The dinoflagellate cyst genus *Epiplosphaera* Klement 1960 - a reappraisal

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ABSTRACT

The dinoflagellate cyst genus *Epiplosphaera* Klement 1960 and its species have been studied in material from the Oxfordian and Kimmeridgian of Poland. The taxonomic history of the genus is summarized and the morphology is discussed. The type species *Epiplosphaera bireticulata* differs from other representatives of the genus in having high septa which are dissected distally. Additional septa in *E. bireticulata* form a second reticulum inside the parasutural septa. *Epiplosphaera reticulata* differs from the other species by having low spines and low, smooth septa. The septa form a second reticulum within the parasutures, as in the case with *E. bireticulata*. *Epiplosphaera areolata* has high spines, but almost no reticulum or parasutures. *Epiplosphaera reticulospinosa* is intermediate between *E. bireticulata* and *E. areolata*. It has a mixture of both high and low septa between the spines. *Epiplosphaera gochtii* has low spines and few, low septa between some of the spines. *Epiplosphaera ornata* is regarded as a junior synonym of *E. gochtii*.

INTRODUCTION

A few dinoflagellate cysts from the Middle and Late Jurassic are characterized by being murochorate. Tabular and intratabular spines are connected with septa, giving the cyst a bireticulum. Klement (1960) described these cysts and created the genus *Epiplosphaera* and the closely related genus *Ellipsoidictyum* to encompass these dinoflagellate cysts.

This paper reports chiefly on the study of some samples very rich in *Epiplosphaera* specimens. The material provided an excellent opportunity to study these cysts in the scanning electron microscope (SEM). They are very difficult to study in the light microscope due to the numerous high septa. Two almost simultaneous and opposing taxonomic proposals of Brenner (1988) and Courtinat (1989) respectively, are compared and reinterpreted using the material studied here.

MATERIAL AND METHODS

Material

*Epiplosphaera bireticulata*, *E. gochtii* (including *Sentusidinium ornatum*), *E. reticulata* and *E. reticulospinosa* were found in large numbers in a sample from the Middle Oxfordian (Transversarium Zone) of the northeast margin of the Holy Cross Mountains (between Kraków and Warszawa, Poland; Fig. 1). Many other Oxfordian and Kimmeridgian samples from the Holy Cross Mountains area (Fig. 1), the Kraków Upland (northnorthwest of Kraków, Poland; Fig. 1) and the Pomeranian Trough (northern central Poland, south of Bydgoszcz; Fig. 1) are rich in *Epiplosphaera* specimens. The sample of the Transversarium Zone was given to me by Dr. Gutowski, University of Warsaw. The other samples were core samples given to me by the University of Warsaw, or were collected by me from outcrops under the guidance of Drs B.A. Matyja and A. Wierzbowski, University of Warsaw.

Methods

The material has been processed following the preparation-method described in Poulsen et al. (1990). Palynological slides have been studied using transmitted light microscopy. In order to study these morphologically complex dinoflagellate cysts, some specimens were mounted as strew mounts on stubs and studied using scanning electron microscopy.

TAXONOMIC HISTORY

Historical review

Klement (1960) proposed the genus *Epiplosphaera* and described three new species belonging to this genus - *E. bireticulata* (the type species), *E. areolata* and *E. reticulospinosa*.

Sarjeant (1984) questionably included *E. areolata* in *Lithodinia*. The transfer of *E. areolata* was not accepted by Brenner (1988), who retained this species in *Epiplosphaera*. Brenner (1988) transferred *Ellipsoidictyum gochtii* Fensome 1979 and *Sentusidinium ornatum* Courtinat 1980 to *Epiplosphaera* as two separate species. Courtinat (1989) considered *E.
Epiplosphaera bireticulata to be a junior synonym of Ellipsoidictyum reticulatum (Valens). Lentin & Williams 1977, and also included E. reticulatum in Epiplosphaera. Furthermore, Courtinat (1989) regarded S. ornatum to be a junior synonym of E. reticulospinosa Klement 1960.

