DEVONIAN MEGASPORES FROM ARCTIC CANADA

by W. G. CHALONER

ABSTRACT. A megaspore assemblage is described from coal and shale deposits of Upper Devonian age from Ellesmere Island, Arctic Canada. All are new species, and two represent new genera: *Biharisporites ellesmerensis* sp. nov., *B. ocksensis* sp. nov., *Triangulatisporites rootsii* sp. nov., *Lagenicula devonica* sp. nov., *Ocksisporites maclarenii* gen. et sp. nov., and *Nikitinsporites canadensis* gen. et sp. nov. All but one of these forms are appreciably smaller than typical Carboniferous megaspores. There appears to be a general rise in the mean size of megaspores from the Devonian to the Carboniferous, followed by a diminution in size through the Mesozoic. This may be correlated with the corresponding rise and decline of the arborescent lycopods.

INTRODUCTION

THE plant microfossils described in this paper were obtained from some samples of bituminous coal and shale of Upper Devonian age from Ellesmere Island, Arctic Canada. The study has been restricted to those spores greater than 200 μ in diameter. With a few exceptions triradiate spores of this size are generally regarded as megaspores of heterosporous plants. The smaller spores present, not dealt with here, may represent the isospores of homosporous plants, the microspores of heterosporous plants, and possibly even pollen (if true seed plants existed in the Devonian).

The occurrence of megaspores of Devonian age is in itself of significance in suggesting the presence of some abundance of heterosporous plants at this time. In the Carboniferous of the northern hemisphere there is a great diversity of megaspores in suitable facies, and many of these have now been correlated with particular genera, and even species, of arborescent lycopods (Felix 1954; Chaloner 1953*a*, *b*). In this context, a Devonian megaspore assemblage has particular significance for comparison with the earliest known Carboniferous megaspores.

I am pleased to express my thanks to Dr. Wayne Fry, to Dr. Colin McGregor of the Canadian Geological Survey and also to the Director of that Survey for making this material available to me.

Source and age of the material. The three specimens from which megaspores were obtained were all collected from Ockse Bay, on the south-west coast of Ellesmere Island. One sample, 4713, was collected from a coal seam at the head of Ockse Bay by E. F. Roots (Canadian Geological Survey Plant Type Locality 13001). The other two samples, collected by D. J. Mclaren, are a sandy shale (sample 4747) from the Ockse Bay section (Plant Type Locality 13003), and a bituminous coal (sample 4742) from the mud-flat talus on the eastern arm of Ockse Bay (Plant Type Locality 13002). The coal of sample 4713, occurring *in situ*, is Upper Devonian, and the spore contents of coal 4742 from the talus is consistent with its having come from the same horizon. According to Dr. Wayne Fry (personal communication) the section from which the samples (4713 and 4747) came 'overlies transitionally beds of known Middle Devonian age, based on a marine fauna; the flora of the upper beds is that described by Nathorst (1904) . . .'.

Methods of spore preparation. The coal samples were macerated for several days in

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Schulze's solution (concentrated nitric acid and potassium chlorate). The residue was then washed and dilute alkali was added. This was decanted off after several hours and replaced by water, and this too was decanted off. Washing and decanting were repeated several times, the residue being allowed to settle out completely each time. The final residue was examined under a binocular microscope and the larger spores picked out with a pipette. Some of the spores were allowed to dry, and mounted as opaque objects (cf. Pl. 55, fig. 7). Others were placed in concentrated nitric acid until transparent, and then transferred to distilled water; these were mounted in glycerine jelly, or dehydrated and mounted in balsam for examination by transmitted light (cf. Pl. 55, fig. 1).

The shale was treated with cold dilute hydrofluoric acid in a polythene beaker for several days. The residue (which still contained quite a lot of undissolved mineral matter) was washed several times by adding water and decanting, and the larger spores were then picked out of the residue as with the coal macerations.

Taxonomy of Palaeozoic megaspores. Prior to 1954 nearly all Palaeozoic megaspores (i.e. spores of more than 200 μ diameter) were placed in a single genus, *Triletes*. Most palaeobotanists accepted this as a genus consisting principally of the megaspores of the heterosporous lycopods. Correlation of a few of these megaspores with their parent plants established that the spores of at least a number of different genera were included in *Triletes* (Schopf, Wilson, and Bentall 1944).

In 1954 Potonié and Kremp published a revision of Palaeozoic spore genera, which they later amplified (1955, 1956*a*, 1956*b*). This revision recognized thirteen genera in place of the old genus *Triletes*, which they rejected completely as a confused name. The basis of their treatment was spore morphology, without regard for the natural relationships of those spores of which the parent plants were known. While this resulted in a seemingly clear-cut definition of genera, some were manifestly very artificial. The spores known to have been borne by *Sigillaria*, for example, a well-circumscribed group (Chaloner 1953*b*), were separated into two genera on features of wall decoration. In a later work Potonié (1958) erected further genera on the basis of species included by other authors in *Triletes*. Many of the diagnostic characters which he uses are of an order which earlier workers had regarded as being only of specific value.

