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# Pithonelloid wall-type of the Late Cretaceous calcareous dinoflagellate cyst genus *Tetratropis*

Jens Wendler*, Helmut Willems

*Universität Bremen, Fachbereich 5, Geowissenschaften, Postfach 330440, D-28334 Bremen, Germany*

## Abstract

The late Cretaceous calcareous dinoflagellate genus *Tetratropis* features both a pithonelloid wall-type (evenly inclined wall-components, proven here by a polarisation optical revision) and a peridinialean paratabulation strongly suggesting a dinoflagellate origin of at least part of the Pithonelloideae. This affinity with dinoflagellates sheds more light on the palaeoecology of the Pithonelloideae (commonly termed "calcispheres"), which are characteristic of the middle to Late Cretaceous. The very short-term stratigraphic occurrence of all *Tetratropis* species is comparable to the distribution pattern of other calcareous dinoflagellate cyst species with a distinctive paratabulation and is thought to reflect a narrow palaeoecological niche. *Tetratropis* species can be interpreted either as paratabulated morphotypes of otherwise atabulate Pithonelloideae formed under exceptional palaeoenvironmental conditions or as invaders from a highly specific palaeoecological niche during short-term palaeoceanographic events probably related to the initiation of the Late Cretaceous global cooling.
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*Keywords:* calcareous dinoflagellate cysts; Pithonelloideae; upper Cretaceous; paratabulation; palaeoecology

## 1. Introduction

Upper Cretaceous chalk characteristically contains a high abundance of spherical calcareous microfossils commonly called "calcispheres". Their walls consist of evenly inclined crystal aggregates (pithonelloid wall-type according to Janofske and Keupp, 1992; Young et al., 1997). These microfossils of the genus *Pithonella* are most probably calcareous dinoflagellate cysts. However, they are taxonomically very problematic and evidence is needed to evaluate their affinity with the dinoflagellates. Wendler et al. (2002b) summarised the arguments on this aspect and gave evidence

to support the dinoflagellate affinity of species of *Pithonella*. Keupp (1987) established the subfamily Pithonelloideae including all pithonelloid wall-type genera. This term is used here to comprise all genera discussed; however, it is not valid in taxonomy as the pithonelloid wall-type is probably present in calcareous remains of various families. In order to make accurate palaeoecological interpretations of these microfossils, it is crucial to understand their taxonomic affinities. Various morphological observations strongly suggest an affinity of some pithonelloid wall-type species with the dinoflagellates. *Pithonella sphaerica* (Kaufmann, 1865), which normally lacks paratabulation, may show hints of tabulation (Keupp, 1987). The shapes of apically antapically flattened pithonelloid species (e.g. *Pithonella discoidea* Willems, 1992; *Bonetocar-*

* Corresponding author. Fax: +49-421-218-4451.

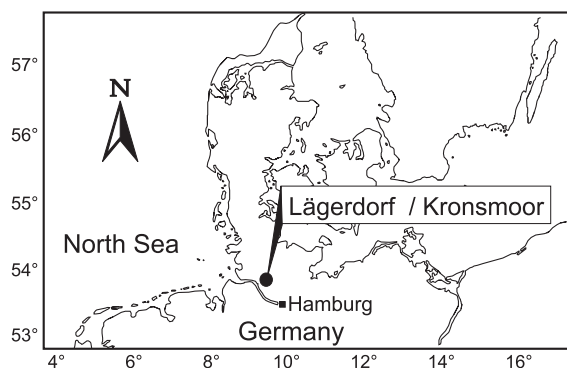*E-mail address:* wendler@uni-bremen.de (J. Wendler).

Fig. 1. Geographical location of the Kronsmoor/Lägerdorf section.

*diella* Dufour 1968; emend. Villain 1975; *Normandia circumperforata* Zügel 1994; *Lentodinella danica* Kienel, 1994) might reflect a paracingulum. Moreover, *Pithonella pyramidalis* (Willems, 1994), *Amphora coronata* (Willems, 1994) and particularly the genus *Tetratropis* (Willems, 1990) represent species that feature both the pithonelloid wall-type and a probable peridinialean paratabulation suggesting that at least part of the Pithonelloideae are of dinoflagellate origin.

