



30 000 years of productivity and salinity variations in the late Quaternary Cariaco Basin revealed by dinoflagellate cysts

KENNETH NEIL MERTENS, CATALINA GONZÁLEZ, IRINA DELUSINA AND STEPHEN LOUWYE

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Dinoflagellate cysts and other palynomorphs were studied from ODP Hole 1002C in the Cariaco Basin over the past 30 000 years. The assemblage shifts between a dominance of heterotrophic dinoflagellate cysts (mainly *Brigantedinium* spp., *Lejeunecysta* spp., *Selenopemphix nephroides* and *Stelladinium reidii*) and autotrophic dinoflagellate cysts (mainly *Spiniferites ramosus*, *Lingulodinium machaerophorum* and *Operculodinium centrocarpum*). These assemblage shifts are associated with stronger upwelling during stadials and stronger river influx during interstadials. Increases in productivity caused by enhanced upwelling are coupled to improved preservation and vice versa. More stratified water is indicated by higher abundances of *L. machaerophorum* and succeeds Heinrich events. The average process length of *L. machaerophorum* can be used to track changes in salinity, since this shows a similar pattern as the $\delta^{18}\text{O}_{\text{SW}}$ (paired Mg/Ca $-\delta^{18}\text{O}$) reconstruction. During the last glacial, conditions were more saline than during the current interglacial. On a millennial scale, changes in salinity are opposite to open ocean salinities and the hydrological proxies, which can be explained by a modulation of the signal by stratification, isolation of the Basin or advection of freshwater masses. These results highlight both generalities and particularities of the palaeoecological record of this tropical semi-enclosed basin.

Kenneth Neil Mertens (e-mail: Kenneth.Mertens@ugent.be), and Stephen Louwye (e-mail: stephen.louwye@ugent.be), Research Unit Palaeontology, Ghent University, Krijgslaan 281/s8, 9000 Ghent, Belgium; Catalina González (e-mail: cataruga@yahoo.com), Geosciences Department, University of Bremen, Klagenfurter Strasse, D-28359 Bremen, Germany; Irina Delusina (e-mail: delusina@geology.ucdavis.edu), Department of Geology, University of California, One Shields Ave., Davis, CA 95616, USA; received 5th December 2008, accepted 12th February 2009.

Large and rapid climate oscillations occurring at sub-orbital and millennial frequencies are not restricted to the northern higher latitudes, but have a global signature which is also prominent in the Caribbean Sea (Peterson *et al.* 2000a; Vink *et al.* 2001; Schmidt *et al.* 2004). The synchronicity of these rapid changes between the Cariaco Basin, the Greenland Ice Cores and California margins shows that these are likely linked through atmospheric processes (Dean 2006, Goni *et al.* 2006). They are expressed as hydrological variations throughout the tropics (Clement & Peterson 2008), variations that have the potential to amplify and perpetuate millennial-scale climate changes (Ivanochko *et al.* 2005).

These rapid climatic changes are well reflected in productivity records, best recorded in coastal areas. Although present-day shelf seas make up 8% of the total ocean surface area, about 10–15% of the global marine primary production takes place in these coastal seas, with 40% of it exported to the deep sea (Muller-Karger *et al.* 2005). The Cariaco Basin, located near to the Venezuelan margin, is characterized by high productivity, which drove the Basin into anoxicity. In this respect, the Basin offers an important opportunity to study productivity changes.

Planktonic organisms such as dinoflagellates are regarded as sensitive recorders of climate change (e.g. Hays *et al.* 2005). Dinoflagellate cysts are the hypnozygotes of unicellular planktonic algae, which are con-

sidered to be useful palaeoceanographical tools in reconstructing late Quaternary palaeoproductivity (Reichart & Brinkhuis 2003; Pospelova *et al.* 2006; de Vernal & Marret 2007). In this respect, they have proved useful also for the Cariaco Basin (González *et al.* 2008b). Since inferred palaeotemperature variations in the Cariaco Basin were relatively small during the last glacial–interglacial transition (max. 3–4°C, based on Mg/Ca, Lea *et al.* (2003) and alkenones, Herbert & Schuffert (2000)), and are of similar magnitude as salinity changes (1.2–2.4‰, based on paired Mg/Ca $-\delta^{18}\text{O}$; McConnell 2008), changes in dinoflagellate cyst assemblages will be mainly related to changes in productivity. However, recent research has shown that dinoflagellate cyst morphology changes with salinity, and, more particularly, process length of *Lingulodinium machaerophorum* shows a linear relationship to salinity, as shown by studying cultures (Hallett 1999) and surface sediments (Mertens *et al.* 2008).

Dinoflagellate cysts from the Caribbean (including the Cariaco Basin) were investigated for the first time by Wall (1967). With the exception of an initial study on dinoflagellate cysts in surface sediments in the close-by Amazon region by Vink *et al.* (2000), organic-walled microfossils have been neglected in this region. Nevertheless, González *et al.* (2008b) have demonstrated that Cariaco dinoflagellate cysts are useful markers for reconstructing productivity during Marine Isotope stages 3 and 4. In this study, the productivity record from the

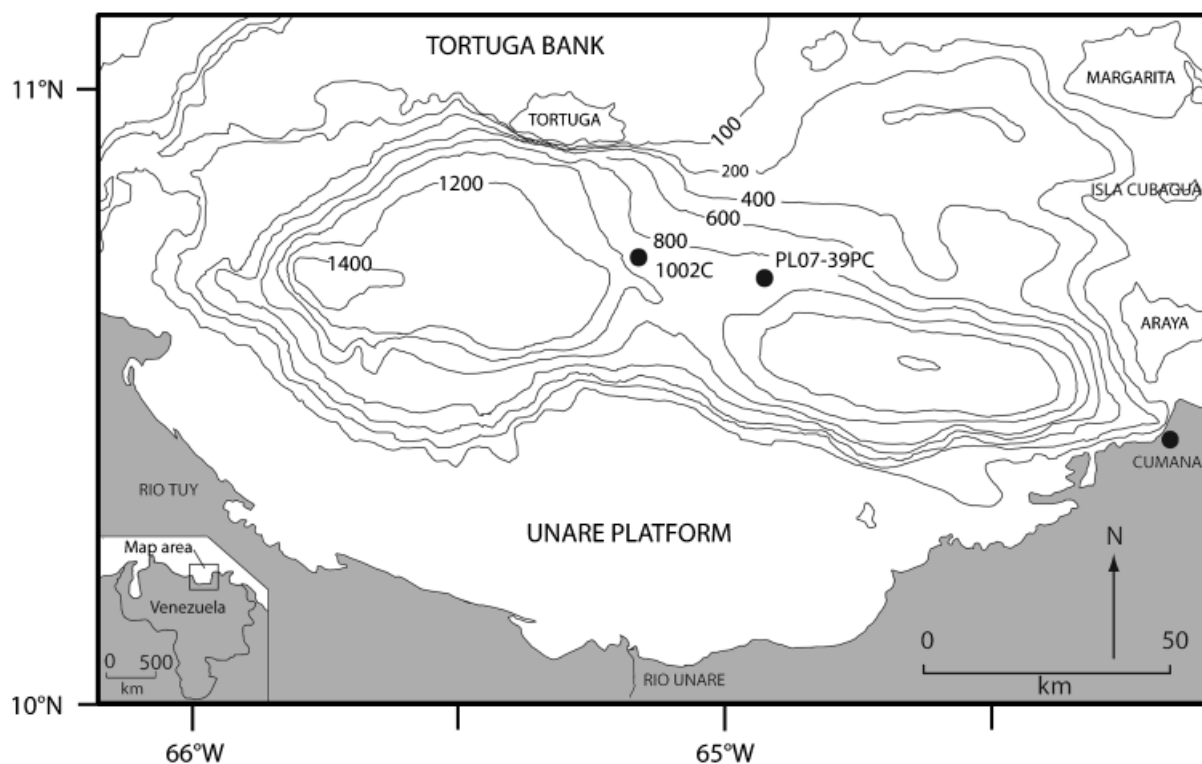


Fig. 1. The Cariaco Basin, with localization of ODP Site 1002 (approximately the same position as core MD03–2620) and core PL07–39PC. The major city Cumaná is denoted with a black dot.

Cariaco Basin is extended throughout the last 30 000 years and compared with other productivity proxies. Additionally, salinity variations are documented using process length variation of *L. machaerophorum* and compared with a paired Mg/Ca- $\delta^{18}\text{O}$ record.

Study area and background

The Cariaco Basin is an east–west trending Quaternary pull-apart basin on the continental shelf, north of Venezuela (Fig. 1). The surrounding topography prevents inflow of deep water from the Caribbean, causing a 100-year residence time of the bottom waters (Deuser 1973). The high oxygen demands, created by upwelling-induced surface productivity, and a strong pycnocline which limits vertical exchange, have led to the present-day anoxic and sulphidic conditions below a depth of 300 m (Peterson *et al.* 1991). The almost complete lack of bioturbation since the start of the Bølling/Allerød implies a nearly uninterrupted sedimentary record.

