Identifying Marine Phytoplankton

Editor

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Contents

Editor's Foreword

This volume is a reprinted version of the two volume series previously published as "Marine Phytoplankton: A Guide to Naked Flagellates and Coccolithophorids" Academic Press, 1993, and "Identifying Marine Diatoms and Dinoflagellates" Academic Press, 1996. It achieves one of the original project objectives of providing in one volume, updated information required for the identification of marine phytoplankton. The response to both volumes was gratifying and confirmed our belief that there was a need for information of this kind. The reprinting of this literature allowed us an opportunity to combine both book texts, to correct errors, and to offer the complete text in a softbound format. While the discipline has not stood still since the first publishing, a complete revision was not possible at this time. Therefore, we urge users of this literature to review the latest journal publications for recent changes. The historical literature is well represented in the reference lists following each chapter and should suffice for returning to original descriptions.

The organization of this book was made with the broadest of outlines to accommodate the specific needs of the contributors—each had their own preference as to how the chapters should be designed. As a result, the reader will recognize that certain elements are common to all chapters. A general introduction, terminology list (in one case illustrated), numerous line drawings as well as SEM and TEM photomicrographs, cryptic descriptions giving essential characters, a synonymy list, index taxa, and extensive reference citations accompany each chapter. Since the material of each chapter varied, a flexible approach was required. Thus readers will find differences in format from chapter to chapter accommodating these differences. I hope this will not be too distracting and that the users will freely move from chapter to chapter with little difficulty.

For the most part, the illustrations are unique and have been produced for this publication. Photographs loaned for inclusion here are noted as are figures taken after published drawings. All original authors were contacted for approval prior to publication of the book. In some instances there are unlabeled illustrations as in a plate series in the Dinoflagellate chapter. These figures, appearing in silhouette, were purposely unlabeled forcing the users to match the silhouette with the corresponding line drawings appearing in the other plates of that chapter. In this manner, the authors of this chapter hoped to encourage researchers to use cell shape and outline as one of the important diagnostic tools in accurate identification of species. This was a deliberate challenge and not an oversight in labeling illustrations.

All chapters have special guides for identification. In the Diatom chapter, there are numerous keys, list of characters, and tables comparing species

to aid the researcher in distinguishing between similar species. In the Coccolithophorid chapter, there are comparisons of similar or problem taxa, which is of particular help with closely related confusing species. In the Flagellate chapter, there is a diagnostic "What to Look For" outline which can serve as a quick reference in narrowing the appropriate class, while in the Dinoflagellate chapter, the illustrated terminology section is oriented at showing the various features used in identifying species. Again, this reflects the preference of the authors. Of particular note, all readers should be aware of the **Taxonomic Index** that appears near the end of the Diatom Chapter. In this section, a new genus, new names and new taxa as well as novel nomenclatural combinations, are presented. **All nomenclatural novelties were validated in the original publications in, Tomas, C. (ed.), "Identifying Marine Diatoms and Dinoflagellates," Academic Press, 1996 and Tomas, C. (ed.), "Marine Phytoplankton: A Guide to Naked Flagellates and Coccolithophorids," Academic Press, 1993.** Additionally, common synonyms are presented at the end of each chapter. The most recently presented valid name is given with the others as equal synonyms including the full author citation.

A word of caution should be mentioned regarding distributions of species. The common feeling was that distributional information was to be given along broad climatic zones such as temperate waters, arctic or antarctic, subtropical, tropical oceans. In some instances, specific locations are mentioned, primarily because the species illustrated may have first been described from that region. The lack of a location reference for any species should not be construed as denoting the absence of that species from a region. Also, it would be impossible to cover all species of marine phytoplankton. The species chosen for description were selected to give a good representation of the commonly important species as well as enough different species as to give a full spectrum of characters to be found in the phytoplankton. The definitive book covering all phytoplankton species in the sea will probably never be realized.

As a final word, I would like again to restate my gratitude to my author/colleagues who devoted considerable effort in creating, revising, and modifying this literature. Without their full commitment, support, and patience this work could not have been completed. Numerous other colleagues also have assisted including those at the Zoological Station of Naples, Italy, the Florida Marine Research Institute, and the students of the International Phytoplankton Course, who have suggested modifications and corrections. Dr. Paul Silva gave invaluable assistance in matters regarding nomenclature. A special word of thanks is due to the editorial staff at Academic Press that has endured numerous modifications, delays, and revisions yet was supportive of the combined book project. Finally, I wish to acknowledge the continued effort and encouragement of my wife Cele, who throughout the various versions of these books has been the constant support without which this work would not have been completed.

Carmelo R. Tomas

Contributors' Forewords

Chapter 2

The diatoms have been studied for almost 300 years. A multitude of monographs and floras covering smaller and larger areas has been published, and the exact number of thousands of species distributed can hardly be given. Although the marine planktonic diatoms probably constitute a smaller fraction of the total number of species described, we are still dealing with some thousands of species. The elaborately and intricately ornamented siliceous diatom frustule was a challenge to the first transmission electron microscopist in the 1940s, and in the 1960s scanning electron microscopy was introduced in diatom studies providing even better insight into the structure of the diatom cell. This information led to new combinations of species, rejection of species, and description of taxa of all taxonomic categories. The thousands of species, the hundreds of years of studies, the clarification of intricate structures and relationships between taxa obtained by electron microscopy, and the confusion caused by introduction of new names may explain the length of the present chapter.

The history and development of the diatom chapter coincide with the rest of the project, starting with a simple text in 1976, mainly based on the authors' own research. The basis for a manuscript was therefore at hand when the possibility to publish the course notes as a book started to materialize in 1989. The first draft for a complete text was ready for the editor's corrections at the end of 1991 and was returned to the authors at the end of 1992. This version went back to the editor in April–May 1993, to be returned to the authors 1 year later. In April 1994, the editor and the senior author sat together for a short week to finally prepare a manuscript ready to submit to Academic Press.

Diatom research fortunately did not stand still between the start and the final step of the preparation of the diatom chapter. Efforts were made to incorporate, although to a limited extent, literature published in 1992–1994, but with the qualification that time and space did not permit a detailed treatment. During the last years of preparation nomenclatural problems related to the diatoms under study came to our notice. Thanks to Dr. Paul C. Silva as the nomenclature specialist on algae, most of the problems have been solved. New taxa and nomenclatural combinations having their first appearance in this chapter will hopefully be dealt with in detail in future publications.

The authors are grateful to Tyge Christensen for correction of the latin, to Paul Silva for his patience with the senior author's numerous questions, to Greta Fryxell for comments on *Pseudo-nitzschia* and *Thalassiosira*, to Frithjof Sterrenburg for comments on *Pleurosigma*, and to Bo Sundström for letting us copy his *Rhizosolenia* drawings. Carmelo Tomas is especially thanked for his editorial assistance; his initiative and sustained effort fulfilled the senior

author's long-dreamt dream to get literature prepared for the International Phytoplankton Courses formally available to a greater audience. E. Paasche and Carina Lange carefully read and commented on parts of the manuscript; Berit Rytter Hasle assisted with the preparation of the line drawings, and the electron micrographs were made at the Electron Microscopical Unit for Biological Sciences at the University of Oslo.

The project was supported by grants from the Norwegian Fisheries Research Council (1202-203.075 to E.E.S.), and from the Norwegian Research Council for Science and the Humanities (457.90/027 to E.E.S., 457.91/001 and 456.92/006 to G.R.H.). The senior author expresses gratitude to the Department of Biology, University of Oslo, for financial support and also for continued working facilities after retirement.

