LLOYD H. BURCKLE

MARINE DIATOMS

Lloyd H. Burckle
Lamont Geological Observatory
Palisades, New York 10964

INTRODUCTION

Those students interested in further work in micropalcontology will find that Diatoms are an interesting, useful and relatively uncrowded field for study. Future work in micropaleontology will stress the solution to correlation and paleoecologic problems in high latitudes—regions which contain few, if any, calcareous microfossils but which are exceedingly rich in diatomaceous remains. In spite of this even in low latitudes the study of fossil Diatoms lags far behind that on other major microfossil groups. This continues despite the fact that they are a demonstrably useful group.

Fossil Diatoms were first studied extensively in the latter half of the 19th century. Although these works have little stratigraphic value they did contribute to our understanding of Diatom taxonomy as well as ferret out and describe numerous classical Diatom collecting localities. Modern work, stressing the stratigraphic applicability of Diatoms, began in the middle 1920's with publications on the extremely diatomaceous California sections. These sections, which range in age from Cretaceous to Pliocene, continue to be the object of considerable study. Workers in other countries particularly the Soviet Union and Japan also began serious study of diatomaceous sections. Such studies were guided by two definitive

works: The Schmidt Diatom Atlas (beginning in 1875) and by the publications of Hustedt (beginning in 1927) which refined taxonomy and added notes on the ecology and distribution of selected Diatom species.

The advent of extensive deep-sea coring programs was accompanied by renewed interest in Diatom biostratigraphy, again with the Russians taking the lead. This interest continues to the present day and most workers in stratigraphic micropaleontology now draw some or all of their material from deep-sea sediments.

There are three uses of fossil Diatoms: (1) They can be used in biostratigraphy. This application has been aided in large part by the use of deep-sea sediment cores, particularly in high latitudes and by the integration of Diatom data with paleomagnetic stratigraphy and with other microfossil groups; (2) They can be used in paleoecological and paleoenvironmental reconstructions. By this it is meant that Diatoms can be used as indicators of such environmental parameters as water chemistry, paleosalinity, paleodepth, paleotemperature and paleonutrient concentrations; and (3) Fossil Diatoms can be used as indicators of paleocurrents and particularly bottom currents. Since many Diatoms are built to remain in suspension they can easily be transported laterally, in some cases for several thousands of miles. In such cases, these displaced Diatoms can be

used as indicators of the historical stability of the transporting currents.

ORGANIZATION AT THE CELLULAR LEVEL

Diatoms are photosynthetic, single celled algae that inhabit many aquatic and subaquatic environments. Some species have adopted a quasi-colonial life style but are capable of living singly. Diatoms may be free floating (planktonic) or attached to some foreign surface (sessile). They, along with the coccolithophoridae, make up the major part of the phytoplankton of the sea and, as such, constitute an important basic link in the food chain. Diatoms are important constituents of many environments, including open ocean, the littoral zone, as well as various fresh water environments.

The Diatom cell contains a nucleus which is usually displaced to one side and is embedded in a protoplasmic mass (Fig. 1). This nucleus is invariably small and may assume a number of shapes. Smaller bodies (nucleoli) are present within the nucleus. Surrounding the nucleus are the chromotophores which vary in number, size, shape and position within the cell according to species. Much of the color imparted by masses of Diatoms is due to the chromotophores.

During certain times of the year, Diatoms produce a fatty substance which is stored in the cell in the form

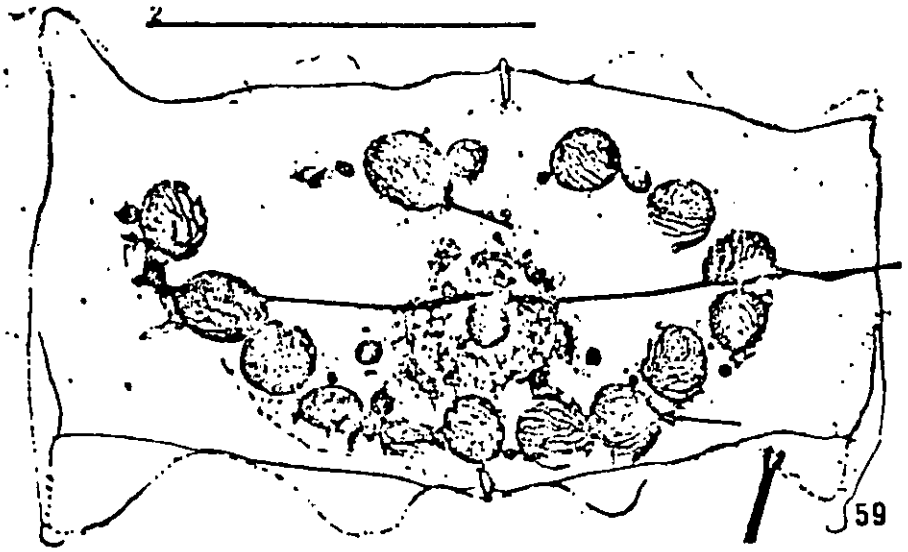
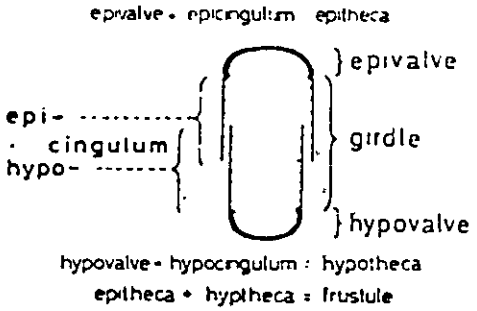
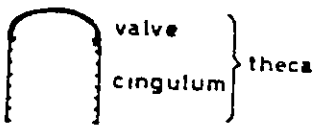


Fig. 1. TEM X5000 of fixed cell of Bellerochea yucatanensis, an Australian planktonic diatom. Protoplasm slightly contracted. Several chloroplasts containing protein fibrils (arrows) visible surrounding cell nucleus. Faint outer line is silica shell. More pronounced darker line inside silica layer is inner diatopectin layer. From Stosch 1977.





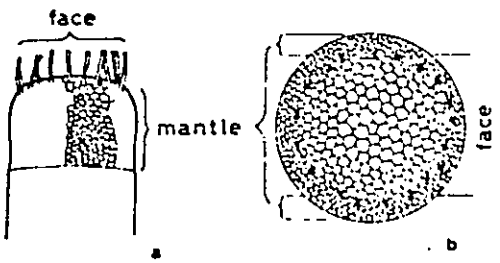


Fig. 2. Components of the frustrule (top); parts of the theca (middle); and valve face and mantle, Stephanopyxis (bottom). From Anonymous 1975.

of several rounded globules. Although the exact purpose of these globules is unknown, it is thought to be a reserve food supply and may play a role in permitting some Diatoms to survive through the winter season.

SKELETAL CONSTRUCTION

Diatoms secrete an external shell or frustule that is often compared to a pill box in which one part of the box or valve fits over the other half and encloses the protoplasmic mass (Fig. 2). Frustules are composed of opaline silica and the larger of the two valves is called the epitheca while the other is called the hypotheca. In the fossil state, most frustules are separated so this distinction is not especially important. The two valves are connected by a usually thin circular band called a girdle— a structure frequently seen in the fossil record, but which has no stratigraphic value. The valve mantle is at the junction of the valve margin and the girdle. For microscopic examination Diatom valves are usually cemented onto a glass slide with the valve face up, and this is referred to as the valve view which is specially desirable since most fossil Diatom taxonomy is based upon the valve view.

According to Hendey, the cell wall may be of two types. A single laminar wall is composed of a single layer of silica. Although the thickness of the wall is generally uniform, there may be local thickenings. A

more complex wall (the locular wall) consists of a double silica wall separated by vertical silica "slats".

A brief morphological note should be introduced here to facilitate further discussion. For many years Diatoms have been split into two major groups: centric forms and pennate forms. Centric forms may be circular, triangular, oblong, etc. but the major distinguishing feature is that the surface markings radiate from a central area. Pennate forms have one long axis and two short axes with the surface markings at right angles to the long axis (Fig. 3).

Diatom symmetry can usually be related to three axes: the apical axis which is parallel to the long dimensions of the valve; the transapical axis which is at right angles to the apical axis and the pervalvar axis which runs through the center of the two valves (Fig. 4). We usually do not find a complete frustule in the fossil state and thus, fossil Diatoms are typically described with reference to the first two axes.

