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Identifying Harmful Marine Dinoflagellates

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ABSTRACT

Faust, Maria A. and Rose A. Gulledge. Identifying Harmful Marine Dinoflagellates. *Smithsonian Contributions from the United States National Herbarium,* volume 42: 144 pages (including 48 plates, 1 figure and 1 table). – A taxonomic identification and reference guide of 48 harmful marine dinoflagellate species present in the world's oceans. This guidebook illustrates the morphology and taxonomy of harmful marine dinoflagellates of the following genera: *Alexandrium, Dinophysis, Gymnodinium, Ostreopsis, Prorocentrum, Coolia, Cochlodinium, Gambierdiscus, Gonyaulax, Gyrodinium, Lingulodinium,* and *Pfiesteria.* These organisms have been implicated in marine life mortality events and/or seafood-borne human diseases. Some species cause problems due to red tide conditions, others produce toxins; e.g. brevetoxins, ciguatoxins, dinophysistoxins, and ichthyotoxins. Detailed taxonomic descriptions of plate and thecal morphology, and cellular structure are presented. Taxonomic treatment of species includes nomenclatural types, type locality, synonyms, and etymology. Information is also available on species reproduction, ecology, biogeography, distribution, and habitat and locality. Species illustrations presented as scanning electron micrographs, differential interference contrast and epifluorescence light micrographs, as well as line drawings. A comprehensive glossary list and literature reference section is included. Kofoidian plate tabulation followed for armored species plate designation. The International Code of Botanical Nomenclature (ICBN) was followed for the taxonomical treatment of species. This fully illustrated laboratory guide is intended for the researcher, instructor, and the student; it is the most comprehensive reference manual for identifying harmful dinoflagellate taxa. It can also serve as a field guide for marine biologists and environmental researchers.

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Cover Design: Illustrations by Alice Tangerini; front *Prorocentrum hoffmannianum* Faust; back *Prorocentrum ruetzlerianum* Faust.

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Identifying Harmful Marine Dinoflagellates

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INTRODUCTION

Interest in identifying harmful dinoflagellate species has received worldwide recognition in recent years due to the increase in red tides, fish kills, and shellfish poisoning events reported from coastal marine ecosystems (Hallegraeff 1991). The publication, *Identifying Harmful Marine Dinoflagellates*, is an effort by the authors to present a fully illustrated identification guide for harmful dinoflagellate taxa. The user will recognize general information on dinoflagellate morphology and other criteria used in species identification. Each taxon is presented with a species overview, and a taxonomic description of cell and thecal plate morphology, reproduction, life cycle, ecology, toxicity, species comparison, habitat and locality, and etymology. This is supplemented with a number of high-resolution light and scanning electron photomicrographs and line drawings. Taxonomic treatment of harmful dinoflagellate taxa includes nomenclatural types, type locality, and synonyms. The nomenclatural name of a species is taken from the original publication of the taxa, with the exception of those where the type species is not known. Species names used in this publication are valid as of those published by 2000. An extensive glossary of terms and relevant literature citations are also provided. This guide will be useful to teachers, researchers and students, as well as professionals involved in environmental water quality assessment and management, fisheries and aquaculture, and public health.

DEDICATION

Dr. Maria Faust would like to dedicate this work to her mentor, Dr. Grethe Hasle, Professor of Marine Botany, University of Oslo, Norway. Dr. Hasle has devoted much of her life to teaching and sharing her understanding of the patterns and order in the diversity of marine phytoplankton species, their morphological relationships, and their global distribution. Nearly 19 years ago Dr. Faust was introduced to identifying marine plankton in a course taught by Dr. Hasle. To this day she is still fascinated by the beauty and diversity of dinoflagellate structures and morphological patterns which manage to restore one's perspective and faith in nature.

IDENTIFYING HARMFUL MARINE DINOFLAGELLATES

Dinoflagellates are unicellular eukaryotic microorganisms. They are free swimming protists with a forward spiraling motion propelled by two dimorphic flagella. They possess a large nucleus with condensed chromosomes, chloroplasts, mitochondria and golgi bodies. Biochemically, photosynthetic species have chlorophylls a and c, and light harvesting pigments peridinin, fucoxanthin and xanthophylls. Dinoflagellates mainly reproduce asexually via binary fission, but some species reproduce sexually and form resting cysts. Their nutrition varies from autotrophy (photosynthesis) to heterotrophy (absorption of organic matter) to mixotrophy (autotrophic cells engulf prey organisms). These features are species-specific (Spector 1984).

Dinoflagellate species are adapted to a variety of habitats: from pelagic to benthic, from temperate to tropical seas, and from estuaries to freshwater. Many species are cosmopolitan and can survive in variety of habitats: in the plankton, or attached to sediments, sand, corals, or macroalgal surfaces. Some species produce resting cysts that can survive in sediments for an extended period of time, and then germinate to initiate blooms (Spector 1984).

Dinoflagellate 'blooms' (cell population explosions) can cause discoloration of the water (known as red tides) which can have harmful effects on the surrounding sea life and their consumers: mass mortalities in fish, invertebrates, birds, and mammals. When toxic species are in bloom conditions the toxins can be quickly carried up the food chain and indirectly passed onto humans via fish and shellfish consumption, sometimes resulting in gastrointestinal disorders, permanent neurological damage, or even death. While harmful dinoflagellate blooms are at times a natural phenomenon and have been recorded throughout history, in the past two decades the public health and economic impacts of such events appear to have increased in frequency, intensity and geographic distribution (Taylor 1987). Toxin production and red tide events of harmful marine dinoflagellates are summarized in Table 1.

Table 1. Toxin production and red tide events of harmful marine dinoflagellates

Species	**Red Tide**	**Produced Toxin**	**Reference**
Alexandrium acatenella	YES	PSP toxins	Prakash & Taylor 1966
A. catenella	YES	Ichthyotoxins; PSP toxins: C1-4, GTX, SXT	Prakash et al. 1971, Fukuyo 1985, Fukuyo et al. 1985, Ogata & Kodama 1986
A. minutum	YES	PSP toxins: GTX1-4	Oshima et al. 1989
A. monilatum	YES	Ichthyotoxins PSP toxins: GTX1, SXT	Gates & Wilson 1960, Ray & Aldrich 1967, Schmidt & Loeblich 1979
A. ostenfeldii	NO	Mild PSP toxins; Spirilides	Cembella et al. 1987, 1988, 2000
A. pseudogonyaulax	NO	Goniodomin A	Murakami et al. 1988
A. tamarense	YES	Strong PSP toxins: GTX1-5, NSXT, SXT	Larsen & Moestrup 1989, Shimizu et al 1975, Oshima et al. 1977
A. tamiyavanichi	NO	Strong PSP toxins: GTX, SXT	Fukuyo et al. 1989, Kodama et al. 1988
Cochlodinium polykrikoides	YES	Ichthyotoxins	Yuki & Yoshimatsu 1989, Kim 1998, Ho & Zubkoff 1979
Coolia monotis	NO	Cooliatoxin	Nakajima et al. 1981, Holmes et al. 1995
Dinophysis acuminata	YES	DSP toxins: OA	Cembella 1989, Lee et al. 1989, Kat 1985
D. acuta	YES	DSP toxins: DTX1, OA	Lee et al. 1989, Yasumoto 1990
D. caudata	YES	Ichthyotoxins	Okaichi 1967
D. fortii	NO	DSP toxins: DTX1-2, OA	Lee et al. 1989, Yasumoto 1990

Species	Red Tide	Produced Toxin	Reference
D. mitra	NO	DSP toxins: DTX1, OA	Lee et al. 1989
D. norvegica	YES	DSP toxins: DTX1, OA	Cembella 1989, Lee et al. 1989, Yasumoto 1990
D. rotundata	NO	DSP toxins: DTX1	Lee et al. 1989
D. sacculus	YES	DSP toxins: OA	Masselin et al. 1992, Giacobbe et al. 1995, Delgado et al. 1996
D. tripos	NO	DSP toxins: DTX1	Lee et al. 1989
Gambierdiscus toxicus	NO	Ciguatoxin, Gambieric acid, Maitotoxin	Murata et al.1990, Yasumoto et al. 1977, 1987, 1993, Yokoyama et al. 1988
Gonyaulax polygramma	YES	Fish and shellfish kills due to anoxia after red tide	Hallegraeff 1991, Koizumi et al. 1996
Gymnodinium breve	YES	NSP toxins: Brevetoxins	Baden 1983, Baden et al. 1982, Hughes 1979
G. catenatum	YES	PSP toxins	Morey-Gaines 1982, Mee et al. 1986
G. mikimotoi	YES	NSP toxin: Gymnodimine; Ichthyotoxins	Hallegraeff 1991, Seki et al. 1996
G. pulchellum	YES	Ichthyotoxins	Onoue et al. 1985, Onoue & Nozawa 1989, Steidinger et al. 1998
G. sanguineum	YES	Ichthyotoxins	Cardwell et al. 1979, Tindall et al. 1984, Carlson & Tindall 1985
G. veneficum	NO	Ichthyotoxins	Ballantine 1956, Abbott & Ballantine 1957, Dodge 1982
Gyrodinium galatheanum	YES	Ichthyotoxins	Braarud 1957, Steemann Nielsen & Aabye Jensen 1957, Pieterse & Van Der Post 1967
Lingulodinium polyedra	YES	PSP toxins: SXT	Bruno et al. 1990
Noctiluca scintillans	YES	Fish and shellfish kills due to high levels of ammonia after red tide	Okaichi & Nishio 1976
Ostreopsis heptagona	NO	Unnamed toxin	J. Babinchak (according to Norris et al. 1985)
O. lenticularis	NO	OTX, Unnamed toxin	Tindall et al. 1990, Ballantine et al. 1988
O. mascarenensis	NO	Ciguatera toxin?	Quod 1994, Morton, S.L. (personal communication)
O. ovata	NO	Unnamed toxin	Nakajima et al. 1981

Species	Red Tide	Produced Toxin	Reference
O. siamensis	NO	Unnamed toxin	Nakajima et al. 1981, Usami et al. 1995
Pfiesteria piscicida	NO	Ichthyotoxins	Burkholder et al. 1995, Noga et al. 1996, Burkholder & Glasgow 1997
Prorocentrum arenarium	NO	DSP toxins: OA	Ten-Hage et al. 2000
P. balticum	YES	Unknown toxin	Silva 1956, 1963, Numann 1957
P. belizeanum	NO	DSP toxins: DTX1, OA	Morton et al. 1998
P. concavum	NO	DSP toxins: OA, FAT, Unnamed toxin	Tindall et al. 1984, Tindall et al. 1989, Dickey et al. 1990, Hu et al. 1993
P. faustiae	NO	DSP toxins: DTX1, OA	Morton 1998
P. hoffmannianum	NO	DSP toxins: OA, FAT	Aikman et al. 1993
P. lima	NO	DSP toxins: DTX1,2,4, OA, FAT, prorocentrolide	Murakami et al. 1982, Yasumoto et al. 1987, Torigoe et al. 1988, Tindall et al. 1989, Lee et al. 1989, Marr et al. 1992, Hu et al. 1993, 1995
P. maculosum	NO	DSP toxins: OA, Prorocentrolide B	Dickey et al. 1990, Hu et al. 1996
P. mexicanum	NO	FAT	Steidinger 1983, Carlson 1984, Tindall et al. 1984
P. micans	YES	Shellfish kills	Pinot & Silva 1956, Horstman 1981
P. minimum	NO	DSP toxin: Venerupin	Nakazima 1965, 1968, Smith 1975, Okaichi & Imatomi 1979, Tangen 1983, Shimizu 1987
P. ruetzlerianum	NO	Unnamed toxin	Quod (personal communication)

ABBREVIATIONS: DSP = diarrhetic shellfish poisoning; DTX1, DTX2, DTX3, DTX4 = dinophysistoxins; FAT = fast acting toxin; GTX1, GTX2, GTX3, GTX4, GTX5 = gonyautoxins; NSP = neurotoxic shellfish poisoning; NSXT = neosaxitoxin; OA = okadaic acid; OTX = ostreotoxin; PSP = paralytic shellfish poisoning; SXT = saxitoxin.

Dinoflagellates exhibit a wide divergence in morphology and size that are essential features used to identify species, as well as surface ornamentation (pores, areolae, spines, ridges, etc.). Armored or thecate species, those that possess a multi-layered cell wall, can be distinguished from unarmored or athecate species, those that lack a cell wall. Surface morphology of thecate cells, often critical to proper identification, can be discerned after cell fixation. However, identification of athecate species is mainly based on live cells since many morphological features may by destroyed by fixation (Steidinger & Tangen 1996).

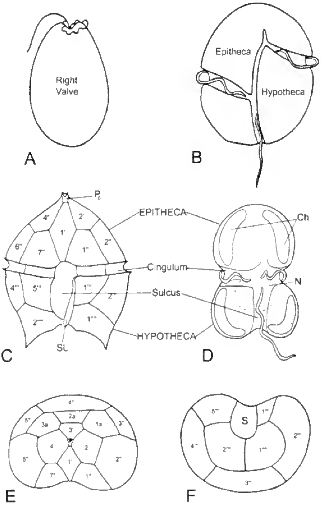

Fig. 1. Identifying dinoflagellates: A. lateral view of a desmokont cell type (two dissimilar flagella apically inserted); B. ventral view of a dinokont cell type (two dissimilar flagella ventrally inserted); C. ventral view of a thecate peridinioid cell; D. ventral view of an athecate gymnodinoid cell; E. apical view of epithecal plates; F. antapical view of hypothecal plates. Ch = chloroplasts; N = nucleus; Po = apical pore plate; SL = sulcal list (Figs. A-B redrawn from Steidinger & Tangen 1996; Figs. C-F redrawn from Taylor 1987)

Another distinction used in dinoflagellate identification is morphological cell type (Fig. 1 A, B): 1. desmokont type where two dissimilar flagella are inserted apically (e.g. *Prorocentrum*); and 2. dinokont type where two dissimilar flagella are inserted ventrally (e.g. *Alexandrium*). Terminology to describe orientation is also used: the forward end when the cell moves is called the apical pole; the opposite end is the antapical pole. Desmokonts are laterally flattened species with two large lateral plates: right valve and left valve. In lateral view the right valve reveals flagellar placement in the anterior V-shaped depression (Fig. 1 A). Dinokonts are, in general, divided into 2 main sections (epitheca and hypotheca) and divided by a girdle (cingulum) (Fig. 1 B-F). The side the flagella arise from is the ventral side, the opposite side is the dorsal. Ventral view (Fig. 1 B) reveals the position of the flagella in relation to the cingulum and sulcus (Taylor 1987).

Other important features include position of the cingulum and whether it is displaced or not (Fig. 1 B). If displaced and the left side is more anterior, the displacement is left-handed. If the opposite is true, it is right-handed. The former is much more common. The degree of displacement is given in cingulum widths (Taylor et al. 1995).

In thecated species the plate pattern, or tabulation, is crucial (see Balech & Tangen 1985) (Fig. 1 C, E, F). The description of new species or any critical taxonomy requires complete elucidation of the plate pattern, which can be difficult, requiring special techniques (see Steidinger et al. 1996).

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Dr. Maria Faust thanks Dr. Klaus Ruetzler, Curator of Sponges, National Museum of Natural History, Smithsonian Institution, for introducing her to the magnificent world of coral reef-mangrove ecosystems at Belize and encouraging her studies.

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Identifying Harmful Marine Dinoflagellate Species

Alexandrium acatenella
(Whedon et Kofoid) Balech, 1985
Plate 1, Figs. 1-4

Species Overview: *Alexandrium acatenella* is an armoured, marine, planktonic dinoflagellate. It is associated with toxic PSP blooms in Pacific coastal regions.

Taxonomical Description: A non-chain forming species, cells of *A. acatenella* are small to medium sized, longer than wide, and angular to round in ventral outline (Figs. 1,2). A characteristic ventral pore is present (Fig. 3). Two short antapical spines are present; no apical horn (Fig. 3). The thecal surface is sculptured with large and small pores. Cells range in size between 35-51 μm in length and 26-35 μm in transdiameter width (Whedon & Kofoid 1936; Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Gonyaulax acatenella* Whedon and Kofoid, 1936: 31, 33-34, figs. 8-13
Type Locality: NW Pacific Ocean: San Diego, California, USA
Synonyms:
Gonyaulax acatenella Whedon and Kofoid, 1936
Protogonyaulax acatenella (Whedon and Kofoid) Taylor, 1979

Thecal Plate Description: The plate formula for *A. acatenella* is: Po, 4', 6'', 6c, 9s, 5''', 2''''. The epitheca in this species is longer than the hypotheca: often it is equal to the length of the hypotheca plus the cingulum. The cone-shaped epitheca is low with convex sides (Figs. 1-3). The apical pore complex (APC) is roughly rectangular. The apical pore plate (Po) is broadly oval and narrows ventrally; it bears a relatively large and comma-shaped foramen (Fig. 4). The first apical plate (1') comes in direct contact with the Po, and also bears the characteristic ventral pore (vp) (Fig. 4)(Whedon & Kofoid 1936; Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

The post-median cingulum is deeply excavated, and displaced in a descending fashion about 1 time its width without overhanging. Narrow lists are present on the cingulum (Figs. 1-3). The deeply excavated sulcus widens posteriorly flaring to the right, slightly invading the hypotheca. The short hypotheca is broadly rounded with two posterior antapical spines (Figs. 1-3). The antapex region between the spines is slightly concave (Whedon & Kofoid 1936; Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

Morphology and Structure: *A. acatenella* is a photosynthetic species with elongated chloroplasts. Cells can be highly pigmented and reddish-brown in color. The elliptical nucleus is C-shaped and equatorial (Whedon & Kofoid 1936; Prakash & Taylor 1966; Balech 1995).

Reproduction: *A. acatenella* reproduces asexually by binary fission (Whedon & Kofoid 1936).

Ecology: *A. acatenella* is a planktonic species associated with paralytic shellfish poisoning (PSP) events and red tides. Populations are most abundant in neritic waters at 15°C. A bloom event in British Columbia caused four human illnesses and one death in 1965, the first reported PSP outbreak associated with *A. acatenella.* Cell densities during this red tide were as high as 13.5×10^6 cells/L (Whedon & Kofoid 1936; Prakash & Taylor 1966).

Toxicity: *Alexandrium acatenella* is a known PSP toxin-producing dinoflagellate species responsible for several illnesses and one death in British Columbia (Prakash & Taylor 1966).

Species Comparison: *A. acatenella* is very similar morphologically (size, shape and thecal plate formula) to the toxic Atlantic species, *A. tamarense*. Differences lie in the general shape of the cell, thecal sculpture, length of epitheca in relation to the hypotheca, and size and shape of the apical plates. The former species is roundish, while the latter is wider (shoulders) and roughly pentagonal. Thecal plates in *A. acatenella* are clearly porolated, while in *A. tamarense* they are relatively smooth. The epitheca in *A. acatenella* is distinctly longer than the hypotheca; they are nearly equal in *A. tamarense.* The size and shape of the apical plates differ in these two species (Balech 1995).

A. acatenella also shares some common characteristics of *A. catenella.* However, the former species is a non-chain former without a posterior attachment pore, bears a ventral pore on 1', and is usually found in warmer waters (Prakash & Taylor 1966; Balech 1995).

Habitat and Locality: *Alexandrium acatenella* is widely distributed in Pacific coastal waters. Populations have been recorded from the north Pacific coast of the United States and Canada, Japan, Argentina and northern Chile (Whedon & Kofoid 1936; Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

Alexandrium catenella
(Whedon et Kofoid) Balech, 1985
Plate 2, Figs. 1-6

Species Overview: *Alexandrium catenella* is an armoured, marine, planktonic dinoflagellate. It is associated with toxic PSP blooms in cold water coastal regions.

Taxonomical Description: A chain-forming species, *A. catenella* typically occurs in characteristic short chains of 2, 4 or 8 cells (Figs. 1,2). Single cells are round, slightly wider than long, and are anterio-posteriorly compressed. A small to medium sized species, it has a rounded apex and a slightly concave antapex (Fig. 1). The thecal plates are thin (Fig. 3) and sparsely porulated. Cells range in size between 20-48 µm in length and 18-32 µm in width (Fukuyo 1985; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Gonyaulax catenella* Whedon and Kofoid, 1936: 25-31, figs. 1-7, 14,15
Type Locality: NW Pacific Ocean: San Diego, California, USA
Synonyms:
Gonyaulax catenella Whedon and Kofoid, 1936
Protogonyaulax catenella (Whedon and Kofoid) Taylor, 1979

Thecal Plate Description: The plate formula for *A. catenella* is: Po, 4', 6'', 6c, 8s, 5''', 2''''. The epitheca and hypotheca are nearly equal in height. The hypotheca bears prominent sulcal lists that resemble spines (Fig. 1). In chain forms, anterior attachment pores (aap) and posterior attachment pores (pap) are present (Fig. 4)(Fukuyo 1985; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

The apical pore complex (APC) is broad, triangular and widens dorsally (Figs. 3,4). The apical pore plate (Po) houses the characteristic fishhook shaped foramen, and, if catenate, an ellipsoidal aap (Fig. 4). There are two diagnostic features of this species: a.) the first apical plate, 1', comes in contact with the Po (Fig. 3); and b.) a ventral pore (vp) is absent. The median cingulum is lipped, deeply concave, and is displaced in a descending fashion one time its width (Figs. 1,5). The sulcus, with prominent lists, is deeply impressed and widens posteriorly (Figs. 1,5). The wide posterior sulcal plate houses the pap near the right margin (Fukuyo 1985; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Morphology and Structure: *A. catenella* is a photosynthetic species with numerous yellow-green to orange-brown chloroplasts. The nucleus is large and U-shaped (Whedon & Kofoid 1936).

Reproduction: *A. catenella* reproduces asexually by binary fission. This species also has a sexual cycle with opposite mating types (heterothallism). After gamete fusion, a planozygote forms which then encysts into a characteristic resting cyst (Fig. 6)(Yoshimatsu 1981).

Ecology: *A. catenella* is a planktonic dinoflagellate species associated with deadly paralytic shellfish poisoning (PSP) events mostly in the Pacific Ocean. Red tides of this species have also been observed (Fukuyo 1985).

This species produces a colorless resting cyst as part of its life cycle which cannot be distinguished from the cyst produced by *A. tamarense* (Fig. 6). The cyst is roughly ellipsoidal with rounded ends; it is covered by a smooth wall and a mucilaginous substance. Cysts have a wide size range: 38-56 μm in length to 23-32 μm in width (Fukuyo 1985; Hallegraeff 1991; Meksumpun et al. 1994).

Toxicity: *Alexandrium catenella* is a known toxin-producing dinoflagellate species; it is the first species ever linked to PSP (Fukuyo 1985; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995). *A. catenella* produces strong PSP toxins which are transmitted via tainted shellfish. These toxins can affect humans, other mammals, fish and birds: c1-c4 toxins, saxitoxins (SXT) and gonyautoxins (GTX)(Schantz et al. 1966; Prakash et al. 1971). Moreover, Ogata and Kodama (1986) report production of ichthyotoxins in cultured media of *A. catenella.*

This species is responsible for numerous human illnesses and several deaths after consumption of infected shellfish. Toxic blooms and PSP in shellfish have been reported in Chile (Avaria 1979), Japan (Onoue et al. 1980; 1981a; 1981b), California (Sharpe 1981) and most of the Pacific coast of the U.S.A. (Nishitani & Chew 1988).

Species Comparison: *A. catenella* is very similar morphologically (size, shape and thecal plate formula) to *A. tamarense*. Differences lie in the shape of the Po, and presence or absence of a vp. The Po in the former species is slightly smaller, and the vp is absent (Fukuyo 1985). Molecular testing conducted on *A. catenella* from Japan and *A. tamarense* from Japan and the U.S.A. revealed a close genetic relationship between the two species, however they remain distinct (Adachi et al. 1995).

Chains of this species are quite distinctive, but can resemble *A. tamiyavanichi*; however, *A. tamiyavanichi* is a warm water species and can be distinguished from *A. catenella* by its conical shape (Taylor et al. 1995).

Habitat and Locality: *Alexandrium catenella* is widely distributed in cold temperate coastal waters. Populations have been recorded from the west coast of North America (from California to Alaska), Chile, Argentina, western South Africa, Japan, Australia and Tasmania (Fukuyo 1985; Fukuyo et al. 1990; Hallegraeff 1991; Hallegraeff et al. 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Alexandrium minutum

Halim, 1960

Plate 3, Figs. 1-6

Species Overview: *Alexandrium minutum* is an armoured, marine, planktonic dinoflagellate. It is a widely distributed species associated with toxic PSP blooms in coastal regions.

Taxonomical Description: Cells of *A. minutum* are small, nearly spherical to ellipsoidal, somewhat dorsoventrally flattened and occassionally longer than wide (Figs. 1,2). Cells are single with a characteristic ventral pore on the first apical plate, 1' (Figs. 1-4). Thecal plates thin. Thecal surface ornamenation can vary from light to heavy reticulation (mostly confined to the hypotheca) with small scattered pores. Intercalary bands are present (Figs. 1-3). Large range in size in this species: between 15-30 µm in length and 13-24 µm in transdiameter width (Balech 1989; 1995; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996; Hwang et al. 1999).

Nomenclatural Types:

Holotype: *Alexandrium minutum* Halim, 1960: 101, figs. Ia-g

Type Locality: Mediterranean Sea: Alexandria Harbor, Egypt

Synonyms:

Alexandrium ibericum Balech, 1985b

Alexandrium lusitanicum Balech, 1985b

Thecal Plate Description: The plate formula for *A. minutum* is: Po, 4', 6'', 6c, 10s, 5''', 2''''. The epitheca is larger than the hypotheca (Figs. 1,2). The apical pore complex (APC) is oval to broadly triangular and pointed posteriorly (Fig. 3). The apical pore plate (Po) is large, narrow and oval with a wide comma-shaped foramen (Figs. 3,5). The Po can be either in direct contact with the first apical plate (1') (Figs. 3,5a) or indirectly connected via a thin suture (thread-like process)(Fig. 5b). A characteristic ventral pore is located on the slender and rhomboidal 1' plate (Figs. 2-4). The distinctive sixth precingular plate (6'') is long and narrow (Fig. 1)(Balech 1989; 1995; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996; Hwang et al. 1999).

The epitheca is hemielliptical to conical with convex sides (Figs. 1,2). The apex is broadly rounded. The short hypotheca is hemielliptical with a convex to flat antapex (Figs. 1,2). The deeply excavated cingulum is displaced in a descending fashion one time its width with thickened margins (Figs. 1,2). The sulcus is shallow with narrow lists (Figs. 1,2)(Balech 1989; 1995; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996; Hwang et al. 1999).

Morphology and Structure: *A. minutum* is a photosynthetic species with an elliptical nucleus (Balech 1989; 1995).

Reproduction: *A. minutum* reproduces asexually by binary fission. This species also has a sexual cycle that produces a characteristic resting cyst (Fig. 6)(Bolch et al. 1991).

Ecology: *A. minutum* is a planktonic dinoflagellate species associated with toxic paralytic shellfish poisoning (PSP) events in coastal regions around the world. This species also produces dense (reddish-brown) red tides (Hallegraeff 1991). A red tide of this species reported from Taiwan had cell densities as high as 2.5 X 10^7 cells/L (Hwang et al. 1999). Another red tide of *A. minutum* reported from South Australia revealed cell levels of 4.8 X 10^8 cells/L (Cannon 1990).

This species produces a clear resting cyst as part of its life cycle. Cysts vary from hemispherical to circular in shape: cyst circular in apical view (24-29 µm in diameter) (Fig. 6); kidney-shaped in lateral view (15-19 µm long). The cyst wall is covered with mucilage (Bolch et al. 1991).

Toxicity: *Alexandrium minutum* is a strong producer of PSP gonyautoxins (GTX): GTX1, GTX2, GTX3 and GTX4 (Oshima et al. 1989). These toxins can affect humans, other mammals, birds and possibly fish (Hallegraeff et al. 1988; Hallegraeff 1991). This species is responsible for PSP events in Taiwan (Hwang et al. 1999), South Australia (Hallegraeff et al. 1988, Cannon 1990), France (Nezan et al. 1989) and New Zealand (Chang et al. 1995).

Habitat and Locality: *Alexandrium minutum* is widely distributed species found in many coastal areas of the world. Populations have been recorded from Alexandria Harbor, Egypt (Halim 1960), Italy (Montresor et al. 1990), northern Adriatic waters (Mediterranean Sea)(Honsell 1993), Turkey (Koray & Buyukisik 1988), Spain and Portugal (as *A. ibericum*)(Balech 1985b), France (Nezan et al. 1989), South Australia (Hallegraeff et al. 1988), and the east coast of the United States (Steidinger & Tangen 1996).

Alexandrium monilatum
(Howell) Balech, 1995
Plate 4, Figs. 1-6

Species Overview: *Alexandrium monilatum* is an armoured, marine, planktonic dinoflagellate. It is a coastal warm water species associated with toxic red tides and massive fish and shellfish kills.

Taxonomical Description: A very distinctive chain-forming species, *A. monilatum* typically occurs in long chains of 16 or more cells. Single cells are medium to large, wider than long, and flattened anterio-posteriorly (Figs. 1,2). Epithecal shoulders are occasionally observed. Thecal plates are thin with many delicate pores. Cells range in size between 28-52 µm in length and 33-60 µm in transdiameter width (Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Gonyaulax monilata* Howell, 1953: 153, figs. 1-5
Type Locality: North Atlantic Ocean: Indian River, Florida, USA
Synonyms:
Gonyaulax monilata Howell, 1953
Gessnerium mochimaensis Halim, 1967
G. monilata (Howell) Loeblich, 1970
Pyrodinium monilatum (Howell) Taylor, 1976

Thecal Plate Description: The plate formula for *A. monilatum* is: Po, 4', 6'', 6c, 10s, 5''', 2''''. The large apical pore complex (APC) is broadly triangular and slightly curving posteriorly. The large apical pore plate (Po) is ovate with a small comma-shaped foramen (Fig. 3). The anterior attachment pore (aap) is large and round (Fig. 3). Small pores are present along the margin of the Po. The characteristic first apical plate (1') is not connected to the Po; it is short and broadly pentagonal (Figs. 2,3). The 1' plate is typically without a ventral pore, however, specimens from Florida reveal a pore at the juncture where the 1', 2' and 4' plates meet (Fig. 2)(Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

The epitheca and hypotheca are nearly equal. The antapex is slightly concave. The median cingulum is deeply excavated, devoid of lists, and is displaced in a descending fashion one time its width (Fig. 2). The sulcus bears a diagnostic feature: a large and rhomboid-shaped posterior sulcal plate (s.p.)(Fig. 4). The s.p. is concave and recessed with radial markings, and contains a large central posterior attachment pore (pap)(Fig. 4)(Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

Morphology and Structure: *A. monilatum* is a photosynthetic species with central radiating brownish chloroplasts. The quarter-moon shaped nucleus is equatorial (Balech 1995).

Reproduction: *A. monilatum* reproduces asexually by binary fission; plane of fission is oblique. This species also has a sexual cycle with armoured isogamous gametes that fuse at oblique angles (Fig. 5). Gametes range in size from 36 X 36 µm to 47 X 56 µm. After fusion, a planozygote forms which then encysts into a characteristic resting cyst (Fig. 6) (Walker & Steidinger 1979).

Ecology: *A. monilatum* is a planktonic estuarine dinoflagellate species associated with toxic red tides and massive fish mortality events in warm coastal waters off Florida, Texas and Venezuela (Howell 1953; Ray & Aldrich 1967). Offshore coastal water blooms have also been reported in Florida and Texas (Williams & Ingle 1972; Wardle et al. 1975). One reported red tide from Texas had cell concentrations ranging from 5 X 10^5 cells/L to 10 X 10^5 cells/L (Gates & Wilson 1960).

This species produces a dark colored resting cyst as part of its life cycle. The cyst is smooth and round to ovoid. Cysts range in size from 60 to 87 µm in diameter (Fig. 6) (Walker & Steidinger 1979).

Toxicity: *Alexandrium monilatum* produces a strong ichthyotoxin resulting in a paralyzing effect (Gates & Wilson 1960, Ray & Aldrich 1967). From laboratory culture studies, Schmidt and Loeblich (1979) report production of paralytic shellfish poison (PSP) toxins: saxitoxin (STX) and gonyautoxins (GTX1); the toxins are hemolytic and neurotoxic (Bass & Kuvshinoff 1982; Clemons et al. 1980). The toxins produced from this species do not accumulate in shellfish (molluscs do not feed on this species) and it is not toxic to birds (Ray & Aldrich 1967). Massive fish kills have been reported from Texas bays in the Gulf of Mexico (Gunter 1942; Connell & Cross 1950; Ray & Aldrich 1967) and on the east coast of Florida in the Atlantic Ocean (Howell 1953).

Habitat and Locality: *Alexandrium monilatum* is a warm water species known from subtropical and tropical regions of the Atlantic Ocean: east coast of Florida (Howell 1953), Venezuela in the Caribbean Sea (Halim 1967), and Texas in the Gulf of Mexico (Gunter 1942; Connell & Cross 1950; Ray & Aldrich 1967). Populations have also been reported from the tropical Pacific Ocean off Ecuador (Balech 1995), and surprisingly in the Chesapeake Bay (Morse 1947).

Alexandrium ostenfeldii
(Paulsen) Balech et Tangen, 1985
Plate 5, Figs. 1-6

Species Overview: *Alexandrium ostenfeldii* is an armoured, marine, planktonic dinoflagellate. Generally, it is a cold-water coastal species found in low numbers mainly along the west coast of Europe.

Taxonomical Description: A distinctive species, cells of *A. ostenfeldii* are large and nearly spherical (Fig. 1). Cells are single, but are often found in two-celled colonies. Epitheca and hypotheca equal in height (Figs. 1). This species has thin thecal plates and a characteristic large ventral pore on the first apical plate (1')(Fig. 2). Faint surface pores are numerous and unevenly distributed. Cells range in size between 40-56 µm in length and 40-50 µm in transdiameter width (Balech 1995; Balech & Tangen 1985; Konovalova 1993; Larsen & Moestrup 1989; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Goniodoma ostenfeldii* Paulsen, 1904: 20, fig. 2
Type Locality: Iceland
Synonyms:
Goniodoma ostenfeldii Paulsen, 1904
Goniaulax tamarensis Lebour var. *globosa* Braarud, 1945
Goniaulax ostenfeldii (Paulsen) Paulsen, 1949
Heteraulacus ostenfeldii (Paulsen) Loeblich, 1970
Gonyaulax globosa (Braarud) Balech, 1971b
Gonyaulax trygvei Parke, 1976
Protogonyaulax globosa (Braarud) Taylor, 1979
Gessnerium ostenfeldii (Paulsen) Loeblich and Loeblich, 1979
Pyrodinium phoneus Woloszynska and Conrad, 1939
Triadinium ostenfeldii (Paulsen) Dodge, 1981

Thecal Plate Description: The plate formula for *A. ostenfeldii* is: Po, 4', 6", 6c, 10s, 5"', 2"". The apical pore complex (APC) is triangular or rectangular in shape. The apical pore plate (Po) is relatively large with a large comma-shaped foramen (Figs. 2,4). It can be either in direct contact with the first apical plate (1')(Fig. 4a) or indirectly connected via a thin suture (thread-like process)(Fig. 4b). The most distinctive plate of this species is the 1' plate: a) it bears a large characteristic ventral pore; and b) a 90 degree angle is formed at the point where the ventral pore and the 4' plate come in contact (Figs. 2,3). The distinctive sixth precingular plate (6") is wider than high (Figs. 2,3)(Balech 1995; Balech & Tangen 1985; Larsen & Moestrup 1989; Taylor et al. 1995).

The broad epitheca is convex-conical, while the hypotheca is hemispherical with an obliquely flattened antapex (Figs. 1,5). The slightly excavated cingulum is equatorial and displaced in a descending fashion less than one time its width; it has narrow lists (Figs. 1,3). The sulcus is slightly depressed and inconspicuous (Balech 1995; Balech & Tangen 1985; Konovalova 1993; Larsen & Moestrup 1989; Taylor et al. 1995).

Morphology and Structure: *A. ostenfeldii* is a photosynthetic species with radiating chloroplasts. The nucleus is U-shaped and equatorial (Fig. 5)(Balech & Tangen 1985).

Reproduction: *A. ostenfeldii* reproduces asexually by binary fission. This species also has a sexual cycle with isogamous mating types; a planozygote is formed (Jensen & Moestrup 1997).

Ecology: *A. ostenfeldii* is a planktonic estuarine dinoflagellate species found in low numbers, mainly along the west coast of Europe, and recently along the southeast coast of Nova Scotia, Canada (Cembella et al. 2000). To date, no blooms have been reported (except in Belgium as *Pyrodinium phoneus* (Woloszynska & Conrad 1939; Hansen et al. 1992).

This species produces temporary resting cysts (Fig. 6). Cysts are large and spherical, ranging in size from 35 to 40 µm in diameter. Cysts are pale in color with a reddish-brown granule, and a well-defined cingular groove. The smooth and clear cell wall is covered with mucilage (Mackenzie et al. 1996; Jensen & Moestrup 1997).

Toxicity: There has long been some doubt as to the toxic potential of this species (Balech 1995; Hansen et al. 1992). Because *A. ostenfeldii* does not form monospecific blooms, it has been difficult to determine this species' toxin producing potential. *A. ostenfeldii*, however, is capable of producing paralytic shellfish poison (PSP) toxins; albeit, it is the least toxic of all the *Alexandrium* species tested for PSP toxins (Cembella et al. 1987; 1988). This species has been associated with shellfish poisoning in Scandinavia (Jensen & Moestrup 1997), and one report of mussel toxicity (as *Pyrodinium phoneus*) has been reported from Belgium (Woloszynska & Conrad 1939).

Recently, a study of aquaculture shellfish from Nova Scotia, Canada, revealed the presence of spirilides, fast-acting neurotoxins, primarily produced by western Atlantic strains of *A. ostenfeldii* (Cembella et al. 2000).

Hansen et al. (1992) conducted studies with a tintinnid ciliate exposed to high concentrations of *A. ostenfeldii*: results were erratic swimming behavior (backwards) followed by swelling and lysis of the ciliates.

Species Comparison: *A. ostenfeldii* is easily misidentified as other *Alexandrium* species; detailed thecal plate observation is often necessary for proper identification (Balech 1995; Larsen & Moestrup 1989).

A. ostenfeldii and *A. tamarense* are often confused for each other since they overlap in size and often co-occur; however, *A. ostenfeldii* is slightly larger and is more widely distributed (has a wider salinity range) than the latter species (Moestrup & Hansen 1988). Other differences between these two species include: *A. ostenfeldii* has a much larger ventral pore on the first apical plate 1'; and the 6" plate is wider than high, whereas the width and height of the 6" plate in *A. tamarense* are equal (Balech 1995; Hansen et al. 1992).

This species also closely resembles another *Alexandrium* species, *A. peruvianum*. Both species are large cells with distinctive large ventral pores on the 1' plate; however, morphological differences are evident in the 1' plate and the APC. Moreover, *A. ostenfeldii* is a larger cell and produces PSP toxins (Balech 1995; Steidinger & Tangen 1996; Taylor et al. 1995).

Habitat and Locality: A cold-water estuarine species, *A. ostenfeldii* was, until recently, believed to be confined to the western european coast: Iceland and Norway (Paulsen 1904; Braarud 1945; Balech & Tangen 1985), Denmark (Moestrup & Hansen 1988), Belgium (as *Pyrodinium phoneus* (Woloszynska & Conrad 1939), and Spain (Fraga & Sanchez 1985). Recently, Balech (1995) collected cells of *A. ostenfeldii* from Alexandria Harbor, Egypt, and also from the NW Pacific Ocean, off of Washington State, U.S.A. Populations have also been observed from British Columbia and the Kamchatka Peninsula in the Pacific Ocean (Konovalova 1993; Steidinger & Tangen 1996; Taylor et al. 1995). In the northwest Atlantic Ocean, cells have been reported from Canada: in the Gulf of St. Lawrence (Levasseur et al. 1998), and southeastern Nova Scotia (Cembella et al. 2000).

Remarks: Belonging to the *Alexandrium* complex, *A. ostenfeldii* has a long and complex taxonomic history.

Alexandrium pseudogonyaulax
(Biecheler) Horiguchi ex Yuki et Fukuyo, 1992
Plate 6, Figs. 1-9

Species Overview: *Alexandrium pseudogonyaulax* is an armoured, marine, planktonic dinoflagellate. It is a toxic species found in coastal regions and brackish environments.

Taxonomical Description: Cells of *A. pseudogonyaulax* are medium to large, irregularly pentagonal-shaped with moderate dorso-ventral flattening. Cells are wider than long; the epitheca is slightly shorter than the hypotheca (Figs. 1,2). The first apical plate (1') is characteristically displaced with a large ventral pore on the anterior margin (Figs. 3-5). The thecal plates are smooth and thin with scattered minute pores. Cells range in size between 34-60 µm in length and 39-69 µm in width (Balech 1995; Montresor et al. 1993; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Goniodoma pseudogoniaulax* Biecheler, 1952: 55, figs. XXX-XXXII
Type Locality: Mediterranean Sea: Thau Lagoon, France
Synonyms:
Goniodoma pseudogoniaulax Biecheler, 1952
Alexandrium pseudogonyaulax (Biecheler) Horiguchi, 1983

Thecal Plate Description: The plate formula for *A. pseudogonyaulax* is: Po, 4', 6'', 6c, 10s, 5''', 2''''. The apical pore plate (Po) is oval shaped, contains a large comma-shaped foramen and a number of irregular pores, and is positioned longitudinally on the apex (Figs. 3,4,6). The distintive 1' plate does not come in contact with the Po (Figs. 3,4,6); it is roughly pentagonal and wider anteriorly (Figs. 3,6). The sloped anterior margin bears a large ventral pore that is wider than long (Figs. 3,4,6). The ventral pore does not penetrate the 4' plate (Balech 1995; Montresor et al. 1993; Yuki & Fukuyo 1992).

The short, convex epitheca is dome-shaped (Figs. 1,2). The hypotheca is slightly longer with an obliquely concave antapex (Figs. 1,2). The shallow cingulum is displaced in a descending fashion less than one time its width (Fig. 5). The sulcus lacks lateral lists. It slightly penetrates the epitheca obliquely on the right (Balech 1995).

Morphology and Structure: *A. pseudogonyaulax* is a photosynthetic species with central radiating yellow-brown chloroplasts. The transversely elongated nucleus is large and curved, and centrally located (Balech 1995; Montresor 1995).

Reproduction: *A. pseudogonyaulax* reproduces asexually by binary fission. This species also has a sexual cycle with isogamous mating types. The smaller rounder gametes (Fig. 7) fuse (one gamete engulfs the other), produce a planozygote which then encysts into a characteristic resting cyst (Fig. 8)(Montresor et al. 1993; Montresor 1995).

Ecology: *A. pseudogonyaulax* is a coastal and brackish water dinoflagellate species. Blooms of this species are commonly reported in the Strait of Georgia, British Columbia (North Pacific Ocean)(Taylor & Haigh 1993).

This species produces a characteristic and unusual resting cyst: a non-smooth cyst. The cysts are round and dark, and are often covered with a mucilaginous layer (Fig. 8). They contain a reddish-orange accumulation body. Size ranges from 40 to 55 µm in diameter. The cyst wall consists of two layers: a smooth inner layer and a paratabular outer layer (Fig. 9). The cyst paratabulation equals the tabulation of a vegetative cell. This is the only reported species in the genus *Alexandrium* to produce a non-smooth cyst (Montresor et al. 1993; Nichetto et al. 1995).

Toxicity: *A. pseudogonyaulax* produces a unique phycotoxin, goniodomin A (GA), that has an antifungal effect (Murakami et al. 1988). The toxin GA targets the liver and thymus (Terao et al. 1989; 1990).

Species Comparison: *A. pseudogonyaulax* closely resembles two other *Alexandrium* species: *A. hiranoi* and *A. satoanum*. Common features include general shape and size, and lack of contact of the first apical plate, 1', with the Po.

Distinguishing features lie in the cell outline, the ventral pore, the 1' plate, cyst morphology and habitat: a) *A. hiranoi* has a round shape, *A. pseudogonyaulax* is wider than long, *A. satoanum* is also wider than long with the general outline resembling a top: the epitheca and hypotheca have straighter sides; b) the ventral pore of *A. hiranoi* is circular and invades the 4' plate, in *A. pseudogonyaulax* the ventral pore is semi-circular and does not invade the 4', and in *A. satoanum*, no ventral pore is present (has a.a.p. and p.a.p); c) the 1' plate in *A. hiranoi* is slender and rectangular, whereas in *A. pseudogonyaulax* the 1' is almost pentagonal; d) the cyst of *A. hiranoi* is smooth, while the cyst of *A. pseudogonyaulax* is paratabulate with thick sutures; and e) *A. hiranoi* is found in rockpools, *A. pseudogonyaulax* is found in coastal brackish habitats (Kita & Fukuyo 1988; Montresor et al. 1993; Steidinger & Tangen 1996).