Some splitting of the genus *Triletes* was clearly desirable, but this increasing multiplicity of megaspore genera has had several disadvantages. Firstly, as already indicated, it cuts across known biological relationships; secondly, it gives an exaggerated impression of the degree of difference between different assemblages; and finally, the generic limits become so finely drawn that almost every new species requires a new genus to accommodate it.

I have not attempted to arrange the spores described here into any supra-generic categories. Where nothing certain is known of the parent plants of the spores concerned, such groups may be misleading in implying affinity of their members, where none is known to exist.

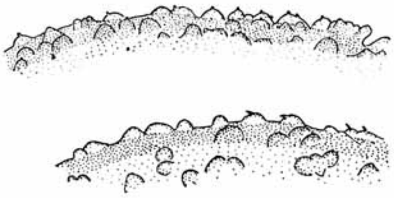
SYSTEMATIC DESCRIPTIONS

Biharisporites ellesmerensis sp. nov.

Plate 55, fig. 2; text-fig. 1

Diagnosis. Triradiate megaspore, circular in the flattened state, with contact faces occupying most of the proximal face of the spore. Greatest diameter 204–304 μ, mean of sixty-four specimens 270 μ. Spore wall apparently of a single layer, covered except on the contact faces with hemispherical to conical warts (coni), typically 7 μ high and 10 μ wide at the base, occasionally having a minute papilla or spine extending from the tip (text-fig. 1). Contact faces lacking warts, bounded by ill-defined arcuate ridges formed by fusion of the warts in that region. Triradiate ridges typically 12 μ wide and rising from about 10 μ in height at their extremities to 25 μ at the pole.

Holotype. The specimen of Pl. 55, fig. 2; slide 4742*a*, Canadian Geological Survey, Ottawa. From sample 4742, a piece of bituminous coal from the mud-flat talus, east arm of Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13002; Upper Devonian.



TEXT-FIG. 1. Decoration of the spore wall of the holotype of *Biharisporites ellesmerensis* sp. nov. × 500, seen in profile at the spore margin. Camera lucida drawing of a transparent preparation. (Slide 4742*a*.)

Discussion. This was the most abundant megaspore present in the two coal samples from Ockse Bay (4742, 4713).

Potonié (1956) recognizes three genera of megaspores having a warty or apiculate decoration, in which this species might be placed: *Tuberculatisporites*, *Verrutriletes*, and *Biharisporites*. Some species of *Tuberculatisporites* obtained from Carboniferous coals are known to be the megaspores of *Sigillaria* (Chaloner 1953*b*). These species have in common a characteristic concavo-convex shape, associated with the peculiar structure of the parent sporangium. It seems desirable to restrict the genus *Tuberculatisporites* to megaspores having this shape, and to exclude from it spores (such as *B. ellesmerensis* sp. nov.) with similar decoration, which were originally more or less spherical.

Potonié (1956) characterizes *Verrutriletes* as having a verrucose decoration of the spore wall, while *Biharisporites* includes similar megaspores with a decoration of uniform coni. The distinction between these two types of decoration depends on the regularity of size and shape of the projections of the spore wall; coni are of uniform size and shape on any one spore, while verrucae are irregular. Clearly, these conditions grade into each other. The projections forming the decoration on these Ellesmere spores approximate to coni in Potonié's sense, and on this basis I include these spores in the genus *Biharisporites*.

The only species of *Biharisporites* recognized by Potonié which is in any sense closely comparable with *B. ellesmerensis* sp. nov., is the Rhaetic *B. myrmecodes* (Harris) Potonié. The Ellesmere spores are about half the diameter of this Rhaetic species, and also differ from it in having the contact faces free of decoration.

While it may seem unwise to include a Devonian spore in a genus based on Gondwanan material, I believe that this is preferable to making a new genus on the basis of very trivial morphological differences. It is inherent in a morphographic system that spores which in all probability are not closely related may be placed in one genus. This is particularly so for spores of a simple, generalized type such as *Biharisporites*. Clearly, other spore genera based on more distinctive or peculiar features (e.g. *Pyrobolospora* Hughes) may represent more natural groups.

Biharisporites ocksensis sp. nov.

Plate 55, figs. 6–8

Diagnosis. Triradiate megaspore, more or less circular in the equatorial plane, 560–1,610 μ diameter, mean of twenty-four spores 925 μ. Spore originally more or less spherical. Triradiate ridges and arcuate ridges slightly elevated; triradiate ridges seven-tenths to nine-tenths of the spore radius. Spore wall up to 40 μ thick; surface finely granular, or covered with minute rounded-conical projections (coni) up to 10 μ high and of about the same width at the base. Decoration uniform over the entire spore surface.

Cotypes. The spores of Pl. 55, figs. 6 and 7; slides 4713*z* and 4713*v* respectively, Canadian Geological Survey, Ottawa. From sample 4713, from a coal seam at the head of Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13001; Upper Devonian.

Discussion. This is the largest of the spore types from Ellesmere, and is comparable in size with some of the large Carboniferous megaspores. The decoration of the wall varies from a fine granular structure (Pl. 62, fig. 7) to minute but well-defined coni visible in profile at the spore margin (Pl. 62, fig. 8). These spores are very similar to some of the large triradiate megaspores of the Lower Carboniferous with a finely granular decoration (cf. *Triletes globuliferus* Dijkstra 1956, *T. subfulgens* Dijkstra); *B. ocksensis* differs from these forms mainly in the character of the wall decoration. It is this feature which excludes it from the several genera of completely smooth-walled megaspores, and I accordingly place it in *Biharisporites* which is characterized by a decoration of small coni. Megaspores of this general type with granular or minutely apiculate walls occur at many horizons from the Devonian onwards.

