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Lower Devonian spores from South Wales[1]

by W. G. CHALONER and M. STREEL[2]
with 2 plates

Inhaltsübersicht: Aus dem Unterdevon (Gedinne, Grenzbereich von Downton-Ditton) wird von einem Fundpunkt bei Newport/South Wales eine Miosporen-Vergesellschaftung beschrieben. Die Sporen werden den Genera *Leiotriletes*, *Punctatisporites*, *Retusotriletes*, *Granulatisporites*, *Emphanisporites* und *Chelinospora* zugeordnet; außerdem können Sporen mit den Genera *Lycospora*, *Murospora* und *Densosporites* verglichen werden.

Summary: A miospore assemblage from near the Downtonian-Dittonian junction (Gedinnian, Lower Devonian) near Newport, South Wales, is described. The spores are assigned to *Leiotriletes*, *Punctatisporites*, *Retusotriletes*, *Granulatisporites*, *Emphanisporites* and *Chelinospora*; specimens compared with *Lycospora*, *Murospora* and *Densosporites* are also present.

Introduction

This paper is an account of a small assemblage of miospores from a horizon approximately one metre above the "*Psammosteus* Limestone" from a locality near Newport, South Wales. The significance of the assemblage is twofold; firstly, the material comes from a surface exposure, and its age is securely established on the basis of fish faunas as being from the lower part of the Lower Devonian (Gedinnian). Secondly, although this early assemblage is of relatively simple spore types at least six genera (possibly nine) are represented.

Source and age of the material

The samples from which spore preparations were made were collected by Dr. H. C. SQUIRRELL of the Geological Survey of Great Britain; we are indebted to him and to the Director of the Geological Survey for making this study possible, and for permission to publish.

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The sample came from a horizon within the Lower Old Red Sandstone, 105 cm. above the "*Psammosteus* Limestone" in a cutting at the eastern end of Crindau tunnel on the Newport By-pass, near Newport, Monmouth, South Wales (Geological Survey One-Inch Sheet, New Series, 249; Six-Inch Sheet Monmouth 28 S. E.; National Grid Reference 30858980). EARP et al. (1964, p. 39) give a brief description of this exposure and mention the occurrence of the spores *Emphanisporites rotatus* and *Punctatisporites* in the mudstone above the "*Psammosteus* Limestone". The lithology at this horizon is a fawn to grey-coloured micaceous silty mudstone containing coalified plant fragments. The only determinable plant macrofossil seen in the present material was a specimen of *Pachytheca* sp. (Pl. 19, figs. 12, 13: Geological Survey and Museum No. GSM 77202). This was in a coalified state so that although the medulla and radiating cortical zone are visible, the detailed structure of the latter is not. As the separation of species within this genus is based principally on the microscopic features of these cortical filaments (KIDSTON and LANG 1924, SCHMIDT 1958) no more precise identification of this specimen is offered.

The horizon of the "*Psammosteus* Limestone" has been discussed fully by WHITE (1950 a & b) and BALL and DINELEY (1961). While there has been considerable controversy as to the position of the Silurian-Devonian boundary in the Welsh Border region, and the "*Psammosteus* Limestone" was at one time included in the Silurian (e. g. by KING, POCOCK and WHITEHEAD; see review in WHITE 1950a) it is now generally placed at or close to the boundary of the Downtonian and Dittonian. WHITE (1950b) regards the "*Psammosteus* Limestone" as probably diachronous, and suggests that while this formation is developed principally within the zone of *Traquairaspis symondsi* it may extend up into the base of the *Pteraspis leathensis* zone. There can be no doubt in any case that our material comes from a horizon very close to the junction of these two zones, and probably within the latter (that is, within the basal Dittonian, close to the Downtonian-Dittonian junction). Following SCHMIDT (1959) this may be regarded as equivalent to the Lower Gedinnian of the Rhineland sequence. It may be noted that our spore assemblage is rather older than the flora of the Senni Beds described by CROFT and LANG (1942) and of approximately the same as, or slightly younger than, the Downtonian flora of LANG (1937).

Preparation proceedure

The major part of the material on which the following descriptions are based was prepared by first mechanically breaking down the mudstone to fragments less than 1 cm. across followed by a treatment with cold 40% hydrofluoric acid for 48 hours. This was followed by centrifugation from

dilute (10%) hydrochloric acid. This treatment was followed by dehydration in acetone and concentration of the spore residue by flotation in bromoform diluted with one sixth its volume of acetone.

