LOWER CARBONIFEROUS MICROFLORAS OF SPITSBERGEN

by G. PLAYFORD

PART TWO

Part I of this paper will be found in Volume 5, Part 3, pages 550-618, with an abstract on page 550; it includes the list of references. Part II continues and concludes the paper; a contents list is placed at the end of this part.

Anulatisporites orbiculatus (Waltz) comb. nov.

Plate 88, fig. 1

1941 Zonotriletes orbiculatus Waltz in Luber and Waltz, p. 24; pl. 4, fig. 60.

1957 Euryzonotriletes orbiculatus (Waltz) Naumova; Kedo, p. 1168.

Diagnosis. The following is the present writer's translation of the diagnosis given by Waltz (in Luber and Waltz 1941, p. 24): 'Diameter—92·5–137·5 μ . Colour brownish yellow. Spore body outline circular; surface of body smooth. Border wide, rather thick, with even or slightly fluted outer edge. On surface of border small wrinkles or folds having concentric orientation are sometimes observed. Thickness of exine on spore body and on border approximately equal. Trilete fissures very prominent, smooth, equal, slightly elevated or thickneed. Length of rays equal to, or slightly less than, spore body radius. Z. orbiculatus Waltz is characterized by a considerable variation in the ratio between diameter of spore body and width of border. Diameter of spore body 50–70 μ . Width of border 15–75 μ .'

Description of specimens. The Spitsbergen specimens conform closely to the above diagnosis. Exine thickness is $2.5-4~\mu$ on spore body. Cingulum of any particular specimen is of uniform width. Surface of cingulum laevigate to infrapunctate (oil immersion); punctate in corroded specimens, particularly around spore-body margin.

Dimensions (12 specimens). Overall equatorial diameter 92–120 μ (mean 105 μ); diameter of spore body 49–71 μ (mean 61 μ); width of cingulum 16–30 μ (mean 22 μ).

Remarks. The species is included in the genus Anulatisporites on the basis of its broad, sculptureless cingulum.

Previous records. Anulatisporites orbiculatus (Waltz) comb. nov. has been recorded from Tournaisian-Viséan strata of the Kizel district, U.S.S.R. (Luber and Waltz 1941), and from the Viséan of White Russia (Kedo 1957, 1958, 1959).

Anulatisporites canaliculatus sp. nov.

Plate 88, figs. 2, 3

Diagnosis. Spores radial, trilete; amb smooth, subtriangular with well-rounded apices and convex sides. Laesurae distinct, straight, length approximately $1.5-4~\mu$ less than [Palaeontology, Vol. 5, Part 4, 1962, pp. 619–678, pls. 88–95.]

spore-body radius; accompanied by conspicuous, flat, smooth, slightly elevated lips, which extend 4–7 μ on either side of laesurae and often have lobed outer margins. Spore body laevigate. Cingulum distinctively incised on proximal surface by a single, continuous, very narrow furrow situated approximately 2·5–5·5 μ from, and more or less conformable with, smooth spore-body margin. Cingulum otherwise undifferentiated, laevigate (irregularly punctate in corroded specimens), uniformly broad, much darker in colour than spore body.

Dimensions (35 specimens). Overall equatorial diameter 54–86 μ (mean 70 μ); diameter of spore body 33–50 μ (mean 41 μ); width of cingulum 11–21 μ (mean 15 μ).

Holotype. Preparation P173/2, 53·1 100·1. L.1125.

Locus typicus. Citadellet (sample G1446), Spitsbergen; Lower Carboniferous.

Description. Holotype 79 μ overall, spore-body diameter 45 μ , width of cingulum 17 μ ; laesurae extending to within 2·5 μ of spore-body margin, lips individually about 4·5 μ wide; furrow incised in cingulum uniformly about 4 μ from spore-body margin, depth about 2 μ . In some specimens the margin between the spore body and the cingulum on the distal hemisphere may be rather undulating showing only general conformity to equatorial outline.

Comparison. The generally larger Zonotriletes sulcatus Waltz (in Luber and Waltz 1938, p. 18; pl. 2, fig. 20) has numerous, rather discontinuous, concentric furrows in the cingulum, which is definitely thickened at its inner margin.

Genus DENSOSPORITES (Berry) Potonié and Kremp 1954

Type species. D. covensis Berry 1937.

Discussion. This genus and the morphographically associated Anulatisporites Loose ex Potonié and Kremp 1954 are presently receiving consideration from a subcommittee of the International Commission for the Microflora of the Palaeozoic; as a result, their redefinition, together with the erection of several other related genera, seems likely. This reappraisal of the densospore group will be based principally upon the sculpture of the cingulum, and it is to be hoped that due regard will be given to the effects of corrosion, both natural and in preparation, which in many cases seems to cause profound cingulate alteration (cf. Bharadwaj 1959, p. 70). Pending publication of the Commission's proposals, the Spitsbergen spores concerned are here assigned to either Densosporites or to Anulatisporites as formally emended by Potonié and Kremp (1954).

Affinity. In view of the abundance of representatives of this genus in sediments (particularly coals) of Carboniferous age, it is surprising that only recently has evidence come forward as to its botanical affinity. Chaloner (1958a) reported microspores similar to Densosporites loricatus (Loose) Schopf, Wilson, and Bentall 1944 from a small Upper Carboniferous lycopod cone compression, which he termed Selaginellites canonbiensis sp. nov. Subsequently, Bharadwaj (1959) obtained microspores conformable with Densosporites from the heterosporous lycopod strobilus Porostrobus zeilleri Nathorst 1914 which had been collected from Lower Carboniferous strata at Pyramiden, Spitsbergen. It will be seen that the abundantly occurring sporae dispersae, described below as Densosporites spitsbergensis sp. nov., resemble closely the microspores obtained by

Bharadwaj (from *P. zeilleri*). In a postscript to his paper, Bharadwaj recommended the inclusion of *Selaginellites canonbiensis* Chaloner within *Bothrostrobus* (Nathorst) Seward.

Densosporites bialatus (Waltz) Potonié and Kremp 1956

Plate 88, figs. 4-7

- 1938 Zonotriletes bialatus Waltz in Luber and Waltz, p. 22; pl. 4, fig. 51.
- 1941 Zonotriletes bialatus Waltz var. undulatus Waltz in Luber and Waltz, pp. 28-29; pl. 5, fig. 71a, b.
- 1941 Zonot iletes bialatus Waltz var. costatus Waltz in Luber and Waltz, p. 29; pl. 5, fig. 72.
- 1952 Hymenozonotriletes aff. bialatus (Waltz) Ishchenko, p. 51; pl. 13, fig. 124.
- 1956 Densosporites bialatus (Waltz) Potonié and Kremp, p. 114.
- 1956 Hymenozonotriletes bialatus (Waltz) var. undulatus (Waltz) Ishchenko, pp. 63–64; pl. 12, figs. 135–7.
- 1957 Cingulizonates tuberosus Dybová and Jachowicz, p. 171; pl. 53, figs. 1-4.
- 1957 Trematozonotriletes bialatus (Waltz) Naumova; Byvsheva, p. 1010.

Description of specimens. Spores radial, trilete; amb roundly subtriangular to oval, more or less conformable with convexly subtriangular body outline. Laesurae perceptible or not visible (corroded specimens); simple, straight to sinuous, length approximately equal to body radius. Where preserved, body exine is finely granulate or punctate. Differentiated cingulum, consisting of: an inner, thickened, opaque portion characteristically sculptured with fine, radially elongated pits; surrounded by a thinner, translucent zone which is approximately one-third to half of the total cingulum width. Conspicuous junction between the two parts of the cingulum may be regular, conforming closely with the spore-body outline; in many cases, however, it is irregularly lobed or dentate due to radial, equatorially tapering extensions of the thickened part projecting into, but rarely attaining margin of, the outer thinner portion.

Dimensions (60 specimens). Overall equatorial diameter 46–77 μ (mean 60 μ); diameter of spore body 21–34 μ (mean 27 μ).

Remarks. In her diagnosis of Zonotriletes bialatus, Waltz (in Luber and Waltz 1938, p. 22) drew attention to the variable structure of the inner thickened portion of the cingulum, suggesting its dependence upon the state of preservation. Subsequently, Waltz (in Luber and Waltz 1941, pp. 28–29) delineated two varieties (undulatus and costatus) within the species, on the basis of this variation. Both varieties are represented in the Spitsbergen assemblages, but their continuous intergradation does not support their recognition as separate morphographical units. The illustrations of Cingulizonates tuberosus Dybová and Jachowicz 1957 (pl. 53, figs. 1–4) strongly suggest conspecificity with Densosporites bialatus (Waltz), and indeed Jachowicz (1958, table 8) subsequently equated the two species.

There seems little doubt of the presence of *D. bialatus* within the Upper Mississippian spore assemblage described by Hacquebard and Barss (1957). These authors remarked (p. 32) that their species *Densosporites irregularis* 'may be conspecific with *Zonotriletes bialatus* Waltz, 1938', and certainly the spores represented by their plate 4, figs. 12, 13 (*D. irregularis*) and by plate 4, fig. 10 (*D. cuneiformis*) show close resemblance to *D. bialatus*.

Previous records. Densosporites bialatus (Waltz) has been recorded by numerous Russian

palynologists from the Lower Carboniferous of the U.S.S.R. (Luber and Waltz 1938, 1941; Ishchenko 1952, 1956, 1958; Byvsheva 1957, 1960; Loginova 1959). It has been recorded also from the Namurian A to Westphalian B interval of the Upper Silesian Coal Measures (Dybová and Jachowicz 1957; Jachowicz 1958), and is probably present in the Upper Mississippian of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Ishchenko (1956) documented occurrences of the species, in the western Donetz Basin, from Viséan to Namurian, and subsequently (1958), in the Dnieper-Donetz Basin, from Tournaisian to Bashkirian.

Densosporites dentatus (Waltz) Potonié and Kremp 1956

Plate 88, figs. 14, 15

1884 Type 274 of Reinsch, p. 27; pl. 20, fig. 128A.

1938 Zonotriletes dentatus Waltz in Luber and Waltz, p. 20; pl. 14, fig. 47.

1956 Densosporites dentatus (Waltz) Potonié and Kremp, p. 115. 1958 Hymenozonotriletes dentatus (Waltz) Ishchenko, pp. 70–71; pl. 7, fig. 96.

Description of specimens. Spores radial, trilete; amb oval to roundly subtriangular. Laesurae simple, straight to sinuous, extending to spore-body margin. Exine of spore body laevigate to granulate; very thin, hence often poorly preserved or absent. Cingulum uniform, relatively dark in colour, width 9–20 μ , equatorial margin regularly dentate.

Dimensions (50 specimens). Overall equatorial diameter 36-65 μ (mean 49 μ); diameter of spore body $20-31 \mu$ (mean 25μ).

EXPLANATION OF PLATE 88

All figures ×500, and from unretouched negatives.

Fig. 1. Anulatisporites orbiculatus (Waltz) comb. nov. Proximal surface; preparation P148/4, 48·2 95·0 (L.1124).

Figs. 2, 3. Anulatisporites canaliculatus sp. nov. 2, Proximal surface; preparation P163/6, 44·2 112·7

(L.1126). 3, Holotype; proximal surface.

- Figs. 4-7. Densosporites bialatus (Waltz) Potonié and Kremp 1956. 4, Distal surface; preparation P164/5, 38·2 93·1 (L.1129). 5, Distal surface; preparation P164/9, 35·3 101·4 (L.1128). 6, Proximal surface; preparation P167B/3, 50·6 95·1 (L.1130). 7, Distal surface; preparation P167B/1, 28·6 94·3 (L.1131).
- Figs. 8, 9. Densosporites subcrenatus (Waltz) Potonié and Kremp 1956. 8, Proximal surface; preparation P145B/32, 41·5 103·3 (L.1134). 9, Proximal surface; preparation P145C/1, 29·0 94·9 (L.1135).

Figs. 10. 11, Densosporites diatretus nom. nov. 10, Proximal surface; preparation P176A/1, 40·9 95·4 (L.1137). 11, Distal surface; preparation P148/1, 25·0 95·4 (L.1136).

- Figs. 12, 13. Densosporites striatiferus Hughes and Playford 1961. 12, Proximal surface; preparation P172/3, 25-9 95-5 (L.1145). 13, Proximal surface; preparation P170/1, 23-8 97-2 (L.1144).
- Figs. 14, 15. Densosporites dentatus (Waltz) Potonié and Kremp 1956. 14, Proximal surface; preparation P148/1, 45·2 95·6 (L.1132). 15, Distal surface; preparation P143B/5, 33·8 106·7 (L.1133).
- Figs. 16, 17. Densosporites aculeatus sp. nov. 16, Holotype; distal surface. 17, Proximal surface; preparation P201/2, 29·8 102·1 (L.1164).

Fig. 18. Densosporites sp. Proximal surface; preparation P167B/13, 38·8 103·0 (L.1166). Figs. 19–22. Densosporites variabilis (Waltz) Potonié and Kremp 1956. 19, 20, Distal and proximal surfaces respectively; preparation P154/6, 22·7 100·8 (L.1140). 21, Proximal surface; preparation P164/9/13/62 103.7 (F.1130). P145B/31, 36·3 102·7 (L.1138). 22, Proximal surface; preparation P158/4, 21·1 93·5 (L.1139).

Comparison. Some of the spores described by Hoffmeister, Staplin, and Malloy (1955, p. 386; pl. 36, figs. 16, 17) as *Densosporites spinifer*, and subsequently recorded as such by Butterworth and Williams (1958, p. 359; pl. 3, fig. 46) and by Love (1960, p. 109), may be representative of *D. dentatus* (Waltz).

Previous records. Recorded initially by Reinsch (1884) from the Russian Carboniferous. Later and more precisely documented Russian occurrences are from the Lower Carboniferous of the Moscow Basin and of the Kizel, Selizharovo, Voronezh, and Borovichi districts (Luber and Waltz 1938, 1941), and from exclusively Viséan sediments of the Dnieper–Donetz Basin (Ishchenko 1958). Thus this Spitsbergen occurrence is the first reported definitely outside Russia.

Densosporites subcrenatus (Waltz) Potonié and Kremp 1956

Plate 88, figs. 8, 9

1938 Zonotriletes subcrenatus Waltz in Luber and Waltz, p. 19; pl. 4, fig. 43.

1956 Densosporites subcrenatus (Waltz) Potonié and Kremp, p. 116.

1958 Hymenozonotriletes subcrenatus (Waltz) Ishchenko, p. 77; pl. 9, fig. 112.

[non Tendosporites subcrenatus (Waltz) Hacquebard and Barss 1957, p. 36; pl. 5, figs. 3, 4.]

Description of specimens. Spores radial, trilete; amb subtriangular, more or less conformable with spore-body outline. Laesurae distinct, simple, straight, length slightly less than body radius. Spore-body exine essentially laevigate, sometimes finely wrinkled; body outline triangular with rounded apices and \pm straight sides. Cingulum laevigate; with crenulate, fringe-like equatorial margin which is often at least partially absent in poorly preserved specimens. Corroded specimens often tend to approach the aspect of *Tripartites*, notably of *T. incisotrilobus* (Naumova; Waltz) Potonié and Kremp 1956 (cf. Waltz *in* Luber and Waltz 1938, p. 19; Ishchenko 1958, p. 77), although incisement or embayment of the cingulum is not necessarily located interradially.

Dimensions (30 specimens). Overall equatorial diameter 44–65 μ (mean 55 μ); diameter of spore body 26–39 μ (mean 32 μ).

Comparison. The specimens described by Hacquebard and Barss (1957, p. 36; pl. 5, figs. 3, 4) as Tendosporites subcrenatus (Waltz) were incorrectly referred to Waltz's species, since they possess a cingulum which is 'irregularly thickened at the periphery'; this is not a feature diagnosed by Waltz or evident from the Spitsbergen representatives. Some of the spores figured by Reinsch (1884, e.g. pl. 3, figs. 38, 41; pl. 17, fig. 41; pl. 19, fig. 41p; pl. 20, fig. 118L) resemble Densosporites subcrenatus (Waltz).

Previous records. Previous definite occurrences are confined to the Russian Lower Carboniferous. Luber and Waltz (1938, 1941) record the species from the Moscow Basin and Kizel region, and Ishchenko (1958, stratigraphical range table 3) found it to be restricted to Viséan–Namurian strata of the Dnieper–Donetz Basin.

Densosporites diatretus nom. nov.

Plate 88, figs. 10, 11; text-fig. 9a

1941 Zonotriletes intermedius Waltz in Luber and Waltz, pp. 27–28; pl. 5, fig: 68. 1956 Hymenozonotriletes intermedius (Waltz) Ishchenko, pp. 64–65; pl. 12, fig. 139. [non Densosporites intermedius Butterworth and Williams, 1958, p. 379; pl. 3, figs. 38, 39.]

Diagnosis. The following is the present writer's translation of the diagnosis given by Waltz (in Luber and Waltz 1941): 'Diameter— $55-70~\mu$. Colour brownish yellow. Outline of spore body roundly triangular. Border wide, thick, bearing superficially two types of sculpture. Nearer to the inside edge of the border is an arrangement of short, radial grooves; on the rest of the surface sparsely distributed tuberculate thickenings can be observed. The former type of sculpture comes close to that of Zonotriletes variabilis Waltz var. valleculosus Waltz, the second shows much similarity to the sculpture of Zonotriletes polyzonalis Waltz. The fact that the species described is found in conjunction with the two others mentioned, and also the similarity of morphological features, argues in favour of the existence of a definite link between them. Diameter of spore body $15-25~\mu$. Width of border $15-30~\mu$.'

Holotype (here designated). Spore illustrated by Luber and Waltz 1941, pl. 5, fig. 68 (here reproduced as Text-fig. 9a).





TEXT-FIG. 9. a, Densosporites diatretus nom. nov., redrawn from Luber and Waltz 1941, pl. 5, fig. 68. b, Lophozonotriletes rarituberculatus (Luber) Kedo 1957, redrawn from Luber and Waltz 1941, pl. 5, fig. 76. c. × 500.

Description of specimens. Those observed in the Spitsbergen assemblages conform closely to the above diagnosis, and to the following additional remarks.

Amb varies from convexly subtriangular to triangular (this variation was noted also by Ishchenko 1956, 1958). The radial grooves are confined to the inner margin of the proximal surface of the cingulum, and are often much finer and more closely spaced than in the spore illustrated by Waltz (in Luber and Waltz 1941; pl. 5, fig. 68) and reproduced herein (text-fig. 9a). The positive sculptural elements on the remainder of the cingulum are usually more strongly developed on the distal surface; in different specimens they range from small coni to larger rod-like thickenings. The cingulum is often rather indistinctly differentiated into an outer light zone and an inner, darker (thicker) zone; this feature was emphasized by Ishchenko (1958, p. 71). Laesurae, apparent only on well-preserved specimens, are distinct, simple, straight to slightly sinuous, length approximately equal to spore-body radius, sometimes extending on to cingulum.

Dimensions (70 specimens). Overall equatorial diameter 55–76 μ (mean 66 μ); diameter of spore body 16–35 μ (mean 25 μ); width of cingulum 14–25 μ (mean 20 μ).

Remarks. This species is included within Densosporites (Berry) Potonié and Kremp on the basis of its massive, distinctively sculptured cingulum. Ishchenko (1956, 1958) transferred Zonotriletes intermedius Waltz 1941 to Hymenozonotriletes Naumova 1937; however, the latter genus as understood by Potonié (1958, p. 29) and evidently by

Naumova (1953) embraces prominently zonate forms having conspicuous spinose sculpture. Thus Ishchenko's assignment of this species is unacceptable.

Comparison. Densosporites diatretus nom. nov. shows some resemblance to Vallatisporites Hacquebard (1957, p. 312) but lacks the distinct 'groove or rampart-like area' characteristic of that genus. Butterworth and Williams (1958, p. 379) described, from the Scottish Lower Carboniferous, a species which they named Densosporites intermedius. These spores are clearly different from those of Hymenozonotriletes intermedius (Waltz 1941); hence it is necessary to erect a new trivial epithet for the species on its inclusion in Densosporites (ref. articles 55 and 64 of the 1961 International Code of Botanical nomenclature).

Previous records. Densosporites diatretus nom. nov. has been recorded previously from Russia only, as follows: Lower Carboniferous of the Moscow Basin and Kizel region (Luber and Waltz 1941); Tournaisian to Middle Viséan only of the western extension of the Donetz Basin (Ishchenko 1956); and Tournaisian, Viséan, and Namurian of the Dnieper-Donetz Basin (Ishchenko 1958).

Densosporites variabilis (Waltz) Potonié and Kremp 1956

Plate 88, figs. 19-22

- 1938 Zonotriletes variabilis Waltz in Luber and Waltz, pp. 20–21; pl. 4, figs. 44–46, and pl. A, fig. 16.
- 1941 Zonotriletes variabilis Waltz var. foveolatus Waltz in Luber and Waltz, p. 26; pl. 5, fig. 66a.
- 1941 Zonotriletes variabilis Waltz var. fossulatus Waltz in Luber and Waltz, p. 26; pl. 5, fig. 66b.
- 1941 Zonotriletes variabilis Waltz var. valleculosus Waltz in Luber and Waltz, p. 27; pl. 5, fig. 66c.
- 1956 Densosporites variabilis (Waltz) Potonié and Kremp, p. 116.
- 1956 Trematozonotriletes variabilis (Waltz) Ishchenko var. foveolatus Waltz; Ishchenko, pp. 102-3; pl. 22, fig. 248.
- 1957 Trematozonotriletes variabilis (Waltz) Naumova; Byvsheva, p. 1010.
- [non Densosporites variabilis (Waltz) Potonié and Kremp; Butterworth and Williams 1958, pp. 380-1; pl. 3, figs. 32-34.]

Description of specimens. Spores radial, trilete; amb roundly subtriangular. Laesurae straight to sinuous, elevated and slightly thickened; frequently not preserved due to delicate spore-body exine. Uniformly thick cingulum prominently sculptured on proximal surface with numerous shallow pits or grooves arranged radially around outer margin of spore body; cavities rarely extend radially beyond centre of cingulum. Additional, irregular pitting on cingulum is often present, and may be attributable to corrosion. Spore body laevigate to granulate; outline more or less conformable with amb. Equatorial margin smooth, undulating, dentate or lobate.

Dimensions (80 specimens). Overall equatorial diameter 41–77 μ (mean 60 μ); diameter of spore body 19–34 μ (mean 26 μ).

Remarks. Three of the four illustrations of Zonotriletes variabilis in Luber and Waltz 1938 (pl. 4, figs. 44–46) were reproduced in Luber and Waltz 1941 (pl. 5, fig. 66a–c) and designated infraspecifically as the following varieties: foveolatus, fossulatus, and valleculosus, respectively. However, continuous morphographical variation between these forms

was noted by Waltz and is confirmed abundantly in the present investigation; as such, their infraspecific recognition does not appear warranted.

Comparison. Densosporites diatretus resembles D. variabilis (Waltz) in possessing similarly disposed radial grooves in the cingulum, which, however, is sculptured additionally with conspicuous tuberculate thickenings. As noted by Waltz (in Luber and Waltz 1941), D. diatretus represents a sculptural intermediate between D. variabilis and D. polyzonalis (Waltz) Potonié and Kremp 1956. In the Spitsbergen assemblages the former two species are commonly although not invariably associated, and are certainly at least morphographically closely related. However, specimens positively identifiable with D. polyzonalis have not been observed by the writer.

Although showing similar sculpture to the specimens described above, *Trematozonotriletes variabilis* (Waltz) var. *trigonalis* Ishchenko 1956 (p. 103; pl. 20, fig. 249) possesses a cingulum which is consistently wider about the spore apices, and as such

probably represents a distinct species.

Butterworth and Williams (1958) incorrectly assigned to Densosporites variabilis (Waltz) a species which they described as being 'abundant throughout' their Scottish Namurian assemblages; these authors implied identity of their specimens with that illustrated by Luber and Waltz 1938 (pl. 4, fig. 46, subsequently Zonotriletes variabilis Waltz var. valleculosus Waltz 1941). However, from the description and photographs given by Butterworth and Williams (1958, pp. 380-1; pl. 3, figs. 32-34) and from the study of a slide kindly loaned to the writer by Dr. Butterworth, it is clear that the Scottish specimens differ from D. variabilis in the following important respects: (1) the spore body is rather poorly defined; (2) the cingulum shows relatively abrupt equatorial reduction in thickness; (3) the cingulate sculpture consists of irregular, elevated, radial thickenings enclosing equally irregular, and not invariably radially disposed, lumina, which are often imperfectly defined and are not concentrated along the inner margin of the cingulum. In contrast, D. variabilis possesses closely spaced, well-defined, pyriform pits, which are radially arranged about the distinct spore body, sharply punctuating an otherwise featureless cingulum of fairly uniform thickness; there is no appearance of the 'radial struts' described by Butterworth and Williams.