As mentioned above, the valve view contains structures significant in taxonomy. Most centric Diatoms and many pennate forms have valves covered with a honeycomb structure, termed areolae. These features are vertical sided chambers within the valve wall (Fig. 5). Their geometry, spacing, etc. is a rather conservative feature and can be used

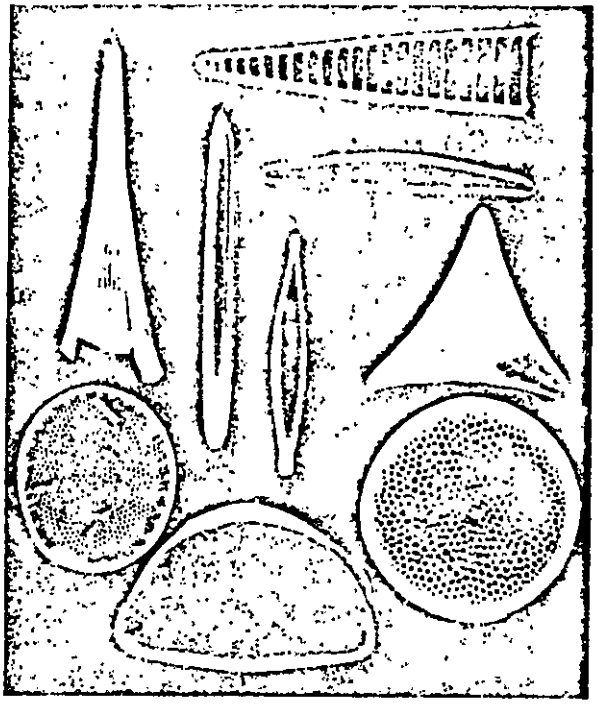


Fig. 3. Representative genera demonstrating basic patterns in centric and pennate diatoms. A. *Rhizosolenia bergonii* H. Peragallo, a pennate form. B. *Nitzschia* sp. a pennate form. C. *Pseudocunotia doliolus* (Wallich) Grunow, a pennate form. D. *Roperia tesselata* var. *ovata* Heiden (Mann), a centric form. E. *Nitzschia marina* Grunow, a pennate form. F. *Nitzschia bicapitata* Cleve, a pennate form. G. *Triceratium cinnamomeum* Greville, a centric form. H. *Hemidiscus cuneiformis* Wallich, a centric form. I. *Coscinodiscus nodulifer* A. Schmidt, a centric form.

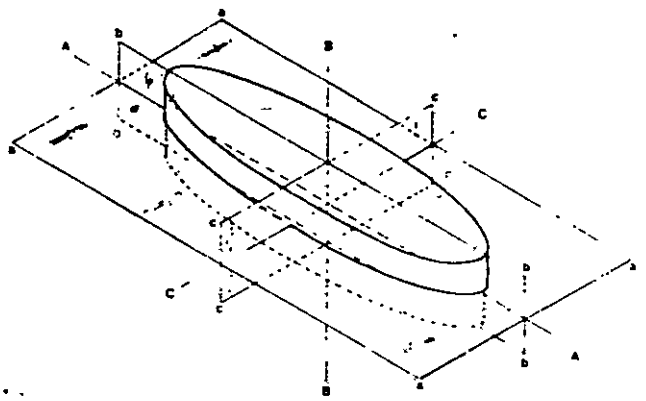


Fig. 4 Axes and planes of symmetry, apical axis A, pervalvar axis B, transapical axis C, valvar plane a, apical plane b, transapical plane c. From HENDEY.

to differentiate species. Frequently a finely perforated plate (termed the sieve plate) may cover the areolae.

Some genera of centric Diatoms possess scattered small pores in the valve view. Such pores perforate the cell wall and, in the pennate forms, may form parallel lines that have the appearance of striations under the light microscope.

Areas of clear structureless silica (termed the hyaline areas) characterize some genera and species of Diatoms. Certain species of *Coscinodiscus*, for example, have clear hyaline central areas, while the genera *Asteromphalus* and *Asterolampra* are characterized by large hyaline central areas (Fig. 5). In the pennate Diatoms, such hyaline regions run down the center of the valve parallel to the apical axis and are called the pseudoraphe. Some genera of the pennates have a V shaped slit (raphe) in the place of the pseudoraphe (Fig. 5).

Additional structures, although seemingly insignificant, are important even at the generic level. A small hyaline area (pseudonodule) near the periphery of centric Diatoms, for example, identifies the genus *Actinocyclus* while two or more pores near the central area characterize the genus *Thalassiosira* and a circlet of spines identifies the genus *Stephanopyxis*. It is essential, therefore, to emphasize that a careful scrutiny of the Diatom valve is necessary for accurate species identification.

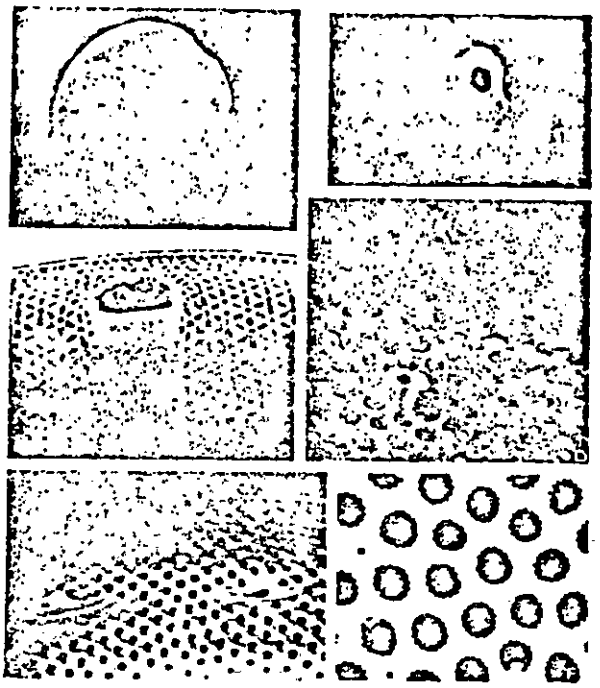


Fig.5. A. *Asteromphalus hiltonianus* showing central hyaline area and hyaline ray. B. Detail of *Asteromphalus* showing hyaline ray. C, D. Detail of areolae with finely perforated sieve plate. The central structure is a pore. E. Detail of labiate process around periphery of centric valve. F. Detail of areolae. Variability in the size of the "dentition" around the areolae is probably due to dissolution.

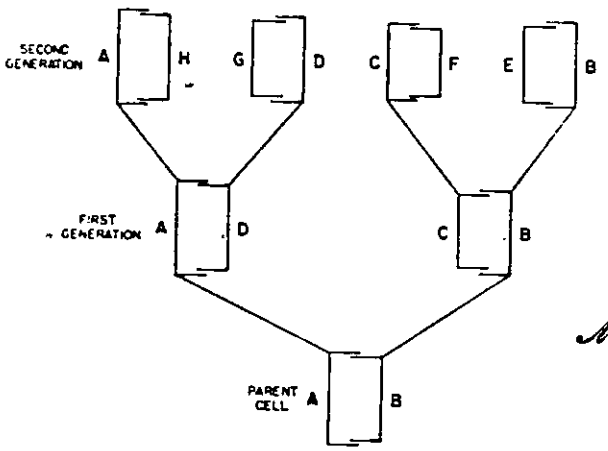


Fig.6. Girdle views of diatom valves through several reproductive phases. Note the progressive decrease in size of some forms.

REPRODUCTION

Diatoms reproduce by simple cell division. Just prior to division, the epitheca and hypotheca move slightly away from each other and separation of the two valves takes place (Fig. 6). New valves are formed on the exposed protoplasm— from the central area outwards and always within the confines of the parent valve. Thus, the original two valves both become epitheca in the new individuals. One can project, therefore, a steady decrease in valve diameter with each succeeding generation. Not only do the valves become smaller, but they also change in geometry as well as in the character of their surface markings.

In some reproductive phases, the Diatom will subdivide to a very small size and to a low level of vitality before dying. In others, cell division will cease at some level and a special cell (called an auxospore) will be formed. The purpose of this auxospore, although the mechanics are not well understood in most species, is to return the Diatom species to its original size from which the process starts anew.

Just as important to species survival as the reproductive cycle is the ability of many Diatoms to survive from one growing season to another. Some species will

persist through the winter months, their life processes greatly reduced. Most, however, form a heavy resting spore which falls to the bottom and is revived when conditions favorable for growth return.

NUTRIENTS

The nutrient content of the water is extremely important to Diatom growth and reproduction. Three nutrients are considered essential for almost all Diatom species. These are phosphorus, nitrate and silica. The Russian worker, T. V. Belayeva, has reported that the giant marine Diatom *Ethmodiscus rex* lives best in waters of low phosphate concentration, but this preference is considered atypical for Diatom species in general. Experience, both in the laboratory and in the field, has shown that when any of these three basic nutrients is missing Diatom growth and reproduction ceases. Some Diatoms are so sensitive that even a reduction in the supply of these dissolved nutrients will inhibit their reproduction.

Given these facts it is relatively easy to point out areas of high Diatom productivity. Any area of upwelling in the ocean will bring a constant supply of these nutrients to the surface and, thus, cause productivity blooms. Coastal regions which receive high

concentrations of nutrients from both run off from land and rain off will support large Diatom populations. Frequently, small ponds become eutrophic* when fertilizer laid in nearby fields runs off during rain storms.

