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SILICOFLAGELLATES AND THEIR GEOLOGIC APPLICATIONS

BY

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ABSTRACT

Marine phytoplankton silicoflagellates have a geologic record from the Mesozoic through the Cenozoic. Their siliceous skeletons can be used as indicators for paleoceanographic currents and upwelling, relative paleotemperatures, and for local and transoceanic biostratigraphic zonations. Deep-ocean coring during the past quarter century has expanded the potential and applications for silicoflagellates to many new areas.

INTRODUCTION

Silicoflagellates are a small group of cosmopolitan marine chrysophyceae -- planktonic unicellular algae with golden-brown chloroplasts and a single flagellum. Their distinguishing characteristic is a single, thinly-enclosed internal skeleton of opaline silica which occurs in simple, geometric open shapes that are formed by hollow tubular rods and spines. These microscopic skeletons (20 - 100 μm), also called silicoflagellates, are the basis of taxonomic classification for the group in modern and fossil materials. The geologic record of fossil species has been documented from the early Cretaceous (Albian) through the Holocene. Work on silicoflagellates, from their discovery by C. G. Ehrenberg in 1837 to the beginning of the JOIDES Deep Sea Drilling Project (DSDP) in 1968, progressed slowly owing to the abbreviated, incomplete geologic record of marine biosiliceous sediment in onshore outcrops. Coring of ocean floor sediment sections in areas of past and present upwelling, where silicoflagellates are most abundant, has enlarged their taxonomy and consequent knowledge of silicoflagellates, stratigraphic succession and global geography. They have become a useful tool for time correlation and for paleoecologic comparisons in ocean history studies, especially in high productivity upwelling areas.

HISTORY OF STUDY

As marine phytoplankton, with specialized cold-water and warm-water taxa, that produce distinctive skeletal hard parts, silicoflagellates have been a subject of biologic, geologic, and oceanographic studies since their identification in the first microscopic studies of C. G. Ehrenberg (1837, 1854). Early studies of silicoflagellates in modern oceans suggested that their distributions were the result of different optimum temperatures. Gemeinhardt (1934) indicated that

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genus <u>Dictyocha</u> dominated warmer Atlantic waters, whereas <u>Distephanus</u> dominated in cooler waters. This general relation was later used by Mandra (1969), and Ciesielski and Weaver (1974) to propose specific paleotemperature curve values for different abundance ratios of genera <u>Dictyocha</u>/<u>Distephanus</u>. Transfer functions derived from modern species' temperature ranges are not applicable to Pliocene floras, as they are for foraminifera, because so few species of the surviving stock of modern silicoflagellates range back into the Pliocene.

Micropaleontologists identified the earliest silicoflagellates as Cretaceous in age (Hanna, 1928; Schulz, 1928; and Deflandre, 1944) and began to develop the stratigraphic succession of species and floras, mainly from diatomaceous deposits. Because early biostratigraphic models were based on few localities from differing latitudes that covered only brief parts of the Mesozoic to Cenozoic continuum, correlation of floras was difficult. Detailed biostratigraphies from pre-Quaternary strata are now becoming possible through the cumulative additions of JOIDES ocean drilling core studies after 1968.

Biologic understanding of silicoflagellates is still limited because only a few living taxa are available for study. Marshall (1934), Lipps (1970), Van Valkenburg (1971ab, 1980), and Boney (1973) have made the most notable contributions to the analysis of cell protoplasmic structures and reproduction of silicoflagellates. This information has been synthesized by Tappan (1980). As a minor part of the ocean plankton with few living relatives, silicoflagellates have been studied mostly by micropaleontologists for biostratigraphic and paleoecologic information. For progress in such studies the reader can refer to the following publications and their reference lists: Mandra, 1960; Loeblich and others, 1968; Bukry, 1981b, 1985b, 1987a; Perch-Nielsen, 1985; Curto, 1990; McCartney and Wise, 1990; Ciesielski, 1991.

PREPARATION AND TERMINOLOGY

No special sample preparation techniques are used for silicoflagellates beyond those developed for the major phytoplankton groups, the coccolithophorids and diatoms. Smear slides or acid residues of marine sediment can be viewed at 250X to 500X magnification for identifications and counts. For the details of biologic preparations, the reader should consult Van Valkenburg (1971b and 1980).

Most taxonomy for silicoflagellates is based on the larger features of skeletal morphology. The terminology for different areas on the one-piece skeleton is

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summarized (Figure 1) and some variations in terms can be seen in Tappan (1980) and Perch-Nielsen (1985). Curto (1990) presented a new set of terms -- nexal, intranexal, extranexal, and vicinexal -- to describe, not structures, but, patterns of basal pike location relative to strut-ring junctions. Such terms might be used for detailed lineage studies or as aids in shortening species descriptions.

TAXONOMY AND MORPHOLOGIC SETS

Taxonomy of silicoflagellates is based on skeletal morphology. Morphologic classification of silicoflagellates uses a combination of characters; principally, the basal ring, apical ring, and basal spines. Empirically, the choice for the most conservative and inclusive characteristics to base generic identification on has led to the basal ring and spine combination. Within the genera, such as triangular Corbisema and hexagonal Distephanus, the different apical structures and proportions or presence/absence of these are used to identify species. Secondary characteristics which have been used much less frequently are pikes on both rings, septae at ring apexes, and surface textures on the tubular elements. Because of the simple geometric shapes, changes produced by subtle variations in these characteristics are used to differentiate species, subspecies, varieties and forms.

Six major geometric groups (sets) are designated to compare and contrast different kinds of silicoflagellates.

1.) The **bachmannocenids**. Typified by the genus Bachmannocena Locker, emended Bukry (neé Mesocena Ehrenberg). This set includes all single ring forms lacking apical structures. The rings are planar and range from circular to polygonal with or without spines and ornamentation (Figure 2).

2.) The **caryochids**. Typified by the genus Caryocha Bukry and Monechi (neé Cannopilus Haeckel). This set contains globular multiportal forms constricted near the base (Figure 3).

3.) The **corbisemids**. Typified by the genus Corbisema Hanna for triangular forms, Arctyocha Bukry and Dictyocha Ehrenberg for quadrangular forms, and Naviculopsis Frenguelli for bipolar forms, this set has an apical bar or strut/bar combination that is elevated above the plane of the basal ring (Figure 4). Basal spines and pikes, and apical bars are typical. Minor modifications include apical bands or plates, and bulbous or flared spines.

4.) The **cornuids**. Typified by genera <u>Cornua</u> Schulz, emended McCartney and others, <u>Lyramula</u> Hanna, and <u>Variramus</u> McCartney and others. This set of Cretaceous taxa has radiating tubular rods and spines that do not close to form portals (Figure 5). <u>Lyramula</u> (wishbone-shaped) is dominant in most Campanian and Maestrichtian floras and has reticulate surface texture like <u>Vallacerta</u>, linking them both to Cenozoic silicoflagellates. <u>Cornua</u> has regular triradiate form and undetermined texture. <u>Variramus</u> has irregular branching tubular spines with smooth texture, making its status as the oldest and simplest silicoflagellate a possibility by size, tubular nature and age. But the lack of typical surface texture seen on later Cretaceous species leaves a question.

