THE EVOLUTION OF CERTAIN UPPER CRETACEOUS HYSTRICHOSPHERES FROM SOUTH AFRICA

by Roger J. Davey

ABSTRACT

This paper traces clearly, for the first time, an evolutionary sequence in dinoflagellate cysts. The sedimentary samples containing the cysts are from northern Natal, South Africa, and are of Upper Cretaceous age. The genera concerned in this study are *Exochosphaeridium* Davey et al. (1966), *Cordosphaeridium* Eisenack (1963b) and an intermediary genus *Amphorosphaeridium* nov. Morphological changes exhibited by the cysts are related to ecological considerations and are shown to be directional; their stratigraphic usefulness is also discussed. In all one genus, three species and two varieties are erected.

INTRODUCTION

Sedimentary samples from the Cretaceous of northern Natal, South Africa, have yielded assemblages of dinoflagellate cysts in a good state of preservation. Eight samples from the upper part of the succession yielded particularly rich assemblages and proved to be of exceptional interest because of the presence of a number of related hystrichospheres—spiny dinoflagellate cysts. Previous micropalaeontological research in this region has dealt with coccoliths (Pienaar 1969) and foraminifera (de Gasparis, personal communication) and indicate that the above samples are of Upper Campanian, Maastrichtian and possibly Danian age. Some of the dinoflagellate cysts identified from the top of the succession have previously only been recorded from the Danian and Lower Palaeocene in other parts of the world (Davey 1969a). Thus younger sediments than have previously been presumed are probably present in this region.

Dinoflagellates are a class of predominantly marine phytoplankton which are typically only capable of very limited movement by means of two flagella. During one stage in their life-cycle encystment takes place and the abandoned cysts, it is believed, are the only dinoflagellate remains that are preserved in sedimentary deposits. The cysts, themselves, are incapable of any self-induced movement and thus are planktonic—drifting with the marine currents and slowly sinking due to the gravitational force. After a certain period has elapsed and environmental conditions are favourable, the dinoflagellate excysts and the next stage in the life-cycle proceeds. Since dinoflagellates are plants they require light for photosynthesis and hence excystment must take place in the photic zone of the sea, i.e. above approximately 300 feet depth. If the cyst sinks beneath this critical level of light intensity and excystment does take place then the dinoflagellate dies because of its inability to photosynthesise; if excystment does not take place death also results. Thus the survival of the encysted dinoflagellate depends to a large extent on its ability to remain suspended in the photic zone. This ability is discussed further in the final section of this paper, with special reference to the aforementioned hystrichospheres from Natal.

The Natal hystrichospheres are attributed to three genera—*Exochosphaeridium* Davey et al. (1966), *Amphorosphaeridium* nov. and *Cordosphaeridium* Eisenack (1963b). They are of a simple basic structure and thus the amount of morphological variation is strictly limited. Each cyst consists of a central or main body composed of two wall layers—an inner endophragm and an outer periphragm. A number of processes or spines are developed from the periphragm and stand more or less perpendicularly to the central body surface. It is only these structures which show morphological variation and vary with respect to their structure, size and numerical abundance. Change in any of these characters must be governed by natural selection and the change must be of such a nature that the cyst remains more or less in equilibrium with its environment. In the above mentioned hystrichospheres, change is demonstrably gradational and directional. The change of one variable necessitates a complementary change in one or more of the other variables in order that the cyst stays in environmental equilibrium. These morphological changes, their inter-relationships and the environmental consequences are dealt with in the final section of this paper; but firstly the classification and detailed morphology of these hystrichospheres must be appreciated. The latter considerations are examined in the systematic section which follows.

Systematics Section

Cyst-Family: EXOCHOSPHAERIDIACEAE Sarjeant and Downie amend.

Amended Diagnosis

Chorate to proximate cysts, spheroidal to ovoidal, bearing solid or hollow intratubular processes. Periphragm fibro-pitted. Distinct polar structures may be present but tabulation rarely discernible. Archaeopyle precingular (type P).

Type Genus

Exochosphaeridium Davey, Downie, Sarjeant and Williams, 1966.

Remarks

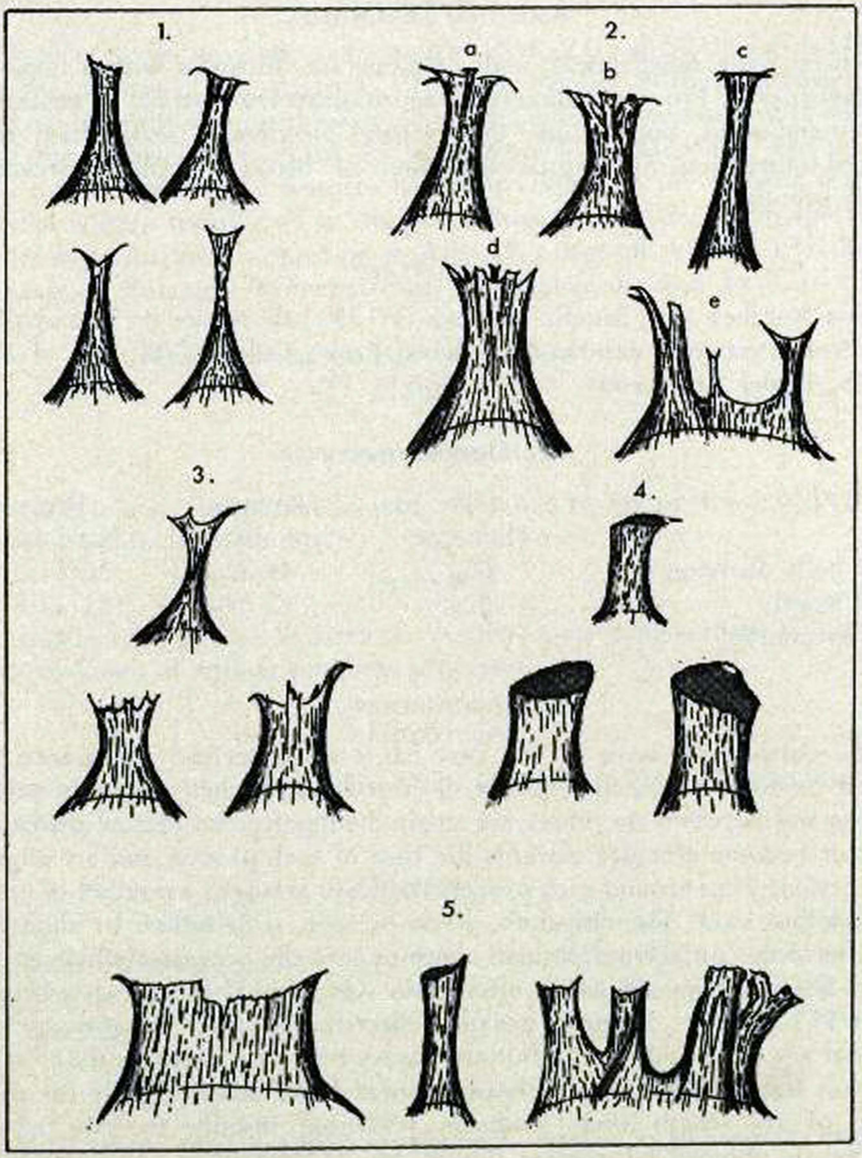
This cyst-family has been expanded to include all chorate to proximate dinoflagellate cysts possessing a precingular archaeopyle but without tabulation except for a weakly defined cingulum which is only rarely present.

