TETRAPTERITES VISENSIS—A NEW SPORE-BEARING STRUCTURE FROM THE LOWER CARBONIFEROUS

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ABSTRACT. *Tetrapterites visensis* gen. et sp. nov. is the name given to examples of a spore-bearing structure from two Lower Carboniferous shales. A spore tetrad is enclosed by a non-cellular membrane of basic tetrahedral shape with wing-like appendages at the apices. These apical modifications (herein designated skiadions) are also found as separate entities in the assemblages and resemble saccate spores. Detailed descriptions of the *Tetrapterites* capsule and component parts are given and an attempt is made to explain its unusual organization.

BOTH authors have been engaged in independent studies of miospores from Lower Carboniferous shales. H. J. S. has been concerned with an assemblage from a shaly intercalation in the Drybrook Sandstone of the Forest of Dean, Gloucestershire, and A. F. H. with plant microfossils from a shale in the Basement Series outcropping on the Caernarvonshire side of the Menai Straits, North Wales. The microfloras from these two shales contained many elements in common; in particular, they were characterized by the presence of pseudosaccate grains which, although usually occurring as separate entities, were also observed as part of a larger structure which is of considerable palaeobotanical interest since it appears to represent a spore tetrad unit of unusual organization. The purpose of this communication is to give a detailed morphological description of the tetrad unit on the basis of material obtained from both shale preparations. The pseudosaccate grains which are a constituent part of this structure may be expected to occur in other spore separations, and because of their distinctive morphology and known presence at similar horizons at two widely separated localities, they may prove to be useful stratigraphical indices.

Location and geological horizon of the samples. The specimen of shale from the Drybrook Sandstone was taken from a level 33 feet above the exposed base of this formation in the more easterly of two quarries on Plump Hill, near Mitcheldean, 160 yards south of the A 4136 Monmouth to Mitcheldean road (Grid ref. SO 661168). The shale was near the base of a 25 feet layer (preserved as a bluff in the quarry) interposed between massive, fine-grained, white, pink, or mottled sandstones with occasional bands of quartz pebbles.

The Drybrook Sandstone was placed in the Seminula Zone [S_2] of the Lower Carboniferous by Sibly (1918, p. 25) on the basis of brachiopods obtained from a calcareous intercalation (the Drybrook Limestone) which is present in the more southerly outcrops. Recently, Allen (1961) and Lele and Walton (1962) have described plant impressions from a siltstone layer in the Drybrook Sandstone of Puddlebrook on the western limb of the Wigpool syncline; the latter have also investigated the miospores from the bed. Lele and Walton (1962) believed that the plant mega- and microfossils indicated that the horizon of the Drybrook Sandstone was below that cited on the brachiopod evidence. However, it is doubtful whether such a conclusion was justified. Lele and Walton (1962,

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pp. 149–50) compare their plant remains with similar forms found at the base of the Lower Brown Limestone of Dyserth, North Wales; and in the Calciferous Sandstone Series of Eskdale, in the Border region of Scotland. The fauna of the Lower Brown Limestone suggest a Lower Dibunophyllum [D_1] Zone age and, therefore, more likely to be younger rather than older than the Drybrook Sandstone. Lacey (1962) in his recent description of the plant remains from the Lower Brown Limestone admits (p. 154) they afford inconclusive evidence of age, but are likely to belong to the Upper Viséan. The correlation with the flora recorded by Kidston (1883) from Eskdale is, at present, of little value in determining the position in the coral/brachiopod zonal scheme because of the uncertainty regarding the equivalence of these rocks with the Dinantian sequences in the Central and Southern Provinces.

The miospores described by Lele and Walton (1962) from the siltstone lacked any distinctive forms on which any assessment of age could be based. The shale sample from the Drybrook Sandstone contained a varied and well preserved microflora (Sullivan, in press) which confirms the Upper Viséan age of these rocks.

The sample from the Basement Series of the Carboniferous Limestone of the Menaian region was collected from a lenticle of shale, maximum thickness 3 feet, referred to by Greenly (1928, pp. 420–1). The shale has an outcrop of 40 yards close to the Britannia Tubular Railway Bridge (Grid. ref. SH 541708) and when traced laterally wedges out into conglomerates.

