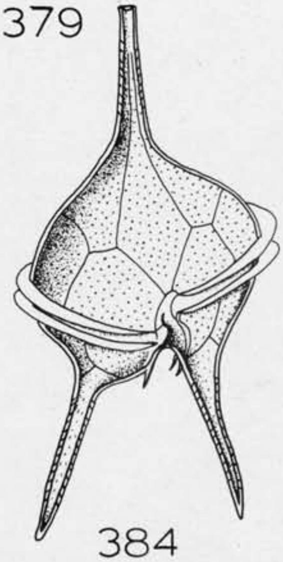

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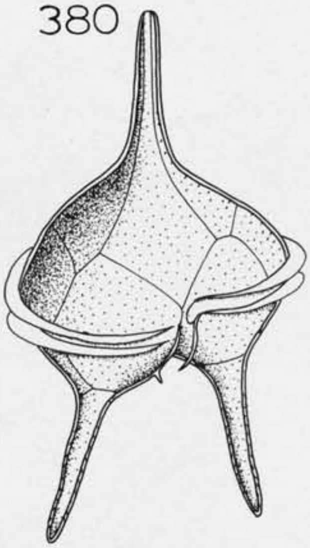

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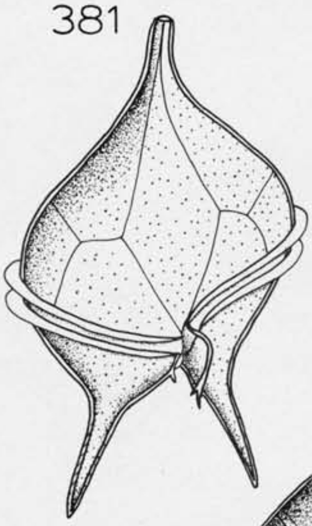

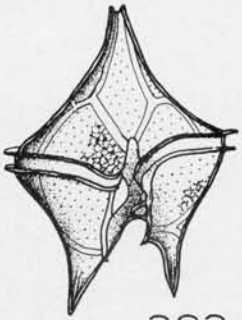

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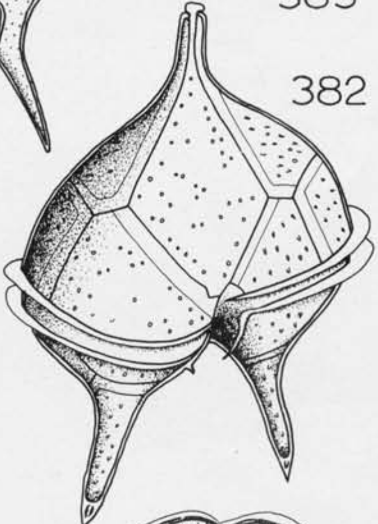

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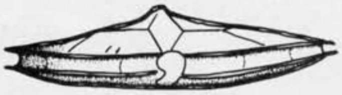

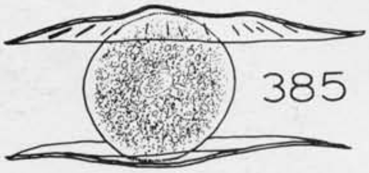

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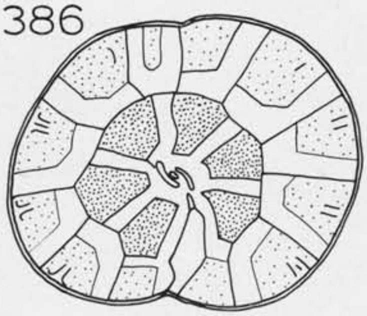

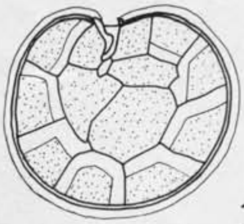

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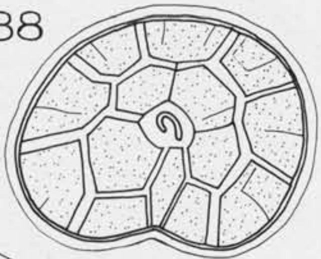

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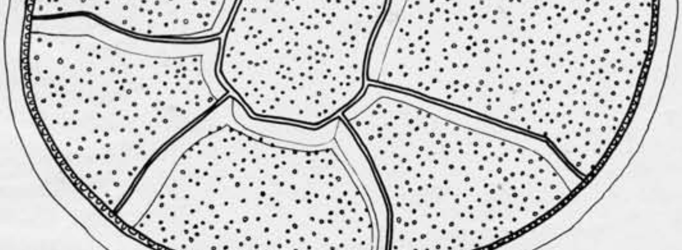

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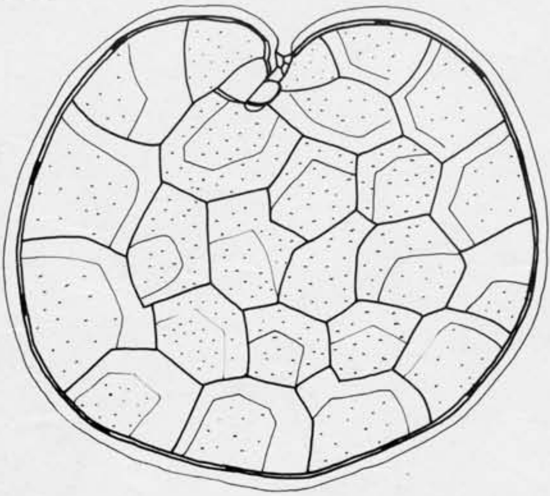

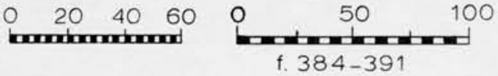

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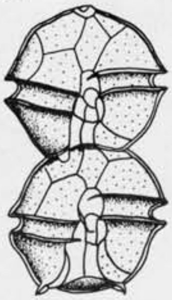

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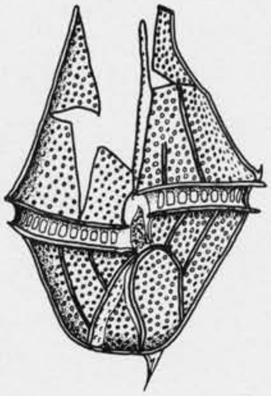

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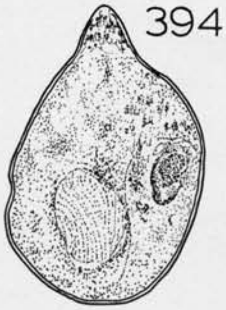

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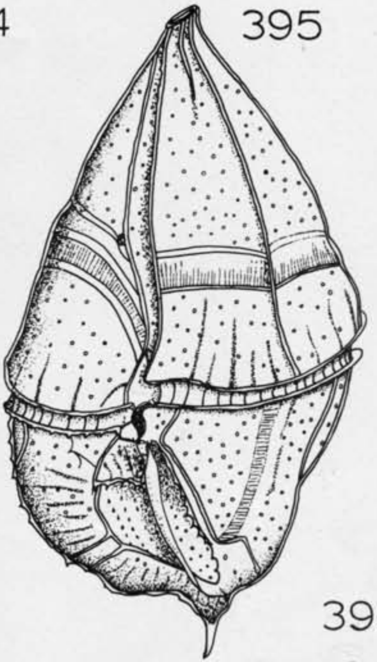

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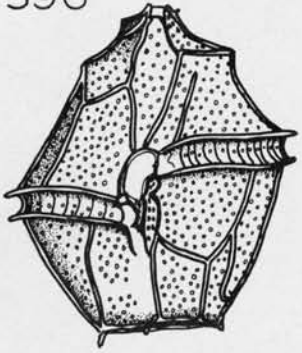

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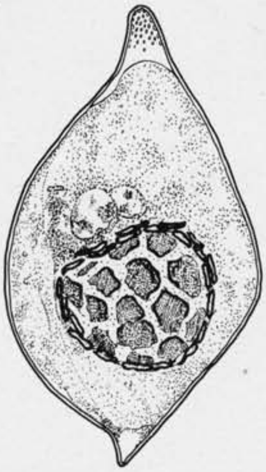

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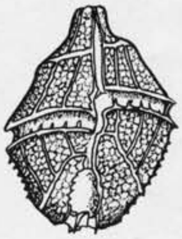

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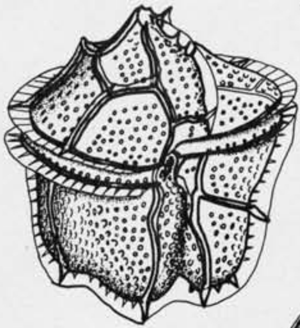