This species roughly resembles *A. tamarense*, however the latter species is not as round, and has a broader APC (Taylor et al. 1995).

Habitat and Locality: *A. pseudogonyaulax* is a coastal species which has been reported from several localities in Europe: France along the Mediterranean coast (Biecheler 1952), Italy in the Gulf of Trieste, North Adriatic Sea (Honsell et al. 1992; Montresor et al. 1993; Nichetto et al. 1995), Portugal and Norwegian fjords (Balech 1995). In the Pacific Ocean this species is a common bloom former in the Gulf of Georgia in British Columbia (Taylor & Haigh 1993), and populations have been observed in coastal waters of Japan (Inoue, in Kita & Fukuyo 1988).

Alexandrium tamarense
(Lebour) Balech, 1985
Plate 7, Figs. 1-6

Species Overview: *Alexandrium tamarense* is an armoured, marine, planktonic dinoflagellate. It is associated with toxic PSP blooms in cold water coastal regions.

Taxonomical Description: Cells of *A. tamarense* are small to medium in size, nearly spherical, and slightly longer than wide (Fig. 1). The first apical plate bears a ventral pore (Figs. 3,5). Cells are commonly found single or in pairs (Figs. 1-3), and less commonly in fours. Paired cells may contain an anterior attachment pore (aap) and a posterior attachment pore (pap)(Fig. 4). Thecal plates are smooth and thin (Fig. 3). The size and shape of this species is highly variable: cells range in size between 22-51 μm in length and 17-44 μm in transdiameter width (Lebour 1925; Fukuyo et al. 1990; Hallegraeff 1991; Hallegraeff et al. 1991; Larsen & Moestrup 1989; Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Gonyaulax tamarensis* Lebour, 1925: 92, plate XIV, figs. 1a-1d
Type Locality: English Channel: River Tamar Estuary, near Plymouth, United Kingdom
Synonyms:
Gonyaulax tamarensis Lebour, 1925
Gonyaulax tamarensis var. *excavata* Braarud, 1945
Gonyaulax excavata (Braarud) Balech, 1971
Gessnerium tamarensis (Lebour) Loeblich and Loeblich, 1979
Protogonyaulax tamarensis (Lebour) Taylor, 1979
Alexandrium excavatum (Braarud) Balech and Tangen, 1985

Thecal Plate Description: The plate formula for *A. tamarense* is: Po, 4', 6'', 6c, 8s, 5''', 2''''. The apical pore complex (APC) is rectangular and narrows ventrally (Fig. 3). The apical pore plate (Po) houses a large fishhook shaped foramen and a small round aap (Figs. 3,4). The first apical plate (1') is variable in shape: from a broad triangle to a narrow rectangle, and bears a small ventral pore (Figs. 3,5). The 1' plate comes in direct contact with the Po (Fig. 3)(Lebour 1925; Fukuyo et al. 1985; 1990; Larsen & Moestrup 1989; Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

The epitheca and hypotheca are nearly equal in height (Figs. 1,2,5). The epitheca is broadly conical, while the hypotheca is roughly trapezoidal (Figs. 1,2,5). The posterior end is slightly indented resulting in two hypothecal lobes; the left lobe is slightly larger than the right (Figs. 1,2). The deeply excavated cingulum is displaced in a descending fashion one time its width with narrow lists (Figs. 2,5). The deep sulcus, with lists, widens posteriorly (Figs. 2,5).

The posterior attachment pore (pap), if present, is small and located in the right half of the posterior sulcal plate (Lebour 1925; Fukuyo et al. 1985; 1990; Larsen & Moestrup 1989; Balech 1995; Taylor et al. 1995; Steidinger & Tangen 1996).

Morphology and Structure: *A. tamarense* is a photosynthetic species with a number of orange-brown chloroplasts. A lunar-shaped nucleus is situated ventrally just inside the cingulum (Fig. 1)(Fukuyo 1985; Larsen & Moestrup 1989).

Reproduction: *A. tamarense* reproduces asexually by binary fission; plane of fission is oblique. This species also has a sexual cycle with anisogamous mating types. The gametes join laterally for sexual fusion, produce a planozygote which then encysts into a characteristic resting cyst (Fig. 6)(Loeblich & Loeblich 1975; Turpin et al. 1978; Silva 1962).

Ecology: *A. tamarense* is a planktonic dinoflagellate species associated with toxic paralytic shellfish poisoning (PSP) events around the world. Toxic blooms are commonly reported in Japan (Fukuyo et al. 1985; Ogata et al. 1982; Oshima et al. 1982). Red tide blooms of *A. tamarense* have been reported in Europe (Mortensen 1985; Moestrup & Hansen 1988), and are common along the NE coast of North America (New England and Canada)(Bicknell & Walsh 1975; Hurst 1975; Loeblich & Loeblich 1975). During a red tide event reported in the Faroe Islands, Norway, in 1984, population levels of *A. tamarense* were estimated at 1 X 10^7 cells/L and completely dominated the plankton (Mortensen 1985; Moestrup & Hansen 1988).

This species produces a ellipsoidal resting cyst that cannot be distinguished from the cyst produced by *A. catenella.* This cyst has rounded ends with a thick cell wall, and is covered in mucilage (Fig. 6). Cysts often contain colorless granules and distinct reddish lipid bodies. Size ranges from 36-56 μm in length and 23-32 μm in width (Turpin et al. 1978; Fukuyo 1985; Bolch & Hallegraeff 1990; Hallegraeff 1991; Hallegraeff et al. 1991).

Toxicity: *Alexandrium tamarense* is a known toxin-producing dinoflagellate species. This species produces very potent paralytic shellfish poison (PSP) neurotoxins which can affect humans, other mammals, fish and birds (Larsen & Moestrup 1989): gonyautoxins (GTX1, GTX2, GTX3, GTX4 and GTX5), neosaxitoxin (NSTX) and saxitoxin (SXT)(Shimizu et al. 1975; Oshima et al. 1977). This species is responsible for numerous human illnesses and several deaths after consumption of infected shellfish: ten deaths in Venezuela in 1977 (Reyes-Vasquez et al. 1979), and one death in Thailand in 1984 (Tamiyavanich et al. 1985). Resting cysts of *A. tamarense* can also harbor PSP toxins. Dale et al. (1978) demonstrated that cysts were more than ten times as toxic as their motile stage counterparts.

Not all strains of *A. tamarense* are toxic: both toxic and nontoxic strains have been reported in New England within the same red tide event (Yentsch et al. 1978). Strains in Australia (Hallegraeff 1991), River Tamar estuary, Britain (type locality)(Moestrup & Hansen 1988) and the Gulf of Thailand (Fukuyo et al. 1988) are all non-toxic.

The usual route of PSP toxin transmission is via contaminated shellfish; however, bloom events of *A. tamarense* have been linked to several massive fish kills: Atlantic herring in the Bay of Fundy, Canada (White 1980); and rainbow trout and salmon in the Faroe Islands, Norway (Mortensen 1985). Hayashi et al. (1982) attribute the fish kills to dinoflagellate toxins accumulated in the food chain; i.e. fish feed on zooplankton infected with PSP poisons and die. However, Ogata and Kodama (1986) report production of ichthyotoxins in cultured media of this species.

Species Comparison: *A. tamarense* can resemble a number of other species within the genus, but it can be distinguished by its cell shape and size, presence of a ventral pore (vp) on the 1' plate, and shape of the thecal plates (Balech 1995; Hallegraeff 1991; Larsen & Moestrup 1989; Steidinger & Tangen 1996).

A. tamarense is very similar morphologically (size, shape and thecal plate formula) to *A. catenella*; both also produce deadly PSP toxins. Morphological differences lie in the shape of the Po, and presence or absence of a vp: the Po in *A. catenella* is slightly smaller than that in *A. tamarense*, and the vp is absent (Fukuyo 1985). Molecular testing conducted on *A. catenella* from Japan and *A. tamarense* from Japan and the

U.S.A. revealed a close genetic relationship between the two species, however they remain distinct (Adachi et al. 1995).

Morphologically, *A. fundyense* is nearly identical to *A. tamarense* except for the missing ventral pore on the 1' plate. *A. minutum* can also be misidentified as *A. tamarense*; however, *A. tamarense* is a smaller species, is always longer than wide, and is found in colder waters than *A. minutum* (Balech 1995; Hallegraeff 1991; Larsen & Moestrup 1989; Steidinger & Tangen 1996).

Habitat and Locality: *A. tamarense* is a widely distributed coastal and estuarine dinoflagellate species (Lebour 1925; Steidinger & Tangen 1996) mainly found in cold to cold-temperate waters in North America, Europe and Japan. However, this species has been reported from warmer waters around the world: Australia, Venezuela and the Gulf of Thailand (Balech 1995; Fukuyo et al. 1990; Hallegraeff 1991; Steidinger & Tangen 1996; Taylor et al. 1995).

Alexandrium tamiyavanichi

Balech, 1994

Plate 8, Figs. 1-6

Species Overview: *Alexandrium tamiyavanichi* is an armoured, marine, planktonic dinoflagellate. It is a producer of strong PSP toxins in the Gulf of Thailand.

Taxonomical Description: A chain-forming species, *A. tamiyavanichi* typically occurs in chains of 8 cells or more. Single cells are small and round to slightly wider than long (Figs. 1,2). A small ventral pore (vp) is present on the first apical plate (1')(Figs. 3-5). The thecal plates are thin and strongly porulated. Cells range in size between 31-41 µm in length and 26-35 µm in transdiameter width (Balech 1995; Fukuyo et al. 1989; Taylor et al. 1995).

Nomenclatural Types:

Holotype: *Alexandrium tamiyavanichi* Balech, 1994: 217-219, figs. 1-6

Type Locality: Gulf of Thailand: Ang Sila, Thailand

Synonyms:

Protogonyaulax cohorticula (Balech) Taylor, sec Kodama et al., (1988); non *Gonyaulax cohorticula* Balech, 1967

Thecal Plate Description: The plate formula for *A. tamiyavanichi* is: Po, 4', 6'', 6c, 10s, 5''', 2''''. The broad apical pore complex (APC) is triangular and narrows ventrally (Figs. 3,4). The apical pore plate (Po) is wide and oval with a large comma-shaped foramen (Figs. 3,4). Several small pores are present along the margin of the Po (Fig. 4). The anterior attachment pore (aap) is large, round and adjacent to the Po (Fig. 4). The 1' plate is large and wide with straight sides, and is in direct contact with the Po (Figs. 3-5). A small ventral pore is present on the anterior right margin of this plate (Figs. 3-5)(Balech 1967; 1995; Fukuyo et al. 1989; Taylor et al. 1995).

The conical epitheca is wider than long with shoulders (Figs. 1,2). The hypotheca is slightly longer than the epitheca (Figs. 1,2). The deeply excavated cingulum is displaced in a descending fashion one time its width (Figs. 2,5). The sulcus is deep and widens posteriorly (Figs. 2,4,5). Two wing-like sulcal lists project anteriorly toward the antapex yielding two antapical spines (Figs. 1,5). The sulcus invades the epitheca via the distinctive anterior sulcal plate (s.a.); this plate is divided into two parts by a transverse rib (Fig. 4). It is the anterior extension of the s.a. plate which projects into a notch in the epitheca (Figs. 2,4,5). The round posterior attachment pore, pap, is present in the center of the posterior sulcal plate (Fig. 6)(Balech 1967; 1995, Fukuyo et al. 1989; Taylor et al. 1995).

Morphology and Structure: *A. tamiyavanichi* is a photosynthetic species. The transversely elongated nucleus is lunate shaped (Balech 1995).

Reproduction: *A. tamiyavanichi* reproduces asexually by binary fission.

Ecology: *A. tamiyavanichi* is a coastal planktonic species (Balech 1994).

Toxicity: *A. tamiyavanichi* produces potent paralytic shellfish poison (PSP) toxins similar to those produced by *A. tamarense*: gonyautoxins

(GTX), and saxitoxin (SXT)(Fukuyo et al. 1989; Kodama et al. 1988). This species has been the main causative organism of PSP in Thailand waters (Kodama et al. 1988).

Etymology: This species, '*tamiyavanichi*', was named in honor of Prof. Suthichai Tamiyavanich, researcher in red tides and toxic dinoflagellates in Thailand (Balech 1994; 1995).

Species Comparison: *A. tamiyavanichi* is often and easily misidentified as *A. cohorticula*: cell size and outline is similar, both with an anterior extention of the s.a. plate, and both species are chain formers. However, there are number of substantial morphological differences between these two species: In *A. cohorticula*, the epitheca is longer than wide; the Po is longer; the first apical plate, 1', is thinner; the pap is larger and oval shaped; and the sulcal lists are larger and projected behind the hypotheca (Balech 1995).

Chains of *A. tamiyavanichi* can resemble *A. catenella*. The epitheca in *A. tamiyavanichi*, however, is conical in comparison to the rounded epitheca of *A. catenella* (Taylor et al. 1995).

Habitat and Locality: *A. tamiyavanichi* is a coastal species that has only been reported from three warm-water localities: Gulf of Thailand (type locality), Manila Bay in the Philippines, and from the Andaman Sea, southwest of Thailand (Balech 1995).

Cochlodinium polykrikoides

Margelef, 1961

Plate 9, Figs. 1-7

Species Overview: *Cochlodinium polykrikoides* is an unarmoured, marine, planktonic dinoflagellate species with a distinctive spiral-shaped cingulum. It is a common red tide former associated with fish kills in Japan and Korea.

Taxonomic Description: *Cochlodinium polykrikoides* is an athecate species; i.e. without thecal plates. Cells are small, oval and slightly flattened dorso-ventrally (Figs. 1,2). Chains, rarely more than eight cells, are common (Figs. 1-4). An apical groove is present on the apex originating from the anterior end of the cingular and sulcal juncture and extending to the dorsal side of the epitheca. Cells range in size from 30-40 um in length to 20-30 um in width (Silva 1967; Yuki & Yoshimatsu 1989; Fukuyo et al. 1990; Taylor et al. 1995; Steidinger & Tangen 1996).

The epitheca is conical and rounded at the apex (Figs. 1,2,4). The hypotheca is bilobed (Fig. 1). The cingulum is deep and excavated (Figs. 1,2,4). It is displaced about 0.6 times the cell length, and descends in a distinct left-handed spiral of 1.8-1.9 turns around the cell. The narrow and shallow sulcus nearly runs parallel to the cingulum making 0.8-0.9 turns around the cell between the proximal and distal ends of the cingulum. The sulcus deepens and widens towards the antapex and divides the hypotheca into two asymmetrical lobes (Fig. 1). The right lobe is narrower and slightly longer than the left lobe (Silva 1967; Yuki & Yoshimatsu 1989; Fukuyo et al. 1990; Taylor et al. 1995; Steidinger & Tangen 1996). Trichocysts have been observed in this species, but the number per cell varies, and not all cells bear them. The presence and number of trichocysts increases with cell and culture age (Silva 1967).

Nomenclatural Types:
Holotype: *Cochlodinium polykrikoides* Margelef, 1961: 76, fig. 27
Type Locality: Caribbean Sea: Puerto Rico
Synonyms:
Cochlodinium heterolobatum Silva, 1967

Morphology and Structure: *C. polykrikoides* is a photosynthetic species with numerous yellowish-green to brown chloroplasts, rod-shaped or ellipsoid in shape (Fig. 1). The nucleus is situated anteriorly in the epitheca (Figs. 2,4). A red stigma is present dorsally in the epitheca (Silva 1967; Yuki & Yoshimatsu 1989; Fukuyo et al. 1990; Taylor et al. 1995).

Reproduction: *C. polykrikoides* reproduces asexually by binary fission; plane of fission is oblique (Silva 1967).

Ecology: *C. polykrikoides* is a planktonic species. It is a common ichthyotoxic 'red water' bloom species in the northwestern Pacific. This species commonly forms cysts (Figs. 5-7) (Fukuyo et al. 1990; Taylor et al. 1995; Steidinger & Tangen 1996).

Toxicity: *Cochlodinium polykrikoides* is a known red tide species associated with extensive fish kills and great economic loss in Japanese and Korean waters (Yuki & Yoshimatsu 1989; Fukuyo et al. 1990; Kim 1998). However, the actual toxin principles have yet to be ellucidated (Taylor et al. 1995). Ho and Zubkoff (1979) suggested that physical contact, not a released toxin, was the cause of oyster larvae (*Crassostrea virginica*) deformation and mortality during a *C. polykrikoides* red tide in the York River (Virginia, USA).

Species Comparison: *C. polykrikoides* closely resembles two other *Cochlodinium* species: *C. helix and C. helicoides*. The degree of rotation of the cingulum and sulcus distinguish the former species from the latter two: a. the cingulum in *C. polykrikoides* makes 1.8-1.9 turns around the cell, while in *C. helix* it is two turns and in *C. helicoides* it is 1.5 turns; and b. the sulcus turns 0.8 times between the proximal and distal ends of the cingulum in *C. polykrikoides*, whereas it is 1 time in *C. helix* and 0.6 times in *C. helicoides* (Silva 1967).

Habitat and Locality: *C. polykrikoides* is a cosmopolitan species found in warm temperate and tropical waters (Steidinger & Tangen 1996). This species was first reported from the Caribbean Sea along the southern coast of Puerto Rico (Margelef 1961). It has since been reported in northern Atlantic waters along the American east coast: Barnegat Bay, New Jersey (Silva 1967), and the York River, Virginia (Ho & Zubkoff 1979; Zubkoff et al. 1979). It is widely distributed in northwestern Pacific waters along the coasts of Japan and Korea (Fukuyo et al. 1990; Kim 1998).

Coolia monotis

Meunier, 1919

Plate 10, Figs. 1-8

Species Overview: *Coolia monotis* is an armoured, marine, benthic dinoflagellate species. It a toxic species with world-wide distribution.

Taxonomic Description: Species in this genus are anterio-posteriorly compressed and are observed in apical or antapical view. A distinguishing feature is the shape and size of the apical pore plate (Po)(Faust 1992).

Cells of *Coolia monotis* are compressed, round and lens-shaped; axis is oblique (Figs. 1-3). The rounded epitheca is slightly smaller than the rounded hypotheca (Fig. 1). The thecal surface is covered with well defined plates delineated by a network of intercalary bands (Figs. 1-3). Cell size ranges from 25 to 45 µm in diameter and 30 to 50 µm in length (Fukuyo 1981; Dodge 1982; Tolomio & Cavolo 1985b; Faust 1992).

The thecal surface is smooth and covered with sparsely scattered large pores with smooth edges (Figs. 1-4). Marginal pores are present on both sides of the lipped cingulum (Figs. 1,3)(Faust 1992).

Nomenclatural Types:

Holotype: *Coolia monotis* Meunier, 1919: plate 19, figs. 13-19

Type Locality: North Sea: Deswartes, Nieuport, Belgium

Synonyms:

Glenodinium monotis (Meunier) Biecheler, 1952

Ostreopsis monotis (Meunier) Lindemann, 1928

Thecal Plate Description: The plate formula of *Coolia monotis* is: Po, 3', 7'', 6c, 6s, 5''', 2'''' (Fig. 8). On the epitheca a distinct oblong apical pore plate (Po)(Fig. 5), positioned off-center, is located adjacent to apical plates 1', 2', and 3' (Figs. 2,8). The Po is about 12 µm long, slightly curved and narrow, and bears a long slit-like apical pore (Fig. 5). Two supporting costae border the slit-like pore. Surrounding the costae and apical pore are evenly spaced round pores (Fig. 5). The large Po is easily observed under LM and is useful for identification (Faust 1992; Steidinger & Tangen 1996).

The lipped cingulum is equatorial, narrow, and enclosed by lists with a smooth edge (Figs. 1-3,6). A ventral pore is located on the right-hand ventral margin between apical plate 1' and precingular plate 6'' (Fig. 1). The ventral pore has an ellipsoidal shape with an average diameter of 0.5 µm (Faust 1992).

The sulcus is narrow, indented, and does not reach the antapex of the cell (Figs. 1,6). It has a deep chamber-like appearance with straight walls. Two slightly curved, wide, flexible lists partially cover the sulcus at two sides (Figs. 1,6)(Faust 1992).

Morphology and Structure: Cells of *C. monotis* are photosynthetic, with many golden-brown discoid chloroplasts. Chloroplasts radiate from the center of the cell. This species has one dorsally situated nucleus located in the hypotheca. A large, round pusule is also present adjacent to the sulcus that seems to open independently into the sulcus (Faust 1992).

Reproduction: *Coolia monotis* reproduces asexually by binary fission. Sexual reproduction has been documented for this species: gametes fuse and a planozygote is formed (Fig. 7)(see Faust 1992).

Ecology: *Coolia monotis* is a planktonic, benthic and epiphytic species (Faust 1992; Steidinger & Tangen 1996). This toxic species has been identified as causing shellfish toxicity (neurotoxin poisoning-like symptoms) in oysters (*Crassostrea gigas*) in Rangauna Harbour, Northland, New Zealand (Rhodes & Thomas 1997).

Toxicity: This species is considered toxic (Nakajima et al. 1981) producing cooliatoxin, a neurotoxic analog to yessotoxin (Holmes et al. 1995, Rhodes & Thomas 1997).

Species Comparison: *Coolia* and *Ostreopsis* species have morphological similarities and differences: 1.) the Po of *Coolia monotis* is similar in architecture, but considerably longer (12 µm) than in *O. heptagona* (8-9 µm) and *O. ovata* (6-7 µm); 2.) the ventral pore of *Coolia monotis* is located on the right-hand ventral margin between apical plate 1' and precingular plate 6" which is similar to the location of the ventral pore of *O. ovata*; and 3.) *Coolia monotis* has a relatively short (20 µm) longitudinal flagellum compared to other benthic dinoflagellate species, but it is significantly longer than the longitudinal flagellum of *O. ovata* (approximately 12 µm) (Besada et al. 1982; Faust 1992; Norris et al. 1985).

Besada et al. (1982) suggested that mucilage secretion occurred through the ventral pore from the pusule of Ostreopsis species. This may also be true for *Coolia monotis* cells since they attach to the bottom of culture plates by mucus threads or are entwined in a veil of mucilage. Mucus formation prompted Besada et al. (1982) to consider a relationship between *Coolia monotis*, *O. ovata* and *Gambierdiscus toxicus*.

Coolia, *Ostreopsis* and *Gambierdiscus* also exhibit a similar internal anatomy (Besada et al. 1982) and sterol composition (Besada 1982). *Gambierdiscus toxicus*, however, differs in having an additional sterol compound (Loeblich & Indelicato 1986) possibly indicating a more distant relationship to the other two species.

Habitat and Locality: *Coolia monotis* is a neritic species that is quite common world-wide in temperate to tropical waters (Steidinger & Tangen 1996). Populations have been observed from plankton samples, oyster beds, brackish habitats and tidal pools, as well as mangrove environments. This species is most common in warm shallow waters of the Caribbean and Mediterranean Seas, and the Pacific Ocean (Faust 1992).

Dinophysis acuminata

Claparède et Lachmann, 1859

Plate 11, Figs. 1-6

Species Overview: *Dinophysis acuminata* is an armoured, marine, planktonic dinoflagellate species. It is a toxic species associated with DSP events and is commonly found in coastal waters of the northern Atlantic and Pacific Oceans.

Taxonomic Description: Species in this genus are laterally compressed with a small, cap-like epitheca and a much larger hypotheca (dorso-ventral depth of epitheca is 1/3 to 1/2 of hypotheca). The shape of the cell in lateral view is the most important criterion used for identification (Taylor et al. 1995). However, size and shape varies considerably in this species (Larsen & Moestrup 1992).

Cells of *Dinophysis acuminata* are small to medium, almost oval or elliptical in shape (Figs. 1-5). The shape can vary from rotund to long and narrow in lateral view. A well-developed left sulcal list (LSL) extends beyond the midpoint of the cell (1/2 to 2/3 of cell length)(Figs. 1-3).

The antapex is rounded, and cells are commonly found with two to four small knob-shaped posterior protrusions; sometimes well-developed and sometimes not (Figs. 2-5)(Balech 1976; Hallegraeff & Lucas 1988; Taylor et al. 1995; Steidinger & Tangen 1996).

The thick thecal plates are covered with prominent circular areolae, each with a pore (Fig. 2). These markings can vary depending on the age of the cell. The variations can range from only pores (Fig. 3), to depressions with scattered pores (Fig. 1), to depressions each with a pore, to areolae each with a pore (Fig. 2). Pores are not found in the megacytic zone (Fig. 3). Cell size ranges: 38-58 µm in length and 30-40 µm in dorso-ventral width (widest near middle of cell)(Lebour 1925; Abè 1967; Dodge 1982; Fukuyo et al. 1990; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:

Holotype: *Dinophysis acuminata* Claparède and Lachmann, 1859: 408, plate 20, fig. 17
Type Locality: North Sea: Norway
Synonyms:
Dinophysis lachmannii Paulsen, 1949
Dinophysis borealis Paulsen, 1949
Dinophysis boehmii Paulsen, 1949

Thecal Plate Description: The epitheca is slightly convex and inclined ventrally (Figs. 1-4). Made up of four plates, it is not visible in lateral view (Balech 1976; Hallegraeff & Lucas 1988; Taylor et al. 1995; Zingone et al. 1998).

The cingulum is made up of four unequal plates, and is bordered by two well-developed lists: an anterior cingular list (ACL), often with ridges, and a smooth posterior cingular list (PCL) (Fig. 1). The dorsal end of the cingulum is strongly inclined and concave (Figs. 1,6)(Balech 1976; Zingone et al. 1998).

The sulcus is comprised of four irregularly shaped plates. The flagellar pore is housed in the sulcal area. The LSL, supported by three ribs, is rather narrow and often sculptured with reticulated ribs, lines and areolae (Balech 1976; Taylor et al. 1995; Zingone et al. 1998). The third rib on the left sulcal list is the longest, and is usually strongly curved posteriorly (Figs. 1,4,6). Sulcal plate development is highly variable in this species (Balech 1976).

The hypotheca, with four large plates, comprises the majority of the cell. The dorsal margin is more or less evenly convex (Figs. 1,2,4). The ventral margin is rarely convex; it is generally oblique and flat (Figs. 2-5)(Balech 1976). The antapex is ventrally off-center (Figs. 2-5)(Abè 1967).

Morphology and Structure: *Dinophysis acuminata* is a photosynthetic species with large chloroplasts, a posterior pyrenoid, and a large central nucleus (Hallegraeff & Lucas 1988; Zingone et al. 1998).

Reproduction: *D. acuminata* reproduces asexually by binary fission. Mackenzie (1991) reported sexual reproduction via the fusion of anisogamous gametes.

Ecology: *D. acuminata* is a planktonic toxic bloom-forming species (Taylor et al. 1995; Steidinger & Tangen 1996). The most extensive blooms have been reported from the summer and fall months (Kat 1989; Taylor et al. 1995). Blooms have been reported from many parts of the world (see Kat 1985); however, they have been particularly extensive/severe along the coasts of Western Europe. Annual blooms of this species from the Netherlands have been reported with cell concentrations greater than 40,000 cells/L (Kat 1985; 1989). Blooms are often associated with toxicity of shellfish (Taylor et al. 1995).

Jacobson and Andersen (1994) found a high number of food vacuoles in cells of *Dinophysis acuminata* and deduced that mixotrophy is an important aspect of its biology. They speculate that this species feeds by way of a peduncle (myzocytosis), the feeding mode used by the heterotrophic species *Dinophysis rotundata* and *D. hastata* (Schnepf & DeichgrAbèr 1983). The peduncle, the proposed feeding apparatus, passes through the cytostomal opening in the theca when the cell is feeding (Jacobson & Andersen 1994).

Toxicity: *D. acuminata* is a toxic species that has been found to produce okadaic acid (OA)(Cembella 1989; Lee et al. 1989) causing diarrhetic shellfish poisoning (DSP) (Kat 1985). Toxicity can vary considerably among seasons and areas where it blooms (Taylor et al. 1995).

This species can cause shellfish toxicity at very low cell concentrations (as low as 200 cells/L)(Lassus et al. 1985). Hoshiai et al. (1997), however, reported a case of nontoxic mussels in Kesennuma Bay, northern Japan, in the presence of high concentrations of *D. acuminata* cells.

Species Comparison: *D. acuminata* can be confused with *D. sacculus, D. norvegica, D. ovum* and *D. punctata*, but is most often misidentified as *D. sacculus* (Steidinger & Tangen 1996; Zingone et al. 1998). The major difference between *D. acuminata* and *D. sacculus* is the shape of the large hypothecal plates: in *D. acuminata* they are shorter, more convex dorsally and often more slender posteriorly; whereas, in *D. sacculus* they are long and sack-like. *D. acuminata* also exhibits more pronounced thecal areolation and sulcal list ornamentation, but these are variable features. Since these two species rarely occur in the same area with the same importance, the possibility of misidentification is reduced (Zingone et al. 1998).

Surface thecal ornamentation in this species is similar to *D. sacculus* (Hallegraeff & Lucas 1988).

Habitat and Locality: Populations of *Dinophysis acuminata* are distributed widely in temperate waters. They are most common and abundant in coastal waters of the northern Atlantic and Pacific Oceans, especially eutrophic areas (Taylor et al. 1995; Steidinger & Tangen 1996).

Remarks: *D. acuminata* has a history wrought with identification problems mainly attributable to the morphological variability of this species. This problem is enhanced by the many synonyms and questionable identifications that have accumulated in the literature over the years (see Zingone et al. 1998).

Compounding the identification problem is the influence of feeding on lateral cell shape; cells containing food vacuoles had a rounder lateral outline than cells devoid of food vacuoles (Jacobson & Andersen 1994).

Many authors consider *Phalacroma* to be synonymous with *Dinophysis* (Steidinger & Tangen 1996).

Dinophysis acuta
Ehrenberg, 1839
Plate 12, Figs. 1-4

Species Overview: *Dinophysis acuta* is an armoured, marine, planktonic dinoflagellate species. It is a toxic species associated with DSP events and is commonly found in cold and temperate neritic waters.

Taxonomic Description: Species in this genus are laterally compressed with a small, cap-like epitheca and a much larger hypotheca (dorso-ventral depth of epitheca is 1/2 to 2/3 of hypotheca). The shape of the cell in lateral view is the most important criterion used for identification (Taylor et al. 1995).

Cells of *Dinophysis acuta* are large and robust, and are among the largest species in the genus *Dinophysis* (Fig. 1). Cells are oblong with a slightly pointed or rounded posterior end (Figs. 1-4). The left sulcal list (LSL) extends beyond the midpoint of the cell (about 2/3 of cell length) ending at or above the widest portion of the cell (Fig. 3)(Balech 1976; Dodge 1982; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

The thick thecal plates of the hypotheca are coarsely areolated, each areola with a central pore (Figs. 1,2,4). The areolation becomes very faint or disappears near the edge of the plates. Cell size ranges: 54-94 µm in length and 43-60 µm in dorso-ventral width (widest below the middle)(Fig. 3)(Balech 1976; Dodge 1982; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Dinophysis acuta* Ehrenberg, 1839: 124, 151, plate 4 (fide Schiller, 1933)
Type Locality: Mediterranean Sea: Gulf of Lion, France

Thecal Plate Description: The small epitheca is made up of four plates. It is low, flat or weakly convex, and is not visible in lateral view (Balech 1976; Larsen & Moestrup 1992; Taylor et al. 1995).

The cingulum is made up of four unequal plates, all with pores. Well developed cingular lists are present: an anterior cingular list (ACL), and a posterior cingular list (PCL). They are generally smooth and rarely ornamented (Fig. 3). The high ACL obscures the low epitheca (Balech 1976; Dodge 1982; Larsen & Moestrup 1992).

The sulcus is comprised of several irregularly shaped plates. The flagellar pore is housed in the sulcal area. The left sulcal list (LSL), supported by three ribs that radiate outward, is rather broad with a convex ventral margin. It is wider posteriorly and slightly areolated. The second sulcal rib is closer to the first than to the third. The third rib is the longest (Figs. 1-4)(Balech 1976; Dodge 1982; Taylor et al. 1995).

The hypotheca, with four large plates, comprises the majority of the cell. The anterior 2/3 of the hypotheca has convex margins, while the posterior third of the hypotheca forms a broad asymmetrical triangle with a straight dorsal edge and occasionally a slightly concave ventral edge (Figs. 1-4). The tapered and roughly pointed antapex is directed slightly ventrally (Figs. 1-4) (Balech 1976; Dodge 1982; Taylor et al. 1995). Balech (1976: figs. 2H, 2I) depicts two specimens with two to three small knob-like spines on the posterior end.

Morphology and Structure: *Dinophysis acuta* is a photosynthetic species with yellow chloroplasts (Dodge 1982; Larsen & Moestrup 1992).

Dimorphic cells, one half resembling *D. acuta* and the other half resembling *D. dens* (the proposed gamete form), have occasionally been observed in this species (Reguera et al. 1990; Hansen 1993; Moita & Sampayo 1993). It is highly probable that these cell forms represent a stage in gametogenesis (Hansen 1993).

Reproduction: *D. acuta* reproduces asexually by binary fission. Hansen (1993) speculates that sexual reproduction, with sexual dimorphism, is part of the life cycle for this species.

Ecology: *D. acuta* is a planktonic oceanic and neritic species (Dodge 1982; Taylor et al. 1995; Steidinger & Tangen 1996). This is a bloom-forming species; blooms are often associated with shellfish toxicity (Taylor et al. 1995).

Toxicity: *D. acuta* is a toxic species that produces okadaic acid (OA), as well as Dinophysistoxin-1 (DTX1)(Lee et al. 1989; Yasumoto 1990). *D. acuta* has been associated with DSP outbreaks in Chile (Larsen & Moestrup 1992), Portugal (Alvito et al. 1990; Sampayo et al. 1990), Scandinavia (Dahl & Yndestad 1985; Krogh et al. 1985; Underdahl et al. 1985; Edler & Hageltorn 1990), and the USA (Freudenthal & Jijina 1985).

Species Comparison: *D. acuta* is very similar to *D. norvegica* in their general shape, and thus can easily be misidentified. *D. acuta* can be differentiated by its larger size and different shape: *D. norvegica* is widest in the middle region of the cell, whereas *D. acuta* is widest below the mid-section. Moreover, *D. acuta* has a longer left sulcal list relative to its cell length (Balech 1976; Dodge 1982; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

D. acuta also strongly resembles a warm-water species, *D. schroederi* Pavillard, 1909 (Schiller 1933; Balech 1976; Burns & Mitchell 1982).

Habitat and Locality: *Dinophysis acuta* is widely distributed in cold and temperate waters world-wide (Larsen & Moestrup 1992; Steidinger & Tangen 1996).

Remarks: Many authors consider *Phalacroma* to be synonymous with *Dinophysis* (Steidinger & Tangen 1996).

Dinophysis caudata
Saville-Kent, 1881
Plate 13, Figs. 1-6

Species Overview: *Dinophysis caudata* is an armoured, marine, planktonic dinoflagellate species. It is a bloom-forming species associated with massive fish kills. It is commonly found world-wide in subtropical and tropical neritic waters.

Taxonomic Description: Species in this genus are laterally compressed with a small, cap-like epitheca and a much larger hypotheca (dorso-ventral depth of epitheca is 1/2 to 2/3 of hypotheca)(Figs. 1,2). The shape of the cell in lateral view is the most important criterion used for identification (Taylor et al. 1995).

D. caudata is a very distinctive species. Cells are large, long and irregularly subovate with a long ventral projection on the hypotheca (Figs. 1-6). The extended process varies in length and shape (Figs. 1-6), and is often toothed on its posterior end (Figs. 4,5). The long left sulcal list (LSL) extends to nearly half of the total length of the cell (Figs. 1,2,5,6). This species is usually widest at the base of the LSL (Lebour 1925; Abè 1967; Dodge 1982; Fukuyo et al. 1990, Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

The thick thecal plates are heavily areolated, each areole with a pore (Figs. 1,4-6). Cell size ranges: 70-110 µm in length and 37-50 µm in dorso-ventral width (at base of LSL) (Lebour 1925; Abè 1967; Dodge 1982; Fukuyo et al. 1990; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Dinophysis caudata* Saville-Kent, 1881: 455, 460
Type Locality: unknown
Synonyms:
Dinophysis homunculus Stein, 1883

Thecal Plate Description: The small epitheca is made up of four plates. The cingulum is narrow with two well-developed lists, anterior cingular list (ACL) and posterior cingular list (PCL), supported by ribs (Figs. 1-6). Both cingular lists are projected anteriorly (Figs. 1,2,5,6). ACL forms a wide and deep funnel obscuring the epitheca (Figs. 1,2). The sulcus is comprised of several irregularly shaped plates. The wide LSL is supported by three ribs spaced equally apart (Figs. 4-6). A right sulcal list (RSL) is also present (Figs. 1,2,5,6). Both sulcal lists are often reticulated (Figs. 4,5)(Lebour 1925; Dodge 1982; Fukuyo et al. 1990; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

The hypotheca, with four large plates, comprises the majority of the cell. It is long and narrows ventrally into a pointed posterior projection (Figs. 1-6)(Lebour 1925). The ventral margin is generally straight or undulate along the main body (Dodge 1982; Fukuyo et al. 1990; Taylor et al. 1995; Steidinger & Tangen 1996). The dorsal contour gradually curves: it is straight or slightly concave along the anterior half of the hypotheca, then is straight or convex in the posterior half running parallel to the ventral margin. The dorsal margin may also curve sharply towards the center where it turns to continue down the ventral posterior projection, which can bear small knob-like spines (Figs. 4,5)(Lebour 1925; Dodge 1982; Fukuyo et al. 1990; Taylor et al. 1995).

Morphology and Structure: *Dinophysis caudata* is a photosynthetic species with chloroplasts and a large posterior nucleus (Fig. 3)(Larsen & Moestrup 1992). Paired cells are common, dorsally joined at the widest point of the hypotheca (Fig. 5)(Dodge 1982; Steidinger & Tangen 1996).

D. diegensis, a species very similar in morphology to *D. caudata* with a reduced hypothecal process, is suspected to be a gamete of *D. caudata* (Moita & Sampayo 1993).

Reproduction: *D. caudata* reproduces asexually by binary fission; paired cells are common (Fig. 5). Moita and Sampayo (1993) speculate that sexual reproduction, with sexual dimorphism, is part of the life cycle for this species.

Ecology: *D. caudata* is a cosmopolitan planktonic species (Abè 1967; Fukuyo et al. 1990; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996). Red tides associated with mass mortality of fish has been reported in the Gulf of Thailand and Seto Inland Sea in Japan (Okaichi 1967).

Toxicity: Although this species is known to create red tides resulting in massive fish mortality in Japan (Okaichi 1967), the toxic potential needs to be examined further (Larsen & Moestrup 1992).

Species Comparison: Cells of *D. caudata* with short hypothecal processes look similar to *D. diegensis* (Taylor et al. 1995); *D. diegensis* has been called a variety of *D. caudata* (Steidinger & Tangen 1996). Some cells of *D. caudata*, bearing a short hypothecal process, can superficially resemble *D. tripos* (Larsen & Moestrup 1992; Steidinger & Tangen 1996).

Habitat and Locality: *D. caudata* is common in temperate to tropical neritic waters (Abè 1967; Fukuyo et al. 1990; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996)

Remarks: The morphology of this species varies considerably, in particular the length of the hypothecal projection and the dorsal expansion. These differences have resulted in descriptions of several different subspecies, varieties and forms (Dodge 1982; Larsen & Moestrup 1992; Taylor et al. 1995). Since this is a cosmopolitan species, Abè (1967) suggests the variations in morphology are due to external environmental factors (e.g. salinity, temperature and nutrients).

Many authors consider *Phalacroma* to be synonymous with *Dinophysis* (Steidinger & Tangen 1996).

Dinophysis fortii

Pavillard, 1923

Plate 14, Figs. 1-4

Species Overview: *Dinophysis fortii* is an armoured, marine, planktonic dinoflagellate species. This species is a bloom forming toxic species associated with DSP events. It has world-wide distribution in cold temperate waters, but is also found in subtropical to tropical waters.

Taxonomical Description: Species in this genus are laterally compressed with a small, cap-like epitheca and a much larger hypotheca (dorso-ventral depth of epitheca is 1/2 to 2/3 of hypotheca). The shape of the cell in lateral view is the most important criterion used for identification (Taylor et al. 1995).

Cells of *Dinophysis fortii* are large, long and subovate, ending in a broadly rounded posterior (a dorsal bulge)(Figs. 1-4). The posterior end is the widest. The left sulcal list (LSL) is well developed and very long; it can extend up to 4/5 of the cell length (Figs. 1-3)(Abè 1967; Taylor et al. 1995; Steidinger & Tangen 1996).

The thick thecal plates of the hypotheca are deeply areolated (Figs. 1,2), each areolae with a pore (Fig. 4). Cell size ranges: 56-83 μm in length and 43-58 μm in dorso-ventral width (at the base of the third rib of the LSL)(Abè 1967; Taylor et al. 1995; Larsen & Moestrup 1992; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Dinophysis fortii* Pavillard, 1923: 881
Type Locality: unknown

Thecal Plate Description: The small epitheca is made up of four plates. Well developed cingular lists, both anteriorly inclined, obscure the epitheca (Figs. 1-4). The anterior cingular list (ACL), which is wider than the posterior list (PCL), forms a wide and shallow cup with the epitheca as its bottom (Figs. 3,4)(Fukuyo et al. 1990; Taylor et al. 1995). The sulcus is comprised of several irregularly shaped plates. The flagellar pore is housed in the sulcal area. The LSL is very long, reticulated (Figs. 1,4) and supported by three ribs (Fig. 3)(Larsen & Moestrup 1992; Taylor et al. 1995). A well-developed triangular right sulcal list (RSL) is also present; it is approximately half the length of the LSL (Figs. 1,4) (Steidinger & Tangen 1996).

The hypotheca, with four large plates, comprises the majority of the cell. The dorsal margin and posterior end are smoothly convex with a slight concavity near the cingulum (Figs. 2,3). The ventral margins are fairly straight, slanting at an angle of 110-120 degrees to the cingulum (Figs. 2,3)(Abè 1967; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

Morphology and Structure: *Dinophysis fortii* is a photosynthetic species with large central chloroplasts and a terminal pyrenoid (Hallegraeff & Lucas 1988; Larsen & Moestrup 1992).

Reproduction: *D. fortii* reproduces asexually by binary fission.

Ecology: *D. fortii* is a planktonic oceanic and neritic species (Abè 1967; Taylor et al. 1995; Steidinger & Tangen 1996). It is a bloom-forming species; noxious blooms have been reported from Australia (Hallegraeff 1987) and Japan (Yasumoto et al. 1980; Osaka & Takabayashi 1985; Igarashi 1986). In northern Japan warm currents in spring and early summer carry populations of *D. fortii* landward where cells filter into coastal areas of intensive shellfish aquaculture (Taylor et al. 1995). Populations seem to be most abundant in early summer (Yasumoto et al. 1980; Osaka & Takabayashi 1985; Igarashi 1986).

Observations of Miyazono and Minoda (1990) suggest that this species prefers high salinity and low temperatures; however, they can tolerate lower salinities. Early studies of Ishimaru et al. (1988) suggest the capablity of *D. fortii* to prey upon cryptomonads.

Toxicity: *Dinophysis fortii* is a known toxin-producing species (Lee et al. 1989; Yasumoto 1990; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996). It is the most noxious cause of diarrhetic shellfish poisoning (DSP) in Japanese waters. This species produces Dinophysistoxin-1 (DTX1), Dinophysistoxin-2 (DTX2), and okadaic acid (OA) (Lee et al. 1989; Yasumoto 1990), although clones in warmer waters show very low toxicity (Taylor et al. 1995). *Dinophysis fortii* was the first species found to be associated with DSP; concentrations as low as 200 cells/L can cause human intoxication (Yasumoto et al. 1980).

Habitat and Locality: *D. fortii* is widely distributed in cold temperate waters world-wide, but is also found in subtropical to tropical areas (Abè 1967; Taylor et al. 1995; Steidinger & Tangen 1996).

Remarks: *D. fortii* is best identified by its wide rounded posterior and the presence of reticulations on the sulcal list (Larsen & Moestrup 1992; Steidinger & Tangen 1996). Variations in cell shape are mostly seen in the placement and size of the hypothecal dorsal bulge (Abè 1967).

Many authors consider *Phalacroma* to be synonymous with *Dinophysis* (Steidinger & Tangen 1996).

Dinophysis mitra
(Schütt) Abè, 1967
Plate 15, Figs. 1-6

Species Overview: *Dinophysis mitra* is an armoured, marine, planktonic dinoflagellate species. It is a toxic species widely distributed in warmer waters.

Taxonomic Description: Species in this genus are laterally compressed with a small, cap-like epitheca and a much larger hypotheca (dorso-ventral depth of epitheca is 1/2 to 2/3 of hypotheca). The shape of the cell in lateral view is the most important criterion used for identification (Taylor et al. 1995).

