

# Calcareous dinoflagellates from the Late Hauterivian (Early Cretaceous) of Frielingen, Germany

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## Abstract

A pale–dark bedded claystone–marlstone succession of Late Hauterivian age (*Simbirskites discofalcatus* ammonite Zone, Early Cretaceous), exposed in the clay-pit Frielingen, Germany (Lower Saxony Basin), was investigated with respect to its calcareous dinoflagellate cyst content. This study aimed at a better understanding of the usefulness of calcareous dinoflagellate cysts to reconstruct palaeoenvironments, and an evaluation of the postulated palaeoenvironmental trends associated with Lower Cretaceous pale–dark bedding rhythms. The ratio of abundant taxa, character traits of cysts, and the results of statistical species analyses were used for that study. Current models of sea level fluctuations and sea surface temperature were modified on the basis of the composition of calcareous dinoflagellate assemblages. Superimposed on a general sea level rise, a regressive interval with high sea surface water temperatures is reflected by the thick bed 118. This distinctively warm interval is represented by a dark bed, which are commonly interpreted to indicate cooler surface waters. It is therefore necessary to review the palaeoenvironmental interpretation of pale–dark bedding rhythms of claystone successions of the Boreal Realm. Factors other than sea surface temperature seem to be important as well.

The species *Pirumella edgarii* was found to favour time intervals with higher sediment input. The newly described species *Pirumella?* sp. nov. may perhaps indicate similar environments in warmer water masses. The species *Pirumella tanyphloia* has been emended, we suggest

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including it in *Pirumella multistrata* forma *tanyphloia*. Moreover, the pithonelloid cysts found in Frielingen are currently the oldest of their kind.

**Keywords:** Lower Saxony Basin, Late Hauterivian, Calcareous dinoflagellate cysts

<b>Content</b>	<b>Page</b>
1 Introduction	242
2 Material and methods	245
2.1 Material	245
2.2 Sample preparation	246
2.3 Data analysis	247
3 Results	248
3.1 Systematic palaeontology	248
3.2 Assemblage of calcareous dinoflagellate cysts in the clay-pit Frielingen	249
4 Discussion	254
4.1 Assemblage of calcareous dinoflagellate cysts in Frielingen	256
4.1.1 Current knowledge about ecological preferences of calcareous dinoflagellate cysts and the environment represented by pale–dark bedded Cretaceous sediments	257
4.1.2 Interpreting the palaeoenvironment on the basis of calcareous dinoflagellate cysts in Frielingen	258
4.2 Morphology of calcareous dinoflagellate cysts in Frielingen	261
5 Conclusions	263
Acknowledgements	263
References	264
Plates	270

## **1 Introduction**

The taxon Dinoflagellata (BÜTSCHLI, 1885) FENSOME et al., 1993 is a highly diverse lineage of mainly unicellular, alveolate eukaryotes. Many dinoflagellates have the ability to build resting cysts, the only form in which these protists are documented in the fossil record. The cysts are either formed during times of unfavourable environmental conditions or for reproductive purposes (BELOW, 1987; DODGE & LEE, 2000). In the latter case, two different types of cysts can be distinguished: (1) cysts built during asexual reproduction and (2) cysts used for sexual reproduction (BELOW, 1987). According to TAYLOR et al. (2008), approximately 15 per cent of the extant taxa produce resting cysts during sexual reproduction, forming the majority of the cysts documented in the fossil record (BELOW, 1987; DALE, 1983). The cyst walls consist either of dinosporine or calcite (DODGE & LEE, 2000; TAYLOR et al., 2008).

The oldest possible calcareous dinoflagellate cysts were described from the Late Triassic (JANOFKSKE, 1992; JANOFKSKE & KEUPP, 1992). Calcispheres described by SERVAIS et al. (2009) from the Silurian are of doubtful affinity to the dinoflagellates. A phylogenetic approach by GOTTSCHLING et al. (2008) calculated Late Jurassic divergence times for the calcareous dinoflagellates. The time of origin of the Dinoflagellata in general is problematic, but is thought to be of Proterozoic/early Palaeozoic (chemical markers found by MENG et al.,

2005; MOLDOWAN & TALYZINA, 1998; PRATT et al., 1991) or Triassic age (BERNEY & PAWLOWSKI, 2006; FENSOME et al., 1996; MOCZYDŁOWSKA et al., 2011).

Calcareous dinoflagellate cysts are characterized by cyst walls composed of calcite. Taxonomically they are included in the taxon *Thoracosphaeraceae* (SCHILLER, 1930) due to evidence for a monophyletic relationship with the extant species *Thoracosphaera heimii*, which develops calcareous coccooid cells (TANGEN et al., 1982). An exception is the taxon ‘Pithonelloideae’ (set in inverted commas hereafter because the validity of the monophyletic nature of the taxon is heavily disputed), a group that has long been included in calcareous dinoflagellate cysts (compare KEUPP, 1987). FENSOME et al. (1993) objected a close relationship between ‘Pithonelloideae’ and other calcareous dinoflagellate cysts, and other authors argue against the possibility that they are dinoflagellate cysts or even dinoflagellates (e.g. STRENG, 2003; STRENG et al., 2009; STRENG et al., 2004; VERSTEEGH et al., 2009). Despite the fact that the ‘Pithonelloideae’ may not even represent a monophylum, WENDLER et al. (2002a) suggested that some of them might comprise coccooid cells homologue to *T. heimii*. Recently, WENDLER & BOWN (2013) also provided evidence that ‘Pithonelloideae’ may yet be strongly recrystallized calcareous dinoflagellate cysts. With these taxonomic problems in mind, the ‘Pithonelloideae’ observed in the samples of the Frielingen section were included in our analyses.

Apart from studies that focus on taxonomic aspects of the calcareous dinoflagellate cysts (e.g. KEUPP, 1981, 1987; KEUPP & MUTTERLOSE, 1984; KOHRING, 1993; REHÁKOVÁ & MICHALÍK, 1996), several authors tried to interpret assemblages of calcareous dinoflagellate cysts with respect to their palaeoenvironmental implications (e.g. ESPER et al., 2000; KEUPP, 1991, 1993, 2001; KEUPP & KOWALSKI, 1992; KOHRING et al., 2005; MONNET, 1993; NEUMANN, 1999; WENDLER et al., 2002a, b). Both taxonomic and palaeoecological interpretations are getting complicated due to a variety of problems described hereafter. Following early studies of calcareous dinoflagellate cysts, two different approaches have been established. Cysts preserved in limestones were investigated using thin sections and a polarisation microscope (e.g. VOGLER, 1941; WANNER, 1940). Isolated cysts from soft rocks were investigated via a scanning electron microscope (SEM) (e.g. ANDRI & AUBRY, 1973; BANNER, 1972; BOLLI, 1974). These two approaches caused different systematic assignments for presumably the same taxa of calcareous dinoflagellate cysts. For a detailed description and comparison of both systematic catalogues see KEUPP et al. (1992). A systematical approach for calcareous dinoflagellate cysts based on the orientation of the crystals in the cyst walls was suggested by KEUPP (1987) and extended by JANOFKSKE (1992) and KOHRING (1993). Other taxonomic systems introduced used the morphology of the archaeopyle (STRENG et al., 2004) or morphological rankings (KEUPP, 1991).

None of these latter taxonomic approaches could be applied here, because the cysts from the Lower Cretaceous neither show complex archaeopyles nor an extensive paratabulation. For our studies, we therefore used a system purely based on cyst wall morphology. Specimens with strictly radially oriented crystals are assigned to the radial group. Since our SEM images did not enable us to measure the crystallographic c-axis of the wall crystals, this group could theoretically include the former subfamilies *Orthopithonelloideae* (KEUPP, 1987) and *Fuetterelloideae* (KOHRING, 1993). The occurrence of specimens of the latter group,

however, is highly unlikely, because they have not yet been found in pre-Cenozoic sediments.

To the pithonelloid group are assigned all specimens with consistently oblique wall crystals, which are all oriented in the same direction. The oblique group contains all specimens with wall crystals that are not ordered in any particular pattern (former *Obliquipithonelloideae* (KEUPP, 1987)).

This method suffers from the problem that different actual species of dinoflagellates may have produced morphologically similar looking cysts thus representing ecophenotypes (hereafter called morphotypes). Consequently, we will only use those descriptive terms in our work, and refer to the old taxonomical subfamilies only where they are required when referring to earlier works.

An additional taxonomical problem arises with the former genus *Orthopithonella*, which was revised by STRENG et al. (2002) and meanwhile only contains the species *Orthopithonella gustafsonii*. All other species of the genus mentioned in this work are therefore marked with question marks behind the genus name, to indicate their uncertain assignment.

The unclear biological subdivision of the calcareous dinoflagellate cysts into subordinated taxa, however, offers one advantage. Investigations by MONNET (1993) revealed that *Orthopithonelloideae* are likely able to actively control the pattern of their cyst walls, but the ultrastructure of the cyst walls of the *Obliquipithonelloideae* is heavily influenced by environmental factors. Different morphotypes of calcareous dinoflagellate cysts are therefore likely to be indicative of different palaeoenvironments. It was suggested that radial forms favour more pelagic sea regions (KEUPP, 1992, 2001; KOHRING, 1993; WENDLER et al., 2002a), although some morphotypes (i.e. *Echinodinella* spp. and *Orthopithonella? porata*) may indicate eutrophic neritic environments (NEUMANN, 1999). ‘Pithonelloideae’ are thought to characterize shelf environments (DIAS-BRITO, 2000; WENDLER et al., 2002a), or transgressive phases (ZÜGEL, 1994); *Pithonella ovalis* indicates a more distant shelf than *Pithonella sphaerica* (WENDLER et al., 2002a). ‘Pithonelloideae’ and *Heptasphaera michaelii* are furthermore taxa known from the Tethys, and therefore indicate Tethyan influxes (KEUPP, 1993). Oblique morphotypes with coarse wall crystals, and *Praecalzigonellum* spp. have been interpreted as cold water indicators (KEUPP, 1991, 2001). Fine crystalline oblique forms, especially *Pirumella multistrata* forma *excentrica*, and *Echinodinella* spp. might indicate the presence of warmer water masses (KEUPP, 1981, 1992, 1993).

All the aforementioned studies only investigated calcareous dinoflagellate cysts in certain areas and time slices. Little is known about the applicability of those ecological preferences of morphotypes of calcareous dinoflagellate cysts across wider spatial and temporal ranges. Nevertheless, a more thorough understanding of the applicability of calcareous dinoflagellate cysts is necessary, if the group should be applied as a palaeo-proxy in the future. Since the pale-dark bedding in the Lower Cretaceous sediments of northern Germany is often attributed to changes in the palaeoenvironment (MUTTERLOSE & RUFFELL, 1999), we hypothesize that assemblages of calcareous dinoflagellate cysts should differ between pale and dark beds in such successions. Consequently, we use the assemblage of calcareous dinoflagellate cysts in Upper Hauterivian sediments from the clay-pit Frielingen to test that hypothesis, and try to use them to reconstruct basic trends of the local palaeoenvironment.