Supplementary material was prepared by maceration in hydrofluoric acid followed by cold concentrated nitric acid, followed by sieving at two size grades to separate the spores from residual insoluble matter. A considerable quantity of material was sieved at 125 μ mesh and the material held on the sieve was searched for any sign of spores of this dimension or greater. No spores were found at this size but much of this larger fraction was found to consist of fragments of organic matter. Further oxidation of these in SCHULZE's solution (for 10 hours) showed that in addition to brown coloured amorphous material there were a number of fragments of sporangial masses similar to those figured by LANG (1937), pl. 13 figs. 7 & 8. None of the spores seen in the sporangial masses showed their exine character and other features clearly enough to make certain of their identity with individual dispersed spores. The material passing the 125 μ sieve was further sieved with a 15 to 20 μ mesh using the apparatus described by STREEL (1965) in order to rid the spores of fine argillaceous residue. Altogether over a thousand spores were examined in unsorted glycerine jelly mounts and over a hundred single-spore mounts were made for study and photography.

Systematic part

All the figured slides are deposited in the palaeontological collection of the Geological Survey and Museum, London. The slide numbers cited here with the prefix "PF" refer to that collection. The observation and photography of the spores were carried out on a Zeiss photomicroscope.

Anteturma: SPORITES H. POTONIÉ.
Turma: TRILETES (REINSCH) R. POTONIÉ et KREMP.
Subturma: AZONOTRILETES LUBER.
Infraturma: LAEVIGATI (BENNIE et KIDSTON) R. POTONIÉ.

Genus: *LEIOTRILETES* (NAUMOVA 1937) POTONIÉ et KREMP 1954.
Type Species: *L. sphaerotriangulus* (LOOSE) POTONIÉ et KREMP 1954.

LEIOTRILETES cf. SIMPLEX NAUMOVA 1953
Pl. 19, Figs. 1 and 2

Description: Triradiate miospores of subtriangular amb, exine typically 1.5 to 2 μ thick, smooth, but occasionally specimens show a minute

O—L pattern (due to ?micropunctate sculpture). Triradiate sutures extend to the extreme margin of the flattened spore; in many specimens, narrow lips are perceptible, especially near the proximal pole (Pl. 19 Fig. 1). Diameter range 23—40 μ, mean 29 μ (for 28 specimens measured).

Discussion. As with the *Punctatisporites*, specific assignation in *Leiotriletes* is somewhat unsatisfactory. We compare our material with NAUMOVA's species, accepting that a number of other Palaeozoic species assigned to this genus are very similar. Comparison might be made particularly with *L. pagius* ALLEN (1965) which differs from our material principally in a wall thickness of 2.5—4 μ (against our 1.5—2 μ).

These spores agree significantly with those found *in situ* in *Cooksonia pertoni* LANG (1937, Pl. 8, Figs. 11, 15) from the Downtonian of Perton Quarry. Evidently, in view of the source and the agreement in horizon of LANG's species, our specimens may well represent the dispersed spores of this plant.

Two specimens which we assign to *L.* cf. *simplex* show inter-radial papillae. Each papilla is a small more or less circular thickening about 3 μ in diameter on the (? outer) surface of the contact face, slightly nearer the margin than the apex, there being a single papilla on each of the three contact faces. These papillae are not sharply defined, and do not photograph well at high magnification (cf. those on *Granulatisporites newportensis*; see below); they are not present on all the spores, and even when present could easily be overlooked. As with the *Granulatisporites*, we do not rate their presence or absence as an important systematic feature.

Genus: *PUNCTATISPORITES* (IBRAHIM 1933) POTONIE & KREMP 1954.
Type Species: *P. punctatus* IBRAHIM 1933.

PUNCTATISPORITES cf. PUNCTATUS IBRAHIM
Pl. 19, Figs. 3—6

Description: Triradiate miospores with circular amb, and triradiate sutures ranging from half to nearly the full spore radius. No lips are present, but the sutures may be open. The exine is smooth and thick (3—4.5 μ) on the distal face, and rather less on the proximal face. The diameter ranges from 58—90 μ (mean of 32 specimens, 66 μ).

Two specimens, otherwise agreeing with this species, have distinct, dark areas of triangular outline around the proximal pole (Pl. 19, Fig. 4). In one case (that figured) this triangular area is outlined by a clearly defined pale line. Lacking further specimens of this type, we prefer to regard these as atypical specimens rather than segregating them as a distinct species.

Most specimens show a series of very minute cavities within the exine and close to its outer surface, and these may be seen in profile at the spore margin (Pl. 19, Fig. 6). As has been pointed out (for example by MCGREGOR 1964, p. 5) such "infrastructure" may well be a product of corrosion (occurring during fossilization or preparation) and accordingly we do not rate this character as a diagnostic feature. A few specimens have irregularly distributed exinous globules adhering to the distal face (Pl. 19, Fig. 3): we do not regard these as constituting a constant feature of the spore ornamentation.