Previous records. Densosporites variabilis has been reported by numerous authors (Luber and Waltz 1938, 1941; Ishchenko 1956, 1958; Bludorov and Tuzova 1956; Byvsheva 1957; Kedo 1957, 1958, 1959; Loginova 1959) as an important constituent of Tournaisian, and particularly Viséan–Namurian strata in the U.S.S.R. Recently Love (1960) recorded the species from the Pumpherston Shell Bed (Viséan) of Scotland, and Hughes and Playford (1961) reported its predominance in one sample (S59a) of the Spitsbergen Lower Carboniferous.

Densosporites duplicatus (Naumova) Potonié and Kremp 1956

Plate 89, figs. 6-8

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1884 Type 336 of Reinsch, p. 33; pl. 16, fig. 125A.
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¹⁸⁸⁴ Type 337 of Reinsch, p. 33; pl. 9, fig. 125.

¹⁹³⁸ Zonotriletes duplicatus (Naumova) Waltz in Luber and Waltz, p. 21; pl. 4, fig. 53.

¹⁹⁵⁶ Densosporites duplicatus (Naumova) Potonié and Kremp, p. 115.

¹⁹⁵⁷ Labiadensites cf. Z. duplicatus (Naumova; Waltz) Hacquebard and Barss, p. 27; pl. 6, fig. 1.

Description of specimens. Spores radial, trilete; amb roundly subtriangular to subcircular. Laesurae distinct, straight, length equal to, or slightly less than, spore-body radius; usually accompanied by minor lip development—lips individually about 3 μ broad, with somewhat irregular outer margins. Spore body concavely or convexly subtriangular to subcircular; laevigate to finely granulate. Outer margin of cingulum strongly and characteristically differentiated into numerous laterally projecting processes which are approximately $10-15~\mu$ long, $3-4~\mu$ in basal diameter, and are conspicuously expanded and thickened apically into crescentic (mushroom-shaped) caps. These prominent peltate processes are usually very closely packed, often appearing to lie in more than one horizontal plane. Cingulum otherwise laevigate, colour slightly darker than body.

Dimensions (70 specimens). Overall equatorial diameter (including processes) $51-77 \mu$ (mean 64μ); diameter of spore body $26-39 \mu$ (mean 32μ).

Remarks. On the basis of a single specimen, Hacquebard and Barss (1957) proposed the assignment of Zonotriletes duplicatus (Naumova) to their new genus Labiadensites, which was said to differ from Densosporites in its invariable possession of 'a strong trilete and greatly developed lips'. It is evident from the examination of numerous Spitsbergen representatives that lips are only sporadically and never strongly developed in this species; furthermore, the earlier descriptions and illustrations given by Reinsch (1884) and Luber and Waltz (1938) contain no reference to such laesurate modification. Hence the species seems more suitably included within Densosporites, as advocated by Potonié and Kremp (1956, p. 115).

Previous records. Densosporites duplicatus was first recorded by Reinsch (1884) from Russian 'Stigmarienkohle' of presumably Lower Carboniferous age. More recently, the species has been reported from Lower Carboniferous deposits of the Moscow Basin and Kizel and Selizharovo regions, U.S.S.R. (Luber and Waltz 1938, 1941); and from Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Densosporites striatiferus Hughes and Playford 1961

Plate 88, figs. 12, 13

Dimensions (40 specimens). Overall equatorial diameter 44–65 μ (mean 54 μ); diameter of spore body 27–45 μ (mean 35 μ); width of cingulum 6–12 μ (mean 9 μ).

Densosporites spitsbergensis sp. nov.

Plate 89, figs. 1-5

Diagnosis. Spores radial, trilete; amb subtriangular, more or less conformable with body outline. Laesurae perceptible to distinct, straight or slightly sinuous; extending on to cingulum as thickened, elevated ridges which often attain equatorial margin. Spore body convexly subtriangular, exine often poorly preserved or absent. Cingulum robust, darker in colour than body; slight and gradual equatorial decrease in thickness. Prominent spinose sculpture on distal surface of spores (body and cingulum); spines

crowded and frequently coalescent around inner margin of cingulum, reduced in size and density in equatorial region; length of spines $1.5-5 \mu$, basal diameter $1-2.5 \mu$. Proximal surface of spores laevigate to sparsely granulate or spinose.

Dimensions (100 specimens). Overall equatorial diameter 55-80 μ (mean 66 μ); diameter of spore body $23-39 \mu$ (mean 31μ).

Holotype. Preparation P163/3, 22-2 96-8. L.1146.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype convexly subtriangular, 64 μ overall; spore-body diameter 28 μ; laesurae distinct, extending to equatorial margin. The species is characterized by its conspicuous distal spinose sculpture, long laesurae, and well-developed cingulum which shows slight reduction in thickness towards the equator; it is a common microfloral constituent of many of the Spitsbergen samples.

Comparison. Densosporites pannosus Knox 1950 (p. 326; pl. 18, fig. 267) is more uniformly and comprehensively spinose and has more prominent, laesurate lips.

Remarks. The sporae dispersae described above as Densosporites spitsbergensis sp. nov. compare closely in all respects with the microspores obtained by Bharadwaj (1959, p. 70; pl. 2, figs. 8-14) from the fructification Porostrobus zeilleri Nathorst 1914, which had been collected in 1882 by Nathorst from the Culm (Lower Carboniferous) at Pyramiden, Spitsbergen, Furthermore, representatives occurring in poorly preserved or overmacerated preparations are very similar to the microspores (from P. zeilleri) which Bharadwaj had treated with excessive potassium hydroxide. From the widespread occurrence of D. spitsbergensis it seems reasonable to assume concomitant widespread distribution of P. zeilleri in Spitsbergen during Lower Carboniferous times.

EXPLANATION OF PLATE 89

All figures ×500, and from unretouched negatives.

Figs. 1-5. Densosporites spitsbergensis sp. nov. 1, Holotype; proximal surface. 2, Distal surface; preparation P162/5, 50.7 104.9 (L.1147). 3, Proximal surface; preparation P163/1, 27.0 96.5 (L.1148). 4, Distal surface; preparation P148/4, 44·2 107·3 (L.1149). 5, Proximal surface; preparation P164/2, 42·3 103·2 (L.1150).

Figs. 6-8. Densosporites duplicatus (Naumova) Potonié and Kremp 1956. 6, Proximal surface; preparation P145A/1, 45·0 110·0 (L.1141). 7, Proximal surface; preparation P145B/1, 23·1 104·7 (L.1142). 8, Proximal surface; preparation P145B/27, 26·3 103·2 (L.1143).

Figs. 9-13. Densosporites variomarginatus sp. nov. 9, Proximal surface; preparation P148/56, 39·2 103·7 (L.1153). 10, Proximal surface; preparation P162/6, 30·0 106·4 (L.1154). 11, Holotype; proximal surface: 12, Proximal surface; preparation P148/27, 35·3 104·5 (L.1156). 13, Proximal surface; preparation P163/6, 38·9 101·2 (L.1155).

Figs. 14, 15. Knoxisporites cinctus (Waltz) Butterworth and Williams 1958. Proximal and distal surfaces respectively; preparation P163/7, 30·4 98·9 (L.1170).

Figs. 16, 17. Lycospora uber (Hoffmeister, Staplin, and Malloy) Staplin 1960. 16, Distal surface; preparation P180B/1, 52.8 105.0 (L.1180). 17, Proximal surface; preparation P180B/4, 43.7 106.4 (L.1181).

Figs. 18-21. Densosporites rarispinosus sp. nov. 18, Proximal surface; preparation P180B/1, 51.5 101.5 (L.1159). 19, Distal surface; preparation P145C/2, 34.7 107.3 (L.1160). 20, Holotype; proximal surface. 21, Distal surface; preparation P145B/1, 17.9 96.7 (L.1161).

Densosporites variomarginatus sp. nov.

Plate 89, figs. 9-13

Diagnosis. Spores radial, trilete, subtriangular. Equatorial margin irregular, i.e. smooth, undulating, dentate or lobate. Laesurae distinct, simple, usually straight, almost attaining spore-body margin. Body laevigate, sometimes finely wrinkled; outline subtriangular with rounded apices and convex to slightly concave sides. Cingulum relatively dense, laevigate or with punctations arranged parallel to spore-body outline. Cingulum has perceptibly to distinctly radiating or striated appearance due apparently to an alternation of intrinsic, non-elevated, usually poorly defined radial 'bands' of differing thickness; the breadth of these bands is (collectively) highly variable.

Dimensions (100 specimens). Overall equatorial diameter 44–102 μ (mean 68 μ); diameter of spore body 27–55 μ (mean 39 μ); (maximum) width of cingulum 7–27 μ (mean 15 μ).

Holotype. Preparation P148/62, 40.8 104.9. L.1152.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype 77 μ overall; spore body microrugulate, outline convexly subtriangular, diameter 43 μ ; cingulum concentrically and finely punctate, width fairly uniform (c. 17 μ), overall distinctly radiating appearance; equatorial margin irregularly undulating.

Despite its generally ill-defined nature (particularly in well-preserved specimens), the radially striated structure of the cingulum is always recognizable. Corrosion, either natural or in preparation, appears to have the effect of emphasizing the structure by embaying the thinner, radial areas, and resulting in an undulating or distinctly lobed equatorial margin. Thus the highly variable nature of the periphery of the cingulum, ranging as a continuous variation from entire to deeply and irregularly incised, is considered to be the result of a concomitant variation in preservation from excellent to poor, respectively. That the margin of the cingulum is highly susceptible to corrosive attack is indicated by the comparative scarcity, even in generally well-preserved assemblages, of specimens possessing an entire, uniformly broad cingulum, and further by the invariable absence of such specimens in poorly preserved assemblages. In some specimens the cingulum appears thickest about the triangular apices of the body.

Comparison. Densosporites striatus (Knox 1950, p. 330; pl. 19, fig. 289) Butterworth and Williams 1958 differs from D. variomarginatus sp. nov. in having a cingulum that is differentiated into an inner thickened portion and an outer, distinctly thinner zone. The cingulum of D. subcrenatus (Waltz) Potonié and Kremp 1956 is marginally crenulate and of essentially uniform, certainly non-striated appearance. Tendosporites subcrenatus (non Waltz) Hacquebard and Barss 1957 (p. 36; pl. 5, figs. 3, 4) has shorter laesurae than D. variomarginatus and is further distinguished by the irregular peripheral thickening of its cingulum, which is otherwise of approximately the same density as the spore body. D. heterotomus (Waltz in Luber and Waltz 1938, pp. 19–20; pl. 2, fig. 28) Potonié and Kremp 1956 may be similar to D. variomarginatus. The drawing given by Luber and Waltz depicts a striate cingulum, which is not, however, described as such in the text or evident from type 612 of Reinsch (1884, p. 60; pl. 38, fig. 257) with which Waltz equated her species. Moreover, and in contrast with D. variomarginatus, D. heterotomus possesses

thickened laesurate lips, is often granulate, and generally much larger (95–120 μ). *D. striatiferus* Hughes and Playford 1961 has much finer and more closely spaced cingulate striations than *D. variomarginatus*.

Densosporites rarispinosus sp. nov.

Plate 89, figs. 18-21; text-fig. 10d

Diagnosis. Spores radial, trilete; amb more or less conformable with convexly subtriangular spore-body outline. Laesurae simple, perceptible to distinct, straight or sinuous, extending equatorially 2–4 μ beyond body margin. Conspicuous distal sculpture of sparsely and irregularly distributed simple spines, which usually project also from equatorial margin; spinae variable in height (1–6 μ), bases circular or subcircular (diameter 0·5–3 μ); subordinate, small verrucae occasionally additionally present. Apart from this sculpture, spore body and cingulum laevigate to finely punctate (corroded specimens). Cingulum non-tapering, and much darker in colour than spore body.

Dimensions (60 specimens). Overall equatorial diameter 37–67 μ (mean 51 μ); diameter of spore body 18–33 μ (mean 24 μ).

Holotype. Preparation P145C/1, 49.6 98.1. L.1158.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype 53 μ overall, spore body 27 μ ; irregularly disposed distal spinae 1·5–6 μ long, 1–2·5 μ broad at base, 4–12 μ apart, progressively sparser towards equator; cingulum and body otherwise infrapunctate; sinuous laesurae extending on to cingulum, 2 μ beyond body margin. This distinctive species is characterized by sparse, but conspicuous, spinose distal sculpture, together with consistent slight extension of the laesurae into the cingulum.

Remarks. Smith (1960) has demonstrated the existence of two distinct wall layers in several species of Densosporites and Anulatisporites—namely an inner membrane (intexine) forming the 'central body' and an outer layer (exoexine) which is equatorially expanded and thickened, thus constituting the cingulum. A similar wall construction is evident in Densosporites rarispinosus sp. nov.; probably overmacerated specimens (e.g. Pl. 89, fig. 19) show a more or less distinct separation of the two wall layers. The same effect has been discussed and illustrated by Bharadwaj (1959, p. 70; pl. 2, figs. 13, 14) in the case of excessively macerated, Densosporites-type microspores of the fructification Porostrobus zeilleri Nathorst.

Comparison. Densosporites spinifer Hoffmeister, Staplin, and Malloy 1955b (pp. 386–7; pl. 36, figs. 16, 17) differs from D. rarispinosus in possessing a coarsely granulate, relatively larger, non-spinose spore body; the spinae of D. spinifer are often closely packed and apparently developed on both proximal and distal surfaces of the cingulum. D. brevispinosus Hoffmeister, Staplin, and Malloy 1955b (p. 386; pl. 36, fig. 22) is subcircular and has a variably differentiated, minutely spinose cingulum enclosing a granulate spore body. The spinose sculpture of D. spinosus Dybová and Jachowicz 1957 (pp. 164–5; pl. 49, figs. 1–4) is more strongly developed than in D. rarispinosus, the cingulum thickness decreases equatorially and the proximal surface is granulate. D.

dentatus (Waltz) Potonié and Kremp 1956 has a regularly dentate equatorial margin, but is laevigate or granulate on the proximal and distal surfaces.

Densosporites aculeatus sp. nov.

Plate 88, figs. 16, 17; text-fig. 10e

Diagnosis. Spores radial, trilete; amb conformable with convexly subtriangular outline of spore body. Laesurae indistinct, simple, straight to curved or sinuous, extending to, or just beyond, body margin; frequently not preserved owing to fragility of proximal body wall. Width and thickness of cingulum fairly uniform, colour much darker than spore body. Equatorial margin and whole of distal surface bear numerous, stout, conspicuously tapering, simple spinae, which have \pm circular bases and are variably spaced (but rarely coalescent); length of spines 2·5–9 μ (usually about 5 μ), basal diameter 1·5–5 μ (average 3·5 μ). Apart from spinose sculpture—spore body laevigate to infragranulate, cingulum laevigate (irregularly punctate in corroded specimens).

Dimensions (36 specimens). Overall equatorial diameter (excluding spinose projections) $31-57\,\mu$ (mean 43 μ); diameter of spore body $18-32\,\mu$ (mean 26 μ).

Holotype. Preparation P164/3, 22-3 96-9. L.1163.

Locus typicus. Birger Johnsonfjellet (sample G1095), Spitsbergen; Lower Carboniferous.

Description. Holotype roundly subtriangular, 40 μ overall; prominently spinose distally and (particularly) equatorially; spinae 4–7 μ long, 3–4 μ broad at base; cingulum otherwise laevigate, spore body finely granulate; body diameter 28 μ .

Comparison. Densosporites aculeatus sp. nov. resembles D. spinifer Hoffmeister, Staplin, and Malloy 1955b (pp. 386–7; pl. 36, figs. 16, 17), but differs in bearing spines on the distal surface of the spore body. Spinozonotriletes'? exiguus Staplin 1960 (p. 22; pl. 4, figs. 26–28) is circular and has comparatively short laesurae, but otherwise seems very similar to D. aculeatus. Another closely allied species is D. rarispinosus sp. nov.; this is distinguishable, however, in its much less strongly developed spinose sculpture, and always clearly discernible laesurae.

Densosporites sp.

Plate 88, fig. 18

Description of specimens. Spores radial, trilete; amb roundly subtriangular. Laesurae distinct, simple, straight, extending to spore-body margin. Body subtriangular with straight to slightly convex sides and rounded to somewhat pointed apices; laevigate or faintly punctate, irregularly thickened on distal surface. Broad cingulum of fairly uniform width and similar density to spore body; sculpture irregularly and minutely scabrate to areolate, particularly in equatorial region.

Dimensions (2 specimens). Overall equatorial diameter 77-92 μ ; diameter of spore body 37-40 μ .

Comparison. The only comparable species to have appeared in the literature is Zonotriletes latizonalis Waltz (in Luber and Waltz 1941, p. 32; pl. 6, fig. 92); this differs from the specimens described above in its marginally serrate cingulum and smaller spore body (diameter $20-25 \mu$).

Genus LABIADENSITES Hacquebard and Barss 1957

Type species. L. attenuatus Hacquebard and Barss 1957.

Affinity. Unknown.

Labiadensites fimbriatus (Waltz) Hacquebard and Barss 1957

Plate 90, figs. 1-3

1938 Zonotriletes fimbriatus Waltz in Luber and Waltz, p. 20; pl. 2, fig. 25.

1956 Hymenozonotriletes fimbriatus (Waltz) Ishchenko, p. 63; pl. 12, fig. 133.

1956 Densosporites fimbriatus (Waltz) Potonié and Kremp, p. 115.

1957 Labiadensites fimbriatus (Waltz) Hacquebard and Barss, p. 28; pl. 4, fig. 2.

Description of specimens. Spores radial, trilete; amb circular to subcircular. Laesurae distinct, straight, almost attaining spore-body margin; flanked by broad, flat lips extending 6– $10~\mu$ on either side of laesurae and having undulating outer margins. Spore body laevigate to infrapunctate. Cingulum smooth, dense; encompassed by a more translucent, less robust equatorial border, which has a frilled, rather membranous appearance; boundary between these is usually well defined and conformable with the smooth, circular spore-body margin. Some specimens were observed in which the membranous border overlaps rather irregularly on to the inner part of the cingulum, particularly on its distal surface. Also, the outer portion sometimes shows considerable variation in width on any one specimen (see Pl. 90, fig. 1), in which case the equatorial outline is broadly undulating.

Dimensions (75 specimens). Overall equatorial diameter 90–144 μ (mean 115 μ); diameter of spore body 50–88 μ (mean 69 μ).

Comparison. Zonotriletes ciliato-marginatus Waltz (in Luber and Waltz 1941, pp. 21–22; pl. 4, fig. 52) has similar, but less concise, differentiation of the cingulum, the outer portion of which is thickly covered with small projections. Some specimens of L. fimbriatus (e.g. Pl. 90, fig. 3), in which the outer membranous border has been partially removed, appear as transitional forms linking this species with Anulatisporites labiatus Hughes and Playford 1961, which has a smooth undifferentiated cingulum. Thus the two species may well be closely related.

EXPLANATION OF PLATE 90

All figures ×500, and from unretouched negatives.

Figs. 1-3. Labiadensites fimbriatus (Waltz) Hacquebard and Barss 1957. 1, Distal surface; preparation P148/41, 34·0 106·6 (L.1167). 2, Proximal surface; preparation P148/5, 52·4 108·9 (L.1168). 3, Proximal surface; preparation P163/7, 27·1 111·3 (L.1169).

Figs. 4-6. Knoxisporites margarethae Hughes and Playford 1961. 4, Distal surface; preparation P173/1, 20·2 112·5 (L.1171). 5, 6, Distal and proximal surfaces respectively; preparation M811/1, 42·5 110·4 (L.1172).

Figs. 7, 8. Knoxisporites literatus (Waltz) comb. nov. 7, Proximal surface; preparation P163/7, 47-7 107-2 (L.1173). 8, Proximal surface; preparation P163/7, 31-4 102-8 (L.1174).

Figs. 9-12. Knoxisporites hederatus (Ishchenko) comb. nov. 9, Proximal surface; preparation P181/5, 35·3 95·8 (L.1178). 10, Proximal surface; preparation P148/5, 47·7 112·8 (L.1175). 11, Proximal surface; preparation P148/5, 24·4 100·9 (L.1177). 12, Proximal surface; preparation P148/55, 37·8 105·4 (L.1176).

Previous records. This distinctive species was apparently widespread in the Northern Hemisphere during Lower Carboniferous times, with previous records from the Tournaisian–Viséan of the Moscow Basin and Kizel region (Luber and Waltz 1938, 1941); from the Tournaisian of the western Donetz Basin (Ishchenko 1956); from the Viséan of the Dnieper–Donetz Basin (Ishchenko 1958); and from Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Genus KNOXISPORITES (Potonié and Kremp) Neves 1961

Type species. K. hageni Potonié and Kremp 1954.

Discussion. Neves (1961) has emended the diagnosis of *Knoxisporites* Potonié and Kremp 1954, and thereby transferred the genus from the Murornati to the Cingulati. Certainly many of the species (including the type) assigned to *Knoxisporites* appear to be definitely cingulate, in addition to their possession of prominent muri variously arranged on the distal hemisphere. In many instances, however, the distinction between cingulum and equatorially disposed mura would not seem as clear as is implied by Neves (1961).

Knoxisporites may be considered analogous to Lophozonotriletes (Naumova) Potonié 1958, differing mainly in sculptural characteristics.

Affinity. Unknown.

Knoxisporites cinctus (Waltz) Butterworth and Williams 1958

Plate 89, figs. 14, 15

1938 Zonotriletes cinctus Waltz in Luber and Waltz, p. 22 (no description); pl. 2, fig. 27.

1956 Anulatisporites cinctus (Waltz) Potonié and Kremp, p. 111.

1958 Euryzonotriletes cinctus (Waltz) Ishchenko, table 3.

1958 Knoxisporites cinctus (Waltz) Butterworth and Williams, p. 370; pl. 2, figs. 11-13.

Dimensions (45 specimens). Overall equatorial diameter $58-94 \mu$ (mean 75μ); diameter of spore body $38-69 \mu$ (mean 54μ).

Previous records. Knoxisporites cinctus (Waltz) has been reported previously (a) from Russia by Luber and Waltz (1938, 1941) from the Lower Carboniferous of the Voronezh and Selizharovo districts, and by Ishchenko (1958) from Namurian rocks of the Dnieper–Donetz Basin; (b) from Scotland by Butterworth and Williams (1958) from the upper part of the Limestone Coal Group (Namurian A); (c) from one sample (B685) of the Lower Carboniferous of Spitsbergen (Hughes and Playford 1961).

Knoxisporites margarethae Hughes and Playford 1961

Plate 90, figs. 4-6

Remarks. Study of numerous additional specimens has indicated that the species is definitely cingulate, with the distal thickened ring developed at or near the cingulum/spore-body margin; and further that the distal extra-reticulum appears to be supported by, although distinct from, the smooth distal muri.

Dimensions (70 specimens). Overall equatorial diameter 64–117 μ (mean 90 μ); diameter of spore body 37–74 μ (mean 53 μ).

Knoxisporites literatus (Waltz) comb. nov.

Plate 90, figs. 7, 8

- 1938 Zonotriletes literatus Waltz in Luber and Waltz, p. 18; pl. 2, fig. 21, and pl. A, fig. 11.
- 1956 Euryzonotriletes literatus (Waltz) Ishchenko, pp. 52-53; pl. 9, fig. 108.
- 1956 Anulatisporites literatus (Waltz) Potonié and Kremp, p. 111.
- 1957 Cincturasporites literatus (Waltz) Hacquebard and Barss, pp. 23-24; pl. 3, figs. 2-5.

Description of specimens. Spores radial, trilete; amb convexly subtriangular, smooth or may show gentle undulation. Laesurae distinct, straight, length equal to, or slightly less than, spore-body radius; bordered by broad, smooth, flat lips which extend approximately $6-10~\mu$ on either side of laesurae. Cingulum broad, usually regular, width $8-19~\mu$; inner margin sometimes darker in colour, possibly indicating poleward extension $(3-5~\mu)$ over spore body. In some specimens the cingulum is slightly narrower at the apices, so that the amb tends to appear more roundly triangular than the equatorial outline of the spore body. Distal surface has characteristic sculpture of several (usually three or four) smooth, rounded muri, which are rather irregularly disposed and often loosely connected; width of muri $6.5-12~\mu$. Apart from lips and distal muri, spore body and cingulum laevigate.

Dimensions (75 specimens). Overall equatorial diameter $56-102 \mu$ (mean 76μ); diameter of spore body $42-74 \mu$ (mean 56μ). This corresponds closely to the combination of the dimensions reported for the species by Waltz (in Luber and Waltz 1938), Ishchenko (1956, 1958), and Hacquebard and Barss (1957).

Remarks. This cingulate species, possessing well-developed distal muri, is conformable with Knoxisporites Potonié and Kremp as emended by Neves (1961). The 'overlap' of the cingulum on to the spore body is infrequently apparent and it was not mentioned in the original specific diagnosis (Waltz in Luber and Waltz 1938, p. 18); thus assignment to Cincturasporites Hacquebard and Barss 1957 is unacceptable.

