

Palaeoecology of calcareous dinoflagellate cysts in the mid-Cenomanian Boreal Realm: implications for the reconstruction of palaeoceanography of the NW European shelf sea



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A transect from the bathyal to proximal shelf facies of the Boreal Realm was investigated to compare spatial and temporal distribution changes of calcareous dinoflagellate cysts (c-dinocysts) throughout the mid-Cenomanian in order to gain information on the ecology of these organisms. Pithonelloideae dominated the cyst assemblages to more than 95% on the shelf, a prevalence that can be observed throughout most of the Upper Cretaceous. The affinity of this group with the dinoflagellates, which is still controversially discussed, can be confirmed, based on evidence from morphological features and distribution patterns. The consistent prevalence of *Pithonella sphaerica* and *P. ovalis* in c-dinocyst assemblages throughout the Upper Cretaceous indicates that they were produced more frequently than cysts of the other species and might, therefore, represent a vegetative dinoflagellate life stage. *P. sphaerica* and *P. ovalis* are interpreted as eutrophic species. *P. sphaerica* is the main species in a marginal-shelf upwelling area, offshore Fennoscandia. Here, sedimentary cyclicality appears to have been reduced to the strongest light/dark changes, while in the outer shelf sediments, light/dark cycles are well-developed and show pronounced temporal assemblage changes. Cyclic fluctuations in the *P. sphaerica*/*P. ovalis* ratio reflect shifts of the preferred facies zones and indicate changes in surface mixing patterns. During periods of enhanced surface mixing most parts of the shelf were well-ventilated, and nutrient-enriched surface waters led to high productivity and dominance of the Pithonelloideae. These conditions on the shelf contrasted with those in the open ocean, where more oligotrophic and probably stratified waters prevailed, and an assemblage with very few Pithonelloideae and dominance of *Cubodinium renei* and *Orthopithonella? gustafsonii* was characteristic. While orbitally-forced light/dark sedimentary cyclicality of the shelf sections was mainly related to surface-water carbonate productivity changes, no cyclic modulation of productivity was observed in the oceanic profile. Therefore, dark layer formation in the open ocean was predominantly controlled by the cyclic establishment of anoxic bottom water conditions. Orbitally-forced interruptions in mixing on the shelf resulted in cyclic periods of stratification and oligotrophy in the surface waters, an expansion of oceanic species to the outer shelf, and a shelfward shift of pithonelloid-facies zones, which were probably related to shelfward directed oceanic incursions.

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1. Introduction

Calcareous dinoflagellate cysts (c-dinocysts) are important contributors to the nanno- and microfossil limestones of Upper Cretaceous depositional sequences. Up to 10% of the carbonate grains of the Cenomanian marly chalks of the NW European shelf are remains of these phytoplankton organisms. Despite this quantitative significance, little is known

about their ecology. Dinoflagellates are unicellular, biflagellate algae that are able to swim actively. A number of dinoflagellate species produce fossilisable cysts during their life cycle. In contrast to organic-walled cysts, most of the c-dinocysts have a long stratigraphic range and cannot be used in biostratigraphy. However, investigation of their ecology can give valuable information on regional oceanographic conditions.

Early approaches to reconstructing palaeofacies zones using c-dinocyst distribution patterns were

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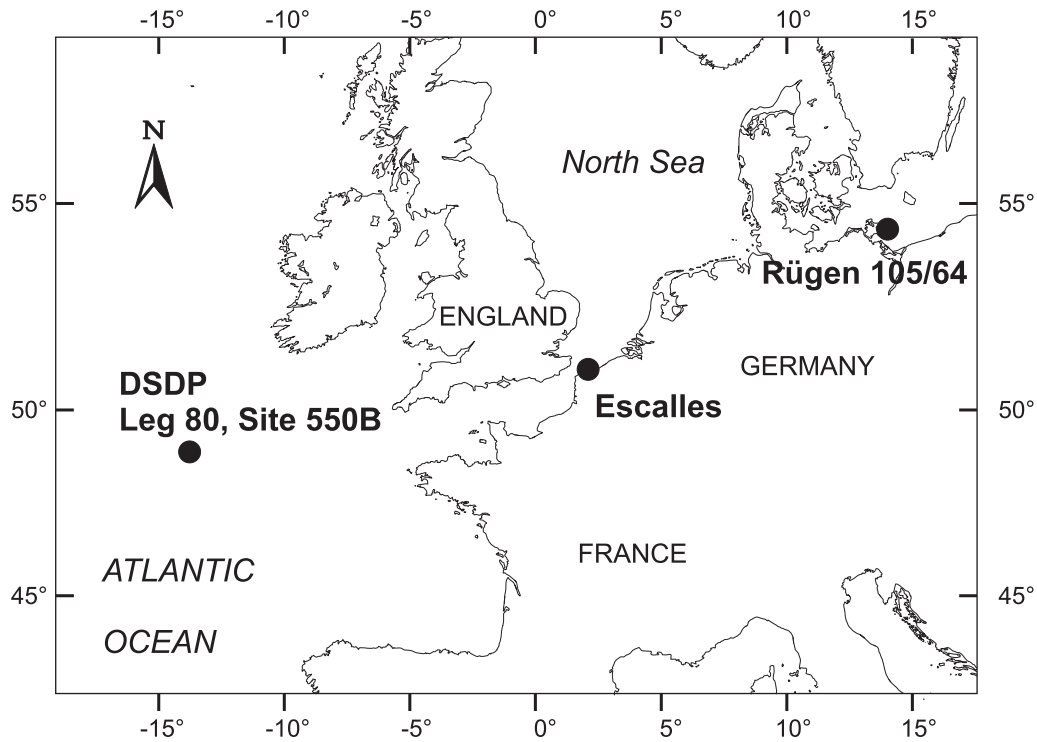


Figure 1. Geographic location of the sections investigated.

made by Keupp (1981, 1987, 1991, 1993, 1995), Keupp & Mutterlose (1984), Keupp & Kowalski (1992) and Zügel (1994). A comprehensive review of studies on pithonelloid *c*-dinocysts and an overview of the global distribution and palaeoecology of the Pithonelloideae was given by Dias-Brito (2000). As the Pithonelloideae are the main element of assemblages investigated in the present study, special focus is put on discussing their affinity to dinoflagellates, which is still debated.

In a recent paper, we reported an analysis of changes in abundance of *c*-dinocysts during orbitally-forced cyclic sedimentary alternations of chalks and marls in the mid-Cenomanian (J. Wendler *et al.*, 2002). These cyclic variations of cyst assemblages can be explained by changes in the intensity of vertical mixing in the surface waters. For a better understanding of the oceanographic changes related to such temporal variations in cyst assemblage it is important to obtain information on the spatial cyst distribution.

The present paper considers the palaeoecology of *c*-dinocysts based on their palaeo-bathymetrical distribution patterns on the NW European shelf within a narrow time period of the mid-Cenomanian. In order to distinguish between oceanic and shelf sea assemblages, we analysed various palaeo-bathymetrical positions around palaeolatitude 40°N at the transition

between the Boreal and Tethyan Realms. The chosen sections represent a transect from a deep marine facies, via an outer shelf position, to proximal shelf. Upwelling throughout the Late Cretaceous has been reconstructed for the marginal shelf location studied, based on numerical models (Parrish & Curtis, 1982; Barron, 1985; Scotese & Summerhayes, 1986). Carbon isotope data of the *R. cushmani* through *H. helvetica* foraminiferal biozone (Hilbrecht *et al.*, 1992) support these models. Thus, this section is suitable for gaining information on the relationship between cyst production and upwelling, which is largely unknown. An approach is made to associate spatial assemblage changes to palaeoceanographic parameters such as differences in nutrient supply, surface water temperature and salinity. We discuss the role of current-induced cyclic oceanic incursion into the shelf environment as indicated by spatial and temporal changes in the cyst-assemblage.