Cells of *D. mitra* are large, broad and wedge-shaped (Figs. 1,2). The ventral hypothecal margin is distinctly concave below the left sulcal list (LSL)(Figs. 1,2). The LSL is relatively short, only half of the total cell length (Fig. 2). This species is widest at the base of the second rib of the left sulcal list (Fig. 2)(Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

The theca are thick and coarsely areolated (Figs. 1-5). Areolae are large; some with a small central pore (Figs. 2,6). Cell size ranges: 70-95 µm in length and 58-70 µm in dorso-ventral width (at base of second rib of LSL)(Larsen & Moestrup 1992; Taylor et al. 1995).

Nomenclatural Types:
Holotype: *Dinophysis mitra* Schütt, 1895: 149, plate 4, fig. 18
Type Locality: unknown
Synonyms:
Phalacroma rapa Stein, 1883
Phalacroma mitra Schütt, 1895
Phalacroma dolichopterygium Jörgensen, 1923

Thecal Plate Description: The small epitheca is slightly convex, appearing as a cap above the cingulum (Figs. 1-4). The four epithecal plates are coarsely areolated. The anteriorly situated cingulum has two narrow, well developed lists, anterior cingular list (ACL) and posterior cingular list (PCL), supported by many ribs (Figs. 1-4). The sulcus is comprised of several irregularly shaped plates. The flagellar pore is housed in the sulcal area. LSL is supported by three short ribs (Fig. 2)(Larsen & Moestrup 1992; Taylor et al. 1995).

The hypotheca, with four large plates, comprises the majority of the cell. The dorsal margin is smoothly convex (Figs. 1-3). The ventral margin is more or less straight in the sulcal region, becoming distinctly concave at the posterior end of the LSL towards the antapex of the cell (Figs. 1,2,5). As the megacytic zone expands during cell growth, the posterio-ventral concavity of the hypotheca becomes much less distinct (Fig. 4)(Larsen & Moestrup 1992; Taylor et al. 1995).

Morphology and Structure: *Dinophysis mitra* is a photosynthetic species with chloroplasts (Schütt 1895).

Reproduction: *D. mitra* reproduces asexually by binary fission.

Ecology: *D. mitra* is a planktonic oceanic and neritic species. No blooms have been reported for this species (Larsen & Moestrup 1992).

Toxicity: *Dinophysis mitra* is a confirmed diarrhetic shellfish poison (DSP) toxin-producing species; it produces Dinophysistoxin-1 (DTX1) and okadiac acid (OA)(Lee et al. 1989; Steidinger & Tangen 1996).

Species Comparison: *Dinophysis mitra* resembles *D. rapa*; Schiller (1933) stated that the two species are probably synonymous. The two species can be distinguished by *D. rapa's* stronger protuberant sulcal ridge at the base of the third rib of the LSL (left ventral margin is angled), and its extreme concavity of the hypothecal posterior ventral margin. *D. rapa* is also a larger species (Abe 1967; Larsen & Moestrup 1992; Steidinger & Tangen 1996).

Habitat and Locality: *D. mitra* is widely distributed in warm temperate to tropical waters world-wide (Abe 1967; Larsen & Moestrup 1992;
Taylor et al. 1995; Steidinger & Tangen 1996).

Remarks: Many authors consider *Phalacroma* to be synonymous with *Dinophysis* (Steidinger & Tangen 1996).

Dinophysis norvegica
Claparède et Lachmann, 1859
Plate 16, Figs. 1-6

Species Overview: *Dinophysis norvegica* is an armoured, marine, planktonic dinoflagellate species. This species is a bloom-forming toxic species associated with DSP events. It is commonly found in cold neritic waters.

Taxonomic Description: Species in this genus are laterally compressed with a small, cap-like epitheca and a much larger hypotheca (dorso-ventral depth of epitheca is 1/2 to 2/3 of hypotheca). The shape of the cell in lateral view is the most important criterion used for identification (Taylor et al. 1995). However, size and shape varies considerably in this species (Larsen & Moestrup 1992).

Cells of *Dinophysis norvegica* are generally large, ovoid and robust (Fig. 1). The posterior end tapers to a triangular shape (Figs. 1-6). The antapex is pointed (Fig. 2) or slightly rounded (Fig. 3), and occasionally with small knob-like protrusions that may extend along the rounded dorsal margin (Figs. 1,4,5). This species is widest at or slightly above the middle of the cell (Fig. 4). The left sulcal list (LSL) extends about 2/3 of cell length (Balech 1976; Dodge 1982; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

The thick thecal plates are coarsely areolated; areolae are large and each with a pore (Figs. 1,3,6). Cell size ranges: 48-80 μm in length and 39-70 μm in dorso-ventral width (widest in the middle)(Balech 1976; Dodge 1982; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Dinophysis norvegica* Claparède and Lachmann, 1859: 407, plate 20, fig. 19
Type Locality: North Sea: Fjord of Bergen, Glesnesholm, Norway
Synonyms:
Dinophysis debilior Paulsen, 1949

Thecal Plate Description: The small epitheca is low, flat or weakly convex, and is obscured by cingular lists. It is made up of four plates with a sinuous sculpture (Balech 1976; Dodge 1982; Taylor et al. 1995).

The cingulum is made up of four unequal plates, all with pores. The cingulum bears two well sculptured lists: an anterior cingular list and a posterior cingular list (Fig. 1). In general, they are covered with irregular coarse or fine sinuous lines or reticulations (Figs. 1,6). Both lists are projected anteriorly (Balech 1976; Dodge 1982).

The sulcus is comprised of several irregularly shaped plates. The flagellar pore is housed in the sulcal area. The LSL, supported by three ribs that radiate outward, is relatively narrow (average maximum width = 10 μm) and curved to the right between the second and third rib (Fig. 1). The first and second ribs project anteriorly;

the third rib is curved or straight and projects posteriorly (Figs. 1,5,6). The third rib is located at the mid-point of the cell or just above it (Fig. 4). The sulcal lists may have surface ornamentation, or they may be smooth (Balech 1976; Dodge 1982; Steidinger & Tangen 1996).

The hypotheca, with four large plates, comprises the majority of the cell. The dorsal margin is smoothly convex to the antapex, while the ventral margin is straight or convex up to the third sulcal rib, then becomes concave or straight to the antapical end (Figs. 1-6)(Balech 1976; Dodge 1982; Larsen & Moestrup 1992).

Morphology and Structure: *Dinophysis norvegica* is a photosynthetic species with yellow chloroplasts and a posteriorly oriented nucleus (Fig. 5)(Schiller 1933; Larsen & Moestrup 1992).

Dimorphic cells of *D. norvegica* were found in Danish waters: one theca half was smaller with rounded margins and a pointed antapex (*D. norvegica* f. *crassior*); the other half was larger with a distinct concave indentation on the lower third of the ventral margin and a more rounded antapex (*D. norvegica* f. *debilor*). It is highly probable that these cells represent a stage in gametogenesis. Or they may be examples of natural variation within the species (Hansen 1993).

Reproduction: *D. norvegica* reproduces asexually by binary fission. Hansen (1993) speculates that sexual reproduction, with sexual dimorphism, is part of the life cycle for this species.

Ecology: *D. norvegica* is a planktonic neritic species (Schiller 1933; Taylor et al. 1995; Steidinger & Tangen 1996). Blooms have been reported from the British Isles (Dodge 1977), Scandinavia (Dahl & Yndestad 1985; Krogh et al. 1985) and the U.S. (Freudenthal & Jijina 1985). Cell numbers of about 80,000 cells/L have been reported from Denmark (Larsen & Moestrup 1992).

Jacobson & Andersen (1994) found a high number of food vacuoles in cells of *Dinophysis norvegica* and deduced that mixotrophy is an important aspect of its biology. They speculate that this species feeds by way of a peduncle (myzocytosis), the feeding mode used by the heterotrophic species *Dinophysis rotundata* and *D. hastata* (Schnepf & Deichgraber 1983). The peduncle passes through the cytostomal opening in the theca when the cell is feeding (Jacobson & Andersen 1994).

Toxicity: *D. norvegica* is a known toxin producer associated with diarrhetic shellfish poisoning (DSP) events. Cembella (1989), Lee et al. (1989) and Yasumoto (1990) reported Dinophysistoxin-1 (DTX1) and okadaic acid (OA) production from this species.

Species Comparison: *Dinophysis norvegica* is very similar to *D. acuta* in shape, and thus can easily be misidentified. Balech (1976) found that the plate patterns of these two species are very similar, but are more variable in *D. norvegica*. These species can be differentiated by their size (although they overlap) and deepest position: *D. acuta* is larger and widest below the mid-section, whereas *D. norvegica* is smaller and widest in the middle region of the cell (Balech 1976; Dodge 1982; Dodge 1985; Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

Other differences between the two species include: *D. acuta* has a longer left sulcal list relative to its cell length (Balech 1976); *D. norvegica* is more pointed at the antapex and lacks the hypothecal bulge evident in *D. acuta* (Dodge 1985); the LSL in *D. norvegica* twists to the right between the second and third rib, and appears narrower than in *D. acuta* (Balech 1976; Dodge 1982).

Habitat and Locality: *D. norvegica* is widely distributed in cold, temperate northern waters (Dodge 1985; Steidinger & Tangen 1996).

Remarks: *D. norvegica* is considerably variable in size and shape (Schiller 1933; Balech 1976). A number of forms and varieties have been described: *D. norvegica* var. *debilor* Paulsen and *D. norvegica* var. *crassior* Paulsen, both of which were subsequently raised to species level (Paulsen 1949). Solum (1962) later considered them as different forms of *D. norvegica*.

Many authors consider *Phalacroma* to be synonymous with *Dinophysis* (Steidinger & Tangen 1996).

Dinophysis rotundata
Claparède et Lachmann, 1859
Plate 17, Figs. 1-5

Species Overview: *Dinophysis rotundata* is an armoured, marine, planktonic dinoflagellate species. It is a toxic heterotrophic species widely distributed in cold and warm waters.

Taxonomic Description: Species in this genus are laterally compressed with a small, cap-like epitheca and a much larger hypotheca (dorso-ventral depth of epitheca is 1/2 to 2/3 of hypotheca). The shape of the cell in lateral view is the most important criterion used for identification (Taylor et al. 1995).

Cells of *Dinophysis rotundata* are medium-sized and broadly rounded in lateral view with convex ventral and dorsal margins (Figs. 1-4). Left sulcal list (LSL) extends over 1/2 to 3/4 of cell length (Figs. 2-4). Greatest dorso-ventral width is between the base of the second and third rib of the LSL (Figs. 2,3)(Lebour 1925; Abè 1967; Balech 1976; Dodge 1982; Larsen & Moestrup 1992; Steidinger & Tangen 1996).

Thecal surface is covered with poroids and scattered pores (Figs. 1,2). Cell size ranges: 36-56 µm in length and 36-43 µm in dorso-ventral width (Lebour 1925; Balech 1976; Dodge 1982; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Dinophysis rotundata* Claparède and Lachmann, 1859: 6, plate 20, fig. 16
Type Locality: North Sea: Glesnesholm, Norway
Synonyms:
Phalacroma rotundatum Kofoid and Michener, 1911
Dinophysis whittingae Balech, 1971a

Thecal Plate Description: The epitheca in this species is visible in lateral view; it is a small convex cap above the cingulum, low and fairly evenly rounded (Figs. 1,3-5)(Abè 1967; Balech 1976; Dodge 1982; Larsen & Moestrup 1992; Taylor et al. 1995). It is made up of four plates, coarsely areolated (Lebour 1925).

The cingulum bears two narrow well developed lists: an anterior cingular list (ACL), and a posterior cingular list (PCL)(Figs. 1,5). The lists are smooth, but may have ornamentation. Both lists incline anteriorly without entirely obscuring the epitheca (Fig. 1)(Lebour 1925; Balech 1976; Dodge 1982; Larsen & Moestrup 1992; Taylor et al. 1995).

The sulcus is comprised of several irregularly shaped plates. The flagellar pore is housed in the sulcal area. The LSL, supported by three ribs, is relatively narrow, often widening posteriorly (Figs. 2,5). The first two ribs are spaced closer together than the second and third ribs (Figs. 2,3,5). Narrower than the LSL, the right sulcal list (RSL) is relatively long, reaching or slightly posterior to the third rib of the LSL (Fig. 2)(Lebour 1925; Balech 1976; Dodge 1982; Taylor et al. 1995).

The hypotheca, with four large plates, comprises the majority of the cell. The ventral margin is almost straight to slightly convex between the first and third LSL ribs (Figs. 3,5). The dorsal margin is much more convex (Figs. 3,4). Posterior region rounded (Figs. 1-4) (Balech 1976).

Morphology and Structure: *Dinophysis rotundata* is a heterotrophic species without chloroplasts. The nucleus is oriented posteriorly (Fig. 4). The protoplasm is clear with numerous food vacuoles (Fig. 3). Megacytic stages frequently observed (Lebour 1925; Balech 1976; Dodge 1982; Larsen & Moestrup 1992).

Reproduction: *D. rotundata* reproduces asexually by binary fission.

Ecology: *D. rotundata* is a planktonic species. No blooms have been reported for this species (Lebour 1925; Balech 1976; Dodge 1982; Larsen & Moestrup 1992). This heterotrophic species feeds phagotrophically: it feeds on loricated and non-loricated ciliates and picoplankton (Faust, M.A., unpublished) which are ingested via a peduncle (Hansen 1991; Inoue et al. 1993).

Toxicity: *Dinophysis rotundata* is a toxic species producing the diarrhetic shellfish poison (DSP) toxin Dinophysistoxin-1 (DTX1). This is the first heterotrophic dinoflagellate in which toxin production has been demonstrated (Lee et al. 1989). However, only Japanese strains of this species have been found to produce the toxins; North American strains have proved non-toxic (Cembella 1989).

Species Comparison: *Dinophysis rotundata* looks similar to *D. rudgei* (or *Phalacroma rudgei*); however, the latter species has a more prominently visible epitheca and is also a larger species (Taylor et al. 1995; Steidinger & Tangen 1996).

Habitat and Locality: *Dinophysis rotundata* is a cosmopolitan species widely distributed in cold and warm waters (Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

Remarks: Many authors consider *Dinophysis* to be synonymous with *Phalacroma* (Steidinger & Tangen 1996).

Dinophysis sacculus
Stein, 1883
Plate 18, Figs. 1-6

Species Overview: *Dinophysis sacculus* is an armoured, marine, planktonic dinoflagellate species. It is a toxic species associated with DSP outbreaks in Europe.

Taxonomic Description: Species in this genus are laterally compressed with a small, cap-like epitheca and a much larger hypotheca (dorso-ventral depth of epitheca is 1/3 to 1/2 hypotheca). The shape of the cell in lateral view is the most important criterion used for identification (Taylor et al. 1995).

Cells of *Dinophysis sacculus* are long and oval with a rounded posterior (Figs. 1-5). It is typically sack-like in shape and highly variable in width. A short left sulcal list (about 1/2 length of the cell) extends midway down the hypotheca (Figs. 1,2). Occasionally cells are found with a few small blunt spines on the posterior end (Figs. 1,3,4,6) (Larsen & Moestrup 1992; Taylor et al. 1995; Zingone et al. 1998).

The thecal surface is covered with small unevenly distributed pores; however, the surface texture can vary from completely smooth (Fig. 3) to coarsely areolate (Figs. 1,2,4). Pores are not found in the megacytic zone (Fig. 3). Cell size ranges: 40-60 µm in length and 20-40 µm in width (Larsen & Moestrup 1992; Taylor et al. 1995; Zingone et al. 1998).

Nomenclatural Types:
Holotype: *Dinophysis sacculus* Stein, 1883: plate 20, fig. 10
Type Locality: Mediterranean Sea: Adriatic Sea, Quarnero, Italy
Synonyms:
Dinophysis reniformis Schröder, 1906
Dinophysis pavillardii Schröder, 1906
Dinophysis ventrecta Schiller, 1933
Dinophysis phaseolus Silva, 1952

Thecal Plate Description: The small epitheca is made up four plates nearly totally obscured by the well-developed cingular lists. The cingulum is bordered by two cingular lists: a wide anteriorly projected anterior cingular list (ACL), and a smooth posterior cingular list (PCL)(Figs. 1-3)(Zingone et al. 1998).

The sulcus is comprised of four irregularly shaped plates. The flagellar pore is housed in the sulcal area. The left sulcal list generally reaches the middle of the cell, however, the length can vary (Figs. 1-3). Three strong supporting sulcal ribs are thin and smooth, and in general, are without ornamentation (Figs. 1,4-6). The right sulcal list is also visible (Fig. 2)(Zingone et al. 1998).

The large hypotheca is made up of four plates. The dorsal and ventral margins of the hypotheca are important morphological characteristics used to identify this species (Zingone et al. 1998). The dorsal margin is straight or undulating: convex below the cingulum, slightly concave in the middle, and convex again posteriorly (Figs. 1,3). The ventral margin also displays some undulation: convex at the middle, and concave below the middle (Figs. 1,6). The shape of these margins is also variable in this species. The convexity of the ventral margin generally corresponds to the region where the third rib of the left sulcal list is inserted (Taylor et al. 1995).

Morphology and Structure: *D. sacculus* is most likely a photosynthetic species; Larsen and Moestrup (1992) state that 'chloroplasts are probably present'. Moreover, Giacobbe (1995) found the possible presence of chlorophyll and phycobilin pigments in using epifluorescence microscopy.

Giacobbe and Gangemi (1997) have shown that the concavity of the dorsal margin can vary in the life history of the species; e.g. the development of the megacytic zone. This area can increase before cell division or following gamete fusion (Giacobbe & Gangemi 1997). Biological factors (i.e. life history and nutrition) can explain the presence of different morphotypes in the same locality (Zingone et al. 1998).

Reproduction: *D. sacculus* reproduces asexually by binary fission (Taylor et al., 1995). Giacobbe and Gangemi (1997) reported sexual reproduction in this species.

Ecology: *Dinophysis sacculus* is a planktonic species (Taylor et al. 1995). Blooms have been reported from Portugal, North Atlantic Ocean (Alvito et al. 1990; Sampayo et al. 1990), and Italy, Mediterranean Sea (Zingone et al. 1998).

Toxicity: *D. sacculus* has been found to produce okadaic acid (OA) (Masselin et al. 1992; Giacobbe et al. 1995; Delgado et al. 1996). It has been linked to diarrhetic shellfish poisoning (DSP) occurrences along the Mediterranean and Atlantic European coasts (Alvito et al. 1990; Sampayo et al. 1990; Lassus & Marcaillou-Le Baut 1991; Belin 1993; Boni et al. 1993; Marasovic et al. 1998).

Species Comparison: *D. sacculus* is most often misidentified as *D. acuminata.* The major difference between these two species is the shape of the large hypothecal plates: in *D. sacculus* they are long and sack-like, whereas in *D. acuminata* they are shorter, more convex dorsally and often more slender posteriorly. *D. acuminata* also exhibits more pronounced thecal areolation and sulcal list ornamentation, but these are variable characteristics. Moreover, since *D. sacculus* and *D. acuminata* rarely occur in the same area with the same importance, the possibility of misidentification is reduced (Zingone et al. 1998).

Surface thecal ornamentation in this species is similar to a number of other *Dinophysis* species: *D. acuta, D. caudata, D. norvegica* and *D. fortii* (Hallegraeff & Lucas 1988).

Etymology: '*Sacculus'* (Latin) refers to the sack-like shape of the hypotheca.

Habitat and Locality: *D. sacculus* is distributed widely in cold and temperate waters (Taylor et al. 1995), most often observed in semi-enclosed basins, estuaries and lagoons (Zingone et al. 1998). Populations have mostly been reported from the Mediterranean Sea (Zingone et al. 1998), with a few reports from the Atlantic Ocean (Murray & Whitting 1900; Cleve 1901; 1902).

Remarks: *D. sacculus* has a history wrought with identification problems mainly attributable to the morphological variability of this species. This problem is enhanced by the many synonyms and questionable identifications that have accumulated in the literature over the years (see Zingone et al. 1998).

Many authors consider *Phalacroma* to be synonymous with *Dinophysis* (Steidinger & Tangen 1996).

Dinophysis tripos

Gourret, 1883

Plate 19, Figs. 1-4

Species Overview: *Dinophysis tripos* is an armoured, marine, planktonic dinoflagellate species. It is a toxic species common in warm temperate to tropical waters.

Taxonomic Description: Species in this genus are laterally compressed with a small, cap-like epitheca and a much larger hypotheca (dorso-ventral depth of epitheca is 1/3 to 1/2 hypotheca). The shape of the cell in lateral view is the most important criterion used for identification (Taylor et al. 1995).

D. tripos is a very distinctive species. Cells are large, anterio-posteriorly elongated and asymmetrical with two posterior hypothecal projections; a longer ventral process and a shorter dorsal one (Figs. 1-4). The V-shaped processes are often toothed on their posterior ends (small knob-like spines) (Fig. 1). The well developed left sucal list (LSL) widens posteriorly and is often reticulated (Figs. 1-3)(Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

The thick thecal plates are heavily areolated (Fig. 1). Cell size ranges: 90-125 µm in length and 50-60 µm in dorso-ventral width (Larsen & Moestrup 1992; Taylor et al. 1995).

Nomenclatural Types:
Holotype: *Dinophysis tripos* Gourret, 1883: 114, plate 3, fig. 53
Type Locality: Mediterranean Sea: Gulf of Marseille, France
Synonyms:
Dinophysis caudata var. *tripos* (Gourret) Gail, 1950

Thecal Plate Description: The small epitheca is made up of four plates. The cingulum is narrow with two well developed lists, anterior cingular list (ACL) and posterior cingular list (PCL), oriented anteriorly (Figs. 1-4). The ACL is supported by many ribs (Figs. 1,4). The wide ACL forms a narrow, funnel-like structure obscuring the epitheca on the bottom. The sulcus is comprised of several irregularly shaped plates. The flagellar pore is housed in the sulcal area. The prominent wide LSL has a straight margin and is supported by three ribs (Figs. 1-4)(Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

The hypotheca, with four large plates, comprises the majority of the cell. It is long, narrowing into two tapered or pointed posterior projections: one short and dorsal, and one longer and ventral (Figs. 1-3). The dorsal projection is sometimes seen with a narrow list connecting two daughter cells during cell division (Fig. 3). The ventral margin of the hypotheca is straight or slightly undulate. The dorsal margin is concave below the cingulum and then convex continuing down to the dorsal projection (Figs. 1,2)(Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

Morphology and Structure: *D. tripos* is a photosynthetic species with chloroplasts (Fig. 2). *D. diegensis*, a smaller form very similar in morphology to *D. tripos* with a reduced hypothecal process, is suspected to be a gamete of the latter species (Moita & Sampayo 1993).

Reproduction: *D. tripos* reproduces asexually by binary fission. Moita and Sampayo (1993) speculate that sexual reproduction, with sexual dimorphism, is part of the life cycle for this species.

Ecology: *Dinophysis tripos* is a planktonic species commonly found in neritic, estuarine and oceanic waters (Steidinger & Tangen 1996). No blooms for this species have been reported (Larsen & Moestrup 1992).

Toxicity: *D. tripos* is associated with diarrhetic shellfish poisoning (DSP) events; it produces Dinophysistoxin-1 (DTX1)(Lee et al. 1989).

Species Comparison: *Dinophysis tripos* can be confused with *D. caudata*; some cells of *D. caudata*, bearing a short hypothecal process, can superficially resemble *D. tripos*. However, *D. tripos* can be distinguished by the presence of two posterior projections (Larsen & Moestrup 1992; Steidinger & Tangen 1996).

Habitat and Locality: *D. tripos* is widely distributed in tropical and temperate waters, and occasionally is found in colder regions (Larsen & Moestrup 1992; Taylor et al. 1995; Steidinger & Tangen 1996).

Remarks: Many authors consider *Phalacroma* to be synonymous with *Dinophysis* (Steidinger & Tangen 1996).

Gambierdiscus toxicus

Adachi and Fukuyo, 1979
Plate 20, Figs. 1-6

Species Overview: *Gambierdiscus toxicus* is an armoured, marine, benthic dinoflagellate species. It is a toxic species that was discovered attached to the surface of brown macroalgae in the Gambier Islands, French Polynesia.

Taxonomic Description: Species in this genus are anterio-posteriorly compressed and are observed in apical or antapical view. The epitheca and hypotheca are not noticeably different in size. A distinguishing feature is the shape and size of the apical pore complex (APC)(Fig. 1)(Faust 1992).

Cells of *Gambierdiscus toxicus* are large, round to ellipsoid (Figs. 1,2,4,5), and flattened anterio-posteriorly. The epitheca and hypotheca are nearly equal in height. The cell surface is smooth with numerous deep and dense pores (Figs. 1,3). Thecal plates are very thick. Cells range in size from 24-60 µm in length, 42-140 µm in transdiameter, and 45-150 µm in dorso-ventral depth (Adachi & Fukuyo 1979).

Nomenclatural Types:
Holotype: *Gambierdiscus toxicus* Adachi and Fukuyo, 1979: figs. 1-7
Type Locality: South Pacific Ocean: Gambier Islands, French Polynesia
Synonyms:
Diplopsalis sp. Yasumoto et al., 1977

Thecal Plate Description: The plate formula of *Gambierdiscus toxicus* is: Po, 3', 7", 6c, 8s, 5"', 1p, 2""(Faust 1995). The apical pore plate (Po) is oval to ellipsoidal with a characteristic fishhook shaped apical pore (Figs. 1,3), the opening of which is always oriented ventrally. Apical plate 2' is subrectangular and is the largest of the three apical plates (Figs. 1,6) (Adachi & Fukuyo 1979). The epitheca is slightly indented ventrally (Figs. 1,4). The hypotheca is deeply excavated ventrally (Figs. 2,5,6) (Adachi & Fukuyo 1979; Fukuyo 1981; Taylor 1979).

In the hypotheca the postcingular plate 1"' is triangular; its right corner extrudes, curves inside, and contacts antapical plate 1"" (Figs. 2,6)(Adachi & Fukuyo 1979; Fukuyo 1981). The posterior intercalary plate (1p) is broad and pentagonal (Figs. 2,6). When the marginal zone widens during thecal growth, the 1p plate changes its shape to rhomboid (Fukuyo 1981).

The cingulum is circular, narrow and deeply excavated, and ascends slightly (Adachi & Fukuyo 1979; Bagnis et al. 1979; Taylor 1979). The cingular wall consists of six plates and measures nearly 5 µm in width. It is bordered by a low, thick ridge which is made up of the folding of pre- and postcingular plates (Figs. 1,4)(Adachi & Fukuyo 1979).

The sulcus is short, deeply concave and pouch-like, and is oriented to the right (Figs. 2,5)(Adachi & Fukuyo 1979; Bagnis et al. 1979; Taylor 1979). Along the sulcal margin, an overhanging ridge continues along the edge of postcingular plate 5"', and antapical plates 1"" and 2""(Fig. 2) (Adachi & Fukuyo 1979).

Morphology and Structure: *G. toxicus* is a photosynthetic species with yellow to golden-brown chloroplasts and a large crescent-shaped nucleus (Fig. 5)(Adachi & Fukuyo 1979).

Reproduction: *G. toxicus* reproduces asexually by binary fission.

Ecology: Cells of *G. toxicus* are frequently found as epiphytes on macroalgae and dead coral. Different strains apparently exhibit a preference for certain algae; e.g. the Hawaiian strain prefers the red alga *Spyridia filamentosa* (Shimizu et al. 1982). Cells readily attach to substrates via mucoid strands originating from the sulcal area (Steidinger & Tangen 1996).

Toxicity: *G. toxicus* is known to produce the following toxins: ciguatoxin (Yasumoto et al. 1987; Murata et al. 1990; Yasumoto et al. 1993); gambieric acid (Yasumoto et al. 1993); and maitotoxin (Yasumoto et al. 1977; 1993; Yokoyama et al. 1988).

Species Comparison: This species resembles *Heteraulacus* in tabulation, but differs by its right-handed girdle torsion, large apical closing plate, and a pouch-like sulcal depression (Taylor 1979).

Gambierdiscus toxicus shares a number of characteristics with *G. belizeanus*. They both have the same plate formula, and have similar apical pore, cingulum, sulcus, general cell shape (lenticulate and antero-posteriorly compressed), and golden brown chloroplasts. However, they differ in a number of distinct features. Architecturally, both species have similar epithecal plates, but differ in thecal surface morphology: *G. toxicus* has a smooth surface with scattered fine pores, whereas *G. belizeanus* has a deeply areolated surface. *G. toxicus* is considerably larger than *G. belizeanus*. And plate 1p is broad in *G. toxicus*, whereas it is long and narrow *in G. belizeanus* (Faust 1995).

Etymology: The genus '*Gambierdiscus*' was named after the Gambier Islands from which it was discovered and also the discoid shape of the cell. The species name '*toxicus*' is derived from the toxin-producing nature of this species.

Habitat and Locality: This species was identified from tropical reefs in the Pacific Ocean (Adachi & Fukuyo 1979; Fukuyo 1981), the Indian Ocean (Quod 1994), and the U.S. Virgin Islands (Carlson & Tindall 1985). Populations have been found in tidal pools and lagoons, as well as in colored sand, in the Caribbean (Faust 1995). In the United States, *G. toxicus* has been collected in waters around Hawaii (Taylor 1979; Shimizu et al. 1982) and the Florida Keys (Bergmann & Alam 1981; Besada et al. 1982; Loeblich & Indelicato 1986).

Gonyaulax polygramma

Stein, 1883

Plate 21, Figs. 1-6

Species Overview: *Gonyaulax polygramma* is an armoured, marine planktonic dinoflagellate species. It is a red tide bloom species associated with massive fish and shellfish kills.

Taxonomic Description: Cells of *Gonyaulax polygramma* are medium-sized, elongate and pentagonal (Figs. 1-6). The tapered epitheca bears a prominent apical horn, and exceeds the symmetrical hypotheca (Figs. 1-3). Longitudinal ridges ornament the thecal surface; reticulations are present between the ridges (Figs. 1-3). On mature cells, longitudinal ridges may be thick and spinulous. Cells range in size from 29-66 µm in length and 26-56 µm in dorso-ventral depth (Dodge 1982; Fukuyo et al. 1990; Hallegraeff 1991; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Gonyaulax polygramma* Stein, 1883: pl. 4, figs. 15-16
Type Locality: unknown

Thecal Plate Description: The plate formula for *G. polygramma* is: Po, 3', 2a, 6'', 6c, 4-8s, 6''', 1''''(Dodge 1989). The epitheca is convex to angular, and bears 12 apical plates (Figs. 1-3). The elliptical apical pore plate (Po) does not extend onto the dorsal side of the cell; it is in direct contact with the first apical plate (1'). The 1' plate with a ventral pore (vp). The left-handed cingulum is post-median and displaced about 1.5 times its width without overhanging (Figs. 1,2,4,6). The slightly excavated sulcus widens posteriorly; it invades the epitheca slightly (Figs. 1,6). The hypotheca is truncate with straight sides and consists of six plates; 1-3 antapical spines present (Figs. 1-4,6)(Dodge 1982; Fukuyo et al. 1990; Hallegraeff 1991; Steidinger & Tangen 1996).

Morphology and Structure: *G. polygramma* is a photosynthetic species with chloroplasts. The large oval nucleus is located posteriorly (Dodge 1982).

Reproduction: *G. polygramma* reproduces asexually by binary fission.

Ecology: *G. polygramma* is a planktonic species commonly found in neritic and oceanic waters (Steidinger & Tangen 1996). This cosmopolitan species is a red tide bloom former associated with shellfish and fish kills. Deadly *G. polygramma* red tides have been reported from Florida (Steidinger 1968), Japan (Nishikawa 1901; Fukuyo et al. 1990; Koizumi et al. 1996), New South Wales (Hallegraeff 1991), South Africa (Grindley & Taylor 1964), and Hong Kong (Lam & Yip 1990). During a bloom in Uwajima Bay, Japan, in 1994, cell levels peaked at 6.8 X 10^4 cell/ml and caused mass mortalities of cultured and natural fish and shellfish stocks (Koizumi et al. 1996).

Toxicity: *G. polygramma* is a non-toxin producing species, but as a red tide species, it has been associated with massive fish and invertebrate kills due to anoxia and high sulfide and ammonia levels resulting from cell decomposition (Hallegraeff 1991; Koizumi et al. 1996).

Habitat and Locality: *G. polygramma* is a cosmopolitan species common in cold temperate to tropical waters worldwide (Hallegraeff 1991; Steidinger & Tangen 1996).

Gymnodinium breve

Davis, 1948

Plate 22, Figs. 1-4

Species Overview: *Gymnodinium breve* is an unarmoured, marine, planktonic dinoflagellate species. It is a toxin-producing species associated with red tides in the Gulf of Mexico, off the coast of western Florida.

Taxonomic Description: *Gymnodinium breve* is an athecate species; i.e. without thecal plates. Cells are small and dorso-ventrally flattened (Figs. 1-3). The cell is ventrally concave and dorsally convex. Cells appear almost square in outline, but with a prominent apical process directed ventrally (Figs. 1,3,4). Cells range in size from 20-40 µm in width to 10-15 µm in depth, and are slightly wider than long (Steidinger et al. 1978; Steidinger 1983; Taylor et al. 1995; Steidinger & Tangen 1996).

The epitheca is rounded with a distinctive overhanging apical process (Figs. 1-3). The epitheca is smaller than the hypotheca (Figs. 1-3). The cingulum is displaced in a descending fashion up to 2 times its width. It houses the transverse flagellum. The sulcus extends into the epitheca up to the antapex adjacent to the apical process (Fig. 4). It houses the longitudinal flagellum. An apical groove, present near the distal epithecal end of the sulcus, extends across the apical process onto the dorsal side of the cell (Figs. 1,2). It is not an extension of the sulcus. The wide hypotheca is notched by the sulcus and is slightly bilobed posteriorly (Figs. 1-4). Discharged trichocysts have been observed (Davis 1948; Steidinger et al. 1978; Steidinger 1983; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Gymnodinium breve* Davis, 1948: 358-360, figs. 1,2
Type Locality: Gulf of Mexico: near Naples, Florida, USA
Synonyms:
Ptychodiscus brevis (Davis) Steidinger, 1979

Morphology and Structure: *Gymnodinium breve* is a photosynthetic species with numerous peripheral yellowish-green chloroplasts and multistalked pyrenoids (Figs. 2,3). The large round nucleus is 6-9 µm in diameter and located in the left half of the hypotheca (Figs. 3,4). Lipid globules have also been observed (Fig. 3). This species does not have peridinin as a major accessory pigment (Davis 1948; Steidinger et al. 1978; Steidinger 1983; Taylor et al. 1995; Steidinger & Tangen 1996).

Reproduction: *G. breve* reproduces asexually by binary fission; cells divide obliquely during mitosis. This species also has a sexual cycle: isogamous gamete production, fusion and formation of a planozygote. The planozygote is morphologically similar to the vegetative cell, but larger. The gametes are rounder and slightly smaller than the vegetative cells (18-24 µm in diameter). It is speculated that temperature controls the onset of the sexual cycle since sexual stages only occurred in fall and winter in both field populations and cultures (Walker 1982).

Ecology: *G. breve* is a planktonic oceanic species, though populations have been documented in estuarine systems under bloom conditions. This species is a bloom-former associated with red tides in the Gulf of Mexico, in particular the west coast of Florida. During a bloom cell levels can reach as high as 1 X 10^7 to 1 X 10^8 cells/L. Blooms initiate offshore requiring high salinities (> 30 o/oo) and high temperatures (Steidinger 1975; Steidinger et al. 1978; Steidinger & Tangen 1996).

G. breve cells are active swimmers resembling 'falling leaves as they swim slowly, turning over and over through the water'. This species forms cysts under adverse conditions. Chain formation reported in very dense concentrations (Steidinger & Joyce 1973).

Toxicity: *G. breve* is a known toxic species that produces a series of brevetoxins (neurotoxins) (Baden 1983). These toxins are responsible for massive fill kills along the west coast of Florida in the Gulf of Mexico. Aerosolization of the toxins (noxious air-borne *G. breve* fragments from sea spray) has been linked to asthma-like symptoms in humans (Baden et al. 1982). Brevetoxins produce neurotoxic shellfish poisoning (NSP) when consumed (Hughes 1979). These toxins are known to cause human illness and distress; however, the poison is not fatal: no human fatalities have been reported from consumption of *G. breve*-infected bivalves (Steidinger & Joyce 1973). So far NSP has been restricted to the western coast of Florida, but more recently it has been documented for New Zealand as well (Steidinger et al. 1973; Baden et al. 1982; Taylor et al. 1995).

Habitat and Locality: *Gymnodinium breve* populations are found in warm temperate to tropical waters, most regularly from the Gulf of Mexico, off the west coast of Florida. *G. breve* and *G. breve*-like species have also been reported from the West Atlantic, Spain, Greece, Japan and New Zealand (Fukuyo et al. 1990; Taylor et al. 1995; Steidinger & Tangen 1996).

Gymnodinium catenatum

Graham, 1943

Plate 23, Figs. 1-7

Species Overview: *Gymnodinium catenatum* is an unarmoured, marine, planktonic dinoflagellate species. It is a chain-forming, toxin-producing, red tide species associated with PSP events throughout the world.

Taxonomic Description: *Gymnodinium catenatum* is an athecate species; i.e. without thecal plates. This species is typically seen in chain formation with up to 64 cells. Cells are small with morphology varying between single cell (Fig. 1) and chain formation (Figs. 2-4). Single cells are generally elongate-ovoid with slight dorso-ventral compression (Figs. 1,5). The apex is truncate or slightly conical while the antapex is rounded and notched (Figs. 1,5). Chain formers, in general, are squarish-ovoid with anterior-posterior compression (Fig. 3). A characteristic horseshoe shaped apical groove encircles the apex (Fig. 1)(Graham 1943; Larsen & Moestrup 1989; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Single cells range in size from 27-43 μm in width to 34-65 μm in length. Chain-forming cells are slightly smaller with sizes ranging from 27-43 μm in width to 23-60 μm in length; terminal cells are slightly larger (Figs. 2,3), similar to single cells (Graham 1943; Blackburn et al. 1989; Larsen & Moestrup 1989; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

The epitheca is smaller than the hypotheca, rounded or truncate (Figs. 1,2). In chain-formers, the epitheca is conical (Figs. 2,4). The larger hypotheca tapers slightly posteriorly (Figs. 2,3). It is notched by the sulcus at the antapex creating a bilobed posterior (Fig. 5). The premedian cingulum displays left-handed displacement, about 2 times its width (Figs. 1,2). The transverse flagellum is housed in the deep cingulum (Figs. 1-3). The sulcus is deep and extends almost the full length of the cell: from just beneath the apex to the antapex (Figs. 1-3)(Graham 1943; Larsen & Moestrup 1989; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:

Holotype: *Gymnodinium catenatum* Graham, 1943: 259-262, figs. 1,2

Type Locality: NE Pacific Ocean: Gulf of California, Mexico

Morphology and Structure: *Gymnodinium catenatum* is a photosynthetic species with numerous yellow-brown chloroplasts and conspicuous pyrenoids. The large nucleus is centrally located. Lipid globules are also common (Graham 1943; Larsen & Moestrup 1989; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Reproduction: *G. catenatum* reproduces asexually by binary fission. This species also has a sexual cycle with opposite mating types (heterothallism). After gamete fusion, a planozygote forms, and after two weeks, this form encysts into a characteristic resting cyst (Fig. 6). Nutrient deficiency induces the sexual phase (Blackburn et al. 1989).

Ecology: *G. catenatum* is a planktonic red tide species. The first *G. catenatum* red tide was reported from the Gulf of California with populations close to 1 X 10^6 cells/L (Graham 1943). Populations of this species have been recorded from Mexico (Mee et al. 1986), Japan (Ikeda et al. 1989), Australia (Hallegraeff et al. 1988; 1989), Venezuela (La Barbera-Sanchez et al. 1993), the Philippines (Fukuyo et al. 1993) and Europe (Estrada et al. 1984; Franca & Almeida 1989; Giacobbe et al. 1995).

G. catenatum produces a characteristic resting cyst (Fig. 6). Cysts are 42-52 μm in diameter, spherical and brown. They have a very distinct morphology: the surface is covered with microreticulate ornamentations. These cysts can germinate after just two weeks of dormancy and initiate new populations (Blackburn et al. 1989).

Cysts are not only a reseeding tool, but also a disbursement agent: *G. catenatum* was introduced to Australian waters via ships' ballast water (Hallegraeff & Bolch 1991).

Toxicity: *G. catenatum* is a known paralytic shellfish poison (PSP) toxin producer (Morey-Gaines 1982; Mee et al. 1986). This species is the only unarmoured dinoflagellate known to produce PSP toxins (Taylor et al. 1995). First reports of PSP associated with *G. catenatum* blooms were recorded in Spain (Estrada et al. 1984).

Species Comparison: *Gymnodinium catenatum* can readily be distinguished from other *Gymnodinium* species by its long chain formations, however, single cells can easily be misidentified. Chains of *G. catenatum* can resemble *Alexandrium catenella*, an anterio-posteriorly compressed species that forms short-chains, however, this species is a cold-water species and is armoured. Chains of *G. catenatum* can also be confused with *Peridiniella catenata*, another armoured chain-forming species. The latter species, however, is not toxic, is a cold-water species and has posterior spines (Larsen & Moestrup 1989; Hallegraeff 1991; Taylor et al. 1995).

Gyrodinium impudicum, recently described from Spain, can superficially resemble *Gymnodinium catenatum* with its similar horseshoe shaped apical groove and its tendency toward chain formation. However, *Gyrodinium impudicum* is smaller in size, differs in shape, forms shorter chains and is not associated with PSP (Fraga et al. 1995).

Habitat and Locality: *G. catenatum* populations are found in warm, temperate coastal waters. Blooms have been reported in Mexico, Argentina, Europe, Australia and Japan (Hallegraeff 1991).

Gymnodinium mikimotoi
Miyake et Kominami ex Oda, 1935
Plate 24, Figs. 1-7

Species Overview: *Gymnodinium mikimotoi* is an unarmoured, marine, planktonic dinoflagellate species. It is a common red tide former in Japan and Korea associated with massive fish kills.

Taxonomic Description: *Gymnodinium mikimotoi* is an athecate species; i.e. without thecal plates. Cells are small, broadly oval to almost round (Figs. 1,2) and compressed dorso-ventrally (Figs. 3,4). Cells are slightly longer than wide with a characteristic long and straight apical groove to the right of the sulcal axis (Figs. 1-3). The apical groove extends from the ventral side to the dorsal side of the epitheca (Fig. 3) creating a slight indentation at the apex of the cell (Fig. 2). Cells range in size from 18-40 µm in length to 14-35 µm in width (Takayama & Adachi 1984; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

The epitheca is broadly rounded and smaller than the hypotheca (Figs. 1,2). The hypotheca is notched by the widening sulcus at the antapex resulting in a lobed posterior (Figs. 1,2). The wide and deeply excavated cingulum is pre-median, and is displaced in a descending spiral about 2 times its width (Figs. 1,5). The sulcus slightly invades the epitheca extending from above the cingulum to the antapex (Figs. 1,5)(Takayama & Adachi 1984; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Gymnodinium mikimotoi* Oda, 1935: 35-48, figs. 1-3
Type Locality: NW Pacific Ocean: Gokasho Bay, Japan
Synonyms:
Gymnodinium nagasakiense Takayama and Adachi, 1984
Gyrodinium aureolum Hulburt, sensu Braarud and Heimdal, 1970

Morphology and Structure: *G. mikimotoi* is a photosynthetic species with several oval to round yellow-brown chloroplasts, each with a pyrenoid. The large ellipsoidal nucleus is located in the left hypothecal lobe (Fig. 6)(Takayama & Adachi 1984; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Reproduction: *G. mikimotoi* reproduces asexually by binary fission; cells divide obliquely during mitosis (Fig. 7)(Yamaguchi & Honjo 1990).

Ecology: *G. mikimotoi* is a planktonic species first described from western Japan (Oda 1935). This species is a recurring bloom former in coastal waters of Japan and Korea; red tides commonly occur in warmer months and are associated with massive fish and shellfish kills (Takayama & Adachi 1984). Reported to be eurythermal and euryhaline, populations of *G. mikimotoi* could presumably over-winter as motile cells, which could then serve as seed populations for a summer red tide (Yamaguchi & Honjo 1989). Moreover, studies conducted in Omura Bay, Japan, revealed that this species can tolerate anoxic or near anoxic conditions utilizing sulfide from the sediment (Iizuka 1972).

Cells have a distinct swimming pattern: turning over through water, like a falling leaf (Takayama & Adachi 1984).