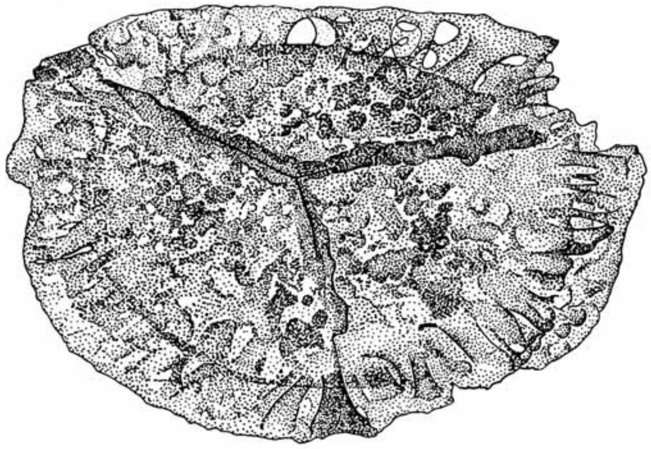
Biharisporites ocksensis differs from previously described species in its relatively large size, and in the dimensions of the coni forming the wall decoration.

Triangulatisporites rootsii sp. nov.

Plate 55, fig. 4; text-fig. 2

Diagnosis. Triradiate megaspore, rounded triangular as seen in an equatorially flattened specimen. Equatorial flange (cingulum) formed of partially fused radiating elements between which gaps occur locally. Diameter, including the flange, measured from one apex of the triangle to the mid-point of the opposite side, 485–524 μ; mean of four specimens 506 μ. Diameter of the spore body 300–370 μ; flange varying in width from 70 μ between the triradiate ridges to 107 μ at the angles. The radiating bars prominent in the flange merge rapidly into a very irregular verrucose to reticulate decoration on the proximal and distal faces.

Holotype. The specimen of Pl. 55, fig. 4; slide 4713*f*, Canadian Geological Survey, Ottawa. From sample 4713, a coal seam at the head of Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13001; Upper Devonian.



TEXT-FIG. 2. *Triangulatisporites rootsii* sp. nov., ×200. Camera lucida drawing of a transparent preparation showing the structure of the flange and decoration of the contact faces. (Slide 4742*d*.)

Discussion. Potonié (1956) recognizes three genera of megaspores with prominent zonal flanges, to which this spore might be referred: *Zonalesporites*, *Superbisporites*, and *Triangulatisporites*. All three are based on Carboniferous holotypes. The first two genera include large megaspores (over 1 mm.) with broad, rather fragile equatorial flanges apparently formed of fused radiating elements. *Triangulatisporites* includes triangular megaspores which are about half this size, and which have a more compact flange, apparently continuous in structure with the spore wall. The flange on this type of spore will not readily break away from the spore body, in contrast to the flange in *Zonalesporites* and *Superbisporites*, which is relatively easily detached.

I include *Triangulatisporites rootsii* sp. nov. in this genus on account of its small size, triangular outline, and the structural continuity of the flange with the spore body wall. This involves a small extension of the limits of the genus both in morphology and in time, but I regard this as preferable to making a new genus at this stage.

Lagenicula devonica sp. nov.

Plate 55, fig. 3

Diagnosis. Triradiate megaspore, with greatly elevated triradiate lips forming an apical prominence. Spore diameter at the equator 270–400 μ, mean of twenty-six spores 337 μ. Height of the spore (measured along the axis) 290–460 μ, mean of fourteen spores 382 μ. Height of the apical prominence alone, from the arcuate ridges to the apex, 97–230 μ, mean of fourteen spores 174 μ. Arcuate ridges prominent, clearly visible in the flattened spore profile. Body of the spore decorated with irregular, more or less conical projections, partially fused to form a verrucose to irregularly reticulate pattern. Apical prominence free of this decoration, but having striate markings or minute corrugations parallel with the spore axis.

Holotype. The spore of Pl. 55, fig. 3; slide 4713*r*, Canadian Geological Survey, Ottawa. From sample 4713, from a coal seam at the head of Ockse Bay, Ellesmere Island. Canadian Geological Survey Plant Type Locality 13001; Upper Devonian.

Discussion. This spore resembles a number of large Carboniferous megaspores with an apical prominence, which are included in the genus *Lagenicula*, e.g. *L. agnina* Zerndt, *L. angulata* Zerndt. It differs from both these species in being less than half their size, and in the very distinctive decoration. The large apical prominence of *Lagenicula devonica* evidently gave the spore a tendency to fall on its side, as with the Carboniferous species. Pl. 55, fig. 3 shows it flattened in this orientation.

Some of the Carboniferous *Lagenicula* species are known to be the megaspores of *Lepidodendron* (Chaloner 1953*a*). It is unlikely that this was the case for *Lagenicula devonica*, but I do not regard this supposition alone as sufficient reason for excluding this spore from the genus *Lagenicula*, with which it agrees in its morphology. This is the only logical way in which a morphographic classification can be applied.