In order to clarify ambiguities regarding the wall-type of *Tetratropis*, the species of this genus were

reinvestigated in the present study. The genus *Tetratropis* comprises the two species *Tetratropis patina* and *Tetratropis corbula* (Fig. 2A,D), which were discovered by Willems (1990), and a recently discovered new species (Bison et al., submitted for publication). They occur in narrow stratigraphic intervals of the middle Coniacian and lower Campanian. *Tetratropis* with its peridinialean paratabulation represents a key genus in the search for dinoflagellate affinities of the taxonomically problematic Pithonelloideae. Although its pithonelloid orientation of the cyst wall-components is clearly visible in scanning electron microscope (SEM) studies (Fig. 2F,I), this observation was later negated by analyses of thin sections with polarised light (Hildebrand-Habel and Willems, 1997). Controversially, whole specimens investigated here show an unequivocal pithonelloid wall-component orientation under polarised light. Therefore, the applicability of the thin section method for the cyst genus investigated had to be checked, and the genus description emended in the present study. In this paper, we evaluate the methodological difficulties of the polarisation-optical analysis and discuss the possible palaeoecological characteristics of *Tetratropis*.

Fig. 2. Scale bars are 30 μm except Fig. 2I.

(A) *Tetratropis patina* (Willems, 1990). SEM image, antapical/side view.

(B) *Tetratropis patina*, split-off epicyst, crossed nicols/gypsum plate, apical view. The distinctive extinction cross is skewed to the right indicating counter clockwise latitudinal wall-component inclination. Note the interference colour arrangement indicative of a radial orientation of the wall-components (bluish in second and fourth quadrant), and the traceability of the extinction cross (arrow) toward the archeopyle.

(C) *Tetratropis patina*, thin section, polarised light/gypsum plate, apical–antapical section. The extinction cross is strongly deformed due to the cyst shape. Blue interference colour is clearly visible in the second and fourth quadrants. The arrow marks a large wall-component, which seems to have different internal orientations. The apical region points to the upper right.

(D) *Tetratropis corbula* (Willems, 1990). SEM image, apical view.

(E) *Tetratropis corbula*, thin section, polarised light/gypsum plate. Note the asymmetrical extinction cross indicating the longitudinal wall-component inclination toward the apex. Bluish interference colour occurs in the second and fourth quadrants. The wall appears to consist of two layers.

(F) *Tetratropis patina*, broken specimen showing the varying thickness of the wall that consists of evenly inclined components. Note the flattening of the cyst. Arrows indicate the wall-components that form the cingular ridge. These are larger and appear more homogenous than the other crystal aggregates. Note that the ridge-components are part of the wall and form the ridges with their distal tips. The dashed area is enlarged in Fig. 2I.

(G) Example of a cyst with the radial wall-type (*Orthopithonella collaris*, Wendler et al., 2001). The wall-crystals appear totally disordered obscuring the extinction cross as a result of destruction during the cutting process.

(H) Pristine thin section of the same species as in (G). Note the clear extinction cross and interference colours.

(I) *Tetratropis patina*, broken specimen, detail of (F) (dashed field). The arrow points at the large wall-component, which is part of the cingular ridge. Note the aggregate-like shape of the wall-components. White dashed lines mark the wall and illustrate the *c*-axis orientation. Red dashed lines indicate the position of the ridges on the cyst surface. Scale bar 10 μm.

