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GEOLOGICAL SURVEY OF CANADA

DEPARTMENT OF MINES AND TECHNICAL SURVEYS

BULLETIN 109

DEVONIAN MIOSPORES FROM THE GHOST RIVER FORMATION, ALBERTA

D. C. McGregor

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By
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PREFACE

Fossil miospores are now recognized to be valuable aids for determining the relative age of sedimentary rocks. In many instances they are the only fossils preserved and may be the sole means of reaching a conclusion. The whole study is however so new that an immense amount of descriptive work has still to be done to supply the basic information on which sound conclusions can be based.

The study reported here has added its quota to this task but, in doing so, has also added to the scanty information on the age of the Ghost River Formation supplied by its stratigraphic position and very fragmentary content of fossil plants. The problem is not yet fully resolved but as our knowledge of miospores grows there is every reason to believe that a solution will be reached.

J. M. HARRISON,
Director, Geological Survey of Canada

OTTAWA, March 1, 1963

Bulletin 109 — Devonische Miosporen der Ghost-River-Formation in Alberta.
Von D. C. McGregor

Es werden 13 Formen von Miosporen beschrieben. Die Zusammensetzung gleicht keiner bisher veröffentlichten Mikroflora, aber sie könnte dem oberen Givet oder dem unteren Frasne angehören.

Бюллетень 109 — Девонские миоспоры из свиты Гост Ривер провинции Альберты.
Д. К. МэкГрегор.

Описано 13 форм миоспор. Комплекс не напоминает ни одной из опубликованных микрофлор, но может происходить из верхнеживетского или нижнефранского яруса.

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DEVONIAN MIOSPORES FROM THE GHOST RIVER FORMATION, ALBERTA

Abstract

Thirteen forms of miospores are described from the type section of the Ghost River Formation of western Alberta: four are new species, three have previously been described, and the remainder are not given species designation. The assemblage as a whole does not resemble any published microflora, but the most abundant species, *Retusotriletes greggsii* n. sp., is similar to certain unpublished forms of upper Givetian to lower Frasnian age. Botanical relationships of the spores are considered, and the possible affiliation of *R. greggsii* with *Svalbardia* is discussed.

Résumé

L'auteur décrit treize formes de miospores qui proviennent de la section type de la formation Ghost River de l'Ouest de l'Alberta: quatre sont de nouvelles espèces, trois ont déjà été décrites et le reste n'a pas été classé par espèce. Dans l'ensemble, ces formes ne ressemblent à aucune microflore connue, mais l'espèce la plus fréquente (*Retusotriletes gregsii* n. sp.) s'apparente à certaines formes non encore décrites que l'on trouve dans le Givetien supérieur et le Frasnien inférieur. L'auteur examine les relations botaniques qui pourraient exister entre les spores et expose les liens de parenté possibles qui existent entre l'espèce *R. greggsii* et l'espèce *Svalbardia.*

Introduction

The type section of the Ghost River Formation is in the Front Range of the Rocky Mountains of Alberta, on Phantom Crag 4 miles northeast of the eastern end of Lake Minnewanka. The formation was originally named and defined by Walcott (1921, 1923)[1] to include 285 feet of red and green shales and buff-weathering dolomite of uncertain (Cambrian to Devonian) age. Recently, Greggs, McGregor, and Rouse (1962) redefined the formation at its type locality to include only the upper 145 feet of Walcott's sequence.[2] So delimited, the Ghost River unconformably overlies the Upper Cambrian Arctomys Formation and apparently grades upwards without break into strata of the Frasnian Fairholme Group.

The age of the Ghost River Formation (*sensu stricto*), based on its stratigraphic position and/or its lithological similarity to other rock units, has been variously designated as Cambrian (e.g., deWit, 1956; Aitken *in* Fitzgerald, 1962), ?Middle Devonian (e.g., Webb, 1951; Clark, 1949), Upper Devonian (e.g., Storey, 1955, 1959), and "uncertain" (e.g., deWit and McLaren, 1950; Harker, Hutchinson, and McLaren, 1954). The formation has, however, most frequently been assigned to the Middle or early Upper Devonian.

The first documented palaeontological evidence for the age of the formation was provided by Greggs, *et al.* (1962) who reported the presence of fragmentary fossil plants, including trilete spores, about 30 feet above the basal unconformity. The megafossil plants most closely resemble Givetian to Frasnian forms from Spitsbergen and Germany, and thus support the age most commonly assigned to the beds on stratigraphic evidence.[3]

The present paper describes in detail the *sporae dispersae* that were obtained by maceration of samples from the plant bed at the type section. According to Greggs, *et al.* (1962) the following spore genera were present: *Leiotriletes, Punctatisporites, Ambitisporites*, and *Retusotriletes*. This list is here revised and enlarged, and now comprises *Pilasporites*, 1 species; *Leiotriletes*, 1 species; *Calamospora*, 1 species (not *Punctatisporites*); *Retusotriletes*, 4 species (not *Ambitisporites*); *Converrucosisporites*, 1 species; *Apiculatasporites*, 1 species; *Planisporites*, 1 species; *Convolutispora*, 1 species; *Cristatisporites*?, 1 species; and *Endosporites*, 1 species.

The writer is grateful to Dr. R. G. Greggs of Shell Oil Company, who discovered the plant bed, and to Dr. Glenn E. Rouse of the University of British Columbia, who was the first palaeobotanist to examine the plants and who has read and commented upon the manuscript. Through their courtesy and the courtesy of Shell Oil Company, the material was donated to the Geological Survey

[1] Names and dates in parentheses are those of *References* cited at the end of this report.

[2] According to J. D. Aitken's interpretation of Walcott's intent (1963: *Bull. Can. Petrol. Geol.*, vol. 11, No. 3, pp. 270-271), the type section is 300 yards north of the locality specified in this paper and in Greggs, *et al.* (1962).

[3] *See* McGregor, 1963: *Bull. Can. Petrol. Geol.*, vol. 11, No. 3, pp. 299-303.

of Canada for study by the writer. Mr. N. F. Hughes of Cambridge University and Dr. F. M. Hueber of the Smithsonian Institution are thanked for permission to quote unpublished data.

Material and Techniques

The samples yielding the spores were collected by R. G. Greggs, G. E. Rouse, and the writer, from 2½ feet of buff-weathering, pale brown, shaly dolomite with much fragmentary plant material. This site has been designated as Geological Survey of Canada (GSC) plant locality 5618. The most abundant megafossils in the beds are parts of unbranched, striate and non-striate plant axes, some as large as 5 inches in diameter and 2 feet long. Associated with them are small clusters of fusiform sporangia, usually the isolated terminal parts of sporangiferous branches only; clusters consisting of numerous fusiform sporangia, more or less joined together and to larger axes; shredded (as if partly decayed) axes or laminae, occasionally approaching flabelliform, with closely spaced carbonaceous 'veins'; and fragments of strobili, of which detailed components are not clearly distinguishable. One of the largest of the latter was found attached to an axis bearing dichotomously branched, leaf-like appendages, and is probably assignable to *Svalbardia* (Greggs, *et al.,* 1962, fig. 1b, p. 930).

Attempts to apply maceration techniques to selected megafossils have not been successful. They are preserved as opaque, shiny, carbonaceous films, which break immediately upon being freed from the supporting matrix. Bulk maceration of samples with hydrofluoric acid for isolation of megafossils was also unrewarding; the largest fragments obtainable were only 166μ in size (specimens of *Cristatisporites*? sp., described below).

Conventional palynological methods involving hydrofluoric and hydrochloric acids and Schulze's reagent were used to extract the spores. Following oxidation, the residues were not treated with a base, as the introduction of potassium or ammonium hydroxide, even in very low concentrations, caused the spores to swell rapidly and disappear. As can be seen from the photographs, specimens commonly were cracked and hence tended to break readily on agitation. All were strongly flattened, so that it was not easy to distinguish between the closely appressed proximal and distal walls, or to detect the actual thickness of the wall. This being so, it was in some specimens only possible to estimate wall thickness by the relative optical density of the specimen.

Specimens were mounted in glycerine jelly, as either mixed or single mounts, and sealed with lacquer. Diaphane and Hoyer's solution were also tested as mounting media, but the spores dissolved immediately on contact with either of these mixtures. The specimens were a rich brown colour thus requiring no stain.

Each type and figured specimen has been given a number in the Geological Survey of Canada Type Series, and stored with the GSC Palaeobotanical Slide Collection in Ottawa. Some are on single specimen mounts, and others are circled on whole-assemblage slides. The specimens here described have been given numbers 13184 to 13213 in the GSC Plant Type Series.

Description of Spores

Anteturma **SPORONITES** (R. Potonié) Ibrahim, 1933

Genus ***Pilasporites*** Balme and Hennelly, 1956a

Type species. *Pilasporites calculus* Balme and Hennelly, 1956a.

Pilasporites plurigenus Balme and Hennelly, 1956a

Plate II, figure 15

"Sporomorpha sp., Pilzspore", Weyland and Greifeld, 1953, p. 46, Pl. 10, fig. 37 (Lower Senonian).
Pilasporites plurigenus Balme and Hennelly, 1956a, p. 64, Pl. 3, figs. 57-59 (Permian).
Sporonites aletes Artüz, 1957, p. 240, Pl. 1, fig. 1; Artüz, 1959, p. 22, Pl. 1, fig. 1 (Namurian-Westphalian).
Inapertisporites laevigatus Rouse, 1959, p. 312, Pl. 2, fig. 30 (Upper Jurassic); Rouse, 1962, p. 208, Pl. 1, figs. 5-6 (Middle Eocene).
Pilasporites plurigenus B. & H. *in* Orlowska Zwolinska, 1962, p. 295, Pl. VI, figs. 5-7 (Zechstein).

Description of specimens. Spores laevigate, circular, alete, but occasionally with one circular or crescentic invagination. Wall opaque and up to 2μ thick, may be folded concentrically.