Toxicity: *G. mikimotoi* is a toxic species associated with massive kills of benthic invertebrates and of both wild and farmed fishes in coastal waters off Japan and Korea; e.g. in 1933 pearl oyster mortalities near Nagasaki, Japan, resulted in an economic loss of $7 million (Oda 1935). For decades red tides of *G. mikimotoi* have resulted in devastating marine life mortalities, yet the toxin mechanism and principles are poorly understood. Research indicates that this species produces hemolytic and ichthyotoxic substances (Hallegraeff 1991; Taylor et al. 1995). Recently, Seki et al. (1996) extracted a lipid-soluble toxin, gymnodimine, from shellfish in Southland, NZ (dubbed 'Southland toxin') after a *Gymnodinium* cf. *mikimotoi* red tide event. This toxin produced a quick kill in both mice and fish, but was less toxic than brevetoxins. No reported human illnesses have resulted from consumption of fish or shellfish from bloom affected areas (Hallegraeff 1991).

Species Comparison: *G. mikimotoi* resembles *G. breve*: both species are dorso-ventrally flattened and their nucleus is located in the left half of the hypotheca. However, these species differ in several features: *G. mikimotoi* does not have an apical process; *G. breve* cells are flatter (dorso-ventral compression is greater); and the sulcal invasion of the epitheca is deeper in *G. breve* (Takayama & Adachi 1984).

The Pacific *Gymnodinium mikimotoi* and the European *Gyrodinium aureolum* are morphologically similar and have been in a state of taxonomic turmoil for over 20 years (Takayama et al. 1998). They are generally regarded as conspecific, although genetic differences between the two populations do exist (Partensky et al. 1988). Controversy, therefore, still remains over the taxonomic status of the Pacific and European populations.

Recently, Takayama et al. (1998) conducted an extensive taxonomic study on the morphological differences between the Pacific *Gymnodinium mikimotoi* and the European *Gyrodinium aureolum*. There were several morphological differences reported, namely swimming behavior, cell thickness, and shape and position of nucleus: cells of *G. aureolum* are thicker; the nucleus of *G. aureolum* is spherical and central, while that of *G. mikimotoi* is longitudinally elliptical and located in the left lobe of the hypotheca.

Habitat and Locality: *G. mikimotoi* is a cosmopolitan species commonly found in temperate to tropical neritic waters. Blooms have been reported from Australia, Denmark, Ireland, Japan, Korea, Norway and Scotland (Taylor et al. 1995; Steidinger & Tangen 1996).

Gymnodinium pulchellum
Larsen, 1994
Plate 25, Figs. 1-6

Species Overview: *Gymnodinium pulchellum* is an unarmoured, marine, planktonic dinoflagellate species. This species produces red tide blooms and has been associated with fish and invertebrate kills in Japan and Florida.

Taxonomic Description: *Gymnodinium pulchellum* is an athecate species; i.e. without thecal plates. Cells are small and broadly oval with slight dorso-ventral compression (Figs. 1-5). The ventral surface is flattened; the dorsal surface is rounded. A conspicuous and well-defined sigmoid apical groove is present on the epitheca (Figs. 1,2); the groove is a characteristic reversed S-shape (Fig. 2). Cells range in size from 16-25 µm in length to 11-16 µm in width (Fukuyo et al. 1990; Larsen 1994; Taylor et al. 1995; Steidinger & Tangen 1996; Steidinger et al. 1998).

The epitheca is slightly smaller than the hypotheca. The wide and deeply excavated cingulum is premedian, and is displaced in a descending fashion 1-1.5 times its width (Figs. 1,3,6). The sulcus slightly invades the epitheca as a finger-like projection (Fig. 2). The sulcus widens and deepens towards the posterior of the cell creating a bilobed hypotheca (Figs. 1,3,4)(Larsen 1994; Taylor et al. 1995; Steidinger & Tangen 1996; Steidinger et al. 1998).

Nomenclatural Types:
Holotype: *Gymnodinium pulchellum* Larsen, 1994: 32, fig. 58
Type Locality: Tasman Sea: Hobsons Bay, Melbourne, Australia
Synonyms:
Gymnodinium type '84-K Onoue et al., 1985

Morphology and Structure: *G. pulchellum* is a photosynthetic species with several yellowish-brown chloroplasts. Pyrenoids are also present (Figs. 3,4). The large nucleus is ellipsoidal and located in the left central part of the cell (Figs. 5,6)(Fukuyo et al. 1990; Larsen 1994; Steidinger & Tangen 1996; Steidinger et al. 1998).

Reproduction: *G. pulchellum* reproduces asexually by binary fission.

Ecology: *G. pulchellum* is a planktonic species first described from southeastern Australia. This species is a bloom-former associated with extensive fish and invertebrate kills in southeast Florida. During one red tide event waters turned an orange-red color with cell levels recorded as high as 19.7 X 10^6 cells/L (Steidinger et al. 1998).

Toxicity: *G. pulchellum* is a toxic species associated with fish and invertebrate kills from southeast Florida. The presence of this species at two separate fish kills in the Indian River, FL, suggests it is ichthyotoxic (Steidinger et al. 1998). Onoue et al. (1985) demonstrated that *G. pulchellum* (as *Gymnodinium* type '84-K) is ichthyotoxic. Three toxic fractions have been isolated from this species: neurotoxic, hemolytic and hemaglutinative (Onoue & Nozawa 1989). *G. pulchellum* is most likely responsible for fish kills in the Melbourne, Australia, region (Larsen 1994).

Species Comparison: Sharing the same habitat and locale, and the same general shape, *G. pulchellum* can be confused with *G. mikimotoi*. *G. pulchellum*, however, is smaller in size and has a distinctive sigmoid apical groove; the apical groove of *G. mikimotoi* is straight (Larsen 1994).

Etymology: The name '*pulchellum*' originates from the Latin word pulchellus, 'beautiful little' (Larsen 1994).

Habitat and Locality: This species is found in temperate to tropical neritic waters. It has been reported from Hobsons Bay (Melbourne area), Australia, where it is often common during the austral summer and early autumn (Larsen 1994). It has also been recorded from Tasmanian waters (Hallegraeff 1991), Japanese waters (Fukuyo et al. 1990; Onoue et al. 1985; Takayama 1985) and from the Mediterranean (Carrada et al. 1991). More recently it has been identified in the western Atlantic off the east coast of Florida (Steidinger et al. 1998). Due to its minute size, *G. pulchellum* may have been greatly overlooked in phytoplankton assessments.

Gymnodinium sanguineum

Hirasaka, 1922

Plate 26, Figs. 1-4

Species Overview: *Gymnodinium sanguineum* is an unarmoured, marine, planktonic dinoflagellate species. This cosmopolitan species is a red tide former that has been associated with fish and shellfish mortality events.

Taxonomic Description: *Gymnodinium sanguineum* is an athecate species; i.e. without thecal plates. This species is highly variable in size and shape. Cells are large, slightly dorso-ventrally flattened and roughly pentagonal (Figs. 1-3). An apical groove is present (Fig. 2). Cells range in size from 40-80 µm in length (Hirasaka 1922; Lebour 1925; Dodge 1982; Fukuyo et al.

1990; Hallegraeff 1991; Steidinger & Tangen 1996).

The epitheca and hypotheca are nearly equal in size. The epitheca is rounded and conical, and the hypotheca is deeply indented by the sulcus creating two posterior lobes (Figs. 1,2). The median cingulum is left-handed and displaced 1-2 times its width (Figs. 2,4). The sulcus does not invade the epitheca, but expands posteriorly into the hypotheca (Hirasaka 1922; Lebour 1925; Dodge 1982; Fukuyo et al. 1990; Steidinger Tangen 1996).

Nomenclatural Types:
Holotype: *Gymnodinium sanguineum* Hirasaka, 1922:161-164, fig.1
Type Locality: NW Pacific Ocean: Kozusa-ura, Gokasho Bay, Japan
Synonyms:
Gymnodinium splendens Lebour, 1925
Gymnodinium nelsonii Martin, 1929

Morphology and Structure: *G. sanguineum* has numerous large, spindle-shaped, reddish-yellow-brown chloroplasts radiating from the center of the cell (Fig. 4). The large nucleus is slightly off-center (Figs. 3,4). Cells can vary from heavily pigmented to pale yellow or nearly colorless (Hirasaka 1922; Lebour 1925; Dodge 1982; Fukuyo et al. 1990; Steidinger & Tangen 1996). Mixotrophy has been observed for this species: in the Chesapeake Bay *G. sanguineum* preys on ciliate protozooplankton (Bockstahler & Coats 1993).

Reproduction: *G. sanguineum* reproduces asexually by binary fission; cells divide obliquely during mitosis (Dodge 1982).

Ecology: *G. sanguineum* is a planktonic species common in estuarine and coastal waters. This cosmopolitan species is a bloom-former associated with shellfish and fish kills. The first *G. sanguineum* red tide was reported from Kozusa-ura, Gokasho Bay, Japan (Hirasaka 1922). Red tide events caused by this species have since been recorded from other coastal regions of Japan (Fukuyo et al. 1990). It is a common red tide bloom species in Australian and New Zealand coastal waters as well (Hallegraeff 1991). *G. sanguineum* is a common red tide species in the Chesapeake Bay where levels as high as 8.8 X 10^5 cells/L have been reported (Bockstahler & Coats 1993). One bloom in Coyote Bay, Gulf of California, Mexico, cell densities reached 1.0 X 10^5 cells/L (Keifer & Lasker 1975).

Robinson and Brown (1983) and Voltolina (1993) observed possible sexual stages of *G. sanguineum* from a recurrent bloom. They speculate that this species may form resting cysts to reseed a region in the next bloom season.

Nakamura et al. (1982) reported that cultures of *G. sanguineum* can tolerate a wide range of temperatures (13-24 °C) and salinities (15-35 o/oo).

Toxicity: *G. sanguineum* is a red tide species associated with fish and invertebrate kills. Cardwell et al. (1979) reported the acute toxicity of this species to larval stages of two species of oysters in Puget Sound, Washington State. And *G. sanguineum* is believed to be responsible for at least one reported fish mortality event in Peru (Jordan 1979).

Tindall et al. (1984) and Carlson and Tindall (1985) demonstrated one isolate of this species to be potentially toxic; however, the toxin principles have yet to be elucidated.

Etymology: The name '*sanguineum*' originates from the Latin word for blood describing the resulting color of the water after a red tide event of this species (Hirasaka 1922).

Habitat and Locality: *G. sanguineum* is commonly found in temperate to tropical neritic waters (Steidinger & Tangen 1996). Blooms have been recorded from Japan (Hirasaka 1922; Fukuyo et al. 1990), Australia and New Zealand (Hallegraeff 1991), and from the Atlantic and Pacific American coasts (Keifer & Lasker 1975; Robinson & Brown 1983; Bockstahler & Coats 1993; Voltolina 1993).

Gymnodinium veneficum

Ballantine, 1956

Plate 27, Figs. 1-3

Species Overview: *Gymnodinium veneficum* is an unarmoured, marine, planktonic dinoflagellate species. This small species has been associated with fish and shellfish mortality events.

Taxonomic Description: *Gymnodinium veneficum* is an athecate species; i.e. without thecal plates. Cells are small and ovoid without dorso-ventral compression (Figs. 1-3). Cells range in size from 9-18 µm in length to 7-14 µm in width (Ballantine 1956; Dodge 1982; Taylor et al. 1995).

The epitheca and hypotheca are equal in size. The cell's anterior end is slightly pointed; the epitheca is without an apical groove (Fig. 1). The hypotheca is rounded with a slight indentation at its posterior end (Fig. 2). The deep cingulum is displaced in a descending spiral 1-2 times its width (Figs. 1,3). The sigmoid sulcus slightly invades the epitheca (Figs. 1,3) (Ballantine 1956; Dodge 1982; Taylor et al. 1995).

Nomenclatural Types:
Holotype: *Gymnodinium veneficum* Ballantine, 1956: 468-474, figs. 6-17
Type Locality: English Channel: off King William Point, Devonport, United Kingdom
Synonyms:
Gymnodinium vitiligo Ballantine, 1956

Morphology and Structure: *G. veneficum* is a photosynthetic species and usually has four irregularly shaped, golden-brown chloroplasts with pyrenoids; occasionally two to eight are present. The large round nucleus is centrally located (Figs. 2,3)(Ballantine 1956; Dodge 1982; Taylor et al. 1995).

Reproduction: *G. veneficum* reproduces asexually by binary fission; cells divide obliquely during mitosis (Ballantine 1956).

Ecology: *G. veneficum* is a planktonic species described from the English Channel (Ballantine 1956).

Toxicity: *G. veneficum* is a known toxic species; it produces an exotoxin lethal to a wide variety of invertebrates and fish (Ballantine 1956; Abbott & Ballantine 1957; Dodge 1982).

Species Comparison: In general cell shape and size, *G. veneficum* can easily be mistaken for *G. micrum*, a non-toxic species. However, the former species usually has four chloroplasts present and is toxic to invertebrates and fish (Taylor et al. 1995).

Habitat and Locality: *G. veneficum* was described from the English Channel. It may be a wide-spread species, but due to its minute size, it most likely has been greatly overlooked in phytoplankton assessments (Ballantine 1956; Dodge 1982).

Gyrodinium galatheanum
(Braarud) Taylor, 1992
Plate 28, Figs. 1-4

Species Overview: *Gyrodinium galatheanum* is an unarmoured, marine, planktonic dinoflagellate species. It is a common red tide former discovered in Walvis Bay, South Africa, associated with fish kills.

Taxonomic Description: *Gyrodinium galatheanum* is an athecate species; i.e. without thecal plates. Cells are small and oval to round in ventral view (Figs. 1-3). A well-defined apical groove is present ventrally on the anterior of the cell (Figs. 1,2,4). The apical groove can produce a slight indentation at the apex (Fig. 1). Cells range in size from 9-17 µm in length to 8-14 µm in width (Braarud 1957; Taylor et al. 1995; Steidinger & Tangen 1996).

The epitheca and hypotheca are both round (Figs. 1-3). The cingulum is displaced in a descending fashion up to 3 times its width (Figs. 1,2,4). The broad cingulum is deeply excavated and houses the transverse flagellum (Figs. 1-3). The short and narrow sulcus slightly invades the epitheca adjacent to the apical groove (Figs. 1,2,4)(Braarud 1957; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Gymnodinium galatheanum* Braarud, 1957: 137-138, fig. 1a-e
Type Locality: South Atlantic Ocean: Walvis Bay, South Africa
Synonyms:
Gymnodinium micrum (Leadbeater et Dodge) Loeblich, III
Woloszynskia micra Leadbeater and Dodge, 1966

Basionym: *Gymnodinium galatheanum* Braarud, 1957

Morphology and Structure: *G. galatheanum* is a photosynthetic species with several round chloroplasts. The large nucleus is round and centrally located (Figs. 3,4). This species does not have peridinin as a major accessory pigment, but has a fucoxanthin derivative and chlorophyll c3 (Braarud 1957; Bjornland & Tangen 1979; Johnsen & Sakshaug 1993; Taylor et al. 1995; Steidinger & Tangen 1996).

Reproduction: *G. galatheanum* reproduces asexually by binary fission.

Ecology: *G. galatheanum* is a bloom-forming planktonic species. Blooms of this species were first recorded from Walvis Bay, South Africa (Braarud 1957). Blooms have since been reported from the Oslofjord, Norway (Bjornland & Tangen 1979) and along the southern coast of Norway (Dahl & Yndestad 1985).

Li et al. (2000) recently observed mixotrophic behaviour in *G. galatheanum* from the Chesapeake Bay. This species was observed to feed on cryptophytes under light and/or nutrient stressed conditions suggesting that this primarily photosynthetic species uses phagotrophy during nutrient-replete conditions to furnish major nutrients necessary for photosynthesis.

Toxicity: *G. galatheanum* is a toxic species associated with fish kills in Walvis Bay, South Africa (Braarud 1957; Steemann Nielsen & Aabye Jensen 1957; Pieterse & Van Der Post 1967). Although this species has been linked to marine life mortalities, mussels and juvenile cod (Nielsen & Stromgren 1991; Nielsen 1993), the toxin principles have yet to be determined (Copenhagen 1953; Pieterse & Van Der Post 1967).

Species Comparison: In shape and size *Gyrodinium galatheanum* resembles two small athecate gymnodinoids, *Gymnodinium veneficum* and *G. micrum* (Taylor et al. 1995). Physiologically *Gyrodinium galatheanum* is closely related to the toxic species *Gyrodinium aureolum*. Both lack peridinin while both have chlorophyll c3, which is characteristic of several bloom-forming prymnesiophytes (Johnsen & Sakshaug 1993).

Habitat and Locality: This species has been reported from cold waters in the North and South Atlantic Oceans: North Sea, British Isles (Larsen & Moestrup 1989); Oslofjord, Norway (Bjornland & Tangen 1979); and Walvis Bay, South Africa (Braarud 1957). *G. galatheanum* may be a wide-spread species but due to its minute size, it most likely has been greatly overlooked in phytoplankton assessments (Taylor et al. 1995).

Lingulodinium polyedrum
(Stein) Dodge, 1989
Plate 29, Figs. 1-6

Species Overview: *Lingulodinium polyedrum* is an armoured, marine, bioluminescent dinoflagellate species. This warm-water species is a red tide former that has been associated with fish and shellfish mortality events.

Taxonomic Description: Cells of *Lingulodinium polyedrum* are angular, roughly pentagonal and polyhedral-shaped (Fig. 1). Cells range in size from 40-54 µm in length and 37-53 µm in transdiameter width. No apical horn or antapical spines present (Fig. 1). Thecal plates are thick, well defined, and coarsely areolate. Distinct ridges are present along the plate sutures (Figs. 1,2). Numerous large trichocyst pores are present within areolae (Fig. 3)(Kofoid 1911; Dodge 1985; 1989 Lewis & Burton 1988; Fukuyo et al. 1990; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Gonyaulax polyedra* Stein, 1883: p. 13, pl. 4, figs. 7-9
Type Locality: unknown
Synonyms:
Gonyaulax polyedra Stein, 1883
Lingulodinium machaerophorum (Deflandre and Cookson) Wall, 1967 (cyst)
Hystrichosphaeridium machaerophorum Deflandre and Cookson, 1955 (cyst)

Thecal Plate Description: The plate formula for *L. polyedrum* is: Po, 3', 3a, 6'', 6c, 7s, 6''', 2''''. The epitheca bears shoulders, nearly straight sides, and an off-center apex which is flattened or slightly pointed (Figs. 1,4). The apical pore plate (Po) contains a raised inner elliptical ridge (Fig. 2). The first apical plate (1') is long and narrow, comes in direct contact with the Po, and bears a ventral pore on its right side (Figs. 1,2,4). The deeply excavated cingulum is nearly equatorial, and displaced one to two times its width. It is descending with narrow ribbed lists (Figs. 1,2,4). The deep sulcus invades the epitheca slightly and widens posteriorly. The hypotheca has straight sides and a truncated antapex (Figs. 1,2,4)(Kofoid 1911; Dodge 1985; Dodge 1989; Lewis & Burton 1988; Fukuyo et al. 1990; Steidinger & Tangen 1996).

Morphology and Structure: *L. polyedrum* is a photosynthetic species with dark orange-brown chloroplasts. The unusual carotenoid, peridinin, is present in the chloroplasts. Also present is a pusule, a C-shaped nucleus, and scintillons (light-emitting organelles)(Kofoid 1911; Schmitter 1971; Jeffrey et al. 1975).

Reproduction: *L. polyedrum* reproduces asexually by binary fission. Sexual reproduction is also part of the life cycle of this species producing spherical spiny cysts.

Ecology: *L. polyedrum* is a bioluminescent planktonic species commonly found in neritic waters. It is responsible for magnificent displays of phosphorescence at night in warm coastal waters (Kofoid 1911). This warm-water species is a red tide former that has been associated with fish and shellfish mortality events. Deadly red tides have been reported from southern California (San Diego region)(Kofoid 1911; Allen 1921), as well as in the Adriatic Sea (Italy and Yugoslavia) where cell levels as high as 2 X 10^7 cells/L have been reported (Marasovic 1989; Bruno et al. 1990).

This species forms colorless spherical spiny cysts (35-50 μm in diameter). The numerous tapering spines can reach up to 17 μm in length, all bearing spinules on their distal ends (Figs. 5,6) (Kofoid 1911; Dodge 1985; 1989; Fukuyo et al. 1990). The cyst of this species is able to fossilize (found in fossil deposits all the way back to the late Cretaceous period): the hystrichosphere (fossilized dinoflagellate cyst) *Lingulodinium machaerophorum* (Deflandre and Cookson) Wall, 1967 was discovered to be the resting spore of *L. polyedrum* (Wall 1967; Fensome et al. 1993).

Marasovic (1989) reported production of temporary resting cysts in a waning red tide dominated by *L. polyedrum* in the Adriatic Sea (Yugoslavia). Near the end of a bloom, the population produced temporary cysts and remained in the plankton. Once environmental conditions were favorable again, the cysts were able to re-seed the area, and thus initiate another red tide event.

Toxicity: Bruno et al. (1990) reported the presence of a paralytic shellfish poison (PSP) toxin, saxitoxin, in water samples taken during a bloom of *L. polyedrum*.

Habitat and Locality: *L. polyedrum* is a widely distributed species found in warm temperate and subtropical waters of coastal areas (Kofoid 1911; Dodge 1985; 1989; Steidinger & Tangen 1996).

Noctiluca scintillans
(Macartney) Kofoid et Swezy, 1921
Plate 30, Figs. 1-4

Species Overview: *Noctiluca scintillans* is an unarmoured, marine planktonic dinoflagellate species. This large and distinctive bloom forming species has been associated with fish and marine invertebrate mortality events.

Taxonomic Description: *Noctiluca scintillans* is a distinctively shaped athecate species in which the cell is not divided into epitheca and hypotheca. Cells are very large, inflated (balloon-like) and subspherical (Figs. 1-4). The ventral groove is deep and wide, and houses a flagellum, a tooth and a tentacle (Figs. 1,2,4). Only one flagellum is present in this species and is equivalent to the transverse flagellum in other dinoflagellates (Fig. 1). The tooth is a specialized extension of the cell wall (Fig. 4). The prominent tentacle is striated and extends posteriorly (Fig. 4). Cells have a wide range in size: from 200-2000 μm in diameter (Zingmark 1970; Dodge 1973; Dodge 1982; Lucas 1982; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Medusa scintillins* Macartney, 1810: 264-265, pl. 15, figs. 9-12
Type Locality: North Sea: Herne Bay, Kent, England
Synonyms:
Medusa scintillins Macartney, 1810
Noctiluca miliaris Suriray, 1836

Morphology and Structure: *Noctiluca scintillans* is a nonphotosynthetic heterotrophic and phagotrophic dinoflagellate species; chloroplasts are absent and the cytoplasm is mostly colorless (Figs. 1,2). The presence of photosynthetic symbionts can cause the cytoplasm to appear pink or green in color (Sweeney 1978). A number of food vacuoles are present within the cytoplasm. A large eukaryotic nucleus is located near the ventral groove with cytoplasmic strands extending from it to the edge of the cell (Fig. 2)(Zingmark 1970; Dodge 1982; Fukuyo et al. 1990; Hallegraeff 1991; Steidinger & Tangen 1996).

Reproduction: *Noctiluca scintillans* reproduces asexually by binary fission (Fig. 3) and also sexually via formation of isogametes. This species has a diplontic life cycle: the vegetative cell is diploid while the gametes are haploid. The gametes are gymnodinioid with dinokaryotic nuclei (Zingmark 1970).

Ecology: *Noctiluca scintillans* is a strongly buoyant planktonic species common in neritic and coastal regions of the world. It is also bioluminescent in some parts of the world.

This bloom-forming species is associated with fish and marine invertebrate mortality events. *N. scintillans* red tides frequently form in spring to summer in many parts of the world often resulting in a strong pinkish red or orange discoloration of the water (tomato-soup). Blooms have been reported from Australia (Hallegraeff 1991), Japan, Hong Kong and China (Huang & Qi 1997) where the water is discolored red. Recent blooms in New Zealand were reported pink with cell concentrations as high as 1.9 X 10^6 cells/L (Chang 2000). In Indonesia, Malaysia, and Thailand (tropical regions), however, the watercolor is green due to the presence of green prasinophyte endosymbionts (Sweeney 1978; Dodge 1982; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

This large cosmopolitan species is phagotrophic, feeding on phytoplankton (mainly diatoms and other dinoflagellates), protozoans, detritus, and fish eggs (Fig. 2)(Dodge 1982; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Toxicity: Toxic blooms of *N. scintillans* have been linked to massive fish and marine invertebrate kills. Although this species does not produce a toxin, it has been found to accumulate toxic levels of ammonia which is then excreted into the surrounding waters possibly acting as the killing agent in blooms (Okaichi & Nishio 1976; Fukuyo et al. 1990). Extensive toxic blooms have been reported off the east and west coasts of India, where it has been implicated in the decline of fisheries (Aiyar 1936; Bhimachar & George 1950).

Habitat and Locality: *Noctiluca scintillans* is a cosmopolitan species distributed world wide in cold and warm waters. Populations are commonly found in coastal areas and embayments of tropical and subtropical regions (Dodge 1982; Fukuyo et al. 1990; Hallegraeff 1991; Taylor et al. 1995; Steidinger & Tangen 1996).

Remarks: This species is frequently referred to as *N. miliaris* although Macartney's specific name has priority. Taylor (1976) suggests that the simplest solution to the problem of nomenclature is to accept the priority of the '*scintillans*' especially as this has been used by two major works (Kofoid & Swezy 1921; Lebour 1925).

Ostreopsis heptagona

Norris, Bomber et Balech, 1985

Plate 31, Figs. 1-6

Species Overview: *Ostreopsis heptagona* is an armoured, marine, benthic dinoflagellate species. It was discovered in the Florida Keys.

Taxonomic Description: Species in this genus are anterio-posteriorly compressed and are observed in apical or antapical view. The epitheca and hypotheca are not noticeably different in size. Unique features of this genus are on the cingulum. In ventral view the cingulum reveals two prominent structures: a ventral plate (Vp) with a ventral pore (Vo), and an adjacent curved rigid plate (Rp). The distinguishing feature at the species level is the shape of the first apical plate (1') on the epitheca (Fig. 1)(Faust et al. 1996).

Cells of *Ostreopsis heptagona* are large, broadly oval, oblong and pointed (Figs. 1-2). Thecal surface is smooth with scattered small round pores (diam.=0.3 µm) that can only be observed at the SEM level (Figs. 1,2). Cells have a dorsoventral diameter of 80-108 µm, and a transdiameter of 46-59 µm (Faust et al. 1996).

Nomenclatural Types:
Iconotype: *Ostreopsis heptagona* Norris, Bomber and Balech, 1985: fig. 1
Type Locality: Gulf of Mexico: Knight Key, Florida, USA

Thecal Plate Description: The plate formula of *Ostreopsis heptagona* is: Po, 3', 7", 6c, 6s?, Vp, Rp, 5"', 1p, 2""(Fig. 5). The epitheca contains 11 plates. The apical pore plate (Po) is 15 µm long, narrow and curved (Figs. 1,3), situated between apical plates 1', 2' and 3', with a long, slit-like apical pore. The 1' plate, the distinguishing plate for this species, is large and irregularly heptagonal (seven-sided)(Figs. 1,5). The hypotheca has eight plates. The posterior intercalary plate (1p) is one of the most characteristic plates of *O. heptagona*; it is long and narrows dorsally, extending along the dorso-ventral axis (Figs. 2,5)(Faust et al. 1996; Norris et al. 1985).

The cingulum is equatorial and narrow (Figs. 1-3). Within the cingulum the Vo is situated on the Vp, adjacent to the Rp (Fig. 4)(Faust et al. 1996). Norris et al. (1985) identified 5 sulcal plates and a transitional plate (t) in this species.

Morphology and Structure: *Ostreopsis heptagona* is a photosynthetic species. Mixotrophy has been documented in other specis of this genus with the Vo as the proposed feeding apparatus (Faust et al. 1996).

Reproduction: Cells of *O. heptagona* reproduce asexually by binary fission.

Ecology: Cells of *O. heptagona* are frequently found as epiphytes on macroalgae in the Caribbean (Morton & Faust 1997). Live cells exhibit an unusual jerky swimming motion and a strong positive geotropic tendency. Cells almost immediately attach to the nearest substrate. Cells attach tenaciously by a network of mucilage strands (Fig. 3) which are expelled by thecal pores (Norris et al. 1985).

Toxicity: This species was determined to be toxic (J. Babinchak, according to Norris et al. 1985).

Species Comparisons: *Ostreopsis heptagona* is distinguished by two major features: a) an irregulary-shaped asymmetric heptagonal (seven-sided) 1' plate that occupies the left center of the epitheca (this plate is hexagonal, six-sided, in all other species of this genus) (Faust et al. 1996; Steidinger & Tangen 1996); and b) the pentagonal and dorso-ventrally elongate 1p plate in the hypotheca (Faust et al. 1996).

In *O. heptagona* plate 5" is pentagonal as it contacts plates 1', 3' and 6", and plate 6" is quadrangular and does not touch 3'. In both *O. siamensis* and *O. ovata* plate 5" is quadrangular and does not touch 1', while 6" is hexagonal and contacts two apical plates, 1' and 3'. Plate 1p in *O. heptagona* is rather narrow, and is always curved, concave to the left and gradually narrows dorsally (Faust et al. 1996). Plate 1p in *O. siamensis* is also narrow, but maintains nearly the same width throughout its length. This plate is different in *O. ovata*: 1p is comparatively wider and shorter, and widens dorsally (Norris et al. 1985).

Etymology: The name *'heptagona'* refers to the distinct seven-sided shape of the first apical plate of this species.

Habitat and Locality: Populations of *O. heptagona* have been reported as epiphytic on macroalgae in the Caribbean Sea (Morton & Faust 1997), and found in the plankton in the Florida Keys (Steidinger & Tangen 1996). Maximum densities were reported for *O. heptagona* associated with *Dictyota dichotoma* (Bomber 1985) and *Acanthophora spicifera* (Morton & Faust 1997).

Ostreopsis lenticularis
Fukuyo, 1981
Plate 32, Figs. 1-8

Species Overview: *Ostreopsis lenticularis* is an armoured, marine, benthic dinoflagellate species. It was discovered as an epiphyte on macroalgae in the Gambier and Society Islands of French Polynesia, and New Caledonia, Pacific Ocean.

Taxonomic Description: Species in this genus are anterio-posteriorly compressed and are observed in apical or antapical view. The epitheca and hypotheca are not noticeably different in size. Unique features of this genus are on the cingulum. In ventral view the cingulum reveals two prominent structures: a ventral plate (Vp) with a ventral pore (Vo), and an adjacent curved rigid plate (Rp). The distinguishing feature at the species level is the shape of the first apical plate (1') on the epitheca (Fig. 1)(Faust et al. 1996).

Cells of *Ostreopsis lenticularis* are lenticulate to broadly oval (Figs. 1,2). The cell surface is smooth and covered with randomly spaced pores (0.4 µm diameter) with smooth raised edges (Figs. 1-4); the pores are large and round (Fig. 3). Cells have a dorso-ventral diameter of 65-75 µm and a transdiameter of 57-63 µm (Faust et al. 1996; Fukuyo 1981).

Nomenclatural Types:
Holotype: *Ostreopsis lenticularis* Fukuyo, 1981: figs. 30-34
Type Locality: South Pacific Ocean: Gambier and Society Islands, and New Caledonia

Thecal Plate Description: The plate formula of *Ostreopsis lenticularis* is: Po, 3', 7'', 6c, 6s?, Vp, Rp, 5''', 1p, 2''''(Fig. 6). The epitheca contains 11 plates. The narrow apical pore plate (Po) is 16 um long (average) with a slit-like apical pore, and is situated adjacent to apical plate 2' (Figs. 1,5). The 1' plate is large, irregularly pentagonal-shaped, and situated in the center (Figs. 1,5)(Faust et al. 1996). The hypotheca is composed of eight plates. Plate 1p, situated centrally, is a narrow, asymmetric, pentagonal plate (Figs. 2,5). Plate 1'''' contacts the sulcal region (Fig. 6)(Faust et al. 1996).

The lipped cingulum is narrow and shallow with a smooth edge (Figs. 1,2,4). Within the cingulum is the Vo located on the Vp, and adjacent to a Rp (Figs. 4,5). The shape of the Vp varies from oblong to circular. The sulcus is small and hidden (Faust et al. 1996).

Morphology and Structure: *Ostreopsis lenticularis* is a photosynthetic species with many golden-brown chloroplasts. A large nucleus is located posteriorly (Fukuyo 1981). There is evidence of mixotrophy in this species: prey organisms are engulfed via the Vo, the proposed feeding apparatus (Faust et al. 1996).

Reproduction: *Ostreopsis lenticularis* reproduces asexually by binary fission.

Ecology: *O. lenticularis* can be benthic, epiphytic or tycoplanktonic (Steidinger & Tangen 1996) commonly associated with macroalgae, in the plankton, attached to soft coral and between sand grains. Engulfed cells were often observed in this species collected from Belizean waters (Faust et al. 1996).

Toxicity: This is a known toxic species; it produces ostreotoxin (OTX), a water-soluble toxin (Tindall et al. 1990), and an unnamed toxin (Ballantine et al. 1988).

Species Comparisons: *Ostreopsis lenticularis* differs from other species in the genus by its lentil-like cell shape, medium size and randomly spaced round pores. The size and location of plates 2''', 3''' and 4''' are also distinguishing features (Faust et al. 1996). This species closely resembles *Gambierdiscus toxicus* in size, shape and color, but *O. lenticularis* has a slightly pointed ventral area while *G. toxicus* has a round and indented one (Fukuyo 1981). *O. lenticularis* is also similar to *O. siamensis* in shape and thecal plate configuration (Fukuyo 1981).

Habitat and Locality: Populations of *O. lenticularis* were originally found in the Gambier and Society Islands and New Caledonia, Pacific Ocean, associated with macroalgae (Fukuyo 1981). Populations can be found from tropical shallow waters to offshore reefs (Steidinger & Tangen 1996). Cells have been observed epiphytic on macroalgae (*Dictyota* sp. and *Acanthophora spicifera*) in the Caribbean region (Carlson & Tindall 1985; Ballantine et al. 1988; Morton & Faust 1997) and the SW Indian Ocean (Quod 1994). In the Caribbean, this species has been observed in the plankton (Faust 1995), attached to soft corals (Ballantine et al. 1985; Carslon & Tindall 1985) and between sand grains (Ballantine et al. 1985; Carslon & Tindall 1985; Faust 1995).

Ostreopsis mascarenensis

Quod, 1994

Plate 33, Figs. 1-8

Species Overview: *Ostreopsis mascarenensis* is an armoured, marine, benthic dinoflagellate species. It was discovered in shallow barrier reef environments and coral reefs in the Mascareignes Archipelago, SW Indian Ocean.

Taxonomic Description: Species in this genus are anterio-posteriorly compressed and are observed in apical or antapical view. The epitheca and hypotheca are not noticeably different in size. Unique features of this genus are on the cingulum. In ventral view the cingulum reveals two prominent structures: a ventral plate (Vp) with a ventral pore (Vo), and an adjacent curved rigid plate (Rp). The distinguishing feature at the species level is the shape of the first apical plate (1') on the epitheca (Fig. 1)(Faust et al. 1996).

Cells of *O. mascarenensis* are very large and broadly oval (Figs. 1,2,7). This is the largest species in the genus. Cells have a dorsoventral diameter of 155-178 µm and a transdiameter of 118-134 µm. The thecal surface is smooth with small evenly distributed pores (Figs. 1-4) that often contain ejected trichocysts (Fig. 6). The pores are round with two small openings (diam.=0.6 µm) with smooth edges (Fig. 3)(Quod 1994; Faust et al. 1996).

Nomenclatural Types:
Holotype: *Ostreopsis mascarenensis* Quod, 1994: fig. 1
Type Locality: West Indian Ocean: Saint Leu, Reunion Island, Mascareignes Archipelago

Thecal Plate Description: *O. mascarenensis* is a large cell with very large plates (Fig. 1). The plate formula for this species is: Po, 3', 7'', 6c, 6s?, Vp, Rp, 5''', 1p, 2''''. On the epitheca, the apical pore plate (Po) bears a long curved slit-like apical pore (26 µm) with an array of minute openings (Fig. 4). The 1' plate is large, long and hexagonal, 102 µm long and 40 µm wide (Fig. 1). In the hypotheca, the posterior intercalary plate (1p) is long and wide (Fig. 2). Plate 1''' is large compared to other species in the genus (Fig. 8)(Quod 1994; Faust et al. 1996).

The lipped cingulum is narrow with a smooth edge (Figs. 1,2,5). It houses the Vo situated on the Vp, and the Rp (Fig. 6). The sulcus is recessed and hidden (Fig. 5)(Quod 1994; Faust et al. 1996).

Morphology and Structure: Cells of *Ostreopsis mascarenensis* are photosynthetic with light golden-colored chloroplasts. This species has two pusules in the sulcus and one dorsal red pyrenoid (Quod 1994). There is evidence of mixotrophy in this species: prey organisms are engulfed via the Vo, the proposed feeding apparatus (Faust et al. 1996).

Reproduction: *O. mascarenensis* reproduces asexually by binary fission.

Ecology: Cells of *O. mascarenensis* are commonly associated with dead corals and sediments and as epiphytes on macroalgae (Quod 1994; Faust et al. 1996). Cells exhibit geotropic swimming. Cells may form blooms, reaching a density of >10,000 cells.g fresh weight of algal tissue (Quod 1994).

Toxicity: This species produces an unnamed toxin which may cause ciguatera (Quod 1994). This toxin has not been detected in fish (Morton, S.L., personal communication 1998).

Species Comparisons: *O. mascarenensis* differs from other species of the genus by its large size, thecal morphology, geotropic swimming behaviour and dissimilar plates, in particular, plates 1',2',3',1''' and 1p (Quod 1994).

Habitat and Locality: Populations of *O. mascarenensis* can be commonly found in shallow (2-5m) barrier reef environments and coral reefs in the SW Indian Ocean. This species has been observed as an epiphyte on *Turbinaria* sp., *Galaxaura* sp., dead corals and sediments at Mayotte, Reunion and Rodriguez Islands (Quod 1994). Cells were also discovered from the lagoonal island, Tobacco Cay, Belize, in the Caribbean Sea (Faust et al. 1996).

Ostreopsis ovata
Fukuyo, 1981
Plate 34, Figs. 1-7

Species Overview: *Ostreopsis ovata* is an armoured, marine, benthic dinoflagellate species. It was discovered from French Polynesia, New Caledonia and the Ryukyu Islands, Pacific Ocean.

Taxonomic Description: Species in this genus are anterio-posteriorly compressed and are observed in apical or antapical view. The epitheca and hypotheca are not noticeably different in size. Unique features of this genus are on the cingulum. In ventral view the cingulum reveals two prominent structures: a ventral plate (Vp) with a ventral pore (Vo), and an adjacent curved rigid plate (Rp). The distinguishing feature at the species level is the shape of the first apical plate (1') on the epitheca (Fig. 1)(Faust et al. 1996).

Cells of *O. ovata* are tear-shaped, ovate and ventrally slender (Figs. 1,2,6). It is the smallest species in the genus. Thecal surface is smooth, ornamented with minute, evenly distributed pores (0.07 μm diameter)(Figs. 1-4). Cells have a dorsoventral diameter of 47-55 μm and transdiameter of 27-35 μm (Faust et al. 1996).

Nomenclatural Types:
Holotype: *Ostreopsis ovata* Fukuyo, 1981: figs. 35-38
Type Locality: Pacific Ocean: French Polynesia, New Caledonia and the Ryukyu Islands

Thecal Plate Description: Thecal plates of *Ostreopsis ovata* are very thin and delicate, and their morphology is very difficult to preserve. The plate formula for this species is: Po, 3', 7", 6c, 6s?, Vp, Rp, 5"', 1p, 2"". In the epitheca, the 1' plate is long and hexagonal, and occupies the left center of the cell (Fig. 1). The apical pore plate (Po) features a short asymmetrical slit-like apical pore, and is associated with narrow apical plate 2' (Figs. 1,4). In the hypotheca, the posterior intercalary plate (1p) is long and narrow (9 X 27 μm) (Fig. 2) (Faust et al. 1996).

Cingulum is equatorial, relatively wide, and bordered by narrow lists (Figs. 1,2). Within the cingulum, the Vo is situated on the Vp surrounded by the Rp (Fig. 5)(Faust et al. 1996). The sulcus contains eight plates (Steidinger & Tangen 1996).

Morphology and Structure: Cells of *Ostreopsis ovata* are photosynthetic containing many golden chloroplasts. Large ovate nucleus is posterior (Fig. 6)(Fukuyo 1981). There is evidence of mixotrophy in this species: prey organisms are engulfed via the Vo, the proposed feeding apparatus (Faust et al. 1996).

Reproduction: *O. ovata* reproduces asexually by binary fission.

Ecology: *O. ovata* can be tycoplanktonic, benthic or epiphytic (Steidinger & Tangen 1996). Engulfed cells were often observed in this species collected from Belizean waters (Faust et al. 1996).

Toxicity: This species produces an unnamed toxin (Nakajima et al. 1981).

Species Comparisons: *O. ovata* differs from the other species in the genus by its small size, very delicate thecal plates and a short, straight Po. It is readily identifiable from *O. siamensis* and *O. lenticularis* by its ovoidal, tear-shaped body (Fukuyo 1981).

Habitat and Locality: *Ostreopsis ovata* is infrequently observed in the field. Populations are usually found in protected, inshore regions from the tropical Pacific Ocean (Fukuyo 1981; Yasumoto et al. 1987; Quod 1994), the Caribbean Sea (Besada et al. 1982; Carlson & Tindall 1985) and the Tyrrhenian Sea (Tognetto et al. 1995). Substrate specificity for this species needs to be determined.

Ostreopsis siamensis
Schmidt, 1902
Plate 35, Figs. 1-8

Species Overview: *Ostreopsis siamensis* is an armoured, marine, benthic dinoflagellate species. It was first identified from plankton samples from the Gulf of Siam (Thailand).

Taxonomic Description: Species in this genus are anterio-posteriorly compressed and are observed in apical or antapical view. The epitheca and hypotheca are not noticeably different in size. Unique features of this genus are on the cingulum. In ventral view the cingulum reveals two prominent structures: a ventral plate (Vp) with a ventral pore (Vo), and an adjacent curved rigid plate (Rp). The distinguishing feature at the species level is the shape of the first apical plate (1') on the epitheca (Fig. 1)(Faust et al. 1996).

Cells of *O. siamensis* are ovate and tear-shaped (Figs. 1,2,7,8). The thecal surface is smooth with evenly scattered round pores (Figs. 1-3). Large (0.5 µm diameter) and small (0.1 µm diameter) pores are present (Fig. 4). Cells have a dorsoventral diameter of 108-123 µm and a transdiameter of 76-86 µm (Faust et al. 1996).

Nomenclatural Types:
Holotype: *Ostreopsis siamensis* Schmidt, 1902: figs. 5-7
Type Locality: Gulf of Thailand: Thailand

Thecal Plate Description: The plate formula for *Ostreopsis siamensis* is: Po, 3', 7", 6c, 6s?, Vp, Rp, 5"', 1p, 2"" (Fig. 8). On the epitheca, a narrow curved apical pore plate (Po) (Fig. 1) is closely associated with the narrow apical plate 2' (Fig. 3). The apical pore appears as a curved slit 2 µm long (Fig. 3). The 1' plate is large, narrow and pentagonal (Fig. 1). The hypotheca is composed of eight plates (Fig. 2). The posterior intercalary plate (1p) is large, elongated (26 X 55 µm), and pentagonal (Fig. 2). Plate 1"" contacts the sulcal region (Figs. 2,5)(Faust et al. 1996).

The narrow cingulum is deep with a smooth edge (Figs. 1-3) and is composed of six plates. In the cingulum the Vo is situated on the Vp next to the Rp (Figs. 5,6). The Vo may be open or closed. The sulcus is small, recessed and hidden below plates 1"" and 2""(Faust et al. 1996).

Morphology and Structure: Cells of *O. siamensis* are photosynthetic and contain numerous golden-brown chloroplasts. A large nucleus is posterior. There is evidence of mixotrophy in this species: prey organisms are engulfed via the Vo, the proposed feeding apparatus (Faust et al. 1996).

Reproduction: *O. siamensis* reproduces asexually by binary fission.

Ecology: *O. siamensis* are benthic, epiphytic, and can be tycoplanktonic (Steidinger & Tangen 1996). They have been observed in plankton samples, but it is most frequently associated with sand and as epiphytes on macroalgae. These cells swim very slowly and spin around the dorso-ventral axis (Fukuyo 1981). Engulfed cells were often observed in this species collected from Belizean waters (Faust et al. 1996).

Toxicity: This species is a known toxin producer; it produces an analog of palytoxin (Nakajima et al. 1981; Usami et al. 1995).

Species comparison: *O. siamensis* differs from other species of the genus by a number of features: a. a tear-drop shape; b. large cell size; and c. small round evenly distributed thecal pores (Faust et al. 1996).