**Morphological review**

The genus *Epiplosphaera* was originally described as: “Ellipsoidal shells with fine, irregularly polygonal, small-meshed reticulate ornamentation on the surface. Processes arising at the points of junction of the basal network are relatively short, simple or with short distal bifurcations, rarely isolated, mostly interconnected by fringes or by thick ledges perpendicular to the surface of the shell. These form either close linear marginal fringes or produce a regularly trapezoidal pattern predominantly in the longitudinal and transverse directions.” -Transcribed from Klement (1960) by Stover & Evitt (1978).

Klement (1960) described (in the holotype description) the archeopyle as a calotte-shaped split in one of the polar ends of the cyst. Stover and Evitt (1978) accepted Klement’s description, the archeopyle type was, however, described as type [fA] with a free operculum in their synopsis and modified description.

The paratabulation formula of this genus was neither described by Klement (1960) nor Stover & Evitt (1978), who also stated that the parasingulum and the parasulcus were not indicated. Brenner (1988), in his emendation of the genus, stated that the paratabulation is visible, depending on the state of reduction of the reticulum or preferential development of the parasutures. In the rich Polish assemblages indications of paratabulation are seen occasionally, including the species with the most complex reticulum of crests, i.e. *E. bireticulata* (Pl. 1, Fig. 4). The paratabulation is gonyaulacoid (Brenner, 1988).

**SYSTEMATICS**

Division Pyrrhophyta Pascher 1914
Class Dinophyceae Fritsch 1929
Order Peridiniales Haeckel 1894
Genus *Epiplosphaera* Klement 1960 emend. Brenner 1988

**Type species.** *Epiplosphaera bireticulata* Klement 1960.

**Diagnosis.** (translated from Brenner, 1988): “Proximochorate dinoflagellate cyst with an apical archeopyle. The cyst wall consists of a thin inner membrane and a solid to fine porous main cyst wall. The surface of the cyst bears an ornament of septa from which normally short bifid spines arise. The spines are often interconnected by delicate septa or membranes. The septa form an irregular network, which occurs in different stages of reduction. The reduction of the ridge network takes place either by shortening, producing an incomplete network, or by preferential development of the parasutures. Depending on the stage of reduction, the paracingulum, the parasutculus, or the parasutures are recognized. The paratabulation is gonyaulacoid.”

**Remarks.** Although this species was originally described as one in which paratabulation is indicated by the archeopyle only (Klement, 1960; Stover & Evitt, 1978), indications of paratabulation may be visible in certain, rather specific, orientations (e.g. Pl. 1, Fig. 4). The gonyaulacoid paraplate pattern is indicated by the archeopyle sutures (Pl. 3, Figs 2, 6). No irregular break is noticed in the archeopyle sutures; the operculum is free as previously stated by Stover & Evitt (1978). *Comparison.* *Epiplosphaera* differs from *Ellipsoidictyum* in having spines, which are interconnected muri or septa that are typically uneven distally. *Ellipsoidictyum* lacks spines and has muri that are essentially uniform in height so that the outline of the cyst is fairly smooth, not irregular and jagged as in *Epiplosphaera*. Aldoria and Valensiella have an autophragm with an ectophragm, the archeopyle of *Aldoria* is precingular. *Egmontadinium* and *Histiophora* have both well expressed parasutures with only minor indication of a non-tabular reticulum (see Brenner, 1988, fig. 19).

**Epiplosphaera bireticulata** Klement 1960 (Pl. 1, figs 1-5)

1960 *Epiplosphaera bireticulata* Klement: 74-75, pl. 8, fig. 1-4.
1988 *Epiplosphaera bireticulata* Klement; Brenner: 51, pl. 15, figs 1a, b (re-illustration of the holotype).

**Remarks.** Courtinat (1989) regarded this species as a junior synonym of *Epiplosphaera reticulata* (Valensi) Courtinat 1989. The spines and crests of *E. bireticulata* are in the type material between 12-15 μm. *Epiplosphaera reticulata* is described by Valensi (1953) as a species with spines about 3μm in length. The crests of *E. bireticulata* are high and dissected whereas the crests of *E. reticulata* are low and smooth (Valensi, 1953, pl. 2, figs 4, 5, 14, 19 and pl. 13, fig. 6). For this reason, it is recommended that *E. bireticulata* should not be considered a junior synonym of *E. reticulata*.

The spines of *E. bireticulata* are difficult to measure; however, in the Polish material the length of the spines is about 8-9 μm. The overall length (including spines) is about 50-62 μm in specimens lacking operculum.