The Basement Series of the Carboniferous Limestone in the Menaian region carries a fragmentary fauna, mainly of brachiopods. The lowest horizon containing abundant animal remains lies near the base of the overlying Lower Brown Limestone. There is a slight divergence of opinion regarding the age of these beds and they have been variously assigned to the base of D_1 or to the top of S_2 (Greenly 1928, Neaverson 1946, George 1958).

Plant remains known from these beds were first described by Walton in Greenly (1928, pp. 408–10) and the list of species later extended by Lacey (1952*a*, *b*). The plants recorded by Lacey (1952*b*, p. 376) were collected from the same shale band and at the same locality as the plant microfossils described in the present paper. Lacey (1952*b*, p. 376) also mentions the varied and well-preserved microflora in which Mrs. E. M. Knox recognized thirty spore types distributed through thirteen genera. A detailed account of this assemblage is being prepared by one of the authors (A. F. H.) as part of a doctoral dissertation on the Viséan and Namurian spores of North Wales.

It will be apparent from the foregoing account that there is a little doubt concerning the exact age of the shales from the Drybrook Sandstone and the Basement Series. A similarity in the composition of the miospore assemblages indicates that one is dealing with closely comparable horizons. An analysis of the stratigraphical information favours the view that the samples belong to the upper part of the Seminula Zone.

Preparation of the samples. The sample of shale from the Drybrook Sandstone was in a very weathered condition and much care was needed in its preparation. The addition of the normal 40 per cent. hydrofluoric acid produced a violent effervescence and so it was necessary to dilute the acid with three times its own volume of distilled water; the polythene container was also immersed in ice to arrest the rise in temperature. Even under these conditions the reaction was complete after only 2 hours. The acid was decanted off and the residue washed with distilled water. No maceration was required, presumably because of the atmospheric oxidation, and the structureless organic debris was removed by the addition of 2 per cent. caustic potash.

The Menaian sample was treated with cold 40 per cent. hydrofluoric acid for several days until all the mineral matter had dissolved. The residue was macerated with fuming nitric acid for 2 hours, washed with progressively more dilute nitric acid and, finally, with distilled water. Both samples were non-calcareous and prior treatment with dilute hydrochloric acid was unnecessary.

SYSTEMATIC DESCRIPTION

Single and compound mounts were made either in glycerine jelly or in cellosize with a balsam cement (Jeffords and Jones 1959). The holotype of *Tetrapterites visensis* and other illustrated specimens have been deposited in the permanent collection of the Micropalaeontological Laboratory of the Department of Geology, Sheffield University.

To facilitate the description of *Tetrapterites*, several morphological terms have been introduced. We propose to apply the term *capsule* to the 'whole' *Tetrapterites* unit, i.e. a structure containing a tetrad of spores. Owing to the uncertainty regarding the precise function of *Tetrapterites*, it is possible that our use of this term may not conform to strict botanical practice, but it is intended to express quite simply the idea of a 'spore receptacle'. The capsule consists of a tetrad of spores surrounded by a non-cellular membrane which is basically tetrahedral in form (text-fig. 1). The outer covering is called the *wall membrane*. The wall membrane is extended into wing-like appendages at the apices. The apical portions of the capsule have been named *skiadions* (Gr. σκιάδειον, umbrella or cover). The skiadions become detached from the rest of the wall membrane and are composed of two distinct parts. The darker-appearing, originally bowl-shaped, central area is called the *cupule* and this encloses the distal hemisphere of the spore (text-fig. 2). The outer, and structurally lower, part of the skiadion is the *wing* (text-fig. 2).

Genus TETRAPTERITES gen. nov.

Type species. Tetrapterites visensis gen. et sp. nov.