Genus *EXOCHOSPHAERIDIUM* Davey et al. 1966.

Exochosphaeridium bifidum (Clarke & Verdier) comb. nov.

Pl. 1, figs. 1-5. Text-fig. 1, no. 1.

1967 *Baltisphaeridium bifidum* Clarke & Verdier: 72, pl. 17, figs. 5, 6; text-fig. 30.



TEXT-FIGURE 1

No. 1. Non-polar processes of *Exochosphaeridium bifidum* (Clarke and Verdier).

No. 2. a-c Non-polar processes of *Amphorosphaeridium fenestratum* sp. nov.
d Antapical process
e Apical process

No. 3. Non-polar processes of *Amphorosphaeridium multibrevum* sp. nov.

No. 4. Non-polar processes of *Amphorosphaeridium latitubulum* sp. nov.

No. 5. Non-polar processes of *Cordosphaeridium fibrospinosum* Davey and Williams.

Amended Diagnosis

Central body subspherical, wall of moderate thickness with a fibro-pitted periphragm layer. Processes numerous, approximately one-third of central body diameter and solid, but fibrous; they expand proximally, and distally to give a reduced bifurcation. Apical process distinctively broad. Precingular archaeopyle typically present.

Holotype

Slide Number 149; Sample Number CV 25. Laborataire de Micropaléontologie, École Practique des Hautes Études, Paris; Culver Cliff, Isle of Wight; Senonian, Upper Cretaceous.

Dimensions

	Holotype	Range of type material	Range of Natal material
Central body diameter ..	66μ	44-72μ	36(51.3)69μ
Process length..	22μ	13-34μ	11(17.8)24μ
No. of specimens			16

Description

The periphragm layer of the cyst has a characteristic appearance which may best be described as fibro-pitted. By this is meant that the outer wall layer is fibrous and between the fibres are situated subpolygonal pits or perforations. The latter become elongate towards the base of each process and are aligned in this direction. Thus around each process there are arranged a number of radiating pits of various sizes. The cingulum, when present, is delimited by aligned pits. The fibres of the surface periphragm continue into the processes which therefore are also fibrous. They are solid, often with subspherical vacuoles, and typically number 55 to 80, i.e. 3-4 processes per reflected plate area. The processes on an individual are of variable width but are always relatively narrow; they vary only slightly in length. Each has a relatively broad base, tapers rapidly for the first quarter of its length then gradually widening distally to give a simple expansion or reduced bifurcation (fig. 1, no. 1). Rarely one or two additional spines are present distally but these are always weakly developed and lie in a plane more or less parallel to the central body surface. Some alignment of the cingular processes may be present and they often occur in pairs which may be partially connected proximally. The sulcal region is often discernible. The sulcal processes are smaller and may be acuminate, but in other specimens sulcal processes are absent and normal processes, connected proximally, outline the sulcal region. The apical process is distinctively complex, broad and usually branches two or three times. The antapical process is apparently of normal process size and shape. The archaeopyle is of a typical precingular form.

Remarks

E. bifidum comb. nov. occurs in samples ZU6, ZU7 and ZU8 and is identical to the type material from England. Clarke & Verdier (1967), although commenting on the probable occurrence of a precingular archaeopyle and an apical process, placed this species in the acritarch genus *Baltisphaeridium*. The presence of these two morphological features has been verified in the present work and this species is here transferred to the genus *Exochosphaeridium*. (This species was incompletely transferred, according to Art. 33, paragraph 4 of the 1961 International Code of Botanical Nomenclature, to *Exochosphaeridium* by Clarke et al. (1968)).

Exochosphaeridium bifidum var. *involutum* nov.
Pl. 2, figs. 1, 3.

Derivation of Name

Latin, *involutus*, complicated—with reference to the presence of both solid and hollow processes.

Diagnosis

A variety of *E. bifidum* (Clarke & Verdier) possessing a small number (less than 50 per cent) of hollow tubiform processes.

Holotype

Bernard Price Institute Colln. slide ZU6/C0. Upper Cretaceous (Campanian/Maastrichtian).

Dimensions

	Holotype	Range
Central body diameter	$47 \times 49\mu$	$45(53.4)69\mu$
Process length	$18\text{-}21\mu$	$14(18.5)24\mu$
No. of specimens		10

Remarks

E. bifidum var. *involutum* nov. resembles *E. bifidum* in all respects except for the presence of hollow tubiform processes. The latter are always in the minority and usually represent less than 25 per cent. of the total processes. They are typically broader than the solid processes and often possess two to four strongly developed fibres which appear as longitudinal thickenings or ribs; they terminate distally with several patulate to recurved spines. As the number of tubiform processes increases, with respect to the solid processes, on specimens belonging to this variety the overall number of processes decreases.

E. bifidum var. *involutum* occurs in three samples from Natal, ZU6, ZU7 and ZU8.

Genus *AMPHOROSPHAERIDIUM* nov.

Derivation of Name

Latin, *amphorum*, two-handled jar; *sphaera*, ball—with reference to the ball-like central body and the two distinctive polar processes.

Diagnosis

Subspherical to ovoidal chorate dinoflagellate cysts possessing a two-layered wall. The periphragm layer is fibrous and variably pitted. Intratabular processes well developed. They are fibrous and typically hollow. Apical and usually antapical processes distinctive. Archaeopyle precingular (type P).

Type Species

Amphorosphaeridium fenestratum sp. nov. Upper Cretaceous (Campanian/Maastrichtian); South Africa.

Remarks

Members of *Amphorosphaeridium* differ from *Exochosphaeridium* Davey et al. (1966) by the possession of hollow and more complex processes, and usually a distinctive antapical process. *Cordosphaeridium* Eisenack (1963) is similar in overall form but does not have distinctive polar processes. *Amphorosphaeridium* appears to occupy a somewhat intermediate position between these two genera both in stratigraphic age and in morphology.

Amphorosphaeridium fenestratum sp. nov.

Pl. 1, fig. 6. Pl. 2, figs. 2, 4. Pl. 3, figs. 1-3. Text-fig. 1, no. 2 a-e.