2. Material and methods

2.1. Material

Three sections of mid-Cenomanian age located along a transect across the European shelf were investigated (Figure 1). The time-span analysed covers three to six

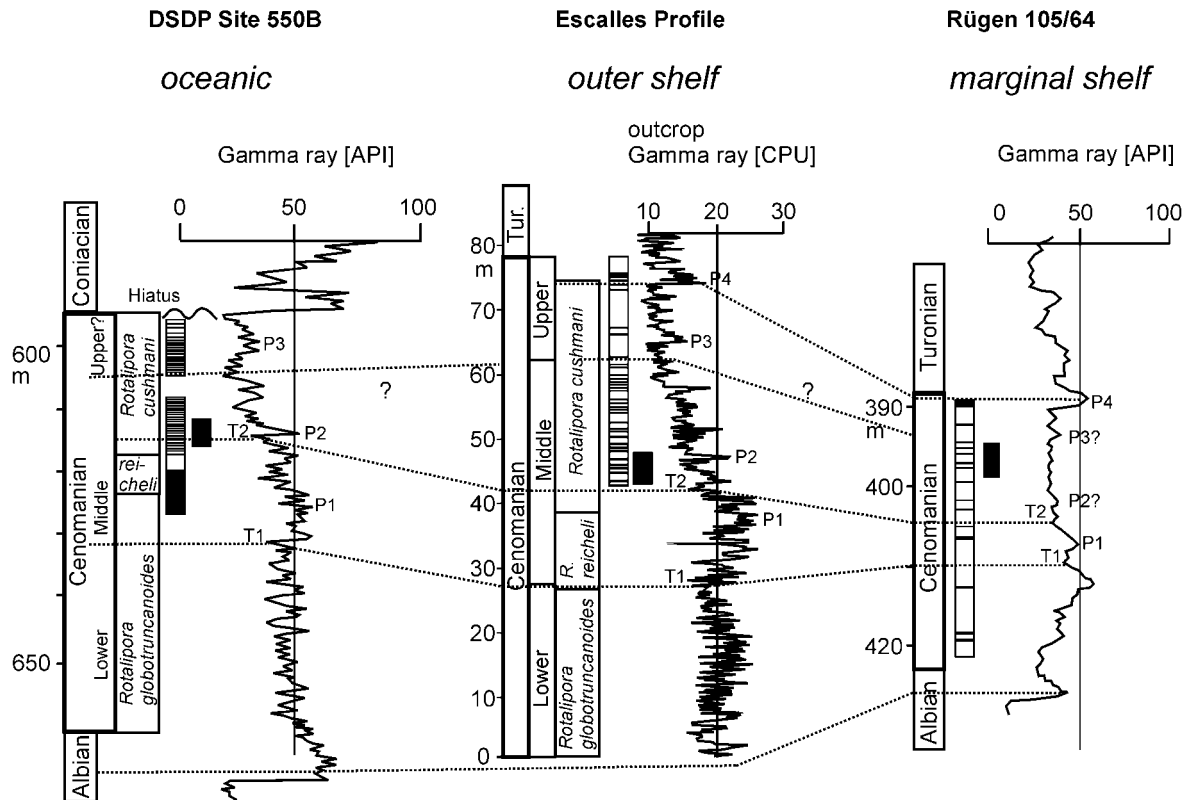


Figure 2. Correlation of the sections investigated based on foraminiferal biostratigraphy, lithology and gamma logs. Lithologic logs show a decreasing frequency of light/dark cycles from ocean/slope towards the marginal shelf; black bars, position of analysed samples; T, trough in the gamma log; P, peak of high gamma values; foraminiferal biozones after Robaszynski & Caron (1995).

precession-controlled light/dark couplets (21 ka). The precession-nature of these cycles has been supported in the literature by spectral analysis (Gale *et al.*, 1999) and analysis of the cycle architecture (J. Wendler *et al.*, 2002). The DSDP drill Site 550B (Leg 80) is situated in the Atlantic Ocean near the Goban Spur and the continental slope. Its bathyal palaeoenvironmental position during the Cenomanian is indicated by oceanic crust bottom rocks of latest Albian age, the dominance of planktic foraminifera (Graciansky *et al.*, 1985) and a low accumulation rate as indicated by the couplet thickness. The investigated core 17 (*Rotalipora cushmani* foraminiferal Zone) of the fully pelagic, deep marine DSDP section consists of a cyclical alternation of dark grey to black, pyrite-rich, 5–20-cm-thick nannofossil marls and 10–50-cm-thick greenish-grey to white nannofossil marls. Pore space is completely cemented throughout the core. The most severe recrystallisation is observed in the dark layers. Ten samples were analysed at a sample spacing of 6–20 cm.

The time span investigated in the outer shelf section 'Escalles' (situated to the south of Calais, France,

Anglo-Paris Basin) is represented by a succession 4 m thick, containing six chalk-marl couplets that represent the basal *Rotalipora cushmani* Zone. The section has a well-established bio-, litho- and sequence-stratigraphy according to Robaszynski & Amédéo (1993), Owen (1996) and Robaszynski *et al.* (1998). Cementation varies throughout the profile and is strong in some light layers and generally weaker in the dark layers. Cyst data were retrieved from 17 samples at a spacing of 10–20 cm.

The Rügen 105/64 borehole represents a proximal shelf position in the northeast of the German Basin, in close vicinity to the Fennoscandian continent. It is less cyclically developed than the two other sections and consists mainly of monotonous white marly limestone. Compared to the two other profiles, a major part of this section contains remains of macrofossils, including bivalves and brachiopods, and mica, which reflect its marginal palaeogeographic position. Because cementation is high in most light layers, sample spacing for cyst analysis is variable and only few values could be obtained from chalks. We examined 16 samples from a 3-m-thick succession of five

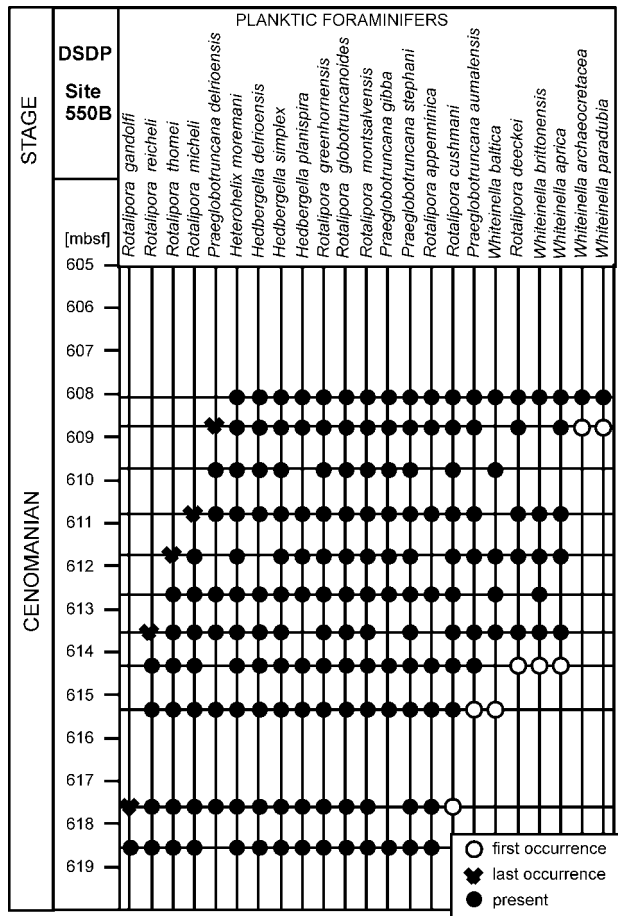


Figure 3. Distribution of planktic foraminifera throughout the core from DSDP Site 550B.

chalk/marl couplets at a spacing of 10–50 cm. The Rügen 105/64 core is stored at the core archive of the Mecklenburg-Vorpommern Geological Survey and is numbered E Rn 105/64. Raw sample material, processed samples and SEM stubs of all analyses are stored at the Division of Historical Geology and Palaeontology of the University of Bremen.

2.2. Methods

Correlation of the three profiles is based on foraminiferal biostratigraphy (zones after Robaszynski & Caron, 1995) and graphic correlation of stratigraphic events (foraminiferal occurrences and gamma ray logs). Graphic correlation and the establishment of the line of correlation were carried out using the work of Carney & Pierce (1995) and MacLeod & Sadler (1995). The gamma ray logs are plotted, using borehole gamma ray data of the DSDP section (Graciansky *et al.*, 1985) and of the Rügen section (courtesy of Mecklenburg-Vorpommern Geological

Survey). For the Escalles section, an outcrop gamma ray log was used (Gräfe, 1999).

For the analyses of foraminifera, 50–100 g of sediment were processed using repeated freezing and thawing in sodium sulphate, and sieved into 125–212 μm , 212–300 μm and 300–425 μm fractions. One hundred specimens per sample were determined by optical microscopy.

The least cemented material of the sections investigated was chosen for cyst analysis as reliable data depend on preservation of specimens. All investigations were done on disaggregated material. One major advantage of analysing calcareous dinoflagellate cysts is that the amount of sample needed is about 100 times less than that required for comparable studies on foraminifera. This is owing to the smaller size of the cysts and a higher volume and weight percentage of the respective grain size fraction in the sediment. Samples comprising 0.5 g of sediment were processed by repeated freezing and thawing in saturated sodium sulphate solution. Ultrasonic cleaning was applied for various durations, depending on the clay content and the degree of interparticle cementation. The cleaning process was controlled by optical microscopy between cleaning steps. The disaggregated samples were sieved into three fractions (<20 μm , 20–75 μm and >75 μm) of which the 20–75 μm fraction covers the size range of Cenomanian c-dinocysts. Information on the grain size distribution of the investigated samples was obtained by measuring the weight of these fractions.

Cysts were counted and picked from weighted splits (1.2–4 mg) of the 20–75 μm fraction, using a Zeiss binocular microscope Stemi2000 at 100 \times magnification. The determination of the species was carried out using a Scanning Electron Microscope (SEM).

