

STUDIA GEOLOGICA POLONICA

Vol. 136, Kraków 2013, pp. 5–197.

*Methods and Applications in Micropalaeontology*

*Edited by J. Tyska*

*Part III*

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**Eocene dinoflagellate cysts from the Popiele beds  
at Koniusza (Skole Nappe, Flysch Carpathians, Poland):  
taxonomy, biostratigraphy, and palaeoenvironmental  
reconstruction of a marginal marine basin<sup>2</sup>**

(Figs 1–89)

KRAKÓW 2013

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<sup>2</sup> Manuscript accepted for publication on October 6, 2013.

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### Abstract

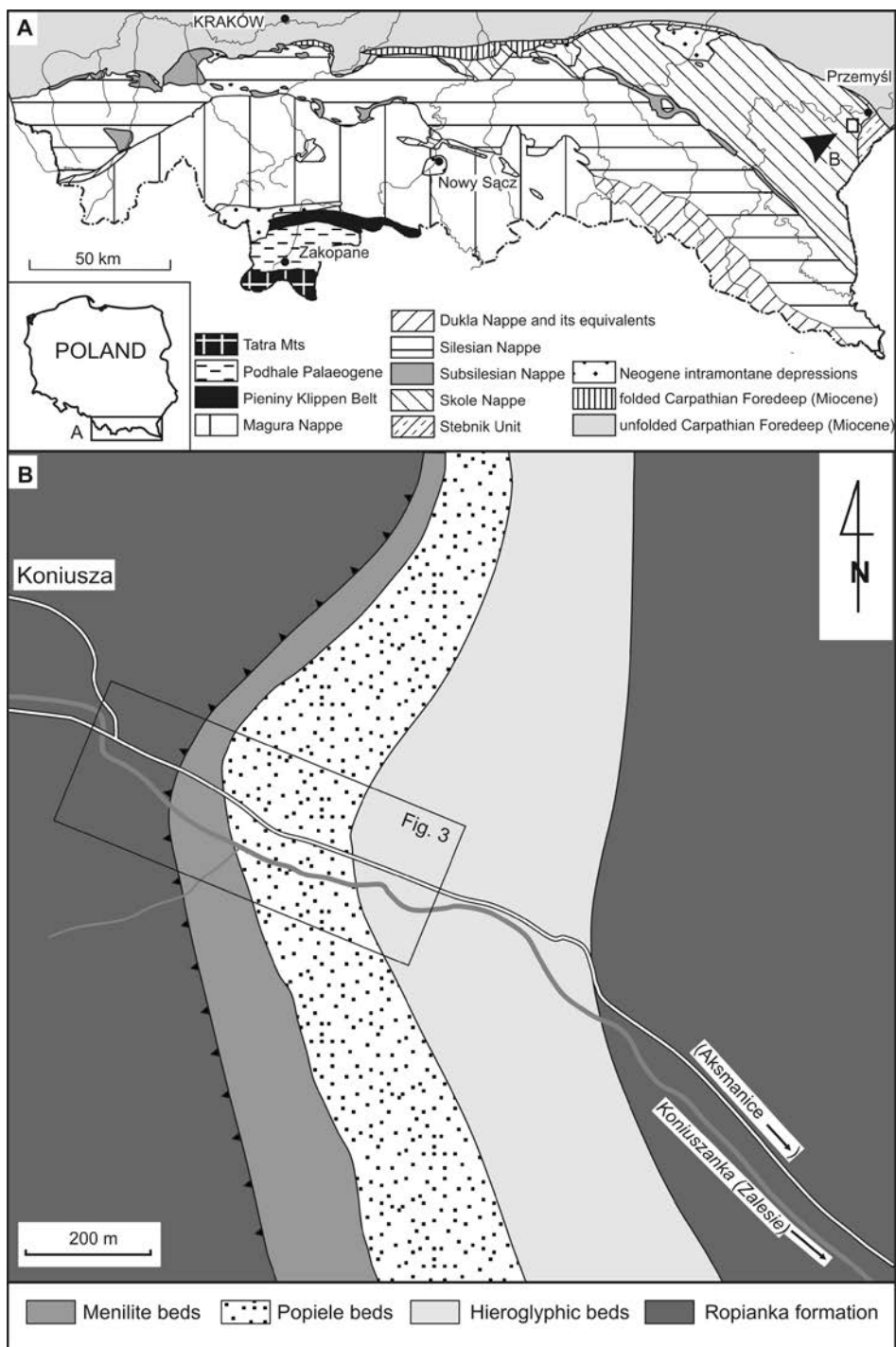
A total of 152 dinoflagellate cyst taxa from the Popiele beds exposed at Koniusza (Skole Nappe, Flysch Carpathians, Poland) are systematically described. The biostratigraphical interpretation of their assemblages suggests Eocene (Bartonian and Priabonian) age. The dark-coloured fossiliferous mudstone that forms bulk volume of the olistostromic Popiele beds is dated as Priabonian; and the pale-coloured marl, mainly forming clasts, is Bartonian and Priabonian. Palaeoenvironmental analysis of palynofacies and dinoflagellate cyst assemblages suggests that the deposits studied were laid down on a shelf (subsequently redeposited into deeper parts of the flysch basin). The pale-coloured Bartonian marl settled down in an environment of relatively calm, hemipelagic deposition with limited terrestrial influx, possibly in an offshore shelf under relatively oligotrophic surface water conditions; their sedimentary setting was presumably influenced by waters from lagoonal environments, manifested by a high ratio of near-shore taxa. The non-calcareous pale-coloured Priabonian mudstone was deposited in an even more offshore setting; its dinoflagellate cyst assemblage shows some similarities with the one from the offshore Hieroglyphic beds. The dark-coloured Priabonian mudstone settled down under a relatively high rate of a terrestrial material influx, presumably during period of a more intense freshwater input into the shelf basin, reflected by a high ratio of land-derived organic particles. This freshwater influx led to a minor eutrophication and a possible salinity decrease in the surface water layer. A comparison of dinoflagellate cyst assemblages from the Popiele beds with coeval ones from the neighbouring areas suggests that the Skole Basin was connected with epicontinental basin of south-eastern Poland during the Bartonian, whereas it was presumably isolated during the Priabonian.

**Key words:** dinoflagellate cysts, Eocene, Popiele beds, Carpathians, palaeoenvironment, biostratigraphy.

### INTRODUCTION

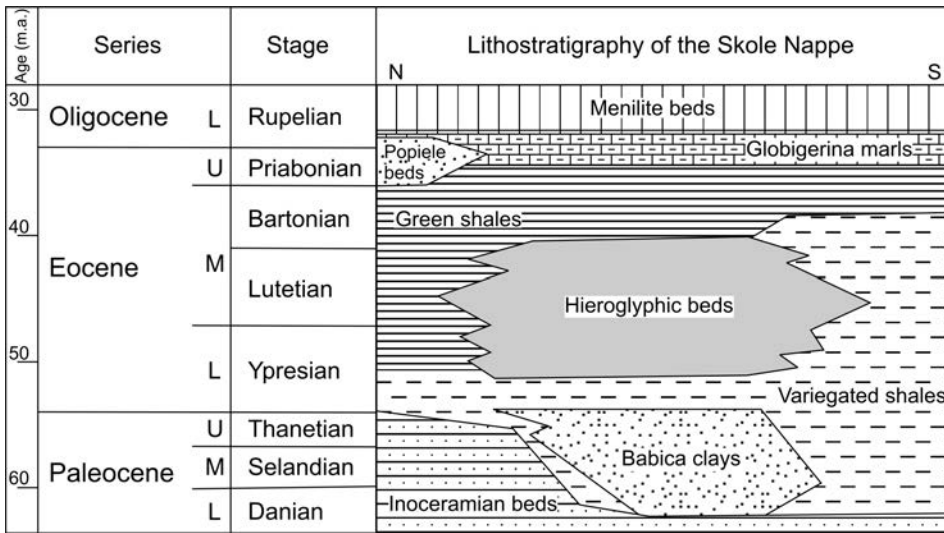
The most of Palaeogene strata of the Flysch (Outer) Carpathians represent the deep-water deposits of turbiditic and hemipelagic origin. The water depth of the flysch basins was estimated on the base of foraminiferal assemblages (e.g., Bieda *et al.*, 1963; Geroch *et al.*, 1967) found in pelagic layers to 2–4 km (Olszewska & Malata, 2006). During the Eocene, the southernmost Magura Basin was the deepest one (over 3.5 km deep), whereas northern basins, including the Skole Basin, were presumably shallower (app. 2.5–3.5 km deep; Olszewska & Malata, 2006). A significant shallowing trend in the Flysch Carpathian basins took place during the Eocene–Oligocene transition (e.g., Uchman *et al.*, 2006) and resulted in water depth reduction of the Skole Basin to barely 200–600 m (Malata & Poprawa, 2006). These depth values refer to the basal parts, whereas palaeoenvironmental conditions on the northern shelf have almost been unknown, covered by a thick sequence of folded and overthrust flysch deposits. Their only traces are fragmentarily preserved slump deposits derived from the northern and north-eastern margins of the Flysch Carpathian basin system. One of them is represented by the Popiele beds. This is a submarine slump deposit formed during the Late Eocene–Early Oligocene in the Skole Basin – the outermost basin of eastern part of the Polish Carpathians (Dzuffyński & Kotlarczyk, 1965) – presumably as a result of the Pyrenean orogenic phase (Dzuffyński *et al.*, 1979a; Kotlarczyk, 1988a).

The Popiele beds consist of dark-coloured massive, unstratified sandy siltstone with lithologically variable intraclasts. Their lithology and specific macrofossil



**Fig. 1.** Geology of study area: **A** – tectonic map of Polish Carpathians (after Książkiewicz, 1977); **B** – geologic map of the Koniusza vicinity (after Kotlarczyk, 1985b; simplified)





**Fig. 2.** Paleocene–Lower Oligocene lithostratigraphy of the Skole Nappe (from Ślaczka & Kaminski, 1998)

content, suggest that these deposits were originally laid down in a proximal sedimentary setting. Analysis of their palynological content from the exposures at Koniusza was intended for palaeoenvironmental reconstruction of sedimentary conditions at the northern margin of the Skole Basin. A biostratigraphic study of dinoflagellate cysts from this unit allows its correlation with coeval flysch and epicontinental deposits. The latter occur on a land north of the flysch basins, which was episodically flooded during the Eocene and Early Oligocene by short-lasting marine transgressions. Their record is fragmentally preserved below a thick cover of Miocene strata in the Carpathian Foredeep (Ślodkańska, 1999; Gedl, 2000a, b, 2003, 2006a; Śmist, 2004; Myśliwiec & Śmist, 2006) and in Roztocze (e.g., Piwocki, 2004).

## GEOLOGICAL BACKGROUND

The Eocene–Miocene flysch sequence of the external parts of the Skole Nappe, the outermost tectonic unit of the Polish Flysch (Outer) Carpathians (Fig. 1A), contains frequent exotic-bearing deposits of submarine slumps (e.g., Dżułyński & Kotlarczyk, 1965; Kotlarczyk, 1979, 1981; Gucik, 1981; Rajchel, 1990). These are usually discontinuous bodies, which consist chiefly of resedimented material from the northern shelf areas of the Skole Basin. One of them is represented by the fossiliferous Popiele beds, which occur between the Eocene Hieroglyphic beds and the Lower Oligocene Menilite beds (Fig. 2). Due to common occurrence of well preserved macrofossils (mainly gastropods and bivalves), this lithostratigraphic unit has been an object of palaeontological studies for over 100 years (Wójcik, 1903; Wiśniowski, 1908). The name “Popiele beds” was introduced by Kropaczek (1919; Polish names: “warstwy z Popiel”, “warstwy popielskie”) after its stratotype

located at Popiele (NW from Borysław) in the Ukrainian Carpathians, then a Polish territory – see Tołwiński (1925, 1928), Horwitz (1926), Hempel (1926), Krajewski (1927), Świdorski (1927–1928). Rajchel (1990) distinguished these strata as an informal lithostratigraphic unit in the rank of member (the “Popiele Member”) of the informal “Hieroglyphic Formation”; in this paper the traditional name “Popiele beds” is used following Ryłko (2004, p. 308).

The Popiele beds crop out in a narrow belt in the northernmost part of the Skole Nappe between Przemyśl (Poland) and the Prut River Valley in the Pokutse Carpathians, Ukraine (Horwitz, 1926; Dżułyński & Kotlarczyk, 1965; Kotlarczyk, 1985b; Fig. 1B). In Poland, their exposures are grouped mainly south of Przemyśl (Wiśniowski, 1908; Rogala, 1925; Watycha, 1964; Rajchel, 1990). Several outcrops of this unit are reported by Rajchel (1990). Ney (1961, 1968, fig. 16E) reported the Popiele beds from the Stebnik Unit in boreholes Jaksmanice-10 and Jaksmanice-25. However, the tectonic position of these flysch deposits is still enigmatic: tectonic slides according to Ney (1968), olistostromes within the Stebnik Unit according to Wdowiarz (1976, fig. 2, cross-section II-II), flysch substratum of the Stebnik Unit according to Kotlarczyk (e.g., 1988b). Majority of the Popiele beds exposures are now in Ukraine (see Rajchel, 1990).

The thickness of the Popiele beds is difficult to estimate; presumably it does not exceed 100 m (Dżułyński & Kotlarczyk, 1965), but Kotlarczyk (1985a) reports a thickness of 200 metres. Kropaczek (1919) estimated their thickness at 120 m. According to Dżułyński & Kotlarczyk (1965), the Popiele beds represent a submarine slump, which consists of variable amounts of small- to several metres thick blocks of shale and marl stacked in a massive, unstratified brownish silty matrix. The latter commonly contains mollusc shells. Blocks and smaller clasts represent material derived from approximately coeval flysch strata incorporated during mass movements (i.e., fragments of Hieroglyphic beds, Menilite beds, Kliwa sandstones – Dżułyński & Kotlarczyk, 1965) and clasts of rocks initially deposited in a proximal shelf area (e.g., pale-coloured marl; see, e.g., Rajchel, 1990). Exotics are rare and represent an older, pre-flysch material derived from the Flysch Carpathian basin substratum, e.g., Jurassic limestone (Dżułyński *et al.*, 1979b), and coal clasts (presumably Carboniferous – Kotlarczyk & Śliwowa, 1963).

Molluscs from the silty matrix were the object of several studies by Wójcik (1903), Wiśniowski (1908), Rogala (1925, 1941 *vide* Krach, 1985) and Krach (1985). The latter author revised collections of Wiśniowski and Rogala, and described a mollusc assemblage consisting of 134 taxa including bivalves, gastropods and scaphopods. Wójcik (1903) and Syniewska (1937) described foraminifers from the Popiele beds, whereas Liszka & Geroch (1979) added new data on foraminifers from Kruhel Mały near Przemyśl, and revised Wójcik's (1903) determinations. As a result, the age of mollusc and foraminifers assemblages from the Popiele beds was interpreted as the late Middle-Late Eocene (Bartonian and Priabonian) according to Bieda *et al.* (1963), Krach (1985) and Liszka & Geroch (1979). Foraminifera and calcareous nannoplankton from the Popiele beds in Poland and Ukraine were recently studied by Garecka *et al.* (2008; without descrip-

tion of the source rocks). Calcareous nannoplankton was correlated by these authors with the assemblages from the Globigerina marls (Upper Eocene–lowermost Oligocene) of the Flysch Carpathians. Presence of *Clausiococcus subdistichus*, *Isthmolithus recurvus*, *Lanternithus minutus*, *Reticulofenestra lockeri*, *R. ornata* and *R. umbilica* was interpreted by these authors as indicative for the Early Oligocene age of the Popiele beds. Foraminiferal assemblages described in that paper, in turn, allowed for a less precise, but generally similar age interpretation – the Eocene/Oligocene turnover (Garecka *et al.*, 2008).

## MATERIAL

The material studied comes from the outcrops of the Popiele beds at Koniusza (Fig. 3). These are the best exposures of this informal lithostratigraphic unit in the Polish Flysch Carpathians described earlier by Dżułyński & Kotlarczyk (1965) and Kotlarczyk (1979a, b). Rajchel (1990) proposed to treat these as the neostratotype, since the stratotype of the Popiele beds is now in Ukraine. The exposures studied by the present author are on the southern bank of a creek east of Koniusza (Fig. 3); note: the creek's name is somehow enigmatic: Koniuszanka according to Krach (1985, fig. 1), and Zalesie Stream according to Kotlarczyk (e.g., 1985b, figs 39 and 40). They begin approximately 160 m east from the place where the Koniusza–Aksmanice road crosses the creek (Fig. 3; GPS: 49° 40.955' N, 022° 42.009' E), and they continue at a distance of 250 m eastwards (see also Krach, 1985, fig. 1; Kotlarczyk, 1985b, fig. 39). The Popiele beds are exposed in two large scarps (exposures A and B; Fig. 3) and in a few smaller sites. One of the large exposures was studied by Dżułyński & Kotlarczyk (1965) and illustrated by Dżułyński *et al.* (1979b, fig. 20). The small exposures of the Popiele beds are also visible in the creek bed; occasionally, large loose blocks lie in the creek bed. The boundaries of the Popiele beds with the Hieroglyphic and Menilite beds at Koniusza are not exposed.

Thirty two samples (Kns1–15, Kns17–33) were collected from the Popiele beds at Koniusza (Figs 3, 4). Two additional samples from the Hieroglyphic beds (KnsH1 and KnsH2), and a single sample from the Menilite beds (Kns16) were taken.

**Sample Kns1** (a massive dark-grey-greenish, micaceous, poorly calcareous mudstone) was collected from the poorly exposed strata, which dip vertically in the creek bed.

**Samples Kns2 and Kns3** were taken 35 m upstream from a small exposure on the southern creek's bank. Sample Kns2 is a dark-greenish, soft, micaceous mudstone with frequent gastropod and mollusc shells. Within this mudstone, a 50-cm in diameter block of a hard greyish-willow-green marl occurs (Kns3).

Much larger blocks of a similar lithology (up to 2–3 m in diameter) occur 15 m upstream in the creek bed (**Kns4**: a hard, pale-willow-green marl). In the scarp, 3 m above these blocks, a soft, brownish sandy mudstone with the shell detritus is exposed (**Kns5**).

15 m upstream, a large scarp begins (exposure B; Fig. 3; Fig. 4G). A dark-coloured (brownish and greenish-brownish), relatively soft (easily disintegrative)

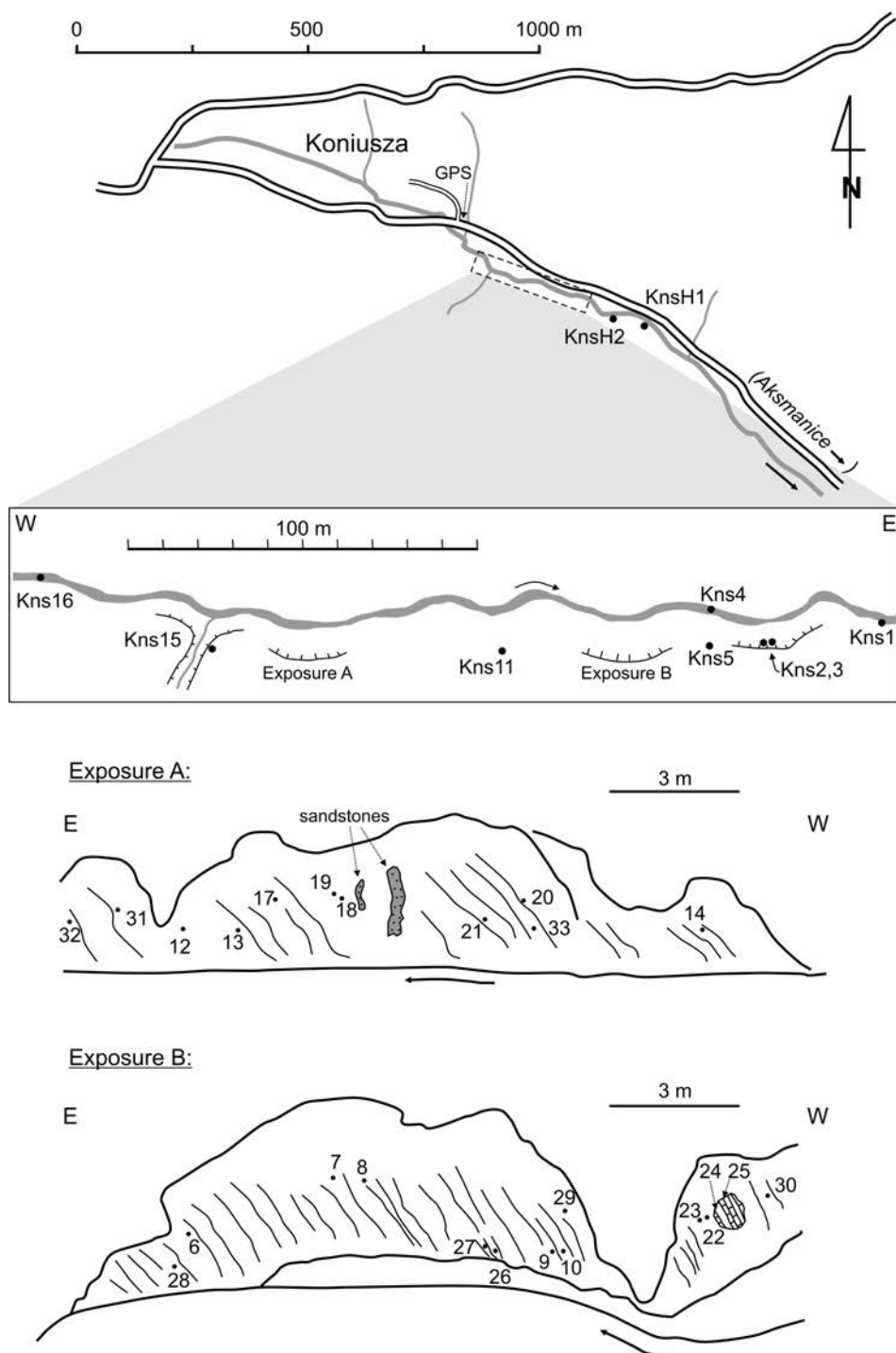


Fig. 3. Location of the studied exposures of the Popiele beds and collected samples





**Fig. 4.** Exposures of the Popiele beds at Koniusza. **A** – fragment of exposure A; **B**, **C** – close-ups of the chaotic deposits of the Popiele beds; **D**, **E** – views on exposure B with block of hard pale-coloured marl (samples Kns24, 25) surrounded by dark-coloured mudstone (sample Kns22); **F** – cross-section through a conglomerate from the Popiele beds: greenish and pale-coloured clasts stick in dark mudstone; **G** – fragment of exposure B; **H** – detail of exposure B with pale-greenish clay (sample Kns27) surrounded by dark-brown micaceous mudstone (sample Kns26)





**Fig. 5.** Macrofauna from the Popiele beds (exposure A). **A** – scaphopod shell; **B–E** – gastropod shells in dark-brown micaceous mudstone; **F** – bivalve shell; **G–I** – extracted gastropod shells (scale bars = 1 cm)

massive mudstone crops out there at a distance of 17 m (**Kns6–10, 22, 26, 28, 29**). Samples Kns6, Kns7 and Kns9, like sample Kns5, contain frequent shell detritus. Sample Kns8 was taken from a pale-greenish, easily disintegrative calcareous mudstone, whereas sample Kns10 is a pale-greenish, relatively hard, poorly calcareous mudstone that occurred within a darker-coloured, soft mudstone. **Sample Kns27** was collected from a non-calcareous pale-greenish shale whereas sample Kns26 from a neighbouring dark mudstone (Fig. 4G, H). A block of hard pale-coloured marl that crops out in the western part of the exposure B was sampled: **Kns24, Kns25** (Fig. 3, Fig. 4D, E). It was contained in a dark-brown mudstone (sample Kns22). There occur also several smaller blocks of pale-greenish (**Kns23**) and olive-greyish (**Kns30**) marl (up to several cm in diameter). Small pebbles of a hard, pale-coloured marl (below 1 cm in diameter) occasionally form conglomerates with a dark-brown micaceous matrix (Fig. 4F).

**Sample Kns11** represents a pale-brownish-beige, soft, calcareous sandy mudstone. It was collected from a small outcrop in the southern creek bank, 20 m upstream.

45-m farther upstream, another large scarp begins (exposure A; Fig. 3, Fig. 4A–C). Eleven samples were taken there (Kns12–14, 17–21, 31–33). **Sample Kns12** is a non-calcareous dark-brown soft claystone showing subtle lamination, collected from the eastern part of the exposure. **Samples Kns17–21** and **Kns33** are poorly calcareous dark-greenish-brownish soft mudstone with frequent calcareous shell detritus. Samples Kns31 and Kns32 are a dark-brownish non-calcareous clay without shell detritus. The dark mudstone in exposure A contains very rich macrofauna (Fig. 5).

There are no good exposures upstream – only a small isolated exposure of a non-calcareous, greenish, soft mudstone (**Kns15**) was found in a scarp of its southern tributary (Fig. 1C). 50-m farther upstream, black and dark-brown calcareous shale and thin-bedded sandstones of the Menilite beds crop out. **Sample Kns16** was taken from a hard, highly calcareous, plate-splitting black shale.

Two samples from the poorly exposed downstream Hieroglyphic beds were taken: **KnsH1** and **KnsH2** (approximately 150 m and 80 m from sample Kns1, respectively; Fig. 3). Both samples represent the same lithology: a pale-greenish non-calcareous soft clay shale.

## METHODS

The samples were processed in the micropalaeontological laboratory of the Institute of Geological Sciences, Polish Academy of Sciences, Kraków. The applied standard palynological procedure included 38% hydrochloric acid (HCl) treatment, 40% hydrofluoric acid (HF) treatment, heavy liquid ( $\text{ZnCl}_2 + \text{HCl}$ ; density  $2.0 \text{ g/cm}^3$ ) separation, ultrasonic cleaning for 10–15 s and sieving at  $15 \mu\text{m}$  on a nylon mesh. No nitric acid ( $\text{HNO}_3$ ) treatment was applied.

The quantity of rock processed was 20 g for each sample. Microscope slides were made from each sample using glycerine jelly as a mounting medium. The rock

samples, palynological residues and slides are stored in the Institute of Geological Sciences, Polish Academy of Sciences, Kraków.

The quantitative analysis of palynological organic matter was done by simple measuring of its column in 2 ml tubes.

The qualitative analysis of the organic particles larger than 15  $\mu\text{m}$ , i.e., the palynofacies *sensu* Combaz (1964) of the samples studied, was calculated by counting 500 palynomorphs and phytoclasts from each sample. Their composition was based on the palynofacies element classifications proposed by Tyson (1995) and Batten (1996). The following main palynofacies element categories have been distinguished:

- **black, opaque phytoclasts** – these are the woody particles most resistant to bacterial decay and oxidation; their accumulation is associated with high energy environments (e.g., Batten, 1996) but they are also known from the low energy off-shore facies (e.g., Tyson, 1989);

- **dark-brown phytoclasts** (commonly opaque in their centres, but translucent at the edges) are poorly structured or unstructured woody fragments;

- **cuticles** – land-plant fragments with well preserved tissue structure; in the most cases they are leaves fragments; their frequency decreases offshore (Batten, 1996), but they are common in turbidites (Gedl & Leszczyński, 2005);

- **sporomorphs** – include spores and pollen grains; land-derived elements, which are transported into marine basin either by rivers or by wind (especially pollen grains); usually accumulated in proximal settings, but due to high buoyancy (particularly pollen grains) they may occur in high ratios in offshore settings (see Batten, 1996 for discussion);

- **dinoflagellate cysts** – the most of their fossil forms is marine plankton associated with proximal settings; peridinioid dominance is usually associated with estuarine or brackish environments, whereas gonyaulacoids are more common offshore; however, peridinioids are also related to upwelling areas (e.g., Powell *et al.* 1992);

- **algae** – this group includes in the material studied the Prasinophycean algae genus *Tasmanites* (see e.g., Guy-Ohlson, 1996), and an *incertae sedis*, which resembles “Genus et species ind.” *sensu* Biffi & Manum (1988, pl. 15, figs 9, 10, 13; this form was tentatively attributed to the Prasinophycean algae genus *Schizosporis* by Brinkhuis, 1992, pl. I, fig. 1). Freshwater algae are represented by very rare specimens of *Botryococcus*; they are not included in this group;

- **foraminiferal organic linings** – these are organic remnants of calcareous foraminiferal tests, mainly benthic forms; they occur almost exclusively in marine deposits (see e.g., Batten, 1996; Stancliffe, 1996).

The first four categories represent land-derived elements, whereas the remaining three categories are aquatic (mainly marine). Amorphous organic particles represent an additional category grouping particles of uncertain origin altered by bacterial decay.

Dinoflagellate cysts were analysed for their frequency and diversity; in this purpose all dinoflagellate cysts from one slide were counted; in a case of less frequent



assemblages, an extra second slide was investigated. On this base, a dominance index (the ratio of summed frequency of the two most numerous species to the total number of dinoflagellate cysts counted) and the Shannon-Weaver diversity index ( $H'$ ) were calculated. The latter index was calculated as:  $H' = -\sum p_i \ln(p_i)$  where  $p_i$  is the relative abundance of each taxon; the Shannon-Weaver index was expressed as:  $e^{H'}$ .

## RESULTS

In this chapter, palynological characteristics of the samples studied is briefly described. Their palynofacies are shown in Figure 6. A special attention is focused on the composition of the organic-walled dinoflagellate cyst assemblages. Species frequencies in the samples studied are shown in Figure 7. Frequencies of other aquatic palynomorphs, when appearing in high ratio, are given.

### The Popiele beds

All samples from the Popiele beds contain rich palynological organic matter; their composition, however, differs between samples. This refers especially to the ratio of the terrestrial to marine elements, and qualitative composition of the dinoflagellate cyst assemblages. The palynofacies compositions reflect sample lithology: palynofacies of the samples collected from the pale-coloured marl characterizes abundance of aquatic palynomorphs (mainly dinoflagellate cysts); the dark-coloured fossiliferous mudstone, in turn, contains a high ratio of land-derived phytoclasts and palynomorphs (Fig. 6).

**Pale-coloured marl.** This rock generally contains a lower amount of palynological organic matter (below 1 mm of residuum column height in 2 ml tube) than the dark mudstone. The terrestrial elements present are sporomorphs (mainly pollen grains) and black opaque phytoclasts, whereas cuticles are evidently subordinate (Fig. 8). The dinoflagellate cyst ratio is high, from 40% to over 80%. The other aquatic palynomorphs are represented by an *incertae sedis* (*Schizosporis*?), whereas *Tasmanites* and foraminiferal organic linings are absent or very rare.

Sample **Kns4** contains a high ratio of dinoflagellate cysts (over 35%; Fig. 8B) and a still higher ratio of black, opaque phytoclasts (60%); cuticles and sporomorphs are rare – below 5%. An *incertae sedis* (*Schizosporis*?) is frequent, whereas *Tasmanites* occurs as single specimens. Dinoflagellate cysts are moderately preserved; some specimens, including a common chorate morphotype (apical archaeopyle, solid short non-tabular processes, questionably included to *Cleistosphaeridium*? sp. – up to 20%), are torn off. Other specimens, including dominating *Spiniferites ramosus* (over 30%), *Homotryblium tenuispinosum* (15%) and *Deflandrea* (12% – mainly *D. granulata*; some specimens show fungi infections) are relatively well preserved. *Impagidinium* is rare.

A high ratio of black opaque phytoclasts is also noted in samples Kns23, Kns24 and Kns25 being the highest in sample **Kns24** – almost 90% (Fig. 6). The latter sample is the only one among the pale-coloured samples, which contains a very low

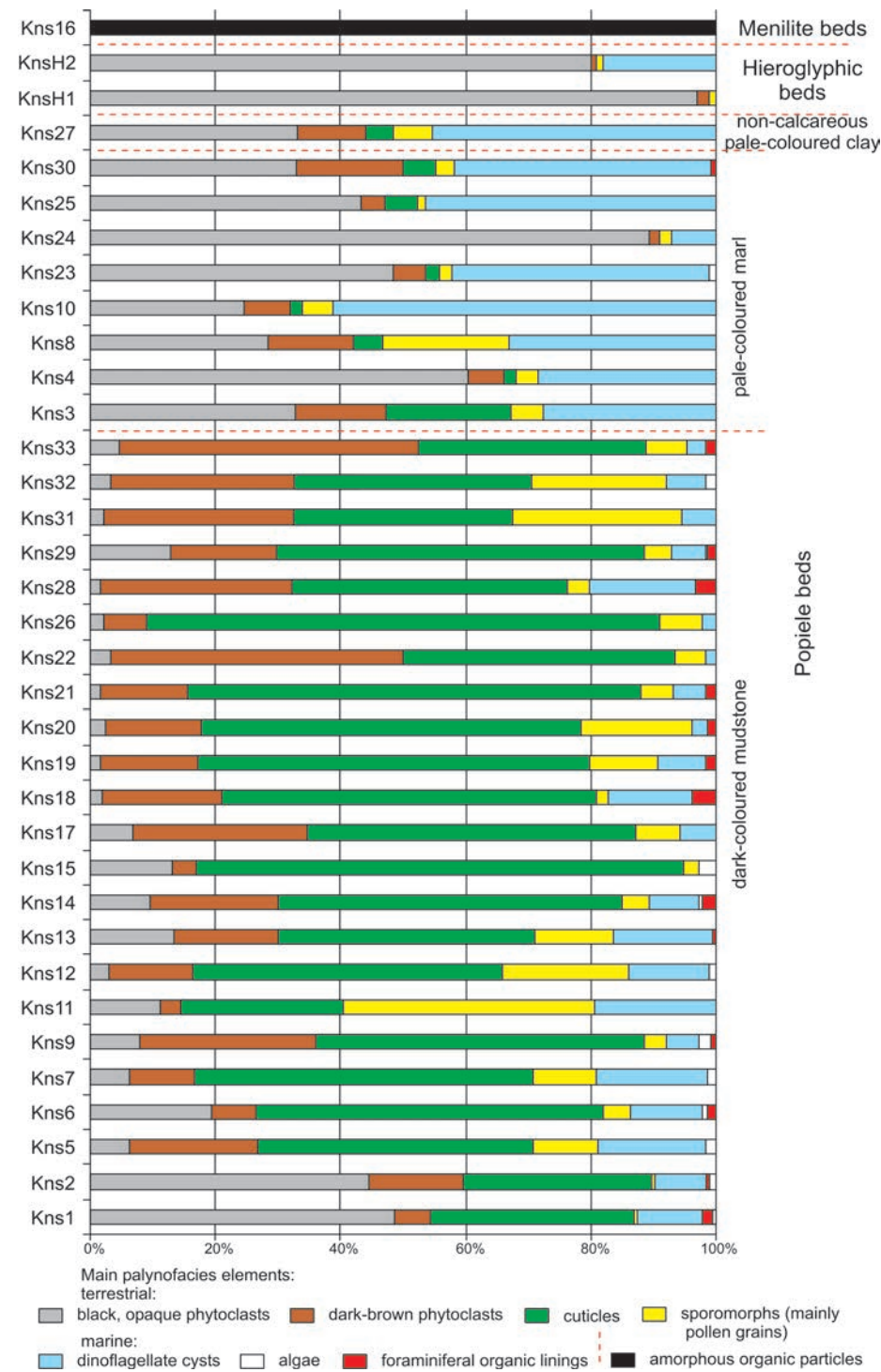


Fig. 6. Palynofacies of the samples studied





ratio of dinoflagellate cysts (8%); their assemblage is dominated by *Homotryblum tenuispinosum* and *Spiniferites ramosus*. Sample **Kns23** contains over 40% of dinoflagellate cysts (although commonly incomplete, torn-off specimens); they are dominated by *Spiniferites ramosus*; *Homotryblum tenuispinosum* is subordinate. Palynofacies of the sample **Kns25** consists in 48% of dinoflagellate cysts; their assemblage is dominated by *Homotryblum tenuispinosum* and *Polysphaeridium subtile*, which in similar proportions represent together almost 85%. Relatively frequent is *Cordosphaeridium gracile*. Peridinioids are nearly absent: single specimens of *Deflandrea phosphoritica* and *D. arcuata* occur. An *incertae sedis* (*Schizosporis*?) occurs in all three samples being the most frequent in sample Kns23.

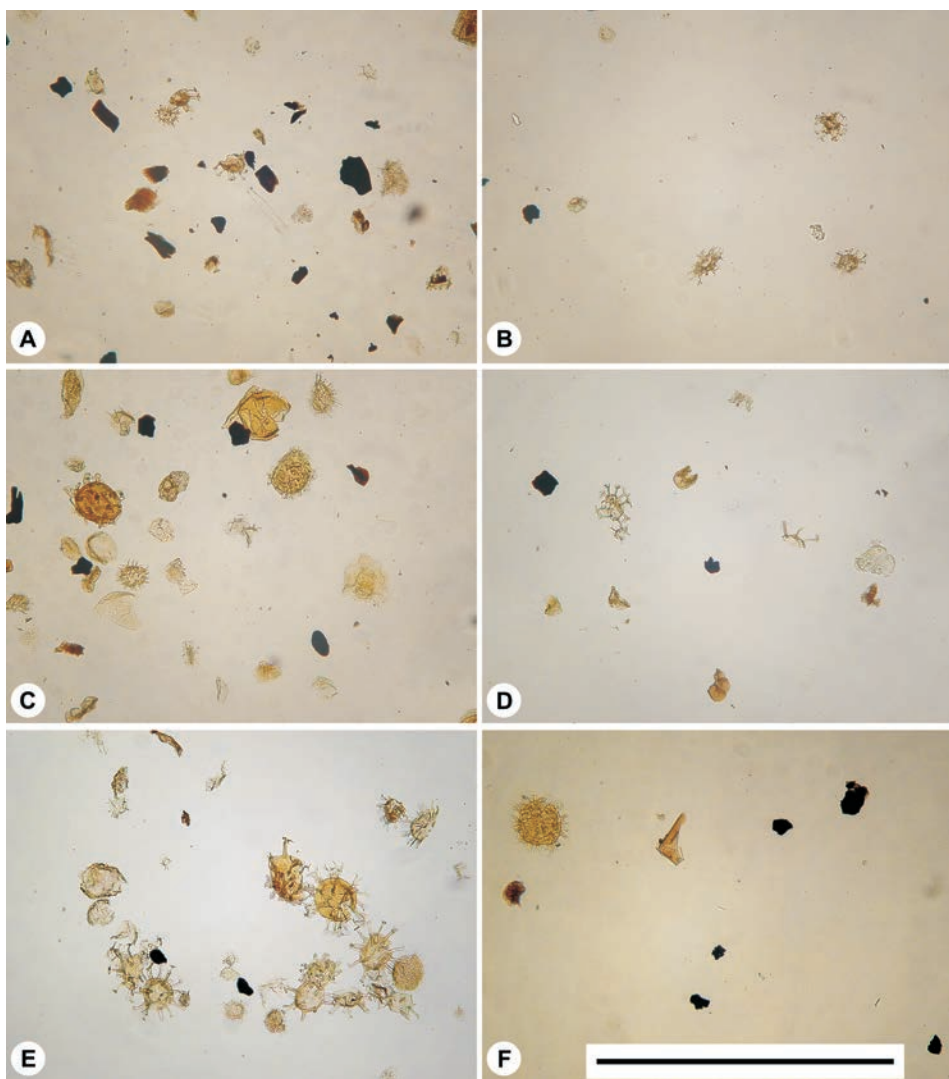
Palynofacies of sample **Kns3** is distinguished by relatively a high proportion of cuticles (almost 20%). Its dinoflagellate cyst assemblage also contains, unusual for pale-coloured marl, a high percentage of *Deflandrea* (up to 20%) represented mainly by *D. phosphoritica* (other species are infrequent: *D. leptodermata*, *D. granulata*). A noteworthy fact is the presence of *Deflandrea* specimens infected by fungi. The most frequent taxa, like in other pale-coloured marl are *Polysphaeridium* (*P. zoharyi*, *P. subtile*; 40%) and *Homotryblum* (*H. tenuispinosum*, *H. abbreviatum*; 30%); an *incertae sedis* (*Schizosporis*?) is also common.

Sample **Kns30**, in turn, is distinguished by a high amount of palynological organic matter characteristic for dark-coloured mudstone. But its palynofacies is typical for pale-colored marl: it consists of frequent dinoflagellate cysts (over 40%) and palynodebris including black, opaque and dark-brown phytoclasts (50%). Dinoflagellate cyst assemblage is dominated by *Homotryblum* (mainly *H. tenuispinosum*; 48%), *Polysphaeridium* (mainly *P. subtile*; 14%), and *Cleistosphaeridium* sp. (6%). Remaining taxa are represented by chorate gonyaulacoids; peridinioids are very rare – mainly *Deflandrea* spp. and single specimens of *Charlesdownia* and *Wetzeliiella*. Some specimens of *Deflandrea*, as in samples Kns3 and Kns4, bear traces of fungi activities.

**Pale-coloured mudstone.** Two samples collected from this rock yielded various palynofacies. The one of sample **Kns10** is similar to palynofacies of pale-coloured marl described above: it is composed mainly of black opaque phytoclasts and dinoflagellate cysts (Fig. 8D). In this sample an *incertae sedis* (*Schizosporis*?) also occurs. Dinoflagellate cyst assemblage consists chiefly of gonyaulacoids, among which *Spiniferites ramosus* is the most numerous. Other frequent chorate gonyaulacoids include *Operculodinium centrocarpum*, *Enneadocysta pectiniformis*, *Homotryblum pallidum*. Representatives of *Impagidinium* are relatively frequent. Peridinioids are infrequent and include mainly *Dracodinium laszczyński* (commonly as isolated endocysts).

A different palynofacies was found in sample **Kns8**: it is characterized by almost 20% of pollen grains (Fig. 6, Fig. 8C) and over 35% of dinoflagellate cysts. Although dinoflagellate cyst assemblage is taxonomically diversified, a frequent occurrence (up to 30%) of *Spiniferites ramosus* and *Achomosphaera* sp. is noted. *Operculodinium centrocarpum* and *Systematophora* cf. *placacantha* are relatively





**Fig. 8.** Palynofacies of pale-coloured marls from the Popiele beds (A–E) and the Hieroglyphic beds (F) at Koniusza. **A** – sample Kns3; **B** – sample Kns4; **C** – sample Kns8; **D** – sample Kns9; **E** – Kns25; **F** – KnsH2 (scale bar in F represents 0.5 mm and refers to all other photomicrographs)

common. Noteworthy is the occurrence of *Impagidinium*, which represents a few percent of the assemblage, and a complete lack of *Deflandrea* and *Charlesdowniea* (peridinioids are represented by rare specimens of *Lentinia serrata*, *Phthano-peridinium* sp. and *Dracodinium laszczyński*). A feature that distinguishes palynofacies of this sample from other pale-coloured marl samples is a rare occurrence of *Homotryblum*. An *incertae sedis* (*Schizosporis*?) occurs relatively frequently, whereas there are neither *Tasmanites* nor foraminiferal organic linings.

The non-calcareous pale-greenish clay (sample **Kns27**) contains 46% of dinoflagellate cysts; phytoclasts (dark-brown and black, opaque equidimensional) represent a similar proportion. Dinoflagellate cyst assemblage is dominated by *Spiniferites ramosus* (48%). *Homotryblum tenuispinosum* and *Dapsilidinium pseudocolligerum* are relatively frequent. It is worthwhile to notice the occurrence of *Impagidinium*. Peridinioids are very rare with single specimens of *Wetzeliiella* sp., *Deflandrea phosphoritica*, *Wilsonidinium* sp. and *Phthanoperidinium? eocenicum*.

The dark-coloured fossiliferous mudstone reveals a higher amount of the palynological organic matter than pale-coloured marl (above 2 mm of residuum column height in 2 ml tube); moreover, it is dominated by terrestrial elements, mainly cuticle remains. Aquatic palynomorphs are subordinate; they commonly include, beside dinoflagellate cysts, *Tasmanites* and foraminiferal organic linings. The main differences in palynofacies between these samples refer to the ratios of cuticles and aquatic elements (Fig. 6).

Palynofacies of the most samples (**Kns5–7**, **Kns9**, **Kns12–15**, **Kns17–22**, **Kns26**, **Kns28**, **Kns29** and **Kns31–33**) are dominated by cuticles (30–60%) associated with dark-brown phytoclasts and sporomorphs (mainly bisaccate pollen grains – from a few to 20%; see Fig. 6). Black, opaque phytoclasts are rare in these samples – their proportion in some samples (e.g., Kns18–21) does not exceed 3% (Fig. 6). Occurrence of *Tasmanites* and foraminiferal organic linings is also characteristic: they occur in all the samples studied, in some being even 2–3% (e.g., Kns15 and Kns18, respectively; Fig. 6). Dinoflagellate cysts are moderately preserved being commonly wrinkled and torn off: some specimens are preserved as undeterminable fragments only. Their assemblages are generally taxonomically diverse in the most of the samples studied (Kns5–7, Kns12, Kns13, Kns17–22, Kns28 and Kns31–33): they are dominated by chorate gonyaulacoids including: *Spiniferites ramosus*, *Homotryblum* spp. (*H. pallidum*, *H. plectilum*, *H. aculeatum*), *Operculodinium* spp. (*O. centrocarpum*, *O. microtriainum*, *O. tiara*), and less frequent *Heterosphaeridium* sp., *Cordosphaeridium* sp., *Areosphaeridium* sp. (Fig. 7). Peridinioids occur in all samples being represented chiefly by *Deflandrea* spp. (*D. heterophlycta*, *D. phosphoritica*) and *Charlesdowniea coleothrypta*. A characteristic feature of the dark-coloured fossiliferous mudstone is nearly the lack of *Impagidinium* – off 20 samples its specimens have been found in Kns5 and Kns13, single specimens in Kns2, Kns18 and Kns28 only.

Samples from the dark-coloured mudstone contain high ratios of cuticles, usually up to 50–60  $\mu\text{m}$  in size; five samples, however, show larger cuticles up to 100  $\mu\text{m}$  and larger: **Kns9**, **Kns14**, **Kns26**, **Kns29** and **Kns31** (Fig. 9F, H). Dinoflagellate cysts from these samples are characterized by a relatively low number of species and, contrary to other samples, by a domination or frequent occurrence of *Deflandrea*. This genus, mainly *D. phosphoritica* and *D. heterophlycta*, dominates in samples Kns9, Kns26, Kns29 and Kns31; it is associated by frequent specimens of *Homotryblum pallidum*. *Spiniferites ramosus* and *Deflandrea* spp. are most frequent in sample Kns14. *Tasmanites* and frequent foraminiferal organic linings are present in all these samples.

Two samples, **Kns1** and **Kns2**, contain much higher ratio (over 40%; Fig. 9A, 9B) of black, opaque phytoclasts; they are often elongated. In these samples, cuticle proportion slightly exceeds 30%. Another characteristic feature is a scarcity of sporomorphs – approximately 1% only. Dinoflagellate cysts represent up to 10%; they are pale-coloured and relatively well preserved, although they are commonly wrinkled and torn-off, thus preserved as fragments. Their assemblages differ between these two samples. Dinoflagellate cysts in sample Kns1 are dominated by *Homotryblum* (mainly *H. plectilum* and *H. tenuispinosum*), which represents over 50%. *Areosphaeridium dityoplokum* is second in frequency (up to 15%); this species occurs mainly as isolated opercula. Also frequent is *Deflandrea* (represented chiefly by *D. phosphoritica*, commonly mechanically damaged) – 10%. This is the most frequent peridinoid in this sample; the others are represented by rare specimens of *Charlesdowniea* sp., *Lentinia serrata* and *Rhombodinium perforatum*. Relatively frequent (up to a few percent) are chorate gonyaulacoids (*Operculodinium microtriainum*, *O. centrocarpum*, *Heterosphaeridium* sp.) and *Thalassiphora pelagica*. Noteworthy is almost complete lack of *Spiniferites*. The assemblage from sample Kns2 is dominated by *Deflandrea* (*D. phosphoritica*, *D. heterophlycta*) – over 40% and *Homotryblum* (mainly *H. plectilum*, *H. pallidum*) – up to 30%. Relatively frequent are *Thalassiphora pelagica*, *Samlandia chlamydophora*, *Operculodinium* spp. There are almost no *Spiniferites*. Both samples contain relatively frequent *Tasmanites* and foraminiferal organic linings, whereas rare specimens of freshwater algae *Botryococcus* occur in Kns2.

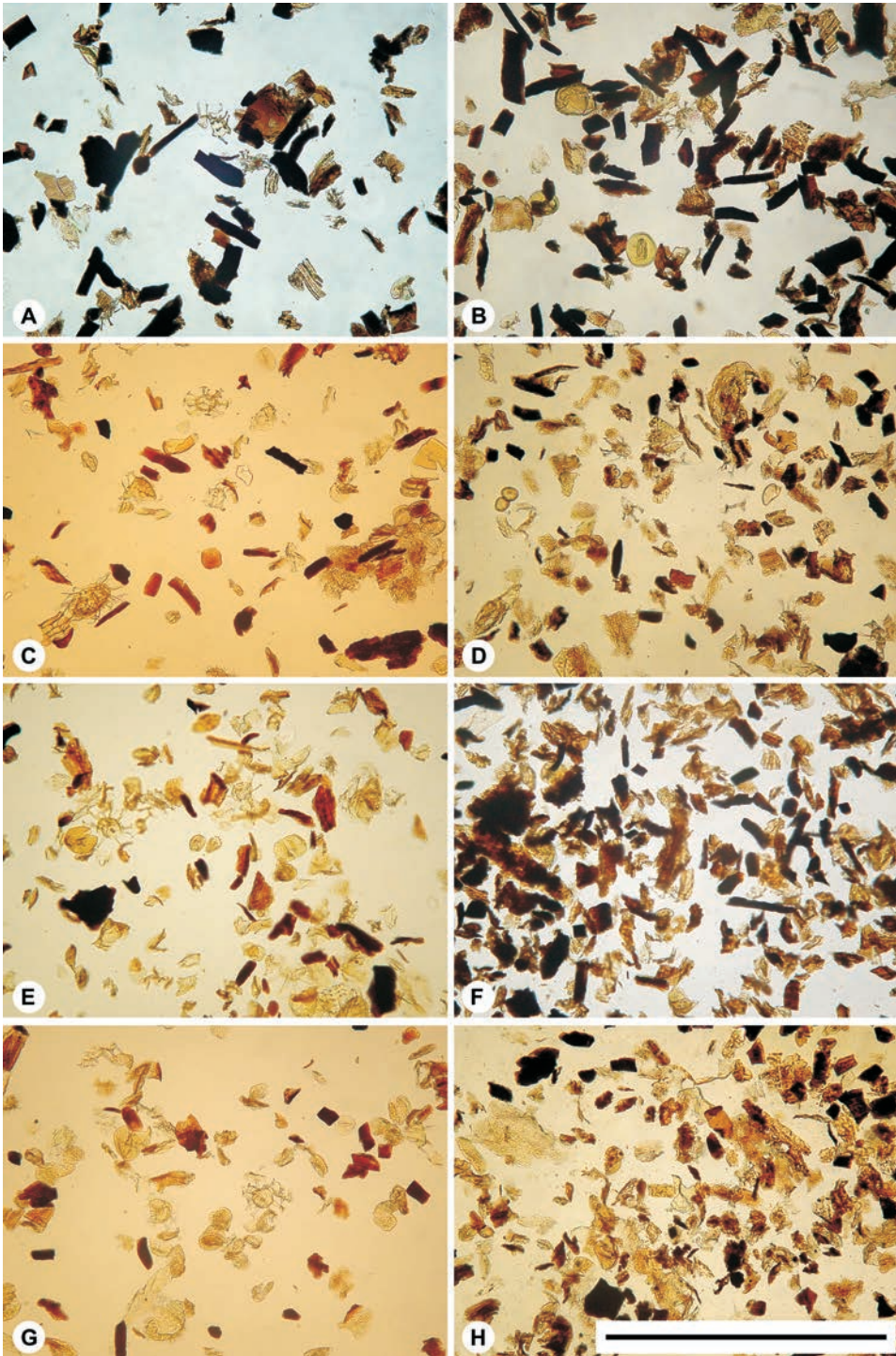
Sample **Kns11** is another dark-coloured sample with a peculiar palynofacies: it contains 40% of pollen grains; dinoflagellate cysts are up to 20% (Fig. 6). Both palynomorph types are strongly damaged. For example, almost all frequent specimens of *Deflandrea* are torn-off. Dinoflagellate cyst assemblage is taxonomically moderately diversified. It is dominated by *Spiniferites ramosus* and *Deflandrea* (*D. phosphoritica* and *D. heterophlycta*). Additionally, relatively frequent are *Operculodinium centrocarpum*, *Homotryblum* (*H. plectilum* and *H. pallidum*). There are no *Impagidinium*. The other aquatic palynomorphs are represented by infrequent *Tasmanites*.

Sample **Kns15** lacks dinoflagellate cysts and contains very low amounts of palynological organic matter. Its particles are represented by large-sized cuticles, which bear traces of corrosion. Infrequent pollen grains and single specimens of *Tasmanites* are also corroded. .

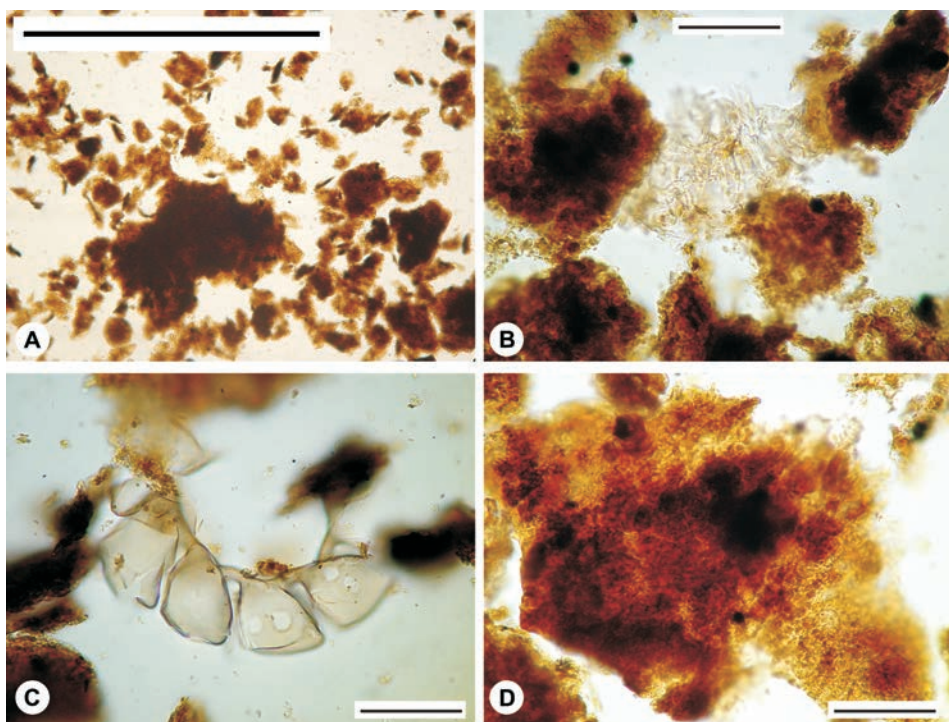


**Fig. 9.** Palynofacies of dark-coloured fossiliferous mudstones from the Popiele beds at Koniusza. **A** – sample Kns1; **B** – sample Kns2; **C** – sample Kns5; **D** – sample Kns6; **E** – sample Kns7; **F** – sample Kns9; **G** – sample Kns12; **H** – sample Kns14 (scale bar in H represents 0.5 mm and refers to all other photomicrographs)









**Fig. 10.** Palynofacies, palynomorphs and phytoclasts of the Menilite beds (sample Kns16) from the Popiele beds at Koniusza. **A** – palynofacies (scale bar = 0.5 mm); **B** – undetermined dinoflagellate cyst surrounded by cloaks of structureless organic matter (scale bar = 25  $\mu$ m); **C** – foraminiferal organic lining (scale bar = 25  $\mu$ m); **D** – cloaks of structureless organic matter (scale bar = 25  $\mu$ m)

### The Hieroglyphic beds

The Hieroglyphic beds exposed east of the Popiele beds outcrops (Fig. 3) yield a different palynological organic matter. Sample **KnsH1** contains low amounts of palynological organic matter composed almost entirely of black opaque phytoclasts. Palynofacies of sample **KnsH2** consists of black opaque phytoclasts and dinoflagellate cysts (10%; Fig. 8F). Their assemblage is composed of gonyaulacoids (only a few single peridinioids occur) dominated by *Spiniferites ramosus*, *Areoligera* cf. *medusettiformis*, *Operculodinium centrocarpum*, and subordinate *Adnatosphaeridium multispinosum* and *Cordosphaeridium gracile*.

### The Menilite beds

Sample **Kns16** yielded extremely high amount of palynological organic matter composed exclusively of structureless organic matter (Fig. 10A), mainly thick cloaks of structureless matter (Fig. 10D) with infrequent black opaque crystals (pyrite?). It seems that in some particles cuticle-like structures are preserved. Palyno-

morphs are represented by rare, but very well preserved foraminiferal organic linings (Fig. 10C). There are also single pale-coloured dinoflagellate cysts coated in amorphous matter, which makes their determination impossible (Fig. 10B).

## BIOSTRATIGRAPHY OF THE POPIELE BEDS

The age interpretation of the assemblages studied is based on stratigraphic ranges of selected dinoflagellate cyst species following Stover *et al.* (1996) and Williams *et al.* (2001), and supported by biostratigraphic data from the north-western Europe (e.g., Bujak *et al.*, 1980; Köthe & Piesker, 2008; Köthe, 2009) and the Polish Carpathians (e.g., Gedl, 2004a, 2005; Fig. 11).

The oldest dinoflagellate cyst assemblages occur in the pale-coloured marl. Samples Kns3 and Kns4 contain *Cerebrocysta bartonensis*, which appeared for the first time during the Early Bartonian. The samples lack species which appeared for the first time during younger stages of the Bartonian (e.g., *Lentinia serrata*, *Corrudinium incompositum*) and during the Priabonian. These two samples contain also *Apectodinium homomorphum* (a species absent from majority of other samples), which according to Stover *et al.* (1996) appeared for the last time during the Early Bartonian. This suggests that these samples represent the Bartonian, presumably the Lower Bartonian. A characteristic feature of these assemblages is a very frequent occurrence of *Homotryblium tenuispinosum*; a common occurrence of this species is also typical for the other pale-coloured marl samples (Kns23–25 and Kns30), and the pale-coloured non-calcareous clay (Kns27). This feature, although indirectly, points to the Bartonian age of the latter samples, which contain assemblages devoid of stratigraphically important species. An exception to this is the occurrence of *Apectodinium homomorphum* in sample Kns24, which suggests an Early Bartonian (or older) age comparable to that of samples Kns3 and Kns4, and the occurrence of *Cerebrocysta bartonensis* (associated by *Areosphaeridium diktyoplokum* and *A. michoudii*) in sample Kns27 (pale-coloured non-calcareous clay), which suggests the Bartonian age. Sample Kns25, which is devoid of stratigraphically important species (except of *A. diktyoplokum*), and contains frequent *H. tenuispinosum*, was collected from the same marl block as was the sample Kns24. Sample Kns23 collected from a small marl block contains, beside frequent *H. tenuispinosum*, species that occur in sample KnsH2 from the Hieroglyphic beds (Ypresian–lower Bartonian; Fig. 2): *Areoligera cf. medusettiformis*, and Gen. et spec. indet. C. The latter species occurs also in sample Kns25. A Bartonian age of the sample Kns30, lacking age-diagnostic species, was tentatively determined on the base of frequent occurrence of *H. tenuispinosum* (Fig. 11).

The most of samples from fossiliferous mudstone contain dinoflagellate cysts, the age of which was interpreted as the Priabonian. This assumption is based mainly on the occurrence of *Rhombodinium perforatum*, its Eocene stratigraphic range being limited to the Priabonian (Bujak *et al.*, 1980). However, this species is very rare in the material studied. Another indicator of the Priabonian age is *Enneadocysta pectiniformis* which, according to Stover & Williams (1995), has the lowest occur-

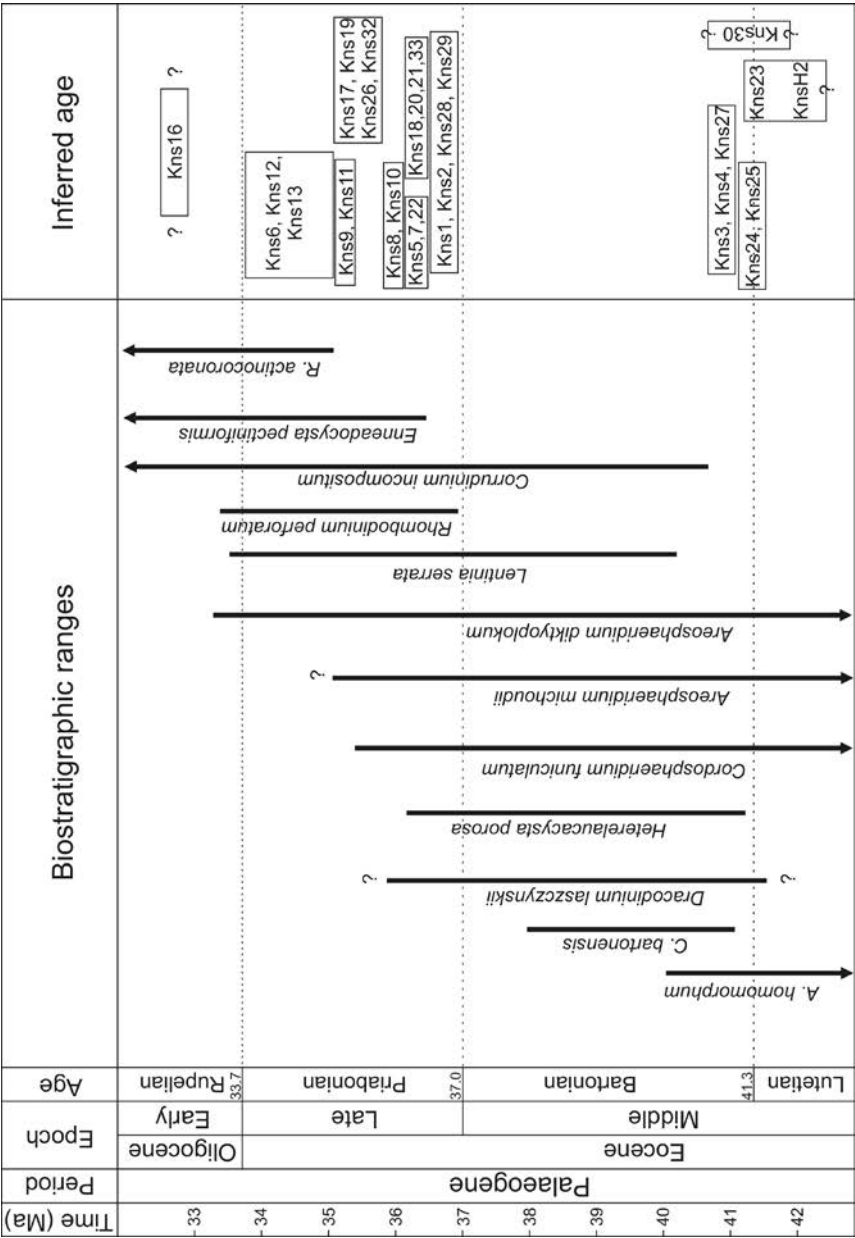


Fig. 11. Biostratigraphic ranges of selected dinoflagellate cyst species from the Popiele beds at Koniusza (based on Stover *et al.*, 1996; Williams *et al.*, 2001 and papers cited there; Gedl, 2004a, 2005a) and suggested ages of the samples studied

rence in the basal Priabonian. Age determination of the Priabonian dinoflagellate cyst assemblages differs slightly between samples. This suggests that the fossiliferous mudstone, which are the main rock that build the Popiele beds, was deposited during different time intervals of the Priabonian.

Presumably the oldest Priabonian dinoflagellate cyst assemblages are those which contain *Rhombodinium perforatum*, and lack *Enneadocysta pectinoforme* (a species which appeared for the first time during the later Early Priabonian); such assemblages have been found in samples Kns1, Kns2, Kns28, Kns29. This interpretation is supported by the presence of *Heterelaucacysta porosa* (its last appearance during the earliest Priabonian; e.g., Köthe & Piesker, 2008; Köthe, 2009) in sample Kns1. Additionally, samples Kns1 and Kns2 yielded single specimens of *Cordosphaeridium? solidospinosum* described from the presumably Middle Eocene strata of the Polish Carpathians (Gedl, 1995b).

The co-occurrence of *Heterelaucacysta porosa*, *Enneadocysta pectiniformis* and *Rhombodinium perforatum* (the two latter specimens appeared for the first time during the Early Priabonian) in samples Kns5, Kns7 and Kns22 suggests that they are slightly younger, but still Early Priabonian (Fig. 11).

The dinoflagellate cyst assemblages from samples Kns8 and Kns10 (pale-coloured mudstone) seem to be younger than the preceding samples, but still Early?-mid? Priabonian. They lack *Heterelaucacysta porosa*, but contain *Enneadocysta pectiniformis* and *Rhombodinium perforatum*. These samples yielded also *Dracodinium laszczynskii*, a species which in the Polish Carpathians seems to have appeared for the last time during the early Priabonian. The highest occurrence of this species was noted in greenish calcareous shale that occur in the basal part of the Leluchów Shale Member (equivalent of the so-called Globigerina marls of the Flysch Carpathian units in Poland; Gedl, 2004a) correlated by Oszczytko (1996) with the calcareous nannoplankton zones NP19–20. *Cordosphaeridium funiculatum*, another species present in both samples, has the highest occurrence in the mid-Priabonian strata.

Samples Kns9 and Kns11 represent, presumably, a slightly higher part of the Priabonian (Fig. 11). This is indicated by the co-occurrence of *Rhombodinium perforatum*, *Enneadocysta pectiniformis* and *Areosphaeridium michoudii*, and by the lack of older species (i.e., *H. porosa*, *C. bartonensis* and *C. funiculatum*). The highest occurrence of *A. michoudii* was noted in the Polish Carpathians within the Globigerina marls (e.g., Gedl, 2004a). This event has no precise dating so far, it presumably took place during the mid-Priabonian, prior to the first appearance of mid-late Priabonian species such as *Reticulatosphaera actinocoronata* (Gedl, 2004a).

The youngest, presumably Late Priabonian, dinoflagellate cyst assemblages occur in samples Kns6, Kns12 and Kns13 (Fig. 11). This assumption is based on the presence of *Reticulatosphaera actinocoronata*. This species appeared for the first time during the mid-late Priabonian. It is recorded from the Polish Flysch Carpathians from the topmost part of the Globigerina marls (Gedl, 2004a, 2005b) or its time-equivalents (Gedl, 2005). The youngest age-range of assemblages from these

samples might be not older than the latest Priabonian. This is suggested by the lack of species which had appeared for the first time during the Eocene–Oligocene transition (*Areoligera semicirculata*) or slightly earlier (*Wetzelietta gochtii*).

Several samples – Kns17–21, Kns26, Kns32, Kns33 – contain assemblages with *Enneadocysta pectiniformis* and some other Eocene species (*Areosphaeridium diktyoplokum*, *A. michoudii*, *Heterelaucacysta porosa*) but without *Rhombodinium perforatum*. Their age can be interpreted as Priabonian, similarly as those samples (e.g., Kns1 and Kns2), which contain the latter species. It should be noted that *R. perforatum* is a rare species in the material studied (1–2 specimens per slide). Among above discussed samples, those with *H. porosa* (Kns18, Kns20, Kns21, Kns33) likely represent basal part of the Priabonian, whereas those without *H. porosa* (Kns17, Kns19, Kns26, Kns32) – are presumably slightly younger.

Dinoflagellate cyst assemblages from samples Kns14 and Kns31 consist of species with long stratigraphic ranges. Presence of *Areosphaeridium diktyoplokum*, and a general similarity to assemblages from the other samples studied, suggests a wide time-span age of these samples – Bartonian–Priabonian.

The age of sample Kns15 cannot be determined due to a lack of dinoflagellate cysts. The same applies to sample Kns16 collected from black shale of the Menilite beds. However, this sample yielded amorphous organic matter, which is typical for the Oligocene Menilite beds (e.g., Gedl, 1999, 2004a).

### Redeposition

A characteristic feature of the dinoflagellate cyst assemblages from Koniusza is almost complete absence of the recycled pre-Eocene species: only one specimen of the Middle Jurassic *Ctenidodinium* sp. (*C. combazii*/*C. ornatum*) was found in sample Kns30. Two reworked specimens (*Ctenidodinium* sp., *Cribroperidinium ?edwardsii* – the latter presumably Early Cretaceous) were found in the Hieroglyphic beds. This points at restricted erosion of Mesozoic rocks during the Middle-Late Eocene in this part of the Carpathian basin margin.

There are also no indications of increased reworking of Palaeogene specimens during the Middle-Late Eocene at northern margin of the Skole Basin. The typical Bartonian species like *Areoligera* cf. *medusettiformis sensu* Eaton (1976), *Wilsonidium?* sp., *Hystrichokolpoma* cf. *rigaudiae*, *Charlesdowniea columna*, *Homotryblum abbreviatum*, *Phthanoperidinium delicatum* or *Apectodinium homomorphum* are present exclusively in the Bartonian samples of the Popiele beds and the Hieroglyphic beds (Fig. 7). Some other species that frequently occur in the Bartonian samples (e.g., *Homotryblum tenuispinosum*, *Polysphaeridium subtile*) are absent from most of the Priabonian samples. Only a few samples dated as Priabonian (Kns10, Kns11, Kns12) yielded also specimens of *Cerebrocysta bartonensis*, which is treated as a Bartonian species (Fig. 11). This indicates that there was virtually no erosion of the Bartonian strata during Priabonian. If there was any, it must have been very limited.



## PALAEOENVIRONMENT

### Diversity of dinoflagellate cyst assemblages

Frequency of dinoflagellate cyst taxa as well as their diversity in the material studied is related to particular lithofacies that build the Popiele beds (Fig. 12).

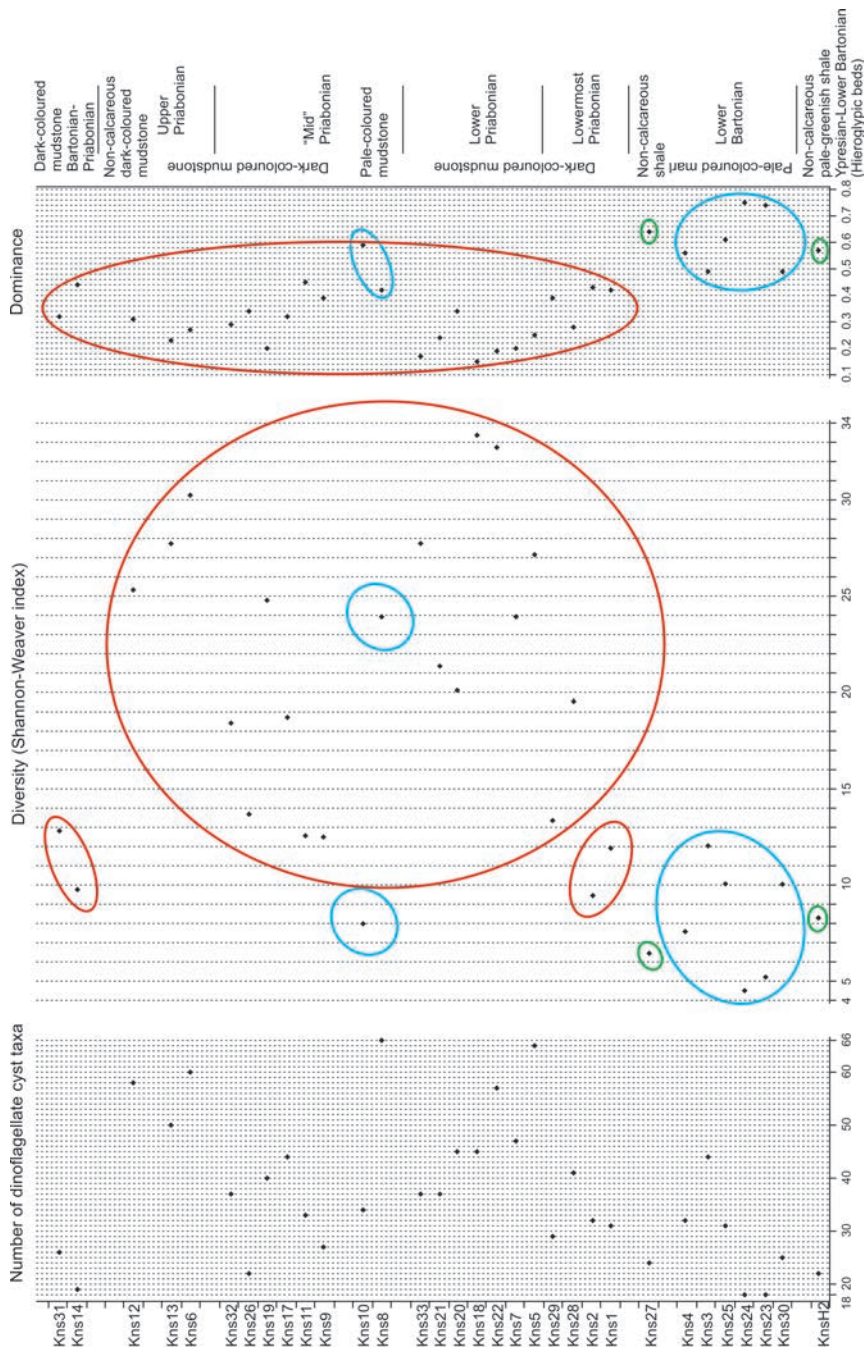
The most taxonomically impoverished assemblages occur in the pale-coloured marl, where number of taxa does not exceed 32 in samples Kns23, Kns24, Kns30, Kns25 and Kns4, being the lowest in samples Kns23 and Kns24 (18 taxa). A low taxa number is recorded in a non-calcareous clay sample Kns27 (24 taxa). Sample KnsH2 from the Hieroglyphic beds (non-calcareous clay) also contains taxonomically impoverished assemblage consisting of 22 taxa. The only exception among samples from pale-coloured lithologies is Kns8 (pale-coloured mudstone), which contains a taxonomically rich assemblage consisting of 66 taxa – the richest one among all samples studied (Fig. 12).

More diversified assemblages are identified in the dark-coloured mudstone: their taxa number usually exceeds 31, with the maximum over 45 taxa (samples Kns22, Kns6 and Kns12) and even 65 in sample Kns5 (Fig. 12). Only a few pale-coloured samples contain impoverished assemblages (i.e., below 32 taxa) comparable to the ones from the pale-coloured lithologies (Kns29, Kns1, Kns2, Kns26, Kns9, Kns14 and Kns31; Fig. 12).

Dinoflagellate cyst assemblages from pale-coloured lithologies are also outstanding when dominance index is considered (Fig. 12): its values exceed 0.49 (maximal values 0.75); there, *Homotryblum* is a dominant taxon. A high dominance index value (0.59) is also noted from the pale-coloured mudstone sample Kns10. In this case, as in sample Kns8, dominating species is *Spiniferites ramosus*. The same refers to the non-calcareous clay assemblages (sample Kns27 and sample KnsH2 from the Hieroglyphic beds), with dominance index relatively high – above 0.55 (Fig. 12). *S. ramosus* is a dominant taxon also in these two samples.

In contrast, assemblages from the dark-coloured lithologies are characterized by much lower values of the dominance index (below 0.43, minimal values 0.15–0.17; Fig. 12).

A difference between dinoflagellate cyst assemblages from pale- and dark-coloured lithologies is visible also when their diversity (calculated as the Shannon-Weaver index) is compared (Fig. 12). The lowest values of this index, pointing to the low diversity, is characteristic for pale-coloured lithologies; assemblages from both marl and non-calcareous clay show index values below 12 (the only exception is sample Kns8, which contains highly diversified assemblage – index value equals 24). The value of the Shannon-Weaver index of samples representing the dark-coloured mudstone is, in turn, much higher – usually above 12, reaching even almost 34; it shows a much higher diversity of the dinoflagellate cyst assemblages from the dark-coloured mudstone than from the pale-coloured lithologies (Fig. 12).



