

Tanta University
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Dinoflagellate cysts: principals

Essay

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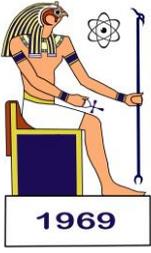
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Rania Abdel Raouf



جامعة طنطا
كلية العلوم
قسم الجيولوجيا

الحويصلات السوطية الدوارة

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بِسْمِ اللَّهِ الرَّحْمَنِ الرَّحِيمِ

قَالُوا سُبْحَانَكَ لَا عِلْمَ لَنَا إِلَّا مَا

عَلَّمْنَا إِنَّكَ أَنْتَ الْعَلِيمُ الْحَكِيمُ

صدق الله العظيم

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ABSTRACT

Dinoflagellates are a major component of the marine microplankton and, from fossil evidence, appear to have been so for the past 200 million years. In contrast, the pre—Triassic record contains only equivocal occurrences of dinoflagellates despite the fact that comparative ultrastructural and molecular phylogenetic evidence indicates a Precambrian origin for the lineage. Thus, it has often been assumed that the dearth of Paleozoic fossil dinoflagellates was due to a lack of preservation or recognition and that the relatively sudden appearance of dinoflagellates in the Mesozoic is an artifact of the record. However, new evidence from a detailed analysis of the fossil record and from the biogeochemical record indicates that dinoflagellates did indeed undergo a major evolutionary radiation in the early Mesozoic....

ARABIC SUMMERY

فريدة من نوعها بين المجموعات الرئيسية للالأولانيات غير المعدنية في وجود السجل الأحفوري واسعة، وهو رقم قياسي تتكون أساسا من أشكال صوانية العضوية الجدران، الجيرية ونادرة، على وجه الحصر تقريبا الخراجات. كوكوليثوفوريد هي المكونات الهامة للبيئة البحرية والكانتات الحية في المياه العذبة اليوم وتمثلها المتحجرات وفرة في الترياسي العلوي والطبقات الأصغر سنا. السجل الأحفوري من كوكوليثوفوريد يعتمد إلى حد كبير هو سمة غريبة على التكيف إلى مرحلة معينة في دورة حياة بعض الأنواع فقط. على سبيل المثال، كوكوليثوفوريد هي السمات المشتركة من الطبقات الرسوبية البحرية. على النقيض من ذلك، رواسب المياه العذبة غير شائعة نسبيا

الميزات لأحدها في الاعتبار عند تحديد الخراجات الأسواط تشمل ما يلي:
الملاح العامة (على سبيل المثال، حجم، وشكل، ومعايير التوجه): الأسواط تتراوح في حجمها من الأصناف واحد إلى آخر. عموما، كوكوليثوفوريد الأحفوري الكبيرة وأوضح خصوصا في أواخر العصر الطباشيري المبكر والتعليم العالي. بالإضافة إلى، شكل الخراجات يلعب دورا هاما في الأهمية ل، توجهات تعتمد على شكل ويفضل بشدة في بعض antapical قمية-direction.there البيولوجية. الخراجات تنحرف عادة من قبل كروية استطالة في الأنواع التي العينات هي تقريبا لم يسبق له مثيل في غيرها من المواقع. هيكل الجدار والسمات السطحية: جدار الكيس، وهيكلها وزخرفة السطح. النظر في العناصر المتنوعة للإغاثة سطح المنخفضة والعالية التي تشكل ما يشار إليه عادة باسم زخرفة، والعلاقة بين الجدار إلى البيولوجي هو أهمية وظيفية من شكل الكيس والإغاثة السطحية في البيئة الهيدروديناميكية على البحر أو من الخصائص التي amixture، والجمع بين لإنتاج cystemorphic و thecamorphic البحرية. ملاح في وعلى جدار الكيس، والتي يمكن تمييزها كما قدر الغرز قرابي لوحات منفصلة قرابي paraplates هو مميز لكل نوع. ملاح أبسط وأكثر وضوحا السطح هي التلال أو الحاجز الذي وضع علامة قبالة أنه كان مسؤولا ليس فقط لتحديد الأول من كوكوليثوفوريد في السجل الأحفوري، ولكن أيضا لقبول المبكر من رفاتهم كما قراب متحجرة .

هو ذو وصاد في معظم الأنواع، ولكنه قد يكون archeopyle: هو فتحة في جدار الكيس من خلالها البروتوبلازم يظهر خلال انقباض. و archeopyle أو thecamorphic تحتل مكانة خاصة بين شخصيات من الخراجات الأسواط. لا يمكن استيعابها في تعاريف إما ميزات archeopyle. و slitlike أيضا cystemorphic، بل تقي بمتطلبات كلا المجموعتين.

، المتكافئة أو الطفيليات. الأنواع الضوئي (ذاتية التغذية) تمثل حوالي phagotrophs ذاتية التغذية، □ agellates على كل، قد يكون الذين يعيشون دينو نصف عدد الذين يعيشون أجناس الأسواط. بعض الأنواع لديها استراتيجية الغذائية أكثر من واحد (سواء الطفيلية والتمثيل الضوئي). وتتميز أجناس في المقام الأول peridinialean وأخيرا، جدولة هو الآن، وبعيدا الطابع المورفولوجي الأكثر أهمية في النظاميات المعيشة كوكوليثوفوريد من خلال أوجه الاختلاف في عدد وترتيب لوحات، والاختلافات الطيفية في شكل لوحة وترتيب وغالبا ما تكون ذات دلالة إحصائية عند مستوى الأنواع. topologic وسوف دائما تكون ممثلة أنماط الجدولة بواسطة الصيغ جدولة متطابقة. فمن المهم للتمييز الجوانب الهندسية و

Chapter I

INTRODUCTION

Dinoflagellates are microscopic in size and occupying a position among the most primitive eukaryotic organisms, dinoflagellates are algal unicells referred to the division of the plant kingdom. Dinoflagellates are important constituents of the marine and freshwater biota today and are represented by abundant fossils in Upper Triassic and younger strata. They are unique among the major groups of non-mineralized protists in having an extensive fossil record, a record composed primarily of organic-walled, calcareous and rare siliceous forms, almost exclusively cysts, in Mesozoic and Cenozoic rocks. It is biological and biochemical evidence indicates an ancient Precambrian origin for the dinoflagellate lineage. However, virtually all fossils recognizable as dinoflagellates are from Mesozoic and Cenozoic sediments.

The name "Dinoflagellata", from the Greek dinos, "whirling rotation and the Latin flagellum, "small

whip". Hence, loosely translated, dinoflagellates are whirling, whip-bearing organisms. They have also been informally termed "the grass of the sea (Bujak & Williams 1980) because of their importance as primary producers in the oceans, and "the dancing dust of the sea" (Harland 1985) in reference to their size and motility.

Preservable cysts produced by only about 13-16% percent of living species (Head 1996) and therefore the fossil record of dinoflagellates is clearly incomplete. This fact has been used to suggest that the fossil record may not reflect the broad pattern of dinoflagellate evolution (Evditt1981). However, new evidence involving:

- 1- A detailed analysis of the fossil record and the evolutionary patterns indicated by it.
- 2- An investigation of biogeochemical markers (Moldowan et al. 1996) supports the premise that, although dinoflagellates probably existed in the Paleozoic, the major diversification of the group occurred during the early Mesozoic and is responsible for the modern dinoflagellate flora.

Dinoflagellates are commonly regarded as a principal component of the modern marine phytoplankton. However, only about half the known species are autotrophic, the remainder being heterotrophic; indeed, some species have both nutritional modes. Dinoflagellates include forms having planktonic to whole benthic lifestyles and they inhabit a range of environments from oceanic to freshwater. They are of major economic importance, aside from their position at or near the base of the food chain, as primary causal agents of paralytic shellfish poisoning and related toxic phenomena (red tides). These primarily single-celled protists are recognizable by one of two features (Fensome, et al.1993):

- (1) a unique type of nucleus termed a dinokaryon, that lacks histones and in which the chromosomes remain condensed throughout the mitotic cycle.
- (2) a stage in the life cycle with two dissimilar flagella. As in related protists such as ciliates dinoflagellates typically have a layer of vesicles in the outer region of the cell. In dinoflagellates these vesicles, termed amphiesmal vesicles, commonly enclose cellulosic (thecal plates. These plates occur in characteristic arrangements (tabulation patterns) that are the principal morphological means of establishing relationships within the group.

As they offer a rich and extensive fossil record characterized by high morphological diversity and rapid evolution-a combination that means excellent potential for geologic dating and correlation, they are important impetus has been given to the study of dinoflagellate cysts in recent years by their role in petroleum exploration, where their small size, abundance in many strata deficient in other fossils and broad geographic distribution combine with their resistant composition and rapid evolution to make them highly useful in subsurface stratigraphic studies. Reciprocally, the wealth of observations that have accumulated over the last 25 years as a consequence of this practical application of dinoflagellate cysts has helped advance their scientific study.

Chapter II

ASPECTS OF THE DINOFLAGELLATE FOSSIL RECORD

2.1. Selectivity of the dinoflagellate fossil record

The fossil record of any group of organisms presents the paleontologist with highly selected data that have been processed by a complicated interplay of many factors. Quantitatively, the record is only an infinitesimal sampling of the individuals that once lived. Both quantitatively and qualitatively, it is strongly biased with respect to certain organisms by circumstances of habit and habitat during life; by the size, shape, and composition of their preservable parts; by the nature of the enclosing sediment; by the post depositional history of the site of deposition; even by the matter of chance that determines the discovery and study of particular fossils. The fossil record of dinoflagellates largely depends is an adaptive feature peculiar to a certain stage in the life cycle of only certain species. That not all species produced cysts has profound consequences for palynologists and for the conclusions they and others draw from their observations.

Four generalizations derived from collective observations on living and fossil dinoflagellates have bearing on this selectivity:

1. Biological considerations imply that dinoflagellates were present throughout the Phanerozoic and probably much earlier, but from the rock record of much of this time we have no recognized dinoflagellate fossils. The primitiveness of dinoflagellates, makes it highly probable that dinoflagellates evolved long before the metazoans appeared about 700 million years ago. That we see no record of their early existence obviously has two possible explanations: either no traces of them have been preserved, or we have not recognized them as dinoflagellates.
2. Production of preservable resting cysts is a limited phenomenon among dinoflagellates. Despite recognition that sexual reproduction is probably a normal part of the life cycle of dinoflagellates, only in a minority of species living today is the cyst enclosed in a wall of geologically resistant material. In the majority, either the sexual phase of the cycle is completed without formation of a resting cyst or the encysted cell lacks a geologically preservable container. In other words, only a relatively few living species produce fossilizable remains. We must conclude that many dinoflagellate species lived without leaving fossilizable traces.
3. Production of preservable resting cysts is a quantitatively variable phenomenon. -Although we do not know precisely what stimuli lead to encystment or what controls determine the number of cysts produced, numerous observations on modern plankton and bottom sediments show that, in any given area, no simple or constant relationship exists between the number of resting cysts, on the one hand, either the number of actively metabolizing vegetative cells or the number of cyst-producing species, on the other. Extrapolated to the fossil record, this implies that, for those dinoflagellate. The relationship between number of cysts,

number of vegetative cells, and number of cyst-producing species varied from time to time and place to place. If that was the case, nothing in the preserved record of dinoflagellates can now reveal to us the changing quantitative values of this relationship.

4. Even within a single reasonably low-level taxon-- say, a genus or family-cyst production may be characteristic during one interval of geologic time, but not another. --This important conclusion cannot be based on observation of the living biota alone, which amounts to drawing samples from a single time plane, but must also take into account evidence that comes from the fossil record. The following three examples germane to this point involve the genera *Ceratium*, *Arpylorus*, and *Protoberidinium*.

That conclusion has some interesting ramifications which we will pursue some interesting ramifications which we will pursue in the following paragraphs.

First. Paleontologists are accustomed to estimating assemblage size and population density by counting numbers of species and individuals. But, from counts of the number of fossil dinoflagellate cysts, one can never arrive at the composition of an assemblage in terms of dinoflagellate species. One cannot estimate the population density in terms of numbers of living individuals per unit of sediment. All that one can determine is the number of species or individuals of dinoflagellate cysts. Lists of dinoflagellate species look like any other species lists. That they tell a different story from one is in no way apparent by inspection. Conceivably the usual 10 species of fossil cysts could represent 20, 50, or 100 dinoflagellate species, and 10 individual cysts could represent 100, 1,000, or 10,000 motile cells- and each at different times or in different samples.

Second. The temporal sequence in which distinctive morphological features appear among fossil dinoflagellates and this includes the highly useful and taxonomically important paratabulation patterns- cannot be accepted as an accurate record of the evolutionary sequence in which these features developed. Thus, it cannot serve either as a reliable guide to phylogenetic ruminations or as an effective constraint upon them. The earliest appearance of a dinoflagellate character in the fossil record establishes only the latest-date by which it had been developed. The much earlier presence of the same features may be unrecorded only because they happened to occur in a non-cyst-producing species that left no detectable remains.