## 2 Material and methods

### 2.1 Material

The clay-pit, from which the samples were collected bed-by-bed, is situated about 20 km northwest of Hanover (Germany), approximately 2 km northwest of the village Frielingen (52°28'46.02" N, 09°30'33.20" E) (Fig. 1). Detailed descriptions of the succession were given by MUTTERLOSE (1984), MUTTERLOSE (1998), and MUTTERLOSE & RUFFELL (1997). Situated in the central part of the Lower Saxony Basin, the southernmost extension of the North Sea Basin (ZIEGLER, 1990), the sediments were deposited in vicinity to Rheno-Bohemia to the south and to the Pompeckj Block to the north (Fig. 2). Floral and faunal exchanges with the Tethys became possible in the middle and latest Hauterivian via the Carpathian Seaway to the east (MUTTERLOSE et al., 1998).

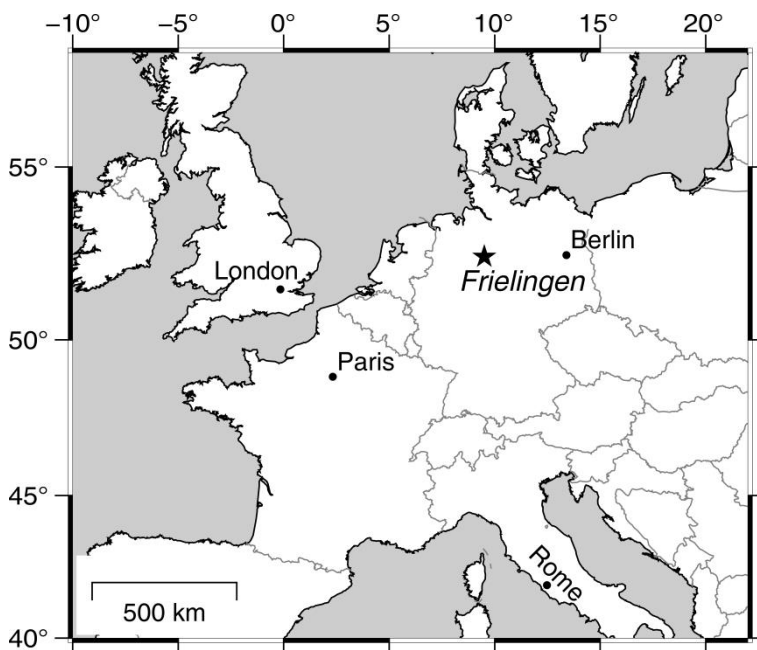


Fig. 1: Location of the clay-pit Frielingen (star) in Germany and northern Europe.

In Frielingen, rhythmically pale–dark bedded (22 rhythms altogether) claystones and marlstones of the *Simbirskites discofalcatus* ammonite Zone (upper Hauterivian) are exposed. These strata represent the topmost unit of Hauterivian sediments and of the regionally so-called *Simbirskites* Beds, which in turn belong to the informal unit of the Clay–Marl Alternating Sequence—an official formation name has not yet been assigned to these strata. The pale beds show thicknesses of about 10–30 cm (MUTTERLOSE, 1984) and are characterized by relatively high carbonate contents of 12–53 per cent and lower  $C_{org}$ -values than the adjacent dark layers (MUTTERLOSE, 1998; MUTTERLOSE & RUFFELL, 1997). The dark beds are generally thicker (MUTTERLOSE, 1984) and contain only 5–23 per cent of  $CaCO_3$ . Thin (10–20 cm) and seemingly continuous layers of calcareous nodules are common throughout the sequence and those nodules appear to be larger in the pale beds (MUTTERLOSE, 1984). Furthermore, the sediment contains pyrite nodules and pyritised burrows of unknown assignment together with ichnofossils of the genera *Chondrites*, *Planolites*, and *Thalassinoides*.

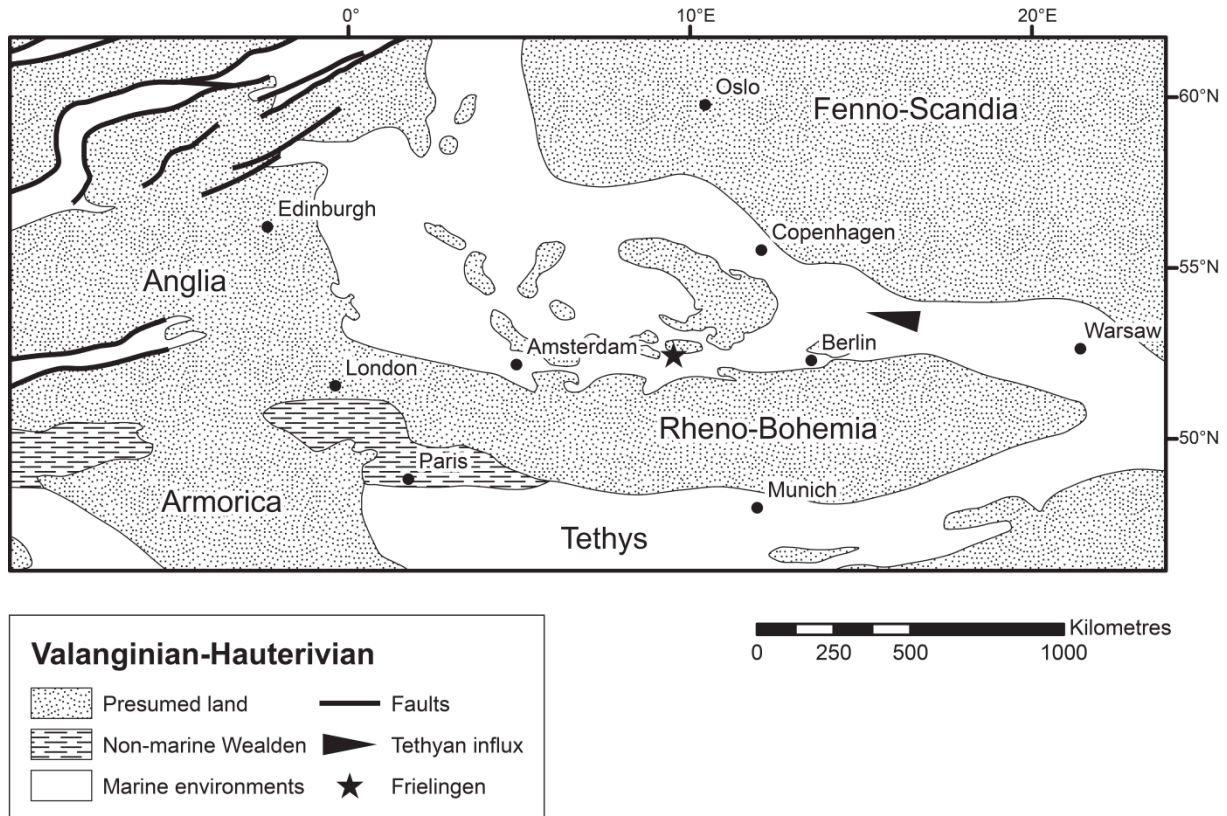


Fig. 2: Palaeogeographic position of the clay-pit Frielingen during Valanginian–Hauterivian times between Rheno-Bohemia (to the south) and the Pompeckj Block (to the north). Tethyan influx occurred several times via the Carpathian Seaway to the east. Redrawn and modified from MUTTERLOSE (1997, fig. 7).

## 2.2 Sample preparation

MUTTERLOSE (1984) established a bed numbering for the clay-pit Frielingen, in which even numbers represent dark beds and odd numbers represent pale beds, respectively. The 25 samples investigated in this study were taken from the lowermost part of the succession, from the beds 101, 102, and 106–119. Samples are not evenly spaced and some thicker beds are represented by more than one sample (Fig. 3). The samples were suspended in tap water and washed through a 20  $\mu\text{m}$  mesh using tap water. The sieved sample-fraction  $>20 \mu\text{m}$  was dried, and calcareous dinoflagellate cysts were picked using a stereomicroscope with a max. magnification of 100 $\times$ . In general 100–200 cysts per sample were picked, however, some samples yielded less abundant assemblages. The cysts were mounted on aluminium stubs of about 1 cm in diameter using adhesive carbon pads, and sputtered with gold. The cysts were then studied with an SEM, using either a Cambridge Instruments Stereoscan 360 or a Zeiss Supra 40VP. After a first investigation of the cysts' exterior surfaces, most of the cysts were cracked with a needle under the stereomicroscope, gold-covered again, and once more investigated with the SEM to obtain information about their wall-structure. A total of 3196 cysts was examined and their morphotype was determined. Furthermore, the cyst-size, number of wall layers, and thickness of each wall was measured. All material is stored at the Freie Universität Berlin, Germany.

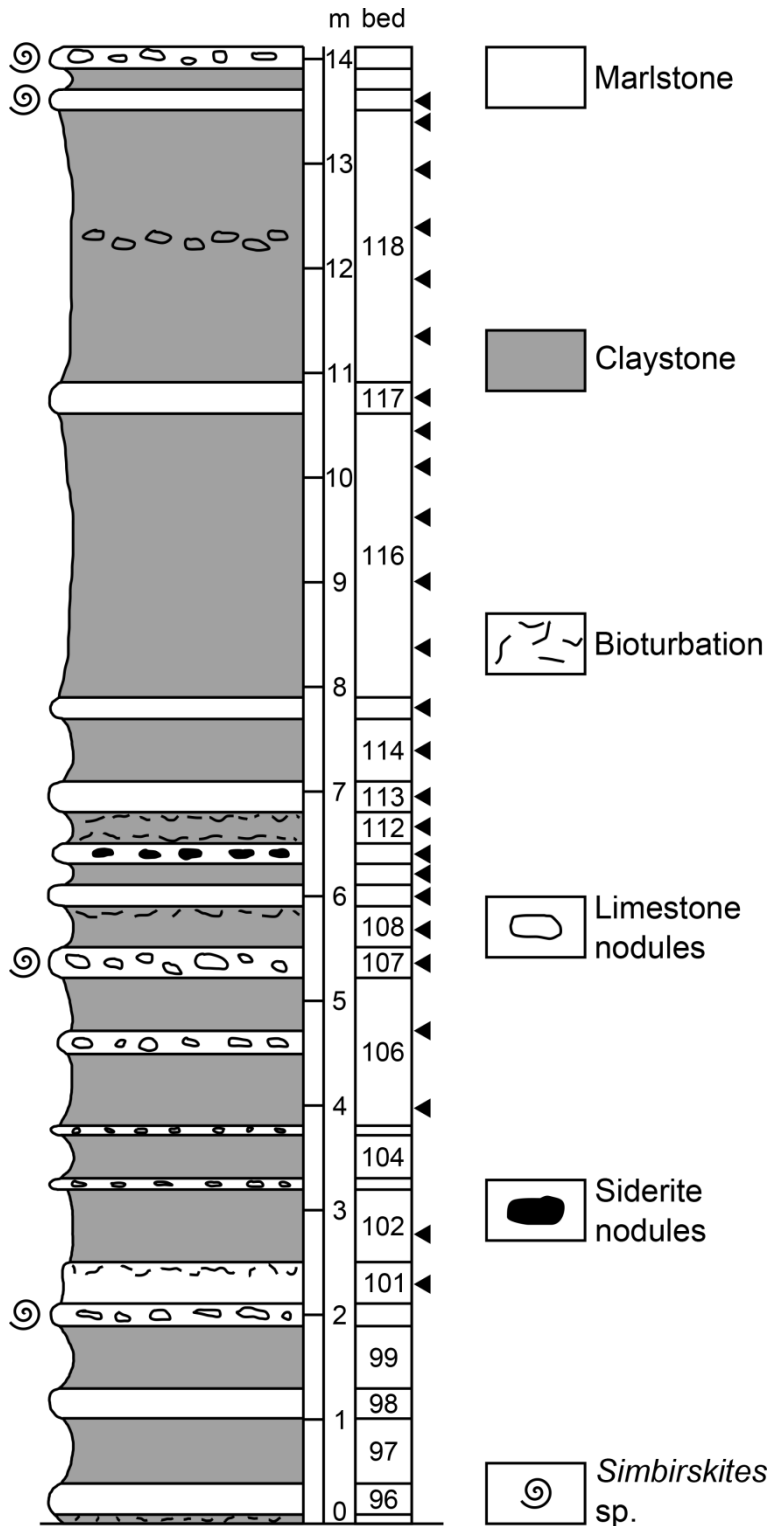


Fig. 3: Lithology of the lower parts of the succession of the clay-pit Frielingen. This part of the section belongs to the *Simbirskites discofalcatus* ammonite Zone, and occurrences of that ammonite genus are indicated in the figure. The solid black triangles to the right of the bed numbering mark the position of the samples (101/1 to 119/1) that were investigated in this work. Based upon MUTTERLOSE & WIEDENROTH (2009, fig. 3).