Previous records. This characteristically Lower Carboniferous species has been reported previously from the U.S.S.R. (Luber and Waltz 1938, 1941; Ishchenko 1956, 1958), Canada (Hacquebard and Barss 1957), and Spitsbergen (Hughes and Playford 1961). Probable representatives occur also in the Upper Devonian of Western Australia (Balme and Hassell 1962, p. 11). On the basis of vertical distribution studies in the Dnieper–Donetz Basin, Ishchenko (1958, stratigraphical range table 3) indicates a range from Upper Devonian to Namurian.

Knoxisporites hederatus (Ishchenko) comb. nov.

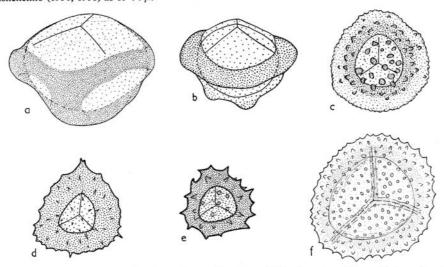
Plate 90, figs. 9-12; text-fig. 10a

1956 Euryzonotriletes hederatus Ishchenko, pp. 58-59; pl. 10, fig. 121.

Description of specimens. Spores radial, trilete; amb circular to subcircular. Distinct spore body encompassed by more or less conformable cingulum (width 6–16 μ , mean 11 μ). Laesurae distinct, simple, straight, length three-quarters of, to almost equal to, spore-body radius. Distal hemisphere bears conspicuous, widely spaced, relatively low, broad, smooth, rounded muri, which are connected in several places to each other and to the cingulum, but do not form a constant, symmetrical pattern; muri slightly sinuous,

breadth 8-17 μ , height 4-7 μ . Apart from muri, exine laevigate to infrapunctate (oil immersion). Marginal distortion, particularly of muri, common.

Dimensions (40 specimens). Overall equatorial diameter $67-112 \mu$ (mean 86μ). Thus the Spitsbergen representatives suggest a considerably less restricted size range for the species than that stated by Ishchenko (1956, 1958) as $85-90 \mu$.



TEXT-FIG. 10. Camera lucida drawings; all magnifications × 500 unless otherwise specified. a, Knoxisporites hederatus (Ishchenko) comb. nov.; lateral view; preparation P174/2, 41·2 114·2 (L.1179). b, Lophozonotriletes appendices (Hacquebard and Barss) comb. nov. (×250); lateral view; preparation P154/5, 53·2 108·7 (L.1190). c, L. variverrucatus sp. nov.; distal surface; preparation P175/2, 33·9 109·0 (L.1193). d, Densosporites rarispinosus sp. nov.; distal surface; preparation P145A/1, 25·6 98·0 (L.1162). e, D. aculeatus sp. nov.; distal surface; preparation P164/2, 43·5 93·3 (L.1165). f, Cristatisporites echinatus sp. nov.; distal surface; preparation P148/1, 31·9 108·9 (L.1184).

Remarks. This species is included within Knoxisporites on the basis of its conspicuous distal sculpture of strongly developed muri together with distinct equatorial girdle. The subgroup Euryzonotriletes Naumova 1939 is an unsatisfactory taxon as it embraces many valid genera, and, as noted by Potonié (1956, p. 87), it appears to lack a type species.

Previous records. According to Ishchenko (1956, 1958) this species is confined to sediments of Tournaisian-Lower Viséan age in the western extension of the Donetz Basin; and to Tournaisian-Viséan strata in the Dnieper-Donetz Basin.

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

Type species. L. micropapillata (Wilson and Coe) Schopf, Wilson, and Bentall 1944.

Affinity. Schopf, Wilson, and Bentall (1944, p. 54) considered that most of the isolated spores conformable with their genus Lycospora represent microspores of arborescent

lepidodendrids. Subsequently, Potonié and Kremp (1954, p. 156) allied the genus with the Lepidophytales, Lepidodendracaeae, and Lepidospermales.

Chaloner (1953b) obtained microspores conformable with Lycospora from two heterosporous lycopod strobili, Lepidostrobus dubius Binney and L. russelianus Binney, both of Upper Carboniferous age. In 1958 Sen reported microspores similar to Lycospora parva Kosanke 1950 from Lepidostrobus goldenbergi Schimper and from L. variabilis Lindley and Hutton.

Lycospora uber (Hoffmeister, Staplin, and Malloy) Staplin 1960

Plate 89, figs. 16, 17

- 1938 Zonotriletes pusillus (non Ibrahim) Waltz in Luber and Waltz, p. 15; pl. 3, fig. 33, and pl. A, fig. 12.
- 1941 Zonotriletes pusillus (non Ibrahim) var. gracilis Waltz in Luber and Waltz, p. 35; pl. 7, fig. 101b.
- 1952 Hymenozonotriletes pusillus (non Ibrahim) Ishchenko, p. 50; pl. 13, fig. 122.
- 1955 Cirratriradites uber Hoffmeister, Staplin, and Malloy, p. 383; pl. 36, fig. 24. 1957 Hymenozonotriletes pusillus (non Ibrahim) Naumova; Byvsheva, p. 1010.
- 1960 Lycospora uber (Hoffmeister, Staplin, and Malloy) Staplin, p. 20; pl. 4, figs. 13, 17, 18, 20.

Description of specimens. Spores radial, trilete; amb convexly subtriangular, conformable with spore-body outline. Laesurae distinct, straight, length approximately equal to body radius; accompanied by narrow, more or less prominent lips. Spore body subtriangular with convex sides and rounded apices; finely granulate to finely rugulate/ verrucate (distal sculpture often coarser); sometimes arcuately folded at periphery. Cingulum ('flange') narrow, laevigate, often diaphanous; equatorial margin smooth in well-preserved specimens.

Dimensions (50 specimens). Overall equatorial diameter $26-39 \mu$ (mean 32μ); diameter of spore body 19-27 μ (mean 23 μ).

Remarks. The numerous species listed by Staplin (1960, p. 20) as synonymous with Lycospora uber (Hoffmeister, Staplin, and Malloy) is a reflection of the variable nature of this species, which is often extremely abundant in the Spitsbergen samples. L. uber is undoubtedly conspecific with forms incorrectly assigned by Russian authors (Waltz, Ishchenko, Byvsheva, &c.) to Ibrahim's species, i.e. L. pusilla (Ibrahim) Schopf, Wilson, and Bentall. Staplin also lists a number of other species, such as L. noctuina Butterworth and Williams 1958 (p. 376; pl. 3, figs. 14, 15), which may well also be representative of L. uber. Certainly much specific subdivision of spores in this category has resulted from their susceptibility to corrosion, and consequent somewhat variable appearance, particularly with respect to spore-body sculpture. As noted by Staplin (1960), a detailed reappraisal of the types of all species included within Lycospora would seem an essential approach to the problem.

Previous records. This species has been recorded by numerous authors from the Russian Carboniferous (Luber and Waltz 1938, 1941; Ishchenko 1952, 1956, 1958; Byvsheva 1957, &c.) and also from the Upper Mississippian of North America (Hoffmeister, Staplin, and Malloy 1955; Hacquebard and Barss 1957; Staplin 1960). Future proven synonymy may show its presence in the Namurian assemblages described by Dybová and Jachowicz (1957) and Butterworth and Williams (1958). As indicated by Ishchenko

(1958, stratigraphical range table 3), it seems likely that *Lycospora uber* did not appear until early Viséan times; its upper limit of distribution is, however, dependent upon resolution of the taxonomic problems discussed above.

Genus CRISTATISPORITES Potonié and Kremp 1954

Type species. C. indignabundus (Loose) Potonié and Kremp 1954.

Discussion. After critical re-examination of the diplotype, and study of other Upper Carboniferous species of Cristatisporites, Bhardwaj (1957, p. 105) came to the conclusion that 'the spores are cingulate having a narrow, subequatorial, thickened peripheral region comparable in structure and organisation to the cingulum of Densosporites and Lycospora'. Richardson (1960, p. 58) followed Bhardwaj in including Cristatisporites within the Cingulati, an assignment which is also supported by the Spitsbergen specimens described below.

Affinity. Unknown.

Cristatisporites echinatus sp. nov.

Plate 91, figs. 1-4; text-fig. 10f

Diagnosis. Spores radial, trilete; amb convexly subtriangular. Differentiation into central area and cingulum distinct to obscure; cingulum width approximately 15–25 per cent. of amb diameter. Laesurae prominent, elevated, with thickened lips (individually 2–4·5 μ wide, and up to 4 μ high); extending on to cingulum, often attaining equatorial margin. Conspicuous echinate sculpture restricted to distal hemisphere and equator, comprising small, fairly closely spaced cones or spines, more or less uniformly distributed, and producing serrate equatorial margin. Sculptural elements \pm equal in size on any one specimen, bases circular to oval, apices pointed or slightly rounded, usually discrete, occasionally fused in small groups; basal diameter of cones/spines $1\cdot5-4~\mu$, length $1\cdot5-5~\mu$. Proximal hemisphere finely granulate to infrapunctate.

Dimensions (25 specimens). Overall equatorial diameter 63–100 μ (mean 81 μ).

Holotype. Preparation P148/31, 39.7 104.2. L.1182.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype 92 μ overall, width of cingulum 14–21 μ ; pronounced laesurae (lips 4 μ wide) attaining serrate equatorial margin; proximal hemisphere sparsely and unevenly granulate (grana up to 1 μ in diameter). In some specimens the distal sculpture shows a gradual, almost imperceptible increase in density towards the equator, so that the cones/spines are fairly closely packed equatorially, and comparatively sparsely distributed in the vicinity of the distal pole. Fusion of these sculptural elements, when encountered, is restricted to the equatorial region, with groups of no more than three. The cingulum usually shows some equatorial decrease in thickness which may be gradual or abrupt; in the latter instance (as with the holotype) a dark ring is evident defining the inner margin of the cingulum. The conspicuous triradiate marks usually appear as uniform, slightly roughened, relatively thick ridges in which dehiscence fissures are frequently not visible.

Comparison. One of two illustrations given by Luber (1955, pl. 5, fig. 111) of Lepidozonotriletes ciliaris (Luber) resembles Cristatisporites echinatus sp. nov., but close similarities are not apparent from either the description (p. 46) or the accompanying figure (pl. 5, fig. 112). Hymenozonotriletes praetervisus Naumova 1953 (pl. 4, fig. 8) may be similar, but an accurate comparison is not possible from Naumova's illustration and brief description. The subgroup Hymenozonotriletes Naumova appears to embrace indiscriminately monosaccate, cingulate, and zonate forms.

Genus LOPHOZONOTRILETES (Naumova) Potonié 1958

Type species. L. lebedianensis Naumova 1953.

Affinity. Unknown.

Lophozonotriletes rarituberculatus (Luber) Kedo 1957

Plate 91, figs. 8, 9; text-fig. 9b

- 1941 Zonotriletes rarituberculatus Luber in Luber and Waltz, pp. 10, 30; pl. 1, fig. 5, and pl. 5, fig. 76.
- 1956 Euryzonotriletes rarituberculatus (Luber) Ishchenko var. triangulatus Ishchenko, p. 51; pl. 8, fig. 104.
- 1957 Lophozonotriletes rarituberculatus (Luber) Kedo, p. 1166.
- 1961 Lophozonotriletes triangulatus Hughes and Playford, pp. 35-36; pl. 3, figs. 3-7.

Remarks. In 1956 Ishchenko instituted the infraspecific taxon 'Euryzonotriletes rarituberculatus (Luber) comb. nov. var. triangulatus var. nov.' Specimens identical to those described by Ishchenko were recorded subsequently from Spitsbergen by Hughes and Playford (1961), who elevated the variety to specific status 'as it occurs alone in considerable numbers in sample B685'. Additional study by the present writer indicates the widespread lateral, and restricted vertical, distribution of this form within Vest-spitsbergen.

After the submission (in April 1960) of the Hughes and Playford manuscript, how-

EXPLANATION OF PLATE 91

All figures $\times 500$, and from unretouched negatives.

- Figs. 1–4. Cristatisporites echinatus sp. nov. 1–3, Holotype. Proximal view: 1, high focus; 2, central focus; 3, low focus. 4, Distal surface; preparation P175/1, 28·5 113·0 (L.1183).
- Fig. 5. Lophozonotriletes dentatus Hughes and Playford 1961. Proximal surface; preparation P226/5, 43·3 113·1 (L.1187).
- Figs. 6, 7. Lophozonotriletes variverrucatus sp. nov. 6, Holotype; proximal surface. 7, Distal surface; preparation M811/1, 40·5 99·6 (L.1192).
- Figs. 8, 9. Lophozonotriletes rarituberculatus (Luber) Kedo 1957. 8, Proximal surface; preparation P163/7, 26·2 94·6 (L.1186). 9, Distal surface; preparation P173/10, 30·3 104·2 (L.1185).
- Figs. 10, 11. Lophozonotriletes appendices (Hacquebard and Barss) comb. nov. 10, Distal surface; preparation P149A/8, 36·3 104·7 (L.1189). 11, Proximal surface; preparation P149A/1, 17·8 113·9 (L.1188).
- Figs. 12, 13. Potoniespores delicatus sp. nov. 12, Holotype; proximal surface. 13, Proximal surface; preparation P149A/29, 34·0 106·4 (L. 1203).
- Figs. 14, 15. Tholisporites foveolatus Hughes and Playford 1961. 14, Proximal surface; preparation P148/40, 36·9 104·0 (L.1200). 15, Distal surface; preparation P172/1, 30·0 104·8 (L. 1201).

ever, the important publication of Luber and Waltz (1941) came to hand, and a detailed comparison of the diagnoses given by Luber (1941, p. 10) for the species, and by Ishchenko (1955, p. 51) for the variety, casts considerable doubt upon the validity of the latter as a distinct morphographical unit. Ishchenko considered his variety distinguishable on the basis of its 'uniformly broad border and regular roundly triangular shape'. However, Luber had clearly described *Zonotriletes rarituberculatus* as being 'roundly triangular', and although noting the margin as somewhat irregular and scallop-like, one of her illustrations (pl. 5, fig. 76: redrawn herein as text-fig. 9b) shows a more or less uniform, entire equatorial margin. It is important to note that Ishchenko included *Z. rarituberculatus* Luber in its entirety within the variety, which must itself, on this basis alone, be considered an unwarranted, superfluous institution.

Of the other illustration given by Luber (1941, pl. 1, fig. 5), which shows an undulating equatorial margin, numerous parallels exist in the Spitsbergen material; these are usually accountable as the result of either folding or corrosion.

Kedo (1957, p. 1166) included *Zonotriletes rarituberculatus* Luber, one of a number of species she listed as characteristic of the Lower Tournaisian of White Russia, within the category of *Lophozonotriletes* Naumova. This assignment remains acceptable under the emendation (by Potonié 1958, pp. 27–28) of Naumova's subgroup (cf. Hughes and Playford 1961, p. 35). *L. rarituberculatus* (Luber) is a highly distinctive species and is undoubtedly of considerable stratigraphical value (see previous records below).

Dimensions (100 specimens). Overall equatorial diameter $50-82 \mu$ (mean 66μ); diameter of spore body $34-59 \mu$ (mean 47μ); width of cingulum $5-15 \mu$ (mean 10μ).

Previous records. Initially described (Luber in Luber and Waltz 1941) from Upper Devonian of the Timan Peninsula and Kizel region and from the lower horizons of the Tournaisian in the southern Moscow Basin and Voronezh region. Ishchenko (1956) found *L. rarituberculatus* to be restricted to Tournaisian strata of the western extension of the Donetz Basin, and Kedo (1957, 1958, 1959) to the Malevka horizon (Lower Tournaisian) of White Russia. Byvsheva (1957, 1960) reported its presence in lowermost Carboniferous from the Melekess and Busuluk deep wells and from the Volga–Ural region. Recently Hughes and Playford (1961) described the species from one sample (B685) of the Spitsbergen Lower Carboniferous, the first-reported occurrence outside the U.S.S.R.

Lophozonotriletes dentatus Hughes and Playford 1961

Plate 91, fig. 5

Dimensions (30 specimens). Overall equatorial diameter 42–69 μ (mean 55 μ); diameter of spore body 28–48 μ (mean 37 μ).

Lophozonotriletes appendices (Hacquebard and Barss) comb. nov.

Plate 91, figs. 10, 11; text-fig. 10b

1957 Cincturasporites appendices Hacquebard and Barss, p. 25; pl. 3, figs. 10-12.

Description of specimens. Spores radial, trilete; amb roundly subtriangular. Laesurae distinct, simple, straight, length approximately equal to spore-body radius. Body subtriangular with convex sides and rounded apices. Cingulum uniform or somewhat

variable in width (average 20 μ), laevigate to finely punctate, often exhibiting narrow concentric furrows; inner margin sometimes darker and well defined, probably indicating poleward 'overlap' (3–5 μ) on spore body. Prominent distal sculpture consisting of from four to twenty-two large, smooth, rounded projections (verrucae) disposed rather irregularly on spore body and sometimes additionally on inner margin of cingulum; occasional sparse development on infrapunctate proximal surface of spore body. Verrucae subcircular to oval in surface view, basal diameter 8–27 μ , height 6–10 μ ; rarely coalescent, most strongly developed around distal pole. Equatorial margin smooth to undulating.

Dimensions (44 specimens). Overall equatorial diameter $110-170 \mu$ (mean 137μ); diameter of spore body $69-117 \mu$ (mean 90μ).

Remarks. Although generally conformable, the above description diverges slightly from the original diagnosis of *Cincturasporites appendices* Hacquebard and Barss 1957. The latter authors evidently did not encounter specimens in which the projections are developed proximally as well as (and much more strongly and abundantly) on the distal surface. Furthermore, many of the Spitsbergen representatives possess projections in excess of the 'three to ten' stated by Hacquebard and Barss.

As discussed previously, *Cincturasporites* Hacquebard and Barss 1957 appears to be an unsatisfactory taxon of doubtful validity; certainly the 'overlap' diagnostic of the genus is recognizable in rather less than half of the specimens described above. On the other hand, the cingulate and conspicuously verrucate nature of the species is in accordance with *Lophozonotriletes* Naumova as emended by Potonié (1958, pp. 27–28).

Previous records. From Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Lophozonotriletes variverrucatus sp. nov.

Plate 91, figs. 6, 7; text-fig. 10c

Diagnosis. Spores radial, trilete; amb convexly subtriangular, finely dentate to almost smooth. Laesurae distinct, simple, straight or slightly sinuous, almost attaining sporebody margin. Spore body usually somewhat lighter in colour than cingulum, which may show gradual, indistinct, equatorial decrease in thickness. Prominent distal sculpture of verrucae and, less commonly, baculae, distributed rather irregularly on both spore body and cingulum. Projections usually discrete, but bases sometimes fused, particularly around inner margin of cingulum; reduced or absent on equatorial region. Projections rather variable in size, shape, and disposition; range $1-7~\mu$ long, $2-12~\mu$ broad. Proximal hemisphere laevigate or infrapunctate.

Dimensions (30 specimens). Overall equatorial diameter $42-68 \mu$ (mean 55μ); diameter of spore body $23-36 \mu$ (mean 30μ); width of cingulum $9-16 \mu$ (mean 12μ).

Holotype. Preparation P175/3, 48.6 94.0. L.1191.

Locus typicus. Citadellet (sample G1450), Spitsbergen; Lower Carboniferous.

Description. Holotype 56μ overall, diameter of spore body 34μ , width of cingulum 11μ ; proximal surface of spore body infrapunctate, of cingulum laevigate; whole distal hemisphere, excepting outer margin of cingulum, bearing numerous verrucae, some

baculae; sculpturing elements $2-7 \mu$ long, $2-12 \mu$ broad, frequently fused at bases in vicinity of spore body/cingulum junction; equatorial margin practically smooth.

Remarks. This cingulate species is included within Lophozonotriletes on the basis of its conspicuously developed verrucate/baculate sculpture. It is distinct from L. rarituberculatus (Luber), which has less numerous, more regular distal projections.

Genus MONILOSPORA (Hacquebard and Barss) Staplin 1960

Type species. M. moniliformis Hacquebard and Barss 1957.

Discussion. The emendation of the genus Monilospora Hacquebard and Barss 1957 by Staplin (1960, p. 28) is here accepted, since it somewhat clarifies the morphological features, particularly in light of the effects of corrosion. The present writer is in agreement with Staplin's statement that three of the species in Hacquebard and Barss 1957—Monilospora moniliformis, Tendosporites subcrenatus (non Waltz), and Densosporites subserratus—perhaps represent different manifestations, due to variable preservation, of the same species.

It seems unfortunate that the terms 'capsula' and 'patella' introduced and utilized by Staplin (1960) in relation to the structure of this and other genera (*Murospora*, *Tendosporites*) are not illustrated or defined in any detail, and are without reference to the layers of the spore wall; in their present form the use of such terms would only add to the confusion at present prevailing in palynological terminology. As understood by the present writer, Staplin's 'outer hull' or 'capsula' in fact refers to the envelopment of the intexine by the exoexine, which may be equatorially expanded and/or thickened, whereas 'patella' (cf. 'patina' of *Tholisporites* Butterworth and Williams 1958, pp. 381–2; text-fig. 3) implies predominantly distal thickening of the exoexine.

Affinity. Unknown.

Monilospora triungensis sp. nov.

Plate 92, figs. 2, 3

Diagnosis. Spores radial, trilete; amb subtriangular. Laesurae distinct, simple, straight, length approximately three-quarters to four-fifths spore-body radius. Spore body laevigate; subtriangular with broadly rounded apices and concave to almost straight sides. Broad cingulum showing gradual and slight equatorial decrease in thickness which is emphasized by corrosion; irregularly scalloped in outer part. Scalloping may be confined to outermost region or, if coarser, may extend about half-way towards spore-body margin.

Dimensions (30 specimens). Overall equatorial diameter $80-117 \mu$ (mean 97μ); diameter of spore body $38-66 \mu$ (mean 52μ).

Holotype. Preparation P145B/36, 38·0 100·9. L.1194.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype 92 μ overall; cingulum width 19 μ , outer margin almost entirely scalloped (indented as much as 10 μ), otherwise laevigate; spore body 53 μ in diameter, laevigate. The species is characterized by its large size and distinctive cingulum.

It is possible that the often highly irregular, scallop-like indentations of the cingulum are the result of corrosive action. However, it is important to note in this connexion that the other microfloral elements, contained in both samples (G1466, G636) from which *Monilospora triungensis* sp. nov. has been recovered, appear exceptionally well preserved.

Comparison. This species resembles Monilospora mutabilis Staplin 1960 (p. 28; p. 6, figs. 1-7, 9) but is consistently larger.

Monilospora dignata sp. nov.

Plate 92, figs. 4, 5

Diagnosis. Spores radial, trilete; amb subtriangular to oval. Laesurae distinct, simple, straight, length almost equal to body radius. Spore body subtriangular with straight to convex sides and rounded apices; laevigate to infrapunctate. Cingulum of somewhat variable width (mean $14\,\mu$); including well-defined, continuous, thickened equatorial region, which is elevated, rounded in cross-section, and superficially either laevigate or finely wrinkled; width of marginal thickening typically variable on any given specimen, about 5–10 μ . Cingulum otherwise smooth.

Dimensions (30 specimens). Overall equatorial diameter 48–64 μ (mean 56 μ); diameter of spore body 25–36 μ (mean 30 μ).

Holotype. Preparation P145B/18, 41·0 101·4. L.1197.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype 62 μ overall; laesurae almost attain spore-body margin; body laevigate, subtriangular with straight to convex sides; cingulum 12–17 μ broad; prominent, elevated, smooth, marginal thickening (5–9 μ in width) appearing to encroach irregularly upon undifferentiated inner part of cingulum.

Comparison. Monilospora dignata sp. nov. is distinguishable from M. moniliformis Hacquebard and Barss 1957 (p. 38; pl. 5, figs. 8, 9) in possessing a smaller spore body, longer laesurae, and continuous marginal thickening. Knoxisporites carnosus (Knox) Butterworth and Williams 1958 (p. 369; pl. 2, figs. 8–10) is larger than M. dignata and its spore body is prescribed by a pronounced zone of cingulate thickening.

EXPLANATION OF PLATE 92

All figures ×500, and from unretouched negatives.

Fig. 1. Cirratriradites solaris Hacquebard and Barss 1957. Proximal surface; preparation P155/15, 40-3 102-8 (L.1206).

Figs. 2, 3. Monilospora triungensis sp. nov. 2, Proximal surface; preparation P145B/34, 34·0 108·5 (L.1195). 3, Holotype; proximal surface.

Figs. 4, 5. Monilospora dignata sp. nov. 4, Holotype; proximal surface. 5, Proximal surface; preparation P145B/1, 46·7 99·8 (L.1198).

Figs. 6, 7. Cirratriradites elegans (Waltz) Potonié and Kremp 1956. 6, Proximal surface; preparation P149A/41, 46·2 100·4 (L.1207). 7, Proximal surface; preparation P149A/2, 45·6 95·2 (L.1208).

Infraturma PATINATI Butterworth and Williams 1958 Genus THOLISPORITES Butterworth and Williams 1958

Type species. T. scoticus Butterworth and Williams 1958.

Affinity. Unknown.

