

# The complex chorate dinoflagellate cysts of the Bathonian to Oxfordian (Jurassic): Their taxonomy and stratigraphic significance

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**ABSTRACT:** The study of chorate dinoflagellate cysts with complex processes is made difficult by their tendency to be damaged or partially obscured by adherent debris. This has resulted in the group being relatively neglected by comparison with the simpler proximate and cavate cysts. To analyse the morphological variation of complex chorate cysts and produce listings of species characteristics, it proved necessary to return to the original descriptions of assigned species and, whenever possible, to re-examine type material. As a consequence of these morphological reassessments, emendations are made to the genera *Compositosphaeridium* Dodekova, *Hystrichosphaerina* Alberti, *Systematophora* Klement and *Polystephanophorus* Sarjeant and the species *P. calathus* (Sarjeant), *P. paracalathus* (Sarjeant), *Hapsidaulax margarethae* Sarjeant, *Adnatosphaeridium caulleryi* (Deflandre) and *Surculosphaeridium cribrotubiferum* Sarjeant. The new combinations *Adnatosphaeridium densifilosum* (Cookson and Eisenack), *Adnatosphaeridium? speciosum* (Alberti) and *Hystrichosphaerina? varispinosa* (Brenner) are proposed and the combination *Surculosphaeridium? vestitum* is retained. This re-evaluation of the group highlights the utility of complex chorate dinoflagellate cysts for biostratigraphic research and allows the postulation of several lineages that might form the basis of the group's continued evolution in the Late Jurassic and Cretaceous.

## INTRODUCTION

The study of Jurassic dinoflagellate cysts with complex processes began early, when C. G. Ehrenberg (1843) illustrated what he termed *Xanthidium penicillatum* from Polish rocks of presumed Corallian (= Late Oxfordian) age. However, there was no accompanying description and the morphology of this species was so long misunderstood that the name fell into disuse.

When studies of Middle and Upper Jurassic dinoflagellate cysts were resumed almost a century later, it was perceived that there were many forms having long processes with elaborate distal branching and connections. Deflandre (1938), in his landmark study of the Villers-sur-Mer section in northern France, described four Oxfordian species with complex processes, all attributed originally to the genus *Hystrichosphaeridium* but since reassigned to other genera. Within the early months of 1960, two new genera were described almost simultaneously: *Systematophora* Klement 1960 from Germany and *Polystephanosphaera* Sarjeant 1960b from England. A second paper from Germany was then in press, describing a third new genus, *Hystrichosphaerina* Alberti 1961. Shortly afterward Pocock (1962) illustrated similar forms from the Jurassic of western Canada.

The three genera proposed during these two years overlapped in their published diagnoses, if not in content. In a later paper by Sarjeant (1961b), *Polystephanosphaera* was abandoned as a junior synonym of *Systematophora*, its type species corresponding too closely to the type species of the latter genus for separation at generic level to be justifiable. However, a fourth genus, *Polystephanophorus* Sarjeant (1961b), was proposed to contain species morphologically outside *Systematophora*. For a long time *Hystrichosphaerina* was also regarded as a junior

synonym of *Systematophora* (see Neale and Sarjeant 1962; Norris and Sarjeant 1965), until resurrected under a revised definition by Stover and Evitt (1978).

Since the 1960's the stratigraphical range of cysts of this general morphological type has been extended downward through the Callovian and Bathonian and upward into the Late Cretaceous and Tertiary. A major review of the group was completed in 1978 by the second author and circulated with the Louisiana State University course notes on Jurassic dinoflagellate cysts. This work proposed the term 'complex chorate cysts' for dinoflagellate cysts having processes or crests of length greater than 30% of the diameter of the cyst and exhibiting complex distal branching and/or linkage. Subsequently Sarjeant (1980) demonstrated that Ehrenberg's *X. penicillatum* was attributable to *Systematophora* and was indeed a senior synonym of one of Klement's species.

The present paper reviews only the cysts having processes longer than 25% of the central body diameter; forms with shorter processes or having high crests (pterochorate forms) are omitted from consideration. The stratigraphic interval examined is from the Bathonian to Oxfordian stages, but consideration is given to the evolution of the group in Kimmeridgian and younger strata.

Current concepts of the species assignable to this group are summarized in tabular form. The accompanying text comments on each species, with an emphasis on its morphology and generic assignment; new observations on some genera and species are presented. In later pages the biostratigraphic potential of the complex chorates is investigated, with an accompanying range chart. The possible evolution of the group is considered, using morphological comparisons and first appearance data.

TABLE 1

A listing of species which have their morphology outlined in Table 6.

<i>Adnatosphaeridium caulleryi</i> (Deflandre 1983, p. 189) emend. nov.
<i>Adnatosphaeridium densifilum</i> (Cookson Eisenack 1974, p. 70) comb. nov.
<i>Adnatosphaeridium ? speciosum</i> (Alberti 1961, p. 37) comb. nov.
<i>Compositosphaeridium bulgaricum</i> Erkmen and Sarjeant 1980, p. 66-67.
<i>Compositosphaeridium polonicum</i> (Górka 1965, p. 306-307) Erkmen and Sarjeant 1980, p. 67-69.
<i>Hapsidaulax margarethae</i> Sarjeant 1975a, p. 144-147; emend. nov.
<i>Hystichosphaerina ? varispinosa</i> (Brenner 1988, p. 87-88) comb. nov.
<i>Perisseiasphaeridium ingegerdiae</i> Nøhr-Hansen 1986, p. 35-36.
<i>Polystephanophorus calathus</i> Sarjeant 1961a, p. 104; emend. nov.
<i>Polystephanophorus paracalathus</i> Sarjeant 1960b, p. 143-144; emend. nov.
<i>Rigaudella aemula</i> (Deflandre 1938, p. 187-189) Below 1982, p. 138-139.
<i>Rigaudella filamentosa</i> (Cookson and Eisenack 1958, p. 47) Below 1982, p. 148.
<i>Surculosphaeridium cribratiferum</i> (Sarjeant 1960b, p. 138) emend. nov.
<i>Surculosphaeridium ? vestitum</i> (Deflandre 1938, p. 189) Davey, Downie, Sarjeant and Williams 1966, p. 162.
<i>Systematophora areolata</i> Klement 1960, p. 62-65.
<i>Systematophora orbifera</i> Klement 1960, p. 66-67.
<i>Systematophora penicillata</i> (Ehrenberg 1843, p. 61, ex 1854, pl. 37, fig. 8.3) Sarjeant 1980, p. 282.
<i>Systematophora valensii</i> (Sarjeant 1960b, p. 142-143) Sarjeant 1961b, p. 1096.
<i>Taeniophora filamentosa</i> Klement 1960, p. 68-69.

## TERMINOLOGY

In describing these cysts, it was found that there are no specific terms for some of the morphological features exhibited and that many workers were inconsistent in their use of existing terms. Table 2 lists these new terms, along with others that are commonly used in descriptions of chorate processes.

Below (1987a, 1987b) has recently proposed far-reaching new approaches to the description of cysts, on the basis of detailed studies under the scanning electron microscope (S.E.M.). While his methodology deserves commendation, the extreme fragility of the processes of the species discussed here makes their remounting for S.E.M. study particularly difficult; the results are rarely satisfactory. For this reason, our work has been undertaken primarily under the optical microscope. Some of the new descriptive terms proposed by Below (idem.)—especially for the precise description of plate shape—appear valuable, but others seem to be superfluous, since the existing terms they replace are not only well established but clearly understood and in wide usage. Consequently, changes would be more disadvantageous than beneficial. It is preferable to adhere, where possible, to the present standard descriptive terminology, as developed in the work of Evitt et al. (1977), Norris (1978a, 1978b), and Sarjeant (1982).

TABLE 2

A listing of terms with definitions used in this paper.

<b>Branch;</b> Secondary extensions arising laterally to the process and forming an acute angle to the process or with other branches. These may or may not join with branches of another process. Branches are proximal to the trabeculae, where developed.
<b>Fenestrate process;</b> A tubular process whose walls are penetrated, to varying degrees, by holes of variable size and shape (Williams, Sarjeant and Kidson 1973, p. 60).
<b>Hapto-process trabecula;</b> A type of trabecula which distally only connects branches of a single process.
<b>Hapto-cluster trabecula;</b> A structure formed by the distal linking of a number of processes, within a single cluster.
<b>Inter-process trabecula;</b> A trabecula which joins two isolated processes.
<b>Inter-cluster trabecula;</b> A trabecula that links process clusters.
<b>Open process;</b> A process which is open distally, closed proximally and forms a tube or funnel.
<b>Order of branching;</b> The number of times a process branches (but not including a distal trabecula, if developed).
<b>Process;</b> An essentially columnar or spine-like projection arising from the surface of a dinoflagellate cyst. Processes may be simple, intricately branched or variably interconnected (Lentin and Williams 1976, p. 174).
<b>Process cluster;</b> A number of processes forming a circular or angular grouping. The processes may be joined proximally by a ridge or crest on the surface of the phragma, or distally by uniting of branches or by hapto-process trabeculae.
<b>Ring trabecula;</b> A circular structure forming the distal termination of a process or process cluster. Proximally supported by secondary branching of the processes while distally often smooth and parallel to the cyst surface.
<b>Trabecula;</b> A thread-like connection between processes, always distal to the last branch and having a span parallel to the cyst surface.
<b>Trans-cingular structure;</b> A crest, ridge or trabecula which crosses the cingulum.

## MORPHOLOGICAL REMARKS AND STUDY METHODS

Those morphological features of complex chorate cysts that are considered to be of taxonomic significance are listed on Table 6. Emphasis is placed upon the paratabulation, style of archaepyle and process form. The order of branching relates to the number of times the process branches distally from the main 'stem'. If the final branch terminates in a trabecula, then the trabecula is not counted as a branch. Recording the order of branching is useful, since it gives an indication of the complexity of process development. The presence of a cingulum and sulcus is important for generic recognition. Commonly, only an area without processes marks their location. Some genera (for example *Surculosphaeridium* and *Perisseiasphaeridium*) have simple, isolated processes or linear process groupings to mark the cingulum. The position of the sulcus may also be marked by processes, e.g. in *Systematophora areolata*, and is consistently indicated by a sulcal notch in the archaepyle margin.

The rigidity imposed by our use of tables for presenting morphological data meant that some information could not conveniently be included. These extra details are contained in a "Remarks" section, wherever necessary. When an emendation to the diagnosis is proposed, a full synonymy is presented. Otherwise, only an abbreviated synonymy is given for each

TABLE 3

Reported occurrences of complex chorate cysts which have not been included in the range chart (Table 4).

**A:** Dinoflagellate species not included in the biostratigraphic chart:

*Adnatosphaeridium densifilum* (Cookson and Eisenack 1974) comb. nov. Range uncertain.

*Hystrichosphaeridium pachydermum* Cookson and Eisenack 1960. Processes too short.

*Hystrichosphaeridium petilum* Gitmez 1970. Processes too simple.

**B:** Reported occurrences which appear to be biostratigraphically anomalous and in need of further study before inclusion in the range chart:

*Compositosphaeridium polonicum* (Górka 1965). Williams and Bujak 1985; Middle Bajocian.

*Hystrichosphaeridium pulchrum* (Deflandre and Cookson 1955). Conway and Cousminer 1981; Lower Oxfordian.

*Oligosphaeridium complex* (White 1842). Conway and Cousminer 1981; Lower Oxfordian.

*Surculosphaeridium cribrotubiferum* (Sarjeant 1960b). Riley and Sarjeant 1972; Bathonian.

*Systematophora areolata* Klement 1960. Bujak and Williams 1977; Bathonian-Callovian.

"*Systematophora fasciculigera*" Klement 1960. Taugourdeau-Lantz and Lachkar, 1984; Upper Bathonian.

"*Systematophora fasciculigera*" Klement 1960. Taugourdeau-Lantz and Lachkar, 1985; Upper Bathonian.

*Systematophora orbifera* (Klement 1960). Dupin 1965; Bathonian.

*Systematophora orbifera* (Klement 1960). Schulz and Mai 1966; Callovian.

*Systematophora penicillata* (Ehrenberg 1843 ex 1854). Thusi and Vigran 1985; Upper Bathonian-Lower Callovian.

*Systematophora penicillata* (Ehrenberg 1843 ex 1854). Conway 1978; Upper Bathonian.

*Systematophora turonica* (Alberti 1961). Bujak and Williams 1977; Callovian-Kimmeridgian.

*Taeniophora iunctispina* Klement 1960. Bujak and Williams 1977; Lower Oxfordian.

**C:** Other complex chorate cysts not included in the biostratigraphic chart:

*Hystrichosphaeridium* sp. A. Quattrocchio 1984, tab. 1.

*Oligosphaeridium* cf. *O. anthophorum*. Vigran and Thusi 1975, tab. 3.

*Polystephanophorus* cf. *paracalathus*. Lund and Pedersen 1985, p. 395.

*Polystephanophorus* sp. Conway 1978, p. 354.

cf. *Systematophora speciosa*. Taugourdeau-Lantz and Lachkar 1984, fig. 1.

*Systematophora* sp. A. Habib 1972, pl. 3, fig. 5.

*Systematophora* sp. Taugourdeau-Lantz and Lachkar 1985, tab. 3.

species, containing the original description and the emendations but omitting all other records.

During the compilation of the taxonomic tables, the possibility of using the Taylor/Evitt plate labelling system (see Evitt 1985, pp. 81–119) was investigated to complement the standard plate notation outlined originally by Kofoid (1907). To use the Taylor/Evitt system, however, it is imperative to know the precise shape of the plates and the relationship of each plate to its neighbors. Unfortunately, the processes or process groups of

TABLE 4

Range chart for complex chorates found in strata of Bathonian to Oxfordian age.

STRATIGRAPHY		GENUS															
		SPECIES		SPECIES		SPECIES		SPECIES		SPECIES		SPECIES		SPECIES		SPECIES	
KIMMERIDGIAN	U	Adnatosphaeridium		Hapidaulax		Compositosphaeridium		Adnatosphaeridium?		Surculosphaeridium		Rigaudella		Compositosphaeridium		Adnatosphaeridium?	
		coulteri		margarethae		bulgericum		sp. A		cribrotubiferum		aemula		polonicum		spectatum	
Oxfordian	U	Adnatosphaeridium		Hapidaulax		Compositosphaeridium		Adnatosphaeridium?		Surculosphaeridium		Rigaudella		Compositosphaeridium		Adnatosphaeridium?	
		coulteri		margarethae		bulgericum		sp. A		cribrotubiferum		aemula		polonicum		spectatum	
Callovian	U	Adnatosphaeridium		Hapidaulax		Compositosphaeridium		Adnatosphaeridium?		Surculosphaeridium		Rigaudella		Compositosphaeridium		Adnatosphaeridium?	
		coulteri		margarethae		bulgericum		sp. A		cribrotubiferum		aemula		polonicum		spectatum	
Bathonian	U	Adnatosphaeridium		Hapidaulax		Compositosphaeridium		Adnatosphaeridium?		Surculosphaeridium		Rigaudella		Compositosphaeridium		Adnatosphaeridium?	
		coulteri		margarethae		bulgericum		sp. A		cribrotubiferum		aemula		polonicum		spectatum	
Bajocian	U	Adnatosphaeridium		Hapidaulax		Compositosphaeridium		Adnatosphaeridium?		Surculosphaeridium		Rigaudella		Compositosphaeridium		Adnatosphaeridium?	
		coulteri		margarethae		bulgericum		sp. A		cribrotubiferum		aemula		polonicum		spectatum	

6'', 6c, 5-6''', 1p, 1''', 1-5s. Processes solid or open, medium to long, slender, often distally flared, and sometimes taeniate. Branching occurs distally, though it may also be developed medially, two stages of branching being common. Trabeculae of variable thickness, distally smooth to finely denticulate, are frequently developed, occasionally linking processes into clusters. Cingulum and sulcus commonly marked by isolated, long thin processes. Archeopyle apical, type (tA), operculum free, often with a sulcal notch.

*Type species:* *Adnatosphaeridium vittatum* Williams and Downie 1966.

*Other accepted species:*

- Adnatosphaeridium buccinum* Hultberg 1985.  
*Adnatosphaeridium caulleryi* (Deflandre 1938) emend. nov.  
*Adnatosphaeridium? chonetum* (Cookson and Eisenack 1962) Davey 1969.  
*Adnatosphaeridium densifilum* (Cookson and Eisenack 1974) comb. nov.  
*Adnatosphaeridium filiferum* (Cookson and Eisenack 1958) Williams and Downie 1969.  
*Adnatosphaeridium huenickenii* Archangelsky 1969.  
*Adnatosphaeridium multispinosum* Williams and Downie 1966.  
*Adnatosphaeridium robustum* (Morgenroth 1966) De Coninck 1975.  
*Adnatosphaeridium? speciosum* (Alberti 1961) comb. nov.  
*Adnatosphaeridium tutulosum* (Cookson and Eisenack 1960) Morgan 1980.  
*Adnatosphaeridium williamsii* Islam 1983.  
*Adnatosphaeridium? williereae* De Coninck 1975.

*Provisionally accepted species:*

- Adnatosphaeridium membraniphorum* Jan du Chêne and Adedirán 1985. The species has a covering membrane, which is not present in other members of the genus.

*Remarks:* Following the separation of *Rigaudella* Below 1982, the genus *Adnatosphaeridium* contains species whose morphological characteristics include an apical archeopyle, intratabular processes, a spherical to ellipsoidal central body (Williams and Downie 1966, p. 215) and processes marking the cingulum and/or sulcus. The addition of the two species *A. densifilum* and *A.? speciosum* does not extend either the stratigraphic or morphological range of the genus.

*Adnatosphaeridium caulleryi* (Deflandre 1938) Williams and Downie 1969 **emend.**

Plate 1, figures 1, 3-5

*Hystrichosphaeridium caulleryi* DEFLANDRE 1938, p. 189, pl. 11, figs. 2-3.

