CURSO BASICO DE DINOFLAGELADOS

06 - 08 DE JULIO DE 1988

INSTRUCTORES:

A.W. VAN ERVE (CORPOVEN, S.A.) Y

A. FASOLA (INTEVEP, S.A.)

LUGAR:

INTEVEP, S.A. - LOS TEQUES

PROGRAMA DEL CURSO

MIERCOLES 06 DE JULIO DE 1988

08.30 - 10.00 INTRODUCCION
REPRODUCCION Y CICLO DE VIDA
MORFOLOGIA

10.30 - 12.00 MORFOLOGIA
ESTRATIFICACION Y COMPOSICION DE LA PARED
DESCRIPCION DE LAS CARACTERISTICAS ESPECIFICAS

01.00 - 04.30 SESION AL MICROSCOPIO (MORFOLOGIA)

JUEVES 07 DE JULIO DE 1988

08.30 - 10.00 DESCRIPCION DE LAS CARACTERISTICAS ESPECIFICAS
DIMENSIONES Y VARIABILIDAD DE LA MORFOLOGIA
TABULACION

10.30 - 12.00 TABULACION Y 'ARQUEOPILO'
LITERATURA ESPECIALIZADA
APLICACION BIOESTRATIGRAFICA EN EL MESOZOICO Y TERCIARIO

01.00 - 04.30 SESION AL MICROSCOPIO (MORFOLOGIA Y ESTRATIGRAFIA)

VIERNES 08 DE JULIO DE 1988

08.30 - 12.00 CLAVE DE DETERMINACION DE FAMILIAS DE DINOFLAG.
DESCRIPCIONES DE LAS FAMILIAS DE DINOFLAGELADOS
DISTRIBUCION BIOESTRATIGRAFICA DE LOS DINOFLAGELADOS MARCADORES

01.00 - 04.30 SESION AL MICROSCOPIO (ESTRATIGRAFIA)

CURSO BASICO DE DINOFLAGELADOS

06 - 08 de julio de 1988

INSTRUCTORES: A.W. VAN ERVE (CORPOVEN, S.A.) Y
A. FASOLA (INTEVEP, S.A.)

LUGAR: INTEVEP, S.A. - LOS TEQUES

INFORMACION GENERAL:

EL ESTUDIO DE LOS DINOFLAGELADOS HA ALCANZADO EN LOS ULTIMOS ANOS, UNA IMPORTANTE POSICION DENTRO DE LA BIOESTRATIGRAFIA, COMO UNA VALIOSA HERRAMIENTA EN EL CONOCIMIENTO DE LAS FORMACIONES GEOLOGICAS DEL SUBSUELO, FUNCIONANDO EN AREAS DONDE OTRAS ESPECIALIDADES TIENEN SERIAS LIMITACIONES. CONSIDERANDO QUE EN VENEZUELA EXISTEN MUY POCOS ESPECIALISTAS EN ESTE GRUPO DE MICROFOSILES, SURGIO LA IDEA DE DICTAR UN CURSO BASICO SOBRE ESTE TEMA EL CUAL SERA COMPLEMENTADO EN EL FUTURO CON UN CURSO AVANZADO.

ESTE CURSO, QUE SE DICTARA EN CASTELLANO, ESTA DESTINADO PARA PERSONAS SIN CONOCIMIENTOS PREVIOS DE DINOFLAGELADOS (MICROPLANCTON VEGETAL).

CONSISTIRA EN CHARLAS SOBRE TOPICOS BASICOS EN EL CAMPO E INCLUIRA OBSERVACION AL MICROSCOPIO DE ALGUNAS MORFOLOGIAS Y ESPECIES DE DINOFLAGELADOS DE DIFERENTES NIVELES ESTRATIGRAFICOS DE VENEZUELA.

EL CURSO ESTA ABIERTO A PROFESIONALES Y TECNICOS EN LOS SIGUIENTES CAMPOS DE LA INDUSTRIA PETROLERA NACIONAL: PALINOLOGIA, MICROPALEONTOLOGIA, NANOPLANCTON, ESTRATIGRAFIA, Y GEOLOGIA.

of the changes that led to them is as yet uncertain. One theory suggests that eucaryotes arose from symbiotic association between formerly free-living procaryotes, each kind giving rise to mitochondria, to chromoplasts or to parts of the flagella (Margulis 1970).

The fossil record suggests that eucaryotes arose between 2000 and 1500 Ma ago, one ancient contender being *Eosphaera* from the Gunflint Chert (Fig. e). This possibly represents a *Volvox*-like, planktonic green algal colony (compare with Fig. 9.1c; see Kazmierczak 1976). Relatively large cells with diameters of 40 μm or more also become widespread in stromatolitic cherts and shales after about 1500 Ma BP (Schopf 1977). Cellular differentiation, root-like structures and the presence of nucleus-like spots are further indications of eucaryotic organisation in microfossils of late Precambrian age. There is even evidence for vegetative reproduction (i.e. mitosis, (Fig. a)) and sexual reproduction (meiotic spore tetrads, (Fig. b)) in the Bitter Springs Chert (about 800 Ma BP, Schopf 1971). The existence of branched cells like those of siphonalean green algae (Fig. d) and of macroscopic, ribbon-like algae about 1300 Ma ago (Cloud 1976, Walter, Oehler *et al.* 1976), suggests that sexual reproduction had evolved by this time. The microfossil evidence for the earliest eucaryotes is discussed more fully by Schopf (1971) and Cloud (1976).

The sexual eucaryote organisation has substantial selective advantages over the asexual procaryote way of life, particularly with regard to the exchange of genes and other forms of genetic recombination. For example, 10 genetic mutations in an asexual population can result in only 11 genotypes, that is the original type and those of the 10 mutants; the same number of mutations in a primitive diploid sexual population could be combined to produce up to 59 049 distinct genotypes (Schopf *et al.* 1973). Hence, in theory, the evolution of eucaryotic sexuality must have resulted in a prodigiously increased genetic variety of organisms, expressed by an increased rate of biological evolution in the fossil record.

4 Division Pyrrhophyta – Dinoflagellates and ebridians

The Pyrrhophyta, better known as dinoflagellates (meaning whirling whips), are single-celled organisms generally between 20 and 150 μm long, with both 'plant' and 'animal' characteristics. They are usually considered as 'plants', however, because of the presence of cellulose in the cell wall and chlorophyll pigments in the protoplasm. It is the carotenoid pigments dinoxanthin and peridinin, though, which give to these organisms the flame-like colours from which they derive their formal, botanical name of Pyrrhophyta (meaning fire plants). The majority of dinoflagellates are equipped with one whip-like and one ribbon-like flagellum for propulsion and have a prominent nucleus and a sculptured cell wall.

Both heterotrophic and autotrophic modes of nutrition occur, although the latter predominate and have formed an important contingent of oceanic phytoplankton since at least mid-Mesozoic times. Although these motile cells are abundant and wide ranging, it is the resistant resting cyst which leaves a fossil record. Dinoflagellate cysts (or dinocysts) have proved to be valuable tools for biostratigraphy and although they have contributed less to ecological and evolutionary palaeontology, these fields promise to become important.

The living dinoflagellate

Dinoflagellates of micropalaeontological interest exhibit two biological states with distinct morphology: a planktonic motile stage and a planktonic or benthic cyst stage. Only the cysts are preserved as fossils, but a knowledge of both stages is necessary for a proper understanding of the group.

The motile stage. Dinoflagellate cells range in size from 5–2000 μm. The cell wall may be either flexible and unarmoured or rigid and armoured. In the former case it comprises a proteinaceous envelope (pellicle) containing flattened cavities near the surface (Fig. 4.1a). In the armoured examples these cavities are occupied by plates of fibrous cellulose to form a closely fitting theca (Fig. 4.1b). The mode of arrangement of these plates, known as tabulation, is constant within each species.

Within the cell is a single, large nucleus and several fluid-filled vessels (pulsules) connected to the exterior via canals. Photosynthetic pigments, where present, are contained in round chromoplasts at the cell margins. Light sensory eye spots may also be present.

The two flagella arise either from pores at the anterior end or from the ventral surface (Figs 4.1c and 4.1d). The cell surface is generally traversed by two furrows, each of which bears a flagellum. One lies in a transverse furrow called the cingulum, which occupies a more or less equatorial position. The other lies in a longitudinal furrow called the sulcus and may trail behind like a tail. That half of the cell anterior to the cingulum is called the epitheca and that posterior to it is termed the hypotheca (Fig. 4.1g). The side bearing the sulcus is ventral (Fig. 4.1f), whilst the opposite side is dorsal (Fig. 4.1g). Many cells are dorso-ventrally compressed so that these two views are the ones usually illustrated.

The sulcus extends in a posterior direction and may terminate in a depression flanked by two antapical horns. The other, apical, end is often rounded, pointed or produced into an apical horn. Overall cell shape can be very varied even within one genus, but includes spherical, subspherical, ovoid, biconical, fusiform, rod-shaped, rectangular, polygonal, discoidal and 'peridinioid'.

Tabulation refers to the arrangement of plates in the armoured motile cells of the Order Peridiniales. In these, five plate series are found to encircle each

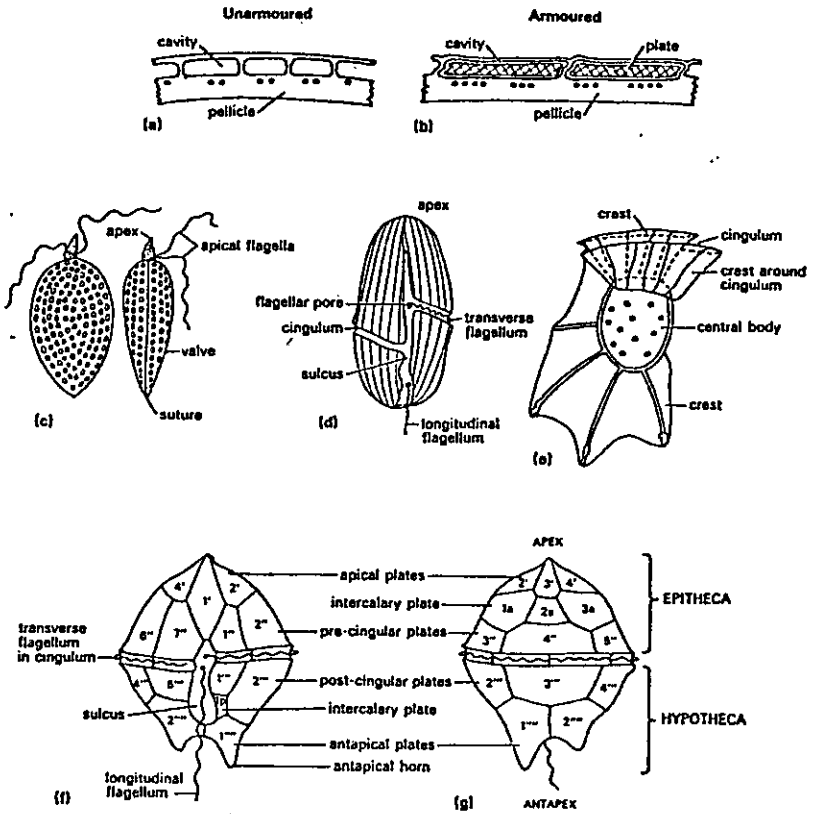


Figure 4.1 Dinoflagellate motile stages. (a) Schematic section through the wall of an unarmoured dinoflagellate; (b) schematic section through the wall of an armoured dinoflagellate; (c) Recent desmophycean *Prorocentrum*, about ×350; (d) Recent gymnodinialean *Gymnodinium*, about ×320; (e) Recent dinophysialean *Ornithocercus*, about ×275; (f) & (g) tabulation of a hypothetical peridinialean motile stage – ((f) ventral side; (g) dorsal side). ((a) & (b) modified from Dodge & Crawford 1970; (c) from Chapman & Chapman 1973; (d) from Kofoid & Swezy 1921; (e) after Barnes 1968 from Chatton; (f) & (g) from Evitt *in* Tschudy & Scott 1969)

cell, each plate being numbered for reference from the ventral area in a counterclockwise direction (Figs 4.1f and g). Around the epitheca occur the apical and precingular series. In the cingulum lie the cingular series whilst the postcingular and antapical series occur on the hypotheca. Additional intercalary plates may also develop at sites between the series, and the sulcus bears small sulcal plates that can be of taxonomic value.

The functional significance of cell shape and tabulation is little understood. As the planktonic forms maintain their position in the water by active

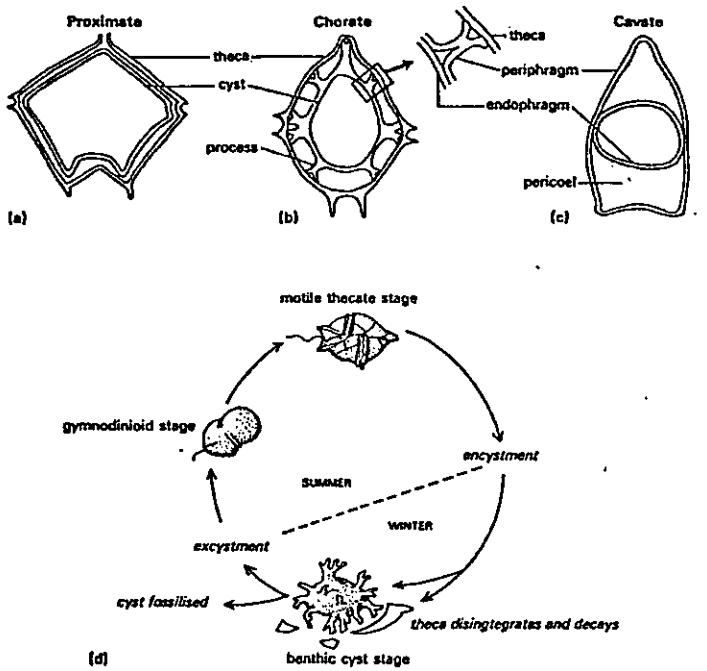


Figure 4.2 Dinoflagellate cysts. (a) Proximate cyst of *Peridinium* (axial section, about ×250); (b) chorate cyst of *Gonyaulax*, with detail of wall (axial section about ×250); (c) cavate cyst of *Deflandrea* (axial section, about ×220); (d) schematic life history of *Gonyaulax* sp., about ×600. ((a) & (b) based on Evitt *in* Tschudy & Scott 1969; (d) on Wall & Dale 1968a)

flagellar propulsion rather than by passive stabilisation, the cells tend to be streamlined. Nevertheless, the long horns of certain genera may serve to retard sinking.

The cyst stage. Although most, if not all, fossil dinoflagellates are cysts, only a few living genera are known to encyst, either in response to adverse environmental conditions or following sexual reproduction. The cyst is formed within the formerly motile cell and contains the same organelles. The cyst wall (phragma) is two-layered and consists of an outer periphragm and an inner endophragm (Fig. 4.2a–c). It is built of organic materials resistant to bacterial decay. Three basic kinds of cyst are recognised, termed proximate, chorate and cavate, although intergradations between these exist.

Proximate cysts develop with the phragma wall in contact with the wall of the enclosing motile cell (Fig. 4.2a). The tabulation, cingulum and sulcus are all reflected in the surface sculpture of proximate cysts.

Chorate cysts develop further within the original cell and are linked to it by spines (processes, Fig. 4.2b). These processes correspond in position with the plates or sutures of the thecal tabulation, but

chorate cysts usually exhibit no traces of a reflected cingulum or sulcus.

Cavate cysts are a type in which the two layers of the cyst wall are partially separated, usually at the poles (Fig. 4.2c). The cavities thus formed (pericoels) may promote buoyancy in the cyst. Traces of the tabulation, the cingulum and the sulcus may also be seen, so it is doubtful whether such cysts formed far below the motile cell wall.

The surface of these cysts may be smooth or bear fine granules (granulate), irregular ridges (reticulate), short spines (spinose), indentations (punctate), raised crests (septate) or processes and horns. Where a reflected cingulum is present, that portion apical to it is called the epitract and the antapical portion is called the hypotract (Fig. 4.3f).

The cyst nature of such structures is demonstrated by the presence of an escape hole, called an archaeopyle. This is formed by the removal of one or several plates (thereby comprising an operculum) from either the apical series, the precingular series, an anterior intercalary plate or a combination of these. The form and position of the archaeopyle is constant within a species.

Further investigation is needed into the functional significance of cyst morphology. The processes of chorate cysts and the pericoels of cavate cysts may both be mechanisms to minimise the downward sinking of oceanic species. If cysts of such forms were to sink far below the photic zone before excystment, their chances of survival would appear to be slender.

Dinoflagellate life history

Sexual reproduction is known in very few Recent dinoflagellates. Asexual reproduction predominates and involves a division of the cell into two halves (by binary fission) without the aid of the guiding nuclear structures found in other eucaryote cells. Hence it may be that dinoflagellates represent an evolutionary condition intermediate between procaryotes and eucaryotes.

The cyst stage of the life cycle is known so far from only a few genera (e.g. *Gonyaulax*, Fig. 4.2d). Cysts form in the autumn with lowered temperatures, remaining dormant on the sea floor through the winter. During this period the surrounding thecal plates may drop away and begin to decay. With the amelioration of conditions in spring, the motile stage excysts through the archaeopyle to leave a resistant phragma for the fossil record. Before developing any armour, however, the new dinoflagellate must pass through a naked gymnodinioid stage (Fig. 4.2d).

Dinoflagellate ecology

Dinoflagellates currently form a major part of the ocean plankton, especially the armoured and autotrophic forms, and they play a prominent rôle in the food chains of the marine realm. The autotrophic forms thrive in areas of upwelling currents that are rich in nutrients such as nitrates and phosphates, whilst they are rarely found alive below 50 m depth because of their need for light. Flagellar locomotion is employed in bringing them to the surface at night and withdrawing them to greater depths in the day because they must avoid harmful ultra-violet light.

As a whole, the group has a wide temperature tolerance (1–35°C) with an optimum for most species of 18–25°C. Many dinoflagellates have geographic distributions which are broadly parallel to oceanic temperature zones (i.e. latitudinal) and hence may be used as indicators of climate oscillations through the Quaternary Era. Certain genera, such as *Gymnodinium* and *Peridinium*, are found in both fresh and salt water although the majority of species are marine and sensitive to changes in water mass, including salinity changes.

Sudden blooms of dinoflagellates, called 'red tides', may occur under optimal conditions but the build up of toxic excretions eventually kills off great numbers of fish and invertebrates. It is possible that some of the dinoflagellates avoid this fate by encystment.

Planktonic forms with a predatory or parasitic mode of life are usually unarmoured and belong mostly to the Order Gymnodiniales. Other orders of limited palaeontological interest contain immobile, benthic, colonial forms and the zooxanthellae which live symbiotically in the tissues of reef-building corals and larger foraminifera.

There are several inherent problems in interpreting the palaeoecology of fossil dinoflagellates. First, those of pre-Quaternary age are not easy to relate to taxa of known habit, although lineages can be traced back in a few cases. Secondly, some of the dinoflagellate flora may not encyst and therefore leave no fossil record. Thirdly, those cysts which are formed may sink and drift to be preserved at depths and conditions beyond the tolerance of the species. Recent studies, however, suggest that modern cyst assemblages from the sea floor in fact bear a strong resemblance to the main overlying water-mass distributions, so that the transport of cysts is probably not very great (see Wall *et al.* 1977). At present, dinoflagellate cysts are most abundant in sediments from the continental rise and slope, with from 1000 to 3000 cysts per gram. There is also a tendency for specific diversity to increase with distance from shore and to be greatest in low latitude waters, as with most other marine plankton. The distribution and ecology of Recent and Quaternary dinoflagellates are reviewed more fully by Williams (pp. 91–5, 231–43 *in* Funnell & Riedel 1971 and pp. 1288–92 *in* Ramsay 1977), by Wall (1971 and pp. 399–405 *in* Funnell & Riedel 1971) and in Wall *et al.* (1977). Palaeoecology is reviewed by Williams (pp. 1292–302 *in* Ramsay 1977). The factors affecting the preservation of dinoflagellate assemblages have been considered by Dale (1976).

Classification

Kingdom PROTISTA
Division PYRRHOPHYTA

Although on the boundary between 'plant' and 'animal' organisation, dinoflagellates are considered to be 'plants' by some because they contain cellulose and chlorophylls. Subdivision of Recent forms takes account of the following in order of importance: position of flagellar insertion, predominant habit (e.g. mobile and flagellate, mobile amoeboid, immobile solitary or immobile colonial), presence of armour, tabulation, shape and sculpture of the motile cell. Fossil dinoflagellate cysts are classified according to cyst type, reflected tabulation, archaeopyle position, general shape and sculpture (see Sarjeant 1974 and Williams pp. 1239–46 *in* Ramsay 1977).