Surface waters entering the Caribbean are the North Brazil Current (NBC) and the North Equatorial Current (NEC). The NBC flows via Trinidad to the west along the continental slope of the Southern Caribbean, while the NEC originates from the North Atlantic gyre. The two upper water masses are the Caribbean Surface Water (CSW) and the Subtropical Under Water

(SUW). The oligotrophic CSW (0–80 m) originates from the NEC and NBC, with a substantial input of low salinity waters from the Amazon and Orinoco Rivers during October and November. The eutrophic SUW (at a depth of 80–120 m) comes from the centre of the North Atlantic, namely the surface waters of the North Atlantic Gyre, and enters the Caribbean between the Lesser Antilles and the Windward Passage between Cuba and the Jamaican Islands (Wust 1964; Nyberg *et al.* 2002). The SUW forms the permanent thermocline and/or nutricline of the Caribbean. The surface water of the Caribbean is generally characterized by low primary productivity, except in coastal regions such as off the Venezuelan coast (Muller-Karger & Aparicio-Castro 1994).

The region is influenced by migrations of the Intertropical Convergence Zone (ITCZ), which causes seasonal variations in the strength of the northeast trade winds (Muller-Karger & Aparicio-Castro 1994). During winter and early spring (January–March), the ITCZ is at its southernmost position; strong trade winds blow along the coast of Venezuela causing upwelling of nutrient-rich waters. The phytoplankton exploits this resource and in January and February primary production rates and carbonate and opal fluxes are at a maximum (Goni *et al.* 2003) and diatoms dominate the phytoplankton population (Ferraz-Reyes 1983). Beginning from about June or July, when the ITCZ

migrates north to a position near the Venezuelan coast, the trade winds weaken markedly and thus also the upwelling. Primary production rates fall to a minimum (Muller-Karger *et al.* 2004). As the upwelling subsides, the northward migration of the ITCZ brings its associated rain belt above the Cariaco Basin. This belt triggers increased fluvial discharge from rivers, affecting the southern Caribbean, and induces a stratification of the water-masses. No large rivers currently discharge into the Basin, but in former times fluvial input was more important (Peterson *et al.* 2000b). During this season, the production is dominated by Cyanobacteria, dinoflagellates (Ferraz-Reyes 1983) and also haptophytes (Goni *et al.* 2003).

The interglacial basin sediments are laminated and reflect migrations of the ITCZ as the high annual sediment flux (20–100 cm/kyr) forms alternating light and dark laminae. The light laminae are mainly composed of diatoms; they reflect high winter–spring production. The micro-organisms appear grouped in aggregates, most likely faecal pellets, and are surrounded by biogenic silica (Hughen *et al.* 1996a). The dark laminae have a higher terrigenous content, and this reflects summer–autumn deposition during the rainy season in combination with reduced productivity. Microorganisms in these laminae are also grouped in aggregates.

As an analogue to the seasonal migrations of the ITCZ, longer-term (orbital-scale, millennial-scale) changes in the mean position of the ITCZ have been proposed as a mechanism linking northern high-latitude and tropical climates (Dean 2006; Peterson & Haug 2006).

Material and methods

Ocean Drilling Programme (ODP) site 1002 (10°42.37'N, 65°10.18'W, 893 m water depth) is located on the western flank of the central saddle of the Cariaco Basin (Fig. 1). The saddle was chosen since varves in the sub-basins tend to be disrupted by microturbidites. Shipboard Scientific Party (1997) gives a detailed description of this core. Marine Calypso core MD03-2620 (10°39.05'N; 65°10.17'W; 876 m water depth) was retrieved during the PICASSO cruise in 2003 (Laj, 2004) and is located close to the location of the ODP site.

Stratigraphy

Hole 1002D is dated with 65 accelerator mass spectrometry (AMS) ^{14}C dates on planktonic foraminifera over the studied interval. After a constant 420-year marine reservoir correction, calendar ages were derived by transferring ages from the GISP II $\delta^{18}\text{O}$ ice core by matching inflection points and interpolation of reflection curves (Hughen *et al.* 2003). Hole 1002C was aligned with hole 1002D through visually matching

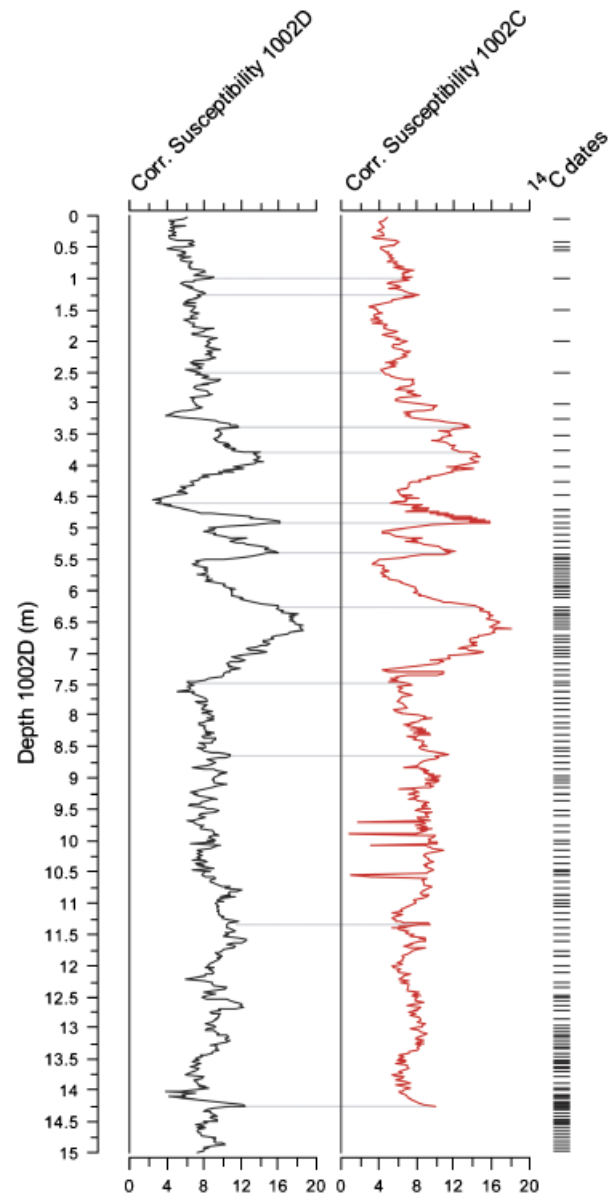


Fig. 2. Alignment of magnetic susceptibilities of 1002C and 1002D using the depth scale of 1002D. Tie-points are shown by grey lines, radiocarbon dates in 1002D by black horizontal lines (Hughen *et al.* 2004).

magnetic susceptibilities provided by Shipboard Scientific Party (1997) (Fig. 2). The studied core sections in Hole 1002C range in age from Late Pleistocene to late Holocene times, covering the time interval that includes Heinrich event 3 (H3), Heinrich event 2 (H2), Last Glacial Maximum (LGM), Heinrich event 1 (H1), Bølling/Allerød Warm Period (B/A), Younger Dryas (YD) and the entire Holocene. Heinrich events are denoted according to their cited ages (Hemming 2004) with respect to the Cariaco Basin age model for Hole 1002C. Sedimentation rates and accumulation rates are discussed in Mertens *et al.* (2008) and range between 32 and 170 cm/kyr.

