# DINOSTRAT 94

**Notes for a workshop on dinoflagellate cyst stratigraphy and associated taxonomic problems : Maastrichtian through Pliocene, Western Venezuela.**

By


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# A. Introduction to Dinoflagellates

## 1. What are dinoflagellates ?

Dinoflagellates are eukarytoic single-celled biflagellated organisms, usually regarded as plant-like but with a variety of nutritional modes, about half of those that are extant being photosynthetic and half being phagotrophs, symbionts and parasites. Many are aquatic occupying marine and freshwater habitats. The majority of fossil dinoflagellates are marine but there are well-documented records of freshwater and brackish species in the Mesozoic and Cenozoic.

The single most unique feature of living dinoflagellates that separates them from all other organisms is the possession of a special nucleus referred to as a **dinokaryon** which remains condensed (and therefore visible) during interphase, has an external mitotic spindle, and lacks histones. None of these features is of much use in identifying fossil dinoflagellates. Fortunately, dinoflagellates generally have a number of other features associated with their distinctive organization which allows ready identification on the basis of morphology of the cell.

Dinoflagellates are motile during part of their life cycle , and have the ability to move through the water column. This is achieved by two **flagellae,** one of which is aligned transversly and beats to the left in multiple waves and the other which is aligned posteriorly and beats with one or fewer waves. The overall motion of the cell is something like a corkscrew, and considerable speed can be achieved by these organisms which are typically in the size range of 50um to 200um (occasionally smaller or larger). Their motion is often related to achieving optimum depths in the water column on a diurnal basis to photosynthesize or respire. The transverse flagellum is usually associated with a helicoid parallel-sided furrow referred to as a **cingulum.** The longitudinal flagellum is associated with a less well defined but nevertheless significant depression referred to as the **sulcus.**

## 2. How are dinoflagellates oriented ?

Definitions are easy, but in practise it can be quite difficult to decide which way is "up" in a fossil dinoflagellate. Dinoflagellates have no well-define symmetry, and therefore they are less readily identified compared with,say, spores or pollen which have a triradial (or higher) axis of symmetry and often a bilateral plane of symmetry.

3. Definitions.

Dinoflagellates have **left** and **right** sides, **anterior** and **posterior** ends, and **ventral** (front) and **dorsal** (back) surfaces. These are defined conventionally using the intersection of the cingulum and sulcus to be the ventral surface. The organism moves in the direction pointed to by the anterior end and the other ends and sides are then defined on this basis.

4. Basic morphologic terms

Given the above basic orientation, it becomes necessary to identify certain salient features of the typical dinoflagellate cell.

The anterior end often but not always has a pointed or otherwise prominent structure or **apical horn** and is referred to as the **apex**. The posterior end may be rounded, or possess one or two **antapical horns** and is referred to as the **antapex**.

The cingulum approximately half way betwen apex and antapex may itself impart a prominence to the cell outline, and it is a combination of these prominences which gives many dinoflagellates a typical polyangular outline. Some dinoflagellates have horns in lateral positions which appear to be developed on the cingulum or in the immediate posticingular positions and these are called **cingular** or **postcingular** horns.

5. Tabulation, plates, and paraplates

Although the shape of a dinoflagellate is often very distinctive, the presence of angular areas bounded by distinctive sutures on the cell wall is one of the most diagnostic features. These areas may be quadrangular, pentagonal, hexagonal, or occasionally with more sides. They are present on most but not all living and fossil dinoflagellates. Some of the early micropaleontologists in the early 1800s correctly identified fossil dinoflagellates in Upper Cretaceous early diagenetic cherts on the basis of the presence of these distinctive angular fields, but it took more than 100 years before it was realized that fossil dinoflagellate represent a special stage of the life cycle which is not motile.

In living motile dinoflagellates, **tabulation** is expressed by **plates** joined along **sutures** which together comprise the **theca**. The theca is often composed largely of cellulose which does not have a high preservation potential in the fossil record. Thecal plates are usually overlapping (imbricate) and during the life of a motile dinoflagellate the plates may be shed or split in various ways to achieve growth or asexual reproduction. Not all living dinoflagellates have plates (are **armoured**); some have a more delicate cell membrane and are called **unarmoured**.

The nature of fossil dinoflagellates became well established during the late 1950's and early 1960's. They were clearly identified as similar to but different in several significant respects compared to the thecate stage. Firstly, the plates were defined by thickenings or other ornament along their edges, but the wall was not in any way imbricated; rather, it was uniformly structured across the boundary of plates. Secondly, fossil dinoflagellate walls were not penetrated by canals or other openings associated with trichocysts or flagellae. Rather, the walls seemed to have localized thickenings in areas which otherwise would be anticipated to have holes. Thirdly, fossil dinoflagellates had other openings in the wall not found in motile dinoflagellates. All this was a puzzle until biologists rather belatedly about the same time started looking at other stages in the life cycle of dinoflagellates. It quickly became clear that fossil dinoflagellates represented th **cyst** stage of the life cycle and not the motile stage. To emphasize this difference, the prefix "**para-**" is often used to indicate that a feature is on the cyst and not on the theca e.g. a cyst has a **paraplate** outlined by **parasutural** features. This might be necessary in studying living populations, but some feel that the term is somewhat contrived in paleontological studies where all dinoflagellates are the encysted stage.

6. Different cysts for different things

Dinoflagellates often form cysts, which may be one of the following:

a) resting cysts (resting spores) following sexual fusion

b) temporary cysts (pellicle cyst, ecdysal cyst) formed in response to adverse conditions

c) vegetative cysts which are metabolically or reproductively active characterize a large part of the life cycle of some living dinoflagellates and this cyst may be organic-walled or calcareous.

c) Digestion cysts are rarely produced in living dinoflagellates after feeding.

The great majority of fossil dinoflagellates appear to represent a resting cyst stage produced after gamete fusion into a zygote and this type of cyst is referred to specifically as a **hypnozygote**. The wall of lving hypnozygotes comprises dinosporin, cellulose, and gelatinous material arranged in several layers and surrounding the shrunken cell contents which are often characterized by a large red-pigmented body. This red body is easily seen in living dinoflagellate cysts which are easily extracted from marine muds and silts by simple sieving and decanting techniques.

7. Composition of fossil dinoflagellates

The fact that dinoflagellates are preserved commonly in the fossil record suggests that they cannot be composed of cellulose. Living dinoflagellates are known to produce various types of cysts which in different families may be of resistant organic material, cellulose, or calcium carbonate. Cellulosic cysts are known to occur in subrecent sediments and can remain viable for several years. Calcium carbonate cysts have also been extracted in sediments from the Cenozoic. The great majority of fossil cysts are known from those composed of organic material (**dinosporin**) which is part of the kerogen component of sedimentary rocks.

8. How are dinoflagellates extracted from rocks ?

It is not known with certainty what organic-walled cysts are composed of - it is conveniently called dinosporin without any precise meaning - but it behaves chemically very much like sporopollenin of the embryopytes. This is very fortunate because no special methods are needed in a palynology laboratory to extract dinoflagellates. Dinoflagellate cysts (which are also commonly referred to for convenience as **dinocysts** or simply **dinos**. by palynologists) are in the size range or behave hydrodynamically like mud, silt or fine sand. These lithologies in drab colours tend to be the best bet for finding dinocysts. In a typical maceration process, calcium carbonate is first removed with dilute hydrochloric acid; then silica and silicates are removed with concentrated hydrofluoric acid (the pretreatment with HCl is necessary to avoid fluoridization of calcium carbonate to calcium fluorite which can be very difficult to subsequently eliminate); one or more washes in strong hydrochloric acid are essential to remove bi-products produced during HF treatment; finally the residue may be oxidized with nitric acid to remove pyrite, and to also remove fusain. The final preparation can be significantly enhanced by sieving in nitex (monofilament nylon cloth with specific mesh sizes) to remove particularly the extra-large and extra-small particles. Dinoflagellates fall in the following size ranges:

small - less than 50um

intermediate - 50 to 100 um

large - more than 100um (some dinocysts are 300um or more in length).

9. More about dinocysts

The earlier workers in the field of micropaleontology were unaware that dinoflagellates were so resistant to chemcial treatment, and for the first one hundred years of study (approximately 1835-1935) all examination was done looking at flint chips or thin sections of cherts. As mentioned earlier, the first fossil dinoflagellates were discovered early in the 19th century. At the same time, it was noticed that there were other microorganisms present with the dinoflagellates covered in spines and processes and clearly -at least to these 19th century paleontologists - not dinoflagellates. At first they were thought to be eggs of invertebrates (perhaps copepods or bryozoa) but gradually these hypotheses were abandoned and by the 1930's it became common practise to call these spiney spheres **hystrichospheres** and simply treat them incertae sedis. It was not until the late 1950's that several palynologists independantly stumbled on the correct identity of hystrichospheres, realizing that they were in fact just another variation of a dinoflagellate cyst. It is now usual to not use the term hystrichosphere, which is too imprecise, and rather term these spiney spheres **skolochorate** cysts.

10. The archeopyle in dinocysts

During the 30s when dinoflagellates were still being studied in thin sections of chert, some exquisite observational work was done on dinocysts and it was noticed that these were often broken in an angular manner. The assumption was made that this was simply random breakage due to mechanical damage during sedimentation or perhaps following compaction and diagenesis. Only later when chemical techniques had been discovered which allowed more precise observation on oriented specimens did it become apparent that far from being random, these breakages were pre-determined, of specific shapes and positions, and of fundamental importance for the dinoflagllates, acting as a means of escape for the cell contents following the resting stage. These angular (or occassionaly rounded) openings are called **archeopyles**, and the lid closing the hole in the wall is the **operculum**.

11. The dinoflagellate life cycle

These fundamental features of dinoflagellates and their cysts can be related to a typical life cycle as follows:

The motile stage of a typical dinoflagellate comprises a biflagellated cell, often covered in cellulosic plates. This cell is believed to be haploid. In response to particular conditions, the motile stage undergoes fission to produce gametes which are also biflagellated and tabulated. These fuse in pairs, each zygote first becoming equipped with double flagellae, becoming imobile and eventually forming a hypnozygote which sinks to the bottom of the water column (sea or lake). During formation of the hypnozygote, the cell contents contract somewhat or a great deal towards the centre of the cell and the dinosporin cyst is formed underneath the theca and encloses the cell contents.

If contraction is not very great, a cyst is formed which looks rather similar to the theca and is called a **proximate** cyst. If contraction is greater, processes and spines tend to form to brace the contracting cyst against the thecal wall. These are termed **chorate**, and those with individual processes rather than high crests are called skolochorate. During cyst formation, for reasons which are not well understood, the dinosporin wall may form as two separate layers which are separated by a space or cavity and are referred to as **cavate** cysts. Cavate cysts are very common in mid- to high latitudes and less common at low latitudes so presumably water temperature and related factors such as viscosity changes and photoperiod may be important in this process.

12. History of research in fossil dinoflagellates.

Given this background, let us review briefly the important players in this field of study.

**Ehrenberg** working in the early 19th century in Germany was the first to discover dinoflagellates in Upper Cretaceous flints. Others in England confirmed these findings. However, little happened for almost one hundred years until O. **Wetzel** - also in Germany and also working on Upper Cretaceous flints - established the morphology of dinocysts and introduced the concept of hystrichospheres. **Deflandre** in France closely followed up on this work and did seminal work on dinocysts in Cretaceous flints starting in the mid-30s and continuing into the 70s, changing preparation teechniques to extract cysts by chemical means.

Added impetus to this work was provided by **Cookson**, an Austalian paleobotanist and palynologist mostly interested in pollen who in mid-career decided to follow up on dinoflagellates and hystrichospheres which were so common in her Upper Mesozoic and Cenozoic residues. She decided to team up with Deflandre and travelled to Paris for this purpose but although a couple of important publications resulted, the two did not get on and she did not return to his laboratory. Rather she teamed up with **Eisenack** at the University of Tubingen which led to a fruitful collaboration spanning almost a quarter century.

Meanwhile, a young palynologist working in the US oil industry, **Evitt**, decided to change career and was appointed to Stanford University where he persued detailed studies of dinoflagellates from the 60s into the 90's. He was very influential and his ideas gained rapid acceptance. He was primarily responsible for correctly identifying the archeopyle and many other important features of dinocysts.

In Britain about the same time, **Downie** at Sheffield University was initiating studies on Paleogene dinocysts which occupied him fand his students for about 30 years. Many notable palynologists were associated with this project, of which **Williams** and **Sarjeant** noteworthy in particular. Williams obtained a position with Amoco (or Pan American Petroleum as it was then called) in Tulsa in the early 60's and subsequently moved on to a position with the Geological Survey of Canada in Dartmouth, Nova Scotia. He has subsequently been responsible for two major endeavours. Firstly, with **Stover** of Exxon in Houston he has catalogued and analyzed genera of dinocysts. Secondly in collaboration with **Lentin** in Calgary he has been responsible for a major ongoing effort to produce an index ofgenera and species of fossil dinoflagellates. At the same time as Williams during the mid-60s, **Norris** became employed at Amoco, having recently arrived from the New Zealand Geological Survey having initiated studies on and application of dinocysts to Mesozoic problems. He subsequently obtained a teaching and research position at the University of Toronto. While in new Zealand, he collaborated with Sarjeant to try and bring order out of chaos to the genera and suprageneric categories for dinocysts. This work has continued to the present day, drawing in a number of other biological and paleontological colleagues. Sarjeant is now at the University of Saskatchewan, and his close work with the dinoflaellate biologist **Taylor** at the University of British Columbia has led to important advances in understanding the relationships between living and fossil dinoflagellates. Meanwhile, during this same period, many petroleum exploration companies became aware of the importance of dinocysts to oil and gas exploration and much but largely unacknowledged work has been done in this field. Of particular interest is the seminal work done by Shell Oil in the Orinoco Delta on distribution of palynomorphs in surface sediments. The work during the 50s of **Kuyl, Muller**, and **Waterbolk** was of fundamental importance in demonstrating that hystrichospheres are neritic organisms closely associated with specific environments in and near delta fronts.

The above history does not do justice to the very many people and important contributions that have been made both within the oil industry and in government and university insitutions. There are many more balanced and scholarly accounts available in the literature. This is simply an individual perspective.

## 13. More about tabulation

Returning to dinoflagellate themselves, it is possible to identify plates or tabulation features on both the motile stage and the encysted stage. The features are different on each stage of the life cycle, but it is possible to think of them as occupying specific sites on the cell. For these purposes, a number of different schemes have been formulated. In these notes, the **Kofoid** scheme will be used; it is still the most popular and most easily understood scheme and was formulated in the early 20th century by a biologist working at Scripps Oceanographic Institute in La Jolla.

Kofoid regarded dinoflagellates as having 4 fundamental features which could be used to define plates - the apex, the antapex, the cingulum, and the sulcus. These features are used to define the following plate series :

**Apical** plates - on and around the apex
**Anterior intercalary** plates - immediately below the apical series
**Precingular** plates - those arranged as a circle of plates anterior to the cingulum
**Cingular** plates - those that form or lie within the cingulum
**Postcingular** plates - those posterior to the cingulum
**Posterior intercalary** plates - between the postcingular plates and the final series:
**Antapical** Plates - plate on and around the antapex

These are designated as a **plate formula** using the following notation:

Apical - single prime '
Anterior intercalary - c
Precingular - double prime"
Cingular - c
Postcingular - triple prime '''
Posterior intercalary - p
Antapical -quadruple prime - ''''

Thus a typical plate formula might be as follows : 4' 3a 7" 6c 5''' 2''''.

There are other schemes which attempt to be more objective or purport to establish plate homologies, but the Kofoid scheme is functional and for most purposes is quite satisfactory in identifying dinoflagellates to the species level.

14. How tabulation is recognized in cysts

It is now apparent that although some dinocysts - notably the proximate cysts - show tabulation features which are rather similar to the plates of the theca, many dinocysts do not and some such as the chorate cysts do not at first sight have any tabulation features.

Much work has been done to solve this problem and it is now apparent that cysts can be regarded as being ornamented in a variety of ways, but with fundamental links to an underlying tabulation. For these purposes, it is assumed that the plate is the fundamental feature. The plate in a theca is bounded by a suture; in a cyst there is no suture but the edge of the paraplate is termed **sutural**. Ornament in this area is thus called sutural e.g. a sutural crest, a sutural row of processes. If the ornament is developed at the centre of the plate, this is called **intra-tabular**. If the ornament bears no obvious relationship to plates, it is termed **non-tabular** (sometimes written nontabular). Sometimes, the ornament is developed close to and parallel to the sutural area, in which case it is called penitabular.

Sutural ornament is often developed as ridges, crests, or linear rows of spines, granules, or other types of processes. Intratabular features are often developed as large or prominent processes at the centre of a plate. Non-tabular features may be large or small and provide a cover of processes which may obscure any obvious tabular features.

15. How are species and genera recognized ?

The following features are used to establish identity :

a) Gross morphology - proximate or chorate, and how many horns
b) Wall relationships - a single wall, a double wall, a cavate wall
c) Tabulation style - how many plates and how they are arranged
d) Archeopyle - where it is located and how many plates are involved
e) Wall features - is the ornament sutural, intratabular, non-tabular.
f) Size - overall, inner body, lenghts of processes
g) Wall structure - thick, thin, diaphanous, fibrous
h) Cingulum development - is it marked by the same or different ornament
i) Other different ornament - is the antapex distinctive

16. More about archeopyles

Probably the most important feature for primary identification of a dinoflagellate cyst is the archeopyle. This can be one of 4 principal types, although there are many variations and some real "odd balls" :

a) **apical archeopyle** , developed on the apical series - often multiplate
b) **intercalary archeopyle** , developed from one or more plates in the anterior intercalary series
c) **precingular archeopyle,** developed from the precingular series; normally single plate but sometimes more
d) **epicystal archeopyle,** involving the entire cyst anterior to the cingulum.

The last archeopyle type is in fact one of a number of archeopyles produced by combination of plates from different series. For convenience, these archeopyle are designated as follows:

apical - A
intercalary - I
precingular - P
combination - use a mixture of the above terms e.g. AIP for epicystal

Much has been written on the archeopyle, and there are many different terms applied to it, but the above is adequate to get started.

17. How to recognize an archeopyle

Although conceptually, the idea of a hole in the wall is easy to grasp, in practise it can be very difficult to see. You *must* have a high quality microscope equipped with differential interference contrast (Nomarski interference contrast) Phase contrast does not help much. Brightfield can be useful but interference contrast is essential.

In inteference contrast, the archeopyle shows up usually quite clearly. If you have trouble, switch to brightfield and look at different absorbition colurs; the archeopyle shows up as a lighter coloured area.

Look for breaks in the wall. Not all archeopyle show up as text book angular areas. In fact, the majority probably do not. Rather, the break in the wall must be related to other cyst features to establish precisely what type of archeopyle is developed. It is extremely important to relate the archeopyle to the cingulum and to the apex.

18. How to identify a cingulum

In proximate cysts, this is reasonably easy, generally the cingulum being seen as a pair of parallel ridges, often helicoid and thus crossing the cyst somewhat obliquely. In skolochorate cysts this is not so easy. The cingulum might have identical processes, different processes, or non at all. One quick way to establish the presence of a cingulum in intratabular cysts is to simply count the total number of processes. Most Cretaceous and Tertiary cysts have about 4 apical plates, 6 each in the precingular, cingular and postcingular region, and about 4-6 antapical, posterior interalary, and anterior intercalary plates combined for a total of about two dozen or slightly more processes. If there are less than 2 dozen processes, very likely you are dealing with a cyst with no processes in the cingulum.

19. How to identify "up" in a cysts

Cysts are conventionally oriented with the apex pointing upwards, which is the way the corresponding theca would swim in the water column. The apex is extremely important to identify, because it holds many of the keys to correct identification of species and genera. In proximate cysts, the apex is often drawn out into an apical horn, and usually but not always the antapex carries 2 antapical horns. Sometimes the antapex is rounded or carries a single antapical horn. In the latter case, you may have difficulty establishing which is the apical and which is the antapical horn. Look for the archeopyle; in all but a single isolated case, the archeopyle of whatever type occurs in the apical end (the **epicyst**). The only known instance of an archeopyle in the antapical end (the **hypocyst**) occurs in the Neogene. In skolochorate cysts, the apical and antapical ends are not usually distinctive. The body of the cyst may be elongated apically-antapically in which case the archeopyle can be used to identify the epicyst. Sometimes, skolochorate cysts have a distinctively larger antapical process but this can also occur in the apical end. Some skolochorate cysts have distinctly smaller cingular processes or none at all which also helps to identify the poles.

# B. Introduction to the Zonation

Methodology

Sections were located in outcrop and in the subsurface for the interval Maastrichtian-Pliocene. No systematic attempt was made to study the pre-Maastrichtian interval but some information was gained from one well on an unconstrained interval referred to as "Senonian" as a basis for comparison of the succeeding Maastrichtian floras.

Zones were established on range tops of selected dinoflagellates to provide an interval zonation. These are listed in morphologic groupings as discussed below. In addition, certain characteristic additional components of the dinoflagellate flora were identified to aid in interpretation of assemblages, and these may be further qualified by the suffix "H" for those with higher occurences, "L" for those with lower occurences, and "C" for those species believed to be confined to the interval under discussion..

Some other algae characteristic of freshwater or hyposaline environments were also used in certain intervals e.g. Pediastrum, Zygnemataceae, prasinophytes, acritarchs.

All species are described in the Maraven dinoflagellate files and provided with a unique number, but these numbers are not provided in the following material.