At one time many dinoflagellate cysts were classed with the problematic 'hystrichospheres'. Evitt (1961, 1963) demonstrated that some of these were true dinoflagellate cysts, designating the remaining problematica to the group Acritarcha (*q.v.*).

Class Desmophyceae. These are thought to be the most primitive dinoflagellates. They have two flagella of equal length inserted at the anterior end of the motile cell, which is unarmoured. Cysts are unknown but may be included amongst the acritarchs. *Prorocentrum* is a living genus involved in red tide blooms. The theca is divided into two equal valves by a longitudinal suture (Fig. 4.1c).

Class Dinophyceae. Most dinoflagellates belong to this class. These have two flagella of unequal length arising from the ventral surface. There are three important orders: the Gymnodiniales, Peridiniales and Dinophysiales.

ORDER GYMNODINIALES. The Gymnodiniales are predatory and parasitic forms lacking armour but having a flexible pellicle. Their cells are commonly spherical, traversed by a deep equatorial cingulum and a shallow longitudinal sulcus. Although resting cysts are known, the lack of tabulation-related features makes it difficult to infer biological affinities. Such uncertain forms may therefore become classified as acritarchs.

The Recent genus *Gymnodinium* (Fig. 4.1d) has a motile cell with an equatorial cingulum. The common late Cretaceous genus *Dinogymnium* (Fig. 4.3a) is probably a proximate cyst and has longitudinal folds, a cingulum and an apical archaeopyle.

ORDER PERIDINIALES. The Order Peridiniales comprises forms with an armoured motile stage. In these the cingulum is equatorial with a slight spiral offset and there is a longitudinal sulcus. The plates are arranged into apical, precingular, cingular, postcingular and antapical series, with additional intercalary and sulcal plates.

Inevitably, classification of the Peridiniales has proceeded along two independent lines, one for the fossil cysts (the bulk of which belong here) and one for the living motile cells. In principle it would be best to combine this divergent information into a single, natural, classification. Unfortunately, however, cyst genera and motile genera do not always correspond, evolution having proceeded at different rates for these different stages of the life cycle.

The motile cell of Recent *Peridinium* (Fig. 4.3b) is laterally compressed and almost bilaterally symmetrical. The cyst stage is proximate with a peridinioid shape, clearly reflected tabulation and

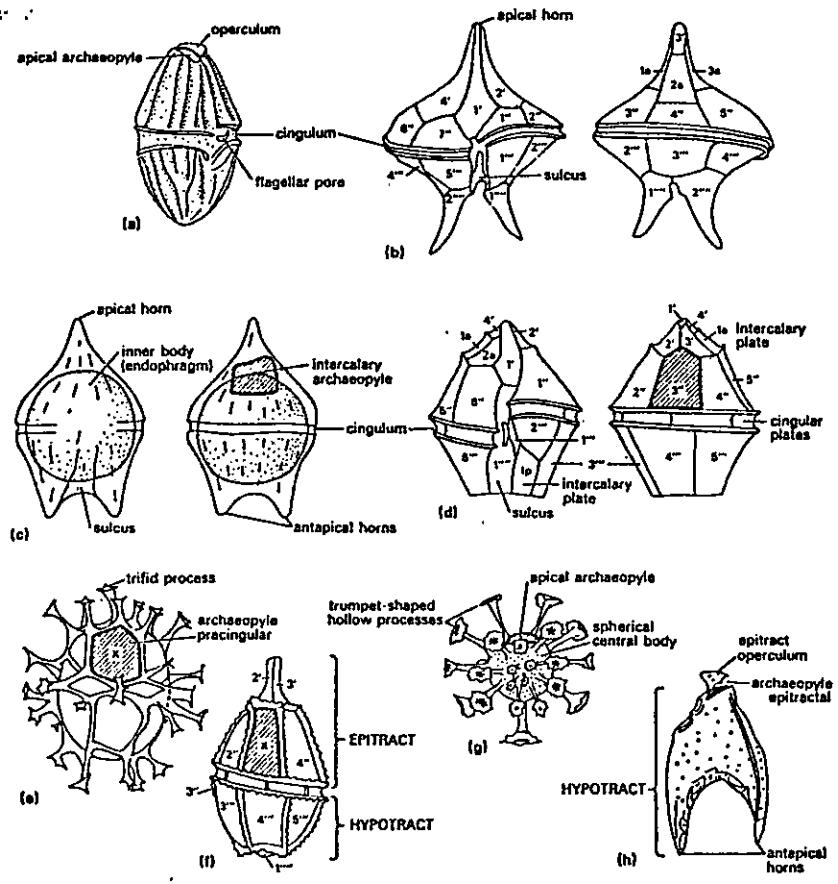


Figure 4.3 Dinoflagellates. (a) *Dinogymnium*, a fossil gymnodinialean cyst, about ×445; (b) motile cell of Recent *Peridinium*, about ×505; (c) cavate cyst of *Deflandrea*, left = ventral and right = dorsal views, about ×360; (d) motile cell of Recent *Gonyaulax*, about ×750; (e) proximochorate cyst of fossil *Spiniferites* ×465; (f) proximate cyst of fossil *Gonyaulacysta*, about ×405; (g) chorate cyst of fossil *Hystrichosphaeridium* ×400; (h) *Nannoceratopsis*, a fossil dinophysialean cyst, about ×680. ((a), (b), (c), (d), (f) & (h) based on Sarjeant 1974; (e) & (g) on Evitt *in* Tschudy & Scott 1969)

furrows. Both theca and cysts may bear two antapical horns (Fig. 4.2a). *Deflandrea* (L.Cret.–U.Olig., Fig. 4.3c) is a fossil cavate cyst of ellipsoidal shape, commonly with horns. The reflected tabulation is rarely visible but of *Peridinium* type with an intercalary archaeopyle.

In Recent *Gonyaulax* (Fig. 4.3d) the motile stage usually lacks horns and the tabulation is relatively asymmetrical. Its cyst is chorate or intermediate between proximate and chorate (proximochorate) with a precingular archaeopyle, being of the type once called *Hystrichosphaera* but now called *Spiniferites* (U. Jur.–Rec., Fig. 4.3e). The fossil proximate cyst *Gonyaulacysta* (M. Jur.–M.Mioc.) also has a reflected tabulation of *Gonyaulax* type with a precingular archaeopyle. The sutures are marked by crests and it bears an apical horn (Fig. 4.3f).

Hystrichosphaeridium (U. Jur.–M.Mioc.) is a fossil chorate cyst with a spherical body and radiating hollow processes, often with trumpet-like openings at the distal ends (Fig. 4.3g). Each process corresponds to the centre of a plate on the once enclosing theca. The archaeopyle is apical.

ORDER DINOPHYSIALES. Although the Dinophysiales are armoured, the plates lack a distinctive tabulation. The cingulum is very anterior in position and less spiralled than in the Peridiniales, uniting with the sulcus in a T- or Y-shaped junction. Both furrows are bordered by flange-like crests, as in Recent *Ornithocercus* (Fig. 4.1e). The cysts are proximate, the archaeopyle and operculum comprising the whole of the epitract (i.e. epitractal). Fossil examples are few but may include *Nannoceratopsis* from the Lower Jurassic (Fig. 4.3h). In this there are two prominent antapical horns and an epitractal archaeopyle.

General history of dinoflagellates

Although biologists hint at the primitive organisation and inferred great age of the group, the acme of peridinalean history appears to have been reached in the Mesozoic and Cainozoic Eras. The late Precambrian and Palaeozoic flowering of acritarchs may represent an earlier stage in dinoflagellate history, when non-tabulate forms thrived.

The earliest recorded peridinialean cyst is *Arpylorus*, a Silurian acritarch with tabulation, a cingulum and a precingular archaeopyle. The main radiation, however, began in the late Triassic Rhaetian Stage with proximate cysts. The latter type remained dominant throughout the Jurassic (e.g. *Gonyaulacysta jurassica*, Fig. 4.3f), although chorate, proximochorate and cavate types had all appeared by the middle Jurassic.

Dinoflagellate cysts of the Cretaceous were predominantly chorate (e.g. *Hystrichosphaeridium*, Fig. 4.3g) or proximochorate (e.g. *Spiniferites ramosus*, Fig. 4.3e) and it was at this time that the greatest diversity of cysts was reached (Fig. 4.4).

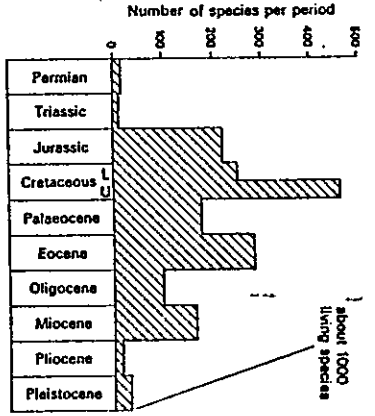


Figure 4.4 Specific diversity of described dinoflagellates through time, omitting the single Silurian record. (Based on Tappan & Loeblich 1973)

Cavate cysts began to flourish in latest Cretaceous times (e.g. *Deflandrea*, Fig. 4.3c) and dominated many Tertiary assemblages until the Oligocene, almost dying out in the Pliocene. Proximate and chorate cysts with complex processes occur in the Eocene and Oligocene, but simpler forms have prevailed since then. Dinoflagellate cysts first appeared in freshwater sediments during the Tertiary.

For fuller accounts of dinoflagellate history see Sarjeant (1967, 1974) and for a review of their evolution see Williams (pp. 1283–8 *in* Ramsay 1977).

Applications of dinoflagellate cysts

Dinoflagellate cysts have proved of considerable value in the biostratigraphy of marine Mesozoic and Cainozoic strata, where they may be used in conjunction with acritarchs, pollen grains and spores. Sarjeant (1967) and Harker & Sarjeant (1975) have outlined the stratigraphical distribution

of dinoflagellate cysts. For examples of their biostratigraphic use we may take Bujak and Williams (pp. 321–9 *in* Swain 1977) for the Jurassic, Habib (1975 and pp. 341–67 *in* Swain 1977) and Aurisano and Habib (pp. 369–87 *in* Swain 1977) for the Cretaceous, and the papers by Costa & Downie (1976) and Manum (1976) for the Cainozoic. Williams (pp. 1246–83 *in* Ramsay 1977) reviews the biostratigraphic zones in use at present.

There is an increasing interest in the palaeoenvironmental value of dinoflagellate cysts. Manum (1976) for example, suggests that changing proportions of cysts to pollen, spores and indeterminate debris through the Cainozoic of the North Atlantic reflect widespread palaeogeographic changes associated with sea-floor spreading events. Dinoflagellate cysts and acritarchs reworked into younger sediments can be used to indicate the provenance of sediments and the directions of transport (see Stanley 1966). Different kinds of cyst may also help to distinguish nearshore from offshore sediments (e.g. Williams & Sarjeant 1967, Downie, Hussain *et al.* 1971, Wall *et al.* 1977). Wall and Dale (1968) found that Quaternary cyst assemblages change in response to probable climatic controls and are therefore of value in the correlation and interpretation of marine strata of this age.

Further reading

Useful introductions to the group may be found in the book by Sarjeant (1974), the chapter by Evitt *in* Tschudy and Scott (1969, pp. 439–68), by Williams *in* Ramsay (1977, pp. 1231–343) and the paper by Harland (1971). Many cysts can be identified with the assistance of the catalogue by Eisenack and Kjellström (1964-to-date) and the index by Norris and Sarjeant (1965).

Hints for collection and study

Dinoflagellate cysts are common in dark grey and black argillaceous rocks of post-Triassic age. They can be disaggregated by methods A to E (especially D) and sorted and concentrated by methods H or K (see Appendix). Temporary or permanent mounts on glass slides should be scanned with well condensed transmitted light at over 400 × magnification. More sophisticated methods of preparation and concentration are reviewed by Gray (pp. 530–86 *in* Kummel & Raup 1965) and by Sarjeant (1974).

EBRIDIANS

The ebridians are unicellular, marine and planktonic with an endoskeleton of silica, but unlike that of the similar silicoflagellates (*q.v.*), it is solid with a tetraxial or triaxial symmetry. Ebridians possess two flagella of unequal length and lack photosynthetic pigments, surviving instead by the ingestion of food (especially diatoms) with the aid of pseudopodia. Reproduction is mostly by asexual division.

Classification of ebridians is complicated by their uncertain biological status, resembling 'algal' groups such as the silicoflagellates and dinoflagellates as much as 'animal' groups like radiolarians. Generally regarded as 'algae' they are placed by some in the division Chrysophyta and by others in the Pyrrhophyta as a distinct class, the Ebriophyceae.

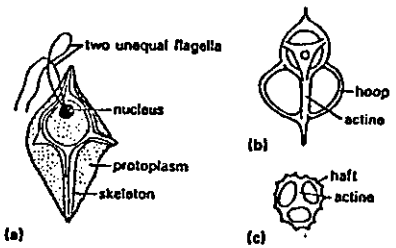


Figure 4.5 Ebridians. (a) Living cell and skeleton of *Hermesinum*; (b) *Hermesinum* skeleton × 500; (c) *Ebria* skeleton × 533. ((a) based on Hovasse 1934)

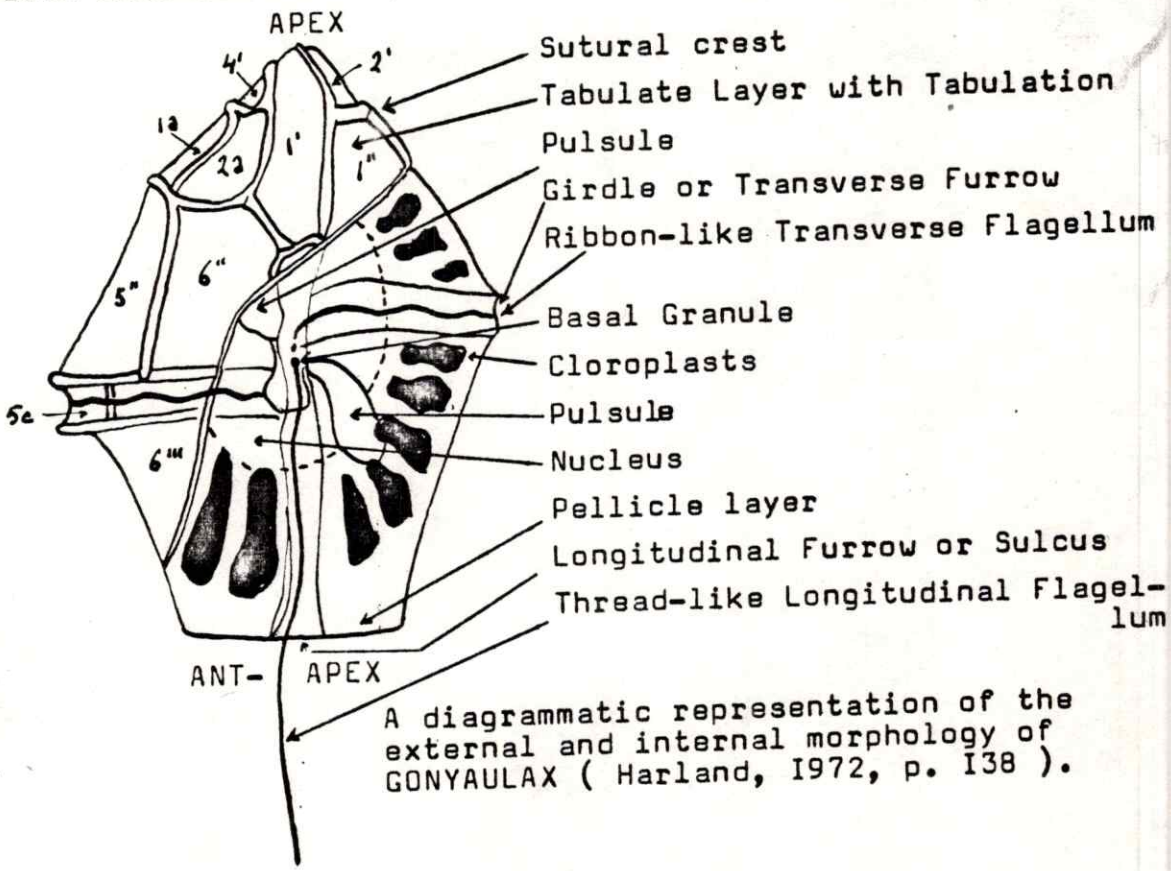
Genera and species are distinguished on the basis of endoskeleton morphology (see Loeblich *et al.* 1968). For example, *Ebria* (Mioc.–Rec., Fig. 4.5c) has three of four radiating bars (actines) with the ends joined by curved hoops called hafts. *Hermesinum* (Palaeoc.–Rec., Fig. 4.5a, b) consists essentially of four actines resembling a sponge spicule in their tetraxial arrangement, the ends of which are joined by a series of subcircular hoops.

Ebridians are known in rocks of Palaeocene age, the majority of genera thriving until the Pliocene when their diversity dropped sharply (Tappan & Loeblich 1972). The geological value of ebridians has been little exploited as yet, largely because they are neither abundant nor uniformly distributed and preserved. None the less, they have been used successfully with silicoflagellates in Cainozoic biozonal schemes, such as those in the north Pacific area (see Ling 1972, 1975).

CONTENTS

Kingdom Plantae
Division Pyrrhophyta Pascher, I914
Class Dinophyceae Pascher
Subclass Diniferophycidae Bergh

The DINOFLAGELLATES occur in enormous numbers in the surface waters of the ocean; there are also a number of freshwater species. A typical dinoflagellate, Gonyaulax, is enclosed in a tight-fitting armour of cellulose plates and has two flagella, one lying in a grove encircling the organism and the other trailing downward. Many dinoflagellates have oil drops which help them to float. Some of them possess a brown pigment in addition to chlorophyll; others are colourless and feed on minute organisms. Some dinoflagellates produce light, as do many other marine and some land animals. One of the most abundant of the luminescent dinoflagellates is Noctiluca, which does not resemble the typical dinoflagellates, but is colourless and ingests solid food. It is spherical, about a millimetre in diameter, with one short thick and one very delicate flagellum. It floats on the surface near shores, often in inconceivable numbers, and, being faintly pink, may in the daytime cause whole areas of the ocean to look like weak tomato soup.



A diagrammatic representation of the external and internal morphology of GONYAULAX (Harland, I972, p. I38).

Gonyaulax sometimes becomes so abundant that it colours the ocean red for miles. These outbreaks of 'red water' cause the death of fish and other animals, which are cast up on the beach and decay. The stench has been compared to that of the Nile when, according to ancient writings, that river 'turned to blood'. Buchsbaum, I938; Kofoid, I909.

Binnen de Subclass Diniferophycidae Bergh zijn voor de onderzoeker van fossiele diniflagellaten de volgende Orders van belang:

Order Peridiniales Schütt, I896 (armoured dinoflagellates)

Order Dinophysiales Lindemann, I928 (armoured, transversely divided by an anteriorly placed girdle)

Order Gymnodiniales Schütt, I896 (unarmoured dinoflagellates).

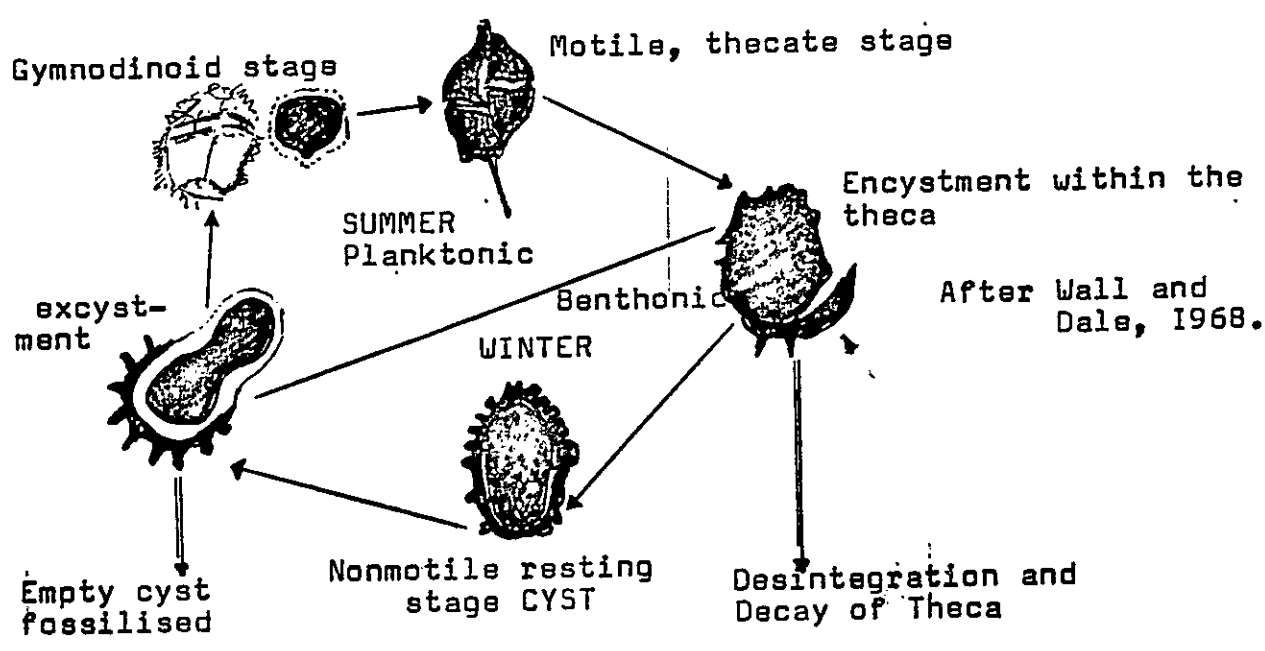
Deze Orders zijn ieder weer onderverdeeld in een aantal Families; een voortreffelijk overzicht van een Classification of Fossil Dinoflagellates, in Orders en Families + bijpassende diagnoses , is te vinden in:
Sarjeant, W.A.S., I974. Fossil and Living Dinoflagellates; pp. I38 - I49. Bovendien is onderhavige classificatie plus alle diagnoses van de Families te vinden in het Dino-systeem.

