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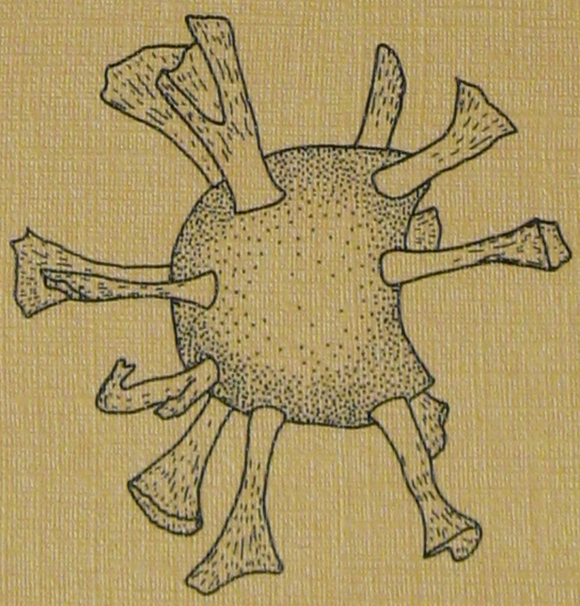
Roger J. Davey



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Contents

Abstract

The dinocyst assemblages were obtained from selected core samples, between the depths 2505′ and 3190′, from the Haldager No. 1 borehole, onshore Denmark. It has been possible to apply the dinocyst zonation of Davey (1979) to these assemblages and they have been dated as Hauterivian (Early Cretaceous) to early Portlandian (Late Jurassic). The placing of the Cretaceous-Jurassic boundary between 2945′ and 2989′ differs significantly from its initial position in Sorgenfrei and Buch (1964) at 2706′. The present revised dating has subsequently been used by Michelsen (1978, p. 23) in his study of the Norwegian – Danish Basin. The study has necessitated the examination of many accurately dated samples of Early Cretaceous and Late Jurassic age from onshore eastern England and the results are incorporated in this paper. Detailed systematics, the key to a detailed stratigraphic breakdown, has necessitated the erection of 2 new genera (*Cymososphaeridium* and *Stiphrosphaeridium*), 12 new species and 2 new subspecies. In addition minor amendments are also made to the dinocyst zonation of Davey (op. cit.).

Introduction

The present investigation, although examining primarily the distribution of dinocysts in the latest Jurassic and Early Cretaceous of the Haldager No. 1 borehole, onshore Denmark, is part of a larger study dealing with rocks of these ages from the Boreal Province of northwest Europe. Thus, in this paper, reference is often made to onshore, accurately dated sections in eastern and southern England. The former include the classic exposure at Speeton, east Yorkshore (Neale, 1974), and the quarries and more temporary exposures in Lincolnshire and Norfolk (Casey, 1973). The sections in southern England include the type localities of the Kimmeridgian and Portlandian in Dorset (Torrens, 1969). Preliminary results of the stratigraphic distribution of dinocysts at this stratigraphic level, both in the Haldager No. 1 borehole and in England, are to be found in Davey (1979), where a formal dinocyst zonation was established. In the present paper recent data on the stratigraphic distribution of certain dinocysts and on the dating of some onshore English sections have neccessitated several revisions in the originally proposed zonation scheme. These are discussed below and the age of the interval examined from the Haldager No. 1 borehole, 2505′–3190′, is reassessed accordingly.

Haldager No. 1 borehole

The Haldager No. 1 borehole was drilled by the Danish American Prospecting Co. (DAPCO.) during the later part of 1950 in northern Denmark to examine the Cretaceous and Jurassic (Sorgenfrei and Buch, 1964). Drilling commenced in a thin Pleistocene and a relatively complete Cretaceous and Jurassic succession was encountered. The borehole terminated in the Liassic at 4989′ (1521 m) depth.

Geological Situation

The core samples analysed are from depths 2505′ to 3190′ (measured in feet below rotary table) and are of Early Cretaceous and Late Jurassic age. Sedimentation during these epochs took place in the Danish Sub-basin of the Norwegian-Danish Basin (Michelsen, 1978). This sub-basin was bordered by positive structural elements to the north and east, the Fennoscandian Shield, and to the south, the Ringkøbing-Fyn High. Seaways existed to the southeast, the Danish-Polish Trough, and to the west into the North Sea Basin. Most of the succession examined is assigned to the Bream Formation which is divided into two members. Only the upper one, the Frederikshavn Member (2576′–3374′), was examined. The Frederikshavn Member is overlain by the Vedsted Formation of which only the basal part was analysed. During the deposition of the Bream Formation, Haldager was situated at or near the depocentre.

Location of Samples

The upper part of the succession analysed, from 2505′ to 3009′, consists predominantly of silty clays and shales with minor siltstone. Between 3009′ and 3080′, sandstones and sands become dominant and below this level, down to 3190′, the lithology consists of clays, shales and silts with minor sands. (Additional, and more detailed, lithological information is to be found in the "Core Descriptions" of the Weekly Report of the Haldager No. 1 borehole obtainable from the Danish Geological Survey).

Although the interval analysed during this study was entirely cored, recovery was often poor and, as the cores have been moved and sampled several times, the exact positions of the analysed samples is usually only approximate. The following is a list of the cores analysed and the approximate position within the core of the actual core piece:–

Core 2505′–2525′ approx. 15′ below top of core.
– 2545′–2565′ approx. 2549′.
– 2585′–2595′ position uncertain, poor recovery.
– 2617′–2627′ probably top of core.
– 2647′–2657′ position uncertain.
– 2667′–2677′ lower part of core.
– 2752′–2762′ approx. 1.5′ below top of core.
– 2772′–2782′ approx. 1′ below top of core.
– 2822′–2832′ near top of core.
– 2832′–2842′ position uncertain.
– 2866′–2876′ approx. 0.5′ below top of core.
– 2896′–2915′ near bottom of core.
– 2935′–2945′ upper part of core.
– 2969′–2989′ approx. 8′ below top of core.
– 2989′–3009′ near top of core.
– 3009′–3015′ near top of core.
– 3030′–3040′ position uncertain.
– 3040′–3060′ approx. 4′ below top of core.
– 3080′–3100′ in upper 4′ of core.
– 3120′–3130′ in upper 4′ of core.
– 3150′–3160′ between 4′ and 8′.
– 3180′–3190′ between 4′ and 8′.

Dating of the Cores

The original stratigraphic account, in Sorgenfrei and Buch 1964, dated the Lower Cretaceous (1369′–2706′) and Portlandian (2706′–2950′) on a combination of ammonites, pelycepods (*Buchia*) and benthonic foraminifera. These ages, and particularly the position of the Cretaceous-Jurassic boundary, were re-evaluated by Davey in 1976 (subsequently incorporated in Davey 1979) using dinocysts. These revised and more detailed datings were used by Michelsen (1978) in his account of the Jurassic of the Norwegian-Danish Basin and are discussed in the present paper.

Palynomorph recovery

Palynomorph recovery from seventeen of the nineteen core samples analysed was good. Two samples, at 2617′–27′ and 3040′–60′, proved to be barren. The latter is understandably barren as it is a fine grained sand which must have undergone winnowing during deposition. The reason for the former sample, a light grey silt, being barren is unclear. A third sample, at 2585′–95′, contains downhole contamination and so has not been included in the detailed stratigraphic analyses.

Dinocyst recovery was generally good to very good and even in the poorest sample, at 3150′–60′, a reasonable number of species are present. Acanthomorph acritarchs, consisting mainly of *Micrhystridium* Deflandre, 1937, are only common in the two youngest samples (2505′–25′ and 2545′–65′) although they are present throughout the analysed sequence. Miospores, of terrestrial derivation, are relatively common to very common in all the cores. Bisaccate pollen grains are typically relatively common in marine sediments but, in the present case, the relatively heavy pteridophyte spores are also consistently common. The latter characteristic is important and indicates strong terrestrial influence at the site of deposition and significant run-off from well vegetated landmasses bordering the depositional basin. As would be expected terrestrically derived plant debris, in the form of woody material (humic) and plant cuticle, is the dominant kerogen component.

Obvious signs of reworking are uncommon and are indicated by Triassic species (*Ovalipollis* spp. and *Ricciisporites tuberculatus* Lundblad, 1954) at 2822′–32′ and 2896′–915′ and by the Liassic species *Chasmatosporites magnolioides* (Erdtman, 1948) at 2822′–32′. In addition, there is some evidence to indicate minor reworking of Ryazanian to lower Valanginian sediments into the Hauterivian. Two occurrences illustrate this; firstly, the present of *Occisucysta* sp. A Davey, 1979, of early Valanginian to late Ryazanian age, at 2545′–65′ and secondly, *Aldorfia dictyota* (McIntyre and Brideaux, 1980) comb. nov. at 2505′–25′.

Revision of dinocyst zonal scheme

The dinocyst zonal scheme for the Barremian to Portlandian, established by Davey 1979, is here slightly modified because of recent changes in ammonite stratigraphy coupled with the reassessment of critical onshore sections and because of recent advances in our knowledge of dinocyst distribution and changes in taxonomy. Davey (op. cit., text-fig. 5) omitted detailed ammonite zonal schemes for the Barremian, Hauterivian and Valanginian and correlated his dinocyst zones/subzones directly to the Speeton Clay litho-units. This omission is here rectified in text–fig. 1. The Barremian and Hauterivian

AGE		BOREAL AMMONITE ZONES	DINOCYST ZONATION (after Davey 1979) SUBZONES	DINOCYST ZONATION (after Davey 1979) ZONES
Barremian	late	*bidentatum*	*Palaeoperidinium cretaceum*	*Odontochitina operculata*
	mid	*rude – fissicostatum*		
	early		*Aptea anaphrissa*	
		rarocinctum	1	
		variabilis	2	*Subtilisphaera terrula*
Hauterivian	late	*marginatus*	*Canningia* cf. *reticulata*	
		gottschei		
		speetonensis	*Batiodinium longicornutum*	*Discorsia nanna*
	early	*inversum*		
		regale		
		noricum	*Kleithriasphaeridium simplicispinum*	
		amblygonium		
Valanginian	late	"Astieria" fauna		*Spiniferites ramosus*
		tuberculata *		
		bidichotomoides *		
		triptychoides *		
		pitrei		
		Dichotomites spp.		
	early	*Polyptychites*		
		Paratollia		
Ryazanian	late	*albidum*		*Pseudoceratium pelliferum*
		stenomphalus	*Scriniodinium pharo*	*Gochteodinia villosa*
		icenii		
	early	*kochi*	*Cannosphaeropsis thula*	
		runctoni		
Portlandian	late	*lamplughi*	*Egmontodinium expiratum*	
		preplicomphalus		
		primitivus		
	early	*oppressus*		
		anguiformis		
		kerberus		*Dingodinium spinosum*
		okusensis		*Avellodinium culmulum*
		glaucolithus		
		albani		

* German Boreal Zones

1 *Cassiculosphaeridia magna*
2 *Nexosispinum vetusculum*

Fig. 1. Correlation of the dinocyst zonation to the Boreal ammonite zonation for the Portlandian to Barremian.

ammonite zonal schemes are taken from Rawson et al. (1978) and the Valanginian scheme from Kemper et al. (in press). In addition, the revision of the early Portlandian ammonite zones by Wimbledon and Cope (1978) have also been incorporated into text–fig. 1.

In more detail, the following emendments have been made to the original ammonite zonation scheme used by Davey (op. cit.): I. It is not internationally agreed as to where the late-early Barremian boundary should be placed. At present, a "mid" interval is retained for practical purposes and is equivalent to the middle Barremian of Davey (op. cit.) and the Cement Beds of the Speeton Clay. For convenience, the late-early Barremian boundary has been placed at the top of the "mid" Barremian.

II. The position of the Barremian-Hauterivian boundary has been revised by Kemper et al. (in press) and is now placed at the base of the *variabilis* Zone which is equivalent to the base of the litho-unit C2C in the Speeton Clay. Davey (op. cit.) and Rawson et al. (1978) had previously placed it at the top of this zone, that is at the base of the litho-unit LB5D.

III. The late-early Hauterivian boundary is placed in the upper part of the *inversum* Zone (Kemper et al., in press).

IV. The upper portion of the Valanginian is represented by a remanié horizon in the Speeton Clay at Speeton and for this reason three German ammonite zones have been utilised at this stratigraphic level.

The majority of the changes made to the dinocyst zonal scheme of Davey (op. cit.) involve taxonomic changes – the reattribution of species to different genera and the erection of new species. These are as follows:

Palaeoperidinium cretaceum substituted for *Astrocysta cretacea.*

Aptea anaphrissa substituted for *Doidyx anaphrissa.*

Nexosispinum vetusculum substituted for *Adnatosphaeridium vetusculum.*

Scriniodinium pharo substituted for *Endoscrinium pharo.*

Gochteodinia villosa substituted for *Pareodinia dasyforma.*

Cannosphaeropsis thula sp. nov. to replace *Cannosphaeropsis* sp. A.

Egmontodinium expiratum sp. nov. to replace *Egmontodinium* sp. A.

The definition of only one subzone is here changed and the lower boundary moved down slightly. This change involves the *Chlamydophorella trabeculosa* Subzone, the lower boundary of which was defined as the first stratigraphic appearance of the nominative species which was considered to be at the base of the Speeton Clay litho-unit C9, in the middle of the *regale* ammonite Zone. Forms that are attributable to, or at least could be easily confused with, *C. trabeculosa* have recently been observed in the early Hauterivian and Valanginian. Thus, the use of this species in a zonation scheme is obviously not desirable and the distinctive species *Batioladinium longicornutum* has been substituted. The first stratigraphic occurrence of this species is marginally lower, at the base of the *regale* ammonite Zone and at the base of the C11 litho-unit in the Speeton Clay. The upper boundary of the *B. longicornutum* Subzone remains the same as that of the former *C. trabeculosa* Subzone. The difinition of the *B. longicornutum* Subzone is as follows:– "The interval from the first appearance of *Batioladinium longicornutum* to the first appearance of *Subtilisphaera terrula.* Age – early to late Hauterivian (C11 to C7F litho-units, Speeton Clay, Speeton).

Systematics

The following section is divided into four parts. The first lists, in alphabetical order, all marine palynomorphs encountered during the present study and indicates, where appropriate, the plates on which they are figured. Figures in brackets refer to the position of that palynomorph on text-fig. 3. New species or those that require certain amplifying remarks are indicated by an asterisk (*) and are dealt with in parts two to four. Parts two and three deal with two groups of related genera – the *Systematophora, Oligosphaeridium* and *Surculosphaeridium* complex and the *Broomea* complex. The final section treats all forms not included in these complexes.

All type material has been assigned MPK numbers and is housed with all the slides examined in this study, in the palynologic slide collection at the Institute of Geological Sciences, Leeds, England. A representative set of slides is also housed at the Danish Geological Survey, Copenhagen.

Marine Palynomorphs

Acanthomorph acritarchs (1)

Achomosphaera neptuni (Eisenack, 1958) Davey & Williams, 1966a (83)

A. cf. *neptuni* (Eisenack, 1958) Davey & Williams, 1966a, in Davey & Verdier, 1974 (105)

**Aldorfia dictyota* (Cookson & Eisenack, 1960b) comb. nov. (63)

**A. spongiosa* (McIntyre & Brideaux, 1980) comb. nov. Pl. 7, figs. 7–10 (55)
Aldorfia sp. A, Pl. 7, figs. 13–15
Aprobolocysta neistosa Duxbury, 1980, Pl. 7, figs. 5–7 (52)
**Apteodinium* sp. A, Pl. 7, figs. 11, 12, 16 (46)
Athigmatocysta grabra Duxbury, 1977 (65)
**Avellodinium culmulum* (Norris, 1965) comb. nov. (16)
A. falsificum Duxbury, 1977 (53)
**Batioladinium longicornutum* (Alberti, 1961) Brideaux, 1975 (106)
**B. pomum* sp. nov. Pl. 5, figs. 2–4 (59)
**B. radiculatum* sp. nov. Pl. 5, figs, 1, 7–9 (60)
**B. varigranosa* Duxbury, 1977, Pl. 5, figs. 5, 6 (102)
**B.* cf. *varigranosa* Duxbury, 1977, Pl. 5, fig. 10 (62)
**Batioladinium* sp. I, Pl. 5, figs. 11–13
Caddasphaera halosa (Filatoff, 1975) Fenton, Neves & Piel, 1980 (2)
Callaiosphaeridium cf. *asymmetricum* (Deflandre & Courteville, 1939) Davey & Williams, 1966b (122)
**Canningia compta* sp. nov. Pl. 8, figs. 3–6 (11)
**Cannosphaeropsis thula* sp. nov. Pl. 8, figs. 7–11 (19)
**Cantulodinium speciosum* Alberti, 1961, Pl. 4, fig. 11 (71)
Cassiculosphaeridia magna Davey, 1974 (31)
C. reticulata Davey, 1969a (94)
**Chlamydophorella membranoidea* Vozzhennikova, 1967, Pl. 8, fig. 12 (41)
C. trabeculosa (Gocht, 1959) Davey, 1978 (107)
Chlamydophorella spp. (87)
Cleistosphaeridium tribuliferum (Sarjeant, 1962a) Davey et al., 1969 (21)
Cleistosphaeridium spp. (3)
Cometodinium whitei (Deflandre & Courteville, 1939) Stover & Evitt, 1978 (76)
Cribroperidinium edwardsii (Cookson & Eisenack, 1958) Davey, 1969a (118)
**Cribroperidinium* sp. A, Pl. 10, figs. 5, 6 (37)
Cribroperidinium spp. (66)
Ctenidodinium elegantulum Millioud, 1969 (84)
Cyclonephelium hystrix (Eisenack, 1958) Davey, 1978 (4)
Cyclopsiella sp. (58)
**Cymososphaeridium validum* sp. nov. Pl. 3, figs. 5, 6, 8, 11 (108)
Cymososphaeridium sp. I, Pl. 3, figs. 9, 12
**Dichadogonyaulax pannea* (Norris, 1965) Sarjeant, 1969. Pl. 9, fig. 10 (22)
Dingodinium albertii Sarjeant, 1966c (32)
D. minutum Dodekova, 1975. (12)
D. spinosum (Duxbury, 1977) Davey, 1979 (47)
Discorsia nanna (Davey, 1974) Duxbury, 1977 (109)
**Egmontodinium expiratum* sp. nov. Pl. 8, figs. 13–16 (39)
E. ovatum (Gitmez & Sarjeant, 1972) Riley, 1979, Pl. 10, figs. 1, 2 (27)
E. polyplacophorum Gitmez & Sarjeant, 1972 (23)
E. torynum (Cookson & Eisenack, 1960b) Davey 1979 (35)
Ellipsoidictyum cinctum Klement, 1960 (38)
Exiguisphaera phragma Duxbury, 1979 (88)
Exochosphaeridium phragmites Davey et al., 1966 (110)
Fromea amphora Cookson & Eisenack, 1958 (73)
Glossodinium dimorphum Ioannides et al., 1977 (40)
**Gochteodinia mutabilis* (Fisher & Riley, 1980) comb. nov. Pl. 6, figs. 9, 12 (26)
**G. villosa* (Vozzhennikova, 1967) Norris, 1978. Pl. 6, figs. 1, 4–6 (45)
**G. villosa* subsp. *multifurcata* nov. Pl. 6, fig. 13 (80)
**G. virgula* sp. nov. Pl. 6, figs. 2, 3, 7, 8, 10, 11 (51)
**Gochteodinia* sp. I, Pl. 6, figs. 14, 15 (49)
**Gochteodinia* sp. II, Pl. 7, figs. 1–4
Gonyaulacysta helicoidea (Eisenack & Cookson, 1960) Sarjeant, 1966b (5)
G. ordocava Duxbury, 1977 (123)
G. pennata Fisher & Riley, 1980 (14)
**Gonyaulacysta* sp. A, Davey, 1979. Pl. 10, fig. 3 (61)
**Gonyaulacysta* sp. B (81)
Heslertonia heslertonensis (Neale & Sarjeant, 1962) Sarjeant, 1966b (95)
H. pellucida Gitmez, 1970 (77)
Hystrichodinium furcatum Alberti, 1961 (124)
H. pulchrum Deflandre, 1935 (6)
H. voigtii (Alberti, 1961) Davey, 1974 (42)
**Hystrichogonyaulax* cf. *cladophora* (Deflandre, 1938b) Stover & Evitt, 1978, Pl. 10, fig. 7 (111)
Hystrichogonyaulax spp (7)
Hystrichosphaeridium cf. *arborispinum* Davey & Williams, 1966b (101)
H. cf. *recurvatum* (White, 1842) Davey & Williams, 1966b. Pl. 10, fig. 4 (125)
**Hystrichosphaerina schindewolfii* Alberti, 1961. (89)
Isthmocystis distincta Duxbury, 1979. Pl. 8, figs. 1, 2 (43)
Kleithriasphaeridium corrugatum Davey, 1974 (28)
K. fasciatum (Davey & Williams, 1966b) Davey, 1974 (67)
**K. porosispinum* sp. nov. Pl. 10, figs. 8–12. (17)
K. simplicispinum (Davey & Williams, 1966b) Davey, 1974 (90)
Lagenorhytis delicatula (Duxbury, 1977) Duxbury, 1979 (92)

