A SEED MEGASPORE FROM THE DEVONIAN OF CANADA

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ABSTRACT. A megaspore tetrad, *Cystosporites devonicus* sp. nov., is described from the Upper Devonian of Scaumenac Bay, Quebec, Canada. *Cystosporites* megaspores have previously been reported only from the Carboniferous, where they have been found in the lycopod seed *Lepidocarpon*. The occurrence of this Canadian *Cystosporites* shows that a level of heterospory equivalent to that reached by *Lepidocarpon* had already been attained by the late Devonian.

THIS paper is an account of some Devonian fossil megaspore exines (briefly described in Chaloner and Pettitt 1963) which had, in at least one respect, reached the level of differentiation achieved in the seed plants. They consist of isolated tetrads, each consisting of one large (about 2 mm.), oval (presumably fertile) megaspore, and three very much smaller (presumably abortive) spores. They closely resemble the seed megaspores formed inside the Carboniferous lycopod seed *Lepidocarpon*. Hitherto the highest degree of heterospory reported in Devonian fossil plants is that in which many megaspore tetrads reached maturity in each megasporangium (e.g. in *Cyclostigma kiltorkense*, *Archaeopteris latifolia*) and were apparently shed, much as in the living *Selaginella* or *Isoetes*. The fossils described here show that a level closely approaching that of seed formation had already been attained in the Devonian.

Materials and methods of investigation. The material from which the megaspore tetrads were obtained was collected from the Upper Devonian Escuminac Formation of Scaumenac (Escuminac) Bay, Quebec, Canada, in 1934 and 1937 by W. Graham-Smith and deposited in the Department of Palaeontology, British Museum (Natural History). The Escuminac Formation is generally accepted as being of early Upper Devonian age (Cooper *et al*. 1942, McGregor 1959). One of the samples, a hard sandstone, bears compressions of *Archaeopteris* foliage and sporangia, whilst the second, a more indurated finer-grained sandstone from the Acanthodian Bed of the same locality, bears compressions of a thickly cutinized plant axis of unknown affinity.

The sandstone was mechanically crushed into small pieces and disaggregated further in commercial (40 per cent.) hydrofluoric acid for several hours. After washing and sieving, the megaspores were picked out and macerated individually in Schulze's solution (potassium chlorate in nitric acid) for 2 to 3 hours, until they were sufficiently transparent for examination by transmitted light. When this oxidative maceration was complete the spores were transferred to dilute ammonia solution for a few minutes and then washed and mounted in glycerine jelly, 'Clearcol' or Canada balsam. Spores of the same type were also seen on the bedding planes of the Acanthodian Bed and one of these spores was removed from the matrix with a needle and treated as outlined above.

To help in resolving the structure of the spore wall, serial sections of several of the macerated specimens were cut. These were dehydrated in 95 per cent. alcohol and cleared in methyl benzoate followed by a solution of 1 per cent. celloidin in methyl benzoate.

[Palaeontology, Vol. 7, Part 1, 1964, pp. 29–36, pls. 3–4.]

After a brief period in benzene, the spores were infiltrated with paraffin wax of melting point 45° C and then transferred to wax of melting point 54° C for about 45 minutes to complete embedding. Serial sections were cut on a microtome at 6 μ; the sections were dewaxed and mounted in Canada balsam.

All the preparations are in the collections of the Department of Palaeontology, British Museum (Natural History), registered numbers V45428 to V45450.

Acknowledgement. We wish to express our thanks to Mr. J. V. Brown for his patient help in taking the photographs.

SYSTEMATIC DESCRIPTION

GENUS CYSTOSPORITES Schopf 1938

Cystosporites devonicus sp. nov.

