Dinoflagellates

Advanced article

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Dinoflagellates are marine or freshwater, photosynthetic or nonphotosynthetic protists that swim by two dissimilar flagella, usually present on the side; one is ribbon-like, winding around to the cell's left, and the other trails behind. Most dinoflagellates have an unusual nucleus, the dinokaryon, throughout their life cycle. Cells are naked or have a theca consisting of cellulose plates lying under the cell membrane; resting cysts have a tough dinosporin wall, which can fossilize readily.

Article Contents

doi: 10.1038/npg.els.0001977

Description and Characterization

Dinoflagellates are eukaryotic, predominantly unicellular flagellate protists, found in marine and freshwater planktonic and benthic communities. They can be found from the poles to the equator. There are over 2000 named living species and 2500 named fossils. Roughly 50% of the living forms are photosynthetic, the remainder being nonphotosynthetic and eating by a variety of mechanisms. The former are major contributors to aquatic primary production, including important endosymbionts: the zooxanthellae of reef-building corals. Some photosynthetic species can also capture food organisms. Others are parasites on many vertebrate, invertebrate, and protist hosts. Some produce toxins that can kill marine fauna or humans by passing up the food chain (red tides, shellfish poisons, ciguatera, and other harmful bloom effects).

The name 'dinoflagellate' is derived from the Greek *dinos*, meaning turning, referring to their movement when swimming.

Form

Dinoflagellates occur principally in a flagellated, swimming form, the dinomastigote, or as an immobile stage, the cyst, which can be seasonally dormant in many species (see Life Cycle below). The cells may be naked (athecate) or may possess a cell wall, the theca, consisting of many cellulose plates (thecate). An additional, continuous layer, the pellicle, may be present (see below). In athecate forms, the pellicle may be the most important layer determining form, in which case the cell is said to be pelliculate. Cyst walls (possibly homologous with the pellicle) are external, continuous, with one or more layers that may contain dinosporin, an extremely resistant sporopollenin-like substance, cellulose, and mucoid material. Both thecae and cyst walls may have ornamentation of remarkable elaborateness, conservative enough to be used in their classification (see below).

The side that the flagella arise from is designated as ventral, thus allowing dorsal, left and right, to be determined by zoological convention. The pole anterior in motion is termed the apical end and the posterior is antapical. In prorocentroids, the flagella are considered to be apical.

The flagellated stage, the dinomastigote

The swimming stage (**Figure 1**) has two flagella: the transverse, which winds around to the cell's left, and the longitudinal, which trails behind. With the exception of prorocentroids (**Figure 1a**) these flagella are associated with surface grooves: the girdle or cingulum and the sulcus, respectively. The cell anterior to the girdle is the episome and that posterior is the hyposome. The transverse flagellum (**Figure 2** and in **Figure 3**) is ribbon-like, with the axoneme running along its longer outer edge and a contractile fibre, the striated strand, running along its shorter inner edge. A single row of simple flagellar hairs is present on the outer edge. The difference in the lengths of the outer and inner edges results in the ribbon being thrown into pleats like a ruffled skirt. The waves produce a forward and turning thrust. With the exception of *Ceratium* and *Noctiluca*, the