Discussion: Collapse of the rather strongly hemispherical distal face has in some cases produced a secondary fold at one edge close to the spore margin (e. g. Pl. 19, Fig. 3, lower edge); this demonstrates incidently that the thickness of the distal face is not appreciably less than that of the exine at the equator. Other secondary folding of the distal face confirms this.

The assignation of species to genera of simple morphology (e. g. *Punctatisporites*, *Leiotriletes* etc.) is becoming increasingly difficult as more and more species are made on undeniably trivial characters (e. g. small differences of size). Some authors have prefered to restrict the uses of species names to a very limited stratigraphic range. Others have taken a broader species concept and have accepted the assignation of, for example, Devonian spores to Carboniferous species (see discussion in PLAYFORD 1962, p. 577 and SULLIVAN 1964, p. 359). We support the sentiment expressed by PLAYFORD, and for this reason prefer to include our spores in "*Punctatisporites* cf. *punctatus*" rather than trying to make a new species for our material on inadequate grounds.

Genus: *RETUSOTRILETES* NAUMOVA 1953 emend. STREEL 1964, non RICHARDSON 1965.
Type Species: *R. simplex* NAUMOVA ("lectogenerotype" of POTONIÉ, 1958).

RETUSOTRILETES sp.
Pl. 2, Fig. 4

Description: Two spores were found (of 26 μ and 30 μ diameter), of more or less circular amb, smooth and thin-walled (about 1 μ) with clearly-defined curvaturae. We regard them as assignable to *Retusotriletes* NAUMOVA, but in view of the limited number of specimens we do not attempt specific assignation.

Two emendations of the genus *Retusotriletes* have been made (STREEL 1964, RICHARDSON 1965). On the basis of the International Code of Botanical Nomenclature (LANJOUW et al 1961), Article 8 ("the author who first designates a lectotype . . . must be followed" etc.), we accept the lectotype of this genus (a "lectogenerotype") designated by POTONIÉ 1958, and accordingly STREEL's emendation based on this species. RICHARDSON expressly rejects POTONIÉ's lectotype and places a rather different interpretation on the genus.

It might be noted that our *Retusotriletes* specimens are in many respects very similar (in size, shape, wall thickness and curvaturae) to our population of *Emphanisporites rotatus*, lacking only the characteristic proximal radiating ornament of the latter. It is conceivable that these *Retusotriletes* represent extreme end-members of the *Emphanisporites* population.

Infraturma: APICULATI (BENNIE et KIDSTON) R. POTONIÉ 1956.

Genus: *GRANULATISPORITES* (IBRAHIM 1933) POTONIÉ et KREMP 1954.
Type Species: *G. granulatus* IBRAHIM.

GRANULATISPORITES NEWPORTENSIS sp. nov.
Pl. 19, Figs. 7, 8, 11

Diagnosis: Triradiate miospores with subtriangular to roundly triangular amb. Exine thin, distally about 1 μ thick, ornamented; proximally thinner, smooth. Triradiate sutures extending to the margin (cf. Pl. 19, Figs. 7, 8), with some specimens apparently showing lips, probably resulting from folds associated with an originally rather pyramidal proximal face. Diameter 20—48 μ (mean, 26 μ for 42 specimens). Distal sculpture of small coni, about 1 μ or less in height and diameter, with rounded apices of rather irregular shape in profile and plan. Density of distribution rather varied; typically about 8—10 along the length of the spore radius. Most specimens show a single rounded papilla 3—4 μ across in each of the three contact areas about one third to one half of the spore radius from the proximal pole.

Holotype: The specimen of Pl. 19, Figs. 7, 8. Greatest diameter 31 μ. Slide No. PF 3239.

Discussion: Inspite of its unsculptured proximal face, we have elected to include this species in *Granulatisporites* rather than *Anapiculatisporites* POT. et KREMP as the latter genus has a sculpture of coni or spines higher than they are broad. *Anaplanisporites* (JANSONIUS 1962, p. 45), also with smooth proximal face and sculptured distal face, while evidently similar to our spore has been based on a species of questionable status (see JANSONIUS, 1962, p. 45). Rather than making yet another new spore genus of relatively simple morphology on the basis of the smooth proximal face, we are including our spore in an existing genus of broad definition.

The papillae on the contact faces of most of the spores we assign to this species are evidently of rather subdued profile, for they are visible only on

rather careful focussing, and are more noticable under low magnifications than under oil immersion.

Comparison: *Granulatisporites newportensis* differs from *Anapiculatisporites devonicus* var. *azonatus* (CHIBR.) VIGRAN 1964 and *Granulatisporites muninensis* ALLEN (1965) in that the latter two species generally have more densely spaced sculptural elements.

