# Calcareous dinoflagellate blooms during the Late Cretaceous 'greenhouse' world - a case study from western Ukraine (#87805)

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# Calcareous dinoflagellate blooms during the Late Cretaceous 'greenhouse' world - a case study from western Ukraine

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The Late Cretaceous was a unique period in the history of the Earth characterized by elevated sea levels, reduced land area, and significantly high concentrations of atmospheric CO<sub>2</sub> resulting in increased temperatures across the globe - a 'Greenhouse world'. During this period, calcareous dinoflagellate cysts (c-dinocysts) flourished and became a ubiquitous constituent of calcifying plankton around the world. An acme in calcareous dinocysts during the Albian to the Turonian coincided with the highest recorded sea water surface temperatures and was possibly linked to certain sportal conditions that favored calcification and a highly oligotrophic system of the European shelf. This study examines the potential applicability of c-dinocysts as a proxy for paleoenvironmental conditions based on their assemblage changes plotted against foraminiferal occurrences and microfacies analysis. The material were extracted from the upper Turonian chalk from the Dubivtsi region of western Ukraine. An inverse correlation was observed between species richness and the number of c-dinocyst specimens. Nutrient availability gradients apparently strongly determined changes in the calcareous dinocyst distribution. These trophic changes were likely caused by the interplay of global eustated sea-level fluctuations and Subhercynian tectonic activity leading to various nutrient inputs from the nearby land.

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#### ABSTRA( 57

The Late Cretaceous was a unique period in the history of the Earth characterized by elevated sea levels, reduced land area, and significantly high concentrations of atmospheric CO<sub>2</sub> resulting in increased temperatures across the globe - a 'Greenhouse world'. During this period, calcareous dinoflagellate cysts (c-dinocysts) flourished and became a ubiquitous constituent of calcifying plankton around the world. An acme in calcareous dinocysts during the Albian to the Turonian coincided with the highest recorded sea water surface temperatures and was possibly linked to certain special conditions that favored calcification and a highly oligotrophic system of the European shelf.

This study examines the potential applicability of c-dinocysts as a proxy for paleoenvironmental conditions based on their assemblage changes plotted against foraminiferal occurrences and microfacies analysis. The material were extracted from the upper Turonian chalk from the Dubivtsi region of western Ukraine. An inverse correlation was observed between species richness and the number of c-dinocyst specimens. Nutrient availability gradients apparently strongly determined changes in the calcareous dinocyst distribution. These trophic changes were likely caused by the



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- leading to various nutrient inputs from the nearby land.
- 31 Subjects Paleontology, Paleoecology, Paleobiology, Taxonom 🔁
- 32 Keywords upper Turonian, Late Cretaceous, calcareous dinocysts, pithonellids,
- nutrient crisis, sea-level fluctuations, Central European Basin.

#### INTRODUCTION

Calcareous dinoflagellate cysts, also known as calcareous dinocysts (c-dinocysts), are minute calcite structures measuring between 10 and 180 µm; they are produced by peridinoid dinoflagellates belonging to the family Thoracosphaeraceae, which is classified under the Order Peridiniales, Class Dinophyceae (*Elbrächter et al., 2008*). Dinoflagellates that produce calcareous cysts are photosynthetic planktonic organisms (*Tangen et al., 1982; Montresor 1994*). Modern c-dinocysts, which are primarily dominated by *Thoracosphaera heimii*, have bee resent in many regions around the world (*Dale, 1992; Montresor et al., 1998; Höll et al., 1992; Vink et al., 2000*). Approximately 30 extant species and about 260 fossil species (morphotypes) (*Nowak, 1963; Reháková, 2000; Fensome and Williams, 2004; Ciurej and Bąk, 2021*) are known so far.

46 The earliest fossil record of c-dinocysts is known from the Upper Triassic (Janofske, 1992). They are widely used as a marker in biostratigraphy, paleoclimate, 47 and paleoenvironmental reconstructions (Keupp, 1991; Zügel, 1994; Dias-Brito, 2000; 48 49 Wendler et al., 2002; Wendler et al., 2013; Omaña et al., 2014; Wiese et al., 2015; 50 Ciurej et al., 2017). In the Late Cretaceous, c-dinocysts were prevalent throughout the 51 world (Keupp 1991; Willems 1994), with Pithonella often dominating the assemblages 52 (Dias-Brito, 2000; Wendler et al., 2002). Pithonellids have been detected in many regions of the world, from both the northern and southern hemispheres, including 53 Western Europe (Wendler et al., 2002; Wiese et al., 2015), Central Europe (Nowak, 54 1963; Reháková, 2000; Ciurej at al., 2017), Tadzhikistan (Andryuschenko and 55 Dolitskaya, 1975), the South Atlantic Ocean (Dias-Brito, 2000), or Middle America 56 (Omaña et al., 2014). The widespread acme of pithonellids during the Albian-Turonian 57 58 coincides with the maximum water surface temperature and the mid-Cretaceous



transgression leading to expansion of relatively shallow and warm epicontinental seas (*Hallam, 1992; Miller et al., 2005; Gale et al., 2008*). One of the reasons for the pithonellid bloom during this period may be attributed to certain favorable conditions of seawater that promoted calcification including high calcium—ion concentration and low Mg/Ca ratio (*Stanley et al., 2005*) together with high concentration of DIC (dissolved inorganic carbon) (*Kelly, 2003*) which is a limiting compound for CaCO<sub>3</sub> precipitation in sea-water today (*Erez, 2003*). The *Pithonella* acme might be also related to the widespread oligotrophic conditions in the early Late Cretaceous shelf seas (e.g., *Wiese et al., 2015*). Pithonellids are interpreted to be opportunistic organisms that can thrive, evolve, and bloom in oligotrophic-mesotrophic environments and were also able to adapt to eutrophic environments (*Dias-Brito, 2000*). Recent dinoflagellates can overcome temporary nutrient deficiency by producing resting cysts (e.g., *Vink et al., 2000*). The abundant but low-diversity c-dinocyst assemblages were documented from surface sediments of oligotrophic areas of the Atlantic Ocean (*Höll et al., 1999; Vink et al., 2000; Zonnevald et al., 2000*).

The upper Turonian pure white chalk of the Ukrainian part of the European epicontinental sea (southeastern part of the Central European Basin), exhibits abundant c-dinocysts (*Bojczuk and Woloszina, 1971; Rozumeyko, 1978; Pasternak, 1984; Olszewska et al., 2012; Dubicka and Peryt, 2012*). In some intervals, c-dinocysts are the main constituents of the chalk deposits. In addition, the strong dominance of one species, *P. ovalis*, indicates single-species blooms. Therefore, during the relatively long period of the late Turonian, the surface waters of this basin were largely inhabited by these organisms. However, c-dinocysts have not been studied in detail in the working area. The published data refer only to general information that mostly mentions their presence. In this study, we present a detailed qualitative and quantitative analysis of the c-dinocysts of the upper Turonian chalk of the Dubivtsi section plotted against microfacies studies and already published foraminiferal assemblage data (*Dubicka and Peryt, 2012*). These data promote our understanding of the environmental factors that caused c-dinocysts to bloom in the Late Cretaceous.