Grethe R. Hasle

Chapter 3

Advances in microscopy have furthered our ability to differentiate genera and species based on morphology and cytology. Concurrent with these advances in equipment and technique were individual studies that clarified useful characters; for example, E. Balech's recognition and characterization of sulcal and cingular plates; D. Wall's, B. Dale's, and L. Pfiester's characterization of life-cycle stages; H. Takayama's characterization of apical grooves or what B. Biecheler described as acrobases; J. Dodge's characterization of apical pore complexes; and F. J. R. Taylor's synthesis and interpretations on dinoflagellate taxonomy, biology, and evolution. These scientists are counted among my heroes. In the future, there will be more heroes who will have worked on optical pattern recognition, biochemical systematics and molecular probes, and other new avenues to identify species and relatedness among species.

My deepest respect and appreciation go to my Norwegian colleagues to whom I am indebted for inviting me to be an instructor and for sharing their knowledge, wisdom, kindness, and sense of humor with me. To Dr. Karl Tangen of OCEANOR, my collaborator, I offer special thanks. To my friend and mentor, Dr. Enrique Balech of Argentina, I offer my sincerest appreciation for teaching me to see beyond what is obvious and to interpret plate patterns and species differences. To Dr. Jan Landsberg (Florida Department of Environmental Protection, Florida Marine Research Institute) and Julie Garrett (Louisiana State University) I offer my gratitude for encouraging and helping me to complete this project. To the editor of this series, Dr. Carmelo Tomas, I express my gratitude for his patience, resolve, and continued friendship. I also thank and acknowledge Dr. Earnest Truby (Florida Department of Environmental Protection, Florida Marine Research Institute) and Dr. Elenor Cox and Clarence Reed (Texas A&M University) for the loan of their exceptional, unpublished scanning electron micrographs of armored species that were used to draw some of the composite illustrations in the plates. Julie Garrett provided most of the scanning electron micrographs of apical pore complexes. Consuelo Carbonell-Moore (Oregon State University) shared her knowledge of the Podolampaceae with me and is credited for photographs in Plate 7. Llyn French (Florida Department of Environmental Protection, Florida Marine Research Institute) assisted in preparation of the plates and provided artistic advice. Diane Pebbles, a biological illustrator and artist, provided 80% of the species illustrations, many of them original drawings based on scanning electron micrograph images. Her work increases the value of this chapter. Dr. Haruyoshi Takayama (Hiroshima Fisheries Experimental Station) provided all the photographs of apical grooves in Plates 1 and 2.

Karen A. Steidinger

Chapter 5

Among today's experts in flagellate taxonomy, the electron microscope has become an indispensable tool for identification of the species. However, the light microscope still remains the main instrument for routine use, and in many cases electron microscopy is merely used to verify identifications already made with conventional light microscopy. For most phytoplankton ecologists, however, the light microscope remains the only accessible equipment for taxonomic identification.

My account of marine planktonic flagellates (excluding dinoflagellates) is an introductory guide to this group and is based primarily on observations using the light microscope. The number of species illustrated for each genus is limited to presumably the most characteristic ones. Within genera such as *Chrysochromulina* (Prymnesiophyceae) and *Pyramimonas* (Prasinophyceae) large numbers of species need electron microscopy for reliable identification. In these cases, reference to features observed using both light and electron microscopy is given. Whenever possible the original description should be consulted, as all later ones depend on the interpretation of the first. Emended diagnoses and descriptions, however, are very important for an up-to-date identification. The variation in morphology common within one flagellate species makes it desirable to give several illustrations, but for practical reasons only one illustration for each species is included here.

When dealing with flagellates, as with other types of plankton, personal experience with each taxon is most important for practical work. The variation within the species required for determining the typical cell shape can be observed by using culture techniques or studying the species during boom conditions. It should be noted, however, that some species vary in appearance with growth condition (such as the number of cells in the *Oltmannsiella* colonies; Carmelo Tomas, personal communication).

The systematics of marine flagellates is presently in a dynamic state. The contents of the plates presented here were fixed to a classification system that becomes further modified as time goes on. The contents of this chapter have,

within practical limits, been updated to accommodate recent systematic revisions.

I am indebted to colleagues at the Institut for Sporeplanter, Copenhagen University; Tyge Christensen for providing Latin diagnoses and critically commenting upon the etymology of terms in the glossary, and Øjvind Moestrup, Helge A. Thomsen, and Jacob Larsen for comments on the manuscript. David Hill, School of Botany, University of Melbourne, Australia, commented on the cryptophycean systematics.

J. Throndsen

Chapter 6

Coccolithophorids, characterized by an outer covering of calcified scales or coccoliths, present special problems in identification due to the small cellular and coccolith size, often requiring observations with electron microscopes for reliable identification. However, species that are larger and/or have characteristic gross morphologies, like *Discosphaera tubifer* and *Scyphosphaera apsteinii,* can be readily identified during routine analysis of water samples with light microscopy. Morphological details of coccolith structure of smaller cells are discernible only under the best optical conditions. Thus, difficulties may be encountered if species like *Emiliania huxleyi* and smaller cells of *Gephyrocapsa oceanica* are present in the same sample. Use of an oil immersion objective and a total magnification of 800–1000 times should allow clear distinction between these species.

My chapter provides an introductory guide to the coccolithophorids. It presents the key literature, which is scattered in numerous publications. The text includes systematic descriptions and line drawings of a number of species as examples of the presumably most common ones encountered in marine samples. The chapter also includes species-related information such as synonyms, characteristics for identification, and distribution.

Several colleagues have kindly read parts of this chapter in manuscript form. This has been a great help. Among the many individuals to whom personal thanks are due, I wish to especially mention the late K. R. Gaarder, who introduced me to the coccolithophorids and so greatly enriched our knowledge of extant species. She has given a solid foundation for future work. Grateful thanks are also due to C. R. Tomas for editorial assistance as well as to R. Heimdal and E. Holm, who assisted with the preparation of the line drawings and other technical aspects of this chapter.

B. Heimdal

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Chapter 1

Introduction and Historical Background

Grethe R. Hasle and Carmelo R. Tomas

The content of this book as well as the earlier companion volume "Marine Phytoplankton: A Guide to Naked Flagellates and Coccolithophorids" had its origins as teaching and "handout" literature developed for the Advanced International Phytoplankton Course. Since the original course in 1976, the literature has been updated, improved, and tested on the talented selected participants for each course. With each course offering, requests were made to have the literature presented in a more permanent format as a published book(s). The urgency for the need of such literature was seen as photocopies of the handouts began to appear in various laboratories around the world. Prior to the 1990 course, an attempt to finalize this goal was realized with the agreement to write one book containing this literature. Here we will briefly present the steps of the procedure leading to the publication of this volume.

The idea of an International Course in Phytoplankton had its origins with Professor Trygve Braarud at the University of Oslo, Norway. Within his archived files are notes where Professor Braarud considered a course to teach young students of phytoplankton. The faculty would consist of Professor F.

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Hustedt (Diatoms), Professor J. Schiller (Dinoflagellates), and Professor E. Kamptner (Coccolithophorids). These names, gurus of the phytoplankton studies of the first half of this century, would have truly made an all-star teaching team. This dream was realized but not with the cast originally designed, as by the time the course was ready to be taught, most of these mentors were deceased.