(J) *Tetratropis patina*, thin section, polarised light/gypsum plate, apical–antapical section. Black bars mark the positions of extinction; white lines indicate the wall-component inclination near the apex; the cyst axis is shown by the dashed white line.
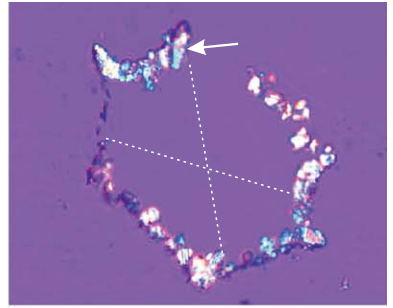
(K) *Tetratropis patina*, thin section, polarised light/gypsum plate, apical–antapical section (same thin section as C). The two specimens illustrated here are from one thin section, which disintegrated into these two layers.
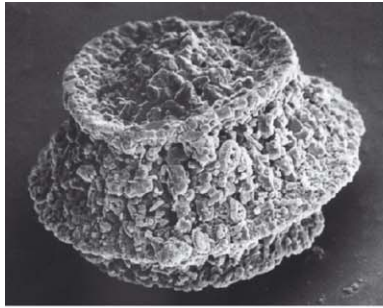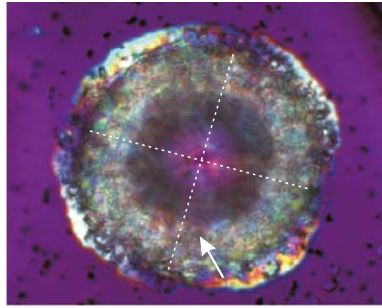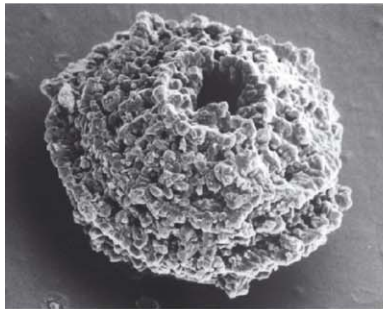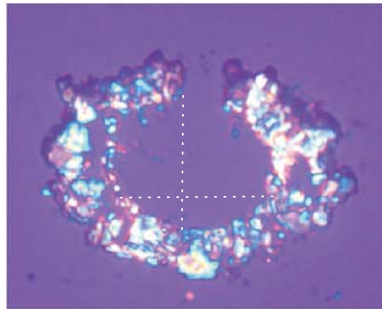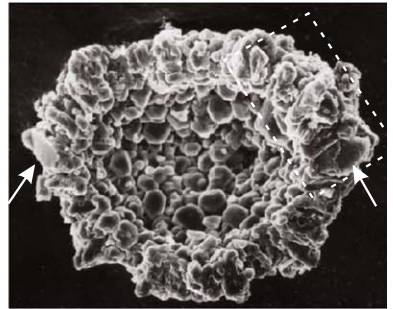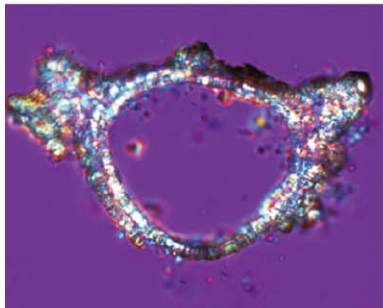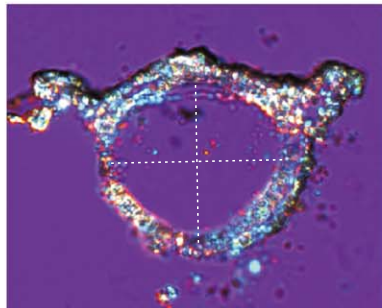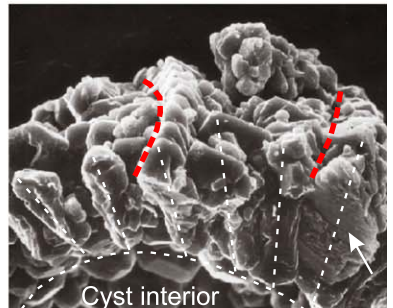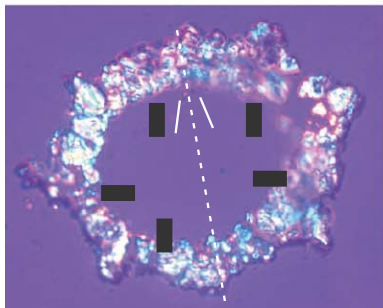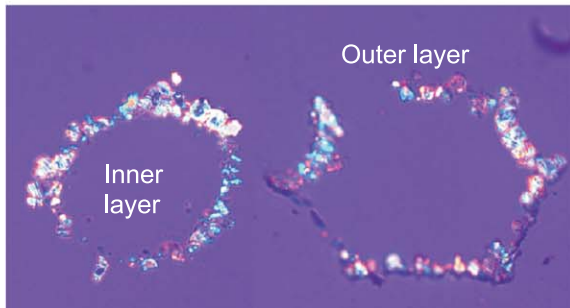
## 2. Materials and methods

For the present reinvestigation of *Tetratropis patina* (Willems, 1990) and *Tetratropis corbula* (Willems, 1990), the original material of Willems (1990) from the "Grube Schinkel" pit near Lägerdorf in NW Germany was used (Fig. 1).

The Kronsmoor/Lägerdorf composite section bearing the material investigated ranges from the middle Coniacian to the upper lower Maastrichtian and is published by Ernst (1984). The sample of white chalk analysed is of mid-Coniacian age. The calcareous dinoflagellate cyst assemblage is dominated by the common Late Cretaceous Pithonelloideae *Pithonella sphaerica* and *Pithonella ovalis* (Kaufmann, 1865), which are accompanied by the rare species of the genus *Tetratropis* during short stratigraphical intervals. The material was processed by repeated freezing and thawing in saturated sodium sulphate solution. Size fractions were separated by wet sieving using mesh sizes of 20 and 125 μm. To clean the cysts, the size fraction 20–125 μm was treated with ultrasound. Cyst specimens were picked with an eyelash from the dried residue using a binocular microscope at a magnification of ×120 and mounted on a stub for SEM studies. For investigation under polarised light, specimens were transferred to a glass slide, embedded in immersion oil and analysed at ×400 magnification.

