# Reconstruction of astronomically-forced cyclic and abrupt palaeoecological changes in the Upper Cretaceous Boreal Realm based on calcareous dinoflagellate cysts

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Meine Bemühungen gründen sich auf dem Glauben, daß die Welt eine völlig harmonische Struktur aufweist.

Albert Einstein

#### Summary

The Upper Cretaceous carbonate sequences of the Boreal NW European shelf sea consist to the major part of pelagic microfossils of which up to 20% can be calcareous dinoflagellate cysts (cdinocysts). Little is known on the palaeoecology of these organisms. The knowledge on the influence of palaeoenvironmental changes on the carbonate-producing organisms is essential to understand the forcing mechanisms of sedimentation of biogenic carbonates. Thus, the present PhD thesis focuses on investigating changes in carbonate productivity related to (i) Milankovitch cycles in the Cenomanian, and to (ii) the environmental catastrophe at the Cretaceous/Tertiary (K/T) boundary, based on the palaeoecology of c-dinocysts. Special emphasis has been placed on discussing the Pithonelloideae which are a controversially discussed group of c-dinocyst that dominates most Upper Cretaceous assemblages and became extinct in the aftermath of the K/T boundary event.

In Chapter 2., the architecture of mid-Cenomanian, precession-controlled light/dark cycles in the section Escalles (Anglo-Paris Basin) is investigated, combining high-resolution analyses of c-dinocyst associations and lithological parameters. Two negatively correlated c-dinocyst assemblages can be distinguished. While the Pithonelloideae (p-assemblage) dominate in light layers (chalks), sculptured (paratabulated) species (s-assemblage) are typical for dark layers (marls). Gradual changes in absolute and relative abundance of the cyst species in these assemblages over several couplets depict a bundling pattern which is interpreted to reflect the modulation of the intensity of the precession cycle by the eccentricity cycle (100 ka). The stacking pattern in the natural gamma ray signal and the carbonate and TOC content has the same period and provides lithological proof of the bundling. A shelf basin circulation model is established to explain the relation between orbitally-forced climate change, its environmental consequences and the resulting sedimentary cyclicity. While the chalks reflect a well-mixed shelf sea environment, the marls, particularly those at the bundle boundaries, can be interpreted as the sedimentary expression of stratified water masses. Stratification during deposition of these marls was caused by low seasonality during strong precession maxima at the eccentricity maxima and led to nutrient depletion and decreased productivity in the surface water masses.

In order to relate the orbitally-forced cyclic changes in c-dinocyst assemblages to spatial distribution patterns of these organisms, a palaeobathymetrical transect (ocean: DSDP Leg 80, Site 550; outer shelf: section Escalles; inner shelf: core Ruegen 105/64) is investigated in **Chapter 3**. The open oceanic environment, where oligotrophic and probably stratified waters prevailed, is dominated by *Cubodinellum renei*, *Orthopithonella ? gustafsonii* which, however, were not exclusively oceanic species. They tolerated a wide range of salinity and nutrient concentrations, but reacted to temperature decrease as is indicated by their absence in the NE part of the European shelf which was probably influenced by cool water masses. The Pithonelloideae were strictly bound to the eutrophic surface waters on the shelf. Lateral changes in c-dinocyst distribution corroborate the shelf basin circulation model discussed in Chapter 2. Intensive surface mixing during light layer deposition caused a basin-wide extension of the Pithonelloideae distribution zones. In contrast, episodes of surface water stratification during dark layer deposition were related to surface water warming, nutrient depletion, occasional downwelling and formation of oxygen-

depleted bottom water. As a consequence, Pithonelloideae distribution zones were shifted shelfward and oceanic, oligotrophy-tolerant species invaded the outer shelf. At the inner shelf, only the strongest stratification events were reflected due to an upwelling zone in this area.

New light is shed on the ecology of *Pithonella sphaerica* and *Pithonella ovalis* which represent indicators of well-mixed, nutrient rich surface waters in which carbonate productivity was enhanced. The affinity of these planktic organisms to the dinoflagellates is plausible according to a summarising review of morphological and ecological aspects. 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, similar to the Recent dinoflagellate *Thoracosphaera heimii*.

The knowledge on Pithonelloideae palaeoecology is further improved by **Chapter 4**., investigating the section Stevns Klint (Denmark). The carbonate breakdown at the K/T boundary is characterised by substantial mass mortality that induced the extinction of Pithonelloideae. Their restriction to the shelf, i.e. a reduced spatial distribution, and a life cycle probably without a resting cyst stage are interpreted as the major disadvantages of Pithonelloideae in surviving this environmental catastrophe. Species that became dominant in the Danian either lived in a broad latitudinal range including oceanic environments, or were coastal species, both being able to adapt to a variety of environmental conditions. Resting cysts of coastal species are particularly characteristic for the assemblage found in the K/T boundary clay ("Fish Clay" in the section Stevns Klint). They represent the only species that lived at the investigated position immediately after the asteroid impact. Coastal species and later invaders from the ocean provided the base of the recolonisation of the Boreal shelf.

In **Chapter 5.**, the new, paratabulated species *Orthopithonella collaris* sp. nov. is described and discussed. The species has been found exclusively in the Fish Clay and shows a pulse-like temporal occurrence which suggests that it may represent an adapted, possibly low latitude invader into the warmed post-impact Boreal Realm, or a stress-controlled morphotype of an otherwise atabulate species. As can be concluded from this example as well as from the cyclic distribution patterns in the Cenomanian, paratabulation appears to play an important role during times of strongly varying environmental conditions that require adaptability.

The various aspects of this thesis that include a reconstruction of the architecture of sedimentary cycles, a palaeoenvironmental interpretation of temporal and spatial c-dinocyst assemblages, and information on species-selective extinction at the K/T boundary show that c-dinocysts can provide a unique tool in the study of environmental changes in the Cretaceous.

## Zusammenfassung

Die Karbonatserien der Oberkreide im borealen Ablagerungsraum des NW-Europäischen Schelfmeeres bestehen zu einem erheblichen Teil aus pelagischen Mikrofossilien. Bis zu 20% der Karbonatpartikel sind kalkige Dinoflagellatenzysten (k-Dinozysten). Die Paläoökologie dieser Organismengruppe ist bisher nur wenig erforscht. Das Wissen über den Einfluß von Paläoumweltveränderungen auf die sedimentbildenden Organismen ist jedoch unerläßlich, um die Steuerungsfaktoren der Sedimentation aus ökologischer Sicht zu verstehen. Hauptziel der vorliegenden Dissertation ist die Vertiefung der Kenntnisse über die Paläoökologie von k-Dinozysten in Beziehung zu Schwankungen in der Karbonatproduktivität. Dabei stehen zum einen die Architektur von Milankovitchzyklen im Cenoman und zum anderen die Umgestaltung der Karbonatproduktion im Boreal an der Kreide/Tertiär Grenze im Mittelpunkt. Besondere Aufmerksamkeit gilt innerhalb der beiden Schwerpunkte dieser Arbeit den Pithonelloideae. Ihre Dominanz in den Assoziationen von "Calcisphaeren" der Oberkreide, ihre kontrovers diskutierte Beziehung zu den Dinoflagellaten und ihr plötzliches Aussterben infolge des Kreide/Tertiär Ereignisses stellen die Schwerpunkte bei der Diskussion dieser Organismengruppe dar.

In Kapitel 2. wird die Architektur von präzessionsgesteuerten Hell/Dunkel-Wechselfolgen des Mittelcenoman im Profil Escalles (Anglo-Pariser Becken) mittels einer hochauflösenden quantitativen Analyse der k-Dinozysten-Assoziationen untersucht. Zwei ökologische Artengemeinschaften können aufgrund ihres gegenläufigen Verteilungstrends unterschieden werden. Während die Pithonelloideae (p-assemblage) in den hellen Lagen dominieren, sind skulpturierte (paratabulierte) Arten (s-assemblage) in dunklen Schichten häufiger. Häufigkeitsschwankungen dieser Artengemeinschaften folgen sowohl der hochfrequenten Hell/Dunkel Zyklik als auch einer niederfrequenten Zyklik, bei der es in einer Folge von etwa fünf sog. Hell/Dunkel-Paketen zu Verstärkung und Abschwächung der Assoziationsunterschiede zwischen hellen und dunklen Lagen innerhalb eines Pakets kommt. Daraus resultiert eine "5'er Bündelung", die mit gleicher Periode auch in den lithologischen Parametern Karbonatgehalt, Gehalt an organischem Kohlenstoff und Gammastrahlung erkennbar ist und auf die übergeordnete Steuerung des Präzessionszyklus durch den Exzentrizitätszyklus hindeutet. Aus der vergleichenden Analyse der ökologischen und der lithologischen Informationen der untersuchten zyklischen Abfolge wurde ein Modell zum Übertragungspfad orbitaler Zyklen über die Epikontinentalmeer-Zirkulation in Sedimentzyklen entwickelt. Durch die Windintensität gesteuerte Oberflächenwassermischung bewirkte eine gute Nährstoffversorgung und steigerte die Karbonatproduktion in Phasen der Ablagerung heller Schichten. Im Gegensatz dazu führten Perioden stärkerer Wasserkörperschichtung zur Nährstoffverarmung im Oberflächenwasser und somit zur Verringerung der Karbonatproduktion, zur zeitweisen Bildung von Bodenwasser-Anoxia und zur Ablagerung dunkler Lagen. Größte Elliptizität der Erdbahn im Exzentrizitätsmaximum verstärkte im Sommerperihel den jahreszeitlichen Temperaturkontrast wodurch es zur Erhöhung der Energie der Windsysteme kam (maximale Oberflächenwassermischung), wohingegen im Winterperihel entsprechend sehr niedriger jahreszeitlicher Kontrast zu häufigen und langen Schichtungsperioden führte.

Um die durch orbitale Zyklen gesteuerten zeitlichen Veränderungen von k-Dinozysten-Assoziationen mit räumlichen Verbreitungsmustern in Beziehung zu bringen, wurden in Kapitel 3. drei Profile auf einem paläobathymetrischen Transekt von der Tiefsee zum inneren Schelf innerhalb des Mittelcenoman untersucht (Ozean: Bohrprofil DSDP Leg 80, Site 550; Außenschelf: Profil Escalles (bei Calais/Frankreich); Innenschelf: Bohrprofil Rügen E Rn 105/64). Der ozeanische Lebensraum ist von den Arten Cubodinellum renei und Orthopithonella ? gustafsonii dominiert, welche aber aufgrund ihrer Verbreitung in einem weiten Spektrum von Salinitäten und Nährstoffkonzentrationen eher als sehr anpassungsfähige Arten interpretiert werden müssen und keine ausschließlich ozeanischen Arten darstellen. Hinsichtlich der Oberflächenwassertemperatur scheint eine Bindung dieser Arten an warme tethyale Verhältnisse zu bestehen, da sie nicht im nordöstlichen Europäischen Schelf auftreten, der vermutlich vom Zustrom kühlen Wassers von Norden beeinflußt war. Die Verteilung der Pithonelloideae Pithonella sphaerica und P. ovalis zeigt eine deutliche Bindung dieser Arten an eutrophe Oberflächenwasserbedingungen. Wechsel im räumlichen Verbreitungsmuster der k-Dinozysten unterstützen das in Kapitel 2 diskutierte Modell zur Entstehung der zyklischen Verteilungstrends der k-Dinozysten. Während der Ablagerung heller Lagen waren gute Oberflächenwassermischung und eutrophe Bedingungen verantwortlich für eine schelfweite Ausbreitung der Pithonelloideae. Wasserschichtung während der Ablagerung dunkler Lagen bewirkte Nährstoffverarmung, Erwärmung des Oberflächenwassers, periodisches Absinken und Bildung sauerstoffarmen Bodenwassers. Dabei wurden die Pithonelloideae Verbreitungszonen schelfwärts verschoben, und ozeanische, an Oligotrophie angepaßte Arten verbreiteten sich auf dem Schelf. In einem Auftriebsgebiet im Innenschelf wurde die Durchmischung nur zeitweise unterbrochen, so daß hier lediglich in den stärksten Wasserschichtungs-Phasen dunkle Karbonatlagen sedimentiert wurden und Pithonelloideae, insbesondere P. sphaerica, fast beständig dominieren.

Für *P. sphaerica* und *P. ovalis* können anhand ihrer zeitlichen und räumlichen Verteilungsmuster und ihrer Häufigkeitsverteilung neue Aussagen zur Ökologie gemacht werden. Die Arten sind Indikatoren für gut durchmischte, nährstoffreiche Oberflächenwässer, in denen es zu hoher Karbonatproduktion in den Schelfmeeren kam. Die Zuordnung dieser planktischen Organismen zu den Dinoflagellaten erscheint nach einer zusammenfassenden Betrachtung morphologischer Merkmale plausibel. Hinsichtlich ihrer außerordentlichen Dominanz in Assoziationen kalkiger Dinozysten lassen sich *P. sphaerica* und *P. ovalis* mit der rezenten Dinoflagellatenart *Thoracosphaera heimii* vergleichen, welche ein vegetativ-coccoides Stadium darstellt, das viel öfter gebildet wird als Zysten und somit in höherer Quantität abgelagert wird. Es wäre daher denkbar, daß diese Pithonelloideae-Arten, ähnlich wie die Skelette von *T. heimii*, keine Ruhezysten sondern vegetative Stadien waren.

Weitere Hinweise auf die Ökologie der Pithonelloideae ergeben sich aus **Kapitel 4.** (Analyse des Profils Stevns Klint/Dänemark). Der Zusammenbruch der Karbonatproduktion an der Kreide/Tertiär Grenze ist geprägt von einem Massensterben der Pithonelloideae, das das Aussterben der Gruppe einleitete. Ihre ökologischen Nachteile im Überleben widriger Umweltbedingungen waren ihre auf die Schelfmeere beschränkte räumliche Ausdehnung und ein Lebenszyklus, der im Gegensatz zu den überlebenden Dinoflagellatenarten vermutlich keine Ruhezystenbildung umfaßte. Viele der Arten, die im Dan erfolgreich die neue Assoziation

aufbauten lebten in weiten geographischen Breitenbereichen bzw. waren Küstenbewohner mit Anpassung an rasch wechselnde Umweltbedingungen. Ruhezysten von Küstenarten sind vor allem typisch für den K/T Grenzton, den Fischton des Profils Stevns Klint. Sie stellen möglicherweise die einzigen Arten dieses Zeitabschnittes direkt nach dem Asteroiden-Impakt dar und bildeten, neben den späteren Einwanderern aus dem Ozean, die Ausgangsformen für die Wiederbesiedelung des NW-Europäischen Schelfmeeres.

In **Kapitel 5.** wird die neue, paratabulierte Art *Orthopithonella collaris* diskutiert. Ihr bisher einzigartiges Auftreten im Stevns Klint - Profil und die Beschränkung auf den K/T Grenzton legen die Vermutung nahe, daß es sich bei dieser Art um einen extrem anpassungsfähigen Einwanderer oder um einen stressbedingten, paratabulierten Morphotyp einer ansonsten atabulaten Art handelt. Die Impakt-Katastrophe am Ende der Kreidezeit, wie auch die klimazyklisch gesteuerten Ereignisse verringerter Karbonatproduktion im Cenoman belegen, daß Paratabulation offenbar eine besondere Rolle in Phasen stark wechselnder Umweltbedingungen spielt, die große Toleranz erfordern.

Die verschiedenen Aspekte der vorliegenden Dissertation von der Rekonstruktion der Zyklenarchitektur sedimentärer Abfolgen, über die paläoozeanographische Interpretation zeitlicher und räumlicher Assoziationsschwankungen bis hin zu Aussagen über artselektive Aussterbemuster an der K/T Grenze zeigen, daß k-Dinozysten einzigartige Informationen über zyklische und abrupte Umweltveränderungen in der Kreide liefern können.

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### 1. Introduction

#### 1.1. Motivation and main objectives

#### Cyclic environmental changes

The Upper Cretaceous of the Boreal Realm is characterised by the deposition of large carbonate sequences that predominantly consist of the remains of calcareous planktic and benthic microfossils (mainly Coccoliths, calcareous dinoflagellate cysts and forminifera). These sequences are characterised by alternation of carbonate rich layers and layers poorer in carbonate content which results in the banded appearance of the deposits. Such light/dark cycles are known as chalk-marl in the Cenomanian. Carbonate cycles have been interpreted to represent variations in (i) terrestrial non-carbonate input, (ii) production of carbonate particles, and (iii) dissolution of carbonate (Einsele et al., 1991). These parameters of sediment formation are controled by palaeoclimatic and palaeoceanographic changes.

According to the Milankovitch theory, sedimentary cycles can reflect changes in solar insolation caused by variations in the Earth's orbital parameters (Milankovitch, 1941). The oscillations in the Milankovitch frequency band are the eccentricity cycle of the Earth's orbit (mean period of 100 ka), modulation of the tilt of the Earth axis, obliquity (about 41 ka cycle), and the precession cycle which modifies the equinoxes so that during one cycle the time of perihelion shifts through the seasons (approximate period of 21 ka). The Milankovitch theory is today widely accepted for the explanation of Quaternary sedimentary cycles.

Bio- and cyclostratigraphical analyses and absolute dating methods combined with spectral analyses have proved orbital forcing to be a plausible cause of Cretaceous chalk/marl couplets (e.g. Bottjer et al., 1986; Einsele et al. 1991; Schwarzacher, 1993; Gale et al., 1999). However, little is known on the exact mechanism how these orbital changes force sedimentation. The path of transformation of a particular orbital constellation via atmospheric and oceanographic processes into the sedimentary system can be extremely variable as is expressed by the various types of carbonate cycles. An important role in depositional environments dominated by carbonate producers, such as the Cenomanian

chalk sea investigated here, play environmental changes that force quantitative and qualitative assemblage changes of these organisms. The present study represents the first high-resolution reconstruction of ecological consequences of orbitally-forced climate change in the Cenomanian based on changes in assemblage of calcareous dinoflagellate cysts (c-dinocysts). Pithonelloideae are the quantitatively most important group of cyst species in the Upper Cretaceous and are, therefore, in special focus throughout this thesis. An introduction to c-dinocysts is given in **Chapter 1.3**.

#### Abrupt environmental changes

In the course of the study on Cenomanian chalk/marls it became clear that cdinocyst assemblage changes are strongly related to changes in carbonate content. In contrast to cyclic disturbances in carbonate production, the Cretaceous/Tertiary (K/T) boundary event represents a catastrophic event of strong carbonate breakdown. While the Pithonelloideae only experienced more or less severe reductions in abundance during cyclic variations in carbonate sedimentation, they became extinct after the K/T event. The reasons for their extinction are unknown as is their ecology. In order to gain insight into a wide range of aspects on Pithonelloideae ecology, it is essential to obtain and compare information on both, the effects of cyclic environmental changes on these organisms, and the abrupt environmental catastrophe at the K/T boundary that likely caused sudden mass mortality. The investigated section at Stevns Klint, Denmark is one of the classic outcrops of the boundary layer that covers this interval of world-wide reduced carbonate production and mass extinction induced by an asteroid impact (e.g. Alvarez et al., 1980; Kastner et al., 1984; Brinkhuis et al., 1998; Smit, 1999). The response of c-dinocyst species to abrupt environmental change, particularly patterns of species-selective survival, can be well studied in this material which contains no major hiatus. Both, cyclic and catastrophic forcing of carbonate productivity appear to require special adaptation which may be indicated in the example of c-dinocyst assemblages by the presence of exotic species or the development of ecological morphotypes.

#### Research questions

As introduced above, the main objective of this PhD is to contribute to the knowledge on the relation between astronomical forcing and biogenic sedimentation, combining investigations on the palaeoecological consequences of (i) cyclical obital variations, and (ii) non-cyclical catastrophic events. Major emphasis has been placed on the following research questions:

#### 1) Methods

Previous studies of Cretaceous c-dinocysts were mainly centered on taxonomical questions concerning the description of species. First steps into palaeoecological interpretation were done by e.g. Keupp (1981, 1987, 1993), Dali-Ressot (1987) and Zügel (1994). The main aim of the present study is to enhance the application of c-dinocysts in palaeoecology, using a quantitative approach. To date, c-dinocyst assemblages were analysed using relative abundances in studies of Mesozoic material. Is it possible to obtain quantitative data, i.e. to actually count cysts in split samples of known weight?

#### 2) Milankovitch cycles and related palaeoenvironmental effects

The architecture of orbitally-forced cycles often reflects the superposition of various frequencies (Schwarzacher, 1993; House, 1995). Can c-dinocysts provide a micropalaeontological tool to decipher such characteristics in the lithologically less distinctive chalk/marls of the European shelf sea?

How is the orbital-forcing signal transformed into sedimentary cycles? To which extent can changes in primary carbonate production versus changes in terrigenous input explain the chalk/marl alternations? Are sea level changes reflected in the high-frequency cylicity? Which palaeoclimatic/palaeoceanographic changes may have had a dominant influence on the temporal distribution pattern of calcareous dinoflagellate cysts?

#### 3) Palaeoecology and spatial distribution patterns

Cyclic temporal association changes throughout a section may have been caused by cyclic shifts in environmental facies zones. Are high-frequency temporal cyst association changes associated with bathymetry-related spatial distribution patterns of calcareous dinoflagellate cysts? Do individual species or c-dinocyst assemblages show restricted distributions which can be related to certain palaeoenvironments?

#### 4) Palaeoecology of Pithonelloideae

The Pithonelloideae are the dominant group of the microfossils investigated here. Which ecological characteristics of the Pithonelloideae can be derived from their spatial and

temporal distribution patterns? What are possible causes of the extinction of the Pithonelloideae after the K/T boundary event?

#### 5) Survival strategies

Most dinoflagellate species survived the K/T boundary event (Brinkhuis et al., 1998; Hildebrand-Habel et al., 1999). What are the ecological controlling factors of the c-dinocyst distribution patterns in the Boreal Realm across the K/T boundary? Which particular assemblages characterise the boundary layer and to what extent do special morphotypes occur?

The cyclicity oriented questions mentioned above have been answered through the integrated analysis of quantitative cyst data and lithological parameters, and are dealt with in **Chapter 2**. which is focused on orbitally-forced temporal changes in mid-Cenomanian c-dinocyst assemblages. **Chapter 3**. represents a picture of spatial distribution patterns of c-dinocysts through the mid-Cenomanian across a palaeo-bathymetrical transect. **Chapter 4**. deals with the response of c-dinocysts to the environmental change related to the K/T impact event. The discussion of patterns of species-selective extinction and survival strategies during an abrupt environmental catastrophe adds to the knowledge obtained from Chapters 2 and 3. The various aspects of Pithonelloideae-palaeoecology are discussed in Chapters 2 to 4. In **Chapter 5**., a new species of c-dinocysts which may represent an example for the development of stress-induced morphotypes at the K/T boundary is described.

Methods applied in the present thesis comprise: *Sampling*) high-resolution sampling of the sediment core Ruegen E Rn 105/64; sample request DSDP Leg 80, Site 550b; field sampling of sections Escalles (France) and Stevns Klint (Denmark); *Processing and preparation*) Disintegration of samples by repeated freezing and thawing in sodium sulphate solution, ultrasonic cleaning, sieving and measurement of grain size fractions (wt%), preparation of SEM stubs and microtom thin sections; *Lithological measurements*) LECO measurement of carbonate content and TOC contents, carbonate bomb, grey scale, Gamma ray logging, XRD clay mineral analysis; *Microscopy*) Optical microscopy (tests of quantitative method, counting, picking of specimens), SEM (determination of species, measurement of cyst-morphometry, EDAX measurement), Polarised-light microscopy (analysis of thin sections), Cathodoluminescence (determination of cementation, characterisation of carbonates, analyses of cyst morphology).

