Dinoflagellata

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Abstract

Dinoflagellates are a major group of aquatic protists responsible for a major part of marine primary productivity, the creation of coral reefs, marine bioluminescence, and most toxic red tides; indirectly they also cause some human diseases like paralytic shellfish poisoning, ciguatera, etc. They are derived from photosynthetic ancestors and early in their evolutionary history exchanged most of the histones in their nuclei for DVNPs, proteins of putatively viral origin that caused a complete reorganization of chromosomes that includes the loss of the typical eukaryotic nucleosomes and a very marked increase in total amounts of DNA per nucleus. Later on, they acquired other types of DNA-binding proteins, so-called HLPs in at least two waves, possibly lateral transfers from bacteria. Dinoflagellate mitochondrial genomes are some of the smallest known, and the genomes of the ancestral plastid type of the group, the peridinin plastids, are atomized into minicircles with usually one single gene per circle. Roughly half of the dinoflagellates are non-photosynthetic, and the majority of the photosynthetic forms have peridinin plastids. Loss of photosynthesis has occurred repeatedly, but all free-living non-photosynthetic forms remain metabolically dependent on cryptic plastids; complete loss of plastid metabolic activity has only been shown in a few parasitic forms. Several lineages show a marked propensity for reacquisition of photosyn-

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thesis, be it in the form of permanent photosynthetic endosymbionts, kleptochloroplasts, or serial secondary and tertiary endosymbioses that produce cells with a wide variety of plastid types. In a few members of the group, peridinin plastids have become the pigment cup/retinoid of complex eyelike structures, so-called ocelli.

Keywords

Dinoflagellates • Syndinians • MALV • Coral reefs • Bioluminescence • Paralytic shellfish poisoning • Ciguatera • DVNP • HLP • Peridinin • Photosynthesis • Kleptochloroplasts • Tertiary endosymbiosis • Theca • Tabulation • Ocelli

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Introduction

General Characteristics

Dinoflagellates (Gr. δίνη/díni, to whirl) are an eukaryotic group containing approximately 4,500 species in more than 550 genera, nearly three quarters of the genera and more than half of the species being fossil. Members of the group can be photosynthetic or non-photosynthetic, walled or naked, parasitic or free-living, and very rarely even multicellular. Of the ca. 2,400 living species, 83% are marine, 8% are benthic, 7% are parasitic, and roughly half are photosynthetic (Gómez 2012); several species are also known from snow and sea ice. Numbers of extant species are sure to grow substantially in the future; recent molecular analyses have shown that there are large numbers of undescribed dinoflagellates in environments like marine picoplankton (Moreira and López-García 2002, de Vargas et al. 2015) or as symbionts ("zooxanthellae") in many types of protists and invertebrates like corals or radiolarians (Coffroth and Santos 2005; Brate et al. 2012). The cell periphery, wall, cyst, nuclear, and flagellar features are very distinctive, dinoflagellates show great diversity of form, and some have highly complex internal differentiation.

Occurrence

Dinoflagellates can be found in most aquatic environments, both freshwater and marine, and in intrazoic habitats (see section "Habitats and Ecology"). Principal sources for dinoflagellate cultures include the Provasoli-Guillard National Center for

Culture of Marine Phytoplankton (CCMP, Boothbay Harbor, Maine, USA), the Canadian Center for the Culture of Microorganisms (CCCM, Vancouver, Canada), the CSIRO Collection of Living Microalgae (CSIRO, Hobart, Tasmania, Australia), the Cawthron Institute Culture Collection of Micro-algae (CICCM, Nelson, New Zealand), the Culture Collection of Algae and Protozoa (CCAP, Oban, UK), and the Microbial Culture Collection at the National Institute for Environmental Studies (MCC-NIES, Tsukuba, Japan).

Literature

Because dinoflagellates have been claimed by botanists as algae and by zoologists as protozoa, and the fossil forms by palynologists and micropaleontologists, literature concerning them is widely scattered. The most comprehensive taxonomic reference work is the two-volume contribution by Schiller (1933, 1937, in German) to Rabenhorst's Kryptogamen Flora, although it is now seriously out of date. Examples of more recent English-language taxonomic monographs covering large numbers of species are those by Steidinger and Williams (1970, Gulf of Mexico), Taylor (1976, Indian Ocean), Dodge (1982, British Isles), and Gómez (2003, Mediterranean). The catalogues of genera (Loeblich and Loeblich 1966) and species by Sournia (1973) and Gómez (2005 and 2012) help in tracking down more recently described taxa. The Center for Excellency in Dinoflagellate Taxonomy (CEDiT, http://www.dinophyta.org) provides authoritative information on taxonomic matters; it includes, for example, lists of valid names, sources of first descriptions, etc. The taxonomy of extant and fossil species was unified for the first time by Fensome et al. (1993). A good summary of the biology of the group is presented in Hackett et al. (2004b); papers concerned primarily with the evolution of the whole group include Taylor (2004), Saldarriaga et al. (2004), Zhang et al. (2005), and Bachvaroff et al. (2014).

A small book by Sarjeant (1974) mostly on fossils and volumes edited by Spector (1984) and Taylor (1987) has brought together much general literature. Major reviews have been provided on particular aspects, e.g., Fensome et al. 1993, classification; Granéli and Turner 2006, biology of harmful species; and Coffroth and Santos 2005, zooxanthellae.

History of Knowledge

The largest dinoflagellate, *Noctiluca*, reaches 2 mm in diameter and can be seen with the naked eye as a grayish sphere, luminescent when disturbed. It is not surprising that it was the first dinoflagellate to be described in 1753 by Henry Baker. Several microscopic forms, both freshwater and marine, were discovered by the early Danish microscopist Otto F. Müller in the 1770s and illustrated in 1786. From then on, there was a slow but steady stream of descriptions, most notably by C.G. Ehrenberg who named many protists, particularly those forming microfossils, in the mid-nineteenth

century. Ehrenberg mistakenly believed that they were scaled-down, multicellular animals (the plastids were interpreted to be gonads). Another common misconception was that there was a ring of cilia in the girdle groove (in the position of the transverse flagellum) additional to the trailing longitudinal flagellum, leading to the name "Cilioflagellates" in use until the end of the nineteenth century. The group was first monographed by F.R. von Stein in 1883, at which time 32 genera were recognized (two not attributed to the dinoflagellates today), 26 of which are still in use. He was the first to recognize the taxonomic usefulness of thecal plate patterns in the group. The nomenclatural system for dinoflagellate thecal plates was standardized by C.A. Kofoid in 1907 and 1909, and the "Kofoid System" is still used universally, although its weakness for generic comparisons is becoming recognized (Taylor 1980; Evitt 1985).

Links to marine luminescence were demonstrated by G.A. Michaelis in 1830, and zooxanthellae symbiotic in colonial radiolarians was described and named by Karl Brandt in the 1880s (their dinoflagellate nature was only later recognized by S. Kawaguti in 1944, and they were cultured by H.D. Freudenthal in the 1950s). Parasitic species were studied largely in the early 1900s by Edouard Chatton.

Freshwater species were first monographed by A.J. Schilling at the end of the nineteenth century, with strong contributions on their biology by George Klebs at the turn of the century.

Ecologists gradually became aware of the importance of the photosynthetic members of the group as beneficial, or sometimes harmful, bloom-forming organisms of the phytoplankton. Their frequent causal association with "red tides" became apparent, with massive kills of fish and marine life being recorded with increasing frequency during this century. Their association with paralytic shellfish poisoning (PSP) was recognized by Hermann Sommer and his colleagues in the 1930s, and the link to ciguatera fish poisoning only in the 1970s by T. Yasumoto and colleagues.

The culture of dinoflagellates was pioneered chiefly by Albert Barker in the 1930s. This permitted the physiology and life cycles to be studied more carefully, principally by T. Braarud and his Norwegian colleagues and B.M. Sweeney in America. The latter, together with J.W. Hastings, focused on luminescence and circadian rhythms.

Much of the current ultrastructural knowledge of the group, including the unusual nuclear features, has come from John Dodge in the 1960s and 1970s, with valuable contributions by many others, including J. and M. Cachon, M.-O. Soyer, C. Greuet, K.R. Roberts, G. Hansen, and Ø. Moestrup. Ultrastructural and biochemical data on the dinoflagellate nucleus led to the proposal of the so-called Mesokaryote hypothesis (Dodge 1965), in which dinoflagellates are thought to represent an intermediate kingdom between prokaryotes and eukaryotes. This view was very prevalent until the advent of molecular data.

Dinoflagellates were thought by many to be entirely asexual in reproduction. Early observations by E. Zederbauer and Karl Diwald of apparent sexual fusion were discounted, and it was only careful documentation and observations of H.A. von Stosch in the 1960s that established its occurrence unequivocably in *Ceratium*. The first genetic studies followed later in 1974, using *Crypthecodinium cohnii*,

coincidentally in two different laboratories (C.A. Beam and M. Himes in Brooklyn; R.C. Tuttle and A.R. Loeblich III at Harvard).

The study of fossil dinoflagellates (reviewed by Sarjeant 1974) accelerated in the 1920s and 1930s with studies by O. and W. Wetzel (unrelated) and the growing realization that the fossils were actually cysts rather than thecae, for the most part, and that many of the spiny "hystrichospheres," formerly of unknown affinities, may also be dinoflagellates. This was only clearly established by W.R. Evitt, using careful observation and encystment experiments, and with the excystment of cysts collected from natural sediments by D. Wall and B. Dale during the 1960s. The zygotic nature of resting cysts (most readily fossilizable) only become evident in the 1970s. Later studies on dinoflagellate life cycles and cyst biology have been made by K. Steidinger, M. Montresor, and J. Lewis, among others.

Practical Importance

Dinoflagellates are perhaps best known as causers of harmful algal blooms, as roughly 75–80% of toxic phytoplankton species belong to the group (Cembella 2003). They are frequent causes of "red tides" that may kill fish and/or shellfish either because of toxin production (Table 1) or because of nontoxic effects caused by large numbers of cells in the water (clugging of animal gills, oxygen depletion, etc., e.g., Smayda 1997). Dinoflagellate toxins are among the most potent biotoxins known and accumulated in shellfish or fish cause human diseases like paralytic shellfish poisoning (PSP), neurotoxic shellfish poisoning (NSP), diarrheic shellfish poisoning (DSP), and ciguatera (Lehane and Lewis 2000). They also have been linked to major human health concerns, especially in estuarine environments (*Pfiesteria*). This is significant to coastal aquaculture in that they prevent otherwise productive areas of coastline from being fully exploited. Parasitic species of the genus *Amoebophrya* infect other dinoflagellates, often toxic ones, and have a significant role in ending harmful algal blooms (Velo-Suárez et al. 2013). The syndinian genus *Hematodinium* causes bitter crab disease in 25 species of crustaceans. When infected, crab meat acquires an aspirin-like, bitter taste, and this has large repercussions for crab fisheries (e.g., Meyers et al. 1987; Stentiford and Shields 2005).

Some dinoflagellates (e.g., *Akashiwo sanguinea*) have been used in aquaculture as a preferred food source for larval fish, for example, for anchovies, because they have a higher caloric content per cell than diatoms. Unfortunately they are sensitive to stirring and bubbling, and this, combined with relatively slow division rates (often 0.5 cell divisions or fewer per day), makes them useful only in special cases.

The main ecological importance of dinoflagellates lies elsewhere, though. They are second only to diatoms as marine primary producers, and so are responsible for a very major fraction of marine primary production worldwide. As phagotrophic organisms, they are also important components of the microbial loop in the oceans and help channel significant amounts of energy into planktonic food webs that would otherwise get lost. Dinoflagellates also have a pivotal role in the biology of reef-

building corals: as zooxanthellae, they build symbioses with corals and other animals and protists, and by removing CO_2 from the medium for photosynthesis, they facilitate the deposition of calcium carbonate.

Habitats and Ecology

Dinoflagellates can be found in most aquatic environments including snow, freshwater, marine, or intrazoic habitats.

Comprehensive treatments of their ecology include the chapters by Taylor and Pollingher in Taylor (1987). Reviews on toxic dinoflagellate blooms (e.g., Lundholm and Moestrup 2006) contain numerous references of ecological interest. Pross et al. (2004) provide a good review on palaeobiogeography based on fossil dinoflagellate cysts.

Nutrition

Roughly half the dinoflagellate species are photosynthetic, but completely autotrophic species are very rare (Gaines and Elbrächter 1987; Schnepf and Elbrächter 1992). Photosynthetic dinoflagellates are generally mixotrophic and rely on a combination of photosynthesis and heterotrophic nutrition; the relative importance of the uptake of dissolved organic nutrients, feeding, and photosynthesis for the nutrition of members of the group is unknown. Non-photosynthetic forms can be either free-living or parasitic, and they rely on both osmotrohy and phagotrophy. Prey capture mechanisms in phagotrophic forms vary greatly. Direct phagocytosis occurs in several species. A distinct cell mouth (cytostome) is present in several large phagotrophic genera (e.g., *Oxyrrhis*, *Noctiluca*, *Kofoidinium*, *Erythropsidinium*, *Gyrodinium s.s.*). Other forms, for example, *Protoperidinium*, extend a delicate, pseudopodial "feeding veil" with which they surround portions of diatom chains and other large prey. Digestion then occurs outside of the theca, and only digested material is taken up; the veil is retracted afterward (Gaines and Taylor 1984; Jacobson and Anderson 1992). A third form of feeding, myzocytosis (e.g., in *Paulsenella* spp., "*Katodinium*" *fungiforme*), involves piercing the cell membrane of prey items with a special organelle, the peduncle, and somehow "sucking" the prey cell's contents as if through a straw (Schnepf and Elbrächter 1992). Peduncles, also present in some photosynthetic species, are c shaped in cross section; the details of the mechanism that underlies this mode of feeding are unknown. Parasitic forms can be intra- or extracellular, and they take up nutrients from their host directly.

Only relatively few non-photosynthetic dinoflagellates have been studied in detail using transmission electron microscopy, and several ostensibly non-photosynthetic species have been shown to carry cryptic plastids (e.g., Sparmann et al. 2008). The ratio of photosynthetic versus non-photosynthetic forms in dinoflagellates may well change in the future as more species are investigated in this regard.

Dinoflagellate Phytoplankton

Dinoflagellates are generally considered second only to diatoms in their importance as primary producers among marine plankton. A deceptive impression has built up in the literature that diatoms predominate in colder, and dinoflagellates in warmer, water. A more accurate picture is that diatoms predominate in coastal waters during the most productive periods and also in open waters of high latitudes (arctic, subarctic, circumantarctic). In the nutrient-poor temperate and tropical oceanic regions, all types of plankton are impoverished, with coccolithophorids less so in the former and dinoflagellates less so in the latter. In fact, the greatest concentrations of dinoflagellates (10^7–10^8/l) occur in temperate coastal waters subject to transient periods of vertical stability (Taylor et al. 2008).

