A SUMMARY REVIEW OF THE MORPHOLOGY AND CLASSIFICATION OF THE FOSSIL PERIDINIALES (DINOFLAGELLATES) WITH RESPECT TO THEIR MODERN REPRESENTATIVES

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ABSTRACT

The biology of the Peridiniales (Dinoflagellates) is reviewed together with the morphology and classification of the fossil forms in an attempt to relate the work of palynologists and phycologists with regard to this group of algae.

INTRODUCTION

It is the purpose of this article to give a summary review of the modern Pyrrhophyta, more particularly the Peridiniales, in addition to a review of the morphology and classification of fossil dinoflagellates. Current research has shown that a knowledge of the modern representatives of this group is essential in order to advance the study of the fossil forms. In the past palynologists have been exclusively concerned with the cyst stage of the organism whereas the phycologist has been almost exclusively concerned with the motile stage. Independently both groups have erected their own taxonomy and co-operation between them is desirable for the further advancement of dinoflagellate studies.

RECENT PERIDINIALES—A SUMMARY REVIEW

Dinoflagellates are contained in the plant division Pyrrhophyta Pascher 1914. The name is derived from the Greek *pyrrhos*—meaning flame coloured, red, yellowish red or tawny, and *phyta*—meaning plants. The distinctive colouration of these organisms is due to the presence of the carotenoid pigments dinoxanthin and peridinin. The Pyrrhophyta are also characterized by possession of chlorophylls a and c, two flagella, a large and prominent nucleus, a variable number of membrane bound pulsules (MORRIS, 1967) or pusules (FRITSCH, 1935) and by distinctive sculpturing patterns on the cell surface.

The division is divided into two classes—the Desmophyceae Fott 1959 and the Dinophyceae Pascher 1914. The former are characterized by a lack of plates on the cell wall, two anteriorly placed flagella, a single longitudinal groove that divides the theca into two valves or an unequal division of the cell by an anteriorly developed transverse girdle. This class has little importance in the geological record although two Jurassic genera, *Nannoceratopsis* Deflandre 1938, Lower to Upper Jurassic, and *Palhistiodinia* Deflandre 1938, Upper Jurassic, have been placed within it. It is possible, however, that many acritarchs belong to this Class (See LISTER, 1970).

The Dinophyceae are, however, important in the fossil record and have a recorded geological range from Silurian to Recent (SARJEANT, 1967). They are characterized by two

flagella arising from the ventral surface, and a single transverse furrow that divides the cell into two equal halves. All other fossil genera of the dinoflagellates may be assigned to this class, which includes free-living single celled forms to palmelloid, colonial, and filamentous non-motile forms. Certain members are endoparasites, some ectoparasites and some symbionts. A description of these specialized forms may be found in FRITSCH (1935). Members of the Dinophyceae occur in fresh, brackish and marine waters and their feeding habits may be holophytic, holozoic or saprophytic and in certain forms a combination of habits is employed. The presence of a cellulosic cell wall and chlorophyll does, however, allow the placement of this group in the plant kingdom.

The palynologist is usually concerned with the marine and freshwater, free-living holophytic forms. The majority of these are referred to one of two orders, the Gymnodiniales Lindemann 1928 and the Peridiniales (Schutt) Lindemann 1928. The major distinction between the two is the lack of a well defined cell wall in the Gymnodiniales ; hence the name. An excellent account of the Gymnodiniales has been published by NORRIS (1966). WALL and DALE (1968a) have demonstrated that certain members of the Gymnodiniales are capable of producing several distinctive cyst morphotypes that resemble acanthomorphitid and herkomorphitid acritarchs, but there is some doubt that these could be fossilized. Recently EVITT (1970) has stated that the genus *Dinogymnium* Evitt, Clarke & Verdier also belongs to this order. It is of interest to note that FRITSCH (1935) and MORRIS (1967) regard the Gymnodiniales as a "primitive" order. Most fossil dinoflagellates are thought to belong to the Peridiniales, although this is not fully proven (EVITT, 1961; WALL, 1965; WALL & DALE, 1968a).

MORPHOLOGY OF THE PERIDINIALEAN CELL

The Peridiniales possess a three-layered cell wall (LOEBLICH III, 1969). The innermost layer, external to the cystoplasmic membrane is called the pellicle, it is unornamented and made up of fibrous cellulose ; the second layer, called the theca, is composed of two to many separable plates, unornamented or ornamented, which are held together by a cementing substance and are also composed of fibrous cellulose ; and a third layer of thecal membranes which surround the theca and are attached along the thecal plate junctions. More recently DODGE and CRAWFORD (1970) published a survey of the theca of several members of the Dinophyceae and found a basic structure of an outer continuous plasma membrane beneath which lies a single layer of flattened vesicles—for both the Gymnodiniales and Peridiniales. In several genera an additional layer of plates is developed within the vesicles. Eight distinct categories of thecal construction are recognised and it is suggested that they are of great taxonomic value. LOEBLICH and LOEBLICH (1966), in discussing cell wall composition of the Pyrrhophyta, quote the results of B. E. Volcani of the Scripps Institute of Oceanography who found the presence of 94% cellulose, minor lipids, minor proteins and inorganic matter.

Some members of the Peridiniales possess an internal structure called the internal skeleton, which consists of opaline silica. This has been observed in the fossil *Actiniscus* Ehrenberg *ex* Downie & Sargeant 1964 [1965] and in the living state by SCHUTT (1891). The "skeleton" consists of four parts ; two large, cupped, five-rayed stars, and two smaller stars. It is uncertain, however, whether these forms should be included within the Peridiniales.