Chronostratigraphic data were obtained from existing company reports. There is some danger of circularity of reasoning in this approach, but until much more details are available on local range zones, it is considered unwise to attempt routinely any long-distance correlations to the better known intervals at mid- to high-latitudes in the northern and southern hemispheres.

Species under each heading are grouped as follows, using archeopyle development as a practical means of distinction of the major dinoflagellate groups:

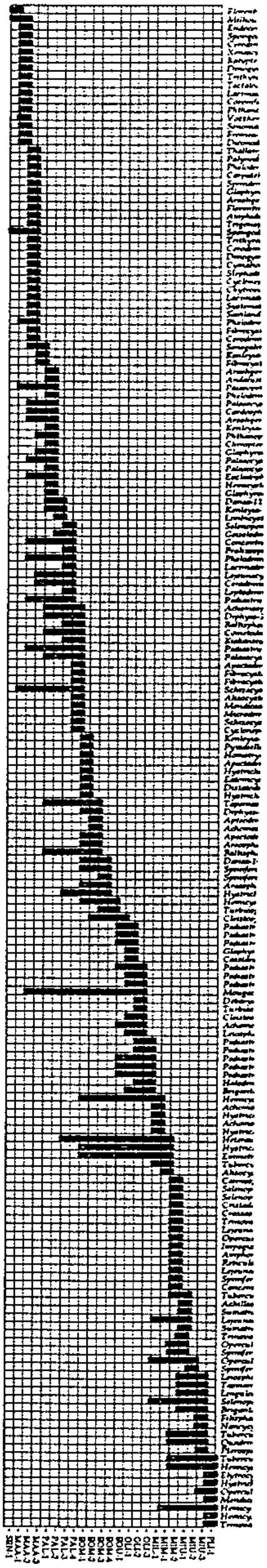
Apical archeopyles
Precingular archeopyles
Intercalary archeopyles
Combination archeopyles
Acritarchs and other algae (freshwater, brackish, or marine)

Under some species entries the following designations are used to indicate extension of ranges upwards or downwards:

H= occurs higher L=occurs lower

The ranges of a few species are constrained adequately by core or outcrop samples to be labelled "C" which indicates that the species is believed to be confined to the interval under discussion.

In the Notes on Identification, the genera are discussed roughly in order of grouping in the zonal scheme. The genus under discussion is placed in bold face and underlined (e.g. **<u>Florentinia</u>**). Other genera cited in comparison are placed only in bold face (e.g. **Hystrichokolpoma**) at their first mention. All other citations of genera are neither underlined nor placed in italics to allow quick identification of the start of each generic discussion.



<u>Senonian through Pliocene zonation based on dinoflagellates and other organic walled algal microfossils, Western Venezuela</u>

Range tops (Last Appearance Datums) are based on well cores, well cuttings, and outcrop

# C. The Zonation in Outline

In this outline, the species with significant last appearances are arranged in alphabetical order. Other species are cited and also designated with the suffix "H" to indicate that the species occurs higher, "L" to indicate lower occurences, and "C" to indicate that these species occuring in core or outcrop appear to be confined to the interval under discussion.

In succeeding sections, the zones are discussed in more detail and the species are grouped into morphological categories to facilitate identification. The attached range chart summarizes the distribution of the important species, emphasizing their last appearance datums (LAD s) and plotting their most likely lowest occurences, taking into account the effects of caving in those assemblages extracted from cuttings samples.

For obvious reasons, actual species numbers are not given but all species are described in detail with colour photographs of representative specimens at critical focus levels and are part of the Maraven palynostratigraphic system.

## Senonian Zones

### Zone SEN-1

SLA-8-2X 17370-80'

Florentinia-
Millioudodinium-(H)
Spongodinium-(H)

## Maastrichtian Zones

### Zone MAA-1

Vega de Asa (superficial-RH)

Cerodinium-
Coronifera-
Diconodinium-
Dinogymnium-
Endoceratium-
Fromea-
Kalyptea-
Laciniadinium-
Millioudodinium-(L)

Palaeoperidinium-
Phelodinium-
Phthanoperidinium-
Schizocystis-
Senoniasphaera-
Senoniasphaera-
Spongodinium-
Tectatodinium-
Trithyrodinium-
Vozzhennikovia-
Xenascus-

## Zone MAA-2

SLA-8-2X 15820-16690'
Rio Guaruries (superficial)

Achomosphaera/Spiniferites spp.
Amphidiadema-
Areoligera-
Areoligera-
Carpatella-
Cerodinium-
Cerodinium-
Chytroeisphaeridia-
Concentrecystis-
Cyclonephelium-
Cymatiosphaera-
Dinogymnium -
Fibrocysta-
Florentinia-
Glaphyrocysta-
Laciniadinium-
Palaeocystodinium-
Palaeoperidinium-
Palynodinium-
Phelodinium-
Phelodinium-
Phelodinium-
Samlandia-
Senegalinium-
Spinidinium-
Spongodinium-
Stephodinium-
Systematophora-
Thallasiphora-
Trigonophyxidia-
Trithyrodinium-

## Zone MAA-3

SLA-4-2X 15740-60'
SLA-8-2X 15800-20'

Cerodinium-(H)
Concentrecystis-(H)
Cordosphaeridium-(H)
Fibrocysta-
Glaphyrocysta-
Kenleyia-
Lejeunecysta-(H)
Palaeocystodinium-(H)
Pediastrum-(H)
Pediastrum-(H)
Senegalinium-

The presence of Tuberculodinium- and Selenopemphix- at 15800-10' at the top of this interval in SLA-8-2X is due to Neogene caving, and the presence of Selenopemphix-at 15770' in this well may be due to contamination from higher Paleogene caving.

# Paleocene Zones

## Zone PAL-1

SLA-4-2X 15600-630'
SLA-8-2X 15700-780'
ALT-11 12570'nucleo
Mesa Bolivar-La Palmita superficial
GUA-1-SX, 11890-900' (?)

Achomosphaera-(H)
Andalusiella-
Areoligera-
Areoligera-
Baltisphaeridium-
Chiropteridium-
Cometodinium-(H)
Cordosphaeridium-
Danea-(H)
Diphyes-(H)
Eocladopyxis-
Glaphyrocysta-
Glaphyrocysta-
Hemicystodinium-
Kenleyia-
Palaeocystodinium-
Palaeocystodinium-(H)
Palaeocystodinium-

Palaeocystodinium-
Palaeoperidinium-
Phelodinium-
Phthanoperidinium-

## Zone PAL-2

ALT-11, 12511-12570'

Danea-
Kenleyia-
Limbicysta-

## Zone PAL-3

ALT-11, 12417-12502'

Cerodinium-(L)
Concentrecystis-1108 (L)
Geiselodinium-1106 (L)
Laciniadinium-1112 (C)
Lejeunecysta-1114 (L)
Leptodinium-1117 (C)
Pediastrum-1120 (L)
Phelodinium-1111 (C)
Prolixosphaeridium-1110 (C)

## Zone PAL-4

ALT-11, 12096-12405'

Alisocysta-1126 (C)
Apectodinium-1122 (C)
Baltisphaeridium-(L)
Cometodinium-(L)
Cyclonephelium-(C)
Diphyes-(L)
Fibrocysta-(C)
Fibrocysta-(C)
Hystrichostrogylon-(H)
Kiokansium-(L)
Mendicodinium-(C)
Microdinium-(C)
Palaeocystodinium-(L)
Pediastrum-(L)
Schizocystis-(L)
Schizocystis-(C)

Although several of the above species in Zone PAL-4 are listed as confined to the zone, this may be due in part to a major environmental shift which occurred in the Upper Paleocene Marcellina Fm overlying Zone 4.

# Eocene Zones

## Middle Eocene

### Zone EOM-1

Pica Pica 1X, 2917-3140'
Corpoven 15-GU-507, 3971-4261

Apectodinium-
Distatodinium-
Eatonicysta-
Hystrichokolpoma-
Hystrichosphaeridium-
Kenleyia-

### Zone EOM-2

Pica Pica 1X, 2660-2877'
Corpoven 15-GU-507, 3902-3916

This is a very diverse interval with considerable variation of species composition. The species cited below are more common or more persistant to the top of the zone:

Achomosphaera-
Apectodinium-
Apteodinium-
Areosphaeridium-
Diphyes-
Heteraulacacysta-
Tapeinosphaeridium-

Lower in the zone, the following LAD's occur:

Cleistosphaeridium-
Homotryblium-
Selenopemphix-

And at the bottom these LAD's occur:

Adnatosphaeridium-
Cannosphaeropis-

## Zone EOM-3

Pica Pica-1X, 1170-2500'
Corpoven 15-GU-507, 3886-3895'

These LAD's occur at or near the top:

Areosphaeridium-
Danea-
Spiniferites-

At lower levels the following species terminate ranges:

Emmetrocysta-
Hystrichostrogylon-
Spiniferites-

## Zone EOM-4

Pica Pica 1X, 220-240'

Hemicystodinium-
Turbiosphaera-

## Upper Eocene

## Zone EOU-1

GUA 1-SX, 11220-11750'

Cleistosphaeridium-
Hemicystodinium-

In the lower part, the LAD's of Pediastrum- and Concentricystis-.

# Oligocene Zones

GUA-1SX, 9310-11210'

## Zone OLI-1

Cassidium-
Pediastrum-
Pediastrum-
Pediastrum-

## Zone OLI-2

Achomosphaera-
Cleistosphaeridium-
Debarya-
Glaphyrocysta-
Leiosphaeridia-
Mougeotia-
Pediastrum-
Pediastrum-
Pediastrum-
Turbiosphaera-

## Zone OLI-3

Brigantedinium-
Halodinium-
Hystrichokolpoma-
Pediastrum (H)
Pediastrum-
Pediastrum-
Pediastrum-
Pediastrum-

# Miocene Zones

### Lower Miocene

## Zone MIL-1

TOC 1-S, 4420-4480'
Hambalek thesis, NNH 170-195

Achomosphaera-
Achomosphaera-
Hemicystodinium-
Heteraulacacysta-(H)
Hystrichokolpoma-
Hystrichosphaeropsis-

### Middle Miocene

## Zone MIM-1

TOC 3067-3110'

Alisocysta-
Emmetrocysta-
Heteraulacacysta-
Hystrichokolpoma-
Tuberculodinium-

## Zone MIM-2

TOC 1-S, 1730-2240'
Hambalek thesis, NHH 148-166 (probably truncated in the mddle part)

*Lower part:*

Impagidinium-
Reticulatosphaera-

*Middle part:*

Lejeunecysta-
Lejeunecysta-
Operculodinium-
Spiniferites-
Trinovantedinium-

*Upper part:*

Amphorosphaeridium-
Cannosphaeropsis-
Concentrecystis-
Crassosphaera-
Cristadinium-
Selenopemphix-
Selenopemphix-

## Zone MIU-1

Hambalek thesis NHH 123-132
TOC 1S, 1340-1580'

Achilleodinium-
Lejeunecysta-
Operculodinium-
Spiniferites-
Sumatradinium-
Sumatradinium-

Trinovantedinium-
Tuberculdoinium-

## Zone MIU-2

TOC 1-S, 1040-1280'

Operculodinium-
Spiniferites-

## Zone MIU-3

TOC 1-S, 650-980'
Hambalek thesis, NHH 220-101

Brigantedinium-
Filisphaera-
Leiosphaeridia-
Lingulodinium-
Nancycysta-
Pterospermella-
Quadrina-
Selenopemphix-
Tasmanites-
Tuberculodinium-

# Pliocene Zones

## Zone PLI-1

TOC 1-S, 460-490'
Hambalek thesis, NHH 217-218

Elytrocysta-
Hemicystodinium-
Hemicystodinium-
Hemicystodinium-
Hystrichogonyaulax-
Mendicodinium-
Operculodinium-
Trinovantedinium-
Tuberculodinium-

# D. Discussion of Senonian Zones

## Zone SEN-1

SLA-8-2X 17370-80'

**Florentinia-**
**Millioudodinium-(H)**
**Spongodinium-(H)**

*Notes on identification*

**Florentinia** is a skolochorate cyst with a precingular archeopyle, intratabular processes of which those in the cingular region are smaller, and often with a distinctively larger antapical process. It resembles **Hystrichokolpoma** which is common in the Tertiary but which has an apical archeopyle. It can also be confused with **Hystrichosphaeridium** which, however, has processes of similar sizes in all positions, and with **Oligosphaeridium** which may show a tendency for the antapical process(es) to be somewhat larger than those elsewhere but which does not have any processes in the cingular region.

**Millioudodinium** is a gonyaulacacean proximate cyst with an autocyst, which immediately distinguishes it from **Gonyaulacysta** which is bicavate but which also has strong sutural ornament, a prominent apical horn, and a precingular archeopyle as in Millioudodinium. **Apteodinium** is similar but does not have sutural ornament or only very obscure and inconsistently expressed ornament.

**Spongodinium** is a proximate cyst with a highly distinctive spongey wall, the vesiculation and thickening usually occurring in the cingular region but also along certain parts of the sutural regions. No other cysts show this distinctive spongey structure to such a high degree, although there are some genera which show very complex alveolar but thinner walls but which are not differentiated markedly in their development e.g. **Fibrocysta** and **Operculodinium** which however are distinctly skolochorate. Some species of **Apteodinium** may show alveolar tissue in the wall but again this is not markedly and differentially thickened.

# E. Lower-Middle Maastrichtian Zones

## Zone MAA-1

Vega de Asa (superficial-RH)

**Dinogymnium-,Endoceratium-,Fromea--,Senoniasphaera-,Xenascus-**

**Coronifera-,Millioudodinium-(L),Spongodinium-,Tectatodinium-**

**Cerodinium-,Diconodinium-,Kalyptea-,Phelodinium-,Phthanoperidinium-,Trithyrodinium-Vozzhennikovia-**

**Laciniadinium-, Palaeoperidinium-**

**Schizocystis-**

*Notes on identification*

**Dinogymnium** is characterized by sub-parallel longitudinal folds and a distinct depressed cingulum. It looks like no other dinocyst but may be confused with ephedroid pollen on cursory examination. Species are recognized on the relative length and width of the cyst and on the distinctive nature of the apical end which carries an atypically small apical archeopyle. Some species are extremely large, very long, and attenuated and may be confused with plant vascular tissue (e.g. tracheids, vessels) and vice versa. It is believed on the basis of ultrastructural examination that Dingymnium may be a gymnodinioid pellicular cyst and not a hypnozygotic cyst which most other fossils appear to be.

**Endoceratium** is circumcavate with sutural ridges, apical archeopyle with offset sulcal notch, and 3 horns - apical, antapical, and cingular. **Pseudoceratium** has a similar shape but is not cavate and does not have sutural ridges.

**Fromea** has an atypical apical archeopyle but is not folded and therefore not confused with **Dinogymnium.**

**Senoniasphaera** is circumcavate and may have sutural ornament or none; it is distinguished from **Endoceratium** by the lack of prominant horns.

**Xenascus** is another ceratioid cyst but its cornucavate wall layers, two unequal lateral horns, and irregular shaped horns together with other projections clearlyh distinguish it from **Endoceratium.**

<u>Coronifera</u> is skolochorate with numerous non-tabular processes, a single larger antapical process, and a precingular archeopyle. **Diphyes** which is common in the Tertiary is similar but has an apical archeopyle and tends to have processes open at the end.

<u>Tectatodinium</u> is a proximate cyst with a precingular archeopyle and a very complex wall structure which was originally likened to the tectate wall of a pollen grain. Recent work on Tertiary species from mid-latitudes indicates that ultrastructurally there is a lot of variation in details of the structure of the wall. The Cretaceous species recognized here is probably not strictly part of the genus but it does have a very thick and complex wall similar to pollen.

<u>Cerodinium</u> is part of a complex of rather similar genera all characterized by cavate walls, little ornament, cingula defined by sutural ridges, and hexa-style intercalary archeopyles. There is still a lot of debate as to whether horn development, pericoel development, or archeopyle development should be considered of prime importance in recognizing genera. **Cerodinium** (also called **Ceratiopsis** in earlier literature) is characterized by cornucavation (with a slight tendency to circumcavation), an isodeltaform archeopyle, and two symmetrical antapical horns. It is distinguished from **Deflandrea** (which probably does not occur in low latitudes) by the well defined horns which tend to project outwards and which are without pericoelar connection (or very little) and the narrower archeopyle which in contrast is very broad in Deflandrea which may also be distinctly circumcavate. However, some authors consider these two genera to be synonymous. It is also noteworthy that Cerodinium is often ornamented or has a wrinkled periphragm, these features being sub-parallel and meridionally distributed along the longitudinal axis.

<u>Phelodinium</u> is distinguished from **Cerodinium** by an archeopyle with a relatively narrow width relative to width of the cyst, and which tends to have an adcingular margin very close to the cingulum. The antapical horns in Phelodinium are typically smaller, pointed, and wider apart than in Cerodinium. However, there is some gradation of these characters and generic assignment can be difficult. **Senegalinium** is a cornucavate genus with small more or less equal antapical horns but these are not as wide apart as in Phelodinium; further, Senegalinium is said to have an epipericoel which is not in communication with the exterior via the archeopyle (cf. **Alterbia** which does have this communication and which also has assymetric antapical horns) .

<u>Trithyrodinium</u> has the same basic structure as **Phelodinium** except that it has a 3-plate intercalary archeopyle and the periphragm is typically diaphanous and often torn or even completely missing. **Ginginodinium** is similar except that it has pandasutural features delimiting tabulation.

Phthanoperidinium is a proximate cyst with an apical horn and a rounded or cornate antapex. Peridiniacean hexa-style tabulation is indicated by sutural features and an intercalary archeopyle. It is distinct from **Palaeoperidinium** which has more prominant antapical horns and a transapical suture forming the archeopyle. Additionally the wall of Palaeoperidinium may be cornucavate to circumcavate.

Laciniadinium may be similar in shape to **Palaeoperidinium** or it can be biconical and it also has a transapical suture but this skirts around the base of the apex due to the exclusion of all apical plates in the archeopyle.

Diconodinium is biconical with only one antapical horn, a cingulum defined by sutural features, non-tabular granules or spines, and an intercalary archeopyle. Vozzhennikovia is similar but has a second antapical horn and is cornucavate.

Kalyptea may have a biconical form and the type species has an intercalary archeopyle. The Cretaceous species described here does not show an archeopyle but the surrounding cloak with complex structure is diagnostic.

# F. Upper Maastrichtian Zones

## Zone MAA-2

SLA-8-2X 15820-16690'
Rio Guaruries (superficial)

**Areoligera-,Chytroeisphaeridia-,Cyclonephelium-DinogymniumGlaphyrocysta,Palynodinium- Spongodinium-SystematophoraTrigonophyxidia-**

**Achomosphaera/Spiniferites spp.,Carpatella-,Fibrocysta-,Florentinia-Samlandia-Stephodinium-,Thallasiphóra-**

**Amphidiadema-,Cerodinium-, Laciniadinium-,Palaeocystodinium-,Palaeoperidinium-Phelodinium, Senegalinium-,Spinidinium-,Trithyrodinium-**

**Concentrecystis-,Cymatiosphaera-**

*Notes on identification*

**Areoligera** is one of several genera with lenticular shape, prominant ornament in the lateral areas and none or very little in the mid-ventral and mid-dorsal areas, together with an apical archeopyle with an offset sulcal notch and usually an assymetric antapex. Areoligera is characterized by complexly branched processes arranged in arcuate penitabular process groups. It is distinguished from **Glaphyrocysta** (which is typically but not exclusively a Tertiary genus) by the lack of trabeculae connecting the ends of the process groups. **Cyclonephelium** is common in the Cretaceous but has subdued ornament (granules, spines) in the lateral areas.

**Palynodinium** is also lenticular with large apical archeopyle and offset sulcal notch and may be confused with some of the above genera on cursory examination but is clearly distinct on the basis of pericoelar development on the right and left sides of the cyst which are also separated by a pronounced indentation on the ventral side giving a reniform outline. Prominant processes occur laterally and on the dorsal surface. **Renidinium** is similar but has penitabular ridges and folds on the periphragm rather than gonal and intergonal processes as in Palynodinium.

**Systematophora** may be confused with **Areoligera** but it is subspherical, has a symmetrical apical archeopyle, uniform process development centrally and laterally, and the processes are arranged in rectilinear, arcuate, or circular process groups for all the major series, together with a few isolated processes. Like Areoligera, the processes are not connected distally. **Hystrichosphaerina** is similar to Systematophora but has the process groups connected distally by trabeculae. **Emmetrocysta** is somewhat similar to Hystrichosphaerina but does not have process groups in the cingular region.

<u>Spongodinium</u> is a proximate cyst with a highly distinctive spongey wall, the vesiculation and thickening usually occurring in the cingular region but also along certain parts of the sutural regions. No other cysts show this distinctive spongey structure to such a high degree, although there are some genera which show very complex alveolar but thinner walls but which are not differentiated markedly in their development e.g. **Fibrocysta** and **Operculodinium** which however are distinctly skolochorate. Some species of **Apteodinium** may show alveolar tissue in the wall but again this is not markedly and differentially thickened.

<u>Chytroeisphaeridia</u> is an essentially featureless proximate cyst with an apical archeopyle. There has been considerable discussion as to whether the archeopyle is apical or precingular. For these purposes, the genus is used for cysts with clearly apical archeopyles. **Tapeinosphaeridium** is similarly featureless but with a precingular arhceopyle. Although in theory the distinction between apical and precingular archeopyles is clear, in practise on featureless cysts which may be crumpled and folded, proper diagnosis of the archeopyle is extremely difficult and may be impossible.