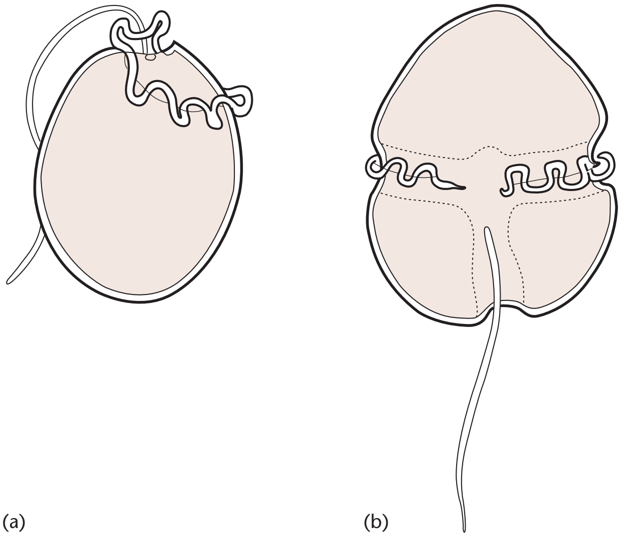

Figure 1 Flagellar arrangements in dinoflagellates. (a) Anterior insertion, found in prorocentroids. (b) The typical flagellar arrangement in dinoflagellates, with both flagellae arising from the ventral side and the transverse flagellum winding to the cell's left (redrawn from Taylor, 1989).

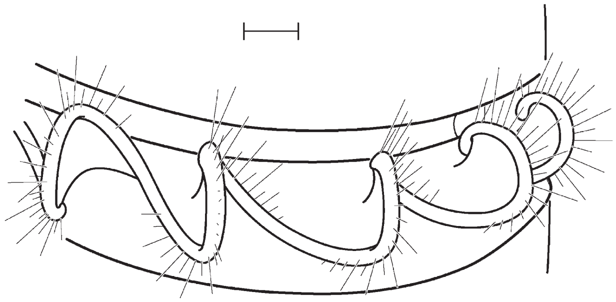

Figure 2 A detail of the transverse flagellum, showing its wavy, ribbon-like form (from Gaines and Taylor, 1985).

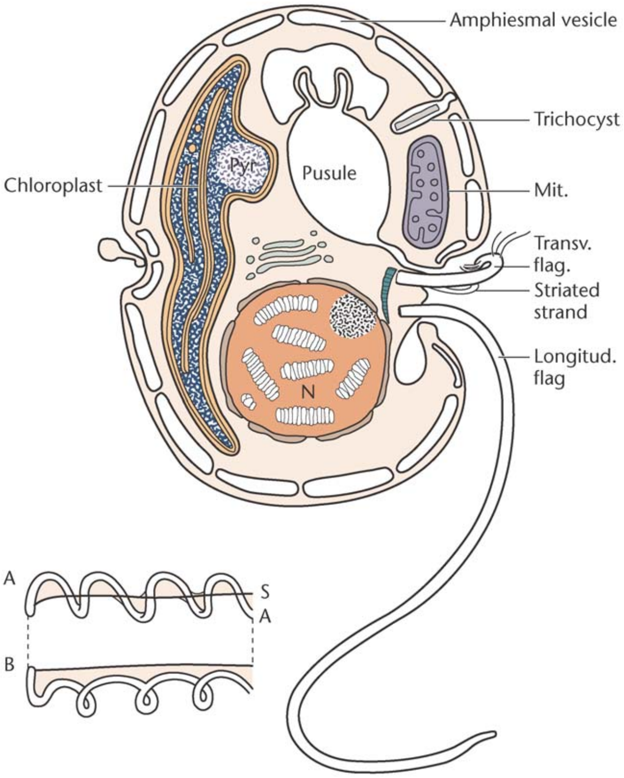

Figure 3 A diagrammatic cross-section of a dinoflagellate, showing the internal organization. Note the single layer of amphiesmal vesicles lying beneath the cell membrane, the prominent nucleus with condensed chromosomes and the pusular cavities (redrawn from Taylor, 1980).

longitudinal flagellum is used mostly for steering. Swimming under natural conditions is probably continuous, with a maximum speed of roughly 1 m per hour.

The typical form of the swimming stage is ovoid, but there are many modifications of this, including torsion (**Figure 4**), horns, and lists (see the theca below). The thecate dinophysoids and the athecate noctilucoids and warnowians exhibit the most unusual modifications of form. *Polykrikos* (**Figure 5**) has the external appearance of several cells stuck together, but inside, these is only one cell with half the number of nuclei as external units. Among those that do not swim except as gametes/spores, *Haplozoon* and *Dinothrix* are multicellular. Cysts (see Life Cycle below) may have simple or highly elaborate forms, the latter often spiny or with strongly developed ridges and crests.