### 2.3 Data analysis

Relative abundances of the different morphological groups and morphotypes, the sizes of selected morphotypes, number and thickness of wall layers, and the abundances of morphotypes with coarse and fine wall crystals were analysed with respect to their palaeoenvironmental implications. All raw data are available via <http://www.pangaea.de/> (doi:10.1594/PANGAEA.816314). Confidence intervals for morphotype abundances were calculated using approaches proposed for multinomial proportions (HESLOP et al., 2011; HOU et al., 2003). Confidence intervals for median cyst sizes were calculated on the basis of

the Binomial distribution (CONOVER, 1980). Statistical tests, as implemented in the software PAST (HAMMER et al., 2001) were applied in order to further emphasize ecological signals in the assemblages. The Shannon–Wiener Index  $H' = \sum p_i \ln p_i$  (with  $p_i$  as proportion of morphotype  $i$ ) was used to calculate the diversity of the assemblage of calcareous dinoflagellate cysts per sample (SHANNON & WEAVER, 1949). On the basis of the diversity, Pielou's Equitability (normalized for species richness)  $J = H'/H_{max}$  was calculated to assess the evenness of the assemblage (PIELOU, 1977). Another parameter of interest was the similarity between samples of pale and dark beds, respectively. The Morisita Similarity Index  $MO$  was used for that purpose, for it is normalized for absolute abundances and robust against changing sample size (MORISITA, 1959). The difference in morphotype composition between pale and dark beds was calculated using ANOSIM (CLARKE, 1993; LEGENDRE & LEGENDRE, 1998).

### 3 Results

#### 3.1 Systematic palaeontology

Dinoflagellata (BÜTSCHLI, 1885) FENSOME et al., 1993

Dinokaryota FENSOME et al., 1993

Dinophyceae PASCHER, 1914

Peridiniphycidae FENSOME et al., 1993

Peridinales HAECKEL, 1894

*Pirumella?* sp. nov.

Plate 1

*Holotype.* Cyst 118.5b-133, (cracked), (Plate 1A), SEM micrographs 'Frielingen 118.5b\_153.tif', 'Frielingen 118.5b\_154.tif'.

*Paratypes.* Cysts 118.2-96, 118.4c-5, and 118.5b-102, (cracked), (Plate 1B–E).

*Repository.* The material is stored at the Freie Universität Berlin, Institut für Geologische Wissenschaften, Malteserstr. 74–100, 12249 Berlin, Germany. Cysts were cracked according to the normal designation procedure, but fragments are still on the SEM stubs and can be investigated.

*Type locality and type horizon.* Clay-pit near Frielingen, northeast of Hanover (Lower Saxony Basin), Germany; Late Hauterivian, *Simbirskites discofalcatus* ammonite Zone.

*Diagnosis.* Ovoid cyst with mean diameter of 31.10  $\mu\text{m}$  (27.77–34.42  $\mu\text{m}$ ). Outer wall composed of coarse, radially arranged crystals (length:width ratio = 2:1), average thickness c. 1.2  $\mu\text{m}$ . Inner wall very thin (0.2–0.6  $\mu\text{m}$ ).

*Description.* The investigated samples contained 27 cysts of this morphotype, most of which were discovered in bed 118. The cysts of that morphotype are mostly slightly ovoid in shape. They are between 28.86 and 41.00  $\mu\text{m}$  in average diameter (average: 32.83  $\mu\text{m}$ ). The outer



wall consists of strictly radially arranged crystals. The crystals are relatively coarse and show a length:width ratio of approximately 2:1. The outer wall is between 0.85 and 1.66  $\mu\text{m}$ , in average 1.23  $\mu\text{m}$  thick. An inner wall layer is mostly, but not always, developed. If it is present, it is always much thinner than the outer wall layer: 0.18–0.59  $\mu\text{m}$ , on average 0.34  $\mu\text{m}$ . The microstructure of the inner wall can therefore hardly be determined. Generally the crystals in the inner wall seem not to be strictly radially arranged. In at least one specimen the inner wall seems to be composed of larger, radially arranged crystals with an approximated length:width ratio of 1:1, but this could be the result of recrystallization.

*Remarks.* Due to the fact that the inner wall is very thin, its microstructure could not be investigated thoroughly. It seems that the inner wall is composed of arbitrary arranged crystals, what would put that morphotype in close vicinity to the genus *Ruegenia* (compare KEUPP et al., 1992; WILLEMS, 1992). This, however, cannot be confirmed without doubt. *Pirumella?* sp. nov. resembles *Ruegenia hadra* KEUPP et al., 1992, but is distinguished from it by the smaller size, the thinner outer wall layer, and the much thinner or even missing inner wall layer. Due to these uncertainties, in combination with the current overturn in taxonomy of calcareous dinoflagellate cysts, the species is described in open nomenclature.

Peridinales HAECKEL, 1894

*Pirumella* (BOLLI, 1980) STRENG et al., 2009

*Pirumella multistrata* forma *tanyphloia* (KEUPP & MICHAEL, 1979) comb. nov.

- 1979 *Pithonella tanyphloia* sp. nov.; KEUPP in KEUPP & MICHAEL, pp. 29–30, plate 6 (figs 1–8).
- 1984 *Obliquipithonella tanyphloia* (KEUPP in KEUPP & MICHAEL, 1979) comb. nov.; KEUPP & MUTTERLOSE, p. 160, plate 22 (figs 4–8).
- 1993 *Pirumella tanyphloia* (KEUPP in KEUPP & MICHAEL, 1979) comb. nov.; LENTIN & WILLIAMS, p. 522.

*Remarks.* KOHRING (1993) introduced a taxonomy to describe species of the genus *Pirumella* (e.g. *Pirumella excentrica*, *Pirumella patriciagreelayae*), which was named *Obliquipithonella* at that time, as formae of *Pirumella multistrata*. According to these interpretations, species which show only minor deviations of a common structure should be seen as a variety of the same species. KOHRING (1993) therefore combined several fine-crystalline oblique species as formae of *Pirumella multistrata*, as they all show the same characteristics with an outer wall composed of fine, obliquely arranged crystals and a fine crystalline inner wall layer. Following this approach we handle the former species *Pirumella tanyphloia* in the same way, since it represents specimens of *Pirumella multistrata* with very thin outer walls.

### 3.2 Assemblage of calcareous dinoflagellate cysts in the clay-pit Frielingen

A total of 32 morphotypes of calcareous dinoflagellate cysts were found in the samples studied (Table 1). Information about these taxa can be obtained from various publications (e.g. KEUPP, 1981; KOHRING, 1993; ZÜGEL, 1994). We want to add, however, some

information on how selected taxa have been treated in this study: *Praecalcionellum mutterlosei* is characterized by a crooking of the sulcus in the cingular region, which cannot be observed when the cyst is mounted on the stub unfavourable. Although to our best knowledge no other species of *Praecalcionellum* has yet been found in sediments of the Hauterivian, we assigned specimens in which the sulcus is not clearly visible to *Praecalcionellum* cf. *mutterlosei*. *Pirumella* aff. *carteri* and *Pirumella* aff. *mcnightii* represent cysts of different morphotypes, in which the outer wall layer had been removed, so that they have a very low taxonomical and analytical value due to their nature as damaged cyst. *Pirumella multistrata* forma *patriciagreeleyae* is further subdivided into two types. In type A, the overgrowing crystals do not exceed the surface area of five or six base crystals, while in type B the cyst surface is overgrown by much larger crystals (KEUPP, 1992). *Pirumella robinsonii* is similar to *P. multistrata* forma *patriciagreeleyae* type B, but in the former morphotype the large surface crystals cover only a small area of the surface area. For consistency, in this study cysts were designated as *P. robinsonii* when the large crystals covered less than 50 per cent of the cysts' surface. It is nevertheless recommended to abandon the morphotype *P. robinsonii* in favour of *P. multistrata* forma *patriciagreeleyae* type B in the future.

The oblique group is the most abundant group of calcareous dinoflagellate cysts in the succession (Fig. 4). Their proportion of the assemblage never drops below 68 per cent and they occur in high abundances in the upper part of the section (despite a considerable decrease between samples 118/5 and 119/1). In the lowermost part of the section, however, the oblique group is partly replaced by high numbers of radially crystalline cysts (up to about 30 per cent in sample 107/1). After a decline of the radial group in sample 108/1, their amount increases subsequently until it reaches nearly 20 per cent in sample 119/1. The pithonelloid group becomes more abundant in the dark beds 102/1 (1 per cent), 106/2 (2 per cent), and 108/1 (9 per cent); though they are completely absent in the pale beds in between. After that interval there are only minor peaks in the abundance of pithonelloid cysts, with the most pronounced one in sample 116/1 (about 4 per cent).

*Echinodinella levata* is abundant in the lower part of the section and reaches peak abundances of more than 13 per cent in sample 102/1 (Fig. 5), after that, *E. levata* only sporadically appears as an accessory part of the flora. *Praecalcionellum mutterlosei* and *P. cf. mutterlosei* reach a maximum abundance shortly afterwards in sample 107/1, after that they occur only sporadically. *Pirumella?* sp. nov. is rare in samples other than those of bed 118 (though small peaks occur in samples 106/2, 110/1, and 116/4). The abundance of *Pirumella?* sp. nov. grows from sample 118/1 (nearly 1 per cent) to 118/2 (about 3.6 per cent). In sample 118/3 the abundance drops and the morphotype is absent in sample 118/4. Sample 118/5 shows a peak value in the proportion of *Pirumella?* sp. nov. (more than 7 per cent), before the morphotype is absent in sample 119/1.