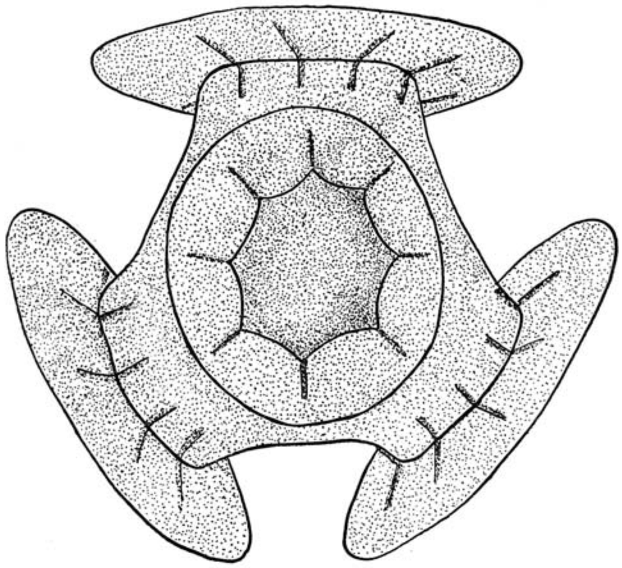
Diagnosis. Spore tetrad enclosed by a non-cellular membrane which has a basic tetrahedral shape and possesses wing-like modifications at the apices.

Tetrapterites visensis gen. et sp. nov.

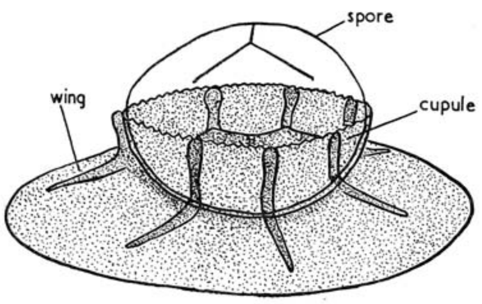
Plate 13, figs. 2–5; Plate 14, figs. 1–6

Holotype. The specimen illustrated (Plate 13, fig. 2) from a shale in the Basement Series of the Carboniferous Limestone of the Menai Straits, Caernarvonshire, North Wales.

Diagnosis. Dimension of capsule approximately 200 μ, diameter of holotype 190 μ; spores radial trilete, amb circular to oval, exine laevigate, size 50–70 μ; as sporae dispersae they would be classified as *Punctatisporites*; wall membrane opaque to translucent (depending on the degree of maceration); skiadions 105–155 μ in diameter, cupule about half of total radius, parallel-sided folds are located on the outer rim of the cupule and continue across the upper surface of the wing; the base of the cupule has a characteristic cuspidate outline with seven to nine angles separated by concave margins; upper border of cupule is irregular.



TEXT-FIG. 1. Diagram to illustrate the basic tetrahedral symmetry of *Tetrapterites visensis* gen. et sp. nov.



TEXT-FIG. 2. Diagrammatic representation of a skiadion of *Tetrapterites visensis* and its associated spore.

Description. Examples of skiadions in their original apical positions are illustrated in Plate 13, figs. 1–2, 4–5. The specimen Plate 13, fig. 1 was photographed while in an open mount. Three skiadions and four spores are present; the fourth skiadion had been attached at the left hand side of the figure. During the preparation of this specimen as a single-grain mount, one of the skiadions and its associated spore broke away from the remainder of the group. The two separated elements are shown as Plate 13, figs. 2, 3. The larger of these two portions (Pl. 13, fig. 2) has been selected as the holotype of *Tetrapterites visensis*. This has three laevigate spores enclosed by a wall membrane with two attached skiadions.

The wall membrane of the capsule (Pl. 13, fig. 4) is reddish-brown in colour and has a resinous texture. The wall is too thick to reveal the details of the spores inside the capsule, although their outlines can be discerned in the region of the apices. The skiadion below the capsule in Plate 1, fig. 4, was probably originally attached in the plane of the photograph. The opacity of the wall membrane is a function of the period of maceration; the Menaian specimens were treated with fuming nitric acid for 2 hours and as a result appear more translucent than those from the Drybrook Sandstone which were unmacerated. The skiadions seem less affected by maceration and the preservation in both separations was very similar.

The skiadion and its associated spore which became detached from the capsule (Pl. 13, fig. 2) is illustrated in Plate 13, fig. 3. It is preserved in semi-lateral view and clearly shows the bowl shape of the cupule (Pl. 14, fig. 2). Another example (Pl. 14, fig. 1) has become distorted during compression and the spore and the skiadion no longer bear their original relationship to one another. One of the rays of the tetrad scar can be seen in the portion of the exine not covered by the cupule (Pl. 14, fig. 3).