REPRODUCTION AND LIFE CYCLE

Reproduction is usually asexual by simple binary fission. The division of the theca usually takes place obliquely along the longitudinal axis with the line of fission passing through the point of insertion of the flagella, such that one flagellum passes to each of the daughter cells. In many forms fission takes place along predetermined thecal plate boundaries. In Ceratium there is sometimes an incomplete division resulting in a chain of individuals being formed.

The existence of sexual reproduction has been recorded in the genus Ceratium. Small individuals within the Ceratium population are the male gametes, the larger ones are the female gametes (or vegetative cells). The females ingest the male gamete during sexual reproduction, the two gametes uniting to form the zygote. (Vide Harland, I972, pp. I38, I39).

Dinoflagellates encyst in response to the oncoming of adverse environmental conditions (Sarjeant, I974, p. 43).



DINOTHECA ASSEMBLAGE (motile dinoflagellate population)
AT A GIVEN TIME AND PLACE

Distribution determined/influenced by a combination of factors, like: temperature, waterdepth, salinity, nutrient supply, current distribution, seasonal fluctuation, bottom substrate, other reasons .

Are cysts produced ?

YES { Not always: a proportion of the motile dinoflagellate population does not or not always produce cysts.

CYST PRODUCTION

Dale (≈30% producers quistes)

Factors determining/influencing the cyst production are virtually unknown; important problems to be investigated:
Quantitatively, what proportion of the motile dinoflagellate population is (possibly) meroplanktonic ? ; and
Quantitatively and qualitatively, how accurately does the cyst assemblage produced reflect the meroplanktonic species in the overlying waters ?

Are the cysts incorporated into the bottom sediment ?

YES { Not always: a proportion of the cysts is not sufficiently resistant to become incorporated into the bottom sediment before degradation has taken place.

INCORPORATION OF CYSTS INTO BOTTOM SEDIMENTS

Incorporation determined/influenced by a combination of factors, like :
sedimentary processes ;
hydrodynamic properties of different cyst species may lead to selective concentration of specific species according to sediment types .

Are the cysts preserved ?

YES { Not always: several destructive forces may be at work : diagenesis, tectonic disturbances and/or corrosion . Generally speaking, cysts may be insufficiently resistant to all kinds of destructive forces and subsequently they are eliminated or rendered unreliable.

CYSTS ARE PRESERVED IN THE PALYNOLOGICAL RESIDUE OF THE SAMPLE
DINOCYST ASSEMBLAGE S.L.

Are the cysts recorded ?

YES { Not always: a proportion of the cysts is not recorded by the investigator for various reasons.

THE CYSTS ARE RECORDED. DINOCYST ASSEMBLAGE S.S.

Figure 7. Schematic representation of factors which determine/influence eventual composition of the dinocyst assemblages.

Chapter 6. MORPHOLOGICAL SYNTHESIS

Faced with a dinoflagellate under the microscope, how does one proceed most effectively to study it? The checklist of features that begins this chapter is intended to facilitate the kind of orderly consideration of a specimen that is the necessary preliminary to identifying it. The remainder of the chapter is devoted to presenting an informal scheme for grouping genera according to cyst morphology. The scheme draws heavily on the ideas of Taylor (1976, 1980) as developed earlier in this manual and is not similar to the formal classification presented by Norris (1978), nor to the views on evolution of tabulation patterns presented by Dörhöfer and Davies (1980) and Eaton (1980). In fact, it sidesteps the issue of a formal family-level classification, about which there is currently no general agreement. It also attempts to accomodate not only cysts with an abundance of evident morphological detail, but also those that are relatively nondescript.

Checklist of Features

No checklist of features can be both brief and comprehensive when dealing with a group that exhibits such diverse morphology as the dinoflagellates. Nevertheless, preparatory to either an idenfification or a description, an outline like the following one can be a help in organizing thoughts into a systematic sequence and assuring that important topics are not overlooked. With such a guide, deficiencies in a published description may be more readily apparent and the missing information can then be sought in the illustrations.

The topics in the following outline are arranged in the sequence one might follow when examining a specimen.

Overall character
- Size, shape, major features of outlines and ornament

Orientation
- To establish dorsal, ventral, apical, antapical and lateral directions
- Some clues to orientation;
  - Elongation and prominent unique processes marking poles
  - Traces of paracingulum and parasulcus - ends of paracingulum offset? Right end normally lower than left.
  - Compression more commonly dorsoventral than lateral or polar
  - Parasulcal notch in outline of apical archeopyle marks ventral surface, offset to left in dorsoventrally compressed specimens
  - Peridinioid outline? Antapical horns are left and right, left one is larger if two are unequal.
  - Ceratioid outline? Horns are apical, antapical, and postcingular; single or larger postcingular one is on right side.
  - Archeopyle - shape and position with respect to pole and equator
  - Paratabulation - certain prominent paraplates may be identifiable by shape and size.

Wall structure
- Number, internal structure, and thickness of wall layers
- Conformity of layers in shape, where in contact, where separated, how interconnected; distribution of cavities
- Relationship of layers to projecting structures
- Openings in wall besides the archeopyle

Surface features
- Projecting structures - processes, septa, horns
  - General type and distribution - nontabular, parasutural, penitabular, intratabular, mixed or nonconforming
  - Number and specific position
  - Internal construction - cross-sectional shape, solid or hollow, hyaline, fibroid, granular
  - Tips - shape, closed or open, interconnecting features
  - Bases - shape, interconnecting features, relationship to other surface ornament or wall structure
  - Uniformity of character, or differences relative to position
- Fine-scale surface ornament - type and distribution
- Special features of areas corresponding to sulcus and cingulum
- Repeat these considerations for each wall layer as appropriate

Archeopyle
- Type, including number and identity of paraplates involved
- Shape and size; reduced or enlarged
- Operculum - simple, compound, free, adnate

Paratabulation
- Which elements express it - processes or septa, finer ornament, features within wall
- How complete is its expression?
- Parasulcus and paracingulum
- General pattern - peridinioid (quadra, hexa), gonyaulacoid (quinqueform; sexiform, L-type or S-type; corniform; partiform), suessioid, other
- Details of relative size, shape, mutual relationships of conspicuous paraplates
- Loci of unmarked or distinctively differentiated paraplates
- Specific modifications in apical and ventral areas
- Summary formula, if appropriate

Variability - as expressed in all features observed, as far as can be judged from available specimens

Major Cyst Categories

Described species of organic-walled dinoflagellate cysts now number about 2000 in more than 300 genera, and these figures are sure to increase. Collectively these cysts show highly diverse morphology; individually they range from nearly featureless to intricately structured. Where appropriate morphological detail abounds, confident placement of genera in families of a conventional taxonomic hierarchy is conceivable, but this is out of the question when the morphology, although perhaps distinctive enough for easy recognition at the

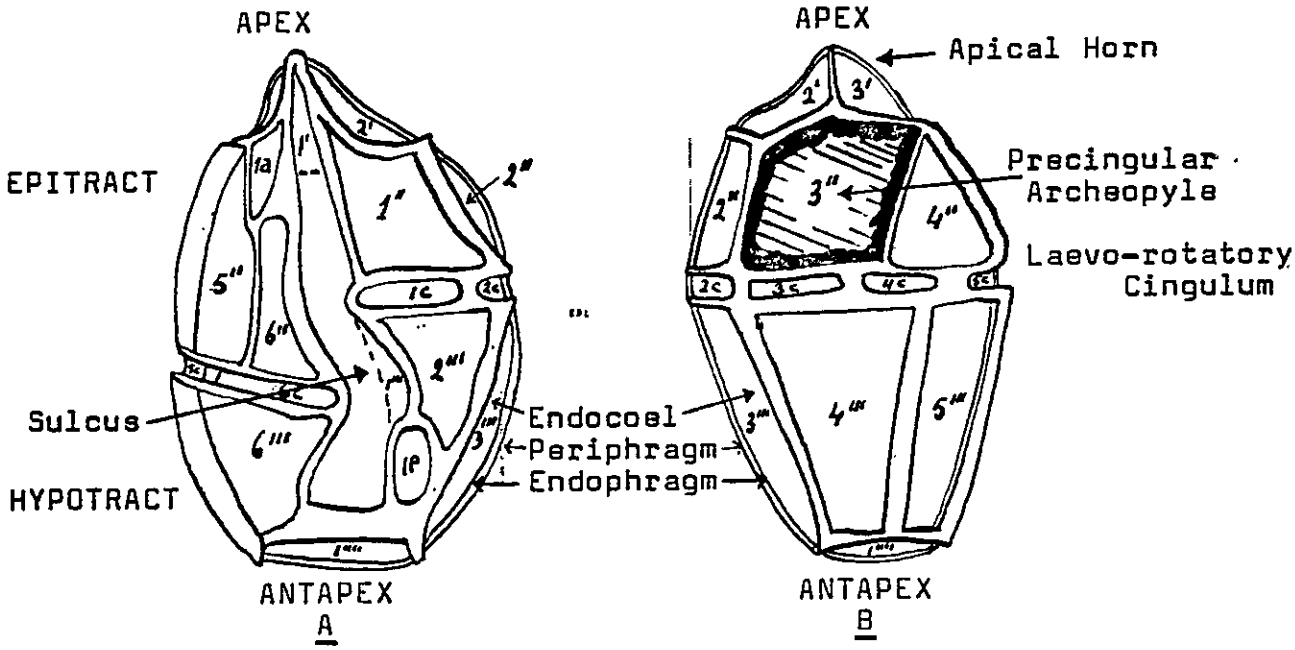
MORPHOLOGY OF DINOCYSTS

Cysts are typically two-layered being composed of an outer periphragm and an inner endophragm (Harland, 1972, p. 142). Norris and McAndrew (1970) have introduced the terms pericorpus and endocorpus to refer to the discrete bodies formed by these respective layers. Evitt (1969) uses the terms periblast and endoblast. The endoblast surrounds a central cavity called the endocoel.

The cyst is usually divided into two halves by the cingulum, which takes the form of a laevo-rotatory spiral, in most cases, into an upper half, the epitract, and a lower half, the hypotract.

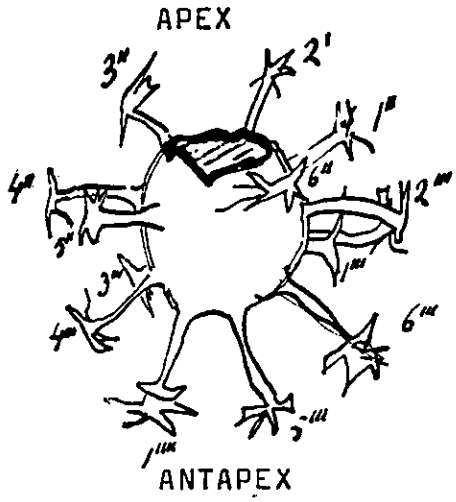
Four main morphological cyst types are recognized, proximate, chorate, proximochorate and cavate. In the proximate cysts, the two wall layers are in general contact, separating only when horns are developed at apex or antapex. The cyst formed in close contact with the inner surface of the wall of the motile dinoflagellate and exhibits the same general form as the parent motile theca, with cingulum, sulcus and tabulation. True proximate cysts are without large processes, though a surface ornament of short spinelets may be developed.

Thus in proximate cysts the wall layers are usually in contact, but small pericoels (cavities developed between the periphragm and endophragm) are sometimes present.



The external morphology of a typical proximate dinoflagellate cyst with a precingular archeopyle. A - Ventral view, B- Dorsal view. I' - 3', apical plates; Ia, anterior intercalary plate; I'' - 6'', precingular plates; Ic - 6c, cingular plates; I''' - 6''', postcingular plates; Ip, posterior intercalary plate; I'''', antapical plate (after Sarjeant, 1967).

Chorate cysts are forms in which the cyst developed well inside the original theca, to whose inner surface it was apparently linked by processes. The processes may be intertabular, intratubular or non-tabular.



Apical Archeopyle

Process
Endophragm
Periphragm
Endocoel

External morphology of a typical chorate dinoflagellate cyst with an apical archeopyle.

Proximate and chorate cysts were originally defined in terms of contraction ratio, the cross-measurement of the processes' span being considered equivalent to the cross-dimension of the original theca; chorate cysts were thus considered to be very contracted, i.e. very much smaller than the original theca, proximate cysts to be scarcely contracted at all, almost equivalent to it in size.

An important instrument in distinguishing between proximate, chorate and proximochorate cysts is the Ratio of the radius of the endocoel (or the diameter of the main body) to the overall diameter of the cyst:

$$\text{RATIO} = \frac{\text{diameter of endocoel}}{\text{overall diameter of cyst}} .$$

Cysts in which the Ratio exceeds 0.8 (R 0.8) may be described as proximate in reference to the supposed proximity of the main cyst wall to the theca at the time of encystment. In contrast, in chorate cysts this Ratio is 0.6 or less (R 0.6), whereas in proximochorate cysts the Ratio lies between 0.6 and 0.8 (0.6 R 0.8). (Evitt, 1969).

Proximochorate cysts show high septa or high processes arising from septa or sutures, suggesting that the cyst developed at some distance inside the thecal wall.

In the fourth group of cysts, the cavate cysts, the two wall layers are to a marked degree separate. The periphragm constitutes a body (periblast) whose outline closely resembles that of the mobile theca. It is separated from the inner layer by cavities at apex and antapex (apical and antapical pericoels - a bicavate cyst) or laterally or equatorially (lateral or equatorial pericoels; in the latter, the cyst is said to be PTEROCAVATE, the wall layers being in contact only at the poles) or virtually on all sides (true cavate or monocavate cysts), the two layers having little more than point contacts.

The shape of the body (endoblast) formed by the endophragm is markedly dissimilar from the periblast: it is most often spherical to ovoidal, rarely elongate, subtriangular or crescentiform.

A group of Cretaceous and earliest Tertiary cavate cysts are distinguished by the possession of extremely elongate horns - apical and antapical (Palaeocystodinium); apical, antapical

, plus one lateral (Odontochitina, Pseudoceratium); apical, antapical, plus two lateral (Muderongia, species of Wetzeliella).

NUMBER OF LAYERS

Not all cysts exhibit two wall layers (endophragm and periphragm) A third wall layer may be developed: in such genera as Chlamydophorella (Family Membranilarnaciaceae : Organic-walled membranate cysts. Enclosing membrane linked to capsule by spines or reticula) it cloaks the tips of spines arising from the periphragm and, being external to the other layers, is termed the ectophragm. In some species of Deflandrea, in contrast, the extra layer is seen by homology to be external to the endophragm but within the periphragm being therefore termed the mesophragm. At the other extreme, some cysts seem to consist of only a single wall layer; however, their outline suggests that of the endoblasts of cavate cysts, the periblast having been perhaps destroyed in diagenesis or laboratory treatment.

CONTINUITY AND PROMINENCE OF EACH LAYER

THICKNESS AND STRUCTURE OF MATERIAL IN EACH LAYER

HORNS

Figure I8-6. HORNS IN FOSSIL DINOFLAGELLATES! At left, shaded areas on a simple, oval theca as seen in dorsal or ventral view show the "cardinal" positions in which horns are most common: a-- apical, aa- antapical, c-- cingular, pc- postcingular.

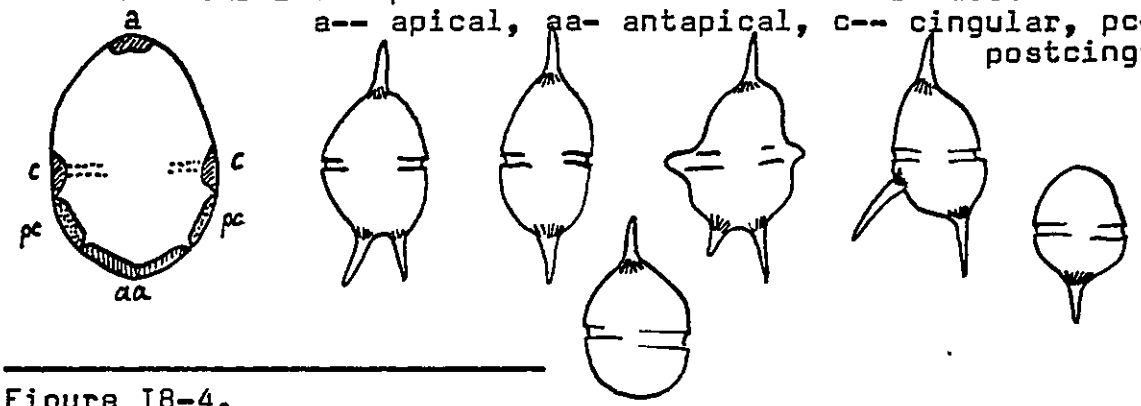
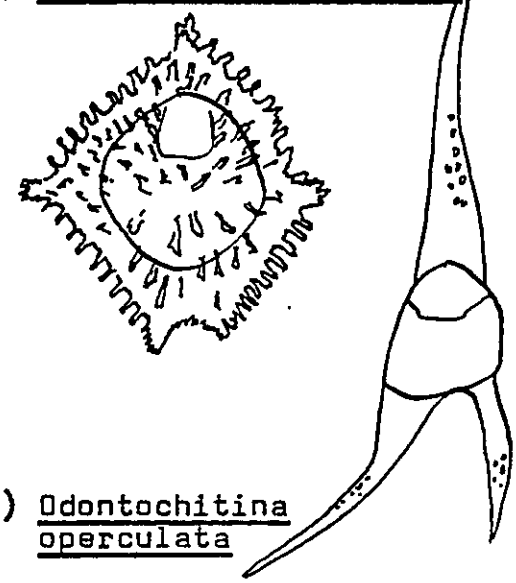
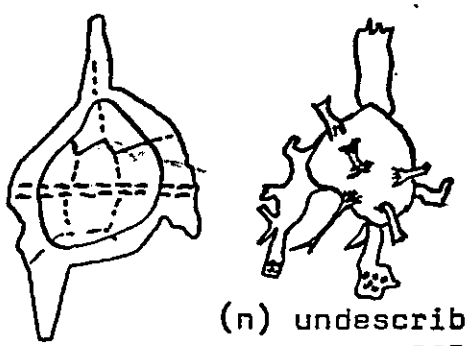


Figure I8-4.

(i) Wetzeliella articulata



(o) Odontochitina operculata



(d) Pseudoceratium ludbrooki

(n) undescribed genus

Evitt, W.R., I969. I8. Dinoflagellates and other organisms in palynological preparations. In: Tschudy, R.H. and Scott , R.A. (Editors), I969. Aspects of Palynology, pp. 439-479.

Horns are major projections of the test. They seldom number more than five and appear to be abbreviated versions of major projections (also called horns) that characterize thecae of many modern dinoflagellates. Figure I8-6 shows the "cardinal" position that may be occupied by horns. Apical and antapical horns occur in a wide assortment of modern and fossil types; cingular horns are relatively rare(fig. I8-4 i). Postcingular horns in modern types are especially characteristic of Ceratium and its close allies, and they occur in tests of several fossil forms (fig. I8-4 o, d, n) that have other traits also suggesting alliance with the Ceratiaceae. Horns in fossil dinoflagellates may be solid or hollow. Their size and prominence may vary within a species.

Horns are characteristic of many proximate, proximochorate and cavate, and a few chorate, cysts. They may be formed by both wall layers, but in many species they are formed as outgrowths from th periphragm, separated from the endephragm by a cavity. Horn development in cysts reached its acme in Cretaceous cavate forms where the length of the horn (especially the apical horn) may greatly exceed that of the tract. (Sarjeant, W.A.S., I974. Fossil and Living Dinoflagellates).

