MIDDLE OLD RED SANDSTONE SPORE ASSEMBLAGES FROM THE ORCADIAN BASIN NORTH-EAST SCOTLAND

by J. B. RICHARDSON

ABSTRACT. Spore assemblages have been found in a variety of Middle Old Red Sandstone deposits sampled from several areas in the Orcadian basin, ranging from the south side of the Moray Firth in the south to the Orkney Islands in the north. New taxa include Subturma Pseudosaccititriletes and four genera, *Acinosporites*, *Corystisporites*, *Dibolisporites*, and *Samarisporites*; eighteen species and two varieties are new, and in addition the genus *Retusotriletes* (Naumova) is emended and restricted to laevigate spores in which well-developed curvaturae perfectae are a constant character; many of the other species described are new combinations of Eisenack (1944), or of various species of Russian authors.

The vertical distribution of spore assemblages in the Orcadian area is described and several points of local correlation discussed. Detailed comparisons with Russian spore assemblages are made and a correlation between the north-west Russian and Orcadian sequences is suggested. Characteristic features of Devonian, especially Middle Devonian spore assemblages are discussed. Apart from the spores no other acid-resistant microfossils have been found except for fragments of plant and fish tissues; the possible significance of this is discussed below.

PLANT microfossils have been obtained from rocks of varied lithological type occurring in the Orcadian basin, north-east Scotland. The lithologies include black bituminous flagstones and subordinate arenaceous flags, siltstones, and shales of Caithness and Orkney. Similar dark bituminous flagstones occur also in the Nairn valley (south-east of Inverness) but, as in other outliers on the south side of the Moray Firth, the strata are more arenaceous, and sequences of sandstones, siltstones, grey-green clays, and nodule beds are more common; this is also true of the dominantly arenaceous sequences of the Black Isle (including the famous Cromarty nodule beds) and Edderton burn to the north of the Moray Firth. These rocks are often prolific of spore assemblages, especially the grey-green clays and siltstones. The microfloras are described and their stratigraphical distribution and relation to lithological type are discussed.

Inter-regional comparisons are made difficult by lack of a uniform classificatory system, nevertheless there are striking similarities especially between the intensively studied Devonian microfloral assemblages from parts of the U.S.S.R. and the Scottish material. Although the volume of literature on Devonian spores is rapidly increasing, comparisons with regions other than the U.S.S.R. are difficult because in many cases the exact stratigraphical horizon of the assemblages is not known. There is thus a need for studies of microfloral assemblages from successions which are well dated by other fossils; only when this is done will it be possible to assess the inter-regional distribution of Devonian microfloras and to realize fully their stratigraphical potential.

During studies of spore assemblages the only other microfossils found have been fragments of plant tissues and fish remains. No chitinozoa, acritarcha, hystrichosphaeridia, or chitinous linings of foraminifera have been found although over 400 slides have been carefully studied.

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STRATIGRAPHY

The Old Red Sandstone of north-east Scotland is divided into three groups, the 'Basement' or Barren group, the Middle Old Red Sandstone, and the Upper Old Red Sandstone. The lower and upper groups are dominantly arenaceous strata while the middle group consists mainly of argillaceous sediments which, in this group's greatest development in Caithness and Orkney, are dark finely banded bituminous and calcareous flagstones. The 'Basement' group rests on igneous and metamorphic rocks of the Highlands, is overlain and in part overlapped by strata containing undoubted Middle Old Red Sandstone fossils. The age of the 'Basement' group is uncertain. On the other hand the Middle Old Red Sandstone of this area has been equated by Westoll (1951), mainly on the basis of fish faunas, with the Upper Eifelian and Givetian. The correlations in text-fig. 1 are based mainly on this work.

Spore assemblages have been isolated from the 'Basement' group and the Middle Old Red Sandstone of this area. The microfloras of the 'Basement' group, however, will be described in a separate publication.

SYSTEMATIC DESCRIPTIONS

All the slides referred to by serial numbers in the text are in the Department of Geology, King's College, London; position on the slide is indicated by the instrument settings of a Zeiss microscope, serial no. 4000349.

Anteturma SPORITES H. Potonié 1893
Turma TRILETES Reinsch 1891
Subturma AZONOTRILETES Luber 1935
Infraturma LAEVIGATI (Bennie and Kidston) Potonié and Kremp 1954
Genus LEIOTRILETES (Naumova 1937) Potonié and Kremp 1954

Type species. L. sphaerotriangulatus (Loose) Potonié and Kremp 1954.

Leiotriletes sp. A

Plate 88, fig. 1

Occurrence. Thurso and Eday flagstone groups, Caithness and Orkney.

EXPLANATION OF PLATE 88

All figures ×300 except where indicated.

Fig. 1. *Leiotriletes* sp. A, proximal view.

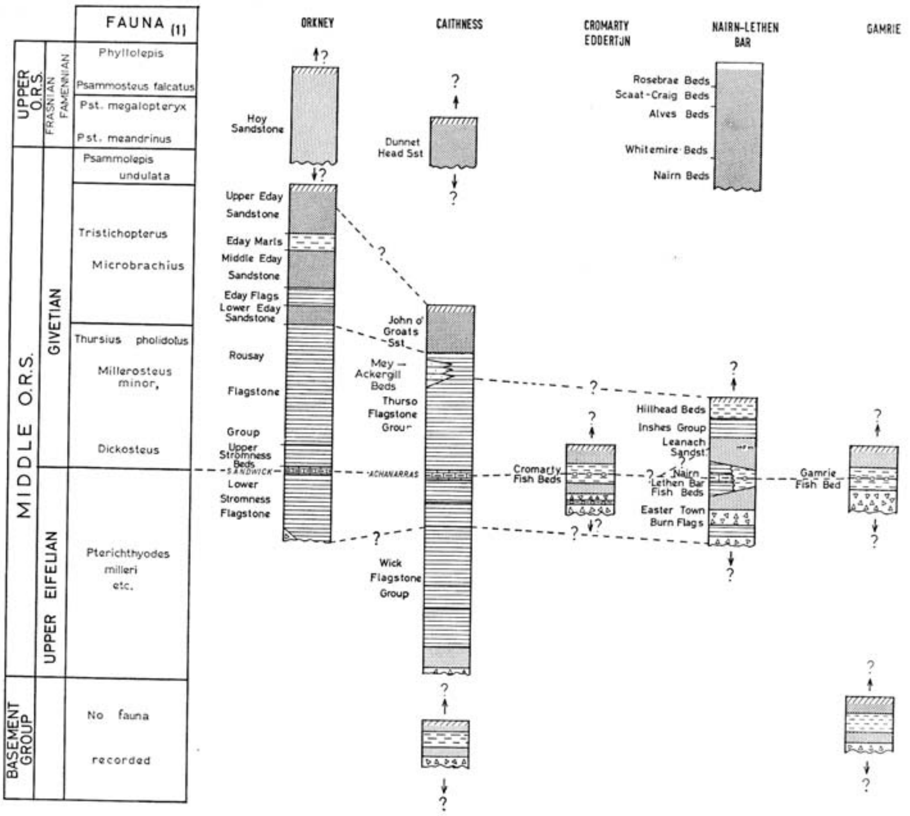
Fig. 2. *Punctatisporites confossus* sp. nov.; holotype, proximal view showing darkened contact areas.

Figs. 3–4. *Calamospora* spp. 3, *C. pannucea* sp. nov., holotype, distal view. 4, *C.* sp. showing darkened contact areas.

Figs. 5–8. *Retusotriletes* spp. 5–6, *R. dubius* (Eisenack) comb. nov. 5, Obliquely compressed specimen showing curvaturae and darkened contact areas, ×500; 6, two specimens showing torn and wrinkled interradial areas and curvaturae. 7–8, *R. distinctus* sp. nov. 7, Holotype, proximal view; 8, oblique compression showing the curvaturae perfectae in plan and profile at the spore margin.

Fig. 9. ? *Stenozonotriletes inequaemarginalis* sp. nov., holotype, proximal view, ×500.

Figs. 10–11. *Trileites langi* sp. nov., ×200. 10, Holotype, proximal view, showing triangular darkened contact areas with thinner areas at the junction of the three rays. 11, Proximal view of specimen showing fine triradiate sutures.



TEXT-FIG. 1. Correlation chart of generalized stratigraphical sections. Fauna (1) based on Westoll (1951), Miles and Westoll (1963), and Tarlo (1961).

Description. Size range 51 to 69 μ (seven specimens), outline triangular with rounded apices and convex interradial margins; exine smooth to infrapunctate, approximately 1 μ thick. Trilete rays three-quarters to equal radius; trilete folds on some specimens.

Comparison. Thomson's group 5a (1944) includes a similar spore (pl. 3, fig. 12).

Genus PUNCTATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. P. punctatus Ibrahim 1933.

Punctatisporites confossus sp. nov.

Plate 88, fig. 2

Holotype. Size 93 × 105 μ; slide OR.45, reference 378991; ? Eday flags, loc. 4.

Occurrence. In all sediments studied but most abundant in ? Eday flags, Inganess.

Diagnosis. Spores with thick exine, externally smooth and strongly infrapunctate, tetrad rays one-half to two-thirds radius; contact areas small and thickened.

Description. Size range 80 to 126 μ (twenty-five specimens measured); outline circular to elliptical. Exine 2 μ thick, occasionally folded; externally smooth but with marked infrapunctation; infrapunctation often exposed by corrosion of the spore wall, corrosion sometimes confined to the interradial areas but more often irregular. Triradiate mark distinct one-half to two-thirds radius, bordered by darkened (thickened) contact areas.

Comparison. This species differs from typical species of *Punctatisporites* by the presence of darkened contact areas. However, the trilete rays are longer, and the exine thicker than typical *Calamospora* species. Further it is strongly infrapunctate and does not show the taper-pointed folding typical of *Calamospora.* The genus *Phyllothecotriletes* Luber has a thick wall, darkened contact areas, but has shorter trilete rays.

Derivation of name. L. confossus—full of holes, referring to the marked infrapunctation.

Genus TRILEITES (Erdtman 1945, 1947) ex Potonié 1956

Type species. T. spurius (Dijkstra) Potonié 1956.

Trileites langi sp. nov.

Plate 88, figs. 10, 11

1925 Type F of Lang; pl. 1, figs. 10–12.

Holotype. Size 209 × 330 μ, exine thick; slide CR.170, reference 379881; Achanarras horizon, loc. 13.

Occurrence. Occurs in most of the beds examined but specimens in Thurso and Eday beds are smaller and have a relatively thinner wall.

Diagnosis. Large, thick-walled spores, tetrad rays four-fifths to nearly equal the radius, surrounded by small, distinct, triangular contact areas.

Description. Colour yellow to reddish-brown. Size range 236 to 400 μ (thirty specimens measured); outline circular to subcircular; spores probably originally subspherical and flattened at the proximal pole. Exine 5 to 13 μ thick; externally smooth with fine infrapunctations, often crumpled into large arcuate folds. Small triangular contact area in the centre of the spores which is thinner than the rest of the spore, bordered by thickened triangle; tetrad rays four-fifths to nearly equal radius of the spore, distinct only in contact areas (one-fourth radius).

Remarks. The spores above could be placed in either *Laevigatisporites* or *Trileites.* Typical members of these genera have distinct curvaturae perfectae which are absent in the spores of *T. langi.* However, some species of *Laevigatisporites* and *Trileites* lack curvaturae, e.g. *L. reinschi* Ibrahim and *T. pinguis* (Harris) Potonié and Kremp. According to Potonié (1956, p. 23) *Trileites* differs from *Laevigatisporites* in having longer Y-rays, whereas Chaloner (1963, p. 108) emphasizes differences in shape; *Laevigatisporites* is regarded as concavo-convex and *Trileites* more or less spherical. Since the spores described by the author appear to have been more or less spherical originally and have long Y-rays they are placed in the genus *Trileites.*

Megaspores from a specimen of the heterosporous plant *Barinophyton richardsoni* (Perry, Maine) are closely similar to the spores described above (Pettitt, in press). Pettitt's spores differ in having short Y-rays; however, in *T. langi* only the innermost parts of the Y-rays are distinct (one-quarter radius), whereas their continuations (i.e. beyond the contact areas) are barely discernible fine sutures in some specimens and in others are not visible.

Comparison. Spores of this type were originally described by Lang (type F). Group 1, form 3, Elovskava (1936, pl. 2, figs. 3 and 4) probably contains spores which are identical to type F; Elovskava's spores are variable in size with a diameter usually about 260 μ. *Calamospora laevigata* (Ibr.) Schopf, Wilson, and Bentall (1944) is also very similar to *T. langi* although in the former the size range is greater (250 to 500 μ), the Y-rays are shorter (only one-third radius), and there are no contact areas. Spores of *Archaeozonotriletes incrustatus* Archangelskaya (1963, pls. 5, 6) are very similar but no sign of the double, partially separated, wall structure is seen in the Scottish specimens. The Russian specimens are from the Lower Frasnian of the Russian platform.

Genus CALAMOSPORA Schopf, Wilson, and Bentall 1944

Calamospora pannucea sp. nov.

Plate 88, fig. 3

Holotype. Size 110 × 123 μ; slide CR.175, reference 422880; Achanarras horizon, loc. 13.

Occurrence. In all the beds examined.

Diagnosis. Spore with thin crumpled exine; triradiate mark one-third to one-half, with triangular contact area.

Description. Size range 62 to 146 μ (forty specimens measured). Outline subcircular to irregular; exine thin and does not retain a definite shape, crumpled into numerous taper-pointed folds. Triradiate mark distinct one-third to one-half radius. A distinct triangular contact area is often seen, the inner part of the triangle is often thinner than the rest of the spore coat.

Comparison. Elovskava described similar spores as Group I, Form 4 (1936, pl. 2, figs. 5, 6). The size range of Elovskava's spores is 110 to 160 μ, slightly greater than that of the spores described here. Triradiate marks and contact areas are not mentioned by Elovskava so further comparison is not possible. The exine of *Leiotriletes nigratus* Naum. 1953 appears more dense.

Derivation of name. L. pannuceus—wrinkled.

Genus RETUSOTRILETES (Naum. 1953) emend.

Type species. R. pychovii Naumova 1953, pl. 14, fig. 5.

Emended diagnosis. Radial trilete miospores; equatorial outline subcircular to subtriangular. Exine externally smooth or finely wrinkled, infra-structure varied. Curvaturae perfectae distinct, often forming a wedge-shaped thickening when seen in lateral compression.

Comparison. Cadiospora Kosanke 1950 has, in addition to curvaturae, well-marked thickened lips. *Divisisporites* (Thomson) Potonié 1956 has curvaturae imperfectae.

Remarks. Potonié (1958, pp. 13, 14) did not formally emend this genus but included it with smooth-walled genera in his classification. The present author restricts this genus to laevigate spores since it is only on such spores (in the assemblages studied) that the curvaturae perfectae form a constant character. In polar compression the thickened curvaturae often dip below the spore margin and give the effect of thickened interradial areas often seen in *R. dubius* (Eisenack); but in lateral compression curvaturae are clearly seen.

Retusotriletes dubius (Eisenack) comb. nov.

Plate 88, figs. 5, 6

1925 Type D of Lang, pl. 1, fig. 8.
1944 *Triletes dubius* Eisenack, p. 115; pl. 2, fig. 7, text-fig. 14.

Holotype. Eisenack 1944, pl. 2, fig. 7; size 92 μ. Triradiate mark five-sixths of the spore radius. Probably Middle Devonian.

Occurrence. Found in all the beds throughout the area. Especially abundant at the Achanarras horizon, Cromarty and Edderton.

Diagnosis. Equatorial outline subtriangular. Relatively thick-walled spores, triradiate mark distinct, two-thirds to nearly equal spore radius, bordered by small darkened contact areas.

Description. Size range 56 to 110 μ (fifty specimens measured). Spore probably originally subspherical. Exine often appears thicker in the interradial areas due to the curvaturae which dip below the margin; externally smooth and finely infrapunctate. The outer smooth layer is often 'torn' from the interradial contact areas and forms arcuate folds, the layer beneath is contorted into minute wrinkles which are usually radially arranged. A distinct triangular, darkened contact area occurs, this is best seen on spores in which the outer layer has been ruptured.

Comparison. This species differs from *R. distinctus* sp. nov. by its smaller size and darkened contact areas. Lang (1925) described similar spores from Cromarty which he named type D. His photograph shows the torn proximal surface often seen in these spores and also darkened contact areas. The size range given by Lang was 60 to 75 μ. Thomson (1940) also figured a spore (group 5A, pl. 3, fig. 13) which closely resembles *R. dubius* from the Middle Devonian of Estonia. Spores designated *Triletes dubius* Eisenack 1944 (pl. 2, fig. 7) are identical to specimens found in the Orcadian deposits, several specimens were examined for comparison including the holotype; the size range of Eisenack's spores is 92 to 104 μ. *R. translaticus* Tchibrickova 1959 is very similar to *R. dubius* but is smaller.

Remarks. The original description of *R. dubius* (Eisenack) did not include a diagnosis. Since there are now a number of comparable species it is here thought desirable to include a diagnosis in common with current practice; however, the original concept of the species has not altered and therefore it is not an emended diagnosis. This procedure is also followed for *D. echinaceus* (Eisenack).

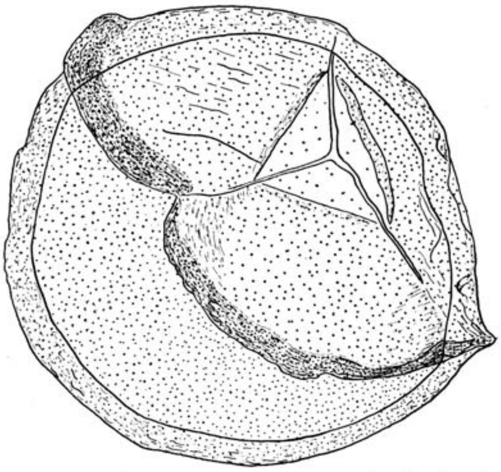
Retusotriletes distinctus sp. nov.

Plate 88, figs. 7, 8; text-fig. 2

1925 Type C of Lang; pl. 1, fig. 7.

Holotype. Size $170 \times 180\,\mu$, exine $8\,\mu$ thick; slide CR.169, reference 259972; Achanarras horizon, loc. 13.

Occurrence. In samples from the Achanarras horizon throughout the area, especially abundant at Coal Heugh, Cromarty. Also occurs consistently in the Upper Wick flagstone group.



TEXT-FIG. 2. *R. distinctus* sp. nov., camera lucida drawing of obliquely compressed specimen showing curvaturae perfectae, $\times 500$.

Diagnosis. Outline circular to subcircular, spores with thick exine, triradiate mark distinct, rays reach the equatorial margin; curvaturae perfectae thickened.

Description. Colour brown to reddish-brown; size range 113 to $218\,\mu$ (thirty-six specimens measured). Equatorial outline circular to subcircular. Exine dense, externally smooth but with pronounced infrapunctation and also minutely wrinkled internally; exine 6 to $15\,\mu$ thick. Spores originally spherical or nearly so. Triradiate mark distinct, rays equal the radius; there are large contact areas and distinct curvaturae perfectae which in laterally compressed spores can be seen projecting at the margin as a wedge-shaped thickening (Pl. 88, fig. 8). Within contact areas a smaller darkened triangular area often occurs.