#### **GEOLOGICAL SETTING**



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The Dubivtsi section is exposed in a quartificated 1 km east of Dubivtsi, near Halych (Fig. 1A). The section contains four lithological units from the bottom to the top (*Dubicka and Peryt, 2012*): 1) white chalk (25 m thick, strongly lithified, with CaCO<sub>3</sub> content ranging from 97.8 to 99.9 %); 2) hardground; 3) inoceramid limestones (4.4 m thick); and 4) marls (1.5 m thick). The total thickness of the studied section is 31 m. The c-dinocysts were studied from the white chalk.

The upper Turonian age of the white chalk of the Dubivtsi section is documented by planktonic foraminifera that indicate, the uppermost part of the Helvetoglobotruncana helvetica and Marginotruncana coronata local foraminiferal zones (Walaszczyk and Peryt, 1998; Peryt et al. 2022); the Marginotruncana coronata Zone of the Central European Basin (Walaszczyk and Peryt, 1998; Peryt et al., 2022) correlates to the Inoceramus costellatus (I. perplexus, see Wiese et al., 2020) and Mytiloides scupini inoceramid zones. In addition, the co-occurrence of Marginotruncal coronata, Marginotruncana marginata, Marginotruncana pseudolinneiana, Dicarinella imbricata and representatives of Falsotruncana indicates the upper Turonian (Huber et al., 2017; Haynes et al., 2016) M. schneegansi standard planktonic foraminiferal zone (Gradstein et al., 2017 The last occurrence of H. helvetica in the Boreal Province (Walaszczyk and Peryt, 1998) seems to be slightly higher than in the Tethyan and Austral realms (Huber and Petrizzzo, 2014). The late Turonian age of the Dubivtsi chalk (below the hardground) is additionally supported by the benthic foraminiferal assemblage: Gavelinella ammonoides (Reuss), Gavelinella vesca (Bykova), Cibicides polyrraphes (Reuss), Globorotalites multiseptus (Brotzen) (see Walaszczyk et al., 2022; Stróżyk et al., 2018). The prominent positive excursion of the  $\delta^{13}$ C curve recorded in the middle of the Dubivtsi section (Dubicka and Peryt, 2012) is probably equivalent to the widespread upper Turonian positive Hitch Wood Event recorded in western and southern Europe (Gale, 1996; Jarvis et al., 2006).

Geologically, this region is situated in the southwestern margin of the East European Platform within the Lviv-Stryi Syncline (*Pasternak et al., 1968; Pasternak et al., 1987; Świdrowska et al., 2008*), which is the southernmost part of a larger tectonic unit called the Border Synclinorium. The Border Synclinorium extends to the northeastern margin of the Mid-Polish Anticlinorium (*Pożaryski et al., 1979*). The



Turonian deposits of the Dubivtsi section belong to the lithological unit here referred to as the Dubivtsi Formation and originally named the "Dubivtsi Suite" (*Ivannikov al., 1987; Gavrilishin et al., 1991; Pasternak, 1959*), which extends over a large area from Volhynia to Podolia in western Ukraine and overlies the Cenomanian limestones. This formation ranges in thickness from 54 to 158 meters and is divided into two distinct intervals. The lower interval, which is of Turonian age, comprises white and gray limestones that are rich in *Pithonella*, as identified by *Rozumeyko* (1978). It also contains flint concretions that appear 15–20 meters above the base of the formation and become more abundant toward the top of the section (*Gavrilishin et al., 1991; Vashchenko et al., 2007*). The upper interval, which is of Coniacian age, consists of limestones, argillaceous limestones and marls that often contain fragments of inoceramids (*Gavrilishin et al., 1991*).

The Upper Cretaceous strata of the Dubivtsi section were deposited in the southeastern part of the Cretaceous Central European Basin, c.a. 100 km south of the Carpathian Basin (*Ziegler 1990*, and Fig. C). During the late Turonian, the Dubivtsi area was submerged under an epicontinental sea (Fig. 1C) with variable water depth from c.a. 50 m up to slightly above 100 m (*Dubicka and Peryt, 2012*) interpreted based on planktonic foraminiferal morphogroups (see Bé, 1977; Hart and Bailey, 1979; Leckie, 1987). During most of the late Turonian, Dubivtsi was far away from the emergent areas; the nearest land (uplifted Ukrainian Shad) was at least 300 km to the east (Fig. 10). An uplift of the 'Krukienic Island asternak (1959) located around 50 km sout set of the Dubivtsi began possibly during the later part of the late Turonian (*Pasternak, 1987; Dubicka et al., 2014*) (Fig. 1C). A previous study of the benthic foraminiferal assemblages (*Dubicka and Peryt, 2012*) showed that sedimentation of the Dubivtsi chalk occurred under oligotrophic conditions, as reflected by the low species richness and extremely low abundance of planktonic and benthic foraminifera and a flood of pithonellids.

#### MATERIAL AND METHODS

Sixteen samples of white chalk from the Dubivtsi section were analyzed for cdinocysts (Fig. 2). These samples were the same as those used for the previously



studied foraminifera (*Dubicka and Peryt, 2012*). Sixteen rock thin sections of dimensions 3×5 cm were prepared for assessing c-dinocyst abundance and diversity as well as microfacies analyses. To estimate the total c-dinocyst content, the thin sections were arbitrarily divided into three laminae. Thin the lower, middle, and upper parts. Each lamina was 0.47 mm thick and 19.6 mm wide. The method used to quantify the dinocysts involved counting the number of species present in each lamina, which had an area of 27 mm² for each sample. The counts for each species were then summed to obtain the total content of c-dinocysts in each sample. The same thin sections were used for microfacies analysis. Observations were made using a Nikon Eclipse LV100N POL polarizing optical microscope with a digital camera and NIS-Elements BR software for capturing photographs of thin sections (Department of Geology and Paleontology, Pedagogical University of Krakow).

Rock samples for c-dinocyst studies were disintegrated using the liquid nitrogen method (*Remin et al., 2011*). The residues obtained were cleaned in an ultrasonic bath and sieved into three fractions: <20  $\mu$ m, 20–75  $\mu$ m, and >75  $\mu$ m. C-dinocyst specimens were handpicked from 20–75  $\mu$ m fraction using a standard optical binocular microscope. Observations were performed using scanning electron microscopy (SEM; HITACHI 3-4700) at the Laboratory of Field Scanning Emission Microscopy and Microanalysis at the Institute of Geological Sciences of Jagiellonian University, Krakow, Poland.

For the taxonomic identification of c-dinocysts, morphological characteristics such as shape, size, aperture, and wall ultrastructure have been observed (Nowak, 1963; Nowak, 1974; Bolli, 1974; Keupp, 1987; Reháková, 2000; Wendler et al., 2002; Wendler et al., 2013; Omaña et al., 2014). Four types of cyst wall ultrastructures, based on the crystal orientation within the wall, have been described: pithonellid, radial, oblique, and tangential (Keupp, 1987; Kohring, 1993; Young et al., 1997). The foraminiferal data set of Dubicka and Peryt (2012) was plotted against the section of the c-dinocyst occurrences.

The material used in this study is housed at the Pedagogical University of Krakow, Institute of Biology and Earth Sciences, Poland (collection no. UPKG/1/2022).