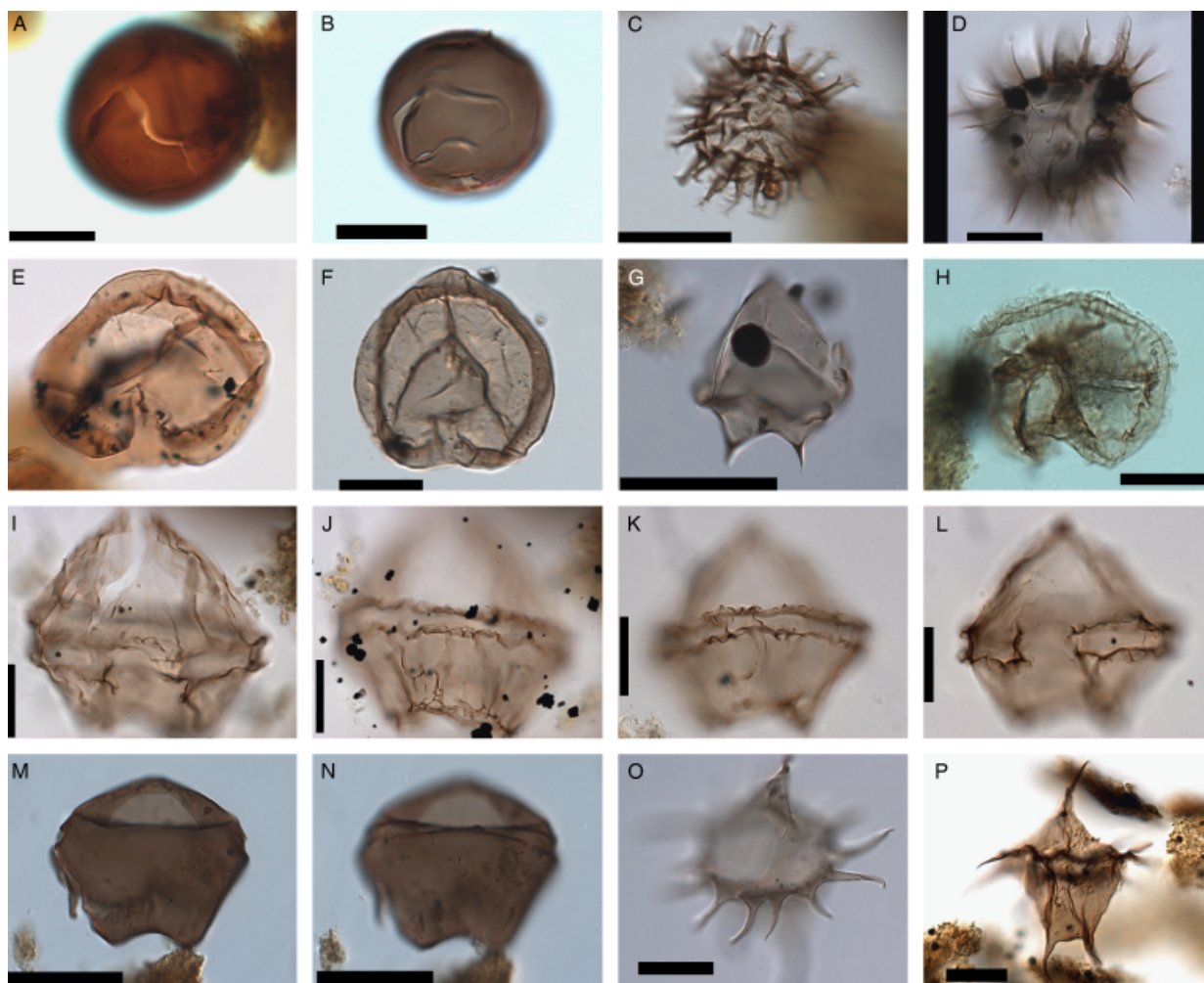


Fig. 3. Micrographs from representative heterotrophic dinoflagellate cysts from ODP 1002C. A. 1H 2W 80–82, *Brigantedinium cariaeoense*. B. 1H 4W 22–24, *Brigantedinium cariaeoense*. C. 1H 4W 22–24, *Echinidinium aculeatum* with characteristic aculeate distal tips. D. 2H 1W 20–23, *Selenopemphix quanta*. E. 1H 2W141–143, *Selenopemphix nephroides*. F. 1H 5W 70–72 *Selenopemphix nephroides*. G. 2H 1W 20–23, *Lejeunecysta marieae*. H–L. 2H 4A 101–103, *Lejeunecysta* sp. A. M–N. 1H 6W 19.5–21.5, *Lejeunecysta oliva* with characteristic pronounced paracingulum. O. 2H 1W 20–23, *Stelladinium reidii*. P. 1H 5W 11–13, *Stelladinium reidii*. All scale bars are 20 μm .

Sample preparation and light microscopy

Samples from Hole 1002C were taken at 20 cm intervals. A few samples of equal ages of core MD03-2620 were processed for comparison. Given the range of sedimentation rates, the sampling interval yields an average temporal resolution of 360 years, ranging between 10 and 1170 years. A total of 88 samples weighing between 1.6 and 23.9 g were prepared for palynological analysis following the maceration technique described in Louwey *et al.* (2004). One to three *Lycopodium* tablets, containing a known number of spores, were added at the beginning of the palynological preparation. The treatment involved decalcification with cold HCl (10%) and subsequent removal of silicates with cold HF (40%). The remaining organic fraction was then sieved at 20 μm on a nylon mesh and mounted with glycerine jelly. A minimum of 300 dinoflagellate cysts

were counted in each sample. In the meantime, all other palynomorphs encountered were counted. *Lycopodium* spores were counted to calculate cyst concentrations (cysts/cm³). Accumulation rates were calculated by multiplying concentrations by sedimentation rates and dry bulk densities based on GRAPE density measurements (Shipboard Scientific Party 1997). Representative dinoflagellate cyst species are illustrated in Figs 3 and 4; other palynomorphs are shown in Fig. 5. All photomicrographs were taken with a Zeiss AxioCam MRc5 camera mounted on a Zeiss Axioskop 2 Plus microscope. Taxonomy used follows Williams *et al.* (1998) and Rochon *et al.* (1999). *Spiniferites ramosus* s.l. includes *Spiniferites bulloideus* and *Spiniferites delicatus*. *Selenopemphix quanta* s.l. includes cysts of *Protoperidinium nudum*.

The morphological variation of *L. machaerophorum* was studied by measuring the three longest processes of

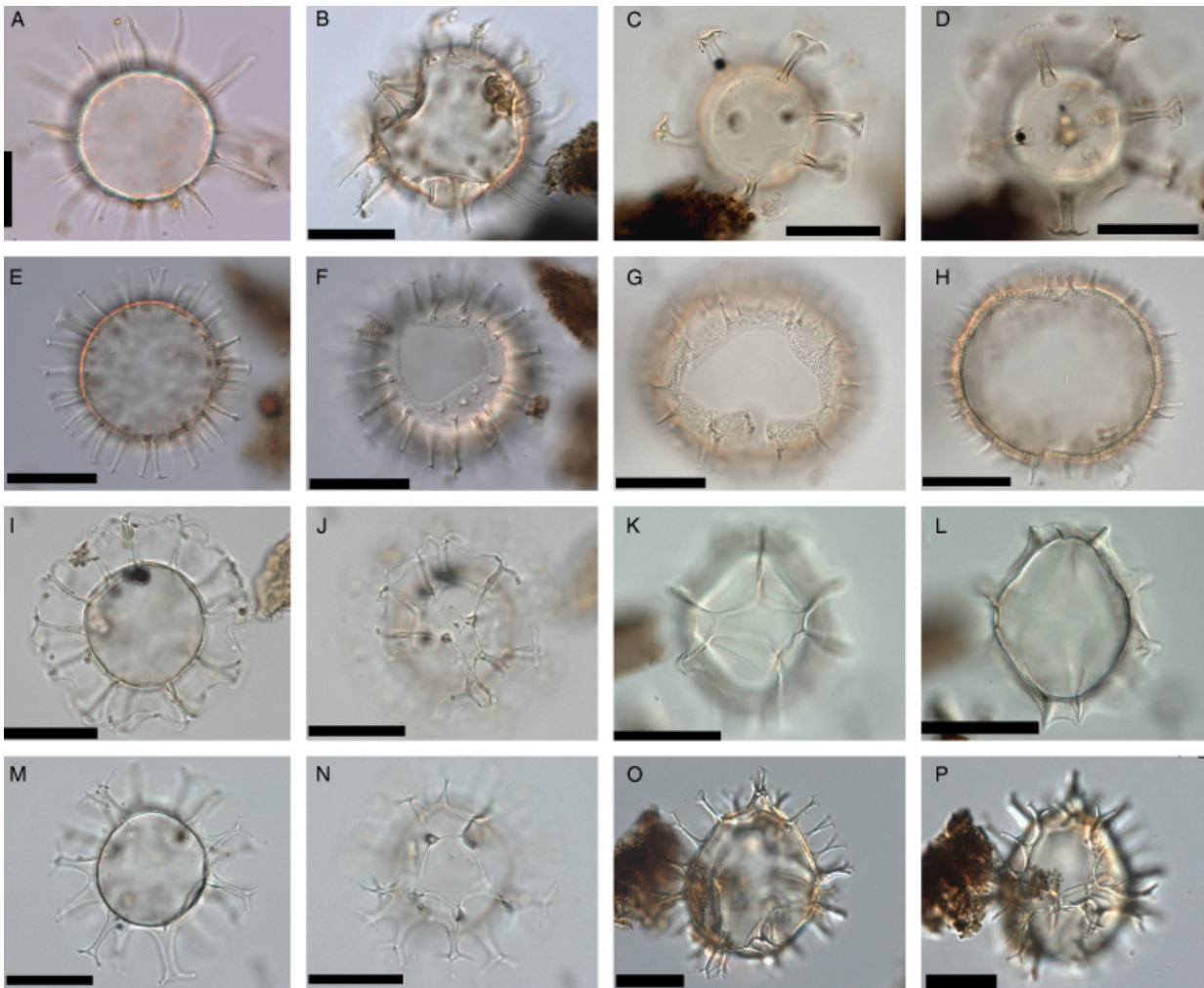


Fig. 4. Micrographs from representative autotrophic dinoflagellate cysts from ODP 1002C. A. 1H 3W 131–133, *Lingulodinium machaerophorum*. B. 1H 2W 80–82, *Lingulodinium machaerophorum*. C–D. 1H 5W 11–13, *Melitasphaeridium choanophorum*. E–F. 1H 4W 81–83, *Operculodinium centrocarpum* var. Wall & Dale, middle focus and upper focus showing archeopyle. G–H. 2H 1W 20–22, *Operculodinium israelianum*, similar views. I–J. 2H 1W 20–23, *Nematosphaeropsis labyrinthus*. K–L. 2H 1W 20–23, *Impagidinium aculeatum*. M–N. 2H 1W 20–22, *Spiniferites ramosus*. O–P. 1H 4W 22–24, *Spiniferites bentorii*. All scale bars are 20 μ m.