Diameter (21 specimens). 13.5-24μ, mean 19.5μ.

Types. Hypotype, GSC No. 13205.

Remarks. Spores of this type occur frequently in Devonian and younger assemblages. They are usually regarded as fungal (Wilson, 1962, p. 94; Rouse, 1959, p. 313; Weyland and Greifeld, 1953, p. 46).

Comparisons. Pilasporites plurigenus appears morphologically identical with individual spores of the Permian species *Reduviasporonites catenulatus* Wilson (1962). However, *R. catenulatus* usually occurs in chains of several individual cells. The true relationship of *R. catenulatus* to *Pilasporites plurigenus* is of course enigmatic. Even so, the close similarity of the individual spores strengthens the probability that *P. plurigenus* is fungal. If it is, Wilson's statement that ". . . those fungi which produce atmospherically borne spores may have evolved at approximately Pennsylvanian-Permian time . . ." can be amended, and the time of origin of these fungi can be extended to at least the Middle Devonian. Of course, it must be remembered that morphographic similarity between such simply constructed spores is less conclusive for deducing botanical affiliation than is similarity between spores of complex structure.

Unaggregated specimens of *Sporonites unionus* (Horst) Dybová and Jachowicz (1957, p. 57, Pl. 2, figs. 2 and 3; 1958, p. 72, Pl. 1, fig. 2) may be similar to *Pilasporites plurigenus*, although the illustrations do not assist in comparison. *S.* (?) *unionus* Horst (1955) has a conspicuous resin-like gloss, so may be of different origin.

"*Laevigataletes*" Type 1, Type 2, and Type 3 (Vishnu-Mittre, 1955) are only briefly described from thin sections of chert. Had it been possible to free them by maceration their identity with *Pilasporites plurigenus* might have been confirmed. They possess the four most obvious criteria that distinguish *P. plurigenus,* i.e., circular outline, small size, unornamented wall, and lack of haptotypic features.

"Spore type C" of Hoffmeister, *et al.* (1955a) differs from *P. plurigenus* only in being larger. A Lower Triassic form, *Spheripollenites elphinstonei* Jansonius (1962), was placed by its author in tentative synonymy with *Pilasporites plurigenus*, but it has a layered wall and very distinct infrapunctation. These features were not mentioned by Balme and Hennelly for *P. plurigenus*, and their photograph shows no trace of such structure. Thus it seems probable that *Spheripollenites elphinstonei* and *Pilasporites plurigenus* are not synonymous.

One of the figured specimens called *Chaetosphaerites*? *pollenisimilis* (Horst) by Staplin (1960), the single cell of his Plate I, figure 13, is like the Ghost River specimens except for its thicker wall.

Small alete (Lower?) Devonian spores associated with *Nematoplexus* Lyon (1962) from the Rhynie Chert are sufficiently similar to the Ghost River type to warrant mention here; they would probably be included in *Pilasporites plurigenus* if found dispersed. This comparison does not however necessarily imply relationship of the latter to the Nematophytales.

Anteturma **SPORITES** H. Potonié, 1893

Infraturma LAEVIGATI (Bennie and Kidston) R. Potonié, 1956

Genus ***Leiotriletes*** (Naumova) Potonié and Kremp, 1954

Type species. Leiotriletes sphaerotriangulus (Loose) Potonié and Kremp, 1954.

Age difference seems to be the main criterion used to justify maintaining *Deltoidospora* Miner and *Leiotriletes* (Naum.) Pot. & Kr. as separate form-genera (*see* Potonié, 1960). Staplin (1960) pointed out the fallacy of this distinction, and in his paper used *Deltoidospora* which has priority. The present writer agrees with his argument for doing so, but on the other hand, almost all workers in Palaeozoic microfloras maintain the distinction, and as Playford (1962) says, this problem in principle involves other form-genera as well (e.g., *Convolutispora* H., S., & M. vs. *Rugulatisporites* Pflug). Furthermore, other genera of triangular, trilete, laevigate spores such as *Cyathidites* Couper, *Hymenophyllumsporites* Rouse, *Matonisporites* Couper, and *Alsophilidites* Cookson ex Potonié should be considered in relation to *Leiotriletes*, since it could be argued that neither age difference nor supposed (unproven) differences in natural affinity for *sporae dispersae* are justifiable criteria for separating them.

The writer is of the opinion that deviation from generally accepted practice at this time should be accompanied by lengthy discussion of the various genera involved. Rather than digress to this extent, it has been decided to follow Potonié (1960) in using *Leiotriletes*, rather than *Deltoidospora* (and *Convolutispora* rather than *Rugulatisporites*), as the former name has been most consistently applied for Palaeozoic spores of this type.

Leiotriletes priddyi (Berry) Potonié and Kremp, 1955

Plate II, figure 16

Zonales-sporites priddyi Berry, 1937, p. 156, fig. 2 (Mississippian).
Levigatisporites marlisae Thomson, 1952, p. 158, Pl. 10, figs. 1-3 (Lower Coblenzian).
Leiotriletes falsus Ishchenko, 1952, p. 10, Pl. 1, fig. 6 (Lower Carboniferous).
Leiotriletes priddyi (Berry) Potonié and Kremp, 1955, p. 38.
Granulati-sporites politus Hoffmeister, Staplin, and Malloy, 1955, p. 389, Pl. 36, fig. 13 (Upper Mississippian).
Leiotriletes parvus Nilsson, 1958, p. 30, Pl. 1, fig. 1 (Liassic), *non L. parvus* Naumova, 1953.
?*Granulatisporites parvigranulatus* Staplin, 1960, p. 15, Pl. 3, figs. 8-9 (Upper Mississippian).

Description of specimens. Spores trilete, laesura simple, rays extend two thirds to four fifths of the distance to the equator. Amb subtriangular, apices broadly rounded, interradial margins slightly concave to slightly convex. Wall about 1μ thick, occasionally folded, laevigate, sometimes infragranulate (*sensu* Potonié and Kremp, 1955).

Diameter (4 specimens). 33-45μ.

Types. Hypotype, GSC No. 13206.

Remarks. Occasional small areas of the wall on some predominantly infragranulate specimens appear devoid of any structure. The infrastructure (or partial lack of it) on these specimens may have been caused by corrosion. Thomson (1952) suspected a similar cause for the slight [infra-?] granulation on some specimens of *Levigatisporites marlisae*. *Granulatisporites politus* H., S., & M. (1955a) is another example of a species, of which the wall may be either smooth or with infrastructure (although its authors do not suggest that the infrapunctation is a result of corrosion). Evidently infrastructure, whatever its origin, is of uncertain value for separating species.

Comparisons. An explanatory note may be appropriate concerning the inclusion here of *Granulatisporites politus* within *Leiotriletes priddyi*. While comparison of Plate II, figure 16 of this paper with Plate 36, figure 13 of Hoffmeister, *et al.* (1955a) may convey the impression that the two are not comparable, the description of *Granulatisporites politus* (op. cit., p. 389) agrees precisely with that of the Ghost River specimens, and encompasses the circumscription of *Leiotriletes priddyi*.

In recent papers on Lower Carboniferous spores from Scotland, Butterworth and Williams (1958, p. 361) and Love (1960, p. 111) have given *Granulatisporites politus* a somewhat different connotation by indicating that it has a tendency for ". . . angular junction of radial and inter-radial areas" (Butterworth and Williams, loc. cit.). Love concluded that this is not a specific character, but it is perhaps still a matter of doubt whether this is so (*see* Playford, 1962, p. 583).

Even so, this feature is scarcely, if at all, evident in the photograph accompanying the original description of *G. politus* (Hoffmeister, *et al.*, 1955a), and probably would be even less evident on specimens of that species that possess convex interradial margins. Considering the above, it seems best at present to exclude the Scottish specimens from *Leiotriletes priddyi*.

Numerous species of triangular, trilete, laevigate spores have been described, many of which are probably synonymous. Those listed above as synonyms of *L. priddyi* have descriptions coinciding with that of the Ghost River type, and there are undoubtedly others, not listed here, that also qualify. Collectively, their ages span a wide range, which is reasonable when one considers the relatively few criteria available for specific distinction. Undoubtedly this form-species, like most others in the genus *Leiotriletes*, incorporates more than one natural species.

Spores found in sporangia of *Zosterophyllum llanoveranum* (Croft and Lang, 1942, p. 148, fig. 40) are slightly larger (45-65μ) than *Leiotriletes priddyi*, but are otherwise apparently similar. When found they were still enclosed in the sporangial walls, and some were still united in tetrads; they may thus have been immature, and if fully developed and dispersed might have been considerably larger.

Genus ***Calamospora*** Schopf, Wilson, and Bentall, 1944

Type species. Calamospora hartungiana Schopf, *in* Schopf, Wilson, and Bentall, 1944.

Calamospora atava (Naumova, 1953) n. comb.

Plate II, figure 17

"Spore-type D", Lang, 1925, p. 256, Pl. 1, fig. 8 (Middle Devonian).
Leiotriletes atavus Naumova, 1953, pp. 23 and 103, Pl. 1, fig. 8, Pl. 16, fig. 3 (Middle and Upper Devonian); Tuzova, 1959, p. 106, Pl. 1, fig. 7 (Middle and Upper Devonian).
?*Leiotriletes atavus* Naum. *in* Kedo, 1955, p. 19, Pl. 1, fig. 5 (Middle and Upper Devonian).

Description of specimens. Spores trilete, laesura simple, rays one half or two thirds as long as the radius of the spore. Amb subcircular. Wall opaque (thickened?) in interradial areas, the darkened areas merging radially with the lighter part of the wall without distinct limits. Exine laevigate, about 1μ thick, tends to fold concentrically.

Diameter (2 specimens). 74μ and 84μ.

Types. Hypotype, GSC No. 13207.