The peridinialean test, generally 20 to 150 microns in length, may be divided by a transverse furrow into an upper half, termed epitheca, and a lower half, termed hy-

potheca. These areas are often subdivided by sutures, grooves or growth areas into thecal plates, for which KOFOID (1909) instituted a nomenclatural system. The epitheca carries two series of plates assignable to an apical series and precingular series. The cingular plate series separates the epitheca from the hypotheca. The hypotheca, like the epitheca, carries two series of plates, the post-cingular and the antapical. Additional plates, if present, are termed anterior or posterior intercalary plates according to their position on the theca. The ventral side of the test may be divided by a longitudinal furrow, the sulcus. A somewhat variable naming system is used for the sulcal plates (KOFOID, 1909 ; BALECH, 1959). Plates are numbered from the ventral area in a counterclockwise direction when viewed from the ventral side.

The two flagella are inserted in two pores or a common pore on the sulcal area. One of the flagella is thread-like, arises from the posterior pore and lies along the longitudinal groove. The other flagellum is ribbon or band shaped, arises from the anterior pore and lies along the transverse furrow. HALL (1923, 1925) described each flagellum as terminating at a basal granule. Each granule is connected by a rhizoplast to an extra-nuclear centrosome which lies adjacent to the nucleus. The only study of flagellar ultra-structure is that of PITELKA and SCHOOLEY (1955), who described that of Gyrodinium Kofoid & Swezy 1921, a member of the Gymnodiniales, although DODGE (1968b) has figured a longitudinal section of a dinoflagellate flagellum.

The typical peridinialean form varies from spherical, subspherical to peridinoid. Other forms may appear as rectangular to polygonal and in some horns are developed; this is especially prominent in Ceratium Schrank ex Loeblich & Loeblich 1966.

The protoplasm commonly consists of an outer dense and granular region containing chloroplasts and an inner region containing the nucleus and pulsules. In the area of the flagellar pores the cytoplasm often becomes more fluid and readily forms pseudopodia. Chloroplasts are of variable form, but most commonly discoid and arranged peripherally in the cell ; some species, however, have a single lobed chloroplast which is often accompanied by pyrenoids. Food is stored as starch in the pyrenoids or as discrete starch granules. DODGE (1968a) gives a full account of chloroplast structure.

The nucleus is a large prominent structure and of particular interest in that its chromosomes remain in the condensed state during interphase. DODGE (1963, 1964, 1966) and LEADBEATER and DODGE (1967), describe the nuclear structure and division in members of the Dinophyceae.

Within the protoplasmic contents of the cell are certain structures called pulsules. These are commonly elongate or bilobed organs which open to the exterior by way of delicate canals. Some species carry two pulsules that are connected. The pulsule canals often open to the exterior at one of the flagellar pores. The function of the structures is debatable (FRITSCH, 1935 ; MORRIS, 1967). In addition an eye spot or ocellus may occur and in some species trichocysts are present. DODGE and CRAWFORD discuss the fine structure of a member of the Gymnodiniales (1969) and similarly a member of the Peridiniales (1970). Text-figure-1 is a diagrammatic illustration of the peridinialean morphology.

PHYSIOLOGICAL ASPECTS OF THE PERIDINIALES

An account of certain physiological and biochemical processes and data for the Pyrrhophyta has been published by LOEBLICH III (1966).

Photosynthetic and non-photosynthetic forms are capable of utilising mono- and disaccharides, fatty acids and amino acids for nutritional purposes. The photosynthetic forms can utilise nitrate, ammonium salts in low concentrations, various amino acids, urea and uric acids as nitrogen sources. All members of the Peridiniales have one or more vitamin requirements ; commonly vitamin B12, less commonly thiamin and biotin.
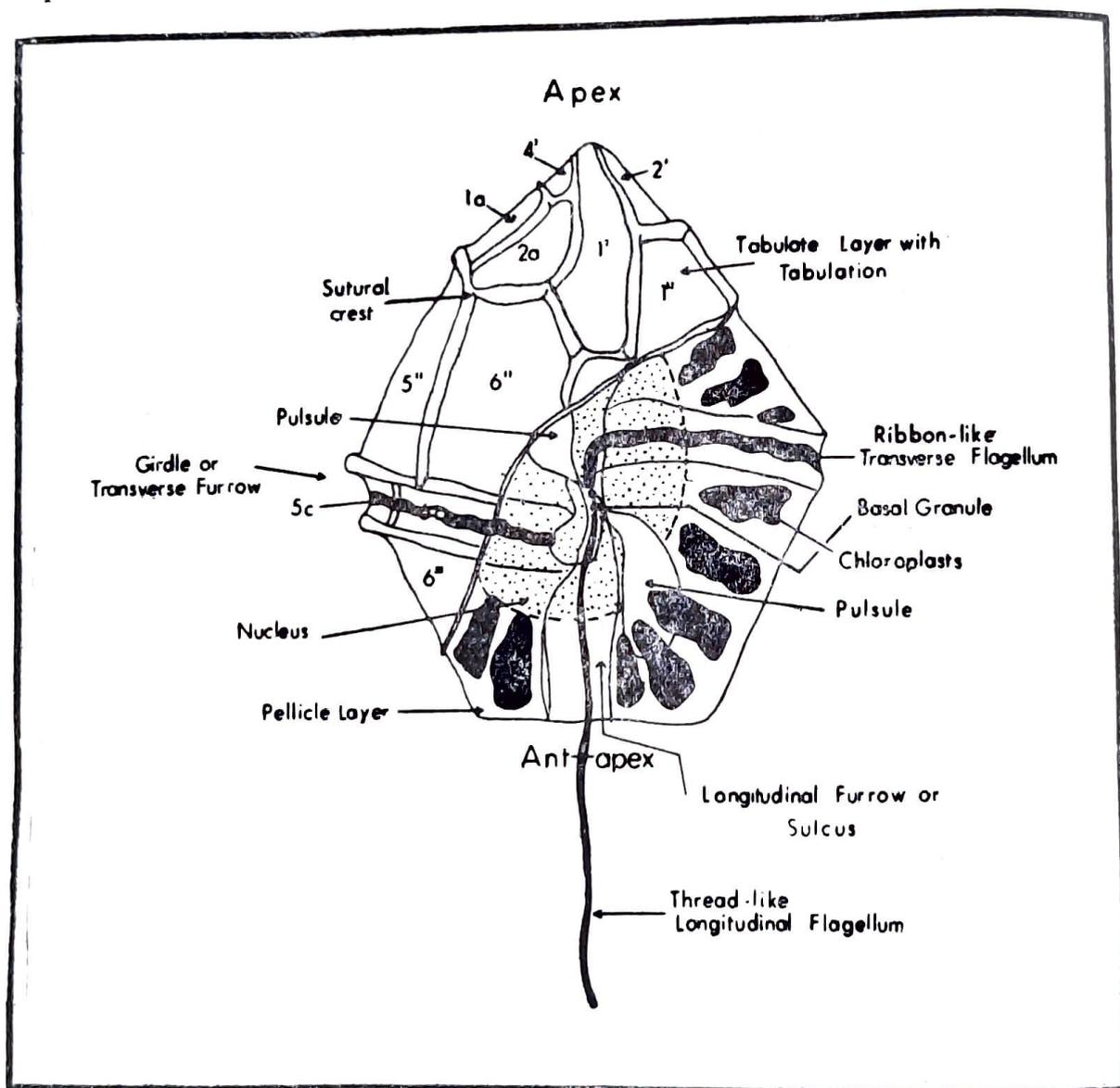
Text-fig. 1. A diagrammatic representation of the external and internal morphology of a typical member of the Peridiniales.

