



Contents lists available at ScienceDirect

Marine Micropaleontology

journal homepage: www.elsevier.com/locate/marmicro

Publisher's Note

Dinocysts as tracers of hydrographical conditions and productivity along the ocean margins: Introduction

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ARTICLE INFO

Article history:

Received 7 April 2008

Accepted 10 April 2008

Available online xxxx

Keywords:

Dinocyst

North Atlantic Ocean

Quaternary

Beaufort Sea

Pacific Ocean

Transfer functions

Primary productivity

Climate change

Preservation

Upwelling

ABSTRACT

Quaternary organic- and calcitic-walled dinoflagellate cysts have received considerable attention within the last two decades due to their potential as tracers of sea surface parameters (temperature, salinity, sea ice cover, productivity). Despite uncertainties about taxonomical identity and limitations due to taphonomical processes, dinoflagellate cysts provide extremely useful and unique information on marine environments of the past. This is illustrated in the present special issue, which contains a selection of papers dealing with various approaches for reconstructing oceanographic parameters such as productivity, sea-ice cover, salinity, temperature, seasonality, and stratification in the upper water mass. All papers use organic-walled dinoflagellate cysts as their main proxy, but most combine the dinocyst information with results from complementary proxies, including benthic foraminifers, coccoliths, pollen, and stable isotopes in carbonates or organic matter. In all contributions, the approaches are based upon rigorous statistical treatment.

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During the last few decades, the discipline of marine micropaleontology has undergone important developments, including the emergence of micropaleontological indicators with diverse biological affinities and chemical composition from a micropaleontological world dominated by carbonate foraminifers. Among these microfossils which recently have received more attention, the organic-walled dinoflagellate cysts known as “dinocysts” occupy an interesting position within the realm of micropaleontology and appear unique in many ways:

- (1) First, the cysts are composed of dinosporin, a complex biomacromolecular substance composed of phenolic, alcoholic and/or carboxylic hydroxides, and fatty acids ranging from C₁₄ to C₁₆, accompanied by tocopherols

and sterols (mostly cholesterol and dinosterol) (Kokinov *et al.*, 1998), resistant to diagenetic processes in environments with high pCO₂ and under-saturated with respect to silica. Therefore, they are well preserved in sedimentary environments where siliceous and carbonate microfossils are affected by dissolution (e.g., de Vernal *et al.*, 1992; Williams, 1990).

- (2) Second, dinocyst assemblages are ubiquitous in sediments deposited along continental margins, and are abundant even under varying salinity levels. Unlike many other oceanic protists, dinocysts occur in sediments deposited under a wide range of settings, including estuaries and epicontinental seas, in addition to inner neritic and outer neritic environments (e.g., Marret and Zonneveld, 2003).
- (3) Third, dinocysts are characterized by a moderately high diversity of morphological species, even in Arctic environments (e.g., de Vernal *et al.*, 2001; Mudie and Rochon, 2001), which makes them useful and makes

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the use of statistical techniques for quantitative analyses possible. Because only ~15% of dinoflagellates produce fossilizable resting cysts, the environmental information preserved within the dinocyst assemblages collected from the sediments remains fragmentary. Nonetheless, the assemblages reflect the environmental conditions in which they developed.

- (4) Finally, dinocysts are produced by dinoflagellates having either heterotrophic, phototrophic or a combination (mixotrophic) of feeding behaviours, so that dinocyst assemblages may provide information on productivity levels (Radi and de Vernal, 2004).

In paleoceanography, the study of dinocysts is complementary to that of other micropaleontological taxonomic groups which are more commonly preserved in sediments deposited in open-ocean including mesopelagic environments, or which live as benthos. Dinocyst assemblages may allow reconstruction of environmental parameters such as salinity, temperature, sea-ice and productivity in surface water of marine environments (e.g., de Vernal et al., 2001, 2005), based on empirical reasoning or quantitative studies. However, dinocysts do not provide a panacea in paleoceanography and many uncertainties deserve special attention:

Cyst–theca relationship: Dinocysts, for the most part, represent the diploid phase of a dinoflagellate's life cycle. Approximately 180 extant marine dinoflagellate species are known to produce resting cysts during sexual reproduction, but formal cyst–theca relationships have been confirmed for about 70 species only through laboratory excystment experiments (Head, 1996). Knowledge of the cyst–theca relationship will therefore provide valuable information on the ecological requirements of the cyst stage, since the latter is commonly the only dinoflagellate evidence available to marine palynologists. **Preservation:** Preservation of organic- and calcitic-walled dinocysts is of primary importance when reconstructing paleoenvironments from fossil dinocyst assemblages. Several studies have shown that the chemical conditions (Zonneveld et al., 1997) and taphonomic processes (Traverse, 2007) in the sediments affect dinocyst assemblage composition, which could lead to biased interpretations. An assessment of the preservation state of dinocyst assemblages must be performed to evaluate the accuracy of paleoenvironmental interpretations.