The carbonate content was measured with a ‘carbonate bomb’ (Carbometer mod. 23) in order to evaluate general differences in carbonate content between sections and between light and dark layers. The grey scale of the dry, unprocessed samples was determined using the Munsell soil-colour chart. Cathodoluminescence, using a Cold Cathode Luminescence System 8200 MK II coupled with an Olympus BH-2 optical microscope, was applied to analyse pithonelloid tests for subtle morphological characteristics.

3. Results

3.1. Correlation

The correlation of the sections investigated by gamma logs and foraminiferal biostratigraphy is shown in Figure 2. The first and last occurrences of

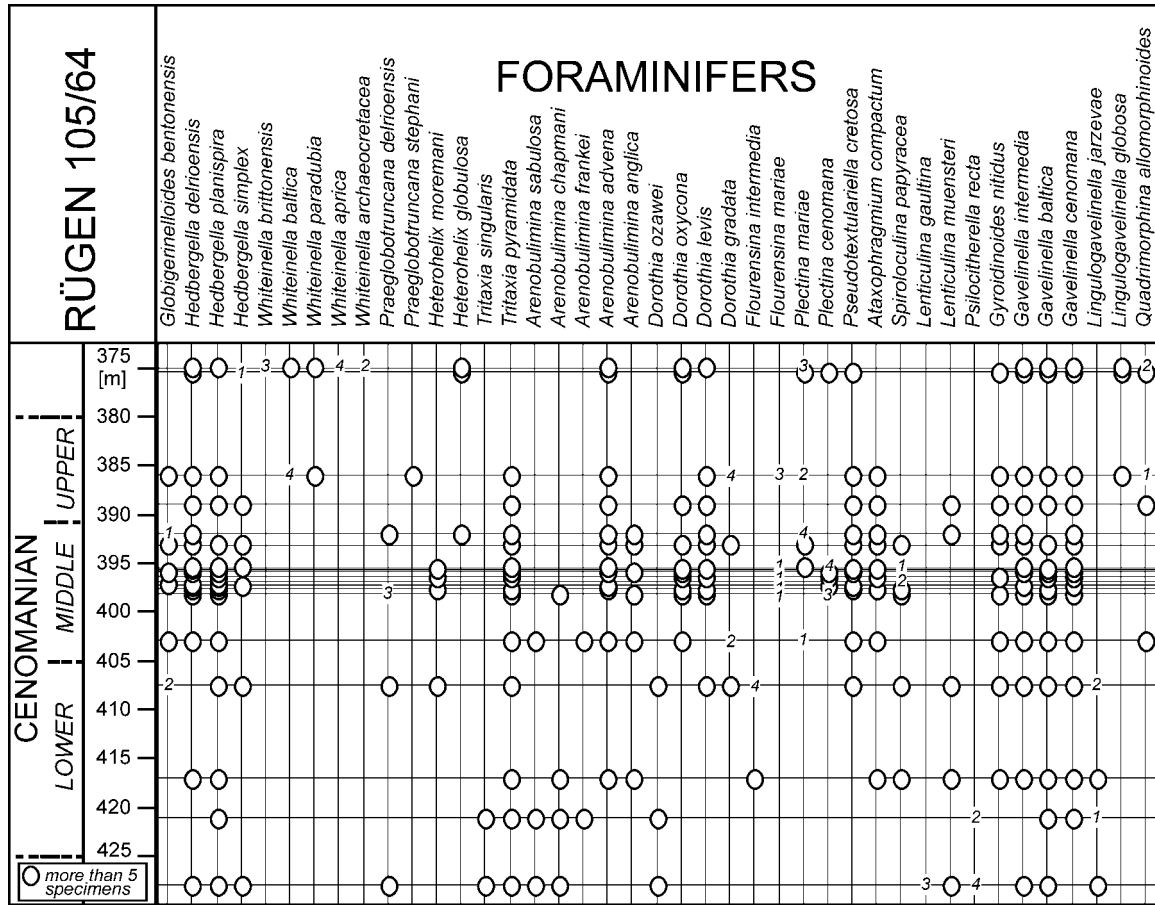
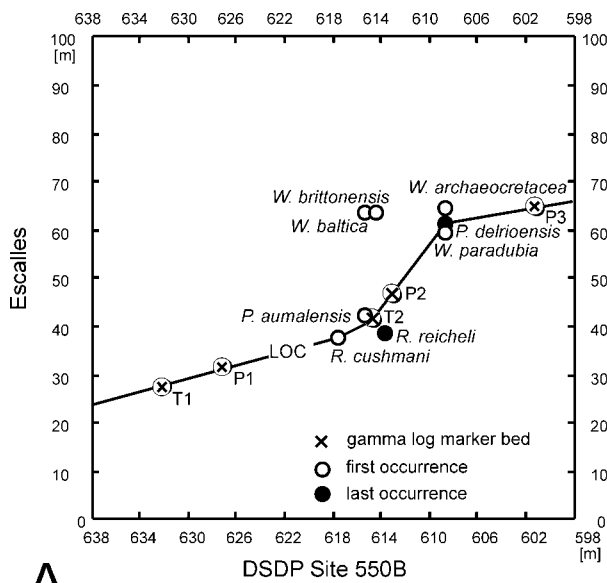


Figure 4. Distribution of benthic and planktic foraminifera throughout the borehole section of Rügen 105/64.

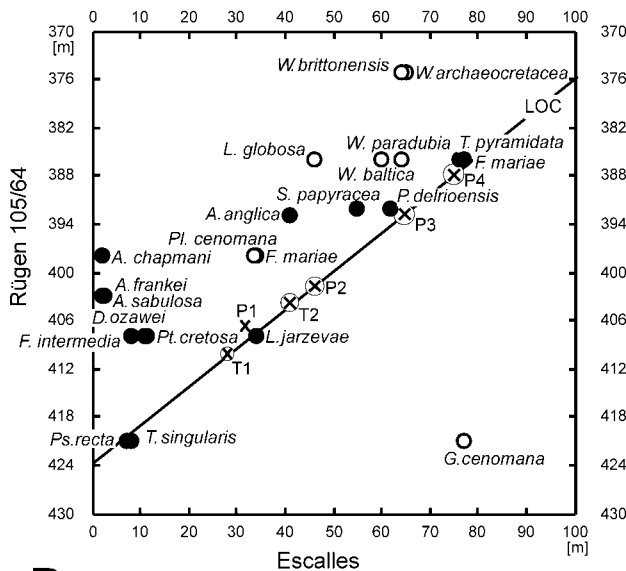
Cenomanian marker species of planktic and benthic foraminifera can be well defined for the succession of the DSDP borehole Site 550B and the Rügen 105/64 section, respectively (Figures 3, 4). The assemblages of benthic foraminifera in the latter are comparable to the fauna of sections in southern England (e.g., Carter & Hart, 1977), which in terms of water depth have been interpreted as deposits of outer shelf environments. The biostratigraphic and gamma ray logging data and information in the literature on benthic foraminifera for the Escalles section (Carter & Hart, 1977; Gräfe, 1999) comprise the input for the graphic correlation of the three profiles (Figure 5A, B).

The Lower/Middle Cenomanian boundary is defined lithologically for Site 550B (Graciansky *et al.*, 1985) and the Escalles sections. Gamma log data provide a new tool in correlating stratigraphic events. Gräfe (1999) and J. Wendler *et al.* (2002) showed that the gamma curve of the outer shelf section of Escalles reflects major changes in clay content (e.g., the CTBE), as well as orbitally-forced variations that are related to bio-productivity, i.e.,

independent from local variations in clay mineral content (terrigenous input). The resulting gamma curve shows a distinctive shape characterised by the troughs and peaks indicated in Figure 2. The gamma ray log shows a trough (T1) at that position (Figure 2). This gamma ray decrease is also recognisable in the Rügen 105/64 core data (Figure 2). The mid-Cenomanian transition from the *Turrilites costatus* to the *T. acutus* ammonite subzones is characterised by a distinct decrease in gamma ray values (T2 in Figure 2). This 'gamma break' is clearly evident in all three sections and the graphic correlation of the planktic foraminiferal data corroborates its synchronicity between Site 550B and Escalles. The Upper Cenomanian Oceanic Anoxic Event can be determined lithologically, and by gamma ray and carbon isotope data, in the Escalles and Rügen 105/64 sections. The entire Upper Cenomanian appears to be missing at Site 550B as a result of a hiatus (Graciansky *et al.*, 1985). However, our analysis of planktic foraminifera suggests that part of the Upper Cenomanian might be present (Figures 3, 5). The



A



B

Figure 5. A, graphic correlation between DSDP Site 550B and the Escalles section based on first and last occurrences of planktic foraminifera marker species and marker beds defined by gamma ray data (T1, T2, P1–P3); for input data see Figures 2 and 3, and Gräfe (1999). B, graphic correlation between the Escalles section and the Rügen 105/64 borehole based on foraminiferal stratigraphic events and marker beds (T1, T2, P1–P4) defined by gamma ray logs; for input data see Figures 2, 4 and Gräfe (1999). Abbreviations: LOC, Line of correlation; *R.*, *Rotalipora*; *P.*, *Praeglobotruncana*; *W.*, *Whiteinella*; *A.*, *Arenobulimina*; *D.*, *Dorothia*; *F.*, *Flourensina*; *G.*, *Gavelinella*; *L.*, *Lingulogavelinella*; *Pl.*, *Plectina*; *Ps.*, *Psilocitherella*; *Pt.*, *Pseudotextulariella*; *S.*, *Spiroloculina*; *T.*, *Tritaxia*.

graphic correlation model supports the synchronicity of the marker events defined by the gamma ray logs and some planktic foraminiferal events. Foraminiferal events that are not aligned on the line of correlation are interpreted to have diachronous occurrences in the sections. The last occurrences (LOs) of the benthic foraminifera *Psilocitherella recta* and *Tritaxia singularis* near the Albian/Cenomanian boundary, and the LO of *Tritaxia pyramidata* and *Flourensina mariae* near the Upper Cenomanian OAE appear to be isochronous events in the Escalles and Rügen sections. Concluding, the analysed sections represent relatively isochronous deposits within the upper part of the middle Cenomanian.