The taxonomy follows the classification of Fensome et al. (1993). The wall-type of the cysts is determined based on the crystallographic orientation of the wall-crystals (Janofske and Keupp, 1992; Young et al., 1997). To analyse the crystallographic orientation, thin sections are usually produced following the procedure of Janofske (1996). However, since thin section preparation bears the risk of destruction of specimens with large and complex wall-components (such as the species investigated), it often results in cuts unsuitable for a crystal-optical analysis (Fig. 2G,H). Therefore, polarisation-optical investigations of thin sections were accompanied by analyses of untreated specimens embedded in immersion oil here.

### 2.1. New terminology of structural elements

The wall of *Tetratropis* and most other pithonelloid wall-type species consists of columnar aggregates formed by individual crystals with a uniform orientation of the c-axes. Accordingly, these crystal-aggregates do not represent crystals. Therefore, we propose the term wall-components.

Unprocessed sample material (sample M200, Willems, 1990, and samples S6, 7, 8, 9, 10, 11, Hildebrand-Habel and Willems, 1997), washed residue, SEM stubs, and the polarisation-optical slides analysed are stored at the Division of Historical Geology and Palaeontology, Bremen University.

## 3. Results

Both species of *Tetratropis* reinvestigated here can be analysed by polarised light optical microscopy of whole specimens and show a distinctive extinction cross, particularly in the ridges (Fig. 2B). This radial to evenly inclined (skewed extinction cross) orientation is a feature of the whole cyst body since the ridges are formed by distally extended wall-components (Fig. 2F,I). Our observation is not in accordance with a disordered (oblique) crystal arrangement of *Tetratropis* as claimed by Hildebrand-Habel and Willems (1997). Fig. 2B shows an apical view of a split-off epicyst of *Tetratropis patina*. This specimen is thin enough to allow for a study under polarised light. In the slightly defocused image, the extinction cross can be followed from the surrounding ridge toward the archeopyle, and the high-order bluish interference colour of the second and fourth quadrant of the extinction cross is visible. Wall-components are inclined counter-clockwise in the transverse plane (latitudinal inclination).

Thirty thin sections were obtained of three specimens and show very different results. The thin sections are generally fragile and subject to mechanical de-

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
Suborder PERIDINIINEAE Autonym
Family PERIDINIACEAE Ehrenberg 1831
Subfamily CALCIODINELLOIDEAE Fensome et al. 1993
Genus *Tetratropis* Willems (1990) and Hildebrand-Habel and Willems (1997)

struction during embedding. A weak zone is frequently observed within the wall. This zone splits the wall into two equally thick layers (Fig. 2K). Such layering of the cyst wall is not visible by SEM imaging (Fig. 2F,I). The separation of these wall-layers can cause a partial disarrangement of the wall-components; however, the extinction cross and arrangement of the interference colours using the gypsum plate can be detected in all thin sections by careful observation of each cyst sector while rotating the slide. From the 30 sections obtained, only 4 are suitable to clearly illustrate the optical polarisation characteristics photographically (Fig. 2C,E,J). The apical–antapical thin section shows a skewed extinction cross and blue interference colour in the second and fourth quadrant. The wall-components are inclined towards the apex (Fig. 2E,F,I) in axial cross section (longitudinal inclination).

The optical analyses prove a radial, uniformly inclined orientation of the *c*-axes of the crystals within each wall-component of the specimens investigated. This means that *Tetratropis* species have to be grouped with the pithonelloid wall-type. Therefore, the affiliation of *Tetratropis* with the oblique wall-type by Hildebrand-Habel and Willems (1997) needs to be emended.

*Original diagnosis* based on the type species *Tetratropis corbula* (Willems, 1990, p. 242, in German), translated: Single-walled calcareous dinoflagellate cysts with a slightly flattened apical–antapical shape. The cyst surface is characterised by four concentric, equator-parallel ridges that divide the cyst body into several segments. The arrangement of the ridges resembles a reduced peridinialean paratabulation, which, however, is mostly obscured within the cyst segments. The equatorial ridge divides the cyst into a trapezoidal-shaped epi- and hypocyst. The round archeopyle is centred in apical position at the epicyst. Columnar wall-components are oriented evenly inclined to radially to the cyst surface and produce apically–antapically arranged crystal rows at the surface.