Plate 3, figs. 1–6; Plate 4, figs. 1–3, 6

Diagnosis. Isolated megaspore tetrads composed of one large, elongated megaspore (presumed fertile), and three small ones (presumed abortive). Fertile spore up to 2,550 μ in length; abortive spores typically 130–70 μ in diameter. Open triradiate suture (laesure) visible at apex of fertile spore when abortive spores are missing; sutures typically 100–150 μ long. Weakly differentiated contact faces on fertile spore correspond to position of abortive spores. Exine of fertile spore minutely granular in texture, without discernible sculpture as seen in profile, 10–15 μ thick. Wall of abortive spores typically 10–12 μ thick, ornamented with conical processes 1–2 μ high and 1–2 μ apart. Distal extremity of fertile megaspore exine sometimes extended as a solid, tapering, truncated stalk-like process.

Holotype. V45428, Department of Palaeontology, British Museum (Natural History); Pl. 3, figs. 1, 2.

Type Locality. Escuminac Formation, Upper Devonian; Scaumenac Bay, Quebec, Canada.

Description

Variation in size and shape. The large fertile megaspore of each tetrad is typically ellipsoidal, being elongated along its polar axis (Pl. 3, figs. 1, 3). The largest is 2,550 μ long, and a typical specimen about 2,000 μ. This is very much larger than average Upper Devonian megaspores of presumably free-sporing type with normal tetrad development. A single, very much smaller, tetrad was isolated (Pl. 3, figs. 4, 7) in which the largest spore was 250 μ in length, and only slightly elongated (Pl. 3, fig. 7); the abortive spores (diameter 50–62 μ) became detached from it during mounting (Pl. 3, fig. 4). It is questionable

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EXPLANATION OF PLATE 3

Figs. 1–7. *Cystosporites devonicus* sp. nov., from the Escuminac Formation, Scaumenac Bay, Quebec, Canada. All the photographs were taken by transmitted light; all the slides are in the British Museum (Natural History). 1, Holotype, V45428; × 50. 2, Part of the same specimen showing the three abortive spores at the apex; × 200. 3, Larger specimen, V45429; the irregular mosaic of pale areas on the exine is attributed to impressions of coarse particles of matrix; × 50. 4, 7, The smallest tetrad found, V45430; the three abortive spores (4) became detached from the fertile spore (7) in mounting; × 200. 5, Fertile spore which ruptured along three splits extending from the triradiate sutures, to form three partial valves, V45431; × 25. 6, Transverse section of a seed megaspore showing the homogeneous character of the exine and a longitudinal secondary fold, V45447; × 200.

how far the observed size variation represents ontogenetic stages; evidently all the spores were sufficiently cutinized to survive fossilization and eventual maceration in Schulze's solution. Chaloner (1952) has observed considerable size variation in the seed megaspores (*Cytosporites*) contained within otherwise typical sporophylls of *Lepidocarpon waltoni*. It may be that some of the smaller tetrads represent those formed in sporophylls near a cone apex, rather than merely immature forms. But the thin (3–4 μ) wall and extremely small size of the tetrad of Plate 3, fig. 4 rather suggests immaturity.

Most of the fertile spores are darker at the ends (poles) and lighter (and probably thinner) in the central (equatorial) region. A number of secondary folds are usually developed, mainly parallel to the long axis presumably corresponding to collapse of an originally ellipsoidal body (Pl. 3, figs. 1, 3; also seen in section in Pl. 3, fig. 6). The polar axial elongation of the fertile spore, which is usually about three times the equatorial width, is a significant feature of agreement between these Devonian spores and the Carboniferous *Cystosporites*. In free-sporing heterosporous plants in which all four members of the megaspore tetrad develop equally, the spore body (aside from any special apical feature such as a gula) is typically more or less equidimensional, or even foreshortened axially. In Carboniferous *Cystosporites* (and possibly in the present case) the polar axial elongation corresponds to the spore expanding to fill the radially elongated sporangium characteristic of the Lepidodendrales.

