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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

F. J. R. Taylor

Institute of Oceanography and Department of Botany,
University of British Columbia, Vancouver, Canada

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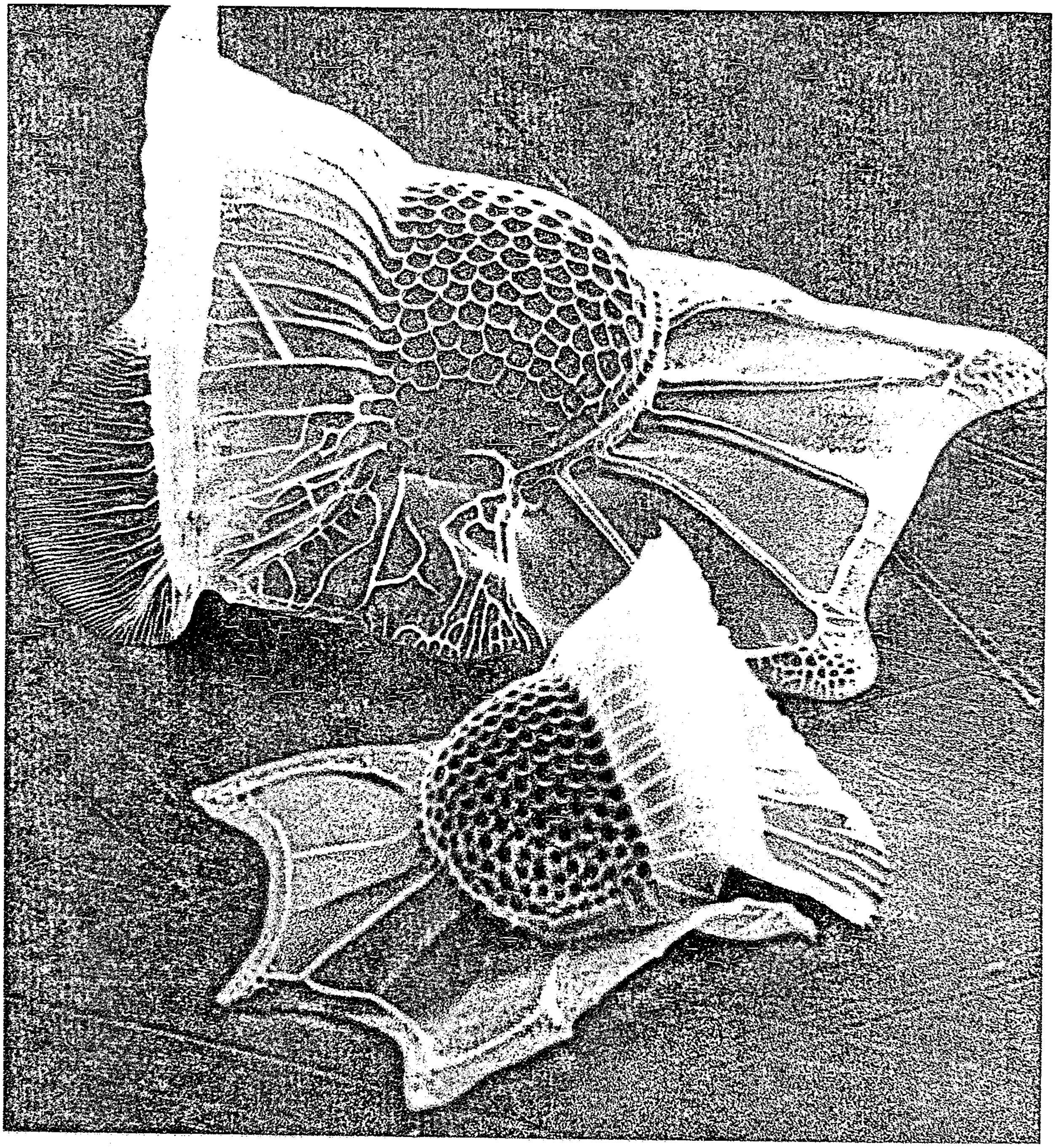
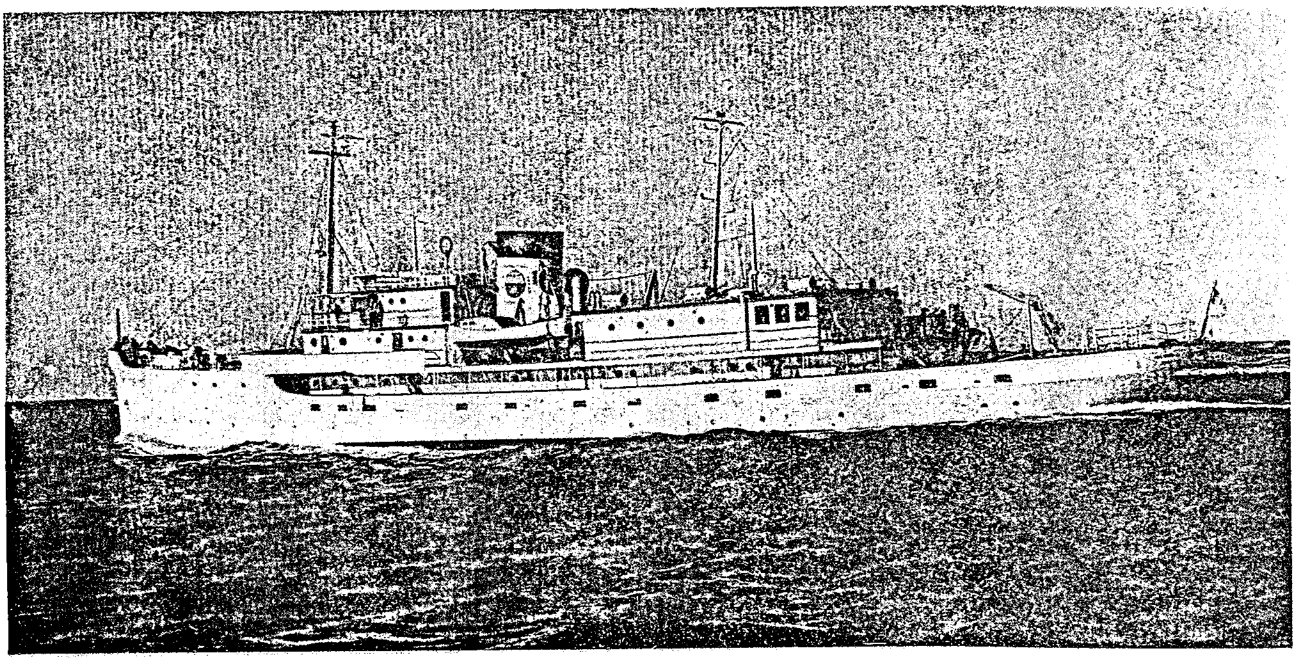