3.2. Lithological differences between the three sections

The sections investigated show considerable differences in the development of light/dark sedimentary cycles (couplets). As the most notable trend, couplets are thin and very narrowly-spaced in the DSDP core, become thicker and more widely spaced towards the Escalles section, and finally appear incomplete, i.e., lower in both number and frequency, in the Rügen 105/64 section (Figure 2).

The carbonate content, grey scale and grain size are compared in Figure 6. In Figure 6A, five couplets of each section are plotted to illustrate differences in thickness and carbonate content. The DSDP section is thinnest. Couplets in this section consist of very fine-grained material without differences in grain-size distribution between light and dark layers (Figure 6D). Very distinctive changes occur in the grey scale (Figure 6C) but the carbonate content between light and dark layers shows only minor fluctuations in this section (Figure 6A, B). The carbonate content of the DSDP section is within 57–65 wt%, considerably lower than in the Escalles and Rügen 105/64 sections, which have carbonate contents of between 71 and 92 wt%. In contrast to the two shelf sections, carbonate contents are higher in the dark layers than in the light layers of the DSDP section. This can be attributed to cementation because the dark layers generally show an increased amount of cement crust around particles. Dark layers in the Escalles and Rügen 105/64 sections have generally decreased carbonate contents; however, in the grey scale there is little contrast with the light layers. It is important to note that in both shelf sections, the difference in carbonate content between dark and light layers (Figure 6A, dashed lines) varies over the section and appears to be modulated by a lower frequency forcing, as discussed for the Escalles section by J. Wendler *et al.* (2002).

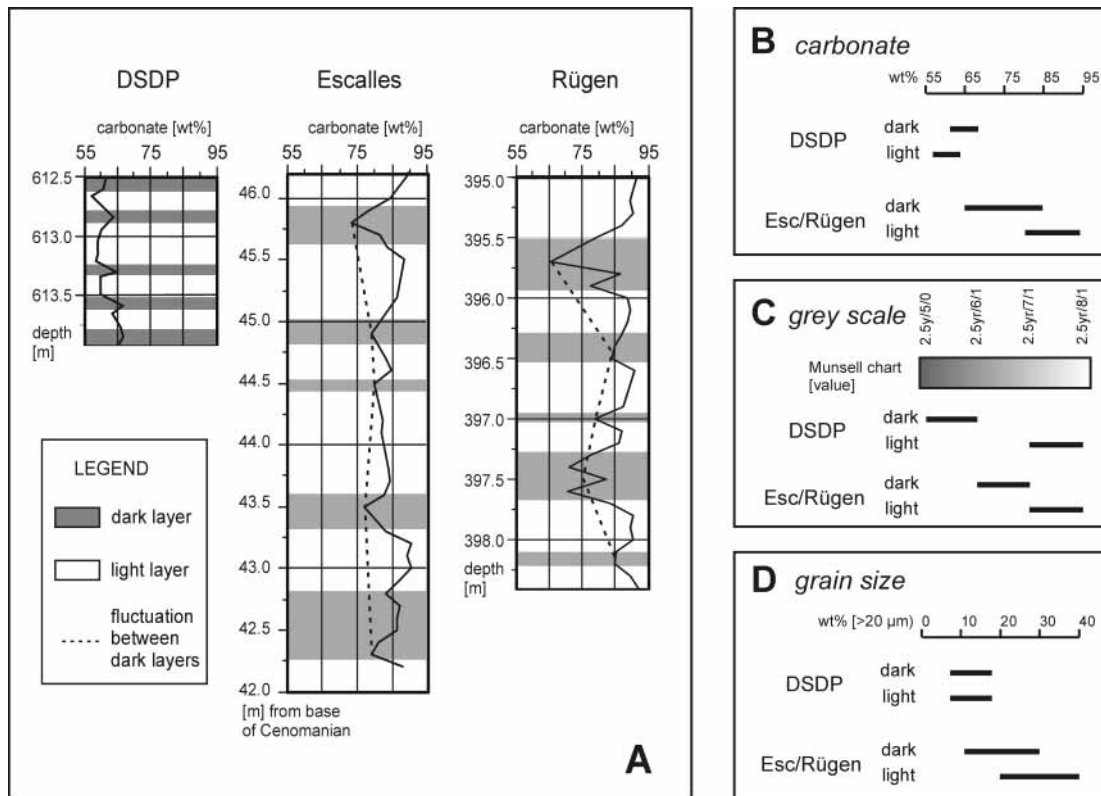


Figure 6. A, comparison of fluctuations in carbonate content through five light/dark couplets in the DSDP, Escalles and Rügen sections; note the reduced thickness of the DSDP section and different type of light/dark alternation showing increased carbonate content in dark layers. B, ranges in the carbonate fluctuation of light and dark layers. C, ranges in the grey scale of light and dark layers; note the strong contrast in the DSDP section. D, ranges in grain size; note the low fluctuation in the fine-grained DSDP section.

3.3. Calcareous dinoflagellate cyst assemblages

The three sections exhibit distinctive differences in c-dinocyst associations. The species investigated for the present paper are illustrated in Figure 7. While the shelf sections Escalles and Rügen 105/64 are dominated by the Pithonelloideae, the DSDP section yielded generally very low c-dinocyst concentrations, and Pithonelloideae are almost absent (Figure 8). The dominant elements of the assemblages in the oceanic section are *Cubodinium renei* Keupp (1987) (often >50% of the assemblage), *Orthopithonella? gustafsonii* Bolli (1974) *sensu* Keupp & Versteegh (1989) and *Pirumella edgari* Bolli (1974) (Figure 8). In contrast to most light/dark couplets in the Escalles section, cyst distribution in the DSDP section does not show any relationship to lithological changes. In the discussion below this c-dinocyst assemblage will be termed the oceanic or o-assemblage.

Two different shelf-assemblages can be distinguished primarily by the distribution of the Pithonelloideae *P. sphaerica* and *P. ovalis* Kaufmann (1865). A dominance of *Pithonella sphaerica* at a ratio of *P.*

sphaerica:*P. ovalis* (Ps/Po ratio) of about 3 is observed in the Escalles section. The Ps/Po ratio is lower in most marls because of a decrease in abundance of *P. sphaerica*. In the Rügen 105/64 section, the Ps/Po ratio is much greater than 10 throughout, including the marls; i.e., the pithonelloid association is dominated by *P. sphaerica* up to more than 90% (e.g., samples R 127, 128 in Figure 8). Substantial changes in cyst assemblage occur only in the most distinctive marls ('marker beds' in Figure 8). Therefore, we can distinguish between a marginal shelf assemblage (MS) represented by the Rügen 105/64 profile, and an outer shelf assemblage (OS) found in the Escalles section. These shelf assemblages can be further characterised by specific occurrences of other c-dinocysts.