<u>Dinogymnium</u> is characterized by sub-parallel longitudinal folds and a distinct depressed cingulum. It looks like no other dinocyst but may be confused with ephedroid pollen on cursory examination. Species are recognized on the relative length and width of the cyst and on the distinctive nature of the apical end which carries an atypically small apical archeopyle. Some species are extremely large, very long, and attenuated and may be confused with plant vascular tissue (e.g. tracheids, vessels) and vice versa. It is believed on the basis of ultrastructural examination that Dingymnium may be a gymnodinioid pellicular cyst and not a hypnozygotic cyst which most other fossils appear to be.

<u>Trigonopyxidia</u> is typically a circumcavate cyst with a triangular outline for both the pericyst and sometimes the endocyst and an apical archeopyle. It is unlikely to be confused with any other dinoflagellate genera but may resemble some acritarchs such as **Veryhachium** which however are single-walled and more typical of the lower Mesozoic and Paleozoic. **Palaeotetradinium (=Inversidinium)** has a quadrate diamond-shaped outline to the pericyst but the endocyst may be triangular. Some spores may simulate Trigonopyxidia but they are usually trilete and do not have an archeopyle.

The <u>Achomosphaera-Spiniferites</u> complex represents a significant problem, particularly so because they are common and may be the only dinoflagellate cysts in inner neritic or lagoonal environments. Both genera are characterized by proximo-chorate or skolochorate cysts with precingular archeopyles and with prominant gonal and intergonal bifurcate or trifurcate processes forked to the 2nd or higher orders. **Achomosphaera** does not have connecting sutural crests whereas **Spiniferites** (**Hystrichosphaera** in the older literature) has prominant sutural crests connecting the process bases together. In practise, the distinction is not always clear (due in part to folding of processes together simulating crests) and there are many gradational forms. Furthermore, it is difficult to describe and illustrate the subtle features which may characterize the species. Size of processes, shape of cross section, nature of the branching, ordination, wall structure, and so on all seem to be important and there are many species described in the literature in attempts to discriminate species. Many of these species have been subsequently misidentified. A few species are described in this study which are particularly distinctive but there are many more which have not been addressed. For paleoenvironmental purposes, the general category Achomosphaera/Spinferites spp. is used. Other genera which are close to Achomosphaera/Spiniferites include **Hystrichosphaeropsis, Rottnestia,** and **Hystrichostrogylon** which are discussed later.

Carpatella is a proximate cyst with apical horn, an antapical protrusion, and a precingular archeopyle together with some sutural features such as cingulum. **Apteodinium** and **Millioudodinium** are similar but lack the antapical protrusion.

Fibrocysta is skolochorate, ovoidal, with many non-tabular, fibrous, hollow or solid processes and a precingular archeopyle but the body is extended by apical and antapical protrusions somewhat similar to those in **Carpatella** (which, however, is proximate). It is distinguished from **Turbiosphaera** by the non-tabular rather than intra-tabular processes; furthermore, Turbiosphaera has a distinctive cingular shelf-like structure and has a mixture of large and small processes, the larger ones being wider and flatter. **Kenleyia** has apical and antapical protrusions but lacks the distinct processes of Fibrocysta, instead having low poorly defined projections and lamellar structures. **Amphorosphaeridium** is similar to Fibrocysta but does not have the apical and antapical protrusions and is spherical rather than ellipsoidal and has complex branching of the processes. **Exochosphaeridium** is a spherical skolochorate cyst with precingular archeopyle and fibrous non-tabular processes but these are solid rather than hollow and the apical processes may be longer or otherwise distinctive.

Florentinia is a skolochorate cyst with a precingular archeopyle, intratabular processes of which those in the cingular region are smaller, and often with a distinctively larger antapical process. It resembles **Hystrichokolpoma** which is common in the Tertiary but which has an apical archeopyle. It can also be confused with **Hystrichosphaeridium** which, however, has processes of similar sizes in all positions, and with **Oligosphaeridium** which may show a tendency for the antapical process(es) to be somewhat larger than those elsewhere but which does not have any processes in the cingular region.

Samlandia (**Palmnickia** in older literature) is a proximate holocavate cyst with reticulate structures covered by ectophragm and a precingular archeopyle. Its structure is quite distinctive and unlikely to be confused with any other taxa in the upper Mesozoic-Cenozoic.

Stephodinium is a camocavate cyst with a spherical endocyst and greatest pericoelar development in the cingular - particularly dorsal cingular - areas. Other camocavate cysts such as **Hystrichostrogylon** have greatest pericoelar development ventrally and in addition have gonal processes.

Thallasiphora is also a camocavate cyst with precingular archeopyle but the wall layers are appressed dorsally and ballooned outwards elsewhere. It is similar in gross structure to **Stephodinium** but has opposite appression and lacks a cingulum which is a prominant feature of Stephodinium.

Amphidiadema is bicavate, elongate, and with an intercalary archeopyle and no real horns. Its bicavate structure distinguishes it from **Deflandrea** and allied genera.

Cerodinium is part of a complex of rather similar genera all characterized by cavate walls, little ornament, cingula defined by sutural ridges, and hexa-style intercalary archeopyles. There is still a lot of debate as to whether horn development, pericoel development, or archeopyle development should be considered of prime importance in recognizing genera. **Cerodinium** (also called **Ceratiopsis** in earlier literature) is characterized by cornucavation (with a slight tendency to circumcavation), an isodeltaform archeopyle, and two symmetrical antapical horns. It is distinguished from **Deflandrea** (which probably does not occur in low latitudes) by the well defined horns which tend to project outwards and which are without pericoelar connection (or very little) and the narrower archeopyle which in contrast is very broad in Deflandrea which may also be distinctly circumcavate. However, some authors consider these two genera to be synonymous. It is also noteworthy that Cerodinium is often ornamented or has a wrinkled periphragm, these features being sub-parallel and meridionally distributed along the longitudinal axis.

Phelodinium is distinguished from **Cerodinium** by an archeopyle with a relatively narrow width relative to width of the cyst, and which tends to have an adcingular margin very close to the cingulum. The antapical horns in Phelodinium are typically smaller, pointed, and wider apart than in Cerodinium. However, there is some gradation of these characters and generic assignment can be difficult. **Senegalinium** is a cornucavate genus with small more or less equal antapical horns but these are not as wide apart as in Phelodinium; further, Senegalinium is said to have an epipericoel which is not in communication with the exterior via the archeopyle (cf. **Alterbia** which does have this communication and which also has assymetric antapical horns) .

Palaeocystodinium comprises generally large fusiform cornucavate cysts with a large prominent pointed apical horn and similarly large pointed antapical horn and a deltaform intercalary archeopyle. **Andalusiella** is similar except that the antapex carries two prominent horns which are close together or with confluent bases. Additionally, some species of Andalusiella may show a cingulum. Species of Palaeocystodinium with an antapical spur on the horn are distinguished from Andalusiella by the fact that the spur is near the tip than the base of the horn.

Laciniadinium may be similar in shape to **Palaeoperidinium** (or it can be biconical) and it also has a transapical suture but this skirts around the base of the apex due to the exclusion of all apical plates in the archeopyle.

Palaeoperidinium has prominant apical andantapical horns and a transapical suture forming the archeopyle which includes apical, intercalary, and precingular plates. Additionally the wall of Palaeoperidinium may be cornucavate to circumcavate, and it may have quasi-tabular ridges in the apical region and pandasutural striations elsewhere. **Saeptodinium** is somewhat similar to Palaeoperidinium with the same archeopyle, but it either lacks or has poorly developed apical and antapical horns.

Trithyrodinium has the same basic structure as **Phelodinium** except that it has a 3-plate intercalary archeopyle and the periphragm is typically diaphanous and often torn or even completely missing. **Ginginodinium** is similar except that it has pandasutural features delimiting tabulation.

Spinidinium is a small cornucavate to circumcavate cyst with apical horns and strongly assymetric antapical horns. Pandasutural regions are smooth and intratabular regions are provided with cones or spines indicating hexa-style peridiniacean tabulation. Archeopyle is interalary as in **Vozzhennikovia** which, however, has non-tabular spines. **Ginginodinium** is similar to Spinidinium but has a 3-plate intercalary archeopyle.

# G. Highest Maastrichtian-Lowest Paleocene Zones

SLA-4-2X, 15600-15760'
SLA-8-2X 15700-15820'
ALT-11 12570' nucleo
Mesa Bolivar-La Palmita superficial
GUA 1-SX, 11890-900' (?)

This interval covers the top Mito Juan and the Guasare Formations and on the basis of associated spore-pollen floras is believed to span the highest Maastrichtian and lowest Paleocene. The highest Maastrichtian assemblage as defined here post-dates the last occurence of Palynodinium- which is often taken as a Cretaceous/Tertiary boundary marker, but this assemblage occurs in a stratigraphic interval - the Mito Juan Fm - usually interpreted as Maastrichtian and lies below the Guasare Fm which is believed to be Paleocene. Whether it eventually proves to be below the Cretaceous-Teritary boundary or above it is less important for basinal correlation than the fact that it includes significant tops of range zones and associated diagnostic elements of use in subsurface correlation.

## Highest Maastrichtian:

### Zone MAA-3

SLA-4-2X 15740-60'
SLA-8-2X 15800-20'

**Glaphyrocysta-**

**Cordosphaeridium-(H),Fibrocysta-,Kenleyia-**

**Cerodinium-(H),Lejeunecysta-(H),Palaeocystodinium-(H),Senegalinium-**

**Pediastrum-(H),Concentrecystis-(H)**

The presence of Tuberculodinium- and Selenopemphix- at 15800-10' at the top of this interval in SLA-8-2X is due to Neogene caving, and the presence of Selenopemphix- at 15770' in this well may be due to contamination from higher Paleogene caving.

## Lowest Paleocene:

### Zone PAL-1

SLA-4-2X 15600-630'
SLA-8-2X 15700-780'
ALT-11 12570'nucleo
Mesa Bolivar-La Palmita superficial
GUA-1-SX, 11890-900' (?)

**Achomosphaera-(H),Danea-(H),Kenleyia-,Cordosphaeridium-**
**-**

**Areoligera-,Chiropteridium-,Cometodinium-(H),Diphyes-(H),Glaphyrocysta-**

**Andalusiella-,Palaeocystodinium-, Phelodinium-**
**Phthanoperidinium-**

**Eocladopyxis-,Hemicystodinium-,Palaeoperidinium-**

**Baltisphaeridium-**

*Notes on identification*

The **Achomosphaera-Spiniferites** complex represents a significant problem, particularly so because they are common and may be the only dinoflagellate cysts in inner neritic or lagoonal environments. Both genera are characterized by proximo-chorate or skolochorate cysts with precingular archeopyles and with prominant gonal and intergonal bifurcate or trifurcate processes forked to the 2nd or higher orders. **Achomosphaera** does not have connecting sutural crests whereas **Spiniferites (Hystrichosphaera** in the older literature) has prominant sutural crests connecting the process bases together. In practise, the distinction is not always clear (due in part to folding of processes together simulating crests) and there are many gradational forms. Furthermore, it is difficult to describe and illustrate the subtle features which may characterize the species. Size of processes, shape of cross section, nature of the branching, ordination, wall structure, and so on all seem to be important and there are many species described in the literature in attempts to discriminate species. Many of these species have been subsequently misidentified. A few species are described in this study which are particularly distinctive but there are many more which have not been addressed. For paleoenvironmental purposes, the general category Achomosphaera/Spinferites spp. is used. Other genera which are close to Achomosphaera/Spiniferites include **Hystrichosphaeropsis, Rottnestia,** and **Hystrichostrogylon** which are discussed later.

**Cordosphaeridium** is a fibrous skolochorate cyst with a precingular archeopyle and fibrous solid or hollow intratabular processes in all major series. **Fibrocysta** has a similar fibrous structure but is ovoidal, with many non-tabular, fibrous, hollow or solid processes and a precingular archeopyle but the body is extended by apical and antapical protrusions.
Cordosphaeridium is distinguished from **Turbiosphaera** which is also fibrous

with intra-tabular processes but this genus has a distinctive cingular shelf-like structure and has a mixture of large and small processes, the larger ones being wider and flatter. **Kenleyia** is fibrous but has apical and antapical protrusions and low poorly defined projections and lamellar structures. **Amphorosphaeridium** is fibrous with mainly non-tabular processes of which the apical and antapical processes are usually distinctive. **Exochosphaeridium** is also a spherical skolochorate cyst with precingular archeopyle and fibrous non-tabular processes but these are solid rather than hollow and the apical processes may be longer or otherwise distinctive. It is possible that Amphorosphaeridium and Exochosphaeridium are synonymous. **Kleithriasphaeridium** has essentially the same general structure as Cordosphaeridium but it is non-fibrous with smooth or only very faintly striated processes.

Kenleyia is a fibrous proximochorate cyst with precingular archeopyle and fibrous sutural processes and apical and antapical protrusions on the body. The processes are discontinuous lamellar structures with tuft-like processes in gonal position, and the cingulum is marked by low ridges.

Tapeinosphaeridium is a small to intermediate sized proximate autophragmal cyst with a featureless wall and precingular archeopyle. It is easy to confuse with **Chytroeisphaeridia** which is essentially the same but with an apical archeopyle. Practical difficulties occur in attempting to interpret archeopyles in such featureless cysts; in fact, the status of Chytroeisphaeridia is in doubt since the type specimen might have an intercalary rather than apical archeopyle. For our purposes, the two genera will be kept distinct, but the effort in distinguishing species in this type of featureless cyst might preclude their everyday application in exploration biostratigraphy.

Areoligera is one of several genera with lenticular shape, prominant ornament in the lateral areas and none or very little in the mid-ventral and mid-dorsal areas, together with an apical archeopyle with an offset sulcal notch and usually an assymetric antapex. Areoligera is characterized by complexly branched processes arranged in arcuate penitabular process groups. It is distinguished from Glaphyrocysta (which is typically but not exclusively a Tertiary genus) by the lack of trabeculae connecting the ends of the process groups. In Glaphyrocysta, the process groups are arcuate or annulate and are complexly branched and joined together within and between groups by a network of trabeculae which may be simple strands or complexly branched or fenestrate. Chiropteridium is also lenticular with an apical archeopyle and offset sulcal notch and with processes joined into groups proximally. The process groups tend to be developed laterally but are absent or reduced in size and number ventrally, unlike in Areoligera where both the dorsal and ventral surfaces are consistantly free of processes. Chiropteridium differs from **Membranophoridium** in that the latter is cavate providing elongate sac-like structures in the lateral areas and totally lacks processes on the mid-dorsal and mid-ventral areas.

Cometodinium is a cyst characterized by numerous closely spaced hair-like processes. Recent work by Monteil has demonstrated that the genus is characterized by an apical archeopyle but this is extremely difficult to see. **Impletosphaeridium** may be similar to Cometodinium but it is so widely circumscribed as to be almost meaningless as a dinoflagellate-taxonomic concept.

Cerodinium is part of a complex of rather similar genera all characterized by cavate walls, little ornament, cingula defined by sutural ridges, and hexa-style intercalary archeopyles. There is still a lot of debate as to whether horn development, pericoel development, or archeopyle development should be considered of prime importance in recognizing genera. **Cerodinium** (also called **Ceratiopsis** in earlier literature) is characterized by cornucavation (with a slight tendency to circumcavation), an isodeltaform archeopyle, and two symmetrical antapical horns. It is distinguished from **Deflandrea** (which probably does not occur in low latitudes) by the well defined horns which tend to project outwards and which are without pericoelar connection (or very little) and the narrower archeopyle which in contrast is very broad in Deflandrea which may also be distinctly circumcavate. However, some authors consider these two genera to be synonymous. It is also noteworthy that Cerodinium is often ornamented or has a wrinkled periphragm, these features being sub-parallel and meridionally distributed along the longitudinal axis. Cerodinium is similar at first glance to **Phelodinium** but the latter has an archeopyle with a relatively narrow width relative to total width of the cyst, and tends to have an adcingular margin of the arhceopyle very close to the cingulum. The antapical horns in Phelodinium are typically smaller, pointed, and wider apart than in Cerodinium. However, there is some gradation of these characters and generic assignment can be difficult.

Senegalinium is a cornucavate genus with small more or less equal antapical horns but these are not as wide apart as in Phelodinium; further, Senegalinium is said to have an epipericoel which is not in communication with the exterior via the archeopyle (cf. **Alterbia** which does have this communication and which also has assymetric antapical horns) .

Lejeunecysta is a cyst with a peridinioid pentagonal outline (sometimes angular, sometimes more rounded) but with an autophragm (which may occassionally separate into layers simulating cavation if the specimens are highly oxidized through weathering or laboratory preparation). The autophragm is usualy featureless other than for folds or very faint ornamentation; the archeopyle is large and wide, centered on the mid-line, and has an adcingular margin close to the cingulum as in **Phelodinium** , which, however, is cavate. and has a narrower archeopyle. The archeopyle is not always developed in Lejeunecysta. **Selenopemphix** is similar to Lejeunecysta but is usually compressed apically-antapically rather than dorso-ventrally and in addition the intercalary archeopyle of Selenopemphix is offset from the mid-line.

**Phthanoperidinium** is a proximate cyst with an apical horn and a rounded or cornate antapex. Peridiniacean hexa-style tabulation is indicated by sutural features and an intercalary archeopyle. It is distinct from **Palaeoperidinium** which has more prominant antapical horns and a transapical suture forming the archeopyle. Additionally the wall of Palaeoperidinium may be cornucavate to circumcavate.

**Palaeocystodinium** comprises generally large fusiform cornucavate cysts with a large prominent pointed apical horn and a similarly large pointed antapical horn and a deltaform intercalary archeopyle. **Andalusiella** is similar except that the antapex carries two prominent horns which are close together or with confluent bases. Additionally, some species of Andalusiella may show a cingulum. Species of Palaeocystodinium with an antapical spur on the horn are distinguished from Andalusiella by the fact that the spur is near the tip than the base of the horn. On the other hand, it is probable that these two genera are closely related and their might be some gradational morphotypes which do not fit neatly into either generic concept. Both genera are characteristic of high latitudes, and it would seem that Andalusiella is confined largely to the equatorial and sub-equatorial belt from South America to central and North Africa and southern Europe. Frequently, either genus can suffer detachment of the apical horn when the archeopyle opens leading to possible misidentification as **Odontochitina**, which, however, is ceratioid with an apical archeopyle. Odontochitina is common in the mid-latitudes to the top of the Cretaceous but is rare or absent in the tropical Upper Cretaceous.

**Eocladophyxis** is a skolochorate cyst with numerous non-tabular processes and a network of sutural features (grooves or ridges) on the wall surface. The archeopyle involves most plates in the epicyst which fall apart individually or in groups. **Hemicystodinium** is somewhat similar with numerous hollow processes and an epicystal archeopyle but no sutural features on the wall surface.

**Pediastrum** is a colonial chlorophycean alga comprising disc-like masses of cells with generally pronounced radial structure, particularly in the peripheral region. The following notes explain the terminology used in describing species in the Maraven files.

Fossil specimens of Pediastrum can be regarded as being oblate spheroids comprising a *central disc*, generally circular in shape, surrounded by a *fringe* of different elements. The structure is that of a multicellular colony and the exact number of cells and the overall size will vary depending on the maturity of the specimen. One side of the colony is arbitrarily referred to as *obverse* and the other as *reverse.*

The colony may be single-layered (*unicameral*) or comprise several layers of cells (often *bicameral*, or sometimes more indicated by *tri-*, *tetra-*, etc.). In multicameral colonies, the cells comprising the fringe may be placed one above the other (*superimposed*) or be *offset* so that some or all of the underlying cell may be seen. The layering may be the same or different between the central cells and the peripheral cells.

From the centre of the central disc outwards to the fringe, the cells may be regarded as comprising a series of encircling rows termed *cycles*, each layer having its own cycle. Thus a colony - or part of a colony - may be *bicyclic, tricyclic, tetracyclic* etc.

The cells are of two different types : the central disc comprises the *central cells* which are surrounded by the *peripheral cells*. The fringe comprises the outer (*distal*) part of the peripheral cells, and this distal part may be referred to as the *fringe element*. The inner (*proximal*) part of the peripheral cells contributes to the central disc. Camerality in the peripheral cell cycles is indicated by the distinctive fringe elements which occur on the obverse and reverse sides. Occassionally the distal part of the central cells may be modified in a distinctive fashion.

The central cells may be *defined* with cell walls or other thickenings. Sometimes the central cells are *undefined*, perhaps due to resorbtion or other processes. The central cells may be *close-packed* with each cell abutting another on all sides. Central cells which are *loose-packed* do not touch their neighbours on all sides and the central disc is characterized by angular or rounded openings. Central cells may be *triangular, quadrangular, pentagonal*, or *hexagonal* in shape, or some rounded modification of these shapes.

The peripheral cells, particularly the fringe elements, usually have highly characteristic shapes. Those fringe elements with a simple triangular outline may be termed *pyramidal* when the basal width is equal to or greater than the height of the fringe part of the cell, or *conical* if the basal width is markedly less. These are general terms and obviously gradational; precise dimensions are needed for accurate description. Some peripheral cells are markedly constricted at their mid-length and are termed *flared*.

Peripheral cells may have a distal finger-like part termed *appendiform*, which may taper or be of constant width and *cylindrical*. This appendiform termination may have a*sharp, rounded*, or *bifid* tip. The appendiform termination is supported on a *base* which may have *convex, concave*, or *straight* sides. In the case of peripheral cells with a distinct base which is supported on a short parallel-sided *footing*, this condition is termed *chimeniform*.

