

# DEVONIAN MEGASPORES FROM THE WYBOSTON BOREHOLE, BEDFORDSHIRE, ENGLAND

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**ABSTRACT.** Nine species of megaspores are described from the Geological Survey Wyboston Borehole, Bedfordshire, England. Of these, five species are new, one forming the basis of a new genus, *Heliosporites*. Two single occurrences of large megaspores referable to Carboniferous genera are recorded, together with a new occurrence of the species *Cystosporites devonicus* Chaloner and Pettitt. The mean maximum size of all the species represented is 810  $\mu$ . While this is a higher figure than that for most Devonian megaspores described hitherto, it is still smaller than the corresponding figure for Carboniferous megaspores. The diversity of megaspores now known from the Devonian suggests that heterosporous plants were more abundant at that time than their representation in the macrofossil record would indicate. Some aspects of the classification of the Palaeozoic dispersed spores are discussed. The assemblage is regarded as probably of Frasnian age.

In the course of preparation of spore assemblages from a Geological Survey boring at Wyboston, Bedfordshire, 18 miles west of Cambridge (Pugh 1956, Edmunds 1956, Edmonds and Dinham 1965), megaspores were found in samples Bt 4284, depth 700 ft. 7 in., Bt 4350, depth 720 ft. 3-4 in., Bt 4354, depth 721 ft., Bt 4356, depth 721 ft. 5 in., and Bt 4358, depth 722 ft. 1 in.

In samples of Bt 3710 and Bt 3711 (counterparts of each other), at depth 560 ft. 3 in., fish fragments occur which have been compared to the genus *Bothriolepis*. Spore assemblages have been obtained from samples at all levels from 611 ft. down to 722 ft. depth. The lowest spore-bearing sample (Bt 4358) directly overlies a basal conglomerate of Old Red Sandstone facies, 14 ft. thick, and this in turn rests on rocks of Cambrian age. The present study offers no basis for separating the spore assemblages from the different horizons between 700 ft. and 723 ft., and these are here treated as a single group for general age considerations, which are discussed below.

*Acknowledgements.* We express our thanks to the Director of the Geological Survey of Great Britain, Sir James Stubblefield, F.R.S., for allowing us access to the cores from Wyboston, and to Mr. M. Mitchell, of the Palaeontological Department, for his help and for the interest he has taken in the palynological investigation.

## PREPARATION TECHNIQUES

Preparations were commenced either by soaking fragments of rock in a hot 50 per cent. solution of non-ionic detergent, or in a cold 20 vol.  $H_2O_2$  solution. Either treatment disaggregated even the more indurated samples, and was followed by treatment with cold 10 per cent. HCl (1 hour), cold 70 per cent. HF until no further reduction in bulk occurred, warm 50 per cent. HCl (ten minutes) and cold concentrated  $HNO_3$  (treatment between 1 and 12 hours, according to the degree of coalification). No alkali treatment was used.

Separation of the organic fraction of the residue from the remaining minerals was achieved either by flotation in zinc bromide solution (of specific gravity 2.0), when the

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residue was large, or by the use of a vibraflute (Tschudy 1960), when the residue was small. A particularly clean preparation was obtained from Bt 4284, which was treated with ultrasound in a tank at 40 kc/s for 2½ minutes, after the warm HCl stage. When a persistent fluo-silicate gel occurred, this was adequately dispersed by the use of ultrasound and the zinc bromide flotation was applied subsequently. Test slides were made before ultrasonic treatment and every 30 seconds during treatment, to check on any selective loss of spores. The megaspores were picked out of the aqueous residues and further macerated individually, in Schulze solution, if necessary. The larger spores were mounted singly in Canada Balsam and the smaller in glycerin jelly.

Sections of the specimens of *Heliosporites variabilis* gen. et sp. nov. and of *Hystricosporites obscurus* sp. nov. were obtained by embedding the spores singly in an Araldite-Epon resin, prepared as described by Mollenhauer (1964). Each spore was embedded in a pre-hardened capsule of resin, orientated so that the equatorial plane of the spore was parallel to the axis of the capsule. Serial sections were then cut parallel to the polar axis of the spore at 1  $\mu$  or 2  $\mu$  intervals, with a glass knife, on a Reichert rotary microtome.

All the slides are deposited in the Palaeontology collection of the Geological Survey and Museum (numbers prefixed PF).

#### SYSTEMATIC TREATMENT

The classification adopted here is that of Potonié and Kremp (1954), as subsequently modified by those authors (1955, 1956) and Potonié (1956, 1958, 1960).

One of the problems innate in a morphographic classification is the degree of importance to be attached to the various criteria available for separating the higher taxa. One feature which has received widely different rating by different authors is the separation of the two layers of the exine to leave a gap (variously referred to as the formation of an air sac, saccus, bladder, cavity, or mesospore). Potonié and Kremp recognized two contrasting situations involving such separation of exine layers. Where a thin, smooth, and crumpled body is sometimes present within a larger thick-walled spore the former was referred to as a mesospore. This term was coined by Fitting (1900) for an apparently comparable structure seen in the megaspore of some living species of *Selaginella*. Other workers (Zerndt 1934, Schopf 1938) had pointed out that spores identical in other respects might differ in the presence or absence of such a mesospore. The presence of this thin-walled inner body was accordingly not rated as of great significance within the morphographic classification, and spores with and without a mesospore were in some cases included within the same genus. This practice has been widely followed by subsequent authors (Dettmann 1961 in *Banksisporites*, McGregor 1960 and Richardson 1965 in *Biharisporites*).

The second possibility distinguished by Potonié and Kremp (1945) was the formation of a saccus; in this case an air-filled cavity (or cavities) are formed within the exine, the sacci of *Pinus* being a typical example. Potonié and Kremp treated this as a feature of much greater taxonomic consequence than the presence of a mesospore and used the possession of sacci as a criterion for including spores (or pollen) bearing them in their *Anteturma* Pollenites. Some of the spores included in Pollenites on the basis of their air sacs had proximal germination (with triradiate sutures) while others had distal germination. These authors were aware that such a grouping (Pollenites) included not merely

true pollen (such as bisaccate conifer pollen) but also the microspores of some heterosporous plants (e.g. *Endosporites*) but evidently accepted this as an unavoidable feature of any such empirical classification.

Dettmann (1963) has since attempted to remove from the Anteturma Pollenites those triradiate spores with an air sac (which she terms cavate) leaving in Pollenites only true pollen grains with distal germination (for which she would reserve the term saccate). In the former category (cavate spores) Dettmann includes megaspores with what earlier workers have called a mesospore, together with those triradiate small spores previously called saccate. All these triradiate 'cavate' spores (her suprasubturma Perinotriletes) she separates from triradiate spores without such a cavity in the exine (her suprasubturma Acavatitriletes).

In the present work a mesospore is noted as a variable character of the species *Hystricosporites multifurcatus*, *H. obscurus*, and *Biharisporites simplex*. In these last three species the specimens with a mesospore comprise less than half the population of the species, so that specimens lacking it are in no sense exceptional. Thus the application of Dettmann's proposed revision of the Anteturma Sporites to Palaeozoic spores encounters the practical difficulty that spores which would otherwise be placed in the same genus or even species may be separated at the level of a suprasubturma.

Richardson (1965) has proposed a new subturma Pseudosaccitriletes as a subdivision within Anteturma Sporites, Turma Triletes. The definition of pseudosaccate, however, corresponds closely with Erdtman's (1952) description of a saccus, so that the term pseudosaccate seems unnecessary. Richardson adds to the diagnosis that the 'exine may have . . . infrastructure' (in the same way as Erdtman adds 'baculoid elements usually sticking to the undersurface of the exine') but in discussing the subturma Richardson removes some genera from Potonié and Kremp's Anteturma Pollenites, Turma Saccites, because they do not show saccus infrastructure. Apart from this difficulty over the definition of terms, the use of the subturma Pseudosaccitriletes would cause the same difficulty in placing spores with a mesospore as the use of Dettmann's suprasubturma Perinotriletes.

It would be very desirable to separate pollen from spores *sensu stricto* in a classification of fossil spores, if this were possible. But at the present time there is no morphological criterion discernible in the fossil spores themselves which will form a basis for separating all pollen from all spores *sensu stricto*. It is implied by both Dettmann and Richardson that the presence of infrastructure in the saccus is such a criterion, but this is not yet certain. Nor is it always easy to determine, in a saccus with small-scale ornament, whether the ornament is on the inner or outer surface, as, for instance, in *Endosporites*. We therefore prefer to adopt Potonié and Kremp's practice of classifying all saccate spores *sensu lato* together, and of keeping together spores which are otherwise similar, whether they possess a mesospore or not.

Anteturma SPORITES H. Potonié 1893

Turma TRILETES Reinsch 1891

Subturma AZONOTRILETES Lubert 1935

Infraturma LAEVIGATI (Bennie and Kidston) R. Potonié 1956

Genus TRILEITES (Erdtman) ex Potonié 1956

*Type species. T. spurius* (Dijkstra) Potonié.

*Trileites langi* Richardson 1965

Plate 26, fig. 1

*Description.* Two specimens have been found. They have oval ambis, diameters  $252\ \mu$  and  $328\ \mu$  and walls  $8\ \mu$  thick. There are several large arcuate secondary folds near the equator. The triradiate markings are  $105\ \mu$  long on both ( $\frac{2}{3}$ – $\frac{5}{8}$  of the radius), but these are clearly visible only for about half their length. There is a small concavely triangular area at the apex where the exine is thinner than elsewhere; the corners of this triangle coincide with the ends of the readily visible triradiate mark. The triradiate mark is continued by faint lines on the exine (not sutures) and at their extremities these are continued by faint curvaturae. The exine is scabrate and one specimen is marked all over with depressions caused by pyrite crystals (as described by Neves and Sullivan 1964).

*Occurrence.* Wyboston Borehole, depths 722 ft. and 700 ft.