Comparison. Spores designated type C by Lang are included in this species; Lang's spores were only slightly variable in size, ranging around $100\,\mu$. Spore type 3C Thomson (1940; pl. 2, fig. 9*a*) is similar to this species but the triradiate mark is about half the spore radius (from the photograph). *P.* ? *limbatus* Hacquebard 1957 has a folded exine and a triradiate mark one-half to two-thirds of the radius. Further, the 'border' in

R. distinctus is not a limbus or any form of equatorial thickening but is due to wall thickness; this can be clearly seen in obliquely compressed spores. *Retusotriletes laevis* Tchibrickova 1959 is smaller (65–75 μ); *R. obliteratus* Tchib. 1962 (Calceola series) is very similar but the contact areas appear thinner than the rest of the spore and the curvaturae are not thickened.

Infraturma APICULATI (Bennie and Kidston) Potonié 1956
Genus APICULATISPORIS (Ibrahim) Potonié and Kremp 1956

Apiculatisporis microconus sp. nov.

Plate 89, fig. 3

Holotype. Size 118 × 146 μ; slide CR.170, reference 383875. Achanarras horizon, loc. 13.

Occurrence. Present in all beds except the Eday beds. Upper Eifelian and Givetian.

Diagnosis. Ornament consists of minute cones; contact areas distinct, triradiate mark one-half to three-quarters radius, lips thickened.

Description. Size range 100 to 164 μ (fifteen specimens measured). Equatorial outline circular to subcircular; exine thin, often folded. Ornament consists of minute cones and small rods less than 1 μ high which are relatively widely spaced. Contact areas distinct, darker in colour.

Comparison. *A. microconus* differs from *Dibolisporites* cf. *gibberosus* Naum. var. *major* Kedo by the minute nature of the ornament but in all other respects they are similar. The extremely small sculptural elements are difficult to resolve, consequently these spores are tentatively assigned to *Apiculatisporis*.

Genus ACANTHOTRILETES (Naumova) Potonié and Kremp 1954
Acanthotriletes multisetus (Luber) Potonié and Kremp 1955

1938 *Azonotriletes multisetus* Luber in Luber and Waltz; p. 15, fig. 61.

Acanthotriletes multisetus var. *major* var. nov.

Plate 89, fig. 7

EXPLANATION OF PLATE 89

All figures × 300 except where indicated.

Figs. 1–2, 4–6. *Dibolisporites* spp. 1–2, *D.* cf. *correctus* (Naum.) comb. nov. 1, Proximal view, × 500; 2, detail of the ornament showing biform elements, × 1000. 4, *D.* cf. *gibberosus* var. *major* (Kedo) comb. nov., obliquely compressed. 5–6 *D. echinaceus* (Eisenack) comb. nov. 5, Distal view; 6, detail of the ornament showing biform elements, × 1000.

Fig. 3. *Apiculatisporis microconus* sp. nov., holotype, proximal view.

Figs. 7–9. *Acanthotriletes* spp. 7, *A. multisetus* var. *major* var. nov., distal view. 8, *A.* sp. B. 9, *A.* cf. *horridus* Hacquebard, polar view.

Fig. 10. *Corystisporites multispinosus* sp. nov., holotype, proximal view.

Fig. 11. *Anapiculatisporites petilus* sp. nov., holotype, distal view, × 500.

Figs. 12–14. *Verrucosisporites* spp., × 500. 12, *V.* cf. *lebedianensis* (Naum.) comb. nov., polar view. 13, *V.* cf. *uncatus* (Naum.) comb. nov., obliquely compressed. 14, *V.* cf. *grandis* (Naum.) comb. nov., distal view.

Holotype. Size 78 × 84 μ; slide OR.35, reference 338948; ? Eday beds, loc. 4.

Occurrence. Hillhead beds and Eday beds; Givetian.

Diagnosis. Ornament consists of fine hair-like processes; size range over 60 μ.

Description. Size 68 to 116 μ (fifteen specimens measured). Outline subcircular to elliptical. Exine relatively thin, consists of two closely adhering membranes. Outer membrane bears short, closely packed, hair-like spines or fimbrae 2 to 4 μ long, which are parallel-sided or only slightly tapered. Inner membrane (intexine) smooth, only seen in torn specimens. Exine often crumpled into taper-pointed folds. Triradiate mark one-half to two-thirds radius, lips elevated.

Comparison. This variety appears to be identical to spores described by Luber except in size, the size range of the latter is 40 to 60 μ. *Dibolisporites echinaceus* (Eisenack) has much coarser, more irregular projections which often have terminal cones.

Remarks. The erection of a new variety of the species *Acanthotriletes multisetus* results in another new variety, based on Luber's type, being automatically set up. This new variety is designated *A. multisetus* var. *multisetus*.

Acanthotriletes cf. *horridus* Hacquebard 1957

Plate 89, fig. 9

Occurrence. Rare; only in ? Eday flags, Inganess shore.

Description. Colour dark brown, spores practically opaque. Size range 118 to 183 μ, excluding spines (on two specimens). Outline subcircular to subtriangular. Exine thick, covered with long, tapering, pointed spines which have very slender apices; spines 25 to 60 μ long. Triradiate mark indistinct.

Comparisons. These spores are similar to those described by Hacquebard from the Horton Group (Mississippian) of Nova Scotia. The spines of the Inganess spores are, however, much longer, and also the elevated lips described by Hacquebard are not seen. This may be a distinct species.

The spores described by Arnold (pl. 4, fig. 5, 1936) and Høeg (type C, pl. 49, fig. 16, 1942) appear to be very similar to those described here; however, their spores are much larger. Arnold's spore is 300 μ (excluding spines) and Høeg's spores are also 300 μ in diameter with spines up to 100 μ long.

Acanthotriletes sp. A

Plate 89, fig. 8

Occurrence. Coal Heugh, Hillhead beds, ? Eday beds (Inganess). Rare.

Description. Size 90 to 118 μ (on five specimens) excluding spines. Outline subcircular. Exine relatively thick, covered sparsely by spines 9 to 15 μ long; spines taper evenly and are sharply pointed. Triradiate mark indistinct.

Comparison. Similar spores have been found by Butterworth in the Lower Carboniferous (pers. comm.).

Genus DIBOLISPORITES gen. nov.

Type species. Dibolisporites echinaceus (Eisenack) comb. nov.

Diagnosis. Radial, trilete, azonate miospores. Equatorial outline subcircular to subtriangular. Sculptural elements dominantly biform (see text-fig. 3) but otherwise very variable, consisting of cones, rod-like processes, pila, verrucae, and spines.

Comparison. Some species of *Biharisporites* have similar ornament but *Biharisporites* is restricted to spores of the megaspore size range. The genus *Acinosporites* gen. nov. has convolute and anastomosing ridges superimposed on which are sculptural elements of various types.

Derivation of name. Gr. dibolus—two pointed; referring to the dominant biform nature of the sculptural elements.

Dibolisporites echinaceus (Eisenack) comb. nov.

Plate 89, figs. 5–6; text-fig. 3 B–D

1944 *Triletes echinaceus* Eisenack, p. 113; pl. 2, fig. 5.

Holotype. Eisenack 1944, pl. 2, fig. 5; size 170 μ, spinose processes 8–10 μ long. Probably Middle Devonian.

Occurrence. Hillhead beds, rare; Eday beds, frequent. Givetian.

Diagnosis. Ornament variable, consists of short spines and also spinose processes and pila which often bear small cones at their apices.

Description. Colour yellow to brown. Size range 92 to 204 μ (Eisenack, 92 to 164 μ; Scottish specimens, 96 to 204 μ, thirty specimens measured). Equatorial outline circular to subcircular. Exine thin, often folded into taper-pointed folds; ornament variable, consists of pointed spines, elongate, more or less parallel-sided spines often with expanded and flattened apices and terminated with small cones, or short pila-like ornament also with small cones at their apices (text-fig. 3); several types of ornament may occur on a single spore; processes 3 to 10 μ long and densely packed. Triradiate mark two-thirds to equal the radius of the spore, lips occasionally elevated; contact areas distinct, externally smooth and infragranular, curvaturae perfectae seen in some specimens.

Comparison. These spores are identical to those described by Eisenack; his preparations have been examined for comparison. Also his description of the variable ornament parallels that found in the Eday beds. They differ from *D.* cf. *gibberosus* var. *major* (Kedo) in having more elongate sculptural elements. *Retusotriletes devonicus* (Givetian, U.S.S.R.) figured but not described by Naumova 1953 (pl. 22, fig. 108) is probably synonymous with *D. echinaceus* but the details of the ornament cannot be seen. *R. devonicus* var. *echinatus* Tchib. 1962 (Calceola series, Upper Eifelian) is also very similar.

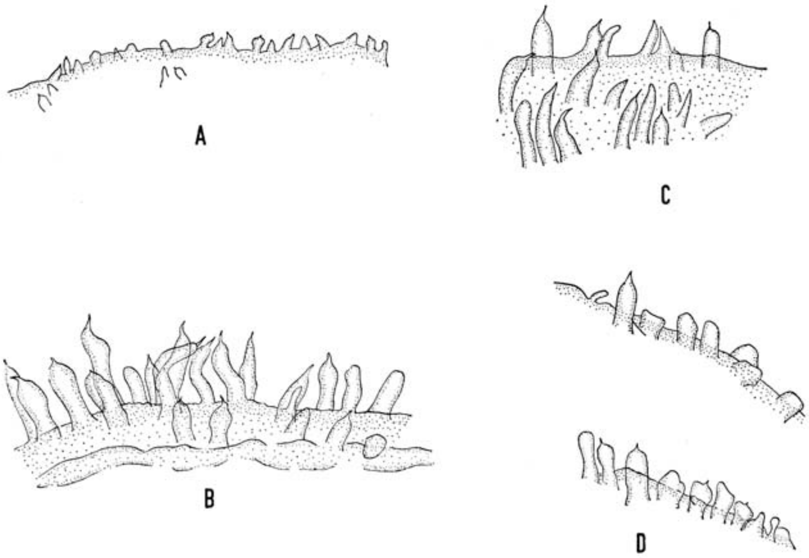
Dibolisporites cf. (al. *Acanthotriletes*) *correctus* (Naum.) comb. nov.

Plate 89, figs. 1, 2

1925 Type E of Lang, p. 256; pl. 1, fig. 9.
Cf. 1953 *Acanthotriletes correctus* Naumova, pl. 1, fig. 22.

Occurrence. Givetian, U.S.S.R. (Naumova); abundant at Achanarras horizon, rare in the Hillhead beds, Givetian.

Description. Size range 53 to 85 μ (thirty specimens measured); outline subcircular to subtriangular. Exine often folded, covered with broad-based, more or less conical warts, warts usually rounded in profile but occasionally terminally flattened; apices of warts often sharply constricted to form fine cone-like terminations; warts 2 to 5 μ high, 3 to 4 μ wide at their bases; in plan view warts rounded, polygonal, or irregular, usually separate but occasionally joined in small groups of two or three elements. Triradiate mark, simple, often indistinct, two-thirds to nearly equal radius.



TEXT-FIG. 3. Camera lucida drawings to show the sculptural details of various species of *Dibolisporites*; A, *D.* cf. *gibberosus* var. *major* (Kedo); B, C, D, *D. echinaceus* (Eisenack), B, holotype; C and D, showing sculptural variation in Scottish assemblages; all × 1500.

Comparison and remarks. Lang recorded two specimens 50 and 60 μ respectively. Naumova's spores appear to be identical to those described above but have a smaller size range (40 to 50 μ). The broad-based warts distinguish this species from other species of *Dibolisporites*.

Dibolisporites cf. (al. *Retusotriletes*) *gibberosus* (Naum.) var. *major* (Kedo) comb. nov.

Plate 89, fig. 3; text-fig 3A

Cf. 1955 *Retusotriletes gibberosus* (Naum.) var. *major* Kedo, pl. 1, fig. 15.

Occurrence. Givetian, Belorussiya (Kedo 1955). Occurs throughout the Middle O.R.S. sequence in Scotland but is most common in the ? Eday beds, loc. 4.

Description. Size range 88 to 160 μ (thirty specimens measured). Exine thin, often crumpled into taper-pointed folds; ornament variable, consists of cones, granules, more elongate rod-like processes and pila; all four types of ornament can occur on a single specimen and on well-preserved specimens are frequently terminated by minute cones; sculptural elements 1–2 μ high. Curvaturae perfectae present in many specimens, contact areas distinct and without any external ornament but with an irregular infrareticulation. Triradiate mark one-half to three-quarters spore radius, lips elevated.

Comparison and remarks. These spores are closely similar to those of Kedo (1955, p. 21) who describes the ornament as tubercles of variable shape from rounded to somewhat elongate. *R. gibberosus* was designated 'Naum. *in litt.*' by Kedo and was figured but not described by Naumova (1953, pl. 22, fig. 110).

The genus *Retusotriletes* is not adopted for this variety since curvaturae perfectae (in the Middle O.R.S. studied) is a character of variable occurrence in spores which are otherwise identical. Again Kedo figures specimens (1955, pl. 1, figs. 18, 19) of a single species of *Retusotriletes* with and without curvature. The genus *Retusotriletes* is here restricted to smooth-walled species, no specimens of which have been seen without curvaturae (see above).

Genus CORYSTISPORITES gen. nov.

Type species. C. multispinosus sp. nov.

Diagnosis. Radial, trilete, azonate miospores, with sculpture consisting of spinose processes with pointed, blunt to slightly expanded apices; triradiate mark with lips elevated in the form of an apical prominence or gula.

Comparison. The prominent triradiate ridges exclude these spores from the genus *Acanthotriletes* Potonié and Kremp; the genus *Lagenicula* is closely similar but is a 'megaspore' genus, whereas the Scottish spores described here are of relatively small size.

Corystisporites multispinosus sp. nov.

Plate 89, fig. 10; text-fig. 4

Holotype. Size 129 μ (excluding spines), spines 15 to 18 μ long, number of spines around the equator fifty-three. Slide MF.9, reference 450893; Hillhead Beds (Thurso flagstone group), loc. 20. Givetian.

Occurrence. Abundant in Hillhead beds, rare in ? Eday beds, Inganess shore.

Diagnosis. Exine covered with closely packed spines; triradiate ridges membranous, elevated to form an apical prominence.

Description. Size range, excluding spines, 70 to 144 μ (thirty specimens measured). Equatorial outline circular to subcircular; outline in lateral view hemispherical with flattened proximal surface. Spores originally subspherical flattened at the proximal pole. Exine thicker in the inter-radial areas covered with spines which often have swollen bases and pointed apices, a few spines have blunt slightly expanded tips; spines occasionally fused in groups and occur in more or less concentric rows; spine length 6 to 13 μ, number around the equator twenty to fifty-three. Triradiate sutures not seen but there are triradiate, membranous ridges, 20 to 32 μ high (lateral compression) which reach the equatorial margin; seen as contorted folds in polar compression.

Comparison. Hymenozonotriletes polyacanthus var. *major* Tchib. 1962 (Eifelian) is similar but has a much larger size range (150 to 250 μ) and appears to have no triradiate lips or apical prominence.

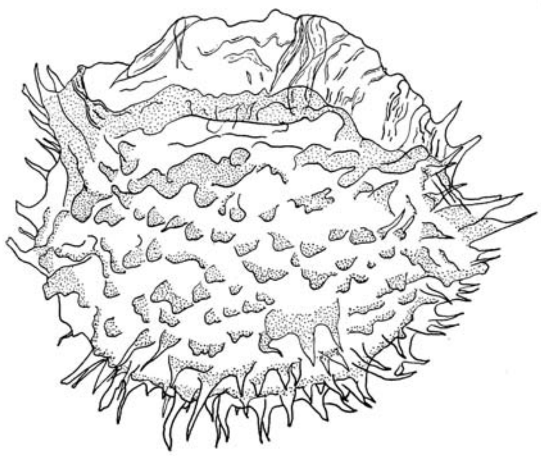
Genus ANAPICULATISPORITES Potonié and Kremp 1954

Type species. A. isselburgensis Potonié and Kremp 1954.

Anapiculatisporites petilus sp. nov.

Plate 89, fig. 11

Holotype. Size 43×50 μ: slide CR.165, reference 3911037. Achanarras horizon, loc. 14.



TEXT-FIG. 4. *Corystisporites multispinosus* sp. nov., lateral compression showing apical prominence, camera lucida drawing, ×600.

Occurrence. Rare; at Achanarras horizon on the Navity shore, also in the Thurso beds, and a single specimen was found in the ? Eday beds.

Diagnosis. Exine thick, ornament consists of short, pointed, slender spines; spine length three to five times greater than width.

Description. Size range 33 to 78 μ (fifteen specimens measured). Equatorial outline subtriangular with convex sides and rounded apices. Spines 2 to 5 μ high less than 1μ wide at their base; ornament confined to the distal surface and equatorial margin; about fifteen around the periphery. Triradiate mark nearly equals radius; folds along tetrad rays, often contorted.

Comparison. A. hispidus Butterworth and Williams 1958 is smaller, has a thinner exine, and a greater concentration of spines around the periphery.

Derivation of name. L. petilus, thin, slender, referring to the thin nature of the spines.

Genus VERRUCOSISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. V. verrucosus Ibrahim 1933.

Verrucosisporites premnus sp. nov.

Plate 90, figs. 1, 2

Holotype. Size 72 μ, verrucae 10 to 12 μ wide, 7 to 12 μ high; slide OR.34 reference 453916; ? Eday flags, loc. 4.

Occurrence. Eday flagstone group, Orkney. Givetian.

Diagnosis. Ornament consists dominantly of large, parallel-sided or slightly tapered verrucae, but smaller sculptural elements are also present.

Description. Size range, excluding ornament, 43 to 96 μ (thirty specimens measured). Equatorial outline circular to subcircular. Spores show no preferred orientation and are often compressed obliquely and laterally. Exine 3 to 4 μ thick. Ornament consists mainly of large, often closely packed, verrucae, but the size and shape is variable on a single spore; sculpture mainly confined to the distal hemisphere and equatorial margin; width of verrucae usually exceeds height but occasionally equals it, width 4 to 26 μ, height 4 to 16 μ; in profile verrucae usually parallel-sided or slightly tapered with flat, slightly curved, and lobed and serrate apices, but occasionally more conical elements with rounded apices occur; ornament in plan view circular to oval, polygonal or irregular. Verrucae often show striations parallel to apices, number around the equator seven to twelve. Triradiate mark distinct, two-thirds to nearly equal radius of the spore.

Comparison and remarks. Spores designated J5 (Radforth and McGregor 1954) from the ? Lower Devonian of Canada resemble *V. premnus*. *Raistrickia*? *gibberosa* Hacquebard 1957 is also similar but is subtriangular in outline and has more regular and widely spaced ornament. *Lophotriletes* aff. *rarituberculatus* (Sadcova) Ischchenko 1958 is closely similar but the maximum height of the tubercles is 3 to 6 μ. *Lophozonotriletes grandis* Naum. 1953 has smaller verrucae. *L. scurrus* var. *jugomaschevensis* Tchib. 1962 (Givetian) is similar but the sculptural elements expand towards their apices.

The presence of large and small sculptural elements on individual specimens of this species is a feature which may eventually warrant generic recognition.

