IN SITU MEGASPORES FROM *LEPIDOSTROBOPHYLLUM FIMBRIATUM* (KIDSTON) ALLEN FROM THE LOWER CARBONIFEROUS OF NORTH-WEST ENGLAND

by M. G. MORTIMER

ABSTRACT. *In situ* megaspores from five sporophylls of *Lepidostrobophyllum fimbriatum* (Kidston) Allen are described from two localities near the English–Scottish border. Each megasporangium contains one tetrad, variously developed, comprising both smaller and larger megaspores. The smaller specimens, presumed abortive, reach a maximum dimension of 2 mm. They differ in gross morphology from the larger ones, presumed fertile, which are from 3·0–6·5 mm in diameter. The larger also show marked differences among themselves in distal inflation and ornament. All are compared with *Setispora pseudoreticulata* Spinner on the basis of the haptotypic features. They are thought to include the largest ever recorded.

LEPIDOSTROBOPHYLLUM FIMBRIATUM was first described as *Lepidostrobus fimbriatum* by Kidston (1883). In common with all later workers, he found only detached leaves, but recognized the raised carbonaceous film in the centre of the basal expansion as a sporangium. Allen (1961) transferred the sporophylls to *Lepidostrobophyllum* Hirmer and gave the first published description of the contents of the sporangium. He described each sporangium as having four spiny megaspores of restricted size range (1·2 to 1·9 mm diameter) but in his material none shows the haptotypic features. On the basis of the spiny ornament and lack of equatorial feature or obvious apical prominence, Allen compared the megaspores with *Triletes echinoides* Chaloner 1954. The megaspores do not appear to be differentiated in development (Allen 1961; text-fig. 4). Lacey (1962) also described megasporangia, probably with four megaspores at maturity. He extended the diameter range of the spores upwards to 4 mm and showed megaspores of unequal size within a tetrad (Lacey 1962; text-fig. 8, diagram C). The haptotypic features remain obscure and Lacey also compared the spores with *T. echinoides* Chaloner 1954.

MATERIAL AND METHODS

The present material is among plant fossils determined by Professor W. G. Chaloner from the Upper Border Group (S2) in the country around Bewcastle (Day 1970), and held in the collections of the British Geological Survey. The hand specimens R1819 and R1821 are from Chirdon Burn, a tributary of the river Black Clough, Northumbria, 1 km west-south-west of Hope House. The hand specimens R1965 and R1966 are from the river Irthing, Northumbria, 1 km south of Lampert. These localities are 4 km apart, and about 10 km from the Lewis Burn, 20 km from Liddel Water, and 25 km from the river Esk, the localities mentioned by Kidston (1883) for the type material of *L. fimbriatum*.

The hand specimens are of carbonaceous shale. The sporophylls lie flat at distances a few centimetres apart from each other, among other compressed fossil plant fragments (Pl. 18, fig. 1). Each sporophyll consists of a rounded-triangular proximal part (pedicel) carrying centrally the remains of a sporangium. The compressed sporangium is a rounded trapezoid in shape. When first seen, it was noted that the additional thickness of the sporangium had resulted in some fracture and flaking, due to handling, but this also provided an indication that its contents might still be present (Pl. 18, figs. 2, 3, 4).

Concentrated nitric acid was dripped slowly on to each sporangium in turn, with frequent water washing and visual monitoring under the binocular microscope. As the fractured edges of the damaged sporangia

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softened, they curled a little, allowing the contents to be picked out with a brush and transferred to a watch glass for further oxidation. A dispersed megaspore noticed on R1821 was removed and treated separately. Fourteen megaspores were recovered in whole or in part from five of the seven sporangia investigated. The distribution is given in Table 1.