GRANULATISPORITES sp.
Pl. 19, Figs. 9, 10

In addition to the above species, we have two specimens with very much finer sculpture than *G. newportensis*. They are of roundly-triangular outline, and aside from the much smaller sculptural elements otherwise similar to that species. The figured specimen is of 26 μ diameter.

Infraturma: MURORNATI POTONIÉ et KREMP 1954.

Genus: *EMPHANISPORITES* McGREGOR 1961.

EMPHANISPORITES ROTATUS McGREGOR 1961 (Type species)
Pl. 20, Figs. 1—3

Description: Triradiate miospores with a circular to subtriangular amb. Triradiate suture present, but lips either absent or not well defined; sutures extending to the spore margin or to the curvaturae where these are visible within the amb. Radiating corrugations (? thickening bands) on the proximal face extending from the pole to the equator or to the curvaturae, if visible. About seven to ten such bands are present on each of the three contact faces. The exine is smooth and thin (about 1 μ). The diameter ranges from 18—40 μ (mean of 18 specimens measured, 26 μ).

Discussion: McGREGOR (1961) included in this species both specimens in which there are not evident curvaturae (his pl. fig. 1) and those in oblique compression with clearly defined curvaturae (his pl. figs. 3 and 4). We accept this range of form seen in variously oriented specimens; probably all specimens of this species have curvaturae (arcuate ridges) but these are only clearly visible when the spore is obliquely compressed (Pl. 20, Fig. 3). Owing to slight variation in the relative area of the proximal and distal surfaces, the curvaturae in a flattened spore may either be coincident with the margin (Pl. 20, Fig. 2), or slightly within the margin (Pl. 20, Fig. 1, at top right edge).

Comparison: *E. neglectus* VIGRAN 1964 (?Givetian-Frasnian) is significantly smaller (with a maximum size of 17 μ to our mean of 26 μ), and has many thick proximal ribs which give an undulating outline to the spore. *E. curvaturus* ALLEN (1965) differs from *E. rotatus* in having a minutely granular distal surface. *E. minutus* ALLEN (1965) is closely comparable to *E. rotatus* but is smaller and appears to lack curvaturae. The difference between *E. minutus* and *E. rotatus* may only be one of size range of different populations of a single species; for this reason we prefer to assign our spores to the earlier described species.

Genus: *CHELINOSPORA* ALLEN (1965).
Type Species: *C. concinna* ALLEN (1965).

CHELINOSPORA VERMICULATA sp. nov.
Pl. 20, Figs. 5—8

Diagnosis: Triradiate miospores with roundly subtriangular amb. Exine rather thick, 2—4 μ distally and equatorially, sculptured; proximally, much thinner (about 1 μ) and smooth. Triradiate sutures extending to the margin, sometimes showing lips apparently produced by folding in the region of the suture (Pl. 20, Fig. 5). Distal sculpture of very fine vermiculi (irregular elongated depressions in the surface) rather less than 1 μ deep and wide, and spaced about 2 μ apart.

Holotype: The specimen of Pl. 20, Figs. 7 and 8. Greatest diameter 34 μ. Slide no. PF 3248.

Discussion: ALLEN's genus *Chelinospora* is founded for patinate spores with variously ornamented (reticulate or foveoreticulate) distal surfaces. BUTTERWORTH and WILLIAMS (1958) originally defined patinate as having "an exinal thickening extending over the entire area of one hemisphere". As a number of "patinate" spores have now been described from the Devonian, it becomes desirable to agree just how great this distal thickening must be before it constitutes a patina. Many spores — probably most — have a slightly thicker distal face than the proximal, but are not regarded as patinate. We consider that in the case of our spores the difference in thickness of the proximal and distal exines warrants this being regarded as patinate. A specimen flattened in the plane of the polar axis is shown forming part of a tetrad in Pl. 20, Fig. 6. This shows the relatively thick distal and equatorial exine in profile.

Only two of the patinate forms of ALLEN — *Chelinospora perforata* and *Cymbosporites catillus* — are somewhat similar to our material, but both of ALLEN's forms have a thicker patina.

Subturma: ZONOTRILETES WALTZ 1935.
Infraturma: CINGULATI POTONIÉ et KLAUS 1954.

Genus: *LYCOSPORA* SCHOPF, WILSON et BENTALL.
Type Species: *Lycospora micropapillata* (WILSON et COE) SCHOPF, WILSON et BENTALL 1944.

cf. *LYCOSPORA* sp.
Pl. 20, Figs. 9, 10

Description: Triradiate miospore of rounded-subtriangular amb, of greatest diameter 28 μ. The internal diameter (diameter of the spore cavity, central area or lumen) is 18 μ. The cingulum appears darker than the central area; it is darkest adjacent to the central area, and becomes progressively lighter towards the periphery producing a slightly bizonate appearance. The triradiate mark is clear, with the rays extending over the cingulum to the spore margin; the lips are relatively tall, apparently broad-based and merging gradually into the spore surface on either side. They diminish in height only towards their extremities. A narrow suture is perceptible. The proximal face is smooth and apparently thin; the distal face is ornamented with a number of low hemispherical sculptural elements; these are more or less circular in outline in plan view, and of rather varied size from less than 1 μ up to 3 μ in diameter. They are aggregated around the periphery of the central area of the spore and do not extend on to the cingulum.