Third and finally, changes, in observed numbers of fossil cysts have any validity as evidence for amounts of photosynthetic activity and consequent changes in levels of atmospheric oxygen or carbon dioxide, which have been speculated to play a role in major events extinction.

2.2. Cysts from freshwater deposits

Reliably identified freshwater deposits are relatively uncommon in the Mesozoic-Cenozoic stratigraphic record, and rather few fossil dinoflagellates have been described from them. Churchill and Sarjeant (1963) reviewed the history of their study, and Bradford (1978a) gave extensive references to Pleistocene and Holocene records from sediments. Pre-Pleistocene freshwater cysts were described from the Eocene by Krutzsch (1962) and Harland and Sharp (1980), from the Oligocene by Evitt (1974), and

from the Miocene by Engelhardt (1976). None are known with certainty from Mesozoic deposits.

2. 3. Fossil dinoflagellates versus acritarchs

When the morphology of a living specimen suggests that it is a dinoflagellate cyst, at least the possibility exists to test the suspicion by examining the cell contents for critical properties. However, identification of empty cysts, must rest on morphological criteria must rest on morphological criteria alone. Comparison of modern cysts with one another quickly teaches us an important lesson in this regard: some have more dinoflagellate-like properties than others, and some have no morphological properties diagnostic of dinoflagellates at to say, there is potential overlap in size, composition, and form between nondescript dinoflagellate cysts and the fossils that have been called acritarchs (Evitt, 1963).

Since calling a specimen an acritarch is to point out that its biological affinity is unknown, the critical question is: What minimum set of particular characteristics will be required of a specimen to justify calling it a dinoflagellate? Of the many possible answers, the one that will guide us here is the following: To be considered a dinoflagellate, a fossil specimen having appropriate size traces of features having the position, extent, and mutual relationships of a cingulum and sulcus, or traces of a pattern of polygons consistent with a thecal tabulation, or both .The traces referred to may be quite incomplete and they may take various forms, some of them quite unlike the thecal features referred to. Therefore, it is pattern, position, extent, and mutual relationship-not form-that are important.

These criteria, even if widely accepted, will not distinguish between dinoflagellates and non-dinoflagellates, but only between objects that can be identified as dinoflagellates with a certain degree of confidence and those that cannot.

2.4. Taxonomy and Nomenclature

Fossil dinoflagellates have been treated by different authors under both the zoological and botanical codes of nomenclature. As appreciation of the morphological differences in detail between fossil and modern dinoflagellates grew, new generic names were proposed for the fossils. In addition, very real uncertainties about detailed biological relationships of modern genera based on thecae with fossils based on cysts. Pertinent considerations include the following:

- a. The greater morphological complexity of the encysted stage, combined with the stratigraphic application of fossil cysts, has favored much narrower circumscription of genera based upon cysts than genera based on modern thecae.
- b. A single species may have more than one cyst morphotype, or that the cysts of two different species may be much more distinct than their thecae.
- c. The fact that many living species do not produce cysts threatens to leave the place of those species in a joint cyst-theca taxonomy.

2.5. Stratigraphic distribution

The oldest fossil known to date that has been accepted widely as a dinoflagellate is *Arpylorus antiquus* from the Late Silurian of North Africa (Evitt, 1967; Sarjeant, 1978). Taxa originally reported from the Permian are either not dinoflagellates (Stover and Evitt, 1978) or probably represent contamination from younger sediments (Jansonius, 1962). No other dinoflagellates have been reported from the Paleozoic or Early Triassic.

Triassic dinoflagellates, first reported from the Rhaetian by (Sarjeant, 1963), are now known to be abundant and varied beginning with strata of Carnian age and possibly older (Anisian). Many show no paratabulation, although shapes and wall structure (proximate and cavate) are more or less "conventional". Some associated spinose bodies may also be dinoflagellate cysts, but so far they have not been shown to include diagnostic dinoflagellate characters.

Chapter III**BASIC ORGANIZATION OF THECA AND CYST****3.1. Major features and cyst orientation**

The terminology for cyst features which we will begin to develop at this point will be a selective one (Williams et al., 1978). The main regions of the cyst that correspond to the epitheca, cingulum, hypotheca, and sulcus of the theca are, respectively, the **epicyst**, **paracingulum**, **hypocyst**, and **parasulcus**. Whereas the theca proper never has more than one visible layer, any one cyst may be constructed of from one to three layers out of a total of at least four different layers. Also unlike the theca, none of these cyst walls is separable into plates along sutures. However, the surface of the cyst may bear **parasutures** in the form of ridges or other linear elements, which, simulate thecal sutures and divide the surface into more or less polygonal areas that resemble thecal plates. Such polygons on the cyst are especially clear and simple examples of **paraplates**, but any features on the cyst whose distribution approximates that of the thecal sutures are said to be **parasutural**.

Just as the tabulation comprises the number and arrangement of plates on the theca, the **paratabulation** encompasses the number and arrangement of paraplates on the cyst. Thecal tabulation has been the single most important criterion for the recognition of genera and species of living thecatellates. Cyst paratabulation has also been important in the taxonomy of fossil dinoflagellates.

Directional terms that apply to cyst and theca are shown in (Figure 3.1 B, D). The **apical**, or anterior end, and the **antapical**, or posterior end, are defined with respect to the principal direction of motion of the swimming cell. The sulcus and parasulcus are taken arbitrarily to mark the **ventral** surface. **Right**, **left**, and **dorsal** then follow automatically from the other directions. **Adcingular** is usable anywhere on the surface for expressing direction or location toward the cingulum.

Dimensional terms **length**, **width**, and **thickness** apply, respectively, to the anterior-posterior, right- left, and dorsal-ventral measurements. Terms such as "polar," "longitudinal," "latitudinal," of revolution are frequently useful and their meaning is normally obvious.

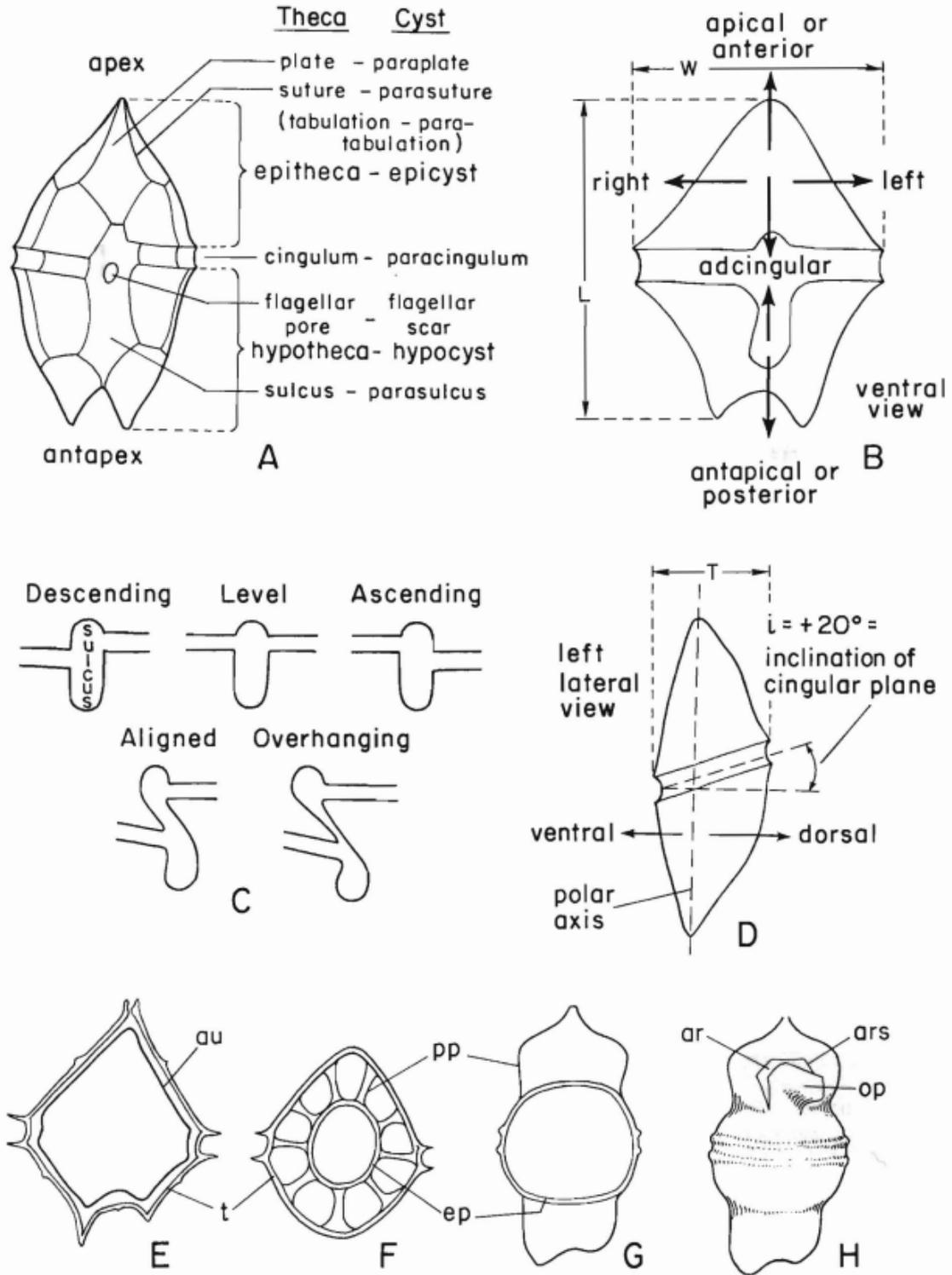


Figure 3.1 - THECA AND CYST - BASIC TERMINOLOGY AND ORGANIZATION

When outlines and patterns are asymmetrical, the taxonomist/microscopist who cannot tell right from left is certain to misidentify critical features and occurs both when viewing a specimen under the microscope and when viewing a photomicrograph or published figure. In each instance, a correct interpretation depends upon two pieces of information about the specimen : the identity of the surface

under inspection, and the direction from which it is being seen.

In most living and fossil species the cingulum is about **level**, or the right end is posterior to the left as the consequence of a **descending** spiral (also called left-handed, sinistral, levorotatory). The opposite condition of an **ascending** cingulum is uncommon among living species and virtually unknown in fossil ones. Therefore, in dealing with fossil specimens it is safe to assume a descending cingulum. Depending upon the width and inclination of the sulcus, one end of a spiral cingulum may or may not **overhang** the other.

Most commonly the cingular plane (or its approxi-) If the cingulum lies closer to the apex on the dorsal surface than it does on the ventral, the cingular plane is said to have a positive inclination, the opposite inclination being negative.

If the cyst wall forms as a layer of material just inside the theca (Figure 3.1 E), the cyst necessarily resembles the theca more or less closely in size and shape. Such cysts are termed **proximate** and their external surfaces may be smooth. In contrast **chorate** cysts (Figure 3.1 F) have a spherical to ellip-soidal or lenticular central. Either proximate or chorate cyst may also be **cavate** (Figure 3.1 G-H); that is having a wall that is separated, at least locally, into an inner and outer layer by an enclosed cavity.

The **archeopyle** is the opening in the cyst wall through which excystment takes place. It is one of the especially important morphological features of the cyst (Figure 3.1 H). It is normally outlined by the **archeopyle suture**, a distinct line of separation in the cyst wall. Rupture of the wall along this suture commonly isolates a portion of the wall, the archeopyle operculum, which is dislodged or lost when the archeopyle opens.

3.2. Kofoid's system for analyzing thecal tabulation

Subdivision of the theca into plates and of the cyst into paraplates follows an orderly plan with differences from one taxon to another was suggested by Kofoid

(1907,1909a).