Lecaniella foveata Singh, 1971 (30)
Lithodinia bulloidea (Cookson & Eisenack, 1960b) Lentin & Williams, 1977 (74)
?*Maduradinium* sp. A Davey, 1978 (85)
Millioudodinium sp. A (18)
Mendicodinium groenlandicum (Pocock & Sarjeant, 1972) Davey, 1979 (15)
Muderongia crucis Neale & Sarjeant, 1962 (119)
M. extensiva Duxbury, 1977 (120)
M. simplex Alberti, 1961 (68)
**M. simplex* subsp. *microperforata* nov. Pl. 9, figs. 4–6 (82)
**Muderongia* sp. A sensu Davey, 1979. Pl. 9, figs. 1–3. (25)
**Muderongia* sp. B (121)
Nelchinopsis kostromiensis (Vozzhennikova, 1967) Wiggins, 1972 (112)
Nematosphaeropsis scala Duxbury, 1977 (113)
Occisucysta tentoria Duxbury, 1977. Pl. 9, figs 13, 14 (86)
**Occisucysta* sp. A Davey, 1979. Pl. 10, figs. 14, 15 (57)
**Oligosphaeridium asterigerum* (Gocht, 1959) Davey & Williams, 1969, Pl. 1, fig. 12 (103)
O. complex (White, 1842) Davey & Williams, 1966b (114)
**O. diluculum* sp. nov. Pl. 2, figs. 1–5 (70)
**Oligosphaeridium* sp. I, Pl. 2, figs. 6–8
Ophiobolus sp. A Davey, 1979 (96)
**Pareodinia* sp. I, Pl. 4, figs. 12–14 (75)
Pareodinia spp. (29)
**Perisseiasphaeridium insolitum* sp. nov. Pl. 4, figs. 8–10 (50)
Phoberocysta neocomica (Gocht, 1957) Millioud, 1969 (99)
P. tabulata Raynaud, 1978 (97)
**Polygonifera staffinensis* (Gitmez, 1970) comb. nov. (24)
Polysphaeridium warrenii Habib, 1976 (98)
Pseudoceratium pelliferum Gocht, 1957. Pl. 10, fig. 16 (78)
Pterospermella aureolata (Cookson & Eisenack, 1958) Eisenack, 1972 (36)
**Pterospermella* sp. A (54)
Pterospermella spp. (79)
Scriniodinium campanulum Gocht, 1959. Pl. 9, figs. 11, 12 (91)
**S. pharo* (Duxbury, 1977) comb. nov. (13)
Sirmiodinium grossii Alberti, 1961 (9)
Spiniferites ramosus (Ehrenberg, 1838) Loeblich & Loeblich, 1966 (100)
S. ramosus (Ehrenberg, 1838) subsp. *primaevus* Duxbury, 1977. Pl. 9, figs. 7, 8 (113)
**Stiphrosphaeridium arbustum* sp. nov. Pl. 3, figs. 1–4 (72)
**S. dictyophorum* (Cookson & Eisenack, 1958) comb. nov. Pl. 2, figs. 10–13 (64)
**Surculosphaeridium* sp. I, Pl. 3, figs. 7, 10 (104)
**Surculosphaeridium* sp. II, Pl. 4, figs. 1, 2
**Surculosphaeridium* sp. III, Pl. 4, figs. 3–6
**Systematophora* cf. *areolata* Klement, 1960, Pl. 1, figs. 5, 6 (10)
**S. palmula* sp. nov. Pl. 1, figs. 1–4 (56)
S. silyba Davey, 1979 (116)
**Systematophora* sp. I, Pl. 1, figs. 7–9 (20)
**Systematophora* sp. II, Pl. 1, figs. 10, 11 (93)
Tanyosphaeridium boletum Davey, 1974 (117)
Tanyosphaeridium spp. (44)
**Tasmanites newtoni* Wall, 1965 (48)
Trichodinium ciliatum (Gocht, 1959) Eisenack, 1964 (33)
Tubotuberella apatela (Cookson & Eisenack, 1960b) Ioannides et al. 1977 (34)
Wallodinium spp. (69)

The Systematophora – Oligosphaeridium – Surculosphaeridium complex

Discussion

The species included within these three genera have in common that they are all skolochorate, gonyaulacacean cysts having an apical archaeopyle and possessing not more than one process or process group per paraplate. Generic differentiation depends on process morphology, i.e. annulate-arcuate, hollow or solid, how the various types are combined, upon the process formula (particularly the presence or absence of paracingular processes) and the presence of ring and linking trabeculae. Thus it is theoretically possible to define many genera using various combinations of the above criteria. The presence of ring trabeculae, either completely or partly linking the distal ends of the processes in annulate complexes, or the distal furcations of solid, fenestrate processes, is used solely at the generic level to differentiate *Hystrichosphaerina* Alberti 1961 from *Systematophora* Klement 1960. This morphological criterion is usually easy to use although, in some instances, adherence to it may cause controversial results as when two morphologically related forms, *S. fasciculigera* Klement 1960 and *H. orbifera* (Klement) Stover and Evitt 1978, are placed in different genera. The linking of processes or process groups by trabeculae, however, as in *Emmetrocysta* Stover 1975 and the »*Adnatosphaeridium*« *aemulum* (Deflandre 1938) complex, is considered to be of greater generic value. A summary of the process arrangements and types in the genera belonging to this complex is shown on table 1. Seven of the genera are already in existence and two new genera, *Stiphrosphaeridium* and *Cymososphaeridium*, are here erected.

The *Systematophora – Oligosphaeridium – Surculosphaeridium* complex is not considered to be a simple lineage in which one genus simply evolves from another and in time gives rise to a further one. More realistically, the basic *Systematophora* type must be regarded as a root stock from which, at certain times in the past, evolved certain variants or morphotypes that are now assigned to different genera. Hence the *Oligosphaeridium* species (described as *O. pulcherrium*, by Ioannides et al. 1977, herein pl. 2, fig. 9) from the mid-Kimmeridgian evolved from the *Systematophora* root stock but did not give rise directly to *O. complex* in the Valanginian. Sometimes associated with this Kimmeridgian *Oligosphaeridium,* and probably closely related to it, is a form here referred to *Perisseiasphaeridium* sp. I (pl. 4, fig. 7) which has solid, paracingular processes. *O. complex*, in all probability, arose from the *Systematophora* root stock in the Ryazanian – early Valanginian perhaps through an intermediate species (see fig. 2). Similarly *Surculosphaeridium cribrotubiferum* (Sarjeant 1960) arose in the Oxfordian probably from ancesters attributable to *Systematophora*. Morphotypes attributable to *Surculosphaeridium* did not reappear until the Valanginian, again probably from a *Systematophora* stock.

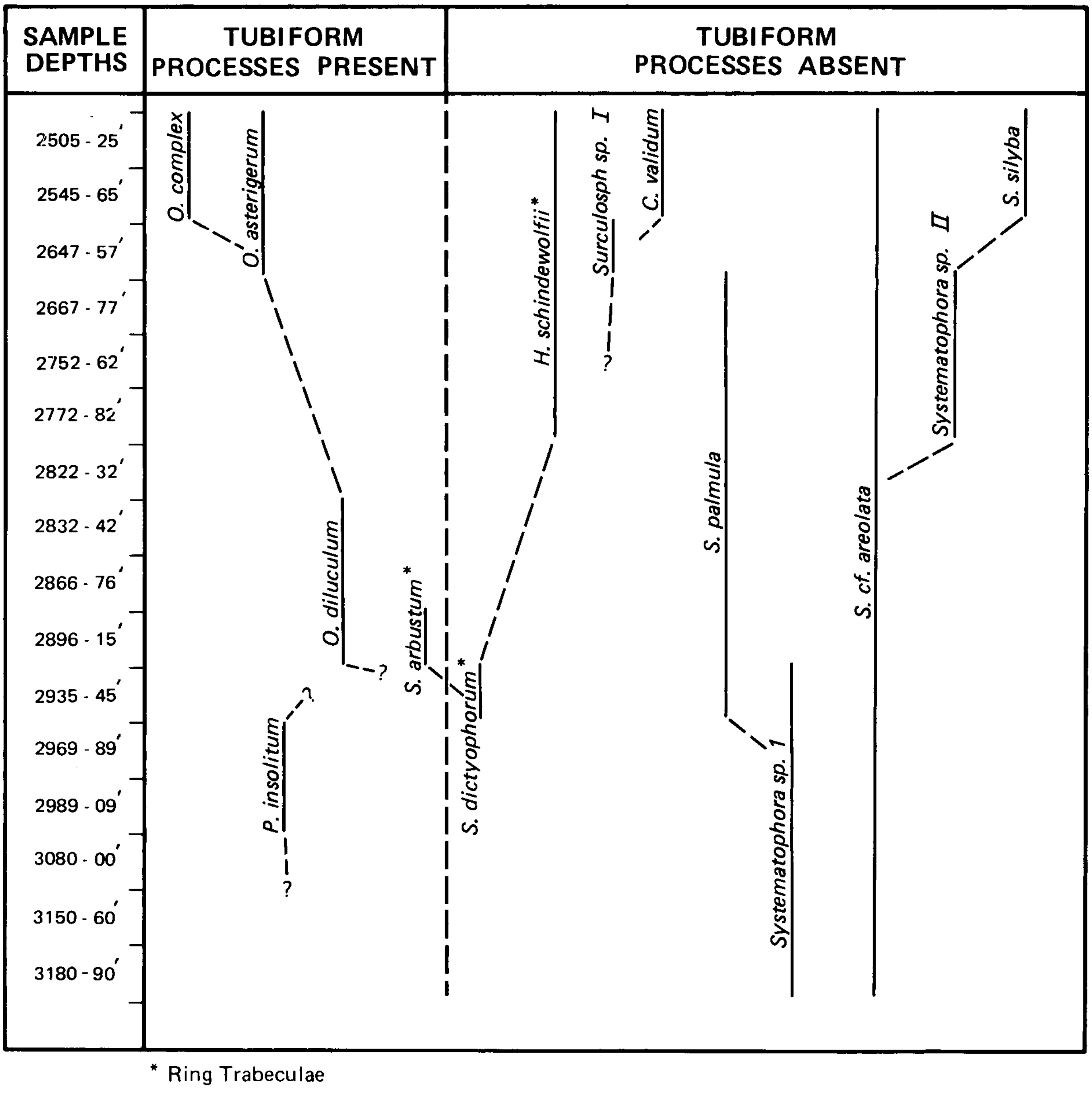

Fig. 2. The ranges of certain chorate dinocysts in the Haldager No. 1 borehole.

Table 1. Summary of the morphological characteristics of similarly structured chorate dinocysts

Genera	Pre- and postcingular process type	Ring trabeculae	Linking trabeculae between processes/ process complexes	Paracingular process type
Systematophora	Annulate-arcuate complexes	Absent	Absent	Solid
Oligosphaeridium	Tubiform	Absent	Absent	Absent
Surculosphaeridium	Solid	Absent	Absent	Solid
Stiphrosphaeridium	Solid-restricted annulate complexes	Present	Absent	Absent
Hystrichosphaerina	Solid?-restricted annulate complexes	Present	Absent	Solid (rarely absent)
Cymososphaeridium	Solid	Absent	Absent	Absent
Perisseiasphaeridium	Tubiform	Absent	Absent	Solid
Hystrichosphaeridium	Tubiform	Absent	Absent	Tubiform
Emmetrocysta	Annulate complexes	Present	Present	Absent
»Adnatosphaeridium« aemulum complex	Solid-annulate complexes. Rarely tubiform	Present	Present	Absent
Polystephanephorus	Annulate complexes	Present	Present	Solid

Genus *Systematophora* Klement 1960

Description. The genus *Systematophora* is characterised by annulate complexes of processes which are best developed in the pre-, postcingular and antapical regions; a single complex occupies each paraplate. When well developed the annulate complexes are penitabular in position but often their size is reduced and they become circular and occupy the central part of the individual paraplate. An additional trend is for the basal ridge of the pre-and postcingular complexes to become reduced on the paracingular margin and the processes to the concentrated on the side of the ridge opposite this margin. In other forms the basal ridge is absent and the individual processes appear to arise immediately from the cyst wall.

The processes are solid, although internal vacuoles may be present; they may be completely separate as in *S. areolata* Klement 1960, the type species, or may be linked to neighbouring processes in the complex by a few simple branches or by numerous branches so that a intricate network is developed. All intermediates extist between isolated processes and simple and intricately linked processes. Restricted annulate complexes, composed of two to three individual processes, may develop in the apical region but often here one paraplate bears a single process. This also happens on the parasulcus and on paraplate 1‴. Two linearly arranged processes usually occupy each cingular paraplate. The process formula appears to be 4′, 6″, 5–6c, 6‴, 1p, 1⁗, 1–5s. The archaeopyle is apical, formed by the detachment of four apical paraplates as a unit (Type Ā).

Remarks. The holotype of *Polystephanephorus calathus* (Sarjeant 1961a) Downie and Sarjeant 1965, which is the type species of the genus, has been reexamined and possesses paracingular processes of the *Systematophora* – type. This is considered to be an important morphological criterion and suggests that *Polystephanephoros* Sarjeant 1961b is closely related to *Systematophora. Polystephanephoros* is distinguished from *Systematophora* by having trabeculae which distally link the process complexes.

Systematophora palmula sp. nov
Pl. 1, figs. 1–4

Derivation of name. Latin, *palma*, hand – with reference to the shape of the major processes.

Diagnosis. Shape. The body was originally spheroidal with only minor dorso-ventral flattening.

Wall. The cyst wall is of moderate thickness and is apparently two-layered, the two layers being closely appressed except where the periphragm alone forms the processes. It is smooth to scabrate. The processes are smooth and may have internal vacuoles.

Processes. These are basically of two types – the pre-, postcingular and antapical annulate processes being membranous and the apical, parasulcal and paracingular processes being simple. The proximal ridges of the annulate complexes tend to be arcuate and, in the pre- and postcingular series, are best developed on the side away from the paracingulum. The single membranous process arising from this arcuate ridge divides medially into two or more branches; additional branching may be present and the distal termination is a small bifurcation. The parasulcal processes are unbranched and solid; they gradually taper-distally to terminate with a small bifuration. The apical processes are similar or slightly membranous. The paracingular processes occur in pairs, two per paraplate, and each pair may be linked proximally by a ridge.

Archaeopyle. An apical archaeopyle always appears to be developed by the detachment of the apical paraplates as a unit (Type Ā). It has a strongly zigzag margin.

Holotype. MPK 2608, slide SAL 4639/III, Haldager No. 1 borehole, core depth 2896′–2915′, Denmark. Ryazanian, Early Cretaceous.

Dimensions

	Holotype (µm)	Range (µm)
Body diameter		
(excluding processes)		
Length		
(archaeopyle developed)	50	34 (45) 53
width	44	39 (43) 48
Process length	18–38	20–38

Description. The width of the membranous processes varies considerably upon an individual specimen and from specimen to specimen. The largest ones, in the antapical and dorsal postcingular positions, divide medially into four to seven subparallel branches; the remaining postcingular processes and the precingular processes are less divided, typically two to four branches, and the division may commence in the lower part of the process.

Remarks. The membranous nature of the major processes in *S. palmula* sp. nov. distinguishes this species from all previously described forms. When some of the major processes become deeply divided, as is sometimes the case, they tend to resemble the larger annulate complexes of *S.* cf. *areolata*, indicating that the two forms are morphologically related.

Occurrence. S. palmula sp. nov. is consistently present from 2935′–45′ to 2667′–77′ (Ryazanian to Valanginian), Haldager No. 1 borehole. It also occurs in the *albidum* (late Ryazanian) and *Paratollia* spp. (early Valanginian) Zones of the Speeton Clay.

Systematophora cf. *areolata* Klement 1960
Pl. 1, figs. 5, 6

Remarks. The present specimens are very similar to the type material from the Lower Kimmeridgian of Germany from which they may be distinguished by, i) the processes being more variable in that they occasionally branch and maybe linked medially or proximally, and, ii) the proximal ridges of the annulate complexes that are subpolygonal in *S. areolata* are reduced to either circular or arcuate ridges, or are apparently absent altogether in *S.* cf. *areolata.*

Occurrence. S. cf. *areolata* occurs in most of the Haldager No. 1 borehole samples and in eastern and northeastern England occurs infrequently in the late Ryazanian and early Valanginian (bed D4, Speeton).

Systematophora sp. I
Pl. 1, figs. 7–9

Description. The cyst is subcircular in outline and is composed of a more or less smooth wall. The anulate complexes are variably developed and proximally usually have a circular ridge from which arise the solid processes. The antapical annulate complex is well developed but in the pre- and postcingular regions the processes tend to be concentrated on the side of the ridge away from the paracingular region. One broad to several finer processes arise from each complex and these divide medially to give several branches which tend to be linked distally by a trabeculum; the trabeculum is arcuate, not circular, in the pre-and postcingular series because of the paucity of processes on the paracingular side of each complex. Alternatively, a process may broaden distally to form a "pseudo-trabeculum" which parallels the cyst surface (pl. 1, figs. 7). The outer margins of the trabeculae bear small spines. The trabeculae and pseudo-trabeculae are formed within an annulate complex and there is no linkage between neighbouring complexes. The apical, cingular and sulcal processes do not form annulate complexes and usually simply branch distally.

Remarks. A reasonable amount of variation as to complexity of process branching has been taken as being acceptable in *Systematophora* sp. I. This variation appears to be continuous and, for the present, there does not seem to be a practical way of subdividing this species. It is characterised by clearly defined pre- and postcingular annulate complexes which distally form arcuate trabeculae or psuedotrabeculae that are distally spiny.

The most similar species to *Systematophora* sp. I appears to be *Adnatosphaeridium caulleryi* (Deflandre) Williams and Downie 1969 which has finer processes and more extensive trabeculae. If true trabeculae are absent from *A. caulleryi* then *Systematophora* sp. I may fall within the range of variation acceptable for this species. *Hystrichosphaerina orbifera* (Klement) Stover & Evitt 1978 is basically similar to *Systematophora* sp. 1 but has considerably more complexly branched processes and the distal trabeculae are typically complete.

Occurrence. Systematophora sp. I is very rare in core 2935′–2945′ (Ryazanian) but is common to moderately common in all the underlying cores of Haldager No. 1. It is moderately common in the early Ryazanian (*kochi* and *runctoni* Zones) of eastern England and becomes common in the Portlandian and Kimmeridgian of this region and southern England.

Systematophora sp.II
Pl. 1, figs. 10, 11

Description. This subspherical cyst has a slightly to heavily granular wall and rather poorly defined annulate complexes. The proximal ridges of the complexes are rarely developed and the processes tend to be concentrated on the side of the complexes away from the paracingulum. The processes are short, less than half the cyst diameter and are of variable width. The broader ones widen distally to terminate with small spines; the narrow processes terminate with a simple bifurcation. The processes are not branched or linked by trabeculae.

Dimensions. Body diameter (excluding processes); length (archaeopyle developed) 35–50μm, width 40–52μm; maximum length of processes 13–19μm.

Remarks. The granular wall, poorly defined annulate complexes and relatively short, broad, processes differentiate *Systematophora* sp. II from *S.* cf. *areolata.*

Occurrence. This form was only recovered in cores 2752′–62′ to 2772′–82′ (early Valanginian) Haldager No. 1 borehole, where it was common to abundant.

Other species

The genus *Surculosphaeridium* is below (p. 16) restricted to species having one process per paraplate in the pre-, postcingular and antapical series. Hence the following species no longer belongs in this genus and is here transferred to *Systematophora.*

Systematophora vestitum (Deflandre) Davey comb. nov. = *Hystrichosphaeridium vestitum* Deflandre, 1938, p. 189, pl. 11, figs. 4–6. Lower Oxfordian, France.

Genus *Oligosphaeridium* Davey and Williams 1966b emend.

Type species. Oligosphaeridium complex (White 1842). Upper Cretaceous, England.

Emended diagnosis. Shape: The body is spherical to subspherical in shape with only minor dorso-ventral flattening.

Wall: The cyst wall is apparently two-layered, the two layers being closely appressed except where the periphragm alone forms the processes. The surface is smooth to coarsely verrucate; an internal structuring maybe present. The processes are generally smooth.

Paratabulation: The parasutures are occasionally defined either by a positive (i.e. ridges) or a negative (i.e. lack of granulation) ornamentation. The paratabulation formula is 4′, 6″, 6c, 6‴, 1p, 1⁗, 5s.

Processes: The plate-centred processes are basically of tubiform shape and flare distally to terminate with several spines. They vary in width according to position on the cyst with the pre-, postcingular and antapical processes being the largest. Rearly a solid process is present in the 1‴ position and one may be present in the parasulcal region. The process formula is 4′, 6″, 5–6‴, 1ps, 1p, 1⁗ plus 0–1s.

Paracingular processes are absent; the only parasulcal process normally present is the posterior parasulcal.

Archaeopyle: An apical archaeopyle is normally developed by the detachment of the apical paraplates as a unit (Type Ā). It has a strongly zigzag margin with a deep parasulcal notch.

Remarks. The diagnosis has been emended mainly to give the paratabulation formula, to indicate process variation, to allow the presence of certain solid processes and to correct the process formula.

The genera *Cymososphaeridium* gen. nov. and *Stiphrosphaeridium* gen. nov. have similar process formulae but the processes are basically solid not tubiform. The process formula of the tubiform processes in *Perisseiasphaeridium* is the same as in *Oligosphaeridium* but fine, solid paracingular and parasulcal processes are also present.

Oligosphaeridium asterigerum (Gocht) Davey and Williams 1969.
Pl. 1, fig. 12

1959: *Hystrichosphaeridium asterigerum* Gocht, p. 67, pl. 3, fig. 1; pl. 7, figs. 1–4.
1969: *Oligosphaeridium asterigerum* (Gocht) Davey and Williams, p. 5.

Remarks. The holotype of *O. asterigerum* (Gocht, pl. 3, fig. 1) comes from a borehole in northwest Germany and is reported to be of early Hauterivian age. Gocht differentiates his new species from *O. complex* (White) Davey and Williams 1966b mainly by the form of the processes which are considered to be narrower and not to widen into funnels. However, from his illustrations of these two species (*O. asterigerum*, pl. 7, fig. 4; *O. complex*, pl. 7, fig. 5) there does not appear to be a significant difference in process form, as he admits in the text (p. 68). I consider that there is a complete graduation between these process types, not only between individuals but upon an individual depending on the position of the process. However, the holotype of *O. asterigerum* does have a narrow, apparently solid, process (upper right of specimen) and this has been found consistently during the present study; its position is 1‴. Thus the occurrence of this process indicates that a more precise way of differentiating the two species is by their process formulae:-

O. asterigerum	4′, 6″, 6‴, 1p, 1⁗, 1ps (1‴ is solid)
O. complex	4′, 6″, 5‴, 1p, 1⁗, 1ps.

Occurrence. O. asterigerum at Speeton has a known range of early Valanginian (bed D4) to latest early Hauterivian (bed C7F) and in the Haldager, No. 1 borehole has a basal occurrence in core 2647′–57′.

O. complex only occurred rarely in the youngest two cores of the Haldager No. 1 borehole and in the Speeton section has an apparent basal occurrence in bed C4C of late Hauterivian age.

Oligosphaeridium diluculum sp. nov.
Pl. 2, figs. 1–5

Derivation of name. Latin, *diluculum*, daybreak or dawn – this species being one of the earliest members of this genus in the Lower Cretaceous.

Diagnosis. Shape: The body is subspherical.

Wall: The thin wall is apparently two-layered. The periphragm is smooth and alone forms the processes.

Paratabulation: None.

Processes: The plate – centred processes vary considerably in size and shape with the larger ones occupying the pre- and postcingular and antapical regions. The processes terminate distally with aculeate and secate spines which maybe branched. Minor fenestration maybe present. One side of the larger processes is often partly lost and in the narrower processes, particularly 1″, 1p and the parasulcal process(es), it may be completely lost and these then appear to be solid. The process formula is 4′, 6″, 6‴, 1p, 1⁗, 1ps plus 0–1s.

Archaeopyle: An apical archaeopyle (Type Ā) is typically developed.

Holotype. MPK 2609, slide SAL 4638/III, Haldager No. 1 borehole, core depth 2866′–76′, Denmark. Ryazanian, Early Cretaceous.