OCKSISPORITES gen. nov.

Type species *O. maclarenii* sp. nov.

Diagnosis. Triradiate megaspore with a broad equatorial flange, having a sharply defined triangular outline. Cavity of the flattened spore circular, diameter less than half the greatest dimension of the whole spore. Flange margin coarsely serrate.

Ocksisporites maclarenii sp. nov.

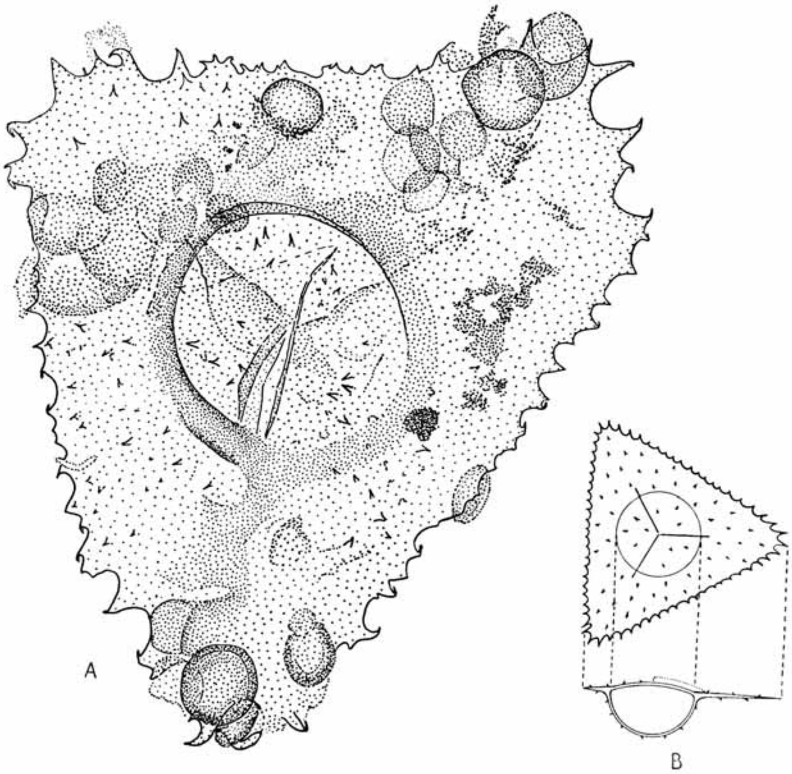
Plate 55, fig. 1; text-fig. 3

Diagnosis. Triradiate megaspore, with a continuous equatorial flange, broadest opposite the triradiate ridges, giving the spore a sharply triangular outline. Sides of the triangle straight to slightly convex. Greatest dimension of flattened spore, from apex of triangle to mid-point of opposite side, 440–630 μ, mean of eight spores 560 μ. Cavity of the flattened spore circular, diameter 240–290 μ, mean of six specimens 260 μ. Width of flange typically 150 μ opposite the triradiate ridges, and 100 μ between them. Triradiate ridges extending to the margin of the spore cavity and sometimes onto the flange; up to 170 μ long and 30 μ high at the pole, diminishing in height towards the margin. Margin of the flange serrate, with sharply pointed teeth typically 20 μ, occasionally up to 60 μ long. Both surfaces of the spore, including the flange, covered with minute spines with swollen bases and sharply drawn-out apices; typically 10 μ long, but smaller on the proximal face over the area of the spore cavity. No arcuate ridges present.

Holotype. The specimen of Pl. 55, fig. 1; slide 4742*e*, Canadian Geological Survey, Ottawa. From sample 4742, a piece of coal from the mud-flat talus, eastern arm of

Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13002; Upper Devonian. This spore was also obtained from samples 4713 and 4747 from the same vicinity.

Discussion. A hypothetical reconstruction of this spore is shown in text-fig. 3B. It can be seen that the thickest part of the flattened spore is around the margin of the spore



TEXT-FIG. 3. *A. Ocksisporites maclarenii* gen. et sp. nov., ×200. Camera lucida drawing of a transparent preparation; some small spores are shown adhering to the megaspore. (Slide 4742*g*.) *B.* Diagrammatic reconstruction ×50, in plan and median section.

cavity. This part accordingly appears darkest in the transparent preparations (Pl. 55, fig. 1). I attribute this thickness to the vertical compression of the equatorial part of the spore wall, where the flange joins the spore.

O. maclarenii differs from previously described megaspores in the relatively large continuous flange with a serrate margin, which gives the spore its sharply triangular outline.