*Remarks.* These spores are considered to fall within the circumscription of *T. langi*. When discussing this species, Richardson remarks on the lack of curvaturae, although he refers to the thin apical triangle as a contact area. The sides of this triangle are seen to be concave, both in Richardson's plate 88, fig. 10 and in the Wyboston specimens, so that they cannot be curvaturae according to the definition of Potonié and Kremp (1955). Consequently the thin apical triangle cannot correspond to the contact area, which is defined both by Potonié and Kremp and by Couper and Grebe (1961) as being bounded by the curvaturae. The observation of the true curvaturae running convexly between the extremities of the triradiate mark confirms this argument and also shows that the contact faces in fact occupy a large part of the proximal face of the spore. This also supports Richardson's placing of the species in the genus *Trileites*, typical members of which have curvaturae. A thin apical area within the contact area has now been noted in several Devonian spore species, *Retusotriletes distinctus* Richardson 1965 (also from the Middle Old Red Sandstone), *Cyclogranisporites* sp. and *Calamospora witneyana* Chaloner (1963) from the Witney Borehole, *Trileites wybostonensis* sp. nov., and the megaspore of *Barinophyton richardsoni* (Dawson) Pettitt (1965) all show an analogous thin apical triangle. All are associated with triradiate marks without lips and in which sutures may be lacking (e.g. *Cyclogranisporites*) or only partly developed (e.g. *T. langi*). Possibly at

## EXPLANATION OF PLATE 26

The slides referred to are in the Geological Survey and Museum Palaeontological Collection. All magnifications  $\times 200$ , unless otherwise stated.

- Fig. 1. *Trileites langi* Richardson. Proximal face of specimen showing faint curvaturae, scattered globules of exinous material around apical area, and polygonal depressions caused by pyrite crystals; Slide PF 3948.
- Fig. 2. *Trileites fulgens* (Zerndt) comb. nov. Proximal face of specimen showing triradiate lips, wedge-shaped arcuate ridges, scabrate exine, and mesospore; PF 3949.
- Figs. 3, 4. *Trileites wybostonensis* sp. nov. 3, Holotype, proximal face,  $\times 100$ ; PF 3950. 4, Detail of haptotypic features,  $\times 1000$ .
- Figs. 5–9. *Hystricosporites multifurcatus* (Winslow) comb. nov. 5, 6, Two types of spine ending, both found on one specimen,  $\times 1000$ . 7, Proximal view of specimen with parallel sided spines; PF 3952. 8, Lateral view showing membranous lips; PF 3953. 9, Proximal face of specimen with tapering spines,  $\times 100$ ; PF 3951.

dehiscence the whole of the thin area was used as an exitus instead of splits occurring along the sutures as in most living triradiate spores.

*Previous records.* *Trileites langi* was found by Richardson in most of the beds examined in the Orcadian basin, Eifelian and Givetian in age. He also records the similarity of *T. langi* to *Archaeozonotriletes incrustatus* Archangelskaya from the lower Frasnian of the Russian platform. The three specimens recorded by Winslow (1962, pl. 17, figs. 10–12) as *Triletes sp.* from the Bedford shale of Ohio (basal Mississippian) are also very similar to *T. langi* in size and appearance, and she has remarked on the unobtrusive continuations of the triradiate mark. An interesting comparison may also be made with the specimens of *Triletes sellingi* Sen (1958) from the Upper Devonian of Bear Island. These resemble *Trileites* in being smooth with a short triradiate mark 'possibly extending up to often indistinguishable arcuate ridges'. The minute tubercular outgrowths, which sometimes occur, could be comparable to the scattered globules of exinous material noted by Chaloner 1963 in *T. oxfordiensis*. Sen's reference of Nathorst's specimens to *Bentzisorites* Potonié and Kremp, remains problematical, as there is no evidence of their possessing a cingulum.

*Trileites fulgens* (Zerndt) comb. nov.

Plate 26, fig. 2

1937 *Triletes fulgens* Zerndt, Type 8, Zerndt, p. 5, pl. 1, figs. 1–9.  
1955 *Laevigatisporites fulgens* (Zerndt) Potonié and Kremp, p. 53.

*Description.* Only one complete specimen has been found in the present material. It has a subcircular amb, with diameters 403  $\mu$  and 428  $\mu$ . The triradiate mark is 150  $\mu$  long, i.e.  $\frac{3}{4}$  radius or more, with labra 30  $\mu$  high at the apex and 25  $\mu$  broad. The triradiate mark terminates at arcuate ridges, wedge-shaped in profile, 10  $\mu$  broad and 15  $\mu$  high, which delimit the contact faces. The wall is 10  $\mu$  thick. By reflected light the exine appears smooth and shiny, but by transmitted light it is seen to be scabrate. With the aid of an oil immersion objective a thin, folded, laevigate mesospore can be seen.

*Occurrence.* Wyboston Borehole, depth 720 ft.

*Remarks.* This spore is excluded from *Biharisporites* because it lacks ornament. The orientation of this spore is slightly oblique, which indicates that it was spheroidal or sub-spheroidal in life, and therefore it does not belong to the genus *Laevigatisporites* (see Chaloner 1953, 1963).

The Wyboston specimen is similar to the type species of *Trileites*, *T. spurius* Dijkstra, in the possession of long, high triradiate lips, strongly developed arcuate ridges, and lack of ornament. Dijkstra measured three specimens, the smallest of which is about double the size of the Wyboston specimen. The other Mesozoic species of *Trileites* all differ from the Wyboston specimen in lacking either high lips or arcuate ridges, or both. The Devonian species *T. langi* Richardson has barely discernible arcuate ridges and *T. oxfordiensis* Chaloner has reduced arcuate ridges.

The Wyboston spore falls at the lower limit of the described size range of *Trileites fulgens* and its measurements are proportionately small. In appearance it closely resembles Zerndt's figures of *T. fulgens*. Zerndt lays emphasis on the 'greasy lustre' of *T. fulgens*,

which he only examined dry, by reflected light. He does not mention the presence of the mesospore, which would, of course, be invisible in a dry specimen. However, the mesospore is sufficiently variable in its presence or absence in other megaspores (see discussion of Systematic Treatment) for this not to be considered an important character.

Zerndt's figures of *T. fulgens* show oblique as well as proximo-distal compressions, indicating that it was spheroidal or subspheroidal in life. Arnold (1950) comments that *T. fulgens* is easily recognized by its (subspheroidal) shape.

It is noted that the only difference between the descriptions of *Trileites spurius* and *Trileites fulgens* is in their size.

*Previous records.* Namurian A and B, Polish Coal Basin. Pennsylvanian, Michigan Coal Basin.

*Trileites wybostonensis* sp. nov.

Plate 26, figs. 3, 4

*Diagnosis.* Triradiate megaspores with circular amb, maximum diameter 250–880  $\mu$  (mean 613  $\mu$ ; 17 specimens). Complete specimens with large arcuate secondary folds. Triradiate mark very short, 15–30  $\mu$  long, averaging  $\frac{1}{16}$  of spore radius, simple, straight, and without lips. Outermost exine layer continuous over thin, circular, apical area, with radius  $\frac{2}{3}$  to  $\frac{3}{4}$  of length of sutures. Inner exine layer forming darkened ring around thin area. Ring 10–20  $\mu$  broad, proximally with steep edge (measured depth 10  $\mu$ ), but distally grading into normal exine thickness and colour; distal margin of dark ring sometimes scalloped. Wall thickness at equator 9–12  $\mu$ , surface scabrate.

*Holotype.* Slide PF 3950, Plate 26, fig. 3.

*Occurrence.* Wyboston Borehole, depths 721 ft., 722 ft.

*Dimensions.* Maximum diameter range 250–880  $\mu$  (mean of 17 spores 613  $\mu$ ); wall thickness 9–12  $\mu$ ; triradiate mark  $\frac{1}{16}$  of spore radius.

*Remarks.* Spores with a short triradiate mark are usually placed in the genus *Calamospora* Schopf, Wilson, and Bentall, but this genus is characterized by its thin, laevigate, much folded wall, and relatively small size (under 350  $\mu$ ), so that to place the large thick-walled scabrate spores of *T. wybostonensis* here would be inappropriate.

Large, relatively thick-walled, smooth megaspores, both with and without curvaturae, have previously been included in *Trileites*. In its very short triradiate mark, the present species differs from all others in the genus. In this respect its inclusion represents an extension of Potonié's circumscription of the genus. *T. wybostonensis* particularly resembles *T. langi* in shape, wall thickness, ornament, and in having a thin apical area. It differs in the extreme shortness of the triradiate mark, the shape of the apical area, and greater size range.

Infraturma APICULATI (Bennie and Kidston) R. Potonié 1956  
Genus HYSTRICOSPORITES McGregor 1960

*Type species.* *H. delectabilis* McGregor.

*Remarks.* Two evidently similar genera have been erected to include megaspores with grapnel-shaped appendages and no prominent equatorial feature; *Dicrospora* Winslow 1962 and *Hystricosporites* McGregor 1960. Despite the two-year interval between these

two works, the description of the genus *Dicrospora* was evidently drawn up before the publication of McGregor's genus. Comparison of the type species of the two genera shows that they are in various respects closely similar. *D. porcata* is characterized by broad radiating ribs on the contact faces, but inspection of McGregor's plate 11, fig. 13, shows that *H. delectabilis* also has this distinctive feature. In addition, both species have a wide size range (*D. porcata* 70–550  $\mu$ , *H. delectabilis* 145–340  $\mu$ , both without the spines); the bifurcate tipped spines may have expanded or bulbous bases.

An apparent point of difference between these authors' descriptions is that *D. porcata* has the contact faces free of spines, whereas *H. delectabilis* has spines on both proximal and distal faces. Evidently McGregor does not mean that the proximal faces are covered with spines, since his plate 11, fig. 13, shows that the contact faces, which occupy about half the proximal face, are free of spines. Winslow's plate 11, fig. 4, shows the same arrangement of spines extending on to the proximal face outside the contact areas. It is thus only difference of wording which at first glance makes the descriptions appear different. Another apparent difference in the descriptions of the two species is that Winslow refers to a 'zonarial ridge' in *D. porcata*, bearing 15–30 spines, whereas McGregor emphasizes that *Hystricosporites* lacks any equatorial flange or concentration of spines in the equatorial region. Winslow's plate 11, fig. 4, shows that the ridge is not equatorial in position, and may better be regarded as representing arcuate ridges. On this interpretation there is no equatorial feature, as McGregor says. There is, however, in both *D. porcata* and *H. delectabilis* a concentration of spines on the arcuate ridges. An estimate of the number of spines on the ridges in McGregor's plate 11, fig. 13, gives 20, which is within Winslow's counts of 15–30.

Another apparent difference is attributable to a difference of view. Winslow figures *D. porcata* in both proximo-distal and lateral orientations, and describes it as having prominent thin lips to the triradiate mark. These are not visible in her plate 11, fig. 4 (proximo-distal compression), but are seen in her plate 22, fig. 15 (lateral compression). McGregor only figures a proximo-distal compression and describes *H. delectabilis* as lacking 'greatly elevated triradiate lips'. However, he does also speak of the lips being 'sometimes raised and convoluted'; which is just the appearance that collapsed high thin lips give in proximo-distal compression.