5.) The **distephanids**. Typified by the genera <u>Distephanus</u> Stöhr and <u>Octactis</u> Schiller which is monospecific. This set has an elevated apical ring that is smaller than the basal ring and connected to it by struts. The polygonal rings are typically hexagonal or quadrangular with spines at the apices (Figure 6). A low frequency of the apical rings are subdivided into binocular and trinocular apical openings. The main exception to the apical ring distinction for distephanids is <u>Distephanus pseudofibula</u> which has apical bars and is used to zone the late Miocene in temperate and cool floras.

6.) The **vallacertids**. Typified by the genus <u>Vallacerta</u> Hanna. The few species in this Cretaceous genus have mostly pentagonal rims with a solid plate covering the central area (Figure 7). Small numbers of quadrangular, hexagonal and heptagonal variants also occur. Reticulate, linear and possible nodular textures occur in the vallacertids.

Certain morphologic characters (apical plates or apical spines) can appear in unrelated lineages at different times. Phenotypic expression repeated in different species of a genus is called iterative evolution. For example, a similar array of low-frequency, polygonal phenotypes can be expected from different species in the same genus. Predominantly five-sided species of <u>Vallacerta</u> can produce four-, six- and seven-sided skeletons (Bukry, 1985b). The same effect can be seen in <u>Dictyocha deflandrei</u> or <u>Distephanus speculum</u>, where the dominant symmetry is accompanied by a low number of polygonal variations. This is considered the normal range of intraspecific variation for silicoflagellates. Quantitative studies establish the dominant morphology. Typical intraspecific variation includes apical plates in species which typically have apical bars, or

subdivided apical rings in species with simple apical rings. Thus, the species concept for silicoflagellates accommodates a wide range of intraspecific variation.

With the beginning of detailed biostratigraphic study of JOIDES DSDP cores, an attempt was made to simplify nomenclature to binomials for different morphospecies. But regionally consistent subspecies were noted for some taxa (subspecies _Dictyocha ornata ornata_ at mid-Atlantic sites) and new or sporadic varieties were identified, thus leading to the use of trinomials for geologic applications. A few geologists use quadrinomials for fossil material.

Development of a natural classification for fossil material will likely be advanced by tracing lineage developments of basal pikes, surface texture and geochemistry of trace elements or isotope ratios. The determination of the status of silicoflagellates as chrysophyte algae from culture studies has led to the classification and taxonomy of silicoflagellates using the International Code of Botanical Nomenclature (ICBN). See Tappan (1980) for higher classification details under Division Chrysophyta Pascher 1914.

BIOLOGY

Silicoflagellates are unicellular (20 to 200 µm) algae with golden-brown chloroplasts in clear cytoplasm. The cytoplasm thinly encloses a basket-shaped skeleton, but it is mostly contained within the perimeter of the skeletal ring. A single long flagellum (200 to 240 µm) extends in an anterior direction relative to cell movement which is achieved by wavelike motion of the flagellum. Reproduction is through simple vegetative fission. This division occurs only after a daughter skeleton has been fully formed.

Skeleton

The tubular opaline skeletons of silicoflagellates have been studied largely through fossil material where most of the taxonomy and structural descriptions have been developed. The major skeletal features are the basal ring, apical ring or bar, and basal-ring spines. Detailed study of modern natural skeletons of _Dictyocha fibula_ s. ampl. (Frenguelli, 1935) and cloned _D. fibula_ (Van Valkenburg and Norris, 1970) have shown considerable variation and irregularity in the skeletal forms produced. Modern _Distephanus speculum_ seems to reproduce with fewer irregularities in the skeletons; Boney (1976) reported consistent mirror-image doubling of the skeleton in dividing cells of _D._

speculum from the Firth of Clyde (United Kingdom), with abnormalities in only 1.78% of the population. However, some abnormal skeletons produced by D. speculum resemble other taxa such as D. pseudofibula, D. crux crux and even Dictyocha pulchella (Figures 4 and 6). The causes or extent of abnormalities and intraspecific variations are still little known because so few culture studies and modern oceanographic studies are available. Studies by Deflandre (1941), Boney (1973), and Van Valkenburg and Norris (1970) have indicated that there is much to learn about intraspecific variation in silicoflagellates.

General skeleton shapes and volumes were studied by McCartney and Loper (1989) using mathematical modelling of skeletal morphology. They concluded that minimization of apical surface area can optimize survivability for Neogene quadrate Dictyocha, but they also noted that the success of Corbisema in the Paleogene implies that high apical surface area may have advantages in warm-water environments. Corbisema then became extinct in the middle Miocene when it became colder.

Dictyocha fibula skeletons from culture studies were noted to possess a spinose collar at the tips of each spine. This collar contains numerous (8 - 10) small projections (Van Valkenburg, 1980). Similar structures with 8 projections were shown on some late Miocene Bachmannocena circulus, middle Miocene and early Pliocene Dictyocha brevispina, and Pleistocene D. perlaevis. The taxonomic and ecologic significance of minor skeletal features, such as the spinose collar, may be an important means to correlate modern culture studies to the fossil record for classification and paleoceanographic analysis.

Takahashi (1991), working on modern sediment trap assemblages, has linked larger skeletal size to higher temperatures. This presents another line of potential study for relating controlled culture and modern oceanic results in order to assist paleoceanographic interpretation of the geologic record.

The complexity of making such correlations was suggested by Kitchell (1983) who proposed that biologic predation pressure intensity is an equally valid cause for skeletal size change. Silicoflagellates could increase their apparent size to a predator (copepods) by developing longer spines and thus reduce predation pressure efficiently, without committing the resources for a full size increase of the skeletal basal ring and other structures. Elongation of spines and rings of silicoflagellates is notable at various times in the Cenozoic and, therefore, is probably a response to changing biotic pressure, not just to abiotic temperature change. Because silicoflagellates, unlike diatoms, are flagellated and motile,

providing a competitive advantage against passive sinking in the acquisition of resources.

A general theory of spine length variation needs to be developed because of the potential advantage of spines in flotation and orientation of the cell so that the chloroplasts can obtain optimum radiation. Spine length variation should be a key to understanding silicoflagellate paleoecology together with information on how cell metabolism is linked to opal formation.

TEXTURE

Electron microscopic examination of silicoflagellates has revealed several kinds of low-relief surface texture on the skeletons (Figure 8). The textures are more robust on apical than abapical surfaces of the skeleton. There are five major kinds of texture:

1.) Crenulate (C). Long subparallel ridges interrupted by periodic peaks.
2.) Linear (L). Long subparallel ridges.
3.) Nodular (N). Rounded protuberances on a smooth surface.
4.) Reticulate (R). Network of intersecting ridges, may have peaks at intersections.
5.) Smooth (S). Uniform, finely granular surfaces with no elevated areas.

Textural differences can be very distinctive, and more than one texture can occur on the same specimen (Figure 8B). To describe this situation with a simple classification code, the individual skeletons are divided into three subsections and are described in this sequence: apical structure/basal ring/spine. Therefore, an individual skeleton having a reticulate apical ring and linear basal ring and spine should have the texture code R/L/L. Comparing such codes from different ages or areas for the same or different taxa can help to show correlations.

Preliminary results of texture analysis have revealed that textures of cold-water specimens are more robust than on warm-water specimens. The reticulate texture common on taxa during the warmer Cretaceous and Paleogene periods is less frequent in the cooler Neogene, when crenulate, linear, nodular and smooth textures are more common. . For example, Bachmannocena specimens from the Eocene are reticulate, but Neogene specimens are predominantly crenulate and smooth (Bukry and Monechi, 1985). Analyzing trends in surface texture from

the Oligocene and early Miocene, when climate was changing to a cooler 'mode', should help to detail the transition from older reticulate texture to the more recently dominant Neogene textures.