#### **1.2.** The Boreal Realm during the Cretaceous – Palaeoclimate and sea level

The sections investigated in this thesis were positioned on the European shelf at the transition between Boreal and Tethyan Realm at mid-northern palaeo-latitude around 40°N according to palaeomagnetic data (Harrison and Lindh, 1982). The Middle-Upper Cretaceous was a period of high sealevel (up to 250 m higher than today) during a greenhouse situation probably without major icecaps (Kemper, 1987). Model simulations suggest the following aspects to have been responsible for the warm climate: (i) the concentration of land masses along the equator (Barron and Washington, 1984; Hay et al., 1990) (ii) a four to seven times higher  $CO_2$  content in the Cretaceous atmosphere as compared to present day values (Berger and Spitzy, 1988; Hay et al., 1997), and (iii) upwelling of warm, saline water at the poles (Hay, 1995). An assumed generally warmer climate of the Cretaceous would have had the thermodynamic consequence of enhanced humidity, resulting in increased rainfall at mid latitudes (Barron et al., 1983, 1989; Mindszenty and D' Argenio, 1993; Voigt, 1996). The equator-pole temperature gradient is believed to have been much smaller than today, reducing the thermohaline circulation and decreasing production of cool bottom water at the poles (Brass et al., 1981, 1982). Instead, bottom water production, as far as the Atlantic Ocean is concerned, is thought to have taken place by downwelling of warm saline water produced in the low- to mid-latitude shelf seas (Bralower and Thierstein, 1984; Hay, 1995). Oxygen depletion of this bottom water probably caused long-term periods of enhanced preservation of organic matter, resulting in the pronounced Middle Cretaceous black shale deposition (e.g. Arthur and Sageman, 1994 and references therein).

Long-term sea level rise related to general climate warming began in the Triassic and reached its maximum in the Upper Cretaceous. The major Cretaceous eustatic sealevel cycle peaked during the Cenomanian/Turonian transition (Hardenbol et al., 1998). During this time, the European shelf was continuously flooded and a number of epicontinental basins developed which were devided from each other by submarine swells (Ziegler, 1990). These sedimentary basins provided the depositional area for thick carbonate sequences. The high sea level disabled the formation of shelf fronts, thus, free exchange of surface water between the North Atlantic Ocean and European shelf sea was possible (Voigt, 1996). Nutrient consumption was high due to extreme productivity in the shelf seas, the primary production in the ocean, in contrast, was very low (Cool, 1982; Bralower and Thierstein, 1984). The main source areas of nutrient input were the North American and Eurasian continents to the north and some smaller paleo-highs as Variscan remains to the South.

#### 1.3. Calcareous dinoflagellate cysts – research history and current knowledge

C-dinocysts are formed during the life cycle of the Calciodinelloideae (Fensome et al., 1993), a subfamily of the dinophyceae. C-dinocysts have been commonly described as "calcispheres" in the fossil record of the Cretaceous, without a further distinction of species. Although most of them do not show any signs of paratabulation, some species do reflect the peridinioid plate pattern of the corresponding motile dinoflagellates very clearly. We know from recent species that Calciodinelloideae are unicellular, autotrophic, primary producers that live in the upper water column. As such, they can play an important role for the reconstruction of climatically-induced changes in surface water conditions. C-dinocysts form one of the three major components of the investigated carbonates, which are almost entirely of biogenic origin. The mean ratio Coccoliths:foraminifera:c-dinocysts is about 70:20:5 (%), these three groups forming 95% of the biogenic components.

The research history of the so-called "calcispheres" can be traced back to Kaufmann (1865) who first described them as species of the foraminifera genus *Lagena*. Lorenz (1902) established the new genus *Pithonella* for the calcispheres which were still assumed to be single-chambered foraminifera. Bonet (1956) rejected the classification of *Pithonella sphaerica* and *P. ovalis* as foraminifera and included them into the *incertae sedis* family Calcisphaerulidae. Theories about the taxonomic affinity of Calcisphaerulidae include: *incertae sedis* protozoans (Adams et al., 1967, Banner, 1972), planktic ciliate organisms (Banner, 1972), spores of chlorophycean algae (Bolli, 1974) and Calpionellids (Villain, 1991). The first SEM studies on isolated Calcisphaerulidae (Banner, 1972; Bolli, 1974) recovered a high variety of surface structures, indicating a rather complex taxonomy, comprising species that differ considerably from the microfossils originally described as *Pithonella* or *Lagena*. All species were, however, grouped in the general genus *Pithonella* Lorenz (1902).

Deflandre (1947) was the first to discover peridinialean paratabulation on some "calcisphere" species and, thus, was able to prove an affinity to dinoflagellates. Wall and Dale (1968) showed with culturing experiments that dinoflagellates produce calcareous cysts. Fütterer (1976) made the first attempt to relate mesozoic Calcisphaerulidae to the Quaternary and Recent calcareous cysts forming dinoflagellates. He also interpreted the

"Thoracosphaeres", formerly interpreted as coccolithophorids, as calcareous cysts of dinoflagellates. Later studies supported and improved this theory, as culturing experiments with *Thoracosphaera heimii* showed that this dinoflagellate species is a vegetative stage (Tangen et al., 1982) and does not represent a cyst.

Intensive research on "*Pithonella*" during the eighties (e.g. Keupp, 1981, 1982, 1987; Keupp and Mutterlose, 1984; Willems, 1985, 1988) induced considerable taxonomic revisions. Firstly, the presence of peridinialaen paratabulation on the inside of the organic lining of *Pithonella patriciagreeleyae* Bolli 1974 and on the surface of some otherwise non-tabulated species proved many mesozoic Calcisphaerulidae as being calcareous dinoflagellate cysts. Secondly, the first palaeoecological studies discovered relations between palaeoenvironmental factors and the morphology of c-dinocysts (Keupp, 1981; 1993). The wall crystal orientation became a diagnostic feature for a first subdivision of Pithonella. Based on these wall types, Keupp (1987) and Kohring (1993) established the systematic concept of 4 subfamilies of calcareous dinoflagellate cysts: Orthopithonelloideae (radial wall type with c-axes of the calcite crystals perpendicular to cyst surface), Obliquipithonelloideae (Kohring, 1993) ("radial" wall type with c-axes tangential to cyst surface).

With the distinction of subfamilies, the incertae sedis genus *Pithonella* was included as subfamily Pithonelloideae to the Calciodinellaceae (Keupp, 1987). According to Keupp (1987) and Dali-Ressot (1987), Pithonelloideae show distribution patterns and morphological features that are closely comparable to other c-dinocysts. However, the affinity of this group to the dinoflagellates is still controversially discussed (e.g. Willems, 1990; Villain, 1991; Keupp and Kienel, 1994; Kienel, 1994; Hildebrandt-Habel et al., 1997; Dias-Brito, 2000) which gave motivation to focus on Pithonelloideae palaeoecology.

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## 2. Analysis of mid-Cenomanian Milankovitch cycles using calcareous dinoflagellate cysts – a reconstruction of orbitally-forced palaeoenvironmental changes and their transformation into sedimentary cycles

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#### Abstract

Mid-Cenomanian, precession-controlled (21 ka) chalk-marl couplets of the Cap Blanc Nez section (Anglo-Paris Basin) have been studied with focus on the effects which Milankovitch cycles have had on the palaeoenvironment. In this paper, we present micropalaeontological and lithological tools that enable the reconstruction of both the cycle architecture and the transformation of the orbitally-forced signal into the sediment. A palaeoecological reconstruction based on changes in the association of calcareous dinoflagellate cysts (c-dinocysts) was carried out, in which two characteristic ecological assemblages of c-dinocysts were identified. Gradual changes in absolute and relative abundance of the cyst species in these assemblages over several couplets depict a bundling pattern which is interpreted to reflect the modulation of the intensity of the precession cycle by the eccentricity cycle (100 ka). The stacking pattern in the natural gamma ray signal and the carbonate and TOC content has the same period and provides lithological proof of the bundling. A shelf basin circulation model is established to explain the relation between orbitally-forced climate change, its environmental consequences and the resulting sedimentary cyclicity. Variations in oceanic circulation are reflected in the sediment by the chalk-marl couplets, the most distinctive couplets ocurring at the base and top of the bundles. While the chalks reflect a well-mixed shelf sea environment, the marls, particularly those at the bundle boundaries, can be interpreted as the sedimentary

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expression of stratified water masses. During deposition of these marls, reduced oceanic mixing due to low seasonality during strong precession maxima at the eccentricity maxima caused periods of water column stratification that in turn led to nutrient depletion and decreased productivity in the surface water masses.

*Keywords*: Cretaceous, Cenomanian, Milankovitch cycles, palaeoceanography, calcareous dinoflagellate cysts, gamma ray.

#### Introduction

Chalk-marl couplets of the Boreal Cenomanian of the Anglo-Paris Basin are characterised by a more or less distinct light/dark cyclicity. These couplets have been interpreted as orbitally-forced sedimentary cycles (e.g. Fischer and Schwarzacher, 1984; Bottjer et al., 1986; Hart, 1987; Gale, 1990, 1995; Schwarzacher, 1993, 1994; Mitchell and Carr, 1998). They are thought to represent the 21 ka precession signal, an interpretation which is supported by (i) correlation with the radiometric dating of the Cenomanian stage based on bentonite bearing sections of the Western Interior Basin, and (ii) spectral analysis (Gale, 1990, 1995; Gale et al., 1999).

The amplitude of the precession signal is modified in amplitude by the 100 ka eccentricity cycle, which leads to an approximate 5:1 bundling of couplets and provides the most conspicuous evidence for the orbital forcing of sedimentary cycles (House, 1995). Such bundling of couplets can, for example, clearly be recognised in the Barremian of the Gubbio section, Italy (Schwarzacher, 1993), where strong variations in grey scale, carbonate content and bed thickness follow the above-mentioned 5:1 ratio. However, the superimposition of precession and eccentricity cycles is often preserved in the sediment as rather subtle changes that cannot be detected in the field. In the couplet succession of the Anglo-Paris Basin, bundling is difficult to prove without the confirmation by microscopic investigations. The current high-resolution micropalaeontological analysis, however, provides an objective measure to recognise this cyclicity.

The main tool used in the present study of the Anglo-Paris Basin couplet succession is the qualitative and quantitative analysis of their calcareous dinoflagellate cyst (cdinocyst) content. C-dinocysts are formed during the life cycle of the Calciodinelloideae, a subfamily of the dinoflagellates (Fensome et al., 1993). C-dinocysts have been commonly described as "calcispheres" in the fossil record, without a further distinction of species. Although most of them do not show any signs of paratabulation, some species do reflect the peridinioid plate pattern of the corresponding motile dinoflagellates very clearly. We know from recent species that the Calciodinelloideae are unicellular, autotrophic, primary producers that live in the upper water column. As such, they can play an important role in reconstructing climatically-induced oceanic changes. C-dinocysts form one of the three major components of the investigated carbonate, which is almost entirely of biogenic origin. The mean Coccoliths:foraminifera:c-dinocysts ratio is about 70:20:5 (%), these three groups forming 95% of the biogenic components of the investigated material.

Our study of c-dinocysts distinguished to the species level is the first to apply them for the interpretation of Cenomamian sedimentary cycles and their stacking patterns. Climatic changes resulting from orbital forcing are reflected in the sediment, as they strongly influence the biogenic (carbonate, organic matter) and abiogenic (siliciclastic) sedimentation. Changes in abundances and distribution of the biogenic components can be caused primarily by variations of environmental parameters, such as surface water temperature, stratification of the water column and nutrient input. Secondarily, diagenesis may have altered the sedimentary distribution of biogenic and abiogenic components but is not considered to have obscured the primary cyclic changes in the investigated section (e.g. R.O.C.C. group, 1986). Here, an approach is made to reconstruct the palaeoceanographic response to variations in orbital parameters through the integrated interpretation of palaeontological and lithological data, such as microfloral changes, which are compared to changes in the carbonate content and the natural gamma ray.

#### Regional geology, palaeogeography

We investigated a 14 m long sedimentary succession in the Middle Cenomanian of the Cap Blanc Nez section near Escalles/SW of Calais, France (Figs. 1 and 2). This 78 m thick profile of the Cenomanian is the reference section for this part of the Anglo-Paris Basin. It represents a central basinal, outer shelf position (Fig. 1), characterised by a continuous deposition of 12 to 110 cm thick chalk/marl alternations. These carbonate sequences were deposited at water depths between 300 m and 500 m (Hart, 1980; Gräfe, 1999), well below the storm-wave base. Palaeogeographically, the investigated section was positioned at around 40° N, i.e. at mid northern latitudes (Ziegler, 1990; Voigt, 1996).

During the Cenomanian and Turonian, a continuous sea level rise led to the worldwide expansion of shelf seas (Haq et al., 1987). The Boreal shelf realm was bordered to the north by the North American and Eurasian continents (Ziegler, 1990). An array of Variscan palaeo-highs formed the border between the Boreal and Tethyan realms to the south. A connection to the opening North Atlantic in the west existed, restricted by the English High and Armorican Massive. Several seaways enabled a connection to the Tethys since the Lower Cretaceous. Both Tethyan and Boreal influence can therefore be expected in the investigated area. The interfingering of these two water masses was thought to be expressed in the lithofacies; Early Cretaceous Tethyan deposits being carbonate-rich and Boreal sediments characterised by high proportions of clay (Keupp, 1993; Mutterlose, 1989; Mutterlose and Ruffell, 1999).

Tectonic activity of the main structural elements of western Europe was relatively calm during the Albian to Lower Turonian (Ziegler, 1975; Ziegler, 1990). Thus, no major disturbances of the sedimentation occurred and reworking, tectonically-induced movement or intercalation of volcanogenic sediments did not disturb the continuous sedimentation.



Fig. 1: Palaeogeography of western Europe during the Middle Cenomanian (after Ziegler, 1990); AM = Amorican Massive, EH = English High, IBM = Iberian Massive, IM = Irish Massive, MC = Massive Centrale, RM = Rheinish Massive.

#### Material

Three main lithofacies types can be distinguished in the studied interval (Gräfe, 1999): (i) grey to white chalk (light-coloured), (ii) marly grey chalk (light-coloured); and (iii) grey marlstone (dark-coloured). It should be kept in mind that the generally used term "marl" for dark layers is lithologically misleading because of their high carbonate content. Bio-, litho- and sequence-stratigraphy according to Robaszynski and Amédro (1993), Robaszynski et al. (1998) and Owen (1996) are summarised in Fig. 2.

We investigated the part of the section ranging from 42.3 m to 56.5 m above the base of the Cenomanian (Fig. 2). Two parts within this succession, termed EscA (Escalles A) and EscB, were analysed for stacking patterns of the couplet succession using various parameters. EscA, covering the interval from 42.3 m to 46.5 m, is positioned in the *A. rhotomagense* zone, its base forming the transition from the *T.costatus* to the *T.acutus* subzone. It represents the lower half of lithostratigraphic member I21 of Robaszynski et al. (1980) and is in the range of couplets >C20 of the couplet numbering scheme of Gale (1990) (Highstand Systems Tract of sequence 3). EscB, covering the interval from 53.8 m to 56.5 m, is a set of couplets in the lower *A. jukesbrownei* zone, within lithostratigraphic members I22 and I23, and couplets D1 to D5 (lower Transgression Systems Tract of sequence 4) according to the subdivisions of Robaszynski et al. (1998) and Gale (1995), respectively.

#### Methods

35 samples from EscA and 25 samples from EscB were analysed for their cdinocyst content, grain size distribution, carbonate content, total organic carbon (TOC) content and natural gamma ray at a sample spacing of 10 cm. To connect the two parts of the section, additional samples with 20 cm to 100 cm sample spacing were studied between the sections with focus on the marls.

All microscopic investigations on microfossils and non-carbonate grains were carried out using disintegrated material. Sample sizes of approximately 0.5 g were processed using repeated freezing and thawing in sodium-sulphate solution. A two minute ultrasonic cleaning was applied to each sample to clean the specimens. The disintegrated samples were sieved into three fractions (<20  $\mu$ m, 20-75  $\mu$ m and >75  $\mu$ m). The two coarse fractions were weighted to obtain information on the grain size distribution, which



Fig. 2: a) Integrated illustration of the bio-, sequence- and lithostratigraphy of the investigated section (modified after Robaszynski and Amédro, 1993; Gräfe, 1999). Sequence and couplet numbering after Gale (1995); Abbreviations: T. = *Turrilites*, I. = *Inoceramus*; scale in meters from base of Cenomanian. Signature in the investigated section: grey = marls, white = chalks. b) Geographic location of the investigated section (arrow).

provides a clearer distinction of lithotypes than is possible from the outcrop observation (e.g. detection of additional "marly" layers).

The micropalaeontological analyses comprise investigation of absolute cyst abundances, relative abundances and ratios between cyst species. Absolute abundances are given in cysts/mg of the 20-75  $\mu$ m fraction. Mean cyst sizes of the species *Pithonella sphaerica* were measured on about 50 randomly picked specimens per sample for a 2 m interval spanning the basal 2 marl/chalk couplets of EscA. In addition to the cyst data, sizes of foraminifera of the 20-75  $\mu$ m size fraction were measured under the SEM (50 tests per sample and 4 samples within EscA).

In order to produce quantitative c-dinocyst data, a weighted microsplit of 1-4 mg of the 20-75  $\mu$ m grain size fraction was taken by measuring the weight of the entire fraction before and after splitting. The complete microsplit was counted using a Zeiss binocular microscope Stemi2000 with magnifications ranging from 80x to 120x. One such microsplit contained at least 300 specimens, in the majority of samples well over 500 specimens. Specimens which could not be taxonomically specified by their light-optical characteristics were picked and studied with the SEM.

The reproducibility of this way of split counting was checked by adding a known number (4000) of glass pearls of 50  $\mu$ m diameter to a sample and counting several splits ranging from 0.8 to 15 mg. The test resulted in a mean deviation from the true content of 11% with maximum errors of +5% (1 of 12 counts) and -20% (2 of 12 counts). Multiple counts of splits of the same sample resulted in maximum differences between the counts of 15-20%, generally being around 10%. Thus, only differences of more than 20% between different counted samples are regarded to reflect significant abundance changes.

In order to obtain a detailed lithological log of the investigated section, the natural gamma ray signal was analysed. Gamma ray and the carbonate content of the marls were cross-plotted to characterise the marl types. The carbonate content and TOC content were determined using LECO measurement.

For the interpretation of the gamma ray data, an analysis of the clay mineralogy was necessary. 6 samples at an approximate sample spacing of 1.5 m, covering two major oscillations of the gamma ray log, were chosen. The variations of the clay content within couplets of several Anglo-Paris Basin sections were analysed by Ditchfield (1990), so we focused on variations between marl types only. The samples were decarbonised with a 10% EDTA (Titriplex III) solution which was buffered with NaOH to pH ~8, at 50°C under continuous stirring for 3 days. 340 ml of this solution dissolves 10 g of carbonate. After filtering and a 5 times cleaning with de-ionised water, the insoluble residue was

centrifuged. The XRD-analysis was performed with a diffractometer D500 on a smear slide containing the  $< 2 \mu m$  fraction.

An overview of the c-dinocyst species studied here is given in appendix A. Appendix B and C contain all raw data of this study. All material is stored at the Division of Historical Geology and Palaeontology, University of Bremen.

#### Results

#### Micropalaeontology

Absolute and relative abundances

The quantitative method applied in this study focuses on the 6 most abundant cdinocyst species (Appendix A, Fig. 11) which are common throughout the section:

Pithonella sphaerica Kaufmann 1865

Pithonella ovalis Kaufmann 1865

Pithonella discoidea Willems 1992

*Pirumella* sp.

Cubodinellum renei Keupp 1987

#### Pentadinellum vimineum Keupp 1987

All cyst species mentioned above are generally present in chalks as well as in marls, but changes in absolute and relative abundance are present between these lithofacies and, in form of subtle variations, also within the litho-types. Marls typically show low absolute abundances and a diverse c-dinocyst association due to the presence of rare species (listed in Appendix A), which cannot, however, be used for quantitative studies. In intervals of high carbonate content (i.e. chalks), high abundances and low diversity are typical.

The micropalaeontological analysis of the abundant species defines two assemblages: (i) the P-assemblage, which consists predominantly of Pithonelloideae (>95%) and *Pirumella* sp.; and (ii) the S-assemblage (S=sculptured/paratabulated), which contains the paratabulated species *Cubodinellum renei* and *Pentadinellum vimineum* that may represent up to 80% of the c-dinocyst association (Figs. 3, 4, 9).

The two assemblages show an inverse absolute abundance pattern (Figs. 3 and 4). In marls, distinct and often sharp-cut peaks in absolute abundances (cysts/mg) of the S-assemblage



**Fig. 3**: C-dinocyst absolute abundances (cysts/mg of the 20-75 μm size fraction) in section EscA. Passemblage: positive peaks relative to mean value are white and are marked with a letter; negative peaks relative to mean value are black and marked with a number (these correlate with excursions (black) of the Sassemblage).



Fig. 4: C-dinocyst absolute abundances (cysts/mg of the 20-75 μm size fraction) in section EscB. Passemblage: positive peaks relative to mean value are white and are marked with a letter negative peaks relative to mean value are black and marked with a number (these correlate with excursions (black) of the S-assemblage). (black, numbered peaks) coincide with very low abundances of the P-assemblage. In contrast, broad maxima in abundance are characteristic of the P-assemblage (white, lettered peaks), and are commonly positioned in chalks where S-assemblage abundances are low. A major peak of *Pirumella* sp. (Fig. 3, peak A1/A2) is correlated with such a broad peak, thereby including this species into the P-assemblage.

#### Distinction of marl types based on cyst association changes

Although the above-mentioned relation between c-dinocyst assemblages and the lithotypes is quite characteristic, the relation of the two groups varies between the chalk-marl couplets. This allows the differentiation between different marl types, which plays a key role in the further analysis of the cyclic pattern.



Fig. 5: Length distribution of *Heterohelix moremani* in 4 samples of the couplet bundle EscA. Note the dominance of smaller specimens in e-marls.

The most distinct marl type is characterised by an almost pure S-assemblage, while Pithonelloideae abundances may decrease to near absence (Figs. 3, 4 and 9). A significant feature is the sharpness of the positive abundance excursions of species of the Sassemblage, such as peaks 1 and 5 in EscA (Fig. 3). The total number of c-dinocysts is low in these beds. Marls of this type will be termed "event-marls" (e-marls) here, because they appear as short-term, exceptional events. The opposite to the e-marls are the so-called pmarls (=Pithonelloideae-rich marl). Relatively high abundances of Pithonelloideae (comparable to chalks) are characteristic for these marls (for example M3(?) and M4 in Fig. 3), while the S-assemblage may be present in low numbers or even absent.

Besides their distinct c-dinocyst association, e-marls are characterised by partial solution of foraminifera and an increased number of very small foraminifera in the 20-75  $\mu$ m fraction. Among these small species, the planktic foraminifer *Heterohelix moremani* Cushman is a common form. Foraminifera of the size fraction <75  $\mu$ m have been scarcely considered in the literature. The length of tests of *H. moremani* was measured in the two e-marls, the p-marl and a chalk of EscA with focus on specimens with not less than 7 chambers (adult forms). The majority of such 7-chambered tests of *H. moremani* have a relatively small size of 50-90  $\mu$ m in the e-marl samples, compared to 70-110  $\mu$ m in the p-marls and in the chalk (Fig. 5).

# Variations within the dominant genus – the Pithonella sphaerica/Pithonella ovalis ratio (Ps/Po-ratio)

Pithonelloideae are the most abundant c-dinocyst species in the investigated material. The present study shows that the *Pithonella sphaerica/Pithonella ovalis* ratio (Ps/Po-ratio) is a statistically powerful indicator of abundance variations within the group of Pithonelloideae. In EscA the Ps/Po-ratio has a relatively constant mean value of 3 but shows distinct negative and positive excursions from this mean value which vary between almost 0 and 6 (Fig. 6). In EscB, the mean value drops to 0,6 but the Ps/Po-ratio still fluctuates significantly between values of 0 and 2 (Fig. 7).

Fig. 6: Relations between lithological data and P-assemblage data of section EscA. Dotted curves = low frequency curves of values in the marls;  $d_m = \underline{d}$  ifference in <u>mean</u> percentage between marl and adjacent chalk. Interpretation = reconstructed Milankovitch cyclicity reflected in the data. Peak numbering and lithological signature as in Fig. 3.