Tholisporites foveolatus Hughes and Playford 1961

Plate 91, figs. 14, 15

Dimensions (75 specimens). Overall equatorial diameter 52-77 μ (mean 64 μ); diameter of proximal central area 24-37 μ (mean 31 μ).

Comparison. Densosporites intermedius (Waltz) comb. nov. shows some general resemblance, but is non-patinate and has different sculpture in the equatorial region.

Infraturma ZONATI Potonié and Kremp 1954 Genus POTONIESPORES Artüz 1957

Type species. P. bizonales Artüz 1957.

Discussion. In her diagnosis of Potoniespores, Artüz (1957, p. 254) refers to the presence of a single V-shaped indentation of the equatorial margin. However, this feature may well prove merely a secondary (preservation) effect and hence its significance as a diagnostic characteristic is doubtful. Concise differentiation of the equatorial girdle into an inner thickened portion and an outer membranous zone permits the discrimination of Potoniespores from Murospora (al. Simozonotriletes).

Affinity. Unknown.

Potoniespores delicatus sp. nov.

Plate 91, figs. 12, 13

Diagnosis. Spores radial, trilete; amb subtriangular, conformable with spore-body outline. Laesurae distinct, simple, straight, length slightly less than spore-body radius. Spore body laevigate to infrapunctate; subtriangular with rounded apices and markedly concave to slightly convex sides. Equatorial girdle entirely laevigate; abruptly and uniformly differentiated into a prominent, dark, thickened, inner part and a thin, outer, diaphanous zone which is frequently folded and torn. Approximately half to two-thirds of the total girdle width is occupied by the inner thickened portion.

Dimensions (35 specimens). Overall equatorial diameter 50–69 μ (mean 58 μ); diameter of spore body 23–33 μ (mean 27 μ).

Holotype. Preparation P180B/4, 24·7 95·1. L.1202.

Locus typicus. Birger Johnsonfjellet (sample G1102), Spitsbergen; Lower Carboniferous.

Description. Holotype 54μ overall; body concavely subtriangular, 24μ in diameter, infrapunctate; equatorial girdle 15μ broad, (inner) two-thirds occupied by dark, thickened portion, outer membranous zone with one conspicuous fold.

Comparison. Potoniespores bizonales Artüz 1957 (p. 254; pl. 6, fig. 47) differs from

P. delicatus sp. nov. in possessing longer laesurae and a relatively broader outer membranous zone. *Hymenozonotriletes concavus* Ishchenko 1956 (p. 63; pl. 12, fig. 134) has a much larger spore body together with somewhat irregular differentiation of the equatorial girdle.

Genus CIRRATRIRADITES Wilson and Coe 1940

Type species. C. saturni (Ibrahim) Schopf, Wilson, and Bentall 1944.

Affinity. Microspores showing close resemblance to Cirratriradites anulatus Kosanke and Brokaw (in Kosanke 1950) have been recovered from the herbaceous, heterosporous lycopod Selaginellites suissei Zeiller (Chaloner 1954), and also from the detached, heterosporous strolibus S. crassicinctus Hoskins and Abbott (1956).

Cirratriradites solaris Hacquebard and Barss 1957

Plate 92, fig. 1

Description of specimens. Spores radial, trilete; amb convexly subtriangular, conformable with spore-body outline. Laesurae distinct, straight, length approximately equal to body radius; bordered by strongly developed lips individually $3-4~\mu$ wide. Spore-body wall very thick (5–9 μ), irregularly punctate to microreticulate. Membranous zona relatively thin, supported by numerous, radially disposed, anastomosing ribs, which tend to be emphasized by corrosion. Well-preserved specimens uncommon.

Dimensions (25 specimens). Overall equatorial diameter $117-252 \mu$ (mean 189μ); diameter of spore body $55-100 \mu$ (mean 78μ). This agrees closely with the combination of the size ranges observed by Hacquebard and Barss (1957) and Staplin (1960).

Comparison. Hymenozonotriletes auranthiacus Naumova (Ishchenko 1956, p. 67; pl. 13, fig. 144), recorded also as Zonotriletes auranthiacus (Naumova) Waltz (in Luber and Waltz 1938, p. 16; pl. 3, fig. 40), is undoubtedly a closely related species. It is distinguishable from C. solaris in its smaller size and in possessing shorter, indistinct, apparently simple laesurae.

Previous records. This species has been reported previously from the Upper Mississippian of Canada (Hacquebard and Barss 1957; Staplin 1960).

Cirratriradites elegans (Waltz) Potonié and Kremp 1956

Plate 92, figs. 6, 7

- 1938 Zonotriletes elegans Waltz in Luber and Waltz, p. 15; pl. 3, fig. 32.
- 1956 Cirratriradites elegans (Waltz) Potonié and Kremp, p. 126.
- 1958 Hymenozonotriletes elegans (Waltz) Ishchenko, p. 67; pl. 7, fig. 88.

Description of specimens. Spores radial, trilete; amb convexly subtriangular, conformable with spore-body outline. Laesurae distinct, straight; extending on to zona, frequently reaching equator; accompanied by conspicuous, smooth, elevated, thickened lips, having maximum development on spore body, extending 4–6 μ on either side of laesurae. Spore body scabrate; non-foveolate. Zona much lighter in colour than spore body, more or less smooth, often folded, shows equatorial decrease in thickness; radially pitted or channelled in corroded specimens.

Dimensions (45 specimens). Overall equatorial diameter 70–128 μ (mean 102 μ); diameter of spore body 44–63 μ (mean 53 μ).

Previous records. Cirratriradites elegans has been known hitherto only from the U.S.S.R. Waltz (in Luber and Waltz 1938) described it initially from Viséan strata of the Moscow Basin, and a recent report is from Viséan to Namurian rocks of the Dnieper–Donetz Basin (Ishchenko 1958).

Genus CAMPTOZONOTRILETES Staplin 1960

Type species. C. vermiculatus Staplin 1960.

Affinity. Unknown.

Camptozonotriletes velatus (Waltz) comb. nov.

Plate 93, figs. 1-3

- 1938 Zonotriletes velatus Waltz in Luber and Waltz, p. 14; pl. 3, fig. 35, and pl. A, fig. 18.
- 1955 Reticulatisporites velatus (Waltz) Potonié and Kremp, p. 112.
- 1958 Hymenozonotriletes velatus (Waltz) Ishchenko, p. 75; pl. 8, fig. 105.

Description of specimens. Spores radial, trilete; amb roundly subtriangular to subcircular. Laesurae distinct, straight, equal to or slightly less than body radius; simple, or bordered by narrow, thickened, elevated lips which often extend, and diverge markedly, immediately beyond radial termini of laesurae, thus appearing rather 'spanner-like' in polar view. Equatorial zone ('flange') uniform, lighter in colour than spore body; outer margin smooth or undulating (due to folding), more or less conformable with spore-body equator. Distal surface marked by development of a variable number of dark, thickened ridges of irregular length and disposition, particularly characteristic of spore body but often extending on to zona. Ridges $4-8~\mu$ wide, simple or divided equally by a narrow longitudinal channel; sometimes connected to form an irregular, wide-meshed reticulum; rarely present on proximal surface.

Dimensions (100 specimens). Overall equatorial diameter 57–116 μ (mean 84 μ); diameter of spore body 33–88 μ (mean 57 μ). This extends considerably the size ranges quoted by Waltz (in Luber and Waltz 1938) and Ishchenko (1958).

Remarks. The spores described above occur abundantly in the upper horizons of the Lower Carboniferous of Spitsbergen; they conform closely to the descriptions given by Waltz (in Luber and Waltz 1938) and by Ishchenko (1958) of respectively Zonotriletes velatus and Hymenozonotriletes velatus. The assignment of the species to Reticulatisporites (Ibrahim) by Potonié and Kremp (1955, p. 112) is clearly incorrect. It is here included within Camptozonotriletes Staplin 1960 on the basis of structure (spore with an equatorial flange) and prominent distal sculpture (irregular muri).

Previous records. Camptozonotriletes velatus (Waltz) comb. nov. has been recorded hitherto exclusively from the U.S.S.R. Luber and Waltz (1938, 1941) report its occurrence in Lower Carboniferous strata of the Moscow Basin and Selizharovo and Voronezh regions. According to the work of Ishchenko (1958) the species is present in Upper Devonian and Viséan rocks of the Dnieper–Donetz Basin, but apparently absent in the Tournaisian.

Genus DIATOMOZONOTRILETES (Naumova) emend.

1939 Diatomozonotriletes Naumova, p. 355; fig. 1.

1956 Reinschospora Schopf, Wilson, and Bentall, β section Diatomozonotriletes (Naumova) Potonié and Kremp, pp. 131–2.

1961 Diatomozonotriletes (Naumova) Potonié and Kremp 1956; Hughes and Playford, p. 40.

Emended diagnosis. Microspores radial, trilete; spore body triangular or subtriangular in equatorial outline. Laesurae usually well defined and long; simple or accompanied by lips. Spore body almost entirely encompassed by prominent zona (corona) consisting of numerous, strongly developed, mainly discrete saetae (fimbriae) emanating radially from equatorial margin of spore body. Saetae are particularly well developed in central interradial equatorial regions, characteristically exhibiting a gradual diminution in size towards the triangular apices of the spore, where they may be either absent or considerably reduced. Saetae pointed or blunt; sometimes fused, at least in part, but always remain recognizable individually within the corona as distinct structural entities. Spore body often sculptured, particularly on distal surface.

Type species (here designated). Diatomozonotriletes saetosus (Hacquebard and Barss 1957, p. 41; pl. 6, fig. 3) Hughes and Playford 1961.

Other species. The following species are now included within Diatomozonotriletes (Naumova) emend.

- 1. Diatomozonotriletes (al. Reinschospora) cervicornutus (Staplin 1960, p. 24; pl. 5, figs. 1-3) comb. nov. Occurrence: Canada (after Staplin 1960)—Golata formation, Alberta; Upper Mississippian.
- 2. Diatomozonotriletes (al. Zonotriletes) curiosus (partim) (Waltz in Luber and Waltz 1938, pl. 4, fig. 49; non pl. A, fig. 13) Ishchenko 1956. Occurrence: U.S.S.R. (after Luber and Waltz 1941)—Moscow Basin, Kizel, Selizharovo, and Voronezh regions; Lower Carboniferous. U.S.S.R. (after Ishchenko 1956, 1958)—western Donetz Basin, Dnieper-Donetz Basin; Viséan.
 - 3. Diatomozonotriletes hughesii sp. nov.
- 4. Diatomozonotriletes (al. Reinschospora) jubatus (Staplin 1960, p. 23; pl. 5, figs. 7, 8) comb. nov. Occurrence: Canada (after Staplin 1960)—Golata formation, Alberta; Upper Mississippian.
- 5. Diatomozonotriletes (al. Reinschospora) nahannensis (Hacquebard and Barss 1957, p. 41; pl. 6, figs. 1, 2) comb. nov. Occurrence: Canada (after Hacquebard and Barss 1957)—South Nahanni River area, Northwest Territories; Upper Mississippian.
- 6. Diatomozonotriletes (al. Reinschospora sect. Diatomozonotriletes) radforthi (Potonié 1956, p. 69; pl. 9, fig. 90) comb. nov. Occurrence: Canada (after Radforth and McGregor 1954, p. 605)—Wabumun Lake; age uncertain (see Radforth and McGregor 1956, footnote on pp. 27–28).
 - 7. Diatomozonotriletes rarus sp. nov.
 - 8. Diatomozonotriletes trilinearis sp. nov.
- 9. Diatomozonotriletes ubertus Ishchenko 1956, p. 100; pl. 19, fig. 242. Occurrence: U.S.S.R. (after Ishchenko 1956, 1958)—western Donetz Basin, Dnieper-Donetz Basin; Viséan to Lower Namurian.
- 10. Diatomozonotriletes (al. Zonotriletes) vesicarius (Waltz in Luber and Waltz 1941, p. 30; pl. 5, fig. 78) comb. nov. Occurrence: U.S.S.R. (after Luber and Waltz 1941)—Selizharovo region; Lower Carboniferous.

Discussion. In anticipation of the possible eventual recognition of Diatomozonotriletes Naumova as a distinct form-genus, Potonié and Kremp (1956a, pp. 131–2) proposed its subgeneric ('sectional') status within the category of Reinschospora Schopf, Wilson, and Bentall. Subsequently, Hughes and Playford (1961) incorrectly attributed generic rank to Diatomozonotriletes (Naumova) Potonié and Kremp 1956 (in Potonié 1956, p. 69), which lacks the designation of a type species.

Species recorded recently (by Ishchenko 1956, 1958; Hacquebard and Barss 1957; Staplin 1960; Hughes and Playford 1961), together with those described below, indicate the consistent presence in the Lower Carboniferous of a distinct group of *Reinschospora*-like spores possessing coronae of relatively coarse, strongly developed saetae. On the other hand, Upper Carboniferous representatives of

Reinschospora, for example the type species R. speciosa (Loose), are characterized by more delicate coronae consisting of a dense aggregation of much finer fimbriae. Such, indeed, is the criterion upon which Potonié and Kremp (1956a) based their sectional subdivision of Reinschospora. Thus the separation of Diatomozonotriletes from Reinschospora is warranted on morphographical grounds and appears also to have definite stratigraphical significance.

Comparison. Some species of Anapiculatisporites Potonié and Kremp 1954, for example A. serratus sp. nov., possess a strongly spinose equatorial margin which may simulate the zona of Diatomozonotriletes. In such cases, however, the sculpture visible at the margin represents an equatorial development of the predominantly distal, spinose sculpture of Anapiculatisporites. In Diatomozonotriletes, distal sculpture is subordinate and quite distinct from the structural components of its encompassing zona.

The present writer is in agreement with Potonié (1960, p. 60) concerning the 'problematical' nature of *Procoronaspora* Butterworth and Williams 1958. This genus appears to overlap the connotations of several previously instituted genera, such as *Lycospora*, but future work may possibly justify its recognition as a discrete form-genus. *Procoronaspora* is undoubtedly closely related to *Diatomozonotriletes* (Naumova) emend., but the 'fine grade' of its diverse sculpture ('grains, verrucae, spines, baculae, &c.') serves to distinguish it from the latter genus. As noted by Potonié (1960, p. 60), Butterworth and Williams's assignment of *Diatomozonotriletes curiosus* (Waltz) is incorrect.

Affinity. Unknown.

Diatomozonotriletes saetosus (Hacquebard and Barss) Hughes and Playford 1961

Plate 93, figs. 4-7

- 1938 Zonotriletes speciosus (non Loose) Waltz in Luber and Waltz, pp. 14–15; pl. 4, fig. 48, and pl. A. fig. 9.
- 1956 Diatomozonotriletes speciosus (non Loose) Ishchenko, pp. 99-100; pl. 19, figs. 239-41.
- 1957 Reinschospora saetosus Hacquebard and Barss, pp. 41-42; pl. 6, fig. 3.
- 1961 Diatomozonotriletes saetosus (Hacquebard and Barss) Hughes and Playford, p. 40; pl. 4, figs. 14, 15.

Description of specimens. Spores radial, trilete; spore body subtriangular with concave sides and rounded to truncated apices. Laesurae distinct, straight, extending almost to equatorial margin; simple or bordered by narrow, slightly thickened lips. Prominent corona comprising nine to fifteen discrete, typically pointed saetae projecting laterally from each interradial portion of the spore-body equator. Saetae $2.5-5 \mu$ broad at base, $3-22 \mu$ long; attain maximum length in central interradial region, diminishing uniformly towards smooth triangular apices. Spore body usually entirely laevigate, occasionally finely granulate on distal surface. Exine thick $(2-4 \mu)$, often distinctly thinner at apices.

Dimensions (85 specimens). Equatorial diameter of spore body 36-63 μ (mean 49 μ).

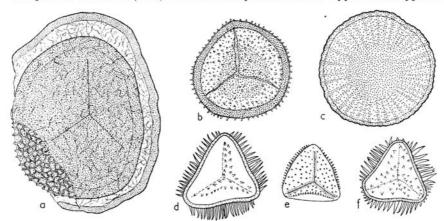
Holotype. As designated by Hacquebard and Barss (1957, p. 42).

Locus typicus. South Nahanni River area, Northwest Territories, Canada (after Hacquebard and Barss 1957); Upper Mississippian.

Previous records. Diatomozonotriletes saetosus has been recorded extensively from the U.S.S.R., as follows: Lower Carboniferous of the Moscow Basin and of the Selizharovo, Borovichi, and Kizel regions (Luber and Waltz 1938, 1941); Lower Viséan only of the

western Donetz Basin (Ishchenko 1956); Lower Carboniferous of the Melekess and Busuluk deep wells (Byvsheva 1957); Viséan–Namurian of the Dnieper–Donetz Basin (Ishchenko 1958); Yasnopolyansky substage (Lower Viséan) of the Saratov–Stalingrad Volga area (Loginova 1959); and Lower Carboniferous of the Volga–Ural region (Byvsheva 1960). Note that these Russian authors invariably incorrectly assign this species to Loose's species, i.e. *Reinschospora speciosa* (Loose) Schopf, Wilson, and Bentall.

Hacquebard and Barss (1957) described the species from the Upper Mississippian of



TEXT-FIG. 11. Camera lucida drawings; all magnifications × 500. a, Velosporites microreticulatus sp. nov.; proximal surface; preparation P163/7, 49·6 110·7 (L.1236). b, Spinozonotriletes balteatus sp. nov.; proximal surface; preparation P149A/3, 42·4 105·8 (L.1244). c, Radialetes costatus gen. et sp. nov.; preparation P159/5, 48·0 112·5 (L.1252). d, Diatomozonotriletes trilinearis sp. nov.; distal surface; preparation P149A/2, 26·9 108·5 (L.1227). e, D. rarus sp. nov.; distal surface; preparation P149B/2, 43·6 110·9 (L.1230). f, D. hughesii sp. nov.; distal surface; preparation P149B/1, 44·6 104·5 (L.1223).

Canada (see above), and Hughes and Playford (1961) reported some specimens from the Lower Carboniferous (sample B609) of Spitsbergen.

Diatomozonotriletes hughesii sp. nov.

Plate 93, figs. 8-11; text-fig. 11f

Diagnosis. Spores radial, trilete; amb subtriangular with rounded apices and concave to almost straight sides. Laesurae perceptible to distinct, simple, more or less straight, almost attaining equatorial margin. Well-developed corona consisting of eleven to seventeen large, mutually dissociated, uniformly tapering saetae projecting laterally from each side of the triangular amb, and having pointed, rarely divided apices. Saetae reach maximum size on centres of sides (up to 16μ long and 4μ in basal diameter); absent or commonly reduced to small coni on triangular apices of spore body. Distal surface of spore body distinctly echinate, bearing scattered, somewhat irregularly distributed

spines (length 2–6 μ); bases of spines rather bulbous (diameter 1–2 μ). Proximal surface laevigate. Exine 1-5–2 μ thick.

Dimensions (80 specimens). Equatorial diameter of spore body 30-47 μ (mean 39 μ).

Holotype. Preparation P149B/1, 47-3 107-6. L.1218.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype body diameter 46 μ ; saetae (interradial) 5–15 μ long; triangular apices of amb each bearing four to five coni, 2–3 μ long, 1·5 μ broad at base; distal spinae congregated in polar region, relatively sparse elsewhere, average length 5 μ ; exine 2 μ thick. This species is characterized by distinctly echinate distal sculpture, together with frequent development of small coni on the radial corners of the spore body.

Comparison. Diatomozonotriletes curiosus (Waltz) Ishchenko (1956, pp. 100–1; pl. 19, fig. 243) and 'Reinschospora sp. A' of Staplin (1960, p. 24; pl. 5, fig. 18) have finer, more numerous saetae.

Diatomozonotriletes trilinearis sp. nov.

Plate 93, figs. 12-14; text-fig. 11d

Diagnosis. Spores radial, trilete; amb subtriangular with straight to slightly concave sides, and rounded to truncated apices. Laesurae distinct, simple, straight, almost reaching equatorial margin. Seventeen to twenty-six closely spaced saetae project radially from sides of spore body amb constituting prominent corona, which is not developed at triangular apices. Saetae pointed, occasionally divided, mutually dissociated, basal diameter $1.5-2~\mu$, longest in central interradial region (up to $14~\mu$), exhibiting a slight, gradual reduction in size towards smooth apices of spore body. Distal surface bearing sharply tapered spinae, $2-4~\mu$ long, $1.5-2~\mu$ broad at base, characteristically congregated in a Y-shaped area, the orientation and radial extent of which conforms with that of the trilete mark on the opposite surface. Each limb of the 'Y' often consists of two parallel lines of spinae. Apart from this restricted spinose sculpture, spore body laevigate. Exine $1.5-2.5~\mu$ thick.

Dimensions (45 specimens). Equatorial diameter of spore body 35-56 μ (mean 45 μ).

Holotype. Preparation P149A/2, 33-5 95-6. L.1224.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype body diameter 50 μ ; coronal saetae 4–13 μ long, less than 1 μ apart; constituent spinae of Y-shaped, distal, sculptured area are less closely spaced in polar region.

Comparison. Type 63 of Reinsch (1884, p. 7; pl. 2, fig. 27) from the Russian (?Lower) Carboniferous may be conspecific with *Diatomozonotriletes trilinearis* sp. nov.

Diatomozonotriletes rarus sp. nov.

Plate 93, figs. 15, 16; text-fig. 11e

Diagnosis. Spores radial, trilete; amb subtriangular with slightly convex to slightly concave sides and rounded apices. Laesurae distinct, straight, length three-quarters of,

to almost equal to, spore-body radius; bordered by thickened, slightly elevated lips, individually about 2 μ wide. Equatorial corona consisting of discrete, closely spaced, pointed saetae attaining maximum size interradially (3·5–5 μ long, 1·5–2 μ in basal diameter) and diminishing gradually and uniformly towards the smooth triangular apices. Proximal surface of spore body laevigate; distal surface echinate, with numerous, small, fairly evenly distributed coni, 1·5–2 μ long, 1–1·5 μ broad at base, and 1·5–4 μ apart. Exine (excluding sculpture) up to 1 μ thick.

Dimensions (15 specimens). Equatorial diameter of spore body 37-48 μ (mean 42 μ).

Holotype. Preparation P145B/19, 38·3 103·4. L.1228.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype body diameter 39 μ ; distal coni reduced in size and density in equatorial region; laesurae conspicuously labiate. This distinctive but very rare species is characterized by relatively short, pointed, equatorial saetae, distal echinate sculpture, together with marked lip development.

Comparison. Diatomozonotriletes rarus sp. nov. is similar to D. curiosus (Waltz in Luber and Waltz 1938, pl. 4, fig. 49) Ishchenko 1956, which is distinguishable, however, in possessing longer saetae and simple laesurae.

Anteturma POLLENITES R. Potonié 1931
Turma SACCITES Erdtman 1947
Subturma MONOSACCITES (Chitaley) Potonié and Kremp 1954
Infraturma TRILETESACCITI Leschik 1955
Subinfraturma INTRORNATI Butterworth and Williams 1958

Discussion. Butterworth and Williams's (1958) suprageneric subdivision of monosaccate grains on the basis of predominantly either internal or external sculpture is

EXPLANATION OF PLATE 93

All figures ×500, and from unretouched negatives.

Figs. 1-3. Camptozonotriletes velatus (Waltz) comb. nov. 1, Proximal surface; preparation P164/15, 32·2 101·5 (L.1210). 2, Distal surface; preparation P149A/27, 38·7 104·4 (L.1211). 3, Proximal surface; preparation P157/4, 23·6 113·6 (L.1212).

Figs. 4–7. Diatomozonotriletes saetosus (Hacquebard and Barss) Hughes and Playford 1961. 4, Proximal surface; preparation P167B/10, 35·9 104·0 (L.1215). 5, Proximal surface; preparation P167B/4, 35·5 100·7 (L.1214). 6, Proximal surface; preparation P167A/2, 25·3 110·3 (L.1216). 7, Proximal surface; preparation P127/3, 53·7 96·9 (L.1217).

Figs. 8-11. Diatomozonotriletes hughesii sp. nov. 8, Proximal surface; preparation P149A/1, 28·2 113·3 (L.1219). 9, Proximal surface; preparation P149A/35, 32·7 102·0 (L.1220). 10, Holotype; distal surface. 11, Distal surface; preparation P157/2, 18·9 108·5 (L.1222).

Figs. 12–14. Diatomozonotriletes trilinearis sp. nov. 12, Holotype; proximal surface. 13, Distal surface; preparation P149B/1, 15·5 99·8 (L.1225). 14, Proximal surface; preparation P149B/2, 38·5 97·4 (L.1226).

Figs. 15, 16. Diatomozonotriletes rarus sp. nov. 15, Holotype; proximal surface. 16, Distal surface; preparation P145C/1, 30·3 106·6 (L.1229).