Comparisons. According to Lang's (1925) brief description, spore-type D corresponds closely with the Ghost River specimens except that its upper size limit is only 75μ (although measurement of Lang's Pl. 1, fig. 8 gives a size of 80μ). Size alone is probably not sufficient criterion for separation, because with only two specimens available, the range of variation for the Ghost River form has not been established.

Leiotriletes atavus Naumova (1953) is only 50-70μ in diameter according to Naumova, but Kedo (1955) records it as 60-80μ. Naumova's description matches the present specimens in all respects except size, but Kedo's specimens have a "thickened margin". On the basis of the descriptions, therefore, the synonymy of Kedo's spores with those of Naumova, and hence with the Ghost River specimens, does not seem certain.

Another discrepancy between descriptions by Naumova and Kedo involves *Leiotriletes nigratus* Naumova (1953, p. 23). Kedo (1955, p. 20) transferred this species to *Trachytriletes* and commented that the surface of the exine is shagreen. The writer can see no alternative but to regard them as separate species for the present but suggests that there may be a typographical error in Naumova's text, since she specifically stated that the exine is laevigate. This possibility is supported by Naumova's illustrations of *L. nigratus* (Pl. 1, fig. 9; Pl. 5, figs. 5, 6) which are stippled as though to indicate an ornamented (shagreen?) exine. *Leiotriletes nigratus* Naumova (smooth exine) would differ from *Calamospora atava* (Naumova) n. comb. only in the length of the rays.

Still another species, *Leiotriletes nigratus* Ishchenko (1958, p. 35) *non* Naumova, is larger than *Calamospora atava* and has slightly shorter rays.

Calamospora saariana Bhardwaj (1957) is smaller, with rays always less than half the spore radius. The wall of *C. membrana* Bhardwaj (1957) is very thin ("membranous") in the equatorial region and thickens noticeably towards the proximal pole, whereas the wall of *C. atava* from Ghost River is not evidently differentiated in this manner.

Genus ***Retusotriletes*** Naumova, 1953

Type species. Retusotriletes simplex Naumova, 1953.

Retusotriletes biarealis n. sp.

Plate I, figures 13 to 15

Description. Spores trilete, laesura simple, length of rays one half to four fifths of the spore radius. Amb subcircular to circular. Wall about 1μ thick, opaque in interradial areas, the darkened area (contact area?) forming a triangle, the apices of which are the extremities of the rays. In addition, the proximal face bears three larger areas delimited near the equator by curvaturae. Curvaturae raised only slightly (ca. 1μ or less) above the spore surface. Ornamentation of the part of proximal surface enclosed by curvaturae, scabrate; remainder of spore laevigate. On some specimens there is a slight appearance of radial alignment of the scabrate ornamentation on the proximal face (*see* fig. 13).

Diameter (11 specimens). 93-127μ, mean 107μ.

Types. Holotype, GSC No. 13192, Pl. I, figs. 13-14; paratype, GSC No. 13193.

Remarks. Some specimens from Ghost River (*see* Pl. I, fig. 15) are scabrate outside the proximal curvaturae. This feature appears to have been caused by corrosion; a part of undamaged laevigate wall is visible at the top of figure 15.

Comparisons. No spore has been described that closely resembles this distinctive species. The specimen that Eisenack (1944) labelled "Sporentyp E? (nach Lang)" and illustrated in his Plate 2, figure 8, is similar in size, has a suggestion of a darkened triangular (contact?) area, and may have curvaturae judging from the photograph. However, it is clearly not conspecific with *R. biarealis* n. sp.

The specimen of "Spore-type D" which Lang (1925) illustrated in Plate I, figure 8, may also have curvaturae, even though Lang does not mention this feature. If it does have curvaturae, it resembles *R. biarealis* except for its smaller size and entirely smooth wall. On the other hand, according to Lang's description alone, Type D is similar to *Calamospora atava* from the Ghost River beds (*q.v.*).

The Middle Devonian species *Retusotriletes translaticius* Chibrikova (1959) possesses both curvaturae and darkened interradial areas, but it is much smaller than *Retusotriletes biarealis* (25-45μ).

Retusotriletes greggsii n. sp.

Plate I, figures 1 to 12

Description. Spores trilete, laesura simple or with thickened or folded margin. Rays at least four fifths as long as the radius of the spore. Ray extremities joined by arcuate thickening of the wall (curvaturae) equatorially or slightly proximally. Arcuate thickening very dark and up to 8μ wide on some specimens (*see* Pl. I, figs. 1, and 3 to 5), or less pronounced, to only slightly noticeable on others (Pl. I, fig. 6); usually slightly wider and invaginated at the tips of the rays. Specimens with lesser thickening of curvaturae may show thin light lines (grooves?) connecting the extremities of the rays. Amb broadly subtriangular to circular. Distal side usually somewhat more rounded than the proximal. Occasionally a part of the distal wall projects to one side as an irregular bulge, even in nearly polar compression (as in Pl. I, fig. 11).

Part of proximal wall enclosed by curvaturae, laevigate or with ornamentation much reduced (Pl. I, fig. 5); remainder of wall with minute coni or apiculae (i.e., taper-pointed, or elongate and blunt), commonly so small that they are clearly distinguishable only under the oil immersion lens (Pl. I, figs. 2, 10, and 12). Ornaments about 0.5-1μ long with basal width slightly less than height; rarely as much as 2μ long with basal width of 1.5μ (*see* Pl. I, figs. 7 and 8).

Diameter (202 specimens). 60-113μ, mean 87μ (*see* Fig. 1).

Types. Holotype, GSC No. 13184, Pl. I, figs. 1-2; paratypes, GSC Nos. 13185, 13186, 13187, 13188, 13189, 13190, 13191.

Remarks. An apparently continuous gradation occurs between the extremes for both the diameter of spores and the size of ornaments in *R. greggsii* n. sp. (compare Pl. I, figs. 6, 7, and 11). The variation in ornamentation may, at least partly, depend on the degree of corrosion of the specimens. However, variation in sculpture together with the relatively wide range of spore diameter suggested that it might be possible to detect two (or more) natural species in this form-species.

With this possibility in mind, the writer plotted the diameter range of 200 specimens of *R. greggsii*. The result (Fig. 1) resembles a normal distribution curve, but has a slight dip at 90-95μ. The dip is too small to be construed as indicative of an overlap in the size ranges of two species, and it is concluded that more than one species cannot be detected on the basis of diameter. In fact, somewhat similar size distributions occur for spores from single megafossil species (although not from single sporangia?), e.g., *Lepidostrobus diversus* Felix, *L. pulvinatus* Felix, and *Lepidocarpon magnificum* And. & Pan. (*in* Felix, 1954).

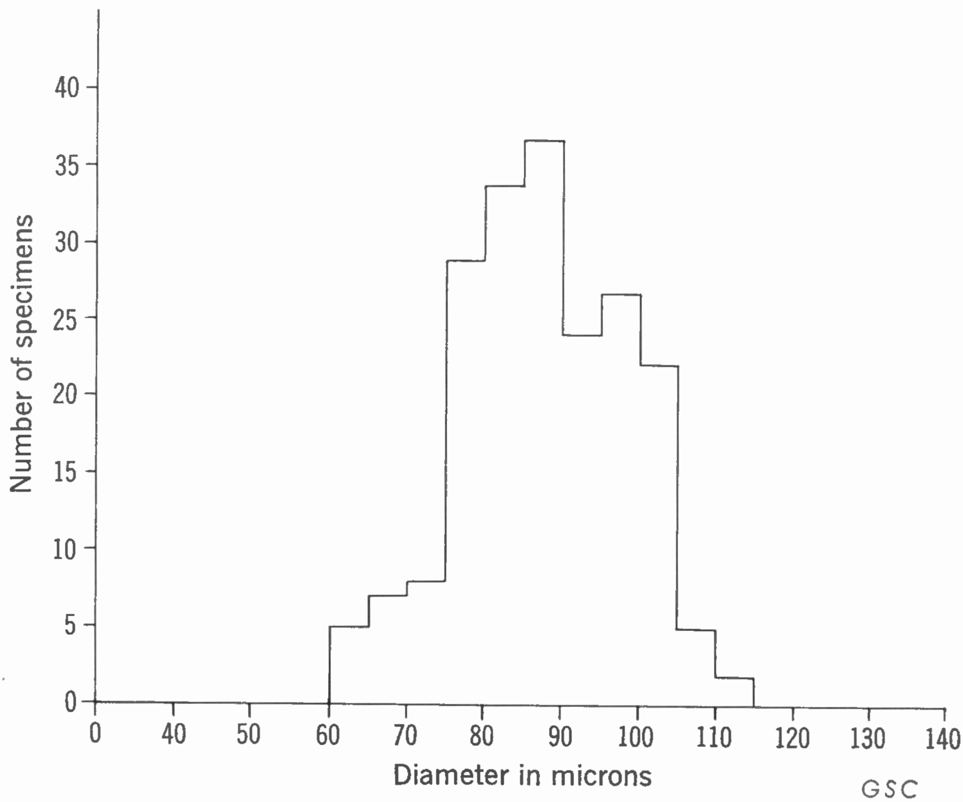

FIGURE 1. Diameter range of 200 specimens of *Retusotriletes greggsii* n. sp.

In Greggs, *et al.* (1962) the present writer placed the spores here assigned to *Retusotriletes greggsii* tentatively in *Ambitisporites* Hoffmeister (1959). Since the former paper was written, it has become clear that assignment to *Retusotriletes* is more appropriate. It might also be mentioned here that the writer is unable to discover any clear distinction between *Ambitisporites* and *Stenozonotriletes* (Naumova) Hacquebard (1957), and regards the two as synonymous.

Comparisons. Russian palynologists have described two species that deviate only slightly from *Retusotriletes greggsii. Retusotriletes verrucosus* Kedo (1955)[1] from the Middle Devonian has a round outline, has small rounded tubercles, and is "somewhat thickened in some specimens along the edge" (translation from Kedo, 1955, p. 22). However, no mention is made of cone-like ornamentation, and the occasional thickening "along the edge" is apparently in addition to the curvaturae as the rays are only two thirds as long as the radius of the spore and the curvaturae therefore are proximal rather than nearly equatorial (op. cit., Pl. 1, fig. 17).