**Fig. 12.** Frequency, diversity (the Shannon-Weaver index) and dominance index of the dinoflagellate cyst taxa from the Popiele beds. Blue circle – pale-coloured marl; green circle – non-calcareous clay; red circle – dark-coloured fossiliferous mudstone

### Dinoflagellate cyst palaeoenvironmental groups

Some Palaeogene dinoflagellate cyst taxa are believed to be good indicators of palaeoenvironmental parameters; they are widely used in palaeoenvironmental reconstructions (see e.g., Brinkhuis, 1994; Sluijs *et al.*, 2005). The following groups, which include taxa of similar palaeoenvironmental preferences, have been distinguished in the material studied:

– ***Homotryblum* group** – includes the genus *Homotryblum*, which mass occurrence in the fossil material is associated by the most authors with increased salinity (e.g., Köthe, 1990; Brinkhuis, 1994; Pross & Schmiedl, 2002). Islam (1984) treated this genus as a near-shore one, and related its process length with increasing distance from shore; Dybkjær (2004) related their length with variable salinity level.

– ***Polysphaeridium* group** – two species are included here: *P. zoharyi* and *P. subtile*; their recent motile stages are commonly found in the littoral hypersaline environments (e.g., Wall & Dale, 1969; Bradford & Wall, 1984; Edwards & Andrieu, 1992; Reichert *et al.*, 2004). A different, euryhaline nature of *Polysphaeridium zoharyi*, was suggested by Marret & Zonneveld (2003) who reported it from the low saline environments.

– ***Operculodinium* group** – consists of representatives of this genus, mainly *O. centrocarpum*; this most likely cosmopolitan species is known from a wide range of environments, from estuarine to open offshore waters (Wall *et al.*, 1977; Harland, 1983; Morzadec-Kerfourn, 1983; Brinkhuis, 1992, 1994; Edwards & Andrieu, 1992).

– ***Thalassiphora* group** – includes representatives of this genus, mainly *T. pelagica*; the high ratio of *Thalassiphora* is believed to be related to periods of stratified water column with enhanced productivity, possibly associated with the oxygen-depleted bottom-water environments (Köthe, 1990; Pross, 1997, 2001; Pross & Schmiedl, 2002).

– ***Spiniferites* group** – includes the genera *Spiniferites* and *Achomosphaera*, which are cosmopolitan, being usually reported from open sea shelf environments (Brinkhuis & Zahariasse, 1988; Islam, 1984; Köthe, 1990; Brinkhuis, 1994).

– ***Impagidinium* group** – includes representatives of the genus *Impagidinium*, and *Ynezidinium brevisulcatum*, which are typical for the offshore environments (e.g., Wrenn & Kokinos, 1986; Brinkhuis *et al.*, 1992; Brinkhuis, 1994; Zevenboom *et al.*, 1994; Dale, 1996; Rochon *et al.*, 1999; Marret & Zonneveld, 2003). The increased frequency of *Impagidinium* was noted from hemipelagic layers of approximately coeval strata of the Magura Nappe, Flysch Carpathians (Gedl, 2005).

– ***Deflandrea* group** – includes mainly *D. phosphoritica* and *D. heterophlycta*; *Deflandrea* reflects near-shore, estuarine environments (e.g. Islam 1984, Köthe 1990). According to Brinkhuis *et al.* (1992), this was a presumably heterotrophic genus which benefited from the nutrient-rich waters, commonly inhabited by peridinioids (e.g., Bradford & Wall, 1984; Harland, 1988;). However, Brinkhuis *et al.* (1992) suggested that this genus may be associated with the eutrophic waters, independently on the distance from a shoreline (see also Gedl, 2005).



– **Wetzeliielloideae group** – includes representatives of the subfamily Wetzeliielloideae (*Charlesdowniea*, *Dracodinium* and *Wetzeliiella*); their motile stages are believed to have appeared in the near-shore lagoonal or estuarine environments characterized by high productivity conditions (e.g., Downie *et al.*, 1971; Goodman, 1979; Islam, 1984; Köthe, 1990; Brinkhuis, 1994). However, some species possibly could benefit from nutrient-rich waters independently on their distance from the shore (see *Deflandrea* group); *Dracodinium laszczynskii* presumably inhabited offshore waters (Gedl & Suruło, 2005). *Rhombodinium perforatum*, which frequently occurs in the hemipelagic deposits of the Magura Nappe at Folusz (Gedl, 2005), presumably also preferred more open offshore environments.

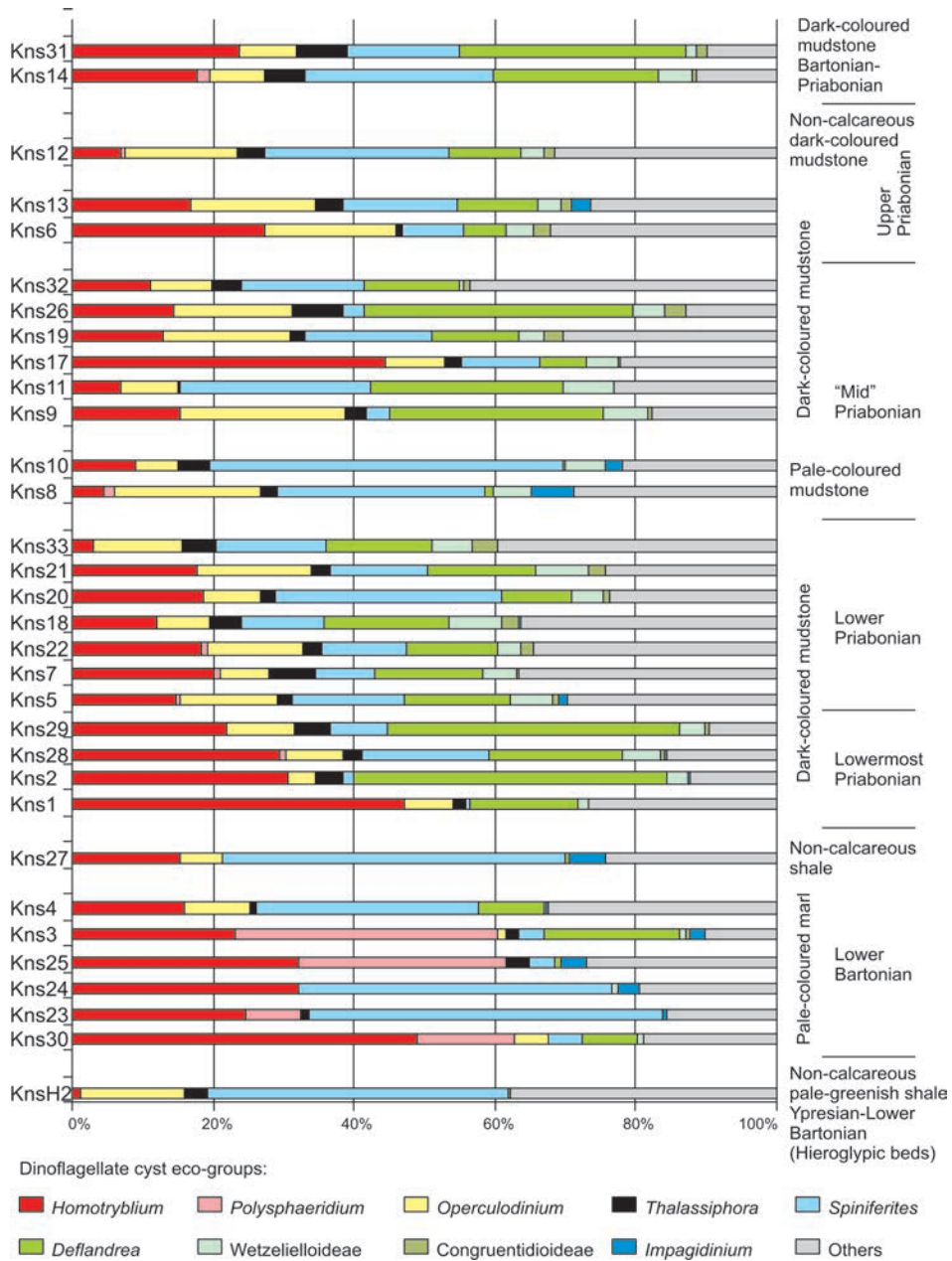
– **Congruentidioidae group** – includes representatives of the subfamily Congruentidioidae (*Selenopemphix*, *Lejeunecysta*), which are believed to be heterotrophic (Fensome *et al.*, 1993). The high proportion of these forms is interpreted as the best indicator of eutrophic conditions (Dale, 1996; see also Biffi & Grignani, 1983; Rochon *et al.*, 1999; Reichert & Brinkhuis, 2003).

Distribution of dinoflagellate cyst palaeoenvironmental groups is shown in Figure 13. Representatives of the *Homotryblum* group occur in a relatively high number in all samples studied (except for the sample KnsH2 from the Hieroglyphic beds, and sample Kns33 from the Popiele beds where frequency of this group hardly exceeds 3%). They are the most frequent in the pale-coloured Bartonian marl (over 20%; maximal frequency in sample Kns30 – almost 50%). Priabonian dark-coloured mudstone contains generally lower values of *Homotryblum* (below 20%), although some samples yielded comparable ratios to the ones from pale-coloured lithologies: ca 30% in Kns2 and Kns28 or even 43% and 47% in Kns17 and Kns1, respectively (Fig. 13). Representatives of the *Homotryblum* group show an important stratigraphical relation: the Bartonian pale-coloured marl contains frequent *Homotryblum tenuispinosum*, whereas the Priabonian samples contain *Homotryblum aculeatum* and *Homotryblum plectilum*.

Representatives of the *Polysphaeridium* group are either absent from most of samples studied (Kns1, 2, 4, 6, 9, 10, 11, 13, 17–21, 24, 26, 27, 29, 31–33; they are also absent from sample KnsH2) or they occur as a few specimens per sample (Kns5, 7, 8, 12, 14, 22, 28). An exception is their frequent occurrence in pale-coloured marl where their proportion reaches 7.7% (Kns23), 14% (Kns30), 29.5% (Kns25), and 37.2% in sample Kns3 (Fig. 13).

*Operculodinium* group is represented by moderate proportions in almost all samples (4–23%; usually its ratio oscillates between 8 and 17%; Fig. 13) except for pale-coloured marl: three samples are devoid of *Operculodinium* specimens (Kns 23–25), two others contain rare specimens (1.2% in Kns3, and 4.9% in Kns30).

*Thalassiphora* group is present in all samples except for samples Kns27 (non-calcareous shale), and Kns24 and Kns30 (pale-coloured marl). It never reaches high ratios – the highest ones are noted in dark-coloured marl samples Kns7 (6.6%), Kns26 (7.2%), Kns31 (7.4%). As a contrast, pale-coloured marl yielded the lowest ratio of *Thalassiphora*: 0.8–1.8%, with maximal value 3.5% in sample Kns25 (absent from two subsequent samples Kns24 and Kns30).



**Fig. 13.** Ratios of dinoflagellate cyst palaeoenvironmental groups from the Popiele beds at Koniusza

Much more frequent are representatives of the *Spiniferites* group, which occur in all samples studied. Distribution of this group shows high quantitative diversity: some samples contain very rare specimens – 0.6–1.6% (Kns1, Kns2), whereas the others contain even over 50% (Kns27 – 48.8%, Kns10 – 50.1%, Kns23 – 50.2%;

Fig. 13). There is no clear correlation of the *Spiniferites* group frequency to the lithology. It seems that representatives of this group are the most common in pale-coloured marl (Kns10 – 50.1%, Kns23 – 50.2%); however, some samples from the same rock type contain low ratios of this group (Kns3 – 3.7%, Kns25 – 3.5%, Kns30 – 4.6%; Fig. 13). Dark mudstone, in turn, contains rather lower ratios of *Spiniferites* group: maximal values hardly exceed 30% (Kns20 – 32.2%; Kns11 – 27.2%, Kns14 – 26.7%, Kns12 – 26%; Fig. 13). A relatively high ratio of *Spiniferites* group in a sample from the Hieroglyphic beds should also be mentioned (KnsH2 – 42.4%; Fig. 13).

Representatives of the *Impagidinium* group are either absent or they are very rare in most of samples representing dark mudstone (absent from seventeen samples: Kns1, Kns6, Kns7, Kns9, Kns11, Kns12, Kns14, Kns17, Kns19–22, Kns26, Kns29, Kns31–33; three remaining samples contain single specimens: Kns2, Kns18, Kns28; Fig. 13). Only two samples representing dark-coloured mudstone contain a higher ratio of *Impagidinium* group: Kns13 – 2.9% and Kns5 – 1%. The *Impagidinium* group is much more frequent in pale-coloured lithologies: pale-greenish mudstone (Kns8 – 5.7%), and non-calcareous pale-greenish shale (Kns27 – 5.1%). Pale-coloured poorly calcareous mudstone Kns10 contains 2.4% of *Impagidinium*. Relatively high ratios of *Impagidinium* group are noted in pale-coloured marls (Kns25 – 3.5%; Kns24 – 3.1%; Kns3 – 2.1%). The only sample representing pale-coloured lithologies, which contains no *Impagidinium* group is sample Kns30 (olive-greyish marl); two other samples contain single specimens of *Impagidinium* only (Kns4, Kns23). Another pale-coloured sample without *Impagidinium* is a non-calcareous clay from the Hieroglyphic beds (KnsH2; Fig. 13).

The *Deflandrea* group occurs in all samples studied, except for two representing pale-coloured marl (Kns23, Kns24). The same rock type contains the lowest values of *Deflandrea* group ratio (from below 1% in samples Kns10, Kns27, to 8% in Kns30 and 9.5% in Kns4; the maximal value occurs in sample Kns3 – 19.2%; Fig. 13). Very rare specimens of *Deflandrea* occur also in pale-coloured clay of the Hieroglyphic beds. In dark lithologies, in contrast, there is a much higher proportion of *Deflandrea* group – the lowest one (6%) occurs in samples Kns6 and Kns17 only, whereas in most of dark-coloured mudstone samples it oscillates around 15%, with maximal values from 30 to 44% in samples Kns9, Kns31, Kns26, Kns29 and Kns2 (Fig. 13).

The *Wetzelilloideae* in the present material are represented almost exclusively by *Charlesdowniea* with rare specimens of *Rhombodinium*, *Dracodinium*, *Apectodinium* and particularly rare *Wetzelilla*. They occur in almost all samples except for a few ones from the pale-coloured marl (Kns23, Kns25, Kns27; remaining samples of this lithology contain single specimens only); pale-coloured clay of the Hieroglyphic beds (KnsH2) contains no *Wetzelilloideae* (Fig. 13). Two pale-coloured samples (Kns8, Kns10) contain a much higher ratio of *Wetzelilloideae* (5.5% and 5.7%, respectively; Fig. 13), but this subfamily is represented there almost exclusively by *Dracodinium laszczynskii* (Fig. 7). A similar percentage of *Wetzelilloideae* (2–8%), but represented chiefly by *Charlesdowniea*, occurs in dark-coloured mudstone (only samples Kns31 and Kns32 contain ratios below 2%).

The Congruentidioideae are generally very rare in the Popiele beds. They are missing from pale-coloured lithologies (except for sample Kns3 where single specimens occur) being commonly below 1% (maximal value of their ratio occurs in sample Kns – 2.9%) in dark-coloured mudstone (they are absent from sample Kns1, Kns2, Kns11).

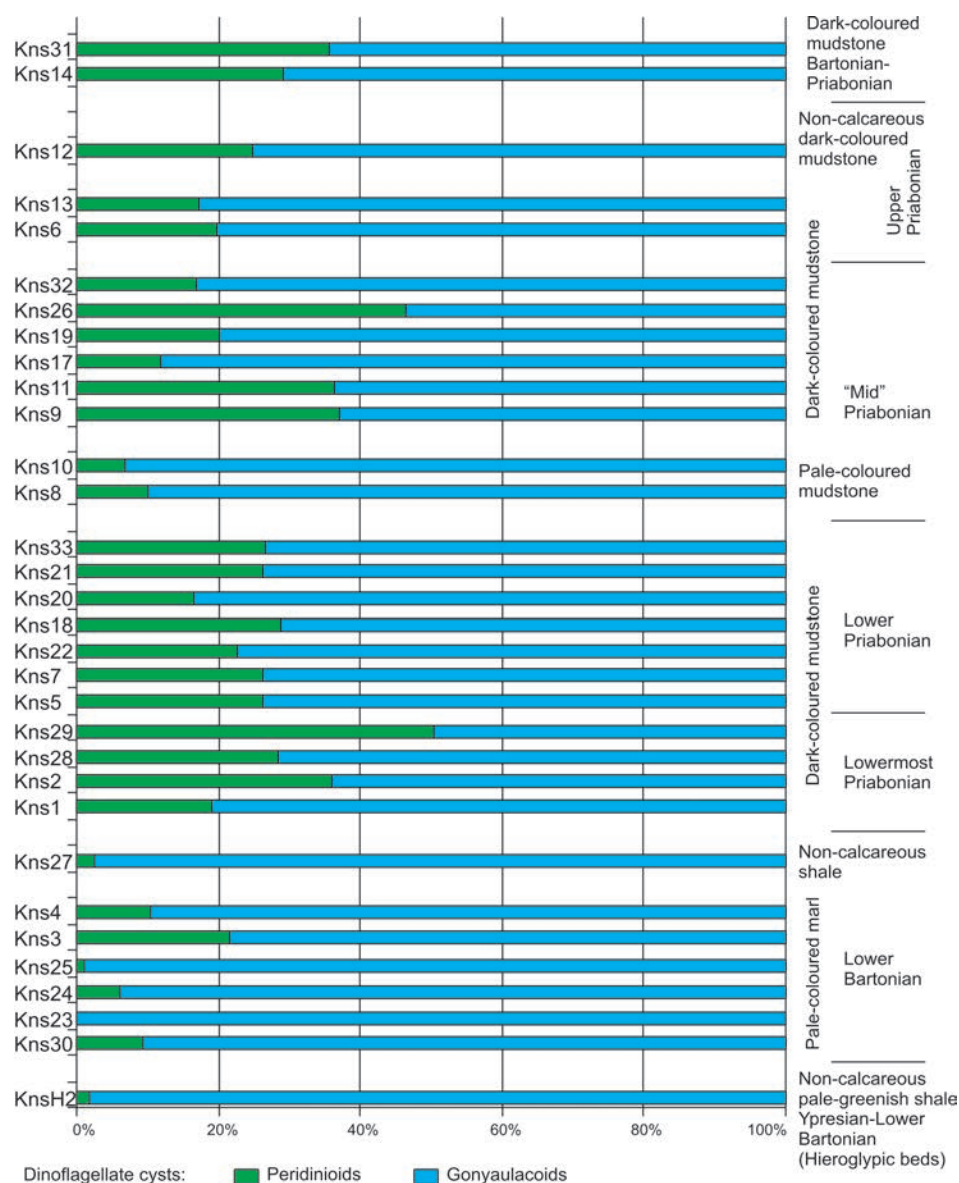
### **Peridinioids vs. gonyaulacoids ratio (P/G)**

Peridinioids, which are partly heterotrophic, are commonly believed to benefit from eutrophic waters; the high ratio of peridinioids versus gonyaulacoids (P/G) in fossil material is used as an indicator of increased palaeoproductivity related to palaeoupwelling or terrestrial nutrient source (river mouths; e.g., Harland, 1973; Lewis *et al.*, 1990; Powell *et al.*, 1992; Firth, 1996; van Mourik *et al.*, 2001). Fossil peridinioids are often interpreted to be indicators of reduced salinity environments (e.g., Köthe, 1990). Because some of the recent peridinioids are also autotrophic, Dale (1996) proposed a heterotrophic versus autotrophic ratio index (H/A), which should more precisely reflect the trophic conditions. However, in a case of the fossil material it is not possible to distinguish whether a particular species was heterotrophic or autotrophic. Therefore, in the present study, the peridinioids versus gonyaulacoids ratio index was calculated.

A characteristic feature of dinoflagellate cyst assemblages from the Popiele beds is a dominance of gonyaulacoids (Fig. 14). Peridinioids are subordinate – their ratio rarely exceeds 30% (in six samples only: Kns2, Kns9, Kns11, Kns26, Kns29, Kns31). In these cases, peridinioids are represented mainly by *Deflandrea*; less frequent Wetzelielloideae are represented chiefly by *Charlesdowniea*. Peridinioids frequency is directly related to lithology. In the most of dark-coloured Priabonian mudstone samples peridinioids represent 15–25%, being the most frequent (45%) in samples Kns26 and Kns29 (Fig. 14). Peridinioids are the rarest in samples from pale-coloured marls: they are absent from sample Kns23, 1% in Kns25, 10% in samples Kns4 and Kns30, being most abundant in Kns3 – over 20%. Peridinioids are also rare in pale-coloured non-calcareous clay: Kns27 (6.4%), Kns8 (6.9%), and Kns10 (6.5%). Peridinioids from two latter samples are represented mainly by *Dracodinium laszczynskii*, which co-occurs in the samples with relatively frequent specimens of oceanic *Impagidinium*.

### **Reconstruction of palaeoenvironment**

Lithological variability of deposits building the Popiele beds exposed at Koniusza suggests that this lithostratigraphic unit incorporates deposits originated from different sedimentary settings (Fig. 15). This view is supported by palaeoenvironmental interpretation of dinoflagellate cyst assemblages found during the present study. The assemblages are generally rich and taxonomically diversified. This is typical for a shelf palaeoenvironment (optimal living conditions of modern dinoflagellate's motile stages in marine realm are usually associated with such environments; e.g., Stover *et al.*, 1996; Dale, 1996), but some taxonomical variations

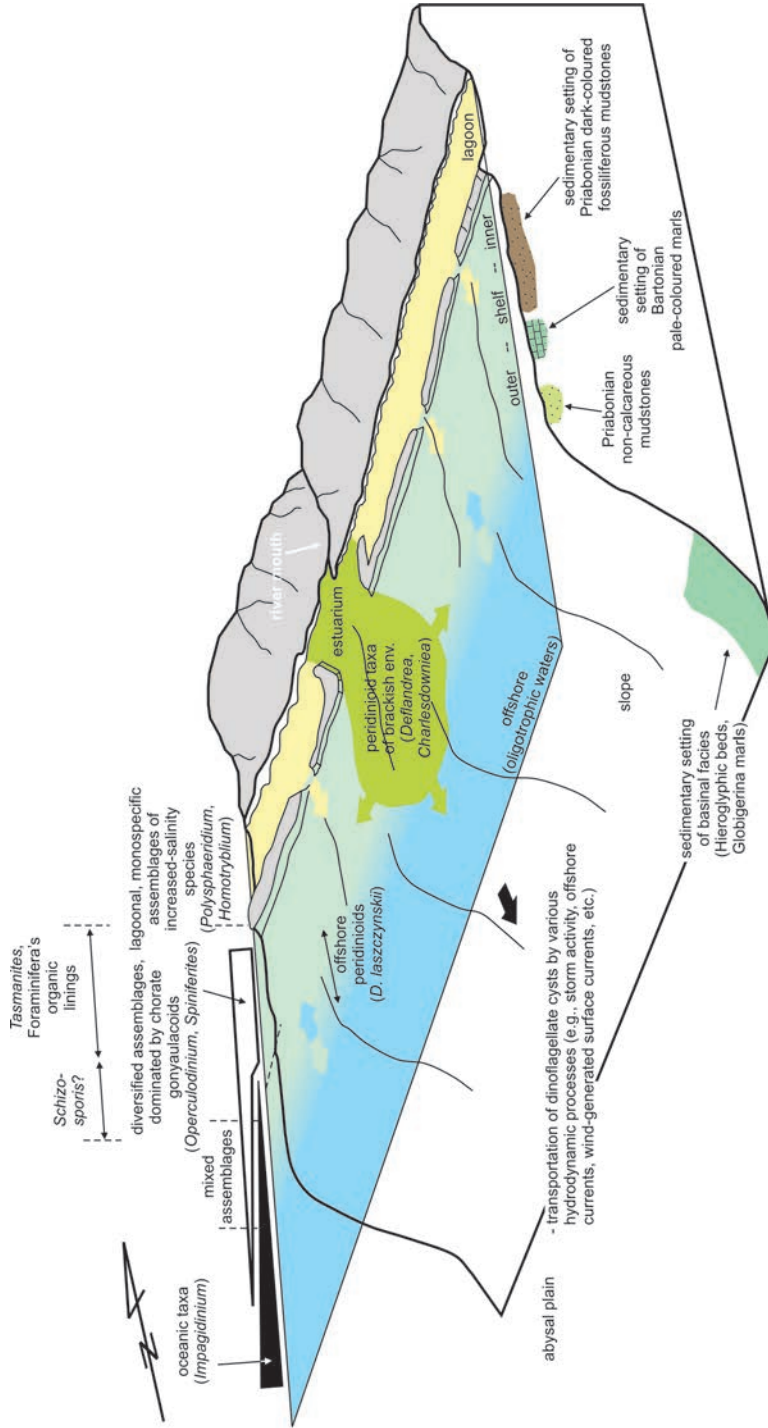


**Fig. 14.** Ratios of peridinioids vs. gonyaulacoids in the material studied

between dinoflagellate cysts in particular samples point at variable settings of their accumulation. These differences are presumably related to such factors like distance from the shore, intensity of terrestrial influx, nutrient availability, salinity, water oxygenation and temperature.

**Distance from shore.** Absence or very rare occurrence of *Impagidinium* in dark-coloured Priabonian mudstone, which form bulk of the Popiele beds volume, suggests that this lithofacies was deposited on a shelf, presumably in its proximal





**Fig. 15.** Conceptual model of palaeoenvironmental and palaeogeographic reconstruction of the Popiele beds sedimentary setting during Bartonian-Priabonian based on data from palynological analysis of the samples studied

part (Fig. 15). This interpretation is supported by the common occurrence of taxa, which motile stages are presumed to have inhabited inner shelf, lagoonal environments, commonly associated with increased salinity – *Polysphaeridium* and *Homotryblum* groups. Their maximal ratio ranges from 47.1% (Kns1), 44.6% (Kns17) through 15–30% in the most of samples studied, to minimal values in samples Kns11 (6.9%), Kns12 (7.6%). Relatively frequent occurrence of oceanic *Impagidinium* in the Bartonian pale-coloured marl (Kns3: 2.1%; Kns24: 3.1%; Kns25: 3.5%; Fig. 13) suggests that this sediment was deposited in a more offshore shelf zone. On the other hand, pale-coloured lithologies contain relatively taxonomically impoverished assemblages, which contrast with more diversified ones that occur in the dark-coloured mudstones (Fig. 12). Impoverished assemblages may be interpreted as indicators of more restricted inner shelf environments – these sediments contain frequent specimens of lagoonal genera *Polysphaeridium* and *Homotryblum* (over 60% in Kns3 and Kns25). The co-occurrence of offshore and near-shore species may indicate either a resedimentation of littoral assemblages into a more offshore shelf zone, or periodical incursions of oceanic water masses onto near-shore environments (e.g., during storm events). Composition of a dinoflagellate cyst assemblage from marl sample Kns30, which contains no *Impagidinium*, whereas its lagoonal genera exceed 62%, may indicate the most proximal site without offshore water influences.

The most offshore sedimentary setting (Fig. 15) may be suggested for pale-coloured non-calcareous clay (Kns8, Kns10, Kns27), which contains the highest ratio of *Impagidinium* (the highest among the all samples studied – 5.7% in Kns8; 5.1% in Kns27 and 2.4% in Kns10; Fig. 13). Representatives of the *Spiniferites* group are the most frequent ones in these samples: 49.3% in sample Kns10, 48.8% in Kns27, and 29.5% in sample Kns8. Ratios of near-shore, lagoonal species (*Homotryblum* and *Polysphaeridium*), in turn, reach their lowest values there: 6.1% (Kns8) and 8.9% (Kns10), 15.4% (Kns27; Fig. 13). However, like pale-coloured marl, samples Kns10 and Kns27 contain taxonomically impoverished dinoflagellate cyst assemblages; they are dominated by the *Spiniferites* group that points at offshore environment. This interpretation is supported by a highly diversified assemblage with frequent *Impagidinium* in sample Kns8.

**Terrestrial influx.** Pale-coloured lithologies from the Popiele beds (Bartonian marls: Kns3, Kns4, Kns23–25, Kns30; Bartonian non-calcareous clay: Kns27; Priabonian calcareous mudstone: Kns8 and Kns10) are characterized by a small amount of palynological organic matter as compared to its high quantity in dark fossiliferous mudstones. Their palynofacies consists chiefly of black opaque phytoclasts and frequent dinoflagellate cysts, which in some samples reach up to 70% of palynofacies (e.g., Kns27). These features suggest that pale-coloured lithologies were deposited in a sedimentary setting characterized by a limited influx of terrestrial elements. The latter, if present, are represented mainly by bisaccate pollen grains, which are commonly accumulated in offshore marine environments as transported by wind and/or floated due to their high buoyancy. Similarly, accumulation of black opaque phytoclasts, which are resistant to oxidation and bacterial

decay, are commonly found as dominating palynofacies element in the Flysch Carpathian offshore hemipelagic deposits (e.g., Lemańska & Gedl, 2005; Gedl, 2007). However, a similar palynofacies may occur in a near-shore environment, e.g. lagoonal environment, which is also characterized by a limited terrestrial influx. Frequent occurrence of *Polysphaeridium* spp. and *Homotryblum abbreviatum* in pale-coloured lithologies may suggest a near-shore, lagoonal environment – the recent motile stages of the former are commonly found in the hypersaline environments (e.g., Wall & Dale, 1969; Bradford & Wall, 1984), whereas mass occurrences of fossil *Homotryblum* are associated by many authors with increased salinity (e.g., Brinkhuis, 1994). But the presence of *Impagidinium* in the same samples suggests a more offshore environment; in this case, the near-shore species should be treated as resedimented from proximal, lagoonal environments into deeper parts of the Skole Basin (see subchapter *Distance from shore*; Fig. 15). This interpretation may be supported by an analysis of sample KnsH2 from the Hieroglyphic beds, which represent basinal deposits, palynofacies of this sample consists of black opaque phytoclasts and dinoflagellate cysts (up to 10%) presumably entirely resedimented from the shelf area (no *Impagidinium* was found there).

Different sedimentary conditions can be suggested for the Priabonian dark-coloured mudstone, which yielded palynofacies composed chiefly of terrestrial palynodebris, with subordinate ratio of marine elements (dinoflagellate cysts rarely exceed here 10%). This suggests that their accumulation happened during a period of intense terrestrial influx, presumably within the inner shelf zone. Land proximity is suggested on the base of composition of dinoflagellate cyst assemblages, which virtually contain no *Impagidinium*, whereas *Homotryblum* is very frequent (e.g., 47.1% in Kns1, and 30.6% in Kns2). It cannot be excluded, however, that both pale- and dark-coloured deposits were laid down at a similar distance from the shore, during periods of variable terrestrial influx.

**Trophic conditions.** Low frequency of peridinioids shows that marl and clay (particularly the pale-coloured ones) of the Popiele beds were deposited in marine environment characterized by a moderate to low nutrient availability (Fig. 15). This is especially well visible when frequency of heterotrophic Congruentidioideae (their high ratio is believed to characterize eutrophic waters; e.g., Biffi & Grignani, 1983) in the material studied is considered. Representatives of this subfamily are very rare (Fig. 13): they occur in dark-brown Priabonian mudstone as a few specimens per sample, being the most common in sample Kns33 – 3.6% (Kns18 – 2.6%, Kns21 – 2.5%, Kns6 – 2.4%, Kns22 – 1.7%, Kns12 – 1.5%, Kns13 – 1.3%, below one per cent in remaining samples). Congruentidioideae are absent from the majority of pale-coloured marl and clay samples (Kns4, Kns23–25, Kns30, Kns8, Kns10, Kns27; Fig. 13). Distribution of Congruentidioideae in the material studied shows negative correlation with distribution of *Impagidinium*: they occur in these samples, which contain no *Impagidinium* specimens (the only exception are samples Kns3, Kns5 and Kns13, Kns18, Kns28). This phenomenon confirms that fossil Congruentidioideae benefited from eutrophic marine environments, whereas *Impagidinium* preferred oligotrophic oceanic waters.



Correlation of Congruentidioideae and *Impagidinium* frequencies suggests various trophic conditions during deposition of lithofacies that form the Popiele beds. Dark-coloured mudstone, which contains assemblages with more frequent Congruentidioideae (but also frequent other peridinioids – up to almost 50%: e.g., Kns26, Kns29; Fig. 14), and devoid of *Impagidinium*, was deposited under moderate eutrophic conditions. Pale-coloured marl and mudstone contain oceanic *Impagidinium* and lack Congruentidioideae (Fig. 13) pointing at relative lower nutrient availability during their accumulation.

Priabonian mudstone (Kns8 and Kns10) is distinctive among the pale-coloured lithologies when trophic conditions are considered: these samples, beside a high ratio of *Impagidinium* (Fig. 13), contain the lowest ratios of peridinioids (7% in Kns8 and 6.5% in Kns10) and they lack Congruentidioideae. Peridinioids in these two samples are represented almost exclusively by *Dracodinium laszczyński*, whereas *Deflandrea*, so common in other samples from the Popiele beds, represents only 1.1% in Kns8 and 0.5% in Kns10. According to Gedl (2004a) and Gedl & Surlu (2005) *D. laszczyński* is an offshore species that presumably benefited from oligotrophic conditions. This would indicate that waters during Priabonian pale-coloured marl deposition were characterized by the lowest nutrient availability.

**Water oxygenation.** According to some authors, a high ratio of *Thalassiphora* may reflect oxygen-depleted water and bottom environment caused by stratified water column and increased productivity conditions (Köthe, 1990; Pross, 1997, 2001). No such conditions could be suggested on the base of infrequent occurrence of this genus in the material studied (from 0.2% in Kns11 to 5.5% in Kns14, and 6.7% in Kns7). However, a slight increase of this genus frequency in dark-coloured mudstone in relation to its occurrence in pale-coloured lithologies (Fig. 13) may reflect a finely oxygen-depleted environment during deposition of the former resulting from decomposition of high amounts of terrestrial organic matter.

**Salinity.** Relative high diversity of the studied assemblages suggests marine environments during deposition. However, the most of samples yield *Polysphaeridium* spp. and *Homotryblium* spp., which are commonly associated with hypersaline environments (e.g., Wall & Dale, 1969; Bradford & Wall, 1984; Brinkhuis, 1994). In some samples, their ratio is very high – even over 60% in some pale-coloured marl samples (Kns3, Kns25, Kns30; Fig. 13). But in the same samples *Impagidinium* occurs (2.1% in Kns3 and 3.5% in Kns25; Fig. 13), which may indicate mixing of near-shore and offshore waters during accumulation of pale-coloured marl (see *Distance from shore*). Frequent occurrence of lagoonal species, particularly in Bartonian samples, suggests existence of lagoons, possibly with increased salinity, along the shore of the Skole Basin.

There are no indications of significantly reduced salinity in the material studied. However, some samples, especially from the dark-coloured mudstone, contain increased ratio of *Deflandrea* (e.g., Kns2 – 44.3%, Kns29 – 41.5%, Kns26 – 38.4%), a peridinioid genus associated by some authors with brackish environments (e.g., Köthe, 1990). Its presence may indicate periodical salinity reductions in marginal zone of the Skole Basin during Priabonian (i.e., during the deposition of dark-col-

oured mudstone) caused by river freshwater input, which was also responsible for a high influx of vascular plant remains preserved in dark mudstone (Fig. 15). This assumption is supported by the occurrence of freshwater algae *Botryococcus* found in sample Kns2. However, magnitude of salinity reduction during Priabonian was relatively small – assemblages with a high number of *Deflandrea* contain also other stenohaline species. Moreover, if present at all, it must have been limited to the surface water zone only, since dark-coloured mudstone contains rich benthic stenohaline fossils. It cannot be excluded that, like in the case of *Homotryblium*-rich assemblages, *Deflandrea* specimens were transported from estuarine waters into more offshore marine environment.

**Sea surface temperature – palaeoclimate.** Fossil dinoflagellate cysts are widely used as a tool for sea surface temperature reconstructions (see Sluijs *et al.*, 2005 for references). Brinkhuis & Biffi (1993) and Brinkhuis (1994) used dinoflagellate cysts as an indicator of climatic cooling phases during the Eocene. They noted the presence of high-latitude species in northeast Italy, and interpreted their appearance as indication of climatic cooling. The most of taxa regarded as the high-latitude ones represent offshore species (see also Bujak, 1984), which seem to be most reliable in palaeoclimatic reconstructions: *Impagidinium pallidum*, *Impagidinium velorum*, *Gelatia inflata*, *Corrudinium incompositum*. The other ones include *Achomosphaera alcornu* and *Rottnestia borussica* and *Svalbardella* (Head & Norris, 1989; Manum *et al.*, 1989; Brinkhuis, 1994; Poulsen *et al.*, 1996). Their use in reconstruction of surface water temperature in case of Koniusza is limited because the dinoflagellate cysts studied represent proximal assemblages. Very rare specimens of *Achomosphaera alcornu*, *Rottnestia borussica* and *Corrudinium incompositum* are the only species believed to be high-latitude ones in the Popiele beds. They are concentrated in offshore marl facies, mainly of Bartonian age, less frequently of Priabonian age. There are no significant increases of their frequency in any sample studied. This makes any attempts of correlation of the material studied with global climatic changes a highly hazardous one. During the Eocene, a long cooling trend took place, starting from the so-called Early Eocene Climatic Optimum to the major cooling phase at the Eocene–Oligocene boundary (e.g., Zachos *et al.*, 2001). Occurrence of high-latitude offshore species, which may be interpreted as indicators of cooling phase, was reported from still younger Carpathian strata. *Gelatia inflata*, *Impagidinium velorum* and *Impagidinium pallidum* have been found in the topmost part of the Globigerina marls (or their equivalents) pointing at the drop of the sea surface temperature during the latest Eocene in the Carpathian basins (e.g., Gedl, 2004a, c, 2005a; Gedl & Leszczyński, 2005).

### Sedimentary implications

Interpretation of palynofacies and dinoflagellate cyst assemblages shows that the main lithologies that build the Popiele beds – pale-coloured marl and mudstone and dark-coloured mudstone – represent two slightly different sedimentary settings, although both located on shelf (Fig. 15).

Pale-coloured lithologies (Bartonian marl and Priabonian mudstone) were accumulated in a more offshore shelf zone, beyond land influences. During Bartonian a lagoon system developed in a most near-shore zone where increased salinity conditions favoured hypersaline dinoflagellates (*Homotryblum* and *Polysphaeridium*). The latter were transported offshore. Priabonian pale-coloured marls were deposited in a presumably even more remote setting where influences of land and lagoonal waters were limited. This relative offshore setting, possibly during a lower river discharge, was characterized by more oligotrophic surface waters and – due to a limited influx of organic matter – by well oxidized bottom waters. Infrequent appearance of high-latitude species may be related to relatively cooler surface waters in an offshore zone of the Skole Basin.

Sedimentary setting of dark-coloured mudstone was originally located in a more proximal shelf zone as compared to the one occupied by pale-coloured lithologies. During Priabonian, this zone was influenced by freshwater influx, which brought land-derived organic particles into the marine basin. This influx, although of limited magnitude, was responsible for at least periodical decrease of salinity in surface waters, and slightly increased nutrient availability. Lagoonal system existed also during Priabonian, but it gradually decreased from early to late Priabonian: the oldest Priabonian samples yield a relatively high ratio of high-salinity dinoflagellate species, which decreases in younger samples.

## DISCUSSION

### Biostratigraphy

Lithological analysis of the Popiele beds at Koniusza showed that this unit consists of clasts representing variable lithologies, which occur in a sandy-loamy fossiliferous matrix (e.g., Dżułyński & Kotlarczyk, 1965; Rajchel, 1990). The present study shows that fossiliferous matrix is of Priabonian age whereas pale-coloured clasts are of Bartonian and Priabonian ages.

The most of palaeontological datings of the Popiele beds is based on fossils, which occur in the sandy-loamy matrix [molluscs studied by Wiśniowski (1908) and Rogala (1925, 1941 *vide* Krach, 1985), and revised by Krach (1985), and Foraminifera studied by Syniewska (1937)]. Their age interpretations are generally similar – Bartonian and Priabonian according to Bieda *et al.* (1963) and Krach (1985). Wójcik's (1903) age interpretations of the Popiele beds from Kruheli Mały were reinterpreted by Liszka & Geroch (1979) as Priabonian. Rajchel (1990) suggested Lower Priabonian age of the Popiele beds at Grochowiec.

The pale-coloured clasts achieved less attention. Dżułyński & Kotlarczyk (1965) distinguished five dominant lithotypes of clasts inserted in the matrix, of which four were attributed to the Eocene Hieroglyphic beds and the Oligocene Menilite beds. The age of the remaining one ("soft and hard marls of green and dark greyish colours") was not determined. Kotlarczyk (1988b) reported occurrence of calcareous nannoplankton characteristic for zone NP21 (co-occurrence of *Disco-*

*aster lodoensis* and *Iribrachiatus orthostylus*) in cream-greenish marl clasts. This uppermost Priabonian–Lower Rupelian interpretation (i.e., the range of Calcareous Nannoplankton Zone NP21; see Martini, 1971) is shifted in contrast to the Bartonian (Kns3, Kns4, Kns23, Kns24, Kns25) and lower?-mid? Priabonian (Kns8, Kns10) of pale-coloured clasts dated based on dinoflagellate cysts in this study (Fig. 11). This indicates that light-coloured clasts may also represent the uppermost Priabonian–Lower Rupelian. Garecka *et al.* (2008) described Early Oligocene calcareous nannoplankton from the Popiele beds, but without detailed sample description.

Age interpretation of microfossil assemblages presented above does not directly solve the problem of the deposition time of the Popiele beds. Due to its olistostromic character, dinoflagellate cysts determine the age of rocks that form this slump deposits, but not the time of the Popiele beds accumulation. The only clue is the age of the youngest samples – Kns6, Kns12 and Kns13 (Fig. 11), which contain late Priabonian dinoflagellate cysts. On this base, it can be stated that deposition of the Popiele beds as a unit at Koniusza took place either during the latest Priabonian, or slightly later, i.e., during the earliest Rupelian.

A similar conclusion may be drawn on the base of the superposition of the Popiele beds at Koniusza, where this lithostratigraphic unit occurs between the Middle/Upper Eocene Hieroglyphic beds and the Lower Oligocene Menilite beds. However, several authors report occurrence of the Popiele beds at other sites within the Eocene strata. Rajchel (1990), on the base of poorly exposed Popiele beds at Turnica, suggested their slightly older age. Also observations in outcrops at Nowe Sady revealed presence of Eocene green shales above the Popiele beds (Morgiel & Żgiet, 1964). Similar position, below green shales, was reported from the Ukrainian Carpathians by Vialov (1951, 1961). Leszczyński (1996, 1997) described a younger position of the Popiele beds, which form a lens within the Globigerina marls, the latter preceded deposition of the menilitic facies in the Flysch Carpathians. Kotlarczyk (1985a, 1988b) and Garecka *et al.* (2008) compare the Popiele beds formation event with deposition of the Globigerina marls (see e.g., Van Couvering *et al.*, 1981; Olszewska, 1983, 1984; Leszczyński, 1996, 1997). On the other hand, occurrence of blocks of rocks derived from the Oligocene Menilite beds and the Kliwa sandstone reported by Dżułyński & Kotlarczyk (1965) and Dżułyński *et al.*, (1979a), indicates that submarine slumps that formed the Popiele beds took place during Oligocene (see also Świdziński, 1948). This conclusion is supported by Garecka *et al.* (2008) who reported the Early Oligocene calcareous nannoplankton suggesting the youngest age of all previous palaeontological datings of the Popiele beds.

All above mentioned indecisive datings of the Popiele beds deposition event may also indicate that such deposition took place during several mass-movement events (as it was already suggested by Dżułyński & Kotlarczyk, 1965) on the northern and north-western margin of the Skole Basin during Priabonian and Rupelian.



### Palaeoenvironment

Interpretation of palynological data presented above, compared to interpretation of micro- and macrofaunistic studies of the Popiele beds, clearly points at neritic, near-shore marine environment (note: palaeontological studies of the Popiele beds focused at fossils that occur in sandy-loamy matrix). Palaeoenvironmental interpretations of dinoflagellate cysts with those of benthic associations (foraminifers and molluscs), especially in relation to water depth may differ, but general conclusions suggesting a near-shore, presumably inner shelf environment, are consistent.

Krach (1985) interpreted macrofossil assemblages (mainly bivalves, gastropods and scaphopods) from Koniusza as typical for marine environment of the neritic zone with water depth not exceeding 100 m.

Liszka & Geroch (1979) analyzed foraminiferal assemblages from the Popiele beds at Kruheli Wielki (near Przemyśl) and made a revision of Wójcik's (1903) foraminiferal collection from the same locality. They found in dark-brownish mudstone and marly shales a rich assemblage composed predominantly of calcareous benthic species (representing *Nodosariidae*, *Buliminidae*, *Discorbidae*, *Anomalinidae*, *Cassidulinidae* and *Alabaminidae*), associated with rare agglutinated (*Ataxophragmiidae* and *Textulariidae*) and planktonic species. According to Liszka & Geroch (1979), the most of foraminiferal species present in the Popiele beds (see also Syniewska, 1938) had broad environmental tolerance: in relation to the water depth they include species, which may inhabit from neritic to bathyal depths. However, high taxonomical diversity, lack of non-calcareous agglutinated species typical for a deep-water flysch sedimentation, and the presence of some neritic species (*Nummulites*, *Asterigerina*) led Liszka & Geroch (1979) to the conclusion that Foraminifera assemblages described from the Popiele beds are indicative for a neritic environment.

Garecka *et al.* (2008) noted among Foraminifera from the Popiele beds the presence of benthic calcareous (*Cibicides*, *Melonis*, *Uvigerina*, *Globobulimina* and *Lenticulina*) and rare agglutinated (*Clavulinoides*) forms, which were interpreted as indicative for a setting at the slope of the Skole Basin (however, these authors did not describe the rock type which yielded foraminifers).

It is not possible to reconstruct water depth of a basin on the base of dinoflagellate cyst assemblages which are planktonic; a distance from shore can be approximately estimated, but this can be masked by intensity of terrestrial influx. Using these criteria it can be suggested that the sedimentary setting of dark-coloured mudstone with frequent macrofauna was located in a proximal shelf zone characterized by intense land-influx that led to a slightly higher trophic level, possibly associated with salinity decrease of the surface waters. This zone was presumably characterized by relatively dynamic conditions since these deposits contain elongated phytoclasts, which are commonly associated with high-energy environments; also preservation of palynomorphs, particularly dinoflagellate cysts, which are commonly torn-off, points at hydrodynamic processes during their accumula-

tion. This interpretation may be supported by those based on macrofossil studies: neritic optimal living conditions for benthic biota – well oxidized bottom waters with sufficient food supply (see Liszka & Geroch, 1979; Krach, 1985). Surface waters in more distal shelf zone (deposition area of pale-coloured lithologies), beyond terrestrial-influx zone, were presumably characterized by lower nutrient availability and lower temperatures, as compared to more inner shelf zone. Such conditions possibly favoured foraminiferal assemblages – described by Garecka *et al.* (2008) – typical for more offshore, deeper environments.

Analysis of dinoflagellate cysts as salinity indicators shows no major changes in surface water chemical composition in the material studied. This interpretation cannot be directly compared with former palaeontological studies, since the latter focused mainly on benthic biotas. Peridinioids, commonly believed to be tolerant to brackish environments, are subordinate in the Koniusza samples pointing at limited freshwater influx. Relatively high ratio of peridinioids of dark-coloured mudstone might be a trace of freshwater influx, but a general lack of freshwater algae (e.g., *Pediastrum* and *Botryococcus*), which commonly occur in marine strata deposited near river mouths, suggests that its influence on salinity of surface waters was minimal (only one sample, Kns2, yields rare specimens of *Botryococcus*). This interpretation can be supported by observations of benthic biota, which were interpreted as stenohaline (e.g., Krach, 1985): a possible decrease of salinity during deposition of fossiliferous marl was either indistinct, or it was limited to the surface zone only. The same refers to the problem of increased salinity conditions postulated on the base of common occurrence of hypersaline species (e.g., *Polysphaeridium*). They were presumably transported by hydrodynamic surface currents from lagoons into more offshore shelf areas where bottom water salinity remained unchanged. Winnowing of near-shore taxa from lagoonal environments into deeper parts of the basin seems to have taken place in flysch basins commonly, leading to occurrence of even monospecific near-shore assemblages in deep-sea deposits (e.g., Gedl & Suruło, 2005).

Nutrient availability is another factor characterizing surface waters. There are two its main sources in surface waters of marine realm: upwelling or freshwater influx. In case of the Koniusza samples the latter seems to be the main source. This interpretation is based on relatively high frequency of peridinioids, particularly Congruentidioideae (these forms are commonly regarded as indicators of fertile, nutrient-rich waters; e.g., Dale, 1996; Reichert & Brinkhuis, 2003) in fossiliferous mudstone, which according to the present interpretation was accumulated in a proximal shelf zone. Palynofacies of this lithology is filled with vascular plant remains obviously derived from a land and was transported by rivers. Richness of benthic biota (e.g., gastropods, bivalves, foraminiferas; see e.g., Liszka & Geroch, 1979; Krach, 1985) in this fossiliferous lithofacies confirms a high rate of food supply. The lowest ratio of peridinioids, and especially of Congruentidioideae, was in samples representing pale-coloured mudstone, which was deposited in more offshore shelf zone (no palaeontological studies of this rock type have been carried out so far). These samples yielded simultaneously the highest ratio of *Impagidinium*,

which is believed to benefit in oligotrophic waters. This relation shows that the near-shore belt of surface water was slightly enriched in nutrients of terrestrial origin whereas the outer shelf waters were more oligotrophic. However, magnitude of this “eutrophication” of coastal waters was very small, since dinoflagellate cysts that could benefit from such conditions (e.g., Congruentidioideae) are very rare in the material studied.

### **Palaeoenvironmental preferences of selected aquatic palynomorphs from the Popiele beds**

A relation of some aquatic palynomorph distribution in the material studied to palaeoenvironmental factors is shortly discussed in this subchapter.

The genus *Impagidinium*, both fossil and recent, is widely associated with off-shore waters (e.g., Brinkhuis, 1994; Zevenboom *et al.*, 1994; Dale, 1996; Rochon *et al.*, 1999), which usually are characterized by low concentration of nutrients. Distribution of this genus in the material studied shows a negative correlation with the occurrence pattern of Congruentidioideae, i.e., the dinoflagellate cyst group, representatives of which are known to benefit from eutrophic waters (e.g., Biffi & Grignani, 1983; Dale, 1996). Samples with *Impagidinium* are generally devoid of Congruentidioideae, and *vice versa* (only three samples of 14 contain mixed assemblages). Such a distribution confirms their generally accepted palaeoenvironmental preferences.

A somehow different from generally accepted seem to be palaeoenvironmental preferences of some Wetzelielloideae. As a group, representatives of this subfamily are commonly treated as forms that have inhabited near-shore, frequently estuarine, waters. Distribution of the genus *Charlesdowniea*, which is present in the most of samples, seems to confirm this rule. But *Dracodinium laszczynskii*, another member of Wetzelielloideae, seems to have had different preferences. This species occurs in two samples (Kns8 and Kns10), which contain dinoflagellate cyst assemblages interpreted as the most offshore ones among all the samples studied. They contain the highest ratios of offshore *Impagidinium*, and one of the lowest ratios of near-shore taxa (*Homotryblum*), and *Deflandrea*. Such a distribution of *Dracodinium laszczynskii* suggests that this species, in contrast to other Wetzelielloideae, has inhabited rather offshore waters (Fig. 15). This interpretation confirms results of earlier studies, which also suggested offshore preferences of this species (Gedl, 2004a; Gedl & Suruła, 2005).

An interesting relation was observed when distribution of peridinioids was considered. Samples with highest ratio of *Deflandrea* (i.e., genus that is believed to benefit from nutrient-rich waters; Kns2, Kns9, Kns11) show lowest ratios of Congruentidioideae. The latter, theoretically, should be also frequent in those samples. In the Koniusza samples, Congruentidioideae are the most common in those with the lowest *Deflandrea* ratio (Kns6, Kns12, Kns13). This points at different palaeoenvironmental preferences of these two groups of peridinioids. Possibly, some other factors including water temperature or water chemistry are responsible

for this distribution pattern. On the other hand, Congruentidioideae are absent from pale-coloured marl, which also contains low ratios of *Deflandrea* (Kns23–25).

Palaeoenvironmental interpretation of other aquatic palynomorphs is somehow enigmatic in the material studied: this refers to foraminiferal organic linings, Tasmanitaceae and *incertae sedis* attributed by Brinkhuis (1992) to Cymatiosphaeraceae (Prasinophyte algae) *Schizosporis*. Their occurrence in the Popiele beds is strictly related to lithology. *Schizosporis*? occurs in pale-coloured marl (Kns3, Kns4, Kns8, Kns10), whereas foraminiferal organic linings and *Tasmanites* have been found in fossiliferous sandy mudstone. Such a distribution of these palynomorphs in the material studied indicates more offshore preferences of *Schizosporis*?, whereas *Tasmanites* and foraminiferal organic linings seem to have been bound with proximal settings. Gedl (2005a) found *Schizosporis*? in samples of hemipelagic origin of coeval flysch deposits (the Szymbark shale, Magura Nappe): this supports thesis of offshore preferences of this taxon.

### Comparison with coeval dinoflagellate cyst assemblages from neighbouring areas

Accumulation of deposits that subsequently were resedimented into deeper parts of the Skole Basin (the Popiele beds) was located at north-western peripheries of the Flysch Carpathian basinal system. Reconstruction of their sedimentary setting suggests that they were deposited in shelf environment. This feature distinguishes the Popiele beds from most of the coeval Carpathian strata, which were accumulated in offshore settings.

**Flysch Carpathians.** Middle and Late Eocene dinoflagellate cysts from the Carpathians have been studied in several localities (Bujak *in* Van Couvering *et al.*, 1981; Gedl, 1995a, b, 2004a, b, c, 2005a, b, c; Gedl & Garecka, 2008; Gedl & Lemańska, 2005; Gedl & Leszczyński, 2005). The majority of these assemblages occur in offshore turbiditic deposits. They represent a mixture of taxa resedimented from shelf area with those that are “*in situ*” (i.e. offshore taxa). Depending on the origin of particular deposits, ratio of inshore and offshore taxa varies significantly: turbiditic parts of a flysch sequence contain chiefly proximal assemblages, whereas pelagic, topmost laminae of the turbidite rhythm yield commonly offshore assemblages (e.g., Gedl & Suruła, 2005; Gedl, 2006b).

The Middle Eocene variegated shales of the Magura Nappe represent oceanic deposits of pelagic/hemipelagic origin (see Dominik, 1977; Leszczyński & Uchman, 1991; Oszczytko, 1992). Red (pelagic) shales of this lithostratigraphic unit exposed at Ptaszkowa (see e.g., Sikora, 1970) are palynologically barren, whereas greenish (hemipelagic) laminae contain dinoflagellate cyst assemblages, which contain a relatively high ratio of oceanic genus *Impagidinium* – over 10% (Gedl & Lemańska, 2005). This confirms oceanic sedimentary setting of this lithofacies. However, greenish laminae contain also a high ratio of near-shore species, including lagoonal *Polysphaeridium*. Frequent occurrence of this genus points at increased transportation of dinoflagellate cysts from lagoonal environ-



ments into offshore parts of the Magura Basin. This phenomenon resembles the one reconstructed for coeval pale-coloured marl from Koniusza, which although deposited much closer to the shore, also shows a mixture of oceanic (*Impagidinium*) and lagoonal species (*Polysphaeridium*).

More diversified dinoflagellate cyst assemblages have been found in coeval strata of the Magura Nappe represented by turbiditic, generally coarse-grained Magura Sandstone Formation. This lithostratigraphic unit is occasionally developed as fine-grained strata like a sequence exposed at Tenczyn, which yielded diverse dinoflagellate cyst assemblages. Pale-coloured non-calcareous lithologies contain low-frequency assemblages consisting of common *Dracodinium laszczyński* and, subordinately, *Impagidinium*, whereas blackish shale yielded almost monospecific assemblages of near-shore *Homotryblum* (Gedl & Suruła, 2005). This distribution pattern suggests the presence of at least two zones inhabited by different dinoflagellate assemblages: the offshore one, with common *Dracodinium laszczyński* and *Impagidinium*, and a near-shore one (lagoonal?) with blooms of *Homotryblum*, which subsequently had been transported into basinal parts of the Middle Eocene Flysch Carpathian sea.

A similar phenomenon of resedimented near-shore assemblages commonly occurs also in the Upper Eocene strata of the Carpathians (e.g., Gedl, 2004b, c). This is well documented in the Folusz section (Szymbark shale and the Magura Formation of the Magura Nappe; see Leszczyński & Malata 2002, and Gedl & Leszczyński, 2005). Hemipelagic samples are enriched in offshore species (e.g., *Impagidinium*), whereas turbiditic ones contain chiefly near-shore taxa (Gedl, 2005).

The Priabonian age of dark-coloured fossiliferous mudstone from Koniusza can be generally correlated with deposition time of the Globigerina marls in the Carpathian basins (Blaicher, 1970; Olszewska, 1983, 1984; see also Leszczyński, 1996, 1997). Dinoflagellate cyst assemblages from this outstanding isochronous horizon usually show no prominent changes in their composition during the terminal Eocene event (Bujak *in van Couvering*, 1981; Gedl, 1999). Rich and diversified assemblages of the Globigerina marls are generally similar to the ones from the Popiele beds. They point to marine conditions, which lasted until deposition of the organic-rich Menilite beds started during the earliest Oligocene (Gedl, 2004a, 2005b, c). The main difference is related to frequent occurrence of oceanic taxa (mainly *Impagidinium*) in the Globigerina marls; their presence suggests more offshore sedimentary setting than that of the Popiele beds (the latter are commonly missing *Impagidinium*). This is especially well visible in a case of the Leluchów Marl Member (an equivalent of the Globigerina marls; Birkenmajer & Oszczytko, 1989) of the Magura Nappe, which contains a high ratio of *Impagidinium* and almost no *Homotryblum* specimens (Gedl, 2004a).

However, some sections of the Globigerina marls in the Flysch Carpathians yielded dinoflagellate cysts assemblages, the composition of which underwent significant changes in their uppermost parts. This refers to a variable ratio of oceanic vs. near-shore taxa and appearance of assemblages dominated by peridinioids (chiefly *Deflandrea*). Monospecific assemblages of *Homotryblum* appear in the

topmost part of the Globigerina marls sequence at Znamyrowice (Silesian Nappe; Gedl, 2005c). Their presence may reflect increased transport from inner shelf areas into deeper parts of the flysch basin, like in the case of Tenczyn. An increase of peridinioid frequency leading to domination of *Deflandrea* is observed in the uppermost part of the section at Ropa (Fore-Magura Nappe – Grybów Unit); this may be interpreted as a result of salinity drop in the surface waters (Gedl, 2005b). The latter event is dated by the first appearance of *Reticulatosphaera actinocoronata*. This bioevent allows precise correlation with youngest samples from the Popiele beds at Koniusza – Kns6, Kns12 and Kns13. Composition of dinoflagellate cyst assemblages of the latter samples, however, shows no similarities: near-shore species (*Homotryblum*) percentage is low (the highest in sample Kns6 – 27.3%), so is the ratio of *Deflandrea* (the highest in samples Kns12 – 10.2%, and Kns13 – 11.2%). Diversified dinoflagellate cyst assemblages from coeval strata suggest variable palaeoenvironmental conditions during the Late Eocene in the Flysch Carpathian basins, which presumably reflect their diversified orography and diversified relation to land areas. Morphology of shelf areas (e.g., existence of lagoon systems), and the presence or lack of estuaries, play important role in the nature of the surface water ecosystems, as reflected in the fossil record by various dinoflagellate cyst assemblages (see Fig. 15). However, distribution of the latter in fossil material is controlled not only by palaeoenvironmental conditions, but also by hydrodynamic processes, which commonly lead to resedimentation of the whole associations from their natural environments (e.g., lagoonal environment) into completely different sedimentary setting – for example abyssal plains. The latter phenomenon, especially when palynological material is considered, seems to have been a very common process in the Flysch Carpathian basins. Palynomorphs, including dinoflagellate cysts, are characterized by high buoyancy, and, compared to other microfossils (e.g., Foraminifera), can easily be transported by hydrodynamic processes without significant resedimentation of clastic material (see e.g., Gedl & Kaminski, 2005; Gedl, 2006b).

**Epicontinental basin.** Middle-Upper Eocene strata of the epicontinental marine basin have recently been found in the Carpathian Foredeep (Tarnogród vicinity) below a thick cover of Miocene strata (Myśliwiec & Śmist, 2006; Gedl, unpubl.). This isolated spot of Eocene strata, together with earlier known occurrence of Eocene deposits in the Sołokija valley in Roztocze (Krzowski, 1993; Cieśliński & Rzechowski, 1993; Buraczyński & Krzowski, 1994; Gaździcka, 1994; Buraczyński & Rzechowski, 1998), are the only traces of a marine basin in south-eastern Poland, south of the Lublin Upland, being the southernmost occurrence of epicontinental marine Eocene strata (Gedl, 2000a, 2006a). Their presence indicates a much larger extension of the Eocene sea than it was previously supposed (e.g., Piwocki, 2004; Słodkowska, 2004), however, its southern limits, and possible connections with the Carpathian basin, are still unsolved.

The age of the Sołokija succession according to Gaździcka (1994) is Bartonian. The results of dinoflagellate cyst studies confirm this interpretation, but also suggest a Priabonian age in the topmost part of the succession (Gedl, in prep.). The

basal part of the Sołokija succession (Bartonian) contains a diversified assemblage dominated by gonyaulacoids, similar to the assemblages from clasts of Bartonian marl of Koniusza. This similarity is supported by the presence of some characteristic species like an undescribed Genus et species indeterminated C (Fig. 84E, H, I) in both sites. However, the basal part of the Sołokija succession contains *Enneadocysta pectiniformis*, which is missing in the pale-coloured marl clasts; this may suggest a slightly younger age of the Sołokija deposits. The topmost part of the Sołokija succession dated as Priabonian (presence of *Rhombodinium perforatum*) can be correlated with the most of the dark-coloured mudstone samples from Koniusza. It yielded a peridinioid-dominated assemblage consisting mainly of *Deflandrea*, which presumably reflects a major drop in water salinity and appearance of brackish conditions in epicontinental basin during the Priabonian. This assemblage contrasts with coeval ones found in dark-coloured mudstone at Koniusza, which taxonomical composition points at marine conditions; their *Deflandrea*-ratios, although higher than in Bartonian samples, show no significant changes in water salinity.

Similarities between Bartonian dinoflagellate cyst assemblages from the Popiele beds at Koniusza, and the Sołokija succession, suggest that the Skole Basin was presumably connected, at least partially, with the epicontinental basin. During the Priabonian an emerged barrier north of the Skole Basin shelf separated it from the epicontinental sea. The latter became gradually a freshwater/brackish basin at Roztocze (the Sołokija succession), whereas marine conditions prevailed in the Skole Basin. At the same time, marine conditions prevailed not only in the Flysch Carpathian basins, but also north of the Lublin Upland (brackish conditions that characterized the Late Eocene epicontinental basin in Poland were most pronounced during its final stage in the northern part; e.g., Grabowska, 1987). The Bartonian–Priabonian Siemień Formation (see Piwocki, 2002) represents marine sediments with stenohaline fauna including foraminifera, calcareous nannoplankton, pelecypods, echinoids, bryozoans, bivalves, brachiopods and corals (e.g., Woźny, 1966, 1967, 1977; Pożaryska and Locker, 1972; Pożaryska, 1977; Szczuchura, 1977; Uberta & Odrzywolska-Bieńkowska, 1977; Kosmowska-Ceranowicz *et al.*, 1990). According to Pożaryska (1977), foraminifera from the Siemień Formation are different from those described by Syniewska (1937) and Wójcik (1903) from the Popiele beds. Pożaryska (1977) suggested on this base that the Siemień Formation is slightly older than the Popiele beds (note: Pożaryska's comparisons are based on foraminiferal data from the fossiliferous mudstone of the Popiele beds, which is Priabonian). Pożaryska (1977) also compared other Eocene Carpathian assemblages and suggested that there was no direct connection between the Late Eocene Carpathian and the epicontinental marine basins in Koniusza area (see also Pożaryska & Odrzywolska-Bieńkowska, 1977; Odrzywolska-Bieńkowska & Pożaryska, 1981). Possible connections between these two basins went through the Moravian Gate (to the west) and through the Black Sea–Caspian Sea area (see Pożaryska, 1977, fig. 3).

## SUMMARY

1. Thirty two samples from the Popiele beds exposed at Koniusza (Flysck Carpathians, Poland) have been studied. They represent various lithologies that build this olistostromic unit: dark-coloured fossiliferous mudstone that forms bulk volume, and clasts of pale-coloured marl and non-calcareous greenish clay. Additionally, two samples from the underlying Hieroglyphic beds and one sample from the overlying Menilitic beds have been investigated.

2. All samples contain rich palynological material. Palynofacies of dark-coloured mudstone is dominated by land-derived remains of vascular plants and sporomorphs. Pale-coloured marly and clay clasts, in turn, yielded mainly black and dark brown phytoclasts and dinoflagellate cysts. Among other aquatic palynomorphs, *Tasmanites* and foraminiferal organic linings are associated with fossiliferous mudstone, whereas *Schizosporis?* sp. occurs in pale-coloured lithologies.

3. A total of 152 dinoflagellate cyst taxa have been described from the Popiele beds. Their assemblages are generally rich and taxonomically diversified, being dominated by gonyaulacoids. Pale-coloured marl samples show lower diversity of dinoflagellate cysts than the dark-coloured mudstone ones; the former are commonly dominated by *Homotryblum*. The latter, in turn, show higher ratio of peridnioids.

4. The ages of the dinoflagellate assemblages from the Popiele beds at Koniusza span the Bartonian and Priabonian. The oldest are Bartonian pale-coloured marl samples. Samples from dark fossiliferous mudstone and pale-coloured non calcareous mudstone contain Priabonian assemblages with *Rhombodinium perforatum*. These interpretations generally coincide with the ones of earlier studies of the Popiele beds based on micro- and macrofauna.

5. There has been almost no pre-Eocene recycled species observed in the material studied. A single specimen of the Jurassic genus *Ctenidodinium* has been found only (two additional specimens have been found in the Hieroglyphic beds sample). The same refers to Palaeogene species: no Paleocene or Early Eocene species have been found. The Priabonian samples contain no Middle Eocene species. This suggests lack of erosion of Mesozoic and pre-Middle Eocene substratum during accumulation of deposits that later formed the Popiele beds.

6. Palynological analysis shows that lithofacies that build olistostromes of the Popiele beds were originally deposited in shelf environments. The most proximal setting was occupied by dark-coloured fossiliferous mudstone. Pale-coloured lithologies accumulated in a more offshore shelf zone, with the Priabonian non-calcareous mudstone deposited as the most offshore one. All studied lithofacies were deposited in marine environment. Marginal shelf zone was presumably slightly influenced by river mouths, leading to faint nutrient enrichment in surface waters and increased influx of terrestrial organic particles. Mixing of shelf waters by hydrodynamic currents resulted in resedimentation of lagoonal dinoflagellate cyst assemblages into a more offshore shelf zone; this phenomenon made palaeoenvironmental reconstructions of the Skole Basin shelf area more complicated. Sedimentolo-



gical relationship of particular samples could not be considered due to olistostromic character of the unit studied. An attempt of palaeoenvironment reconstruction resulted in distinguishing the following palaeoenvironmental zones at the shelf of the Skole Basin during Bartonian and Priabonian (Fig. 15):

(i) Lagoons occupied the near-shore belt; their hypersaline waters were inhabited by motile stages of *Polysphaeridium* and *Homotryblum*; there are no preserved deposits of this environment among the lithologies studied – their dinoflagellate cysts occur as winnowed into more offshore lithologies.

(ii) Basinwards, a shelf zone extended where fossiliferous mudstone accumulated. This zone was characterized by relatively high hydrodynamic conditions responsible for common mechanical damage of dinoflagellate cysts; on the other hand they prevented water stratification, and, despite a high influx of terrestrial matter, they ensured optimal living conditions at the bottom inhabited by diversified benthic assemblages, mainly gastropods and bivalves. Its surface waters were inhabited by diversified dinoflagellate assemblages pointing to a normal saline water, although freshwater influx of a minor magnitude was marked by a high ratio of land-derived plant particles. Freshwater influx was possibly responsible for a relatively high ratio of peridinioids, which benefited from slightly increased nutrient availability.

(iii) Farther basinwards, a zone of pale-coloured marl accumulation occurred. It was located on a shelf, offshore with relation to the sedimentary setting of the fossiliferous dark mudstone, and beyond the zone of intense land influences. Lack of the latter led to more oligotrophic conditions characteristic for basinal waters; their which influences are manifested by the presence of oceanic genus *Impagidinium*. Marine currents were responsible not only for water exchange with offshore zone, but also with lagoonal ones: as a result of the latter, monospecific assemblages of hypersaline species appeared in offshore sedimentary setting of the pale-coloured marl.

(iv) Farther offshore, during the Middle-Late Eocene, deposition of the Hieroglyphic beds and the *Globigerina* marls took place on slope and in basinal parts of the Skole Basin (Fig. 15).

7. The shelf area of the Skole Basin, where deposition of the lithofacies that build the Popiele beds took place, was presumably connected during the Bartonian with the epicontinental sea of the south-eastern Poland. This interpretation takes into account taxonomical similarities between Bartonian assemblages of both basins. During the Priabonian these two basins were presumably separated by a narrow land barrier. The southernmost part of the Late Eocene epicontinental basin became brackish then, whereas the Carpathian basins remained fully marine.

## SYSTEMATIC PART

A total of 152 dinoflagellate cyst taxa have been recognized in the Eocene of the Popiele beds exposed at Koniusza (their frequencies are shown in Fig. 7). They are illustrated in Figs 15–82, and listed below in alphabetic order. Taxa from the Hieroglyphic beds are shown in Figs 83 and 84. Taxonomy of the species described in this section [arranged alphabetically, per family or subfamily; classification by Fensome *et al.* (1993) is used] follows Fensome & Williams (2004). Terminology applied to the morphology of dinoflagellate cysts follows Williams *et al.* (2000). Beside dinoflagellate cysts, some other aquatic palynomorphs are illustrated in Figs 85–88 in this chapter. They are listed at the end of dinoflagellate cyst list.