In January 1969, a working Group of Phytoplankton Methods (WG 33) was established during the executive meeting of the Scientific Committee in Oceanic Research (SCOR). During this meeting, Professor Braarud pointed out the urgent need for considering phytoplankton methods other than those involving pigment and other chemical analyses. The IOC Working Group on Training and Education also commented on the need for modern textbooks and manuals (Unesco technical papers in marine science no. 18, Paris, 1974).

In Item 4 of the Terms of Reference to WG 33, the Working Group was asked to prepare a report including reference to literature in taxonomy of the main groups and on methods for using quantitative phytoplankton data in ecological studies. To fulfill this request, the Working Group suggested a list of the contents of such a manual and a tentative plan for a "Phytoplankton Course for Experienced Participants." The University of Oslo was chosen as the place for the course and the Marine Botany Section as responsible for the teaching program.

The preparation of a Phytoplankton Manual of Methodology started with a meeting at the University of Oslo under the auspices of SCOR in 1974. The "phytoplankton manual" was published in 1978 by Unesco as "Monographs on Oceanographic Methodology 6" with A. Sournia as the editor. No further steps were taken to prepare a corresponding manual on phytoplankton taxonomy although a need had been expressed by some members of WG 33.

The first "Phytoplankton Course for Experienced Participants" was held at the University of Oslo during 4 weeks in August–September 1976 with 17 participants from 13 different countries. After the first offering, the length of the course was cut to 3 weeks, and the next two courses, in the autumns of 1980 and 1983, were held at the Biological station in Drøbak, belonging to the University of Oslo. Stazione Zoologica "Anton Dohrn," Naples, Italy, hosted and organized the courses now called "Advanced Phytoplankton Courses, Taxonomy and Systematics" in 1985, 1990, and 1995. Another session of this course is presently being planned for Spring 1998 to be held in the Naples area.

From the very beginning interest in the courses was considerable and increased with each offering. In 1995, more than 170 applications were received for the 15–17 places available. The apparent need for a course dealing with identification of phytoplankton species became more evident with the increased activity in mariculture, the recurrence of harmful phytoplankton blooms, the

documented toxicity of certain species, the apparent increased pollution of the sea, and global atmospheric changes.

A total number of 99 participants, representing 38 countries, participated in the five courses to date. The instructors in 1976 were the late Karen Ringdal Gaarder (coccolithophorids, dinoflagellates), Grethe Rytter Hasle (diatoms, dinoflagellates), E. Paasche (algal physiology, cultures), Karl Tangen (dinoflagellates), Jahn Throndsen (naked flagellates), and Berit Riddervold. All the instructors with the exception of Berit Riddervold Heimdal (coccolithophorids), from the University of Bergen, were from the University of Oslo. In 1983, Karen A. Steidinger, Florida Marine Research Institute, and Karl Tangen, now Oceanor, Trondheim, Norway, taught dinoflagellates and Barrie Dale, University of Oslo, lectured on dinoflagellates cysts. Erik E. Syvertsen, University of Oslo, assisted G. R. Hasle with the diatoms. From 1985 the staff of Stazione Zoologica also participated in the teaching.

The courses were sponsored by SCOR and IABO, and financially by UNESCO, NORAD (Norwegian Agency for International Development), the Norwegian Ministry of Foreign Affairs, the Italian Ministry of Foreign Affairs, the Italian National Research Council, the U.S. Office of Naval Research, Stazione Zoologica "A. Dohrn" di Napoli, and the University of Oslo.

Despite the unique collection of reprints and identification literature available during the course at the University of Oslo, and later at the Stazione Zoologica, class notes and handouts had to be prepared. They started out with a few pages on each group and increased gradually with additional information from the literature and the respective instructor's own research. In 1983, mainly by Karen Steidinger's initiative, contacts were made with publishing companies to formalize an officially published text. These attempts failed, but in 1989 Carmelo R. Tomas (participant of the 1983 course) started successful negotiations with publishing companies for a text to be used in the 1990 course. Again this deadline was not accomplished but a firm commitment from the authors, editor, and publishing company was definitely made. Consequently, the course notes changed in format and increased in content to form the basis of a manuscript for publication. It became evident that the flagellate and coccolithophorid texts would be completed ahead of those on the diatoms and dinoflagellates. This plus the fact that the newly expanded version of the diatom and dinoflagellate sections exceeded the original project would make a book containing all parts too large for a handy volume. After renegotiation between Academic Press and Carmelo Tomas as the editor, it was decided that a volume on flagellates and cocclithophorids would be published first to be followed by the present one on diatoms and dinoflagellates.

Running expenses inside Norway, related to the manual project, were covered by grants from the Department of Biology, University of Oslo; the Norwegian Research Council for Science and the Humanities (NAVF 457.90/041); and from the Norwegian Fisheries Research Council (project 66170).

Planning funds for the literature were also awarded to the editor from UNESCO while funds for illustrations, technical assistance, postage, and communications were given by Stazione Zoologica of Naples. Since no member of this team was funded to work full-time on this project, each person gave of their personal time and effort to accomplish the goal of completing these manuals. The respective institutions gave support, as was possible, affording each author and editor the opportunity to work on this project. The support notwithstanding, each member of this team worked on this literature while assuming full duties of their permanent work assignments.

Chapter 2

Marine Diatoms

Grethe R. Hasle and Erik E. Syvertsen

INTRODUCTION

The study of diatoms began in the 18th century. The name of the class Bacillariophyceae was derived from the genus *Bacillaria* Gmelin 1791, whereas "Diatom" refers to the genus *Diatoma* De Candolle 1805. Despite more than a century of devoted morphological and taxonomic investigations, electron microscopy, introduced to diatom research in the middle of the 20th century, revealed additional information. A reevaluation of the established classification systems and the current ideas and information on biogeography was required, and a new era of diatom investigations began.

Simonsen (1979) introduced a diatom system based on results from light and electron microscopy and constructed a key to the diatom families. Other ideas on classification, evolution, and critical evaluations at the higher taxonomic levels followed, based on the increasing amount of information (Cox, 1979; Round & Crawford, 1981, 1984; Fryxell, 1983; Glezer, 1983; Nikolaev, 1984; Williams & Round, 1986, 1987), resulting in two partially diverging diatom systems (Glezer et al., 1988; Round et al., 1990).

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Publications summarizing the new information on diatom morphology as well as a revision of the classical identification literature were needed. To meet this requirement several diatom atlases, floras and handbooks were published during the past decade or so, most of them concentrating on a particular geographical region. Ricard (1987) constructed keys to families and genera with genus as the lowest rank, the genera being illustrated with light and electron micrographs of one or a few species of each. The diatom handbooks by Priddle & Fryxell (1985) and Medlin & Priddle (1990) both deal with polar species. The focus of the former is on some planktonic diatoms commonly recorded in the Southern Ocean. The latter, a more comprehensive handbook, includes the two polar regions and has an ecological as well as a taxonomic part with keys to species. The diatom atlas from India and the Indian Ocean region (Desikachary, 1986–1989) contains only light micrographs of the diatoms recorded in the area with no additional text, and the phytoplankton atlas by Delgado & Fortuño (1991) has text as well as line drawings and scanning electron micrographs of diatoms from the Mediterranean.