In addition to the nutrient supply many species have special requirements. A number, for example, are known to require cobalamin (vitamin B_{12}) as well as thiamin (vitamin B_1). Sulphur, iron and manganese are also considered essential for many Diatoms. In addition to this, various Diatom species are known to respond to trace elements in the water. Thus, a number of nutritional variables may be operating to promote or inhibit the presence of specific Diatom species.

ECOLOGY

Within both fresh water and marine environments Diatoms can be found occupying a great number of specific niches. On land they arefound in soils and ocassionally on wetted rocks (aerial epilithic) and plants (aerial epiphytic). In streams, lakes and ponds they are found attached to rocks and plants as well as in bottom muds

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*The term eutrophic essentially means that there is an ample supply of dissolved nutrients in the aquatic environment. The danger in this is that ponds and small lakes that are eutrophic may become overstocked, in effect, choking off the environment, reducing circulation and finally killing off all but the hardiest forms.

(epipelic). Although no fresh water Diatom species are known to be true planktonics many of them do spend a portion of their life cycle afloat.

In the marine realm, two broad Diatom habitats are recognized: (1) benthonic; and (2) planktonic. Benthonic Diatoms live in littoral environments either attached to something (sessile) or capable of some movement along the bottom (vagile). They are of considerable importance in that they serve as the major food for many shallow water marine feeders. In addition, certain species produce enough cementing mucus to cement sediment grains together and thus inhibit submarine erosion, while other Diatom species are known to form a dense mat at the sediment/water interface and thus prevent any continued reworking of the sediment.

Planktonic species are considered as part of the oceanic or neritic plankton. Oceanic (or holoplanktonic) forms spend their entire existence in the open ocean and pass through the various phases of their life cycle in that environment. Neritic forms are found in association with coastlines. Since such forms frequently pass through a benthic stage, these coastal regions must possess rather shallow shelves.

N. Ingram Hendey (1964) considers the neritic plankton under three catagories:

A. Holoplanktonic

B. Meroplanktonic

C. Tychopelagic

The holoplanktonic existence was considered previously and is mentioned here only because some neritic plankton appear to be holoplanktonic. Meroplanktonic species live close to the coastline in the plankton but spend part of their existence in bottom sediments, probably as resting spores. It is sometimes difficult to differentiate holoplanktonic and meroplanktonic species. Tychopelagic species probably spend most of their lives on the bottom (Fig. 7).

Frequently it happens that a Diatom Thanatocoense far from the present coastline may contain representatives of both the neritic and oceanic plankton as well as a number of sessile and vagile forms. This is understandable since bottom currents or storms may dislodge shallow water forms and transport them many miles from their original habitat.

Factors which control Diatom distribution vary with the habitat. A complex of chemical and physical factors controls the distribution of fresh water and terrestrial Diatoms. These factors are light, salinity, pH, temperature and the concentration of such elements as silicon, nitrogen, sulphur, calcium and iron.

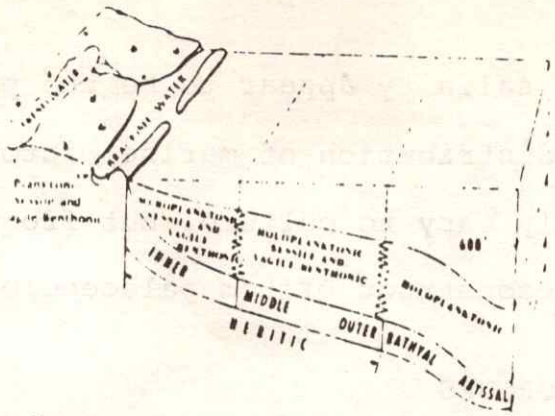
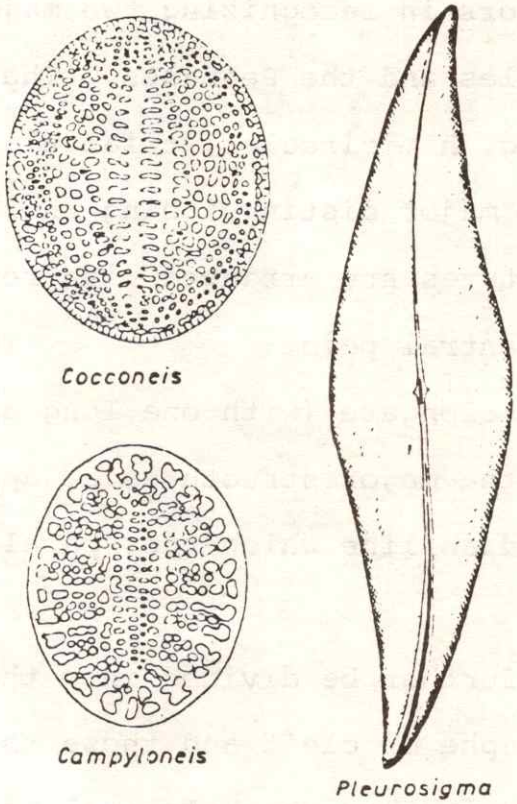


Fig. 7 Marine and fresh-water environments occupied diatoms. (From Wornardt, 1969).



B

Fig. 8. Linear diatoms. Diagnosis: One long axis (apical axis) and two shorter axes (transapical and pervalvar axes). Isopolar, symmetrical about the apical axis with clear silica area running down center of valve parallel to apical axis. May contain raphe, pseudoraphe, central nodule, polar nodule, ridges, costae and pores.

Temperature and salinity appear to be the principle factors controlling distribution of marine Diatoms. Thus, Diatoms are relatively easy to culture, but frequently it is difficult to reconstruct Diatom paleoecology.

MAJOR MORPHOLOGICAL GROUPS

Diatoms take on a great many shapes and thus it is difficult to present a simple picture of the major morphological groups. Most Diatomists follow the lead of their 19th century predecessors in recognizing two major divisions— the Centrales and the Pennales. The Centrales may be circular, oblong, hemicircular, triangular, quadrangular, etc. but the major distinguishing character is that the surface structures are arranged with reference to some central or near central point. The Pennales, on the other hand, are elongate (with one long axis and two very short ones) with the major structures at approximately right angles from a median line which runs parallel to the long axis.

The Pennales can further be divided into those forms which possess a true raphe or cleft and those that do not (pseudoraphe). Any further morphological breakdown beyond this point is largely dependent upon such features as shell geometry, surface structures, etc. Although the many different kinds of shapes, geometrics and structures in the Diatom present a somewhat confusing picture, N.

Ingram Hendey (1964) has succeeded in assigning most Diatoms to one of seven "shape groups". These seven minor groups can be lumped together into two major groups: (1) Those whose valves usually have a raphe or pseudoraphe; and (2) Those whose valves are without a raphe or pseudoraphe. In the first category, Hendey recognized four "shape groups": the Linear Diatoms, the Cuneate Diatoms, the Cymbiform Diatoms and the Carinoid Diatoms.

Linear Diatoms have one long axis (the apical axis) and two shorter axes (the transapical and pervalvar axes). They are isopolar, symmetrical about the apical axis (with a few exceptions) and possess a clear silica area running down the center of the valve parallel to the apical axis. If this area is free of any structure it is termed the pseudoraphe. If, however, it possesses a V shaped slit (usually seen as a narrow line under the light microscope) running parallel to the apical axis it is termed the raphe. Linear Diatoms which contain raphe also have a central nodule and, at the apical ends, polar nodules. Surface markings, in the form of ridges (costae) or pores, may radiate away from the raphe or pseudoraphe (Fig. 8).

Cuneate Diatoms differ from the Linear forms in their symmetry. Although Cuneate forms are symmetrical about the apical axis, they are assymetrical about the transapical axis. They may have a raphe or a pseudoraphe (Fig. 9A). Symmetry

is also a major distinguishing characteristic in the Cymbiform Diatoms. In this groups the asymmetry is about the apical axis, while it is symmetrical about the trans-apical axis. The valves are isopolar and may have a raphe or a pseudoraphe, depending upon the genus (Fig. 9B).

The last group, the Carinoid Diatoms, are based upon the placement and structure of the raphe. Symmetry and valve shape are relatively unimportant. The raphe is usually on a raised keel and the group may be subdivided into those genera that have one raphe and those genera having two raphe (in both subgroups the raphe is situated along the margin of the valve) - Fig. 10.

In the second category, Hendey recognized three "shape groups". Discoid Diatoms have a relatively simple structure, are circular in valve view and rectangular in girdle view. The valve surface may be flat, concave, convex or concavo- convex. Possible surface structures on the valve face include: areolae, pores, ribs, spines, etc. - Fig. 11A.

The Gonioid Diatoms are usually angular in outline but, otherwise, are difficult to characterize. The shape may be circular, elliptical or triangular. Since a definitive description of this group is difficult, the reader is referred to Figure 11B for sample shapes.