As we have only a single specimen of this type of spore we have not made it the basis of a new species; indeed even its generic assignment might reasonably be questioned. It appears to be distinct from any species of *Lycospora* described from the Carboniferous or Devonian, although it may be compared in general terms with strongly sculptured species with a broad cingulum such as *Lycospora noctuina* BUTTERWORTH and WILLIAMS (Namurian). The sculpture is more comparable with that of some *Lophozonotriletes* species (e. g. *L. rarituberculatus* (LUBER) KEDO; cf. PLAYFORD 1963). Those who favour the current trend of making encreasingly narrow generic limits might regard this specimen as generically distinct. As we have only the single specimen we prefer to make a tentative generic assignment, realising that even this is open to criticism. We figure and describe this spore because it represents the most clear-cut case of a cingulate spore in the assemblage.

Genus: *DENSOSPORITES* BERRY 1937.
Type Species: *Densosporites covensis* BERRY.

cf. *DENSOSPORITES* sp.
Pl. 20, Fig. 11

Description: Subtriangular miospore with a greatest diameter of 38 μ, and a cingulum up to 7 μ wide. The exine is smooth, and both proximal and distal surfaces of the exine are present as very thin smooth membranes extending over the central area; one surface has a transverse crack. Owing to a certain amount of adhering debris in the central area it is difficult to affirm or deny the possible presence of a triradiate mark. The cingulum is optically much denser than the central area, but is of more or less uniform density throughout its width. It therefore conforms with *Densosporites, sensu stricto* (i. e. *Densosporites* in the sense of BUTTERWORTH et al 1964). It is similar to several Carboniferous species but as only a single specimen was found, no specific assignation was attempted.

Genus: *MUROSPORA* SOMERS.

Type Species: *M. kosankei* SOMERS 1952.

cf. *MUROSPORA* sp.
Pl. 20, Fig. 12

Triradiate miospore of subtriangular amb; sides slightly concave to slightly convex; 34 μ in greatest diameter, with an equatorial feature about 6 μ wide, which we interpret as a cingulum, appearing darker than the central area. The exine is smooth. The triradiate lips are broad (up to 4 μ wide) with a clear suture and an irregularly undulating outer edge. The suture ends at the margin of the central area; the lips continue on to the equatorial feature, and merge into it. As with the last species, this may be superficially compared with Lower Carboniferous species such as *M. varia* STAPLIN 1960 (from which our spore differs in, amongst other things, its much smaller size and more prominent lips). While PLAYFORD (1962) describes the equatorial feature of *Murospora* as a cingulum, STAPLIN regards species included within this genus as having some variety of structure — a cingulum, a distal patella or a capsula. Our spore appears comparable on the basis of the structure of its equatorial feature to *Murospora kosankei*, and we accordingly describe it as cingulate. Having only a single specimen, we prefer to assign our spore only tentatively to this genus.

General discussion

The significance of this small assemblage lies in its position close to the base of the Devonian system — that is, approximately of the same age as the earliest generally accepted record of a vascular land plant. Relatively few

accounts of Lower Devonian spores have been published. The only records from Britain of Lower Devonian dispersed spores are those figured but not named by LANG (1932), the small assemblage from the Witney Borehole described by CHALONER (1963), (of which the "early Devonian" age was itself deduced principally from the spores) and the mention of the occurrence of the two genera *Emphanisporites* and *Lophotriletes* by RICHARDSON et al. (1964). DOWNIE (1963) describes *Punctatisporites? dilutus* and *Lophotriletes* sp. from the Wenlockian (Silurian) and this must be regarded as the earliest record of triradiate spores from Britain.

Outside Britain, one of the most important works describing Lower Devonian spores is that of ALLEN (1965). In the Spitzbergen succession ranging from Gedinnian through Middle Devonian ALLEN records six genera from rocks believed to be of Gedinnian age, viz.: *Leiotriletes, Punctatisporites, Calamospora, Granulatisporites, Cyclogranisporites* and *Emphanisporites*. Earlier work on Lower Devonian and pre-Devonian spores is reviewed in OBRHEL (1958) and CHALONER (1960, 1963).