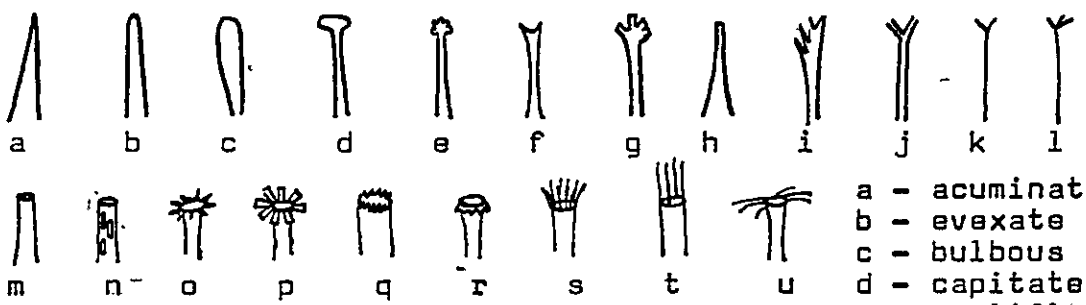
PROCESSES

In contrast to horns, processes seem not to represent structures that projected from the theca but to be unique features of the cyst that formed within the theca. They are more numerous than horns and less restricted in position. Processes are essentially columnar or spinelike projections and range from simple to intricately branched and interconnected.

Processes and septa may occur separately or in combination, merging into one another. They also grade downward in size into lesser structures - processes into features such as spinules, denticles, or granules.

Like horns, processes form in proximate, proximochorate and chorate cysts and on the periblasts of cavate cysts, as outgrowths from the periphragm which generally produce no modifications of the endophragm. At their origins (their proximal end), the processes may arise virtually at right angles to the cyst surface or may be modified to gentler angles by basal thickening. In some species, rootlike proximal outgrowths may be observed.

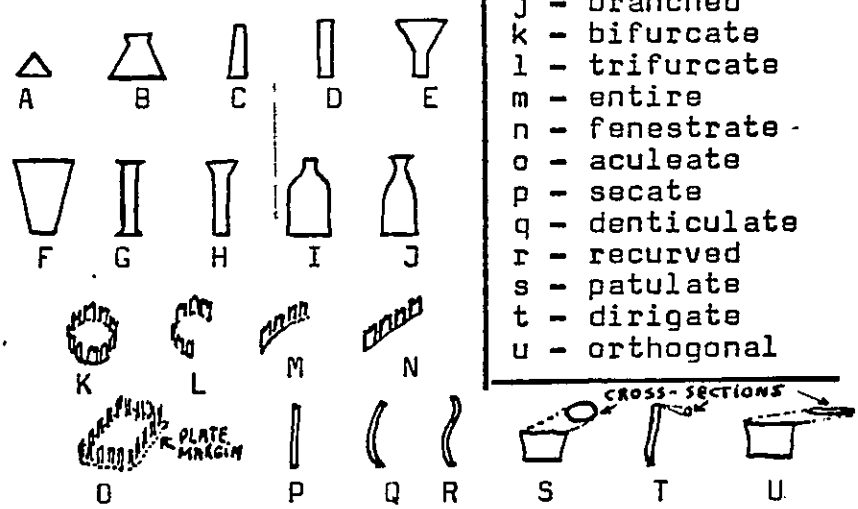
A detailed descriptive terminology for processes of different shapes and arrangement is presented by Downie and Sarjeant (in Davey et al., 1966).



Morphological terminology applied to the form of the distal ends of processes of dinoflagellate cysts.

a - acuminate
b - evexate
c - bulbous
d - capitate
e - cauliflorate
f - bifid
g - foliate
h - oblate
i - digitate
j - branched
k - bifurcate
l - trifurcate
m - entire
n - fenestrate
o - aculeate
p - secate
q - denticulate
r - recurved
s - patulate
t - dirigate
u - orthogonal

A - conical
B - subconical
C - tapering
D - cylindrical
E - infundibular
F - flared
G - tubiform
H - buccinate
I - lagenate
J - bulbose
K - annular complex
L - soleate complex
M - arcuate complex
N - linear complex
O - simulate complex
P - erect
Q - curved
R - sinous
S - latispinous
T - slender
U - taeniate

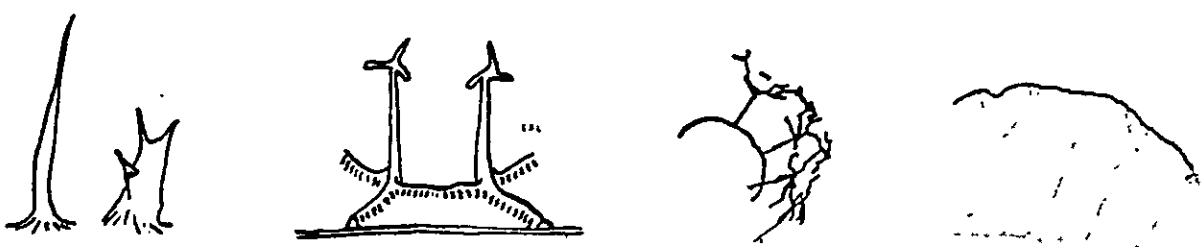


Morphological terminology applied to the general form and arrangement of processes of dinoflagellate cysts.

In some genera (e.g. Dinogymnium) the wall is penetrated by systems of perforations radiating outwards from the endocoel (wall or mural canals), but this is uncommon. The surface of the periphragm and, where separate, the endophragm may bear irregular wart-like outgrowths (verrucate), very short spines (spinose) or thick or thin rods (baculate or papillate): it may be coarsely and irregular granular (chagrinate) or may bear granules of more uniform size (granulate); or it may bear ridges, irregular in form and distribution (vermiculate) or forming a polygonal mesh, sometimes of very regular character (reticulate). Alternatively, a negative ornament of indentations may be developed; large and rounded, with a regular spacing (foveolate), smaller and, generally, more closely spaced (punctate), or of irregularly polygonal shape and variable size (infrareticulate). Only in a very few species does the surface appear smooth (laevigate) and most forms appearing laevigate at normal magnifications (x 100 to x 450) are discovered to have a surface ornament when studied under higher magnifications (x 1000+). Sarjeant, 1974.

Processes may be solid or hollow, open or closed at their tips and/or bases, in substance fibrous or hyaline (Evitt, 1969).

Processes may stand entirely free and separate from one another; however, adjacent processes may be confluent at their bases by ridges or low septa or linked at higher levels by outgrowths: the tips by thin filaments (trabeculae) forming an overall mesh, or by a membraneous layer. Also the processes may be linked in groups (their distribution reflecting the tabulation). (Evitt, 1969; Sarjeant, 1974).



FREE LINKED TRABECULATE MEMBRANOUS LAYER

The form and arrangement of the projecting structures are important taxonomic features. Their position is tabular if it reveals the pattern of thecal tabulation, nontabular if it does not. Tabular projections are either sutural or intratabular; nontabular ones may be disposed regularly or irregularly. Sutural features correspond in position to the sutures between thecal plates and may include processes, septa, or other projecting structures. If sutural projections in the position of suture junction (i.e., corresponding to the corners of thecal plates) are different from those in between, they may be distinguished as gonal and intergonal projections, respectively. Intratabular features occupy positions on the test corresponding to more or less of the central portions of thecal plates rather than to the lines of separation between them. (Evitt, 1969).

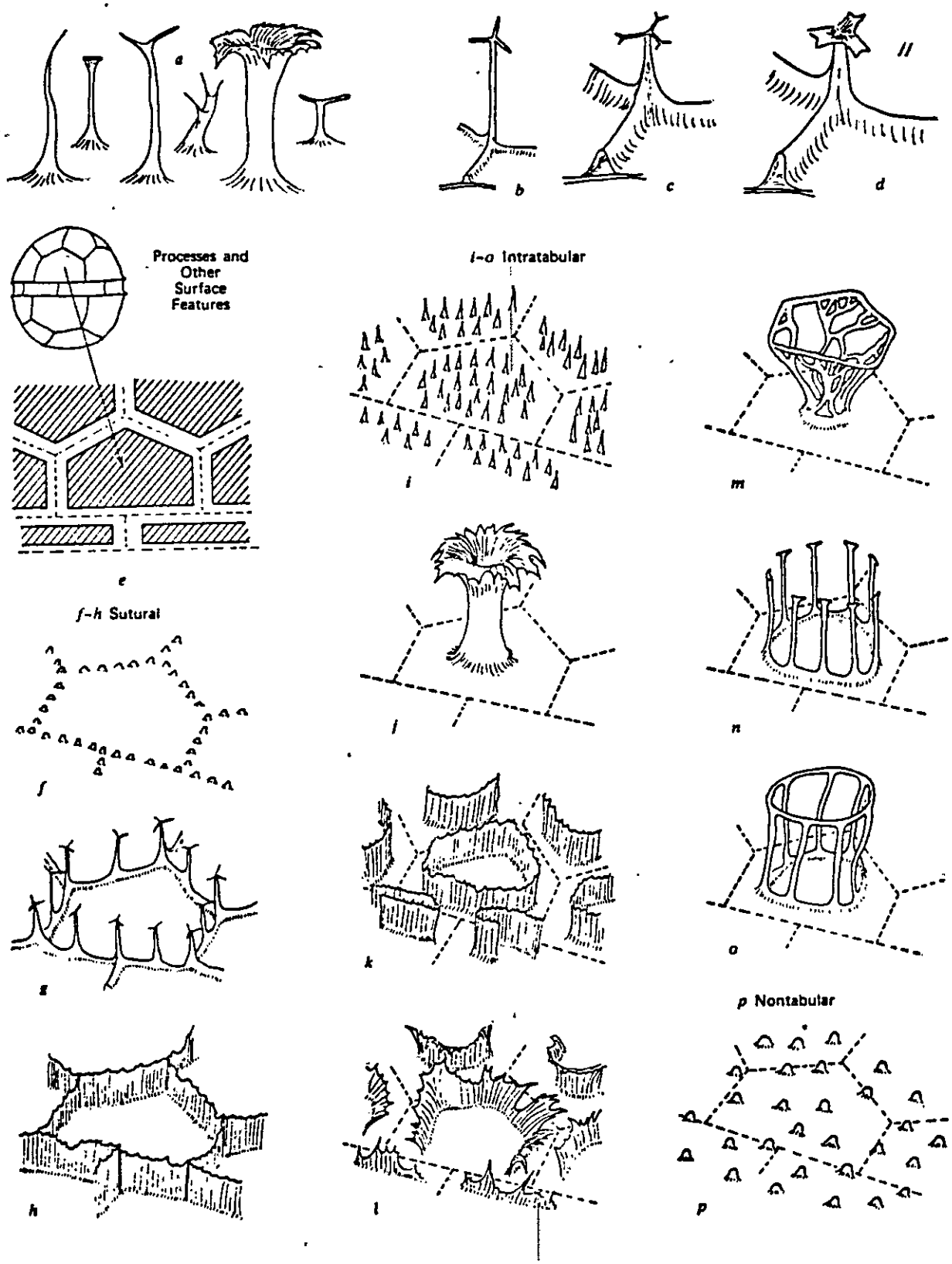


Figure 18-7. Surface features of fossil dinoflagellates. (*a*) Diagrams of several different styles of processes. (*b–d*) Three types of processes that occur in *Hystrichosphaera*. Prongs of trifurcate tips alternate with folds in outer wall layer that radiate from bases. Processes vary from solid (*b*) to hollow but closed at the tip (*c*) to hollow and open at the tip (*d*). (*e*) Diagram of small portion of dinoflagellate test and inset diagram of tabulate theca to show relationships of areas portrayed in perspective diagrams (*f–p*). Dashed lines on test correspond in position to suture lines on theca; shaded areas correspond to inner areas of thecal plates. (*f–o*) are tabular patterns; (*p*) is nontabular. (*f–h*) Surface features in sutural arrangement, corresponding to dashed lines in (*e*): (*f*) large granules; (*g*) trifurcate gonal and bifurcate intergonal processes joined by basal ridges (as in *Hystrichosphaera*); (*h*) thin septa forming a reticulum, as in *Pterodinium*. (*i–o*) Surface features in intratabular arrangement, corresponding to all or part of shaded areas in (*e*): (*i*) apiculate granules or spines; (*j*) trumpet-shaped hollow processes (as in some *Hystrichosphaeridium*); (*k*) thin septa around isolated areas, not forming a reticulum (as in *Schematophora*); (*l*) like (*k*), but septa deeply dissected and incomplete (as in *Areoligera*); (*m*) large process with constricted base, polygonal tip and wall of strands (as in some *"Hystrichosphaeridium"*); (*n*) ring of processes rising from a connecting basal ridge, free at tips (as in *Systematophora*); (*o*) like (*n*), but process tips joined by ringlike trabeculum (as in *Polystephanephorus*). (*p*) Coarse granules in nontabular arrangement. Distribution pattern of projections does not reveal either a pattern of sutural lines or a pattern of rounded to polygonal platelike areas.

SEPTA

SEPTA are essentially planar structures (varying from membraneous to relatively thick and stiff) that rise more or less perpendicularly from the main body. They have been called wings, ledges, crests, lists, and membranes. Processes and septa may occur separately or in combination, marging into one another. They also grade downward in size into lesser structures - septa into simple ridges or the low muri of a surface reticulum. (Evitt, 1969).

Septa may be smooth at their outer (distal) margin or may be denticulate or spinose, the denticles or spines being of constant or variable height and spacing. The septa themselves may be solid, perforate or fenestrate: this may be an original feature or, in fossil cysts, may result from diagenetic effects or from physical and/or chemical treatment in the laboratory. In proximate and proximochorate cysts and on the periblasts of cavate cysts, the septa arise as folds or outgrowths of the periphragm; in all species so far studied in thin section, the endophragm beneath them is unmodified. In instances where septa arise on the endoblasts of cavate cysts, they are presumably formed directly from the endophragm, though this has not yet been confirmed by thin-section studies. (Sarjeant, 1974).

Voor wat betreft the arrangement of the septa zie onder PROCESSES.

SPECIAL FEATURES OF AREAS CORRESPONDING TO CINGULUM AND SULCUS.

TABULATION

It is always necessary to give a detailed analysis of the distribution of cyst features (such as projections, surface ornament and archaeopyle) that may relate to a thecal tabulation pattern, together with as complete an estimate as possible of that tabulation.

Tabulation is the pattern of plate arrangement in a dinoflagellate theca. There may be no trace of tabulation on the test of a fossil dinoflagellate - or it may be reflected by various structures and may range from obvious, through obscure but demonstrable, to faint and uncertain. This reflected tabulation may be revealed in one or both of two ways: by polygonal areas that at least superficially look like true plates or by a wide variety of other structures that are not at all platelike.

A very important, if only partial, indication of tabulation is the archaeopyle, which is treated in a separate section.

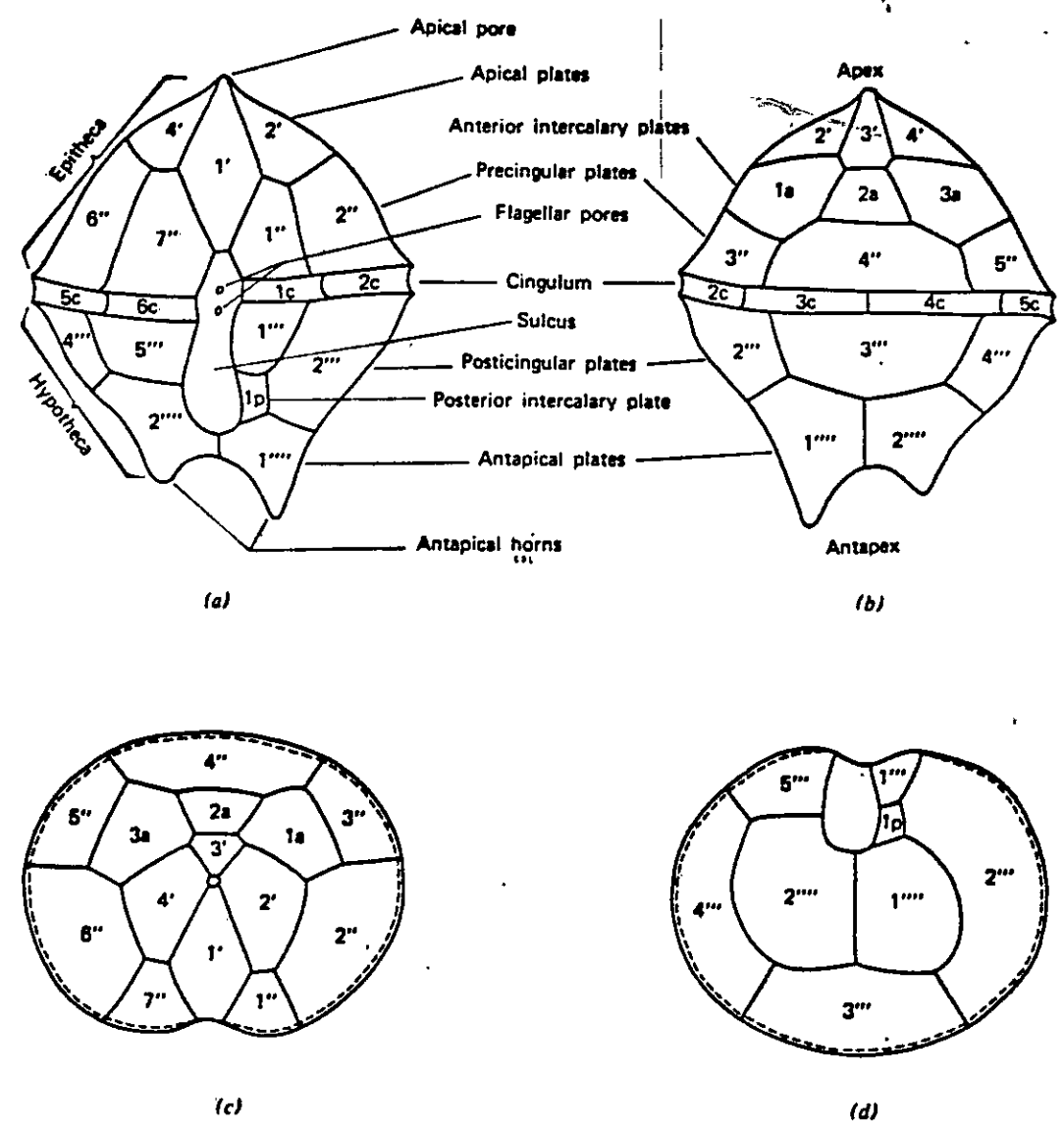


Figure 18-2. Dinoflagellate terminology and tabulation. Diagrams of a hypothetical dinoflagellate theca to illustrate the terminology for the principal thecal structures and the symbols used to designate individual plates (slightly modified from Kofoid, 1909): (*a*) ventral view; (*b*) dorsal view; (*c*) apical view; (*d*) antapical view. The complete tabulation of this example can be described in an abbreviated "formula" as follows: 4', 3a, 7'', 6''', 5'''', 1p, 2'''', meaning that the theca is composed of four apical plates, three anterior intercalary plates, seven precingular plates, six cingular plates, five postcingular plates, one posterior intercalary plate, and two antapical plates. A similar terminology and the same symbols can be used in describing the distribution of structures on the tests of fossil dinoflagellates.

THE ARCHEOPYLE

The archeopyle is the excystment aperture in the resistant wall of a dinoflagellate resting cyst. Its shape and position are closely related to a pattern of thecal tabulation. Rarely the archeopyle is a slitlike separation in the wall, but the opening is usually formed by the partial or complete release of a portion of the wall, the operculum, which corresponds to one or more thecal plates. The operculum is freed by parting of the wall along the principal archeopyle suture. The operculum is simple if it is a single unit or compound if it is divided into two or more separate pieces by accessory archeopyle sutures. The operculum (or part of it, if it is compound) is described as free if the primary archeopyle suture surrounds it completely and attached if a connection with the rest of the wall is maintained because the principal archeopyle suture is incomplete.

The shape and position of the archeopyle generally suffice to identify the thecal plates that are reflected by the portion of the test wall involved in its formation. It is typically more or less polygonal, but in some fossils the archeopyle suture runs roughly parallel to, instead of exactly along, a reflected suture line. The operculum may be smaller than the plate area (a reduced archeopyle) or it may overlap the boundary and include narrow strips surrounding plate-areas and of the cingulum (an enlarged archeopyle); its corners may be rounded.

In the past the archeopyle has often been overlooked or only superficially described, but it is now proving to be a feature of unusual value in discriminating between dinocyst taxa. A description that does not adequately treat the archeopyle cannot be considered complete. Details of archeopyle form and structure, together with examples, are given by Evitt (1967); a few are shown in figure 18-8.