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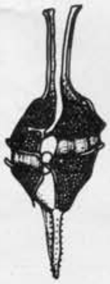

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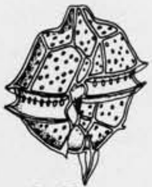

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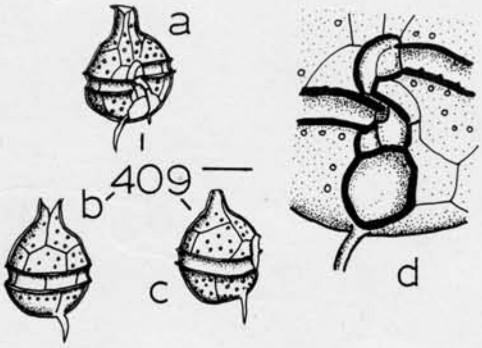

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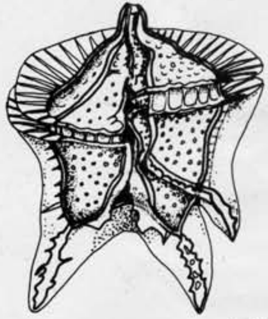

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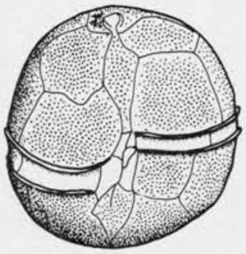

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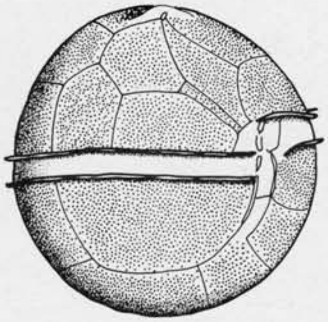

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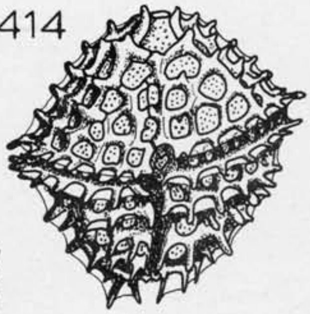

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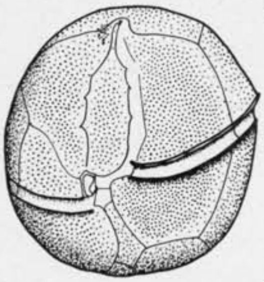

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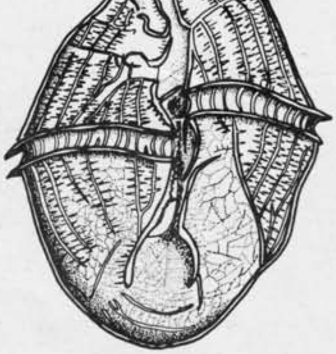

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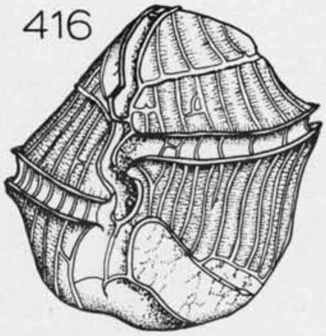

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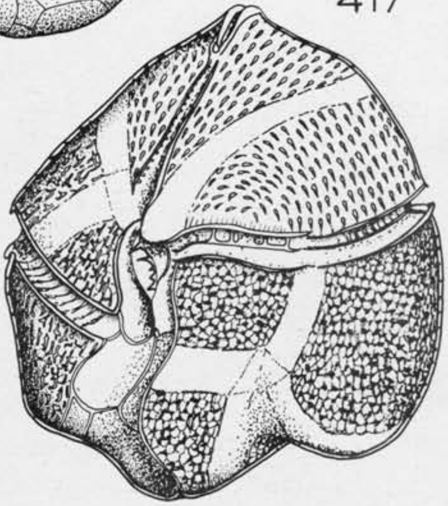

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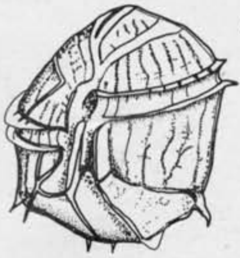

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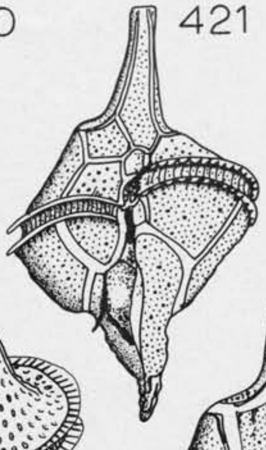

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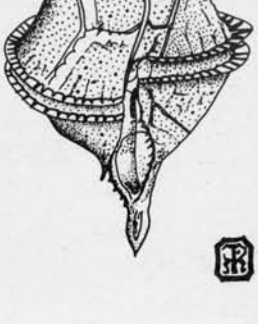

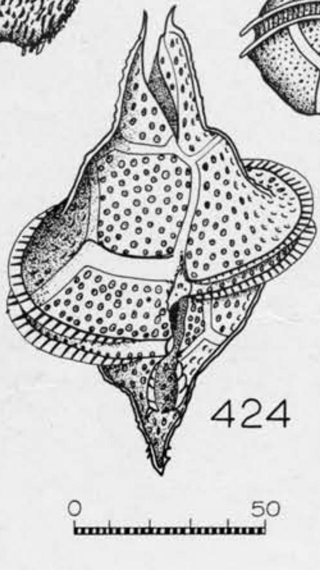

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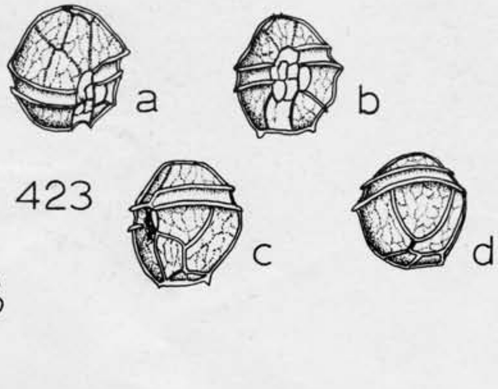

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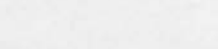

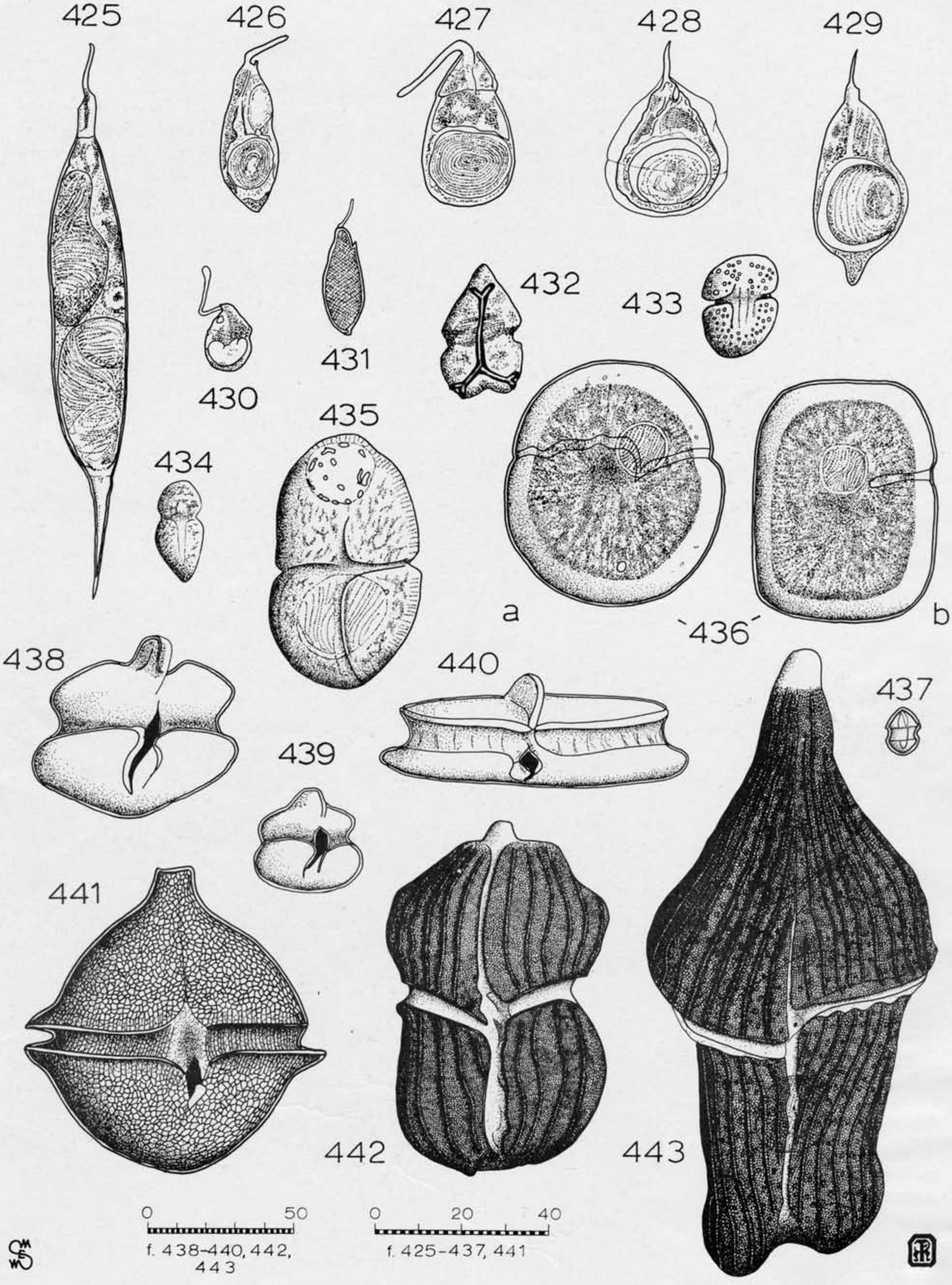
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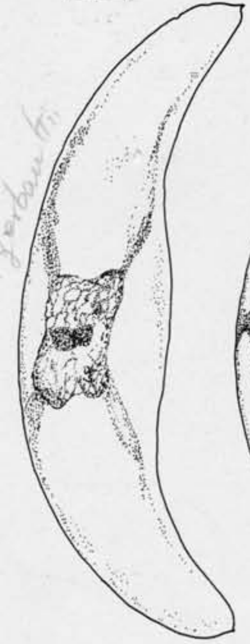
f. 438-440, 442, 443
0
20
40
f. 425-437, 441