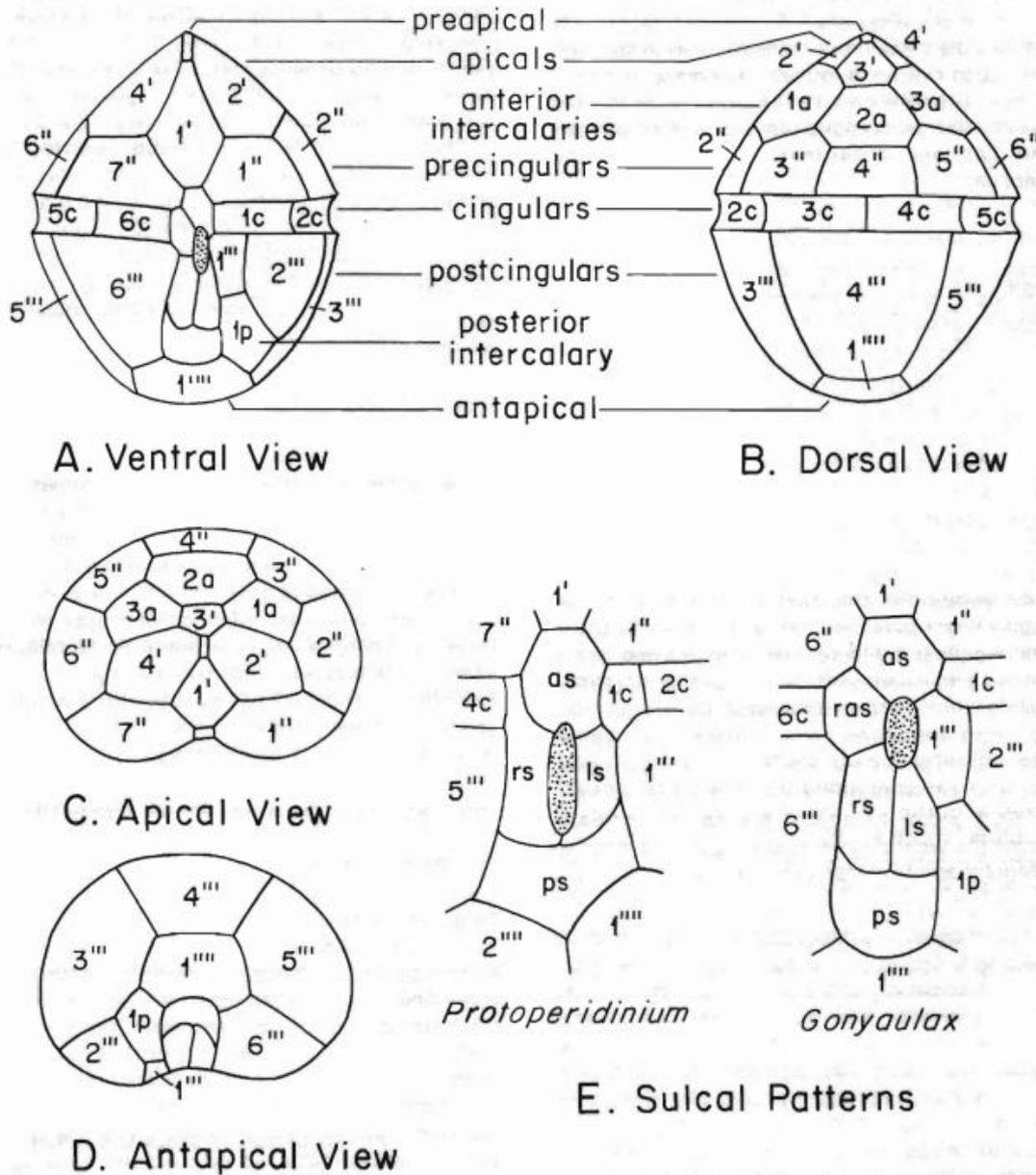


Figure 3.2 - KOFOIDIAN SYSTEM OF TABULATION

3.3. Size, shape, and preferred orientation of cysts

Although dinoflagellate cysts exhibit a great range of size, both within a single species and from one taxon to another, the impression seems well founded that the mean size of fossil dinoflagellate cysts is greater than that of the cells of living species. The reason for this size difference is not clear. Fossil cysts - in excess of 100µm are not uncommon but, with a few exceptions, cells with such a dimension would be considered relative giants among modern species. Large fossil dinoflagellates are especially conspicuous in the Late Cretaceous and Early Tertiary.

Zygotic cysts observed in sexually reproducing cultures of some modern dinoflagellates form within thecae that grow considerably larger than vegetative cells of the same species. Therefore, cyst size

may not be a safe guide to the dominant size of motile cells in a living population. Also, cyst size may be influenced by environmental conditions.

Subspherical to ellipsoidal cysts are common, just as are similarly shaped motile cells among living dinoflagellates. The possible adaptive significance of the more elaborate shapes is unknown.

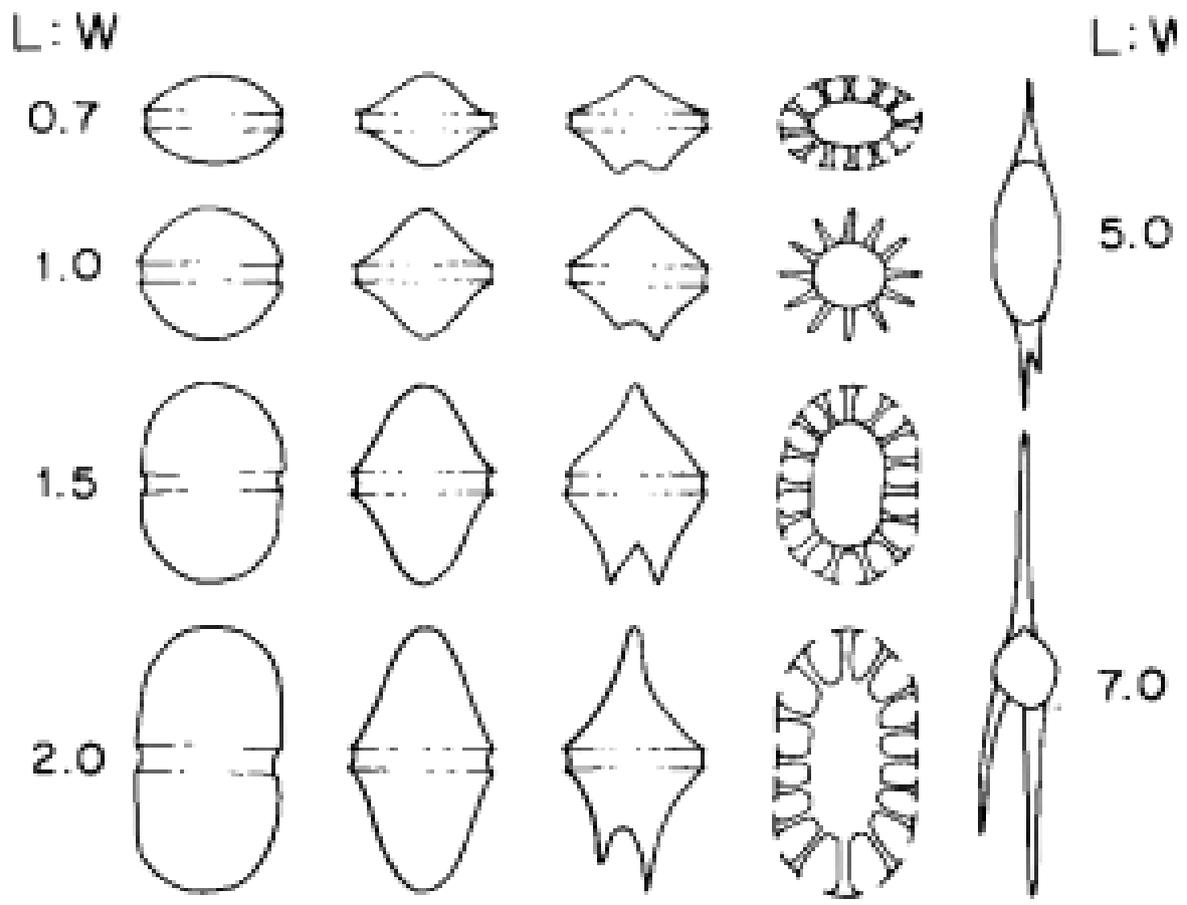
Cyst shape plays an important role in paleopalynology, quite apart from its biological significance, by influencing specimen orientation at two stages:

First, as the cyst settles on the original depositional interface. Any postdepositional compaction that may follow original sedimentation will normally serve only to accentuate those primary equidimensional shapes that determined an original departure from selective orientation. Orientations dependent upon shape are so strongly favored in some species that specimens are virtually never seen in other positions.

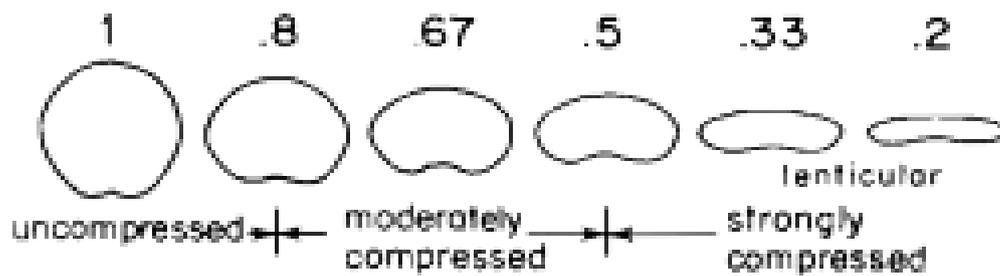
Cysts commonly deviate from sphericity (Figure 3.4): by elongation in the apical-antapical direction (= axial or longitudinal elongation); by primary compression or flattening, most frequently in a dorsoventral direction. Besides, dorsoventral compression is extremely rare in dinoflagellate cysts. Consequently, apical, antapical, and lateral views are relatively uncommon and for many species, truly exceptional. While lateral views are seldom critical for species identification, a polar view may be essential to reveal details of paratabulation critical for a reliable identification.

The transverse cross-section of the cyst may depart from circular in varying amounts. Commonly the parasulcus lies in a local excavation near the ventral midline, and much of the ventral surface may be a broad concavity. Alternatively, dorsal and ventral surfaces may be nearly planar and parallel, and the lateral surfaces reduced to narrow strips. The term **lenticular** has been applied to cysts whose main body shows strong dorsoventral compression without pronounced elongation.

One to several major projections, or **horns**, rise at specific locations from the thecae of many species of dinoflagellates and vary greatly in size. It on the cyst may also include short, solid projections, in addition to hollow extensions of the main body. Probably all horns on cysts represent what were slender continuations of the thecal cavity, rather than the solid projections.



A. Length : width ratios



B. Primary Compression

Figure 3.3 - DIMENSION RATIOS AND COMPRESSION

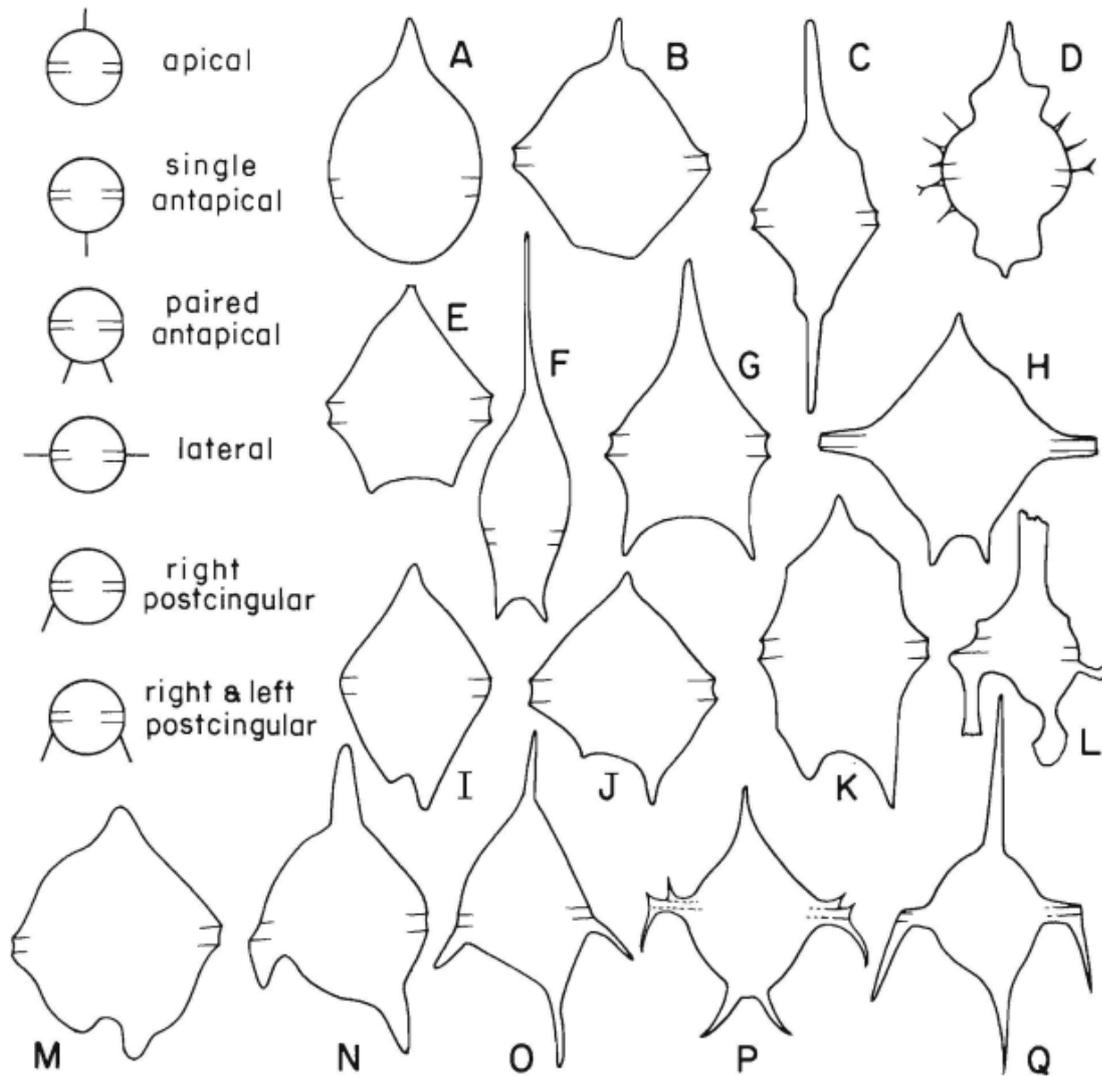


Figure 3.4- HORNS: CARDINAL LOCATIONS AND COMBINATIONS

Chapter IV

THE CYST WALL

4.1. Introduction

The relation of the wall to the biological processes that go on within the cell during encystment is

unknown, as is also the functional significance of cyst shape and surface relief in the hydrodynamic environment of the sea or lake. Study of fossil cysts especially has revealed great diversity in wall layering, internal structure of the layers, and relief on their surfaces. Electron microscopic examination of the wall has been tremendously informative, and scanning electron microcopy is becoming routine in conjunction with taxonomic studies. Nevertheless, up to this time only a small fraction of known species have been studied at the high magnification and with the special preparation that will be required before the wall gives up even those secrets that relate to its physical structure.