Dimensions

	Holotype (μm)	Range (μm)
Body diameter		
(excluding processes)		
length		
(archaeopyle developed)	48	46 (48) 50
width	56	42 (48) 56
Process length	24–36	18–36

Description. The cyst wall is relatively thin (less than 1μm) and consequently it is often distorted. The processes vary from approximately 1 to 6μm in stem width with the pre- and postcingular and antapical processes being the largest. The walls of these processes sometimes appear to be fibrous and this may be related to incipient fenestration which is usually best developed, when present, at the bases of the processes. When the process stem is short, the rather irregular distal furcations may extend to the body surface.

Remarks. O. diluculum sp. nov. is characterised by its deeply and irregularly furcate, basically tubiform processes. It is thought to be related to *Stiphrosphaeridium arbustum* sp. nov. which differs by having strongly fenestrate processes that terminate with distal trabeculae. *Oligosphaeridium pulcherrimum* (Deflandre and Cookson 1955) Davey and Williams 1966b may be distinguished by its more regularly tubiform processes, 18 in number, whick are strongly fenestrate distally.

Occurrence. O. diluculum is moderately common at depths 2832′–42′ to 2896′–2915′ in the Haldager No. 1 borehole but in eastern England only occurs, with certainty, in the *stenomphalus* Zone, late

Ryazanian. It was also recovered from bed D7G at Speeton which probably belongs to the same zone.

Oligosphaeridium sp. I
Pl. 2, figs. 6–8

Description. The cyst is subspherical in shape and is composed of a thin, smooth to scabrate wall. The basically tubiform processes are short, broad and are usually finely fenestrate. They may have short stems (pl. 2, fig. 6) and then flare widely to give a broad funnel or the stem may be absent and flaring or funneling commences directly from the endocyst (pl. 2, fig. 7). In the latter case they simulate annulate complexes, particularly when the fenestration is coarse and irregular so that the process wall begins to disintegrate (pl. 2, fig. 8). The process formula appears to be 4′, 6″, 5‴, 1ps, 1p, 1⁗.

Remarks. Oligosphaeridium sp. 1 appears most similar to *Amphorula metaelliptica* Dodekova 1969, described from the Tithonian of Bulgaria, which differs by having arcuate processes and significantly both paracingular and parasulcal processes.

Occurrence. Oligosphaeridium sp. I is a rare but distinctive form which, as yet, has only been found in eastern England, in the *runctoni* Zone (early Ryazanian) and in bed E at Speeton. Distortion of the rare specimens observed makes measurements rather meaningless.

Genus *Surculosphaeridium* Davey, Downie, Sarjeant and Williams 1966 emend.

Type species. Surculosphaeridium cribrotubiferum (Sarjeant 1960) Davey et al. 1966. Upper Jurassic (Lower Oxfordian), England.

Emended Diagnosis. Shape: The body is spherical to subspherical in shape with only minor dorso-ventral flattening.

Wall: The cyst wall is apparently two-layered, the two layers being closely appressed except where the periphragm alone forms the processes. The surface is smooth to lightly ornamented and the processes are generally smooth.

Paratabulation: Parasutures not observed.

Processes: The processes are solid, often with internal vacuoles, and simply to complexly branched. The apical, pre-, postcingular, parasulcal and antapical processes are plate-centred. Although the paracingular processes are usually deeply bifurcate and also plate-centred, sometimes the bifurcation extends to the cyst wall so forming two processes per cingular paraplate. The processes vary in width according to position on the cyst with the pre-, postcingular and antapical being the largest. The process formula is 4′, 6″, 6c, 6″, 1p, 1⁗, 1–5s.

Archaeopyle: An apical archaeopyle is normally developed by the detachment of the apical paraplates as a unit (Type Ā). It has a strongly zigzag margin with a deep parasulcal notch.

Remarks. The diagnosis has been emended principally to correct the process formula and to limit the genus to species having only one process per paraplate in the apical, pre-, postcingular and antapical series. For the latter reason *Surculosphaeridium vestitum* (Deflandre) is transferred to *Systematophora* on p. 14.

Surculosphaeridium sp. I
Pl. 3, figs. 7, 10

Description. The cyst is subspherical in shape and composed of a thin, more or less smooth wall. The processes are solid, often with internal vacuoles (particularly the larger processes), and are of variable shape; their distribution conform with the process formula for the genus. The larger processes – the pre-, postcingular and antapical – are relatively broad proximally, sometimes with arcuate bases, sometimes bifurcate medially and typically widen distally into a broad, fenestrate fan which distally may be slightly denticulate. The paracingular processes are narrow, deeply furcate and bifid distally; the parasulcal processes are similarly narrow and briefly bifurcate distally. An apical archaeopyle is typically developed.

Dimensions. Cyst diameter (excluding processes) 38–53μm; process length 10–25 *μm*.

Occurrence. This species was only found in one sample, core 2647′–57′, Haldager No. 1 borehole, where it was relatively common. Undistorted specimens are rare.

Surculosphaeridium sp. II
Pl. 4, figs. 1, 2

Discription. The cyst is subspherical in shape and composed of a thin, more or less smooth wall. The stout, solid processes are strongly vacuolate, vary somewhat in size depending on their position and indicate the process formula 4′, 6″, 6c, 6‴, 4–5c, 1p, 1''''. The larger processes, belonging to the pre-, postcingular and antapical series, are unbranched but recurve distally to form a membranous, subcircular flange orientated parallel to the cyst wall. The paracingular processes are moderately to deeply furcate and terminate distally with a small pad or are briefly bifurcate. The narrow parasulcal processes are rather irregularly branched. An apical archaeopyle is typically developed.

Dimensions. Cyst diameter (excluding processes) 32–50μm; process length 14–22μm, process width up to 2μm.

Remarks. This rare but distinctive species is undoubtedly best assigned to *Surculosphaeridium* even though the major process are unusual, in that they are not branched.

Occurrence. As yet this species has only been found in beds D4 and D3 of the early Valanginian at Speeton, northeast England.

Surculosphaeridium sp. III
Pl. 4, figs. 3–6

Description. The cyst is subspherical in shape and composed of a smooth wall of moderate thickness. The stout, solid processes are often strongly vacuolate and appear to be distributed according to the generic process formula. The pre-, postcingular and antapical processes divide initially either medially or distally into two to several branches which may then subdivide further. When the branching is restricted distally a radiating secate margin may develop. The larger processes may be arcuate proximally. The paracingular processes occur in pairs that may be joined by a small proximal ridge. Both the paracingular and parasulcal processes are briefly bifurcate distally. An apical archaeopyle is typically developed.

Remarks. Except for the presence of paracingular processes, this species is very similar to *Cymososphaeridium* sp. I. All the specimens encountered have been damaged and so meaningful measurements have not been possible.

Occurrence. As yet *Surculosphaeridium* sp. III has only been found in beds D4 and D3 of the early Valanginian at Speeton, northeast England.

Genus *Stiphrosphaeridium* gen. nov.

Type species. Stiphrosphaeridium dictyophorum (Cookson & Eisenack, 1958) comb. nov. Upper Jurassic, Papua.

Derivation of name. Greek, *stiphros*, solid or stout – with reference to the strong, solid processes.

Diagnosis. Shape: The body is spherical to subspherical in shape with only minor dorso-ventral flattening.

Wall: The cyst wall is apparently two-layered, the two layers being closely appressed except where the periphragm alone forms the processes. The surface is smooth to scabrate.

Paratabulation: Parasutures not observed.

Processes: The plate-centred processes are solid and fenestrate. Paracingular processes are absent. The pre-, postcingular (2–6''') and antapical processes are the largest but do vary in size depending on their position on the cyst. The processes may be solid for most of their length before becoming fenestrate, or the fenestrations may extend down to the body surface. Distally these larger processes each terminate in a more or less complete circular trabeculum; in the smaller process (1–4', 1ps, 1p) the trabeculae are sometimes incompletely developed. The process formula is 4', 6'', 6''', 1p, 1'''', 1ps, plus 0–4s.

Archaeopyle: An apical archaeopyle is developed by the apical paraplates as a unit (Type Ā). The archaeopyle has a strongly zigzag margin.

Remarks. An alternative way of defining most of the processes is to describe them as fenestrate funnels which may become solid proximally. *Stiphrosphaeridium* gen. nov. is considered to be most closely related to *Systematophora* and differs principally by never having paracingular processes. Processes occupying the major plate series (i.e. pre-, postcingular and antapical) of *Systematophora* are never solid, one per paraplate, but always form annulate complexes which proximally typically extend over a large proportion of a paraplate. It is possible to interpret the larger processes of *Stiphrosphaeridium*, when they are fenestrate down to the cyst wall, as representing narrow or reduced annulate complexes. The processes of *Oligosphaeridium* are similarly distributed on the cyst surface but are tubiform.

Stiphrosphaeridium dictyophorum (Cookson & Eisenack) comb. nov.
Pl. 2, figs. 10–13

1958: *Hystrichosphaeridium dictyophorum* Cookson and Eisenack, p. 44, pl. 11, fig. 14.
1969: *Oligosphaeridium dictyophorum* (Cookson and Eisenack) Davey and Williams, p. 5.

1979: *Polystephanephorus sarjeantii* Gitmez, Davey, p. 65, pl. 3, figs. 4, 5.

Description. S. dictyophorum comb. nov. illustrates all the characteristics of the genus. Most of the major processes are solid proximally for up to half their length and only in the largest processes, mainly the dorsal postcingular and the antapical, do the fenestrations extend to the body surface. Thus, in the latter cases, it could be interpreted that the 2 to 4 processes arising from the surface constitute narrow or restricted annulate process complexes. Parasulcal processes, additional to the posterior parasulcal, are rare as is the first postcingular process (1‴). The trabeculae are smooth to slightly denticulate distally. An apical archaeopyle is usually developed.

Remarks. S. dictyophorum is very similar to *S. anthophorum* (Cookson & Eisenack 1958) comb. nov. which appears to have broader and more fenestrate processes. The holotype of *S. anthophorum* (Cookson & Eisenack 1958, pl. 11, fig. 12) is reported as occurring in the Apto-Albian of Papua; the other specimen illustrated as this species by Cookson & Eisenack in the same paper (pl. 11, fig. 13) is reported as occurring in sample 27 (I.E.C. well 1) from the Upper Jurassic of Papua, as does the holotype of *S. dictyophorum.* This specimen, attributed to *S. anthophorum*, has more solid (less fenestrate) processes than the holotype of *S. anthophorum* and more closely resembles the holotype of *S. dictyophorum;* it should probably be re-assigned to this latter species.

Specimens previously assigned to *Polystephanephorus sarjeantii* by Davey (1979) are here re-assigned to *S. dictyophorum. P. sarjeantii* is similar to *S. anthophorum* although if paracingular processes are present then this species belongs to *Hystrichosphaerina* Alberti 1961 and closely resembles *H. orbifera* (Klement) Stover & Evitt 1978.

Occurrence. S. dictyophorum only occurs in one sample (2935′–45′) in the Haldager No. 1 borehole and it is there very common. It is similarly very common in the two ammonite zones of the early Ryazanian, eastern England (*runctoni* and *kochi* Zones). Its reported occurrence by Davey 1979 in the *oppressus* Zone of the Portlandian of eastern England is now considered probably due to contamination.

Stiphrosphaeridium arbustum sp. nov.
Pl. 3, figs. 1–4

Derivation of name. Latin, *arbutus*, with trees – with reference to the tree – like form of the processes.

Diagnosis. Shape: The body is subspherical in shape.

Wall: The two layers of the cyst wall are closely appressed except where the periphragm forms the processes. The surface is almost smooth.

Processes: The plate-centred processes vary considerably in size, particularly in width, with the smallest being 1‴, 1p and the parasulcal process(es). The larger processes are poorly to complexly fenestrate; distally each terminates with an incompletely developed circular trabeculum which is slightly spinous distally. Where trabeculae are not developed the processes are distally irregularly aculeate and secate. The more proximal parts of the incompletely fenestrate processes are solid, hollow with a restricted lumen or very rarely hollow. Internal vacuoles are often present. The process formula is 4′, 6″, 6‴, 1⁗, 1ps, plus 0–1s.

Archaeopyle: An apical archaeopyle (Type Ā) is typically developed.

Holotype. MPK 2610, slide SAL 4639/III, Haldager No. 1 borehole, core depth 2896′–2915′, Denmark. Ryazanian, Early Cretaceous.

Dimensions

	Holotype (µm)	Range (µm)
Body diameter		
length (archaeopyle developed)	44	44 (50) 62
width	50	40 (59) 69
Process length	18–34	18–38

Description. The cyst wall is relatively thin (less than 1µm) and because of this is easily distorted and broken. The processes vary from approximately 1 to 7µm in stem width with the pre-, postcingular and antapical processes being the widest. In some of these latter processes the fenestration continues to the body surface so giving rise to what could be termed "narrow-based annulate complexes". Usually, however, fenestration commences medially to distally and the more proximal parts of the processes are solid. Occasionally the internal vacuoles in the processes appear to have joined so giving a hollow process. Rarely this is well developed and the lumen of the stem appears to be confluent with the distal fenestrate funnel of the process so giving a "tubiform" process. Typically the stem walls of these processes are fenestrate.

Remarks. S. arbustum sp. nov. is characterised by possessing strongly fenestrate processes which terminate distally by incompletely developed trabeculae. The processes are very variable and the above features do not occur on all the processes. This species is intermediate between *Oligosphaeridium diluculum* sp. nov., which has basically tubiform processes that are not strongly fenestrate and never have distal trabeculae, and *Stiphrosphaeridium dictyophorum* in which practically all the processes are strongly fenestrate with circular, distal trabeculae.

Occurrence. S. arbustum is relatively common in core 2896′–2915′, Haldager No. 1 borehole, and infrequently in the *icenii* and *stenomphalus* Zones of eastern England.

Other species

The following species is here transferred to *Stiphrosphaeridium.*
Stiphrosphaeridium anthophorum (Cookson and Eisenack) Davey comb. nov. = *Hystrichosphaeridium anthophorum* Cookson and Eisenack 1958, p. 43, pl. 11, fig. 12. Lower Cretaceous (Apto – Albian), Australia.

Genus *Cymososphaeridium* gen. nov.

Type species. Cymososphaeridium validum sp. nov. Early Cretaceous, Hauterivian, Denmark.

Derivation af name. Latin, *cymosus*, full of shoots – with reference to the branching nature of the processes.

Diagnosis Shape: The body is spherical to subspherical in shape with minor dorso-ventral flattening.

Wall: The cyst wall is apparently two-layered, the two layers being closely appressed except where the periphragm alone forms the processes. The surface is smooth to scabrate.

Paratabulation: Parasutures not observed.

Processes: The solid, plate-centred processes vary in size with 1′′′ being particularly small. Paracingular processes are absent. The processes branch, usually medially or distally, to give rise to two to four main branches and these may give rise to further branches. The process formula is 4′, 6′′, 6′′′, 1p, 1′′′′, 1ps.

Archaeopyle: An apical archaeopyle is developed by the detachment of the apical paraplates as a unit (Type Ā). The archaeopyle has a strongly zigzag margin.

Remarks. The form of the processes in *Cymososphaeridium* gen. nov. is practically identical to that of *Surculosphaeridium* Davey *et al.* 1966 but the latter genus can easily be distinguished by the presence of paracingular processes. The process formula of *Cymososphaeridium* is the same as for *Oligoshaeridium* and *Stiphrosphaeridium* gen. nov.; the former genus, however, has tubiform processes whereas the processes in the latter genus are strongly fenestrate.

Cymososphaeridium validum sp. nov.
Pl. 3, figs. 5, 6, 8, 11

Derivation of name. Latin, *validus*, strong and powerful – with reference to the stout processes.

Diagnosis. Shape: The body is spherical to subspherical.

Wall: The two wall layers are closely appressed except where the periphragm forms the processes. The surface is more or less smooth.

Processes: The plate-centred process vary somewhat in size with 1′′′ being particularly narrow and flimsy. They are smooth and solid, except sometimes for internal vacuoles. The processes are parallel sided before branching to initially give two to four branches which then branch further. The initial branching is typically medial to distal although in the postcingular processes it is proximal. The process formula is 4′, 6′′, 6′′′, 1p, 1′′′′, 1ps.

Archaeopyle: An apical archaeopyle (Type Ā) is typically developed.

Holotype. MPK 2611, slide SAL 4628/I, Haldager No. 1 borehole, core depth 2505′–25′, Denmark. Hauterivian, Early Cretaceous.

Dimensions

	Holotype (μm)	Range (μm)
Body diameter (excluding processes) length (archaeopyle developed)	49	48–56
width	52	44–66
Process length	24–34	20–36

Description. The wall is thin, less than 1μm in thickness, and the cyst is often distorted. The narrow process 1′′′ is approximately 1μm thick and the other processes are between 2 and 6μm in thickness. The internal vacuoles are not abundant and are often noticeably concentrated at the bases of the processes.

Remarks. The presence of solid branching processes and the lack of paracingular processes distinguishes *C. validum* sp. nov. from all previously described species. It may be identical to specimens wrongly attributed to *Hystrichosphaeridium ramuliferum* by Gocht 1959 (pl. 3, fig. 9) from the Valanginian and Hauterivian of Germany.

Occurrence. It occurs moderately commonly in cores 2505′–25′ and 2545′–65′ in the Haldager No. 1 borehole and in the Hauterivian of the North Sea Basin.

Cymososphaeridium sp. I
Pl. 3, figs. 9, 12

Description. The cyst is of subspherical shape and is composed of a moderately thick wall from which arise 19 solid, stout processes. They are strongly vacuolate. They occasionally branch medially but typically they divide distally to give several short branches which bear spines; the branches are sometimes broad, being spinous distally, and resemble the "pseudo-trabeculae" of *Systematophora* sp. I. Process 1‴ is noticeably narrower than the other processes. The larger processes, mainly the postcingular, may be arcuate proximally.

Remarks. Cymososphaeridium sp. I differs from *C. validum* principally by the lack of complexly branched processes. It appears to be most similar to a form described herein as *Surculosphaeridium* sp. II which has very similar major processes but also has paired paracingular processes.

Occurrence. Cymosophaeridium sp. I occurs consistently in beds D3 and D2 (early Valanginian) at Speeton, northeastern England.

Genus *Perisseiasphaeridium* Davey and Williams 1966b

Remarks. The presence of both tubiform and solid processes differentiates *Perisseiasphaeridium* from all described genera except *Callaiosphaeridium* Davey and Williams 1966b which, however, has hollow paracingular processes and an epicystal archaeopyle. *Perisseiasphaeridium* is morphologically intermediate between *Oligosphaeridium*, which has the same arrangement of tubiform processes, and *Systematophora*, which has comparable paracingular and parasulcal processes.

Perisseiasphaeridium insolitum sp. nov.
Pl. 4, figs. 8–10

Derivation of name. Latin, *insolitus*, unusual or uncommon – with reference to the unusual occurrence of both hollow and solid processes in this species.

Diagnosis. Shape: The body is subspherical in shape.
Wall: The two wall layers are closely appressed except where the periphragm forms the processes. The surface is more or less smooth.
Processes: The plate-centred, tubiform processes are arranged 4′, 6″, 5‴, 1p, 1⁗, 1ps; they flare distally to give rise to several aculeate spines. There are six pairs of solid, paracingular processes and up to four additional parasulcal processes; these processes typically bifurcate distally. The 1‴ process, when present, is of the latter type.
Archaeopyle: An apical archaeopyle (Type Ā) is typically developed.

Holotype. MPK 2612, slide SAL 5254/2, bed 1 (Casey 1973), Spilsby Sandstone, Portlandian (*giganteus* or *anguiformis/kerberus/okusensis* Zones). Nettleton Top Barn Pit, Lincolnshire, eastern England.

Dimensions

	Holotype (μm)	Range (μm)
Body diameter (excluding processes)	44×58	40–62
Tubiform process stem length	18–28	14–28

Description. The cyst wall is thin, being under 1μm in thickness, and is consequently often distorted and/or broken. The solid and tubiform processes are of comparable length and approximately equal to half the body diameter. The tubiform processes are sometimes faintly striate along their lengths and proximally adjacent to the cyst body; the stem width varies from 3 to 6μm. The solid processes measure less than 2μm in thickness. The paracingular region appears usually to possess aligned, low, ovoidal ridges (pl. 4, fig. 9), one per paraplate, with each process of the paracingular pair arising from one end of the ridge.

Remarks. Although *P. insolitum* sp. nov. is often distorted or broken, the combination of tubiform and solid processes is very distinctive and differentiates it from all previously described species except *P. pan-*

nosum Davey and Williams 1966b. The latter species has irregularly branched and fenestrate tubiform processes in contrast to the simple tubiform processes of *P. insolitum.*

Occurrence. In the Haldager No. 1 borehole, *P. insolitum* is moderately common in core 2969′–89′ and infrequent in core 2989′–3009′, cores that are dated as early Portlandian to early Ryazanian. In eastern England, it is common in the *oppressus* Zone and infrequent in the *giganteus* Zone (*anguiformis – okusensis* Zones).

Genus *Hystrichosphaerina* Alberti 1961

Remarks. The suggested synonymy of *Polystephanephorus* Sarjeant, 1961b and *Hystrichosphaerina* by Duxbury, 1980, is herein rejected. The type species of the former genus, *P. calathus* (Sarjeant, 1961a) Downie and Sarjeant, 1965, possesses trabeculae linking the annulate complexes and this feature is considered to be of generic importance. *Hystrichosphaerina* never has linking trabeculae.

Hystrichosphaerina, however, is considered to be much more closely related to *Stiphrosphaeridium* gen. nov. which possesses solid and annulate complexes in the pre- and postcingular regions but no paracingular processes. *Hystrichosphaerina* has similar annulate complexes which are rarely, if ever, solid and, generally, well defined paracingular processes. These thin long solid processes were noted in the original diagnosis by Alberti, 1961, who considered them probably equatorial in position. Examples of these processes can plainly be seen on *H. schindewolfii* Alberti, 1961, illustrated as *Perisseiasphaeridium eisenacki* by Davey, 1974 (pl. 6, fig. 5) from the late Barremian. The paracingular processes number 1 or 2 per paraplate and bifurcate once or twice distally. The paracingular processes illustrated on a specimen of *H. schindewolfii* by Duxbury, 1980 (pl. 6, fig. 6; text-fig. 10) are very poorly developed being none, 1 or 2 per paraplate. In slightly younger sediments, in the Apto-Albian, a comparable species occurs which completely lacks paracingular processes and is assignable to *Stiphrosphaeridium anthophorum* (Cookson & Eisenack, 1958) comb. nov. Identical specimens are illustrated by Davey, 1979c, (pl. 7, figs. 1, 4, 9) from the Apto-Albian of northwest Europe as *Polystephanephorus anthophorum.*

Hystrichosphaerina schindewolfii Alberti, 1961

1961: *Hystrichosphaerina schindewolfii* Alberti, pp. 38, 39, pl. 10, figs. 1–3, 6, 7.
1965: *Systematophora schindewolfi* (Alberti) Downie & Sarjeant, p. 146
1969: *Perisseiasphaeridium eisenacki* Davey & Williams, p. 6
1980: *Hystrichosphaerina schindewolfii* Alberti, Duxbury, p. 126, pl. 6, fig. 6

Remarks. See above, under generic "Remarks".