D. gerbaultii

D. hamulus ✓

444



D. gerbaultii

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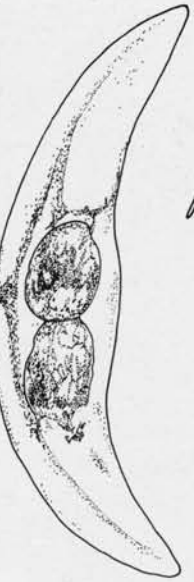

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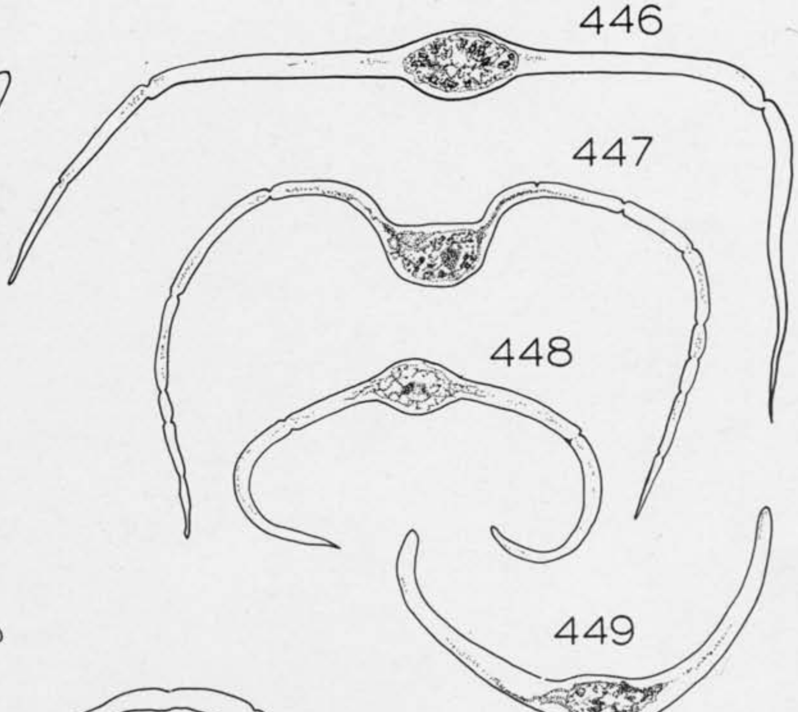

D. ham

450 D. hamulus

D. lunula

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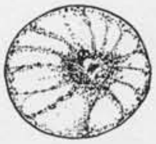
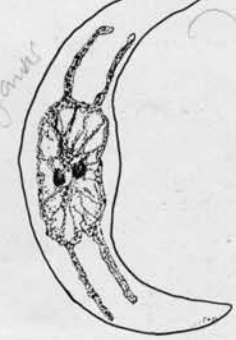
452 D. lunula



458 D. elegans



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P. robusta

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453

bicorne D.

D.

454

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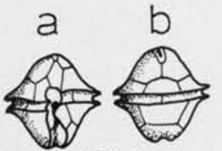
464



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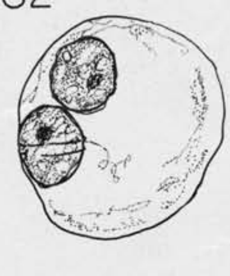

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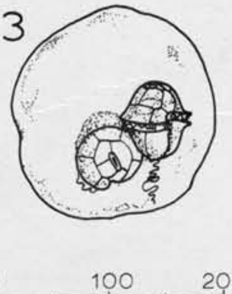

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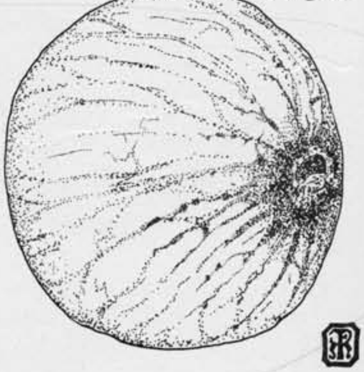


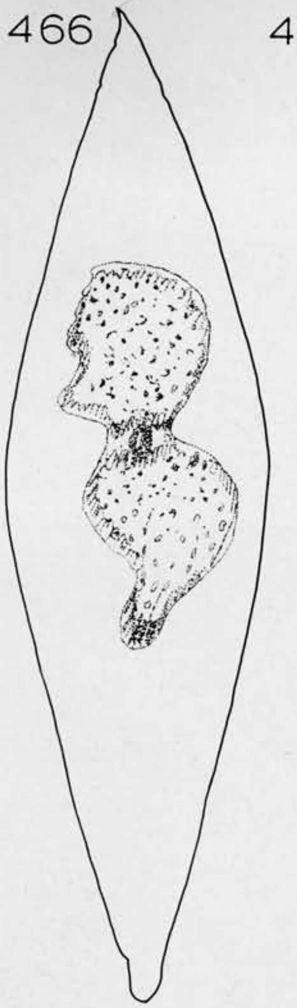
P. noctiluca

P. noctiluca

P. fusiformis

P. rhomboides

466



P

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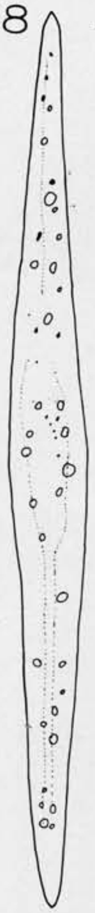

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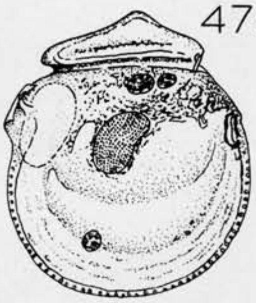

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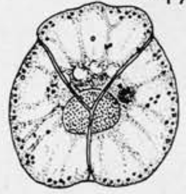
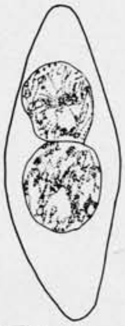


P. fusiformis



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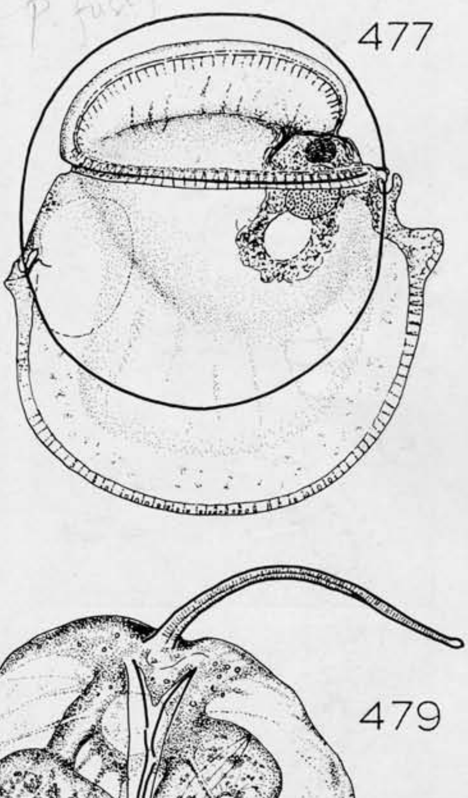