The MS-assemblage does not contain cysts of *Cubodinium renei* nor species with orthogonal wall crystal orientation. It thus differs considerably from the o-assemblage. Along with *Pithonella sphaerica*, *Pentadinellum vimineum* Keupp (1987) is the characteristic species of the MS-assemblage. Furthermore, an increased presence of spiny cysts is noted (Figure

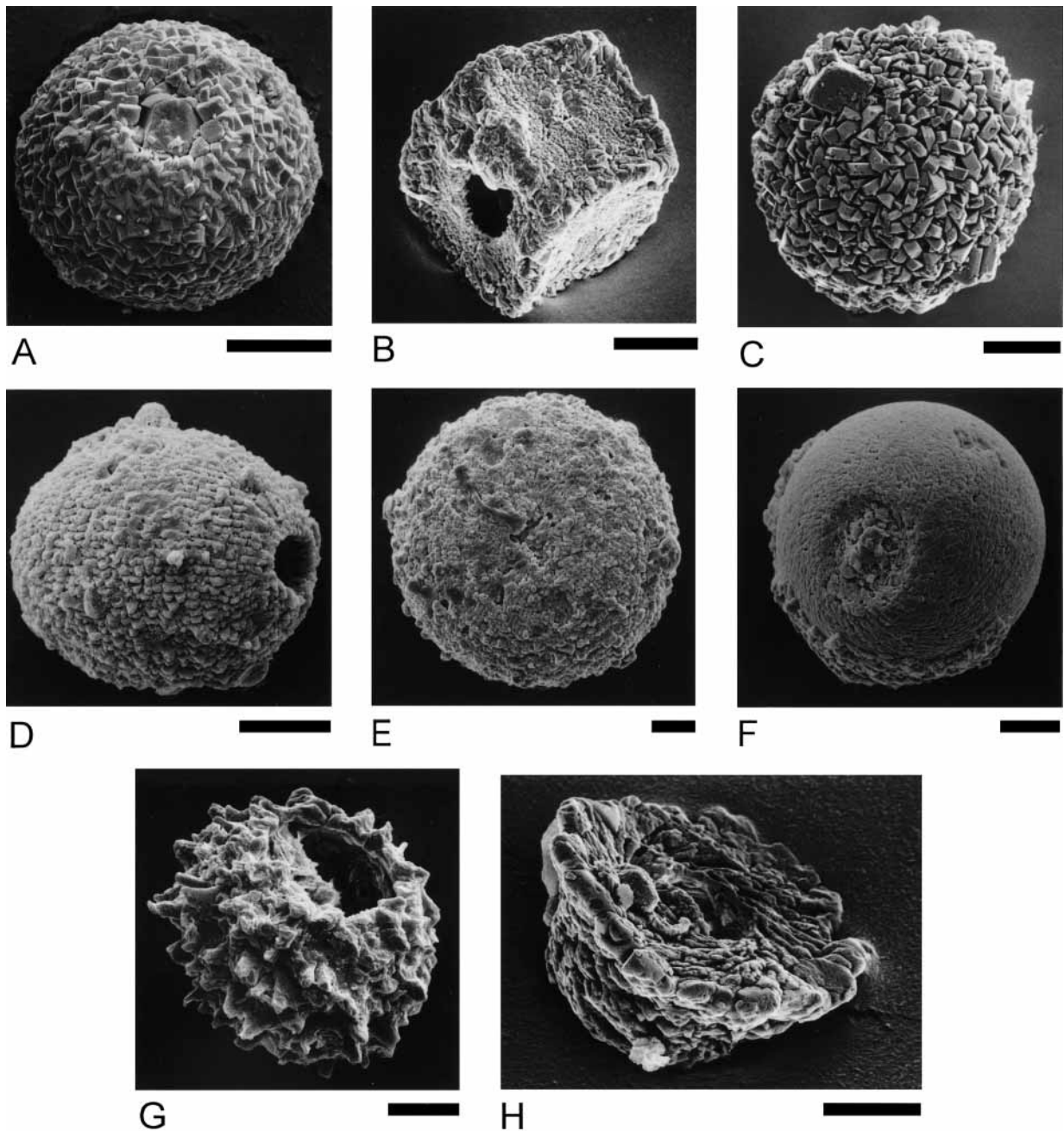


Figure 7. Calcareous c-dinocyst species investigated in the present study; scale bars represent 10 μm . A, *Orthopithonella? gustafsonii* Bolli (1974), o-assemblage, DSDP 17-4-1. B, *Cubodinellum renei* Keupp (1987), o-assemblage, DSDP 17-4-3. C, *Pirumella edgarii* Bolli (1974), o-assemblage, DSDP 17-4-5. D, *Pithonella ovalis* Kaufmann (1865), OS-assemblage; Escalles I-5. E, *Pithonella sphaerica* Kaufmann (1865), MS-assemblage (OS-assemblage), Escalles I-12. F, *Pithonella sphaerica*, showing the inner wall and contours of archeopyle, Escalles I-6. G, spiny morphotype, MS-assemblage, Rügen-135. H, *Pentadinellum vimineum* Keupp (1987), OS-, MS-assemblage (o-assemblage); Rügen-120.

8). The OS-assemblage is characterised by the presence of both the species of the o-assemblage and *Pentadinellum vimineum* (Figure 8), as would be expected from its intermediate position between the other two profiles.

In summary, a clear ocean to shelf distribution trend is indicated by shelfward-increasing abundances of Pithonelloideae, an increasing Ps/Po ratio, and decreasing numbers of *Cubodinellum renei* and *Orthopithonella? gustafsonii*. While *C. renei* and *O.?*

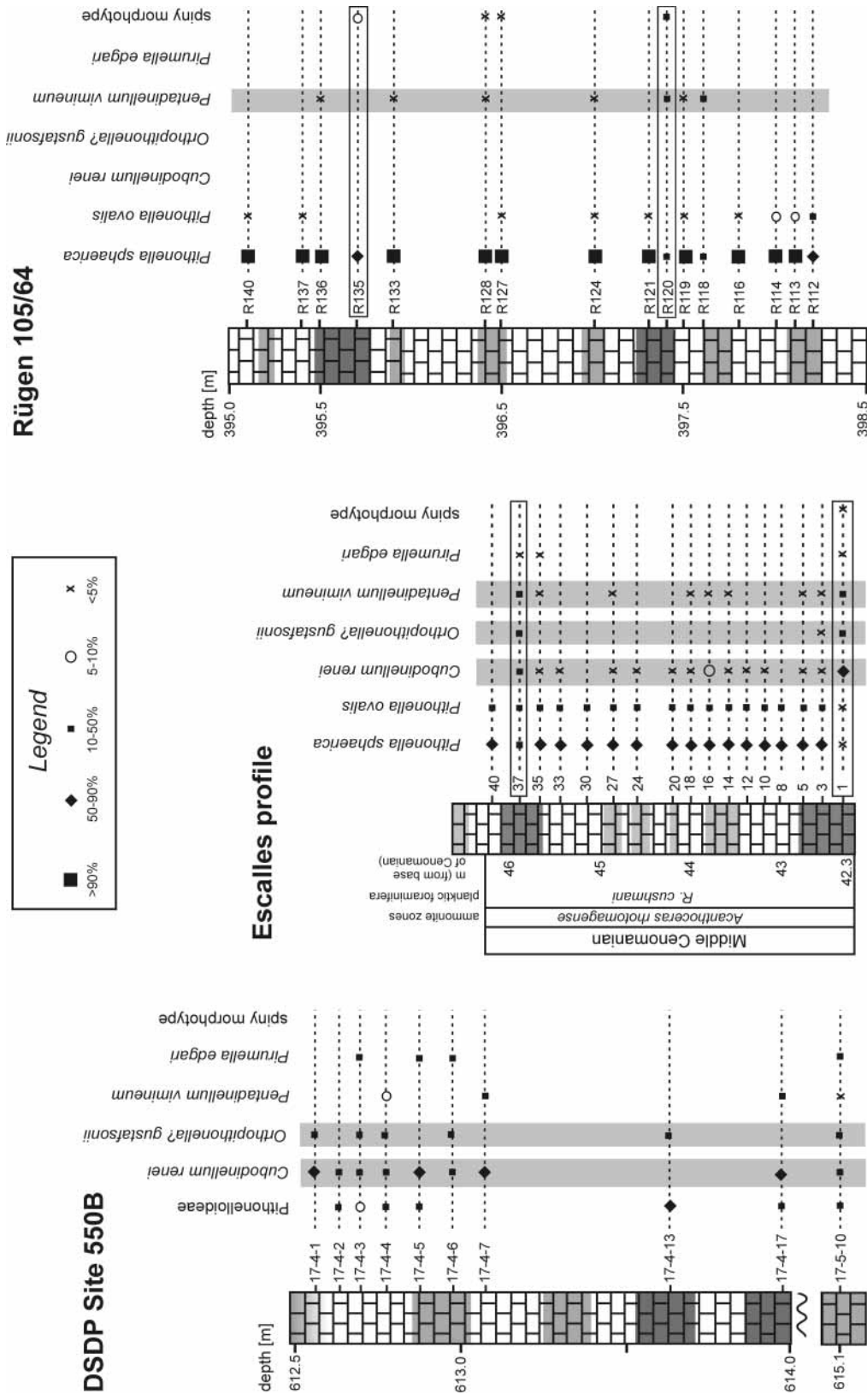


Figure 8. Comparison of relative cyst abundances in the shelf sections of the investigated sections. Facies-indicative species (except for the Pithonelloideae) are indicated by a grey background; marker beds in the shelf sections are framed. Note (1) low overall Pithonelloid abundances in the DSDP section; (2) lower Pithonelloid abundances and occurrences of the o-assemblage in dark layers (marker beds) of the Escalles section; (3) *Pithonella sphaerica* dominance also within dark layers of the Rügen section.