**Age.** Early Oxfordian to the Late Kimmeridgian (Autissiodorensis Zone). In the material studied, it occurs from the Middle Oxfordian (Transversarium Zone) to the Early Kimmeridgian (Hypselocyclum Zone). The species has been recorded from the Early Oxfordian to the Late Kimmeridgian (Eudoxus Zone) of Germany by Klement (1960), Brenner (1988) and Dürr (1988), from the Middle Oxfordian to

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**Explanation of Plate 1**

Magnification: Scale bars represent 10μm. Fig. 1 taken under SEM, all others taken in transmitted light. All specimens are from Poland.

**Figs 1-5.** *Epiplosphaera bireticulata* Klement 1960. Figs 1-2, 4-5. Transversarium Zone. Oxfordian; Zarzecze-Baltów, northeastern margin of Holy Cross Mountains (sample B-JG-7); Fig. 3. Planula Zone, Oxfordian; Kobyłczyce-VI-10 borehole, 30.5 m, Kraków-Wielun Upland. Figs 2-5, DGU catalogue No.: 1991-NEP-22, 23, 24 and 25 respectively.

**Fig 6.** *Epiplosphaera reticulata* (Valensi) Courtinat 1989. Spongy Limestone Formation; Binammatum Zone, Hyspeli Subzone, Oxfordian; Barcin-Pakosc 3 borehole, 137.4 m, Pomeranian Trough. Specimen E: DGU-catalogue-No.: 1991-NEP-26.
The dinoflagellate *Epiplosphaera*
the mid Kimmeridgian of France by Courtinat (1989), and from England from the Oxfordian or Kimmeridgian by Thomas and Cox (1988) and the Late Kimmeridgian (Mutabilis - Autissiodorensis Zones) by Cox et al. (1987).

**Epiplosphaera areolata** Klement 1960

(Pl. 2, figs 1, 3, 5)

1960 *Epiplosphaera areolata* Klement: 76-77, pl. 8, figs 5-9.

1984 *Lithodinia?* areolata (Klement); Sarjeant p. 166.

1988 *Epiplosphaera areolata* Klement; Brenner: 50-51, pl. 15, figs 5a, b (re-illustration of the holotype).

**Remarks.** Both Brenner (1988) and Courtinat (1989) retained *E. areolata* as a species of *Epiplosphaera*. The emendation of *Epiplosphaera* by Brenner (1988) fully justifies this. In the Polish material the spines of this species are about 8 µm in length. The total length of the species is about 55-75 µm including spines.

**Age.** Early Oxfordian to the earliest Volgian/Tithonian. In the Polish material it occurs from the Late Oxfordian (Bimammatum Zone, Hypselocyclum Subzone) to the earliest Volgian (Klimovyi Zone). The species has been recorded from the Early Oxfordian to the Late Kimmeridgian (Eudoxus Zone) of Germany (Klement, 1960; Brenner, 1988; Dürr, 1988), and from the Middle Oxfordian to the earliest Tithonian (Plicatilis - Gravesia Zones) of France (Courtinat, 1989).

**Epiplosphaera gochtii** (Fensome 1979) Brenner 1988

(Pl. 3, figs 1-6)

1979 *Ellipsoidictum gochtii* Fensome: 20-22, pl. 2, figs 8, 9, 11, 12 and text-fig. 8.

1980 *Sentusidinium ornatum* Courtinat in Courtinat and Gaillard: 61-62, pl. 9, figs 2, 3, 5, text-fig. 10a.

1988 *Epiplosphaera gochtii* (Fensome); Brenner: 51, pl. 15, figs 6a, b.

1988 *Epiplosphaera ornata* (Courtinat); Brenner: 52, pl. 15, figs 4a, b.

**Remarks.** In accordance with the emendation of *Epiplosphaera* by Brenner (1988), this species is best placed in this genus, rather than in *Ellipsoidictum* or in *Sentusidinium* as it has spines interconnected by septa, which is not characteristic of the two latter genera. Fensome (1979) and Courtinat (in Courtinat & Gaillard, 1980) published, independently and within a few months of each other, descriptions of two new species, *E. gochtii* and *E. ornata* that, I believe, are clearly conspecific. The two species have identical shaped spines which, however, original were described with minor differences in length and thickness (Fensome, 1979; Courtinat, in Courtinat & Gaillard 1980).