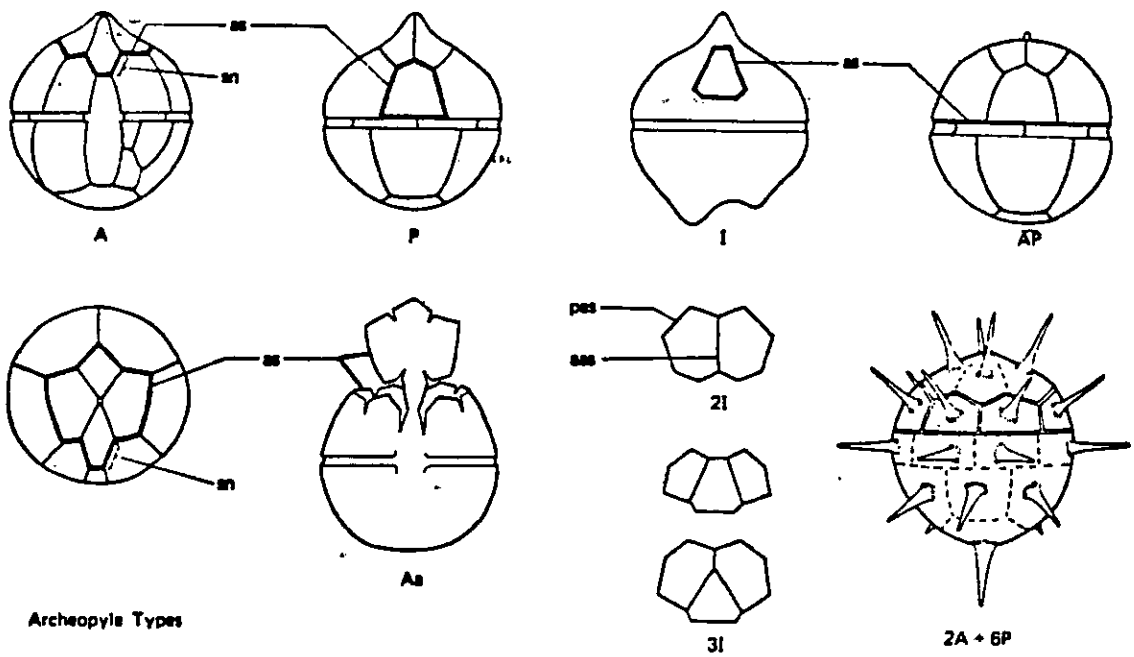


Figure 18-8. Archeopyle types in fossil dinoflagellates. (Symbols: as—archeopyle suture, pas—principal archeopyle suture, aas—accessory archeopyle suture, sn—sulcal notch. The four best known types are shown in the upper diagrams, selected details and variations are shown below. The symbols, fully explained by Evitt (1967) identify the series of thecal plates reflected by the portion of the cyst wall that is released to form the opening and give additional information about the operculum as follows: "A," "P," and "I" stand for apical, precingular, and intercalary series, respectively. A single capital letter (e.g., P), or two capitals without spacing, indicates a simple operculum, and a bar above the letter (e.g., $\bar{A}$ or $\bar{A}\bar{P}$) indicates that the simple operculum corresponds to two or more thecal plates. The operculum is known to be attached only when the symbol includes a small "a" (e.g., Aa). A numeral or a plus sign indicates a compound operculum, the numeral showing the number of pieces to the operculum (e.g., 3I) and the plus sign indicating coincidence of archeopyle sutures with boundaries between two plate series (e.g., 2A + 6P). In figure at lower right dashed lines are not represented by any visible features or specimen, but are drawn in order to show arrangement of processes with respect to thecal tabulation; only some of the secondary archeopyle sutures are visible. Figure at lower left is apical view of one above.

KEY TO THE DINOCYST-FAMILIES

1. Dinocyst marginate. ---------- (35) Family AREOLIGERACEAE (19)
   Areoligera
   Chiropteridium
   Cyclonephelium.

2. Dinocyst not marginate.
   2a. Dinocyst membranate, see 3
   2b. Dinocyst trabeculate, see 4
   2c. Dinocyst proximate, proximochorate, chorate or cavate, see 5.

3. Dinocyst membranate.
   3a. membranate dinocyst with an apical archeopyle ----------
   ---------- (26) Family MEMBRANILARNACIACEAE (22)
   Membranilarnacia
   Chlamydophorella
   Samlandia
   Tubidermodinium
   Valensiella.
   3b. membranate dinocyst with an intercalary + precingular or a precingular archeopyle -- (27) Family SCRINIOCASSIACEAE (24)
   Scriniocassis
   Gardodinium
   Palmnickia
   Tuberculodinium.

4. Dinocyst trabeculate.
   4a. trabeculate dinocyst with an apical archeopyle ----------
   ---------- (37) Family Adnatosphaeridiaceae (17)
   Adnatosphaeridium.
   4b. trabeculate dinocyst with a precingular archeopyle ----------
   ----------(36) Family CANNOSPHAEROPSITACEAE (25)
   Cannosphaeropsis.

5. Dinocyst proximate, proximochorate, chorate or cavate.
   5a. Dinocyst proximate, see 6
   5b. Dinocyst proximochorate, see 7
   5c. Dinocyst chorate, see 8
   5d. Dinocyst cavate, see 9.

6. Dinocyst proximate.
   6a. proximate dinocyst with an apical archeopyle, see 6.I
   6b. proximate dinocyst with an intercalary or intercalary+ apical archeopyle, see 6.2
   6c. proximate dinocyst with a precingular archeopyle, see 6.3
   6d. proximate dinocyst with an epitractal archeopyle, see 6.4.

   6.I. proximate dinocyst with an apical archeopyle.
   6.I.a. Tabulation clearly marked - (3) Family MICRODINIACEAE (6)
   Microdinium
   (?) Belodinium
   Clathroctenocystis
   Dapcodinium
   Eisenackia
   Fibradinium
   Glyphanodinium
   Lithodinia

(?) Maturodinium
→ Meiourogonyaulax.

6.I.b. Tabulation weakly indicated or absent, see 6.I.I.
6.I.I.
6.I.I.a. Cingulum usually distinct ----------
---------- (40) Family DINOGYMNIACEAE
(2) Dinogymnium
(?) Cystodiniopsis.
6.I.I.b. Cingulum weakly indicated or not at all, see 6.I.I.I.
6.I.I.I.
6.I.I.I.a. Spines lacking, other superficial ornamentation reduced or absent ---------- (5) Family FROMEACEAE
(3) Fromea
Horologinella.
6.I.I.I.b. Surface psilate, covered with irregular ridges (sometimes forming a reticulum) or ornamented with verrucae or short spines ----- (6) Family CANNINGIACEAE
(9) Canningia
Batiacasphaera
Chytroeisphaeridia
Dictyopyxidia
Epelidosphaeridia
Histiocysta
Membranocysta
Rhombodella
Tenua.

6.2. proximate dinocyst with an intercalary or intercalary+ apical archeopyle.
6.2.a. Tabulation vestigial or absent, see 6.2.I
6.2.b. Tabulation : sutures are delinated by low ridges, ridges, crests, septal membranes or lines of spines, see 6.2.2.
6.2.I.
6.2.I.a. Two antapical horns present ----------
---------- (7) Family BROOMEACEAE
(39) Broomea.
6.2.I.b. Rarely with an antapical prominence or horn ----------
---------- (I2) Family PAREODINIACEAE
(8) Pareodinia
Imbatodinium
Pyxidiella.
6.2.2.
6.2.2.a. Archeopyle intercalary- (I3) Family PhTHANOPERIDINIACEAE
(34) Phthanoperidinium.
6.2.2.b. Archeopyle apically situated; operculum includes apical and anterior intercalary plates ----------
---------- (4) Family NELCHINOPSACEAE
(3) Nelchinopsis.

6.3. proximate dinocyst with a precingular archeopyle.
6.3.a. Tabulation vestigial or absent ----------
---------- (2) Family APTEODINIACEAE
(24) Apteodinium
Ellipsoidinium
Emslandia
Kenleyia
Soaniella

Spongodinium
Tectatodinium
Trichodinium
Xenicodinium.

6.3.b. Tabulation I-6', 0-5a, 6-8'', 5-6+c, 5-7''', I-2p, 0-Ipv, 0-??pc, 0-I''''; sutures marked by low ridges, by crests of variable form or by lines of spines ---------- (I) Family GONYAULACYSTACEAE
(7) Gonyaulacysta
Acanthaulax
Carpodinium
Cribroperidinium
Cryptarchaeodinium
Egmontodinium
Herendeenia
Hystrichogonyaulax
Lanterna
Leptodinium
Muratodinium
Occisucysta.

6.4. proximate dinocyst with an epitractal archeopyle.
6.4.a. Shape triangular -------- (39) Family NANNOCERATOPSITACEAE
(3) Nannoceratopsis
(?) Nannoceratopsiella

6.4.b. Shape spheroidal, ovoidal, polygonal or polyhedral, see 6.4.I.

6.4.I.
6.4.I.a. Very high crests are present on one or both boundaries of the cingulum ------- (9) Family CTENIDODINIACEAE
(25) Ctenidodinium
Wanaea.

6.4.I.b. No enlarged sutures or a 'fringe' bounding the cingulum on one or both sides, see 6.4.2.

6.4.2.
6.4.2.a. Peridinium-shaped with two antapical horns ----------
---------- (I9) Family PalaeoPERIDINIACEAE
(13) Palaeoperidinium.

6.4.2.b. Shape spheroidal, ovoidal, polygonal or more or less polyhedral, see 6.4.3.

6.4.3.
6.4.3.a. Tabulation 3', 7'', 5''', 3''''; sutures delineated by low crests or ridges -- (I0) Family HETERAULACYSTACEAE
(33) Heteraulacysta.

6.4.3.b. Tabulation 3-5', 0-3a, 6-7'', ?6c, 5-7''', Ip, o-Ipv, I''''. Clearly or feebly tabulate, with sutures marked by lines, low ridges, raised crests or lines of spines -
---------- (8) Family DICHADOGONYAULACACEAE
(15) Dichadogonyaulax
Eodinia
Luehndea
Mancodinium
(?) Rhaetogonyaulax

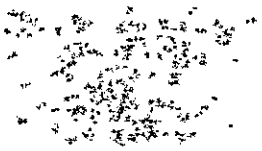
7. Dinocyst proximochorate.
7a. proximochorate dinocyst with an apical archeopyle ----------
---------- (14) Family XIPHOPHORIDIACEAE
(3) Xiphophoridium.
7b. proximochorate dinocyst with a precingular archeopyle ------
---------- (11) Family SPINIFERITACEAE
(4) Spiniferites
Achomosphaera
(?) Danea
Gonyaulax
Heliodinium
Heslertonia
Hystrichodinium
Hystrichostrogylon
Nematosphaeropsis
Planinosphaeridium
Protoellipsodinium
Pterodinium
Turbiosphaera.
7c. proximochorate dinocyst with an epitractal archeopyle -------
---------- (15) Family TOOLONGIACEAE
(3) Toolongia
Dinopteryoium
Dodnadattia.

8. Dinocyst chorate.
8a. chorate dinocyst with an apical archeopyle, see 8.I
8b. chorate dinocyst with a precingular archeopyle, see 8.2
8c. chorate dinocyst with an epitractal archeopyle ----------
---------- (30) Family HOMOTRYBLIACEAE
(7) Homotryblium
Callaiosphaeridium.
8.I. chorate dinocyst with an apical archeopyle.
8.I.a. Processes non-tabular --- (33) Family CLEISTOSPHAERIDIACEAE
(21) Cleistosphaeridium
Anthosphaeridium
Impletosphaeridium
Linqulasphaera
Polysphaeridium.
8.I.b. Processes tabular, see 8.I.I.
8.I.I.
8.I.I.a. Processes generally tubular and distally open, sometimes hollow and closed, sometimes solid ----------
---------- (28) Family HYSTRICHOSPHAERIDIACEA
(14) Hystrichosphaeridium
Araeosphaeridium
Hystrichokolpoma
Litosphaeridium
Oliqosohaeridium
Perisseiasphaeridium
Surculosphaeridium
Tanyosphaeridium.

8.I.I.b. Processes in the form of high, raised crests (supported by spines or lacking such support) or groups or lines of processes, sometimes simple, often branching or anastomosing, sometimes linked proximally by crests or distally by trabeculae. The processes may be solid, tubula or hollow but closed distally ----------
---------- (32) Family SystematoPHORACEAE
(13) Systematophora
Amphorula
Coronifera
Diphyes
Epiplosphaera
Hemiplacophora
Heterosphaerdium
Polystephanophorus
Prolixosphaeridium
Taeniophora.

8.2. chorate dinocyst with a precingular archeopyle.
8.2.a. Processes trumpet-shaped and intratabular ----------
---------- (3I) Family CORDOSPHAERIDIACEAE
(16) Cordosphaeridium
Amphorosphaeridium.
8.2.b. Processes not trumpet-shaped, see 8.2.I.
8.2.I.
8.2.I.a. Processes non-tabulate, solid, hollow but closed distally, or tubular and distally open. Archeopyle formed by the los of (from one to) four or five plates ----------
---------- (34) Family LinguloDINIACEAE
(33) Lingulodinium
Operculodinium
Protoceratium.
8.2.I.b. Processes numerous, solid (or closed hollow); their situation may be intratabular or peritabular ----------
---------- (29) Family EXOCHOSPHAERIDIACEAE
(27) Exochosphaeridium
(?) Cometodinium
Lanternosphaeridium
Trioperculodinium.

9. Dinocyst cavate.
9a. cavate dinocyst with an apical or combined apical+intercalary archeopyle, see 9.I
9b. cavate dinocyst with an intercalary archeopyle ----------
---------- (16) Family DEFLANDREACEAE
(16) Deflandrea
Albertia
Australiella
Bulbodinium
Ceratiopsis
Cerodinium
Chatangiella
Cooksoniella
Dingodinium
Evittodinium
Geiselodinium
Kisselevia
Komewuia



Palaeocystodinium
(?) Pseudodeflandrea
Svalbardella
Spinidinium
Trithyrodinium
(?) Uvatodinium
Eoceno → Wetzeliella
Xenikoon.

9c. cavate dinocyst with a precingular archeopyle, see 9.2.

9.I. cavate dinocyst with an apical or combined apical+ intercalary archeopyle.

9.I.a. One apical horn, one or more antapical horns (variously developed) and two lateral horns or prominences ---------- (22) Family Muderongiaceae
(12) Muderongia
Phoberocysta.

9.I.b. One apical horn, one antapical horn or prominence and one lateral horn or outbulge ---------- (2I) Family PSEUDOCERATIACEAE
(11) Pseudoceratium
Aptea
Endoceratium
Odontochitina
Odontochitinopsis.

9.I.c. With or without an apical horn and one or two antapical horns or prominences; no lateral horn, prominence or outbulge ---------- (20) Family HEXAGONIFERACEAE
(3f) Hexagonifera
Ascodinium
Parvocavatus
Senoniasphaera.

9.2. cavate dinocyst with a precingular archeopyle.

9.2.a. Cyst enclosed in a mucilaginous envelope ---------- (23) Family NETRELYTRACEAE
(5) Netrelytron
Kalyptea
Paranetrelytron.

9.2.b. Cyst not enclosed in a mucilaginous envelope, see 9.2.I.

9.2.I.

9.2.I.a. Cyst pterocavate ----- (25) Family STEPHODINIACEAE
(23) Stephodinium
(?) Actinotheca.

9.2.I.b. Cyst not pterocavate, see 9.2.2.

9.2.2.

9.2.2.a. Tabulation 4', 0-Ia, 6'', 6c, 5-6''', I-Op, 0-I'''' --- ---------- (I7) Family ENDOSCRINIACEAE
(26) Endoscrinium
Hystrichosphaeropsis
(?) Palaeohystrichopho
Pentadinium
Psaligonyaulax
Scriniodinium
Smolenskiella
Triblastula
Tubotuberella.

9.2.2.b. Tabulation 4', 2-3a, 7'', 5''', 2'''' ---------- (18) Family NELSONIELLACEAE (36)
Nelsoniella
Amphidiadema.

9.2.2.c. Tabulation I', Ia, 5'', 4''', I'''' ---------- (24) Family THALASSIPHORACEAE (23)
Thalassiphora
Erikania.

10. FAMILY UNCERTAIN.

(35) (46) The following pre-Quaternary organic-walled genera are not allocated to families, either because their morphology in general or the mode of archeopyle formation in particular is uncertain, or because they appear to represent new familial groupings about which it is felt further information is needed before firm proposals can be made:

Aireiana
Artemisiocysta
Astrocysta
Caligodinium
Cantulodinium
Cauca
Diconodinium
Dorocysta
Duosphaeridium
Eocladopyxis
Gillinia
Ginginodinium
Gorkadinium
Lejeunia
Mathurosphaera
Microsphaeridium
Mikropithon
Palaeoglenodinium
Palaeosphaeridinium
Phanerodinium
Pluriarvalium
Raphidodinium
Schematophora
Selenopemphix
Sirmiodinium
Stenopyxinium
Stephanolytron
Valveodinium
Wetzelodinium.

END OF THE KEY TO THE DINOCYST - FAMILIES

Distribution of biostratigraphically diagnostic dinocysts

(naar gegevens van de AASP en het IKU)

Gonyaulacysta jurassica komt in het Midden-Kimmeridgien niet meer voor, wél vinden we Gonyaulacysta granulata, G. longicornis en G. nuciformis. Verder wordt Leptodinium dominant. Karakteristiek is ook Heslertonia. Endoscrinium en Scriniodinium zijn nog steeds present.

Gedurende het Boven-Kimmeridgien voltrekken zich opmerkelijke veranderingen: Endoscrinium en Scriniodinium sterven uit. Veel nieuwe soorten van Gonyaulacysta komen in, alsmede vertegenwoordigers van de genera Fromea en Tenua. Ook Chytroeisphaeridia is present. Ook treden in deze periode voor het eerst Krijt-vormen op zoals Spiniferites ramosus, Phoberocysta, Muderongia, Broomea en Dingodinium.

Volgien en Berriasien

Voor een karakterisering van het dino-bestand tijdens deze perioden moet men te rade gaan bij Norris en Dörhöfer.

Gedurende dit interval gaat de "verkrijtisatie" door, en gesteld kan worden dat eigenlijk pas in het Valanginien we met een echt volwassen Krijt assemblage te maken hebben (whatever that may be !).

Valanginien

Aanwezig zijn onder andere de volgende vormen: Gonyaulacysta parorthoceras, Gonyaulacysta perforans, Cribroperidinium, Tenua, Chytroeisphaeridia, Canningia, Muderongia, Phoberocysta en Broomea. Verder komen Spiniferites ramosus en vertegenwoordigers van Hystrichosphaeridium in grote getale voor.

In het Boven-Valanginien/Onder-Hauterivien zien we de opkomst van Clathroctenocystis en Omatia.

Hauterivien

Aanwezig zijn onder andere: Dingodinium, Gardodinium, "gekamde" Gonyaulacysta's, weer veel Spiniferites ramosus.

Tevens zien we het eerste inkomen van Oligosphaeridium en Callaiosphaeridium.

In het Boven-Hauterivien komen de eerste Pseudoceratium's voor.

Barremien

In het Barremien vinden opmerkelijke veranderingen plaats: we zien het geleidelijk uitsterven van Heliodinium, Gardodinium, Pareodinia en Netrelytron.

Verder zien we aanwezigheid van grote vormen van de genera Gonyaulacysta, Cribroperidinium, Pseudoceratium, Odontochitina, Muderongia en Broomea. Ook Tenua/Cyclonephelium en Spiniferites ramosus zijn present.

Aptien

De volgende vormen verschijnen voor het eerst: Aptea, Coronifera, Pterodinium, Microdinium, Cauca en Trichodinium. Canninginopsis tabulata komt voor tot en met het Aptien en is een uitstekende marker voor de Aptien-Albien grens.

Albien

In het Albien zijn Muderongia en Aptea weer verdwenen. Al met al blijft een zekere Onder-Krijt invloed gehandhaafd door het nog steeds aanwezig-zijn van Cribroperidinium, Odontochitina, Pseudoceratium, Broomea, Phoberocysta en Dingodinium. Tegelijkertijd echter komen nieuwe aspect-bepalende vormen in zoals Achomosphaera, Spiniferites cingulatus, Hystrichosphaeridium tubiferum en H. arundum.

In het Boven-Albien zien we het eerste optreden van Ovoidinium en van twee zeer belangrijke Boven-Krijt genera, namelijk Dinogymnium en Deflandrea. Het eerste optreden van Dinogymnium en Deflandrea is erg lokaal bepaald en beide genera zijn eigenlijk pas in het Turonien pas volledig tot ontwikkeling gekomen.

De "gekamde" Gonyaulacysta's sterven tijdens het Albien uit.