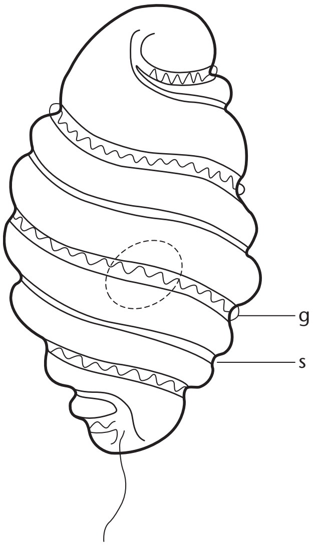

Figure 4 Torsion at its extreme in *Cochlodinium.*

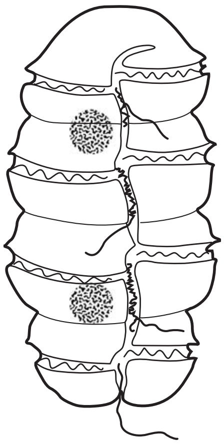

Figure 5 *Polykrikos*, which resembles a fused state in which the number of nuclei in the single cellular compartment is half the number of external flagella pairs and girdles.

The theca

Many dinoflagellates have a cell wall, the theca, composed of many cellulose plates (**Figure 8**). Dinoflagellates with a theca are said to be thecate (= old term 'armoured') and those without it are considered athecate. The theca anterior to the cingulum is the epitheca and that behind it is the hypotheca. The plates are usually perforated by pores, all of which seem to be exit points for trichocysts. The pattern of plates is conservative and is used extensively in taxonomy and within-group classification and phylogeny. Each plate lies within a cortical vesicle or alveolus, formerly termed an amphiesmal vesicle. The vesicles form a single layer internal to the cell membrane. In athecate dinoflagellates, the vesicles are empty or have very thin platelets not obvious in light microscopy.

The boundaries of the plates are termed sutures and the plate pattern is often referred to as the tabulation pattern. Taylor (1980) recognized five basic sutural patterns among living dinoflagellates prorocentroid, dinophysoid, gonyaulacoid, peridinioid and gymnodinioid, the latter being athecate. A fifth thecate form, heterocapsoid, should probably be added to this (Fensome *et al.*, 1993).

The plates of all these, except prorocentroids and gymnodinioids, can be assigned to a series using the Kofoid System. There are five principal latitudinal series encircling the cell: apicals and precingulars on the epitheca, cingulars, and postcingulars and antapicals on the hypotheca. Apicals contact the apex where there is usually an apical pore complex (APC) contained within one or two concentric plates. Precingulars are anterior to and contact the cingulum. The cingulars line the cingulum. Postcingulars are posterior to the cingulum and antapicals are at the antapex. Additional plates are termed intercalaries (intercalaries are frequent on the epitheca in peridinioids where they can form an almost complete series between apicals and precingulars), except for the sulcus, which is lined by sulcal plates. Each plate is numbered in the Kofoid System, proceeding around each series to the cell's left. The first apical plate often extends from the anterior of the sulcus to the APC. Sometimes, it is difficult to decide which series a plate belongs to, in which case a plate homology system may be used. The most commonly used is the Taylor–Evitt System, which is also best for generic comparisons (see Fensome *et al.*, 1993).

Within-group Relationships and Classification

The tree shown in Taylor (1987) indicates the major lineages recognized within living dinoflagellates and gives a visual impression of the morphological diversity within the group. The most recent comprehensive classification is that of Fensome *et al.*, (1993), which was the first to integrate the classification of living and fossil dinoflagellates. Until then, fossils had been classified almost entirely separately, primarily using ornamentational features but, with the application of scanning electron microscopy, it has become possible to determine a tabulational pattern on many fossils. This character has proved to be extremely useful in the classification of modern thecate dinoflagellates. This allowed the combination of both classifications.