#### **RESULTS**



#### **Microfacies**

Five microfacies (Fig. 3 and 2L) were distinguished within the Dubivtsi white chalk:

Planktonic and benthic foraminiferal wackestone. This microfacies occurred in the lowest part of the Dubivtsi section (sample 1). It contain contain the penthic and planktonic foraminifera (Fig. 3A) and rare bioclasts. No c-dinocysts were observed. The groundmass was mostly a micritic matrix, locally slightly recrystallized.

Benthic foraminiferal wackestone-packstone (Figs. 3D and E). This microfacies occurred in samples 2 and 13. Grain components were represented by benthic and planktonic foraminifera (where the benthics dominate, reaching up to 80% of the foraminiferal assemblages), common bioclasts, and pers (Fig. 3D). Only a few calcareous dinocysts represented by pithonellids were found. The components were embedded in micritic matrix, locally slightly recrystallized. Locally, some roughly parallel streaks composed of chaotically, and tightly packed bioclasts were observed in sample 2 (Fig.3E).

Pithonellid-rich wackestone-packstone (Figs. 3B and C). This microfacies occurred in samples 3–10. Pithonellid floods, which can exceed 80% of grain components, were observed (Fig. 3B). Calcareous dinocysts were represented by two species only: *Pithonella ovalis* and *P. sphaerica*. Small numbers of benthic and planktonic foraminifera were also observed. Benthic foraminifera dominated and locally exceeded 80% of the foraminiferal assemblages. Bioclasts were locally common. Pellets and pseudorets were common and very common locally (Fig. 3C). The groundmass was a dark gray micritic matrix that locally can be slightly recrystanced.

Calcareous dinocyst, foraminiferal wackestone-packstone (Figs. 3F and G). This microfacies occurred in the middle and upper parts of the section (samples from 17 to 25). It contained various c-dinocysts (Fig. 3F), represented by eight species (Assemblage no. 2; see chapter below). Benthic and planktonic foraminifera were also observed. Pellets and bioclasts were locally common (Fig. 3G). The components were embedded in slightly recrystallized micrite matter. Streaks composed of chaotically and tightly packed, more or less fragmented skeletons were locally visible.



Calcareous dinocyst, foraminiferal wackestone (Fig. 3H). This microfacies occurred in the uppermost part of the section in samples 29–32. It contained a moderate number of c-dinocysts represented by four species (Assemblage no. 3; see chapter below). Benthic and planktonic foraminifera were also observed. Bioclasts were less prevalent. Pellets and pseudopellets were number locally. Some orientations of the components, visible as streaks composed of chaotically, tightly packed organic skelet, were locally observed. These components were embedded mainly in the micritic matrix.

#### Vertical distribution of calcareous dinocysts

Calcareous dinocysts were present in fifteen of the sixteen samples (Supplementary 1, Fig. 4–7). Only one sample (no. 1) did not contain c-dinocysts (Fig. 2B.). The preservation of the c-dinocysts observed in the thin sections was generally good, even when the matrix was recrystallized. Locally, the specimens were poorly preserved therefore detailed identification was not possible. These specimens were included as problematic taxa in the statistical analysis (Supplementary 1).

Only eight species belonging to three genera (*Pithonella*, *Bonetocardiella*, and *Stomiosphaerina*) were identified. *Pithonella* accounted for 93–100%, dominating all assemblages. The assemblages were predominantly represented by *Pithonella ovalis* (Kaufmann in Heer 1865) orenz 1902; *Pithonella sphaerica* (Kaufmann in Heer 1865) *Zügel 1994* was less common; and *Pithonella lamellata* Keupp in Keupp & Kienel 1994 and *P. cardiiformis* Zügel 1994 were rare. *Bonetocardiella* represented by *Bonetocardiella conoidea* Bonnet 1956 appeared in smaller numbers. The genus *Stomiosphaerina* represented by *Stomiosphaerina biedai* Nowak 1974 and *Stomiosphaerina bakae* Ciurej 2023, recently created from the material of the Dubivtsi section (see Ciurej, under review), also occurred in small numbers. Small amounts of unidentified specimens, namely Species A, were also detected. These species are illustrated in Figs. 4–7.

Species diversity and the number of specimens that varied among individual samples were calculated. The three c-dinocyst assemblages were distinguished based on the vertical profile distribution (Table 1). These are as follows:



Assemblage no. 1 observed within samples 2 – 13 (Fig. 2H), contained a strongly depleted assemblage, represented by only two species, *P. ovalis* and *P. sphaerica*. *P. ovalis* prevailed in all samples. Three sub-assemblages were distinguished based on the number of specimens. Sub-assemblage 1A, observed in sample 2, was characterized by a negligible number of 37 specimens of pithonellids, including 27 of *P. ovalis* and 8 of *P. sphaerica*. Sub-assemblage 1B, occurred in samples 3 – 10, was characterized by a flood abundance of pithonellids; the pithonellids varied from 1480 to 2656 specimens, including 1045 to 2041 specimens of *P. ovalis* and 375 to 599 specimens of *P. sphaerica*. *P. sphaerica* showed a decreasing trend in younger samples. Sub-assemblage 1C, observed in sample 13, was marked by a significant decrease in c-dinocysts: the number of pithonellids dropped to 174 specimens, with 123 specimens of *P. ovalis* and 46 specimens of *P. sphaerica*.

Assemblage no.-2 was characterized by an increase in c-dinocyst diversity but a decrease in their numbers. Eight species, namely *P. ovalis*, *P. sphaerica*, *P. lamellata*, *P. cardiiformis*, *B. conoidea*, *S. bakae*, *S. biedai*, and Species A, were recognized. This assemblage occurred in samples 17–25 (Fig. 2H). A very high number of c-dinocysts, at 1568 specimens, was observed in sample 17, followed by a marked decrease to 652 specimens in sample 20, and a gradual decrease to 484 specimens in sample 25. The most abundant species within Assemblage no.-2 was *P. ovalis* (ranging from 1118 to 296 specimens), and *P. sphaerica* was less abundant (from 337 to 134 specimens). Other species included from 35 to 3 specimens.

Assemblage no.-3 was characterized by a half-decrease in c-dinocyst diversity compared with Assemblage no.-2. Four species observed herein were represented by *P. ovalis, P. sphaerica, B. conoidea,* and Species A, all known from previous assemblages. The number of specimens ranged from 454 to 403. The dominant species, *P. ovalis*, ranged from 411 to 329. The second species, *P. sphaerica*, ranged from 54 to 31 specimens and showed a clear downward trend toward the younger sediments. Other species included from 12 to 6 specimens. This assemblage occurred in the highest part of the section (samples 29–32) (Fig. 2H).

#### Paleoecological intervals



Based on the assemblages of c-dinocysts and planktonic and benthic foraminifera, together with microfacies analysis four paleoecological intervals were distinguished (Fig. 2O) as follows:

Interval 1 is characterized by the absence of calcareous dinocysts (sample 1). Planktonic and benthic foraminifera were relatively diverse and abundant. Planktonic foraminifera in samples from this interval represented almost 50% of the assemblage and were composed of deep- and shallow-dwelling taxa belonging to the following genera: Helvetoglobotruncana Marginotruncana, Dicarinella, Whiteinella, Falsotruncana, Globigerinelloides Heterohelix, and Hedbergella. Benthic foraminifera were dominated by Gavelinella, Gyroidinoides, Lenticulina, Globorotalites, Marssonella, Arenobulimina, and Valvulineria. This interval corresponds to the microfacies described as planktonic and benthic foraminiferal wackestone (Fig. 2L).