Derivation of name. G. premnos—stump, referring to the shape of the dominant ornament.

Verrucosisporites cf. (al. *Acanthotriletes*) *uncatus* (Naumova) comb. nov.

Plate 89, fig. 13

Cf. 1953 *Acanthotriletes uncatus* Naumova, pl. 1, figs. 23, 24.

Occurrence. Eday flags, Orkney; Givetian. Top of Givetian and base of Frasnian, U.S.S.R.

Description. Size range 38 to 60 μ (excluding ornament); Naumova's spores 40 to 45 μ. Equatorial outline subcircular to subtriangular; spores show no preferred orientation. Exine thick, covered by variable ornament consisting of verrucae and spines, verrucae in profile, parallel-sided to slightly tapered, with flattened, lobed, or slightly rounded apices; in plan view rounded, polygonal, or irregular; width of verrucae 2 to 10 μ; height 2 to 6 μ, width usually greater than height but occasionally equals the height;

number around the equator nine to fifteen. Triradiate mark distinct, rays equal or nearly equal to the spore radius.

Comparison and remarks. These spores appear identical to those figured by Naumova (1953, pl. 1, figs. 23, 24), the ornament is very similar, consisting of a mixture of parallel-sided verrucae with flattened or lobed apices and more rounded verrucae and cones. However, many of the Scottish specimens are more rounded in outline. *Filicitriletes densus* Luber 1955 is also similar.

Verrucosisporites cf. (al. *Lophozonotriletes*) *grandis* (Naumova) comb. nov.

Plate 89, fig. 14

Cf. 1953 *Lophozonotriletes grandis* Naumova, pl. 11, figs. 5, 6.

Occurrence. Eday flags, Orkney, Givetian; Givetian and Frasnian, U.S.S.R., Naumova (1953) and Kedo (1957).

Description. Equatorial outline subcircular. Size range 51 to 60 μ (on five specimens). Sculptural elements sparse, consist dominantly of verrucae with occasional cones; number around the periphery nine to eleven; verrucae in profile more or less parallel-sided with rounded or flattened apices; in plan usually subcircular but occasionally irregular; usually 2 to 5 μ wide (occasional elements up to 10 μ wide) and 2 to 4 μ high. Triradiate mark simple, Y-rays nearly equal radius of spore.

Remarks. Typical specimens of *V*. cf. *grandis* have sparse, more rounded, and smaller sculptural elements than *V*. cf. *proscurrus* (cf. Naumova 1953, pl. 11, figs. 5, 6); however, they tend to show gradation to specimens of the *V*. cf. *proscurrus* and *V*. cf. *uncatus* types.

Verrucosisporites cf. (al. *Lophozonotriletes*) *lebedianensis* (Naumova) comb. nov.

Plate 89, fig. 12

Cf. 1953 *Lophozonotriletes lebedianensis* Naumova, pl. 17, fig. 42.

Occurrence. ? Eday flags, loc. 4.

Description. Equatorial outline subcircular. Size 57 μ (one specimen). Spore covered by thin-walled 'vesicles' which are more or less globular in shape; ornament confined to the distal surface and equatorial margin; 'vesicles' 8 μ high and 8 μ wide. Triradiate mark distinct nearly equal to the radius of the spore.

Comparison. This spore closely resembles the spore figured by Naumova (1953, pl. 19, fig. 34) which is from the Famennian of the U.S.S.R. Naumova's species does not appear to have true zona but there appears to be a concentration of ornament around the equator; there is no such concentration in the specimen described above.

Verrucosisporites cf. (al. *Lophozonotriletes*) *proscurrus* (Kedo) comb. nov.

Plate 90, figs. 10, 11

Cf. 1957 *Lophozonotriletes proscurrus* Kedo, pl. 4, figs. 18, 19.

Occurrence. Eday flagstone group, Orkney. Givetian. Kaluga beds (Givetian) and Serotsvet (Famennian), B.S.S.R. (Kedo 1955, 1957).

Description. Size range 45 to 64 μ (fifteen specimens measured). Equatorial outline circular to subcircular. Ornament consists of closely packed, broad verrucae; in profile usually parallel-sided with flat apices but occasionally rounded, in plan view rounded to irregular and convolute; a few small cones occur on most specimens; width of verrucae usually twice the height but occasionally equal to it, width 4 to 12 μ, height 2 to 6 μ; number round the equator seventeen to twenty-six. Triradiate mark indistinct, equal or nearly equal to radius of spore.

Comparison and remarks. This species differs from *V. premnus* in the smaller, more densely packed ornament. In *V.* cf. *uncatus* the ornament is more sparse and irregular. *Lophozonotriletes scurrus* Naum. 1953 (pl. 3, figs. 22, 23) has sculpture which is more sparse, is not dominantly broad and parallel-sided, and appears to be fused around the periphery to give a zonate or pseudozonate structure. *L. gromosus* Naum. has more rounded sculptural elements but forms figured by Kedo 1955 (pl. 6, figs. 11, 12) as *L. scurrus* and *L. gromosus* respectively, closely resemble some Scottish spores.

Genus RAISTRICKIA (Schopf, Wilson, and Bentall) Potonié and Kremp 1954

Raistrickia sp. A

Plate 90, fig. 3

Occurrence. Rare. Cromarty nodule beds, Navity shore and ? Eday beds, Inganess, Orkney. Givetian.

Description. Equatorial outline subcircular. Size 39 to 66 μ (on two specimens). Exine relatively thick but folded; covered with densely packed baculae interspersed with slender spines and cones: baculae often spatulate, sometimes nearly parallel-sided, 5 to 10 μ high and 2 to 10 μ wide; height usually twice the width or greater but occasionally equal to width. Triradiate mark indistinct.

Raistrickia sp. B

Plate 90, fig. 4

Occurrence. ? Eday beds, Inganess, Orkney. Givetian.

EXPLANATION OF PLATE 90

All figures $\times$500 except where indicated.

Figs. 1–2. *Verrucosisporites premnus* sp. nov. 1, Holotype, oblique compression. 2, Specimen with some spatulate sculptural elements and showing sculptural elements of variable size.

Figs. 3–5. *Raistrickia* spp. 3, *R.* sp. A, distal view. 4, *R.* sp. B, oblique compression. 5, *R.* cf. *clavata* Hacquebard 1957; polar compression.

Figs. 6–7. *Convolutispora cerebra* Butterworth and Williams 1958. 6, Oblique compression. 7, Damaged specimen showing presence of two layers, the inner layer is not visible in undamaged specimens.

Figs. 8–9. *Camptotriletes* spp. 8, *C. verrucosus* Butterworth and Williams 1958; distal view. 9, *C.* cf. *corrugatus* (Ibrahim) Potonié and Kremp 1955; oblique compression.

Figs. 10–11. *Verrucosisporites* cf. *proscurrus* Kedo. 10, Distal view showing dominantly flat topped, parallel-sided ornament. 11, Distal view showing sculpture in plan, sculptural elements joined together in groups by narrow connecting ridges.

Figs. 12–13. *Biharisporites parviornatus* sp. nov. 12, Holotype, lateral view, $\times$200. 13, Specimen, laterally compressed, showing smooth proximal surface and inner body connected to the proximal surface only, $\times$300.

Description. Size range (excluding baculae) 64 to 103 μ (three specimens). Equatorial outline subcircular. Exine thick, bears large spatulate or parallel-sided processes which are often greatly expanded at their apices; 10 to 24 μ high, base 8 to 18 μ wide, apices 24 to 36 μ wide; baculae show transverse striae and occur on the distal surface and equatorial margin. Triradiate mark indistinct, equal to two-thirds of spore radius.

Comparison. Raistrickia sp. A has cones and spines interspersed with the baculae. *R. clavata* Hacquebard (1957) has a triangular outline and smaller baculae.

Raistrickia cf. *clavata* Hacquebard 1957

Plate 90, fig. 5

Occurrence. Rare. ? Eday beds, Inganess, Orkney. Givetian.

Description. Size 54 to 60 μ (two specimens). Baculae parallel-sided or club-shaped, 4 to 12 μ wide, 6 to 12 μ high, width usually two-thirds the height but occasionally equals it. Number around the equator eight, nine.

Genus BIHARISPORITES Potonié 1956

Biharisporites parviornatus sp. nov.

Plate 90, figs. 12, 13; text-fig. 5

Holotype. Size 328 × 344 μ. Slide OR.35, reference 301962; ? Eday beds, loc. 4.

Occurrence. Eday flagstone group.

Diagnosis. Relatively large triradiate spores, exoexine bears small, closely packed sculptural elements of varied type which are dominantly biform; biform elements have a basal part of varied form, terminated by minute cones.

Description. Size range 208 to 368 μ (twenty-two specimens measured). Outline circular to subcircular, spores originally spherical or subspherical; show no preferred orientation on compression. Exoexine thick, commonly folded, covered by closely packed sculpture except on the contact areas which are externally smooth but infrapunctate. Sculptural elements of variable size and shape on a single spore, occasionally fused together in small groups or interconnected by narrow ridges; sculpture consists of small spines, cones, rods, and rounded tubercles, all four types are often terminated by minute cones. Elements 1 to 4 μ wide, 0·5 to 3·5 μ high; height usually equal to, or less than, width but occasionally greater than width. Contact areas smooth and ornament surrounding the contact areas is usually smaller than that on the distal pole. Some specimens have a thin-walled intexine (mesosporium) which is often folded and clearly separated by a cavity from the exoexine. Triradiate mark distinct one-quarter to one-half the radius of the spore, bordered by thickened lips 4 to 5 μ wide, occasionally the exoexine is folded along the Y-rays. Curvaturae perfectae are present on some specimens.

Comparison. B. ellesmerensis Chaloner 1959 has a similar size range but larger sculptural elements, *B. submamillarius* McGregor 1960 has a greater size range and larger sculptural elements. *Retusotriletes loxuriosus* Tchib. 1962 (Lower Eifelian) is similar in size (300 to 400 μ) but the sculptural details cannot be discerned from her figure. Similar spores have been found in the sporangia of *Archaeopteris* cf. *jacksoni* (Pettitt, in press), from the Upper Devonian, Scaumenac, Canada.

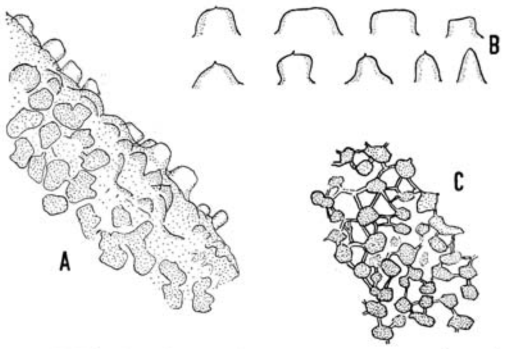
Infraturma MURORNATI Potonié and Kremp 1954
Genus CAMPTOTRILETES Naumova 1937

Type species. *C. corrugatus* (Ibrahim) Potonié and Kremp 1954.

Camptotriletes verrucosus Butterworth and Williams 1958

Plate 90, fig. 8

Occurrence. Only in the Basal beds, Easter Town Burn, the Eday sandstone and the flagstone groups, Upper Eifelian, and Givetian. The type material is from the Lower Carboniferous, Scotland; also Neves (1961) has described them from Lower Namurian A, northern England.



TEXT-FIG. 5. *Biharisporites parviornatus* sp. nov.; A, portion of wall showing sculptural elements; sculptural elements in profile, B, and in plan view, C; camera lucida drawings, ×1500.

Remarks. These spores are indistinguishable from those described by Butterworth and Williams. The original material has been examined and the holotype closely compared with spores found in the Eday beds.

Camptotriletes cf. *corrugatus* (Ibrahim) Potonié and Kremp 1955

Plate 90, fig. 9

Occurrence. ? Eday beds, loc. 4. Givetian. Westphalian B and C (Potonié and Kremp 1955).

Remarks. Only one specimen has been found. The ornament consists of a series of low ridges which bear cones (compare pl. 16, fig. 290, Potonié and Kremp 1955).

Genus CONVOLUTISPORA Hoffmeister, Staplin, and Malloy 1955
Convolutispora cerebra Butterworth and Williams 1958

Plate 90, figs. 6, 7

Occurrence. ? Eday beds (Inganess) and Eday flags, Givetian. Type material from the Lower Carboniferous, Scotland.

Remarks. The Orcadian spores are indistinguishable from those described by Butterworth and Williams (1958). Type material has been examined for comparison.

Genus ACINOSPORITES gen. nov.

Type species. *A. acanthomammillatus* sp. nov.

Diagnosis. Radial, trilete spores. Equatorial outline subcircular to subtriangular. Ornament consists of a series of convoluted and anastomosing ridges which bear verrucae with spines, spinose projections, or cones.

Comparison. The genus *Acinosporites* has ornament of various types superimposed on convoluted ridges, whereas in *Convolutispora* Hoffmeister, Staplin and Malloy (1955) the ornament consists solely of convolute and anastomosing ridges.

Derivation of name. L. acino—berry.

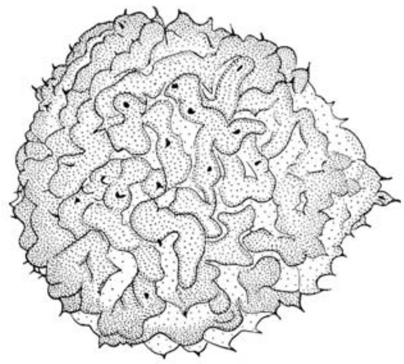
Acinosporites acanthomammillatus sp. nov.

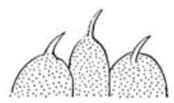
Plate 91, figs. 1, 2; text-fig. 6

1925 Type I of Lang, pl. 1, fig. 21.

Holotype. Size 100×106 μ, verrucae 5 μ high, cones 1·5 to 5 μ high, width of ridges 5 to 6 μ. Slide CR.80, reference 290905; Cromarty nodule beds, loc. 14.

Occurrence. Regularly at the Achanarras horizon, especially common in Navity shore samples, but not found in the highest beds examined (Thurso and Eday beds). A similar type of spore occurs in the ? Eday beds (Inganess) but it is much smaller (*c*. 45 μ) and has no apical prominence. Givetian.





TEXT-FIG. 6. *Acinosporites acanthomammillatus* sp. nov., holotype, camera lucida drawing of distal view, ×600.

Diagnosis. Ornament consists of rounded verrucae which bear slender cones or short slender cones or short slender spines at their apices. Tubercles are borne on contorted and anastomosing ridges. Triradiate folds equal the radius of the spore.

Description. Size range 85 to 141 μ (thirty specimens measured). Equatorial outline subtriangular with convex sides and rounded apices, one apex often more pronounced than others. Exine thick; bears contorted anastomosing ridges 5 to 6 μ wide; superimposed on the ridges are rounded verrucae 3 to 6 μ high, surmounted by slender cones or spines with pointed or occasionally blunt and expanded apices, 1·5 to 5 μ long and 1 to 2 μ wide at their base; ornament confined to the distal surface and equatorial margin, ridges fused into tight concertina-like folds around the equator. Proximal surface externally smooth and infrapunctate. A thin-walled central body is present in some specimens but is usually not discernible. Triradiate membranous ridges 6 to 28 μ high in lateral view, from contorted folds in polar view which reach the equatorial margin.

Comparison. This species is distinguished from *Acinosporites macrospinosus* and *Acinosporites* sp. A by having short rounded verrucae whose height is more or less equal to their width. *Apiculatisporis* (*Azonotriletes*) *spinotuberosus* Luber 1938 resembles *Acinosporites acanthomammillatus* in that both show a similar outline and have rounded verrucae tipped by cones, however it is not known whether in Luber's species the verrucae were borne on anastomosing ridges. *Archaeozonotriletes arduus* Archangelskaya (1963, pl. 8, fig. 3) is similar but is smaller and other spores placed in this species (pl. 8, figs. 1, 2, 4, 5) appear to have a zona. This species is from the Upper Eifelian of the Russian platform.

Remarks. The closely crowded tubercles seen in profile around the periphery of the spore are not entirely due to the height of the muri as in plan view distinct swellings can be made out along the ridges which bear slender cones or spines at their apices.

Acinosporites parviornatus sp. nov.

Plate 91, fig. 8

Holotype. Size 62×66 μ; verrucae 3 μ high, cones approximately 0·5 μ long, ridge width 2 to 3 μ. Slide CR.192, reference 289888; shales in basal conglomerate, loc. 12.

Occurrence. Abundant in the shale intercalations in basal conglomerate, Millers Bay, Cromarty. Upper Eifelian.

Diagnosis. Ornament consists of narrow anastomosing ridges which bear slender-pointed cones.

Description. Size range 50 to 104 μ (on fifteen specimens). Equatorial outline subtriangular with convex sides and rounded apices. Exine bears contorted ridges 2 to 3 μ wide; ridges covered by closely packed verrucae 2 to 3 μ high; surmounted by small cones 0·5 to 1 μ long. Ornament confined to the distal surface and equatorial margin. Proximal surface smooth. Triradiate mark indistinct.

Comparison. The small verrucae and minute cones distinguish this species from *A. acanthomammillatus*.

Acinosporites macrospinosus sp. nov.

Plate 91, figs. 3–6

EXPLANATION OF PLATE 91

All figures ×300 except where indicated.

Figs. 1–9. *Acinosporites* gen. nov. 1–2, *A. acanthomammillatus* sp. nov.; holotype, at different levels of focus, polar compression, distal view. 1, Showing the tubercles tipped with cones; 2, showing convolute ridges. 3–6, *A. macrospinosus* sp. nov. 3, Holotype, polar compression, proximal view; 4, lateral compression showing apical prominence; 5, distal view with convolute ridges; 6, distal surface of triangular specimen with convolute ridges partially opened out. 7, *A.* cf. *macrospinosus* sp. nov.; distal view of specimen closely similar to the holotype but much larger, ×200. 8, *A. parviornatus* sp. nov.; holotype, obliquely compressed. 9, *A.* sp. A; distal view.

Figs. 10–12. *Perotrilites* spp. 10–11, *P. conatus* sp. nov. 10, Holotype; 11, proximal view showing fine wrinkling of the outer membrane, ×500. 12, *P. sp.*, specimen with finer ornament than *P. conatus*.

Holotype. Size 103×105 μ, spines 10–18 μ long. Slide CR.19, reference 318900; Cromarty nodule beds, loc. 12.

Occurrence. Common in the Cromarty nodule beds especially at Millers Bay; also in the Lower Stromness beds, Orkney, Basal beds, Millers Bay, and Thurso beds, Caithness, and south side of the Moray Firth (Winewell fish band). Upper Eifelian and Givetian.

Diagnosis. Ornament consists of spinose processes with pointed apices. Triradiate mark distinct with elevated ridges in the form of an apical prominence.

Description. Colour brown to reddish-brown. Size range, excluding spines, 80 to 160 μ (thirty-five specimens measured). Equatorial outline circular, subcircular, or triangular; hemispherical in lateral compression, flattened at the proximal pole. Exine thick covered by anastomosing ridges which are often convolute and closely packed but on some specimens the ridges form a loose, irregular, reticulate pattern; ridges bear spines 10 to 50 μ long with stout often swollen or bulbous bases, and pointed apices. Ridges fused into tight 'concertina' folds around the contact areas. Triradiate mark with pronounced elevated, membranous ridges which form a distinct apical prominence; 21 to 52 μ high in lateral view; in polar compression the apical prominence forms contorted folds which reach the equatorial margin.