The publications by Rivera (1981), Makarova (1988) and Rines & Hargraves (1988) have the character of monographs of the marine planktonic genera *Thalassiosira* (the former two publications) and *Chaetoceros* (the latter publication), although based on material from specific geographical areas. The investigation of *Rhizosolenia*, a third important marine planktonic genus, by Sundström (1986) is based on material from almost all oceans, and the Unesco Manual on Harmful Microalgae has a chapter on this category of diatoms (Hasle & Fryxell, 1995).

The monumental diatom volume by Round et al. (1990) differs from all the publications mentioned previously in content as well as size; it consists of sections on the biology of the diatoms, a summary of the introduced classification, and a generic atlas. Linnaeus, a catalogue and expert system for the identification of protistan species (Estep et al., 1992), includes diatoms, and the catalogue by Gaul et al. (1993) lists papers containing electron micrographs of diatoms and is thus useful to those studying the fine structure of the diatom frustule.

Despite these recent publications, teaching experience tells us that there is still a need to fill in respect to the global aspect of the identification of marine planktonic diatoms at the specific level. We hope to fill a part of this need with this chapter.

GENERAL CHARACTERISTICS

Systematics: Class Bacillariophyceae in the division Chromophyta.

Closest relatives: Chrysophyceae and Xanthophyceae. (See Round et al., 1990, p. 122.)

Number of species: 10,000–12,000, approx 50,000 (Round & Crawford, 1984, p. 169), or in excess of 100,000 (Round & Crawford, 1989, p. 574); or in marine plankton approx 1400–1800 (Sournia et al., 1991, p. 1085).

Size: ca. 2 μm–ca. 2 mm.

Level of organization: Unicellular, often in colonies.

Cell covering: Siliceous wall and organic layer.

Flagella: Male gametes with one flagellum with stiff hairs.

Chloroplasts: Lamellae with three thylakoids, girdle lamella, and four membranes around the chloroplast.

Pigments: Chlorophylls *a* and *c*, betacarotene, fucoxanthin, diatoxanthin, and diadinoxanthin.

Mitochondria: Tubular type.

Storage products: Chrysolaminarin and oil.

Motility: Present in pennate diatoms with a raphe.

Biotopes: Marine and freshwater, plankton, benthos, epiphytic, epizoic (e.g., on whales and crustaceans), endozoic (e.g., in foraminifera), endophytic (e.g., in seaweed), on and in sea ice, and "air diatoms."

Geological age: Centrics: Jurassic (a few species) and Early Cretaceous (Gersonde & Harwood, 1990). Araphid pennates: Late Cretaceous (Medlin et al., 1993, with references). Raphid pennates: Middle Eocene (Medlin et al., 1993, with references).

LIFE CYCLES

Reproduction (Figs. 1a and 1b)

Diatoms reproduce vegetatively by binary fission, and two new individuals are formed within the parent cell frustule. Each daughter cell receives one parent cell theca as epitheca, and the cell division is terminated by the formation of a new hypotheca for each of the daughter cells. This type of division, with formation of new siliceous components inside the parent cell, leads to size reduction of the offspring. The possible size range of the diatom cells seems to be species dependent, and the specific variation may be as large as 8 to 10 times the length of the apical axis or the diameter.

The considerable size variation is often accompanied by a pronounced size dependent change in cell proportions, normally in the form of an increase in the ratio between the length of the pervalvar axis and the apical axis or diameter. In addition, size variation often causes changes in valve ornamentation, like a reduction in the number of central clustered processes in *Thalassiosira* spp. (E. Syvertsen, personal observations), a loss of special structures like the pili of certain species of the Cymatosiraceae (Hasle et al., 1983), and an alteration of the valve outline of morphologically bipolar species from elongate toward almost circular, e.g., *Fragilaria* spp. (Hustedt, 1959) and Cymatosiraceae.

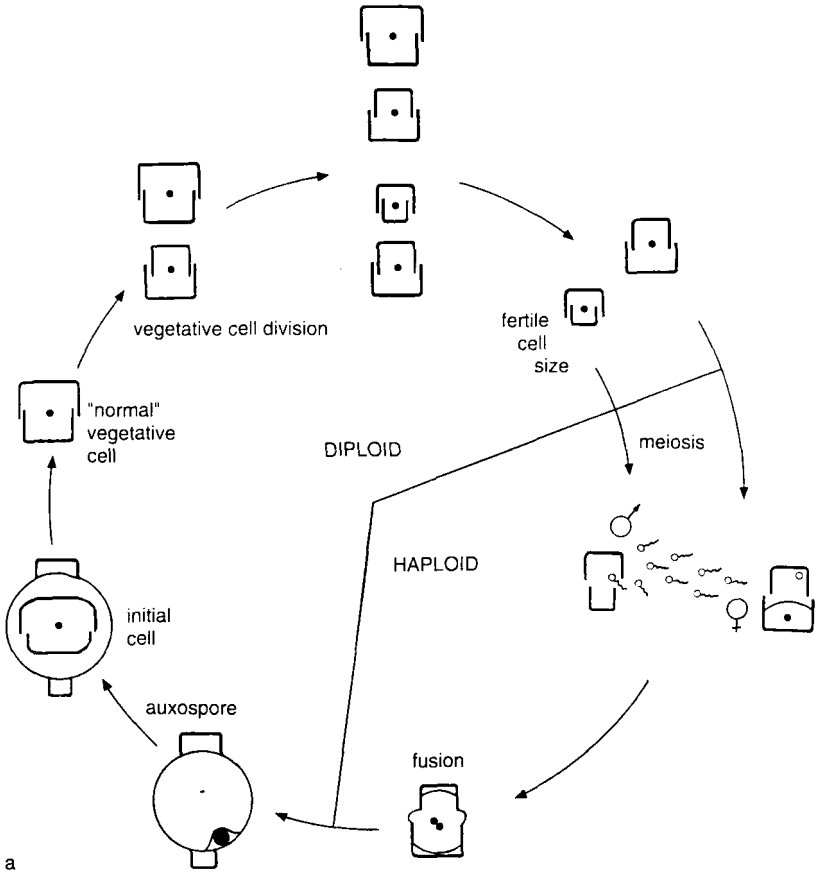


FIGURE 1 (a) Sexual reproduction of a centric diatom (oogamy) and (b) of a pennate diatom (morphological isogamy, physiological anisogamy). ●, Zygote; •, nucleus; ○, pycnotic nucleus.

The decrease in the average cell size of a diatom population during vegetative growth implies a need for a means of restoring the cell size. This is made possible by auxospore formation, in which a cell sheds its siliceous theca, thereafter forming a large sphere surrounded by an organic membrane. Within this sphere, a new diatom frustule of maximal size is formed, and the cycle starts anew. The first cell formed inside the auxospore, the initial cell, may have a morphology deviating in girdle structure, valve outline, and process pattern from that of a "normal" vegetative cell (*vide*, *Thalassiosira decipiens*, Hasle, 1979, Fig. 41; *Cymatosira lorenziana*, Hasle et al., 1983, Fig. 19).