Thecamorphic features are always homologs of thecal features, as is evident from an toward similarity that may depend upon similar topography and relief (e.g., elevated margins of the cingulum, depression of the parasulcus) or on a similar position or distribution with alters (e.g., "negative" parasutures as grooves incised on the inner surface of the endocyst, or processes arranged along parasutural lines).

In contrast to the camorphic features, **cystomorphic features** (of which processes are a prime example) have no equivalents in outwardly similar features on the theca.

4.2. Wall layers

It employs three word stems to distinguish between a wall layer (**-ophragm**), the cavity which it encloses (**-coel**), and the three-dimensional body which it forms (**-cyst**). To these stems may be added a variety of prefixes which identify particular wall layers: **auto-**, **endow-**, **peri-**, **meson-**, and **ecto-**. The additional prefixes epic- and hypo- may also be used to specify the particular portion (i.e., "hemisphere") of the layer, cavity, or body under consideration. Examples, auto cyst, endophragm, epipericoel. Various types of wall stratification and terms applied to them are shown in (Figure 4.1).

In cysts with the simplest wall construction, a single wall, the **autophragm**, surrounds an internal cavity, the **autocoel**; and the three-dimensional body so formed is an **auto cyst** (Frontispiece D). Many cysts have a wall composed of only one layer or more. But the junction between closely appressed layers may be nearly impossible to see clearly, whereas phenomena of light refraction (i.e., Becke lines) may create the appearance of layering where none exists.

Endophragm and **periphragm** are, respectively, the inner and outer layers in many cysts with definitely two-layered walls. These layers may be in close contact or separated by a **pericoel** (Frontispiece B).

An **ectophragm**, a layer of highly varied character, is present external to either a periphragm or autophragm of some cysts (Figure 4.1 B-E). It may consist of a membrane that is continuous, perforate, or interrupted along parasutures, or it may be reduced in varying measure to rodlike or ribbonlike .

A further type of wall layer, the **mesophragm**, a thin layer lying between two other layers easily identified as periphragm and endophragm by comparison with other species.

It is useful to focus attention on the **cavation** of the wall (Stover and Evitt, 1978); that is, the form and distribution of the major cavities between layers, especially the pericoel. Thus, the terms **epicavate**, **hypocavate**, and **epicavate** may be used to describe cysts in which one cavity is confined to either the epicyst (Figure 4.1 L) or the hypocyst, or two cavities occur, one at each pole (Figure 4.1 G, I).

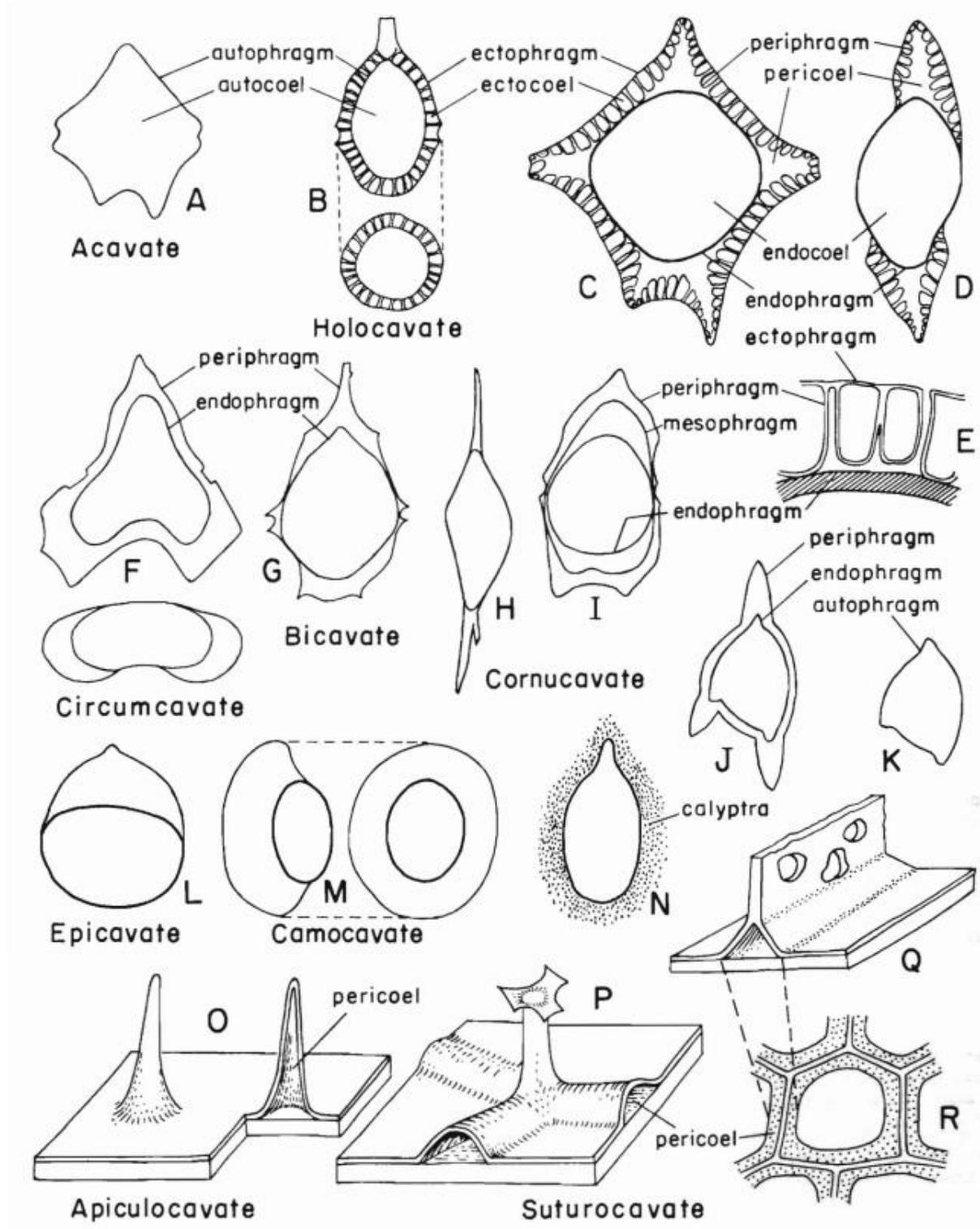


Figure 4.1 - SCHEMATIC EXAMPLES OF WALL STRUCTURE

In **holocavate** cysts an encircling cavity is evident in all directions of view, and supporting structures of some kind extend between the wall layers (Figure 4.1 B). By contrast, in **circumcavate** cysts, the cavity is continuous around the margin of the cyst as seen in dorsoventral view, (Figure 4.1 F). **Camocavate** cysts have the wall layers in contact or close together on one surface (Figure 4.1 M). Cysts in which cavities occur only at or near the bases of horns or equivalent structures are **cornucavate** (Frontispiece J, Figure 4.1 H); they are **suturocavate** (Benedek et al., 1982) if the cavities are restricted to the lines of parasutures (Figure 4.1 P-R) and **apiculocavate** (new) if restricted to the bases of spines or processes. **Acavate** cysts are without wall cavities.

A final kind of enveloping material, although hardly to be considered a part of the wall, is a **calyptra** (Figure 4.1 N). Looking like a gelatinous mass, irregular in thickness and closely surrounding the cyst, and are associated especially with certain pyriform to fusiform cysts of Late Jurassic and Early Cretaceous age.

4.3. Surface relief

The inner surfaces of autophragm, endophragm and periphragm are usually smooth, and the outer surface of the endophragm is either smooth or has features of only low to moderate relief. In contrast, the outer surface of an autophragm or periphragm may be extended into a great variety of projecting structures (Figure 4.2, 4.3).

Most projections from the autophragm or periphragm fall into two general categories: those which rise essentially from a point or very limited basal contact with the underlying surface, and those which rise from a linear base. The former, depending upon their height, include granules, verrucae, spinules, spines, and a host of structures collectively termed **processes**. Similarly, the linear elements grade from ridges or low folds into higher, fence-like **septa**, which have also been termed ledges, crests, or lists.

For cysts having projections in the lower part of the range (between about one to three-tenths of the main body diameter), the term **proximochorate** has been used, chorate cysts may be **skolochorate**, with processes, and **murochorate**, with septa.