Transport: Marine dinoflagellates are found mostly in neritic environments where nutrient concentrations are high enough to sustain phytoplankton blooms of phototrophic forms. Dinoflagellates and their cysts are mobile in the water column, and are subject to transport by surface or bottom currents like other planktonic organisms. Lateral transport is believed to account for a large part of the dinocyst assemblages found in the deeper part of ocean basins (Dale, 1992), and thus must be considered when interpreting dinocyst assemblages in terms of paleoenvironments. Calibration of the distribution of motile (planktonic) and cyst (benthic) stages, when available, is extremely helpful in assessing dinocyst transport, and therefore may increase accuracy of paleoenvironmental interpretations.

Despite uncertainties resulting from questions about the taxonomical identity and from limitations due to taphonomic processes, dinoflagellate cysts provide extremely useful and unique information on marine environments of the past. This is illustrated in the present special issue, which contains a selection of papers dealing with various approaches for reconstructing oceanographic parameters such as productivity, sea-ice cover, salinity, temperature, seasonality, and stratification in the upper water mass. All papers use organic-walled dinoflagellate cysts as their main proxy, but most combine the dinocyst information with results from complementary proxies, including benthic foraminifers, coccoliths, pollen, and stable isotopes in carbonates or organic matter. In all contributions, the approaches are based upon rigorous statistical treatment.

From a geographical point of view, the papers present a wide coverage (Fig. 1): some present databases developed at hemispheric spatial scales, whereas others present more regionally focused datasets for low to high latitudes of the Atlantic or Pacific continental margins, in addition to a paper from the Beaufort Sea margins. Most papers are methodologically oriented with emphasis on reference datasets based on the analyses of surface sediment samples. Applications developed in some manuscripts cover the late Quaternary.

The paper by T. Richerol and co-authors, titled “Evolution of paleo sea-surface conditions over the last 600 years in the Mackenzie Trough, Beaufort Sea (Canada)”, discusses the recent evolution of quantitative sea-surface parameters in an Arctic continental shelf environment (A in Fig. 1), which had never been done in this area before. They use dinocyst assemblages to document the actual warming trend that began in the western Canadian Arctic prior to the onset of the Industrial Era.

V. Pospelova and colleagues investigate the spatial distribution of dinocysts in the northeastern Pacific (area delimited by solid line (B) in Fig. 1), over an area characterized by strong upwelling, in their contribution titled: “Distribution of dinoflagellate cysts in surface sediments from the northeastern Pacific Ocean (43–25°N) in relation to sea-surface temperature, salinity, productivity and coastal upwelling”. The study reveals a strong coupling between cyst distribution and annual productivity and sea-surface temperature over the northeast North Pacific Ocean.

L. F. Vasquez Bedoya and co-authors document modern dinocyst assemblages in surface sediments from the southern Gulf of Tehuantepec (Mexico; C in Fig. 1) in their paper titled: “Last century record of organic-walled dinoflagellate cysts and benthic foraminifera in coastal sediments from the Gulf of Tehuantepec, South Pacific of Mexico”. This is an area marked by polluting industrial activities and characterized by an intense upwelling. By combining dinocyst and benthic foraminifer analyses, the authors investigate a core covering the last century for the reconstruction of productivity and the evaluation of human activity impact.

M.-S. Seidenkrantz and colleagues discuss paleoenvironmental change in the Labrador Sea and North Atlantic region during the late Holocene in their contribution “Variable North Atlantic climate seesaw patterns documented by a late Holocene marine record from Disko Bugt, West Greenland”. They describe the evolution of sea-surface conditions over the last 3000 years along the west coast