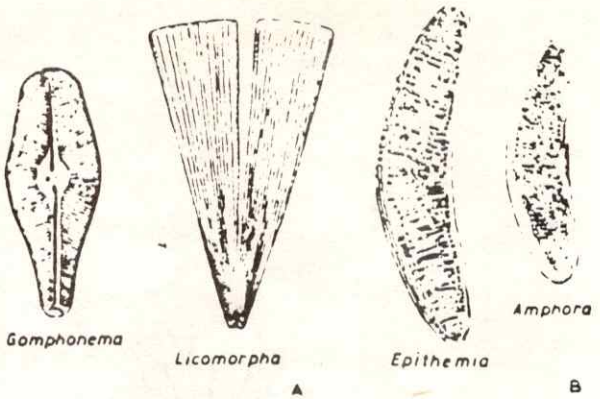


Fig. 9. A. Cuneate diatoms. Diagnosis: Symmetrical about the apical axis and asymmetrical about the transapical axis. May have a raphe or pseudoraphe. B. Cymbiform diatoms. Diagnosis: Asymmetrical about the apical axis. Valves are isopolar and may have a raphe or pseudoraphe.

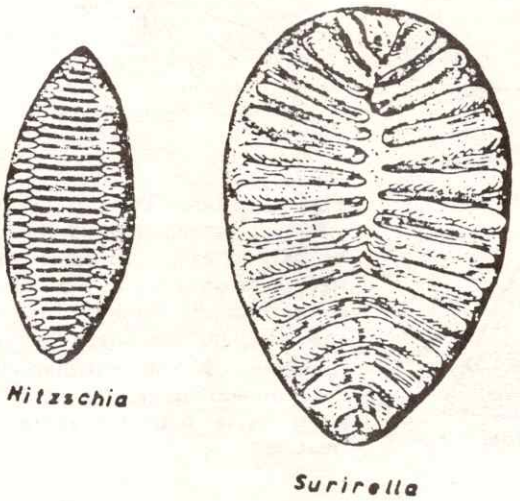
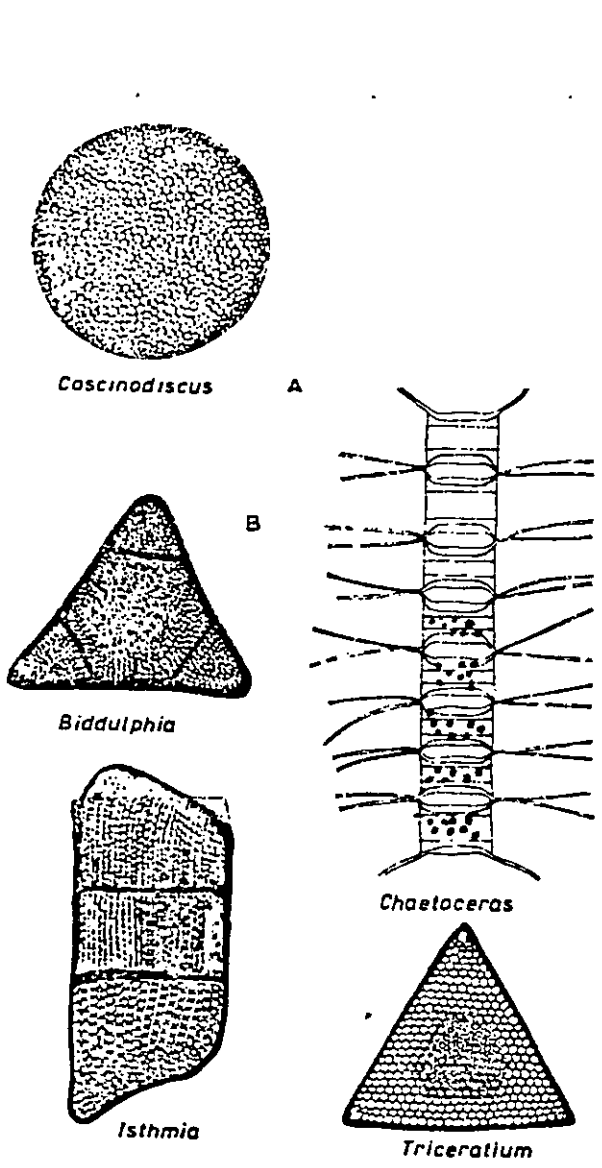


Fig. 10. Carinoid diatoms. Diagnosis: Based on placement and structure of raphe. Raphe placed on raised keel near valve margin. Symmetry and valve shape relatively unimportant.



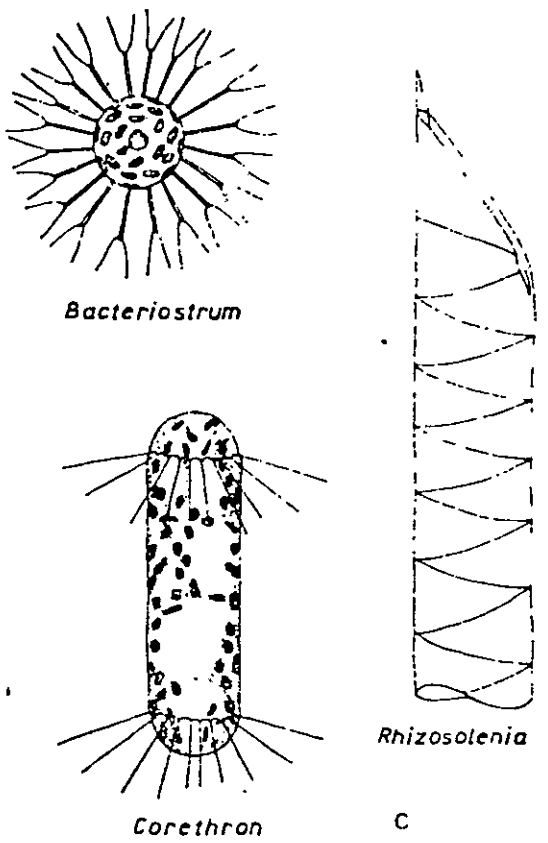


Fig.]] A. Discoid diatoms. Diagnosis: Circular in valv view and rectangular in girdle view. Valve surface may be flat, concave, convex or concavo-convex. Surface structures on valve face include: areolae, pores, ribs, spines, etc. B. Gonioid diatoms. Diagnosis: Usually angular in outline. Shape may be circular, elliptical or triangular. C. Solenoid diatoms. Diagnosis: Unusual development of girdle band. Girdle length many times valve diameter resulting in tubular-shaped frustule.

Solenoid Diatoms feature exceptional development of the girdle band. The girdle length may be many times the valve diameter, resulting in a frustule with a tubular shape. In valve view, the cell is usually circular or elliptical in outline. However, because of its expanded girdle, members of this group are also always cemented on a glass slide with the girdle view up (Fig. 11C).

EVOLUTIONARY TRENDS

The earliest Diatoms date from the Middle Cretaceous, although there are unsubstantiated reports of their occurrence in the Jurassic and even the Late Paleozoic. Since these Cretaceous Diatoms occur in assemblages it has been argued that Diatoms really developed in Late Paleozoic or Early Mesozoic time and either existed as naked protoplasm or were simply not fossilized. Isolated, heavily silicified Diatom valves found in Early to Middle Cretaceous sediments suggest that selective solution is the final arbiter of Diatom first appearance rather than any biochemical changes.

The Centrales are the only group of Diatoms to occur in the Cretaceous and earliest Paleocene with Pennate forms first appearing in the late Paleocene and increasing somewhat in abundance during the Eocene. Tappan and Loeblich (1971) pointed out that the expansion of the

Centrales had stabilized by Eocene time and, except for a burst in the Miocene, their diversity was essentially unchanged throughout the Tertiary. The Pennales, on the other hand, have undergone an exponential increase since at least Miocene time and, at present, far surpass the Centrales in numbers of living species. The centric forms tend to dominate the plankton while the Pennate forms are more abundant in the benthic realm.

Therefore, it is not surprising that the earliest fresh water Diatoms (Eocene) are Pennate forms. Indeed, at present most fresh water Diatoms, including benthics and quasi planktonics, are Pennate forms. Diatoms were probably introduced into the fresh water environment via brackish water littoral forms.

Unfortunately, we do not see a progressive increase in complexity of the Diatom valve with time. Cretaceous forms show as much variation in shell structure as do the Tertiary forms. Because of this, it is difficult to use "stage of evolutionary development" as a gross stratigraphic tool. It seems more likely that if the complete Diatom record were preserved we would see the missing primitive forms in the Late Paleozoic and Early Mesozoic.

REASONS FOR EVOLUTIONARY CHANGE

In considering benthic and fresh water Diatoms it is relatively easy to account for evolutionary change.

At the very least we can invoke geographic isolation followed by progressive changes in the composition of the gene pool to explain any character shifts. With planktonic communities, many species appear to be restricted to specific water masses, thus achieving some degree of geographic isolation.