There are thus no significant points of difference and many striking points of similarity between *D. porcata* and *H. delectabilis*, as described and figured by their authors. Generally the measurements of the former encompass those of the latter, probably because Winslow measured 17 specimens and McGregor about 10. A puzzling feature is that Winslow estimates proximo-distally and laterally compressed specimens to be equally abundant in her population, whereas McGregor apparently only observed proximo-distal compressions. However, this does not affect the material similarity of the two species, which are concluded to be conspecific. The name *Hystricosporites delectabilis* McGregor has priority and *Dicrospora porcata* Winslow becomes its junior synonym. The other species of the genus *Dicrospora* described by Winslow including *Dicrospora multifurcata* should accordingly be referred to *Hystricosporites*.

*Hystricosporites multifurcatus* (Winslow) comb. nov.

Plate 26, figs. 5–9

1962 *Dicrospora multifurcata* Winslow, p. 52, pl. 11, figs. 4, 5, pl. 12, fig. 5, pl. 22, fig. 15.

*Description.* Triradiate megaspores with rounded triangular amb, body diameter 114–233  $\mu$  (mean of 11 spores 173  $\mu$ ) plus long spines 70  $\mu$  to 120  $\mu$  (mean 86  $\mu$ ). The triradiate mark is long, reaching the equator, and has thin membranous lips. In lateral compression the lips may be up to 60  $\mu$  high at the apex. In proximo-distal compressions the curvaturae are seen as a membranous structure 15–20  $\mu$  broad. The proximal face is scabrate. The remainder of the exine is covered with long, parallel-sided or, occasionally, tapering appendages, slightly expanded at the bases, and sometimes joined to an adjacent spine for part of their length. The spines do not taper at the tips, but are baculate, with 2–5 small spines, 1–5  $\mu$  long, arising from the flat tops. The main spines are usually longitudinally grooved or fluted, but sometimes cylindrical, and the minute apical spines are always homogeneous in texture. Wall thickness 6–10  $\mu$  distally, less proximally. A mesospore is seen in five spores, i.e. in about half the observed specimens.

*Occurrence.* Wyboston Borehole, depths 700 ft., 721 ft., 722 ft.

*Remarks.* These spores are very close to the description and figures of *Dicrospora multifurcata*. Winslow only describes spores with striate spines and suggests that this appearance may be due to collapse of a hollow structure. Our observation of homogeneous spines on some well-preserved specimens suggests that the striation may be an effect of corrosion. Winslow does not mention a mesospore, but since specimens with and without it, but comparable in all other respects, are about equally abundant in the Wyboston material, this is not considered a specific difference.

*Previous records.* *D. multifurcata* is recorded by Winslow from the uppermost Middle Devonian to basal Mississippian of Ohio.

*Hystricosporites obscurus* sp. nov.

Plate 27, figs. 1–5

*Diagnosis.* Triradiate megaspores 177–440  $\mu$  in equatorial diameter (mean of 31 spores 303  $\mu$ ), plus spines 18–60  $\mu$  high; body characteristically dark and difficult to clear by maceration. Amb in proximo-distal compressions circular or rounded subtriangular. Lateral and oblique compressions frequently encountered. In lateral compression with subdued apical prominence formed by contact faces and high triradiate lips. Angle at apex approximately a right angle, maximum distance from apex to curvatura about  $\frac{1}{3}$  polar axis. Lips 60–150  $\mu$  high at apex, thin. Contact faces about 10  $\mu$  thick, remainder of wall 15–30  $\mu$  thick. Curvaturae emphasized by close-set palisade of bifurcate spines. Bifurcate spines also scattered over remainder of exine, from 10–25 being seen at the margin of the spore. Spines 18–60  $\mu$  high, i.e.  $\frac{1}{7}$  to  $\frac{1}{6}$  of body diameter. In some spores spines

EXPLANATION OF PLATE 27

All magnifications  $\times 200$ , unless otherwise stated.

Figs. 1–5. *Hystricosporites obscurus* sp. nov. 1, Holotype, oblique view; Slide PF 3954. 2, Lateral view of characteristically dark specimen; PF 3955. 3, Proximal view of specimen sectioned, photographed in open glycerin jelly mount. 4, Section, showing shrunken mesospore; PF 3957. 5, Lateral view of specimen showing membranous lips and mesospore; PF 3956.

Figs. 6–8. *Biharisporites simplex* sp. nov. 6, Ornament of small rods and coni,  $\times 1000$ . 7, Proximal view of specimen showing scabrate contact areas and characteristic secondary folds; PF 3959. 8, Holotype, slightly oblique view showing triradiate mark and mesospore; PF 3958.



arising directly from the exine and tapering from  $12\ \mu$  wide at their bases to  $3\ \mu$ , then bifurcating to form pitchfork or anchor-shaped ends, each prong tapering from 2 or  $3\ \mu$  to zero over a length of  $7\text{--}10\ \mu$ . In other spores spines arising from either conical or bulbous bases,  $25\text{--}30\ \mu$  wide at base and  $6\text{--}9\ \mu$  high, and tapering sharply to  $12\ \mu$  wide at base of main spine. Contact faces free of spines, scabrate. Remainder of exine between spines scabrate. Spines homogeneous in texture. Mesospore observed as a thin, folded inner membrane in eight spores, i.e. a quarter of the specimens.

*Holotype.* Slide PF 3954. Body diameter  $315\ \mu$ , spines  $45\ \mu$ . Plate 27, fig. 1.

*Occurrence.* Wyboston Borehole, depths 720 ft., 721 ft., 722 ft.

*Dimensions.* Body diameter  $177\text{--}440\ \mu$  (mean of 31 spores  $303\ \mu$ ); wall thickness  $15\text{--}30\ \mu$ ; spines  $18\text{--}60\ \mu$  high; triradiate lips  $60\text{--}150\ \mu$  high.

*Remarks.* The section parallel to the polar axis (Pl. 27, fig. 4) shows that the main wall thickness is spongy in texture and envelops a thin, homogeneous layer (the mesospore), which is free from it. Dettmann and Playford (1963) illustrate a free homogeneous inner wall layer in *Spinozonotriletes uncatus* Hacquebard. They argue that this is intexine and refer to the 'granular' main wall as exoexine. *H. obscurus* differs in structure from *S. uncatus* in a homogeneous zone at the inner margin of the exoexine.

The spores of *H. obscurus* agree well with the generic diagnoses of McGregor (*Hystricosporites*) and Winslow (*Dicrospora*) (see discussion of the genus *Hystricosporites*). *H. obscurus* differs from *H.* (al. *Dicrospora*) *amherstensis* in its relatively much shorter spines ( $\frac{1}{7}$  to  $\frac{1}{8}$  body diameter compared with  $\frac{1}{3}$ ) and generally smaller size, and from *H.* (al. *D.*) *bedfordi* in lacking a pseudoflange. *H. obscurus* lacks radiating ribs on the contact faces and thus differs from *H. delectabilis* McGregor, *H. corystus* Richardson, *H. porrectus* (Balme and Hassell) Allen, and *H. costatus* Vigran, all of which can be seen from their authors' plates to possess this feature. It also lacks the distal extension of the exoexine ('crumina' of Allen) of *H. coronatus* Vigran.

The five specimens assigned to '*Dicrospora* sp. B' by Winslow (body diameter  $130\text{--}50\ \mu$ ), however, have shorter spines ( $\frac{1}{7}$  to  $\frac{1}{8}$  body diameter) and may be small specimens of *H. obscurus*. The figure (Winslow, pl. 12, fig. 2) shows them to have a dark body. '*D.* sp. B' is from the Bedford shale in Ohio, i.e. basal Mississippian in age.

#### Genus BIHARISPORITES Potonié 1956

*Type species.* *B. spinosus* (Singh) Potonié.

*Biharisporites simplex* sp. nov.

Plate 27, figs. 6-8

*Diagnosis.* Triradiate megasporites, originally more or less spheroidal,  $200\text{--}630\ \mu$  in diameter (mean of 43 specimens,  $309\ \mu$ ), characteristically with large secondary folds. Triradiate mark  $\frac{1}{3}\text{--}\frac{2}{3}$  of spore radius, simple, straight, and without labra. No arcuate ridges. Curvaturae not present as structures, but represented by a sharp or gradual change in surface ornament. Curvaturae emphasized, in about 10 per cent. of specimens, by secondary arcuate folding, but more often obscured by the large secondary folds

referred to above. Contact faces scabrate. Remainder of exine ornamented with small, close-set conii, standing  $1-1\frac{1}{2}\mu$  high, and tapering evenly from bases  $1\mu$  in diameter. Conii homogeneous in texture and remarkably constant in size, shape, and dense distribution. Conii usually entire, and often with axis of each cone curved. In a region  $5-15\mu$  wide, bordering the contact faces, sculptural elements reduced in size, but not coalesced. Wall thickness  $3-6\mu$ . A thin walled, laevigate, folded mesospore observed in 19 spores, i.e. under half of specimens.

*Holotype.* Slide PF 3958; specimen with mesospore; Plate 27, figs. 6, 8.

*Occurrence.* Wyboston Borehole, depths 700 ft., 720 ft., 722 ft.; most commonly found at 700 ft.

*Dimensions.* Diameter range  $200-630\mu$ , mean of 43 spores,  $309\mu$ ; wall thickness  $3-5\mu$ ; triradiate mark  $\frac{2}{3}$  of spore radius; conii  $1-1\frac{1}{2}\mu$  high,  $1\mu$  diameter at base.

*Remarks.* Chaloner, in 1959, when describing *B. ellesmerensis*, has discussed whether Devonian spores should be placed in a genus based on Gondwanan (i.e. Carbo-Permian) material. *B. submamillarius* McGregor 1960 and *B. parviornatus* Richardson 1965, both based on Devonian material, have since been included in the genus. The tubercles of *B. submamillarius* bear tiny spines and the varied sculptural elements of *B. parviornatus* are terminated by short cones, so that both are as nearly 'approximate to conii in Potonié's sense' (Chaloner 1959, p. 323) as *B. ellesmerensis*. *B. simplex* has conii less than twice as high as broad, which is clearly within Potonié's sense. The mesospore reported in the type species, *B. spinosus* (Singh) Potonié, and also in *B. myrmecodes* (Harris) Potonié and *B. datmensis* (Srivastava) Potonié, is not mentioned in the case of *B. echinatus* (Miner). Potonié (1956, p. 31) appears to regard it as a specific character of the types species. This has allowed freedom for the inclusion in the genus of *B. ellesmerensis* and *B. ocksensis* neither of which shows the mesospore, and *B. submamillarius* and *B. parviornatus* in which it is sometimes developed. A greater or lesser separation of the intexine to form a mesospore has also been noted in several other Palaeozoic megaspores, e.g. in *Triletes globosus* by Winslow (1959).