Comparison. This species differs from *A. acanthomammillatus* and *A.* sp. A in the form of ornamentation that is superimposed on the convolute ridges. In the case of *A. macrospinosus* the ornament consists of prominent, pointed spines.

Derivation of name. L. spinosus—thorny, macro—long.

Acinosporites sp. A

Plate 91, fig. 9

Occurrence. Hillhead beds, rare.

Description. Size around 90 μ (on four specimens). Equatorial outline subtriangular with convex sides and rounded apices. Exine thick, no folds seen. Ornament consists of anastomosing ridges 5 to 8 μ thick; ridges bear irregularly shaped spinose processes, more or less parallel-sided with rounded extremities and widened bases; processes 15 to 21 μ long and number about sixteen around the equator. Small cones are borne on the extremities of the processes, cones 1 to 5 μ long. Ornament confined to the distal surface and equatorial margin. Proximal surface externally smooth but infrapunctate. Triradiate mark distinct, rays equal to one-third radius of the spore.

Comparison. These spores are very similar to those of the species *A. acanthomammillatus* but differ from them in having irregular processes. Both *A. acanthomammillatus* and *A.* sp. A have blunted ornament which bear cones at their extremities *A. macrospinosus* does not have this feature. *Lepidozonotriletes aculeatus* Hacquebard appears similar and has ornament consisting of 'plate-like, scalloped units, fused at the base and with small spines at the top'; however, Hacquebard's species does not appear to have the convolute ridges typical of the genus *Acinosporites*.

Subturma PERINOTRILITES Erdtman 1947
Genus PEROTRILITES (Erdtman) Couper 1953

Perotrilites conatus sp. nov.

Plate 91, figs. 10, 11

Holotype. Size 88 μ, central body 77 μ; slide CR.173, reference 426899; Achanarras horizon locality 13.

Occurrence. Cromarty nodule beds, Achanarras horizon; Clava and Winewell fish beds, Mey beds, and Eday flags.

Diagnosis. 'Perispore' ornamented by cones, short pointed spines, or both.

Description. Colour of perispore yellow, body brown. Size range 60 to 132 μ, central body 52 to 103 μ (thirty specimens measured). Equatorial outline subcircular. Perispore thin, delicate, transparent, often minutely wrinkled and contorted; usually not much greater than the body in diameter but occasionally much larger. Central body completely enclosed by 'perispore', attached by the proximal surface only. Central body smooth. 'Perispore' ornamented by minute cones, 1 μ or less high, or short spines 3 to 4 μ long with pointed tips. 'Perisporal' membrane often formed into contorted triradiate folds. Triradiate mark on the spore body, simple, rays equal, or nearly equal to body radius.

Comparison. This species differs from other species of *Perotrilites* in the possession of cones or short pointed spines. The 'perispore' of *Diaphanospora riciniata* is 'apparently unornamented' and that of *D. perplexa* Balme and Hennelly 1962 is infragranulate. *Perotrilites sp.* McGregor 1960 is very similar but has a granulate ornament. *Hymenozonotriletes discors* Tchib. 1962 (Givetian, Bashkir) is similar but the nature of the outer membrane cannot be made out from Tchibrickova's figures.

Remarks. Specimens from the Eday beds, Orkney, are larger and many of them do not have a closely adhering 'perispore'.

Subturma ZONOTRILETES Waltz 1935
Infraturma CINGULATI Potonié and Klaus 1954
Genus DENSOSPORITES (Berry) Potonié and Kremp 1954

Type species. *D. covensis* Berry 1937.

Densosporites orcadensis sp. nov.

Plate 92, figs. 1, 2

Holotype. Size 121 × 134 μ, cingulum 35 μ wide, slide OR.26, reference 3751021; ? Eday beds, loc. 4. Givetian.

Occurrence. All samples examined from the Eday flagstone group.

Diagnosis. Dark and light zones of cingulum clearly separated, width of dark zone less than, or equal to, that of light zone; distal surface and equatorial margin covered with pointed a bifurcate spines. Rays of tetrad mark equal spore radius.

Description. Colour pale yellow to brown, inner zone of cingulum dark brown. Size range 103 to 157 μ (thirty specimens measured); cingulum 22 to 51 μ wide. Equatorial outline subtriangular. Dark and light zones of cingulum distinct; dark zone usually half the width of light zone but occasionally equals it; outer (light) zone membranous sometimes with a scalloped margin and often of unequal width being wider at the radial apices. Outer margin of dark zone sharply defined from light zone, inner margin usually clearly separated from central area but sometimes this is indistinct. A thin-walled, folded intexine can be seen in some specimens. Distal surface and equatorial margin of spore bear pointed or bifurcate spines; bifurcate spines are slightly tapered for two-thirds of their length, then often sharply constricted so that the bifurcation is borne on a slender stem; alternatively they may be uniformly tapered throughout their length; spines 3 to 13 μ long occur on distal surface and equatorial margin. Triradiate folds often accompany the Y-rays.

Comparison. D. orcadensis differs from *D. devonicus* Richardson 1960 by the greater width of the light zone, in relation to the dark zone, of the cingulum. Also the outer margin of the dark zone is more regular in *D. orcadensis. Hymenozonotriletes polyacanthus* Naum. 1953 has a similar ornament but the spines are not so clearly bifurcate and the size range is smaller. *H. spinosus* Naum. 1953 has pointed spines. *H. meonacanthus* var. *rugosus* Kedo 1955 has a narrow dark zone but has pointed spines and a smaller size range.

Genus STENOZONOTRILETES Hacquebard 1957

Type species. S. conformis Naumova 1953.

? *Stenozonotriletes inequaemarginalis* sp. nov.

Plate 88, fig. 9

Holotype. Size 50×59 μ, border 6 μ; slide CR.164B, reference 3131049; Cromarty nodule beds, loc. 14.

Occurrence. Rare. Cromarty and Edderton nodule beds, Achanarras horizon.

Diagnosis. Equatorial outline subtriangular with convex sides and rounded apices, inner margin of border more distinctly triangular with angular apices; border thinner opposite one or more of the tetrad rays; triradiate mark simple, two-thirds to four-fifths, rays do not cross border.

Description. Colour brown to reddish-brown. Size range 46 to 66 μ, maximum width of border 5 to 6 μ (sixteen specimens measured). Exine thick, externally smooth, polar area strongly infrapunctate.

Comparison. S. simplex Naum. is similar but does not have radial thinning of the border or the strong infrapunctation of the polar area.

Remarks. These spores have not been seen in oblique compression consequently it is not certain that the wide border is an equatorial structure.

Infraturma ZONATI Potonié and Kremp 1954
Genus SAMARISPORITES gen. nov.

Type species. S. (Cristatisporites) orcadensis (Richardson) comb. nov.

Diagnosis. Radial trilete zonate spores. Ornament confined to the distal surface consists of conical to rounded conical projections, verrucae, or both, which often bear cones or short spines; elements may be clearly separated, arranged in concentric patterns, fused together in regular rows or groups, or fused into irregular convolute groups.

Comparison. Cristatisporites has sculpture on the proximal and distal surfaces. *Cirratriradites* does not have such prominent distal sculpture. Spores of the genus *Samarisporites* are closely similar to certain spores included in *Hymenozonotriletes* Naumova 1953. The latter genus, however, has a wide circumscription and was subsequently emended by Potonié 1958 who limited the genus to spores with a distinct cingulum similar to that of *Densosporites* (see Potonié 1958, p. 29).

Remarks. The intexine is clearly seen in most specimens although in distal view it is often obscured by a heavy concentration of ornament over the central area.

Derivation of name. L. samara—winged fruit.

Samarisporites megaformis sp. nov.

Plate 92, fig. 6

Holotype and occurrence. Size 216 × 254 μ; central area 130 μ. Slide CR.188, reference 469899; Basal beds, loc. 11. Upper Eifelian.

Diagnosis. Large spores; ornament consists of rounded and pointed cones and warts on the central area and the zona.

Description. Colour yellow with yellow to dark-brown central area. Size range 184 to 254 μ (on eight specimens). Equatorial outline subtriangular with convex sides and rounded to pointed apices; central area rounded or subtriangular in proximal view. Central area and zona clearly separated. Ornament consists of rounded verrucae and cones, and verrucae which bear cones at their apices; ornament often arranged in concentric rows and sometimes fused into groups, which may form a convolute pattern, often densely packed over the central area. Verrucae and cones 6 to 16 μ wide on the central area, smaller and more cone-like on the flange. Number of cones around the periphery twenty to forty. Prominent triradiate folds reach the equatorial margin, trilete sutures not seen.

Comparison. This species is closely similar to some spores placed in *S. orcadensis* but is larger. *Hymenozonotriletes macrotuberculatus* Archangelskaya (1963) Upper Eifelian is similar but the sculptural elements on the Russian spores are more densely packed.

Remarks. Spores placed in the genus *Samarisporites* and particularly in *S. megaformis* appear to resemble, in general organization, those of the genus *Calyptosporites* (Richardson 1960, 1962). However, the spores of the latter genus often show folding of the outer

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EXPLANATION OF PLATE 92

All figures × 300.

Figs. 1–2. *Densosporites orcadensis* sp. nov. 1, Holotype, distal polar view. 2, Corroded specimen showing thin-walled intexine partially separated from the exoexine.

Figs. 3–5. ? *Spinozonotriletes* cf. *naumovii* (Kedo) comb. nov. 3, Proximal view. 4, Specimen with body asymmetrically placed, ? pseudosaccate. 5, Smaller specimen with a narrow and less dissected margin than fig. 3, distal view.

Fig. 6. *Samarisporites megaformis* sp. nov., holotype, distal view.

membrane which does not affect the inner one, proving that the spores membranes are separated by a cavity (pseudosaccate). Similarly some of the species placed by Naumova (1953) and Kedo (1955, 1957) in the genus *Hymenozonotriletes* can be distinguished as pseudosaccate since they show similar folds.

Other species recorded previously in *Cristatisporites* (Richardson 1960) are:

Samarisporites (al. *Cristatisporites*) *orcadensis* (Richardson 1960) comb. nov. Occurrence in all assemblages except those from the Eday group.

Samarisporites (al. *Cristatisporites*) *conannulatus* (Richardson 1960) comb. nov. Occurrence in Achanarras horizon, rare.

Samarisporites (al. *Cristatisporites*) *mediconus* (Richardson 1960) comb. nov. Occurrence in Lower Stromness beds and Achanarras horizon (Black Isle).

Genus SPINOZONOTRILETES Hacquebard 1957

? *Spinozonotriletes* cf. (al. *Archaeozonotriletes*) *naumovii* (Kedo) comb. nov.

Plate 92, figs. 3–5; text-fig. 7

Cf. 1955 *Archaeozonotriletes naumovii* Kedo, pl. 4, fig. 8.

Occurrence. Givetian, B.S.S.R. (Kedo 1955). Only in the Eday beds (Givetian), Scotland.

Description. Size range, excluding spines, 85 to 231 μ (thirty-three specimens measured), central area 62 to 157 μ. Equatorial outline subcircular to subtriangular, central area subcircular to subtriangular in proximal view. Exine consists of two layers; the outer layer (exoexine) is thick, minutely wrinkled, infrapunctate, and extends at the equator in the form of a thick flange; the inner layer (intexine) is also thick. Exoexine bears relatively long, widely spaced, stout spines, confined to the distal surface and equatorial margin; the spines have pointed apices, taper uniformly for much of their length but have wider bases, they are 15 to 44 μ long and number fourteen to twenty-one around the equator. Triradiate mark indistinct, equal to the radius of the 'body' of the spore; occasionally there are well-developed triradiate folds which reach the equatorial margin.

Comparison. The spores described here closely resemble *Archaeozonotriletes naumovii* Kedo (pl. 4, fig. 8, 1955). The size range of the Scottish spores is greater but in the nature of the flange and the nature and distribution of the spines they appear identical. The type species *Spinozonotriletes uncatus* Hacquebard 1957 also resembles *S.* cf. *naumovii* but has an indistinct central body. The size range of the Scottish spores (85 to 206 μ) almost equals the sum of Hacquebard's and Kedo's ranges which are 82 to 148 μ and 150 to 200 μ respectively.

Remarks. The structure of the flange appears very similar to that seen in *Ancyrospora grandispinosa* Richardson (1962), both forms differ from typical members of the Zonati in the thick nature of the flange. However, it is possible that a cavity exists, in some of these spores, between the two membranes but none of the spores shows any sign of a lumen in optical section, with the possible exception of the specimen figured (Pl. 92 fig. 5). If many of these forms prove to have a well-developed cavity then a strong case could be made for the inclusion of these specimens in the genus *Grandispora*.

Subturma PSEUDOSACCITITRILETES subturma nov.

Diagnosis. Trilete spores with a well-developed cavity separating any two layers of the exine and which do not have, in addition, a solid flange. The exine may have sculpture, infrastructure, or both.

Comparison. Spores of Pseudosaccititriletes differ from those of other subgroups of turma Triletes in having a well-developed cavity separating layers of the exine. It would

TEXT-FIG. 7. ? *Spinozonotriletes* cf. *naumovii* (Kedo), camera lucida drawing, ×500.

seem preferable to restrict the term monosaccate to pollen-like forms with a well-developed columellate structure and to include only such forms in subturma Monosaccites, anteturma Pollenites. Examples of pseudosaccate spores are *Endosporites*, *Grandispora*, *Remysporites* and the genera described below.

Discussion. The genera and species described below are usually placed in the group Monosaccites, they have a variably inflated outer membrane which is commonly folded. Further, they differ from certain members of Monosaccites, such as *Florinites*, in that they do not have an infrareticulate (columellate) structure. So far the earliest record of spores with this structure is from the Frasnian of the U.S.S.R. (*Archaeoperisaccus*

Naumova, 1953); the latter genus includes pollen-like, monolete, monosaccate grains, some of which show an infrareticulate structure. In contrast to *Florinites* (and similar pollen-like grains) the spores described below do not show this typical saccus infrastructure, and in many cases their outer wall is much thicker than in *Florinites*. Therefore the following spores, formerly placed in the monosaccate group, are here excluded from it and are referred to as pseudosaccate. The growing number of such genera, especially from the Devonian and Carboniferous, is here considered to warrant suprageneric recognition; especially since the inclusion of such forms (which may have prominent spinose ornamentation, e.g. *Grandispora*) in subturma Monosaccites, anteturma Pollenites, could be misleading.

Dettman (1963) reviews the major spore classifications and proposes a new classification for Sporites (spores *sensu stricto*). In her classification a new group Perinotrilites (Erdtman) is proposed for 'cavate' spores. This group consists of some genera previously included within the group Monosaccites in addition to other spores, with a diaphanous outer membrane, which in the present paper are included in Perinotriletes Erdtman (*sensu* Potonié). While the writer is in sympathy with much of the criticism of present classifications (Dettman, pp. 12–16), Dettman's new group Perinotrilites is not used here for the following reasons. First, the use of the group name Perinotrilites in another sense could cause confusion. Secondly, in the author's view, spores with a 'perispore'-like outer membrane, e.g. *Perotrilites*, are sufficiently distinct to be classified separately. If Potonié's classification is to be changed in this respect, evidence is needed to show that the outer membranes of spores of the genus *Perotrilites* are basically the same as in forms which are here regarded as typically pseudosaccate, e.g. *Endosporites* and *Calyptosporites*. Although there is some doubt as to whether the outer membrane of spores belonging to *Perotrilites* (and similar genera) is a true perispore, the outer membranes of such spores are very distinctive. Dettman herself points to the similarity between the outer membrane ('outer layer of sculptine') of her new genus *Crybelosporites* and the perine of microspores of the extant genera *Pilularia*, *Marsilea*, and *Regnellidium* stating that 'similar, if not identical, features are shown by all three species of *Crybelosporites*' (Dettman 1963, p. 80). Consequently, in the present paper, the group Perinotrilites (*sensu* Potonié) is retained and a new group is proposed as outlined above.

Remarks. The term cavate is not adopted here because it has several current usages, and in its original definition by Faegri and Iversen (1950) is used for pollen grains with a a columellate structure; as such it is synonymous with the term saccate.

Subsidiary taxa. Since the spores originally placed in the subgroup Intrornati and Extrornati (Butterworth and Williams 1958) are here regarded as pseudosaccate the taxa Intrornati and Extrornati are retained.

Infraturma INTRORNATI Butterworth and Williams 1958

Genus AURORASPORA (Hoffmeister, Staplin, and Malloy) Richardson 1960

Auroraspora macromanifestus (Hacquebard) Richardson 1960

Occurrence. All the beds throughout the area, most abundant at the Achanarras horizon; Upper Eifelian and Givetian. Lowermost Mississippian, Canada (Hacquebard, 1957), and, 'very infrequent' similar forms, from the Upper Mississippian (Staplin 1960).

Auroraspora macromanifestus (Hacquebard) var. *major* var. nov.

Plate 93, fig. 3

Holotype. Size 290 μ, central body 100 μ. Slide OR.19, reference 349855; Lower Stromness flagstone, loc. 1. Upper Eifelian.

Occurrence. In Lower Stromness flagstones, and Basal beds, Easter Town burn. Upper Eifelian. Rare specimens also at the Achanarras horizon.

Diagnosis. Large spores with dominantly subtriangular equatorial outline; spores have prominent folds along the tetrad mark which reach the equatorial outline.

Description. Size range 270 to 306 μ, central body 90 to 143 μ (ten specimens measured). Central body tends to be small in relation to the bladder.

Comparison. These spores differ from those of *A. macromanifestus* only in size.

Auroraspora micromanifestus (Hacquebard) Richardson 1960

Plate 93, fig. 1

Occurrence. Achanarras and Eday beds, Givetian. Rare.

Remarks. Specimens of *Auroraspora* from the Achanarras horizon have a range in size and body/bladder ratio which includes Hacquebard's *micromanifestus* and *macromanifestus*. However, in the Orcadian sediments *A. micromanifestus* is rare, whereas *A. macromanifestus* and larger forms are most abundant.

Auroraspora minuta sp. nov.

Plate 93, fig. 2

Holotype. Size 95 × 98 μ, body 80 μ. Slide OR.31, reference 290102; ? Eday beds, loc. 4.

Occurrence. Abundant in ? Eday beds (Inganess shore) and also in the Eday flags, but not in other beds. Givetian.

Diagnosis. Small pseudosaccate spores; central body only slightly less than the bladder and often eccentrically placed, attached to bladder on proximal surface only. Triradiate mark equals radius of spore body.

Description. Colour, bladder pale yellow, central body brown. Size range 50 to 108 μ, body 51 to 90 μ (100 specimens measured). Ratio of central body diameter to whole diameter 68 to 95 per cent. (mode 80 to 85 per cent.). Equatorial outline of bladder and

EXPLANATION OF PLATE 93

All figures × 300 except where indicated.

Figs. 1–3. *Auroraspora* spp. 1, *A. micromanifestus* Hacquebard 1957, proximal view, specimen from the Eday beds. 2, *A. minuta* sp. nov., holotype, polar view. 3, *A. macromanifestus* var. *major* var. nov., holotype, central body displaced, proximal view.