The reticulate and linear texture of Caryocha specimens (Bachmann and Keck, 1969; Martini and Müller, 1976) has confirmed the classification of this previously problematic genus as a silicoflagellate.

ECOLOGY AND PALEOTEMPERATURE

Silicoflagellate ecology is not well known compared to other more widely studied modern phytoplankton such as the coccolithphorids and diatoms. Van Valkenburg (1980), describing biological studies, indicated that silicoflagellates are highly temperature sensitive. The chief claim to fame of silicoflagellates has been the widely cited Gemeinhardt (1934) observation that Dictyocha fibula was dominant in warm waters and Distephanus speculum in cool waters of the Atlantic. This general relation was converted into specific temperature curves based on the ratio of Dictyocha/Distephanus and applied to fossil floras (Mandra, 1969; Cornell, 1974; Ciesielski and Weaver, 1974). The warm-water association of Dictyocha in the Southern Ocean correlates positively with fluctuations in warm-water diatoms and is useful in defining the position of the modern Polar Front in the southern ocean (Defelice and Wise, 1981). Similarly, Juillet-Leclerc and Schrader (1987) reported diatoms analyzed as cold-water by oxygen-isotope study were correlated to the lowest abundance of the 'warm' silicoflagellate genus Dictyocha.

Modern Distephanus speculum blooms are related to optimum temperature and nutrients such as nitrogen and phosphorus, so the abundance of D. speculum indicates cool upwelling conditions. Caution has been raised, however, that productivity factors other that temperature may cause blooms (Bukry, 1987b; Takahashi, 1989). For example, Fanuko (1989) reported a large bloom (653,000 cells/liter) of D. speculum in the Gulf of Trieste in August 1983, at 18°C temperature, a warm temperature where D. fibula would be expected. The D. speculum bloom ceased when phosphorus was exhausted. For diatoms, Egge and Aksnes (1992) have experimentally shown silicate concentration is a limiting factor for dominance over other nonsiliceous phytoplankton. A similar relation may affect silicoflagellate blooms.

Because almost all pre-Pleistocene species are extinct, a scheme for determining relative paleotemperature is based on the relative percentages of warm, temperate and cool water genera. The initial basis for this relative paleotemperature analysis has been proposed for Cenozoic floras. For the late Cenozoic, the TS= Xw + 0.5Xt formula adds the percentage of warm-indicator taxa Corbisema and Dictyocha and one half the percentage of temperate taxa Distephanus (quadrate) and Bachmannocena (quadrate) to produce a relative paleotemperature value from 0 to 100 (Bukry, 1981b, 1985a; Bukry and Monechi, 1985). The formula was empirically determined for Neogene latitudinal temperature distributions along western North America, and was successfully applied to a latitudinal transect at the Kuroshio-Oyashio current boundary area in the northwestern Pacific and in the North Atlantic (Bukry, 1981b).

Because the genus Dictyocha first evolved in the early to mid Miocene, a different system should be developed for the genera of the Paleogene. The Paleogene system should concentrate on species' distributions because Paleogene genera, such as Naviculopsis, included both cool and warm water species which could be used to construct a ratio. For example the tropical species of Naviculopsis occupied a similar niche to that of Dictyocha. Within the genus Naviculopsis, N. lata and N. foliacea are considered warm species, whereas N. quadrata and N. constricta are considered cool-water species (Bukry, 1985a, 1987a). In the Cretaceous, Vallacerta hortonii has a distribution indicating it was a warm species, whereas V. siderea and V. tumidula indicate higher latitude cooler conditions (Bukry, 1985b; Ballance and others, 1989). The Paleogene ratio must take into account changes in temperature preference through time. At different times in the Paleogene, the species of Distephanus had different temperature ranges. During the Oligocene, quadrangular Distephanus were dominant; the hexagonals first achieved dominance at high latitude in the early Miocene. In the tropics it took until the late Miocene for hexagonal domination, as quadrangulars were phased out (Bukry, 1985a). More JOIDES drilling and quantitative techniques should result in improved silicoflagellate paleotemperature estimates for the Paleogene.

GEOLOGIC HISTORY

Evolution

Silicoflagellate evolutionary adaptation to changing oceanic conditions for 110 million years from early Cretaceous to Holocene has been preserved as a succession of different skeletal morphologies in marine sediment. Following the early evolution of simple skeletons with radiating rods and spines that lack portals in the early Cretaceous, the more regular closed triangular and quadrangular skeletons of Corbisema and Arctyocha appeared in the late Cretaceous. The closed geometric taxa were the only ones to survive the Mesozoic/Cenozoic boundary extinction event. A morphologic radiation in the Paleocene added two new long-ranged genera, Naviculopsis and Bachmannocena which produced many new species until their extinctions in the Miocene and Pleistocene, respectively. Distephanus with an apical ring above the basal ring appeared in the Eocene and persists into modern floras. Caryocha is a globular, multi-portal silicoflagellate that appeared in the early Miocene but was not very abundant. Following the extinctions of Corbisema and Naviculopsis near the lower to middle Miocene boundary, silicoflagellate floras took on a more modern appearance with a variety of new species of Dictyocha, Distephanus and Bachmannocena. Bachmannocena, the simple ring silicoflagellate disappeared between the upper Pliocene and mid Pleistocene in different areas, leaving Dictyocha, Distephanus and new monospecific Octactis as the remaining living silicoflagellates. Bignot (1985) notes that they are on their way to extinction. Although they are a physically smaller and less diverse group now than in the past, they still have a broad range of intraspecific variation and occur in all oceans.

Using stratigraphic relations in a small region, lineages of successive species can be designated. For example, in oceanic strata off the east coast of North America, the Bachmannocena lineage, covering most of the Eocene (15 m.y.), includes five successive species beginning with the earliest Bachmannocena connudata, then → B. venusta → B. oamaruensis → B. apiculata apiculata → B. apiculata monolineata. Such lineages are evidence for the rate of structural change in a widespread genus used for biostratigraphy.

Zonation

The short duration and widespread occurrence of certain silicoflagellates has made them useful for transoceanic correlation of marine strata. Because there are distinct differences in the species arrays of cold- and warm-water floras, low and high latitude zonations were developed for the Neogene. Later work on Southern Ocean Paleogene floras has also produced detailed zonal systems which are distinct from tropical systems. The Cretaceous floras are not as extensively known, but these have provincial distributions also. Owing to the larger planetary surface area distributions in the low- to mid-latitudes, low to mid latitude zonations are most widely applicable. A representative late Mesozoic and Cenozoic zonation is summarized (Figure 9).

In addition to biostratigraphic zones and subzones even shorter units, termed horizons, have been described. Because of the relatively high degree of intraspecific variation shown in silicoflagellate skeletons, some very short-lived unusual morphologies can be used as stratigraphic horizon index fossils for a thin stratum within a thick zone. Alternatively, the sudden arrival of a new morphology could indicate migration of a taxon from an area that had been previously ecologically isolated. For example one cold-water taxon, Distephanus quinquangellus, suddenly appeared in Pliocene tropical assemblages of the Pacific from higher latitude areas where it had existed since Miocene time. Some short subzones (several hundred thousand years) are similar to horizons in duration. The short Dictyocha neonautica Subzone of the Dictyocha fibula Zone is based on the brief widespread flourishing a naviculopsoid species that appeared in the latest Miocene and disappeared near the Miocene/Pliocene boundary.