Potonié describes the exine of *Biharisporites* as 'thick, with small conii'. Particularly thick walls have been recorded in the cases of *B. datmensis* ( $15-20\mu$ ) and *B. ocksensis* (up to  $40\mu$ ), but a thick wall has not been noted as a feature of other species, including the type species *B. spinosus*. In *B. simplex* the wall is not thick compared with the spore diameter, but from the figures it appears to be about the same relative thickness as in *B. spinosus*. It thus involves no morphographic extension of Potonié's circumscription to include *B. simplex* in *Biharisporites*.

*Comparison.* *B. simplex* differs from all other species of the genus in the absence of labra bordering the triradiate sutures. *B. parviornatus* most closely resembles *B. simplex* in general aspect and both have very small sculptural elements. *B. simplex* is different, however, in having regular ornament all of one type. Pettitt (1965) has recently described megaspores from *Archaeopteris* cf. *jacksoni* some of which show an evenly developed ornament of tiny conii, similar to that of *B. simplex*. In spite of a strong similarity in this and other aspects, these spores differ from *B. simplex* in having labra  $5\mu$  thick and in their smaller size.

## Subturma LAGENOTRILETES Potonié and Kremp 1954

## Genus LAGENOISPORITES Potonié and Kremp 1955

*Type species.* *L. rugosus* (Loose) Potonié and Kremp.

*Lagenoisporites* sp.

Plate 28, fig. 1

*Description.* Only two specimens have been found in the present material. The most complete and better preserved is a flask-shaped triradiate megaspore  $378\ \mu$  in maximum diameter including apical prominence. The prominence is equal in height to half the polar axis. The better-preserved specimen is split into three valves, the splits following the triradiate sutures and extending nearly to the distal pole. The contact faces thus lie free and flat. Each shows two darkened lines connecting the ends of an arcuate ridge and meeting at an angle of  $120^\circ$ . These lines represent the junction of lips and contact faces. The upper part of the contact face (about  $\frac{2}{3}$  of the median length) formed the elevated lips. The contact faces are delimited by low, gently curving arcuate ridges  $6\text{--}9\ \mu$  high. The ridges are about  $15\ \mu$  broad, fading distally into the exine surface. The spore wall is  $20\ \mu$  thick. The contact faces are  $5\ \mu$  thick. The exine is scabrate.

*Occurrence.* Wyboston Borehole, depth 721 ft.

*Remarks.* The apical prominence in this species differs from that of *Lagenicula paulispinosa* sp. nov. in showing a clear demarcation between what may be regarded as contact areas and the elevated lips.

Potonié and Kremp (1955) give the lack of any distinct ornament and a more or less smooth exine, coupled with possession of a gula, as the essential characters of the genus *Lagenoisporites*. They include in the genus both forms in which the gula (apical prominence) is formed by expansion of the whole contact faces (e.g. *L. rugosus*), and those in which it is formed only by parts of the contact faces near the apex (e.g. *L. simplex*). Spinner (1965) has recently discussed the name *Lagenoisporites* and emphasized the importance of restricting this genus to megaspores with a completely smooth exine. The specimens from the Wyboston boring are not laevigate, but scabrate. They lack any measurable ornament, however, and so fall within Potonié and Kremp's slightly wider circumscription 'more or less smooth'. Consequently, these specimens are placed in *Lagenoisporites* sensu Potonié and Kremp.

The Carboniferous type species *L. rugosus* has a more or less smooth exine, and the apical prominence shows some variety of form. It has a wide size range, but the smallest specimens are larger than the Wyboston spores and have a relatively smaller apical prominence and punctate exine. *Lagenoisporites nudus* (Nowak and Zerndt) Potonié and Kremp has a smooth smaller apical prominence and the exine may be rugose.

There thus seems to be no suitable species to which to assign these spores, but the material is so far insufficient for the erection of a new species.

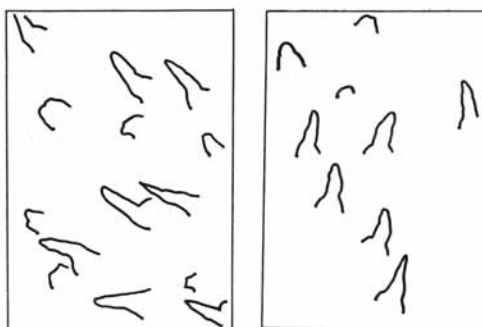
## Genus LAGENICULA (Bennie and Kidston) Potonié and Kremp 1954

*Type species.* *L. horrida* Zerndt.

*Lagenicula paulispinosa* sp. nov.

Plate 28, figs. 4-5; text fig. 1

**Diagnosis.** Flask-shaped triradiate megaspores 390–565  $\mu$  in maximum dimension (mean of 5 spores 473  $\mu$ ), including apical prominence. Conical prominence formed by the whole of the contact faces and at its maximum extent equal in height to half the polar axis. Contact faces delimited by low gently curving arcuate ridges about 15  $\mu$  broad and 10  $\mu$  high. Spore wall 15  $\mu$  thick. Body with scattered relatively short spines 9–12  $\mu$  high standing on conical bases approximately 5  $\mu$  at base and 5  $\mu$  high, and then tapering gradually to the apex. Spines homogeneous, remainder of exine finely granular. Ornament continued on to the contact faces as cones and verrucae diminishing in height towards spore apex.



TEXT-FIG. 1. Ornament on two typical areas of exine of *Lagenicula paulispinosa*. Drawn on photographic prints, which were afterwards bleached out;  $\times 500$ .

**Holotype.** Slide PF 3961; Plate 28, fig. 4.

**Occurrence.** Wyboston Borehole, depth 721 ft.

**Remarks.** The spines are commonly broken off leaving the conical bases only as ornament. *L. paulispinosa* is distinguished from *L. subpilosus* forma *major* (Dijkstra) ex Chaloner by its shorter, sparser, and stouter spines, and by its much smaller size

## EXPLANATION OF PLATE 28

All magnifications  $\times 200$ , unless otherwise stated.

Fig. 1. *Lagenoisporites* sp., lateral view of specimen flattened into three segments,  $\times 100$ ; Slide PF 3960.

Figs. 4, 5. *Lagenicula paulispinosa* sp. nov. 4, Holotype, lateral view showing well-developed apical prominence; PF 3961. 5, Free segment showing reduced ornament on raised lip,  $\times 100$ ; PF 3962.

Figs. 2, 3, 6–10. *Heliosporites variabilis* gen. et sp. nov. 2, Proximal face of specimen with spines on cingulum,  $\times 100$ ; PF 3963. 3, Holotype, proximal face, showing short triradiate ridges on exoexine and cingulum of bizonate appearance with radial striae,  $\times 100$ ; PF 3964. 6, Specimen with relatively short triradiate ridges and thin outer part to cingulum,  $\times 100$ ; PF 3967. 7, Proximal view of separation between intexine and exoexine,  $\times 500$ ; PF 3966. 8, Specimen sectioned, photographed in open plastic mount. 9, Section, showing separation of intexine and exoexine, high lips and wedge-shaped cingulum; PF 3965. 10, Proximal view of spore lumen, showing folded intexine,  $\times 500$ ; PF 3968.

(about half). *L. devonica* Chaloner, which is of comparable size, has a lower apical prominence and lacks spines, being ornamented with rugulae and muri, and indeed *L. devonica* differs from all other species of the genus in its very subdued apical feature.

The ornament of *L. paulispinosa* is of such small dimensions that it is not evident when a specimen is observed dry, by reflected light. When viewed under these conditions, the exine then comes within the description 'more or less smooth' which is Potonié's criterion for *Lagenosporites*. These two megaspore genera were originally founded on species described from observation of dry specimens, so that it is possible that spores belonging to *Lagenicula paulispinosa*, if only observed dry, might be placed in *Lagenosporites*. However, megaspores should ideally be observed by transmitted as well as reflected light, which may provide extra information, as in this case. Since *L. paulispinosa* has a small-scale ornament of discrete sculptural elements, it is assigned to *Lagenicula* rather than *Lagenosporites*.

Turma ZONALES (Bennie and Kidston) Potonié 1956

Subturma ZONOTRILETES Waltz 1935

Infraturma CINGULATI Potonié and Klaus 1954

Genus HELIOSPORITES gen. nov.

*Heliosporites variabilis* sp. nov.

Plate 28, figs. 2, 3, 6-10

*Diagnosis.* Triradiate megaspores with rounded sub-triangular amb, maximum diameter 190-535  $\mu$  (mean of 35 specimens 318  $\mu$ ). Exine two-layered. The outer layer, or exoexine, spongy in texture and entirely enclosing the intexine. The two layers attached over the entire distal face of the spore lumen, but with a cavity between them in the region of the proximal face, deepest at the proximal pole and diminishing towards the equator (Pl. 28, fig. 9). In optical section a slight gap may be seen around the periphery of the inner body (Pl. 28, fig. 7). Exoexine thickened centrifugally to form a massive wedge-shaped cingulum which tapers towards the equator, sometimes evenly, giving the cingulum a homogeneous appearance in plan view, and sometimes unevenly, giving a slightly bizonate appearance with an indistinct thicker inner part near the spore lumen, and an outer membranous part. The cingulum, in either case, may be simple and entire, or show fine radiating striae, or foveae of various sizes, or develop a small number of wide-based spines or baculi. Triradiate lips formed only of exoexine, highest at the proximal pole and extending on to and sometimes across the cingulum. Lips membranous, and in well-preserved specimens showing fine close-set parallel ribs. Surface of exoexine scabrate.

Inner layer, or intexine, homogeneous in structure and forming a thin (1-3  $\mu$ ) laevigate wall to the central lumen with distinct sutures extending about  $\frac{1}{4}$  of its own radius. The central lumen occupying about  $\frac{2}{5}$  of the total diameter of the spore, sometimes with the proximal face secondarily folded (Pl. 28, fig. 10).

*Holotype.* Slide PF 3964; Plate 28, fig. 3.

*Occurrence.* Wyboston Borehole, depths 700 ft., 720 ft., 721 ft., 722 ft.

*Dimensions.* Maximum diameter 190-535  $\mu$  (mean of 35 spores 318  $\mu$ ); ratio of spore lumen to total

diameter, 1:2.5; length of lips from  $\frac{2}{3}$  to length of total radius; height of lips up to  $35\ \mu$  at apex. Number of spores having spines on cingulum, 4 out of 35 examined.