Fig. 4. *Calyptosporites velatus* (Eisenack) Richardson 1962; specimen showing large triradiate folds and also distal folding of the exoexine.

Figs. 5–7. *Rhabdosporites parvulus* sp. nov. 5, Holotype, × 500. 6, Obliquely compressed specimen with asymmetrical central body, × 500. 7, *R.* sp. A, spore showing three layers, distal polar view.

body rounded, to rounded triangular or irregular; central body distinct, only slightly smaller than the bladder and often eccentrically placed. Bladder thin, often strongly folded; externally smooth and infrapunctate, occasionally infragranular; body smooth. Triradiate mark distinct, rays equal to radius of body, lips thickened.

Comparison. A. minuta differs from other species of *Auroraspora* by the large size of the central body in relation to the bladder, further the bladder is a loose structure as indicated by the frequent asymmetrical position of the central body. In contrast *A. macromanifestus* and *A. micromanifestus* show a symmetrical arrangement of body and bladder and were probably elliptical in cross-section with a more rigid bladder. Further, no triradiate folds have been seen on specimens of *A. minuta* although bladder folds are common. *Hymenozonotriletes variabilis* Naum. 1953 resembles *A. minuta* but has a triradiate mark which reaches the equatorial outline.

Infraturma EXTRORNATI Butterworth and Williams 1958
Genus CALYPTOSPORITES Richardson 1962

Type species. C. velatus (Eisenack) Richardson 1960.

Calyptosporites velatus (Eisenack) Richardson 1962

Plate 93, fig. 4

1944 *Triletes velatus* Eisenack, p. 108 pars; pl. 1, figs. 1–3.
1960 *Cosmosporites velatus* (Eisenack) Richardson, p. 52.
1962 *Calyptosporites velatus* (Eisenack) Richardson, p. 192.

Occurrence. All the horizons examined. Abundant generally at Achanarras horizon and especially in Coal Heugh shales; Upper Eifelian, Givetian, Scotland. Middle and Upper Givetian, U.S.S.R.

List of similar forms

Hymenozonotriletes echiniformis Kedo 1955 (pl. 4, fig. 1). Upper Givetian.

H. spinulosus Naum. 1953 (pl. 8, fig. 14), Frasnian.

H. proteus Naum. 1953 (pl. 4, fig. 5), Upper Givetian, Kedo 1955 (pl. 3, fig. 10), Middle Devonian; this form differs from *C. velatus* in the nature of the ornament which consists of small rounded tubercles.

H. facilis Kedo 1957 (pl. 3, fig. 2), Famennian; this form is pseudosaccate but is smaller than *C. velatus* and the ornament is coarser.

H. tener Tchib. var. *concinnus* Tchib. 1962 (pl. 15, fig. 3), Eifelian, appears identical to spores placed in the above species.

Also the writer has seen forms identical to *C. velatus* in Upper Givetian assemblages presented by Naumova to Alpern (C.I.M.P. stratotype collection, Department of Geology, University of Sheffield).

Calyptosporites microspinosus Richardson 1962

1960 *Cosmosporites microspinosus* Richardson, p. 53; pl. 14, figs. 5–6.

Occurrence. Lower Stromness beds, and Basal beds, Easter Town burn. Also found consistently at the Achanarras horizon but not found above this level. Upper Eifelian, Lower Givetian.

Genus RHABDOSPORITES Richardson 1960

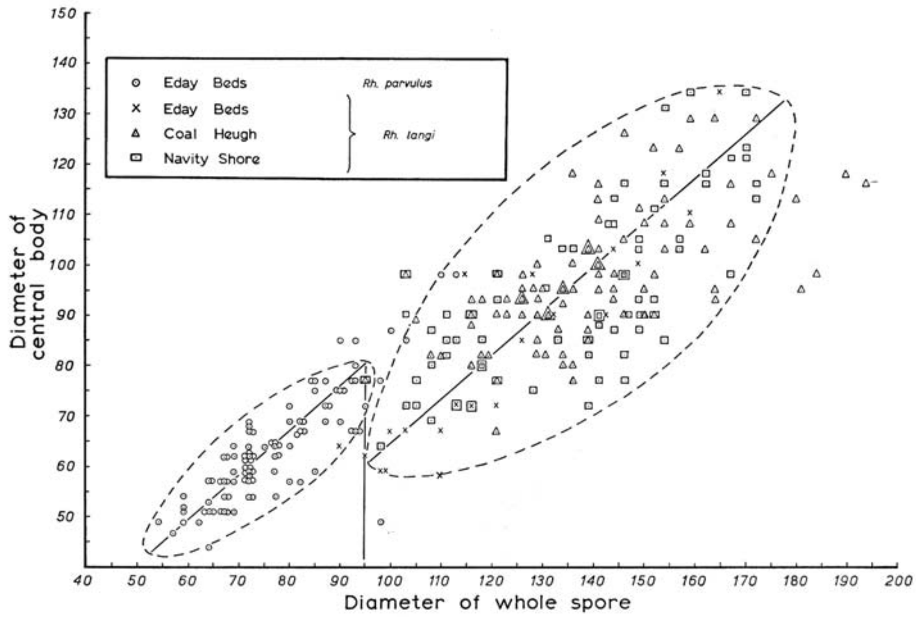
Type species. R. langi (Eisenack) Richardson 1960.

Rhabdosporites parvulus sp. nov.

Plate 93, figs. 5, 6; text-fig. 8

Holotype. Size 80 μ, body 67 μ. Slide OR.25, reference 364980; ? Eday beds, loc. 4.

Occurrence. Abundant in the ? Eday beds (Inganess) and Eday flagstone groups but rare in lower beds where it is subordinate to *R. langi*. Upper Eifelian and Givetian.



TEXT-FIG. 8. Comparison of size variation in *Rhabdosporites* from the Cromarty nodule beds and the Eday beds.

Diagnosis. Small pseudosaccate spores; bladder (exoexine) covered with fine rods.

Description. Colour of bladder and body yellow to brown. Size range 59 to 94 μ (mode 75 μ); central body 44 to 87 μ (mode 55μ); ratio of body to spore diameter 69 to 93 per cent. (mode 80 to 85 per cent.) (on 100 specimens measured). Equatorial outline of both bladder and central body subcircular to subtriangular; central body usually placed eccentrically and often indistinct. Bladder ornamented, uniformly covered by densely packed rods which are parallel sided and have truncated tips. Central body smooth. Bladder usually shows folds. Triradiate mark distinct, often splayed open; rays equal to the radius of the body of the spore, occasionally slightly less.

Comparison. This species differs from that of *R. langi* by its smaller size range, and the larger size of the central body in relation to the whole diameter (text-fig. 8). Since the bladder is not as loose as *R. langi* the large bladder folds are not present although small folds are often seen. Several of Naumova's species of *Archaeozonotriletes* resemble *R. parvulus* but unfortunately the ornament of the Russian forms cannot be clearly discerned from the drawings or descriptions. With this reservation the following species are thought to be comparable with the Scottish forms.

Archaeozonotriletes micromanifestus Naum. 1953 (pl. 2, fig. 18), most of the spores figured have a smaller body/bladder ratio. Upper Givetian and Lower Frasnian.

A. micromanifestus var. *minor* Naum. 1953 (pl. 2, fig. 19) has a similar body/bladder ratio but smaller size range. Upper Givetian.

A. rugosus Naum. 1953. Frasnian.

Hymenozonotriletes varius Naum. 1953 (pl. 3, fig. 2, Kedo 1955) has a smaller size range. Upper Givetian.

Similar spores have been found in sporangia of *Archaeopteris* cf. *jacksoni* (Pettitt, in press).

Rhabdosporites langi (Eisenack) Richardson 1960

Occurrence. In all samples examined; abundant at the Achanarras horizon (Cromarty nodule beds) where sporangia occur containing this species, much less abundant in the Eday beds. Upper Eifelian and Givetian Scotland. The writer has also seen this species in samples from Scaumenac Bay (Canada), Upper Devonian (regarded as basal Frasnian by Westoll, pers. comm.).

List of similar species

Hymenozonotriletes polymorphus Naumova in litt. (in Kedo 1955, pl. 3, fig. 8). Eifelian (Nara group), size range 100–120 μ. This corresponds with the lower part of the size range of *R. langi*.

H. facetus Archangelskaya 1963 (pl. 15, figs. 1–6). Uppermost Eifelian (Mosolov group), size range 105 to 176 μ. Probably synonymous with *R. langi*.

Archaeozonotriletes macromanifestus Naum. 1953. Upper Givetian.

A. micromanifestus Naum. 1953. Top of the Givetian and base of the Frasnian. Kedo 1955 states the same range and records this species from the Luga-Oredezh beds. Size range 80 to 120 μ, Kedo 90 to 135 μ.

Rhabdosporites sp. A

Plate 93, fig. 7

Occurrence. ? Eday beds, loc. 4.

Description. Spores show three distinct membranes, outer membrane covered by small, closely packed rods. Size range 146 to 224 μ, second layer 129 to 172 μ, central layer 90 to 127 μ (on six specimens). Triradiate mark simple, rays equal to the radius of the inner layer.

Comparison. These spores are like *R. langi* except that they show three distinct layers.

THE SEQUENCE OF SPORE ASSEMBLAGES

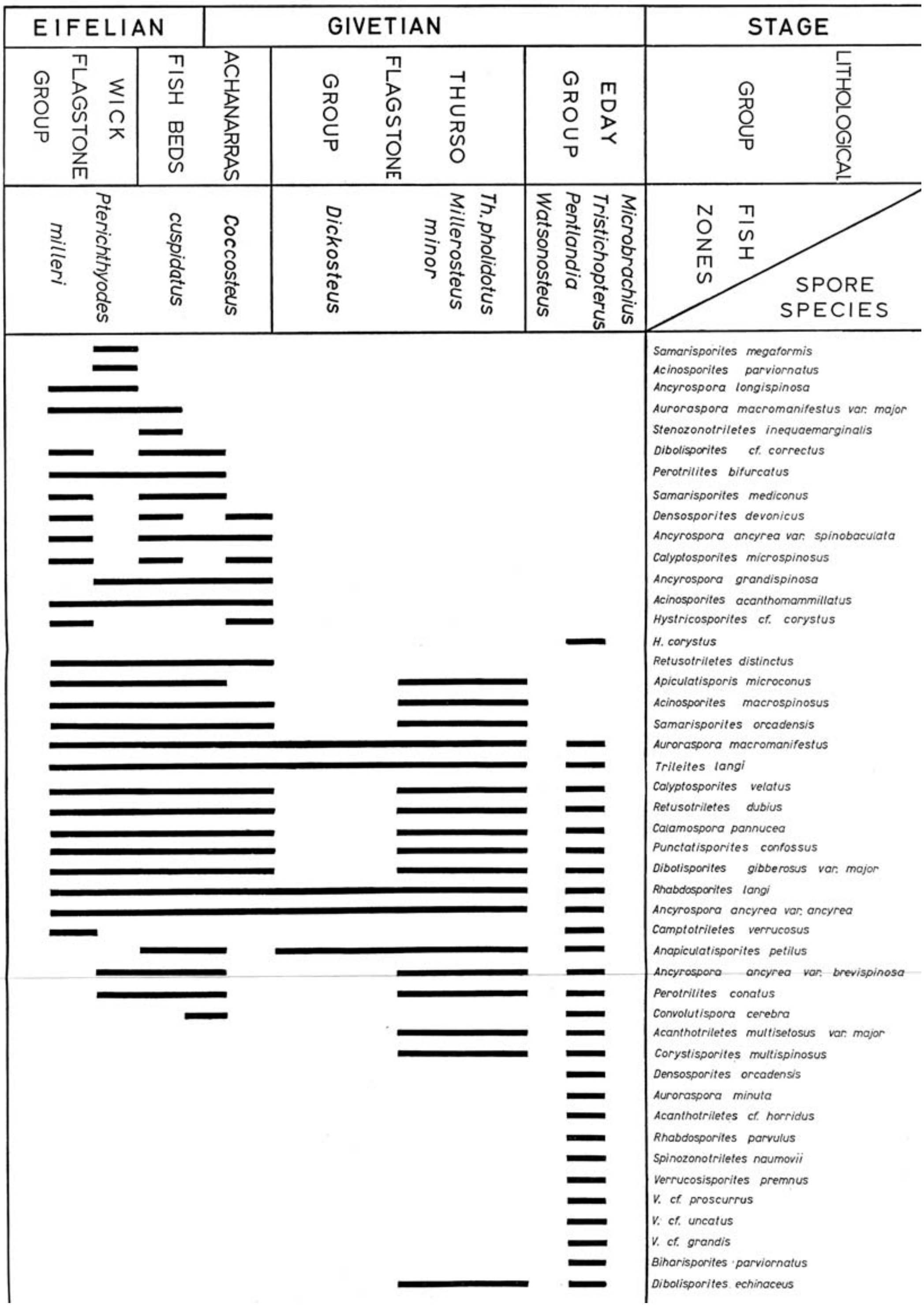
Four microfloral assemblages can be distinguished (text-fig. 9) in the Middle Old Red Sandstone of the Orcadian basin. The lower two are equivalent to the upper part of *Pterichthyodes* Zone of Westoll. The third is more or less equivalent to the *Millerosteus minor* Zone whilst the uppermost spore assemblages are equivalent to the lower part of *Microbrachius–Tristichopterus* Zone. The most striking changes in the microfloral assemblages occur between the uppermost microflora and those of the lower microfloras.

Pterichthyodes Zone (Upper Wick flagstone group and Achanarras horizon). Strata below the Achanarras horizon are collectively referred to as equivalents of the Upper Wick flagstone group and not the Passage beds (Caithness succession) since Miles and Westoll (1963) have demonstrated that the stratigraphical position of the Passage beds is uncertain. Strata examined in this zone are, first, the Upper Wick flagstone group equivalents in Orkney, Cromarty, and the south side of the Moray Firth, and secondly, the Achanarras fish bed and equivalents throughout the area. In strata below the Achanarras horizon several large spore types have been found, *Auroraspora macromanifestus* var. *major*, *Samarisporites megaformis*, and *Ancyrospora longispinosa*. The latter two types have so far only been found in these beds and not at the Achanarras horizon. Apart from these spore types the assemblages of the Upper Wick flagstone group closely resemble those of the Achanarras horizon but certain species prominent at the latter horizon are rare or absent in lower strata.

Achanarras horizon. This horizon is distinctive because first, certain types are associated at this horizon and at no other, and secondly, because of the variety and abundance of forms with bifurcate processes. The species *Acinosporites acanthomammillatus* or *A. macrospinosus* are frequently abundant, and several species (*Densosporites devonicus*, *Ancyrospora grandispinosa*, and *Calyptosporites microspinosus*) have not been found above the Achanarras horizon.

Millerosteus minor Zone. Spore assemblages have been examined from samples of the Thurso flagstone group (Mey beds), Caithness, and the Inshes and Hillhead beds on the south side of the Moray Firth. However, they are too few to give an accurate representation of the strata of the *Millerosteus* Zone. The most notable features of these beds are first the absence of certain species especially characteristic of the Achanarras horizon and lower strata, and secondly that spores with pointed spines are important, e.g. *Acanthotriletes multisetosus* var. *major* and *Corystisporites multispinosus*; the latter species is very abundant in the Hillhead beds.

Microbrachius–Tristichopterus Zone. Spore assemblages from the ? Eday flags (Inganess shore) and Eday flagstone group show only minor differences between them but together differ very considerably from the underlying microfloral assemblages. Prominent new species include *Rhabdosporites parvulus*, *Spinozonotriletes* cf. *naumovii*, *Auroraspora minuta*, *Biharisporites parviornatus*, and various species of *Verrucosisporites*, although some species of the latter genus appear to have a rather sporadic distribution. *Ancyrospora ancyrea* var. *brevispinosa* is abundant whilst several other species of this genus found at lower horizons are absent (Richardson 1962). One curiosity is the occurrence



TEXT-FIG. 9. Range chart showing spore distribution in the Middle Old Red Sandstone of the Orcadian basin.

of small specimens of the genus *Emphanisporites* which are, however, very rare. This genus has not been found in any of the other samples described in the present paper but more robust specimens of this genus are frequently encountered in the Basement Group.

STRATIGRAPHICAL CORRELATION

Several points concerning local stratigraphical correlation within the M.O.R.S. of north-east Scotland have emerged from these studies. At present these are mainly of a general nature and a great deal of further work remains to be done. However, on the basis of the present evidence the following points can be made.

First, in the upper part of the Wick Flagstone group (i.e. below the Achanarras horizon) the assemblages from the upper part of the Lower Stromness beds (Orkney) agree very well with those from the Basal flagstones of Easter Town Burn (south side of the Moray Firth), a prominent species in both is *Ancyrospora longispinosa*. In the Cromarty shore section the latter species is found only at the base of the sequence in the lowest shale band intercalated in the Basal conglomerate (text-fig. 1). It therefore seems likely that *A. longispinosa* will be a reliable indicator of the upper part of the Wick flagstone group.

The second point concerns the close similarity between the microfloras of the Achanarras Fish Beds of Orkney, Caithness, and the Black Isle with those from the Winewell fish band and '*Ptilophyton*' bed (Easter Tillybo) on the south side of the Moray Firth. Both the '*Ptilophyton*' and Winewell spore assemblages contain *Densosporites devonicus* and *Ancyrospora grandispinosa* which so far have only been found together at the Achanarras horizon. These two species occur in the lower part of the nodule beds of the Cromarty, Navity shore, and Eathie burn sections, whereas in the succession on the south side of the Moray Firth, they have only been found together in the Winewell and '*Ptilophyton*' beds. In the underlying strata, however, *A. grandispinosa* occurs in the Nairn–Clava fish band. It is interesting to note that Westoll (1951) stated that the fish faunas of the Leanach sandstones (which include the Winewell fish band) contained four typical Achanarras forms, whereas the underlying Nairn–Clava bands had yielded only one characteristic Achanarras form.

If the above correlation is correct, the Nairn–Clava fish band represents a lower horizon. Unfortunately the dark flags of the Nairn fish band have so far yielded relatively few spore types and these mainly belong to long ranging species. Consequently detailed comparisons cannot be made, but it is noteworthy that there are some similarities between the Nairn fish-bed assemblages and microfloras from the upper part of the shale intercalations in the Basal conglomerate of the Cromarty section.