The Maastrichtian-Paleocene species of Pediastrum are quite distinctive and different compared with those in the Eocene and Oligocene.

Mougeotia is a highly distinctive zygnematacean cyst whose prime feature is a levigate wall with an exceptionally high refractive index. This refraction is so high as to be confused at first glance with refraction associated with, for example, quartz grains. The wall is usually colourless but has a bright almost bluish appearance due to the high refraction. Mougeotia also often folds in a very distinctive manner with folds on one surface at right angles to those on the other, and where the folds intersect the amb, an angulation is created which may be quadrate.

<u>Concentrecystis</u> is a discoidal cyst which splits equatorially into two hemispheres. Each hemisphere is characterized by a series of concentric, coaxial thickenings parallel to the amb and more or less parallel to each other. The wall may be coloured and the cyst could be confused with striate spores or pollen.

# H. Lower Paleocene Zones

SLA-8-2X 15680-15780' Guasare Fm
ALT-11 12073-12570' Guasare Zones 14/15
Mesa Bolivar-La Palmita superficial

The very lowest Paleocene (**Zone PAL-1**) has already been discussed in the previous section for the above localities. The higher Lower Paleocene zones are defined on the basis of cores from Alturitas-11. Although the primary approach has been interval zones based on last appearance datums (LAD's), the presence of this cored section has allowed some first appearance datums (FAD'S) to be determined also.

## Zone PAL-2

ALT-11, 12511-12570'

**Danea-,Kenleyia-**

**Limbicysta-**

*Notes on identification*

**Kenleyia** is proximochorate with a precingular archeopyle, horn-like protrusions apically and antapically, a fibrous wall, and fibrous processes and lamellar structures which may be sutural in position, together with low features associated with the cingulum. **Fibrocysta** is generally somewhat similar but has longer more distinct processes and these appear to be non-tabular. **Turbiosphaera**, another fibrous genus, is similar to Kenleyia but has distinct processes which are intratabular, and a shelf-like structure marking the cingulum.

**Danea** is another proximochorate fibrous cyst with precingular archeopyle and it has an prominant apical projection and a smaller antapical projection or none at all. It is distinctive on account of its pentitabular septa or discontinuous sutural septa which distinguish it from **Kenleyia, Fibrocysta,** and **Turbiosphaera** discussed above. **Muratodinium** is quite similar to Danea but has only sutural septa rather than being mixed with penitabular septa.

**Limbicysta** is a cornucavate cyst with prominant horns including two in the cingular region. It was originally described from Late Cretaceous freshwater environments but it is possible that the specimens could be allochthonous and "washed in" to neritic environments from coastal-terrestrial freshwater or lagoonal environments.

## Zone PAL-3

ALT-11, 12417-12502'

**Leptodinium-(C)**

**Prolixosphaeridium-(C)**

**Cerodinium-(L),Geiselodinium-(L),Laciniadinium-(C),Lejeunecysta-(L),Phelodinium-(C)**

**Concentrecystis-(L),Pediastrum-(L)**

*Notes on identification*

**Leptodinium** is a proximo-chorate gonyaulacoid cyst with or without an apical horn, with a precingular archeopyle and characterized by strong sutural septa and a large 6". It therefore is distinguished from **Impagidinium** which has the same basic structure but is equipped with a triangular 6". **Millioudodinium** is somewhat similar but is proximate and has a strong apical horn and rather low sutural septa. All these genera are distinguished from **Gonyaulacysta** by their autophragm; in Gonyaulacysta the wall is 2-layered, the cyst is bicavate, and the sutural septa may be strongly ornamented.

Heteraulacacysta is a proximate or proximochorate gonyaulacoid dinoflagellate with anterior-posterior compression which leads to polar views quite frequently. It has an epicystal archepyle, and the tabulation is indicated by usually high and delicate sutural folds or septa with no ornment or only delicate ornament on the sutural features. It is similar to **Dinopterygium** which, however, has quite strong tubercles in the intratabular areas and may show a covering wall layer usually called ectophragm; in other words, the tubercles are developed between an inner and outer wall layer.

**Prolixosphaeridium** is an elongate, skolochorate cyst with an apical archeopyle and numerous, probably non-tabular, hollow processes with closed tips. **Tanyosphaeridium** is very similar but is distinguished by having processes with open tips and these are often relatively longer than in Prolixoshpaeridium. **Peridictyocysta** is a related genus with the solid processes arranged in longitudinal rows and connected together distally by a meshwork of trabeculae. **Distatodinium** is also elongate, skolochorate, with an apical archeopyle but has tubular or blade-like processes which are multiply bifurcate and some may be connected together by trabeculae.

Lejeunecysta is a cyst with a peridinioid pentagonal outline (sometimes angular, sometimes more rounded) but with an autophragm (which may occassionally separate into layers simulating cavation if the specimens are highly oxidized through weathering or laboratory preparation). The autophragm is usualy featureless other than for folds or very faint ornamentation; the archeopyle is large and wide, centered on the mid-line, and has an adcingular margin close to the cingulum as in **Phelodinium** , which, however, is cavate. and has a narrower archeopyle. The archeopyle is not always developed in Lejeunecysta.

Selenopemphix is similar to **Lejeunecysta** but is usually compressed apically-antapically rather than dorso-ventrally and in addition the intercalary archeopyle of Selenopemphix is offset from the mid-line. Selenopemphix-in polar view is characterized by strong cingular septa which are superimposed giving the outline a double-edged appearance. The cingular septa may be smooth or highly ornamented with serrations and spines. In most cases, the cingular ends overlap in a depressed area of the sulcus leading to a characteristic reniform outline in polar view.

Cerodinium is part of a complex of rather similar genera all characterized by cavate walls, little ornament, cingula defined by sutural ridges, and hexa-style intercalary archeopyles. There is still a lot of debate as to whether horn development, pericoel development, or archeopyle development should be considered of prime importance in recognizing genera. **Cerodinium** (also called **Ceratiopsis** in earlier literature) is characterized by cornucavation (with a slight tendency to circumcavation), an isodeltaform archeopyle, and two symmetrical antapical horns. It is distinguished from **Deflandrea** (which probably does not occur in low latitudes) by the well defined horns which tend to project outwards and which are without pericoelar connection (or very little) and the narrower archeopyle which in contrast is very broad in Deflandrea which may also be distinctly circumcavate. However, some authors consider these two genera to be synonymous. It is also noteworthy that Cerodinium is often ornamented or has a wrinkled periphragm, these features being sub-parallel and meridionally distributed along the longitudinal axis. Cerodinium is similar at first glance to Phelodinium but the latter has an archeopyle with a relatively narrow width relative to total width of the cyst, and tends to have an adcingular margin of the arhceopyle very close to the cingulum. The antapical horns in Phelodinium are typically smaller, pointed, and wider apart than in Cerodinium. However, there is some gradation of these characters and generic assignment can be difficult.

Laciniadinium may be similar in shape to Palaeoperidinium (or it can be biconical) and it also has a transapical suture but this skirts around the base of the apex due to the exclusion of all apical plates in the archeopyle. **Palaeoperidinium** has prominant apical andantapical horns and a transapical suture forming the archeopyle which includes apical, intercalary, and precingular plates. Additionally the wall of Palaeoperidinium may be cornucavate to circumcavate, and it may have quasi-tabular ridges in the apical region and pandasutural striations elsewhere. **Saeptodinium** is somewhat similar to Palaeoperidinium with the same archeopyle, but it either lacks or has poorly developed apical and antapical horns.

Geiselodinium is a peridinioid cyst with virtually no wall features other than very poorly developed apical and 2 antapical horns which are usually low and blunt. It is cavate with a very small pericoel. Thus its lack of features and poorly developed horns distinguish it from **Palaeoperidinium** and **Saeptodinium**.

## Zone PAL-4

ALT-11, 12096-12405'

**Alisocysta-(C),Cometodinium-(L),Cyclonephelium-(C),Diphyes-(L),Microdinium-(C)**

**Fibrocysta-(C),Hystrichostrogylon-(H),Kiokansium-(L)**

**Apectodinium-(C),Palaeocystodinium-(L)**

**Mendicodinium-(C)**

**Baltisphaeridium-(L),Pediastrum-(L),Schizocystis-(L)**

Although several of the above species in Zone PAL-4 are listed as confined to the zone, this may be due in part to a major environmental shift which occurred in the Upper Paleocene Marcellina Fm overlying Zone 4.

*Notes on identification*

Alisocysta is proximochorate with an apical archeopyle and penitabular ridges in all major series, the ridges bounding pandasutural regions with no ornament or uniform light ornament. **Eisenackia** is similar but has penitabular platforms with pandasutural dpressions inbetween.

Cometodinium is skolochorate, covered with closely spaced hair-like processes and may have a cingular feature. It has been proved to have an apical archeopyle but generally this is difficult to see and interpret.

Cyclonephelium is proximate with a rounded outline and with an assymetric antapical concavity and a large apical archeopyle with offset sulcal notch. Ornamentation is low and always reduced or lacking in the midventral and middorsal areas. **Glaphyrocysta** is related but has long processes which are connected together distally.

Diphyes is skolochorate with an apical archeopyle and numerous hollow non-tabular processes and a single larger and distinctive antapical process which often has a distal pore. **Coronifera** is similar but has a precingular archeopyle and there is a tendency for its processes to be open distally.

Microdinium is a small smooth proximate cyst with a short epicyst and a large apical archeopyle which may also include some intercalary plates. Sutural ridges outline a complex tabulation. **Fibradinium** is similar but has a fibrous autophragm. **Druggidium** is similar to Microdinium and Fibradinium in many respects but has a 2-plate precingular archeopyle.

Fibrocysta has been discussed earlier.

Hystrichostrogylon is skolochorate, camocavate, with gonal and intergonal bifurcate spines and ȃ precingular archeopyle. The first impression is that of a **Spiniferites** which is distorted and damaged, but closer examination shows the endophragm and periphragm with a pericoel which may ballon outwards on one side. There is sme difference of opinion as to whether the pericoel is better developed dorsally or ventrally.

Kiokansium is skolochorate with numerous nontabular solid processes and 2-plate precingular archeopyle. **Operculodinium** is similar but has a single-plate precingular archeopyle and partially hollow processes and often a complex wall. **Exochosphaeridium** is similar but has solid fibrous processes and a single-plate precingular archeopyle.

Apectodinium is a proximochorate cornucavate genus with a rounded or angular outline depending on whether all or only some horns are developed; at its maximum development there are apical, antapical, and 2 lateral horns. There are numerous short hollow brnached or simple processes in nontabular position. The archeopyle is intercalary in quadra style. **Wetzeliella** is related with strong pentagonal outline, often circumcavate, and with nontabular and intratabular processes and pandasutural features, but it is rare or absent in low latitudes.

**Palaeocystodinium** has been discussed earlier.

Mendicodinium is an essentially featureless cyst with an epicystal archeopyle. It may be uniformly or irregularly reticulate but has no sutural ornament.

# J. Middle Eocene Zones

Sections of the Lower Eocene and Upper Paleocene examined to date have not yielded dinoflagellates or other aquatic algae so no zonation is possible at this time.

The following two sections have yielded well preserved floras which allow zonation of some of the Middle Eocene on the basis of range tops (LAD's):

Pica Pica 1X, 220-3140'
Corpoven 15-GU-507, 3886-4261'

## Zone EOM-1

Pica Pica 1X, 2917-3140'
Corpoven 15-GU-507, 3971-4261

**Eatonicysta-,Distatodinium-,Hystrichosphaeridium-,Hystrichokolpoma-**

**Kenleyia-**

**Apectodinium-**

*Notes on identification*

**Eatonicysta** looks to be skolochorate but is characterized by a delicate outer wall (ectophragm) which covers or connects the processes when perfectly preserved. The processes are intratabular (none on the cingulum), solid, and fibrous and have at least traces of the ectophragm which may be smooth or distinctly reticulate, and the archeopyle is apical. **Adnatosphaeridium** has more processes and thhe tips are connected together by trabeculae which some consider to be traces of an ectophragm. **Areosphaeridium** is definitely skolochorate with solid fibrous intrtabular processes with platform-like distal terminations which may be perforate, arcuate, or denticulate, and is distinguished from Eatonicysta by the lack of ectophragm.

**Hystrichosphaeridium** is another skolochorate genus with apical archeopyle but the intratabular processes are hollow, open, often flared distally, and present and equally developed on all major series including the cingulum. **Oligosphaeridium** is similar but does not have cingular processes. **Surculosphaeridium** is essentially the same as Hystrichosphaeridium but the processes are solid rather than hollow. **Perisseiasphaeridium** is similar to Hystrichosphaeridium but has complxly branched intratabular processes except on the cingulum which features solid processes. **Hystrichokolpoma**

has processes of different shape on the cingulum and also has a distinctive antapical process. Areosphaeridium has solid processes with distinctive terminations. **Homotryblium** is similar to Hystrichosphaeridium but has an epicystal archeopyle.

Pyxidiella is a featurelss elongate ovoidal cyst with little or no ornament and an intercalary archeopyle.

## Zone EOM-2

Pica Pica 1X, 2660-2877'
Corpoven 15-GU-507, 3902-3916'

This is a very diverse interval with considerable variation of species composition. The species cited below are more common or more persistant to the top of the zone:

**Areosphaeridium-,Diphyes-**

**Achomosphaera-,Apteodinium-,Tapeinosphaeridium-**

**Apectodinium-**

**Heteraulacacysta-**

Lower in the zone, the following LAD's occur:

**Cleistosphaeridium-**

**Selenopemphix-**

**Homotryblium-**

And at the bottom these LAD's occur:

**Adnatosphaeridium-**

**Cannosphaeropis-**

*Notes on identification*

Most of these genera have been discussed above.

Cleistosphaeridium is a skolochorate cyst with apical archeopyle and numerous non-tabular processes or spines which are usually closed.

**Operculodinium** is similar but has a precingular archeopyle. **Hemicystodinium** is superficially similar but has an epicystal archeopyle.

Cannosphaeropsis is a skolochorate cyst with precingular archeopyle and with gonal processes with distal ends connected together by single-strand trabeculae which are inserted between the triradiate forks of the processes. **Nematosphaeropsis** is somewhat similar but the trabeculae may be single or paired and represent extensions of the trifurcate ends of the gonal processes.

## Zone EOM-3

Pica Pica-1X, 1170-2500'
Corpoven 15-GU-507, 3886-3895'

These LAD's occur at or near the top:

**Areosphaeridium-**

**Danea-,Spiniferites-**

At lower levels the following species terminate ranges:

**Emmetrocysta-**

**Hystrichostrogylon-,Spiniferites-**

*Notes on identification*

Most genera have been discussed above.

Emmetrocysta is a skolochorate cyst with with an apical archeopyle and intratabular process groups in all major series except the cingulum. The process groups are cylindrical to trumpet-shaped and are linked by distal ring trabeculae, and some process groups are linked together by trabeculae. **Hystrichosphaerina** is similar but features process groups in the cingulum. **Systematophora** is also similar but lacks the ring trabeculae distally and furthermore usually has basal ridges connecting the slender projections in the group; the cingulum is marked by distinctive processes.

## Zone EOM-4

Pica Pica 1X, 220-240'

**Turbiosphaera-**

**Hemicystodinium-**

*Notes on identification*

Most genera have been discussed earlier.

**Hemicystodinium** is a skolochorate cyst with an epicystal archeopyle and numerous non-tabular processes. The operculum tends to break up into several pieces. The edge of the archeopyle has a distinctive sulcal tab flanked by a low depression corresponding to the low sixth precingular plate. **Polysphaeridium**is similar but is said to have an apical archeopyle, although this has been challenged and it might be synonymous with Hemicystodinium. **Homotryblium** is similar to Hemicystodinium but has intratabular processes. **Eocladopyxis** has numerous nontabular processes and an epicystal archeopyle like Hemicystodinium, but the hypocyst is distinctive with sutural grooves.
**Turbiosphaera**, is a fibrous proximochorate genus with polar protrusions, is similar to Kenleyia, but has distinct processes which are intratabular, and a shelf-like structure marking the cingulum.

# K. Upper Eocene Zones

The following zone is identified with the Upper Eocene because it occurs immediately below the Eocene/Oligocene boundary as determined by pollen zones and lithostratigraphic considerations. The actual age of its lower boundary is not known. It represents a fluctuating inner neritic-lagoonal-lacustrine environment and as such some of the range tops and bases may be determined by environmental factors; their chronostratigraphic significance remains to be assessed as more information from other areas becomes available.

## Zone EOU-1

GUA 1-SX, 11220-11750'

**Cleistosphaeridium-**

**Hemicystodinium-**

In the lower part the LAD's of Pediastrum- and Concentricystis- occur.

*Notes on identification*

**Cleistosphaeridium** is skolochorate with an apical archeopyle with numerous nontabular processes or spines which are normally closed distally. **Polysphaeridium** is similar but with open processes, although this genus has been reinterpreted as having an epicystal archeopyle and therefore more similar with or identical to **Hemicystodinium**.

# L. Oligocene Zones

GUA-1SX, 9310-11210'

## Zone OLI-1

**Cassidium-**

**Pediastrum-spp.**

*Notes on identification*

**Cassidium** is a subspherical proximate cyst with a rugulate or reticulate surface, an apical archeopyle, and gonyaulacacean tabulation indicated by sutural grooves. **Eisenackia** is similar but has better defined sutural grooves giving a strong impression of raised intratabular platforms also it has an unornamented surface. **Alisocysta** differs in having penitabular ridges tracing out the tabulation and does not have sutural grooves as such.

**Pediastrum** is a colonial chlorophycean alga comprising disc-like masses of cells with generally pronounced radial structure, particularly in the peripheral region. The following notes explain the terminology used in describing species in the Maraven files.

Fossil specimens of Pediastrum can be regarded as being oblate spheroids comprising a *central disc*, generally circular in shape, surrounded by a *fringe* of different elements. The structure is that of a multicellular colony and the exact number of cells and the overall size will vary depending on the maturity of the specimen. One side of the colony is arbitrarily referred to as *obverse* and the other as *reverse*.

The colony may be single-layered (*unicameral*) or comprise several layers of cells (often *bicameral*, or sometimes more indicated by *tri-*, *tetra-*, etc.). In multicameral colonies, the cells comprising the fringe may be placed one above the other (*superimposed*) or be *offset* so that some or all of the underlying cell may be seen. The layering may be the same or different between the central cells and the peripheral cells.

From the centre of the central disc outwards to the fringe, the cells may be regarded as comprising a series of encircling rows termed *cycles*, each layer having its own cycle. Thus a colony - or part of a colony - may be *bicyclic, tricyclic, tetracyclic* etc.

The cells are of two different types : the central disc comprises the *central cells* which are surrounded by the *peripheral cells*. The fringe comprises the outer (*distal*) part of the peripheral cells, and this distal part may be referred to as the *fringe element*. The inner (*proximal*) part of the peripheral cells contributes to the central disc. Camerality in the peripheral cell cycles is indicated by the distinctive fringe elements which occur on the obverse and reverse sides. Occassionally the distal part of the central cells may be modified in a distinctive fashion.

The central cells may be *defined* with cell walls or other thickenings. Sometimes the central cells are *undefined*, perhaps due to resorbtion or other processes. The central cells may be *close-packed* with each cell abutting another on all sides. Central cells which are *loose-packed* do not touch their neighbours on all sides and the central disc is characterized by angular or rounded openings. Central cells may be *triangular, quadrangular, pentagonal*, or *hexagonal* in shape, or some rounded modification of these shapes.

The peripheral cells, particularly the fringe elements, usually have highly characteristic shapes. Those fringe elements with a simple triangular outline may be termed *pyramidal* when the basal width is equal to or greater than the height of the fringe part of the cell, or *conical* if the basal width is markedly less. These are general terms and obviously gradational; precise dimensions are needed for accurate description. Some peripheral cells are markedly constricted at their mid-length and are termed *flared*.

Peripheral cells may have a distal finger-like part termed *appendiform*, which may taper or be of constant width and *cylindrical*. This appendiform termination may have a*sharp, rounded*, or *bifid* tip. The appendiform termination is supported on a *base* which may have *convex, concave*, or *straight* sides. In the case of peripheral cells with a distinct base which is supported on a short parallel-sided *footing*, this condition is termed *chimeniform*.

The Pediastrum species in the Oligocene and Upper Eocene interval are highly distinctive and have restricted ranges. Whether these ranges are controlled by shifting environments or time-related evolutionary events is still being investigated. In any event, the Oligocene species are quite different from the Paleocene species and there is no overlap of ranges between the two groups.

## Zone OLI-2

**Glaphyrocysta-,Cleistosphaeridium-**
**,Achomosphaera-**
**Turbiosphaera-**
**,Leiosphaeridia-,Pediastrum-spp,Mougeotia-,Debarya-**

The dinoflagellate cysts have been discussed above.

Mougeotia is a probable freshwater zygnematacean cyst characterized by a colourless highly refractive wall, a rounded often quadrate outline, and distinctive folds in which the sets on opposing faces are often at right angles. Its most distinctive feature is the high refraction leading to a blue grey colour under differential interference contrast illumination and therefore simulating minerals such as quartz.

Debarya is also a freshwater cysts and has a short cylindrical or cone shaped form with one end usually open.