BARKER (1935) indicated a predominance of carbohydrate synthesis in the photosynthetic processes of *Peridinium* Ehrenberg 1832. Many workers have recently been concerned with the diurnal rhythms of photosynthetic rates, photosynthetic capacity and bioluminescence (HASTINGS, 1959 ; HASTINGS *et al.*, 1961 ; SWEENEY, 1960, 1964, 1965, 1969). Members of the Peridiniales are very efficient at photosynthesis ; the rate of respiration is approximately 10% of the maximum rate of photosynthesis and the respiratory and photosynthetic quotients are approximately at unity.

Reproduction in the Peridiniales 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. The theca may be lost during asexual reproduction so that each daughter cell must regrow a new theca ; in other cases half the theca is lost so that half of the theca is regrown. In *Ceratium* there is sometimes an incomplete division resulting in a chain of individuals being formed. Initial daughter cells closely resemble the gymnodinialean dinoflagellate ; this is taken by some as a possible indication of the "primitive" condition (FRITSCH, 1935 ; MORRIS, 1967). SOUSA E SILVA (1967) described asexual reproduction in *Goniodoma* sp. as occurring by mitosis or as a result of direct division without the production of mitotic figures. Actual division takes place within the theca whilst the organism is in a sedentary state.

The existence of sexual reproduction in the Peridiniales is doubted by some but it has been recorded by ZEDERBAUER (1904) and ENTZ (1909, 1924) and more recently by VON STOSCH (1964, 1965). In all cases this was 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. MORRIS (1967) described sexual reproduction again in *Ceratium*, where a conjugation tube was employed and in which the gametes fused. Vegetative cells appear to be haploid, but the zygotes have not been observed to form a resting stage with a subsequent reduction division. It has, however, been suggested that dinoflagellate cysts are the resting stage of members of the Peridiniales, but this is not as yet proved.

The life cycle of the Peridiniales is described in WALL and DALE (1968a), and that of *Pyrodinium bahamense* Plate 1906 in WALL and DALE (1969). Text-Figure 2 summarizes details of the life cycle. Particularly interesting is the existence of a short lived "gymnodinoid" stage immediately after excystment, which is thin-walled and temporarily uniflagellate in the case of *Gonyaulax digitale* (Pouchet) Kofoid and is avalvate in the case of *Pyrodinium bahamense*. Also of importance in the process of excystment is the formation of the archeopyle. It is suspected that it forms as a result of an enzymatic dissolution along predetermined lines, usually closely related to suture lines (EVITT & WALL, 1968 ; WALL & DALE, 1969). Ecdysis has also been described in *Pyrodinium* by WALL and DALE (1969), but the significance of this is as yet unclear.

Conditions of encystment are also imperfectly known. It may occur as a natural phase in the life history following a period of exponential growth (as Text-Figure 2 suggests), as a means of sexual reproduction, as protection against adverse conditions or as a hibernation device (WALL & DALE, 1970). The development of the cyst within the theca is also imperfectly known. EVITT and WALL (1968) described the process in *Peridinium limbatum* (Stokes) Lemmermann. Encysting cells are recognized by their dense cellular contents and lack of mobility. The endoblast (capsule) is secreted at a later stage of the encystment often after the formation of the outer wall ; it is a primary structure and its proper development is necessary if the cyst is to survive. NORRIS and McANDREW (1970) have also described various developmental stages, but these may in fact be inviable cysts and as such not typical. The cyst itself is an important part of peridinialean study but is generally neglected by modern phycologists. It is preserved in the fossil record and will be fully described later.