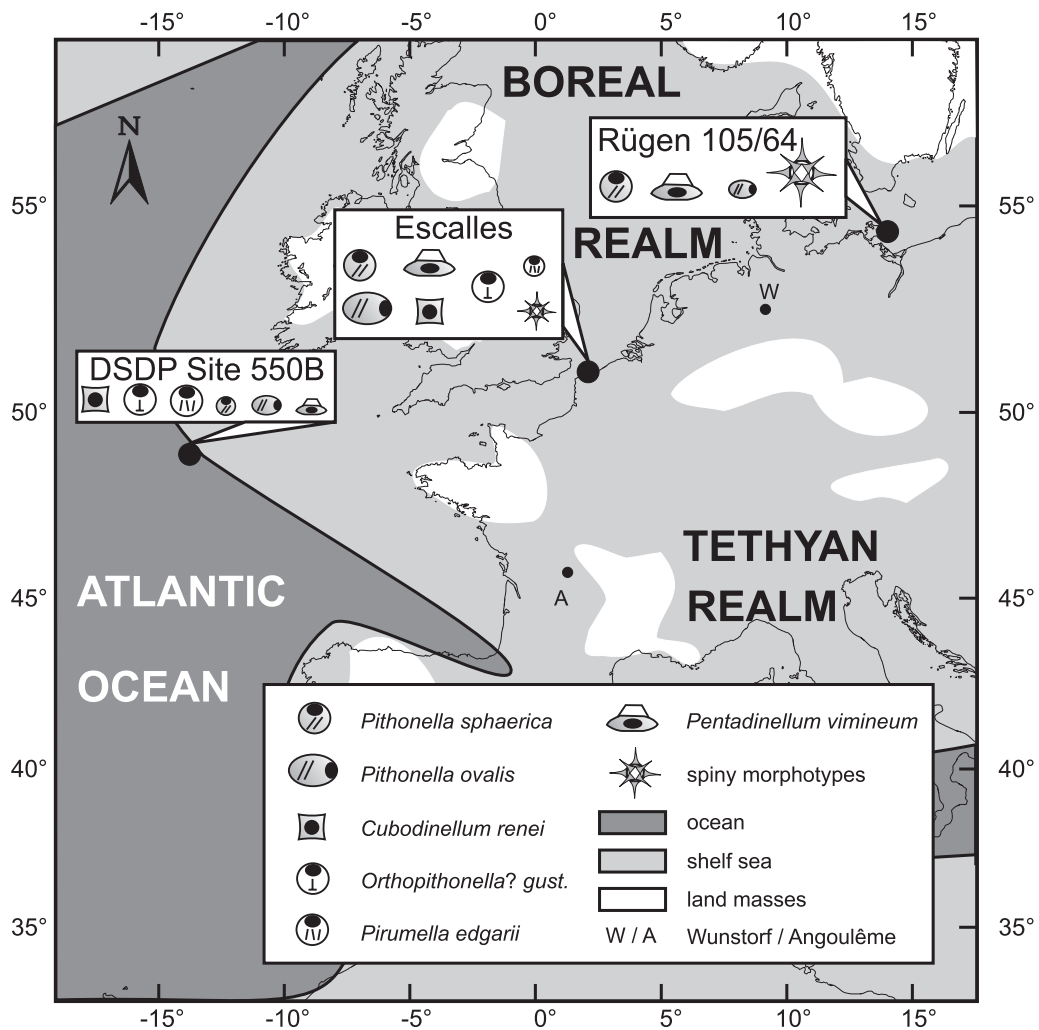


Figure 9. Palaeogeographic distribution of mid-Cenomanian c-dinocysts; note the distinction between typical oceanic and shallow sea species.

gustafsonii are present in outer shelf cyst assemblages, significant abundances are restricted to the occasional occurrence in certain marls, and the species disappear towards the inner shelf.

Pithonella sphaerica and *P. ovalis* show no optically visible features of paratabulation. The cathodoluminescence investigations performed did not provide hints of subtle structures that could resemble ridges of a peridinialean paratabulation. The test surfaces are monotonous in both luminescence colour and intensity.

4. Discussion

4.1. Oceanic environment: absence of the Pithonelloideae, and o-assemblage palaeoecology

The distribution of c-dinocyst assemblages throughout the transect investigated (Figures 8, 9) can be

interpreted to reflect general oceanographic differences between the shelf and oceanic environment. The near absence of Pithonelloideae in the oceanic assemblage may be interpreted as (1) highly selective dissolution of carbonate at the bottom of the ocean, or (2) adaptation to shelf environments only. Dissolution appears unlikely as a few, quite well preserved specimens of Pithonelloideae were found. A more plausible explanation for the presence of these specimens is that they were transported to the site of deposition from shallower environments, or that these specimens mark the outer fringes of the Pithonelloideae habitat. A restriction of Pithonelloideae to shelf environments, excluding coastal areas, is described in the literature from the entire Tethyan Realm, the area between latitudes 40° South and North which was their preferred habitat (e.g., Kaufmann, 1865; Bignot & Lezaud, 1964; Bein & Reiss, 1976; Masters & Scott,

1978; Bouyx & Villain, 1986; Dali-Ressot, 1987; Zügel, 1994; Dias-Brito, 2000). Thus, evidence is strong that the Pithonelloideae did not live in the oceanic environment. A dependence of these species on (1) water depth, or (2) certain surface water conditions may have determined the boundaries of their habitat. If the Pithonelloideae represent cysts in the sense of a benthic resting stage (Dale, 1983), then water depth in the open ocean would be too deep for the hatching dinoflagellates to swim back to the photic zone.

It is, however, also possible that the dinoflagellates stayed only a short time within the cyst and hatched in the water column. If so, they would have been independent of water depth because their complete life cycle took place in surface waters. In this case, other factors, such as nutrient supply, salinity and surface-water temperature, can be assumed to have limited the habitat of these planktic organisms to the shelf seas. Low carbonate productivity, suggesting oligotrophic conditions in the oceanic facies, is indicated lithologically by a lower carbonate content combined with decreased thickness (i.e., lower accumulation rates), and finer grain sizes in the DSDP section as compared to the shelf sections.

The o-assemblage species *Cubodinellum renei* and *Orthopithonella? gustafsonii* are not restricted to the oceanic environment (DSDP Site 550B). Zügel (1994) observed significant amounts of these species in coastal facies of the Anglo-Paris Basin (Angoulême section, Figure 9) which have been interpreted as brackish on the basis of foraminiferal data (Moreau, 1978). Therefore, we interpret *Cubodinellum renei* and *Orthopithonella? gustafsonii* as a species that lived in a broad range of salinity and trophic conditions, from estuarine, eutrophic to oceanic, oligotrophic environments. They are negatively correlated with the Pithonelloideae, which as eutrophic/euryhaline species (Dias-Brito, 2000) were nearly absent in both the oceanic and the coastal environments. Thus, a wide-ranging environmental tolerance enabled *C. renei* and *O.? gustafsonii* to occupy a wide range of niches and to live in a variety of surface water conditions.

Despite their adaptability, cysts of these species cannot be found in the northernmost of the sections investigated (Rügen 105/64). There is a gradient of northeastward-decreasing abundance of the *C. renei* and *O.? gustafsonii* species on the transect investigated. This is supported by low abundances of these species in the Wunstorf section (Zügel, 1994), which is located between the Escalles and Rügen 105/64 sections (Figure 9). Temperature was probably the controlling factor of this pattern as cool waters, originating from the bathyal seaway between the

Atlantic and Arctic oceans as reconstructed by Gradstein *et al.* (1999), may have entered this part of the European shelf sea. The absence of *C. renei* and *O.? gustafsonii* suggests that the Rügen section was situated outside the temperature range tolerated by these species. The outer shelf and oceanic parts of the transect were apparently not influenced by cold water masses and instead were supplied with warm Tethyan water.

4.2. Shelf environments: surface mixing and upwelling

Along the shelf, the distribution of the Pithonelloideae can be interpreted in terms of (1) dependence on water depth, or (2) dependence on nutrients. Zügel (1994) interpreted increased abundances of *Pithonella ovalis* to indicate transgressive episodes. His conclusion is based on the observation of a *P. ovalis*-dominance during the Turonian sea-level maximum. A relationship between *P. ovalis* increase and transgression has been widely observed in the Cenomanian of Western Europe (Villain, 1975; Keupp, 1987, 1991; J. Wendler *et al.*, 2002) and the Tethys (Dali-Ressot, 1987). Thus, a bathymetry-related zonation across the shelf appears to be a consistent feature of the distribution of the Pithonelloideae, *P. sphaerica* being dominant in marginal shelf areas and *P. ovalis* preferring somewhat deeper outer shelf environments (Figures 9, 10). Because of the life strategy of these planktic organisms that inhabited the surface water, it is difficult to explain, however, how water depth itself could control their spatial distribution. It appears more plausible that environmental differences such as gradients in nutrient availability and salinity caused by the interplay of oceanic and shelf-sea influence determined the distribution of these species.