*Remarks.* These spores are seen in section to have a wedge-shaped cingulum, as defined by Potonié and Kremp (1955), and figured in sections of *Densosporites* by Hughes, Dettmann, and Playford (1962). *Zonalesporites brasserti* (Zerndt) Potonié and Kremp has an equatorial feature which, although described by Potonié and Kremp as a 'cingulum', differs somewhat from that of *Densosporites* in being composed of many overlapping and partially fused hair-like elements. This equatorial feature is, moreover, of different texture from the body of the spore and is often found separated from it (e.g. Zerndt 1934, pl. 23, figs. 7, 12). Damaged specimens from the Wyboston boring do not break in this way, but may be broken across both cingulum and central area, or part of the cingulum may be chipped away. This cohesion is due to the continuity of the cingulum with the exoexine over the central area. In addition to this difference in structure, in *Zonalesporites* the ratio of the body to the total diameter is much larger (1:1.5 mean value taken from measurements of published figures) than in the Wyboston spores (1:2.5).

The type species of the genus *Triangulatisporites* Potonié and Kremp, *T. triangulatus*, which appears by transmitted light to have a homogeneous equatorial feature, also differs in structure from *H. variabilis*. Guennel (1954) has demonstrated that in *T. triangulatus* the central body is free of exoexinous covering over the contact faces. The central body may be entirely freed from this covering either in fossilization or preparation, and either part of the spore may be found separately (Guennel, pl. 1, fig. c; Hoskins and Abbott, fig. 14). The megaspores of *Selaginellites suissei* Zeiller (Chaloner 1954) and *S. crassinctus* Hoskins and Abbott (1956) agree closely with *T. triangulatus*. Hoskins and Abbott's sections show the flange to have a dense margin against the central body, and not to thin out progressively towards the outer margin, which is rounded in section. Sections of *H. variabilis* show all parts of the exoexine to be of equal density, and the outer margin is acute in section.

Thus the structure of *Heliosporites variabilis* is such that it cannot be included within any existing megaspore genus, and we accordingly propose a new genus based on this species.

The cingulum and small cavity between the exoexine and the intexine of *H. variabilis* recall the structure of the microspore genus *Densosporites* (Berry) Butterworth *et al.* A small cavity between the exoexine and the intexine was first demonstrated in *Densosporites* by Smith (1960), and later in sections by Hughes, Dettmann, and Playford (1962). Allen (1966) has emphasized that *Densosporites* is excluded from the category of 'cavate' spores, and we accept this. *Heliosporites* is therefore placed with *Densosporites*, in the infraturma Cingulati.

The sections of *Cirratriradites avius* figured by Allen show an interesting proximal separation between the spore wall layers, analogous to that seen in *H. variabilis*. In other respects, of course, the structure of *C. avius* is very different, since the exine is three layered and the exoexine across the distal face surprisingly thick (as also demonstrated in *C. elegans* by Hughes, Dettmann, and Playford). *Cirratriradites*, of course, falls within the usually accepted size limits for assignation to a microspore rather than a megaspore; indeed, certain species are known to represent lycopod microspores (Chaloner 1954; Hoskins and Abbott 1956).

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*Previous records.* No megaspores comparable with *H. variabilis* have been recorded previously, with the possible exception of *Hymenozonotriletes corrugatus* Archangelskaya (1963) from the lower Frasnian of the Russian platform. This is a spore of the same general shape and size range as *Heliosporites variabilis* and with a wide 'otorochka'. The 'otorochka' is described as having a finely or deeply notched margin (similar to the chipped margin of corroded specimens of *H. variabilis*). It sometimes shows isolated spines or ramifying small folds and veinlets; the triradiate mark has high lips and may or may not extend across the 'otorochka'. All these features may be seen in *H. variabilis*. It is unfortunate that the Russian word 'otorochka' covers both a solid border (cingulum or zona) and a hollow border (saccus). However, Archangelskaya evidently understands her spore to be saccate, since she says 'spore coats meet only in polar regions'; and this is borne out by her mention of small folds in the 'otorochka'. Her figures (Pl. 14, figs. 1, 2) throw no further light on this aspect. Fig. 1 shows such small folds, but fig. 2 is very similar to corroded *H. variabilis* (several of the Wyboston specimens show such a darkened central area, and radial folding in the thinner part of the cingulum). In view of Archangelskaya's comment, we prefer to treat our spore as specifically distinct for the time being.

Infraturma ZONATI Potonié and Kremp 1954

Genus TRIANGULATISPORITES Potonié and Kremp 1954

*Type species.* *T. triangulatus* (Zerndt) Potonié and Kremp

*Triangulatisporites* sp.

Plate 29, figs. 1-3

*Description.* Triradiate megaspore with rounded triangular amb, 1450  $\mu$  in maximum diameter (only one complete specimen measured). It has a relatively narrow equatorial flange (zona) from 50  $\mu$  to 125  $\mu$  wide, not always widest at radial extremities. The sutures are long, equal to radius of spore cavity. The lips are 125  $\mu$  high at apex, decreasing to about  $\frac{1}{3}$  of original height at margin of spore cavity, there diverging and merging with flange. The proximal face in the immediate vicinity of the apex is free of ornament. About  $\frac{1}{3}$  distance towards equator radiating rugulae develop, about 15  $\mu$  high and wide. These either continue in radiating alignment to margin of the spore or interconnect to form an irregular reticulum. The flange is either membranous with radiating ribs, or somewhat thicker with verrucae and rugulae on its surface. The ornament is continued on the distal surface as an irregular polygonal reticulum with lumina 60  $\mu$  to 100  $\mu$  across.

*Occurrence.* Wyboston Borehole, depth 720 ft.

*Remarks.* This species is readily recognizable by its distinctive ornament and equatorial feature. Twelve fragments with a maximum dimension of 800  $\mu$  or more, have been found, usually representing one-third of a spore, which has split along the triradiate sutures. The specimens are always strongly compressed. The equatorial feature is usually attached.

The Mesozoic megaspore genus *Horstisporites* Potonié 1956, has variable reticulate ornament, but lacks any equatorial feature. Species of the Palaeozoic genus *Triangulatisporites* have been demonstrated by Guennel 1954 and by Spinner 1965 to consist of a

simple central body which may be detached from an outer layer forming the lips, equatorial feature, and reticulum, but in our spore there is no sign of this double structure. The equatorial feature in our spore is not a typical zona, but it does in some cases resemble the compound equatorial feature of the Upper Devonian species *T. rootsi* Chaloner, although always without gaps. The ratio of the spore lumen to the total diameter is 1:1.2, compared with a typical figure for other species of *Triangulatisporites* of 1:1.3 (taken from measurements of published figures). In other respects our spore agrees well with *Triangulatisporites*, and in view of the limited material available this seems the most appropriate generic assignment.

Genus ZONALESPORITES (Ibrahim) Potonié and Kremp 1954

*Type species.* *Z. brasserti* (Stach and Zerndt) Potonié and Kremp.

*Zonalesporites* sp.

Plate 29, fig. 4

*Description.* Only one near-complete specimen has been found. It is a triradiate megaspore with rounded-triangular amb. The dimension from the apex of the triangle to the midpoint of the opposite side is 1400  $\mu$ . The triradiate mark has straight raised ridges, 65  $\mu$  broad at the apex of the spore, and running onto and across the cingulum, 25  $\mu$  broad at extremities. It has a massive wedge-shaped cingulum 125–225  $\mu$  broad, broadest opposite the ends of the triradiate sutures. The cingulum has a narrow, darkened inner ring near the spore lumen. The darkened ring is further emphasized by a secondary fold in the distal surface. The cingulum is continuous with the exine over the spore lumen. The exine is apparently of two layers, which peel apart at the broken edges. On the proximal face the exine is relatively thick, without folds, and on the distal face it is thinner.

*Occurrence.* Wyboston Borehole, depth 700 ft.

*Remarks.* This species resembles those of *Triangulatisporites* in having a homogeneous equatorial structure, but it is not a zona, nor is it detachable from the central body. The species further differs from *Triangulatisporites* in the thickness of the distal face (in *Triangulatisporites* this carries the reticulum and is continuous with the zona), in the absence of any trace of a reticulate ornament and in the markedly larger size (about

EXPLANATION OF PLATE 29

All magnifications  $\times 50$  unless otherwise stated.

Figs. 1–3. *Triangulatisporites* sp., Proximal view of specimen, photographed by transmitted light to show narrow zona; PF 3969. 2, Distal view of same specimen, photographed dry by reflected light to show reticulum. 3, Part of zona, by transmitted light,  $\times 200$ .

Fig. 4. *Zonalesporites* sp., Proximal view of near-complete specimen, showing continuity of cingulum with central area and long triradiate ridges; PF 3970.

Figs. 5–7. *Cystosporites devonicus* Chaloner and Pettitt. 5, Lateral view of large fragment with apex: PF 3971. 6, Miospore appressed to surface of same specimen,  $\times 500$ . 7, Detail of haplotypic features of same specimen,  $\times 200$ .

Figs. 8–10. *Cystosporites* sp. 8, Lateral view of fragment, possibly with distal extremity, showing longitudinal striae in equatorial region; PF 3973. 9, Miospore appressed to same specimen,  $\times 200$ . 10, Lateral view of fragment broken along triradiate sutures and showing darkened apical area; PF 3972.



double). The ratio of the spore lumen to the total diameter is 1:1.5, which is less than the mean value for *Triangulatisporites* but the same as the mean value for *Zonalesporites* (1:1.5). Spinner (1965) has emended the genus *Zonalesporites* to include megaspores with some range of equatorial features from a corona to a zona. However, *Zonalesporites* sp. differs from other members of *Zonalesporites* s.l. in the continuity of the body and cingulum, and in the unusual feature of a distal face thinner than the proximal. It is, however, included in the size range for the genus and lacks any body ornament, in addition to the points of similarity mentioned above, so that this generic assignation is preferred for the time being.

Fragments of this species are quite frequently encountered in the Wyboston material, usually representing a sector of the spore, broken apart along the triradiate mark.

Turma CYSTITES Potonié and Kremp 1954  
Genus CYSTOSPORITES Schopf 1938

*Type species. C. breretonensis* Schopf.

*Cystosporites devonicus* Chaloner and Pettitt 1964

Plate 29, figs. 5-7

*Description.* Two specimens have been found, each representing the large ('fertile') member of the tetrad, but neither of them complete. Both are of an elongate shape, oval at one end and broken off at the other, lengths 880  $\mu$  and 1200  $\mu$ . The triradiate mark is near the rounded end, 150  $\mu$  in maximum extent, and on the better-preserved specimen showing lips 3  $\mu$  wide. The contact areas are weakly developed and the arcuate ridges not discernible. The entire exine is scabrate. The exine is 3-5  $\mu$  thick in one case and 5-10  $\mu$  in the other, apparently of a single layer. Arcuate and longitudinal folds follow the shape of the spores. The distal end of the spore is missing in each case. No other abortive spores were found adhering to the contact faces.