Derivation of Name

Latin, *fenestrum*, window—with reference to the typical presence of an archaeopyle.

Diagnosis

Central body subspherical, wall moderately thick, fibrous and pitted. Processes one or two, rarely three, per plate-area, of variable width but constant length (approximately one-third central body diameter); they are typically hollow, tubiform and spinous distally. Apical process broad, branching; antapical process tubiform, distinctively large. Archaeopyle usually present.

Holotype

Bernard Price Institute Colln. slide ZU6/C8. Upper Cretaceous (Campanian/Maastrichtian).

Dimensions

	Holotype	Range
Central body diameter	57 x 64μ	52(59.6)77μ
Process length	25-27μ	19(21.3)27μ
No. of specimens		12

Description

The wall of the central body is 1 to 1.5μ thick and is fibrous with subpolygonal to elongate pits or perforations between the fibres. The cingulum, which is rarely present, may be delimited by parallel rows of aligned pits. The processes are also fibrous, the fibres of each process splaying out proximally over the surface of the central body. The majority of the processes are tubiform and are angular in cross-section, usually quadrilateral, due to three or four longitudinal ribs (fig. 1, no. 2a, b, d). Solid processes sometimes also occur but are always in a minority and are usually restricted to the sulcal region. The processes vary considerably in width on an individual and on different specimens depending mainly on the number of processes per plate-area present. The processes on specimens possessing one process per plate-area are typically broader than those with two or three per plate-area. Normally, however, there are one or two processes per plate-area and any additional ones are finer, perhaps solid, although being of equal length to the normal processes. The processes have broad bases and taper distally before expanding to produce a small number of spines. The latter of the tubiform processes are usually formed by extensions of the more strongly developed fibres (longitudinal ribs) of the processes and are often recurved to some extent. The broader processes are very rarely fenestrate. The sulcal region, as mentioned earlier, may either bear relatively fine solid processes or may be devoid of any processes. In the latter case this region is surrounded by normal processes which tend to be joined proximally and so clearly delimit it (Pl. 1, fig. 6). Some process alignment may be noticeable along the cingulum. The apical process is a broad fibrous structure which gives rise medially to two to four subsidiary processes; the antapical process is similar to the normal processes in structure but is larger. The archaeopyle is of a rounded triangular shape and is formed by the loss of the reflected precingular plate 3″—Type P of Evitt (1967).

Remarks

A. fenestratum sp. nov. is very similar to *Exochosphaeridium bifidum* in overall form, differing only in the possession of hollow processes and an enlarged antapical process. *E. bifidum* var. *involutum* is intermediate between these two species but is defined such that the majority of the processes are solid. *A. fenestratum* differs from *A. bipolare* comb. nov. (Cookson & Eisenack 1965) only in the shape of the antapical process which is tubiform in the former and acuminate in the latter. The processes of *A. axiale* comb. nov. (Eisenack 1965) are similar to those of *A. fenestratum* but they differ in the form of the apical process.

A. fenestratum occurs in two samples, ZU5 and ZU6, and is particularly abundant in the former sample.

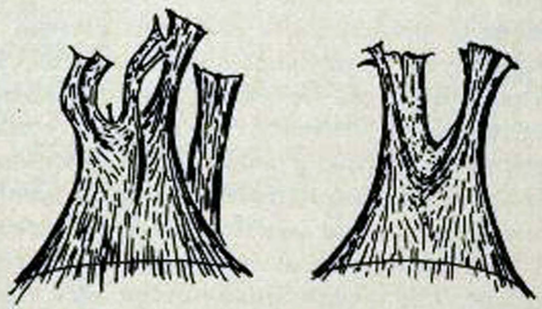
Amphorosphaeridium fenestratum var. *dividum* nov.
Pl. 2, figs. 5, 6. Text-fig. 2.

Derivation of Name

Latin, *dividus*, separated or divided—with reference to the branched nature of the processes.

Diagnosis

A variety of *A. fenestratum* Davey possessing strongly developed processes which are sometimes branched.



TEXT-FIGURE 2
Processes of *Amphorosphaeridium fenestratum* var. *dividum* nov.

Holotype

Bernard Price Institute Colln. slide ZU5/C4. Upper Cretaceous (Campanian/Maastrichtian).

Dimensions

	Holotype	Range
Central body diameter	56 x 63μ	50(60.1)77μ
Process length	28μ	25(27.0)31μ
No. of specimens		10

Description

The proportion of branched to unbranched processes varies considerably—from two to three to over half the processes may be affected. Normally the process bifurcates simply, either proximally or medially, but occasionally each branch in turn subdivides once or twice more. Thus one process may give rise to as many as six branches, all of which terminate at a more or less constant distance from the central body. The finer processes appear to be solid and terminate more simply than the tubiform processes. There are one to two processes per plate-area.

Remarks

A. fenestratum var. *dividum* nov. differs from *A. fenestratum* by the possession of branched processes. An additional difference is that the processes of the former are, on the average, longer than those of *A. fenestratum*. The two mean lengths are respectively 29.0μ and 21.3μ.

A. fenestratum var. *dividum* occurs in two samples, ZU5 and ZU6. In the former it is a rare variant whereas in the latter sample it is the most abundant one but is still rare since the assemblage obtained from this sample was extremely meagre.

Amphorosphaeridium multibrevum sp. nov.

Pl. 3, figs. 5, 6. Pl. 4, fig. 1. Text-fig. 1, no. 3.

Derivation of Name

Latin, *multus*, much; *brevis*, short—with reference to the large number of short processes present in this species.

Diagnosis

Central body subspherical, wall fibrous and pitted. Processes numerous, four, rarely three, per plate area; hollow, tubiform and spinous distally. They are relatively short (approximately one-quarter central body diameter), of constant length but variable width. Apical and antapical processes not very distinctive. Archaeopyle typically present.

Holotype

Bernard Price Institute Colln. slide ZU4/C3. Upper Cretaceous (Campanian/Maastrichtian).

Dimensions

	Holotype	Range
Central body diameter	54 x 57μ	47(58.1)73μ
Process length	13μ	12(14.0)18μ
No. of specimens		10

Description

The structure of the processes is similar to that of the processes of *A. fenestratum* except that they are shorter and may be joined proximally. Distally the processes are spinous, the spines on one side of each process typically being longer than those of the other side (fig. 1, no. 3). The apical and antapical processes are similar in height to the normal processes and are, thus, rather difficult to distinguish. The antapical process is slightly larger than the surrounding processes whereas the apical process is considerably broader and more complex. The cingulum is discernible on some specimens and is delimited by two parallel rows of processes.

Remarks

A. multibrevum sp. nov. differs from *A fenestratum* mainly in the possession of shorter and more numerous processes. It has been recorded from samples ZU2, ZU3, and ZU4.