Retusotriletes punctatus Chibrikova (1959), an Upper Givetian-Lower Frasnian species, possesses minute tubercles, but neither their shape nor their size is described specifically. It is, however, smaller (40-50μ) than *R. greggsii.*

Some specimens of *R. greggsii,* in which the curvaturae are not greatly thickened, resemble spores from sporangia associated with *Eospermatopteris* (Kräusel and Weyland, 1935, p. 16). At least some of the latter, from the Middle Devonian of New York, are "körnige", and the photographs show the curvaturae plainly.

R. greggsii may also resemble spores believed to belong to *Svalbardia polymorpha*, described from Spitsbergen by Høeg (1942, p. 77, Pl. XXXI, figs. 5-9).

Retusotriletes semizonalis n. sp.

Plate II, figures 1–5 and 7–8

Description. Spores trilete, laesura simple or with narrow lips. Rays extend to or almost to the equator. Amb subtriangular to subcircular, wall about 1μ thick. More or less thickened (up to 3μ) opaque curvaturae join the extremities of the rays. Curvaturae, which are equatorial or nearly so except where they are connected to the ray tips slightly proximally, form a pseudo "otorochka" in the sense of Luber (1955, p. 9, item 1). Ornamentation consists of extremely minute, closely spaced coni (fig. 4), which may only be distinguishable under an oil immersion objective.

Diameter (19 specimens). 50-67μ, mean 60μ.

Types. Holotype, GSC No. 13197, Pl. II, figs. 3-4; paratypes, GSC Nos. 13194, 13195, 13196, 13198, 13199.

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[1] Both Kedo (1955, p. 22) and Andreeva (1962, p. 200) refer to this species as "*Retusotriletes verrucosus* Naum. in litt.". However, the first published description seems to be that of Kedo (1955).

Remarks. In this species the degree of thickening of the curvaturae varies somewhat. Some specimens (e.g., Pl. II, figs. 3, 8) apparently resemble *Stenozonotriletes* (Naum.) Hacquebard except for the slight incurving of the thickenings (curvaturae) to meet the extremities of the rays. The latter feature is clearly *Retusotriletes*-like, and the fact that in occasional specimens the curvaturae are partly proximal allows its recognition as *Retusotriletes.* The spore illustrated in Plate II, figure 7, is an extreme form (overmacerated?).

Comparisons. This species agrees with the diagnosis of *R. communis* Naumova (1953, p. 97: "rays a little shorter than the radius of the spore body"), but according to Naumova's drawings (Pl. XV, figs. 15-17; Pl. XVI, fig. 42; and Pl. XVIII, figs. 20, 21) the rays of *R. communis* are distinctly shorter and the curvaturae are entirely proximal.

Retusotriletes semizonalis n. sp. apparently resembles the Lower Carboniferous species *Asterocalamotriletes marginellus* (Luber) Luber (1955) in all respects except in ornamentation. In 1955 Luber did not mention ornamentation of *A. marginellus*, but in 1938 she described the same spore as *Zonotriletes marginellus* and at that time stated that the exine was unornamented.

One specimen of *Retusotriletes semizonalis* (Pl. II, fig. 7) compares fairly closely with the spore of *Protopteridium minutum* Halle (1936, particularly Pl. V, fig. 12). The resemblance may be just superficial, and could only be verified by examination of the specimens.

Retusotriletes sp.

Plate II, figure 6

Retusotriletes sp. A, Balme, 1960, p. 28, Pl. 4, fig. 7 (Lower Carboniferous).
Retusotriletes sp. cf. *R. pychovii* Naumova var. *major* Naumova *in* Balme & Hassell, 1962, p. 7, Pl. I, fig. 13 (Famennian).
Retusotriletes cf. *R. pychovii* Naumova *in* Balme, 1962, p. 4, Pl. 1, figs. 3-4 (Frasnian).

Description. Spores trilete, laesura slightly thickened and raised above the spore surface, rays one half to two thirds the length of the spore radius. Amb subcircular. Curvaturae distinct, raised very slightly above the general spore surface, and very convex although they rarely extend to the equator. Area enclosed by curvaturae lighter in colour than remainder of spore. One of the areas slightly smaller than the other two. Wall laevigate to minutely scabrate under oil immersion lens, rigid in appearance, thickness not determinable.

Diameter (4 specimens). 66-77μ, figured specimen 66μ.

Types. Hypotype, GSC No. 13200.

Remarks. Each of the specimens from the Ghost River Formation has "areas" of unequal size. Although this inequality might possibly be a phenotypic feature, it is not an unusual occurrence in other species of *Retusotriletes,* and is therefore of doubtful value for distinguishing species.

Comparisons. One of the characters by which Naumova distinguishes *R. pychovii* is its thick wall, or at least the thickening of the wall as seen at the equator in polar compression. It is not clear from her description whether all the wall outside the proximal "areas" of *R. pychovii* is thickened, or whether the thickening is only equatorial. Nevertheless, the four Ghost River specimens are apparently not greatly thickened, and thus not conspecific with *R. pychovii.* They do agree closely with *R.* sp. cf. *R. pychovii* Naumova var. *major* Naumova of Balme and Hassell (1962, p. 7) which has a wall about 1μ thick. They are also similar to *R.* sp. A of Balme (1960, p. 28), which Balme compares to *R. pychovii* cf. *major* Naumova, and with *R.* cf. *R. pychovii* Naumova of Balme (1962, p. 4) from the Lower Carboniferous and the Frasnian, respectively, of Western Australia. The latter only differs from the Canadian specimens in slightly smaller size (58-67μ), according to Balme's description. On the other hand measurement of the photograph in Balme (1962, Pl. I, fig. 4) gives a size of 76μ for the specimen of *R.* cf. *R. pychovii,* which leads one to suspect that the 67μ figure quoted in the size range may be a typographical error.

Azonotriletes lemniscatus Luber (*in* Luber and Waltz, 1941, p. 53), from the Lower and Upper Carboniferous of Kazakhstan, seems to differ only in possession of "small hair-like outgrowths" along the curvaturae.

Evidently, smooth or nearly smooth *Retusotriletes*-like spores occur through a large part of the geological column, albeit not in large numbers. See *Calamospora diversiformis* Balme and Hennelly (1956b, p. 246) from the Permian, *Retusotriletes mesozoicus* Klaus (1960, p. 120) from the Triassic, and *Leiotriletes harpeformis* Bolkhovitina (1953) from the Lower Cretaceous.

Infraturma APICULATI (Bennie and Kidston) R. Potonié, 1956

Genus ***Converrucosisporites*** Potonié and Kremp, 1954

Type species. Converrucosisporites triquetrus (Ibrahim) Potonié and Kremp, 1954.

Converrucosisporites sp.

Plate II, figures 18, 23, and 24; Figure 2

Description. Spores trilete, rays reach to or nearly to the equator of the spore, commissure indistinct because of ornamentation of the exine. Amb roundly subtriangular. Wall probably thin, but precise thickness indeterminable; covered overall by closely spaced slightly tapering rounded ornaments, variable in size, up to 2.5μ in height and up to 3μ in basal width. Ornaments circular to sinuous in plan.

Diameter (3 specimens). 40μ, 41μ, and 47μ.

Types. Hypotypes, GSC Nos. 13208, 13209.

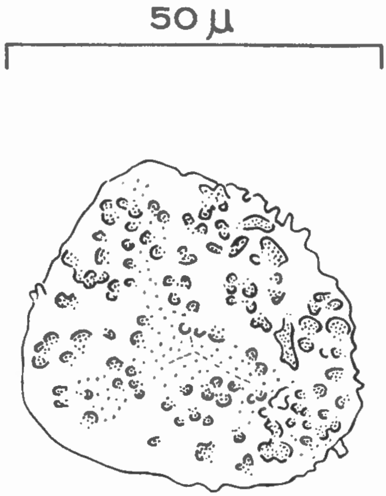

FIGURE 2. *Converrucosisporites* sp., camera lucida drawing, distal side.

Remarks. These specimens were at first regarded as variants of *Convolutispora paraverrucata* n. sp., but further study indicated that they lie well outside the size range of that species and have somewhat smaller non-anastomosing verrucae.

Comparisons. Converrucosisporites parvinodosus Playford (1963) has lower, more rounded verrucae and a distinct negative reticulum. *Acanthotriletes impolitus*, according to the drawings in Naumova (1953, Pl. I, fig. 18), Tuzova (1959, Pl. I, fig. 21), and Chibrikova (1959, Pl. I, fig. 14), has more widely spaced ornaments, and in fact Chibrikova (1959, p. 44) mentions this feature. *A. denticulatus* Naumova (1953) and *A. crenatus* Naumova (1953) have sharp-tipped "thorns". *Converrucosisporites subverrucosus* Bhardwaj (1957) is smaller, but otherwise is apparently similar to *C.* sp. *C. triquetrus* (Ibr.) Pot. & Kr. (1954) has larger verrucae which may be "plattenförmige". *C. varietus* (Imgrund) Pot. & Kr. (1955) has wart-like ornaments that are not variable in size and shape as are those of *C.* sp.

Genus ***Apiculatasporites*** Ibrahim, 1933 (*sensu* Potonié, 1960)

Type species. Apiculatasporites spinulistratus (Loose) Ibrahim, 1933.

Apiculatasporites dilucidus (McGregor, 1960) n. comb.

Plate II, figures 12 to 14

? "Spore-type E", Lang, 1925, p. 256, Pl. I, fig. 9 (Middle Devonian).

? *Azonotriletes punctulatus* Waltz (*pars*) in Luber & Waltz, 1941, p. 14, Pl. II, figs. 16a, 16b (Lower Carboniferous).