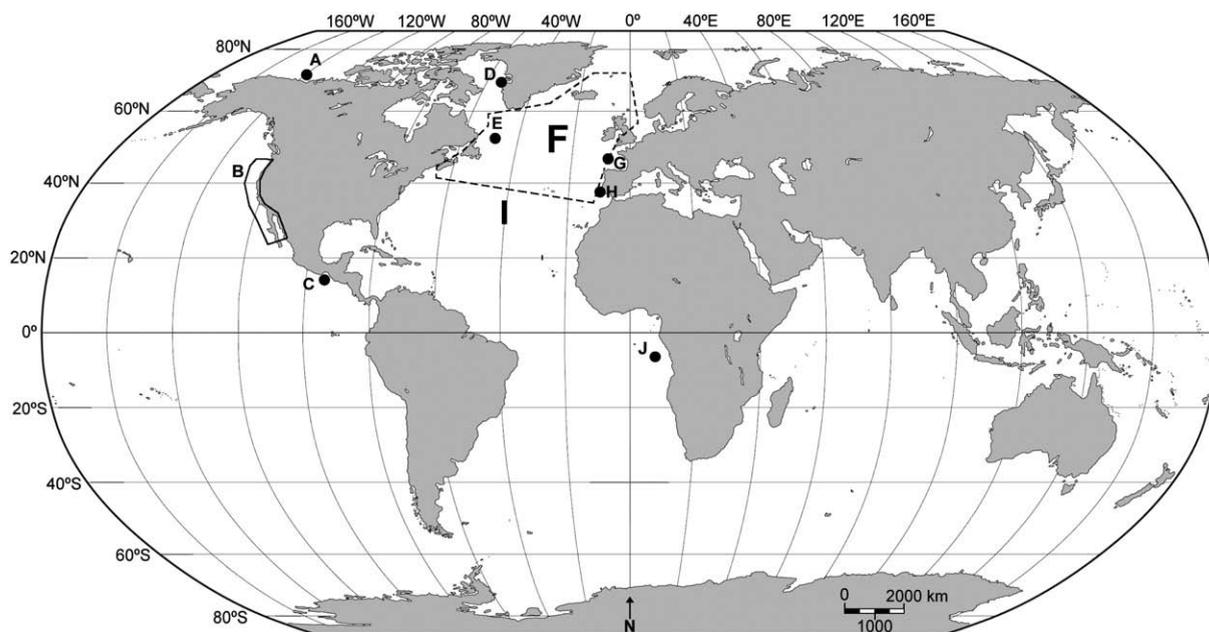


Fig. 1. Geographical location of contributions from the present special issue: A = T. Richerol et al.; B (area delimited by solid line) = V. Pospelova et al.; C = L.F. Vázquez-Bedoya et al.; D = M.-S. Seidenkrantz et al.; E = T. Radi and A. de Vernal; F (area delimited by dashed lines) = S. Solignac et al.; G = A. Penaud et al.; H = S. Ribeiro and A. Amorim; I = K. Zonneveld and G. Versteeg; J = F. Marret et al.

of Greenland (D in Fig. 1), with emphasis on recent historical climatic events including the Little Ice Age and the Medieval Warm Period, and relate their findings to North Atlantic circulation patterns.

The work of T. Radi and A. de Vernal titled; “Dinocysts as proxy of primary productivity in mid-high latitudes of the Northern Hemisphere”, also addresses an important issue from a methodological point of view. It explores the relationships between productivity in overlying waters and dinoflagellate cyst assemblages in the sediments using a database composed of information on dinocyst assemblages in 1171 surface sediment samples and satellite information on productivity for the northern hemisphere. They conclude that dinocysts can be used to reconstruct productivity with an accuracy equivalent to that of primary productivity estimated from satellite observations and applied the approach for the reconstruction of productivity during the last 25000 years in the northwest North Atlantic (E in Fig. 1).

The northern North Atlantic Ocean is investigated by S. Solignac and colleagues in their contribution; “Comparison of coccolith and dinocyst assemblages in the northern North Atlantic: how well do they relate with surface hydrography?” They address the relevant question on how to compare and integrate the response of two dominant phytoplankton groups to changes in sea-surface environmental parameters, and integrate the information from both groups. Using a database combining dinocyst and coccolith assemblages from surface sediments (see area delimited by dashed line (F) in Fig. 1), they demonstrate an excellent correspondence between the responses of the two groups, and thus are able to document the distribution of surface water masses in the temperate domains. They show that surface temperature is

the primary environmental parameter influencing the distribution of both groups in the region studied.

In a paper titled “Interglacial variability (MIS 5 and MIS 7) and dinoflagellate cyst assemblages in the Bay of Biscay (North Atlantic)”, A. Penaud and colleagues present a multiproxy interpretation of paleoenvironmental conditions in the Bay of Biscay (G in Fig. 1) during the last two interglacial periods. They also highlight the potential of the dinocyst species *Spiniferites septentrionalis* and *Spiniferites mirabilis* as tracers of surface water mass temperatures.