Besides these lateral distribution zones, the Pithonelloideae show temporal abundance changes at high-frequency cyclicity that can be related to nutrient availability. J. Wendler *et al.* (2002) showed that variations in carbonate production in light/dark cycles can be related to orbitally-forced cyclic fluctuations between periods of strong surface-water mixing and high nutrient concentrations (light layers), and stratified, oligotrophic conditions (dark layers). *Pithonella sphaerica* dominates the cyst-assemblage in the light layers (chalks) and, thus, was interpreted as a species of eutrophic conditions. Among previous studies, Noel *et al.* (1995) in particular interpreted the Pithonelloideae as productivity indicators. Generally high productivity of carbonate during chalk deposition is corroborated by ecological studies on planktic and benthic foraminifera (Hart, 1980; Leary & Hart,

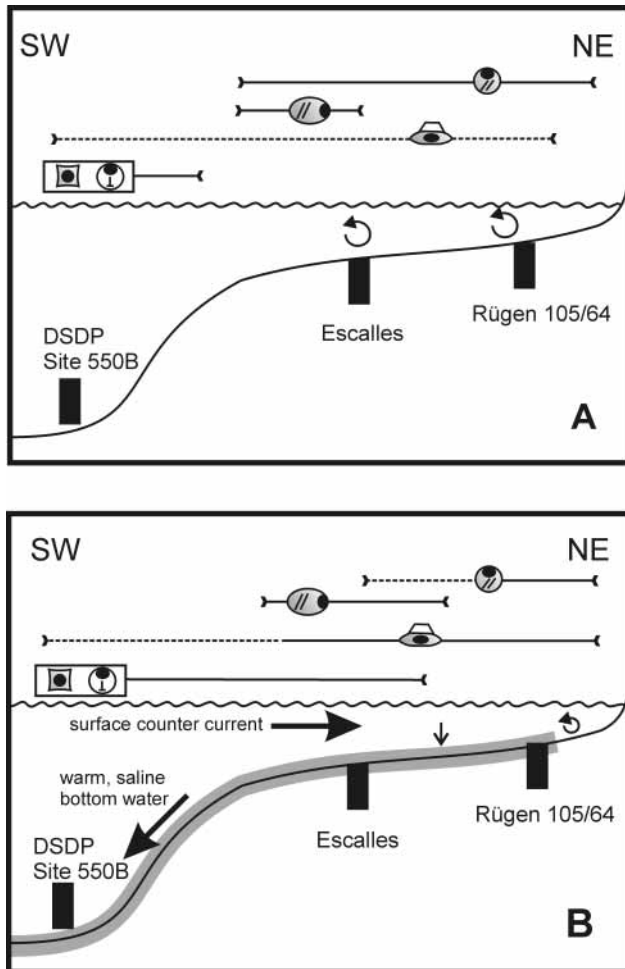


Figure 10. Illustration of the shifts in distribution of c-dinocysts and changes in circulation associated with light/dark sedimentary alternations. A, light layer deposition, surface mixing. B, dark layer deposition, stratification and occasional downwelling; note spread of the o-assemblage, shift of Pithonelloideae distribution zones towards the shelf, and reduction of inner shelf upwelling area (for c-dinocyst symbols, see legend of Figure 9).

1992; Mitchell & Carr, 1998; Gräfe, 1999), and coccoliths (Roth & Krumbach, 1986; Watkins, 1989; Young *et al.*, 1998).

The continuous dominance of *P. sphaerica* in the Rügen section (Figure 8) suggests that strong surface mixing prevailed throughout most of the time-span represented. Such a situation could have been caused by (1) convective overturning owing to decreased surface water temperature or salinity increase, or (2) upwelling. An upwelling zone offshore Fennoscandia during the Late Cretaceous has been predicted by numerical simulations (Parrish & Curtis, 1982; Barron, 1985), and upwelling during Late Cenomanian–Early Turonian times was reconstructed

by Hilbrecht *et al.* (1992), based on regional stable carbon isotope variations. The influence of a cool surface water current (section 4.1. above) would have decreased the temperature contrast between surface and deep water, providing a basis for continuous convective overturning. The wide spacing of light/dark couplets in the Rügen section supports the hypothesis of continuous mixing, as it shows that carbonate production was quite stable, and only the strongest episodes of stratification were sufficient to influence this well-circulated proximal shelf area. In addition, nutrient depletion of the surface water during most stratification phases was probably less effective owing to continuous or even increased terrigenous input of nutrient rich material from the nearby Fennoscandian continent.

Although *Pithonella sphaerica* dominated the area in which the influence of cool water masses is assumed, it cannot be interpreted as a cool-water species, because it was widely distributed throughout the warm Tethyan Realm. Their restriction to the Tethyan Realm suggests that all Pithonelloideae were thermophilic, planktic organisms (Dias-Brito, 2000). Therefore, the cool waters must have mixed with the warm Tethyan waters sufficiently to remain in the temperature range required by the Pithonelloideae. The dominance of *P. sphaerica* could indicate that this species was best adapted to temperature changes, i.e., it represents the most opportunistic of the Pithonelloideae, or required the highest nutrient concentrations. To conclude, owing to their dominance in chalks deposited under eutrophic conditions in well-mixed surface waters *P. sphaerica* (and *P. ovalis* in the outer shelf) are interpreted as indicators of nutrient-rich water masses of relatively stable salinity. Cyclic fluctuations in the Ps/Po ratio through the section, which can be interpreted to reflect temporal shifts of the preferred facies zones, probably indicate changes in surface current patterns.

The distribution of *Pentadinellum vimineum* suggests that this species also preferred the shelf environment, especially during episodes of dark layer deposition [Figures 8 (marker beds), 10] for which oligotrophic conditions were reconstructed (J. Wendler *et al.*, 2002). While oligotrophy is a likely reason for increased abundance of *P. vimineum* in the OS-facies, the presence of significant abundances (8% of the cyst assemblage) of *Pentadinellum* in the estuarine environment (Zügel, 1994; section A in Figure 9) suggests that this species tolerated a wide range of salinity and nutrient concentrations, similar to the species of the o-assemblage (section 4.1.). Thus, its higher abundance in dark as compared to light layers seems to reflect other environmental parameters. We interpret

P. vimineum as an indicator of increased surface water temperature as, according to Neumann (1999), the invasion of this species into the Boreal Realm was related to episodes (deposits up to 10 m thick) of possible incursions of warm surface waters from the Tethys during the mid-Cretaceous. If water temperature was a limiting factor, then the increased *P. vimineum* abundances during deposition of the dark layers investigated here indicates cyclic surface-water warming, supporting our hypothesis of stratification during these periods. Enhanced mixing during light-layer deposition, in contrast, would have resulted in lower surface-water temperatures.

4.3. Ocean–shelf interactions

In Figure 10, an overview of the c-dinocyst distribution along the investigated ocean–proximal shelf transect is given. Orbitally–forced cyclic changes in the intensity of wind-driven mixing are most likely to have caused the light/dark sedimentary cyclicity of the epicontinental shelf sections (e.g., Tyson & Pearson, 1991; J. Wendler *et al.*, 2002). An explanation for the interplay of the o- and the MS-assemblage may be that during periods of enhanced surface mixing most parts of the shelf were well-ventilated, and nutrient enriched surface waters led to an increased productivity and dominance of the Pithonelloideae. These conditions on the shelf differed from those in the open North Atlantic Ocean where, indicated by generally low primary productivity (e.g., Cool, 1982; Bralower & Thierstein, 1984), more oligotrophic and probably stratified waters prevailed (Figure 10A). Orbitally–forced interruptions of mixing on the shelf resulted in cyclic periods of oligotrophy in the surface waters and a shelfward extension of the oceanic conditions (Figure 10B). It can be postulated that during such stratification events the occasional downwelling of high saline, oxygen-depleted water and its outflow into the ocean induced a shelfward-directed surface current (Voigt, 1996). Such an oceanographic situation would lead to the observed expansion of typical oceanic species to the outer shelf and initiate the shelfward shift of Pithonelloideae-facies zones, which is indicated by the narrowing of the facies dominated by *Pithonella sphaerica* and shelfward extension of the *P. ovalis* distribution zone (low Ps/Po ratios) during these periods (Figures 8, 10).

The assumed influence of oxygen-poor bottom waters at DSDP Site 550B is supported by the lithological data, which indicate that light/dark alternations were predominantly redox-controlled and reflect varying preservation of organic particles. Changes in carbonate production or non-carbonate input are not

evident. In contrast to the shelf sections, assemblages of c-dinocysts do not change between light and dark layers in this section, i.e., the surface plankton production remained stable while, on the sea floor, cyclic anoxic conditions prevented decay of organic matter during dark layer deposition. Early diagenetic cementation was enhanced, as indicated by the abundant carbonate crusts around particles that are responsible for the increased carbonate values measured in the black layers. Authigenic carbonate crusts in present day oxygen–minimum zones suggest that early diagenetic cementation is promoted by anoxic conditions under which sulphate reduction and methanogenesis play an important role (e.g., von Rad *et al.*, 1996).

4.4. Pithonelloideae ecology: probable vegetative dinoflagellate stages?

The Pithonelloideae are the most important group of c-dinocysts throughout the Upper Cretaceous; however, they are taxonomically very problematic. Arguments for their affinity with the dinoflagellates are summarised here.