In the type material of *E. gochtii* from East Greenland the length of the spines was between 4-6 µm (Fensome, 1979). In the type material of *E. ornata*, the length of the spines was between 5-8 µm (Courtinat in Courtinat and Gaillard, 1980). In the Polish material, *E. gochtii* occurs in large numbers in one sample. There is a transition between shorter (3 µm) slender spines to longer (4-7 µm) and more solid spines. The two species express only intraspecific variation with minor differences in length and in thickness of the spines. The name *E. ornata* is a junior subjective synonym of *Epiplosphaera gochtii*.

Courtinat (1989) placed "*Sentusidinium ornatum*" in synonymy with *E. reticulospinosa*, which has long spines of 9-15 µm and a pronounced reticulum. "*Sentusidinium ornatum*" has low spines of 4-8 µm and a less distinct reticulum. The synonymy proposed by Courtinat (1989) is rejected in this paper.

**Age.** Late Bathonian to the Late Kimmeridgian. In the Polish material, this species occurs from the Middle Oxfordian (Transversarium Zone) to the Late Kimmeridgian (Mutabilis-Eudoxus Zones). The species has been recorded from the Early Callovian (Calloviense Zone) in East Greenland (Fensome, 1979), from the Late Bathonian to the Late Kimmeridgian (Hodsoni to Eudoxus Zones) of Germany (Brenner, 1988; Dürr, 1988; Prauss, 1989), and from the Late Oxfordian of France (Courtinat and Gaillard, 1980).

**Epiplosphaera reticulospinosa** Klement 1960

(Pl. 2, figs 2, 4)

1960 *Epiplosphaera reticulospinosa* Klement: 75-76, pl. 8, figs 10-12.

1988 *Epiplosphaera reticulospinosa* Klement; Brenner: 51, pl. 15, figs 3a, b (re-illustration of the holotype).

1991 *Sentusidinium ornatum* Courtinat 1980 in Courtinat & Gaillard 1980: 61-62, pl. 9, figs 2, 3, 5 textfig. 10a.

**Remarks.** The length of the spines and the height of the crests ranges from 15-12 µm in the type material to 9 µm in the Polish material. (See *E. ornata* for discussion of synonymy with that species).

**Age.** Early Oxfordian to the earliest Volgian/Tithonian. In the studied material, *E. reticulospinosa* occurs from the Middle Oxfordian (Transversarium Zone) to the Late Kimmeridgian (Eudoxus-Autissiodorensis Zones). The species has been recorded from the Early Oxfordian to the Late Kimmeridgian (Eudoxus Zone) of Germany (Brenner, 1988; Dürr, 1988; Klement, 1960). It has been recorded from the Middle Oxfordian to the earliest Tithonian of France (Courtinat, 1989; Ioanides et al., 1988). It is recorded in the Late Oxfordian.

Explanation of Plate 2

Magnification: Scale bars represent 10 µm. **Figs 1-3** taken under SEM, **Figs 4-5** taken in transmitted light. All specimens are from Poland.

**Figs 1, 3, 5. Epiplosphaera areolata** Klement 1960. *Fig. 1.* Oolite Platy Member, Hypselocyclum Zone, Kimmeridgian. Małogoszcz Quarry (sample MQ-9). southwestern margin of the Holy Cross Mountains. *Fig. 3.* sample details as for Pl. 3, fig. 6. *Fig. 5.* Dobromierz Marl, Hypselocyclum Zone, Kimmeridgian. Trojanów-83 borehole, 67.7 m, northwestern margin of the Holy Cross Mountains. *Fig. 5:* DGU-catalogue-No.: 1991-NEP-21.

**Figs 2, 4. Epiplosphaera reticulospinosa** Klement 1960. *Fig. 2.* sample details as for Pl. 1, fig. 1. *Fig. 4.* sample details as for Pl. 1, fig. 3. *Fig 4,* DGU-catalogue-No.: 1991-NEP-20.
to mid Kimmeridgian (Serratum to Mutabilis Zones) of England (Nørh-Hansen, 1986; Thomas and Cox, 1988).

**Epiplosphaera reticulata** (Valensi 1953) Courtinat, 1989. (Pl. 1, fig. 6)

1953 *Palaeoperidinium reticulatum* Valensi: 28, pl. 2, figs 4, 5, 14, 19, pl. 13, fig. 6, texfig. 2d.