- Achilleodinium biformoides* (Eisenack 1954) Eaton 1976 (p. 70; Fig. 7.94; Fig. 27L, M)  
*Achomosphaera alcornu* (Eisenack 1954) Davey et Williams 1966 (p. 101; Fig. 7.49; Fig. 44N, Fig. 85E)  
*Achomosphaera crassipellis* (Deflandre et Cookson 1955) Stover et Evitt 1978 (p. 101; Fig. 7.109; Fig. 44P, Fig. 85B)  
*Achomosphaera ramulifera* (Deflandre 1937) Evitt 1963 (p. 101; Fig. 7.41; Fig. 44I–M)  
*Achomosphaera* sp. *sensu* Brinkhuis 1992 (p. 103; Fig. 7.113; Fig. 44O)  
*Adnatosphaeridium multispinosum* Williams et Downie 1966 (p. 121; Fig. 7.40; Fig. 20D, E, Fig. 54A–C, E, F, K–P, Fig. 85G)  
*Adnatosphaeridium vittatum* Williams et Downie 1966 (p. 121; Fig. 7.42; Fig. 54D, G–J)  
*Apectodinium homomorphum* (Deflandre et Cookson 1955) Lentin et Williams 1977 (p. 164; Fig. 7.50; Fig. 80I, Fig. 82A–C, Q)  
*Araneosphaera araneosa* Eaton 1976 (p. 70; Fig. 7.137; Fig. 28S)  
*Areoligera coronata* (Wetzel 1933) Lejeune-Carpentier 1938 (p. 124; Fig. 7.130; Fig. 55M, N, Fig. 84A, L)  
*Areoligera* cf. *medusettiformis sensu* Eaton 1976 (p. 124; Fig. 7.151; Fig. 84 F, G)  
*Areosphaeridium diktyoplokum* (Klumpp 1953) Eaton 1971 (p. 61; Fig. 7.2; Fig. 17A–F, Fig. 18A, B, Fig. 20A–C)  
*Areosphaeridium ebdonii* Bujak 1994 (p. 61; Fig. 7.108; Fig. 18D–F)  
*Areosphaeridium michoudii* Bujak 1994 (p. 61; Fig. 7.76; Fig. 18C, H–L, Fig. 19G)  
*Batiacasphaera hirsuta* Stover 1977 (p. 145; Fig. 7.69; Fig. 52F, G)  
*Batiacasphaera micropapillata* Stover 1977 (p. 145; Fig. 7.55; Fig. 52H, I, M)  
*Batiacasphaera?* *reticulata* (Davey 1969) Davey 1979 (p. 145; Fig. 7.133; Fig. 52P–S)  
*Batiacasphaera* sp. A (p. 145; Fig. 7.58; Fig. 52L)  
*Batiacasphaera* sp. B (p. 146; Fig. 7.63; Fig. 52J, K, Fig. 53A, F)  
*Batiacasphaera* sp. C (p. 146; Fig. 7.68; Fig. 52O, T, Fig. 53C)  
*Cerebrocysta bartonensis* Bujak in Bujak *et al.* 1980 (p. 146; Fig. 7.48; Fig. 45T–X, Fig. 51E)  
*Cerebrocysta* cf. *bartonensis* Bujak 1980 (p. 147; Fig. 7.150; Fig. 45Y–Z1)  
*Charlesdowniea clathrata* (Eisenack 1938) Lentin et Vozzhennikova 1989 (p. 165; Fig. 7.98; Fig. 75B, C, G, H, Fig. 76A–F)  
*Charlesdowniea coleothrypta* (Williams et Downie 1966) Lentin et Vozzhennikova 1989 (p. 166; Fig. 7.8; Fig. 75A, D, E, Fig. 77A–I, Fig. 78A–I, Fig. 79A–G, Fig. 80A–E)  
*Charlesdowniea columna* (Michoux 1988) Lentin et Vozzhennikova 1990 (p. 167; Fig. 7.66; Fig. 76G–I)  
*Chlamydothorella* sp. (p. 147; Fig. 7.122; Fig. 16U–W)  
*Cleistosphaeridium ancyreum* (Cookson et Eisenack 1965) Eaton, Fensome, Riding et Williams 2001 (p. 64; Fig. 7.78; Fig. 21D, E, G, H, J, K, Fig. 22A, M, N, P–S, Fig. 23M–O, Fig. 25A–C, F–I, Fig. 26J, K)  
*Cleistosphaeridium placacanthum* (Deflandre et Cookson 1955) Eaton, Fensome, Riding et

- Williams 2001 (p. 67; Fig. 7.83; Fig. 24A–P, Fig. 21A–C, F, I, L, Fig. 25D)  
*Cleistosphaeridium* sp. (p. 67; Fig. 7.44; Fig. 22B, Fig. 23Q–U, Fig. 26F)  
*Cleistosphaeridium?* sp. A (p. 70; Fig. 7.105; Fig. 22C–L, O, Fig. 23A–L, P, Fig. 26A, D, E, G–I)  
*Cordosphaeridium cantharellus* (Brosius 1963) Gocht 1969 (p. 73; Fig. 7.11; Fig. 28P, Q, Fig. 29A–F)  
*Cordosphaeridium fibrospinosum* Davey et Williams 1966 (p. 73; Fig. 7.86; Fig. 28R, T, U)  
*Cordosphaeridium funiculatum* Morgenroth 1966 (p. 73; Fig. 7.129; Fig. 30G, L–N)  
*Cordosphaeridium funiculatum sensu* Brinkhuis 1992 (p. 79; Fig. 7.107; Fig. 31J–L)  
*Cordosphaeridium gracile* (Eisenack 1954) Davey et Williams 1966 (p. 79; Fig. 7.18; Fig. 29J–L, Fig. 85J, K, L)  
*Cordosphaeridium inodes* (Klumpp 1953) Eisenack 1963 (p. 79; Fig. 7.77; Fig. 32B, S, T, Fig. 85F)  
*Cordosphaeridium minimum* (Morgenroth 1966) Benedek 1972 (p. 80; Fig. 7.57; Fig. 28F–O)  
*Cordosphaeridium?* *solidospinosum* Gedl 1995 (p. 80; Fig. 7.23; Fig. 29G–I)  
*Cordosphaeridium* sp. A (p. 80; Fig. 7.126; Fig. 28A–E)  
*Corrudinium incompositum* (Drugg 1970) Stover et Evitt 1978 (p. 103; Fig. 7.29; Fig. 45J–S)  
*Corrudinium?* sp. A *sensu* Gedl 2005 (p. 103; Fig. 7.75; Fig. 32Q, R)  
*Cribroperidinium giuseppeii* (Morgenroth 1966) Helenes 1984 (p. 84; Fig. 7.14; Fig. 33A–P)  
*Dapsilidinium pseudocolligerum* (Stover 1977) Bujak *et al.* 1980 (p. 147; Fig. 7.88; Fig. 20J, K, Fig. 34S–Z, Fig. 53E)  
*Deflandrea arcuata* Vozzhennikova 1967 (p. 151; Fig. 7.37; Fig. 68E–G)  
*Deflandrea granulata* Menéndez 1965 (p. 152; Fig. 7.62; Fig. 69E–N)  
*Deflandrea heterophlycta* Deflandre et Cookson 1955 (p. 152; Fig. 7.20; Fig. 68H–J, L–O, Fig. 80J)  
*Deflandrea leptodermata* Cookson et Eisenack 1965 (p. 152; Fig. 7.61; Fig. 68A–D)  
*Deflandrea phosphoritica* Eisenack 1938 (p. 155; Fig. 7.4; Fig. 68K, Fig. 69A–D, O, P, Fig. 70A–N, Fig. 80K)  
*Dinopterygium cladoides sensu* Morgenroth 1966 (p. 134; Fig. 7.24; Fig. 62A–H, J–M)  
*Diphyes colligerum* (Deflandre et Cookson 1955) Cookson 1965 (p. 84; Fig. 7.87; Fig. 34N–Q)  
*Distatodinium craterum* Eaton 1976 (p. 148; Fig. 7.110; Fig. 55E, I)  
*Distatodinium ellipticum* (Cookson 1965) Eaton 1976 (p. 148; Fig. 7.91; Fig. 55A, B, F–H)  
*Distatodinium?* *scariosum* Liengjarern, Costa et Downie 1980 (p. 148; Fig. 7.146; Fig. 55O–Q)  
*Distatodinium virgatum* Stover 1977 (p. 149; Fig. 7.143; Fig. 55C, D)  
*Dracodinium laszczynskii* Gedl 1995 (p. 168; Fig. 7.116; Fig. 80F, Fig. 81A–F)  
*Dracodinium cf. laszczynskii* Gedl 1995 (p. 168; Fig. 7.131; Fig. 63G, H)  
*Enneadocysta arcuata* (Eaton 1971) Stover et Williams 1995 (p. 64; Fig. 7.135; Fig. 19E, F)  
*Enneadocysta pectiniformis* (Gerlach 1961) Stover et Williams 1995 (p. 64; Fig. 7.80; Fig. 19A–D, H–J, L, M, Fig. 20G)  
*Escharisphaeridia* sp. (p. 115; Fig. 7.128; Fig. 16D, E, Fig. 53B)  
*Fibrocysta axialis* (Eisenack 1965) Stover et Evitt 1978 (p. 117; Fig. 7.33; Fig. 40C, F, I–K)  
*Fibrocysta radiata* (Morgenroth 1966) Stover et Evitt 1978 (p. 117; Fig. 7.52; Fig. 40G, H)  
*Fibrocysta* sp. A (p. 117; Fig. 7.34; Fig. 40D, E)  
*Glaphyrocysta exuberans* (Deflandre et Cookson 1955 ex Eaton 1976) Stover et Evitt 1978 (p. 125; Fig. 7.70; Fig. 84J, M)  
*Glaphyrocysta intricata* (Eaton 1971) Stover et Evitt 1978 (p. 126; Fig. 7.97; Fig. 56M, P–T)  
*Glaphyrocysta semitecta* (Bujak in Bujak *et al.* 1980) Lentin et Williams 1981 (p. 126; Fig. 7.7; Fig. 53I, Fig. 57A–P, Fig. 56A–L, N, O)  
*Heslertonia?* sp. (p. 149; Fig. 7.95; Fig. 32A, N, O)  
*Heterelaucacysta campanula* Drugg et Loeblich Jr. 1967 (p. 129; Fig. 7.115; Fig. 61C, G, H, J, K)  
*Heterelaucacysta cf. campanula* Drugg et Loeblich Jr. 1967 (p. 129; Fig. 7.134; Fig. 62O, P)  
*Heterelaucacysta leptalea* Eaton 1976 (p. 131; Fig. 7.35; Fig. 61A, B, D, E)  
*Heterelaucacysta porosa* Bujak in Bujak *et al.* 1980 (p. 133; Fig. 7.15; Fig. 62N, Fig. 61F, I, L)  
*Heterelaucacysta pustulata* Jan du Chêne et Adediran 1985 (p. 134; Fig. 7.127; Fig. 62I)

- Heterosphaeridium* sp. A (p. 149; Fig. 7.3; Fig. 26B, C, Fig. 59A–C, E–T, Fig. 60B–T)  
*Homotryblium abbreviatum* Eaton 1976 (p. 136; Fig. 7.51; Fig. 63I–L, Fig. 64P, Q, Fig. 85C)  
*Homotryblium aculeatum* Williams 1978 (p. 136; Fig. 7.22; Fig. 63A–H, Fig. 64R, S)  
*Homotryblium caliculum* Bujak in Bujak *et al.* 1980 (p. 136; Fig. 7.90; Fig. 67Q–T)  
*Homotryblium conicum* Gedl 1995 (p. 137; Fig. 7.142; Fig. 47M–P)  
*Homotryblium plectilum* Drugg et Loeblich Jr. 1967 (p. 138; Fig. 7.5; Fig. 64E–J, Fig. 66I–K)  
*Homotryblium* cf. *plectilum* Drugg et Loeblich Jr. 1967 (p. 138; Fig. 7.31; Fig. 64K–O, T, Fig. 66H)  
*Homotryblium tenuispinosum* Davey et Williams 1966 (p. 138; Fig. 7.1; Fig. 63M–T, Fig. 65A–H)  
*Homotryblium vallum* Stover 1977 (p. 142; Fig. 7.47; Fig. 64A, D)  
*Homotryblium* cf. *vallum* Stover 1977 (p. 142; Fig. 7.60; Fig. 64B, C)  
*Hystrichokolpoma cinctum* Klumpp 1953 (p. 87; Fig. 7.132; Fig. 35M, N)  
*Hystrichokolpoma rigaudiae* Deflandre et Cookson 1955 (p. 87; Fig. 7.13; Fig. 36A–P, Fig. 35A–C, O–Q, Fig. 32C–E)  
*Hystrichokolpoma* cf. *rigaudiae* Deflandre et Cookson 1955 (p. 87; Fig. 7.149; Fig. 35R–U)  
*Hystrichokolpoma salacia* Eaton 1976 (p. 89; Fig. 7.101; Fig. 35D, I–L, Fig. 32K–M)  
*Hystrichosphaeridium salpingophorum* (Deflandre 1935) Deflandre 1937 (p. 142; Fig. 7.85; Fig. 18H, Fig. 19K, N–S)  
*Hystrichostrogylon coninckii* Heilmann–Clausen 1985 (p. 105; Fig. 7.138; Fig. 44D)  
*Hystrichostrogylon membraniphorum* Agelopoulos 1964 (p. 105; Fig. 7.81; Fig. 44A–C)  
*Impagidinium aculeatum* (Wall 1967) Lentin et Williams 1981 (p. 106; Fig. 7.46; Fig. 46A–F, K)  
*Impagidinium maculatum* (Cookson et Eisenack 1961) Stover et Evitt 1978 (p. 106; Fig. 7.124; Fig. 46Q, R)  
*Impagidinium margaritifera* (Cookson et Eisenack 1960) Stover et Evitt 1978 (p. 106; Fig. 7.121; Fig. 46S)  
*Impagidinium velorum* Bujak 1984 (p. 108; Fig. 7.59; Fig. 46O, P)  
*Impagidinium* sp. A *sensu* Gedl 2005 (p. 108; Fig. 7.36; Fig. 46U–Z2)  
*Impagidinium* sp. B *sensu* Gedl 2005 (p. 108; Fig. 7.125; Fig. 46N, Z3, Z4, Fig. 51A, B)  
*Impagidinium* sp. C *sensu* Gedl 2005 (p. 108; Fig. 7.123; Fig. 46G–J, L, M, T, Fig. 51D)  
*Lejeunecysta fallax* (Morgenroth 1966) Artzner et Dörhöfer 1978 (p. 176; Fig. 7.141; Fig. 83T, U)  
*Lejeunecysta globosa* Biffi et Grignani 1983 (p. 180; Fig. 7.136; Fig. 83O)  
*Lejeunecysta lata* Biffi et Grignani 1983 (p. 181; Fig. 7.100; Fig. 83W)  
*Lejeunecysta* sp. (p. 181; Fig. 7.106; Fig. 83V)  
*Lentinia serrata* Bujak 1980 (p. 158; Fig. 7.27; Fig. 71A–P)  
*Lingulodinium machaerophorum* (Deflandre et Cookson 1955) Wall 1967 (p. 89; Fig. 7.38; Fig. 20H, I, L, Fig. 27D–F)  
*Melitasphaeridium asterium* (Eaton 1976) Bujak *et al.* 1980 (p. 119; Fig. 7.89; Fig. 34L, M)  
*Melitasphaeridium pseudorecurvatum* (Morgenroth 1966) Bujak *et al.* 1980 (p. 119; Fig. 7.74; Fig. 34A–K, R, Fig. 53J, Fig. 84C)  
*Membranophoridium aspinatum* Gerlach 1961 (p. 129; Fig. 7.21; Fig. 53G, H, Fig. 55K, L, Fig. 58A–L, Fig. 59D, Fig. 60A)  
*Microdinium reticulatum* Vozzhennikova 1967 (p. 59; Fig. 7.117; Fig. 16A–C, F–M)  
*Microdinium* aff. *reticulatum* Vozzhennikova 1967 (p. 59; Fig. 7.119; Fig. 16P–T)  
*Microdinium* sp. (p. 60; Fig. 7.118; Fig. 16N, O)  
*Nematosphaeropsis labyrinthus* (Ostenfeld 1903) Reid 1974 (p. 109; Fig. 7.93; Fig. 47A–D)  
*Nematosphaeropsis lemniscata* Bujak 1984 (p. 109; Fig. 7.112; Fig. 47E–H, Y)  
*Nematosphaeropsis reticulensis* (Pastiels 1948) Sarjeant 1986 (p. 109; Fig. 7.92; Fig. 47I–X, Z–Z1)  
*Operculodinium centrocarpum* (Deflandre et Cookson 1955) Wall 1967 (p. 90; Fig. 7.26; Fig. 37A–R, Fig. 84K)  
*Operculodinium divergens* (Eisenack 1954) Stover et Evitt 1978 (p. 93; Fig. 7.9; Fig. 30A–F, H, K, Fig. 31A–C, F–I)  
*Operculodinium microtriainum* (Klumpp 1953) Islam 1983 (p. 93; Fig. 7.6; Fig. 20F, 24I, J, Fig. 38G, Fig. 39J–O, Fig. 40A, B)



- Operculodinium tiara* (Klumpp 1953) Stover et Evitt 1978 (p. 93; Fig. 7.30; Fig. 31D, E, Fig. 39F–I)
- Operculodinium* sp. A (p. 94; Fig. 7.56; Fig. 39A–E)
- Palaeocystodinium golzowense* Alberti 1961 (p. 159; Fig. 7.96; Fig. 72S)
- Pentadinium laticinctum* Gerlach 1961 (p. 111; Fig. 7.84; Fig. 32P, U, V–X, Fig. 51F, G)
- Phthanoperidinium alectrolophum* Eaton 1976 (p. 160; Fig. 7.103; Fig. 73S–V, Fig. 74D, E, G–I)
- Phthanoperidinium comatum* (Morgenroth 1966) Eisenack et Kjellström 1972 (p. 160; Fig. 7.19; Fig. 73C–K, Fig. 74B, C)
- Phthanoperidinium delicatum* Michoux 1985 (p. 160; Fig. 7.79; Fig. 73N–R, Fig. 85A)
- Phthanoperidinium? eocenicum* (Cookson et Eisenack 1965) Lentin et Williams 1973 (p. 162; Fig. 7.102; Fig. 72A–L, Fig. 74A)
- Phthanoperidinium stockmansii* (de Coninck 1975) Lentin et Williams 1977b (p. 162; Fig. 7.28; Fig. 73A, B, L, M, Fig. 74F)
- Polysphaeridium subtile* Davey et Williams 1966 (p. 143; Fig. 7.45; Fig. 67A–L)
- Polysphaeridium zoharyi* (Rossignol 1962) Bujak *et al.* 1980 (p. 143; Fig. 7.43; Fig. 53D)
- Pyxidinospis* sp. A sensu Gedl 2005 (p. 119; Fig. 7.64; Fig. 52N)
- Pyxidinospis* sp. C sensu Gedl 2005 (p. 121; Fig. 7.65; Fig. 45A–H, Z1, Z2)
- Reticulosphaera actinocoronata* (Benedek 1972) Bujak et Matsuoka 1986 (p. 150; Fig. 7.104; Fig. 32F–J)
- Rhombodinium perforatum* (Jan du Chêne et Châteauneuf 1975) Lentin et Williams 1977 (p. 169; Fig. 7.10; Fig. 82E–G)
- Rottnestia borussica* (Eisenack 1954) Cookson et Eisenack 1961 (p. 111; Fig. 7.71; Fig. 44E, H)
- Samlandia chlamydophora* Eisenack 1954 (p. 94; Fig. 7.17; Fig. 27A–C, G–K, N, O)
- Selenopemphix armata* Bujak 1980 (p. 183; Fig. 7.53; Fig. 83J–N, P)
- Selenopemphix nephroides* Benedek 1972 (p. 183; Fig. 7.82; Fig. 83A, D–I, Q–S)
- Selenopemphix selenoides* Benedek 1972 (p. 183; Fig. 7.145; Fig. 83B, C)
- Sepispinula? ambigua* (Deflandre 1937) Masure 2004 (p. 150; Fig. 7.140; Fig. 16X, Y)
- Spiniferites pseudofurcatus* (Klumpp 1953) Sarjeant 1970 (p. 112; Fig. 7.16; Fig. 48O)
- Spiniferites ramosus* (Ehrenberg 1838) Mantell 1854 (p. 112; Fig. 7.25; Fig. 44F, G, Fig. 48A–N, P, Q, Fig. 49A–L, Fig. 84B)
- Tectatodinium pellitum* Wall 1967 (p. 115; Fig. 7.54; Fig. 45I, Fig. 51H–K, Fig. 52U–Y)
- Thalassiphora delicata* Williams et Downie 1966 (p. 97; Fig. 7.111; Fig. 41F, Fig. 42A, E)
- ?Thalassiphora dynamica* (Morgenroth 1966) Stover et Evitt 1978 (p. 100; Fig. 7.99; Fig. 55J)
- Thalassiphora patula* (Williams et Downie 1966) Stover et Evitt 1978 (p. 100; Fig. 7.114; Fig. 27A–F, Fig. 85I)
- Thalassiphora pelagica* (Eisenack 1954) Eisenack et Gocht 1960 (p. 100; Fig. 7.12; Fig. 43G–K, Fig. 41A–E, Fig. 42B–D, Fig. 85D)
- Thalassiphora reticulata* Morgenroth 1966 (p. 100; Fig. 7.144; Fig. 42F)
- Vectidinium?* sp. (p. 162; Fig. 7.73; Fig. 72M–R, T–X)
- Vozzhennikovia* sp. (p. 159; Fig. 7.39; Fig. 71U–X, Fig. 80H)
- Wetzeliiella* sp. (p. 175; Fig. 7.72; Fig. 82D, J, O, P)
- Wilsonidium?* sp. (p. 175; Fig. 7.147; Fig. 81J–L)
- Ynezidium brevisulcatum* (Michoux 1985) Lucas-Clark et Helenes (p. 115; Fig. 7.67; Fig. 50A–K, Fig. 51C)
- Genus et species indetermined A (p. 150; Fig. 7.120; Fig. 52A–C)
- Genus et species indetermined B (p. 151; Fig. 7.139; Fig. 52D, E)
- Genus et species indetermined C (p. 151; Fig. 7.148; Fig. 84E, H, I)
- Indetermined peridinoids (p. 164; Fig. 7.32; Fig. 71Q, R, S, T, Fig. 80G)

#### Reworked pre-Eocene dinoflagellate cyst taxa:

*Ctenidodinium* sp. (Fig. 6.152; Fig. 84D)

*Cribooperidinium?edwardsii* (Fig. 6.153; Fig. 85H; this species occurs in the Hieroglyphic beds exclusively)

**Other aquatic palynomorphs:***Botryococcus* sp. (Fig. 86H)*Tamanites* sp. (Fig. 86B, F, G, I–Q, Fig. 89F)*Incertae sedis* (*Schizosporis*? sp.) (Fig. 86A, E, R–U, Fig. 89A–D)

Foraminiferal organic linings (Fig. 87A–M, Fig. 88C–F, Fig. 89E)

Scolecodonts (Fig. 88A, B)

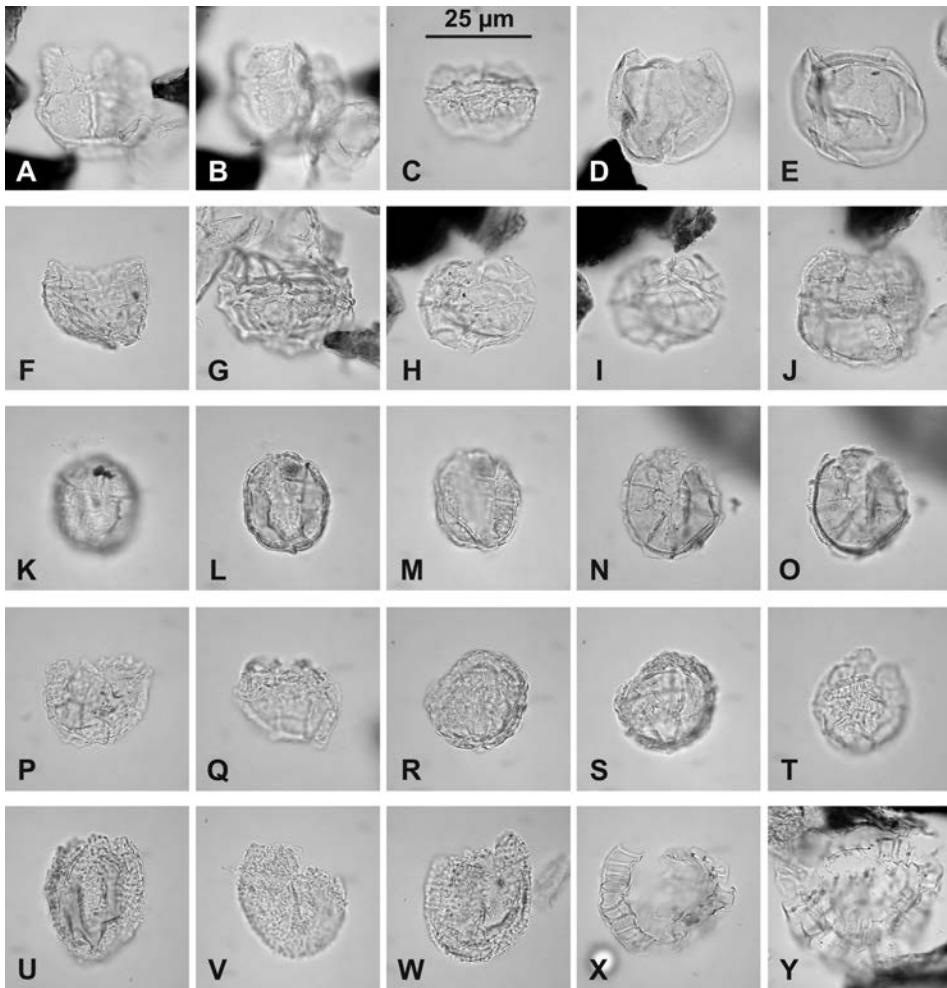
Division **DINOFLAGELLATA** (Bütschli 1885) Fensome *et al.* (1993)Subdivision **DINOKARYOTA** Fensome *et al.* (1993)Class **DINOPHYCEAE** Pascher 1914Subclass **PERIDINIPHYCIDAE** Fensome *et al.* (1993)Order **GONYAULACALES** Taylor 1980Suborder **CLADOPYXIINEAE** Fensome *et al.* (1993)Family **CLADOPYXIACEAE** Stein 1883Genus *Microdinium* Cookson et Eisenack 1960Type species: *Microdinium ornatum* Cookson et Eisenack 19601960 *Microdinium* n. gen.; Cookson & Eisenack (1960), p. 61966 *Microdinium* Cookson et Eisenack 1960 emend.; Sarjeant (1966), p. 148–1491978 *Microdinium* Cookson et Eisenack 1960 emend.; Stover & Evitt (1978), p. 65–661994 *Microdinium* Cookson et Eisenack 1960 emend.; Slimani (1994), p. 24*Microdinium reticulatum* Vozzhennikova 1967

(Fig. 16A–C, F–M)

1967 *Microdinium reticulatum* n. sp.; Vozzhennikova (1967), p. 96–97, pl. 37, figs. 2–5.**Material.** Rare; this species occurs in samples Kns8, Kns10–13, Kns21, Kns22, Kns25, Kns27 and Kns28.**Description.** Cyst small, ovoidal to slightly ellipsoidal, with hypocyst larger than epicyst. Paratabulation expressed by low and smooth crests of equal height. Crest width variable; it ranges from thin and delicate (e.g., Fig. 16A, B, F) to massive (Fig. 16G). Paraplates reticulate.*Microdinium* aff. *reticulatum* Vozzhennikova 1967

(Fig. 16P–T)

**Material.** Five specimens in sample Kns8.**Description.** A species of *Microdinium* with relatively thick cyst wall and prominent paraplate reticulation pattern. Muri large, they seem to at least partly overlap parasutural crests.**Discussion.** This species is similar to *M. reticulatum*. It differs by thicker cyst wall and more prominent reticulate structure of the cyst wall.



**Fig. 16** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Microdinium* sp. (same specimen, various foci; Kns13); **C** – *Microdinium* sp. (Kns8); **D** – *Escharisphaeridia* sp. (Kns8); **E** – *Escharisphaeridia* sp. (Kns8); **F** – *Microdinium* sp. (Kns10); **G** – *Microdinium* sp. (Kns11); **H, I** – *Microdinium* sp. (same specimen, various foci; Kns11); **J** – *Microdinium* sp. (Kns12); **K–M** – *Microdinium* sp. (same specimen, various foci; Kns8); **N, O** – *Microdinium* sp. A (same specimen, various foci; Kns8); **P** – *Microdinium* sp. B (Kns8); **Q** – *Microdinium* sp. B (Kns8); **R, S** – *Microdinium* sp. B (same specimen, various foci; Kns8); **T** – *Microdinium* sp. B (Kns8); **U** – *Chlamydophorella* sp. (Kns10); **V** – *Chlamydophorella* sp. (Kns11); **W** – *Chlamydophorella* sp. (Kns8); **X** – *Sepispinula? ambigua* (Kns12); **Y** – *Sepispinula? ambigua* (Kns14)

*Microdinium* sp.

(Fig. 16N, O)

**Material.** Two specimens in sample Kns8.

**Description.** Ovoidal species of *Microdinium* with smooth, low and discrete parasutural crests delimiting smooth paraplates areas.

Suborder **GONYAULACINEAE** (Autonym)  
 Family **GONYAULACACEAE** Lindemann 1928  
 Subfamily **LEPTODINIOIDEAE** Fensome *et al.* (1993)

Genus ***Areosphaeridium*** Eaton 1971

Type species: *Areosphaeridium diktyoplokum* (Klumpp 1953) Eaton 1971

- 1971 *Areosphaeridium* n. gen.; Eaton (1971), p. 357–358  
 1995 *Areosphaeridium* Eaton 1971 emend.; Stover & Williams (1995), p. 100

*Areosphaeridium diktyoplokum* (Klumpp 1953) Eaton 1971

(Fig. 17A–F, Fig. 18A, B, Fig. 20A–C)

- 1953 *Hystichosphaeridium diktyoplokum* n. sp.; Klumpp (1953), p. 392, pl. 18, figs. 3–7  
 1971 *Areosphaeridium diktyoplokum* comb. nov.; Eaton (1971), p. 358–359  
 1971 *Areosphaeridium diktyoplokum* Klumpp 1953 emend.; Eaton (1971), p. 359  
 1995 *Areosphaeridium diktyoplokum* Klumpp 1953 emend.; Stover & Williams (1995), p. 102

**Material.** This species occurs in almost all samples except of Kns4, Kns11, Kns21, Kns23, Kns24, Kns30 and Kns33. It is very common in sample Kns1. Isolated processes frequently occur.

**Description.** Cyst wall on majority of specimens smooth to finely granular. Process stems solid and always smooth. Distal terminations of processes in shape of regularly fenestrate platforms. Their margins are of two types, constant in each specimen: smooth (Fig. 17E, F, Fig. 20C) and irregular (Fig. 17A–D, Fig. 19A, B, Fig. 20B).

*Areosphaeridium ebdonii* Bujak 1994

(Fig. 18D–F)

- 1994 *Areosphaeridium ebdonii* n. sp.; Bujak (1994), p. 119–121, pl. 2, figs. 8–9

**Material.** Single specimens were found in samples Kns17 and Kns22; isolated operculum was found in sample Kns6.

**Description.** Cyst subspherical, chorate with intratabular thick, solid, relatively short processes distally terminated with with fenestrate oval platform typical for *A. diktyoplokum*. Process length does not exceed 15  $\mu$ m; the ones at hypocyst are slightly longer. Operculum found in sample Kns6 (Fig. 18D) consists of four apical paraplates, each with single intratabular process.

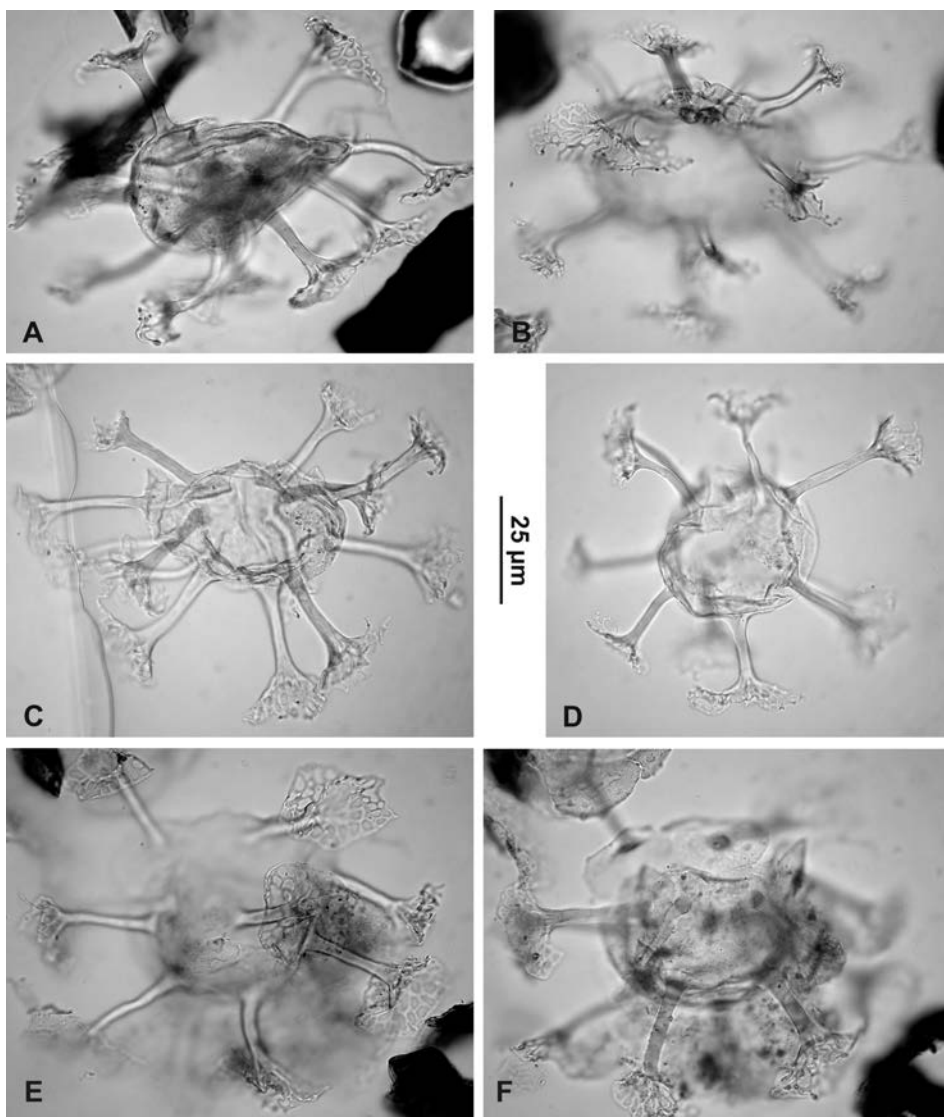
*Areosphaeridium michoudii* Bujak 1994

(Fig. 18C, H–L, 13G)

- 1994 *Areosphaeridium michoudii* n. sp.; Bujak (1994), p. 121, pl. 1, figs. 1–3

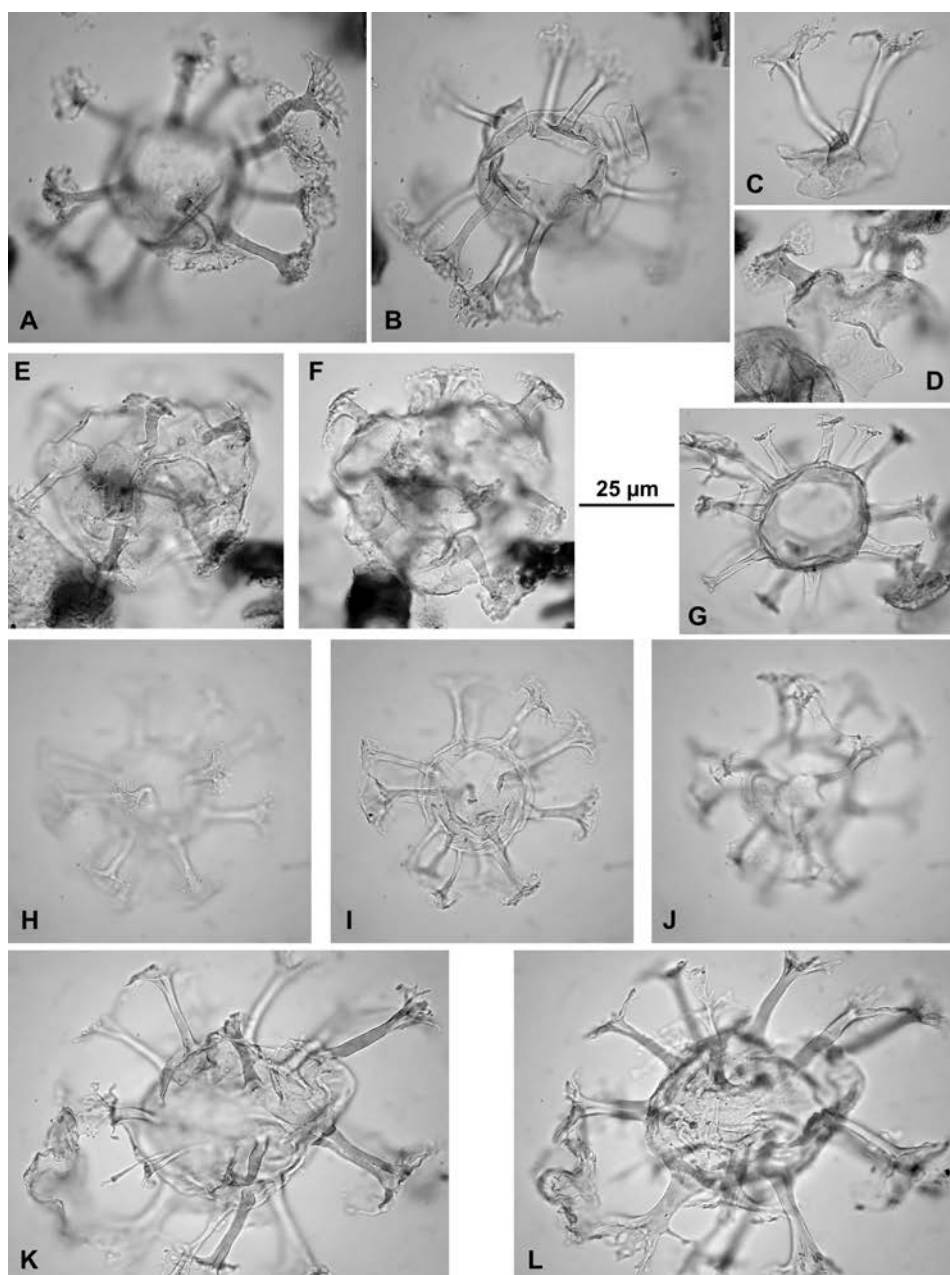
**Material.** Single specimens occur in samples Kns4–6, Kns8, Kns9, Kns26–28 and Kns31; more frequent specimens were found in samples Kns10, Kns11, Kns17, Kns20–22 and Kns32.





**Fig. 17.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–F** – *Areosphaeridium diktyoplokum* (A: Kns1; B: Kns3; C, D: Kns8; E, F: Kns6, same specimen, various foci)

**Description.** Cyst large, chorate with solid intratabular processes and apical archaeopyle. No paracingular processes. Cyst wall rather smooth, some specimens have finely granular surface. Stems always smooth. Processes distally expanded and branched into irregular network.



**Fig. 18.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Areosphaeridium diktyoplokum* (Kns6, same specimen, various foci); **C** – *Areosphaeridium michoudii* (fragment of isolated operculum with two processes; Kns5); **D** – *Areosphaeridium ebdonii* (isolated operculum; Kns6); **E, F** – *Areosphaeridium ebdonii* (same specimen, various foci; Kns17); **G** – *Hystrichosphaeridium salpingophorum* (Kns33); **H–J** – *Areosphaeridium michoudii* (small spherical specimen, various foci; Kns8); **K, L** – *Areosphaeridium michoudii* (same specimen, various foci; Kns4)

Genus *Enneadocysta* Stover et Williams 1995

Type species: *Enneadocysta pectiniformis* (Gerlach 1961) Stover et Williams 1995

1995 *Enneadocysta* n. gen.; Stover & Williams (1995), p. 108–109

*Enneadocysta arcuata* (Eaton 1971) Stover et Williams 1995

(Fig. 19E, F)

1971 *Areosphaeridium arcuatum* sp. nov.; Eaton (1971), p. 360–363, pl. 3, figs 1–9; text-figs 4–5

1995 *Enneadocysta arcuata* comb. nov.; Stover & Williams (1995), p. 108

1995 *Enneadocysta arcuata* Eaton 1971 emend.; Stover & Williams (1995), p. 109

**Material.** Rare specimens in samples Kns12, Kns22, Kns25, Kns26, Kns29 and Kns32.

**Description.** Cyst relatively large, chorate with intratabular processes terminated with horse-shoe branching. Processes generally solid and smooth, finely fibrous. Processes at hypocyst slightly broader with irregularly scattered perforations (Fig. 19E).

*Enneadocysta pectiniformis* (Gerlach 1961) Stover et Williams 1995

(Fig. 19A–D, H–J, L, M, Fig. 20G)

1961 *Baltisphaeridium pectiniforme* n. gen.; Gerlach (1961), p. 195–196, pl. 28, fig. 14, text-fig. 18

1978 *Areosphaeridium pectiniforme* comb. nov.; Stover & Evitt (1978), p. 20

1984 *Areosphaeridium pectiniforme* (Gerlach 1961) emend.; Sarjeant (1984), p. 83–84, 86

1995 *Enneadocysta pectiniformis* comb. nov.; Stover & Williams (1995), p. 108

1995 *Enneadocysta pectiniformis* (Gerlach 1961) emend.; Stover & Williams (1995), p. 114

**Material.** Rare in samples Kns6, Kns8, Kns9, Kns19–22, Kns26, Kns32 and Kns33; common in samples Kns5, Kns7, Kns10–13 and Kns18.

**Description.** Cyst small, chorate with smooth to finely granular autophragm and solid, smooth, intratabular processes that distally branch into horse-shoe-like terminations. Small spines regularly spaced at these branches. Paracingular processes absent.

Genus *Cleistosphaeridium* Davey, Downie, Sarjeant et Williams 1966

Type species: *Cleistosphaeridium diversispinosum* Davey, Downie, Sarjeant et Williams 1966

1966 *Cleistosphaeridium* n. gen.; Downie *et al.* (1966), p. 166

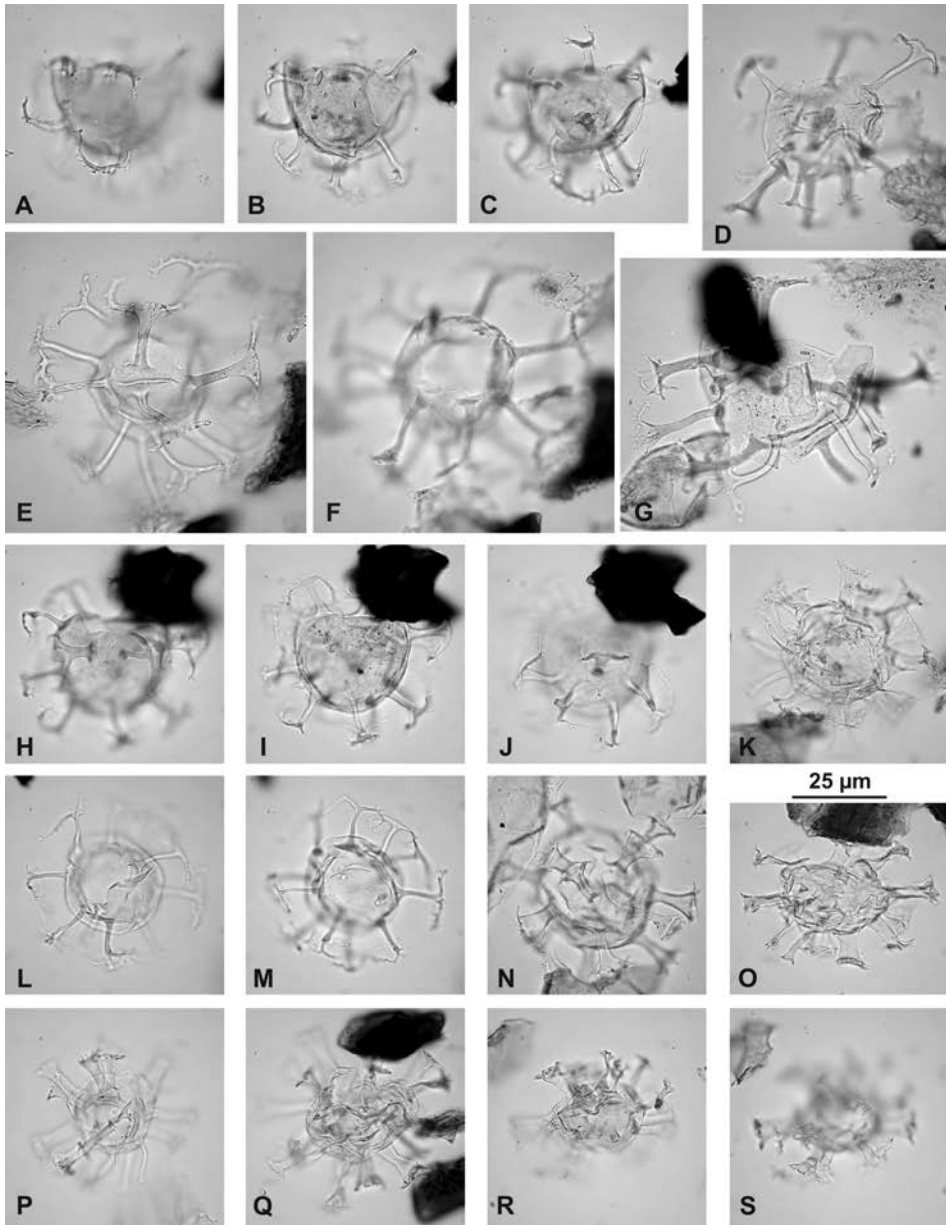
2001 *Cleistosphaeridium* Davey, Downie, Sarjeant et Williams 1966 emend.; Eaton *et al.* (2001), p. 176

*Cleistosphaeridium ancyreum* (Cookson et Eisenack 1965) Eaton, Fensome, Riding et Williams 2001

(Fig. 21D, E, G, H, J, K, Fig. 22A, M, N, P–S, Fig. 23M–O, Fig. 25A–C, F–I, Fig. 26J, K)

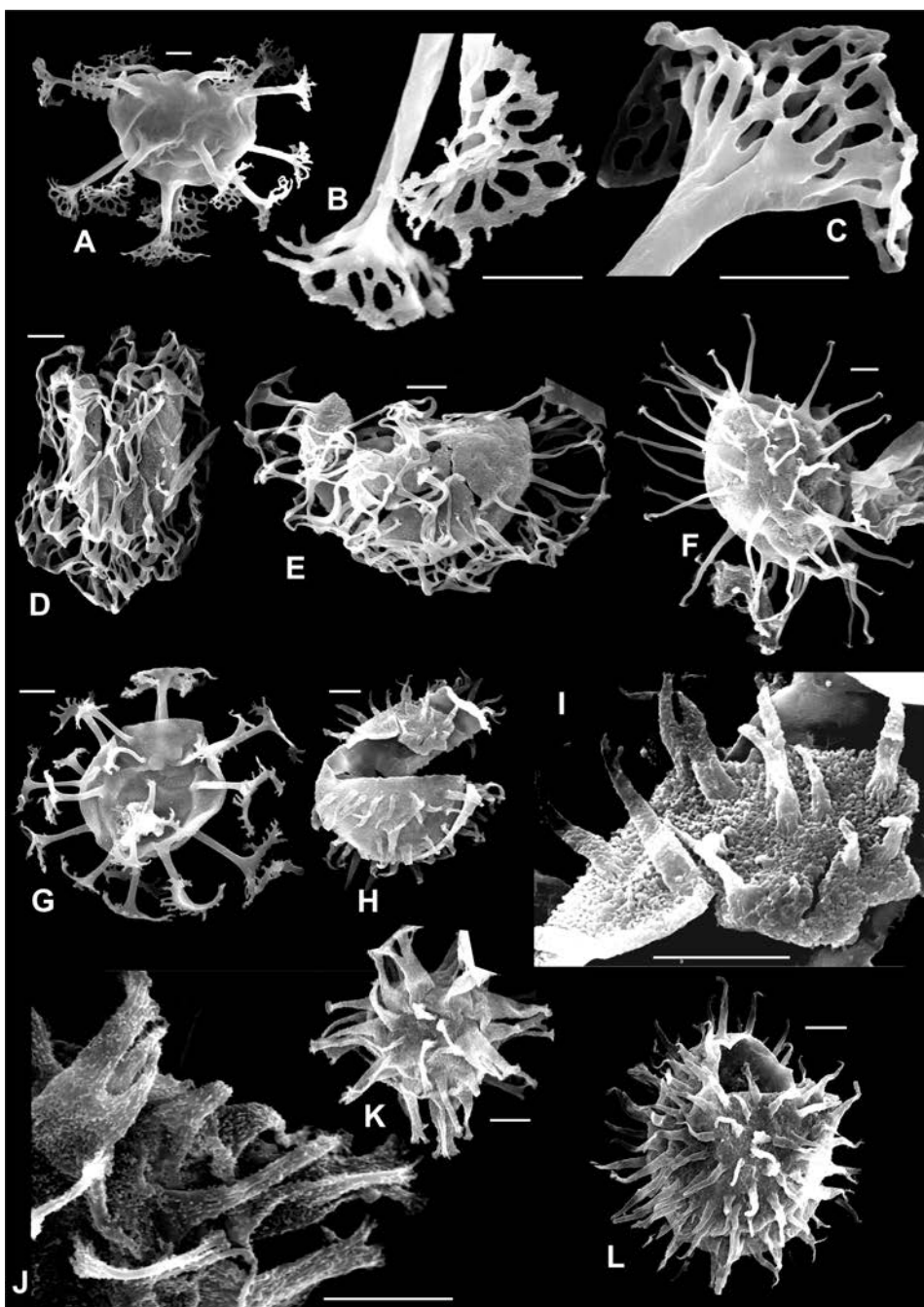
1965 *Systematophora ancyrea* n. sp.; Cookson & Eisenack (1965a), p. 126, pl. 14, figs. 1–3

2001 *Cleistosphaeridium ancyreum* comb. nov.; Eaton *et al.* (2001), p. 191



**Fig. 19.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–C** – *Enneadocysta pectiniformis* (same specimen, various foci; Kns6); **D** – *Enneadocysta pectiniformis* (Kns7); **E, F** – *Enneadocysta arcuata* (same specimen, various foci; Kns12); **G** – *Areosphaeridium michoudii* (Kns8); **H–J** – *Enneadocysta pectiniformis* (same specimen, various foci; Kns8); **K** – *Hystrichosphaeridium salpingophorum* (Kns12); **L, M** – *Enneadocysta pectiniformis* (same specimen, various foci; Kns8); **N–S** – *Hystrichosphaeridium salpingophorum* (N: Kns8; O: Kns12; P: Kns5; Q: Kns5; R, S: Kns6, same specimen, various foci)





**Material.** Rare in samples Kns4, Kns22 and Kns29; more frequent in samples Kns8 and Kns18–20; three specimens in the Hieroglyphic beds (KnsH2).

**Description.** Cyst central body subspherical, with thick, granular wall and numerous processes. The latter are smooth, relatively long and slender, distally simply

**Fig. 20.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10 µm). **A–C** – *Areosphaeridium diktyoplokum* (A, B: sample Kns8; C: sample Kns5; A: a complete specimen with well visible apical archaeopyle margin, smooth cyst wall and intratabular processes; B, C – details of distal process' terminations in shape of perforated platforms); **D, E** – *Adnatosphaeridium multispinosum* (Kns5); **F** – *Operculodinium microtriainum* (Kns3); **G** – *Enneadocysta pectiniformis* (Kns8; a specimen with adnate archaeopyle; intratabular processes terminated with horse-shoe-like denticulate terminations); **H, I** – *Lingulodinium machaerophorum* (Kns8; H: specimen with 5P archaeopyle; I: detail of the surface showing its granular structure); **J, K** – *Dapsilodinium pseudocolligerum* (Kns8; J: detail of the surface showing a cover of thread-like very small projections, which give an coarse appearance under transmitted-light microscope; K: complete specimen); **L** – *Lingulodinium machaerophorum* (Kns8; specimen with 2P archaeopyle)

branched. Processes are chaotically united proximally by low smooth ridges, which do not form complete intratabular proximal complexes (Fig. 25B, H, I). Commonly two or three adjoining processes only are united (Fig. 26K).

*Cleistosphaeridium placacanthum* (Deflandre et Cookson 1955) Eaton,  
Fensome, Riding et Williams 2001  
(Fig. 21A–C, F, I, L, Fig. 24A–P, Fig. 25D)

- 1955 *Hystrichosphaeridium placacanthum* n. sp.; Deflandre & Cookson 1955, p. 276–277, pl. 9, figs. 1–3  
1969 *Systematophora placacantha* comb. nov.; Davey, Downie, Sarjeant & Williams 1969, p. 17  
1980 *Systematophora placacantha* (Deflandre et Cookson 1955) emend.; May 1980, p. 68  
2001 *Cleistosphaeridium placacanthum* comb. nov.; Eaton *et al.* (2001), p. 190

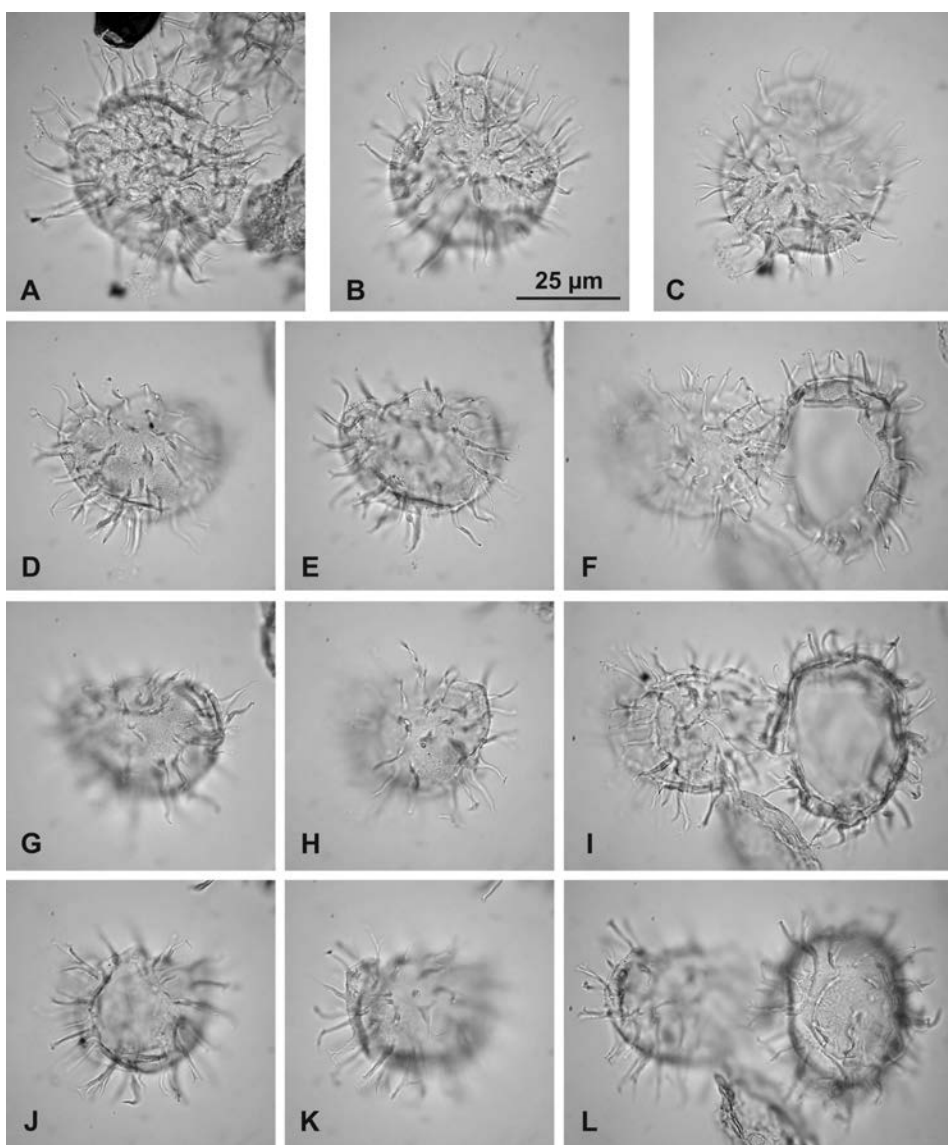
**Material.** Rare to moderately common in samples Kns5–9, Kns11–14, Kns18–20, Kns22–25, Kns29, Kns31 and Kns33.

**Description.** Cyst subspherical, chorate, with solid, long, slender, distally slightly expanded processes arising from low circular ridges. Some ridges not fully developed. Processes of the same length on a specimen but usually long in relation to the main body diameter. Periphragm granular and relatively thick. Archaeopyle apical with typical zigzag margin.

**Remarks.** *Cleistosphaeridium placacanthum* is very similar to *C. ancyreum*. Main difference is more complete development of proximal ridges by *C. placacanthum*. But in the material studied some specimens attributed to this species do not always possess all ridges complete. Another difference, also not applicable for all specimens, refers to usually longer processes by *C. placacanthum*.

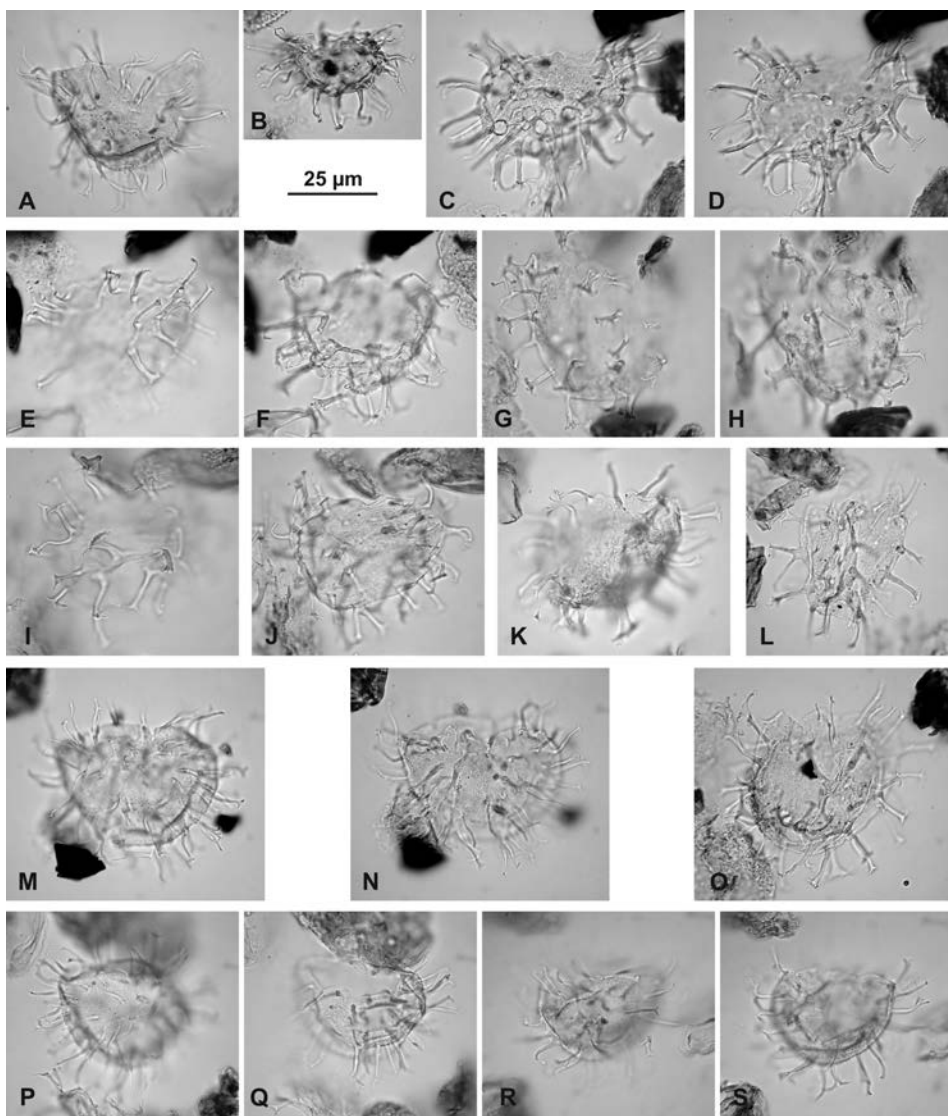
*Cleistosphaeridium* sp.  
(Fig. 22B, Fig. 23Q–U, Fig. 26F)

**Material.** Rare to moderately common in samples Kns3, Kns8–10, Kns13, Kns18, Kns19, Kns22, Kns30, Kns32 and Kns33; very common in sample Kns4 (up to 20% of the whole dinoflagellate cyst assemblage).



**Fig. 21.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Cleistosphaeridium placacanthum* (Kns8); **B**, **C** – *Cleistosphaeridium placacanthum* (same specimen, various foci; Kns8); **D**, **E**, **G** – *Cleistosphaeridium ancyreum* (same specimen, various foci; Kns8); **F**, **I**, **L** – two specimens of *Cleistosphaeridium placacanthum* (same specimens, various foci; Kns8); **H**, **J**, **K** – *Cleistosphaeridium ancyreum* (same specimen, various foci; Kns8)

**Description.** Cyst subpherical, chorate, with relatively small central body and numerous non-tabular, isolated, solid and long processes. Processes distally branched. Periphragm smooth or finely granular. Archaeopyle apical.



**Fig. 22.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Cleistosphaeridium ancyreum* (Kns8); **B** – *Cleistosphaeridium?* sp. (Kns3); **C, D** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns12); **E, F** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns12); **G, H** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns8); **I, J** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns12); **K** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns13); **L** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns12); **M, N** – *Cleistosphaeridium ancyreum* (same specimen, various foci; Kns8); **O** – *Cleistosphaeridium* sp. A (Kns12); **P, Q** – *Cleistosphaeridium ancyreum* (same specimen, various foci; Kns8); **R, S** – *Cleistosphaeridium ancyreum* (same specimen, various foci; Kns8)



*Cleistosphaeridium?* sp. A

(Fig. 22C–L, O, Fig. 23A–L, P, Fig. 26A, D, E, G–I)

**Material.** Rare in samples Kns5, Kns6, Kns8, Kns13, Kns18, Kns27 and Kns31; moderately common in samples Kns12, Kns17, Kns19–22, Kns29 and Kns33; frequent in samples Kns30 and Kns32.

**Description.** Cyst subspherical to lenticular, chorate, with granular periphragm and solid, nontabular processes. Processes isolated, although occasionally a pair of adjoining processes united proximally, distally expanded or simply branched. In some specimens their arrangement seems to be grouped at peripheral areas, whereas midventral and middorsal areas are free. Process length constant on a specimen, ranges from 1/3 to 1/2 of the central body diameter. Apical archaeopyle with zigzag margin.

**Remarks.** General cyst arrangement resembles the genus *Cleistosphaeridium*, but lenticular shape and typical for Areoligeraceae process distribution observed in some specimens made this taxonomical allocation questionable.

Subfamily **CRIBROPERIDINIOIDEAE** Fensome *et al.* (1993)Genus *Achilleodinium* Eaton 1976Type species: *Achilleodinium biformoides* (Eisenack 1954) Eaton 19761976 *Achilleodinium* n. gen.; Eaton (1976), p. 234*Achilleodinium biformoides* (Eisenack 1954) Eaton 1976

(Fig. 27L, M)

1954 *Hystriosphæridium biformoides* n. sp.; Eisenack (1954), p. 68, pl. 11, figs. 16–201976 *Achilleodinium biformoides* comb. nov.; Eaton (1976), p. 234

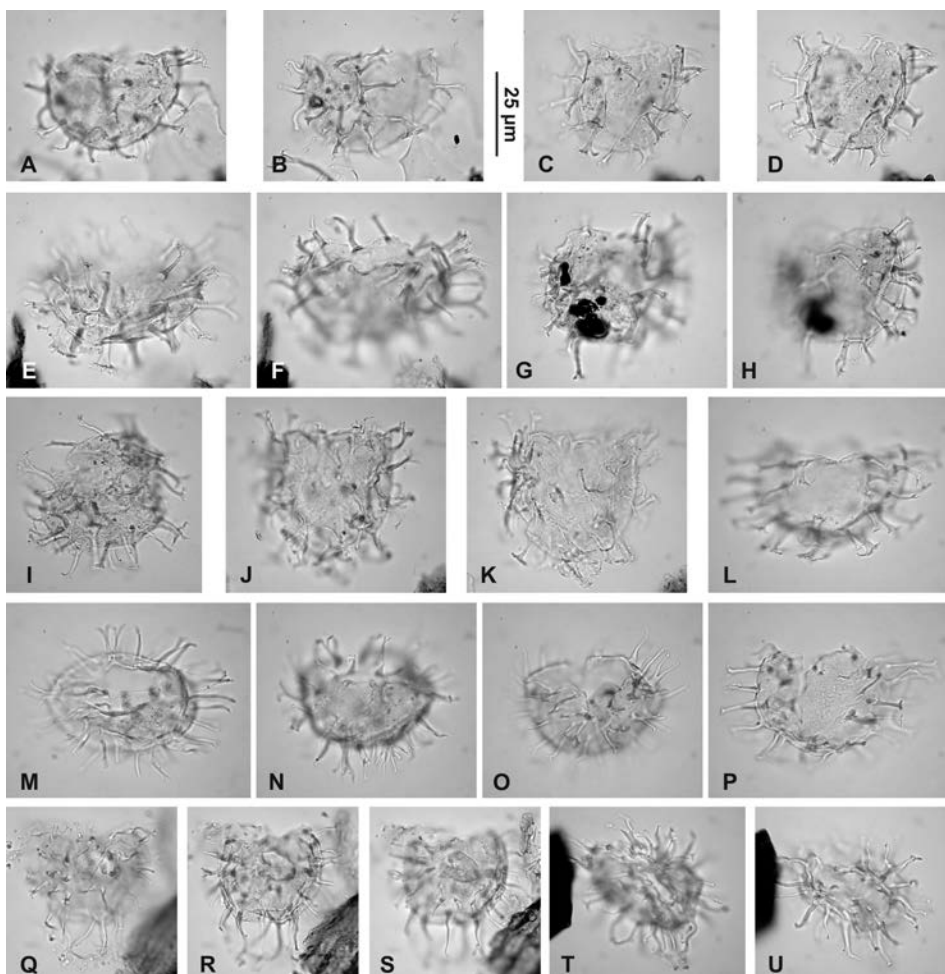
**Material.** Rare specimens occur in samples Kns5–7 and Kns30.

**Description.** All specimens of *A. biformoides* from the material studied have typical slightly elongated central body with very finely granulate cyst wall and finely fibrous box-like, precingular and postcingular processes. Slender para-cingular processes smooth.

Genus *Araneosphaera* Eaton 1976Type species: *Araneosphaera araneosa* Eaton 19761976 *Araneosphaera* n. gen.; Eaton (1976), p. 239–240*Araneosphaera araneosa* Eaton 1976

(Fig. 28S)

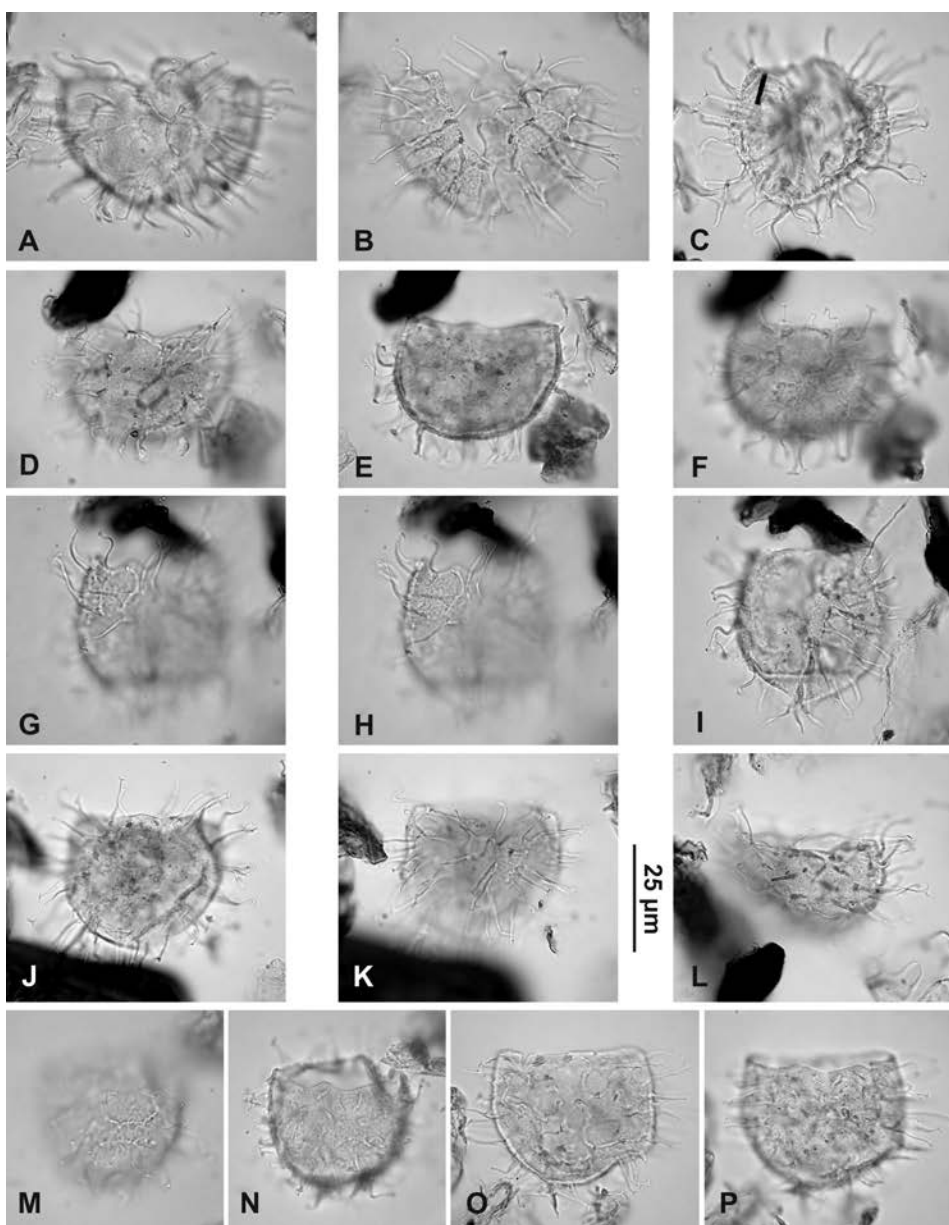
1976 *Araneosphaera araneosa* n. sp.; Eaton (1976), p. 240, 242, pl. 2, figs. 5–8; text-figs. 6A–D



**Fig. 23.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns6); **C, D** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns6); **E, F** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns6); **G, H** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns6); **I** – *Cleistosphaeridium* sp. A (Kns6); **J, K** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns6); **L, P** – *Cleistosphaeridium* sp. A (same specimen, various foci; Kns5); **M** – *Cleistosphaeridium ancyreum* (Kns8); **N, O** – *Cleistosphaeridium ancyreum* (same specimen, various foci; Kns8); **Q–S** – *Cleistosphaeridium?* sp. (same specimen, various foci; Kns3); **T, U** – *Cleistosphaeridium?* sp. (same specimen, various foci; Kns4)

**Material.** A single specimen occurs in sample Kns12.

**Description.** This poorly preserved specimen has ellipsoidal central body and intratabular fibrous processes distally expanded. Process height not equal – the longest processes are at hypocyst; here, they tend to fuse distally.



**Fig. 24.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–P** – *Cleistosphaeridium placacanthum* (**A, B**: Kns5, same specimen, various foci; **C**: Kns5; **D–F**: Kns5, same specimen, various foci; **G–I**: Kns5, same specimen, various foci; **J, K**: Kns5, same specimen, various foci; **L**: Kns6; **M, N**: Kns12, same specimen, various foci; **O, P**: Kns12, same specimen, various foci)

Genus *Cordosphaeridium* Eisenack 1963Type species: *Cordosphaeridium inodes* (Klumpp 1953) Eisenack 1963

- 1963 *Cordosphaeridium* n. gen.; Eisenack (1963), p. 261  
 1968 *Cordosphaeridium* Eisenack 1963 emend.; Morgenroth (1968), p. 548  
 1969 *Cordosphaeridium* Eisenack 1963 emend.; Davey (1969c), p. 35  
 1981 *Cordosphaeridium* Eisenack 1963 emend.; Sarjeant (1981), p. 100–101  
 1991 *Cordosphaeridium* Eisenack 1963 emend.; He Chengquan (1991), p. 157–158, 213

*Cordosphaeridium cantharellus* (Brosius 1963) Gocht 1969

(Fig. 28P, Q, Fig. 29A–F)

- 1963 *Hystrichosphaeridium cantharellus* n. sp.; Brosius (1963), p. 40–41, pl. 6, fig. 1; text-fig. 2  
 1969 *Cordosphaeridium cantharellus* comb. nov.; Gocht (1969), p. 45

**Material.** Rare to moderately common in majority samples (Kns1, Kns2, Kns5–9, Kns11, Kns12, Kns14, Kns18, Kns20–22, Kns28, Kns29, Kns31, Kns33); absent from pale-coloured marl.

**Description.** Central body subspherical with intratabular, fibrous, distally strongly expanded processes. Antapical process occasionally larger than the others (Fig. 29C). Distal terminations usually highly fibrous, felty, although some specimens show considerably smoother processes (Fig. 28P, Q). Archaeopyle precingular, operculum free.

*Cordosphaeridium fibrospinosum* Davey et Williams 1966

(Fig. 28R, T, U)

- 1966 *Cordosphaeridium fibrospinosum* n. sp.; Davey & Williams (1966b), p. 86, pl. 5, fig. 5  
 1969 *Cordosphaeridium fibrospinosum* Davey et Williams 1966 emend.; Davey (1969c), p. 36

**Material.** Single specimens in samples Kns5, Kns6, Kns17 and Kns25.

**Description.** Specimens of *Cordosphaeridium fibrospinosum* from Koniusza possess wide, highly fibrous, relatively short, tubiform intratabular processes. One of these specimens has processes distally expanded (Fig. 28R), whereas the second one has processes tubiform with irregular margins (Fig. 28T, U). Processes of the latter specimen show also a high degree of irregular perforations, increasing in distal processes' parts, where they give rise to an irregular margin.

*Cordosphaeridium funiculatum* Morgenroth 1966

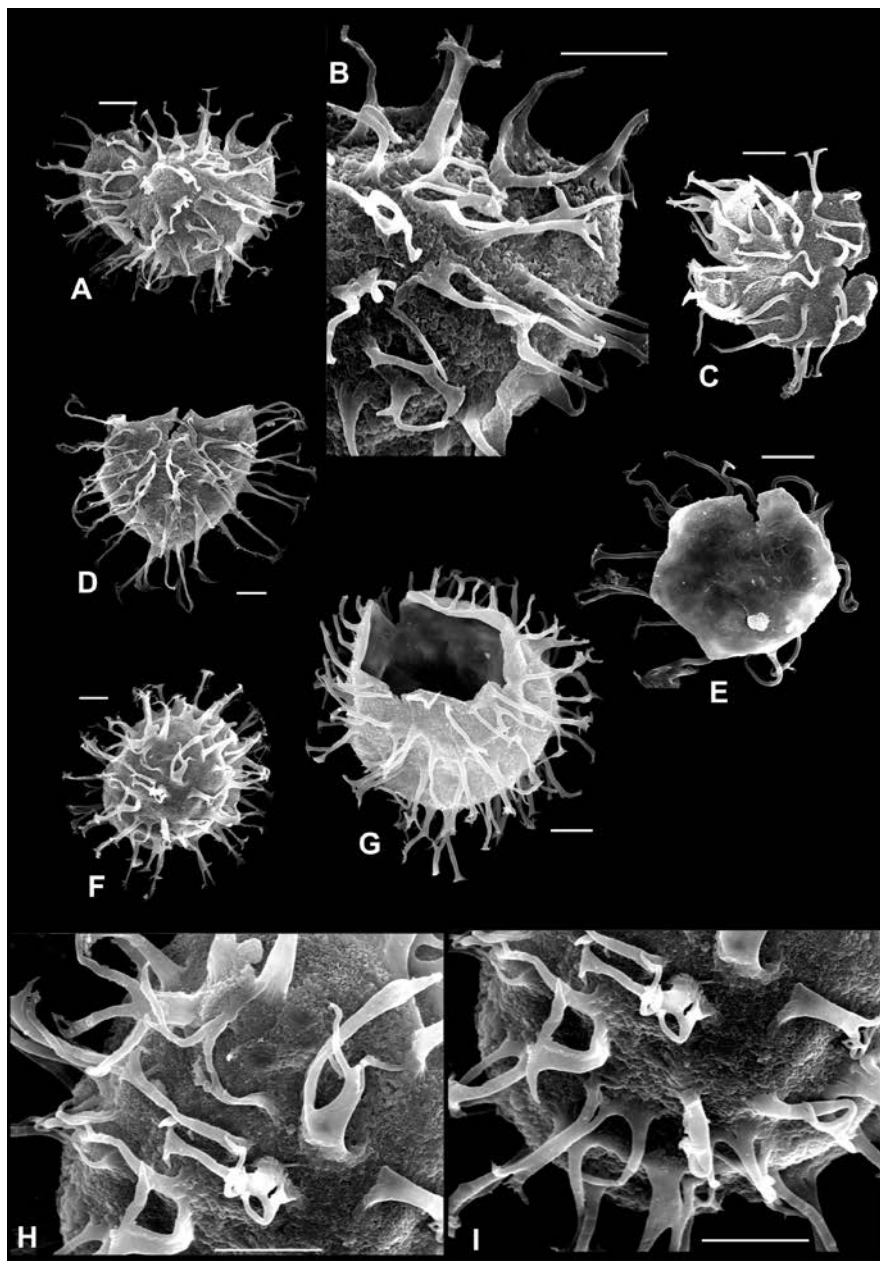
(Fig. 30G, L–N)

- 1966 *Cordosphaeridium funiculatum* n. sp.; Morgenroth (1966a), p. 22–23, pl. 6, figs. 2–3  
 1992 *Cordosphaeridium funiculatum* Morgenroth 1966 emend.; Brinkhuis (1992), p. 97

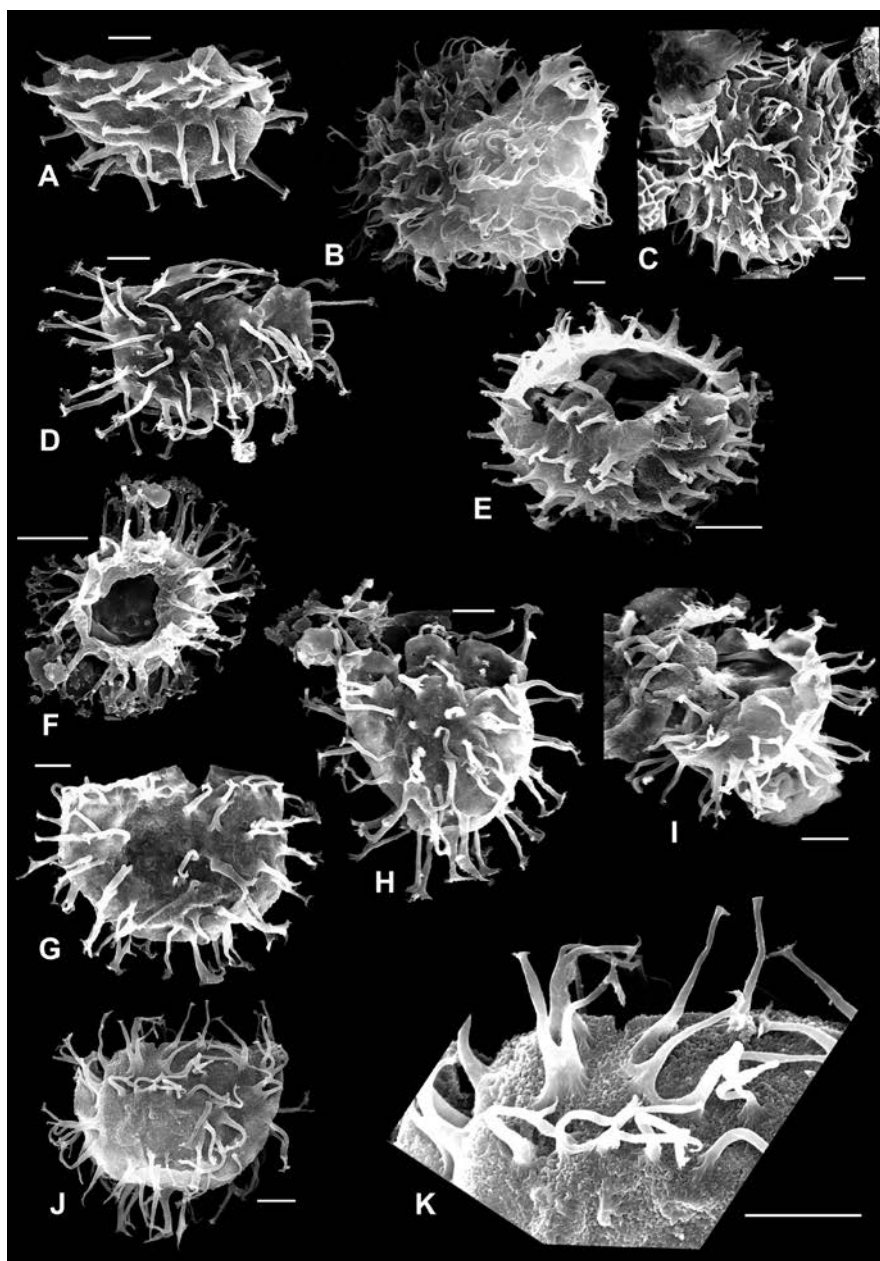
**Material.** Two specimens occur in sample Kns8, single specimens in samples Kns10 and Kns18.