Auxospore formation is size dependent and normally takes place when the cell has reached about one-third of its maximal size (Drebes, 1977). Below

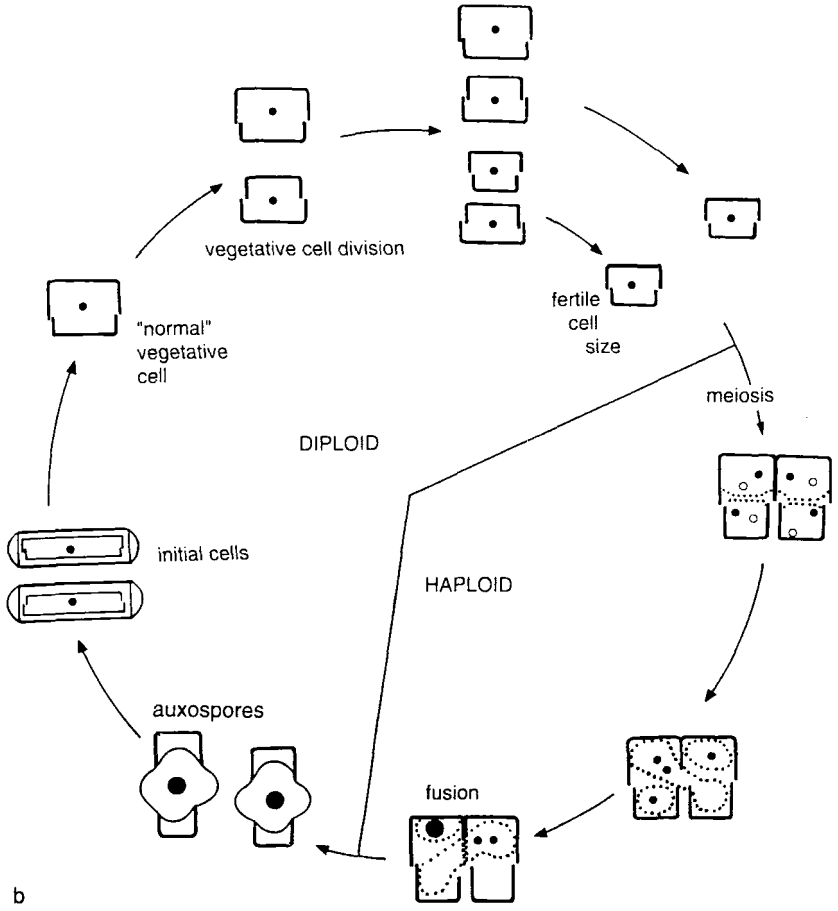


FIGURE 1 (*Continued*).

this limit the diatoms seem unable to rejuvenate themselves, and they continue to divide until they reach a stage at which cell division is no longer possible. There are reports in the literature of taxa which do divide without a simultaneous size reduction (Drebes, 1977), and some species seem to be able to multiply at their lower size limit without further size reduction for an extended length of time (E. Syvertsen, personal observations). For most species, however, auxospore formation is a necessary and normal occurrence in their life cycle. It may take place as a vegetative event or as the result of sexual reproduction.

All diatoms are diplonts with a meiosis at the end of the gametogenesis. The zygote develops into an auxospore. In the centric diatoms, sexual reproduc-

tion is by oogamy with flagellated male gametes, while most pennate diatoms are morphologically isogamous lacking a flagellated stage. A few araphid species have been shown to be anisogamous (Drebes, 1977) and are considered to represent a transitional stage between centric and pennate diatoms. Since the diatoms are thought to have evolved from centrics toward pennates (see also Geological age), this implies a development from oogamy toward isogamy, contrary to what is considered the normal evolution in other groups.

One peculiar consequence of the diatom mode of vegetative multiplication is the possible "eternal life" of larger valves, resulting from the fact that one of the daughter cells inherits one of the parent cell thecae. Nothing seems to be known about how many times a theca can be "reused" in this way. Theoretically, it could go on indefinitely if the cells are not destroyed by external factors. But even if the thecae are reused only a few times, the valve morphology of certain cells may reflect earlier events in the life of the population. As discussed below, a vegetative cell may have a resting spore epitheca documenting previous resting spore formation. In the same way, various valve morphotypes may be found in a population of a species capable of developing morphologically distinct forms in response to environmental influences.

Heteromorphy

Many diatoms are heterovalvate, i.e., the two valves of a frustule are dissimilar. This is most prominent within the family Achnanthaceae, where the cells have one valve with a raphe and the other without a raphe, and in the Cymatosiraceae, where one valve has a tubular process and the other does not.

Chain-forming species with cells linked together by siliceous structures may, in addition, have separation valves. These valves are morphologically different from the valves within the chain. Thus, *Cymatosira lorenziana* has four morphologically distinct types of valves: a separation valve with a tubular process, a separation valve without a tubular process, and intercalary valves with and without a process, respectively. In the genera *Bacteriastrum, Chaetoceros, Paralia,* and *Skeletonema,* the intercalary valves of the chains are all alike and different from the separation valves (Fryxell, 1976; Crawford, 1979).

Another type of heteromorphy may be found with species in which the morphology varies in response to changes in the environment. These morphotypes are generally considered to be forms of the species. During and after environmental changes specimens may be found which have two different valves reflecting different environmental conditions. This type of morphological adaptation has been found in *Thalassiosira rotula.* In this species, the valve morphology changes in response to variations in temperature and the girdle morphology changes in response to available nutrients (Syvertsen, 1977).

Resting Spore Formation (Fig. 2)

The diatom resting spores are first and foremost recognized by their heavily silicified frustules. The resting spore morphology of some species is similar to that of the corresponding vegetative cells, whereas in other species, the resting spores and the vegetative cells differ drastically (Syvertsen, 1979, 1985).

Diatom resting spores are normally formed as a response to unfavorable environmental conditions, and germination occurs when the conditions improve (see Hargraves & French, 1983, for a review). Resting spore formation is common in centric, but rare in pennate marine planktonic diatoms. Whereas resting spores of several centric marine planktonic diatoms germinate in culture within a few days, the freshwater benthic pennate species, *Eunotia soleirolii* (Kützing) Rabenhorst, requires a dormancy of several weeks (von Stosch & Fecher, 1979) before germination. *Achnanthes taeniata* and *Fragilariopsis oceanica* are pennate marine planktonic diatoms known to form resting spores; whether a dormancy period is present in these species is unknown.

Three types of resting spores can be distinguished: exogenous resting spore—the mature resting spore is not physically in contact with a parent cell theca; semiendogenous resting spore—the spore hypovalve is enclosed within one of the parent cell thecae; and endogenous resting spore—the whole spore is enclosed within the parent cell frustule. Normally two or more exogenous resting spores [e.g., a chain of 13 resting spores of *Detonula confervacae* (Syvertsen, 1979)], two semiendogenous resting spores [e.g., *Thalassiosira australis* (Syvertsen, 1985)], and one endogenous resting spore [e.g., *Chaetoceros* spp. (Hargraves, 1979)] are formed. All three types were found in clonal cultures of *Thalassiosira nordenskioldii* and *T. antarctica* with the semiendogenous type as the most common (Syvertsen, 1979).