Abortive spores and haptotypic features. Most of the fertile spores still have the abortive members of the tetrad adhering to the proximal pole (Pl. 3, figs. 1–3). The abortive spores show a sculpture of minute coni, 1–2 μ high and 1–2 μ apart. This ornament is variable, and in some specimens is barely discernible. The substance of the abortive spore exine is more or less granular, as in the fertile spores. The fertile spores show a clear triradiate suture when the three abortive spores have been removed (Pl. 4, fig. 1). In one case (Pl. 3, fig. 5) splitting had extended from the original sutures almost to the distal pole to divide the spore into three valves; this may have occurred before fossilization, or as a result of compaction in the matrix. In those spores where the proximal polar area of the fertile spore is visible, the areas of contact with the abortive spores are rather thinner than the adjacent exine and so are paler in colour (Pl. 4, fig. 1). The contact faces are bounded by weakly developed arcuate ridges, which appear darker than the surrounding exine.

The nature of the exine. The wall of the fertile megaspore is typically 10–15 μ thick, and under $\times 500$ magnification it shows a small-scale heterogeneity of a finely porous or granular nature (Pl. 4, fig. 6). Superimposed on this is an irregular, much larger scale pattern, of slightly thinner areas (Pl. 3, fig. 3; Pl. 4, fig. 1) which we attribute to coarse grained particles in the enclosing matrix which have left their impression on the exine. There is no clearly defined exine stratification; in section the fertile megaspore shows a more or less uniform exine (Pl. 4, fig. 6) with the fine granular texture extending throughout.

The basal stalk. Several of the fertile megaspores have at their base (the distal end with respect to the tetrad) an irregular prolongation of the exine in the form of a tapering, usually abruptly truncated, 'stalk' (Pl. 4, fig. 3). A closely similar feature has been described by Bochenski (1936) in *Cystosporites giganteus* found inside *Lepidocarpon* *major* (Brongt.) Piérart (1961), and also on isolated **Cystosporites giganteus** (Dijkstra 1946).

Associated miospores. Several of the fertile megaspores have miospores adhering to them. While some of these are rather obscure, others have a prominent triradiate mark and an equatorial feature (Pl. 4, fig. 2), and may be assigned to the dispersed spore genus *Lycospora*. *Lycospora*, in addition to representing the microspores of many *Lepidostrobus* species, probably includes the microspores of *Lepidocarpon* (see, for example, Felix 1954). The occurrence of *Lycospora* in this context is of particular interest in view of the paucity of lycopod macrofossils at this horizon (see below). However, this occurrence of the *Lycospora* appressed to several of the specimens of *Cystosporites devonicus* cannot be regarded as being anything more than a suggestive association.

ASSIGNATION TO *CYSTOSPORITES*

In making the genus *Cystosporites* Schopf (1938) begins the diagnosis, 'Seed megaspores . . .'. It is amply demonstrated that many species of *Cystosporites* were borne on Lepidocarp megasporophylls (e.g. *C. giganteus*, *C. varius*) and were in this sense seed megaspores, but this is a piece of information which is not derived from an innate character of the dispersed megaspores themselves, and is only deduced from the circumstances of occurrence of certain specimens. The genus *Cystosporites*, which is based on dispersed megaspores, must be defined in terms of the megaspores alone, although it may be surmised that most (probably all) species included in the genus do indeed represent Lepidocarp seed megaspores. The main feature of *Cystosporites* is the development of the tetrad in such a way that the fertile spore becomes very large and sack-like in shape while the three abortive members of the tetrad remain relatively small and rounded. A further feature on which Schopf lays considerable emphasis is the fibrous character of the fertile spore exine. He reasonably correlates this with the supposition that this made it possible for food reserves to pass into the seed megaspore from the parent plant at a late stage in its development (while still enclosed in the sporangium). The thick continuous exine of the megaspores of *Lepidostrobus* and *Sigillariostrobus* (free-sporing plants) would presumably have prevented the inward passage of food reserves after the development of the spore wall was complete.

Since Scott's original (1901) description of petrified *Lepidocarpon* a number of species based on compression fossils have been put in the genus. The main problem involved in doing this is one commonly encountered in palaeobotany—that of extending a genus

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EXPLANATION OF PLATE 4

Figs. 1, 3, 6. *Cystosporites devonicus* sp. nov. 1, Fertile spore apex showing triradiate sutures (laesurae) and pale areas of the contact faces, V45428; ×200. 3, Distal end of a fertile spore showing the 'stalk', V45433; ×200. 6, Exine, showing its porous-granular character, V45434; ×500.