Many photosynthetic dinoflagellates behave as annual species. They are generally ecophysiologically diverse and tend to be more specialized to particular habitats/hydrographic regimes than diatoms, for example. For this reason, dinoflagellate blooms tend to be monospecific (Smayda and Reynolds 2003).

Polar waters have relatively few photosynthetic dinoflagellate species (e.g., McMinn and Scot 2005). In temperate coastal and also in freshwaters, dinoflagellates usually bloom in mid- to late summer when sunshine and vertical stability allow strong aggregations to develop at vertical and/or horizontal discontinuities, referred to as clines (e.g., thermocline, nutricline) or fronts. The swimming abilities of the cells (maximum approximately 1 m/h) allow them to resist moderate downward water movements and to occupy compromise positions in the water column relative to light (maximum upward) and inorganic nutrients (maximum downward; Cullen and MacIntyre 1998 and references therein). Subsurface maxima may occur at 1% surface light levels or even less (Anderson and Stolzenbach 1985). In ice-covered lakes, dinoflagellates can accumulate just under the ice if it is not too thick and may bloom early in the season or even in winter.

Daily patterns of vertical migrations are also seen, with the cells rising as far toward the surface as the nutrients allow during the day and downward at night (e.g., *Lingulodinium polyedrum* and *Akashiwo sanguinea* off California or *Ceratium hirundinella* and *Peridinium cinctum* in lakes; Cullen and MacIntyre 1998). *Prorocentrum* spp., *Ceratium fusus*, and *C. furca* tend to predominate in estuarine water. Several of the coastal bloom formers are harmful to marine life or humans when in high concentrations ("red tides"): see Table 1. In higher latitudes (but not polar), the summer community is generally similar but of shorter duration than in warmer temperate waters (e.g., the Bering Sea/Gulf of Alaska relative to southern California or southern Chile compared with Peru; Taylor et al. 2008). Many of the bloom formers overwinter as benthic cysts.

In temperate lakes, the dominants in summer can vary considerably according to many factors, including degree of eutrophy (nutrient level), pH, depth, and surrounding vegetation. Dinoflagellates are represented chiefly by *Ceratium* spp. (especially *C. hirundinella*), when grazing is intense, or *Peridinium* and "*Gymnodinium*" spp. when it is not. In tropical lakes, other protist groups usually predominate, but

Table 1 Examples of toxic dinoflagellates

Species	Toxin	Effect
Alexandrium spp.	Saxitoxins	PSP
Amphidoma spp.	Azaspiracid	Azaspiracid poisoning
Azadinium spp.	Azaspiracid	Azaspiracid poisoning
Cochlodinium polykrikoides	Unknown	Fish kills, smothered corals
Coolia monotis	Cooliatoxin	
Dinophysis spp.	Dinophysistoxin	DSP
Gambierdiscus toxicus	Maitotoxin, ciguatoxin	Ciguatera
Gymnodinium catenatum	Saxitoxins	PSP
Karenia spp.	Brevetoxins	NSP, fish kills
Karlodinium veneficum	Brevetoxins	NSP
Lingulodinium polyedrum	Yessotoxin	
Ostreopsis spp.	Ostreotoxin	
Pfiesteria spp.	*Pfiesteria* toxin	Possible estuary-associated syndrome (PEAS)
Prorocentrum spp.	Okadaic acid, dinophysistoxin	DSP
Protoceratium reticulatum	Yessotoxin	
Pyrodinium bahamense	Saxitoxins	PSP
Takayama spp.	Brevetoxins	NSP
Vulcanodinium rugosum	Pinnatoxins	

Peridinium gatunense is a major dominant in Lake Kinneret, Israel, where it "oversummers" as a benthic cyst (Pollingher 1987).

Tropical nearshore waters are usually diatom dominated, but brief dinoflagellate blooms may occur, and some tropical Atlantic mangrove-lined bays have become famous for persistent blooms of the bioluminescent species *Pyrodinium bahamense* var. *bahamense*; with the development of the shoreline, these blooms have been greatly reduced. Several toxic species bloom in tropical coastal waters. In the oceanic tropics, although a great variety of *Ceratium* spp. are most obviously present, they are not abundant; *Pyrocystis* spp. and in the nanoplankton size range (<20 μm) *Oxytoxum* spp. are usually more abundant.

Dinoflagellate Microzooplankton

Non-photosynthetic forms depend on the presence of their food for nutrition; as might be expected, they are most abundant at the end of blooms of their prey organisms. *Protoperidinium* spp. and *Noctiluca scintillans*, for example, typically

follow diatom blooms. From a biogeographic standpoint, they are most abundant where the latter are. Species of *Protoperidinium* are important in polar waters and are generally coastal in distribution. The effect of non-photosynthetic dinoflagellates on marine (or freshwater) ecosystems is very understudied, but at least in coastal food webs, it can be very large (e.g., Lessard and Swift 1985).

Benthic Dinoflagellates

Dinoflagellates (both photosynthetic and non-photosynthetic) are common inhabitants of benthic sediment habitats, but details of their biology are scarce (Hoppenrath et al. 2014). Early data suggests that benthic marine communities are remarkably similar across locations of similar latitudes, but investigations are too few and geographically restricted to allow for generalized biogeographic conclusions so far. Photosynthetic forms can bloom in benthic habitats; several *Amphidinium* and *Prorocentrum* species may discolor marine sand flats. *Crypthecodinium cohnii* and *Oxyrrhis marina* are often associated with seaweed (brown and green algae, respectively), and the latter also forms intense pink tide-pool blooms. On tropical, bushy seaweeds several toxic species occur, e.g., *Gambierdiscus toxicus*, which adheres to the surface of the weeds and is the ultimate cause of ciguatera (Anderson and Lobel 1987).

Symbioses

Mutualistic Associations

Most zooxanthellae (golden-brown endosymbionts of marine animals and protists) are dinoflagellates. The association between dinoflagellates and reef-building corals was mentioned above, but dinoflagellate endosymbionts inhabit a great number of other invertebrates and protists, for example, many sea anemones, jellyfish, nudibranchs, the giant clam *Tridacna*, and several species of radiolarians and foraminiferans (for a review, see, e.g., Trench 1997). The effect that these associations have on organisms and ecosystems can be massive. They use waste products of their host (e.g., waste nitrogen and phosphorus compounds) as nutrients and release up to 40% or more (possibly more than 90%) of their photosynthate to their hosts, chiefly in the form of glycerol, with smaller amounts as sugars and amino acids. Furthermore, by taking CO_2 from the water for photosynthesis, zooxanthellae facilitate the deposition of calcium carbonate (Marshall 1996) and the production of coral reefs, large foraminiferal skeletons, the massive shells of *Tridacna*, etc.

Dinoflagellate zooxanthellae often belong to the genus *Symbiodinium*, which divides in the coccoid stage and has very transient flagellated stages. But at least seven dinoflagellate genera from four orders have been found in symbiotic associations (Banaszak et al. 1993). For a long time, *Symbiodinium* was considered to be a monospecific genus, but now it is clear that it contains a large cryptic diversity. Coral bleaching is the expulsion/digestion of zooxanthellae in temperature-stressed corals.

Dinoflagellates can also function as hosts of mutualistic symbioses. They may, for example, carry extracellular cyanobacteria ("phaeosomes") that may help fix nitrogen in nutrient-poor oceanic regions, e.g., the dinophysoids *Ornithocercus*, *Histioneis*, and *Citharistes*; other endosymbiotic bacteria are not at all uncommon: Sinophysis and Triposolenia contain for example cyanobacterial endosymbionts. Eukaryotic endosymbionts are also found in many dinoflagellates. *Noctiluca scintillans*, for example, exists in the Pacific in at least two populations: one of them always harbors *Protoeuglena*, a green alga, as an endosymbiont and the other one never seems to contain them. Other noctilucales, for example, *Spatulodinium*, and at least one *Kofoidinium*-like species also contain green endosymbionts (Gómez and Furuya 2007). Two other such endosymbioses that may well be permanent (definitive proof is lacking at the moment) are the genus *Amphisolenia*, which always seems to contain pelagophyte endosymbionts (Daugbjerg et al. 2013), and *Podolampas bipes*, which seems to contain a pedinellid dictyochophyte (Schweikert and Elbrächter 2004). Diatom-carrying dinoflagellates (so-called dinotoms, *Kryptoperidinium*, *Durinskia*, *Dinothrix*, *Galeidinium*, "*Peridinium*" *quinquecorne*, "*Peridiniopsis*" sp.) show a similar situation; they contain (almost) complete diatom endosymbionts and are thus binucleated. Molecular phylogenetic trees put all dinotoms in a clade, and this would seem to suggest that the diatom endosymbiosis occurred before the divergence of the different species. However, things are not that simple: the type of diatom endosymbiont (pennate vs. centric) is different in the different genera (Takano et al. 2008). This situation is very close to being a true tertiary endosymbiosis, but no diatom genes seem to have moved to the dinoflagellate nucleus. True tertiary endosymbioses do exist in dinoflagellates; they involve plastids of haptophyte origin (Patron et al. 2006; Nosenko et al. 2006) and will be discussed in the plastid section below.

Parasitism

Many extant dinoflagellates are parasites (here defined as organisms that eat their prey from the inside, i.e., endoparasites, or that remain attached to their prey for longer periods of time, i.e., ectoparasites), and of those, a majority branch early in the dinoflagellate molecular tree. Syndinians, early-branching parasitic dinoflagellates, are characterized by a plasmodial (multinucleate) stage (references in Cachon and Cachon 1987; Fensome et al. 1993). Core-dinoflagellate parasites on the other hand seem to have originated repeatedly from within the group, and their trophic stages are generally much easier to relate morphologically to the flagellated stages from which they arise. Dinoflagellates can parasitize animal or protist hosts. Ectoparasitic forms show the least modification; they attach to and penetrate the host by a stalklike projection from the sulcus, probably homologous to the peduncle of motile forms. *Chytriodinium* actively penetrates the chorion of crustacean eggs by extraordinary rapid "drilling" movements with its extensible hyposome, while the motile stages of parasites on fish, such as *Piscinoodinium*, *Amyloodinium*, and *Crepidoodinium*, have a pedunclelike organelle with which they penetrate the host. *Blastodinium* inhabits the gut of copepods, maintaining its position by rows of small spines. *Protoodinium*, *Crepidoodinium*, *Piscinoodinium*, and *Blastodinium* retain their plastids while feeding on their zooplanktonic or fish hosts.

Circadian Rhythms

In a number of species, many cellular phenomena are rhythmic, exhibiting daily (circadian) differences. Processes such as bioluminescence, photosynthesis, cell division, and motility have been studied intensively, especially in *Lingulodinium polyedrum* (Sweeney 1987; Akimoto et al. 2004), but it is likely that many other cellular processes are under circadian control and that this cellular "clock" occurs in many – possibly all – dinoflagellates. A key feature of the circadian (about 1 day) control is that the mechanism responsible is endogenous, not directly dependent upon the light-dark cycles, which, however, serve to confer phase to the system (Johnson and Hastings 1986).

Toxins

The toxic species that have caused illness or death of humans or marine fauna, as listed in Table 1, produce two principal types of toxins: (a) water-soluble, small molecular weight substances that block the entry of sodium into the nerves of some animal groups, including humans, and (b) larger, water-, or lipid-soluble compounds that increase membrane permeability to various ions, including sodium and/or calcium. Additionally, there are a few toxic substances such as cholinesterase-like compounds in *Amphidinium carterae* known only from laboratory testing. Toxins in the first group include the saxitoxin complex (saxitoxins, neosaxitoxin, gonyautoxins), heterocyclic guanidines produced by *Alexandrium* species, *Pyrodinium bahamense*, and *Gymnodinium catenatum*, which produce paralytic shellfish poisoning. Saxitoxin, by mass, is 1,000 times more potent than cyanide and 50 times more toxic than curare (Sako et al. 2001). Toxins in the second group are polyether compounds. They include the brevetoxin complex from *Karenia brevis* which kills fish and causes neurotoxic shellfish poisoning, okadaic acid from tropical *Prorocentrum lima*, ciguatoxin and maitotoxin from *Gambierdiscus toxicus*, the dinophysistoxins from *Dinophysis* and *Prorocentrum* spp., pectenotoxin from *Dinophysis*, yessotoxin from *Protoceratium reticulatum* and *Lingulodinium polyedrum*, and azaspiracid from Azadinium spp. and Amphidoma spp. (Van Dolah 2000). They cause ciguatera (Lehane and Lewis 2000), diarrheic shellfish poisoning, and azaspiracid shellfish poisoning. Maitotoxin is one of the most potent biogenic toxins known (Terao et al. 1989).

The functions of the toxins are presently unknown. They do not prevent predation on the producers, and most of their grazers, such as copepods, pteropods, or bivalve mollusks, remain unharmed. However, they can cause massive kills of fish and other marine life (dolphins, manatees, birds, etc.). Toxins produced by benthic dinoflagellates that do not often bloom generally do not cause fish kills: the toxin is taken orally by the fish with its food and is accumulated in the animal's tissues (mostly the liver) where it causes comparatively little damage. Toxins produced by blooming, planktonic dinoflagellates are much more likely to cause fish kills. When the blooms end and the cells die, toxins are released into the water, and fish take the toxin via their

gills, a much more direct way into their bloodstream. In these cases, the effects of the toxin are much more severe. Both brevetoxin and maitotoxin have been shown to accumulate in fish tissues if taken orally, but brevetoxin is more likely to cause fish kills because of the ecology of its producing organism.

Most toxin producers are photosynthetic, but *Protoperidinium crassipes*, producer of azaspiracid, is an exception. Toxicity in benthic coral reef dinoflagellates is a common occurrence (Anderson and Lobel 1987); this is not the case in planktonic dinoflagellates.

Characterization and Recognition

The typical dinoflagellate is a biflagellated eukaryotic unicell, between 10 and 100 μm in length (the extreme range is 2–2,000 μm). One ribbonlike flagellum, the transverse, winds to the left around the cell causing it to turn as well as providing forward thrust. The second flagellum, the longitudinal, beats posteriorly. Although providing some forward thrust (Gaines and Taylor 1985), its principal function seems to be directional (an exception is *Ceratium*). Cell shape is highly variable but is often pyriform.

In most dinoflagellates, the two flagella arise from the side (designated as ventral) and lie in surface grooves: the transverse in the girdle (or cingulum) and the longitudinal in the sulcus (Fig. 1), although its distal portion projects freely behind the cell. This is known as the dinokont condition. If the distal and proximal ends of the girdle do not meet at an equal level at the sulcus, they are said to be displaced. Displacement may be left handed (the most common condition), in which the proximal (left) end is more anterior, or right handed, and the degree is measured in girdle widths, given from the upper edges.

The girdle divides the cell into an anterior body portion, the episome (or epicone), and a posterior hyposome (hypocone). The sulcal groove stops at the posterior of the cell. In athecate (wall-less) cells, there is a thin, anterior extension of the sulcus, the acrobase, which reaches the cell's apex. Acrobases can be straight, sigmoid, or form loops around the apex of the cell.