Resting spore morphology is a more constant, specific feature than the type and mode of formation and, thus, is of greater taxonomic value. Until disproven by Syvertsen (1979) for centric diatoms and by von Stosch & Fecher (1979) for pennate diatoms, it was generally believed that resting spores had no girdle and thus differed from vegetative cells. Among the centric diatoms, the general trend seems to be that resting spores of species, possibly early in the phylogenetic diatom system (e.g., *Thalassiosira* and *Stellarima*), have a girdle and are often morphologically similar to the vegetative cells. Resting spores of species in the possibly more advanced part of the system (e.g., *Bacteriastrum* and *Chaetoceros*) are usually very different from the vegetative frustules and often lack a girdle. This seems to coincide with a suggested development from exogenous or semiendogenous toward endogenous resting spores (Syvertsen, 1979). On the other hand, phylogenetically advanced pennate diatoms, e.g., *Achnanthes taeniata* and *Fragilariopsis oceanica,* form resting spores with a girdle. A special case occurs when resting spores are formed within auxospores. This takes place, for instance, in *Chaetoceros eibenii* (von Stosch et

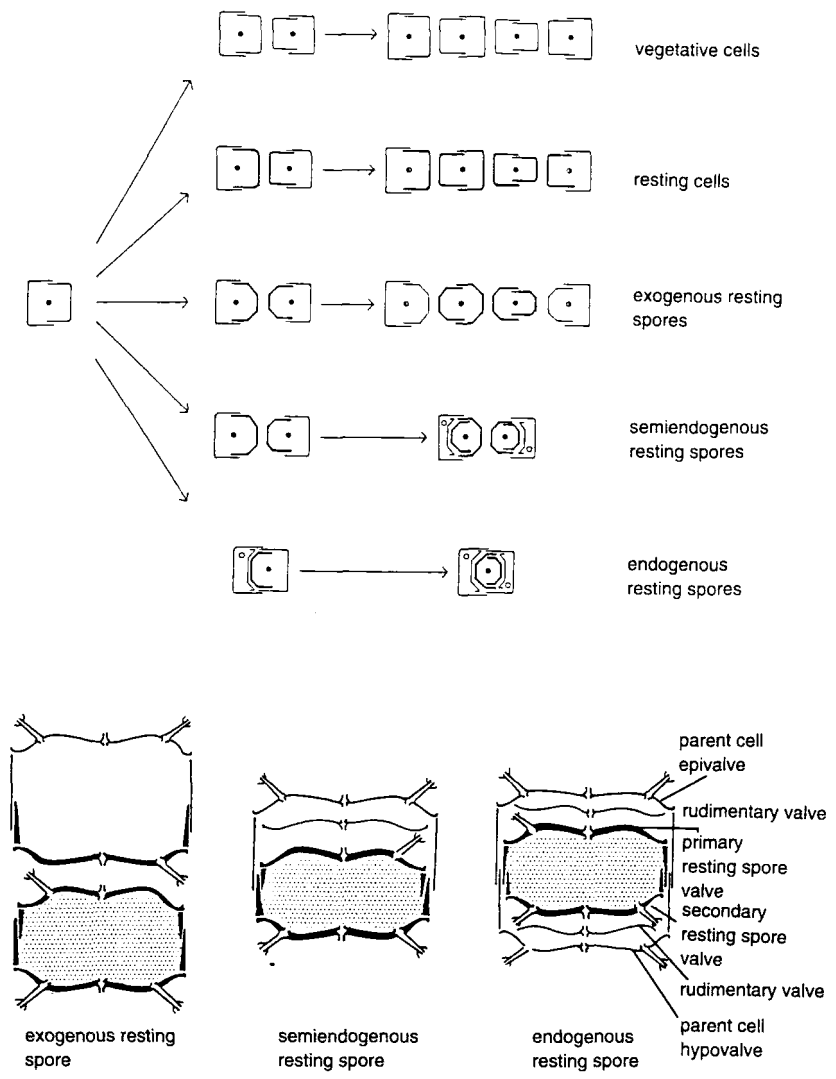


FIGURE 2 Formation of vegetative cells, resting cells, and resting spores from a vegetative parent cell. *Thalassiosira nordenskioeldii* is an example of a species forming all three types of resting spores.

al., 1973) and in *Leptocylindrus danicus* and *L. minimus* (Hargraves, 1990). Unlike other diatoms known so far, the resting spores are an obligate part of the life cycle of *L. danicus* (French & Hargraves, 1985).

Resting spore formation includes two cytokinetic mitoses (von Stosch et al., 1973), where one or both may be unequal. Depending on the degree of dissimilarity, the rudimentary cells may or may not be visible (Syvertsen, 1979). In terms of morphology, the rudimentary valves are often intermediate between vegetative and resting spore valves, but may be sufficiently different to risk being described as separate species unless their origin is known [*vide Thalassiosira australis* (Syvertsen, 1985)].

The two valves of a resting spore may be similar or distinctly different. Often the first valve formed (primary resting spore valve) is more similar to the valves of the vegetative cells than is the second valve (secondary resting spore valve). Thus, during resting spore formation at least four morphologically different valve types may be found which can easily be and probably often have been identified as belonging to different species. These valve types are (1) normal vegetative valves, (2) rudimentary valves, (3) primary resting spore valves, and (4) secondary resting spore valves. In addition, intermediate valve types between those mentioned and representing various degrees of development are often seen (E. Syvertsen, personal observations). This diversity of valve types belonging to one and the same species calls for caution in identification work using cleaned diatom material.

Resting spores germinate in two ways, according to whether or not they have a girdle. Spores with a girdle germinate to form two new vegetative cells where the resting spore thecae serve as epithecae [e.g., *Thalassiosira* (E. Syvertsen, personal observations)], while spores lacking a girdle shed the spore valves in the process of vegetative cell formation, as with *Bacteriastrum* and *Chaetoceros* (von Stosch et al., 1973). In the first case, chains formed after resting spore germination have the resting spore valves as epivalves on the end cells, and these cells are thus heterovalvate.

MORPHOLOGY AND TERMINOLOGY

With an increasing amount of information on details of the siliceous diatom cell wall, especially that obtained with electron microscopy, a need for a generally accepted terminology became evident in the early 1970s. The first attempt along this line was published in 1975 as "Proposals for a Standardization of Diatom Terminology" (Anonymous, 1975; von Stosch, 1975) followed by "An Amended Terminology for the Siliceous Components of the Diatom Cell Wall" (Ross et al., 1979). These publications contain glossaries in Latin, English, German, and French. A Russian translation of Anonymous (1975) was published by Makarova (1977).

When the fine structure of pennate diatoms became more extensively studied, new terms were introduced (Mann, 1978, 1981; Cox & Ross, 1981; Williams, 1985, 1986). Terms specific to certain centric diatom families or genera, partly applicable to light microscopy, were also suggested (Hasle et al., 1983; Sundström, 1986; Rines & Hargraves, 1988).

The text of this chapter follows the current terminology, including, in part, that of Barber & Haworth (1981). The gross morphology of the diatom frustule and structures more generally distributed within the class are defined in this chapter. Terms specific to particular taxa are defined in the introductory text to these taxa. The definitions of the terms may include elements not readily revealed by light microscopy. This does not exclude the possibility to recognize the presence of a particular structure. For example, the tubular parts of strutted processes may be visible in the light microscope, while the satellite pores are usually not observable.

Gross Morphology (Figs. 3 and 4)

Apical axis—long axis of a bilateral diatom—axis between the poles of a frustule.

Pervalvar axis—axis through the center point of the two valves.

Transapical axis—third axis of a bilateral diatom.

Valvar plane—parallel to the valves—plane of division.

Apical plane—perpendicular to the transapical axis.

Transapical plane—perpendicular to the apical axis. (If more specified terms are required, see Round et al., 1990, p. 23, Fig. 18.)

Valve view—frustule seen from top or bottom.

Broad girdle view—frustule seen from broad side.

Narrow girdle view—frustule seen from narrow side.

Frustule—the whole diatom box.

Epitheca—upper overlapping part of frustule.

Hypotheca—lower part of frustule.

Valve—epi-, hypo-.