Fig. 2. Two miospores, cf. *Lycospora sp.*, adhering to the exine of a fertile spore of *Cystosporites devonicus*, near to the distal end, V45432; ×500.

Fig. 4. Exine of *Cystosporites giganteus* (from the holotype of *Lepidocarpon waltoni*, from the Lower Carboniferous of Scotland) showing the fibrous character of the fertile spore wall, V45451; ×500.

Fig. 5. Exine of *Cystosporites verrucosus* (from *Lepidocarpon braidwoodensis*, Upper Carboniferous of England), showing the more or less granular character of the fertile spore wall, and two spines, V45452; ×500.

All the slides are in the British Museum (Natural History).

based on a petrifaction to include species based on compressions which do not show all the features seen in the petrified material. In this particular case, compressions of *Lepidocarpon* could hardly be expected to show clear evidence of the thin integumentary flaps, an important character of *Lepidocarpon* as seen in the petrified state. Schopf (1941), Chaloner (1952), Bharadwaj (1959), and Piérart (1961) have reviewed the basis for extending *Lepidocarpon* to include such compression fossils. In effect the possession of *Cystosporites* megaspores contained in otherwise *Lepidostrobus*-like sporophylls has been accepted by these authors as a legitimate basis for assigning the sporophylls to *Lepidocarpon*. We regard this as a more reasonable and preferable expedient to the alternative of assigning such sporophylls to *Lepidostrobus*.

Two Upper Carboniferous species of *Lepidocarpon* based on compressions are particularly relevant in their bearing on our Devonian *Cystosporites*: *Lepidocarpon major* (Brongt.) which contains *Cystosporites giganteus* megaspores and *Lepidocarpon braidwoodensis* (Arnold) Piérart, which contains *Cystosporites verrucosus* (of which Arnold's *Lagenicula saccata* is a synonym—see Dijkstra 1955). Both of these *Lepidocarpon* species were previously assigned to *Lepidostrobus*, but have been reassigned by Piérart (1961) on the basis of their containing *Cystosporites*.

The *Cystosporites giganteus* megaspores enclosed in *Lepidocarpon major* were shown by Bochenski (1936) to have a basal stalk (Stiel) extending from the megaspore to the adaxial end of the sporangium. A similar but much larger structure extends from the megaspore to fill the whole adaxial half of the megasporangium in *L. braidwoodensis*. (This can be seen in the specimens of this species figured by Chaloner 1954 as *L. monospora*, a species now shown to be a later synonym of *L. braidwoodensis*—see Dijkstra 1955.) We accordingly regard the similarity of the stalk in our *Cystosporites* to that in *C. giganteus*, which is known to be a Lepidocarp seed megaspore, as a significant feature of agreement.

The probable biological significance of the fibrous character of the exine in some *Cystosporites* has been mentioned above. That of *C. giganteus* is shown in Plate 4, fig. 4. However, *C. verrucosus* has a much more compact, homogeneous texture (Pl. 4, fig. 5), and is ornamented with small ridges and spines near the apex. These two species may be said to show the extremes of wall texture among those already assigned to *Cystosporites*. The exine of *C. devonicus* (Pl. 4, fig. 6) is not significantly less porous or granular than that of *C. verrucosus*, and we accordingly discount its non-fibrous exine as a basis for excluding it from *Cystosporites*.

In summary, our megaspore tetrads show the following features in common with Carboniferous species of *Cystosporites*:

1. Development of one member of the tetrad, the fertile spore, at the expense of the three abortive members, which adhere to the fertile spore apex.
2. The fertile spore is elongated axially to between two and three times its width.
3. Some of our spores have a basal stalk, similar to that of *C. giganteus*.
4. The exine is of a granular or porous character, similar to that of *C. verrucosus*.