In the Thurso flagstone group spore assemblages have been obtained from the Inshes and Hillhead groups on the south side of the Moray Firth and the Mey beds from Caithness. Unfortunately spores from the Inshes flagstones are badly preserved and, in Caithness, the flags from Spital quarries (immediately overlying the Achanarras horizon) have not yielded any spores. The Mey beds are thought 'to correspond to an upper part of the Rousay beds of Orkney' (Miles and Westoll 1963) and contain the fish *Millerosteus minor* and *Thursius pholidotus*. The Hillhead beds on the south side of the Moray Firth also contain *Millerosteus* (*Coccosteus*) *minor*. Spore assemblages so far obtained from the Mey beds are very different from those of the ? Eday beds (Inganess, Orkney)

TABLE 1. Spore species distribution, south of Moray Firth

	Easter Town burn flagstone	Nairn fish bed	Ptilo-phyton bed ? Acha-narras horizon	Leanach Sandstone Group (Winewell fish band)	Inshes Group	Hillhead beds
Auroraspora macromanifestus var. *major*	×					
Ancyrospora longispinosa	×					
A. ancyrea var. *spinobaculata*	×					
Calyptosporites microspinosus	×					
Retusotriletes distinctus	×		×			
Samarisporites orcadensis	×		×	×		
Auroraspora macromanifestus	×	×	×	×	×	×
Trileites langi	×		×		×	
Calyptosporites velatus	×		×	×		×
Retusotriletes dubius	×		×	×		×
Calamospora pannucea	×	×	×	×		×
Punctatisporites confossus	×		?	×		×
Rhabdosporites langi	× (A)	×	×	×	×	× (A)
A. ancyrea var. *ancyrea*	× (A)	×	×	×	×	×
A. ancyrea var. *brevispinosa*		×	×	×	×	×
Perotrilites conatus		×	×	×		
Ancyrospora grandispinosa		×	×	×		
Acinosporites macrospinosus		×	×	×		
Perotrilites bifurcatus		?	?			
Densosporites devonicus			×	×		
Acinosporites acanthomammillatus			×	×		
Hystricosporites sp.			× (R)			
Dibolisporites cf. *correctus*				×		×
Acanth. multisetosus var. *major*				×		×
Corystisporites multispinosa						× (A)
Dibolisporites echinaceus						×
Spinozonotriletes sp.						×

(R) rare, less than 0·1 per cent. of total assemblage; (A) abundant, more than 10 per cent. of total assemblage.

and the Eday flags, and show greater similarities to the Hillhead beds. Both the Hillhead and Mey beds apparently lack many of the species characteristic of the Achanarras horizon, viz. *Retusotriletes distinctus*, *Calyptosporites microspinosus*, *Perotrilites bifurcatus*, *Densosporites devonicus*, *Ancyrospora ancyrea* var. *spinobaculata*, and *A. grandispinosa*. At the same time there are some differences between spore assemblages from the Mey beds and the Hillhead beds. Further work is necessary to determine whether the Thurso flagstone group can be subdivided on the basis of the spores and whether differences between the Mey and Hillhead beds are stratigraphically important.

Strata from the cliff section below Inganess farm (Orkney), previously placed by the Survey in the Upper Rousay group, have recently been equated by Miles and Westoll (1963) with the Eday flags. Excellent spore assemblages have been obtained from the Inganess section and notably from grey shales immediately above the lower of the two 'thin bands of dark flags' referred to by Miles and Westoll (p. 205). Spore assemblages have also been obtained from the Eday flags of Weethick Point and Newark Bay. Samples from both these localities have yielded closely similar spore assemblages to those from the Inganess cliff section and assemblages from all three localities are strikingly different from spore assemblages found at any other lower horizon in the Orcadian basin (Table 2). In particular the Hillhead and Mey beds (equivalent to the Upper Rousay group) have very different assemblages from those of the Inganess shore section. Consequently the evidence provided so far by spore assemblages supports the correlation made by Miles and Westoll. However, it is not yet known exactly where this marked change in spore assemblages takes place, further the junction between the Eday and Rousay groups is not clearly defined (for discussion see the Orkney Memoir 1935, and Miles and Westoll 1963, p. 204) and therefore in the present paper the Inganess strata are referred to as ? Eday flags.

COMPARISONS WITH OTHER REGIONS

Comparative studies are hampered first by lack of a uniform classificatory system along with inadequate description and illustration, and secondly by the fact that the precise age of the Devonian spore bearing rocks is not known accurately in many cases. Spore assemblages which most closely resemble those from Scotland were described by Eisenack (1944) from an erratic block (Baltic shore, Germany) and secondly by Kedo (1955) from Eifelian and Givetian deposits (north-east Belorussiya).

Eisenack's original slides have been examined and the spores are strikingly similar to those found in the Orcadian deposits at the Achanarras horizon. All his species are comparable with Orcadian species with the exception of *Triletes balticus* and *Emphanisporites erraticus* (Eisenack) McGregor 1961; however, Eisenack only recorded one specimen of the latter species. More specifically, species of *Auroraspora* and *Calyptosporites* are the same in both Eisenack's assemblage and the Scottish material. Also spores of the genus *Ancyrospora* are closely comparable although there are minor differences. Spores of these three genera are abundant, show a similar range of variation and a comparable size range in both assemblages. Specimens of *Rhabdosporites langi* (Eisenack), *Dibolisporites echinaceus* (Eisenack), and *Retusotriletes dubius* (Eisenack) are identical. *Triletes paravelatus* Eisenack resembles *Samarisporites orcadensis* but is one of the few species which is not exactly comparable. Other species which occur at the Achanarras horizon but do not occur in Eisenack's assemblage, although persistently present in Orcadian strata, tend to be only locally abundant, e.g. *Acinosporites* spp. and *Densosporites devonicus* Richardson 1960, or only of minor importance quantitatively, e.g. *Perotrilites* spp. Exceptions to this are *Calamospora pannucea* and *Retusotriletes distinctus* which are abundant in the Orcadian sediments but do not occur in Eisenack's assemblage.

The sequence of spore assemblages described by Kedo (1955) is from the Nara (Narowa), Kaluga, and Luga-Oredezh series which were all regarded as Givetian in age. However, the Nara beds are now considered by Russian workers to be Eifelian (Tchibrickova, pers. comm.).

Microfloras from the Nara and Kaluga beds (especially the latter) closely resemble Scottish microfloras, although the present use of a different nomenclatural system by

TABLE 2. Spore species distribution, Caithness and Orkney

	Lower Stromness flags	*Achanarras Sandwick fish bed*		*Thurso Flag-stone Group (Mey beds)*	*Lower Eday Sand-stone*	*? Eday flags*	*Eday flags*
		Ach.	*Sand.*				
Ancyrospora longispinosa	×						
Auroraspora macromanifestus var. *major*	×		?				
Perotrilites bifurcatus	×						
Samarisporites mediconus	×						
Densosporites devonicus	×	×	×				
Ancyrospora ancyrea var. *spinobaculata*		×					
Calyptosporites microspinosus	×	×	×				
Ancyrospora grandispinosa		×					
Acinosporites acanthomammillatus	×		×				
Hystricosporites cf. *corystus*	×	×	×				
Retusotriletes distinctus	×		×				
Apiculatisporites microconus	×			×			
Acinosporites macrospinosus	×	×		×			
Samarisporites orcadensis	×	×	×	×			
Auroraspora macromanifestus	× (A)	×	×				
Acanthotriletes cf. *horridus*	×	×				×	
Trileites langi	×	×		×		×	×
Calyptosporites velatus	×	×	×	×		×	×
Retusotriletes dubius	×	×	×	×		×	×
Calamospora pannucea	×	×	×	×		×	×
Punctatisporites confossus	×	×	×	×		×	×
Dibolisporites gibberosus var. *major*	×	×	×	×		×	×
Rhabdosporites langi	×	× (A)	×	× (A)		×	×
Ancyrospora var. *ancyrea*	× (A)	× (A)	× (A)	× (A)		× (R)	× (R)
Leiotriletes sp.				×	×	×	×
Camptotriletes verrucosus					×	×	
Anapiculatisporites petilus				×		×	?
A. ancyrea var. *brevispinosa*				×		× (A)	× (A)
Perotrilites conatus				×		×	
Convolutispora cerebra						×	×
Acanth. multisetosus var. *major*						×	
Densosporites orcadensis						×	×
Auroraspora micromanifestus						×	?
Auroraspora minuta						×	?
Rhabdosporites parvulus					×	× (A)	× (A)
?*Spinozonotriletes* cf. *naumovii*						×	×
Verrucosisporites premnus						×	×
V. cf. *proscurrus*						×	×
V. cf. *grandis*						×	
Biharisporites parviornatus						×	×
Dibolisporites echinaceus						×	×
Emphanisporites cf. *rotatus*						× (R)	× (R)

(R) rare, less than 0·1 per cent. of total assemblage; (A) abundant, more than 10 per cent. of total assemblage.

scientists in the U.S.S.R. tends to obscure the great similarities. The following species are thought to be comparable if not synonymous.

Nara–Kaluga beds (Kedo 1955)	Upper Wick flagstone group–Achanarras–Thurso flagstone group–Eday group
Retusotriletes gibberosus var. *major* Kedo 1955	*Dibolisporites gibberosus* var. *major* (Kedo) nov. comb.
R. devonicus (Naum.) Kedo 1955 } *R. antiquus* (Naum.) Kedo 1955 }	*Dib. echinaceus* (Eisenack) nov. comb.
Lophozonotriletes scurrus Naum. 1953 } *L. grumosus* Naum. 1953 }	*Verrucosisporites proscurrus* (Kedo) nov. comb.
Hymenozonotriletes meonacanthus Naum. 1953	*Densosporites devonicus* Richardson 1960
H. polyacanthus Naum. 1953	*Den. orcadensis* Richardson sp. nov.
Archaeozonotriletes naumovii Kedo 1955	? *Spinozonotriletes naumovii* (Kedo) comb. nov.
H. proteus Naum. 1953 } *H. echiniformis* Kedo 1955 }	*Calyptosporites velatus* (Eisenack) Richardson 1960, 1962
H. polymorphus (Naum.) Kedo 1955	*Rhabdosporites langi* (Eisenack) Richardson 1960
H. varius Naum. 1953	*R. parvulus* Richardson sp. nov.
Archaeotriletes ancylius (Naum.) Kedo 1955	*Ancyrospora ancyrea* (Eisenack) Richardson 1962

Seven of these Russian species are important quantitatively in the Nara and Kaluga beds and are similarly well represented in the Scottish succession. A striking difference, however, is the relative development of spores with prominent bifurcate spines in the two areas. There is a wide variety of such spores in the Orcadian deposits and many of these are quantitatively important. On the other hand, spores with this distinctive ornament are present in the Nara and Kaluga beds but are not so abundant or varied.

The overlying Luga-Oredezh beds have a distinct microflora; nothing comparable to this has been found in the Orcadian strata although some species resemble those more commonly found in the Eday group. In the Luga-Oredezh beds there is an abundance of *Archaeozonotriletes* (*sensu* Naumova) species which have thick walls with sculpture of verrucae, cones, and spines, and are pseudosaccate (see p. 584). Similar spores are abundant in Naumova's assemblages from the upper part of the Starooskol beds (D_2^2), Upper Givetian, of the Russian platform.

Naumova (1953) does not describe spores from the Ryazhsko-Morsov and Kaluga beds (Upper Eifelian and Givetian respectively, Tchibrickova pers. comm.) but figures them in her stratigraphical distribution table (table 22). Few species were figured by Naumova from these beds but several of these spores closely resemble those from Orcadian deposits. They are as follows:

Leiotriletes atavus Naum. 1953	*Calamospora pannucea* sp. nov.
Retusotriletes gibberosus Naum. 1953	*Dibolisporites gibberosus* var. *major* (Kedo)
R. devonicus Naum. 1953 } *R. antiquus* Naum. 1953 }	*D. echinaceus* (Eisenack) comb. nov.
Hymenozonotriletes polymorphus Naum. 1953	*Rhabdosporites langi* (Eisenack) Richardson 1960
H. polyacanthus Naum. 1953	*Densosporites orcadensis* sp. nov.

The proportions of the main spore species for these beds are not given by Naumova. The absence of spores with bifurcate processes on Naumova's chart may indicate that such spores, if present, are not abundant in these strata. Spore complexes from the higher beds (complexes 5 to 15) are dealt with in detail, and there, spores with bifurcate processes are present but not abundant; however, none of the various species with this distinctive ornament is plotted by Naumova in the relative abundance charts.

More recently Archangelskaya (1963) has described spores from the Upper Eifelian to Lower Frasnian from the eastern part of the Russian platform. Unfortunately the whole assemblage is not described as the work only deals with those spores which are thought to be new; as a result only specific comparisons can be made:

RUSSIAN PLATFORM	SCOTLAND
Archaeozonotriletes incrustatus (Lower Frasnian)	*Trileites langi* sp. nov.
A. arduus (Upper Eifelian)	*Acinosporites acanthomammillatus* sp. nov.
Hymenozonotriletes macrotuberculatus (Upper Eifelian)	*Samarisporites megaformis* sp. nov.
H. longus (Upper Eifelian)	*Calyptosporites velatus* (Eisenack)
H. facetus (Upper Eifelian)	*Rhabdosporites langi* (Eisenack)
H. hexus (Upper Eifelian–Lower Givetian)	*Perotrilites conatus* sp. nov.

The general similarity between the spores from the Upper Eifelian is interesting. For instance, broadly similar structural types such as large zonate and pseudosaccate types occur in both the Russian platform and Scotland. In addition the same typical sculptural patterns are developed in spores from both areas; in particular spores with biform sculptural elements and prominent bifurcate spines are a feature of the Russian and Scottish assemblages.

Further east in the region of Bashkiri (south-west Urals) and in the southern Urals Tchibrickova has examined spore assemblages of Middle Devonian age (Tchibrickova 1959, 1962). Spores from the Takata and Calceola beds (Upper Eifelian) contain a number of similar forms to the Scottish beds, notably forms similar to *Dibolisporites gibberosus* var. *major* (Kedo) comb. nov., *D. echinaceus* (Eisenack) comb. nov., and *Calyptosporites velatus* (Eisenack). However, as with other Russian assemblages, spores with bifurcate processes occur but are not abundant (Tchib., pers. comm.). Also monolete spores occur in the Calceola beds but have not been found among any of the Scottish assemblages.

Spores from the Barzas coals (Kutznetsk basin, western Siberia, U.S.S.R.) were described by Elovskava (1936). These beds were assigned to the lower part of the Upper Givetian (Markovsky 1958), however, in the size of the spores and the presence of spores similar to *Auroraspora*, *Calyptosporites*, and *Rhabdosporites*, the assemblage closely resembles the Upper Eifelian and Lower Givetian spore assemblages from Scotland. No spores with bifurcate spines were recorded.

Similarly Thomson (1940, 1952) records no spores with anchor-shaped processes from the 'Pterichthyoidesstufe' of Estonia (Pernau group regarded as Lower to Middle Givetian by Thomson). Apart from this, many elements of the microfloras appear very similar to those found in the Orcadian succession. The lack of spores with bifurcate processes may be related to the original distribution of the parent plants, or alternatively may be stratigraphical if, for instance, the Pernau beds were older than Givetian. With regard to the latter it is interesting to note that the problematic Basement group which lies below the Upper Eifelian and Lower Givetian beds in Scotland has so far not yielded spores with bifurcate spines but zonate spores are present. Also the Pernau beds lie below the Nara beds which are now regarded by workers in the U.S.S.R. as Eifelian.

Considering the U.S.S.R. as a whole the microfloras compare very closely to the Scottish assemblages in many respects. This is especially true of spore assemblages described from western Belorussiya. Further to the east Tchibrickova's assemblages are very similar and she has found similar spores to *Rhabdosporites langi*, *Samarisporites orcadensis*, *S. mediconus*, and *Ancyrospora grandispinosa* in strata of Uppermost Eifelian and Lowermost Givetian age (pers. comm.). However, although these are close similarities, the low proportion and, possibly in certain cases (Elovskava and Thomson), absence of spores with bifurcate processes in all these assemblages is equally striking. Since the beds containing these assemblages are either marine, or in areas where marine and continental strata interdigitate, it is possible that the two facts are related, and it is tempting to suggest that plants producing spores having this distinctive ornament were more common in, or bordering, fresh-water environments. However, it is equally possible that some of the anomalies in the distribution of these spores may be more apparent than real and due to differences in age. Further work on more accurately dated deposits may show if either of these interpretations is correct.

In the North American continent spores have been recorded from Lower and ? Middle Devonian, Radforth and McGregor (1954, 1956), McGregor (1961), and Scott and Rouse (1961). From the Upper Devonian, Arnold (1936), Hoffmeister, Staplin, and Malloy (1955), McGregor (1960), and Winslow (1962).

Since no spore assemblages from strata definitely of Middle Devonian age have been described in the literature no detailed comparison is possible. On the whole the Lower and ? Middle Devonian assemblages, so far described, do not have any great points of similarity with Middle Devonian spores from Scotland or Eurasia. However, some Middle Devonian (Upper Gaspe sandstone) spore assemblages currently being investigated by McGregor (pers. comm.) are more comparable and spores of the genera *Calyptosporites* and *Ancyrospora* are present. One or both of these spore types are characteristic of Middle and Upper Devonian deposits of Europe and Asia. More detailed comparison must await full description of these assemblages.

Upper Devonian assemblages so far described from North America are on the whole very different from the Scottish spores but several genera notably *Biharisporites*, *Hystricosporites*, and *Ancyrospora* occur in both. Only one Upper Devonian assemblage from Canada has been described in detail (McGregor 1960) and this was from a coal which may represent a restricted microflora. Probably greater similarities will be detected when microfloras are fully described from Upper Devonian deposits other than coals.

More recently Winslow (1962) published a comprehensive and valuable paper which deals with megaspores, miospores, and micro-plankton. These assemblages are from Ohio (U.S.A.) and range in age from Middle Devonian to Mississippian. The majority of spore types, however, are from the uppermost Devonian and lowermost Carboniferous parts of the succession. Several of these forms could be included in genera prominent in Middle and Upper Devonian assemblages elsewhere. These include two major spore types; first large, more or less triangular, pseudosaccate forms ('*Endosporites*' of Winslow, placed in this paper in *Auroraspora* and *Calyptosporites*) and secondly spores with prominent bifurcate processes. Both of these groups, each of which include several genera, figure prominently in Middle and Upper Devonian assemblages from various parts of the world. The pseudosaccate forms referred to are also known from Lower Carboniferous deposits of many regions, whereas spores with bifurcate processes apparently decline rapidly in importance in the Lower Carboniferous (Richardson 1962). Winslow's work tends to corroborate this, as in her sequence '*Dicrospora*' (possibly in part *Ancyrospora* and *Hystricosporites* but including species with multifurcate spines not described from elsewhere) and '*Endosporites*' occur together in the uppermost Devonian and lowermost Carboniferous, whereas higher in the Carboniferous (Upper Tournaisian) spores with bifurcate processes were not recorded (Winslow 1962, pl. 23). Many other spore types described by Winslow distinguish her assemblages from those of Middle Devonian age described in the present paper and elsewhere. Two points arise from the comparisons: first, there is a greater development of megaspore species, and many of the latter have a greater size range than any spore types so far recorded from Middle Devonian deposits; secondly, there are spores with well developed equatorial and distal thickenings '*Canthospora*' (? *Annulatisporites*) and *Reticulatisporites crassus* (? *Knoxisporites*) occurring in the uppermost Devonian and Lower Carboniferous (Winslow succession); it is interesting to note that similar forms occur in Upper Devonian deposits elsewhere (particularly Famennian, U.S.S.R.).