In the studied material, a low Ps/Po-ratio is always the result of a stronger decrease in abundance of *Pithonella sphaerica* relative to *P. ovalis*. This is characteristic for the marls and corresponds with generally decreased Pithonelloideae abundances. There is a gradual variation in Ps/Po values between marls (low frequency curve in Fig. 6), with lowest Ps/Po values observed in the e-marls. The ratio stays close to the mean value around the p-marls. Thus, the distinction of marl types on the basis of changes in absolute cyst number as described above is supported by the Ps/Po-ratio.

Contrary to the marls, chalks are generally characterised by a high Ps/Po-ratio due to an increase in abundance of *Pithonella sphaerica* relative to *P. ovalis*. A significant minimum in the size of specimens of *P. sphaerica* occurs within the basal chalk of EscA, which was analysed for morphometric changes (Fig. 3). This minimum is accompanied by a simultaneous decrease in abundances of Pithonelloideae, a peak of the Ps/Po-ratio, and a particularly high carbonate content (Fig. 6).

#### Cycle architecture of EscA compared to EscB

A systematic succession of marl types is present in EscA (Figs. 3 and 6). M1 and M6 are e-marls whereas M2 and M5 are less distinctive marls. Towards the middle of this section, differences between chalks and marls concerning the relation between the P- and S-assemblages and the Ps/Po-ratio are least developed. An interference between the S-assemblage and the P-assemblage is characteristic of this interval (p-marls M3(?) and M4). The resulting pattern is a bundling of 5 couplets, bounded by e-marls. From the base towards the top of this bundle, the abundance patterns of the c-dinocyst assemblages gradually oscillate from the event-marl situation to the p-marl situation in the middle of the bundle, and then back to the next e-marl situation.

The c-dinocyst abundances of EscB are shown in Fig. 4. The abundances of the species of the S-assemblage are lower than in EscA, leading to a lower resolution of this parameter. Whereas in EscA, all numbered peaks (in the marls) were correlatable between the P- and S-assemblage, only peak 1 can be correlated between the two assemblages in EscB. The associated marl (M1) can be characterised as an e-marl due to its minima of (i) *Pithonella discoidea* and *Pithonella sphaerica*, which are correlated to a weak S-assemblage excursion (Fig. 4); and (ii) the low Ps/Po-ratio (Fig. 7). This e-marl is much less distinctive then those in EscA. Note that the absolute abundance of Pithonelloideae in the e-marl of EscB is not as low as in EscA. 4 peaks in the absolute abundances of the


Fig. 7: Relations between lithological data and P-assemblage data of section EscB. Dashed curves – low frequency curve between values in the marls; d<sub>m</sub> – <u>difference in mean percentage between marl and adjacent chalk</u>. Dotted curve: low frequency variation in the Ps/Po-ratio. Couplet succession of EscB enables no interpretation as in EscA. Peak numbering and lithological signature as in Fig. 4.

Pithonelloideae (A-D) can be distinguished in EscB (Fig. 4). All are situated in the chalks. The double peak C1/C2 is associated with a broad increase of abundance of the S-assemblage (peak 4). It is thus comparable to the peak region B1/B2 which is in interference with peak 3 (p-marl M3 (?)) in EscA. The double peak D1/D2 is similar but corresponds with only a weak increase in abundance of paratabulated forms. It can, therefore, be better compared to A1/A2 of EscA, which marks the most distinctive chalk layer of this section. A near-symmetric cycle architecture, as is present in EscA, cannot be reconstructed in EscB, as only e-marl M1 is unambiguous. No bundling of couplets can be reconstructed from the low frequency curves in Ps/Po-ratio and Pithonelloid abundances (Fig. 7).

# Lithology

#### Gamma ray

The gamma ray data for EscA and EscB are shown in Figs. 6 and 7. The plot for the entire investigated section is given in Fig. 9 (page 31). The gamma ray is a proxy for the clay content of sediments. High counts per unit (cpu) represent layers rich in radioactive elements (K, U or Th) which are mainly incorporated in clay minerals. Thus, large excursions generally occur in the marls, whereas chalks show low values caused by their higher carbonate/clay ratio. Due to the declining overall clay content from EscA to EscB, the gamma values continuously decrease throughout the entire section (Fig. 9; Gräfe 1999, Figs. 5, 6).

Fig. 6 shows that a positive correlation exists between the low frequency curve of the gamma ray log of marls and the Pithonelloideae distribution throughout EscA. This curve shows a gradual increase from low values in the e-marls (M1, M6) to higher values inbetween them. In EscB, only the gamma ray variations between chalks and marls can be recognised. Changes between marls, as in EscA are not clearly reflected, probably since the lower overall gamma value leads to a lower resolution.



**Fig. 8**: Cross plot of gamma ray data and carbonate content of the marls from EscA and bundle 2. Note the eccentricity-controlled shift (b) of e-marls compared to the normal relation (a).

In Fig. 8, the gamma ray signature of marls is plotted against their carbonate content. Interestingly, the different marl types plot in different areas within this diagram. The general trend from high carbonate content and low gamma ray values to low carbonate content and high gamma values is shifted in the e-marls to generally lower values of both parameters. This could be due to the composition of the clay mineral fraction. To test this hypothesis, we chose 6 samples from e-marls and p-marls (for sample positions see Fig. 9) and examined their relative content of kaolinite, chlorite and illite and the half value width (crystallinity measure) of illite (Apendix C). Variations in the relative quantities of these clay minerals are on the order of 1% only. The half value width of illite, as a measure for the crystallinity, varies between 0.48 and 0.57 and can be regarded as constant.

The results reveal a stable clay association which varies very little between the samples (Fig. 9). Though the small variation in the illite/kaolinite-ratio seems to correlate positively with the gamma ray data in EscA, it fails to explain the gamma ray peak the second p-marl analysed (Fig. 9). Additionally, it is not significant enough to cause the changes in the gamma ray log. Besides clay minerals, a major source for elevated gamma ray values is uranium-binding organic matter (ten Veen and Postma, 1996). However, no relation between the TOC content and the low frequency curve in the gamma ray log could be found (Figs. 6 and 7).

#### Grain size distribution

The percentage of grains with a size larger than 20  $\mu$ m in EscA is clearly related to the light/dark lithological changes, chalks being coarser grained than marls (Fig. 6). It is 10-25% in the dark layers and 20-70% in the light layers. These ranges of grain size represent a clearer distinction between the light and dark layers than the carbonate content does. As the marls contain less grains with a size >20  $\mu$ m but still have a high carbonate content (see following chapter), the light/dark-cyclicity is to some extent a simple optical expression of these grain size changes.

In three exceptional samples of EscA, minimum values of less than 10% grain size  $>20 \ \mu\text{m}$  occur. Two of these samples occur in e-marls (Fig. 6, peaks 1 and 5), and relate to minima of the carbonate content. The third sample, however, is situated in the middle of the couplet set and this thin bed does not appear in the outcrop as a dark layer (Fig. 5, peak 3; named M3 (?)). Because of the deviation from the characteristic grain size ranges of chalks, this peak would define the layer "M3 (?)" as a marl.

The percentage of grains >20  $\mu$ m in marls is 20-40% in EscB (Fig. 7). A grain size minimum in a chalk was also identified (peak 4), which hints at the presence of a marly layer at this position as well (M4 (?)). The overall higher grain size in marls of EscB compared to EscA is also expressed by the less distinct outcrop appearance of marls higher up in the section. The grain size distribution of both EscA and EscB shows no clear relation to the c-dinocyst data and the gamma ray log.

#### *Carbonate content and total organic carbon (TOC)*

The carbonate content of EscA varies between 74% and 90% (Fig. 6). It is positively related to the absolute abundances of the P-assemblage species and the Ps/Poratio. A gradual change can be recognised in the amplitude of variation between marls and chalks ( $d_m$  in Fig. 6). The contrast is largest for the e-marls (12-15%) while in the middle of the bundle, the difference in carbonate content between marls and chalks is only about 5%. This trend is negatively related to the low frequency curve in gamma ray values and the c-dinocyst data (Fig. 6) and also resembles the bundling of couplets in section EscA.

TOC values of the marls in EscA range from 0.15-0.26%, whereas those of the chalks range from 0.1-0.2%. There are no significant changes in TOC values and carbonate content between the marl types but, as with the carbonate content, the differences in TOC values between marls and chalks are largest in the couplets that contain the e-marls (Fig. 6).

In EscB (Fig. 7), the variations in carbonate content between marls and chalks is lower than in EscA (2-10%). Chalks have carbonate values as low as 85% while some marls show a maximum carbonate content of 88%. TOC values are between 0.15% and 0.32% in marls and range from 0.1%-0.2% in the chalks.

### Cycles between EscA and EscB, defined by the succession of marl types

An analysis of c-dinocysts of the interval from 46 m to 54 m between the section parts EscA and EscB was performed, with focus on the succession of the different marl types to test for continuous bundling. Fig. 9 shows the variations and trends. The couplets following EscA can again be bundled into a set of 5 ("bundle 2" in Fig. 9). This bundle shows a comparable architecture to that of EscA, being bounded by e-marls and gradually developing a p-marl in the middle of the succession (Fig. 9). Above this bundle, couplets



Fig. 9: Integrated illustration of the investigated section, showing trends in (i) e-marl characteristics; (ii) variations in mean *Pithonella sphaerica* and *P. ovalis* abundances and the Ps/Po-ratio; (iii) bundling of gamma ray log and clay mineral distribution; and (iv) sequence stratigraphy after Robaszynski and Amédro (1993): SMW = Shelf Margin Wedge, TST = Transgressive Systems Tract, HST = Highstand Systems Tract.

cannot be bundled anymore by a systematic marl succession. The gamma ray signal and the lack of lows in mean absolute abundance of the P-assemblage suggest a relatively thick bundle of 4 couplets or a discontinuity in the succession (Fig. 9). The most important characteristic of this interval is the change which occurs in the Pithonelloideae assemblage. An increase of *P. ovalis* numbers between 52 m and 53 m leads to a significant shift of the mean Ps/Po-ratio from about 3 to 0.6.

#### Discussion

# Transformation of the orbital-forcing signal into micropalaeontological cyclicity – bundling pattern and palaeoenvironmental interpretation

The Middle Cenomanian chalk-marl alternations of the Anglo-Paris Basin have been previously analysed by spectral analysis and the results support orbital forcing of the cycles (Gale et al., 1999). Here, an attempt is made to reconstruct the coupled effect which orbital forcing on the one hand and oceanographic changes on the other have had on the palaeoenvironment. The observed bundling of five chalk-marl-couplets (Figs. 3, 6 and 9) strongly suggests the presence of a 5:1 modulation in amplitude of the precession signal by the 100 ka eccentricity cycle.

In EscA, the cyclicity is well reflected by the palaeontological and sedimentological parameters analysed in this study. A bundling pattern in palaeontological parameters was recently reported in a study of the sedimentology, macrofossil events and foraminiferal successions of the Lower to Middle Cenomanian by Mitchell and Carr (1998). Using different proxies, the present study provides an integrated approach to explain the transformation of the orbital signal into the sediment by interpreting the cyclic succession of different couplet types (defined here as marl types).

Couplets containing e-marls show the most pronounced contrast between chalk and marl (Figs. 3, 6 and 9). The amplitudes of all investigated micropalaeontological parameters peak in the e-marls and adjacent chalks. These couplets form the boundaries of the bundles. The observed amplification of couplets suggests increased low-frequency (eccentricity) modulation of the precession cycle. Thus, these bundle parts can be interpreted to have been deposited at eccentricity maxima. Contrary to these positions, interference of the usually negatively correlated abundances of the P-assemblage and the S-assemblage, the buffered positive and negative peaks of the Ps/Po-ratio around their mean value, and the small changes in TOC and carbonate content in the middle of the bundles (p-marls) all indicate a smaller contrast between the precession extremes during eccentricity minima. Since the bundling is well reflected by the c-dinocyst assemblages, we can attempt to palaeoecologically interpret the influence of the orbital variations on the palaeoenvironment.

A pattern of negatively related abundance trends of Pithonelloideae to the cdinocysts contained in the S-assemblage has already been observed by various authors in connection with sequence-scale sea level changes and water mass changes (Keupp, 1982, 1989, 1991; Zügel, 1994; Neumann, 1999). Although the species involved might indicate conditions which characterise a certain facies zone (e.g. lagoon), they could also have been spread over the entire epicontinental basin under certain oceanographic and climatic conditions (e.g. during periods of basin-wide, reduced circulation). Thus, cyst association changes do not necessarily reflect sea level change.

Particularly for the high frequency precession cycles investigated here, a sea level control appears unlikely for the following controversy in ecological interpretation. On the one hand side, the paratabulated species discussed in the present study have been attributed to a group of Tethyan invaders into the Boreal realm during transgressions in the Albian (Keupp, 1992; Neumann, 1999). At that time, Pithonelloideae contributed insignificantly to the dinocyst association of the Tethyan and Boreal realm. In the Cenomanian, on the other hand side, the Tethyan c-dinocyst assemblages rarely contain species of the S-assemblage and were dominated by *Pithonella ovalis* (Dali-Ressot, 1987; Wendler, unpubl. data). This species should then be the main element of a Tethyan invasion which cannot be observed in the e-marls. On the contrary, an invasion of *Pithonella ovalis* indeed occurs with the 3<sup>rd</sup> order transgression of sequence 4 (Fig. 9) and can be interpreted to indicate increased Tethyan influence towards the Upper Cenomanian.

Though there is a shift to a *P. ovalis* dominance amongst the Pithonelloideae, the main character of the e-marls is the unusually high percentage of paratabulated forms (Fig. 3). Pithonelloideae are interpreted as being typical for the outer shelf (Bein & Reiss, 1976; Villain, 1981), whereas the species of the S-assemblage were observed to be more abundant in marginal facies (Zügel, 1994). The distribution patterns in the marls (Fig. 9) would thus suggest a sea level fall during these episodes. However, it is unlikely that marginal facies zones expanded over the central areas of the Anglo-Paris Basin. Therefore, it seems more plausible that the observed distribution pattern of dinocysts reflects oceanographic changes which are not primarily controlled by sea level fluctuations, but instead led to basin-wide conditions typical of the marginal environment (e.g. a lagoonal or estuarine circulation).

*Pithonella sphaerica* has been interpreted as an indicator of high carbonate production (Noel et al., 1995), so that the very high Ps/Po-ratios in the chalks seem to indicate productivity peaks. In today's oceans, productivity of planktic organisms depends primarily on nutrient supply. Thus, a change from high to low abundance of calcareous primary producers in chalks and marls, respectively, may point to lower nutrient

availability during marl formation with the most oligotrophic conditions prevailing during e-marl deposition.

Investigations on Recent calcareous dinoflagellates have shown that they are especially adapted to rather oligotrophic conditions and well stratified surface water masses (Höll et al., 1998; Vink, 2000). On the other hand, the highest diversity of c-dinocysts can be found in shelf areas where also stratified, but eutrophic conditions persist near the coast (Wall et al., 1977; Dale, 1983). An example is the Mediterranean Sea which has a highly diverse c-dinocyst association in both, oligotrophic and eutrophic environments (Montresor et al., 1998; and in the fossil record e.g.: Versteegh, 1993).

In conclusion, the significant changes in the investigated section between phases of low diversity/high numbers of specimens (chalks) and phases of high diversity/low numbers of specimens (e-marls) can be interpreted to reflect alternations between mixed and less circulated (possibly stratified) oceanographic conditions, respectively. Such oceanographic changes influence the supply of nutrients to the surface water environment. Oligotrophic conditions probably prevailed during times of greater stratification (e-marls), when transport of nutrients to the surface waters was hampered by stagnation. The observed pattern gives biological evidence for a productivity-controlled sedimentation. Low productivity during marl deposition in the investigated basin was also concluded from data on coccoliths (Young et al., 1998) and foraminifera (Hart 1980; Leary and Hart, 1992; Mitchell and Carr, 1998; Gräfe, 1999). The e-marls detected in the present study apparently reflect extremely low productivity, which was partly accompanied by selective dissolution at the water/sediment interface (especially of foraminifera) due to decreased accumulation rates of carbonate particles. The maximum abundances of Heterohelix moremani in the e-marls corroborate this interpretation of low productivity. This opportunist (Nederbragt et al., 1998) is known to have flourished during the uppermost Cenomanian oceanic anoxic event, when an extended oxygen minimum zone caused environmental stress on planktonic life (Hart, 1996).

# Transformation of the orbital-forcing signal into lithological cyclicity – gamma ray signature of the bundles

Governing the surface water carbonate productivity, precessional forcing passively influenced the quantity of non-carbonate in marls and chalks (Gräfe, 1999). This is reflected in the marls by a lower carbonate content, a smaller grain size and a higher gamma radiation compared to the chalks. However, although the carbonate content of the e-marls is low, they also have relatively low gamma ray values (Fig. 8). Additionally, the very low variation in carbonate content between the marl types cannot account for the differences in gamma ray values. Thus, an alternative explanation is needed for the low frequency mean curve of the gamma ray, which reflects the bundling of couplets and thus seems to reflect the eccentricity cycle (higher gamma ray values during eccentricity minima compared to the eccentricity maxima) (Figs. 6 and 9).

The low frequency mean gamma ray curve is a prominent feature throughout the entire Middle Cenomanian (Fig. 5 in Gräfe, 1999). It could be interpreted on the basis of the clay minerals as (i) a change in the clay mineral association caused by climatic change; or (ii) a sea level change during the eccentricity cycle. Substantial climatic change causes qualitative variations in the association of clay minerals, especially the kaolonite:illite ratio (Mutterlose and Ruffell, 1999; Deconinck and Bernoulli, 1991; Deconinck et al., 1999). Kaolinite is the major clay mineral of erosion under the warm, humid conditions proposed for the Upper Cretaceous (Aróstegui et al., 1991; Deconinck and Chamley, 1995; Hallam et al., 1991; Thiery and Jacquin, 1993). It contains no radioactive elements. The most important clay mineral producing a gamma ray signal is illite. Illite-rich clay assemblages develop by erosion under rather dry conditions (Rösler, 1981; Singer, 1984). It could thus be postulated that more humid conditions under increased seasonality of the eccentricity maxima were replaced by a slightly drier climate during the eccentricity minima in the Anglo-Paris Basin. However, changes of the kaolinite/illite ratio in the clay mineral assemblage are also caused by sea level change (Singer, 1984; Van Buchem et al., 1992; Kunow et al., 1998). Kaolinite is deposited in the marginal facies whereas the smaller crystallites of illite are transported further into the basin. If a transgressive/regressive pattern had partly controlled the clay mineral association of the investigated cycles, then the increased gamma ray signal at the eccentricity minima would characterise these periods as regressive units.

The almost constant kaolinite/illite-ratio between marls and chalks (Ditchfield, 1990), as well as between the e-marls and p-marls, suggests, however, that no significant climate change or sea level-controlled facies shift took place on the couplet (precession) and bundle (eccentricity) scale, respectively. Since changes in the clay association and TOC content are obviously insignificant, two factors that are related to productivity, the contribution of (i) phosphate (Glenn and Arthur, 1985; Wray, pers. com.) and (ii) the Sr/Ca ratio of the carbonate, could have influenced the low frequency gamma ray mean curve.

Due to the previously discussed relation between the bundling and surface water productivity, a plausible explanation for the gamma ray curve would be a higher phosphate content and/or an increased Sr/Ca ratio at the eccentricity minima, caused by an uninterrupted and high productivity. The addition of such a signal to the radiation caused by the clay minerals theoretically results in the observed low frequency curve.

Besides clay minerals, organic matter and phosphate, other components of the marls and chalks may cause gamma radiation, such as, authigenic glaucony or radioactive detrital minerals. Future work on the mineralogy of the non-carbonate fraction is needed to completely solve the problem of the radiation sources.

# Influence of the long-term sea level change on the transformation of the orbital-forcing signals

The long-term sea level trend seems to be critical for the preservation of the shortterm orbital signals. The 100 ka eccentricity signals are more distinctly developed in the Highstand Systems Tract (HST) of sequence 3 (EscA) than in the Transgression Systems Tract (TST) of sequence 4 (EscB). Positioned in an interval of maximum sea level change, EscB is considered to represent a different, possibly less distinct or even incomplete succession due to fusing or erosion of individual couplets. The disturbed cyclicity above bundle 2 is related to the lowstand and subsequent transgression that have been reconstructed for this interval (Figs. 2 and 9). Niebuhr and Prokoph (1997) suggest that obscured symmetry in sedimentary successions is caused by chaotic sedimentation under the influence of transgression and lowstand conditions which overprints Milankovitchrelated cyclicity. Poor preservation of the orbital signal within regressive units was also shown by Ricken (1994) in mid-Cretaceous cycles of the Western Interior Basin.

Besides disturbing the cyclical deposition, the long-term sea level change also appears to have influenced the distribution of Pithonelloideae in the investigated section. From 48.8 m to 52 m, the abundances of both *Pithonella sphaerica* and *P. ovalis* are significantly lower than in EscA, bundle 2 and EscB (Fig. 9). This interval is interpreted as the Shelf Margin Wedge (SMW) of sequence 3. Thus, the relative sea level lowstand is reflected by a Pithonelloideae minimum, indicating a basinward shift of their preferred facies zone which was the outer shelf. With the beginning of the *A. jukesbrownei* zone (TST of sequence 4), Pithonelloideae abundance increases considerably. The dominance of *P. ovalis*, which characterises this transgression may reflect an increased Tethyan influence (as discussed

above). The sea level-controlled, increased overall abundance of *P. ovalis* would also explain the low relative abundance of the S-assemblage (3%) in the e-marl (M1 of EscB, Fig. 4). In addition to the influence of sea level change on the sedimentary preservation of orbitally-forced signals, non-linear dynamics in the sedimentation have to be considered an important factor that may have obscured the reflection of the Milankovitch signal (Smith, 1994).

#### The palaeoenvironmental model

Simulation of Cretaceous climate shows that the largest effect of precession-controlled climate forcing is the modulation of the atmospheric (e.g. monsoonal) circulation (Park and Oglesby, 1990). Thus, the relation between orbital cycles, climate change and light/dark sedimentary cycles can be generally explained by two different mechanisms of wind-driven changes in sub-surface water circulation: (i) a monsoonal, salinity-driven model; and (ii) an anti-monsoonal, temperature-driven model (Herbert and Fischer, 1986).

Dark layers, which are organic-rich, can be thought to represent episodes of increased monsoonal intensity and enhanced atmospheric circulation in general, during which high terrigenous influx of freshwater and nutrients caused stratification (a freshwater surface layer) and very high bioproductivity, respectively (model (i)). This mechanism of eutrophication of the surface water is thought to have controlled, for example, the Pliocene/Pleistocene sapropel formation of the Mediterranean (e.g. Rossignol-Strick et al., 1982; Versteegh, 1994) and various Upper Cretaceous light/dark sedimentary cycles (e.g. Boyd et al., 1994; Caron et al., 1999; Watkins, 1989). As discussed before, marls of the studied section represent periods of low productivity and constant terrigenous influx, so this model cannot be applied here. Mitchell and Carr (1998) combined sea level change with this eutrophication model. In their "stratified water column model" for the Cenomanian of the Anglo-Paris Basin, they suggest that under peak oceanic influence, increased nutrient influx (supplied by flooding of shelf areas) led to high production which in turn caused oxygen depletion of the bottom waters. The problem with this mechanism is that it applies oxygen depletion to force stratification, which is not possible. Oxygen depletion follows as a consequence of reduced circulation and stratification caused by density contrast between water layers.

Neither significant sea level changes nor varying terrestrial input by alternations between a humid and arid climate can be reconstructed in the present study. Therefore, we think that an anti-monsoonal mechanism, controlling basin circulation via wind stress instead of terrestrial run-off, caused the light/dark rhythmicity and its bundling (model (ii)). In this model, decreased energetic influence of wind systems, which at the investigated palaeogeographic position would be the Westerlies (e.g. Voigt, 1996), is considered to be the dominant factor controlling water column stratification. Thus, in an "anti-monsoonal" model, deposition of dark layers took place during periods of low seasonal contrast, i.e. weakened atmospheric dynamics.