These features form the basis of our assigning *C. devonicus* to that genus. We do not consider that this assignation begs the question of whether or not it represents a Lepidocarp seed megaspore, or even whether its enclosing sporangium was integumented, although both of these are likely.

COMPARISON WITH SIMILAR STRUCTURES

Cystosporites devonicus compares most closely with the several Carboniferous species of this genus. It may also be compared in more general terms with the seed megaspore enclosed in the Carboniferous lycopod seed *Miadesmia*. This is of comparable size to *C. devonicus*, but *Miadesmia* did not apparently form an exine on the three abortive members of the (presumed) megaspore tetrad, and only a single large seed megaspore is seen in the megasporangium. The *Miadesmia* megaspore also differs from *Cystosporites* in lacking any visible tetrad mark or other haptotypic features. We have examined Scott's material of *Miadesmia* seeds in the British Museum (Natural History) in which the megaspore membrane, although apparently yellow and translucent, was thin and uniform in texture.

The megasporangium of the Lower Carboniferous coenopterid fern *Stauropteris burntislandica* represents an instance in which a single megaspore tetrad was reduced to two fertile and two abortive spores (Surange 1952, Chaloner 1958)—a situation analogous to the more extreme reduction in *Lepidocarpon*. The similarity of the megaspore tetrad in *S. burntislandica* and *Cystosporites* does not extend beyond this; but the situation in *S. burntislandica* is of interest in that while it is a megaphyllous plant it parallels *Lepidocarpon* in having a modified single tetrad, but in this case in a non-integumented megasporangium.

Comparison with *Hirsutocarpon extensum*, described by Maslov (1957) from a section of Devonian limestone, is limited by our rather meagre knowledge of this Russian fossil. Maslov compared it with *Lepidocarpon* and with *Miadesmia*, but as it is known only in one plane of section, its real shape and the nature of the enclosed megaspore (if any) is quite conjectural and its similarity to these or any other seeds is problematical (see Banks 1960, Chaloner 1960).

Finally, *Cystosporites devonicus* may be compared with the megaspore membranes isolated from Lower Carboniferous Pteridosperm seeds—for example, those of *Eosperma oxroadense* (Barnard 1959) and *Geminitheca scotica* (Smith 1959). These and other Carboniferous seed megaspore membranes resemble our fossil in being more or less oval, elongated sack-like structures. They all differ from this and other species of *Cystosporites* in having no abortive spores or haptotypic features at the apex, and no basal stalk to the megaspore membrane.

THE PARENT PLANT OF *CYSTOSPORITES DEVONICUS*

All the fructifications in which Carboniferous *Cystosporites* megaspores have been found so far may be included in the genus *Lepidocarpon* s.l., or at least in the Lepidocarpaceae (Schopf 1941, Chaloner 1952, Bharadwaj 1959, Piérart 1961). Indeed, the various features which characterize the *Cystosporites* tetrad correspond to its retention to constitute the seed megaspore inside a Lepidocarp seed. Accordingly the most obvious interpretation of our fossil is simply that it represents a Devonian Lepidocarp seed megaspore. However, such an interpretation would presuppose the nature of the parent megasporangium, and, in particular, that it was integumented. A considerable number of large, and probably arborescent, lycopod genera are now known from the late Devonian, including *Cyclostigma*, *Archaeosigillaria*, *Lepidosigillaria*, and *Lepto-*

phloeum. Any of these are possible parent plants for a lycopod (*Lepidocarpon*-like) fructification. However, lycopod macrofossil remains in the Escuminac beds are rare. Dawson (1882) reported *Knorria* (a genus representing a variety of arborescent lycopods in a decorticated state) and an 'obscure' *Lepidostrobus* from Scaumenac Bay. These appear to be the only lycopod macrofossils recorded from that locality.