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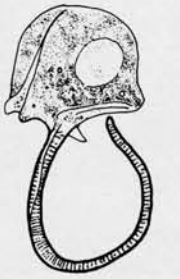

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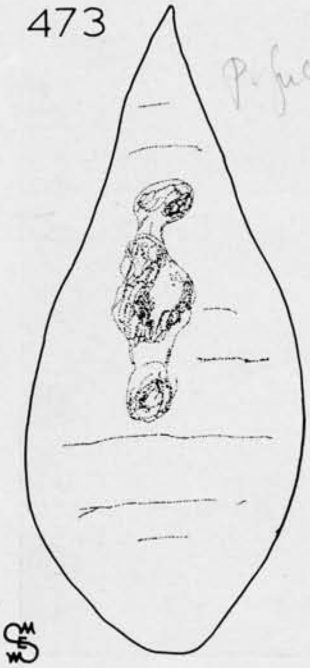

P. fusiformis

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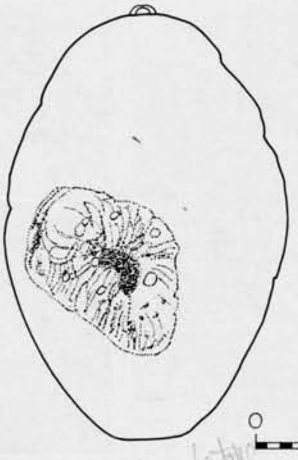

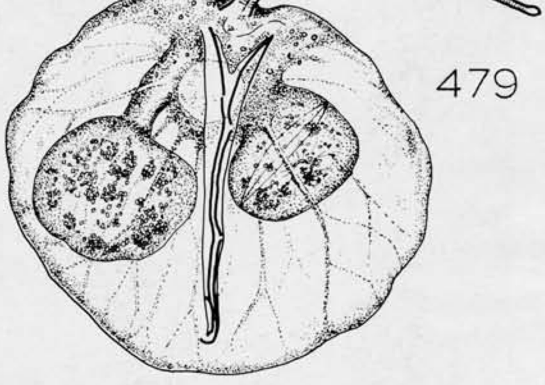

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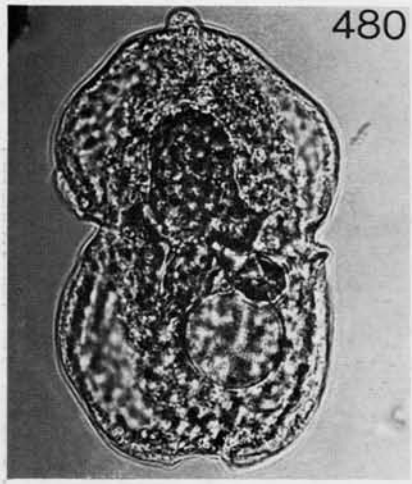
P. apiculatus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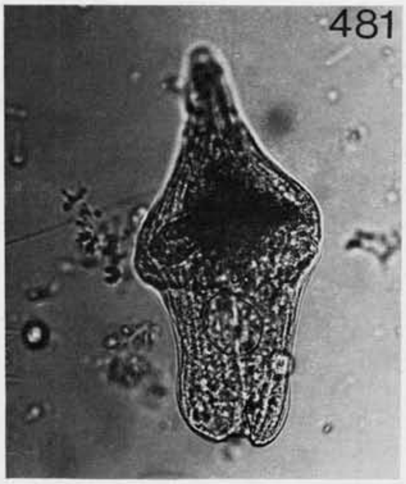
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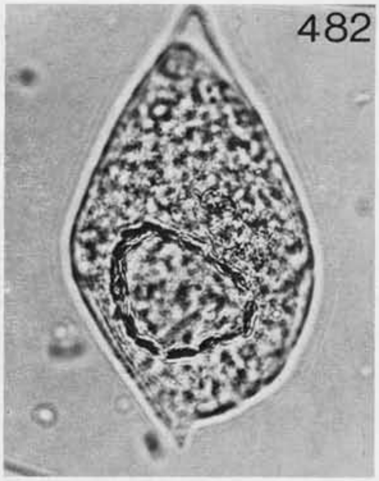
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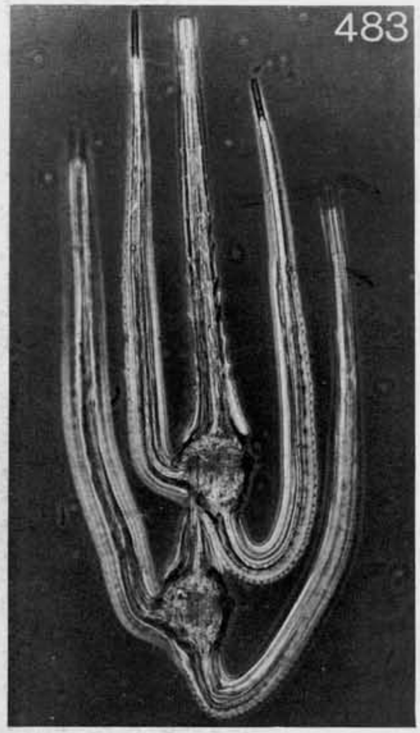
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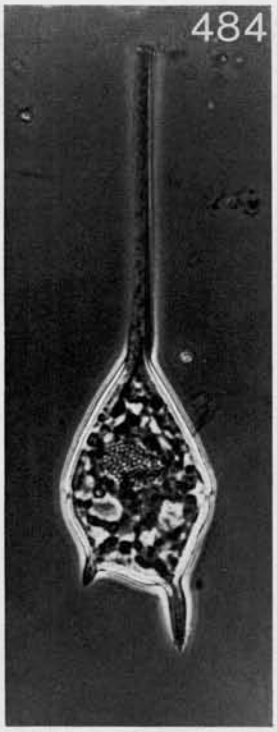
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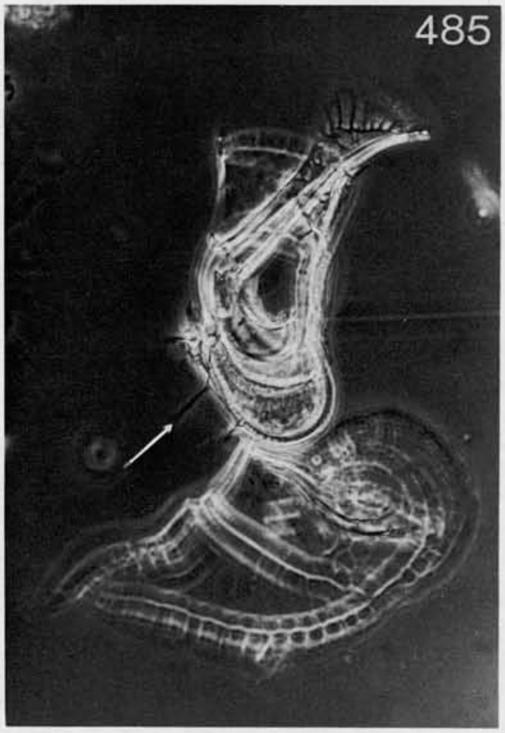
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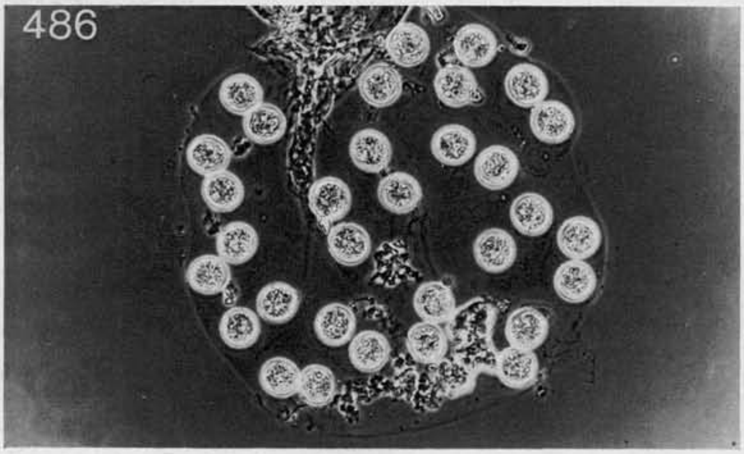
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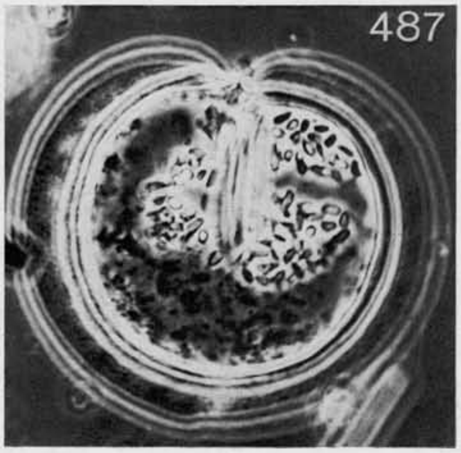
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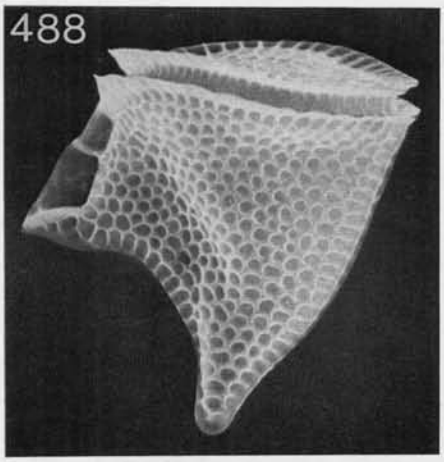