In a few genera, most notably *Prorocentrum*, the two flagella arise from the anterior (apex) of the cell and are not associated with grooves, although they are differentiated as in dinokonts and beat differently. This is the desmokont condition (Fig. 2).

Flagella

The longitudinal flagellum is relatively conventional in appearance, with few or no hairs (mastigonemes). It may be ribbonlike, and in some, e.g., *Ceratium* (in which it is the main propulsive unit) and *Oxyrrhis*, an accessory fibrillar band may be present, running parallel to the axoneme. It beats with only one or two periods to its wave. In *Ceratium*, it can contract rapidly up to the body.

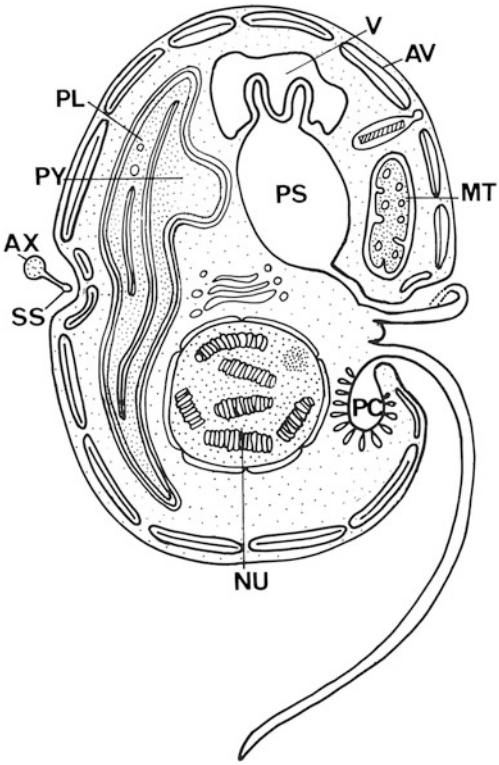

Fig. 1 Longitudinal section through a generalized dinoflagellate (re drawn from Taylor 1980). *AV* amphiesmal vesicle; *AX* axoneme; *MT* mitochondrion; *NU* nucleus; *PC* collecting pusule; *PL* plastid; *PS* sac pusule; *PY* pyrenoid; *SS* striated strand; *V* vacuome

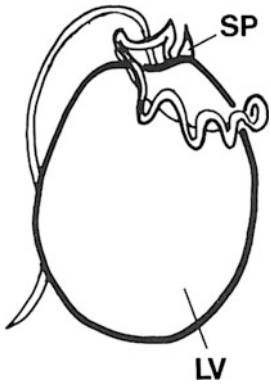

Fig. 2 Flagellar arrangement of *Prorocentrum*. *LV* left valve; *SP* spine

The transverse flagellum (Fig. 3) is generally a wavy ribbon in which only the outer edge undulates from base to tip, due to the action of the axoneme which runs along it. The beat of the axoneme is approximately spiral, but because the ribbon is anchored on its inner edge by an accessory fibrillar band, the striated strand, the

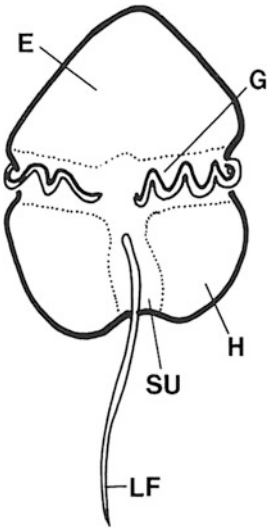

Fig. 3 Flagellar arrangement in a dinokont dinoflagellate seen from the ventral side. *E* episome; *G* girdle (=cingulum); *H* hyposome; *LF* longitudinal flagellum; *SU* sulcus

ribbon forms a travelling ruffle rather than a spiral, the outer advancing faces being inclined forward and downward. The axonemal edge has simple hairs, which can be of varying length. The form of the ruffle as it beats and the hairs act in such a way that there is forward propulsion and also a turning force. Curiously, the cells rotate in the direction of the wave, i.e., always to the cell's left (Gaines and Taylor 1985). Early-branching dinoflagellates (*Oxyrrhis*, the syndinians, and *Noctiluca*) do not seem to have a striated strand in their transverse flagellum.

Amphiesma (Cortex)

The cells may be naked (athecate) or possess a wall (thecate, pelliculate). In a few species of *Oxyrrhis*, *Heterocapsa*, and *Lepidodinium*, very small delicate, star-, or basketlike organic scales occur external to the cell membrane, but in walled dinoflagellates, the close-fitting cellulosic plates which together form the theca are intracellular.

The organization of the outer cortical region of the cell is distinctive. This entire structural complex, regardless of the presence or absence of cellulose plates, is the amphiesma (Morrill and Loeblich 1983; also known as the cortex; Netzel and Dürr 1984). Beneath the cell membrane of the motile cell, a single layer of vesicles is usually present, the alveolae (Fig. 4; the term "alveolus" comes from the ciliate literature, but it is starting to be used in dinoflagellates and apicomplexans to underline the homologous nature of these structures in the three groups). It is within these alveolae (traditionally called amphiesmal vesicles) that the cellulose plates are formed, one per vesicle in thecate (= armored) dinoflagellates. In

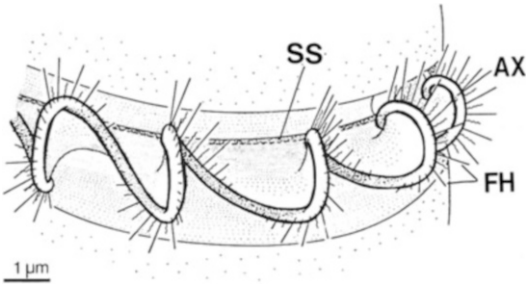

Fig. 4 Detail of the transverse flagellum, modified from Gaines and Taylor (1985). *AX* axoneme; *FH* flagellar hairs; *SS* striated strand

athecate (= naked) species, the vesicles are either empty or contain amorphous material, and the vesicles themselves play a structural role. In some species of *Gymnodinium*, there is a very thin "membrane" within the vesicles that resembles the membranous layer that acts as a plate precursor in *Ceratium* and other more heavily thecate species. The thecal plates usually fit tightly together, the margins often overlapping in a predictable way (imbrication pattern). There is a general trend to overlap from dorsal to ventral and from girdle to pole. The boundaries of the plates are the sutures. Cell growth is permitted by the addition of wall material along some of the margins of the thecal plates. These growth zones, often striated, are termed intercalary bands. In gonyaulacoids, plate growth is usually along only one margin of the suture, whereas it is on both in peridinioids. Pores do not usually occur in the intercalary growth zones. The patterns formed by the thecal plates (tabulation) are of critical importance in taxonomy and are discussed here following the description of other internal components, life cycles, and cysts. Recent molecular phylogenetic trees suggest that thecate dinoflagellates are monophyletic (Janouškovec et al. 2016).

Throughout part or all of the life cycle in some species, there may be a thin continuous fibrous layer, the pellicle, usually lying internally to the alveolae. It consists of cellulose, usually with sporopollenin added to varying degrees. It may form the principal strengthening layer of the amphiesma of athecate genera such as *Ptychodiscus*, *Balechina*, *Sclerodinium*, and *Kofoidinium*. In thecate genera such as *Alexandrium* or *Scrippsiella*, it is present beneath the theca for much of the life cycle and forms the wall of temporary cysts, which are formed rapidly and asexually by the shedding of the theca (ecdysis). Athecate cells with a well-developed pellicle are here termed pelliculate.

Microtubules are also usually present below the vesicles of both thecate and athecate forms, presumably adding some strength to the latter and aiding in morphogenesis. Both microtubular and fibrous (banded, rhizoplast) flagellar roots (portions of kinetids) are present, with sphincterlike collars around the flagellar insertion pockets. Peduncles are tubular structures through which food may be drawn, e.g., in "*Katodinium*" *fungiforme*, *Paulsenella*, *Pfiesteria*, etc.

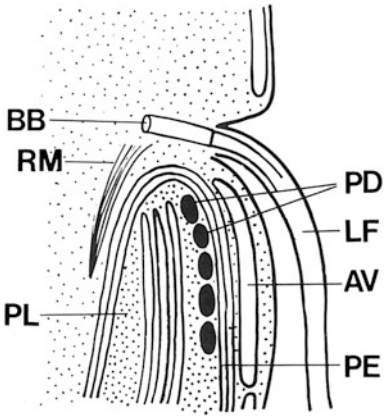

Fig. 5 A typical eyespot, located beneath the longitudinal flagellum (drawn from micrographs by Dodge 1973). *AV* amphiesmal vesicle; *BB* basal body (=centriole); *LF* longitudinal flagellum; *PD* pigment droplets; *PE* plastid envelope; *PL* plastid; *RM* microtubular root

In addition to cholesterol, most dinoflagellate membranes contain a rare 4α,23,24 (R)-trimethyl-5α-cholest-22-en-3-ol, so-called dinosterol, a fossilizing biomarker (Alam et al. 1979); the abundance of dinoflagellate fossils from the Mesozoic onward correlates with levels of derivatives of dinosterols. Early-branching dinoflagellates like syndinians, *Noctiluca*, *Amphidinium*, *Gyrodinium*, and the Kareniaceae lack dinosterol, but the Gymnodiniaceae, *Akashiwo*, and all thecates seem to be able to produce it (Janouškovec et al. 2016).

Ejectile Bodies (Extrusomes)

The most common type of extrusome, of almost universal occurrence in the motile phase, is trichocysts: rod-shaped bodies (Fig. 5) which, when mature, usually lie in the amphiesma perpendicular to the cell membrane. The shaft is a paracrystalline, proteinaceous rod a few micrometers in length, rectangular in cross section. At its distal end, it extends as a group of twisted fibers. The whole is enclosed within a membranous sac, and there is a sheathing material between the rod and the membrane (Livolant 1982a, b). The tip of the sac is in contact with the cell membrane, passing through the amphiesmal vesicles (and thecal plates, if present). The exact mechanism of extrusion is unknown, but it is suspected that the sac ruptures at the contact point at the cell surface, and water entering causes a change in the polymerization of the rod, resulting in an elongation of eight times or more. Trichocysts are formed in the vicinity of the Golgi apparatus (Bouck and Sweeney 1966) and subsequently move to the cell periphery. It appears that most pores in the thecal plates are associated with trichocysts, but this is difficult to establish. Their function is unknown but is assumed to be defensive, excretory, or both. They are most similar to those of ciliates. A less ordered type of extrusome in dinoflagellates is the mucocyst, a simple sac with granular contents, associated with the release of mucoid material.

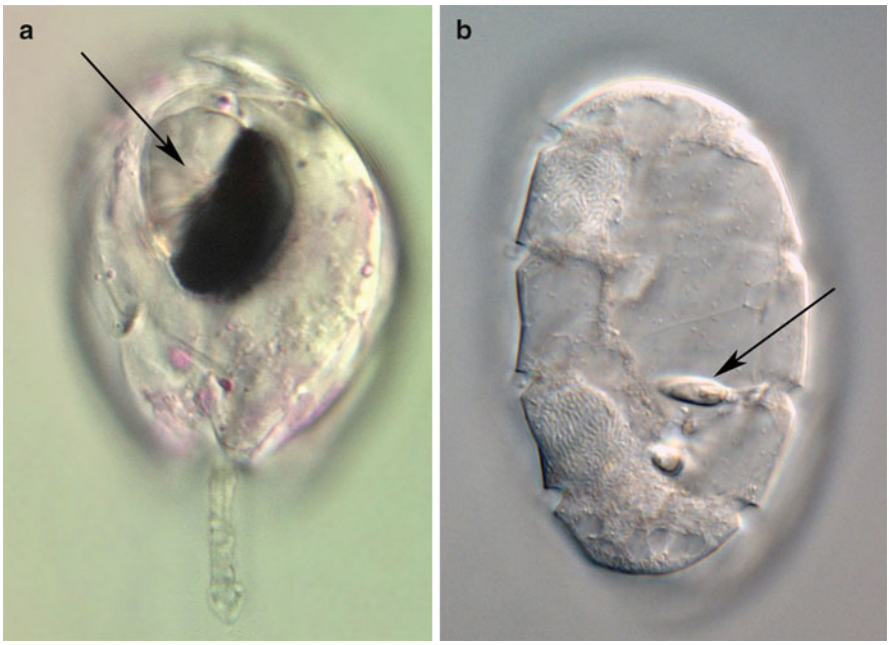

Fig. 6 (**a**) Light micrograph of *Erythropsidinium* sp. *Arrow*: Ocelloid. (**b**) Light micrograph of *Polykrikos kofoidii*. *Arrow*: Nematocyst (Courtesy of Greg Gavelis, Arizona State University)

Much more elaborate extrusomes are found in polykrikoids and warnowiids. These are nematocysts (Fig. 6), named for their resemblance to the stinging organelles of cnidarians (also known as cnidocysts), although their ontogeny differs in a few details (Westfall et al. 1983). Nematocysts are larger than trichocysts and can reach 20 μm in length. They are conical, fluid-filled sacs with a capitate blunt end. Most of the body consists of a large posterior chamber, supported by longitudinal ribs in *Nematodinium*, from which a smaller anterior chamber is isolated; the whole structure is capped by a lidlike operculum. A sharp stylet in the anterior chamber is connected to a tubular filament in the posterior chamber. In *Polykrikos*, it is coiled much like those in cnidarians, and the nematocysts fire by inversion, the stylet driving through the operculum. In *P. schwartzii*, two other structures are invariably associated with the nematocysts: a taeniocyst, which resembles a trichocyst in that it is a solid rod but with more elaborate differentiation (Fig. 6), and a chute with chute organelles, which appears to act as a safe conduit to the exterior when the complex discharges (Westfall et al. 1983). The taeniocyst projects from the cell surface near the kinetosomes. The whole complex originates by coordinated, linked differentiation from Golgi complexes near the nucleus, the primordial forms (anlage) being referred to as the nematogene and taeniogene.

Mitochondria, Golgi Bodies, and Microbodies

Dinoflagellate mitochondria have tubular cristae constricted at the base and arising from the inner membrane. Their genomes are highly unusual (Waller and Jackson 2009): like those of their close relatives, for example, apicomplexans, they encode for only three proteins: cytochrome oxidase 1 (cox1), cytochrome oxidase 3 (cox3), and cytochrome b (cob) as well as ribosomal RNA genes that are fragmented into separate pieces. In dinoflagellates, however, the modification of mitochondrial genomes has gone further than in apicomplexans. For example, all dinoflagellate mitochondrial transcripts need to be edited extensively before translation, and transcripts for at least cox3 need to be trans-spliced (Lin et al. 2002, Zhang and Lin 2005).

Golgi bodies are common, usually near the nucleus; and they may play a role in mitosis, surrounding the zones from which the spindle arises. They give rise to extrusomes. Microbodies are usually present, and some of them seem to be linked with bioluminescence (see below).