Interval 2 correlates to c-dinocysts Assemblage no. 1 (samples 2–13) including sub-assemblage of very low species diversity, composed of only two species, and a very high number of c-dinocysts (samples 3–10) and sub-assemblage with a much lower number of specimens (samples 2 and 13). Planktonic foraminiferal assemblage in samples from this interval differs from that of Interval 1 by a drastic decline in the number of planktonic foraminifera and disappearance of deep-dwelling forms (Helvetoglobotruncana Marginotruncana, Dicarinella, and Falsotruncana). Benthic foraminiferal assemblages differed from those of Interval 1, primarily due to the disappearance of representatives of the genus Valvulineria. The benthic foraminifera of the upper part of Interval 2 had very low diversity and were composed of only five genera: Gavelinella, Gyroidinoides, Lenticulina, Globorotalites, and Arenobulimina. Interval 2 correlates with two different microfacies: pithonellid-rich wackestone-packstone (samples 3–10) (Fig. 2L) and wackestone-packstone microfacies (samples 2 and 13) (Fig. 2L).

**Interval 3** is characterized by c-dinocysts Assemblage no. 2 (samples 17–25) that is moderately diverse (eight species) with an intermediate number of c-dinocyst specimens. Planktonic foraminiferal assemblages in samples from this interval were similar to those of Interval 2, whereas benthic foraminiferal assemblages differed mainly



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in the occurrence of deep-infaunal *Praebulimina*. This interval corresponds to the c-dinocystand foraminiferal wackestone-packstone microfacies (Fig. 2L).

Interval 4 correlates to c-dinocysts Assemblage no.—3 (samples 29–32) characterized by low diversity (four species) and a moderate number of c-dinocysts. Planktonic foraminiferal assemblages in samples from this interval differed from that of Intervals 1 and 2 by the re-appearance of deep-dwelling forms (*Marginotruncana* and *Dicarinella*), while benthic foraminiferal assemblages differed by the disappearance of *Praebulimina* and the occurrence of *Eponides*. This interval is correlated with the c-dinocyst-and foraminiferal wackestone microfacies (Fig. 2L).

#### **DISCUSSION**

#### Calcareous dinocyst distribution in relation to the water depth

In the Dubivtsi section, two species of the genus Pitonella (P. ovalis and P. sphaerica) are the main components of the assemblages, with evident dominance of Pithonella ovalis. The P. sphaerica to P. ovalis ratio (Ps/Po ratio) was introduced by Keupp (1991), Zügel (1994), and Wendler et al. (2002) to assess the water depth of the basin and distance from the shoreline. According to these authors, a high Ps/Po ratio ~10 characterizes shelf assemblages with eostal influence. A low Ps/Po ratio ~3 suggests that the assemblages originated from the outer shelf/distal environment. Throughout the entire Dubivtsi section, the *Ps/Po* ratio was very low, ranging from 0.42 to 0.08. This ratio may demonstrate that the Dubivtsi chalk was deposited in the outer shelf environment. However, the question arises as to how to interpret the inner and outer shelves of the Cretaceous. A continental shelf is part of a continent that is submerged under seawater. Following this definition, the entire Cretaceous epicontinental sea should be interpreted as a shelf. Therefore, a direct link between the present and the 'non-actualistic' Cretaceous marined epositional environment is difficult to establish. So we accept, that low Ps/Po ratio in case of the studied Dubivtsi section indicates instead a far distance from an emerged area. 🕦 Dubivtsi chalk was deposited in rather shallow epicontinental sea that was influenced by sea-level fluctuations. Based on planktonic foraminiferal water depth indices (see Bé and Hamlin, 1967, Bé, 1977; Hart and Bailey, 1979; Caron and Homewood, 1983; Leckie, 1987), it



can be concluded that the water depth during deposition of Intervals 2 and 3 was ca. 50–100 meters, while during intervals 1 and 4 greater than 100 meters, (*Dubicka and Peryt, 2012*). The sea level drop, during Interval 2 is believed to be related to global eustatic regression during the Hyphantocera Event (see *Wiese and Kröger, 1998; Wiese et al., 2004*).

The sea level curve interpreted from foraminiferal data correlates with recent studies of c-dinocyst assemblages and also with the microfacies analysis (see Fig. 2H-M). A significant sea level drop marked in the lowest part of the section (between samples 1 and 2) correlates with the appearance of c-dinocysts in the chalk deposits, though still with negligible numbers of specimens and with very low species diversity (Sub-assemblage no. 1A). The low sea level occurred during Interval 2, which corresponds to a flood abundance but very low diversity Sub-assemblage no. 1B. The transgressive episode likely started within Interval 3, which correlates with an increase in c-dinocyst diversity (eight species) but a decrease in their numbers (Assemblage no. 2). A significant sea level rise observed in the uppermost part of the section (Interval 4), corresponds to low abundance and diversity c-dinocyst Assemblage no. 3. The microfacies analysis from Interval 4 also suggests a transgressive event, as bioclasts are less common.

#### Nutrient availability and evolution of the basin

The study of the Ukrainian chalk revealed a relatively shallow water setting c.a. between 50 and 100 m depth during Intervals 2 and 3 (Fig. 2O) which were, however, enhanced by a small amount of terrigenous influx from the land area. The minimal terrigenous influx into the basin is indicated by nearly pure calcareous facies, with little or no detrital content, such as quartz or clay minerals (*Dubicka et al., 2014*). The Dubivtsi chalk has an exceptionally high CaCO<sub>3</sub> content, ranging from 97.8% to 99.9%. Additionally, the chalk displays diamagnetic properties that are characterized by a very low negative value of magnetic susceptibility ( $\chi$ ), with a mean value of  $-0.5 \times 10^{-8}$  m³ kg<sup>-1</sup> (*Dubicka et al., 2014*). Individual samples exhibited slightly increased values up to  $0.8 \times 10^{-8}$  m³ kg<sup>-1</sup> (sample 15). This phenomenon is likely due to the basin's paleogeographic position and its relatively large distance from the shoreline (Fig. 1C).



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During sedimentation of Intervals 1–3 the nearest land area might be associated with the Ukraine Slied (*Pasternak et al., 1968; Gavrilishin et al., 1991*, and Fig. 1 which could have been situated at a distance of 200–300 km away.