DISSOLUTION

Whereas stages of progressive dissolution have been shown for coccoliths and diatoms (Bukry, 1973b, 1978; Mikkelsen, 1980), such sequential solution has not been recorded for silicoflagellates. During mass dissolution studies of biosiliceous sediment in the laboratory, silicoflagellate disappearance values are similar to the range for the more susceptible diatoms (Mikkelsen, 1980; Pichon and others, 1992). Laboratory dissolution of Pliocene biosilica showed that all the silicoflagellates were destroyed at an early stage when diatom abundance had only been reduced by 20 percent. Dissolution must proceed very quickly once begun. Examination of thousands of silicoflagellate assemblages from Cretaceous

to Holocene also has not revealed an obvious series of solution stages. This may be the result of the unusual tubular structure of almost all of the silicoflagellate skeleton. Monty and others (1991), in their study of bacterial attack on biosilica in diatoms, note that bacterial action or solution strips the outer surface layer exposing a granular opaline ultrastructure underneath. Applying this to the problem of silicoflagellate solution, a constant solution rate could attack and could remove a uniformly thick surface layer and open any underlying ultrastructure to solution all around the tubular diameter -- doubling the cross-sectional removal rate. Also, uniform tubular diameters would be removed simultaneously (unlike diatoms with differential central and girdle thicknesses of many species). Ultrastructural details of silicoflagellate skeletons are still unknown. The empirical evidence is that the external layer has solution resistance similar to that of diatoms, but once breached solution destruction must be rapid.

Some Quaternary silicoflagellate floras appear 'ghostlike' because their tube thickness is obviously thinner than is typical for the species (Bukry, 1980a). This could be solution thinning, or original weak silicification. Other siliceous groups include weakly silicified species or ecophenotypes.

In normal marine conditions silicoflagellates may avoid solution during sinking through the water column by the physical protection and rapid sinking afforded inside zooplankton fecal pellets (Takahashi, 1991). Evidence that this process happened in the past is given by fossil floras from different water depths which show little solution nor any range of dissolution stages. Most damage to skeletons appears to be mechanical breakage. Some taxa may be differentially solution susceptible. For example, the warm-water species Octactis pulchra was reported as abundant in North Pacific Ocean sediment traps, with abundance at two stations reaching 15% and 50%. But examination of surface sediments at both stations revealed no specimens of O. pulchra, indicating strong dissolution control over the distribution of this warm-water, upwelling guide species (Pisias and others, 1986). Similarly, cold-water diatoms from the North Pacific suffered less weight loss than warmer water floras during dissolution experiments (Mikkelsen, 1980). Dissolution rankings have not been established for silicoflagellates. This could be studied by subjecting silicoflagellate-rich sediment to the laboratory dissolution process and recording the results at different stages by a taxonomic specialist. Attention to the sediment composition, such as clay-rich/silica or carbonate-rich, might reveal the influence of differing pore-water

chemistry in the resulting dissolution rankings. Silica-rich sediment typically has pore waters with more acid pH where biogenic opal is more stable than in carbonate sediment where more basic pore water can promote opal dissolution.

NEW APPLICATIONS

The principal phytoplankton groups of the Mesozoic and Cenozoic oceans are the coccolithophorids and diatoms. The chief value of silicoflagellates has been to provide paleoecological and stratigraphic determinations for certain high-latitude deposits where the other groups are more dissolved or where their floras are not well known. The wide salinity tolerance of modern silicoflagellates (optimum 30 to 40‰, minimum 20‰) implies that some silicoflagellate species may have been more cosmopolitan than diatoms in the Cretaceous and early Paleogene. Thus, they may be useful over a broader geographic range.

Because of high intraspecific variation and regional phenotypes it is possible to use silicoflagellate floras to evaluate tectonic plate motions. For example, in the early Miocene Naviculopsis ponticula Zone at DSDP Sites 572 and 495 on the East Pacific Rise, specific species successions and abundances have been matched on either side of this fast-spreading ridge (van Andel and Bukry, 1973; Bukry, 1985a). Also, the relocating of some Cretaceous sediment sites to their original Cretaceous latitudes (backtracking) in the Indian and Pacific Ocean from tropical to temperate latitudes was supported by paleoecologic application of cool-water silicoflagellate taxa such as Vallacerta tumidula (Ballance and others, 1989). V. tumidula is only known at high latitude in the Northern Hemisphere.

Biostratigraphic zonations developed from silicoflagellate floras in DSDP cores are being applied to correlation with land outcrops. For example, the first coccolith and silicoflagellate-bearing sediment of Paleocene age from western North Atlantic DSDP Site 384 permitted a new age assignment for the noncalcareous "Eocene diatomite" beds at Fur and Mor in Denmark. The same silicoflagellate biostratigraphic guide species reported from Denmark occur at DSDP Site 384. The coccoliths at DSDP 384 are late Paleocene, thus suggesting a more extensive Paleocene section onshore in Denmark.

In northeast Japan, Yanagisawa and Suzuki (1987) used silicoflagellates in the Oligocene Shirasaka Formation to restrict biosiliceous assemblages to an early Oligocene age, using the oceanic Dictyocha deflandrei Zone and the Bachmannocena apiculata apiculata Subzone. Also in Japan, Kobayashi (1988)

adopted silicoflagellate biostratigraphic guide taxa from DSDP sections to design a specific detailed zonation for the Neogene of the Japan Sea coastal region. Several new regional zones were developed to augment the existing oceanic zones.

Some silicoflagellates may indicate discrete ecologic events. The widespread but brief occurrence of elongate <u>Dictyocha neonautica</u> in the latest Miocene of the North Pacific is a distinctive recurrence of the <u>Naviculopsis</u> morphology which became extinct 10 m.y. earlier. This brief occurrence followed a major shift in carbon isotope ratios (Loutit and Kennett, 1979), and may represent a singular perturbation in ocean near-surface conditions, since there are no younger recurrences of this abundance or geographic extent (Bukry, 1980b).

Relative paleotemperature (TS) trends from silicoflagellate quantitative abundance data can be used for local fine-scale correlation. Matching of the TS values across the Miocene/Pliocene boundary at tropical Pacific DSDP Sites 503A and 504 shows that similar cool events (TS=42,46) before the boundary are followed by a warming trend (TS= 63,73), until matching values (TS=86) adjacent to the boundary indicate near-identical surface conditions at the two sites (Bukry, 1984). In a detailed study of paleotemperature records for the Pliocene at the Bianco section of Italy, the silicoflagellate TS trends paralleled those derived from coccoliths and planktonic foraminifera (Rio and others, 1989).

Modern silicoflagellates have been used in biologic oceanography to help demonstrate phytoplankton similarities between long term (1964 - 1975) central and edge stations some 3200 km apart in the North Pacific central gyre (Venrick, 1992). <u>Dictyocha fibula</u> was tabulated among the 20 dominant species. The eastern edge station was colder and fresher and <u>D</u>. <u>fibula</u> abundance, like that of associated coccolithophorids and diatoms, was more stable there.

Many of the applications of silicoflagellates to biologic, ecologic, geologic, and oceanographic studies are in their initial stages. Van Valkenburg (1980) has suggested that study of silica metabolism and skeleton formation in phytoplankton would benefit from detailed work on silicoflagellates. Determining the integrated ecostratigraphy for this environmentally sensitive group would be an important contribution to Mesozoic and Cenozoic paleoceanography.