? *Trachytriletes punctulatus* (Waltz) Ishchenko (*pars*), 1952, p. 21, Pl. IV, figs. 35 to 37 (Middle Carboniferous).

Planisporites dilucidus McGregor, 1960, p. 30, Pl. 11, fig. 10 (Upper Devonian).

Diameter (11 specimens). 50-69μ, mean 62μ.

Types. Hypotypes, GSC Nos. 13203, 13204.

Remarks. The number of cones visible at the equator varies from 75 to 124, with 91 the mean. This is slightly greater than for *Apiculatasporites* (*Planisporites*) *dilucidus* from Melville Island (McGregor, 1960), but not sufficiently different to justify placing them in different species.

Comparisons. Lang (1925) found two specimens from the Middle Devonian of Scotland, "Spore-type E", which are 50-60μ in size and bear "numerous small, pointed projections or papillae". According to Lang's illustration of type E, it may have slightly larger, less numerous ornaments. In other respects it seems to be identical with *Apiculatasporites dilucidus.*

The Middle Devonian Spore-type VIA of Thomson (1940, p. 12, Pl. 3, fig. 16) described as "mit sehr kleinen Papillen bedeckt" may be very much like *Apiculatasporites dilucidus,* but the ornamentation was not described in detail, and specimens of type VIA have not been examined by the present writer. Another of Thomson's types, VIB, was likened by him (p. 12) to type E of Lang (1925), but Thomson's photograph and description suggest that type VIB has larger and less regular ornaments.

Azonotriletes punctulatus Waltz in Luber and Waltz (1941, p. 14; =*Trachytriletes punctulatus* (Waltz) Ishchenko, 1952, p. 21) differs only slightly in ray length (one third to two thirds of the spore radius) from the Ghost River species. According to Luber and Waltz there are several varieties that differ in size, the smallest being 25-45μ and the largest 90-115μ. The same authors described the wall as very thin, but remarked that it increases in thickness with the size of the spore. They described the sculpture as "fine-grained or punctate" while Ishchenko (1958, p. 41) called it "fine-grained or almost tuberculate". *A. punctulatus* is obviously extremely variable, and if its ornaments are coni, its scope encompasses *Apiculatasporites dilucidus.* It is long-ranging in the U.S.S.R., being widespread in the Lower Carboniferous and occurring also in the Permian (Luber and Waltz, 1941, p. 14).

Microspores of *Crossotheca hughesiana* Kidston (1923, p. 338, text-fig. 25) may be referable to *A. dilucidus* if the "apiculae" are cones. *Punctatisporites fissus* Hoffmeister, *et al.* (1955a, p. 393) has granules rather than cones, is commonly folded, and has shorter rays.

Hacquebard and Barss (1957) described a species, *Punctatisporites nahannensis,* from the Lower Carboniferous of the Nahanni River area of western Canada, which differs from *Apiculatasporites dilucidus* in somewhat wider spacing of the cones, unequal length of the rays, and smaller size. Two lowermost Mississippian spores called *Punctatisporites* sp. *C.* by Winslow (1962) have slightly longer ornaments, and a "vaguely defined contact area".

Planisporites furfuris Balme and Hassell (1962) from the Famennian of Western Australia has somewhat shorter rays than *Apiculatasporites dilucidus.* Slight differences in ray length (as between one half and two thirds of body radius), however, like slight differences in number of ornaments at the periphery, are perhaps of doubtful value for making fine distinctions between form-species. The main difference between *A. dilucidus* and *Planisporites furfuris* seems to lie in the tendency of the latter to be rounded-triangular rather than circular (p. 6, op. cit.).

According to Naumova (1953, p. 27), *Lophotriletes subrotundatus* has rays equal in length to the spore radius. In the specimen that she illustrated however, they are about two thirds to four fifths as long as the radius. The ornaments of the species are not described in detail, which prevents evaluation of its similarity to *Apiculatasporites dilucidus*.

Trachytriletes solidus Naumova *in* Kedo (1957, p. 15) may also be similar to *A. dilucidus*. Neither Kedo nor Naumova (1950, 1953) described this "species", although all three papers include drawings of it. In Kedo's paper its size range coincides with that of *A. dilucidus*, but according to Naumova (1953) it is only 15-40μ in diameter. Spore diameter is a feature that some Russian palynologists (e.g., Naumova, Luber, Kedo) apparently regard as very variable within species, and of relatively less importance for distinguishing species than ornamentation, shape, wall thickness, "perispore" development, etc. For example, Naumova cited four different diameter ranges for *Trachytriletes solidus* (1953, pp. 46, 95, 104, and 121) and she repeated this procedure for several other species in the same paper. The considerable size latitude for *Azonotriletes punctulatus* Waltz is another example (*see above*). Evidently, it is not the intention of these workers to set rigid limits of size for their species. They seem to devote more attention to spore size as a function of evolution and palaeoecology (*see* Naumova, 1953, pp. 9-10), an aspect that might be explored profitably by other palynologists.

Genus ***Planisporites*** (Knox) Potonié, 1960

Type species. Planisporites granifer (Ibrahim) Knox, 1950.

Planisporites sp.

Plate II, figure 19; Figure 3

? *Azonotriletes resistens* Luber *in* Luber and Waltz, 1941, p. 54, Pl. XII, fig. 183 (Middle and Upper Carboniferous).

Description. Spores trilete; ray length indistinct, but with thickening or folds along two of the rays almost to the equator. Amb subtriangular, sides convex. Wall about 1μ thick, densely covered by cones up to 1.5μ long and less than 1μ wide at their base, most only very slightly tapered. Little variation in size and shape of cones. Eighty-two cones visible at margin.

Diameter (one specimen). 53μ.

Types. Hypotype, GSC No. 13210.

Comparisons. Synonymy of *Azonotriletes resistens* Luber (*in* Luber and Waltz, 1941, p. 54) with *Planisporites* sp. is questioned because Luber did not describe the ornamentation in detail. *Azonotriletes parvispinus* Luber, described in the same paper (p. 67), is less densely covered with spines of variable shape.

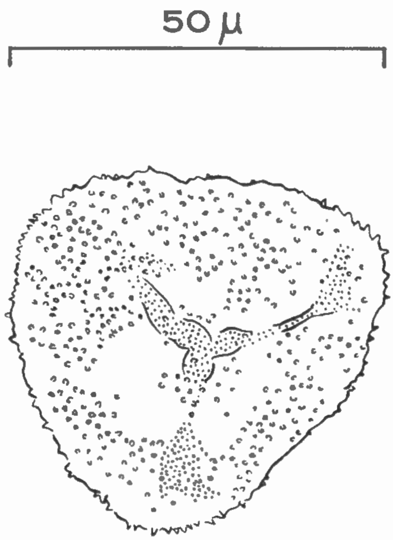

FIGURE 3. *Planisporites* sp., camera lucida drawing, proximal side.

Both Lang and Thomson have published photographs and short descriptions of spores that may fairly closely resemble the present specimen. In these accounts, however, the descriptions are brief, and the illustrations inadequate to show the finer details of structure. The spores concerned are Spore-type E of Lang (1925; *see also* comments under *Apiculatasporites dilucidus* in this paper), spores of group VIB of Thomson (1940), and *Levigatisporites eiserfeyensis* Thomson (1952).

Azonotriletes echinatus Andreeva (1953), Pl. III, fig. 38, *nomen nudum,* (?) *non* Andreeva, 1956, p. 260) apparently has larger coni. *Acanthotriletes tenuispinosus* Naumova (1953, p. 25) has "rather short thorns", but the drawing (Pl. I, fig. 17) indicates that they are longer than those of *Planisporites* sp. *Acanthotriletes tenuispinosus* var. *famenensis* Naumova (Pl. I, fig. 18, op. cit.) is not described but may be more like the Ghost River specimen. *Acanthotriletes circumactus* Ishchenko (1956) has slightly concave sides (op. cit., p. 33, but *see* Pl. 5, fig. 53), which may not be sufficient criterion for distinction from *Planisporites* sp. However, since the ornamentation is not described in detail, its degree of similarity to *Planisporites* sp. is uncertain.

Infraturma MURORNATI Potonié and Kremp, 1954

Genus ***Convolutispora*** Hoffmeister, Staplin, and Malloy, 1955a

Type species. Convolutispora florida Hoffmeister, Staplin, and Malloy, 1955a.

Convolutispora paraverrucata n. sp.

Plate II, figures 9 to 11

Description. Spores trilete, laesura simple, rays more than half the length of the radius. Laesura usually obscured by the opaque ornamentation of the exine. Amb circular to very roundly subtriangular. Wall, exclusive of ornamentation, apparently thin but exact thickness not determinable. Ornamentation consisting of closely spaced round-topped, flat-topped, or conical, sometimes anastomosing rugulae or verrucae, irregularly elongate, S-, Y-, or V-shaped, or subcircular in plan view. Ornaments variable in size, usually no more than 7μ long, rarely as much 2.5μ wide, maximum height about 4μ. Marginal outline of spore irregular because all variations of ornamentation may occur on a single specimen.

Diameter (35 specimens). 54-83μ, mean 65μ.

Types. Holotype, GSC No. 13202, Pl. II, fig. 10; paratype, GSC No. 13201.

Remarks. Playford (1963) comments on the close morphographic relationship between *Convolutispora* and *Verrucosisporites.* Certainly there is justification for considering inclusion of the Ghost River species in *Verrucosisporites* as its ornamentation is rugulate-verrucate. It was however placed in *Convolutispora* because some of the ornaments anastomose.

Comparisons. Probably the species that most closely resembles *Convolutispora paraverrucata* n. sp. is *C. tuberculata* (Waltz) Hoffmeister, *et al.* (1955a). It has not been possible to examine the types from the Karaganda Basin, but according to description and figures of Luber and Waltz (1938) and other Russian authors, *C. tuberculata* seems to possess more rounded and relatively lower ornaments, giving its marginal outline a more regularly undulating appearance. *C. tuberculata* from the Lower Carboniferous of Spitsbergen (Playford, 1962, p. 592) has wider rugulae (2-5μ) and an undulating equatorial margin.