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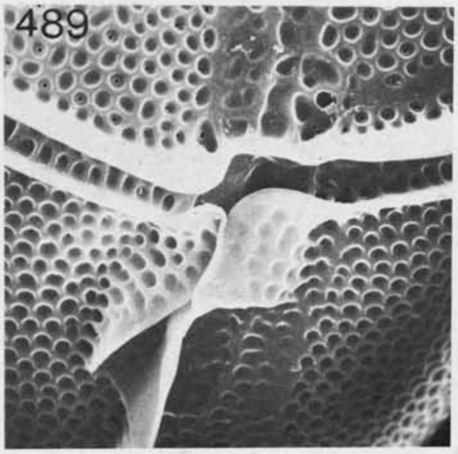

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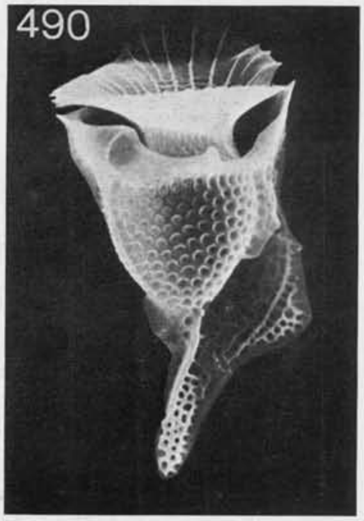

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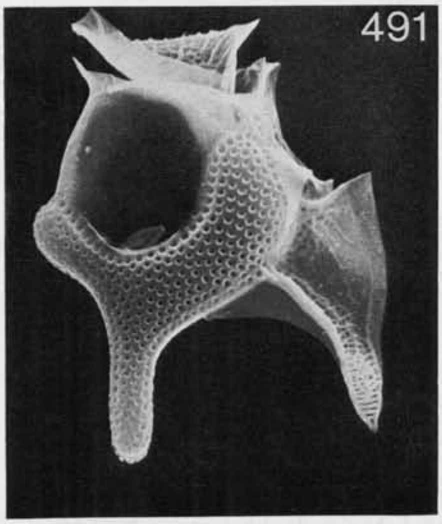

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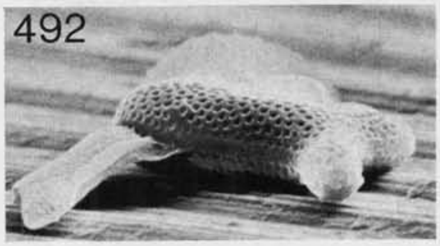

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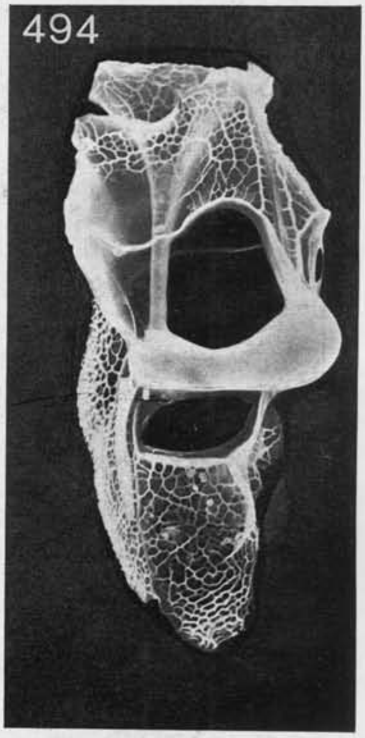

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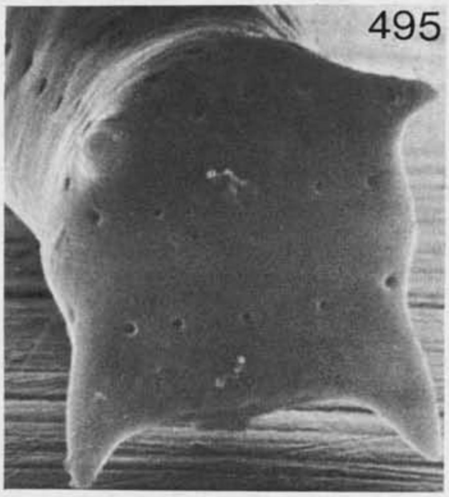

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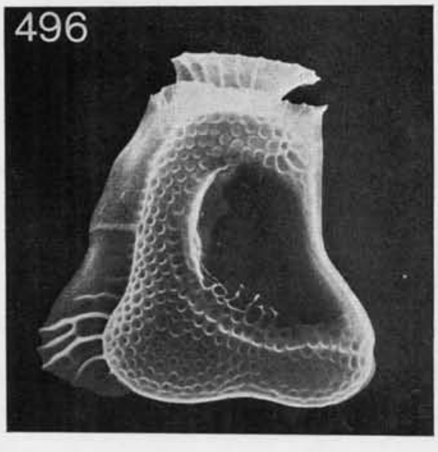

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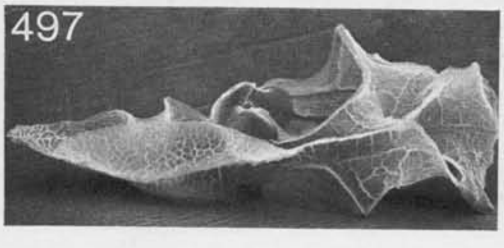