BEHAVIORAL AND ENVIRONMENTAL ASPECTS OF THE PERIDINIALES

Members of the Peridiniales are noted for their bioluminescence ; the light is blue-green and is produced as a result of a certain enzymatic reactions (HASTINGS & SWEENEY,
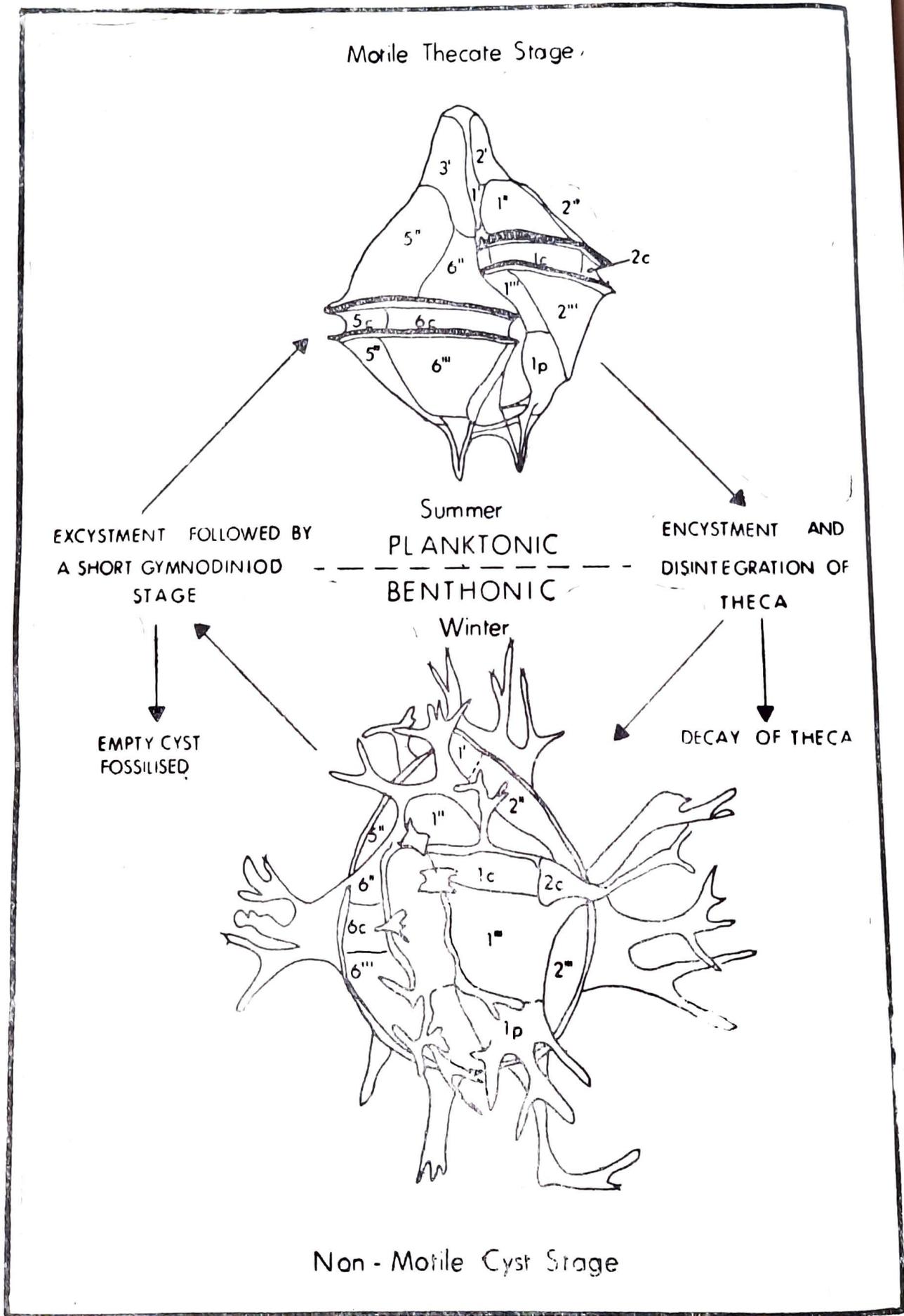
Text-fig. 2 A diagrammatic representation of the peridinialean life cycle as exemplified by *Gonyaulax digitalis* (after WALL & DALE, 1968a).

1957 ; SOLI, 1966 ; HASTINGS & BODE, 1961). The luminescence is of two types, either a rapid flashing or a steady dim glow ; the former is produced as a result of an external stimulus. KELLY (1968) described bioluminescence at Woods Hole, Massachusetts and concluded that dinoflagellates are responsible for most near surface bioluminescence. It was also suggested that bioluminescent forms are derived from a common ancestor.

Locomotion is achieved by beating the flagella (Kofoid & Swezy, 1921 ; Jahn et al 1963), but it is of interest that the transverse flagellum also contributes towards the forward drive. The organism moves through the water in a spiral manner, apex first (JAHN et al., 1963). A maximum mean velocity of 1 metre per hour has been achieved at 3% salinity and at 24°C. (HAND et al., 1965).

Phototaxis is a variable feature in the Peridiniales and it may be negative or positive. This response leads both to concentrations of cells where optimum conditions occure and to diurnal vertical migrations.

The products of excretion passed out into the surrounding fluid often contain toxins. A recent account of a dinoflagellate bloom and subsequent toxin production has been reported by WOOD (1968), ROBINSON (1968), COULSON et al. (1968), ADAMS et al. (1968) and INGHAM et al. (1968). Glycolic acid is the normal major product of excretion.