50 cysts per sample, when possible. The longest processes were chosen for three reasons. First, they would reflect unobstructed growth during formation of the cyst. Second, since only a restricted number of processes are measurable per cyst, it is necessary to make a consistent approach by choosing the longest processes. Third, the largest variation is obtained by choosing the longest processes, and this provides a more accurate proxy. The methodology is explained more in detail in Mertens *et al.* (2009). Often less than 50 cysts were measured when there were not enough available.

Results

Dinoflagellate cyst relative abundance data

A total of 47 dinoflagellate cyst taxa were identified in the studied sequence (Appendix 1). Only five taxa reach

relative abundances of more than 15% (Fig. 6): *Brigantedinium* spp. (3–94%), *Brigantedinium cariacense* (0–35%), *S. ramosus* (0–94%), *Selenopemphix nephroides* (0–45%) and *L. machaerophorum* (0–63%). Other species of minor importance are *Stelladinium reidii* (0–14%), *Islandinium minutum* (0–14%), *S. quanta* (0–9%), *Quinquecuspis concreta* (0–9%), *Spiniferites mirabilis* (0–7%), *Brigantedinium simplex* (0–8%), *Lejeunecysta sabrina* (0–13%), *Operculodinium centrocarpum* sensu Wall & Dale (0–9%) and *Operculodinium israelianum* (0–6%). Similar species were identified as in González *et al.* (2008b). The cyst mentioned in González *et al.* (2008b) as *Selenopemphix* cf. *divaricatum* is corrected here as *Lejeunecysta* sp. A.

The samples are generally dominated by Proto-peridiniacean heterotrophic cysts (4–98%, average 84%), mainly *Brigantedinium* spp., *Echinidinium* spp., *Selenopemphix* spp. and *S. quanta*. Autotrophic cysts from the Gonyaulacales occasionally dominate the

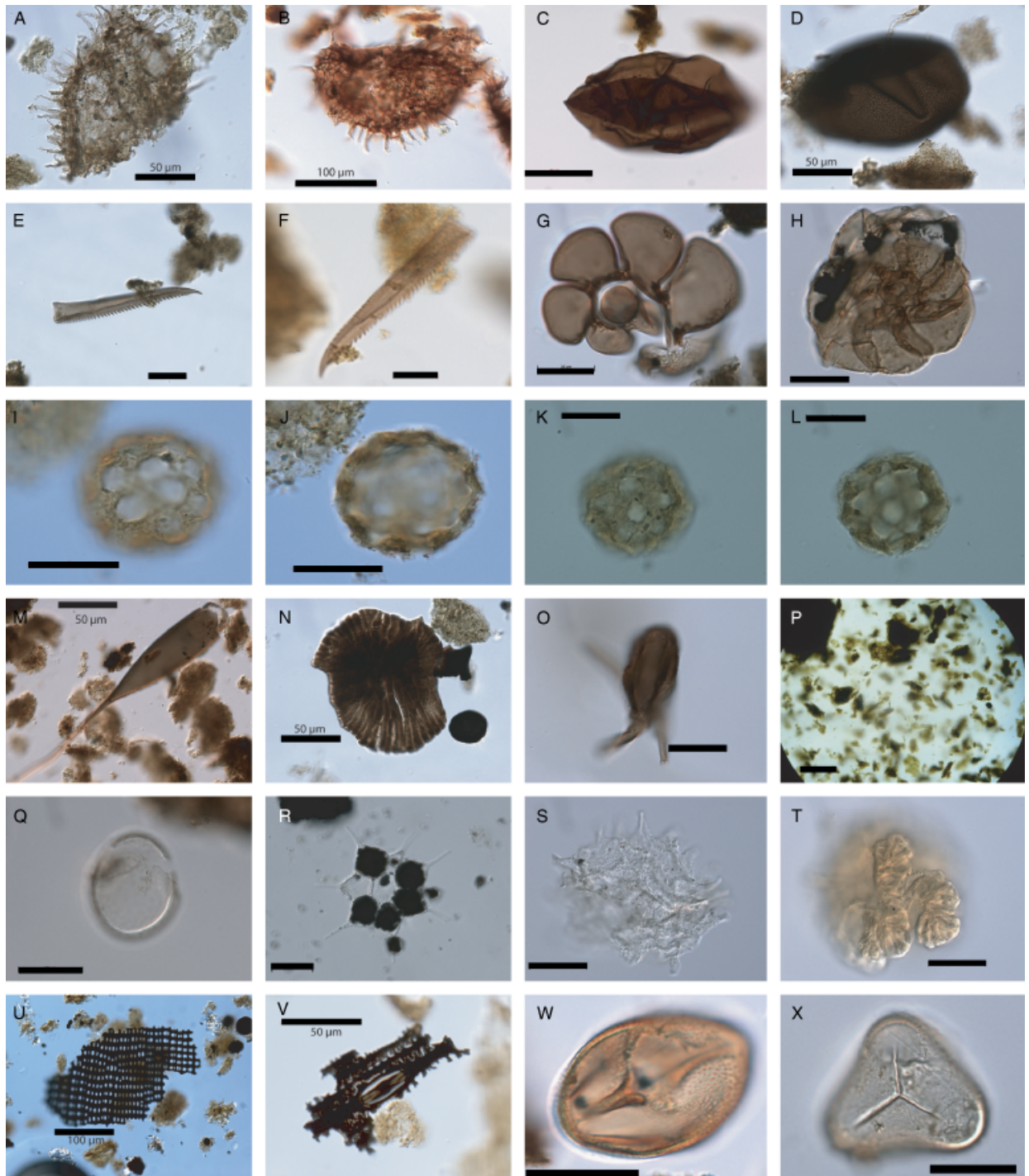


Fig. 5. Micrographs from representative other palynomorphs from ODP 1002C. Faunal remains: A. 1H 4W 0–2, copepod egg. B. 1H 4W 22–24, copepod egg. C. 1H 5W 11–13, copepod egg. D. 1H 4W 22–24, copepod egg. E. 1H 2W 80–82, scolecodont. F. 1H 2W 141–143, scolecodont. G. 1H 2W 80–82, planispiral microforaminiferal lining. H. 2H 1W 20–23, trochospiral microforaminiferal lining. I–L. 2H 4A 101–103, organic ‘wrappings’ of Ascidian spicule. M. 1H 2W 80–82, tintinnid lorica. Fungal remains: N. 2H 1W 20–23, fruiting body. O. 2H 1W 20–23, *Tetraploa* sp. P. 1H 1W 1.5–3.5, typical microscopic view of anoxic Cariaco Basin palynological samples filled with amorphous organic matter (AOM). Q. Organic lining of calcareous dinocyst. Chlororophyta: R. 2H 4W 101–103, *Pediastrum* sp. with characteristic stellate outline. S. 2H 1W 20–22, less well-preserved *Pediastrum* sp. T. 2H 1W 20–22, *Botryococcus* sp. Floral remains: U. 2H 1W 60–62, charcoal fragment, preservation of fine structures suggests charcoal origin V. 1H 4W 22–24, charcoal fragment. W. 1H 4W 22–24, pollen grain. X. 1H 2W 80–82, trilete spore. All scale bars are 20 μm , except where noted.

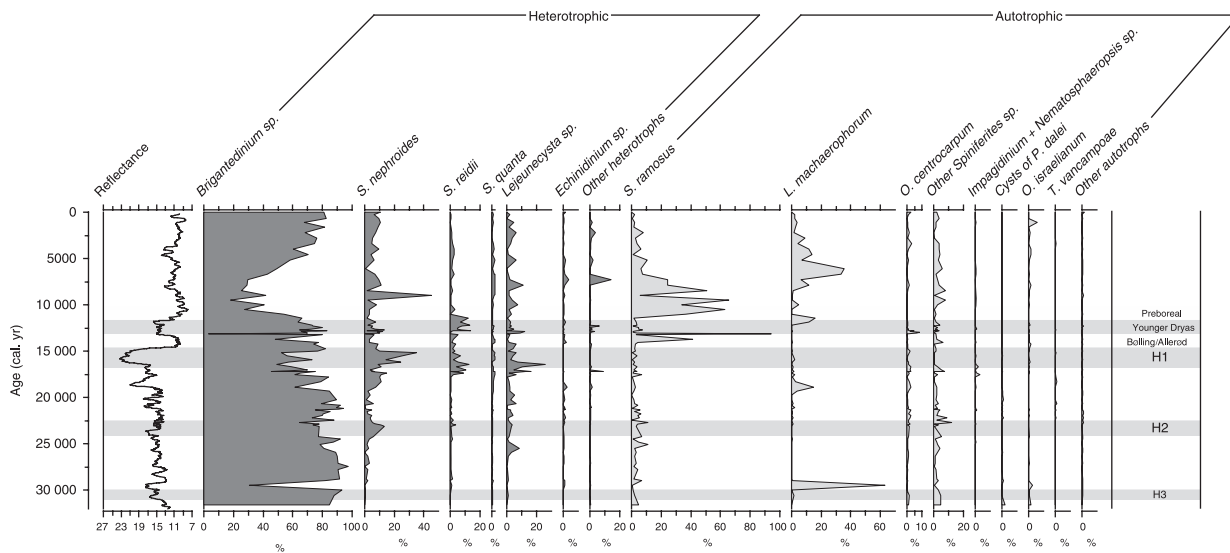


Fig. 6. Relative abundances of the most important dinoflagellate cyst taxa expressed in percentages of total cysts from Hole 1002C. Reflectance curve from Peterson *et al.* (2000a). Grey bars indicate stadials.