*Occurrence.* Wyboston Borehole, depths 720 ft., and 721 ft.

*Remarks.* These spores have the polar axial elongation characteristic of the fertile member of a *Cystosporites* tetrad. In the haplotypic features, in the finely granular nature of the whole exine and in the longitudinal folding, they are closely comparable to *C. devonicus*, which is from the basal Frasnian of Scaumenac Bay, Quebec (Westoll in Richardson 1965).

*Associated miospores.* There are two spores adhering to the exine of one specimen, of 55  $\mu$  and 60  $\mu$  diameter respectively. They have long, simple triradiate marks and a narrow equatorial feature (about 5  $\mu$ ). They are very similar to the two miospores found by Chaloner and Pettitt adhering to the surface of *C. devonicus* and referred by them to cf. *Lycospora* sp.

Chaloner and Pettitt have discussed the significance of the occurrence of their *Cystosporites* at this Upper Devonian horizon. This additional record (and the following one) confirms their report, and demonstrates that this extreme development of heterospory was not an exceptional isolated occurrence in the Scaumenac Beds.

*Cystosporites* sp.

Plate 29, figs. 8–10

*Description.* Three elongated fragments of megaspores have been found, 504  $\mu$ , 1385  $\mu$ , and 1575  $\mu$  in length respectively. Two are split along the triradiate sutures, leaving only one valve in the apical region (Pl. 29, fig. 10) and the third has an irregular prolongation of the exine obscuring the intact end. The apices are darkened in a region of 20–25  $\mu$  radius, which probably represents the contact areas. The exine is scabrate, except in the central (equatorial) regions, where longitudinal striae give a fibrous appearance. The wall is 9–12  $\mu$  thick, splitting into two layers at the rough edges. There are no secondary folds.

*Occurrence.* Wyboston Borehole, depth 721 ft.

*Remarks.* These spores have the polar axial elongation characteristic of the fertile megaspore *Cystosporites*. The irregular prolongation of the exine at the end of one specimen may be a distal stalk similar to that of *C. devonicus* and *C. giganteus* (Zerndt) Schopf but it is not certain that it is in fact at the distal end of the spore. The spores differ from *C. devonicus* in the small contact areas and the nature of the exine in the central area.

*Associated miospore.* One thin-walled spore, diameter 60  $\mu$ , and with a short simple triradiate mark is appressed to one fragment.

## THE AGE OF THE MEGASPORES

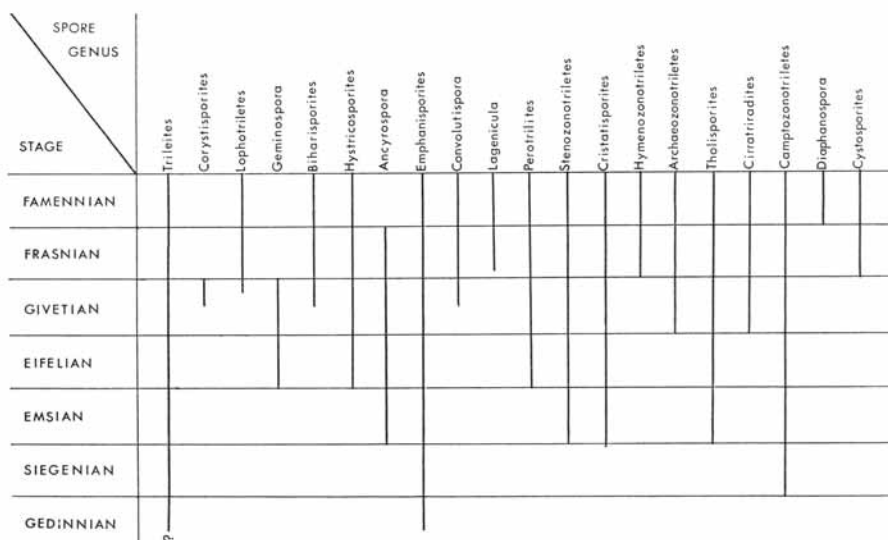
The megaspores have been found at depths between 700 and 720 ft. in the Wyboston Borehole. Fish fragments which occur at depth 560 ft. 3 in. have been compared to the genus *Bothriolepis*, which indicates a Middle or Upper Devonian age, with a probability in favour of the latter (H. A. Toombs pers. comm. to W. G. C. 1965).

Only three of the megaspore species have been reported previously. *Trileites langi* is known from the Eifelian and Givetian of the Orcadian basin (Richardson 1965), and similar forms from the lower Frasnian of the Russian platform (Archangelskaya 1963), the Upper Devonian of Bear Island (Sen 1958), and the basal Mississippian of Ohio (Winslow 1962). *Hystricosporites* (al. *Dicrospora*) *multifurcatus* is only known in Ohio, and there ranges from Upper Middle Devonian to basal Mississippian. *Cystosporites devonicus* is only known from the basal Frasnian of Quebec (Chaloner and Pettitt 1964). To these may be added the occurrence of *Hymenozonotriletes corrugatus* (which may be comparable with *Heliosporites variabilis*) in the lower Frasnian of Bashkir (Archangelskaya 1963). Together these suggest a late Middle Devonian or more probably early Upper Devonian age.

The megaspores are accompanied by well-preserved assemblages of miospores, showing a wide diversity of morphology. Spores with bifurcate appendages are especially abundant. It is hoped that these will form the subject of a later paper.

The occurrences of spores with bifurcate spines, and of other distinctive genera found in the Wyboston Borehole and previously recorded in other places, are summarized in text-fig. 2. In comparing these records it must be noted that the Orcadian Old Red Sand-

stone sequence comes to an end in the Givetian, and the Spitsbergen Devonian succession low in the Frasnian. In Western Australia only Frasnian sediments were sampled in the Caernarvon Basin and Famennian in the Canning Basin. More weight must therefore be given to the records from the succession of the Russian platform which runs from the Eifelian to the top of the Devonian system and on into the Carboniferous, and



TEXT-FIG. 2. Chart of the ranges in the Devonian period of some spore genera found in the Wyboston Borehole.

has been studied by several workers. These Russian records indicate a Givetian or lower Frasnian age for the Wyboston assemblage. It must be noted, however, that some important papers (e.g. Tchibrikova 1959, 1962 and Archangelskaya 1963) are, like the present paper, based on material from borings which is dated only on palynological evidence. This tentative dating does, however, give some support to that suggested by the megaspores alone, and it is in line with the indication of the fish remains.

#### POPULATION STUDIES OF SPORES WITH BIFURCATE SPINES

It is emphasized that the assemblages here studied were not consciously selected in any way. As mentioned above, test slides were made in the various stages of the preparation procedures, to reassure us that there had been no sensible loss of any of the constituents. It is, however, also recognized that any preparation procedure is in its nature a selection of the spores out of all the other constituents of the rock samples, and that the 100 per cent. recovery of the total spore assemblage is an ideal rarely achieved. Different procedures do discriminate to some extent against varying elements of the assemblage. This

has been quantified for three rock samples of diverse type by Hughes *et al.* (1964; see especially tables 6–8). Any attempt to compare spore assemblages must take account of this factor, and any difference between them must be of a greater order than that attributable to laboratory selection, before it can be significant.

Large spores with bifurcate spines were abundant in all the samples discussed in this paper, but especially so in sample Bt 4284, at depth 700 ft., where they comprise over 75 per cent. of the assemblage. Spores with bifurcate spines have been widely reported from sediments of Middle and Upper Devonian age but only Richardson has commented

TABLE 1. Relative percentages of species with bifurcate spines at depth 700 ft., Wyboston Borehole. \* Species recorded by Richardson from the Orcadian basin.

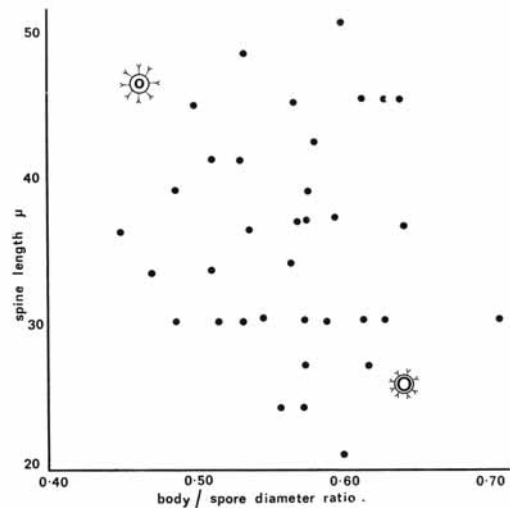
	%
* <i>Ancyrospora grandispinosa</i>	9
* <i>A. ancyrea</i> var. <i>brevispinosa</i>	20
* <i>A. ancyrea</i> var. <i>ancyrea</i>	3
<i>A. trocha</i>	19
* <i>A. longispinosa</i>	2
<i>A. langi</i>	1
Other species of <i>Ancyrospora</i>	31
<i>Hystricosporites delectabilis</i>	14
* <i>Perotrilites bifurcatus</i>	1
	100

on an abundance of them. He estimates them often to form as much as 50 per cent. of the assemblage from localities throughout the Orcadian Basin (Richardson 1962). Some comparison has been made with Richardson's work on the stratigraphic distribution of such spores in the Orcadian basin. Table 1 shows the relative percentages of the various species with bifurcate spines at depth 700 ft. Richardson's table (1962, fig. 14) shows that in Orcadia *Ancyrospora ancyrea* is not associated with *A. grandispinosa*, *A. longispinosa*, and *Perotrilites bifurcatus* above the Achanarras horizon, which straddles the Eifelian–Givetian boundary. However, only 35 per cent. of the bifurcate-spined spores from Wyboston correspond with the species found in the Orcadian basin. Text-fig. 3 shows a plot of spine length against body to spore-diameter ratio, similar to Richardson's 1962 table, and shows a scatter distinct from either of the two populations plotted by him (Eifelian–Givetian and M. Givetian respectively). If this were due to a slight evolutionary difference between the Wyboston spores and the Orcadian spores, the inference would be that the former are of earlier age than the latter. The available palaeontological evidence indicates the reverse to be the case. A small difference in depositional environment could, however, readily account for such a difference in population. Spores recovered from clastic sediments must have been subject, in the process of sedimentation, to the normal processes of sorting which are highly sensitive to differences of size and weight in the transported and deposited particles. The representatives of a single species in such a sedimentary environment will have a 'population structure' which may be a very modified version of that of the biological population from which it was derived.