What we are at a loss however to explain is the evolution of one species into another in what was apparently the same water mass. We cannot invoke geographical isolation nor can we see any measurable ecological reason why there should be this time-sequential grading of one species into another. We are lead to suspect that some property of the environment (vitamin composition, trace element abundance, minor though long term changes in temperature, salinity, or upwelling) has promoted a character shift.

Many species whose evolution can be documented last a relatively short time in the geologic record. For example, from the Late Miocene to Recent of the Equatorial Pacific we can observe the evolution of six species. One of these survives to the present while the other five become extinct. Most of them become extinct within a half million years of their first appearance. This fact suggests that there was something inherently unstable in the new species or that they evolved in response to some transitory (in a geological sense) phenomenon in the environment.

The fact that we know so little about the multitude of environmental influences operating on the Diatoms leaves us relatively free to speculate on the cause of their evolution.

PALEOECOLOGY

Prior to discussing the paleoecological importance of Diatoms, certain restraints in the form of "words of caution" must be placed upon the reader. Because planktonic Diatoms are built to remain in suspension, they can easily be transported laterally by both bottom and surface currents. This may result in an anomalously high concentration of planktonic forms where none existed in the local biocoenose. Simonsen (1969), for example, reported on marine and brackish water Diatoms which were carried far up the Amazon by the tidal bore. Burckle and Biscaye (1971) found that in the Antarctic high southern latitude neritic and oceanic Diatoms are carried northward by Antarctic Bottom Waters as far as the Equatorial regions (Fig.12). The possibility of such displacements must be considered in any paleoecological reconstruction.

Secondly, we should keep in mind that selective solution both in the water column and in the sediments may significantly alter Diatom Thanatocoenosis. In the Equatorial Pacific the solution rate may remove more than 80%

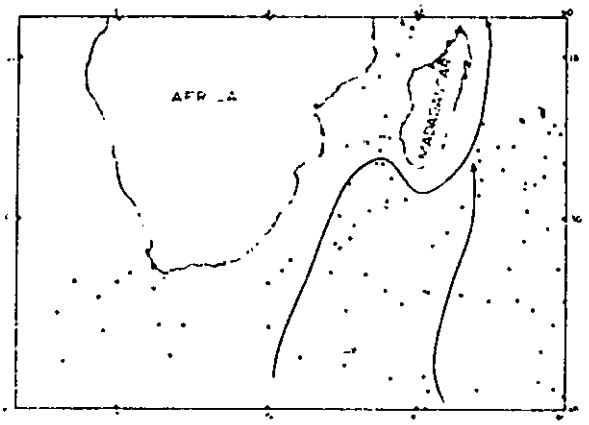


Fig. 12. Distribution of displaced Antarctic diatoms (solid circles) in surface sediments of the southwest Indian Ocean. The arrows indicate the probable avenues by which Antarctic Bottom Water moves northward.

of the biocoenose and in those sections where monospecific oozes are recovered we suspect that solution has removed everything else.

A final point to keep in mind before we discuss the paleoecology of Diatoms is that the word paleoecology when applied to micropaleontology should be read as quantitative paleoecology. In order to achieve maximum results the floras must be subjected to some sort of mathematical treatment. Such treatment may range from extremely simple to algebraically complex.

The initial step in quantitative paleoecology is counting and categorizing (by taxonomic entity) a minimum number of Diatoms per sample. Experience has shown us that no fewer than 300 individuals per sample ought to be counted. Where species diversity is low the count should be increased to that level where no new species are encountered. The resulting Diatom spectrum showing the relative percent abundance for each species versus time is useful in demonstrating time-sequential changes in the Diatom flora.

However, some Diatomists prefer to integrate such a spectrum into a single curve and thereby determine the relative importance of various ecological parameters upon the changing Diatom community. The achieve this end, several avenues are open. The simpl est is the Td value:

$$Td = \frac{X_w}{X_c+X_w} X100$$

where X_W = total count of warm water Diatom species and X_C = total count of cold water Diatom species. Td stands for Diatom temperature and is used in a relative sense in reference to cold or warm assemblages.

In some cases we already know the temperature preferences of the Diatoms with which we are dealing. In others, it may be necessary to determine the constituency of a Diatom assemblage and its relationship to latitude and water mass (and, we presume, temperature). To divide Diatom assemblages along a North-South gradient into a number of species groups we can use a Recurrent Group Analysis:

$$\alpha ab = \frac{JAB}{\sqrt{N_A \, N_B}} - \frac{1}{\sqrt{N_B}}$$

Where N_A = total number of occurrences of species A

N_B = total number of occurrences of species B

JAB = joint occurrences of species A and B

When $N_B \geq N_A$ then pairs of species are considered to show affinity (ie. they belong to the same group) when $\alpha ab \geq 0.5$. This permits the eventual definition of a number of species groups all of whose members show positive affinity for one another.

In addition to these relatively simple statistical techniques a number of more sophisticated mathematical tools are open to the student. Cluster analysis may be

used to define fossil associations and the reader is encouraged to become familiar with the treatment of this subject given in Michener and Sokal (1957). A final method, and one which will come into increasing use in the future is the Biological Response Model of Imbrie and Kipp (1971). This method uses factor analysis to group species relative to some ecologic gradient but, further, it attempts to define the causal influences responsible for these groups to determine the relative importance of each cause and to project this information into the past.

With planktonic species, the principle paleoecological parameter sought is temperature. Paleoecological equations developed by John Imbrie also permit the construction of other parameters such as salinity, nutrient supply, etc. but these factors usually can be related to temperature. Also, since most paleoecological work deals with the Pleistocene, we are naturally most interested in temperature change during that period. Kanaya and Koizumi (1966), for example, used Recurrent Group Analysis and Td values in reconstructing Late Pleistocene temperature change in the North Pacific.

Although there was little time control, they were able to document at least three warm intervals during the Late Pleistocene. Td values have also been used in the Equatorial Pacific (Fig.13). You can readily see that a

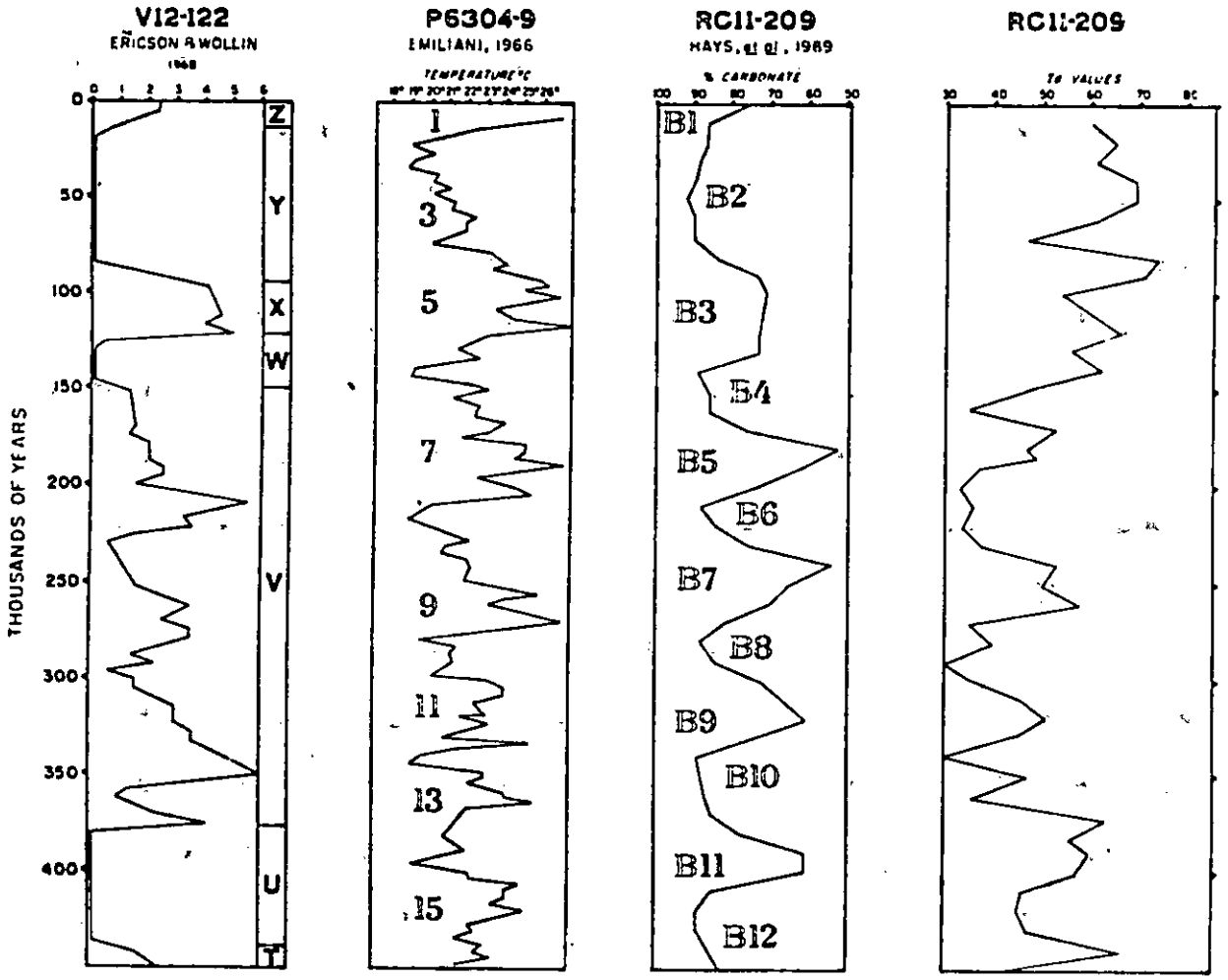


Fig. 13. Comparison of T_d values obtained from a core from the Equatorial Pacific with temperature data based upon Foraminifera (Ericson and Wollin, 1968), $^{18}O/^{16}O$ isotope ratios (Emiliani, 1966) and abundance of biogenic calcium carbonate (Hays et al., 1969).