Amphorosphaeridum latitubulum sp. nov.

Pl. 4, figs. 2, 7. Text-fig, 1, no. 4.

Derivation of Name

Latin, *latus*, broad; *tubulatus*, tubular—with reference to the broad, tubular processes.

Diagnosis

Central body ovoidal bearing two, rarely three, fibrous processes per plate-area, Processes tubiform, short (less than one-quarter central body diameter), of variable width with entire distal margins. Apical process broad and branched; antapical process relatively large and tubiform. Archaeopyle typically present.

Holotype

Bernard Price Institute Colln. slide ZU3/C6. Upper Cretaceous (Campanian ?/Maastrichtian).

Dimensions

	Holotype	Range
Central body diameter	49 x 56μ	49(60.6)73μ
Process length	11μ	11(13.0)15μ
No. of specimens		10

Description

The ovoidal central body is elongated along the polar axis and possesses the fibro-pitted periphragm typical of this genus. The short tubiform processes, although being of constant length, are extremely variable in width. The processes possess longitudinal fibres which extend on to the surface of the central body. The walls of the processes, however, are weak and distortion is common. Distally the processes expand slightly and typically have an entire undulatory margin (fig. 1, no. 4), but very occasionally one or two processes may bear spines. The cingulum is sometimes aligned by pits or processes. The apical process is abnormally broad proximally and typically subdivides into two or three branches either proximally or medially.

Remarks

A. latitubulum sp. nov. in overall appearance most closely resembles *A. multibrevum*. They differ primarily in that the processes of the latter species are often ribbed and are spinous distally. The processes of the former also are more variable in width and fewer in number.

A. latitubulum occurs only in three samples examined, ZU1, ZU2 and ZU3.

Other Species

The following two species are here included in *Amphorosphaeridium* gen. nov. on the basis of the type of processes, the polar structure(s) and the precingular archaeopyle:

Amphorosphaeridium axiale (Eisenack 1965), p. 150 (as *Cordosphaeridium axiale*) in *Neues. Jb. Geol. Paläont., Abh.*, **123**, pt. 2, pp. 149-159.

Amphorosphaeridium bipolare (Cookson & Eisenack 1965), p.135 (as *Cordosphaeridium bipolare*) *in Proc. R. Soc. Vict.* **79,** pt. 1, pp. 133-137.

Genus: CORDOSPHAERIDIUM Eisenack 1963 amend.

Amended Diagnosis

Chorate, subspherical dinoflagellate cysts possessing a two-layered wall. The periphragm is fibrous and variably pitted, and gives rise to well developed intratabular fibrous processes. Polar processes not distinctive. Archaeopyle precingular (type P).

Type Species

Cordosphaeridium inodes (Klumpp 1953) Eisenack 1963. Eocene, Germany.

Remarks

The archaeopyle of *Cordosphaeridium* was previously considered to be formed by the loss of a single apical plate (Davey & Williams 1966b). However, detailed morphological and evolutionary studies reported in the present paper now show conclusively that the archaeopyle is precingular and is formed by the loss of a single plate corresponding to the precingular thecal plate 3″. The shape of the archaeopyle may be polygonal (six-sided), but is more usually that of a triangle with rounded apices—a shape typically associated with precingular archaeopyles. This kind of archaeopyle was termed "type P" by Evitt (1967). The fibro-pitted nature of the periphragm appears to be exhibited by all members of this genus and is, thus, included in the diagnosis.

Cordosphaeridium differs from *Exochosphaeridium* and *Amphorosphaeridium* by the absence of distinctive, abnormally large or complex polar structures. The lack of these structures causes orientation difficulties and was the reason for the misidentification of the archaeopyle position. Orientation may now be effected by the utilisation of archaeopyle shape.

Cordosphaeridium fibrospinosum Davey & Williams 1966b.
Pl. 3, fig. 4, Pl. 4, fig. 5. Text-fig. 1, no. 5.

1966 *Cordosphaeridium fibrospinosum* Davey & Williams: p. 86, pl. 5, fig. 5.

Revised Diagnosis

Central body ovoidal with wall up to 0.5μ thick, composed of smooth endophragm and fibro-pitted periphragm. Processes fibrous, one per plate-area, often very broad and ovoidal in cross-section; walls perforate. Processes open distally with entire or undulose margin. Archaeopyle typically present.

Dimensions

	Range
Central body diameter	49-63μ
Process length	14-20μ
No. of specimens	6

Description

This species is characterised by a thin-walled fibro-pitted central body and one process per plate-area. The width of the processes is variable and may sometimes be equal to the process length. Their length on each specimen is more or less constant and approximately equal to one-third of the central body diameter. The processes are typically tubiform but occasionally they do subdivide distally. The walls of the processes are extremely fine and fibrous, and usually appear to be fenestrate or perforate. The apical and antapical processes appear to be of equal size to the remaining processes.

Remarks

The diagnosis of this species has been revised such that the possession of an apical archaeopyle has been omitted. The specimens from northern Natal agree very well with the type material from the London Clay (Lower Eocene, Ypresian) of southern England. *C. fibrospinosum* differs from *C. axilimurum* Davey & Williams (1966b) by the absence of fine processes and by the relatively broader processes.

C. fibrospinosum was recorded in three samples, ZU1, ZU2 and ZU3.

Cordosphaeridium sp.
Pl. 4, figs. 3, 4, 6.

Description

Two specimens have been located, one each in samples ZU1 and ZU2, which may not be attributed to any previously described species. The central body is subspherical possessing a wall of moderate thickness and a fibro-pitted periphragm layer. The processes, one or two per plate-area, are extremely fibrous, delicate and typically fenestrate. They are basically tubiform and broaden slightly both proximally and distally. All are of similar length but vary considerably in width. The narrow processes terminate distally with an entire, serrate or spinous margin. The broader processes are more complex and may divide medially or distally into two to four branches. They splay out distally and are serrate or spinous. The apical and antapical processes are not distinctive. The archaeopyle is of a rounded triangular shape and is precingular in position.