SUGGESTIONS FOR FURTHER READING

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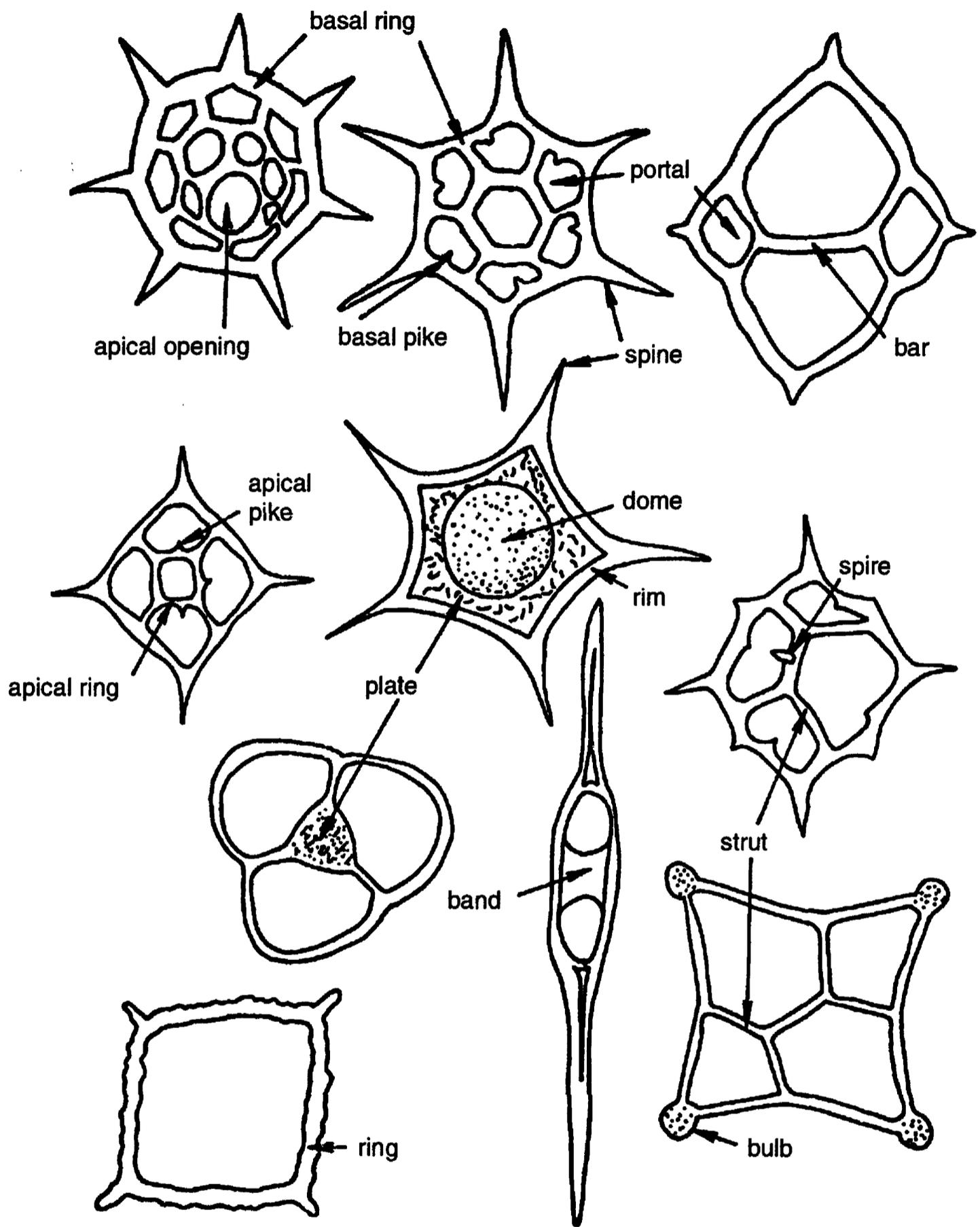
Figure 1. Terminology for principal structural elements used in description of silicoflagellate skeletons (Bukry, 1976).
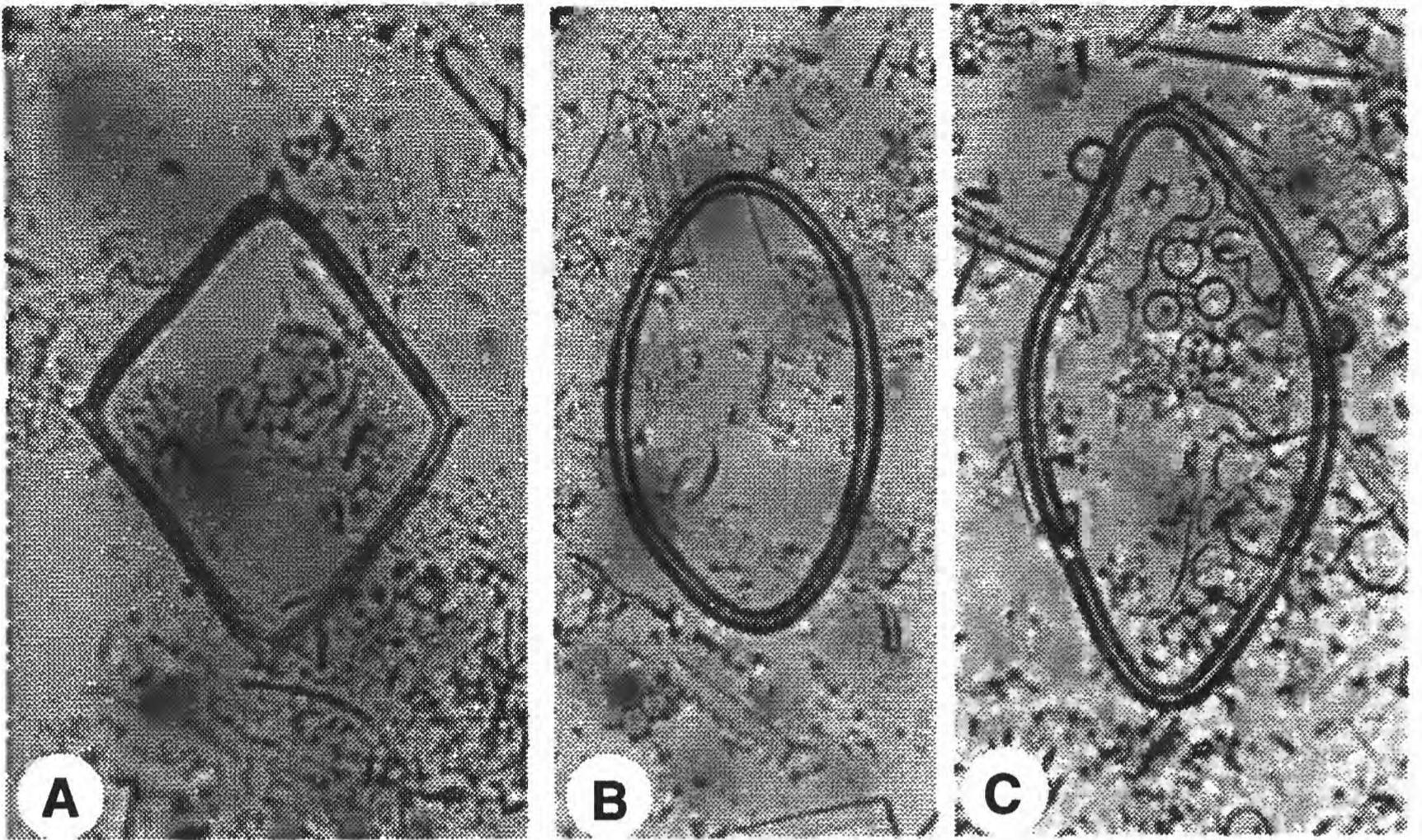
Figure 2. Bachmannocenids. A. *Bachmannocena quadrangula* (Ehr. ex Haeck.).
B. *B. ovata* (Buk.). C. *B. venusta* (Buk.).
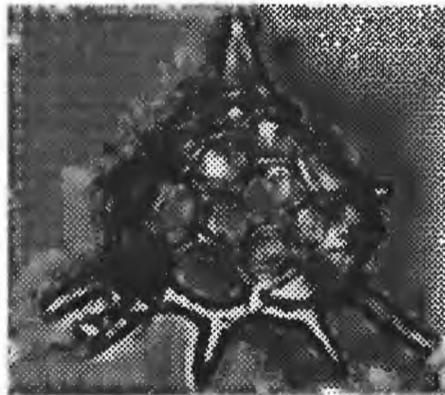
Figure 3. Caryochids. *Caryocha depressa* (Ehr.).
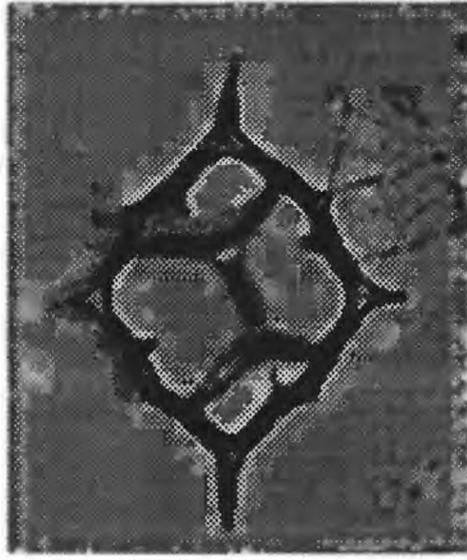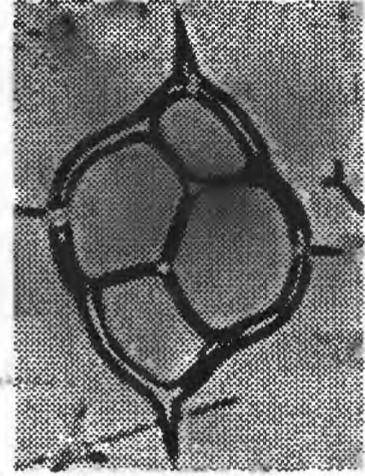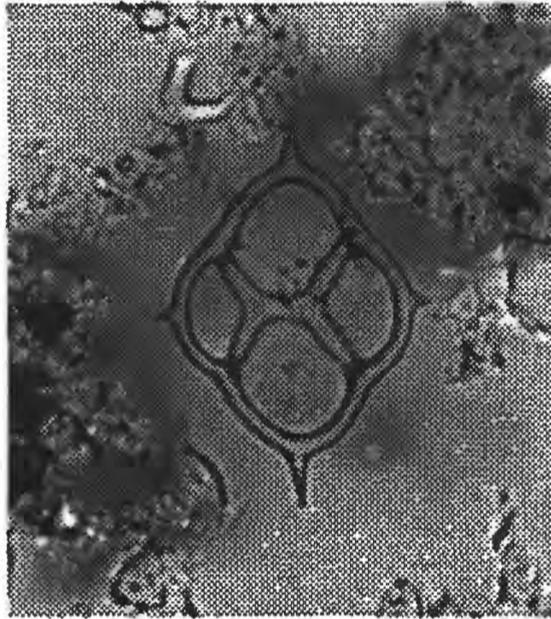