substitution is necessary in the original equation since cold water forms are not present. However, if we substitute cosmopolitan species for cold water we find that the Equatorial assemblage can be broken down into two groups: a tropical/subtropical group and a cosmopolitan group. As shown in Figure 13 there are signficant changes in the assemblages— changes which essentially agree with climatic oscillations founded on other methods. You will note also a shift from a tropical/subtropical assemblage to a cosmopolitan assemblage near the end of the Matuyama Reversed Epoch— a climatic shift which has also been observed using other geologic evidence.

A. P. Jousé of the Soviet Union came to a similar conclusion in the North Pacific after analyzing a Diatom spectrum from this region. She noted a rather significant upward change in the Diatom assamblage from water to cold during the Middle Pleistocene. Sharp increases (in effect, recurrences) in the warm-water species *Raphoneis arcuatum* var. *ventricosum* defined the extreme warm conditions in the North Pacific during the later Pleistocene. Subsequent workers have found as many as five recurrences of this species in the North Pacific.

In 1954 Kolbe performed a rather simple but time consuming experiment in Diatom paleoecology which has seldom been repeated. You will recall that Belayeva noted

that certain species show a marked increase in size (in this case, valve diameter) over areas of strong upwelling. This size increase appears to be related to the nutrient supply which in turn is governed by the rate of upwelling. It follows, then, that if nature can modulate the rate of upwelling in a specific area it will also be modulating the nutrient supply and the size of specific Diatom species. In 1952, Arrenhius proposed a rather simple model governing vertical and horizontal oceanic circulation and their relationship to climate— during glacial period the temperature gradient between the poles and the equator increased, resulting in more intense circulation, while interglacial periods demonstrated the opposite effect.

In a deep-sea core from the eastern equatorial Pacific (an area of upwelling) Kolbe measured the valve diameters of 300 specimens per sample of *Coscinodiscus nodulifer*, a species which ranges from approximately 10 microns to over 100 microns in diameter. His work showed good correlation between maximum diameter values and glacial periods and offered promise for use of valve size in paleoecology. Unfortunately, as mentioned previously, this type of study has been rarely used because it consumes a great deal of time. Recent technological advances involving the light microscope, however, now make it possible to measure both valve diameter and valve area rapidly and thus make it possible to use this paleoecological tool.

Marine benthic and brackish water communities can also be utilized in paleoecological reconstruction. One must repeat the caution, however, that currents, particularly bottom currents, may displace these Diatoms from their normal habitat and result in faulty interpretation. Sedimentary structures may provide some clue as to whether or not displacement has taken place. The condition of the Diatom valve may also be a key. If they are broken and partially dissolved they most certainly have been displaced. In the South Atlantic well preserved benthic Diatoms of Eocene age have been recovered from depths of approximately 500 fathoms on the Argentine Continental Slope— clear evidence, it would seem, of considerable subsidence along this Slope since the Eocene.

We can use brackish water Diatoms to reconstruct sea level changes in the recent past as well as any signficant changes in temperature or water chemistry. Many of these species have very narrow temperature, salinity and chemical tolerances. Changes in any parameter of the environment, therefore, lead to a change in the Diatom community. By careful analysis of the Diatom biocoenosis we should be able to reconstruct shoreline changes and, thereby, reconstruct past climates.

Fresh water Diatoms cannot be applied as easily as marine forms to delineate temperature change with time.

Rather, they are more important in defining changes in water chemistry, nutrient supply, compositional and mechanical properties of sediment, and in determining past changes in basin geometry. To put these parameters on a rudimentary basis, Peter Kilham (1971), for example, postulated a relationship between species dominance and silica concentration. His data indicate that *Stephanodiscus astrea* is likely to be dominant at low silica concentrations and *Melosira granulata* is likely to dominate at higher silica concentrations.

Work done by the French in the Chad Basin indicate that the relative abundance of these two species may also reflect basin geometry. *Stephanodiscus astrea* was most abundant at times when the Chad Basin was at a higher lake level, while *M. granulata* was more abundant at intermediate or lowered lake levels.

From time to time, fresh water Diatoms provide us with a most important link between the continental detritus (including fresh water Diatoms) from the Asian mainland to the Sea of Japan where it is incorporated into marine sediments. Changes in volume and species content give us some clue to the species content of fresh water lakes as well as to changes in wind stress with time.

A more integrated picture illustrating this point emerges when data from Northwest Africa and the Equatorial

Atlantic are compared and correlated. Along the southwest edge of the Sahara a long wet season alternates with a much shorter dry season. Intermittent lakes (usually containing abundant Diatoms) dry out during the dry season and the ever present Trade Winds carry the lake sediment out to sea where it is incorporated into marine sediments. By studying paleomagnetically dated deep-sea cores from the Equatorial Atlantic we can determine the time of first influx of wind blown continental detritus into the Atlantic (about 1.2 m.y. B.P.) as well as changes in volume of continental detritus. Of special interest is the observation that *Stephanodiscus astrea* was a common constituent of Equatorial Atlantic sediment from about 1.2 m.y. B.P. to approximately 400,000 years B.P. Such a convergence of evidence and circumstance suggests that this section of North Africa was more humid prior to 1.2 m.y. B.P. and that, prior to that time, present day intermittent lakes were perennial..

Two additional measurements which may have some paleoecological significance is total Diatom abundance per gram of sediment and Diatom diversity.. Diatom numbers per gram of sediment has been much used by modern day Diatomists as an indication of past changes in surface productivity. The reader can appreciate some of the problems involved in using this method. Obviously, the investigator does not count a gram of Diatom valves. Rather, he or she counts the Diatoms

in a aliquot of the original sample and then, by simple ratio, determine numbers per gram. The problem arises in the method used— no two Diatomists employ the exact same methods in sample preparation and sample counting. Therefore, the results usually differ by a great deal. It should further be pointed out that recent studies indicate that high Diatom counts in surface sediments are not especially useful indicators of surface productivity. Such studies indicate a correlation coefficient of r = .6 between Diatom abundance in surface sediment and the sea surface. Other physical parameters (temperature, salinity, etc.) show a much higher correlation coefficient with Diatoms in surface sediments.

Diatom diversity has also been used as a barometer of surface productivity. The usual method of determining diversity is to determine the numbers of species encountered in a random count of 300 specimens. This method has been found unreliable because it does not account for the relative abundance of individual species. In our work we have found good results using the Shannon-Wiener Information Measure as a Diversity Index:

$$H_s = - \sum_{i=1}^{S} P_i \log_e P_i$$

Where s= number of species in a random count of 300 individuals

P_i= the relative abundance of the ith species measured from 0 to 1.0

$\text{Log}_e P_i$ = the logarithm of P_i to the base e

A high value for H indicates a very diverse assemblage while a 0 or low value indicates a monospecific or near monospecific assemblage. In the Equatorial Pacific we find high diversity values during a glacial period. This agrees essentially with the thinking of Arrenhius, namely that vertical and horizontal circulation is stimulated during cold periods resulting in increased surface nutrients and productivity.

As mentioned earlier, Diatoms are easily displaced by currents and, as an example, the action of Antarctic Bottom Waters in carrying high latitude Diatoms toward the equator is noted. It can be seen that the transportability of the Diatom valve can be turned into a plus factor and that we might use the distribution of Antarctic Diatoms in surface sediments to trace the northward flow of Antarctic Bottom Water. Figure 12 shows the distribution of these Diatoms in surface sediments of the Southwest Indian Ocean. One can clearly trace the influence of bottom water to the South and East of Malagasy. Similar distribution are observed in other parts of the Southern Hemisphere.