The Peridiniales form an important part of the total modern microplankton and are primarily controlled in vertical and areal distribution by temperature, salinity, light intensity and nutritional requirements. LOEBLICH III (1966) quotes a figure of 20% as being the optimum salinity for certain marine species, well below that of the open sea (35%). Studies of one species of tide-pool dinoflagellate suggests that the ability to adapt to a sudden decrease in salinity is greater than the ability to adapt to a sudden increase. Temperature toleration limits are from 1° to 35°C but the optimum lies between 18°C and 25°C according to the species under consideration. MULLER (1959) quotes 20°C as the optimum temperature. Marine photosynthetic forms can tolerate very high light intensities and VOZZHENNIKOVA (1965) states that the Peridiniales are confined to the top 50 metres of the oceanic photic zone ; the major concentration being within 5 to 40 metres depth. KISELEV (1950) found that the position of the densest concentration of dinoflagellates was a function of light intensity such that in continuous solar illumination it is placed at 10 to 15 metres depth and, under prolonged cloud cover, at the surface.

CLASSIFICATION OF THE PERIDINIALES

The Peridiniales have in the past been variously classified as botanical and zoological entities and the present classification has evolved with the work of PASCHER (1914, 1931), LINDEMANN (1928), SCHILLER (1937), FRITSCH (1935), GRAHAM (1951), CHATTON (1952) and KISELEV (1954). A modern classification, based exclusively on the thecate stage of the dinoflagellate life cycle, is given below after FRITSCH (1935) and MORRIS (1967). The classification has remained stable since about 1930 except for such differences of opinions as to whether the Dinophyceae, for instance, should be regarded as a Subdivision or as a Class.

Division Pyrrhophyta Pascher 1914

Class *Desmophyceae* Fott 1959
Order Desmomonodales Pascher 1914   —naked, longitudinal divided forms.
Order Thecatales Lindemann 1928   —armoured, longitudinal divided forms with an apical "tooth".

Order Dinophysiales Lindemann 1928	—armoured, transversely divided by an anteriorly placed girdle.
Class *Dinophyceae* Pascher 1914	
Order Gymnodiniales Lindemann 1928	—unarmoured *dinoflagellates.
Order Peridiniales (Schutt) Lindemann 1928	—armoured *dinoflagellates.
Order Rhizodiniales Pascher 1931	—amoeboid forms.
Order Dinocapsales Pascher 1931	—palmelloid forms.
Order Dinococcales Pascher 1931	—coccoid forms.
Order Dinotrichales Pascher 1931	—filamentous forms.

Wood (1954) is of the opinion that the genus concept in the Linnean sense can have no significance in dinoflagellate taxonomy because of the apparent lack of sexual reproduction. This view is also held by certain palynologists (Cox, pers. comm.). Bursa (1963) described certain morphogenetic factors that give rise to aberrant dinoflagellates, which have been described as separate species by some workers. There is a possibility that such aberrent fossil cysts also occur.

MORPHOLOGY AND CLASSIFICATION OF FOSSIL MICROPLANKTON

That part of the life cycle of living dinoflagellates (Peridiniales) which is represented in the fossil record is generally believed to be the cyst (Evitt & Wall, 1968 ; Wall & Dale, 1968a). There is no positive evidence that the motile theca is found fossilised. Consequently the following account refers to the cyst stage of the peridinialean life cycle only.

Morphology and Composition

In overall shape most members of the Peridiniales can be described as spherical, ovoidal, peridinoid, rhomboidal or pentagonal. Many modern forms are somewhat flattened dorso-ventrally ; a property which is accentuated on fossilisation. Morphological terms useful in describing dinoflagellate cysts have recently appeared in Downie and Sarjeant (1966), Sarjeant (1969) and Evitt (1969) and a glossary of terms is at present in press by Sarjeant and Williams (Sarjeant, pers. comm.).

Dinoflagellate cysts have resistant walls, mineralised in some rare forms, composed of an acid-insoluble organic substance. Wall and Dale (1968b) described mineralised cysts with a two-layered wall structure. The outer mineralised layer is composed of calcite (aragonite ?) in radial or microgranular habit. The inner layer is of an organic composition. A totally organic cyst wall is found in the majority of the Peridiniales. Staplin (1969) and Van Gijzal (1967a, 1967b) have, in effect, demonstrated that the composition of the cyst wall of dinoflagellates is not the same as the walls of pollen and spores. Kjellstrom (1968) recognized the presence of COOH, CH_2 and CH_3 groups, carboxylic groups and long chain alifatic saturated carbohydrates in the walls of Palaezoic leiospheres [acritarchs, but possibly related to dinoflagellates].

Cysts are typically two-layered being composed of an outer periphragm and an inner endophragm. 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

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*The term dinoflagellates is used here in the palynological sense.

endocoel. Jux (1968a, 1968b), in recent electron microscope studies of the walls of *Hystrichosphaera bentori* Rossignol 1964 [Recent] and *Cordosphaeridium inodes* (KLUMPP, 1953) [Eocene] has revealed the two layers, similar in overall structure but differing in the frequency of small vesicles that were conspicuously present.

Three layered cysts are also known. The third layer either develops between the periphragm and endophragm and is called the mesophragm (EVITT, 1969) or it develops outside the periphragm, in which case it is termed the ectophragm. In some forms a single layered cyst wall is present; the single layer is most often the endophragm, but where this is not demonstrable the term autophragm is to be preferred (EVITT, 1969).

In adhering to these rather strict terms homologous relationships are implied. This should be avoided if possible as homology in dinoflagellate cyst walls has been adduced only between the modern species *Peridinium limbatum* and the fossil *Deflandrea* spp. by EVITT and WALL (1968). Caution is therefore advised in the use of these terms. Cox (1971) has instituted a new objective numerical system of referring to cavities, bodies and walls in dinoflagellate cysts in an attempt to deal with this problem.