Dinoflagellates without a theca have been classified using other criteria. In dinoflagellates, the presence or absence of plastids has not been a generic character even though it is in other groups with both photosynthetic and nonphotosynthetic members, for example, euglenoids and cryptomonads. This is likely to change as molecular comparisons indicate whether they are truly closely related or not.

Fensome *et al.* (1993) chose the flagellar dimorphism and lateral insertion as the main unifying feature of the Phylum/Division Dinoflagellata. All dinoflagellates have closed mitosis (the nuclear envelope does not break down during mitosis), but this feature is present in many protists. Most dinoflagellates have a mitotic spindle external to the nucleus, but syndinians have a spindle internal to the nucleus, like those of the groups considered to be ancestral to them. Most dinoflagellates lack histones permanently, but one group, the syndinian parasites, has histone-like proteins all the time, whereas two others, the blastodinians (also parasites) and the noctilucoids, have histone-like proteins part of the time. All other dinoflagellates lack histones at all stages of their life cycles. Fensome *et al.* (1993) adopted the hypothesis that dinoflagellates evolved from ancestors with histones, gradually losing them until, in the majority, histones were completely lost. Applying this principle, the Subdivision Dinokaryota includes all those which have a dinokaryon (see below) at any time in their life cycle; the Class Dinophyceae includes the great majority of dinoflagellates lacking histones at any stage, the Subdivision Syndinea having histone-like proteins. The Noctiluciphyceae and Blastodiniphyceae have a status equal to that of the Dinophyceae. The basal position of syndinians has been confirmed by small subunit ribosomal deoxyribonucleic acid (rDNA) sequencing of *Amoebophrya,*with *Oxyrrhis* diverging earlier, in accordance with the classification.

Within the Dinophyceae, the use of tabulation, where available, has been well supported by molecular sequencing. Thus, the tabulation groupings of Taylor (1980) have held up. A major question remains. What is the basal group of the Dinophyceae? It has long been acknowledged that gymnodinioids, with little or no theca, are probably polyphyletic (Taylor, 1980), but are all or some more basal than thecate forms? Taylor (1980) placed forms with anterior flagellar insertion (*Desmomastix, Pleromonas, Prorocentrum*) basal to other dinoflagellates. However, the view that gymnodinioids are more basal than those with thecal plates has also been supported. Unfortunately, small subunit rDNA (ssrDNA), the most commonly used molecular phylogenetic tool, has not resolved this unequivocally so far. Gonyaulacoids form a well-resolved group that seem to have evolved from peridinioids, but the gymnodinioids, prorocentroids and peridinioids form a 'GPP' complex that is an unresolved with *ss*rDNA (Saunders *et al.*, 1997). This grouping appears to be a failure of the method since there is no obvious resemblance between these entities and it is unlikely that peridinioids and prorocentroids evolved more than once. Prorocentroids could be very derived dinoflagellates or close to the base. Small subunit rDNA consistently places *Crypthecodinium*, which has a tabulation somewhat intermediate between gonyaulacoids and peridinioids, basal to other histone-less dinoflagellates.

Internal Cell Structure

The arrangement of major cell organelles is shown in **Figure 3**.

Amphiesma or cortex

There is usually a single layer of vesicles lying just beneath the cell membrane. These are the amphiesmal or cortical vesicles. Also part of the outer complex are the trichocysts, rod-like structures, contained within vesicles that fit between the amphiesmal vesicles and contact the cell membrane. The whole complex including the theca, if present, is termed the amphiesma.

Pusules, mitochondria, plastids, and ocelli

Each cell has two specialized vacuoles, the pusules, which open to the exterior at the flagellar bases by means of canals. They have a close contact with the general cell vacuolar system, the vacuome, which ramifies throughout the cell. They are most developed in nonphotosynthetic species and at least one is considered to be for excretion.