*Systematic position of the genus Tetratropis according to* Hildebrand-Habel and Willems (1997, p. 183): "...A revision of the original material and further tests of the type species *Tetratropis corbula* as well as *T. patina* by using the thin section method established by Janofske (1996) for the examination of the crystallographic ultrastructure of the wall has shown that the c-

axes of all calcite crystals in fact are arranged in typical obliquipithonelloid structures. This optical character of the wall-crystals requires a new combination of the genus, placing the two species *T. corbula* and *T. patina* within the Obliquipithonelloideae Keupp (1987)."

*Here proposed systematic position of Tetratropis:* A re-examination of the light-optical characteristics of *Tetratropis patina* and *T. corbula* using whole cysts, a split-off epicyst of *T. patina*, and 30 thin sections revealed a distinctive radial, uniformly inclined, i.e. pithonelloid orientation of the wall-components. Thus, *Tetratropis* cannot be grouped with the Obliquipithonelloideae Keupp (1987) as proposed by Hildebrand-Habel and Willems (1997). Thin section analysis also suggests a layering of the wall. The pithonelloid wall-type of all *Tetratropis* species indicates a generic relation to other Pithonelloideae.

## 4. Discussion

The species of *Tetratropis* are examples of pithonelloid wall-type microfossils, taxonomically related to the dinoflagellates. The splitting into wall-layers observed during thin section analysis can be interpreted to reflect the presence of a thin organic layer, which separated two wall layers. Such wall architecture is the basis of the biomineralisation model of all Pithonelloideae established by Keupp and Kienel (1994) and has been considered to be of high taxonomic importance regarding the affiliation of *Tetratropis* with the Pithonelloideae (Willems, 1994). The layered appearance of the wall could, however, also be an effect caused by the uniform inclination of the wall-components.

Why is the wall-component orientation hardly seen by polarised light optical analyses of the thin sections? One reason could be the destructive aspect of the method. The blade, which cuts the thin sections, produces a short pressure on the material. Pristine wall-crystals will be cut smoothly while recrystallised crystal aggregates (which are typical for the material investigated, Fig. 2I) may be grown together and, therefore, have a stronger resistance against the cutting force. Thus, they may get disordered in the cutting process. Fig. 2G + H for example shows the variable thin cutting results of a radial wall-crystal orientation of the calcareous di-

noflagellate cyst *Orthopithonella collaris* (Wendler et al., 2001) with a similar diagenetic overprint. Additional destruction may occur during embedding of the thin section when large specimens in particular are subject to deformation (curl) of the thin section.

A second factor that may significantly influence both the cutting process and the optical analysis is the morphology of the wall-components. As can be seen in Fig. 2I, the wall of *Tetratropis* species consists of rather complex columnar aggregates of oriented crystals, which are more fragile than homogenous crystals and, therefore, are susceptible to disordering. Occasionally, individual crystals of some wall-components appear to vary in orientation (Fig. 2C). It is, however, difficult to verify whether this characteristic is primary or caused by the cutting. As a result of partly varying orientation, the entire wall-component would not show a single light-optical orientation, thus obscuring the polarised light image of the whole cyst.

Thirdly, the latitudinal inclination of the wall-components results in an angle between their $c$-axes and the cutting plane inhibiting total polarised light extinction and obscuring the extinction cross. The longitudinal inclination toward the archeopyle obscures the extinction cross by separating its apically pointing axis into two parts, one extinction sector on each side of the apical–antapical axis (Fig. 2J).