BIOSTRATIGRAPHY

The fundamental tenet of biostratigraphy is that species evolve and become extinct. Since we can document these events in Diatoms it stands to reason that they

should have some value as stratigraphic tools. Besides the great abundance of Diatom species (10,000) we must also remember that initial studies in marine Diatoms dealt mainly with marine sections exposed on land. In other words, these were shallow water marine sections which played host to benthonic and neritic planktonic communities rather than holoplanktonic communities.

Such assemblages are strongly effected by even minor changes in the environment; for example, salinity, sea level changes, etc. Such changes affect the vertical continuity of species within the assemblage. Thus, a first or last appearance of a species may be due to some shift in ecological parameters rather than evolution or extinction. In spite of these drawbacks, G. Dallas Hanna, beginning in the 1930's, has used Diatoms to show that a gross correlation is possible between the Miocene of California and the Miocene of the U.S. East Coast.

Because the appearance of benthic Diatoms, like any other benthic organism, can be time-transgressive, true time-stratigraphic correlations are best drawn using planktonic Diatoms. It seems natural, therefore, that increases in our understanding of planktonic Diatoms as stratigraphic tools is directly related to the recovery of numerous deep sea sediment cores. These cores provide continuous or nearly continuous depostional records and permit us to

"see" and measure discrete evolutionary steps. Since several microfossil groups are present in the same core, it is also possible to cross correlate and thus relate Diatom zones to the type reference sections in Europe.

Although Diatoms were among the first of the microfossils to be studied, it is only recently that they have been used to define biostratigraphic zones. The problem is one of solution, preservation, and vertical continuity particularly in the Cretaceous and Paleogene. Diatoms respond to favorable conditions by living in great profusion or "blooming". Those sections which contain abundant Diatoms, therefore, usually represent short time intervals even though the section may be quite thick.

Nevertheless, there are a number of species which can be used to define and differentiate the Cretaceous and Paleogene. Greater vertical continuity is seen in the Neogene, thus permitting zones to be defined during this time interval (Fig. 14).

The Cretaceous may be defined by several species of *Triceratium*, *Coscinodiscus*, *Aulacodiscus* and *Biddulphia* which appear to be restricted to the Mesozoic. The "crisis in life" which occurred at the Mesozoic/Cenozoic boundary apparently also affected the Diatoms because there is a difference between the late Cretaceous and Paleogene forms. The true extent of this difference has not

yet been determined because of the paucity of Paleogene diatomites. However, the Paleogene witnessed the first appearance of the Pennales.

The Eocene may be defined by several species of the genus *Pyxilla* as well as *Cyclotella hannae, Coscinodiscus oblongus* and several species of *Triceratium*. *Pyxilla* spp. had a rather broad distribution during the Eocene, occurring in the South Atlantic, the Southwest Pacific, the California section and the Norwegian Sea. Some of these forms extend upward into the early Oligocene. However, little is known about the Oligocene floras, particularly the younger part. Burckle (1972) described a high latitude Oligocene flora from the North Atlantic but reported a low diversity assemblage dominated by the genus *Stephanopyxis*. A major reason why we have so little information about Oligocene Diatoms is that we have recovered so little Oligocene age sediment from the deep sea floor. Those sediments of this age that have been recovered frequently contain only calcareous biogenic remains.

In Miocene and younger sediments, we have more vertical continuity and thus a greater opportunity to define biostratigraphic zones. Hans Schrader (1973) has defined 25 Diatom zones in the North Pacific for the interval from the Middle Miocene to the Recent while Japanese workers have named 7 for the same interval of time from the

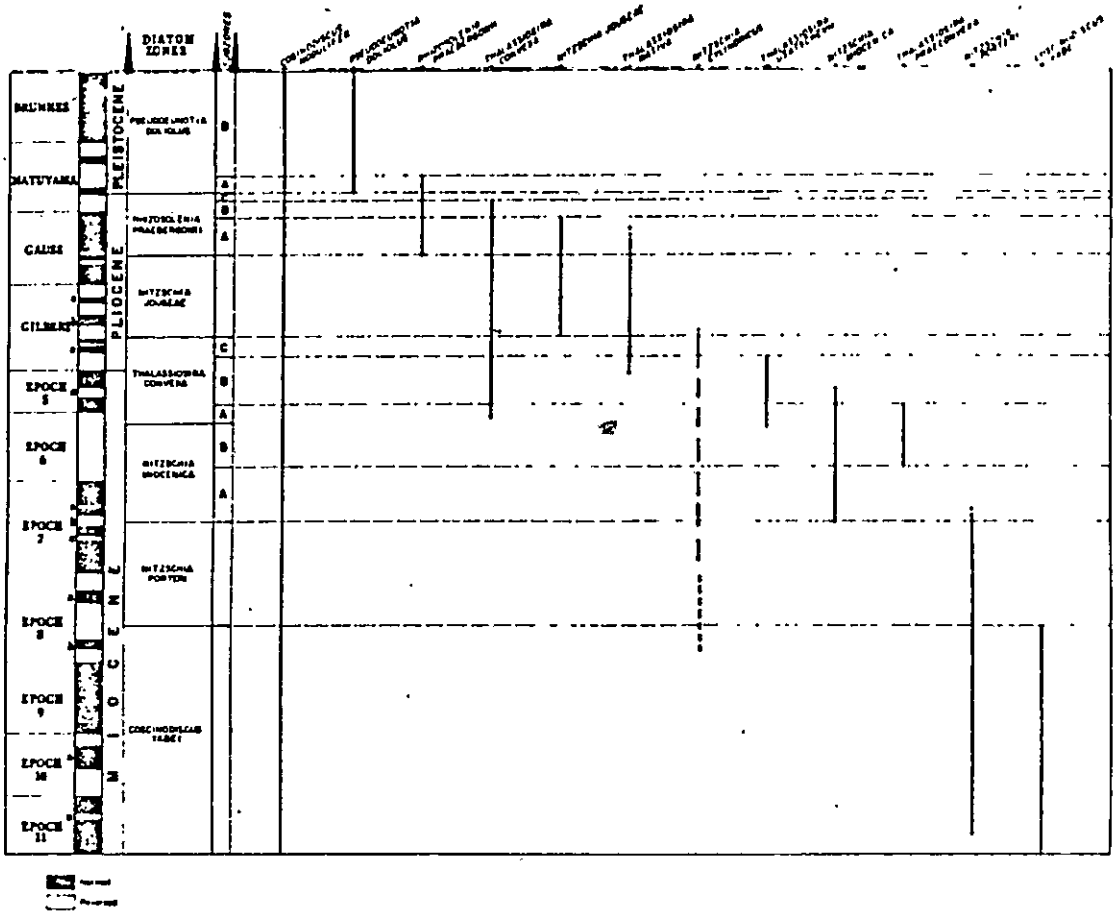


Fig. 14. Ranges of selected diatom species from the late Miocene to Recent of the Equatorial Pacific. (From Burckle, 1972).

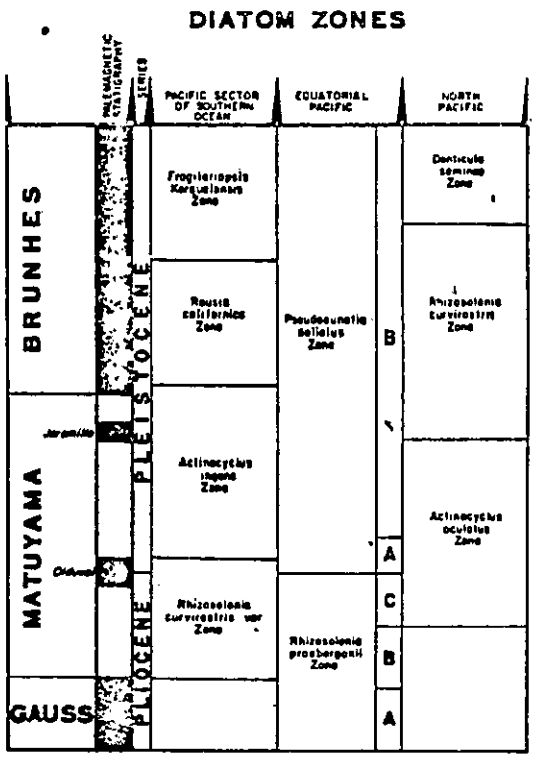


Fig. 15. Late Pliocene and Pleistocene diatom zones for the Pacific. (From Donahue, 1970, and Burckle, 1972.)

Japanese mainland. Since both continental and deep-sea Neogene sections are diatomaceous we can correlate between the two.

In general, we can characterize the Diatom composition of marine Neogene sections as follows: The Early Miocene in low latitudes can be defined by the occurrence of such forms as *Coscinodiscus lewisianus* var. *lewisianus* and *C. lewisianus* var. *similus*, *Raphododiscus marylandicus* and *Coscinodiscus praepaleoceus*. The last mentioned species is found as a constituent of high latitude Diatom assemblages as well. In intermediate latitudes (Northern and Southern Italy, Maryland and California) *C. lewisianus* var. *lewisianus* and *similus*, *C. praepaleoceus* and *R. marylandicus* are found. The late Early Miocene and early Middle Miocene may be characterized by the problematical Diatom, *Macrora stella*. This form is found most abundantly in intermediate latitudes but has also been found in the Equatorial regions as well as higher latitude sections of Japan.