The contribution by S. Ribeiro and A. Amorim, “Environmental drivers of temporal succession in recent dinoflagellate cyst assemblages from a coastal site in the North-East Atlantic (Lisbon Bay, Portugal)”, describes the interannual distribution of dinoflagellate cysts as related to bloom occurrences and environmental conditions along the Portuguese coast (H in Fig. 1). In particular, the authors highlight the fact that dinocyst assemblages in the sediments are the integration of abiotic factors affecting cyst production, transport and sedimentation.

K. Zonneveld, and G. Versteegh present a thorough review of the effect of diagenetic and taphonomic processes on preservation of dinocysts in sediments in their paper; “Preservation and organic chemistry of late Cenozoic organic-walled dinoflagellate cysts; a review”. They document that cysts of modern heterotrophic species are more susceptible to oxidation and degradation than gonyaulacoid cysts and that Mesozoic cysts have different preservation characteristics than Cenozoic species. In addition, they propose that the rate of degradation of dinocyst assemblages may serve as proxy for the ventilation rate of the deep ocean and use examples throughout the Atlantic sector (I in Fig. 1) to illustrate some of their findings.

The manuscript by F. Marret and co-authors, titled: "Marine Production in the Congo-influenced SE Atlantic over the past 30 000 years: a novel dinoflagellate-cyst based transfer function approach", describes the evolution of sea-surface conditions and productivity in the Congo fan area (J in Fig. 1) since the last Glacial Maximum, and discusses the accumulation of organic carbon in the sediments. These authors present a new database of surface dinocyst assemblages for paleoenvironmental reconstructions in the deep part of the basin.

The special issue thus provides new insights into the dinoflagellate cyst distribution in sediments as related to environmental parameters, notably productivity, in addition to hydrographic conditions. The selection of papers presented illustrates the usefulness of dinoflagellate cysts for documenting natural and human-related changes in marine environments and addressing paleoceanographical and environmental issues.

Appendix A

Taxonomic list of dinoflagellate cyst taxa from this special issue: references follow Turon (1984) and Rochon et al. (1999). The nomenclature conforms to Fensome and Williams (2004) and Head et al. (2001).

Division: Dinoflagellata Bütschli 1885 Fensome et al. 1993
 Subdivision: Dinokaryota Fensome et al. 1993
 Class: Dinophyceae Pascher 1914
 Gonyaulacoid cysts
Achomosphaera ramulifera (Deflandre 1937) Evitt 1963
Achomosphaera spp.
Alexandrium excavatum (Braarud 1945) Balech & Tangen 1985
Ataxiodinium choane Reid 1974
Bitectatodinium spongium (Zonneveld 1997)
Bitectatodinium tepikiense (Wilson 1973)
Dalella chathamensis McMinn & Sun 1994
Impagidinium plicatum Versteegh & Zevenboom 1995
Impagidinium aculeatum (Wall 1967) Lentin & William 1981
Impagidinium japonicum Matsuoka 1983
Impagidinium pallidum Bujak 1984
Impagidinium paradoxum (Wall 1967) Stover & Evitt 1978
Impagidinium patulum (Wall 1967) Stover & Evitt 1978
Impagidinium sphaericum (Wall 1967) Lentin & Williams 1981
Impagidinium spp. Undet. Stover & Evitt 1978
Impagidinium striatum (Clarke and Verdier 1967) Stover & Evitt 1978
Impagidinium variaseptum Marret & de Vernal 1997
Impagidinium velorum Bujak 1984
Lingulodinium machaerophorum (Deflandre & Cookson 1955) Wall 1967
Nematosphaeropsis labyrinthus (Ostenfeld 1903) Reid 1974
Operculodinium centrocarpum (Deflandre & Cookson 1955) Wall 1967
Operculodinium centrocarpum short processes form
Operculodinium israelianum (Rossignol 1962) Wall 1967
Operculodinium janduchenei Head et al. 1989
Operculodinium longispinigerum Matsuoka 1983
Polysphaeridium zoharyi (Rossignol 1962) Bujak et al. 1980 =
Pyrodinium bahamense
Pyxidinospis reticulata (McMinn & Sun 1994) Marret & de Vernal 1997