The spores which occur as tetrads within the capsule range from 50–70 μ in diameter. They have laevigate exines, often with crescentic secondary folds, and are circular to oval in outline: as sporae dispersae they would be classified as *Punctatisporites*. It is presumed that the spores were not tightly clasped by the cupule because of the infrequency in which they occur together. Furthermore, in the rare cases when the spore is observed within the cupule, the position of the trilete is variable.

The most common remains recognizable as belonging to *T. visensis* are the skiadions (Pl. 14, figs. 4–6). They vary in size from 105 to 155 μ and are usually oval in outline (Pl. 14, figs. 4, 5), rarely circular. The cupule is sharply defined from the wing and occupies approximately half of the total radius of the skiadion. The cupule is composed of a depressed, saucer-shaped base surrounded by a rim about 10 μ high, but now compressed in the horizontal plane. The upper border of the cupule is ragged and it is along this line that the skiadion separates from the remainder of the wall membrane. This feature is clearly evident in Plate 14, fig. 6. The base of the cupule displays a characteristic cuspidate outline; there are between seven and nine cusps separated by concave margins (Pl. 14, fig. 6). There is a darker, and presumably thicker, zone around the base of the

EXPLANATION OF PLATE 13

Specimen references; DS, Drybrook Sandstone of the Forest of Dean; MS, Basement Series of the Carboniferous Limestone Series of the Menai Straits.

Figs. 1–5. *Tetrapterites visensis* gen. et sp. nov. 1, Capsule with three skiadions and four spores: this specimen separated into two parts on mounting; $\times 400$. 2, Holotype, MS1a; the larger portion of the group illustrated in fig. 1; $\times 400$. 3, Skiadion containing spore which separated from the base of the specimen illustrated in fig. 1, MS1b; $\times 500$. 4, Capsule with three skiadions attached at the apices and a fourth below the group which may possibly have been attached in the plane of the photograph, DS1/1; $\times 250$. 5, Enlarged view of one of the skiadions in fig. 4 (this plate); the folds can be seen to originate at a concentric zone of thickening above the cupule, DS1/1; $\times 1000$.

cupule which has an ill-defined inner limit (e.g. Pl. 14, fig. 5). Parallel-sided folds are located at the angles of the cuspidate base and are disposed in a radial manner. The folds run down the exterior of the cupule rim and continue across the upper (proximal) surface of the wing. In the skiadion (Pl. 13, fig. 5) the folds appear to arise from a concentric zone of thickening below which the wall membrane ruptures. In some cases the folds at the cupule margin have terminal thickenings (Pl. 13, fig. 3; Pl. 14, fig. 2). There are usually the same number of folds as there are cusps at the base of the cupule, but it sometimes happens that folds are absent at one or two (never more) of the angles (e.g. Pl. 14, figs. 5, 6). In no instance were folds observed between the cusps.

The significance of the cuspidate outline of the base of the cupule is still a matter of conjecture. It may result from, or merely be accentuated by, compression. It is possible that the cusps may be the points at which the cupule is attached to the wing. Whatever the explanation, the constancy in the number and arrangement of the cusps is indicative of a control by some inherent structural character of the skiadion. The wing and the cupule are without ornamentation. The only visible structure is an irregular pitting which is probably due to corrosion.

Remarks. The capsules and skiadions of *T. visensis* were only minor elements in the preparations from the two samples. An estimated frequency is in the region of 0·02 per cent. This figure excludes the spores of *Punctatisporites* which may have arisen from tetrads enclosed within the wall membranes of *Tetrapterites*. The proportions of spores morphologically similar to those observed in *T. visensis* were 26 per cent. and 9 per cent. for the Drybrook and Menaian samples, respectively. These spores have been referred to *Punctatisporites platirugosus* (Waltz) by Sullivan (in press). It is unlikely that more than a small fraction of the total were derived from *Tetrapterites*. Indeed, *P. platirugosus* was observed in the Drybrook Sandstone preparations as large masses containing upwards of forty or fifty specimens and obviously represented the contents of sporangia. The number of complete or incomplete capsules (spores enclosed by a wall membrane which has two or more skiadions attached at their original apical positions) present in both assemblages was six. The skiadions totalled seventy-five and, of these, only two had retained the spore in the cupule. It was surprising that examples of wall membrane without skiadions or spores were not identified in the preparations. It is not implied that they do not exist, merely that they present problems in recognition.