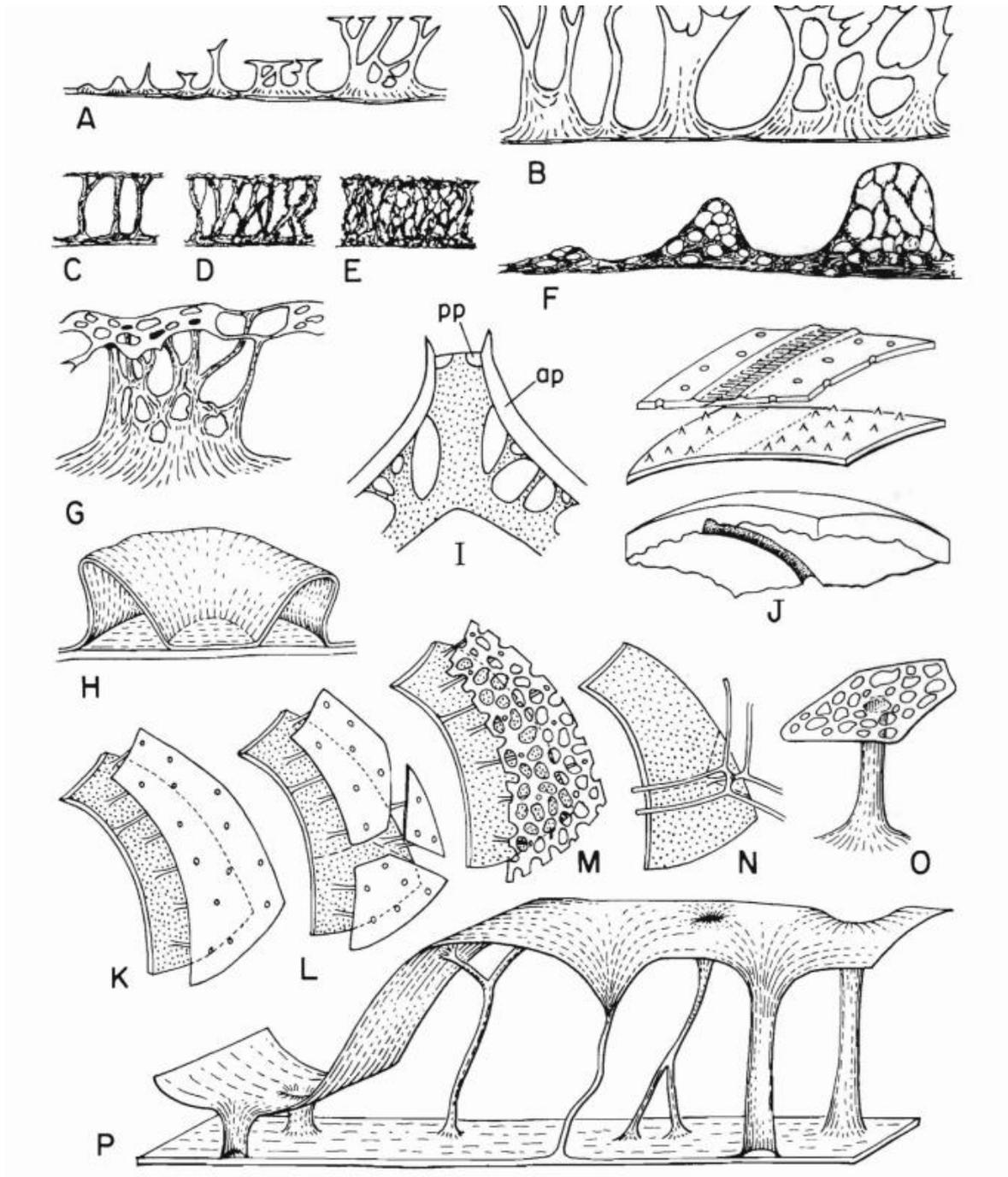


Figure 4.2 - SCHEMATIC DETAILS OF WALL FEATURES

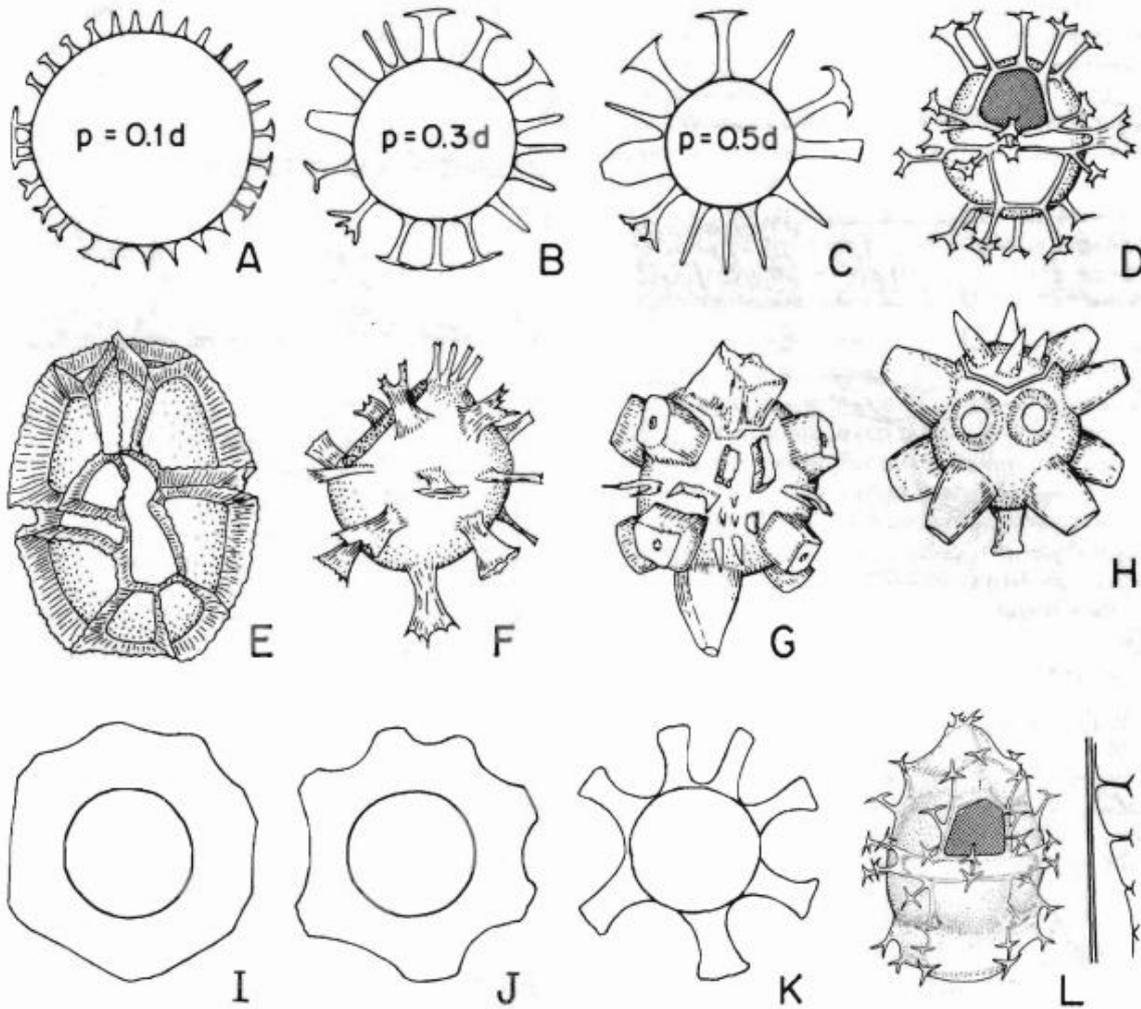


Figure 4.3 - SOME EXAMPLES FOR SURFACE RELIEF

4.4. Distribution of relief

The local elements of wall structure, whatever may be their exact form and whether or not they involve surficial or internal detail, may be distributed in different ways (Figure 4.4).

A distribution which gives no indication of paratabulation is termed **nontabular** and its elements may be uniformly or irregularly spaced. In contrast, a **tabular** distribution does indicate paratabulation and is said to be **parasutural** when it emphasizes the boundaries between paraplates or **intratabular** when it accentuates the central portions of paraplates more or less remote from these boundaries.

If the basal diameter of an intratabular feature is imagined to increase until it encloses most of the area of the paraplate, then the special case of a **penitabular** feature results. Penitabular features on adjacent paraplates may approximately parallel the paraplate boundaries. In principle, they form closed lines around each paraplate. When they run very close to the parasuture, the pairs of lines from adjacent paraplates may give the appearance of a single parasutural feature.

The simplest and most apparent parasutural features are ridges or septa which mark off paraplates much as thecal sutures separate thecal plates. It was responsible not only for the first identification of dinoflagellates in the fossil record, but also for the early acceptance of their remains as fossilized thecae.

Parasutural projections on a single cyst may be of uniform or varied design. Projections localized at the angles of paraplates are termed **gonal**, while those along paraplate sides between triple junctions are **intergonal**.

The zones of incremental plate growth intercalated along the thecal sutures in many modern species are clearly represented in some fossils by what have been called **pandasutural bands**. Like their thecal counterparts, these may even be transversely striate and vary in width from one part of the cyst to another.

Both external relief features and features within the wall may be affected. In External features may include elaborate processes or septa, often intricately expanded or interconnected. Internal features may include the empty pericoel or connecting structures of various types extending between inner and outer walls. Central reduction and marginal prominence of features is usually greater for the ventral surface than for the dorsal one.

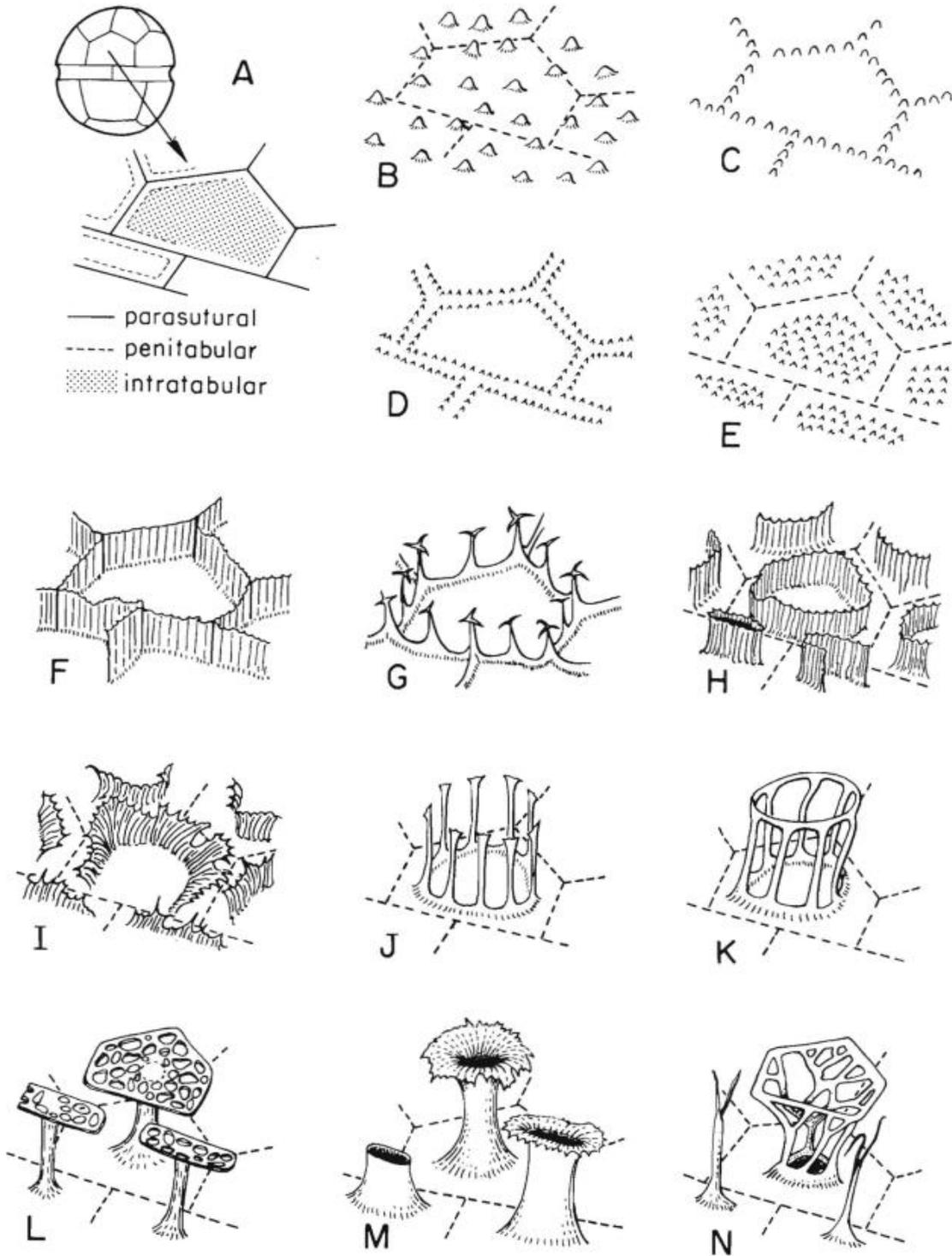


Figure 4.4 - DISTRIBUTION OF FEATURES

Chapter V

TABULATION AND PARATABULATION

Tabulation is far and away the most significant morphological character in the systematics of living peridinialean dinoflagellates. Genera are distinguished primarily by differences in the number and arrangement of plates, and minor differences in plate shape and arrangement are often significant at the species level. Aside from tabulation, the taxonomic criteria based on thecal morphology which are available to the systematist are limited to such features as thecal shape and surficial relief of the plates including the distribution of trichocyst pores. In the study of dinoflagellate cysts the conditions are rather different. Here two factors assure that paratabulation will never be so uniquely important a taxonomic character as is tabulation for dinoflagellate thecae. **First**, paratabulation is frequently expressed incompletely or imperfectly and, when this is so, no technique equivalent to dissection can make obscure paraplate boundaries more readily visible.

Second, the cyst commonly shows a greater diversity of morphological detail than the theca (in, for example, wall structure, surface ornament, and the archeopyle) and this detail is frequently more obvious and easier to analyze than paratabulation. Paratabulation provides a vitally important "conceptual" framework for organizing into a consistent whole the often incomplete observations assembled from multiple specimens.

The details of its patterns are important taxonomic criteria in those cases where the patterns are clearly and more or less completely displayed, just as tabulation patterns are for living thecate forms. Actually, paraplate shape for identifying particular paraplates, has been criticized by specialists on modern dinoflagellates (e.g., Balech, 1967b; Taylor, 1976a).

Given the broad spectrum of variation in plate shapes and tabulation patterns among modern thecate dinoflagellates. Differences in paratabulation depend mainly on one or a combination of the following four variables: **1)** the presence or absence of paraplates, **2)** the failure of certain parasutures to be recognizable, resulting in a lowered paraplate count, **3)** differences in the particular contacts made by a given paraplate with those near it, and **4)** differences in paraplate shapes resulting from different relative lengths of their sides. **The first**, or what may be called the distributional aspect of tabulation, pertains to the number of plates and their general placement in the theca.

The second aspect, is essentially topologic and concerns the mutual relationship of plates in the tabulation mosaic. **The third**, aspect is strictly geometric, involving the sizes and shapes of plates. Although these factors are obviously related to both plate distribution and topology, the concern here is specifically the number and dimensions of the sides and angles on the individual plates.

For the tabulation of a theca or the paratabulation of a cyst to be fully characterized, the first three of these aspects must all be considered, either explicitly or implicitly. Only the first, or distributional, aspect can be indicated by a tabulation formula in Kofoidian style. Unfortunately, the connotation given to "tabulation" is commonly limited to just this distributional aspect, and failure to give adequate attention to the topologic and geometric aspects of tabulation as well is responsible for the serious deficiency of many

taxonomic descriptions the topologic aspect concerns properties that are, probably, less familiar or less obvious. Topology, as a field of mathematical inquiry, is concerned with those properties of geometric configurations which are unaltered by elastic deformations (Figure 5.1).