DESCRIPTION OF *IN SITU* MEGASPORES

Triradiate megaspores with prominent fimbriate lips to the triradiate mark, with a subcircular or oval outline in oblique compression (Pl. 19, fig. 1; Pl. 20, figs. 1, 4, 8, 15, 17) or a flask-shaped outline in lateral compression (Pl. 19, figs. 6 and 7; Pl. 20, figs. 10 and 20). Diameter 1·0–6·5 mm, those from 3·0–6·5 mm being found in oblique compression and the smaller ones in lateral compression. Laesurae from one-third to equal to the spore radius in length, being relatively shorter in the larger specimens, accompanied by thick, high lips about 200 μm in width and 150–200 μm high, increasing in height towards the apex. In oblique compression the lips are turned over on each other at the apex to form a crestal knot of densely bunched material (e.g. Pl. 19, fig. 1; Pl. 20, fig. 15). The lips are densely ornamented with fimbriae consisting of discrete, parallel-sided spines, 125–150 μm in length, and about 20 μm in diameter (Pl. 19, fig. 8). These spines have truncated, rounded, or papillate tips. In the smaller specimens the contact faces bear a similar but less dense ornament of spines up to 50 μm in length, 20–30 μm in diameter, interspersed with granules 10–15 μm in basal diameter (Pl. 19, figs. 7 and 8). In the larger specimens the contact faces bear a scattered ornament of similar spines, up to 50 μm in length and 20–30 μm in diameter, some with papillate tips, interspersed with similar granules (Pl. 19, fig. 4). The contact faces are delimited from the remainder of the exine in some of the larger specimens by low arcuate ridges 10–15 μm high (Pl. 19, fig. 1), and in others simply by an angle in the outline of the spore (Pl. 20, Figs. 1 and 4). In the smaller megaspores the arcuate ridges are well developed and contorted into a sinuous pattern (Pl. 19, fig. 7). Distally the megaspores bear an ornament of spines. In the larger specimens this is variously developed with a marked effect on the appearance of the spores (see below). In the smaller ones the spines are broken off (Pl. 19, fig. 5) and the ornament consists of their stumps and closely packed broad bulbous bases.

Developed and abortive megaspores

All the megaspores are characterized by prominent fimbriate lips to the triradiate mark and by an ornament of large spines. The larger specimens are further characterized by the lack of an apical prominence involving the contact faces, and of an equatorial feature. In the smaller ones the apical prominence occupies half the polar dimension, the arcuate ridges are pronounced and equatorially placed, and the distal exine is densely ornamented.

The larger and smaller megaspores also differ in their response to nitric acid: the larger specimens become translucent and can be studied by transmitted light, whereas the smaller are still opaque. The difference in chemical response is thought to be due simply to greater density. The megaspores were not treated with other acids, but it is unlikely that mineralization would affect members of the same tetrad differently. Moreover, the fimbriate lips to the triradiate mark show normal transparency and colour at the outer edges (Pl. 20, figs. 9 and 21), indicating that the remainder of the exine is still of sporopollenin.

These smaller and larger megaspores are so different in gross morphology that it is probable they would be assigned to different form genera if found dispersed. However, it can be seen that further

EXPLANATION OF PLATE 18

Figs. 1–4. *Lepidostrobophyllum fimbriatum* (Kidston) Allen. 1, R1821 hand specimen, showing scattered sporophylls including 1, 2, and 3, and dispersed megaspore A, ×1. 2, R1966, part of hand specimen with megasporangiate sporophyll, ×3. 3, R1965, part of hand specimen showing megasporangiate sporophyll 2, ×3. 4, R1819, part of hand specimen with empty sporophyll, ×3.

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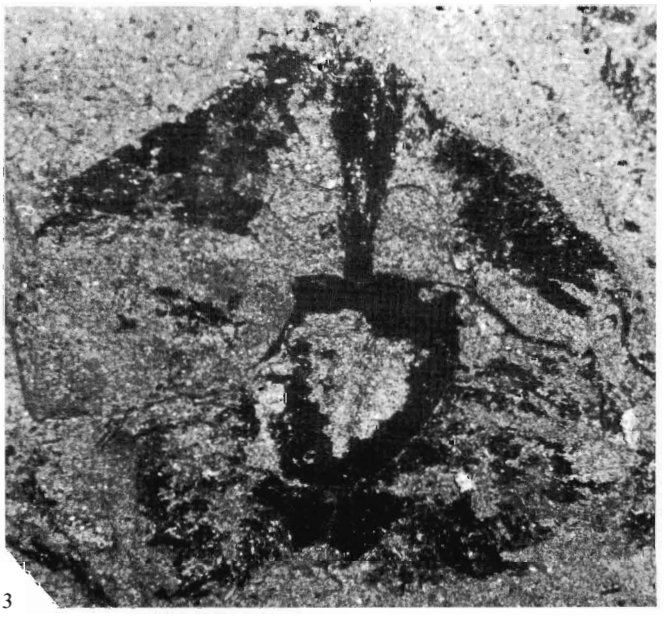

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MORTIMER, *Lepidostrobophyllum* sporophyll

distal inflation of the smaller spores would alter the relative size importance of the haptotypic features, smooth out the ridges, and separate the spine bases to achieve the morphology of the larger spores. Chaloner and Pettitt (1964) recorded *Cystosporites* megaspore tetrads with one large and three very small members, where the morphologic difference between the large and small members is just such distal inflation. The smaller megaspores of *L. fimbriatum* differ from those of *Cystosporites* in having attained about half the size of the larger ones, while retaining the features of immaturity. They are presumed to have aborted at a later stage.