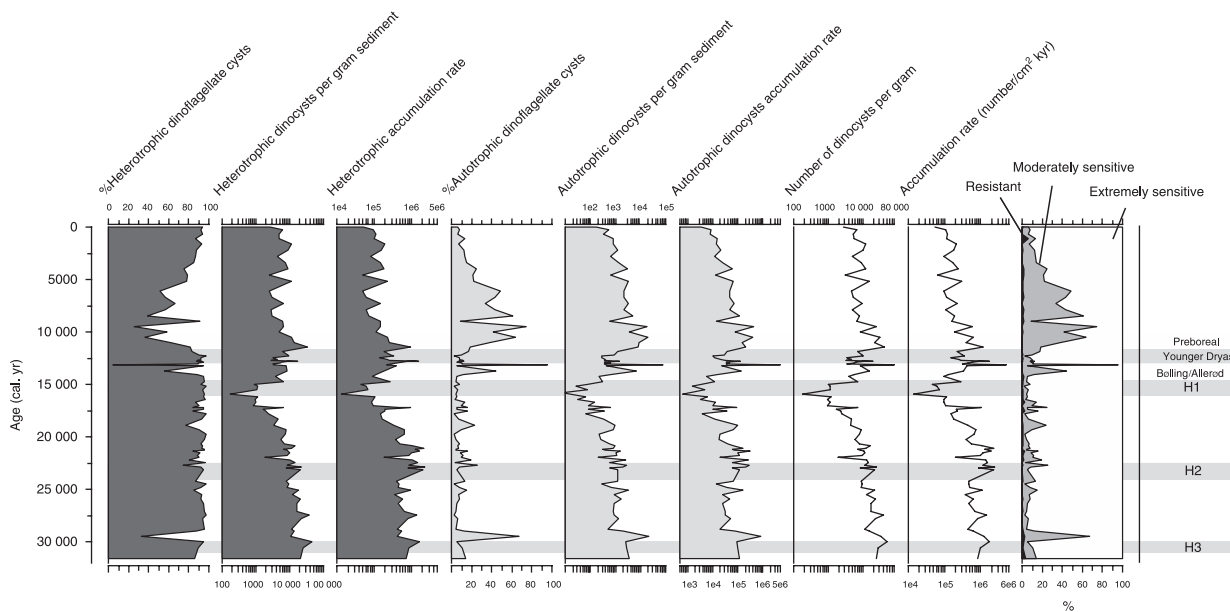


Fig. 7. Relative absolute abundances and accumulation rates of heterotrophic and autotrophic dinoflagellate cyst taxa next to absolute and accumulation rates of total dinoflagellate cysts. The last curves show the grouping according to preservation in percentages: resistant, moderately sensitive and extremely sensitive cysts. Grey bars indicate stadials. Absolute abundances and accumulation rates are shown on a logarithmic scale.

assemblage during the B/A and Preboreal (2–96%, average 16%), during which *Spiniferites* species (mainly *S. ramosus*) are accompanied by *O. centrocarpum* sensu Wall and Dale and *L. machaerophorum*.

Dinoflagellate cyst concentrations and accumulation rates

Dinoflagellate cyst concentrations range from 180 to 79603 cysts per gram of sediment and show distinct fluctuations (Fig. 7). High dinoflagellate cyst concentrations coincide with warm interstadials (B/A and

Preboreal) and low cyst concentrations with cold stadials (YD and H1). Highest concentrations are attained during B/A and Preboreal, when peaks of *S. ramosus* can be recorded. Autotrophic species reach abundances of 8 to 76 247 cysts per gram sediment, whereas abundances of heterotrophic species range from 172 to 34 021 cysts per gram sediment. Autotrophic cyst concentrations show similar fluctuations as relative abundance of autotrophic species, whereas heterotrophic cysts show distinct differences compared to relative abundance of heterotrophic species (Fig. 7).

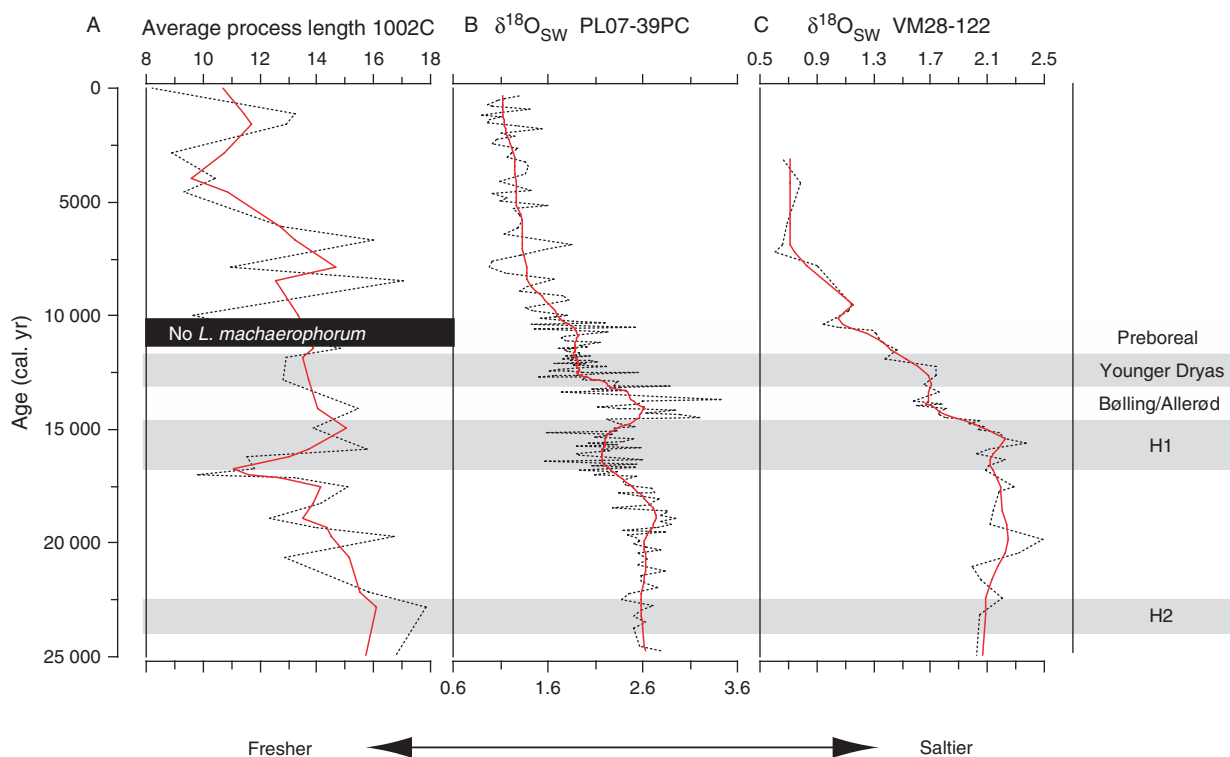


Fig. 8. A. Salinity reconstruction based on *Lingulodinium machaerophorum* average process length. B. Paired Mg/Ca $-\delta^{18}\text{O}$ reconstruction from core PL07-39PC from data of Lea *et al.* (2003) and Lin *et al.* (1997). C. Core VM28-122 from Schmidt *et al.* (2004). Grey bars indicate stadials. The Mg/Ca and $\delta^{18}\text{O}$ only extend the last 25 000 years.

Accumulation rates range between 13 and 5135 cysts/cm² yr, and average 640 cyst/cm² yr, which is comparable to the older record from the Cariaco Basin (González *et al.* 2008b) and the Santa Barbara Basin record (Pospelova *et al.* 2006). All fluctuations of accumulation rates are similar to dinoflagellate cysts per gram of sediment.

It is stressed that the residue was sieved on a 20 µm mesh, and that some of the *Lycopodium* spores were probably lost during sieving (Lignum *et al.* 2008; Mertens *et al.* in prep.). However, presumably, the large amount of amorphous organic matter in the samples will inhibit this process by quickly clogging up the filters. Also, the large fluctuations in concentrations and accumulation rates cannot solely be attributed to methodological issues.