Figure 4. Corbisemids. A. *Corbisema hastata* (Lemm.). B. *Dictyocha aculeata aculeata* (Lemm.). C. *D. flexatella* (Buk.). D. *D. pulchella* (Buk.). E. *Naviculopsis lata* (Defl.).
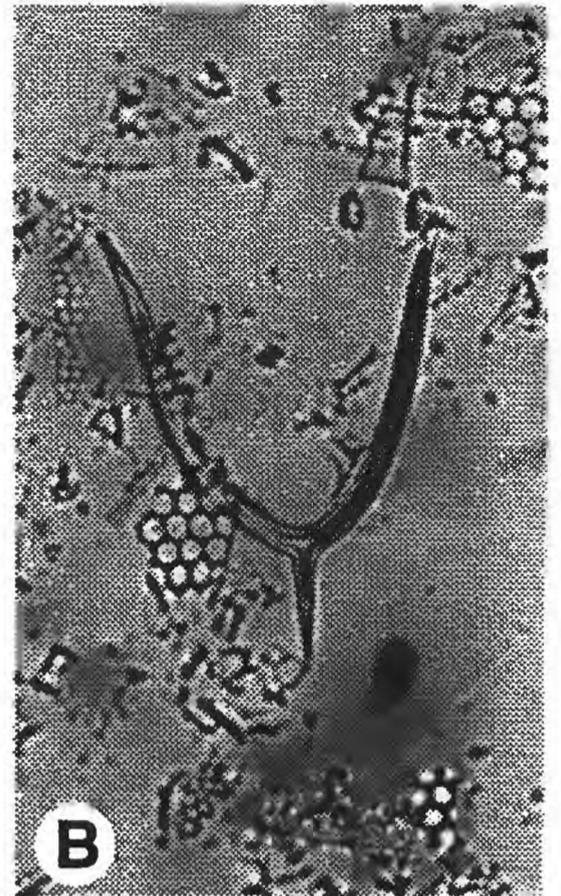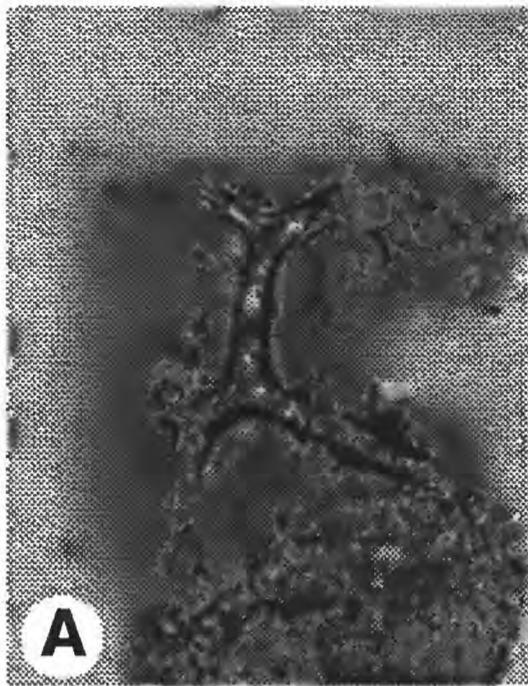
Figure 5. Cornuids. A. *Cornua* sp. cf. *C. trifurcata* Schulz.
B. *Lyramula furcula* Hanna.
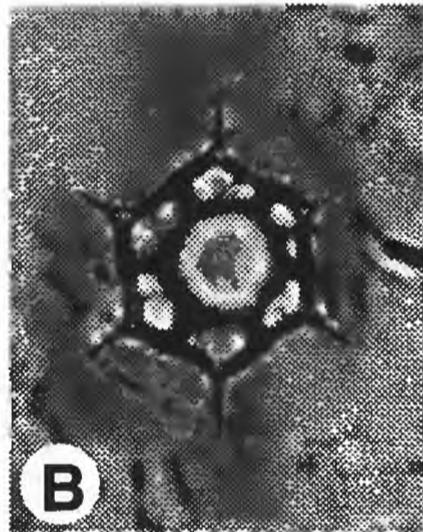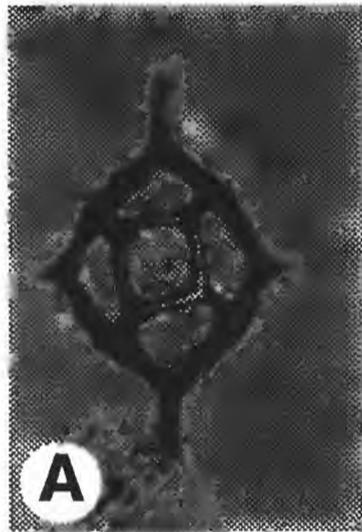
Figure 6. Distephanids. A. *Distephanus crux crux* (Ehr.). B. *D. speculum speculum* (Ehr.)
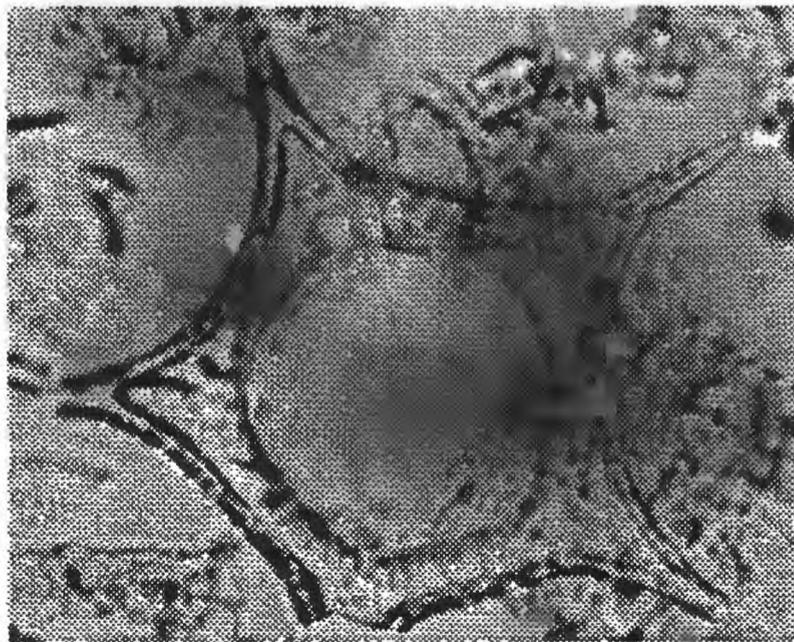