The Broomea complex

Remarks. Recently there has been considerable discussion regarding this lineage (Wiggins 1975, Brideaux 1975) and, in particular, the type of archaeopyle present (Dörhöfer, Duxbury and Eaton pers. comm.). The procedure adopted here regarding the archaeopyle is that it is either formed by the removal of the apical paraplates or one to three anterior intercalary paraplates. The latter are so called simply because they located beneath the apical horn and above the precingular paraplates – no direct relationship between these anterior intercalary paraplates and those present in peridinacean species is implied.

This lineage contains mainly elongate forms with an apical and two antapical horns and an anterior intercalary or apical archaeopyle. The generic distinctions are summarised below:–

Broomea Cookson and Eisenack, 1958 emend. Lentin and Williams 1976. One elongate, hexagonal intercalary paraplate (2a) is lost from the mid-dorsal epicystal surface during archaeopyle formation.

Batioladinium Brideaux, 1975. The archaeopyle is apical; it has a deep parasulcal notch and the breakage is high on the dorsal epicystal surface above the intercalary paraplates which remain in place. *Necrobroomea* Wiggins, 1975 is accepted as being a junior synonym of *Batioladinium.*

Imbatodinium Vozzhennikova, 1967. At the present time I reject Wiggins, 1975 synonymisation of *Imbatodinium* and *Pareodinia* for two reasons. Firstly, the type species *I. kondratjevii* has the unusual morphology of an indented paracingulum and a noticeable parasulcus. Secondly, and perhaps of even greater importance, is that there is still considerable confusion as to whether the archaeopyle is apical or intercalary.

Gochteodinia Norris, 1978. This genus contains forms with a 2 – paraplate intercalary archaeopyle and a spinose ornament.

Pareodinia Deflandre, 1947c emend. Wiggins 1975. This genus is restricted to forms with a 2–3 paraplate intercalary archaeopyle, low non-spinose ornament and no distinctive antapical horn. A kalyptra may be present. (My interpretation of *Pare-*

odinia differs from that of Stover and Evitt only in that spinose forms are considered to belong to *Gochteodinia*).

Aprobolocysta Duxbury, 1977 emend. Duxbury, 1980. This genus is here restricted to include forms that apparently possess walls of two layers, the periphragm being distinctly membranous, with or without minor antapical projections, and an apical archaeopyle with deep parasulcal notch.

Kalyptea Cookson and Eosenack, 1960b emend. Wiggins 1975 has a 1 to 3 paraplate intercalary archaeopyle but has only single horns at the apex and antapex.

Cantulodinium Alberti 1961 is pear-shaped, has a 2–3 paraplate intercalary archaeopyle and 3 or more hollow hypocystal horns.

Genus *Batioladinium* Brideaux 1975

Batioladinium longicornutum (Alberti) Brideaux 1975

1961: *Broomea longicornuta* Alberti, p. 27, pl. 5, figs. 18–21; pl. 6, figs. 1–2

1975: *Batioladinium longicornutum* (Alberti) Brideaux, p. 1240

Occurrence. At Speeton *B. longicornutum* has a recorded occurrence of early Hauterivian, bed C11, (Davey, 1974) to earliest late Barremian, basal Upper B beds, Duxbury 1980. In Haldager No. 1, it occurs at 2505′–25′ and 2545′–65′.

Batioladinium pomum sp. nov.

Pl. 5, figs. 2–4

Derivation of name. Latin, *pomum*, fruit of any kind – with reference to the characteristic shape of this species.

Diagnosis. Shape: Basically elongate – ovoidal with some dorso-ventral flattening; broadest in the paracingular region. Apical horn moderately long, slender, gradually tapering and arising relatively abruptly from the main part of the cyst. Typically two low, rounded antapical horns.

Wall: Apparently autophragm only.

Paratabulation: Paracingulum sometimes indicated by alignment of granules. Other paratabulation absent.

Ornament: Increases in coarseness from apical to antapical region. Pitting and low granules are typical of the apical region; the granulation becomes more pronounced towards the paracingulum and particularly on the hypocyst. Irregular spinules and small tubercles may be present here.

Archaeopyle: Apical with deep parasulcal notch; operculum usually remains attached.

Holotype. MPK 2613, slide SAL 4640/I, Haldager No. 1 borehole, core depth 2935′–45′, Denmark. Ryazanian, Early Cretaceous.

Dimensions

	Holotype (μm)	Range (μm)
Cyst length	94	83 (88) 94
Cyst width	40	33 (37) 40

Description. The length of the apical horn is typically 1/4 to 1/3 of the overall cyst length.

Remarks. B. pomum sp. nov. is distinguished from *B. jaegeri* (Alberti) Brideaux, 1975 by its shorter apical horn, rounded antapical horns and its distinctively variable granulate ornament. *B. micropodum* (Eisenack and Cookson) Brideaux, 1975 is distinguished by its very short apical horn and densely granulate thick wall.

Occurrence. B. pomum occurs in the early Valanginian to Ryazanian in cores 2832′–42′ to 2935′–45′, Haldager No. 1 borehole and only in the *lamplughi* Zone of Eastern England.

Batioladinium radiculatum sp. nov.

Pl. 5, figs. 1, 7–9

Derivation of name. Latin, *radicula*, small root – with reference to the form of the antapical horns.

Diagnosis. Shape: Basically elongate, dorso-ventrally flattened; broadest in the paracingular region. Apical horn long, gradually tapering and proximally merges with the main part of the cyst body; distal part is solid with internal vacuoles. Two relatively short antapical horns are present; they taper rapidly distally and are strongly vacuolate throughout. They may give rise to irregular branches or may be bifurcate.

Wall: Apparently autophragm only.

Paratabulation: Paracingulum may be defined by aligned granules.

Ornament: Epicyst mainly smooth to lightly punctate. Granules and tubercles gradually start to appear towards or in the paracingular region and become more abundant on the hypocyst.

Archaeopyle: Apical with deep parasulcal notch.

Holotype. MPK 2614, slide SAL 4640/I, Haldager

No. 1 borehole, core depth 2935′–45′, Denmark. Ryazanian, Early Cretaceous.

Dimensions

	Holotype (μm)	Range (μm)
Cyst length (not incl. antapical horns)	168	120–168
Cyst length (not incl. antapical horns; archaeopyle developed)		60–67
Antapical horns	38 and 49	23–49

Remarks. B. radiculatum sp. nov. is differentiated from the rather similar species *B. longicornutum* by its generally weaker and shorter antapical horns and by its ornamented hypocyst. In addition, *B. radiculatum* appears to become extinct within the late Ryazanian whereas *B. longicornutum* does not have its basal occurrence until much higher in the sequence, in the early Hauterivian.

Occurrence. B. radiculatum occurs in the Ryazanian of Haldager No. 1 borehole, in cores 2866′–76′ and 2935′–45′, and in the *runctoni* to *icenii* Zones of eastern England.

Batioladinium varigranosum (Duxbury) comb. nov.
Pl. 5, figs. 5, 6

1977: *Aprobolocysta varigranosa* Duxbury, p. 53, pl. 14, figs. 6, 7; fig. 20

Remarks. Numerous examples of this interesting species have been examined in the Valanginian and Hauterivian of eastern England and in the Haldager No. 1 borehole. The cyst wall is relatively thick and densely granular with additional verrucae and irregular spinules usually more concentrated towards the antapex. This distribution of ornament is a common feature of the genus *Batioladinium.* Antapical horns, if developed at all, are small and rounded; an apical horn is absent. Complete specimens are relatively rare so the latter characteristic is normally impossible to determine. Very similar forms exist that do have a short apical horn (placed in *B.* cf. *varigranosum*, see below) which cannot be differentiated from *B. varigranosum* if the archaeopyle is completely developed. The evidence available suggests that the two forms are closely related and probably intergrade. Hence, because of the apical archaeopyle, the type of ornament and the intergrading with forms having an apical horn and antapical horns (therefore definitely belonging to *Batioladinium*), the present species is here transferred from *Aprobolocysta* to *Batioladinium.*

Occurrence. B. varigranosum occurs from the early Valanginian (bed D4, Speeton) to the basal Hauterivian (bed D2, Speeton, Duxbury 1977). It occurs in cores 2505′–25′ to 2647′–57′, Haldager No. 1 borehole of Hauterivian to Valanginian age.

Batioladinium cf. *varigranosum* (Duxbury 1977) comb. nov.
Pl. 5, fig. 10

Remarks. This form is identical to *B. varigranosum* in size and type of ornamentation (see above). However, a low apical horn is present. The two forms are clearly related and as *B.* cf. *varigranosum* is the stratigraphically older it is quite possible that *B. varigranosum* is derived from it.

Occurrence. B. cf. *varigranosum* occurs in the Ryazanian cores 2866′–76′ to 2935′–45′, Haldager No. 1 borehole and in the *runctoni, icenii* and *stenomphalus* Zones of eastern England.

Batioladinium sp. I
Pl. 5, figs. 11–13

Description. This is an elongate species with overall length greater than twice the width. The apical horn is relatively short and merges into the main part of the cyst; the antapical horns are low and rounded. The wall is thickish and may be densely granular and pitted. The ornament becomes stronger towards the antapex, becoming coarsely granular with irregular spinules. The latter may also be granular and sometimes are particularly well developed on the antapical horns. The archaeopyle is apical. A paracingulum may be defined by ornament alignment.

Dimensions. Range – overall length 78μm (one specimen), length (archaeopyle developed) 57–72μm, width 30–38μm.

Remarks. The most similar species in overall appearance is *Imbatodinium krondratjevii* Vozzhennikova, 1967 which appears to possess only isolated tubercles.

Occurrence. This species occurs only in the *lamplughi, runctoni,* and *kochi* Zones of eastern England.

Genus *Gochteodinia* Norris, 1978
Gochteodinia villosa (Vozzhennikova) Norris, 1978
Pl. 6, figs. 1, 4–6

1967: *Imbatodinium villosum*, p. 56, pl. 12, figs. 1–3; pl. 13, figs. 1–3; pl. 14, figs. 1, 2; pl. 15, figs. 1, 2.
1975: *Pareodinia dasyforma* Wiggins, p. 107
1978: *Gochteodinia villosa* (Vozzhennikova) Norris, p. 7

Remarks. G. villosa, as accepted here, is extremely variable in overall size, and length and density of process cover. A paracingulum (pl. 6, fig. 6) is occasionally discernible. The holotype (Vozzhennikova, pl. 12, fig. 3a) has a more or less even cover of relatively short, acuminate or slightly bifid processes. This type (pl. 6, fig. 6) is prevalent in the earlier part of the species range but higher in the sequence the larger and longer processed forms (pl. 6, fig. 1) are dominant. The earliest forms of this lineage (pl. 6, fig. 5), in the *giganteus* Zone of eastern England, have very short, blunted processes. An interesting variant are specimens which have ball-like distal process terminations (pl. 6, fig. 4); these are particularly common in the *kochi* Zone of eastern England. An archaeopyle is typically developed and, although the breakage often appears to be somewhat irregular, probably two anterior intercalary paraplates (2 I) are involved.

Occurrence. G. villosa occurs in the *giganteus* to *albidum* Zones of eastern England. It is rare in the *giganteus* Zone, approximately 4% in the *oppressus* Zone, 0.5% in the *runctoni* Zone, 14% in the *kochi* Zone, 9.5% in the *icenii* Zone, 4.5% in the *stenomphalus* Zone and very rare in the *albidum* Zone. It is very rare in the *giganteus* Zone of Dorset, southern England. *G. villosa*, therefore has a peak abundance in the mid Ryazanian.

Gochteodinia villosa subsp. *multifurcata nov.*
Pl. 6, fig. 13

1977: *Pareodinia dasyforma* Wiggins, Duxbury, p. 56, pl. 14, fig. 3
1978: *P. dasyforma* Wiggins, Duxbury, pl. 1, fig. 2
1978: *Gochteodinia villosa* (Vozzhennikova) Norris, pl. 11, fig. 10

Derivation of name. Latin, *multus*, much; *furcatus*, forked – with reference to the presence of distally furcate processes.

Diagnosis. A subspecies of *G. villosa* possessing one to many processes which flare distally to give three to several small spines.

Type. MPK 2616, slide "Upper D4"/1′, bed D4, Speeton Clay, early Valanginian, Speeton, Yorkshire, eastern England.

Dimensions

	Type (μm)	Range (μm)
Body length	70	56–79
Body width	32	24–36
Process length	7–10	5–12

Remarks. G. villosa, at present, is accepted as being a rather variable species (see above) and can bear processes which briefly bifurcate distally. However, if three or more distal spines occur then the specimen is attributable to *G. villosa* subsp. *multifurcata* nov. It is distinguished from *G. judilentinae* McIntyre & Brideaux, 1980, by having many more processes.

Occurrence. This subspecies is considered to have evolved from *G. villosa* at or near the Valanginian – Ryazanian boundary. It occurs in the early Valanginian (Duxbury, 1978; personal observation); in the Canadian Valanginian (McIntyre & Brideaux, 1980); and probably into the early Hauterivian (as *Pareodinia dasyforma* in Duxbury, 1977). This subspecies only occurs at 2647′–77′ (Valanginian) and 2832′–42′ (early Valanginian – late Ryazanian) in the Haldager No. 1 borehole.

Gochteodinia virgula sp. nov.
Pl. 6, figs. 2, 3, 7, 8, 10, 11

Derivation of name. Latin, *virga*, twig or branch – with reference to the irregularly branched nature of the processes.

Diagnosis. Shape: Ovoidal to elongate-ovoidal with minor dorso-ventral ventral flattening. Apical horn small and rounded, antapical horns absent.

Wall: Apparently two-layered with the layers being closely appressed except where the periphragm alone forms the processes. The wall is thick and densely intraperforate so having a spongy appearance. The processes are smooth.

Paratabulation: The paracingulum and parasulcus are sometimes discernible by a lack of processes.

Processes: Basically short but of variable length and are typically branched (terminating distally in a small or large bifurcation) or, more rarely, are simple.

Archaeopyle: Large and appears to be formed by the displacement of 2–3 anterior intercalary paraplates (2–3I).

Holotype. MPK 2615, slide SAL 5014/2, bed 3 (Casey 1973), Spilsby Sandstone, Portlandian (*primitivus* Zone). Nettleton Top Barn Pit, Lincolnshire, eastern England.

Dimensions

	Holotype (μm)	Range (μm)
Body length	56	54–60
Body width	38	30–44
Process length	6–12	6–18

Description. The distinctive, relatively thick wall is approximately 2μm thick.

Remarks. G. virgula sp. nov. is distinguished from *G. villosa* by its thicker, intraperforate wall and the consistent presence of short bifurcating processes.

Occurrence. This is a rare species in the *oppressus* and *lamplughi* Zones of eastern England and in core 2989′–3009′, Haldager No. 1 borehole.

Gochteodinia mutabilis (Riley) comb. nov.
Pl. 6, figs. 9, 12

1980: *Pareodinia mutabilis* Riley, p. 324, pl. 3, figs. 6, 10

Remarks. Because of the presence of a spinose ornament, this species is here re-attributed to *Gochteodinia* Norris, 1978.

Occurrence. This rare but distinctive species has a top known stratigraphic range in the *albani* Zone of the earliest Portlandian of southern England. It occurs rarely at 3150′–60′ and 3180′–90′ (early Portlandian) of the Haldager No. 1 borehole. The specimens recorded in the "*giganteus*" Zone of eastern England (pl. 6, figs. 9, 12) are, at the present, considered to have been reworked.

Gochteodinia sp. I
Pl. 6, figs. 14, 15

Description. This form is closely related to *G. virgula* and differs in that firstly, the apical horn is more or less absent and secondly, that the processes are longer and more complex; they tend to be linked distally by trabeculae.

Occurrence. Gochteodinia sp. I occurs rarely in cores 2969′–2989′ and 2989′–3009′ (early Ryazanian – Portlandian), Haldager No. 1 borehole.

Gochteodinia sp. II
Pl. 7, figs. 1–4

Description. This form has an elongate-ovoidal shape with a moderate length apical horn which is rounded distally. The wall is scabrate. The ornament consists of peritabular ridges and low crests which give rise to somewhat fibrous processes of varying length and width; these usually bifurcate distally. The pre-, postcingular and cingular paraplate series are clearly present although it is impossible to determine accurately the number in each.

Occurrence. Gochteodinia sp. II is rare in the *giganteus* Zone (*anguiformis – okusensis* Zones) of eastern England.

Genus *Pareodinia* Deflandre, 1947c
Pareodinia sp. I
Pl. 4, figs. 12–14

Description The cyst shape is elongate to ovoidal with an apical horn of moderate length arising abruptly from the main body of the cyst. The wall is of moderate thickness and is smooth but densely intraperforate giving a spongy appearance. Vestiges of a kalyptra are sometimes present. The archaeopyle appears to be formed by three intercalary paraplates (3I) although they usually remain in position.

Remarks Pareodinia sp. I superficially resembles *P. groenlandica* Sarjeant, 1972, which differs by having a stronger, subconical apical horn and a strongly reticulate surface pattern.

Occurrence. It is rare to infrequent in cores 2647′–2657′, 2832′–2842′ and 2866′–2876′, Haldager No. 1 borehole.

Genus *Aprobolocysta* Duxbury, 1977, emend Duxbury, 1980.

Remarks. See the introduction to this section (p. 22).

Aprobolocysta neistosa Duxbury, 1980
Pl. 7, figs. 5–7

1980: *Aprobolocysta neistosa* Duxbury, p. 112, pl. 2, figs. 8, 9.

Remarks. The present specimens are very similar to those described by Duxbury, 1980, except that they are smaller and have lower crests. The length of the cyst body (archaeopyle developed and without crests) is 47–59μm, width (without crests) is 30–33μm and the height of the crests is up to 8μm.

Occurrence. Duxbury, 1980, records *A. neistosa* from the early (including mid) and basal late Barremian at Speeton, England. In the present study this species occurs only in bed D3 (early Valanginian) at Speeton and spasmodically in the Haldager No. 1 borehole (cores 2505′–25′, 2545′–65′ and 2969′–2989′; Hauterivian – early Ryazanian/late Portlandian).

Genus *Cantulodinium* Alberti, 1961
Cantulodinium speciosum Alberti, 1961
Pl. 4, fig. 11

1961: *Cantulodinium speciosum* Alberti, p. 23, pl. 3, figs. 20–23; pl. 12, fig. 3

Remarks. The present specimen agrees very closely with those described by Alberti, 1961. In addition, it may be added, that the epicyst is more or less smooth whereas the hypocyst bears an irregular scatter of tubercles. The archaeopyle is wide, has a more or less smooth precingular margin and is apparently formed by the loss of two anterior intercalary paraplates (2 I).

Occurrence. C. speciosum has previously been reported from the Valanginian of Germany by Alberti 1961, and from the Upper Jurassic of Denmark by Stover and Evitt (1978). Single specimens occur only in cores 2545′–65′ and 2896′–2915′ of the Haldager No. 1 borehole. (The reported Upper Jurassic occurrence from Denmark may be incorrect and due to wrongly dated borehole material).

Other taxa

Genus *Aldorfia* Stover & Evitt, 1978
Aldorfia sp. A
Pl. 7, figs. 13–15

Description. This is a moderately large, subspherical to rhomboidal form having a hollow, conical apical horn formed only of periphragm. The paracingulum may also be marked by a slight extension of the periphragm; the parasulcus is defined by a weak depression. The endophragm and periphragm are separated by a distinct pericoel which is traversed by isolated collumellae which sometimes coalesce to form short muri. A precingular archaeopyle (3″) is typically developed.

Dimensions. Overall length 77 (89) 103 μm, overall width 57 (70) 80 μm.

Remarks. Aldorfia sp. A is similar to *A. aldorfensis* (Gocht) Stover & Evitt 1978 from the Bajocian – Bathonian. The latter differs by not having a true apical horn and by having generally longer columellae which are particularly well developed at the cyst apices. *A. spongiosa* McIntyre & Brideaux 1980 comb. nov., of Portlandian – Ryazanian (–?Valanginian) age has broad, sponge-like thickenings linking the periphragm and endophragm

Occurrence. Aldorfia sp. A is relatively common in the *anguiformis – kerberus* Zones (formerly *giganteus* Zone) of Lincolnshire, England, where it occurs with *A. spongiosa.*

Other Species

The following two species are here attributed to the genus *Aldorfia* on the basis of their wall structure and general form:
Aldorfia dictyota (Cookson & Eisenack, 1960b) comb. nov. = *Scriniodinium dictyotum* Cookson & Eisenack, 1960b, p. 248–9, pl. 37, figs. 8, 9.
Aldorfia spongiosa (McIntyre & Brideaux, 1980) comb. nov. = *Apteodinium spongiosum* McIntyre & Brideaux, p. 12, pl. 2, figs. 8–12

Genus *Apteodinium* Eisenack, 1958
Apteodinium sp. A
Pl. 7, figs. 11, 12, 16

Description. This, moderately large, subspherical species is characterised by a thick, intraperforate or spongy wall which can measure up to 7μm in thickness. The wall surface is smooth. A short apical horn is present. The paracingulum is typically well defined by parallel ridges which are particularly noticeable at the cyst margins. The parasulcus is marked by a shallow, elongate indentation.

Dimensions. Overall length 72–103 μm, overall width 56–76 μm, maximum wall thickness 4–7 μm.

Occurrence. Apteodinium sp. A is common in the *kerberus* Zone (early Portlandian) of Dorset (7%) and the *kochi* Zone (early Ryazanian) of Norfolk (8%). It is rare in the *oppressus* to *runctoni* Zones (early Ryazanian – early Portlandian) of eastern England and in cores 2866′–76′, 2896′–2915′, 2969′–89′ and 2989′–3009′, Haldager No. 1 borehole. The age of these cores is late Ryazanian to late early Portlandian which is, at the present, this forms longest range.

Genus *Avellodinium* Duxbury, 1978

The following species is here attributed to the genus *Avellodinium* on the basis of its process type and distribution, the presence of an epicystal archaeopyle and its general form.
Avellodinium culmulum (Norris, 1965) comb. nov. = *Gonyaulax culmula* Norris, p. 793–5, figs. 1, 2, 6–9.

Genus *Canningia* Cookson & Eisenack 1960b
Canningia compta sp. nov.
Pl. 8, figs. 3–6

Derivation of name. Latin, *comptus*, ornamented – with reference to the nature of the cyst surface.