Dimensions

	Central body diameter	Process length
Pl. 4, fig. 3	51 x 56μ	Up to 20μ
Pl. 4, fig. 4	42 x 56μ	Up to 19μ

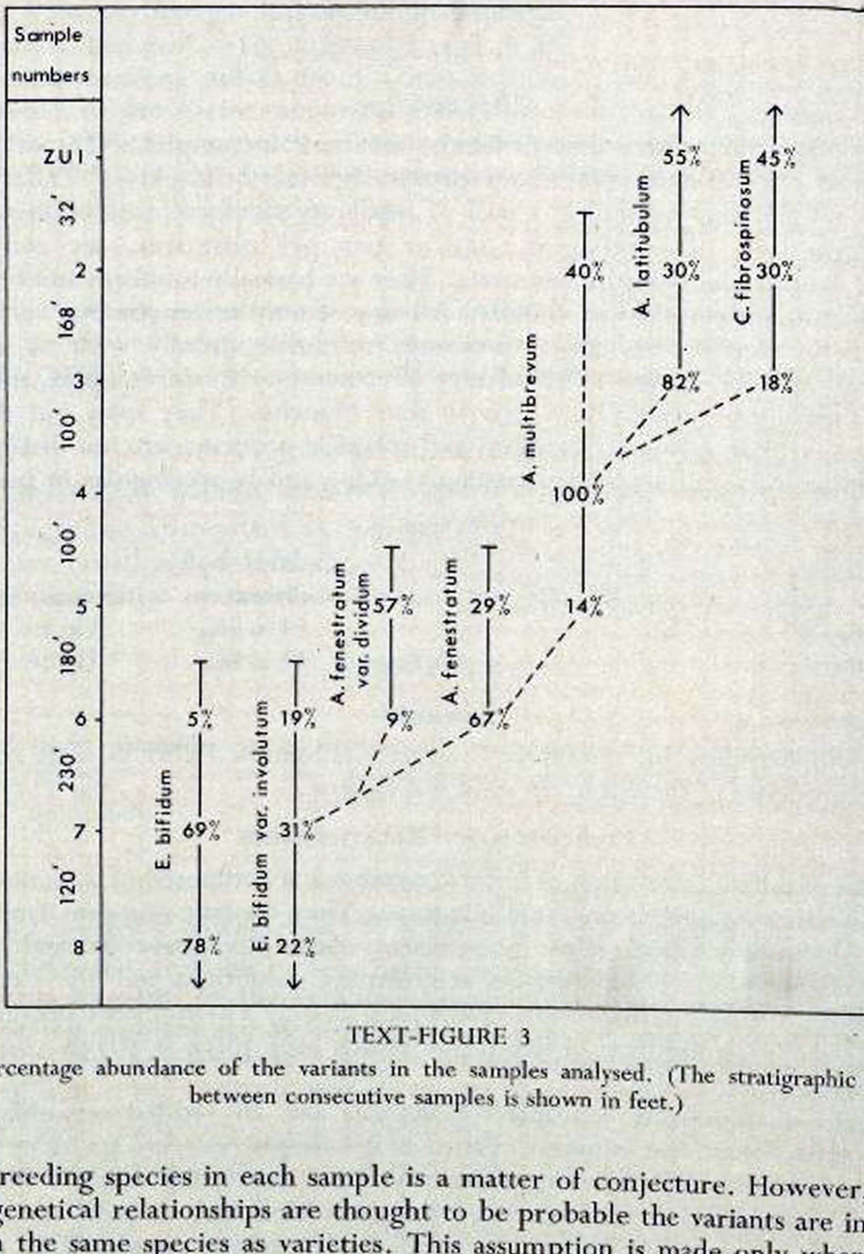
Remarks

Cordosphaeridium sp. resembles *C. gracilis* (Eisenack 1938) in most respects but the processes of the latter are solid not hollow.

Evolutionary Relationships

The examined succession of Natal Cretaceous is composed of a monotonous series of calcareous mudstones and siltstones. They contain abundant land-plant debris, spores and pollen grains, foraminifera, coccoliths, ostracodes and various molluscan remains. The unchanging sedimentary conditions and the flora and fauna indicate that a rather stable subtropical marine environment prevailed in this region during the time of deposition which took place relatively close to a land mass.

Eight samples were available for analysis and all yielded assemblages of dinoflagellate cysts. One group of related hystrichospheres were found in all the samples and their detailed examination yielded interesting results. Morphological studies enabled this group to be subdivided into a small number of distinct and recognisable variants. In each sample (except sample ZU4) two to four variants could be identified although a certain amount of overlap and gradation between the variants existed. Each variant occurred in more than one sample and it was clear that any new variant had evolved from one of the pre-existing variants. The percentage abundance of each variant was calculated with respect to the other variants in that sample and abundance trends may be traced as the succession is ascended (see fig. 3). Which of the variants formed a natural,



TEXT-FIGURE 3

The percentage abundance of the variants in the samples analysed. (The stratigraphic distance between consecutive samples is shown in feet.)

interbreeding species in each sample is a matter of conjecture. However, when such genetical relationships are thought to be probable the variants are included within the same species as varieties. This assumption is made only when intermediary forms are present linking the two variants, as for instance with *E. bifidum* and *E. bifidum* var. *involutum*.

The species and varieties of hystrichosphere described in the systematics section are placed in the cyst-family Exochosphaeridiaceae, which is, at present, restricted to the Upper Cretaceous and Tertiary. Members of this cyst-family are characterised by the possession of intratabular processes, a precingular

TABLE 1

PROCESS VARIATION IN THE VARIANTS DESCRIBED

	E. bifidum	*E. bifidum* var. *involutum*	*A. fenestratum*	*A. fenestratum* var. *dividum*	*A. multibrevum*	*A. latitubulum*	*C. fibrospinosum*
Type of processes	Solid	Solid and Hollow	Hollow and Solid	Hollow and Solid	Hollow	Hollow	Hollow
Length of processes	Long	Long	Long	Longer	Short	Short	Short
Breadth of processes	Narrow	Narrow	Narrow	Narrow	Narrow	Moderately Broad	Broad
No. of processes per plate-area	3-4	2-4	1-	1-2	3-4	2-3	1
Presence of fenestrate process walls	Absent	Absent	Very rare	Very rare	Very rare	Rare	Abundant

archaeopyle and a fibro-pitted periphragm layer. Cyst variability is exhibited chiefly in the structure, length, breadth and number of processes and by the presence or absence of distinctive polar structures. It is these factors which vary in the assemblages examined.

E. bifidum has previously been recorded throughout most of the Upper Cretaceous (Cenomanian-Campanian) of the Isle of Wight, England, by Clarke & Verdier (1967). In Natal is only occurs in the lower three samples here discussed (ZU6, ZU7 and ZU8) and progressively decreases in percentage abundance, at the expense of its variety, as the succession is ascended. *E. bifidum* is characterised by numerous long solid processes and its variety, *E. bifidum* var. *involutum*, by fewer processes, of similar length, but also by the presence of hollow processes which are of necessity broader (see fig. 1 and table 1). In sample ZU6 a new variant, *A. fenestratum*, occurs which possesses predominantly hollow processes. The latter species has been placed in a new genus since *Exochosphaeridium* is restricted to forms possessing solid processes. There is, in fact, a complete gradation between *E. bifidum* var. *involutum*, possessing few hollow processes, and *A. fenestratum*, possessing few solid processes, but specimens exactly intermediate in character, i.e. having equal number of both types of processes, are exceedingly rare. Accompanying this change in process structure is a decrease in the number of processes.