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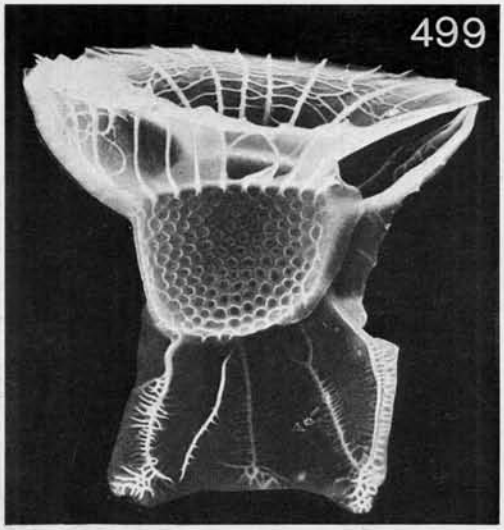
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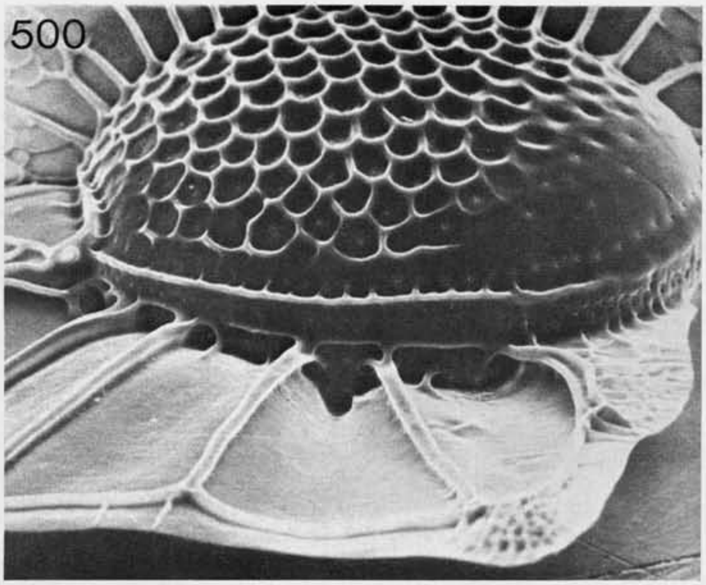
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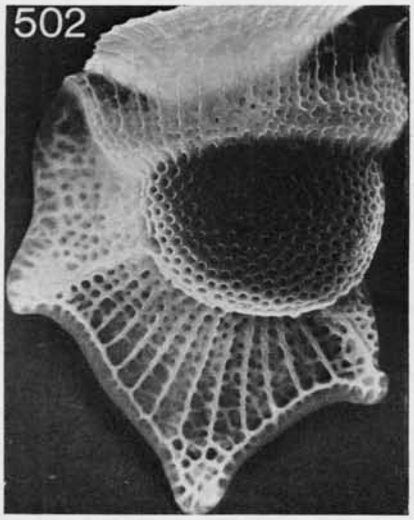
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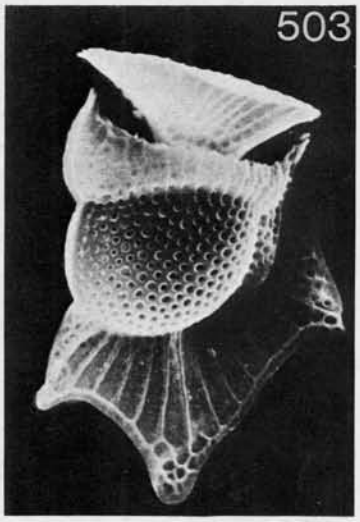
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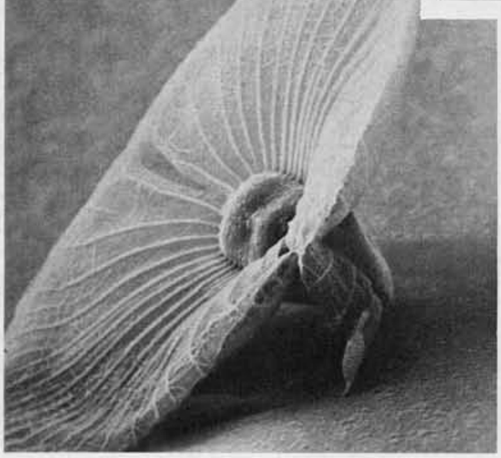
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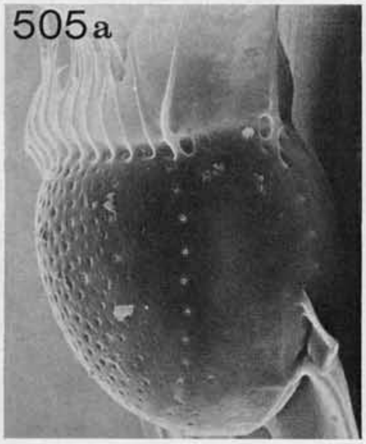
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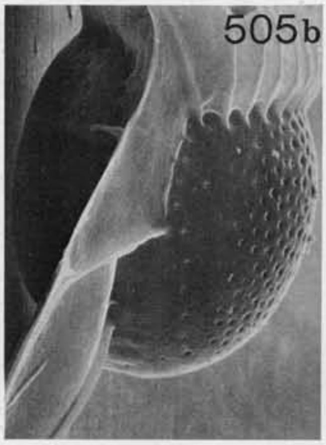
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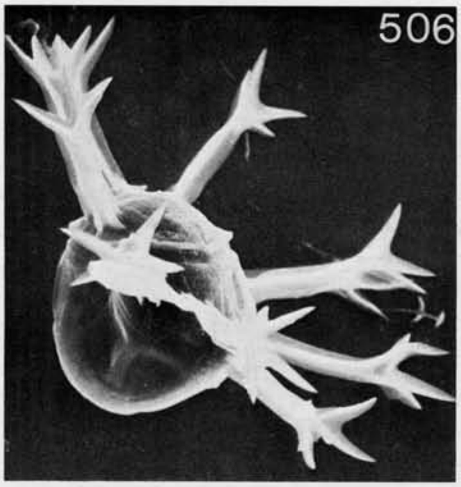
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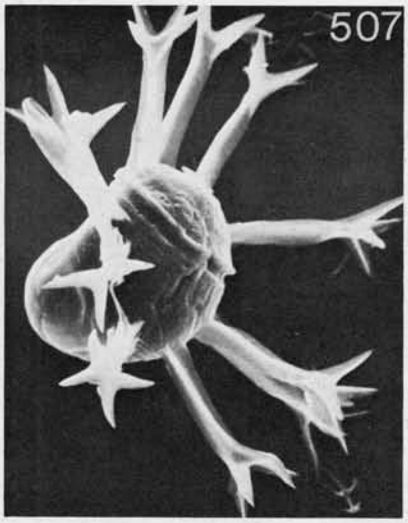
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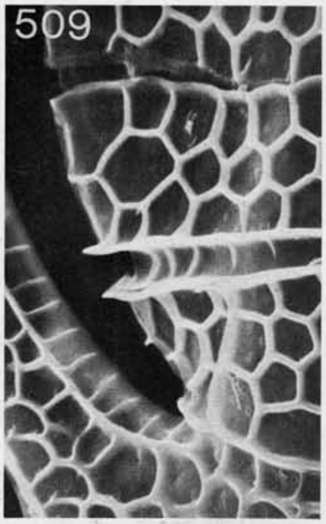
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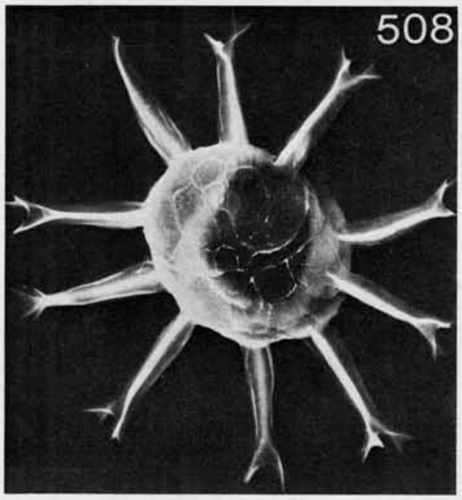
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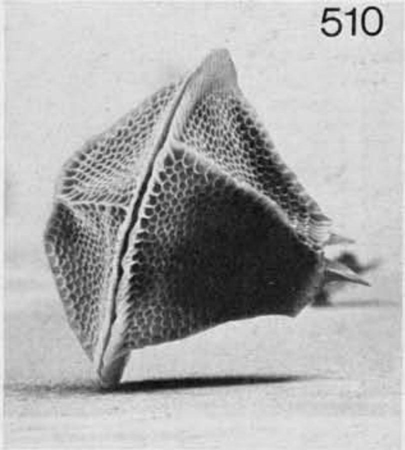
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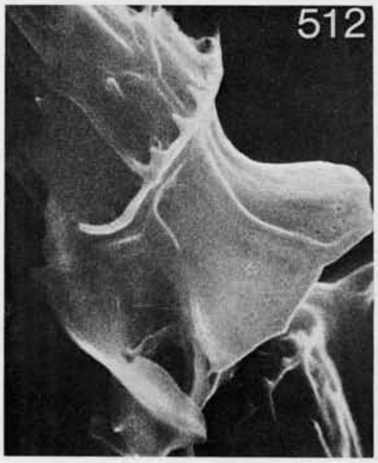
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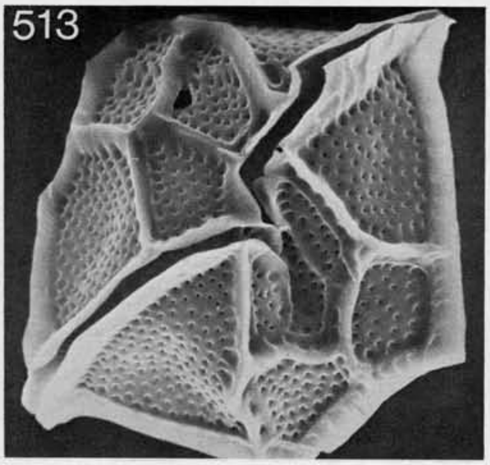
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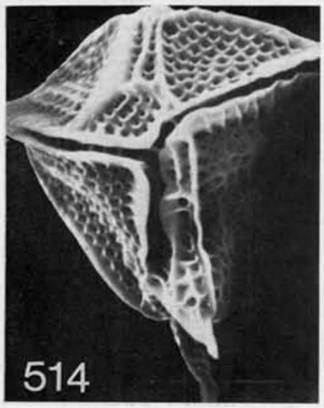
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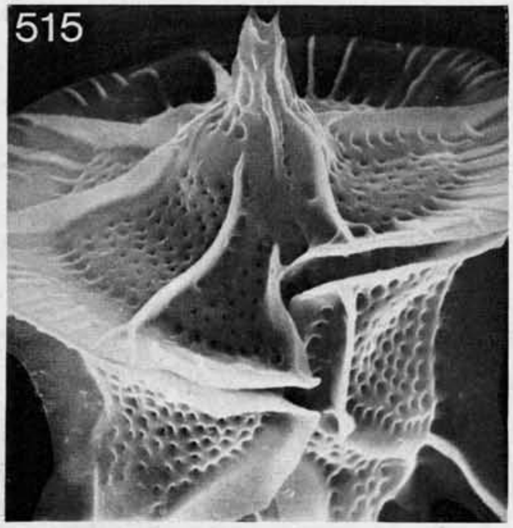
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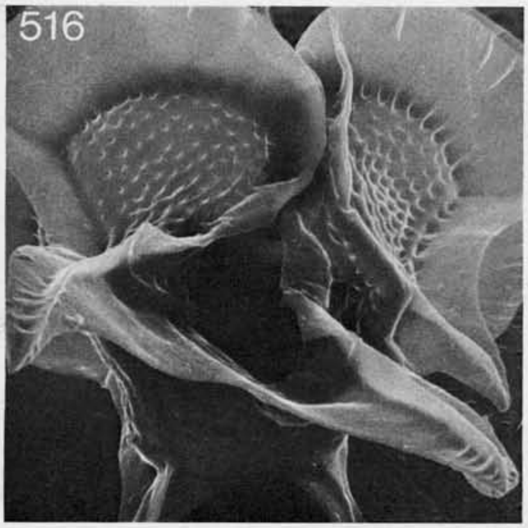
