

1 **Encyclopaedia of Marine Geosciences**

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4 **Cover sheet**

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27

28 **DINOFLAGELLATES**

29

30 **Definition**

31 Dinoflagellates (Greek $\delta\iota\nu\eta$, *dino* “whirl”, and Latin *flagellum* “whip, scourge”) are
32 unicellular protists that have two distinctive flagella during at least part of their life cycle.

33

34 **Introduction**

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

47

48 **General Characteristics**

49 Dinoflagellates (*c.* 2 to 2000 μm) are primarily unicellular eukaryotes but some species are
50 colonial, and chain formation is common (Taylor et al., 2008). Organisms are assigned to the
51 division Dinoflagellata (kingdom Alveolata) based on possession of one or more of a suite of
52 characters including an amphiesma, two dissimilar flagella, and a unique type of nucleus

53 (Taylor, 1987). The amphiesma is the complex outer region of the cell wall, usually
54 containing a single layer of flattened vesicles. These amphiesmal vesicles may contain thecal
55 plates usually composed of cellulose (thecate or armoured forms). Six basic types of
56 tabulation, i.e. arrangement of amphiesmal vesicles are known (Fensome et al., 1993).
57 Dinoflagellates without thecal plates are called athecate, naked or unarmored.

58

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

65

66 The unique type of nucleus, the dinokaryon, is characterized by chromosomes that remain
67 condensed between cell divisions, and a lack of histones. Dinoflagellates may have special
68 vacuole-like structures of unknown function called pusules (usually two per cell). The
69 accessory pigment peridinin that enables energy transfer may be present in photosynthetic
70 cells.

71

72 **Ecology of Dinoflagellates**

73 Dinoflagellates live in all aquatic environments and have been observed both in snow and sea-
74 ice (Taylor et al., 2008). They are most abundant in shallow marine settings, but also occur in
75 fully oceanic environments. The biogeographic distribution is primarily determined by
76 temperature, and the same species occur within similar climatic zones in both hemispheres.
77 True endemism is rare, and some species have a bipolar distribution. More than 2300 species
78 have been described (Gómez, 2012) of which more than 180 are marine benthic (Hoppenrath

79 et al., 2014) and 350 freshwater species (Mertens et al., 2012).

80

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

91

92 **Dinoflagellate cysts (= dinocysts)**

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

104

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

114

115 **Fossil Record of Dinoflagellates**

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

124

125 Fossil cysts first occurred in the Triassic with a subsequent major radiation from late Triassic
126 to mid-Jurassic, but molecular biomarkers indicate that ancestors of dinoflagellates originated
127 in the Proterozoic (Hackett et al., 2004). Species diversity was highest in the Cretaceous
128 declining throughout the Cenozoic, and followed the global sea level record with high
129 diversity corresponding to intervals of high sea level and large shelf seas (Pross and
130 Brinkhuis, 2005). To date more than 4000 fossil cyst species have been described.

131

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

145

146 **Ecology of Extant Dinoflagellate Cysts**

147 Like dinoflagellates, their cysts are found in all aquatic environments, and occur even in
148 regions with a seasonal sea-ice cover (e.g. Dale, 1996; Matthiessen et al., 2005; Mertens et al.,
149 2012; Zonneveld et al., 2013). In general, diversity is highest in shallow marine settings
150 (continental shelf and rise), and decreases towards the poles as a function of annual mean sea-
151 surface temperature (Chen et al., 2011). Apart from changes in assemblage composition in
152 relation to environmental gradients, cyst morphology (e.g. process morphology and length)
153 may be affected by environmental stress such as temperature and salinity variability (Dale,
154 1996; Rochon et al., 2009; Jansson et al., 2014). The assemblage composition generally
155 depends on both water mass properties and surface water circulation pattern. Application of
156 multivariate ordination methods (canonical correspondence, detrended correspondence, and