## Zone OLI-3

**Hystrichokolpoma-**

**Brigantedinium-**

**Halodinium-Pediastrum-spp**

*Notes on identification*

**Brigantedinium** is a small proximate cyst with an intercalary archeopyle and an autophragm with the typical protoperidinioid brown colour. Cysts of this type are very common and often cannot be identified closely if crumpled and due to their general lack of other features. It is common practise to informally refer to these as "round browns", and indeed this is the name used for a dinoflagellate newsletter ! **Selenopemphix** has a similar brown appearance but it has distinct cingular crests which may be ornamented.

**Halodinium** is best described as an acritarch even though it has the double layered wall characteristic of dinoflagellates. However, it has a sub-apical rounded pylome which cannot be identified as an archeopyle.

# M. Miocene Zones

Tocuyo 1-S, 650-4480'
Hambalek thesis, Falcon (NNH 220 and lower to NHH195)

## Lower Miocene

### Zone MIL-1

TOC 1-S, 4420-4480'
Hambalek thesis, NNH 170-195

**Hystrichokolpoma-**

**Hystrichosphaeropsis-,Achomosphaera-spp**
-

**Hemicystodinium-**
**Heteraulacacysta-(H)**

*Notes on identification*

**Hystrichokolpoma** is a skolochorate cyst with an apical archeopyleand processes in all major series but characterized by smaller processes in the cingulum. The process bases may be very large and almost fill the plate to its boundary. **Florentinia** and **Achilleodinium** are similar but have precingular archeopyles in the latter or combination precingular-apical archeopyles in the former.

## Middle Miocene

### Zone MIM-1

TOC 3067-3110'

**Hystrichokolpoma-,Emmetrocysta-,Alisocysta-**

**Tuberculodinium-,Heteraulacacysta-**

### Zone MIM-2

TOC 1-S, 1730-2240'
Hambalek thesis, NHH 148-166 (probably truncated in the mddle part)

*Lower part:*

**Reticulatosphaera-,Impagidinium-**

*Middle part:*

**Operculodinium-,Spiniferites-**
**-**
**Lejeunecysta-spp,Trinovantedinium-**

*Upper part:*

**Amphorosphaeridium-,Cannosphaeropsis-**

**Selenopemphix-spp-**

**,**
**Concentrecystis-**
**Crassosphaera-**

*Notes on identification*

Reticulatosphaera as used in this species is a chorate cyst with an apical archeopyle and very high sutural crests which support a distinct ectophragmal trabeculate system on their distal edge.

**Impagidinium** is a proximochorate cyst with a precingular archeopyle, subspherical shape, and distinct sutural cress or septa. The tabulation is distinct by the development of a triangular-sahped 6". **Leptodinium** is similar but has a more quadrate 6".

**Operculodinium** is a skolochorate or proximochorate cyst with numerous nontabular capitate processes and a precingular archeopyle. The processes may be solid or hollow and are usually closed. The wall may be complex. Exochosphaeridium is similar but has fibrous processes. **Lingulodinium** is similar but has closed blade-like processes and a multiplate precingular archeopyle. **Cleistosphaeridium** is generally somewhat similar but has an apical archeopyle.

**Trinovantedinium** is autophragmal with a pentagonal outline (one apical and two antapical horns), an intercalary archeopyle, and numerous nontabular short processes or spines. It is distinguished from **Lejeunecysta** by the strong nontabular ornament.

Cristadinium is a proximate protoperidiniacean pentagonal cyst with a triangular epicyst, 2 antapical horns, intercalary archeopyle, and sutural ornament, the latter distinguishing it from **Trinovantedinium**.

<u>Sumatradinium</u> is ovoidal sometimes with an antapical depression and with an intercalary archeopyle. It is distinctive on account of nontabular spines and short processes in addition to a granulate or reticulate wall.

<u>Amphorosphaeridium</u> is a skolochorate cyst with precingular archeopyle and a subspherical body covered in numerous nontabular fibrous hollow processes. **Exochosphaeridium** is similar but has solid processes. In **Fibrocysta**, which has similar processes, the body is terminated by apical and antapical protrusions.

<u>Cannosphaeropsis</u> is a skolochorate cyst with precingular archeopyle and with gonal processes with distal ends connected together by single-strand trabeculae which are inserted between the triradiate forks of the processes. **Nematosphaeropsis** is somewhat similar but the trabeculae may be single or paired and represent extensions of the trifurcate ends of the gonal processes.

<u>Lejeunecysta</u> is a cyst with a peridinioid pentagonal outline (sometimes angular, sometimes more rounded) but with an autophragm (which may occassionally separate into layers simulating cavation if the specimens are highly oxidized through weathering or laboratory preparation). The autophragm is usualy featureless other than for folds or very faint ornamentation; the archeopyle is large and wide, centered on the mid-line, and has an adcingular margin close to the cingulum as in **Phelodinium** , which, however, is cavate. and has a narrower archeopyle. The archeopyle is not always developed in Lejeunecysta.

<u>Selenopemphix</u> is similar to **Lejeunecysta** but is usually compressed apically-antapically rather than dorso-ventrally and in addition the intercalary archeopyle of Selenopemphix is offset from the mid-line. Selenopemphix in polar view is characterized by strong cingular septa which are superimposed giving the outline a double-edged appearance. The cingular septa may be smooth or highly ornamented with serrations and spines. In most cases, the cingular ends overlap in a depressed area of the sulcus leading to a characteristic reniform outline in polar view.

## Zone MIU-1

<u>Hambalek thesis NHH 123-132</u>
<u>TOC 1S, 1340-1580'</u>

**Spiniferites-,Operculodinium-,Achilleodinium-**
**Trinovantedinium-,Sumatradinium-,Lejeunecysta-,Sumatradinium-**

**Tuberculodinium-**

*<u>Notes on identification</u>*

**Tuberculodinium** is a large proximate cyst with a double wall, the outer (ectophragm) often damaged or draped closely against the inner (periphragm). Large processes support the outer layer and may be variable in size and shape and may be hollow or solid. The archeopyle is very unusual in being multiplate at the antapex, but this is not immediately obvious; rather, the prominent tubercles are very obvious and identify even fragments of this distinctive genus.

**Trinovantedinium** is autophragmal with a pentagonal outline (one apical and two antapical horns), an intercalary archeopyle, and numerous nontabular short processes or spines. It is distinguished from **Lejeunecysta** by the strong nontabular ornament.

## Zone MIU-2

TOC 1-S, 1040-1280'

**Operculodinium-, Spiniferites-**

**Operculodinium** is a skolochorate or proximochorate cyst with numerous nontabular capitate processes and a precingular archeopyle. The processes may be solid or hollow and are usually closed. The wall may be complex. Exochosphaeridium is similar but has fibrous processes. **Lingulodinium** is similar but has closed blade-like processes and a multiplate precingular archeopyle. **Cleistosphaeridium** is generally somewhat similar but has an apical archeopyle.

## Zone MIU-3

TOC 1-S, 650-980'
Hambalek thesis, NHH 220-101

**Filisphaera-,Lingulodinium-**

**Quadrina-,Selenopemphix-,Brigantedinium-**

**Tuberculodinium-**

**Tasmanites-Leiosphaeridia-,Nancycysta-,Pterospermella-**

*Notes on identification*

**Filisphaera** is an ovoidal proximate cyst with a complex granular wall and precingular archeopyle; the details of the wall structure are different compared with **Tectatodinium** which is said to have a layered wall similar to tectate pollen.

**Quadrina** is probably but not certainly a protoperidinioid cyst with a distinctive brown wall and clusters of spine-like processes at each of its four angular corners. The orientation of the cyst is uncertain, some belieiving that two of the angles are aligned apically-antapically and others believing that the flat ends are terminal. No archeopyle has been identified with certaintly but if it is, the matter should be solved.

**Brigantedinium** is a small proximate cyst with an intercalary archeopyle and an autophragm with the typical protoperidinioid brown colour. Cysts of this type are very common and often cannot be identified closely if crumpled and due to their general lack of other features. It is common practise to informally refer to these as "round browns". **Selenopemphix** has a similar brown appearance but it has distinct cingular crests which may be ornamented.

**Tasmanites** is a marine green algal cyst with a very thick wall penetrated by many delicate canals. **Leiosphaeridia** is an acritarch with a thinner wall and no other features.

**Nancycysta** is an acritarch with a wall extended into finger-like protuberances as in a glove.

# N. Pliocene Zones

## Zone PLI-1

TOC 1-S, 460-490'
Hambalek thesis, NHH 217-218

**Elytrocysta-**

**Hystrichogonyaulax-,Operculodinium-**

**Trinovantedinium-**

**Hemicystodinium-spp,Tuberculodinium-,Mendicodinium-**

*Notes on identification*

**Elytrocysta** is a proximate holocavate cyst with an apical archeopyle and numerous nontabular projections covered by thin ectophragm. Batiacasphaera is distinguished by its lack of ectophragm.

**Hystrichogonyaulax** is a proximate cyst with precingular archeopyle and sutural ridges surmounted by isolated spines.

**Hemicystodinium** is a skolochorate cyst with an epicystal archeopyle and numerous non-tabular processes. The operculum tends to break up into several pieces. The edge of the archeopyle has a distinctive sulcal tab flanked by a low depression corresponding to the low sixth precingular plate. **Polysphaeridium**is similar but is said to have an apical archeopyle, although this has been challenged and it might be synonymous with Hemicystodinium. **Homotryblium** is similar to Hemicystodinium but has intratabular processes. **Eocladopyxis** has numerous nontabular processes and an epicystal archeopyle like Hemicystodinium, but the hypocyst is distinctive with sutural grooves on the wall surface.

# O. Selected References

The following list is a highly selective group of references which might be useful in gaining a quick entry to the topic of fossil dinoflagellate cysts, covering both stratigraphic and taxonomic aspects and also their biological relationships. A brief summary of the significance of the publication is indicated following each entry. Very full references to the primary literature at low taxonomic levels and high stratigraphic resolution can be found in, for example, Fensome et al. (1993), Lentin and Williams (1989), and Williams et al. (1993).

Artzner, D.G., Davies, E.H., Dorhofer, G., Fasola, A., Norris, G. and Poplawski, S., 1979. A systematic illustrated guide to fossil organic-walled dinoflagellate genera. Royal Ontario Museum, Life Sciences Division, Miscellaneous Publication, : 1-119. Provides line drawings of holotypes of fossil genera arranged in a morphographic scheme.

Evitt, W.R., 1985. Sporopollenin Dinoflagellate Cysts. American Association of Stratigraphic Palynologists, Austin : 1-333. An exhaustive treatment of the morphology of dinoflagellate cysts.

Fensome, R.A., Taylor, F.J.R., Norris, G., Sarjeant, W.A.S., Wharton, D.I. and Williams, G.L., 1993. A classification of living and fossil dinoflagellates. Micropaleontology, Special Publication, 7, : 1-351. Reviews all extant and extinct taxa at the generic and higher levels, integrates information gained from cysts and thecae, and reconciles biological and paleontological classifications in a unified scheme.

Head, M.J. and Wrenn, J.W. (Ed.), 1992. Neogene and Quaternary dinoflagellate cysts and acritarchs. American Association of Stratigraphic Palynologists Foundation, Dallas : 1-438. Provides a series of perspectives on Miocene-Holocene dinoflagellates and some original contributions on ecology/paleoecology of Neogene dinoflagellates which hitherto had been a somewhat neglected group.

Jan du Chene, R., Masure, E., Becheler, I., Biffi, U., De Vains, G., Fauconnier, D., Ferrario, R., Foucher, J.-C., Gaillard, M., Hochuli, P., Lachkar, G., Michoux, D., Monteil, E., Moron, J.-M., Rauscher, R., Raynaud, J.-F., Taugourdeau, J. and Turon, J.-L., 1986. Guide pratique pour la determination de kystes de Dinoflagelles fossiles. Le complexe *Gonyaulacysta*. Centres de recherches exploration-production Elf-Aquitaine, Bulletin, Memoir, 12, : 1-479. A detailed guide to gonyaulacoid species.

Lentin, J.K. and Williams, G.L., 1989. Fossil dinoflagellates: index to genera and species, 1989 edition. American Association of Stratigraphic Palynologists, Contributions Series, 20, 1-473. The latest in a series of publications which tabulates systematically all species and genera of fossil dinoflagellates, tracks synonyms, and places species and genera in correct combinations. Also available on IBM-compatible floppy disk.

Norris, G. and Sarjeant, W.A.S., 1965. A descriptive index of genera of fossil Dinophyceae and Acritarcha. New Zealand Geological Survey, Paleontological Bulletin, 40, 1-72. The first attempt to integrate fossil dinoflagellate genera in a comprehensive overview. Subsequently superceded by others (the latest being Fensome et al. (1993)) but still useful for information taken from the primary literature, often in difficult-to-get journals, and translated into English.

Powell, A.J. (Ed.), 1992. A Stratigraphic Index of Dinoflagellate Cysts. Chapman and Hall, London : 1-290. A review of Mesozoic-Cenozoic dinocysts and a detailed discussion of their zonal use particularly applicable to northwest Europe.

Sarjeant, W.A.S., 1974. Fossil and Living Dinoflagellates. Academic Press, London : 182. A useful book reviewing the paleontology and some aspects of the biology of dinoflagellates, the latter now somewhat dated..

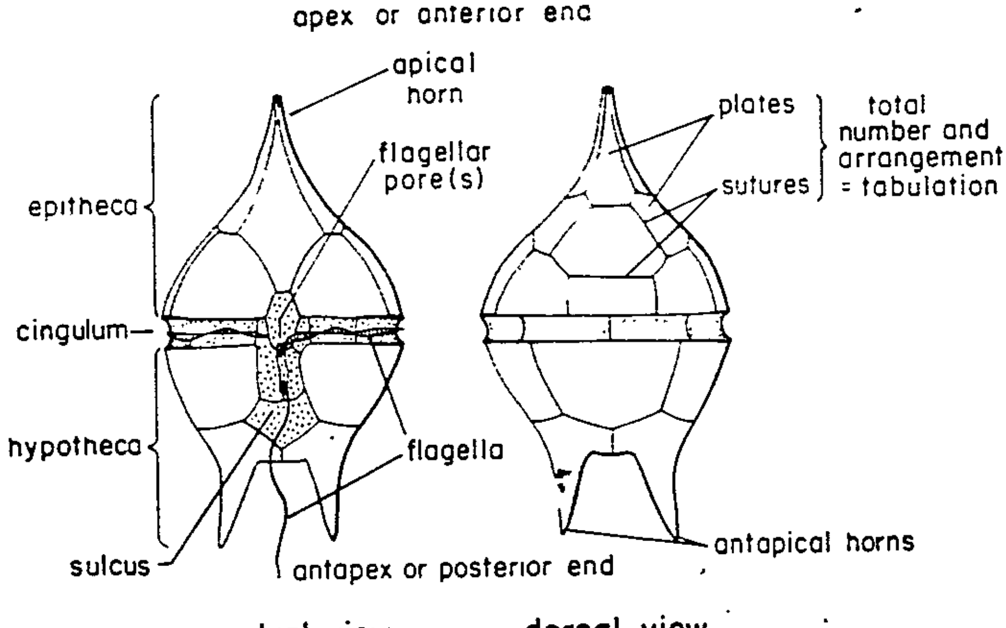
Stover, L.E. and Evitt, W.R., 1978. Analyses of pre-Pleistocene organic-walled dinoflagellates. Stanford University Publications, Geological Sciences, 15, : 1-300. A seminal work analyzing dinoflagellate cyst morphology and assessing their significance at the generic level. A continuation of this approach appears in Stover and Williams (1987).

Stover, L.E. and Williams, G.L., 1987. Analyses of Mesozoic and Cenozoic organic-walled dinoflagellates 1977-1985. American Association of Stratigraphic Palynologists, Contributions Series, 18, 1-243. A continuation of Stover and Evitt (1978)but enhanced by the addition of schematic illustrations of the genera reviewed.

Taylor, F.J.R. (Ed.), 1987. The Biology of Dinoflagellates. Blackwell Scientific Publications, Oxford 21 : xii+785. A thorough review of various aspects of dinoflagellate biology with contributions from leading authorities in various specializations.

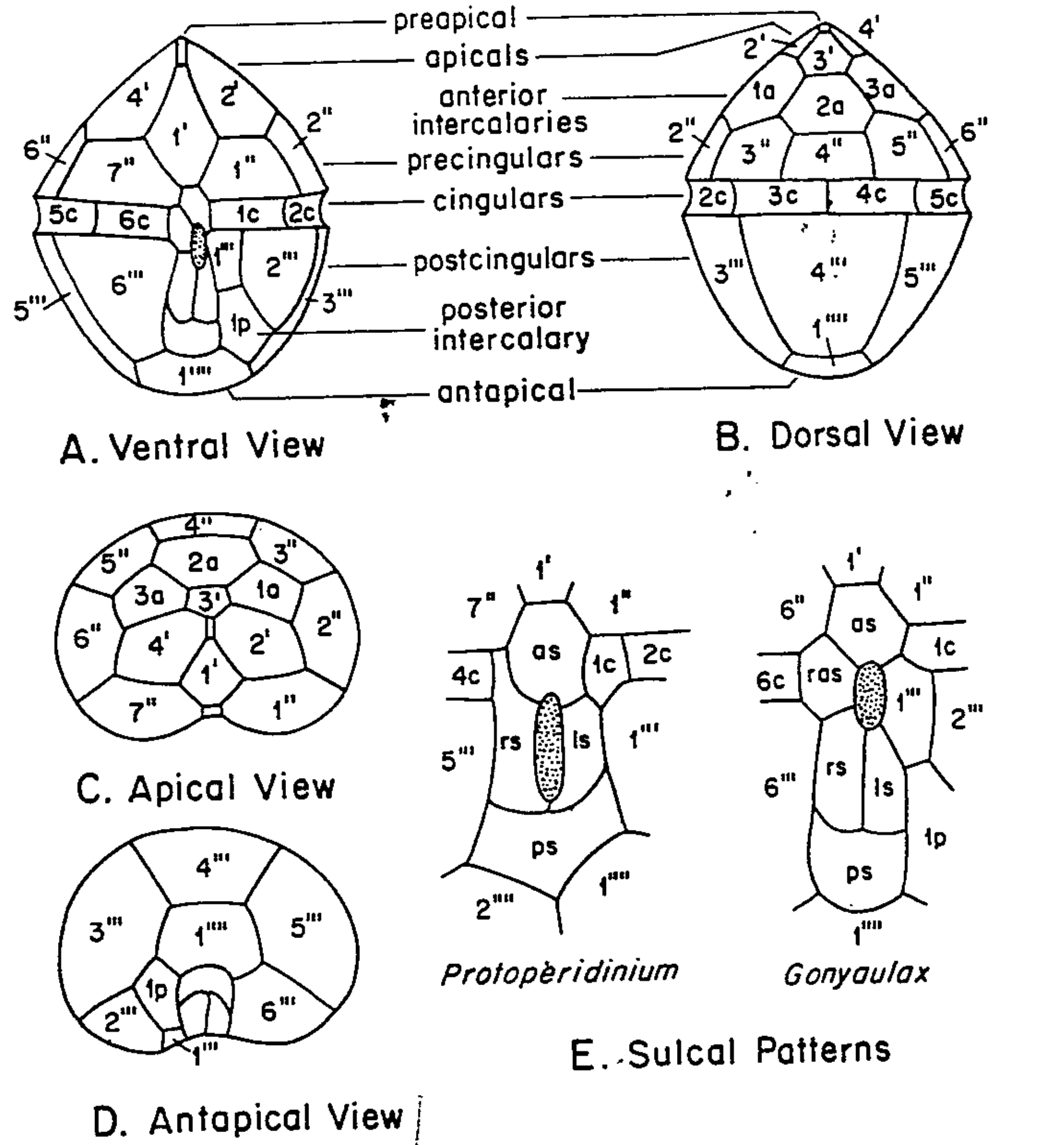
Williams, G.L. and Bujak, J., 1985. Mesozoic and Cenozoic dinoflagellates. In: H. M. Bolli, J. B. Saunders and K. Perch-Nielsen (Eds.), Plankton Stratigraphy. Cambridge University Press, Cambridge : 847-964. A review on a global basis of stratigraphically significant Jurassic, Cretaceous and Tertiary dinoflagellate species. Superceded in part by Williams et al. (1993).

Williams, G.L., Stover, L.E. and Kidson, E.J., 1993. Morphology and stratigraphic ranges of selected Mesozoic-Cenozoic dinoflagellate taxa in the northern hemisphere. Geological Survey of Canada, Paper, 92-10, : 1-137. A recent compilation of stratigraphically significant genera, species, and other morphologic groupings. Illustrations are arranged both taxonomically and stratigraphically, and useful hints to identification are provided. The title is somewhat misleading because coverage is almost exclusively confined to the extra-troical regions, but nevertheless a very useful work.