The energetic influence of the local wind system on the sea surface can control the circulation of a shelf basin in a coupled atmosphere-ocean system (Barron, 1983; Bottjer et al., 1986). Global temperature variation modifies the rate of precipitation (Barron et al., 1989) and the intensity of the wind systems in general. During times of high seasonality, wind systems such as the monsoon are stronger due to stronger pressure gradients between continents and oceans (De Boer and Smith, 1994). It is likely that the Cretaceous climate was generally characterised by intense mid-latitude depressions (Price et al., 1998) which would intensify the atmospheric circulation. Stronger winds lead to a more intense mixing of the surface waters, whereas low seasonality weakens this process. This can result in an intensely stratified upper water column during periods of low seasonality and reduced circulation in the basin. It is possible that saline, warm, oxygen-depleted, nutrient-poor surface water forms which can be subject to occasional downwelling if it becomes too dense. On a global scale, the latter is thought to have predominantly caused the production of warm, saline bottom water in low latitude shelf areas, leading to a deepening of the redoxcline that in turn caused the anoxic sedimentation during the mid-Cretaceous (Brass et al., 1982; Bralower and Thierstein, 1984; Roth and Krumbach, 1986; Thierstein, 1989).

The relation between seasonality, the wind system, oceanic mixing and its influence on the c-dinocyst distribution is illustrated in Fig. 10. Orbital forcing amplifies seasonality in the northern hemisphere when our planet passes through perihelion during the northern summer. This situation is defined as the precession minimum (Berger, 1978; Hilgen et al., 1995; ten Veen and Postma, 1996). At this position, Earth receives the most summer insolation. During aphelion in the northern winter, when the irradiation angle is lowest, the Sun-Earth distance is highest and causes long, cold winters. In addition, the perihelion and aphelion distances are modified by the eccentricity cycle, which modulates the intensity of the seasonality. Consequently, lowest seasonality occurs during intervals of winter perihelion (precession maximum) and high eccentricity, which are the periods of e-marl deposition (i.e. the bundle boundaries). Well developed chalks, on the contrary, would



Fig. 10: Model of shelf basin circulation changes related to orbital forcing for the mid-Cenomanian of the Anglo-Paris Basin.

represent peak seasonality at the summer perihelion, during which a well-mixed basin promoted high productivity. Organic matter was effectively recycled in the welloxygenated water, leading to the deposition of a light, carbonate-rich limestone.

In the eccentricity minima (for example the middle part of the bundle EscA), lithological changes are less distinct, and the c-dinocysts are very abundant in marls as well as in chalks. Thus, we suggest that during times of decreased eccentricity with both summer and winter perihelion being less pronounced, i.e. without strong variations in seasonality, stratification occurred only temporarily and did not hamper bioproduction.

## Double peaks – obliquity signal or negative biological feedback?

Several high abundance peaks of Pithonelloid species appear as double peaks in the thickest chalks (i.e. peaks "A" in EscA and "C" and "D" in EscB: Figs. 3 and 4). These double peaks may reflect (i) the additional influence of the obliquity cycle; or (ii) a negative ecological feedback to the precession minima. An expression of the obliquity cycle would be realistic, as this could well have buffered the precession signal (due to the modulation of insolation into an irregular sum-curve containing double peaks: see, for example, House, 1995), and could lead to the production of a "hidden marl" within a chalk. Especially peak "C" in EscB is related to a weak peak of paratabulated cysts, suggesting a short-term development of conditions typical for marl formation. It is striking that all 3 double peaks occur in exceptionally thick chalks, indeed suggesting that a "marl" may be hidden. Theoretically, the obliquity signal could be present at the mid-latitudinal position of the section, but it was not found to be significant in time series analysis in the study area (e.g. Gale, 1999). In contrast, the Lower Cretaceous of the even more southward positioned Vocontian Basin is made up of carbonate cycles that are dominated by the obliquity cycle (Giraud et al., 1995). Thus, it is possible that a weak obliquity signal might be recorded in the investigated material.

The presence of a negative ecological feedback would be supported by the analysis of *Pithonella sphaerica* diameters in EscA (Fig. 3). The distinctive decrease in diameter at the double peak "A" suggests environmental pressure, possibly due to competition with the other organisms that flourished during these episodes of generally enhanced bioproductivity. Thus, although the environmental conditions during the precession minima seem to have favoured productivity, a negative feedback in the size of *P. sphaerica* cysts can be observed which may indicate a decreased intensity of biomineralisation. Interestingly, a drop of mean as well as maximum test sizes in the middle of Cenomanian chalks has also been observed in benthic foraminifera (Leary and Hart, 1992). These authors assumed enhanced rates of gametogenesis or dwarfism due to an enhanced "carbonate rain", i.e. ecological stress being the reason. No decrease in abundances was recorded for the benthic foraminifera. A temporary decrease of abundances of both benthic foraminifera and "Calcispheres" (=Pithonelloideae) in the middle of chalks of the Cenomanian from Folkstone/GB was also recorded by Ditchfield (1990). Although the double peaks may reflect an obliquity signal, the most straightforward explanation,

because of the absence of size-decrease in the two analysed marls (M1 and M2 in EscA), is a negative biological feedback to enhanced productivity.

# Conclusions

Precession-controlled light/dark couplets of the Middle Cenomanian show amplification and buffering by the superimposed eccentricity cycle.

- Bundling of couplets can be recognised by c-dinocyst association changes that are in phase with variations in gamma ray and carbonate content. Bundles are defined by different marl types. The cyclicity in the micropalaeontological data clearly points to a palaeoecological origin of the signal.
- 2. Couplets showing strongest contrast in cyst association are interpreted as bundle boundaries that mark the eccentricity maxima, whereas weak couplets developed during eccentricity minima.
- 3. Orbitally-forced climate change during the eccentricity cycle primarily controlled the basin circulation patterns but did not cause significant changes in terrestrial runoff or sea level.
- 4. The variations in oceanic circulation are reflected in the sediment by the chalk-marl couplets. Marls can be interpreted as the sedimentary expression of stratified surface water masses while chalks are representative of a well-mixed shelf sea environment. Reduced oceanic mixing due to low seasonality during strong precession maxima at the eccentricity maxima caused periods of water column stratification that in turn led to nutrient depletion and decreased productivity in the surface water masses (e-marls). As a consequence, slightly increased surface temperatures in contrast to the well mixed chalk episodes can be assumed.

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### Appendix

#### Taxonomy

The classification of calcareous dinoflagellate cysts is based on the four types of wall crystal orientation of these microfossils (Keupp and Mutterlose, 1984; Keupp, 1987; Janofske and Keupp, 1992). The 4 wall types of the Calciodinelloideae (Fensome et al., 1993) after Young et al. (1997) are: pithonelloid, oblique, radial and tangential.

Division: DINOFLAGELLATA (Bütschli, 1885) Fensome et al., 1993 Subdivision: DINOKARYOTA Fensome et al., 1993 Class: DINOPHYCEAE Pascher, 1914 Subclass: PERIDINIPHYCIDAE Fensome et al., 1993 Order: PERIDINIALES Haeckel, 1894 Family: PERIDINIACEAE Ehrenberg, 1831 Subfamily: CALCIODINELLOIDEAE Fensome et al., 1993

#### <u>P-assemblage</u>

Cenomanian assemblages of c-dinocysts are dominated by Pithonelloideae, commonly called "calcispheres" Pithonelloideae are double-walled cysts, each wall consisting of pithonelloid orientated calcite crystals (uniquely oblique, linear rows between apex and antapex on the cyst surface); (for detailed information on biomineralisation see Keupp and Kienel, 1994).

Genus *Pithonella* Lorenz, 1902; emend. Bignot and Lezaud, 1964; emend. Villain, 1977 *Pithonella sphaerica* Kaufmann, 1865

Shape: Sphaerical cysts 20-120  $\mu$ m diameter, cysts >70  $\mu$ m rare; height/width ratio 0.9 to 1; mostly round archeopyles, 4-14  $\mu$ m diameter; a row of crystals occasionally surrounds the opening.

Stratigraphic range: Upper Barremian (Keupp, 1987) to Lower Danian? (Kienel, 1994).

*Pithonella ovalis* Kaufmann, 1865 Shape: Ovoid, apically-antapically elongated form of the genus *Pithonella*. Stratigraphic range: as *P. sphaerica* 



Fig. 11: Calcareous dinoflagellate cysts used in the quantitative analysis; scale bar is 10 µm.

- 1) Pithonella sphaerica
- 2) Pithonella ovalis
- 3) Pithonella discoidea
- 4) Pirumella sp.
- 5) Cubodinellum renei
- 6) Pentadinellum vimineum

#### Pithonella discoidea Willems, 1992

Shape: Disc-shaped; apical-antapically flattened cysts of the genus *Pithonella* with a height/width ratio below 0.5 and an equatorially running suture line (similar to *Normandia circumperforata* Zügel, 1994); 29-70 µm in equatorial diameter.

Stratigraphic range: mid-Cenomanian to Maastrichtian (range extended from originally only Maastrichtian to the mid-Cenomanian due to the findings of the present study).

The following species are characterized by a cyst wall with an oblique crystal orientation. The most abundant species are *Cubodinellum renei* and *Pentadinellum vimineum*, which show a reduced paratabulation. Having a wide lateral and stratigraphical range and specific ecological demands, they are not of biostratigraphic value but are very suitable for the study of cyclical environmental changes. Due to their distinctive paratabulation, they are easy to determine with the binocular microscope and used for countings without extensive SEM-studies being necessary.

#### Genus Pirumella Bolli, 1980

The most abundant oblique spherical cysts in the studied material all belong to the same species whose exact affinity is not unequivocally determinable. The 2 possibilities are: (i) *Pirumella carteri* Bolli, 1974; or (ii) remains of double-walled cysts (*Pirumella multistrata* group) with the outer wall having been mechanically removed (as described by Keupp, 1989).

Shape: 29-55  $\mu$ m in diameter, most likely with oblique wall crystal orientation. Only one thin wall is present. Surface crystals are lath-shaped and obliquely oriented. Appearance in the light microscope: transparent, slightly reflective surface in contrast to *Pithonella* spp. The archeopyle diameter varies from 7 to 15  $\mu$ m, commonly about <sup>1</sup>/<sub>4</sub> of the cyst diameter. The archeopyle is often elongated or slightly 8-shaped and frequently has an elevated rim.

Rare species:

Normandia circumperforata Zügel, 1994 Pithonella cardiiformis Zügel, 1994

# S-assemblage

### Cubodinellum renei Keupp, 1987

Shape: 20-35  $\mu$ m in size, showing a paratabulation pattern giving it a cubic shape. The paratabulation is formed by perpendicular edges of coarser crystals on a sphaerical inner cyst body. The single wall consists of thin, needle-shaped, obliquely orientated crystals. Stratigraphic range: mid-Albian to Late Cenomanian.

#### Pentadinellum(?) vimineum Keupp, 1987

Shape: Carinate, hat-shaped cyst; paratabulation consists of an occasionally asymmetric pentagonal cingular ridge, 20-53  $\mu$ m in diameter. This ridge is attached to a sphaerical inner cyst body, 15 – 22  $\mu$ m in diameter. The archaeopyle is 7.4-17  $\mu$ m in diameter. The single wall consists of thin, needle-shaped, obliquely orientated crystals. Stratigraphic range: mid-Albian to Maastrichtian (Wendler and Willems, subm.)

Rare species:

[oblique wall type] Gonellum kurti Keupp, 1987 Pirumella labyrinthica Zügel, 1994 Pirumella cf. porosa (Pflaumann & Krasheninnikov, 1978) Pirumella scobidota Zügel, 1994 Saumuria sp. Zügel, 1994

[radial wall type]

Orthopithonella cf. gustafsoni Bolli, 1974

# Absolute c-dinocyst abundances

depth (m)	sample	P. sphaerica cysts/mg	P. ovalis cysts/mg	Ps/Po- ratio	P. discoidea cysts/mg	total P. spp. <i>C.renei</i> cysts/mg cysts/mg		P. vimineum cysts/mg	<i>Pirumella</i> sp. cysts/mg
		diameter							
56.3	141	(µm)] 280	570	0.48	27	877	0	0	5
56.2	140	320	900	0.35	- 11	1231	0	2	7
56.1	139	280	500	0.56	9	789	1	1	13
56.0	138	540	800	0.67	30	1370	0	0	14
55.9	137	460	730	0.63	10	1200	3	1	2
55.8	136	600	900	0.66	15	1515	0	0	5
55.7	135	190	160	1.20	6	356	0	0	6
55.6	134	230	440	0.53	17	687	0	1	3
55.5	133	260	340	0.76	8	608	0	0	5
55.4	132	200	500	0.40	5	705	1	1	0
55.3	131	200	410	0.48	8	618	0	0	2
55.2	130	270	290	0.93	15	575	1	0	15
55.1	129	250	520	0.46	7	777	0	0	0
55.0	128	270	520	0.51	6	796	0	1	12
54.9	127	600	1150	0.51	23	1773	2	3	15
54.8	126	425	650	0.65	12	1087	2	5	35
54.7	125	430	710	0.60	4	1144	0	3	7
54.6	124	650	300	1.90	62	1012	1	0	13
54.5	123	360	410	0.86	8	778	0	0	15
54.4	122	100	370	0.27	1	471	0	0	0
54.3	121	270	360	0.75	11	641	0	0	0
54.2	120	500	370	1.30	40	910	0	0	30
54.1	119	160	145	1.10	10	315	0	0	0
53.8	116	18	220	0.08	0	238	3	4	0
53.7	115	420	460	0.91	6	886	0	2	0
52.9	107	195	325	0.60	1	521	2	3	2
51.4	92	190	94	2.00	0	284	1	2	0
49.7	75	0	0	/	0	0	0	1	0
49.3	71	110	31	3.50	0	141	4	3	0
48.5	63	50	30	1.66	0	80	9	10	0
48.0	58	180	95	1.90	0	275	1	2	2
47.2	50	164	35	4.60	0	199	0	1	3
46.7	45	203	64 25	3.20	0	267	0	0	12
40.0	44	90	20 114	3.00 2.12	4	119	0	0	5
40.5	43	243	114	2.13	10	250	0	0	5
40.4	42	200	140	1.45	10	460	2	2	0
46.0	38	200	80	3.00	10	340	2	1	0
45.0	37	12	24	0.00	10	36	15	10	2
45.8	36	34	25	1 10	1	60 60	8	4	35
45.7	35	70	50	1 20	0	120	4	4	6
45.6	34	110	50	2.10	0	160	5	3	9 10
45.5	33	300	45	7.00	15	360	3 1	0	10
45.2	30	200	80	2.50	.0	281	0	0	0
44.9	27	160	130	1.20	3	293	10	2	0
44.8	26	210	86	2.50	10	306	6	2	16
44.7	25	300	110	2.70	25	435	1	1	10
44.6	24	550	200	2.70	25	775	2	0	0

44.5	23		506	153	3.30	12	671	3	2	15
44.2	20	56	410	190	2.20	7	607	13	10	20
44.1	19		220	71	3.10	14	305	9	0	3
44.0	18	50	170	32	5.30	8	210	9	2	7
43.9	17	49	238	72	3.30	7	317	12	1	24
43.8	16	64	195	54	3.60	2	251	17	2	12
43.7	15		402	131	3.10	8	541	12	8	20
43.6	14	60	240	89	2.70	2	331	8	2	21
43.5	13		430	160	2.70	3	593	9	7	4
43.4	12	61	700	130	5.40	5	835	5	3	4
43.3	11	44	590	130	4.50	35	755	4	0	150
43.2	10	44	330	90	3.70	30	450	1	0	125
43.1	9	62	400	106	3.80	27	533	2	1	90
43.0	8	67	780	260	3.00	40	1080	0	0	200
42.9	7	56	710	240	3.00	9	959	5	1	10
42.8	6	63	210	64	3.30	4	278	4	1	3
42.7	5	58	290	115	2.50	10	415	9	4	12
42.6	4	57	310	62	5.00	15	387	8	2	20
42.5	3	54	210	70	3.00	11	291	2	0	22
42.4	2		18	20	1.00	1	39	18	9	10
42.3	1		3	3	1.00	0	6	50	20	10
42.2	0	46	110	17	6.50	12	139	0	1	23

# Lithological data

depth [m]	sample	sample weight [mg]	size 20-75µm [wt%]	size >75µm [wt%]	gamma ray [CPU]	TOC [wt%]	carbonate [wt%]
56.3	141	588.0	28.10	3.30	14.33		
56.2	140	718.6	20.10	5.80	15.00	0.145	82.5
56.1	139	694.5	19.30	8.50	15.33	0.143	85.6
56.0	138	482.0	18.00	23.80	14.33	0.125	89.5
55.9	137	695.4	25.30	21.20	15.33	0.178	86.5
55.8	136	692.0	33.20	8.20	13.67	0.228	86.2
55.7	135	452.5	22.70	29.50	15.00	0.149	85.3
55.6	134	461.5	31.80	7.60	15.00	0.108	92.1
55.5	133	492.0	20.00	39.00	16.67	0.107	89.5
55.4	132	581.7	25.60	7.50	17.00	0.233	83.2
55.3	131	786.6	26.00	13.20	14.00	0.181	87.6
55.2	130	674.0	32.00	5.20	15.33	0.185	85.3
55.1	129	679.6	28.50	11.00	17.00	0.159	86.6
55.0	128	765.0	26.70	16.37	16.00	0.157	85.7
54.9	127	606.3	23.40	5.00	15.00	0.172	85.3
54.8	126	807.7	25.50	7.30	15.00	0.226	84.6
54.7	125	760.5	22.00	4.60	14.33	0.217	84.6
54.6	124	752.0	22.50	29.00	14.00	0.128	91.1
54.5	123	518.0	26.00	11.30	15.67	0.180	82.9
54.4	122	611.4	24.00	5.10	16.00	0.160	86.2
54.3	121	564.5	26.60	11.80	15.00	0.249	88.7
54.2	120	592.7	31.60	6.20	14.67	0.166	90.1
54.1	119	581.3	22.70	22.70	15.67	0.303	89.1
53.8	116	629.0	15.40	19.20	16.33	0.222	76.4
53.7	115	536.0	17.40	6.50	16.00		76.3
52.9	107	534.0	17.40	7.00	15.00		71.9
51.4	92	629.5	19.50	8.20	14.70		77.8

49.7	75	586.0	20.70	12.70	16.67		83.1
48.5	63	506.4	12.00	3.10	16.67		75.4
48.0	58	529.5	13.00	1.70	15.33		72.8
47.2	50	533.3	19.50	30.00	22.00		86.8
46.7	45	530.0	29.60	2.70	14.33		
46.6	44	530.0	29.30	7.50	15.64		
46.5	43	530.0	19.60	4.90	19.00		
46.4	42	530.0	1.95	91.26	16.00		
46.2	40	605.4	1.95	63.04	15.33	0.097	89.5
46.0	38	597.6	23.83	13.14	16.67	0.108	84.2
45.9	37	584.4	11.70	1.64	16.33	0.223	78.4
45.8	36	568.6	14.54	4.22	17.00	0.222	73.5
45.7	35	505.6	18.39	6.15	16.33	0.202	81.6
45.6	34	605.6	22.29	5.94	17.33	0.145	83.6
45.5	33	550.0	24.87	18.11	17.00	0.123	88.2
45.2	30	550.0	22.05	24.91	16.00	0.155	86.5
44.9	27	550.0	28.44	12.31	20.00	0.187	79.2
44.8	26	550.0	16.82	2.45	18.67	0.231	81.2
44.7	25	550.0	16.35	51.47	17.67	0.174	82.9
44.6	24	550.0	29.71	31.73	18.67	0.151	84.5
44.5	23	550.0	31.73	11.62	19.67	0.168	79.9
44.2	20	587.2	11.36	1.64	20.00	0.186	82.1
44.1	19	601.6	14.28	6.22	18.67	0.214	82.0
44.0	18	591.5	16.30	13.70	19.00	0.170	
43.9	17	643.1	19.23	6.77	18.33	0.178	
43.8	16	614.8	15.15	3.05	20.00	0.205	83.8
43.7	15	594.5	12.66	4.14	19.00	0.211	84.1
43.6	14	688.2	13.16	4.44	21.33	0.197	82.7
43.5	13	658.5	13.70	4.70	22.33	0.261	77.1
43.4	12	628.7	22.73	4.07	18.00 /	/	
43.3	11	729.5	20.41	26.99	18.67	0.152	82.9
43.2	10	569.5	18.18	37.12	17.00	0.117	90.3
43.1	9	500.0	21.74	23.66	19.00	0.129	89.0
43.0	8	590.2	20.00	18.00	17.33	0.132	90.2
42.9	7	599.5	22.22	4.38	18.33	0.166	87.0
42.8	6	612.5	14.28	2.22	18.33	0.202	83.2
42.7	5	591.6	13.70	2.50	17.67	0.217	87.2
42.6	4	636.7	15.87	6.93	17.00	0.191	86.5
42.5	3	492.9	20.41	6.29	17.67	0.195	86.2
42.4	2	626.5	14.28	2.12	17.67	0.243	81.1
42.3	1	614.4	10.42	0.78	16.00	0.232	78.9
42.2	0	535.4	23.81	9.49	17.00	0.287	88.0

# Clay mineral data

sample	weighted peak	weighted peak	weighted peak	illit [%]	kaolinite	chlorite	illite/kaolinite	half value
	size illite [mm <sup>2</sup> ]	size kaolinite	size chlorite	!	[%]	[%]	ratio	width of illite
		[mm²]	[mm²]					
1	550	146.19	27.2	76.0	20.2	3.7	3.8	0.50
13	929	229.35	43.0	77.3	19.1	3.6	4.0	0.48
23	618	154.11	28.4	77.2	19.3	3.6	4.0	0.50
37	732	210.54	32.2	75.1	21.6	3.3	3.5	0.53
50	470	151.14	25.6	72.7	23.4	4.0	3.1	0.50
63	573	151.47	32.4	75.7	20.0	4.3	3.8	0.57

# 3. 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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#### Abstract

A transect from the bathyal to inner shelf facies of the mid-Cenomanian European shelf sea (Boreal Realm) was investigated in order to compare spatial and temporal distribution changes of calcareous dinoflagellate cysts (c-dinocysts) and 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 still controversially discussed affinity of this group to the dinoflagellates can be confirmed, based on evidence from morphological features and distribution patterns. The consistent prevalence of Pithonella sphaerica and P. ovalis in cdinocyst 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 an inner shelf upwelling area offshore Fennoscandia. Here, cyclicity appears to be reduced to the strongest events, while outer shelf light/dark cycles are well-developed and show strong temporal assemblage changes. Cyclic fluctuations in the Ps/Po 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 lead to high productivity and dominance of the Pithonelloideae. These conditions on the shelf were contrasting the conditions in the open ocean, where more oligotrophic and probably stratified waters prevailed, showing an assemblage with very few Pithonelloideae and

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dominance of *Cubodinellum renei* and *Orthopithonella ? gustafsonii* is characteristic. While orbitally-forced light/dark sedimentary cyclicity of the shelf sections is 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 of 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 Pithoelloideae - facies zones, probably related to shelfward directed oceanic ingressions.

*Keywords*: Cenomanian, palaeoecology, calcispheres, calcareous dinoflagellate cysts, Pithonelloideae, Boreal Realm, epicontinental seas.

#### 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 on their ecology. Dinoflagellates are unicellular, biflagellate algae, of which some 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.

First approaches of reconstructing palaeofacies zones using c-dinocyst distribution patterns were made e.g. by Keupp (1981, 1987, 1991, 1993), Keupp and Mutterlose (1984), Keupp and Kowalski (1992), Zügel (1994). A comprehensive review of studies on pithonelloid c-dinocysts and an overview of the global distribution and palaeoecology of the Pithonelloideae is 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 under debate.