**Description.** This species has a very outstanding net-like structure of the cyst wall,

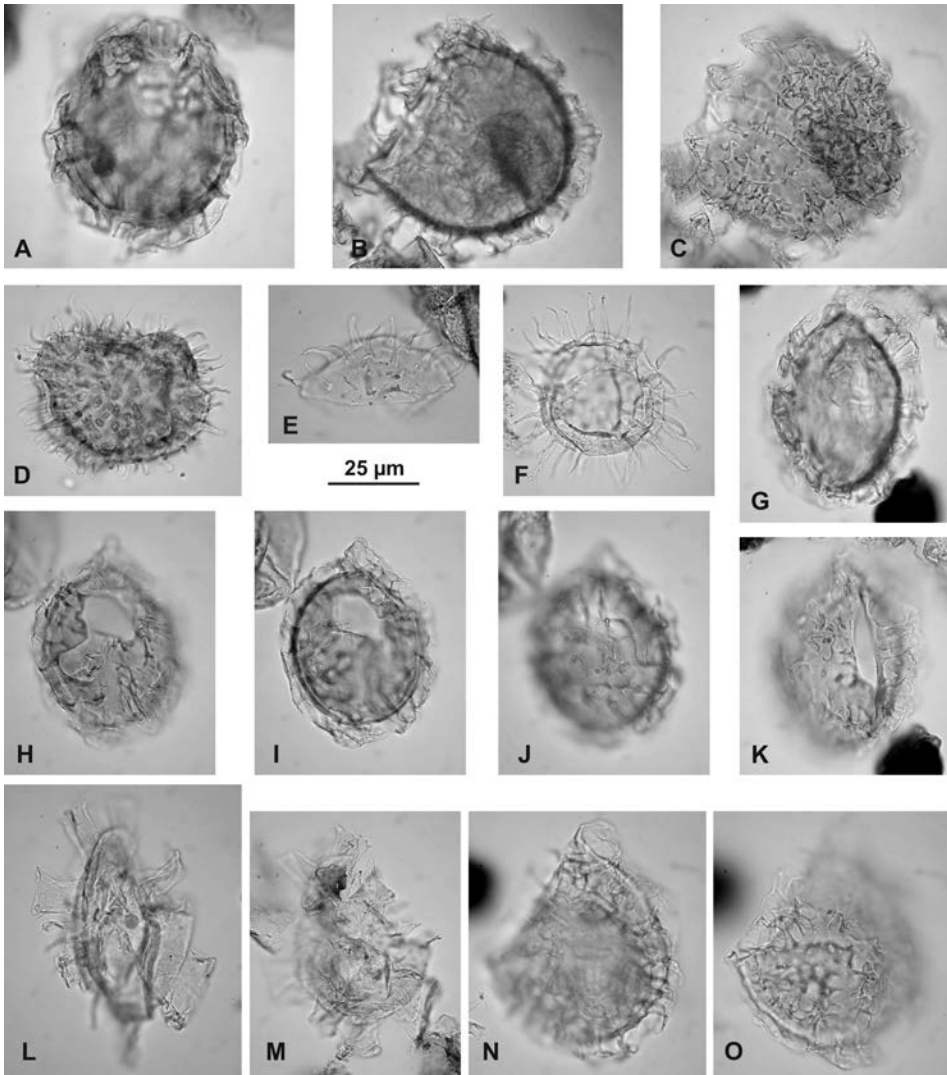




**Fig. 25.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10  $\mu$ m). **A, B** – *Cleistosphaeridium ancyreum* (Kns8; **A** – complete specimen; **B**: detail showing periphragm structure and intratabular process complexes united proximally by incomplete ridges); **C** – isolated operculum of *Cleistosphaeridium ancyreum* (Kns8); **D** – *Cleistosphaeridium placacanthum* (Kns8); **E** – isolated operculum of *Cleistosphaeridium ancyreum* or *Cleistosphaeridium placacanthum*: smooth inner side of endophragm visible (Kns8); **F, H, I** – *Cleistosphaeridium ancyreum* (Kns8; **F**: complete specimen; **H, I**: details showing granular structure of periphragm, and process complexes with incomplete proximal ridges); **G** – *Cleistosphaeridium ancyreum* (Kns8)

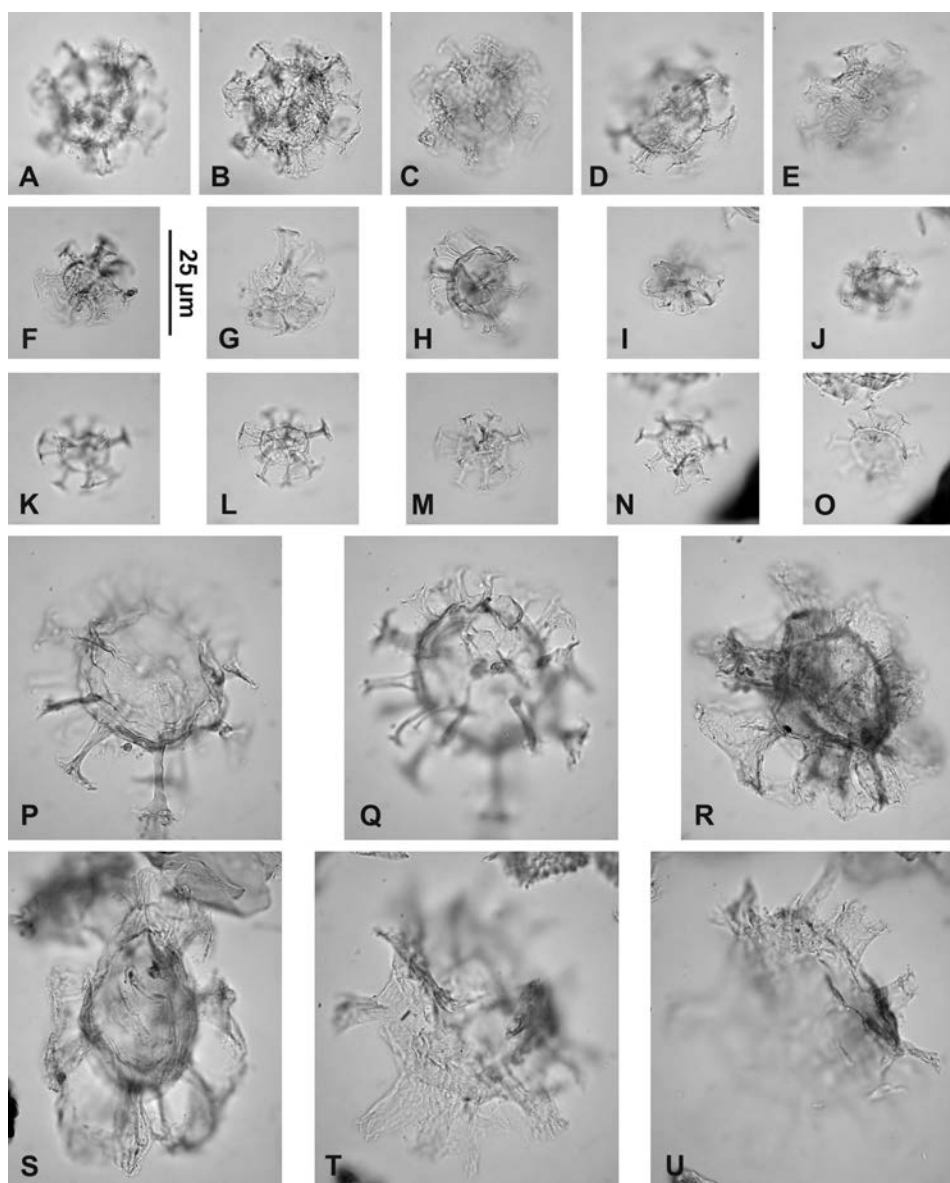


**Fig. 26.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10  $\mu$ m). **A** – *Cleistosphaeridium* sp. A (Kns5); **B**, **C** – *Heterosphaeridium* sp. A (**B**: Kns8; **C**: Kns5); **D** – *Cleistosphaeridium* sp. A (Kns5; specimen with smooth periphragm and long simple processes); **E** – *Cleistosphaeridium* sp. A (Kns5; specimen with perforated periphragm and relatively short and massive processes); **F** – *Cleistosphaeridium* sp. (Kns8); **G–I** – *Cleistosphaeridium* sp. A (specimens with smooth periphragm and long simple processes; **G**, **H**: Kns4; **I**: Kns3); **J**, **K** – *Cleistosphaeridium ancyreum* (Kns8; **J**: complete specimen; **K**: detail of periphragm and process complexes)



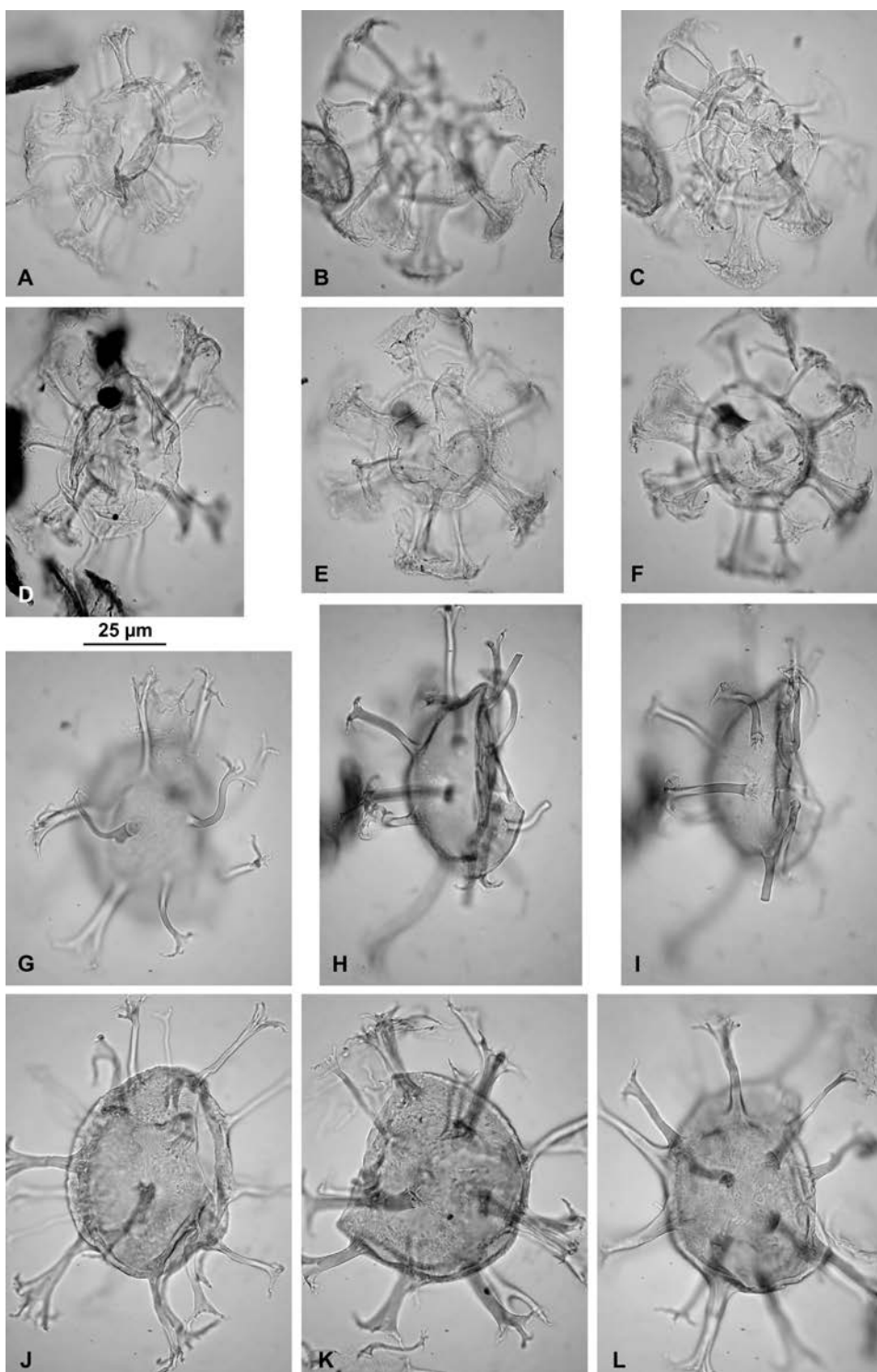
**Fig. 27.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Samlandia chlamydophora* (Kns1); **B**, **C** – *Samlandia chlamydophora* (same specimen, various foci; Kns1); **D** – *Lingulodinium machaerophorum* (Kns3); **E** – *Lingulodinium machaerophorum* (Kns5); **F** – *Lingulodinium machaerophorum* (Kns8); **G**, **K** – *Samlandia chlamydophora* (same specimen, various foci; Kns7); **H**–**J** – *Samlandia chlamydophora* (same specimen, various foci; Kns5); **L** – *Achilleodinium biformoides* (Kns5); **M** – *Achilleodinium biformoides* (Kns6); **N**, **O** – *Samlandia chlamydophora* (same specimen, various foci; Kns8)

identical to that of *Operculodinium divergens* (see e.g., Fig. 30H, K, Fig. 31A–C, G, H). Intratabular, hollow, smooth and relatively slender processes that arise from this structure are slightly expanded distally with an irregular margin splitting into short spines. Processes smooth to massive fibrous. Brinkhuis (1992) emended this



**Fig. 28.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–C** – *Cordosphaeridium* sp. A (same specimen, various foci; Kns8); **D, E** – *Cordosphaeridium* sp. A (same specimen, various foci; Kns8); **F** – *Cordosphaeridium minimum* (Kns3); **G** – *Cordosphaeridium minimum* (Kns5); **H** – *Cordosphaeridium minimum* (Kns5); **I, J** – *Cordosphaeridium minimum* (same specimen, various foci; Kns5); **K–M** – *Cordosphaeridium minimum* (same specimen, various foci; Kns7); **N, O** – *Cordosphaeridium minimum* (same specimen, various foci; Kns8); **P, Q** – *Cordosphaeridium cantharellus* (same specimen, various foci; Kns6); **R** – *Cordosphaeridium fibrospinosum* (Kns6); **S** – *Araneosphaera araneosa* (Kns12); **T, U** – *Cordosphaeridium fibrospinosum* (same specimen, various foci; Kns5)





species to include also specimens, which possess the same net-like wall structure but differ by shorter, thicker processes devoid of distal expanding (see below).

*Cordosphaeridium funiculatum* Morgenroth 1966 *sensu* Brinkhuis 1992

(Fig. 31J–L)

1992 *Cordosphaeridium funiculatum* Morgenroth 1966 emend.; Brinkhuis (1992), p. 97

**Material.** Single specimens in samples Kns6, Kns20 and Kns22.

**Description.** Cyst subspherical, with net-like structure of the wall bearing intratabular hollow, relatively short, distally open tubiform processes. Distal processes' termination smooth. Process wall consists of root-like structure.

**Discussion.** Brinkhuis' (1992) emendation made that this species is included in *C. funiculatum*. However, in the author opinion, morphological differences between this species and *C. funiculatum sensu* Morgenroth 1966, allow treating them as separate species.

*Cordosphaeridium gracile* (Eisenack 1954) Davey et Williams 1966

(Fig. 29J–L, Fig. 85J, K, L)

1954 *Hystriosphraeridium inodes* subsp. *gracile* n. subsp.; Eisenack (1954), p. 66, pl. 8 fig. 17; pl. 10, figs. 3–8; pl. 12, figs. 7, 21

1954 *Cordosphaeridium gracile* comb. nov.; Davey & Williams (1966b), p. 84

1954 *Cordosphaeridium gracile* (Eisenack 1954) emend.; Davey & Williams (1966b), p. 84–85

**Material.** Single to rare specimens occur in samples Kns1, Kns20, Kns22, Kns24, Kns27, Kns28 and Kns32; frequent in samples Kns25 and Kns30 (pale-coloured marl) and in sample KnsH2 (the Hieroglyphic beds).

**Description.** This specimen has spherical central body with smooth cyst wall and relatively long, thin, hollow, finely fibrous intratabular processes. Processes slightly expanded distally, terminating with serrate margins, commonly Y-shaped branched. Archaeopyle precingular.

*Cordosphaeridium inodes* (Klumpp 1953) Eisenack 1963

(Fig. 32B, S, T, Fig. 85F)

1953 *Hystriosphraeridium inodes* n. sp.; Klumpp (1953), p. 391, pl. 18, figs. 1–2

1963 *Cordosphaeridium inodes* comb. nov.; Eisenack (1963), p. 261

1968 *Cordosphaeridium inodes* (Klumpp 1953) emend.; Morgenroth (1968), p. 549–550

1981 *Cordosphaeridium inodes* (Klumpp 1953) emend.; Sarjeant (1981), p. 102–105

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**Fig. 29.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Cordosphaeridium cantharellus* (Kns7); **B, C** – *Cordosphaeridium cantharellus* (same specimen, various foci; Kns5); **D** – *Cordosphaeridium cantharellus* (Kns2); **E, F** – *Cordosphaeridium cantharellus* (same specimen, various foci; Kns6); **G** – *Cordosphaeridium? solidospinosum* (Kns10); **H, I** – *Cordosphaeridium? solidospinosum* (same specimen, various foci; Kns1); **J–L** – *Cordosphaeridium gracile* (Kns25)

**Material.** Single specimens occur in samples Kns4–6, Kns25, Kns27 and Kns28; a single specimen was found in the Hieroglyphic beds (KnsH2).

**Description.** Cyst small to intermediate, subspherical, chorate, with finely granular wall and fibrous, tubiform intratabular processes, slightly expanded distally. Distal margins denticulate. Length of processes does not exceed " of the central body diameter. Archaeopyle precingular.

*Cordosphaeridium minimum* (Morgenroth 1966) Benedek 1972

(Fig. 28F–O)

1966 *Cordosphaeridium inodes* subsp. *minimum* n. subsp.; Morgenroth (1966a), p. 24, pl. 5, figs. 6–7

1972 *Cordosphaeridium minimum* comb. nov.; Benedek (1972), p. 25–26

**Material.** Single specimens occur in samples Kns3–5, Kns7, Kns17, Kns22, Kns26 and Kns33; rare in samples Kns19 and Kns20.

**Description.** Cyst very small, spherical, with smooth to granular wall. Processes relatively long, up to the diameter of the central body, tubiform, covered by longitudinal ribs. Processes distally strongly expanded, in some cases into platform-like structure (e.g., Fig. 28K–M). Well developed archaeopyle was not observed.

*Cordosphaeridium? solidospinosum* Gedl 1995

(Fig. 29G–I)

1995 *Cordosphaeridium? solidospinosum* n. sp.; Gedl (1995b), p. 197, pl. 4, fig. 2; pl. 5, figs. 7–8

**Material.** Single specimens occur in samples Kns1, Kns2, Kns10, Kns19 and Kns22; moderately common in sample Kns18.

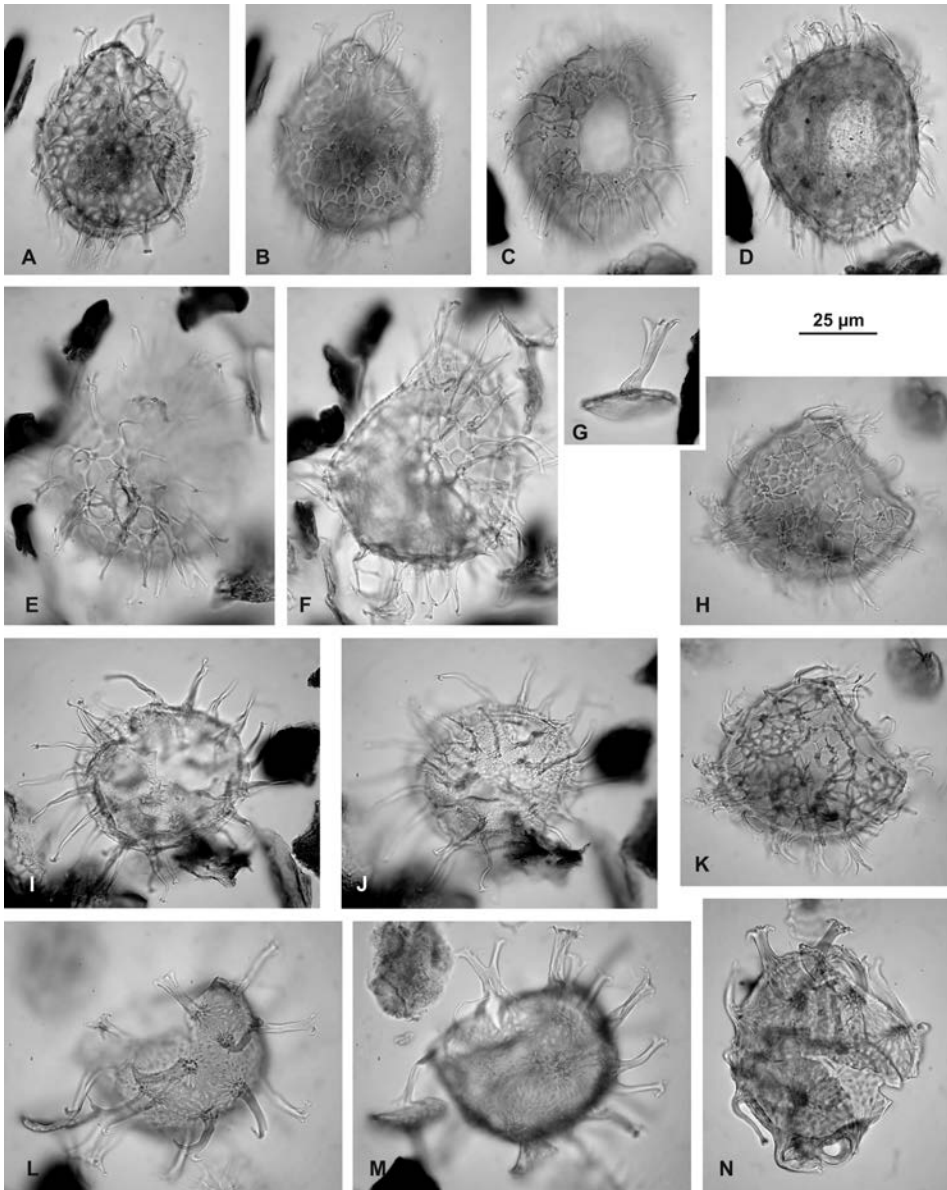
**Description.** This species has subspherical central body with smooth cyst wall. Intratabular processes solid, smooth, of equal height, distally simply branched into short spines, which occasionally show further bifurcations. Archaeopyle precingular.

*Cordosphaeridium* sp. A

(Fig. 28A–E)

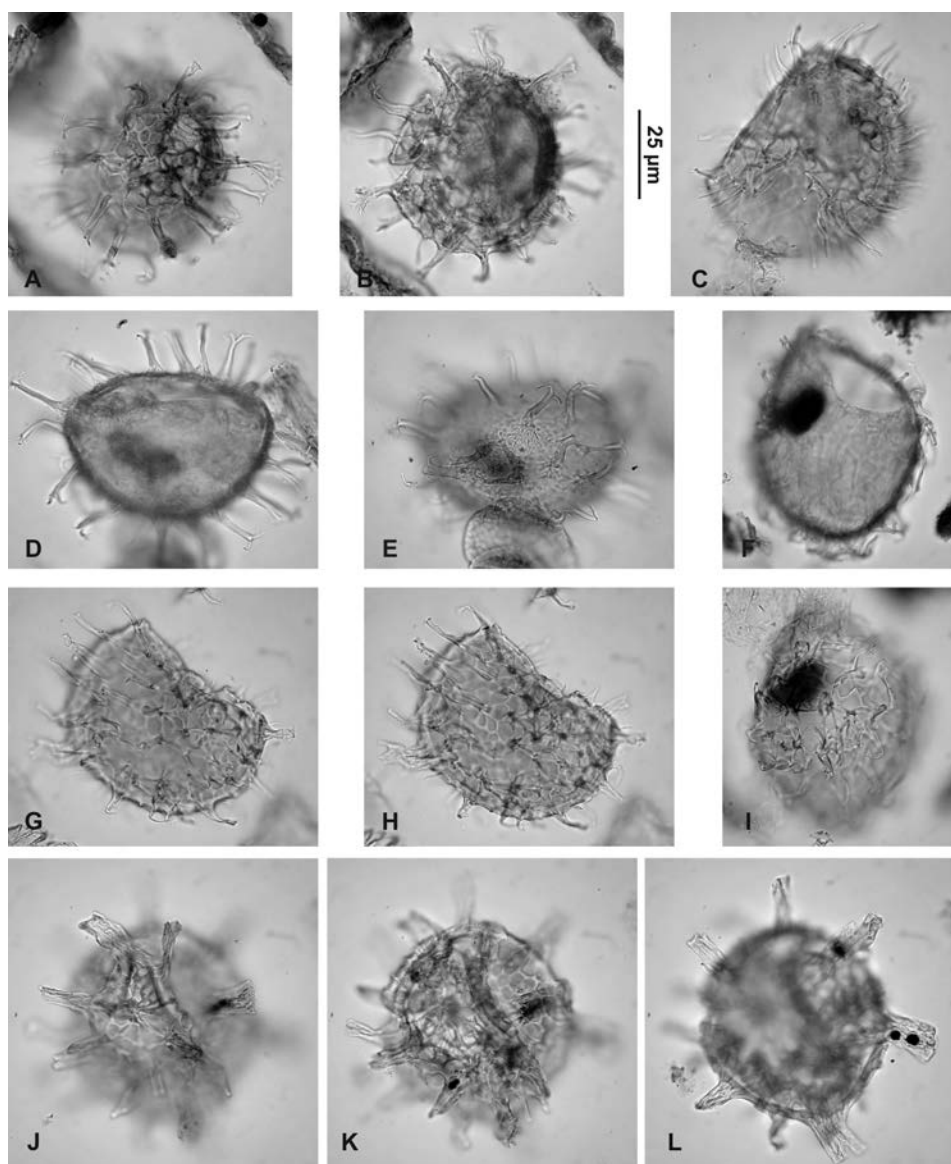
**Material.** Two specimens occur in sample Kns8.

**Description.** Cyst small, spherical, with central body covered with fine net-like structure similar to that on *Operculodinium divergens* (this structure by this latter species is more robust). Intratabular processes short, massive (their height slightly exceeds width) with clearly indicated longitudinal ribs. Processes distally expanded and terminated with smooth margin. Archaeopyle precingular.

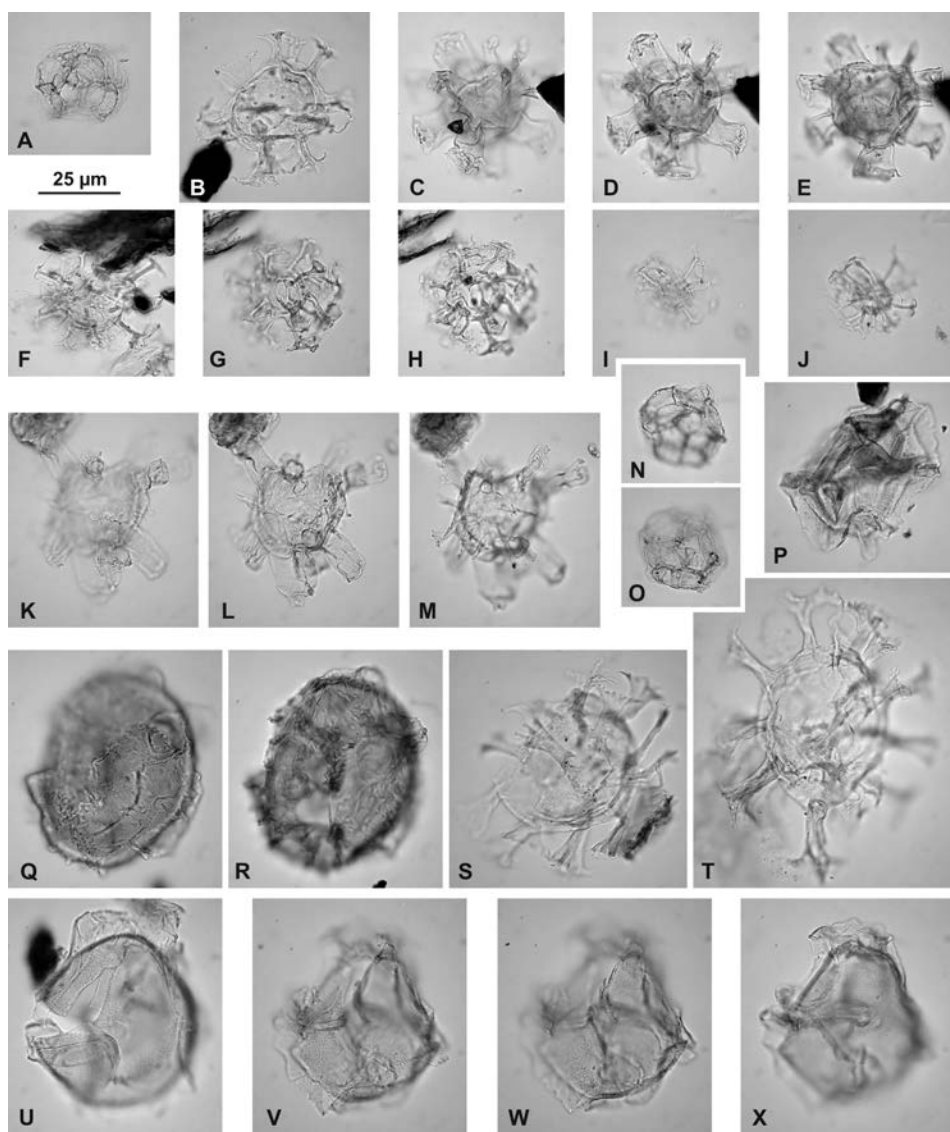


**Fig. 30.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Operculodinium divergens* (same specimen, various foci; Kns5); **C, D** – *Operculodinium divergens* (same specimen, various foci; Kns7); **E, F** – *Operculodinium divergens* (same specimen, various foci; Kns13); **G** – *Cordosphaeridium funiculatum* (isolated opercular paraplate with intratratabular process; Kns8); **H, K** – *Operculodinium divergens* (same specimen, various foci; Kns5); **I, J** – *Operculodinium microtriainum* (same specimen, various foci; Kns2); **L, M** – *Cordosphaeridium funiculatum* (same specimen, various foci; Kns8); **N** – *Cordosphaeridium funiculatum* (Kns8)





**Fig. 31.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Operculodinium divergens* (same specimen, various foci; Kns6); **C** – *Operculodinium divergens* (Kns7); **D, E** – *Operculodinium tiara* (same specimen, various foci; Kns5); **F, I** – *Operculodinium divergens* (same specimen, various foci; Kns5); **G, H** – *Operculodinium divergens* (same specimen, various foci; Kns5); **J–L** – *Cordosphaeridium funiculatum sensu* Brinkhuis 1992 (same specimen, various foci; Kns6)



**Fig. 32.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Heslertonia?* sp. (Kns8); **B** – *Cordosphaeridium inodes* (Kns4); **C–E** – *Hystrichokolpoma rigaudiae* (same specimen, various foci; Kns6); **F** – *Reticulatosphaera actinocoronata* (Kns8); **G, H** – *Reticulatosphaera actinocoronata* (same specimen, various foci; Kns8); **I, J** – *Reticulatosphaera actinocoronata* (same specimen, various foci; Kns12); **K–M** – *Hystrichokolpoma salacia* (same specimen, various foci; Kns8); **N, O** – *Heslertonia?* sp. (same specimen, various foci; Kns5); **P** – *Pentadinium laticinctum* (Kns13); **Q, R** – *Corrudinium?* sp. A sensu Gedl 2005 (same specimen, various foci; Kns4); **S** – *Cordosphaeridium inodes* (Kns5); **T** – *Cordosphaeridium inodes* (Kns8); **U** – *Pentadinium laticinctum* (Kns8); **V–X** – *Pentadinium laticinctum* (same specimen, various foci; Kns5)

Genus *Cribroperidinium* Neale et Sarjeant 1962Type species: *Cribroperidinium sepimentum* Neale et Sarjeant 1962

- 1962 *Cribroperidinium* n. gen.; (Neale & Sarjeant 1962), p. 443  
 1969 *Cribroperidinium* Neale et Sarjeant 1962 emend.; Davey (1969a), p. 125  
 1982 *Cribroperidinium* Neale et Sarjeant 1962 emend.; Sarjeant (1982), p. 40  
 1984 *Cribroperidinium* Neale et Sarjeant 1962 emend.; Helenes (1984), p. 112

*Cribroperidinium giuseppeii* (Morgenroth 1966) Helenes 1984

(Fig. 33A–P)

- 1966 *Gonyaulax giuseppeii* sp. nov.; Morgenroth (1966a), p.5, pl.2, figs.3–6  
 1984 *Cribroperidinium giuseppeii* comb. nov.; Helenes (1984), p. 121

**Material.** Rare (samples Kns1, Kns8, Kns11, Kns13, Kns14, Kns20–22, Kns27, Kns28, Kns31 and Kns33) to moderately common (samples Kns5–7 and Kns12); absent from pale-coloured marl.

**Description.** Cyst proximal, ovoidal, with epicyst and hypocyst of approximately the same size (the former may be slightly narrower). Short apical horn present. Periphragm smooth. Paratabulation indicated by low and delicate parasutural ridges. Additional parallel ridges commonly present. Areas between ridges covered with radial ridges, whereas the central areas of the paraplates covered with irregular network of similar delicate ridges (e.g., S11L). Archaeopyle precingular, isolated opercular paraplates also occur (Fig. 33D).

Genus *Diphyes* Cookson 1965Type species: *Diphyes colligerum* (Deflandre et Cookson 1955) Cookson 1965

- 1965 *Diphyes* n. gen.; Cookson (1965), p. 85  
 1966 *Diphyes* Cookson 1965 emend.; Davey & Williams (1966b), p. 95–96  
 1985 *Diphyes* Cookson 1965 emend.; Goodman & Witmer (1985), p. 76

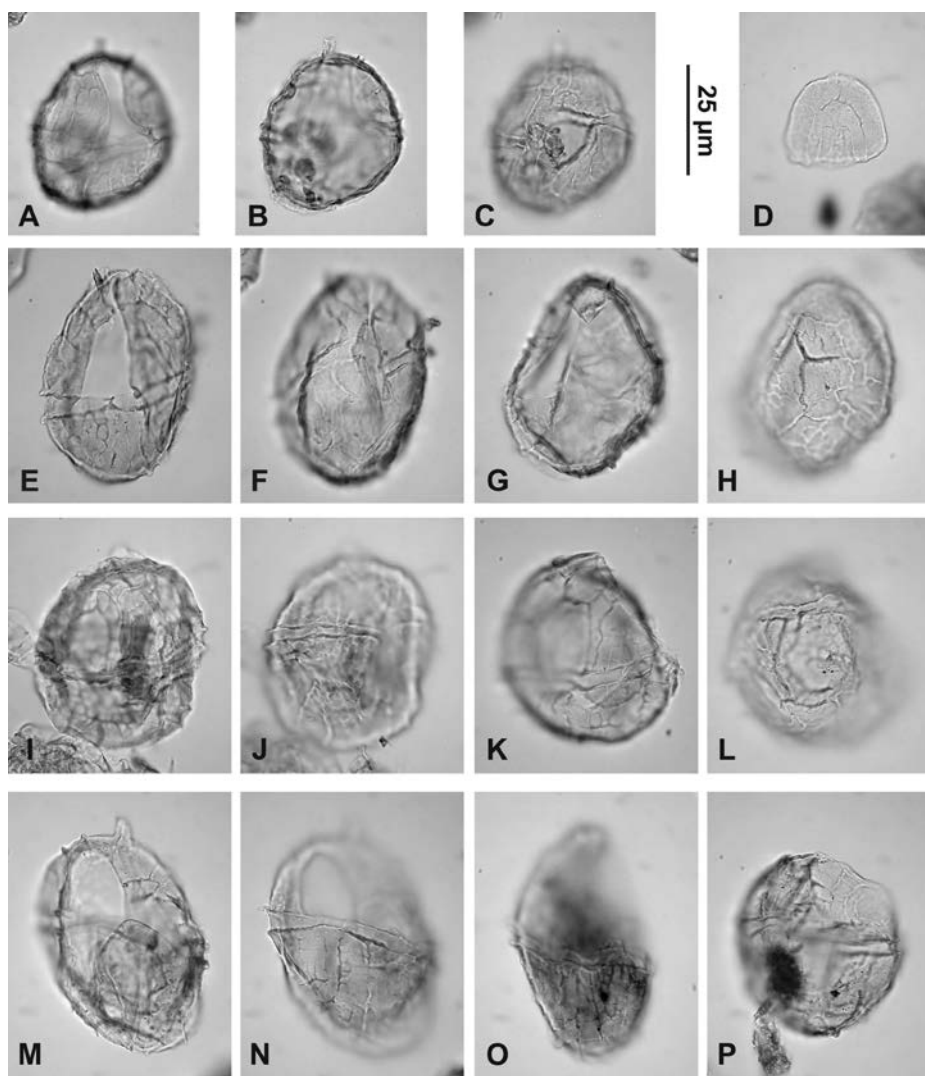
*Diphyes colligerum* (Deflandre et Cookson 1955) Cookson 1965

(Fig. 34N–Q)

- 1955 *Hystriochosphaeridium colligerum* n. sp.; Deflandre & Cookson (1955), p. 278–279, pl. 7, fig. 3  
 1965 *Diphyes colligerum* comb. nov.; Cookson (1965), p. 86–87  
 1965 *Diphyes colligerum* (Deflandre et Cookson 1955) emend.; Cookson (1965a), p. 86  
 1985 *Diphyes colligerum* (Deflandre et Cookson 1955) emend.; Goodman & Witmer (1985), p. 77–78

**Material.** Rare specimens occur in samples Kns5, Kns6 and Kns12.

**Description.** Cyst small, spherical, with densely granular wall covered with numerous nontabular processes. Processes smooth, hollow, broad at the base, getting narrow upwards, distally slightly expanded and open. One outstanding antapical process much larger, smooth, broad, hollow, distally open. Archaeopyle apical.



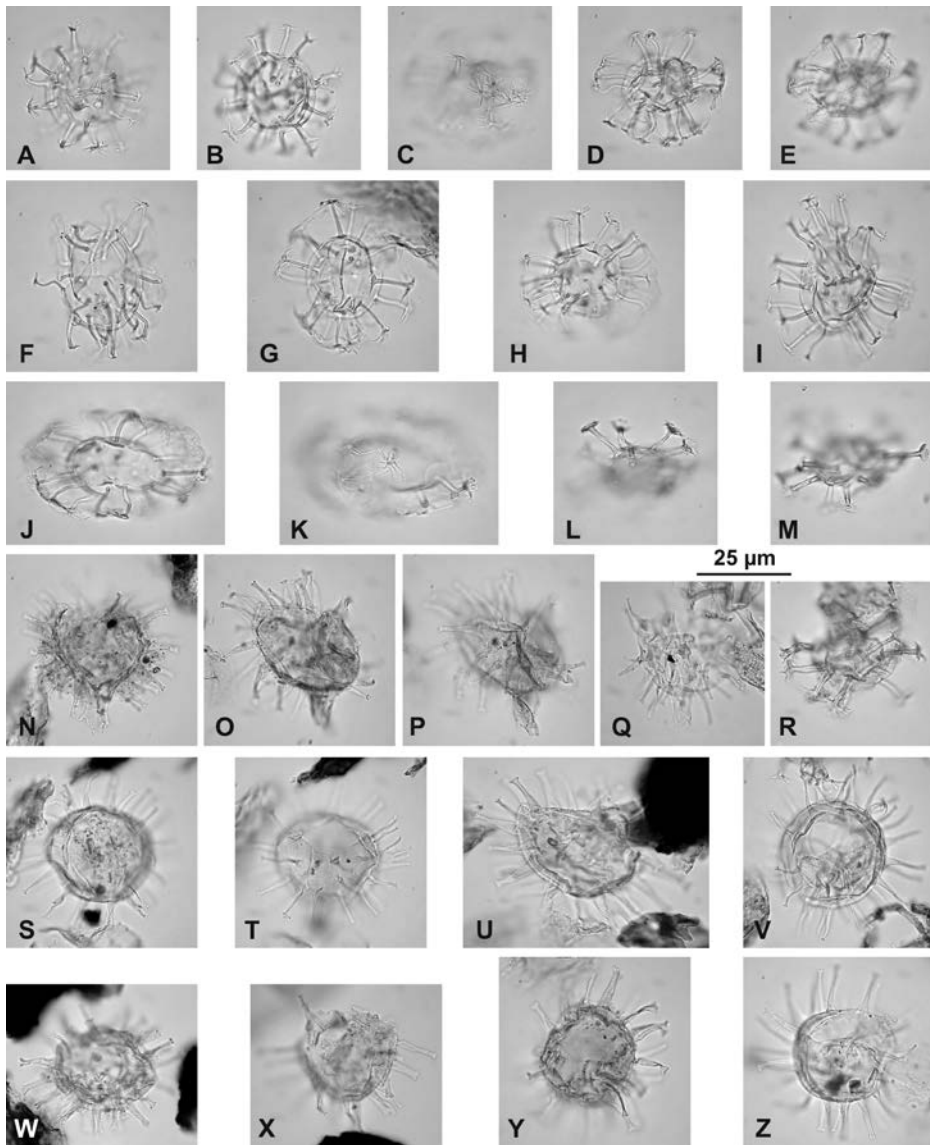
**Fig. 33.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–P** – *Cribroperidinium giuseppeei* (A–C: same specimen, various foci, Kns5; D: isolated opercular paraplate, Kns12; E, F: same specimen, various foci, Kns5; G, H: same specimen, various foci, Kns5; I, J: same specimen, various foci, Kns5; K, L: same specimen, various foci, Kns12; M, N: same specimen, various foci, Kns7; O: Kns1; P: Kns12)

### Genus *Hystrichokolpoma* Klumpp 1953

Type species: *Hystrichokolpoma cinctum* Klumpp 1953

- 1953 *Hystrichokolpoma* n. gen.; Klumpp (1953), 388
- 1966 *Hystrichokolpoma* Klumpp 1953 emend.; Williams & Downie (1966a), p. 176
- 1995 *Hystrichokolpoma* Klumpp 1953 emend.; Zevenboom & Santarelli in Zevenboom (1995), p. 136
- 2004 *Hystrichokolpoma* Klumpp 1953 emend.; Foucher in Fauconnier & Masure (2004), p. 281





**Fig. 34.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Melitasphaeridium pseudorecurvatum* (same specimen, various foci; Kns4); **C–E** – *Melitasphaeridium pseudorecurvatum* (same specimen, various foci; Kns5); **F** – *Melitasphaeridium pseudorecurvatum* (Kns8); **G** – *Melitasphaeridium pseudorecurvatum* (Kns8); **H** – *Melitasphaeridium pseudorecurvatum* (Kns8); **I** – *Melitasphaeridium pseudorecurvatum* (Kns8); **J, K** – *Melitasphaeridium pseudorecurvatum* (same specimen, various foci; Kns10); **L, M** – *Melitasphaeridium asterium* (same specimen, various foci; Kns6); **N** – *Diphyes colligerum* (Kns6); **O, P** – *Diphyes colligerum* (same specimen, various foci; Kns6); **Q** – *Diphyes colligerum* (Kns5); **R** – *Melitasphaeridium pseudorecurvatum* (Kns6); **S, T** – *Dapsilidinium pseudo-colligerum* (same specimen, various foci; Kns12); **U** – *Dapsilidinium pseudo-colligerum* (Kns12); **V** – *Dapsilidinium pseudocolligerum* (Kns12); **W** – *Dapsilidinium pseudocolligerum* (Kns6); **X** – *Dapsilidinium pseudocolligerum* (Kns13); **Y** – *Dapsilidinium pseudocolligerum* (Kns13); **Z** – *Dapsilidinium pseudocolligerum* (Kns8)

*Hystrichokolpoma cinctum* Klumpp 1953

(Fig. 35M, N)

1953 *Hystrichokolpoma cinctum* n. sp.; Klumpp (1953), p. 389, pl. 17, figs. 3–4, 5a–d**Material.** Single specimens occur in samples Kns10, Kns18 and Kns20.**Description.** Central body subspherical, with thick and smooth cyst wall. Two types of processes, as typical for the genus: large, dome-like intratabular processes of the precingular and postcingular series are thin-walled and finely granular, distally narrowed, open; their broad bases almost outline the shape of whole paraplates. Paracingular and parasulcal processes thin, small and faint, distally open. Antapical process broad at the base, tubular, distally narrowed and open (much longer than the other processes).*Hystrichokolpoma rigaudiae* Deflandre et Cookson 1955

(Fig. 36A–P, Fig. 35A–C, O–Q, Fig. 32C–E)

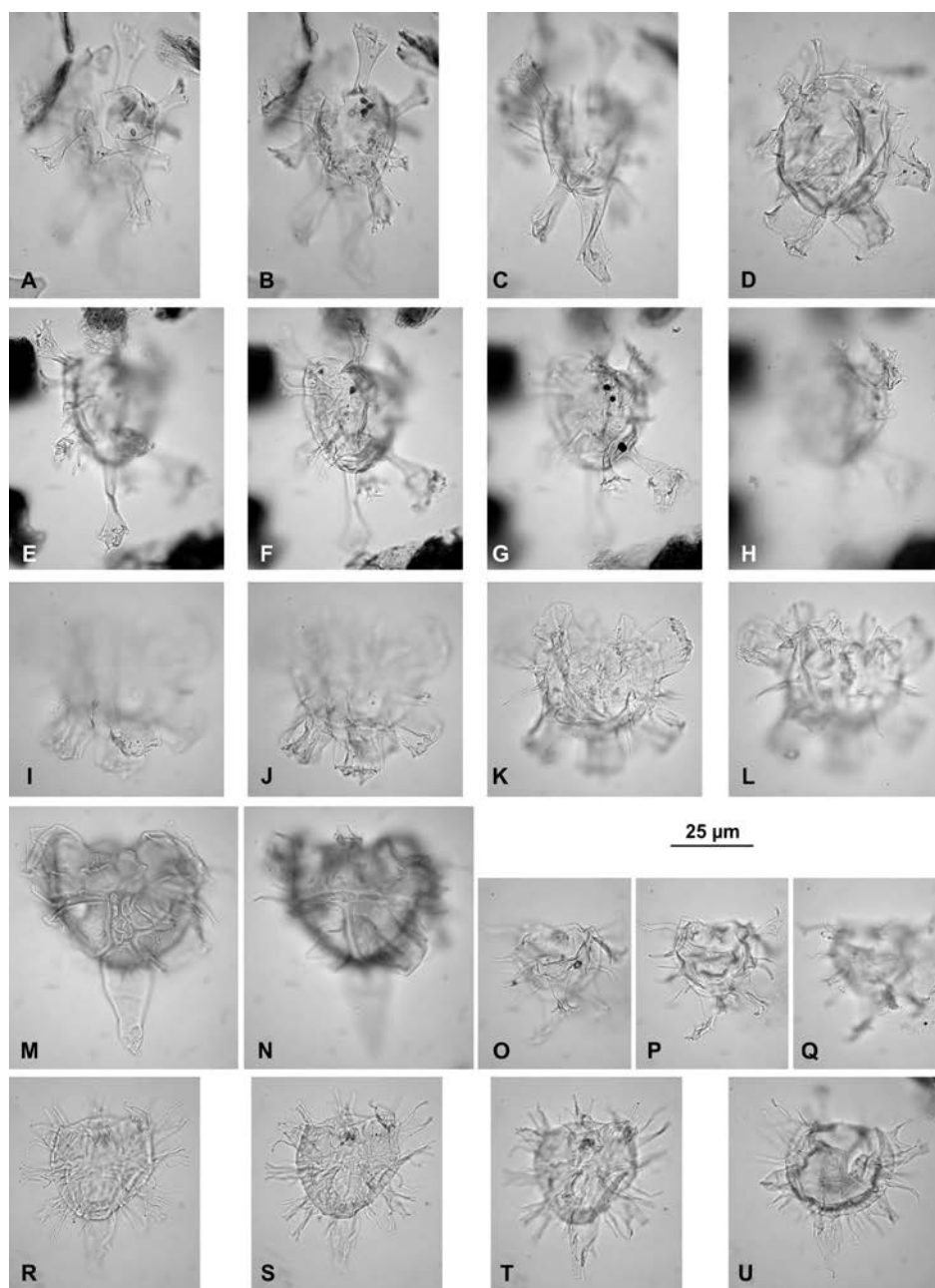
1955 *Hystrichokolpoma rigaudiae* n. sp.; Deflandre & Cookson (1955), p. 279–281, pl. 6, figs. 6, 10; text-fig. 42**Material.** Rare to moderately common in most of samples from dark mudstone (samples Kns1, Kns2, Kns5–7, Kns9, Kns11, Kns13, Kns14, Kns17–22 and Kns31), frequent in sample Kns32; absent from pale-coloured marl, except of sample Kns8.**Description.** Central body subspherical to slightly elongated, smooth. It bears two types of processes: the large ones, typical for paracingular and postcingular series, wide, tubiform, smooth, each distally terminated with a few small tube-like processes. Narrow processes hollow, smooth, usually distally closed, but also open are present. Prominent antapical process tubiform, distally becomes narrowed.

This species shows a considerable variation in process length, regarding their length and width. There is a specimen with very short, almost box-like cylindrical processes terminated with short tubes (sample Kns6; Fig. 36K, L, P). Two specimens found in samples Kns6 (Fig. 35E–H) and Kns7 (Fig. 35A–C) have very long, slender tubiform processes. Another morphotype included in *H. rigaudiae* has very thin processes (Kns8; Fig. 35O–Q).

*Hystrichokolpoma* cf. *rigaudiae* Deflandre et Cookson 1955

(Fig. 35R–U)

**Material.** A few specimens occur in pale-coloured marl only (samples Kns23 and Kns25).**Description.** This species is similar to *H. rigaudiae* in general shape of the cyst and process arrangement, but it differs by the shape of paracingular and postcingular processes, which possess very long tubes that arise from their lower parts.



**Fig. 35.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–C** – *Hystrichokolpoma rigaudiae* (same specimen with long, slender processes, various foci; Kns7); **D** – *Hystrichokolpoma salacia* (Kns5); **E–H** – *Hystrichokolpoma rigaudiae* (same specimen with long, slender processes, various foci; Kns6); **I–L** – *Hystrichokolpoma salacia* (same specimen, various foci; Kns8); **M, N** – *Hystrichokolpoma cinctum* (same specimen, various foci; Kns10); **O–Q** – *Hystrichokolpoma rigaudiae* (same specimen with long and thin processes, various foci; Kns8); **R–T** – *Hystrichokolpoma* cf. *rigaudiae* (same specimen, various foci; Kns25); **U** – *Hystrichokolpoma* cf. *rigaudiae* (Kns25)

*Hystrichokolpoma salacia* Eaton 1976

(Fig. 35D, I–L, Fig. 32K–M)

- 1976 *Hystrichokolpoma salacia* n. sp.; Eaton (1976), p. 271–272, pl. 11, figs. 1–3; text-figs. 16A–B

**Material.** Rare specimens occur in samples Kns5, Kns6, Kns8, Kns12, Kns20–22 and Kns32.

**Description.** Central body subspherical, with thin and smooth cyst wall. Intratabular precingular and postcingular processes cylindrical, distally closed. However, their morphology may differ. They may be relatively short, box-like, smooth (sample Kns5; Fig. 35D), or finely striated (sample Kns8; Fig. 35I–L). Another specimen from sample Kns8 has much thinner and longer cylindrical processes (Fig. 32K–M). Remaining paracingular processes short, narrow, distally closed. Antapical process large, inflate, distally closed. Its height, in contrast to other species of *Hystrichokolpoma*, equals that of other pre- and postcingular processes (Fig. 35J) or only slightly exceeds it (Fig. 32L).

Genus *Lingulodinium* Wall 1967

Type species: *Lingulodinium machaerophorum* (Deflandre et Cookson 1955) Wall 1967

- 1967 *Lingulodinium* n. gen.; Wall (1967), p. 109  
 1973 *Lingulodinium* Wall 1967 emend.; Wall & Dale in Wall, Dale & Harada (1973), p. 23–24  
 1989 *Lingulodinium* Wall 1967 emend.; Dodge (1989), p. 291

*Lingulodinium machaerophorum* (Deflandre et Cookson 1955) Wall 1967

(Fig. 20H, I, L, Fig. 27D–F)

- 1955 *Hystrichosphaeridium machaerophorum* n. sp.; Deflandre & Cookson (1955), p. 274, pl. 9, figs. 4–9  
 1967 *Lingulodinium machaerophorum* comb. nov.; Wall (1967), p. 109

**Material.** Single to rare specimens in samples Kns2, Kns3, Kns5, Kns7, Kns8, Kns11–13, Kns18, Kns19, Kns23–25, Kns27–30, Kns32 and Kns33; moderately frequent in sample Kns20.

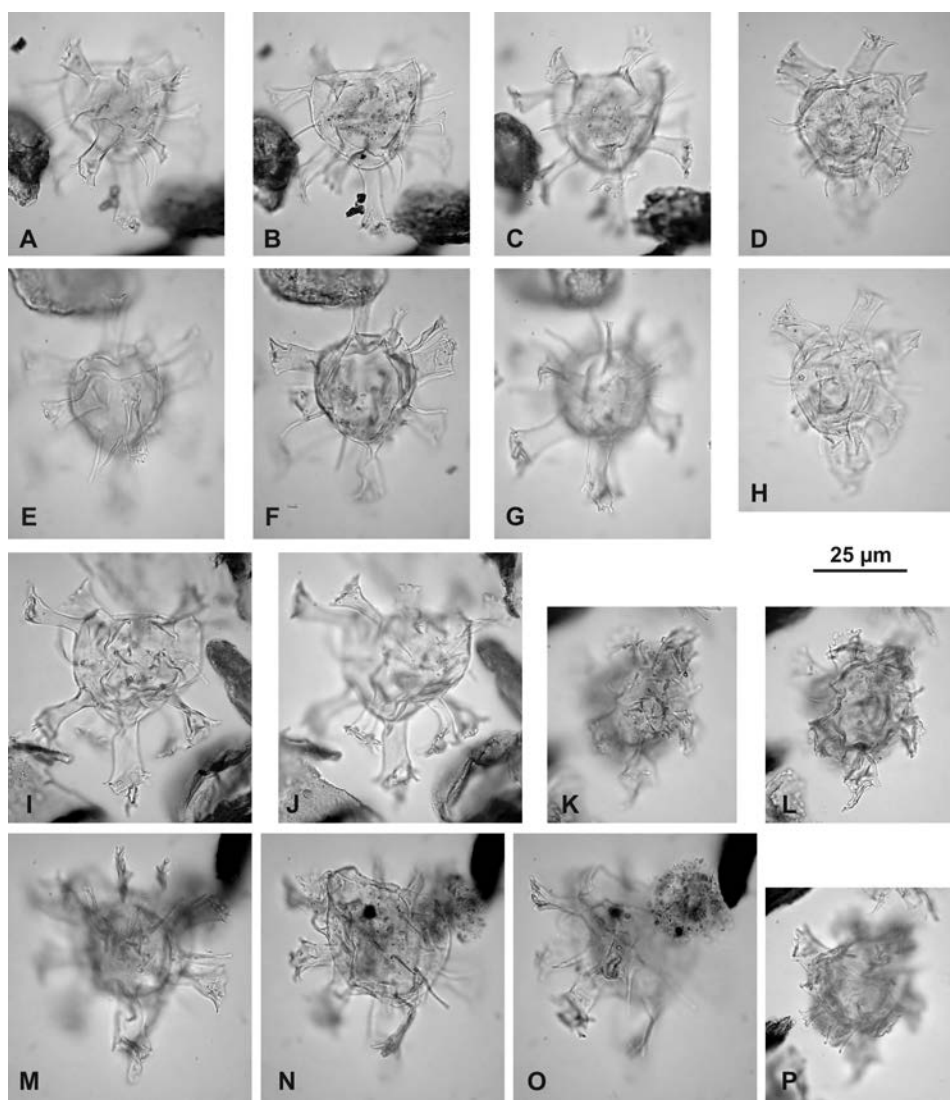
**Description.** Cyst spherical, chorate, with granular wall (Fig. 20I) covered by numerous, nontabular, hollow, distally closed blade-shaped processes. Number of processes and their length variable: some specimens possess longer and less frequent processes (Fig. 27E, F), whereas the others, less frequent, covered with shorter but more numerous processes (Fig. 27D). Processes covered with tiny granulae, which in some specimens become larger and more frequent, especially in distal parts of processes (Fig. 27F).

Genus *Operculodinium* Wall 1967

Type species: *Operculodinium centrocarpum* (Deflandre et Cookson 1955) Wall 1967

- 1967 *Operculodinium* n. gen.; Wall (1967), p. 110–111  
 1997 *Operculodinium* Wall 1967 emend.; Matsuoka, McMinn & Wrenn (1997), p. 22





**Fig. 36.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–P** – *Hystrichokolpoma rigaudiae* (**A–C**: same specimen, various foci; Kns12; **D, H**: same specimen, various foci; Kns5; **E–G**: same specimen, various foci; Kns12; **I, J**: same specimen, various foci; Kns12; **K, L, P**: specimen with short processes, same specimen, various foci; Kns6; **M–O**: same specimen, various foci; Kns6)

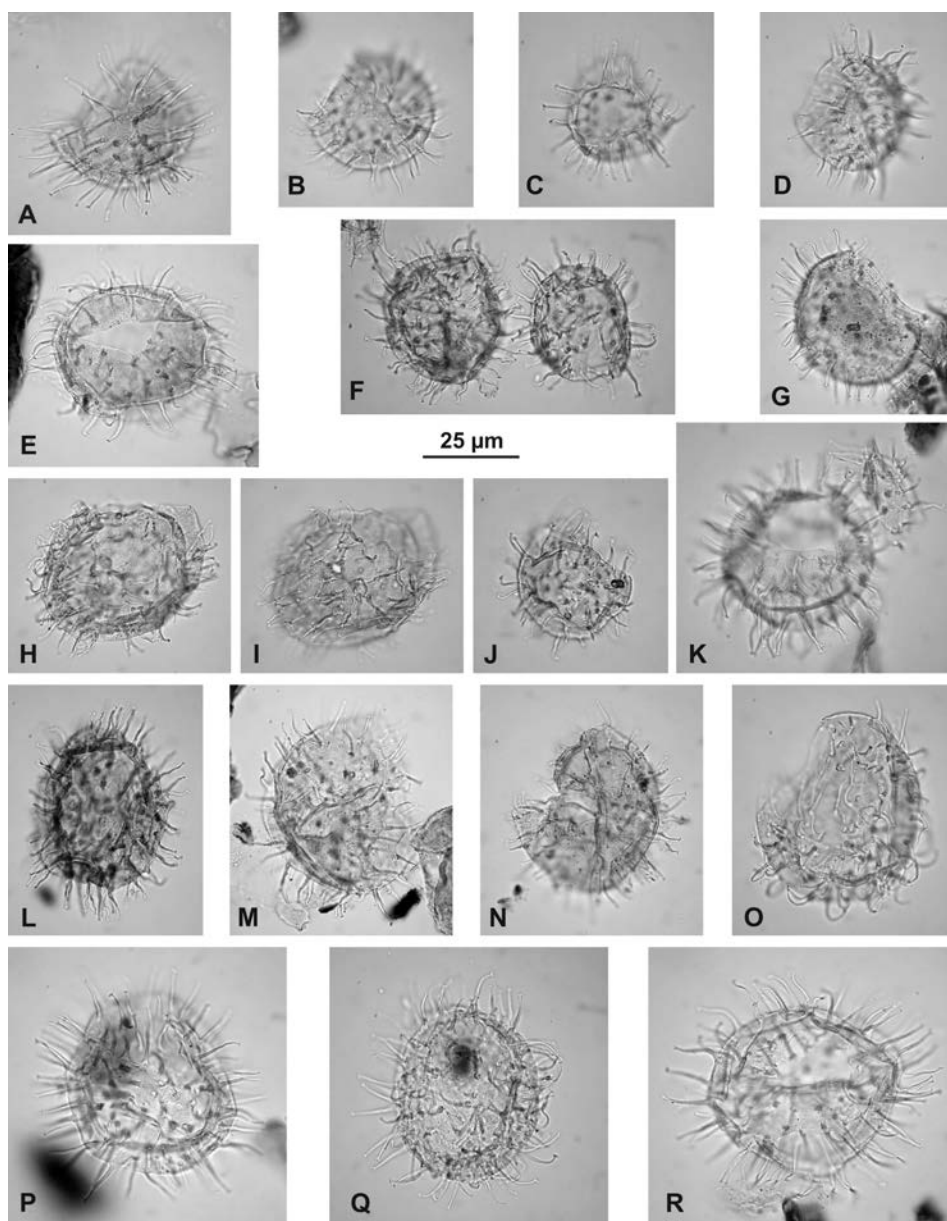
*Operculodinium centrocarpum* (Deflandre et Cookson 1955) Wall 1967

(Fig. 37A–R, Fig. 38A–F, H, I, Fig. 84K)

1955 *Hystrichosphaeridium centrocarpum* n. sp.; Deflandre & Cookson (1955), p. 272–273, pl. 8, figs. 3–4

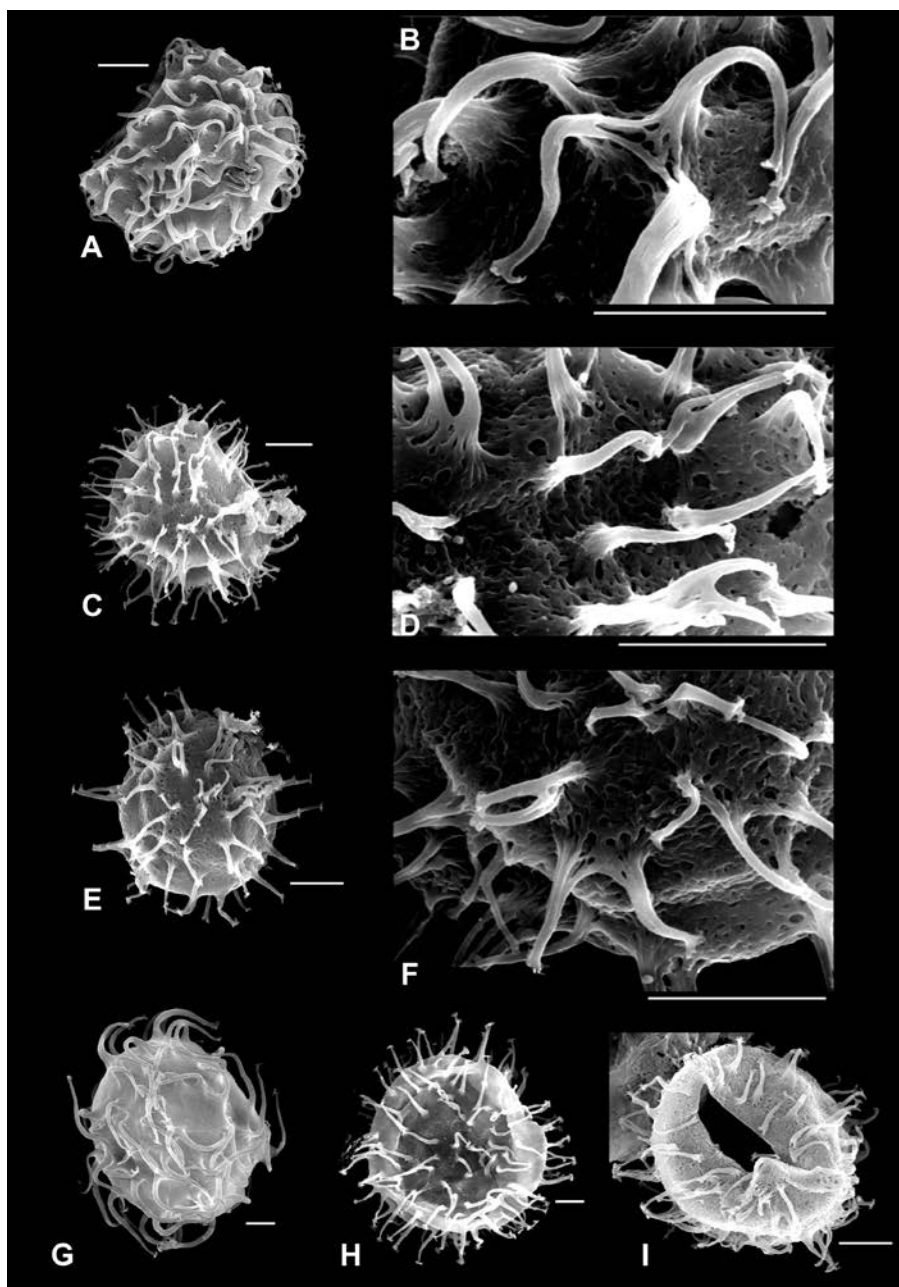
1967 *Operculodinium centrocarpum* comb. nov.; Wall (1967), p. 111

**Material.** Very common species at Koniusza; it occurs in most of samples, being



**Fig. 37.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–R** – *Operculodinium centrocarpum* (A–D: Kns8; E: Kns5; F: two specimens, Kns4; G: Kns12; H, I: same specimen, various foci, Kns4; J: Kns4; K: Kns8; L: Kns4; M, N: Kns6; O–R: Kns8)

frequently a dominating species. Absent from most of samples representing pale-coloured marl (Kns3, Kns23–25). Frequent in the Hieroglyphic beds (sample KnsH2).



**Fig. 38.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10  $\mu$ m). **A–F, H, I** – *Operculodinium centrocarpum* (A, B: Kns8 – specimen with long and relatively massive processes arising from net-like wall structure, A: complete specimen, B: detail of the wall and process structure; C, D: Kns8 – specimen with thin processes, C: complete specimen, D: detail showing the cyst surface and processes; E, F: Kns8 – E: complete specimen, F: detail showing the structure of the cyst surface and processes; H: Kns8 – specimen with smooth and non-perforated surface; I: Kns5); **G** – *Operculodinium microtriainum* (Kns5)

**Description.** Cyst subspherical, with wall consisting of very dense net-like structure, which gives rise to numerous solid, nontabular, distally capitate processes (Fig. 38B, D, F). Process bases arise from this wall structure in a form of root-like construction, which passes into homogenous solid process stems. Process length constant at each specimen; it rarely exceeds 1/3 of the main body diameter. Archaeopyle precingular.

*Operculodinium divergens* (Eisenack 1954) Stover et Evitt 1978

(Fig. 30A–F, H, K, Fig. 31A–C, F–I)

1954 *Hystriosphæridium divergens* n. sp.; Eisenack (1954), p. 67, pl. 9, figs. 13–16

1978 *Operculodinium divergens* comb. nov.; Stover & Evitt (1978), p. 178

**Material.** This species occurs as rare to moderately common in almost all samples representing dark-coloured mudstone (except of Kns17 and Kns18); it is absent from most of pale-coloured marl samples (except of Kns8 and Kns10).

**Description.** Cyst relatively large, chorate, with thick wall composed of net-like structure consisting of solid ribs densely crossing irregularly with each other. Nontabular processes smooth, hollow, frequently united proximally, distally split into two or more branches. Processes distally closed or open, the latter commonly slightly expanded.

Cyst wall net-like structure of *Operculodinium divergens* is identical to that of *Cordosphaeridium funiculatum*. The latter species differs by intratabular processes, which generally are of the same size at particular specimen.

*Operculodinium microtriainum* (Klumpp 1953) Islam 1983

(Fig. 20F, 24I, J, Fig. 38G, Fig. 39J–O, Fig. 40A, B)

1953 *Hystriosphæridium microtriainum* n. sp.; Klumpp (1953), p. 390, pl. 17, figs. 6–7

1983 *Operculodinium microtriainum* comb. nov.; Islam (1983a), p. 241

**Material.** Moderately to very frequent in samples representing dark-coloured mudstone (except of sample Kns14); absent or very rare (Kns3 and Kns4) in samples representing pale-coloured marl. Two specimens occur in the Hieroglyphic beds (KnsH2).

**Description.** Cyst intermediate to large, spherical to subspherical, chorate, with wall composed of dense net-like structure, which gives rise to numerous nontabular, solid, smooth, long processes that distally terminate with tiny hook-like branches. Base of processes consists of root-like structure, which directly arises from the wall. Archaeopyle precingular.

Wall and process structure of *Operculodinium microtriainum* is similar to that of *Operculodinium centrocarpum*. The latter is much smaller, its processes are capitate.

*Operculodinium tiara* (Klumpp 1953) Stover et Evitt 1978

(Fig. 31D, E, Fig. 39F–I)

1953 *Hystriosphæridium tiara* n. sp.; Klumpp (1953), p. 390–391, pl. 17, figs. 8–10

1978 *Operculodinium tiara* comb. nov.; Stover & Evitt (1978), p. 179



**Material.** Single or very rare specimens occur in samples Kns1, Kns5, Kns17, Kns22, Kns28, Kns33; more frequent in sample Kns6.

**Description.** Cyst spherical, chorate, with nontabular, numerous, relatively short and massive processes, distally branched into tiny tips. Cyst wall felty, relatively thick. Archaeopyle precingular.

*Operculodinium* sp. A

(Fig. 39A–E)

2005    *Operculodinium* aff. *centrocarpum*; Gedl (2005), p. 35–36, pl. 3, fig. 23

**Material.** Rare specimens occur in samples Kns3, Kns6, Kns11, Kns17, Kns20 and Kns21.

**Description.** Cyst small, spherical, chorate, with wall composed of dense net-like structure, and short, straight processes, acuminate or terminated with tiny branching. Cyst diameter does not exceed 30 µm. Archaeopyle precingular.

Genus *Samlandia* Eisenack 1954

Type species: *Samlandia chlamydophora* Eisenack 1954

1954    *Samlandia* n. gen.; Eisenack (1954), p. 76

*Samlandia chlamydophora* Eisenack 1954

(Fig. 27A–C, G–K, N, O)

1954    *Samlandia chlamydophora* n. sp.; Eisenack (1954), p. 76, pl. 11, figs. 12–15

**Material.** Rare in most of samples (Kns4–8, Kns11–13, Kns17, Kns19–22, Kns28, Kns32), moderately common in samples Kns1, Kns2 and Kns18; absent from samples Kns3, Kns9, Kns10, Kns14, Kns23–27, Kns29–31 and Kns33.

**Description.** Cyst subspherical to ellipsoidal, with wall thick and smooth. Some specimens have indistinct apical protrusion (Fig. 27G–K). Cyst wall covered by thin membranaceous processes of variable shape and morphology. These are both isolated processes commonly united proximally by low ridges (Fig. 27K, N, O) and processes united in shape of anastomosing complexes (ridges); processes distally united forming irregular ectophragmal network. The latter forms apical “horn” in case of specimens with apical protrusion (Fig. 27G–K). Archaeopyle precingular.