Cenomanien

Kenmerkend voor het Cenomanien is het voorkomen van Palaeohystrichophora infusoroides; Cleistosphaeridium huguonioiti sterft aan het einde van het Cenomanien uit. Het tesamen voorkomen van deze twee vormen is karakteristiek voor het Cenomanien. Verder zien we het inkomen van Eisenackia; er zijn nog steeds veel Spiniferites ramosus maar weinig Gonyaulacysta's.

Tijdens het Cenomanien zien we tevens het laatste voorkomen van Broomea, Pseudoceratium, Apteodinium, Xiphophoridium, Surculosphaeridium, Pterodinium en Tanyosphaeridium.

Turonien, Coniacien, Santonien en Campanien

Gedurende deze perioden zien we een dominantie vanvormen zoals Spiniferites, Achomosphaera, Coronifera, Hystrichokolpoma, Hystrichosphaeridium, Cordosphaeridium, Oligosphaeridium, Litosphaeridium, Polysphaeridium, Cleistosphaeridium, Prolixosphaeridium en Cannosphaeropsis.

Verder zijn de volgende genera nog steeds vertegenwoordigd: Gonyaulacysta, Leptodinium, Cribroperidinium, Microdinium, Cyclonephelium en Thalassiphora.

Aiora en Nematosphaeropsis komen in tijdens het Santonien; Areoligera komt ook in tijdens het Neocomien.

Gedurende het Campanien gaat het genus Dinogymnium een zeer prominente plaats innemen.

Maastrichtien

Tijdens het Maastrichtien vindt een opmerkelijke verandering plaats mede door het voorkomen van de karakteristieke genera Palaeoperidinium, Lejeunia, Deflandrea, Australiella, Cooksoniella, Chtangiella, Palaeocystodinium en Svalbardella.

Aan het einde van het Maastrichtien hebben de dino-assemblages al een écht Tertiair aspect !

Dinogymnium is nagenoeg uitgestorven.

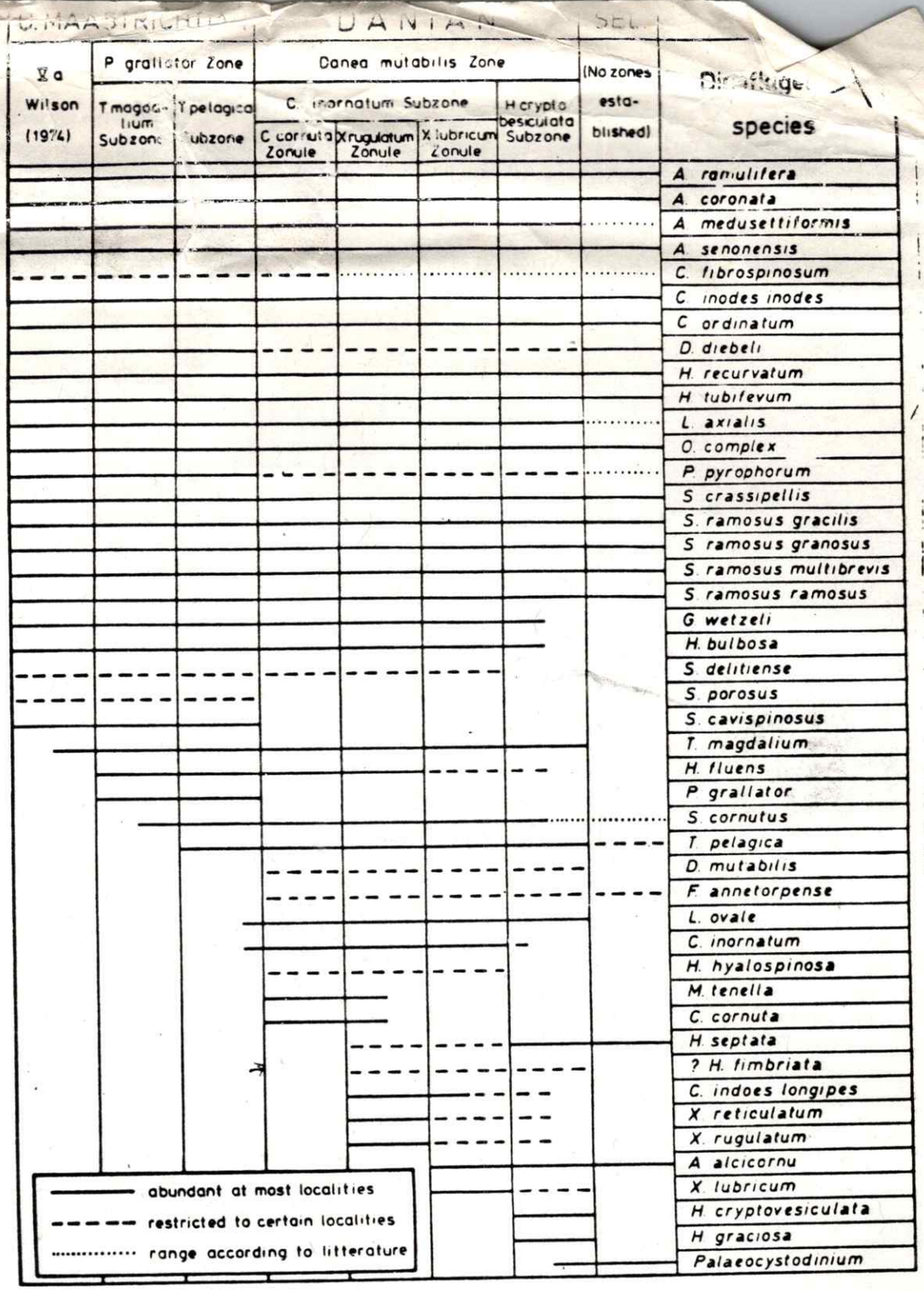
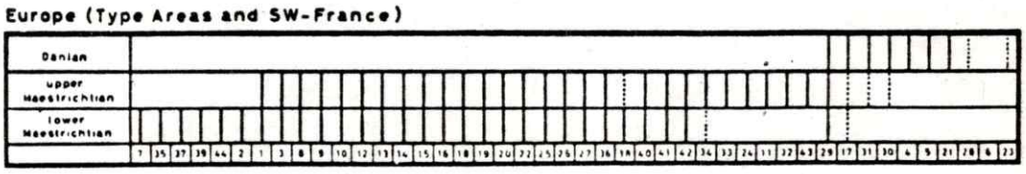


Fig. 3. Stratigraphical range of 45 common species.

Europe (Type Areas and SW-France)



North America (Alabama)

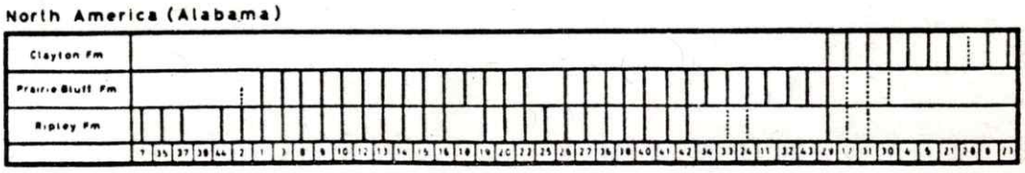


FIGURE 69.1
Distribution of calcareous nannoplankton in stratigraphic arrangement. Shows change at top of Maestrichtian, and equivalent in Alabama. Numerals correspond to names of taxa as given by Bramlette and Martini [9], where this illustration first appeared.

Las siguientes publicaciones son referencias recientes que darán una idea del estado actual de conocimientos sobre ecología/paleoecología de los dinoflagelados y rangos de especies de dinoflagelados desde el Jurásico hasta el Cuaternario.

--- --- ---

Duffield, S.L.; Stein, J.A. 1986. Peridiniacean-dominated dinoflagellate cyst assemblages from the Miocene of the Gulf of Mexico shelf, offshore Louisiana. AASP Contribution Ser. 17: 27-45. Ecol & Rang

Harland, R. 1983. Distribution maps of Recent dinoflagellate cysts in bottom sediments from the North Atlantic Ocean and adjacent seas. Palaeontology, 26: 321-387. Ecol.

Sarjeant, W.A.S.; Lacalli, T.; Gaines, G. 1987. The cysts and skeletal elements of dinoflagellates: speculations on the ecological causes for their morphology and development. Micropaleontology, 33 (1): 1-36. Ecol.

Wall, D.; Dale, B; Lohmann, G.P.; Smith, W.K. 1977. The environmental and climatic distribution of dinoflagellate cysts in modern marine sediments from regions in the North and South Atlantic oceans and adjacent seas. Marine Micropaleontology, 2: 121-200. Ecol.

Williams, G.W. 1977. Dinocysts. Their classification, biostratigraphy and paleoecology. En: Oceanic Micropaleontology; Ramsay, ed.: 1231-1325. Rang.

Williams, G.W.; Bujak, J.P. 1985. Mesozoic and Cenozoic dinoflagellates. En: Plankton Stratigraphy; Bolli et al ed.: 847-964 Rang.

Wrenn, J.H.; Kokinos,J.P. 1986. Preliminary comments on Miocene through Pleistocene dinoflagellate cysts from De Soto Canyon, Gulf of Mexico. AASP Contribution Series, 17: 169-225. Ecol & Rang

FILE: WRENN KOKINOS A INTEVEP S.A.

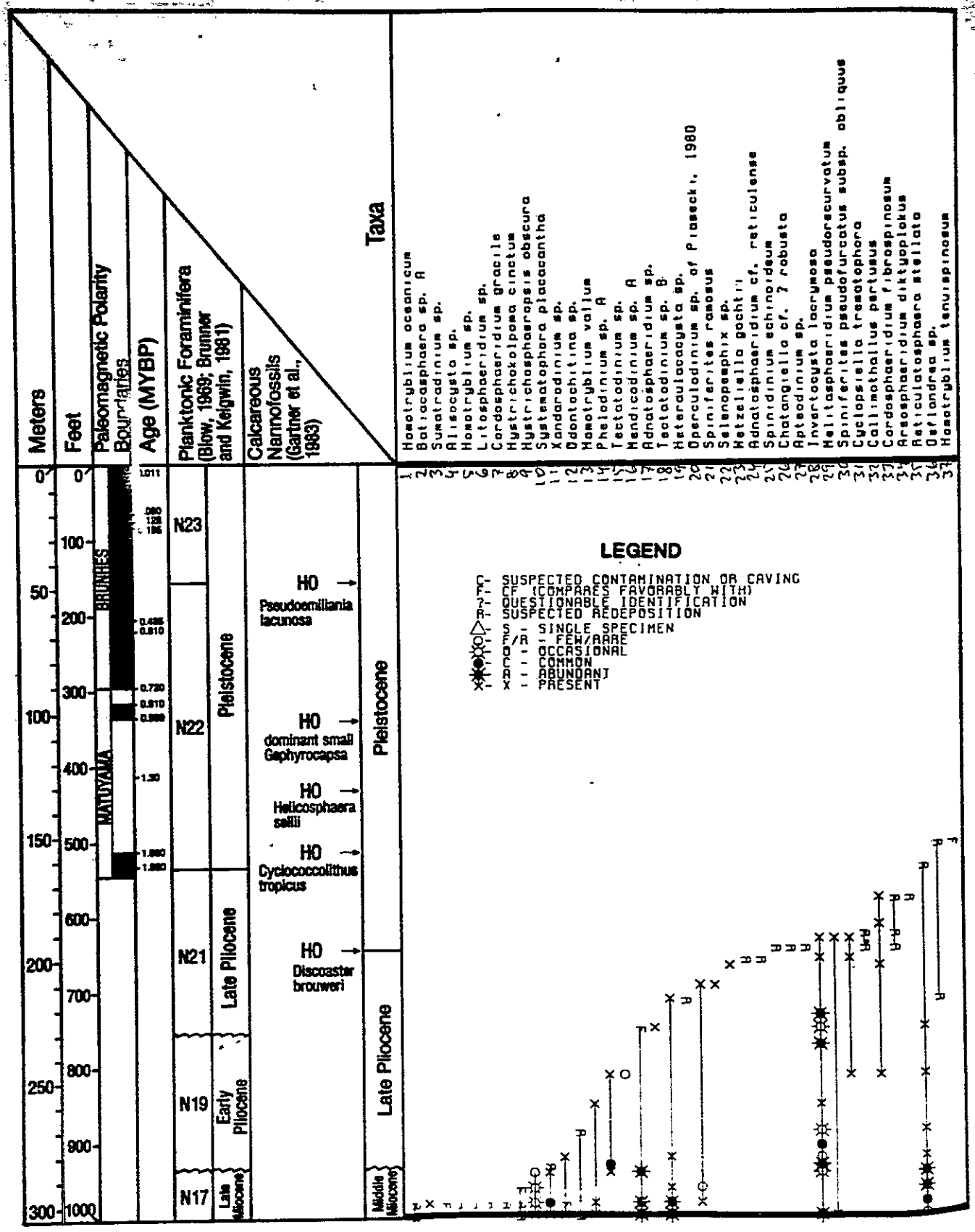
WRENN KOKINOS; 84

111 Achomosphaera andalousiensis
129 Achomosphaera spp
24 Adnatosphaeridium cf reticulense
17 Adnatosphaeridium sp
4 Alisocysta sp
151 Alterbidinium spp
59 Andalusiella sp
27 Apteodinium sp
73 Areoligera sp
34 Areosphaeridium diktyoplokus
121 Ascodinium verrucosum
65 Ascostomocystis sp
80 Batiacasphaera sp
2 Batiacasphaera sp a
64 Bitectatodinium tepikiense
128 Brigantedinium cariacoense
126 Brigantedinium spp
32 Callimothallus pertusus
87 Canningia spp
110 Cannosphaeropsis sp a
60 Ceratiopsis pannucea
131 Ceratiopsis sp
26 Chatangiella cf ? robusta
152 Chatangiella spp
97 Chlamydophorella cf nyei
82 Cleistosphaeridium sp
33 Cordosphaeridium fibrospinosum
7 Cordosphaeridium gracile
99 Cordosphaeridium sp
157 Cribroperidinium spp
122 Cyclonephelium distinctum
88 Cyclonephelium spp
69 Cyclopsiella elliptica
113 Cyclopsiella sp
31 Cyclopsiella trematophora
81 Cymatiosphaera sp
42 Dapsilidinium sp
112 Dapsilidinium sp a
49 Deflandrea phosphoritica
36 Deflandrea sp
58 Dinogymnium spp
123 Epelidosphaeridia sp
95 Florentinia deanei
62 Florentinia ferox
154 Forma a
130 Forma b
102 Forma c
67 Forma d
53 Forma e
66 Fromea sp a
132 Glaphyrocysta sp
98 Gonyaulacysta sp
43 Heteraulacacysta campanula

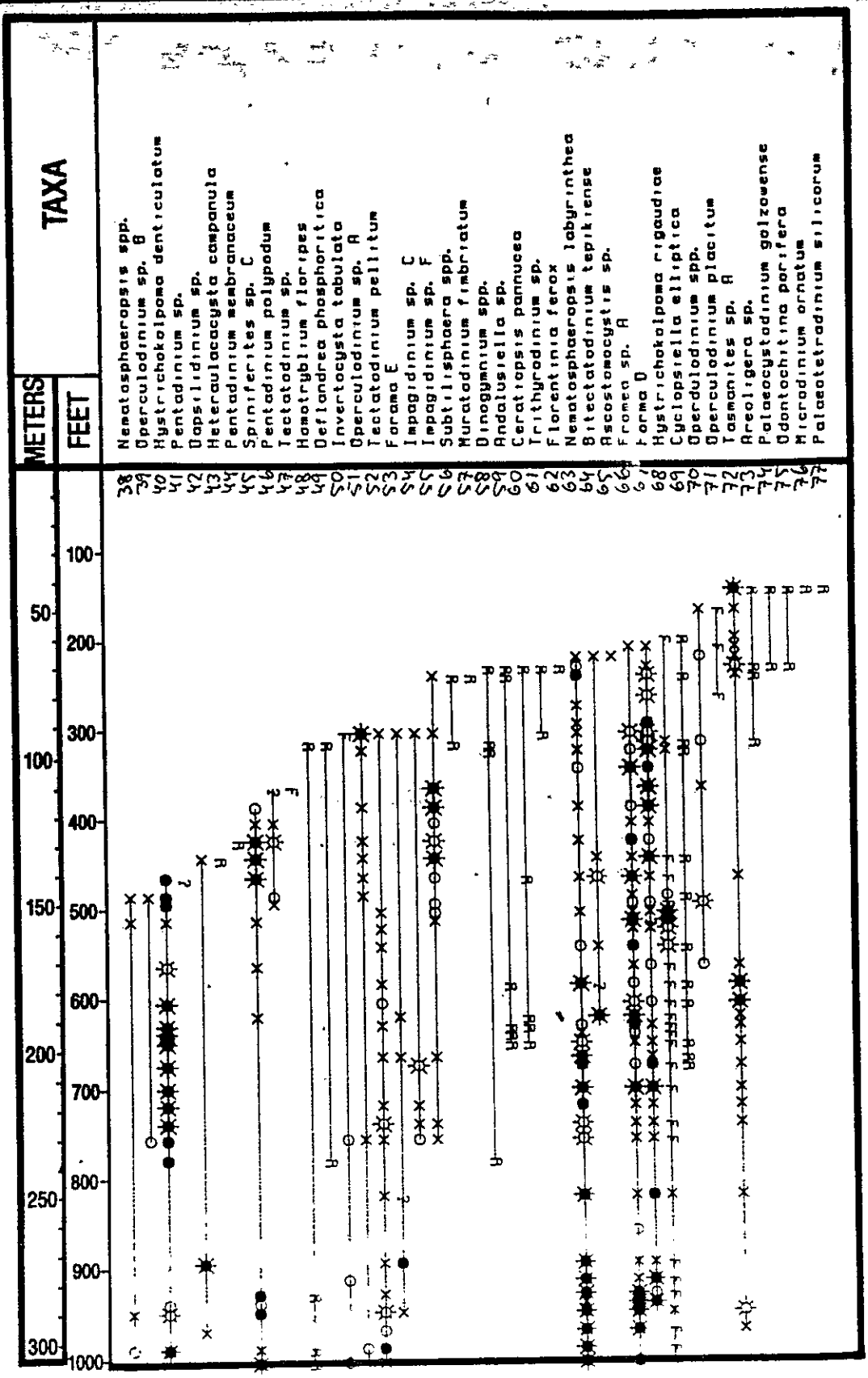
FILE: WRENN KOKINOS A INTEVEP S.A.