1977 *Ellipsoidictyum reticulata* (Valensi); Lentin and Williams: 56.

1989 *Epiplosphaera reticulata* (Valensi); Courtinat: 176.

**Remarks.** The emendation of *Epiplosphaera* Klement 1960, by Brenner (1988) justifies the transfer of *E. reticulata* to *Epiplosphaera* as done by Courtinat (1989); it has low spines and indications of paracingulum and parasulcus and is, therefore, best placed in *Epiplosphaera* rather than in *Ellipsoidictyum* which is characterized by the lack of spines.

Courtinat (1989) considered *E. bireticulata* to be a junior subjective synonym of *E. reticulata*. This is in my view highly questionable; they differ in spine length and crest height. Furthermore the septa of *E. reticulata* are smooth (Valensi, 1953, pl. 2, figs 4, 5), whereas the crests of *E. bireticulata* are dissected. *E. reticulata* is similar to *E. bireticulata* in having a reticulum with low smooth crests and similar form of the spines. *E. reticulata* differs from *E. bireticulata* in having much lower spines and crests. The synonymy proposed by Courtinat (1989) is rejected in this paper.

**Age.** Early Bajocian to Late Kimmeridgian. In the Polish material studied, *E. reticulata* occurs from the Middle Oxfordian (Transversarium Zone) to the Late Kimmeridgian (Eudoxus-Autissiodorensis Zones). The holotype is of Bajocian age and the paratype of Bathonian age (Valensi, 1953). Sarjeant (1979) reported the range of this species as Early Bajocian to Late Oxfordian to Early Kimmeridgian (Serratum - Bayley Zones) in England.

**Table 1: Summary of the morphological characteristics.**

| Species                      | Parasutural septa | Nontabular septa | Spines                  |
|------------------------------|-------------------|------------------|-------------------------|
| *Epiplosphaera bireticulata* | High              | High             | Absent                  |
| *Epiplosphaera areolata*     | ±Low              | Low              | High                    |
| *Epiplosphaera gochtii*      | Absent            | Low (rare)       | Low - medium            |
| *Epiplosphaera reticulospinosa* | Mixture of high and low | Mixture of high and low | High                   |
| *Epiplosphaera reticulata*   | Low               | Low              | Low                     |

**Genus Valensiella Eisenack 1963**

*Valensiella groenlandica* (Smelror 1988) comb. nov.

**Remarks.** This species is attributed to *Valensiella* because the cyst wall organisation is an autophragm with an ectophragm (Smelror, 1988). The species cannot be placed in *Ellipsoidictyum* as it is a genus without an ectophragm.

**CONCLUSIONS**

Based on the scanning electron microscopy and transmitted light microscopy of the Polish material the genus *Epiplosphaera* is believed to consist of five species at present, i.e. *E. bireticulata* (the type species) and *E. areolata, E. gochtii, E. reticulata* and *E. reticulospinosa*. *Epiplosphaera bireticulata* and *E. reticulata* are not regarded as synonyms, as suggested by Courtinat (1989). *Sentusidinium ornatum* is regarded as a junior subjective synonym of *E. gochtii* and not of *Epiplosphaera reticulospinosa* as proposed by Courtinat (1989).

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**Explanation of Plate 3**

Magnification: Scale bars represent 10 μm. Figs 1-2, 6 taken under SEM. Figs 3-5 taken in transmitted light. All specimens are from Poland.

*Epiplosphaera gochtii* (Fensome) Brenner 1988.

Figs 1-3, 5. Sample details as for Pl. 1, fig. 1. Fig. 3, DGU-catalogue-No.: 1991-NEP-27. Fig. 5, DGU-catalogue-No.: 1991-NEP-29.

Fig. 4. Dobromierz Marls, Hypselocyclum Zone, Kimmeridgian; Trojánów-83 borehole, 81.4 m, northwestern margin of the Holy Cross Mountains.

Fig. 4: DGU-catalogue-No.: 1991-NEP-28.

Fig. 6. Upper Platy Limestone, Mutabilis? Zone, Kimmeridgian, Małogoszczyzna Quarry (sample MQ-1), southwestern margin of the Holy Cross Mountains.
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