Plastids

All dinoflagellates arose from photosynthetic ancestors, and the plastids of a large majority of the photosynthetic members of the group share genetic similarities to the apicomplexan apicoplast and the plastids of chrompodellids like *Chromera* and *Vitrella* (Janouškovec et al. 2015). These so-called peridinin plastids are characterized by triple-membraned (sometimes double-membraned) envelopes, the lack of a girdle lamella, thylakoids usually in groups of unappressed threes, and various types of pyrenoids (Schnepf and Elbrächter 1999). They contain chlorophyll a and c_2 as well as peridinin (a type of carotenoid only found in dinoflagellates), β-carotene, and small amounts of diadinoxathin and dinoxanthin (Jeffrey et al. 1975). DNA-containing areas may be single or multiple, sometimes in prominent "nucleoid-like" regions; they never form a peripheral ring like in some heterokonts (Dodge 1973). In these peridinin-containing plastids, genes appear to exist as minicircles with usually one gene per circle (but two to four in a circle also exist) flanked by a variety of noncoding sequences (Zhang et al. 1999; review in Howe et al. 2008). The absolute number of genes coded in the dinoflagellate peridinin plastids also seems to be much lower than in other algae: while the plastid of cryptomonads, diatoms, and other photosynthetic chromalveolates codes for around 165–185 genes, no more than 16 genes have ever been found in any dinoflagellate peridinin plastid (Green 2004; Nisbet et al. 2004). Some of the missing genes appear to have been moved to the nucleus of the organisms involved (e.g., Hackett et al. 2004a; Bachvaroff et al. 2004), but there are still a number of them that are missing altogether. There are data that suggest that in at least some species, these minicircles may be located in the nucleus, not in the plastids (Laatsch et al. 2004). Peridinin plastids have a bacterial

type of rubisco (evidently a lateral gene transfer) that has a much lower specificity for CO_2 over O_2 when compared to the more common "eukaryotic" rubisco found in other algae (Whitney et al. 1995; Morse et al. 1995). The usual storage products in peridinin dinoflagellates are starch, produced exterior to the plastid, and oils.

In spite of their photosynthetic ancestry, not all dinoflagellates are photosynthetic: roughly half of the members of the group have secondarily lost the ability to photosynthesize and may or may not contain traces of the ancestral plastid. *Oxyrrhis*, *Noctiluca*, and *Crypthecodinium*, for example, contain plastid-targeted proteins even if an organellar plastidial remnant has not been identified, but the syndinian *Hematodinium* appears to have lost all traces of a plastid (Gornik et al. 2015; Janouškovec et al. 2016).

The diversity in types of photosynthesis that exists within dinoflagellates is unparalleled within any group of eukaryotes (Schnepf and Elbrächter 1999), but in this group, it is not always easy to distinguish between true plastids (here defined as organelles that include proteins encoded in their host's nucleus), endosymbionts that have not transferred genes to the host's nucleus but that nevertheless may well be permanent, and other phenomena related to photosynthesis acquisition, for example, kleptoplastidy. The green symbionts in *Noctiluca*, diatoms in the dinotom clade, pelagophytes in *Amphisolenia*, and dictyochophytes in *Podolampas* are (probably) examples of endosymbioses with no genetic transfer to the nucleus (only the dinotoms have been studied in detail in this respect, E. Hehenberger, pers. comm.); at least in dinotoms, this endosymbiosis seems to be permanent. Genetic transfers to the host's nucleus seem to have occurred in at least two lineages that have replaced their peridinin plastids for plastids with completely different origins: the Kareniaceae (*Karenia*, *Karlodinium*, and *Takayama*), which have obtained a haptophyte-derived plastid through tertiary endosymbiosis (Ishida and Green 2002; Patron et al. 2006; Nosenko et al. 2006), and the gymodiniacean genus *Lepidodinium*, which has a plastid derived from a green alga (Watanabe et al. 1991; Minge et al. 2010).

In addition to permanent plastid replacements, non-photosynthetic dinoflagellates may reacquire photosynthesis through the temporary use of plastids from their prey, so-called kleptochloroplasts (stolen chloroplasts; Schnepf and Elbrächter 1999; Janson 2004). Plastids acquired in this way are either eventually digested or lost because of imperfect distribution to daughter cells following division. This is not a rare phenomenon; it has been shown to occur in several eukaryotic lineages like foraminiferans, ciliates, katablepharids, and even animals (sea slugs). In dinoflagellates, kleptochloroplasts have been found in several lineages, for example, *Dinophysis*/*Phalacroma*, *Amylax*, and *Nusuttodinium*, and in an undescribed member of the Kareniaceae, but details are different in the different lineages. *Nusuttodinium* and the undescribed kareniacean use plastids that they take directly from their prey, cryptomonads, and the haptophyte genus *Phaeocystis*, respectively (Onuma and Horiguchi 2015; Sellers et al. 2014). In *Nusuttodinium aeruginosum*, the prey's nucleus and nucleomorph are retained together with the plastid, but as the dinoflagellate lacks the mechanism to initiate the cryptomonad nucleus' division, this is only passed on to one daughter cell after the dinoflagellate's cell division.

Dinoflagellate daughter cells containing cryptomonad nuclei have large, healthy kleptochloroplasts, but in the ones that lack it, the plastids start to degenerate (Onuma and Horiguchi 2015). *Dinophysis* and *Amylax* also have cryptomonad-derived kleptochloroplasts, but they acquire them indirectly by feeding on another kleptoplastidic organism, the ciliate *Mesodinium rubrum*. However, while *Amylax*, like *Mesodinium*, retains the cryptomonad's nucleus and nucleomorph as well as the plastid (Kim et al. 2014), *Dinophysis* seems to digest the cryptomonad nucleus and nucleomorph and retains only the plastid itself. In spite of this, *Dinophysis* kleptochloroplasts can remain viable for at least 10 weeks, a similar amount of time to what is observed in *Mesodinium rubrum*. One possible reason for this is that the *Dinophysis* nucleus contains plastid-targeted genes that may help keep the plastid active; while some of these genes seem to be remnants of the original peridinin plastid of dinoflagellates, others seem to have been obtained from cryptomonads, haptophytes, and other algae (Wisecaver and Hackett 2010). At least one species of *Dinophysis*, *D. mitra*, contains kleptochloroplasts of haptophyte origin (Koike et al. 2005) that may be obtained by preying on kleptoplastidic ciliates like *Tontonia*, *Laboea*, or *Strombidium* (Nishitani et al. 2012).

Eyespots and Ocelloids

No protist group displays so many eyespot types as dinoflagellates (Hansen et al. 2007). Four types (not including ocelloids; see below) have been distinguished, all situated in the sulcal area close to the flagellar roots where they are likely to be shadowed by the proximal part of the longitudinal flagellum. In many dinoflagellates, like in many photosynthetic heterokonts, eyespots consist of osmiophilic, carotene-containing globules inside the plastid, usually as a single or double layer between the plastid envelope and the outermost thylakoids. In some groups, an elongated vacuole that contains brick-like vesicles is located in front of the eyespot but outside the plastid (e.g., the *Borghiella*/*Baldinia* clade; Hansen et al. 2007; Moestrup et al. 2008). In suessialean dinoflagellates, these brick-like vesicles form multiple layers. Another type of eyespot, found in genera like *Esoptrodinium*, *Jadwigia*, *and Tovellia*, consists of osmiophilic globules not bounded by any membrane, floating free in the cytoplasm. And in dinotoms osmiophilic granules are surrounded by three membranes, a situation that has given rise to the hypothesis that this organelle represents the remnant of the original peridinin-containing plastid (see section on "Evolutionary History"). The detailed structure of the eyespot in other dinoflagellates, for example, in non-photosynthetic species like *Oxyphysis oxytoxoides*, is unknown. In *Protoperidinium* species, numerous large carotenoid-like masses occur throughout the cell periphery prior to cyst formation and may act as a reserve material for the wall or for metabolism.

The ocelloid (ocellus) found in the seven genera of the warnowiaceans is a complex organelle showing extraordinary resemblances to metazoan eyes, but at a subcellular level and without any neurological connection to a brain. It consists of four primary components: a darkly pigmented cup called the retinal body; a lenslike,

refractile hyalosome; iris-like rings; and a transparent, cornea-like layer over the lens. The lens is constructed of secretions of unknown material within endoplasmic reticulum and is surrounded by constricting fibers that have been suggested to change the shape of the lens (Greuet 1978, but experimental proof of this is lacking). The "cornea," a transparent layer covering the lens, is composed of mitochondria that extend into a network in the surrounding cytoplasm (Gavelis et al. 2015). The retinal body consists of a cuplike structure containing very precisely aligned membranes backed by a layer of reddish brown to black pigment droplets (Greuet 1978). This retinal body turns out to be a heavily modified plastid: it contains DNA that encodes plastidial genes and dedifferentiates into a plastid of more standard morphology at the end of interphase. The outer membrane of the retinal body of *Nematodinium* is contiguous with that of peridinin plastids that also exist in this cell, and so appears to be a part of a larger netlike plastid. At least some warnowiaceans (e.g., *Nematodinium*) feed on other dinoflagellates, and because the dinoflagellate dinokaryon polarizes light, it has been suggested that function of the ocellus may be to recognize polarized light (Gavelis et al. 2015).

Pusules

In the motile cell, there are usually two specialized vacuoles that arise from ducts that open at the flagellar bases, in addition to the generalized cell vacuolar system (vacuome). These pusules are particularly large in *Protoperidinium*, where they are differentiated into a sac pusule, which can occupy a third or more of the episome, and a collecting pusule, which resembles a cluster of grapes. Each has evaginations, which can be highly elaborate, running close to the vacuome membrane where exchange presumably takes place. Although they resemble water-regulating vacuoles, they do not behave like them. They are most developed in non-photosynthetic marine species. They may be for excretion, uptake, or both (one for each). They do not participate in phagotrophic ingestion, and large particles are usually absent from them. At the ultrastructural level, a flaky material may coat the surface of one of them.

Luminous Organelles

Marine dinoflagellates in at least 18 genera have been documented as being capable of bioluminescence (Poupin et al. 1999); they account for much of the planktonic bioluminescence in oceans. *Pyrocystis noctiluca* and *Noctiluca scintillans* are particularly important in oceanic tropical and coastal temperate regions, respectively. The luminescence occurs as a brief (0.1 s) blue flash (max 476 nm) when stimulated, usually by mechanical disturbance. Flashes have been seen to emanate from individual cytoplasmic bodies ca. 0.5 μm in diameter distributed mainly in the cortical region of the cell (Johnson et al. 1985; Hastings 1986) as pockets that protrude into the main cell vacuole. These so-called scintillons contain luciferase, the main

enzyme involved in dinoflagellate bioluminescence (Nicolas et al. 1985), and luciferin, a tetrapyrrole ring structurally similar to chlorophyll that acts as the substrate to the light-producing reaction. At physiological pHs, (pH 7–8), luciferase is inactive, and luciferin is bound to a protein. Light generation occurs when the pH in the scintillon is lowered to about pH 6, the luciferin is released, and the luciferase takes its active conformation (Hastings 1996). The triggering mechanism for the whole reaction is most commonly mechanical: shearing pressure deforms the cell's plasma membrane, where mechanoreceptors signal a release of calcium ions into the cytoplasm. This forms an action potential across vacuolar membranes in the cell and causes the opening of proton channels in the membrane that release hydrogen ions into the cytoplasm and into the scintillons. The consequent lowering of the pH in the scintillons triggers the light-producing reaction. Luciferin production probably occurs in plastids (cryptic ones in non-photosynthetic dinoflagellates) from precursors repurposed from heme and chlorophyll production (Janouškovec et al. 2016).

Predation on zooplankton by fish and cephalopods is facilitated by dinoflagellate luminescence (Mensinger and Case 1992; Fleischer and Case 1995). The idea proposed to explain this, the so-called burglar-alarm hypothesis, postulates that shearing stress caused by copepod feeding currents trigger dinoflagellate bioluminescence and that this bioluminescence is then used by visual predators like fish and squid to find their zooplankton prey. This, in the end, benefits the dinoflagellates. An alternative possibility is that bioluminescence may startle predators and discourage their feeding (Buskey and Swift 1983).

Luminescent and nonluminescent strains can occur in the same species, e.g., *Alexandrium tamarensis* and *Noctiluca scintillans*.

Dinoflagellate bioluminescence is controlled by circadian rhythms and only occurs at night (e.g., Knaust et al. 1998)

Skeleton

Internal skeletal elements, siliceous in some species, are known in genera of the actiniscaceans and dicroerismaceans. In *Dicroerisma*, there is a single, branching skeleton in the shape of an inverted Y. In *Actiniscus*, the siliceous internal elements are also paired and are star shaped. Basketlike peripheral skeletons are present in *Achradina* and *Monaster*.

Nucleus

The dinoflagellate nucleus is so different from that of typical eukaryotes that it is usually given its own name, the dinokaryon; in the 1960s, the ultrastructural and biochemical differences between dinokarya and typical eukaryotic nuclei were deemed to be important enough to warrant the establishment of an intermediate kingdom between prokaryotes and eukaryotes, the so-called Mesokaryota (Dodge 1965). This view was subsequently disproved by molecular data.

Dinoflagellate nuclei lack nucleosomes (e.g., Rizzo 1991), and the ratio of basic proteins to DNA in them is much lower than in any other eukaryotes (1:10 in dinoflagellates, as opposed to the equimolar ratios found in other eukaryotes). The main basic components in dinoflagellate nuclei are not histones but other types of basic proteins that interact with DNA: so-called DVNP's (dinoflagellate/viral nucleoproteins) that are otherwise only known from a group of large algal viruses (Gornik et al. 2012) and HLPs (histone-like proteins, Wong et al. 2003), which seem to have entered dinoflagellates in two separate waves of lateral transfer from bacterial sources (Janouškovec et al. 2016). Dinoflagellates also contain very high amounts of DNA per cell: 3,000–215,000 Mbp weighing up to 250 pg in a haploid nucleus (in humans those numbers are 2,900 Mbp DNA/cell and 3 pg in a haploid cell). Chromosomes remain continuously condensed and visible during interphase and mitosis, but whereas syndinians have few chromosomes (four in *Syndinium*, Ris and Kubai 1974), some species may have up to 143 (*Alexandrium fundyense*, Oakley and Dodge 1974).

In the so-called core dinoflagellates, chromosomes appear fibrillar, the 3–6 nm fibrils being packed in a highly ordered state (up to six levels of coiling), consisting of arches and whorls (e.g., Dodge 1966; Spector et al. 1981). A prominent nucleolus is also persistent. In those species investigated, there is an unusual substitution (12–68%) of the base thymine by 5-hydroxymethyluracil (Rae 1976).

All nuclear-encoded messenger RNAs investigated in a wide diversity of members of the dinoflagellate lineage (including *Perkinsus marinus*) have been recently shown to be trans-spliced to a universally conserved 22 base pair fragment that is added to their 5′ end (Zhang et al. 2007; Lidie and Van Dolah 2007). In core dinoflagellates, many highly expressed genes are arranged in tandem arrays, a feature that is very rare in eukaryotes (Bachvaroff and Place 2008).