Differences and similarities—developed megaspores

Attention is drawn above to the morphologic differences between the abortive and developed megaspores found in the present study. The eleven developed megaspores also show variability in the density, size, and style of the distal ornament, which is illustrated in Plates 19 and 20 (where figures of megaspores belonging to the same tetrad have as far as possible been placed together) and summarized in Table 1.

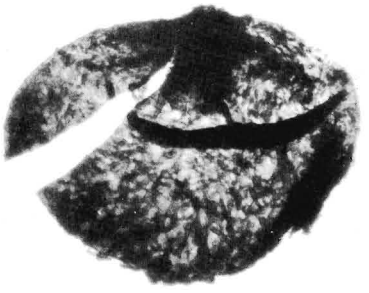
The most complete developed megaspore, R1966b, is from the river Irthing locality. It has a distal ornament of large spines, typically 200–400 μm high, densely packed and without bare patches. Many of the spines are buttressed at the base and branched at the tip, giving a pseudoreticulate effect in compression (Pl. 19, figs. 1 and 2). The other developed megaspore of the same tetrad, R1966a, also has large, dense ornament (Pl. 19, fig. 3). However, the developed megaspores from the other hand specimen from the river Irthing locality show some differences in ornament. The single megaspore of R1965(1) is the largest found, its diameter being 6·5 mm. The distal ornament is obscure, but a few spines similar to the large branched ones of R1966b can be made out, interspersed with some that are narrower and simpler. No spines appear at the periphery, indicating that the ornament is genuinely sparse (Pl. 20, fig. 17). The one developed megaspore of R1965(2) is represented by a fragment extending from the apex to the distal margin (Pl. 20, fig. 18). The ornament is again sparse and also reduced in size, typically 75–100 μm high. Some of the spines are slightly buttressed at the base or forked at the tip, but the majority are simple (Pl. 20, fig. 19). The area near the distal margin is bare.

In contrast to the differences among the developed spores from the river Irthing, at Chirdon Burn, the six known from sporophylls from the hand specimen R1821 consistently show the sparser, lower ornament, with the bare area around the distal pole (Pl. 20, figs. 1–8, 11–14). The dispersed megaspore R1821A, however, has distal ornament of further reduced size, typically 50 μm high, all of simple spines and more evenly distributed (Pl. 20, figs. 15 and 16).

In all these megaspores the ornament of the contact faces is of knobs and short, stubby or papillate spines (Pl. 19, fig. 4). The features of the crest, where seen, are also always the same. Individual spines in the distal ornament can also be matched for features of shape (simple, broadened or buttressed base; branched, stubby, papillate or pointed tips). Importance is given to these similarities by the knowledge that all are megaspores of *L. fimbriatum*. The differences of size and distribution of the ornament have a marked effect on the appearance of the spores, however, and it is doubtful if all would be assigned to the same form species if found dispersed.

EXPLANATION OF PLATE 19

Figs. 1–8. *Lepidostrobophyllum fimbriatum* (Kidston) Allen. Megaspore tetrad of R1966. 1, developed megaspore (b), × 10. 2 and 4, ornament of megaspore (b), × 100. 2, typical large spine with buttressed base and branched tip, with other simpler spines; 4, reduced ornament of short, blunt-tipped spines and papillae on contact face. 3, developed megaspore (a). Large simple spines with blunt tips interspersed with narrower pointed spines, × 100. 5 and 8, abortive megaspore (c), stereoscan, × 250. 5, body ornament of broken-off spines on bulbous bases, 8, detail of fimbriate lips on apical prominence and sinuous arcuate ridges. 6 and 7, abortive megaspore, dry, by reflected light, × 10. 6, (c), 7, (d).