The c-dinocyst assemblage in the studied Dubivtsi section was characterized by 363 low species richness dominated by Pithonella, with some shifts from two species 364 occurring in the lower part (Assemblage no. 1) to eight taxa in the middle part 365 (Assemblage no. 2) and four species in the highest part (Assemblage no. 3). A similar 366 367 very low-diverse c-dinocyst assemblage, represented by only seven species and dominated by *Pithonella* was also observed in the upper Turonian of the German Basin 368 (Wiese et al., 2015). Such a low species richness was interpreted as a 'nutrient crisis 369 caused by the drowning of source areas of nutrient input during the early Late 370 371 Cretaceous sea-level highstand' (Wiese et al., 2015, p.1). Furthermore, Gale et al. (2000) linked a high abundance of c-dinocysts in southern England with a reduction in 372 373 water productivity during the Cenomanian-Turonian boundary interval (see also Dubicka et al., 2021). A spread of calcareous nannoplankton/planktonic foraminifera/c-374 375 dinocyst-rich sediments of the Cenomanian and Turonian has been previously recognized (Hay, 2008; Pearce et al., 2009; Linnert et al., 20 p from England to the 376 377 Russian Platform. In general, it is interpreted that during the Turonian the highly oligotrophic system of the European shelf sea was established (Haq, 2014; Gale et al., 378 379 2000; Pearce et al., 2009; Linnert et al., 2010). Thus, considering the above, the highly abundant but low-diversity c-dinocyst 380 Assemblage no. 1 (Interval 2), apparently resulted from reduced surface water 381 productivity and an oligotrophic environment, which is additionally supported by data 382 from foraminiferal assemblages (Fig. 2J, K, M). Oligotrophic conditions of Interval 2, 383 384 coinciding with season vel, that correlates with the Hypanthocer Event (the period with lower relative sea level recognized in western Europe; Wiese et al., 2004), may appear 385 surprising. Usually, regression is related to less oligotrophic conditions as the sea 386 retreat exposes land areas, affecting winnowing increase and a higher input of nutrients 387 from the land to the sea. However, the large distance between Dubivtsi and land areas 388 (Fig. 1C) likely limited the supply of nutrients from hinterland sources even during sea-389 level fall. On the other hand, shelf upwelling (Merino, 1997; Zaytsev et al., 2003; Jing et 390



al., 2009) from the nearby Carpathian Basin (today the Carpathian Orogen is located ca. 50 km to the south), that likely injected nutrients during sea-level highstand, might have been halted during the discussed sea level lowstand.

The Assemblage no. 2 characteristic for Interval 3 is likely related to more mesotrophic conditions within the photic zone, which could have favored an increase in the species richness into eight species (six new species of c-dinocysts and *P. ovalis* and *P. sphaerica*). The higher trophic level is also supported by the significant increase in the deep-infaunal benthic foraminifera *Praebulimina* (Fig. 2K). During Interval 3, the studied area was still under a relatively low sea level, however, likely during progressive deepening that might have affected more nutrient input from the Carpathian Basin. In addition, some nutrient supply might have had runoff from the adjacent land in the Stryi region, named "Krukienic Island" (Pasternak, 1959), located some 40–50 km from Dubivtsi. The island became uplifted ouring the Subhercynian tectonic phase that commenced in the late Turonian and caused extensive basin inversions in Central Europe (see *Walaszczyk*, 1992; Vejbæk and Andersen, 2002; Voigt et al., 2021). The uplift of this area close to the European continental margin might be supported by the increase in mass magnetic susceptibility and the decrease in CaCO<sub>3</sub> content (*Dubicka et al.*, 2014).

A slight decrease in nutrients under mesotrophic/oligotrophic conditions (Interval 4) could have influenced the c-dinocyst Assemblage no. 3 (Fig. 2H). This is interpreted by a half- in c-dinocyst species richness in relation to Interval 3 (Fig. 2O) and the disappearance of the infaunal foraminifera *Praebulimina* (Figs. 2F, K). The renewed drop of the trophic conditions could have been related to the sitting of the emerging areas during transgression as shown by the reappearance of deep-dwelling planktonic foraminifera. This theory was confirmed by the shift in the negative direction of the mass magnetic susceptibility of the samples from this interval (*Dubicka et al., 2014*).

In summary, the data from this study show that nutrient availability gradients, which are a function of water depth and distance from the shore, strongly determined changes in the calcareous dinocyst assemblage

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#### 431 Author contributions

- 432 AC examined and determined the calcareous dinocysts and performed the microfacies
- analysis. ZD provided the samples for this study. Both authors discussed the results.
- 434 AC wrote the first version of the manuscript. Both authors edited the final version of the
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#### 436 Competing Interests

The authors declare there are no competing interests.

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Zonneveld AF, Brune A, Willems H. 2000. Spatial distribution of calcareous 690 dinoflagellate cysts in surface sediments of the Atlantic Ocean between 13"N and 691 36"s. Review of Palaeobotany and Palynology 11:197–223. 692 Zonneveld KAF, Meier KJS, Esper O, Siggelkow D, Wendler I, Willems H. 2005. 693 The (palaeo) environmental significance of modern calcareous dinoflagellate 694 cysts: a review. Paläontologische Zeitschrift. 79(1):61-77. 695 **Zügel P. 1994.** Verbreitung kalkiger Dinoflagellaten-Zysten im Cenoman/Turon von 696 Westfrankreich und Norddeutschland. Courier Forschungsinstitut Senckenberg 697 **176**:1–159. 698 699 Figure 1 Location of the Dubivtsi section. (A) Paleogeographical man during 700 Turonian time (~ 91.1 Ma), (modified after Pasternak, 1959; Ziegler, 1990; Scotese, 701 2014), and (B) sketch map with location of the studied Dubivtsi section. 702 Figure 2 Microfossil assemblage changes within the upper Turonian chalk of the 703 **Dubivtsi section.** (A)  $\delta^{13}C_{carb}$  curve for Dubivtsi chalk. (B)-(D) Percentage content of c-704 dinocysts (calculated in thin sections). (E) Total number of c-dinocysts (calculated in 705 thin sections). (F) Sample c-dinocysts species diversity (calculated in thin section view). 706 (G) P. sphaerica/P. ovalis ratio. (H) Calcareous dinocysts assemblages based on 707 changes of diversity and total number. (I) P/B ratio. (J) Distribution of particular 708 morphotypes of planktonic foraminifera. (K) Abundance fluctuation of species and group 709 of species of benthic foraminifera in foraminiferal assemblages. (L) Microfacies 710 distinguished within section. (M) Water depth fluctuations in western Ukraine based on 711 712 planktonic foraminifera. (N) Trophic conditions fluctuations. (O) Paleoecological intervals. A, I, J, K, M after Dubicka and Peryt, 2012). Local planktonic foraminiferal 713 714 zonation after Walaszczyk and Peryt (1998). Figure 3 Microfacies of the white chalk of the Dubivtsi section observed in 715 transmitted light microscope. (A) Planktonic and benthic foraminiferal wackstone 716 showing foraminifera dispersed within slightly recrystallized micritic matrix (sample 1). 717 (B), (C) Pithonellid-rich wackstone-packstone with large amount of pithonellids (oval 718 and spherical cross sections) marked by blue arrows, rare foraminifera (yellow arrow), 719



