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Chapter · January 2015

DOI: 10.1007/978-94-007-6644-0_55-1

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Dinoflagellates

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Definition

Dinoflagellates (Greek, **δύω**, *dino*, “whirl” and Latin *flagellum*, “whip, scourge”) are unicellular protists that have two distinctive flagella during at least part of their life cycle.

Introduction

Dinoflagellates are a biologically complex group of protists that comprise planktonic, meroplanktonic, and benthic species. They have different modes of nutrition making it difficult to attribute the group as a whole to animals or plants. Some species produce toxins that impact human health through consumption of contaminated seafood or water or aerosol exposure (Hackett et al., 2004). Toxic algae blooms are increasingly documented over the past decades (<http://oceanservice.noaa.gov/hazards/hab>) and may have a considerable economic impact. Extensive blooms of dinoflagellates may cause a coloration of water known as red tide. Some species are an important source of bioluminescence (Hackett et al., 2004). Since it has been finally accepted more than 50 years ago that the fossil hystrichospheres in Mesozoic and Cenozoic sediments are cysts of dinoflagellates (e.g., Dale, 1983), dinoflagellate cysts have become important in stratigraphy and understanding past environments.

General Characteristics

Dinoflagellates (c. 2 to 2,000 µm) are primarily unicellular eukaryotes but some species are colonial, and chain formation is common (Taylor et al., 2008). Organisms are assigned to the division Dinoflagellata (kingdom Alveolata) based on possession of one or more of a suite of characters including an amphiesma, two dissimilar flagella, and a unique type of nucleus (Taylor, 1987). The amphiesma is the complex outer region of the cell wall, usually containing a single layer of flattened vesicles. These amphiesmal vesicles may contain thecal plates usually composed of cellulose (thecate or armored forms). Six basic types of tabulation, i.e., arrangement of amphiesmal vesicles, are known (Fensome et al., 1993). Dinoflagellates without thecal plates are called athecate, naked, or unarmored.

A distinctive flagellar apparatus consisting of a coiled transverse flagellum within a cingular groove and a posterior flagellum within a sulcal groove enables a spiral motion and to move freely in the water column (Taylor, 1987). Swimming speeds range from centimeters to a few meters per hour. Vertical migration is a result of endogenous rhythms. This motility permits to optimize position in the euphotic zone to a limited extent to take full advantage of light and nutrients and avoids sinking under very stable water conditions.

The unique type of nucleus, the dinokaryon, is characterized by chromosomes that remain condensed between cell divisions, and a lack of histones. Dinoflagellates may have special vacuole-like structures of

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unknown function called pusules (usually two per cell). The accessory pigment peridinin that enables energy transfer may be present in photosynthetic cells.

Ecology of Dinoflagellates

Dinoflagellates live in all aquatic environments and have been observed both in snow and sea ice (Taylor et al., 2008). They are most abundant in shallow marine settings but also occur in fully oceanic environments. The biogeographic distribution is primarily determined by temperature, and the same species occur within similar climatic zones in both hemispheres. True endemism is rare, and some species have a bipolar distribution. More than 2,300 species have been described (Gómez, 2012) of which more than 180 are marine benthic (Hoppenrath et al., 2014) and 350 freshwater species (Mertens et al., 2012).

Dinoflagellates have diverse feeding mechanisms and utilize various modes of nutrition: they may be phototrophic, heterotrophic, and mixotrophic and may be free living, endosymbionts, or parasites (Jeong et al., 2010). Most species are probably mixotrophic or heterotrophic feeding on diverse preys such as bacteria, picoeukaryotes, nanoflagellates, diatoms, other dinoflagellates, heterotrophic protists, and metazoans or ingest particulate matter or dissolved substances. They are important in planktonic marine food webs since they may have both a considerable grazing impact on natural populations and are excellent prey for mixotrophic protists and metazoans. Together with diatoms and coccolithophores, dinoflagellates are among the most prominent marine primary producers today, thus playing an important role in the global carbon cycle.