Variation of *L. machaerophorum* process length

L. machaerophorum average process length varies between 8.2 and 17.8 µm and shows distinct fluctuations (Fig. 8). It is compared to another salinity proxy, a paired Mg/Ca $-\delta^{18}\text{O}$ from *Globigerinoides ruber* (white) from the close-by Cariaco Basin core PL07-39PC constructed from Mg/Ca data from Lea *et al.* (2003) and $\delta^{18}\text{O}_c$ data from Lin *et al.* (1997). For the calculation of $\delta^{18}\text{O}_{\text{SW}}$, temperature is removed from the $\delta^{18}\text{O}_c$ record

using the temperature $-\delta^{18}\text{O}_c$ equation calibrated by Thunell *et al.* (1999a, b). Furthermore, *G. ruber* (white) can be considered to be representative of annual-average conditions in the near-surface water (Lin *et al.* 1997).

Despite the scatter in the process length record and a possible dependence of temperature (Mertens *et al.* 2009), consistencies between both independent proxies suggest that both approximate the same environmental variable, i.e. salinity. Both short process lengths and low $\delta^{18}\text{O}_{\text{SW}}$ can be associated with lower salinities and vice versa, and thus both proxies indicate a fresher interglacial and a more saline glacial. On a millennial time scale, H1 and YD both indicate a fresher basin, while the LGM, B/A and Preboreal indicate a saltier environment. These trends on millennial time scales contrast with those from a paired Mg/Ca $-\delta^{18}\text{O}$ by Schmidt *et al.* (2004) core VM28-122 from the Colombian Basin (Fig. 8).

Other palynomorphs

Concentrations of all other palynomorphs show similar fluctuations as their accumulation rates, so only accumulation rates are discussed (Fig. 9).

Most abundant other palynomorphs in the samples are faunal remains of zooplankton (copepod eggs,

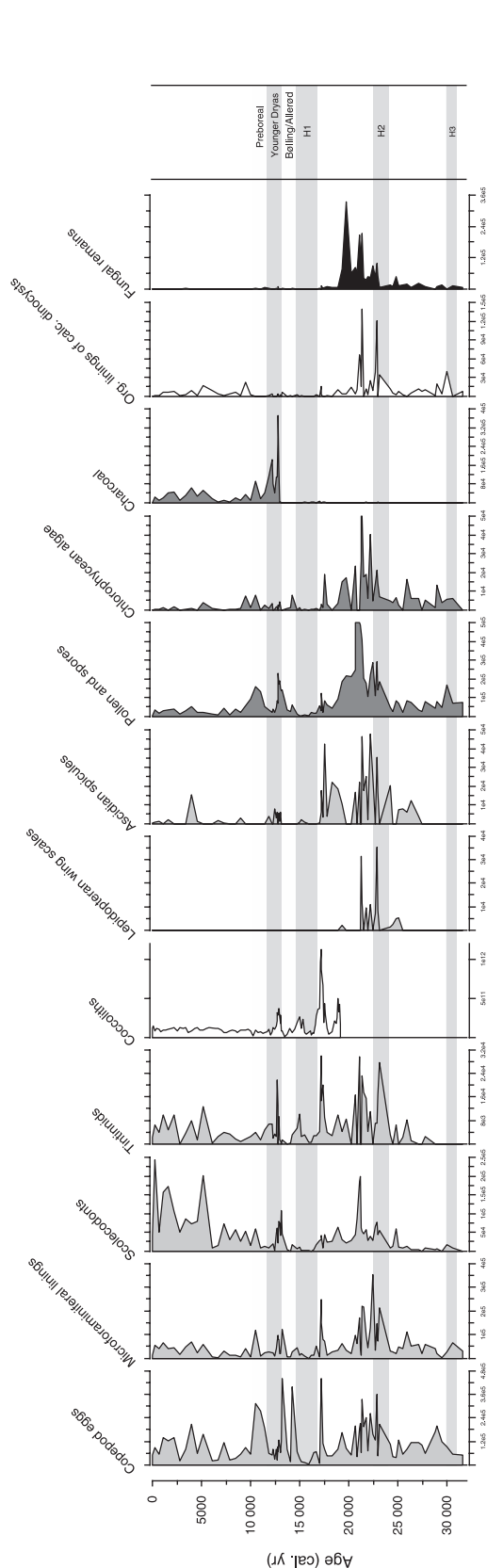


Fig. 9. Accumulation rates of other palynomorphs (in number/cm² kyr): zooplankton (copepod eggs, microfaminiferal linings, scolecodonts and tintinnids), coccoliths (Mertens *et al.* 2008), other faunal remains (Lepidopteran wing scales and Ascidian spicules), floral remains (pollen and spores, Chlorophyta, charcoal), organic linings of calcareous dinocysts and fungal remains. Grey bars indicate stadials.

microforaminifer linings, scolecodonts and tintinnids). Tintinnids and scolecodonts show very similar fluctuations with peaks during YD and H1, whereas copepod eggs and microforaminifer linings show a different pattern with peaks during B/A and Preboreal (Fig. 9). Other faunal remains are lepidopteran wing scales and organic ‘wrappings’ of ascidian spicules. This last new faunal palynomorph has been identified, and radiating crystals are clearly visible even after dissolution of aragonite crystals during palynological preparation (Fig. 5). Lepidopteran wing scales and ascidian spicules show similar patterns, with a distinct peak during the LGM. Fungal remains (fruiting bodies, ascospores, etc.) were also quantified and show a similar manifest peak during the LGM.

The most abundant floral remains are pollen and spores next to charcoal and chlorophyte algae. It has to be noted that the samples were filtered on 20 µm, so a substantial amount of pollen might have been lost, resulting in a bias towards larger pollen. Despite this, results are similar to those of González *et al.* (2008a), where sieves of 8 µm were used. Interstadials can be characterized by high pollen concentrations. Pollen grains are mainly transported into the basin by river influx (González *et al.* 2008a) and together with Chlorophycean algae can be used to indicate increased freshwater influx. Taxa of the class Chlorophyceae (*Pediastrum* and *Botryococcus*) show similar fluctuations as pollen and spores. Charcoal accumulations show a marked peak during the YD, implying the occurrence of frequent fires and thus drier conditions. The charcoal peak in accumulation during the YD was presumably caused by another type of more open vegetation and would have prevented the return of preceding dense and more humid forests (Ledru *et al.* 2002), and can be associated with a forest-savanna turnover (Rull 2007). This peak during the YD is not surprising, since frequent regional burning correlates with periods of rapid climate change (Haberle & Ledru 2001).

Other palynomorphs include organic linings of calcareous dinocysts, *Halodinium* sp. and acritarchs. Only organic calcareous dinocysts reached high enough numbers to show reliable fluctuations, and these show a marked peak during the LGM.

Discussion

Transport

Pollen and spores in the Cariaco Basin are primarily transported into the basin by rivers (González *et al.* 2008a). Enhanced river transport is indicated by higher pollen fluxes during the interstadials (B/A and Preboreal) relative to the stadials (H1 and YD) (Fig. 9). The higher abundance of autotrophic dinoflagellate cysts during these periods (Fig. 7) could reflect

transport of these cysts from the shelf. However, this does not seem to be the case. Other palynomorphs which must be transported from the shelf, e.g. ascidian spicules and lepidopteran scales, do not show enhanced shelf transport during the B/A and the Preboreal periods, but rather during the YD. Ascidians are sessile filter feeding tunicates and are important members of marine benthonic communities throughout shelf seas (Varol & Houghton 1996), and can thus be considered to be indicative of transport from the shelf. Lepidopteran wing scales must also be transported from the shelf. The only time when manifest enhanced transport from the shelf is recorded is during the LGM, since most other palynomorphs show enhanced accumulations during this period (Fig. 9). This is related to the sea-level lowering during the LGM exposing the shelf, which is corroborated by the observations of Piper & Dean (2002).

Another transport issue is turbidite deposition, associated with earthquake activity, which has been previously reported in the Cariaco Basin (Thunell *et al.* 1999a, b; Scranton *et al.* 2001). All turbidites clearly stand out in the Cariaco Basin record and all samples were carefully selected outside the turbidite deposited layers.

Preservation

To see whether selective preservation can be an issue in the Cariaco Basin, a similar grouping as in Zonneveld *et al.* (2001) and Mertens *et al.* (in prep.) was used, to which we added a few species that can be assumed to have had similar resistance to degradation:

- 1 Extremely sensitive: Round brown cysts (*Brigantedinium* spp.), Spiny Brown cysts (*Echinidinium* spp. and *I. minutum*), *Stelladinium* spp., *Lejeunecysta* spp., *Selenopemphix* spp., *Tuberculodinium vancampoe*.
- 2 Moderately sensitive: *L. machaerophorum*, *Melittasphaeridium choanophorum*, *O. centrocarpum* sensu Wall and Dale, *Operculodinium janduchenei*, *Spiniferites* spp., *Achomosphaera* spp., *Q. concreta* and *Votadinium* spp.
- 3 Resistant cysts: *Nematosphaeropsis labyrinthus*, *Impagidinium* spp., *O. israelianum*, *Pentapharsodinium dalei*, *Polysphaeridium zoharyi*, *Ataxiodinium choane* and *Bitectatodinium* spp.