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. The surface of the cyst may be ornamented by granules, punctae, vermiculae, a reticulation or it may be smooth. Text-figure 3 illustrates the gross morphology of a dinoflagellate cyst.
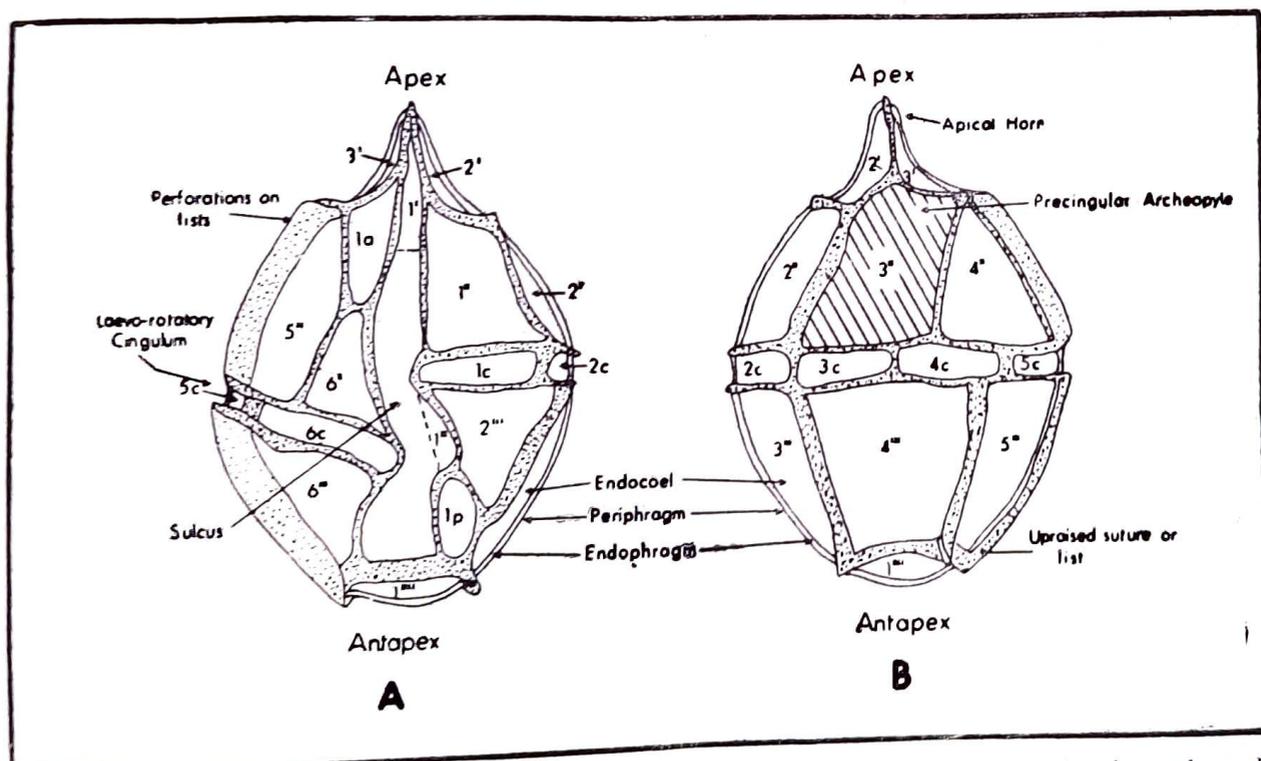
Text-fig. 3. The external morphology of a typical proximate dinoflagellate cyst with a precingular archeopyle (type P of EVITT, 1967). A—Ventral view, B—Dorsal view. 1'-3', apical plates, 1a, anterior intercalary plate; 1"-6", precingular plates; 1c-6c, cingular plates; 1'''-6''', postcingular plates; 1p, posterior intercalary plate; 1'''', antapical plate, (after Sarjeant, 1967a).

Three main morphological cyst types are recognized, proximate, chorate and cavate. Proximate cysts are thought to exhibit the same general form as the parent motile theca, with cingulum, sulcus and tabulation. Cyst tabulations are described and labelled in much the same way as for the motile theca and are likewise variable. The wall layers are usually in contact, but small pericoels (cavities developed between the periphragm and endophragm) are sometimes present beneath processes and horns.

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Chorate cysts are characterised by processes, often reflecting the original tabulation of the parent theca. The processes may be intertabular (zonal or sutural), intratabular or non-tabular. This kind of cysts is also characterised by an 0.5—0.6 condensation ratio (an expression of the possible position of cysts growth within the parent theca), derived from the following expression :

$$\frac{\text{Radius of Endocoel}}{\text{Overall radius}}$$

There is also a proximo-chorate 'subgroup' that is transitional between the two groups discussed above. These typically have a 0.6—0.8 condensation ratio, carry a tabulation and also possess processes, usually of the intertabular type.