Topologically entical tabulation patterns will always be represented by identical tabulation formulae. The importance of distinguishing the geometric and topologic aspects of tabulation patterns is illustrated in (Figure 5-1). Although the shapes of plates and paraplates are almost endlessly varied in detail, an effort to distinguish two general shapes that have proved descriptively useful has led to several alternative terms among which the "fittest" have yet to be selected.

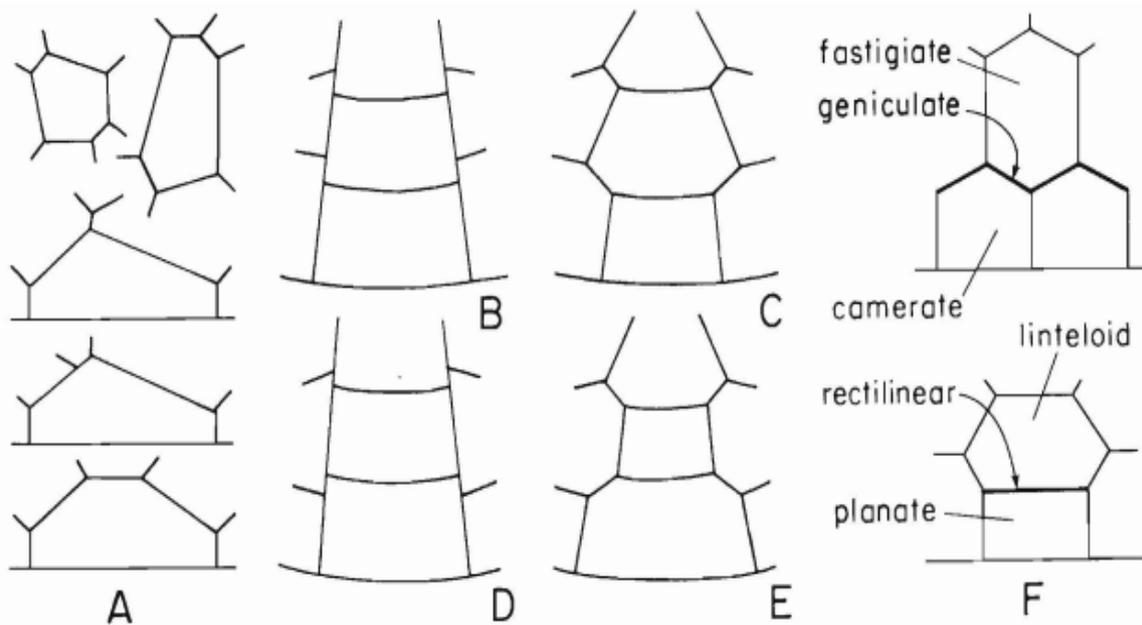


Figure 5.1- TOPOLOGY AND SHAPE OF PLATES

The somewhat overlapping scopes of these terms should be clear if the following definitions are considered along with the diagrams in (Figure 5.1 F): **Planate** (Bujak, 1980) describes a plate that appears to contact the next more poleward series along a line essentially parallel to the cingulum . **Geniculate** (Evvit, 1978) refers to the angular boundary between two latitudinal series in fossil Representation.

This is one of the two most commonly encountered groups of patterns among fossil cysts, occurring in many distinctive species with diverse morphologies. Both proximate and cavate cysts are common but chorate cysts are extremely rare. Modern Examples. These include *Protoperidinium*, hundred marine species until recently (Balech, 1974) attributed to *Peridinium*; *Peridinium* S.S., now represented by a moderate number of almost exclusively freshwater species; and a small number of other marine genera with one to a few species each.

Thecae of modern peridinioid species vary in shape from subspherical to peridinioid and are often

dorsoventrally compressed. In modern peridinioid thecae, preapicals may be quite obvious, but equivalent paraplates in cysts are only rarely apparent, for they are small and occur in an area where cyst details are commonly difficult to observe. On the ventral surface, the variations involve the shape of the first apical plate (depending upon whether it contacts two, three or four precingulars) and these three styles are known, respectively, as **ortho**, **meta**, and **para**. On the dorsal surface, the second intercalary contacts one, two, or three precingulars, and these arrangements long have been referred to **quadra**, **penta**, and **hexa** (Evitt, 1978).

Chapter VI

THE ARCHEOPYLE

The archeopyle (Evitt, 1961, 1967) is the opening in the cyst wall through which the protoplast emerges during excystment. The archeopyle is operculate in most species, but it may also be slitlike. The etymological reference of the term to an opening in ancient (i.e., fossil) dinoflagellates is no longer appropriate, for archeopyles are well known in cysts of living species, although this was not so at the time it was proposed.

Gocht, (1983, p. 268-269) commented that the archeopyle occupies a special position among the characters of dinoflagellate cysts. In the first place, it cannot be accommodated in the definitions of either thecamorphic or cystomorphic features; it meets the requirements of both groups. Further, the formative process of the archeopyle is different from that of the other cyst structures. On the one hand, the archeopyle is a thecamorphic feature of the cyst in that it most frequently expresses an easily recognizable fraction of the paratabulation. On the other hand, it is typically cystomorphic, because comparable mechanisms are not known on the theca.

Little is known about the biological processes related to archeopyle formation and function. Normally it is defined by a line of actual or potential separation through the cyst wall, which may be visible as a fine line under the microscope. Many archeopyles provide communication directly between the innermost cavity of the cyst and the exterior. Others, in some cavate cysts, provide obvious connection only between the pedicel or the ectocoel and the exterior, whereas the more inward wall layer (i.e., ophragm or autophragm) shows no opening.

6.1. Structure and Terminology

As more has been learned about the archeopyle, the concept of its structure and the descriptive terminology applied to it has changed.

The **principal archeopyle suture** is the primary determinant of the archeopyle. This line of structural and probably also compositional discontinuity in the wall apparently originates at the time of wall formation and localizes the opening that develops during excystment. It is often visible in an unopened cyst as a line whose brightness contrasts with that of the rest of the wall (transmitted light), or as a fine linear depression in the wall surface. A difference in ultra-structure of the wall material at the locus of the suture may also be apparent (Jux, 1968). In a modern cyst, the suture may be opened by chemical treatment (acetolysis) as well as by excystment of the living cell.

Most commonly the principal archeopyle suture more or less completely surrounds a portion of the cyst wall, the **archeopyle operculum**, whose release forms the opening when the wall ruptures along the suture. It is common for the suture to run approximately along a sequence of parasutures and for the

operculum to comprise one or more entire paraplates. we know from evidences of paratabulation independent of the archeopyle that the archeopyle suture in many species deviates from a parasutures.

A combination archeopyle is a polyplacoid opening that involves paraplates from more than one series.

The principal archeopyle suture may be unbranched (straight, curved, or angled), or it may have branches in the form of **accessory archeopyle sutures** which extend onto either the operculum or the rest of the cyst, or both. Accessory sutures may range from in the archeopyle margin to relatively long branches from the principal suture. In the latter case, the accessory sutures may separate flaplike portions of the cyst wall, or fully subdivide the operculum into two or more separable **opercular pieces**. If the operculum is entire or only incompletely divided by accessory sutures, it is a **simple operculum**; but if accessory sutures divide it completely, the operculum is **compound**. A monoplacoid operculum is necessarily simple; polyplacoid opercula may be simple or compound.

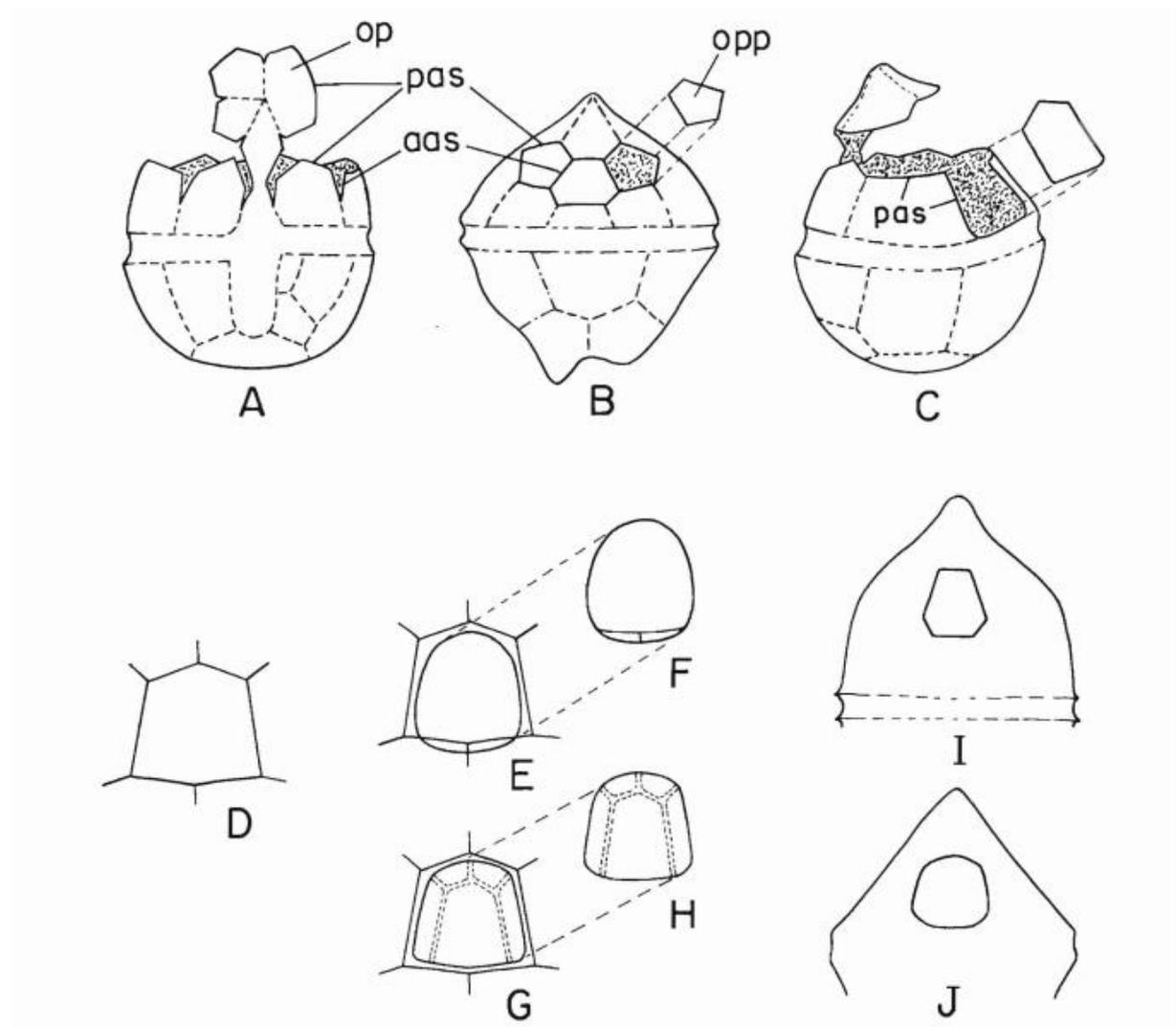


Figure 6.1- BASIC ARCHEOPYLE FEATURES

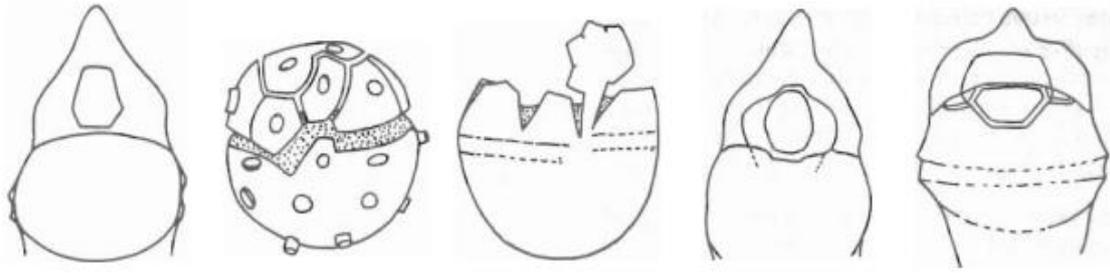


Figure 6.2- RELATION OF ARCHEOPYLE TO THE CYST WALL; SIZE OF OPENNINGS

An operculum completely surrounded by the principal suture is said to be **free**, and it will separate fully from the rest of the cyst if the suture opens along its entire length. A free operculum (or free opercular pieces, if the operculum is compound) may also remain locally **adherent** (connotation: joined or united, although usually separate) wherever the suture does not open, but such adherence is an incidental condition and cannot be recognized unless the suture is partly open elsewhere. Contrasting with a free operculum (whether adherent or not) is an **adnate** operculum, which is incompletely surrounded by the archeopyle suture. An adnate operculum is locally continuous with the rest of the cyst where the suture is interrupted and this continuity can often be recognized, even if the suture is nowhere open. The free or adnate condition of the operculum is constant within most species and has been used as the principal criterion for distinguishing a few genera. Laterally adnate opercula possibly occur in cysts of some Pleistocene and living species.