Apart from spores with bifurcate spines, little comparison with the Orcadian assemblages is possible, since both spores with bifurcate appendages and spores with pointed spines are infrequent in our material.

## THE DISTINCTION BETWEEN MEGASPORES AND MIOSPORES

McGregor (1960), Richardson (1962), and Winslow (1962) have remarked on the considerable range in size observed in some Middle and Upper Devonian species, straddling the  $200\ \mu$  figure which in the Carboniferous is a practical, if arbitrary, dividing line between megaspores and miospores. This feature is illustrated again in two species from the Wyboston material, *Heliosporites variabilis* (diameter range  $190\text{--}535\ \mu$ ), and



TEXT-FIG. 3. Scatter diagram to show 'body'/spore diameter ratio plotted against spine length of *Ancyrospora ancyrea*; based on 35 specimens from depth 700 ft., Wyboston Borehole.

*Hystricosporites obscurus* (diameter  $177\text{--}440\ \mu$ ). Richardson and Winslow have suggested that the variable size of these spores may be related to the incomplete establishment of heterospory in the parent plants. Winslow mentions the possibility that while larger specimens of *D. multifurcata* (size range  $100\ \mu$  to  $300\ \mu$  without spines) may have functioned as megaspores, the smaller specimens may have functioned as their corresponding miospores.

## DISCUSSION

*The affinities of the megaspores.* In addition to these genera whose sizes range across the  $200\ \mu$  limit discussed above, several of the species described in this paper are smaller than the average size of Carboniferous megaspores. The upper size limit of *Trileites langi* is  $400\ \mu$  (Richardson 1965), of *Hystricosporites obscurus*  $440\ \mu$ , of *Lagenicula paulispinosa*  $565\ \mu$ , of *Lagenoisporites* sp.  $420\ \mu$ , and of *Biharisporites simplex*  $630\ \mu$ . However, others (e.g. *Triangulatisporites* sp., *Zonalesporites* sp.) are not much smaller than Carboniferous species of these genera. Such large megaspores have long been known from the Upper Devonian. Sen (1958) redescribed three species from the Upper

Devonian of Bear Island with size ranges between 1000  $\mu$  and 2000  $\mu$  which had been originally described but not named by Nathorst. Chaloner (1959) found specimens of *Biharisporites ellesmerensis* up to 1610  $\mu$  in diameter in the Upper Devonian of Ellesmere Island, and, commenting on the rise in mean size of megaspores from the Devonian into the Upper Carboniferous, sought to correlate this with the rise of the arborescent lycopods during the latter period. The species of megaspores described in this paper have a mean maximum size of 810  $\mu$ , considerably below the Upper Carboniferous mean of 1600  $\mu$  cited by Chaloner, and to this extent they are consistent with the pattern of progressive size increase suggested by the earlier evidence.

Although many of the very large Carboniferous megaspores are now known to be correlated with arborescent lepidodendrids and sigillarians, size of the megaspore alone is no reliable indication of size of the parent plant. Some of the largest lepidostrophi (e.g. *Lepidostrobus browni*) were presumably borne on arborescent lepidodendrids and yet bore relatively small megaspores. Perhaps the only aspect of the present megaspore assemblage from which palaeobotanical deductions may safely be made is their considerable diversity of form. Only one Devonian lycopod (*Cyclostigma kiltorkense*) has been shown to be heterosporous. Only three other genera of Devonian plants (*Enigmophyton*, *Barinophyton*, and *Archaeopteris*) are believed to be heterosporous and these have singularly simple azonate megaspores. It is evident from the present study that the heterosporous plants of the Devonian must have far exceeded in number, and perhaps in diversity, their known representation in the megafossils.

*The rock samples.* The samples between 700 ft. and 722 ft. 1 in. depth, in which the megaspores were found, are medium-grey flaggy siltstones or mudstones with silty partings. The horizontally bedded sequence is interrupted at depth 719 ft. 8–11 in. by a thin conglomerate.

Plant remains of two kinds occur, and are concentrated on particular bedding planes. The more common are compressions of fragments of naked axes from 1 to 3 mm. broad and up to 5 cm. long. None show any spines, leaves, or other emergences. Many are longitudinally striate, some with one or more stronger central striae. They are probably fragments of spineless psilophytes. The less common are billets of wood up to 4.5 cm. broad and 9.5 cm. long, being limited in length by the size of the hand specimens. They have thickness up to 0.5 cm., are mostly coalified and partly pyritized, with subregular cross-fractures of the type described by Arnold (1934). One end of each piece is preserved on any one core, and is the rounded shape characteristic of water-worn wood. The wood is of the 'gymnospermous type', either Progymnospermopsida or possibly, true Gymnosperms. Although on some fragments individual wood elements could be recognized, the details of pitting could not be discerned.

There are fish teeth in the mudstone at 700 ft. depth (Bt 4284). Mica is common in the siltstone, sometimes covering a bedding plane. Pyrite is also common, in places forming groups of crystals in the body of the mudstone and partly replacing plant fragments. There is limonite staining round the larger plant fragments. Small particles of coaly material are common throughout. There is very little calcium carbonate. Other samples, less rich in spores, show fragmentary lamellibranchs and ostracods, also concentrated on particular bedding planes.

All the fossils so far mentioned could have been deposited in a freshwater environ-

ment. Some other microfossils have also been found in the spore preparations. These are rare acritarchs and occasional chitinozoans and conodonts. The first two groups belong to simple long-ranging types and it is possible that they have been reworked from older sediments. In the case of the conodonts this seems less likely, since they are well preserved. Cases of reworked conodonts are known and have been discussed by Lindström (1964) and Krebs (1964). Both admit that well-preserved conodonts may be reworked. On the other hand, the occurrence of the conodonts accords with Youngquist's observation (1951) that these fossils are commonly associated with plant remains in a near-shore environment, and also frequently with fish remains.

The oscillation in grain size and fossil content, suggests a shallow-water environment, with occasional downwashes of plant material from nearby land, but the degree of salinity of the environment is not known.