C. ampla Hoffmeister, *et al.* (1955a, p. 384) has distinct rugulae of less relief than those of *C. paraverrucata. C. fromensis* Balme and Hassell (1962, p. 8) and *C.* sp. of the same authors have wider ridges, which are rounded in cross-section. *C. clavata* (Ishchenko) Hughes and Playford (1961) is larger and has low (2μ) and flattened ornaments.

Genus ***Cristatisporites*** Potonié and Kremp, 1954

Type species. Cristatisporites indignabundus (Loose) Potonié and Kremp, 1954.

Cristatisporites? sp.

Plate II, figures 20 to 22; Figure 4

Description. Spores trilete, laesura simple, rays almost as long as the radius of the spore. Amb subcircular, wall very dark, opaque except for the equatorial flange-like extension; thickness unknown. Ornamentation consisting of coni, truncated coni, or warts, about 2-8μ wide at base, more or less as high as basal width, and about 2-9μ apart. Some of the ornaments may be connected to one another at their bases by very low ridges of approximately the same width as the bases of the ornaments. At the equator, ornaments in lateral view are confluent in such a way that they resemble a flange-like structure of variable width, up to 10μ wide (*see* fig. 21).

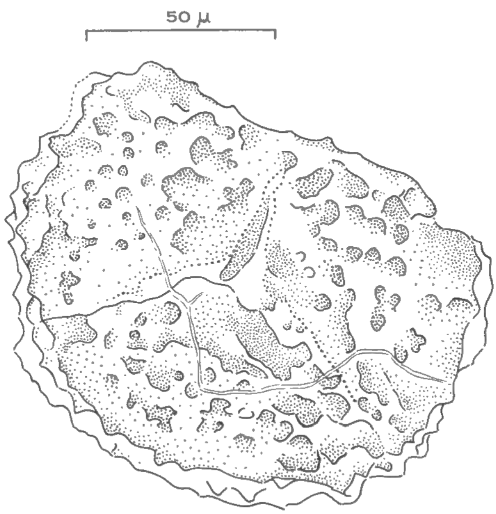

FIGURE 4. *Cristatisporites*? sp., camera lucida drawing, proximal side.

Diameter (6 specimens). 132-166μ. Dimensions are quoted only for specimens that are more than half a spore. All the Ghost River spores are brittle, and this relatively large type was usually fragmented. The most nearly complete specimen is illustrated in Plate II, figure 20.

Types. Hypotypes, GSC Nos. 13211, 13212.

Remarks. The flange-like structure visible at the equator of some specimens is possibly not confined to the equatorial region. It may rather represent the general extension of the exine in the form of enlarged ornament bases. The writer has also not discarded the possibility that the "flange" represents an ornamented exoexine or perispore, although no inner body or mesospore has been detected.

The writer is in doubt as to the generic assignment of this species. Two form-genera, *Apiculatisporis* and *Cristatisporites,* have been considered, but neither seems entirely suitable. Neither the tendency for interconnection of the bases of the ornaments by low ridges nor the presence of a flange are features of *Apiculatisporis*. The absence of a cingulum does not fit the current interpretation of *Cristatisporites* (*see* Bhardwaj, 1957, p. 105, and Potonié, 1958, p. 27) but on the other hand it does not violate the (unemended) diagnosis of that genus (*see*

Potonié and Kremp, 1954, p. 142). For this reason, the Ghost River specimens are tentatively assigned to *Cristatisporites* and included in the infraturma Murornati.

Comparison. The Givetian species *Archaeozonotriletes firmus* Chibrikova (1959, Pl. 10, fig. 1) resembles this spore in several respects, but Chibrikova does not mention interconnection of the bases of the ornaments, and *A. firmus* is usually larger (160-200μ). Chibrikova interprets the peripheral structure of *A. firmus* as the projecting edge of a "perispore".

Infraturma TRILETESACCITI Leschik, 1955

Genus ***Endosporites*** Wilson and Coe, 1940

Type species. Endosporites ornatus Wilson and Coe, 1940.

Endosporites sp.

Plate II, figure 25

Description of specimen. Spore monosaccate or mesosporate; trilete, rays simple, extending almost to equator of central body. Amb rounded-triangular, exoexine or saccus granulate, granules rounded or flat-topped, about 1-1.5μ wide, 1-1.5μ high, and 1-4μ apart. Central body also rounded-triangular, probably unornamented, its wall thin and slightly darkened in angles of rays.

Dimensions (one specimen). Total diameter 60μ; diameter of central body 45μ.

Types. Hypotype, GSC 13213.

Comparisons. Several species of *Archaeozonotriletes* described by Naumova (1953) are sufficiently close to this specimen to warrant comparison. Synonymies are not determinable because that author did not give measurements of size, shape, or distance separating the ornaments.

Archaeozonotriletes basilaris Naum. (op. cit., p. 33) has, according to the illustrations, a larger ratio of body width to total spore width, but in the species assigned to *A. basilaris* in Kedo (1955) this ratio is (according to Kedo's illustration) closer to that of *Endosporites* sp. His species also has a size range that includes the Ghost River specimen. The main difference may lie in the more closely spaced granules of the Russian species. *Archaeozonotriletes luteolus* Naum. (op. cit., p. 128) seems to differ from *A. basilaris* in shape, so it may be excluded from consideration. *A. pustulatus* Naum. (p. 35) and *A. famenensis* Naum. (p. 117) may have larger, more widely spaced ornaments. *A. devonicus* Naum. (p. 86) is smaller, and has "medium-sized" protuberances that in her illustration are so close together that they touch.

Zonotriletes graniferus Luber *in* Luber and Waltz (1941, p. 70) is much larger. *Hymenozonotriletes opacus* Ishchenko (1958, p. 75) is at least superficially similar to *Endosporites* sp.

Archaeozonotriletes sp., recorded by Balme (1960) from the Lower Carboniferous of Western Australia, is certainly similar in construction. The only difference detectable, based on interpretation of Balme's photograph (1960, Pl. 5, fig. 31), is closer spacing and smaller size of granules on the bladder.

Description of the Assemblage

The Ghost River microflora comprises thirteen species, assigned to ten genera. The abundance of each species in the assemblage, shown by a count of 320 specimens, is as follows:

Retusotriletes greggsii n. sp.	202
Convolutispora paraverrucata n. sp.	35
Pilasporites plurigenus B. & H.	21
Retusotriletes semizonalis n. sp.	19
R. biarealis n. sp.	11
Apiculatasporites dilucidus (McG.) n. comb.	11
Cristatisporites? sp.	6
Leiotriletes priddyi Berry	4
Retusotriletes sp.	4
Converrucosisporites sp.	3
Calamospora atava (Naum.) n. comb.	2
Planisporites sp.	1
Endosporites sp.	1

Most of the spores are broadly rounded-triangular in polar compression. Sculpture, where present, is in general of low relief, composed of grana, coni, or ridges. All species except *Pilasporites plurigenus* are trilete, and the rays extend nearly to the equator in most species.

Only three species have diameter ranges extending beyond 100μ; *Cristatisporites*? sp., with an upper size limit of 166μ, is by far the largest.

Botanical Relationships of the Spores

Several of the species present in the Ghost River assemblage have been assigned to form-genera of relatively simple construction, i.e., *Apiculatasporites, Calamospora, Converrucosisporites, Leiotriletes*, and *Planisporites*. The most that can be said concerning the natural affiliations of these groups is that they are probably isospores or microspores of bryophytic, psilophytic, or pteridophytic plants. Of the other genera represented, *Convolutispora* has not been allied with any natural taxon, and the same is true for *Retusotriletes*. *Endosporites* has been aligned with the lycopods (Chaloner, 1958) and the pteridosperms (Remy, 1953), but the Ghost River specimen that has been placed in that genus does not closely resemble the species discussed by those authors, and may not belong with either of those natural groups. As discussed elsewhere in this paper, *Pilasporites plurigenus* may be fungal. This suggestion has, however, a rather tenuous basis, and may be difficult to either prove or disprove.

The only species that lends itself to more profitable speculation as to natural affinity is *Retusotriletes greggsii*. This form resembles spores believed to be from *Svalbardia polymorpha* Høeg, a Givetian to perhaps Frasnian plant from Spitsbergen. Høeg (1942, p. 77, Pl. 31, figs. 5 to 9) described spores

> . . . which evidently belong to the plant [*Svalbardia polymorpha*] itself . . . [as] . . . oblong, about 60-70μ long or a little more, and somewhat narrower. . . . The wall is nearly smooth, but has minute tubercles which are only visible under strong magnification; in some spores, which are probably better preserved than others, each tubercle may end in a little tooth-like projection. There are distinct tetrad marks.

In addition, Høeg's photographs, particularly figure 6 and possibly figure 9, suggest that the spores possess curvaturae which are, as on some specimens of *Retusotriletes greggsii*, not greatly thickened. The comparison must be treated cautiously as *R. greggsii* does not possess the 'little tooth-like projections' mentioned by Høeg. These may never have been present in *R. greggsii* or alternatively, if present, they may have been very delicate and removed during either preservation or laboratory preparation. The writer has not been able to compare *R. greggsii* directly with the spore preparations of Høeg, but a study of Devonian spores of Spitsbergen which is now being directed by Høeg (pers. comm.) may present information that will facilitate comparison of *R. greggsii* with the spores of *Svalbardia*.