*Cannosphaeropsis caulleryi* (Deflandre 1938) DEFLANDRE 1947a, text-fig. 5, no. 4. — DEFLANDRE 1947b, p. 1575, fig. 4. — SARJEANT 1960a, pl. 12, fig. 6. pl. 14, fig. 5, tab. 2. — SARJEANT 1961a, p. 103, pl. 13, fig. 8, pl. 15, fig. 4. — SARJEANT 1962a, pl. 70, fig. 3, tab. 2-3. — SARJEANT 1962b, pl. 2, fig. 4, tab. 4. — DOWNIE and SARJEANT 1964, p. 100. — HOROWITZ 1970, p. 179, pl. 5, fig. 8.

*Adnatosphaeridium caulleryi* (Deflandre 1938) WILLIAMS and DOWNIE 1966, p. 218, nomen nudum. — WILLIAMS and DOWNIE 1969, p. 17. — EISENACK and KJELLSTRÖM 1971, p. 47-48. — RILEY and SARJEANT 1972, tab. 2a, 3a, 4a. — SARJEANT 1975b, pl. 3, fig. 13. — IOANNIDES,

STAVRINOS and DOWNIE 1976, p. 448, pl. 1, figs. 4-6. — BJAERKE 1977, pl. 9, fig. 4. — BUJAK and WILLIAMS 1977, text-fig. 2a. — WILLIAMS 1977, pl. 1, fig. 7. — SARJEANT 1978, p. 26. — STOVER and EVITT 1978, p. 15. — BARSS, BUJAK and WILLIAMS 1979, p. 36. — ERKMEN and SARJEANT 1980, p. 69-70, pl. 8, fig. 4, 7, tab. 2. — WILLIAMS and BUJAK 1985, fig. 21, no. 5. — RIDING 1987, fig. 8, no. 13. — LENTIN and WILLIAMS 1989, p. 6. — DÜRR 1989, p. 57, pl. 1, fig. 10.

*?Adnatosphaeridium caulleryi* (Deflandre 1938) SARJEANT 1968, tab. 2b, nomen nudum.

*Polystephanephorus caulleryi* (Deflandre 1938) COURTINAT 1989, p. 171.

*Emended diagnosis:* Skolochorate dinoflagellate cysts, with central body spherical to subspherical and of intermediate to large overall size. Phragma smooth to finely granulate. Central body surmounted by numerous solid, slender processes which are consistently bifurcate or multifurcate and may be distally expanded. Processes may be deeply or medially furcate and occasionally branch proximally. Processes variably interconnected distally by solid, slender, smooth to irregularly denticulate trabeculae. Paratabulation gonyaulacacean, indicated by intratabular processes (or clusters of processes). Process clusters irregular, occasionally exhibiting annulate or arcuate organisation; this is shown best in the precingular, postcingular and antapical areas. Apical, cingular, sulcal and posterior intercalary paraplates give rise to single processes or to small, closely-spaced process clusters. Trabeculae may or may not interconnect process clusters. Paratabulation formula probably 4', 6'', 6c, 6''', 1p, 1''', x-?s. Archeopyle apical, type (tA), operculum free.

*Holotype:* Slide AM 22, Institut de Paléontologie, Centre Scientifique Georges Deflandre, Paris.

*Type locality:* Villers-sur-Mer, Calvados, France; Jurassic (Oxfordian).

*Holotype dimensions:* See Table 6.

*Description:* This species of *Adnatosphaeridium* has a spherical to subspherical, smooth to finely granulate cyst body bearing numerous thin, solid processes, interpreted as extensions of the periphragm. The process length is variable within a population (20-31% of the overall cyst diameter), but relatively consistent on any individual specimen. The processes, though consistently furcate, are otherwise variable in distal morphology; they may be expanded and interconnected by irregularly denticulate trabeculae. Medial branching of the processes may occur and rarely they bifurcate proximally. The larger paraplate areas (precingular, postcingular and antapical) are characterised by distinct intratabular process clusters which are typically irregular, rarely annulate or arcuate, in organisation. Individual processes within these relatively large clusters are normally trabeculate. The size, complexity and trabecular connections between adjacent clusters render some precingular and postcingular clusters difficult to distinguish. The smaller apical, paracingular, parasulcal and posterior intercalary paraplates have solitary, generally bifurcate, processes or small, closely-spaced process clusters. The large number and complexity of the processes renders the paratabulation formula difficult to determine precisely; however, it appears to be standard gonyaulacacean. The archeopyle is apical, type (tA), with a free operculum.



TABLE 5

<b>Kimmeridgian</b>	<i>Hystriosphæridium</i>	<i>Emmetrocyta</i>	<i>Oligosphæridium</i>	<i>Amphorula</i>
<b>Oxfordian</b>				<i>Taeniophora</i>
<b>Callovian</b>	<i>Polystephanephorus</i>		<i>Systematophora</i>	
<b>Bathonian</b>	<i>Surculosphaeridium</i>		<i>Rigaudella</i>	<i>Compositosphaeridium</i>
		<i>Adnatosphaeridium</i>	<i>Hapsidaulax</i>	

**Remarks:** The diagnosis of *Adnatosphaeridium caulleryi* has been emended to incorporate the detailed process morphology and its variation and to note the archeopyle type and gonyaulaccean paratabulation. *A. caulleryi* is a relatively variable species and has been used by some workers as a "catch-all" taxon. Bathonian forms with a dense cover of (apparently) nontabular, solid trabeculate processes are here excluded from *A. caulleryi* and placed into open nomenclature, as *Adnatosphaeridium* sp. A. It seems possible that the latter and *A. caulleryi* were the evolutionary precursors of younger Jurassic skolochorate forms such as *Systematophora* and *Taeniophora*, this postulated evolutionary pathway progressively giving rise to types with more ordered intratabular process clusters.

The holotype illustrated by Deflandre (1938, pl. 11, figs. 2–3) has an endocoel densely packed by pyrite. However, the processes can be seen to be grouped distally into poorly developed clusters. The cingulum appears to be marked by isolated single processes, not linked by distal trabeculae. These processes show that the original photograph is orientated at 90 degrees to the apical-antapical axis.

Below (1982) stated that *Adnatosphaeridium* belongs to the "*Cyclonephelium* lineage" (i.e. is a Gv-cyst of Evitt 1985), which infers that the genus falls within the Family Areoligeraceae Evitt 1963, emend. Sarjeant and Downie 1966. His judgement was based on the apparently lenticular nature of the type species, *A. vittatum* Williams and Downie 1966. However, it is preferable to retain *Adnatosphaeridium* within the Family Hystriosphæridiaceae Evitt 1963, emend. Norris 1978a (i.e. Gi-cysts of Evitt 1985), pending a restudy of the holotype of *A. vittatum*.

Berger (1986) noted Below's comments and referred to the morphological variability of *A. caulleryi* and the difficulties in the generic assignment of forms belonging to the *Adnatosphaeridium*, *Systematophora*, and *Polystephanephorus* plexus. The emendation of *Polystephanephorus*, proposed below, makes the recent transfer of *A. caulleryi* to that genus by Courtinat (1989, p. 171) inappropriate. *A. caulleryi* differs from other species of *Adnatosphaeridium* in possessing relatively long, slender processes in intratabular positions all over the central body and in the variability of the processes in their branching and development of trabeculae.

***Adnatosphaeridium densifilum*** (Cookson and Eisenack 1974) **comb. nov.**

Plate 4, figure 1

*Cannosphaeropsis densifilosa* COOKSON and EISENACK 1974, p. 70, pl. 24, fig. 13. — LENTIN and WILLIAMS 1989, p. 47.

**Holotype:** Slide P31289. Lodged at the National Museum of Victoria, Melbourne, Australia.

**Type locality:** 1405–37ft., Broome no. 3 borehole, Canning Basin, Australia; Upper Jurassic.

**Remarks:** It is considered necessary to reassign this species to *Adnatosphaeridium*, since its inclusion into *Cannosphaeropsis* does not accord with the current understanding of the latter genus. Stover and Evitt (1978, p. 143) listed the characteristics of *Cannosphaeropsis* as including a precingular archeopyle and triradiate accessory branches at the end of each gonial process. These features are not developed in *A. densifilum*, whereas it does have an apical archeopyle and complex trabeculae (see pl.

4, fig. 1), thus conforming with the morphology of *Adnatosphaeridium*.

***Adnatosphaeridium? speciosum* (Alberti 1961) comb. nov.**

Plate 5, figure 6

*Cannosphaeropsis speciosa* ALBERTI 1961, p. 37, pl. 9, fig. 13.  
— LENTIN and WILLIAMS 1989, p. 302.

*Polystephanophorus speciosus* (Alberti 1961) RILEY and SARJEANT 1972, p. 3.

**Holotype:** Preparation number A34, present location unknown.

**Type locality:** Hildesheim, Federal Republic of Germany; Oberer Dogger (Middle Jurassic; Callovian).

**Remarks:** For reasons similar to those outlined above for *A. densifilum*, this species cannot be retained in *Cannosphaeropsis* and is here transferred to *Adnatosphaeridium*. Stover and Evitt (1978, p. 143) indicated that the species probably has an apical archeopyle and 15–17 process clusters. The holotype, illustrated by Alberti (1961, pl. 9, fig. 13), has well developed trabeculae and processes that appear to be neither gonial nor sutural in location. The holotype is in the German Democratic Republic, its exact whereabouts unknown. Until it is located and restudied, or until a lectotype can be designated and described, this generic reassignment must be considered provisional.

***Adnatosphaeridium? sp. A***

Plate 1, figures 6–7

*Adnatosphaeridium caulleryi* auct. non (Deflandre 1938) Williams and Downie 1969. RIDING, PENN and WOOLLAM 1985, pl. 5, fig. 1.

**Description:** Central body ellipsoidal, phragma smooth to granular with a dense cover of processes which are apparently largely nontabular. The processes are long, thin, and solid; they flair distally and may contain internal vacuoles. Medial branching is not commonly developed, though distally the processes normally bifurcate and may be connected by thin trabeculae. The archaeopyle appears to be apical.

**Figured specimens:**

BGS Specimen MPK4185

BGS Specimen MPK6488

**Lodgement:** British Geological Survey, Keyworth, Nottingham, England.

**Section:** Atworth Borehole, near Bath, England; Upper Fuller's Earth, Hodsoni Zone, Upper Bathonian (Jurassic).

Size (µm)	minimum	average	maximum
Overall diameter	67.2	76.2	84.0
Cyst body diameter	36.1	43.2	48.2
Process length	19.2	21.6	24.3

four specimens measured.

**Remarks:** This form is not named because, as yet, too few well-preserved specimens have been encountered to make a population sufficiently large to show the full morphological variation. It is only questionably assigned to *Adnatosphaeridium*, since the processes are largely nontabular; one of the chief generic parameters of that genus is the possession of intratabular processes (Stover and Evitt 1978, p. 14).

*Adnatosphaeridium* sp. A is known only from the Bathonian of England.

***Compositosphaeridium* Dodekova 1974 emend.**

*Compositosphaeridium* DODEKOVA 1974, p. 25–26. — STOVER and EVITT 1978, p. 33. — ERKMEN and SARJEANT 1980, p. 65–66. — LENTIN and WILLIAMS, p. 71. — COURTINAT 1989, p. 164.

**Emended diagnosis:** Skolochorate dinoflagellate cyst; body subspherical with a smooth to slightly granular wall consisting of an endophragm and a periphragm. The latter forms about 24 intratabular processes of which the larger are polytubular. Proximally the main processes can be linked by ridges. Distally they are open, with spines at their corners, and may be interconnected by trabeculae. Paracingular and parasulcal processes are thinner, monotubular or bitubular, and distally closed. Paratabulation formula 0-1pr, 4', 0-1?a, 6'', 6c, 5''', 1p, 1''', 1-?s. Archeopyle apical with a zig-zag margin, without well developed auxiliary sutures. Operculum simple polyplacoid; it may incorporate a preapical paraplate as well as four apical paraplates and an anterior intercalary paraplate.

**Type species:** *Compositosphaeridium polonicum* (Górka 1965) Erkmen and Sarjeant 1980.

**Other accepted species:**

*Compositosphaeridium bulgaricum* Erkmen and Sarjeant, p. 66–67.

**Remarks:** The complex taxonomic history of this genus is outlined by Lentin and Williams (1989, p. 71): "When published the genus was monotypic, with *Hystrichosphaeridium costatum* Davey and Williams being the nomenclatural type. Beju (1971, p. 292) considered this species to be a junior synonym of *Hystrichosphaeridium polonicum* Górka 1965, p. 306. Dodekova (1974) did not include Beju (1971) in her bibliography. Erkmen and Sarjeant (1980, p. 65–67) supported the synonymy given by Beju (1971) and proposed the new name *Compositosphaeridium bulgaricum* Erkmen and Sarjeant for the specimens described and illustrated by Dodekova (1974). They also included *C. polonicum* (= *C. costatum*) in the genus, but proposed that *C. bulgaricum* should rightfully be considered as the type species, because it was on the basis of this material that Dodekova had formalised her concept of the new genus *Compositosphaeridium*. This is contrary, however, to the I.C.B.N. .... (T)he correct name of the type species is *Compositosphaeridium polonicum* (Górka) Erkmen and Sarjeant."

The recent emendation by Courtinat (1989, p. 164) is here superseded, in view of inconsistencies in the diagnosis and description. He states, in justification of his emendation, that "Dodekova defined the genus as having two walls, an endophragm and a periphragm, and polytubular processes. An examination, using the S.E.M., of forms attributable to *C. polonicum* indicates without ambiguity that the cyst is formed by only one autophragm and that the processes are monotubes" (free translation of original French text).

The use of an S.E.M. to search for an inner wall of a cyst seems inappropriate. The instrument can only resolve the outer surface of a cyst and cannot prove or disprove the presence of an inner wall. A study using a transmission electron microscope (T.E.M.) would be necessary to prove the contention by Courtinat of a single wall.

The accompanying illustrations (Courtinat 1989, pl. 12, fig. 2; pl. 13, fig. 4), using an optical microscope show the presence of two walls, as is usual in chorate cysts. The term "autophragm" as defined by Williams, Sarjeant and Kidson (1978, p. 10) is therefore used incorrectly and the diagnosis, outlined above, retains the terms "periphragm" and "endophragm". Courtinat also emends the paratabulation formula of the genus but does not mention the antapical plate (probably a typographical error?) or the sulcal plates.

The process morphology, displayed by the two species assigned to *Compositosphaeridium*, is unique and represents an evolutionary experiment in cyst form which was only temporarily successful.

***Compositosphaeridium bulgaricum* Erkmen and Sarjeant 1980**

Plate 5, figures 4–5; text-figure 3, number 5

1974 *Compositosphaeridium costatum* auct. non Davey and Williams, DODEKOVA p. 26–29, pl. 1, figs. 1–11, pl. 2, figs. 1–9, text-figs. 1–2.

*Compositosphaeridium bulgaricum* ERKMEN and SARJEANT 1980, p. 66–67.

**Remarks:** *C. bulgaricum* has polytubes with up to twelve subtubes, the dorsal and antapical polytubes being the largest. From the thickened sides of the polytubes, spines are developed distally, while proximally all processes may exhibit rootlike extensions (Erkmen and Sarjeant 1980, p. 67). A ridge or septum may be developed between process bases, measuring from 3u–15u in height (Dodekova 1974, p. 26–29).

***Compositosphaeridium polonicum* (Górka 1965) emend. Erkmen and Sarjeant 1980**

Plate 3, figure 1

*Hystichosphaeridium polonicum* GÓRKA 1965, p. 306–307, pl. 3, figs. 5–6.

*Hystichosphaeridium costatum* DAVEY and WILLIAMS 1966, p. 62, pl. 10, fig. 4.

*Cordosphaeridium costatum* (Davey and Williams 1966) GÓRKA 1970, p. 489–490, pl. 5, figs. 1a–b, pl. 6, fig. 7, text-fig. 6.

*Compositosphaeridium costatum* (Davey and Williams 1966) DODEKOVA 1974, p. 26, pl. 1, figs. 1–11, pl. 2, figs. 1–9, text-figs. 1–2.

*Compositosphaeridium polonicum* (Górka 1965) emend. ERKMEN and SARJEANT 1980, p. 67–69. — COURTINAT 1989, p. 164, pl. 12, fig. 2; pl. 13, fig. 4; pl. 14, figs. 8, 9; text-fig. 73h.

**Remarks:** The emendation of the genus by Courtinat (1989, p. 164) is here rejected and that by Erkmen and Sarjeant (1980) instead retained. This species has relatively short intratabular processes, not linked by crests or trabeculae: the polytubes consist of fewer than four subtubes. These features differentiate it from *C. bulgaricum* (Erkmen and Sarjeant 1980, p. 67), though intermediate forms with long intratabular processes have been recorded by Górka (1970, p. 48–49). *C. costatum* is a subjective junior synonym of this species. Erkmen and Sarjeant (1980, p. 69) postulate that *C. bulgaricum* evolved into *C. polonicum*.

***Hapsidaulax* Sarjeant 1975a**

**Type species:** *Hapsidaulax margarethae* Sarjeant 1975a, emend herein.

**Remarks:** This genus is thought to be one of the earliest examples, with *Adnatosphaeridium*, of the complex chorate morphology. It is thus of particular interest even though monospecific and rarely reported.

***Hapsidaulax margarethae* Sarjeant 1975a emend.**

Text-figure 3, numbers 1, 3; text-figure 4, numbers 1–3

*Hapsidaulax margarethae* SARJEANT 1975a, p. 144–147, pl. 1a–d, 2a–d, text-figs. 1–3. — STOVER and EVITT 1978, p. 231–232. — SARJEANT 1978, p. 26. — SARJEANT 1979, pl. 1, fig. 7, text-fig. 3b. — RIDING 1982, p. 16, fig. 2, pl. 1, fig. 6. — LENTIN and WILLIAMS 1989, p. 164.