Habitat and Locality: *Ostreopsis siamensis* has been observed in various tropical regions of the world. Populations were originally discovered in plankton samples collected from the Gulf of Siam (Thailand) (Schmidt 1902, figs. 5-7) and then seldom observed again for over 70 years. Cells were later found as epiphytes on macroalgae in the Pacific Ocean (Taylor 1979; Yasumoto et al. 1980; Fukuyo 1981; Nakajima et al. 1981; Holmes et al. 1988), the SW Indian Ocean (Quod 1994), the Florida Keys (Bomber 1985), and the Caribbean region (Carlson 1984; Tindall et al. 1984; Ballantine et al. 1988; Faust 1995; Faust & Morton 1995). They have also been associated with sand in the Caribbean (Faust et al. 1996).

Pfiesteria piscicida
Steidinger et Burkholder, 1996
Plate 36, Figs. 1-9

Species Overview: *Pfiesteria piscicida* is a putatively toxic dinoflagellate species with flagellated and cyst stages. This species, dubbed the 'ambush predator', was first observed in the Pamlico Sound, North Carolina, USA, in 1991 after a massive fish kill. *Pfiesteria piscicida* has been associated with fish kills, and then feeds on the dead prey (Burkholder et al. 1992; 1995; Steidinger et al. 1996).

Taxonomic Description: *Pfiesteria piscicida* is a polymorphic and multiphasic dinoflagellate species with a number of unicellular stages throughout its life cycle: bi- and triflagellated zoospores, and nonmotile cyst stages. Within the different life stage forms there is a wide range in size and morphology (Steidinger et al. 1996).

The flagellated stages are small, oblong thecate cells that resemble gymnodinioid cells, although they are actually small cryptic peridinioid cells (Figs. 1-4). The biflagellated stages, zoospores, have two size groups: 5-8 µm (gametes) and 10-18 µm (Fig. 3). The larger triflagellated stage, 25-60 µm, is a planozygote with the features of a vegetative cell along with one transverse and two longitudinal flagella (Fig. 4). Cyst stages, with highly resistant cell walls, range in size from 25-33 µm (Fig. 5). The flagellated forms are typically planktonic and ephemeral, whereas the cyst stages are benthic (Steidinger et al. 1996).

Nomenclatural Types:
Holotype: *Pfiesteria piscicida* Steidinger, Burkholder, Glasgow, Hobbs, Garrett, Truby, Noga and Smith, 1996: 160, fig. 2
Type Locality: North Atlantic Ocean: Pamlico River Estuary, North Carolina, USA
Synonyms:
Pfiesteria piscimorte Burkholder et al., 1993
Pfiesteria piscimortuis Burkholder et al., 1995
"phantom dinoflagellate" Burkholder et al., 1992

Etymology: The genus *'Pfiesteria'* is named in honor of Dr. Lois A. Pfiester, a pioneer in describing and unravelling the sexual life cycles of freshwater dinoflagellates. The species name *'piscicida'* is taken from the Latin words *'pisces'* for fish, and *'cida'* for killer (Steidinger et al. 1996).

Thecal Plate Description: The biflagellated stages of *P. piscicida* have thin thecal plates with a plate formula unique to the Dinophyceae: Po, cp, X, 4', 1a, 5'', 6c, 4s, 5''', 2'''' (Figs. 6-9). Raised sutures designate plate tabulation (Figs. 1,4). Thecal nodules border plate sutures (Fig. 6). Theca is smooth with scattered pores; trichocysts are present. The epitheca is equal to or exceeds the hypotheca in height (Fig. 1). The apical pore complex (APC) houses a broadly ovate apical pore plate (Po) and closing plate (cp)(Figs. 6-8). The elongate canal plate (x plate) is at a slight angle to the APC (Figs. 7,8). The first apical plate (1') is rhomboid in shape (Fig. 6). The broad and shallow cingulum is without lists, and descends almost 1 time its width. The sulcus is excavated, without lists, descends to the right, and slightly invades the epitheca via the anterior sulcal plate (s.a.)(Figs. 1,9) (Steidinger et al. 1996).

Morphology and Structure: *P. piscicida* exhibits a number of different life cycle stages. This species uses both heterotrophic and mixotrophic nutritional modes depending on the life stage. Flagellated stages are mixotrophic: they use a peduncle (Figs. 1,2) to capture and ingest prey (myzocytosis), and kleptochloroplasts (chloroplasts retained from ingested algal prey) to photosynthesize when prey supply is low. Large food vacuoles are often found in the epitheca, the mesokaryotic nucleus is located in the hypotheca (Schnepf et al. 1989; Elbrächter 1991; Fields & Rhodes 1991; Stoecker 1991; Steidinger et al. 1996; Lewitus et al. 1999).

Reproduction: Biflagellated zoospores reproduce asexually via temporary cysts. Sexual reproduction has also been documented for this species: biflagellated zoospores produce anisogamous gametes (Fig. 3), which fuse to produce triflagellated planozygotes (two longitudinal flagella and one transverse) (Fig. 4). Sexual and asexual reproduction can occur on either a fish or algal diet (Tester, P., personal communication).

Species Comparisons: *P. piscicida* is a distinct free-living estuarine dinoflagellate (Fensome et al. 1993, Burkholder & Glasgow 1995; 1997).

Ecology and Toxicity: *P. piscicida* is an estuarine species with a wide temperature and salinity tolerance. A cryptic heterotrophic species, it is a prey generalist that feeds on bacteria, algae, microfauna, finfish and shellfish, and may well represent a significant estuarine microbial predator. Feeding mode is governed by the presence or absence of fish and fish material. Life cycle stage is governed by the presence of live or dead fish (Burkholder 1995; Burkholder & Glasgow 1997).

In the absence of fish, biflagellated stages feed myzocytotically on bacteria, algae and microfauna; i.e. prey is suctioned into a food vacuole via a feeding tube or peduncle (Fig. 2), and then digested (Burkholder & Glasgow 1995; Glasgow et al. 1998). Similar to other heterotrophic dinoflagellate species, a large food vacuole allows *P. piscicida* to phagocytize large prey items (Gaines & Elbrächter 1987; Schnepf & Elbrächter 1992; Burkholder et al. 1998).

Pfiesteria piscicida is a strong ichthyotoxic dinoflagellate species: in the presence of live fish, *P. piscicida's* behavior is stimulated by a chemosensory cue, an unknown substance in fish secreta/excreta. Benthic stages (Fig. 5) then rapidly emerge as flagellated forms that swarm, immobilize, and kill the prey. Some prey experience ulcerative fish disease (open skin lesions) before dying. *P. piscicida* is lethal to fish at relatively low concentrations (> 250-300 cells/ml). At lower levels (~100-250 cells/ml) ulcerative fish disease results. Similar ulcers have been reported from shellfish as well. After a kill benthic stages form which inconspicuously descend back to the sediments (Burkholder & Glasgow 1995; 1997; Burkholder et al. 1995; 1998; Noga et al. 1996; Steidinger et al. 1996).

P. piscicida and possibly other *Pfiesteria*-like species are suspected to be responsible for a number of major fish and shellfish kills in the North Carolina Albemarle-Pamlico estuary, and in the Maryland Chesapeake Bay (Burkholder et al. 1995; Burkholder & Glasgow 1997). The ever changing morphology of this species may give answers to a number of mysterious fish kills along the southeast coast of the United States (Steidinger et al. 1996).

This species was initially linked to serious health problems in humans who had come in direct contact with it (narcosis, respiratory distress, epidermal lesions, and short-term memory loss); however, a study sponsored by the Centers for Disease Control (CDC) has revealed no such relationship (Swinker et al. 2001). Other CDC-funded studies are currently addressing possible associated human health problems with *Pfiesteria* and *Pfiesteria*-like species in several states, including Maryland and North Carolina (P. Tester, personal communication).

Habitat and Locality: *Pfiesteria piscicida* was first identified from the Pamlico Sound in North Carolina. Since its emergence; however, *P. piscicida* and *Pfiesteria*-like species have been reported from other eutrophic, temperate to subtropical estuarine systems in the eastern United States: from Delaware inland bays to Mobile Bay, Alabama (Burkholder et al. 1993; Burkholder et al. 1995; Lewitus et al. 1995). This natural range is expected to expand, considering the warming trend in global climate, and the increased human impact on coastal areas resulting in decreased water quality (Smayda 1992; Adler et al. 1993; Epstein et al. 1993; Hallegraeff 1993; Burkholder & Glasgow 1997).

Prorocentrum arenarium

Faust, 1994

Plate 37, Figs. 1-6

Species Overview: *Prorocentrum arenarium* is an armoured, marine, sand-dwelling, benthic dinoflagellate species. This toxic species is associated with coral rubble and colored sand in tropical embayments of the Caribbean Sea.

Taxonomic Description: *Prorocentrum arenarium* is a bivalvate species often observed in valve view. Cells are round to slightly oval in valve view (Figs. 1,2,6); cell size ranges between 30 to 32 μm in diameter. Both valves are concave in the center. The thecal surface is smooth (Figs. 1-3) with distinct randomly distributed valve poroids (65-73 per valve). The valve centers are devoid of pores. The poroids vary from kidney-shaped to oblong (Figs. 1-5), with an average size of 0.62 µm long and 0.36 µm wide. Spacing between poroids is 2-3 µm. Valve margins exhibit evenly spaced marginal poroids, 50-57 per valve, and are similar in size to valve poroids (Figs. 1-5). These poroids are useful diagnostic features of this species and are easily viewed under the light microscope. The intercalary band is smooth and wide (Figs. 2,3)(Faust 1994).

The periflagellar area, which lacks ornamentation, is a broad triangle on the right valve at the anterior end of the cell (Figs. 1,3,5). The anterior region of the right valve is excavated; the left valve margin is flattened (Fig. 2). The flagellar and auxiliary pores are unequal in size (Fig. 5). The longitudinal flagellum is short (average length of 11 µm) (Fig. 1)(Faust 1994).

Nomenclatural Types:
Holotype: *Prorocentrum arenarium* Faust, 1994: figs. 14, 15
Type Locality: Caribbean Sea: Carrie Bow Cay, Belize, Central America

Morphology and Structure: *Prorocentrum arenarium* is a photosynthetic species with a prominent central pyrenoid and a posterior nucleus (Fig. 6). A small (2-3 µm), narrow, tubular, peduncle-like structure in the periflagellar area has been observed in this species. This structure originates and emerges from the flagellar pore (Faust 1994).

Reproduction: *Prorocentrum arenarium* reproduces asexually by binary fission.

Ecology: *Prorocentrum arenarium* is a benthic and epiphytic species. Cells are motile, propelled by two flagella, or are attached to sand or coral rubble. This species can be a significant component of benthic *Prorocentrum* assemblages in colored sand patches in the Caribbean (1200-6000 cells/g sand) (Faust 1994).

The presence of a peduncle-like structure may indicate mixotrophic feeding within the sand (Faust 1994).

Toxicity: This is a known diarrhetic shellfish poison (DSP) toxin-producing species, producing okadaic acid (OA)(Ten-Hage et al. 2000).

Species Comparison: Only a few round to nearly round *Prorocentrum* species are known: *P. arenarium* (Faust, 1994) is smaller than *P. emarginatum* (cell diameter 35-40 µm)(Faust 1990b), but larger than *P. ruetzlerianum* (cell diameter 28-35 µm) (Faust 1990b) and *P. compressum* (cell diameter 36 µm)(Matzenauer 1933; Böhm 1936; Schiller 1937; Tafall 1942; Dodge 1975).

The valve poroids of *P. arenarium* are distinct from similarly known benthic *Prorocentrum* species: P. lima has approximately 58-86 round pores per valve and 55-72 marginal pores with a diameter of 0.3-0.7 µm (Faust 1991); *P. maculosum* has about 85-90 valve poroids and 65-75 marginal poroids with a diameter of 0.6 µm (Faust 1993b).

The architecture of the periflagellar area of *P. arenarium*, with no ornamentation (Faust 1994), is similar to that of *P. concavum*, *P. ruetzlerianum* (Faust 1990b), *P. foraminosum* (Faust 1993b), and *P. tropicalis* (Faust 1997).

P. arenarium has a smooth intercalary band. This feature is also characteristic of other benthic *Prorocentrum* species: *P. lima* (Faust 1991), *P. hoffmannianum* (Faust 1990), and *P. foraminosum* (Faust 1993b).

The peduncle-like organelle in *P. arenarium* is similar in structure to the peduncle observed in *P. norrisianum* (Faust 1997).

Habitat and Locality: *Prorocentrum arenarium* is associated with coral rubble and colored sand in tropical embayments of the Caribbean Sea and the SW Indian Ocean (Faust 1994; Ten-Hage et al. 2000).

Prorocentrum balticum
(Lohmann) Loeblich III, 1970
Plate 38, Figs. 1-4

Species Overview: *Prorocentrum balticum* is an armoured, marine, planktonic, bloom-forming dinoflagellate species. This cosmopolitan species is commonly found in cold temperate to tropical waters world-wide.

Taxonomic Description: *P. balticum* is a bivalvate species often observed in valve view. Cells are small (< 20 µm in diameter), and round to ovoid in valve view (Figs. 1,2,4), with two minute and distinct apical projections (Figs. 1,3,4). Although cells are nearly spherical, some have broad shoulders. Thecal valves are covered with many tiny interconnected spines (Figs. 1-4) which form narrow transverse rows on the intercalary band (Fig. 1). Many scattered rimmed pores are present on the cell surface (Fig. 2)(Dodge 1975; 1982; Toriumi 1980; Steidinger & Tangen 1996; Faust et al. 1999).

Two minute apical spines (Figs. 1,3,4) border the relatively small periflagellar area. The periflagellar pores are different sized (Fig. 3)(Dodge 1975; Toriumi 1980; Steidinger & Tangen 1996; Faust et al. 1999).

Nomenclatural Types:
Holotype: *Exuviaella baltica* Lohmann, 1908: 265, plate 17, fig. 1a,b
Type Locality: unknown
Synonyms:
Prorocentrum pomoideum Bursa, 1959
Exuviaella aequatorialis Hasle, 1960

Morphology and Structure: *Prorocentrum balticum* is a photosynthetic species with a round nucleus situated posteriorly (Dodge 1975; Dodge 1982; Toriumi 1980).

Reproduction: *P. balticum* reproduces asexually by binary fission.

Ecology: *P. balticum* is a planktonic species. It is a neritic and oceanic species with world-wide distribution (Dodge 1975; Dodge 1982; Steidinger & Tangen 1996). Cells are active swimmers.

This species has been reported to form red tides in many parts of the world (see Lassus 1988). Many blooms have occurred in brackish water habitats (Tangen 1980; Zotter 1979; Edler et al. 1984) confirming Braarud's (1951) earlier growth experiments that revealed *P. balticum*'s highest growth rates were at low salinities (10-15 o/oo).

Toxicity: Although toxicity in *P. balticum* has never been confirmed, it has been associated with toxic red tides (Silva 1956; Silva 1963; Numann 1957). Steidinger (1979) regards it as a questionable toxic species.

Species Comparison: *P. balticum* is not easily distinguished from *P. minimum* and a critical assessment of its taxonomic status is still needed. Both are small species, valves covered with small spines, and periflagellar areas are relatively small with two pores. *P. balticum* is distinguished by its small size, its almost spherical shape (Toriumi 1980), and its two minute apical projections (Faust et al. 1999).

Because of its small size, records of *P. balticum* may actually include closely related, but undescribed species (Steidinger & Tangen 1996).

Habitat and Locality: *Prorocentrum balticum* is commonly found in marine waters all over the world: cosmopolitan in cold temperate to tropical waters (Dodge 1975; 1982; Steidinger & Tangen 1996).

Prorocentrum belizeanum

Faust, 1993

Plate 39, Figs. 1-9

Species Overview: *Prorocentrum belizeanum* is an armoured, marine, benthic dinoflagellate species. This species is associated with floating detritus and sediment in tropical embayments of the Caribbean Sea.

Taxonomic Description: *Prorocentrum belizeanum* is a bivalvate species often observed in valve view. Cells are round to slightly oval (Figs. 1,2,4,7,8). Cells measure between 55-60 μm in length and 50-55 μm in width. Valves are concave in the center (Figs. 2,4) (Faust 1993a).

Thecal surface is heavily areolated; approximately 853-1024 areola are present on each valve (Figs. 1-5). The areolae are round to oval (0.66-0.83 μm in diameter) (Figs. 1-6). Some bear trichocyst pores at their base. Ejected trichocysts are often observed. The intercalary band is smooth; however, marginal areolae give the appearance of a transversely striated intercalary band (Figs. 7,8)(Faust 1993a).

The periflagellar area is a V-shaped triangle located apically on the right valve (Figs. 1,4,6,8). Both the left and right valves are excavated (Figs. 1,4). Two periflagellar pores, flagellar and auxiliary, are equal in size. The auxiliary pore is surrounded by a flared periflagellar collar (Fig.

6). Accessory pores are also present. The left valve anterior margin bears a large rounded and flared curved apical collar that borders the periflagellar area (Figs. 1-4,6,8). In lateral and apical view, the curved apical collar resembles a rounded lip (Figs. 3,4)(Faust 1993a).

Nomenclatural Types:
Holotype: *Prorocentrum belizeanum* Faust, 1993: figs. 1,2
Type Locality: Caribbean Sea: Twin Cays, Belize, Central America

Morphology and Structure: *Prorocentrum belizeanum* is a photosynthetic species with a centrally located pyrenoid and a large kidney-shaped posterior nucleus (Fig. 7)(Faust 1993a).

Reproduction: *Prorocentrum belizeanum* reproduce asexually by binary fission.

Ecology: *P. belizeanum* is a benthic species that can be a major component (1200 cells/mL) of benthic *Prorocentrum* assemblages in floating detritus and sediments in tropical coastal waters of the Caribbean. Cells are motile or are often attached to sediments and detrital particles (Faust 1993a).

Toxicity: This is a known diarrhetic shellfish poison (DSP) toxin-producing species producing okadaic acid (OA) and small amounts of Dinophysistoxin-1 (DTX1)(Morton et al. 1998).

Species Comparison: Only a few round or near-round *Prorocentrum* species are known: *P. belizeanum* is larger then *P. hoffmannianum* (45-55 μm long and 40-45 μm wide)(Faust 1990b) and larger than *P. compressum* (36 μm in diameter)(Matzenauer 1933; Böhm 1936; Schiller 1937; Tafall 1942; Dodge 1975).

The areolae of *P. belizeanum* are distinct from similar known benthic *Prorocentrum* species (Faust 1993a): *P. hoffmannianum* has approximately 670 areola per valve (diam.=1.0-1.15 μm), and *P. ruetzlerianum* has about 550 pentagonal-shaped areola per valve (diam.=1.0 μm)(Faust 1990b).

The architecture of the periflagellar area of *P. belizeanum* is similar to *P. lima* (Taylor 1980) and the planktonic species *P. playfairi* (Croome & Tyler 1987). *P. hoffmannianum* (Faust 1990b), however, has a more complex platelet configuration (Faust 1993a). The periflagellar area of *P. belizeanum* lacks an apical spine (Faust 1993a), which is similar to *P. hoffmannianum* (Faust 1990b) and *P. lima* (Faust 1991), but different from *P. compressum*, which has two apical spines (Tafall 1942; Dodge 1975). *P. reticulatum* (Faust 1997), *P. sabulosum* (Faust 1994), *P. belizeanum* (Faust 1993a) and *P. hoffmannianum* (Faust 1990b) share a distinct feature in the periflagellar area: three small accessory pores adjacent to a periflagellar pore (Faust 1997).

The flared curved apical collar (or 'raised anterior ridge') on the left anterior margin of *P. belizeanum* is similar to the curved apical collar of *P. hoffmannianum*. However, *P. belizeanum* has a more prominent and rounder collar than *P. hoffmannianum*, which is broader (Faust 1990b; Faust 1993a; Steidinger & Tangen 1996).

Habitat and Locality: Cells of *P. belizeanum* are common in tropical coastal waters (Steidinger & Tangen 1996) associated with floating detritus (Faust 1993a).

Prorocentrum concavum
Fukuyo, 1981
Plate 40, Figs. 1-7

Species Overview: *Prorocentrum concavum* is an armoured, marine, benthic dinoflagellate. This toxic species is often associated with floating detritus and sediments in tropical and neritic waters.

Taxonomic Description: *P. concavum* is a bivalvate species often observed in valve view. Cells are broadly ovoid. Valve centers are concave and flattened (Figs. 1,2,5-7). Cells measure 50-55 μm in length and 38-45 μm in width. The valve surface is covered with 1000-1100 prominent shallow areolae. The areolae are round to oval with smooth edges (Figs. 1,3) and often observed with a central pore (0.8 μm diameter) (Fig. 3). No marginal pores are present and the cell center is devoid of areolae (Fig. 5). The intercalary band is granulated and horizontally striated (Figs. 1,2)(Fukuyo 1981; Faust 1990b).

The periflagellar area is a narrow, rimmed, V-shaped depression on the right valve (Figs. 1,4,5,7). It is composed of eight apical plates, without ornamentation, fitted with a large flagellar pore, and a much smaller auxiliary pore (Fig. 4). The left valve is slightly indented anteriorly with a thickened apical ridge (raised margin) bordering the periflagellar area (Fig. 1)(Fukuyo 1981; Faust 1990b).

Nomenclatural Types:
Holotype: *Prorocentrum concavum* Fukuyo, 1981: figs. 13-19,49
Type Locality: Pacific Ocean: French Polynesia, New Caledonia and the Ryukyu Islands

Morphology and Structure: *Prorocentrum concavum* is a photosynthetic species with golden-brown chloroplasts (Faust 1990b). Two cup-shaped pyrenoids are also present (Fukuyo 1981).

Reproduction: *Prorocentrum concavum* reproduces asexually by binary fission.

Ecology: *P. concavum* is a benthic species that can also be tycoplanktonic. Cells can be either motile or embedded in mucus attached to detritus (Faust 1990b; Steidinger & Tangen 1996).

Toxicity: This species is known to be toxic, producing the following toxins: fast-acting toxin (FAT)(Tindall et al. 1984), diarrhetic shellfish poison (DSP) toxins (Hu et al. 1993), okadaic acid (OA)(Dickey et al. 1990), and an unnamed toxin (Tindall et al. 1989).

Species Comparisons: *Prorocentrum concavum*, at the LM level, is difficult to differentiate from a number of other *Prorocentrum* species due to their similar size and shape; e.g. *P. concavum* is often confused with *P. lima* (Fukuyo 1981; Faust 1990b), but *P. lima* is not areolate and bears marginal pores (Faust 1990b).

The location and arrangement of areolae on the surface of *P. concavum* closely resembles that of *P. hoffmannianum* (about 670/valve)(Faust 1990b) and *P. belizeanum* (about 950/valve) (Faust 1993a); however, the latter two species have fewer areolae per valve and also have marginal pores, while *P. concavum* does not (Faust 1990b).

P. concavum and *P. tropicalis* (Faust 1997) have similar intercalary bands: granulated and horizontally striated.

Habitat and Locality: *P. concavum* populations are often associated with floating mangrove detritus and sediments in tropical and neritic waters (Faust 1990b; Steidinger & Tangen 1996).

Prorocentrum faustiae
Morton, 1998
Plate 41, Figs. 1-4

Species Overview: *Prorocentrum faustiae* is an armoured, marine, benthic dinoflagellate species. This species is associated with macroalge from the Australian Barrier Reef.

Taxonomic Description: *Prorocentum faustiae* is a bivalvate species often observed in valve view. Cells are broadly ovate to rotundate with a rugose appearance (Figs. 1-3). Valve centers are concave (Figs. 1-3). Cells are 43-49 µm long and 38-42 µm wide. Small pores (0.1 µm in diameter), probably containing trichocysts, are dense on the valve surface and along the valve perifery (Figs. 1-3). The intercalary band is transversely striated (Fig. 3) (Morton 1998). The periflagellar area is a wide triangular, V-shaped region located apically on the right valve (Figs. 1,4). Sixteen apical platelets make up the periflagellar area. Included also are two pores: a large flagellar pore, and a smaller auxiliary pore (Fig. 4)(Morton 1998).

Nomenclatural Types:
Holotype: *Prorocentrum faustiae* Morton, 1998: 567, figs. 1-4
Type Locality: Coral Sea: Heron Island, Australia

Morphology and Structure: *Prorocentrum faustiae* is a photosynthetic species containing numerous golden-brown chloroplasts and a centrally located pyrenoid (Figs. 1,2). A large kidney-shaped nucleus is situated posteriorly (Morton 1998).

Reproduction: *Prorocentrum faustiae* reproduces asexually by binary fission.

Ecology: *Prorocentrum faustiae* is a benthic species epiphytic on macroalgae (Morton 1998).

Toxicity: *P. faustiae* is a diarrhetic shellfish poison (DSP) toxin-producing species producing okadaic acid (OA) and Dinophysistoxin-1 (DTX1)(Morton 1998).

Species Comparison: *Prorocentrum faustiae* is similar in shape and size to *P. hoffmannianum* (45-55 µm long and 40-45 µm wide); however, the former lacks thecal areolae, which are very abundant on the latter. *P. faustiae* lacks a distinct ridge along the valve perifery which distinguishes this species from *P. maculosum* (Morton 1998).

Etymology: The species '*faustiae*' is named in honor of Dr. Maria Faust, Smithsonian Institution, for her advancements in the taxonomy of non-planktonic dinoflagellates (Morton 1998).

Habitat and Locality: Populations of *P. faustiae* are associated with macroalgae from Heron Island, Australia (Morton 1998).

Prorocentrum hoffmannianum
Faust, 1990
Plate 42, Figs. 1-6

Species Overview: *Prorocentrum hoffmannianum* is an armoured, marine, benthic dinoflagellate species. This species is associated with floating detritus and sediment in tropical embayments of the Caribbean Sea.

Taxonomic Description: *Prorocentrum hoffmannianum* is a bivalvate species often observed in valve view. Cells are ovoid, broadest in mid-region, tapering slightly apically (Figs. 1,2,5,6). Cells are 45-55 µm long and 40-45 µm wide. Both valves are slightly concave in the center. The intercalary band is smooth and appears as a flared ridge around the cell (Figs. 1,2,5). Observed under LM, the marginal areolae can give the appearance of a striated intercalary band (Fig. 5)(Faust 1990b).

The valve surface is deeply areolate; areolae are dense, large, and round to oblong (Figs. 1-4). Small round to ovoid pores are found within deep areolae; these pores have smooth margins, are 1.0-1.5 µm in diameter, and many bear trichocyst pores (Fig. 3). There are approximately 650-700 areolae on each valve (Faust 1990b).

The periflagellar area is a wide triangle situated apically on the right valve (Figs. 1,4). It houses eight periflagellar platelets and two periflagellar pores: a flagellar pore and auxiliary pore (equal in size); accessory pores are also present. The flagellar pore is surrounded by a small flared periflagellar collar (Fig. 4). Both left and right valves are apically excavated (Figs. 1,4). The left valve exhibits a flared and flattened curved apical collar that borders the periflagellar area (Figs. 1,2)(Faust 1990b).

Nomenclatural Types:
Holotype: *Prorocentrum hoffmannianum* Faust, 1990: figs. 13,14
Type Locality: Caribbean Sea: Twin Cays, Belize, Central America
Synonyms:
Exuviaella hoffmannianum (Faust) McLachlan, Boalch and Jahn, 1997

Morphology and Structure: *Prorocentrum hoffmannianum* is a photosynthetic species containing golden-brown chloroplasts, a centrally located pyrenoid, and a large posterior nucleus (Fig. 5)(Faust 1990b).

Reproduction: *Prorocentrum hoffmannianum* reproduces asexually by binary fission.

Ecology: *Prorocentrum hoffmannianum* is a benthic species. Cells are motile or attached to detritus by mucilage (Faust 1990b).

Toxicity: This species is considered toxic producing fast-acting toxin (FAT) and diarrhetic shellfish poison (DSP) toxin: okadaic acid (OA)(Aikman et al. 1993).

Species Comparison: *Prorocentrum hoffmannianum* is similar in shape to *P. lima*, but larger and broader with dense areolae. *P. hoffmannianum* is often misidentified as *P. concavum*, but can be distinguished by its ovoid shape and presence of areolae in the center of the valve (Fukuyo 1981; Faust 1990b; 1991).

The architecture of the periflagellar area of *P. hoffmannianum* is similar to *P. lima, P. concavum* (Fukuyo 1981) and *P. playfairi* (Croome & Tyler 1987); however, *P. hoffmannianum* has a more complex platelet configuration (Faust 1990b). *P. reticulatum* (Faust 1997), *P. sabulosum* (Faust 1994), *P. belizeanum* (Faust 1993a) and *P. hoffmannianum* (Faust 1990b) share a distinct feature in the periflagellar area: three small accessory pores adjacent to a periflagellar pore (Faust 1997).

Both *P. hoffmannianum* and *P. belizeanum* have a prominent flared curved apical collar on the left valve bordering the periflagellar area, although the curved apical collar of the latter species is rounder, whereas that of the former is flatter (Faust 1993a).

Etymology: This species is named in honor of Dr. Robert S. Hoffmann, Assistant Secretary for Research, Smithsonian Institution, for his encouragement, support and scientific leadership (Faust 1990b).

Habitat and Locality: Populations of *P. hoffmannianum* are often associated with floating detritus in tropical coastal regions of the Caribbean Sea (Faust 1990b).

Remarks: In Carlson (1984), *P. concavum* identified on Plate 5, figs. n-s, is *P. hoffmannianum* based on thecal surface morphology, periflagellar area and intercalary band characteristics. In addition, the illustration of *P. concavum* (fig. 17) by Steidinger (1983) is neither *P. concavum* nor *P. hoffmannianum*, but is an unidentified species (Faust 1990b).

Prorocentrum lima

(Ehrenberg) Dodge, 1975

Plate 43, Figs. 1-7

Species Overview: *Prorocentrum lima* is an armoured, marine, benthic dinoflagellate species with world-wide distribution.

Taxonomic Description: *P. lima* is a bivalvate species often observed in valve view. Cells are oblong to ovate, small to medium-sized, broadest in the mid-region, and narrow toward the anterior end (Figs. 1,2,4-6). Cell size ranges between 32-50 µm in length and 20-28 µm in width. Thecal valves are thick and smooth with scattered surface pores (Figs. 1-4). Each valve contains about 50-80 small round marginal pores evenly spaced around the perifery of the valve (0.6 µm in diameter)(Figs. 1,3), and about 60-100 larger round to oblong unevenly distributed valve pores with trichocysts (0.48 µm in diameter) (Figs. 1,2,4). All pores have smooth edges (Figs. 3,4). The center is devoid of pores (Figs. 1,2,4). Marginal pores is a useful diagnostic feature of this species distinguishing it from other *Prorocentrum* species. Occasionally *P. lima* can be found without marginal pores or with partially filled pores. In older cells, the thecal surface can become vermiculate. The intercalary band appears as a thick, smooth, and well-defined margin at the periphery of the valve giving the appearance of a flared ridge (Figs. 1,2,4-6) (von Stosch 1980; Dodge 1975; Faust 1990b; Faust 1991; Steidinger & Tangen 1996).

The periflagellar area is a shallow V-shaped depression on the right valve (Fig. 3) made up of eight platelets and two pores: a larger flagellar pore and a smaller auxiliary pore (Figs. 1,3-5). A protruding periflagellar collar surrounds the auxiliary pore (Fig. 3). Both valves are anteriorly indented; the left valve margin has a flattened apical ridge that borders the periflagellar area (Figs. 1,2,6)(Faust 1991; Steidinger & Tangen 1996).

Nomenclatural Types:
Holotype: *Prorocentrum lima* (Ehrenberg) Dodge, 1975: 109, figs. 1E,F, plate 1B,C
Type Locality: unknown
Synonyms:
Exuviaella marina Cienkowski, 1881
Exuviaella lima (Ehrenberg) Bütschli, 1885
Exuviaella marina var. *lima* (Ehrenberg) Schiller 1933
Basionym: *Cryptomonas lima* Ehrenberg, 1860

Morphology and Structure: *Prorocentrum lima* is a photosynthetic species containing two chloroplasts, a central pyrenoid and a large posterior nucleus (Figs. 5,6)(Dodge 1975).

Reproduction: *P. lima* reproduces asexually by binary fission. This species also exhibits an alternate form of asexual reproduction in which a chain of cell pairs is enclosed within a thinwalled cyst. In this mode multiple vegetative divisions occur within a hyaline envelope (a division cyst) which may contain a chain of 4 to 32 cells (Faust 1993d). Sexual reproduction has also been documented: isogamous gametes form, conjugation takes place, and a large hypnozygote (resting cyst) is produced (Fig. 7)(Faust 1993c).

Ecology: *P. lima* is a benthic and epiphytic species that can be tycoplanktonic. Cultured cells readily adhere to the culturing vessel via mucous strands and rarely swim freely (Fukuyo 1981; Steidinger & Tangen 1996).

This species produces a pale colored resting cyst as part of its life cycle. Cysts are large (70-75 µm diameter) and round with a smooth triple-layered wall (Faust 1993c).

Toxicity: *Prorocentrum lima* is a toxic dinoflagellate species known to produce a number of toxic substances: fast-acting toxin (FAT)(Tindall et al. 1989); prorocentrolide (Torigoe et al. 1988); and diarrhetic shellfish poison (DSP) toxins (Yasumoto et al. 1987): okadaic acid (OA)(Murakami et al. 1982; Lee et al. 1989; Marr et al. 1992); Dinophysistoxin-1 (DTX1)(Marr et al. 1992); Dinophysistoxin-2 (DTX2)(Hu et al. 1993); and Dinophysistoxin-4 (DTX4)(Hu et al. 1995).

Species Comparison: *P. lima* is difficult to identify due to its similar morphology to several other *Prorocentrum* species with a triangular periflagellar area and an oval or ovoid shape (e.g. *P. foraminosum*, *P. concavum* and *P. hoffmannianum*). *P. lima* can be distinguished by its size, shape, narrow periflagellar area and the presence of valve and marginal pores. *P. concavum*, however, is larger, broader, has more valve pores and does not have marginal pores. *P. foraminosum* and *P. hoffmannianum* are also similar in shape to *P. lima*, though both are larger species with very different valve pore numbers and arrangements. *P. hoffmannianum*, moreover, is much broader and its valve surface is deeply areolated (Steidinger 1983; Steidinger & Tangen 1985; 1996; Fukuyo 1981; Faust 1990b; 1991; 1993b).

Steidinger (1983) recognized that the marginal pores of *P. lima* can be used to differentiate this species at the light microscope level from completely areolated species such as *P. concavum* or *P. compressum* which are similar in shape.

Habitat and Locality: *Prorocentrum lima* is a neritic, estuarine species with world-wide distribution (Steidinger & Tangen 1996). Cells can be found in temperate (Lebour 1925; Schiller 1933; Carter 1938) as well as tropical oceans (Fukuyo 1981; Steidinger 1983; Carlson 1984; Faust 1990b). This species occurs in sand (Lebour 1925; Drebes 1974; Dodge 1985), attached to the surface of red and brown algae and benthic debris (Fukuyo 1981; Steidinger 1983; Carlson 1984), associated with coral reefs (Yasumoto et al. 1980; Fukuyo 1981; Bomber et al. 1985; Carlson & Tindall 1985), or can be found attached to floating detritus in mangrove habitats (Faust 1991).

Prorocentrum maculosum

Faust, 1993

Plate 44, Figs. 1-6

Species Overview: *Prorocentrum maculosum* is an armoured, marine, benthic dinoflagellate species. This toxic species is often associated with floating detritus in tropical coastal regions of the Caribbean Sea.

Taxonomic Description: *Prorocentrum maculosum* is a bivalvate species often observed in valve view. Cells are 40-50 µm long and 30-40 µm wide, broadly ovate with the maximum width behind the middle region, and slightly tapered at the anterior end (Figs. 1,2). The thecal surface is rugose with distinct scattered valve poroids (85-90 per valve)(Figs. 1-3). The poroids vary from kidney-shaped to circular or oblong (average diam.=6.0 µm), 2-4 µm apart (Fig. 3). Valve center is devoid of poroids (Figs. 1,2,6)(Faust 1993b).

The valve margins form a distinct ridge which appears as a flange around the cell (Figs. 1,2). Marginal pores are equally spaced (65-75 per valve), and appear larger and more uniform than the valve poroids (Figs. 1,2)(Faust 1993b).

The periflagellar area is a broad triangle on the anterior end of the right valve (Figs. 1,4) made up of 8 platelets and 2 pores (Fig. 4). A thin apical ridge (raised margin) on the left valve surrounds the periflagellar area (Figs. 2,4). The flagellar and auxiliary pores are about equal in size, both surrounded by a curved and flared periflagellar collar (Fig. 4)(Faust 1993b).

Nomenclatural Types:
Holotype: *Prorocentrum maculosum* Faust, 1993: figs. 1,2
Type Locality: Caribbean Sea: Twin Cays, Belize, Central America
Synonyms:
Exuviaella maculosum (Faust) McLachlan, Boalch and Jahn, 1997

Morphology and Structure: *Prorocentrum maculosum* is a photosynthetic species containing golden-brown chloroplasts and a centrally located pyrenoid. A large posterior nucleus is situated adjacent to the pyrenoid (Fig. 5)(Faust 1993b).

Reproduction: *Prorocentrum maculosum* reproduces asexually by binary fission.

Ecology: *P. maculosum* is a benthic species. Cells are motile or attach to detritus or sediment by mucous strands (Faust 1993b).

Toxicity: This is a known toxic species that produces prorocentrolide B, a fast-acting toxin (Hu et al. 1996). A diarrhetic shellfish poison (DSP) toxin, okadaic acid (OA), has also been reported from one Caribbean clone previously identified as *P. concavum* (Dickey et al. 1990), but reassigned to *P. maculosum* (Faust 1996b; Zhou & Fritz 1996).

Species Comparison: The use of scanning electron microscopy has revealed major differences in the micromorphology of benthic species within the genus *Prorocentrum* (Faust 1990a; Faust 1993b). Under LM *P. maculosum* may be confused with *P. lima* (Faust 1991) which has round valve pores and a smooth thecal surface. Dodge (1975), when revising the taxonomy of the genus *Prorocentrum*, described *P. lima* to be a morphologically variable species. However, the architecture of the flagellar pore area was not considered.

P. maculosum and *P. lima* can be distinguished by a number of surface features. The thecal surface of *P. maculosum* is rugose, covered with large kidney-shaped poroids; a periflagellar collar surrounds both equally-sized flagellar and auxiliary pores (Faust 1993b). In *P. lima* the thecal surface is smooth with round pores; only the larger flagellar pore is surrounded by a curved periflagellar collar (Faust 1991).

The valve margins of *P. tropicalis* form a distinct ridge that appears as a flange around the cell, similar to *P. maculosum* (Faust 1993b).

The periflagellar architecture of *P. maculosum* is similar to *P. hoffmannianum* (Faust 1990b), *P. compressum* (Abe 1967; Dodge 1975), *P. playfairi* and *P. foveolata* (Croome & Tyler 1987).

Etymology: The name '*maculosum'* originates from Latin and refers to 'speckled, spotted', which describes the thecal surface of this species (Faust 1993b).

Habitat and Locality: Populations of *P. maculosum* are often associated with floating detritus in tropical coastal regions of the Caribbean Sea (Faust 1993b).

Prorocentrum mexicanum
Tafall, 1942
Plate 45, Figs. 1-7

Species Overview: *Prorocentrum mexicanum* is an armoured, marine, benthic dinoflagellate species. This toxic species is commonly found in tropical shallow embayments.

Taxonomic Description: *Prorocentrum mexicanum* is a bivalvate species often observed in valve view. Cells are ovate to oblong with straight sides (30-38 μm long and 20-25 μm wide) (Figs. 1,2,6). The valve surface of young cells is smooth (Fig. 2), but in older cells it may appear rugose (Figs. 1,3,5). Both valves have many large trichocyst pores (100 per valve) radially arranged in furrowed depressions (Figs. 1-5), and 80 marginal pores (Fig. 3). Trichocyst pores are round with a smooth edge (0.5 μm in diameter) and even in size (Fig. 4). Ejected trichocysts are common. Valve center devoid of pores. The intercalary band is broad and transversely striated (Figs. 3,5)(Faust 1990b).

The periflagellar area, located apically and off-center on the right valve, is a relatively small, V-shaped, shallow depression (Figs. 1,5). It houses a prominent curved periflagellar collar adjacent to the auxiliary pore (Figs. 1,2,5). Opposite is a smaller periflagellar plate adjacent to the flagellar pore (Fig. 5). The large periflagellar collar (2 X 6 µm) may appear as an apical spine, and has been reported as such (Fukuyo 1981; Carlson 1984). Both valves are excavated (Figs. 1,2)(Faust 1990b).

Nomenclatural Types:
Holotype: *Prorocentrum mexicanum* Tafall, 1942: plate 34, figs. 3,8
Type Locality: North Pacific Ocean: Mexico
Synonyms:
Prorocentrum maximum Schiller, 1937
Prorocentrum rhathymum Loeblich, Sherley and Schmidt, 1979

Morphology and Structure: *P. mexicanum* is a photosynthetic species with a posterior nucleus (Faust 1990b).

Reproduction: *Prorocentrum mexicanum* reproduces asexually by binary fission. Sexual reproduction has also been observed in natural cell populations (Faust, M.A., pers. com.).

Ecology: *P. mexicanum* is a benthic species that can be tycoplanktonic (Steidinger & Tangen 1996). Cells swim freely or attach to floating detritus with mucous strands. Cells are often found embedded in mucilage (Faust 1990b).

Toxicity: *P. mexicanum* is a known toxin-producing species (Steidinger 1983; Carlson 1984; Tindall et al. 1984) producing fast-acting toxin (FAT)(Tindall et al. 1984).

Species Comparison: With its prominent periflagellar collar, *P. mexicanum* most resembles *P. caribbaeum* in general cell shape; however, *P. caribbaeum* is a larger species, is broader and heart-shaped, and broadest in the anterior region (Dodge 1975; Faust 1993a).

Trichocyst pore morphology is also similar in these two species; however, significant differences lie in the number of trichocyst pores: *P. caribbaeum* has a greater number of pores per valve (145-203) than *P. mexicanum* (100 per valve). Ejected trichocysts are often observed in cells of both species (Faust 1990b; 1993a).

P. mexicanum, *P. emarginatum* and *P. caribbaeum* all have radially arranged valve pores and display two different sized pores (Loeblich et al. 1979; Fukuyo 1981; Steidinger 1983; Faust 1990b; 1993a).

The periflagellar area and platelet architecture of *P. caribbaeum* is similar to that of *P. mexicanum* (Carlson 1984; Faust 1993a).

The intercalary band of *P. mexicanum* is transversely striated. This is similar to *P. caribbaeum* and *P. emarginatum* (Faust 1990b; 1993a).

Habitat and Locality: *Prorocentrum mexicanum* is a common species found in tropical and subtropical benthic communities (Steidinger & Tangen 1996) of shallow protected areas of the Pacific and Atlantic Oceans (Faust 1990b).

Prorocentrum micans
Ehrenberg, 1833
Plate 46, Figs. 1-6

Species Overview: *Prorocentrum micans* is an armoured, marine, planktonic, bloom-forming dinoflagellate. This is a cosmopolitan species in cold temperate to tropical waters.

Taxonomic Description: *P. micans* is a bivalvate species often observed in valve view. Cells of this species are highly variable in shape and size (Figs. 1-5)(see Bursa 1959; Dodge 1975). Cells are tear-drop to heart shaped, rounded anteriorly, pointed posteriorly, and broadest around the middle (Figs. 1,2,4-6). This species is strongly flattened with a well-developed winged apical spine (10 µm long) on the left valve (Figs. 1,3). Cells are medium-sized (35-70 µm long, 20-50 µm wide) with a length:width ratio usually less than two. The cell surface is rugose, covered with shallow minute depressions (Figs. 1,2). Numerous tubular trichocyst pores are also present in short rows arranged radially (Figs. 1,5,6). Intercalary band is smooth and wide (Figs. 1,4-6)(Wood 1954; Toriumi 1980; Dodge 1975; 1982; 1985; Fukuyo et al. 1990; Steidinger & Tangen 1996; Faust et al. 1999).

The periflagellar area is a relatively small, shallow, broad triangular depression situated apically on the right valve off-center (Fig. 3). Two periflagellar pores are present: one large flagellar pore and one smaller auxiliary pore (Fig. 3). Adjacent to the flagellar pore is a small, slightly curved periflagellar plate (Fig. 3). The large pointed apical spine lies adjacent to the periflagellar area, directly opposite the periflagellar plate (Fig. 3)(Taylor 1980; Toriumi 1980).