Upper Devonian deposits from U.S.S.R. have assemblages (Naumova 1953; Kedo 1957) which are on the whole very different from the Middle Old Red Sandstone spores from Scotland. However, spores probably belonging to the genera *Auroraspora*, *Calyptosporites*, *Rhabdosporites*, *Hystricosporites*, *Ancyrospora*, and *Perotrilites* occur in both. In addition to these similar forms there are spore genera in the Upper Devonian which have not been found in the Middle Devonian and which are also found in the Lower Carboniferous, notably forms with well-developed equatorial and distal thickenings (? *Reticulatisporites* and ? *Knoxisporites*) and also forms with prominent ornament and an equatorial rim (*Lophozonotriletes*). In the Upper Devonian (Famennian) of Western Australia the same applies with '*Diaphanospora*' (*Perotrilites*), '*Archaeotriletes*' (*Hystricosporites*), and forms similar in structure to *Auroraspora* and *Calyptosporites* ('*Leiozonotriletes*') occurring with *Reticulatisporites*, ? *Knoxisporites*, *Cincturasporites*, and *Pulvinispora* (the last two genera have equatorial and radial proximal thickenings respectively).

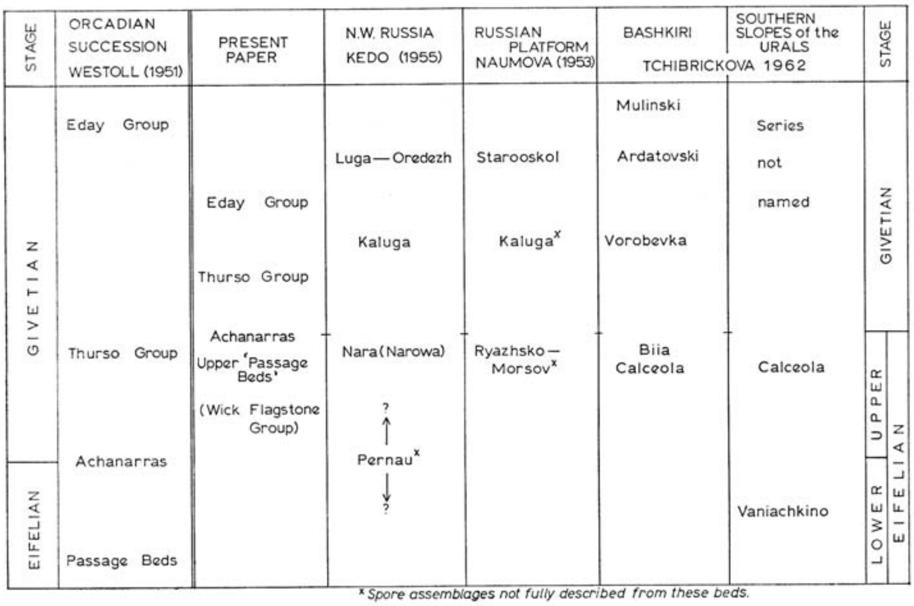
Although assemblages of Carboniferous spores are very different from those from the Orcadian basin, certain genera, and occasionally species, are very similar. For example, spores of the genus *Auroraspora* occur in the Lower Carboniferous deposits of Russia (Luber and Waltz 1938), U.S.A. (Hoffmeister *et al.* 1954), Canada (Hacquebard 1957 and Staplin 1960), and the British Isles (Butterworth and Williams 1958). The majority of spores of this type are much smaller than the Middle Devonian species. An exception is '*Endosporites*' *pseudoradiatus* (Winslow 1962), but this species has other features which distinguish it from Devonian forms.

Hacquebard's (1957) microflora, of lowermost Mississippian age, is especially interesting since several of the spores described closely resemble spores found in the M.O.R.S. of Scotland. The species *Auroraspora macromanifestus* and *A. micromanifestus* are identical to spores in the Orcadian deposits. The size range of the Canadian spores most closely resembles the spores found in the Eday beds. Also certain spinose species, *Acanthotriletes horridus* and *Spinozonotriletes uncatus*, are similar to forms found in the Eday beds. On the whole, however, Hacquebard's assemblage is different from those found in the Middle Old Red Sandstone.

Several species described by Butterworth and Williams from the Lower Carboniferous of Scotland are identical to spores in the Eday beds. However, the whole assemblage is very different.

Stratigraphical importance of the comparisons. Several points concerning correlation of Orcadian sediments arise from the comparisons (text-fig. 10) of Orcadian microfloras with those from other regions.

First, the exact equivalent of the Pernau microfloras described by Thomson has not yet been found in Scotland and these beds may be Lower or lower Upper Eifelian in age, although it must be noted that no recent description has been made of the Pernau microfloras and therefore comparisons are difficult.



TEXT-FIG. 10. Inter-regional correlation chart showing the suggested correlations between Scotland and the U.S.S.R., based on comparison of spore assemblages.

Secondly, from the remarkable similarity between Orcadian M.O.R.S. spore assemblages and those from Nara and Kaluga beds (Upper Eifelian and Lower Givetian), it seems that the M.O.R.S. succession studied in Scotland can be correlated with the Nara and Kaluga beds of north-west Russia. On the microfloral evidence it would therefore seem necessary to adjust the stratigraphical table published by Westoll (1951) so that strata from the Upper Wick flagstone group to the Eday group become more or less equivalent to the Nara and Kaluga beds of north-west Russia.

Thirdly, Nara–Ryazsko–Morsov beds are now equated by Russian workers with the Upper Eifelian. If this fact is taken into account with the above comparisons and applied to the Orcadian succession, then the Achanarras horizon would more or less represent the junction between Upper Eifelian and Lower Givetian in terms of current Russian usage. This correlation is in agreement with the earlier suggestion of Westoll (1951), although Westoll partly based his correlations on comparison between the

Achanarras and Pernau floras (Westoll 1951, p. 12). Further Tchibrickova's record (pers. comm.) of *Rhabdosporites langi*, *Samarisporites orcadensis*, *S. mediconus*, and *Ancyrospora grandispinosa* from strata of uppermost Eifelian or lowermost Givetian age supports this correlation since all these forms are prominent at the Achanarras horizon and the latter two species have only been found in the upper part of the Wick flagstone group and at the Achanarras horizon.

CHARACTERISTICS OF DEVONIAN MICROFLORAS

The above comparisons and studies of Middle Old Red Sandstone spore assemblages reveal several distinctive features of Devonian microfloras in general.

First, spores with thickened curvaturae perfectae and, or, darkened contact areas appear to be numerous and widespread in Devonian strata. The darkened contact areas occur in spores of *Calamospora* type but in addition occur in thicker walled spores *Punctatisporites* and *Retusotriletes*.

Secondly, spores with proximal radial thickenings are common in Devonian deposits, they appear to be most common in the Lower Devonian but also occur in Middle and Upper Devonian, and Tournaisian. Besides the genera *Emphanisporites* and *Pulvinospora* such thickenings are seen in some spores with bifurcate processes (*Dicrospora porcata* Winslow 1962).

Monolete spores have not so far been recorded from the Lower Devonian; there is one record of their occurrence in the Middle Devonian (south Urals, Tchibrickova 1962) but in the Upper Devonian they are much more frequently encountered and have been recorded from the U.S.S.R. (Naumova 1953; Kedo 1955), North America (Hoffmeister, Staplin, and Malloy 1955; McGregor 1960; and Winslow 1962), and Australia (Balme and Hassell 1962).

Large zonate and pseudosaccate spores, often with sculpture consisting of rods, cones, pointed or bifurcate spines, are typical of Middle Devonian deposits along with spores bearing large bifurcate processes.

Another type of ornamentation frequently found in the Middle Old Red Sandstone of Scotland is formed by verrucae or spinose processes which bear slender spines or cones at their apices. This biform sculpture (see text-figs. 3, 5, 6) occurs on spores of the genus *Dibolisporites* (*D.* cf. *gibberosus* var. *major*, *D. echinaceus*, *D.* cf. *correctus*), *Biharisporites parviornatus*, *Acinosporites acanthomammillatus*, *Acinosporites sp.*, *Samarisporites orcadensis*. Spores of the first two species appear to be widespread in Europe and *Biharisporites* with biform ornament has been recorded from the Upper Devonian of Canada (Chaloner 1959 and McGregor 1960). While this type of ornament is not exclusively Devonian, since it occurs on *Lycopoditriletes spinotuberosus* (Lower Carboniferous, Luber 1955), it may nevertheless prove to be a feature most conspicuous in Devonian deposits with waning importance in the Lower Carboniferous. Luber states that her species occurs very rarely in the Karaganda coals but has not been found elsewhere.

Spores so far described from the Upper Eifelian and Lower Givetian tend to be relatively large. In the Orcadian deposits several genera decrease in size upwards in the succession (e.g. *Auroraspora*, *Ancyrospora*, *Rhabdosporites*). In the higher beds (Eday group) the size difference between the smaller and larger spores is more marked than in the lower part of the succession. It is possible that the largest spores found, *Trileites* *langi* and *Biharisporites parviornatus*, are megaspores, but no direct evidence for this has been found, and size alone is an unsatisfactory criterion. However, it is interesting to note that Pettitt (in press) has found similar spores from heterosporous plants; he has obtained megaspores and microspores from *Archaeopteris* cf. *jacksoni* (Lower Frasnian, Scaumenac, Canada) similar to *Biharisporites parviornatus* and *Rhabdosporites parvulus* respectively; and spores which are closely similar to *Trileites langi* from *Barinophyton richardsoni* (Upper Devonian, Perry, Maine, U.S.A.). If spores from *Archaeopteris* cf. *jacksoni* prove to be diagnostic of this plant genus then this would indicate the presence of *Archaeopteris* in the Middle Devonian. Although there is insufficient evidence to form a basis for correlation between the dispersed spores and those associated with *Archaeopteris* cf. *jacksoni*, the fact that *Biharisporites* and *Rhabdosporites parvulus* occur together in the Eday beds and are not found elsewhere in the succession may be significant.

Biharisporites and *Trileites* from the Middle O.R.S. of Scotland are small in comparison with many Carboniferous megaspores and the megaspore content so far described from Middle Devonian microfloras is small (in size, variety, and numbers) compared with Upper Devonian and Carboniferous microfloras (Chaloner 1959 and Winslow 1962).

Microfloras so far described from the Upper Givetian are distinct from those of the lower. Spore assemblages from the Starooskol and Luga-Oredezh beds (Upper Givetian, U.S.S.R., Naumova 1953; Kedo 1955) contain abundant thick-walled pseudosaccate spores (often with external ornament) of the genus *Archaeozonotriletes* (*sensu* Naumova). No exact parallel of this microflora has been found so far in the Scottish succession. However, several similar species of *Archaeozonotriletes* are reported from the Lower Givetian of Bashkiri (Tchibrickova 1962).

CONCLUSIONS

The close correspondence between the Scottish microfloras and those from north-west Russia illustrated the potential use of Devonian spores for inter-regional correlation. There are also some interesting microfloral differences which may be ecologically controlled.

Local correlation within the Orcadian basin can also be achieved on a broad basis and the findings so far have tended to corroborate some of the views of Westoll (1951) and Miles and Westoll (1963) on correlation within this area.

In the Orcadian sequences the genera *Ancyrospora* and *Rhabdosporites* are the most numerous components; together they constitute 50 per cent. of the assemblages in many samples. This is especially true in sequences in the Cromarty nodule beds where the proportions of *A. ancyrea* var. *ancyrea* ranges from 20 to 50 per cent. whilst the proportions of *R. langi* range from 6 to 32 per cent. In the majority of samples, however, *A. ancyrea* is by far the most abundant species ranging from 40 to 50 per cent. The occasional abundance of *R. langi* in sediments of siltstone and fine sandstone can be correlated with the presence of sporangia containing this spore species. The species *Acinosporites macrospinosus* is relatively abundant in certain samples, namely the mudstone-nodule beds Millers Bay, Eathie and Killen burns, Winewell fish band, but, although it is a persistent component, in other samples it is relatively rare (less than 1 per cent.). There is also some evidence for the association of the abundance of certain spores with lithological type, e.g. the laevigate species *Calamospora pannucea* and *Trileites langi* occur more abundantly in coarser sediments; these features are being further investigated. In spite of the variations referred to, the spore assemblages are generally well mixed and differences at a particular horizon are usually quantitative rather than qualitative.

Finally, during the studies of spore assemblages no acritarchs, hystrichospheres, or chitinozoa have been found and, since these fossils are often abundant in brackish and marine sediments, their absence strongly supports the prevalent view that the sediments of the Orcadian basin were laid down in fresh-water environments.

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APPENDIX. LIST OF SAMPLE LOCALITIES

West Mainland, Orkney

1. Exposure on Rackwick foreshore half a mile south of Billia Croo (G.R.220097). Calcareous and arenaceous flagstone. *Lower Stromness flagstone group.*
2. Foreshore, north side of Bay of Skaill (GR.234196). Grey calcareous flagstones. *Sandwick fish bed.*
3. Stream exposure, quarter of a mile west-south-west of Bryameadow (G.R.253224). Grey calcareous flagstone. *Sandwick fish bed.*

East Mainland, Orkney

4. Cliff section east of Inganess Farm (G.R.473093). Series of grey shales, sandstones, and sandy limestone exposed. ? *Eday flagstone group.*
5. Foreshore, quarter of a mile south-east of Weethick Point (G.R.494095). Grey-green shales and dark flagstones. *Eday flagstone group.*
6. Foreshore west of Newark Bay, near Muckle Castle (G.R.563032). Light grey calcareous flagstone. *Eday flagstone group.*

Eday Island

7. Foreshore, south of Rushacloust (G.R.546301). Dark bituminous fish band. Dark laminated shales and grey calcareous shales. Base of *Eday flagstone group.*

Caithness

8. Foreshore, south-east side of Murkle Bay (G.R.173693). Grey calcareous flagstone. *Thurso flagstone group* (Mey beds).
9. Achanarras quarry, west of Spital village (G.R.150545). Dark grey, finely banded calcareous and bituminous flagstones overlain by light-grey arenaceous and calcareous flagstone. *Achanarras fish bed.*

Edderton

10. Edderton burn, half a mile south of Blackpark farm (G.R.674826). Sandstones, grey-green shales with limestone nodules. *Achanarras horizon.*

Cromarty–Blackisle area

11. Foreshore, east of Millers Bay (G.R.801673). Black shales and thin limestone bands in conglomerates at the base of the sequence. *Wick flagstone group.*
12. Foreshore, Millers Bay (G.R.796674). Red and green sandstones, grey-green siltstones, shales and clays with limestone nodules. *Achanarras horizon.*
13. Coal Heugh, stream immediately south of Millers Bay (G.R.796672). Sandstones grey-green siltstones and clays.
14. Foreshore, south of Navity Farm (G.R.790646). Red and green sandstones, shales, grey-green shales with limestone nodules. *Achanarras horizon.*
15. Eathie burn (G.R.782642). Grey-green shales with limestone nodules and red-grey siltstones. *Achanarras horizon.*
16. Killen burn (G.R.671573). Sandstones, grey siltstones, shales, and clays. *Achanarras horizon.*

SOUTH SIDE OF THE MORAY FIRTH

Inverness-shire

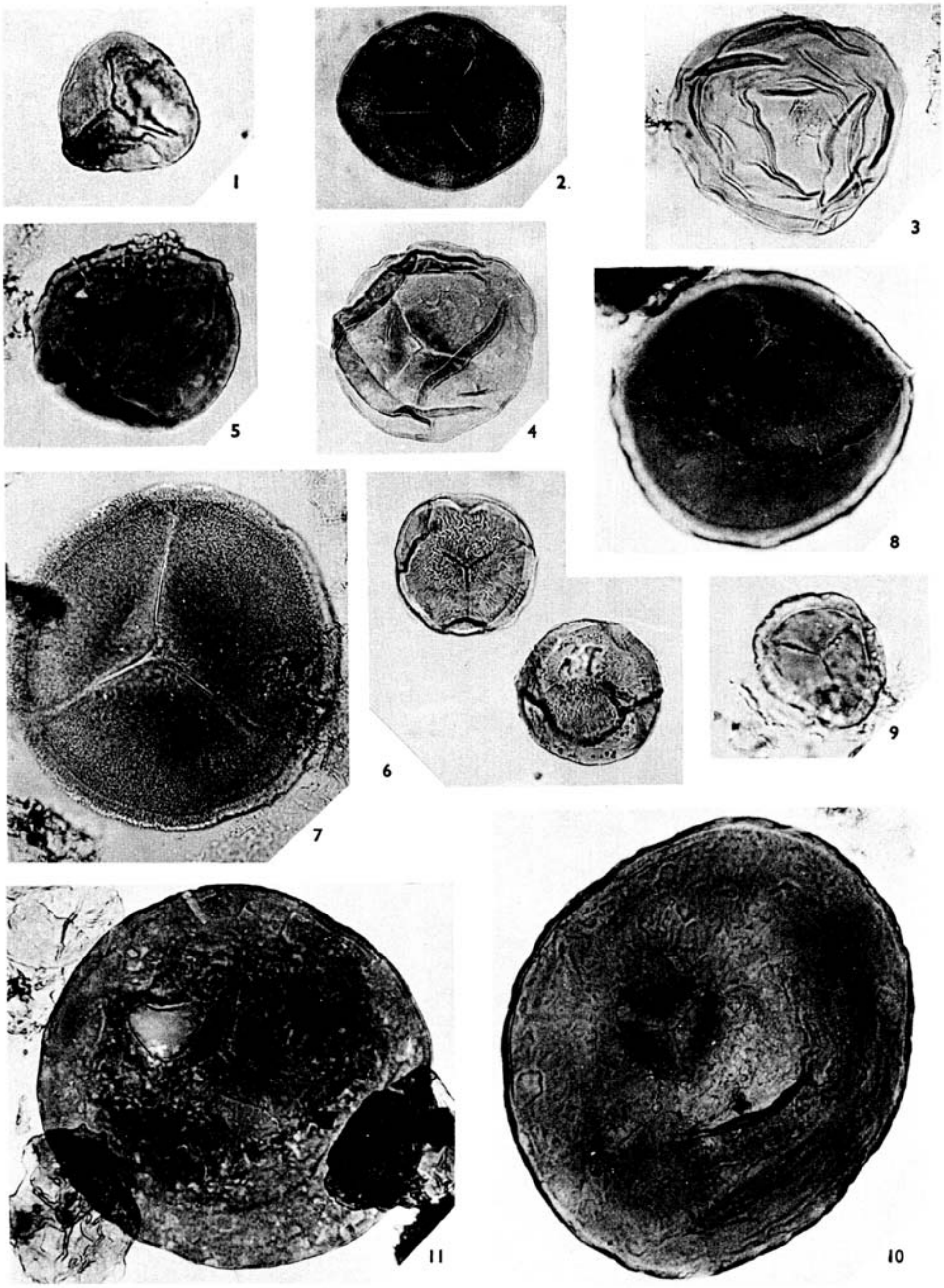
17. Stream exposure, 300 yards north of Tower (G.R.716442). Black calcareous shales with nodules. *Inshes group.*
18. Stream exposure, Eastern Town burn (G.R.753428). Black calcareous shales with limestone nodules associated with conglomerates. *Wick flagstone group.*
19. Clava bridge, Strathnairn (G.R.759449). Grey-green sandstone, overlain by black calcareous flagstone. ? *Achanarras horizon.*
20. Hillhead quarry, 1 mile south-east of Dalcross station (GR.776499). Dark grey shales and grey micaceous flagstone. *Hillhead group.*