The base of the Middle Miocene is defined by the first appearance of *Annelus californicus*. This is an extremely important species, particularly useful in Circum-pacific correlations. It occupies a very short time range during the early Middle Miocene and is found in both continental marine and deep sea sections (California, Japan, Java, Equatorial Pacific, South Pacific, etc.). A number of workers (Nakaseko, et al. 1972; Burckle, 1975) have reliably

correlated the range of this species with the foraminiferal zones N.8 and N.9 of Blow (1969). In California, it occurs in uppermost Relizian and basal Luisian sediments.

Ranging concurrently with *A. californicus* is a low latitude marker species, *Cestodiscus peplum*. It ranges to just above the last occurrence of *A. californicus* but is not especially useful in any long range correlation.

In equatorial regions a number of species are found in association with one another and do not range above the Middle Miocene. Such associations, therefore, may be used to define the Middle Miocene and include *Coscinodiscus lewisianus* var. *lewisianus*, *Craspedodiscus coscinodiscoides*, *Actinocyclus ingens*, *Cestodiscus pulchellus* var. *pulchellus* and *C. pulchellus* var.*maculatus*. Besides these, there are a number of forms which provide specific information on stratigraphic levels within the Middle Miocene. A significant contribution to Neogene Diatom stratigraphy has been made by Simonsen and Kanaya (1961) and Schrader (1973) who documented successive time-dependent change in the genus *Denticula*. Simonsen and Kanaya (1969) showed that *Denticula lauta* was the earliest representative of this species in the California section where it occurs in Relizian, Luisian and Mohnian sediments. Schrader (1973) subsequently found this form in Middle Miocene deep-sea sediments.

An important first appearance of *Denticula nicobarica* occurs in the early Middle Miocene, followed by the first occurrence of *Denticula hustedtii* in the middle Middle Miocene. The middle Middle Miocene is also characterized by the first occurrence of plicated species of the genus *Coscinodiscus*. These forms go under a variety of names (*C. plicatus, C. yabei, C. praeyabei, C. miocenica*) but are all characterized by a distinct plication cutting the valve in half and by having rather coarse areolae. Members of this group characterize the late Middle Miocene and early Middle Miocene of many low and intermediate latitude sections.

Ranging concurrently with the early part of the range of the plicate *Coscinodiscus*, is the species *Mediera splendida*. This form is found in intermediate and high latitudes and provides an important link in correlating equatorial and high latitude sections. On the basis of such a comparison, Burckle and Todd (1973) concluded that the range of *Mediera splendida* covers the upper part of the Middle Miocene.

The Late Miocene is characterized in equatorial regions by such forms as *C. paleaceus* and *C. yabei* which both disappear around the middle of the Late Miocene. Two *Denticula* species (*D. nicobarica* and *D. hustedtii*) disappear near the Middle/Late Miocene boundary but are

found higher up in the section in the higher latitudes. *Actinocyclus ingens* is another form whose last occurrence is time-transgressive from low to high latitudes. In equatorial sections it disappears around the Middle/Late Miocene boundary, but lingers on into the early Pleistocene of Japan (Koizumi, 1968; Burckle, 1971) and the Middle Pleistocene of the South Pacific (Donahue, 1970).

The latest Miocene is also characterized by a number of evolutionary first appearances. *Nitzschia miocenica*, for example, evolves from its ancestor *N. porteri*, and ranges to just before the Miocene/Pliocene transition. *Thalassiosira convexa* evolves before the Miocene/Pliocene transition and ranges to the latest Pliocene (Fig. 14). Both these species are fairly cosmopolitan and were distributed from the equator to about 40° North and South of the equator. An equally important species with a much broader distribution is *Nitzschia reinholdii*. This form evolved during the latest Miocene and ranged into the Middle Pleistocene. Besides its wide distribution in the deep-sea it has been reported from Italy, Japan, California and Java. The reader should be cautioned that, in my experience, an increase in abundance of this species indicates a Middle Pliocene or younger age.

High northern latitudes may be characterized during the Late Miocene by the first appearance of *Rhizosolenia*

barboi (called *Rhizosolenia curvirostrus* or *Pyxilla barboi* by some authors), *Denticula kamtschatica* and *Denticula seminae*. *D. kamtschatica* disappeared near the end of the Pliocene but *D. seminae* survives to the present.

During the Pliocene a number of first and last appearances provide us with stratigraphic markers. *Nitzschia jouseae* makes an evolutionary first appearance during the Early Pliocene and disappears during the middle Late Pliocene. This form is abundant in equatorial sediments but has been found as far away as 40° of latitude from the Equator. The Early/Late Pliocene boundary is the approximate position of the first appearance of *Rhizosolenia praebergonii*. This species ranges to just after the Pliocene/Pleistocene transition and is generally restricted to low latitudes (Fig. 14). Koizumi (1972), however, reported it from the Japanese section; a fact which permits correlation of Pliocene sections between equatorial regions and Japan.

In high northern latitudes of the Pacific region, a number of forms define the Pliocene; *Actinocyclus ochotensis*, *Thalassiosira punctata*, *Rhizosolenia barboi* to mention a few. A number of species of the genus *Thalassiosira* are also used in the North Pacific. However, species of this genus are especially difficult to differentiate. The beginning student, therefore, is not encouraged to work

with this group, except in those cases mentioned above where indentification is relatively easy.

The base of the Pleistocene is marked by the first evolutionary appearance of *Pseudoeunotia doliolus*. It is found mainly in equatorial regions but is also present in intermediate latitudes as much as 40° from the equator. By early Pleistocene times an essentially modern Diatom flora had developed in most marine environments of the world. In the equatorial regions, besides *Pseudoeunotia doliolus*, important elements of the Pleistocene flora consisted of *Coscinodiscus nodulifer*, *Coscinodiscus crenulatus*, *Nitzschia marina*, *Thalassiosira oestrupii*, *Thalassionema nitzschioides* var. *nitzschioides* and *Th. nitzschioides* var. *parva*. Many other forms are present in the assemblage, but these are the most important.

In the high northern latitudes, we observe a distinct provincialism. In the North Pacific, the flora is dominated by *Denticula*, several species of *Rhizosolenia*, several species of *Thalassiosira* and the genus *Coscinodiscus*. In the North Atlantic, *Denticula* is not present and the assemblages appear to be dominated by *Thalassiosira gravida* on the one hand and *Thalassionema nitzschioides* on the other.

The reader has probably noted by now that most of the discussion regarding Diatom biostratigraphy has neglected the high Southern latitudes. The reason for this is that

little work has been done in this region as yet, particularly for the interval of time between the Early Oligocene and the Late Pliocene. It is not a question of a lack of good biostratigraphic material to study. McCollum (1973), for example, has noted that two species of the genus *Trinacrea* provide useful datums for the Early Pliocene.

The Pleistocene Diatoms of the Anatarctic region have been studied by a number of workers (Jousé *et al.*, 1963; Kozlova, 1964; Donahue, 1970 to mention a few). Jousé *et al.* (1963) defined a number of abundance zones based upon the alternation in abundance of Antarctic and subantarctic forms. Donahue (1970) define three zones based upon last appearances (Fig. 15). The last occurrence of *Actinocyclus ingens* occurs during the Middle Pleistocene while the last occurrence of *Rouxia california* comes in the early Late Pleistocene.

In addition to these, there are numerous Diatoms which serve as indicators to the Pleistocene and are unique to the Antarctic region. These include at least six species of the genus *Nitzschia* (of which *N. kerguelensis* is the most abundant), *Eucampia balaustium*, *Coscinodiscus lentiginosis*, *C. margaritae* and *Thalassiosira gracilis*.

The foregoing discussion dealt primarily with the fossil record of planktonic Diatoms. There is good reason for this stress since these forms are more suitable for

stratigraphy and for long distance correlation. Benthonic and neritic species have greater value in paleoecologic and paleo-oceanographic studies and as indicators of sediment sources. Yet, when necessary these forms can be used for biostratigraphic work. Walter Wornardt, for example, defined two principle assemblage floras for the Miocene/Pliocene transition in California. Although planktonic elements were present most of the species were benthonic or neritic in habitat. In Java, Th. Reinhold defined several zones in the interval from the Middle Miocene to the Pliocene— largely using benthonic and neritic species.

Fresh water Diatoms are little used in precise biostratigraphic work owing to the obvious difficulty in correlating with marine sections. When independent dating techniques are used, fresh water forms may be used in biostratigraphy especially in the Pleistocene. However, the real application of fresh water forms is in paleoecological interpretations.

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