Nomenclatural Types:
Holotype: *Prorocentrum micans* Ehrenberg, 1834: 307
Type Locality: North Sea: near Kiel, Berlin, Germany
Synonyms:
Cercaria sp. Michaelis, 1830
Prorocentrum schilleri Böhm in Schiller, 1933
Prorocentrum levantinoides Bursa, 1959
Prorocentrum pacificum Wood, 1963

Morphology and Structure: *P. micans* is a photosynthetic species with two golden-brown chloroplasts situated peripherally. A large kidney-shaped nucleus is situated posteriorly. Two anterior vacuoles are usually present (Dodge 1975; 1982; Toriumi 1980; Fukuyo et al. 1990).

Reproduction: *P. micans* reproduces asexually by binary fission.

Ecology: *P. micans* is one of the most common and diversified species in the genus *Prorocentrum*. It is a planktonic species commonly found in neritic and estuarine waters, but it is also found in oceanic environments; it is cosmopolitan in cold temperate to tropical waters. This species is also known to tolerate very high salinity: populations have been reported from hypersaline salt lagoons (>90 o/oo) in the Caribbean islands (Steidinger & Tangen 1996). Cells are active swimmers (Dodge 1982; Steidinger & Tangen 1996).

This species forms extensive red tides in many parts of the world (Fukuyo et al. 1990; 1999).

Toxicity: Although *P. micans* is capable of forming extensive blooms, it is usually considered harmless (see Taylor & Seliger 1979; Anderson et al. 1985; Graneli et al. 1990). It may excrete substances that inhibit diatom growth, but apparently these substances do not enter the food chain or affect organisms at higher trophic levels (Uchida 1977).

There are only a few reports of *P. micans* having caused problems: shellfish kills in Portugal (Pinto & Silva 1956) and South Africa (Horstman 1981). Claims for toxicity of this species need confirmation. Early reports on *P. micans* being a paralytic shellfish poison (PSP) producer (Pinto & Silva 1956) are unconfirmed, and recent incidents involving shellfish mortality have been attributed to oxygen depletion (Lassus & Berthome 1988).

Species Comparison: This species varies considerably in shape and size and may be confused with closely related species; e.g. *P. gracile, P. scutellum* and *P. caribbaeum*. *P. gracile* has a very strong winged apical spine, is not as broad, and has a length:width ratio usually larger than 2; *P. scutellum* is in the same size range as *P. micans*, but bears a shorter and broader apical spine (Dodge 1975; 1982). *P. caribbaeum* is also in the same size range, but is heart-shaped and broadest around the anterior end, whereas *P. micans* is more tear-drop shaped and broadest around the middle (Dodge 1985; Faust 1993a).

P. gracile and *P. micans* share two distinct features: a.) similar trichocyst pore pattern (Steidinger & Williams 1970; Steidinger & Tangen 1996); and b.) similar arrangement of apical spine: the spines lie adjacent to the periflagellar area (Toriumi 1980).

Trichocyst pore number is highly variable in this species (Dodge 1985): 83 pores per valve were illustrated for one *P. micans* specimen (Dodge 1965), 101 pores per valve for another specimen (Dodge 1985), and 139 pores per valve in yet another specimen (Sournia 1986). Trichocyst pore morphology of this species resembles that of *P. caribbaeum*; however, the latter species has a much greater number of pores per valve: 145-203 (Faust 1993a).

Habitat and Locality: *P. micans* is commonly found in marine waters all over the world (Dodge 1975).

Prorocentrum minimum
(Pavillard) Schiller, 1933
Plate 47, Figs. 1-7

Species Overview: *Prorocentrum minimum* is an armoured, marine, planktonic, bloom-forming dinoflagellate. It is a toxic cosmopolitan species common in cold temperate brackish waters to tropical regions.

Taxonomic Description: *Prorocentrum minimum* is a bivalvate species often observed in valve view. Cells are small (14-22 µm long to 10-15 µm wide) and shape is variable: cells range from triangular (Fig. 1), to oval (Figs. 3,5,7), to heart-shaped (Fig. 6). Cells are laterally flattened (Fig. 3). A short apical spine is sometimes observable (Figs. 1-4,7). Valves with short, evenly shaped broad-based spines (about 600-700 per valve) arranged in a regular pattern (Figs. 1-4). These can appear as rounded papillae depending on angle of view. There are two sized pores present: smaller pores are scattered (Figs. 1,4), while larger pores are located at the base of some peripheral spines. The intercalary band is transversely striated (Figs. 2,5,6) (Parke & Ballantine 1957; Faust 1974; Dodge 1982; Steidinger & Tangen 1996).

The broad anterior end is truncate with a relatively small, shallow, broadly V-shaped depressed periflagellar area located apically on the right valve, slightly off-center (Figs. 1-7). The periflagellar area bears eight apical platelets and two pores of unequal size: a large flagellar pore and a smaller auxiliary pore (Fig. 2). Adjacent to the flagellar pore is a small apical spine (Figs. 2,7). Adjacent to the auxiliary pore is a small, curved and forked periflagellar collar (Figs. 1,2) (Parke & Ballantine 1957; Dodge & Bibby 1973; Faust 1974).

Nomenclatural Types:
Holotype: *Exuviaella minima* Schiller, 1933: figs. 33a,b
Type Locality: Mediterranean Sea: Gulf of Lion, France
Synonyms:
Exuviaella minima Pavillard, 1916
Prorocentrum triangulatum Martin, 1929
Exuviaella marie-lebouriae Parke and Ballantine, 1957
Prorocentrum cordiformis Bursa, 1959
Prorocentrum mariae-lebouriae (Parke and Ballantine, 1957) Loeblich III, 1970

Morphology and Structure: *Prorocentrum minimum* is a photosynthetic species with golden-brown chloroplasts, one large pyrenoid and two pusules. The nucleus is broadly ellipsoidal and posteriorly situated (Parke & Ballantine 1957; Faust 1974; Dodge 1982).

Reproduction: *P. minimum* reproduces asexually by binary fission.

Ecology: *P. minimum* is a bloom-forming planktonic species. Cosmopolitan in cold temperate brackish waters to tropical regions; mostly estuarine, but also neritic (Steidinger & Tangen 1996; Faust et al. 1999). Due to its small size, this species is probably often lost or overlooked in field samples (Dodge, 1982). Cells are active swimmers (Parke & Ballantine 1957).

Recently, Stoecker et al. (1997) reported mixotrophy in this species; ingested cryptophytes were observed in cells of *P. minimum*.

Toxicity: *P. minimum* is a toxic species; it produces venerupin (hepatotoxin) which has caused shellfish poisoning resulting in gastrointestinal illnesses in humans and a number of deaths. This species is also responsible for shellfish kills in Japan and the Gulf of Mexico, Florida (Nakazima 1965; Nakazima 1968; Smith 1975; Okaichi & Imatomi 1979; Tangen 1983; Shimizu 1987; Steidinger & Tangen 1996).

Species Comparisons: *P. minimum* can be confused with *P. balticum*; however, the former species differs by its larger size and different shape, and by having only one apical spine and a forked periflagellar collar (Faust et al. 1999).

Habitat and Locality: *P. minimum* is commonly found along the west coast of the USA, Japan, Gulf of Mexico, Caspian, Adriatic, Mediterranean and Black Seas, and Scandinavian waters; often in large numbers (Dodge 1982; Tangen 1980; 1983; Marasovic et al. 1990).

Prorocentrum ruetzlerianum
Faust, 1990
Plate 48, Figs. 1-6

Species Overview: *Prorocentrum ruetzlerianum* is an armoured, marine, benthic dinoflagellate species. This species is associated with floating detritus and sediment in tropical embayments of the Caribbean Sea.

Taxonomic Description: *P. ruetzlerianum* is a bivalvate species often observed in valve view. Cells are round to ovoid (Figs. 1,4-6) with an average diameter of 28-35 µm. Valve centers are slightly concave (Fig. 1). The entire valve surface is deeply areolate; the areolae are ovate to pentagonal deep depressions (Figs. 1,2,6). Each areola houses a central round pore (1 µm diameter) (Fig. 2). Approximately 500-550 areolae are present on each theca, along with 70-80 evenly spaced marginal areolae. The intercalary band is broad and transversely rugose with long sinuous rugae (Figs. 1,2). Viewed with LM, the valve margins have a distinct striated pattern (Figs. 4,5). This type of intercalary band is unique to this species (Faust 1990b).

The periflagellar area is relatively small, without ornamentation, and set into a shallow, V-shaped depression on the right valve (Figs. 1-3). The flagellar pore is much larger than the auxiliary pore (Fig. 3)(Faust 1990b).

Nomenclatural Types:
Holotype: *Prorocentrum ruetzlerianum* Faust, 1990: figs. 21-23
Type Locality: Caribbean Sea: Twin Cays, Belize, Central America

Morphology and Structure: *Prorocentrum ruetzlerianum* is a photosynthetic species with golden chloroplasts, a centrally located pyrenoid (Figs. 4,5), and a posterior nucleus (Faust 1990b).

Reproduction: *Prorocentrum ruetzlerianum* reproduces asexually by binary fission.

Ecology: *P. ruetzlerianum* is a benthic species associated with floating detritus and sediment. This is not a common species and is often in low numbers when present. Cells are motile or attach to detrital particles (Faust 1990b).

Toxicity: Quod (1996, pers. com.) has shown that this species is a toxin producer; however, the toxin principals have yet to be determined.

Species Comparison: There are several deeply areolated *Prorocentrum* species all with varying amounts of areolae per valve: *P. hoffmannianum* has approximately 670 round to oval areolae per valve (1.1 µm diameter)(Faust 1990b); *P. belizeanum* has about 853-1024 round to oval areolae per valve (0.73 µm diameter)(Faust 1993a); and *P. sabulosum* has about 391 round to oval areolae per valve (1.3 µm diameter)(Faust 1994).

Etymology: This species was named after Dr. Klaus Ruetzler, Invertebrate Zoologist, National Museum of Natural History, Smithsonian Institution, for his extensive investigations on Twin Cays mangrove ecology, his patience, advice, encouragement, and generous support of microbial ecology investigations.

Habitat and Locality: Populations of *P. ruetzlerianum* are often associated with floating detritus and sediments in tropical coastal regions of the Caribbean Sea (Faust 1990b).

GLOSSARY

anisogamous - Sexual reproduction in which the gametes differ from each other morphologically (Taylor 1987); e.g. *Alexandrium tamarense.*

amphitrophy - Nutrition mode of photosynthetic dinoflagellates in which either heterotrophy or autotrophy alone can support cell functions.

antapex - The posterior-most part of the cell.

antapical - In dinokonts, the posterior pole of the cell.

antapical plates - In thecated dinokont species, the plates covering the posterior end of the cell (designated with '''') not in contact with the cingulum.

anterior - In desmokonts, the top part of the cell.

apex - The anterior-most part of the cell.

apical - In dinokonts, the anterior pole of the cell.

apical collar - A topographic feature of some prorocentroids (desmokonts). It is an extension of the intercalary band on the left valve along the anterior margin bordering the periflagellar area (e.g. *P. belizeanum* and *P. hoffmannianum*). This feature can be curved, flared, rounded or flattened. Oftentimes, this feature can only be viewed via SEM.

apical horn - A prominent apical extention of the cell formed by apical plates; it is a feature only found on thecate species. In these species, the apical horn constitutes the apex of the cell (Steidinger & Tangen 1996).

apical plates - In thecated dinokont species, the thecal plates that surround and are in contact with the apex of the cell (designated with ') not in contact with the cingulum. In those species with an apical pore complex (APC), the plates that touch the APC.

apical pore (ap) – Pore located on the Po plate. This feature is not always a round or oval hole, but can be long and narrow and/or curved, or even fishhook shaped. In *Alexandrium* spp. the ap is referred to as a foramen. If the ap is a hole, then it may have a closing/cover plate (cp) or canopy.

apical pore complex (APC) – This feature is located on the epitheca of many marine, armoured (thecated) dinokont species. It includes an apical pore plate (Po), which bears an apical pore (ap), and often times, small periferal pores. In addition, there can be a ventral apical plate or canal plate (X plate). The X plate is always posterior and ventral to the Po.

apical pore plate (Po) - Part of the apical pore complex (APC); a feature located on the epitheca of many marine, armoured (thecated) dinokont species. The Po houses an apical pore (ap), and often times, small periferal pores. The Po can be long and narrow, as in *Ostreopsis* spp., or wide and triangular, as in *Gambierdiscus* spp.

areolae - Surface ornamentation on thecal plates that approximates deep depressions with or without raised sides. The sides may be round to polygonal and are closely appressed. Areolae can contain pores, even double pores.

armoured - Dinoflagellate species that have thecal plates of varying thickness and orientation in identifiable tabulation series. Often the plates are thickened or ornamented with reticulations, spines, grooves, etc... which are often characteristic to a species.

asexual reproduction - A method of reproduction where a 1N cell produces two to four cells with the same chromosome number. This can be by binary fission of a motile stage or a nonmotile stage. In many armoured dinokonts the original cell divides along predetermined sutures and then each half produces a new half with new thin plates.

autotrophy – Photosynthetic nutritional mode in which inorganic compounds (CO_2 and carbonates) are utilized for growth, metabolism and reproduction.

auxotrophy - Heterotrophic nutritional mode in which specific external organic compounds (usually the vitamins B_{12}, biotin and thiamine) are required in small amounts by most photosynthetic dinoflagellates.

benthic - Occuring at the bottom of the water column.

binary fission - A method of asexual reproduction in which the parent cell divides into two equal, or nearly equal, parts, each of which develops to parental size and form.

bioluminescence - The emission of light from certain species of dinoflagellates by either mechanical or chemical stimulation.

bloom - High concentrations of planktonic organisms due to enhanced cell division (growth) rates. Seasonal blooms are often related to periodical increase in nutrient and light conditions (e.g. spring bloom). Exceptional blooms are often dominated by one or a few species and may discolor the water a reddish-brown color, hence the name 'red tide'.

canal plate (X-plate) – A narrow elongated plate found on the epitheca of some thecate dinokont species ventral to the APC.

catenate – Cells connected in a series; cells in chain formation.

chlorophyll - Plant pigments found in chloroplasts which function as photoreceptors of light energy for photosynthesis.

chloroplast - Membrane-bound organelle found in the cytoplasm of various eukaryotic organisms that contain the chlorophyll pigments and the enzyme systems for photosynthesis.

chromosomes - Complex, helical structures in plant and animal nuclei that carry the linearly arranged genetic units, DNA and RNA.

ciguatera - A human intoxication caused by ingestion of tropical piscivorous reef fishes contaminated with toxin-producing benthic/epiphytic dinoflagellates. These fish accumulate biotoxins through the food chain (Steidinger 1993). More than 175 separate gastrointestinal, neurotoxic, or cardiovascular symptoms may be associated with this poisoning (Becker & Sanders 1991). In extreme cases death can result from respiratory failure. Although incidence is high, human mortality is low (Hallegraeff 1995).

cingular plates - In thecate dinokont species, the plates that make up the cingulum (designated with a 'c').

cingulum - In dinokont species, this structure is usually a furrow (girdle) encircling the cell once or several times, and it can be displaced. In thecated species, the cingulum is made up of plates. This structure is missing in some desmokont-type cells (e.g. *Prorocentrum*).

closing plate (cp) - A small plate located in the apical pore complex (APC) of some marine, armoured dinokont species, and associated with the apical pore (ap).

concave - Hollowed or rounded inward resembling the inside of a bowl.

convex - Curved or rounded resembling the exterior of a sphere or circle.

costae - A rib or rib-like structure, often located in the apical pore complex of thecated species; e.g. *Coolia monotis*.

cyst - Any dormant or resting nonmotile cell possessing a distinct cell wall.

cytoplasm - Protoplasm within a plant or animal cell external to the nucleur membrane.

DAPI (4',6-Diamidino-2-Phenylindole) - A highly specific and sensitive fluoresceing DNA stain used in epifluorescent microscopy to observe structures containing DNA. DAPI specifically binds to double stranded DNA, and when excited with light the DAPI-DNA complex fluoresces a bright blue (Porter & Feig 1980).

desmokont - A dinoflagellate cell type in which two dissimilar flagella emerge from the anterior part of the cell; e.g. *Prorocentrum* sp. This morphological type does not have a cingulum or a sulcus.

diameter - With the exception of the Prorocentroids, the maximum cell width measured between the lateral extremes of the cingular flanges (Balech 1995).

Diarrhetic Shellfish Poisoning (DSP) - A human gastrointestinal disease caused by the ingestion of toxic marine shellfish (filter-feeding bivalves) from cold and warm temperate regions of the Atlantic and Pacific Oceans (Steidinger 1993). Shellfish can accumulate and store large quantities of red tide dinoflagellate toxins without apparent harm to themselves (Steidinger & Baden 1984). Symptoms include diarrhea, nausea and vomiting lasting a few days. No human deaths have been reported (Hallegraeff 1995).

dinoflagellate - Biflagellated unicellular alga member in the Phylum Pyrrhophyta.

dinokont - A dinoflagellate cell type in which two flagella are inserted ventrally; one flagellum is transverse and housed in a cingulum and the other is longitudinal and housed in a sulcus. A dinokont dinoflagellate can be a thecate species (with thecal plates) or an athecate species (without thecal plates)(Steidinger & Tangen 1996).

dinophysoid - Group of dinokont type dinoflagellates. Members of this group are the only thecate dinoflagellates fundamentally divisible into two lateral halves and have an anterior cingulum and a narrow sulcus. They are laterally compressed, and their shapes in lateral view are essential for genus and species identification (Taylor et al. 1995).

diploid - A cell that has a nucleus with two sets of chromosomes (2N).

dorsal - Of or relating to the back side of an organism. In dinokonts, opposite the ventral side (front side)(Steidinger & Tangen 1996).

dorsoventral - Extending along the axis joining the dorsal and ventral sides.

encystment - To form or become enclosed in a cyst (resting spore). There are several types of encystment. Stressed cells can 'round up' and settle out of the water column and yet be viable if the stress conditions are removed. Others involve temporary cysts for asexual reproduction, flotation, and other functional aspects of individual survival. Yet another type of encystment involves sexual reproduction and the production of thick-walled hypnozygotes which can remain encysted for months, even years (Steidinger & Tangen 1996).

epibenthic - Attached to the bottom.

epifluorescence microscopy - A method of microscopy used to view light-excited regions of an organism stained with a fluorochrome dye.

epiphyte - An alga which attaches itself and lives nonparasitically on another plant or on some nonliving object. Cell can attach via a mucoid holdfast or thread(s).

epitheca - The anterior part of the dinokont-type cell above the cingulum.

eukaryote - A cell with a membrane-bound nucleus.

excystment - When the hypnozygote matures and is ready to produce a motile cell from the resting cell, a naked cell will emerge from an opening in the cyst wall. This emerging cell will either be flagellated or amoeboid. Typically, this cell will undergo meiosis and produce four vegetative 1N cells that are motile in the water column (Steidinger & Tangen 1996).

flagellar pore - In desmokont dinoflagellates, the pore in which flagella emerge located in the periflagellar area (flagellar pore area).

flagellum - Whip-like structures arising from the cell and responsible for propelling cells in a watery fluid. All dinoflagellates at some time in their life cycle have two dissimilar flagella: a transverse flagellum (provides propulsion) and a longitudinal flagellum (provides direction). They either emerge through one pore or two separate pores.

fluorescence - Emission of energy as visible light.

foramen - A relatively large comma-shaped cavity (apical pore) on the Po plate of *Alexandrium* spp. (sometimes fishhook shaped as in *Alexandrium catenella* and *A. tamarense*). It is a diagnostic feature of the APC.

gametes - In armoured and unarmoured species a 1N cell that fuses with another 1N cell to produce a zygote (2N).

geotropic - Oriented by gravity.

growth - Increase of body volume, and proliferation of a cell.

haploid - Vegetative or gametic cells that have one set of chromosomes (1N).

hepatotoxic - Toxic to the liver.

heterothallism - Sexual cycle in dinoflagellates which involves opposite mating types; e.g. *Gymnodinium catenatum*.

heterotrophy - Nutritional mode in which absorption of organic matter is required for growth, metabolism and reproduction; e.g. auxotrophy, mixotrophy, myzocytosis, phagotrophy and organotrophy.

horn - In armoured cells an extension of the apical or antapical plates.

hypnozygote - A thick-walled zygote formed following fusion of two motile gametes (diploid-2N).

hypotheca - The posterior part of a dinokont-type cell below the cingulum.

hystrichosphere - A fossilized dinoflagellate cyst.

intercalary band - Marginal growth zones between thecal plates; usually straited horizontally or transversely.

isogamous - Sexual reproduction in which the fusing gametes differ morphologically from the vegetative cells, but are morphologically identical to each other (Taylor 1987); e.g. *Alexandrium monilatum*.

lacerate - With a deeply and irregularly incised margin.

lanceolate - Tapering at both ends.

lateral - In desmokonts oriented toward the left or right side of the cell.

lenticulate - Shaped like a double convex lens; shaped like a lentil.

life cycle - A continuum of phases and cell types in the reproduction and growth of a species. The life cycle usually contains at least an asexual phase in which a cell can divide by binary fission and produce two similar cells (1N). It may also contain a sexual phase in which gametes fuse to form zygotes (2N) and these zygotes produce 1N cells.

list - Membranous thecal extensions of armoured dinoflagellates (often associated with the cingulum and sulcus); some extensions are curved or ribbed.

lobe - A rounded projection on a structure.

megacytic growth zone - The cell growth that occurs at the suture between the two valves of the Prorocentrales or the fissure halves of the Dinophysiales. When this usually horizontally striated zone is at its maximum extent, the cell will be at its greatest depth or width, respectively (Steidinger & Tangen 1996).

mesokaryotic - Dinoflagellate nucleus which possesses characteristics of both prokaryotes and eukaryotes.

mixotrophy - Heterotrophic nutritional mode of some photosynthetic dinoflagellates in which ingestion of food particles is required for existence.

mucocyst - An ejectile organelle; a minute structure that emerges through pores in the theca of armoured dinoflagellates that releases mucous or mucous threads when discharged.

myzocytosis - Heterotrophic nutritional mode in which prey is suctioned into a food vacuole via a feeding tube or peduncle, and then digested (Schnepf & Deichgraber 1983).

neritic - The region of shallow water adjoining the seacoast; e.g. bays, lagoons, mangroves, salt marshes, etc.

Neurotoxic Shellfish Poisoning (NSP) - A human neurological disease caused by the ingestion of toxic marine shellfish (filter-feeding bivalves). Symptoms are similar to those of ciguatera poisoning and include temperature reversal sensations, as well as headache, chills, and muscle and joint pain (Hallegraeff 1995, Steidinger 1993). Cases have been reported from the southeast US and eastern Mexico (Steidinger 1993).

nucleus - A membrane-bound organelle in eucaryotic cells which contains a large percentage of the genetic material in the cell. In dinoflagellates, it is most often referred to as a mesokaryon or a dinokaryon due to its unique feature: chromosomes are permanently condensed.

organelle - A specialized subcellular structure having a special function; e.g. mitochondria.

organotrophy - Heterotrophic nutritional mode of dinoflagellates without chloroplasts; i.e. total nutrition and growth is derived exclusively from organic compounds.

osmotrophy - Active uptake of dissolved organic substances for nutrition.

ovate - Shaped like an egg; one end broader than the other.

Paralytic Shellfish Poisoning (PSP) - A human neurological disease caused by the ingestion of toxic marine shellfish (filter-feeding bivalves) as well as other harvested seafood. PSP has been reported from cold and warm seas (Steidinger 1993). Shellfish can accumulate and store large quantities of bloom or red tide dinoflagellate toxins without apparent harm to themselves (Steidinger & Baden 1984). Symptoms include: tingling sensation around lips gradually spreading to face and neck; prickly sensation in fingertips and toes; headache, dizziness, nausea, vomiting, diarrhea. In extreme cases, muscular paralysis occurs resulting in death from respiratory paralysis (Hallegraeff 1995).

peduncle - A small, flexible, finger-like appendage located near the flagellar pores in some photosynthetic as well as nonphotosynthetic species. Its functions are not fully understood, but it has been associated with feeding behavior (phagotrophy).

pellicle - A retaining envelope which may be found around certain dinoflagellates or which can develop at a certain stage of the life history.

periflagellar area - In prorocentroids (desmokonts) this region is located on the anterior end of the right valve within a notched area (V-shaped triangular depression). It consists of several plates or platelets around one or two periflagellar pores, the auxilliary pore (A) and the flagellar pore (F). Accessory pores, apical spine(s), periflagellar collars and/or periflagellar plates may also be present.

periflagellar collar - A topographic feature of the periflagellar area of some prorocentroids (desmokonts). It is a thecal extension of a periflagellar plate that can lie adjacent to the periflagellar pores (flagellar and auxiliary) and/or surround one or both pores (e.g. *Prorocentrum maculosum*). A periflagellar collar can be flared and/or protuberant, or appear as a winged spine (e.g. *Prorocentrum mexicanum*). Oftentimes, this feature can only be viewed via SEM.

periflagellar plates - A topographic feature of the periflagellar area of some prorocentroids (desmokonts); platelets situated around the periflagellar pores.

periflagellar pores - In prorocentroids (desmokonts), large apical pores found in the periflagellar area: auxiliary pore (A) and/or the flagellar pore (F). A periflagellar collar can surround these pores; e.g. *P. maculosum*.

phagotrophy - Heterotrophic feeding mode of generally non-photosynthetic dinoflagellates in which whole prey (or parts of) are ingested or engulfed, with digestion occurring in phagocytic vacuoles.

photosynthesis - The use of only inorganic compounds for growth, metabolism and reproductionin presence of light.

phytoplankton - Planktonic plant life.

pigments - Any coloring matter in plant or animal cells.

plankton - Refers to free-living organisms in aquatic environments that have little or no self-motility and therefore float and drift under the action of water movement.

plastids – Cytoplasmic organelles of photosynthetic cells that serve as centers of specialized metabolic activities.

pore - Openings or channels in the theca of dinoflagellates that can be involved in extrusion of trichocysts or mucocysts and other active processes. Pore number and location are variable within a species, but in many groups, the pattern is a reliable, but variable character for identification of species (Steidinger & Tangen 1996).

poroid - Shallow surface depressions on the valve surface.

post-cingular plates - In thecated dinokont species, the plates touching the cingulum in the hypotheca (designated with ''').

posterior - In desmokonts, the bottom end of the cell.

pre-cingular plates - In thecated dinokont species, the plates touching the cingulum in the epitheca (designated with '').

premedian cingulum - In dinokont-type cells when the cingulum is above the midpoint of the cell.

prokaryote - A cell that contains a primitive nucleus where the DNA-containing region lacks a definitive membrane; e.g. bacteria and cyanobacteria.

prorocentroids - Group of desmokont type dinoflagellate. Two anteriorly inserted flagella and two large laterally flattened valves easily distinguish the species of this group. The right valve has a small indentation, the periflagellar area, that houses the flagellar pore(s) (Taylor et al. 1995).

pustule - A small elevation on the valve surface resembling a blister or pimple.

pyrenoid – Cytoplasmic structure made of protein or appended to the chloroplasts in most phytoflagellates. They are associated with the formation or storage of polysaccharide food reserves (usually starch)(Steidinger & Tangen 1996).

reticulae - Surface ornamentation on thecal plates where raised straight lines or ridges cross one another creating a complex pattern resembling a network of fibers, veins or lines.

rugose - Uneven surface covered with shallow minute depressions.

Scanning Electron Microscopy (SEM) – Instrumentation used to observe minute surface details of small organisms/objects at high magnification by means of electron lenses. SEM techniques are often employed and needed to correctly identify a dinoflagellate species.

sexual reproduction - A method of reproduction that involves two gametes (1N) that fuse to produce a zygote (2N).

striae - Surface ornamentation on unarmoured or armoured dinoflagellates that appear as longitudinal lines, ridges or grooves; on armoured species the striae can be interrupted by pores and may be associated with other markings, such as reticulations.

sulcus - Longitudinal area on the ventral surface of dinokont-type cells that forms a pronounced furrow or depression that houses the longitudinal flagellum. In thecated species, the sulcus is made up of sulcal platelets (designated by 's'). This feature is not present in some desmokont-type cells (Steidinger & Tangen 1996).

sutures - In armored species, visible linear boundaries between thecal plates (Steidinger & Tangen 1996).

theca - Dinoflagellate membrane system encompassing the whole cell consisting of a complex of three to six membranes.

thecal plates - Plates of armoured (thecated) species which are composed of cellulose or polysaccharide microfibrils. Their particular size, shape and arrangement on the cell are characteristic to a species (Steidinger & Tangen 1996).

transdiameter - With the exception of the Prorocentrales, the cell width measured between the lateral extremes of the cingulum bottom; i.e. the flanges are excluded. Minimum cingular width; a measurement of width used in armoured dinokonts (Balech 1995).

trichocysts – A cytoplasmic ejectile organelle; a minute structure that emerges through pores in the theca of armoured dinoflagellates that releases filamentous or fibrillar threads when discharged.

tycoplanktonic - Benthic dinoflagellate species found at some time in the water column.

unarmoured - Dinokont-type cells that do not have an identifiable plate series and do not have apical pore complexes.

vacuole - A cytoplasmic membrane-bound cavity within a cell that may function in digestion, storage, secretion or excretion.

valves - In the thick-walled desmokonts, two opposing halves of the theca are called valves (right and left). The right valve is the one most indented anteriorly by the periflagellar plates.

ventral - The front side of an organism (opposite dorsal side): in dinokonts, side of sulcus and juncture of the cingulum-sulcus; in dinokonts, the side of flagellar insertion (Steidinger & Tangen 1996).

ventral pore (vp) - In some armored species, a ventral pore may be present at the juncture of the first apical plate (1') and an anterior intercalary or another apical plate on the epitheca. Sometimes the pore is in one of the apical plates. The presence of a ventral pore or its placement may be diagnostic for certain species (Steidinger & Tangen 1996).

ventral ridge - In dinokonts, an identifiable ridge on the right side of the sulcal intrusion onto the epitheca.

vermiculate - Surface ornamentation on thecal plates in which the plates are marked with irregular fine lines or with wavy impressed lines.

zygote - A cell (2N) formed by the union of two gametes (1N) during sexual reproduction.

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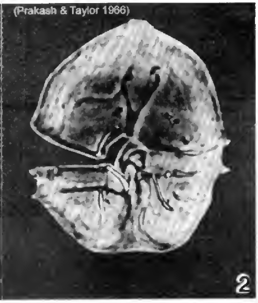
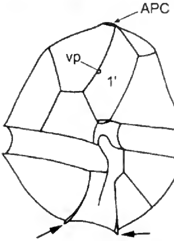
PLATE 1





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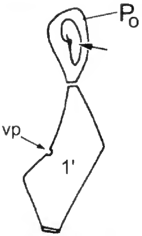

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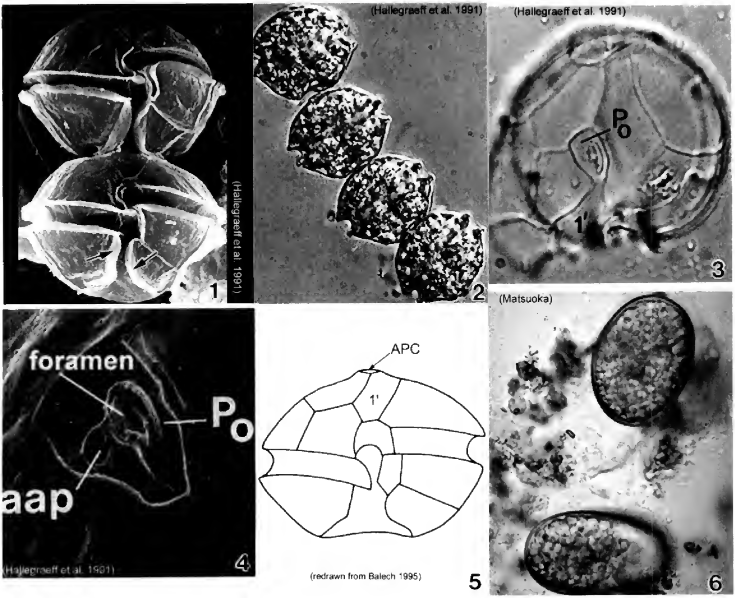
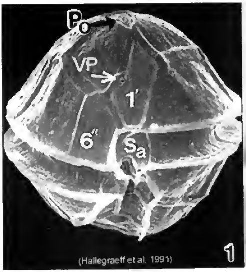
Alexandrium acatenella. Figs. 1-2. LM: ventral view of empty thecae. Cell small to medium, longer than wide, angular to round. Conical epitheca with shoulders; larger than hypotheca. Figs. 3-4. Line drawings. Fig. 3. Ventral view: 1' plate bears ventral pore (vp). Hypotheca with two antapical spines (arrows). Fig. 4. Po comes in direct contact with 1' plate. APC: comma-shaped foramen (arrow).

PLATE 2



Alexandrium catenella. Fig. 1. SEM: ventral view. Two cell chain. Cells round; wider than long. Rounded apex and slightly concave antapex. Cingulum deep and lipped; sulcus deeply impressed and widens posteriorly. Hypotheca with prominent sulcal lists (arrows). Fig. 2. LM: four cell chain. Cells anterior-posteriorly compressed. Fig. 3. LM: apical view. First apical plate (1') comes in direct contact with apical pore plate (Po). Ventral pore absent from 1' plate. Fig. 4. SEM: apical pore complex (APC). Foramen fishhook shaped; anterior attachment pore (aap) adjacent. Fig. 5. Line drawing: thecal plates depicted. Fig. 6. LM: resting cyst elliptical with rounded ends.

PLATE 3



(Hallegraeff et al. 1991)

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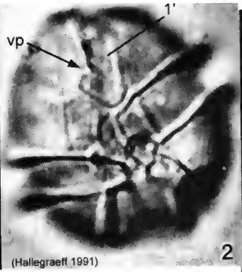

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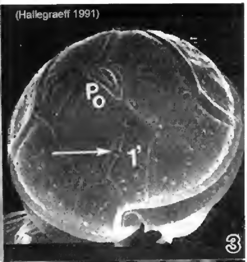

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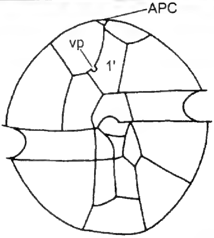

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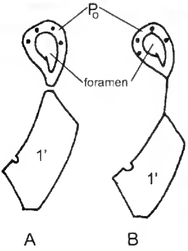

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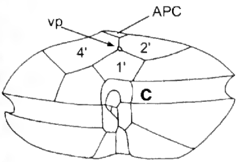
(Matsuoka & Fukuyo)

6

Alexandrium minutum. Fig. 1. SEM: ventral view. Cell small and ellipsoidal. Epitheca conical, larger than hypotheca. Hypotheca short and wide; antapex obliquely flattened. Intercalary bands present. Cingulum deep, lipped; displaced 1X its width. Sulcus shallow (sa=anterior sulcal plate). Apical pore plate (Po) in direct contact with 1' plate. Fig. 2. LM: ventral view. Ventral pore (vp) present on 1' plate. Fig. 3. SEM: apical view. Po large, narrow and oval; indirectly connected to 1' plate. Vp present (arrow). Figs. 4-5. Line drawing. Fig. 4. Ventral view. 1' plate slender and rhomboidal. Fig. 5. Po connection to 1' plate: a. direct; b. indirect via thin suture. Fig. 6. LM: cyst circular in apical view.

PLATE 4

(Walker & Steidinger 1979)



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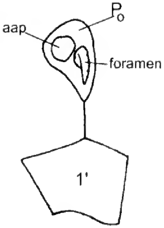

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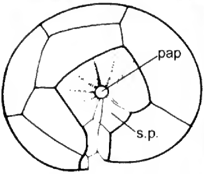

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4

(Walker & Steidinger 1979)

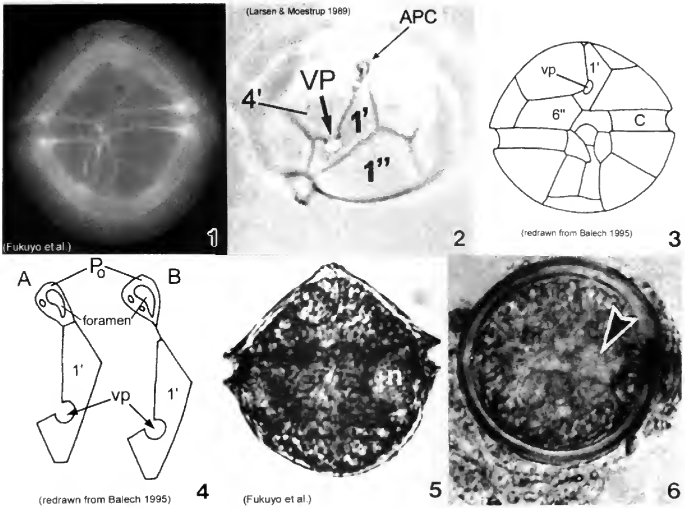
5

(Walker & Steidinger 1979)

6

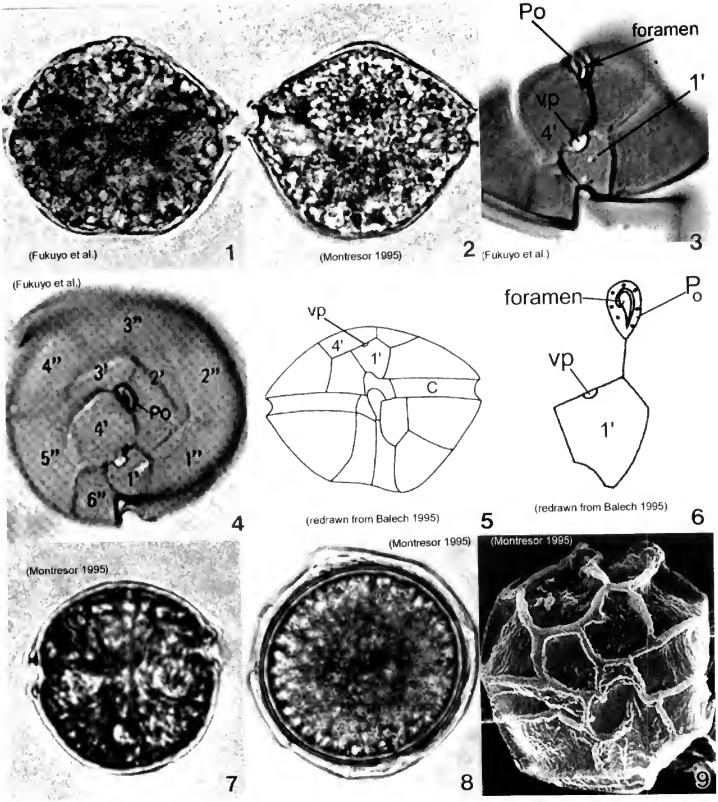
Alexandrium monilatum. Fig. 1. LM: four-cell chain. Cells large, wider than long, flattened anterio-posteriorly. Antapex slightly concave (arrow). Figs. 2-4. Line drawings. Fig. 2. Ventral pore (vp) depicted (Florida specimens) at anterior margin of 1' plate where it comes in contact with plates 2' and 4'. Cingulum (C) deeply excavated, wide, descending; displaced one time its width. Fig. 3. Apical pore plate (Po) does not come in contact with 1' plate. Anterior attachment pore (aap) large, round and dorsally situated in the APC. Foramen comma-shaped. Fig. 4. Antapical view: posterior sulcal plate (sp) large, rhomboid and concave with radial markings. Posterior attachment pore (pap) large and centrally located. Figs. 5-6. LM. Fig. 5. Two isogamous gametes fusing at oblique angles. Fig. 6. Mature resting cysts: dark and round, with a triple layered wall.

PLATE 5



Alexandrium ostenfeldii. Figs. 1-3. LM. Fig. 1. Ventral view. Cell large and nearly spherical. Cingulum deeply excavated. Epitheca broad and convex-conical. Hypotheca hemispherical with an obliquely flattened antapex. Fig. 2. Epitheca: apical view. Ventral pore (vp) large and distinct. First apical plate (1') forms a 90 degree angle at the point where vp and 4' plate come in contact. Apical pore complex (APC) with comma-shaped foramen. Figs. 3-4. Line drawings. Fig. 3. Ventral view: 6'' plate wider than high. Cingulum (C) slightly excavated. Fig. 4. APC and 1' plate: a. Po in direct contact with 1'; b. Po in indirect contact with 1' via thin suture. Fig. 5. LM: vegetative cell. Small equatorial nucleus (n). Fig. 6. LM: temporary cyst large and spherical, covered in mucilage. Nucleus visible (arrowhead)(Mackenzie et al. 1996).

PLATE 6



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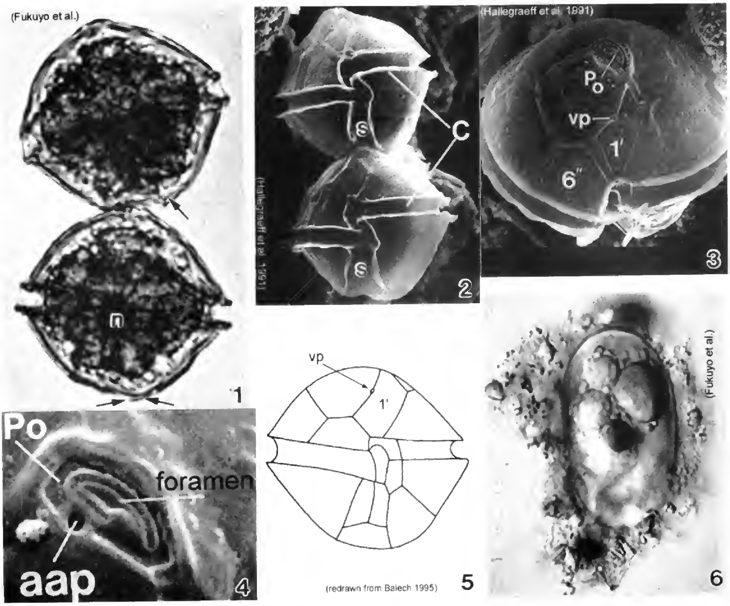
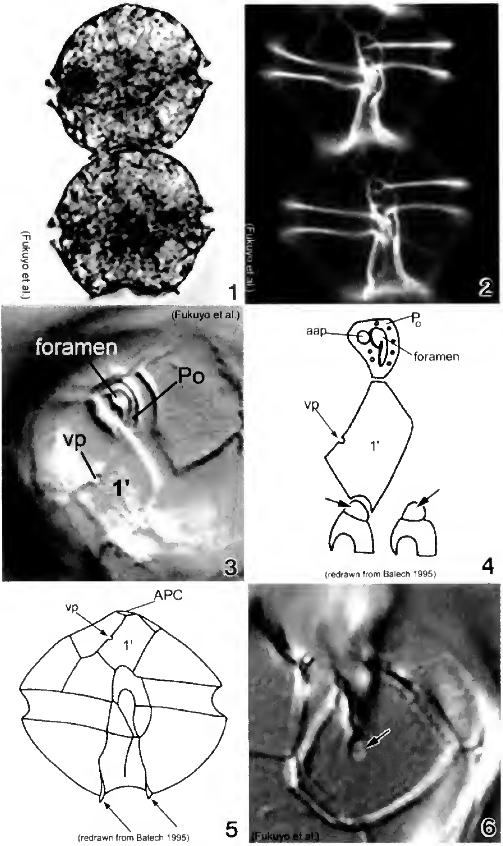
Alexandrium pseudogonyaulax. Figs. 1-4. LM. Fig. 1. Ventral view. Cell broadly pentagonal; wider than long. Epitheca short and dome-shaped. Hypotheca longer than epitheca. Cingulum shallow and barely displaced. Fig. 2. Dorsal view. Antapex obliquely concave. Fig. 3. Epitheca: ventral view. Apical pore plate (Po) with comma-shaped foramen. 1' plate pentagonal with large wide ventral pore (vp) on 4' plate margin. Fig. 4. Epitheca: apical view. 1' plate does not come in contact with Po. Po oval and longitudinal on apex. Figs. 5-6. Line drawings. Fig. 6. Po and 1' plate not in contact. Fig. 7. LM: isogamous gametes smaller and rounder than vegetative cells. Fig. 8. LM: round resting cyst. Fig. 9. SEM: paratabulate cyst.

PLATE 7



Alexandrium tamarense. Fig. 1. LM. Two cell chain: cells small to medium; slightly longer than wide, nearly spherical. Cingulum (C) deeply escavated and lipped. Left hypothcal lobe slightly larger than right. Nucleus (n) visible. Figs. 2-4. SEM. Fig. 2. Two cell chain: cingulum displaced 1X its width. Deep sulcus (s) widens posteriorly. Fig. 3. Epitheca: apical view. Apical pore plate (Po) rectangular; narrows ventrally. Po and first apical plate (1') in direct contact. Small ventral pore present on 1' plate. Fig. 4. Apical pore complex (APC): foramen large and fishhook shaped. Small round anterior attachment pore (aap) present (Hallegraeff 1991). Fig. 5. Line drawing. Fig. 6. LM. Oblong resting cyst with rounded ends, reddish lipid bodies; covered in mucilage.