As fluctuations between resistant and sensitive cysts are exactly a reflection of changes between autotrophic and heterotrophic dinoflagellate cysts (Fig. 7), ecological changes cannot be discarded. By studying the coccolith assemblage in the same core over the same interval, Mertens *et al.* (2008) came to the conclusion that high productivity should be considered in sync with less degradation of coccoliths and vice versa. This seems to be similar for dinoflagellate cysts: periods of

high productivity, such as the YD, resulted in low degradation of dinoflagellate cysts, while periods characterized by lower productivity, like the B/A and the Preboreal, resulted in higher degradation of dinoflagellate cysts.

Pronounced disparities can be observed between fluctuations of the relative abundance record and the concentration of heterotrophic dinoflagellate cysts (Fig. 7). These disparities suggest that preservation is an important factor in interpretation of the relative abundance record of the heterotrophic dinoflagellate cysts. On the other hand, this difference between both relative abundance and concentration is not observable in the autotrophic dinoflagellate cysts (Fig. 7), and could be explained by relative enrichment of resistant material causing synchronous increases in relative and absolute abundance of these species.

Degradation could have taken place in the water column, in the sediment or after coring. To assess whether selective preservation is caused by postdepositional degradation after coring, samples from Hole 1002C were compared with samples from similar intervals from MD03-2620, but we found no significant differences in assemblage composition over the selected intervals. Presumably, the degradation process can be considered to have the most important influence in the water column (Mertens *et al.* 2008). Only 1.33% of the surface primary productivity is delivered to the bottom of the Cariaco Basin (Muller-Karger *et al.* 2004). Losses of organic matter occur mostly in the water column, and postdepositional losses are negligible (Wakeham & Ertel 1988). Furthermore, Thunell *et al.* (2007) have shown that particulate organic carbon fluxes strongly correlate with mineral fluxes in the Cariaco Basin. This mineral ballasting could potentially cause enhanced preservation of sensitive dinoflagellate cysts.

The formation of a pyritized 'gley' horizon has been described by Blazhchishin & Lukashina (1995). It corresponds to a zone of sulphide diffusion underlying the transition from oxic to anoxic conditions (Lyons *et al.* 2003) and spans H1 in Hole 1002C. This zone corresponds to a zone of low accumulations of both heterotrophic and autotrophic dinoflagellate cysts, and very likely to a zone of degradation within the sediment, possibly related to pyritization of the cysts.

To conclude, preservation is an issue in the productive Cariaco Basin which can be related to degradation within the water column (from B/A to recent) and postdepositional degradation (during H1). However, since high productivity can be related to enhanced preservation and vice versa, and since absolute abundances of heterotrophic species can be considered to reflect changes in primary productivity (Reichart & Brinkhuis 2003), changes in productivity can still be reconstructed, which will be discussed in the next section.

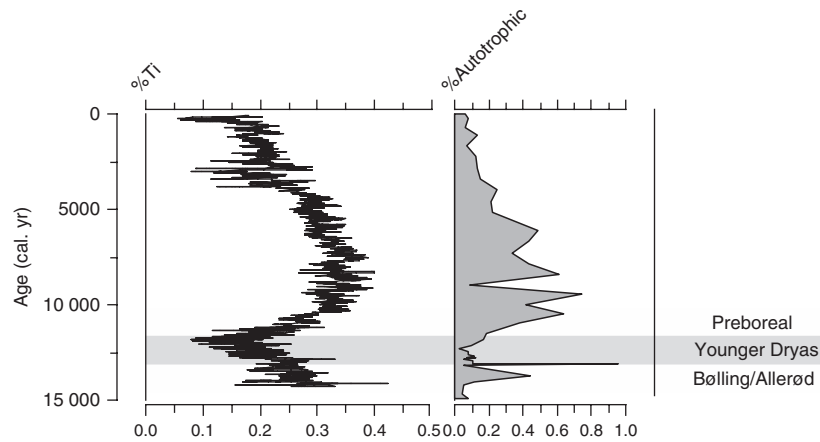


Fig. 10. Comparison between two hydrological proxies, %Ti (XRF data from Haug *et al.* 2001) and % autotrophic dinoflagellate cysts (this study). Grey bars indicate stadials. The Ti XRF data have only been published for the last 14 600 years.

Productivity

In terms of ecology, the shifts between heterotrophic and autotrophic cysts require an explanation. Dinoflagellate plankton studies are rare in the Caribbean (e.g. Marshall 1973), so it is difficult to make direct links to current dinoflagellate blooms in the Caribbean. Despite this fact, insights gained from dinoflagellate studies in other basins can be used to draw inferences about palaeoproductivity changes in the Cariaco Basin.

Globally, heterotrophic species generally dominate areas with enhanced nutrient conditions and active upwelling (Marret & Zonneveld 2003), and absolute abundances of heterotrophic cysts reflect changes in primary productivity (Reichart & Brinkhuis 2003). Both relative and absolute abundances indeed reach higher numbers during the YD (Fig. 7), a period associated with enhanced upwelling in the Cariaco Basin (Peterson *et al.* 2000a, b; Lea *et al.* 2003; Mertens *et al.* 2008). We presume that the time interval that correlates with H1 was also a period of enhanced productivity, as noted by Mertens *et al.* (2008), although the sulphidic overprint mentioned above makes it difficult to recognize it as such. The other stadials associated with Heinrich events (H2 and H3) show peaks of the accumulations of heterotrophic dinoflagellate cysts and confirm previous observations of the older record by González *et al.* (2008b), although it is stressed that other peaks of a similar amplitude can be observed in this part of the record; these peaks cannot thus serve unambiguously to identify these Heinrich events. Other heterotrophic species (*S. nephroides*, *S. reidii*, *Lejeunecysta* spp.) show similar peaks during these HE (Fig. 6). Additionally, we record an event around 8.44 ka by a peak in *S. nephroides*, which can be related to stronger trade winds in the Cariaco Basin (Hughen *et al.* 1996b). This event has also been reflected as a major freshwater event in the Gulf of Mexico from 8.6 to 8.3 kyr, where it can be related to episodic megaflooding of the Mississippi river system or large-scale changes in precipitation patterns over the Gulf of Mexico (LoDico *et al.* 2006).

The autotrophic species are to a large extent determined by relative abundances of *S. ramosus* and *L. machaerophorum* (Fig. 6). In the Amazon region, *S. ramosus* can be related to oligotrophic, shelfward conditions (Vink *et al.* 2000), as in British Columbia estuarine environments, where autotrophic taxa, including *S. ramosus*, are related to stratified coastal waters under the influence of coastal runoff (Radi *et al.* 2007). Also, the abundance of *S. ramosus* shows similar fluctuations as the coccolith *Gephyrocapsa oceanica*, responding to warming of the surface water and high river influx, simultaneously with weakening of upwelling rates, most pronounced during B/A and Preboreal (Mertens *et al.* 2008). Furthermore, the correspondence of Ti (XRF) data (Haug *et al.* 2001) and the relative abundance of autotrophic dinoflagellate cysts (Fig. 10) suggests a rapid response of autotrophic dinoflagellate cysts to high river influx, a similar conclusion as González *et al.* (2008b).

L. machaerophorum shows a very different pattern compared to *S. ramosus* (Fig. 6). According to Vink *et al.* (2003), *L. machaerophorum* can be related to neritic, warm, low-density, stratified environments in the Equatorial Atlantic. The stadials associated with Heinrich events are followed by short events of water column stratification. The middle Holocene also shows a similar stratification of the water column. The different pattern between *S. ramosus* and *L. machaerophorum* suggests that high river influx inhibits *L. machaerophorum* blooms, which could be due to the combination of a number of processes, including enhanced shelfal transports due to heavy monsoonal rainfall (Jordan & Winter 2000) and stagnation of sulphidic waters (Lyons *et al.* 2003) inhibiting excystment (e.g. Kremp & Anderson 2000).

The recorded shifts between an autotrophic dinoflagellate-cyst-dominated record, coupled to river influx, and a heterotrophic dinoflagellate-cyst-dominated record, coupled to higher upwelling rates, confirm the models of González *et al.* (2008b) and Mertens *et al.* (2008), who assert that these rapid changes can be

linked to migrations of the ITCZ. Again, no asynchronicity between the terrestrial and the marine signal can be recorded, as stated in Mertens *et al.* (2008).

The shifts between autotrophic and heterotrophic dinoflagellates can also explain differences between reconstructions using sterol biomarkers of Werne *et al.* (2000) and Dahl *et al.* (2004). In the first study, which solely used dinosterol, little difference was found between YD and Holocene, whereas the latter authors found significant differences between both periods using a larger suite of sterols (chlorine sterol esters, CSEs). Since dinosterol is produced by both autotrophic and heterotrophic dinoflagellates, a differentiation between YD and Holocene will be less pronounced. The approach used by Dahl *et al.* (2004), where specific CSEs are used to track changes in dinoflagellate abundance, enables differentiation between YD and Holocene, and can probably be attributed to these CSEs being mainly produced by autotrophic dinoflagellates. Culture studies on which dinoflagellates produce which CSEs could elucidate this further.