Diagnosis. Shape: Cysts subspherical to slightly angular with some dorso-ventral flattening. Apical region broadly conical; antapex rounded to slightly indented. Widest portion of the cyst is in the paracingular region.

Wall/Ornament: Wall of moderate thickness. Lightly pitted to foveolate and verrucate. Ornament less pronounced towards the centre of the dorsal postcingular paraplate and in the parasulcal region.

Paratabulation: Absent to poorly defined by relatively stronger ornamentation along the boundaries of the paracingulum on the dorsal surface and towards the margins of the dorsal postcingular paraplate. Parasulcus often defined by a distinct groove which extends across the ventral surface from the antapex towards the parasulcal notch and terminating in the paracingular region.

Archaeopyle: Apical; parasulcal notch strongly indented and offset to the left of the mid-line. Margin is strongly zig-zag.

Holotype. MPK 2617, slide SAL 5011/1, Sandringham Sands, Brook Farm, North Runcton, Norfolk, England. *Lamplughi* Zone, Portlandian.

Dimensions

	Holotype (μm)	Range (μm)
Pericyst length		68–82
Pericyst length (archaeopyle developed)	54	54 (59) 65
Pericyst width	52	52 (61) 74

Description The wall is approximately 1 to 1.5 μm in thickness (including ornament). The ornament is most easily observed in plan view and appears to consist of well developed verrucae. When the ornament is high it is noticeable at the lateral margins of the cyst but when low the cyst margins appear to be almost smooth. In the latter case it is probable that a foveolate wall structure is present.

Remarks. The type of ornament, together with the strongly zig-zag archaeopyle margin with the deep parasulcal notch distinguishes *C. compta* sp. nov. from other members of this genus.

Occurrence. C. compta occurs only rarely in the *kerberus* (formerly *giganteus*) Zone of Dorset and eastern England. However, it occurs abundantly in eastern England from the *oppressus* to *stenomphalus* Zone and typically makes up between 20 and 40% of the dinocyst assemblage; its greatest recorded abundance is in a sample from the *primitivus* Zone where it attains 74%. Undoubtedly, this species flourished in the relatively shallow shelfal seas established over eastern England during the Portlandian and the Ryazanian for it does not occur in the same abundance over most of the North Sea Basin. *C. compta* is rare in the *albidum* Zone and has only very rarely been recorded from the basal Valanginian.

In Haldager No. 1 borehole *C. compta* is moderately to very common in cores 2866′–76′ to 2989′–3009′ (late Ryazanian to early Portlandian) and rarer at 2772′–82′, 2832′–42′, 3080′–3100′ and 3180′–90′. Thus the overall range here, as onshore, is early Valanginian to early Portlandian.

Genus *Cannosphaeropsis* O. Wetzel 1933
Cannosphaeropsis thula sp. nov.
Pl. 8, figs. 7–11

1977: *Adnatosphaeridium apiculatum* (Cookson and Eisenack) Lentin and Williams; Duxbury, pl. 10, fig. 1
1979: *Cannosphaeropsis* sp. A Davey, p. 56, pl. 1, figs. 6, 9, 12

Derivation of name. Latin, *thule*, furthest north – with reference to its boreal occurrence.

Diagnosis. Shape: The pericyst, excluding processes, is ovoidal to oviform with very little dorso-ventral flattening.

Wall: The cyst wall is apparently two-layered, the two layers being closely appressed except where the periphragm alone forms the processes. The wall is of moderate thickness and the surface is smooth to lightly pitted.

Paratabulation: Parasutures are occasionally visible along the paracingulum and, more rarely, surrounding the parasulcal region.

Processes: These are parasutural in position. The gonal processes are trifurcate distally whereas the parasutural processes bifurcate distally. The furcations join with neighbouring ones to form a trabeculum which reflects the paratabulation. Distally the trabeculum bears small spines. The processes are longest on the dorsal hypocyst and decrease in size away from this region, being lowest on the ventral epicyst.

Archaeopyle: Precingular, Type P (3″ only), with free operculum.

Holotype. MPK 2618, slide SAL 5260/4, Sandringham Sands, cut off channel, West Abbey, Norfolk, England. *Kochi* Zone, Ryazanian.

Dimensions

	Holotype (μm)	Range (μm)
Pericyst diameter (excluding processes)		
length	56	48 (56) 68
width	39	38 (42) 48
Maximum height of trabecula	18	14–28

Description. The number of parasutural processes tends to increase in the lower Portlandian to upper Kimmeridgian and are often free distally. In these forms the trabeculum tends to become more irregular.

Remarks. C. thula sp. nov. is distinguished from previously described species of this genus by the relatively large size of the cyst body compared with the overall cyst size and also by the much greater height of the processes on the dorsal hypocyst than on the ventral epicyst. *C. thula* appears to be the only member of this genus represented at this stratigraphic level in northwest Europe.

Occurrence. The total range of *C. thula*, deduced from onshore English sections, appears to be from the Zone of *Epipallaceras* sp. (uppermost Kimmeridgian) to the *icenii* Zone (late Ryazanian). However it is only consistently present, and relatively common (1–5%), from the *kerberus (giganteus)* to the *kochii* Zones. In the Haldager No. 1 borehole it has a topmost occurrence in core 2935′–45′ but only becomes relatively common in cores 2969′–89′ and 2989′–3009′. It also occurs at 3150′–60′ and 3180′–90′.

Genus *Chlamydophorella* Cookson and Eisenack 1958

Chlamydophorella membranoidea Vozzhennikova 1967

Pl. 8, fig. 12

1967: *Chlamydophorella mambranoidea* Vozzhennikova, p. 114, pl. 48, figs. 1–10

1979: *Chlamydophorella* sp. A Davey, p. 56, pl. 3, figs. 10–13

Remarks. The density and regularity of the processes and the amount of parasutural alignment they exhibit appears to be rather variable in *C. membranoidea*, a species described from the Upper Jurassic of the USSR. Of note in some of the present specimens and in the type material is the occasional presence of a rudimentary corona of the *Stephanelytron* – type. This was not described by Vozzhennikova but is clearly illustrated by her holotype (pl. 48, fig. 9b) and by other specimens (pl. 48, figs. 5, 10). As in *Stephanelytron* the corona does not occupy the antapex but is situated on the antapical paraplate which is displaced onto the ventral surface. *S. scarburghense* Sarjeant 1961 is similar but has a much more strongly developed corona which is always present. *C. membranoidea*, however, does indicate that there is a complete gradation from *Stephanelytron* to *Chlamydophorella.*

Occurrence. Specimens assignable to *C. membranoidea* probably range from the basal Kimmeridgian to the late Hauterivian. The reduced corona, however, has not been observed below the *kerberus (giganteus)* Zone in Dorset or below the core 2989′–3009′, Haldager No. 1 borehole. Forms with a corona occur rather spasmodically in the Ryazanian and Valanginian of eastern England but are relatively common in the Hauterivian.

Genus *Cribroperidinium* Neale and Sarjeant 1962

Cribroperidinium sp. A

Pl. 10, figs. 5, 6

Description. This is a large ovoidal species of *Cribroperidinium* composed of a thick, densely intraperforate wall and possessing a long apical horn. The latter is hollow for approximately half its length. The paratabulation is moderately well defined by low ridges which bear small to large spines. The latter are particularly well developed at the base of the apical horn, along the paracingular margins and around the antapical paraplate where they are sometimes complexly linked. A large precingular (Type P) 3″ only archaeopyle is usually developed.

Remarks. In gross morphology *Cribroperidinium* sp. A is similar to *Gonyaulacysta longicornis* (Downie) Sarjeant, 1969 especially because of the length of the apical horn. *G. longicornis* is differentiated from *Cribroperidinium* sp. A by being more spherical in shape, being thinner walled, having a very poor paratabulation and almost completely lacking spines. In the Upper Kimmeridgian, Portlandian and Ryazanian less destinctive forms than *Cribroperidinium* sp. A occur which have shorter apical horns and are less spinose. In this study these forms are assigned to *Cribroperidinium* spp.

Occurrence. Cribroperidinium sp. A is very common in the *anguiformis – okusensis (giganteus), oppressus* and *primitivus* Zones of eastern England and may represent up to 46% of the dinocyst assemblage. It is common in only one core sample (2989′–3009′, early Portlandian) in Haldager No. 1 borehole and is present rarely at 2896′–2915′ and 3080′–100′.

Genus *Dichadogonyaulax* Sarjeant 1966b
Dichadogonyaulax pannea (Norris) Sarjeant 1969
Pl. 9, fig. 10

1965: *Leptodinium panneum* Norris, p. 796, figs. 3, 10–13
1969: *Dichadogonyaulax pannea* (Norris) Sarjeant, p. 14

Occurrence. D. pannea is a consistently occurring species from the *giganteus* Zone of Dorset, where it can attain up to 7% of the dinocyst assemblage, to the *pectinatus* Zone of the Kimmeridgian. Below this zone it has been recorded infrequently down to the *mutabilis* Zone of the Kimmeridgian. It occurs in samples 3080′–3100′ to 3180′–3190′, Haldager No. 1 borehole, and is most common in the deepest sample.

Genus *Egmontodinium* Gitmez & Sarjeant, 1972
Egmontodinium expiratum sp. nov.
Pl. 8, figs. 13–16

1979: *Egmontodinium* sp. A, Davey p. 61, pl. 1, figs. 7, 10

Derivation of name. Latin, *expiratus*, to cease – with reference to the disappearance of the paratabulation in this species.

Diagnosis. Shape: Cysts ovoidal to elongate with rounded apices. Dorso-ventral flattening is only minor.

Wall: The wall is apparently two-layered and of moderate thickness; it is smooth to scabrate. The crests and processes are smooth.

Paratabulation: This is only partly defined by low parasutural crests and appears to be 4′, 6″, 6‴, 1p, 1⁗. The crests are basically penitabular although the precingular crests may be parasutural at or towards the paracingular region and diverge from here towards the apices. The limits of the parasulcus may be also, partly defined, as may the paraplates 1‴ and 1p. Penitabular crests define the position of the antapical paraplate (1⁗). The boundaries of the paracingulum are practically absent.

Processes: These are located on the crests and, although are of variable width, they are usually broadly membranous. Distally the gonal processes are briefly trifurcate and the parasutural processes briefly bifurcate. Rarely isolated processes are present in parasutural or penitabular positions, particularly in the paracingular region.

Archaeopyle: Apical; margin strongly zig-zag with a deep parasulcal notch. The archaeopyle breakage occurs midway between the penitabular crests of the apical and precingular series.

Holotype. MPK 1264, slide GB 424/2, Bed J (Arkell 1933), Cherty series, Tilly Whim Caves, Dorset, England. Portlandian, *kerberus* Zone.

Dimensions

	Holotype (µm)	Range (µm)	Single Speciman (µm)
Cyst length			63
Cyst length (archaeopyle developed)	64	50 (61) 70	
Cyst width	40	40 (44) 52	
Maximum height of processes	10	8–13	

Description. The crests are sometimes striate or vacuolate and vary in height from simple ridges to membranous crests. The majority of the processes are extensions of the crests and are linked by the crests. The crests are usually best developed and most noticeable in the antapical region. Often in the parasulcal and apical regions it is difficult to determine whether or not the crests are parasutural or penitabular. The apical region is rarely seen because it is detached in archaeopyle formation.

Remarks. E. expiratum sp. nov. is intermediate between *E. polyplacophorum* Gitmez and Sarjeant, 1972, and *E. torynum* (Cookson and Eisenack) Davey 1979. The former lacks processes entirely whereas the latter has many parasutural processes but lacks crests and a paratabulation.

Occurrence. E. expiratum is a rare species occurring from the *anguiformis – okusensis (giganteus)* to the *runctoni* Zones (basal Ryazanian) of eastern England and only in the *kerberus (giganteus)* Zone of Dorset. In the Haldager No. 1 borehole it occurs at 2667′–77′, 2896′–915′, 2969′–89′ and 3080′–100′.

It is possible that the younger two occurrences could be due to reworking.

Egmontodinium ovatum (Gitmez and Sarjeant) Riley 1979
Pl. 10, figs. 1, 2

1970: *Systematophora* sp. Gitmez, p. 296, pl. 8, fig. 5
1972: *Systematophora ovata* Gitmez and Sarjeant, p. 237, pl. 14, figs. 2, 3
1979: *Egmontodinium ovatum* (Gitmez and Sarjeant) Riley, p. 221

Description. The cyst is elongate to ovoidal, thin walled and bears a moderate number of short processes. The processes are membranous and distally bifurcate to give two relatively thin, often flexuous, recurved spines. These may terminate in brief bifurcations. The processes appear to be sutural and are aligned along the precingular, postcingular and paracingular boundaries. The membranous part of each process extends along the paraplate boundaries although sutural crests or ridges do not appear to be present. The archaeopyle is apical.

Remarks. The holotype of *E. ovatum* has been reexamined and has identical processes to those figured here. The elongate shape of the cyst and the shape and distribution of the processes is very similar to that found in *E. torynum* (Cookson and Eisenack) Davey 1979 and the two species are considered to be closely related.

Occurrence. Rare in the *hudlestoni* Zone to the top of the Zone of *Epipallasceras* sp. (Kimmeridgian) in Dorset; rare in the *pectinatus* Zone (Kimmeridgian) of Yorkshire. The holotype is described from the *baylei* Zone (basal Kimmeridgian) of Cambridgeshire, England; its position at this stratigraphic level is anomalous since this is considerably lower than its known stratigraphic range. *E. ovatum* did not occur in the Haldager No. 1 borehole.

Genus *Gonyaulacysta* Deflandre 1964
Gonyaulacystra sp. A
Pl. 10, fig. 3

1979: *Gonyaulacysta* sp. A Davey, p. 61, pl. 4, fig. 6

Remarks. The specimens attributed to this species from the Haldager No. 1 well are extremely similar in overall form to the originally described material from eastern England.

Occurrence. Previous to this study *Gonyaulacysta* sp. A had only been recorded from two localities (Norfolk and Yorkshire) in eastern England and extremely rarely in the North Sea Basin. In the Haldager No. 1 borehole it occurs relatively infrequently in cores 2866′–76′ to 2935′–45′ (late Ryazanian – ?early Ryazanian).

Gonyaulacysta sp. B

Description. The present species is very similar to *Gonyaulacysta* sp. A Davey 1979 but possesses intratabular and parasutural spines that may be complexly linked.

Occurrence. This form was only noted in the Haldager No. 1 borehole in cores 2772′–82′ and 2832′–42′ (early Valanginian – late Ryazanian).

Genus *Hystrichogonyaulax* Sarjeant 1969
Hystrichogonyaulax cf. *cladophora* (Deflandre, 1938b) Stover and Evitt, 1978
Pl. 10, fig. 7

1977: *Gonyaulacysta cladophora* (Deflandre) Dodekova, Duxbury, p. 33, pl. 2, fig. 5
1979: *Gonyaulacysta* cf. *cladophora* (Deflandre), Davey p. 77

Occurrence. This large species, which is superficially similar to *G. cladophora*, has a known Hauterivian to late Valanginian range although its peak abundance is in the early Hauterivian. In the Haldager No. 1 borehole it is common at 2505′–25′ and rare at 2545′–65′.

Genus *Kleithriasphaeridium* Davey 1974
Kleithriasphaeridium porosispinum sp. nov.
Pl. 10, figs. 8–12

1979: *Kleithriasphaeridium* sp. A Davey, p. 61, pl. II, figs. 10, 11

Derivation of name. Latin, *poros*, porous; *spina*, thorn – with reference to the perforate appearance of the processes.

Diagnosis. Shape: The body is of ovoidal shape with only minor dorsoventral flattening.

Wall: The wall is apparently two-layered and of moderate thickness. The periphragm is extremely fibrous and alone forms the processes. Fibres radiate from the bases of the processes over the body and the surface region between processes may be fibrous or strongly to weakly reticulate.

Processes: These are tubiform and terminate with a smooth, or slightly to strongly serrate margin. Rarely they bifurcate medially or distally. Usually two of the apical processes are linked by a crest. The width and length of the processes vary according to their position on the cyst; the largest are dorsal hypocystal and antapical in position and the smallest are the parasulcals. The apical and paracingular processes are intermediate in size. The process formula appears to be 1pr, 4′, 6″, 6c, 5‴, 1p, 1⁗ plus xs. Fewer processes sometimes occur apparently resulting from a reduction in the number of processes in and around the parasulcal region.

Archaeopyle: Precingular, Type P (3″ only) with free operculum.

Holotype. MPK 2620, slide GB 424/2, Bed J (Arkell 1933, Cherty Series, Tilly Whim Caves, Dorset, England. Portlandian, *kerberus* Zone.

Dimensions

	Holotype (μm)	Range (μm)
Pericyst diameter (excluding processes)	40×48	32 (44) 57
Length of processes	11–20	10–24
Maximum length of processes	20	16 (21) 26

Remarks. K. porosispinum sp. nov. is characterised, and distinguished from other members of the genus *Kleithriasphaeridium*, by the presence of highly fibrous processes. There appears to be a difference in the degree of ornamentation between the onshore English specimens and those recovered from Denmark. Whereas the surface of the cyst is strongly fibro-reticulate on the English specimens, the Danish specimens tend to be smooth to slightly reticulate.

Occurrence. This species is common (5%) in the *kerberus ("giganteus")* Zone of Dorset and has been reported down to the *pectinatus* Zone (late Kimmeridgian). In eastern England it has a definite range of *stenomphalus* Zone (late Ryazanian) to the *anguiformis – okusensis* (formerly *giganteus*) Zones. It has been reported from the latest Ryazanian and early Valanginian here but these rare occurrences may be due to reworking. In the Haldager No. 1 borehole it occurs from 2866′–76′ (late Ryazanian) to the base of the examined section.

Genus *Muderongia* Cookson and Eisenack 1958
Muderongia sp. A
Pl. 9, figs. 1–3

1979: *Muderongia* sp. A Davey, p. 64, pl. 2, figs. 4, 5

Occurrence. Muderongia sp. A is a rare to relatively common species from the *giganteus* Zone to the *pallesioides* Zone (Riley 1974) in Dorset, England. It is a relatively common species from 3080′–3100′ to 3180′–90′ in the Haldager No. 1 borehole.

Muderongia simplex Alberti, 1961, subsp. *microperforata* subsp. nov.
Pl. 9, figs. 4–6

Diagnosis. A subspecies of *M. simplex* possessing a perforate periphragm. The perforations are numerous, small and are circular to subpolygonal in outline.

Type. MPK 2619, slide SAL 4637/III, Haldager No. 1 borehole, core depth 2832′–42′, Denmark. Early Valanginian – late Ryazanian, Early Cretaceous.

Dimensions

	Type (μm)	Range (μm)
Overall length	85	78–85
Overall width	74	51–70
Overall length (archaeopyle developed)		42–60

Description M. simplex subsp. *microperforata* closely resembles *M. simplex* in all respects except for the very characteristic perforation of the periphragm. The perforations are often better developed, and more easily observed, on the horns. Typically an apical horn, two lateral and two antapical horns are present although the lateral horns and one of the antapical horns may be reduced to bulges. A clear paracingulum is usually present and extends along the lateral horns to give a lateral indentation to them. The inner body is rounded in shape and may be slightly asymmetric antapically.

Occurrence. This subspecies only occurs in one core, 2832′–42′, in the Haldager No. 1 borehole (early Valanginian to late Ryazanian) and it is here abundant. It has also been observed, albeit rarely, in coeval sediments in the North Sea Basin.

Muderongia sp. B

Remarks. This form is similar to *M. simplex* subsp. *microperforata* except that the perforations are confined to the distal portions of the horns.

Occurrence. Muderongia sp. B occurs rarely in core 2545′–65′ (probable early Hauterivian) and also in the North Sea Basin in Hauterivian – Valanginian sediments.

Genus *Occisucysta* Gitmez 1970
Occisucysta sp. A
Pl. 10, figs. 14, 15

1977: *Occisucysta evitti* (Dodekova) Gitmez; Duxbury, p. 43, pl. 3, figs. 1, 5
1979: *Occisucysta* sp. A Davey, p. 64, pl. 3, figs. 7, 8 (figured as *Occisucysta* cf. *evittii*)

Occurrence. Davey (1979) published the range of this species as late Ryazanian (*albidum* Zone) to early Valanginian. It has also been recovered from the *stenomphalus* Zone of eastern England thus extending its known range. In the Haldager No. 1 borehole, it is found rarely in core 2822′–32′ to core 2935′–45′ (early Valanginian – Ryazanian). The specimen in core 2545′–65′ (Hauterivian) is considered to have been reworked.

Genus *Polygonifera* Habib, 1972
Polygonifera staffinensis (Gitmez, 1970) comb. nov.

1970: *Meiourogonyaulax staffinensis* Gitmez, p. 276–8, pl. 3, fig. 1
1972: *Meiourogonyaulax staffinensis* Gitmez, Gitmez & Sarjeant, p. 224–5, pl. 9, fig. 4
1972: *Hexagonifera jurassica* Gitmez & Sarjeant, p. 240–1, pl. 14, figs. 5, 8
1976: *Lithodinia staffinensis* (Gitmez) Gocht, p. 334

Remarks. P. staffinensis comb. nov. is basically a cavate dinocyst, with or without incipient antapical horn development, having weak to moderate paratabulation and a large, apical archaeopyle. It is recognised as being a rather variable morphotype especially with respect to the amount of cavation developed. However, being cavate this species does not belong in *Lithodinia*, nor can it be attributed to *Hexagonifera* which possesses an intercalary archaeopyle. In most respects this species closely resembles the Jurassic species *Polygonifera evittii* Habib 1972 and for this reason *staffinensis* is transferred to this genus.

Occurrence. P. staffinensis occurs consistently, and is often common (10% *albani* Zone of Dorset) from the *albani* Zone to the *elegans* Zone of the Kimmeridgian in Dorset. Spasmodic occurrences above this range, in the Portlandian and Ryazanian are considered to be probably due to reworking. Similarly, it has also been recorded very rarely below this range down to the *pseudocordata* Zone of the late Oxfordian. *P. staffinensis* was only recorded from the two basal samples analysed in the Haldager No. 1 borehole.

Genus *Pterospermella* Eisenack, 1972
Pterospermella sp. A

Description. The present forms are closely comparable to *Pterospermella aureolata* (Cookson & Eisenack, 1958) except that there is a distinctive, thickened outer border to the flange.

Occurrence. Pterospermella sp. A is restricted to cores 2935′–45′ and 2969′–89′ in the Haldager No. 1 borehole and mainly to the later part of the Portlandian in eastern England.

Genus *Scriniodinium* Klement, 1957
Scriniodinium pharo (Duxbury, 1977) comb. nov.