FRANKE (1965) describes an interesting assemblage of spores of late Lower Devonian age from the German Emsian, which he assigns to twenty-four genera (of which eleven are new). As FRANKE adopts a very narrow generic concept, perhaps this figure gives a somewhat misleading impression of diversity in the flora if used as the sole basis for comparison with other assemblages. Aside from FRANKE's record of a monosulcate pollen, *Gynkgaletes* (apparently based on a single specimen, which might be interpreted as a secondarily folded spore rather than as a pollen grain) the whole assemblage shows no greater complexity of spore structure than ALLEN's from comparable horizons.

There are two aspects of a spore assemblage from rocks of this age which are worth considering. Firstly, the establishing of the earliest appearance of the various known Devonian genera is important in their use as stratigraphic indices. Secondly, they are of interest simply as plant fossils offering some evidence on the progress of early land plant evolution. On average, land plant spores stand a much better chance of being preserved as fossils than the parent plant which produced them, because of the relatively large numbers in which they are produced, and the chemically resistant nature of the exine. (As a generalization this is of course limited to free-sporing vascular plants depending on wind for their spore dispersal, and does not apply to those Angiosperms which depend exclusively on insect pollination). The palaeobotanical interest in an assemblage of this age centres on the question of whether it indicates a more diversified land flora than the macrofossils have hitherto suggested for that horizon. The time of first appearance of vascular land plants has been debated as between Pre-Cambrian and late lower Palaeozoic (ANDREWS 1960, AXELROD 1959, STEWART 1960). While there are no pre-Gedinnian fossil vascular plants which are generally acceptable to palaeobotanists, a number of claims have been made of both vascular plant macrofossils and spores in the Lower Palaeozoic. AXELROD accepts a number of these — both macrofossil and spore records — and sees in them evidence of a diverse Lower Palaeozoic and possibly even Pre-Cambrian land flora of vascular plants. Other authors have taken a narrower view of what constitutes a land-plant spore and regard the Silurian as the earliest date of appearance of triradiate spores, followed by only a rather limited diversity of land flora in the early Devonian (STEWART 1960, CHALONER 1960). Any new evidence from spores as to the state of diversity of the early Devonian land flora is therefore worth examining.

The general suggestion of spore records published so far is one of a very limited number of spore types occurring in the Lower Devonian building up progressively and steadily to a greater number of types, representing spores of more elaborate morphology, by the late Devonian (cf. RICHARDSON et al. 1964). It is obviously important to establish wether or not the apparently restricted number of spore genera, of limited morphological complexity, so far reported in the Lower Devonian is a representative picture and not simply a result of inadequate study of samples of this age. No study of a single assemblage such as that described here can, on its own, offer conclusive evidence of this kind — particularly since such evidence from its very nature must be negative. However, our assemblage does contribute a little more to the general picture. In our assemblage, only five genera are represented in any number (the record of the other four genera resting, insecurely, on one or two specimens).

A count based on 200 specimens gave the following figures:

Leiotriletes	cf. *simplex*	8%
Punctatisporites	cf. *punctatus*	19%
Granulatisporites	*newportensis*	31%
Emphanisporites	*rotatus*	23%
Chelinospora	*vermiculata*	19%

The spores show only a limited range of sculptural elements: these include coni, vermicular depressions and proximal muri. One shows pronounced differential thickening of proximal and distal hemispheres (i. e. a patina). Of the spores represented by single specimens, two show a clear cingulum. In this respect our assemblage shows a slightly greater complexity than any recorded by ALLEN from the Gedinnian of Spitzbergen but is more comparable with ALLEN's Siegenian material (where not only *Lycospora* but *Stenozonotriletes, Camptozonotriletes, Cirratriradites* and *Rhabdosporites* are present). Despite this all our spores are basically simple and triradiate. None have morphologically elaborate appendages or any evidence of

double structure of the wall (saccate or cavate walls, of various authors) — features common in Middle and Upper Devonian and Carboniferous spores.

It might be added that the macrofossil record of the Downtonian flora (LANG 1937), the closest in age to our spore assemblage, includes only three vascular plants: *Zosterophyllum myretonianum*, and two species of *Cooksonia*. It seems fair to say that in terms of the number of genera present our spore assemblage represents a more diverse flora than the macrofossils, but that it does not suggest a flora of materially greater complexity.

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Explanation of Plates

Plate 19

All the photographs are × 1000, unless otherwise stated.
All the photographs are unretouched.

Figs. 1—2. *Leiotriletes* cf. *simplex* NAUMOVA. Slide numbers PF 3233 and PF 3234.

Figs. 3—6. *Punctatisporites* cf. *punctatus* (IBR.) POT. et LOOSE. 3—5. X 500. Slide numbers PF 3235, PF 3236 and PF 3237 respectively. 4 shows the proximal triangular marking. 6, part of the same specimen, X 2500, to show the minute cavities within the exine. Slide number PF 3238.