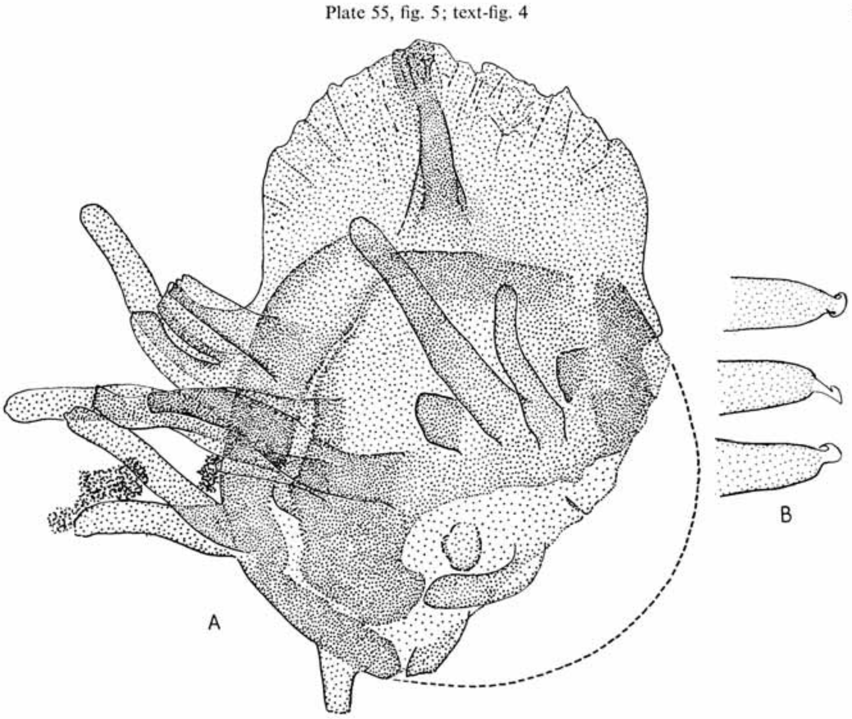
NIKITINSPORITES gen. nov.

Type species *N. canadensis* sp. nov.

Diagnosis. Megaspore with greatly elevated triradiate lips forming an apical prominence; spore body, except for the lips, covered with thick spines, parallel sided for most of their length, tapering sharply at the apex to end in an anchor-shaped bifurcation.

Nikitinsporites canadensis sp. nov.

Plate 55, fig. 5; text-fig. 4



TEXT-FIG. 4. *A. Nikitinsporites canadensis* gen. et sp. nov., ×200. Camera lucida drawing of a transparent preparation of one of the cotypes. The apical prominence is uppermost; the anchor-shaped spine apices are missing. The dotted line shows the outline of the missing part of the body of the spore. *B.* Anchor-shaped spine apices from another specimen, ×400. (Slides 4713*ac* and 4713*ab* respectively.)

Diagnosis. Triradiate megaspore, body more or less circular when flattened, 390–610 μ diameter, mean of eleven specimens 525 μ. Triradiate lips greatly expanded to form an apical prominence, up to 195 μ high, mean of eleven specimens 140 μ. Height of spore, including the apical prominence, 390–710 μ, mean of ten specimens 573 μ. Spore wall, excluding the triradiate lips and contact faces, covered with thick spines typically 200 μ long and 30 μ diameter. Spines tapering very gradually from the base, contracting rapidly at the apex to a bifurcated anchor-shaped tip. Width of this anchor-shaped apex always less than that of the main part of the spine. Spore wall typically 25 μ thick, up to 40 μ in the largest spores.

Cotypes. The specimens of Pl. 55, fig. 5 and text-fig. 4A, both on slide 4713*ac*, Canadian Geological Survey, Ottawa. From sample 4713, from a coal seam at the head of Ockse Bay, Ellesmere Island; Canadian Geological Survey Plant Type Locality 13001; Upper Devonian.

Discussion. The anchor-shaped apices of the spines on these spores are evidently very fragile, and are missing from many of the spines. Usually, when this is the case, a small papilla is left at the apex of the relatively thick spine (text-fig. 4A and B). These spores are clearly very similar to those described by Nikitin (1934) occurring in sporangia of Upper Devonian age, to which he gave the name *Kryshtofovichia africani*. The megaspores of *Kryshtofovichia* have an even taller apical prominence than those described here, but in all other respects are closely similar. Nikitin's name, *Kryshtofovichia africani*, is based on both mega- and microsporangia, which he believed with good reason to have belonged to the same plant. This name could not therefore be used for isolated megaspores, however similar to those in the sporangia (see discussion in Schopf and others 1944, p. 21). I regard the genus *Nikitinsporites* as including spores of the type contained in *Kryshtofovichia africani*, if found isolated.

A much smaller spore than those just described, but having a triradiate symmetry and anchor-shaped spine apices has long been known from the Devonian under the name 'Lang's Type G'. This was first described by Lang (1925) from the Middle Old Red Sandstone of Scotland. This type of spore was subsequently described from a number of other localities in rocks of similar age (Kräusel and Weyland 1929, Middle Devonian of Elberfeld; Arnold, 1936, Upper Devonian of Scaumenac, Canada and Pittston, Pa., U.S.A.; Høeg 1942, Middle Devonian of Spitzbergen; Hoffmeister and others 1955, Middle Devonian of Alberta; I have also obtained them from the Upper Devonian of Perry, Maine, U.S.A.). Eisenack 1944, described new material of Lang's Type G and gave it the name *Triletes ancyreus*. His material differed from that described by the other authors in having elevated triradiate lips forming an apical prominence, and he figured spores flattened laterally to show this feature.

Finally, Naumova (1953) described various triradiate spores with anchor-shaped spines, some similar to Lang's Type G, under the generic name *Archaeotriletes*. Potonié (1958) has emended this genus, and validated it by citing a type species and a holotype.