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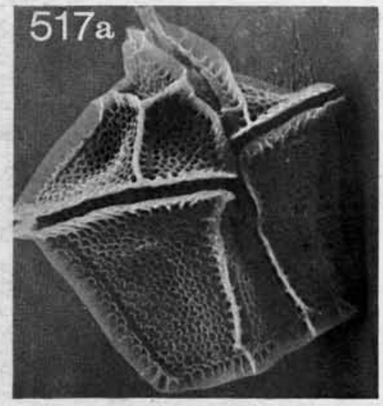
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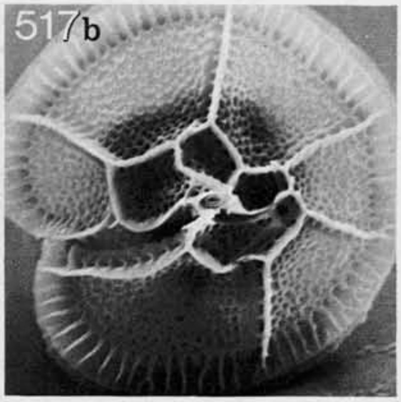
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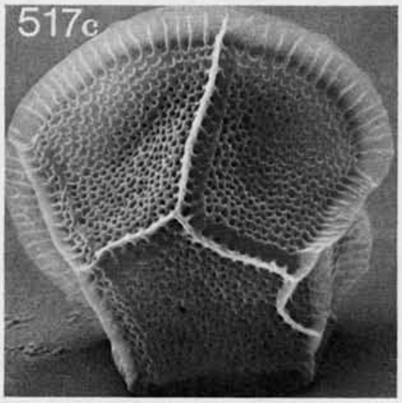
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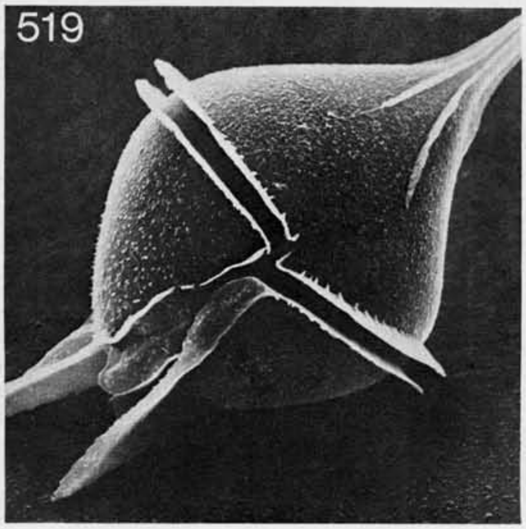
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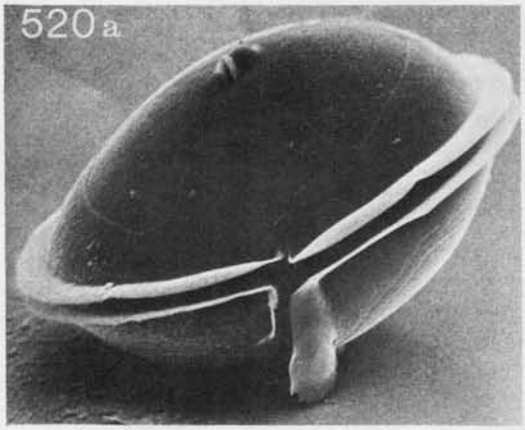
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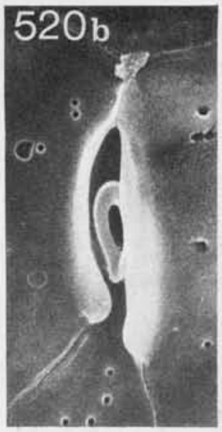
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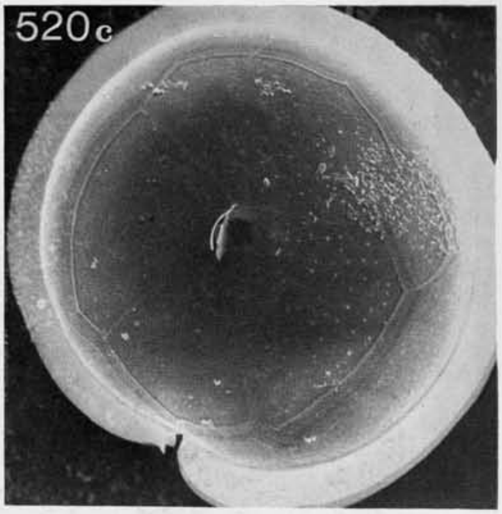
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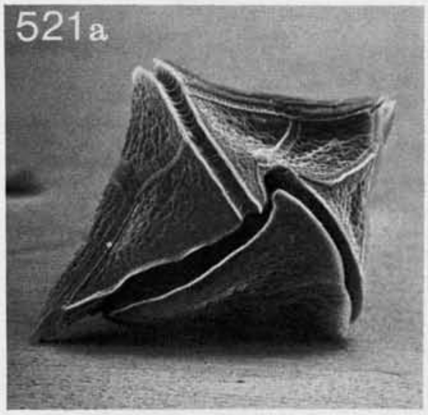
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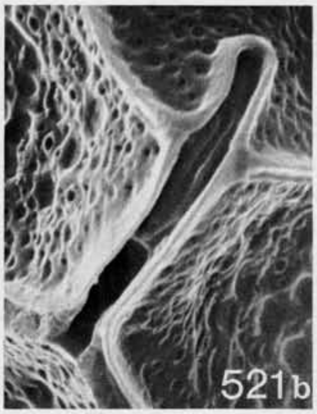
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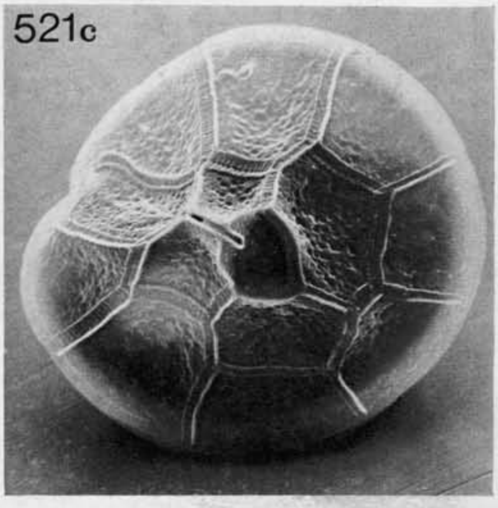
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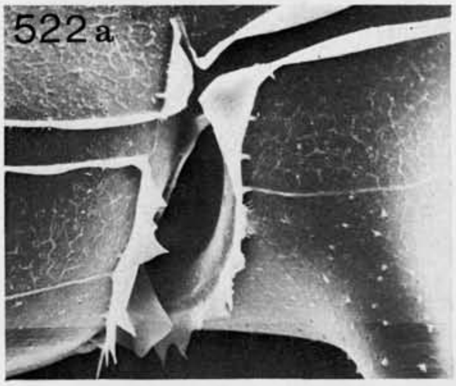
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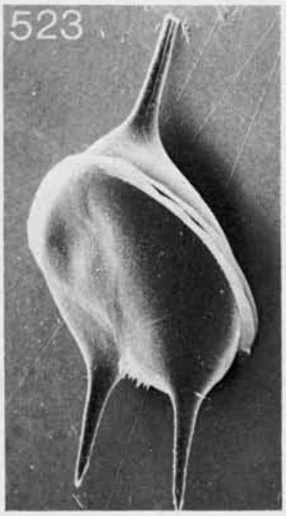
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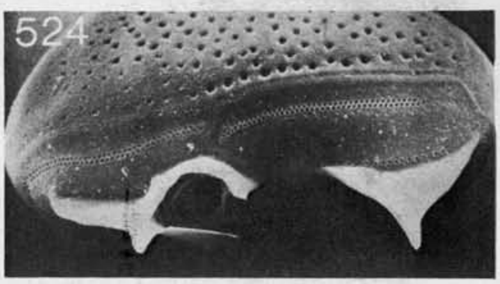
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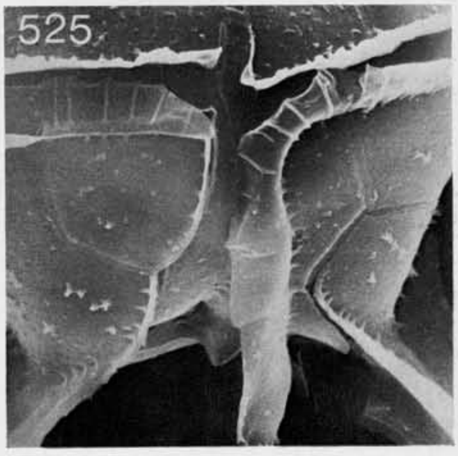
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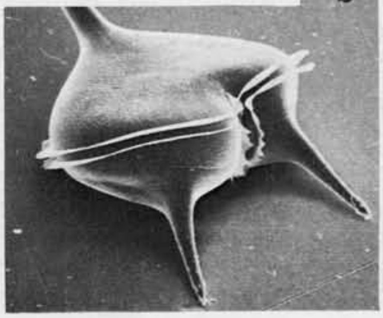
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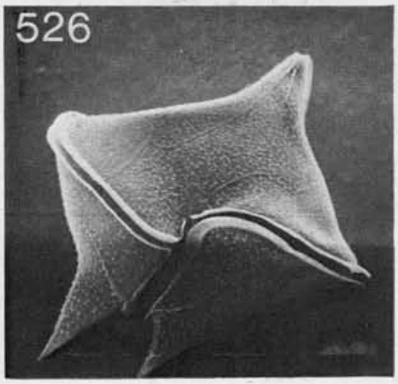
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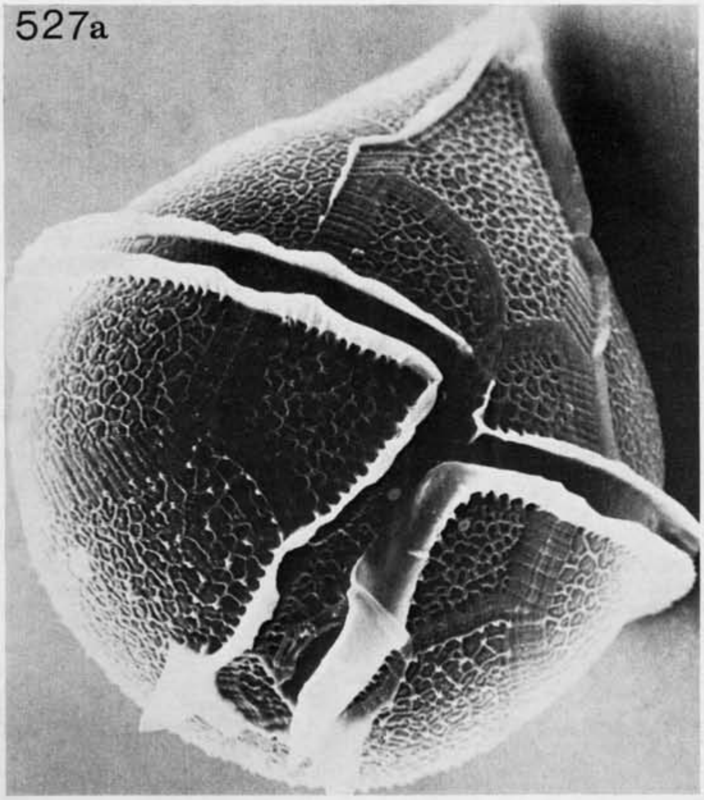