Mitochondria present in each cell have short tubular cristae. Plastids (= chloroplasts) are unusual in having envelopes consisting of three membranes, only known elsewhere in euglenoid flagellates, their thylakoids being loosely grouped into threes. Photosynthetic pigments consist of chlorophylls a and c_2, β carotene and several xanthophylls, of which peridinin is group distinctive. Photosynthetic dinoflagellates are notable for the presence of anomalous pigment spectra in some species or subgroups. Some of these, such as the fucoxanthin- and chlorophyll *b*-containing taxa have been shown to have foreign endosymbionts or kleptochloroplasts. However, those with 19′ hexanoyloxyfucoxanthin (mostly gymnodinioid fishkillers, e.g. the genus *Karenia*) and phycoerythrin (photosynthetic dinophysoids) do not have obvious endosymbionts although their plastids resemble haptophytes and cryptomonads, respectively.

Storage consists of chunks of starch in the cytoplasm and oils. The membranes contain a distinctive sterol, dinosterol. The presence, in old sediments, of its derivative, dinosterane, has been used as an evidence of their existence more than 600 million years ago.

Some dinoflagellates have photosensing structures. Eyespots, consisting of clusters of carotene droplets located within a plastid beneath the base of the longitudinal flagellum, are present in *Glenodinium* and some gymnodinioids. Much more elaborate are the ocelli, or ocelloids, of warnowian gymnodinioids such as *Warnowia, Nematodinium* and *Erythrodiniopsis* (reviewed by Greuet in Taylor, 1987). These amazing examples of convergent evolution consist of a lens-like body, a fluid-filled cavity and a pigment-backed membrane array, the retinoid in the pigment cup. The structural resemblances to a vertebrate eye are astounding, especially when one recalls that these are organelles of a single cell. Taylor (1980,1987) has suggested that they may act as rangefinders in heterotrophic feeding since the possessor cell has no known way of analysing an image projected on the retinoid.

The dinokaryon (nucleus) and dinomitosis

The normal nuclear state of dinoflagellates is so unusual that it has been given the name dinokaryon. Dinoflagellates have been defined primarily by their unique flagellar type and arrangement (Fensome *et al.*, 1993). Within this assemblage, one group, the parasitic syndinians, has a conventional-looking nucleus containing histone-like proteins in which the chromosomes de-condense during interphase. Two other groups, the noctilucoids and blastodinians, alternate between a eukaryon and the dinokaryon. All other dinoflagellates have a dinokaryon at all times.

The dinokaryotic state consists of continuously condensed chromosomes lacking histones. The number of chromosomes varies from as little as five in parasites to more than 180, and they are genetically haploid. The amount of DNA is usually anomalously large and can be seen as tightly packed fibres making up the chromosomes. Nucleosomes are lacking. As much as 70% of the thymine may be replaced by 5 hydroxy methyluracil, an indication that much of the DNA is genetically inactivated. Transcription is probably restricted to loops that extend beyond the chromosomes (see Spector (1984) for details).

Another oddity is that during mitosis, the nuclear envelope remains intact, the nucleolus persists and the spindle is extranuclear. This combination is found only in hypermastigote flagellates. Chromosomes are attached to the nuclear envelope by their kinetochores, chromosome-associated microtubules passing through tunnels that form in the nucleus during mitosis, to pull the daughter chromosomes apart after replication by dragging the split kinetochores and their daughter chromosomes towards the poles of the dividing nucleus. This extraordinary process is termed dinomitosis.