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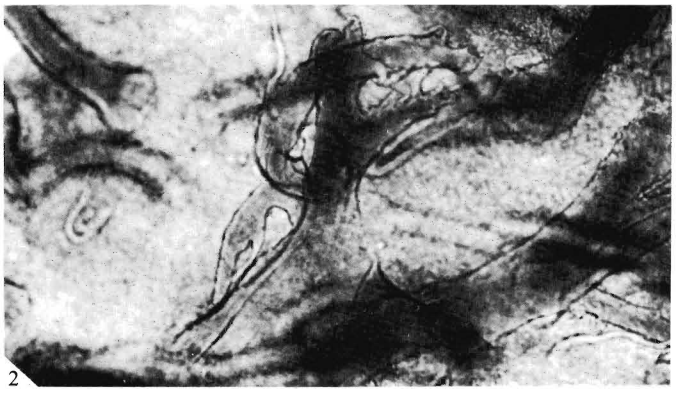

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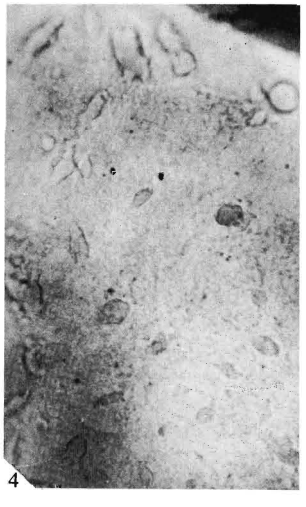

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MORTIMER, *Lepidostrobophyllum* megaspore

Life association

In the present material only some megaspores consistently show the same style of distal ornament. In the hand specimen R1821 the megaspores from R1821(1) and R1821(3) are consistent, but R1821(A) is different. R1965(1) and R1965(2) do not show the same ornament. Those of a third hand specimen, R1966, are different again. As noted at the outset the sporophylls of R1821 and of R1965 lie near each other (as in Pl. 18, fig. 1). This proximity indicates a probability that in life the sporophylls were in each case associated in the same cone. This may account for the consistency in the ornament of the *in situ* spores of R1821. This leaves the differences between the megaspores of R1965 unaccounted for.

Tetrad development

Table 1 shows a variable pattern of development among the members of a tetrad. The two complete tetrads are differently developed: in 1821(3) there are three developed megaspores and one abortive and in R1966 there are two developed and two abortive. R1821(1) appears to follow the first pattern, although it is possible that the fourth member is another small, developed megaspore. In R1965(1) the one megaspore found is of such a large size that it may be the only developed member. The list of megaspore sizes in R1821(1), R1821(3), and R1966 also shows a tendency among the developed members of the tetrad for one to reach a larger size than the others. This lends support to the possibility that in some cases only one developed at the expense of the other three.

R1821(1) and R1821(3) thus show consistency in the style of all the known developed megaspores, and most probably also in the development of the tetrads. R1965(1) and R1965(2), although less well known, may well be different in both respects.

COMPARISON WITH PREVIOUSLY DESCRIBED DISPERSED MEGASPORES

The developed megaspores of *L. fimbriatum* are characterized by the presence of pronounced fimbriate lips, the absence of a true apical prominence and of an equatorial feature, and a distal ornament of spines. Four species of dispersed megaspores showing this combination of characters have been described; the first by Chaloner (1954) as *Triletes echinoides* (transferred to *Setispora* by Spinner in Butterworth and Spinner 1967), the second and third by Alvin (1965, 1966) as

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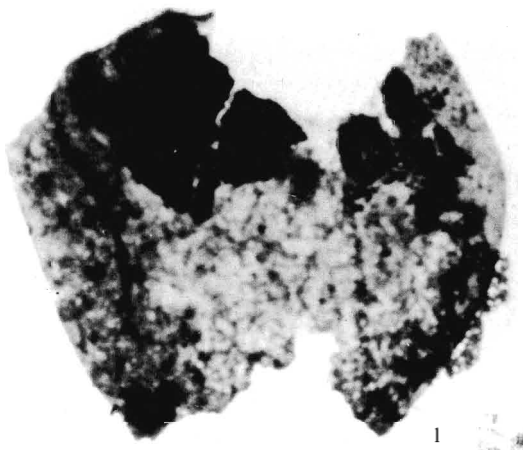
EXPLANATION OF PLATE 20