Figure 7. Vallacertids. *Vallacerta tumidula* (Glez.).
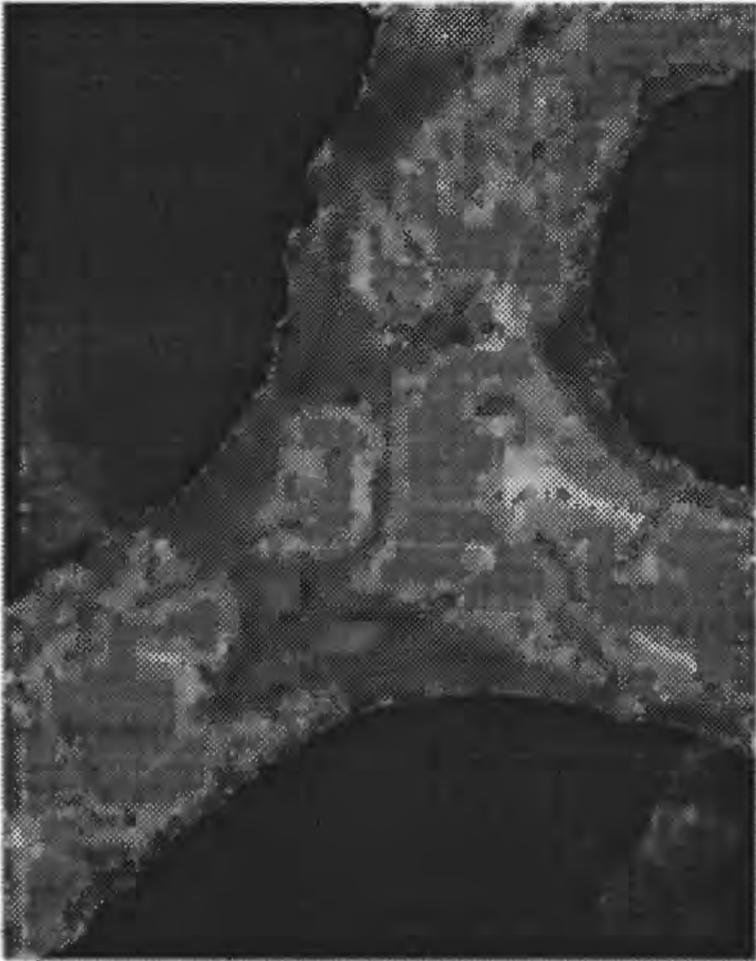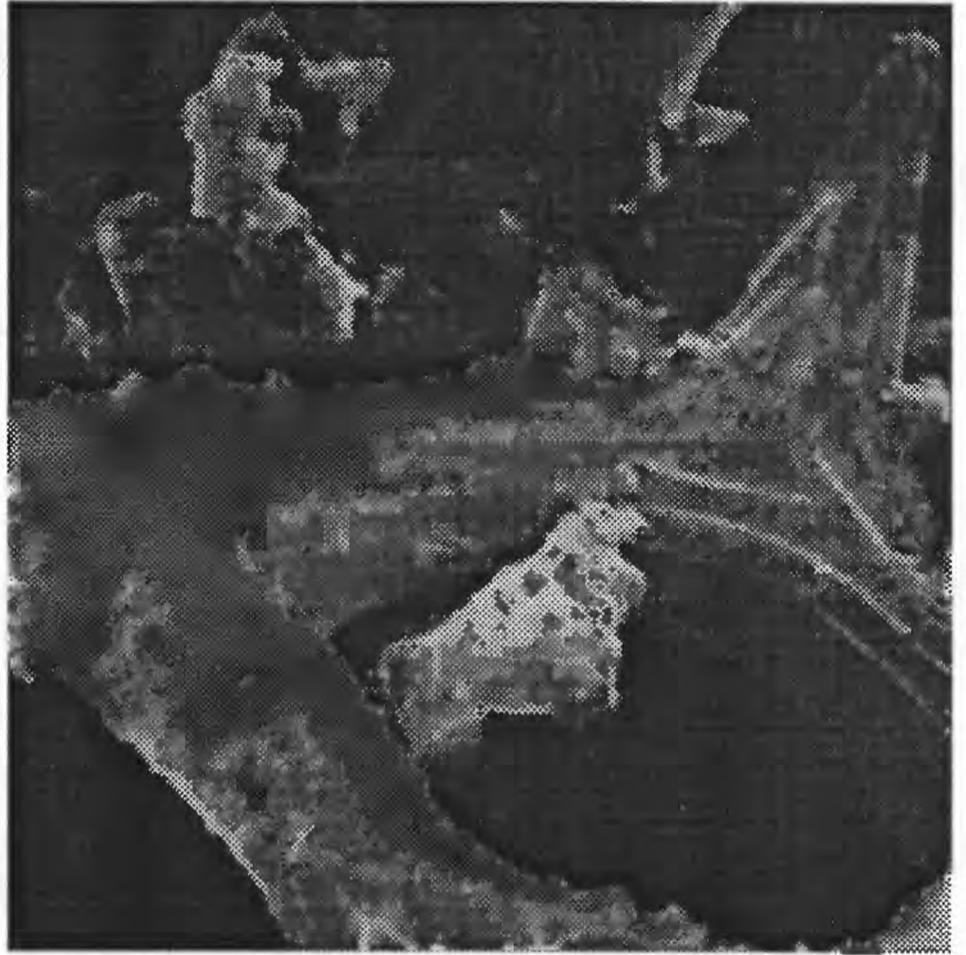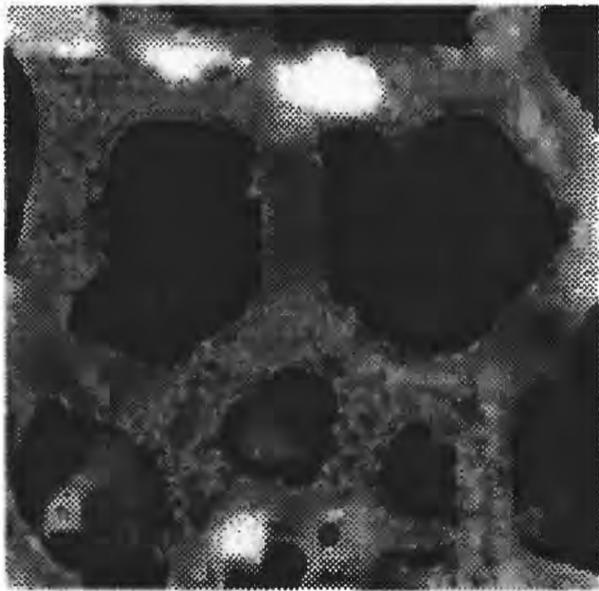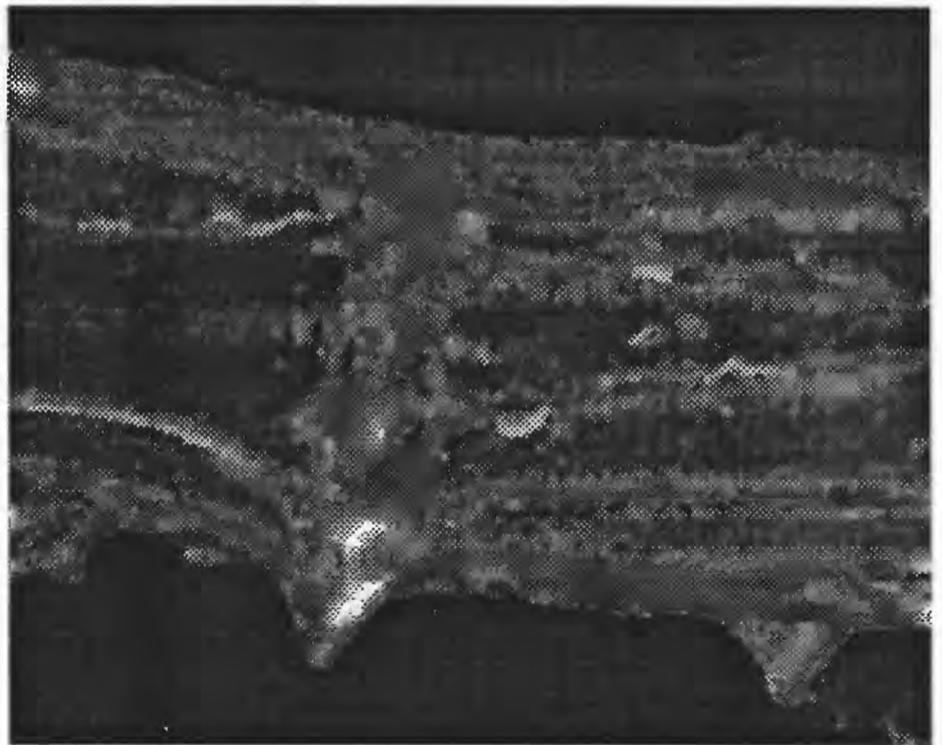
Figure 8. Silicoflagellate textures (Bukry and Monechi, 1985). A. Reticulate.
B. Reticulate and linear on the same specimen. C. Nodular. D. Crenulate.