Figs. 17, 18. Endosporites micromanifestus Hacquebard 1957. 17, Proximal surface; preparation P145B/2, 24·5 94·3 (L.1232). 18, Proximal surface; preparation P174/2, 25·5 112·0 (L.1231).

undoubtedly of morphographical significance. However, in many cases the distinction is not readily ascertainable. Although Butterworth and Williams (1958) assigned their genus *Remysporites* to the Extrornati, Potonié (1960, p. 72) included it within the Intrornati since he considered that the often 'externally microreticulate' bladder appearance of this genus may well be due to the development of infrareticulate structure rather than to external sculpture of the exoexine. According to Potonié similar manifestation of internal bladder structure is evident in other genera (*Endosporites*, *Wilsonia*, *Guthörlisporites*, *Microsporites*). Hence, *Velosporites* Hughes and Playford 1961, which shows 'fine external sculpture' of the saccus, is also probably more correctly included within the Intrornati.

Genus ENDOSPORITES Wilson and Coe 1940

Type species. E. ornatus Wilson and Coe 1940.

Discussion. Richardson (1960, p. 49) has with justification drawn attention to the overlapping connotations of Auroraspora Hoffmeister, Staplin, and Malloy 1955 and Endosporites Wilson and Coe 1940. However, Richardson's statement that Auroraspora 'differs from Endosporites in the absence of a limbus' is questionable, since the original diagnosis of the latter genus (Wilson and Coe 1940, p. 184), which is still accepted unemended, and a recent morphological amplification of the type species (Wilson 1960) contain no reference to an equatorial bladder thickening (limbus). Admittedly, some authors (Potonié and Kremp 1954; Bhardwaj 1957; Chaloner 1953a, 1958b) have noted the characteristic presence of a limbus in representatives of Endosporites, and it is undoubtedly an important morphographical feature which may well have generic significance. However, there are many species included within Endosporites, and presently recognized as such, which appear to lack the development of a limbus. In all, therefore, a complete reappraisal of the type species of this and other related monosaccate genera (particularly Auroraspora) would seem advisable. Pending this, the present writer considers it preferable at this stage to retain the original generic assignment of the two species instituted by Hacquebard (1957), E. micromanifestus and E. macromanifestus, both of which Richardson (1960) transferred to Auroraspora.

Perhaps the least unsatisfactory distinction between *Auroraspora* and *Endosporites* was expressed by Hoffmeister, Staplin, and Malloy (1955b, p. 381) on the basis of relative thicknesses of bladder and body walls. According to these authors *Auroraspora* possesses a central body having a 'moderately thick wall' enclosed by a 'transparent and very thin bladder'; whereas in *Endosporites* the body wall 'approximates the bladder in thickness' (cf. Wilson 1960, pl. 1, fig. 5—explanation p. 31). As Richardson (1960, p. 49) implies, little diagnostic importance can be attached to actual or relative colour which is partially dependent upon preservation and maceration procedures.

Wilson (1960) has demonstrated conclusively that in *Endosporites ornatus* the central body is attached to the bladder on the proximal side only; this method of attachment was interpreted earlier by Potonié and Kremp (1954, p. 149; fig. 81).

Affinity. Chaloner (1953a, 1958b) has reported the occurrence of microspores very similar to *Endosporites globiformis* (Ibrahim) Schopf, Wilson, and Bentall 1944 in the lycopod cone *Polysporia mirabilis* Newberry 1873 (syn. *Lepidostrobus zea* Chaloner 1953a). Earlier, Schopf, Wilson, and Bentall (1944, p. 45) stated that 'Endosporites is

related to some of the Pennsylvanian Cordaitaleans' because of the presence of E. pelucidus-type spores within the strobilus Cordaianthus shuleri Darrah 1940. This attribution of Endosporites has been discounted by Wilson (1960, p. 31) because he has shown that E. pelucidus is more correctly assigned to the genus Florinites (see Wilson 1958).

Endosporites micromanifestus Hacquebard 1957

Plate 93, figs. 17, 18

1956 Hymenozonotriletes aff. variabilis Naumova; Ishchenko, p. 62; pl. 11, figs. 129, 130.

1957 Endosporites micromanifestus Hacquebard, p. 317; pl. 3, fig. 16. 1960 Auroraspora micromanifestus (Hacquebard) Richardson, p. 51.

Description of specimens. Spores radial, trilete; amb convexly subtriangular. Laesurae distinct, accompanied by elevated, rather irregular, flange-like lips that frequently extend to the equator. Central body thin, smooth, well defined; outline more or less conformable with amb. Bladder thin, often folded, infragranulate.

Dimensions (50 specimens). Overall equatorial diameter 42-95 μ (mean 67 μ); diameter of central body 28-65 μ (mean 44 μ).

Previous records. Described initially by Hacquebard (1957) from lowermost Misissippian strata of Nova Scotia, this species has been recorded subsequently from the Scottish Viséan by Love (1960) and from one sample (B685) of the Lower Carboniferous of Spitsbergen (Hughes and Playford 1961). It evidently occurs also throughout the Tournaisian-Viséan-Namurian succession of the western extension of the Donetz Basin (Ishchenko 1956, p. 62).

Genus REMYSPORITES Butterworth and Williams 1958

Type species. R. magnificus (Horst) Butterworth and Williams 1958.

Discussion. Contrary to the statement of Butterworth and Williams (1958, p. 386), the saccus in this genus is now considered to envelop the central body entirely (see discussion herein of Velosporites).

Affinity. Affinity with the Cycadofilices is suggested by the similarity between the type species and the spores borne by Paracalathiops stachei (Stur) Remy 1953 (see Butterworth and Williams 1958, p. 387; Potonié 1960, p. 72).

Remysporites albertensis Staplin 1960

Plate 94, fig. 3

Description of specimens. Spores radial, trilete; amb and body outline subcircular to circular. Smooth central body completely enveloped by loosely fitting bladder; both commonly folded, and probably attached at conspicuous proximal polar (contact) area. Contact area convexly subtriangular, distinctly sculptured with mixed rugulae and verrucae; bladder surface otherwise smooth. Central body and bladder walls both thin (about 1-1.5 μ). Laesurae distinct, simple, straight, length half to two-thirds central body radius.

Dimensions (25 specimens). Overall equatorial diameter 146–205 μ (mean 178 μ); diameter of central body 113–150 μ (mean 130 μ).

Comparison. The specimens conform closely with the diagnosis given by Staplin (1960, p. 35), except that they extend the size range considerably. However, Staplin does not state the number of specimens he measured, and in any case it seems likely that such large monosaccate species exhibit considerable size diversity, dependent probably upon mode of preservation and/or maceration (cf. Butterworth and Williams 1958, p. 388).

Previous records. From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

Genus VELOSPORITES Hughes and Playford 1961

Type species. V. echinatus Hughes and Playford 1961.

Discussion. This genus includes large monosaccate spores (as diagnosed by Hughes and Playford 1961, p. 42) characterized by relatively minor but distinctive body-wall sculpture. It is also important to state that a limbus may or may not be present.

According to Butterworth and Williams (1958, p. 386) the genus *Remysporites* is characterized by 'bladder enveloping central body except on proximal side'; and it was principally on this basis that Hughes and Playford (1961) decided to erect the genus *Velosporites* to incorporate a species rather similar to *Remysporites magnificus* (Horst) Butterworth and Williams but possessing comprehensive bladder envelopment. Recently, however, through the courtesy of Drs. M. A. Butterworth and A. H. V. Smith of the National Coal Board, the opportunity has been taken of examining the material from which Butterworth and Williams diagnosed *Remysporites*. As a result the present writer came to the conclusion—jointly with Dr. Butterworth—that the bladder in *R. magnificus* (the type species) does, in fact, envelop the central body entirely. This is substantiated further by a more recently described representative of *Remysporites*, *R. albertensis* Staplin 1960 (p. 35; pl. 8, figs. 8, 10), which is also recorded herein. The characteristic sculpture and relatively thick wall of the central body, exhibited by the two species recorded below, is, however, considered sufficient to justify the continued recognition of *Velosporites* as a distinct form-genus.

Affinity. Unknown.

Velosporites echinatus Hughes and Playford 1961

Plate 94, fig. 1

Remarks. The surface of the central body characteristically bears minute, sparsely distributed coni or very low, mound-like elevations, which are often evident only under oil immersion. The bladder is commonly folded on both large and small scale, the latter resulting in a microrugulate effect.

Dimensions (80 specimens). Overall equatorial diameter $102-194 \mu$ (mean 140μ); diameter of central body $70-128 \mu$ (mean 100μ).

Velosporites microreticulatus sp. nov.

Plate 94, fig. 2; text-fig. 11a

Diagnosis. Spores radial, trilete; monosaccate; amb circular to oval, more or less entire. Laesurae simple, straight, length approximately four-fifths central body radius, not evident on bladder. Central body distinct, circular to subcircular, thick-walled $(4-9 \, \mu)$; distinct, finely reticulate sculpture of very narrow, pointed muri up to $1.5 \, \mu$ high, enclosing small, polygonal lumina which are $1.5-7 \, \mu$ broad (average $3.5 \, \mu$); surrounded completely by thin, transparent bladder. Bladder extending $9-27 \, \mu$ beyond central body margin; definite equatorial thickening (limbus) $3-6.5 \, \mu$ wide, smooth, imposing comparative rigidity to bladder. Bladder often densely microrugulate or vermiculate, frequently corroded or torn, thickness about $0.5 \, \mu$.

Dimensions (16 specimens). Overall equatorial diameter $100-140\,\mu$ (mean $118\,\mu$); diameter of central body $73-102\,\mu$ (mean $88\,\mu$).

Holotype. Preparation P163/7, 22-3 94-7. L.1235.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype 120 μ overall, subcircular; central body 92 μ in diameter, 5 μ in thickness, circular, colour much darker than bladder; bladder partially removed thereby revealing detail of conspicuous microreticulate sculpture of central body; limbus 6 μ wide.

Subturma POLYSACCITES Cookson 1947 Genus ALATISPORITES Ibrahim 1933

Type species. A. pustulatus Ibrahim 1933.

Affinity. Unknown.

Alatisporites tessellatus Staplin 1960

Plate 95, fig. 10

Description of specimens. Spores radial, trilete. Central body circular, finely and densely rugulate. Laesurae indistinct, simple, straight, length half to two-thirds body radius. Approximately seven to eight thin, overlapping, frequently strongly folded bladders are prominent equatorially but attached to distal surface of body.

Dimensions (17 specimens). Overall equatorial diameter 75–109 μ (mean 87 μ); body diameter 52–61 μ (mean 56 μ).

EXPLANATION OF PLATE 94

All figures \times 500, and from unretouched negatives.

Fig. 1. Velosporites echinatus Hughes and Playford 1961. Proximal surface; preparation M811/5, 58·2 108·9 (L.1234).

Fig. 2. Velosporites microreticulatus sp. nov. Holotype; proximal surface.

Fig. 3. Remysporites albertensis Staplin 1960. Proximal surface; preparation P149A/15, 40·4 100·1 (L.1233).

Figs. 4-6. Spinozonotriletes uncatus Hacquebard 1957. 4, Proximal surface; preparation P175/2, 42-8 108-9 (L.1238). 5, Proximal surface; preparation P148/5, 38-8 93-0 (L.1240). 6, Distal surface; preparation P148/51, 39-1 107-0 (L.1237).

Remarks. Apart from extending the range of overall size, the Spitsbergen specimens conform very closely to the diagnosis given by Staplin (1960, p. 31; pl. 7, fig. 10).

Previous records. Described initially from the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

Turma Aletes Ibrahim 1933 Subturma Azonaletes (Luber) Potonié and Kremp 1954 Infraturma RETICULONAPITI (Erdtman) Vimal 1952 Genus RETIALETES Staplin 1960

Type species. R. radforthii Staplin 1960.

Discussion. In his diagnosis of this genus, Staplin (1960, p. 6) states: 'spores alete, but sometimes split along a few fine grooves that originate at one end and parallel the long axis'. Similar but usually more extensive splitting has been observed in certain Mesozoic microspores, e.g. Schizosporis Cookson and Dettmann 1959 and Psophosphaera Naumova (in Bolkhovitina 1959). In Retialetes, rupturing, when present, is always longitudinally situated, and suggests a possible mechanism for germination.

Affinity. Unknown.

Retialetes radforthii Staplin 1960

Plate 95, figs. 1-3

Description of specimens. Spores alete, ellipsoidal. Comprehensive reticulate sculpture comprised of rounded or flat-topped, low, smooth muri (1–3 μ high, 1–2·5 μ broad) enclosing subcircular to polygonal lumina 4–22 μ in longest diameter (usually about 8 μ). Exine (excluding muri) 3–5 μ thick; often split along one, occasionally two or more, narrow grooves that parallel the long axis of the spore.

Dimensions (25 specimens). $102-182 \mu$ (mean 144μ) by $66-107 \mu$ (mean 84μ).

Previous records. This distinctive species was originally described by Staplin (1960) from the Upper Mississippian Golata formation of Alberta, Canada.

Genus RADIALETES gen. nov.

Type species. R. costatus sp. nov.

Diagnosis. Microspores radial, alete. Outline circular or subcircular. Distinctive sculpture consisting of radially disposed muri or incipient thickenings which thus give the spores an overall radiating appearance. Muri sometimes considerably diminished towards central portions of spores.

Comparison. The spore illustrated by Hoffmeister, Staplin, and Malloy (1955a, pl. 3, fig. 7) as 'Radiaspora' sp. has similar, albeit exclusively distal, sculpture but differs from Radialetes gen. nov. in being distinctly trilete. As noted by Potonié (1956, p. 42), Radiaspora has yet to be validated as a generic name. Radialetes is distinct from Aumancisporites Alpern 1958 (p. 84), which is sculptured with more or less parallel grooves disposed transversely with respect to the long axis of the spore. Undulatasporites Leschik 1955 (p. 28) has irregular rugulate sculpture.

Affinity. Unknown.

Radialetes costatus sp. nov.

Plate 95, figs. 7-9; text-fig. 11c

Diagnosis. Spores radial, alete. Outline circular to subcircular; commonly distorted due to folding. Both surfaces sculptured with more or less distinct, low, non-anastomosing, radially disposed muri which attain maximum development at the margin, and may be lacking or considerably diminished centrally; muri $1.5-5 \mu$ broad, $1-3 \mu$ apart, up to 2μ high. Folding of exine usually results in marked apparent discordance of muri on opposing surfaces producing an overall 'cross-hatched' effect. Exine (including sculpture) $2-6 \mu$ thick; apart from muri, laevigate to finely granulate or punctate.

Dimensions (50 specimens). Diameter 42-117 μ (mean 70 μ).

Holotype. Preparation P145B/38, 40·7 105·9. L.1249.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype 48 μ , circular; conspicuous radial muri 1·5–3 μ broad, 1–1·5 μ high, 1·5–3 μ apart; muri do not extend to central portion of either surface; exine otherwise laevigate, total thickness 2 μ .

Remarks. This distinctive, alete species, characterized by simple, radially disposed muri, has not been recorded in available literature. It shows considerable size variation, but is otherwise morphographically constant. R. costatus sp. nov. occurs in many of the Spitsbergen Lower Carboniferous samples, but is always a minor constituent.

INCERTAE SEDIS

Genus SPINOZONOTRILETES Hacquebard 1957

Type species. S. uncatus Hacquebard 1957.

Discussion. This and several other genera were instituted by Hacquebard (1957, pp. 314–15) as convenient subdivisions of the broad subgroup Archaeozonotriletes Naumova 1953. Both Naumova and Hacquebard used the term 'perispore' to denote the usually strongly developed, often conspicuously sculptured outer membrane which encloses and frequently almost obscures the central body of many of the spores embraced by the subgroup. It is, however, highly questionable whether a true perispore (perine), as usually understood (cf. Erdtman 1952; Harris 1955), is represented.

Potonié (1960, p. 42) suggested that the 'central body' seen in *Spinozonotriletes* may be a mesospore, a feature which, according to Potonié (1958, p. 21), is present also in the type species of *Grandispora* Hoffmeister, Staplin, and Malloy 1955.

From text-figs. 5, 6c of Richardson (1960) it is evident that his genus Ancyrospora shows wall features similar to those of Spinozonotriletes. Richardson (p. 55) applied the term 'bladder' to the thick, strongly sculptured, outer membrane (which he regarded as the exoexine) enveloping the central body (intexine), and thus assigned Ancyrospora to the Monosaccites. There seems to be considerable doubt, however, as to whether the outer enveloping layer of the exine in these spores is truly comparable to the exoexine (bladder) of typical Palaeozoic monosaccate types (e.g. Endosporites, Remysporites, Velosporites). Thus until further work is done on the structure of such forms as Spinozonotriletes, their non-committal suprageneric assignment seems preferable.

Grandispora was described by Hoffmeister, Staplin, and Malloy (1955) as possessing a 'central body wall only slightly thicker than the bladder wall', a feature which together with its constantly subcircular amb permits clear discrimination from *Spinozonotriletes*.

Affinity. Unknown.

Spinozonotriletes uncatus Hacquebard 1957

Plate 94, figs. 4-6

Description of specimens. Spores radial, trilete; amb convexly subtriangular. Laesurae with prominent, folded, flange-like lips (up to $5\,\mu$ wide and $7\,\mu$ high) extending to equator. Exoexine conspicuously sculptured with large, simple spines which are particularly frequent around the equatorial regions, less abundant in the polar areas; some specimens were noted in which the spines were reduced or absent on finely granulate contact areas. Spines have broad, circular bases (2–6 μ wide) which often appear rather bulbous in lateral view; length 4–19 μ . This wide variation in spine dimensions is between specimens rather than within specimens, which individually bear spines of markedly uniform size. Exoexine thickness 3–5·5 μ (exclusive of spines); commonly folded. Intexine rather indistinct, more or less conformable with equatorial outline, diameter roughly three-quarters overall diameter.

Dimensions (66 specimens). Overall equatorial diameter (exclusive of spines) 74–150 μ (mean 104 μ). This is closely conformable with the size range stated by Hacquebard (1957, p. 316).

Comparison. Spinozonotriletes uncatus may be conspecific with Acanthozonotriletes senticosus Ishchenko 1956 (p. 87; pl. 16, fig. 200), which is somewhat smaller $(67-70 \mu)$, but is otherwise very similar.

Previous records. From the Horton group (lowermost Mississippian) of Nova Scotia, Canada (Hacquebard 1957). The possibly identical species *Acanthozonotriletes senticosus* is confined to Tournaisian strata of the western Donetz Basin (Ishchenko 1956).

Spinozonotriletes balteatus sp. nov.

Plate 95, figs. 4-6; text-fig. 11b

Diagnosis. Spores radial, trilete; amb roundly subtriangular to oval. Laesurae obscured by elevated, narrow, membranous, flange-like lips, frequently contorted due to compression and extending to limbate equatorial margin. Intexine indistinct to perceptible, roundly subtriangular. Distal surface of exoexine densely and uniformly sculptured with small, simple spinae which sometimes coalesce to form a rugulate pattern; spines usually evident at equator, sparsely scattered to absent on proximal surface. Spines have rounded to polygonal bases (diameter $0.5-2.5 \mu$); length $1-2 \mu$. Equatorial margin of exoexine marked by well-defined limbus $3.5-7 \mu$ broad in polar view.

Dimensions (40 specimens). Overall equatorial diameter $51-102 \mu$ (mean 73μ); diameter prescribed by intexine $30-59 \mu$ (mean 42μ).

Holotype. Preparation P149A/3, 30.5 97.5. L.1241.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype 77 μ overall, irregularly roundly subtriangular; sinuous laesurate lips extend to conspicuously limbate margin; intexine perceptible, 44 μ in diameter; distal surface of exoexine covered with small, crowded spinae which are often coalescent at their bases; apart from spines, exoexine laevigate. Obliquely compressed specimens common; in such cases the limbus appears as a well-defined, dark, transgressive band, marking the true equatorial margin.

Remarks. This species, characterized by the presence of a limbus and of predominantly distal spinose sculpture, appears unparalleled in available literature. On the basis of its exoexinal sculpture and somewhat obscure intexine, the species finds suitable inclusion within *Spinozonotriletes* Hacquebard.

Genus TETRAPORINA Naumova 1939 ex Naumova 1950

Type species. T. antiqua Naumova 1950 (designated by Potonié 1960, p. 130).

Discussion. This genus, recently validated by Potonié (1960), was instituted by Naumova (1939, p. 357) as a subgroup of her group Tetraporosa, which she included within the class Porosa Naumova. The original diagnosis of Tetraporina stated 'pollen with four pores, without folds', and according to Naumova the class Porosa 'belongs exclusively to the Angiospermae'. Subsequently, Naumova (1950) and Teteriuk (1956) have described a number of Russian Lower Carboniferous species of Tetraporina, and reaffirmed their belief in the angiospermous affinity of such forms. More recently, the names Azonotetraporina and Zonotetraporina were introduced by Teteriuk (1958, pl. 1 explanation) merely as captions to some drawings of further Lower Carboniferous Tetraporina-like spores, and must therefore at this stage be considered nomina nuda. Thus Staplin's (1960, p. 6) usage of Azonotetraporina as a valid generic entity is unacceptable. Furthermore, from the figures given by Teteriuk (1958) it seems likely that the forms were differentiated only on the basis of wall thickness.

Tetraporina Naumova is rather an unsatisfactory taxon in that the supposedly diagnostic four 'pores' are often either incompletely or not developed; this is apparent from both Naumova's and Teteriuk's illustrations and also from the Spitsbergen specimens described below. These latter represent an interesting new Lower Carboniferous occurrence, but are insufficient basis for the seemingly necessary, comprehensive reappraisal of the genus, the most significant feature of which appears to be constantly quadrangular shape.

Affinity. The angiospermous attribution (Naumova 1939, 1950; Teteriuk 1956, 1958) of Tetraporina has been regarded doubtfully by many subsequent authors (Staplin 1960, p. 6; Scott, Barghoorn, and Leopold 1960, p. 287; Hughes 1961, p. 89). Certainly the brief descriptions and line drawings of the Russian forms are inadequate for a critical assessment of botanical affinity. The possible algal affinity of the genus was discussed recently by Scott et al. (1960, p. 287), who noted its close morphological similarity with species of the unicellular green alga Tetraëdron. Valuable support in this connexion is apparent from a paper by Churchill (1960), who figured a number of Cainozoic and living unicellular algae and aplanospores; of his illustrations, fig. 1, nos. 3, 4, 6, 8, 11, 12, and 13 show striking superficial resemblance to Tetraporina. Moreover, Dr. Churchill

has kindly examined the specimens described below and he considers that there is little doubt of their algal affinity.

Tetraporina incrassata Naumova 1950

Plate 95, figs. 12, 13

Description of specimens. Spores alete; outline quadrangular with distinctly concave sides and rounded corners. Exine scabrate to almost smooth, generally about 2 μ thick; locally \pm conspicuously thickened at corners, which may occasionally show aperture-like perforations.

Dimensions (12 specimens). Diagonal length 46-70 μ (mean 60 μ).

Previous records. From the Lower Carboniferous of the Moscow Basin (Naumova 1950).

Tetraporina glabra Naumova 1950

Plate 95, fig. 11

Description of specimens. Spores alete; outline quadrangular with concave sides and rounded angles. Exine uniformly thick (3 μ), laevigate. In the figured specimen one minute perforation is present in the vicinity of each corner; the other specimens encountered appear non-perforate.

Dimensions (3 specimens). Diagonal length $50-54 \mu$.

Previous records. From Lower Carboniferous deposits of the Moscow Basin (Naumova 1950).

Tetraporina horologia (Staplin) comb. nov.

Plate 95, figs. 14, 15

1960 Azonotetraporina? horologia Staplin p. 6; pl. 1, figs. 4, 6.

Description of specimens. Spores alete; outline quadrangular with concave to almost straight sides and rounded corners. Exine thin, hence readily folded and distorted; surface finely granulate to slightly roughened. Apertures rarely evident, but often simulated by arcuate folds at the corners.

Dimensions (14 specimens). Diagonal length 44-71 μ (mean 56 μ).

Remarks. As discussed above, Azonotetraporina Teteriuk is not a valid genus and in any case appears to be a misconceived subdivision of Tetraporina Naumova. Accordingly Staplin's species, which was questionably referred to Azonotetraporina, is here transferred to Tetraporina.

Comparison. Tetraporina glabra Naumova 1950 (pl. 1, figs. 5, 28) is thicker-walled, but otherwise similar to T. horologia (Staplin) comb. nov.

Previous records. From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

MICROFLORAL ASSEMBLAGES AND STRATIGRAPHICAL APPLICATIONS

The primary object of this section is to assess the stratigraphical significance of the microfloral elements, described above, of the Lower Carboniferous succession of Spitsbergen. It will be shown below that two distinct, successive, microfloral suites (assemblages) are distinguishable, each characterized by a number of distinctive microspore species of restricted stratigraphical ranges and hence of considerable correlative value both within and outside Spitsbergen. Evidence will be adduced as to the age of these assemblages, with reference to the standard European stage subdivisions of the Carboniferous, on the admittedly indirect basis of Russian and North American microfloral parallelism.

As noted previously, the microfloras examined in the present study have been recovered from a wide variety of lithologies (especially clastic rock types), and are thus probably fairly representative of the overall contemporary flora. Collecting has been insufficiently detailed, however, to permit palaeoecological inferences based upon quantitative/ qualitative studies of the microflora observed throughout a limited stratigraphical succession (cf. Neves 1958).