19 Heteraulacacysta sp
5 Homotryblium sp
48 Homotryblium floripes
1 Homotryblium oceanicum
37 Homotryblium tenuispinosum
13 Homotryblium vallum
8 Hystrichokolpoma cinctum
40 Hystrichokolpoma denticulatum
68 Hystrichokolpoma rigaudiae
159 Hystrichosphaeridium sp
9 Hystrichosphaeropsis obscura
116 Hystrichostrogylon sp
125 Impagidinium aculeatum
138 Impagidinium patulum
86 Impagidinium sp
149 Impagidinium sp a
115 Impagidinium sp b
54 Impagidinium sp c
107 Impagidinium sp d
117 Impagidinium sp e
55 Impagidinium sp f
141 Impagidinium strialatum
109 Incertae sedis sp I
28 Invertocysta lacrymosa
50 Invertocysta tabulata
84 Labyrinthodinium truncatum
114 Lejeunecysta cf hyalina
118 Lejeunecysta diversiforma
145 Lejeunecysta spp
43 Lingulodinium machaerophorum
6 Litosphaeridium sp
137 Melitasphaeridium choanophorum
29 Melitasphaeridium pseudorecurvatum
78 Membranophoridium aspinatum
16 Mendicodinium sp a
79 Microdinium opacum
76 Microdinium ornatum
136 Multispinula quanta
57 Muratodinium fimbriatum
63 Nematosphaeropsis labyrinthea
100 Nematosphaeropsis sp a
134 Nematosphaeropsis sp b
38 Nematosphaeropsis spp
155 Odontochitina costata
90 Odontochitina operculata
75 Odontochitina porifera
12 Odontochitina sp
94 Oligosphaeridium complex
91 Oligosphaeridium pulcherrimum
92 Oligosphaeridium spp
127 Operculodinium centrocarpum
156 Operculodinium cf centrocarpum
124 Operculodinium giganteum
139 Operculodinium israelianum
71 Operculodinium placitum

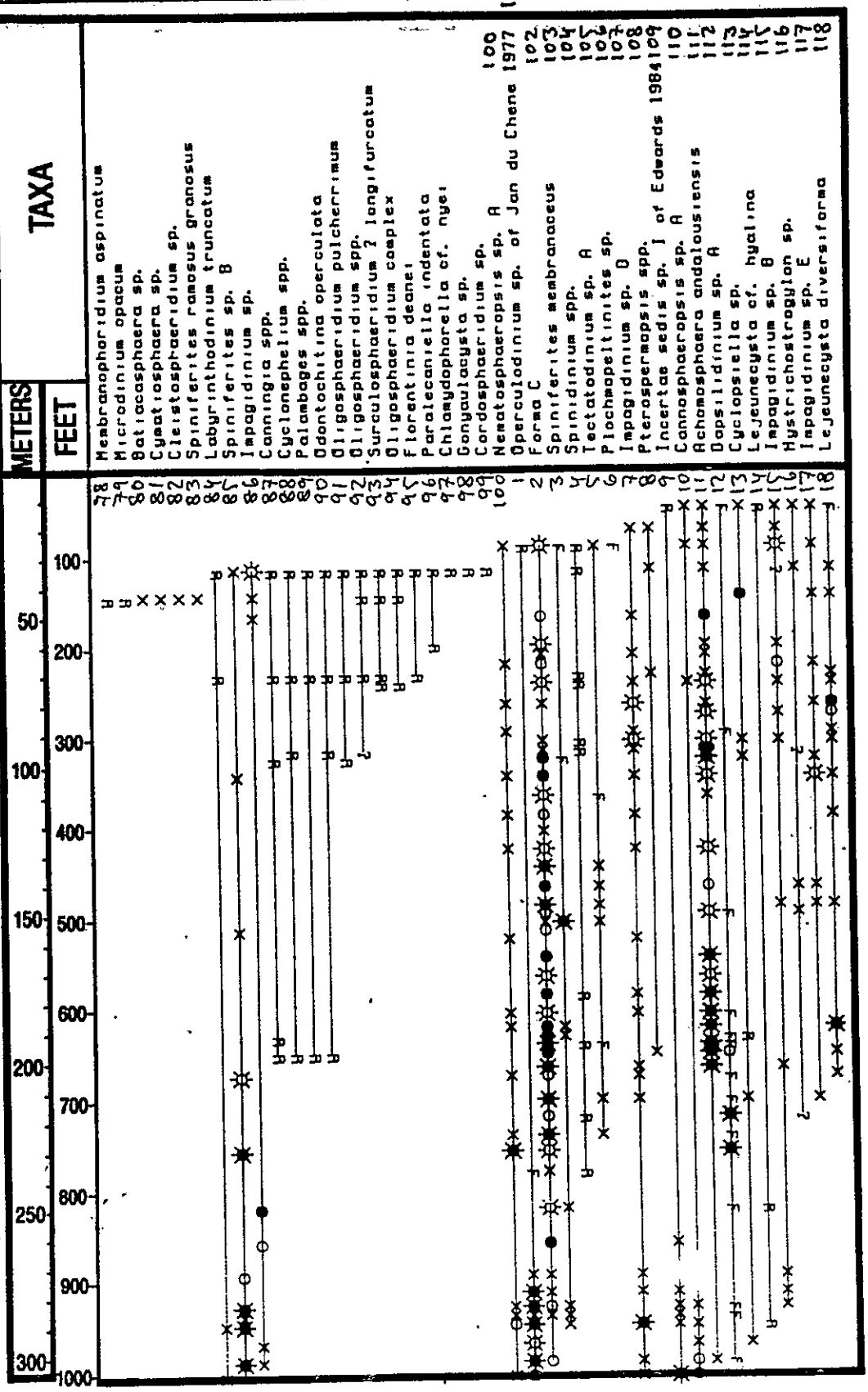
101,20 Operculodinium sp
51 Operculodinium sp a
39 Operculodinium sp b
70 Operculodinium spp
74 Palaeocystodinium golzowense
119 Palaeohystrichophora infusorioides
133 Palaeoperidinium cretaceum
77 Palaeotetradinium silicorum
89 Palambages spp
96 Paralecaniella indentata
44 Pentadinium membranaceum
46 Pentadinium polypodum
41 Pentadinium sp
14 Phelodinium sp a
106 Plochmopeltinites sp
146 Polysphaeridium zoharyi
108 Pterospermopsis spp
35 Reticulatosphaera stellata
148 Rhizophagites sp a
22 Selenopemphix sp
150 Selenophemphix nephroides
25 Spinidinium echinoideum
104 Spinidium spp
103 Spiniferites membranaceus
140 Spiniferites mirabilis
135 Spiniferites pachyderma
80 Spiniferites pseudofurcatus subsp obliquus
21 Spiniferites ramosus
83 Spiniferites ramosus granosus
158 Spiniferites ramosus ramosus
142 Spiniferites sp a
85 Spiniferites sp b
45 Spiniferites sp c
144 Spiniferites spp
56 Subtilisphaera spp
3 Sumatradinium sp
93 Surculosphaeridium ? longifurcatum
10 Systematophora placacantha
153 Tasmanites sinuosus
72 Tasmanites sp a
52 Tectatodinium pellitum
47,15 Tectatodinium sp
105 Tectatodinium sp a
18 Tectatodinium sp b
61 Trithyrodinium sp
147 Tuberculodinium vancampoae
120 Veryhachium sp
23 Wetzeliella gochtii
11 Xandarodinium sp



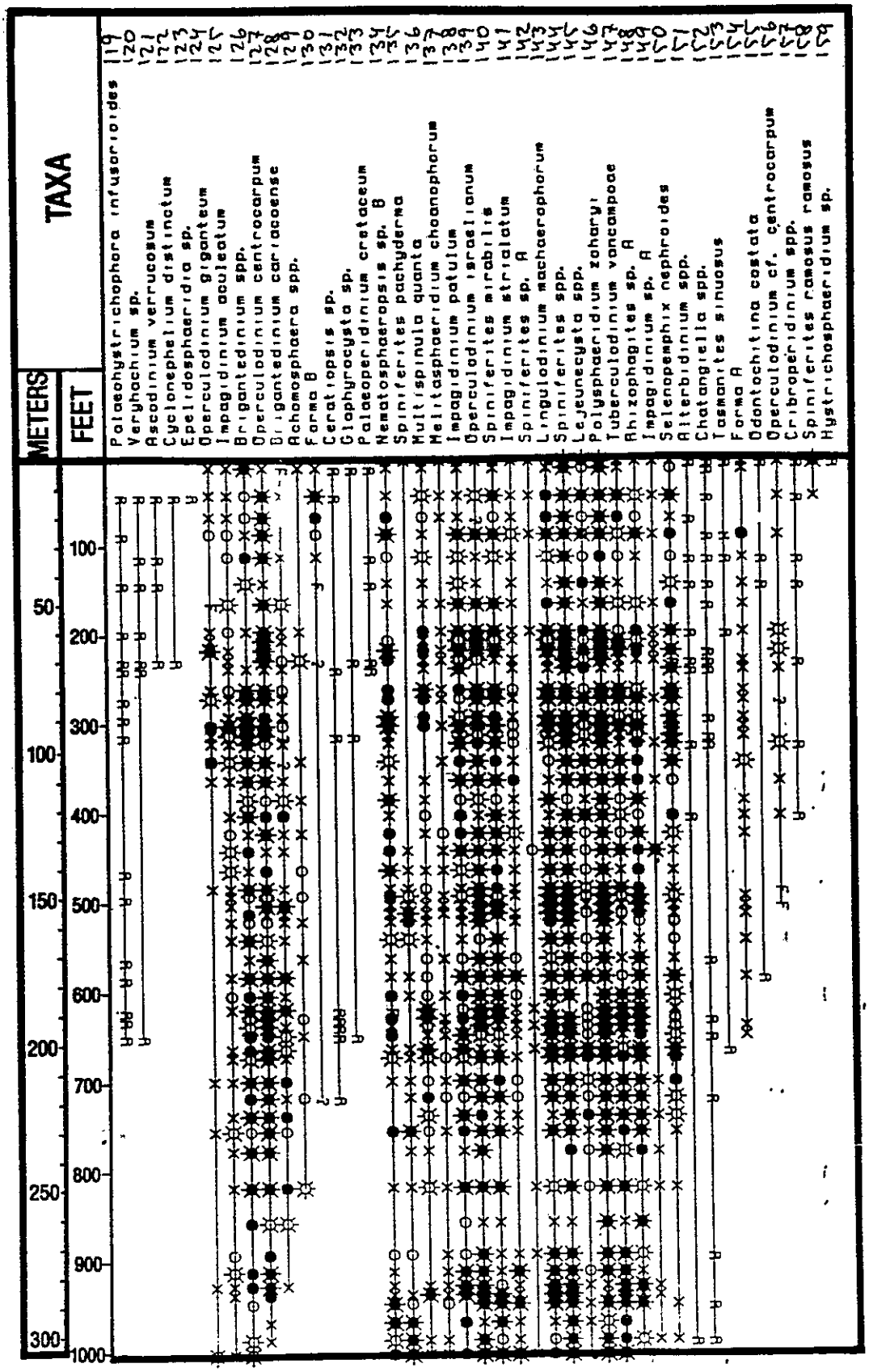
Text-Figure 2. Range chart of the palynomorphs recovered from the E67-135 core. The inferred paleomagnetic polarity boundaries are from Williams (1984) and the inferred ages are from Ledbetter (1984) and Thunell (1984).



Text-Figure 2 (continued)



Text-Figure 2 (continued).

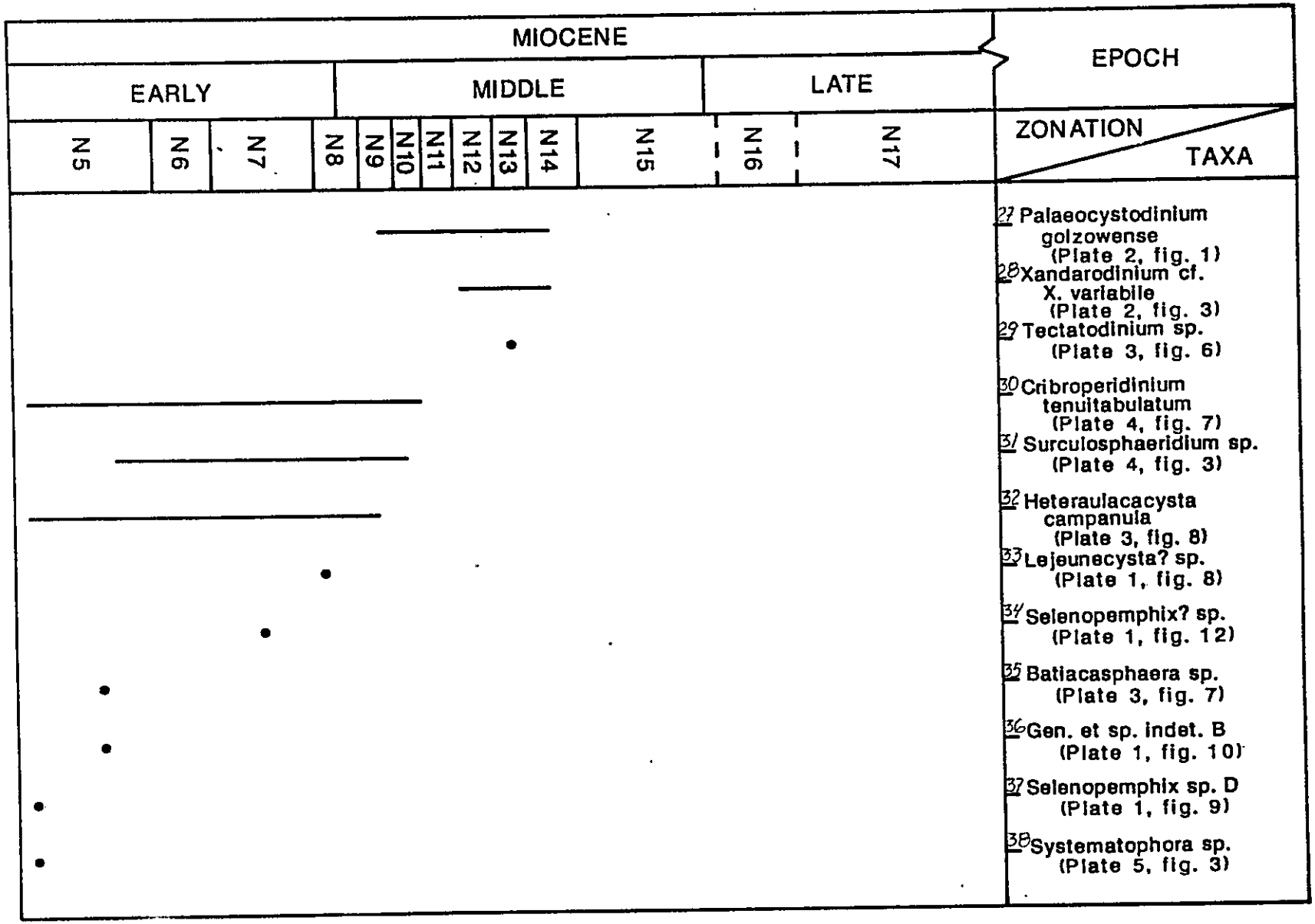


Text-Figure 2 (continued).

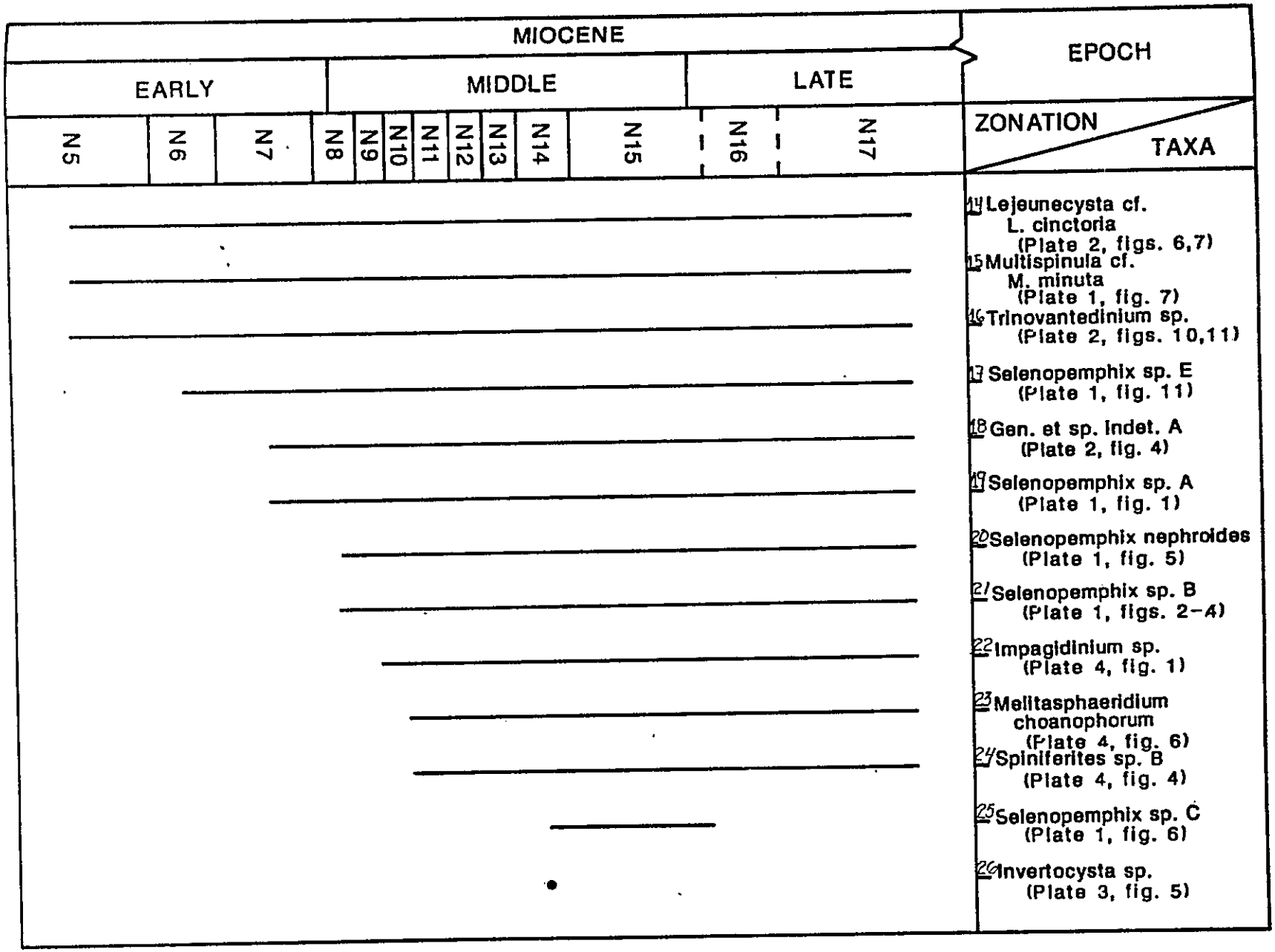
FILE: DUFFIELD STEIN A INTEVEP S.A.

DUFFIELD & STEIN, 1986

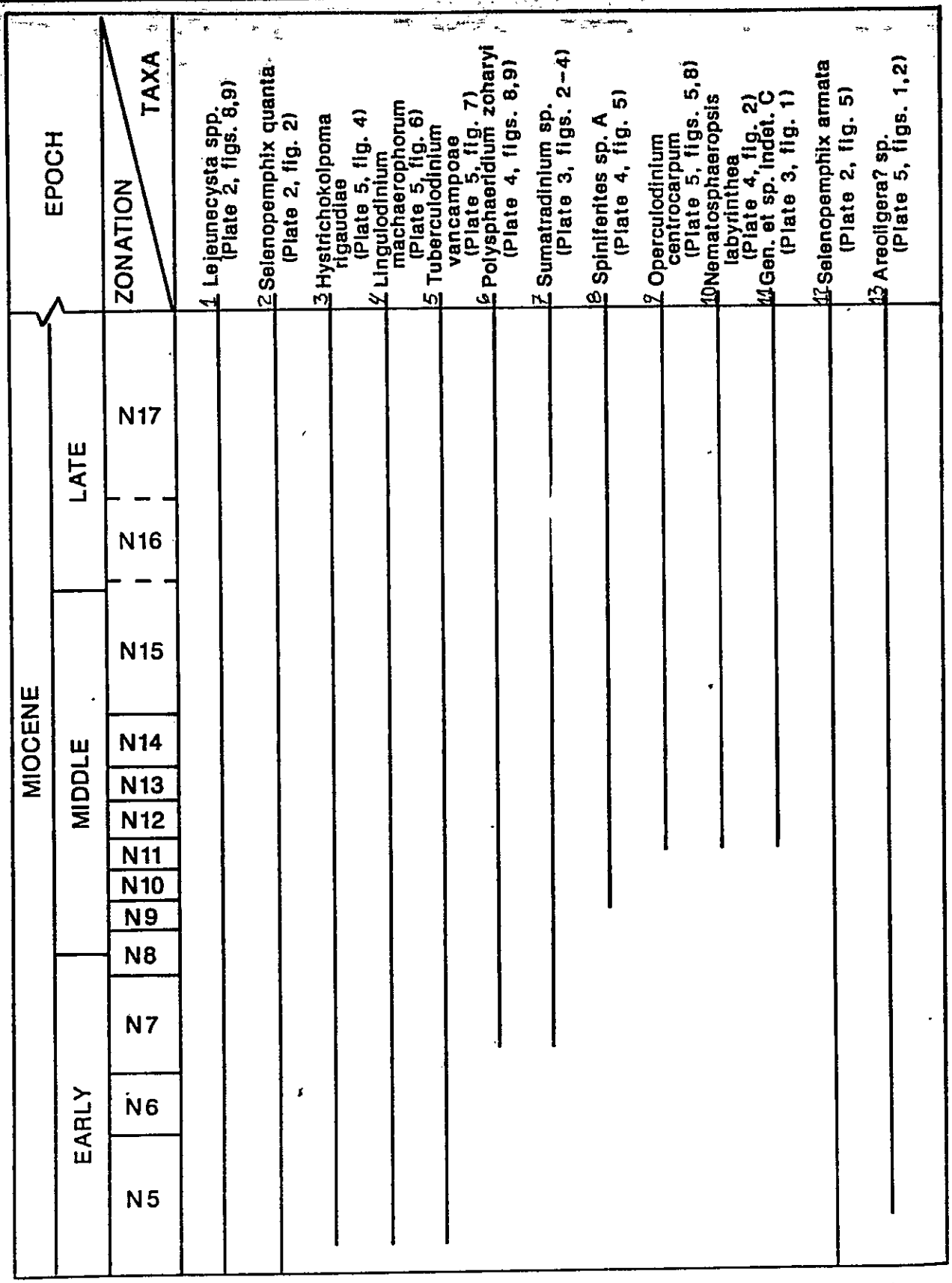
13 Areoligera? sp
35 Batiacasphaera sp
30 Cribroperidinium tenuitabulatum
18 Gen et sp indet A
36 Gen et sp indet B
11 Gen et sp indet C
32 Heteraulacacysta campanula
3 Hystrichokolpoma rigaudiae
22 Impagidinium sp
26 Invertocysta sp
14 Lejeunecysta cf L cintoria
1 Lejeunecysta spp
33 Lejeunecysta? sp
4 Lingulodinium machaerophorum
23 Melitasphaeridium choanophorum
15 Multispinula cf M minuta
10 Nematosphaeropsis labyrinthea
9 Operculodinium centrocarpum
27 Palaeocystodinium golzowense
6 Polysphaeridium zoharyi
12 Selenopemphix armata
20 Selenopemphix nephroides
2 Selenopemphix quanta
19 Selenopemphix sp A
21 Selenopemphix sp B
25 Selenopemphix sp C
37 Selenopemphix sp D
17 Selenopemphix sp E
34 Selenopemphix? sp
8 Spiniferites sp A
24 Spiniferites sp B
7 Sumatradinium sp
31 Surculosphaeridium sp
38 Systematophora sp
29 Tectatodinium sp
16 Trinovantedinium sp
5 Tuberculodinium vancampoae
28 Xandarodinium cf X variabile



Text-Figure 3 (continued).