Apart from the fact that *Tetratropis* has the same wall-type as *Pithonella sphaerica* Kaufmann (1865) and *P. ovalis* Kaufmann (1865), they also share similar archeopyle sizes and shapes, and similar cyst surface characteristics (Willems, 1994). These similarities suggest that *Tetratropis* species represent paratabulated Pithonelloideae closely related to the above mentioned species. *P. sphaerica* and *P. ovalis* dominate the dinoflagellate cyst assemblage of the samples containing *Tetratropis* so their ecological demands may have been similar. So far, species of *Tetratropis* have only been reported from the Kronsmoor/Lägerdorf section. A striking aspect is their narrow stratigraphic occurrence. *T. patina* and *T. corbula* are only known from two narrow intervals in the mid-Coniacian (Hildebrand-Habel and Willems, 1997) and early Campanian (unpublished data) of the Kronsmoor/Lägerdorf section. The recently discovered new *Tetratropis* species has so far been found exclusively in one sample of latest Campanian age of the same section (Bison et al., submitted for publication). As the section investigated is very well studied, these short-term occurrences can be interpreted as primary signals rather than being an effect of inappropriate stratigraphic coverage. Such narrow temporal occurrences suggest a highly specific ecology of the cyst species investigated. *Tetratropis* show a distinctive type of paratabulation, which strongly deforms the spherical cyst body by predominantly reflecting sulcal and cingular features. Generally, calcareous dinoflagellate cysts with a paratabulation of this type are found in the stratigraphic record in short-term, often event-like occurrences or abundance peaks in relation to transgressive/regressive trends and Milankovitch cyclicity (Keupp, 1991; Zügel, 1994; Neumann, 1999; Keupp, 2001; Wendler et al., 2002a,b), and the K-T impact event (Willems, 1996; Wendler et al., 2001; Wendler and Willems, 2002). Therefore, it is possible that *Tetratropis* species are (1) paratabulated morphotypes of otherwise atabulate forms developed during the short-term establishment of specific environmental conditions (favourable or stress conditions), or (2) they are invaders from a different palaeoenvironmental niche representing the short-lived extension of these specific palaeoenvironmental conditions into the palaeogeographic position investigated. If (1) is the case, the most likely atabulate equivalents of these species in the material investigated are *P. sphaerica* and *P. ovalis*. The morphological modification can either reflect a reversible change in the phenotype or document a short-term evolution in genotype. But why are not all specimens paratabulated in the samples deposited during the appropriate conditions? This fact either points at a period of environmental conditions too short-lived for the bioturbation/reworking resolution of the chalk, or a high frequency cyclic, possibly seasonal, establishment of the required conditions allowing for the deposition of both atabulate and paratabulated cysts. Further, possibly morphologically intermediate, species in the material investigated are *P. cardiiformis* Zügel (1994), which is heart-shaped, and the disc-shaped *P. discoidea* Willems (1992). The shape of these species probably reflects a cingulum and suggests that they could be a link between the atabulate Pithonelloideae and *Tetratropis* species. However,

the apical inclination of the wall-components, which is typical for *Tetratropis* species, differs from *Pithonella* species but instead is characteristic for *Bonetocardiella conoidea* Bonet (1956) analysed by Zügel (1994). If the inclination type of the wall-components is of high generic order, this difference speaks against a relation of *Tetratropis* and *Pithonella*.

In the case of (2) short-term events related to the late Coniacian, early Campanian and Campanian/Maastrichtian coolings (e.g. Frakes, 1999; Barrera and Savin, 1999) may have initiated the invasion of *Tetratropis* species from their preferred habitat into the area investigated. Future high-resolution studies on this aspect and particularly a better coverage of the spatial distribution of *Tetratropis* are needed to reach a final conclusion about their palaeoecology.

It has to be kept in mind that the similarities between *Tetratropis* species and other Pithonelloideae discussed in this paper cannot be used to prove a dinoflagellate affinity for all microfossils, which have the pithonelloid wall-type. Several examples of pithonelloid microfossils incompatible with known dinoflagellate morphology and ecology have been described in the literature (e.g. Villain, 1981; Willems, 1996).

## 5. Conclusions

A revised light-optical analysis of all known species of *Tetratropis* clearly proves the affinity of these calcareous dinoflagellate cysts with the pithonelloid wall-type.

Three factors may strongly inhibit a successful light-optical study of thin sections of *Tetratropis* species: (1) coarse wall-components with additional diagenetic overprint are rigid and can be disturbed from their original arrangement during cutting; (2) the aggregate-like nature of the wall-components increases the likelihood of destruction, and there is the additional possibility of different primary orientations of the crystals that form the aggregates; (3) latitudinal wall-component inclination causes a dull extinction cross while longitudinal wall-component inclination toward the archeopyle modifies the shape of the extinction cross.

The peridinialean paratabulation of *Tetratropis* unequivocally proves affinity of the genus with the dinoflagellates. Its strong relation to other pithonelloid

wall-type microfossils such as *Pithonella sphaerica*, *Pithonella ovalis* and *Bonetocardiella conoidea* adds support to the hypothesis that these genera lacking paratabulation are also dinoflagellate cysts.