Archaeopteris, on the other hand, is relatively common at Scaumenac Bay (Arnold 1936). One species of this genus was shown by Arnold (1939) to be heterosporous, and Beck (1960), on the basis of its wood anatomy and other features, has grouped *Archaeopteris* with some similar genera in a new group, the Progymnospermopsida. Fertile pinnae of *A.* cf. *jacksoni* Dawson from Scaumenac Bay have been found by one of us (J. M. P.) to bear sporangia which contain either 9 to 48 megaspores 202–370 μ in diameter, or several hundred microspores 45–70 μ in diameter. It is evident that heterospory was not confined to one species of *Archaeopteris*, and it may have been general in the genus. It is at least conceivable that *Cystosporites devonicus* could represent a megaspore tetrad of a plant similar to *Archaeopteris* in which reduction of the megaspore number had reached the *Lepidocarpon* level. In this case, similarity of *C. devonicus* to Lepidocarp megaspores would constitute a remarkable degree of parallel evolution in the lycopods and a macrophyllous plant. But whatever the nature of its parent plant, the character of the *C. devonicus* tetrad itself indicates the attainment of a level of heterospory previously unknown in the Devonian.

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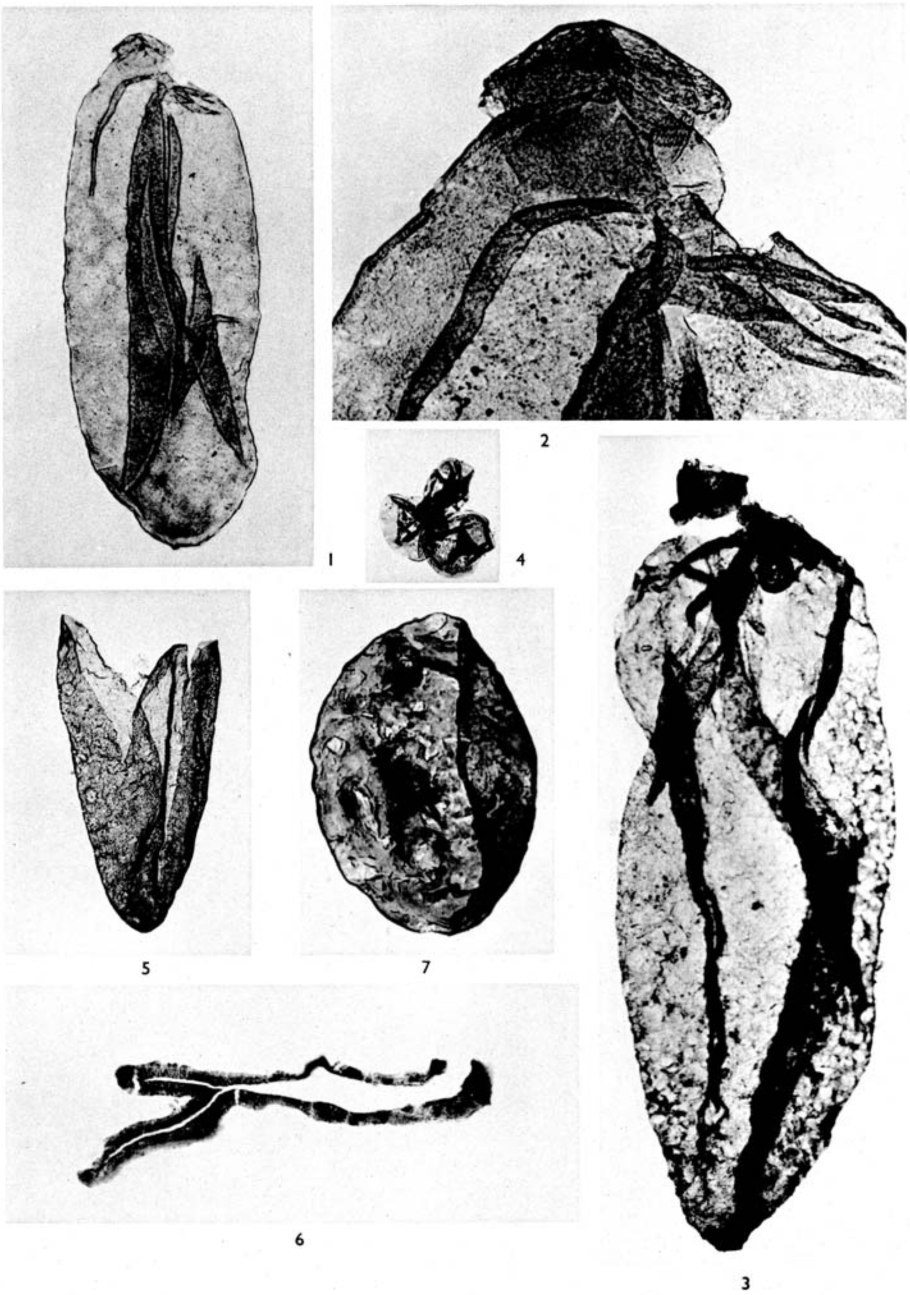
Manuscript received 9 May 1963