Mitosis

Dinoflagellate mitosis is also unusual. The nuclear envelope persists during mitosis ("closed"), as it does in many other eukaryotes (Raikov 1994). However, with the exception of *Oxyrrhis marina* and several species of the genus *Amoebophrya* (Triemer 1982; Moon et al. 2015), the mitotic spindle is extranuclear and passes through furrows and tunnels that form in the nucleus at prophase (Dodge 1987 and references therein). With the exception of the centrioles in *Syndinium*, there are no obvious spindle pole bodies other than concentric aggregations of Golgi bodies ("archoplasmic spheres"). Some microtubules contact the nuclear envelope, lining the tunnels at points where the chromosomes also contact. The chromosomes usually have differentiated, dense regions inserted into the envelope.

Cytokinesis

The plane of cell cleavage is typically oblique between anterosinistral and posterodextral moieties, passing through the kinetid. In thecate species, the theca may be

shared by the offspring, with synthesis of the missing components (desmoschisis), or the parent theca may be cast off, each offspring forming a complete new theca (eleutheroschisis).

In photosynthetic forms, the time of division is phased; this is controlled by an endogenous (circadian) mechanism (see below). Division typically occurs near the end of the dark period, but in several species, it is phased at other times (Hastings and Sweeney 1964). Division rates are usually relatively slow, many species dividing only once every 2 or more days. *Amphidinium carterae* can divide twice in 1 day. The non-photosynthetic species *Crypthecodinium cohnii* is the most rapidly reproducing dinoflagellate known, dividing three times per day, although parasites may divide faster during sporogenesis via palintomy.

Life Cycle

Most dinoflagellates appear to be haploid, with post-zygotic meiosis. Clearly established sexual fusion is known for only a few species, but, because of its cryptic nature (gametes grossly resembling regular motile cells, slow fusion, occurring at night in photosynthetic species), it is probably widespread.

Syngamy may involve equal (isogamy) or unequal (anisogamy) motile gametes (see Fig. 7). Both heterothallism (no fusion in clonal strains) and homothallism are known. The product of fusion is a tri- or quadriflagellate planozygote (later biflagellate in some), which may remain motile for hours or days. Eventually a nonmotile resting cyst (hypnospore) is formed. After a varying length of time (see section "Cysts" below), excystment occurs. Meiosis, heralded by a peculiar churning and rotation of the nucleus termed nuclear cyclosis, associated with the pairing of homologous chromosomes, may precede or follow excystment and may be accomplished in two conventional, successive divisions (e.g., *Ceratium cornutum*) or possibly one (*Crypthecodinium cohnii*). In some species, the planozygote that emerges from the cyst may again be tri- or quadriflagellate.

In most dinoflagellates, the motile phase (mastigote) is dominant, but in some, most of their life cycle is spent in a coccoid or other nonmotile form. Those living as intracellular symbionts (e.g., *Symbiodinium)* are photosynthetically and reproductively active in the coccoid state (vegetative cyst: see section "Cysts" below). Some marine planktonic forms, such as *Pyrocystis*, live predominantly as greatly inflated trophic cysts, as do the benthic phases of genera like *Halostylodinium*, *Spiniferodinium*, *Cystodinium*, etc. *Thoracosphaera* and *Pfiesteria* are other genera that can divide in the cyst stage. These coccoid life stages usually lack amphiesmal vesicles, trichocysts, and pusules, as well as flagella, and as a consequence are often difficult to identify as dinoflagellates. A continuous, fibrous wall that may be greatly reduced in the symbionts appears to be homologous with the pellicular layer and cyst wall. In the broadest sense, they represent cysts that are metabolically active rather than dormant. Transient mastigote phases occur in these species; they are suspected to be gametes, although no fusion has been seen.

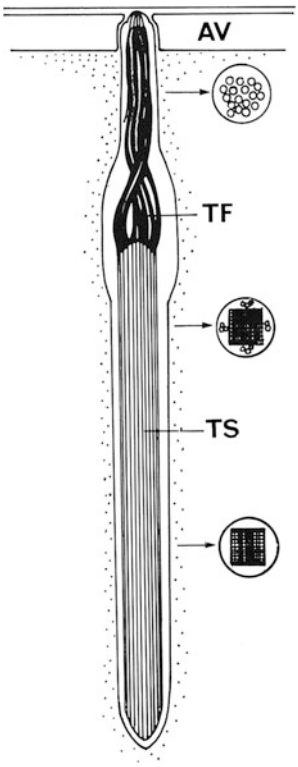

Fig. 7 Longitudinal section of a trichocyst (redrawn from Bouck and Sweeney 1966). *AV* amphiesmal vesicle, *TF* trichocyst fibers, *TS* trichocyst shaft.

Cysts

In dinoflagellates the protozoological term cyst, rather than the approximately equivalent botanical term spore, has been used for nonmotile, continuous walled stages. Fewer than 15% of the living forms are known to form cysts, although the figure is climbing steadily; virtually all fossils appear to be cyst stages; see below. Dale (1983) has reviewed cyst biology, and Fensome et al. 1993 has unified the classification of extant and fossil dinoflagellates.

Cysts can be of several types, according to their roles in the life cycle, and the literature may be confusing because of earlier lack of awareness of this and the lack of standardization of terms. Here, the following are recognized:

1. Resting cyst (resting spore, hypnozygote) –
   A dormant stage, generally resistant to adverse conditions. In several instances (see above), these result from sexual fusion, but it is not known if this applies to most of them. The wall may contain a sporopollenin-like material, additional to cellulose and/or gelatinous material, and may be of several layers. Internally, the contents often shrink (due to loss of water), storage products become polymerized (oils, starch), photosynthetic pigments are gradually reduced, and a large, red-pigmented body is often formed.

2. Temporary cyst (pellicle cyst, ecdysal cyst) –
   In those thecate species with a well-developed pellicular layer (e.g., *Alexandrium* and *Scrippsiella* spp.), the cell may respond to rapid adverse changes by shedding the theca (*ecdysis*), including the outer amphiesmal layers and axonemes, the pellicular layer becoming the cyst wall. In *Pyrophacus* and *Protoperidinium*, this accompanies eleutheroschisis.
3. Trophic cyst (coccoid cells) –
   Nonmotile, usually photosynthetic cells that are metabolically and reproductively active in this phase. Surrounded by a continuous wall homologous with the pellicle (e.g., *Symbiodinium*, *Pyrocystis*, *Spiniferodinium*, *Thoracosphaera*).
4. Digestion cyst –
   This type, in which the organism encysts after feeding, is common in some phagotrophic protist groups but is rare in dinoflagellates. "*Katodinium*" *fungiforme* is an example.

In the first two types, encystment, or the sexual events leading to it, can be triggered by nutrient stress (e.g., nitrogen starvation, the most common experimental method used) or changes in light intensity, photoperiod, or temperature (von Stosch 1964), but other factors are probably also involved. Cyst formation is most commonly observed toward the end of blooms or in the senescent phase of batch cultures.

In many cases, cysts "reflect" the tabulation of the motile cells that gave rise to them by way of ridges or other features like spines, processes, the shape of excystment apertures (archeopyles), etc., that mark the position of thecal boundaries in the motile cells (Fig. 7). This "pseudotabulation" is critical for the taxonomy of fossil taxa.

Excystment will occur after a relatively fixed period at constant temperature. Lower temperature generally prolongs the period. A rapid rise in temperature often triggers excystment. Light may or may not be required. Anaerobic conditions inhibit excystment (see Dale 1983; Pfiester and Anderson 1987 for further details). A residual body, dark brown in color, is often left behind in the empty cyst. It may correspond to an accumulation body or the red body of the cyst (Fig. 8).

Thecal Patterns (Tabulation)

The tabulational patterns formed by the alveolae and the thecal plates contained in them have been used in taxonomy for more than 100 years. Six fundamental types can be recognized (Fig. 9):

1. *Gymnodinoid*. Alveolae are numerous and often hexagonal, the girdle and sulcus being the only clearly distinguishable series. The plates may be too delicate to see or entirely absent. Gymnodinoid tabulations are present in the gymnodiniales and in some members of the distantly related Symbiodiniaceae and Borghiellaceae.

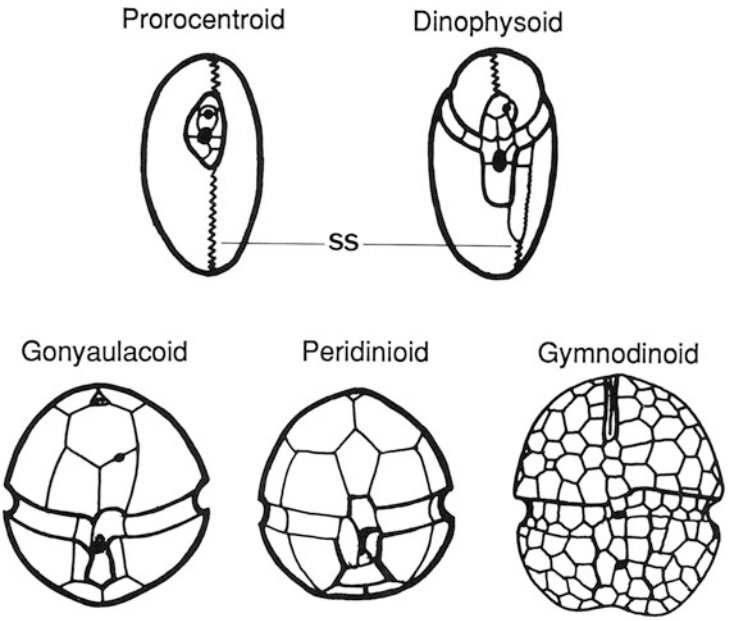

Fig. 8 Basic thecal organizational types (From Fensome et al. 1999)

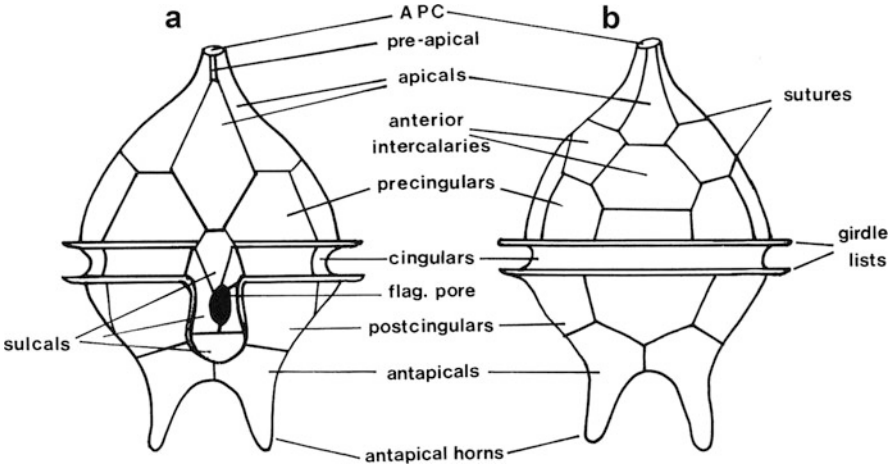

Fig. 9 Thecal plate terminology for a peridinioid or gonyaulacoid taxon. (**a**) ventral view. (**b**) dorsal view

2. *Suessioid*. Amphiesmal vesicles arranged in 6–11 latitudinal series. The number of plates per series, or even the number of series, varies with species. The cingulum is well marked, and it may contain one or two rows of plates. Named after the fossil genus *Suessia*. Extant genera with a suessioid tabulation include

Symbiodinium and *Polarella*, but recent data suggest that fossil Suessiales are not related to *Symbiodinium* and its relatives (Janouškovec et al. 2016).

3. *Peridinioid and Gonyaulacoid*. In these there are five distinct primary latitudinal series termed from apex to antapex/posterior the apicals, precingulars, cingulars (girdle), postcingulars, and antapicals. Plates lying between these series are termed *intercalaries* (anterior or posterior on the epi- or hypotheca, respectively), and those lying within the sulcus are *sulcals*. The midventral epithecal plate often spans both the precingular and apical series. By convention it has been termed the first apical plate (1′). At the apex, an apical pore complex (APC) is often present, consisting of an outer (Po) and inner (Pi) pore plate, and a small pre-apical platelet (Pp) is often present in peridinioids. Apical plates are those that contact the APC. Peridinioid tabulations are defined by a more-or-less symmetrical first apical plate and by the presence of two antapical plates; in gonyaulacoid tabulations, the first apical plate is asymmetrical; and there are two to four fundital plates.
4. *Nannoceratopsioid (fossil only)*. Laterally-flattened cells with a reduced episome. Only cysts are known, and they reflect a sagittal suture dividing the hyposome into right and left halves, like in dinophysoid tabulations. Episomes, however, reflect a gonyaulacoid-peridinioid type of tabulation.
5. *Dinophysoid*. The theca is fundamentally divisible into two halves by a vertical sagittal suture, but a girdle and sulcus are "superimposed" on it, separating an epitheca and hypotheca, and there are small plates on the ventral surface of the epitheca, hypotheca, and in the sulcus around the single large flagellar pore. A simple apical pore is located on the ventral side of the epitheca. The arrangement of the plates varies little within the group, with 18 or 19 being the usual number. Lists (ridges or extensions of the edge of thecal plates) along the girdle and sulcus edges may be prominent and developed to an extraordinary degree in some genera (e.g., *Ornithocercus*, *Histioneis*, and *Citharistes)*, producing bizarre forms, some forming a "phaeosome chamber" from the girdle lists in which extracellular coccoid cyanobacteria occur.
6. *Prorocentroid*. The theca is composed of two large plates, the valves, which join along a toothed margin, the sagittal suture (Figs. 2 and 6). An apical cluster of small platelets of regular arrangement, 8–12 in number (nomenclature in Hoppenrath et al. 2013), surrounds the two pores from which the desmokont flagella arise. The periflagellar platelets lie principally in an excavation of the right valve. A small spine often arises from the periflagellar plate designated as "a" (Taylor 1980).