- bioclasts (green arrows), and pellets and pseudo relets (red circles), (samples: B 4, C 720 - 8). (D), (E) Benthic foraminiferal wackstone-packstone with foraminifera (yellow arrow) 721 and pellets (red arrows) dispersed within recrystallized micrite matrix, and streak-like 722 structures composed of chaotically, tightly packed organic keletons, including 723 foraminifera; streak and ground mass undary marked by orange arrow (samples: D -724 13, E - 2). (F), (G) Calcareous dinocysts, foraminiferal wackstone-packstone, showing 725 c-dinocysts (oval and spherical cross-sections) marked by blue arrows, and foraminifera 726 (yellow arrows) and common bioclasts (green arrows), (samples: F - 20, G - 17). (H) 727 Calcareous dinocysts, foraminiferal wackstone with c-dinocysts (blue arrows) and 728 foraminifera (vellow arrows), dispersed within recrystallized micrite matrix (sample 3) 729 Figure 4 Transmitted light microscopy images of calcareous dinocysts from the 730 **Dubivtsi section.** (A) - (C) Bonetocardiella conoidea Bonnet 1956 showing the 731 pithonellid wall (yellow arrows) and aperture (blue arrows), (sample 17). (D), (E) 732 Pithonella lamellata Keup in Keupp and Kienel 1994 showing wall with the double layer 733 734 (blue arrows), and extinction cross (red arrows), (sample 17), (F) – (K) Pithonella ovalis (Kaufmann in Heer 1865) Lorenz 1902, (F, G, I - sample 4; H - sample 7, J, K - sample 735 17) showing the thick wall with double layer (yellow arrows), and the pithonellid wall 736 type (green arrows), the aperture (blue arrows) and extinction cross (red arrows): (F) – 737 (H) longitudinal sections; (I) - (K) axial sections. All images were taken from thin 738 sections under plain-polarized light, except E2 and J2 which are under crossed polarized 739 740 light. Figure 5 Transmitted light microscopy images of calcareous dinocysts from the 741 **Dubivtsi section.** (A) – (E) *Pithonella sphaerica* (Kaufmann in Heer 1865) Zügel 1994; 742 showing the thick wall with double layer (yellow arrows), and the aperture (blue arrows) 743 and extinction cross (red arrows), (samples: A - 3, B - 4, C - E - 7). (F) – (H) *Pithonella* 744 cardiiformis Zügel 1994, with aperture (blue arrow), (sample 17). All images were taken 745 from thin sections under plain-polarized light, except E2 that was under crossed polars 746 light. 747
- 748 Figure 6 Transmitted light microscopy images of calcareous dinocysts from the
- 749 **Dubivtsi section.** (A), (B) *Stomiosphaerina biedai* Nowak 1974, (samples: A 20; B –

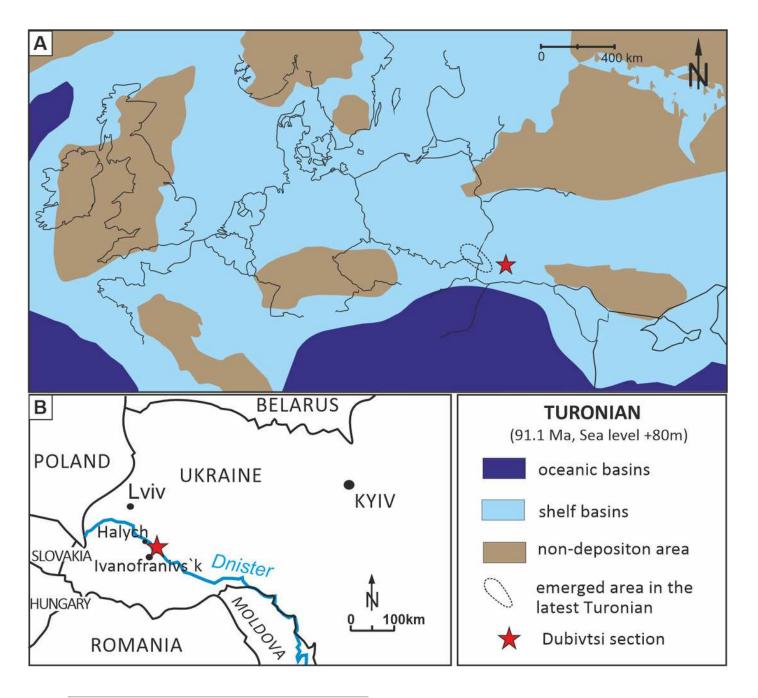
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22). (C), (D) Stomiosphaerina bakae Ciurej 2023, (sample 17). (E), (F) Species A 750 (samples: E - 17, F - 32). Thin sections, plain-polarized light, except B2, C2, E2 -751 crossed polars light. 752 Figure 7 SEM images of calcareous dinocyst from the Dubivtsi section. (A) – (C) 753 Pithonella ovalis (Kaufmann in Heer 1865) Lorenz 1902: (A) Longitudinal view of P. 754 ovalis showing outer wall with diagenetic calcited ystals overgrowths (sample 2). (B) 755 Longitudinal view of P. ovalis showing outer wall texture (sample 3). (B1) Magnified 756 view of the same specimens (sample 3). (C) Longitudinal view of *P. ovalis* of outer wall 757 with blocky calcite structures (sample 6). (C1) Magnified view of the same specimens 758 showing details of aperture (sample 6). (D) - (H) Pithonella sphaerica (Kaufmann in 759 Heer 1865) Zügel 1994 in various stage of preservation: (**D**) Outer wall with blocky, 760 secondary calcite structure (sample 3). (E) Specimen with partially removed thin outer 761 wall (sample 4). (E1) Close-up of the same specimens with details of inner wall (sample 762 4). (F), (G) Variously diagenetically altered outer wall where the blocky, recrystallized 763 calcite structure is visible (F - sample 3, G - sample 6). (H, H1) outer wall with blocky, 764 recrystallized calcite structure (sample 7). 765

## Figure 1 📮

Location of the Dubivtsi section

(A) Paleogeographical map during Turonian time (~ 91.1 Ma), (modified after Pasternak, 1959; Ziegler, 1990; Scotese, 2014), and (B) sketch map with location of the studied Dubivtsi section.



Microfossil assemblage changes within the upper Turonian chalk of the Dubivtsi section.

**A)**  $\delta^{13}C_{carb}$  curve for Dubivtsi chalk. **(B)-(D)** Percentage content of c-dinocysts (calculated in thin sections). **(E)** Total number of c-dinocysts (calculated in thin sections). **(F)** Sample c-dinocysts species diversity (calculated in thin section view). **(G)** *P. sphaerica/P. ovalis* ratio. **(H)** Calcareous dinocysts assemblages based on changes of diversity and total number. **(I)** P/B ratio. **(J)** Distribution of particular morphotypes of planktonic foraminifera. **(K)** Abundance fluctuation of species and group of species of benthic foraminifera in foraminiferal assemblages. **(L)** Microfacies distinguished within section. **(M)** Water depth fluctuations in western Ukraine based on planktonic foraminifera. **(N)** Trophic conditions fluctuations. **(O)** Paleoecological intervals. A, I, J, K, M after Dubicka and Peryt, 2012). Local planktonic foraminiferal zonation after Walaszczyk and Peryt (1998).