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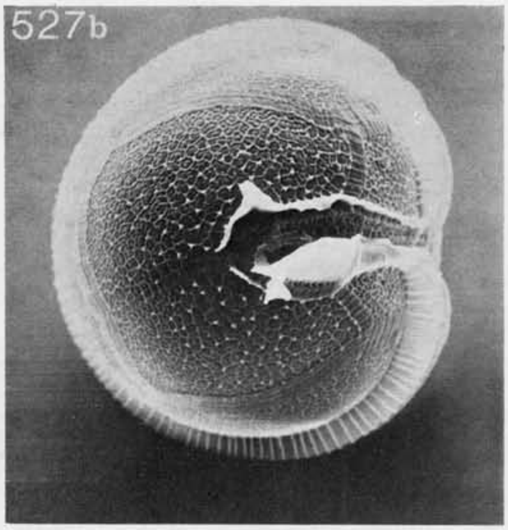

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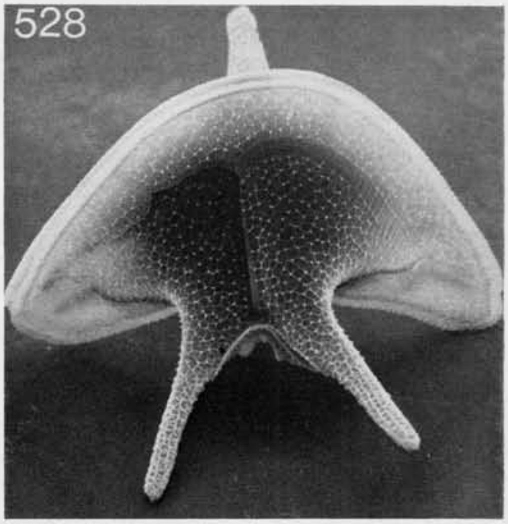

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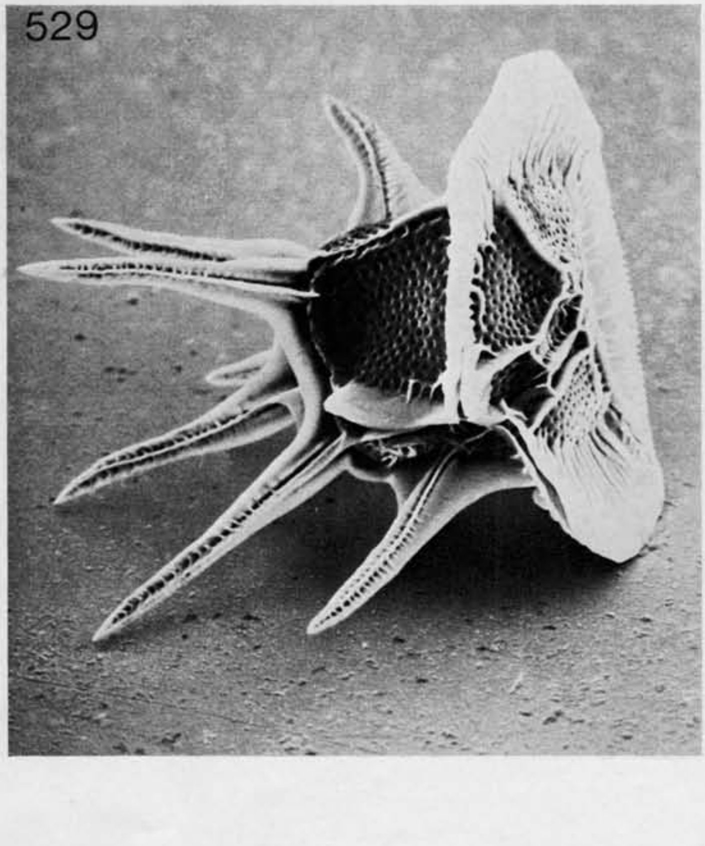

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