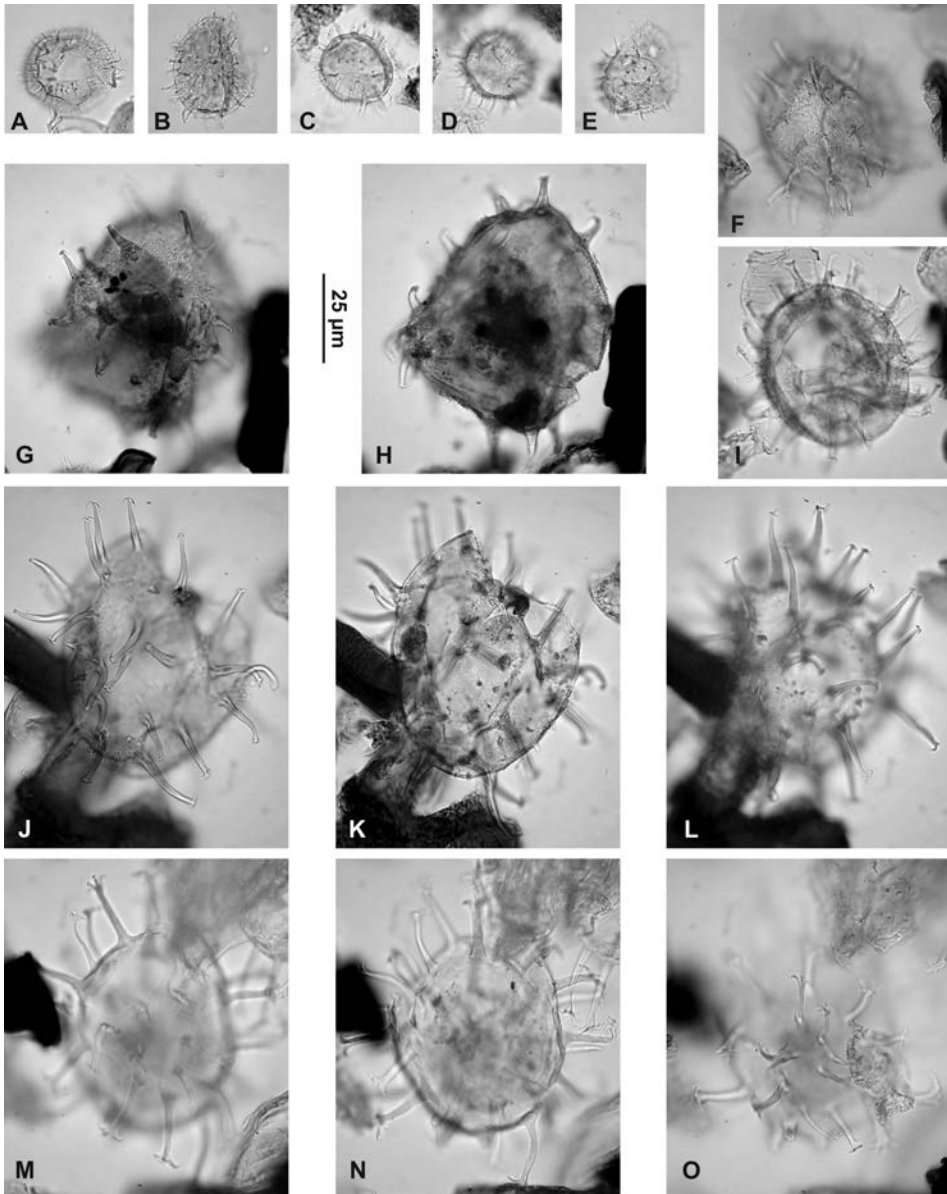
Genus *Thalassiphora* Eisenack et Gocht 1960

Type species: *Thalassiphora pelagica* (Eisenack 1954) Eisenack et Gocht 1960

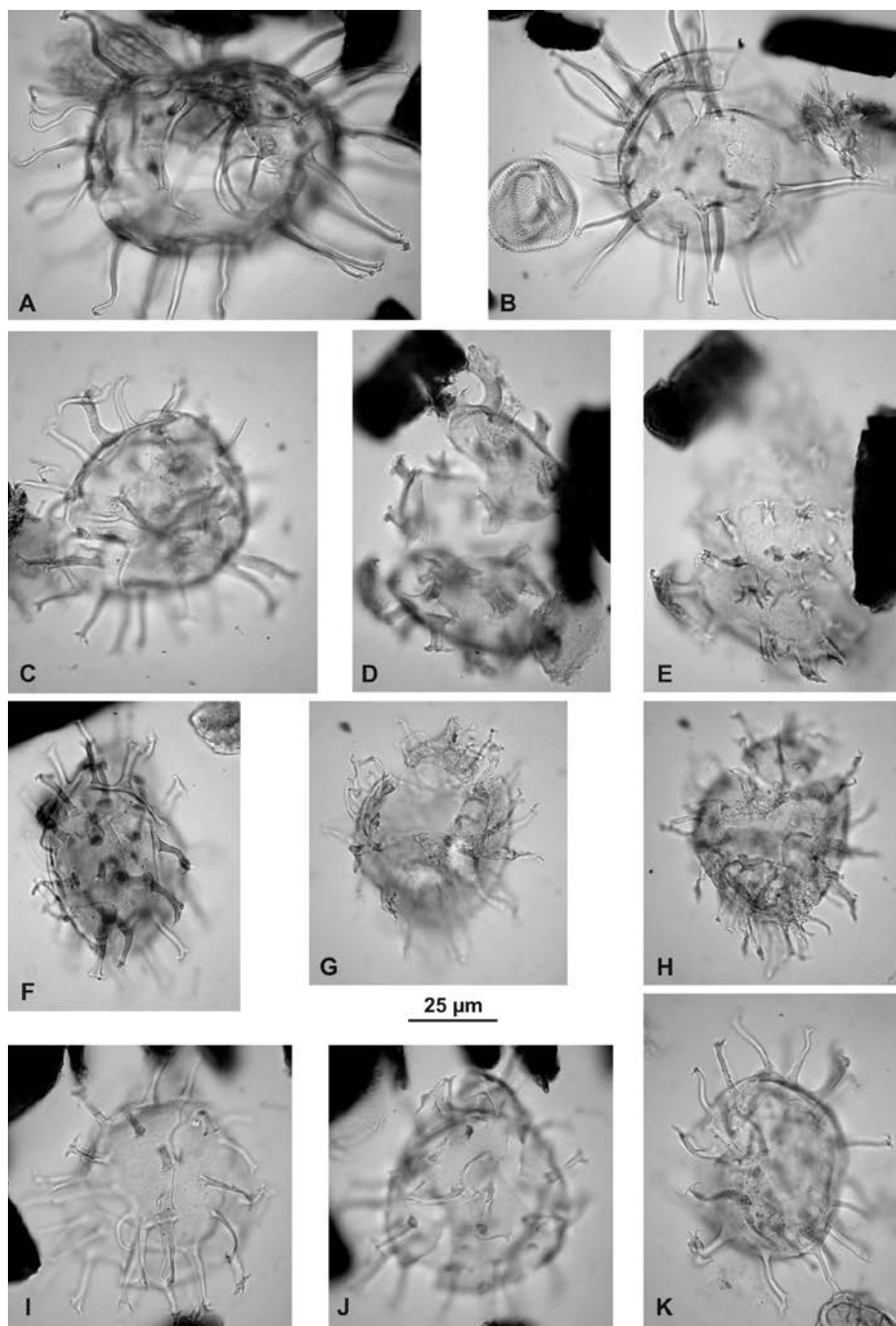
1960    *Thalassiphora* n. gen.; Eisenack & Gocht (1960), p. 513

1968    *Thalassiphora* Eisenack et Gocht 1960 emend.; Gocht (1968), p. 153

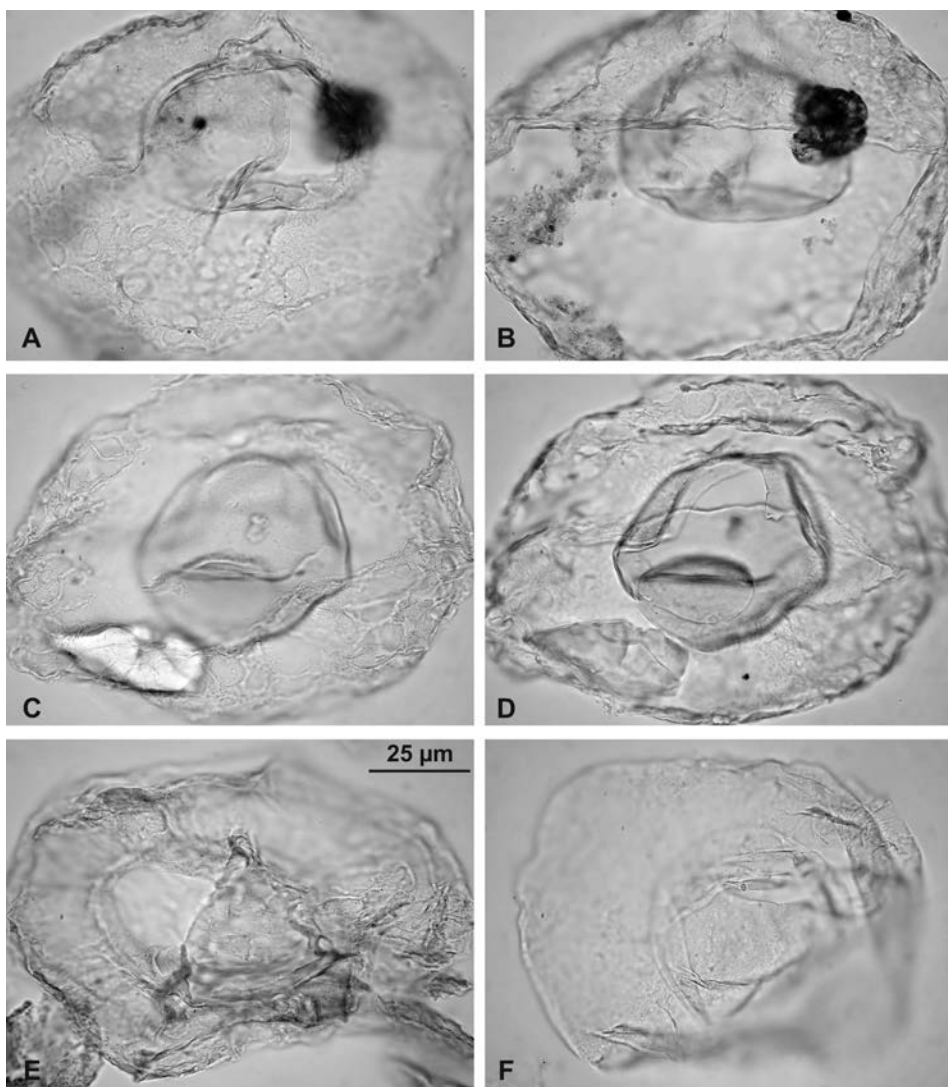
1981    *Thalassiphora* Eisenack et Gocht 1960 emend.; Benedek & Gocht (1981), p. 59



**Fig. 39.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Operculodinium* sp. A (Kns3); **B** – *Operculodinium* sp. A (Kns3); **C**, **D** – *Operculodinium* sp. A (same specimen, various foci; Kns6); **E** – *Operculodinium* sp. A (Kns11); **F**, **I** – *Operculodinium tiara* (same specimen, various foci; Kns5); **G**, **H** – *Operculodinium tiara* (same specimen, various foci; Kns6); **J**–**L** – *Operculodinium microtriainum* (same specimen, various foci; Kns1); **M**–**O** – *Operculodinium microtriainum* (same specimen, various foci; Kns7)



**Fig. 40.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Operculodinium microtriainum* (Kns1); **B** – *Operculodinium microtriainum* (Kns2); **C** – *Fibrocysta axialis* (Kns6); **D**, **E** – *Fibrocysta* sp. **A** (same specimen, various foci; Kns2); **F** – *Fibrocysta axialis* (Kns3); **G**, **H** – *Fibrocysta radiata* (same specimen, various foci; Kns3); **I**, **J** – *Fibrocysta axialis* (same specimen, various foci; Kns2); **K** – *Fibrocysta axialis* (Kns8)



**Fig. 41.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–E** – *Thalassiphora pelagica* (A, B: same specimen, various foci; Kns6; C, D: same specimen, various foci; Kns10; E: Kns12); **F** – *Thalassiphora delicata* (Kns8)

*Thalassiphora delicata* Williams et Downie 1966

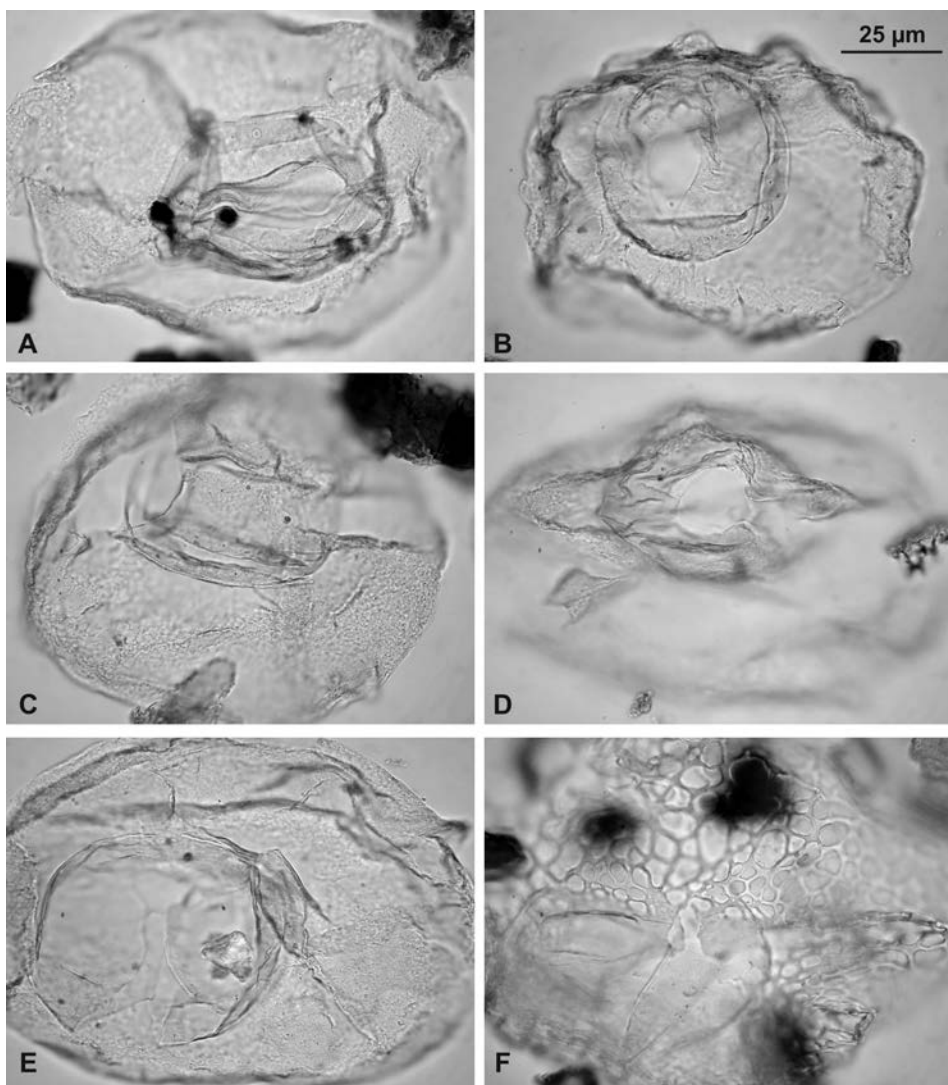
(Fig. 41F, Fig. 42A, E)

1966 *Thalassiphora delicata* n. sp.; Williams & Downie (1966c), p. 235, pl. 26, fig. 8

1976 *Thalassiphora delicata* Williams et Downie 1966 emend.; Eaton (1976), p. 287

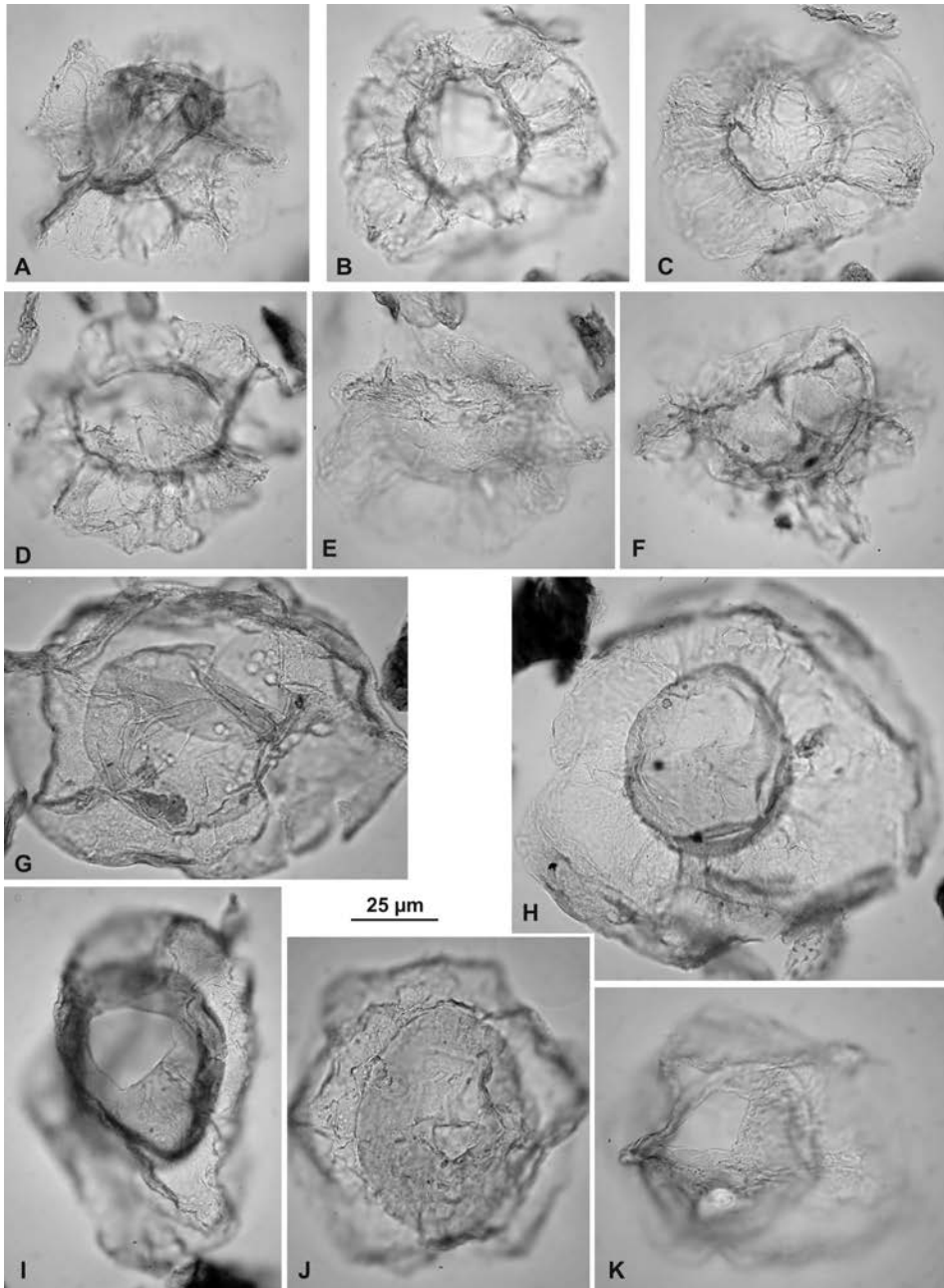
**Material.** Single specimens occur in samples Kns6, Kns7 and Kns11; moderately common in samples Kns8 and Kns10.





**Fig. 42.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bar at B refers to all other photographs). **A** – *Thalassiphora delicata* (Kns6); **B** – *Thalassiphora pelagica* (Kns7); **C** – *Thalassiphora pelagica* (Kns7); **D** – *Thalassiphora pelagica* (Kns7); **E** – *Thalassiphora delicata* (Kns11); **F** – *Thalassiphora reticulata* (Kns13)

**Description.** Cyst camocavate, with endocyst spherical, relatively large in comparison to pericyst. Endophragm smooth, homogenous, devoid of fenestrations and parasutural features except of precingular archaeopyle.Periphragm thin and although seemingly smooth, it has finely spongy structure.



**Fig. 43.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Thalassiphora patula* (Kns8); **B, C** – *Thalassiphora patula* (same specimen, various foci; Kns12); **D, E** – *Thalassiphora patula* (same specimen, various foci; Kns12); **F** – *Thalassiphora patula* (Kns8); **G** – *Thalassiphora pelagica* (Kns5); **H** – *Thalassiphora pelagica* (Kns6); **I** – *Thalassiphora pelagica* (Kns3); **J** – *Thalassiphora pelagica* (Kns4); **K** – *Thalassiphora pelagica* (Kns4)

*?Thalassiphora dynamica* (Morgenroth 1966) Stover et Evitt 1978

(Fig. 55J)

1966 *Erikania dynamica* n. sp.; Morgenroth (1966a), p. 27–28, pl. 6, figs 7–81978 *Thalassiphora dynamica* comb. nov.; Stover & Evitt (1978), p. 195**Material.** A single specimen in sample Kns5.**Description.** Central body spherical, with smooth wall; shape of archaeopyle not certain due to cyst compression. Central body surrounded by thin, smooth membrane with large opening, which remains in contact with central body by narrow portions of the outer membrane.**Discussion.** This specimen has been questionably assigned to this species described by Morgenroth (1966a) from Lower Eocene. It is partly compressed and folded, and complete arrangement of the cyst, particularly relations between inner body and outer membrane, cannot be univocally estimated.*Thalassiphora patula* (Williams et Downie 1966) Stover et Evitt 1978

(Fig. 27A–F, Fig. 85I)

1966 *Thalassiphora patula* n. sp.; Williams & Downie (1966c), p.235, pl.26, fig.81978 *Thalassiphora patula* (Williams et Downie 1966) emend.; Stover & Evitt (1978), p.287**Material.** Rare specimens occur in samples Kns7, Kns8, Kns10, Kns12, Kns13, Kns21, Kns22, Kns25 and Kns26; a single specimen occur in sample KnsH2 (the Hieroglyphic beds).**Description.** Cyst camocavate, with endocyst subspherical, with smooth, thin and nonperforated endophragm. Pericyst of irregular shapes consisting of highly incomplete, commonly fenestrate periphragm, which seems to be connected to endocyst by thickened portions in shape of massive “processes”.*Thalassiphora pelagica* (Eisenack 1954) Eisenack et Gocht 1960

(Fig. 43G–K, Fig. 41A–E, Fig. 42B–D, Fig. 85D)

1954 *Pterospermopsis pelagica* n. sp.; Eisenack (1954), p. 71, pl. 12, figs. 17–181960 *Thalassiphora pelagica* comb. nov.; Eisenack & Gocht (1960), p. 513–5141981 *Thalassiphora pelagica* (Eisenack 1954) emend.; Benedek & Gocht (1981), p. 59–61**Material.** Moderately common to common in all samples except of Kns8, Kns11, Kns24, Kns27 and Kns30 where this species is missing; moderately common in sample KnsH2 (the Hieroglyphic beds).**Description.** Cyst camocavate, with subspherical endocyst, with thin and smooth to finely granular endophragm, which remains in contact with pericyst dorsally. Periphragm massive, densely irregularly fenestrate, which makes a spongy structure.*Thalassiphora reticulata* Morgenroth 1966

(Fig. 42F)

1966 *Thalassiphora reticulata* n. sp.; Morgenroth (1966b), p. 6–7, pl.2, figs. 1–2

**Material.** A single specimen was found in sample Kns13.

**Description.** Cyst camocavate, with endocyst subspherical, composed of thin, smooth, homogenous endophragm. Periphragm perforated by regular net of oval, ellipsoidal to polygonal openings.

### Subfamily **GYNYAULACOIDEAE** (Autonym)

#### Genus *Achomosphaera* Evitt 1963

Type species: *Achomosphaera ramulifera* (Deflandre 1937) Evitt 1963

1963 *Achomosphaera* n. gen.; Evitt (1963), p. 163

#### *Achomosphaera alcicornu* (Eisenack 1954) Davey et Williams 1966

(Fig. 44N, Fig. 85E)

1954 *Hystichosphaeridium alcicornu* n. sp.; Eisenack (1954), p. 65, pl. 10, figs. 1–2

1966 *Achomosphaera alcicornu* comb. nov.; Davey & Williams (1966a), p. 50

**Material.** This species occurs almost exclusively in pale-coloured marl: its single specimens were found in samples Kns3, Kns24, more frequent in sample Kns30; a single specimen occurs in dark-coloured mudstone (Kns32); a single specimen also was found in sample KnsH2 (the Hieroglyphic beds).

**Description.** Cyst chorate, subspherical, large, with thick and smooth wall. Processes gonol, massive, long, smooth, and distally trifurcate. No parasutural ridges or septa. Archaeopyle precingular.

#### *Achomosphaera crassipellis* (Deflandre et Cookson 1955) Stover et Evitt 1978

(Fig. 44P, Fig. 85B)

1955 *Hystichosphaera crassipellis* n. sp.; Deflandre & Cookson (1955), p. 265, pl. 6, figs. 2–3; text-fig. 20

1978 *Achomosphaera crassipellis* comb. nov.; Stover & Evitt (1978), p. 138

**Material.** Single specimen in samples Kns6 and Kns21; another specimen was found in the Hieroglyphic beds (KnsH2).

**Description.** Cyst subspherical, with densely reticulate, rather thin wall. Tiny lumina of the same size, densely distributed make a perforate appearance of the wall. Gonol processes show the same type of reticulation. No parasutural ridges at process bases. Archaeopyle precingular.

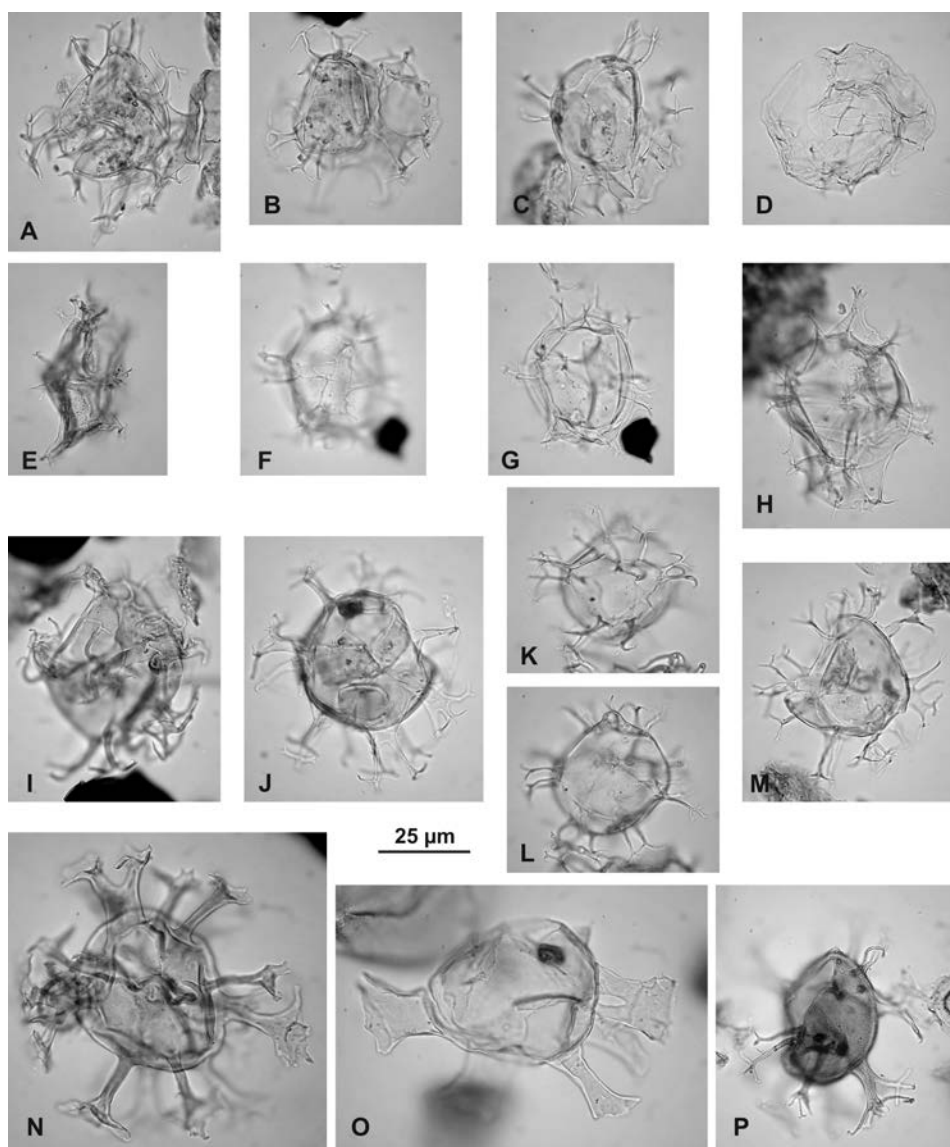
**Discussion.** This species has relatively thin cyst wall. Deflandre & Cookson (1955) described *A. crassipellis* as having a very thick reticulate membrane.

#### *Achomosphaera ramulifera* (Deflandre 1937) Evitt 1963

(Fig. 44I–M)

1937 *Hystichosphaeridium ramuliferum* n. sp.; Deflandre (1937), p. 74, pl. 14, figs. 5–6; pl. 17, fig. 10





**Fig. 44.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Hystrichostrogylon membraniphorum* (Kns5); **B** – *Hystrichostrogylon membraniphorum* (Kns5); **C** – *Hystrichostrogylon membraniphorum* (Kns11); **D** – *Hystrichostrogylon coninckii* (Kns12); **E** – *Rotnestia borussica* (Kns4); **F**, **G** – *Spiniferites ramosus* – specimen with relatively large endocyst, indistinct parasutural ridges and short and slender gonial processes (same specimen, various foci; Kns8); **H** – *Rotnestia borussica* (Kns5); **I** – *Achomosphaera ramulifera* (Kns2); **J** – *Achomosphaera ramulifera* (Kns8); **K**, **L** – *Achomosphaera ramulifera* (same specimen, various foci; Kns13); **M** – *Achomosphaera ramulifera* (Kns12); **N** – *Achomosphaera alvicornu* (Kns3); **O** – *Achomosphaera* sp. *sensu* Brinkhuis (1992; Kns7); **P** – *Achomosphaera crassipellis* (Kns6)

1963 *Achomosphaera ramulifera* comb. nov.; Evitt (1963), p. 163

**Material.** This species is rare (Kns2, Kns6, Kns21, Kns29, Kns30 and Kns33) to moderately common (samples Kns8, Kns12, Kns13, Kns17–20, Kns22 and Kns32); moderately common in sample KnsH2 (the Hieroglyphic beds).

**Description.** Cyst spherical to slightly subspherical, with smooth to shagreenate periphragm. Processes gonal and intergonal, neighbouring processes frequently arising from common ridges. However, generally neither ridges nor septa are present. Processes generally of two types: thin, solid or broader, membranaceous. Archaeopyle precingular.

*Achomosphaera* sp. *sensu* Brinkhuis 1992

(Fig. 44O)

1992 *Achomosphaera* sp.; Brinkhuis (1992), p. 96, pl. II, figs. 1–3; pl. XX, figs. 10–11

**Material.** A single specimen occurs in sample Kns6.

**Description.** Cyst chorate, large, subspherical, with infrequent large, hollow, broad processes, with distally expanded margins. These margins are presumably trifurcated although due to their broadness it is difficult to estimate. Number of processes is also not certain: the studied specimen possesses six processes, but it seems to be damaged, incomplete. Periphragm smooth, no parasutural ridges.

Genus *Corrudinium* Stover et Evitt 1978

Type species: *Corrudinium incompositum* (Drugg 1970) Stover et Evitt 1978

1978 *Corrudinium* n. gen.; Stover & Evitt (1978), p. 148–149

*Corrudinium incompositum* (Drugg 1970) Stover et Evitt 1978

(Fig. 45J–S)

1970 *Gonyaulacysta incomposita* n. sp.; Drugg, (1970), p. 810–811, figs. 1E–O, 2A

1978 *Corrudinium incompositum* comb. nov.; Stover et Evitt (1978), p. 149

**Material.** Rare specimens occur in samples Kns1, Kns8, Kns10–13 and Kns27.

**Description.** Cyst small, ovoidal, proximate, with paratabulation expresses by low, smooth ridges of equal height and smooth margins. Paraplate areas covered by incomplete additional ridges, occasionally united with parasutural ones, and regularly spaced, isolated tubercles. Archaeopyle precingular.

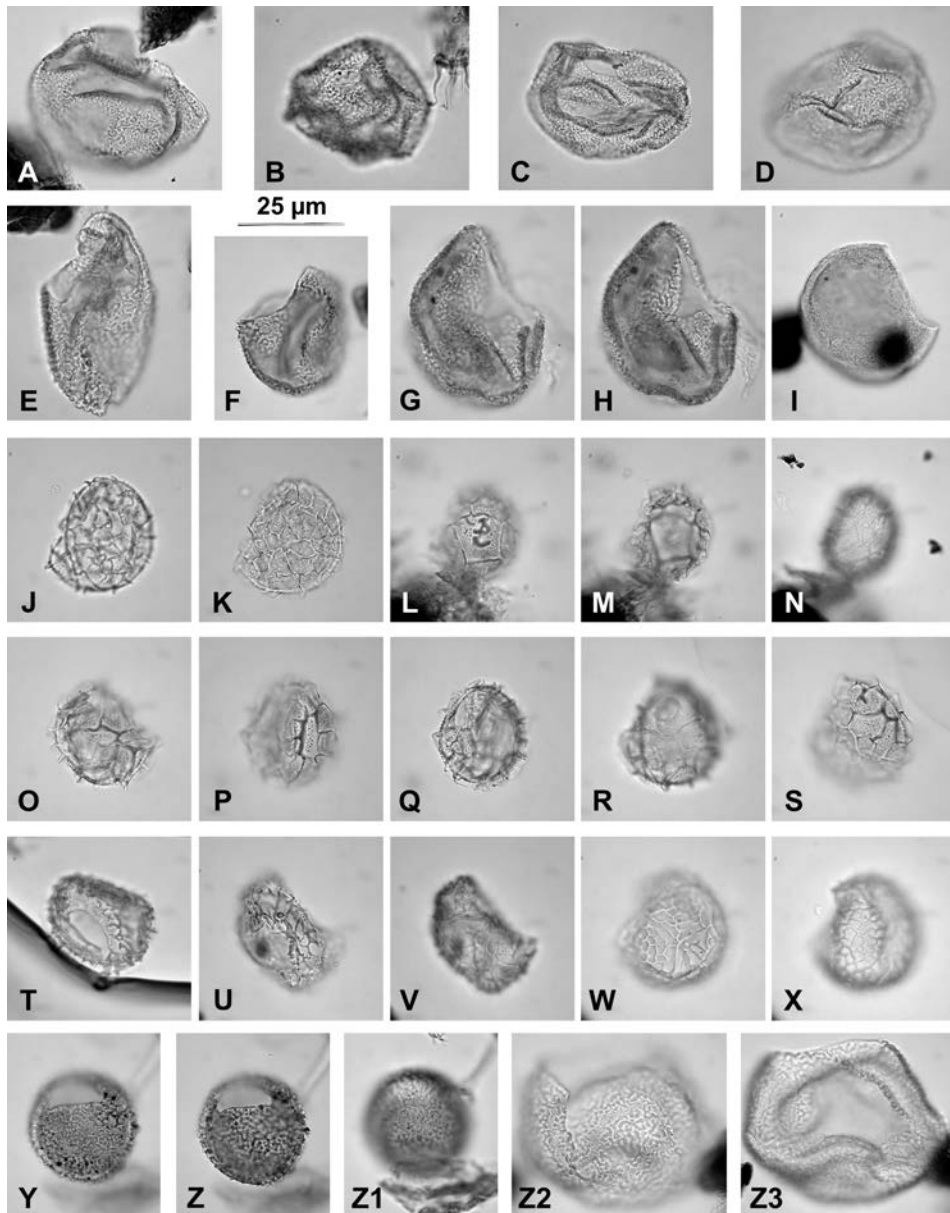
*Corrudinium?* sp. A *sensu* Gedl 2005

(Fig. 32Q, R)

2005 *Corrudinium?* sp. A; Gedl (2005a), p. 36, pl. 4, figs. 6–9, 11, 12

**Material.** A single specimen in sample Kns4.

**Description.** Cyst large, subspherical, proximate, with thick wall. Periphragm



covered with tubercles and elongated ribs, which form noncontinuous positive relief, mainly in shape of low ridges. Their arrangement is irregular, some of them seem to form concentric forms, the others are rather linear. Archaeopyle pre-cingular.

**Discussion.** This species was described for the first time by Gedl (2005a) from Upper Eocene [uppermost Eocene? – for age determination of these strata see Leszczyński & Malata (2002), and Gedl & Leszczyński (2005)] strata of the

**Fig. 45.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Pyxidinospis* sp. *C sensu* Gedl 2005 (Kns3); **B** – *Pyxidinospis* sp. *C sensu* Gedl 2005 (Kns3); **C** – *Pyxidinospis* sp. *C sensu* Gedl 2005 (Kns4); **D** – *Pyxidinospis* sp. *C sensu* Gedl 2005 (Kns4); **E** – *Pyxidinospis* sp. *C sensu* Gedl 2005 (Kns13); **F** – *Pyxidinospis* sp. *C sensu* Gedl 2005 (Kns3); **G, H** – *Pyxidinospis* sp. *C sensu* Gedl 2005 (same specimen, various foci; Kns13); **I** – *Tectatodinium pellitum* (Kns8); **J, K** – *Corrudinium incompositum* (same specimen, various foci; Kns10); **L–N** – *Corrudinium incompositum* (same specimen, various foci; Kns8); **O** – *Corrudinium incompositum* (Kns8); **P, Q** – *Corrudinium incompositum* (same specimen, various foci; Kns8); **R, S** – *Corrudinium incompositum* (same specimen, various foci; Kns8); **T** – *Cerebrocysta bartonensis* (Kns10); **U, V** – *Cerebrocysta bartonensis* (same specimen, various foci; Kns11); **W, X** – *Cerebrocysta bartonensis* (same specimen, various foci; Kns12); **Y–Z1** – *Cerebrocysta* cf. *bartonensis* (same specimen, various foci; Kns25); **Z2, Z3** – *Pyxidinospis* sp. *C sensu* Gedl 2005 (same specimen, various foci; Kns17)

Magura Nappe (Polish Flysch Carpathians). It was questionably assigned to the genus *Corrudinium*. Single, rather poorly preserved specimen from Koniusza does not allow further taxonomical allocation of this species.

### Genus *Hystrichostrogylon* Agelopoulos 1964

Type species: *Hystrichostrogylon membraniphorum* Agelopoulos 1964

1964 *Hystrichostrogylon* n. gen.; Agelopoulos (1964), p. 673–674

1978 *Hystrichostrogylon* Agelopoulos 1964 emend.; Stover & Evitt (1978), p. 164

### *Hystrichostrogylon coninckii* Heilmann-Clausen 1985

(Fig. 44D)

1994 *Hystrichostrogylon coninckii* n. sp.; Heilmann-Clausen in Thomsen & Heilmann-Clausen (1985), p. 353, 355, pl. 7, figs. 9–12; text-figs. 10A–F

**Material.** A single specimen in sample Kns12.

**Description.** Periphragm and endophragm very thin and smooth, both layers in contact dorsally. Faint and very indistinct parasutural ridges present on endocyst and pericyst (especially in paracingular position). Processes gonial and intergonal short and slender.

### *Hystrichostrogylon membraniphorum* Agelopoulos 1964

(Fig. 44A–C)

1964 *Hystrichostrogylon membraniphorum* n. sp.; Agelopoulos (1964), p. 674; text-figs. 1–2

**Material.** Rare specimens in samples Kns5, Kns11, Kns17, Kns23 and Kns25.

**Description.** Central body subspherical, with smooth cyst wall and gonial processes long, distally trifurcate, with farther tiny further branching. No ridges connecting processes proximally. Antapical and dorsal processes united by a broad periphragm. Archaeopyle paracingular.



Genus *Impagidinium* Stover et Evitt 1978Type species: *Impagidinium dispersitum* (Cookson et Eisenack 1965) Stover et Evitt 19781978 *Impagidinium* n. gen.; Stover & Evitt (1978), p. 165–166*Impagidinium aculeatum* (Wall 1967) Lentin et Williams 1981

(Fig. 46A–F, K)

1967 *Leptodinium aculeatum* n. sp.; Wall (1967), p. 104–105, pl. 14, figs. 18–19; text-figs. 3C–D1981 *Impagidinium aculeatum* comb. nov.; Lentin & Williams (1981), p. 153**Material.** A single specimen occurs in sample Kns3, more frequent in sample Kns8.**Description.** Cyst thin-walled, small, ovoidal, with very thin parasutural septa slender, of unequal height: concavities of septa proceed into distinct acuminate corners, presumably in gonal positions.*Impagidinium maculatum* (Cookson et Eisenack 1961) Stover et Evitt 1978

(Fig. 46Q, R)

1961 *Leptodinium maculatum* n. sp.; Cookson & Eisenack (1961), p. 40, pl. 2, figs. 5–61978 *Impagidinium maculatum* comb. nov.; Stover & Evitt (1978), p. 166**Material.** Single specimens in samples Kns8 and Kns27.**Description.** Cyst subspherical, murochorate, with parasutural ridges hyalinous, very low, smooth, of equal height, with smooth margins. Intratabular area covered with uniformly, densely distributed, flat, isolated tubercules.*Impagidinium margaritifera* (Cookson et Eisenack 1960) Stover et Evitt 1978

(Fig. 46S)

1960 *Gonyaulax margaritifera* n. sp.; Cookson & Eisenack (1960), p. 5–6, pl. 2, figs. 1–2; text-fig. 1

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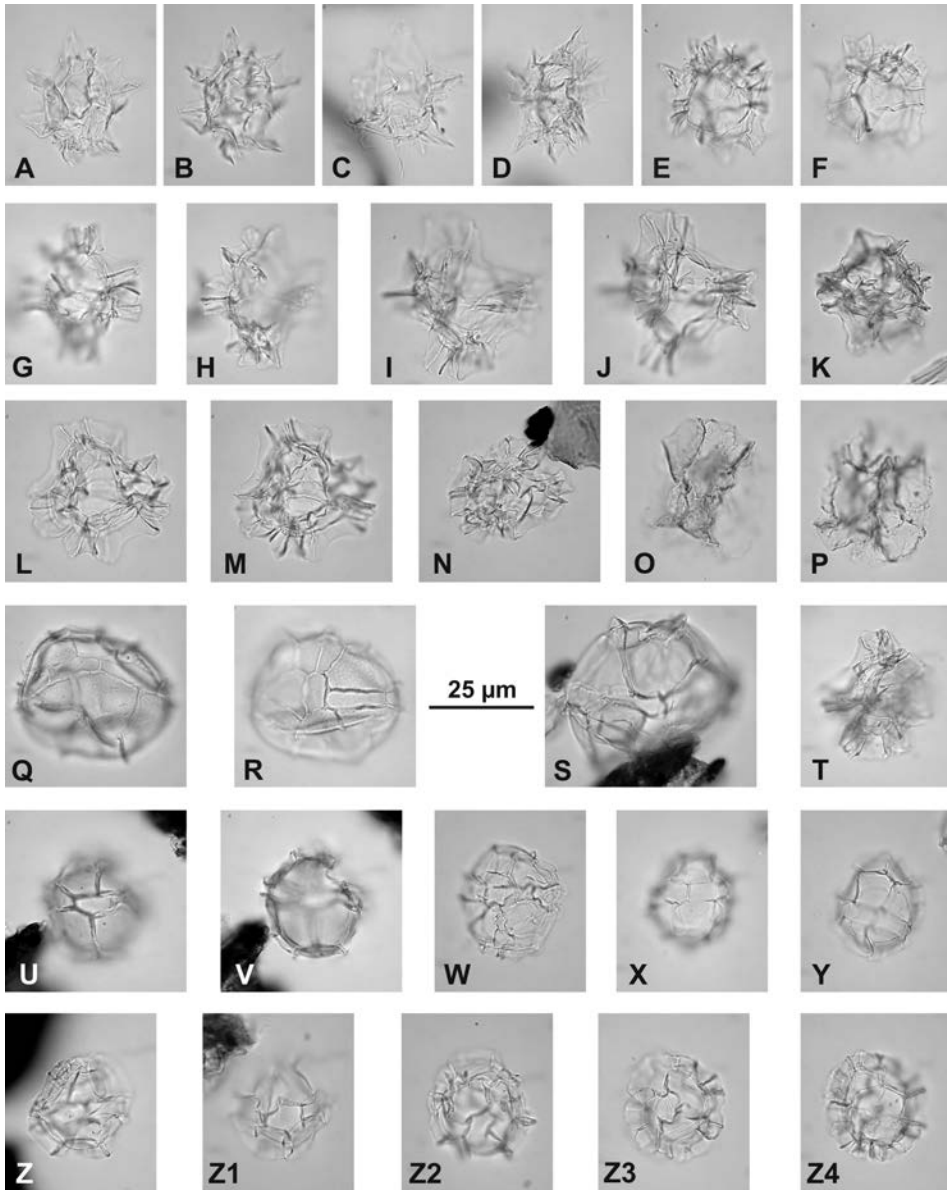
**Fig. 46.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Impagidinium aculeatum* (same specimen, various foci; Kns8); **C** – *Impagidinium aculeatum* (Kns8); **D** – *Impagidinium aculeatum* (Kns8); **E, F** – *Impagidinium aculeatum* (same specimen, various foci; Kns8); **G, H** – *Impagidinium* sp. C sensu Gedl 2005 (same specimen, various foci; Kns8); **I, J** – *Impagidinium* sp. C sensu Gedl 2005 (same specimen, various foci; Kns8); **K** – *Impagidinium aculeatum* (Kns6); **L, M** – *Impagidinium* sp. C sensu Gedl 2005 (same specimen, various foci; Kns8); **N** – *Impagidinium* sp. B sensu Gedl 2005 (Kns10); **O, P** – *Impagidinium velorum* (same specimen, various foci; Kns3); **Q, R** – *Impagidinium maculatum* (same specimen, various foci; Kns8); **S** – *Impagidinium margaritifera* (Kns8); **T** – *Impagidinium* sp. C sensu Gedl 2005 (Kns10); **U, V** – *Impagidinium* sp. A sensu Gedl 2005 (same specimen, various foci; Kns13); **W** – *Impagidinium* sp. A sensu Gedl 2005 (Kns8); **X, Y** – *Impagidinium* sp. A sensu Gedl 2005 (same specimen, various foci; Kns8); **Z** – *Impagidinium* sp. A sensu Gedl 2005 (Kns8); **Z1** – *Impagidinium* sp. A sensu Gedl 2005 (Kns8); **Z2** – *Impagidinium* sp. A sensu Gedl 2005 (Kns8); **Z3–4** – *Impagidinium* sp. B sensu Gedl 2005 (same specimen, various foci; Kns8)

1978 *Impagidinium margaritifera* comb. nov.; Stover & Evitt (1978), p. 166

**Material.** A single specimen in sample Kns8.

**Description.** Cyst spherical, murochorate, with thin and smooth wall. Parasutural ridges indistinct, of equal height, with smooth margins. Bases of ridges perforated with a single row of densely and regularly spaced holes.

**Discussion.** Perforations by *I. margaritifera* described by Cookson & Eisenack (1960) were much thicker than in this specimen, which possesses dense but delicate



perforations; they are also of the same size, so they never form ledges like in the type material.

*Impagidinium velorum* Bujak 1984

(Fig. 46O, P)

1984 *Impagidinium velorum* n. sp.; Bujak (1984), p. 187–188, pl. 2, figs. 13–16

**Material.** A single species occurs in sample Kns3.

**Description.** Cyst small, ovoidal, murochorate, with hyalinous, very thin, smooth wall and very high septa, whose height equals central body diameter.

*Impagidinium* sp. A *sensu* Gedl 2005

(Fig. 46U–Z2)

?1989 *Impagidinium* sp. cf. *I.* sp. B; Head & Norris (1989), p. 547, pl. 10, fig. 4

?2000 *Impagidinium* sp. cf. *I.* sp. B of Head & Norris (1989); Gedl (2000), p. 193, fig. 100d–f,  
m

2005 *Impagidinium* sp. A; Gedl (2005a), p. 36, pl. 8, figs 1–6

**Material.** Single specimens in samples Kns2, Kns4, Kns18, Kns23–25, Kns27 and Kns28; more common in samples Kns3, Kns5, Kns8 and Kns10. Most frequent is sample Kns13.

**Description.** Cyst subspherical to slightly ellipsoidal, murochorate, with thin and smooth wall. Parasutural ridges low, of equal height, delicate, smooth, with smooth margins.

**Remarks.** This taxon closely resembles a specimen of *Impagidinium* sp. cf. *I.* sp. B figured but not described by Head & Norris (1989; p. 547, pl. 10, fig. 4).

*Impagidinium* sp. B *sensu* Gedl 2005

(Fig. 46N, Z3, Z4, Fig. 51A, B)

2005 *Impagidinium* sp. B; Gedl (2005a), p. 36, pl. 8, figs 7–12, 14

**Material.** Single specimens were found in samples Kns8 and Kns10.

**Description.** Cyst small, subspherical, murochorate, with smooth periphragm and relatively thick and high parasutural ridges. Ridges of equal height or slightly depressed, their distal margins smooth or finely irregular (Fig. 46Z3, Z4). Ridges junctions show clear thickenings. Archaeopyle precingular.

*Impagidinium* sp. C *sensu* Gedl 2005

(Fig. 46G–J, L, M, T, Fig. 51D)

2005 *Impagidinium* sp. C; Gedl (2005a), p. 37, pl. 8, fig. 13

**Material.** Rare specimens occur in samples Kns8, Kns10, Kns25 and Kns27. A single specimen was found in sample Kns4 during SEM observation.

**Description.** Cyst ellipsoidal, murochorate, with pear-shaped central body (hypo-

cyst broader but lower than epicyst). Parasutural ridges high, relatively massive, deeply concave being the highest in paracingular and polar areas. This gives a characteristic cruciform shape of the cyst.

Genus *Nematosphaeropsis* Deflandre et Cookson 1955

Type species: *Nematosphaeropsis balcombiana* Deflandre et Cookson 1955

- 1955 *Nematosphaeropsis* n. gen.; Deflandre & Cookson (1955), p. 268  
 1966 *Nematosphaeropsis* Deflandre et Cookson 1955 emend.; Williams & Downie (1966c), p. 222  
 1988 *Nematosphaeropsis* Deflandre et Cookson 1955 emend.; Wrenn (1988), p. 137

*Nematosphaeropsis labyrinthus* (Ostenfeld 1903) Reid 1974

(Fig. 47A–D)

- 1903 *Pterosperma labyrinthea* n. sp.; Ostenfeld (1903), p. 578, fig. 127  
 1974 *Nematosphaeropsis labyrinthus* comb. nov.; Reid (1974), p. 592

**Material.** Single specimens occur in samples Kns5 and Kns8.

**Description.** Cyst small, subspherical to slightly ellipsoidal, chorate, trabeculate, with thin, solid, relatively long, mainly trifurcate processes. Central body smooth. Processes connected distally by delicate trabeculae.

*Nematosphaeropsis lemniscata* Bujak 1984

(Fig. 47E–H, Y)

- 1984 *Nematosphaeropsis lemniscata* n. sp.; Bujak (1984), p. 189–190, pl. 3, figs. 5–7  
 1988 *Nematosphaeropsis lemniscata* Bujak 1984 emend.; Wrenn (1988), p. 142, 144

**Material.** Rare specimens occur in samples Kns7 and Kns8.

**Description.** Cyst subspherical, chorate, trabeculate, with smooth wall; no proximal parasutural developed. Processes relatively short (usually less than central body diameter), hollow, massive, distally trifurcate, proceed into ectophragmal network. These trabeculae of equal width, massive, seem to be u-shaped in transverse cross-sections.

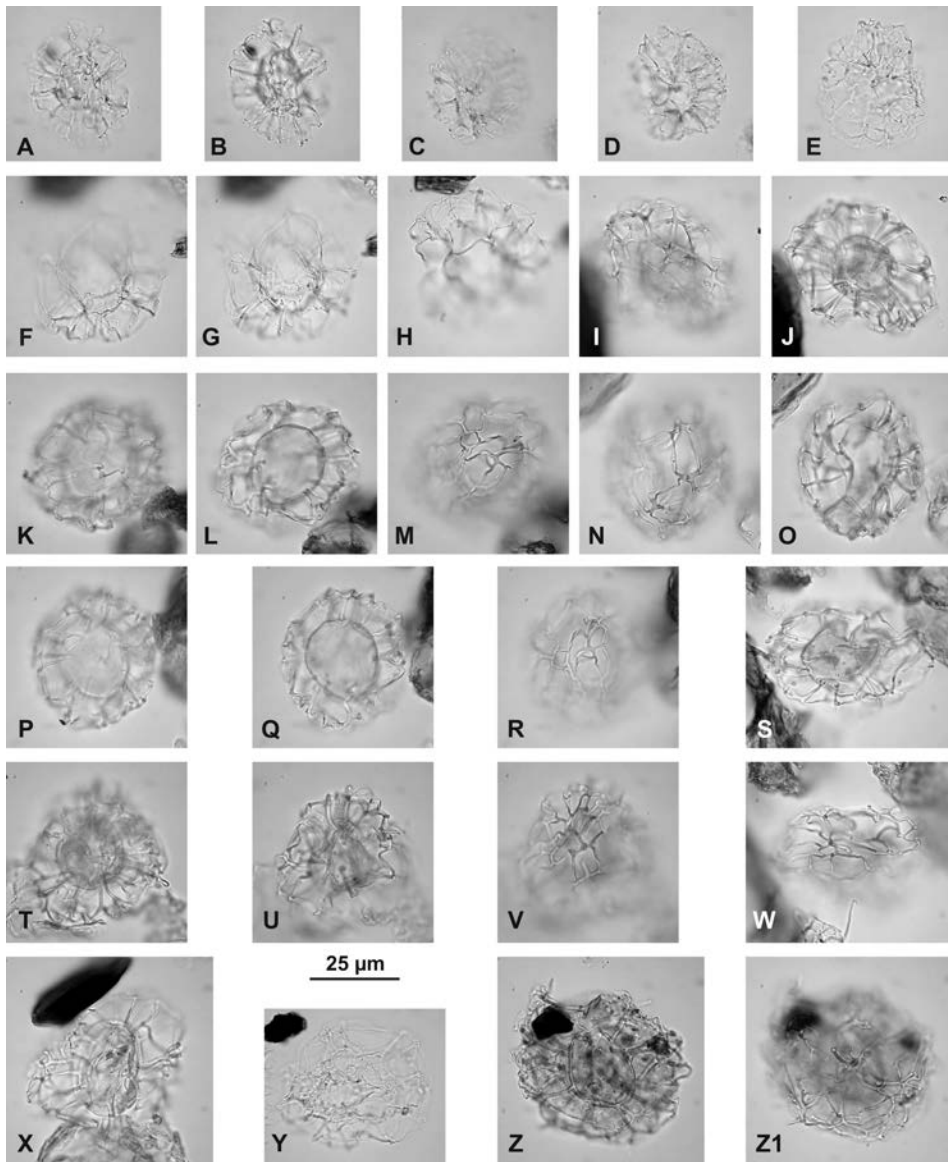
*Nematosphaeropsis reticulensis* (Pastiels 1948) Sarjeant 1986

(Fig. 47I–X, Z–Z1)

- 1948 *Cannosphaeropsis reticulensis* n. sp.; Pastiels (1948), p. 49, pl. 5, figs. 7–10  
 1986 *Nematosphaeropsis reticulensis* comb. nov.; Sarjeant (1986), p. 9  
 1986 *Nematosphaeropsis reticulensis* (Pastiels 1948) emend.; Sarjeant (1986), p. 9, 11

**Material.** Single specimens occur in samples Kns5–7, Kns9, Kns12; common in sample Kns13.

**Description.** Cyst subspherical, trabeculate, with thick and smooth wall. Long (up to the central body diameter), solid, mainly trifurcate processes distally connected by solid trabeculae. Additional spines present at distal process terminations.



**Fig. 47.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Nematosphaeropsis labyrinthus* (same specimen, various foci; Kns8); **C, D** – *Nematosphaeropsis labyrinthus* (same specimen, various foci; Kns8); **E** – *Nematosphaeropsis lemniscata* (Kns8); **F–H** – *Nematosphaeropsis lemniscata* (same specimen, various foci; Kns7); **I, J** – *Nematosphaeropsis reticulensis* (same specimen, various foci; Kns13); **K–M** – *Nematosphaeropsis reticulensis* (same specimen, various foci; Kns13); **N, O** – *Nematosphaeropsis reticulensis* (same specimen, various foci; Kns13); **P–R** – *Nematosphaeropsis reticulensis* (same specimen, various foci; Kns13); **S, W** – *Nematosphaeropsis reticulensis* (same specimen, various foci; Kns7); **T–V** – *Nematosphaeropsis reticulensis* (same specimen, various foci; Kns5); **X** – *Nematosphaeropsis reticulensis* (Kns12); **Y** – *Nematosphaeropsis lemniscata* (Kns8); **Z–Z1** – *Nematosphaeropsis reticulensis* (same specimen, various foci; Kns6)



Genus *Pentadinium* Gerlach 1961Type species: *Pentadinium laticinctum* Gerlach 1961

- 1961 *Pentadinium* n. gen.; Gerlach (1961), p. 164–165  
 1982 *Pentadinium* Gerlach 1961 emend.; Benedek, Gocht & Sarjeant (1982), p. 266–268

*Pentadinium laticinctum* Gerlach 1961

(Fig. 32P, U, V–X, Fig. 51F, G)

- 1961 *Pentadinium laticinctum* n. sp.; Gerlach (1961), p. 165–166, pl. 26, figs. 5–6; text-figs. 6–7  
 1982 *Pentadinium laticinctum* Gerlach 1961 emend.; Benedek, Gocht & Sarjeant (1982), p. 268–272

**Material.** Rare specimens occur in samples Kns5, Kns8, Kns10, Kns13, Kns17, Kns22, Kns25, Kns30 and Kns33.

**Description.** Cyst suturocavate, proximochorate, with subspherical to polygonal (in lateral view) endocyst. Pericyst appressed, except of parasutural areas where it forms high septa of inconsistent width at their bases. Endophragm thicker than periphragm, brain-like, with vermiculate structure (Fig. 51G). Periphragm densely, but finely, granular.

Genus *Rottnestia* Cookson et Eisenack 1961Type species: *Rottnestia borussica* (Eisenack 1954) Cookson et Eisenack 1961

- 1961 *Rottnestia* n. gen.; Cookson & Eisenack (1961), p. 40, 42

*Rottnestia borussica* (Eisenack 1954) Cookson et Eisenack 1961

(Fig. 44E, H)

- 1954 *Hystrichosphaera borussica* n. sp.; Eisenack (1954), p. 62, pl. 9, figs. 5–7  
 1961 *Rottnestia borussica* comb. nov.; Cookson & Eisenack (1961), p. 42

**Material.** Single specimens occur in samples Kns4 and Kns5.

**Description.** Cyst elongated, bicavate, with spherical to subspherical endocyst. Pericyst wide at hypocyst, whereas it forms an apical horn on epicyst. Two specimens found at Koniusza differ by periphragm, which is thicker and coarser granular on specimen from sample Kns4 (Fig. 44E), while specimen from sample Kns5 posses a much thinner and finer granular one (Fig. 44H). Short and slender gonial trifurcate processes arise from low and indistinct parasutural ridges.

Genus *Spiniferites* Mantell 1850Type species: *Spiniferites ramosus* (Ehrenberg 1838) Mantell 1854

- 1850 *Spiniferites* n. gen.; Mantell (1850), p. 191  
 1970 *Spiniferites* Mantell 1850 emend.; Sarjeant (1970), p. 75

*Spiniferites pseudofurcatus* (Klumpp 1953) Sarjeant 1970

(Fig. 48O)

- 1953 *Hystrichokibotium pseudofurcatum* n. sp.; Klumpp (1953), p. 388, pl. 16, figs. 12–14  
 1970 *Spiniferites pseudofurcatus* comb. nov.; Sarjeant (1970), p. 76  
 1981 *Spiniferites pseudofurcatus* (Klumpp 1953) emend.; Sarjeant (1981), p. 108–109

**Material.** Rare specimens of this species occur in samples Kns1, Kns2, Kns5, Kns8, Kns11, Kns13, Kns14, Kns18, Kns19, Kns24, Kns25, Kns27, Kns31 and Kns32; more frequent in samples Kns7, Kns17, Kns20 and Kns33.

**Description.** Cyst subspherical, relatively large, chorate, with thick and smooth endophragm and thinner periphragm that occasionally bears irregular small granules. The latter forms low parasutural ridges that connect proximally gonol processes. Processes hollow, commonly massive, distally trifurcate. Process length up to the half of the central body diameter.

*Spiniferites ramosus* (Ehrenberg 1838) Mantell 1854

(Fig. 44F, G, Fig. 48A–N, P, Q, Fig. 49A–L, Fig. 84B)

- 1838 *Xanthidium ramosum* n. sp.; Ehrenberg (1838), pl. 1, figs. 1–2, 5  
 1854 *Spiniferites ramosus* comb. nov.; Mantell (1854), p. 239

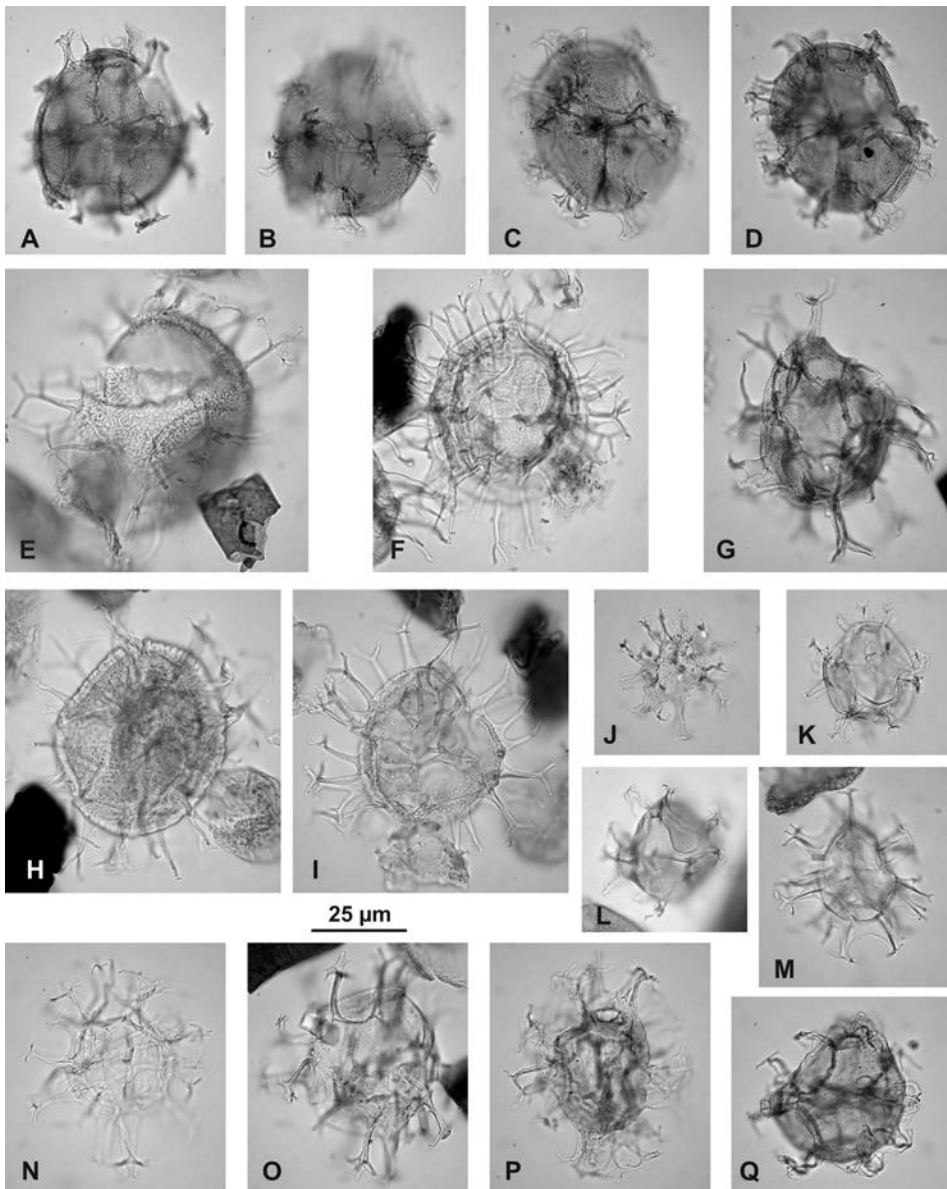
**Material.** Very frequent species occurs in all samples, being dominating in some samples; rare in samples Kns1, Kns2 and Kns26.

**Description.** Cyst spherical to subspherical and slightly ellipsoidal, chorate, with thin and smooth to finely granular both cyst layers. Periphragm forms parasutural ridges, usually low and indistinct, with gonol (and intergonol at some specimens) processes, which are solid or hollow. Their length is variable but constant at particular specimen; they terminate with bifurcations (intergonol) and trifurcations. Archaeopyle precingular.

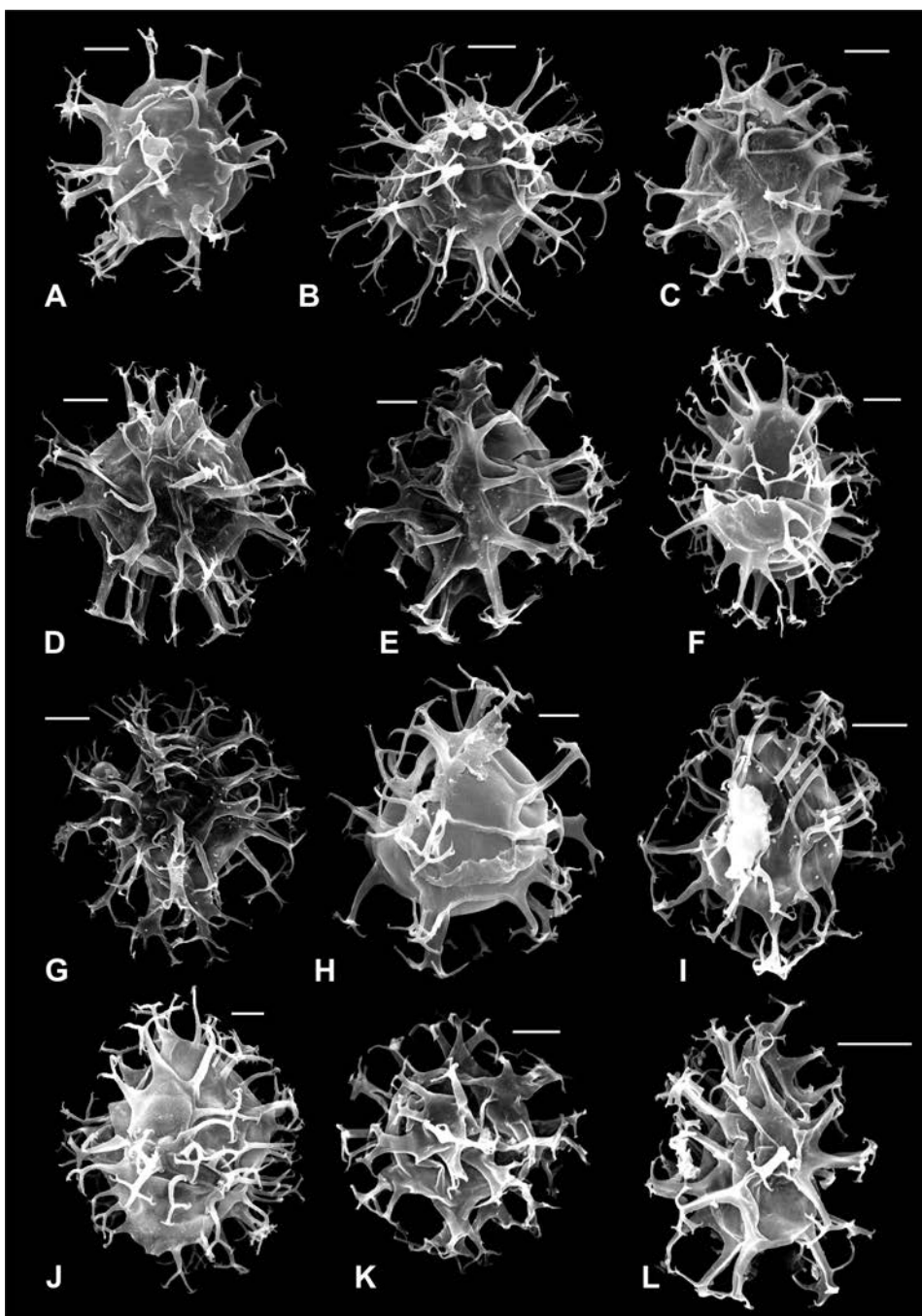
**Discussion.** This species shows a considerable variability of morphology, mainly related to presence or absence of intergonol processes; their length and height of parasutural ridges, which commonly are high close to process, are much lower in between processes (Fig. 48A–N, P, Q). Lesser diversity is visible in endophragm structure: majority of specimens attributed here to *Spiniferites ramosus* have relatively thin and smooth endophragm. Only very rare specimens have thick endophragm (Fig. 48E, H); one of them presumably represents *Spiniferites ramosus* subsp. *meandriiformis* [single specimen occurs in sample Kns7; this subspecies, although described from Upper Cretaceous strata by Corradini (1973), was reported from Eocene by Gocht (1969)].

Genus *Tectatodinium* Wall 1967Type species: *Tectatodinium pellitum* Wall 1967

- 1967 *Tectatodinium* n. gen.; Wall (1967), p. 112–113  
 1994 *Tectatodinium* Wall 1967 emend.; Head (1994), p. 306



**Fig. 48.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Spiniferites ramosus* (same specimen, various foci; Kns3); **C, D** – *Spiniferites ramosus* (same specimen, various foci; Kns3); **E** – *Spiniferites ramosus* (Kns6); **F** – *Spiniferites ramosus* (Kns6); **G** – *Spiniferites ramosus* (Kns3); **H** – *Spiniferites ramosus* (Kns12); **I** – *Spiniferites ramosus* (Kns12); **J** – *Spiniferites ramosus* (Kns4); **K** – *Spiniferites ramosus* (Kns4); **L** – *Spiniferites ramosus* (Kns1); **M** – *Spiniferites ramosus* (Kns13); **N** – *Spiniferites ramosus* (Kns8); **O** – *Spiniferites pseudofurcatus* (Kns1); **P** – *Spiniferites ramosus* (Kns3); **Q** – *Spiniferites ramosus* (Kns4)



**Fig. 49.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10  $\mu\text{m}$ ). **A–L** – *Spiniferites ramosus* (**A–G**: Kns8; **H–L**: Kns5)

*Tectatodinium pellitum* Wall 1967

(Fig. 45I, Fig. 51H–K, Fig. 52U–Y)

1967 *Tectatodinium pellitum* n. sp.; Wall (1967), p. 113, pl. 16, figs. 11–121994 *Tectatodinium pellitum* Wall 1967 emend.; Head (1994), p. 308, 310

**Material.** Single specimens occur in samples representing pale-coloured marl (Kns3, Kns4, Kns8, Kns10 and Kns25); a single specimen occurs in dark-coloured mudstone (Kns17).

**Description.** Cyst spherical, proximate, with wall composed of thin inner layer and much thicker outer layer, consisting of spongy luxuriae, which are very densely packed making a felty appearance (Fig. 51I, K). The outer cyst surface is relatively smooth, no isolated fibres appear. Archaeopyle precingular, operculum free.

Genus *Ynezidinium* Lucas-Clark et Helenes 2000Type species: *Ynezidinium malloyii* Lucas-Clark et Helenes 20002000 *Ynezidinium* n. gen.; Lucas-Clark & Helenes (2000), p. 114–115*Ynezidinium brevisulcatum* (Michoux 1985) Lucas-Clark et Helenes 2000

(Fig. 50A–K, Fig. 51C)

1985 *Impagidinium brevisulcatum* n. sp.; Michoux (1985), p. 144–145, pl. 1, figs. 9–11; text-fig. 42000 *Ynezidinium brevisulcatum* comb. nov.; Lucas-Clark & Helenes (2000), p. 118

**Material.** Rare to moderately common specimens occur in samples representing pale-coloured marl (Kns3, Kns8, Kns10, Kns24, Kns25 and Kns27); a single specimen occurs in sample representing dark-coloured mudstone (Kns13).

**Description.** Cyst large, spherical to ellipsoidal, murochorate. Endophragm and periphragm smooth, the latter is relatively thin forming low parasutural ridges of equal height. Parasutural ridges by some specimens show slightly sinusoidal course (e.g., Fig. 50G); they can be smooth or striated at their bases (Fig. 50H, J).

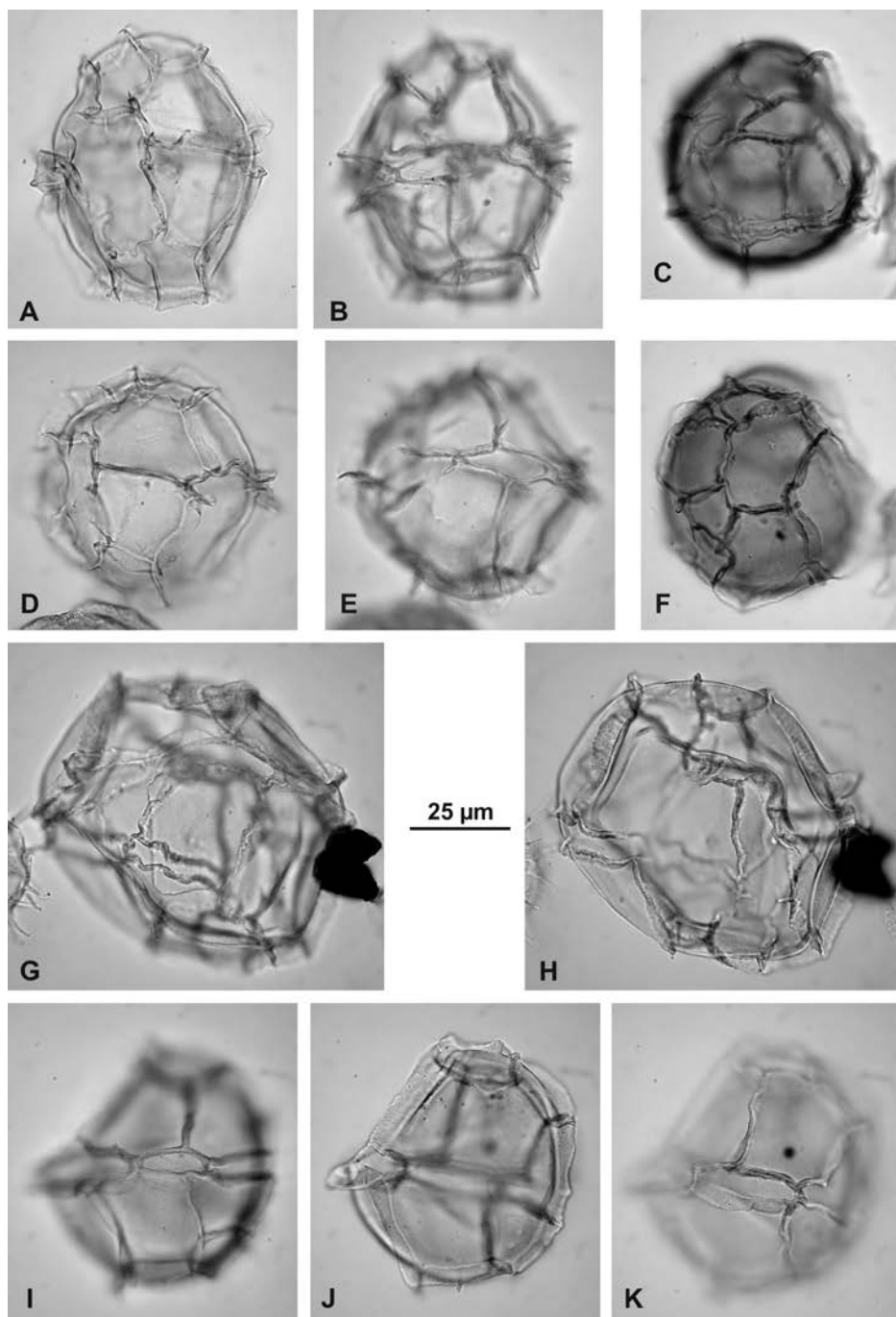
Subfamily **UNCERTAIN**Genus *Escharisphaeridia* Erkmen and Sarjeant 1980Type species: *Escharisphaeridia pocockii* (Sarjeant 1968) Erkmen et Sarjeant 19801980 *Escharisphaeridia* n. gen.; Erkmen & Sarjeant (1980), p. 62–63*Escharisphaeridia* sp.

(Fig. 16D, E, Fig. 53B)

**Material.** Two specimens in sample Kns8, a single specimen in sample Kns28.

**Description.** Autocyst spherical, thin-walled, with finely shagreenate autophragm. No indication of paratabulation except of apical archaeopyle, margin of which is well visible at both specimens.





**Fig. 50.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–K** – *Ynezidinium brevisulcatum* (**A, B**: same specimen, various foci; Kns10; **C, F**: same specimen, various foci; Kns3; **D, E**: same specimen, various foci; Kns8; **G, H**: same specimen, various foci; Kns8; **I–K**: same specimen, various foci; Kns8)

Genus *Fibrocysta* Stover et Evitt 1978Type species: *Fibrocysta bipolaris* (Cookson et Eisenack 1965) Stover et Evitt 19781978 *Fibrocysta* n. gen.; Stover & Evitt (1978), p. 155*Fibrocysta axialis* (Eisenack 1965) Stover et Evitt 1978

(Fig. 40C, F, I–K)

1965 *Cordosphaeridium axialis* n. sp.; Eisenack (1965), p. 150, pl. 15, figs. 1–41978 *Fibrocysta axialis* comb. nov.; Stover & Evitt (1978), p. 155

**Material.** Single specimens occur in samples Kns2, Kns3, Kns6, Kns8, Kns13, Kns18, Kns21, Kns22, Kns28, Kns29 and Kns33.

**Description.** Cyst ovoidal, with nontabular, solid, relatively long, slender, distally slightly expanded processes, except of apical one, which is remarkably larger, distally terminating with two parallel branched tips. Cyst wall smooth (Fig. 40C) to finely granular (Fig. 40F, K). Archaeopyle precingular.

*Fibrocysta radiata* (Morgenroth 1966) Stover et Evitt 1978

(Fig. 40G, H)

1966 *Lanternosphaeridium radiatum* n. sp.; Morgenroth (1966a), p. 37–38, pl. 10, figs. 7–91978 *Fibrocysta radiata* comb. nov.; Stover & Evitt (1978), p. 155

**Material.** A single specimen was found in sample Kns3.

**Description.** Cyst ovoidal, with wall consisting of relatively thick fibrous structure, which passes into lower parts of processes giving a fibrous appearance; higher parts of processes smooth. Processes nontabular, slender, solid, distally narrowing, terminated with tiny expandings. Antapical process larger, tubiform, hollow, fibrous at the base, distally open. Apical protrusion present; presumably, this could be the base of a broken apical process (Fig. 40G). Archaeopyle precingular.