Valve mantle—marginal part of valve, set off from valve face at an angle.

Valve face—part of valve surrounded by mantle.

Girdle—part of frustule between epi- and hypovalves consisting of epi- and hypocingula.

Cingulum—portion of the girdle associated with a single valve.

Band or segment—a single element of the girdle.

Intercalary band(s)—**copula(e)**—element(s) nearest to the valves, different in structure from elements farther away from the valves.

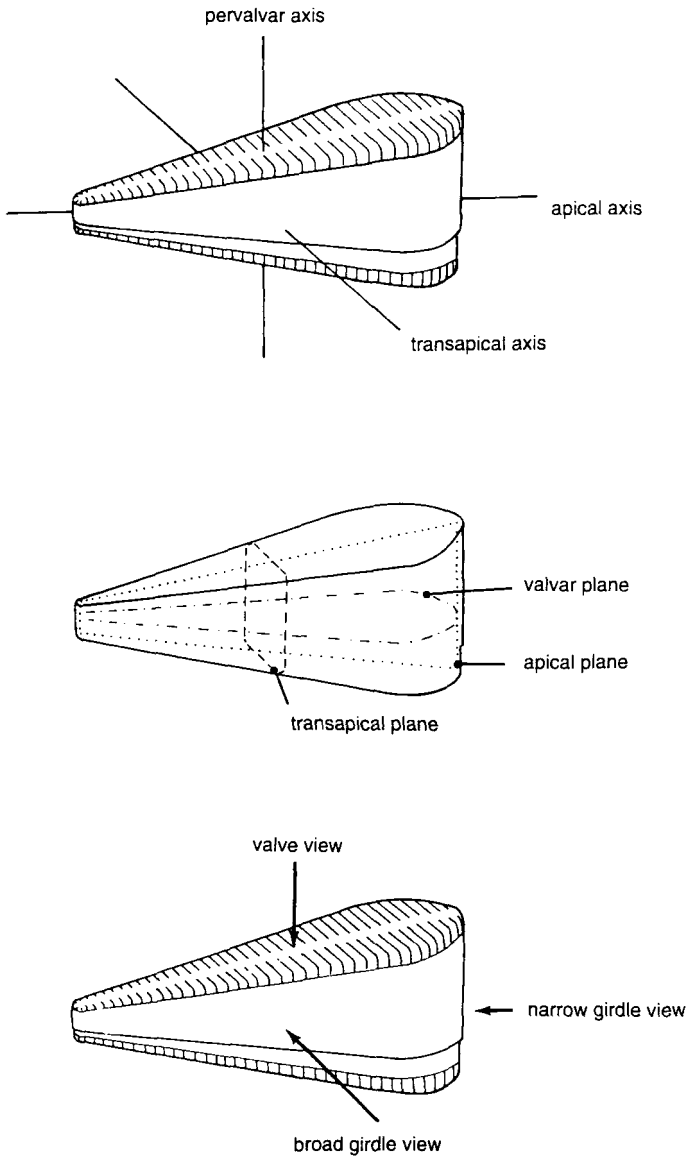


FIGURE 3 Axes and planes of a diatom frustule.

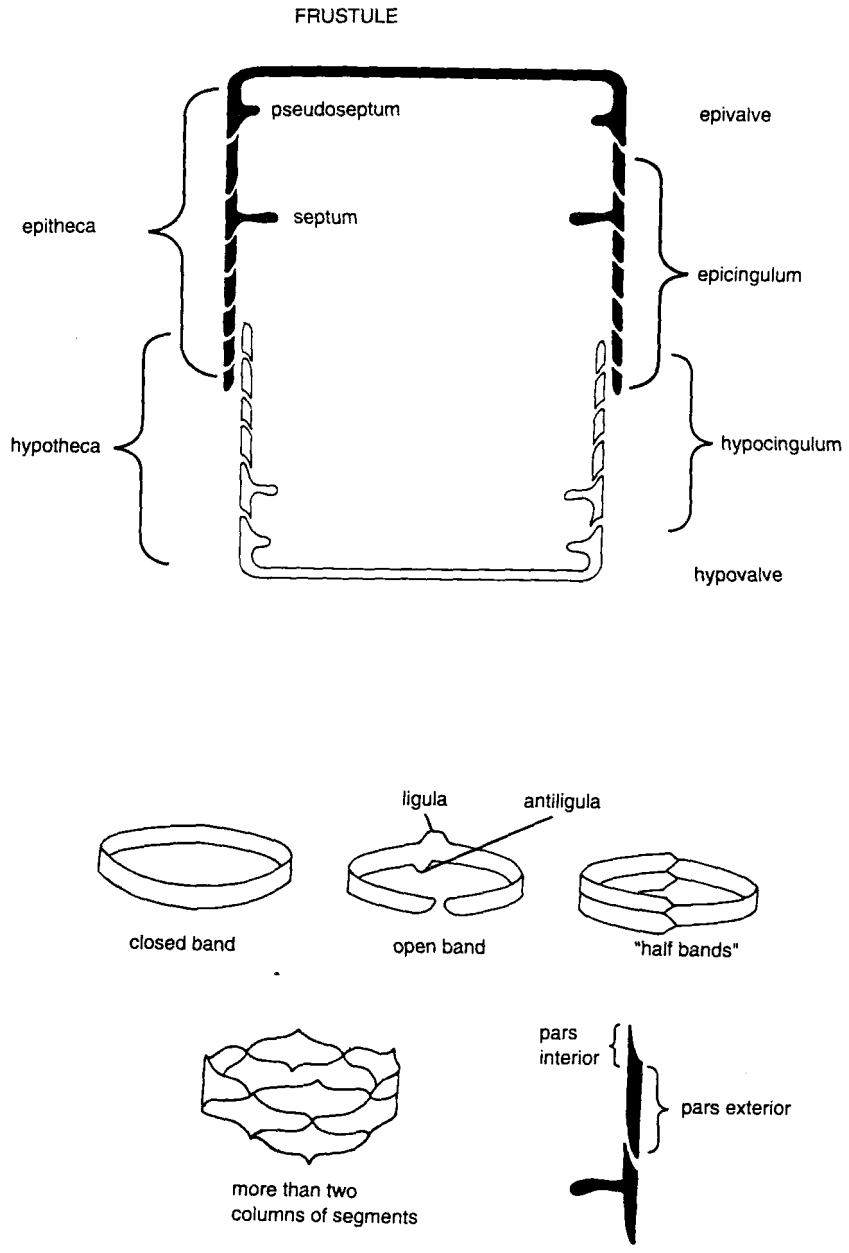


FIGURE 4 Gross morphology of the frustule, types of girdle bands and segments, and overlapping of bands.

Valvocopula—band adjacent to a valve.

Connecting band(s)—pleura(e)—element(s) in the middle of the girdle when intercalary bands are present or any element when no intercalary bands are present.

Septum—a sheet or ridge in the valvar plane projecting from a girdle band into the interior of the frustule, often with several openings.

Hyaline band—element of girdle with no perforations (see Hemidiscaceae).

Fine Structure of the Siliceous Cell Wall (Figs. 5 and 7)

Basal siliceous layer—the layer that forms the basic structure of the various components of the frustule.

Annulus (von Stosch, 1977)—a ring of costal thickness, often surrounding one or more processes and with a structure different from that of the rest of the valve (see *Porosira* and *Actinocyclus*).