Additional information regarding the degree of similarity of *R. greggsii* to dispersed spores from Spitsbergen is nevertheless available to the writer, from slides kindly supplied by N. F. Hughes of the University of Cambridge. The slides referred to are from the Mimer Valley Series of Vestspitsbergen, and one of them, from Munindalen, contains a few spores that are remarkably like *R. greggsii*. As the age of the Mimer Valley Series is uppermost Givetian to lowermost Frasnian according to Friend (1961), *R. greggsii* apparently occurs in Spitsbergen in rocks of about the same age as those from which Høeg reported *Svalbardia*. When this information is considered, together with the occurrence in the Ghost River Formation of a plant probably assignable to *Svalbardia*, the possibility that *Retusotriletes greggsii* represents spores of *Svalbardia* receives further support. If *R. greggsii* was indeed derived from *Svalbardia*, its affinities would be with the fern-like order *Protopteridiales* Høeg (op. cit., p. 178). However, the arguments offered here give merely a suggestion of the affiliation of *Retusotriletes greggsii*, which can only be confirmed or refuted by more direct evidence.

Some tentative conclusions may be advanced concerning the environment from which the Ghost River spores originated. The microflora comprises relatively few species, one of which is distinctly dominant. This may indicate that the spores were produced by a specialized florule with a single dominant element (that which bore *R. greggsii*) growing at most a few miles from the site of deposition of the spores. This would be consistent with the presence, in the sediments containing the spores, of numerous megafossil fragments of one (*Svalbardia*?) or only a few plant species. The megafossils are sufficiently fragmented to suggest some transport from site of origin, but intact condition of a few specimens (such as the one figured by Greggs, *et al*., 1962) suggests that they were not subject either to long transportation or to strong wave action. Local deposition in the Ghost River beds of *sporae dispersae* from a specialized, restricted flora would also provide a reasonable explanation for the absence of any representative of the bifurcate-spined complex of spores (*Ancyrospora*, *Archaeotriletes*, etc.). Spores with this bizarre type of ornament are present in most other Middle and Upper Devonian microfloras, and perhaps are the record of a less specialized, more widespread component of the Devonian vegetation.

Comparison with Other Assemblages

There are at least twenty published papers describing Devonian *sporae dispersae* in some detail, in addition to numerous others that give extensive spore lists (e.g., Filimonova, 1958). Most of these concern material of Givetian or younger age, a few describe assemblages that are perhaps as old as Eifelian (Lang, 1925; Chibrikova, 1957; Richardson, 1960, 1962), and two describe spores from older Devonian deposits (Thomson, 1952; McGregor, 1961). Two spore assemblages of Upper Devonian, possibly Frasnian, age have been recorded from the Canadian Arctic Islands (Chaloner, 1959; McGregor, 1960). The first contains exclusively megaspores, while the second contains only one species, *Apiculatasporites dilucidus* (McG.) n. comb., in common with the Ghost River microflora. The 'Upper Devonian' spores mentioned and figured but not described by Hoffmeister, Staplin, and Malloy (1955b, p. 10, Pl. 1) do not appear to include any that are similar to those from the Ghost River Formation. No record of known Givetian to lower Frasnian spores has been published from North America, although there are strata of this age that do contain spores and these are referred to below. One must look beyond this continent for published material comparable in age to the Ghost River microflora.

Chibrikova, Kedo, and Naumova described species, from Givetian and Frasnian strata of Bashkiria, Byelorussia, and the Moscow Basin that are similar to *Calamospora atava, Retusotriletes greggsii, Cristatisporites*? sp., and *Endosporites* sp. (*see* Table I). However, only in one (*Calamospora* (*Leiotriletes*) *atava*), is similarity sufficiently demonstrable to warrant synonymy. Other Ghost River species (e.g., *Apiculatasporites dilucidus, Retusotriletes* sp., *Converrucosisporites* sp.) are comparable to Givetian-to-Frasnian forms from the U.S.S.R., but resemble Famennian or even Carboniferous species just as closely.

The Ghost River assemblage does not readily fit into any of Naumova's nineteen Middle or Upper Devonian complexes (1953, Pl. 22), Kedo's three Givetian complexes (1955, p. 11), or Chibrikova's Givetian-Frasnian chart (1959, Pl. 15). Neither is it accommodated in Tuzova's Givetian-Frasnian material from Tataria, which in that author's opinion agrees with complexes 14 and 15 of Naumova.

The French Lower Frasnian assemblage of Taugourdeau-Lantz (1960) is quite different from the present microflora. It contains several species of *Archaeotriletes* and *Hymenozonotriletes*, thus presenting a more conventional 'Upper Devonian' appearance. In addition, it contains no species that is greatly predominant in numbers.

Table I

Summary of species comparable to those from the Ghost River Formation

Ghost River Formation	Comparable Species	Age
Pilasporites plurigenus Balme & Henn.	Various	Namurian to Eocene
Leiotriletes priddyi (Berry) Pot. & Kr.	Various	Coblenzian to at least Liassic
Calamospora atava (Naum.) n. comb.	*Leiotriletes atavus* Naum.	Middle and Upper Devonian
	Type D, Lang	Middle Devonian
Retusotriletes biarealis n. sp.		
R. greggsii n. sp.	*Retusotriletes verrucosus* Kedo	Middle Devonian
	R. punctatus Chibr.	Upper Givetian and Lower Frasnian
R. semizonalis n. sp.	*Asterocalamotriletes marginellus* (Luber) Luber	Lower Carboniferous
R. sp.	*Retusotriletes* sp. A, Balme	Lower Carboniferous
	R. sp. cf. *R. pychovii* var. *major* Naum. *in* Balme & Has. (1962)	Famennian
	R. cf. *R. pychovii* Naum. *in* Balme (1962)	Frasnian
Converrucosisporites sp.	Various	Givetian to Upper Carboniferous
Apiculatasporites dilucidus (McG.) n. comb.	Various	Middle Devonian to Middle Carboniferous
Planisporites sp.	*Azonotriletes resistens* Luber	Middle and Upper Carboniferous
Convolutispora paraverrucata n. sp.	Various	Famennian to Lower Carboniferous
Cristatisporites? sp.	*Archaeozonotriletes firmus* Chibr.	Givetian
Endosporites sp.	*A. basilaris* Naum.	Frasnian
	Hymenozonotriletes opacus Ishch.	Tournaisian to Viséan
	Archaeozonotriletes sp., Balme	Lower Carboniferous

The Ghost River material comprises relatively few species, one of which is distinctly dominant, and several new species. In these respects it resembles three other described assemblages: the Melville Island Frasnian one of McGregor (1960), the Western Australian Frasnian one of Balme (1962), and the Western Australian Famennian one from Core 24 of Balme and Hassell (1962). On the other hand, it is not qualitatively like any of these three. Perhaps the explanation for the apparent uniqueness of these four florules may be not so much that they are geographically restricted, as that our knowledge of Devonian microfloras is as yet very imperfect.

Comparison has also been made with Lower and early Middle Devonian assemblages from the Gaspé Sandstone and from New Brunswick and Maine, and Lower or early Middle Devonian spores from northern Ontario (unpublished data). These assemblages contain a high proportion of species with membranous perispore or bladder, membranous equatorial flange, radial ribs, and verrucate, foveolate, or reticulate walls. They thus have little resemblance to the spores from Ghost River.

The writer has recently found *Retusotriletes greggsii* in a small population of spores from strata about 35 miles north of the Ghost River type section. The material was collected by J. Aitken of the Geological Survey of Canada, from beds suspected by Aitken (pers. comm.) to be stratigraphic equivalents of the plant-bearing beds at Ghost River. *R. greggsii* occurs also in the Onteora Formation (early Upper Devonian) of New York state, in material supplied by F. M. Hueber, formerly of the Geological Survey of Canada. Finally, as mentioned earlier, a species probably synonymous with *R. greggsii* has also been seen by the writer in material from Spitsbergen, supplied for comparative purposes by N. F. Hughes. Considering these occurrences of *R. greggsii*, it seems likely that this species is of rather wide geographical distribution near the Givetian-Frasnian boundary.

Age

Estimates of the age of the Ghost River Formation, based on stratigraphic and plant megafossil evidence, have been discussed elsewhere in this paper. It was stated that a late Middle or earliest Upper Devonian age has been most widely accepted on stratigraphic grounds, and that evidence from plant megafossils, particularly the *Svalbardia*-like fragment illustrated by Greggs, *et al.* (1962), supports this dating. Neither *Svalbardia* nor *Archaeopteris,* with which the fertile parts of *Svalbardia* could most easily be confused, are known from beds older than Givetian.

The spores themselves, when compared with those from published literature, do not add much to this. However, preliminary comparison with unpublished data from western Canada, New York, and Spitsbergen (*see above*) reinforces the conclusion that they are late Givetian or perhaps Frasnian. If Frasnian, they would be very earliest Frasnian, as the overlying Cairn Formation has been placed early in that stage (McLaren, 1962, fig. 1).

The Ghost River plant bed is therefore considerably younger than the Lower Devonian plant-bearing channel fill at Beartooth Butte, Wyoming. Some workers (e.g., Sandberg, 1961) have regarded the Ghost River and Beartooth Butte Formations as approximately equivalent in age. Recently, however, McMannis (1962, pp. 6-7) suggested that lithologically similar deposits with fish and plant remains may occur in Montana in both the Lower Devonian (Beartooth Butte Formation) and the late Middle Devonian (Maywood (?) Formation). If McMannis is correct, the latter deposits and the plant bed at Ghost River would be of about the same age.

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PLATES I and II

Plate I

(×400, except where otherwise stated)

Figures 1–12 *Retusotriletes greggsii* n. sp. (Page 8)
1, holotype, GSC 13184; 2, holotype, polar part of distal wall ×1000; 3-12, paratypes: 3, 4, GSC 13185, 13186, specimens slightly tipped; 5, GSC 13187, specimen laterally compressed; 6, GSC 13188, large specimen showing proximal position of curvaturae; 7, GSC 13189, distal view, specimen with unusually large ornaments; 8, same specimen, part of distal wall, ×1000; 9, GSC 13190, showing proximal position of curvaturae; 10, same specimen, ×1000; 11, GSC 13191, small specimen; 12, same specimen, part of distal wall, ×1000.