Dinoflagellate Cysts (Dinocysts)

Dinoflagellates may form different types of cysts during various stages of their complex life cycle that involve asexual and sexual and motile and nonmotile stages (Taylor, 1987). Resting cysts represent a dormant stage in which normal life processes are greatly reduced. They are part of the sexual reproduction cycle (hypnozygotes) but may also be formed asexually (Kremp, 2013). Vegetative cysts are metabolically and/or reproductively active nonmotile cells. Temporary cysts are formed asexually as a result of adverse conditions. Digestion cysts that form after feeding are rare. Dale (1983) suggests that resting cysts may have three possible functions: protection, propagation, and dispersion. The latter may be extremely effective in introducing viable dinocysts into new geographic areas via transport in ships' ballast water (Taylor et al., 2008). Resting cysts may remain viable in sediments for centuries (Ribeiro et al., 2011).

Formation of resting cysts is a complex process and may be induced by various biotic and abiotic factors but is often related to peak abundances of the vegetative cells occurring at various times of the year (e.g., Matthiessen et al., 2005). After a mandatory dormancy period of variable length, excystment is triggered by different environmental factors. The cytoplasm excysts through an opening in the cell wall, the archeopyle, which is an important feature for taxonomic definition of cyst genera. Only a minority of living dinoflagellates produce resting cysts (less than 20 %, Head, 1996). Establishing cyst-theca relations are complicated by the fact that a single dinoflagellate species may produce cyst morphotypes attributable to different cyst species (Rochon et al., 2009).

Fossil Record of Dinoflagellates

Dinoflagellates are preserved in the fossil record predominantly through their resting cysts. Micropaleontologists mainly focus on organic-walled cysts (i.e., consisting of a refractory biomacromolecule called dinosporin, Fensome et al., 1993) but calcified cysts are increasingly recognized in tropical to temperate environments (Zonneveld et al., 2005). Siliceous skeletons are rare. Taphonomic processes that alter dinocyst assemblages while sinking through the water column are relatively little known (Matthiessen et al., 2005), but species-selective aerobic degradation at the seafloor is an important process (Zonneveld et al., 2008).

Fossil cysts first occurred in the Triassic with a subsequent major radiation from late Triassic to mid-Jurassic, but molecular biomarkers indicate that ancestors of dinoflagellates originated in the Proterozoic (Hackett et al., 2004). Species diversity was highest in the Cretaceous declining throughout the Cenozoic and followed the global sea level record with high diversity corresponding to intervals of high sea level and large shelf seas (Pross and Brinkhuis, 2005). To date more than 4,000 fossil cyst species have been described.

Separate classification schemes have been developed by biologists and paleontologists for living dinoflagellates and fossil cysts before their natural relationship was discovered. Therefore, the resting cysts are often attributed to a different genus and species than their motile stage. Due to their nutritional strategies, dinoflagellates have been handled under the International Code either of Botanical or Zoological Nomenclature. Based on morphological characteristics, a phylogenetic classification at suprageneric level including both extant and fossil vegetative cells and cysts has been proposed by Fensome et al. (1993). Cyst species are generally described based on morphology, but molecular genetic studies become increasingly important to unravel the intricate phylogenetic relationship between taxa difficult to distinguish by morphology (Matsuoka and Head, 2013 and references therein). The database dinoflaJ2 comprises the classification of fossil and living dinoflagellates down to the generic rank; an index of fossil dinoflagellates at generic, specific, and intraspecific rank; and the references of original descriptions (Fensome et al., 2008b).

Ecology of Extant Dinoflagellate Cysts

Like dinoflagellates, their cysts are found in all aquatic environments and occur even in regions with a seasonal sea-ice cover (e.g., Dale, 1996; Matthiessen et al., 2005; Mertens et al., 2012; Zonneveld et al., 2013). In general, diversity is highest in shallow marine settings (continental shelf and rise) and decreases toward the poles as a function of annual mean sea-surface temperature (Chen et al., 2011). Apart from changes in assemblage composition in relation to environmental gradients, cyst morphology (e.g., process morphology and length) may be affected by environmental stress such as temperature and salinity variability (Dale, 1996; Rochon et al., 2009; Jansson et al., 2014). The assemblage composition generally depends on both water mass properties and surface water circulation pattern. Application of multivariate ordination methods (canonical correspondence, detrended correspondence, and regression analysis) on regional and global data sets confirms a relationship to different physical (e.g., mean annual and seasonal surface temperature, salinity, upwelling intensity, sea-ice cover), biological (e.g., chlorophyll-a concentration, primary productivity), and chemical (e.g., phosphate, nitrate, and bottom water oxygen concentration) water mass properties. Ecological preferences are relatively well defined for a number of extant species (Zonneveld et al., 2013). The sensitivity for nutrient availability makes them ideal to identify areas of high productivity such as polynyas and upwelling regions and also of human-induced pollution and eutrophication if these signals can be differentiated from climate change (Dale, 2009). Biogeographic

distributions of assemblages on regional and hemispheric scale have been widely used to develop transfer functions (using primarily the modern analogue technique) in order to quantitatively reconstruct sea-surface temperature and salinity, seasonal extent of sea-ice cover, and primary productivity in Quaternary sediments (e.g., de Vernal and Marret, 2007; de Vernal et al., 2007; Bonnet et al., 2012).