In a recent paper, we analysed abundance changes of c-dinocysts during orbitallyforced cyclic sedimentary alternations of chalks and marls in the mid-Cenomanian (**Chapter 2.**). These cyclic variations of cyst assemblages can be explained by changing circulation intensity of 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 study aims at investigating the palaeoecology of c-dinocysts based on their bathymetrical distribution patterns on the NW European shelf within a narrow time period. In order to distinguish between oceanic and shelf sea assemblages, we analysed various bathymetrical positions along around 40° N palaeo-latitude 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 the inner shelf facies. Upwelling has been reconstructed for the studied inner shelf location based on carbon isotope studies (Hilbrecht et al., 1992) and numeric models (Parrish and Curtis, 1982; Barron, 1985; Scotese and Summerhayes, 1986). Thus, this section is suitable to gain information on the relationship between cyst production and upwelling which is largely unknown. An approach is made to associate spatial assemblage changes to differences in nutrient supply, surface water temperature and salinity. We discuss the role of current-induced cyclic oceanic ingression into the shelf environment as indicated by spatial and temporal changes in the cyst assemblage.

#### Material

Three sections of mid-Cenomanian age located along a transect across the European shelf were investigated (Fig. 1). The analysed time span covers about five precession-controlled light/dark couplets. The fully pelagic, deep marine profile "DSDP" (DSDP Leg 80, Site 550) is situated near the continental slope. The drill site is located in the Atlantic Ocean near the Goban Spur. Its bathyal palaeoenvironmental position during the Cenomanian is indicated by oceanic crust bottom rocks of latest Albian age, sedimentology and the dominance of planktic foraminifera (Graciansky et al., 1985). The investigated core 17 of the DSDP section recovered 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. Microfossils pore space is completely cemented throughout the core. The most severe recrystallisation is observed in the dark layers. Ten samples were analysed at 6-20 cm sample spacing.



Fig. 1: Geographic location of the investigated sections.

The investigated time span in the outer shelf section "Escalles" (situated S of Calais, France, Anglo-Paris-Basin) is represented by a four metres thick profile part containing six chalk-marl couplets. Its base lies at the transition of the *T.costatus* to the *T.acutus* subzone. The section has a well-established bio-, litho- and sequence-stratigraphy according to Robaszynski and Amédro (1993), Robaszynski et al. (1998) and Owen (1996). Cementation varies throughout the profile and is strong in some light layers and generally less strong in the dark layers. Cyst data were retrieved from 17 samples at 10 to 20 cm spacing.

Profile "Rügen" represents an inner shelf position in the Northeast 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, section Rügen contains to a major part remains of macro fossils (bivalves, brachiopods etc.) and mica which reflect its relatively marginal palaeo-geographic 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. The results presented in this paper are the first available data on this section. We studied 16 samples of
a 3 m thick succession of 5 chalk/marl couplets at 10 to 50 cm spacing. The Rügen section is stored at the core archive of the Geological Survey Mecklenburg-Vorpommern and has the core number 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.

#### Methods

Correlation of the three profiles is based on foraminiferal biostratigraphy, graphic correlation of foraminiferal occurrences, and gamma ray logs. The gamma ray logs are plotted using bore hole gamma ray data of the DSDP section (Graciansky et al., 1985) and of the Rügen section (courtesy of Geological Survey Mecklenburg-Vorpommern). For the Escalles section, an outcrop gamma ray log was used (Gräfe, 1999).

For the foraminifera analyses, 50-100 g were processed using repeated freezing and thawing in sodium sulphate, and sieved into fractions  $63-125 \,\mu\text{m}$ ,  $125-500 \,\mu\text{m}$  and  $>500 \,\mu\text{m}$ . 100 specimens were determined per sample, using optical microscopy at 40x magnification.

The least cemented material of the investigated sections was chosen for cyst analysis as reliable data depend on good preservation of specimens. All investigations were done on disintegrated material. One major advantage of analysing calcareous dinoflagellate cysts is that the sample amount needed is about 100 times less than what is needed for comparable studies with foraminifera. This is due to the smaller size of the cysts and a higher volume and weight percentage of the respective grain size fraction in the sediment. 0.5 g of sediment were processed by repeated freezing and thawing in sodium sulphate. Ultrasonic cleaning was applied at various duration, depending on the clay content and the degree of interparticle cementation. The cleaning process was controlled by optical microscopy between cleaning steps. The disintegrated samples were sieved into three fractions (<20  $\mu$ m, 20-75  $\mu$ m and >75  $\mu$ m) of which the 20-75  $\mu$ m 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 with 100x magnification. The determination of the species was carried out by Scanning Electron Microscopy (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 Pithonelloideae tests for subtle morphological characteristics.



Fig. 2: Correlation of the investigated sections based on foraminifera biostratigraphy, lithology and gamma logs. Lithologic logs show decreasing frequency of light/dark cycles from ocean/slope towards the inner shelf. Black bars – position of analysed samples.

Fig. 3: Distribution of planktic foraminifera throughout the DSDP section.



	DIJGEN 105/64		Globigerinelloides bentonensis	Hedbergella delrioensis	Hedbergella planispira	Hedbergella simplex	Whiteinella brittonensis	Whitehella baltica	Whiteinella paradubia	Whiteinella aprica	Whiteinella archaeocretacea	Praealobotruncana delrioensis	Praealobotruncana stephani	Heterohelix moremani	Hatarohaliy alobi iloso	Tritavia einai Ilaris		iritaxia pyramiaara	Arenobulimina sabulosa	Arenobulimina chapmani <b>O</b>	Arenobulimina frankei <b>J</b>	Arenobulimina advena						Dorothia gradata	Flourensing Intermedia	Flourensing maride	Plectina mariae	Plectina cenomana	Pseudotextulariella cretosa	Ataxophragmium compactum	Shiroloci iling papyraced	lenticulina adultina		Lenticulina muensteri	Psilocitherella recta	Gyroidinoides nitidus	Gavelinella intermedia	Gavelinella baltica	Gavelinella cenomana	Lingulogavelinella jarzevae	Lingulogavelinella globosa	Quadrimorphina allomorphinoides
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Fig. 4: Distribution of benthic and planktic foraminifera throughout the Rügen section.

### Results

### **Correlation**

The correlation of the three investigated sections by gamma logs and foraminiferal biostratigraphy is shown in Fig. 2. The first and last occurrences of Cenomanian marker species of planktic foraminifera and benthic foraminifera can be well defined for the drill hole section DSDP and the Rügen section, respectively (Figs. 3, 4). The data form the basis of correlation of these sections with the well established foraminifera biostratigraphy of the Escalles section, whereby a graphic correlation of planktic foraminifera first and last occurrences could be performed (Fig. 5). This correlation gives low resolution determination of the main boundaries.



Fig. 5: Graphic correlation between DSDP section and Escalles section based on first and last occurrences of planktic foraminifera marker species, LOC = line of correlation.

The Lower/Middle Cenomanian boundary is defined lithologically in the DSDP (Graciansky et al., 1985) and the Escalles sections. The gamma ray log shows a valley of low values at that position. This gamma ray decrease can also be noted in the Rügen section. The mid-Cenomanian transition from the *Turrilites costatus* to the *T. acutus* ammonite subzone is characterised by a distinct decrease in gamma ray values. This "gamma break" can be clearly noticed in all three section and the graphic correlation of the foraminifera data corroborates its synchronicity between DSDP and Escalles. The Upper Cenomanian Oceanic Anoxic Event can be determined lithologically, by gamma ray and carbon isotope data in the Escalles and Rügen sections. The entire Upper Cenomanian is missing in the DSDP section due to a hiatus (Graciansky et al., 1985), however, our analysis of planktic foraminifera suggests that part of the Upper Cenomanian might be present (Figs. 3, 5). Concluding, the analysed profile parts represent a relatively isochronous period of time in the upper part of the mid-Cenomanian.



Fig. 6: (A) Comparison of DSDP, Escalles and Rügen section concerning fluctuations in carbonate content through 5 light/dark couplets. 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 carbonate fluctuation of light and dark layers; (C) ranges in grey scale of light and dark layers, note the strong contrast in DSDP section; (D) ranges in grain size, note the low fluctuation in the fine-grained DSDP section.

#### Lithological differences between the three sections

The investigated profiles show considerable differences in the development of light/dark sedimentary cycles (couplets). As the most notable trend, couplets are thin and occur very narrowly-spaced in the DSDP section, get thicker and wider spaced towards the Escalles section, and finally appear incomplete, i.e. in lower number and frequency, in the Rügen profile (Fig. 2).

The parameters carbonate content, grey scale and grain size are compared in Fig. 6. In Fig. 6a, five couplets of each section are plotted to illustrated differences in thickness and carbonate contents. The DSDP section shows the lowest thickness. Couplets of the DSDP section consist of very fine-grained material without differences in grain size distribution between light and dark layers (Fig. 6d). Very distinctive changes occur in grey scale (Fig. 6c) but the carbonate content between light and dark layers shows only minor fluctuations in this section (Figs. 6a, b). The carbonate content in the DSDP profile is with 57 to 65 wt% considerably lower than in the Escalles profile and the Rügen profile which have carbonate contents 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 assigned to cementation as the dark layers generally show an increased rate of cement crusts around particles. Dark layers in the Escalles and Rügen profiles have generally decreased carbonate contents, however, there is contrast in grey scale to the light layers. It is important to note that in both shelf sections, the difference in carbonate content between dark and light layers (Fig. 6a, dashed lines) varies over the section and appears to be modulated by a lower frequency forcing, as is discussed for the Escalles section in **Chapter 2**.

#### Calcareous dinoflagellate cyst assemblages

The 3 profiles exhibit distinctive differences in c-dinocyst associations. The species investigated in the present study are illustrated in Plate 1. While the shelf sections Escalles (Figs. 8, 10) and Rügen (Figs. 9, 10) are dominated by the Pithonelloideae, the DSDP profile displays very low c-dinocysts concentrations in general, and Pithonelloideae are almost absent (Figs. 7, 10). The dominant elements of the assemblages in the oceanic section are *Cubodinellum renei* Keupp (1987) (often >50% of the assemblage), *Orthopithonella ? gustafsonii* Bolli (1974) sensu Keupp and Versteegh (1989) and *Pirumella edgari* Bolli (1974) (Fig. 7, 10). In contrast to most light/dark couplets in the Escalles section, the cyst distribution in the section DSDP does not show a relation to lithological changes. In the further discussion the c-dinocyst assemblage will be termed the (<u>oceanic</u>) o-assemblage.

Two different shelf-assemblages can be distinguished primarily by the distribution of the Pithonelloideae *P. sphaerica* and *P. ovalis* Kaufmann (1865). The investigated time slice is dominated by *Pithonella sphaerica* at a ratio of *P. sphaerica* : *P. ovalis* (Ps/Po ratio) of about 3 in the Escalles section (Fig. 8). The Ps/Po ratio is lower in most marls due to a decrease in *P. sphaerica*. In the Rügen profile, the Ps/Po ratio by far exceeds ten throughout the section (Fig. 9), i.e. the Pithonelloideae association is dominated to more than 90% by *P. sphaerica* including marls (e.g. samples R 127, 128 in



Fig. 7: Cyst distribution (based on abundance per 3 mg of the 20-75 μm grain size fraction) in the DSDP section. Note generally low abundance of c-dinocysts with *Cubodinellum renei* and *Orthopithonella* ? gustafsonii being most frequent.

Fig. 10). Substantial changes in cyst assemblage of the Rügen section occur only in the most distinctive marls ("marker beds" in Fig. 10). Therefore, we can distinguish between an inner shelf assemblage (IS) represented by the Rügen profile, and an outer shelf assemblage (OS) that is found in the Escalles section. These shelf assemblages can be further characterised by specific occurrences of other c-dinocysts.



Fig. 8: Cyst distribution in the Escalles section (for legend, see Fig. 7). Note the dominance of Pithonelloideae and the decreased Ps/Po ratio in dark layers. Species of the o-assemblage occur in higher abundances in the dark layers.

The IS-assemblage does not contain cysts of *Cubodinellum 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 IS-assemblage. Furthermore, an increased presence of spiny cysts can be noted (Figs. 9, 10). The OS-assemblage is characterised by the presence of both, the species of the o-assemblage and *Pentadinellum vimineum* (Fig. 10) as could be expected from its intermittend position between the other two profiles.

In summary, a clear ocean to shelf distribution trend can be noted by shelfward increasing abundances of Pithonelloideae, an increasing Ps/Po ratio and decreasing occurrence of *Cubodinellum renei and Orthopithonella* ? *gustafsonii*. While *C. renei* and *O.* ? *gustafsonii* are still present in outer shelf cyst assemblages, although significant

abundances are restricted to the short-term occurrence in certain marls, the species disappear at the inner shelf.

The Pithonelloideae *P. sphaerica* and *P. ovalis* show no optically visible features of paratabulation. The cathodoluminescence investigations performed in the present study did not provide hints of subtle structures that could resemble ridges of a peridinialaen paratabulation. Test surfaces are monotonous in luminescence colour and luminescence intensity.



Fig. 9: Cyst distribution illustrated as ranges in cyst number throughout the Rügen section (for legend, see Fig. 7). *Pithonella sphaerica* dominates the assemblage also within the dark layers.

#### Discussion

#### Oceanic environment - absence of the Pithonelloideae, and o-assemblage palaeoecology

The distribution of c-dinocyst assemblages throughout the investigated transect (Figs. 10, 11) 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 (i) highly selective dissolution of carbonate at the bottom of the ocean, or (ii) 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 40° North which was their preferred habitat (e.g. Kaufmann, 1865; Bignot and Lezaud, 1964; Bein and Reiss, 1976; Masters and Scott, 1978; Bouyx and Villain, 1986; Dali-Ressot, 1987; Zügel, 1994; Dias-Brito, 2000). Thus, evidence is strong that Pithonelloideae did not live in the oceanic environment. A dependence of these species on (i) water depth, or (ii) certain surface water conditions may have determined the boundaries of their habitat. If Pithonelloideae would 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 stay only a short time within the cyst and hatch already in the water column which would make them independent from water depth. 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. Probably, oceanic surface waters fell short of the lower limit of nutrient availability for Pithonelloideae to live. Low carbonate productivity, suggesting oligotrophic conditions in the oceanic facies is indicated lithologically by lower carbonate



Fig. 10: Comparison of relative cyst abundances of the investigated sections. Facies-indicative species (except for the Pithonelloideae) are marked with grey background; marker beds in the shelf sections with particularly low Pithonelloideae abundances are framed.

contents 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 profile). Zügel (1994) observed significant amounts of these species in a coastal facies (section Agoulême, Fig. 11) which has been interpreted as brackish on the basis of foraminifera data (Moreau, 1978). Therefore, we interpret *Cubodinellum renei and Orthopithonella ? gustafsonii* as species that lived in a broad range of salinity and trophy, from estuarine, eutrophic to oceanic, oligotrophic environments. They are anti-correlated to the Pithonelloideae which as eutrophic/euryhaline species were nearly absent in both, the oceanic and the coastal environments. Thus, large environmental tolerance enabled *C. renei and O. ? gustafsonii* to occupy a wide range of niches and to live under a variety of surface water conditions.

Despite their adaptability, cysts of these species cannot be found in the northernmost of the investigated profiles (Rügen). There is a gradient of NE-ward decreasing abundance of the *C. renei and O. ? gustafsonii* species on the transect investigated here, supported by the data of the Wunstorf section (Zügel, 1994) which is located between the Escalles and Rügen sections (Fig. 11). Temperature was probably the controlling factor of this pattern as cool waters, originating from a bathyal sea way between the Atlantic and Arctic Ocean reconstructed by Gradstein et al. (1999), may have entered this part of the European. 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 probably were supplied with warm Tethyan water masses.

### Shelf environments - surface mixing and upwelling

Along the shelf, the Pithonelloideae distribution can be interpreted in terms of: (i) dependence on sea-level, or (ii) dependence on nutrients. Zügel (1994) interpreted increased abundances of *Pithonella ovalis* to indicate transgressive episodes. His

conclusion is mainly based on sequence stratigraphy and the observation of *P. ovalis*dominance during the Turonian sea level maximum. A relation between *P. ovalis* increase and transgression was widely observed in the Cenomanian of Western Europe (Villain, 1975; Keupp, 1987; Keupp, 1991; **Chapter 2.**) and the Tethys (Dali-Ressot, 1987; Robaszynski et al., 1993). Thus, a bathymetry-related zonation across the shelf appears to be a consistent feature of the Pithonelloideae distribution, *P. sphaerica* being dominant in inner shelf areas and *P. ovalis* preferring somewhat deeper outer shelf environments (Figs. 11, 12). It is difficult to explain, however, how water depth itself could control the Pithonelloideae 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.



Fig. 11: Palaeogeographic distribution of mid-Cenomanian c-dinocysts. Note the distinction between typical oceanic and shallow sea species (Palaeogeography after Ziegler, 1990).

Besides these lateral distribution zones, Pithonelloideae show temporal abundance changes at high-frequency cyclicity that can be related to nutrient availability. It was shown in **Chapter 2.** 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, especially Noel et al. (1995) interpreted 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 and Hart, 1992; Mitchell, S.F. and Carr, I.T., 1998; Gräfe, 1999), and coccoliths (Roth and Krumbach, 1986; Watkins, 1989; Young et al., 1998).

The continuous dominance of *P. sphaerica* in the Rügen profile (Fig. 10) suggests that strong surface mixing prevailed throughout most of the investigated time span. Such a situation can be caused by (i) convective overturning due to decreased surface water temperature or salinity increase, or (ii) upwelling. An upwelling zone offshore Fennoscandia was predicted by numeric simulations (Parrish and Curtis, 1982; Barron, 1985) and studies on regional carbon isotope variations (Hilbrecht et al., 1992). The influence of a cool surface water current (as discussed above) would have decreased the temperature contrast between surface and deep water, providing the basis of continuous convective overturning. The mentioned upwelling caused by the SE ward directed mayor wind vector for Europe (Barron, 1985) can be regarded as a second plausible mixingsource. The wide spacing of light/dark couplets in the Rügen profile supports the hypothesis of continuous mixing, as it shows that carbonate production was guite stable, and only the strongest episodes of stratification were sufficient enough to influence this inner shelf area. In addition, nutrient depletion of the surface water during most stratification phases was probably less effective due to continuous terrigenous input of nutrient rich material from the nearby Fennoscandian continent.

Although *Pithonella sphaerica* dominated in the area for which an influence of cool water masses is assumed, it cannot be interpreted as cool water species, as this species was widely distributed throughout the warm Tethyan Realm. Their distribution confined to the Tethys suggests that all Pithonelloideae were thermophilic, planktic organisms (Dias-Brito, 2000). Therefore, the cool waters must have mixed with the warm Tethyan waters sufficiently enough 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. represents the most opportunistic of the Pithonelloideae or required the highest nutrient concentrations. Concluding, due to their dominance in chalks deposited under eutrophic conditions and in an upwelling zone *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 which can be caused by shifts of the preferred facies zones probably indicate changes in surface current patterns or sea level.

The distribution of *Pentadinellum vimineum* suggests that this species also preferred ecological conditions of the shelf environment, especially during episodes of dark layer deposition (Figs. 8, 9, 10 (marker beds), 12) for which oligotrophic conditions were reconstructed (Chapter 2.). 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 Fig. 11) suggests that this species tolerated a wide range of salinity and nutrient concentrations, similar to the species of the o-assemblage. Thus, its higher abundance in dark as compared to light layers seems to reflect other environmental parameters. P. vimineum could be an indicator of increased surface water temperature as, according to Neumann (1999), pulses of this species were related to episodes (up to 10 m profile thickness) of possible ingressions of warm surface waters from the Tethys into the Boreal Realm 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 might basically indicate 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.

### **Ocean** – shelf interactions

In Fig. 12, an overview over the c-dinocyst distribution along the investigated ocean – inner 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 and Pearson, 1991; **Chapter 2.**). An explanation for the interplay of the o- and the IS-assemblage is the following scenario. During periods of enhanced surface mixing most parts of the shelf were well-ventilated, and nutrient enriched surface waters lead to high productivity and dominance of the

Pithonelloideae. These conditions on the shelf were contrasting the conditions in the open ocean where more oligotrophic and probably stratified waters prevailed (Fig. 12a). 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 (Fig. 12b). 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).

The assumed influence of oxygen poor bottom waters is supported by the lithological data which indicate that light/dark alternations of the DSDP section were predominantly redox-controlled and reflect varying preservation of organic particles. Changes in carbonate production or non-carbonate input are not evident. Assemblages of c-dinocysts do not change between light and dark layers in this profile, i.e. the surface plankton production remained stable while, at the sea floor, cyclic anoxic conditions prevented organic matter decay during dark layer deposition. Early diagenetic cementation was enhanced as indicated by the abundant carbonate crusts around particles which 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 and methanogenesis play an important role (e.g. von Rad et al., 1996).

A shelfward directed surface current would explain the expansion of typical oceanic species to the outer shelf. The fact that these species occur in the Escalles section but are absent throughout the Rügen profile indicates that the above-mentioned counter current to the bottom water outflow did not reach the inner shelf. This distribution pattern may indicate a gradient of decreasing energy of the ingression and/or, as discussed earlier, a gradient of decreasing surface water temperature. A further aspect of the oceanic ingression is the shelfward shift of Pithoelloideae - facies zones which is indicated by the narrowing of the facies dominated by *Pithonella sphaerica* and a shelfward extension of the *P. ovalis* distribution zone (low Ps/Po ratios) during these periods (Fig. 12).



Fig. 12: Illustration of the shifts in distribution of c-dinocysts and changes in circulation during light/dark sedimentary alternations. (A) light layer deposition, surface mixing, (B) dark layer deposition, stratification and occasional downwelling; note spread of o-assemblage, shift of Pithonelloideae distribution zones towards the shelf and reduction of inner shelf upwelling area. (for c-dinocyst symbols see legend Fig. 11)

### 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. In this chapter, arguments for their affinity to dinoflagellates are summarised. The Pithonelloideae, commonly termed "calcispheres" 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 and Tappan, 1964) and c-dinocysts (Rehánek and Cecca, 1993). A relation of Pithonelloideae via Cadosinidae to the tintinnida was excluded by Banner (1972) due to the multi-layered, calcareous wall of most species of *Pithonella*. Pithonelloideae show some similarity in size and shape with the Calpionellids (Villain, 1977, 1981, 1991), which also seem to have a pithonelloid wall crystal orientation. However, as Calpionellids were marine planktic Protozoa *incertae sedis*, typical of Jurassic to Lower Cretaceous deep sea deposits (Remane, 1978), Pithonelloideae differ substantially from this group in terms of stratigraphical and palaeoecological distribution. During the past two decades, evidence to consider Pithonelloideae as c-dinocysts has been growing (e.g. Keupp, 1987; Dali-Ressot, 1987; Willems, 1990, 1992, 1994).

Modern c-dinocyst species predominantly live in oligotrophic, oceanic environments and are found in much lower abundance. These two aspects in comparison to the distribution patterns of Pithonelloideae may speak against their affinity to dinoflagellates with calcareous life stages: (i) they are absence in oligotrophic surface waters, and (ii) they dominate in abundance relative to the other c-dinocyst species. Aspect (i) likely reflects their special adaptation to the eutrophic epicontinental seas of the Cretaceous which lack a comparable counter part in the Recent. Restriction to eutrophic environments is also typical of some recent neritic species (Montresor et al., 1998). Thus, aspect (i) does not apply to exclude Pithonelloideae from the group of dinoflagellates. Their dominance in abundance suggests to differentiate Pithonelloideae from dinoflagellates and rather interpret them as foraminifera which equally dominate in the respective grain size of the investigated material. However, the recent dinoflagellate species *Thoracosphaera heimii* (Lohmann, 1920) Kamptner, 1944 represents an example to weaken argument (ii) as this species shows overwhelming dominance within most assemblages of the Recent (e.g. Dale, 1992; Höll et al., 1999; Vink et al., 2000; Wendler et al., in press).