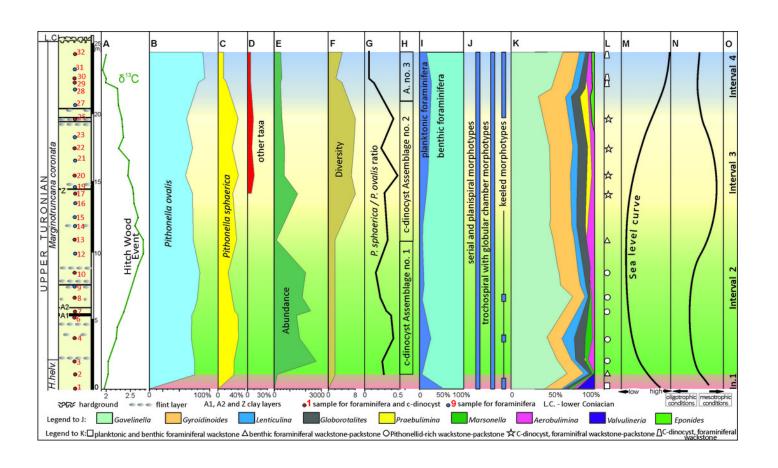




Table 1(on next page)

Supplementary 1

Supplementary 1 Table 1. Distribution of calcareous dinocysts in the Dubivtsi section.

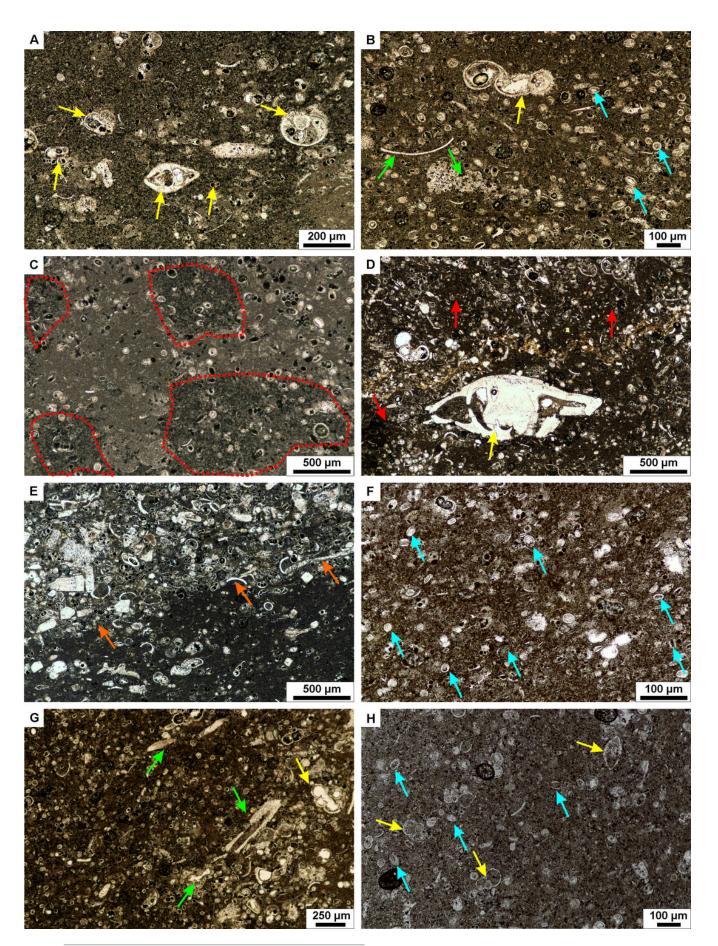
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1 2

	Interval	Species/ Sample	Bonetocardiella conoidea	Pithonella cardiformis	Pihonella lamellata	Pithonella ovalis	Pithonella sphaerica	Stomiosphaerina bakae	Stomiosphaerina biedai	Species A	Problematic	Abundance	Diversity	Ps/Po ratio
		32	7			348	31			7	10	403	4	0.09
Interval 3	30				411	34				9	454	2	0.08	
		29	12			329	54			6	13	414	4	0.16
		25	15	4	4	296	140	12	6	3	4	484	8	0.47
	Interval 2	22	13	6	11	467	134	9	4	5	9	658	8	0.29
THICT VALUE		20	17	10	9	385	195	17	8		11	652	7	0.51
		17	35	18	21	1118	337	14	6	4	15	1568	8	0.30
	Subinterval C	13				123	46				5	174	2	0.37
	Subinterval B	10				1683	320				13	2016	2	0.19
Interval 1		8				1450	375				9	1834	2	0.26
		7				1757	555				11	2323	2	0.32
		6				1045	426				9	1480	2	0.41
		4				1121	470				10	1601	2	0.42
		3				2041	599				16	2656	2	0.29
	Subinterval A	2				27	8				2	37	2	0.30

Microfacies of the white chalk of the Dubivtsi section observed in transmitted light microscope.

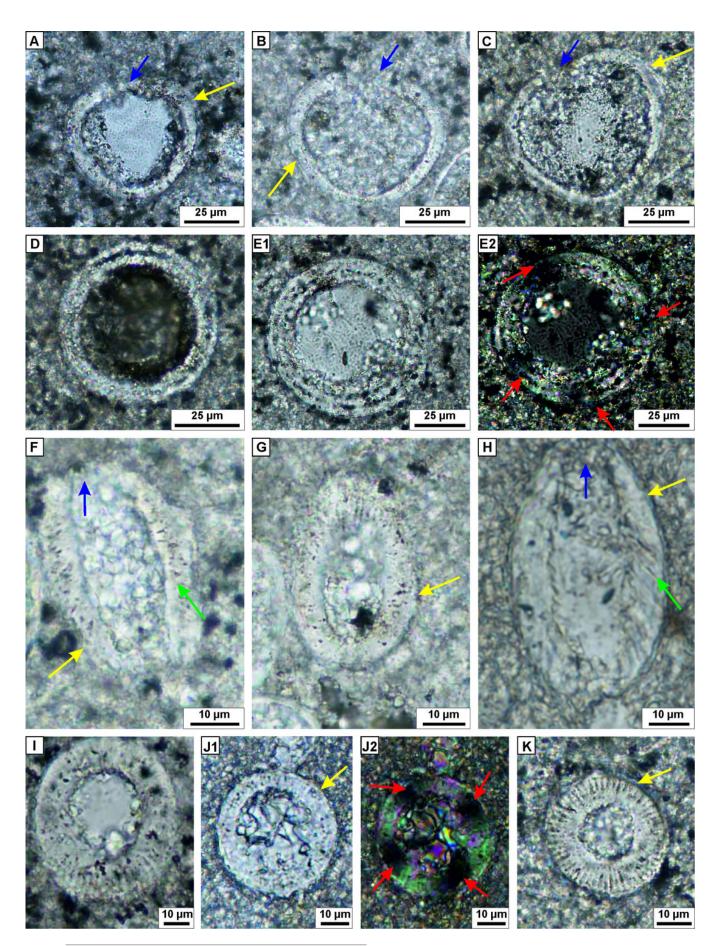
(A) Planktonic and benthic foraminiferal wackstone showing foraminifera dispersed within slightly recrystallized micritic matrix (sample 1). (B), (C) Pithonellid-rich wackstone-packstone with large amount of pithonellids (oval and spherical cross sections) marked by blue arrows, rare foraminifera (yellow arrow), bioclasts (green arrows), and pellets and pseudopellets (red circles), (samples: B - 4, C - 8). (D), (E) Benthic foraminiferal wackstone-packstone with foraminifera (yellow arrow) and pellets (red arrows) dispersed within recrystallized micrite matrix, and streak-like structures composed of chaotically, tightly packed organic skeletons, including foraminifera; streak and ground mass boundary marked by orange arrow (samples: D - 13, E - 2). (F), (G) Calcareous dinocysts, foraminiferal wackstone-packstone, showing c-dinocysts (oval and spherical cross-sections) marked by blue arrows, and foraminifera (yellow arrows) and common bioclasts (green arrows), (samples: F - 20, G - 17). (H) Calcareous dinocysts, foraminiferal wackstone with c-dinocysts (blue arrows) and foraminifera (yellow arrows), dispersed within recrystallized micrite matrix (sample 32).