Areola—regularly repeated perforation through the valve wall, often marked by more or less elaborate multiangular walls or ribs (definition slightly deviating from Ross et al., 1979, p. 527).

Velum—a thin perforated layer of silica across an areola.

Cribrum—a velum perforated by regularly arranged pores.

Foramen—the passage through the constriction at the surface opposite the velum.

Poroid areola or poroid—an areola not markedly constricted at one surface of the valve.

Loculate areola or loculus—an areola markedly constricted at one surface of the valve and occluded by a velum at the other.

Alveolus—an elongated chamber running from the central part of the valve to margin, open to the inside and covered by a perforate layer on the outside.

Stria—one or more rows of areolae or pores, or an alveolus. Uniseriate, one row; biseriate, two rows; multiseriate, many rows.

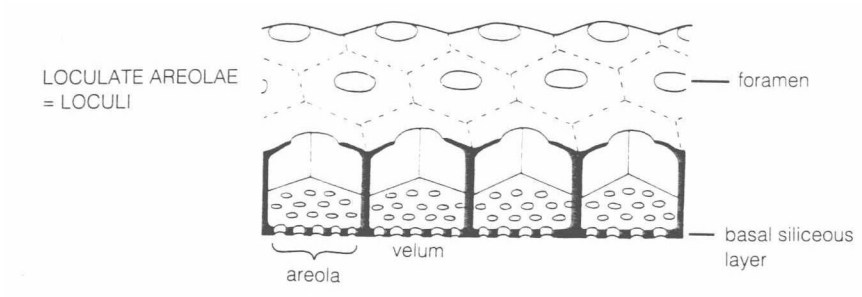
Interstria—the nonperforate siliceous strip between two striae.

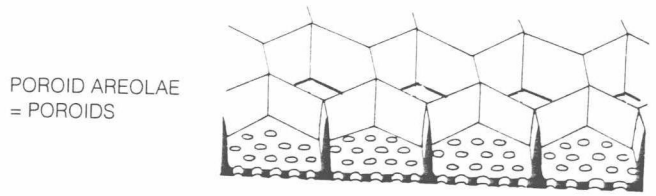
Processes (Figs. 6–8)

Process—projection with homogeneously silicified walls.

Labiate process—rimoportula—a tube or an opening through the valve wall with an internal flattened tube or longitudinal slit surrounded by two lips.

Spine—a closed or solid structure projecting out from the surface of the frustule.





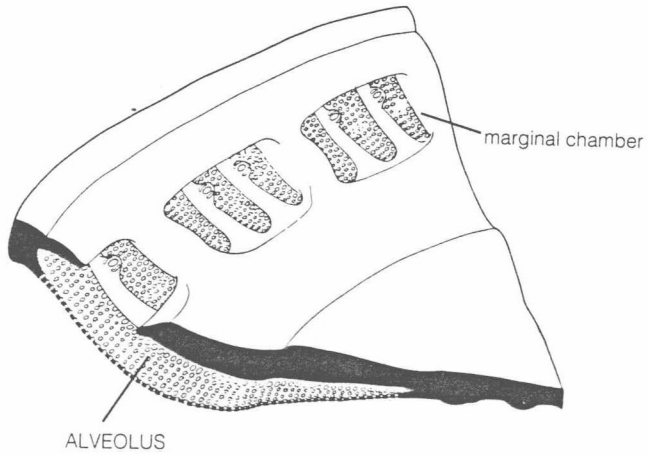


FIGURE 5 Fine structure of the siliceous cell wall.

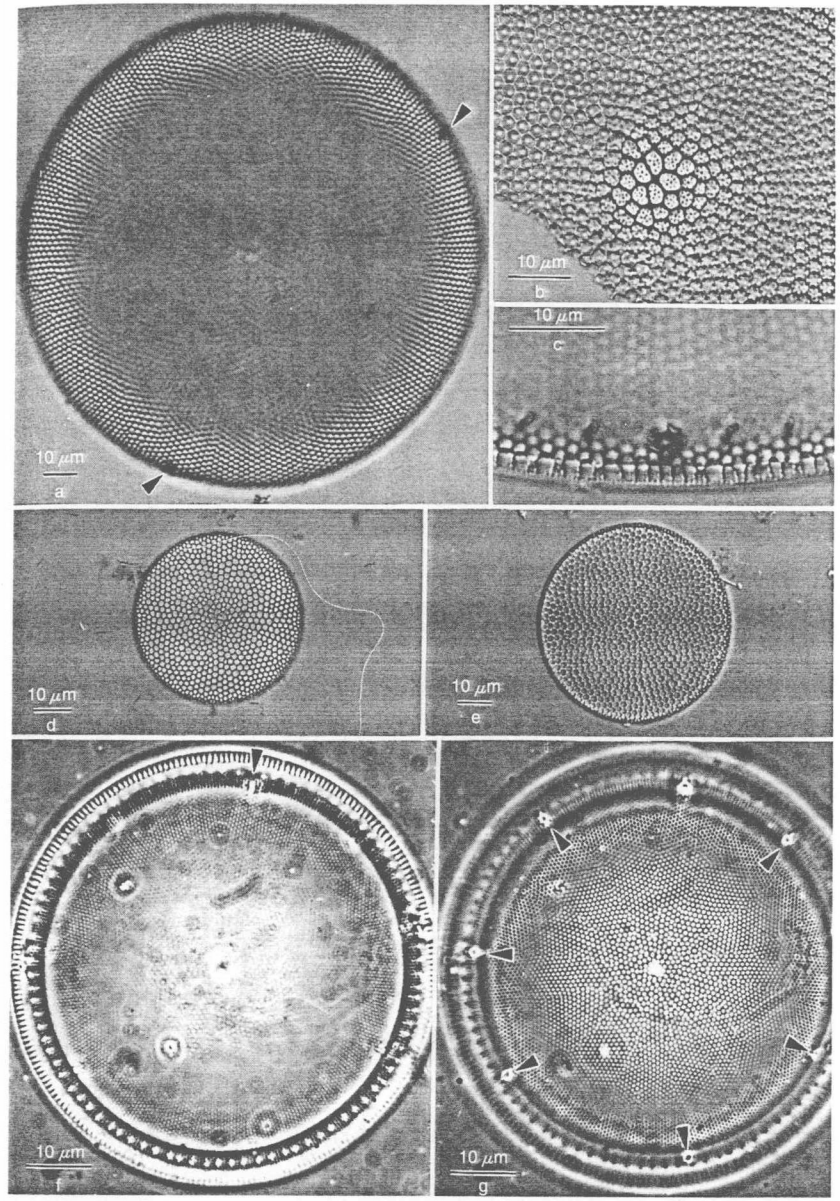


FIGURE 6 Light micrographs showing areola and process patterns. Scale bars = 10 μm. (a) *Coscinodiscus centralis*, radial areolation with striae incerted from valve margin, one marginal ring of smaller and two larger (arrows) labiate processes; (b) *C. centralis*, central rosette of larger areolae, cribra discernible, decussating arcs of areolae; (c) *C. centralis*, four smaller long-necked labiate processes and one larger process; (d and e) *Coscinodiscus radiatus*, radial areolation, indistinct decussating rows and fasciculation with striae parallel to the edge row; (f) *Thalassiosira punctigera*, ribbed margin, one marginal ring of small, densely spaced strutted processes, one larger labiate process (arrow); (g) *T. punctigera*, bases of occluded processes (arrows), fasciculate areolation with striae parallel to the middle row.