Paleoecology of Extinct Dinoflagellate Cysts

Dinocysts are increasingly used for paleoenvironmental reconstructions (Pross and Brinkhuis, 2005) but the definition of ecological preferences of extinct species remains a challenge. Various combinations of actuo-paleontological, empirical, and statistical approaches including comparison with the morphology and ecology of co-occurring extant genera and species, the identification of latitudinal and onshore-offshore gradients from paleobiogeographic data, the interpretation of statistical analyses (e.g., correspondence analysis) on dinocyst distribution in relation to independent paleoenvironmental information, and the relation between dinocyst assemblages and geochemical proxies for water mass properties may yield qualitative and quantitative ecological information on, e.g., temperature, salinity, onshore-offshore gradients, bottom water oxygenation, and productivity (e.g., Versteegh and Zonneveld, 1994; Pross and Brinkhuis, 2005; De Schepper et al., 2011; Bijl et al., 2011; Masure et al., 2013; Schreck and Matthiessen, 2013). These ecological parameters are qualitatively known for some extinct species, groups of taxa or complexes of genera (e.g., Pross and Brinkhuis, 2005), and the correlation of species abundance to geochemical proxies (e.g., Mg/Ca temperatures on co-occurring planktonic foraminifera, De Schepper et al., 2011) is promising for providing quantitative data.

Biostratigraphy

Since the middle of the twentieth century, palynostratigraphy has emerged as a routine tool in both hydrocarbon exploration and academic research in Mesozoic and Cenozoic sediments, and numerous biostratigraphic zonations have been erected for Triassic to Neogene sediments (Stover et al., 1996). Dinocysts typically exhibit high abundances in neritic settings; thus, the derived stratigraphic information is complementary to that obtained from typically more offshore groups such as planktonic foraminifers, coccolithophores, and radiolarians (Pross and Brinkhuis, 2005). Significant progress has been made during the past four decades of scientific ocean drilling (DSDP, ODP, IODP) by assessing stratigraphic ranges against independent chronostratigraphic information. Recently, the focus is slowly moving from defining new zonations toward calibrating bioevents to the geological time scale on both regional (De Schepper and Head, 2008; Fensome et al., 2008a; Schreck et al., 2012) and global scales (Williams et al., 2004). This avoids the inherent problem of zonations that zones named after the same species may have different age ranges. However, few studies illustrate that dinocyst bioevents are rarely synchronous worldwide, and low-, mid-, and high-latitude bioevents should be distinguished to account for the observed latitudinal control on species ranges. Nonetheless, some bioevents are useful on regional and/or supraregional scale and enable stratigraphic correlations between different basins in the mid- and high latitudes (Schreck et al., 2012).

Conclusion

In recent years, biological and paleontological studies have provided a wealth of new information relevant for the application of recent and fossil dinocysts in marine geosciences. However, our knowledge of their ecology is still biased to coastal and shelf environments, and many open ocean regions such as the Pacific yet remain largely unexplored. The phylogenetic relationship to the motile form of many extant species is unknown, and molecular genetic studies will be particularly useful to address the long-standing question whether a single dinoflagellate species forms different cyst species. In the geological record, dinocysts are of eminent importance for paleoenvironmental interpretation and biostratigraphy in high latitudes where preservation of calcareous and biosiliceous microfossils is poor, but data from lower latitudes are required to inevitably improve independent age calibration of bioevents. This will also provide new data on the temporal and spatial distribution of fossil dinocysts, which together with calibration of species abundances to geochemical proxies for, e.g., surface temperature, will lead to a better understanding of cyst paleoecology.

Cross-References

- ▶ [Deep-Sea Sediments](#)
- ▶ [Marine Microfossils](#)
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