The short-term stratigraphic occurrence of species of *Tetratropis* is comparable to the distribution pattern of other strongly paratabulated calcareous dinoflagellate cyst species. *Tetratropis* can be interpreted as (1) morphotypes formed under favourable palaeoenvironmental conditions (or possibly stress) or (2) invaders from a specific palaeoecological niche that extended into the area investigated during short-term palaeoceanographic events most likely related to pulses in the late Cretaceous global cooling.

## Acknowledgements

## References

Barrera, E., Savin, S.M., 1999. Evolution of late Campanian–Maastrichtian marine climates and oceans. In: Barrera, E., Johnson, C.C. (Eds.), Evolution of the Cretaceous Ocean–Climate System. Special Paper-Geological Society of America, Boulder, Colorado, vol. 332, pp. 245–282.

Bison, K.-M., Wendler, J., Versteegh, G.J.M., Willems, H., submitted. *Tetratropis terrina* sp. nov., a new calcareous dinoflagellate cyst from the Upper Campanian (polyplocum zone) of Lägerdorf (N Germany). Journal of Micropalaeontology.

Bonet, F., 1956. Zonificacion Microfaunistica de las Calizas Cretácicas del Este de México. Boletin de la Asociacion Mexicana de Geologos Petroleros 8, 389–488.

Bütschli, O., 1885. Protozoa. In: Bronn, H.G. (Ed.), Klassen und Ordnungen des Thier-Reichs, Wissenschaftlich Dargestellt in Wort und Bild, vol. 1. Wintersche Verlagsbuchhandlung, Leipzig, pp. 865–1088.

Dufour, T., 1968. Quelques remarques sur les organismes incertae sedis de la famille des Calcisphaerulidae Bonet, 1956. Compte Rendu de l'Académie Sciences, D 266, 1947–1949.

Ehrenberg, C.G., 1831. Animalia evertebrata. In: Hemprich, P.C., Ehrenberg, C.G. (Eds.), Symbolae physicae seu icones et

descriptiones naturalium novorum aut minus cognitorum quae ex itineribus Lybiam Aegyptum Nubiam Dongalam Syriam Arabiam et Habessinian. Pars Zoologica. Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin.

Ernst, H., 1984. Bericht über eine Grossprobenserie im Schreibkreide-Richtprofil von Lägerdorf/Kronsmoor (M-Coniac bis U-Maastricht). Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg 57, 137–145.

Fensome, R.A., Taylor, F.J.R., Norris, G., Sarjeant, W.A.S., Wharton, D.I., Williams, G.L., 1993. A classification of living and fossil dinoflagellates. Micropalaeontology, Special Publication 7. 351 pp.

Frakes, L.A., 1999. Estimating the global thermal state from Cretaceous sea surface and continental temperature data. In: Barrera, E., Johnson, C.C. (Eds.), Evolution of the Cretaceous Ocean–Climate System. Special Paper-Geological Society of America, Boulder, Colorado, vol. 332, pp. 49–57.

Haeckel, E., 1894. Systematische Phylogenie. Entwurf eines natürlichen Systems der Organismen auf Grund ihrer Stammesgeschichte: I. Systematische Phylogenie der Protisten und Pflanzen Reimer, Berlin. 400 pp.

Hildebrand-Habel, T., Willems, H., 1997. Calcareous dinoflagellate cysts from the Middle Coniacian to Upper Santonian chalk facies of Lägerdorf (N Germany). Courier Forschungsinstitut Senckenberg 201, 177–199.

Janofske, D., 1996. Ultrastructure types in recent "calcispheres". Bulletin de l'Institut océanographique (Monaco) 14 (4), 295–427.

Janofske, D., Keupp, H., 1992. Mesozoic and Cenozoic "calcispheres" update in systematics. International Nannoplankton Association Newsletter 14, 14–16.

Kaufmann, F.J., 1865. Polythalamien des Seewerkalkes. In: Heer, O. (Ed.), Die Urwelt der Schweiz. Friedrich Schlothess, Zürich, pp. 194–199.

Keupp, H., 1987. Die kalkigen Dinoflagellaten-Zysten des Mittelalb bis Untercenoman von Escalles/Boulonnais (N-Frankreich). Facies 16, 37–88.

Keupp, H., 1991. Kalkige Dinoflagellatenzysten aus dem Eibrunner Mergel (Cenoman-Turon-Grenzbereich) bei Abbach/Süddeutschland. Berliner Geowissenschaftliche Abhandlungen. Reihe A, Geologie und Paläontologie 134, 127–145.