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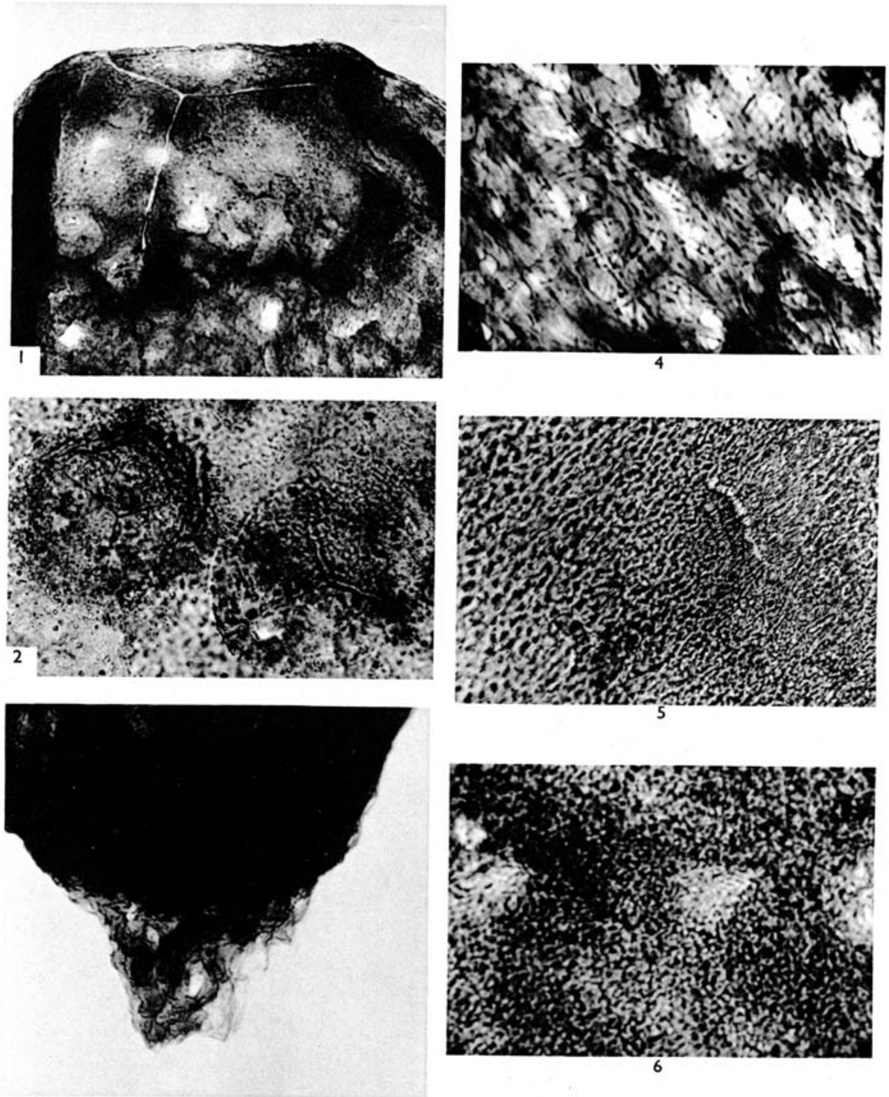

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