Comparative morphology. The mode of occurrence of spores in sediments (sporae dispersae) or in fructifications ('*sporae in situ*' of Potonié (1962), but perhaps *sporae inclusae* would be a better name) is either as individuals, or as isolated tetrads, or as tetrads making up the whole or part of a sporangial cluster. The contents of a mature sporangium can take the form of a single tetrad as is the case with many megasporangia, but in those cases the tetrad is surrounded by a sporangial wall which has a cellular structure. The wall membrane of *Tetrapterites* is non-cellular and cannot therefore be equivalent to a sporangial wall or even the remains of one.

The organization of *Tetrapterites* is unusual; a search through the literature of both living and fossil plants has not revealed any comparable structure. However, attention may be drawn to *Didymosporites scotti*, a megaspore tetrad described by Chaloner (1958) from the coenopterid fern *Stauropteris burntislandica*, consisting of two large fertile spores and two small abortive ones surrounded by a cuticular network. It is possible that the wall membrane of *T. visensis* could have the same origin as that of the cuticular network of *D. scotti* which Chaloner (1958, p. 201) believes to be the remains of a tapetum. The remains of *D. scotti* have been observed in the Drybrook preparations, but the possible significance of its association with *T. visensis* is not known.

Certain features observed in living plants may have a bearing on the interpretation of the structural organization of *T. visensis*. In the Order Hepaticae certain species of the genus *Sphaerocarpus* liberate spores in the form of tetrads. A special wall develops between the spore mother cell wall and the individual spores. This wall is thick and is arranged in the pattern of the future ornamentation of the spore exine; it thickens distally before the spores themselves have completed wall formation on their proximal faces. A special wall would thus surround the tetrad and one would observe the following sequence of mutually enclosing membranes: sporangium wall, spore mother cell wall (which disappears at maturity), special wall and, finally, spore wall (exine). It is conceivable that the wall membrane of *T. visensis* could be equivalent to a special wall which is non-cellular.

Another possible explanation is that the laevigate spores represent the inner layer (intexine) of the exine and that the wall membrane is the outer layer (exoexine). In an immature condition the intexine may become separated at both poles whilst the exoexine is detached at the distal pole only. This stage in development has been observed in some species of *Pellia* (Hepaticae).

Whatever the explanation of the organization of *T. visensis* it is possible to suggest its function in the reproductive cycle. The wing-like modifications of the wall membrane are clearly a morphological adaptation to facilitate transport of the capsule through the air or water. The rupture of the wall membrane takes place near the apices and the skiadions separate to release the spores.

The separated skiadions of *Tetrapterites* do sometimes display a superficial resemblance to certain genera of Acritarchs. In the genus *Pterospermopsis* Wetzel 1952, the spherical capsule is surrounded by an equatorial wing which may bear radial folds, e.g. *P. helios* Sarjeant 1959 from the Cornbrash of Yorkshire. Several species of *Cymatiosphaera* (Wetzel 1933) Deflandre 1954, e.g. *C. mirabilis* Deunff 1958 from the Ordovician of Brittany and *C. miloni* Deunff 1957 from the Devonian of Canada, have membranes which are supported by rodlets: these on compression can simulate the wing of *Tetrapterites*.

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EXPLANATION OF PLATE 14

Figs. 1–6. *Tetrapterites visensis* gen. et sp. nov. 1, A skiadion with its associated spore, MS2; ×500. 2, Enlarged view of the cupule and spore of the skiadion illustrated in Plate 13, fig. 3; note the bowl-shaped nature of the cupule, the thickened termini of the radial folds, and the irregular upper margin of the cupule, MS1b; × 1000. 3, Enlarged view of portion of fig. 1 (this plate) to show the spore in the cupule; one of the rays of the trilete is clearly visible, MS2; ×1000. 4–6, separated skiadions of *T. visensis*. 4, DS3/1; ×500. 5, DS2/1; ×500. 6, Enlarged view of cupule of skiadion illustrated in fig. 5 (this plate); to show the cuspidate outline of the base and the irregular upper margin, DS2/1; ×1000.