PLATE 8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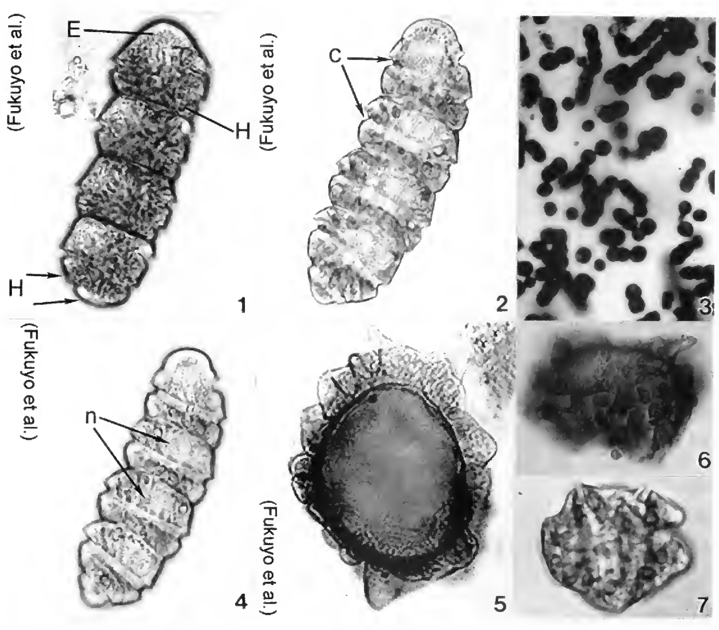
(Fukuyo et al.)

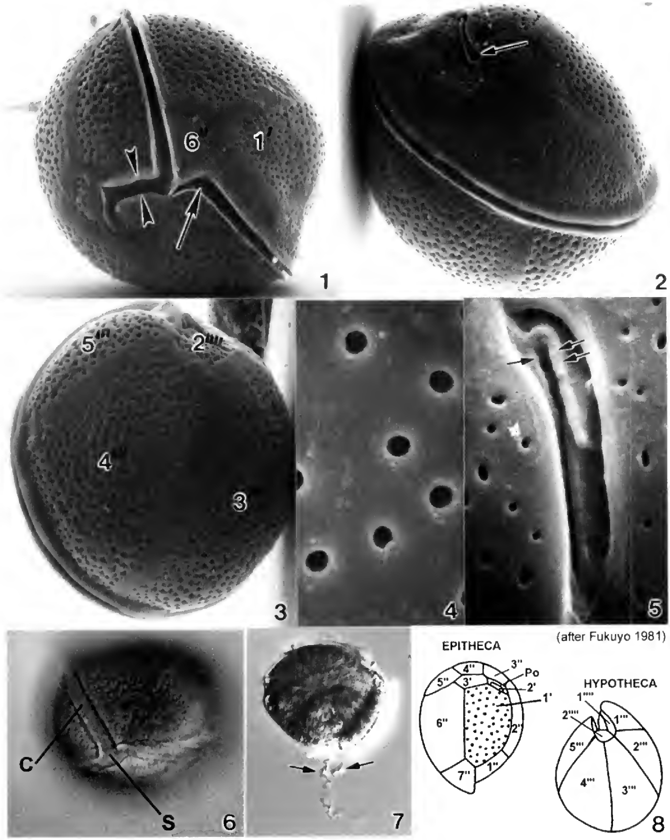
Alexandrium tamiyavanichi. Figs. 1-3. LM. Fig. 1. Two cell chain: cells medium-sized; round to slightly wider than long. Epitheca with shoulders. Fig. 2. Cells stained with calcofluor white: cingulum displaced 1X its width; sulcus widens posteriorly. Fig. 3. Apical view: apical pore plate (Po) houses comma-shaped foramen. First apical plate (1') with ventral pore (vp). Figs. 4-5. Line drawings. Fig. 4. 1' plate in direct contact with Po. Po with large central foramen surrounded by small pores. Anterior sulcal plate (s.a.) invades epitheca: an anterior projection of s.a. fits into a notch in the 1' plate (arrows). Fig. 5. Ventral view: sulcal lists project anteriorly (arrows). Fig. 6. Posterior sulcal plate (s.p.) with round posterior attachment plate (pap) in center (arrow).

PLATE 9



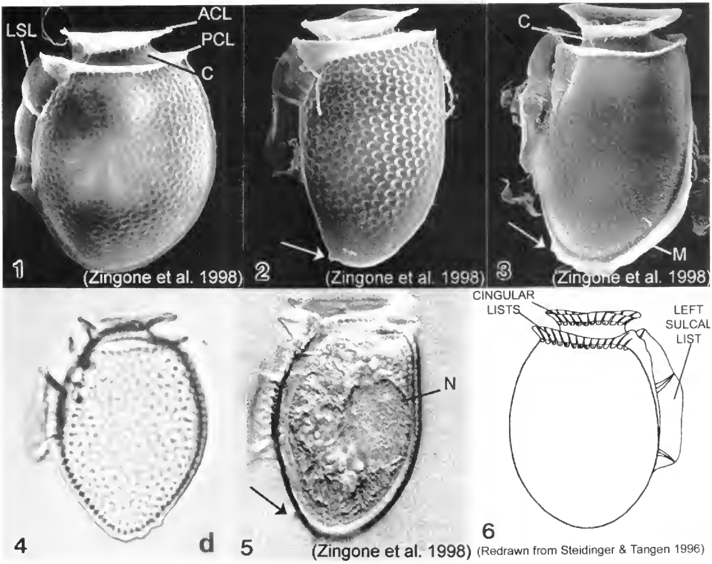
Cochlodinium polykrikoides. Figs. 1-7. LM. Fig. 1. Four cell chain. Single cell small and ellipsoid. Epitheca (E) rounded and conical. Hypotheca (H) divided into two posterior lobes (arrows). Numerous rod-shaped chloroplasts. Fig. 2. Cingulum (c) deeply excavated; circles cell 1.8-1.9 times. Fig. 3. Colony of single and chained cells. Fig. 4. Large nucleus (n) in epitheca. Figs. 5-7. Cysts. (Figs. 3,6,7 by Matsuoka & Fukuyo)

PLATE 10



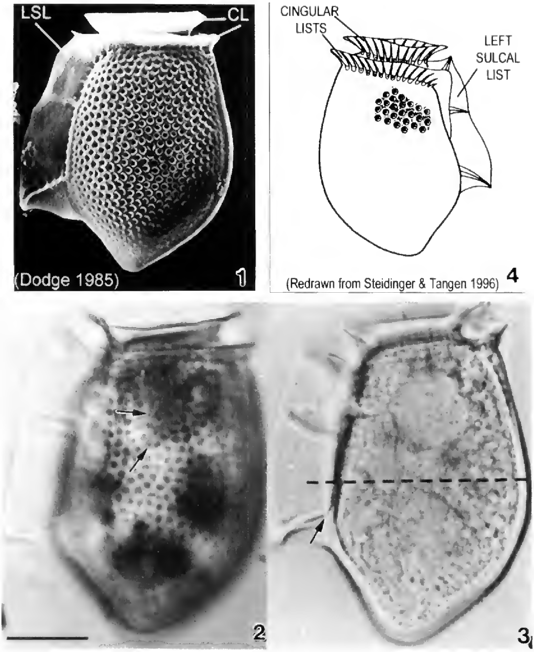
Coolia monotis: Figs. 1-5. SEM. Fig. 1. Ventral view: spherical shape. Cingulum lipped and equatorial. Sulcus with flexible lists (arrowheads). Ventral pore present (arrow). Fig. 2. Dorsal view: apical pore plate (arrow), Po, located off-center on epitheca. Fig. 3. Antapical view: hypothecal plates. Fig. 4. Smooth edged thecal pores unevenly distributed. Fig. 5. Po about 12 µm long, slightly curved and narrow with a slit-like apical pore. Two supporting rib-like costae (arrows) and evenly spaced round pores surround the pore. Figs. 6,7. LM. Fig. 6. Ventral view of lipped cingulum and sulcus. Fig. 7. Planozygote with two longitudinal flagella (arrows). Fig. 8. Line drawing: thecal plate arrangement.

PLATE 11



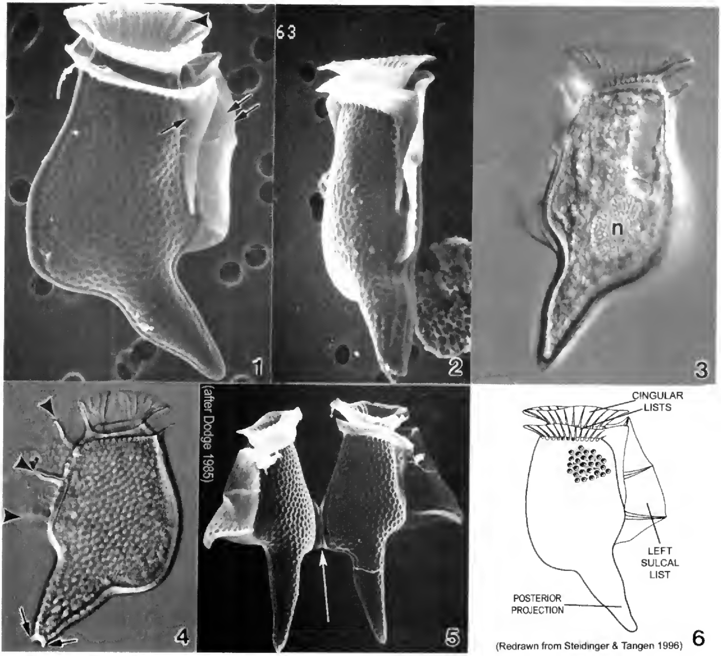
Dinophysis acuminata. Figs. 1-5. SEM: lateral view. Fig. 1. Cell oval and rotund; thecal surface with shallow depressions and scattered pores. Left sulcal list (LSL) extends beyond midpoint of cell. Well-developed cingular lists: anterior cingular list (ACL); posterior cingular list (PCL). C=cingulum. Fig. 2. Long and narrow cell with prominent surface areolae, each with a pore. Antapex tapered and ventrally off-center. Small posterior protrusion present (arrow). Fig. 3. Long and narrow cell. Thecal surface smooth with small scattered pores. Megacytic zone (M) void of pores. Posterior protrusions on antapex (arrow). Figs. 4-5. LM: lateral view. Fig. 4. Surface areolae and tapered antapex (from Larsen & Moestrup 1992: fig. 1d). Fig. 5. Large dorsal nucleus (N). Small, blunt projections on tapered antapex (arrow). Fig. 6. Line drawing.

PLATE 12



Dinophysis acuta. Fig. 1. SEM: lateral view. Cell oblong and robust; theca heavily areolated. Well developed cingular lists (CL) and left sulcal list (LSL). Pointed antapex. Figs. 2-3. LM: lateral view (from Larsen & Moestrup 1992: figs. 2a,d; scale bars=20 µm). Fig. 2. Large areolae, each with a pore (arrows). Fig. 3. Widest point below mid-section (dashed line) aligned with third sulcal rib (arrow). Fig. 4. Line drawing.

PLATE 13

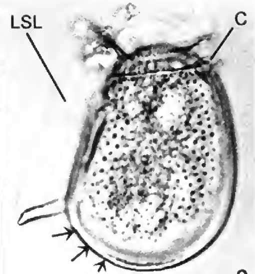


(Redrawn from Steidinger & Tangen 1996)

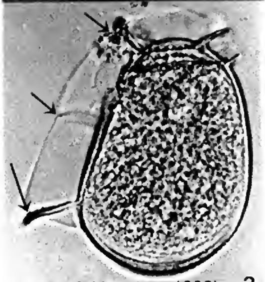
Dinophysis caudata. Figs. 1-2. SEM. Fig. 1. Large, long and distinctive cell with extended ventral hypothecal process. Cingulum narrow; lists supported by ribs (arrowhead). Strong left sulcal list (double arrows). Right sulcal list present (single arrow). Fig. 2. Ventral view: cell compressed laterally. Figs. 3-4. LM. Fig. 3. Large posterior nucleus (n). Fig. 4. Left sulcal list with three supporting ribs (arrowheads); posterior projection with small knob-like spines (arrows). Surface areolae evident. Fig. 5. SEM. Paired cells joined at dorsal expansion (arrow). Fig. 6. Line drawing.

PLATE 14

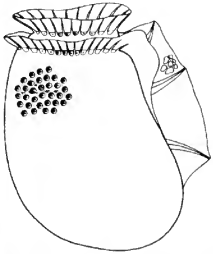
(Honsell) 1



(Larsen & Moestrup 1992) 2



(Larsen & Moestrup 1992) 3

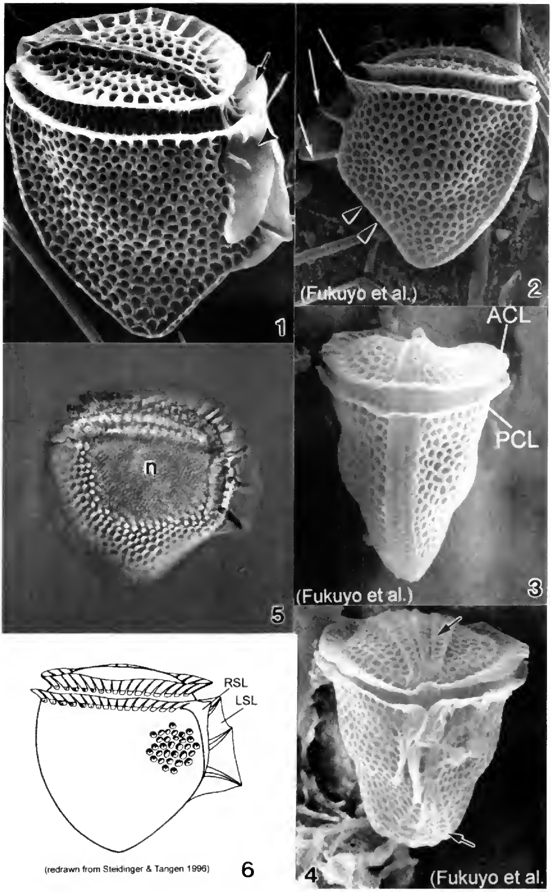


4

(redrawn from Steidinger & Tangen 1996)

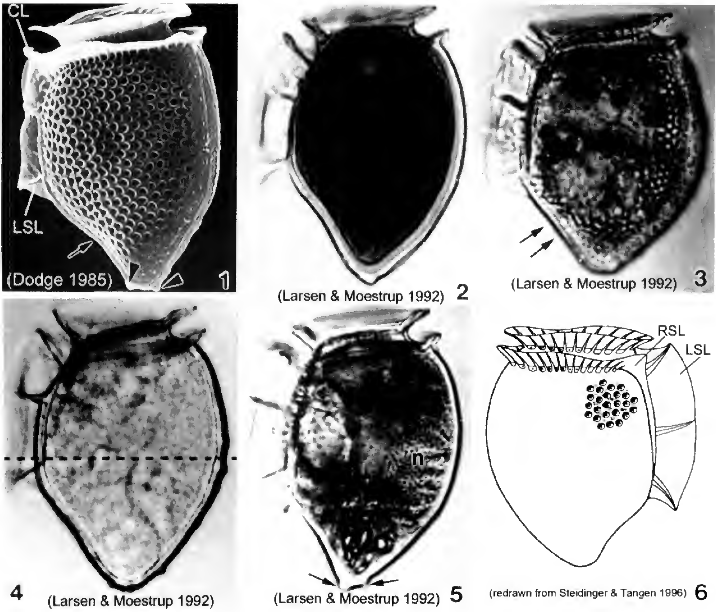
Dinophysis fortii. Fig. 1. SEM: lateral view. Left sulcul list (LSL) long and well-developed. Right sulcal list (RSL) present. Cingulum (C) obscures low and small epitheca. Thecal surface covered with areolae. Figs. 2-3. LM: lateral view. Fig. 2. Cell subovate with a wide round posterior bottom (dorsal bulge)(arrows). Fig. 3. LSL supported by three strong ribs (arrows). Smoothly convex dorsal margin. Fig. 4. Line drawing.

PLATE 15



Dinophysis mitra. Figs. 1-4. SEM. Fig. 1. Lateral view: cell broad and wedge-shaped; epitheca visible. Left sulcal list (LSL) short (arrow). Right sulcal list (RSL) small (arrowhead). Theca heavily areolated. Fig. 2. Epitheca cap-like; greatly reduced. LSL supported by three short ribs (arrows). Ventral hypothecal margin concave below LSL (arrowheads). Fig. 3. Dorsal view: hypothecal margin smoothly convex. Short anterior cingular list (ACL) and posterior cingular list (PCL) supported by numerous ribs. Fig. 4. Ventral view: dividing cell. Megacytic zone expanding (arrows). Epitheca, sulcus, RSL and LSL visible. Fig. 5. LM: large nucleus (n). Fig. 6. Line drawing *(Phalacroma mitra).*

PLATE 16



(Dodge 1985) 1

(Larsen & Moestrup 1992) 2

(Larsen & Moestrup 1992) 3

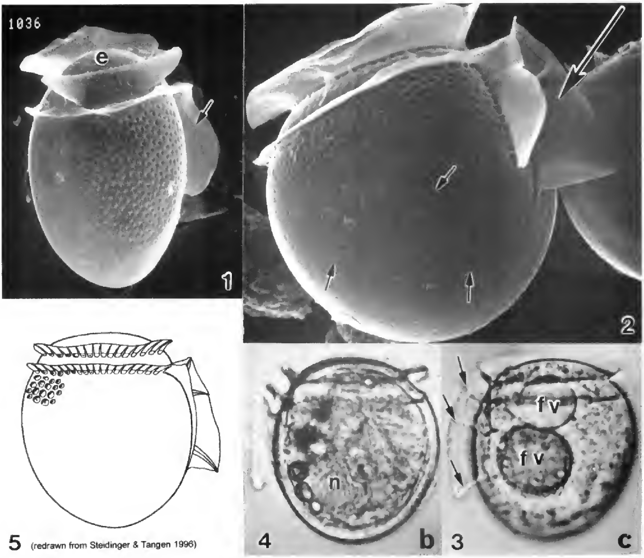
4 (Larsen & Moestrup 1992)

(Larsen & Moestrup 1992) 5

(redrawn from Steidinger & Tangen 1996) 6

Dinophysis norvegica. Fig. 1. SEM: lateral view. Cell heavily areolated with pointed antapex and posterior protrusions (arrowheads). Ventral margin concave below left sulcal list (LSL)(arrow). Well developed cingular lists (CL) and LSL. Figs. 2-5. LM: lateral view. Fig. 2. Cell less robust than in Fig. 1; pointed antapex. Fig. 3. Robust cell with rounded antapex. Heavily areolated. Ventral margin straight below LSL (arrows). Fig. 4. Deepest point of cell through mid-point (dashed line), just above third rib of LSL. Fig. 5. Large posterior nucleus (n). Pointed antapex with posterior projections (arrows). Fig. 6. Line drawing. Right sulcal list depicted (RSL).

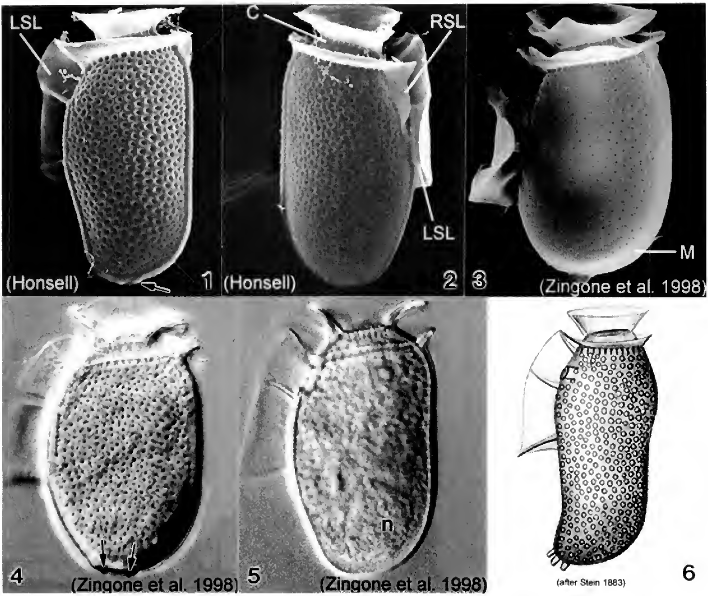
PLATE 17



5 (redrawn from Steidinger & Tangen 1996)

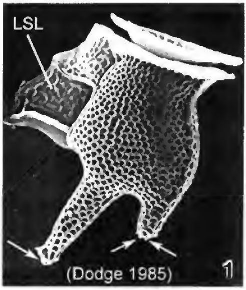
Dinophysis rotundata. Figs. 1-2. SEM: lateral view. Fig. 1. Cell broadly rounded. Small cap-like epitheca (e) not obscured by cingular lists. Right sulcal list (arrow). Fig. 2. Left sulcal list (LSL) (large arrow), over 1/2 the cell length, widens posteriorly. Surface pores present (small arrows). Figs. 3-4. LM (from Larsen & Moestrup 1992: figs. 8b,c). Fig. 3. Large food vacuoles (fv). LSL supported by three ribs (arrows). Widest width of cell between second and third rib. Fig. 4. Posterior nucleus (n). Fig. 5. Line drawing (as *Phalacroma rotundata*).

PLATE 18

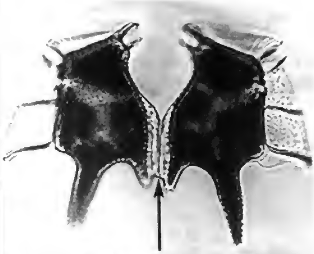


Dinophysis sacculus. Figs. 1-3. SEM: lateral view. Fig. 1. Cell oblong with rounded posterior. Hypotheca long, margins undulate. Thecal surface coarsely areolated. Short left sulcal list (LSL). Cingulum with two well developed lists. Small blunt posterior projections (arrow). Fig. 2. Cingulum lined with pores. Right sulcal list (RSL) visible. Fig. 3. Smooth thecal surface with pores. Metacytic zone (M) devoid of pores. Figs. 4-5. LM: lateral view. Fig. 4. Hypotheca sack-like with deep thecal pores. Posterior end with two blunt projections (arrows). Fig. 5. Large posterior nucleus (n). Fig. 6. Line drawing: morphotype from Stein (1883).

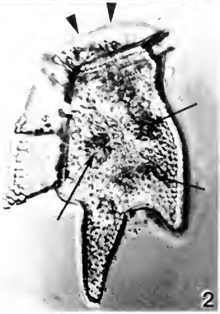
PLATE 19



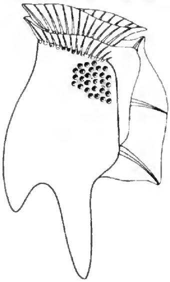
(Dodge 1985)



(Larsen & Moestrup 1992)



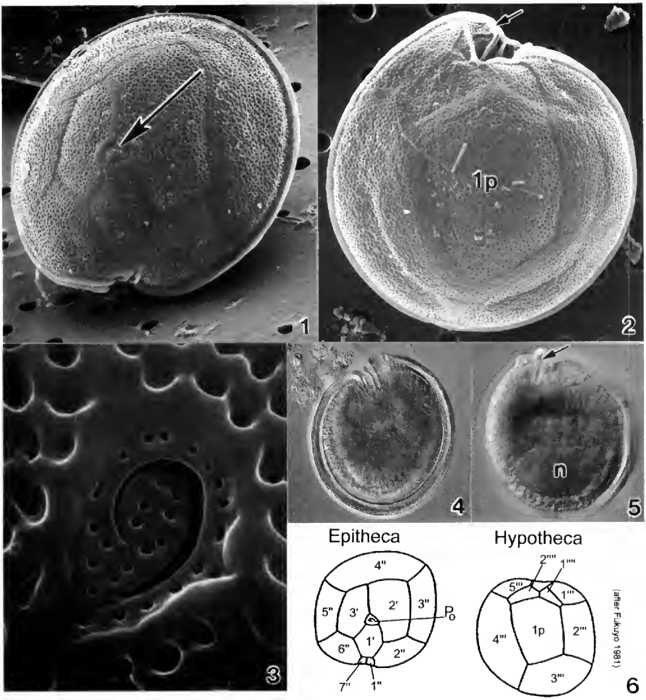
(Larsen & Moestrup 1992)



(redrawn from Steidinger & Tangen 1996)

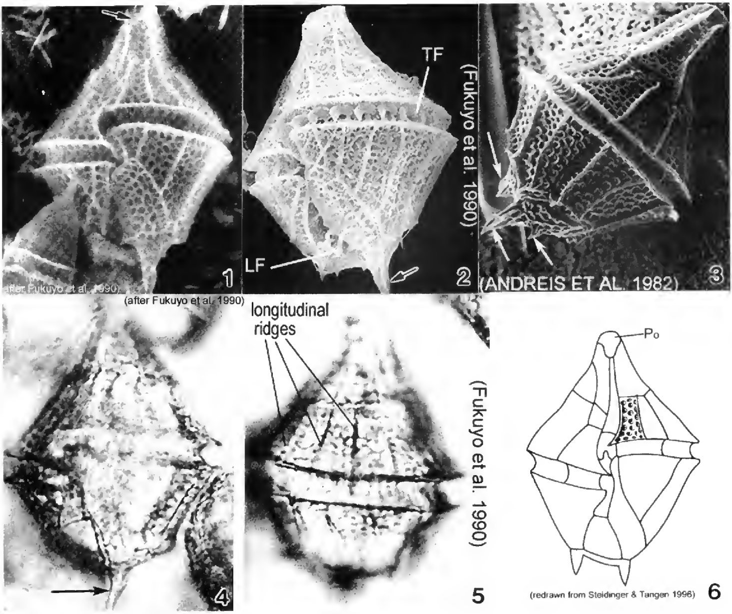
Dinophysis tripos. Fig. 1. SEM: lateral view. Cell large, oblong and heavily areolated. Hypothecal projections with toothed posterior ends (arrows). Left sulcal list (LSL) large, wide and reticulated. Figs. 2,3. LM: lateral view. Fig. 2. Anterior cingular list (ACL) projected anteriorly obscuring low epitheca (arrowheads). Narrow cingulum. Chloroplasts visible (arrows). Fig. 3. Paired cells. Hypothecal projection on dorsal margin sometimes seen with a narrow list (arrow) connecting two daughter cells during cell division. Fig. 4. Line drawing.

PLATE 20



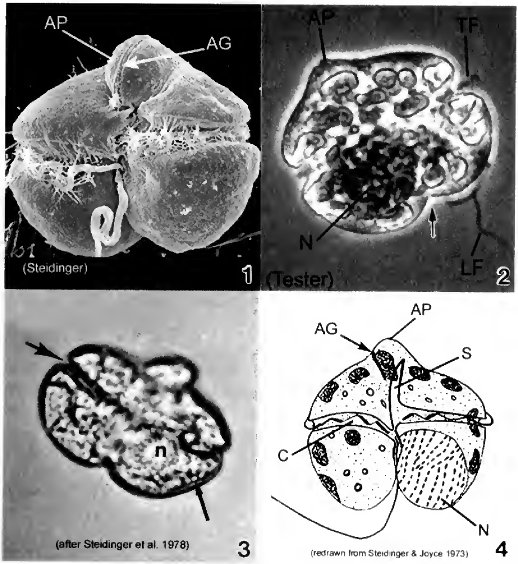
Gambierdiscus toxicus. Figs. 1-3. SEM. Fig. 1. Epitheca: cell round to ellipsoid; anterior-posteriorly compressed. Cell surface smooth with small scattered pores. Apical pore complex located at the apex (arrow). Fig. 2. Hypotheca: 1p plate large and pentagonal. Sulcal region deeply excavated (arrow). Fig. 3. Apical pore plate with characteristic fishhook shaped apical pore. Fig. 4. LM. Epitheca: cingulum and sulcal region in focus. Fig. 5. LM. Hypotheca: sulcal ridge (arrow); large nucleus (n). Fig. 6. Line drawing: thecal plate arrangement.

PLATE 21



Gonyaulax polygramma. Figs. 1-3. SEM. Fig. 1. Ventral view: cell large, elongate and quadrilateral. Epitheca with prominent apical horn (arrow). Cingulum left-handed, displaced 1.5 X its width; sulcus widens posteriorly. Longitudinal ridges on thecal surface with reticulations in between. Fig. 2. Lateral ventral view: transverse (TF) and longitudinal (LF) flagella present. One antapical spine (arrow). Fig. 3. Dorsal view: hypotheca truncate with straight sides. Three antapical spines (arrows): one large and two small. Figs. 4-5. LM. Fig. 4. Ventral view: reticulations evident; one long antapical spine (arrow). Fig. 5. Dorsal view: prominent longitudinal ridges. Fig. 6. Line drawing.

PLATE 22



(Steidinger)

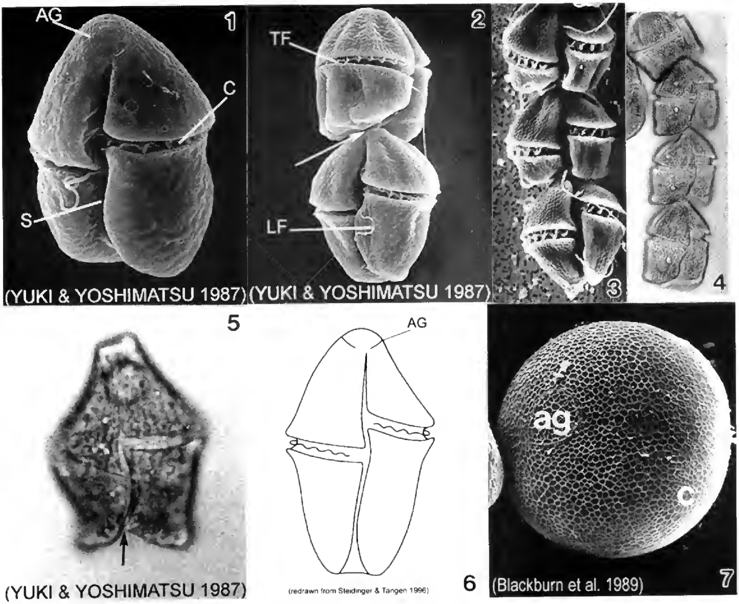
(Tester)

(after Steidinger et al. 1978)

(redrawn from Steidinger & Joyce 1973)

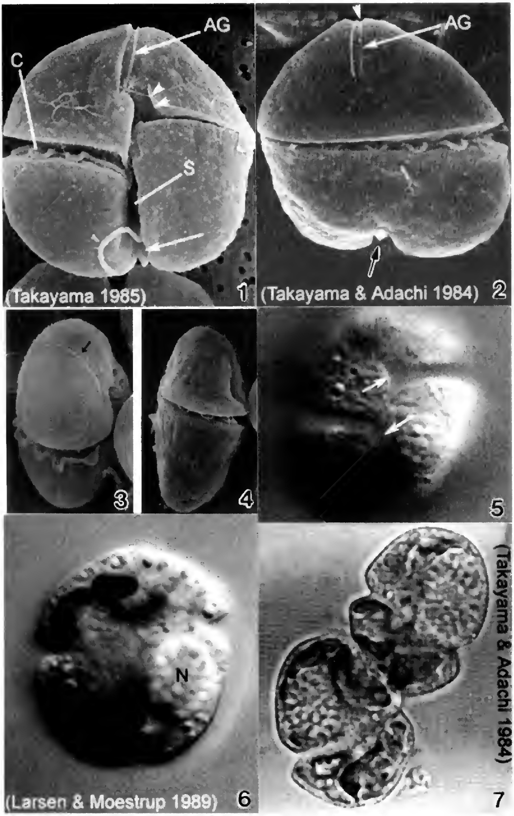
Gymnodinium breve. Fig. 1. SEM: ventral view. Cell small, wider than long, dorso-ventrally flattened. Cell nearly square in outline; prominent apical process (AP) directed ventrally. Apical groove (AG) present on apical process, adjacent to sulcus. Figs. 2-3. LM. Fig. 2. Dorsal view: large nucleus (N) in hypotheca. Transverse (TF) and longitudinal (LF) flagella present. Hypotheca bilobed (arrow). Fig. 3. Ventral view: displaced cingulum (large arrow) and lipid globule (small arrow). Fig. 4. Line drawing. Cingulum (C) displaced, descending. Long sulcus (S) extends to apex of cell.

PLATE 23



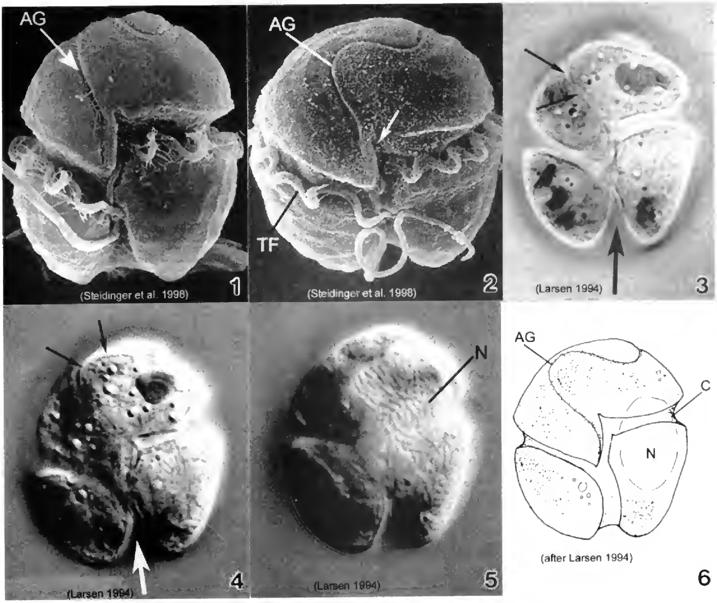
Gymnodinium catenatum. Figs. 1-3. SEM: ventral view. Fig. 1. Cell small, elongate-ovoid with slight dorso-ventral compression. Conical apex; rounded and notched antapex. Cingulum (C) excavated; sulcus (S) long. Distinctive horse-shoe shaped apical groove (AG) encircles apex. Fig. 2. Two cell chain; attachment point visible (arrow). Premedian cingulum displaced 2X its width. Longitudinal (LF) and transverse (TF) flagella visible. Fig. 3. Chain cells with anterior-posterior compression. Terminal cell slightly longer. Thecal surface rugose to smooth (Blackburn et al. 1989). Figs. 4-5. LM. Fig. 4. Chain-formation (Yuki and Yoshimatsu 1987). Fig. 5. Single cell. Conical epitheca with concave to flat apex. Bilobed hypotheca (arrow). Fig. 6. Line drawing. Fig. 7. SEM: cyst with microreticulations. ag=apical groove; c=cingulum

PLATE 24



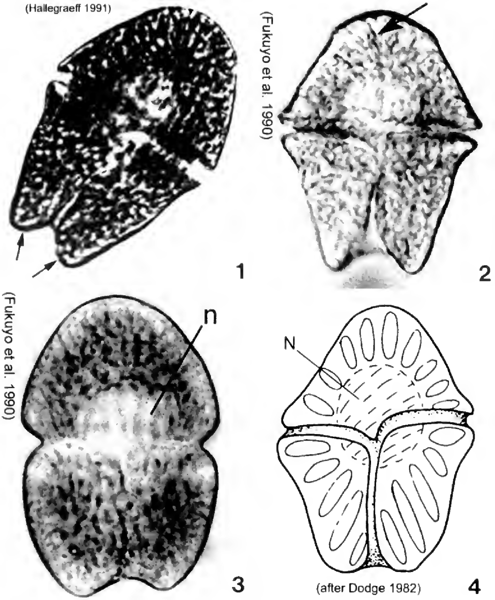
Gymnodinium mikimotoi. Figs. 1-4. SEM. Fig. 1. Ventral view: cell small, broadly oval to almost round. Epitheca slightly smaller than hypotheca. Characteristic straight apical groove (AG). Cingulum (C) deep, displaced 2 times its width. Sulcus (S) slightly invades epitheca (arrowheads). Hypotheca notched by widening sulcus (arrow). Fig. 2. Dorsal view: apical groove extends to dorsal side of epitheca creating slight indentation at the apex (arrowhead). Hypotheca bilobed (arrow). Fig. 3. Apical view of apical groove (arrow)(after Fukuyo et al.). Fig. 4. Cell compressed dorso-ventrally (after Fukuyo et al.). Figs. 5-7. LM. Fig. 5. Cingulum displaced 2 times its width (arrows)(from Larsen & Moestrup 1989: fig. 16g). Fig. 6. Large nucleus (N) in left lobe of hypotheca. Fig. 7. Vegetative division. Division plane oblique.

PLATE 25



Gymnodinium pulchellum. Figs. 1-2. SEM: ventral view. Fig. 1. Cell small and broadly oval. Cingulum wide, displaced 1-1.5 X its width. Deeply excavated sulcus creates lobed hypotheca. Conspicuous undulating apical groove (AG). Fig. 2. Well-developed apical groove: reverse S-shape. Transverse flagellum (TF) housed in cingulum. Sulcus slightly invades epitheca with finger-like projection (arrow). Figs. 3-5. LM: ventral view. Figs. 3-4. Apical groove distinguishable (small arrows). Chloroplasts and pyrenoids present. Lobed hypotheca (large arrow). Fig. 5. Large elliptical nucleus (N) in left central part of cell. Fig. 6. Line drawing. C=cingulum

PLATE 26



(Hallegraeff 1991)

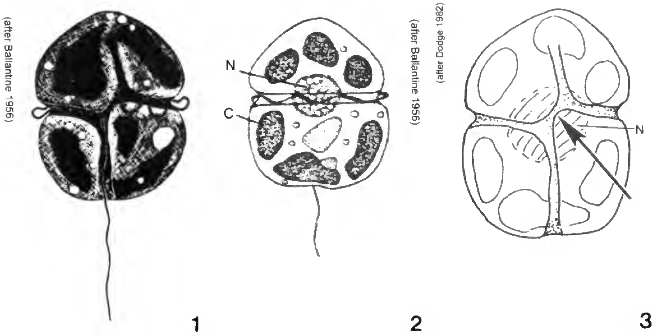
(Fukuyo et al. 1990)

(Fukuyo et al. 1990)

(after Dodge 1982)

Gymnodinium sanguineum. Figs. 1-3. LM. Cell large, pentagonal, and slightly dorso-ventrally flattened. Cells vary in shape and size. Fig. 1. Ventral view. Epitheca and hypotheca nearly equal in size: epitheca conical, hypotheca bilobed (arrows). Fig. 2. Ventral view. Deep cingulum median, displaced 1-2 times its width. Sulcus deeply notches hypotheca. Apical groove present (arrow). Fig. 3. Cell deeply pigmented; central nucleus (n). Fig. 4. Line drawing. Spindle-shaped chloroplasts radially arranged.

PLATE 27



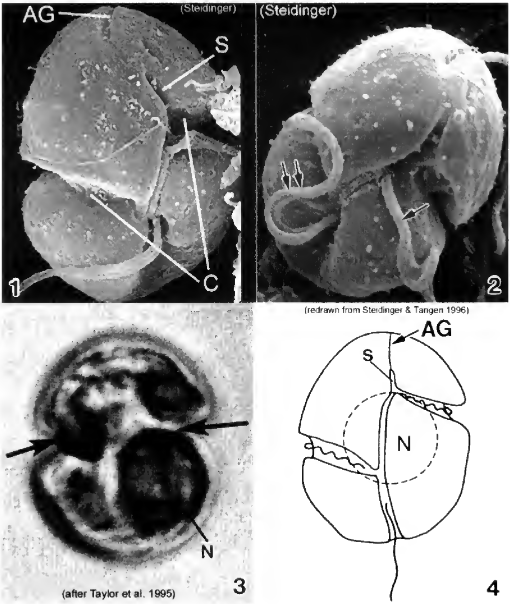
(after Ballantine 1956)

(after Ballantine 1956)

(after Dodge 1982)

Gymnodinium veneficum. Figs. 1-3. Line drawings. Fig. 1. Ventral view: cell small and ovoid. Epitheca slightly pointed, without apical groove. Cingulum deep and displaced 1-2 times its width. Fig. 2. Dorsal view: large central nucleus (N). Two to eight irregular chloroplasts present (C). Fig. 3. Sigmoid sulcus slightly invades epitheca (arrow).

PLATE 28


(Steidinger)

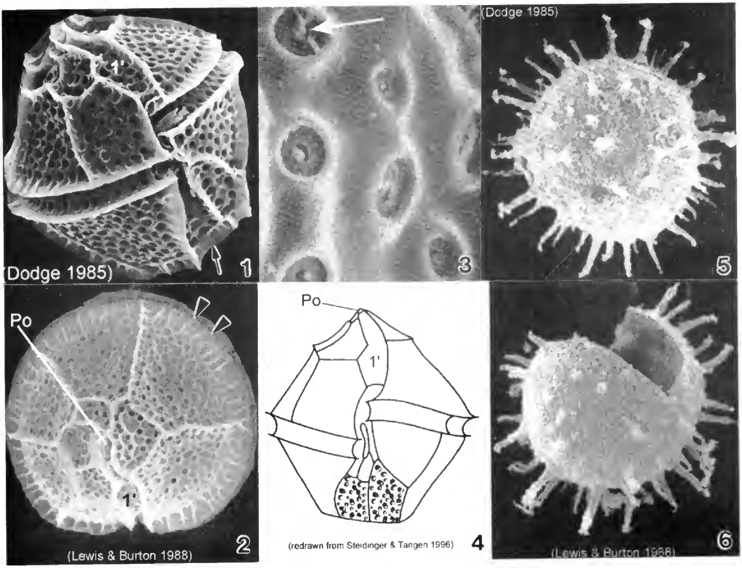
(Steidinger)

(after Taylor et al. 1995)

(redrawn from Steidinger & Tangen 1996)

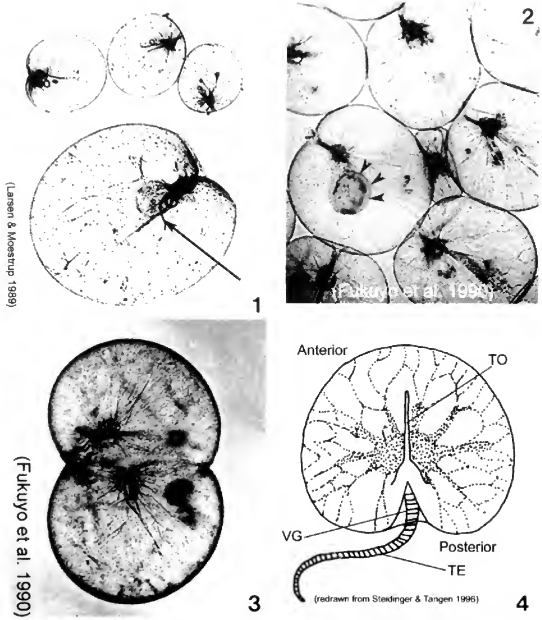
Gyrodinium galatheanum. Figs. 1-2. SEM: ventral view. Fig. 1. Cell small, oval to round, with distinct apical groove (AG). Cingulum (C) displaced 3 times its width. Short and narrow sulcus (S) slightly invades epitheca. Fig. 2. Epitheca and hypotheca round. Cingulum wide, houses transverse flagellum (single arrow). Longitudinal flagella present (double arrow). Fig. 3. LM: ventral view. Cingulum deeply excavated (arrows). Nucleus (N) large and central. Fig. 4. Line drawing.

PLATE 29



Lingulodinium polyedrum. Figs. 1-3. SEM. Fig. 1. Ventral view: cells angular and polyhedral-shaped. Thick plates well defined and coarsely areolate. Epitheca with shoulders and nearly flattened apex. Hypotheca with straight sides and flattened antapex (arrow). Cingulum deep and displaced 1-2 X its width. Sulcus widens posteriorly. Fig. 2. Apical view: first apical plate (1') long and narrow. Apical pore plate (Po) with raised inner elliptical ridge. Cingulum with lists (arrowheads). Strong ridges along sutures outline thecal plates. Fig. 3. Thecal areolae with large trichocysts (arrow)(Lewis and Burton 1988). Fig. 4. Line drawing. Figs. 5-6. SEM: resting cysts. Fig. 5. Cyst sperical with numerous tapering spines. Fig. 6. Cyst theca after excystment.