A

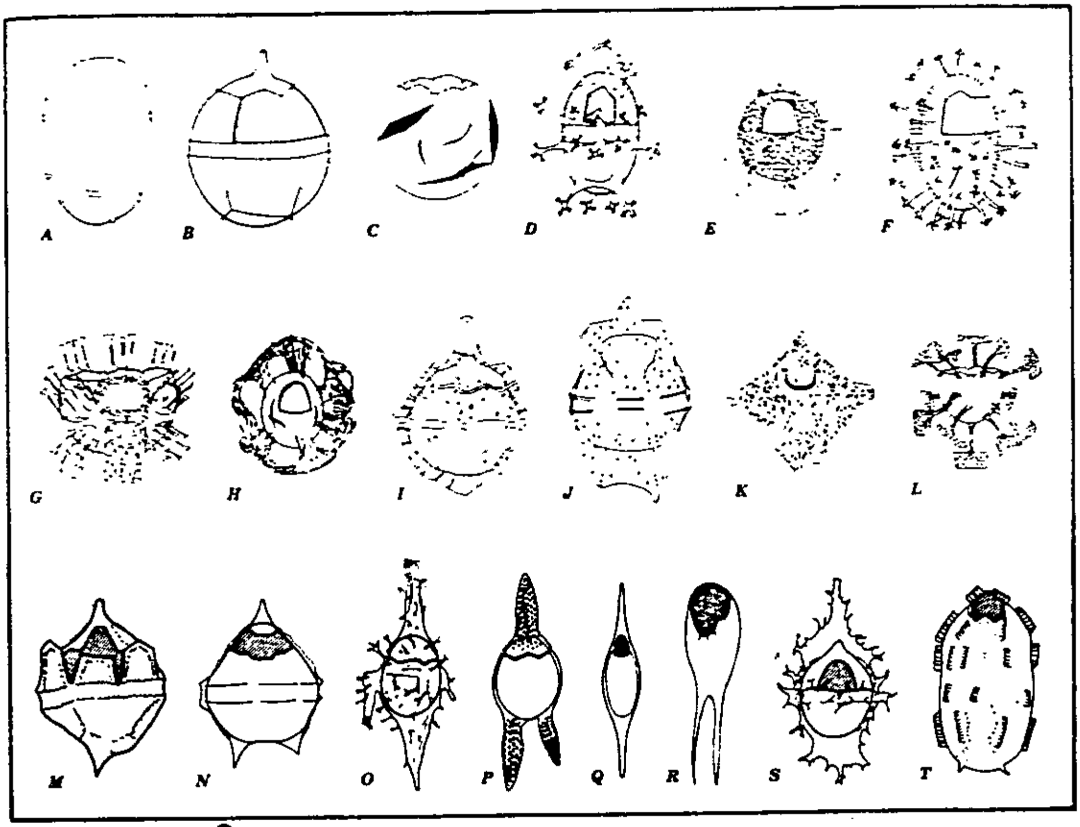
**Figure 1.2 - PRINCIPAL FEATURES OF THE THECA IN A PERIDINIALEAN DINOFLAGELLATE**
(For corresponding terms applicable to the cyst, see Figure 3.1)




B

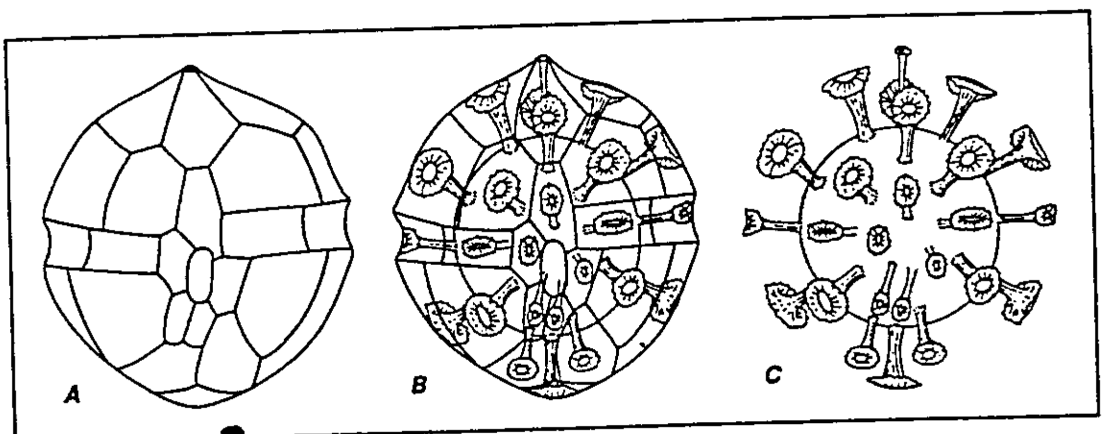
**Figure 3.2 - KOFOIDIAN SYSTEM OF TABULATION**
A-D - Tabulation of a hypothetical peridinialean theca. This pattern would be represented by the formula: *1pr, 4', 3a, 7'', 6c, 6''', 1p, 1'''', 5s*.
... and *Gonyaulax*. Additional smaller plates may also be present. Flagellar

2



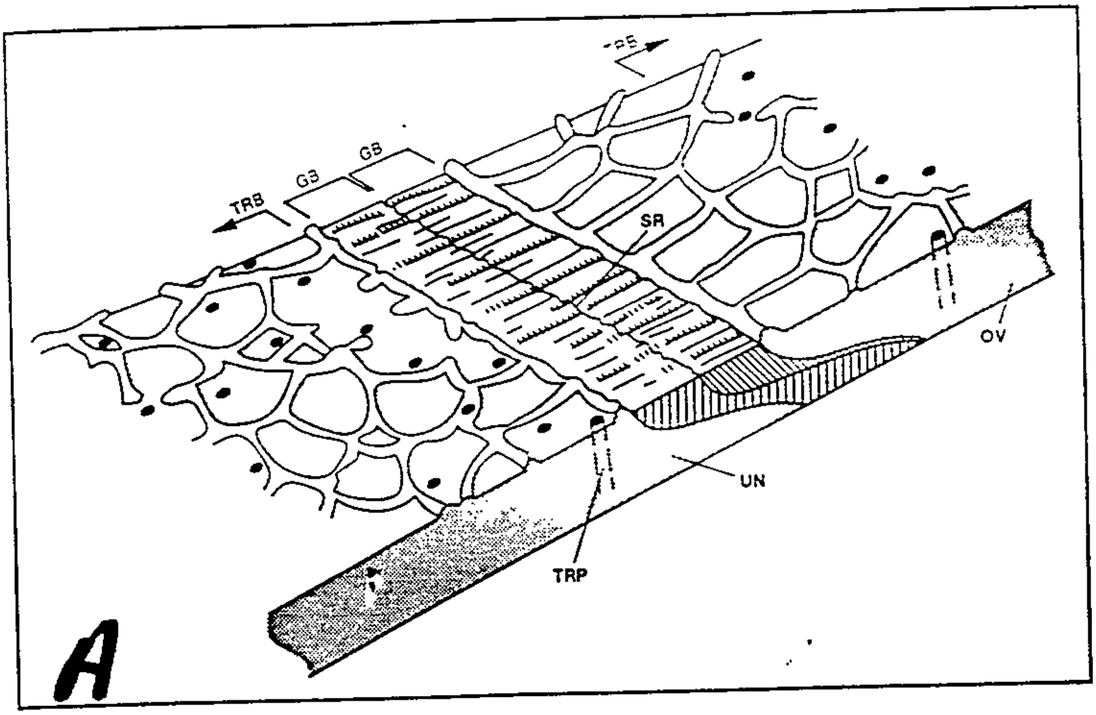

A

TEXT-FIGURE 36
A variety of fossil cysts. A. *Druggidium* sp. B. *Rhynchodiniopsis cladophora.* C. *Batiacasphaera micropapillata.* D. *Spiniferites ellipsoideus.* E. *Cordosphaeridium funiculatum.* F. *Kiokansium williamsii.* G. *Systematophora placacantha.* H. *Thalassiphora patula.* I. *Gardodinium trabeculosum.* J. *Chatangiella verrucosa.* K. *Rhombodinium porosum.* L. *Areosphaeridium diktyoplokus.* M. *Chichaouadinium vestitum.* N. *Trithyrodinium* sp. O. *Xenascus* sp. P. *Odontochitina porifera.* Q. *Palaeocystodinium golzowense.* R. *Batioladinium longicornutum.* S. *Triblastula utinensis.* T. *Valvaeodinium lineatum.* All views dorsal except A, C, L, O and R, which are ventral. SOURCE: adapted from Williams et al. (1993).

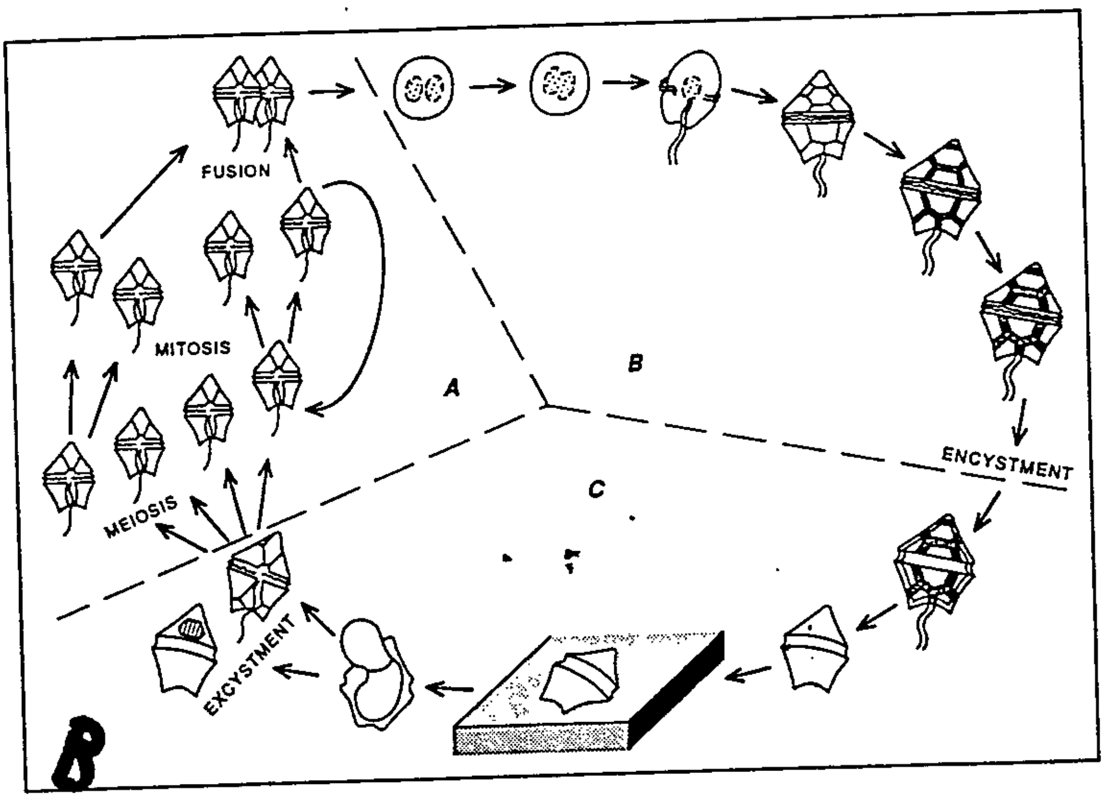



B

TEXT-FIGURE 38
Interpretation of a chorate cyst. Development of the fossil cyst species *Hystrichosphaeridium tubiferum* from a hypothetical parent theca. KEY: Central body of cyst is shaded. SOURCE: adapted from Evitt (1985, text-fig. 3.3A-C).




TEXT-FIGURE 10
Block diagram showing a suture of a theca of *Protoperidinium grande* with growth bands. KEY: GB = growth band, OV = overlapping plate, SR = suture, TRB = trichocyst bearing region, TRP = trichocyst pore, UN = underlapping plate. SOURCE: adapted from Gocht and Netzel (1974, text-fig. 3A).




TEXT-FIGURE 8
Idealized life-cycle involving sexual reproduction and cyst formation. A. Cells in this segment are motile and haploid. B. Cells in this segment are motile and diploid: note the double set of flagella in the motile cells. C. Cells in this segment are nonmotile (except for the excysted cell shown to the left) and diploid. KEY: Nucleus is represented by dotted areas in first three cells in B; hachured area in discarded cyst in C represents archeopyle. SOURCE: adapted from Evitt (1985, text-fig. 1.3).

4

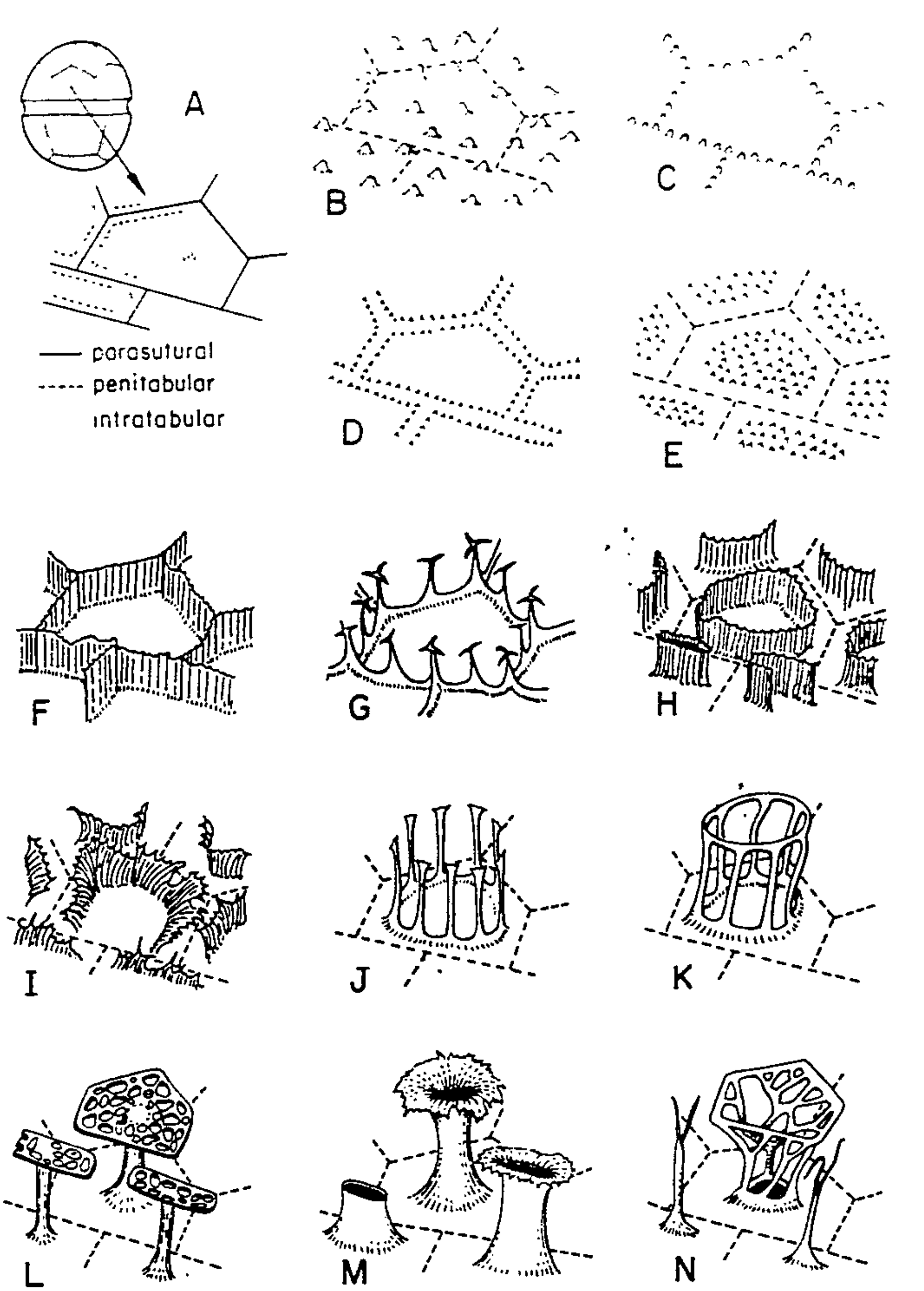



Figure 4.4

**Figure 4.4 - DISTRIBUTION OF FEATURES**

A - Schematic dorsal view of a theca (above) and portion of dorsal surface of its cyst (below), to identify parasutures shown by dashed lines in other figures and to show location of parasutural, penitabular, and intratabular ornament.

B-E - Four principal types of distribution: nontabular (B), parasutural (C), penitabular (D), and intratabular (E).

F - Parasutural septa (e.g., Cretaceous-Holocene *Impagidinium*).

G - Parasutural ridges combined with gonal and intergonal processes (e.g., Cretaceous-Holocene *Spiniferites*).

H - Closed penitabular septa (e.g., Tertiary *Alisocysta*).

I - Penitabular septa with adcingular interruptions on larger paraplates; paracingular projections of different design (e.g., some Late Cretaceous *Areoligera*).

J - Penitabular to intratabular process group rising from a basal ridge (e.g., Jurassic-Tertiary *Systematophora*).

K - Similar to J, but processes united distally by ring-trabecula (e.g., Early Tertiary *Emmetrocysta*).

L-N - Single intratabular processes. L - Solid processes with tips expanded into perforate ectophragm (e.g., Early Tertiary *Areosphaeridium diktyoplokus*). M - Hollow tubiform processes (e.g., Late Cretaceous-Early Tertiary *Hystrichosphaeridium tubiferum*). N - Complex process (or process group) on major paraplates (condition intergrades with that shown in K), cingular processes of contrasting design (e.g., Early Cretaceous *Hystrichosphaerina*).

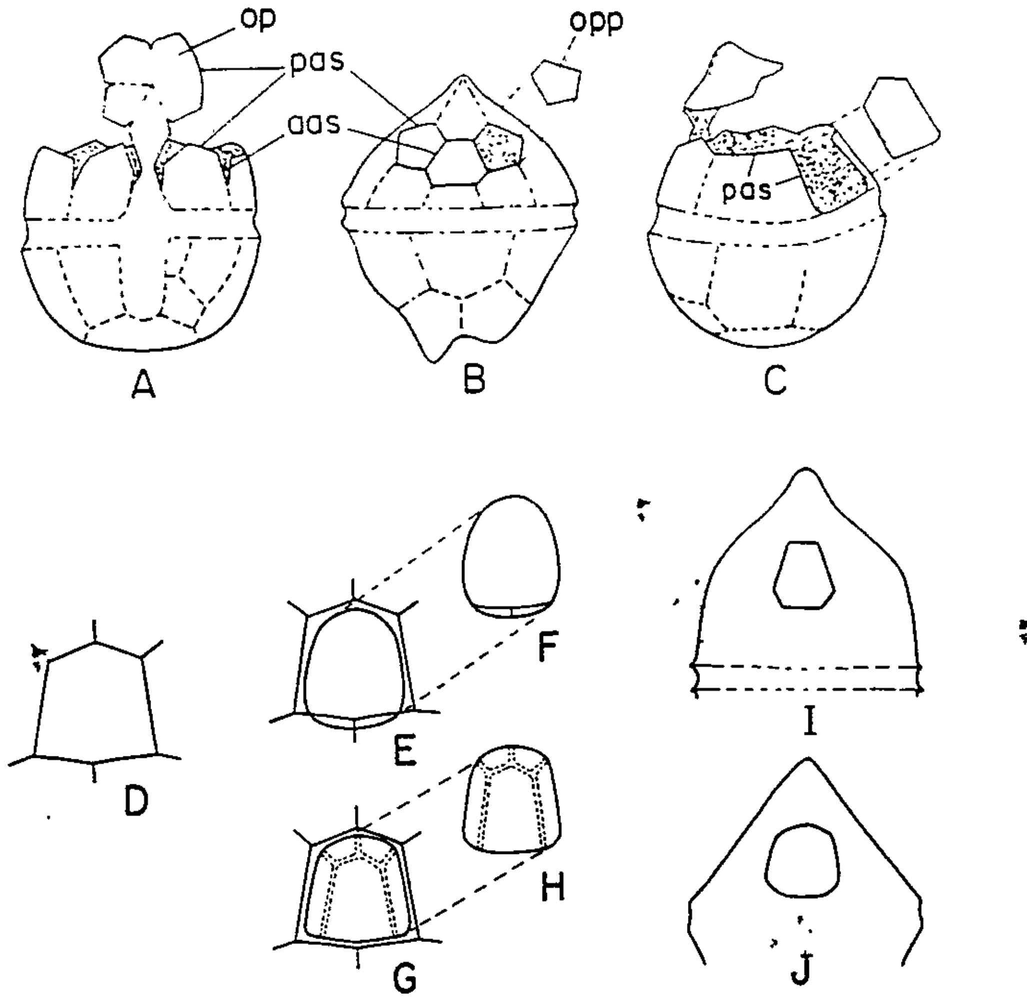



**Figure 6.1 - BASIC ARCHEOPYLE FEATURES**

aas - accessory archeopyle suture; pas - principal archeopyle suture; op - operculum; opp - opercular piece of compound operculum

A - Apical archeopyle with ventrally adnate, simple, polyplacoid operculum comprising the apical paraplates; accessory archeopyle sutures developed along parasutures between precingular paraplates.

B - Intercalary archeopyle with compound operculum divided by accessory sutures into three opercular pieces, all of them free and two of them in place.

C - Combination archeopyle with compound operculum: apical portion polyplacoid, simple, and adnate; precingular portion monoplacoid and free.

D - Complete congruence of archeopyle and the paraplate to which it corresponds.

E-F - Archeopyle not congruent with paraplate as outlined by parasuture. E -Opening reduced along lateral and apical margins, enlarged posteriorly to include part of paracingulum. F - Operculum of E.

G-H - Reduced archeopyle involving a paraplate whose surface bears accessory ridges related to overlap and growth of thecal plates (e.g., *Cribroperidinium*). H - Operculum of G. Note that accessory ridges on operculum falsely suggest that extensive enlargement has incorporated portions of adjacent paraplates.

I-J - Angularity of the opening. I - Shape and position of the opening are sufficient to indicate equivalence of the archeopyle to paraplate 2a of a peridinioid cyst, despite absence of definitive paratabulation. J - Rounded opening whose shape and position are ambiguous indicators of paraplate equivalence.