Various morphometric observations strongly suggest an affinity of species with pithonelloid wall type to the dinoflagellates. *Pithonella pyramidalis* (Willems, 1994), *Lentodinella danica* (Kienel, 1994) and particularly the genus *Tetratropis* (Willems, 1990) represent species that feature both, the pithonelloid wall type (uniquely declined wall crystals) and a probable peridinialaen 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 refused later by analyses of thin sections with polarised light (Hildebrand-Habel and Willems, 1997), however, a new species of *Tetratropis* shows unequivocal pithonelloid wall crystal orientation in polarised light (unpubl. data). Further evidence for a dinoflagellate affinity is the biomineralisation of Pithonelloideae shells which follows the same principles as known c-dinocyst biomineralisation patterns (Keupp and Kienel, 1994).

It has to be kept in mind that analogy between tabulate and atabulate species may probably be no evidence for a dinoflagellate affinity of all Pithonelloideae because findings of morphotypes that are incompatible to the 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 got extinct after the K/T boundary event (Hildebrand-Habel et al., 1999; **Chapter 4.**). In summary, evidence is strong that Pithonelloideae are related to the dinoflagellate subfamily Calciodinelloideae 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 Pithonella 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 cysts of other species are formed. All known calcareous dinoflagellate microfossils from the Mesozoic through 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, (i) the cyst stage, and (ii) the vegetative-coccoid life-stage, the latter only known from Thoracosphaera heimii. The low abundance of most species is due to the fact that, as far as is known from culturing of recent species, only part of the motile Calciodinelloideae cells form calcareous cyst, resulting in a low cyst turn-over rate during the dinoflagellate life cycle (Karwath, 2000). Significant abundances require a faster way of calcareous shell formation. In contrast to the cyst-formation of Calciodinelloideae, almost each 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 and Pienaar, 1983). In the present day upwelling area of the Arbabian 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 show (I. Wendler, pers. comm.). The much higher abundance of *T. heimii* skeletons relative to cysts can be explained by the species' rapid life-cycle during which a calcareous shell is formed every one to three days (Inouye and Pienaar, 1983). The dominance of some Pithonelloideae in the Upper Cretaceous appears to be an analog 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.

### Conclusions

The oceanic section 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, however, were not restricted to the oceanic environment, but also occupied various shelf environments and, therefore, appear to have lived in a broad range of salinity and trophy. A gradient of decreasing temperature is likely to have controlled their decreasing abundance towards the inner shelf area of the investigated transect. While orbitally-forced light/dark sedimentary cyclicity of the shelf sections is mainly related to surface water carbonate productivity changes, 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.

Along the shelf the Pithonelloideae dominate the assemblages whereby the individual species show a bathymetry-related zonation. *P. sphaerica* (and *P. ovalis* in the outer shelf) were indicators of nutrient rich water masses due to their dominance in chalks deposited under eutrophic conditions. Cyclic fluctuations in the Ps/Po ratio which can be caused by shifts of the preferred facies zones indicate changes in surface current patterns. A continuous dominance of *P. sphaerica* in the inner shelf profile indicates continuous mixing related to convective overturning or upwelling. A low frequency of light/dark alternations in the inner shelf section can be interpreted to reflect a reduced effect of orbital forcing on wind-driven surface mixing. Besides Pithonelloideae, *Pentadinellum vimineum* was an important shelf sea species. It apparently tolerated a wide range of salinity and

trophy and preferred warm temperatures, indicating cyclic surface water warming during stratification events.

During periods of enhanced surface mixing most parts of the shelf were wellventilated, and nutrient enriched surface waters lead to high productivity and dominance of the Pithonelloideae. These conditions on the shelf were contrasting the conditions in the open ocean where more oligotrophic and probably stratified waters prevailed. Orbitallyforced interruptions of mixing on the shelf resulted in cyclic periods of oligotrophy in the surface waters and 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 ingressions during these periods. The c-dinocyst distribution pattern may indicate a gradient of decreasing energy of the ingressions and/or, a gradient of northward decreasing surface water temperature towards the investigated inner shelf section.

The modulation of their distribution by surface currents and changes in surface mixing gives new evidence that Pithonelloideae lived planktic. Our present review of morphological aspects makes an affinity of Pithonelloideae to the dinoflagellates 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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# Appendix

# Section DSDP

# C-dinocysts

sample	depth	counted mg F	P. vimineum	edgari	ortho sp.	spiny oblique	spiny	blocky	blocky
	т					•		ortho	oblique
0-17-4-1	612.55	1.5	0	0	4	0	0	1	0
0-17-4-2	612.65	1.1	0	0	0	1	0	0	2
0-17-4-3	612.71	3.7	0	7	6	0	0	9	0
0-17-4-4	612.79	1.6	2	0	3	0	0	1	0
0-17-4-5	612.89	1.3	0	1	0	0	0	0	0
O-17-4-6	612.99	1.9	0	2	2	0	0	0	0
0-17-4-7	613.09	3	2	0	0	0	0	0	0
0-17-4-13	613.64	3.2	0	0	0	0	0	3	0
0-17-4-17	613.97	1.9	1	0	0	0	0	0	0
O-17-5-7	614.75	3.9	1	2	0	1	0	2	0
O-17-5-10	615.09	2.2	1	7	5	1	1	1	0

sample	depth	counted mg	gonellum	P. sphaerica	P. ovalis	C. renei	total cysts
	т						
0-17-4-1	612.55	1.5	0	0	0	5	10
0-17-4-2	612.65	1.1	1	2	1	1	8
0-17-4-3	612.71	3.7	0	2	2	18	44
0-17-4-4	612.79	1.6	0	4	8	12	30
0-17-4-5	612.89	1.3	0	1	0	2	4
O-17-4-6	612.99	1.9	0	0	0	3	7
0-17-4-7	613.09	3	0	0	0	5	7
0-17-4-13	613.64	3.2	0	4	0	0	7
0-17-4-17	613.97	1.9	0	2	0	3	6
O-17-5-7	614.75	3.9	0	3	1	0	10
O-17-5-10	615.09	2.2	0	2	5	8	31

# Lithology

sample	depth	pyrite	glaukony	mica	spicules	fish remains	black pariticles
	т						
0-17-4-1	612.55	0	0	0	0	0	0
0-17-4-2	612.65	0	0	0	0	0	0
0-17-4-3	612.71	low	0	0	0	0	0
O-17-4-4	612.79	present	0	0	0	0	0
O-17-4-5	612.89	low	0	low	0	present	present
O-17-4-6	612.99	low	low	low	0	present	present
O-17-4-7	613.09	very low	0	very low	0	0	0
0-17-4-13	613.64	high	low	low	0	low	high
0-17-4-17	613.97	present	low	low	0	low	low
O-17-5-7	614.75	low	0	present	0	0	0
O-17-5-10	615.09	0	present	low	0	low	present

sample	depth	carbonate	g.>20 µm	grey sc.	sample	depth	carbonate	grains>20 μm	grey scale
	m	wt%	wt%			m	wt%	wt%	
0-17-2-1	609.5	57.5	12	5y 6-1	0-17-4-1	612.55	61.5	14	5y 6-1
0-17-2-2	609.64	60	11	5y 7-1	0-17-4-2	612.65	61	10	5y 6-1
0-17-2-3	609.74	63	13	5y 7-1	0-17-4-3	612.71	57.5	10	5y 7-1
0-17-2-4	609.84	66	17	5y 7-1	0-17-4-4	612.79	60.5	12	5y 7-1
0-17-2-5	609.97	67.3	13	5y 7-1	0-17-4-5	612.89	64	13	5y 7-1
O-17-2-6	610.08	61	9	5y 6-1	O-17-4-6	612.99	60.3	10	5y 7-1
0-17-2-7	610.17	59.5	14	5y 6-1	0-17-4-7	613.09	59	8	5y 7-1
O-17-2-8	610.27	61.5	15	5y 4-1	O-17-4-8	613.2	59		5y 7-1
O-17-2-9	610.4	65	18	5y 7-1	O-17-4-9	613.26	58.5		5y 7-1
O-17-2-10	610.44	64.3	12	5y 7-1	O-17-4-10	613.35	64.5	17	7.5yr 6-0
0-17-2-11	610.59	64	14	2.5y 4-0	0-17-4-11	613.39	60	15	7.5yr 7-0
0-17-2-12	610.68	63.3	17	5y 7-1	O-17-4-12	613.54	60	11	5y 7-1
0-17-2-13	610.79	63.5	16	5y 8-1	O-17-4-13	613.64	67	11	7.5yr 5-0
O-17-2-14	610.9	63.5	17	5y 7-1	O-17-4-14	613.7	63.5	14	5y 7-1
					O-17-4-15	613.82	66		5y 8-1
mean:		60.5	14.5		O-17-4-16	613.9	67		7.5yr 5-0
					0-17-4-17	613.97	65.5	16	7.5yr 7-0

## Section Escalles

C-dinocysts

depth	sample	P. sphaerica	P. ovalis	Ps/Po-ratio	O. ? gust.	C.renei	P. vimineum	P. edgarii	spiny spp.
m		cysts/mg	cysts/mg		cysts/mg	cysts/mg	cysts/mg	cysts/mg	cysts/mg
46.2	40	280	160	1.75	0	0	0	0	0
46	38	250	80	3	0	2	1	0	0
45.9	37	12	24	0.5	12	15	10	5	0
45.8	36	34	25	1.1	10	8	4	2	0
45.7	35	70	50	1.2	6	4	4	1	0
45.6	34	110	50	2.1	0	5	3	0	0
45.5	33	300	45	7	0	1	0	0	0
45.2	30	200	80	2.5	0	0	0	0	0
44.9	27	160	130	1.2	0	10	2	0	0
44.8	26	210	86	2.5	0	6	2	0	0
44.7	25	300	110	2.7	0	1	1	0	0
44.6	24	550	200	2.7	0	2	0	0	0
44.5	23	506	153	3.3	0	3	2	0	0
44.2	20	410	190	2.2	0	13	10	0	0
44.1	19	220	71	3.1	0	9	0	0	0
44	18	170	32	5.3	0	9	2	0	0
43.9	17	238	72	3.3	0	12	1	0	0
43.8	16	195	54	3.6	0	17	2	0	0
43.7	15	402	131	3.1	0	12	8	0	0
43.6	14	240	89	2.7	0	8	2	0	0
43.5	13	430	160	2.7	0	9	7	0	0
43.4	12	700	130	5.4	0	5	3	0	0
43.3	11	590	130	4.5	0	4	0	0	0
43.2	10	330	90	3.7	0	1	0	0	0
43.1	9	400	106	3.8	0	2	1	0	0
43	8	780	260	3	0	0	0	0	0
42.9	7	710	240	3	0	5	1	0	0

42.8	6	210	64	3.3	0	4	1	0	0
42.7	5	290	115	2.5	0	9	4	0	0
42.6	4	310	62	5	0	8	2	0	0
42.5	3	210	70	3	0	2	0	0	0
42.4	2	18	20	1	8	18	9	5	2
42.3	1	3	3	1	10	50	20	5	4
42.2	0	110	17	6.5	0	0	1	5	0

# Lithology

sample	depth	carbonate	grains >20	sample	depth	carbonate	grains >20
	т	wt%	wt%		т	wt%	wt%
40	46,2	89,5		16	43,8	83,8	18
38	46	84,2	37	15	43,7	84,1	17
37	45,9	78,4	13	14	43,6	82,7	18
36	45,8	73,5	19	13	43,5	77,1	18
35	45,7	81,6	25	12	43,4	/	27
34	45,6	83,6	28	11	43,3	82,9	47
33	45,5	88,2	43	10	43,2	90,3	45
30	45,2	86,5	47	9	43,1	89	45
27	44,9	79,2	41	8	43	90,2	38
26	44,8	81,2	19	7	42,9	87	27
25	44,7	82,9	30	6	42,8	83,2	17
24	44,6	84,5	28	5	42,7	87,2	16
23	44,5	79,9	43	4	42,6	86,5	23
20	44,2	82,1	13	3	42,5	86,2	27
19	44,1	82	21	2	42,4	81,1	16
18	44	82.5	30	1	42,3	78,9	11
17	43,9	83	26	0	42,2	88	33

## Section Rügen

# C-dinocysts

sample	depth	Diagenesis	P.sphaerica	P.ovalis	Ps/Po	P. vimineum	Pirumella	Pir.	grobplatti	cysts total
							sp.	echinosa	ge	
		(estimate)	cysts/mg	cysts/mg		cysts/mg				cysts/mg
R 112	398.2	3	750	103	7	0	0	0	0	853
R 113	398.1	2.5	1080	115	10	0	0	0	0	1195
R 114	398	1	111	10	11	0	1	0	0	121
R 116	397.8	2	63	3	21	0	0	0	0	66
R 118	397.6	3	1	0	/	1	0	0	0	2
R 119	397.5	3	435	16	27	3	1	0	0	455
R 120	397.4	3	4	0	>>	8	0	3	3	18
R 121	397.3	3	240	2	120	0	0	0	0	242
R 124	397	3	146	6	24	2	0	0	0	154
R 127	396.5	3	386	7	55	0	0	1	0	394
R 128	396.4	3	355	6	59	3	0	3	0	367
R 135	395.7	3	6	0	>>	0	0	2	0	8
R 136	395.5	3	165	0	>>	1	0	0	0	166
R 137	395.4	2.5	108	3	36	0	0	0	0	111
R 140	395.1	1.5	500	2	250	0	0	0	0	502

# Lithology

sample	depth	Diagenesis	grey scale	carbonate	sponge spic.	glauconite	mica	pyrite
R 110	398.4	1	2.5 8/2	92.2				
R 111	398.3	2	2.5 8/2	89.6				
R 112	398.2	3	5y 5/2	84.7	0	0	0	0
R 113	398.1	2.5	5y 8/1	85.5	0	0	0	
R 114	398.0	1	2.5y 8/2	90.5	0	0	low	0
R 115	397.9	1.5	5y 8/1	89.6				
R 116	397.8	2	2.5y 8/2	90.5	0	0	0	0
R 117	397.7	1	5y 6/2	83.7				
R 118	397.6	3	5y 6/1	70.9	present	present	high	0
R 119	397.5	3	5y 8/2	82.2	low	low	low	0
R 120	397.4	3	5y 7/2	71.1	low	low	present	0
R 121	397.3	3	2.5y 8/2	77.4	0	0	low	0
R 122	397.2	1.5	5y 8/1	86.1				
R 123	397.1	1	2.5y 8/2	87.2				
R 124	397.0	3	2.5y 7/2	78.7	present	low	low	0
R 125	396.9	1	2.5y 8/2	87.4				
R 126	396.6	1	2.5y 8/2	90.9				
R 127	396.5	3	2.5y 7/2	83.9	present	low	0	0
R 128	396.4	3	5y 7/1. lighter	84.9	present	low	low	0
R 129	396.3	1	2.5y 8/2	86.9				
R130	396.2	1	2.5y 8/2	88.6				
R 131	396.1	1.5	2.5y 8/2	89.8				
R 132	396.0	1	2.5y 8/2	88.6				
R 133	395.9	3	5y 7/1	77.5	0	low	0	0
R 134	395.8	2	2.5y 8/2	86.6				
R 135	395.7	3	5y 6/2	65.4	present	present	present	high
R 136	395.5	3	5y 7/1	79.3	low	low	low	0
R 137	395.4	2.5	5y 7/1	87	0	0	low	0
R 138	395.3	2.5	2.5y 8/2	90.6				
R 139	395.2	1	2.5y 8/2	89.5				
R 140	395.1	1.5	2.5y 8/2	88.8	0	0	low	0

Diagenesis (preservation)

1: bad

2: middle

3: good

## Plate I

Calcareous c-dinocyst species investigated in the present study, scale bar is 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); IS-assemblage, (OS-assemblage); Escalles I-12
- f) *Pithonella sphaerica*; showing the inner wall and contures of archeopyle; Escalles I-6
- g) Pentadinellum vimineum Keupp (1987); OS-, IS-assemblage, (o-assemblage); Rügen-120
- h) spiny morphotype; IS-assemblage; Rügen-135







е












## 4. The distribution pattern of calcareous dinoflagellate cysts across the Cretaceous/Tertiary boundary (Fish Clay, Stevns Klint, Denmark) -Implications for our understanding of species selective extinction

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## Abstract

The distribution patterns of calcareous dinoflagellate cysts were studied in the classic Cretaceous/Tertiary (K/T) boundary section of Stevns Klint, Denmark, focusing mainly on the response of the cyst association to an abrupt environmental catastrophe. A major part of the Fish Clay, which covers the K/T boundary at its base and is exposed in the investigated section, contains fallout produced by an asteroid impact. Calcareous dinoflagellate cysts (dinocysts) are the best preserved remains of carbonate-producing phytoplankton in this layer. The potential of this group of microfossils for the analysis of survival strategies and extinction patterns has been previously underestimated. The cyst species of the investigated section can be grouped into 4 assemblages that represent victims, survivors, opportunists and specially adapted forms. The victims (Pithonelloideae) were an extremely successful group throughout the upper Cretaceous, but were restricted to the narrow outer shelf. This restriction minimized their spatial distribution, which generally should be large to facilitate escape from unfavorable conditions. Spatial restriction optimized the population decrease by mass mortality, disabling a successful recovery. In contrast, the survivors that became the dominating group in the Danian had a wide spatial range from the shelf environment to the oceanic realm. A unique calcareous dinocyst assemblage in the Fish Clay shows that even under the stressed conditions immediately following the impact event, some species flourished due to special adaptation or high ecological tolerance. The ability of these dinoflagellate species to form calcareous resting cysts in combination with their generally wide spatial distribution in a variety of environments appears to be the main reason for a low extinction rate at the K/T boundary

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as opposed to the high extinction rate of other phytoplankton groups, such as the coccolithophorids.

*Keywords*: Cretaceous/Tertiary boundary, Fish Clay, calcareous dinoflagellate cysts, paleoecology.

## Introduction

The Stevns Klint section represents one of the classic Cretaceous/Tertiary (K/T) boundary sections and has been extensively studied during the twentieth century (e.g. Christensen et al., 1973; Birkelund and Håkansson, 1982; Schmitz et al., 1992). The boundary clay in this section, the so-called Fish Clay, consists for a major part of products of impact-fallout at its base (Alvarez et al., 1980; Kastner et al., 1984; Smit, 1999) and can be considered to represent the abrupt change following an impact event which had global consequences, most probably the Chicxulub impact (Hildebrand et al., 1991).

The extinction event at the end of the Cretaceous is still hotly debated because of the controversy of paleontological data which obviously reflect two different scenarios, namely (i) a long-term faunal and floral change causing extinction of taxa throughout the upper Maastrichtian and (ii) the sudden impact-catastrophe. A comprehensive discussion on this aspect is given by Ward (1995). The gradual decline in species richness of e.g. ammonites (Marshall and Ward, 1996) and planktic foraminifera during the Maastrichtian was probably related to long-term global climate change, characterized by strong cooling and sea level regression (Keller et al., 1995; Keller, 2000). Evidence from e.g. molluscs (Marshall and Ward, 1996), foraminifera (e.g. Smit, 1982, Olsson and Liu, 1993, Molina et al., 1998) and coccolithophorids (Pospichal et al., 1992; Pospichal, 1994), however, show that the major extinction at the K/T boundary was related to a sudden catastrophe rather than culmination of long-term environmental stress. An important role for the understanding of the exact extinction mechanism of the impact play fossil groups with low extinction rates, since their association changes may provide information on migration events and survival strategies and can in turn improve our knowledge of the ecological effects of the catastrophic events. Most calcareous plankton groups were strongly affected by extinction at the K/T boundary. Organic walled dinoflagellate cysts, on the contrary,

reflect no extinction at all but show characteristic lateral distribution changes that can be used to reconstruct variations in sea surface temperatures (Brinkhuis et al., 1998).

In the present study we focus on the distribution patterns of calcareous cystproducing dinoflagellates (Calciodinelloideae) over the K/T boundary in the Stevns Klint section, which also show no accelerated extinction rate (Hildebrand-Habel et al., 1999). The study aims at ecologically interpreting the pattern of selective extinction of these organisms over the boundary, which is clearly related to the impact-event.

The subfamily Calciodinelloideae (Fensome et al., 1993) comprises all dinoflagellates that form calcareous resting cysts as part of their life cycle. These fossilisable cysts are mostly spherical in shape and do not show any signs of paratabulation, although some species do reflect the peridinioid plate pattern (paratabulation) of the corresponding motile dinoflagellates very clearly. Calcareous dinoflagellate cysts (dinocysts) show a high diversity of forms throughout the entire Cretaceous. Their recent descendants are autotrophic organisms, so that we assume that Cretaceous dinocysts are also remains of phytoplanktonic organisms, reflecting conditions within the photic zone. Therefore, they can be applied as a tool for the reconstruction of conditions in the upper water column, an area which is strongly influenced by atmospheric change and thus plays a key role in the reaction of the ocean to both short-term catastrophes and long-term climate change.

This study represents the first high-resolution analysis of calcareous dinocysts across the Fish Clay. Calcareous dinocysts of the stratigraphic interval containing the K/T boundary were studied by Kienel (1994) in various palaeogeographic positions of the Boreal realm including Stevns Klint, without however sampling the Fish Clay. Worldwide, studies of the calcareous dinocysts throughout the Maastrichtian to Paleocene period of time are scarce. Important work has been done in the southern Atlantic Ocean (Fütterer, 1984, 1990; Hildebrand-Habel et al., 1999) and the Boreal realm (Willems, 1994, 1995, 1996). In many cases, a hiatus prevents detailed studies exactly at the boundary.

## **Material and Methods**

The sampled section is located approximately 500 m NE of Højerup "gamle kirke" at Stevns Klint, near Copenhagen, Denmark (Fig. 1). Details of the lithostratigraphy of the Fish Clay are given in Christensen et al. (1973); foraminiferal biostratigraphy and isotope stratigraphy are provided by Schmitz et al. (1992). Four main lithofacies types can be

distinguished: 1) white Maastrichtian limestone, rich in bryozoan fragments; 2) reddish and black to gray, pyritic, laminated clay (Fish Clay); 3) yellowish, highly burrowed and intensively cemented limestone (Cerithium Limestone); and 4) white Danian limestone, very rich in bryozoans. Preservation of the calcareous dinoflagellate cysts is good in the Maastrichtian limestone and very good in the Bryozoan Limestone. In contrast, the carbonate grains of the Cerithium Limestone (sample Fi9) and the uppermost part of the Fish Clay (sample Fi8) are strongly altered. Preservation of carbonate grains in the lower Fish Clay appears to have been selective, planktic foraminifera showing signs of dissolution (see also Schmitz et al., 1992) while dinocysts are particularly well preserved.



Fig. 1: Geographic location and lithological profile of the investigated section, including sample positions.

Samples were taken with a micro carve at 1 cm sample spacing. Approximately 2 g of sediment were disintegrated in water (clay samples). The limestone samples were disintegrated by repeated freezing and thawing in a saturated solution of sodium sulfate. The disintegrated clay samples were treated with a clay dispersant (Rewoquat) for 24 hours to remove clay particles during washing. The material was wet-sieved using mesh sizes of 15  $\mu$ m, 20  $\mu$ m, 75  $\mu$ m and 125  $\mu$ m and dried.

Counts were done by optical microscopy (120x magnification) using weighted splits of 1-2.8 mg of the 20-75  $\mu$ m grain size fraction, which encompasses the size range of

most specimens of calcareous dinoflagellate cysts. Exceptions are large Maastrichtian specimens which were analyzed in the size fraction  $>75 \,\mu\text{m}$ , and the lower size limit of Danian species which were analyzed qualitatively in smear slides of the 15-20 µm size fraction, using a CamScan CS 44 Scanning Electron Microscope (SEM). Due to the dominance of one species in the Maastrichtian, the presence of rare species in samples Fil to Fi4 could only be assessed qualitatively by SEM-analyses of the 20-28 µm size fraction, where these are enriched. This fraction was dry-sieved from 4 mg of the 20-75 µm fraction (qualitative evaluation of results: 1 to 10 specimens per SEM stub = present [<0.5% of the dinocyst assemblage]; more than 10 specimens per SEM stub = common). Each specimen counted in the splits under the light microscope was picked, excluding the optically determinable Pithonelloideae, and mounted on a stub for SEM studies for taxonomic determination. The taxonomy follows the classification of Fensome et al. (1993) and Young et al. (1997). The carbonate content of each sample was measured in order to evaluate the comparability of dinocyst counts of the clay to the counts in the limestones. Measurement was carried out using a "carbonate bomb" (Carbometer mod. 23: 1 g of crushed sample is placed in a small pressure vessel along with a plastic boat containing 6N hydrochloric acid. The vessel which has a manometer attached is sealed and the carbonate is reacted with the acid. The amount of pressure registered by the gauge is proportional to the carbonate content.). Due to strong variations in carbonate content, the results of the counts only represent a semi-quantitative estimate of the concentration of specimens per sample.