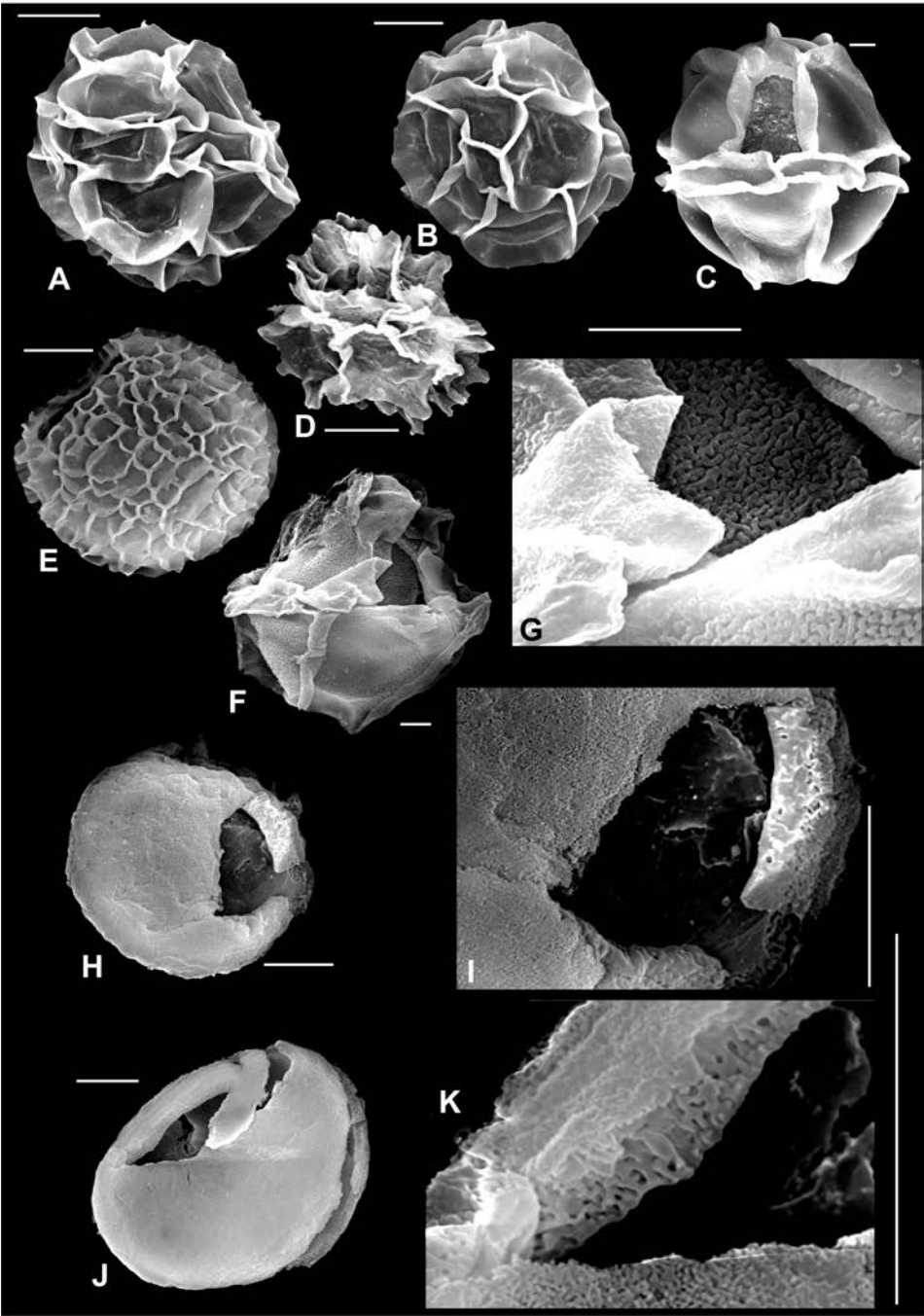
*Fibrocysta* sp. A

(Fig. 40D, E)

**Material.** A single specimen was found in sample Kns2.

**Description.** Cyst presumably ovoidal to subspherical (broken specimen does not allow precise determination of the cyst shape), with finely fibrous wall and short, massive, solid, fibrous processes, distally slightly expanded, with seccate margin. Apical process considerably larger, longer, terminated with three very short, massive branches (Fig. 40D).

Genus *Melitasphaeridium* Harland et Hill 1979Type species: *Melitasphaeridium choanophorum* (Deflandre et Cookson 1955) Harland et Hill1979 *Melitasphaeridium* n. gen.; Harland & Hill (1979), p. 38–39



**Fig. 51.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10 µm). **A, B** – *Impagidinium* sp. B *sensu* Gedl 2005 (both specimens Kns8); **C** – *Ynezidinium brevisulcatum* (Kns8; note scale bar length, which shows large dimension of this species compared to other illustrated *Impagidinium* specimens); **D** – *Impagidinium* sp. C *sensu* Gedl 2005 (Kns4); **E** – *Cerebrocysta bartonensis* (Kns5); **F, G** – *Pentadinium laticinctum* (Kns5; F: complete specimen; G: detail showing periphragm and endophragm structures); **H, I** – *Tectatodinium pellitum* (Kns8; H: complete specimen; I: detail showing outer surface structure and a cross-section through the cyst wall); **J, K** – *Tectatodinium pellitum* (Kns8; J: complete specimen; K: detail showing outer surface structure and a cross-section through the cyst wall)

*Melitasphaeridium asterium* (Eaton 1976) Bujak, Downie,  
Eaton et Williams 1980

(Fig. 34L, M)

1976 *Hystrichosphaeridium asterium* n. sp.; Eaton (1976), p. 273, pl. 11, figs. 7–10

1980 *Melitasphaeridium asterium* comb. nov.; Bujak, Downie, Eaton & Williams (1980), p. 30

**Material.** Single specimens occur in samples Kns5, Kns6 and Kns17.

**Description.** Cyst small, spherical, chorate, with smooth and thin wall bearing long, thin, straight, cylindrical processes that distally expand into circular platforms with aculeate margins. Archaeopyle precingular.

*Melitasphaeridium pseudorecurvatum* (Morgenroth 1966) Bujak, Downie,  
Eaton et Williams 1980

(Fig. 34A–K, R, Fig. 53J, Fig. 84C)

1966 *Hystrichosphaeridium pseudorecurvatum* n. sp.; Morgenroth (1966a), p. 30–31, pl. 8, figs. 5–6

1980 *Melitasphaeridium pseudorecurvatum* comb. nov.; Bujak, Downie, Eaton & Williams (1980), p. 30

**Material.** Single specimens occur in samples Kns4–6, Kns12, Kns20, Kns23 and Kns28; more frequent in sample Kns8, Kns17–19, Kns25 and Kns27, very frequent in sample Kns10; relatively common in the Hieroglyphic beds (KnsH2).

**Description.** Cyst small, spherical, chorate, with smooth and very thin wall. Over 20 processes thin, hollow, smooth, cylindrical, distally aculeate. Serrations long and slender, radially arranged. Archaeopyle precingular.

Genus *Pyxidinopsis* Habib 1976

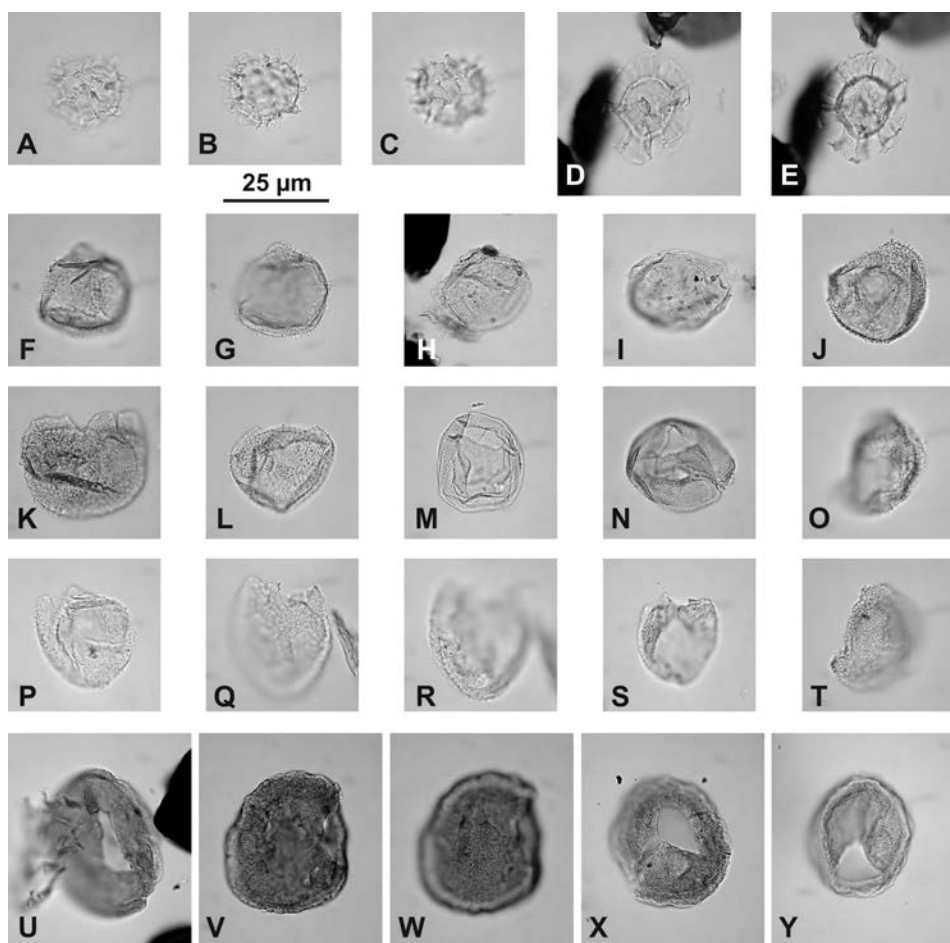
Type species: *Pyxidinopsis challengerensis* Habib 1976

1976 *Pyxidinopsis* n. gen.; Habib (1976), p. 382

*Pyxidinopsis* sp. A *sensu* Gedl 2005

(Fig. 52N)

2005 *Pyxidinopsis* sp. A; Gedl (2005), p. 37–38, fig. 3.104; pl. 10, fig. 10



**Fig. 52.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–C** – Genus et species indeterminated A (same specimen, various foci; Kns8); **D, E** – Genus et species indeterminated B (same specimen, various foci; Kns12); **F, G** – *Batiacasphaera hirsuta* (same specimen, various foci; Kns4); **H** – *Batiacasphaera micropapillata* (Kns6); **I** – *Batiacasphaera micropapillata* (Kns6); **J** – *Batiacasphaera* sp. B (Kns8); **K** – *Batiacasphaera* sp. B (Kns3); **L** – *Batiacasphaera* sp. A (Kns3); **M** – *Batiacasphaera micropapillata* (Kns4); **N** – *Pyxidinospis* sp. A sensu Gedl 2005 (Kns3); **O, T** – *Batiacasphaera* sp. C (same specimen, various foci; Kns8); **P** – *Batiacasphaera?* *reticulata* (Kns11); **Q, R** – *Batiacasphaera?* *reticulata* (same specimen, various foci; Kns11); **S** – *Batiacasphaera?* *reticulata* (Kns11); **U** – *Tectatodinium pellitum* (Kns3); **V, W** – *Tectatodinium pellitum* (same specimen, various foci; Kns4); **X** – *Tectatodinium pellitum* (Kns10); **Y** – *Tectatodinium pellitum* (Kns10)

**Material.** A single specimen occurs in sample Kns3.

**Description.** Cyst small, proximate, wrinkled, presumably subspherical. Cyst wall covered with tiny, densely packed elongated granules, which commonly fuse with each other giving rise to finely vermiculate pattern. No other forms of positive relief. No indication of paratabulation except of precingular archaeopyle.



*Pyxidinospis* sp. C *sensu* Gedl 2005

(Fig. 45A–H, Z1, Z2)

2005 *Pyxidinospis* sp. C; Gedl (2005), p. 38, fig. 3.114; pl. 10, fig. 13

**Material.** Rare specimens occur in samples Kns3, Kns4, Kns8, Kns13, Kns17 and Kns22.

**Description.** Cyst subspherical, commonly wrinkled. Cyst wall covered by anastomosing rugulate pattern composed of tiny ribs. Ribs connected to each other but their distribution is rather loose and smooth areas separate these wrinkles. Archaeopyle precingular. No indication of paratabulation except of archaeopyle.

**Discussion.** This species differs from *Pyxidinospis* sp. A by larger dimension, thicker cyst wall and generally coarser sculpture of its morphology. Ornamentation by *Pyxidinospis* sp. A is much finer, and positive elements (wrinkles) are densely packed, whereas by *Pyxidinospis* sp. C it is much thicker, and anastomosing ribs are commonly separated by smooth areas.

## Family AREOLIGERACEAE Evitt 1963

Genus *Adnatosphaeridium* Williams et Downie 1966Type species: *Adnatosphaeridium vittatum* Williams et Downie 19661966 *Adnatosphaeridium* n. gen.; Williams & Downie (1966c), p. 2151990 *Adnatosphaeridium* Williams et Downie 1966 emend.; Stancliffe & Sarjeant (1990), p. 199–200*Adnatosphaeridium multispinosum* Williams et Downie 1966

(Fig. 20D, E, Fig. 54A–C, E, F, K–P, Fig. 85G)

1966 *Adnatosphaeridium multispinosum* n. sp.; Williams & Downie (1966c), p. 216–217, pl. 24, fig. 5

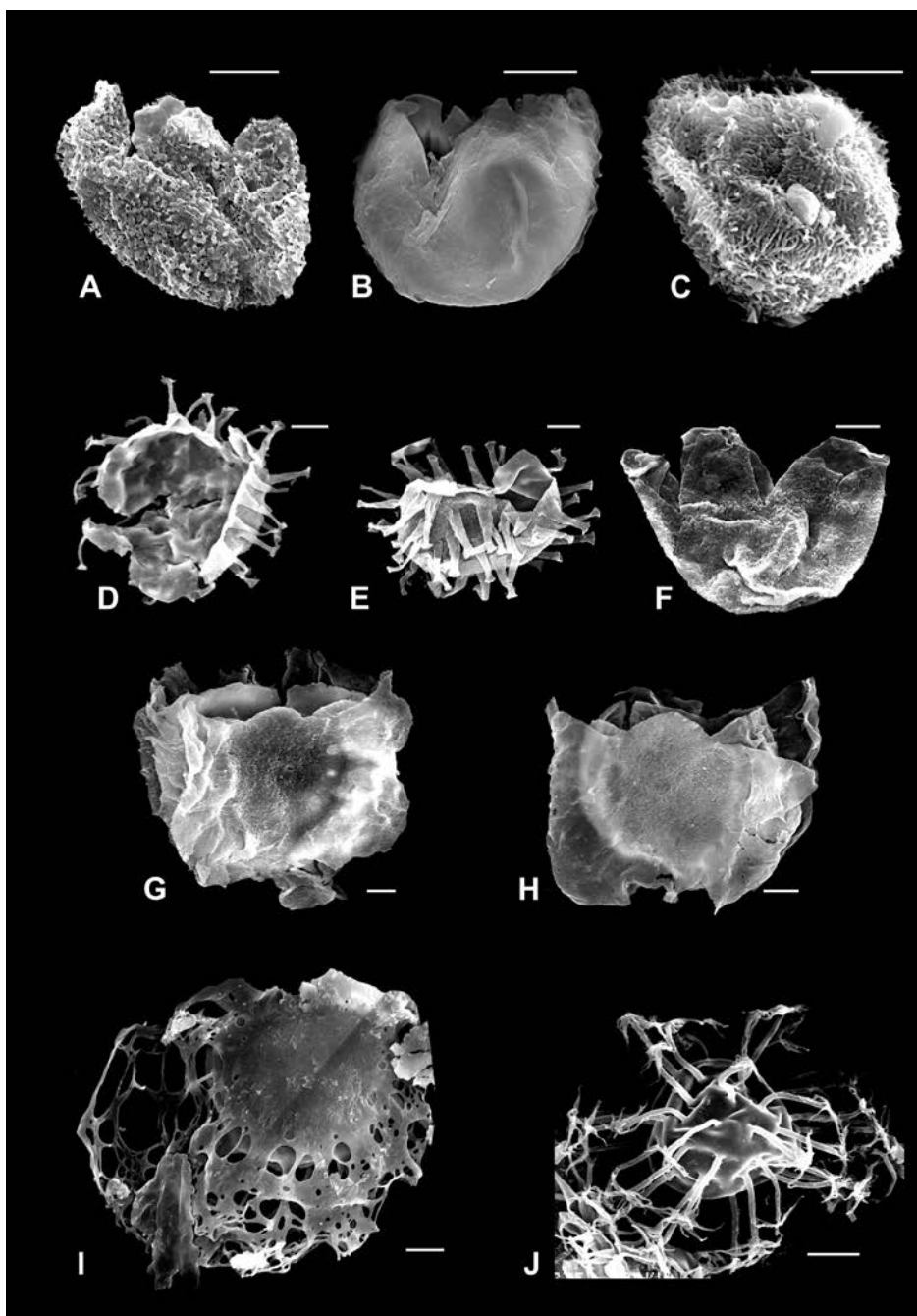
**Material.** Single to rare specimens in samples: Kns2, Kns3, Kns5–7, Kns10–13, Kns17, Kns19–22, Kns26, Kns28, Kns29, Kns32 and Kns33; moderately common in sample KnsH2 (the Hieroglyphic beds).

**Description.** Cyst subspherical to slightly lenticular; some specimens show well developed antapical lobation (Fig. 54A–C). Endophragm usually finely to strongly granular (e.g., Fig. 20E, Fig. 54A, B, N), some specimens have smooth endophragm (Fig. 54E, F). Periphragm smooth and thin, forms numerous thin, smooth, long and slender processes, which distally branch to form trabeculae. Short acuminate spines present on some specimens' trabeculae. Archaeopyle apical; typical zigzag margin present.

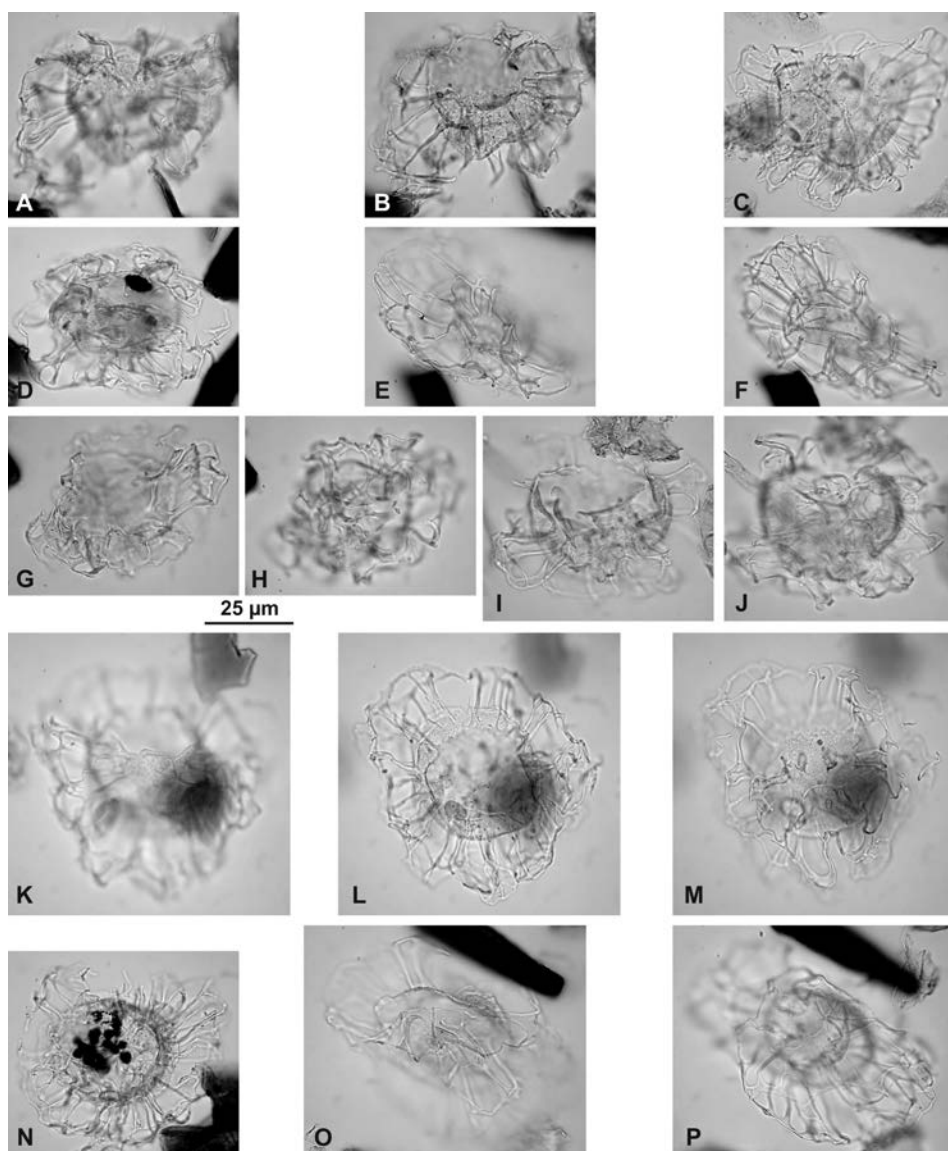
*Adnatosphaeridium vittatum* Williams et Downie 1966

(Fig. 54D, G–J)

1966 *Adnatosphaeridium vittatum* n. sp.; Williams & Downie (1966c), p. 215, pl. 24, figs. 3, 7; text-fig. 56



**Fig. 53.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10  $\mu\text{m}$ ). **A** – *Batiacasphaera* sp. B (Kns8); **B** – *Escharisphaeridia* sp. (Kns8); **C** – *Batiacasphaera* sp. C (Kns4); **D** – *Polysphaeridium* *zoharyi* (Kns3); **E** – *Dapsilidinium* *pseudocolligerum* (Kns5); **F** – *Batiacasphaera* sp. B (Kns5); **G, H** – *Membranophoridium* *aspinatum* (G: Kns8; H: Kns5); **I** – *Glaphyrocysta* *semitecta* (Kns5); **J** – *Melitasphaeridium* *pseudorecurvatum* (Kns8)



**Fig. 54.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Adnatosphaeridium multispinosum* (same specimen, various foci; Kns6); **C** – *Adnatosphaeridium multispinosum* (Kns6); **D** – *Adnatosphaeridium vittatum* (Kns2); **E, F** – *Adnatosphaeridium multispinosum* (same specimen, various foci; Kns2); **G, H** – *Adnatosphaeridium vittatum* (same specimen, various foci; Kns3); **I, J** – *Adnatosphaeridium vittatum* (same specimen, various foci; Kns5); **K–M** – *Adnatosphaeridium multispinosum* (same specimen, various foci; Kns7); **N** – *Adnatosphaeridium multispinosum* (Kns6); **O, P** – *Adnatosphaeridium multispinosum* (same specimen, various foci; Kns12)

**Material.** Single specimens occur in samples Kns2, Kns3 and Kns5; a single specimen occurs in sample KnsH2 (the Hieroglyphic beds).

**Description.** Cyst subspherical with granular endophragm and smooth periphragm. The latter forms two types of processes: numerous, thin and slender processes that distally are united by trabeculae, and rare massive, wide, hollow buccinate processes, distally open with highly expanded margins; the latter seems to be interconnected to the trabeculae. Archaeopyle apical.

### Genus *Areoligera* Lejeune-Carpentier 1938

Type species *Areoligera senonensis* Lejeune-Carpentier 1938

1938 *Areoligera* n. gen.; Lejeune-Carpentier (1938), p. B164

1966 *Areoligera* Lejeune-Carpentier 1938 emend.; Williams & Downie (1966c), p. 227–228

#### *Areoligera coronata* (O. Wetzel 1933) Lejeune-Carpentier 1938

(Fig. 55M, N, Fig. 84A, L)

1933 *Hystriosphæra penicillata* forma *coronata* n. sp.; O. Wetzel (1933), p. 41, pl. 4, fig. 17

1938 *Areoligera coronata* comb. nov.; Lejeune-Carpentier (1938), p. B170

**Material.** A single specimen was found in sample Kns8; two specimens were found in the Hieroglyphic beds (KnsH2).

**Description.** Cyst large, subspherical, with thick and smooth wall bearing intratabular process complexes, except of mid-dorsal and mid-ventral areas. Complexes arise from circular ridges; their bases are developed as membranous or solid processes – both forms fuse higher forming irregularly perforated structure. Process complexes distally terminate with irregularly digitate distal margins. Archaeopyle apical with typical zigzag margin.

#### *Areoligera* cf. *medusettiformis* sensu Eaton 1976

(Fig. 84F, G)

1971 *Areoligera* cf. *medusettiformis*; Eaton (1976), p. 242–246, fig. 7C, pl. 3, fig. 7

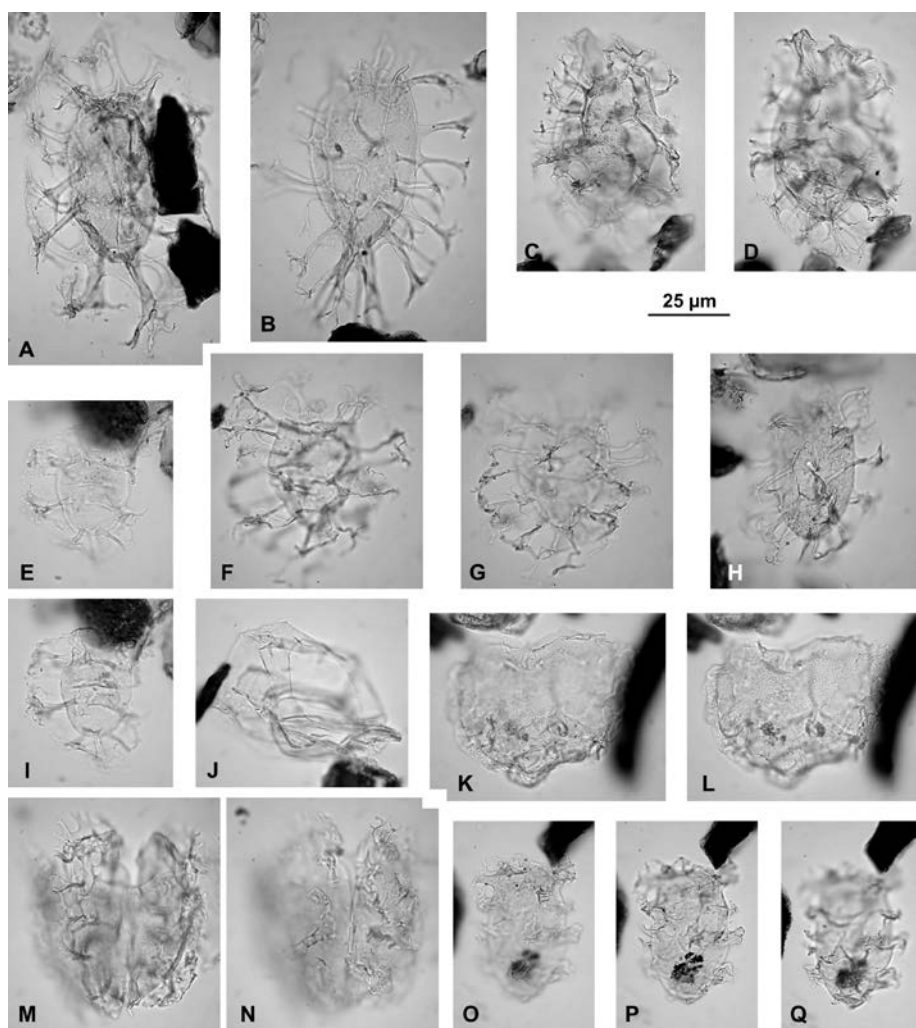
**Material.** Rare specimens occur in samples Kns23 and Kns25. Very frequent occurrence of this species is noted from the Hieroglyphic beds (sample KnsH2).

**Description.** Cyst subspherical to lenticular, with intratabular process complexes developed on whole cyst surface, including the mid-dorsal and mid-ventral areas. Process complexes similar to *A. coronata*, but less massive and membranous. Archaeopyle apical with typical zigzag margin.

### Genus *Glaphyrocysta* Stover et Evitt 1978

Type species: *Glaphyrocysta retiintexta* (Cookson 1965) Stover et Evitt 1978

1978 *Glaphyrocysta* n. gen.; Stover & Evitt (1978), p. 49–50



**Fig. 55.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Distatodinium ellipticum* (Kns6); **B** – *Distatodinium ellipticum* (Kns5); **C**, **D** – *Distatodinium virgatum* (same specimen, various foci; Kns13); **E**, **I** – *Distatodinium craterum* (same specimen, various foci; Kns7); **F**, **G** – *Distatodinium ellipticum* small specimen (same specimen, various foci; Kns12); **H** – *Distatodinium ellipticum* small specimen (Kns12); **J** – ?*Thalassiphora dynamica* (Kns5); **K**, **L** – *Membrano-phoridium aspinatum* specimen with low membranes (same specimen, various foci; Kns13); **M**, **N** – *Areoligera coronata* (same specimen, various foci; Kns8); **O**–**Q** – *Distatodinium* ?*scariosum* (same specimen, various foci; Kns17)

*Glaphyrocysta exuberans* (Deflandre et Cookson 1955 ex Eaton 1976)  
Stover et Evitt 1978

(Fig. 84J, M)

- |      |  |
|------|--|
| 1955 | <i>Cyclonephelium exuberans</i> n. sp.; Deflandre & Cookson (1955), p. 285 (nom. nud.) |
| 1971 | <i>Cyclonephelium exuberans</i> ; Eaton (1976), p. 255–256                             |
| 1978 | <i>Glaphyrocysta exuberans</i> comb. nov., Stover & Evitt (1978), p. 50.               |



**Material.** Rare specimens, commonly poorly preserved occur in samples Kns4, Kns6, Kns18–20, Kns22 and Kns29; two specimens have been found in the Hieroglyphic beds (KnsH2).

**Description.** Cyst lenticular with relatively long solid and thin processes, which distally are interconnected forming anastomosing and membranaceous structure. Archaeopyle apical with zigzag margin.

*Glaphyrocysta intricata* (Eaton 1971) Stover et Evitt 1978

(Fig. 56M, P–T)

1971 *Cyclonephelium intricatum* n. sp.; Eaton (1971), p. 365, pl. 4, figs. 8–10

1978 *Glaphyrocysta intricata* comb. nov.; Stover & Evitt (1978), p. 50

**Material.** Rare specimens occur in samples Kns5, Kns7, Kns11 and Kns12.

**Description.** Cyst lenticular with foveolate wall. Solid, thin, smooth processes arranged in annulate complexes grouped in peripheral areas – mid-ventral and mid-dorsal areas free of processes. Processes in particular complexes connected in two-third of height by simple branches or membranaceous structures; their distal margins digitate. Process complexes connected distally by simple trabeculae. Archaeopyle apical with zigzag margin.

*Glaphyrocysta semitecta* Bujak (1980) Lentin et Williams 1981

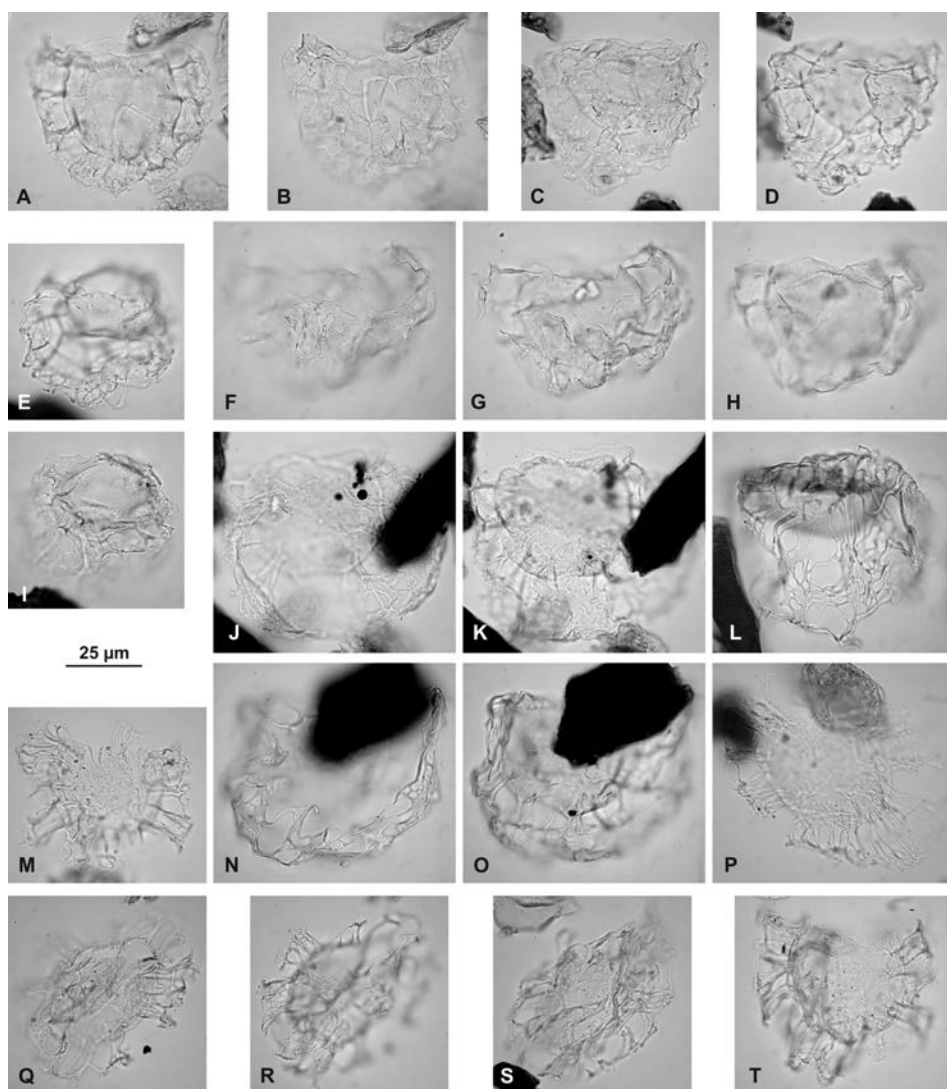
(Fig. 53I, Fig. 57A–P, Fig. 56A–L, N, O)

1980 *Cyclonephelium semitectum* n. sp.; Bujak in Bujak, Downie, Eaton & Williams (1980), p. 46, 48, 50, pl. 14, figs. 2–9; text-fig. 13

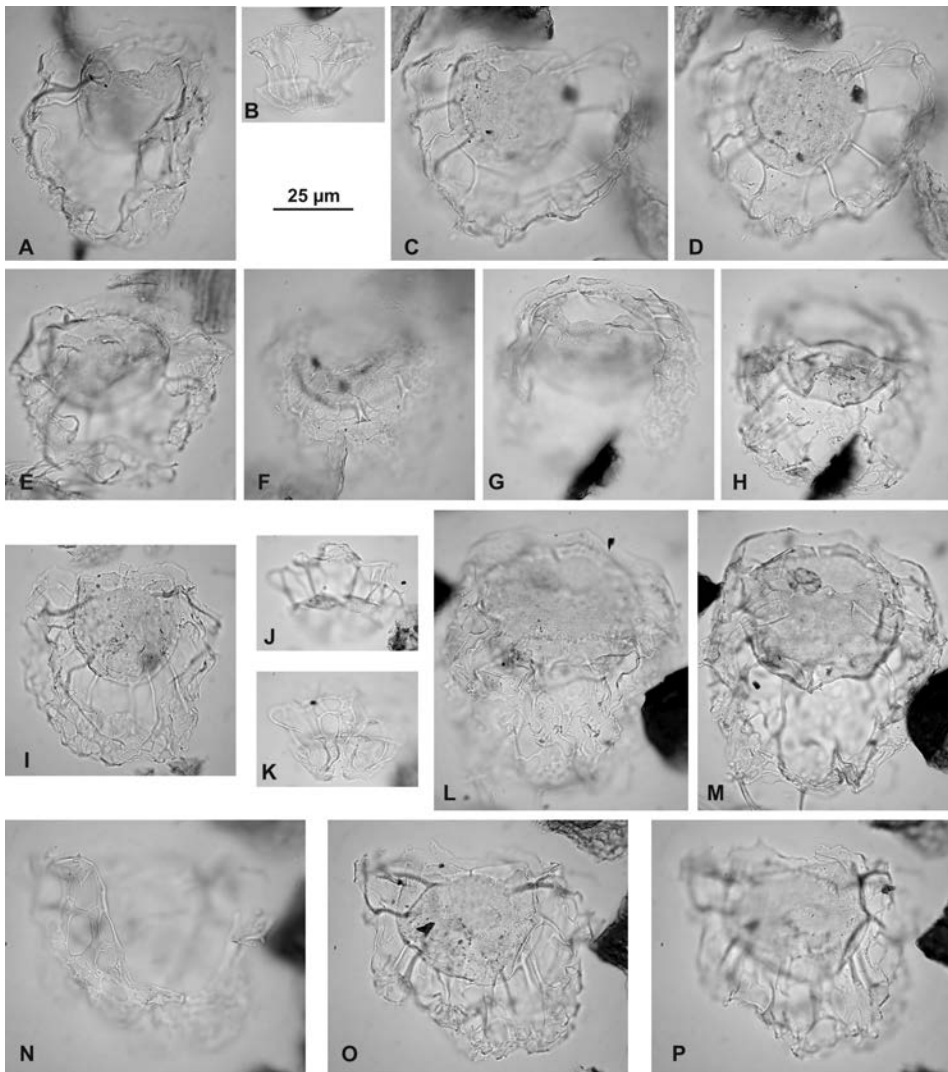
1981 *Glaphyrocysta semitecta* comb. nov.; Lentin & Williams (1981), p. 111

**Material.** Rare to moderately common, occurs mainly in samples representing dark-coloured mudstone; absent in samples Kns4, Kns10, Kns14 and Kns23–28; very frequent in sample Kns32.

**Description.** Central body subspherical, lenticular, with finely granular cyst wall. Antapical lobation present on some specimens (Fig. 57O, P, Fig. 56K, O). Solid and slender processes arise from cyst peripheries being absent from mid-dorsal and mid-ventral areas. Additional rare processes arise from precingular paraplates of the ventral side. Processes distally united by hyalinous, smooth membrane, which show a variable degree of perforation: from small, numerous holes to large openings. Membrane remains fully developed on the dorsal side where it is in contact with the central body; it is absent from the ventral side (e.g., Fig. 57 L, M, N–P). Processes and membrane length variable: the shortest at precingular and postcingular areas, usually become much longer toward the antapex (Fig. 57A, I, L, M, Fig. 56C–E, L). This length difference is usually rather high, but some specimens show it considerably smaller, even to specimens with all processes of the same height (e.g., Fig. 56A, B). Archaeopyle apical with zigzag margin. Operculum free, frequently found as isolated specimens (Fig. 57B, J, K).



**Fig. 56.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Glaphyrocysta semitecta* (same specimen, various foci; Kns12); **C, D** – *Glaphyrocysta semitecta* (same specimen, various foci; Kns12); **E, I** – *Glaphyrocysta semitecta* (same specimen, various foci; Kns13); **F–H** – *Glaphyrocysta semitecta* (same specimen, various foci; Kns11); **J, K** – *Glaphyrocysta semitecta* (same specimen, various foci; Kns2); **L** – *Glaphyrocysta semitecta* (Kns1); **M** – *Glaphyrocysta intricata* (Kns11); **N, O** – *Glaphyrocysta semitecta* (same specimen, various foci; Kns1); **P** – *Glaphyrocysta intricata* (Kns7); **Q, R** – *Glaphyrocysta intricata* (same specimen, various foci; Kns5); **S** – *Glaphyrocysta intricata* (Kns7); **T** – *Glaphyrocysta intricata* (Kns11)



**Fig. 57.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–P** – *Glaphyrocysta semitecta* (A: Kns13; B: isolated operculum, Kns1; C, D: same specimen, various foci, Kns12; E, F: same specimen, various foci, Kns5; G, H: same specimen, various foci, Kns6; I: Kns7; J, K: same specimen of isolated operculum, various foci, Kns6; L, M: same specimen, various foci, Kns6; N–P: same specimen, various foci, Kns13)

### Genus *Membranophoridium* Gerlach 1961

Type species: *Membranophoridium aspinatum* Gerlach 1961

1961 *Membranophoridium* n. gen.; Gerlach (1961), p. 198

1978 *Membranophoridium* Gerlach 1961 emend.; Stover & Evitt (1978), p. 64–65

*Membranophoridium aspinatum* Gerlach 1961

(Fig. 53G, H, Fig. 55K, L, Fig. 58A–L, Fig. 59D, Fig. 60A)

196 *Membranophoridium aspinatum* n. sp.; Gerlach (1961), p. 199–201, pl. 21, figs. 7–8

**Material.** Single or rare specimens occur in samples Kns1, Kns3–5, Kns7–10, Kns12, Kns13, Kns17–21, Kns28, Kns29 and Kns33.

**Description.** Cyst proximochorate with lenticular central body. Antapical lobation present on some specimens (Fig. 58A, B, J, K). Apical lobation present on specimens with attached opercular paraplates (Fig. 58F, I). Endophragm relatively thick, foveolate. Periphragm much thinner, usually shagreenate to finely foveolate; periphragm on a single specimen shows large holes (Fig. 58D, E). Periphragm separated from endophragm in peripheral areas at both sides of the central body where the former forms pericoels. Pericoels have smooth margins and usually constant height, except of the antapical area where they form antapical lobations. Archaeopyle apical with zigzag margin. Operculum usually free; if attached, rupture suture visible (Fig. 58F, I).

Suborder **GONIODOMINEAE** Fensome *et al.* (1993)Family **GONIODOMACEAE** Lindemann 1928Subfamily **GONIODOMOIDEAE** (Autonym)Genus *Heteraulacacysta* Drugg et Loeblich Jr 1967Type species: *Heteraulacacysta campanula* Drugg et Loeblich Jr 19671967 *Heteraulacacysta* n. gen.; Drugg & Loeblich Jr (1967), p. 1831980 *Heteraulacacysta* Drugg et Loeblich Jr 1967 emend.; Bujak *in* Bujak, Downie, Eaton & Williams (1980), p. 58*Heteraulacacysta campanula* Drugg et Loeblich Jr 1967

(Fig. 61C, G, H, J, K)

1967 *Heteraulacacysta campanula* n. sp.; Drugg & Loeblich Jr (1967), p. 183–184, pl. 1, figs. 6–7, 8a–c; text-fig. 2

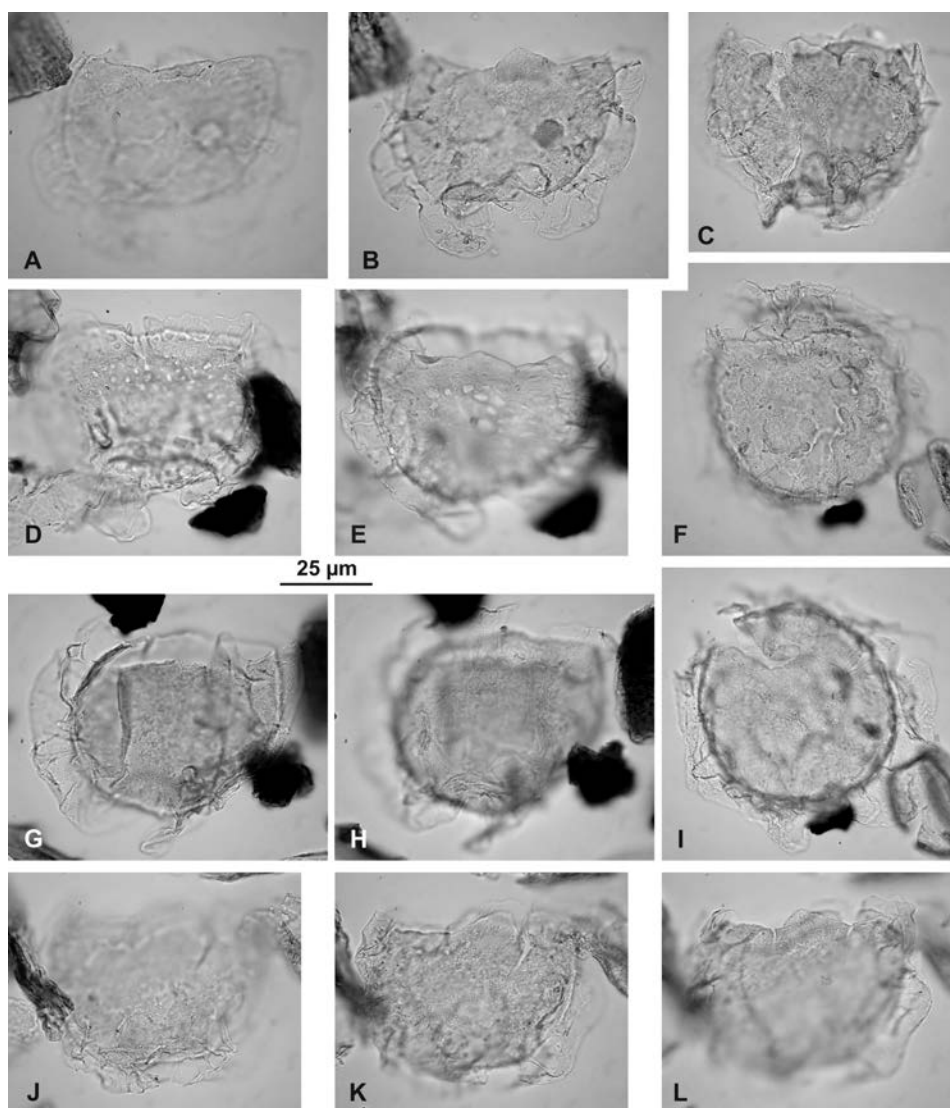
**Material.** Rare specimens occur in samples Kns7–9 and Kns17.

**Description.** Specimens of *H. campanula* in the material studied are visible in polar view only. Periphragm and endophragm thin and rather smooth, the former may also be finely foveolate. Periphragm forms indistinct parasutural ridges, except of paracingular one, which is prominent. The latter also shows indistinct radial striations at its base.

*Heteraulacacysta cf. campanula* Drugg et Loeblich Jr 1967

(Fig. 62O, P)

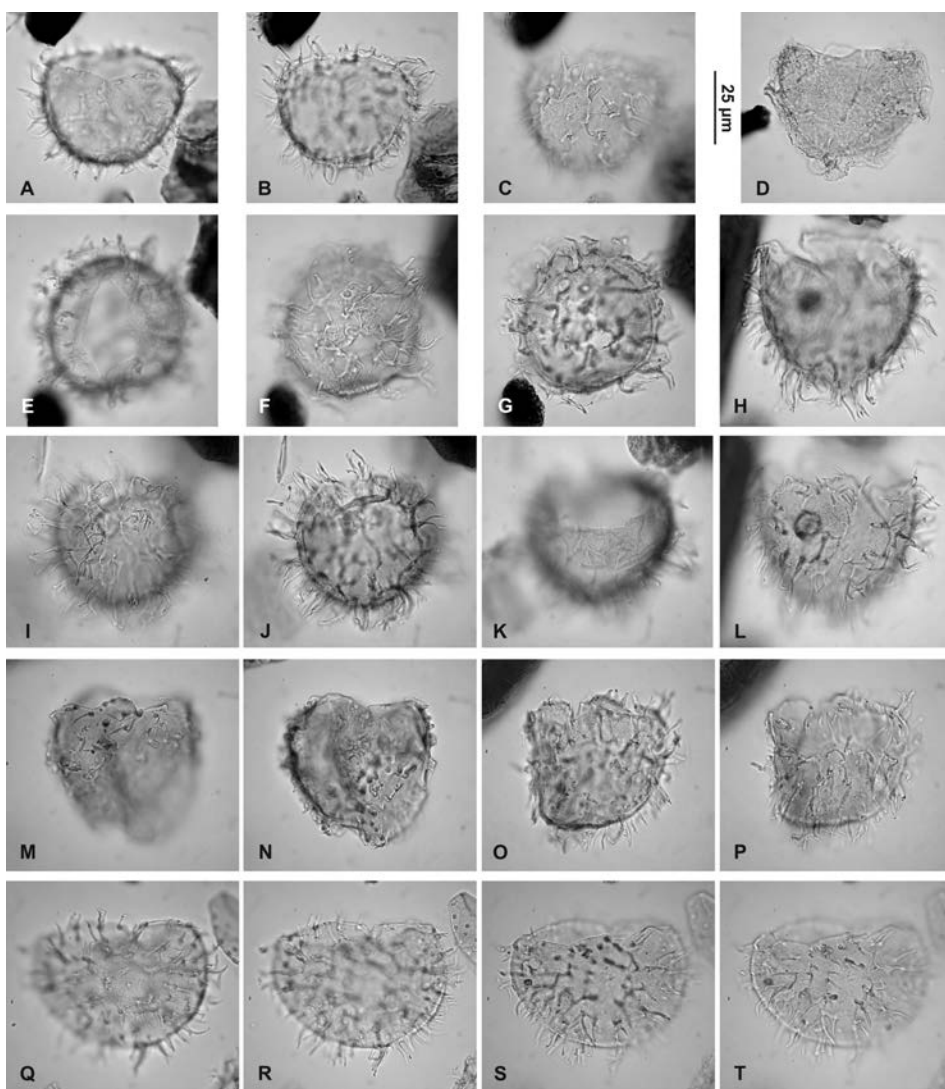
**Material.** A single specimen occurs in sample Kns12.



**Fig. 58.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–L** – *Membranophoridium aspinatum* (A, B: same specimen, various foci, Kns5; C: same specimen, various foci, Kns5; D, E: specimen with holes (same specimen, various foci, Kns13; F, I: complete specimen, same specimen, various foci, Kns8; G, H: same specimen, various foci, Kns5; J–L: same specimen, various foci, Kns5)

**Description.** This specimen resembles *H. campanula* in general arrangement of parasutural features. It differs by numerous irregular, relatively large foveolae in central parts of the cyst. Radial striations at the base of paracingular flange are well developed.



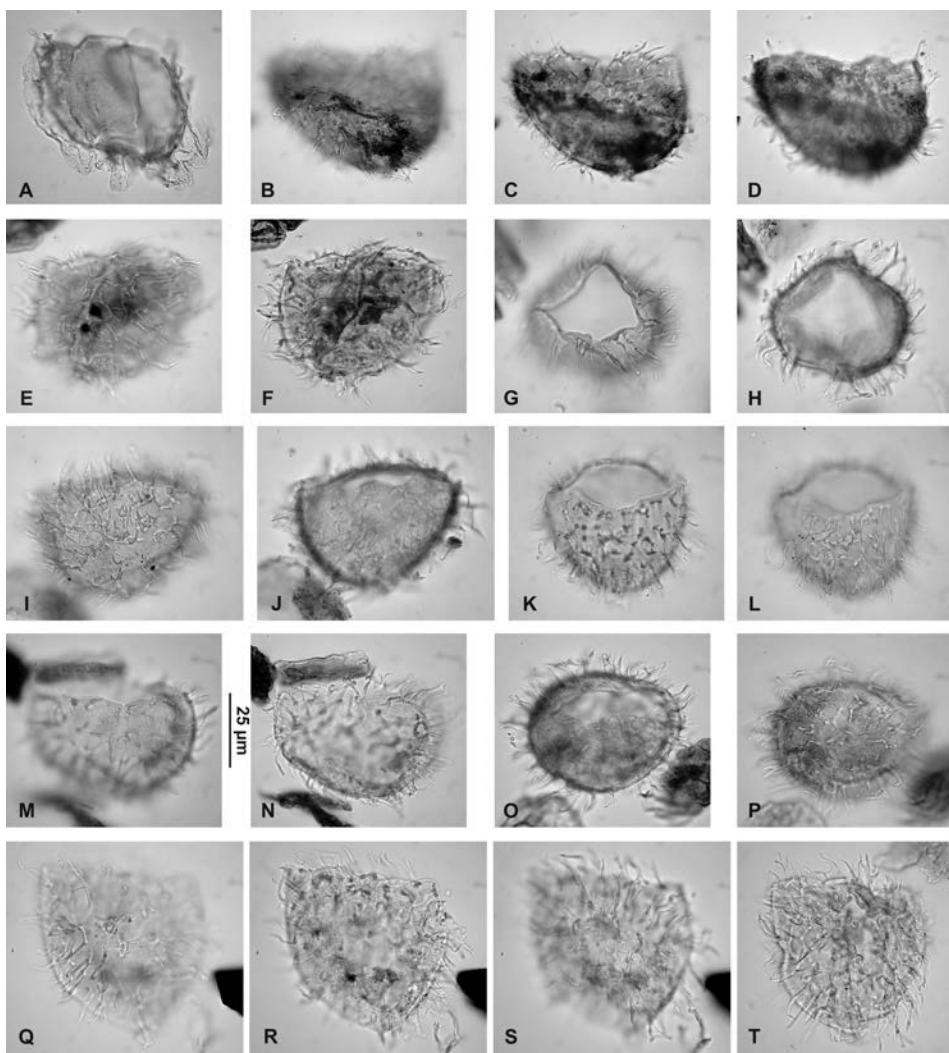


**Fig. 59.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–C** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns5); **D** – *Membranophoridium aspinatum* (Kns3); **E–G** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns5); **H, L** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns1); **I–K** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns1); **M, N** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns1); **O, P** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns1); **Q–T** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns5)

*Heteraulacacysta leptalea* Eaton 1976

(Fig. 61A, B, D, E)

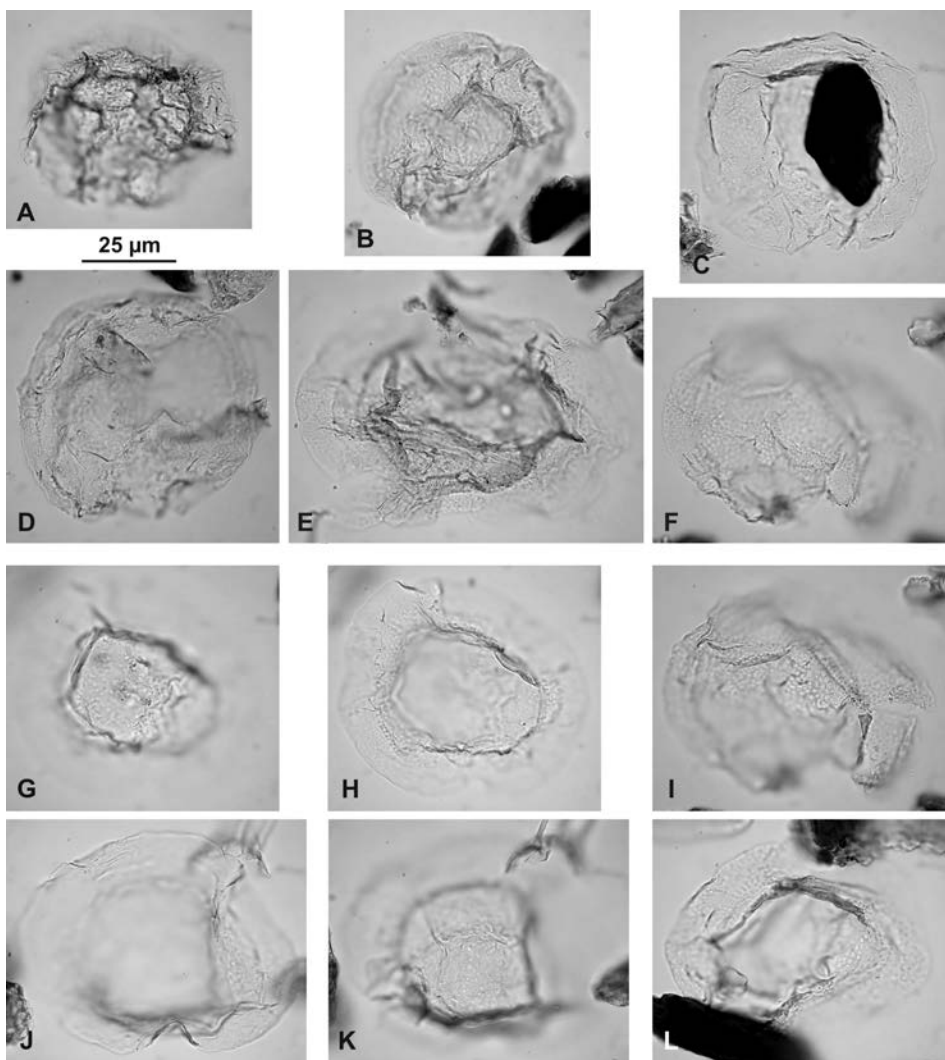
- 1976 *Heteraulacacysta? leptalea* n. sp.; Eaton (1976), p. 305–306, pl. 21, figs. 1–2  
 1980 *Heteraulacacysta leptalea*; Bujak in Bujak, Downie, Eaton & Williams (1980), p. 60



**Fig. 60.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Membranophoridium aspinatum* (Kns1); **B–D** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns6); **E, F** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns6); **G, H** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns6); **I, J** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns6); **K, L** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns11); **M, N** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns5); **O, P** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns5); **Q–S** – *Heterosphaeridium* sp. A (same specimen, various foci; Kns11); **T** – *Heterosphaeridium* sp. A (Kns12)

**Material.** Rare specimens occur in samples Kns2, Kns5 and Kns6, Kns17, Kns18, Kns20, Kns28 and Kns33.

**Description.** Cyst subcircular to elliptical in polar view, proximate, with concavity in parasulcal area. Endophragm finely granular or covered by larger, isolated



**Fig. 61.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Heterelaucacysta leptalea* (Kns3); **B** – *Heterelaucacysta leptalea* (Kns6); **C** – *Heterelaucacysta campanula* (Kns8); **D** – *Heterelaucacysta leptalea* (Kns5); **E** – *Heterelaucacysta leptalea* (Kns5); **F, I** – *Heterelaucacysta porosa* (same specimen, various foci; Kns5); **G, H** – *Heterelaucacysta campanula* (same specimen, various foci; Kns8); **J, K** – *Heterelaucacysta campanula* (same specimen, various foci; Kns7); **L** – *Heterelaucacysta porosa* (Kns7)

granulae (Fig. 61A, B). Periphragm thin, densely wrinkled, foveolate. Parasutural ridges poorly developed and hardly determinable.

*Heterelaucacysta porosa* Bujak 1980

(Fig. 62N, Fig. 61F, I, L)

1980 *Heterelaucacysta porosa* n. sp.; Bujak in Bujak, Downie, Eaton & Williams (1980), p. 62, pl. 15, figs. 10–13; text-figs. 14B–C

**Material.** Rare specimens occur in samples Kns1, Kns5–7, Kns12, Kns13, Kns18, Kns20–22, Kns32 and Kns33.

**Description.** Cyst subcircular in polar view, proximate. Endophragm smooth. Periphragm forms small ridges on hypo- and epicyst, and a prominent paracingular flange. Periphragm all over densely and uniformly perforated by small isometric holes. No concentric arrangement of perforations on paracingular crest, as noted by Bujak (*in Bujak et al.*, 1980), was observed. However, some specimens show amalgamation of neighbouring pores in basal part of paracingular flange in the form of elongated empty spaces (Fig. 61L). Majority of specimens have densely perforated paracingular crests, but some have entire distal margins of these flanges (Fig. 62N).

*Heterelaucacysta pustulata* Jan du Chêne et Adediran 1985

(Fig. 62I)

1985 *Heterelaucacysta pustulata* n. sp.; Jan du Chêne & Adediran (1985), p. 15, pl. 19, figs. 1–7, 9–10; text-figs. 3d–3g

**Material.** Single specimens occur in samples Kns8 and Kns17.

**Description.** Cyst subcircular in polar view, proximate. Periphragm smooth and thin, finely wrinkled on the central body, forms a paracingular crest with smooth margins. Ornamentation of the cyst is limited to the central body, which is covered with irregularly loosely scattered pustulae – tiny granulae with cylindrical perforation within. It is not visible if these pores go through endophragm as well. Paracingular crest free of pustulae.

Subfamily **PYRODINIOIDEAE** Fensome *et al.* (1993)

Genus *Dinopterygium* Deflandre 1935

Type species: *Dinopterygium cladoides* Deflandre 1935

1935 *Dinopterygium* n. gen.; Deflandre (1935), p. 231

1978 *Dinopterygium* Deflandre 1935 emend.; Stover & Evitt 1978, p. 204–205

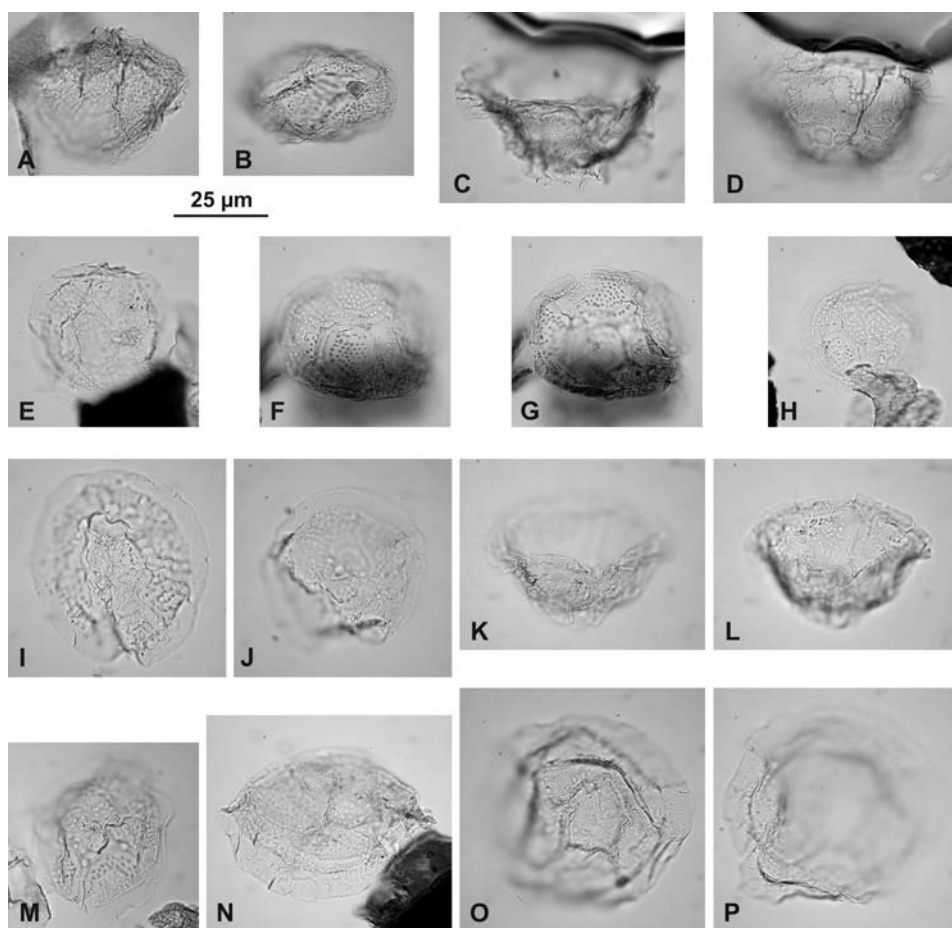
*Dinopterygium cladoides sensu* Morgenroth 1966

(Fig. 62A–H, J–M)

1966 *Dinopterygium cladoides*; Morgenroth (1966a), p. 12, pl. 2, fig. 11

**Material.** Single to rare in samples Kns2, Kns3, Kns5–9, Kns12, Kns13, Kns19, Kns20, Kns22, Kns23, Kns25, Kns28, Kns32; moderately common in sample Kns1.

**Description.** Cyst subcircular in polar view, polygonal in lateral view, proximate. Endophragm and periphragm smooth and thin, the latter forms membraneous crests: relatively low, smooth and indistinct with smooth distal margin on majority of specimens (e.g., Fig. 62A, B, G, L), and higher, with foveolate bases and



**Fig. 62.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Dinopterygium cladoides* (Kns1); **B** – *Dinopterygium cladoides* (Kns1); **C, D** – *Dinopterygium cladoides* (same specimen, various foci; Kns3); **E** – *Dinopterygium cladoides* (Kns6); **F, G** – *Dinopterygium cladoides* (same specimen, various foci; Kns6); **H** – *Dinopterygium cladoides* (Kns12); **I** – *Heterelaucacysta pustulata* (Kns8); **J** – *Dinopterygium cladoides* (Kns8); **K, L** – *Dinopterygium cladoides* (same specimen, various foci; Kns8); **M** – *Dinopterygium cladoides* (Kns5); **N** – *Heterelaucacysta porosa* (Kns12); **O, P** – *Heterelaucacysta* cf. *campanula* – specimen with irregular perforation (same specimen, various foci; Kns12)

irregular distal margin on specimen from sample Kns3 (Fig. 62C, D). Parasutural ridges of the same height, except of antapical part of the cyst where they are slightly higher (Fig. 62K, L). Paraplates covered by densely distributed, isolated, relatively large granulae, which occupy central parts of the paraplates. These intratabular granule groups are separated by wide smooth bands with parasutural crests.



Genus *Homotryblium* Davey et Williams 1966Type species: *Homotryblium tenuispinosum* Davey et Williams 19661966 *Homotryblium* n. gen.; Davey & Williams (1966b), p. 100*Homotryblium abbreviatum* Eaton 1976

(Fig. 63I–L, Fig. 64P, Q, Fig. 85C)

1976 *Homotryblium abbreviatum* n. sp.; Eaton (1976), p. 267–268, pl. 10, figs. 2–4

**Material.** Rare specimens in samples representing pale-coloured marl (Kns3, Kns4, Kns23 and Kns25); a few specimens were found in the Hieroglyphic beds (KnsH2).

**Description.** Cyst spherical, chorate, with densely granular periphragm. Processes intratabular, hollow, tubular, smooth, open, distally expanded. Broad circular areas around process stems smooth, devoid of granular periphragm. Boundary between granular periphragm and smooth endophragm visible as a typical circle beneath the process base. Length of processes up to one third of the central body diameter. Archaeopyle epicystal.

*Homotryblium aculeatum* Williams 1978

(Fig. 63A–H, Fig. 64R, S, Fig. 66A–G)

1978 *Homotryblium aculeatum* n. sp.; Williams (1978), p. 797, pl. 4, figs. 5–6, 8–9

**Material.** A very common species in samples representing dark-coloured mudstone (except of sample Kns33 where it is absent); absent from samples representing pale-coloured marl except of two samples Kns8 and Kns10 that yielded frequent specimens of this species, and sample Kns4 (two specimens).

**Description.** Cyst spherical, chorate, with relatively thin and smooth wall (Fig. 66C, G). Intratabular processes thin, smooth, tubiform, hollow, distally slightly expanded with aculate to denticulate margins (Fig. 66B). Archaeopyle epicystal.

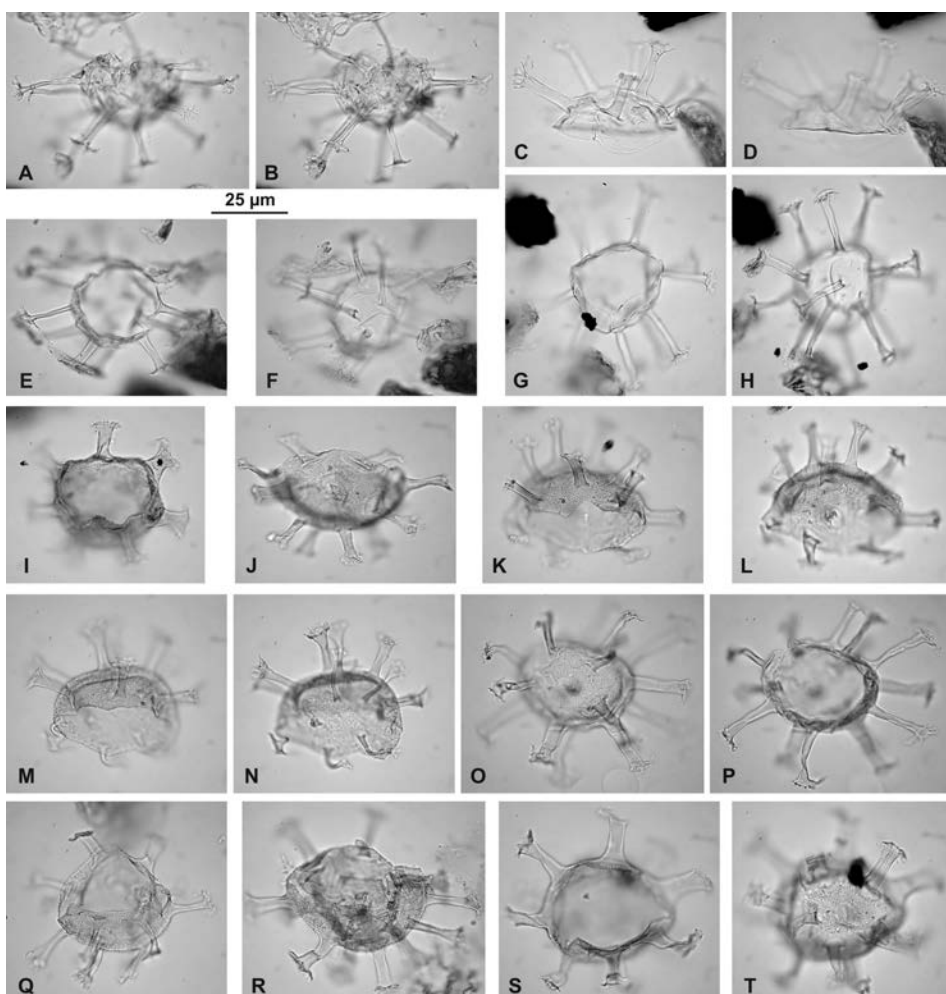
*Homotryblium caliculum* Bujak (1980)

(Fig. 67Q–T)

1980 *Homotryblium caliculum* n. sp.; Bujak in Bujak, Downie, Eaton & Williams (1980), p. 62, 64, pl. 16, fig. 4

**Material.** Single specimens occur in samples Kns5, Kns10, Kns12 and Kns25.

**Description.** Cyst subspherical, proximochorate, with shagreenate (Fig. 67S, T) to finely granular periphragm (Fig. 67Q, R). Processes intratabular, short, hollow, with relatively thin base, distally strongly expanding in form of a cup, distally open. Distal process margins with digitations (Fig. 67Q, R) or seccae (Fig. 67S, T). Archaeopyle epicystal.



**Fig. 63.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Homotryblum pallidum* (same specimen, various foci; Kns6); **C, D** – *Homotryblum pallidum* (same specimen, various foci; Kns12); **E, F** – *Homotryblum pallidum* (same specimen, various foci; Kns1); **G, H** – *Homotryblum pallidum* (same specimen, various foci; Kns6); **I** – *Homotryblum abbreviatum* (Kns3); **J** – *Homotryblum abbreviatum* (Kns4); **K, L** – *Homotryblum abbreviatum* (same specimen, various foci; Kns3); **M, N** – *Homotryblum tenuispinosum* (same specimen, various foci; Kns3); **O, P** – *Homotryblum tenuispinosum* (same specimen, various foci; Kns4); **Q** – *Homotryblum tenuispinosum* (Kns3); **R** – *Homotryblum tenuispinosum* (Kns3); **S, T** – *Homotryblum tenuispinosum* (same specimen, various foci; Kns3)

*Homotryblum conicum* Gedl 1995

(Fig. 47M–P)

1995 *Homotryblum conicum* n. sp.; Gedl (1995b), p. 202–203, pl. 6, figs. 1–4

**Material.** A single specimen occurs in sample Kns13.

**Description.** Cyst subspherical, with intratabular, very short conical processes, smooth, hollow, distally open, with smooth margin. Periphragm densely granular. Circular smooth areas appear at the process bases. Archaeopyle epicystal.

*Homotryblum plectilum* Drugg et Loeblich Jr 1967

(Fig. 64E–J, Fig. 66I–K)

1967 *Homotryblum plectilum* n. sp.; Drugg & Loeblich Jr (1967), p. 184–186, pl. 2, figs. 1–9; text-fig. 3

**Material.** Moderately to very frequent in samples representing dark-coloured mudstone (except of samples Kns 14 and Kns33 that lack this species); absent from samples representing poale-coloured marl except of samples Kns23 and Kns25 that yielded single specimens of this species.

**Description.** Cyst subspherical, chorate, with granular wall. Intratabular processes smooth, hollow, cylindrical, with striated surface, distally open (Fig. 66K). Distal margins digitate with short lists incised along striations and slightly expanded. Processes rather short in comparison to the main body, their length rarely exceeds a half of its diameter.

*Homotryblum cf. plectilum* Drugg et Loeblich Jr. 1967

(Fig. 64K–O, T, Fig. 66H)

**Material.** It occurs in dark-mudstone samples only; it is rare (Kns1, Kns6, Kns13, Kns18), moderately frequent (Kns19–22, Kns31 and Kns32) and very frequent (Kns17, Kns28 and Kns29).

**Description.** This species differs *H. plectilum* by processes that are longer and usually much more expanded distally. They are commonly thicker than at *H. plectilum*, and due to their length they commonly are slightly curved in contrast to straight processes by *H. plectilum*. However, some specimens have thin and long processes (Fig. 64O, T). Distal terminations of processes consist of strongly expanded lists that are longer than at *H. plectilum*. (Fig. 64L).

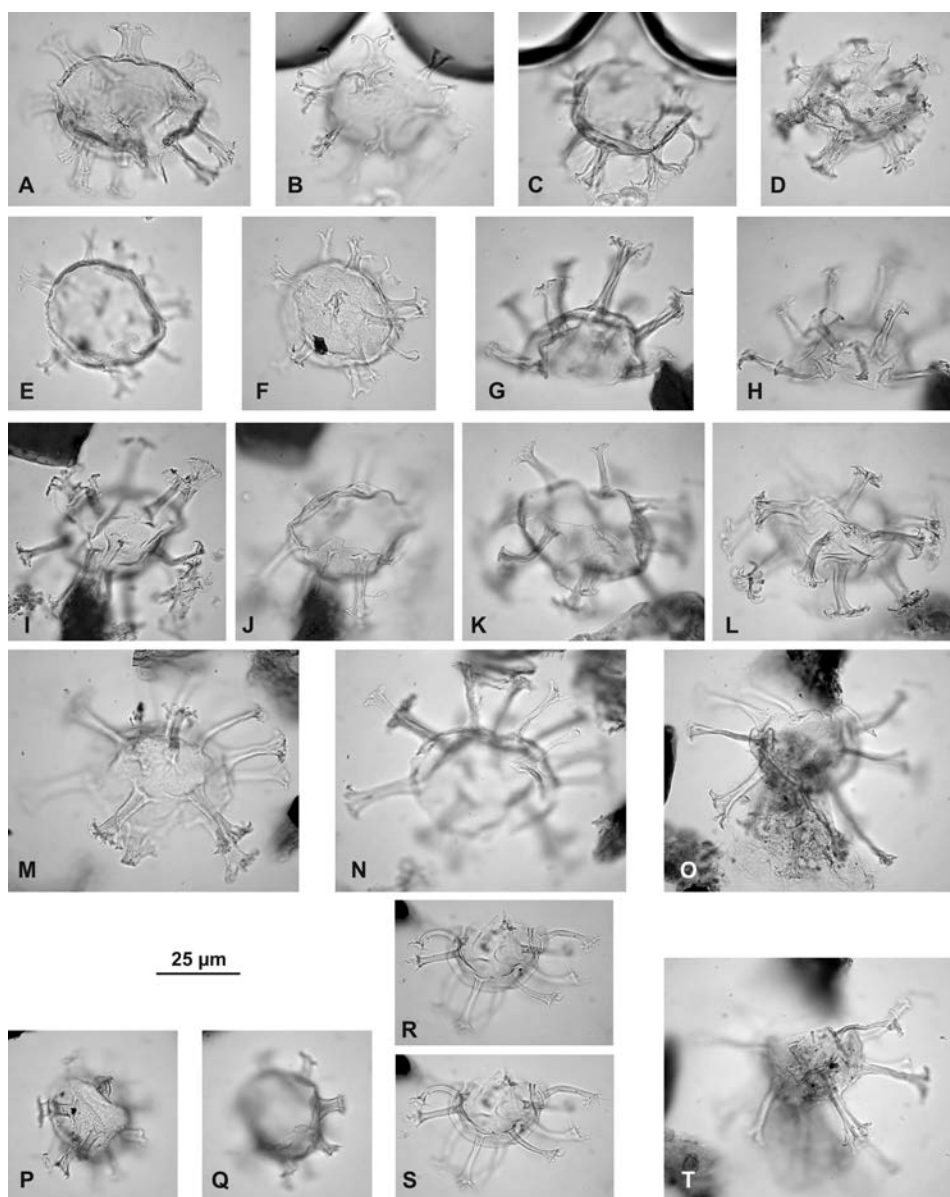
*Homotryblum tenuispinosum* Davey et Williams 1966

(Fig. 63M–T, Fig. 65A–H)

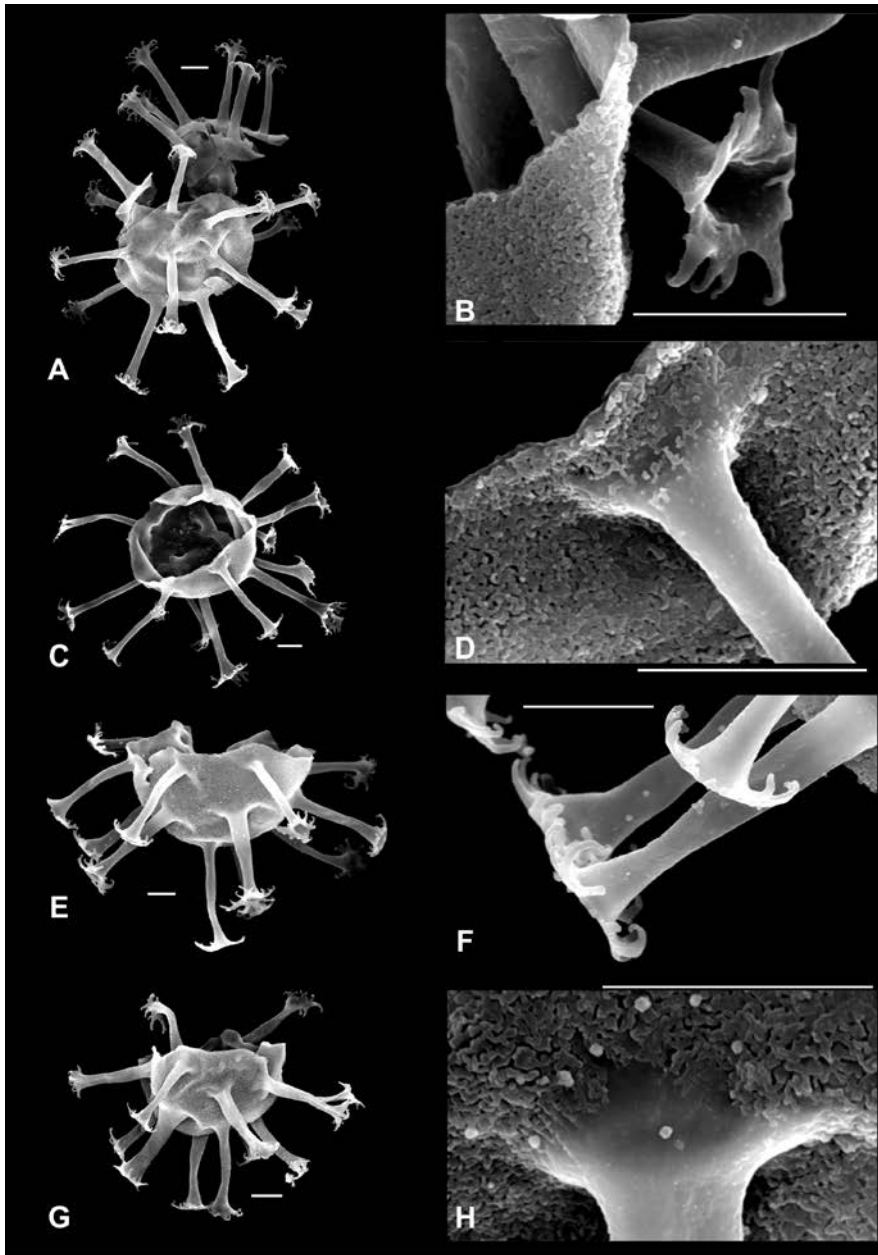
1966 *Homotryblum tenuispinosum* n. sp.; Davey & Williams (1966b), p. 101–102, pl. 4, fig. 11; pl. 12, figs. 1, 5, 7; text-fig. 21

**Material.** A very frequent species in samples representing pale-coloured mudstone (Kns3, Kns4, Kns23–25, Kns27 and Kns30) except of samples Kns8 and Kns10 that lack this species; samples representing dark-coloured mudstone lack this species or they contain relatively rare specimens (Kns12, Kns13, Kns18, Kns28 and Kns33).