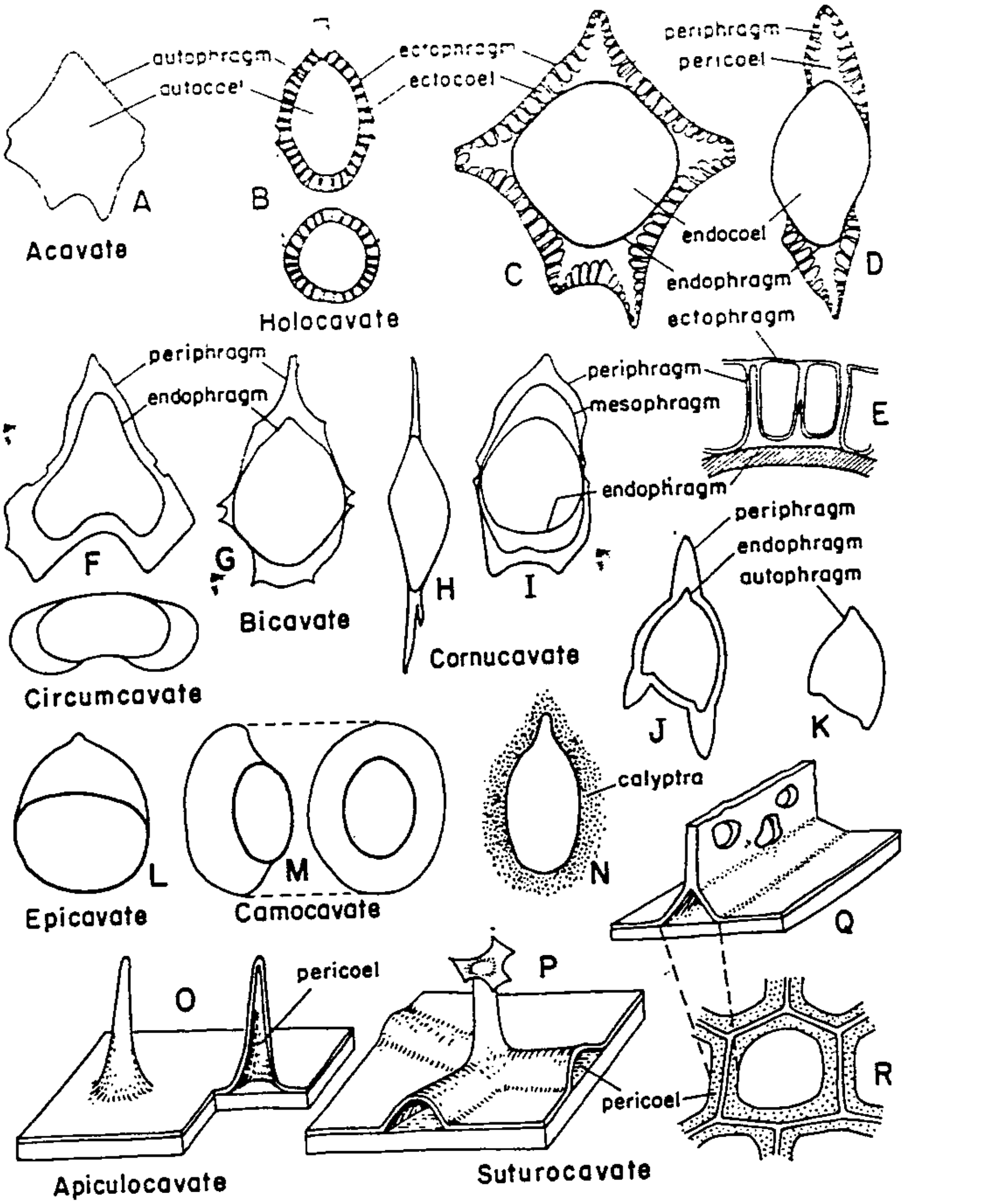



Figure 4.1

**Figure 4.1 - SCHEMATIC EXAMPLES OF WALL STRUCTURE**

(Dorsoventral views in optical section except as noted)

A - Acavate cyst with single wall layer (as in Recent *Trinovantedinium*).

B - Holocavate cyst (polar view below) with autophragm and ectophragm (e.g., Late Jurassic-Early Cretaceous *Gardodinium*).

C-E - Cyst with endophragm, periphragm and ectophragm; cornucavate with respect to pericoel; irregularly cavate with respect to ectocoel. D - lateral view in optical section. E - Detail section of wall showing continuity of periphragm and ectophragm and variable extent of pericoel into process shafts. (e.g., Eocene *Kisselovia*).

F - Circumcavate cyst (polar view below; e.g., Late Jurassic-Early Cretaceous *Sirmiodinium*).

G - Bicavate cyst (e.g., Late Jurassic *Gonyaulacysta jurassica*).

H - Cornucavate cyst (e.g., Late Cretaceous-Early Tertiary *Palaeocystodinium*).

I - Bicavate cyst with mesophragm (e.g., occasional species of Late Cretaceous *Isabelidinium*).

J - Circumcavate cyst (e.g., Early Cretaceous *Endoceratium ludbrookiae*).

K - Acavate autocyst (outline as in Early Cretaceous *Aptea*), suggesting that this is really an endocyst, as in J, without pericyst.

L - Epicavate cyst (e.g., Late Cretaceous *Nelsoniella*).

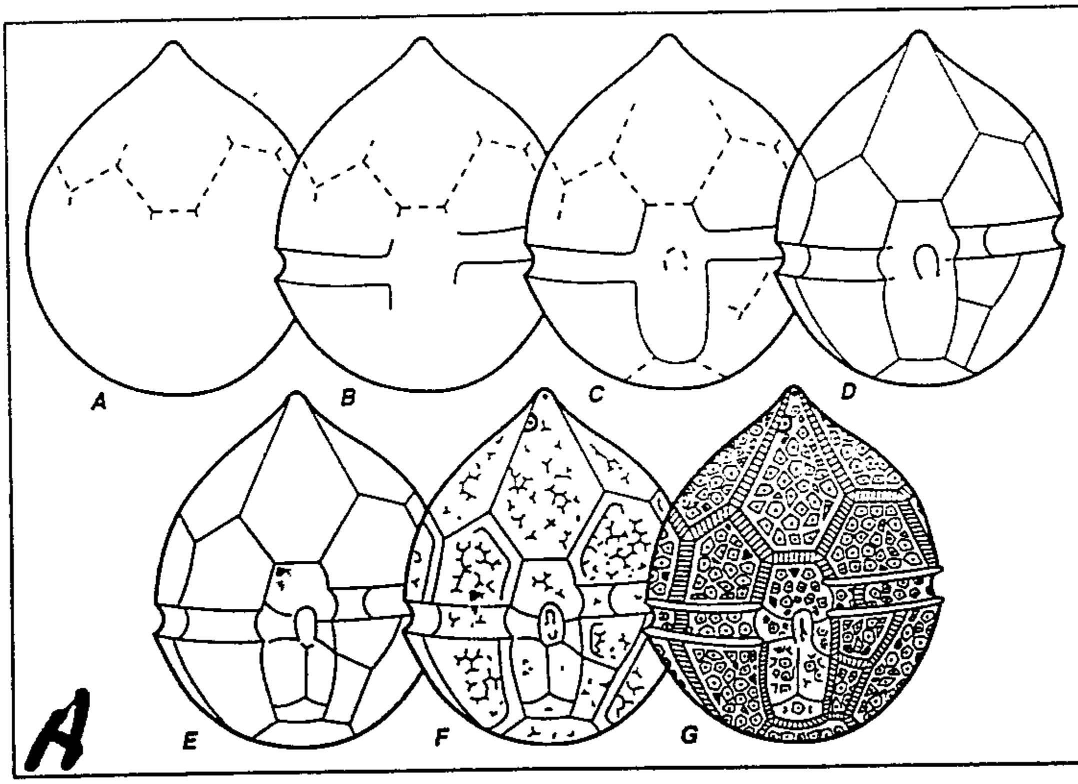
M - Camocavate cyst (left lateral view on left; e.g., Early Tertiary *Thalassiphora pelagica*).

N - Autocyst with calyptra (e.g., some Late Jurassic *Pareodinia*).

O - Oblique detail and section of apiculocavate wall, showing pericoel completely restricted to interior of processes.

P-R - Suturocavate wall. P - Oblique detail and section, showing pericoel restricted to parasutural ridges and interior of open-tipped processes (as in some *Spiniferites*). Q-R - Pericoel confined to base of parasutural septa. Q - Oblique view and section; R- plan view, showing extent of pericoel (stippled); septa (paired parallel lines), and line of contact between periphragm and endophragm encircling central portion of paraplate.

7




TEXT-FIGURE 37
Schematic sketches of fossil gonyaulacacean cysts showing a morphological series (A-G) in which there is increasingly strong representation of thecamorphic features. Note the "reflection" of a ventral pore (i.e. the presence of a porichnion) and an "apical pore" in F and G. SOURCE: adapted from Gocht (1983, fig. 1).

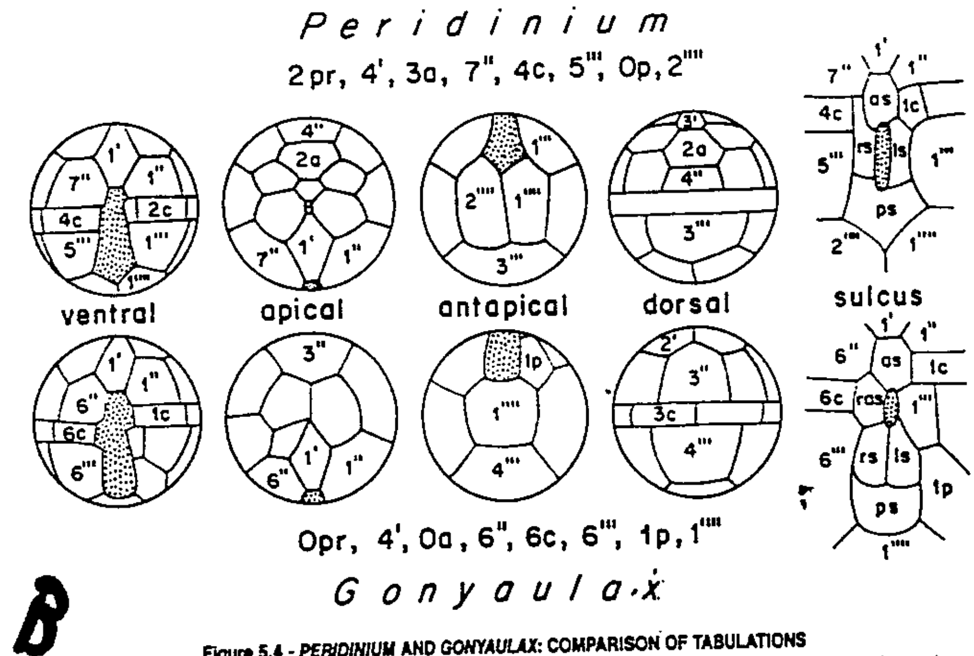
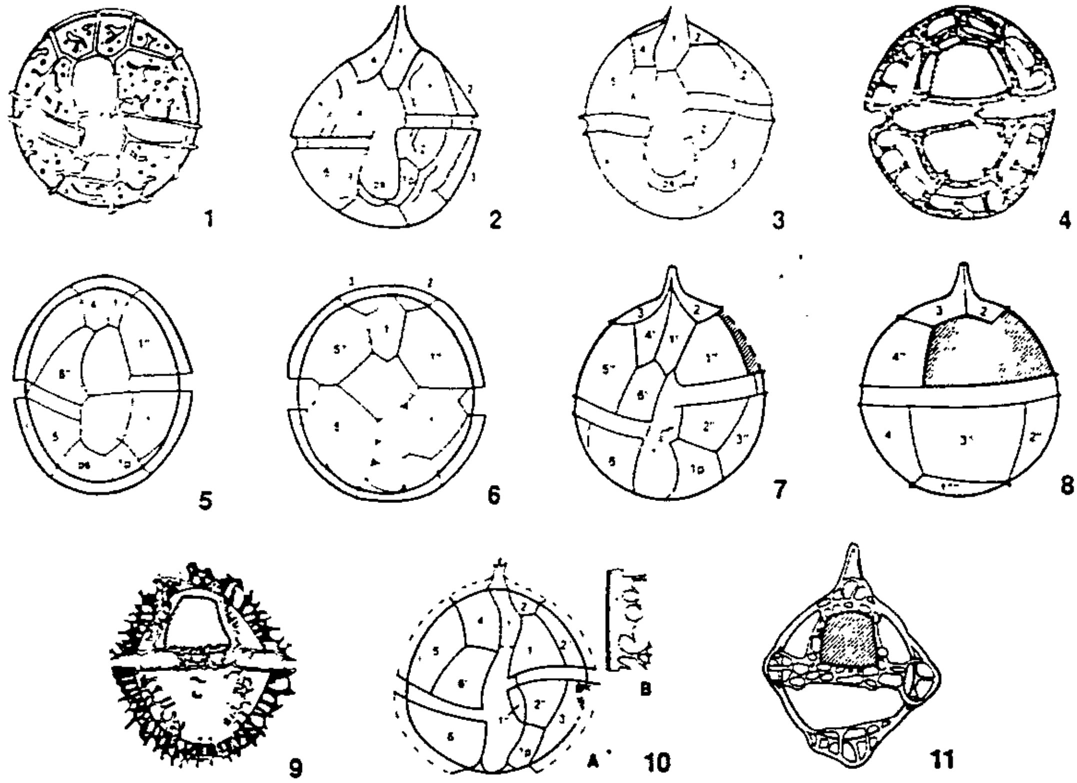



**Figure 5.4 - *PERIDINIUM* AND *GONYAULAX*: COMPARISON OF TABULATIONS**

Schematic representation of one pattern for each genus. Diagrams show different views of entire pattern and detail of the sulcus. Kofoid tabulation formulae are shown, and key plates on the diagrams are labeled with the Kofoid designations conventionally used. Designations for sulcal plates are: *as* - anterior, *rs* - right, *ls* - left, *ras* - right accessory, *ps* - posterior. Sulcus patterned in principal views; flagellar pore regions stippled in details of sulcus.




1. *Corrudinium incompositum* (T-52), ventral surface
2. *Cribroperidinium edwardsii* (C-60), ventral surface
3. *Cribroperidinium tenuitabulatum* (T-35), ventral surface
4. *Impagidinium aquaeductum* (T-24), dorsal surface
5. *Impagidinium dispertitum* (T-46), ventral surface
6. *Impagidinium patulum* (T-2), ventral surface

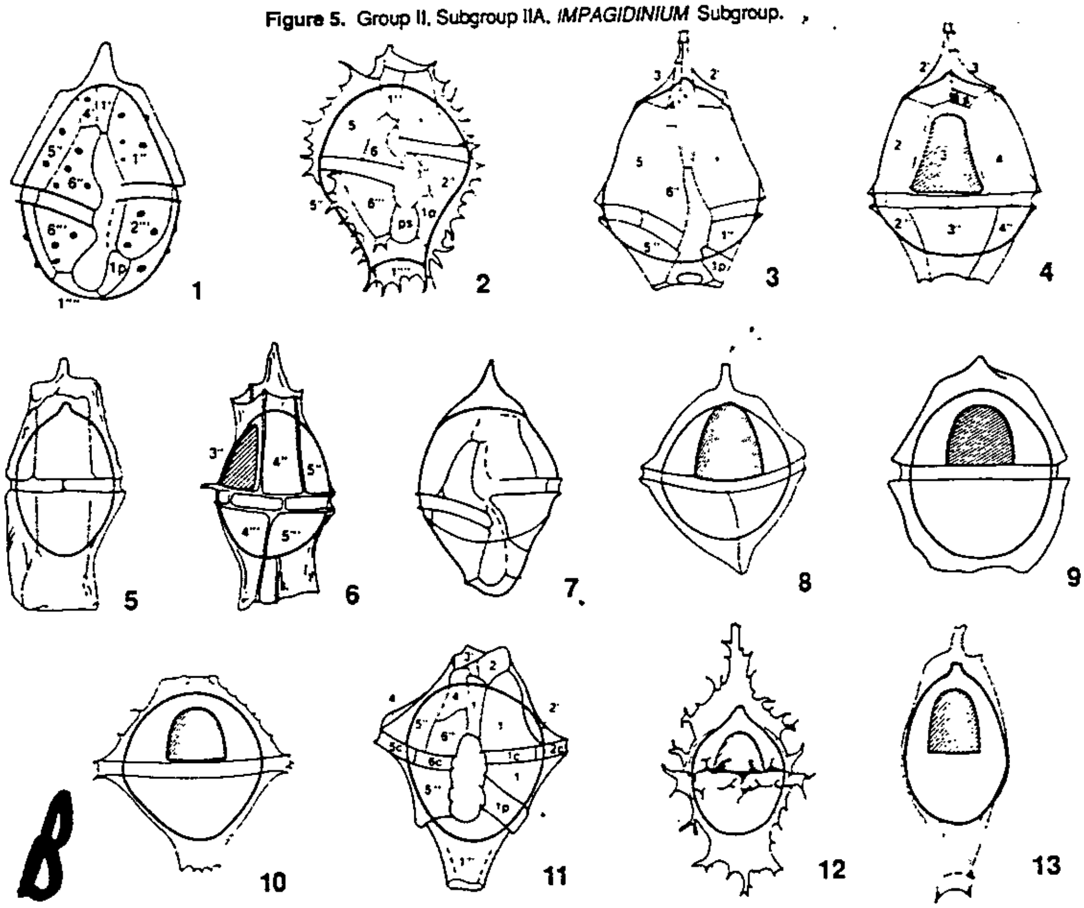
7-8 *Rhynchodiniopsis cladophora* (J.-22), ventral and dorsal surfaces, respectively

9. *Rhynchodiniopsis? regalis* (J.-44), dorsal surface

10A,B *Occisucysta balios* (J.-18), dorsal surface (10A)

11. *Spongodinium delitiense* (T-108), dorsal surface

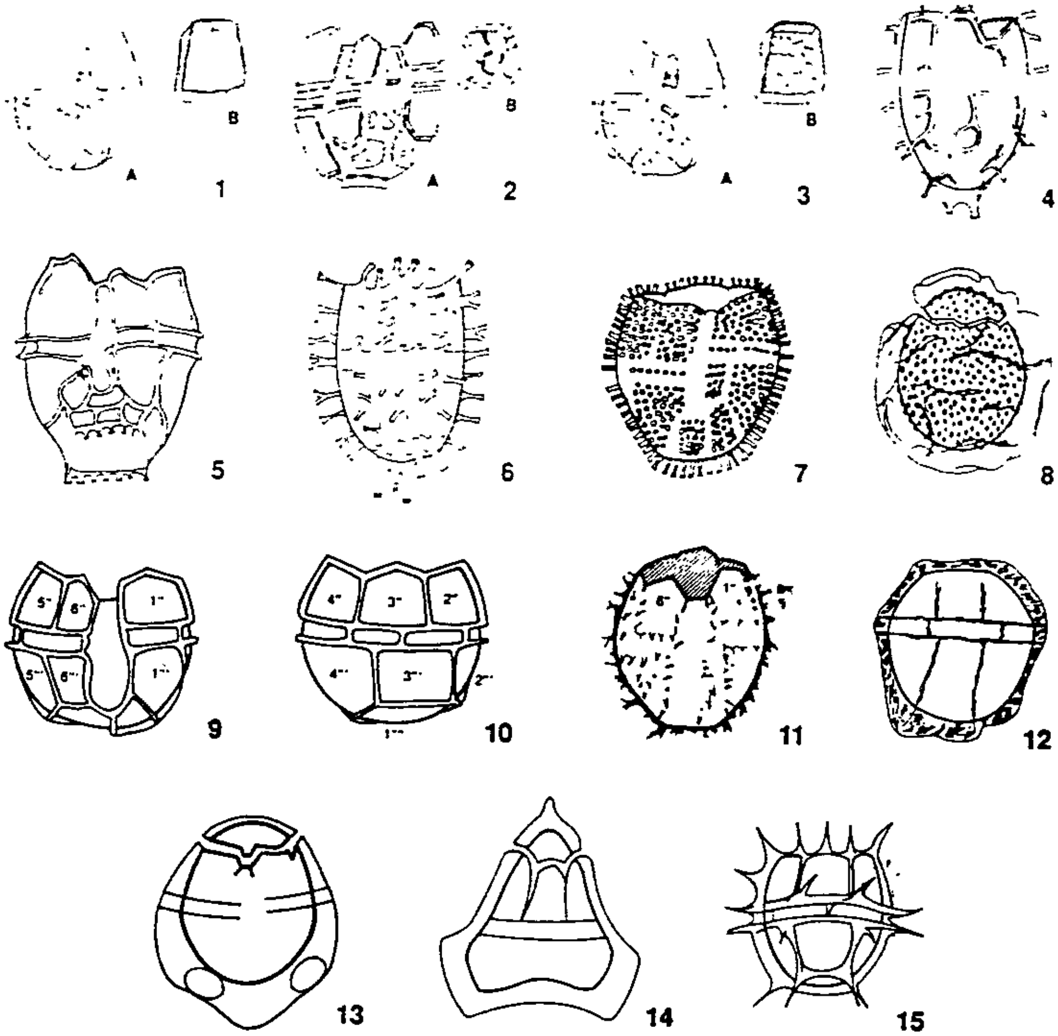
**Figure 5.** Group II, Subgroup IIA, *IMPAGIDINIUM* Subgroup.




