1   **Encyclopaedia of Marine Geosciences**

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4   **Cover sheet**

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27

DINOFLAGELLATES

29

Definition

Dinoflagellates (Greek δινη, *dino* "whirl", and Latin *flagellum* "whip, scourge") are

unicellular protists that have two distinctive flagella during at least part of their life cycle.

33

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.

47

General Characteristics

Dinoflagellates (*c*. 2 to 2000 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

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 reproductive 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 dispersal. 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 cytoplast

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**

226   **Michael Schreck**

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352   **Cross-references**

353   Deep-sea sediments

354   Marine microfossils

355   Paleoceanography

356   Paleoceanographic proxies