A. fenestratum var. *dividum*, occurring in samples ZU6 and ZU5, appears to be an offshoot from the main line of evolution in which branching of the processes is present. In addition this variety illustrates an increase in process length when compared with *A. fenestratum* and a decrease in process number.

A. multibrevum, possessing relatively numerous but short processes, first appears in sample ZU5 and in sample ZU4 is the only form present. From this species are derived *A. latitubulum* and *C. fibrospinosum* which are present in the upper three samples—ZU1, ZU2 and ZU3. *A. latitubulum* differs from *A. multibrevum* in that although the relatively short processes are retained, their breadth is usually greater and they are fewer in number. *C. fibrospinosum* is characterised by short broad processes, few in number, with fenestrate walls.

The study of these variants show that the evolution of this group of hystrichospheres is governed by a small number of morphological variables. Basically evolutionary change was from a form with numerous solid long narrow processes (*E. bifidum*) to one with few hollow short broad processes (*C. fibrospinosum*). This is by no means a direct simple line of descent but rather one in which various combinations of process type have been tried, then retained or discarded. The gradual change in the structure and number of processes is clearly shown in table 1. There apparently are four major breakthroughs in process form—the change from solid to hollow processes; in relative length, from long to short; in relative width, from narrow to broad; and in the ability of the processes to have fenestrate walls. These changes are throughout accompanied by and govern the variation in process number.

The evolution of any group of organisms is a slow and gradual process taking place over an extensive period of time. The organism evolves towards a goal that is seldom, if ever, attained—that is to be in perfect equilibrium with its environment. In the examples under discussion change has almost entirely been confined to the processes and it is these that govern the ability of the encysted dinoflagellate to remain in a favourable environment, that is the oceanic photic zone (see Introduction and Davey 1969b). Thus a change of any single variable necessitated a compensatory change in one or more of the other variables so that the cyst could remain in the same favourable environment. It is evident from the information available that a change from solid to hollow processes permits a corresponding decrease in the number of processes without detracting from the flotation qualities of the cyst. However, with the change from long hollow processes to relatively short hollow processes the number required for stability in the photic zone had to be again increased. In *A. multibrevum* the processes become broader and finally extremely broad in *C. fibrospinosum* with a corresponding decrease in the number of processes. The latter species possesses an additional characteristic which is often present in later species of this genus, that of fenestrate process walls. Presumably this characteristic increases the buoyancy of the cyst.

The above study traces clearly, for the first time, an evolutionary sequence in dinoflagellate cysts. The genus *Cordosphaeridium* is shown to evolve from the genus *Exochosphaeridium* via the intermediary genus *Amphorosphaeridium*. The structural changes in this sequence are gradational and may be directly related to environmental conditions. Each variant has a limited stratigraphic range (fig. 3) and in addition at any particular horizon the variants are in definite proportions to one another. Thus, such an evolutionary sequence is of great taxonomic and stratigraphic value.

References

Clarke, R. F. A., Davey, R. J., Sarjeant, W. A. S. and Verdier, J. P., 1968. A Note on the Nomenclature of some Upper Cretaceous Dinoflagellate Taxa. *Taxon*, **17**: 181-3.

Clarke, R. F. A. and Verdier, J. P., 1967. An investigation of microplankton assemblages from the chalk of the Isle of Wight, England. *Verh. K. ned. Akad. Wet.*, **24**: (3): 1-96, pls. 1-17.

Cookson, I. C. and Eisenack, A., 1965. Microplankton from the Dartmoor Formation, S.W. Victoria. *Proc. R. Soc. Vict.* **79**: 133-137.

Davey, R. J., 1969a. Non-Calcareous Microplankton from the Cenomanian of England, northern France and North America. *Bull. Br. Mus. nat. Hist.* **17**, (3), 105-180.

—1969b. Some Dinoflagellate Cysts from the Upper Cretaceous of northern Natal, South Africa. *Palaeont. afr.* **12**: 1-23.

Davey, R. J. and Williams, G. L., 1966b. The genus *Hystrichosphaeridium* and its allies. *Bull. Br. Mus. nat. Hist.*, Suppl. **3**: 53-106.

Davey, R. J., Downie, C., Sarjeant, W. A. S. and Williams, G. L., 1966. Fossil Dinoflagellate Cysts attributed to *Baltisphaeridium*. *Bull. Br. Mus. nat. Hist.*, Suppl. **3**: 157-175.

Eisenack, A., 1938. Die Phosphoritknollen der Bernstein-formation als überlieferer tertiären Planktons. *Schr. phys.-okon. Ges. Konigsberg*, **70**: 181-188, figs. 1-6.

—1963. *Cordosphaeridium* n.g., ex *Hystrichosphaeridium*, Hystrichosphaeridea. *Neues Jb, Gesl. Paläont., Abh.*, **118**: 260-265, pl. 29.

—1965. Über einige Mikrofossilien des samländischen und norddeutschen Tertiärs. *Neues Jb. Geol. Paläont., Abh.*, **123**: 149-159.

Evitt, W. R., 1967. Dinoflagellate Studies, II. The Archaeopyle. *Stanford Stud. Geol.*, **10**, (3): 1-83, pls. 1-11.

Pienaar, R. N., 1969. Upper Cretaceous Calcareous Nanno-plankton from Zululand, South Africa. *Palaeont. afr.* **12**: 75-147.

Sarjeant, W. A. S. and Downie, C., 1966. The Classification of Dinoflagellate Cysts above Generic Level. *Grana palynol.* **6**, (3): 503-527.

PLATE 1

Exochosphaeridium bifidum (Clarke and Verdier).

Fig. 1. Slide ZU8/C10. x 500.

Fig. 2. Specimen illustrating branched apical process to the north. Slide ZU8/C10. x 500.

Fig. 3. Specimen bearing unusually short processes and illustrating the characteristically shaped precingular archaeopyle. Slide ZU8/C7. x 500.

Fig. 4. Detached precingular operculum of less characteristic shape. Slide ZU8/C10. x 500.

Fig. 5. Specimen illustrating faint cingulum, archaeopyle to the north-west. Slide ZU6/CN. x 500.

Amphorosphaeridium fenestratum sp. nov.

Fig. 6. Specimen illustrating ventral area devoid of processes; large, antapical process seen to the south. Slide ZU6/CN. x 500.