For the oblique group, *P. multistrata* forma *patriciagreeleyae*, *Pirumella sheilasantawae*, and *Pirumella thayerii* are abundant in the lower part of the section (up to sample 116/1). From sample 111/1 to the top they are accompanied by *Pirumella pachystrata* (Figs 6, 7). *Pirumella loeblichii* also shows peak abundances in the lower part of the section. This morphotype is, together with *Pirumella multistrata* forma *tanyphloia* comb. nov., furthermore abundant in bed 116. *Pirumella multistrata* forma *excentrica* shows a bimodal distribution. A first interval of higher abundance occurs in samples 111/1–115/1, followed by a drop in bed 116 and a

pronounced bloom in bed 118. *Pirumella edgarii* is present throughout the complete succession, but both of the thicker dark beds 116 and 118 show particularly large amounts of that morphotype (Fig. 7).

Table 1: List of morphotypes of calcareous dinoflagellate cysts found in the samples from the clay-pit Frielingen.

MORPHOTYPE	SAMPLE
<b>Radial group</b>	
<i>Orthopithonella</i> aff. <i>gustafsonii</i> (BOLLI, 1974)	113/1, 114/1, 116/1, 117/1
<i>Orthopithonella?</i> <i>porata</i> (KEUPP, 1982)	101/1–106/2, 111/1, 114/1–116/2, 116/4, 116/5, 118/1–118/3, 118/5, 119/1
<i>Orthopithonella?</i> cf. <i>compsa</i> (KEUPP, 1982)	102/1, 106/1, 116/1
<i>Praecalcionellum mutterlosei</i> (KEUPP in KEUPP & MICHAEL, 1979)	101/1–107/1, 116/3, 118/1, 118/2, 118/4, 119/1
<i>Praecalcionellum</i> cf. <i>mutterlosei</i>	102/1, 106/1, 107/1, 109/1, 116/2, 116/4, 116/5, 118/1, 118/2, 118/4–119/1
<i>Echinodinella levata</i> (KEUPP, 1981)	101/1–106/1, 108/1, 110/1, 117/1
<i>Keuppisphaera</i> sp.	118/4
<i>Pirumella?</i> sp. nov.	106/2, 110/1, 116/4, 118/1–118/3, 118/5
<b>Oblique group</b>	
<i>Pirumella multistrata</i> (PFLAUMANN and KRASHENINNIKOV, 1978)	101/1–119/1
<i>Pirumella</i> cf. <i>multistrata</i>	101/1–107/1, 109/1–119/1
<i>Pirumella multistrata</i> forma <i>tanyphloia</i> (KEUPP in KEUPP & MICHAEL, 1979) comb. nov.	101/1–106/1, 108/1–111/1, 113/1–117/1, 118/2, 119/1
<i>Pirumella multistrata</i> forma <i>excentrica</i> (KEUPP, 1979)	106/2–116/3, 116/5–119/1
<i>Pirumella quiltyi</i> (BOLLI, 1974)	101/1–119/1
<i>Pirumella pachystrata</i> ZÜGEL, 1994	101/1, 107/1, 109/1, 111/1–116/2, 117/1, 118/1
<i>Pirumella robinsonii</i> (BOLLI, 1974)	101/1–106/2, 113/1, 114/1, 116/1, 116/2, 118/3–118/5
<i>Pirumella multistrata</i> forma <i>patriciagreeleyae</i> (BOLLI, 1974)	101/1–116/1, 116/4–118/2, 118/4–119/1
<i>Pirumella thayerii</i> (BOLLI, 1974)	101/1, 106/1–114/1, 116/1–118/1, 118/4, 119/1
<i>Pirumella echinosa</i> (KEUPP, 1982)	106/1
<i>Pirumella</i> aff. <i>carteri</i> (BOLLI, 1974)	101/1–108/1, 110/1–118/5
<i>Pirumella loeblichii</i> (BOLLI, 1974)	101/1–119/1
<i>Pirumella strobila</i> (KEUPP in KEUPP & MICHAEL, 1979)	101/1–106/1, 109/1–111/1, 113/1, 116/2–116/4, 118/2, 118/4, 118/5
<i>Pirumella spinosa</i> (KEUPP in KEUPP & MICHAEL, 1979)	102/1, 107/1, 109/1, 111/1, 113/1, 116/4, 117/1, 118/2, 118/3
<i>Pirumella sheilasantawae</i> (BOLLI, 1974)	102/1, 106/1, 107/1–112/1, 115/1, 117/1, 118/2–119/1
<i>Pirumella edgarii</i> (BOLLI, 1974)	102/1–106/2, 110/1, 111/1, 113/1, 114/1, 116/1–116/5, 118/1–118/5
<i>Pirumella</i> cf. <i>sphenifera</i> (KEUPP, 1987)	102/1–106/2, 114/1, 116/1, 116/4–118/2
<i>Pirumella</i> aff. <i>mcnightii</i> (BOLLI, 1974)	102/1, 106/1, 108/1, 113/1, 114/1, 116/1, 116/2, 116/4, 118/2, 118/3, 118/5
<i>Bicarinellum calvum</i> (KEUPP in KEUPP & MICHAEL, 1979)	113/1, 117/1, 118/1
<i>Bicarinellum cristatum</i> KEUPP, 1982	113/1
<i>Heptasphaera michaelii</i> (KEUPP in KEUPP & MICHAEL, 1979)	101/1, 102/1, 111/1, 113/1, 116/3, 117/1, 118/4
<i>Alasphaera tuberculata</i> (PFLAUMANN & KRASHENINNIKOV, 1978)	110/1
<b>Pithonelloid group (Plate 1)</b>	
<i>Pithonella sphaerica</i> (KAUFMANN, 1865)	106/2, 108/1, 116/1, 118/4
<i>Pithonella ovalis</i> (KAUFMANN, 1865)	102/1, 106/2, 108/1, 111/1, 116/1, 118/2, 118/3

Moreover, in both of the thick beds the abundance of *P. edgarii* is low at the beginning (samples 116/1 and 118/1, respectively), gradually increases, and reaches the highest values in the uppermost samples 116/5 and 118/5 (Fig. 7).

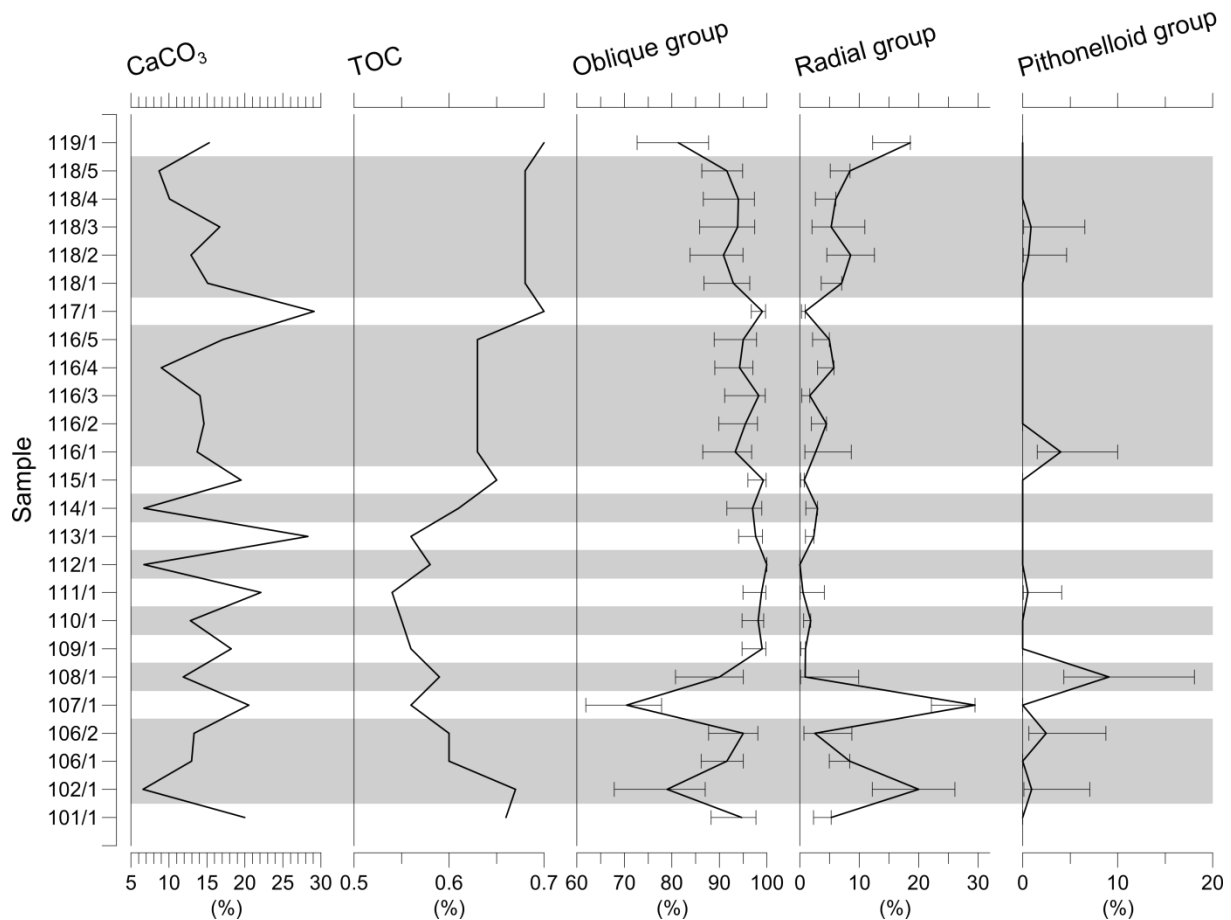


Fig. 4: Proportions of cysts of the radial group, oblique group, and pithonelloid group throughout the section in the clay-pit Frielingen. Values for  $\text{CaCO}_3$  and total organic carbon (TOC) according to MUTTERLOSE & RUFFELL (1997). Grey shades indicate dark beds.

*Pirumella quiltyi* is the most abundant taxon in the succession, with average proportions of over 30 per cent and a minor preference for pale beds. Above sample 118/1, the abundance of *P. quiltyi* decreases rapidly, and never again exceeds 4 per cent. *Pirumella echinosa* is restricted to sample 106/1. *Bicarinellum calvum* only appears in samples 113/1, 117/1 and 118/1, always in low abundances. One cyst of *Bicarinellum cristatum* was found in sample 113/1, and one cyst of *Alasphaera tuberculata* in sample 110/1. *Heptasphaera michaelii* is occurring consistently with low abundances throughout the succession. A peak abundance marks sample 111/1, and throughout the section samples that contain some specimens of *H. michaelii* alternate with samples which appear to lack that morphotype. Since *H. michaelii* always appears in relative low abundances, it is likely that it has been overlooked in some samples. *Pirumella strobila* and *Pirumella spinosa* do not follow a particular distribution pattern. *Pirumella strobila* shows a peak abundance in sample 109/1, otherwise *P. strobila* and *P. spinosa* show a random distribution over the whole succession. Periods in which they are relatively abundant alternate with periods in which they are absent. *Pirumella* cf.

*sphenifera* is more or less abundant between samples 102/1 and 106/2, and between samples 114/1 and 118/2, respectively.

*Pirumella* aff. *carteri* is rare throughout the succession, and is only common in samples 118/4 and 118/5, where it comprises about 50 per cent and 40 per cent of the assemblage. *Pirumella* aff. *mcnightii* is evenly distributed over the succession.