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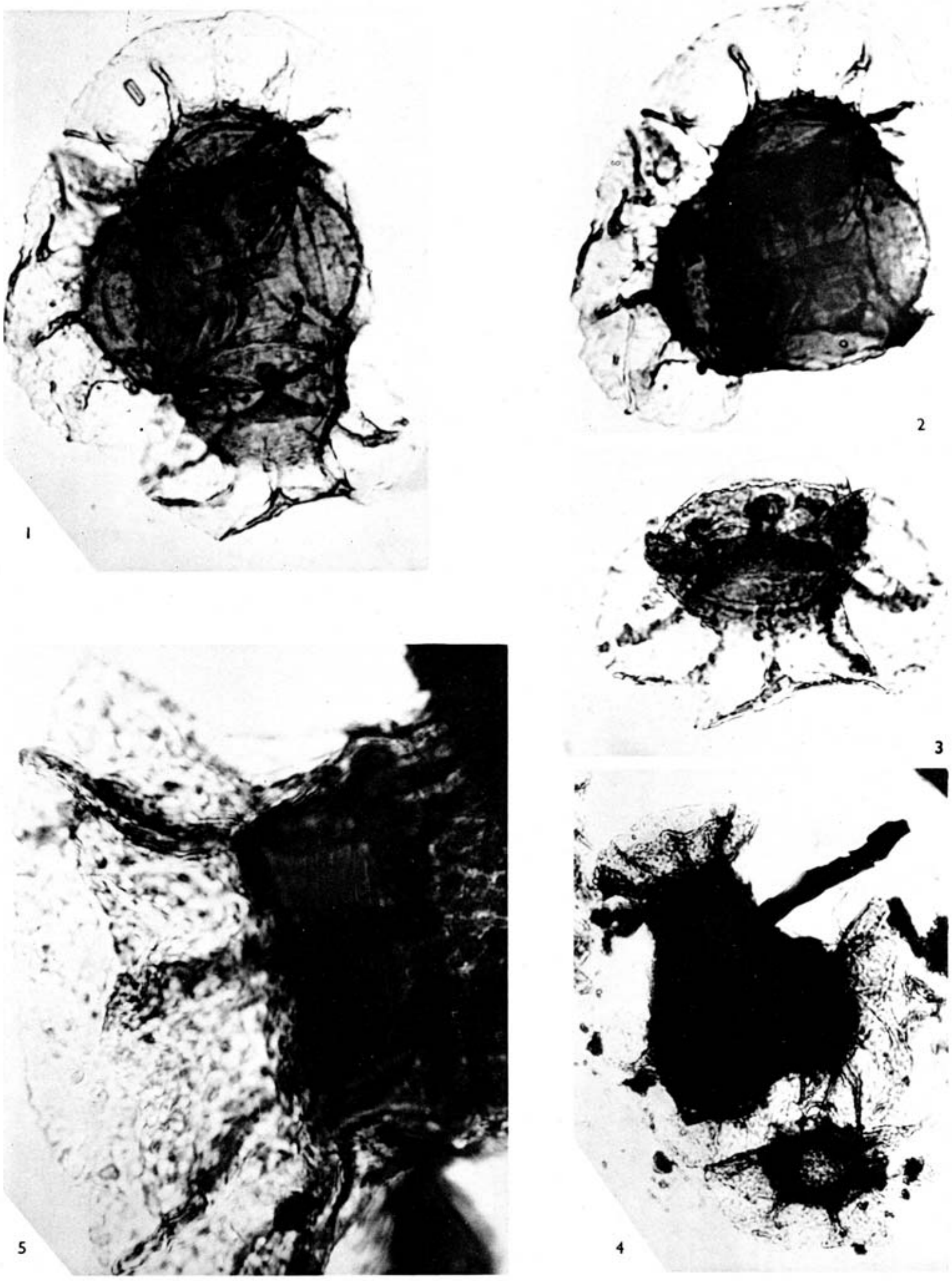
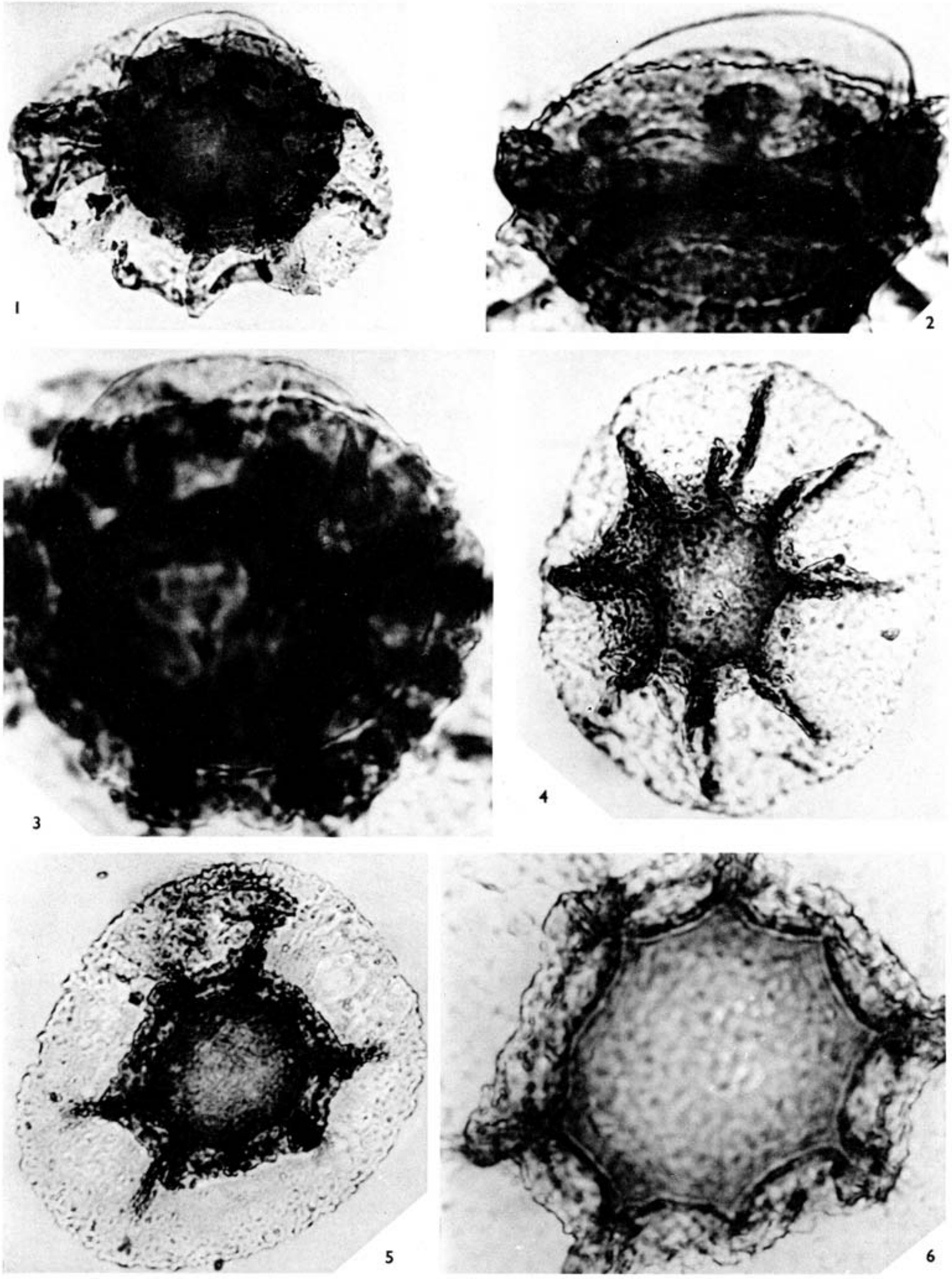


SULLIVAN and HIBBERT, Lower Carboniferous spore-bearing structure



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