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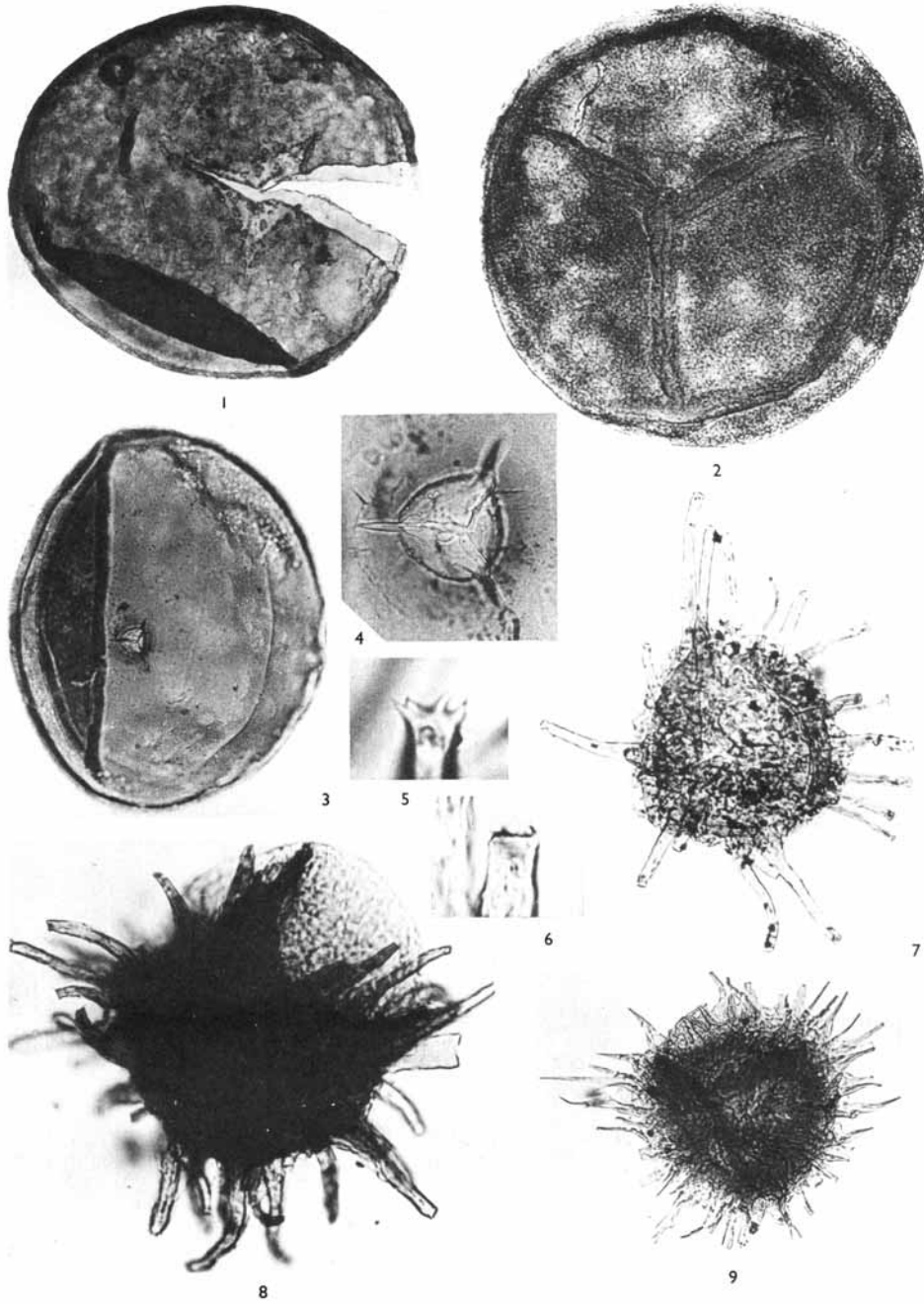
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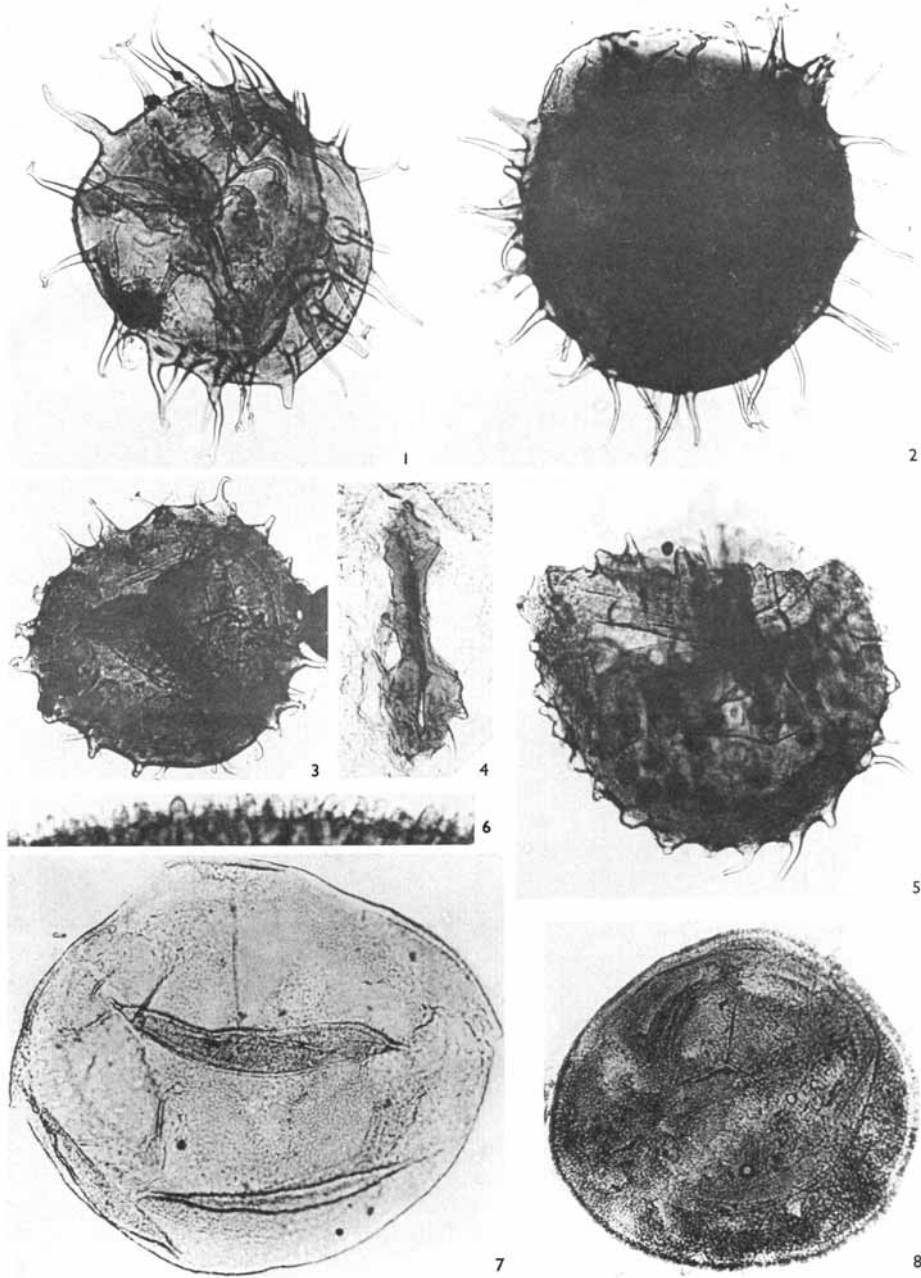
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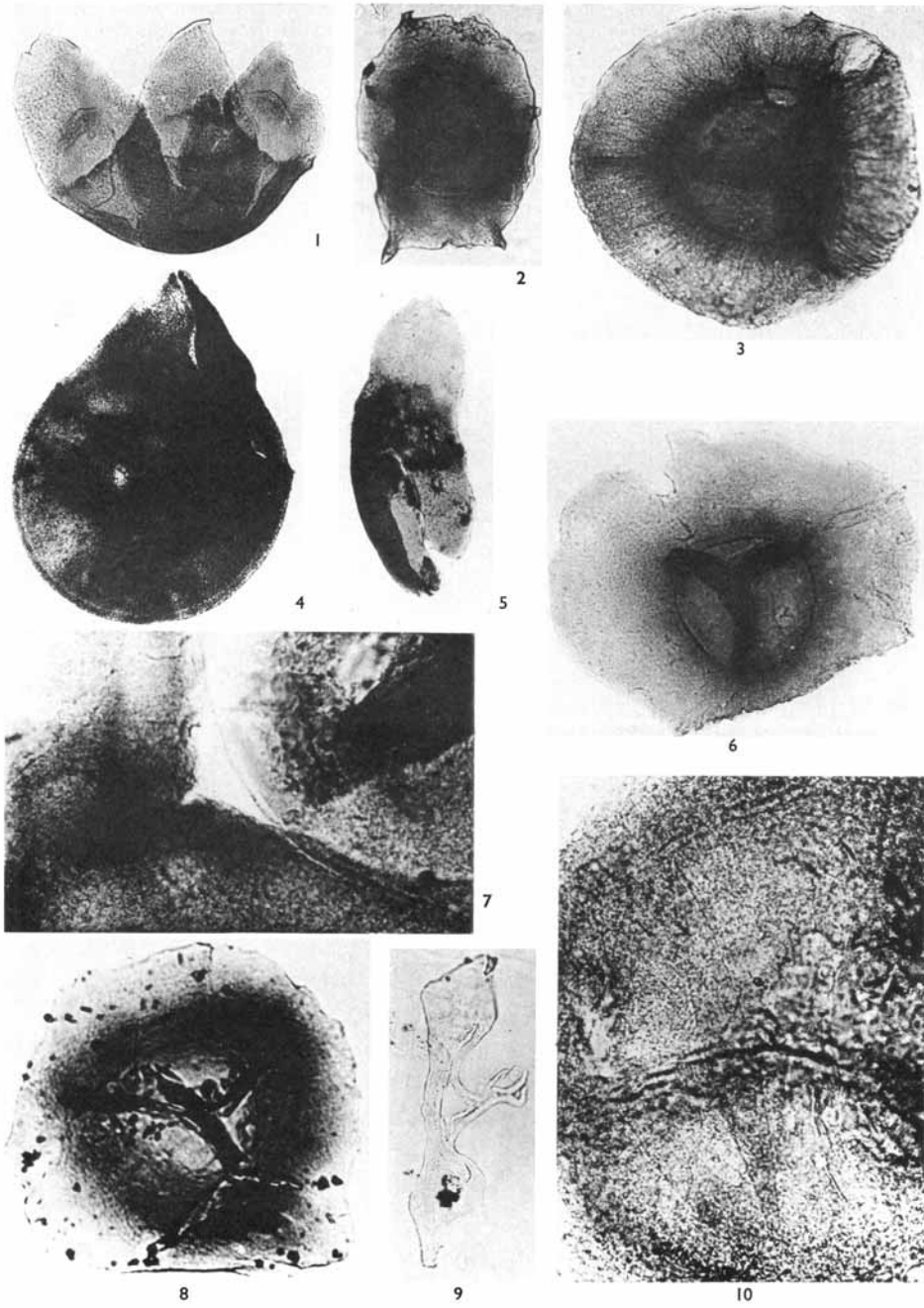
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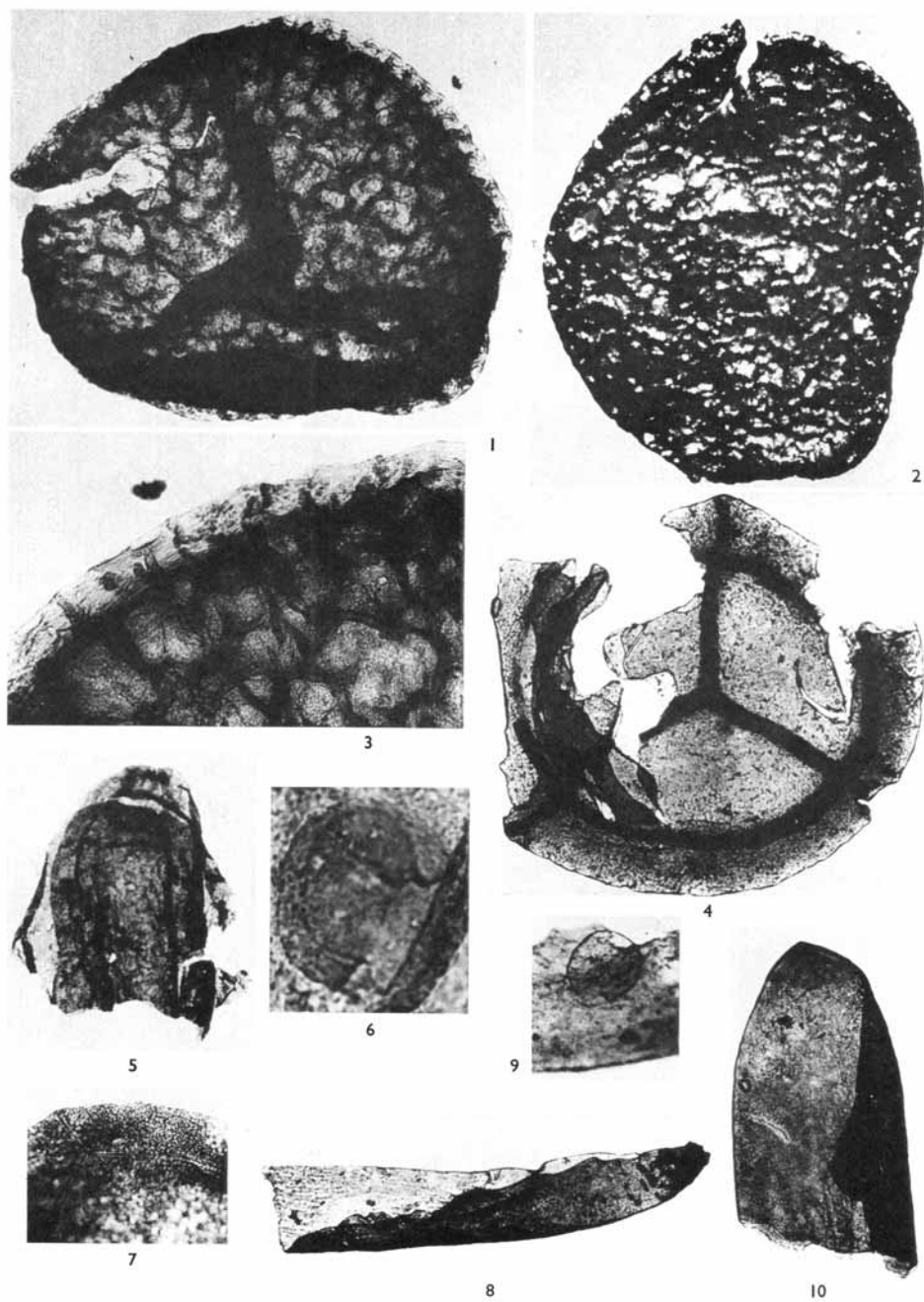
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