While it is important to distinguish between adnate and adherent opercula, to do so may require careful observation under high magnification with critical lighting. Persistent presence of the operculum, combined with apparently complete confluence of the wall surface across the gap between the visible ends of the archeopyle suture, is positive indication of the adnate condition. Loss of adnate opercula through tearing is indicated by an irregular break.

The characters of the archeopyle and its operculum relate closely to the wall structure at the locus of the opening. If the wall is an autophragm or is composed of two layers closely linked in the archeopyle area, only a single opening (with a single operculum) is developed. However, if wall layers are separated in the area of the archeopyle (e.g., in some cavate cysts), two distinct openings (peri- and endoarcheopyle, or ecto- and autoarcheopyle) may occur. In most cases the openings in different wall layers of one specimen are of the same type.

An ectophragm, if present, normally is either incomplete in the region of the archeopyle (e.g. *Kisselovia*) or opens as part of the periphragm or autophragm on which it is supported. Therefore, the features of ectoarcheopyle and ectoperculum in such cysts usually need not be detailed separately.

The relative sizes and shapes of archeopyles through the separated walls of cavate cysts are

strongly influenced by the contours and spacing of the two walls, even if both archeopyles are of the same type. Archeopyle dimensions as a fraction of cyst dimensions vary greatly. At one extreme, exemplified by some peridinioid cysts with relatively small intercalary archeopyles, the opening is so small that only a severely distorted or subdivided protoplast could pass through it. At the other extreme, an archeopyle whose principal suture runs approximately along the equator of a spherical cyst would allow the entire protoplast to leave the cyst as one body without distortion.

Archeopyles apparently may be situated on any part of the cyst, archeopyles are located in the hypocyst (involving antapical paraplates and postcingular paraplates in the siliceous cysts of Peridinites). Note that the term **epicystal archeopyle** has the special connotation of a large combination archeopyle that involves all (not just any) paraplates of the epicyst, the archeopyle suture running approximately along the paracingulum. The term **archeopyle type** applies to the sum of the characteristics of the excystment aperture in a single specimen. However, **an archeopyle formula**, in which symbols stand for the most important morphologic features.

Chapter VII

SAMPLE PREPARAION

Case study from the Eocene sediments, Fayoum Area, Egypt.

7.2. Palynology processing

Four samples have been selected from the Eocene sediments in the Fayoum area, Egypt in purpose to test their palynofloral content. The standard palynological techniques have been applied for all samples. The two marly samples from Gebel Mudarawa are being productive in terms of dinoflagellates cysts and other palynomorphs. In contrast, the three samples from Gebel Na'alou are being barren from palynomorphs but contain some palynodebris and amorphous organic matters (AOM) (Fig. 7.1).



Fig. 7.1- A photograph of the Mudawara Mt. Fayoum Depression, Egypt.

Methods

(A) Initial processes: The palynological preparation of the samples began with taken suitable amount of each sample, if available 5-10g were taken (Fig. 7.2).

(B) Demineralisation:

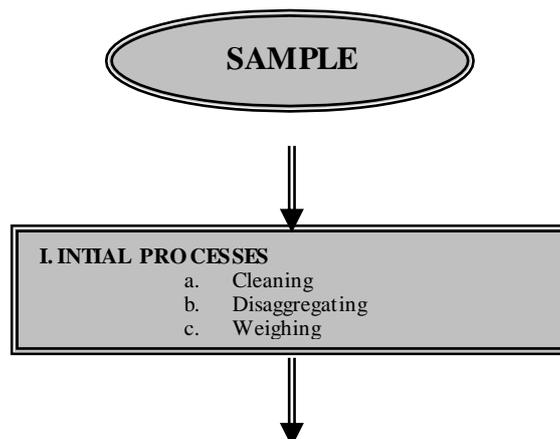
Removal of carbonates: Up to 50 ml of 35 % HCl was added to dissolve any carbonates. Care must be taken to ensure that all carbonates have been dissolved to avoid calcium fluoride precipitation. The acid was siphoned off and the samples were washed several times with distilled water until neutral, calibrated litmus paper was used to test neutrality of the sample before further treatment.

(1) Removal of silicates: This procedure requires care because HF has extremely corrosive and toxic nature. So, it should be carried out in a well-ventilated laboratory with an efficient fume cupboard and wearing protective clothes, respiratory filter, clear plastic eyeglasses and rubber gloves. In polypropylene cups, the samples were macerated in 30 to 50 ml of cold concentrated 48 % HF for 48 hrs to 72 hrs to dissolve all silicates. The samples were occasionally agitated and stirred with a polypropylene stirring rod. If the sample is highly siliceous excess of HF can be added. The residue was washed several times with distilled water until neutrality. The residue was treated, if necessary, with 10 % HCl to remove any fluorides (CaF_2) which might have formed in the residue. It can be heated and then washed as stated before.

(2) Sieving: Before sieving, residues were treated for a few seconds in an ultrasonic bath and for removing any undissolved heavy minerals by decantation. Material coarser than 125 μm was

removed by brass sieving. The fine fractions ($< 125 \mu\text{m}$) were sieved and washed through a $10 \mu\text{m}$ nylon sieve. Residues are checked for their palynomorph content as well as for their colour.

- (C) Oxidation:** The organic residue contains in addition to the desired microfossils, plant and animal tissues fragment, fine material of uncertain origin and wood fragments. Unless coarse enough to be removed by sieving, the wood fragments, being resistant to oxidation than other organic matter and maybe concentrated by a combined process of oxidation and filtration. Schulz's solution (mixture of HNO_3 + KClO_3 in a proportion of 50% to 50%) was used to remove amorphous organic material at least partly from the residue.
- (D) Removal of oxidation products:** Adding NaOH solution (7.5 %) for few a seconds and washing two times at least with distilled water. This was carried out by using MRS (Modified Reissinger System) in fume cupboard (Traverse, 1988).
- (E) Staining:** Since most palynomorphs are colourless to pale yellowish brown, it is advantageous to artificially stain them. The residues were stained with red Safranin "O" (1 g. of Safranin "O" + 100 ml of 2 % NaOH), using an ultrasonic bath for a few seconds. Safranin "O" stain does not mask the brown pigment of the protoperidinacean cysts but does enhance the details in pale cysts (de Verteuil & Norris, 1992). Then residues were sieved using a 10 and $20\mu\text{m}$ mesh.
- (F) Slide preparation:** 2 slides of each sample were made using glycerine jelly as mounting media. Using glass slides (26 x 76 mm) and glass cover slips (24 x 50 mm). Ethyl alcohol and soapy solution were used for cleaning slides.
- (G) Examination:** The prepared slides examined by traversing each slide at magnification 200 using microscope. Further detailed taxonomic work was carried out at higher magnifications utilising light microscopical and digital photographic facilities. Preservation varies from good to poor. All major palynomorph groups were documented.
- (I) Photography:** Well preserved specimens photographed using an Olympus Microscope.



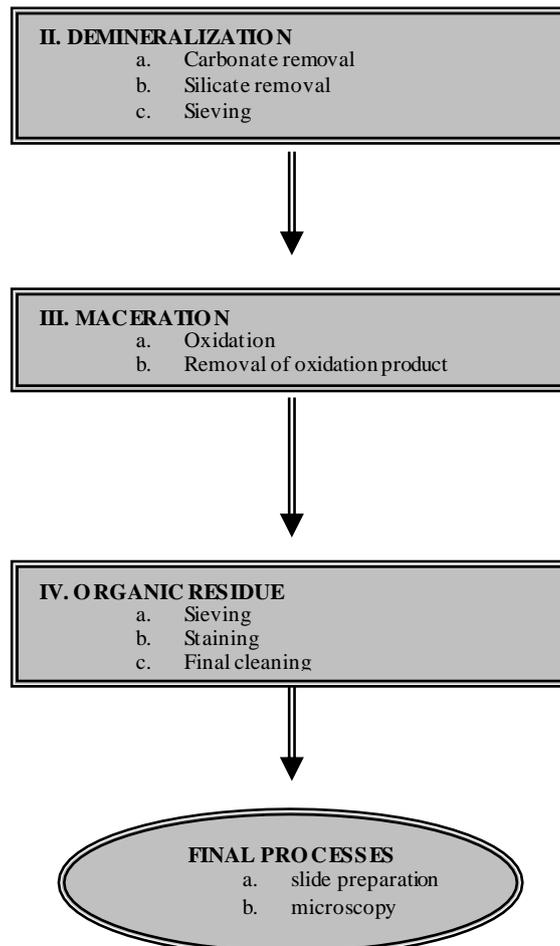
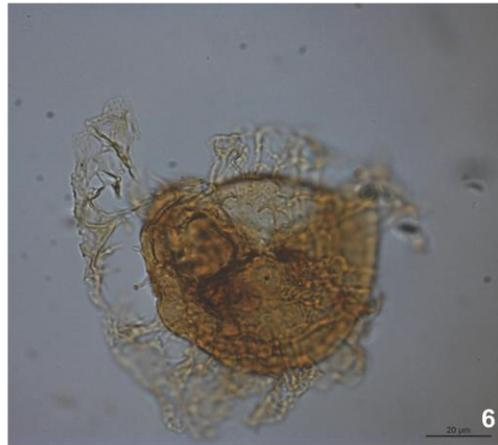
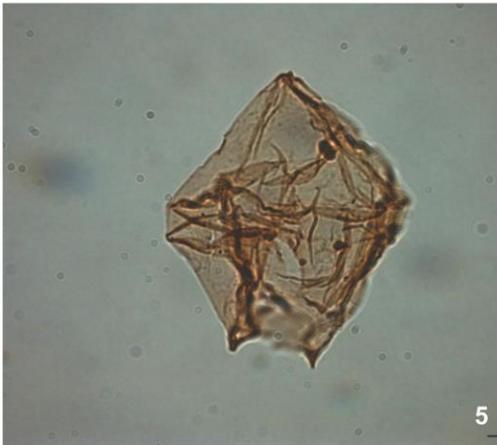
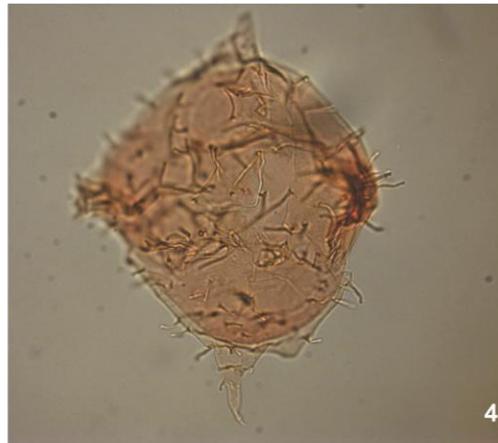
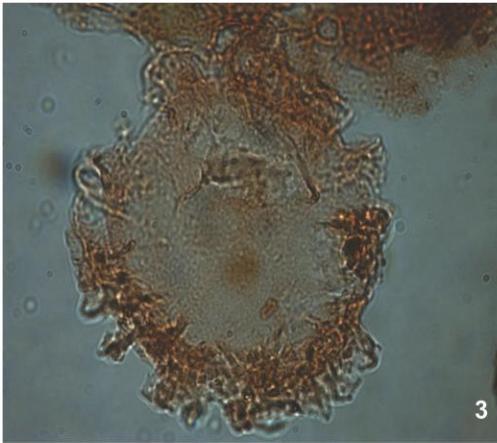
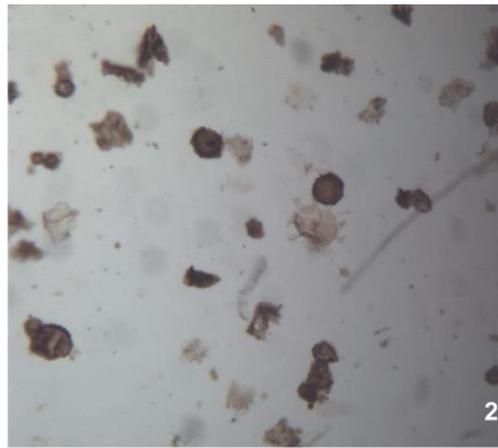
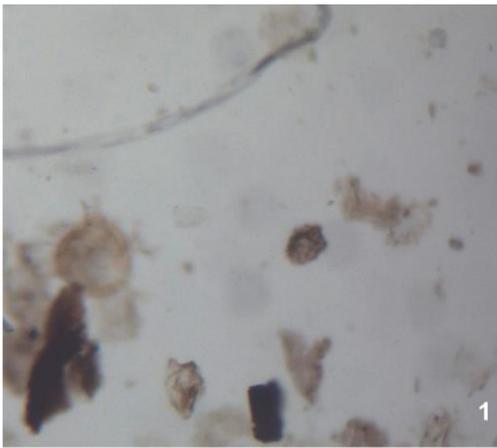


Fig. 7.2- Basics of palynological sample processing (Soliman, 2006).