Figs. 1–21. *Lepidostrobophyllum fimbriatum* (Kidston) Allen. 1–7, three developed megaspores of R1821(1). 1–3, megaspore (a), 6 mm diameter, crestal knot missing. 1, ×10; 2, dry, by reflected light, showing distribution of ornament, ×4; 3, detail of ornament showing broken-off spine with buttressed base, ×64, 4, megaspore (b), 4 mm diameter, haptotypic features largely missing, scattered ornament of broken-off spines, ×10. 5*a*, *b*, fragments of megaspore (c), approx. 2 mm diameter, part of fimbriate lips on each. 6, detail of fimbriate lips on megaspore (c), ×64. 7, detail of ornament on megaspore (c), showing scattered stumpy spines, ×64. 8–14, megaspore tetrad of R1821 (3). 8, developed megaspore (b), crestal knot on right, ×10. 9 and 10, abortive megaspore (d). 9, detail of fimbriate lips, ×64, 10, transmitted light showing failure to clear on simple oxidative treatment, ×10. 11 and 12, developed megaspore (a), haptotypic features missing. 11, ×10; 12, detail showing ornament of scattered stumpy spines, ×64. 13 and 14, developed megaspore (c). 13, detail of fimbriate lips, ×64; 14*a*, *b*, two fragments comprising large part of megaspore, including some haptotypic features at upper right, ×10. 15 and 16, dispersed developed megaspore R1821A: 15, large part of body, 5 mm diameter, bunched fimbriate lips forming crestal knot at upper right, ×10; 16, ornament of scattered stumpy spines, ×100. 17, developed megaspore of R1965(1), large part of body, approx. 6·5 mm diameter, with ornament of discrete blunt-tipped spines, ×10. 18–21, two megaspores of R1965(2). 18 and 19, developed megaspore (a). 18, fragment with part of fimbriae at lower left, ×10; 19, ornament showing large blunt-tipped spines, ×64. 20 and 21, abortive megaspore. (b) 20, transmitted light, ornament of broken-off spines on bulbous bases evident at periphery, ×10; 21, apex showing fimbriae, ×100.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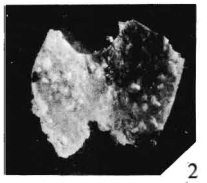
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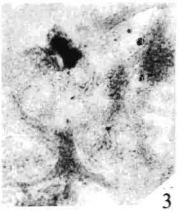
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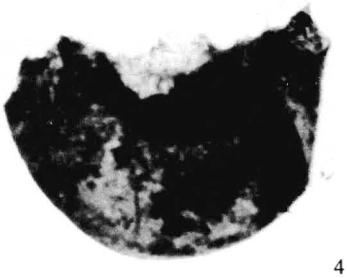
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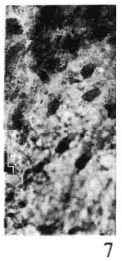
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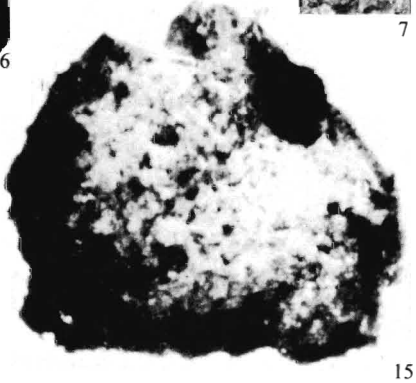
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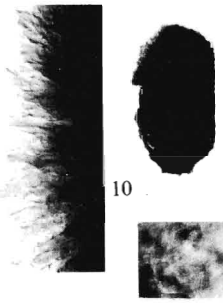
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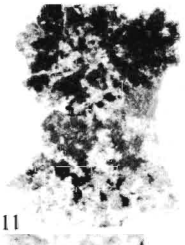
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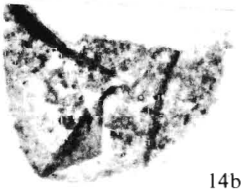
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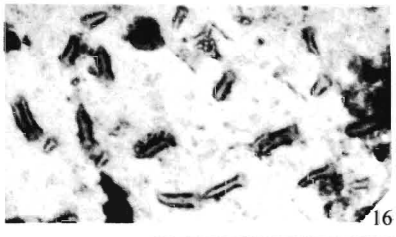
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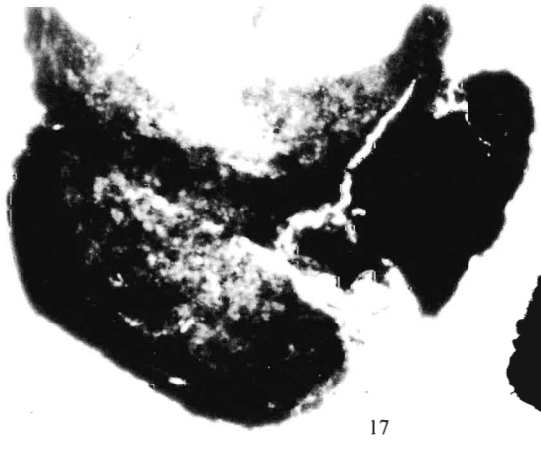
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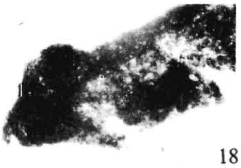
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MORTIMER, *Lepidostrobophyllum* megaspore

TABLE 1. Occurrence of megaspores with observations on size, orientation and ornament.