The third major group, cavate cysts, are readily distinguished by their possession of large pericoels. The endophragm and periphragm are typically not in contact except along an equatorial zone, in which case the cyst may be termed bicavate, or at the apex and antapex, when the cyst may be termed pterocavate. Text-figures 3 and 4, illustrate the types of dinoflagellate cysts.
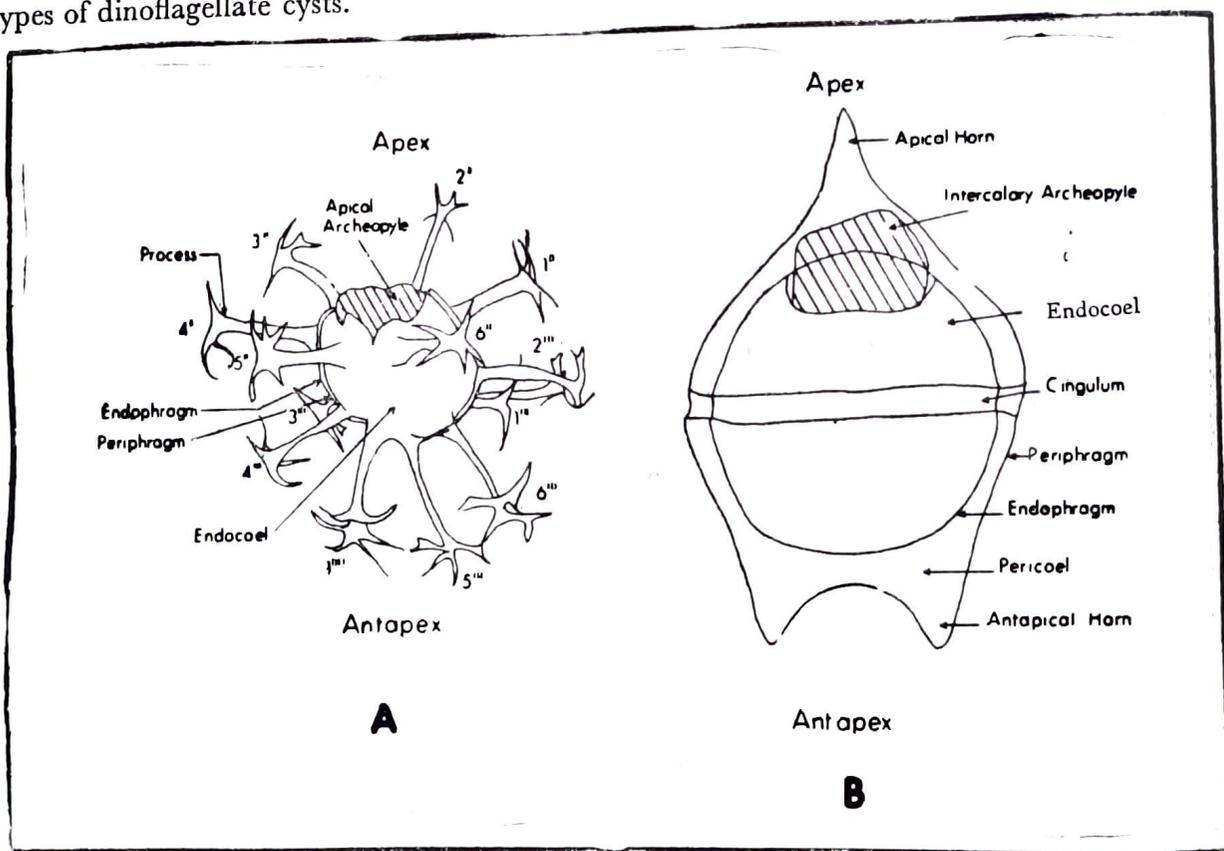
Text-fig. 4. A—External morphology of a typical chorate dinoflagellate cyst with an apical archeopyle (type A of Evitt, 1967). B—External morphology of a typical cavate dinoflagellate cyst with an intercalary archeopyle (type I of Evitt, 1967), (after Sarjeant,1967a).

Since 1960 cyst types have been linked to a functional (growth or developmental) definition, the condensation ratio. Proximate cysts may form just below the cell wall of the parent theca whereas chorate cysts condense and may form well within the parent cell. In describing these various cysts an objective descriptive terminology should be used without the implication of any functional purpose. Cavate cysts, for instance, could be termed proximate in a functional sense as some forms carry a tabulation, indicative of cyst three main formation in juxtaposition to the parent cell wall.

In the literature there is some confusion over the terms "spine" and "process", as pointed out by HARLAND (in press). All projections arising from the cyst should, in the

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author's opinion, be termed processes and fully described using the terminology of DOWNIE and SARJEANT (1966) and SARJEANT (1969). Processes may, in a functional sense, then be regarded as merely a form of "ornamentation", may support the cyst within the parent theca or may be used to facilitate flotation.

The term horn is applied to a major extension of the cyst body, which may carry portions of the tabulation (see EVITT, 1969). This term must also be used with care so that it is not confused with "process".

A morphological feature of dinoflagellate cysts is the archeopyle (EVITT, 1961, 1967). This is an opening in the cyst wall through which the organism escapes during excystment (WALL, 1965). In most fossil forms this opening is conspicuous. The archeopyle is usually equivalent to one or more reflected plates of the thecal tabulation. It may develop within a reflected plate area as a reduced archeopyle or it may include parts of surrounding plates as an enlarged archeopyle. Cavate cysts may possess an archeopyle in the periblast and/or the endoblast. That portion of the cyst which is lost or swings free of the archeopyle is called the operculum. Free opercula are often seen in palynological preparations. EVITT (1967) discussed the archeopyle extensively and erected a scheme to designate the various types :

(1) Apical—involving loss of apical plates : $\overline{A}$, Aa.
(2) Intercalary—involving loss of intercalary plates, I, 2I, 3I.
(3) Precingular—involving loss of precingular plates ; P, 2P, 3P, 6P.
(4) Combination—involving loss of plates from more than one plate series ; $\overline{Ai}$, $\overline{A}$+P, $\overline{AP}$, 2A+6P.

The epithecal or epitractal archeopyle of NORRIS (1965) is included in the combination type. Other forms of archeopyle termed $\overline{AID}$+2 Pa, Aa+3I and $\overline{AID}$ have been described from freshwater dinoflagellate cysts by NORRIS and MCANDREW (1970). HARLAND (in press) has also noted other possible archeopyle types in dinoflagellate cysts from a hypersaline environment. In any description of dinoflagellate cysts a full account of archeopyle structure is essential.