The use of cathodoluminescence to distinguish reworked Maastrichtian from Danian specimens was tested, using a Cold Cathode Luminescence System 8200 MK II coupled with an Olympus BH-2 optical microscope. However, there is no difference in luminescence color and/or intensity between Maastrichtian and Danian carbonates.

All material is stored at the Division of Historical Geology and Paleontology of the University of Bremen.

## Results

The carbonate content and grain size distribution of the investigated samples are given in Fig. 2 to illustrate the significant lithological variations throughout the profile. The basal Fish Clay shows an abrupt breakdown in carbonate content and contains an increased amount of coarse grains, which are predominantly non-carbonate. Towards the top of the clay, the carbonate content increases gradually and the grain size distribution indicates fining upward. The deposition of coarse grains (mainly fish remains, spherules and corroded foraminifera) at the base of the Fish Clay is followed by a clay that almost lacks carbonate grains larger than 125  $\mu$ m but shows a first carbonate recovery in the fraction less than 125  $\mu$ m.



Fig. 2: Carbonate content and grain size distribution of the investigated samples; gray underlain areas of the diagrams mark the common ranges in percentage throughout the Cretaceous; note the significantly higher amount of the coarse fraction in the Danian sample.

The Cretaceous chalk and the Danian Bryozoan-limestone have a similar carbonate content but show a considerable difference in the percentage of the coarse fraction with higher values in the Danian. The percentages of the dinocyst-bearing fraction 20-125  $\mu$ m, however are approximately equal.

While the cyst counts of these limestones can be compared to each other due to the lithological similarity, the cyst amount counted in the clay samples is biased incalculably by selective carbonate dissolution (foraminifera) and dilution by non-carbonate.

Assemblage	species	Samples	Comments
P-assemblage	Pithonella sphaerica Kaufmann	Fi1, Fi2, Fi3,	most abundant species,
(Pithonella)	Pithonella discoidea Willems	Fi4	formerly known as
	Pithonella ovalis Kaufmann	Fi8*, Fi9*,	calcispheres
		Fi10*	
D-assemblage	Operculodinella operculata Kienel,	Fi1, Fi2, Fi3,	Operculodinella operculata
(common in the	1994, emend. Hildebrand-Habel et	Fi4,	was formerly described as
<u>D</u> anian)	al., 1999	Fi8*, Fi9*,	Thoracosphaera operculata
	Operculodinella costata Kienel	Fi10	(Bramletti et Martini, 1964)
	Operculodinella reticulata Kienel		and Obliquipithonella
	Lentodinella danica Kienel		operculata (Fütterer, 1990)
	Orthotabulata obscura Kienel		
	Calcicarpinum tetramurus Kienel		assemblage is named for its
			dominance in the Danian but
			is also present in the
			Maastrichtian
B-assemblage	Orthopithonella sp.	Fi1 – Fi10	present throughout the
(Background)	Rhabdothorax spp. (2 species)		section; increased abundance
			in the Fish Clay
C-assemblage	Orthopithonella collaris (n. sp.)	Fi5, Fi6, Fi7	pulse-like occurrence
( <u>C</u> lay-specific)	Pirumella lepidota Keupp		exclusively in the Fish Clay
	Pentadinellum vimineum Keupp		

## TABLE 1: ASSEMBLAGES OF CALCAREOUS DINOFLAGELLATE CYSTS

\*probably reworked specimens



Fig. 3: Common calcareous dinoflagellate cysts of the Stevns Klint K/T boundary section. All scale bars are

10 µm.

- 1) *Pithonella sphaerica*, main species of the P-assemblage, sample Fi1.
- 2) Orthopithonella sp., B-assemblage, sample Fi6.
- **3)** *Rhabdothorax* sp., B-assemblage, sample Fi5.
- 4) Orthopithonella collaris (spec. nov., Chapter 5.), C-assemblage, sample Fi5.
- 5) *Pirumella lepidota*, C-assemblage, sample Fi5.

6) *Pentadinellum vimineum*, C-assemblage, sample Fi5.

- 7) *Operculodinella operculata*, D-assemblage, sample Fi3.
- 8) *Operculodinella reticulata*, D-assemblage, sample Fi10.
- 9) *Operculodinella costata*, D-assemblage, sample Fi10.
- **10)** *Calcicarpinum tetramurus*, D-assemblage, sample Fi10.
- 11) *Lentodinella danica*, D-assemblage, sample Fi10.
- 12) Orthotabulata obscura, D-assemblage, sample Fi10.

## Stratigraphical distribution of cyst assemblages in the studied section

The 15 common species of calcareous dinocysts of the studied material (Fig. 3) were grouped into 4 assemblages according to their stratigraphical distribution (Tab. 1), which were given the abbreviations P- (*Pithonella* spp.), D- (dominant in the Danian), C- (clay-specific) and B- (background). In Fig. 4 the distribution patterns of these 4 assemblages are illustrated.

The uppermost Maastrichtian samples (Fi1 – Fi4) are characterized by a typical upper Cretaceous dinocyst association which consists to about 99% of species of the P-assemblage. This group represents the dominant element of the Boreal microflora since the Albian. Cyst abundances are in the order of 1000 cysts per mg (fraction 20-75  $\mu$ m). The remaining 1% of the cyst association is formed by the D- and B-assemblages. Approaching the uppermost Maastrichtian, abundances of the P-assemblage decrease.

Cyst abundances are extremely low in the Fish Clay (Fi5-Fi7) compared to the Maastrichtian chalk due to the abrupt, complete disappearance of the P-assemblage and the D-assemblage. The lowermost 4 mm of the reddish layer contain almost no cysts. The C-assemblage is immediately present just above the base of the clay layer. Specimens are exceptionally well preserved in contrast to planktic foraminifera and coccoliths. The occurrence of a new species, *Orthopithonella collaris* n.sp. (Chapter 5.), is particularly

prominent since it is restricted to the K/T boundary clay only. The B-assemblage shows increased abundance in the Fish Clay. No calcareous dinocysts were found in the <20  $\mu$ m size fraction.



**Fig. 4**: Qualitative and semi-quantitative distribution patterns of the 4 assemblages (described in table 1) of calcareous dinocyst species throughout the Fish Clay section.

Abundances of calcareous dinocysts remain low in the entire clay succession. Towards the top (Fi8), the C-assemblage disappears and the species of the B-assemblage decrease in number while the P- and D-assemblage reappear. Preservation of specimens, especially those of the P-assemblage, is mostly poor in this upper part of the clay. No data could be obtained from the Cerithium Limestone due to extremely poor preservation.

In the Bryozoan Limestone (Fi10), the total abundances of cysts in the 20-75  $\mu$ m fraction are about 80 cysts per mg (fraction 20-75  $\mu$ m). The D-assemblage represents approximately 75% of the association. The size fraction 15-20  $\mu$ m contains *Operculodinella operculata* (1,4 % of that fraction). A decrease in abundance of the B-assemblage can be noted. The C-assemblage is absent. Very few specimens (3% of the

dinocyst association) of the P-assemblage can be found. The good preservation provides no clear hints that these specimens have been reworked.

## Discussion

## The duration of deposition of the boundary clay

The Fish Clay is generally considered to be a condensed layer (Schmitz, 1990; MacLeod and Keller, 1991). The amount of time represented by this layer is, however, still a matter of debate. An evaluation of the duration of deposition, which is certainly variable due to local circumstances, is important for the understanding of the mechanisms of ecological change which are associated with the impact.

We consider the reddish and dark-gray layers as representing the first decades or centuries following the impact because of their mineralogical particularities: featuring only traces of quartz as terrigenous component, an almost pure smectitic clay mineral assemblage, and spherules of probable impact origin (Kastner et al., 1984). Alvarez et al. (1980) point out that, in contrast to the terrigenous clays found in the chalks below and above the Fish Clay, the completely different clay mineral assemblage of this layer is likely the product of alteration of fallout material. Had the time of deposition been in the order of millennia, the continual terrestrial input and reworking would have diluted the comparably small amount of fallout. Furthermore, fining upward covering the reddish and dark-gray layers suggests a fast, continuous sedimentation under decreasing energy. Accordingly, the presence of non-Maastrichtian carbonate producers, causing a gradual increase in carbonate content already during deposition of the fallout, indicates a fast recovery of an initially low carbonate production. This supposition is corroborated by the results of Pope et al. (1994) who modeled the impact winter cooling and a subsequent warming pulse, which took place during the discussed interval, to have had a duration of decades only. Especially the warming pulse was independently recognized to occur at the base of the Fish Clay by Brinkhuis et al. (1998), using dinoflagellate-based sea surface temperature reconstruction. However, based on biostratigraphical results, these authors considered the period of warming to have had a longer duration of up to 10000 years, which is inconsistent with the conclusions drawn from the mineralogical and sedimentological characteristics of the basal Fish Clay discussed above.

## The distribution patterns of calcareous dinocysts

## Victims

The 4 characteristic assemblages of calcareous dinocysts show specific reactions to the impact catastrophe. Most strikingly, the dominance of the Pithonelloideae ended abruptly with the onset of clay deposition. These species that were characteristic for the boreal realm throughout the whole Upper Cretaceous were clearly victims of the K/T event. It is ambiguous whether the P-assemblage experienced a weak recovery in the Danian which, according to Kienel (1994), ends at the top of the *Cruciplacolithus intermedius* nannofossil-zone. In the Geulhemmerberg K/T boundary section (Limburg, SE Netherlands) (Willems, 1996) no break at all in the dominance of the species of the P-assemblage can be found. This is most likely due to reworking. In the Stevns Klint section, a few specimens of this assemblage can also be found above the K/T boundary. Those are likely reworked, though their mostly poor preservation could also derive from increased cementation, i.e. diagenetic overprinting. Despite the possibility of a weak and short-lived recovery, this assemblage is an example for the sudden end of an era of extremely successful Cretaceous organisms initiated by the impact catastrophe.

As changing distribution patterns of Pithonelloideae are known to reflect sea level change (Dali-Ressot, 1987; Keupp, 1991; Zügel, 1994), the decrease in number towards the end of the Maastrichtian can be interpreted as a reaction to the long-term global eustatic sea level fall (Haq et al., 1987; Hardenbol et al., 1998). This major regression resulted in a pronounced sea level lowstand during the late Maastrichtian to early Danian period of time, and in turn reduced the area of epicontinental shallow seas (Håkansson and Thomsen, 1999). Additionally, short term regression, estimated to have been on the order of 70-100 m in the Tethys (Keller, 1988), is reflected by the uppermost Maastrichtian associations of planktic foraminifera and dinoflagellates (Brinkhuis and Zachariasse, 1988; Schmitz et al., 1992).

One reason for the extinction of the P-assemblage may be found in their restriction to the outer shelf environment of these seas (e.g. Villain, 1981; Zügel, 1994), which was progressively reduced during the sea level fall. Because of their restriction to a shrinking environmental niche, they were strongly affected by the environmental catastrophe since they could not escape into other environments where they might have found niches to survive.

Furthermore, the ability to form a resting cyst as part of the life cycle appears to be an important general factor in dinoflagellate survival, as also suggested by Brinkhuis et al. (1998) for the dinoflagellates that form organic-walled cysts. The production of long-term resting cysts can be considered a survival strategy (Lewis et al., 1999). Experimental data (Dale, 1983; Lewis et al., 1999) on resting cysts confirm a wide range of survival time between 12 and 66 months for different dinoflagellate species, coastal and fresh water species having the longest dormancy periods. These differences could account for selective extinction, although it must be noted that still little is known about the ability of dinoflagellates to adjust their dormancy period according to certain natural environmental conditions that could never be simulated in experiments. Experiments performed by Griffis and Chapman (1989, 1990) showed that light blackout exceeding 3 months and the effect of acid rain on the growth of cells are critical factors for survival of the motile dinoflagellate stage. We hypothesize that the species of the P-assemblage, in addition to their disadvantage of diminished spatial distribution, had a rapid life cycle with a short resting stage. Thus, they were subject to extinction because their dormancy period was not long enough to survive the impact winter and prolonged period of unfavorable conditions.

### Survivors

The D- and B-assemblages were not significantly affected by the impact and survived into the Tertiary. The first appearance of species of the D-assemblage in the Late Maastrichtian at Stevns Klint and in a section from the South Atlantic Ocean (Hildebrand-Habel et al., 1999) most likely reflects a change in the cyst association as a consequence of long-term environmental change and evolution.

The disappearance of the D-assemblage in the K/T boundary layer could be the result of environmental stress or of selective dissolution. The latter seems unlikely, since the assemblage contains a wide range of cyst sizes, various wall thickness and all wall types. Therefore, the absence of the D-assemblage in the Fish Clay is interpreted to mainly reflect an ecological signal. It may indicate that these species experienced instant regional migration due to a major facies shift at the investigated location. However, the species of the D-assemblage seem to have lived in a wide range of environments as they are known from shelf environments (Kienel, 1994; Willems, 1996; and the present study) as well as the oceanic realm (Hildebrand-Habel et al., 1999). Such an extended habitat can provide a large variety of ecological niches that increases the chance of survival for at least part of

the species' population. Even if 99,9% of the population dies, the species can still survive (Smit, 1999, 2000).

## Adapters and opportunists

In contrast to the species of the D- and P-assemblages, the species of the C- and Bassemblages present in the Fish Clay seem to have adapted themselves to the special environmental conditions following the impact or they were opportunists. The spiny cysts of the B-assemblage might be compared to the recent calcareous dinoflagellate species *Scrippsiella trochoidea* (von Stein), which forms similar spiny cysts and is exclusively found in coastal environments (Janofske, 2000 and references therein) where unstable conditions are typical. This species is considered an euryhaline species and is occasionally described from brackish environments. Lewis et al. (1999) found in a study including *Scrippsiella* sp. that "... the species to have the greatest longevity are amongst the most common members of coastal phytoplankton assemblages". This means that the coastal environment could have been a reservoir of cysts that are capable of surviving a long period of unfavorable conditions at the K/T boundary (Lewis et al., 1999). This idea is corroborated by the increased presence of spiny cysts within the Fish Clay, which probably represent species that successfully pioneered the post-impact marine environment.

Special adaptation to the environment established during Fish Clay deposition must be assigned particularly to the C-assemblage. The new species *Orthopithonella collaris* and *Pentadinellum vimineum* with their distinctive reduced paratabulation and *Pirumella lepidota* are exotic elements in the dinocyst association of the boreal realm. *Pentadinellum vimineum* represents a group of reduced paratabulated species that shows a specific distribution pattern throughout the Cretaceous which is characterized by restricted temporal ranges. They were observed to occur sporadically in short-term events related to ingressions of warm Tethyan water masses into the Boreal realm during the lower-middle Cretaceous (Keupp et al., 1991; Neumann, 1999). Zügel (1994) stated that the development of paratabulated cysts, which he found to be dominating in coastal areas, must be related to short-term, regional, ecological events.

Possible reasons for the C-assemblage pulse occurrence in the Fish Clay are (i) the above mentioned advantage in survival strategy, probably connected with the development of stress-controlled, ecological morphotypes, or (ii) a migration of the species into the studied area. A comparable pulse of organic-walled dinoflagellate cysts exactly at the K/T

boundary is discussed by Brinkhuis et al. (1998). They discovered a short-term dominance of an equatorial species in the lower parts of the Fish Clay and interpreted it as representing a migration of a tropical species into higher latitudes due to the aerosolforced, post-impact warming event. So far, too little is known on the ecological affinities of the C-assemblage species to check if such an interpretation also applies for this group of dinoflagellates. While it is possible that the pulse-like occurrence in the Fish Clay was caused by a migration event, the most straightforward explanation is that the C- as well as the B-assemblages represent a pioneer flora of robust species that flourished during the time of diminished carbonate production, which was later replaced by a newly developed ecosystem.

The dinocyst association of the Fish Clay is similar to the calcareous dinocyst assemblages found in the "C-" clay of the Geulhemmerberg K/T section (Willems, 1996). According to paleogeographic distribution patterns, including those of the Pithonelloideae, this association was interpreted as indicative of maximum transgression. Considering (i) the fact that reworking played a major role in the P-assemblage distribution in the Stevns Klint and Geulhemmerberg sections; (ii) the pulse-like appearance of the C-assemblage in the Fish clay; and (iii) the distinct breakdown of the P-assemblage in the clay, we interpret the C- and B-assemblage-equivalents of the Geulhemmerberg section to reflect a unique ecological situation rather than a sea-level-controlled facies shift.

Although the Fish Clay is an exceptional example of breakdown of carbonate production which is clearly related to an impact and subsequent substantial extinctions, there is a striking analogy between its dinocyst distribution and that of cyclic sediments throughout the Mid-Cenomanian which are interpreted as orbitally forced sedimentary cycles (Gale et al., 1999). Reduced paratabulated species occur in high relative abundance in certain marls of the chalk-marl couplets of the Anglo-Paris Basin, while simultaneously, an almost complete disappearance of Pithonelloideae can be observed (**Chapter 2.**). These short-term disruptions of the chalk deposition can be related to climatically forced stratification events on the basis of paleoceanographic models (e.g. Mitchell and Carr, 1998). If the similar dinocyst distribution patterns of this long-term climate change on the one hand and the impact catastrophe on the other hand were caused by the same oceanographic changes, it may be suggested that stratification was another important local factor of the extinction mechanism related to the impact.

## Conclusions

Two main ecological factors were apparently important for the survival over the K/T boundary of the dinoflagellates investigated in this study. Firstly, the ability to form a resting cyst as part of the life cycle appears to be an important advantage for dinoflagellate survival. Secondly, the distribution of species over large areas and a wide range of ecosystems was crucial for survival. A combination of both factors appears to be the main reason for a low extinction rate at the K/T as opposed to the high extinction rate of other phytoplankton groups, such as the coccolithophorids.

The P-assemblage distribution shows that even though some specimens occur above the K/T boundary which may represent a short recovery, the complete disappearance of taxa right at the base of the boundary clay is an abrupt biotic response clearly related to the impact. So, our definition of an impact-related extinction should not necessarily require the instant disappearance of a taxon but rather accept the impact catastrophe as an event, initiating a substantial ecological change which allowed for a limited survival time of some victims.

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## Appendix

sample No.	fraction <20 μm [wt%]	fraction 20-125 µm [wt%]	fraction >125 µm [wt%]	carbonate [wt%]
Fi1	59.1	27.8	13.1	95
Fi2	60.4	29.1	10.5	95
Fi3	73.0	17.0	10.0	95
Fi4	62.3	26.4	10.3	95
Fi5a	49.4	27.3	23.3	77
Fi5b	29.9	26.2	42.9	32
Fi6	44.9	45.5	9.6	43
Fi7	61.3	36.7	2.0	58
Fi8	63.8	30.0	6.2	77
Fi9	35.0	33.6	31.4	91
Fi10	32.1	25.2	42.7	96

GRAINSIZE FRACTIONS AND CARBONATE CONTENT

## COUNTS OF CALCAREOUS DINOFLAGELLATE CYSTS

sample No.	counted split [mg] of 20-75 µm fraction	counted cysts (total)	Pithonella sphaerica	Pithonella ovalis	Pithonella discoidea	<i>Rhabdothorax</i> spp.	Orthopithonella sp.
Fi1	1.4	1280	1230	10	30	1	2
Fi2	0.9	772	720	10	40	0	1
Fi3	0.7	436	400	4	20	1	1
Fi4	0.8	428	350	2	70	0	0
Fi5b	2.8	64	0	0	0	18	24
Fi6	2.2	74	0	0	0	18	28
Fi7	1.0	28	0	0	0	3	4
Fi8	1.2	48	24	0	0	5	4
Fi9	no count						
Fi10	1.2	92	3	0	0	10	11

sample No.	split [mg] of 20- 75 µm fraction	Orthotabulata obscura	Operculo- dinella spp.	Calcicarp. tetramurus	Lentodinella danica	Pirumella lepidota	Orthopithonella collaris
Fi1	1.4	1	1	2	3	0	0
Fi2	0.9	0	0	0	1	0	0
Fi3	0.7	1	2	3	4	0	0
Fi4	0.8	1	1	2	2	0	0
Fi5b	2.8	0	0	0	0	10	12
Fi6	2.2	0	0	0	0	22	8
Fi7	1.0	0	0	0	0	9	0
Fi8	1.2	0	8	0	7	0	0
Fi9	no count						
Fi10	1.2	17	16	11	24	0	0

qualitative analysis of the 20-28 µm size fraction						<i>sphaerica</i> >75µm
sample No.	Orthotabulata obscura	Operculodinella spp.	Calcicarpinum tetramurus	Lentodinella danica	Pithonella sphaerica	split [mg] of >75µm fraction
Fi1	р	р	р	р	770	2.2
Fi2	р	р	р	р	660	3.3
Fi3	р	С	С	С	312	3.3
Fi4	р	р	р	р	265	2.8

a – absent; p – present ( $\sim 0.5\%$ ); c – common

# 5. *Orthopithonella collaris* sp. nov., a new calcareous dinoflagellate cyst from the K/T boundary (Fish Clay, Stevns Klint/Denmark)

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## Abstract

A new calcareous dinoflagellate cyst species, *Orthopithonella collaris* sp. nov., is described from the Cretaceous/Tertiary (K/T) boundary clay (Fish Clay) of Stevns Klint, Denmark, on the basis of SEM studies and light-microscopic analyses of thin sections of single specimens. The species has been found exclusively in the Fish Clay and as such may be a potential marker for the K/T boundary. Its pulse-like occurrence is thought to be due to the abrupt, relatively short-term ecological catastrophe associated with the K/T boundary event.

Keywords: calcareous dinoflagellate cysts, K/T boundary, Boreal, Fish Clay, Stevns Klint

## Introduction

The so-called Fish Clay, exposed at Stevns Klint, Denmark (near Copenhagen) represents one of the classic Cretaceous/Tertiary (K/T) boundary layers and has been extensively studied (e.g. Christensen et al., 1973; Birkelund and Håkansson, 1982; Schmitz et al., 1992). The base of this section displays the products of impact-fallout (Alvarez et al, 1980; Kastner et al., 1984; Smit, 1999) and can be considered to represent relatively short-term, exceptional environmental conditions following an impact event which had global consequences, most probably the impact that caused the Chicxulub impact crater. In the

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Fish Clay, a distinctive flora of calcareous dinoflagellate cysts (Calciodinelloideae) was found, containing a new species which is described in this paper.

The subfamily Calciodinelloideae (Fensome et al., 1993) comprises all dinoflagellates that form calcareous resting cysts as part of their life cycle. These fossilisable cysts are mostly spherical in shape. Although most of them do not show any signs of paratabulation, some species do reflect the peridinioid plate pattern of the corresponding motile dinoflagellates very clearly. Paratabulation may be holotabulate (i.e. complete plate pattern shown), however, usually paratabulation is reduced to particular elements of the corresponding motile cell, often the sulcal and cingular areas where the flagellae were positioned. Calcareous dinoflagellate cysts with reduced paratabulation are of particular interest as their occurrence in the stratigraphic record is characterised by short-term, often event-like abundance peaks in relation to transgressive/regressive trends and Milankovitch cyclicity (Keupp, 1991; Zügel, 1994; Neumann, 1999; **Chapter 2.**).