Hand specimen		Megaspores	Dimension (mm)	Orientation	Ornament
R1819	1 sporophyll	empty			
R1821	3 sporophylls	(1) 3 developed	6, 4, ?3	Oblique	Intermediate, sparse, distal pole bare
		? abortive			
		(2) empty			
		(3) 3 developed	5, 3+, 3	Oblique	Intermediate, sparse, distal pole bare
		1 abortive	2	Lateral	Dense
R1821A	Dispersed megaspore		5	Oblique	Low, evenly distributed
R1965	2 sporophylls	(1) 1 developed ?others	6·5	Oblique	Large elements, sparse
		(2) 1 developed	4	Oblique	Intermediate, sparse
		1 abortive ?others	2	Lateral	Dense
R1966	1 sporophyll	2 developed	4·5, 3	Oblique	Large elements, pseudo-reticulate
		2 abortive	2, 2	Lateral	Dense

T. subpalaeocristatus and *T. pannosus*, and the fourth by Spinner (in Butterworth and Spinner 1967) as *S. pseudoreticulata.*

Comparison between the megaspores of *L. fimbriatum* and *T. echinoides* was made by Allen (1961) and Lacey (1962), and indeed the largest specimens of this species (2 mm diameter, Winslow 1959) are the only ones of this morphology to approach the size of the large megaspores of *L. fimbriatum*. However, the prominent lips of *T. echinoides* are tall, narrow, and fluted with dentate margins, rather than the thick lips ornamented with spines in *L. fimbriatum.*

T. subpalaeocristatus and *T. pannosus* resemble the megaspores of *L. fimbriatum* in having raised lips to the triradiate mark which are covered with capillae. In *T. subpalaeocristatus* the capillae are proportionately narrower and longer than in *L. fimbriatum* and appear to be largely fused.

S. pseudoreticulata Spinner resembles the megaspores of *L. fimbriatum* in the features of the crest, which consists of raised lips covered with capillate elements, and in the distal ornament of large spines which may be simple or branching at the tip, and have a conical base which may be buttressed (Butterworth and Spinner 1967, Pl. 4, fig. 4). The ornament is densely arranged and overlaps in compression to give a pseudoreticulate appearance, as in some specimens of *L. fimbriatum* megaspores (notably R1966a). Moreover, the dry specimen figured by Spinner (Pl. 4, fig. 6) shows an area denuded of spines as in some megaspores of *L. fimbriatum* (e.g. R1966b and c). The spores described by Spinner are generally smaller than those described here (diameter range approximately 1–2 mm compared with 2·0–6·5 mm) but other than this, *S. pseudoreticulata* shows all the haptotypic features of the large megaspores of *L. fimbriatum*, while individual distal features can be matched.

The smaller, presumed abortive, megaspores are also compared with *S. pseudoreticulata* Spinner on the basis of the dense fimbriate ornament of the raised laesurae, which can extend to the equatorial margin. The polar axis is longer than the equatorial, resulting in preferred lateral compression, as in *Lagenicula* (Bennie and Kidston) Potonié and Kremp 1954. However, about half of the polar length of the apical priminence is formed by the length of the fimbriae, and not by involvement of the contact faces and laesurae as in *Lagenicula.*

The comparison with *S. pseudoreticulata* Spinner is supported by the geographical proximity of the sources of the present material with that of Butterworth and Spinner (1967). All the localities are in the country around Bewcastle, and from horizons within the Border Group (Lower Carboni-

ferous), and three are in the Lewis Burn, which, as noted above, is also the source of some of the type material of *L. fimbriatum* (Kidston 1883).

ABSENCE OF MICROSPORANGIA

The sporangia of R1819 and of R1821(2) were also investigated. No megaspores were found. If these sporangia were microsporangiate, even if dehisced, it was hoped to find microspores in considerable numbers and all of one kind. Small spores were, however, found only in ones and twos and were not all of the same morphology. These are concluded to have been adpressed to the sporangial wall and the sporangia are considered to be empty megasporangia. All sporophylls of *L. fimbriatum* with contents known to date are megasporangiate.

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