**Emended diagnosis:** Central body spherical to subspherical; phragma thin, with or without granular ornament. Paratabulation formula 5', 2a, 7'', 0c, 6''', 1p, 1pv, 1''', 1s. Trabeculae of very variable thickness, sometimes broadening at their junctions; frequently they have internal vacuoles of variable size. The trabeculae are supported by parasutural processes and may be linked to the parasutures by tenuous crests, entire or fenestrate, occasionally faintly striate; however some cysts, especially those with coarse trabeculae, entirely lack crests. Cingulum not developed, so that the precingular paraplates contact the postcingular paraplates. Only one elongate sulcal paraplate is discernible.

**Holotype:** Specimen SWS 2460/2/104, slide G.Mus. Pd. 2. England Finder co-ordinate D42/1, with G.Mus. label to the right.

**Paratypes:** 1. Specimen SWS 2460/1/106, slide G.Mus. Pd. 1. England Finder co-ordinate B44/4, with G.Mus. label to the right.

2. Specimen SWS 2460/1/109, slide G.Mus. Pd. 1. England Finder co-ordinate F44/2, with G.Mus. label to the right.

**Lodgement:** Slides housed in the Palynology Laboratory, University of Saskatchewan, Saskatoon, Canada.

**Type locality:** Duntulm Formation, Great Estuarine Group, Duntulm, Isle of Skye, Scotland; Middle Jurassic (Bathonian).

**Holotype dimensions:** see Table 6.

**Remarks:** The holotype and both paratypes are in good condition. The holotype and paratype II both conform well with the original descriptions and drawings; however, it should be stressed that these drawings do not show the processes supporting the trabeculae, nor do they show the trabeculae on the opposite side of the cyst. Paratype I was chosen because it displays free trabeculae, unfused to the phragma by crests; and these are indeed well shown. However, the specimen is not crushed (as originally thought) but folded, so that half of the trabeculae lie beneath the central body. The restudy found that the original description and interpretive diagram are incorrect; unfortunately, it was not possible to formulate a satisfactory reinterpretation of the paratabulation of this specimen. Since this aspect of the information that paratype I was thought to provide cannot now be used, the paratabulation formula of the species was proved incorrect. An emendation of the diagnosis is therefore necessary.

The paratabulation formula remains unique among Jurassic dinoflagellates, in particular in its lack of any reflection of a cingulum and the wide separation of the two anterior intercalary

plates. However, in modern dinoflagellates, tabulate thecae without a cingulum are known; for example *Podolampas palmipes* Stein 1883. The absence of a medial groove would seem to indicate that the motile dinoflagellate, of which *H. margarethae* was the cyst, did not have one for its transverse flagellum. Perhaps the dinoflagellate did not have a transverse flagellum for locomotion, which might infer the dinoflagellate was less mobile than those with two flagella; or perhaps, as in some living Dinophysalean genera, the flagellum was enclosed.

The general process morphology is very variable, with gradation from processes joined only distally by trabeculae to processes joined by high crests rising from the body. In cross-section these crests swell distally, being supported by a much thinner proximal portion. This could be a precursor to the development of a fully separate trabecula or it could indicate that the wall had grown outward and fused with the trabecula. When separately developed, the trabeculae frequently are perforate.

Despite a re-examination of the entire type material, no specimens were observed with a recognizable archaeopyle.

The lack of a reflected cingulum and the presence of the species in the Middle Bathonian seems to indicate its primitive morphology in respect to succeeding genera; but, so far as presently known, it had no descendants. Probably there was an environmental control on its distribution, since the two studies recording its occurrence are from geographically close localities, namely western Scotland by Sarjeant (1975a) and eastern England by Riding (1982).

#### *Hystrichosphaerina* Alberti 1961 emend.

*Hystrichosphaerina* ALBERTI 1961, p. 38. — NEALE and SARJEANT 1962, p. 455. — DOWNIE and SARJEANT 1964, p. 169. — NORRIS and SARJEANT 1965, p. 34. — STOVER and EVITT 1978, p. 57–58. — WILSON and CLOWES 1980, p. 56. — DUXBURY 1980, p. 125–126. — LENTIN and WILLIAMS 1989, p. 190.

**Emended diagnosis:** Central body spherical to subspherical, with a smooth to granular phragma. About 18 large intratabular clusters, with approximately 5 to 10 processes per cluster, are developed; the clusters flare distally in a trumpet-like fashion. Processes thin, solid, occasionally thickening distally, with smooth to granular walls. Complex branching occurs along the length of the processes, two orders of branching being commonly developed. The process clusters are capped by ring trabeculae which may be denticulate distally. Inter-cluster trabeculae may be present or absent. Cingulum marked either by a few isolated long, thin, distally bifid processes or by an area devoid of processes. Paratabulation ?4', 6'', 4-6c, 5-6''', 1p, 1'''. Archeopyle apical, type (tA), with a zig-zag margin and free operculum.

**Type species:** *Hystrichosphaerina schindewolfii* Alberti 1961, p. 38.

**Holotype:** From preparation no. A35.

**Lodgement:** Unknown.

**Type locality:** Hildesheim, Federal Republic of Germany; Middle Jurassic (Callovian).

#### *Other accepted species:*

*Hystrichosphaerina neuquina* Quattrocchio and Volkheimer 1983.

*Hystrichosphaerina sarjeantii* (Gitmez 1970) Duxbury 1980.

*Hystrichosphaerina turonica* Alberti 1961.

*Hystrichosphaerina varians* (May 1980) Lentin and Williams 1981.

#### *Provisionally accepted species:*

*Hystrichosphaerina? varispinosa* (Brenner 1988) comb. nov.

**Remarks:** The diagnosis presented by Alberti (1961) is very general and, in modern studies, difficult to use. The emendation here presented is an update, using contemporary morphological concepts with a view to restricting the genus. The new diagnosis incorporates the work of Stover and Evitt (1978) and data gleaned from the original illustrations. A re-examination of the type material is needed to properly define the genus, but its present whereabouts in the German Democratic Republic is unknown to the authors.

*Hystrichosphaerina* differs from *Polystephanophorus* in that the latter has a different paratabulation formula, with fewer process clusters and with the bifurcation of one process per cluster to form a ring trabecula.

*Emmetrocysta* has been differentiated from *Hystrichosphaerina* by Stover and Evitt (1978) on the absence from the former of both cingular processes and inter-cluster trabeculae. Inter-cluster trabeculae may be visible on the photograph of the holotype of *Hystrichosphaerina schindewolfii* Alberti (pl. 10, fig. 3); in particular, a triple junction appears present at the upper right of the photograph. However, this apparent feature remains to be confirmed. If our interpretation is correct, the presence of cingular processes would become the only differentiating feature between *Hystrichosphaerina* and *Emmetrocysta*; moreover, Alberti's diagnosis states that cingular processes are only sometimes, not consistently, present. Both supposed differentiating features, then, appear questionable in view of the uncertainty of the morphology of the type species of *Hystrichosphaerina*. The two genera are not here united, however, pending a re-examination of the type material or, if this remains unavailable, the designation of a neotype.

#### *Hystrichosphaerina? varispinosa* (Brenner 1988) comb. nov.

*Systematophora varispinosa* Brenner 1988, p. 87–88, pl. 16, figs. 2, 5.

**Holotype:** Preparation N7II; catalogue number 1655.

**Lodgement:** Institute and Museum of Geology and Paleontology, Tübingen, Federal Republic of Germany.

**Type locality:** 1800 meters west-southwest of Neuffen Church, near Stuttgart, Federal Republic of Germany; Malm gamma, *Platynota* Zone, Upper Jurassic.

**Remarks:** The morphology of the processes of *Hystrichosphaerina? varispinosa* is very variable within a cluster and from one cluster to another. The processes may have hapto-cluster ring trabeculae, which is at variance with the generic diagnosis of *Systematophora* Klement 1960 as here emended. Brenner's diagnosis fails to describe the body shape, archeopyle location or form, full paratabulation formula,



phragma surface features or holotype size; also no paratypes were designated to show the full range of morphological variation. For these reasons the species is only provisionally placed in *Hystrichosphaerina* Alberti 1961 pending a fuller reconstruction.

The development on the postcingular plates 4''' and 5''' of a gap in the ring trabeculae directed toward the cingulum is of note. This suggests a possible relationship between this species and *Systematophora daveyi* Riding and Thomas 1988. The latter species has all its precingular and postcingular processes arranged in arcs open toward the cingulum.

***Perisseiasphaeridium* Davey and Williams 1966**

*Type species: Perisseiasphaeridium pannosum* Davey and Williams 1966.

*Remarks:* Only one of the three species assigned to this genus has been recorded from the Bathonian to Oxfordian interval under consideration.

***Perisseiasphaeridium ingegerdiae* Nøhr-Hansen 1986**

Text-figure 4, numbers 4, 6

*Perisseiasphaeridium ingegerdii* NØHR-HANSEN 1986, p. 35–36, pl. 3, fig. 11, pl. 4, figs. 8–9, text-fig. 6.

*Remarks:* The original name of the species, *P. ingegerdii*, as proposed by Nøhr-Hansen, did not conform with Article 73.10 and Recommendation 73C (b) of the International Code of Botanical Nomenclature (Voss et al., 1983). This section concerns the creation of a species using a female name which ends in a consonant. The termination is here corrected.

The distal morphology of the major processes is less complex than that of the type species, *P. pannosum* Davey and Williams 1966. The proximal ends of the major processes of *P. ingegerdiae* have striate roots flaring out onto the central body (Nøhr-Hansen 1986, p. 35–36). The type material is from the Lower Kimmeridgian of southern England (Nøhr-Hansen 1986, p. 36). However, an occurrence of this species is known from the Oxfordian of southern France (Smelror and Leereveld, pers. comm.).

***Polystephanephorus* Sarjeant 1961b emend.**

*Polystephanephorus* SARJEANT 1961b, p. 1096. — DOWNIE and SARJEANT 1964, p. 141. — NORRIS and SARJEANT 1965, p. 50. — SARJEANT 1976, p. 18. — STOVER and EVITT 1978, p. 236–237. — DUXBURY 1980, p. 125–126. — WILSON and CLOWES 1980, p. 83. — LENTIN and WILLIAMS 1989, p. 301.

*Emended diagnosis:* Central body spherical to subspherical; phragma single layered (or apparently so), with a smooth to granulate surface. Paratabulation reflected by intratabular process clusters or single processes, giving a formula of ?4', 5'', x or 5c, 6''', 1''', x or 4s. Process clusters are developed on the major paraplates; processes forming the clusters are thin and solid with smooth to granular walls. Branching can occur medially along the process length or distally, with up to two orders of branching, though this is not common. Approximately five to nine processes form each ring cluster; these are connected distally by a trabecula arising from the bifurcation of one of the processes. Process clusters may or may not be interconnected by trabeculae. When cingular or sulcal processes are developed, they are isolated, solid, small and thin with a brief

distal bifurcation. Archeopyle apical, type (tA), with a distinct sulcal notch and free operculum.

*Type species: Polystephanephorus calathus* (Sarjeant 1961b) emend. nov.

*Other accepted species:*

*Polystephanephorus euryanthus* Cookson and Eisenack 1974.

*Polystephanephorus paracalathus* (Sarjeant 1960b) emend. nov.

*Remarks:* This genus occurs rarely, the type species being known only from the type locality. The ambiguity of the described morphology of the two assigned species has been a hindrance to their recognition. The emended diagnoses and diagrams, presented here, demonstrate that the genus has a distinctive morphology. However, more specimens of both species need to be studied to fully determine the possible morphological variation.

The genus differs from *Systematophora* in that *Polystephanephorus* has ring trabeculae and inter-process cluster trabeculae. *Taeniophora* and *Rigaudella* exhibit transingular structures; these are not developed on *Polystephanephorus*. *Emmetrocysta* and *Hystrichosphaerina* have a paratabulation formula which includes six precingular paraplates, while *Polystephanephorus* has only five. The process clusters with many processes developed by *Polystephanephorus* are not formed by *Rigaudella*.

***Polystephanephorus calathus* (Sarjeant 1961a) Sarjeant 1961b emend.**

Plate 2, figures 1, 4; text-figure 1

*Polystephanosphaera calathus* SARJEANT 1960b, p. 140, text-fig. 3a, nomen nudum. — SARJEANT 1961a, p. 104, pl. 14, fig. 7, text-fig. 7

*Polystephanosphaera calathus* (Sarjeant 1961a) SARJEANT 1961b, p. 1096. — SARJEANT 1962a, tab. 3. — SARJEANT 1964, tab. 3. — DOWNIE and SARJEANT 1964, p. 141. — SARJEANT 1967, tab. 7. — EISENACK and KJELLSTRÖM 1971, p. 931. — RILEY and SARJEANT 1972, tab. 3b. — WILLIAMS 1977, tab. 2. — STOVER and EVITT 1978, p. 237. — DUXBURY 1980, p. 126. — WILLIAMS and BUJAK 1985, fig. 19, fig. 43, no. 16. — LENTIN and WILLIAMS 1989, p. 301.

*Emended diagnosis:* Cyst phragmochoate, acavate and without crests. The major paraplates are each defined by a cluster of straight, simple or distally branching processes. Processes may be interconnected medially or proximally, or may repeatedly branch. One single process per cluster bifurcates to form a ring trabecula, which may be smooth or may give rise to very short spinelets. Isolate processes, distally closed and usually with bifid tips, mark the cingulum and sulcus. Paratabulation: ?4', 5'', 5c, 6''', 0p, 1''', 4s. Surface of phragma laevigate, punctate, or infrareticulate. Archeopyle apical, type (tA); operculum free.

*Holotype:* Slide SC 2/11/9.

*Lodgement:* Centre for Palynological Studies, Department of Geology, University of Sheffield, England.

*Type locality:* Scarborough Castle Cliff. Oxford Clay (*Mariae* Zone), Upper Jurassic (Lower Oxfordian).

*Type dimensions:* See Table 6.

**Remarks:** For this, the type species of *Polystephanephorus*, only a holotype and one paratype were originally designated. The holotype suffered damage when made into a single mount during the 70's, and the paratype has not been located. The epittract of the holotype was folded, some of the trabeculae being broken and some processes folded. Nevertheless, the holotype remains in fair condition and, using the technique outlined on p. 2, it proved possible to make a much fuller paratabulation reconstruction than has been ascertained hitherto. However, on the accompanying line drawing (text-fig. 1), the area around clusters 2'' and 2''' remains difficult to resolve and the detail should be considered as tentative.

***Polystephanephorus paracalathus* (Sarjeant 1960b) Sarjeant 1961b emend.**

Plate 2, figures 2, 3, 5; text-figure 2

*Polystephanosphaera paracalathus* SARJEANT 1960b, p. 143–144, pl. 6, fig. 4, text-fig. 3b

*Polystephanephorus paracalathus* (Sarjeant 1960b) SARJEANT 1961b, p. 1096. — SARJEANT 1962a, tab. 3. — SARJEANT 1962b, tab. 3, 4. — SARJEANT 1964, tab. 3. — DOWNIE and SARJEANT 1964, p. 141. — SCHULZ and MAI 1966, tab. 1. — SARJEANT 1967, tab. 7. — SARJEANT 1968, p. 233, 236, pl. 1, fig. 15, tab. 2b. — SARJEANT 1969, fig. 46.1. — EISENACK and KJELLSTRÖM 1971, p. 933. — RILEY and SARJEANT 1972, tab. 3b. — SARJEANT 1976, p. 18–19, pl. 1, figs. 1–2, text-fig. 6. — WILLIAMS 1977, pl. 4, fig. 8, tab. 2. — STOVER and EVITT 1978, p. 237. — DUXBURY 1980, p. 126. — WILLIAMS and BUJAK 1985, fig. 19, fig. 36, no. 4. — LENTIN and WILLIAMS 1989, p. 301

non *Polystephanephorus paracalathus* (Sarjeant 1960b) COURTINAT 1989, p. 171, pl. 13, fig. 11.

**Emended diagnosis:** Body spherical to subspherical, with a smooth to granular autophragm. Five to nine processes are arranged in intratabular clusters which, when viewed laterally, are seen to flare distally. Paratabulation probably ?4', 5'', 0c, 6''', 1''', 0s. Processes thin, thickening distally, solid with occasional medial branching; only one order of branching being developed. Processes terminate in a ring trabecula of variable thickness, which originates from the bifurcation of one process. Each cluster can develop inter-cluster trabeculae. These may join between clusters to form a triple junction and can have dagger-like extensions on the proximal side, usually halfway between adjacent clusters. No cingular or sulcal processes are developed. The archeopyle is apical, type (tA), with a well developed sulcal notch.

**Holotype:** Slide WC 90/2/12.

**Lodgement:** Centre for Palynological Studies, University of Sheffield, England.

**Type locality:** Crook Hill Brickyard, Chickerell, near Weymouth, Dorset, Oxford Clay (Jason Zone). Middle Jurassic (Middle Callovian).

**Holotype dimensions:** See Table 6.

**Remarks:** The holotype of *P. paracalathus* was remounted at the same time as that of *P. calathus*. It was damaged during this procedure and is now in a very poor state. Upon re-examination in 1987, it was found impossible to decipher the paratabulation completely. Nevertheless, using original and new observations, a revised and more refined drawing of the holotype was obtained (text-fig. 2). This confirms and extends the original

diagnosis. However, a more detailed morphological description should be compiled, perhaps using a lectotype, to understand completely the paratabulation and morphological range of this species. Unfortunately, none of the seven other cysts comprising the type material was available for study.

A feature of the species is the uniting of the inter-cluster trabeculae to form triple junctions; however, the inter-process trabeculae are frail and easily broken. Though the poor state of the holotype precludes any conclusive judgement, the trabeculae seem to correspond in position to the sutures. This and the absence of cingular processes could be used to separate the species from *Polystephanephorus* and to erect a new genus, which would make *Polystephanephorus* accord with the concepts of Davey (1982, tab. I). However, owing to the poor state of its holotype, the species is left in the genus *Polystephanephorus* for the time being.