PLATE 30



(Larsen & Moestrup 1989)

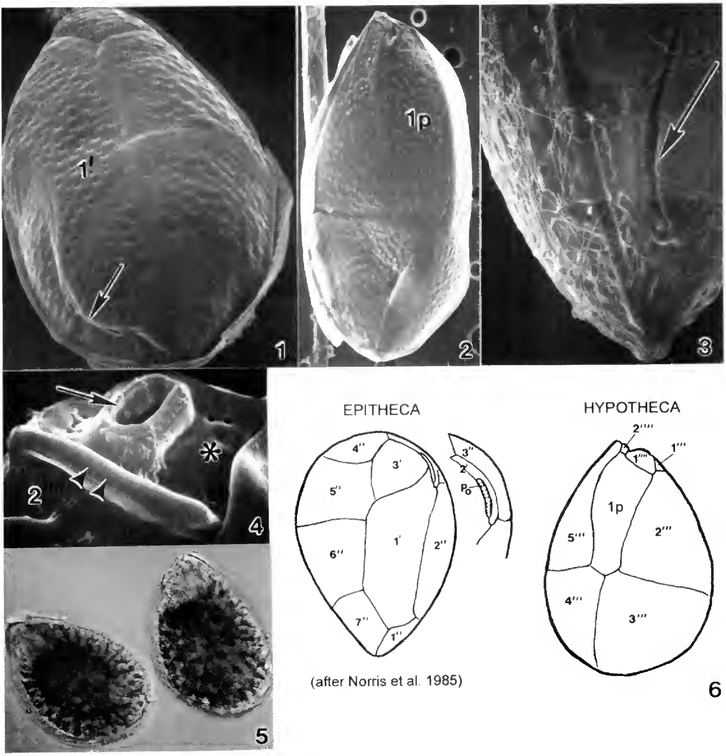
(Fukuyo et al. 1990)

(Fukuyo et al. 1990)

(redrawn from Steidinger & Tangen 1996)

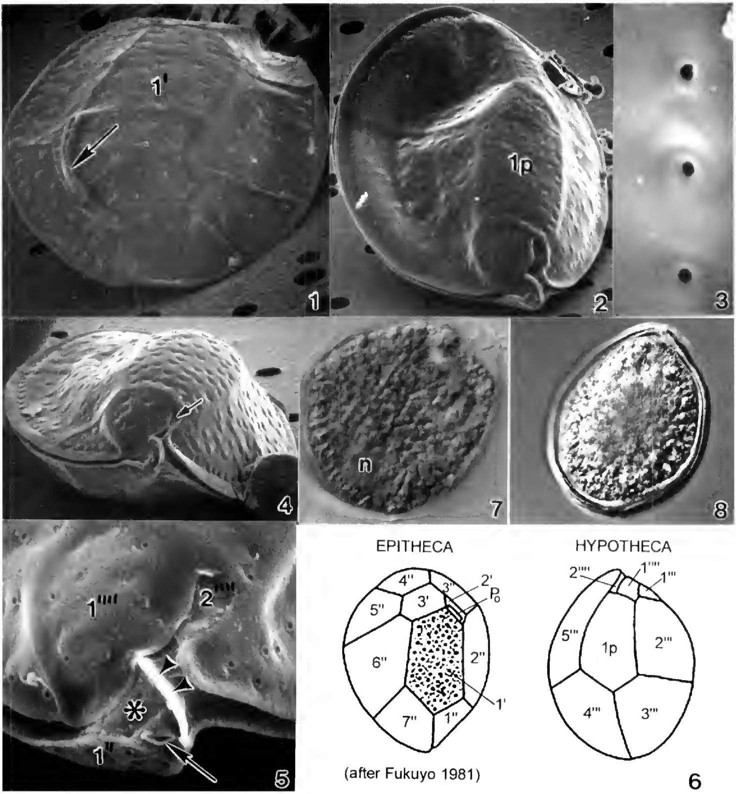
Noctiluca scintillans. Figs. 1-3. LM. Fig. 1. Cells large, balloon-shaped, nearly spherical, and colorless. A single flagellum housed in the ventral groove (arrow). Fig. 2. Cytoplasmic strands extend from nucleus (near the groove) to cell perifery. Engulfed cell (arrowheads). Fig. 3. Asexually dividing cell. Fig. 4. Line drawing. Deep and wide ventral groove (VG) houses the tooth (TO), an extension of the cell wall. Striated tentacle (TE).

PLATE 31



Ostreopsis heptagona. Figs. 1-4. SEM. Fig. 1. Epithecal view: cells broadly oval, oblong and pointed. Long curved apical pore plate, Po, off-center (arrow). Plate 1' heptagonal and distinctive. Fig. 2. Hypothecal view: plate 1p pentagonal and dorso-ventrally elongate. Fig. 3. Po long, narrow and curved. Narrow mucilage strands cover cell surface. Fig. 4. Ventral view: location of ventral opening (arrow), ventral plate (asterisk), and rigid plate (asterisk) within cingulum. Fig. 5. LM. Two cells. Fig. 6. Line drawing: thecal plate arrangement.

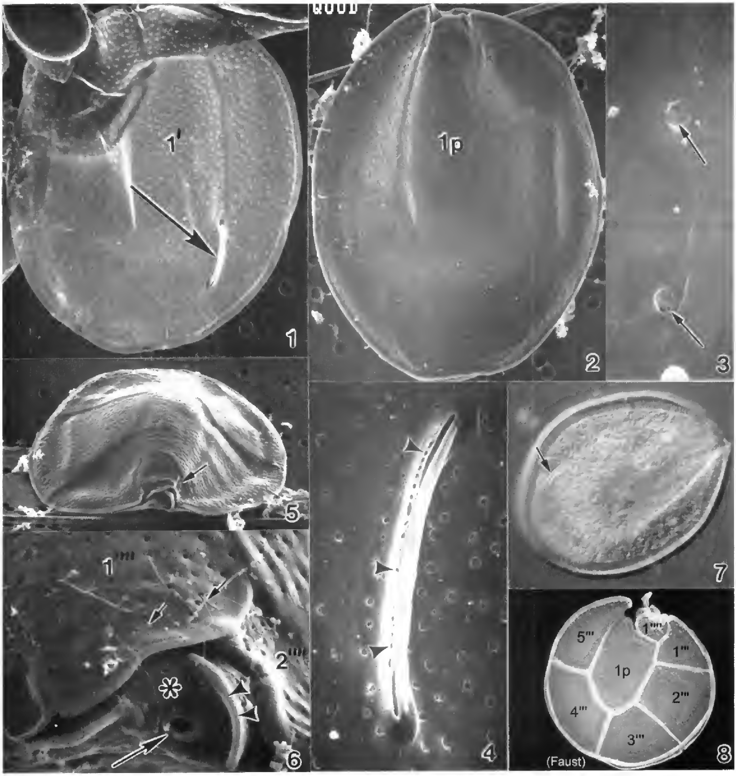
PLATE 32



(after Fukuyo 1981)

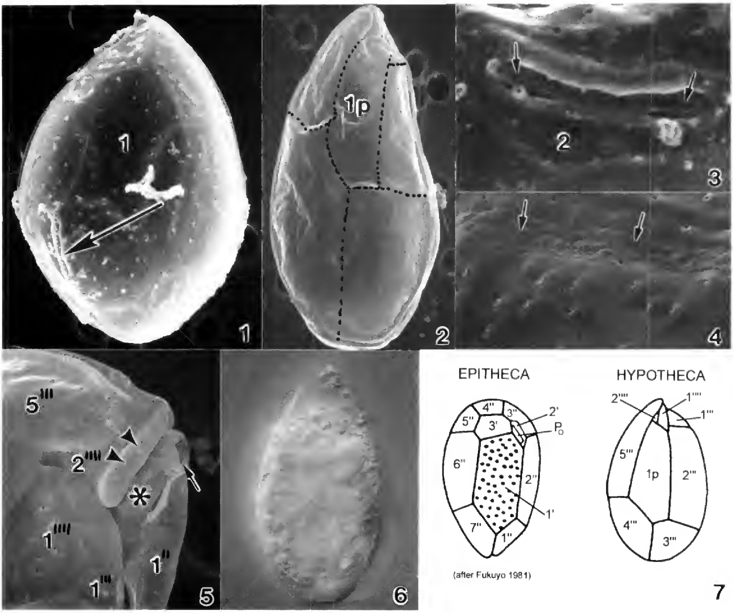
Ostreopsis lenticularis. Figs. 1-5. SEM. Fig. 1. Epithecal view: cell lenticulate to broadly oval. Curved off-center apical pore plate with a slit-like apical pore (arrow). Plate 1' irregularly pentagonal. Fig. 2. Hypothecal view: plate 1p central and pentagonal. Fig. 3. Smooth thecal surface. Round pores with smooth raised edges. Fig. 4. Hypothecal ventral view: cell anterio-posteriorly compressed. Shallow cingulum with smooth edge. Small sulcus hidden (arrow). Fig. 5. Location of ventral opening (arrow), ventral plate (asterisk), and rigid plate (arrowheads) within cingulum. Fig. 6. Line drawing: thecal plate arrangement. Figs. 7,8. LM. Fig. 7. Cytoplasma granulated; posterior nucleus (n). Fig. 8. Distinct cingular list.

PLATE 33



Ostreopsis mascarenensis. Figs. 1-5. SEM. Fig. 1. Epitheca: inner thecal surface. Cell very large, broadly ovate, large plates. Plate 1' elongate and hexagonal. Apical pore plate (Po) nearly straight. Fig. 2. Hypotheca: plate 1p long and wide. Fig. 3. Smooth cell surface with round pores; pores with two small openings (arrows). Fig. 4. Po with long narrow apical pore; small pores line the opening (arrowheads). Figs. 5-6. Ventral view of epitheca. Fig. 5. Cell compressed anterio-posteriorly; cingulum narrow with smooth edge. Small sulcus hidden (arrow). Fig. 6. Location of ventral opening (large arrow), ventral plate (asterisk), and rigid plate (arrowheads) within cingulum. Pores with ejected trichocysts (small arrows). Fig. 7. LM. Epitheca: Po (arrow) and cingulum in focus. Fig. 8. Line drawing: hypotheca plate arrangement.

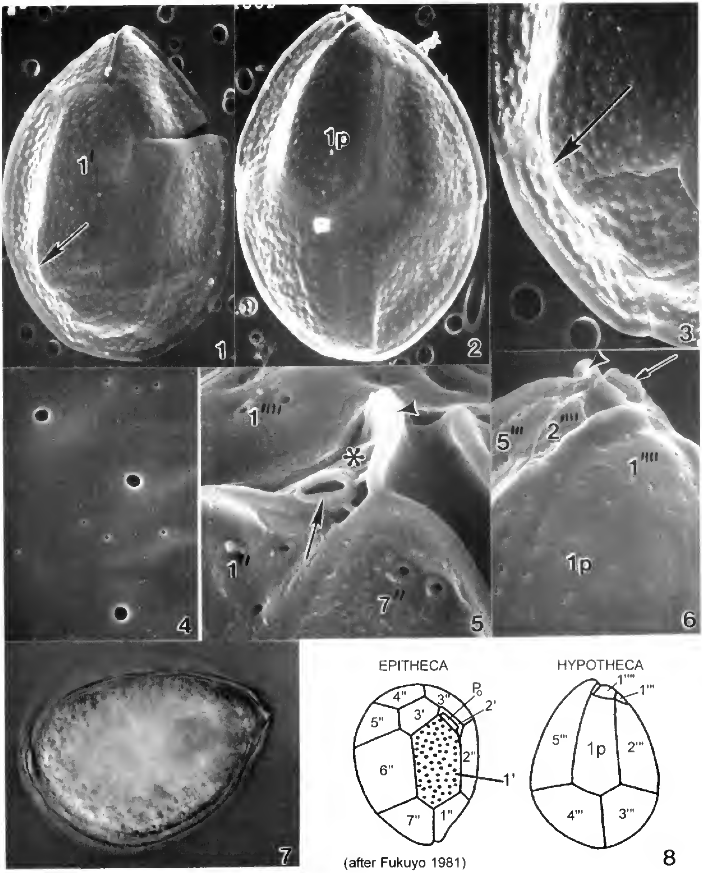
PLATE 34



(after Fukuyo 1981)

Ostreopsis ovata. Figs. 1-5. SEM. Fig. 1. Epithecal view: cell slender and tear-shaped. Apical pore plate (Po) off-center (arrow). Plate 1' large and hexagonal. Cingulum wide with narrow lists. Fig. 2. Hypothecal view: plates delicate. Plate 1p long and narrow. Fig. 3. Po: short and straight, adjacent to plate 2'. Fig. 4. Thecal surface smooth with scattered small pores. Suture line uneven and bumpy (arrows). Fig. 5. Hypothecal view: ventral opening (arrow), ventral plate (asterisk), and rigid plate (arrowhead) on cingulum. Fig. 6. LM. Large posterior nucleus. Fig. 7. Line drawing: thecal plate arrangement.

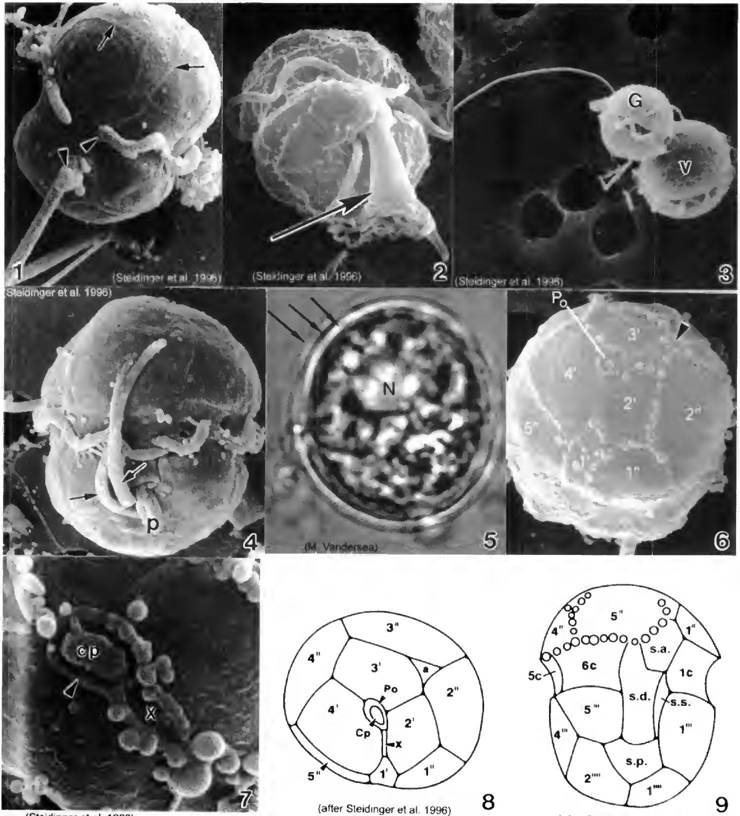
PLATE 35



(after Fukuyo 1981)

Ostreopsis siamensis. Figs. 1-6. SEM. Fig. 1. Epithecal view: cell broad and tear-shaped. Thecal surface smooth with scattered pores. Apical pore plate (Po) off-center (arrow). Narrow cingulum with smooth edge. Plate 1' narrow and pentagonal. Fig. 2. Hypothecal view: plate 1p long and pentagonal. Fig. 3. Po: long, curved and narrow. Fig. 4. Large and small pores on thecal surface. Fig. 5. Ventral view: location of ventral opening (arrow), ventral plate (asterisk), and rigid plate (arrowhead) on cingulum. Fig. 6. Hypothecal view: Vo (arrow) and Rp (arrowhead). Fig. 7. LM. Hypotheca. Fig. 8. Line drawing: thecal plate arrangement.

PLATE 36



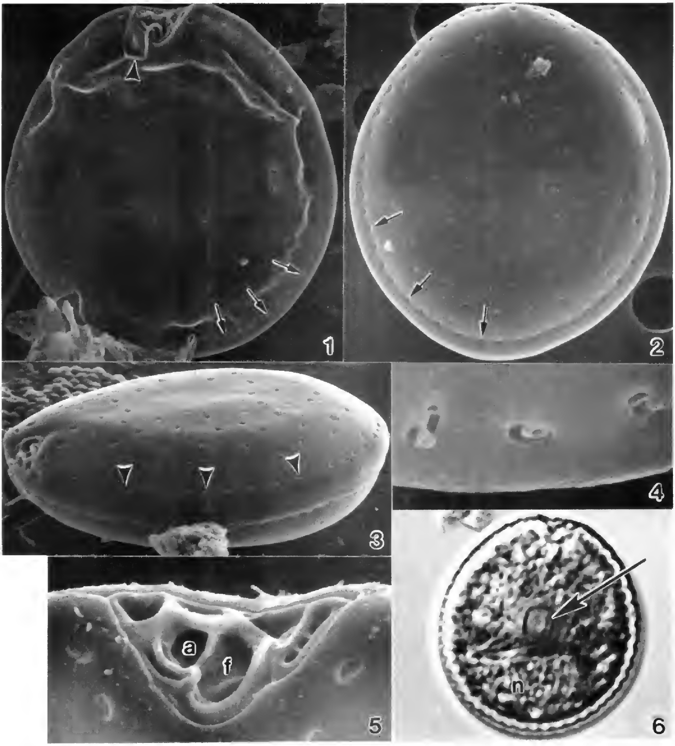
(Steidinger et al. 1996)

(after Steidinger et al. 1996)

(after Steidinger et al. 1996)

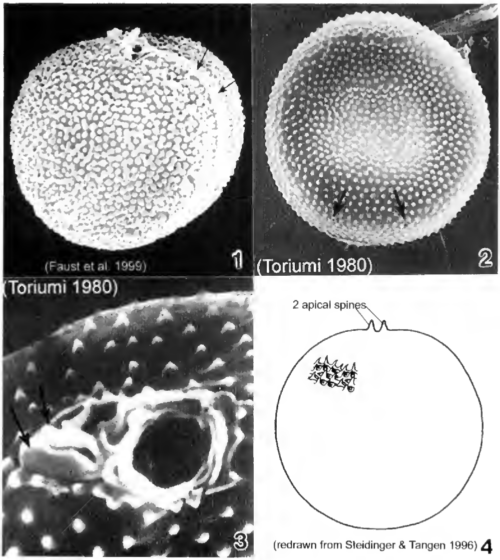
Pfiesteria piscicida: Figs. 1-4. SEM. Figs. 1-2. Biflagellated stage resembles a gymnodinioid cell. Cells small, oblong and thecated. Fig. 1. Plate sutures apparent (arrows). Both flagella present (arrowheads). Fig. 2. Peduncle deployed (arrow). Fig. 3. Biflagellated stage with 2 size groups: large vegetative (V) cell; small gamete (G) cell. Fig. 4. Flagellated stage. Planozygote: larger triflagellated stage; similar to vegetative cell with 2 longitudinal flagella (arrows) adjacent to peduncle (P). Fig. 5. LM. Triple layer cyst (arrows): benthic stage. Nucleus (N) stained with DAPI (courtesy of P. Tester). Figs. 6-7. SEM: biflagellate stage. Fig. 6. Epithecal plate morphology: thecal nodules apparent. Small 1a plate triangular (arrowhead). Plate 1' rhomboid (after Steidinger et al. 1996). Fig. 7. Apical view of APC: Po (arrowhead), cp, X plate. Figs. 8-9. Line drawings: plate tabulation. Fig. 8. Apical view: epitheca. Fig. 9. Ventral view: thecal nodules depicted.

PLATE 37



Prorocentrum arenarium. Figs. 1-5. SEM. Fig. 1. Right valve: cells round to ovoid. Periflagellar area is a broad, V-shaped depression. Short longitudinal flagellum visible (arrowhead). Marginal poroids present (arrows). Fig. 2. Left valve: surface smooth, with scattered valve and marginal poroids (arrows). Fig. 3. Lateral view: intercalary band smooth; marginal poroids evenly spaced (arrowheads). Fig.4. Marginal poroids oblong to kidney-shaped. Fig. 5. Periflagellar area: triangular and unornamented with large flagellar pore (f) and smaller auxiliary pore (a). Fig. 6. LM. Right valve: posterior nucleus (n) and prominent central pyrenoid (arrow).

PLATE 38



(Faust et al. 1999)

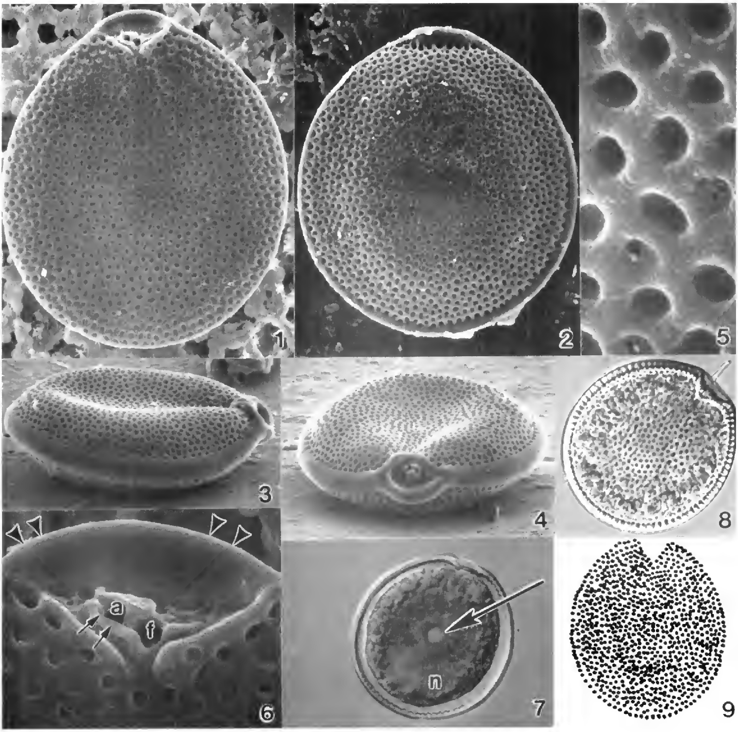
(Toriumi 1980)

(Toriumi 1980)

(redrawn from Steidinger & Tangen 1996)

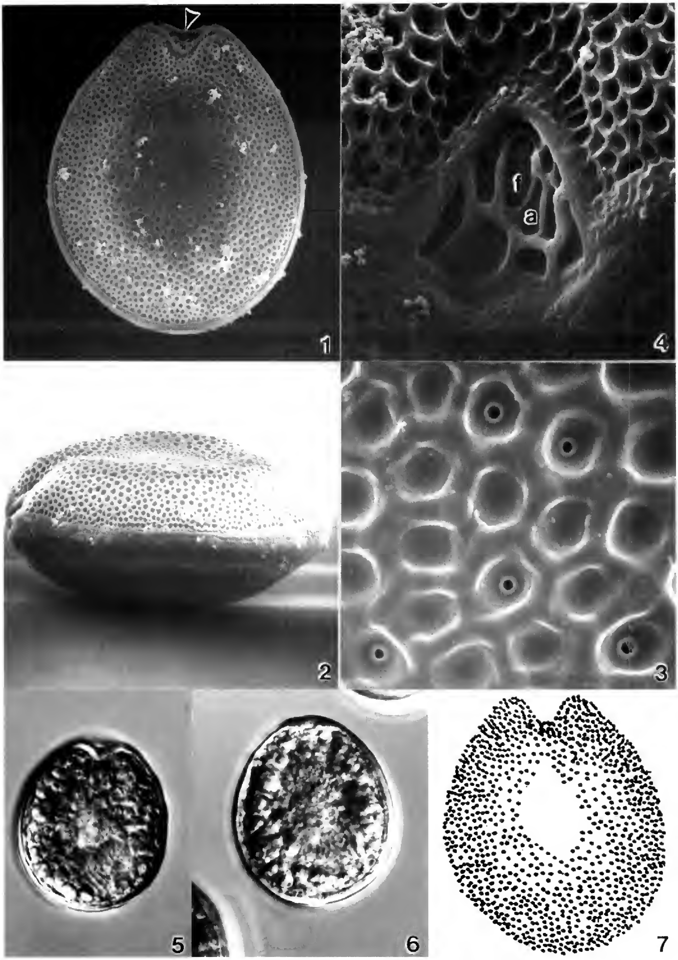
Prorocentrum balticum. Figs. 1-3. SEM. Fig. 1. Valve view: cell round to spherical, covered with many tiny spines. Apical spine apparent. Intercalary band broad, transversely striated (arrows). Fig. 2. Surface with scattered rimmed pores (arrows). Fig. 3. Periflagellar region: two different sized pores and two small apical projections (arrows). Fig. 4. Line drawing.

PLATE 39



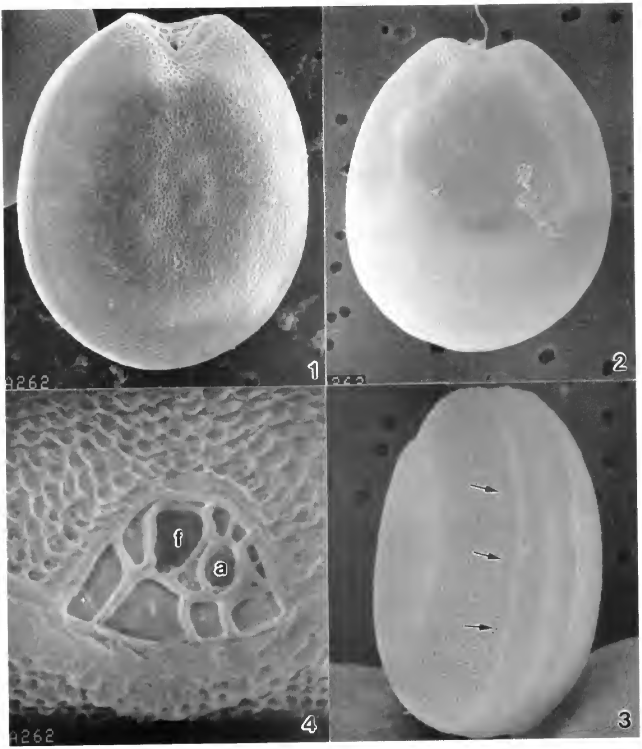
Prorocentrum belizeanum. Figs. 1-6. SEM. Fig. 1. Right valve: cell round to oval; surface heavily areolated. Fig. 2. Left valve: anterior margin with flared curved apical collar. Marginal areolae visible. Fig. 3. Lateral view: valve center concave; intercalary band smooth and wide. Fig. 4. Apical view: apical area with rounded lip; both valves excavated. Fig. 5. Areolae round to ovoid with smooth margins; some with pores. Fig. 6. Periflagellar area: auxiliary pore (a) surrounded by curved periflagellar collar (arrows); adjacent to flagellar pore (f). Left valve with flared apical collar (arrowheads). Fig. 7. Left valve: central pyrenoid (arrow) and posterior nucleus (n). Fig. 8. LM: right valve; flagella present. Fig. 9. Line drawing: areolae arrangement (after Faust 1993a).

PLATE 40



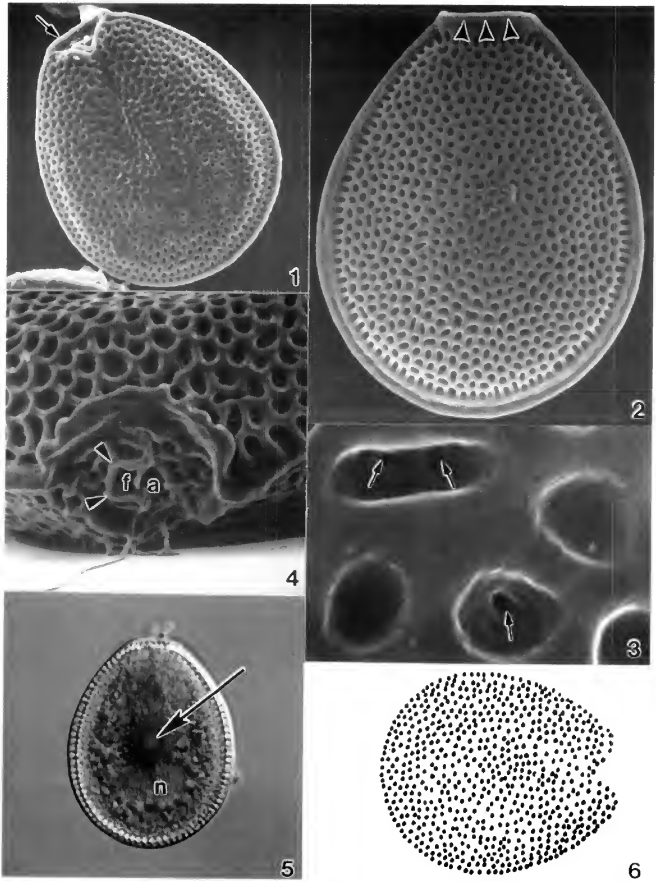
Prorocentrum concavum. Figs. 1-4. SEM. Fig. 1. Right valve. Cell ovate and heavily areolate. Valve center devoid of areolae. Left valve with anterior apical ridge (arrowhead). Fig. 2. Lateral view. Valve center concave and flattened. Intercalary band granulated and horizontally striated. Fig. 3. Valve areolae round to oval with smooth edges; some with small central pores. Fig. 4. Periflagellar area a V-shaped depression. Two pores: small auxiliary pore (a); large flagellar pore (f). Figs. 5-6. LM (M.A. Faust). Fig. 5. Right valve. Fig. 6. Left valve. Fig. 7. Line drawing: areolae arrangement. (Figs. 1-4,7 after Faust 1990b)

PLATE 41



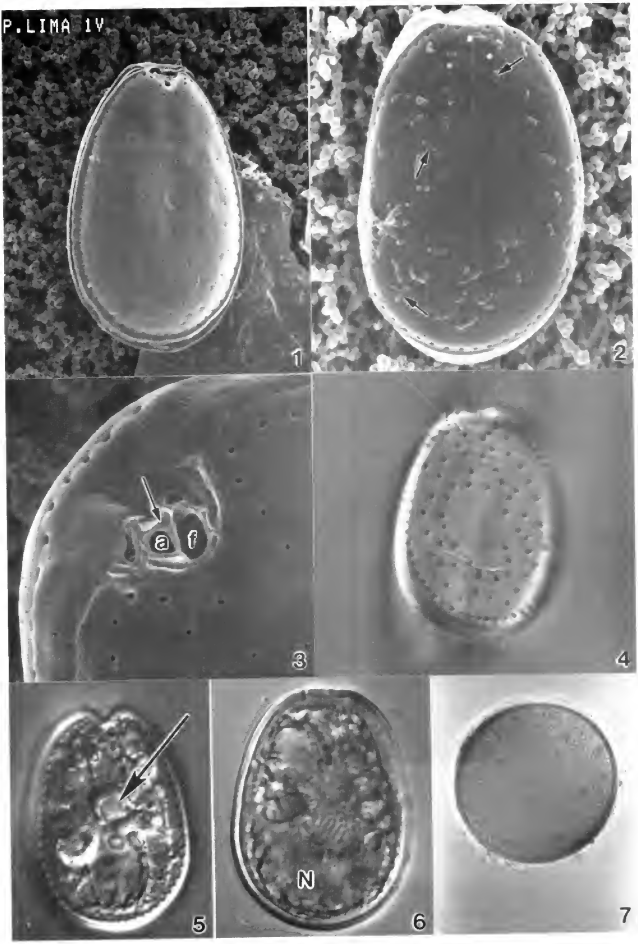
Prorocentrum faustiae. Figs. 1-4. SEM. Fig. 1. Right valve. Cells broadly ovate to rotundate with slightly concave center. Valve surface rugose. Periflagellar area situated apically. Fig. 2. Left valve: apical region slightly excavated. Fig. 3. Intercalary band wide and transversely striated. Small marginal pores evenly spaced along cell perifery (arrows). Fig. 4. Periflagellar area: apical view. Broad V-shaped depression; larger flagellar pore (f) adjacent to smaller auxiliary pore (a). (All figures donated by S.L. Morton)

PLATE 42



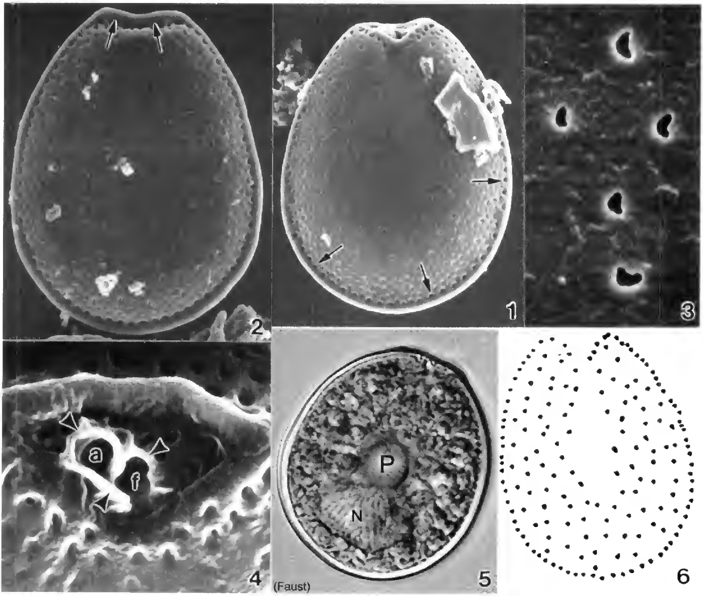
Prorocentrum hoffmannianum. Figs. 1-4. SEM. Fig. 1. Right valve: cell ovoid, tapering slightly apically. Valve surface areolated, slightly concave. Curved apical collar (arrow). Fig. 2. Left valve: distinct flared apical collar bordering periflagellar area (arrowheads). Marginal areolae large. Intercalary band smooth. Fig. 3. Areolae round to ovoid with smooth margins. Some with small pores (arrows). Fig. 4. Periflagellar area: flagellar pore (f) surrounded by flared periflagellar collar (arrowheads), adjacent to auxiliary pore (a); pores equal in size. Fig. 5. LM. Left valve: central pyrenoid (arrow); posterior nucleus (n). Intercalary band appears striated (M.A. Faust). Fig. 6. Line drawing: areolae arrangement. (Figs. 1-4,6 after Faust 1990b)

PLATE 43



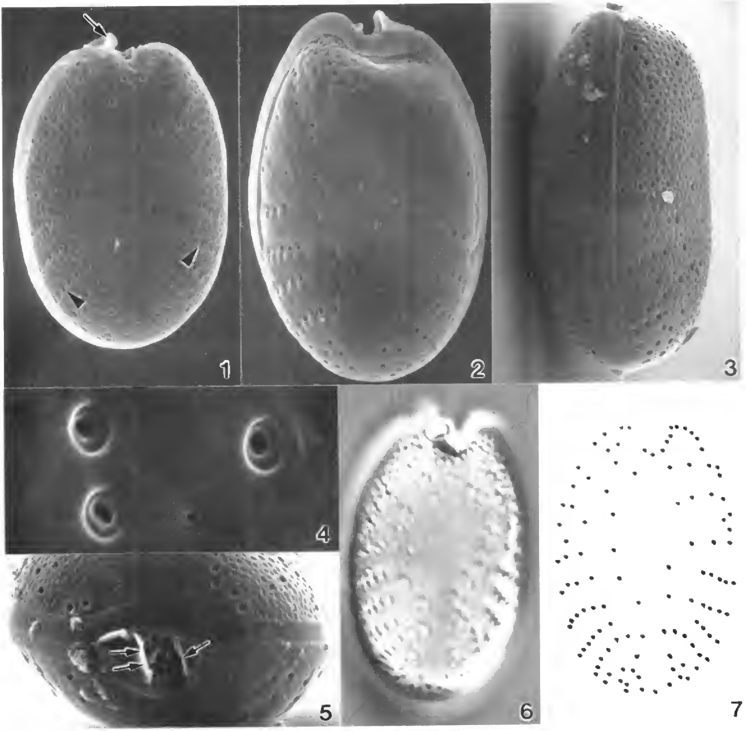
Prorocentrum lima. Figs. 1-3. SEM. Fig. 1. Right valve. Cells oblong to ovate with narrowed anterior. Marginal pores and scattered surface pores present; valve center devoid of pores. Intercalary band smooth and wide. Fig. 2. Left valve; bacteria attached (arrows). Fig. 3. Periflagellar area: shallow, broad, V-shaped depression on right valve. Flared periflagellar collar encircles auxiliary (a) pore (arrow); larger flagellar pore (f) adjacent (after Faust 1991). Figs. 4-7. LM. Fig. 4. Thecal pore arrangement. Fig. 5. Right valve with central pyrenoid (arrow). Fig. 6. Left valve and posterior nucleus (n). Fig. 7. Triple-layered resting cyst. (Figs. 1,2,4-7 after Faust 1993c)

PLATE 44



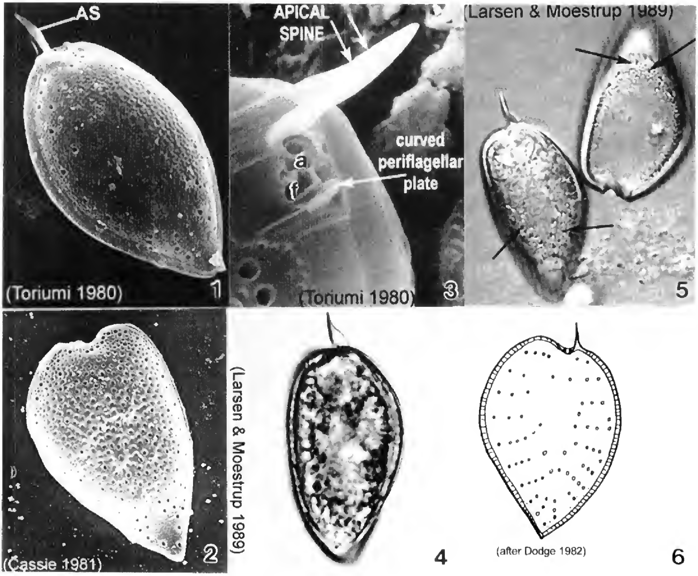
Prorocentrum maculosum. Figs. 1-4. SEM. Fig. 1. Right valve: cell broadly ovate, narrowing apically. Valve surface rugose with scattered poroids; valve center devoid of poroids. Marginal pores evenly spaced (arrows). Fig. 2. Left valve: anterior end flat to slightly concave with raised apical ridge (arrows). Valve margins appear as a flange around cell. Fig. 3. Valve poroids: unevenly distributed on valve surface; circular to oblong or kidney-shaped. Fig. 4. Periflagellar area: broad V-shaped depression on right valve. Apical ridge (raised margin) on left valve. Flagellar (f) and auxiliary (a) pores surrounded by protuberant periflagellar collar (arrowheads); equal in size. Fig. 5. LM. Right valve: central pyrenoid (P) and large posterior nucleus (N) (M.A. Faust). Fig. 6. Line drawing: valve poroid and marginal pore arrangement (Figs. 1-4,6 after Faust 1993b)

PLATE 45



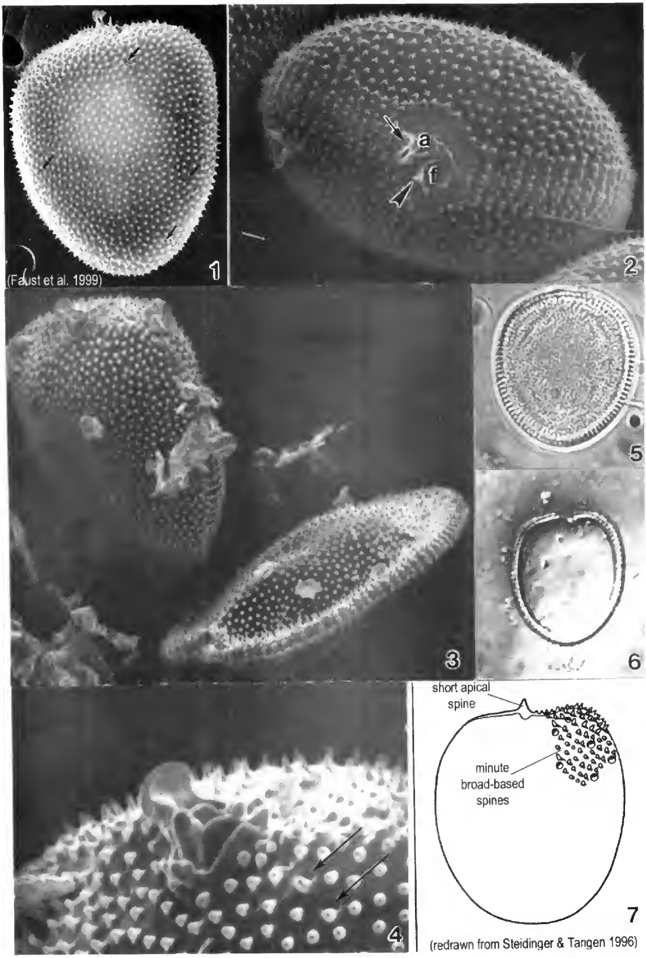
Prorocentrum mexicanum. Figs. 1-5. SEM. Fig. 1. Right valve: cell oval. Periflagellar collar curved and prominent (arrow). Trichocyst pores radially arranged (arrowheads). Fig. 2. Left valve. Apical area excavated (M.A. Faust). Fig. 3. Lateral view: cell ovate to convex; intercalary band broad and transversely striated. Cell surface rugose. Fig. 4. Trichocyst pores round with smooth edge, within deep furrowed depressions. Fig. 5. Periflagellar area: small, V-shaped shallow depression. Prominent curved periflagellar collar (double arrows) adjacent to auxiliary pore; protuberant periflagellar plate (single arrow) opposite and adjacent to flagellar pore. Fig. 6. LM. Right valve: radial pore arrangement visible (M.A. Faust). Fig. 7. Line drawing: trichocyst pore arrangement. (Figs. 1,3-5,7 after Faust 1990b)

PLATE 46



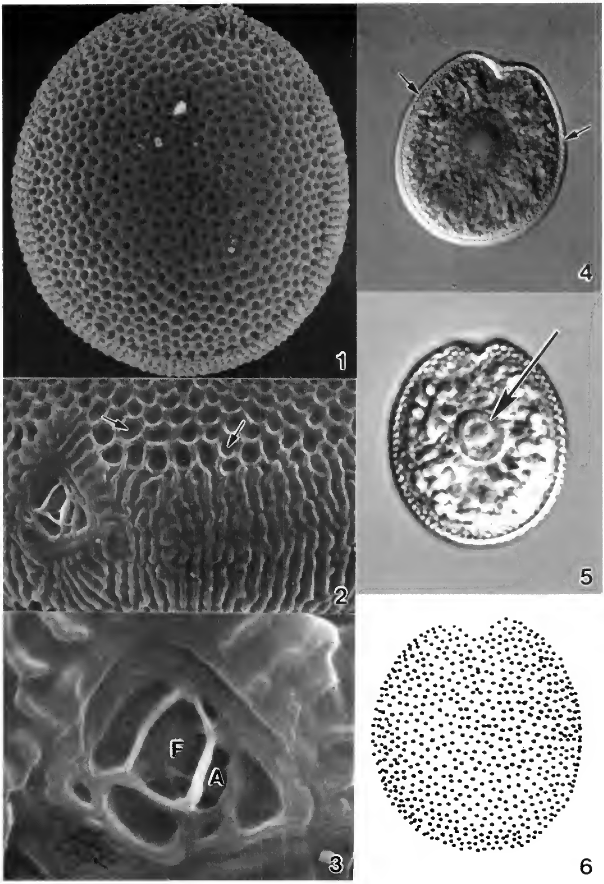
Prorocentrum micans. Figs. 1-3. SEM. Fig. 1. Right valve: cell tear-drop shaped; rounded anteriorly, pointed posteriorly, broadest in the middle. Apical spine (AS) winged. Rugose thecal surface. Intercalary band smooth and wide. Fig. 2. Heart-shaped cell. Apical spine missing. Fig. 3. Periflagellar area: small, shallow triangular depression on right valve. Flagellar (f) and auxiliary (a) pores present; curved periflagellar plate adjacent to f. Large winged AS directly opposite. Figs. 4-5. LM: Left valve. Winged AS visible. Fig. 5. Empty theca with visible trichocyst pores (arrows). Fig. 6 Line drawing: trichocyst pore arrangement.

PLATE 47



Prorocentrum minimum. Figs. 1-4. SEM. Fig. 1. Right valve. Cell oval; broad truncate apical region. Thecal surface with numerous short broad spines. Small scattered pores (arrows). Fig. 2. Lateral apical view. Periflagellar area with 2 pores: large flagellar (f) and small auxiliary (a). Small apical spine (arrowhead) adjacent to f; small curved forked periflagellar collar (arrow) adjacent to a. Intercalary band wide; transversely striated. Fig. 3. Cells oval; ventrally flattened. Fig. 4. Apical view. Short thecal spines and small scattered pores (arrows). Figs. 5-6. LM. Surface features and intercalary band visible. Fig. 7. Line drawing. (Figs. 1-6 after Faust 1974)

PLATE 48



Prorocentrum ruetzlerianum. Figs. 1-3. SEM. Fig. 1. Right valve: cell round to ovoid, covered with pentagonal areolae. Cell surface rugose. Fig. 2. Anterio-lateral view. Each areola with small circular pore at its base (arrows). Intercalary band broad, transversely rugose. Fig. 3. Periflagellar area: small, shallow, unornamented depression on right valve; large flagellar (f) pore and smaller auxiliary (a) pore. Figs. 4-5. LM (M.A. Faust). Right valve: striated valve margins (small arrows); large central pyrenoid (large arrow). Fig. 6. Line drawing: areolae arrangement. (Figs. 1-3,6 after Faust 1990b)