The plates in each latitudinal series are numbered from the cell's left to right, beginning with the plate closest to the midventral position. This convention, the "Kofoid System," is currently in universal use (Fig. 10). It also uses a notation to designate the series, using primes to indicate the apical (′), precingular (″), postcingular (‴), and antapical (⁗) plates, both when labelling plates on figures and when producing a plate formula. The latter is a listing of the total plates in each series for a species or genus. Thus *Gonyaulax* is represented by Po, Pi, 3′, 2a, 6″, 6C + t, 6S, 6‴, 1p, 1⁗, and *Peridinium* by OP, 4′, 3a, 7″, 5C + t, 6S, 5‴, 2⁗. Cingulars (C),

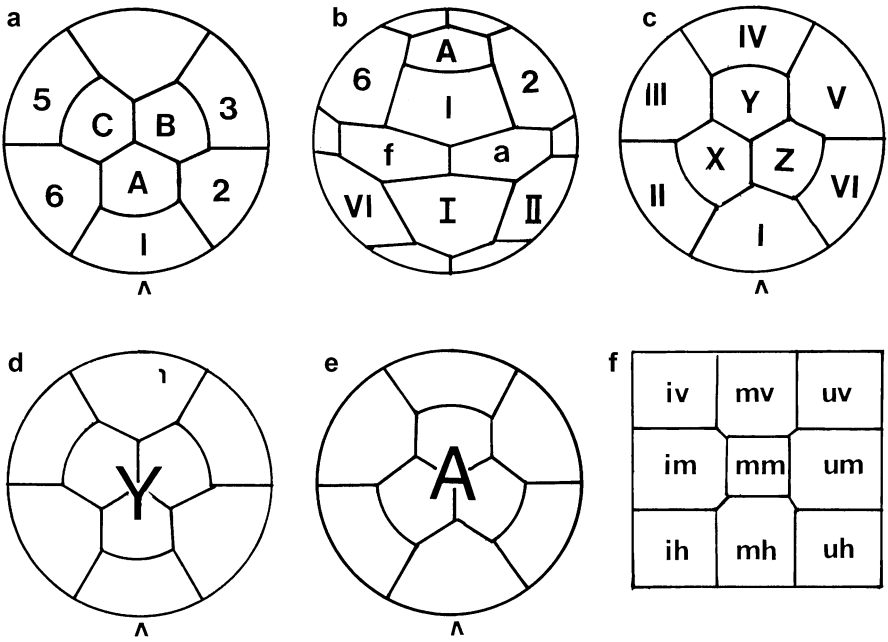

Fig. 10 Model and plate designation used in the Taylor homology system (from Taylor 1980, with modifications by Evitt 1985). (**a**) Polar view; (**b**) ventral view; (**c**) antapical polar view; (**d**) the "Y" arrangement of polar plates relative to the flagellar insertion; (**e**) the "A" arrangement; (**f**) designations for subdivision of a primary plate area (maximum subdivision) using Evitt's modification; *i* initialis; *u* ulter; *m* medialis; *v* vorner; *h* hinter (the latter selected because they are not letters used for whole plates in either system)

sulcals (S), anterior intercalaries (a), and posterior intercalaries (p) are designated by letters. The *t* plate is a small transitional plate between the cingulars and the sulcals at the proximal end of the girdle in peridinioids and at the distal end in gonyaulacoids. Other distinctions between gonyaulacoids and peridinioids include the common occurrence of 6″, 6‴, 1p, and 1⁗ in the former and 2–3a, 7″, 5‴, and 2⁗ in the latter (exceptions being due to apparent suture loss or plate subdivisions); intercalary growth from the overlapping plate margin only in gonyaulacoids versus both sides of a suture; and basic symmetry: the former showing evident torsion, the latter tending to bilateral symmetry.

Although the Kofoid System is usually easy to apply, ambiguities in the attribution of some plates to one series or another can cause problems, resolved by following consensus. This, combined with the mechanical, consecutive numbering, renders the system poor for intergeneric comparisons. Taylor (1980) has introduced a basic model (Figs. 9 and 10) elaborated on by Evitt (1985), consisting of three epithecal polar (A–C), six pre-equatorial (1–6), six equatorial (a–f), six post-equatorial (I–VI), and three hypothecal polar (X–Z) sectors, which represent hypothetical primary plates from which homologous plates can be recognized by

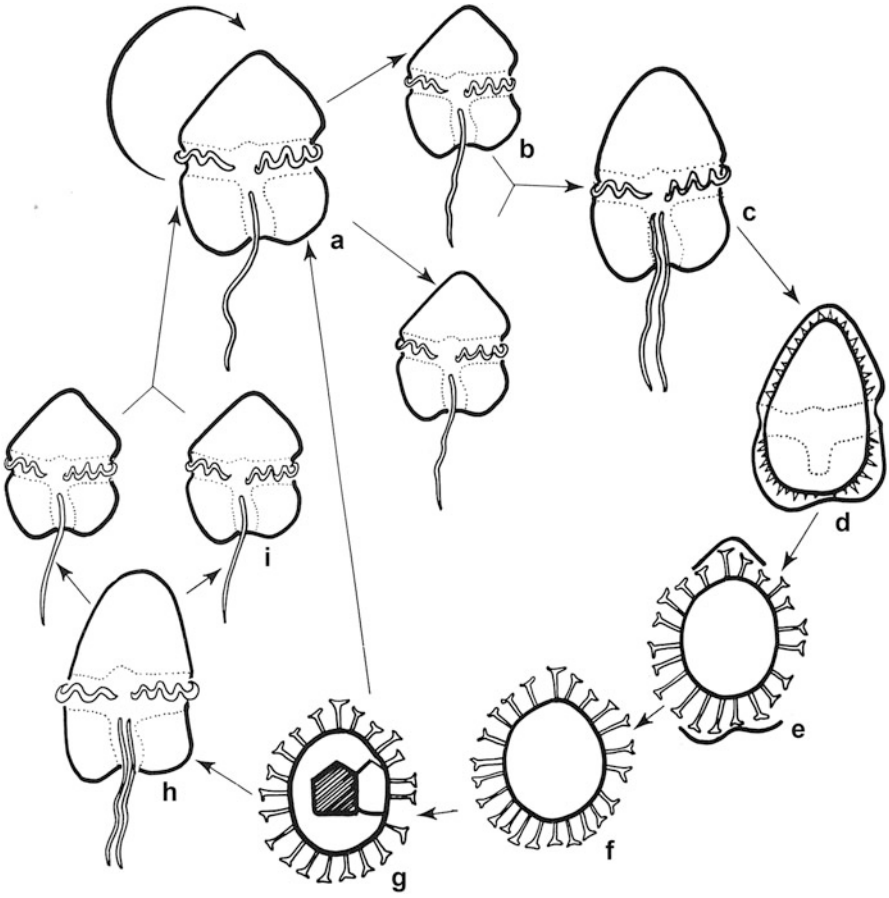

Fig. 11 Common dinoflagellate life cycle (modified from Dale 1983). (**a**) Asexually reproducing motile cell (mastigote); (**b**) gametes (can be iso- or anisogametes); (**c**) planozygote; (**d**) hypnocyst (resting cyst) formation within the theca; (**e**) theca discarded (cysts may be smooth, rigid or spiny); (**f**) dormancy; (**g**) excystment through the archaeopyle; (**h**) meiocytic planozygote; (**i**) meiotic division (**h** and **i** may take place in the cyst and meiosis may involve one or two divisions). Not shown: temporary cysts may be asexually produced from asexually reproducing motile cells (**a**). Pyrocystis and other photosynthetically active amastigotes may be in sexually or asexually produced, pellicle-surrounded "cysts"

assuming subdivisions, suture losses, and plate size and position changes. The first step is to normalize the cell to a sphere, removing obvious plate distortions. Then the primary plates and their sutures are determined by studying the relationships of the plates to each other (see examples given by Evitt 1985).

Cyst walls often exhibit patterns of ridges, spines, or other surface ornamentation, which correspond to the tabulation of the parent theca, although some sutures are often not reflected on the cyst. The pattern discernable on the cyst wall is termed paratabulation and is used extensively in fossil cyst taxonomy (Figs. 11 and 12).

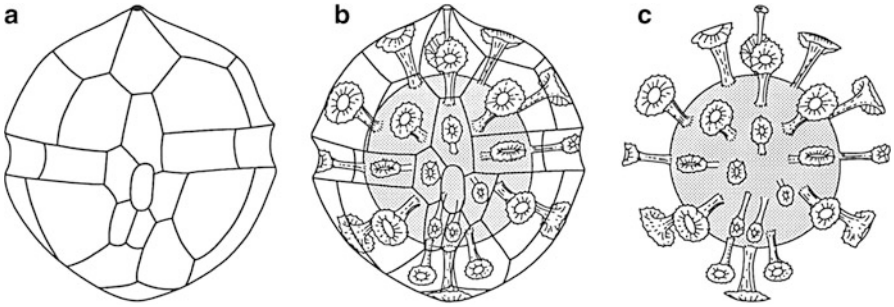

Fig. 12 Development of the fossil cyst species *Hystrichosphaeridium tubiferum* from a hypothetical parent theca. Central body of cyst is shaded (Adapted from Evitt (1985), Fensome et al. (1993). Copyright Micropaleontology Press)

Fossils

If one disregards acritarchs (microfossils with ambiguous morphologies that may or may not be of dinoflagellate origin), a large majority of dinoflagellate fossils consist of cyst stages of forms with gonyaulacoid or peridinoid tabulations (Fensome et al. 1999). Dinoflagellate fossils of other types are rare; they include, for example, suessialean forms, forms with possible dinophysoid affinities (*Nannoceratopsis*), a few Cenozoic gymnodinoid cysts, and fossil chemical traces like dinosterols. In a few cases, some otherwise ambiguous cyst morphologies have been shown to be of dinoflagellate origin through the study of cyst stages of extant forms.

About 15% of extant dinoflagellates produce fossilizable cysts (Head 1996). This does not mean that that was the case in the geologic past, but it does seem to be clear that the fossil record of dinoflagellates is highly incomplete. Nevertheless, certain patterns regarding the evolutionary history of the group can still be recognized.

Fossil dinoflagellates are controversial or absent in strata prior to the early Mesozoic, but quantities of dinosteranes (derivatives of dinosterols, chemical compounds as of yet associated almost exclusively with dinoflagellates) correlate well with some acritarch species' abundance in the Paleozoic (Moldowan and Talyzina 1998). Nevertheless, pre-Mesozoic dinosteranes are unlikely to have originated from dinoflagellates: in extant dinoflagellates, dinosterol is only produced by thecate dinoflagellates and a few of their closest athecate relatives (Janouškovec et al. 2016), and the earliest confirmed (thecate) dinoflagellate fossil is from the mid-Triassic (Fensome et al. 1999). Dinosteranes in early Triassic sediments could be derived from athecate relatives of the thecate clade, but it is unlikely that dinosterol-producing dinoflagellates were present earlier than that. After the mid-Triassic, species diversity increases steadily until the early Cenozoic, and then it declines toward the present day (MacRae et al. 1996). By the mid-Jurassic, practically all major morphological variations of peridinioid and gonyaulacoid forms were already present, and late innovations are very minor. *Nannoceratopsis*, a striking "missing link" between peridinioids and dinophysoids, lived also in the

early Jurassic, as did forms with a suessialean tabulation (already there since the mid-Triassic). Paleontological evidence points to an evolutionary radiation of thecate, cyst-forming dinoflagellates in the late Triassic/early Jurassic that involved early experimentation, stabilization later, and the early presence of "missing links." Whether this evolutionary radiation involved fossil-poor gymnodinoid forms cannot be determined by paleontological data alone.

Maintenance and Cultivation

Dinoflagellates are usually grown in enriched, filtered, and sterilized marine or freshwater. The methods and the media used have been described in detail by Guillard and Keller (1984). The most commonly used media for photosynthetic marine forms are dilutions of Guillard's *f* medium or modifications of Provasoli's *ES*, with Chu's no. 10 for freshwater species. Totally artificial media rarely support vigorous growth, and agar is not suitable for most species. Dinoflagellates are inhibited by strong agitation and prefer light/dark cycles (typically 14:10) to continuous illumination. Many are difficult or impossible to grow axenically (bacteria-free) at present.

Phagotrophic non-photosynthetic species are usually fed smaller, photosynthetic flagellates, with precautions to avoid overgrowth by the latter. Organism-free organic media have been developed for *Oxyrrhis marina* and *Crypthecodinium cohnii*.

Evolutionary History

Molecular evidence shows that the closest relatives of dinoflagellates are apicomplexans and ciliates. These three eukaryotic clades, together with the paraphyletic group that includes their ancestors, the protalveolates (perkinsids, *Colponema*, etc.), form the so-called Alveolates (Cavalier-Smith 1991), one of the best-supported groupings that have emerged from the analysis of molecular phylogenetic data in eukaryotes (e.g., Fast et al. 2002; Cavalier-Smith and Chao 2004 and many others). Morphological data also strongly supports this clade (e.g., Taylor 2004). The closest relatives of alveolates are the stramenopiles (also called heterokonts), the grouping that contains oomycetes, labyrinthulids, opalinids, chrysophytes, diatoms, and brown algae, among others. The relationship between alveolates and stramenopiles is also very well supported with molecular data (e.g., Fast et al. 2001; Harper and Keeling 2003; Hackett et al. 2004a).

The question of whether dinoflagellates evolved from photosynthetic ancestors was answered by the discovery of *Chromera*, a photosynthetic endosymbiont of corals that in phylogenetic trees branches at the base of the apicomplexans (Moore et al. 2008) and whose plastid genes strongly resemble those of the apicomplexans' apicoplast and the peridinin plastids of dinoflagellates (Janouškovec et al. 2010). *Chromera* is only one member of a clade that contains several photosynthetic and many non-photosynthetic members, the so-called chrompodellids, and by comparing

the patterns of the presence, absence, and localization of metabolic pathways involving plastidial elements in chrompodellids, apicomplexans, and dinoflagellates, it was possible to explain the presence of photosynthetic plastids in some members of these groups and not others (Janouškovec et al. 2015). Some non-photosynthetic members of the dinoflagellate lineage have now been shown to contain either plastid-targeted genes or major plastid-associated biosynthetic pathways, e.g., the perkinsozoan *Perkinsus marinus* (Stelter et al. 2007; Matsuzaki et al. 2008; review in Fernández Robledo et al. 2011), *Oxyrrhis marina* (Slamovits and Keeling 2008), *Noctiluca scintillans* (Janouškovec et al. 2016), and *Crypthecodinium cohnii* (Sánchez-Puerta et al. 2007), but in the syndinians, plastids appear to be completely lost (Gornik et al. 2015).

Initially dinoflagellate phylogenetic trees had backbones that were poorly resolved, and so it was difficult to determine phylogenetic relationships of large groups to each other based on this kind of data alone (Daugbjerg et al. 2000; Saldarriaga et al. 2004; Orr et al. 2012); the main value of molecular phylogenetic data was to clarify in-group phylogenies, for example, within groups like calciodinellids, pfiesteriaceans, polykrikoids, or the genera *Symbiodinium* or *Alexandrium*, as well as to underline the differences between groupings of gymnodinoids. More recent phylogenetic studies based on large concatenations of protein sequences (101 genes in Janouškovec et al. 2016) have started to produce phylogenetic trees with better resolved backbones. They suggest that *Oxyrrhis marina* is the earliest branch of the dinoflagellates, followed by the syndinians; whether the Syndiniales are a monophyletic or a paraphyletic group is still unclear. The next group to branch off are the Noctilucales, and the Gymnodiniales build a paraphyletic group that gave rise to thecate dinoflagellates, which are monophyletic. Only a few gymnodinialean lineages are as of yet present in large protein-based trees, but it looks like *Amphidinium* makes the earliest branch after the Noctilucales, followed by the Kareniaceae, the *Gymnodinium* group of families (a single clade that includes *Gymnodinium*, *Togula*, and *Polykrikos*), and *Akashiwo*, the sister group to thecates. The branching order of the thecate groups is not yet clear, but the group includes the Symbiodiniaceae; it looks like the suessioid and gymnodinoid tabulations of the Symbiodiniaceae and Borghiellaceae represent secondary losses of theca (Janouškovec et al. 2016).