Figs. 7, 8 a. 11. *Granulatisporites newportensis* sp. nov. 7, 8, the holotype; proximal and distal surfaces respectively in the plane of focus. Slide number PF 3239. 11, slide number PF 3240.

Figs. 9—10. *Granulatisporites* sp. Two planes of focus. Slide number PF 3241.

Figs. 12—13. *Pachytheca* sp., X 10. 12. Specimen on the matrix with a quadrant removed and lying with the inner surface uppermost at right. 13. Illuminated to show radiating cortical filaments. Specimen number GSM 77202.

Plate 20

All the photographs are × 1000. All the photographs are unretouched.

Figs. 1—3. *Emphanisporites rotatus* McGREGOR. Slide numbers PF 3242, PF 3243 and PF 3244 respectively.

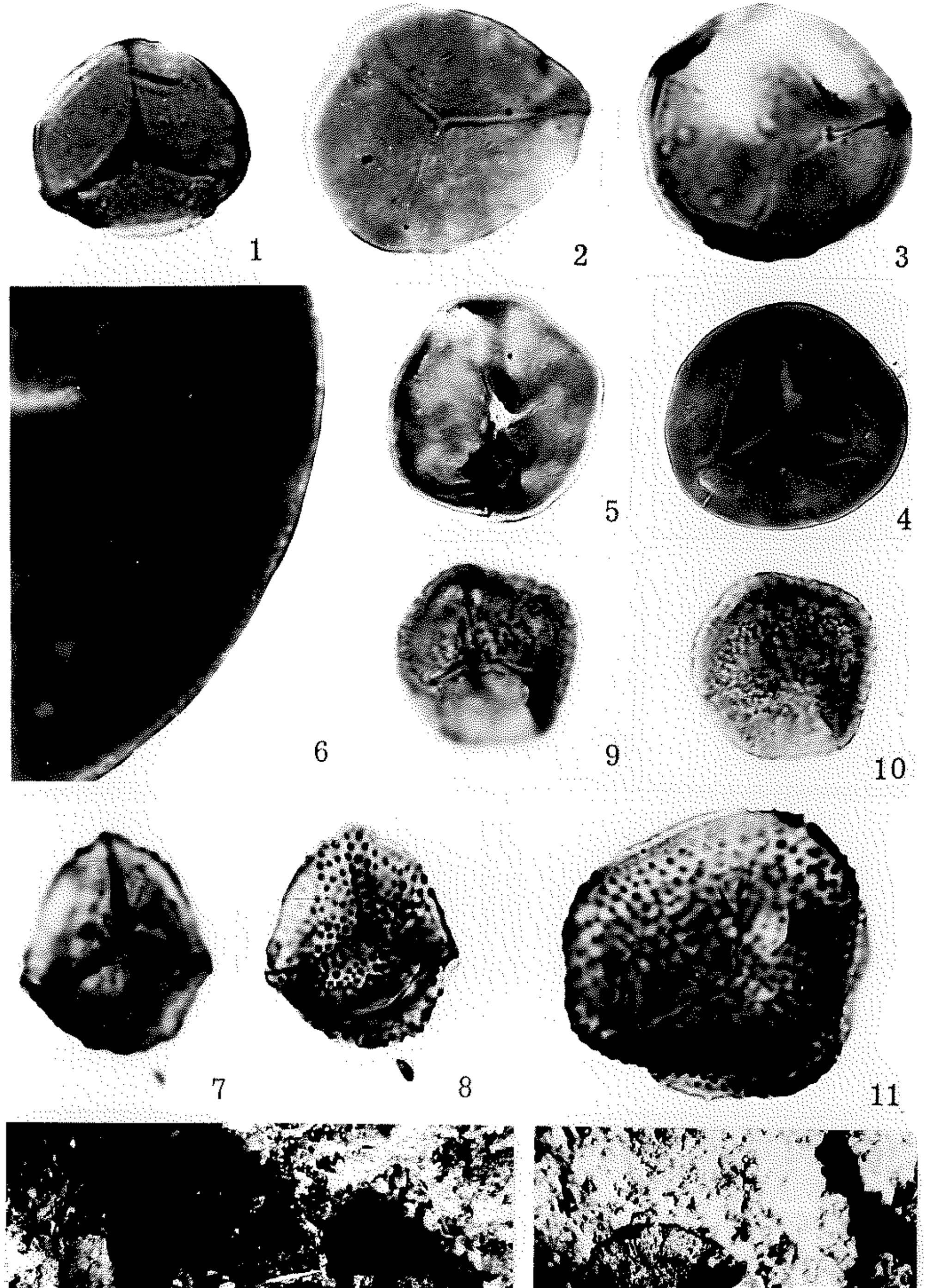
Fig. 4. *Retusotriletes* sp. Slide number PF 3245.