Life Cycle

The basic life cycle of dinoflagellates is shown in **Figure 6**. The metabolically active dinomastigote of dinoflagellates is haploid. Populations undergo numerous asexual

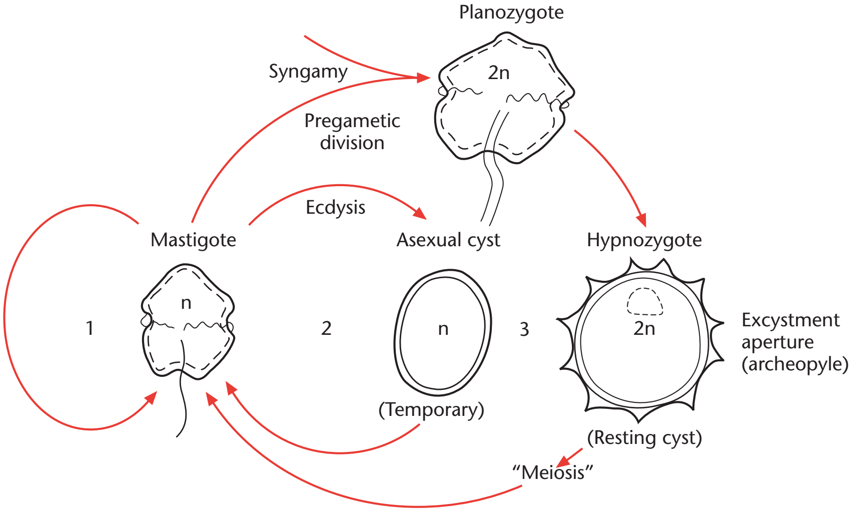

Figure 6 The basic dinoflagellate life cycle. (1) The asexual phase of repeated divisions of the haploid swimming cell (mastigote). (2) Formation of a temporary cyst from a single cell shedding its theca (not in all dinoflagellates). (3) The sexual cycle, involving the fusion of gametes resembling normal cells, a swimming zygote, encystment to produce a dormant resting cyst with a tough wall (not in all dinoflagellates) and meiosis after excystment.

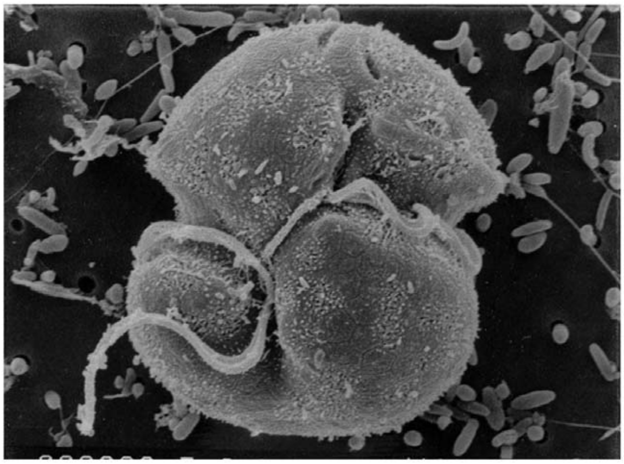

Figure 7 Scanning electron micrograph (SEM) of *K. micrum,* an athecate dinoflagellate, showing the two flagella, the transverse lying in the girdle depression, the longitudinal arising from the sulcus. The episome is anterior to the girdle and the hyposome is the part posterior to the girdle, cell diameter 8 μm. The small objects in the background are bacteria.

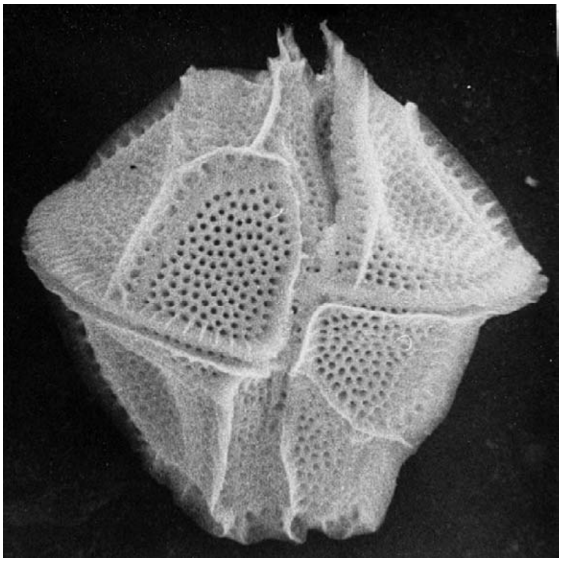

Figure 8 SEM of the cellulose theca of *Lingulodinium polyedra.* Most of the plate boundaries are marked by ridges. The apical plates are gaping slightly. The plates are densely pored, cell diameter 60 μm.