Calcareous dinoflagellate cysts of the stratigraphic interval containing the K/T boundary were studied by Kienel (1994) in various palaeogeographic locations in the Boreal realm including Stevns Klint, although the Fish Clay was not sampled. World-wide, studies of the calcareous dinoflagellate cysts throughout the Maastrichtian to Palaeocene period of time are scarce and generally only include investigations of the southern Atlantic Ocean (Fütterer, 1984; 1990; Hildebrand-Habel et al., 1999) and the Boreal realm (Willems, 1994, 1995, 1996). In many cases, a hiatus prevents detailed studies exactly at the boundary. Wendler and Willems (**Chapter 4.**) studied the changes in assemblages of calcareous dinoflagellate cysts throughout the Stevns Klint section, and found that the new species is exclusively present in the Fish Clay. This lends it an outstanding biostratigraphic role as marker for post-K/T environmental conditions in continental shelf areas. In the present paper we give a detailed taxonomic description of the new species and discuss its restricted occurrence within the Fish Clay.

### **Material and Methods**

The sampled section is located near Højerup at Stevns Klint, Denmark (Fig. 1). Details of the lithostratigraphy of the Fish Clay are given in Christensen et al. (1973); foraminiferal biostratigraphy and isotope stratigraphy were investigated by Schmitz et al. (1992). The Fish Clay is a reddish to black, pyritic clay which marks an interval of almost complete breakdown of carbonate accumulation. Preservation of carbonate grains appears



to have been selective in this layer, the planktic foraminifera and coccoliths showing signs of dissolution while the calcareous dinoflagellate cysts are particularly well preserved.

Fig. 1: Geographical location and lithological profile of the investigated section, including the position of the samples which contain *Orthopithonella collaris* sp. nov.

Approximately 2 g of the sediment were disintegrated in water and treated with a clay dispersant (Rewoquat) for 24 h to remove clay particles during washing. The material was wet-sieved using mesh sizes of 20  $\mu$ m and 75  $\mu$ m and the residue was consequently dried. Cyst specimens were picked with an eyelash using a binocular microscope at a magnification of x120 and mounted on a stub for SEM studies. Morphological details of the cysts were investigated by rotating the 45° inclined SEM-stub throughout 360°. The description of *Orthopithonella collaris* sp. nov. in the present study is based on the analysis of 38 cysts.

The taxonomy follows the classification of Fensome et al. (1993) which subdivides the Calciodinelloideae according to their wall type and type of archeopyle. To analyse the crystallographic orientation of the wall crystallites, thin sections of 7 specimens were prepared following the procedure of Janofske (1996). The crystallographic orientation defines the wall type of the cyst (Young et al., 1997) and is essential for determining the species' generic affinity. Unprocessed sample material (sample numbers are: Fi5, Fi6 and Fg which is a composite sample of the lower 3 cm of the Fish Clay), washed residue and the analysed SEM stubs and thin sections are stored at the Division of Historical Geology and Palaeontology, University of Bremen.

## Taxonomy

Division DINOFLAGELLATA (Bütschli, 1885) Fensome et al., 1993

Subdivision DINOKARYOTA Fensome et al. 1993

Class DINOPHYCEAE Pascher, 1914

Subclass PERIDINIPHYCIDAE Fensome et al., 1993

Order PERIDINIALES Haeckel, 1894

Family PERIDINIACEAE Ehrenberg, 1831

Subfamily CALCIODINELLOIDEAE Fensome et al., 1993

Genus Orthopithonella Keupp and Mutterlose, 1984

Original diagnosis (Keupp and Mutterlose, 1984: p. 158): "Cysts with mostly single walls consisting of block-like to columnar crystallites. Crystallites are strictly radially oriented. In most cases, cysts are without paratabulation."

Emendation (Keupp and Versteegh, 1989, p. 210): "Spherical, non- to reduced paratabulated cysts; mostly single-walled; c-axes of the wall-crystallites are radially oriented. The archeopyle is mostly formed by the apical plates 2' - 4'."

Comment: A narrower definition of the genera-specific characteristics, particularly regarding the number of walls, is currently in progress (Streng, pers. com.). Presumably, the new definition will result in a subdivision of the original genus *Orthopithonella*.

## Orthopithonella collaris Wendler et al., sp. nov.

**Derivation of name**: *collaris* (Latin, m.) = collar; according to the prominent ridge that reflects the paratabulation and is distinctively arranged on the cyst surface, resembling a collar.

**Diagnosis**: A spherical to apically-antapically flattened species of *Orthopithonella* with a paratabulation consisting of a prominent ridge that deliniates two separate, unequal but confluent heptagonal regions (Plate II, Fig. 6). The double-layered wall consists of radially

oriented crystallites in both layers (Plate I, Figs. 5, 6). The apical archeopyle shows a weakly sub-angular shape.

Holotype: Cyst Fi5c/e4 (SEM micrographs 390/22-31, Fig. 2; Plate I, Figs. 1,2; Plate II, Fig. 1).

**Type locality**: Cliff section, 500 m NE of Højerup, Stevns Klint, Denmark (near Copenhagen).

Type stratum: Basal Danian "Fish Clay", sample Fi5.

**Paratypes**: Fi5a/b3, Fi5a/c5, Fi5a/d1, Fi5a/d4, Fi5a/e3, Fi5a/e4, Fi5a/e6, Fi5a/f4, Fi5a/i3; Fi5b/h1; Fi5c/a1-4, Fi5c/b1-2, Fi5c/d1-4, Fi5c/e1-3; Fi6/l4, Fi6/h5, Fi6/h6, Fi6/i1; Fg/b4, Fg/e2, Fg/j6; cysts for thin sections: Fi5/DS/1-7.

**Repository**: Collection at the Division of Historical Geology and Palaeontology, Department of Geosciences, University of Bremen, Germany.

## **Description and measurements:**

Spherical to slightly apically-antapically flattened cysts. Cysts are 40–70 µm in diameter.

<u>Paratabulation pattern</u>: The prominent ridge can be interpreted to reflect the cingulum and sulcus (Fig. 2a, b). This interpretation is based on the position of the two heptagonally shaped parts of the ridge at an angle of 80-90° to the cyst surface. The slightly flattened, apical surface of the cyst is encircled by the weakly six-sided, 63–89  $\mu$ m wide part of the ridge (termed cingular ridge) which is not developed in the sulcal region. It encompasses the occasionally visible, sub-angular, ventrally flattened archeopyle (Plate II, Fig. 3). The six sides of the cingular ridge reflect 6 cingular or precingular plates (Fig. 2b). This ridge devides the cyst into a smaller epicyst (about 1/3 of the sphere) and a larger hypocyst (Plate II, Fig. 4; Fig. 2a). The smaller, 35–60  $\mu$ m wide, heptagonal area is found on what is interpreted as the ventral surface and is surrounded by the remaining part of the ridge (hereafter termed sulcal ridge) on all but the apical side (Plate II, Fig. 4). This region can be interpreted to reflect the sulcal area and the neighbouring plates (Fig. 2b). The ridges are 12–25  $\mu$ m high. The comparison of different specimens shows that the ridge size

is independent of the cyst body diameter, which might in part be due to diagenetic growth of the ridge-crystallites.

<u>Asymmetry</u>: Both sulcal and cingular ridges form a wider arc to the left side of the cyst, leading to an asymmetrical shape that is characteristic of this species (Fig. 2a, b; Plate I, Fig. 3). The angle between the cyst surface and the ridges is smaller on the ventral and apical side than on the dorsal side (Plate I, Fig. 2). Also the angle between the apical-antapical axis and the cingular ridge varies on one individual, being smaller on the right than on the left side of the cyst (angle y in Fig. 2a). The angle at the connection points between cingular and sulcal ridges (Fig. 2a) is larger on the right (angle x (r): ca. 100°) than on the left side (angle x (l): ca. 45°). The left side is closer to the apex than the right side (dashed horizontal lines in Fig. 2a). The span between these transition points can be interpreted to reflect the sulcal width, which is 17–33  $\mu$ m wide.



Fig. 2: a) Holotype cyst Fi5c/e4 of Orthopithonella collaris sp. nov.; ventral view. ci = cingular ridge, su = sulcal ridge; lines show the symmetrical characteristics of the cingular and sulcal ridge: marked with solid lines: angles x (right/left) = angles of transition between cingular and sulcal ridge; angles y (right/left) = different attachment angles of the cingular ridge; dashed horizontal lines indicate the shift between left and right side relative to the apical-antapical axis.

**b**) Schematic sketch of the interpreted paratabulation pattern of *Orthopithonella collaris* sp. nov. with the cingular and sulcal ridge tilted into one plane; the interpretation of the reflected plate pattern follows the Kofoidian tabulation system. A = archeopyle; S = sulcus.

<u>Walls</u>: The wall is double-layered (Plate I, Figs. 5, 6). The crystals on the cyst surface are arranged in an irregular array, resembling an oblique orientation (Plate I, Fig. 4). This appearance, which is probably caused by diagenetic overprinting does not reflect the true orientation of the crystals of the outer wall. During thin section analysis, a radial orientation of the crystals of both layers orthogonal to the cyst surface could be clearly identified (Plate I, Fig. 6). The inner wall is  $3-4 \mu m$  thick and consists of slim, rhombohedral crystals, whereas the outer wall, also  $3-4 \mu m$  in thickness, is built up of larger, block-like, rhombohedral crystals (Plate I, Fig. 5). The ridges appear to be hollow and seem to represent an extension of the outer wall (Plate I, Fig. 6). Crystals forming the ridges are larger than those of the cyst surface (Plate I, Fig. 4).

## **Comparison and discussion**

Orthopithonella collaris shows a unique pattern of reduced paratabulation which clearly distinguishes it from any other calcareous dinoflagellate cyst described to date. In the following, similarities with a few other Orthopithonella species concerning the cyst wall will be mentioned, that might indicate a closer relationship between O. collaris and those species. The wall characteristics of O. collaris are comparable to those of Orthopithonella duplicata Kohring (1993), which is described from the Valanginian and the K/T boundary. However, the latter species is smaller and without paratabulation. A second comparable species in terms of its wall type, is the double-walled cyst Orthopithonella? globosa Kohring (1993). However, this species does not show unambiguous radial orientation of crystallites. The crystals show a slightly declined orientation in the material of Fütterer (1984), who firstly described the species as Pithonella globosa. The size of ?O. globosa (84-134 µm) is comparable to that of O. *collaris* and it is also restricted to a short period of time ranging from mid-Maastrichtian to early Danian. However, ?O. globosa is described as a strictly spherical form without paratabulation. Orthopithonella aequilamellata Willems (1988) is another spherical species comparable to O. collaris with respect to the cyst diameter, crystal shape and thickness of the double-layered wall. This species, however, also lacks any signs of paratabulation.

Due to its unique paratabulation pattern, *O. collaris* is a distinctly new calcareous dinoflagellate cyst species, and appears to be limited to the narrow stratigraphic interval of the Fish Clay, where it is common. Investigations of more continuous K/T boundary

sections are needed to understand its ecological and stratigraphical significance. This species can be interpreted as being either (i) a morphotype which is formed under environmental stress, or (ii) an invader into the Boreal realm from higher or lower latitudes due to a short-term shift in environmental conditions caused by catastrophic cooling or warming. Brinkhuis et al. (1998) reconstructed a pulse-like northward migration of a Tethyan warm water organic-walled dinoflagellate cyst species during the time of deposition of the Fish Clay. Although such migration of low latitude species might also be hypothesised for calcareous dinoflagellate cyst species, data on the geographic distribution of *O. collaris* would be needed to support this idea. Therefore, the most straightforward interpretation for the short-term occurrence of *O. collaris* in the Fish Clay is that this species represents a paratabulated morphotype formed under specific post-K/T environmental conditions. *O. collaris* is an exotic member of a calcareous dinoflagellate cyst assemblage that probably represents a pioneer flora (**Chapter 4.**).

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## Plate I

- Holotype Fi5c/e4 of *Orthopithonella collaris* sp. nov.; ventral view. Note the characteristically steeper right side of the cingular ridge. Scale bar 30 μm.
- 2) Holotype Fi5c/e4; apically shifted lateral view showing the thick cingular ridge which consists of larger crystals than those on the cyst body. Note the difference in angle between cyst surface and ridge on ventral and dorsal side. Scale bar 30 μm.
- Cyst Fi5c/a1; ventral view. Particularly asymmetric specimen which clearly shows the larger arc of both ridges to the left of the cyst. Scale bar 30 μm.
- Cyst Fi5c/a1; surface crystal pattern, large crystals to the lower left belong to the apical ridge. Scale bar 3 μm.
- Cyst Fi5a/b3; detail of the outer and inner wall showing the smaller size of the inner wall crystals.
   Scale bar 3 µm.
- Cyst Fi5/DS/7; thin section showing the distinct double-layered wall and the cingular ridge. Note the apically flattened cyst shape, the approximate 1:3 ratio of epicyst:hypocyst and the hollow ridge. Polarised light; scale bar 30 μm.



## Plate II

- Holotype Fi5c/e4; apical view. Note the difference in angle between cyst surface and cingular ridge to the right and left of the sulcus (S). Scale bar 10 μm.
- Cyst Fi5/DS/6; antapical view. Note the antapically pointed, slightly asymmetric sulcal ridge. Sulcus points to the upper left. Scale bar 10 μm.
- 3) Cyst Fi5a/e4; laterally tilted apical view showing a round to sub-angular archeopyle. Scale bar 30 µm.
- 4) Cyst Fi5c/e3; ventral view. Note the angular shape of both sulcal and cingular ridge and the larger diameter of the cingular ridge compared to the sulcal ridge, and the approximate 1:3 ratio of epicyst:hypocyst. Scale bar 10 μm.
- 5) Cyst Fg/b4; apically tilted dorsal view (apex pointing to the left). Scale bar 30 µm.
- 6) Cyst Fi5c/a1; lateral view showing the angle between sulcal and cingular ridge (apex pointing to the right). Scale bar 10 μm.




## 6. Conclusions and prospects for future research

Orbitally-forced climate variability appears to have had a major influence on the surface water circulation and on the ecology of c-dinocysts in the mid-Cenomanian European shelf sea. The variations in oceanic circulation are reflected in the sediment by chalk-marl couplets. Two negatively correlated c-dinocyst assemblages can be distinguished. While the Pithonelloideae (p-assemblage) dominate in light layers (chalks), sculptured (paratabulated) species (s-assemblage) are typical for dark layers (marls). Gradual changes in absolute and relative abundance of the cyst species in these assemblages over several couplets depict a bundling pattern which is interpreted to reflect the modulation of the intensity of the precession cycle by the eccentricity cycle (100 ka). The stacking pattern in the natural gamma ray signal and the carbonate and TOC content has the same period and provides lithological proof of the bundling. Bundles are defined by different marl types. Couplets showing the strongest contrast in cyst association are interpreted as bundle boundaries that mark the eccentricity maxima, whereas weakly developed couplets were deposited during eccentricity minima.

A shelf basin circulation model based on a temperature-driven forcing of stratification can explain the observed cyclic changes. While chalks are representative of a well-mixed shelf sea environment, the marls can be interpreted as the sedimentary expression of stratified surface water masses. Reduced oceanic mixing due to low seasonality during strong precession maxima (winter perihelion) at the eccentricity maxima caused periods of thermal water column stratification that led to nutrient depletion and decreased productivity in the surface water masses (e-marls).

Temporal changes in c-dinocyst assemblage can be related to spatial interactions between different facies zones across an ocean-shelf-transect. 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, whereby the individual species show a bathymetry-related zonation. Dominance of *P. sphaerica* in the inner shelf profile indicates continuous mixing related to convective overturning or upwelling. A low frequency of light/dark alternations in the inner shelf section can be interpreted to reflect a reduced effect of orbital forcing on wind-driven surface mixing. Besides Pithonelloideae, *Pentadinellum vimineum* was an important shelf sea species. It

apparently tolerated a wide range of salinity and trophy and preferred warm temperatures, indicating cyclic surface water warming during stratification events.

The conditions on the shelf were contrasting the conditions in the open ocean where more oligotrophic and probably stratified waters prevailed and Pithonelloideae were nearly absent. Orbitally-forced interruptions of mixing on the shelf resulted in cyclic periods of oligotrophy in the surface waters and 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 ingressions during these periods. The c-dinocyst distribution pattern may indicate a gradient of decreasing energy of the ingressions and/or, a gradient of northward decreasing surface water temperature towards the investigated inner shelf section. The species of the oceanic c-dinocyst assemblage, Cubodinellum renei and Orthopithonella ? gustafsonii, were not restricted to the oceanic environment, but also occupied various shelf environments and, therefore, appear to have lived in a broad range of salinity and trophy. While orbitally-forced light/dark sedimentary cyclicity of the shelf sections is mainly related to surface water carbonate productivity changes, 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 following conclusions on the Pithonelloideae ecology can be summarised: Both species did not live in the oceanic environment. *P. sphaerica* (and *P. ovalis* in the outer shelf) are interpreted as indicators of nutrient rich water masses due to their dominance in chalks deposited under eutrophic conditions. Long-term sea level change and high frequent shifts of the preferred facies zones are indicated by Ps/Po-ratio fluctuations in a temporal succession. The modulation of their distribution by surface currents and changes in surface mixing gives new evidence that Pithonelloideae lived planktic. The present review of morphological aspects makes an affinity of Pithonelloideae to the dinoflagellates plausible. 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.

The idea that Pithonelloideae represent a vegetative life stage is supported from a second point of view, when discussing the extinction of Pithonelloideae at the K/T boundary. While apparently all c-dinocyst species seem to indicate survival of their producers, the Pithonelloideae disappeared abruptly. A major advantage of dinoflagellates

to survive stress situations is their ability to form resting cysts that may persist considerable time at the shallow sea floor. The coastal environment with its characteristic species seems to have been a reservoir of cysts that successfully pioneered the post-impact marine environment. However, the Pithonelloideae, obviously did not benefit from such strategy although they lived at appropriately shallow water depths. Their extinction was probably additionally triggered by their disability to migrate into the oceanic realm where niches at deeper water depth or in less affected areas of the globe probably provided shelter for the motile cells. A number of survivor species, particularly *Operculodinella operculata*, likely benefited from a wide spatial distribution in various environments.

Finally, the distribution of paratabulated species in response to cyclic and abrupt environmental changes allows the following conclusions. The most prominent paratabulated species of the Cenomanian, *Cubodinellum renei* and *Pentadinellum vimineum*, are characterised by their temporal and spatial distribution patterns to have been very tolerant species. The newly discovered species *Orthopithonella collaris* with its distinctive paratabulation seems to be restricted in temporal occurrence to the stressed, presumably highly variable environment of the post-K/T Boreal epicontinental sea. The paratabulation of those three species is realised by particularly pronounced ridges that reflect the cingular and sulcal areas of the corresponding motile stages. It might be speculated that for some reasons of adaptation these regions of the dinoflagellate cell, where the flagellae were positioned, were strengthened. It appears as if paratabulation played an important role whenever adaptability was required. *O. collaris* may even be interpreted as a paratabulated morphotype of an otherwise atabulate cyst species. Did *C. renei* and *P. vimineum* also have atabulate counterparts?

The knowledge obtained in the present study can be further improved by future research on the following aspects. The distinctive temporal distribution pattern of c-dinocysts across the Fish Clay, especially the origin and palaeoecology of *O. collaris*, may be related to latitudinal migration events similar to those known from the organic-walled dinoflagellate cysts (Brinkhuis et al., 1998). Studying the marine K/T boundary clay in a wide global area can provide information on such distribution changes.

The results on distribution patterns of c-dinocysts in the European epicontinental sea showed that these microfossils provide a good tool for high-resolution palaeoenvironmental reconstructions. Analyses of their occurrences in a broader range of sedimentary basins would help to refine our understanding of the astronomical forcing of sedimentary cycles in different environmental settings. Comparison of the model of wind-

driven surface mixing (temperature-driven stratification) with the model of runoffcontrolled surface salinity (salinity-driven stratification) shows that the corresponding paths of signal transformation from an orbital constellation via climate variability into the sediment can lead to opposite types of light/dark cyclicity. In the first scenario, a low seasonal temperature gradient (winter perihelion) would decrease wind-driven surface mixing, leading to stratification, decreased nutrient supply to the surface, low productivity and preservation of organic matter, resulting in dark layer deposition. In the second scenario, high seasonal temperature contrast (summer perihelion) is needed to strengthen wind systems and cause increased precipitation, high runoff, eutrophic surface conditions and stable estuarine salinity stratification, again resulting in dark layer deposition. In other words, dark layers at one site can contain indicators of high productivity while dark layers at the other site reflect low productivity, depending on which climatic forcing dominates in different basins. The controversy that exists in correlating Cenomanian chalk/marls of North-western Europe and the Crimean (Young et al., 1998) may be explained by this effect that should be focused on in detail in future studies.

Biostratigraphy has reached a high degree of resolution for many sections particularly of Cenomanian age (Ditchfield, 1990). It appears a promising approach to use this resolution in combination with the equally detailed cyclostratigraphic time scale (Gale et al., 1999) to study lateral distribution patterns of c-dinocyst in extremely narrow time spans and obtain Cretaceous biogeographic data comparable in resolution to surface sediment investigations in the Recent. The reconstruction of palaeo-current patterns in the Cretaceous would benefit from such an approach.

The successful application of c-dinocysts in the reconstruction of palaeoenvironmental changes in the Cretaceous encourages further studies of their distribution patterns in cyclic sequences of different periods of time. Their high tolerance and the survival potential of catastrophes make c-dinocysts a promising tool in the study of events, when other organisms experienced substantial extinction that disables comparison of pre- and post-event-assemblages.

Interdisciplinary studies that combine harmonic science, astronomy and geology should be improved in order to fully understand the harmonics present in sedimentary cycles. Countless studies in the present days, including this thesis, have put emphasis on orbital forcing, which certainly provides plausible mechanisms to cause variability of processes that influence sedimentation. However, the role of long-term solar cycles has been previously under-estimated and evidence is growing that they played an important role in creating Pleistocene/Holocene climate cyclicity (e.g. Gauthier, 1999; Perry and Hsu, 2000). Thus, it appears an exciting field for future studies to find out whether solar cycles caused light/dark cycles in the further past. Cyclicity is found in almost all processes in the universe and all the various cycles, be it orbital changes, solar cycles or even galactic cycles, are parts of a concert of harmonics which we have yet to discover.

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## Curriculum vitae; international presentation of this thesis

Jens Wendler was born in Apolda, Germany, on the 30<sup>th</sup> of Juli 1970. From 1991 to 1997, he studied Mineralogy and Geology at the TU Bergakademie Freiberg. His Diploma thesis, under supervision of Prof. Dr. J. Schneider (Division of Palaeontology and Stratigraphy), dealt with the investigation of the sequence stratigraphy, micropalaeontology and diagenetic evolution of Permian carbonates of the Southern Permian Basin and was part of an industrial research project of the Erdöl – Erdgas Gommern GmbH. From June 1997 to 2001, Jens Wendler was involved in the research project "Cycle architecture and integrated stratigraphy" at the University of Bremen, supervised by Prof. Dr. H. Willems (Division of Historical Geology and Palaeontology) and wrote the present PhD thesis. Results of this project were published as talk- and poster presentations at the following international conferences:

- 7<sup>th</sup> Conference of the International Nannoplankton Association, Puerto Rico, 1998
- 6<sup>th</sup> International Conference on Modern and Fossil Dinoflagellates, Trondheim, 1998
- Geo-Berlin '98, Berlin, 1998
- 19th Regional European Meeting of Sedimentology IAS, Copenhagen, 1999
- Spring Meeting Astronomische Gesellschaft & Deutsche Geologische Gesellschaft; Asteroids, Meteorites, Impacts and their Consequences, Nördlingen, 2000
- Conference on Catastrophic Events and Mass Extinctions, Vienna, 2000 (*Chapter 4 of this thesis appears in the Proceedings of this Conference*)
- 6<sup>th</sup> Cretaceous Symposium, Vienna, 2000
- 8<sup>th</sup> Conference of the International Nannoplankton Association, Bremen, 2000.