1. *Gonyaulacysta cassidata* (C-69), ventral surface
2. *Gonyaulacysta eisenackii* (J.-29), ventral surface

3,4 *Gonyaulacysta jurassica* (J.-24), ventral and dorsal surfaces, respectively

5. *Hystrichosphaeropsis obscura* (T-19), lateral view
6. *Hystrichosphaeropsis ovum* (C-40), right lateral view
7. *Psaligonyaulax deflandrei* (C-49), ventral surface
8. *Scriniodinium? campanula* (C-57), dorsal surface
9. *Scriniodinium crystallinum* (J.-28), dorsal surface
10. *Scriniodinium luridum sensu* Deflandre (1938b) (J.-21), dorsal surface
11. *Scriniodinium luridum sensu* Gocht (1970b) (J.-42), ventral surface
12. *Triblastula utinensis* (C-26), dorsal surface
13. *Tubotuberella apatela* (C-100), dorsal surface




All views of ventral surfaces unless otherwise stated (inserts included)

1A,B *Alisocysta circumtabulata* (T-94)
2A,B *Alisocysta margarita* (T-92)
3A,B *Alisocysta reticulata* (T-98)
4. *Egmontodinium expiratum* (J.-11)
5. *Egmontodinium polyplacophorum* (J.-13)
6. *Egmontodinium torynum* (C-97)
7. *Lanterna* sp. (J.-12)
8. *Leberidocysta chlamydata* (C-41)
9,10 *Lithodinia deflandrei* (J.-36), dorsal surface
11. *Lithodinia jurassica* (J.-39)
12. *Lithodinia stoveri* (C-87), dorsal surface
13. *Sirmiodiniopsis orbis* (J.-27)
14. *Sirmiodinium grossii* (C-86), dorsal surface
15. *Xiphophoridium alatum* (C-50), dorsal surface

**Figure 19.** Group XI, *LITHODINIA* Group.

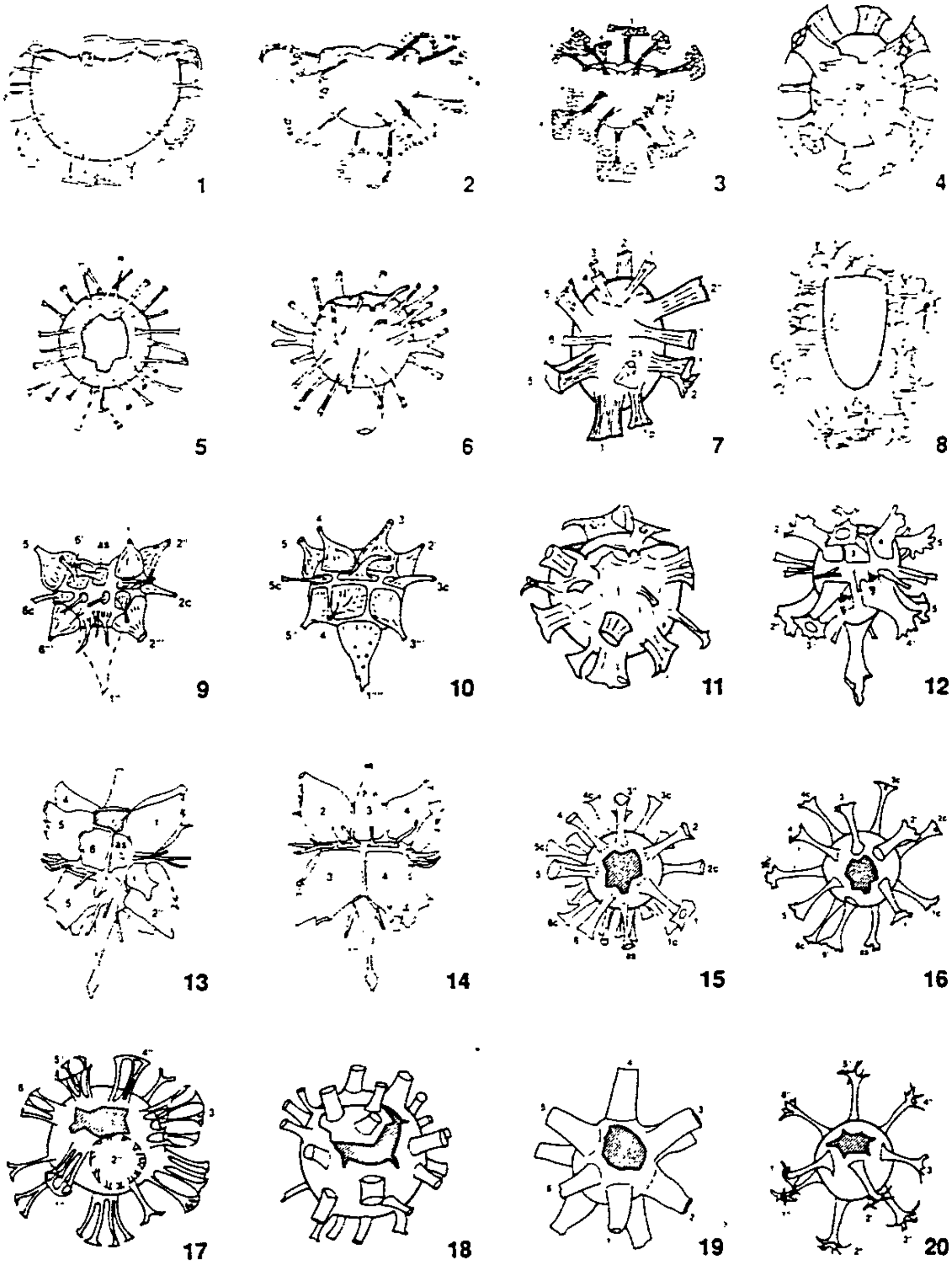


**Figure 9.** Group III, Subgroup IIIB, *HYSTRICHOSPHAERIDIUM* Subgroup.

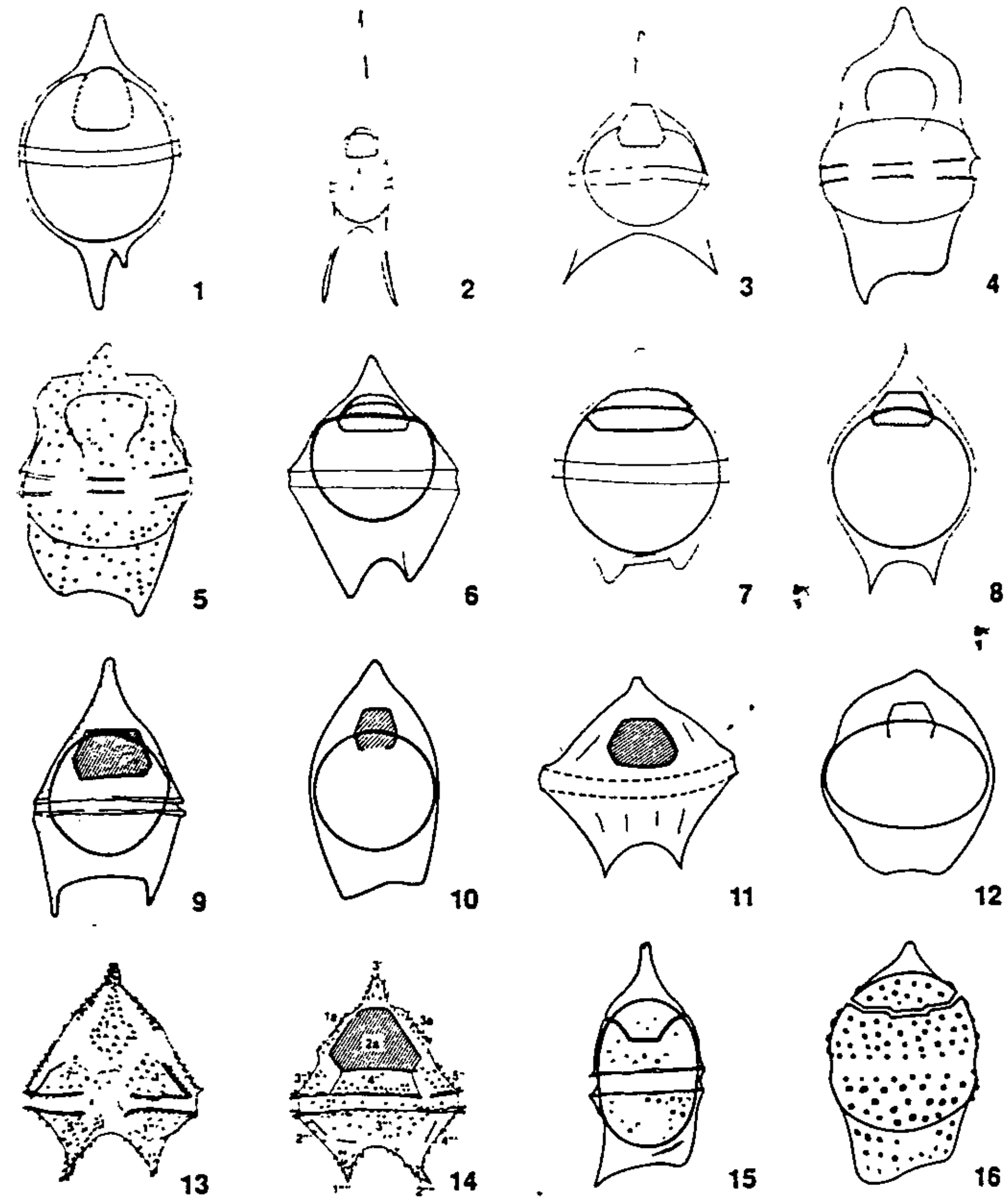
1. *Adnatosphaeridium multispinosum* (T-75), ventral surface
2. *Areosphaeridium arcuatum* (T-53), ventral surface
3. *Areosphaeridium diktyoplokus* (T-66), ventral surface
4. *Compositosphaeridium polonicum* (J.-33), ventral surface
5. *Dapsilidinium pseudocolligerum* (T-25), apical surface
6. *Diphyes colligerum* (T-69), ventral surface
7. *Discorsia nanna* (C-79), ventral surface
8. *Distatodinium paradoxum* (T-37), lateral surface

9,10 *Hystrichokolpoma bulbosum* (T-105), ventral and dorsal surfaces, respectively

11. *Heterosphaeridium difficile* (C-52), ventral surface
12. *Hystrichokolpoma rigaudiae* (T-15), dorsal surface

13,14 *Hystrichokolpoma cinctum* (T-43), ventral and dorsal surfaces, respectively

15. *Hystrichosphaeridium salpingophorum* (T-87), apical surface
16. *Hystrichosphaeridium tubiferum* (T-83), apical surface
17. *Hystrichosphaerina schindewolfii* (C-78), oblique apical surface
18. *Litosphaeridium arundum* (C-70), oblique apical surface
19. *Litosphaeridium siphoniphorum* (C-59), apical surface
20. *Oligosphaeridium complex* (T-81), apical surface



All views of dorsal surfaces unless otherwise stated
1. *Andalusiella* sp. (T-101)
2. *Cerodinium diebelii* (T-106)
3. *Cerodinium speciosum* (T-86)
4. *Chatangiella ditissima* (C-44)
5. *Chatangiella verrucosa* (C-42)
6.-8. *Deflandrea phosphoritica* (T-45)
9. *Deflandrea oebisfeldensis* (T-91)
10. *Isabelidinium* sp. (C-31)
11. *Lejeunecysta* sp. (T-8)
12. *Manumiella? cretacea* (T-107)
13,14. *Lentinia serrata* (T-70), ventral surface (13)
15. *Ovoidinium cinctum* (C-67)
16. *Ovoidinium verrucosum* (C-65)

**Figure 14.** Group VII, *DEFLANDREA* Group.

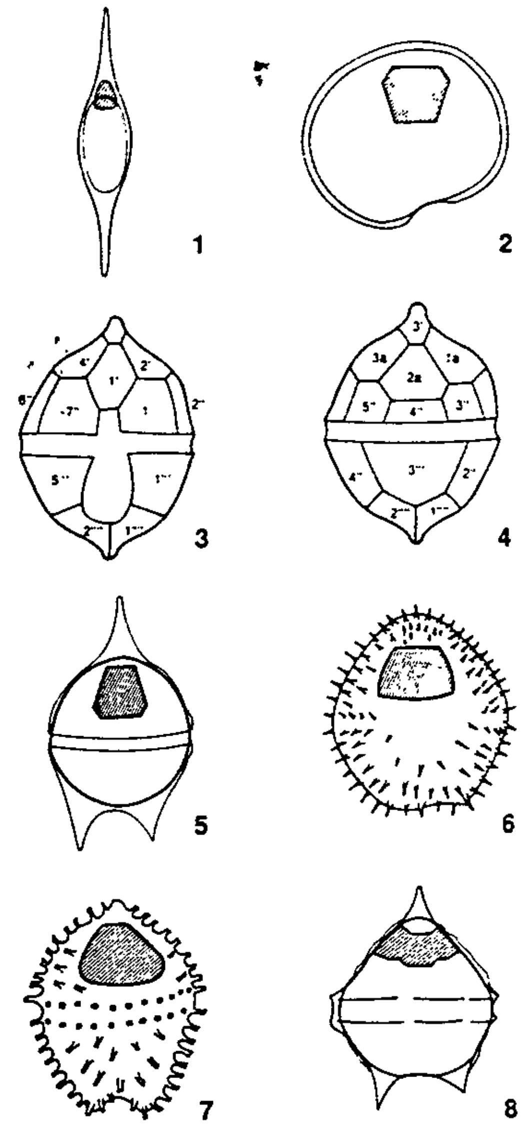
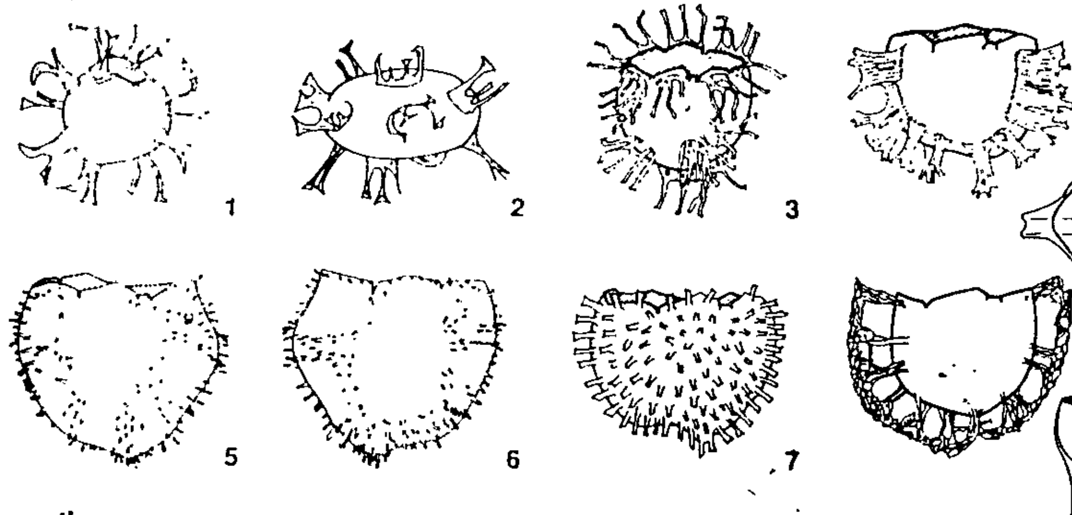


**Figure 15.** Group VII, *DEFLANDREA* Group. (cont.)

All views of dorsal surfaces unless otherwise stated
1. *Palaeocystodinium golzowense* (T-26)
2. *Selenopemphix* sp. (T-7), apical surface
3,4 *Phthanoperidinium* sp. (T-51), ventral surface (3)
5. *Senegalinium* sp. (T-59)
6. *Sumatradinium* sp. (T-22)
7. *Trinovantedinium capitatum* (T-4)
8. *Trithyrodinium* sp. (T-99)



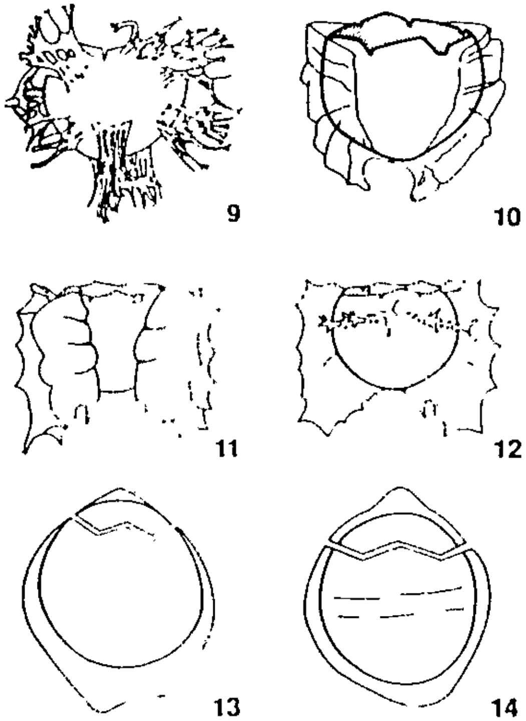
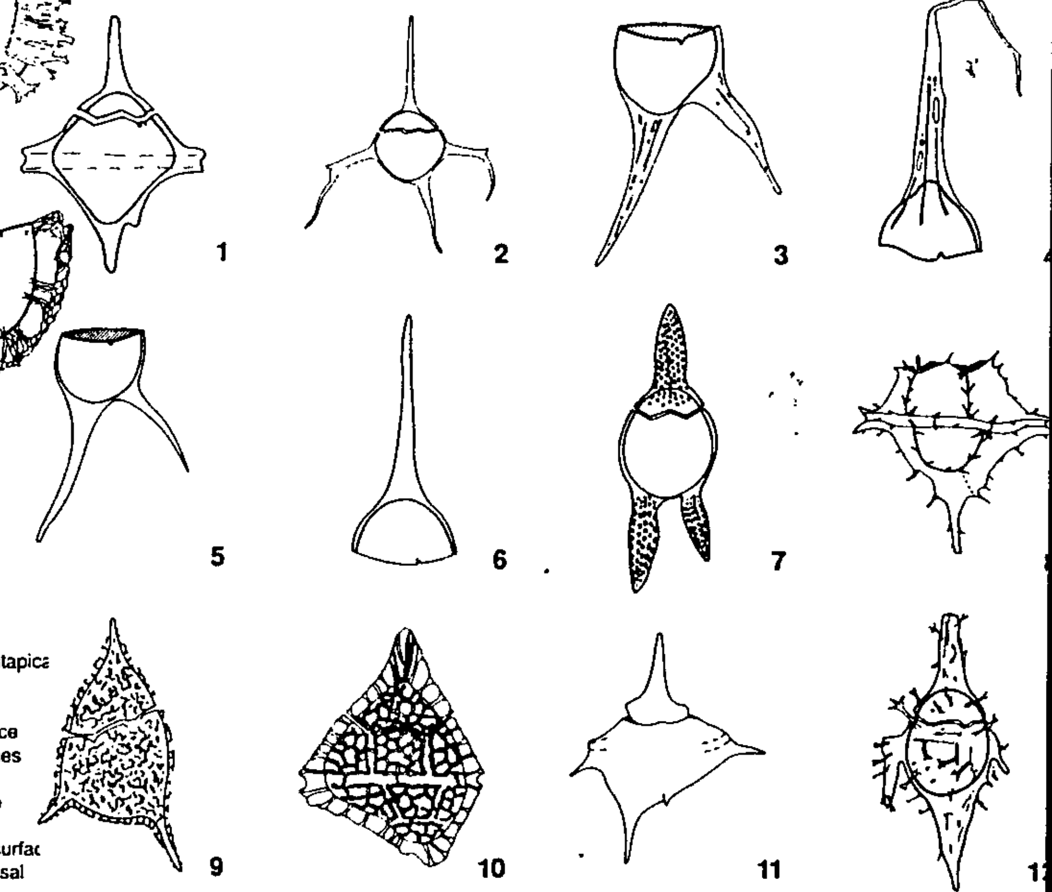


**Figure 13.** Group VI, *GLAPHYROCYSTA* Group.

1,2 *Areoligera? semicirculata* (T-55), ventral and antapical surfaces, respectively
3. *Areoligera senonensis* (T-82), ventral surface
4. *Chiropteridium mespilanum* (T-36), ventral surface
5,6 *Cerbia tabulata* (C-82), ventral and dorsal surfaces
7. *Circulodinium distinctum* (C-28), ventral surface
8. *Glaphyrocysta exuberans* (T-73), ventral surface
9. *Glaphyrocysta ordinata* (T-85), dorsal surface
10. *Membranophoridium aspinatum* (T-42), ventral surface
11,12 *Palynodinium grallator* (C-25), ventral and dorsal surfaces, respectively
13. *Senoniasphaera inornata* (T-103), dorsal surface
14. *Senoniasphaera jurassica* (J.-14), dorsal surface



1. *Muderongia simplex* (C-94), dorsal surface
2. *Muderongia tetracantha* (C-83), ventral surface
3,4 *Odontochitina costata* (C-39), ventral surface and operculum
5,6 *Odontochitina operculata* (C-35), ventral surface and operculum
7. *Odontochitina porifera* (C-51), dorsal surface
8. *Phoberocysta neocomica* (C-88), dorsal surface
9. *Pseudoceratium pelliferum* (C-85), dorsal surface
10. *Pseudoceratium polymorphum* (C-73), dorsal surface
11. *Vesperopsis* sp. (C-66), ventral surface
12. *Xenascus* sp. (C-32), ventral surface

**Figure 12.** Group V, *MUDERONGIA* Group.