PLATE 1

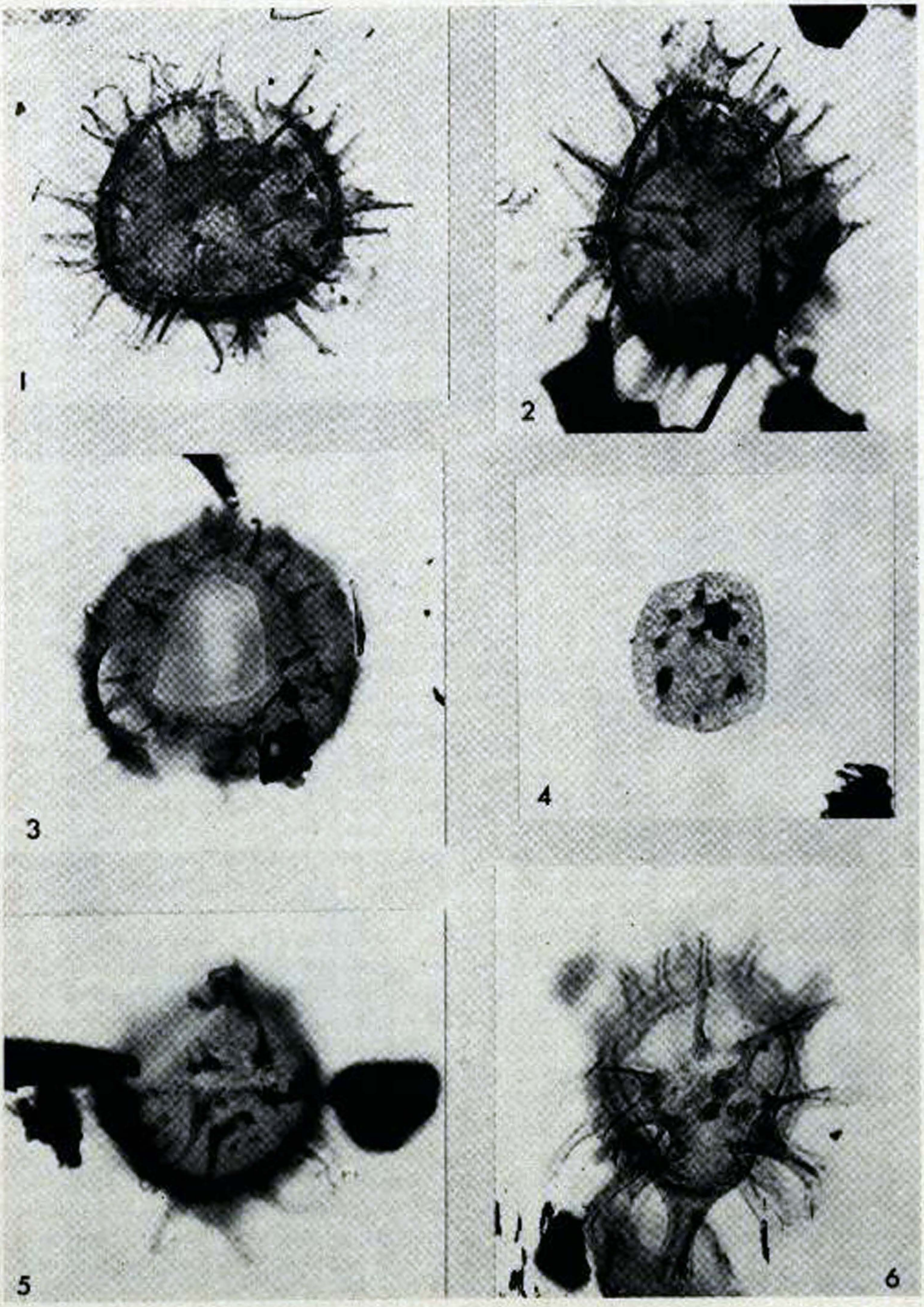


PLATE 2

Exochosphaeridium bifidum var. *involutum* nov.

Fig. 1. High magnification of holotype to show solid and hollow processes. Slide ZU6/C0. x 1000.

Fig. 3. Holotype. Slide ZU6/C0. x 500.

Amphorosphaeridium fenestratum sp. nov.

Fig. 2. Detached operculum bearing two processes. Slide ZU6/C8. x 500.

Fig. 4. Specimen possessing branched apical and large tubiform antapical processes. Slide ZU6/C8. x 500.

Amphorosphaeridium fenestratum var. *dividum* nov.

Fig. 5. Holotype. Slide ZU5/C4. x 500.

Fig. 6. Slide ZU6/C0. x 500.