Morphological data and palaeontological "missing links" do suggest a close relationship between the four thecate dinoflagellate groups: one theory (unsupported as of yet by molecular data) suggests that the more-or-less symmetric peridinioids arose from gymnodinoids and constitute a paraphyletic grouping that gave rise certainly to the (much more asymmetric) gonyaulacoids, as well as to the *Symbiodinium* group and the dinophysioids (Taylor 2004). The fossil genus *Nannoceratopsis* is a morphological intermediate between peridinioids and dinophysioids (Fensome et al. 1993). The sixth thecate group, the prorocentroids, may have originated from dinophysioid ancestors (Taylor 1980).

A recent study using large phylogenies has suggested that dinoflagellates are primarily a marine group and that transitions to freshwater environments have only happened in a small fraction of the marine lineages (Logares et al. 2007).

Classification

Dinoflagellates have been studied and classified by botanists, zoologists, and paleontologists, and this has resulted in differing taxonomic practices and dual (or even triple) classification schemes. Fensome et al. (1993) unified dinoflagellate classification, and their system builds the scaffolding of the classification system that is presented below. One recent (and very welcome) trend has been the reinvestigation of the type species of large, polyphyletic genera of gymnodinoid dinoflagellates like *Gymnodinium*, *Gyrodinium*, *Amphidinium*, etc., with both ultrastructural and molecular methods (e.g., Daugbjerg et al. 2000; Hansen and Daugbjerg 2004; Flø-Jørgensen et al. 2004). This has enabled a more phylogenetically accurate circumscription of those large genera and has caused a flood of description of new gymnodinoid genera that are not particularly closely related to those types (e.g., *Karenia*, *Karlodinium*, *Takayama*, *Togula*, *Testudodinium*, *Prosoaulax*, *Apicoporus*, *Tovellia*, *Borghiella*, *Baldinia*, *Jadwigia*, etc.). It should be noted, however, that *Gymnodinium*, *Gyrodinium*, *Amphidinium*, etc., are formally still polyphyletic; they contain many species that have not been reinvestigated recently or that have not yet been given new taxonomic placements. Recent papers have used the terms sensu lato and sensu stricto to distinguish between the polyphyletic and the newly defined versions of these genera. In the case of *Gymnodinium*, even the "sensu stricto" version of the genus is still paraphyletic; it has been shown that entire families of dinoflagellates (Polykrikaceae, Warnowiaceae, Actiniscaceae) are descended from it (Hoppenrath and Leander 2007); the corresponding taxonomic changes have not yet been made. In this work, as in much of the primary literature, when there is reason to belive that a species is misclassified into a certain genus, that generic name is given inside apostrophes (e.g., "*Amphidinium*" *longum*).

The classification presented below includes many temporary names and unnamed clades, something that reflects the instability of dinoflagellate classification at the moment. For a more formal classification of the group, see Fensome et al. 1993.

Annex

An informal, annotated classification of living dinoflagellate genera based primarily on molecular data, but using Fensome et al.'s (1993) classification when sequencing data is not available. Note that dinoflagellate classification is currently very unstable, mostly because phylogenies based on small subunit ribosomal genes lack support in many crucial branches.

Perkinsids: Apparently paraphyletic ancestral group to the dinoflagellates. Motile stages have a conoid, micronemes, and rhoptries. External mitotic spindle. Trans-spliced leaders in RNAs from nuclear genes (Zhang et al. 2007), transversal flagellum present in the motile stage of *Parvilucifera prorocentri* (Leander and Hoppenrath 2008). Ancestrally photosynthetic. Inclusion of *Psammosa* in the group seems to render perkinsids paraphyletic, but confirmation of this needs further study (Okamoto et al. 2012).

Perkinsus, *Parvilucifera*, *Psammosa*, *Xcellia*, *Gadixcellia*, *Rastrimonas*?

Dinoflagellates: Eukaryotes lacking nucleosomes and in which histones have been replaced to a large degree by dinoflagellate/viral nucleoproteins (DVNPs); DNA content much higher than in other eukaryotes, chromosomes condensed throughout the life cycle. Ancestrally photosynthetic, with dinokont flagellation (one flagellum takes a transversal orientation), added trans-spliced leaders to nuclear transcripts (Zhang et al. 2007), and an external mitotic spindle (but reversions back to an internal one exist in *Oxyrrhis* and in some species of *Amoebophrya*, Moon et al. 2015).

1. Oxyrrhids: Free-living dinoflagellates with an internal mitotic spindle. Chromosomes continuously condensed, but lacking the fibrillar appearance of core dinoflagellate chromosomes. Molecular data suggests that this monotypic group may be drastically underclassified (Lowe et al. 2005).

Oxyrrhis

2. Syndinians: Parasitic dinoflagellates with at least two life cycle stages: a plasmodial (multinucleate) trophont, and motile, dinokont stages. At least one species has lost all traces of a plastid (*Hematodinium* sp., Gornik et al. 2015); all other described ones are non-photosynthetic. Syndinians may be paraphyletic, but the issue needs more research.

2.1. Ellobiopsids: Trophonts are plasmodial ectoparasites of crustacean zooplankton attached to the host by a nutrient-absorbing rhizoid. Motile stages appear to have dinokont flagella, but this has not been studied in detail. Not always considered to be dinoflagellates; tentatively treated as such here in the absence of nuclear data because of the plasmodial nature of the vegetative stages, because of the apparently dinokont condition of the motile stages, and because molecular data puts the genus *Thalassomyces* within the alveolates with good support, where it weakly clusters with dinoflagellates (Silberman et al. 2004).

Ellobiopsis, *Thalassomyces*, *Parallobiopsis*, *Ellobiocystis*, *Rhizellobiopsis*

2.2. Eduboscquellids and other group 1 alveolates: Most of the members of this group are known only as environmental molecular sequences from the picoplankton of virtually all the world's oceans (de Vargas et al. 2015). Recent data has shown that at least one member of this clade is the genus *Eduboscquella*, a syndinian characterized by a trophont that only becomes multinucleate (i.e., plasmodial) late in its development (as *Duboscquella* in Harada et al. 2007, nomenclatural change in Coats et al. 2012). The fish-egg parasite *Ichthyodinium* also seems to be a member of this group (Skovgaard et al. 2009). Whether the environmental sequences obtained correspond to free-living organisms or to the motile stages of parasites is unknown at present.

Ichthyodinium, *Eduboscquella*, *Dogelodinium*, *Keppenodinium*, symbionts/parasites of radiolarians and phaeodarians (Dolven et al. 2007), and many undescribed species with picoplanktonic life stages in both aerobic and anaerobic environments (Takishita et al. 2007).

2.3. Syndinids and other group 2 alveolates: Another clade whose members are known mostly as environmental sequences from marine picoplankton. A riboclade at the moment, morphological synapomorphies for the group have not been discovered. In molecular trees, there seem to be two distinct groups that correspond to families; a third family exists for which no molecular data has been obtained. Syndinids can be either intracellular or extracellular parasites of copepods, appendicularians, crabs, radiolarians, or other dinoflagellates.

2.3.1. Syndiniaceae: Syndinids in which the trophont consists of a plasmodium with no fixed shape and no internal cavities.

Syndinium, *Hematodinium*, *Merodinium*, *Solenodinium*, *Trypanodinium*

2.3.2. Amoebophryaceae: Syndinids with a wormlike multiflagellated swimming stage, the vermiform.

Amoebophrya

2.3.3. Sphaeriparaceae: Syndinids in which the plasmodial trophont is organized into two segments separated by a sharp constriction, forming an anterior, episome-like region, and a posterior basal disc. Parasitic on appendicularians and radiolarians. No molecular data is available for members of this family.

Atlanticellodinium

2.3.4. Syndinians incertae sedis: *Atelodinium*, *Coccidinium*

3. Core dinoflagellates: Dinoflagellates in which chromosomes are fibrillar in appearance. Mostly free-living, but a few parasitic forms are also known.

3.1. Noctilucales: Dinoflagellates in which trophonts are large and inflated by vacuoles. Only the gametes have a dinokont flagellation and the fibrillar chromosomes that are typical for core dinoflagellates.

Noctiluca, *Kofoidinium*, *Pomatodinium*, *Spatulodinium*, *Leptodiscus*, *Abedinium*, *Cachonodinium*, *Craspedotella*, *Cymbodinium*, *Petalodinium*, *Scaphodinium*

3.2. Gymnodiniales: Paraphyletic group of core dinoflagellates with numerous amphiesmal vesicles arranged non-serially (gymnodinoid alveolar arrangement). Amphiesmal vesicles do not contain thecal plates. Several genera of

this group (e.g., *Gymnodinium*, *Gyrodinium*, *Amphidinium*, *Katodinium*, *Woloszynskia*, *Cochlodinium*) are large and polyphyletic as defined traditionally and are in the process of being reclassified; the classification below only refers to those genera in sensu stricto.

3.2.1. Amphidiniaceans: Benthic or endosymbiotic dinoflagellates with small triangular- or crescent-shaped epicones deflected to the left. Cells dorsoventrally flattened may or may not have chloroplasts.

Amphidinium

3.2.2. Kareniaceans, the "haptophore" lineage: Dinoflagellates with haptophyte-derived plastids and kleptochloroplasts.

Karlodinium, *Karenia*, *Takayama*, *Brachydinium*, *Asterodinium*, *Microceratium*, and the Ross Sea dinoflagellate, an as yet unnamed species from Antarctic ice with haptophyte-derived kleptochloroplasts. *Apicoporus* is related to this clade and may have plastids of very variable sizes, some being not much more than pigmented granules (Sparmann et al. 2008; some cells are entirely unpigmented). These are thought to be peridinin plastids, but no molecular data exists on this.

3.2.3. The *Gyrodinium* s.s. clade: Gymnodinialeans with surface ridges and an elliptical, bisected apical groove. Vesicular chambers around the nucleus. In many species of *Gyrodinium*, there is a tough nuclear capsule either outside of the nuclear envelope or between its two membranes.

Gyrodinium s.s.

3.2.4. Torodiniales: Gymnodinoids in which the episome is much larger than the hyposome and has a hat- or bill-like apical projection. Cells striated longitudinally, vesicular chambers around the nucleus.

3.2.4.1. Kapelodiniaceans: Non-photosynthetic torodiniales with a cap-like apical projection and three rows of vesicles under the rim of the cap.

Kapelodinium

3.2.4.2. Torodiniaceans: Photosynthetic torodiniales with a bill-like apical projection on top of which lies a structure shaped like a counterclockwise inward spiral.

Torodinium

3.2.5. The *Gymnodinium* family group: Molecularly defined grouping of gymnodinoids; many groups have a horseshoe-shaped apical groove running

in an anticlockwise direction and vesicular chambers around the nucleus. Originally conceived as the genus *Gymnodinium* sensu stricto, it later turned out that several families of naked dinoflagellates are contained in the group.

3.2.5.1. Gymnodiniaceans: Paraphyletic family, only definable in a negative way: naked dinoflagellates with no internal skeletons, surface ridges, nematocysts, or ocelli. As defined here, gymnodiniaceans have given rise to polykrikaceans, warnowiaceans, and actiniscaceans.

Gymnodinium s.s., *Paragymnodinium*, *Gyrodiniellum*, *Levanderina*, *Barrufeta*, *Gymnoxanthella*, *Dissodinium*, *Chytriodinium*, *Lepidodinium*, *SpiniferodiniumNusuttodinium*, *Pellucidodinium*, *Pheopolykrikos*, *Togula*, *Syltodinium*/"*Gyrodinium*" *undulans*, "*Cochlodinium*" *polykrikoides*/"*Cochlodinium*" *fulvescens*

3.2.5.2. Polykrikaceans: Pseudocolonial dinoflagellates with half (or a quarter) as many nuclei as zooids. They have the ability to dissociate into pseudocolonies with fewer zooids and just one nucleus. Nematocyst complexes are present. The genus *Pheopolykrikos* is also pseudocolonial (same number of zooids and nuclei), but it is not related to *Polykrikos* in molecular trees (Hoppenrath and Leander 2007).

Polykrikos

3.2.5.3. Warnowiaceans: Dinoflagellates with ocelli, i.e., elaborate light-receiving organelles. Nematocysts also commonly present.

Warnowia, *Erythropsidinium*, *Greuetodinium*, *Nematodinium*, *Nematopsides*, *Proterythropsis*, *Protopsis*

3.2.5.4. Actiniscaceans: Gymnodinialeans with an internal skeleton.

Actiniscus, *Diaster*, *Dicroerisma*

3.2.5.5. Ptychodiscaceans: Naked dinoflagellates in which the pellicle is strongly developed and is the principal structural element in the amphiesma of the motile cell. Few ultrastructural studies, for example, of the nucleus. Probably polyphyletic: *Ceratoperidinium* branches close to the *Gymnodinium* family group in molecular trees, but it is unclear whether the other ptychodiscaceans are related to it.

Tovellia, *Jadwigia*, *Esoptrodinium*, *Opisthoaulax*

3.2.6. Haplozoaceans: Ribbonlike, multicellular dinoflagellates parasitic in appendicularians and polychaetes.

Haplozoon

– Gymnodiniales incertae sedis:
  (a) Genera with uncertain positions in molecular-based phylogenetc trees or whose familiar relationships are unclear: *Akashiwo*, *Ankistrodinium*, *Bispinodinium*, *Moestrupia*, *Testudodinium*. In addition "*Cochlodinium*" *convolutum*/"*Gyrodinium*" *falcatum* makes clades in molecular trees that may represent an undescribed genus.
  (b) Putatively polyphyletic genera with understudied type species: *Cochlodinium*, *Katodinium*, *Woloszynskia*
  (c) Gymnodiniales for which no molecular data exist: *Bernardinium*, *Crepidoodinium*, *Filodinium*, *Gynogonadinium*, *Pavillardia*, *Pyramidodinium*, *Schizochytriodinium*

3.3. Thecates: Dinoflagellates with cellulosic plates inside the alveolae. Primarily with alveolae in a pattern of five or six latitudinal plate series, but these increase in the suessiales and decrease in dinophysiales and prorocentrales.

3.3.1. Gonyaulacales: Thecates in which the first apical plate is asymmetrical and in which there are two to four (usually three) fundital plates (Fig. 10)

3.3.1.1. Cladopyxineans: Gonyaulacales with a partiform tabulation pattern, that is, the first antapical homologue ("Y" plate) contacts the distalmost postcingular plate and in which the posterior sulcal homologue ("Z") is within the sulcus and extends further to the anterior than the posterior intercalary homologue ("X"), thus contacting the first postcingular homologue (Fig. 10). Molecular data are not available for the group.

Cladopyxis, *Acanthodinium*, *Palaeophalacroma*, *Sinodinium*

3.3.1.2. Gonyaulacineans: Gonyaulacales with a sexiform tabulation pattern (Fig. 10), that is, the first antapical homologue ("Y" plate) contacts the distalmost postcingular plate and in which the posterior intercalary homologue ("X") extends further to the anterior than the posterior sulcal homologue ("Z").