The Pithonelloideae, commonly termed ‘calci-spheres’ in the literature, have been interpreted as, e.g., proloculi of foraminifera, chlorophycean algal spores (Bolli, 1974), *incertae sedis* benthic organisms (Villain, 1977), planktic ciliate organisms (Banner, 1972) and Cadosinidae, the latter being interpreted as foraminifera (Wanner, 1940), tintinnida (Loeblich & Tappan, 1964) and c-dinocysts (Rehánek & Cecca, 1993). A relationship of the Pithonelloideae via the Cadosinidae to the tintinnida was excluded by Banner (1972) because most species of *Pithonella* have a multi-layered calcareous wall. The size and shape of the Pithonelloideae and the calpionellids (Villain, 1975, 1977, 1981, 1991), which also seem to have a pithonelloid wall-crystal orientation, are similar. However, as calpionellids were marine planktic Protozoa, typical of Jurassic–Lower Cretaceous deep-sea deposits (Remane, 1978), the Pithonelloideae differ substantially from this group in terms of stratigraphical and palaeoecological distribution. During the past two decades, evidence in favour of the Pithonelloideae being c-dinocysts has been growing (e.g., Keupp, 1987; Keupp & Kienel, 1994; Dali-Ressot, 1987; Willems, 1990, 1992, 1994).

Modern c-dinocyst species live predominantly in oligotrophic, oceanic environments and are found in much lower abundance. These two aspects in comparison to the distribution patterns of Pithonelloideae may argue against their affinity to dinoflagellates with calcareous life stages because (1) they were absent from oligotrophic surface waters, and (2) they were

much more common than the other c-dinocyst species. The former is likely to reflect their special adaptation to the eutrophic epicontinental seas of the Cretaceous Period, which lack a comparable counterpart today. Restriction to eutrophic environments is also typical of some recent neritic species (Montresor *et al.*, 1998). Thus, point 1 does not exclude Pithonelloideae from dinoflagellate group. Their dominance suggests differentiation of the Pithonelloideae from dinoflagellates and rather interprets them as foraminifera, which equally dominate in the respective grain size of the material investigated. However, the Recent dinoflagellate species *Thoracosphaera heimii* (Lohmann, 1920) Kamptner, 1944 is an example that weakens argument 2 as this species dominates most Recent assemblages (e.g. Dale, 1992; Höll *et al.*, 1999; Vink *et al.*, 2000; I. Wendler *et al.*, in press).

Various morphometric observations strongly suggest an affinity of species with a pithonelloid wall-type to the dinoflagellates. *Pithonella pyramidalis* (Willems, 1994), *Lentodinema danica* (Kienel, 1994) and particularly the genus *Tetratropis* (Willems, 1990) represent taxa that feature both the pithonelloid wall-type (uniquely declined wall crystals) and a probable peridinialean paratabulation which strongly hints at a dinoflagellate origin of at least part of the Pithonelloideae. The pithonelloid orientation of the wall of *Tetratropis* spp. that is clearly visible under the SEM, was negated later by analyses of thin sections with polarised light (Hildebrand-Habel & Willems, 1997); however, a new species of *Tetratropis* shows unequivocal pithonelloid wall crystal orientation in polarised light (unpublished data). Further evidence for a dinoflagellate affinity is the biomineralisation of pithonelloidean shells, which follows the same principles as known c-dinocyst biomineralisation patterns (Keupp & Kienel, 1994).

It has to be kept in mind that analogy between tabulate and atabulate species may not be evidence for a dinoflagellate affinity of all of the Pithonelloideae because findings of morphotypes that are incompatible with known dinoflagellate biology (Villain, 1981, 1991; Willems, 1996) strengthen the belief that the pithonelloid wall-type may have been realised by different groups of organisms that produced calcareous microfossils. If so, it is, however, a puzzling fact that the 'pithonelloid wall-type', i.e., all possibly different organisms that had this particular crystal orientation, substantially declined and finally became extinct after the K/T boundary event (Hildebrand-Habel *et al.*, 1999; Wendler & Willems, in press). In summary, evidence is strong that Pithonelloideae are related to the dinoflagellate subfamily Calcio-

dinelloideae (Fensome *et al.*, 1993) and as such can be interpreted here in terms of ecology as part of dinoflagellate assemblages.

The dominance of *Pithonella sphaerica* and *P. ovalis* by two orders of magnitude in the shelf assemblages is striking and suggestive of the dinoflagellate life stage they may represent. Their prevalence could reflect their ability to form large amounts of calcareous shells in a shorter time than the cysts of other species. All known calcareous dinoflagellate microfossils from the Mesozoic through to the Recent contribute only insignificant amounts to the sediment with two exceptions: the Pithonelloideae in the Cretaceous and, as mentioned above, *Thoracosphaera heimii* in the Cenozoic. Among present-day dinoflagellates, two life strategies are known to produce calcareous shells: (1) the cyst stage, and (2) the vegetative-coccoid life-stage, the latter only known from *Thoracosphaera heimii*. The low abundance of most species is as a result of the fact that, as far as is known from culturing recent species, only part of the motile calciodinelloidean cells form calcareous cysts, resulting in a low cyst turn-over rate during the dinoflagellate life cycle (Karwath, 2000). Significant abundances require a faster way to calcareous shell formation. In contrast to the cyst-formation of the Calciodinelloideae, almost all of the cells of *T. heimii* form a calcareous skeleton (Tangen *et al.*, 1982). These shells are the dominant part of the two cell cycles of this species (Inouye & Pienaar, 1983). In the present-day upwelling area of the Arabian Sea, the formation of calcareous skeletons of *T. heimii* exceeds the formation of calcareous dinoflagellate cysts often by two orders of magnitude, as sediment trap studies have shown (I. Wendler, pers. comm., 2001). The much higher abundance of *T. heimii* skeletons relative to cysts can be explained by the rapid life-cycle of the species during which a calcareous shell is formed every one to three days (Inouye & Pienaar, 1983). The dominance of some Pithonelloideae in the Upper Cretaceous appears to be an analogue to the dominance of *T. heimii* in the Cenozoic, both probably formed in a similar way. Therefore, we propose the idea that some pithonelloid calcispheres, namely the two dominant species *P. sphaerica* and *P. ovalis*, represent skeletons produced by dinoflagellates with a vegetative-coccoid life-stage.

5. Conclusions

The oceanic section considered in this paper is characterised by a near absence of Pithonelloideae, which are interpreted to have required high nutrient concentrations. The main species of the oceanic

c-dinocyst assemblage are *Cubodinellum renei* and *Orthopithonella? gustafsonii*, which were not, however, restricted to the oceanic environment, but also occupied various shelf environments and, therefore, appear to have lived in a broad range of salinity and trophic conditions. A gradient of decreasing temperature is likely to have controlled their decreasing abundance towards the proximal shelf area of the transect investigated. While orbitally-forced light/dark sedimentary cyclicity of the shelf sections is mainly related to surface-water changes in carbonate productivity, a cyclic modulation of productivity was not observed in the oceanic profile. Dark layer formation in the open ocean was predominantly controlled by the cyclic establishment of anoxic bottom-water conditions.

The Pithonelloideae dominated the assemblages on the shelf where individual species were bathymetrically zoned. *P. sphaerica* (and *P. ovalis* on the outer shelf) were abundant in nutrient-rich water masses, as indicated by their dominance in chalks deposited under eutrophic conditions. Cyclic fluctuations in the Ps/Po ratio, which were probably caused by shifts of the preferred facies zones, indicate changes in surface-current patterns. A continuous dominance of *P. sphaerica* in the marginal-shelf section implies continuous mixing related to convective overturning or upwelling. A low frequency of light/dark alternations in the marginal-shelf section may reflect a reduced effect of orbital forcing on wind-driven surface mixing. Besides Pithonelloideae, *Pentadinellum vimineum* was an important shelf species. It apparently tolerated a wide range of salinity and trophic conditions and preferred warm temperatures, indicating cyclic surface-water warming during stratification events.

During periods of enhanced surface mixing most parts of the shelf were well-ventilated, and nutrient-enriched surface waters led to high productivity and dominance of the Pithonelloideae. These conditions contrasted with those of the open ocean where more oligotrophic and probably stratified waters prevailed. Orbitally-forced interruptions of mixing on the shelf resulted in cyclic periods of oligotrophy in the surface waters, an expansion of oceanic species to the outer shelf, and a shelfward shift of Pithonelloideae-facies zones. Cyclic downwelling-induced export of warm, saline, bottom water from the shelf towards the ocean induced occasional shelfward-directed oceanic incursions during these periods. The c-dinocyst distribution pattern may indicate a gradient of decreasing energy of the incursions and/or a gradient of northward-decreasing surface-water temperature towards the marginal-shelf section investigated.

The modulation of their distribution by surface currents and changes in surface mixing provide new evidence that Pithonelloideae were planktic. Our review here of morphological aspects indicates that an affinity of Pithonelloideae to the dinoflagellates is plausible. The consistent prevalence of *P. sphaerica* and *P. ovalis* in c-dinocyst assemblages throughout the Upper Cretaceous indicates that they were produced more frequently than cysts of the other species and might, therefore, represent a vegetative dinoflagellate life stage.

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