***Rigaudella* Below 1982**

**Type species:** *Rigaudella aemula* (Deflandre 1938) Below 1982.

**Remarks:** This genus has transcingular trabeculae uniting processes situated on the precingular and postcingular paraplates and forming several large process groupings. *Taeniophora* also exhibits connection between the processes of the pre- and postcingular paraplates, but the linkage is by raised ridges on the phragma, not by trabeculae. Nevertheless, these cross-cingular connections indicate a relationship between the two genera. The lack of cingular and sulcal processes is one of the features distinguishing *Rigaudella* from *Adnatosphaeridium* Williams and Downie 1966, as here emended.

***Rigaudella aemula* (Deflandre 1938) Below 1982**

Plate 1, figure 2

*Hystichosphaeridium aemulum* DEFLANDRE 1938, p. 187–189, pl. 9, fig. 12, pl. 10, figs. 5–8, pl. 11, figs. 1–7.

*Cannosphaeropsis aemula* (Deflandre 1938) DEFLANDRE 1947b, p. 1576.

*Cannosphaeropsis paucispina* KLEMENT 1960, p. 72, pl. 10, figs. 9–10.

*Adnatosphaeridium aemulum* (Deflandre 1938) WILLIAMS and DOWNIE 1969, p. 17.

*Adnatosphaeridium paucispinum* (Klement 1960) GITMEZ and SARJEANT 1972, p. 234, pl. 10, figs. 1–4.

*Rigaudella aemula* (Deflandre 1938) BELOW 1982, p. 139, 140, 143–4, 147, figs. 1–6, 8, 11–23, 27–28, 31–33.

**Remarks:** Below (1982) furnished a detailed interpretative drawing of this species, illustrating the large processes which branch along their length and distally develop hapto-ring trabeculae. The processes are also linked by inter-process trabeculae to form large ellipses connecting a number of processes. The ellipses cross from epittract to hypottract, forming transcingular structures.

***Rigaudella filamentosa* (Cookson and Eisenack 1958) Below 1982**

Plate 4, figures 3–4

*Cannosphaeropsis filamentosa* COOKSON and EISENACK 1958, p. 47, pl. 7, figs. 8–9, pl. 8, figs. 1–3.

*Cannosphaeropsis perforata* ALBERTI 1961, p. 37, pl. 9, fig. 14.

*Adnatosphaeridium filamentosum* (Cookson and Eisenack 1958) WILLIAMS and DOWNIE 1969, p. 17.

*Adnatosphaeridium perforatum* (Cookson and Eisenack 1958) RILEY and SARJEANT 1972, p. 3.

*Rigaudella perforata* (Cookson and Eisenack 1958) BELOW 1982, p. 148–149, fig. 34.

**Remarks:** The diagram given by Below, in his restudy of this species (1982, text-fig. 34), shows trabeculae which do not always form complete rings. Cookson and Eisenack (1958) did not mention this feature. Moreover, Below (1982, p. 149) noted the variability of the process morphology, as illustrated by the two paratypes. The division of the processes can start anywhere along their length and the resulting complexity of fenestration is variable. Below (ibid., p. 149) noted that *R. filamentosa* is probably a senior synonym of *R. perforata*. The holotype of the latter is in the German Democratic Republic, its exact whereabouts unknown, so that no further information could be obtained to supplement Alberti's original description and illustration (1961, p. 37; see Table 6 herein). Despite this, we concur with Below 1982 in considering *R. perforata* to be a junior synonym of *R. filamentosa*.

Helby and Partridge (1980), in their re-illustration of Australian holotypes, noted that the holotype of *R. filamentosa* was not available for examination. Their illustrations of two paratypes are here reproduced (pl. 4, figs. 3–4).

***Surculosphaeridium*** Davey, Downie, Sarjeant and Williams, 1966

**Type species:** *Surculosphaeridium cribrotubiferum* (Sarjeant 1960b) emend. herein

**Remarks:** The emendation by Davey (1982, p. 15) of *Surculosphaeridium* excludes the species *Surculosphaeridium? vestitum* (Deflandre 1938) Davey, Downie, Sarjeant and Williams 1966, because the species has three antapical plates. While it is believed that the genus generally has intratabular processes, the exclusion of this species from *Surculosphaeridium* on this morphological criterion alone is not accepted and its placement into *Systematophora* is rejected. Davey's emendation of the genus is therefore likewise rejected.

***Surculosphaeridium cribrotubiferum*** (Sarjeant 1960b) emend.

Text-figure 3, numbers 4, 6

*Hystrichosphaeridium cribrotubiferum* Sarjeant 1960b, p. 137, pl. 6, figs. 2–3, text-fig. 1. — DOWNIE and SARJEANT 1964, p. 120

*Surculosphaeridium cribrotubiferum* (Sarjeant 1960b) DAVEY, DOWNIE, SARJEANT and WILLIAMS 1966, p. 161–162, pl. 9, fig. 6, text-fig. 41. — RILEY and SARJEANT 1972, tabs. 3–4. — LAM and PORTER 1977, fig. 4. — STOVER and EVITT 1978, p. 83. — SARJEANT 1978, p. 26. — SARJEANT 1979, text-fig. 3d. — WOOLLAM 1980, pl. 5, fig. 10, text-fig. 4. — WOOLLAM and RIDING 1983, fig. 8. — LENTIN and WILLIAMS 1989, p. 357. — COURTINAT 1989, p. 172, pl. 12, fig. 1; pl. 13, fig. 5; text-fig. 73d.

**Emended diagnosis:** Body subspherical, skolochorate, without crests. Phragma composed of two layers. Intratabular processes reflect the tabulation formula 4', 6'', 6c, 6''', 1p, 3''', ?1s. Processes large, thick, solid, and distally closed. Proximally the main processes have striations on their walls, extending onto the surface of the phragma. Processes may develop first and second order branching. Process walls typically exhibit circular depressions between the striations: these are of variable size and depth, with steep sides. The cingulum is marked by six thin

processes, which may be deeply bifurcate; the sulcus may be devoid of processes or may bear a single thin, solid process.. The apical archeopyle, type (tA), has short accessory archeopyle sutures and a deep sulcal notch.

**Holotype:** Slide V.51735(1), WF 108/13/3.

**Lodgement:** British Museum of Natural History, London.

**Type locality:** Furzy Cliff, Weymouth, Oxford Clay (*Cordatum* Zone). Late Jurassic (Lower Oxfordian).

**Holotype dimensions:** See Table 6.

**Remarks:** In 1987, the holotype was examined at the British Museum of Natural History, London and found to be in good condition. Though the cyst has organic debris around the body, this does not obscure its morphology significantly. The principal processes have striations on their walls extending to their bases. Between the ridges are structures which Davey et al. (1966, p. 161) termed 'pores'; however, they do not open into the interior of the processes, appearing instead to be circular depressions of varying size with steep sides (see text-fig. 3, no. 6). The apical archeopyle has a sulcal notch and short accessory archeopyle sutures.

The original diagnosis designated only the holotype out of the eight specimens seen in the assemblage. Davey (1982), in his restrictive emendation, stated that the genus has only one antapical paraplate. However, the type species *S. cribrotubiferum* has three antapical paraplates (Davey did not publish an emended diagnosis of the species but only of the genus). His emendation is therefore rejected.

***Surculosphaeridium? vestitum*** (Deflandre 1938) Davey, Downie, Sarjeant and Williams, 1966.

Plate 3, figure 9

*Hystrichosphaeridium vestitum* DEFLANDRE 1938, p. 189–190, pl. 11, figs. 4–6.

*Baltisphaeridium vestitum* (Deflandre 1938) SARJEANT 1960a, p. 397, pl. 13, fig. 8, pl. 14, figs. 13–14.

*Surculosphaeridium vestitum* (Deflandre 1938) DAVEY, DOWNIE, SARJEANT and WILLIAMS 1966, p. 162, pl. 9, fig. 8, text-fig. 42.

*Surculosphaeridium? vestitum* (Deflandre 1938) STOVER and EVITT 1978, p. 83.

*Systematophora vestita* (Deflandre 1938) DAVEY 1982, p. 13.

**Remarks:** The proposal by Davey (1982, p. 15) to transfer *Surculosphaeridium? vestitum* to *Systematophora* Klement 1960 is here rejected. This species does not have proximally linked processes which form ring clusters, as shown by the type species of *Systematophora*; instead, the processes are isolate. Davey noted that the species has more than one antapical paraplate but did not publish a paratabulation formula. It is considered preferable to leave the species in *Surculosphaeridium*, pending further study of the relationship of process locations to paraplate boundaries. The type specimen was illustrated by Deflandre (1938, pl. 9, fig. 5) only as a line drawing and there is also an urgent need for a full restudy.

***Systematophora*** Klement 1960 emend.

*Systematophora* KLEMENT 1960, p. 61–62. — SARJEANT 1961b, p. 1095–1096. — DOWNIE and SARJEANT 1964, p. 146. — NORRIS and SARJEANT 1965, p. 57. — SARJEANT

1984, p. 167. — BRENNER 1988, p. 83–86. — LENTIN and WILLIAMS 1989, p. 360.

*Polystephanosphaera* SARJEANT 1960b, p. 140–142.

Emended diagnosis: Phragmochorate dinoflagellate cyst; central body spherical to ellipsoidal with a smooth to granular phragma. Paratabulation 0-2pr, 4", 6", 5-6c, 5-6"', 1p, 1"', 1-5s. Penitabular to intratabular clusters of processes are developed on the precingular, postcingular and antapical paraplates. Proximally, each process of a cluster is linked to its neighbor, to a greater or lesser degree, by a crest on the phragma; the resulting grouping can form a circle or ellipse. Processes are solid, of moderate length; branching varies from a single distal bifurcation to very intricate complexes with numerous stages of branching. Inter-process trabeculae or ring trabeculae are not normally developed. The number of processes per cluster varies from 3 to many. In the apical region four penitabular to intratabular clusters may be present or single or paired processes may be developed instead. At the apex, preapical paraplates can be indicated by a single process, a ridge, or not at all. The cingular and sulcal paraplates may be devoid of processes; alternatively, they may have single isolated processes or pairs of processes joined together proximally by a wall or ridge. Archeopyle apical, type (tA); often with a sulcal notch.

Type species: *Systematophora areolata* Klement 1960.

*Other accepted species:*

*Systematophora ancyrea* Cookson and Eisenack 1965.

*Systematophora complicata* Neale and Sarjeant 1962.

*Systematophora conspicua* He and Li 1981.

*Systematophora cretacea* Davey 1979a.

*Systematophora orbifera* Klement 1960.

*Systematophora palmula* Davey 1982.

*Systematophora penicillata* (Ehrenberg 1843, ex 1854) Sarjeant 1980.

*Systematophora placacantha* (Deflandre and Cookson 1955) Davey, Downie, Sarjeant and Williams, 1969.

*Systematophora silyba* Davey 1979b.

*Systematophora valensii* (Sarjeant 1960b) Sarjeant 1961b.

*Systematophora? variabilis* (Cookson and Eisenack 1967) Stover and Evitt 1978.

*Provisionally accepted species:*

*Systematophora? curta* Matsuoka and Bujak 1988. This species can have incomplete development of the basal connection of processes within a cluster and, where formed, the clusters are rectangular in shape unlike those of any other species of the genus.

*Systematophora? daveyi* Riding and Thomas 1988. The assignment of this species to *Systematophora* is questionable, owing to its incomplete development of circular process clusters.

*Note:* The species *Systematophora? austinii* (Merrill 1895) Sarjeant 1964 is included by Lentin and Williams in their latest dinoflagellate index (1989, p. 360). However, this species was rejected by Sarjeant (1966, p. 5), who showed that its holotype is a specimen of *Spiniferites ramosus* (Ehrenberg 1838) Loeblich and Loeblich 1966. *S.? austinii* is thus a subjective junior synonym of that species and should be rejected.

*Remarks:* This emended diagnosis is based, to a large degree, on the description of the genus by Davey (1982, p. 11). The primary characteristic of this genus is the basal linkage of most processes into clusters. The presence or absence of paired

processes marking the cingulum and sulcus cannot be used as the sole criterion to distinguish this genus from others. Brenner (1988, p. 83) records a solitary process marking the apex, while in certain Argentinian forms studied by Volkheimer and Sarjeant (unpublished data), preapical paraplates are indicated by lesser surficial ornament. The recent emendation by Brenner (1988, p. 83–85) is not utilised here, since it does not sufficiently stress the morphology of the processes.

The genus is distinguished from *Taeniophora* Klement 1960 by its lack of transcingular structures. *Polystephanophorus* Sarjeant 1961b has only five precingular paraplates and *Emmetrocysta* Stover 1975 does not have cingular processes. *Hystrichosphaerina* Alberti 1961 has intratabular clusters with very complex branching and ring trabeculae; the latter are not consistently developed by *Systematophora*. However, these two genera are morphologically and stratigraphically close; indeed, they were considered synonymous by Neale and Sarjeant (1962) and Norris and Sarjeant (1965).

*Systematophora areolata* Klement 1960

Plate 5, figures 3, 7; text-figure 4, number 5

*Systematophora areolata* KLEMENT, p. 62–65, pl. 9, figs. 1–8, text-figs. 32–35.

*Remarks:* The holotype was taken by the late Dr. Karl Klement to Texas; since his death in 1982, its whereabouts is unknown. Fortunately the original description is very detailed, with a number of drawings and good plates. The paratypes are still in Tübingen (Brenner 1988, p. 86); a lectotype or neotype should be selected.

*Systematophora orbifera* Klement 1960

Plate 5, figures 1–2

*Systematophora orbifera* KLEMENT 1960, p. 66–67, pl. 9, figs. 9–10, pl. 10, fig. 7.

*Hystrichosphaerina orbifera* (Klement 1960) STOVER and EVITT 1978, p. 58.

*Remarks:* The transfer of this species to *Hystrichosphaerina* Alberti by Stover and Evitt (1978) is here rejected, owing to the general lack of complete ring trabeculae from most process clusters of the holotype. Indeed, the complex nature of the processes makes it difficult to be certain that any ring trabeculae are developed (Gocht, pers. comm.). The paratypes do have hapto-cluster trabeculae, occasionally with ring trabeculae. The variability in morphology of the processes within clusters is great, but no more than is typical of the genus.

*Systematophora penicillata* (Ehrenberg 1843, ex 1854) Sarjeant 1980

Text-figure 3, number 2

*Xanthidium penicillatum* EHRENBURG 1843, p. 61, nomen nudum. — EHRENBURG 1854, pl. 37, fig. 8.3.

*Ovum hispidum* (*Xanthidium*) *penicillatum* (Ehrenberg 1843, ex 1854) LOHMANN 1904, p. 21.

*Hystrichosphaera penicillata* (Ehrenberg 1843, ex 1854) WETZEL 1933, p. 41.

*Systematophora fasciculigera* KLEMENT 1960, p. 65–66, pl. 9, figs. 11–12, pl. 10, fig. 8.

*Hystrichosphaeridium penicillatum* (Ehrenberg 1843, ex 1854) DOWNIE and SARJEANT 1964, p. 121.

*Systematophora penicillata* (Ehrenberg 1843, ex 1854) SARJEANT 1980, p. 282–283, pl. 37.



**Remarks:** In the redescription of this species by Sarjeant (1980, p. 282), *S. fasciculigera* Klement 1960 was shown to be its subjective junior synonym. The photograph here reproduced (pl. 6, fig. 2) was taken in 1980 by the second author and is necessarily of indifferent quality, since the holotype is embedded in chert and very difficult to photograph. Through inadvertence, the paratabulation formula given in the emended diagnosis did not include the postcingular processes. (The formula should be ?3-4', 6'', 5-6c, 6''', 1p, 1''', ?0s.) However, in view of the subsequent full description presented by Sarjeant (op. cit.), it is not considered necessary to emend the diagnosis formally.

***Systematophora valensii*** (Sarjeant 1960b) Sarjeant 1961b Plate 3, figures 5, 7, 10

*Polystephanosphaera valensii* SARJEANT 1960b, p. 142-143, pl. 6, figs. 5-7, text-fig. 3c.

*Systematophora valensii* (Sarjeant 1960b) SARJEANT 1961b, p. 1096.

**Remarks:** The original erection of this species by Sarjeant (1960b, p. 142-143) followed the International Code of Zoological Nomenclature, being published prior to the article by Downie et al. (1961) in which the use henceforward of the International Code of Botanical Nomenclature for dinoflagellate taxonomy was advocated. Consequently, despite the statement to the contrary by Lentin and Williams (1973, p. 134 and subsequent editions), the transfer of the species from *Polystephanosphaera* to *Systematophora* by Sarjeant (1961b) was valid (Article 48). The species therefore did not require validation by Downie and Sarjeant (1964, p. 146), as was claimed by Lentin and Williams (1973, p. 134).

Recently the holotype was re-examined and photographed by Downie (pers. comm.) on behalf of the present authors. The cyst is in a very poor state of preservation, having suffered severe damage during transfer from the original strew-mount to a single mount. The morphology of the process clusters can be seen to accord with the original diagnosis, but no new details could be determined. It is suggested that a neotype should be selected for this species, as soon as a suitable specimen becomes available.

***Taeniophora* Klement 1960 emend. Sarjeant 1984**

**Type species:** *Taeniophora iunctispina* Klement 1960.

**Remarks:** The basal linkage of processes across the cingulum is an important characteristic of the genus. However, the presence of organic material often obscures the cyst surface, making the differentiation of this genus from *Systematophora* Klement 1960 difficult. Courtinat (1989, p. 174) remarks that his specimens do not always exhibit the characteristic pattern of basal cross-cingular linkage, so that the resulting morphology may resemble that of *Amphorula* Dodekova 1969, suggesting a possible relationship between the two genera.