Figures 13–15 *Retusotriletes biarealis* n. sp. (Page 7)
13, holotype, GSC 13192, ×1000; 14, holotype; 15, paratype, GSC 13193, laesura in focus.

PLATE I

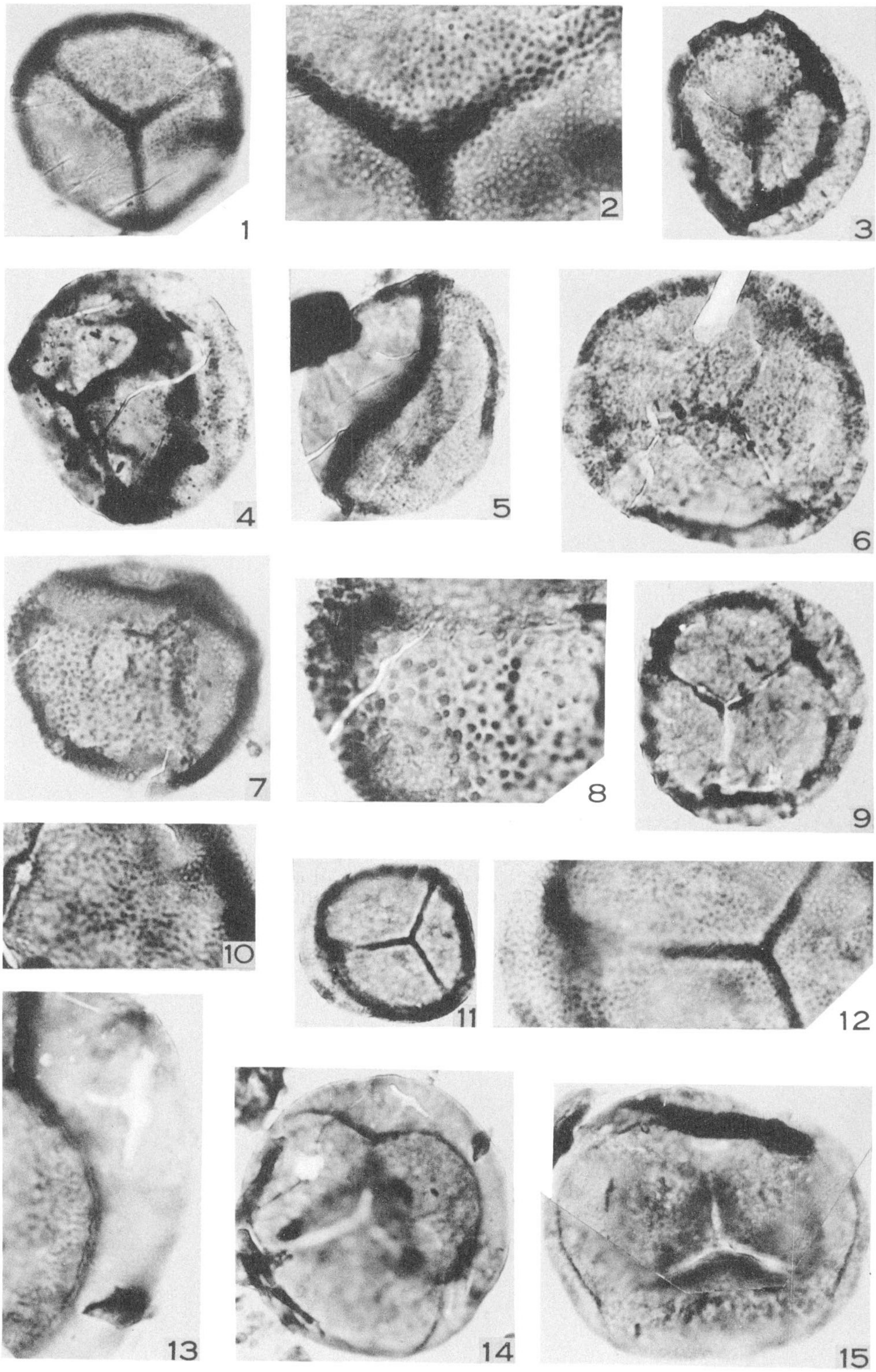
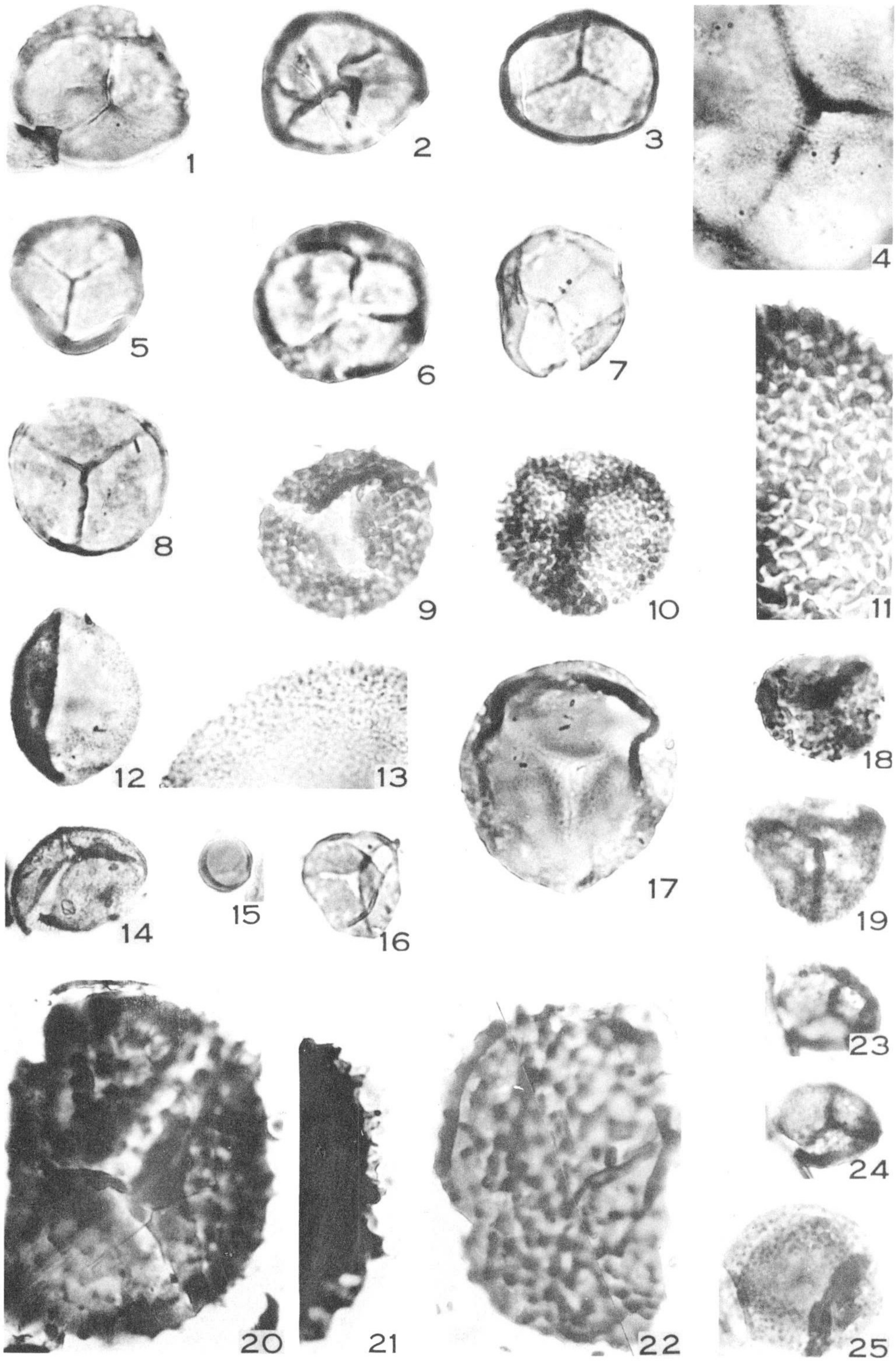


Plate II

(×400, except where otherwise stated)

Figures 1–5, 7–8	*Retusotriletes semizonalis* n. sp. (Page 10) 1, paratype, GSC 13194, curvaturae only slightly thickened; 2, 5, paratypes, GSC 13195, 13196, curvaturae heavily thickened; 3, holotype, GSC 13197; 4, holotype, polar part of distal wall, ×1000; 7, paratype, GSC 13198, possibly overmacerated; 8, paratype, GSC 13199, curvaturae equatorial.
Figure 6	*Retusotriletes* sp. (Page 11) GSC 13200.
Figures 9–11	*Convolutispora paraverrucata* n. sp. (Page 17) 9, paratype, GSC 13201, with large ornaments; 10, holotype, GSC 13202; 11, holotype, ×1000.
Figures 12–14	*Apiculatasporites dilucidus* (McG.) n. comb. (Page 13) 12, GSC 13203, largest specimen; 13, same, part of wall, ×1000; 14, GSC 13204, small specimen.
Figure 15	*Pilasporites plurigenus* Balme and Hennelly (Page 3) GSC 13205.
Figure 16	*Leiotriletes priddyi* (Berry) Pot. & Kr. (Page 5) GSC 13206.
Figure 17	*Calamospora atava* (Naumova) n. comb. (Page 6) GSC 13207.
Figures 18, 23–24	*Converrucosisporites* sp. (Page 12) 18, GSC 13208; 23, 24, GSC 13209.
Figure 19	*Planisporites* sp. (Page 15) GSC 13210.
Figures 20–22	*Cristatisporites*? sp. (Page 17) 20, GSC 13211; 21, same specimen, part of margin showing projecting ornaments, ×1000; 22, GSC 13212, some ornaments connected by ridges.
Figure 25	*Endosporites* sp. (Page 19) GSC 13213.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