Delineation of microfloral assemblages

Detailed study of microfloras contained in samples collected from the three successions, at Birger Johnsonfjellet, Triungen, and Citadellet (see text-fig. 2), has given an overall picture, as comprehensive as sampling intervals permit, of the microfloral succession in the Spitsbergen Lower Carboniferous. Tables 1 and 2 list all the microspore species present in the samples from these localities; in the preparations of most samples, abundance and sufficiently good preservation of the microfloral elements has permitted representation on a quantitative basis, resulting from a count of 250 specimens per sample. It will be evident from these Tables that, whilst many species are ubiquitous, a fairly large number possess restricted vertical distribution. A more or less uniform microfloral suite occurs in samples from the lower parts of the Birger Johnsonfjellet and Triungen sections and in the entire collected Citadellet section (see Table 1). This distinctive suite is here conveniently designated as the Rarituberculatus Assemblage. The

EXPLANATION OF PLATE 95

All figures × 500, and from unretouched negatives.

Figs. 1-3. Retialetes radforthii Staplin 1960. 1, Preparation P155/7, 36·0 106·0 (L.1246). 2, Showing longitudinal rupture; preparation P155/13, 33.9 105.2 (L.1247). 3, Preparation P155/10, 36.9 103·3 (L.1248).

Figs. 4-6. Spinozonotriletes balteatus sp. nov. 4, Holotype; distal surface. 5, Tetrad; preparation P149A/1, 26·4 100·4 (L.1243). 6, Proximal surface; preparation P145B/1, 17·9 95·6 (L.1242).

Figs. 7-9. Radialetes costatus gen. et sp. nov. 7, Preparation P163/1, 38·7 107·9 (L.1250). 8, Preparation P145B/7, 35·2 106·0 (L.1251). 9, Holotype.

Fig. 10. Alatisporites tessellatus Staplin 1960. Proximal surface; preparation P163/2, 40·4 113·5 (L. 1245).

Fig. 11. Tetraporina glabra Naumova 1950. Preparation P145B/5, 35·5 104·2 (L.1255). Figs. 12, 13. Tetraporina incrassata Naumova 1950. 12, Preparation P139/4, 30·1 103·6 (L.1253). 13, Preparation P145A/1, 44·7 102·6 (L.1254).

Figs. 14, 15. Tetraporina horologia (Staplin) comb. nov. 14, Preparation P181/3, 32·1 105·5 (L.1256). 15, Preparation P202/3, 31.9 97.7 (L.1257)."

microspore	BI	RGER	JOH	NSON	FJELL	ET	TRIU	NGEN		CITADELLET								
species	01086	G1087	G1088	G1089	G1090	G1091	G1473	G1472	G1445	G1446	G1448	G1450	G1451	G145				
Chaetosphaerites pollenisimilis								×										
Leiotriletes inermis L. subintortus var. rotundatus L. ornatus L. microgranulatus	x x	2.0 x	0.4 1.6	2.8 0.4	x	3.6 x 1.6	1.2 x	2.4 x x	4.4 x o.8	1.6 1.2 0.4	4.4 2.0 0.8	5.2 2.0 1.6 0.8	2.4 1.6 0.8 0.8	4. 4. 1. 4.				
Punctatisporites glaber P. parvivermiculatus P. labiatus P. pseudobesus	×	3.6	2.8 x	2.8 2.0 0.4	x	3.6 1.6 x	0.4	1.6 x x 0.4	5.6 0.4 x	6.4	7.2 X 0.4	10.0 2.0 1.6	5.6	8.1				
Calamospora microrugosa	x	2.4	2.0	1.2		0.8	1.2	0.8	3.2	2.8	3.6	3.2	4.0	2.				
Phyllothecotriletes rigidus			x			x			1.2		0.8	×	2.8	2.8				
Granulatisporites planiusculus	x					- 100												
Cyclogranisporites lasius C. flexuosus	×	2.4	0.4			0.4	U	0.4	3.2 x	1.6	5.6	5.2	2.8	2.				
Verrucosisporites gobbettii				x	x			x			0.4	1.2	1.2	1.:				
Lophotriletes coniferus						x			4.4	1.2	x	0.4	×	Х.				
Apiculatisporis macrurus	-	-	-	0.4	-	_	3.2	0.4	-		0.4	0.8						
Acanthotriletes multisetus A. mirus				×				0.8 x	2.4	11.2	12.0 x	6.4	5.2	4.8 x				
Convolutispora tuberculata C. vermiformis C. harlandii C. crassa	×	4.8	0.4	3.6 2.0 2.0 0.4	x	1.2	0.8 6.8	0.8 0.4 2.8 0.4	3.6	1.6 3.2 0.8	1.2 1.6 0.4	4.4 1.6 0.4 0.8	2.8 0.8 1.6	0.4				
Microreticulatisporites lunatus				0.8		0.4	0.8	0.4			1.6	2.8	2.0	0.8				
Dictyotriletes caperatus		217	×	0.4				2.8	0.8	1.2	0.8	-		9				
Reticulatisporites cancellatus R. planus		0.4	0.8	4.8	x	0.8 x		12.8	0.8	0.8	0.8 x	х	2.8	1.				
Perotrilites perinatus P. nagnus	×	2.0	0.4	1.2	x	0.4	0.4	0.4	1.2 x	1.6	1.2 x	1.2	0.4	0.				
Triquitrites batillatus					x	1.6					303							
Tripartites incisotrilobus				19.2	x	2.8		2.8			0.4	1.2	2.8	7.6				
Stenozonotriletes stenozonalis S. facilis var. praecrassus S. simplex S. inductus S. clarus S. perforatus S. perforatus S. cf. spetcandus	×××	2.0 *	x 3.2	0.4 x 0.8 x		x	1.6 x 0.4 2.0	x 0.8	2.4 0.8 × 0.4 0.8	0.8 1.6 0.4 2.0	0.4 x	x	x					
Murospora intorta M. conduplicata S. sublobata	×	2.0		3.6		1.6 x		0.8	×	0.4	4.4	x 0.8	1.6	1.6				
Anulatisporites anulatus A. labiatus A. orbiculatus A. canaliculatus			3.2	3.2 x	x x	6.4 1.6	10.8	8.0 x 0.8	18.8	8.4	5.2 2.8	2.4 0.4 x 0.8	3.2 5.2 x	2.4 0.8				
Densosporites dentatus D. intermedius D. variabilis		21.2	2.4 x	2.4	x	36.0	30.4	1.6 0.4 1.2	x	0.4	4.0 0.8	4.8	6.4	4.8 6.4 3.2				
D. striatiferus D. spitsbergensis D. variomarginatus		2.8	2.8 8.4	16.8	x	8.0		1.6	•	1.2	3.6	3.6 6.4	5.6 16.8	10.8				
Labiadensites fimbriatus				1.2				0.4					×	0.4				
Knoxisporites cinctus K. margarethae K. literatus K. hederatus		0.8		0.8 1.6		0.8 1.6	0.4	0.4 x	1.6 2.8 0.4	6.0	0.8 X 0.4	0.4 0.8	x 0.4 0.8	x 8.0 8.0				
Cristatisporites echinatus								x	- 1			x	×	×				
Lophozonotriletes rarituberculatus L. dentatus L. varivernucatus	x	7.2	1.2	2.8	x	0.8 x	0.4	0.4	4.4 1.6 1.2	2.8 x 2.4	0.8	0.8	0.8	0.8 x				
Tholisporites foveolatus	-	3.6	43.6	2.4			14.8	26.0	18.4	22.0	2.0	0.8	0.8					
Endosporites micromanifestus		2.4	0.4	0.4		x		×	0.8	0.8	4.4	5.2	1.2	2.4				
Velosporites echinatus V. microreticulatus		0.4	0.4	0.8		0.4	6.0	×	×	0.8	0.4 X	×	0.4	×				
V. microreticulatus Spinozonotriletes uncatus				x		-	0.4	1.2		×	×	1.2	0.4	1.2				
Alntisporites tessellatus				0.4										×				
Radialetes costatus			0.4	x		x	x	x	X.	0.8	0.4		х	0.4				
Tetraporina incrassata T. horologia						x								×				

TABLE 1. Microspore distribution in samples from the Citadellet succession and from the lower parts of the sections exposed at Birger Johnsonfjellet and Triungen. In most samples, constituent species are recorded as percentages, which are based upon individual counts of 250 specimens. Indeterminable specimens in each case comprise the percentage complementary to that of specifically determinable specimens. '×' indicates observed presence in a particular sample, but not in actual count. Relatively sparse and poorly preserved spores were recovered from samples G1086 and G1090, and hence neither was considered suitable for quantitative specific estimation. Correction: for *Densosporites intermedius* read *D. diatretus* (see p. 623).

microspore		BIR	GER	JOH	NSO	NFJE	LLET	P .			TR	IUNG	EN		
species	01092	01093	G1095	01096	G1098	G1099	G1101	01102	G1471	G1470	G1469	G1468	G1467	G1466	G14
Chaetosphaerites pollenisimilis	0.4	1.2		2.4	1.2	x		0.4	-	0.4			x	3.6	
Leiotriletes inermis L. subintortus var. rotundatus	1.6	0.8	1.6	2.4	2.0	x	x	0.8		0.8	x	x x	1.6	0.4	,
L. ornatus L. curiosus	0.4	^	2840	1.2	x	•	•	1.6	×	0.8		0.4	×	0.4 X	
Punctatisporites glaber P. parvivermiculatus	0.8	0.4	1.2	3.2	1.2	X-		2.4	×	5.6 4.8	x	1.2	2.0	0.8	
P. pseudobesus P. stabilis	1.2	0.4	x	0.4						1.000	ļ.,		x	2.0	
Calamospora microrugosa	0.8	0.4	0.8	2.4	0.4		x	0.4	x	2.8		2.0	2.4	1.2	_
Phyllothecotriletes rigidus	x	x	x		x	x		x	x	0.4		x	0.4	x	Н
Waltzispora lobophora W. albertensis W. sagittata				x	*			0.8 x		*			x	0.4 6.4	
Cyclogranisporites lasius C. flexuosus	x x	x	0.4	0.8	x	x		0.4			x	5.2	0.8	x	
Verrucosisporites eximius					x	x	x			0.8			0.4	X	
Anapiculatisporites concinnus A. serratus			0.4					1.2		0.8	x			8.8	
Acanthotriletes multisetus												0.4			
Hystricosporites sp.			2.0			7	×		×	0.4	x	36.0	2.4	×	
Convolutispora tuberculata C. clavata C. harlandii C. crassa	2.0 x	0.4 x	0.8		x		×		x	0.4		36.0	x		
C. labiata C. usitata	0.4			0.4	x					0.8	x		x		
Microreticulatisporites lunatus	x		0.4		x					х	х				
Reticulatisporites rudis R. cancellatus R. variolatus R. peltatus	4.4 1.6	2.0	2.8 0.8 x	2.4	0.4 x	x	x	2.0 x x	×	0.8 0.4 0.4	x	x	x x x	0.4 x x	
R.? sp. Poveosporites insculptus			0.4		0.4	x		x	×	4.4	×	0.8	4.0	x	
Perotrilites perinatus P. magnus	x	0.4	o.8			_			x	x					
Triquitrites trivalvis T. batillatus	5.6	1.2	0.8	0.4	0.8	x	x	0.8	-	0.4			0.4	0.4 X	
Tripartites incisotrilobus	1.2	1.2	0.4	0.4	2.8	x	x	0.8		0.8		1.2	0.8	1.2	
T. complanatus Stenozonotriletes clarus	- ×	-	_		x	10000	×	X	x	x	-		0.4	0.4	
S. facilis var. praecrassus S. perforatus S. cf. spetcandus	0.4	0.4	x x							×			×	x	
Murospora intorta M. aurita	0.8	0.4 24.8 0.4	0.4 4.8 1.2	0.4	0.8	x x	×	7.2	x	1.2		0.4	0.4 0.4	5.2	,
M. conduplicata M. sublobata	0.4	0.4	1.2 x	0.4	0.4	x x	x	0.4 X	x	0.4	x	0.8 x	0.4 X	5.2 2.0 1.2	
M. dupla M. strigata			1		x	x	15555	100111						0.4	
M. tripulvinata M. friendii		2.0			x	×		x		0.4		0.4		0.4	
Anulatisporites anulatus A. labiatus	1.2	0.8	4.8	2.0	0.4	x	×	0.4	x	2.0		1.2	4.0 X	0.8	
A. lablatus Densosporites bialatus D. dentatus			18.4	1.6	0.8	×		1.2		8.4		0.8	0.8	1.2	
D. subcrenatus	3.2	2.0	12.0	2.0	4.0 X	×	×	4.0 x	x	×	×	x	0.4	0.8	
D. intermedius D. variabilis	3.6	6.8	16.8	1.2	4.0		x	1.6	x	3.6	x	0.8	46.0	6.4	
D. duplicatus D. spitsbergensis	10.0	13.2	3.6	2.0		x	x	0.4	x	1.2	×	0.8	0.8	×	
D. rarispinosus D. aculeatus		100	2.4	×	0.8	×		4.4 x	x	0.8	x		0.8	2.4	
D. sp. Labiadensites fimbriatus	5.6	0.8	0.8	x	0.4	x	x	x	x	x		6.4	2.0	0.4	
Knoxisporites cinctus K. margarethae	x		1.2									7.0505	Quanta I	in the	
K. literatus	6.4	11.2	2.4	25.0	x	x	x	0.8	-	5.6	x	2.4	2.4	32.4	-
Lycospora uber Lophozonotriletes appendices	+	-	2.0	56.8	43.2	x	x	61.2	x	0.4	x	2.4	0.4	1.6	
Monilospora triungensis										0.4				0.4	
M. dignata	-	-	-	-	1.2	×		0.4		x	-		0.4	0.8 x	
Potoniespores delicatus Cirratriradites solaris			×		21.2	^		×					5.4	x	
C. elegans Camptozonotriletes velatus	2.4	0.4	2.0	x		-	-	×	×	1.6	×	0.4	1.2	x	
Diatomozonotriletes velatus	1		x		1.6	x	x	0.4						x	
D. hughesii D. trilinearis D. rarus			×	×		x	x	0.8	x	6.0 4.0		0.8	0.8	2.4 0.4 x	
Endosporites micromanifestus	x		0.4	x	x	x	x	0.4	-	-	-		×	x	-
Remysporites albertensis	-	-	+	-		-	-		-	×	-	_	x	-	
Velosporites microreticulatus Spinozonotriletes balteatus	×	1	+-	-		-		-		13.6	x	21.6	0.8	2.8	
Alatisporites tessellatus				0.4				х							
Retialetes radforthii							x							х	-
Radialetes costatus	-	1.2	0.4	-	-	-	-		. x	x	-		0.4	x	\vdash
Tetraporina incrassata T. glabra T. horologia										x				0.4	

TABLE 2. Microspore distribution in Birger Johnsonfjellet and Triungen samples succeeding those documented in Table 1. In most samples, constituent species are recorded as percentages, which are based upon individual counts of 250 specimens. Indeterminable specimens in each case comprise the percentage complementary to that of specifically determinable specimens. 'x' indicates observed presence in a particular sample, but not in actual count. Counting was precluded in samples G1099, G1101, G1471, G1469, and G1465, owing to sparse occurrence and/or poor preservation of the recovered spores. Correction: for *Densosporites intermedius* read *D. diatretus* (see p. 623).

younger microfloral suite, termed the Aurita Assemblage, is present in samples from Birger Johnsonfjellet and Triungen, immediately succeeding those documented in Table 1. It includes many species unknown from the Rarituberculatus Assemblage and lacks a considerable number characteristic of the latter. The detailed microfloral analysis of the samples from Birger Johnsonfjellet and Triungen which contain the Aurita Assemblage is presented in Table 2. This microfloral subdivision is not intended to suggest finality, as it is recognized that subsequent work on more detailed collections may well provide a more precise microflorally based zonation.

In the Birger Johnsonfjellet section, the change in microspore content occurs stratigraphically between samples G1091 and G1092, at respectively 128 metres and 138 metres above base. At Triungen the change occurs between samples G1472 and G1471, at respective heights above base of 100 metres and 132 metres. The apparent abruptness of this 'change' would possibly be in fact reduced to a transition if intermediate samples from both sections were available. It is important to note, however, that none of the samples from other localities contains evidence of a mixture of the diagnostic representatives of the two assemblages discussed below.

The Rarituberculatus Assemblage. The older assemblage, which is named from the most consistently occurring species (see Table 1), is characterized diagnostically by the following microspore species:

Lophozonotriletes rarituberculatus (Luber) Kedo 1957 Verrucosisporites gobbettii sp. nov. Lophotriletes coniferus Hughes and Playford 1961 Convolutispora vermiformis Hughes and Playford 1961 Dictyotriletes caperatus sp. nov. Reticulatisporites planus Hughes and Playford 1961 Stenozonotriletes inductus Ishchenko 1956 Anulatisporites canaliculatus sp. nov. Densosporites striatiferus Hughes and Playford 1961 Densosporites variomarginatus sp. nov. Knoxisporites hederatus (Ishchenko) comb. nov. Cristatisporites echinatus sp. nov. Lophozonotriletes dentatus Hughes and Playford 1961 Lophozonotriletes variverrucatus sp. nov. Tholisporites foveolatus Hughes and Playford 1961 Velosporites echinatus Hughes and Playford 1961 Spinozonotriletes uncatus Hacquebard 1957

Other species apparently exclusive to the older assemblage, but of less common occurrence, are: *Punctatisporites labiatus* sp. nov., *Leiotriletes microgranulatus* sp. nov., *Acanthotriletes mirus* Ishchenko 1956, and *Stenozonotriletes stenozonalis* (Waltz) Ishchenko 1958.

The following species are common but not diagnostic components of the Rarituberculatus Assemblage: Cyclogranisporites flexuosus sp. nov., Convolutispora tuberculata (Waltz) Hoffmeister, Staplin, and Malloy 1955, Reticulatisporites cancellatus (Waltz) comb. nov., Perotrilites perinatus Hughes and Playford 1961, P. magnus Hughes and Playford 1961, Tripartites incisotrilobus (Naumova) Potonié and Kremp 1956, Stenozonotriletes clarus Ishchenko 1958, Murospora conduplicata (Andrejeva) comb. nov., M. sublobata (Waltz) comb. nov., Anulatisporites anulatus (Loose) Potonié and Kremp 1954, A. labiatus Hughes and Playford 1961, Densosporites dentatus (Waltz)

Potonié and Kremp 1956, D. diatretus nom. nov., D. spitsbergensis sp. nov., Knoxisporites cinctus (Waltz) Butterworth and Williams 1958, K. margarethae Hughes and Playford 1961, K. literatus (Waltz) comb. nov., Endosporites micromanifestus Hacquebard 1957, and Radialetes costatus gen. et sp. nov.

The Aurita Assemblage. From a comparison of Tables 1 and 2 it is evident that this assemblage comprises an even more diverse microflora than that represented by the Rarituberculatus Assemblage. In particular, zonate forms (Cirratriradites, Camptozonotriletes, Potoniespores, Diatomozonotriletes) appear significantly; the older assemblage appears to be entirely devoid of zonate (s. str.) spores: Other striking generic introductions are Lycospora, Anapiculatisporites, Waltzispora, Monilospora, Foveosporites, Remysporites, and Retialetes. Furthermore, the genera Reticulatisporites, Convolutispora, Densosporites, and Murospora are represented prolifically by numerous species in this younger assemblage. Especially significant is the total absence of Lophozonotriletes rarituberculatus (Luber), the 'index' species of the older microfloral suite.

The following microspore species are considered diagnostic components of the Aurita Assemblage, and have not been observed in the older assemblage:

Murospora aurita (Waltz) comb. nov., emend. Waltzispora lobophora (Waltz) Staplin 1960 Waltzispora albertensis Staplin 1960 Waltzispora sagittata sp. nov. Verrucosisporites eximius sp. nov. Anapiculatisporites concinnus sp. nov. Reticulatisporites variolatus sp. nov. Reticulatisporites peltatus sp. nov. Foveosporites insculptus sp. nov. Triquitrites trivalvis (Waltz) Potonié and Kremp 1956 Murospora friendii sp. nov. Densosporites bialatus (Waltz) Potonié and Kremp 1956 Densosporites subcrenatus (Waltz) Potonié and Kremp 1956 Densosporites duplicatus (Naumova) Potonié and Kremp 1956 Densosporites rarispinosus sp. nov. Densosporites aculeatus sp. nov. Lycospora uber (Hoffmeister, Staplin, and Malloy) Staplin 1960 Lophozonotriletes appendices (Hacquebard and Barss) comb. nov. Potoniespores delicatus sp. nov. Cirratriradites elegans (Waltz) Potonié and Kremp 1956 Camptozonotriletes velatus (Waltz) comb. nov. Diatomozonotriletes saetosus (Hacquebard and Barss) Hughes and Playford 1961 Diatomozonotriletes hughesii sp. nov.

The Assemblage name is based upon the species *Murospora aurita* (Waltz), which is almost invariably present, often as the predominating species (see Table 2).

Spinozonotriletes balteatus sp. nov.

Other species which are much rarer than those of the foregoing list, but which nevertheless appear similarly restricted to the younger assemblage, are as follows: Leiotriletes curiosus sp. nov., Anapiculatisporites serratus sp. nov., Convolutispora clavata (Ishchenko) Hughes and Playford 1961, Reticulatisporites rudis Staplin 1960, Reticulatisporites? sp., Tripartites complanatus Staplin 1960, Murospora dupla (Ishchenko) comb. nov., M. strigata (Waltz) comb. nov., M. tripulvinata Staplin 1960, Monilospora triungensis sp. nov., M. dignata sp. nov., Cirratriradites solaris Hacquebard and Barss 1957, Diatomo-

zonotriletes trilinearis sp. nov., D. rarus sp. nov., Remysporites albertensis Staplin 1960, and Retialetes radforthii Staplin 1960.

The following species, which are also components of the Rarituberculatus Assemblage, are often present in significant proportions: Chaetosphaerites pollenisimilis (Horst) Butterworth and Williams 1958, Convolutispora tuberculata (Waltz) Hoffmeister, Staplin, and Malloy 1955, Reticulatisporites cancellatus (Waltz) comb. nov., Triquitrites batillatus Hughes and Playford 1961, Tripartites incisotrilobus (Naumova) Potonié and Kremp 1956, Murospora intorta (Waltz) comb. nov., M. conduplicata (Andrejeva) comb. nov., M. sublobata (Waltz) comb. nov., Anulatisporites anulatus (Loose) Potonié and Kremp 1954, A. labiatus Hughes and Playford 1961, Densosporites dentatus (Waltz) Potonié and Kremp 1956, D. spitsbergensis sp. nov., Labiadensites fimbriatus (Waltz) Hacquebard and Barss 1957, Knoxisporites literatus (Waltz) comb. nov., Endosporites micromanifestus Hacquebard 1957, and Radialetes costatus gen. et sp. nov.

The Birger Johnsonfjellet and Triungen samples, from which the Aurita Assemblage has been recovered, are lithologically more diverse than those from which the older assemblage has been studied. It seems relevant, therefore, to consider the general relationships observed between rock-type and contained microfloral elements, although, as noted previously, detailed palaeoecological inferences are not possible. For this purpose a series of histograms (text-fig. 12) has been constructed to represent the relative proportions of common microfloral constituents observed in five lithological types, all of which contain the Aurita Assemblage. The microflora of the dull coal (E363) and of the highly carbonaceous (coaly) shale (R38) are notably restricted in comparison with those of the other sediments represented on text-fig. 12. In E363 the predominating forms are species of Densosporites, and Reticulatisporites cancellatus (Waltz) is also an important constituent. The microflora of R38 is marked by an extremely high percentage of Murospora aurita (Waltz). In the fine-grained sandstone (G1102) and the two carbonaceous shales (G1098, G1466) the microfloras exhibit considerable diversity, with Lycospora uber (Hoffmeister, Staplin, and Malloy) as the most abundant component. By contrast this species is comparatively rare in E363 and R38. These spore associations are probably representative of a more or less contemporary flora as preserved in sediments which accumulated in different ecological situations; possible botanical implications will be discussed subsequently in this paper.

A summary compilation of the species characteristic of the two microfloral assemblages is presented on Table 5.

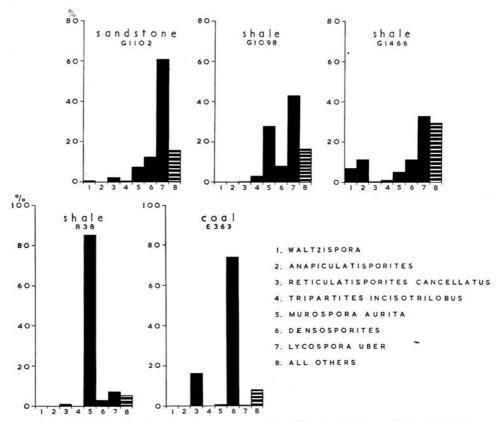
Age of the microfloral assemblages

The Rarituberculatus Assemblage. The 'index' species of this assemblage, Lophozonotriletes rarituberculatus (Luber), is a characteristic constituent of Russian strata of Tournaisian age (Luber and Waltz 1941; Ishchenko 1956; Kedo 1957, 1958, 1959; Byvsheva 1957, 1960). It has not been recorded from Viséan or younger rocks, but was reported by Luber and Waltz (1941) from allegedly Upper Devonian sediments of the Timan Peninsula and Kizel region. However, more recent Russian work (as cited above) seems to suggest that L. rarituberculatus is an exclusively Tournaisian form.