1977: *Endoscrinium pharo* Duxbury, p. 32, pl. 9, fig. 5

Remarks. I agree with Stover and Evitt's (1978) interpretation that *Endoscrinium* (Klement, 1960) is a junior synonym of *Scriniodinium* Klement, 1957. Hence the present species is here formally transferred to the latter genus.

Occurrence. Very rare examples of *S. pharo* occur in the *giganteus* of Norfolk, eastern England. Onshore in England, it is next recorded in the *lamplughi* Zone and above this zone it is relatively common (always under 5%) until the *albidum* Zone where it is rare. Recent unpublished studies show that this species does range into the early Valanginian. In the Haldager No. 1 borehole it occurs consistently from sample 2772′–82′ to 2969′–89′ and has an isolated occurrence in sample 3180′–90′.

Genus *Tasmanites* Newton 1875
Tasmanites newtoni group Wall 1965

Remarks. The overall size, the wall thickness and details of the wall structure of the tasmanitids near the Jurassic – Cretaceous boundary vary considerably and in the present instance they are all included under the taxon *Tasmanites newtoni* group. The presence or absence of large pore – canals does not appear to be a particularly diagnostic feature. In general appearance the present specimens compare most closely to *T. tardus* Eisenack 1957 and *T. newtoni* Wall 1965.

Occurrence. In eastern England, tasmanitids occur consistently from the "*giganteus*" Zone to the *runctoni* Zone. In Dorset they occur consistently and often abundantly from the "*giganteus*" Zone to the *mutabilis* Zone (early Kimmeridgian). Lam and

Porter (1977) report this group from the *pallasioides* Zone to the *cymodoce* Zone of Brora, northeast Scotland. In Haldager No. 1 borehole they occur only at 2866′–76′ and 2989′–3009′. Tasmanitids are characteristic of the Kimmeridge Clay Formation in the North Sea Basin and are particularly common in the late Portlandian; their occurrence is closely linked to the distribution of *Pterospermella aureolata* (Cookson & Eisenack, 1958) Eisenack, 1972 in this formation.

Discussion of the dinocyst distribution and zonation/age of the analysed cores

The distribution of dinocysts in the Haldager No. 1 borehole is very similar to their distribution outlined in Davey 1979 where a zonation for the Barremian to Portlandian was established. This zonation was erected principally after the detailed studies of dinocyst distributions in accurately dated onshore sections in England. By comparing the distribution of dinocysts in the Haldager No. 1 borehole to the known distributions (op. cit. and Systematics of this paper), the borehole samples analysed can be zoned and the age determined (text fig. 3). The following section discusses how the above dinocyst zonation is applied to the analysed section of the borehole and the cores dated.

Batioladinium longicornutum Subzone, Discorsia nanna Zone. Cores 2505′–25′ and 2545′–65′ (late? – early Hauterivian).

The presence of *B. longicornutum* and the lack of the suceeding subzonal markers (*Canningia* cf. *reticulata* sensu Duxbury 1977, *Subtilisphaera* spp. and *Ophiobolus* sp. A Davey 1979) indicates the presence of the *B. longicornutum* Subzone. *Hystrichogonyaulax* cf. *cladophora* is common in the higher sample and is suggestive of the earlier part of this zone. *Discorsia nanna*, the base of which is used to define the underlying *Kleithriasphaeridium simplicispinum* Subzone, was not recorded during this study; hence this subzone could not be identified with certainty. However the occurrence of *Muderongia extensiva* in the deeper core suggests the possibility that this subzone may have been penetrated. *Heslertonia heslertonensis* (see Davey 1979) is not now considered to have a base in this subzone and probably ranges down to at least the early Valanginian where it possibly grades into the smaller *Heslertonia pellucida*.

Additional distinctive species characteristic of the Hauterivian include *Cymososphaeridium validum, Nematosphaeropsis scala* and *Spiniferites ramosus primaevus*.

Spiniferites ramosus Zone. Cores 2647′–57′ and 2667′–77′ (Valanginian)

The base of *S. ramosus*, in the deeper sample, is used to define this zone. The presence of *Gochteodinia villosa multifurcata* is consistent with this zone and the occurrence of *Systematophora palmula* in the deeper sample suggests an early Valanginian age at this level. The base of *Oligosphaeridium* is in the higher sample; its absence in the lower sample is similarly suggestive of an early Valanginian age.

The base of *Phoberocysta neocomica* occurs at 2667′–77′ and, when considering its distribution in Davey 1979, appears to be unusually high. However, Davey, at that time, included forms since attributable to *P. tabulata* in *P. neocomica* and the former species does occur deeper in the borehole.

Spiniferites ramosus/Pseudoceratium pelliferum Zones. Cores 2752′–62′ and 2772′–82′ (early Valanginian)

Although *S. ramosus* is absent from these cores, the deeper one does nevertheless contain *Kleithriasphaeridium simplicispinum* and *Exochosphaeridium phragmites* which are characteristic of this zone. However, the top occurrences of *Canningia compta, Scriniodinium pharo* and *Gonyaulacysta* sp. B at this level do suggest the basal part of the *S. ramosus* Zone to *P. pelliferum* Zone of earliest Valanginian age.

Pseudoceratium pelliferum Zone. Cores 2822′–32′ and 2832′–42′ (early Valanginian – late Ryazanian)

The base of this zone is defined, in the deeper sample by the basal occurrence of *P. pelliferum.* The top occurrence of *Occisucysta* sp. A. Davey 1979 in the higher sample, indicates the upper part of this zone.

Davey (1979) wrongly considered that *Ctenidodi-*

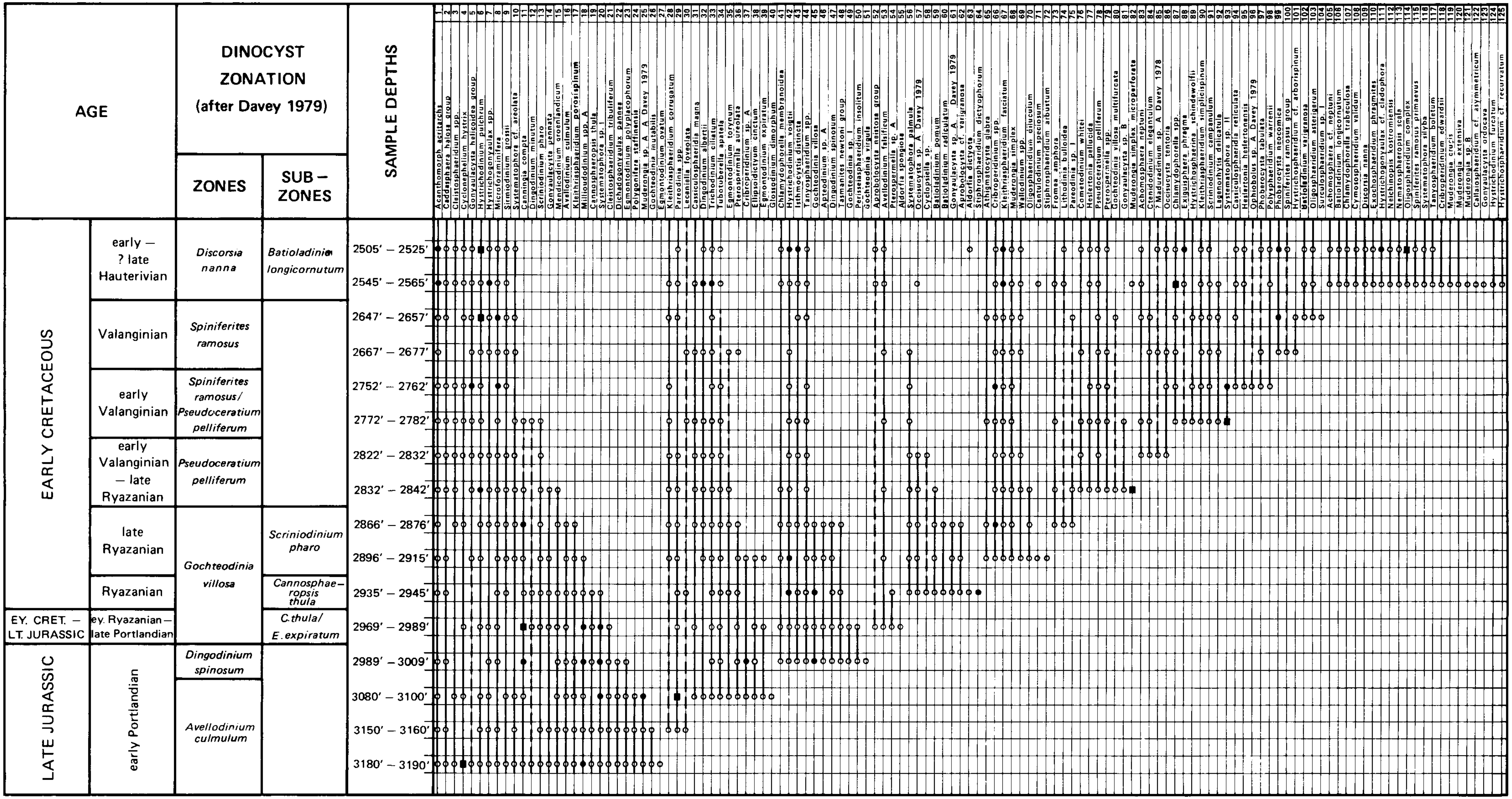

Fig. 3. Distribution-range chart of the microplankton encountered in the Haldager No. 1 borehole.

nium elegantulum did not occur beneath the *Chlamydophorella trabeculosa (Batioladinium longicornutum)* Subzone of Hauterivian age. It has since been observed down to the lower part of the *P. pelliferum* (latest Ryazanian) Zone and in the present borehole has a basal occurrence at 2822′–32′.

The continued presence of *Gochteodinia villosa multifurcata* down to 2832′–42′ is indicative of an early Valanginian age although a late Ryazanian age cannot be dismissed. Such an age is suggested by *Oligosphaeridium diluculum* at this level.

Scriniodinium pharo Subzone. Cores 2866′–76′ and 2896′–915′ (late Ryazanian)

The top of this zone is identified by the top occurrence of *Avellodinium culmulum* in core 2866′–76′. *Kleithriasphaeridium porosispinum* (*Kleithriasphaeridium* sp. A of Davey 1979) also has a top occurrence at this level and was reported by Davey (op. cit) to mark this boundary. However, it now appears probably, that this species does in fact range into the early Valanginian. The top consistent occurrence of *Pterospermella aureolata* also occurs in this core. Although it is realised that this is a strongly environmentally controlled form, it does have a practical top occurrence in northwest Europe at the top of the Kimmeridge Clay Formation which is, at its youngest, at the top of this subzone. Additional species first appearing in this core, and consistent with this subzone, include *Gonyaulacysta* sp. A Davey 1979, *Dingodinium spinosum* and *Gochteodinia villosa.*

The absence of *Cannosphaeropsis thula* in core 2896′–915′ indicates that this core is similarly attributable to the *S. pharo* Subzone. Several forms have basal occurrences in this core and include *Kleithriasphaeridium corrugatum, K. fasciatum, Muderongia simplex* and *Athigmatocysta glabra.*

Although the first three species were considered by Davey (op. cit) to have stratigraphical bases in the overlying *Pseudoceratium pelliferum* Zone, there is now strong evidence to suggest in this core, and the overlying core, that their bases are indeed lower and in the *S. pharo* Subzone. The base of *Oligosphaeridium diluculum* (only recorded onshore from the *stenomphalus* Zone) is in this core and *Stiphrosphaeridium arbustum* (recorded onshore from the *icenii* and *stenomphalus* Zones) only occurs here; both these occurrences are consistent with the *S. pharo* Subzone determination.

Cannosphaeropsis thula Subzone. Core 2935′–45′ (Ryazanian)

The top of this subzone in this borehole is marked by the first downhole occurrence of the nominative species. The following species have their basal occurrences at this level:– *Batioladinium radiculatum, Systematophora palmula, Occisucysta* sp. A Davey 1979 and *Gonyaulacysta* sp. A Davey 1979. Both the latter two species have their basal stratigraphical occurrences in the *stenomphalus* Zone of England. Hence, there is here strong evidence to suggest they do range slightly lower in the Ryazanian. *B. radiculatum* has only been recorded onshore in the *runctoni* and *icenii* Zones and *Stiphrosphaeridium arbustum*, which is common in this core, is only found abundantly in the *runctoni* and *kochi* Zones. *C. thula* has also been found extremely rarely in the *icenii* Zone. Hence the top of this subzone may be slightly higher than reported by Davey (op. cit) and be within the lower part of the *icenii* Zone.

Cannosphaeropsis thula/Egmontodinium expiratum Subzones. Core 2969′–89′ (early Ryazanian – Portlandian)

These two subzones are always difficult to differentiate because of the rarity of the marker species, *E. expiratum.* It does occur in this core, but also in core 2896′–915′ where it is probably reworked. *Canningia compta* occurs abundantly for the first time at 2969′–89′ and has been recorded in similar numbers from Zones *oppressus* to *stenomphalus* onshore. It is, however, recognised that this is a somewhat facies controlled form and is particularly characteristic of "nearshore" shallow water sediments. *Perisseiasphaeridium insolitum* is also present and onshore has only been recovered from the "*giganteus*" and *oppressus* Zones. This suggests that this core could belong to the lower part of the *E. expiratum* Subzone.

Dingodinium spinosum Zone. Core 2989′–3009′ (early Portlandian)

The marker species for this zone, *Dichadogonyaulax pannea*, has its top occurrence in this core and indicates that sediments of early Portlandian age are present. However there is evidence, by the presence of *Gochteodinia virgula* (onshore in the *oppressus* and *lamplughi* zones), that younger aged Portlandian sediments may also be present in this core. This conclusion is strengthened by *Gochteodinia villosa* which occurs commonly in this core. Although this species is known from the "*giganteus*" Zone of onshore England, it is only present in any abundance above this level.

Additional species having basal occurrences in this core are *Dingodinium spinosum* and *Perisseiasphaeridium insolitum* which both have bases onshore in the "*giganteus*" Zone. *Egmontodinium polyplacophorum*, which has a top occurrence onshore in the *oppressus* Zone, similarly has a youngest occurrence in this core.

Avellodinium culmulum Zone. Cores 3080′–100′ to 3180′–90′ (early Portlandian)

This zone is identified by the absence of *Dingodinium spinosum*, the top occurrence of *Polygonifera staffinensis* in core 3080′–100′ and the continued presence of *A. culmulum* to the base of the cored sequence at 3180′–90′. Of significance in the highest core is the top and common occurrence of *Muderongia* sp. A. Davey 1979 which, for practical purposes, is regarded as marking the top of this zone. Several species have their basal occurrences in this core but these are regarded primarily as being only of local interest.

Core 3150′–60′ contains the top occurrence of *Gochteodinia mutabilis* which onshore is known only from the *albani* Zone and late Kimmeridgian.

Although *A. culmulum* is found in core 3180′–90′, the distinctive species *Egmontodinium ovatum* also occurs here. This species has only previously been observed in pre-Portlandian sediments and suggests that the base of the *A. culmulum* Zone may be within the uppermost Kimmeridigian. *Scriniodinium pharo* occurs in this core and has previously been found to have a stratigraphical base in the "*giganteus*" Zone; its occurrence here could be possibly due to contamination.

Acknowledgements

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(All references to dinocysts mentioned in the text but not listed below are to be found in Lentin and Williams 1973, 1975, 1977).

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Plate 1

All magnifications ×500. All type material is stored in the collections of the Institute of Geological Sciences, Leeds.

Systematophora palmula sp. nov.

Figs. 1–3 Slide SAL 4639/III, holotype.

Fig. 4. Slide SAL 4639/I, Haldager No. 1 borehole, core depth 2896′–2915′; Ryazanian, Denmark.

Systematophora cf. *areolata* Klement

Fig. 5. Slide 4635/II, Haldager No. 1 borehole, core depth 2772′–82′; Valanginian, Denmark.

Fig. 6. Slide 4638/III, Haldager No. 1 borehole, core depth 2866′–76′; Ryazanian, Denmark. Interference contrast.

Systematophora sp. I

Figs. 7–9. Slide Warlingham VI, Warlingham borehole, Surrey, core depth 2285′ 7″; Upper Kimmeridge Clay, Kimmeridgian (? *rotunda* Zone).

Systematophora sp. II

Figs. 10, 11. Slide SAL 4635/II, Haldager No. 1 borehole, core depth 2772′–82′; Valanginian, Denmark. Fig. 11, phase contrast.

Oligosphaeridium asterigerum (Gocht) Davey & Williams

Fig. 12. Slide SAL 4628/I, Haldager No. 1 borehole, core depth 2505′–25′; Hauterivian, Denmark. Note solid first postcingular process (1‴) on lower right of specimen.

Plate 1

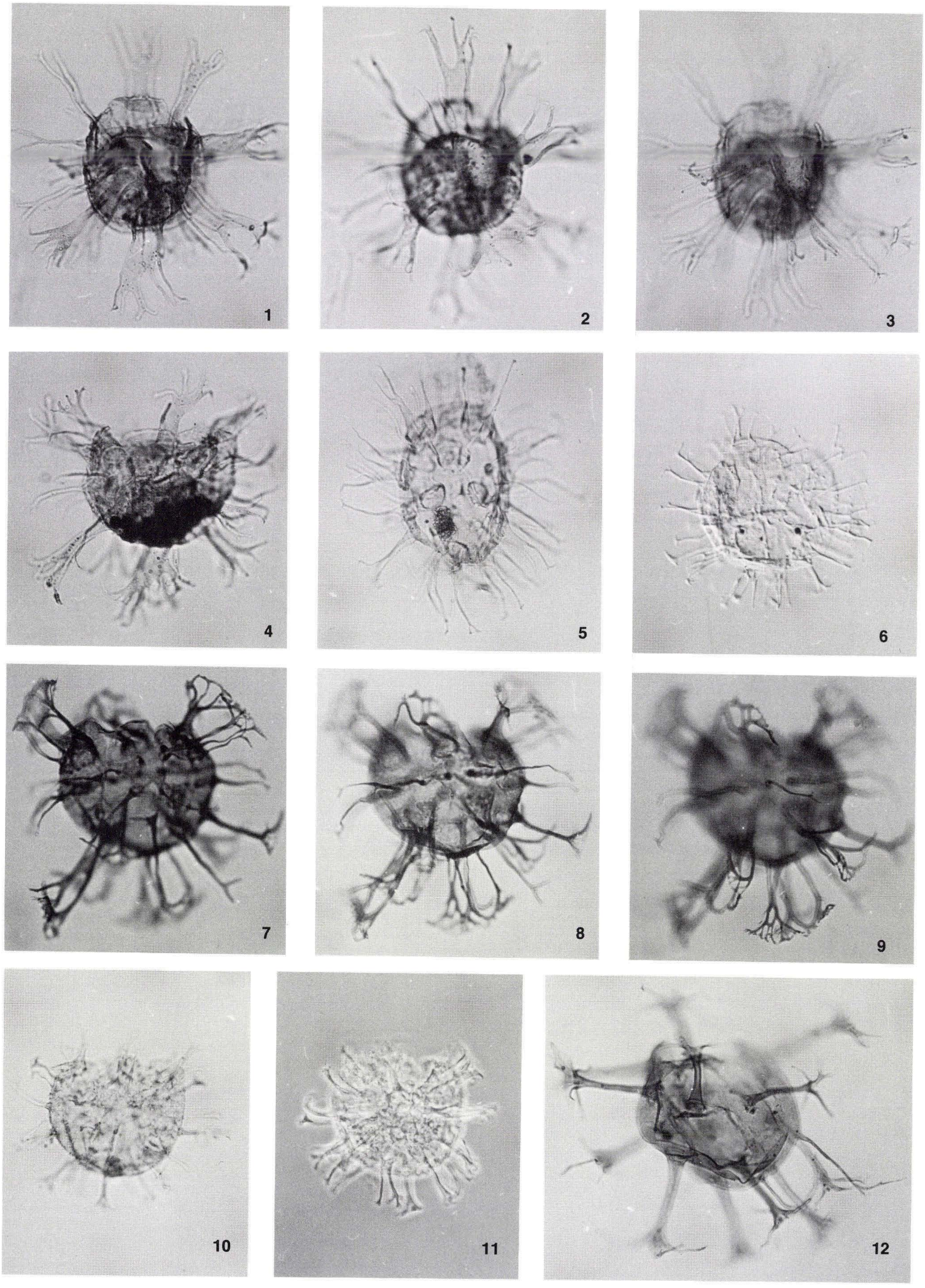

Plate 2
All magnifications ×500.

Oligosphaeridium diluculum sp. nov.
Figs. 1, 2. Slide SAL 4638/III, holotype.
Fig. 3. Slide SAL 5003/1, Sandringham Sands, Ryazanian (*stenomphalus* Zone); Mintlyn Wood Road Cutting, Kings Lynn By-Pass, Norfolk.
Fig. 4. Slide SAL 4638/II, Haldager No. 1 borehole, core depth 2866′–76′; Ryazanian, Denmark.
Fig. 5. Slide SAL 4639/I, Haldager No. 1 borehole, core depth 2896′–2915′; Ryazanian, Denmark.

Olgosphaeridium sp. I
Figs. 6, 7. Slide Sp. E/1, Bed E, Speeton Clay, Ryazanian; Speeton, Yorkshire.
Fig. 8. Slide SAL 5009/1, Bed 6 (Casey 1973), Sandringham Sands; Ryazanian (*runctoni* Zone); Manor Farm, Norfolk.

Oligosphaeridium pulcherrimum sensu Ioannides et al. 1977
Fig. 9, Slide SAL 5426/1, North Wooton borehole, core depth 41.30 m; Kimmeridgian (*wheatleyensis* Zone). Note funnel-shaped processes, complexly and irregularly divided distally.

Stiphrosphaeridium dictyophorum (Cookson & Eisenack) comb. nov.
Figs. 10, 11. Slide 5009/2, Bed 6 (Casey 1973), Sandringham Sands; Ryazanian (*runctoni Zone*); Manor Farm, Norfolk.
Figs. 12, 13. Slide 5258/1, Bed 6 (Casey 1973), Sandringham Sands; Ryazanian (*runctoni* Zone); Manor Farm, Norfolk. 12, two paraplates bearing restricted annulate process complexes. 13, detached operculum having four, basically solid, processes.