***Taeniophora filamentosa* Klement 1960 emend. Sarjeant 1984**

Plate 3, figures 4, 6

*Taeniophora iunctispina* subsp. *filamentosa* KLEMENT 1960, p. 70, pl. 10, figs. 5-6.

*Systematophora iunctispina filamentosa* (Klement 1960) STOVER and EVITT 1978, p. 84.

*Taeniophora filamentosa* (Klement 1960) SARJEANT 1984, p. 169-170, pl. 2, figs. 3-4.

**Remarks:** The holotype was redescribed by Sarjeant (1984, p. 170) and shown to have transcingular ridges. The presence of a defined cingulum and the smaller process length (40-45% of the breadth of the cyst's body) distinguish this species from *T. iunctispina* Klement 1960.

***Taeniophora iunctispina* Klement 1960 emend. Sarjeant 1984**

Plate 3, figures 3, 8

*Taeniophora iunctispina* KLEMENT 1960, p. 68, pl. 10, figs. 1-6.

*Systematophora iunctispina* (Klement 1960) STOVER and EVITT 1978, p. 84.

*Taeniophora iunctispina* Klement 1960; emend. SARJEANT 1984, p. 168-169.

**Remarks:** The species has transcingular ridges on the phragma. The length of the processes is 50-60% of the breadth of the cyst and the process walls are coarsely granular. The cingulum is marked by deflections of the transcingular ridges (Sarjeant 1984, p. 168-169).

## PHYLOGENETIC RELATIONSHIPS

The morphology of complex chorate dinoflagellate cysts lends to the study of their evolutionary lineage. In 1960 the second author published the earliest speculations concerning the evolution of process structure in this group of cysts (Sarjeant 1960b, p. 142, text-fig. 4). Five basic morphologies, of which only four had then been recognised in the fossil record, were postulated as the likely 'root-stock' of the group.

When that diagram was published, very little was known of the stratigraphical distribution of these morphologies. A more detailed evolutionary lineage can now be hypothesized. Possible Early Jurassic precursors to the complex chorate group include the spinose genera *Dapsilidinium* Bujak, Downie, Eaton and Williams 1980, *Luehndea* Morgenroth 1970, and *Valvaeodinium* Morgenroth 1970, but direct relationships are difficult to demonstrate. These three genera all have simple processes, gonial, sutural, or nontabular. At this stratigraphical level there are no species with multi-staged, distally branching processes, trabeculae or intratabular process clusters. Of these early genera, the species occurring latest, *Luehndea spinosa* Morgenroth 1970, ranges up into the Early Toarcian, leaving the Aalenian and Bajocian devoid (to the authors' knowledge) of complex chorate cysts.

*Adnatosphaeridium caulleryi* (Deflandre 1938) Williams and Downie 1969 has been recorded from the Lower Bathonian (Riding 1982; Taugourdeau-Lantz and Lachkar 1984) and *Hapsidaulax margarethae* Sarjeant 1975a has been reported from the base of the Middle Bathonian (Riding 1982). In theory, either of these species might form the basis from which other complex chorate dinoflagellate cysts evolved. *Adnatosphaeridium caulleryi* has a complex network of processes and trabeculae, while *Hapsidaulax margarethae* has complex processes and lacks a cingulum. This would seem to indicate that the possession of a complex network of trabeculae is a primitive feature.

However, *Hapsidaulax margarethae*, with its variable morphology of walls and trabeculae positioned along the plate sutures

TABLE 6

A listing of features for complex chorate dinoflagellates. Asterisk (\*) indicates type species. "Inf. Plate" indicates authors inference.

	<i>Adnatosphaeridium caulleryi</i> (Deflandre 1938, p. 189) emend nov.	<i>Adnatosphaeridium densifilosum</i> (Cookson & Eisenack, 1974 p. 70) comb. nov.	<i>Adnatosphaeridium? speciosum</i> (Alberti, 1961, p. 37) comb. nov.	<i>Compositosphaeridium bulgaricum</i> Erkmen & Sarjeant 1980, p. 66-67.	* <i>Compositosphaeridium polonicum</i> (Górka, 1965, p. 306-307) Erkmen & Sarjeant 1980, p. 67-69.
Shape of body	globose (1)	oval (1)	nearly spherical (1)	ovoid (1)	spherical to oval
Paratabulation	4', 6'', 6c, 6''', 1p, 1''', x-?s'		not resolved	4', ?a, 6'', 6c, 5''', 1p, 1pv, 1''' (1)	4', ?a, 6'', 6c, 5''', 1p, 1''' (1)
Archaeopyle type & position	apical		? apical (2)	apical (1)	apical. Inf. plate (1)
Archaeopyle suture				auxiliary suture developed with sulcal notch. Inf. pl. (2)	unrecorded
Process type	solid slender (1)	cylindrical to slightly conical (1)		large polygonal tubes, 2-12 components (1)	monotubes or polytubes (1)
order of branching	yes; 2 stages	yes; 2 at least. Inf. plate (1)	at least 2 stages. Inf. plate (1)	1 stage. Inf. plate (2)	no branching (1)
clustered proximally	yes		yes (3)		no (1)
number of clusters	? 18		15-17 (1)		
trabeculae & type	inter-process trabeculae	yes (1)	hapto-cluster. Inf. plate (1)	rare inter-process trabeculae (1)	not present (1)
ring trabeculae	not present		yes. Inf. plate (1)	not developed. Inf. plate (2)	
Process location	intratabular			intratabular (1)	intratabular (1)
Processes closed distally	yes			only some on cingulum and sulcus (1)	no (1)
Cingulum marked by	single processes		not evident on holotype photograph	small processes; solid, thin monotubes or polytubes (1)	monotubes or spines (1)
Sulcus marked by	not resolved			small processes; solid, monotubes or polytubes (1)	thin processes with furcate tips (1)
Wall details	not ornamented (1)	thin (1)	smooth to slightly granular (1)	mesh-like ornament (2)	
Body size	total cyst 45-50µm (1)	body 70:52µm (1) overall 166:142µm (1)	width of shell 52µm (1)	body length (no operculum): 47-55µm (2)	diameter 21-42µm (1)
Process length	10-17µm (1)		18-23µm (1)	17-23µm (2)	12-28µm (1)
References used in compiling table	(1) Deflandre 1938, p. 189, pl. 11., figs. 2-3.	(1) Cookson & Eisenack, 1974, p. 70, pl. 24 fig. 13.	(1) Alberti 1961, p. 37-38, pl. 9 fig. 13., (2) Stover & Evitt 1978, p. 144., (3) Riley & Sarjeant 1972, p. 3.	(1) Erkmen & Sarjeant 1980, p. 66-67., (2) Dodekova 1974, p. 26-27, text-fig. 1.	(1) Erkmen & Sarjeant 1980, p. 68

TABLE 6  
Continued

<i>*Hapsidaulax margarethae</i> Sarjeant 1975; emend. nov.	<i>*Polystephanophorus calathus</i> (Sarjeant 1961a, p. 104) emend. nov.	<i>Polystephanophorus paracalathus</i> (Sarjeant 1960b, p. 143-144) emend. nov.	<i>*Rigaudella aemula</i> Below 1982, p. 139-147.	<i>Rigaudella filamentosa</i> (Cookson & Eisenack 1958, p. 47) Below 1982, p. 148-149.	<i>*Surculosphaeridium cribratiferum</i> (Sarjeant 1960b, p. 137) emend. nov.
spherical to ellipsoidal $\pm$ slight apical prominence(1)	ellipsoidal	spherical	spheroidal (1)	sphaerical (1)	subspherical
5', 2a, 7'', 0c, 6''', 1p, 1pv, 1''', 1s	?4', 5'', 5c, 6''', 1''', 4s	probably ?4', 5'', 0c, 6''', 1''', 0s.	4', 6'', 0c, 5(-?6)''', 1pv, 1pv, 1''', 0s. (1)	not recorded	4', 6'', 6c, 6''', 1p, 3''', 1-?s
? precingular (1)	apical (2)	apical (1)	apical (1)	apical. Inf. plate (2)	apical (2)
not recorded	short auxiliary sutures	sulcal notch developed	zig-zag with auxiliary sutures. Inf. plate(1)		auxiliary sutures and sulcal notch developed
highest antapically (1)	simple (1)	simple or branched (2)	proximally solid, dis- tally branched (1)	distally complex,, ramiform	solid (2)
1 stage	1 stage	1 stage	2 stage. Inf. plate (1)	2 staged. Inf. plate (2)	1-2 stages
no	yes (3)	yes (2)	no. Inf. plate (1)	no. Inf. plate (1)	no
	12-16 (3)	unrecorded			
variable thickness, inter-process (1)	hapto-cluster trabeculae	hapto-cluster and inter-cluster trabeculae(2)	inter-process and hapto-process trabeculae (1)	inter-process and hapto-process. Inf. plate (2)	no
no	yes (3)	yes (2)	hapto-process (1)	no (not true rings). Inf. plate (2)	
sutural processes (1)	intratabular	intratabular	intratabular Inf. plate (1)	intratabular Inf. plate (2)	intratabular (3)
yes	yes	yes	yes. Inf. plate (1)	Yes. Inf. plate (2)	yes
not marked (1)	single isolated small processes	lack of processes	no processes (1)	process free area	deeply branched processes
one sulcal plate	single isolated small processes	lack of processes	no processes, sulcal notch(1)	process free area	sulcal notch
thin, granular or psilate (1)	shagrinata	moderately thin	2 layered (1)	moderately thick	2 layered, smooth to lightly ornamented(2)
central body 23- 34 $\mu$ m by 20-37 $\mu$ m (1)	holotype diameter 45 $\mu$ m (3)	holotype diameter 40 $\mu$ m (3)	body 25-45 $\mu$ m (2)	holotype 48 $\mu$ m (1)	holotype body diame- ter 43 $\mu$ m by 39 $\mu$ m, (1)
up to 17 $\mu$ m	22-23 $\mu$ m (3)	26 $\mu$ m (3)	18-25 $\mu$ m (2)	not recorded	up to 24 $\mu$ m (1)
(1)Sarjeant 1975a, p. 144-147, text-fig. 2.	(1)Sarjeant 1978, p. 23, (2)Sarjeant 1976, p. 18. (3)Sarjeant 1961a, p. 104.	(1)Sarjeant 1976, p. 19. (2)Sarjeant 1978, p. 24. (3)Sarjeant 1960b, p. 143.	(1)Below 1982, p. 138, 147, text-fig. 23. (2)Deflandre 1938, p. 188.	(1)Cookson & Eisenack 1958, p. 47, pl. 8 fig. 8. (2)Below 1982, p. 149, text-fig. 34.	(1)Davey et al. 1966, p. 161. (2)Davey 1982, p. 15. (3)Sarje- ant 1978, p. 26.

TABLE 6  
Continued

	<i>Surculosphaeridium? vestitum</i> (Deflandre 1938, p. 189) Davey et al. 1966, p. 162.	* <i>Systematophora areolata</i> Klement 1960, p. 62-65.	<i>Systematophora orbifera</i> Klement 1960, p. 66-67.	<i>Systematophora penicillata</i> (Ehrenberg 1843 ex 1854) Sarjeant 1980, p. 282-3.	<i>Systematophora valensii</i> (Sarjeant 1960b, p. 142) Sarjeant 1961b, p. 1096.
Shape of body	ellipsoidal (1)	ellipsoidal to circular (1)	spherical to ellipsoidal (1)	subspherical (1)	spherical (1)
Paratabulation	unresolved	?, 6'', 26c, 6''', 1p, 1''', 2s (2)	4', 6'', 24c, 25''', 1'''' (2)	?3-4', 6'', 5-6c, 6''', 1p, 1''', 20s (1)	unrecorded
Archaeopyle type & position	unrecorded	apical (1)	apical (1)	apical (1)	unrecorded
Archaeopyle suture		slightly zig-zag (3)	not recorded	unrecorded	
Process type	slender and variable (2)	branched distally (2)	variable thickness (1)	simple, bifid or ramiform (1)	fused for up to half of length (2)
order of branching	1-3 staged	1-2 stages. Inf. plate (1)	2 stage. Inf. plate (1)	yes (1)	2 stage. Inf. plate (1)
clustered proximally	no	yes (2)	yes (1)	yes (1)	yes (1)
number of clusters		14+. Inf. plate (2)	?16. Inf. plate (2)	17-18. Inf. plate (1)	12-16 (1)
trabeculae & type	no (2)	no. Inf. plate (2)	inter-cluster (3)	hapto-cluster. Inf. plate (1)	no (2)
ring trabeculae			generally no (3)	no (1)	
Process location	intra-tabular (3)	penitabular. Inf. plate (3)	not recorded	penitabular (1)	unrecorded
Processes closed distally	yes	yes (1)		yes. Inf. plate (1)	yes (1)
Cingulum marked by	deeply furcate or separated processes (3)	rectilinear paired process groupings. Inf. Plate (1)	single, isolated processes. Inf. plate (1)	paired processes (1)	an area without processes
Sulcus marked by	area without process development	2 rectilinear process groupings of 3 processes each (1)	unresolved	area without processes	an area without processes
Wall details	shagrinate., moderately thick	reticulate (1)	occasional fine reticulation (1)	unrecorded	
Body size	body length up to 70µm (1)	body: length 58-63µm; breadth 46-50µm (1)	body length 35-70µm; breadth 43-58µm (1)	body length 40-70µm; breadth 40-65µm (1)	holotype: body diameter 62µm (1)
Process length	up to 30µm (3)	12-26µm (1)	20-29µm (1)	17-25µm (1)	about 20µm (1)
References	(1)Deflandre 1938, p. 189. (2)Sarjeant 1978, p. 26. (3)Davey et al. 1966, p. 162-163.	(1)Klement 1960, p. 62-65, text-fig. 33, 35. (2)Sarjeant 1978, p. 25. (3)Stover & Evitt 1978, p. 84.	(1)Klement 1960, p. 66-67; (2)Courtinat & Gaillard 1980, p. 35; (3)Gocht (pers. comm.).	(1)Sarjeant 1980, p. 282-283, pl. 37.	(1)Sarjeant 1960b, p. 142, text-fig. 3c. (2)Sarjeant 1978, p. 25.



TABLE 6  
Continued

<i>Taeniophora filamentosa</i> (Klement 1960, p. 70) emend. Sarjeant, 1984, p. 169-170.	* <i>Taeniophora iunctispina</i> Klement 1960, p. 68-69 emend. Sarjeant 1984, p. 168-9.	<i>Perissosphaeridium ingegerdiae</i> Nøhr-Hansen 1986, p. 35-36.
ovoid (1)	spherical (1)	subspherical body (1)
unresolved	1-5", 2-6"', 1''''; partial tabulation formula (1)	4', 6'', 6c (?), 5''', 1p (?), 1''''', ?s(1)
apical (1)	apical (1)	apical (1)
auxiliary sutures (1)	accessory sutures developed (1)	auxiliary sutures. Inf. plate (1)
slender to very slender, distally variably branching (1)	slender, distally branched (1)	2 types; large thick hollow tubiform or slender massive processes (1)
1-2 stages. Inf. plate (1)	1-2 stages (1)	distal tips; 1 stage. Inf. plate (1)
surficial lines or ridges join processes (1)	connected by low walls (1)	no
5+(1)	7 at least. Inf. plate (1)	
occasional inter-process (1)	inter-process. Inf. plate (1)	no
no. Inf. plate (1)	no. Inf. plate (1)	
some are gonial (1)	on a low ridge. Inf. plate (1)	intratabular (1)
yes. Inf. plate (1)	yes (1)	only cingular processes. Inf. plate (1)
low ridges (1)	flexure in cluster-connecting ridges (1)	6 pairs of processes (1)
sulcal notch (1)	sulcal notch (1)	isolated single processes (1)
punctate (1)	punctate to fine graulation; ridges on wall (1)	2 layered (1)
length 52-58µm; breadth ± 52µm (2)	length± 58µm; breadth 46-52µm (2)	body diameter 42-60µm (1)
15-23µm (2)	maximum 29-35µm (2)	20-30µm (1)
(1)Sarjeant 1984, p. 170, pl. 2 fig. 4. (2)Klement 1960, p. 70.	(1)Sarjeant 1984, p. 168, pl. 3, figs. 1-2, text-fig. 6., (2)Klement 1960, p. 69.	(1)Nøhr-Hansen 1986, p. 35-36, text-fig. 6.

and its lack of any indication of a cingulum, is unique and seems not to be directly related to the later complex chorate genera.

In contrast, *Adnatosphaeridium caulleryi* can readily be interpreted as the precursor of those later genera, all of which have a similar morphology of thin, branching processes. The accompanying chart (Table 5) is speculative, but suggests that trabecular development becomes progressively reduced in younger strata, whereas the position of the processes becomes more ordered. The table suggests some probable interconnections of genera, with three separate lineages starting from *Adnatosphaeridium* Williams and Downie 1966.

In the Upper Bathonian *Compositosphaeridium* Dodekova 1974 is first reported. Like *Hapsidaulax*, it has a unique morphology in this case consisting of tabulate polytubes; this is not encountered above the Upper Jurassic. The earlier species *Compositosphaeridium bulgaricum* Erkmen and Sarjeant 1980 can have up to twelve subdivisions of its polytubes, but this number is reduced in the later (and only other) species *Compositosphaeridium polonicum* (Górka 1965) emend. Erkmen and Sarjeant 1980, which only develops up to three subdivisions.