**Description.** Cyst spherical, chorate, with strongly granular periphragm (Fig. 65). Intratabular processes smooth, hollow, tubiform, distally open, with serrate margin

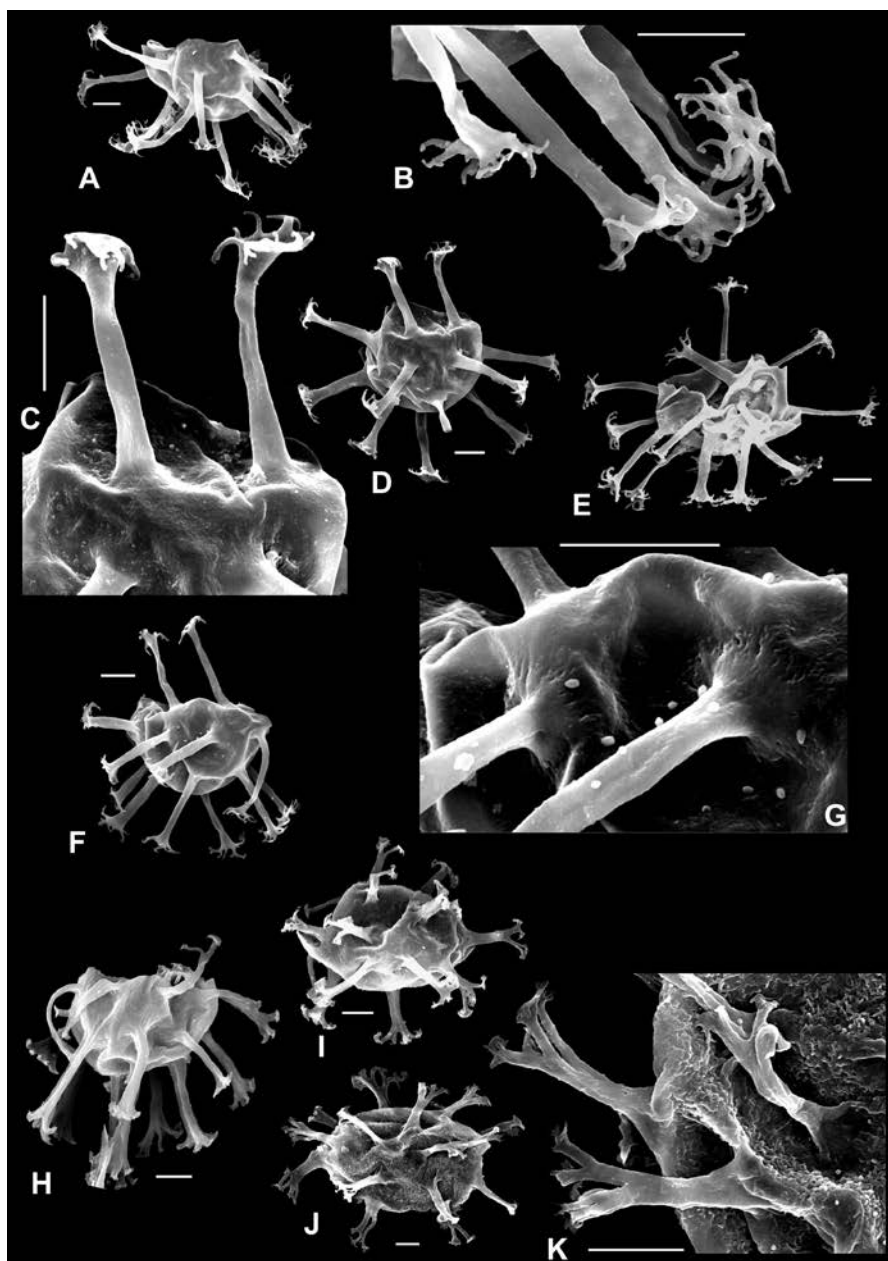


**Fig. 64.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Homotryblium vallum* (Kns3); **B, C** – *Homotryblium* cf. *vallum* – deeply incised processes (same specimen, various foci; Kns3); **D** – *Homotryblium vallum* (Kns6); **E, F** – *Homotryblium plectilum* – specimen with short and thin processes (same specimen, various foci; Kns8); **G, H** – *Homotryblium plectilum* (same specimen, various foci; Kns1); **I, J** – *Homotryblium plectilum* (same specimen, various foci; Kns1); **K, L** – *Homotryblium* cf. *plectilum* (same specimen, various foci; Kns1); **M, N** – *Homotryblium* cf. *plectilum* – large specimens (same specimen, various foci; Kns6); **O, T** – *Homotryblium* cf. *plectilum* – large specimens (same specimen, various foci; Kns6); **P, Q** – *Homotryblium abbreviatum* (same specimen, various foci; Kns3); **R, S** – *Homotryblium pallidum* (same specimen, various foci; Kns6)



**Fig. 65.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10 μm). **A–H** – *Homotryblum tenuispinosum* (**A, B**: Kns8 – **A**: complete specimen with detached opercular part; **B**: detail showing granular structure of periphragm and smooth endophragm; inner side of the latter is well visible; process' expanded distal margin with spines visible; **C, D**: Kns8 – **C**: specimen of a hypocyst; **D**: detail showing relation of periphragm and endophragm at the base of a process; **E, F, H**: Kns8 – **E**: specimen of a hypocyst; **F**: detail showing distal termination of a process; **H**: detail of a process base showing relation of granular periphragm and smooth endophragm; **G**: specimen with processes covered by very delicate reticulate structure, Kns8)





**Fig. 66.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10  $\mu$ m). **A, B** – *Homotryblum aculeatum* (Kns5; **A**: hypocyst; **B**: detail showing long spines that terminate distal part of processes); **C, D** – *Homotryblum aculeatum* (Kns5; **C**: detail of smooth periphragm; **D**: hypocyst); **E** – *Homotryblum aculeatum* (Kns5); **F, G** – *Homotryblum aculeatum* (Kns5; **F**: hypocyst; **G**: detail of the cyst showing its smooth surface); **H** – *Homotryblum* cf. *pectilum* (Kns5); **I** – *Homotryblum plectilum* (Kns5); **J, K** – *Homotryblum plectilum* (Kns8; **J** – complete specimen; **K**: detail showing periphragm and processes)

(Fig. 65F). Boundaries between granular periphragm and smooth endophragm at process bases visible as dark circles (Fig. 65D, H). Archaeopyle epicystal.

*Homotryblium vallum* Stover 1977

(Fig. 64A, D)

1977 *Homotryblium vallum* n. sp.; Stover (1977), p. 79–80, pl. 3, figs. 45–48

**Material.** Rare specimens occur in samples Kns3, Kns6, Kns8, Kns13 and Kns33; more frequent in sample Kns17.

**Description.** Cyst subspherical, proximochorate, with finely granular periphragm and rather smooth to shagreenate endophragm. Intratabular processes short and wide, tubular, hollow. Longitudinal ribs occur at the whole process length. Processes distally open. Distal process parts slightly incised along ribs, forming secate margins, which tend to expand.

*Homotryblium cf. vallum* Stover 1977

(Fig. 64B, C)

**Material.** Three specimens in sample Kns3.

**Description.** Cyst subspherical, with shagreenate periphragm and smooth endophragm. Intratabular processes moderately long (approximately of a half of the central body diameter), smooth, hollow, open, characterized by very deep incisions along longitudinal ribs. Incisions depth variable, from up to a half of the process height, even up to the process base. In the latter case, a single process consists of isolated lists arising from a circular base. Archaeopyle epicystal.

Genus *Hystrichosphaeridium* Deflandre 1937

Type species: *Hystrichosphaeridium tubiferum* (Ehrenberg 1838) Deflandre 1937

1937 *Hystrichosphaeridium* n. gen.; Deflandre (1937), p. 68

1966 *Hystrichosphaeridium* Deflandre 1937 emend.; Davey & Williams (1966b), p. 55–56

*Hystrichosphaeridium salpingophorum* (Deflandre 1935) Deflandre 1937

(Fig. 18H, Fig. 19K, N–S)

1935 *Hystrichosphaera salpingophora* n. sp.; Deflandre (1935), p. 232, pl. 9, fig. 1

1937 *Hystrichosphaeridium salpingophorum* comb. nov.; Deflandre (1937), p. 70

1966 *Hystrichosphaeridium salpingophorum* (Deflandre 1935) emend.; Davey & Williams (1966b), p. 61–62

**Material.** Rare specimens occur in samples Kns5–8, Kns12, Kns13, Kns17–19, and Kns33; moderately common in Kns32.

**Description.** Cyst subspherical, chorate, with smooth to finely granular wall (majority of specimens have smooth cyst wall – only one specimen has a granular wall – Fig. 19N). Intratabular processes tubiform, hollow, smooth, distally open and expanded. Distal margins denticulate. Parasulcal processes much thinner and

slender (Fig. 19K, O, P). Process length usually equals half of the central body diameter; occasionally their length slightly exceeds it (Fig. 19P, Q).

**Discussion.** Specimens of *H. salpingophorum* from Koniusza have relatively short processes. This feature resembles specimens from the London Clays described by Davey & Williams (1966b).

### Genus *Polysphaeridium* Davey et Williams 1966

Type species: *Polysphaeridium subtile* Davey et Williams 1966

- 1966 *Polysphaeridium* n. gen.; Davey & Williams (1966b), p. 91–92  
 1980 *Polysphaeridium* Davey et Williams 1966 emend.; Bujak, Downie, Eaton & Williams (1980), p. 32, 34

### *Polysphaeridium subtile* Davey et Williams 1966

(Fig. 67A–L)

- 1966 *Polysphaeridium subtile* n. sp.; Davey & Williams (1966b), p. 92, pl. 11, fig. 1  
 1980 *Polysphaeridium subtile* Davey et Williams 1966 emend.; Bujak, Downie, Eaton & Williams (1980), p. 34

**Material.** A very frequent species in three samples representing pale-coloured marl (Kns3, Kns25 and Kns30), rare in samples Kns8 and Kns23, absent from Kns4, Kns10, Kns24 and Kns27; rare specimens occur in samples representing dark-coloured mudstone: Kns5, Kns7, Kns12 and Kns14.

**Description.** Cyst subspherical chorate with densely granular periphragm. Numerous nontabular processes hollow, cylindrical, thin and slender, distally open and slightly expanded with a smooth margin. Archaeopyle epicystal.

### *Polysphaeridium zoharyi* (Rossignol 1962) Bujak, Downie, Eaton et Williams 1980

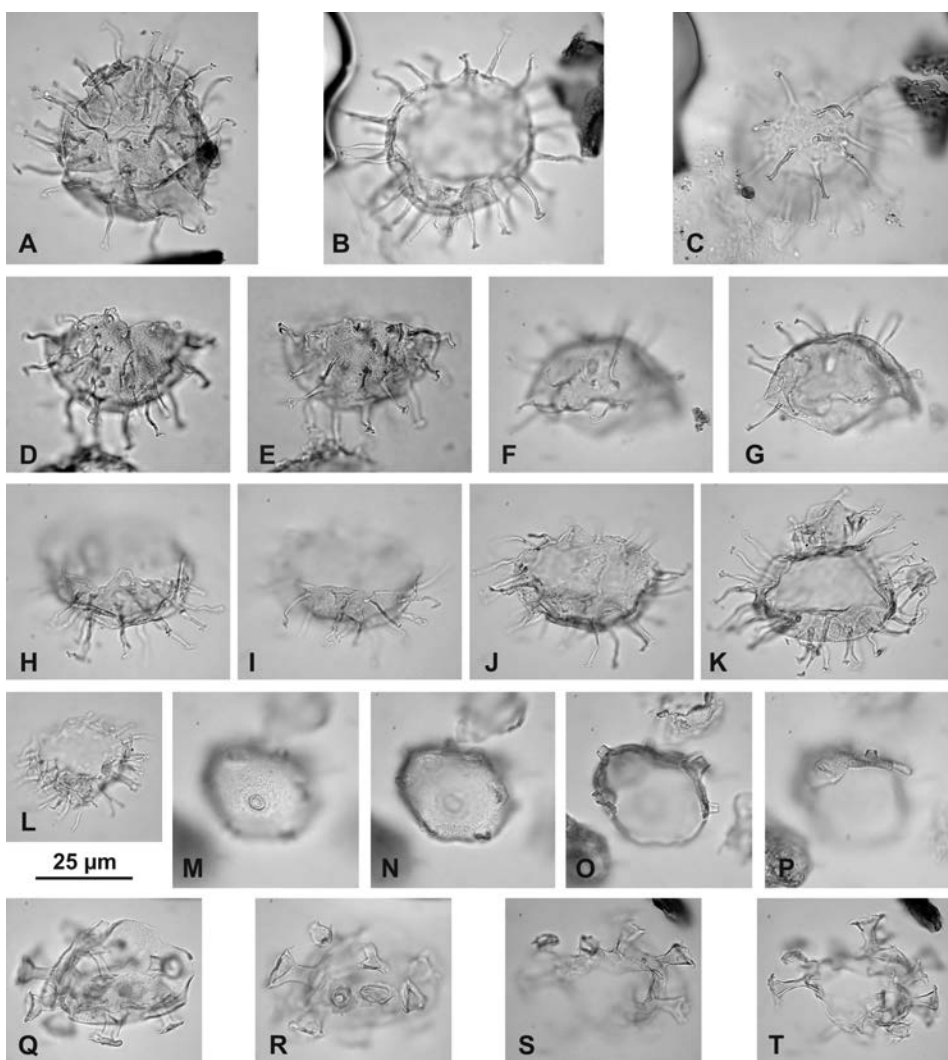
(Fig. 53D)

- 1962 *Hystichosphaeridium zoharyi* n. sp.; Rossignol (1962), p. 132, pl. 2, fig. 10  
 1980 *Polysphaeridium zoharyi* comb. nov.; Bujak, Downie, Eaton & Williams (1980), p. 34

**Material.** Frequent species in three samples representing pale-coloured marl (Kns3, Kns23, 30), rare in Kns24; absent from most of samples representing dark-coloured mudstone except of Kns22 and Kns28 that yielded rare specimens.

**Description.** Cyst subspherical, chorate, with finely granular periphragm. Nontabular processes smooth, cylindrical, hollow, distally open. Archaeopyle epicystal.

**Discussion.** This species is very similar to *Polysphaeridium subtile*. *P. zoharyi* is distinguished from *P. subtile* by less numerous processes, which are shorter and straight in contrast to longer and slender processes by *P. subtile*.



**Fig. 67.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Polysphaeridium subtile* – specimen with paraplates of epicyst (Kns3); **B, C** – *Polysphaeridium subtile* (same specimen, various foci; Kns3); **D, E** – *Polysphaeridium subtile* (same specimen, various foci; Kns3); **F, G** – *Polysphaeridium subtile* (same specimen, various foci; Kns3); **H** – *Polysphaeridium subtile* (Kns3); **I, J** – *Polysphaeridium subtile* (same specimen, various foci; Kns3); **K** – *Polysphaeridium subtile* (Kns3); **L** – *Polysphaeridium subtile* – small specimen (Kns5); **M–P** – *Homotryblum conicum* (same specimen, various foci; Kns13); **Q, R** – *Homotryblum caliculum* (same specimen, various foci; Kns10); **S, T** – *Homotryblum caliculum* (same specimen, various foci; Kns5)

Suborder **UNCERTAIN**  
Family **UNCERTAIN**

Genus *Batiacasphaera* Drugg 1970

Type species: *Batiacasphaera compta* Drugg 1970

- 1970 *Batiacasphaera* n. gen.; Drugg (1970), p. 813  
1975 *Batiacasphaera* Drugg 1970 emend.; Morgan (1975), p. 161  
1980 *Batiacasphaera* Drugg 1970 emend.; Dörhöfer & Davies (1980), p. 40

*Batiacasphaera hirsuta* Stover 1977

(Fig. 52F, G)

- 1977 *Batiacasphaera hirsuta* n. sp.; Stover (1977), p. 72–73, pl. 1, figs. 1–3

**Material.** A single specimen occurs in sample Kns4.

**Description.** Cyst small, spherical, with wall covered by dense hair-like projections. Hairs densely packed but isolated: single ones do not connect each other. No other forms of positive relief. Apical archaeopyle is the only trace of paratabulation.

*Batiacasphaera micropapillata* Stover 1977

(Fig. 52H, I, M)

- 1977 *Batiacasphaera micropapillata* n. sp.; Stover (1977), p. 73, pl. 1, figs. 7–8

**Material.** Rare specimens in samples Kns3, Kns4 and Kns6, Kns17, Kns19–22, Kns28 and Kns30; moderately frequent in sample Kns18.

**Description.** Cyst subspherical (all specimens wrinkled), thin-walled, proximate, with apical archaeopyle and homogenous wall (under optical microscop), with granulate to papillate outer surface. Distribution of these relief elements is very dense, particular granulae are spaced very close to each other, which gives a roughly appearance of outer surface of the cyst wall.

*Batiacasphaera?* *reticulata* (Davey 1969) Davey 1979

(Fig. 52P–S)

- 1969 *Chytroeisphaeridia reticulata* n. sp.; Davey (1969b), p. 14, pl. 4, figs. 3–4, 6  
1979 *Batiacasphaera reticulata* comb. nov.; Davey (1979), p. 217  
1997 *Batiacasphaera?* *reticulata*; Mohr & Mao Shaozhi (1997), p. 58

**Material.** Three specimens in sample Kns11.

**Description.** Cyst ellipsoidal, slightly elongated, with relatively thick and rigid wall covered with irregular, densely distributed granulae, some of which tend to fuse.

*Batiacasphaera* sp. A

(Fig. 52L)

**Material.** Single specimens in samples Kns3, Kns17, Kns21 and Kns33.



**Description.** Cyst subspherical, proximate, with thin wall covered by densely distributed but isolated, tiny tuberculae. Tuberculae cone-shaped, with truncated, slightly rounded distal terminations.

*Batiacasphaera* sp. B

(Fig. 52J, K, Fig. 53A, F)

**Material.** Single specimens in samples Kns3 and Kns5 and two specimens in sample Kns8.

**Description.** Cyst subspherical, proximate, with wall composed of very thin pedium and dense, irregular luxuriae. The latter give in optical microscope view a granular structure of the cyst wall (Fig. 52J, K). Pedium and luxuriae are well visible under higher magnification (SEM view: Fig. 53A, F). Irregular perforations of the luxuriae may result from their alveolate nature.

*Batiacasphaera* sp. C

(Fig. 52O, T, Fig. 53C)

**Material.** Single specimens in samples Kns4 and Kns8.

**Description.** Cyst subspherical, proximate, with wall composed of an inner thin and smooth layer (pedium), and hair-like projections densely arising from pedium. Projections do not branch; they also show no connections with each other. Generally, they grow horizontally or at low angle, and tend to trail. Archaeopyle with angular margins, presumably apical.

**Discussion.** This species resembles *Batiacasphaera hirsuta* by hairy cover of the cyst wall. The latter, however, tend to trail at *Batiacasphaera* sp. C in contrast to vertical growth of the hairs at *B. hirsuta*.

Genus *Cerebrocysta* Bujak 1980

Type species: *Cerebrocysta bartonensis* Bujak 1980

1980 *Cerebrocysta* n. gen.; Bujak in Bujak, Downie, Eaton & Williams (1980), p. 42

*Cerebrocysta bartonensis* Bujak 1980

(Fig. 45T–X, Fig. 51E)

1980 *Cerebrocysta bartonensis* n. sp.; Bujak in Bujak, Downie, Eaton & Williams (1980), p. 42, pl. 13, figs. 4–11

**Material.** Rare specimens occur in samples Kns10–12, Kns27 and Kns29; moderately common in samples Kns3 and Kns4,.

**Description.** Cyst small, subspherical, proximate, with smooth wall covered by low, randomly arranged crest network. Some crests show linear arrangement; it rather cannot be linked to parasutural features. Archaeopyle precingular, single paraplate involved.

*Cerebrocysta* cf. *bartonensis* Bujak 1980

(Fig. 45Y–Z1)

**Material.** Rare specimens occur in sample Kns25.

**Description.** This species is similar to *C. bartonensis*, from which it differs by thicker cyst wall and more densely arranged crest network.

Genus *Chlamydophorella* Cookson et Eisenack 1958Type species: *Chlamydophorella nyei* Cookson et Eisenack 19581958 *Chlamydophorella* n. gen.; Cookson et Eisenack (1958), p. 561983 *Chlamydophorella* Cookson et Eisenack 1958 emend.; Duxbury (1983), p. 41*Chlamydophorella* sp.

(Fig. 16U–W)

**Material.** Single specimens in samples Kns8, Kns10 and Kns11.

**Description.** Cyst ellipsoidal, elongated, proximate, with periphragm covered with very short, solid processes, occasionally united to form short ridges, distally connected by ectophragmal membrane. Membrane very thin, commonly disrupted. Archaeopyle apical.

Genus *Dapsilidinium* Bujak, Downie, Eaton et Williams 1980Type species: *Dapsilidinium pastielsii* (Davey et Williams 1966b) Bujak, Downie, Eaton et Williams 19801980 *Dapsilidinium* n. gen.; Bujak, Downie, Eaton & Williams (1980), p. 27–28*Dapsilidinium pseudocolligerum* (Stover 1977) Bujak, Downie, Eaton et Williams 1980

(Fig. 20J, K, Fig. 34S–Z, Fig. 53E)

1977 *Polysphaeridium pseudocolligerum* n. sp.; Stover (1977), p. 74–75, pl. 1, figs. 14–191980 *Dapsilidinium pseudocolligerum* comb. nov.; Bujak, Downie, Eaton & Williams (1980), p. 28

**Material.** Rare specimens occur in samples Kns5, Kns6, Kns8, Kns11, Kns13, Kns17, Kns19, Kns23, Kns25 and Kns31; more common in samples Kns10 and Kns12, Kns18; very frequent in sample Kns27. A single specimen was found in the Hieroglyphic beds (KnsH2).

**Description.** Cyst subspherical, chorate, with finely (e.g., Fig. 34S, Z) to coarsely (Fig. 20J, Fig. 34U) granular wall and numerous nontabular processes. Processes hollow, smooth to finely fibrous, commonly covered with very tiny thorn-like projections (well visibly under SEM: see Fig. 20J), generally thin, broad at base, getting narrow towards, distally open with slightly expanded smooth margins. Archaeopyle apical.

Genus *Distatodinium* Eaton 1976Type species: *Distatodinium craterum* Eaton 19761976 *Distatodinium* n. gen.; Eaton 1976, p. 262–263*Distatodinium craterum* Eaton 1976

(Fig. 55E, I)

1976 *Distatodinium craterum* n. sp.; Eaton (1976), p. 263–264, pl. 9, figs 1–5**Material.** Single specimens occur in samples Kns6–9.**Description.** Cyst elongated, ellipsoidal, relatively small, chorate, with smooth wall and processes in precingular, postcingular and antapical positions (specimen has no apical part). Processes hollow, smooth, distally branched with irregular branch system. Processes isolated, no distal connection among processes branchings. Archaeopyle apical.*Distatodinium ellipticum* (Cookson 1965) Eaton 1976

(Fig. 55A, B, F–H)

1965 *Hystichosphaeridium ellipticum* n. sp.; Cookson (1965a), p. 87–88, pl. 11, figs. 1–3, 3a1976 *Distatodinium ellipticum* comb. nov.; Eaton (1976), p. 264**Material.** Rare specimens occur in samples representing dark-coloured mudstone: Kns5–7, Kns9, Kns12 and Kns13, Kns18, Kns20–22.**Description.** Cyst elongated, chorate, with numerous (more than 40) hollow, distally branched processes, and shagreenate to finely granular cyst wall. Processes usually isolated except of antapical ones, which occasionally arise from common base (e.g., Fig. 55B). Distal branching irregular, long; no distal connection among processes. Archaeopyle apical. Majority of specimens relatively large (Fig. 55A, B), but some specimens have shorter central bodies and relatively longer processes (Fig. 55F–H).*Distatodinium ?scariosum* Liengjarern, Costa et Downie 1980

(Fig. 55O–Q)

1980 *Distatodinium scariosum* n. sp.; Liengjarern *et al.* (1980), p. 477, 481, pl. 54, fig. 3**Material.** A single specimen was found in sample Kns17.**Description.** Cyst elongated, with short, hollow, distally slightly expanded processes terminated with short spines. Processes seem to be intratabular arising from each paraplate including the paracingular series, except of the antapical area where more numerous processes are present**Discussion.** This species was questionably assigned to *D. scariosum* on the base of overall shape and processes morphology. However, *D. scariosum* lacks paracingular processes, which are present on the specimen from Koniusza.

*Distatodinium virgatum* Stover 1977

(Fig. 55C, D)

1977 *Distatodinium virgatum* n. sp.; Stover (1977), p. 75–76, pl. 1, figs. 20–21**Material.** A single specimen in sample Kns13.**Description.** Cyst elongated, chorate, with smooth wall and numerous, nontabular processes. Processes hollow, smooth, and relatively short in relation to the main cyst body, distally bifurcated or trifurcated without further branching. Some processes are proximally connected by low membranous ridges with convex margins. Described specimen has adnate operculum.Genus *Heslertonia* Sarjeant 1966Type species: *Heslertonia heslertonensis* (Neale et Sarjeant 1962) Sarjeant 19661966 *Heslertonia* n. gen.; Sarjeant (1966), p. 1331980 *Heslertonia* Sarjeant 1966 emend.; Duxbury (1980), p. 123*Heslertonia?* sp.

(Fig. 32A, N, O)

**Material.** Single specimens in samples Kns5 and Kns8.**Description.** Central body small, spherical, with smooth cyst wall and high ridges. Ridges height almost equal to the central body diameter, smooth, hyalinous, with thickenings along the arched distal margins. Archaeopyle not observed.Genus *Heterosphaeridium* Cookson et Eisenack 1968Type species: *Heterosphaeridium conjunctum* Cookson et Eisenack 19681968 *Heterosphaeridium* n. gen.; Cookson et Eisenack 1968, p. 1151981 *Heterosphaeridium* Cookson et Eisenack 1968 emend.; Yun Hyesu 1981, p. 45–46*Heterosphaeridium* sp. A

(Fig. 26B, C, Fig. 59A–C, E–T, Fig. 60B–T)

**Material.** Rare (Kns2, Kns18, Kns22, and Kns31) to moderately frequent (Kns1, Kns5–7, Kns9, Kns11–14, Kns17, Kns19–21 and Kns28) in samples representing dark-coloured mudstone; absent from samples representing pale-coloured marl, or present there as single specimens only (Kns3 and Kns4).**Description.** Cyst subspherical, proximochorate, with relatively thick and smooth periphragm and nontabular processes of various shapes. Processes slender, solid and hollow, usually with broad bases, commonly united in pairs or three, distally tapering and closed. Archaeopyle apical with zigzag margin.Genus *Reticulosphaera* Matsuoka 1983Type species: *Reticulosphaera actinocoronata* (Benedek 1972) Bujak et Matsuoka 19861983 *Reticulosphaera* n. gen.; Matsuoka (1983), p. 116

1986 *Reticulosphaera* Matsuoka 1983 emend.; Bujak & Matsuoka (1986), p. 238

*Reticulosphaera actinocoronata* (Benedek 1972) Bujak et Matsuoka 1986  
(Fig. 32F–J)

1972 *Cleistosphaeridium actinocoronatum* n. sp.; Benedek (1972), p. 34, pl. 12, fig. 13; text-fig. 13

1986 *Reticulosphaera actinocoronata* comb. nov.; Bujak & Matsuoka (1986), p. 238

1986 *Reticulosphaera actinocoronata* (Benedek 1972) emend.; Bujak & Matsuoka (1986), p. 238–239

**Material.** Rare specimens in samples Kns6, Kns12, Kns13.

**Description.** Cyst small, spherical, chorate, with smooth wall and solid, relatively massive, long processes (up to the central body diameter). Processes distally simply branched, usually into two thick branches, which further branch into irregular net of thin and slender branches. These delicate branches of particular process do not connect with the ones of another process.

Genus *Sepispinula* Islam 1993

Type species: *Sepispinula ancorifera* (Cookson et Eisenack 1960) Islam 1993

1993 *Sepispinula* n. gen.; Islam (1993), p. 88

*Sepispinula? ambigua* (Deflandre 1937) Masure 2004  
(Fig. 16X, Y)

1937 *Micrhystridium ambiguum* n. sp.; Deflandre (1937), p. 81, pl. 16, figs 8–9

1978 *Cleistosphaeridium ambiguum* comb. nov.; Jiabo (1978), p. 60

1981 *Polysphaeridium ambiguum* comb. nov.; Yun Hyesu (1981), p. 44

1987 *Chlamydophorella ambigua* comb. nov.; Stover & Helby (1987), p. 277

1990 *Dapsilidinium ambiguum* comb. nov.; Wheeler & Sarjeant (1990), p. 310–311

1994 *Gorgonisphaeridium ambiguum* comb. nov.; Sarjeant & Stancliffe (1994), p. 31

2004 *Sepispinula? ambigua* comb. nov.; Masure in Fauconnier & Masure (2004), p. 500

**Material.** Single specimens in samples Kns12 and Kns14.

**Description.** Cyst subspherical, proximochorate, with smooth wall and nontabular processes. Processes tubiform, slightly broader and hollow at the base, gradually narrowing and getting solid in the middle part. Process tubes distally slightly broader, terminated with parallel branchings. The latter commonly united by very thin, noncontinuous membrane. Archaeopyle apical.

Genus et species indetermined A

(Fig. 52A–C)

**Material.** A single specimen in sample Kns8.

**Description.** Cyst small, spherical, proximate, with low ridges, presumably in parasutural position. Ridges of irregular height: elevated sections with smooth margins pass into much lower, poorly developed ones. Archaeopyle type not recognizable.



**Discussion.** Genus et species indet. A resembles the genus “*Imperfectodinium*” proposed by Zevenboom & Santarelli (in Zevenboom, 1995), which was regarded by Fensome & Williams (2004) as not validly published. A characteristic feature of this genus is incomplete development of parasutural features expressed mainly by crests or septae. This feature made taxonomical allocation of the specimen from Koniusza to this genus. However, not certain archaeopyle type makes this questionable.

Genus et species indetermined B

(Fig. 52D, E)

**Material.** A single specimen in sample Kns12.

**Description.** Cyst small, with spherical central body and long processes (their length equals or slightly exceeds “ of the central body diameter). Processes connected by membranous septa, their height equals that of processes. Archaeopyle type not certain, presumably apical.

**Discussion.** This specimen superficially resembles the genus *Labyrinthodinium*. But the latter genus has much shorter processes and apical archaeopyle; its stratigraphic range is limited to Miocene (see de Verteuil & Norris, 1996).

Genus et species indetermined C

(Fig. 84E, H, I)

**Material.** This species occurs relatively frequently in samples Kns23 and Kns25; a few specimens of this species were found in the Hieroglyphic beds (KnsH2).

**Description.** Cyst large, proximate, with foveolate wall. Lumina circular, up to 2–3 µm in diameter, regularly distributed and isolated. Upper surface of the cyst wall finely rugulate. Archaeopyle apical, operculum free.

Order **PERIDINIALES** Haeckel 1894

Suborder **PERIDINIINEAE** (Autonym)

Family **PERIDINIACEAE** Ehrenberg 1831

Subfamily **DEFLANDREOIDEAE** Bujak et Davies 1983

Genus *Deflandrea* Eisenack 1938

Type species: *Deflandrea phosphoritica* Eisenack 1938

- 1938 *Deflandrea* n. gen.; Eisenack (1938), p. 187
- 1966 *Deflandrea* Eisenack 1938 emend.; Williams & Downie (1966c), p. 231
- 1974 *Deflandrea* Eisenack 1938 emend.; Stover (1974), p. 169–170
- 1976 *Deflandrea* Eisenack 1938 emend.; Lentin & Williams (1976), p. 35–36

*Deflandrea arcuata* Vozzhennikova 1967

(Fig. 68E–G)

- 1967 *Deflandrea arcuata* n. sp.; Vozzhennikova (1967), p. 143–144, pl. 66, fig. 1; pl. 68, figs. 3a–b

1990 *Deflandrea arcuata* Vozzhennikova 1967 emend.; Lentin & Vozzhennikova (1990), p. 50

**Material.** Rare to moderately common specimens in samples Kns2, Kns3, Kns18, Kns19, Kns22, Kns25, Kns26 and Kns33.

**Description.** Cyst circumcavate to bicavate, with ovoidal endocyst and almost ovoidal pericyst, its width is slightly higher than its length. Endophragm thick and granular (Fig. 68E) to vermiculate (Fig. 52G); periphragm much thinner and smooth. One short apical horn, and two antapical ones, broad and short. Antapical horns separated by short concavity.

*Deflandrea granulata* Menéndez 1965

(Fig. 69E-N)

1965 *Deflandrea granulata* n. sp.; Menéndez (1965), p. 9-10, pl. 1, fig. 4.

**Material.** This species is frequent in two samples representing pale-coloured marl (Kns3 and Kns4); a few specimens occur in samples Kns30 and Kns33. A single specimen occurs in the Hieroglyphic beds (KnsH2).

**Description.** Cyst bicavate, with ovoidal endocyst and thin periphragm composed of closely spaced irregular grains and elongated granulae, which make an appearance of an abrasive paper. Apical and two antapical horns blunt; antapical horns poorly developed, they are separated by weakly developed concavity.

*Deflandrea heterophlycta* Deflandre et Cookson 1955

(Fig. 68H-J, L-O, Fig. 80J)

1955 *Deflandrea heterophlycta* n. sp.; Deflandre & Cookson (1955), p. 249-250, pl. 5, fig. 6; text-fig. 5

**Material.** Moderately common to very frequent in all samples representing dark-coloured mudstone; absent in most of samples representing pale-coloured marl except of sample Kns30 that yielded a few specimens.

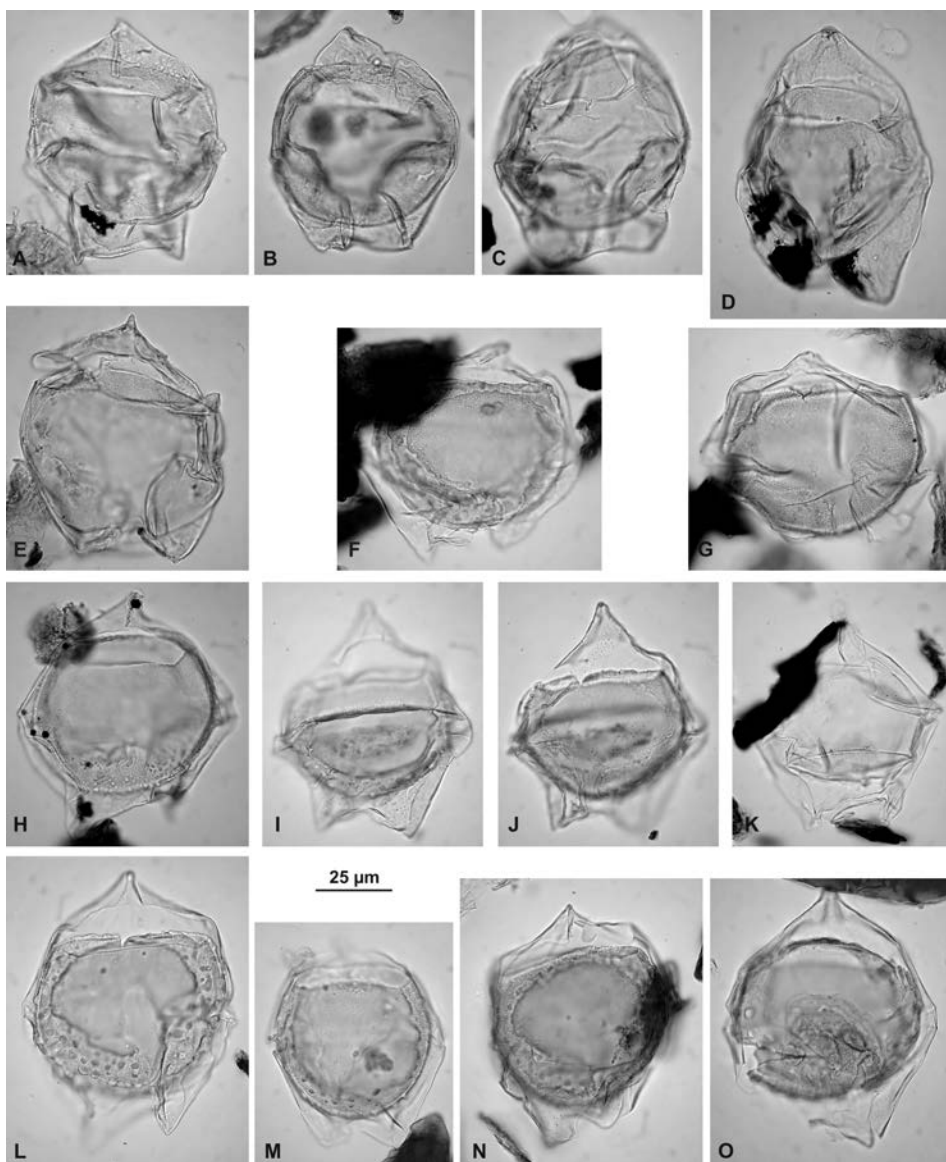
**Description.** Cyst peridinioid, circumcavate to bicavate, with ovoidal endocyst, with thick, finely granular endophragm covered by very prominent tubercles (Fig. 80J). The latter tend to group in peripheral areas of the endocyst, especially at antapical part; central part is completely free of tubercles. Periphragm smooth; some specimens bear very tiny spicules grouped in intratabular areas separated by parasutural bands free of spicules. Well developed apical and two antapical horns; the latter of almost equal size, separated by concave antapex margin.

*Deflandrea leptodermata* Cookson et Eisenack 1965

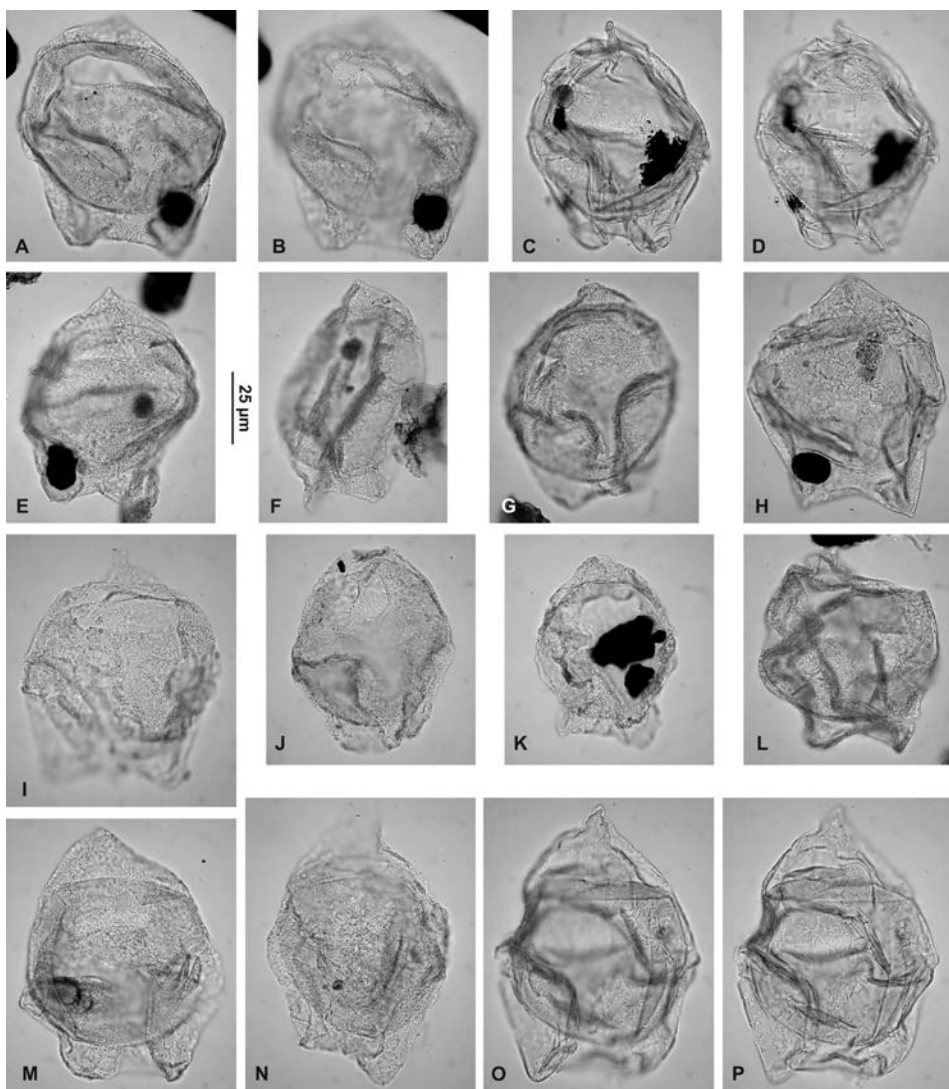
(Fig. 68A-D)

1965 *Deflandrea leptodermata* n. sp.; Cookson & Eisenack (1965a), p. 121-122, pl. 11, figs. 6-7

**Material.** Rare specimens in samples Kns3, Kns4, Kns30 and Kns33.



**Fig. 68.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Deflandrea leptodermata* (Kns3); **B** – *Deflandrea leptodermata* (Kns3); **C** – *Deflandrea leptodermata* (Kns3); **D** – *Deflandrea leptodermata* (Kns4); **E** – *Deflandrea arcuata* (Kns3); **F** – *Deflandrea arcuata* (Kns2); **G** – *Deflandrea arcuata* (Kns2); **H** – *Deflandrea heterophlycta* (Kns2); **I, J** – *Deflandrea heterophlycta* (same specimen, various foci; Kns5); **K** – *Deflandrea phosphoritica* (Kns13); **L** – *Deflandrea heterophlycta* (Kns5); **M** – *Deflandrea heterophlycta* (Kns1); **N** – *Deflandrea heterophlycta* (Kns5); **O** – *Deflandrea heterophlycta* (Kns1)



**Fig. 69.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Deflandrea* with fungi traces (same specimen, various foci; Kns3); **C, D** – *Deflandrea* with fungi traces (same specimen, various foci; Kns4); **E** – *Deflandrea granulata* (Kns3); **F** – *Deflandrea granulata* (Kns4); **G** – *Deflandrea granulata* (Kns3); **H** – *Deflandrea granulata* (Kns3); **I** – *Deflandrea granulata* (Kns4); **J** – *Deflandrea granulata* (Kns3); **K** – *Deflandrea granulata* (Kns3); **L** – *Deflandrea granulata* (Kns3); **M** – *Deflandrea granulata* (Kns4); **N** – *Deflandrea granulata* (Kns4); **O, P** – *Deflandrea* with fungi traces (same specimen, various foci; Kns4)

**Description.** Cyst peridinioid, bicavate, with ovoidal endocyst, with finely to coarsely granular endophragm. Periphragm thin, smooth to shagreenate. Pericyst relatively long, with short blunt apical horn, and two antapical horns, poorly developed, blunt, forming almost straight line of the antapex margin between them.

*Deflandrea phosphoritica* Eisenack 1938

(Fig. 68K, Fig. 69A–D, O, P, Fig. 70A–N, Fig. 80K)

1938 *Deflandrea phosphoritica* n. sp.; Eisenack (1938), p. 187, text-fig. 187

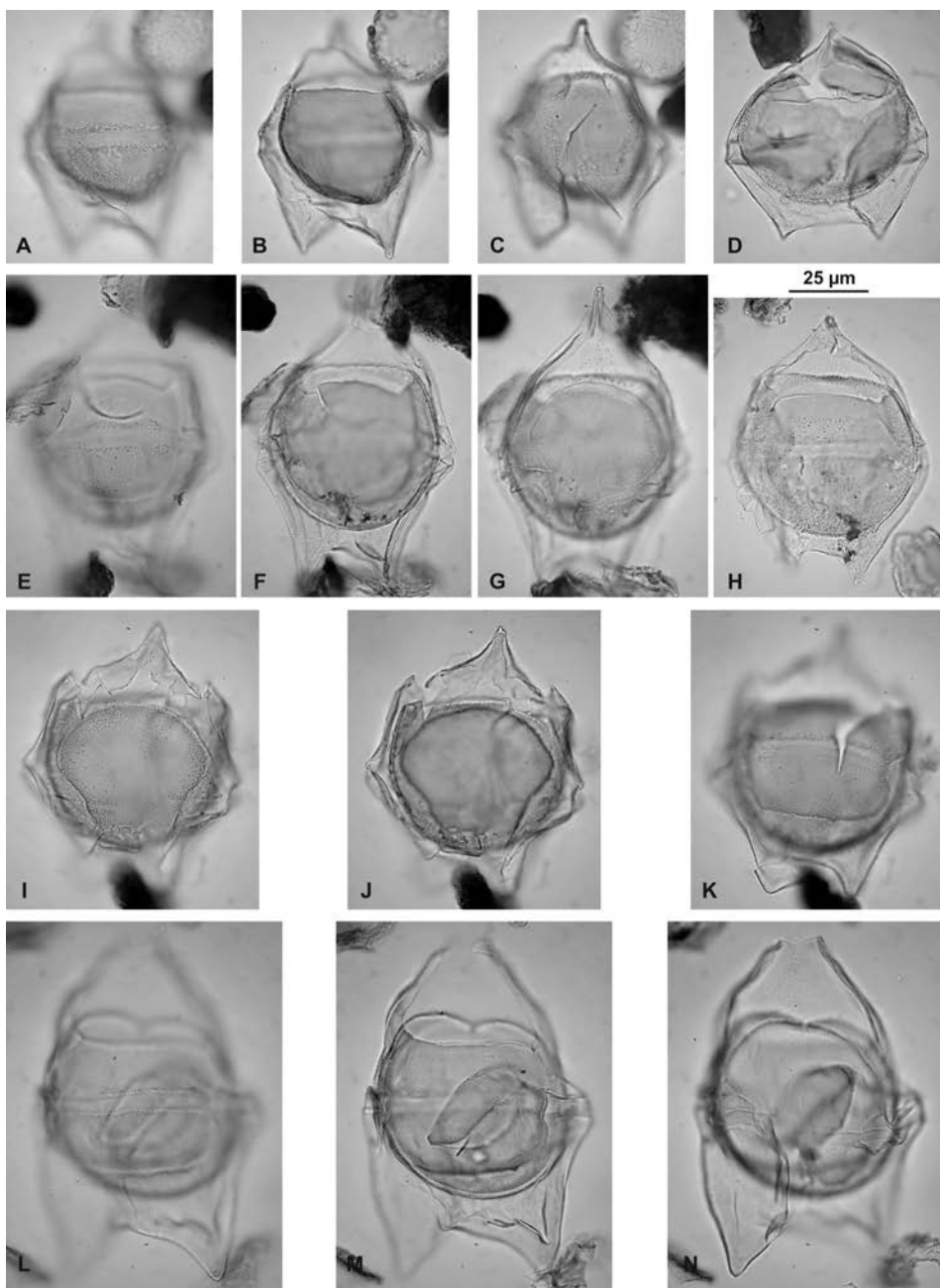
**Material.** Frequent in all samples representing dark-coloured mudstone; absent in most of samples representing pale-coloured marl show various frequencies of this species: frequent in samples Kns3 and Kns30, rare in samples Kns4, Kns8, Kns10, Kns25 and Kns27, absent from samples KnsKns23 and Kns24.

**Description.** Cyst peridinioid, bicastrate to circumcavate, with one apical and two antapical horns, the latter usually of similar lengths, separated by concavity. Endocyst ovoidal, with endophragm thicker than periphragm, shagreenate to finely granular. Periphragm smooth, covered in majority of specimens by very fine projections grouped in intratabular areas, separated from each others by smooth parasutural bands. Paracingulum usually indicated by linear arrangement of these projections. Parasulcus usually not visible or only detectable as small depression devoid of positive relief. Archaeopyle intercallary.

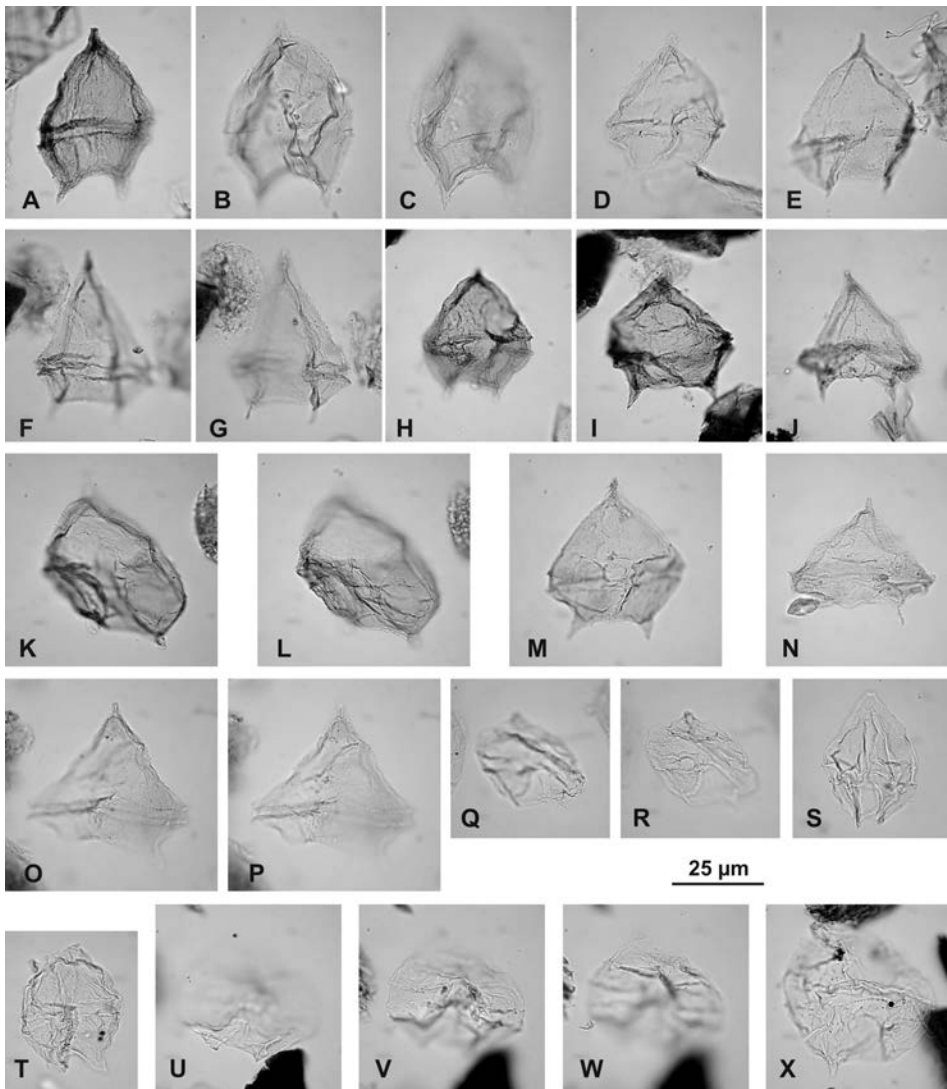
**Remarks.** Specimens included to this species show certain variability in morphology related mainly to pericyst shape and its relation to endocyst. Some specimens are bicastrate forms, rounded, with pericyst in close contact with endocyst in paracingular areas (Fig. 70H). The others are pentagonal, having periphragm separated from endophragm in paracingular area. Some differences are also observed in periphragm relief, which include smooth to variously ornamented specimens; positive ornamentation is never prominent, usually consists of tiny granules or spines, commonly arranged in intratabular clusters.

Some specimens of *Deflandrea* in samples Kns3 and Kns4 have periphragm covered with amoebiform, radial structures in the shape of asterisks (Fig. 69A–D, O, P). Distribution density of these structures may vary from specimen to specimen: in case of denser ornamentation, periphragm becomes slightly granular appearance (Fig. 69A, B). Other specimens have smooth periphragm with infrequent, isolated amoebiform structures. It is not certain if the presence of these radial structures on *Deflandrea* specimens from samples Kns3 and Kns4 reflects taxonomical diversity. Similar structures were described by Gocht (1969, p. 87, 89) on some Palaeogene dinoflagellate cysts. He interpreted them as traces of fungi activity and noted some similarities to those described by Elvik (1966) on fossil sporomorphs (see also e.g., Palamarczuk & Barreda, 1998, pl. 3, fig. 11). Gocht (1966, p. 89) noted selective occurrence of these structures: they appear on *Wetzelialla* and *Deflandrea* specimens only, whereas specimens of other taxa from the same sample are intact. The same phenomenon is observed in Koniusza material. Amoebiform structures appear on some *Deflandrea* specimens only, whereas other species from the same samples show no similar traces.

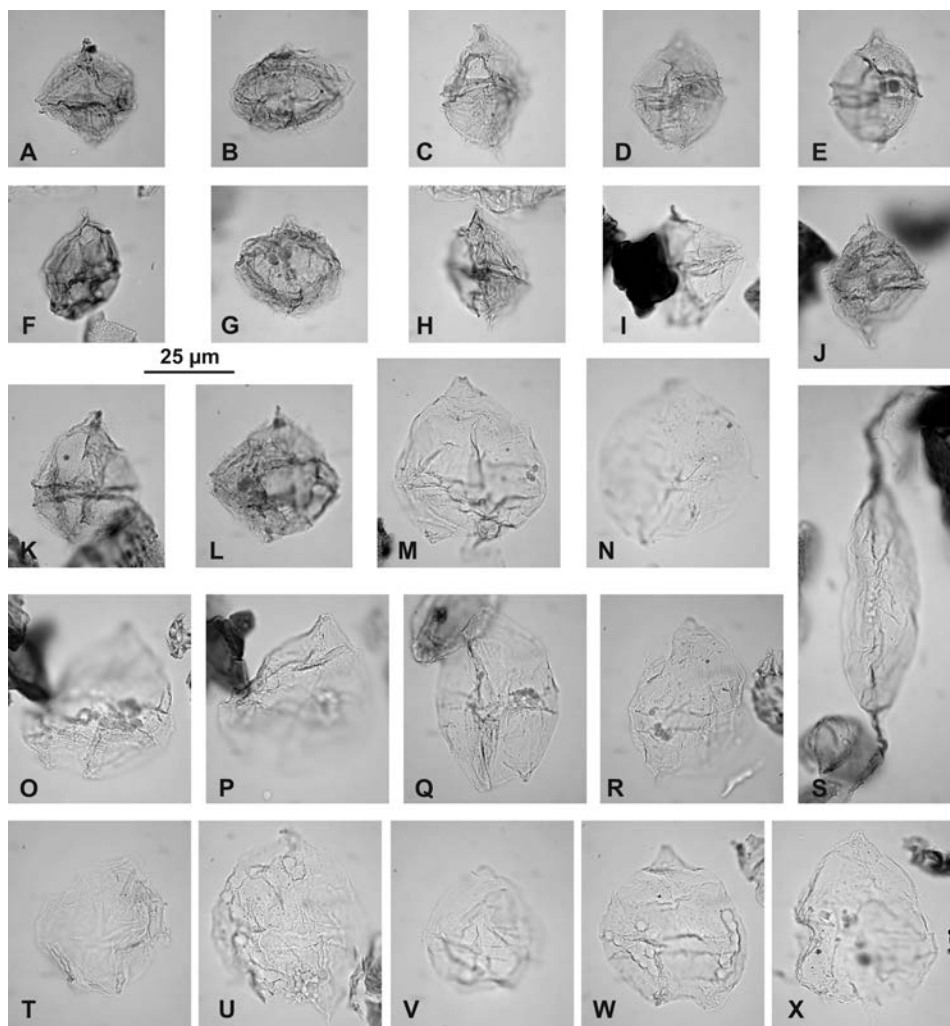




**Fig. 70.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–N** – *Deflandrea phosphoritica* (**A–C**: same specimen, various foci; Kns1; **D**: Kns1; **E–G**: same specimen, various foci; Kns5; **H**: Kns12; **I–K**: same specimen, various foci; Kns1; **L–N**: same specimen, various foci; Kns5)



**Fig. 71.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Lentinia serrata* (Kns13); **B, C** – *Lentinia serrata* (same specimen, various foci; Kns1); **D** – *Lentinia serrata* (Kns5); **E** – *Lentinia serrata* (Kns5); **F, G** – *Lentinia serrata* (same specimen, various foci; Kns5); **H** – *Lentinia serrata* (Kns6); **I** – *Lentinia serrata* (Kns6); **J** – *Lentinia serrata* (Kns6); **K, L** – *Lentinia serrata* (same specimen, various foci; Kns12); **M** – *Lentinia serrata* (Kns12); **N** – *Lentinia serrata* (Kns7); **O, P** – *Lentinia serrata* (same specimen, various foci; Kns7); **Q–T** – Indetermined peridinoids (Q: Kns1, R: Kns5, S: Kns5, T: Kns3); **U–W** – *Vozzhennikovia* sp. (same specimen, various foci; Kns2); **X** – *Vozzhennikovia* sp. (Kns2)



**Fig. 72.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–L**– *Phthanoperidinium?* *eocenicum* (A–F: Kns5, D, E: same specimen, various foci; G: Kns7; H, I: Kns12; J–L: Kns6); **M–R**, **T–X**– *Vectidinium?* sp. (M, N: Kns6; O–R: Kns5, O, P: same specimen, various foci; T–X: Kns11); **S**– *Palaeocystodinium golzowense* (Kns5)

### Genus *Lentinia* Bujak 1980

Type species: *Lentinia serrata* Bujak 1980

1980 *Lentinia* n. gen.; Bujak in Bujak *et al.* (1980), p. 69

### *Lentinia serrata* Bujak 1980

(Fig. 71A–P)

1980 *Lentinia serrata* n. sp.; Bujak in Bujak *et al.* (1980), p. 71–72, pl. 18, figs. 7–12; text-figs. 18A–F, 19

**Material.** Rare in samples Kns1, Kns5, Kns6, Kns12, Kns13, Kns22, Kns26 and Kns32, more frequent in samples Kns7 and Kns8.

**Description.** Cyst peridinioid, cornucavate with one apical and two, symmetrically placed antapical horns of equal length. Pericyst widest in paracingular area. Periphragm smooth with small denticles, commonly of linear arrangement. Archaeopyle intercalary 2a, large. This species in the material studied shows diversity in epi- and hypocyst length ratio. Some specimens have paracingulum placed symmetrically, dividing pericyst into epicyst and hypocyst of approximately equal length (Fig. 71K). Majority of specimens have longer epicyst than hypocyst (e.g., Fig. 71A, B, E), but some specimens have very unsymmetrically placed paracingulum that divides pericyst into very short hypocyst and much longer epicyst (Fig. 71F, G, J, O, P). Colouration of pericyst is uniform: some specimens are brownish-pigmented (Fig. 71A, H, I), whereas majority of *L. serrata* specimens are pale-coloured.

Genus *Palaeocystodinium* Alberti 1961

Type species: *Palaeocystodinium golzowense* Alberti 1961

1961 *Palaeocystodinium* n. gen.; Alberti (1961), p. 20

*Palaeocystodinium golzowense* Alberti 1961

(Fig. 72S)

1961 *Palaeocystodinium golzowense* n. sp.; Alberti (1961), p. 20, pl. 7, figs. 10–12; pl. 12, fig. 16

**Material.** Single specimens in samples Kns5, Kns7, Kns8, Kns12 and Kns22.

**Description.** Cyst cornucavate, strongly elongated, with one apical and one antapical, long, capitate horn. Periphragm smooth and thin, densely folded. Archaeopyle not visible.

Genus *Vozzhennikovia* Lentin et Williams 1976

Type species: *Vozzhennikovia apertura* (Wilson 1967a) Lentin et Williams 1976

1976 *Vozzhennikovia* n. gen.; Lentin & Williams (1976), p. 65–66

*Vozzhennikovia* sp.

(Fig. 71U–X, Fig. 80H)

**Material.** Two specimens in sample Kns2. A single specimen was found in sample Kns3 during SEM observations.

**Description.** Cyst peridinioid, ovoidal, compressed, cornucavate, with smooth and thin periphragm covered by irregular echinae. One blunt apical horn and one acuminate short antapical horn [right antapical horn absent (Fig. 71X) or strongly reduced (Fig. 71U)]. Paracingulum indicated by two parallel faint denticulate ridges. Archaeopyle not visible.

Subfamily **PALAEOPERIDINIOIDEAE** (Vozzhennikova 1961) Bujak et Davies 1983

Genus ***Phthanoperidinium*** Drugg et Loeblich Jr. 1967

Type species: *Phthanoperidinium amoenum* Drugg et Loeblich Jr. (1967)

- 1967 *Phthanoperidinium* n. gen.; Drugg & Loeblich Jr. (1967), p. 182  
 1981 *Phthanoperidinium* Drugg et Loeblich Jr. 1967 emend.; Edwards & Bebout (1981), p. 36  
 1982 *Phthanoperidinium* Drugg et Loeblich Jr. 1967 emend.; Islam (1982), p. 306

*Phthanoperidinium alectrolophum* Eaton 1976

(Fig. 73S–V, Fig. 74D, E, G–I)

- 1976 *Phthanoperidinium alectrolophum* n. sp.; Eaton (1976), p. 295, 298, pl. 17, figs. 10–11; text-fig. 23A

**Material.** Rare specimens in samples Kns5, Kns6, Kns8, Kns18 and Kns30.

**Description.** Cyst subspherical, proximate, with short apical horn. Cyst wall smooth, parasutural ridges low with denticulate margins (Fig. 74E, I).

*Phthanoperidinium comatum* (Morgenroth 1966) Eisenack et Kjellström 1972

(Fig. 73C–K, Fig. 74B, C)

- 1966 *Peridinium comatum* n. sp.; Morgenroth (1966b), p. 1, pl. 1, figs. 1–2  
 1972 *Phthanoperidinium comatum* comb. nov.; Eisenack & Kjellström (1972), p. 907

**Material.** Rare to moderately frequent in most of samples representing dark-coloured mudstone (Kns1, Kns5–7, Kns13, Kns14, Kns20–22, Kns28, Kns29, Kns31 and Kns32); frequent in sample Kns12; absent from samples representing pale-coloured marl.

**Description.** Cyst elongated ellipsoidal to slightly polygonal, chorate, with short, blunt apical horn and tiny projection present on antapex. Paracingular ridges low, smooth. Long solid, slender, distally slightly branched processes arise from these ridges. However, some specimens from Koniusza show incomplete development of smooth ridges, which partially are replaced by rows of short hair-like projections (Fig. 75C). Paraplate areas smooth, covered with various forms of positive relief (best visible under SEM – Fig. 75B, C). Some specimens have intratabular areas covered with irregularly scattered small granulae (Fig. 75C). More common are specimens with additional rows of hair-like projections separated from parasutural ridges by smooth bands (Fig. 75B).

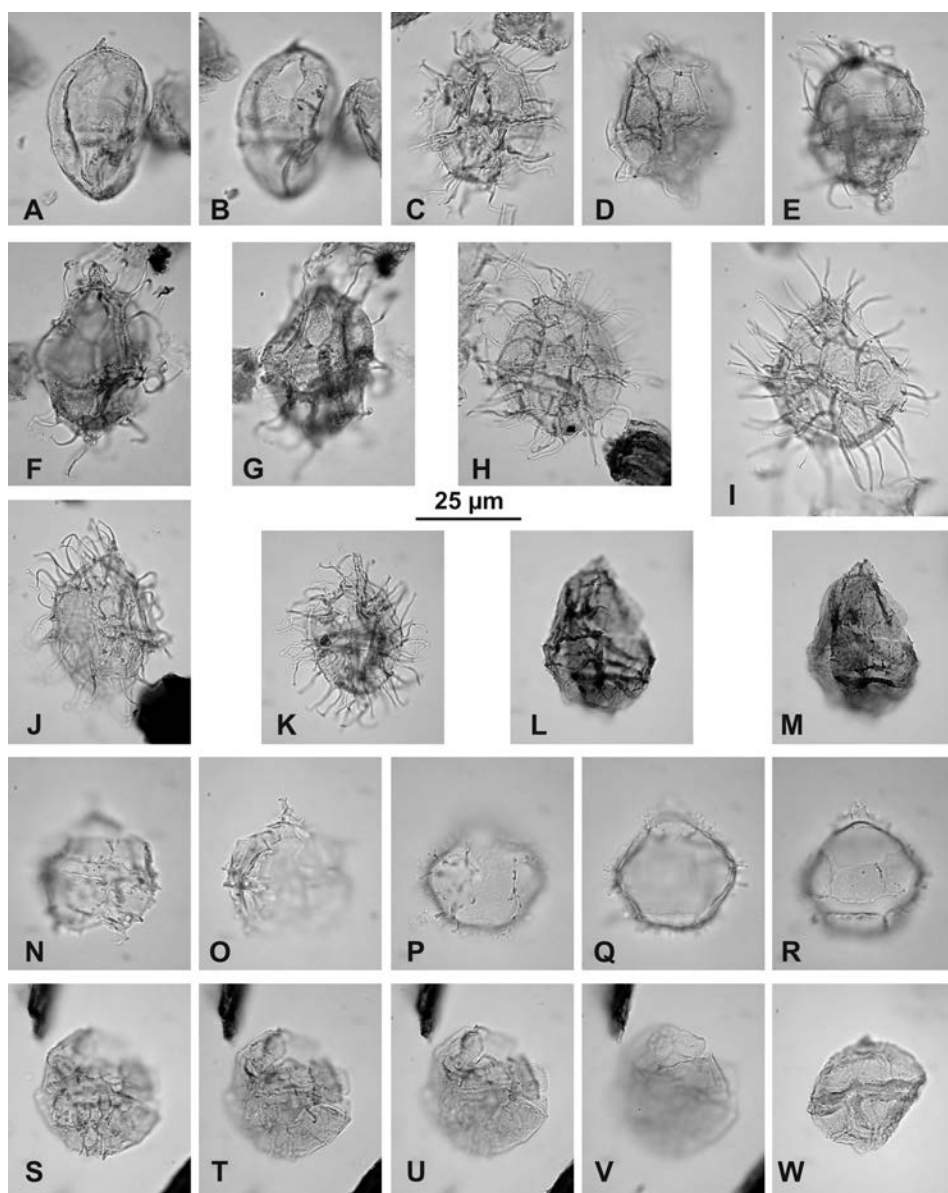
*Phthanoperidinium delicatum* Michoux 1985

(Fig. 73N–R, Fig. 85A)

- 1985 *Phthanoperidinium delicatum* n. sp.; Michoux (1985), p. 147–148, pl. 2, figs. 1–4; pl. 3, figs. 1–5, 13–14

**Material.** Two specimens in sample Kns4; three specimens in the Hieroglyphic beds (KnsH2).





**Fig. 73.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Phthanoperidinium stockmansii* (same specimen, various foci; Kns1); **C** – *Phthanoperidinium comatum* (Kns1); **D, E** – *Phthanoperidinium comatum* (same specimen, various foci; Kns5); **F, G** – *Phthanoperidinium comatum* (same specimen, various foci; Kns1); **H** – *Phthanoperidinium comatum* (Kns6); **I** – *Phthanoperidinium comatum* (Kns12); **J** – *Phthanoperidinium comatum* (Kns6); **K** – *Phthanoperidinium comatum* (Kns5); **L, M** – *Phthanoperidinium stockmansii* (same specimen, various foci; Kns6); **N, O** – *Phthanoperidinium delicatum* (same specimen, various foci; Kns4); **P–R** – *Phthanoperidinium delicatum* (same specimen, various foci; Kns4); **S–V** – *Phthanoperidinium alectrolophum* (same specimen, various foci; Kns6); **W** – *Phthanoperidinium alectrolophum* (Kns8)

**Description.** Cyst peridinioid, subspherical to rounded polygonal, with short blunt apical horn and two poorly developed antapical ones. Parasutural ridges very low. Short processes of irregular shape, commonly bifurcate, arise from these ridges.

*Phthanoperidinium? eocenicum* (Cookson et Eisenack 1965)

Lentin et Williams 1973

(Fig. 72A–L, Fig. 74A)

1965 *Peridinium eocenicum* n. sp.; Cookson & Eisenack (1965), p. 119–120, pl. 11, figs. 1–5

1973 *Phthanoperidinium? eocenicum* comb. nov.; Lentin & Williams (1973), p. 113

**Material.** Rare specimens in samples Kns5–7, Kns12, Kns19 and Kns27.

**Description.** Cyst peridinioid, fusiform, with one apical and two antapical horns; one of the latter usually reduced. Epicyst and hypocyst separated by helicoidal paracingulum. Paraplates separated by smooth ridges, which occasionally bear rare short processes.

*Phthanoperidinium stockmansii* (de Coninck 1975) Lentin et Williams 1977

(Fig. 73A, B, L, M, Fig. 74F)

1975 *Peridinium stockmansii* n. sp.; de Coninck (1975), p. 97–98, pl. 17, figs. 18–37

1977 *Phthanoperidinium stockmansii* comb. nov.; Lentin & Williams (1977b), p. 131

**Material.** Single specimens in samples Kns1, Kns3, Kns5 and Kns6.

**Description.** Cyst peridinioid, slightly elongated, subpolygonal, with short apical horn. Parasutural features shown, beside the archaeopyle, by rows of very tiny spines located along the paraplates boundaries. Archaeopyle intercalary.

Genus *Vectidinium* Liengjarern, Costa et Downie 1980

Type species: *Vectidinium stoveri* Liengjarern, Costa et Downie 1980

1980 *Vectidinium* n. gen.; Liengjarern *et al.* (1980), p. 490

*Vectidinium? sp.*

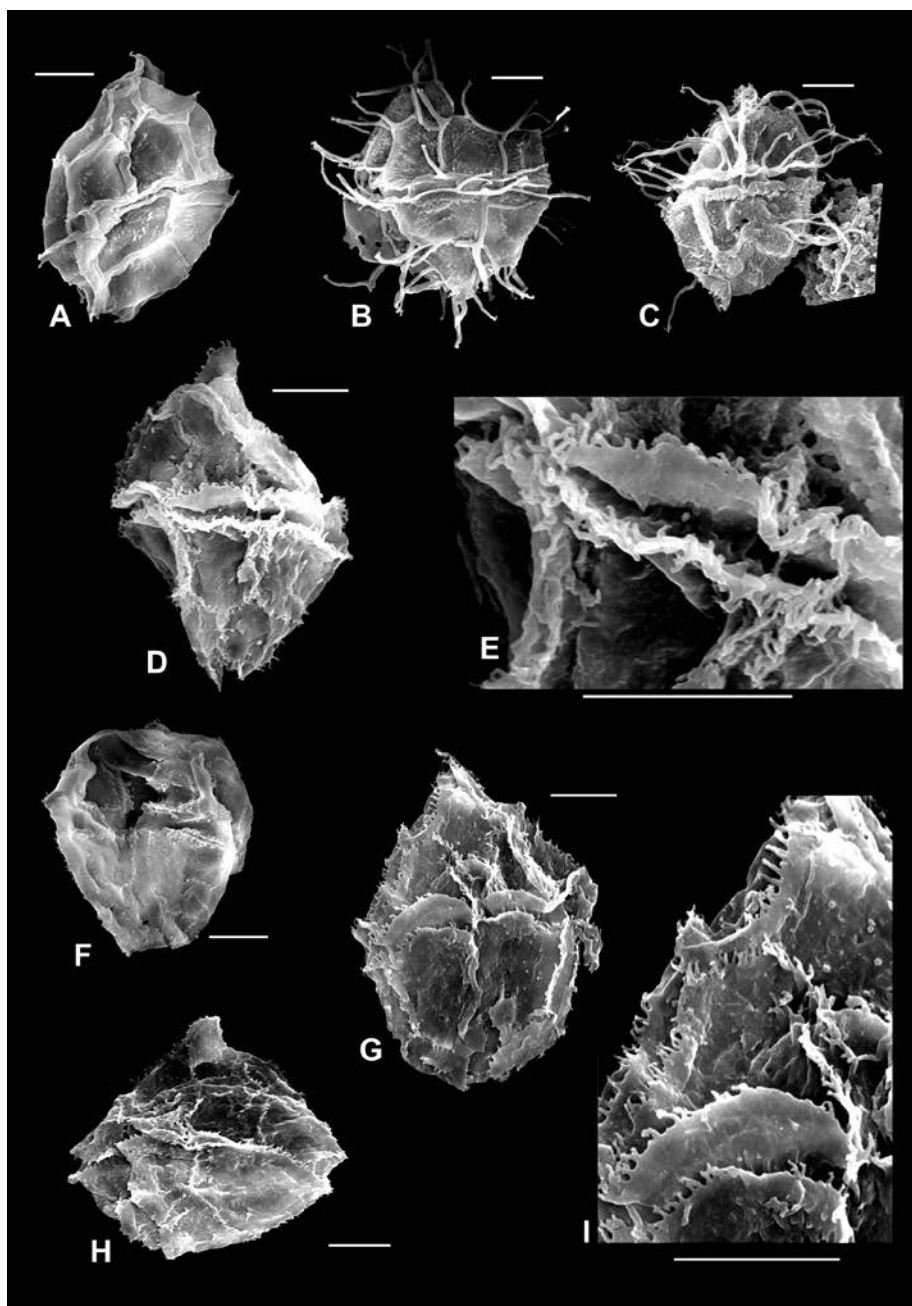
(Fig. 72M–R, T–X)

2004 *Vectidinium* sp.; Gedl (2004a), fig. 8a

**Material.** Rare in samples Kns4–7, Kns22 and Kns28; moderately frequent in samples Kns11 and Kns12.

**Description.** Cyst compressed peridinioid, with one blunt apical horn and two acuminate short antapical horns, of which one may be reduced. Cyst wall smooth and thin, covered by irregular, sparsely distributed echinae. Paracingulum indicated by a depression bordered by two parallel denticulate ridges. Archaeopyle intercalary, three intercalary paraplates involved. Paraplates adnate to the paracingular paraplates along their margins, separated elsewhere.