Scanning electron micrograph of two common members of the Indian Ocean dinoflagellate community; *Ornithocercus magnificus* STEIN (foreground) and *Ornithocercus quadratus* SCHÜTT. Magnification: 1035x.



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.

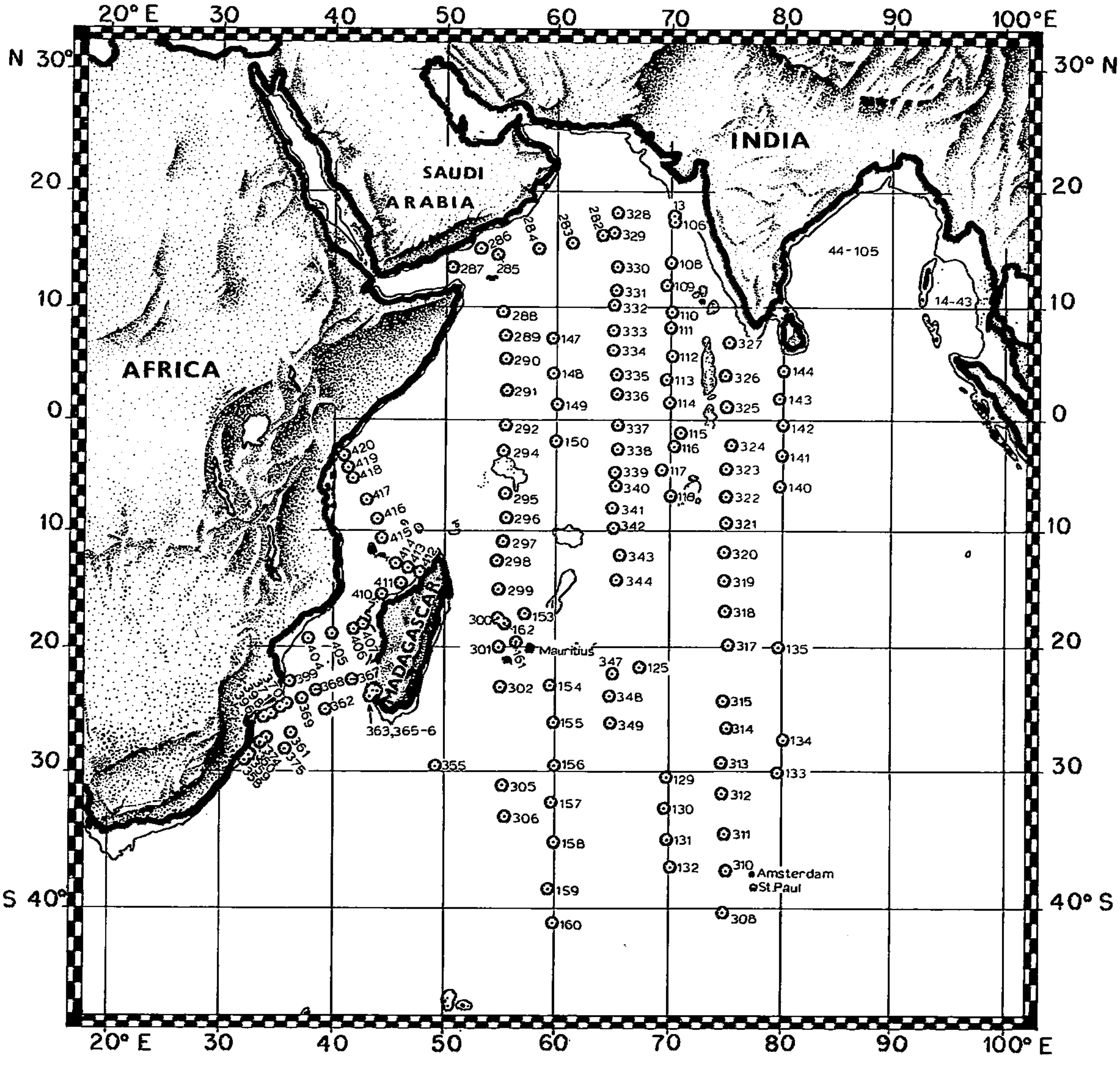

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Chart 1. Stations from which dinoflagellate material was collected by the R.V. "Anton Bruun" during the International Indian Ocean Expedition, 1963–1964. For details of the Bay of Bengal/Andaman Sea area please refer to Chart 2. The periods during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