Nairnshire

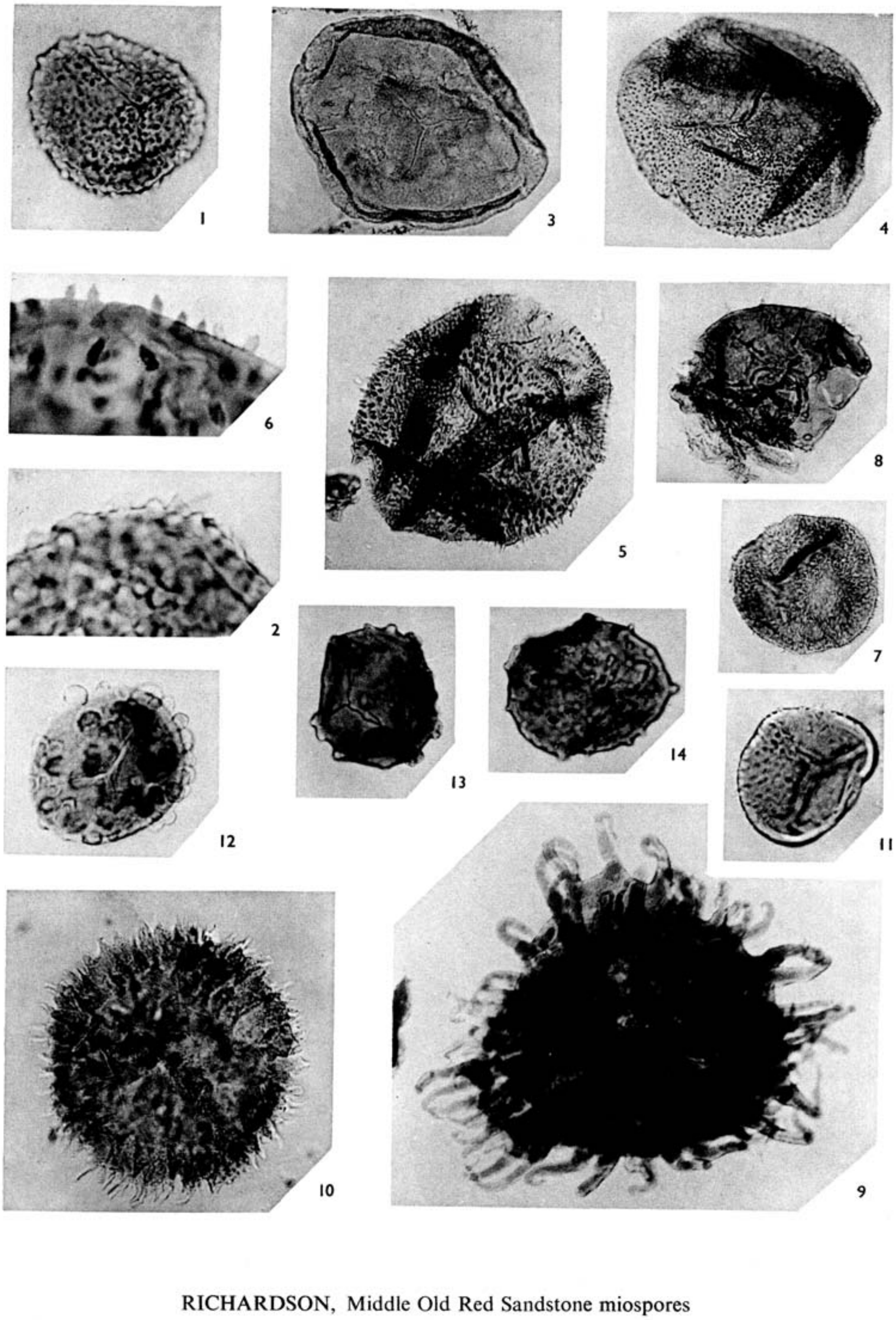
21. Lethen House quarry, north bank of Muckle burn (G.R.935516). Red and green siltstones, shales with limestone nodules. *Achanarras horizon.*
22. Winewell, roadside exposure (G.R.906519). Limestone and purple and green shales. Fish band, ? *Achanarras horizon.*

Aberdeenshire

23. Roadside exposure, half a mile east of Easter Tillybo (G.R.791592). Yellow shales. *Achanarras horizon.*



RICHARDSON, Devonian miospores



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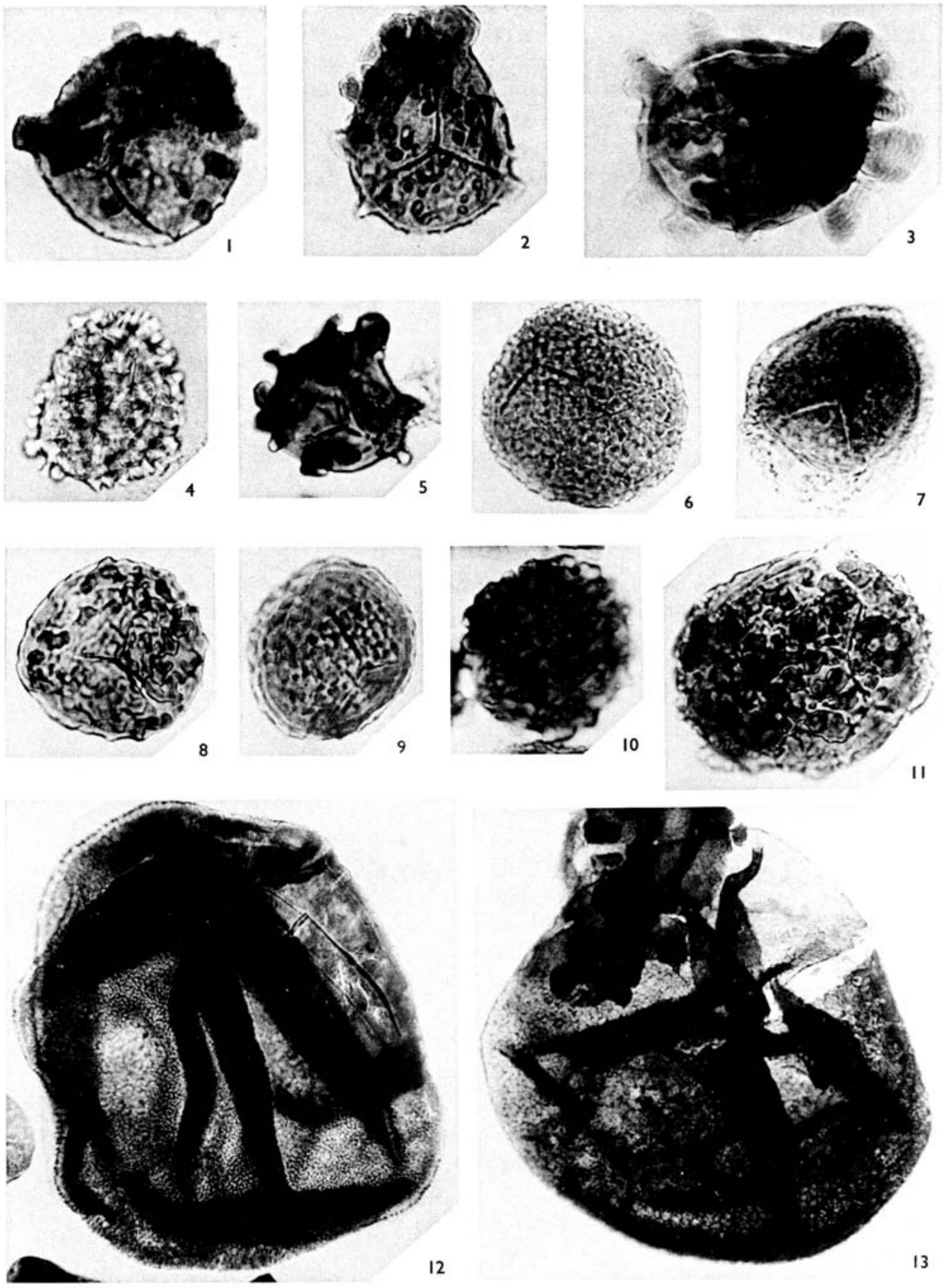

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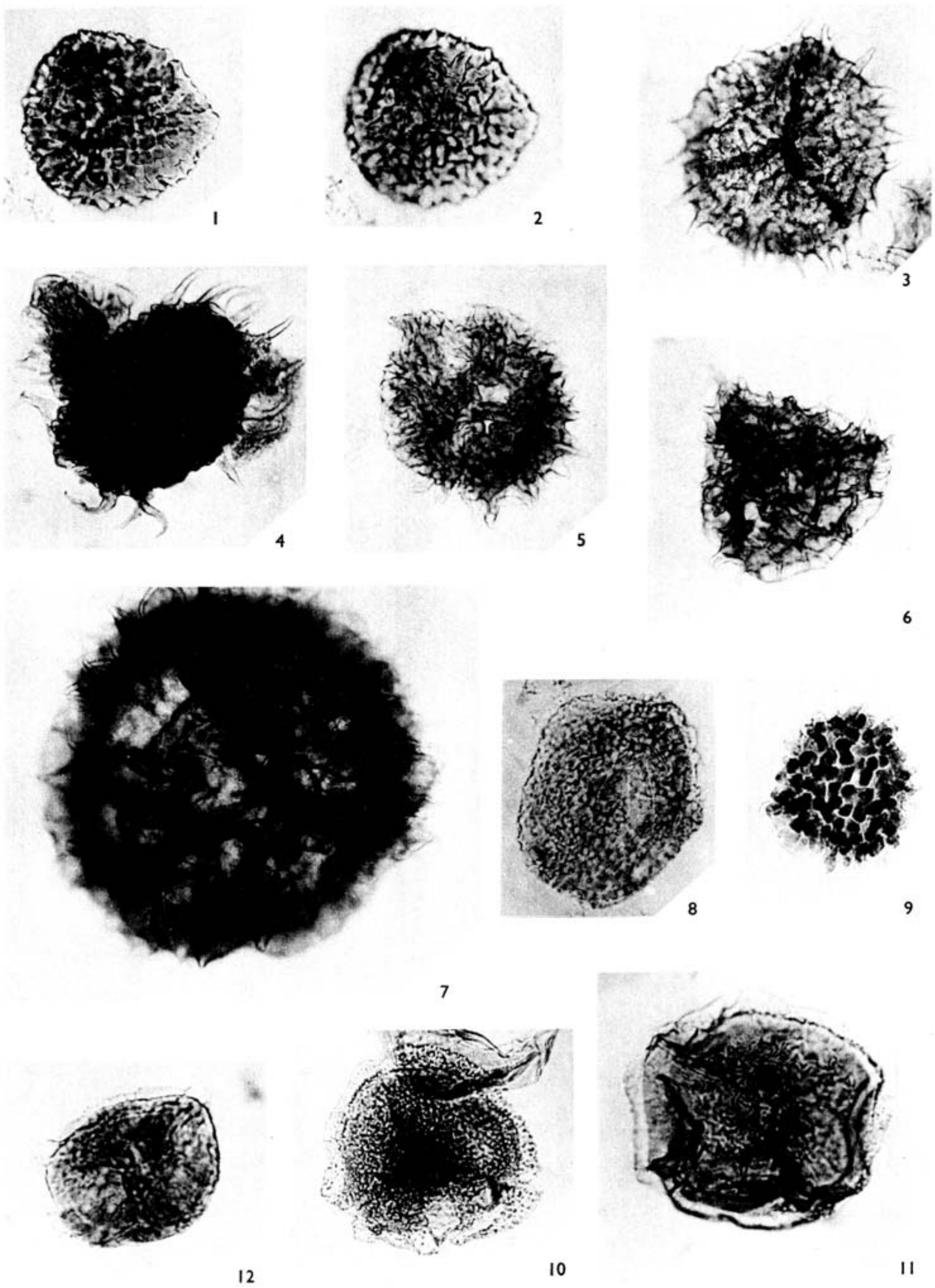

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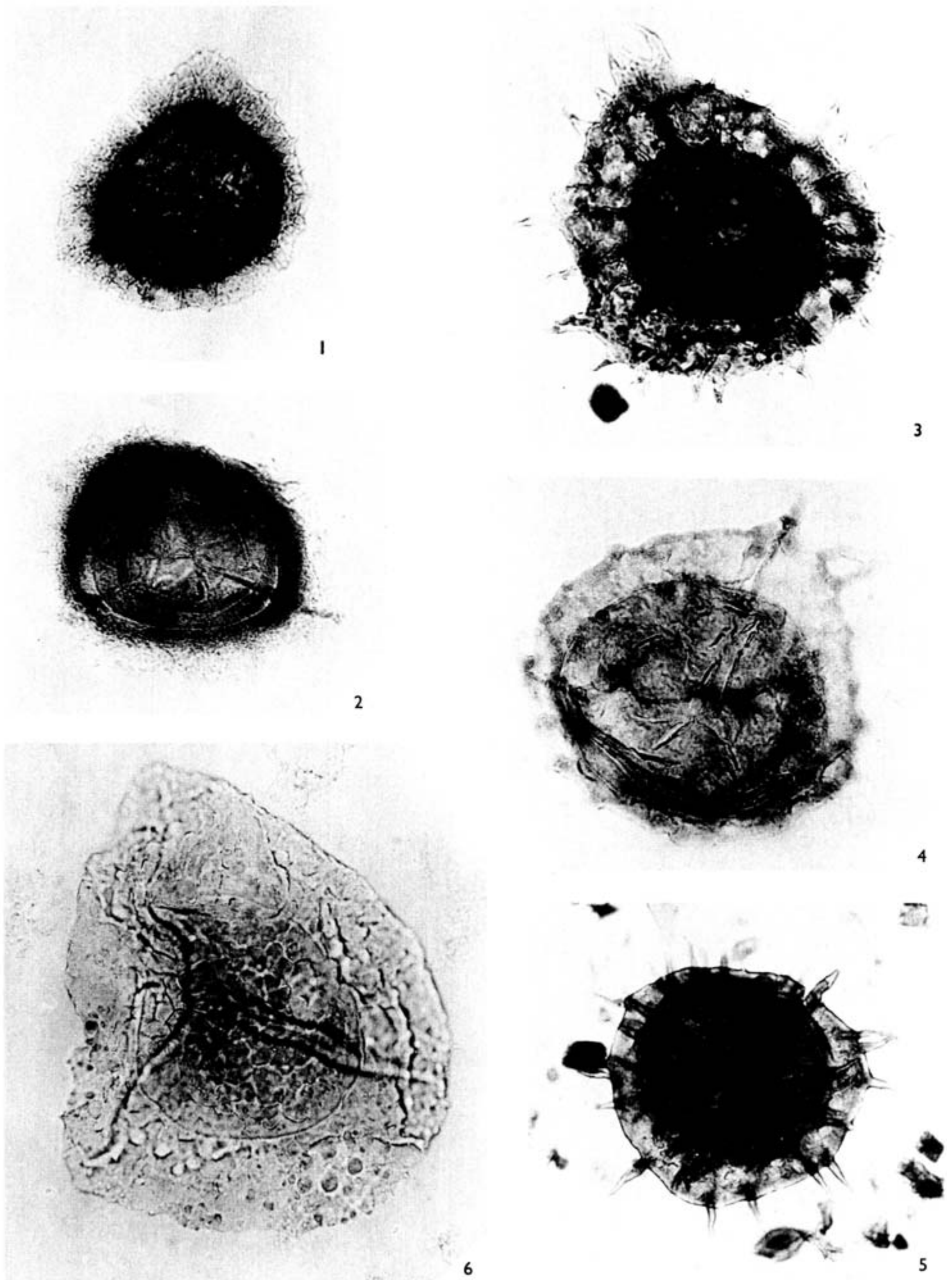

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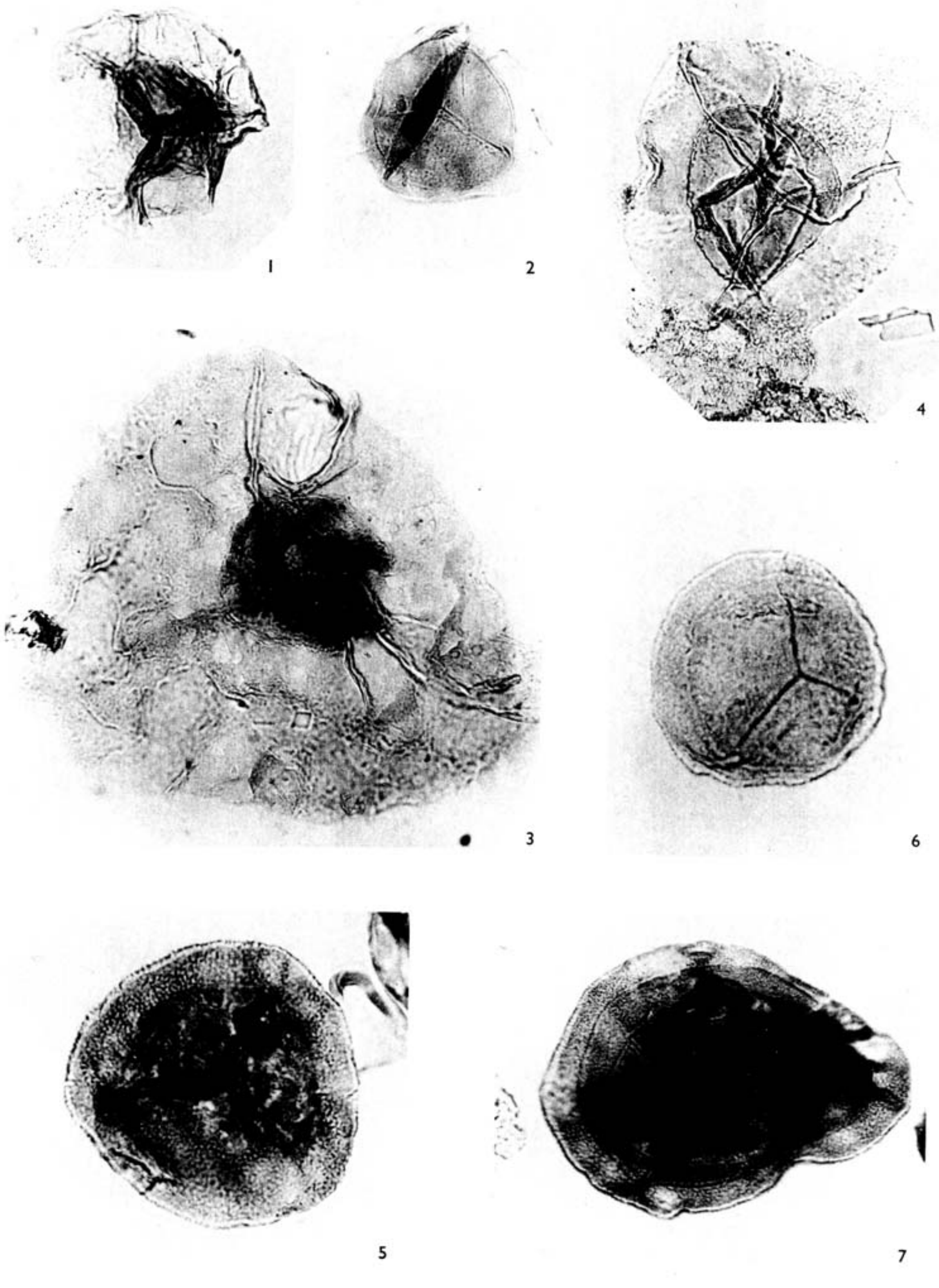

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