divisions in this phase while conditions are suitable for growth. Division occurs usually during the late dark period and it has been shown that the onset of dark sets the division process in motion. This light/dark phasing means that division rates of more than once a day are unlikely. A cell dividing at a rate less than once per day will divide every two, three or more days, still during the dark period. This phasing is most clear in photosynthetic species but is also present at least in some nonphotosynthetic species.

Although at one time it was thought that sexual reproduction was rare or absent in the group, it appears that it is probably present in most members of the group and has not been recognized because the gametes resemble asexual cells. Gametes may be isogamous (plus and minus) or anisogamous (the smaller male, the larger female by convention). In the latter case, the two gametes were often described as distinct species.

Sexual reproduction can be induced in the laboratory by nutrient starvation, particularly of nitrogen, and this probably is the case in the field, occurring at the end of blooms.

The zygote has an initial swimming phase, the planozygote, recognizable by its double flagella set. In many, this probably undergoes meiosis shortly afterwards to return to normal asexual cells (but this has not been well documented); but in 10–20%, a nonmotile cyst follows. This process is termed encystment. If this becomes dormant, then it is termed a hypnozygote.

The continuous wall of the hypnozygote, usually known as a resting cyst, is often strongly impregnated with dinosporin, a polymer of carotene, which is strongly resistant to decomposition. After a certain period of time, an internal or external trigger (light, temperature) leads to the development of an opening in the cyst wall, the archeopyle, as part of excystment and a swimming cell with double flagella emerges. This undergoes meiosis to produce normal haploid cells.

This life cycle is termed haplophasic because the haploid phase usually predominates.

Fossils

Dinoflagellates have a rich fossil record in the Mesozoic and Cenozoic eras. It consists almost exclusively of the remains of resting cysts. From other phylogenetic considerations, the lineage almost certainly diverged in the late Proterozoic (at least 800 Ma; Ma = mega anna, or million years); but records prior to the Triassic (245 Ma) are somewhat equivocal. *Arpylorus* in the Devonian Period (400Ma) appeared to have sufficient dinoflagellate-like features to be attributed to the group, but is now doubted to be one. Some of the enigmatic Palaeo- and Proterozoic fossils referred to as Acritarchs are probably dinoflagellates, especially the spiny 'acanthomorphs'. Due to the presence of dinosterane, the hydrogenated form of dinosterol (currently unique to the group), in Cambrian deposits (600 Ma), the existence of the group at that time has been claimed. Nevertheless, the record indicates a huge radiation of peridinioid and gonyaulacoid fossils in the late Triassic through to the Cretaceous, possibly due to the availability of large areas of shallow seas.

Dinoflagellate fossils are extracted from rock formed primarily from coastal or lacustrine sediments by a method that also yields pollen grains and Tasmanitids (cysts of Prasinophyceans). Therefore, practitioners of this are termed palynologists. The results are of considerable interest as indicators of ancient coastal sediments to petroleum geologists.

Special Features of Interest

In addition to their practical value as fossils, dinoflagellates have ecological and toxicological interests.

Ecology

Dinoflagellates are important marine and freshwater primary producers in the microplankton size range (20–200 µm), only diatoms surpassing their contribution in coastal waters. Periodic intense 'blooms' of individual species can discolour the water a reddish brown and at such times may have harmful effects (see below). Heterotrophic dinoflagellates can be important grazers on the smaller producers of the 'microbial loop' and thus play a role as recyclers. The impact of the parasitic forms has not been adequately evaluated yet. However, the beneficial symbionts known as zooxanthellae, which are mostly dinoflagellates, have been shown to be extremely important, especially in their contribution to the reef-building activities of coral animals and as primary producers of tropical coral ecosystems. They live inside cells of the coral and may 'leak' as much as 90% of their photosynthate. It has been estimated that, without their contributions to the coral animals, erosional forces would outweigh carbonate deposition by the animals and large reefs could not exist.