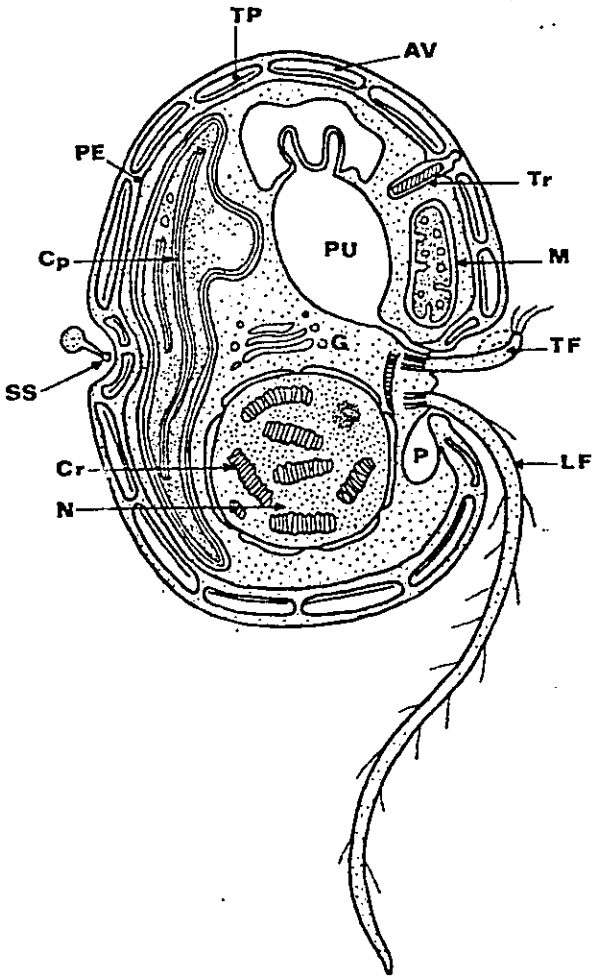
Text-Figure 3 (continued)



Text-Figure 3. - Range chart of dinoflagellate cyst taxa. The foraminiferal zonation is that of Blow (1969) adapted from Stude (1984).

by Dodge (1971, 1973). Features of some of the more unusual members (parasites, noctilucoids) will receive a more extensive treatment in a supplement, prepared by J. and M. Cachon (in press at this time of writing), to Chatton's useful but now outdated chapter in the first volume of the Traité de Zoologie (1952). Only features of particular relevance to the present discussion will be summarized here.

Text Fig. 1 illustrates the basic organization of a generalized dinoflagellate. This



Text Fig. 1. A diagrammatic longitudinal section through a gymnodinoid dinoflagellate. *AV:* amphiesmal vesicle; *Cp:* chloroplast; *Cr:* chromosome; *G:* Golgi complex; *LF:* longitudinal flagellum; *M:* mitochondrion; *N:* nucleus; *PE:* pellicular layer; *P, PU:* pusule; *SS* striated strand; *TF:* transverse flagellum; *TP:* thecal plate; *Tr:* trichocyst.

shows an essentially eukaryotic organization common to many other flagellated protists. However there are several noteworthy peculiarities by means of which members of the group may be recognized and which give suggestions about their evolution.

The commonest arrangement among the protists is two, anteriorly inserted flagella. This type is found in only a small percentage of dinoflagellates, in the "desmokonts", e.g. *Prorocentrum*, but this feature may be used to argue for primitiveness of the desmokonts relative to other dinoflagellates. Flagellar dimorphism, found in all dinoflagellates, is common in protists although it usually involves an anterior hairy flagellum and a posteriorly-directed smooth one, e.g. in many of the chlorophyll *c*-containing groups (see Taylor, 1976b, 1978 for details). The ribbon-like flagellum present in all dinoflagellates is unusual but not unique to the group. Some of the pedinelloid chrysophytes have a somewhat similar modification on their single anterior flagellum. The presence of simple, rather than compound, flagellar hairs (although sometimes in complex arrangements) on one or both flagella is unlike chrysophytes and more like euglenoids. The functional association of ribbon-like flagellum and surface furrow found in most dinoflagellates (the "dinokonts", in which the flagella are inserted laterally) is distinctive of the group. LeBlond and Taylor (1976) have discussed the functional aspects of this arrangement and the flagellar wave.

In the motile cell ("mastigont") a wall consisting of multiple cellulose plates may be absent or developed to varying degrees. Unlike other cellulose-producing protists and higher plants this wall (the theca *sensu stricto*) is internal, being formed within a single layer of vesicles, the amphiesmal vesicles, below the cell membrane. Internal walls are also formed by other flagellate groups, e.g. cryptomonads and euglenoids, but these are of different composition.

In some dinoflagellates other types of

formula provisional, given as *?2', ?6-7a, 6'', 6c, 6''', 1p, 1''''*, but archeopyle type is uncertain, and the presence of six or seven anterior intercalary paraplates is unusual.

Archeopyle. Apical, type uncertain.

Paracingulum. Indicated by six paraplates (see Note below).

Parasulcus. Longitudinally elongate area between paraplates *1'* and *1''''*, which widens antapically; epicystal part may be subdivided.

Size. Small.

Note: The provisional paratabulation formula provided by Morgenroth (1968) indicates six paracingular plates, but his illustration of the ventral surface shows seven; the seventh paraplate may lie within the parasulcus.

COMPARISON

Subtilidinium may be congeneric with either *Cladopyxidium* or *Microdinium*. However, Morgenroth's description and illustrations do not provide sufficient information to demonstrate conclusively whether *Subtilidinium* is congeneric with those genera or, if not, to specify exactly how they differ.

SPECIES

Type Species:

Subtilidinium minutum Morgenroth 1968; monotypic.

SURCULOSPHAERIDIUM

Davey *et al. in* Davey *et al.* 1966

ORIGINAL DESCRIPTION

"Subsphaerical chorate cysts bearing a moderate number of intratabular processes, considered to reflect the tabulation *4', 6'', 6c, 6''', 1p, 3''''*. Processes solid, closed distally and branched. Archeopyle apical." — From Davey *et al. in* Davey *et al.* (1966, p. 161).

SYNOPSIS

Cysts skolochorate, body subspherical with approximately 25 solid, isolated, distally branched, intratabular processes; paratabulation gonyaulacacean, indicated by intratabular processes; archeopyle apical, Type $\overline{\text{tA}}$.

MODIFIED DESCRIPTION

Shape. Body subspherical.

Wall Relationships. Autophragm only.

Wall Features. No parasutural features. Intratabular processes relatively slender, solid, branched distally, and may be perforate; autophragm smooth.

Paratabulation. Indicated by intratabular processes, gonyaulacacean; process formula: *4', 6'', 6c, 6''', 1p, 1''''*, *1s*. Presence of three antapical processes unusual and requires confirmation.

Archeopyle. Apical, probably Type $\overline{\text{tA}}$. Operculum free; exact shape of operculum and trace of principal archeopyle suture unknown.

Paracingulum. Indicated by six intratabular processes.

Parasulcus. Position suggested by a few slender processes in midventral part of hypocyst.

Size. Intermediate to large.

Note: Paratabulation shown by Davey *et al. in* Davey *et al.* (1966) indicates three antapical processes; this we consider anomalous, particularly on a cyst that otherwise shows normal gonyaulacacean paratabulation. The process formula given above reflects our interpretation of the paratabulation on the type species.

COMPARISON

Surculosphaeridium differs from *Hystrichosphaeridium* in having solid rather than tubular processes. It differs from *Areosphaeridium*, which also has solid intratabular processes, in not having fenestrate, arcuate, or platformlike features at the ends of the processes.

SPECIES

Type Species:

Surculosphaeridium cribrotubiferum (Sarjeant 1960) Davey *et al. in* Davey *et al.* 1966.

Provisionally Accepted Species:

S.? longifurcatum (Firtion 1952) Davey *et al. in* Davey *et al.* 1966—archeopyle may be precingular rather than apical; if so, process distribution requires reinterpretation.

S.? vestitum (Deflandre 1938b) Davey *et al. in* Davey *et al.* 1966—no verification of archeopyle type.

PALAEOCYSTODINIUM
Alberti 1961

ORIGINAL DESCRIPTION
Body fusiform, more or less flattened dorsoventrally. With hornlike processes at both ends; these taper towards their free ends. With a rounded-trapezoidal pylome below the apex. Always with a roundish to ellipsoidal inner body closely appressed against the outer shell. — Translated from Alberti (1961, p. 20).

SUPPLEMENTAL DESCRIPTION
See Lentin & Williams (1976, p. 88-89).

SYNOPSIS
Cysts proximate, cornucavate or circumcavate, elongate ellipsoidal, with single slender pointed apical and antapical horns at each pole; paratabulation indicated by archeopyle only; archeopyle intercalary, Type I; archeopyle index generally <0.5.

MODIFIED DESCRIPTION
Shape. Elongate ellipsoidal; apical and antapical horns pointed and generally significantly narrower than part of cyst containing the endocyst.

Wall Relationships. Cysts cornucavate or circumcavate; endocyst subspherical to elongate ellipsoidal.

Wall Features. No parasutural features. Periphragm smooth to faintly ornamented; scattered spinulae or granulae may be anywhere on periphragm, but tend to be found most frequently at or near ends of horns. Antapical horn may have short lateral spur.

Paratabulation. Indicated by archeopyle only.

Archeopyle. Intercalary, Type I (*2a* only); height greater than width; archeopyle index generally <0.5; operculum free.

Paracingulum. Generally not indicated.

Parasulcus. Not indicated.

Size. Large.

COMPARISON
Palaeocystodinium differs from *Svalbardella* in having slender pointed apical and antapical horns and in lacking indications of paratabulation other than the archeopyle.

SPECIES
Type Species:

Palaeocystodinium golzowense Alberti 1961.

Other Accepted Species:

P. australinum (Cookson 1965b) Lentin & Williams 1976.

P. benjaminii Drugg 1967.

P. denticulatum Alberti 1961.

P. gabonense sp. nov. = Svalbardella australina Cookson & Eisenack 1965b of Malloy (1972, p. 63, pl. 1, fig. 17, 20); holotype, pl. 1, fig. 17, herein designated.

P. granulatum (Wilson 1967b) Lentin & Williams 1976.

P. lidiae (Gorka 1963) Davey 1969b.

P. scabratum Jain, Sah & Singh 1975.

Provisionally Accepted Species:

P.? deflandrei Gruas-Cavagnetto 1968— provisional assignment by original author.

P.? hyperxanthum (Vozzhennikova 1963) Vozzhennikova 1967—archeopyle stated to be absent.

P.? rhomboides (O. Wetzel 1933a) Lentin & Williams 1973—provisional assignment by transferring authors [originally described as *Ceratium* cf. *fusca* forma *rhomboides*].

PARAGONYAULACYSTA
Johnson & Hills 1973

ORIGINAL DESCRIPTION
"Proximate cysts, ellipsoidal in outline, surmounted by a short, thin, apical horn. Tabulation: *2', 2a, 6'', 6C, 6''', 1p, 1''''*. Cingulum broad, helicoid, displaced ventrally by 1 × its width, sulcus extends onto epitract and abuts against plate *1'*. Sutures in form of low ridges which, at junctions with cingulum, bear short spines; surface of cyst smooth. Intercalary archeopyle formed by loss of plates 1a and 2a." — From Johnson & Hills (1973, p. 207).

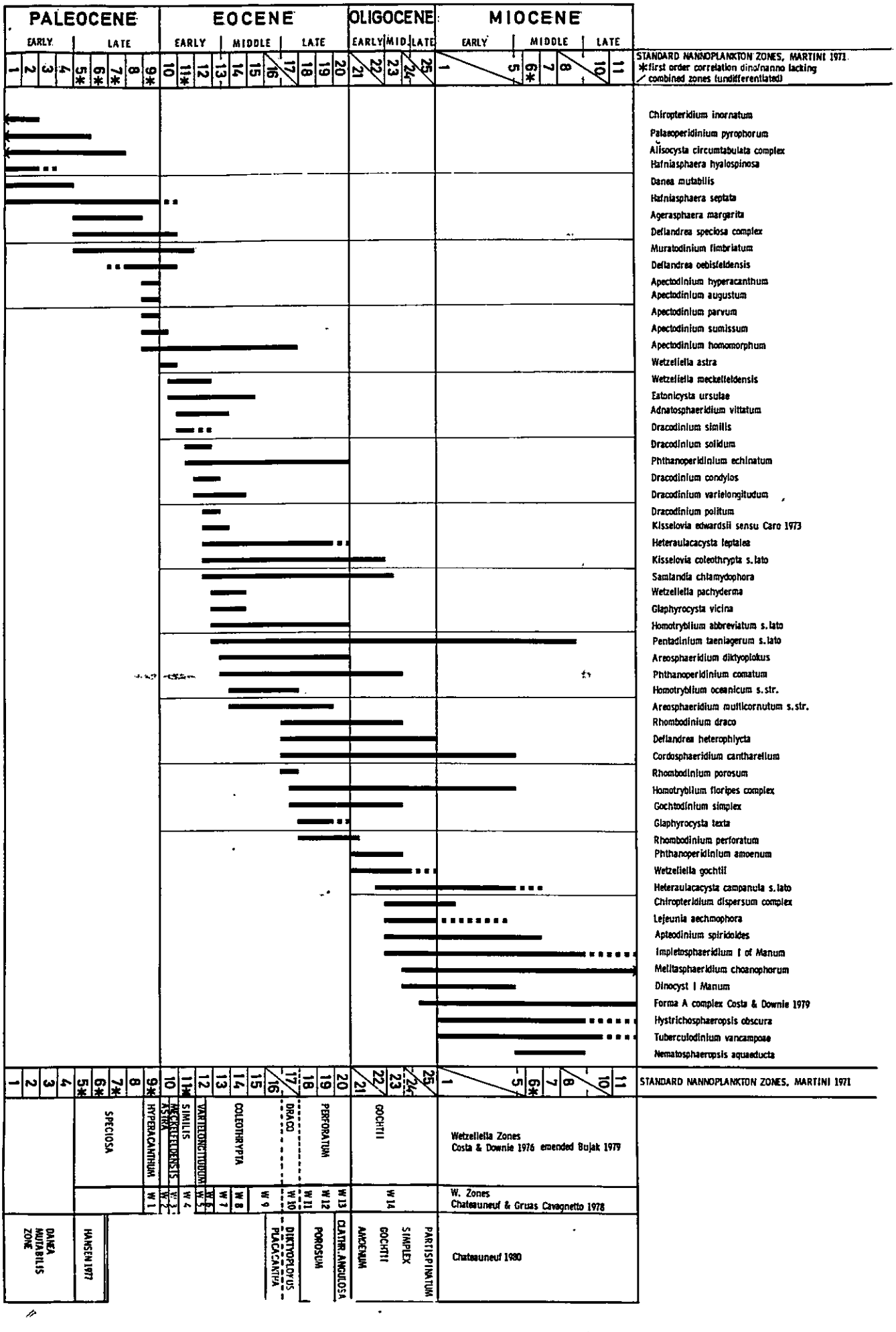
SYNOPSIS
Cysts proximate, ellipsoidal, with an apical horn; paratabulation indicated by low parasutural ridges; autophragm smooth; archeopyle intercalary, Type 2I; archeopyle index >0.5.

MODIFIED DESCRIPTION
Shape. Ellipsoidal with an apical horn.

Wall Relationships. Autophragm only.

LAMINILLAS PARA OBSERVAR AL MICROSCOPIO EN PARTE PRACTICA DEL CURSO DE DINOFLAGELADOS

Slide	1	La Viana-1	4129'	lám.	1
	2	"	2646'	"	1
	3	"	2214'	"	1
	4	"	1565'	"	1
	5	"	1138'	"	1
	6	"	544'	"	1
	7	Mamón-14	11430'	"	1
	8	"	10620'	"	1
	9	"	7710'	"	1
	10	"	7190'	"	2
	11	"	6290'	"	3
	12	"	6290'	"	1
	13	UV-201	3428'	"	2
	14	"	3385'	"	1
	15	"	3212'	"	1
	16	"	3139'	"	1
	17	"	3051'	"	2
	18	"	2991'	"	1
	19	Mitare-1	4900'	"	1
	20	"	4690'	"	1
	21	MPE-159	Sup.	"	5
	22	"	Sup.	"	4
	23	"	Sup.	"	1
	24	M2PE12	Sup	"	6
	25	M14PE108	Sup.	"	2
	26	MPE-226	Sup.	"	1
	27	Sup-71	Sup.	"	2
	28	NZZ-88	5880'	"	3
	29	DX-2	3290'	"	1
	30	JX-4	1090'	"	1
	31	P.Azul-1	6861'	"	2


PALEOCENE
EARLY
LATE
EOCENE
EARLY
MIDDLE
LATE
OLIGOCENE
EARLY
MID
LATE
MIOCENE
EARLY
MIDDLE
LATE
STANDARD NANNOPLANKTON ZONES, MARTINI 1971.
*first order correlation dino/nanno lacking
/ combined zones (undifferentiated)
Chiropteridium inornatum
Palaeoperidinium pyrophorum
Alisocysta circumtabulata complex
Hafniasphaera hyalospinosa
Danea mutabilis
Hafniasphaera septata
Agerasphaera margarita
Deflandrea speciosa complex
Muratodinium fimbriatum
Deflandrea oebisfeldensis
Apectodinium hyperacanthum
Apectodinium augustum
Apectodinium parvum
Apectodinium sumissum
Apectodinium homomorphum
Wetzeliella astra
Wetzeliella meckelfeldensis
Eatonicysta ursulae
Adnatosphaeridium vittatum
Dracodinium similis
Dracodinium solidum
Phthanoperidinium echinatum
Dracodinium condylos
Dracodinium varielongitudum
Dracodinium politum
Kisselovia edwardsii sensu Caro 1973
Heteraulacacysta leptalea
Kisselovia coleothrypta s.lato
Samlandia chlamydophora
Wetzeliella pachyderma
Glaphyrocysta vicina
Homotryblium abbreviatum s.lato
Pentadinium taeniagerum s.lato
Areosphaeridium diktyoplokus
Phthanoperidinium comatum
Homotryblium oceanicum s.str.
Areosphaeridium multicornutum s.str.
Rhombodinium draco
Deflandrea heterophlycta
Cordosphaeridium cantharellum
Rhombodinium porosum
Homotryblium floripes complex
Gochtodinium simplex
Glaphyrocysta texta
Rhombodinium perforatum
Phthanoperidinium amoenum
Wetzeliella gochtii
Heteraulacacysta campanula s.lato
Chiropteridium dispersum complex
Lejeunia aechmophora
Apteodinium spiridoides
Impletosphaeridium I of Manum
Melitasphaeridium choanophorum
Dinocyst I Manum
Forma A complex Costa & Downie 1979
Hystrichosphaeropsis obscura
Tuberculodinium vancampoae
Nematosphaeropsis aquaeducta
STANDARD NANNOPLANKTON ZONES, MARTINI 1971
SPECIOSA
HYPERACANTHUM
SIMILIS
MECKELFELDENSIS
ASTRA
VARIELONGITUDUM
COLEOTHRYPTA
DRACO
PERFORATUM
GOCHTII
Wetzeliella Zones
Costa & Downie 1976 emended Bujak 1979
W. Zones
Chateauneuf & Gruas Cavagnetto 1978
DANEA MUTABILIS ZONE
HANSEN 1977
DIKTYOPLOKUS PLACACANTHA
CLATHR. ANGULOSA
POROSUM
AMOENUM
GOCHTII
SIMPLEX
PARTISPINATUM
Chateauneuf 1980