This species has been questionably included to the genus *Vectidinium* due to uncertain problem of cyst wall relation. Majority of specimens are acavate (e.g., Fig.



**Fig. 74.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10  $\mu$ m). **A** – *Phthanoperidinium?* *eocenicum* (Kns5); **B** – *Phthanoperidinium comatum* (Kns5); **C** – *Phthanoperidinium comatum* (Kns5); **D, E** – *Phthanoperidinium alectrolophum* (Kns5; **D**: complete specimen; **E**: detail showing parasutural ridges with denticulate margins); **F** – *Phthanoperidinium stockmansii* (Kns5); **G, I** – *Phthanoperidinium alectrolophum* (Kns5; **D**: complete specimen; **E**: detail showing parasutural ridges with denticulate margins); **H** – *Phthanoperidinium alectrolophum* (Kns5)

72T, U, X) but some of them seem to be cornucavate (Fig. 72M, Q, R) with developed epipericoel. However, due to very delicate cyst wall, which is commonly folded, presence of these epipericoels is not certain. Similar species was described by Gedl (2004a) from the topmost part of the Leluchów Marl Member (Magura Nappe, Carpathians, Poland).

#### Indetermined peridinioids

(Fig. 71Q, R, S, T, Fig. 80G)

**Material.** Rare specimens in samples Kns1, Kns3, Kns5, Kns17, Kns19, Kns20, Kns22, Kns28 and Kns33. A single specimen was found in sample Kns8 during SEM observations.

**Description.** A few specimens of peridinioids, which due to their preservation have not been precisely determined. These are small, compressed peridinioid cysts with one apical horn and two acuminate short antapical horns, of which one may be reduced. Their cyst wall is smooth, thin and commonly densely folded. Pericoel presence and archaeopyle type is uncertain.

#### Subfamily **WETZELIELLOIDEAE** (Vozzhennikova 1961)

Bujak et Davies 1983

#### Genus *Apectodinium* (Costa et Downie 1976) Lentin et Williams 1977

Type species: *Apectodinium homomorphum* (Deflandre et Cookson 1955) Lentin et Williams 1977

1976 *Wetzelietta Apectodinium* n. subg.; Costa & Downie (1976), p. 608

1977 *Apectodinium* comb. nov.; Lentin & Williams (1977b), p. 8

#### *Apectodinium homomorphum* (Deflandre et Cookson 1955) Lentin et Williams 1977

(Fig. 80I, Fig. 82A–C, Q)

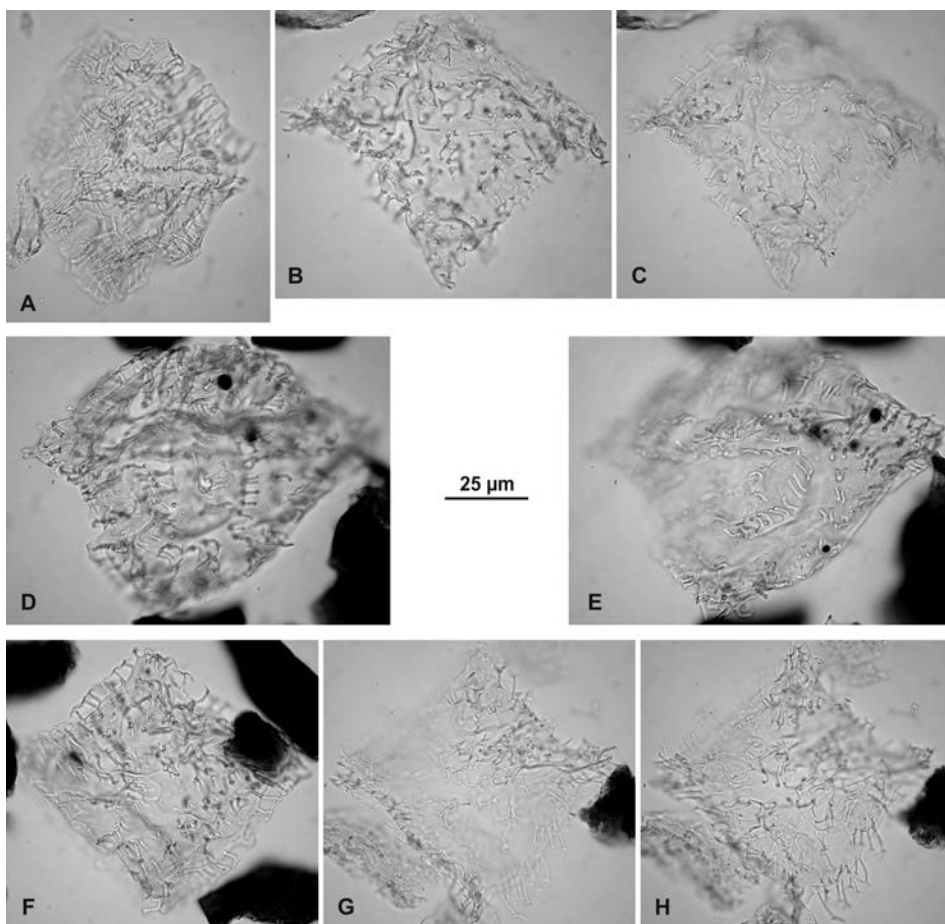
1955 *Wetzelietta homomorpha* n. sp.; Deflandre & Cookson (1955), p. 254, pl. 5, fig. 7

1977 *Apectodinium homomorphum* comb. nov.; Lentin & Williams (1977b), p. 8

1979 *Apectodinium homomorphum* (Deflandre et Cookson 1955) Lentin et Williams 1977 emend.; Harland (1979c), p. 64

**Material.** It occurs in samples representing pale-coloured marl: single specimens in samples Kns3 and Kns4, a few specimens in sample Kns24.

**Description.** Cyst proximochorate, with rounded pentagonal outline; two specimens from samples Kns3 and Kns4 show faintly developed antapical horns, which make them similar to *Apectodinium parvum*. Wall layers closely adpressed, except of the latter examples where small pericoels are developed (Fig. 82B, D). Cyst wall smooth (Fig. 82A) to finely granular (Fig. 82C). Processes numerous, hollow, evexate, occasionally branched. Archaeopyle not visible.



**Fig. 75.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Charlesdowniea coleothrypta* (Kns5); **B, C** – *Charlesdowniea clathrata* (same specimen, various foci; Kns11); **D, E** – *Charlesdowniea coleothrypta* (same specimen, various foci; Kns2); **F** – *Charlesdowniea coleothrypta* (Kns2); **G, H** – *Charlesdowniea clathrata* (same specimen, various foci; Kns12)

### Genus *Charlesdowniea* Lentin et Vozzhennikova 1989

Type species: *Charlesdowniea coleothrypta* (Williams et Downie 1966) Lentin et Vozzhennikova 1989

1989 *Charlesdowniea* n. gen.; Lentin & Vozzhennikova (1989), p. 225, 227

### *Charlesdowniea clathrata* (Eisenack 1938) Lentin et Vozzhennikova 1989

(Fig. 75B, C, G, H, Fig. 76A–F)

1938 *Wetzeliella clathrata* n. sp.; Eisenack (1938), p. 187; text-fig. 5

1989 *Charlesdowniea clathrata* comb. nov.; Lentin & Vozzhennikova (1989), p. 227

**Material.** Rare specimens occur in samples mainly representing dark-coloured



mudstone: Kns5, Kns7, Kns10 and Kns12, Kns18, Kns20, Kns22, Kns26, Kns28 and Kns30; frequent in sample Kns11.

**Description.** Cyst rhomboidal, with four reduced horns: one apical, two lateral and one antapical (right antapical horn hardly discernible). Lateral horns are occasionally most developed (e.g., Fig. 75B, C). Periphragm smooth. Relatively short processes hollow, distally branched and connected in rows by distal thin trabeculae.

*Charlesdowniea coleothrypta* (Williams et Downie 1966) Lentin et  
Vozzhennikova 1989

(Fig. 75A, D, E, Fig. 77A–I, Fig. 78A–I, Fig. 79A–G, Fig. 80A–E)

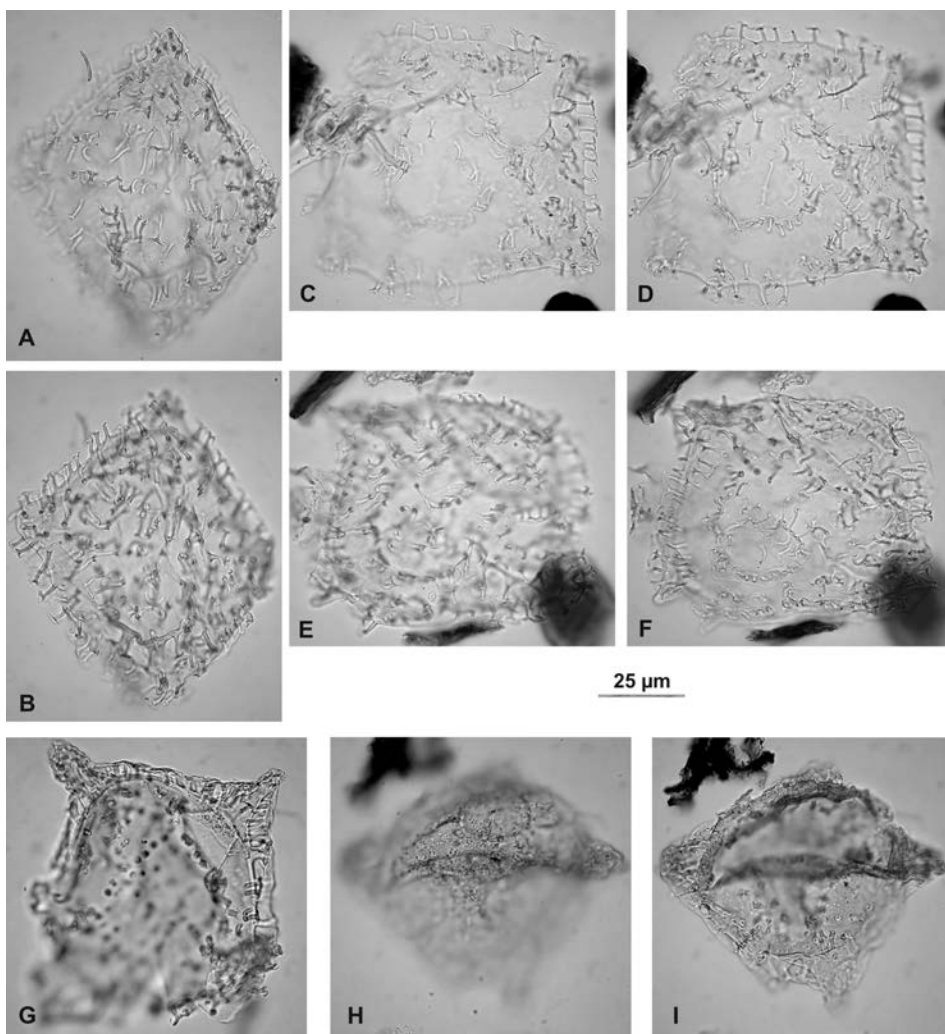
1966     *Wetzeliiella coleothrypta* n. sp.; Williams & Downie (1966b), p. 185–186, pl. 18, figs. 8–9; text-fig. 47

1989     *Charlesdowniea coleothrypta* comb. nov.; Lentin & Vozzhennikova (1989), p. 225

**Material.** This is the most frequent species of the genus *Charlesdowniea* in the Koniusza material. Frequent specimens occur in most of samples representing dark-coloured mudstone (rare in samples Kns31 and Kns 32); absent in most of samples representing pale-coloured marl (except of samples Kns3 and Kns24 where single specimens occur, and sample Kns8 that yielded frequent specimens).

**Description.** Pericyst rhomboidal to pentagonal (see *Remarks*), with smooth to finely granular wall covered by hollow processes. The latter united distally by isolated ectophragmal portions, which shape reflects paraplates.

**Remarks.** *Charlesdowniea coleothrypta* from Koniusza shows a high morphological diversity. It refers to general shape of the cyst, process length and morphology of the ectophragm that distally unites the processes. Specimens attributed here to *Charlesdowniea coleothrypta* have well developed ectophragmal pattern reflecting paraplate arrangement. General cyst shape is bimodal: specimens with typical for *Wetzeliielloideae* well developed horns (two lateral, apical and two antapical, of which the right one is reduced) co-occur with oval specimens almost devoid of pronounced horns. The latter presumably represents subgenus *C. coleothrypta rotundata* described by Châteauneuf & Gruas-Cavagnetto (1978). There are two morphotypes of *C. coleothrypta* varied by process length: the one with short processes, and the morphotype with long, slender processes. The latter predominate on specimens with well developed horns. The third morphological feature that differ specimens of *C. coleothrypta* from Koniusza refers to the morphology of the ectophragm. Majority of specimens have rather smooth ectophragmal platforms that distally terminate processes. However some specimens possess perforated ectophragm (Fig. 80C, E). Perforation pattern is not stable among specimens with such an ectophragm: some specimens possess perforation consisting of holes irregular in shape and diameter, usually grouped in central portions of ectophragmal platforms. The other have regularly perforated platforms in a way resembling perforations on periphragm of *Rhombodinium perforatum*. Williams & Downie (1966b) in their original diagnosis of *C. coleothrypta* state that the ectophragmal



**Fig. 76.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Charlesdowniea clathrata* (same specimen, various foci; Kns5); **C, D** – *Charlesdowniea clathrata* (same specimen, various foci; Kns7); **E, F** – *Charlesdowniea clathrata* (same specimen, various foci; Kns7); **G** – *Charlesdowniea columna* (Kns3); **H, I** – *Charlesdowniea columna* (same specimen, various foci; Kns3)

membrane is “finely perforate”. They do not mention if this feature is diagnostic for this species. It is also difficult to recognize this feature from illustrations of *C. colethrypta* in literature. If not described in text, only SEM microphotographs allow clear determination of ectophragm nature (see e.g., Downie *et al.* 1971, pl. 2, fig. 5).

*Charlesdowniea columna* (Michoux 1988) Lentin et Vozzhennikova 1990  
(Fig. 76G–I)

1988 *Kisselevia columna* n. sp.; Michoux (1988), p. 28, 30, pl. 1, figs. 2–3, 6–5; pl. 2, figs. 3–5; text-figs. 7A–B

1990 *Charlesdowniea columna* comb. nov.; Lentin & Vozzhennikova (1990), p. 74

**Material.** Two specimens in sample Kns3.

**Description.** Cyst pentagonal, circumcavate to cornucavate, with short columnar hollow processes united distally by ectophragmal membrane. Processes occur all over pericyst, but most common are at ambital margins. Five horns well developed, although right antapical horn is shorter than the left one. Endocyst ovoidal.

### Genus *Dracodinium* Gocht 1955

Type species: *Dracodinium solidum* Gocht 1955

1955 *Dracodinium* n. gen.; Gocht (1955), p. 87

1980 *Dracodinium* Gocht 1955 emend.; Bujak, Downie, Eaton & Williams (1980), p. 28

### *Dracodinium laszczynskii* Gedl 1995

(Fig. 80F, Fig. 81A–F)

1995 *Dracodinium laszczynskii* n. sp.; Gedl (1995b), p. 205, pl. 7, figs. 11, 13

**Material.** This species occurs in two samples only (pale-coloured marl), being moderately frequent in sample Kns8, and frequent in sample Kns10.

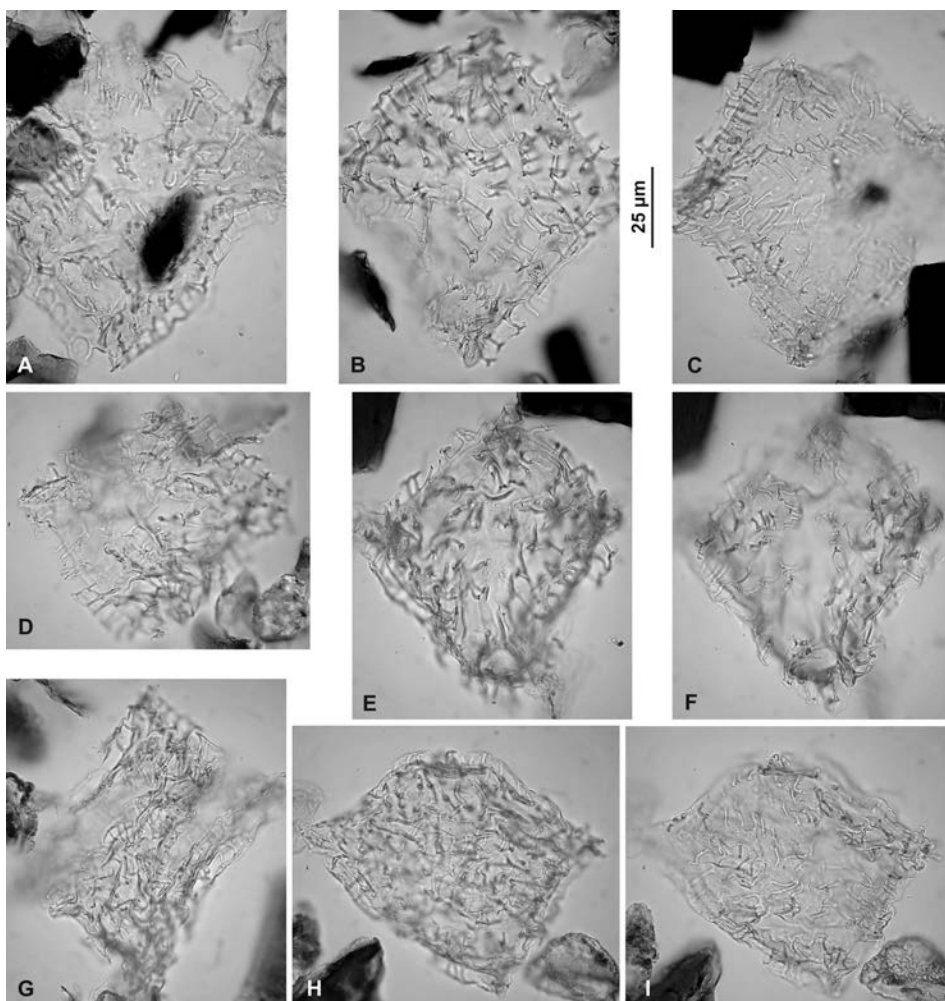
**Description.** Cyst cornucavate, ovoidal, with apical, lateral and antapical horns strongly reduced and appressed to ovoidal endocyst. Pericystal horns very broad, indistinct, tapering with rounded tips. Lateral horns commonly almost not developed. Two antapical horns, left one reduced. Periphragm shape closely follows the shape of endocyst, which makes an ovoidal appearance of the whole cyst (Fig. 81D, E). However, some specimens have more prominent horns, especially apical ones, which taper sharply (Fig. 81A, B). Isolated endocysts, presumably of this species, frequently occur in samples Kns8 and Kns10. Endophragma thick and granular; some specimens seem to have additional membrane developed on granular endophragm (Fig. 82H). Periphragm thin and smooth. Archaeopyle intercalary, operculum free. Periarchoepyle higher than endoarchaeopyle, breadth of both is of the same size.

### *Dracodinium* cf. *laszczynskii* Gedl 1995

(Fig. 63G, H)

**Material.** A single specimen in sample Kns10.

**Description.** Specimen found in sample Kns10 resembles closely *Dracodinium laszczynskii*. It differs, however, by larger epi- and hypopericoels. Apical horn is more prominent, it tapers rather sharply. The latter feature, although not typical for *D. laszczynskii*, was also noted on some specimens attributed to this species (e.g., Fig. 81A). Additional membrane on endocyst is also present (Fig. 81H).



**Fig. 77.** Dinoflagellate cysts from the Popiele beds at Koniusza. A–I – *Charlesdowniea coleothrypta* (A: Kns6; B: Kns13; C: Kns2; D: Kns1; E, F: same specimen, various foci, Kns1; G: Kns1; H, I: same specimen, various foci, Kns5)

### Genus *Rhombodinium* Gocht 1955

Type species: *Rhombodinium draco* Gocht 1955

1955 *Rhombodinium* n. gen.; Gocht (1955), p. 85

1979 *Rhombodinium* Gocht 1955 emend.; Bujak (1979), p. 313–314

#### *Rhombodinium perforatum* (Jan du Chêne et Châteauneuf 1975)

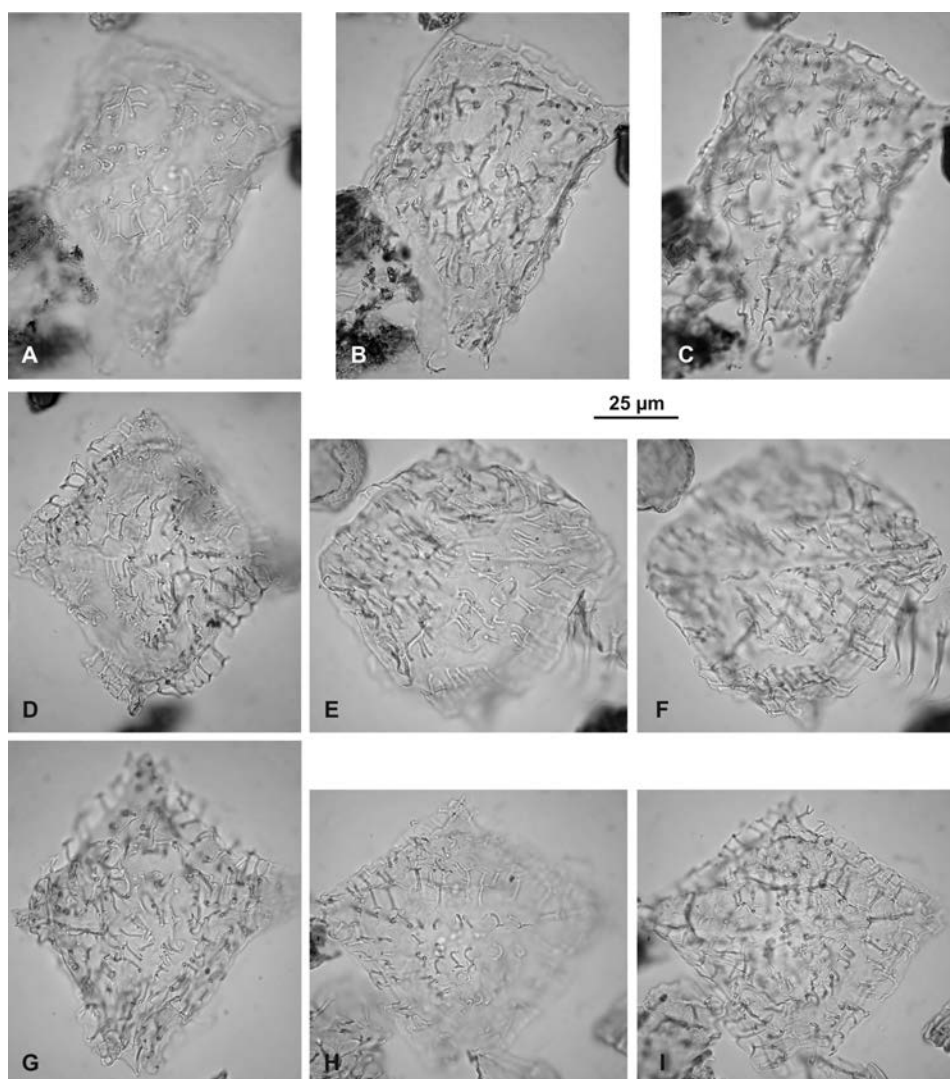
Lentin et Williams 1977

(Fig. 77E–G)

1975 *Wetzelialla Rhombodinium perforatum* n. sp.; Jan du Chêne & Châteauneuf (1975), p. 30–31, pl. 1, figs. 8–14; pl. 3, figs. 7–10

1977 *Rhombodinium perforatum* comb. nov.; Lentin & Williams (1977b), p. 139



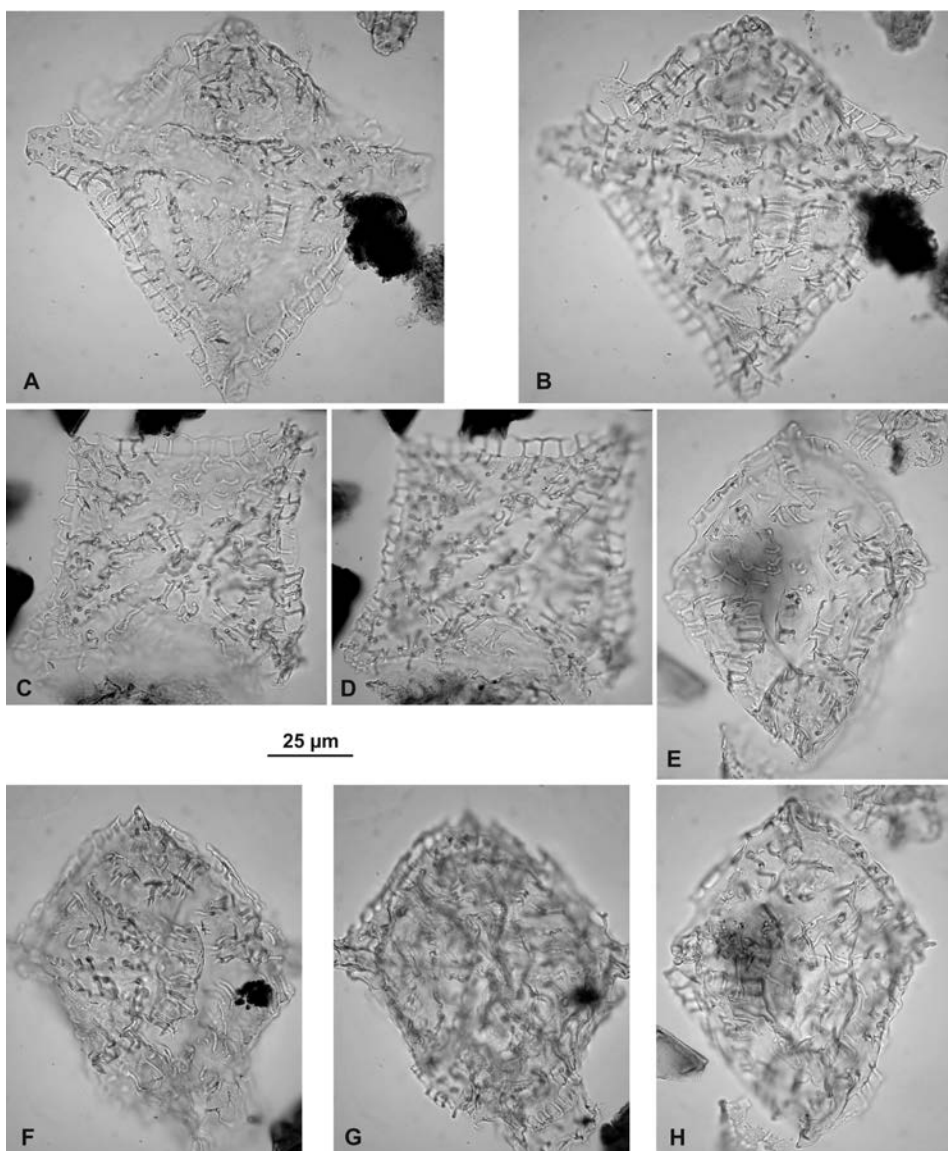


**Fig. 78.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–I** – *Charlesdowniea coleothrypta* (A–C: same specimen, various foci, Kns5; D: Kns12; E, F: same specimen, various foci, Kns5; G: Kns5; H, I: same specimen, various foci, Kns5)

**Material.** Rare specimens occur in samples Kns1, Kns2, Kns5–9, Kns11, Kns22, Kns28 and Kns29.

**Description.** Cyst rhomboidal, circumcavate, with rhomboidal endocyst and pericyst with four horns: apical, two lateral, and one antapical (second antapical reduced). Endophragm thin and smooth, periphragm thin and smooth, densely perforated with tiny holes, approximately circular, of uniform diameter. Periarthacaeopyle of *Wetzeliella articulata* type.



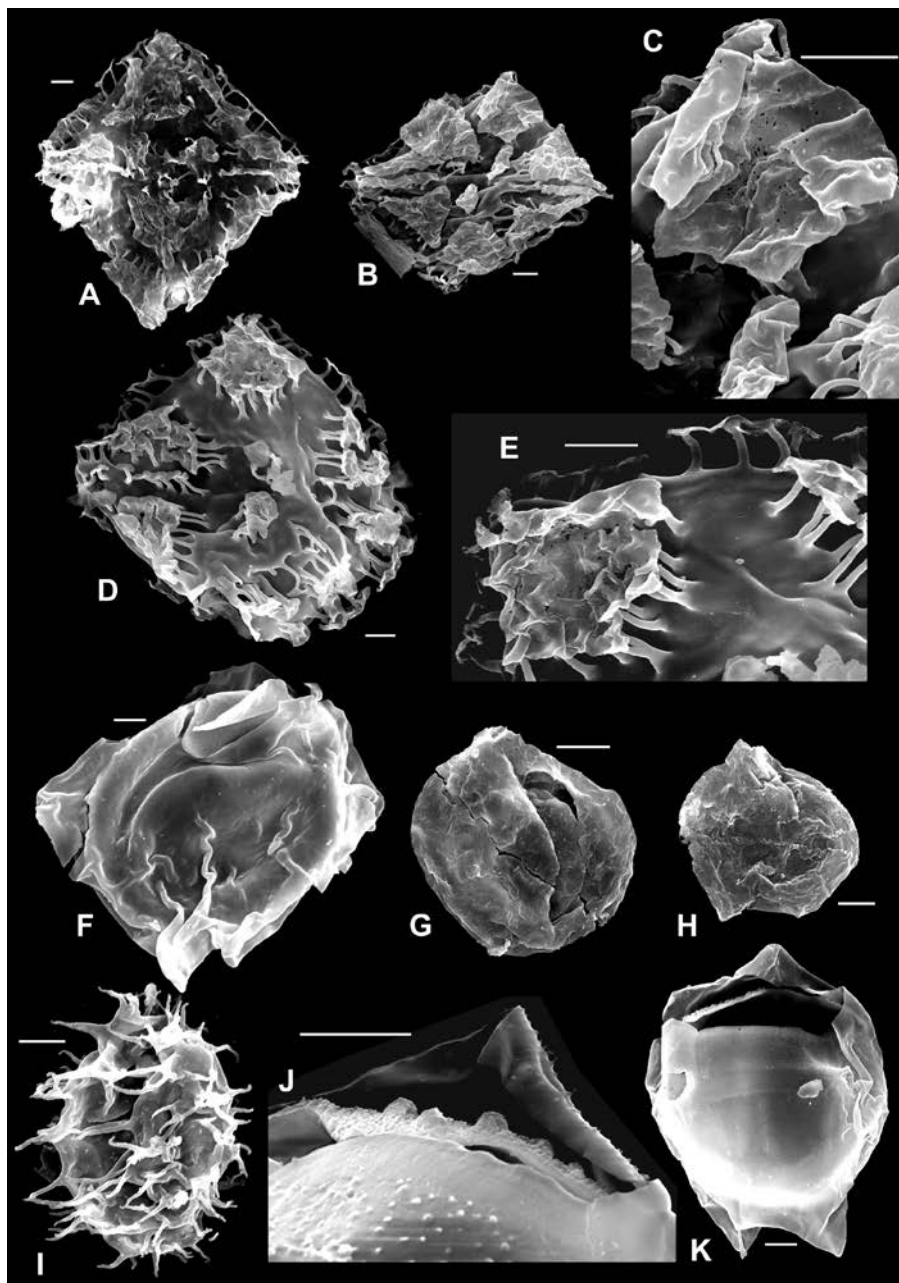


**Fig. 79.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A–H** – *Charlesdowniea coleothrypta* (A, B: same specimen, various foci, Kns6; C, D: same specimen, various foci, Kns2; E, H: same specimen, various foci, Kns5; F, G: same specimen, various foci, Kns5)

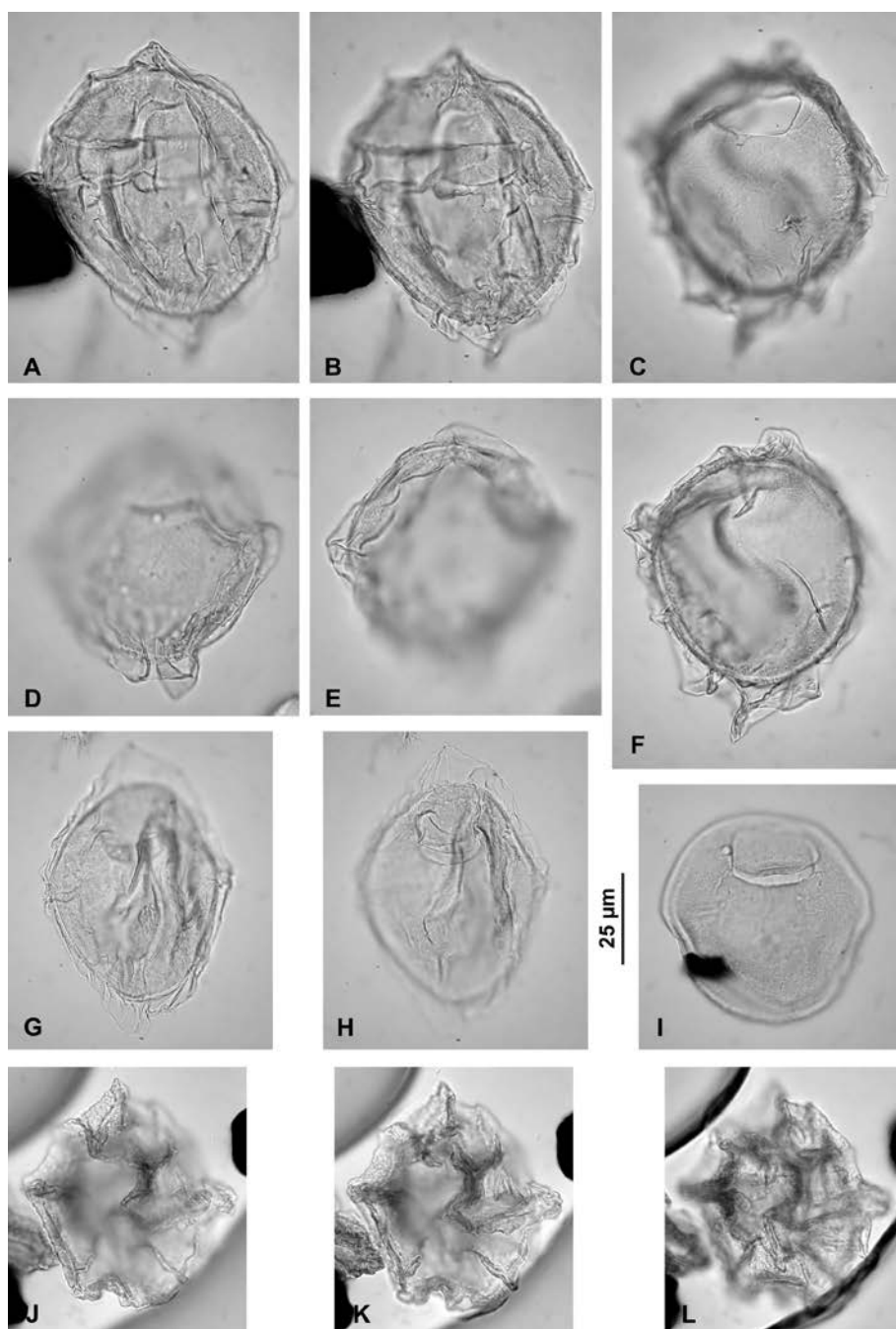
### Genus *Wetzeliiella* Eisenack 1938

Type species: *Wetzeliiella articulata* Eisenack 1938

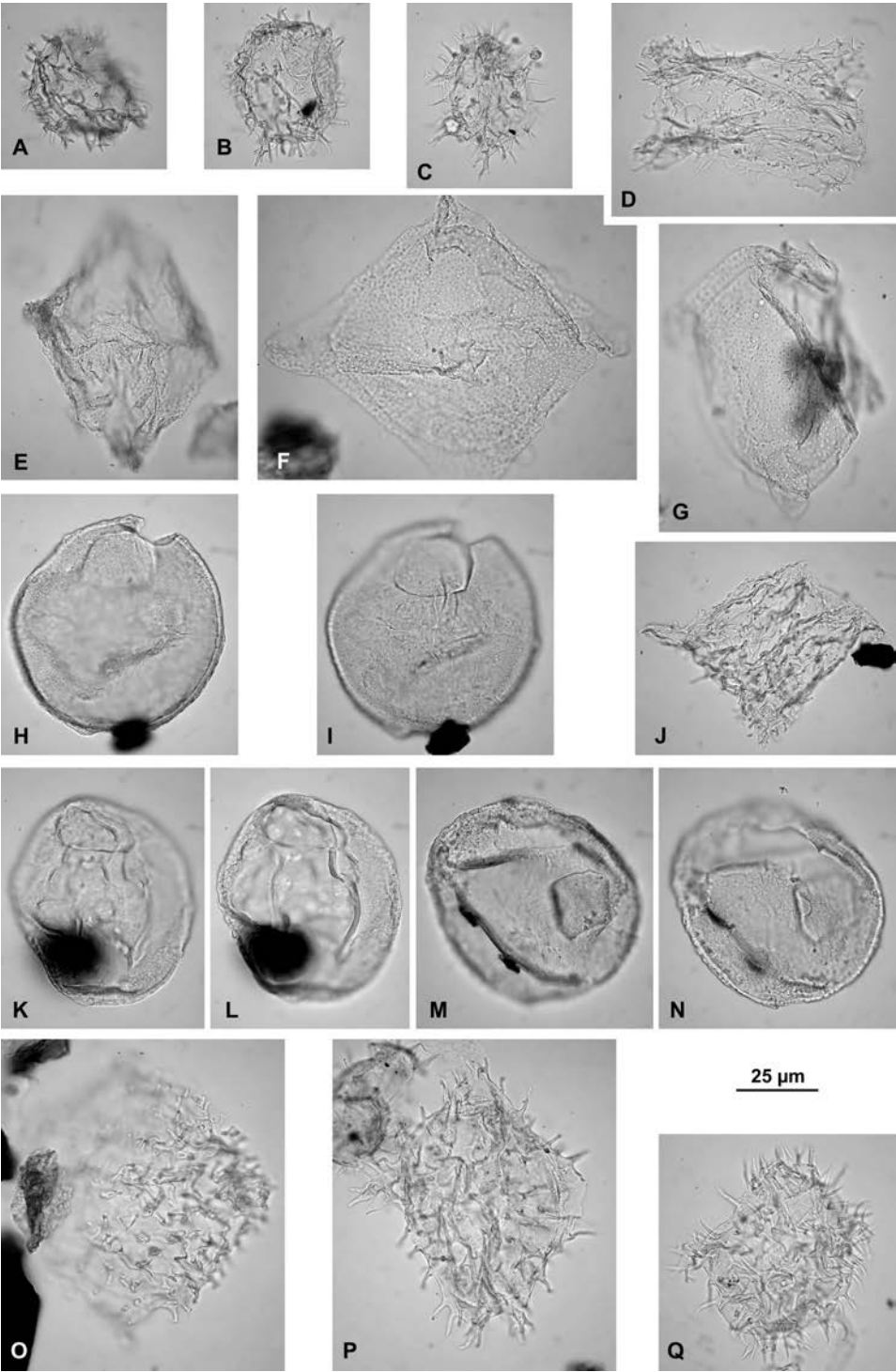
- |      |  |
|------|--|
| 1938 | <i>Wetzeliiella</i> n. gen.; Eisenack (1938), p. 187                           |
| 1966 | <i>Wetzeliiella</i> Eisenack 1938 emend.; Williams & Downie (1966b), p. 182    |
| 1976 | <i>Wetzeliiella</i> Eisenack 1938 emend.; Lentin & Williams (1976), p. 129–130 |



**Fig. 80.** Dinoflagellate cysts from the Popiele beds at Koniusza (scale bars refer to 10  $\mu$ m). **A–E** – *Charlesdowniea coleothrypta* (**A**: ventral view, Kns8; **B**: ventral view, **C**: detail showing perforated ectophragm, Kns5; **D**: ventral view, **E**: detail showing smooth periphragm and processes united distally by finely perforated ectophragm, Kns5); **F** – *Dracodinium laszczynskii* (Kns8); **G** – indetermined peridinioid (Kns8); **H** – *Vozzhennikovia* sp. (Kns3); **I** – *Apectodinium homomorphum* (Kns4); **J** – *Deflandrea heterophlycta* – detail showing granular endophragm with tubercles and an intratabular group of spines on periphragm (Kns5); **K** – *Deflandrea phosphoritica* (Kns5)



**Fig. 81.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A, B** – *Dracodinium laszczynskii* (same specimen, various foci; Kns8); **C, F** – *Dracodinium laszczynskii* (same specimen, various foci; Kns8); **D, E** – *Dracodinium laszczynskii* (same specimen, various foci; Kns10); **G, H** – *Dracodinium* cf. *laszczynskii* Gedl 1995 (same specimen, various foci; Kns10); **I** – endocyst of *Dracodinium* sp. (*D. laszczynskii*?; Kns10); **J–L** – *Wilsonidium*? sp. (Kns27)





**Fig. 82.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Apectodinium homomorphum* (Kns3); **B** – *Apectodinium homomorphum* (Kns3); **C** – *Apectodinium homomorphum* (Kns4); **D** – *Wetzeliiella* sp. (Kns8); **E** – *Rhombodinium perforatum* (Kns8); **F** – *Rhombodinium perforatum* (Kns8); **G** – *Rhombodinium perforatum* (Kns5); **H, I** – endocyst of *Dracodinium* sp. (*D. laszczynskii*?; same specimen, various foci; Kns8); **J** – *Wetzeliiella* sp. (Kns10); **K, L** – endocyst of *Dracodinium* sp. (*D. laszczynskii*?; same specimen, various foci; Kns8); **M, N** – endocyst of *Dracodinium* sp. (*D. laszczynskii*?; same specimen, various foci; Kns8); **O, P** – *Wetzeliiella* sp. (O: Kns30, P: Kns23); **Q** – *Apectodinium homomorphum* (Kns24)

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*Wetzeliiella* sp.

(Fig. 82D, J, O, P)

**Material.** This genus is extremely rare in the Koniusza material. Single specimens were found in samples Kns4, Kns8 and Kns10, Kns23, Kns27, Kns30 and Kns33. A single specimen occurs in the Hieroglyphic beds (KnsH2)

**Remarks.** Each of three specimens found is poorly preserved, wrinkled, making specific determination impossible.

Genus *Wilsonidium* Lentin et Williams 1976

Type species: *Wilsonidium tabulatum* (Wilson 1967) Lentin et Williams 1976

1976 *Wilsonidium* n. gen.; Lentin & Williams (1976), p. 138–139

*Wilsonidium*? sp.

(Fig. 81J–L)

**Material.** Two specimens occur in sample Kns27.

**Description.** Cyst peridinioid, of rhomboidal shape of the pericyst with poorly developed horns (one apical, two lateral and two broad antapical). Periphragm thick, densely rugulate, presumably perforated. Endocyst not visible. Periphragm folded forming (parasutural?) ridges. Archaeopyle not discernible.

**Discussion.** This species was questionably included to the genus *Wilsonidium* on the base of ridges that presumably are in parasutural positions.

Family CONGRUENTIDIACEAE Schiller 1935

Subfamily CONGRUENTIDIOIDEAE (Autonym)

Genus *Lejeunecysta* Artzner et Dörhöfer 1978

Type species: *Lejeunecysta hyalina* (Gerlach 1961) Artzner et Dörhöfer 1978

1961 *Lejeunia* n. gen.; Gerlach (1961), p. 169

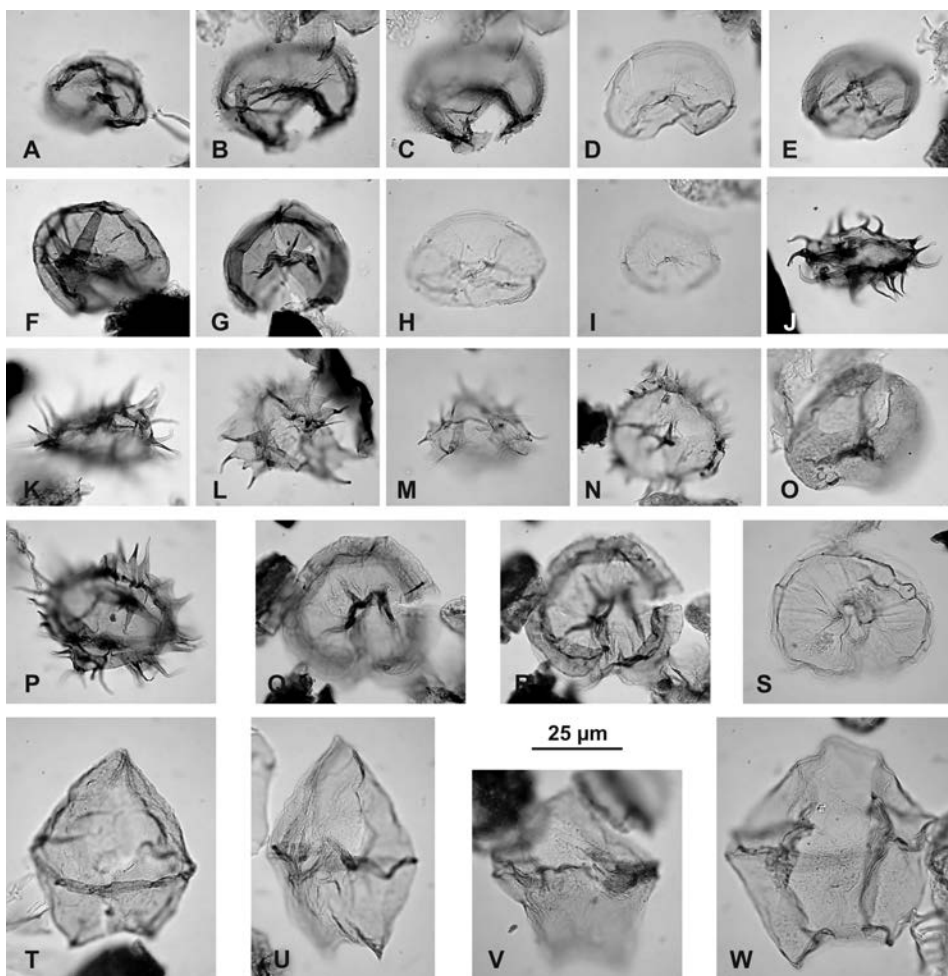
1972 *Lejeunia* Gerlach 1961 emend.; Kjöllstrom (1972), p. 467

1976 *Lejeunia* Gerlach 1961 emend.; Lentin & Williams (1976), p. 68–69

1978 *Lejeunecysta* nom. nov.; Artzner & Dörhöfer (1978), p. 1381

1980 *Lejeunia* Gerlach 1961 emend.; Bujak in Bujak *et al.* (1980), p. 68



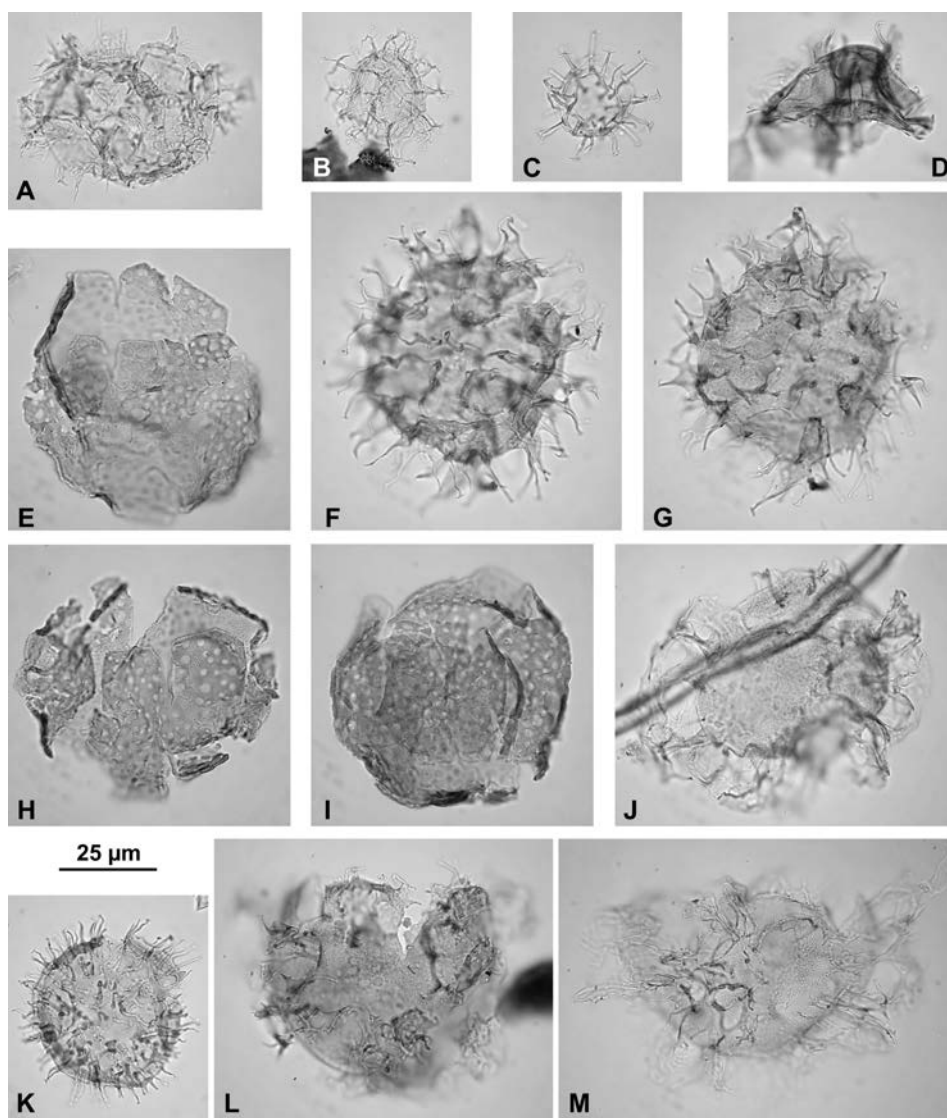


**Fig. 83.** Dinoflagellate cysts from the Popiele beds at Koniusza. **A** – *Selenopemphix nephroides* (Kns6); **B, C** – *Selenopemphix selenoides* (same specimen, various foci; Kns12); **D** – *Selenopemphix nephroides* (Kns12); **E** – *Selenopemphix nephroides* (Kns12); **F** – *Selenopemphix nephroides* (Kns6); **G** – *Selenopemphix nephroides* (Kns6); **H** – *Selenopemphix nephroides* (Kns5); **I** – *Selenopemphix nephroides* (Kns5); **J** – *Selenopemphix armata* (Kns3); **K** – *Selenopemphix armata* (Kns6); **L** – *Selenopemphix armata* (Kns6); **M** – *Selenopemphix armata* (Kns12); **N** – *Selenopemphix armata* (Kns13); **O** – *Lejeunecysta globosa* (Kns12); **P** – *Selenopemphix armata* (Kns6); **Q, R** – *Selenopemphix nephroides* (same specimen, various foci; Kns13); **S** – *Selenopemphix nephroides* (Kns13); **T** – *Lejeunecysta fallax* (Kns12); **U** – *Lejeunecysta fallax* (Kns12); **V** – *Lejeunecysta* sp. (Kns7); **W** – *Lejeunecysta lata* (Kns5)

*Lejeunecysta fallax* (Morgenroth 1966) Artzner et Dörhöfer 1978

(Fig. 83T, U)

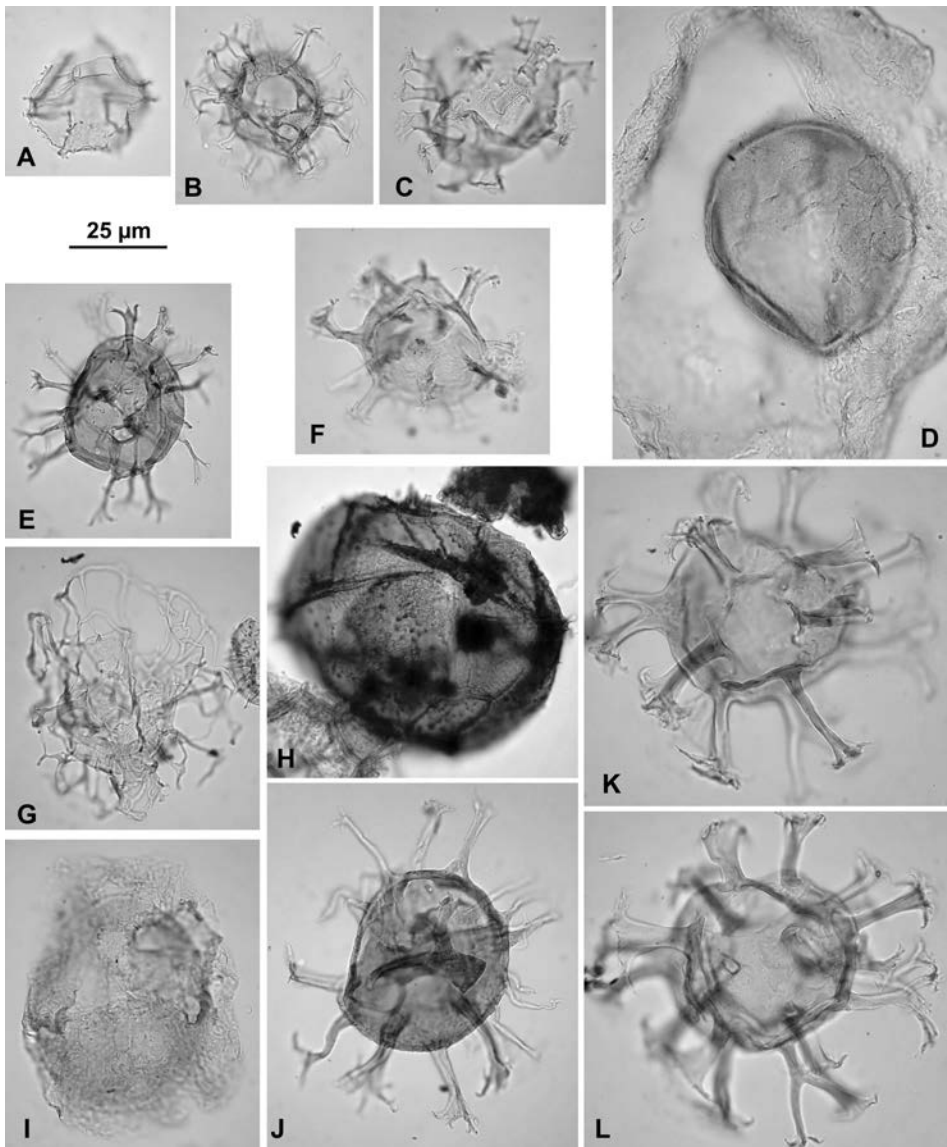
- |      |  |
|------|--|
| 1966 | <i>Lejeunia fallax</i> n. gen.; Morgenroth (1966b), p. 2–3, pl. 1, figs. 6–7         |
| 1978 | <i>Lejeunecysta fallax</i> comb. nov.; Artzner & Dörhöfer (1978), p. 1381            |
| 1983 | <i>Lejeunecysta fallax</i> (Morgenroth 1966) emend.; Biffi & Grignani (1983), p. 132 |



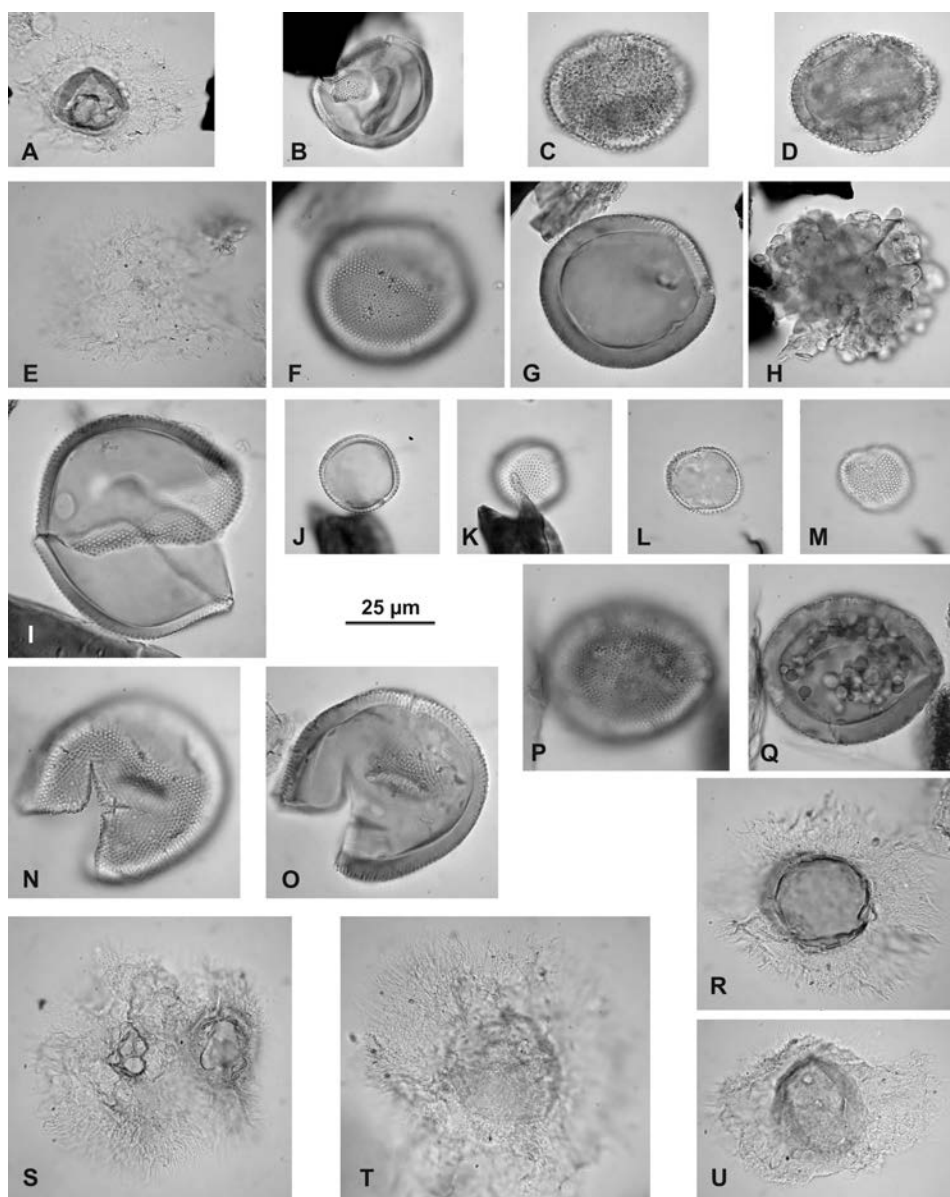
**Fig. 84.** Dinoflagellate cysts from the Hieroglyphic beds at Koniusza (sample KnsH2). **A** – *Areoligera coronata*; **B** – *Spiniferites ramosus*; **C** – *Melitasphaeridium pseudorecurvatum*; **D** – *Ctenidodinium* sp. (reworked Mesozoic species); **E** – Gen. et spec. indet. C; **F**, **G** – *Areoligera* cf. *medusettiformis* sensu Eaton (1976; same specimen, various foci); **H**, **I** – Gen. et spec. indet. C; **J** – *Glaphyrocysta exuberans*; **K** – *Operculodinium centrocarpum*; **L** – *Areoligera coronata*; **M** – *Glaphyrocysta exuberans*

**Material.** Two specimens in sample Kns12.

**Description.** Autocyst compressed peridinioid, with smooth autophragm. Paracingularium indicated by transverse folds. Apical and two well developed antapical horns, the latter acuminate. Distinctive concavity between antapical horns.

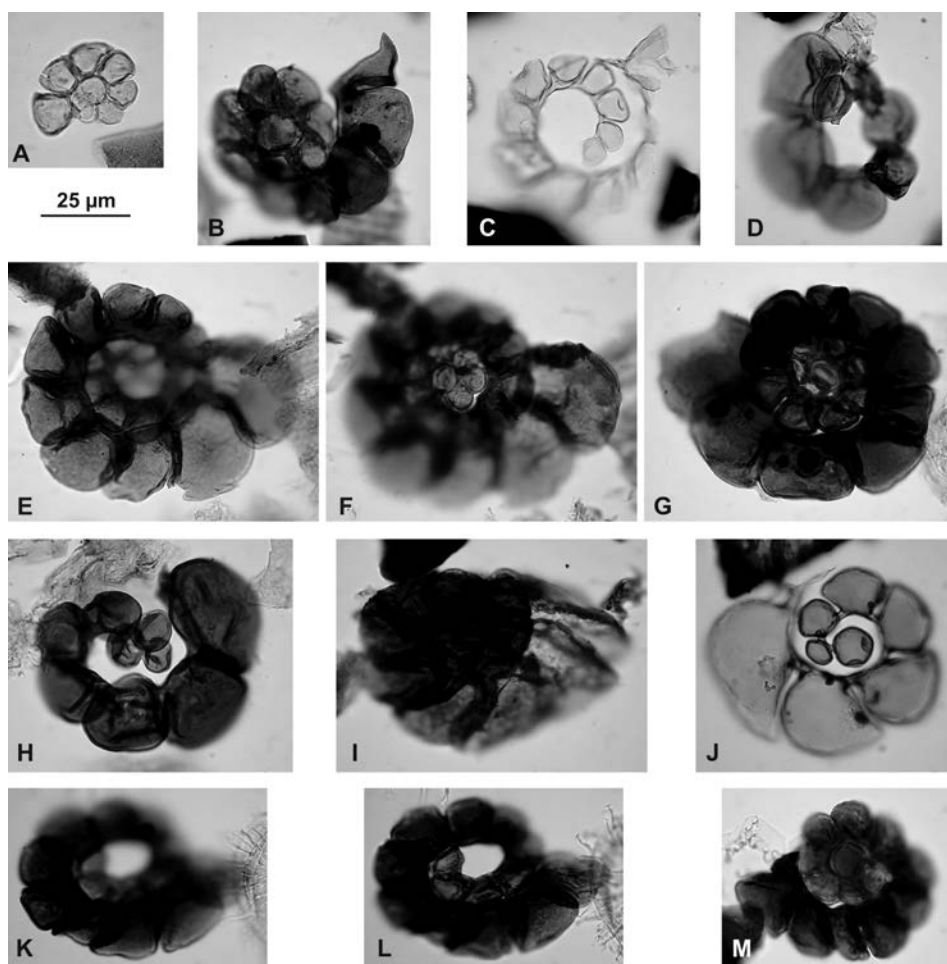


**Fig. 85.** Dinoflagellate cysts from the Hieroglyphic beds at Koniusza (sample KnsH2). **A** – *Phthanoperidinium delicatum*; **B** – *Achomosphaera crassipellis*; **C** – *Homotryblium abbreviatum*; **D** – *Thalassiphora pelagica*; **E** – *Achomosphaera alcicornu*; **F** – *Cordosphaeridium inodes*; **G** – *Adnatosphaeridium multispinosum*; **H** – *Cribroperidinium ?edwardsii* (reworked Mesozoic species); **I** – *Thalassiphora patula*; **J, K, L** – *Cordosphaeridium gracile*



**Fig. 86.** Aquatic palynomorphs from the Popiele beds at Koniusza. **A** – *incertae sedis* (*Schizosporis*?; Kns8); **B** – *Tasmanites* (Kns1); **C, D** – *Tasmanites* (same specimen, various foci; Kns1); **E** – *incertae sedis* (*Schizosporis*?), specimen without “central body” (Kns8); **F, G** – *Tasmanites* (same specimen, various foci; Kns5); **H** – *Botryococcus* sp. (Kns2); **I** – *Tasmanites* (Kns1); **J, K** – *Tasmanites* (same specimen, various foci; Kns12); **L, M** – *Tasmanites* (same specimen, various foci; Kns12); **N, O** – *Tasmanites* (same specimen, various foci; Kns6); **P, Q** – *Tasmanites* (same specimen, various foci; Kns1); **R–U** – *incertae sedis* (*Schizosporis*?; all specimens Kns8)





**Fig. 87.** Aquatic zoomorphs from the Popiele beds at Koniusza. **A–M** – foraminiferal organic linings (A: Kns1; B–D: Kns2; E–M: Kns6, E, F and K, L: same specimens, various foci)

*Lejeunecysta globosa* Biffi et Grignani 1983

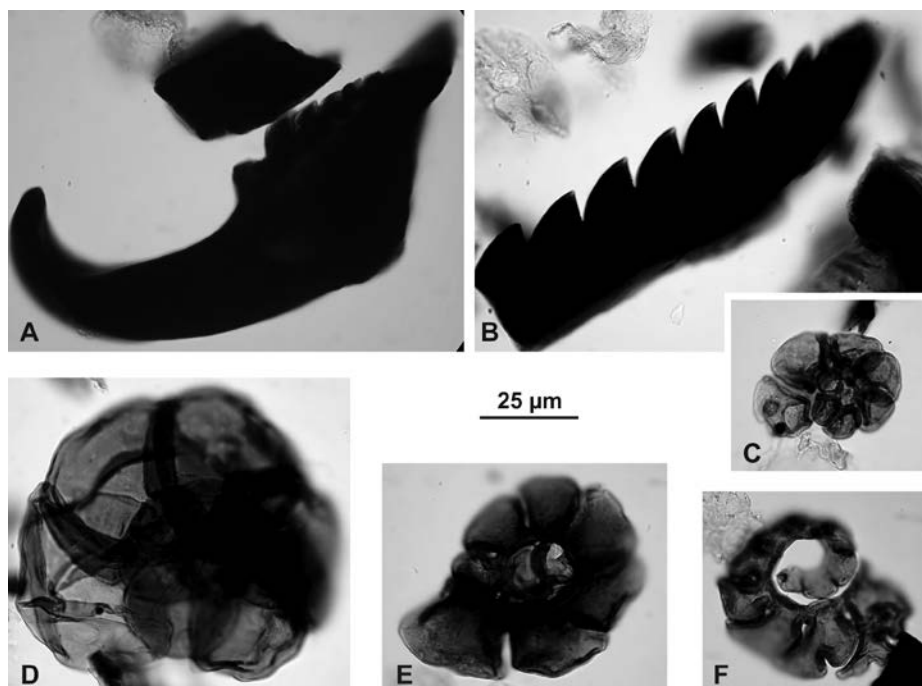
(Fig. 83O)

1983 *Lejeunecysta globosa* n. sp.; Biffi & Grignani (1983), p. 132–134, pl. 2, figs. 6–7, 10; text-fig. 2E

**Material.** A single specimen was found in sample Kns12.

**Remarks.** Autocyst compressed peridinioid, with rounded pentagonal outline. Autophragm smooth, dark-brown coloured. Two antapical horns indistinct, oblate. Apical horn not developed. Paracingulum indicated by faint, noncontinuous transverse fold. Archaeopyle intercalary 2a, opiculum free.





**Fig. 88.** Aquatic zoomorphs from the Popiele beds at Koniusza. **A** – scolecodont (Kns3); **B** – scolecodont (Kns9); **C–F** – foraminiferal organic linings (all Kns6)

*Lejeunecysta lata* Biffi et Grignani 1983

(Fig. 83W)

1983 *Lejeunecysta lata* n. sp.; Biffi & Grignani (1983), p. 134–136, pl. 3, figs. 1–2, 4; text-fig. 2G

**Material.** A single specimen was found in sample Kns5.

**Description.** Autocyst compressed peridinioid, with pentagonal outline. Two antapical horns poorly developed separated by weak antapical concavity. Paracingularium developed as transverse folds that divides cyst into equal epi- and hypocyst. Autophragm finely granular.

*Lejeunecysta* sp.

(Fig. 83V)

**Material.** Single to rare specimens in samples Kns6, Kns7, Kns12, Kns19, Kns21, Kns22 and Kns31.

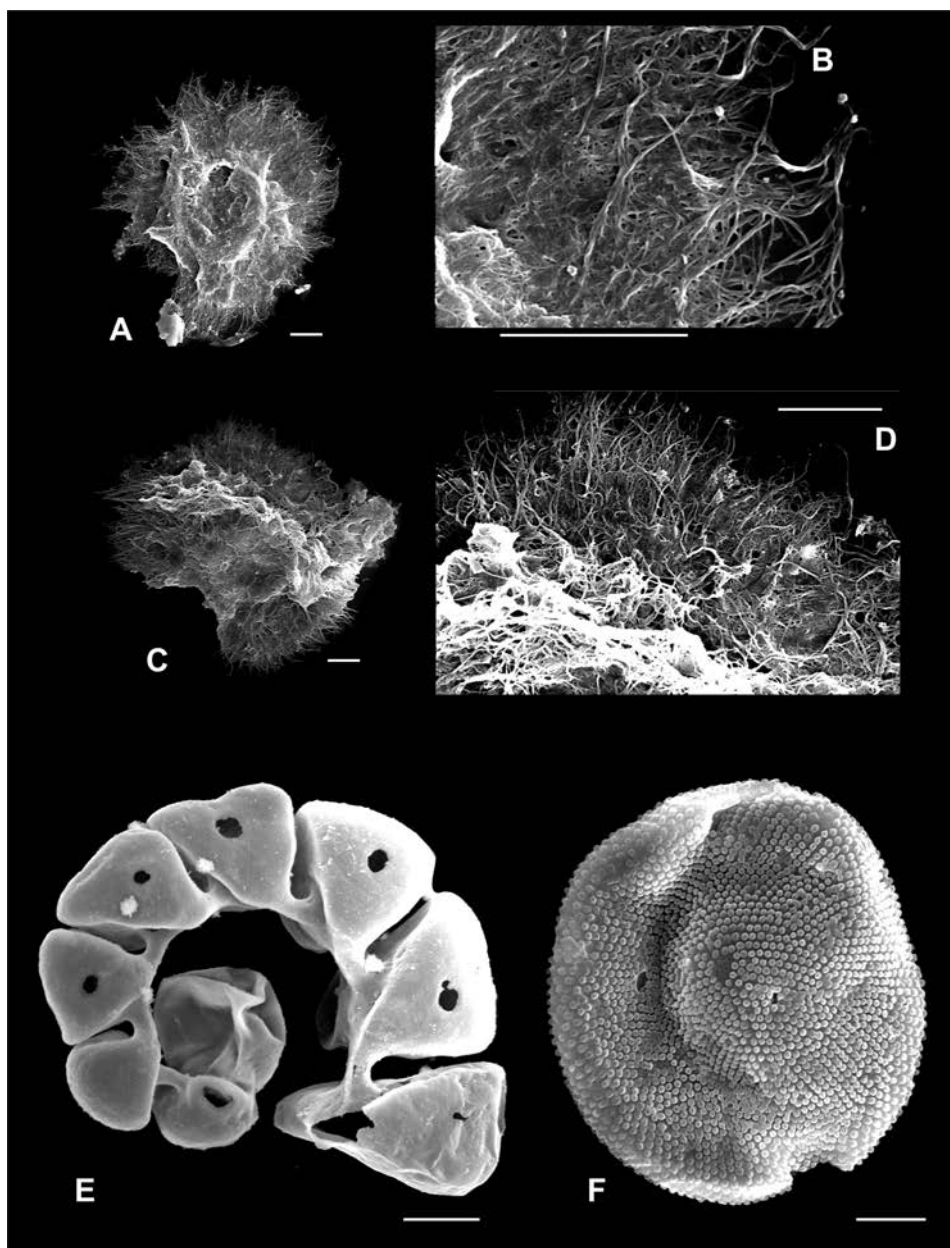
Genus *Selenopemphix* Benedek 1972

Type species: *Selenopemphix nephroides* Benedek 1972

1972 *Selenopemphix* n. gen.; Benedek (1972), p. 47

1980 *Selenopemphix* Benedek 1972 emend.; Bujak in Bujak *et al.* (1980), p. 82

1993 *Selenopemphix* Benedek 1972 emend.; Head (1993), p. 32



**Fig. 89.** Aquatic palynomorphs from the Popiele beds at Koniusza (scale bars refer to 10  $\mu\text{m}$ ). **A–D** – *incertae sedis*, presumably *Schizosporis* (both specimens Kns8; **A**, **C**: complete specimens, **B**, **D** – details); **E** – foraminiferal organic lining (Kns3); **F** – *Tasmanites* (Kns3)

*Selenopemphix armata* Bujak 1980

(Fig. 83J–N, P)

- 1980 *Selenopemphix armata* n. sp.; Bujak in Bujak *et al.* (1980), p. 83–84, pl. 21, figs. 1–3; text-figs. 23D, 24

**Material.** Single to rare specimens in samples Kns3, Kns6, Kns7, Kns12, Kns13, Kns18, Kns19, Kns21, Kns22, Kns26, Kns31 and Kns33.

**Description.** Autocyst compressed in polar view, ellipsoidal to kidney-shaped, with long, solid, acuminate processes at paracingulum. Hollow acuminate processes in central parts of the autocyst represent apical and antapical horns. Autophragm thin and smooth, dark-brown coloured.

*Selenopemphix nephroides* Benedek 1972

(Fig. 83A, D–I, Q–S)

- 1972 *Selenopemphix nephroides* n. sp.; Benedek (1972), p. 47–48, pl. 11, fig. 13; pl. 16, figs. 1–4  
 1980 *Selenopemphix nephroides* Benedek 1972 emend.; Bujak in Bujak *et al.* (1980), p. 84  
 1981 *Selenopemphix nephroides* Benedek 1972 emend.; Benedek & Sarjeant (1981), p. 333–334, 336

**Material.** Rare specimens occur in most of samples representing dark-coloured mudstone (except of samples Kns1, Kns7, Kns11 and Kns14); absent from samples representing pale-coloured marl.

**Description.** Autocyst compressed in polar view, kidney-shaped, with smooth autophragm. Some specimens have very faint striations going radially from the central part to the paracingular margin (Fig. 83S). Parasulcal area indicated by a small depression. Paracingulum indicated by a band, which occurs in marginal areas. The latter, independently of the cyst size, may be relatively thin (e.g., Fig. 83D, H) or much broader (e.g., Fig. 83G, Q, R). No positive relief elements. Majority studied specimens have dark-brown colouration of the autophragm (e.g., Fig. 83F, G). Some specimens are pale-coloured (Fig. 83H).

*Selenopemphix selenoides* Benedek 1972

(Fig. 83B, C)

- 1972 *Selenopemphix selenoides* n. sp.; Benedek (1972), p. 48, pl. 11, fig. 15; pl. 16, figs. 5–8; text-fig. 22  
 1980 *Selenopemphix selenoides* Benedek 1972 emend.; Bujak in Bujak *et al.* (1980), p. 86  
 1981 *Selenopemphix nephroides* Benedek 1972 emend.; Benedek & Sarjeant (1981), p. 336–338

**Material.** Single specimens in samples Kns14 and Kns22, three specimens in sample Kns18.

**Description.** Autocyst compressed in polar view, crescent-shaped, with smooth autophragm. Paracingulum band ornamented with tiny spines. Parasulcus forms a huge depression, which gives this rescentic shape in polar view. Autophragm smooth, dark-brown coloured.

## Acknowledgements

I would like to thank Prof. Jacek Rajchel and Prof. Jörg Pross for critical reading the manuscript and valuable comments. Prof. Krzysztof Birkenmajer and Dr Jarosław Tyska are kindly acknowledged for editorial remarks and linguistic corrections. Dr Ryszard Orłowski is kindly acknowledged for help during SEM observations.

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