Keupp, H., 2001. Palaeoenvironmental interpretation of late Albian calcareous dinoflagellate cysts from Kirchrode I borehole (Lower Saxony Basin, NW Germany). Palaeogeography, Palaeoclimatology, Palaeoecology 174 (1–3), 251–267.

Keupp, H., Kienel, U., 1994. Wandstrukturen bei Pithonelloideae (Kalkige Dinoflagellaten-Zysten): Biomineralisation und systematische Konsequenzen. Abhandlungen der Geologischen Bundesanstalt-A. 50, 197–217.

Kienel, U.,1994. Die Entwicklung der kalkigen Nannofossilien und der kalkigen Dinoflagellaten-Zysten an der Kreide/Tertiär-Grenze in Westbrandenburg im Vergleich mit Profilen in Nordjütland und Seeland (Dänemark) [PhD thesis]. Berliner

Geowissenschaftliche Abhandlungen. Reihe E, Paläobiologie 12, 87 pp.

Neumann, Chr., 1999. Diversitäts- und Häufigkeitsmuster kalkiger Dinoflagellatenzysten aus dem Alb der Bohrung Kirchrode II (zentrales Niedersächsisches Becken, NW-Deutschland) und ihre möglichen Steuerungsmechanismen. Berliner geowissenschaftliche Abhandlungen. Reihe E, Paläobiologie 31, 79 pp.

Pascher, A., 1914. Über Flagellaten und Algen. Berichte der Deutschen Botanischen Gesellschaft, Berlin 32, 136–160.

Villain, J.-M., 1975. "Calcisphaerulidae" (incertae sedis) du Crétacé Supérieur du Limbourg (Pays-Bas), et dautres régions. Palaeontographica A 149, 193–242.

Villain, J.-M., 1981. Les Calcisphaerulidae: intérêt stratigraphique et paléoécologique. Cretaceous Research 2, 435–438.

Wendler, J., Willems, H., 2002. The distribution pattern of calcareous dinoflagellate cysts at the Cretaceous/Tertiary boundary (Fish Clay, Stevns Klint, Denmark)—implications for our understanding of species selective extinction. In: Koeberl, C., MacLeod, K.G. (Eds.), Catastrophic Events and Mass Extinctions: Impacts and Beyond. Special Paper-Geological Society of America, vol. 356, pp. 265–275.

Wendler, J., Wendler, I., Willems, H., 2001. *Orthopithonella collaris* sp. nov., a new calcareous dinoflagellate cyst from the Cretaceous/Tertiary boundary (Fish Clay, Stevns Klint/Denmark). Review of Palaeobotany and Palynology 115, 69–77.

Wendler, J., Gräfe, K.-U., Willems, H., 2002a. Reconstruction of mid-Cenomanian orbitally-forced palaeoenvironmental changes based on calcareous dinoflagellate cysts. Palaeogeography, Palaeoclimatology, Palaeoecology 179, 19–41.

Wendler, J., Gräfe, K.-U., Willems, H., 2002b. Palaeoecology of calcareous dinoflagellate cysts in the mid-Cenomanian Boreal Real: implications for the reconstruction of palaeoceanography of the NW European shelf sea. Cretaceous Research 23, 213–229.

Willems, H., 1990. Tetratropis, eine neue Kalkdinoflagellaten-Gattung (Pithonelloideae) aus der Oberkreide von Lägerdorf (N-Deutschland). Senckenbergiana Lethaea 70, 239–257.

Willems, H., 1992. Kalk-Dinoflagellaten aus dem Unter-Maastricht der Insel Rügen. Zeitschrift für Geologische Wissenschaften 20, 155–178.

Willems, H., 1994. New calcareous dinoflagellates from the Upper Cretaceous White Chalk of northern Germany. Review of Palaeobotany and Palynology 84, 57–72.

Willems, H., 1996. Calcareous dinocysts from the Geulhemmerberg K/T boundary section (Limburg, SE Netherlands). Geologie en Mijnbouw 75, 215–231.

Young, J.R., Bergen, J.A., Bown, P.R., Burnett, J.A., Fiorentino, A., Jordan, R.W., Kleijne, A., van Niel, B.E., Romein, A.J.T., von Salis, K., 1997. Guidelines for coccolith and calcareous nannofossil terminology. Palaeontology 40, 875–912.

Zügel, P., 1994. Verbreitung kalkiger Dinoflagellaten-Zysten im Cenoman/Turon von Westfrankreich und Norddeutschland. Courier Forschungsinstitut Senckenberg 176, 159 pp.