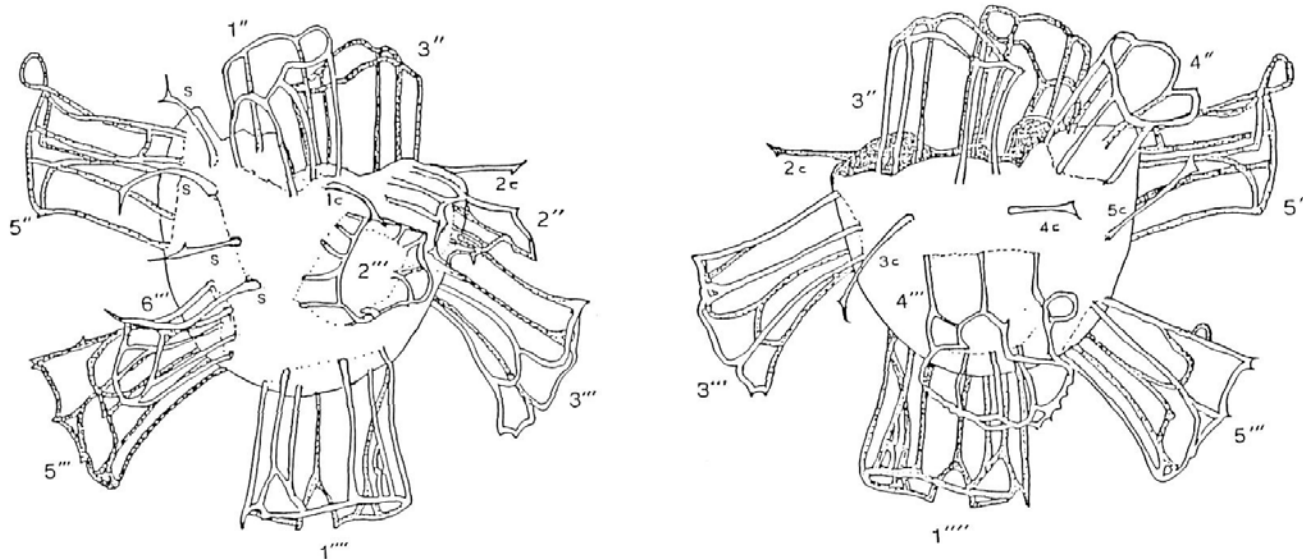
The postulated *Adnatosphaeridium* - *Rigaudella* - *Taeniophora* - *Amphorula* lineage is based on the development of transingular structures in the second and third genera. *Amphorula* Dodekova 1969 has crescent-shaped walls on the preingular and postingular paraplates that open toward the cingulum; these may be the last vestiges of transingular walls as developed by *Taeniophora* Klement 1960. The newly described species *Systematophora? daveyi* Riding and Thomas 1988 might also fit better into this grouping of genera. A second hypothetical lineage from *Adnatosphaeridium* includes *Systematophora* - *Oligosphaeridium*, based initially on the grouping together of processes into process clusters and subsequently on the development of walls connecting processes within a cluster. If this connecting wall becomes as high as the processes, a tube would be formed with distal spines, which is a morphology similar to *Oligosphaeridium* Davey and Williams 1966. The third hypothetical lineage of *Adnatosphaeridium* - *Surculosphaeridium* - *Hystrichosphaeridium* is based on the separation of contact between individual processes leading to the development of isolated intratabular processes, without trabeculae.

#### BIOSTRATIGRAPHY, PALEOGEOGRAPHY AND PALEOECOLOGY

During the collation of biostratigraphic range data, it was noted that certain reported occurrences appear anomalous and require further study before their inclusion into the range chart. These are listed in Table 3 and were not taken into account in the discussion that follows.

The complex chorate dinoflagellate group is well represented from the Bathonian to the Oxfordian and beyond. The group is first recorded from the Lower Bathonian of Northwest Europe by Riding et al. (1985), with cysts assigned to *Adnatosphaeridium caulleryi*. As discussed above, it appears that these cysts are a precursor to all succeeding complex chorates and are directly related to *Adnatosphaeridium? sp. A*.

In the Middle Bathonian only *Hapsidaulax margarethae* has been recorded with certainty. In the Upper Bathonian two morphotypes, *Adnatosphaeridium sp. A* and *Com-*



TEXT-FIGURE 1

Interpretive drawing of the holotype of *Polystephanephorus calathus* (Sarjeant 1961a) emend. nov.; magnification  $\times 890$ .

*positosphaeridium bulgaricum*, first appear. The base of the Callovian Stage is marked by the occurrence of *Surculosphaeridium* and *Rigaudella*; *Polystephanephorus* is first recorded in the Middle Callovian; and *Perisseiasphaeridium* and *Systematophora* are first reported from the Upper Callovian. However, the last genus may have evolved earlier, perhaps in the Bathonian (Davey, pers. comm.). In the Oxfordian *Taeniophora* is the only new complex chorate genus, while genera first occurring in the Kimmeridgian include *Hystrichosphaerina*, *Hystrichosphaeridium*, *Emmetrocyta*, and *Oligosphaeridium*.

The biostratigraphic utility of the complex chorates is affected to some extent by the relative scarcity of records from outside northwest Europe and offshore eastern North America. The Tethyan realm seems to have a limited number of species. *Adnatosphaeridium caulleryi*, *Rigaudella aemula*, *Surculosphaeridium penicillatum* and *Systematophora orbifera* have been recorded from Libya (Thusu, Van Der Eem, Elimehdawi and Bu-Argob, pers. comm.), near the edge of the Tethyan ocean, while only *Rigaudella aemula* has been reported from Australia (Helby et al. 1987). In the Arctic fewer species are recorded than are known from northwest Europe. Nine species (*Compositosphaeridium polonicum*, *Rigaudella aemula*, *Rigaudella filamentosa*, *Surculosphaeridium cribrotubiferum*, *Surculosphaeridium vestitum*, *Systematophora orbifera*, *Systematophora penicillata*, *Taeniophora fasciculigera*, and *Taeniophora iunctispina*) have been recorded from East Greenland and Central Norway (Poulsen 1985; Aarhus et al. 1989; and Piasecki 1980). The Sverdrup Basin of Arctic Canada has yielded only one complex chorate species, *Rigaudella aemula*, during this interval (Davies 1983, fig. 4).

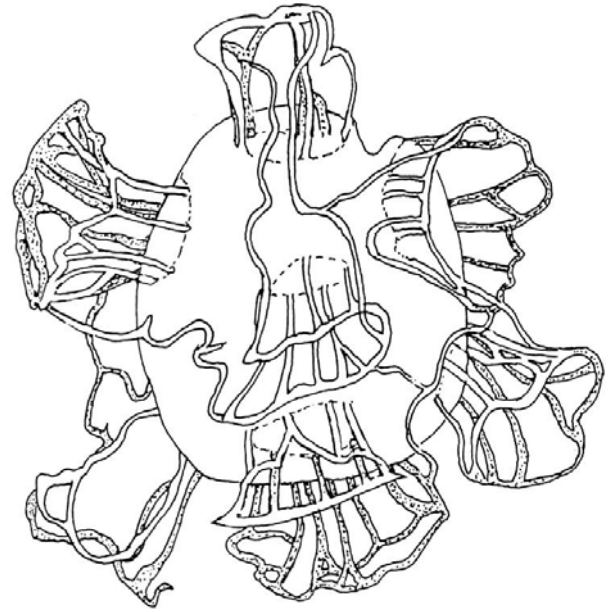
Paleoenvironmental controls may have limited the ability of the cysts to survive outside the seas of northwest Europe. Paleogeog-

raphical distance and currents might also be factors, since the sparsest assemblages are those furthest away from northwest Europe. Vozzhennikova (1965) and Scull et al. (1966) suggested that processes might have lengthened and elaborated to aid the flotation of the cyst, by increasing surface area relative to volume and by facilitating attachment to vagile organisms or floating organic debris. The experiments of Sarjeant et al. (1987) support this hypothesis. Yet these features seem not to have been enough to facilitate a wide distribution of the complex chorates. Perhaps current-flow patterns made it difficult for the rapidly evolving group to populate the oceans more widely. However, it must be reiterated that the apparent distribution of complex chorates, discussed above, might be merely a result of the lack of detailed palynological studies from most of the world.

The use of complex chorate cysts as paleoenvironmental indicators has not been a primary subject of this study. However, Jurassic assemblages with abundant complex chorate cysts usually contain low numbers of small acritarchs (micrhystridia). Wall (1965) demonstrated a loose correlation between water depth and acritarch distribution and process length. Sarjeant (1968, p. 240) postulated a direct relationship between declining numbers of small acritarchs and the progressive increase of water depth offshore. This indicates that complex chorate dinoflagellate cysts were formed in more open marine, deeper water environments. Cysts with smooth walls or shorter processes or crests occurred nearer shore, along with larger acritarchs and long-spined micrhystridia, while the shortest-spined micrhystridia occurred in the shallowest waters, living perhaps even within the sands of beaches.

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We are deeply indebted to Dr. James Riding for his constructive suggestions throughout our preparation of this manuscript and,



TEXT-FIGURE 2

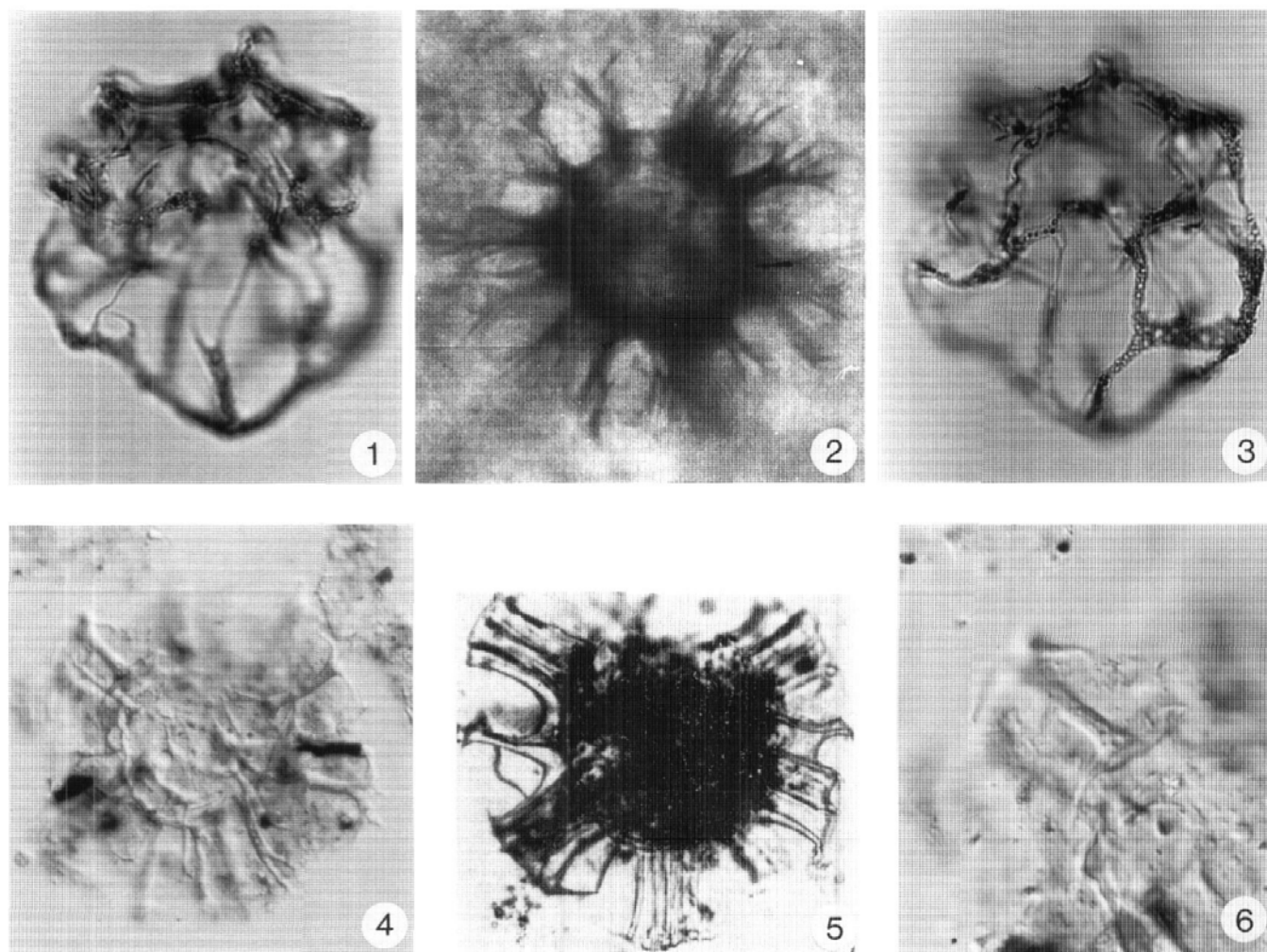
Interpretive drawing of the holotype of *Polystephanephorus paracalathus* (Sarjeant 1960b) emend nov.; magnification  $\times 1050$ .

in particular, for providing us with information concerning *Adnatosphaeridium caulleryi* and *Adnatosphaeridium?* sp. A in the Bathonian of England. Dr. Rex Harland courteously brought the holotypes of *Polystephanephorus calathus* and *P. paracalathus* from England to the International Palynological Congress in Brisbane, Queensland, for a confirmatory restudy by the second author. We would also like to thank all the researchers who sent pre-publication copies of their work for inclusion in this paper. Dr. Hans Gocht assisted us in the examination of a type species. Dr. Henrik Nøhr-Hansen, Dr. Robin Helby, and Professor Charles Downie kindly let us reproduce their illustrations, while Dr. Edward Davies spent valuable time carefully reviewing the work. All their help is gratefully acknowledged. However, the opinions and any errors contained in this paper are solely the responsibility of the authors.

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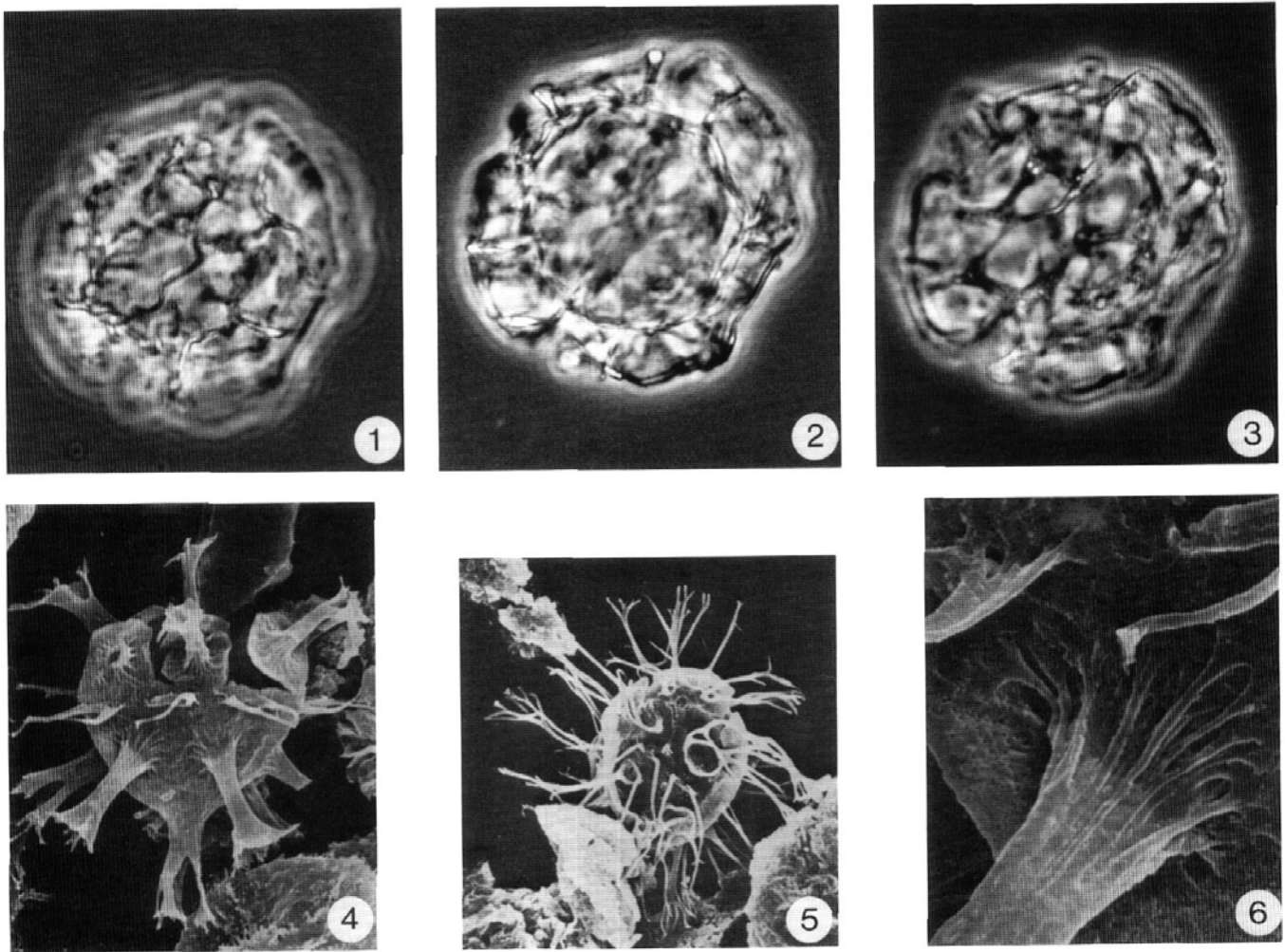
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TEXT-FIGURE 3

- |   |  |
|---|--|
| <p>1 <i>Hapsidaulax margarethae</i> Sarjeant 1975a, paratype I, lower surface; magnification <math>\times 1140</math>.</p> <p>2 <i>Systematophora penicillata</i> (Ehrenberg 1843 ex 1854), lectotype, upper, ventral surface; re-illustration from Sarjeant 1980, pl. 37; magnification <math>\times 1000</math>.</p> <p>3 <i>Hapsidaulax margarethae</i> Sarjeant 1975a, paratype I, upper surface; magnification <math>\times 1140</math>.</p> | <p>4 <i>Surculosphaeridium cribrotubiferum</i> (Sarjeant 1960b), holotype; magnification <math>\times 615</math>.</p> <p>5 <i>Compositosphaeridium bulgaricum</i> Erkmen and Sarjeant 1980, holotype; re-illustration of Dodekova 1974, pl. 1, fig. 5; magnification <math>\times 1285</math>.</p> <p>6 <i>Surculosphaeridium cribrotubiferum</i> (Sarjeant 1960b), holotype, close-up of the pits and striations on the process wall; magnification <math>\times 1260</math>.</p> |
|---|--|