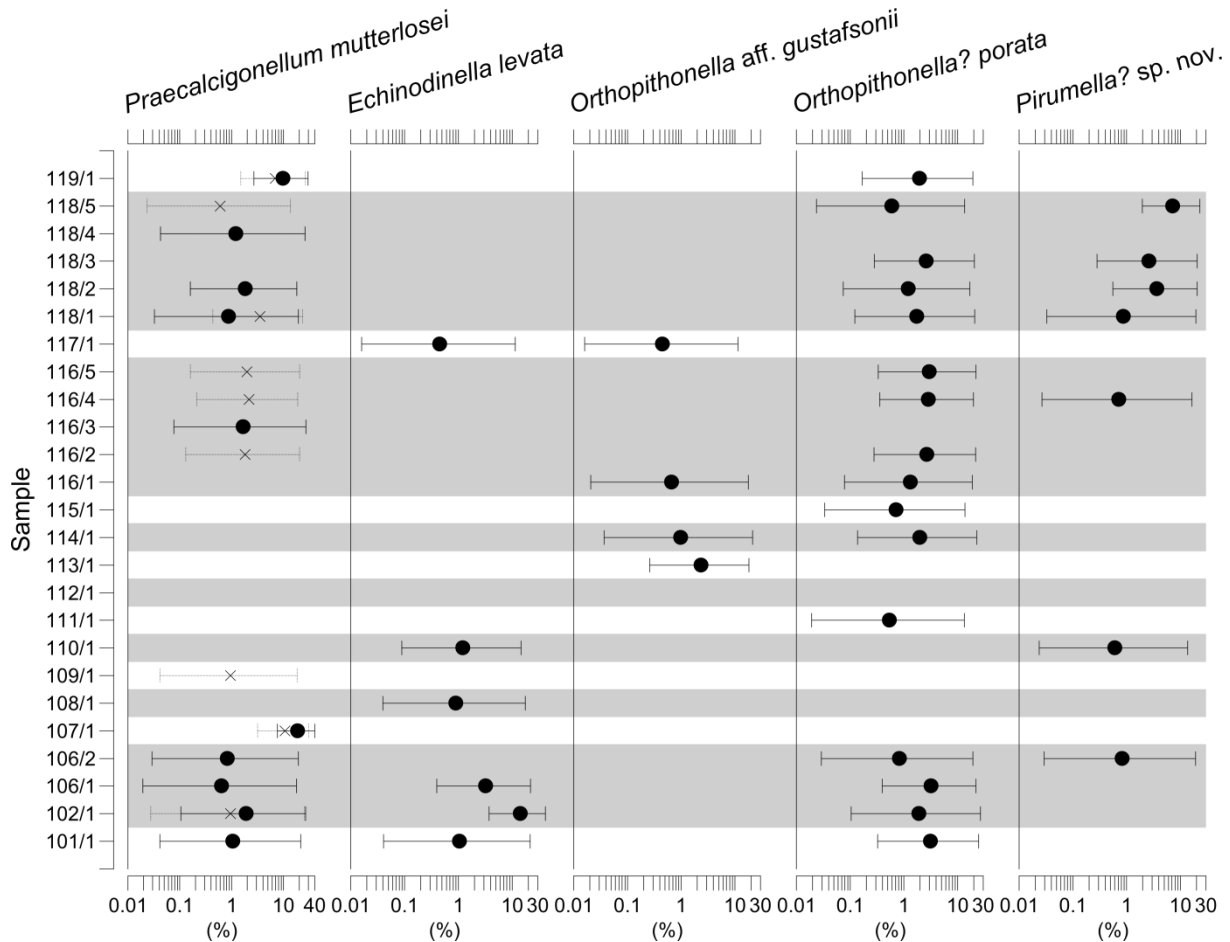


Fig. 5: Relative abundance of most abundant morphotypes of the radial group. Abundances of *Praealcalcionellum mutterlosei* (circles, solid error bars) and *P. cf. mutterlosei* (crosses, dotted error bars) were plotted into the same graph. Their good agreement furthers the belief that *P. cf. mutterlosei* indeed represents specimens of *P. mutterlosei* that simply cannot be certainly identified. Grey shades indicate dark beds.

The pithonelloid cysts generally show low abundances in the samples investigated and are often relatively poorly preserved. *Pithonella sphaerica* is most common, it was observed in samples 106/2, 108/1, 116/1, and 118/4, with peak abundances in sample 108/1 (8 per cent). *Pithonella ovalis* sporadically occurs throughout the section without any obvious pattern but never exceeds abundances of 1 per cent.

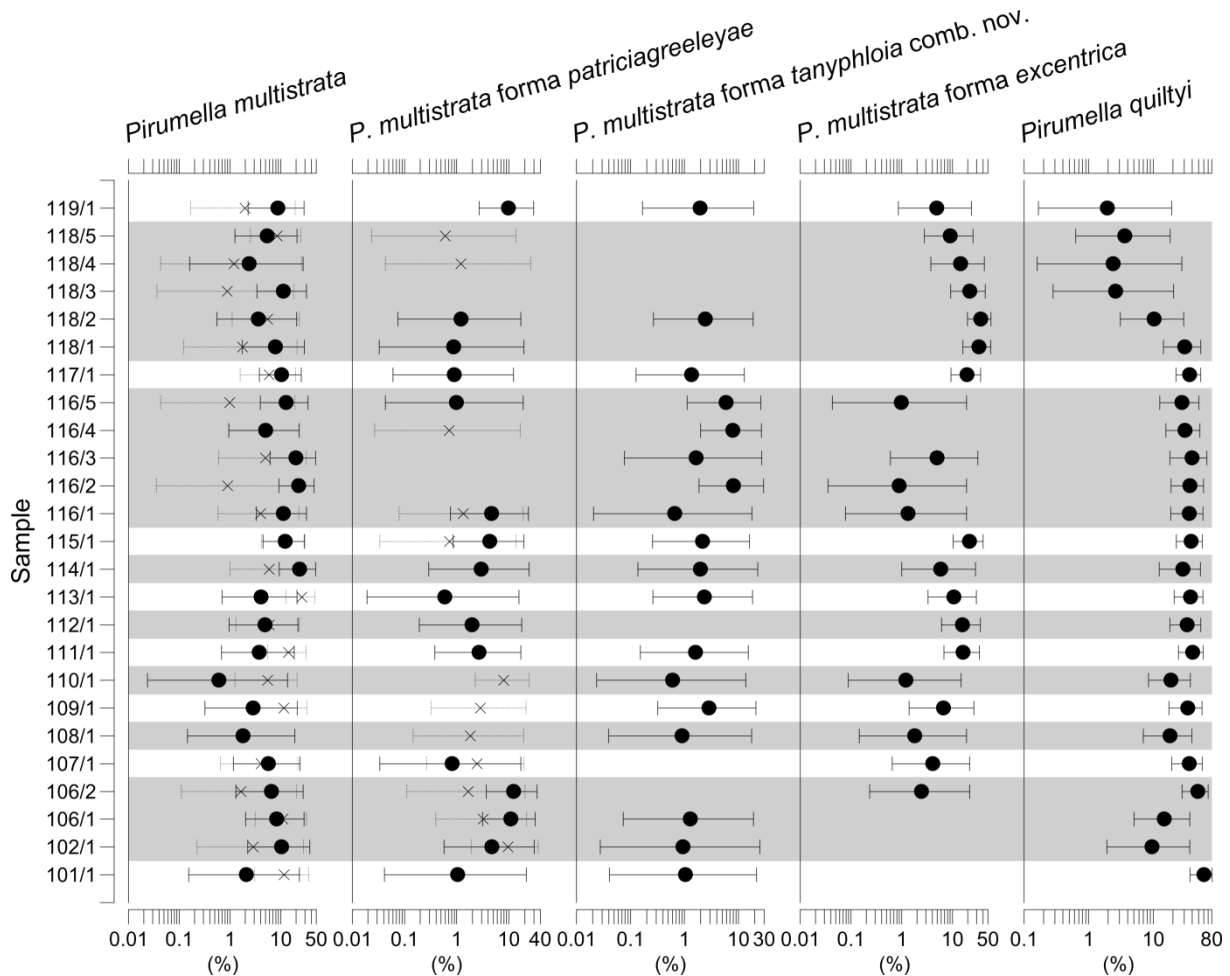


Fig. 6: Relative abundance of some oblique-walled morphotypes in the sediments of Frielingen. *Pirumella multistrata* (circles, solid error bars) and *P. cf. multistrata* (crosses, dotted error bars) were plotted together in one graph, as well as types A (circles, solid) and B (crosses, dotted) of *P. multistrata* forma *patriciagreeleyae*. Note the high abundance of *P. multistrata* forma *excentrica* in bed 118. Grey shades indicate dark beds.

#### 4 Discussion

If calcareous dinoflagellate cysts should be useful for the reconstruction of past environments, it is crucial to understand whether or not they are reacting at all to the supposed environmental change that took place in the Lower Saxony Basin during the Upper Hauterivian. For that, following approaches by NEUMANN (1999), the diversity distribution of the cysts found in Frielingen was investigated. The diversity (Shannon–Wiener Index) and equitability (Pielou's Equitability) show a first prominent peak in sample 102/1 (Fig. 8). Both values are subject to fluctuations for the rest of the succession but generally increase towards the top of the section. This gives evidence for an increasing diversity towards younger sediments and an increasing evenness of morphotype composition. However, in both indices the increase towards the top of the investigated section is not significant according to Spearman's rank order correlation ( $p_H = .262$ ,  $p_J = .302$ ).