Spiniferites belerius Reid 1974
Spiniferites bentorii (Rossignol 1964) Wall & Dale 1970
Spiniferites bulloideus (Deflandre & Cookson 1955) Sarjeant 1970
Spiniferites delicatus Reid 1974
Spiniferites elongatus Reid 1974
Spiniferites frigidus Harland & Reid, in Harland et al. 1980
Spiniferites hyperacanthus (Deflandre & Cookson 1955) Cookson & Eisenack 1974
Spiniferites lazus Reid 1974
Spiniferites membranaceus (Rossignol 1964) Sarjeant 1970
Spiniferites mirabilis (Rossignol 1964) Sarjeant 1970
Spiniferites pachydermus (Rossignol 1964) Reid 1974
Spiniferites ramosus (Ehrenberg 1838) Mantell 1854
Spiniferites septentrionalis Harland 1977
Spiniferites spp. Indet. Mantell 1850
Tectatodinium pellitum Wall 1967
Tuberculodinium vancampoae (Rossignol 1962) Wall 1967 (= cyst of *Pyrophacus steinii*)
 Peridinioid cysts
Brigantedinium cariacense (Wall 1967) Reid 1977 = cyst of
Protoperidinium avellanum (Heunier) Balech
Brigantedinium simplex (Wall 1965) Reid 1977 = cyst of
Protoperidinium conicoides (Paulsen) Balech
Brigantedinium spp. Reid 1977 (includes all the specimen of *Brigantedinium* species grouped because of crumpled aspect of the cysts) = *Protoperidinium* spp.
 Cyst of *Pentapharsodinium dalei* Indelicato & Loeblich III 1986
 Cyst of *Protoperidinium americanum* (Gran & Braarud 1930) Balech 1974
 Cyst of *Protoperidinium nudum* (Meunier 1919) Balech 1974
 Cyst of *Protoperidinium stellatum* (Wall 1968) Balech 1994
 Cyst of *Scrippsiella trifida* Lewis 1991 ex Head, 1996
Echinidinium aculeatum Zonneveld
Echinidinium bispiniformum
Echinidinium delicatum Zonneveld
Echinidinium echinatum
Echinidinium granulatum Zonneveld 1997 ex Head et al., 2001
Echinidinium karaense
Echinidinium transparantum
Islandinium brevispinosum Pospelova & Head
Islandinium minutum (Harland & Reid in Harland et al., 1980; Head et al., 2001)
Islandinium? cezare (de Vernal et al. 1989 ex de Vernal in Rochon et al., 1999; Head et al., 2001)
Leipokatium invisitatum Bradford 1975
Lejeunecysta oliva (Reid 1977) Turon & Londeix 1988 (= *Protoperidinium leonis*)
Lejeunecysta sabrina (Reid 1977) Bujak 1984
Lejeunecysta spp.
Quinquecuspis concreta (Reid 1977) Harland 1977
Selenopemphix brevispinosum Head et al. 1989
Selenopemphix nephroides (Benedek 1972) Bujak in Bujak et al. 1980, Benedek & Sargeant 1981 = cyst of *Protoperidinium subinermis* (Paulsen)
Selenopemphix quanta (Bradford 1975) Harland 1981 = *Multispinula quanta* (Bradford 1975) = cyst of *Protoperidinium conicum* (Gran) Balech
Stelladinium reidii Bradford 1975
Stelladinium sp.
Stelladinium stellatum (Wall & Dale 1968) Reid 1977

Trinovantedinium applanatum = *Trinovantedinium capitatum* Reid 1977 = *Protoperidinium pentagonum* (Gran 1902) Balech 1974

Trinovantedinium variabile

Tuberculodinium vancampoae (Rossignol 1962) Wall 1967

Votadinium calvum Reid 1977 = cyst of *Protoperidinium oblongum* (Aurivillius) Parke & Dodge

Votadinium spinosum Reid 1977 = cyst of *Protoperidinium claudicans* (Paulsen) Balech

Xandarodinium xanthum Reid 1977 = cyst of *Protoperidinium divaricatum*

Others

Cyst of *Gymnodinium catenatum* Graham 1943

Cyst of *Gymnodinium nolleri* Ellegaard et Moestrup 1999

Dubridinium caperatum Reid 1977

Dubridinium ulesterum Reid 1977

Palaestomocystis fritilla

Palaestomocystis subtilithea

Polykrikos kofoidii Chatton 1914

Polykrikos schwartzii Bütschli 1873

Protoceratium reticulatum (Claparède et Lachmann 1859) Bütschli 1885

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