Figs. 5—8. *Chelinospora vermiculata* sp. nov. 5. Smooth proximal face and triradiate mark in focus in upper left of photo. Slide number PF 3246. 6. Tetrad showing the relative thickness of the wall in the proximal and distal areas. Slide number PF 3247. 7, 8. The holotype in two focal planes. Slide number PF 3248.

Figs. 9 a. 10. cf. *Lycospora* sp. 9. Focal plane more or less coincident with proximal face. 10. Distal face. Slide number PF 3249.

Fig. 11. cf. *Densosporites* sp. Slide number PF 3250.

Fig. 12. cf. *Murospora* sp. Slide number PF 3251.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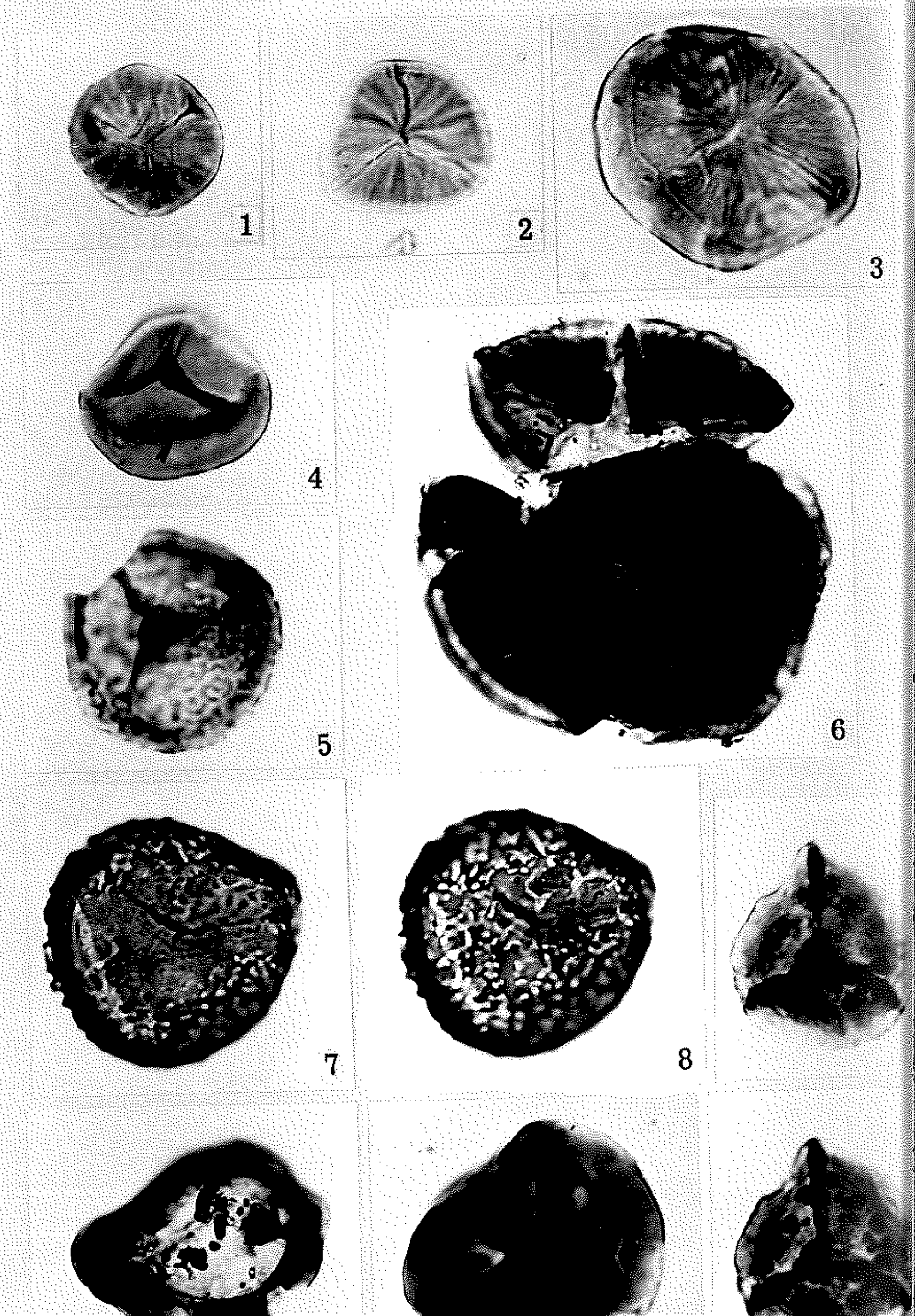
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