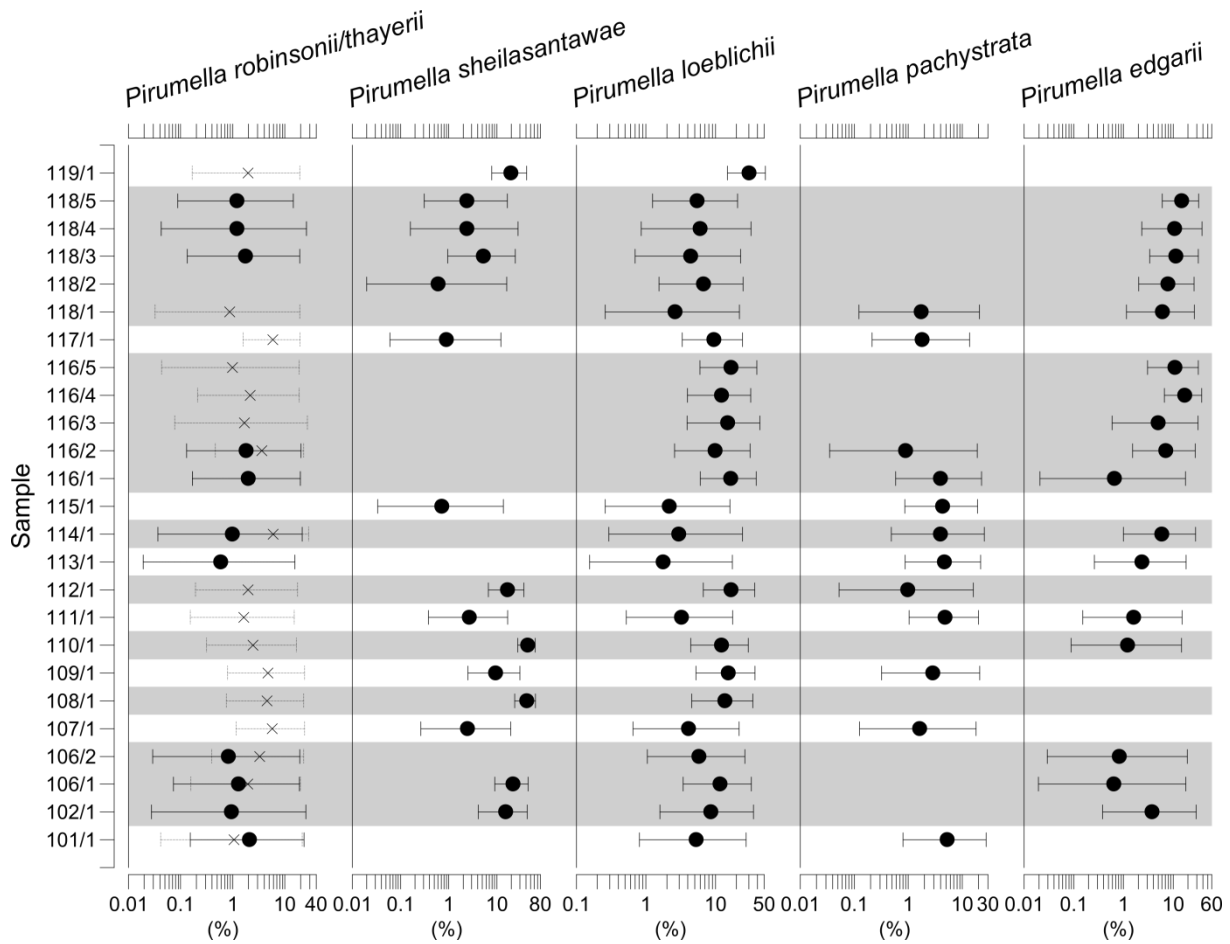


Fig. 7: Relative abundance of coarse crystalline morphotypes of the oblique group in the sediments of Frielingen. *Pirumella robinsonii* (circles, solid error bars) and *Pirumella thayerii* (crosses, dotted error bars) were plotted together into the same graph. Grey shades indicate dark beds.

To investigate the impact of bed colour on the assemblage of calcareous dinoflagellate cysts, the assemblage differences between pale and dark beds were calculated. ANOSIM provides relatively small values for  $R$ , depending on the method of distance measurement. The Bray–Curtis Distance (BRAY & CURTIS, 1957), commonly applied in ANOSIM, supplied a small value  $R = 0.112$  ( $p = .114$ ). Other distance measurements result in higher values for  $R$  (the Manhattan Distance (SWAN & SANDILANDS, 1995) suggests a considerable difference between pale and dark beds with a high significance of  $R = 0.2841$ ,  $p = .006$ ). The difference in the assemblages of pale and dark beds seems to be small. A cluster analysis (Fig. 9) reveals that the sediment colour somehow influences the expected cyst assemblage, especially beds 116 and 118 form distinct clusters. However, the confidence intervals of the nodes are relatively low.

Those results imply that there may be no reaction in the assemblage of those protists to the proposed environmental change between pale and dark beds, and most certainly there is no long-term trend throughout the profile regardless of short-term pale–dark rhythms. Keeping that in mind, a basic interpretation of the assemblage of the calcareous dinoflagellate cyst assemblage in the clay-pit Frielingen remains questionable, but should be tried here.

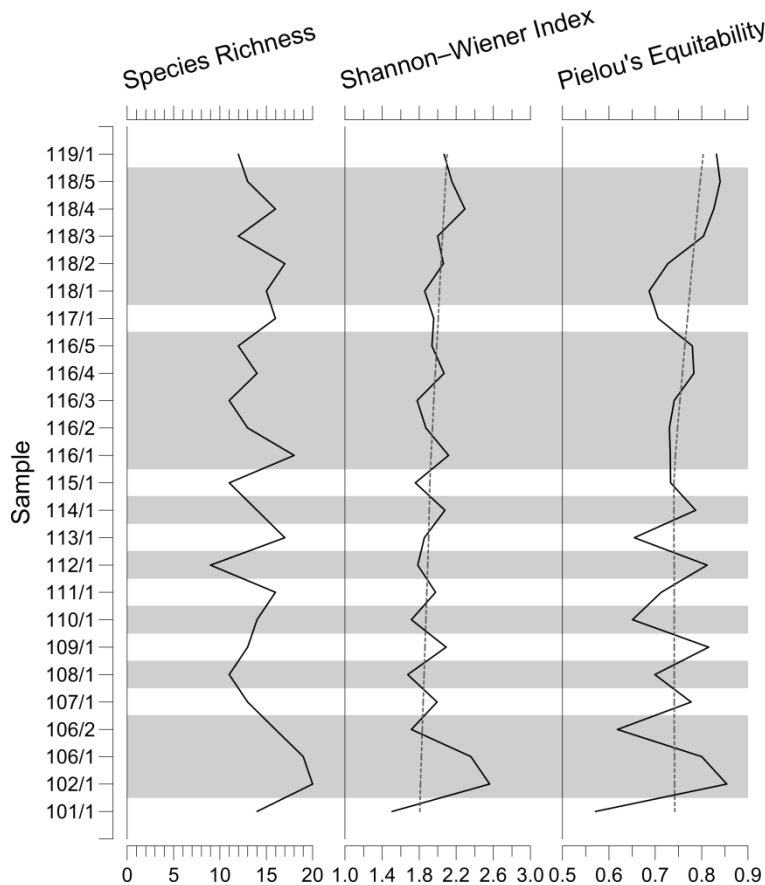


Fig. 8: Species richness, Shannon–Wiener Index, and Pielou's Equitability for calcareous dinoflagellate cysts assemblages in sediments from the clay-pit Frielingen. Although a general increase in both values might be assumed, these trends are insignificant at  $q = .05$ . Grey shades indicate dark beds.

#### 4.1 Assemblage of calcareous dinoflagellate cysts in Frielingen

When interpreting assemblages of calcareous dinoflagellate cysts, preservation has to be kept in mind. Although most cysts are relatively well preserved, there is evidence for some alteration throughout the succession. Particularly, the remarkable increase in the abundance of *Pirumella* aff. *carteri* in samples 118/4 and 118/5 must be noted. This morphotype represents damaged fine-crystalline cysts of the oblique group, in which the outer wall layer was removed, and in which only the inner wall layer was preserved. What processes caused this increase in abundance must remain speculative: enhanced ground water circulation through the layers those samples were taken from is a possible explanation, but mechanical abrasion during sample preparation is more likely.

The specimens of the genus *Pithonella* are the oldest undoubted occurrences of their kind—not considering the very disputable 'Pithonelloideae' found by JANOFKSKE (1987) in Triassic rocks. According to DIAS-BRITO (2000), *Pithonella sphaerica* is hardly known from sediments older than the Late Albian. *Pithonella ovalis* originated most likely in the Albian, possibly in the Barrémian (BORZA, 1964). The occurrence of the two morphotypes found in the Frielingen section principally allows extending the first occurrence of this taxon into the Late Hauterivian. It should be marked here, however, that the cysts are highly abraded and badly preserved, making reworking likely. Since the samples do not come from a core section, a down-core contamination can be ruled out, and if the cysts are reworked it may be reasonable to assume that they are even older than the Upper Hauterivian. Nevertheless it is possible, that a contamination of samples occurred in the field or during sample preparation, so that the in-situ nature of the pithonelloid cysts cannot be considered unquestionable.



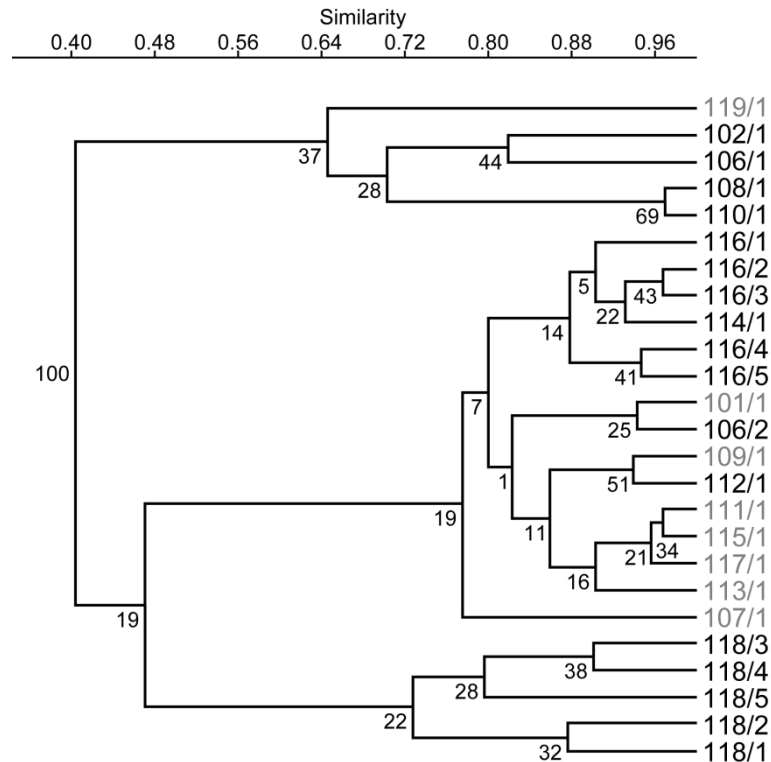


Fig. 9: Cluster analysis of the assemblage of calcareous dinoflagellate cysts in the samples from Frielingen (on the basis of abundance data), using the Morisita Similarity Index (MORISITA, 1959) and a Paired Group algorithm. Confidences for each node were calculated via bootstrapping (10000 replications). Samples of bed 118 and bed 116 (the latter together with sample 114/1) form distinct clusters. Most samples of pale beds (grey letters) and dark beds (black letters) also lie in close vicinity to each other. Values for *Pirumella* aff. *carteri* and *Pirumella* aff. *mcnightii* were removed prior to analysis, because they represent damaged cysts.

#### 4.1.1 Current knowledge about ecological preferences of calcareous dinoflagellate cysts and the environment represented by pale–dark bedded Cretaceous sediments

Cysts of the radial group are commonly interpreted to favour pelagic settings (KEUPP, 1992, 2001; KOHRING, 1993; WENDLER et al., 2002a). On the other hand, NEUMANN (1999), for instance, suggested that some morphotypes of the radial group (i.e. *Echinodinella* spp. and *Orthopithonella? porata*) are indicative of eutrophic conditions of surface waters of a neritic environment. *Echinodinella levata* is supposed to be a warm-water-indicating ecophenotype of *Praecalcionellum mutterlosei* (KEUPP, 1992), which itself is indicative of the influence of cool water masses (KEUPP, 1991).