Similar trends in productivity are observed in the other palynomorphs (Fig. 9). Copepod eggs are more abundant during the B/A and the Preboreal (Fig. 9). Copepods are known to prey on dinoflagellates (e.g. Huntley *et al.* 1986; Abrahams & Townsend 1993), which then show the highest accumulations (Fig. 7). Also, the low abundance of copepod eggs during the strong upwelling in the YD could possibly be related to aldehyde production by diatoms inducing reduced hatching success (e.g. Romano *et al.* 2003; Wichard *et al.* 2008). Tintinnid accumulations, on the other hand, are similar to coccolith accumulations (Mertens *et al.* 2008) (Fig. 9), which show their peak during H1 and YD (Mertens *et al.* 2008). This suggests that coccolith accumulations are linked to tintinnid faecal pellet production, which is not surprising since tintinnids are known to feed on coccolithophores (e.g. Winter *et al.* 1986) and material is grouped in aggregates, most likely pellets (Hughen *et al.* 1996a).

Salinity reconstruction

On a glacial–interglacial scale, both the average process length of *L. machaerophorum* and $\delta^{18}\text{O}_{\text{SW}}$ reconstruction indicate a more saline environment during the last glacial, and a fresher basin during the current interglacial (Fig. 8). Increased glacial high-salinity and interglacial low-salinity conditions were also suggested by Peterson *et al.* (1991) studying foraminiferal assemblage changes in Cariaco Basin cores V12-104 and V12-99. Similar observations are made for Hole 1002C (Herbert & Schuffert 2000; Peterson *et al.* 2000b), which can be linked to a greater aridity in the Cariaco Basin during glacial periods (Yarincik & Murray 2000; Martinez *et al.* 2007). Similarly, in the Caribbean Sea,

higher salinity estimates have been inferred during glacial isotope stages based on palaeoecological analyses of coccoliths (Giraudeau 1992) and paired Mg/Ca– $\delta^{18}\text{O}$ measurements (Schmidt *et al.* 2004), so this is not a local phenomenon and can be linked to shifts of the ITCZ causing changes in the thermohaline circulation (Schmidt *et al.* 2004).

On a millennial scale, both salinity proxies indicate a saline LGM and a fresh H1 followed by a more saline B/A and a fresh YD again followed by a more saline Preboreal. A negative excursion during H1 was previously noted by Lin *et al.* (1997) in the oxygen isotope records, and was considered to be related to increased rainfall or meltwater pulse. However, when compared to the salinity reconstruction from core VM28-122 located in the Colombia Basin (Schmidt *et al.* 2004), we observe an opposing pattern, most pronounced during LGM, H1, B/A and YD (Fig. 8). This millennial-scale variability is also opposite to variations in river influx in the Cariaco Basin, indicated by pollen and spores, Chlorophycean algae, autotrophic dinoflagellate cyst accumulations (Figs 7, 9) and plant biomarkers (Hughen *et al.* 2004). The fresh YD also contrasts with an arid YD, which can be inferred from the upwelling record (Lea *et al.* 2003; Mertens *et al.* 2008), but also the charcoal accumulations (Fig. 9) and continental pollen (Salgado-Labouriau 1980; Leyden, 1985) and plant biomarker records (Xu & Jaffé 2008). Also, Amazon river discharge was 40% reduced during the YD (Maslin & Burns 2000). Furthermore, the fresh H1 contrasts with González *et al.* (2008b), who suggested the development of hypersaline coastal environments during HEs. This asynchronicity between salinity records and hydrological records is enigmatic. Sea-level variations do not help to explain the differences. Rapid sea-level rises during meltwater pulses can cause mobilization of the sediment upshelf and drops downslope during lower sea level (Summerhayes *et al.* 1975), and it has been shown to only change the magnitude of terrigenous pulses at the Brazil continental margin (Arz *et al.* 1999), although higher shelf transport during the LGM (see above) does seem to suggest this. Three possible mechanisms can be thought of. The first is an influence of stratification on the salinity records. An increased stratification during interstadials could result in higher salinities if the microfossils recording the salinities were to form deeper in the water column, where salinities are higher. In fact, the dinoflagellate cyst *L. machaerophorum* has been found to occur deeper in the water column (cf. Mertens *et al.* (2009) for a review) and variants of the foraminifer *G. ruber* (white) can also be associated with deeper depth habitats (Wang 2000; Kuroyanagi *et al.* 2008), resulting in different Mg/Ca temperatures (Steinke *et al.* 2008). Another possibility is the more isolated nature of the Cariaco Basin during these times, resulting in anomalous temperatures (Lea *et al.* 2003) and salinities (this

study) for the Caribbean, also suggested by modelling studies (Wan *et al.* 2008). A last possibility is the intrusion of low salinity Antarctic Intermediate Water (AAIW) into the Caribbean during H1 and YD, evidenced by neodymium isotopic variations (Pahnke *et al.* 2008), which then supposedly did not reach as far west as the Columbian Basin.

Conclusions

Assemblage changes of dinoflagellate cysts are determined by productivity changes and show rapid shifts between heterotrophic-dominated assemblages and autotrophic-dominated assemblages, which can be related to shifts of the ITCZ. Owing to the occurrence of large losses in the water column, relative abundance records have to be interpreted with care, and always compared to accumulation records. Stadials (including those associated with Heinrich events) can be characterized by higher upwelling, interstadials by higher river influx preceded by high stratification. The LGM is characterized by influx from the shelf caused by the concurrent sea level lowering.

The average process length of *L. machaerophorum* shows similar fluctuations as a constructed paired Mg/Ca $-\delta^{18}\text{O}$ record and can serve as a semi-quantitative salinity proxy. These salinity proxies show a millennial-scale pattern contrasting to a salinity reconstruction from the open Caribbean Sea and to what would be expected from the hydrological proxies (autotrophic dinoflagellate cysts, Ti (XRF), pollen and spores and Chlorophyta). Changes in the stratification, isolation of the Cariaco Basin or advection of fresh water-masses could explain this discrepancy.

These results confirm previous findings, but also emphasize the uniqueness of this extraordinary environmental setting.

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Appendix I

Species list

- Achomosphaera* Evitt 1963
- Ataxiodinium choane* Reid 1974
- Bitectatodinium spongium* Zonneveld 1997
- Bitectatodinium tepikiense* Wilson 1973
- Brigantodinium* Reid, 1977 ex. Lentin and Williams 1993
- Brigantodinium cariacense* (Wall 1967) Lentin and Williams 1993
- Brigantodinium simplex* Wall 1965 ex. Lentin and Williams 1993
- Echinidinium* Zonneveld 1997
- Echinidinium aculeatum* Zonneveld 1997
- Echinidinium delicatum* Zonneveld 1997
- Echinidinium euaxum* (Head 1993) Zonneveld 1997
- Echinidinium granulatum* Zonneveld 1997
- Echinidinium transparentum* Zonneveld 1997
- Impagidinium aculeatum* (Wall 1967) Lentin and Williams 1981
- Impagidinium paradoxum* (Wall 1967) Stover and Evitt 1978
- Impagidinium patulum* (Wall 1967) Stover and Evitt 1978
- Impagidinium striatum* (Wall 1967) Stover and Evitt 1978
- Impagidinium* Stover & Evitt 1978
- Islandinium minutum* Harland and Reid in Harland *et al.* 1980
- Lejeunecysta marieae* Harland in Harland *et al.* 1991 ex. Lentin and Williams 1993
- Lejeunecysta oliva* (Reid 1977) Turon and Londeix 1988
- Lejeunecysta sabrina* (Reid 1977) Bujak 1984
- Lejeunecysta* sp. A

- Lingulodinium machaerophorum* (Deflandre and Cookson 1955) Wall 1967
Melitasphaeridium choanophorum (Deflandre and Cookson, 1955) Harland and Hill, 1979
Nematosphaeropsis labyrinthus (Ostenfeld 1903) Reid 1974
Operculodinium centrocarpum (Deflandre and Cookson 1955) Wall 1967
Operculodinium israelianum (Rossignol 1962) Wall 1967
Operculodinium janduchenei Head *et al.* 1989
Polysphaeridium zoharyi (Rossignol 1962) Bujak *et al.* 1980
Quinquecuspis concreta (Reid 1977) Harland 1977
Selenopemphix nephroides Benedek 1972; emend. Bujak in Bujak *et al.* 1980; emend. Benedek and Sarjeant 1981
Selenopemphix quanta (Bradford 1975) Matsuoka 1985
Selenopemphix selenoides Benedek, 1972
Spiniferites bentorii (Rossignol 1964) Wall and Dale 1970
Spiniferites elongatus Reid 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) Loeblich and Loeblich 1966; emend. Davey and Williams 1966
Spiniferites scabratus (Wall 1967) Sarjeant 1970
Spiniferites Mantell, 1850; emend. Sarjeant 1970
Stelladinium reidii Bradford 1975
Tuberculodinium vancampoae (Rossignol 1962) Wall 1967
Votadinium calvum Reid 1977