Luminescent dinoflagellates

Dinoflagellates are one of the most common causes of bioluminescence in seawater. They give off a blue–white flash when disturbed. In dinoflagellates, the substance that is oxidized in this process, luciferin, is a tetrapyrole. Members of the genera *Noctiluca, Pyrocystis, Pyrodinium, Alexandrium, Gonyaulax* and *Protoperidinium* are those most implicated in this phenomenon. It is believed to reduce grazing on them by zooplankton. In some tropical Atlantic bays, such as Phosphorescent Bay in Puerto Rico, their luminescence is a tourist attraction.

Toxic dinoflagellates

Some dinoflagellates produce potent toxins that can be lethal to humans if they contaminate seafood (shellfish or fish) or kill marine fauna when the toxins are released into the water. These phenomena and others caused by members of other groups, are collectively called harmful algal blooms (HABs).

Paralytic shellfish poisoning (PSP) is caused by saxitoxin, a blocker of sodium channels in nerves, produced by dinoflagellates of the genera *Alexandrium*, *Pyrodinium* and *Gymnodinium*. Neurotoxic shellfish poisoning (NSP) is similar, but is caused by brevetoxins from *Karenia brevis*. Diarrhoeic Shellfish Poisoning (DSP) is caused by okadaic acid and other toxins produced by species of *Dinophysis* and *Prorocentrum lima*. Ciguatera fish poisoning (CFP) causes tropical reef fish to become toxic due to a food chain originating in the dinoflagellates *Gambierdiscus, Ostreopsis* and *Prorocentrum*. The principal toxins, ciguatoxin and maitotoxin, are produced by *Gambierdiscus*, but the others add other potentially toxic compounds, leading to a complex symptomatology.

Fish killers release toxic substances into the water, which harm gills, the liver or other organs. Species of *Karenia* (formerly placed in the genus *Gymnodinium*), such as *K. brevis, K. mikimotoi* and *Karlodinium micrum,* are responsible for most dinoflagellate-caused fish kills. *Heterocapsa circularisquama* kills oysters in Japan.

Phylogenetic Position of the Group

As protists, dinoflagellates are members of the great radiation of eukaryotic unicells from which the plant, animal and fungal lineages eventually arose. But where within this radiation? Given that they are the only eukaryotes that, like prokaryotes, lack histones, one view, the Mesokaryote hypothesis, placed them at the base of the eukaryotic tree, in which case their lineage would be more than 1.5 billion years old. However, we know that some do have histones and the placement of these at the base of the dinoflagellate subtree by molecular techniques (see above) is not consistent with this idea. Therefore, their lineage diverged later, although still before the Metazoans of the late Precambrian (Neoproterozoic), that is, roughly 800 million years ago. Biogeochemical evidence, the presence of dinosteranes, hydrogenated dinosterols that are unique to the group, confirms their presence in Early Cambrian sediments.

Their possession of tubular mitochondrial cristae, a feature of surprising conservativeness in protists, places them within a large complex of groups that includes the Chromists (chrysomonads, diatoms, brown algae, oomycete fungi), radiolarians, foraminiferans and far from the flat cristae assemblage that includes animals, plants and true fungi. The strong structural resemblance between the cortex of dinoflagellates and ciliates, with the single layer of vesicles/cortical alveoli and rod-like trichocysts led to a suggestion of close affinity between them. Less obviously, Apicomplexans (sporozoans) have a peripheral vesicle and also have rod-like structures. Molecular phylogenetic comparisons now place these three groups as members of a lineage named the Alveolates by Cavalier Smith, with Apicomplexans and dinoflagellates closer together than ciliates. Several genera are considered to be 'predinoflagellates', among them *Oxyrrhis, Colponema*, and *Perkinsus*.

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