Another significant species is Spinozonotriletes uncatus Hacquebard, which has been described from the lowermost Mississippian of Canada. Its possible Russian equivalent,

Acanthozonotriletes senticosus Ishchenko, is confined to Tournaisian deposits of the western Donetz Basin. Two other species described by Ishchenko (1956), Stenozonotriletes inductus and Acanthotriletes mirus, have similar vertical restriction.

Convolutispora vermiformis Hughes and Playford occurs in Canadian strata of lowest Mississippian and of probable Upper Devonian age.



TEXT-FIG. 12. Histograms showing microspores present in different rock-types containing the Aurita Assemblage.

Numerous other components of the Rarituberculatus Assemblage, most of which are also present in the younger assemblage, are unknown from pre-Tournaisian strata. These are: Chaetosphaerites pollenisimilis (Horst), Acanthotriletes multisetus (Luber), Microreticulatisporites lunatus Knox, Tripartites incisotrilobus (Naumova), Stenozonotriletes facilis Ishchenko var. praecrassus Ishchenko, Murospora intorta (Waltz), M. conduplicata (Andrejeva), M. sublobata (Waltz), Zonotriletes macrodiscus Waltz (probable Russian equivalent of Anulatisporites labiatus Hughes and Playford), Anulati-

sporites orbiculatus (Waltz), Densosporites dentatus (Waltz), D. diatretus, D. variabilis (Waltz), Labiadensites fimbriatus (Waltz), Knoxisporites cinctus (Waltz), K. hederatus (Ishchenko), and Endosporites micromanifestus Hacquebard.

From the above evidence it is concluded that the Rarituberculatus Assemblage is of

Tournaisian age.

The Aurita Assemblage. The younger assemblage is marked by the absence of the characteristic Tournaisian species cited above and especially notable is the sudden dis-

appearance of Lophozonotriletes rarituberculatus (Luber).

Murospora aurita (Waltz), the 'index' species of the Aurita Assemblage, was described initially (Luber and Waltz 1938, 1941) from Russian strata, the age of which was not specified more precisely than 'Lower Carboniferous'. Subsequent investigations (Hacquebard and Barss 1957; Staplin 1960) indicate its presence in Canadian deposits of Upper Mississippian age. These latter occurrences, together with evidence from the present study of the complete absence of M. aurita in the older assemblage, suggest strongly that the species is post-Tournaisian. It is noteworthy also that M. aurita is unknown in rocks definitely assignable to the Namurian stage.

Numerous other Russian, Canadian, and British species are important constituents of this assemblage. *Convolutispora clavata* (Ishchenko), *Murospora dupla* (Ishchenko), *M. strigata* (Waltz), and *Triquitrites trivalvis* (Waltz) have been recorded as exclusively Viséan species in the U.S.S.R., although the latter species is known also from Namurian A coals of Scotland (Butterworth and Williams 1958). *Waltzispora sagittata* sp. nov. occurs in the Scottish Viséan (Love 1960).

The following species are unknown from Namurian or younger strata of the U.S.S.R.: Reticulatisporites cancellatus (Waltz), Stenozonotriletes clarus Ishchenko, Murospora conduplicata (Andrejeva), Densosporites dentatus (Waltz), Labiadensites fimbriatus (Waltz), and Camptozonotriletes velatus (Waltz).

Densosporites subcrenatus (Waltz), Cirratriradites elegans (Waltz), and Diatomozonotriletes saetosus (Hacquebard and Barss) are apparently confined in Russia to rocks of Viséan and Namurian age.

Lycospora uber (Hoffmeister, Staplin, and Malloy), which is often an extremely abundant constituent of the assemblage, appears from previous records to range from

lowest Viséan to at least Westphalian A.

The following species have been reported hitherto from strata ranging in age from Tournaisian to Namurian: Convolutispora tuberculata (Waltz), Tripartites incisotrilobus (Naumova), Stenozonotriletes facilis Ishchenko var. praecrassus Ishchenko, Densosporites intermedius (Waltz), D. variabilis (Waltz), Knoxisporites literatus (Waltz), and Endosporites micromanifestus Hacquebard. Densosporites bialatus (Waltz) is also known to be similarly long-ranging, but appears to be especially abundant in Russian strata of Viséan-Namurian age.

A number of species, confined to the Aurita Assemblage, are common to the coal microflora described by Hacquebard and Barss (1957), which is probably equivalent in age to the Middle Chester series of the United States. These comprise: Waltzispora albertensis Staplin, which is present also in the Russian Lower Carboniferous (Reinsch 1884) and was formally described by Staplin (1960); Cirratriradites solaris Hacquebard and Barss, also recorded by Staplin (1960); Densosporites duplicatus (Naumova),

initially reported by Luber and Waltz (1938) from the Russian Lower Carboniferous; and *Lophozonotriletes appendices* (Hacquebard and Barss).

The microflora described by Staplin (1960) is from the Golata formation of Canada, which is equivalent in age to the Lower Chester series of the United States and is thus probably slightly older than the coal investigated by Hacquebard and Barss (1957). The following species, all described for the first time by Staplin (1960), are restricted in Spitsbergen to the Aurita Assemblage: Reticulatisporites rudis, Tripartites complanatus, Murospora tripulvinata, Remysporites albertensis, and Retialetes radforthii. In particular, the latter species appears to be confined at Birger Johnsonfjellet and Triungen to the stratigraphically highest beds containing the younger assemblage.

Very little obvious similarity exists between the Aurita Assemblage and the Namurian microfloras described by Horst (1955), Dybová and Jachowicz (1957), Butterworth and Williams (1958), and Neves (1961). Indeed, the only species in common are those which are known from the work of other authors to occur also in strata of greater age, i.e. at least Viséan. Furthermore, none of the definitely post-Viséan Russian species, as documented by Ishchenko (1956, 1958), is present in the assemblage.

It is evident that the Aurita Assemblage conforms closely at specific level with microfloras reported by numerous authors from Viséan strata of the U.S.S.R. Significant correlation can also be made with Lower-Middle Chester microfloras of Canada. As noted previously in this paper, the European equivalence of the Chester series is somewhat uncertain, but more recent goniatite and conodont studies suggest correlation of the lower part of the series with the Upper Viséan rather than with the Namurian A.

Collectively, the above evidence strongly indicates that the Aurita Assemblage is of Viséan age, although a possible extension into the older Namurian is not precluded. Definite pronouncement in this latter respect must necessarily await more conclusive palaeontological evidence concerning the European equivalence of the Chester series, coupled with further palynological investigation of the North American Mississippian, the microfloras of which are as yet only sparsely known (see text-fig. 4).

As discussed previously, the two microfloral assemblages are represented successively in the sections at Birger Johnsonfjellet and Triungen. Thus the Billefjorden Sandstones as developed at these localities incorporate strata ranging in age from Tournaisian to Viséan, possibly to lowest Namurian. Certainly the presence (in the stratigraphically highest beds) of *Retialetes radforthii*, together with a number of other forms described by Staplin (1960) and Hacquebard and Barss (1957), seems to indicate an upper age limit of either topmost Viséan or alternatively lowest Namurian.

Samples from the Citadellet succession contain exclusively the Rarituberculatus Assemblage, hence indicating a Tournaisian age. However, the uppermost part of this section has not been sampled (see text-fig. 2) and it is possible therefore that beds of Viséan age are represented at Citadellet. *In situ* samples were unobtainable from basal Billefjorden Sandstones of the three reference successions; thus the precise age of the lowermost part of the series at Birger Johnsonfjellet, Triungen, and Citadellet is unknown.

Correlation within Syalbard

The microfloral assemblages delineated above have been observed in preparations of samples from various other localities in Vestspitsbergen and from Nordkapp, Bjørnøya.

Thus the rocks exposed at these localities (listed below) may be correlated with the palynologically documented successions at Birger Johnsonfjellet, Triungen, and Citadellet. Two comprehensive check lists (Tables 3 and 4) record the microspore species

present in samples from localities other than those of the three successions. Table 3 incorporates samples containing the Rarituberculatus Assemblage, whilst the younger assemblage is represented (in a relatively large number of samples) in Table 4.

Citation is made below of some of the more stratigraphically significant constituent species of each sample which, in containing one or other of the microfloral assemblages, is referable implicitly to appropriate portions of the reference successions. The localities are shown on text-fig. 1; data on their stratigraphy have already been presented.

Vestspitsbergen

- 1. Citadellet. Samples B685 (studied earlier by Hughes and Playford 1961) and B687 both contain prolific microfloras representative of the Rarituberculatus Assemblage, and as such are conformable with the other Citadellet samples recorded palynologically in Table 1. Age—Tournaisian.
- 2. Triungen. Sample G1461 contains an abundant and well-preserved microflora which is typical of the Aurita Assemblage. In particular, the presence of the rare forms Reticulatisporites? sp. and Retialetes radforthii suggests a similar horizon to that of sample G1466 of the known Triungen succession. Age—Upper Viséan, or possibly lowermost Namurian.
- 3. Ebbadalen (north side). Sample B706 yielded a fairly well-preserved microflora including the following diagnostic representatives of the younger assemblage: Murospora aurita, Waltzispora albertensis, Reticulatisporites peltatus, Densosporites bialatus, Lyco-

	LOCALITY		В		
5	AMPLE NO.	8685	B687	8680	
Leiotriletes inermis L. subintortus var. r L. ornatus L. microgranulatus	otundatus	x x	x x x	x	
Punctatisporites glab P. parvivermiculatus P. labiatus	er	x	x	x	
Calamospora microrugo	na	×	x	x	
Phyllothecotriletes r	igidus	×			
Cyclogranisporites las C. flexuosus	sius	x	x		
Verrucosisporites gob	bettii		x	x	
Lophotriletes conifer	18	×	×		
Acanthotriletes multis	setus		×		
Convolutispora vermifo	ormis	х	x x	×	
Microreticulatisporit	es lunatus	×	x		
Dictyotriletes capera	tus		x	x	
Reticulatisporites car R. planus	ncellatus	×	x	x	
Perotrilites perinatus P. magnus	,	x	x		
Tripartites incisotri	lobus	×	- 11/2		
Stenozonotriletes ster S. inductus S. clarus S. perforatus S. of. spetcandus	nozonalis	×	x x x x		
Murospora conduplicate	1	×	x		
Anulatisporites anula: A. labiatus A. orbiculatus A. canaliculatus	tus	×	x x x	x x	
Densosporites dentatus D. intermedius D. variabilis D. stristiferus D. varionarginatus	1	x	x x x	x x	
Labiadensites fimbria	tus		x		
Enoxisporites cinctus K. margarethae		x x	x	×	
Lophozonotriletes rari	tuberculatus	×	x	x	
L. dentatus L. variverrucatus		×	×	×	
Tholisporites foveolat	tus	x	×		
Endosporites micromani	festus	×	x	-	
Velosporites echinatus		x	×	×	
Spinozonotriletes unce	itus	x			
Radialetes costatus		×			

TABLE 3. Check list of microspore species, representative of the Rarituberculatus Assemblage, present in samples other than those documented in Table 1. Locality index—A, Citadellet; B, Odellfjellet. Correction: for Densosporites intermedius read D. diatretus (see p. 623).

spora uber, Camptozonotriletes velatus, Diatomozonotriletes saetosus, &c. Age—Viséan. Sample W860 contains a somewhat poorly preserved microflora recognizably conformable with the Aurita Assemblage. Significant species present include Murospora aurita, Convolutispora clavata, Reticulatisporites peltatus, Densosporites bialatus, Lycospora uber, Diatomozonotriletes saetosus, and Camptozonotriletes velatus. The additional presence of Convolutispora harlandii suggests correlation with a horizon

comparable with that of G1095 in the Birger Johnsonfjellet succession. Age—Viséan.

Both these samples are from near the base of the Billefjorden Sandstones, suggesting that Culm sedimentation commenced at this particular locality relatively late in the Lower Carboniferous.

- 4. Ebbadalen (south side). Samples B609 (recorded in Hughes and Playford 1961), B604, F531, F774, G332, G334, G366, and G382 are all from the same horizon, which is well above the base of the Culm. None yielded a well-preserved microflora. The following are some of the species, indicative of the Aurita Assemblage, which were observed in these complementary samples: Murospora aurita, Anapiculatisporites concinnus, Reticulatisporites peltatus, Foveosporites insculptus, Triquitrites trivalvis, Tripartites complanatus, Murospora friendii, Densosporites bialatus, D. duplicatus, D. rarispinosus, Lycospora uber, Potoniespores delicatus, Cirratriradites solaris, Diatomozonotriletes saetosus, Remysporites albertensis, and Retialetes radforthii. Age—Upper Viséan, or possibly lowermost Namurian.
- 5. Wordiekammen (north side). The coal S59a (studied by Hughes and Playford 1961) contains a rather restricted microflora including such representatives of the younger assemblage as: Murospora aurita, Convolutispora clavata, Lycospora uber, and Spinozonotriletes balteatus. Age—Viséan.
- 6. Adolfbukta (north shore). A particularly well-preserved microflora, typical of the Aurita Assemblage, was obtained from sample W217. Species present include: Murospora aurita, Leiotriletes curiosus, Waltzispora lobophora, W. albertensis, Verrucosisporites eximius, Triquitrites trivalvis, Tripartites complanatus, Densosporites bialatus, D. duplicatus, Lycospora uber, Lophozonotriletes appendices, Cirratriradites solaris, Diatomozonotriletes saetosus, D. hughesii, D. rarus, and Retialetes radforthii. Age—Upper Viséan, or possibly lowermost Namurian.
- 7. De Geerfjellet. Samples G636 and T269, which are from the same outcrop and horizon, both yielded well-preserved microfloras characteristic of the Aurita Assemblage. Stratigraphically important species include: Murospora aurita, Waltzispora albertensis, W. sagittata, Anapiculatisporites serratus, A. concinnus, Reticulatisporites? sp., R. rudis, R. peltatus, Tripartites complanatus, Triquitrites trivalvis, Murospora tripulvinata, Densosporites bialatus, D. duplicatus, Lycospora uber, Monilospora triungensis, Cirratriradites solaris, Diatomozonotriletes saetosus, D. hughesii, D. trilinearis, D. rarus, Spinozonotriletes balteatus, and Retialetes radforthii. Age—Upper Viséan, or possibly lowermost Namurian.
- 8. Ragnarbreen. A somewhat restricted microflora was obtained from the coal R38 (see text-fig. 12). Constituent species include the following, all representative of the younger assemblage: Murospora aurita, Waltzispora albertensis, Reticulatisporites peltatus, Triquitrites trivalvis, Murospora friendii, Densosporites bialatus, Lycospora uber, Camptozonotriletes velatus, Diatomozonotriletes saetosus, &c. Age—Viséan.
- 9. Anservika. The microfloras obtained from samples R5, F20, D120, G1283, G1280, G1278, and G1276 are specifically similar and, as they were collected from approximately the same horizon, may be considered here collectively. The Aurita Assemblage is represented by such forms as Murospora aurita, Waltzispora albertensis, W. sagittata, Verrucosisporites eximius, Convolutispora clavata, Reticulatisporites variolatus, R. peltatus, Foveosporites insculptus, Murospora friendii, Densosporites bialatus, D. dupli-

Chaetospharites pollenisimilis		LOCALITY	A		9		_		с		_			٥	ε	-	-	c				н			T	,	,		Τ	K	4	Γ	м	N O P			-	2			
Section Sect		SAMPLE NO.	61461	8706	WB60	8604	6098	F531	F774	6332	6334	9989	6382	5590	W217	6636	T269	838	R S	F20	0150	G1283	61280	G1278	61276	08015	300	100	61339	G1344	£363	8624	H267	8616	6198	8443	M365	550	950	P702	P725
International Note	Chaetosphaerites p	ollenisimilis							x					×	×	x	×			_	-			×	x		x x	×	×		\vdash	\vdash	\vdash		×		×	×	×		
Lamental	Leiotriletes inerm	is				x	х			х		x		х	х	X		х				X		X	×						X	×			X		×	Х	х	Х	
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тавье 4. Check list of microspore species, representative of the Aurita Assemblage, present in samples additional to those documented in Table 2. Locality index—A, Triungen; в, Ebbadalen (north side); с, Ebbadalen (south side); р, Wordiekammen (north side); в, Adolfbukta (north shore); г, De Geerfjellet; G, Ragnarbreen; н, Anservika; I, Carronelva; I, Gerritelva; к, Margaretbreen; L, Svenbreen; м, Odellfjellet; N, Ålandvatnet; о, Lemströmfjellet; Р, Blårevbreen; Q, Nordkapp, Bjørnøya. Correction: for Densosporites intermedius read D. diatretus (see p. 625)

catus, D. rarispinosus, Lycospora uber, Lophozonotriletes appendices, Cirratriradites solaris, &c. Age—Viséan.

- 10. Carronelva. Sample G1080 contains a very sparse microflora, which, in containing Murospora aurita, M. tripulvinata, and Lycospora uber, is referable to the Aurita Assemblage. Age—Viséan.
- 11. Gerritelva. Sample 353 yielded a sparse microflora, including the following species diagnostic of the younger assemblage: Murospora aurita, M. tripulvinata, Densosporites rarispinosus, Lycospora uber, Lophozonotriletes appendices, Diatomozonotriletes saetosus, and Monilospora dignata. In particular, the presence of the latter species suggests correlation with the stratigraphically highest sample (G1102) of the Birger Johnsonfjellet succession. Age—Upper Viséan, or possibly lowermost Namurian.

More abundant and diverse assemblages were recovered from samples 390 and 391. The following forms, diagnostic of the Aurita Assemblage, were identified from both samples: *Murospora aurita*, *Reticulatisporites peltatus*, *Lycospora uber*, and *Cirratriradites solaris*. Age—Viséan.

12. Margaretbreen. Sample G1339 contains a diverse and well-preserved microflora with many species characteristic of the younger assemblage. These include: Murospora aurita, M. friendii, Triquitrites trivalvis, Densosporites bialatus, D. duplicatus, D. aculeatus, Lycospora uber, Camptozonotriletes velatus, Diatomozonotriletes saetosus, and Spinozonotriletes balteatus. Age—Viséan.

A much less abundant microflora was obtained from sample G1344. Although *Murospora aurita* was not identified, the Aurita Assemblage is represented by such forms as *Lycospora uber*, *Camptozonotriletes velatus*, and *Retialetes radforthii*. The latter species suggests correlation with the uppermost parts of the successions at Triungen and Birger Johnsonfjellet. Age—Upper Viséan, or possibly lowermost Namurian.

- 13. Svenbreen. Sample E363, from just above the base of the Billef jorden Sandstones, includes the following representatives of the younger assemblage: Murospora aurita, Reticulatisporites variolatus, Densosporites bialatus, D. rarispinosus, Lycospora uber, Cirratriradites elegans, Camptozonotriletes velatus, and Diatomozonotriletes hughesii. Also present is Convolutispora harlandii, which, together with the above species, suggests correlation of this sample with approximately the same horizon as sample G1095 of the Birger Johnsonfjellet succession. Age—Viséan.
- 14. Odellfjellet. Sample B680 yielded a well-preserved microflora. The Rarituberculatus Assemblage is represented diagnostically by such forms as Lophozonotriletes rarituberculatus, L. variverrucatus, Punctatisporites labiatus, Verrucosisporites gobbettii, Dictyotriletes caperatus, Anulatisporites canaliculatus, and Velosporites echinatus. Age—Tournaisian.

From stratigraphically higher beds, samples B624 and H267 yielded diverse microfloras referable to the Aurita Assemblage. Species common to both samples include: *Murospora aurita*, *Reticulatisporites peltatus*, *Densosporites aculeatus*, *Lycospora uber*, *Lophozonotriletes appendices*, *Cirratriradites elegans*, and *Camptozonotriletes velatus*. Age—Viséan.

15. Alandvatnet. Comparatively poorly preserved microfloras were recovered from samples B616 and B619. Both contained the following species, which are diagnostic of the younger assemblage: Murospora aurita, Densosporites bialatus, Lycospora uber, Cirratriradites elegans, and Camptozonotriletes velatus. Age—Viséan.

16. Lemströmfjellet. Sample B443 contains a sparse microflora, including the following characteristic representatives of the Aurita Assemblage: Murospora aurita, Anapicu-

latisporites concinnus, and Lycospora uber. Age-Viséan.

17. Blårevbreen. Prolific and closely similar microfloras were recovered from samples M365, Q55, and Q56. Amongst the forms, common to all or at least two of these samples, and diagnostic of the Aurita Assemblage, are: Murospora aurita, M. friendii, M. strigata, Waltzispora albertensis, Reticulatisporites variolatus, R. peltatus, Triquitrites trivalvis, Densosporites bialatus, D. duplicatus, D. rarispinosus, Lycospora uber, Cirratriradites elegans, Camptozonotriletes velatus, Diatomozonotriletes saetosus, D. hughesii, Remysporites albertensis, and Retialetes radforthii. This spore association is very similar to that encountered in the stratigraphically highest samples from Triungen and Birger Johnsonfjellet. Age—Viséan, or possibly lowermost Namurian.

Bjørnøya

1. Nordkapp. A few species only were positively identifiable in the poorly preserved microfloras recovered from samples P702 and P725. Sample P702 contains the following stratigraphically significant forms: Densosporites bialatus, Lycospora uber, and Diatomozonotriletes saetosus. Sample P725 includes Anapiculatisporites concinnus, Lycospora uber, and Spinozonotriletes balteatus. Although neither sample appears to contain the 'index' species Murospora aurita, their microfloras are clearly referable to the Aurita Assemblage. Age—Viséan.

From the above it is evident that the majority of the samples may be correlated with the upper parts of the Birger Johnsonfjellet and Triungen successions, by virtue of their content of representatives of the Aurita Assemblage. Moreover, the fact that many of these younger samples—specifically those from Ebbadalen (north side), Svenbreen, and Blårevbreen—are from basal beds suggests that in some places Culm deposition may have commenced relatively late in the Lower Carboniferous.

Apart from the localities of the three reference successions, only one sample (from Odellfjellet) contained the Rarituberculatus Assemblage. In addition two samples from higher in the Odellfjellet section yielded the younger assemblage. Thus this section is comparable in age (Tournaisian–Viséan) to those of Birger Johnsonfjellet and Triungen.

BOTANICAL RELATIONSHIPS

The outstandingly successful stratigraphical applications of dispersed-spore studies over the past two decades have tended to transcend the fundamentally botanical nature of palynology. Indeed, the botanical origin of many Carboniferous spore genera is at present unknown. Such workers as Chaloner (1953a, b; 1954; 1958a, b), W. and R. Remy (1957), and Sen (1958) have contributed considerably to our knowledge of the botanical affinities of some of the more characteristic *sporae dispersae* of Carboniferous age. As a result it is now possible to deduce the existence of certain plant groups solely on the basis of dispersed-spore evidence.