GEOLOGIC AGE	Ma	SILICOFLAGELLATE		ZONE MARKERS
		ZONE	SUBZONE	
PLEISTOCENE		*Dictyocha aculeata aculeata*		
		Bachmannocena quadrangula		*B. quadrangula* - A
	1.6 (1.8)	*Dictyocha stapedia stapedia*	*Dictyocha delicata*	*D. delicata* - FO
PLIOCENE			*Dictyocha ornata*	*D.s. stapedia* - FO
		Dictyocha fibula	*Dictyocha angulata*	*D. pulchella* - LO
			Dictyocha pulchella	*D. neonautica* - LO
	5.3 (5.4)		*Dictyocha neonautica*	*D. longa, D. neonautica* - FO
		Dictyocha brevispina	———	
			Bachmannocena hexalitha	*B. hexalitha* - A
MIOCENE			———	*C. triacantha* - LO
		Corbisema triacantha	*Distephanus stauracanthus*	*D. stauracanthus* - FO
			Caryocha schulzii	*Naviculopsis* - LO
		Naviculopsis ponticula		*N. ponticula* - FO
		Naviculopsis quadrata		*N. quadrata* - FO
		Naviculopsis lata		*N. lata* - FO
	23.7 (23.8)	*Naviculopsis biapiculata*	*Distephanus speculum haliomma*	*D.s. haliomma, D.s. hemisphaericus* - FO
OLIGOCENE			*Corbisema triacantha mediana*	*N. biapiculata* - FO, *C. apiculata* - LO
		Corbisema apiculata		*C. hastata* - LO
	36.6 (33.7)			*D. hexacantha* - LO
		Dictyocha hexacantha		
EOCENE				*D. hexacantha* - FO
		Naviculopsis foliacea	*Dictyocha spinosa*	
			Naviculopsis robusta	*D. spinosa* - FO
	57.8 (55.0)			*N. foliacea* - FO
		Naviculopsis constricta		
PALEOCENE				*N. constricta* - FO
		Corbisema hastata		
	66.4 (66.0)			*C. hastata* - FO
CRETACEOUS		*Lyramula furcula*		*L. furcula* - FO

Figure 9. A representative Cenozoic and Mesozoic biostratigraphic zonation for oceanic floras from tropical and subtropical areas (Bukry, 1981a, 1985a, Perch-Nielsen, 1985). Geologic boundary ages (Ma) from Berggren and others, 1985, and Cande and Kent, 1992 (in parentheses). Abbreviations for zone marker events are A = acme, FO = first occurrence, and LO = last occurrence.