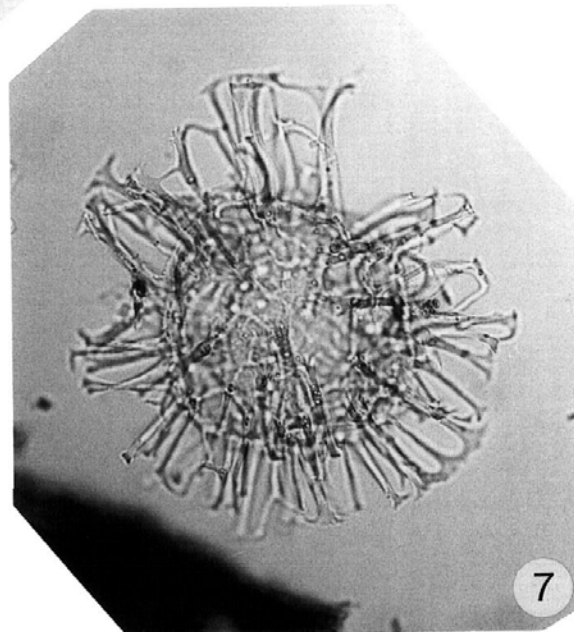
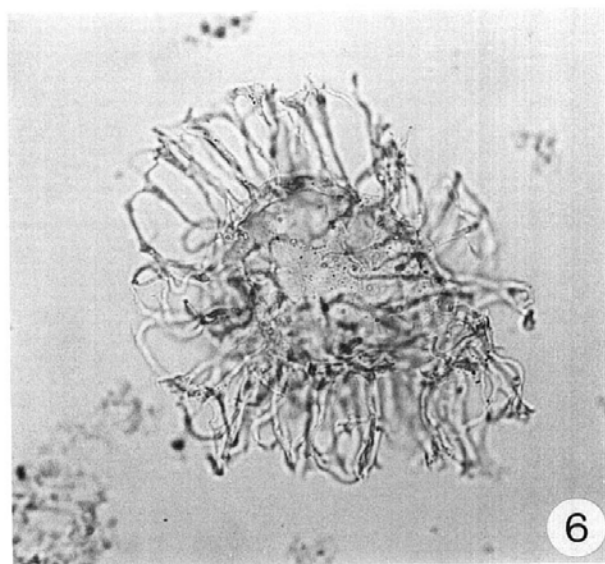
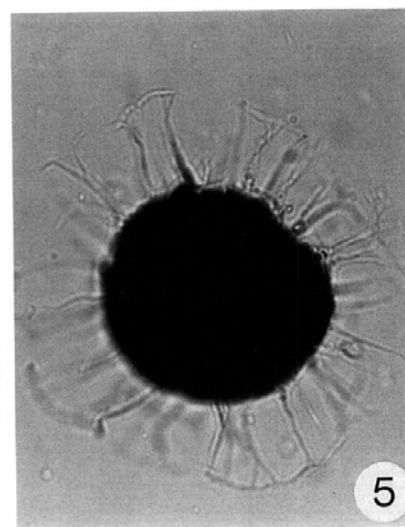
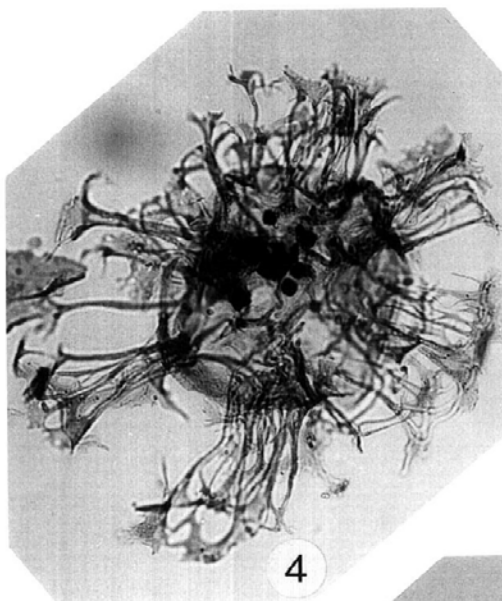
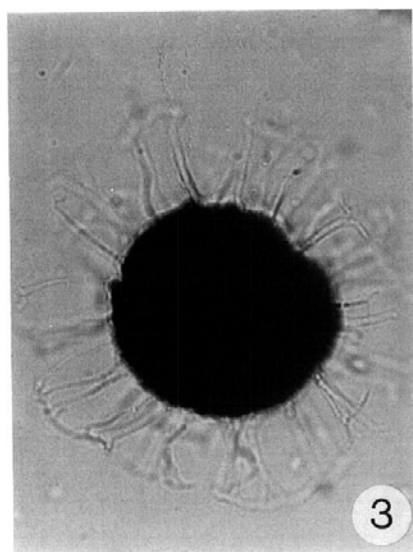
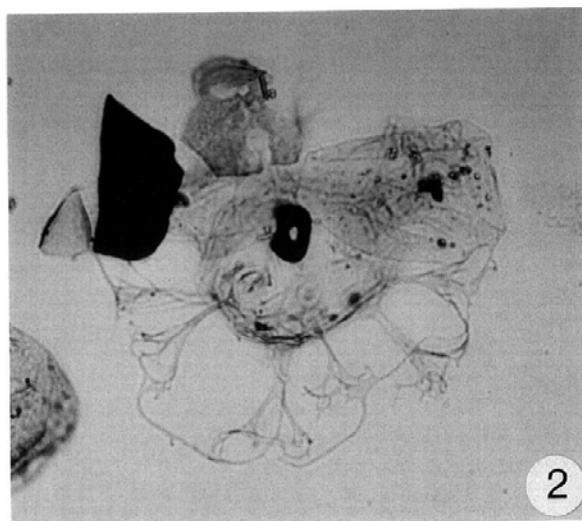
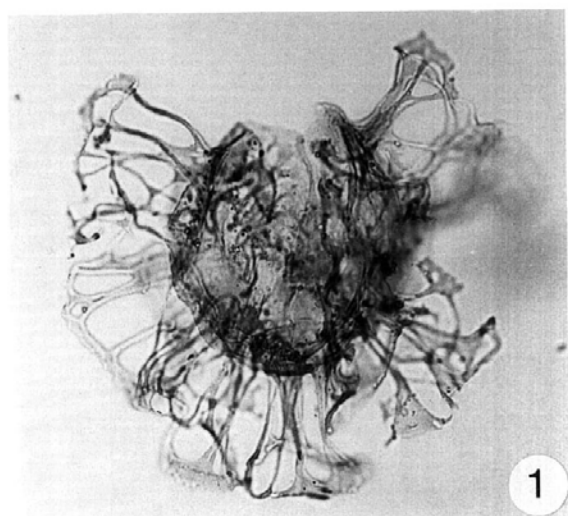
TEXT-FIGURE 4

- 1 *Hapsidaulax margarethae* Sarjeant 1975a, holotype; oblique apical view, phase contrast; magnification  $\times 1000$ .
- 2 *Hapsidaulax margarethae* Sarjeant 1975a, holotype; medial view, phase contrast; magnification  $\times 1000$ .
- 3 *Hapsidaulax margarethae* Sarjeant 1975a, holotype; oblique antapical view, phase contrast; magnification  $\times 1000$ .
- 4 *Perisseiasphaeridium ingegerdiae* Nøhr-Hansen 1986, S.E.M. photograph, re-illustration from Nøhr-Hansen 1986, pl. 4, fig. 8; magnification  $\times 760$ .
- 5 *Systematophora areolata* Klement 1960, S.E.M. photograph, re-illustration from Nøhr-Hansen 1986, pl. 2, fig. 9; magnification  $\times 600$ .
- 6 *Perisseiasphaeridium ingegerdiae* Nøhr-Hansen 1986, S.E.M. photograph showing the striae on the base of the processes; re-illustration from Nøhr-Hansen 1986, pl. 4, fig. 8; magnification  $\times 3125$ .

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# PLATE 1

- |   |  |   |  |
|---|--|---|--|
| 1 | <i>Adnatosphaeridium caulleryi</i> (Deflandre 1938), BGS specimen MPK6489, Cornbrash, <i>Macrocephalus</i> Zone (Callovian), Yorkshire, England; magnification ×855. |   |  |
| 2 | <i>Rigaudella aemula</i> (Deflandre 1938), slide S02447/1/1, Highworth Grit, <i>Densiplicatum</i> Zone (Oxfordian), Oxfordshire, England; magnification ×710.        | 5 | <i>Adnatosphaeridium caulleryi</i> (Deflandre 1938), holotype; magnification ×700.   |
| 3 | <i>Adnatosphaeridium caulleryi</i> (Deflandre 1938), holotype; magnification ×700.   | 6 | <i>Adnatosphaeridium?</i> sp. A, BGS specimen MPK 4185, Atworth Borehole, Upper Fuller's Earth, <i>Hodsoni</i> Zone (Bathonian); magnification ×855. |
| 4 | <i>Adnatosphaeridium caulleryi</i> (Deflandre 1938), BGS specimen MPK6490, Cornbrash, <i>Macrocephalus</i>   | 7 | <i>Adnatosphaeridium?</i> sp. A, BGS specimen MPK 6488, Atworth Borehole, Upper Fuller's Earth, <i>Hodsoni</i> Zone (Bathonian); magnification ×855. |

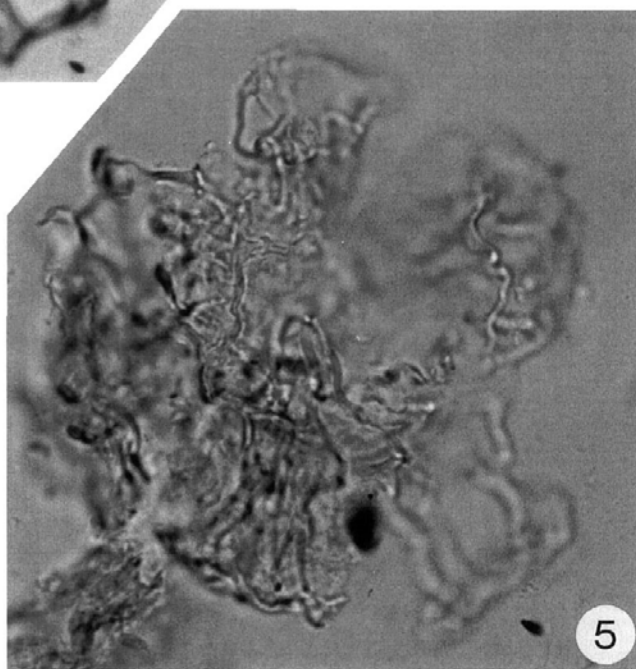
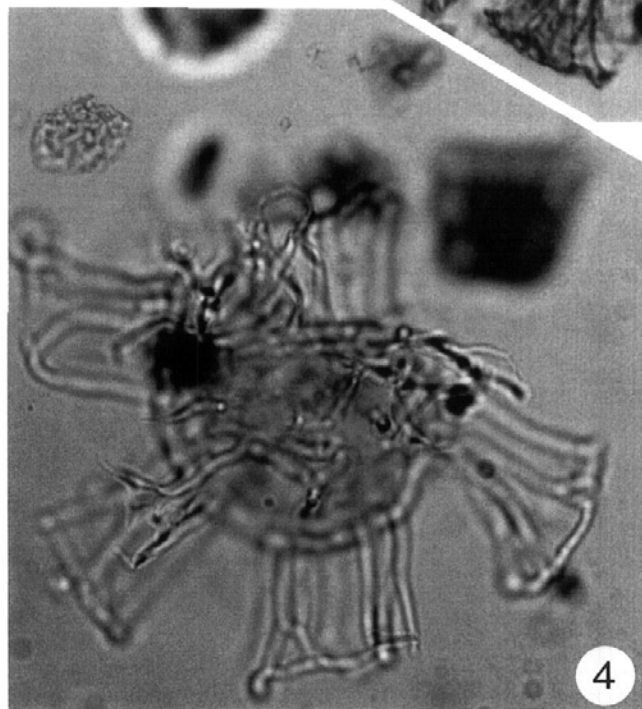
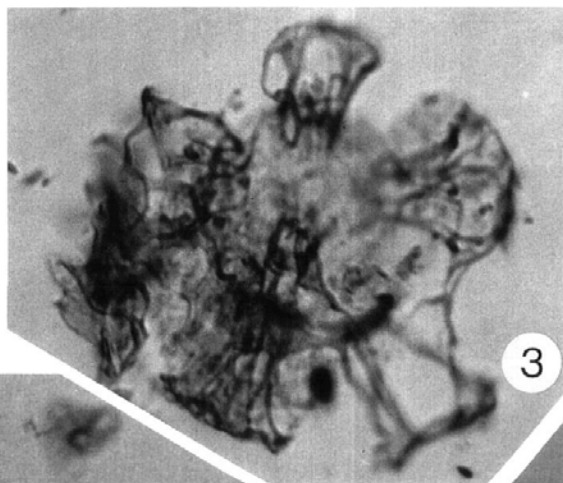
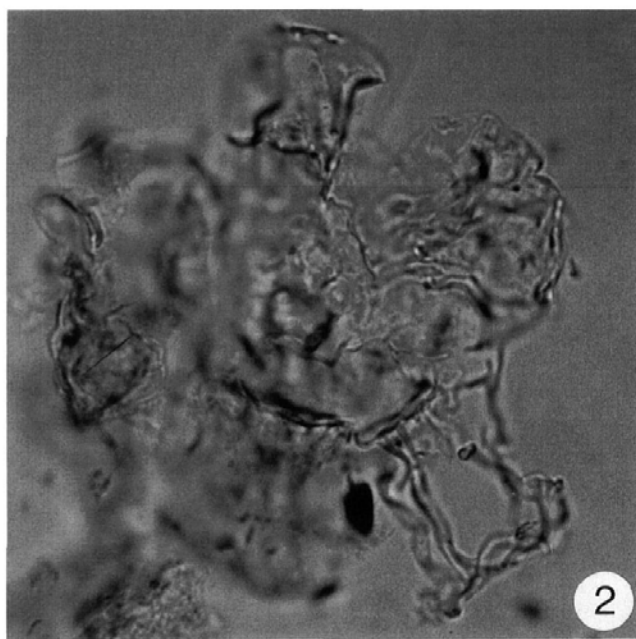
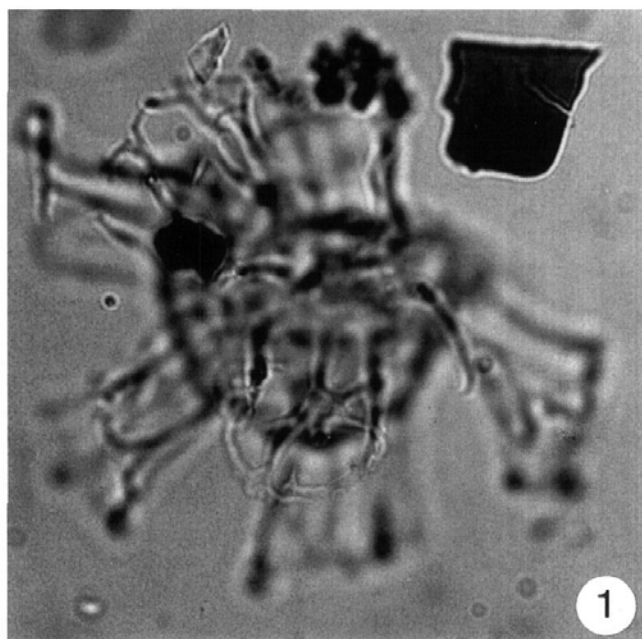


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## PLATE 2

- 1 *Polystephanephorus calathus* (Sarjeant 1961a), holotype; magnification  $\times 1055$ .
- 2 *Polystephanephorus paracalathus* (Sarjeant 1960b), holotype; magnification  $\times 990$ . Photograph taken in 1987.
- 3 *Polystephanephorus paracalathus* (Sarjeant 1960b), holotype; magnification  $\times 840$ . Photograph taken in 1961.
- 4 *Polystephanephorus calathus* (Sarjeant 1961a), holotype; magnification  $\times 1055$ .
- 5 *Polystephanephorus paracalathus* (Sarjeant 1960b), holotype; magnification  $\times 990$ .