3.3.1.2.1. Gonyaulacaceans: Gonyaulacineans with six precingular plates in which the sulcus is more-or-less midventral (may be straight, oblique, or sigmoideal). The antapical outline is more-or-less symmetrical, no dorsoventral compression.

Protoceratium, *Lingulodinium*, *Gonyaulax*, *Acanthogonyaulax*, *Amylax*, *Spiraulax*, *Ataxiodinium*, *Bitectatodinium*, *Halostylodinium*, *Impagidinium*, *Pentadinium*, *Schuettiella*

3.3.1.2.2. Ceratocoryaceans: Gonyaulacineans with five precingular plates and a midventral, L-type sulcus. There is a strong dextral torsion.

Ceratocorys

3.3.1.3. Ceratiineans: Gonyaulacales with at least three horns and in which the first antapical plate ("Y") contacts six or seven adjacent plates including the distalmost postcingular.

Ceratium, *Tripos*

3.3.1.4. "Goniodomineans": Gonyaulacales with a quinqueform tabulation pattern, that is, the first antapical homologue ("Y" plate) does not contact the distalmost postcingular plate. Plate growth occurs only at overlapping plate margins. Note: because of multiple taxonomic and nomenclatural problems (Kretschmann et al. 2015), the generic name *Goniodoma* has been replaced by *Pyrrhotriadinium*. Suprageneric taxon names based on *Goniodoma* (e.g., Goniodomineans, Goniodomaceans, etc.) have not yet followed suit and are given here in quotation marks.

3.3.1.4.1. "Goniodomaceans": "Goniodomineans" in which the principal life-cycle stage is a motile thecate cell.

3.3.1.4.1.1. "Goniodomoideans": "Goniodomaceans" in which the posterior sulcal homologue ("Z") is external to the sulcus and cells are not anteroposteriorly compressed. Dinosporin cysts. Molecular data are not available for the group.

Pyrrhotriadinium, *Pachydinium*

3.3.1.4.1.2. Gambierdiscoideans: "Goniodomaceans" in which the posterior sulcal homologue ("Z") is external to the sulcus and cells anteroposteriorly compressed. No ventral pore.

Gambierdiscus, *Fukuyoa*, *Coolia*, *Ostreopsis*

3.3.1.4.1.3. Helgolandinioideans: "Goniodomaceans" with either of the following characters: tabulation has more than the typical number of plates in at least two plate series or the presence of a smooth cellulosic cyst in the life cycle.

Helgolandinium, *Alexandrium*, *Fragilidium*, *Pyrophacus*

3.3.1.4.1.4. Pyrodinioideans: "Goniodomaceans" in which the posterior sulcal homologue ("Z") and right sulcal homologue are within the sulcus.

Pyrodinium

3.3.1.4.2. Pyrocystaceans: "Goniodomineans" in which the principal life cycle stage is a nonmotile vegetative cyst.

Pyrocystis

3.3.1.5. Gonyaulacales incertae sedis: *Adenoides*, *Heterodinium*, *Crypthecodinium*, *Centrodinium*, *Dolichodinium*, *Goniodinium*, *Peridiniella*, *Planodinium*, *Thecadiniopsis*, *Thecadinium*, *Pseudothecadinium*, *Stylodinium*, *Pseudadenoides*

3.3.2. Dinophysiales: Dinoflagellates with a sulcus, a cingulum, and a sagittal suture that extends the entire length of the cell

3.3.2.1. Dinophysiaceans: Dinophysiales in which the motile cell is never more than three times as long as it is broad. Ventral pore on the ventral episome, and flagellar pore immediately posterior to the cingulum.

Dinophysis, *Phalacroma*, *Citharistes*, *Dinofurcula*, *Latifascia*, *Histioneis*, *Histiophysis*, *Metadinophysis*, *Metaphalacroma*, *Ornithocercus*, *Pseudophalacroma*, *Sinophysis*, *Thaumatodinium*, *Oxyphysis*

3.3.2.2. Amphisoleniaceans: Dinophysiales in which the motile cell is more than four times as long as it is wide. The ventral pore is on the ventral episome, and the flagellar pore is significantly posterior to the cingulum.

Amphisolenia, *Triposolenia*

3.3.3. Prorocentrales: Dinoflagellates with no sulcus or cingulum, apically inserted flagella.

Prorocentrum, *Mesoporos*

3.3.4. The *Symbiodinium* order ("Symbiodiniales," once the taxon is described formally): *Symbiodinium* and several fossil genera have motile stages with seven latitudinal series of amphiesmal vesicles, i.e., a suessioid tabulation, and this feature was used in the past to define the order Suessiales. Nevertheless, the fossil genus *Suessia* has morphological features that distinguish it from extant Symbiodiniaceae (and Borghiellaceae), and is now thought that the two groups are not related (Janouškovec et al. 2016). The term Suessiales should be used for the group that includes *Suessia* and its fossil relatives, not *Symbiodinium*. Several dinoflagellates with a typically gymnodinoid tabulation group strongly with *Symbiodinium* in molecular trees, there is obviously a strong trend within the group to

increase the number of alveolae and reduce the theca. Eyespots in members of this group are associated with one or more rows of brick-like vesicles.

3.3.4.1. Borghiellaceans: Eyespot consists of rows of globules arranged in a single layer within the chloroplast, and a large, narrow vesicle containing a single layer of translucent bricklike structures.

Borghiella, *Baldinia*, "*Woloszynskia*" *pesheri*

3.3.4.2. Symbiodinaceans: Eyespot contains many layers of brick-like structures. No globules inside a chloroplast.

Symbiodinium, *Polarella*, *Protodinium*, *Prosoaulax*, *Pelagodinium*, *Biecheleria*, *Biecheleriopsis*, *Piscinoodinium*, *Haidadinium*, *Ansanella*, *Asulcocephalium*, *Leiocephalium*, "*Gymnodinium*" *natalense*, "*Gymnodinium*" *linucheae*, "*Katodinium*" *fungiforme*

3.3.4.3. "Symbiodiniales" incertae sedis: *Sphaerodinium*

3.3.5. Peridiniales: Thecates in which the first apical plate is roughly symmetrical, and that have two antapical plates placed more-or-less symmetrically about the midventral/middorsal plane (may be fused or subdivided secondarily).

3.3.5.1. Amphidomataceans: Molecularly-defined clade, six or four apical plates.

Amphidoma, *Azadinium*

3.3.5.2. Heterocapsids: Peridiniales with five apical plates, not laterally compressed.

Heterocapsa

3.3.5.3. Glenodinoids: Peridiniales with four apical plates and six postcingular plates.

Glenodinium, *Glenodiniopsis*, "*Gymnodinium*" *impatiens*

3.3.5.4. Peridiniineans: Peridiniales with three or four apical plates and five postcingular plates.

3.3.5.4.1. Peridiniaceans: Peridiniineans with a distinct cingulum of four to six cingular plates (exclusive of a transitional plate that is sometimes present) and with at least one intercingular boundary on the dorsal surface.

3.3.5.4.1.1. Peridinioideans: Peridiniaceans with seven precingular plates and peridinin-containing plastids, and without calcareous cysts (often build cysts of dinosporin). In all likelihood paraphyletic. The apical pore complex may be absent.

Peridinium, *Vulcanodinium*

3.3.5.4.1.2. Dinotoms: Peridiniaceans with diatom-derived plastids

Kryptoperidinium, *Durinskia*, *Dinothrix*, *Galeidinium*, "*Peridinium*" *quinquecorne*, "*Gymnodinium*" *quadrilobatum*, "*Peridiniopsis*" *penardii*, "*Peridiniopsis*" cf. *kevei*

3.3.5.4.1.3. The *Zooxanthella* clade: Symbionts in radiolarians and hydrozoans

Zooxanthella

3.3.5.4.1.4. Endodiniaceans: Endosymbionts in the cnidarian *Velella velella*.

Endodinium

3.3.5.4.1.5. Thoracosphaeraceans: Peridiniaceans with five or six precingular plates that often form calcareous cysts. Preliminary data suggest that they may be paraphyletic, having given rise to the blastodinioids.

Pentapharsodinium, *Duboscquella*, *Duboscquodinium*, *Ensiculifera*, *Calcicarpinum*, *Pernambugia*, *Scrippsiella*, *Brandtodinium*, *Calciodinellum*, *Calcigonellum*, *Calciperidinium*, *Caracomia*, *Follisdinellum*, *Fuettererella*, *Lebessphaera*, *Pentadinellum*, *Praecalcigonellum*, *Wallidinellum*, *Leonella*, *Melodomuncula*, *Posoniella*, *Thoracosphaera*, *Bysmatrum*, *Chimonodinium*, *Theleodinium*, *Bicarinellum*, *Tintinnophagus*, *Aduncodinium*, *Stoeckeria*, *Paulsenella*, *Pfiesteria*, *Cryptoperidiniopsis*, *Luciella*, *Amyloodinium*, *Tyrannodinium*, *Naiadinium*, "*Peridinium*" *aciculiferum*/"*Scrippsiella*" *hangoei*/ "*Peridinium*" *baicalense*/"*Peridinium*" *euryceps*, "*Peridiniopsis*" *niei*, "*Peridiniopsis*" *penardii*

3.3.5.4.1.6. Blastodinioids: Parasitic dinoflagellates living unattached in the gut of copepods and producing a very distinctive trophont. Only the motile stages have an obvious dinokaryon.

Blastodinium

3.3.5.4.1.7. Peridiniopsids: A group of fresh-water dinoflagellates with rDNA sequences similar to those of *Peridiniopsis borgei* from brackish/limnic habitats (Logares et al. 2007).

Peridiniopsis, *Palatinus*, "*Peridinium*" *umbonatum*, "*Peridinium*" *inconspicuum*, "*Peridinium*" *centenniale*

3.3.5.4.1.8. Peridiniaceans incertae sedis: *Ailadinium*, *Amphidiniella*, *Kansodinium*, *Madanidinium*, *Pileidinium*

3.3.5.4.2. Protoperidiniaceans: Peridiniineans with a well-imprinted cingulum with three cingular plates excluding a transitional plate; there are no intracingular boundaries on the dorsal surface.

3.3.5.4.2.1. Protoperidinioideans: Protoperidiniaceans with two antapical plates.

Protoperidinium, *Congruentidium*, *Archaeperidinium*, *Amphidiniopsis*, *Glochidinium*, *Brigantedinium*, *Echinidinium*, *Herdmania*, *Islandinium*, *Minuscula*, *Multispinula*, *Quinquecuspis*, *Stelladinium*, *Trinovantedinium*, *Votadinium*, *Xandarodinium*

3.3.5.4.2.2. Diplopsaloids: Protoperidiniaceans with six precingular and one antapical (=fundital) plate.

Diplopsalis, *Kolkwitziella*, *Boreadinium*, *Diplopelta*, *Diplopsalopsis*, *Dissodium*, *Dubridinium*, *Gotoius*, *Oblea*, *Preperidinium*, *Zygabikodinium*, *Niea*, *Qia*, "*Protoperidinium*" *depressum*/"*Protoperidinium*" *claudicans*

3.3.5.4.2.3. The *Lessardia/Roscoffia* clade: Protoperidiniaceans with five precingular plates.

Lessardia, *Roscoffia*, *Rhinodinium*, *Cabra*

3.3.5.4.3. Podolampaceans: Peridiniineans in which the cingulum is not indented, but is composed of three cingular plates.

Podolampas, *Blepharocysta*, *Gaarderiella*, *Heterobractum*, *Lissodinium*, *Mysticella*

3.3.5.5. Peridiniales incertae sedis: *Chalubinskia*, *Hemidinium*, *Heteraulacus*, *Nephrodinium*, *Oodinium*, *Plagiodinium*, *Protoodinium*, *Sabulodinium*, *Staszicella*, *Thaurilens*

3.3.6. Thecates incertae sedis: *Archaeosphaerodiniopsis*, *Dinosphaera*, *Melanodinium*, *Oxytoxum*, *Thompsodinium*

3.4. Core dinoflagellates incertae sedis: *Actinodinium*, *Adinimonas*, *Apodinium*, *Bargoniella*, *Cachonella*, *Caryotoma*, *Cystodinedria*, *Cystodinium*, *Desmocapsa*, *Desmomastix*, *Dinamoebidium*, *Dinastridium*, *Dinoclonium*, *Dinococcus*, *Geodinium*, *Gloeodinium*, *Glenoaulax*, *Halophilodinium*,

Hypnodinium, *Micracanthodinium*, *Myxodinium*, *Oodinioides*, *Parapodinium*, *Phytodinium*, *Pleromonas*, *Proaulax*, *Pseliodinium*, *Rhizodinium*, *Rufusiella*, *Schizodinium*, *Tetradinium*
Ptychodiscus, *Balechina*, *Berghiella*, *Ceratoperidinium*, *Lissaiella*, *Lophodinium*, *Sclerodinium*, *Amphitholus*, *Achradina*, *Monaster*

Tovelliaceans: Dinoflagellates with a thin theca and an eyespot composed of pigment globules not bound by membranes and not located in a chloroplast. Members of this group also have an apical line of narrow plates, i.e., a small number of narrow thecal plates arranged in a row, level with the cell surface and lined on each side by another row of wider plates.

Genera in dinoflagellate species lists that are not considered to be dinoflagellates by Fensome et al. (1993): *Chilodinium*, *Entomosigma*, *Glyphidium*, *Pelagorhynchus*, *Pronoctiluca* (see Gawryluk et al. 2016), *Protodinifer*

Genera considered to be taxonomic junior synonyms by Fensome et al. (1993), but that have not been formally transferred: *Amphiceratium*, *Aureodinium*, *Biceratium*, *Bourrelyella*, *Branchiophilus*, *Cachonina*, *Caledonidinium*, *Ceratodinium*, *Clathrocysta*, *Clipeodinium*, *Corythodinium*, *Dimastigoaulax*, *Dinoceras*, *Dinopodiella*, *Dinopyxis*, *Discodinium*, *Epiperidinium*, *Exuviaella*, *Gessnerium*, *Gymnocystodinium*, *Hemicystodinium*, *Heteroceras*, *Hirundinella*, *Hyalosaccus*, *Latifascia*, *Lebouraia*, *Leptospathium*, *Manchudinium*, *Melodinium*, *Microtaeniella*, *Murracystis*, *Nectocystis*, *Parahistioneis*, *Parelion*, *Parrocelia*, *Pavillardinium*, *Pentadinium*, *Philozoon*, *Photocystis*, *Phyllodinium*, *Phytodinedria*, *Planinosphaeridium*, *Plectodinium*, *Polysphaeridium*, *Poroceratium*, *Prorocentrum*, *Prodinophysis*, *Proheteroschisma*, *Properidinium*, *Protogonyaulax*, *Pseudoactiniscus*, *Roulea*, *Schillingia*, *Spiraulaxina*, *Sporodinium*, *Steiniella*, *Trochodinium*, *Tuberculodinium*

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