PLATE 2

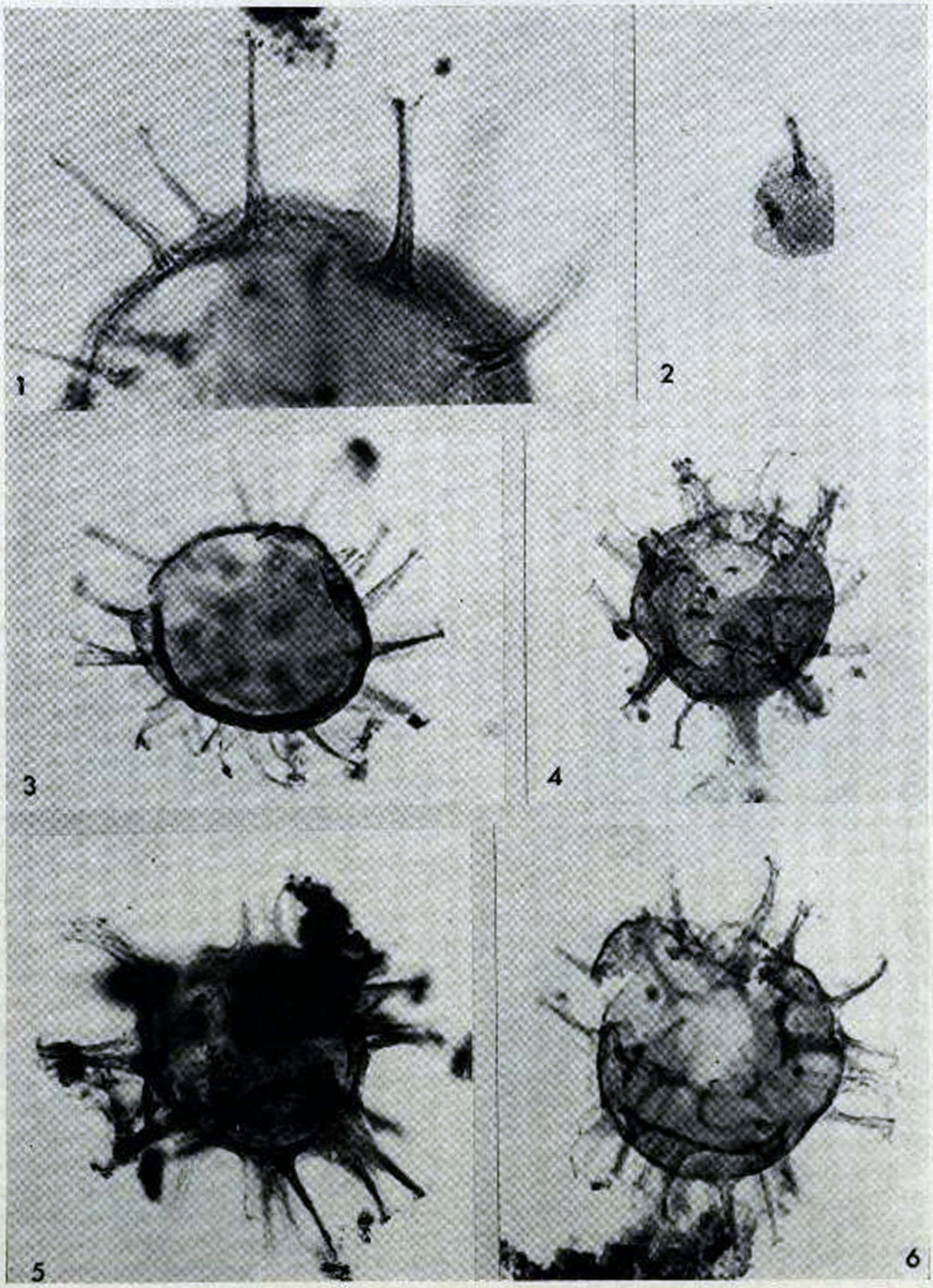


PLATE 3

Amphorosphaeridium fenestratum sp. nov.

Fig. 1. Holotype—view of precingular archaeopyle. Slide ZU6/C8. x 500.

Fig. 2. Enlargement of holotype to show wall structure, and hollow and fibrous structure of the processes. Slide ZU6/C8. x 1000.

Fig. 3. Slide ZU6/C0. x 500.

Cordosphaeridium fibrospinosum Davey and Williams

Fig. 4. Specimen with archaeopyle to the north-west. Slide ZU2/1. x 500.

Amphorosphaeridium multibrevum sp. nov.

Fig. 5. Holotype. Slide ZU4/C3. x 500.

Fig. 6. Slide ZU4/C8. x 500.

PLATE 3

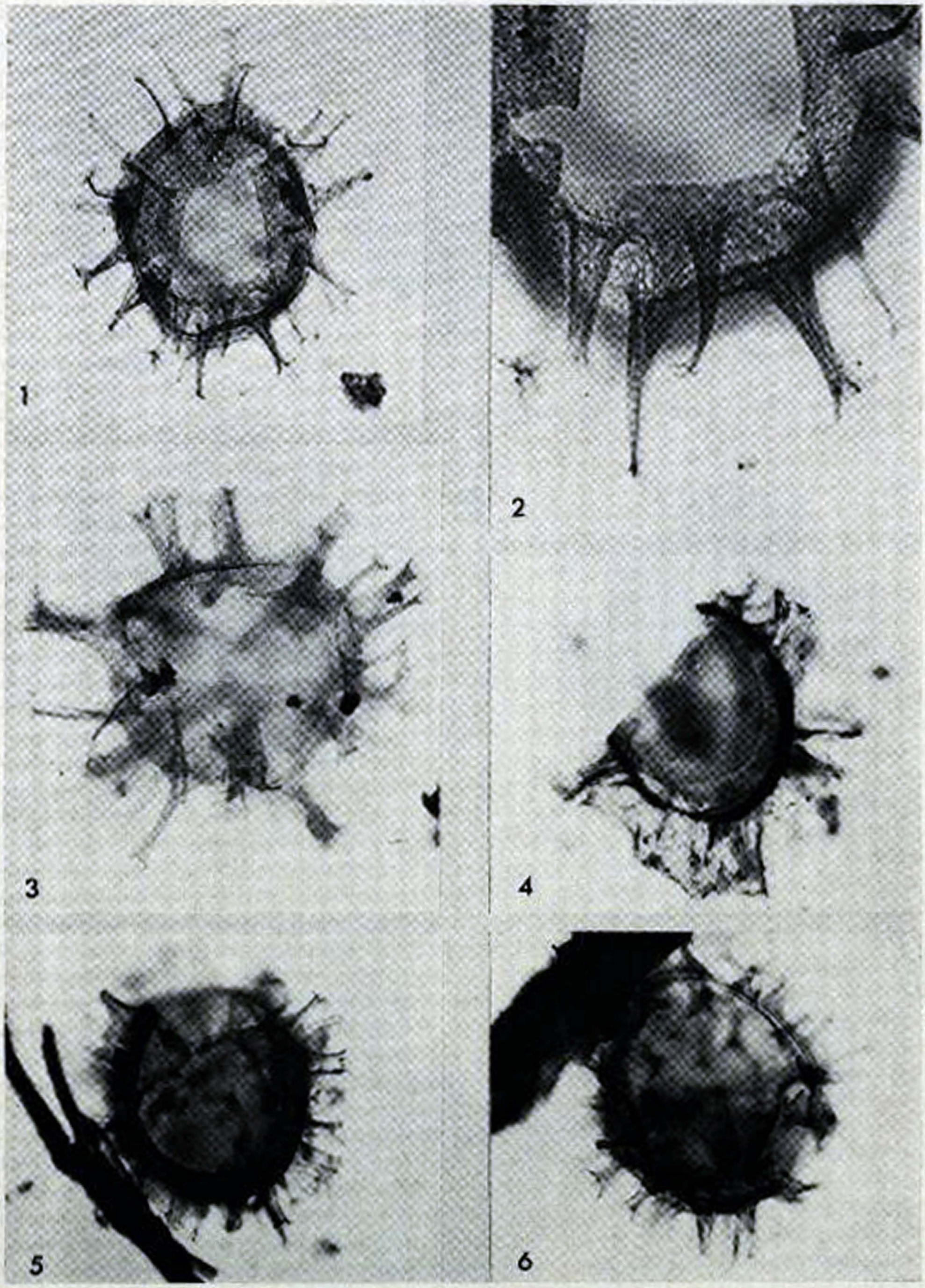


PLATE 4

Amphorosphaeridium multibrevum sp. nov.

Fig. 1. Slide ZU2/1. x 500.

Amphorosphaeridium latitubulum sp. nov.

Fig. 2. Holotype illustrating branched apical and broad antapical processes. Slide ZU3/C6 x 500.

Fig. 7. Detached precingular operculum. Slide ZU3/C6. x 500.

Cordosphaeridium sp.

Fig. 3. Slide ZU2/2. x 500.

Fig. 4. Slide ZU1/C4. x 500.

Fig. 6. High magnification to show the delicate and fibrous nature of the processes. Slide ZU1/C4. x 1000.

Cordosphaeridium fibrospinosum Davey and Williams

Fig. 5. Slide ZU2/1. x 500.

Plate 4