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Transmitted light microscopy images of calcareous dinocysts from the Dubivtsi section.

(A) – (C) Bonetocardiella conoidea Bonnet 1956 showing the pithonellid wall (yellow arrows) and aperture (blue arrows), (sample 17). (D), (E) Pithonella lamellata Keup in Keupp and Kienel 1994 showing wall with the double layer (blue arrows), and extinction cross (red arrows), (sample 17). (F) – (K) Pithonella ovalis (Kaufmann in Heer 1865) Lorenz 1902, (F, G, I - sample 4; H – sample 7, J, K – sample 17) showing the thick wall with double layer (yellow arrows), and the pithonellid wall type (green arrows), the aperture (blue arrows) and extinction cross (red arrows): (F) – (H) longitudinal sections; (I) – (K) axial sections. All images were taken from thin sections under plain-polarized light, except E2 and J2 which are under crossed polars light.

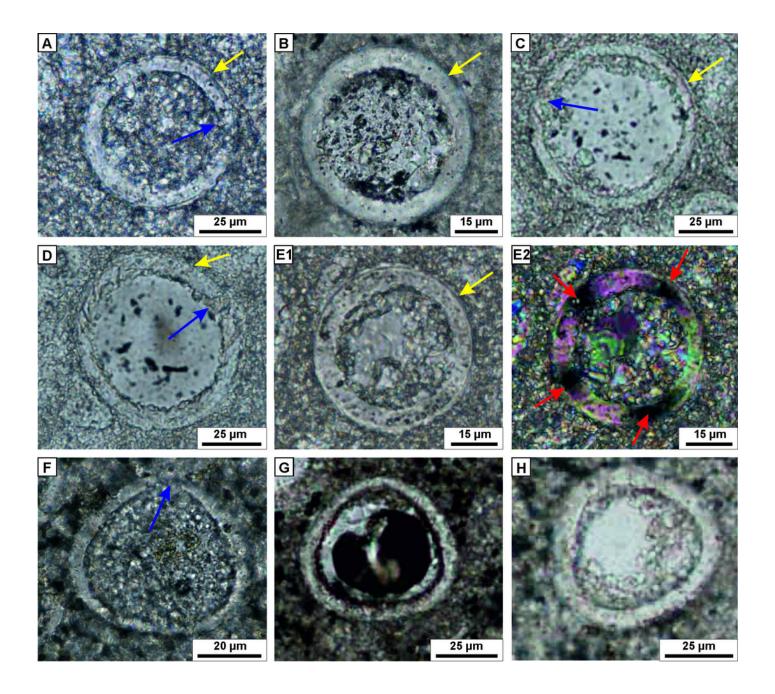


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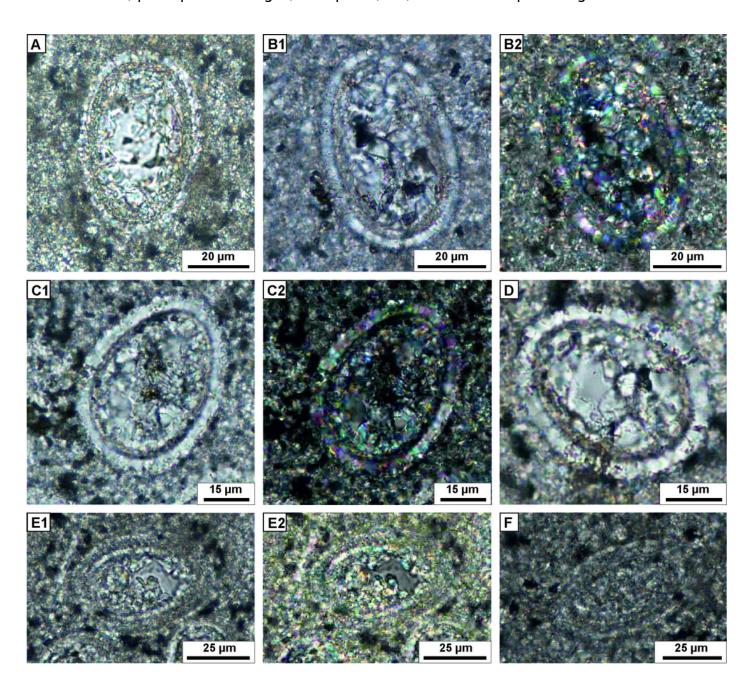
Transmitted light microscopy images of calcareous dinocysts from the Dubivtsi section.

(A) – (E) *Pithonella sphaerica* (Kaufmann in Heer 1865) Zügel 1994; showing the thick wall with double layer (yellow arrows), and the aperture (blue arrows) and extinction cross (red arrows), (samples: A – 3, B – 4, C – E – 7). (F) – (H) *Pithonella cardiiformis* Zügel 1994, with aperture (blue arrow), (sample 17). All images were taken from thin sections under plain-polarized light, except E2 that was under crossed polars light.



Transmitted light microscopy images of calcareous dinocysts from the Dubivtsi section.

(A), (B) Stomiosphaerina biedai Nowak 1974, (samples: A - 20; B - 22). (C), (D) Stomiosphaerina bakae Ciurej 2023, (sample 17). (E), (F) Species A (samples: E - 17, F - 32). Thin sections, plain-polarized light, except B2, C2, E2 - crossed polars light.



SEM images of c-dinocyst from the Dubivtsi section.

(A) - (C) Pithonella ovalis (Kaufmann in Heer 1865) Lorenz 1902: (A) Longitudinal view of P. ovalis showing outer wall with diagenetic calcite crystals overgrowths (sample 2). (B) Longitudinal view of P. ovalis showing outer wall texture (sample 3). (B1) Magnified view of the same specimens (sample 3). (C) Longitudinal view of P. ovalis of outer wall with blocky calcite structures (sample 6). (C1) Magnified view of the same specimens showing details of aperture (sample 6). (D) - (H) Pithonella sphaerica (Kaufmann in Heer 1865) Zügel 1994 in various stage of preservation: (D) Outer wall with blocky, secondary calcite structure (sample 3). (E) Specimen with partially removed thin outer wall (sample 4). (E1) Close-up of the same specimens with details of inner wall (sample 4). (F), (G) Variously diagenetically altered outer wall where the blocky, recrystallized calcite structure is visible (F - sample 3, G - sample 6). (H, H1) outer wall with blocky, recrystallized calcite structure (sample 7).