There is now evidently partial synonymy between 'Lang's Type G', certain of Naumova's *Archaeotriletes* species, and *Triletes ancyreus* Eisenack. The spore described here as *Nikitinsporites canadensis* differs from all of them in its much greater size, its very thick scarcely tapering spines and the large apical prominence. I have accordingly preferred to make a new genus, *Nikitinsporites*, rather than to include this spore as a species of *Archaeotriletes*.

GENERAL DISCUSSION

Origin of the spores. There are several groups of heterosporous plants in the Upper Devonian flora which could have produced the megaspores described here. The more important are the lycopods and the heterosporous ferns (cf. *Archaeopteris*). However, it is possible that other groups, including even non-vascular plants, might be represented. At least one plant, believed to be of a non-vascular nature, produced large (*c.* 200 μ) resistant spores with a triradiate mark (Kidston and Lang 1924; Arnold 1954). Any generalization concerning parent plants of the Ellesmere megaspores must therefore be very tentative.

Two of the six species described here show some similarity with Carboniferous megaspores which have been attributed to the lycopods (*Triangulatisporites* and *Lagenicula*). While such a correlation cannot be reliably extended, even at a generic level, beyond the species for which it was established, such similarity offers at least a suggestion of relationship. Nikitin (1934) believed that his *Kryshtofovichia africani* was a lycopod. If he was right, this implies a similar origin for the *Nikitinsporites* megaspores described here.

Spores similar to Lang's Type G have been recorded in close association with *Aneurophyton* (Kräusel and Weyland 1929), but there is no conclusive evidence that they actually represent the spores of this plant. In view of their widespread occurrence in the upper part of the Devonian, a correlation with their parent plant would be particularly interesting.

Comparison with other megaspore assemblages. Sen (1958) has recently redescribed and figured some megaspore casts from the Upper Devonian of Bear Island, originally figured by Nathorst. They are remarkable in being far larger than any other Devonian forms known (including those described here), and in this and other respects resemble Carboniferous ones. Sen identifies one spore from the Bear Island assemblage with a species previously known only from the Upper Carboniferous. As there is no reason to doubt the age of the Bear Island material, the similarity of these spores to Carboniferous forms is disconcerting. The apparent anomaly presented by Sen's results emphasizes the need for further work on Devonian megaspores.

If the various assemblages of megaspores from different horizons are compared on the basis of size alone, those from the Carboniferous are by far the largest (excluding the Bear Island material just mentioned). As Dijkstra (1949, p. 30) has pointed out, Mesozoic megaspores are distinguishable from Carboniferous ones, taken collectively, simply on the basis of their much smaller size, without regard to their morphology. This

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EXPLANATION OF PLATE 55

The photograph of fig. 7 was taken by reflected light, the remainder by transmitted light. Fig. 8 is × 800, the remainder are all × 100.

Figs. 1–8. Megaspores from the Upper Devonian of Ockse Bay, Ellesmere Island.

Fig. 1. *Ocksisporites maclarenii* gen. et sp. nov., holotype. From sample 4742, slide 4742*e*.

Fig. 2. *Biharisporites ellesmerensis* sp. nov., holotype. From sample 4742, slide 4742*a*.

Fig. 3. *Lagenicula devonica* sp. nov., holotype. From sample 4713, slide 4713*r*. The apical prominence is uppermost, and the arcuate ridges lie more or less across the centre of the flattened spore; one of the triradiate ridges is slightly to the right of the centre.

Fig. 4. *Triangulatisporites rootsii* sp. nov., holotype. From sample 4713, slide 4713*f*.

Fig. 5. *Nikitinsporites canadensis* gen. et sp. nov., Cotype. From sample 4713, slide 4713*ac*.

Figs. 6–8. *Biharisporites ocksensis* sp. nov. 6, 7, Cotypes; sample 4713, slides 4713*z*, and 4713*v* respectively. 8, Part of the spore margin, showing the decoration in profile.

All the slides are in the Canadian Geological Survey, Ottawa, Canada.

general trend of size decrease can be seen from Table 1. Obviously these data depend on a whole series of subjective and other extraneous factors (e.g. the limits that are placed on species) and new discoveries may completely alter this picture.

TABLE 1

Age	*Number of species*	*Mean spore diameter for all species*
Upper Cretaceous (Dijkstra 1949)	13	402 μ
Lower Cretaceous (Dijkstra 1951)	26	431 μ
Middle Jurassic (Kendall 1942; Murray 1939)	7	421 μ
Rhaetic (Harris 1935)	14	603 μ
Permian (Surange and others 1953)	18	685 μ
Carboniferous (Dijkstra 1946)	34	1,600 μ

Table 1. Showing the mean size for all the species, taken collectively, of each of several megaspore assemblages. The second column gives the number of species recognized in each assemblage. The figures show a general decrease in the mean size of the megaspores from the Carboniferous to the Cretaceous.