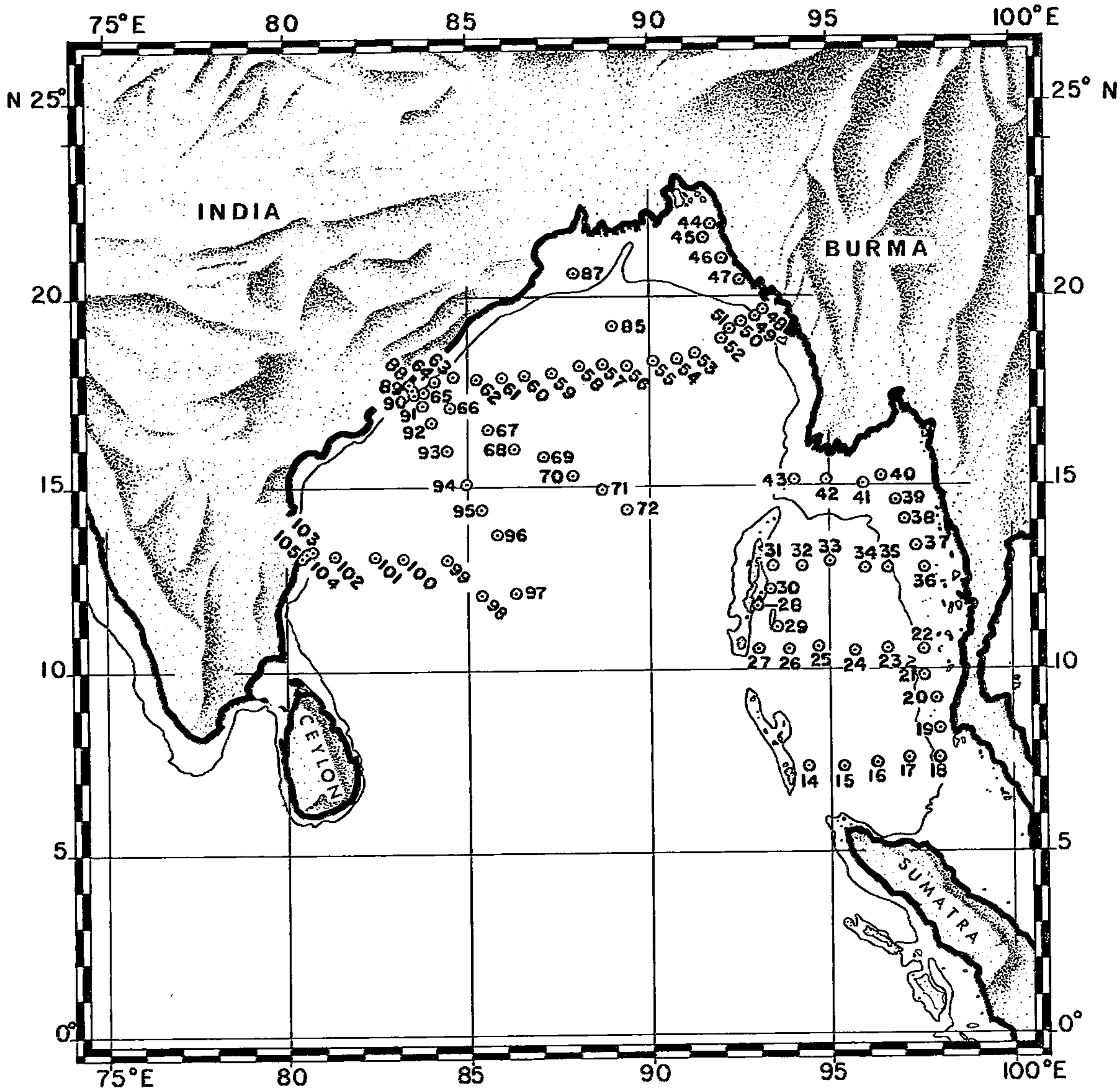
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Chart 2. The station positions within the Bay of Bengal and the Andaman Sea. All these stations were occupied during cruise I (March – May, 1963).

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 ° 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, 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.

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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, 1963) 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 bore 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. highleyi* 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.

ings 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.?)

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;