The oblique group has shown to be less able to control the ultrastructure of their cyst walls (MONNET, 1993), so that coarse crystalline forms are interpreted to indicate cooler water masses, while fine crystalline forms favour warmer water (KEUPP, 1991, 2001). Additionally, KOHRING (1993) proposed that the reduction of the inner wall in *Pirumella* cf. *multistrata* may display an adaptation towards slightly colder water, though not as cold as is indicated by coarse crystalline cysts. Conversely, *P. multistrata* forma *excentrica* is often described as prospering during intervals strongly influenced by warm water masses (e.g. KEUPP, 1981, 1993). The occurrence of *P. loeblichii* and *P. multistrata* was suggested to be an indicator of transgressive trends (NEUMANN, 1999).

The pithonelloid group is a typical invader from the Tethys, so that their occurrence is indicative of high sea levels which enabled water exchange via the Carpathian Seaway (compare Fig. 2). Pithonelloid cysts are furthermore believed to characterize shelf environments (DIAS-BRITO, 2000; WENDLER et al., 2002a) or transgressive phases (ZÜGEL, 1994).

Pale-dark bedding rhythms in Cretaceous sediments from northern Germany are often interpreted as the result of changes in temperature and precipitation. As such, dark beds are believed to have been formed during times with decreased surface water temperatures (MUTTERLOSE & RUFFELL, 1999). NEBE (1999) proved that the pale-dark-bedding in the sediments of Frielingen is most likely caused by Milanković cycles. For the clay-pit Frielingen, NEBE (1999) calculated an average sedimentation rate of 1.89 cm/kyr for the lower part of the section (up to bed 115). According to these studies, the two thick dark beds were produced during time intervals of strongly increased sedimentation rates, representing time spans comparable to the other beds. These beds were, however, not included into the calculations due to the risk that they might corrupt them, effectively failing to proof the working hypothesis.

#### 4.1.2 Interpreting the palaeo-environment on the basis of calcareous dinoflagellate cysts in Frielingen

The proportion of cysts of the coarse crystalline oblique group (Table 2) is uncorrelated with TOC content ( $p = .692$ ) but shows a correlation with the sediments  $\text{CaCO}_3$  content ( $r = -0.438$ ,  $p = .029$ , Pearsons product-moment correlation) (Fig. 10). Given that higher carbonate contents are associated with pale beds in Frielingen (MUTTERLOSE, 1998; MUTTERLOSE & RUFFELL, 1997), this negative correlation can be interpreted in a way, that dark beds are indeed generally indicative of cooler palaeoenvironments.

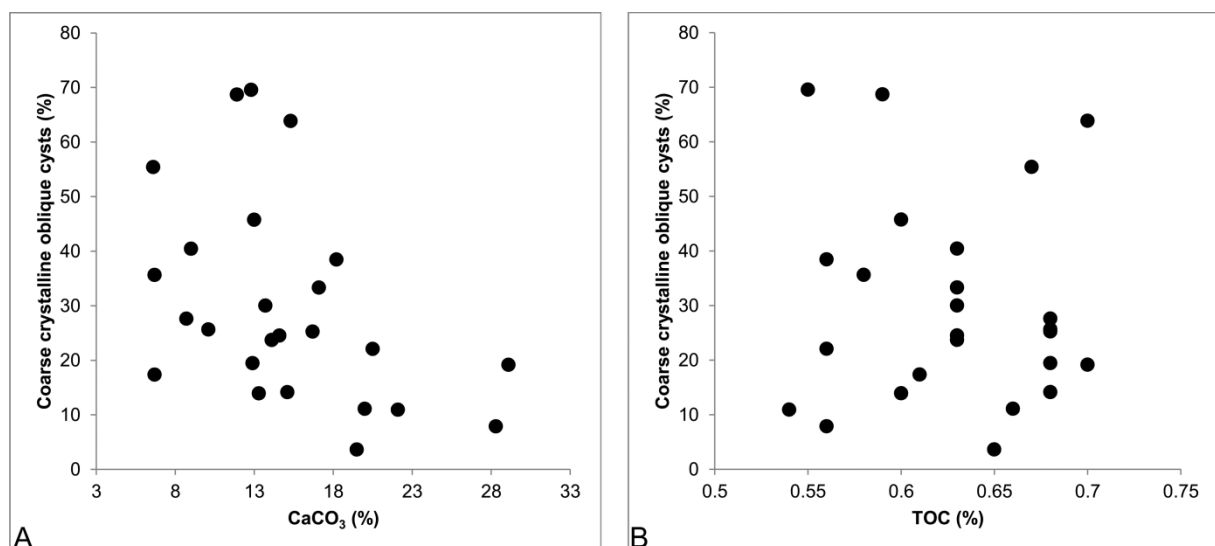


Fig. 10: Correlation between the relative abundance of coarse crystalline morphotypes of calcareous dinoflagellate cysts of the oblique group in sediments from the clay-pit Frielingen and the  $\text{CaCO}_3$  (A) and TOC (B) content of the sediment.

Table 2: Categorisation of obliquely crystalline calcareous dinoflagellate cysts from the clay-pit Frielingen into coarse and fine crystalline morphotypes for analysis purposes. *Pirumella* aff. *carteri* and *Pirumella* aff. *mcnightii* were omitted due to their nature as damaged cysts of undeterminable affinity.

COARSE CRYSTALLINE	FINE CRYSTALLINE
<i>Pirumella thayerii</i>	<i>Pirumella multistrata</i>
<i>Pirumella robinsonii</i>	<i>Pirumella</i> cf. <i>multistrata</i>
<i>P. multistrata</i> forma <i>patriciagreeleyae</i> type B	<i>P. multistrata</i> forma <i>patriciagreeleyae</i> type A
<i>Pirumella echinosa</i>	<i>P. multistrata</i> forma <i>excentrica</i>
<i>Pirumella loeblichii</i>	<i>P. multistrata</i> forma <i>tanyphloia</i> comb. nov.
<i>Pirumella sheilasantawae</i>	<i>Pirumella quiltyi</i>
<i>Pirumella strobila</i>	<i>Pirumella pachystrata</i>
<i>Pirumella spinosa</i>	<i>Heptasphaera michaelii</i>
<i>Pirumella edgarii</i>	<i>Alasphaera tuberculata</i>
<i>Pirumella</i> cf. <i>sphenifera</i>	<i>Bicarinellum cristatum</i>
<i>Bicarinellum calvum</i>	

In more detail, the high abundances of *Echinodinella levata*, *Orthopithonella? porata*, and *Orthopithonella? cf. compsa* in the lower parts of the section may be interpreted as a signal for a restrictive neritic environment. This is also supported by higher proportions of *Pithonella sphaerica* and the first occurrence of *Pithonella ovalis*.

The high abundances of *E. levata* are followed by a prominent peak of *Praecalzigonellum mutterlosei* and *P. cf. mutterlosei* in sample 107/1. Further up, *Pirumella multistrata* forma *patriciagreeleyae* type B, *Pirumella thayerii*, *Pirumella sheilasantawae*, and *Pirumella strobila* appear in high abundances and a first peak of *Pirumella loeblichii* is visible as well. The lower part of the section above sample 106/1 is therefore considered to represent cooler water conditions. The distribution of *P. sheilasantawae* (more abundant in dark layers) supports the hypothesis, that dark beds generally represent time intervals with colder surface waters. The increase in *P. loeblichii* could also mark a further transgression.

In the ensuing samples above 109/1, *P. cf. multistrata* and *Pirumella pachystrata* become more abundant, and are then replaced by *P. multistrata* and *P. multistrata* forma *tanyphloia* comb. nov. This trend may signify a continuous warming of the surface waters. The presence of *P. multistrata* could also be interpreted as a signal for a continued transgression towards an open neritic environment. The increase in the abundance of *P. multistrata* forma *excentrica* in sample 111/1 may be considered as a signal for a further increase in water temperature.

*Pirumella multistrata* forma *excentrica* then nearly ceases from the sediment record in bed 116, well correlated with a strong increase in the proportions of *P. loeblichii*, *Pirumella robinsonii*, and *P. thayerii*. This interval is very likely characterized by cooler surface waters (though not cold enough to re-establish a *P. mutterlosei* community). The dominance of *P. loeblichii* could also mark a transition back to lower sea levels (re-establishing a more restricted neritic environment) and/or nutrient depletion (NEUMANN, 1999). The latter can be ruled out, though, at least for sample 116/1, due to the content of pithonelloid cysts and high TOC values.

The upper part of the sediment column is characterized once again by an increase in the abundance of *O. ? porata*, whereas *P. multistrata* grows less abundant beyond sample 116/5 and *Pirumella quiltyi* (that was present throughout the succession) nearly ceases beyond sample 118/2. Instead *P. loeblichii* and *P. mutterlosei*/*P. cf. mutterlosei* grow abundant in sample 119/1. This can be interpreted as a renewed transgressive phase in combination with cooling of the surface waters.

The reduced amounts of *P. quiltyi* in the topmost samples cannot be interpreted easily, however. Throughout the succession *P. quiltyi* is more common in warm intervals, since a decline of abundance occurs mainly in the dark beds. The morphotype is not influenced by the presumably increased sedimentation rate in bed 116. A combination of a more restricted environment and warmer surface waters with a high sediment input might have been less suitable for *P. quiltyi*.

The limitation of *P. sphaerica* to the dark beds supports the idea, that this morphotype favoured eutrophic conditions, since the higher TOC levels in dark beds have been interpreted in this way (MUTTERLOSE & RUFFELL, 1997). *Pithonella ovalis*, however, also seems to prefer dark beds, which are thought to mark intervals of colder surface waters. This finding does not contradict the interpretation of *P. sphaerica* as a Tethyan morphotype, since it may be more eurytherm than other 'Pithonelloideae' (WENDLER et al., 2002a). However, even the presence of the presumably more stenotherm morphotype *P. ovalis* in dark beds does not exclude that the dark beds represent sediments of colder surface waters. The continuous presence of the Tethyan morphotype *Heptasphaera michaelii* shows that the surface waters were presumably considerably warm during the whole time interval investigated here.

The nature of the two thick dark beds (i.e. beds 116 and 118) remains questionable. The calcareous dinoflagellate cysts assemblages suggest the following: The drop in the abundance of *P. multistrata* forma *excentrica* and the rise in the abundance of *P. loeblichii* indicate surface water cooling for bed 116. Bed 118, in contrast, is dominated by *P. multistrata* forma *excentrica* and contains only small amounts of *P. loeblichii*. Both beds show increasing proportions of *Pirumella edgarii* through time, always reaching peak abundances in the uppermost sample of each bed. The cluster analysis revealed high intra-bed similarities, but low inter-bed similarities for the thick dark beds 116 and 118. It must be assumed that bed 116 represents an interval of cold surface waters whereas bed 118 was deposited under warmer surface waters (despite the slightly increasing abundances of *P. cf. mutterlosei* in sample 118/1). The higher abundance of *P. loeblichii* and *P. multistrata* in bed 116 may reflect a slightly more open neritic environment. The dominance of *P. multistrata* forma *excentrica*, together with high abundances of *O. ? porata*, in bed 118 support the interpretation as a restricted neritic environment (NEUMANN, 1999), though.