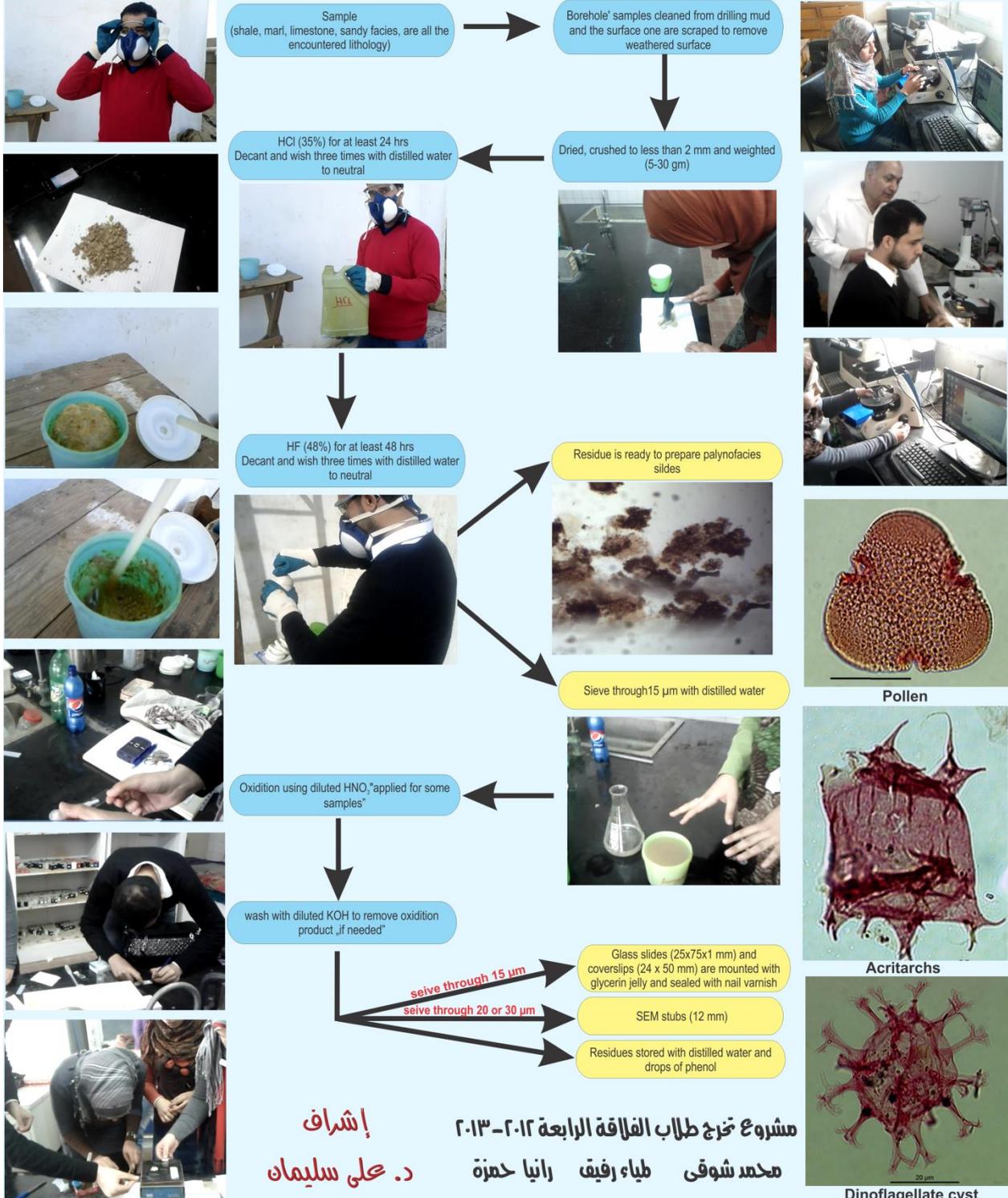


Some recovered dinoflagellate cyst from the prepared samples from the Mudwara Mt.

- 1-2- Palynodebris containing amorphous organic material and dinoflagellates
- 3- Cyclonephelium sp.
- 4- Wetzeliella sp.
- 5- Lejeunecysta sp.
- 6- Glaphyrocysta sp.



Flow chart for processing palynological samples

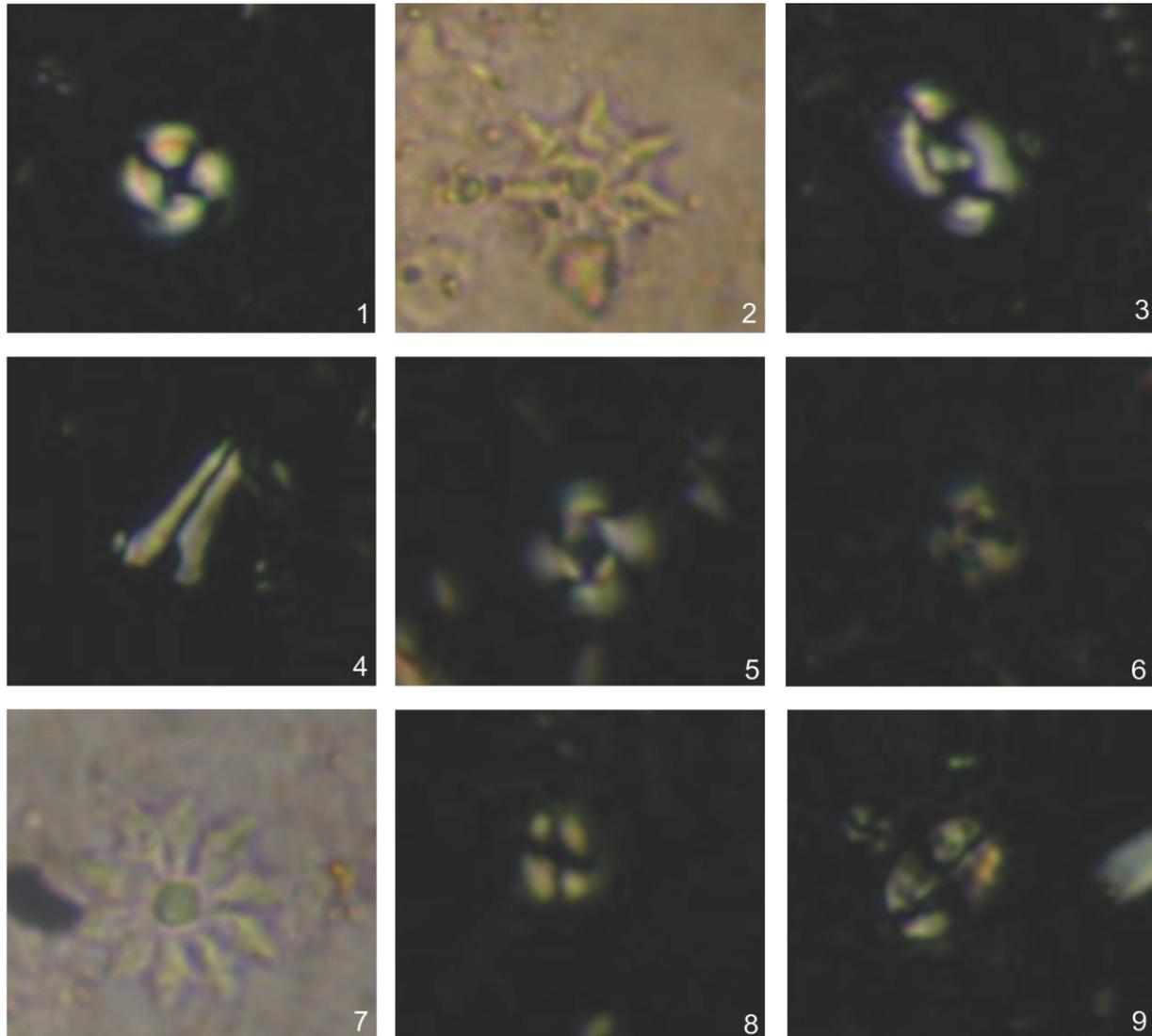


مشروع تخرج طلاب الفلاقة الرابعة ٢٠١٢-٢٠١٣
 محمد شوقي طياء ريف رانيا حمزة
 د. علي سليمان إشراف

7.2- Calcareous Nannoplankton processing

For the calcareous nannofossil study, the same samples were processed by smear slide preparation from raw sediments samples. Smear slides were examined by using polarized microscope with 1250 x magnification. Due to the small size of nannofossils, special care is taken for cleaning laboratory ware in order to prevent the chances of contamination. Samples were processed by using the standard preparation technique in Bowen and Young (1998) with the following minor modification:

- 1-a small sample, approximately thumbnail size, was scraped from the surface and gently crushed in a mortar.
- 2-the powdered sediments was placed into a bottle and soaked in distilled water.
- 3-the sample was agitated and left to settle.
- 4-by using a plastic pipette, a few drops of the suspended particulate matter are put on a glass slide and dried on a hot plate.
- 5-when the sediments were dry, the mounting medium such as Canada balsam was added to the cover slip. The latter was pressed down onto the sample to remove air bubbles.
- 6-the slide was later cooked on a hot plate at about 120 °C for 1-2 minutes, the slides were labeled and left to cure the adhesive and to make the slide more durable and easier to store.
- 7-high quality smear slide was prepared from each sample, for nannofossil viewing and photographing.



Some Nannoplankton taxa recovered from the prepared samples

- 1- *Discoaster saipanensis* Bramlette & Riedel (1954).
- 2- *Reticulofenestra umbilica* (Levin, 1965) .
- 3- *Pontosphaera multipora* (Kamptner, 1948) .
- 4- *Cyclicargolithus floridanus* (Roth & Hay in Hay et al. 1967).
- 5- *Ericsonia formosa* (Kamptner, 1963) .
- 6- *Zygrhablithus bijugatus* (Deflandre in Deflandre & Fert, 1954) .
- 7- *Cribocentrum reticulatum* (Gartner & Smith, 1967) .
- 8- *Discoaster barbadiensis* Tan (1927) .
- 9- *Helicosphaera lophota* Bramlette & Sullivan (1961) .

SUMMARY & CONCLUSION

Dinoflagellates were introduced as they are unique among the major groups of non-mineralized protists in having an extensive fossil record, a record composed primarily of organic-walled, calcareous and siliceous forms are rare. Dinoflagellates are important constituents of the marine and freshwater biota today

and are represented by abundant fossils in upper Triassic and younger strata.

The fossil record of dinoflagellates largely depends is an adaptive feature peculiar to a certain stage in the life cycle of only certain species. For example, dinoflagellates are common features of marine sedimentary strata. On contrast, freshwater deposits are relatively uncommon.

Over all, living dinoflagellates may be autotrophs, phagotrophs, symbionts or parasites. Photosynthetic species (autotrophs) account for about half the number of living dinoflagellate genera. Some species have more than one nutritional strategy (both parasitic and photosynthetic).

The features to be considered when identifying dinoflagellate cysts include the following:

General features (e.g. size, shape, criteria for orientation): dinoflagellate range in size from one taxon to another. Generally, large fossil dinoflagellates are especially conspicuous in the late cretaceous and early tertiary. In addition to , cysts shape plays an important role in biological significance. Cysts commonly deviate from sphericity by elongation in the apical-antapical direction. there for, orientations dependent upon shape are so strongly favored in some species that specimens are virtually never seen in other positions.

Wall structure and surface features: the cyst wall, its structure and surface ornament. consider the varied elements of low and high surface relief that constitute what is usually referred to as the ornament, the relation of the wall to the biological is a functional significance of cyst shape and surface relief in the hydrodynamic environment of the sea or lake. The features in and on the cyst wall, which can be distinguished as theca-morphic and cystomorphic, combine to produce a mixture of properties that is distinctive for each species. The simplest and most apparent surface features are ridges or septa which mark off paraplates much as thecal sutures separate thecal plates it was responsible not only for the first identification of dinoflagellates in the fossil record, but also for the early acceptance of their remains as fossilized thecae.

The archeopyle: is the opening in the cyst wall through which the protoplast emerges during excystment. The archeopyle is operculate in most species, but it may also be slitlike. The archeopyle occupies a special position among the characters of dinoflagellate cysts. It cannot be accommodated in the definitions of either thecamorphic or cystomorphic features; it meets the requirements of both groups.

Finally, tabulation is far and away the most significant morphological character in the systematics of living peridinialean dinoflagellates. Genera are distinguished primarily by differences in the number and arrangement of plates, and minor differences in plate shape and arrangement are often significant at the species level. Tabulation patterns will always be represented by identical tabulation formulae. It is important for distinguishing the geometric and topologic aspects.

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