Most of the large Carboniferous megaspores are known to have been borne by arborescent lycopods (Felix 1954; Chaloner 1958*a*) which were one of the main elements in the coal swamp vegetation. It is significant that two of the smallest Carboniferous megaspores were apparently borne by herbaceous lycopods (Chaloner 1954, 1958*b*). Such evidence as is available from the macrofossils suggests that most Mesozoic lycopods, in contrast to the Carboniferous ones, were at least small, if not entirely herbaceous types. It is therefore a plausible hypothesis (accepting the provisos made above) that the decline in megaspore size shown in Table 1 may be correlated with the decline in the arborescent lycopods, as distinct from the herbaceous ones.

The megaspores described here, as with most of the larger spores recorded from the Devonian (Lang, Høeg, loc. cit.) are far smaller than the Carboniferous ones. On size alone the Ellesmere megaspore assemblage looks much more like a Mesozoic than a Carboniferous or Permian one. It may be that they represent, at least in part, the herbaceous lycopod stock which was later to continue side by side with the arborescent forms so prominent in the Carboniferous, and which ultimately survived them into the Mesozoic.

REFERENCES

ARNOLD, C. A. 1936. Observations on fossil plants from the Devonian of eastern North America. *Contrib. Mus. Paleont. Univ. Mich.* **5** (2), 37–48.

—— 1954. Fossil Sporocarps of the Genus *Protosalvinia* Dawson, with special reference to *P. furcata* (Dawson) comb. nov. *Svensk. bot. Tidsk.* **48** (2), 293–300.

CHALONER, W. G. 1953*a*. On the megaspores of four species of *Lepidostrobus*. *Ann. Bot., Lond.* n.s. **17**, 263–93.

—— 1953*b*. On the megaspores of *Sigillaria*. *Ann. Mag. nat. Hist.* **6**, 881–97.

—— 1954. Notes on the spores of two British Carboniferous Lycopods. Ibid. **7**, 81–91.

—— 1958*a*. *Polysporia mirabilis* Newberry, a fossil Lycopod cone. *J. Paleont.* **32**, 199–209.

—— 1958*b*. A Carboniferous *Selaginellites* with *Densosporites* microspores. *Palaeontology*, **1**, 245.–53.

DIJKSTRA, S. J. 1946. Eine monographische Bearbeitung der karbonischen Megasporen. *Med. Geol. Sticht.* C-3-1 (1), 1–101.

—— 1949. Megaspores and some other fossils from the Aachenian (Senonian) in South Limburg, Netherlands. *Med. Geol. Sticht.* n.s. **3,** 19–32.

—— 1951. Wealden megaspores and their stratigraphic value. Ibid. **5,** 7–21.

—— 1956. Lower Carboniferous megaspores. Ibid. **10,** 5–18.

EISENACK, A. 1944. Über einige pflanzliche Funde in Geschieben, nebst Bemerkungen zum Hystrichosphaerideen-Problem. *Zeit. f. Geschiebeforschung*, **19,** 103–24.

FELIX, C. J. 1954. Some American arborescent Lycopod fructifications. *Ann. Mo. Bot. Gdn.* **41** (4), 351–88.

HARRIS, T. M. 1935. The fossil flora of Scoresby Sound, East Greenland, Pt. IV. *Medd. om. Grønl.* **112,** 1–176.

HØEG, O. A. 1942. The Downtonian and Devonian flora of Spitsbergen. *Norges Svalbord- og Ishavs-undersøkelser*, **83,** 1–228.

HOFFMEISTER, W. S., STAPLIN, F. L., and MALLOY, R. E. 1955. Geologic range of Paleozoic plant spores in North America. *Micropaleontology*, **1** (1), 9–27.

HUGHES, N. F. 1954. Wealden plant microfossils. *Geol. Mag.* **92,** 201–17.

KENDALL, M. 1942. Jurassic Lycopod megaspores from the Gristhorpe Plant Bed. *Ann. Mag. nat. Hist.* (11) **9,** 920–3.

KRÄUSEL, R. and WEYLAND, H. 1929. Beiträge zur Kenntnis der Devonflora III. *Abh. Senckenberg. naturf. Ges.* **41** (7), 315–60.

KIDSTON, R. and LANG, W. H. 1924. On the presence of Tetrads of resistant spores in the tissue of *Sporocarpon furcatum* Dawson from the Devonian of America. *Trans. Roy. Soc. Edinb.* **53** (3), 597–601.

LANG, W. H. 1925. Contributions to the study of the Old Red Sandstone flora of Scotland. Ibid. **54** (2), 253–72.

MURRAY, N. 1939. The microflora of the Upper and Lower Estuarine Series of the East Midlands. *Geol. Mag.* **76,** 478–89.

NATHORST, A. G. 1904. Die oberdevonische Flora des Ellesmerelandes. *Report of the second Norwegian Arctic Expedition in the 'Fram'* 1898–1902. No. 1. A. W. Brøgger, Kristiania.

NAUMOVA, S. N. 1953. Complexes sporo-polliniques du Dévonien Supérieur de la platforme russe et leur signification stratigraphique (translated from the Russian by the Centre d'Étude Docum. Pal., Paris 5); *Trav. Inst. Sci. géol., S.S.S.R.* **43,** ser. géol. (60), 1–204.

NIKITIN, P. A. 1934. Fossil plants of the Petino horizon of the Devonian of the Voronezh region. I, *Kryshtofovichia africani* n. gen. et sp. *Bull. Acad. Sci., U.R.S.S.* **7,** 1079–92.