The hypothesis, that the dark bed 118 represents an interval of warmer surface waters contradicts the explanation of MUTTERLOSE & RUFFELL (1999), who suggested that dark beds generally represent colder time intervals. They, however, also suggest that dark beds are indicative of lower sea levels in that area, what is in accordance with the higher abundances of *P. multistrata* forma *excentrica* in bed 118. The dominance of *P. loeblichii* in bed 116 does support the interpretation of dark beds as low-temperature deposits. If the assumption of NEBE (1999) is correct that these beds reflect the same time span as the other beds, the sedimentation rates for beds 116 and 118 must have been very high. It is therefore suggested here that *P. edgarii* might be a morphotype that prefers environments with a very high

sediment input. That interpretation is in accordance with the models of MUTTERLOSE & RUFFELL (1999), which suggest higher sediment runoff from the continents during time intervals represented by dark beds. Whether the relative increase in the abundance of *P. edgarii* towards the top of beds 116 and 118 is due to an increasing sedimentation rate or a progressive establishment of the *P. edgarii* community under favourable conditions must remain speculative. The dominance of *Pirumella?* sp. nov. in bed 118 (that follows a similar distribution as *P. edgarii*) may indicate a preference of that morphotype towards warm surface waters with a high sediment input in restricted neritic environments.

The generally observable transgressive trend suggested for the *Simbirskites discofalcatus* ammonite Zone (compare HAQ et al., 1987; LUTAT, 1996; MUTTERLOSE, 1991) can in general be supported by the data obtained here. The known development can, however, be slightly modified by a short but pronounced regression in bed 118 on the basis of the obtained data.

#### 4.2 Morphology of calcareous dinoflagellate cysts in Frielingen

BELOW (1987) argued that a high intraspecific variance in cyst size could be due to the fact that they belong to different stages of the life cycle. KEUPP (1995), however, suggested that the cysts of a continuous sediment column exhibit a normal distribution, indicating the presence of specimens of the whole life cycle in the preserved community. Therefore, it was suggested that all calcareous dinoflagellate cysts comprise hypnocygotes and that cyst size may be linked to Milanković cycles (KEUPP, 2001). Small cysts may thereby indicate nutrient-rich environments, in which dinoflagellates reproduce often (NEUMANN, 1999). If the surface waters are oligotrophic, growth periods are prolonged due to reduced reproduction rates, effectively leading to the development of larger calcareous dinoflagellate cysts. Both hypotheses were examined based on the samples from Frielingen.

Three relatively abundant morphotypes were chosen to apply these tests: *Pirumella multistrata*, *Pirumella quiltyi*, and *Pirumella loeblichii*. *Pirumella quiltyi* and *P. loeblichii* show a vague negative correlation between cyst size and TOC. The size of the cysts of *P. multistrata* is positively correlated with carbonate content of the sediment (Fig. 11). It is possible to document that the cyst size at least partly correlates with TOC levels, where high TOC values go hand in hand with smaller cysts at least in some morphotypes (compare Fig. 11A). These trends, however, are unpronounced and statistically insignificant. Considering these findings and the interpretation of MUTTERLOSE & RUFFELL (1997) and (1999), according to which the pale beds represent phases of warm, oligotrophic surface waters, one would expect larger cysts in the pale beds. In Frielingen, however, the cyst size of most taxa is rather uninfluenced by the CaCO<sub>3</sub> content of the beds. Only *Pirumella multistrata* shows a weak and insignificant positive correlation of cyst size and CaCO<sub>3</sub>. We therefore follow NEUMANN (1999), who postulated that the cyst size seems to have been influenced by more than one environmental factor.

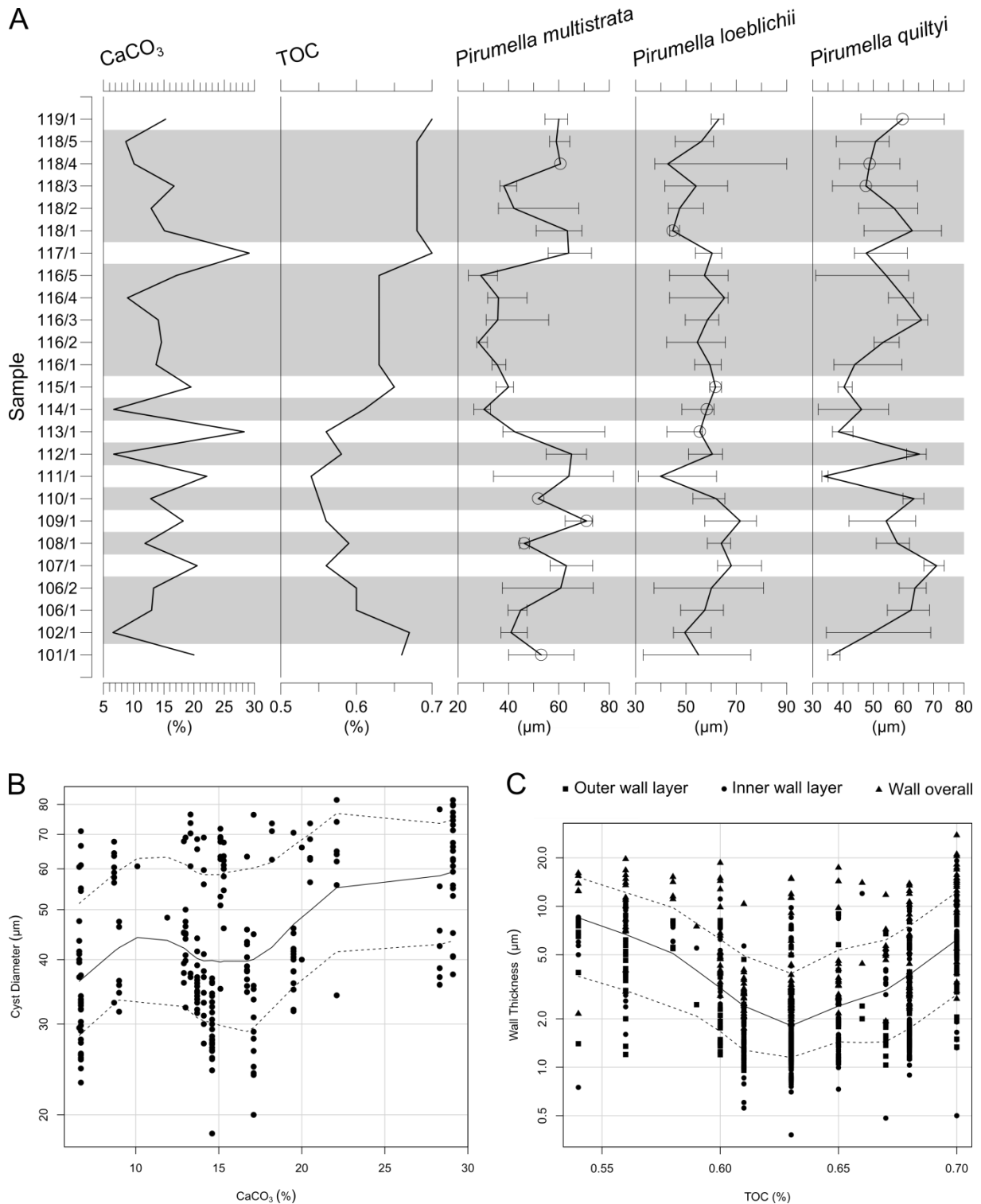


Fig. 11: A, Median cyst sizes of three selected morphotypes of calcareous dinoflagellate cysts in the clay-pit Frielingen. In some morphotypes the cyst size seems to be correlated to the TOC of the sediment. An unpronounced negative correlation is visible in scatter plots for *Pirumella quiltyi* and *Pirumella loeblichii*. Grey shades indicate dark beds. Circles indicate samples with insufficient specimens to calculate reliable confidence intervals. A, B, *Pirumella multistrata* shows a general trend to grow larger in samples with higher  $\text{CaCO}_3$  contents. C, *Pirumella multistrata* shows a correlation of wall thickness and sediment TOC. LOESS regression line (solid) with root-mean-square residuals (dashed) in Subfigs. B and C.

It has been suggested that the thickness of the cyst wall correlates with the CaCO<sub>3</sub> content of the samples (NEUMANN, 1999), a hypothesis not supported by the data from Frielingen. While the thickness of the inner wall layer in cysts of the oblique group seems not to be influenced by CaCO<sub>3</sub> or TOC, a relatively good negative correlation between the TOC and the thickness of the outer wall layer is visible in the lower parts of the section. This correlation, however, becomes less pronounced above sample 115/1 and ceases entirely above sample 116/5. *Pirumella multistrata* shows a certain correlation of cyst wall thickness and TOC, building thinnest walls at TOC values of c.0.63 per cent (Fig. 11C). This correlation is, however, not related to higher reproduction rates. Due to the process of wall formation the cyst size can hardly influence the wall thickness significantly. It might be, though, that the smaller cells encysting in eutrophic water cannot deposit as much carbonate and therefore must produce thinner walls. Once again the correlation of the cyst walls of *P. multistrata* with both parameters is the most pronounced (especially towards TOC). This morphotype, possibly due to its wide morphological range, seems to be most useful for palaeoecological analyses.

## 5 Conclusions

The investigation of the sediments from the clay-pit Frielingen offered new insights into the upper Hauterivian palaeoenvironment of the Lower Saxony Basin. The assemblages indicate a transgressive phase, an observation in accordance with the results of other authors. This transgressive phase is punctuated by a short regressive interval in bed 118. Sea surface temperatures are high throughout the entire interval investigated. The clear signal that the dark bed 118 comprises deposits of warmer surface waters contradicts the hypothesis, that dark beds generally comprise colder environmental conditions than their adjacent pale beds. Bed 116, however, shows that dark beds can indeed represent sediments of cooler time intervals, as does the distribution of coarse-crystalline taxa, such as *Pirumella sheilasantawae*. Therefore, the hypothesis that dark beds often indicate time intervals with cooler surface waters can be confirmed, but other environmental factors seem to be important as well. The simplified interpretation of dark beds as cold water sediments should be approached with caution in the future.

*Pirumella edgarii* seems to favour time intervals with higher terrigenous sediment input, whereas it seems to be uninfluenced by the water temperature. The favoured environment of *Pirumella?* sp. nov. might be similar in terms of sedimentation rate, though it is likely to prefer warmer surface waters. Those two morphotypes may therefore be useful as (partly temperature-independent) proxies for sediment input in the future.

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## Plates

### Plate 1

Figs A–E: *Pirumella?* sp. nov.

Figs A & B: *Pirumella?* sp. nov. from the clay-pit Frielingen is small, slightly oval in shape, and shows a structure of neatly arranged, pointed crystals on the surface (A: cyst 118.5b-133, B: cyst 118.2-96).

Figs C–E: The outer wall is rather thin and clearly consists of radially arranged crystals. The inner wall, if developed at all, is even thinner. Its ultrastructure is hardly accessible and seems to be recrystallized to some extent (C: cyst 118.5-8, D: cyst 118.4c-5, E: cyst 118.5b-102).

Figs F–J: The sediments of Frielingen bear the oldest undoubted occurrences of ‘Pithonelloideae’:

Figs F & G: *Pithonella sphaerica* is often poorly preserved but it shows the typical parquet like crystal structure on the surface.

Figs H–J: *Pithonella ovalis* is often better preserved.