157 regression analysis) on regional and global data sets confirm a relationship to different
158 physical (e.g. mean annual and seasonal surface temperature, salinity, upwelling intensity,
159 sea-ice cover), biological (e.g. chlorophyll-a concentration, primary productivity), and
160 chemical (e.g. phosphate, nitrate, and bottom water oxygen concentration) water mass
161 properties. Ecological preferences are relatively well-defined for a number of extant species
162 (Zonneveld et al., 2013). The sensitivity for nutrient availability make them ideal to identify
163 areas of high productivity such as polynyas and upwelling regions, but also of human-induced
164 pollution and eutrophication if these signals can be differentiated from climate change (Dale,
165 2009). Biogeographic distribution of assemblages on regional and hemispheric scale have
166 been widely used to develop transfer functions (using primarily the modern analogue
167 technique) in order to quantitatively reconstruct sea-surface temperature and salinity, seasonal
168 extent of sea-ice cover, and primary productivity in Quaternary sediments (e.g. de Vernal and
169 Marret, 2007; de Vernal et al., 2007; Bonnet et al., 2012).

170

171 **Paleoecology of Extinct Dinoflagellate Cysts**

172 Dinocysts are increasingly used for paleoenvironmental reconstructions (Pross and Brinkhuis,
173 2005) but the definition of ecological preferences of extinct species remains a challenge.
174 Various combinations of actuo-paleontological, empirical, and statistical approaches
175 including comparison with the morphology and ecology of co-occurring extant genera and
176 species, the identification of latitudinal and onshore-offshore gradients from paleo-
177 biogeographic data, the interpretation of statistical analyses (e.g. correspondence analysis) on
178 dinocyst distribution in relation to independent paleoenvironmental information, and the
179 relation between dinocyst assemblages and geochemical proxies for water mass properties
180 may yield qualitative and quantitative ecological information on e.g. temperature, salinity,
181 onshore-offshore gradients, bottom water oxygenation and productivity (e.g. Versteegh and
182 Zonneveld, 1994; Pross and Brinkhuis, 2005; De Schepper et al., 2011; Bijl et al., 2011;

183 Masure et al., 2013; Schreck and Matthiessen, 2013). These ecological parameters are
184 qualitatively known for some extinct species, groups of taxa or complexes of genera (e.g.
185 Pross and Brinkhuis, 2005), and the correlation of species abundance to geochemical proxies
186 (e.g. Mg/Ca temperatures on co-occurring planktonic foraminifera, De Schepper et al., 2011)
187 is promising for providing quantitative data.

188

189 **Biostratigraphy**

190 Since the middle of the 20th century, palynostratigraphy has emerged as a routine tool in both
191 hydrocarbon exploration and academic research in Mesozoic and Cenozoic sediments, and
192 numerous biostratigraphic zonations have been erected for Triassic to Neogene sediments
193 (Stover et al., 1996). Dinocysts typically exhibit high abundances in neritic settings, thus the
194 derived stratigraphic information is complementary to that obtained from typically more
195 offshore groups such as planktonic foraminifers, coccolithophores, and radiolarians (Pross
196 and Brinkhuis, 2005). Significant progress has been made during the past four decades of
197 scientific ocean drilling (DSDP, ODP, IODP) by assessing stratigraphic ranges against
198 independent chronostratigraphic information. Recently, the focus is slowly moving from
199 defining new zonations towards calibrating bioevents to the Geological Time Scale on both
200 regional (De Schepper and Head, 2008, Fensome et al., 2008a, Schreck et al., 2012) and
201 global scale (Williams et al., 2004). This avoids the inherent problem of zonations that zones
202 named after the same species may have different age ranges. However, the few studies
203 illustrate that dinocyst bioevents are rarely synchronous worldwide, and low-, mid-, and high
204 latitude bioevents should be distinguished to account for the observed latitudinal control on
205 species ranges. Nonetheless, some bioevents are useful on regional and/or supraregional scale
206 and enable stratigraphic correlations between different basins in the mid- and high latitudes
207 (Schreck et al., 2012).

208

209 **Conclusion**

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

224

225 **Jens Matthiessen**

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351

352 **Cross-references**

353 Deep-sea sediments

354 Marine microfossils

355 Paleooceanography

356 Paleooceanographic proxies