POTONIÉ, R. 1956. Synopsis der Gattungen der Sporae dispersae, I. *Beih. Geol. Jb.* **23,** 1–103.

—— 1958. Synopsis der Gattungen der Sporae dispersae. II. Ibid. **31,** 1–114.

POTONIÉ, R. and KREMP, G. 1954. Die Gattungen der paläozoischen Sporae dispersae und ihre Stratigraphie. *Geol. Jb.* **69,** 111–94.

—— 1955. Die Sporae dispersae des Ruhrkarbons, I. *Palaeontographica*, **98**B, 1–136.

—— 1956*a*. II. Ibid. **99**B, 85–191.

—— 1956*b*. III. Ibid. **100**B, 65–121.

SCHOPF, J. M., WILSON, L. R., and BENTALL, R. 1944. An annotated synopsis of Paleozoic fossil spores and the definition of Generic Groups. *Ill. Geol. Surv., Rept. Inv.* **91,** 1–66.

SEN, J. 1958. On the megaspores described by Nathorst from the Upper Devonian of Bear Island. *Geol. Fören. Stockh. Förh.* **80** (2), 141–8.

SURANGE, K. R., SINGH, P., and SRIVASTAVA, P. N. 1953. Megaspores from the West Bokaro Coalfield (Lower Gondwanas) of Bihar. *Palaeobotanist*, **2,** 9–17.

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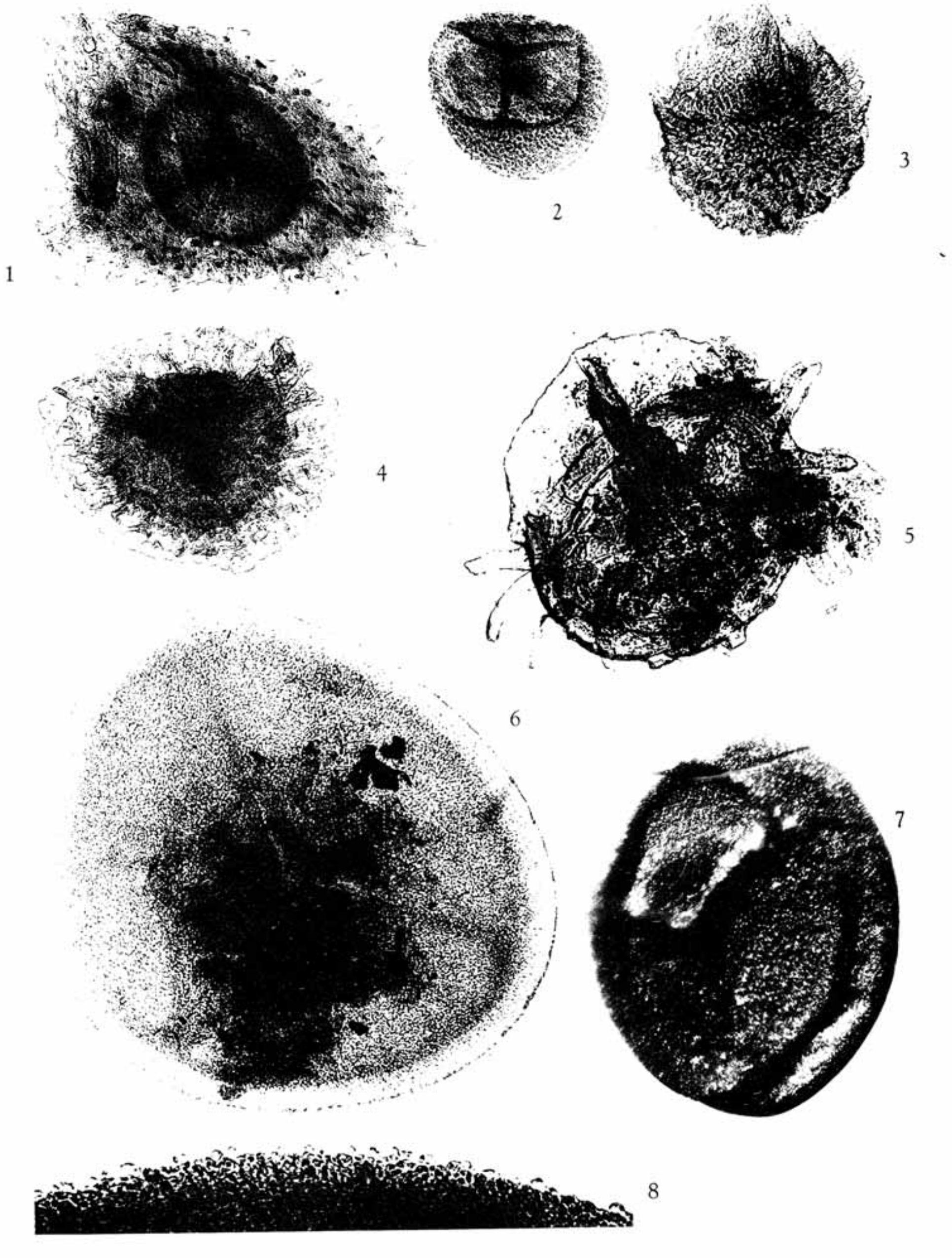

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