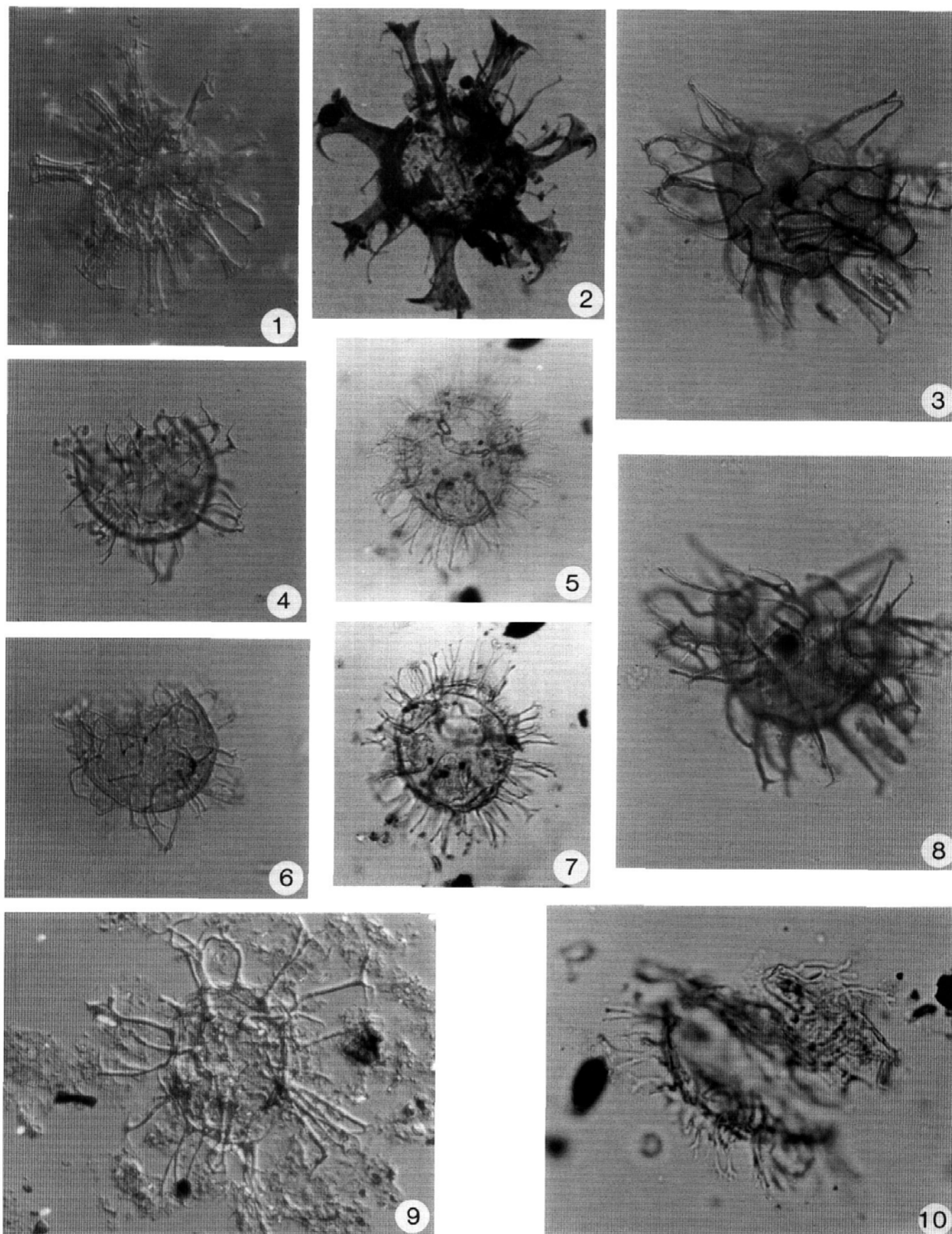




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### PLATE 3

- 1 *Compositosphaeridium polonicum* (Górka 1965), phase contrast. Specimen illustrated by Davey, Downie, Sarjeant and Williams (1966, pl. 10, fig. 4) as the holotype of *Hystrichosphaeridium costatum*; magnification  $\times 500$ .
- 2 *Perisseiasphaeridium ingegerdiae* Nøhr-Hansen 1986, holotype, reprint from Nøhr-Hansen (1986, pl. 3, fig. 11); magnification  $\times 625$ .
- 3 *Taeniophora iunctispina* Klement 1960, holotype, ventral view; magnification  $\times 620$ .
- 4 *Taeniophora filamentosa* Klement 1960, holotype, dorsal view; magnification  $\times 475$ .
- 5 *Systematophora valensii* (Sarjeant 1960b), holotype; magnification  $\times 600$ .
- 6 *Taeniophora filamentosa* Klement 1960, holotype, ventral view; magnification  $\times 475$ .
- 7 *Systematophora valensii* (Sarjeant 1960b), holotype in original condition; magnification  $\times 400$ .
- 8 *Taeniophora iunctispina* Klement 1960, holotype, slightly oblique view; magnification  $\times 620$ .
- 9 *Surculosphaeridium? vestitum* (Deflandre 1938) of Davey, Downie, Sarjeant and Williams 1966, sample V51736(1); phase contrast, magnification  $\times 600$ .
- 10 *Systematophora valensii* (Sarjeant 1960b), holotype, in present condition; magnification  $\times 670$ .

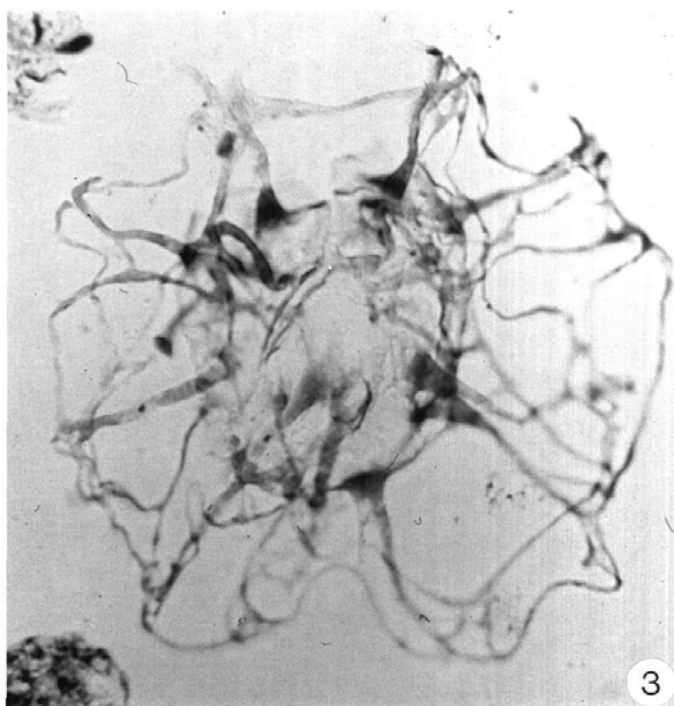
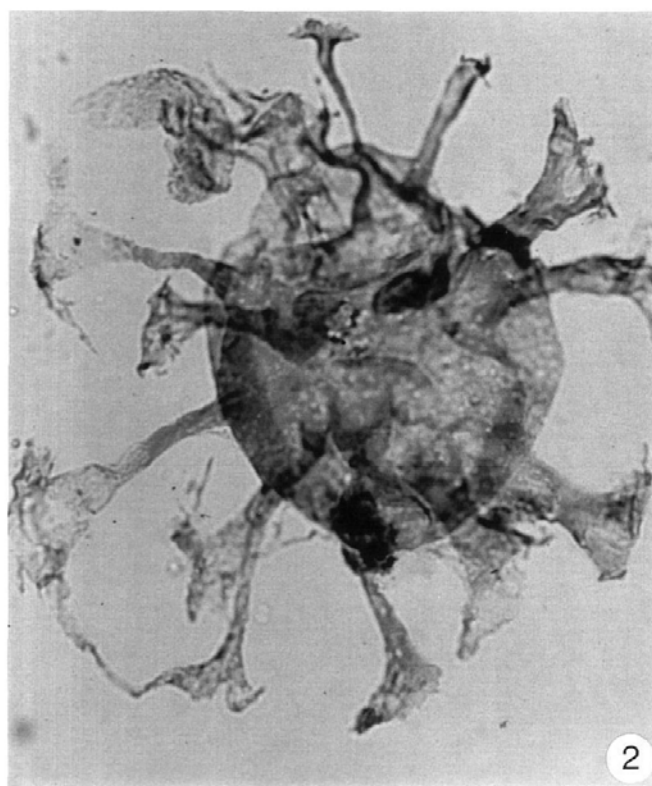
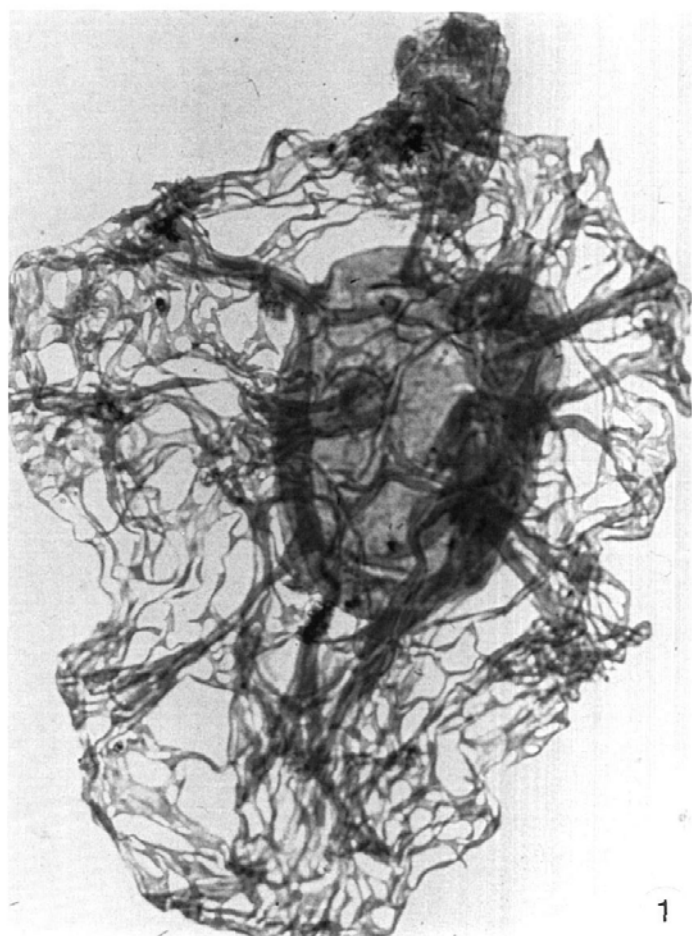


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# PLATE 4

- 1 *Adnatosphaeridium densifilum* (Cookson and Eisenack 1974), holotype, reprint of Helby and Partridge (1980) slide 38; magnification  $\times 790$ .
- 2 *Rigaudella aemula integra* (Cookson and Eisenack 1958), holotype, reprint of Helby and Partridge (1980) slide 3; magnification  $\times 1085$ .
- 3 *Rigaudella filamentosa* (Cookson and Eisenack 1958), paratype A, reprint of Helby and Partridge (1980) slide 5; magnification  $\times 840$ .
- 4 *Rigaudella filamentosa* (Cookson and Eisenack 1958), paratype B, reprint of Helby and Partridge (1980) slide 6; magnification  $\times 840$ .

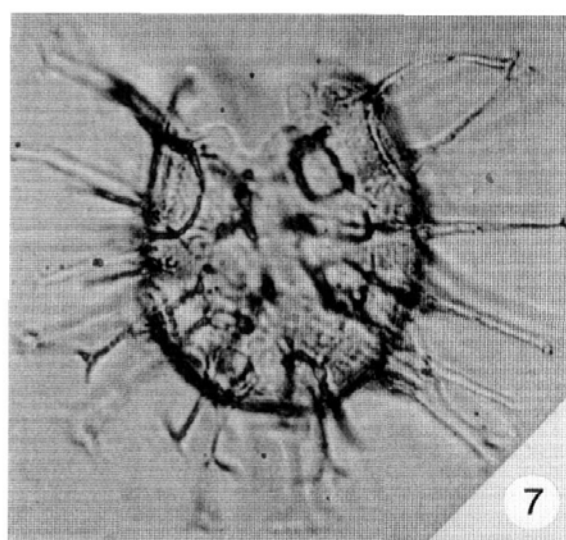
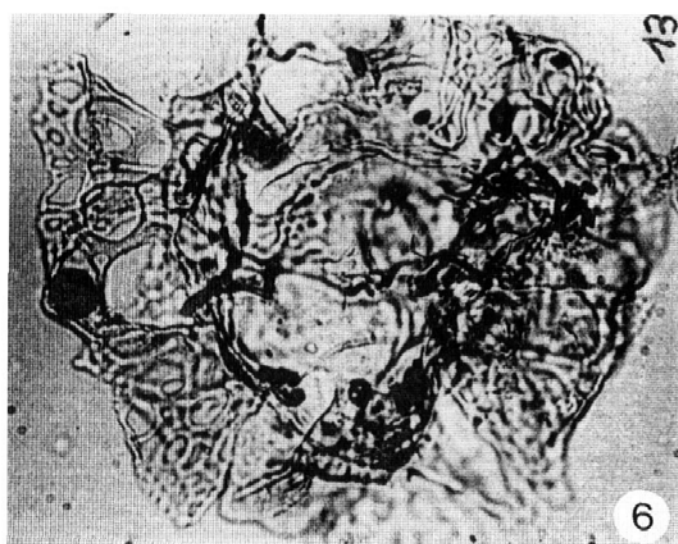
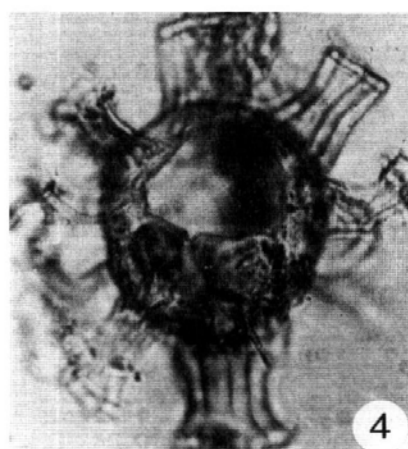
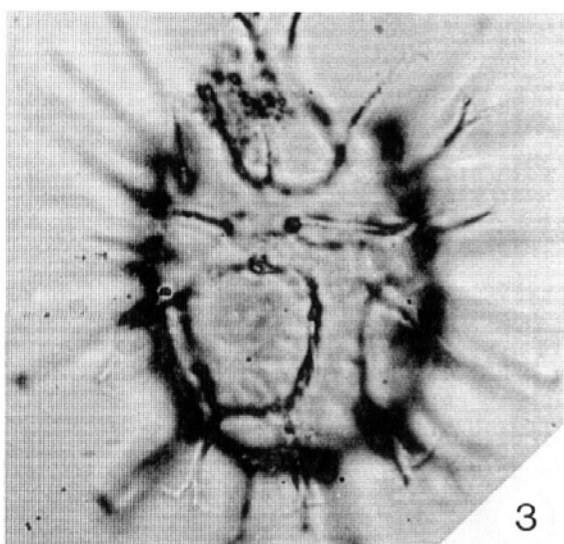
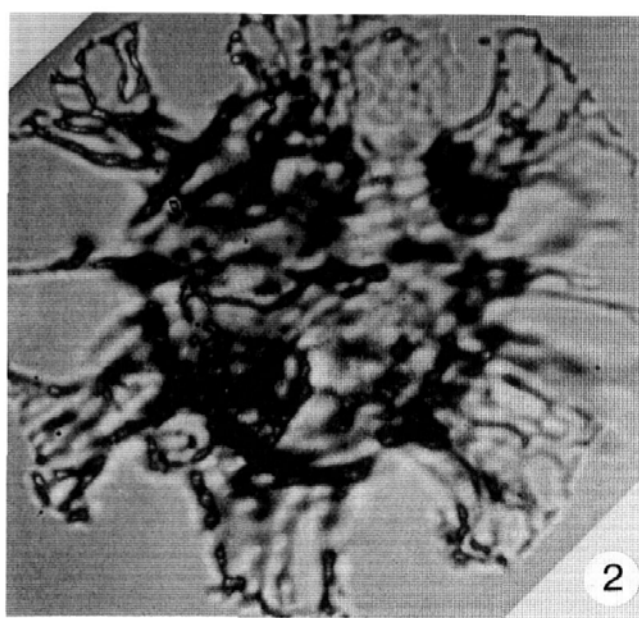
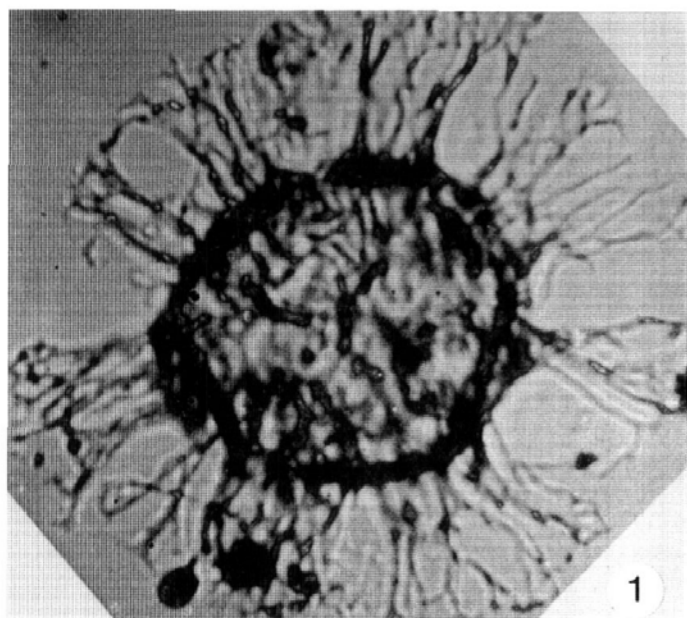




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## PLATE 5

- 1 *Systematophora orbifera* Klement 1960, paratype, re-illustration from Klement 1960, pl. 9, fig. 10; magnification ×860.
- 2 *Systematophora orbifera* Klement 1960, holotype, re-illustration from Klement 1960, pl. 9, fig. 9; magnification ×860.
- 3 *Systematophora areolata* Klement 1960, paratype, re-illustration from Klement 1960, pl. 9, fig. 4; magnification ×860.
- 4 *Compositosphaeridium bulgaricum* Erkmen and Sarjeant 1980, re-illustration from Dodekova 1974, pl. 1, fig. 3; magnification ×750.
- 5 *Compositosphaeridium bulgaricum* Erkmen and Sarjeant 1980, holotype, re-illustration from Dodekova 1974, pl. 1, fig. 6; magnification ×1400.
- 6 *Adnatosphaeridium? speciosum* (Alberti 1961), holotype, re-illustration from Alberti 1961, pl. 9, fig. 13; magnification ×850.
- 7 *Systematophora areolata* Klement 1960, holotype, re-illustration from Klement 1960, pl. 9, fig. 2; magnification ×860.



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