As listed by Nathorst (1914) and Forbes *et al.* (1958), the macroflora of the Spitsbergen Culm consists predominantly of arborescent lycopods including numerous representatives of *Lepidodendron* and *Bothrodendron*. The presence of *Lepidodendron* is almost certainly reflected in the microflora by the abundance of *Lycospora* (occurring as

MICROFLORAL ASSEMBLAGE	RARITUBERCULATUS	AURITA
SUGGESTED AGE	TOURNAISIAN	VISÉAN, possibly to NAMURIAN A
Leiotriletes microgranulatus		
Punctatisporites labiatus		
Verrucosisporites gobbettii		
Lophotriletes coniferus		
Acanthotriletes mirus		
Convolutispora vermiformis		
Dictyotriletes caperatus		
Reticulatisporites planus		
Stenozonotriletes stenozonalis		
Stenozonotriletes inductus		1
Anulatisporites canaliculatus		
Densosporites striatiferus		
Densosporites variomarginatus		
Knoxisporites hederatus		
Cristatisporites echinatus		
Lophozonotriletes rarituberculatus		
Lephozonotriletes dentatus		
Lophozonotriletes dentatus Lophozonotriletes variverrucatus		()
Tholisporites foveolatus		
Velosporites echinatus		
Spinozonotriletes uncatus		
Cyclogranisporites flexuesus		
Convolutispora tuberculata		
Reticulatisporites cancellatus		
Tripartites incisotrilobus		
Stenozonotriletes clarus		
Anulatisporites labiatus		
Densosporites dentatus		
Densosporites intermedius		
Densosporites spitsbergensis		
Labiadensites fimbriatus		
Knoxisporites literatus		
Endosporites micromanifestus		
Radialetes costatus		
Waltzispora lobophora	1	
Waltzispora albertensis	· ·	
Verrucosisporites eximius		
Reticulatisporites variolatus	1	
Reticulatisporites peltatus	-	
Foveosporites insculptus		
Triquitrites trivalvis		
Tripartites complanatus		
Murospora aurita		
Murospora friendii		
Densosporites bialatus		
Densosporites duplicatus		
Densosporites rarispinosus		
Densosporites aculeatus		
Lycospora uber		
Lophozonotriletes appendices		
Potoniespores delicatus		
Cirratriradites solaris	° [
Cirratriradites elegans		
Camptozonotriletes velatus		
Diatomozonotriletes saetosus		
Diatomozonotriletes hughesii		
Spinozonotriletes balteatus		
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TABLE 5. Summary compilation of important constituent species of the two Microfloral Assemblages delineable in the Lower Carboniferous of Spitsbergen. The indicated probable age of each Assemblage is discussed in detail in the text. Correction: for *Densosporites intermedius* read *D. diatretus* (see p. 623).

a single species, Lycospora uber), since this spore genus has been found associated elsewhere only with various species of the cone Lepidostrobus (see Chaloner 1953b; Sen 1958). In view of the total absence of Lycospora uber in the older microfloral assemblage, it is tempting to surmise the appearance, in Spitsbergen at least, of its parent plant in early Viséan times. Lycopods are probably also represented by the numerous species of Densosporites which occur throughout the Spitsbergen Culm. Chaloner (1958a) attributed a heterosporous cone, containing Densosporites-type microspores, to the herbaceous lycopod Selaginellites, but Bharadwaj (1959) recommended the inclusion of this cone in the genus Bothrostrobus. The spores described herein as Densosporites spitsbergensis are closely similar to those recovered by Bharadwaj (1959) from the Spitsbergen Lower Carboniferous fructification Porostrobus zeilleri (described originally by Nathorst 1914). Bharadwaj considered that P. zeilleri 'shows lepidodendroid as well as sigillarioid characters'. Other probable Lycopsidean derivatives are the genera Endosporites (see Chaloner 1953a, 1958b) and Cirratriradites (see Chaloner 1954; Hoskins and Abbott 1956). These genera are represented respectively in the Lower Carboniferous of Spitsbergen by Endosporites micromanifestus, and by Cirratriradites elegans and C. solaris. It should be noted, however, that the two species of Cirratriradites bear little resemblance to the C. annulatus-type microspores recovered from Selaginellites suissei and from S. crassicinctus by Chaloner (1954) and Hoskins and Abbott (1956) respectively.

From available literature, no definite pronouncement can be made concerning the origin of the numerous other microspore genera represented in the Spitsbergen Culm. Especial caution is necessary in assessing the botanical relationships of simple, relatively unsculptured generic groups such as Calamospora, Punctatisporites, and Leiotriletes. Forms of this general type are known to derive from numerous plant groups including, for example, Bryophyta, Psilophytales, Equisetales, and Filicales. Fern-like plants probably contributed the bulk of azonate, often prominently sculptured, trilete spores such as Cyclogranisporites, Acanthotriletes, Anapiculatisporites, Verrucosisporites, Convolutispora, and Reticulatisporites (cf. Potonié and Kremp 1956b; W. and R. Remy 1957). There appears to be no evidence regarding the affinity of cingulate forms such as Murospora, Stenozonotriletes, Anulatisporites, Labiadensites, Knoxisporites, Lophozonotriletes, &c., but some of these may well be of lycopsid origin. The genus Florinites, which is well known from the Upper Carboniferous as derived from cordaite and conifer vegetation, is conspicuously absent in the Spitsbergen Culm. Indeed, Monosaccites comprises an essentially minor element of the microfloras; such genera as Remysporites and Velosporites may perhaps be of pteridosperm origin. The presence in minor amounts of Chaetosphaerites and Tetraporina suggests strictly subordinate fungal and algal contributions respectively.

Some consideration has already been given to differences in microspore composition of various lithological types (see text-fig. 12), all of which contain the Aurita Assemblage. In the coal (E363) and the highly carbonaceous shale (R38), Densosporites spp. and Murospora aurita are respectively the dominating forms in microfloras which show a marked paucity in generic and specific representation. These species are relatively heavy, cingulate forms and were probably not very readily dispersed by wind or water. Thus their extreme abundance in coaly sediments may suggest that the parent plants were components of the coal swamp vegetation. Lycospora uber is a relatively trivial constituent of both E363 and R38. In contrast, the shales (G1098, G1466) and the sand-

stone (G1102) all contain diverse, essentially similar microfloras (having high specific and generic representation) which are probably fairly representative of the overall contemporary flora. In all three samples, *Lycospora uber* is the most abundant type, but accompanied by significant amounts of *Densosporites spp.* and *Murospora aurita*. *L. uber* is a small, relatively light spore which was probably dispersed widely from its parent arborescent lepidodendrid, and was perhaps eclipsed in the coal microflora by a dominance of heavier, less dispersable forms (as *Densosporites spp.* and *Murospora aurita*).

CONCLUSIONS

The Lower Carboniferous sediments of Spitsbergen contain diverse and some exceptionally well-preserved microfloras. The vertical distribution of the microspore species, as observed in the Billefjorden Sandstones sections at Birger Johnsonfjellet, Triungen, and Citadellet, provides an effective means of stratigraphical correlation both within and outside Spitsbergen. Indeed, the present study lends considerable support to the view expressed by Ishchenko (1956, p. 135) to the effect that terrestrial sequences of Lower Carboniferous age may be subdivided precisely on the exclusive basis of their microspore content.

There is some evidence that a third microfloral assemblage may be delineable. This would incorporate the youngest microfloral elements (e.g. *Retialetes radforthii*) which indicate an Upper Viséan or lowest Namurian age. A subdivision of the Aurita Assemblage would thus be entailed, but precise delimitation is not possible from samples available at present.

External correlation is afforded by the strikingly close similarity between the microfloras described herein and those reported previously from the Lower Carboniferous of Russia, and from portions of the Mississippian of Canada. In terms of the standard European stages, the age of the Billefjorden Sandstones is shown to range from Tournaisian to at least Viséan and perhaps lower Namurian; this endorses and strengthens the preliminary view of Hughes and Playford (1961). In terms of North American (Mississippian) nomenclature, the series ranges in age from Kinderhook to lower or middle Chester.

The fact that basal Culm samples, from often not widely separated localities, are of different ages suggests that the initiation of Culm sedimentation was not everywhere contemporaneous. Such variation in the age of local base levels is not unusual in a continental sequence which developed over an irregular landscape.

The disconformity at the top of the Billefjorden Sandstones at both Triungen and Birger Johnsonfjellet indicates that Culm sedimentation may have continued well into the Namurian. As noted previously the highest collected Culm sediments from the south side of Ebbadalen (samples B609, F531, &c.) indicate an Upper Viséan or lowermost Namurian age. However, this coaly horizon is succeeded by a further 220 feet of Culm which passes by vertical transition into the Lower Gypsiferous Series (see McWhae 1953, fig. 6, stratigraphical column H). These upper Culm beds may well be Namurian A in age; the age of the Lower Gypsiferous Series is not definitely known, but is thought to be Upper Namurian or Bashkirian (Forbes et al. 1958, p. 470 and table 2).

APPENDIX A. DATA ON SAMPLES STUDIED

Samples are listed and described macroscopically under headings of the localities from which they were collected. Actual collector is referred to by initials: M. B. Bayly, D. E. T. Bidgood, M. H. P. Bott, C. L. Forbes, J. L. Fortescue, P. F. Friend, D. G. Gee, D. J. Gobbett, W. B. Harland, J. R. H. McWhae, B. Moore, G. Playford, O. P. Singleton, M. S. Thornton, C. B. Wilson, J. M. Wordie. The initials are followed by the preparation numbers of each sample—those prefixed with 'M' were prepared by Mrs. Margaret Mortimer; 'P' indicates preparation by the writer.

Birger Johnsonfjellet

- G1086 sandstone, pale grey, hard, medium-grained, micaceous, with plant fragments; D. J. G.;
- G1087 sandstone, dark grey, hard, medium-grained, carbonaceous, micaceous; D. J. G.; P161,
- G1088 shale, black, silty, carbonaceous, micaceous, with plant fragments; D. J. G.; P162, P171.
- G1089 siltstone, black, carbonaceous, micaceous, with plant fragments; D. J. G.; P163.
- G1090 siltstone, reddish-brown to black, very hard, ferruginous, carbonaceous; D. J. G.; P177.
- shale, black, highly carbonaceous, with plant fragments; D. J. G.; P139, P143. G1091
- shale, black, highly carbonaceous, with plant fragments; D. J. G.; P158. G1092
- shale, black, highly carbonaceous, with plant fragments; D. J. G.; P159. G1093
- shale, dark grey, silty, carbonaceous, micaceous, with plant fragments; D. J. G.; P164. sandstone, pale grey, hard, medium-grained; D. J. G.; P178. G1095
- G1096
- G1098 shale, black, carbonaceous; D. J. G.; P167.
- shale, black, carbonaceous; D. J. G.; P160.
- G1101 shale, black, highly carbonaceous, with plant fragments; D. J. G.; P168.
- sandstone, dark grey, fine-grained, silty, carbonaceous, micaceous; D. J. G.; P180, P188. G1102

Triungen

- G1473 shale, dark grey, carbonaceous; D. J. G.; P147.
- G1472 siltstone, black, carbonaceous, micaceous; D. J. G.; P148.
- sandstone, pale grey, hard, fine-grained, with carbonaceous, silty lenses; D. J. G.; P179. G1471
- G1470 shale, black, carbonaceous, with plant fragments; D. J. G.; P149.
- G1469 shale, black, highly carbonaceous, with plant fragments; D. J. G.; P152.
- G1468 shale, black, highly carbonaceous; D. J. G.; P151.
- shale, black, highly carbonaceous; D. J. G.; P154, P157. G1467
- shale, black, carbonaceous, micaceous, with coaly lenses; D. J. G.; P145. G1466
- G1465 shale, black, clayey, highly carbonaceous; D. J. G.; P153.
- G1461 shale, black, carbonaceous; D. J. G.; P155.

Citadellet

- B685 sandstone, grey, fine-grained, massive, carbonaceous, micaceous, with plant fragments; B. M.; M811, M928, M949, P003.
- B687 sandstone, grey, fine-grained, silty, carbonaceous, micaceous, with plant fragments; B. M.; P226.
- G1445 sandstone, grey-black, fine-grained, silty, carbonaceous, micaceous; D. J. G.; P172.
- G1446 shale, black, carbonaceous, micaceous; D. J. G.; P173.
- G1448 shale, grey-black, carbonaceous, micaceous, very fissile; D. J. G.; P174.
- G1450 shale, black, carbonaceous, very fissile; D. J. G.; P175.
- G1451 shale, black, carbonaceous, very fissile; D. J. G.; P176.
- G1452 sandstone, dark brown, fine-grained, massive, carbonaceous, ferruginous; D. J. G.; P206.
- G1453 shale, grey-black, carbonaceous, very fissile; D. J. G.; P181.

Ebbadalen (north side)

- B706 sandstone, grey, fine-grained, silty, carbonaceous, micaceous, with 'Knorria'; B. M.; P012.
- W860 shale, black, carbonaceous, micaceous; C. B. W.; P017.

Ebbadalen (south side)

- B604 bright coal; B. M.; P018.
- B609 siltstone, grey, carbonaceous, micaceous, with Cardiopteridium ? spetsbergense Nathorst; B. M.; M803.
- F531 shale, black, highly carbonaceous, with Lepidodendron rhodeanum Sternberg; P. F. F.; M788, P225.
- F774 siltstone, black, carbonaceous, micaceous, with plant fragments; P. F. F.; P021.
- G332 shale, black, carbonaceous, with plant fragments; D. J. G.; P024.
- G334 shale, black, highly carbonaceous, with plant fragments; D. J. G.; P076.
- G366 shale, black, carbonaceous, with Lepidophloios scoticus Kidston; D. J. G.; P077.
- G382 siltstone, black, carbonaceous, micaceous, with Cardiopteridium? spetsbergense Nathorst; D. J. G.; P029.

Wordiekammen (north side)

S59a dull coal; O. P. S.; M883, P150.

Adolfbukta (north shore)

W217 shale, black, highly carbonaceous, with plant fragments; J. M. W.; P034.

De Geerfiellet

- G636 shale, black, carbonaceous, with plant fragments; D. J. G.; P026, P186.
- T269 shale, black, highly carbonaceous, some layers consisting almost entirely of megaspores; M. S. T.; P141.

Ragnarbreen

R38 shale, black, highly carbonaceous, with plant fragments; J. R. H. McW.; M821, P182.

Anservika

- R5 sandstone, grey, fine-grained, hard, micaceous, slightly carbonaceous; J. R. H. McW.; P011.
- F20 dull coal; C. L. F.; M822, P083.
- D120 sandstone, dark grey, fine-grained, hard, carbonaceous, micaceous, with plant fragments; D. E. T. B.; P033.
- G1283 siltstone, dark grey, carbonaceous, micaceous, with plant fragments; D. J. G.; P236.
- G1280 sandstone, grey-black, fine-grained, carbonaceous, micaceous, with plant fragments; D. J. G.; P156.
- G1278 siltstone, grey, sandy, carbonaceous, micaceous, with plant fragments; D. J. G.; P235-
- G1276 sandstone, grey-black, fine-grained, silty, carbonaceous, micaceous; D. J. G.; P234.

Carronelva

G1080 siltstone, grey-black, sandy, carbonaceous, micaceous, weathered, with plant fragments; D. J. G.; P207.

Gerritelva

- 353 bright coal; W. B. H.; P015.
- 390 shale, grey-black, carbonaceous, micaceous, with Lepidophloios sp. and Cardiopteridium ? spetsbergense Nathorst; W. B. H.; P064.
- 391 shale, grey-black, carbonaceous, micaceous, with Cardiopteridium? spetsbergense Nathorst; W. B. H.; M810, P004.

Margaretbreen

- G1339 shale, black, carbonaceous, with plant fragments; D. J. G.; P184.
- G1344 shale, dark grey, carbonaceous, micaceous, with plant fragments; D. J. G.; P203.

Svenbreen

E363 dull coal; D. G. G.; P140.

Odellfjellet

- B680 shale, black, carbonaceous, micaceous, with Cyclostigma sp.; B. M.; M809, P224.
- B624 siltstone, grey, carbonaceous, micaceous, with plant fragments; B. M.; M806, P002.
- H267 shale, black, highly carbonaceous, with Stigmaria; W. B. H.; M797, P086.

Ålandvatnet

- B616 sandstone, pale grey, fine-grained, massive, with plant fragments; B. M.; M807, P089.
- B619 sandstone, grey, fine-grained, massive, with plant fragments; B. M.; P081.

Lemströmfjellet

8443 sandstone, pale grey, medium-grained, massive, with irregular intercalations of carbonaceous, fine-grained sandstone and siltstone; M. H. P. B.; P053.

Blårevbreen

- M365 shale, black, silty, carbonaceous, micaceous, with plant fragments; M. B. B.; P202.
- Q55 shale, black, carbonaceous; J. L. F.; P146, P165.
- Q56 shale, black, carbonaceous, with plant fragments; J. L. F.; P166.

Nordkapp, Bjørnøya

- P702 shale, black, carbonaceous, weathered, with plant fragments; G. P.; P127.
- P725 shale, grey-black, carbonaceous, with Lepidodendron spetsbergense Nathorst, 'Knorria', and Carpolithus sp.; G. P.; P134.

APPENDIX B. NOTE ON SPECIMENS ILLUSTRATED BY HUGHES AND PLAYFORD (1961)

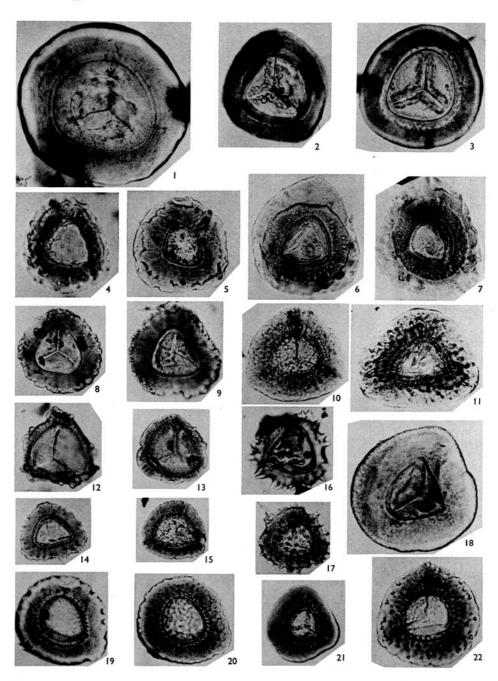
Sedgwick Museum Specimen numbers (L.880-L.938) have been allocated to type and other figured specimens of the preliminary study by Hughes and Playford (1961).

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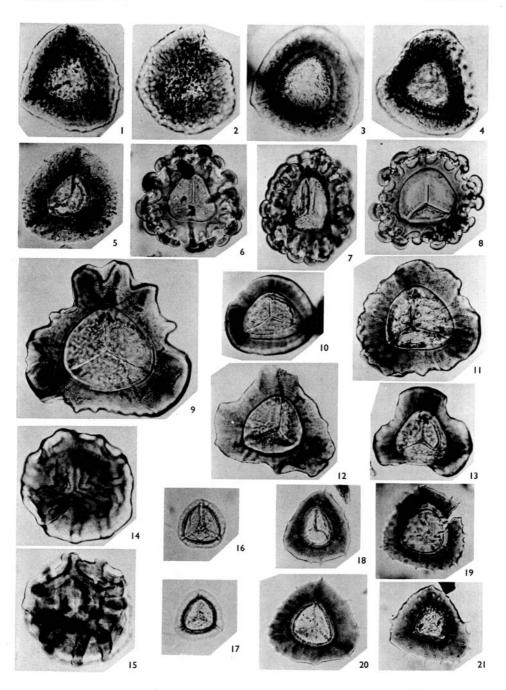
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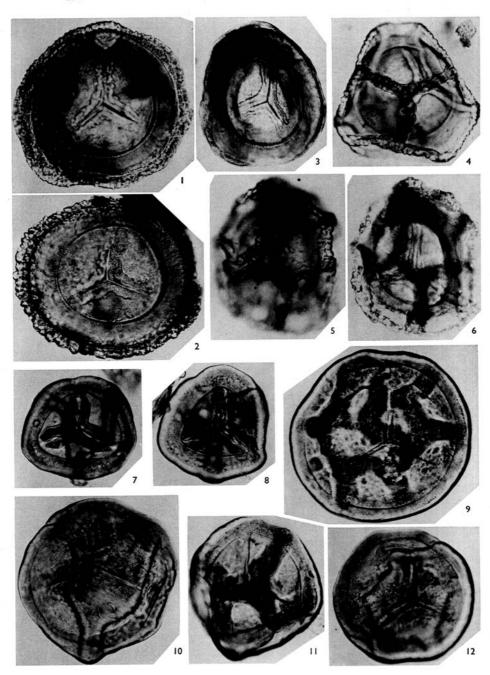
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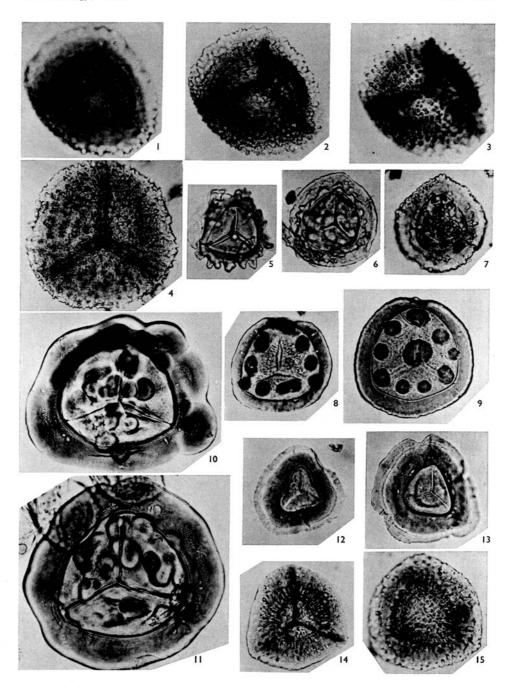
PLAYFORD, Lower Carboniferous microspores



PLAYFORD, Lower Carboniferous microspores

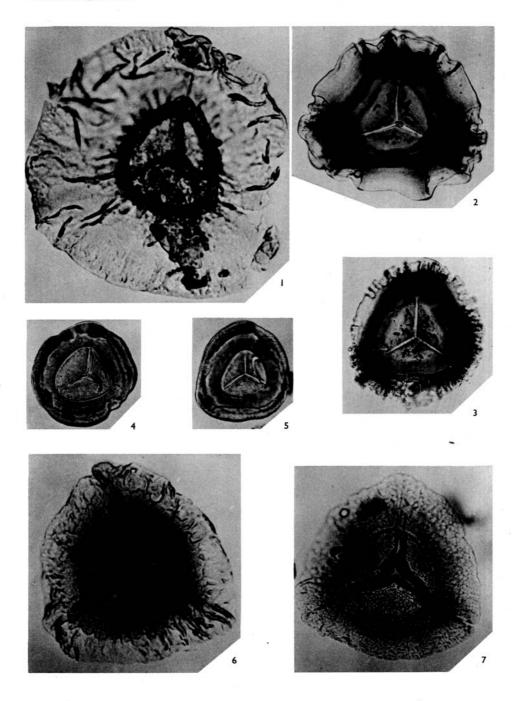


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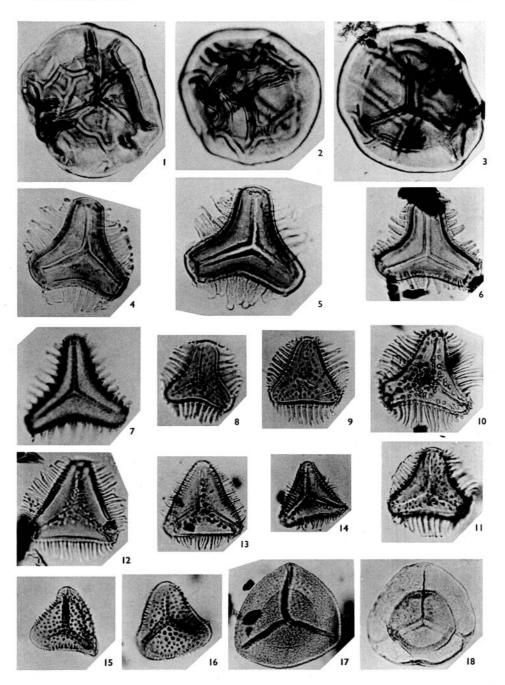


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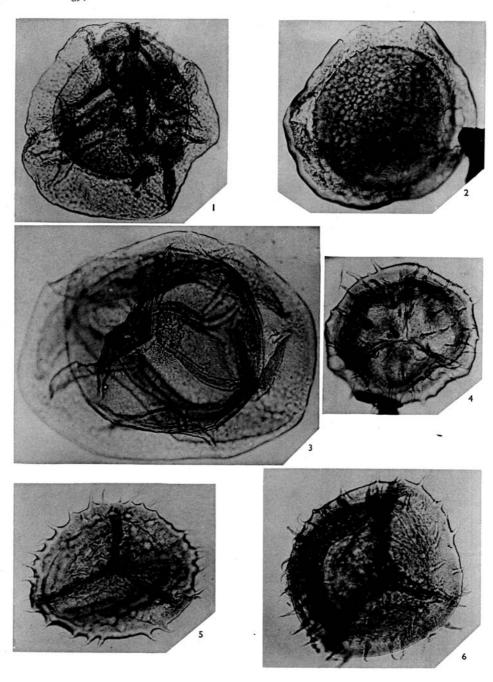
PLATE 92



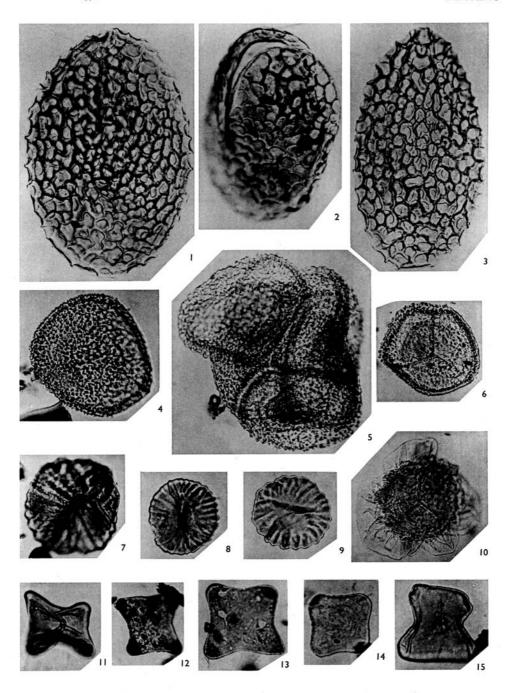
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