CLASSIFICATION

The classification of dinoflagellate cysts has passed through a number of phases. At first it was usual not to classify dinoflagellates beyond generic level. They were regarded as animal or plants according to a writers particular view ; either being placed in the class Dinoflagellata or the class Dinophyceae respectively. EISENACK (1961), for instance, erected a zoological scheme, although he claims that from 1938 he regarded them as algae (EISENACK, 1963a). In 1961 it was suggested by DOWNIE et al. that dinoflagellates should be treated as plants under the International Code of Botanical Nomenclature (I.C.B.N.); this is the practice today. A similar system was employed by VOZZHENNIKOVA (1965, 1967) with a mixture of fossil and modern genera being placed into families. An important consideration in Vozzhennikova's scheme is that cavate cysts are fundamentally different from the other cyst types. A separate subclass, the Endoflagellatophycidae, was erected to acommodate cavate types.

SARJEANT and DOWNIE (1966) reviewed the situation as it stood then and erected a purely morphological classification for fossil dinoflagellates to exist alongside and independently of the natural classifications of the thecate stage. The form-generic concept was used and because such genera cannot be grouped into natural families (Article 3, I.C.B.N.)

a number of artificial cyst-families were erected. Morphological parameters used in the scheme were overall form, shape, archeopyle formation and tabulation. It was pointed out that the relative importance of these parameters varied according to the cyst group under consideration. It is unfortunate that in using overall form, i.e. proximate, chorate and cavate groupings, a 'growth' hypothesis is implied which leads into certain diffi-culties ; in particular that a cavate cyst (morphological) can be considered to be proximate with a chorate component if the 'growth' hypothesis is accepted. These terms, in the author's opinion, must be used in their morphological sense only, as the various processes of cyst formation are, as yet, largely unknown.

A subsequent approach is that of MÄDLER (1967) who placed fossil dinoflagellates into a new division—the Hystrichophyta, called a class by Mädler, of the plant kingdom. This division includes the order Hystrichosphaerales Mädler 1963 which in turn includes the family Hystrichosphaeraceae (O. Wetzel 1933) Mädler 1963, (Mädler's designation). It appears that the true nature of the 'hystrichospheres' was not well understood by Mädler.

WALL and DALE (1968a) suggested the erection of a comprehensive taxonomic ap-proach to unite the fossil and modern dinoflagellates into a "natural" classification. Tabula-tion and archeopyle formation were regarded as the only taxonomically stable morpho-logical characters. The scheme of SARJEANT and DOWNIE (1966) was criticised on three main grounds : (1) two phases of the dinoflagellate life cycle could be assigned to different taxa at generic and family level : (2) too much emphasis was placed on the growth hy-pothesis, and (3) the classification effectively and unnaturally divides modern from fossil representatives. WALL and DALE (1968a) suggested that taxa should be formulated with re-ference to all phases of the organism's life history : that if a taxon is erected on only one stage of the life cycle, then it can only be treated as a natural taxon if a population is studied ; that one valid name be used, preferable the name of the extant organism ; and that extinct taxa must be defined on morphological features having the greatest taxonomic potential. Certain taxonomic emendations would be required ; modern taxa should be redefined to attribute some importance to the cyst stage of the life cycle ; fossil and living synonymous dinoflagellates should adopt a single epithet. Extinct forms should be allocated to taxa at the family level on tabulation patterns, and to taxa at the generic level on tabulation, archeopyle formation and the nature of any ornamentation.

NORRIS and McANDREW (1970) favour separate classifications for the cyst and thecate stages. They question the taxonomic stability of archeopyle formation because certain freshwater cysts (see NORRIS & McANDREW, 1970) have unique archeopyles but are quite clearly of *Peridinium* affinity. This is also supported by the work of the writer (in HARLAND & SARJEANT, 1970 ; HARLAND, in press).

In offering a compromise between the comprehensive scheme of WALL and DALE (1968a) and the purely morphological scheme of SARJEANT and DOWNIE (1966) HARLAND in press) suggested that Quaternary dinoflagellates be dealt with under a 'natural' com-prehensive classification as suggested by WALL and DALE (1968a). It seems most likely that the majority if not all Quaternary fossil dinoflagellate cysts will be ultimately assigned to their parent thecae, in much the same way as Quaternary pollen and spores are assigned to their parent plants. This would allow a full revision of Modern and Quaternary dino-flagellates to be achieved without further difficulties. All pre-Quaternary dinoflagellate cysts would be classified on morphological grounds alone, but with their natural affinities stated where known or reasonably assured. In this way it will still be possible to erect pro-bable dinoflagellate lineages, as WALL and DALE (1969) have done for *Pyrodinium bahamense* Plate 1906.

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If the taxonomic hierachy of WALL and DALE (1968a) is applied to fossil dinoflagellates two natural families and two artificial families would be recognized : the Gonyaulacaceae having a basic tabulation of 3-6', 6'', 6c, 6'' ', 1'' ''; the Peridiniaceae with a basic tabulation of 4', 7'', 4c, 5'' ', 2'' '', plus anterior intercalary plates ; a family to include all those fossil cysts that do not carry a tabulation ; and a family (or even families ?) for forms with tabulations not assignable to either the Gonyaulacaceae or Peridiniaceae. Sub-families or genera then be erected on archeopyle formation and genera or species erected on overall form, 'ornamentation', process structure, etc. It would, however, be premature to attempt such a scheme in the present state of knowledge available.

CONCLUSION

It is hoped that this review will stimulate the palynologist to take an interest in modern dinoflagellates and the phycologist to become interested in the fossil record of dinoflagellates, especially as this is a time when dinoflagellate research is expanding at an ever-increasing rate.

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