Plate 2

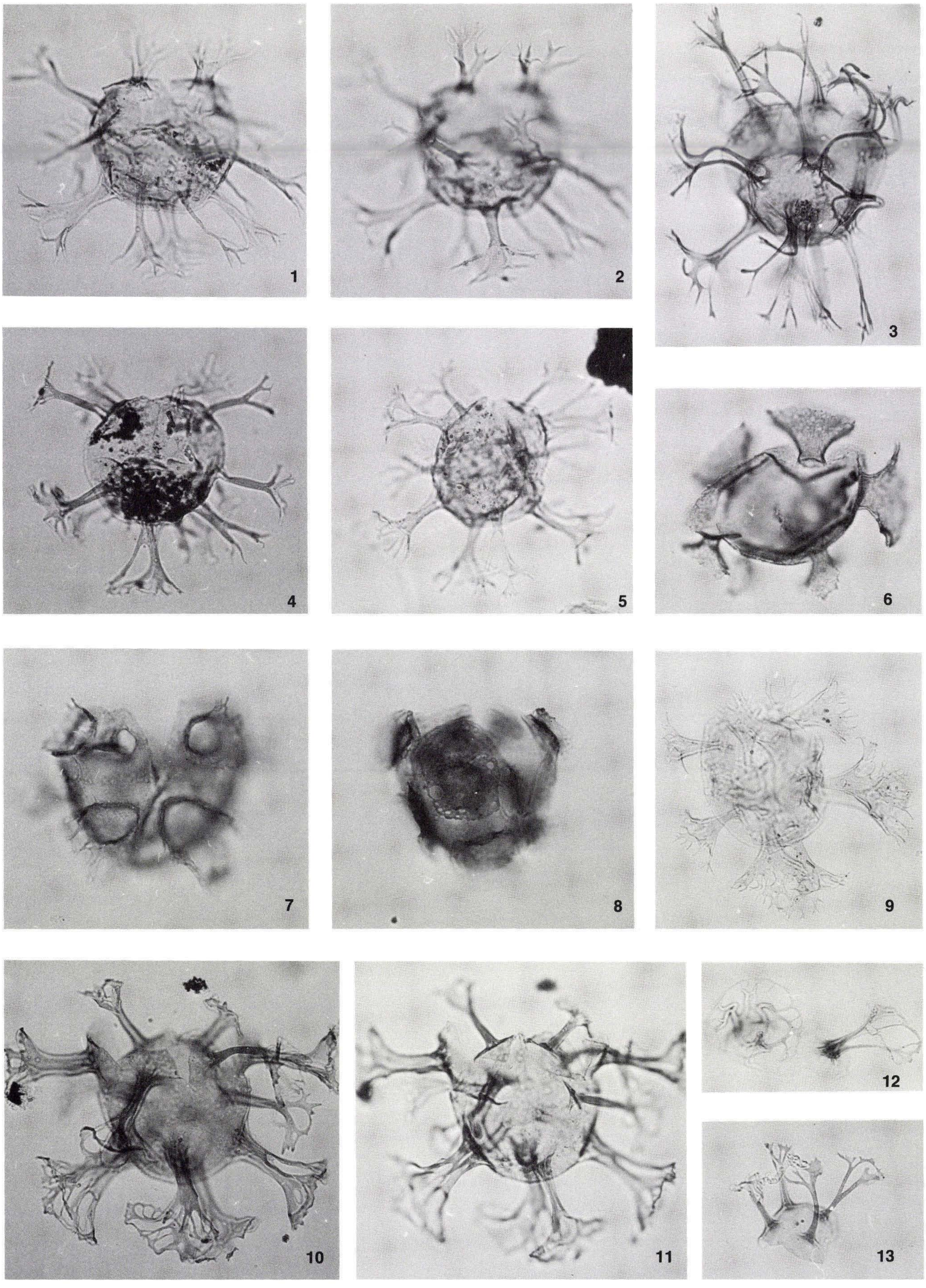

Plate 3

All magnifications ×500.

Stiphrosphaeridium arbustum sp. nov.
Figs. 1, 2. Slide SAL 4639/III, holotype.
Figs. 3, 4. Slide SAL 4639/I, Haldager No. 1 borehole, core depth 2896′–2915′; Ryazanian, Denmark.

Cymososphaeridium validum sp. nov.
Figs. 5, 8, 11. Slide 4628/I, holotype.
Fig. 6. Slide 4628/I, Haldager No. 1 borehole, core depth 2505′–25′; Hauterivian, Denmark. Interference contrast.

Surculosphaeridium sp. I
Fig. 7. Slide 4632/I, Haldager No. 1 borehole, core depth 2647′–57′; Valanginian, Denmark.
Fig. 10. Slide 4637/IV, Haldager No. 1 borehole, core depth 2832′–42′; early Valanginian – late Ryazanian, Denmark.

Cymososphaeridium sp. I
Figs. 9, 12. Slide Sp. D3 base/1′, Bed D3, Speeton Clay; early Valanginian; Speeton, Yorkshire.

Plate 3

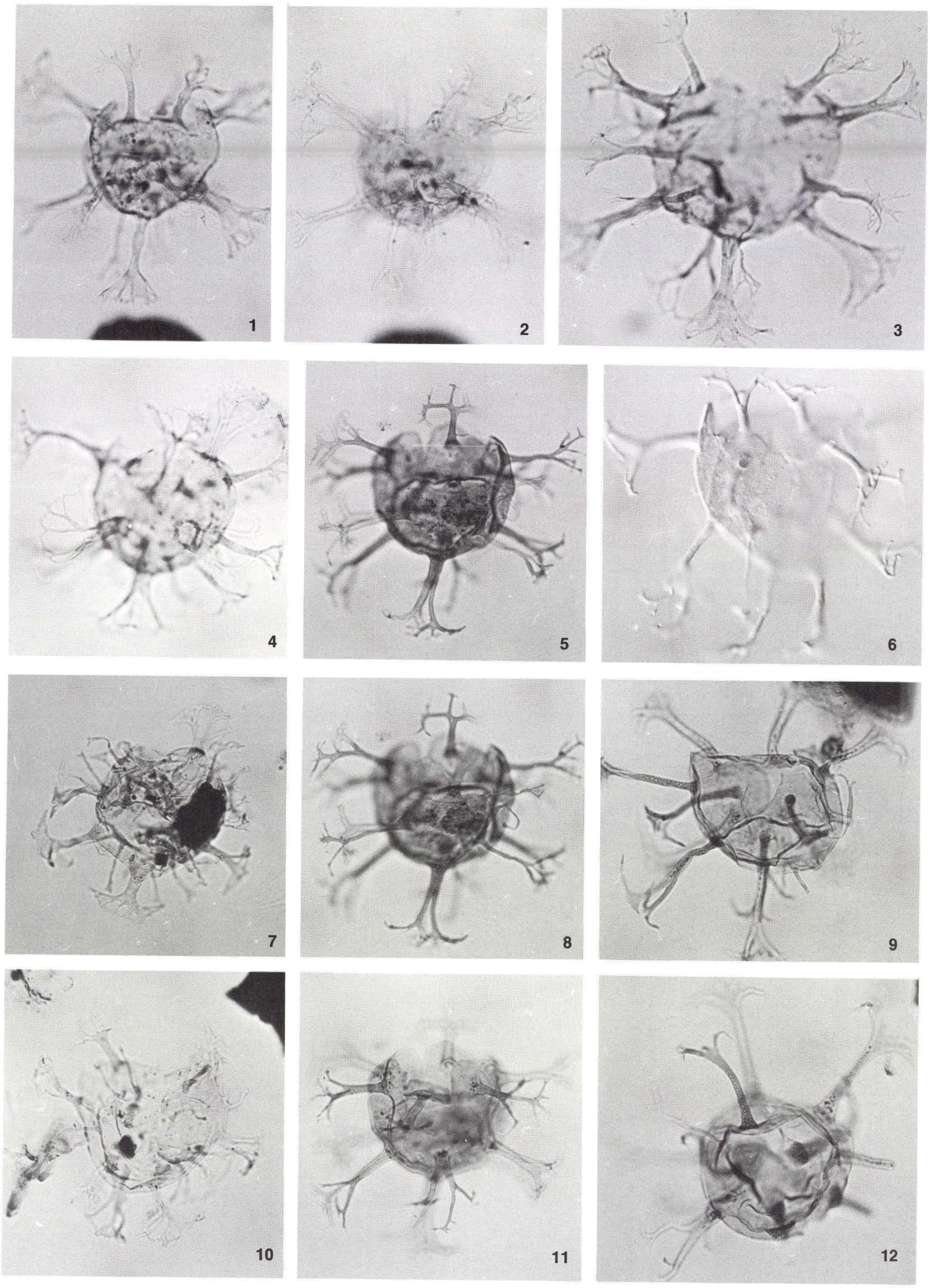

Plate 4

All magnifications ×500.

Surculosphaeridium sp. II

Fig. 1. Slide Sp. D3 middle/1, Bed D3, Speeton Clay; early Valanginian; Speeton, Yorkshire.

Fig. 2. Slide Sp. D4/1, Bed D4, Speeton Clay; early Valanginian; Speeton, Yorkshire.

Surculosphaeridium sp. III

Figs. 3, 4. Slide Sp. D4 pale stripe/3′, Bed D4, Speeton Clay; early Valanginian; Speeton, Yorkshire. 4, note clearly defined paracingular processes.

Figs. 5, 6. Slide Sp. D3 base/1′, Bed D3, Speeton Clay; early Valanginian; Speeton, Yorkshire. Note arcuate bases to larger processes.

Perisseiasphaeridium sp. I

Fig. 7. Slide SAL 5433/1, North Wooton borehold, core depth 55.50 m; Kimmeridgian (*autissiodorensis* Zone). Note very complexly branching tubiform processes and solid parasulcal and paracingular processes. Phase contrast.

Perisseiasphaeridium insolitum sp. nov.

Fig. 8. Slide SAL 5254/2, holotype.

Figs. 9, 10. Slide SAL 5254/1, Bed 1 (Casey 1973), Spilsby Sandstone, Portlandian ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire.

Cantulodinium speciosum Alberti

Fig. 11. Slide 4639/I, Haldager No. 1 borehole, core depth 2896′–2915′; Ryazanian, Denmark. Note the apparent loss of two intercalary paraplates in archaeopyle formation.

Pareodinia sp. I

Figs. 12, 13. Slide 4638/II, Haldager No. 1 borehole, core depth 2866′–76′; Ryazanian, Denmark. 13, interference contrast.

Fig. 14. Slide 4632/I, Haldager No. 1 borehole, core depth 2647′–57′; Valanginian, Denmark. Interference contrast.

Plate 4

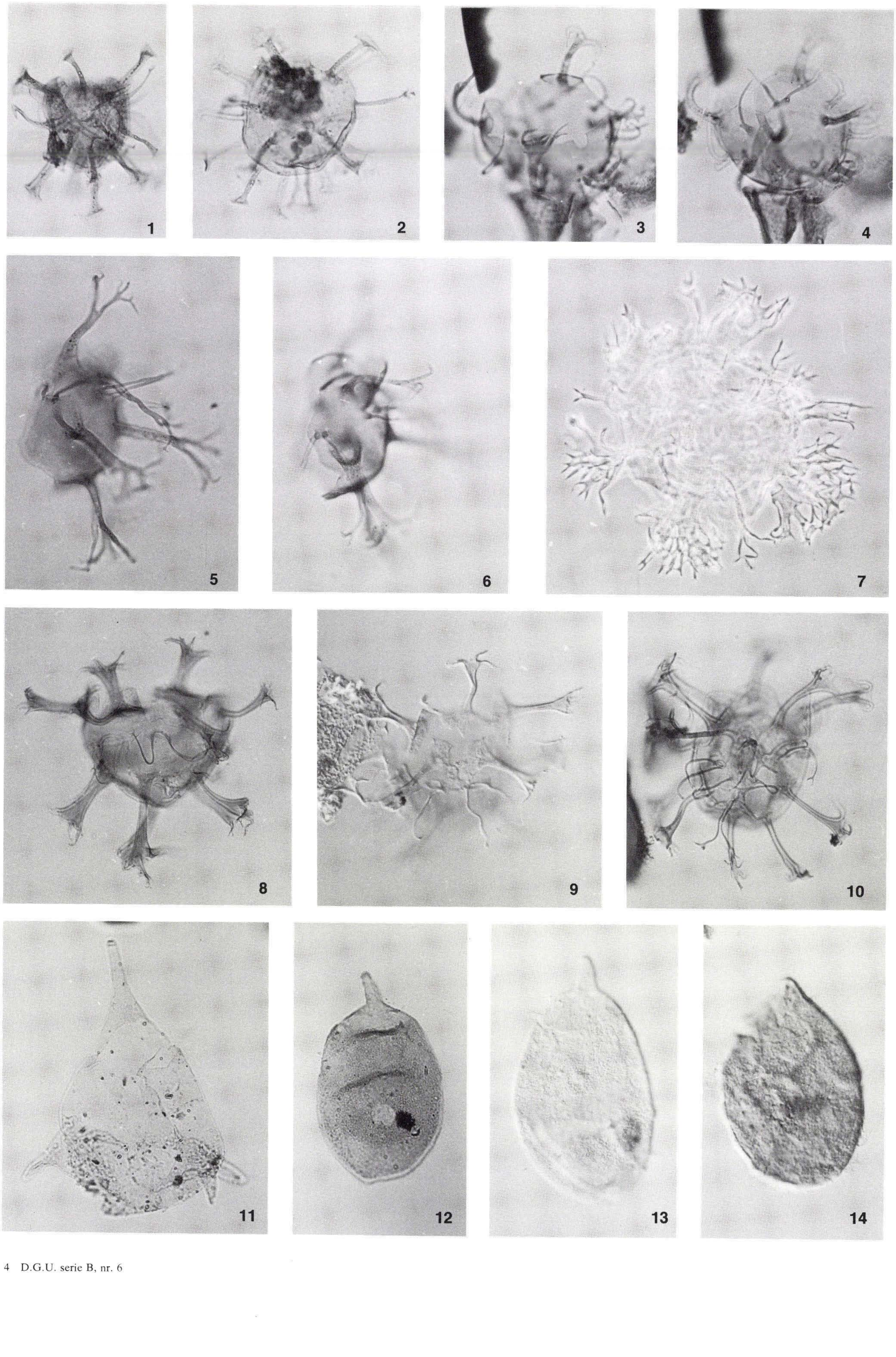

Plate 5
All magnifications ×500.

Batioladinium radiculatum sp. nov.
Fig. 1. Slide SAL 4640/I, Haldager No. 1 borehole, core depth 2935′–45′; Ryazanian, Denmark.
Fig. 7. Slide SAL 4640/II, Haldager No. 1 borehole, core depth 2935′–45′; Ryazanian, Denmark.
Fig. 8. Slide SAL 4640/I, holotype.
Fig. 9. Slide SAL 5258/1, Bed 6 (Casey 1973), Sandringham Sands; Ryazanian (*runctoni* Zone); Manor Farm, Norfolk. Apical archaeopyle developed.

Batioladinium pomum sp. nov.
Fig. 2. Slide SAL 4639/I, Haldager No. 1 borehole, core depth 2896′–2915′; Ryazanian, Denmark.
Fig. 3. Slide SAL 4640/I, holotype.
Fig. 4. Slide SAL 4638/II, Haldager No. 1 borehole, core depth 2866′–76′; Ryazanian, Denmark.

Batioladinium varigranosum (Duxbury) comb. nov.
Fig. 5. Slide Sp. D3 top/I', Bed D3, Speeton Clay; early Valanginian; Speeton, Yorkshire.
Fig. 6. Slide SAL 4628/I, Haldager No. 1 borehole, core depth 2505′–25′; Hauterivian, Denmark. Apical archaeopyle developed.

Batioladinium cf. *varigranosum* (Duxbury) comb. nov.
Fig. 10. Slide SAL 4640/I, Haldager No. 1 borehole, core depth 2935′–45′; Ryazanian, Denmark. Interference contrast.

Batioladinium sp. I
Fig. 11. Slide SAL 5260/4, Sandringham Sands; Ryazanian (*kochi* Zone); cut off channel, West Abbey Station, Norfolk. Apical archaeopyle developed.
Fig. 12. Slide Sp. D3 top/I′; Bed D3, Speeton Clay; early Valanginian; Speeton, Yorkshire. Apical archaeopyle developed.
Fig. 13. Slide Sp. D3 base/I′, Bed D3, Speeton Clay; early Valanginian; Speeton, Yorkshire. Apical archaeopyle developed.

Plate 5

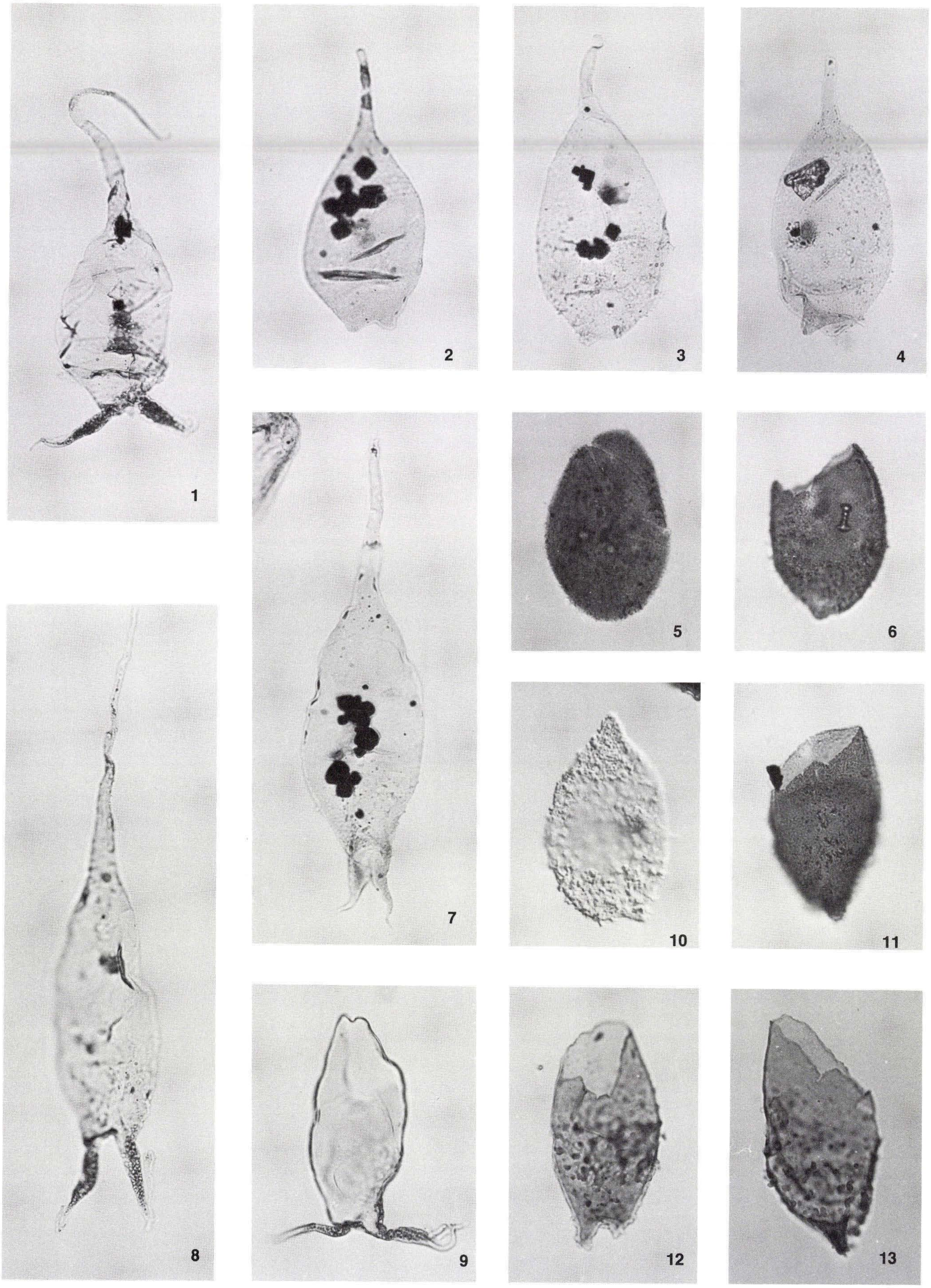

Plate 6

All magnifications ×500.

Gochteodinia villosa (Vozzhennikova) Norris

Fig. 1. Slide SAL 5259/2, Bed 10 (Casey 1973), Sandringham Sands; Ryazanian (*stenomphalus* Zone); Mintlyn Sands, Norfolk. Unusually large specimen.

Fig. 4. Slide SAL 5260/4, Sandringham Sands; Ryazanian (*kochi* Zone); cut off channel, West Abbey Station, Norfolk. Note bulbous extremities to the spines.

Fig. 5. Slide SAL 5254/1, Bed 1 (Casey 1973), Spilsby Sandstone, Portlandian ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire. Note very short, blunt spines.

Fig. 6. Slide SAL 4640/II, Haldager No. 1 borehole, core depth 2935′–45′; Ryazanian, Denmark. Note 2 I archaeopyle and short, acuminate processes. Interference contrast.

Gochteodinia virgula sp. nov.

Figs. 2, 7, 10. Slide SAL 5014/2, holotype.

Figs. 3, 8, 11. Slide SAL 5018/1, Haldager No. 1 borehole, core depth 2989′–3009′; Portlandian, Denmark.

Gochteodinia mutabilis (Fisher & Riley) comb. nov.

Figs. 9, 12. Slide SAL 5024/1, Haldager No. 1 borehole, core depth 3150′–60′; Portlandian, Denmark. Note short, very irregular spines.

Gochteodinia villosa subsp. *multifurcata* nov.

Fig. 13. Slide Sp. "Upper D4"/1′, type.

Gochteodinia sp. I

Fig. 14. Slide SAL 4641/II, Haldager No. 1 borehole, core depth 2969′–89′; early Ryazanian – late Portlandian, Denmark. Note distal trabeculae.

Fig. 15. Slide SAL 5018/1, Haldager No. 1 borehole, core depth 2989′–3009′; Portlandian, Denmark. Note branching processes with occasional trabeculae.

Plate 6

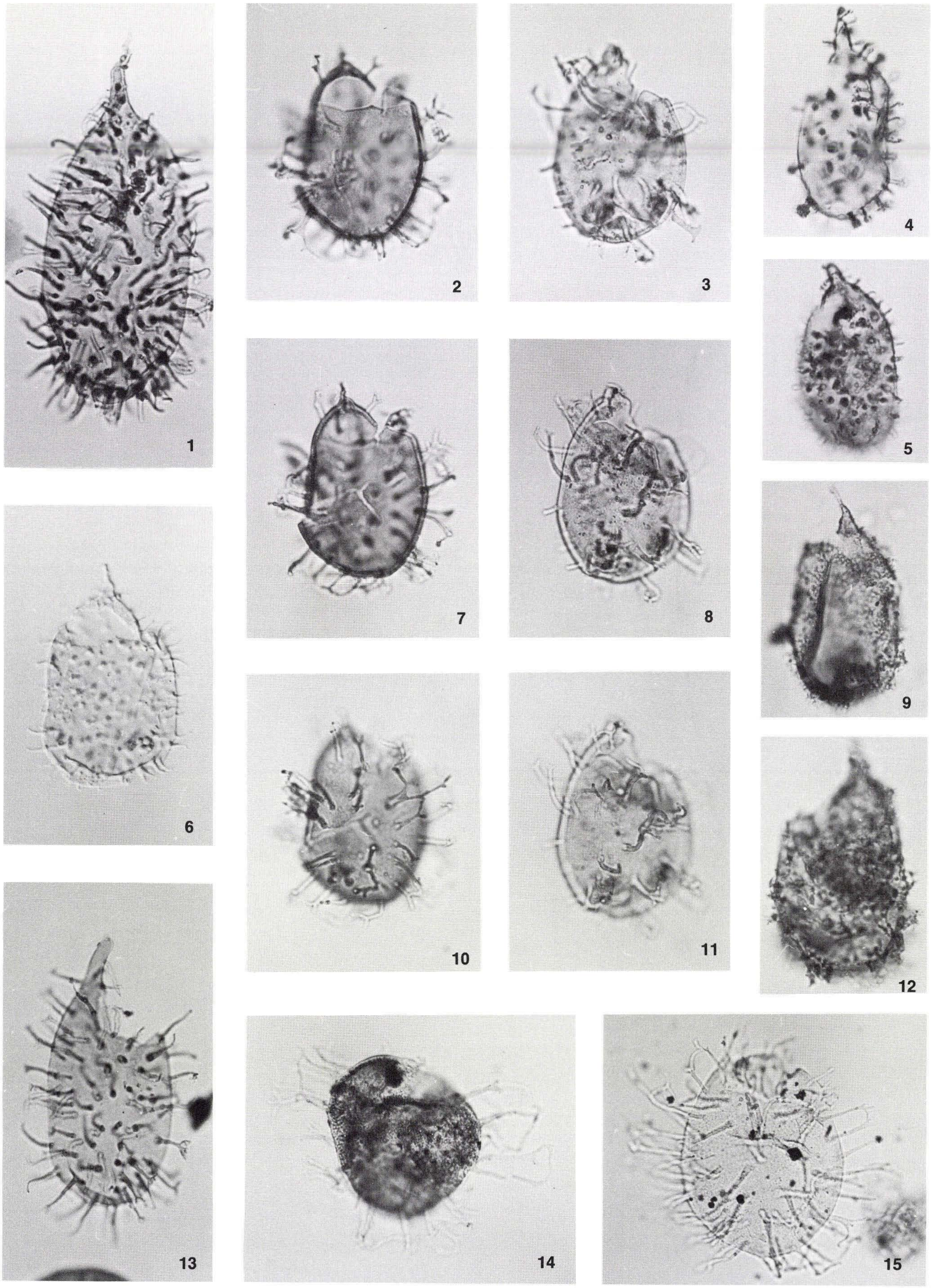

Plate 7

All magnifications ×500.

Gochteodinia sp. II

Figs. 1–4. Slide SAL 5254/1, Bed 1 (Casey 1973), Spilsby Sandstone; Portlandian ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire. 1, 2, 4, note peritabular crests.

Aprobolocysta neistosa Duxbury

Figs. 5, 6. Slide SAL 4629/3, Haldager No. 1 borehole, core depth 2545′–65′; Hauterivian, Denmark. 5, ventral view. 6, dorsal view.

Fig. 7. Slide Sp. D3 top/I′, Bed D3, Speeton Clay; early Valanginian; Speeton, Yorkshire.

Aldorfia spongiosa (McIntyre & Brideaux) comb. nov.

Fig. 8. Slide SAL 4641/II, Haldager No. 1 borehole, core depth 2969′–89′; early Ryazanian – late Portlandian, Denmark. Note large precingular archaeopyle and characteristic ornamentation.

Figs. 9, 10. Slide SAL 5254/1, Bed 1 (Casey 1973), Spilsby Sandstone; Portlandian ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire. 9, dorsal view with operculum partially detached. 10, ventral view.

Apteodinium sp. A

Fig. 11. Slide SAL 5254/1, Bed 1 (Casey 1973), Spilsby Sandstone; Portlandian ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire. Datached operculum; note pitted or perforate surface appearance.

Figs. 12, 16. Slide SAL 5254/3, Bed 1 (Casey 1973), Spilsby Sandstone; Portlandian ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire. 12, ventral view; note apical horn which is an extension of the wall. 16, medial view; note thick, spongy wall.

Aldorfia sp. A

Figs. 13–15. Slide SAL 5254/3, Bed 1 (Casey 1973), Spilsby Sandstone; Portlandian, ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire. 13, dorsal view. 14, ventral view. 15, medial view.

Plate 7

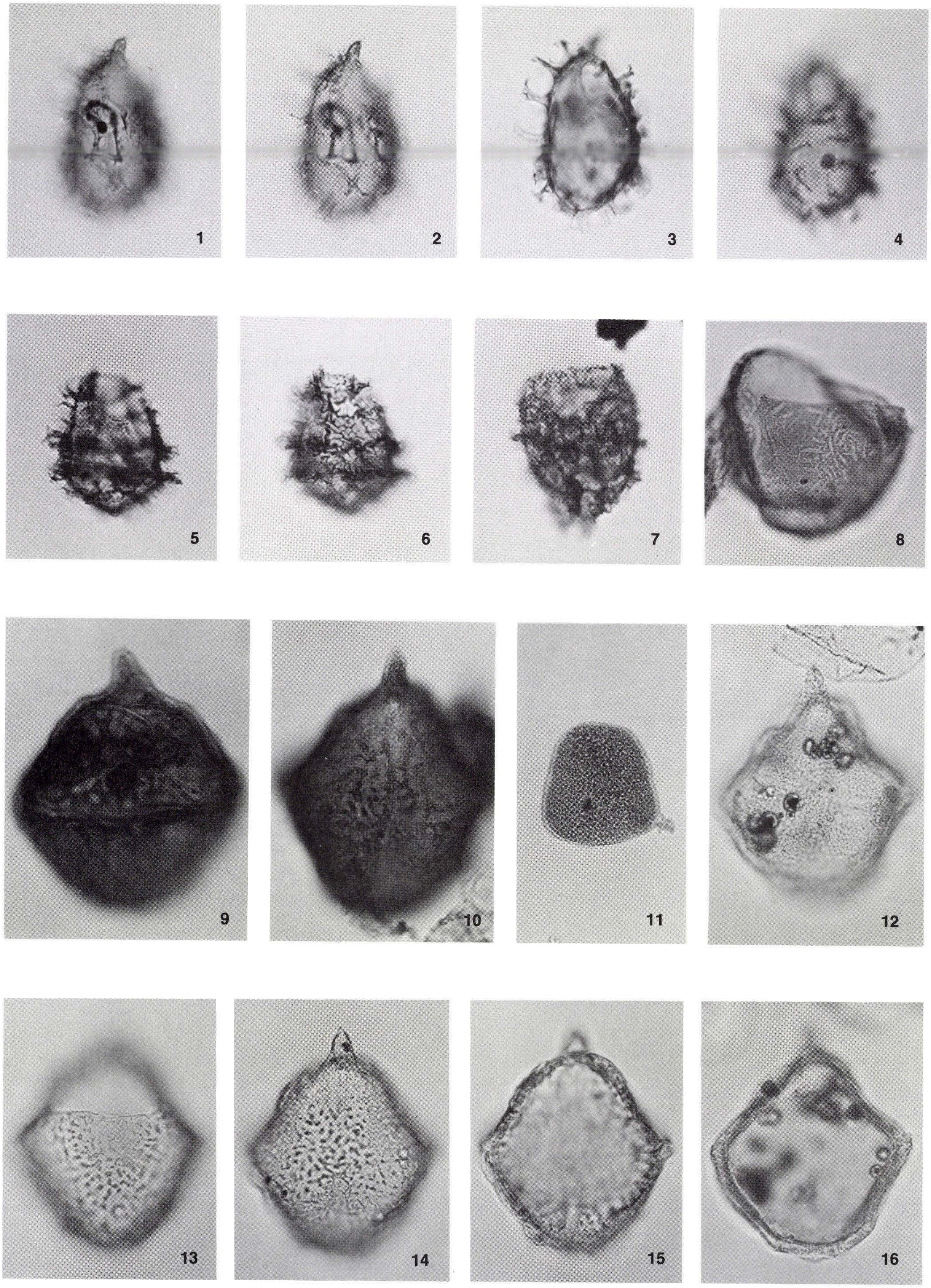

Plate 8

All magnifications ×500.

Isthmocystis distincta Duxbury

Fig. 1. Slide SAL 4629/4, Haldager No. 1 borehole, core depth 2545′–65′; Hauterivian, Denmark. Apical view; note detachment of precingular paraplates in archaeopyle formation, parasulcal/apical region still in place and membranous paracingular flange.

Fig. 2. Slide SAL 4628/1, Haldager No. 1 borehole, core depth 2505′–25′; Hauterivian, Denmark. Lateral view; apical region, with small apical horn visible, and attached to cyst by the parasulcal region.

Canningia compta sp. nov.

Fig. 3. Slide SAL 5011/1, holotype.

Figs. 4, 5. Slide SAL 5009/2, Bed 6 (Casey 1973), Sandringham Sands; Ryazanian (*runctoni* Zone); Manor Farm, Norfolk. 4, ventral view; note parasulcus and parasulcal notch.

Fig. 6. Slide SAL 4641/II, Haldager No. 1 borehole, core depth 2969′–89′; early Ryazanian – late Portlandian, Denmark. Complete specimen, with partially detached operculum.

Cannosphaeropsis thula sp. nov.

Fig. 7. Slide SAL 4641/I (MPK 1272), Haldager No. 1 borehole, core depth 2969′–89′; early Ryazanian – late Portlandian, Denmark. Lateral view; precingular archaeopyle to the northeast.

Figs. 8–11. Slide SAL 5260/4, holotype. 8, dorsal view. 9, dorso-medial view. 10, ventral view. 11, distal ventral view illustrating trabeculae.

Chlamydophorella membranoidea Vozzhennikova

Fig. 12. Slide SAL 5258/1, Bed 6 (Casey 1973), Sandringham Sands. Ryazanian (*runctoni* Zone); Manor Farm, Norfolk. Note offset antapical corona.

Egmontodinium expiratum sp. nov.

Figs. 13, 14. Slide GB 424/2, holotype. 13, dorsal view. 14, ventral view.

Fig. 15. Slide 5009/1, Bed 6 (Casey 1973), Sandringham Sands; Ryazanian (*runctoni* Zone); Manor Farm, Norfolk. A more spinose variety than usual although the crests are still clearly visible.

Fig. 16. Slide GB 424/1, Bed J (Arkell 1933), Cherty Series; Portlandian, *kerberus* Zone; Tilly Whim Caves, Dorset. Specimen with very reduced spines and a vacuolated appearance.

Plate 8

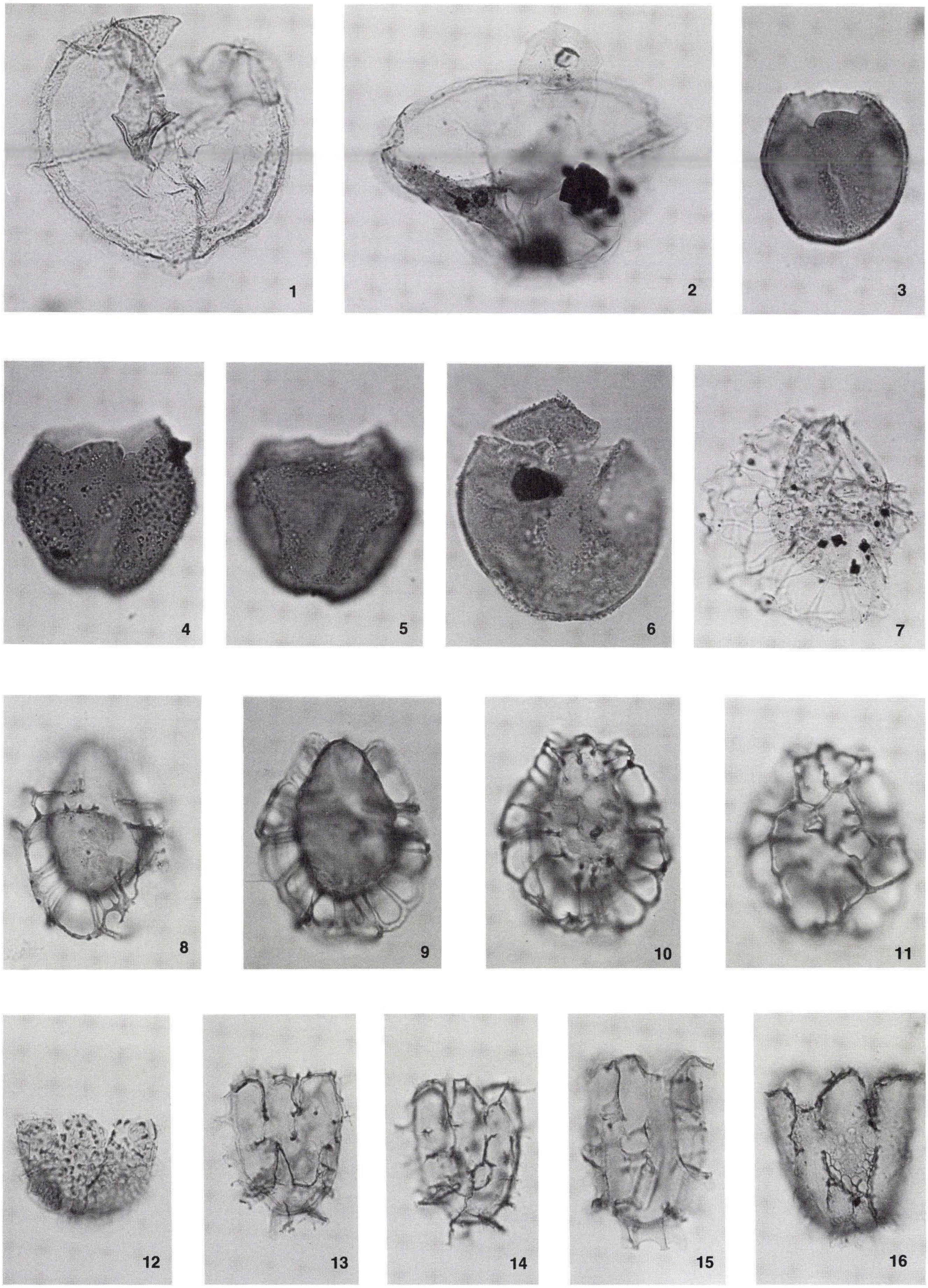

Plate 9
All magnifications ×500.

Muderongia sp. A sensu Davey
Figs. 1–3. Slide SAL 5254/1, Bed 1 (Casey 1973), Spilsby Sandstone; Portlandian ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire. 1, note irregular shape of the inner body. 2, dorsal view; note paratabulation. 3, ventral view.

Muderongia simplex subsp. *microperforata* subsp. nov.
Figs. 4, 5. Slide SAL 4637/III, type. Complete specimen.
Fig. 6. Slide SAL 4637/III, Haldager No. 1 borehole, core depth 2832′–42′; early Valanginian – late Ryazanian, Denmark. Note numerous, clearly defined perforations of the periphragm.

Spiniferites ramosus subsp. *primaevus* Duxbury
Figs. 7, 8. Slide SAL 4629/3, Haldager No. 1 borehole, core depth 2545′–65′; Hauterivian, Denmark. 7, detail of process terminations.

Spiniferites ramosus (Ehrenberg) Loeblich & Loeblich group
Fig. 9. Slide Sp. "Upper D4"/I', Bed D4, Speeton Clay; early Valanginian; Speeton, Yorkshire.

Dichadogonyaulax pannea (Norris) Sarjeant
Fig. 10. Slide SAL 5025/2, Haldager No. 1 borehole, core depth 3180′–90′; Portlandian, Denmark. Note posterior paracingular crest. Interference contrast.

Scriniodinium campanulum Gocht
Figs. 11, 12. Slide SAL 4629/4, Haldager No. 1 borehole, core depth 2545′–65′; Hauterivian, Denmark. 11, dorsal view. 12, ventral view.

Occisucysta tentoria Duxbury
Figs. 13, 14. Slide Sp. C11B/1, Bed C11, Speeton Clay; Hauterivian; Speeton, Yorkshire.

Plate 9

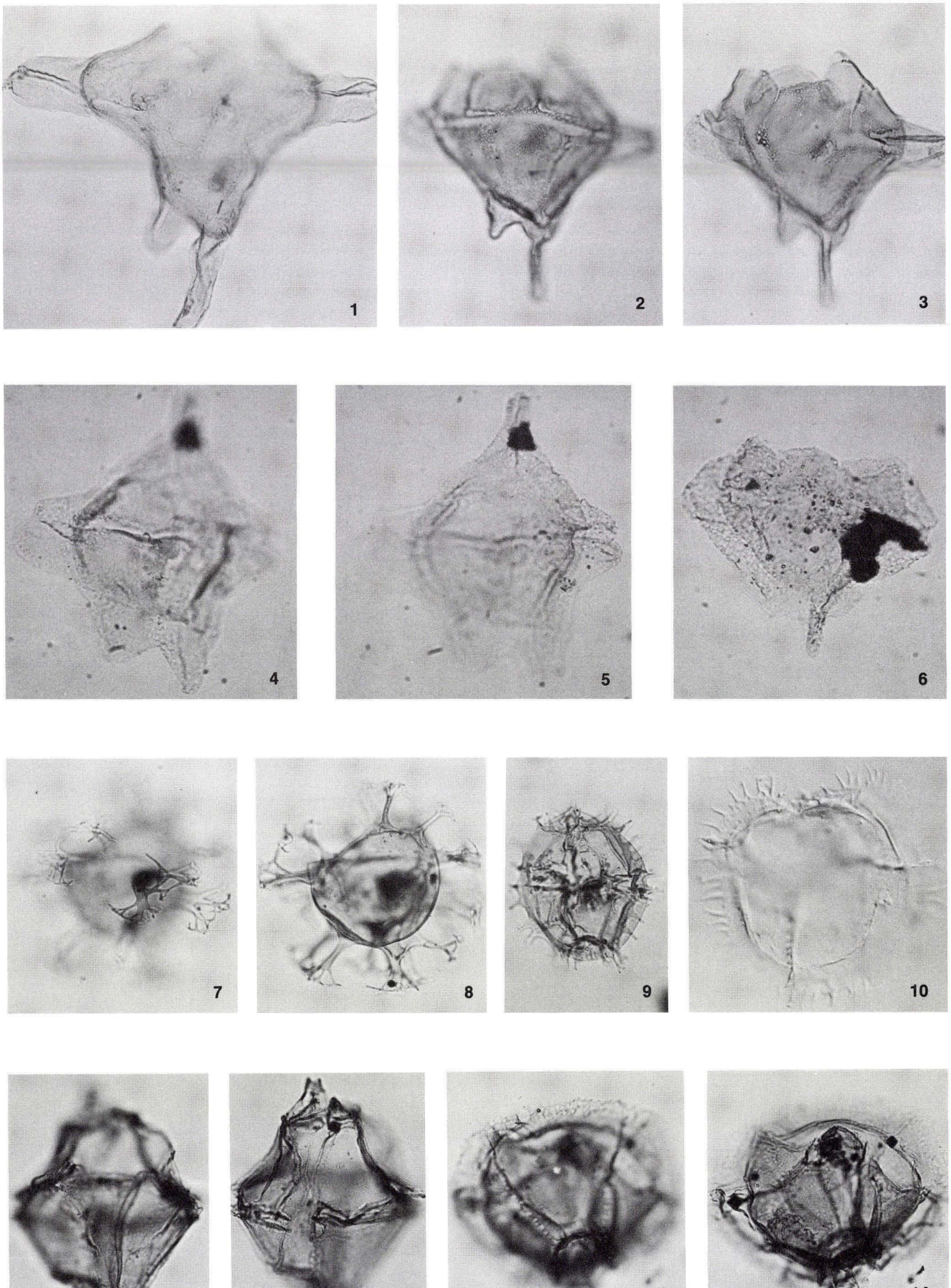

Plate 10

All magnifications ×500 unless otherwise stated.

Egmontodinium ovatum (Gitmez & Sarjeant) Riley

Figs. 1, 2. Slide GH 4/1, Kimmeridge Clay Formation; Kimmeridgian (*pectinatus* Zone); Golden Hill Pit, Yorkshire. 1, enlargement (×1500) to show process terminations; phase contrast.

Gonyaulacysta sp. A Davey

Fig. 3. Slide SAL 4639/II, Haldager No. 1 borehole, core depth 2896′–2915′; Ryazanian, Denmark.

Hystrichosphaeridium cf. *recurvatum* (White) Davey & Williams

Fig. 4. Slide SAL 4629/I, Haldager No. 1 borehole, core depth 2545′–65′; Hauterivian, Denmark.

Cribroperidinium sp. A

Figs. 5, 6. Slide SAL 5254/3, Bed 1 (Casey 1973), Spilsby Sandstone; Portlandian ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire. 5, detail of apical horn. 6, medial view.

Hystrichogonyaulax cf. *cladophora* (Deflandre) Stover & Evitt

Fig. 7. Slide SAL 4628/I, Haldager No. 1 borehole, core depth 2505′–25′; Hauterivian, Denmark.

Kleithriasphaeridium porosispinum sp. nov.

Fig. 8. Slide SAL 5254/3, Bed 1 (Casey 1973), Spilsby Sandstone; Portlandian ("*giganteus*" Zone); Nettleton Top Barn Pit, Lincolnshire. Note large precingular archaeopyle.

Fig. 9. Slide SAL 4639/II, Haldager No. 1 borehole, core depth 2896′–2915′; Ryazanian, Denmark. Note fibrous/perforate nature of process. ×1500, phase contrast.

Figs. 10–12. Slide GB 424/2, holotype.

? *Maduradinium* sp. A Davey

Fig. 13. Slide SAL 4629/4, Haldager No. 1 borehole, core depth 2545′–65′; Hauterivian, Denmark. Note granular apical, antapical and paracingular regions.

Occisucysta sp. A Davey

Fig. 14. Slide SAL 4634/III, Haldager No. 1 borehole, core depth 2752′–62′; early Valanginian, Denmark. Dorsal view showing 2P archaeopyle.

Fig. 15. Slide SAL 4637/IV, Haldager No. 1 borehole, core depth 2832′–42′; early Valanginian – late Ryazanian, Denmark. Lateral view showing well developed parasutural crests and intratabular ornamentation.

Pseudoceratium pelliferum Gocht

Fig. 16. Slide SAL 4636/I, Haldager No. 1 borehole, core depth 2822′–32′; early Valanginian – late Ryazanian, Denmark. Note the wide body and short horns of this early representative of this species. Phase contrast.

Plate 10