MEGASPORE ASSEMBLAGES FROM VISÉAN DEPOSITS AT DUNBAR, EAST LOTHIAN, SCOTLAND

by EDWIN SPINNER

ABSTRACT. Megaspore assemblages are described from two coal seams in the lower Limestone Group. Two new species are proposed: Sétissopites pseudoreticulatus and Zonalesporites fasciatus. The genera Lagentiulia (Bennie and Kidston) Potonié and Krempp 1954 and Sétissopites (Jrahim) Potonié and Krempp 1954 are emended. Two new combinations are proposed: Sétissopites indianaicus (Chaloner) and Sétissopites splendidus (Zördli). The assemblages are compared with published records of megaspores from North America and Europe.

DUNBAR, East Lothian, is situated on the east coast of southern Scotland, some 25 miles east of Edinburgh. Exposed on the foreshore approximately 2 miles east of the town centre near the Barns Ness lighthouse are a group of alternating limestones, shales and sandstones, the prominent members of which are named as follows (from a detailed succession given by Lumsden, in press):

- Upper Skateraw Limestone
- shales etc.
- Middle Skateraw Limestone
- Skateraw Coal
- shales, sandstones etc.
- Lower Skateraw Limestone
- shales etc.
- Upper Longeraig Limestone
- shales etc.
- Longeraig Coal
- Middle Longeraig Limestone

Of two thin coal seams, approximately 10–22 cm. thick, the lower, named here Longeraig Coal, can be seen at the base of a low ridge (high-water mark) formed by the overlying Upper Longeraig Limestone (NT 7155 7730). The upper seam, named here Skateraw Coal, occurs 3–6 m. above the Longeraig seam in the succession and crops out on a small promontory 200 m. farther east towards the lighthouse. Both localities are clearly indicated on the geological map permanently exhibited on a wall in the derelict limestone kiln situated just above the shoreline as well as by marker pegs on the ground.

This succession is locally assigned to the lower Limestone Group of the Carboniferous Limestone and is probably upper P1 or basal P2 age (pers. comm. Dr. R. B. Wilson, Institute of Geological Sciences, Edinburgh, based on the tentative correlation of the Upper Longeraig Limestone with the Hurlet Limestone of the Glasgow area; see also Currie 1954, p. 533). By its geographical position, this succession probably represents part of a link between the depositional areas of the Midland Valley of Scotland, and the Northumberland Trough of England in Upper Viséan–Namurian time.

The succession was brought to the writer's attention by Dr. R. H. Wagner as a result of a field excursion, led by A. Davies and D. C. Greig (Institute of Geological Sciences) and subsequent discussion of the stratigraphic age of the strata.

Although the work began as a study of the presence, preservation, and variety of megaspores in this deposit and of the possibilities of changes in megaspore assemblages as an aid in the subdivision and correlation of Viséan deposits in this area, it was found during the work that some revision of the systematic descriptions was desirable, and that some new taxa were necessary. A comparative account is also given of published records of megaspore assemblages from deposits of Lower Carboniferous age in other areas.

Channel samples were taken of both seams and megaspores were obtained by using Schulze's solution (2 days) followed by repeated washings with 5% Potassium hydroxide solution. Specimens were prepared for both transmitted and reflected light examination.

SYSTEMATIC DESCRIPTIONS

No suprageneric classification is employed, and the arrangement is in alphabetical order. The type material is deposited in the reference collections, Microplaeontology Laboratory, Geology Department, University of Sheffield, England.

Genus LAGENICULA (Bennie and Kidston) Potonie and Kremp emend.

1962 Rostratispora Bharadwaj and Venkatachala, p. 25.

Type species: Lagenicula hirrida Zerdt 1934.

Emended diagnosis. Trilete megaspores with an apical prominence formed by the progressive expansion of the laesurae along most of their length from the junction with the curvature to the proximal pole, and the thickening of the exine of the greater part of the contact areas.

Description. This expansion often, but not necessarily, results in a longer polar than equatorial axis of the spore body. There is a tendency for lateral compression to be most common, but polar oblique compressions are found. Spores compressed laterally are bottle-shaped in outline, polar compressions circular to oval in outline. Originally the spore body was more or less spherical in shape. Contact areas are usually distinct, laevigate or ornamented with elements, similar in form to but smaller in size than those which characterize the distal surface. Exine ornamentation is varied consisting of basic elements e.g. verrucae, cones, spines, pilae, baculae, capillae 'hair-like' forms, or more complex elements with features of two or more of the basic type, or the exine may be laevigate. Often two layers of exine can be distinguished (transmitted light) the inner layer when distinguishable being thin and often folded.

Comparison and remarks. Lagenicula is most similar to Setosisporites (Ibrahim). However, in Setosisporites the apical prominence is formed mainly by the expansion of the laesurae, which generally occurs only in the area immediate to the proximal pole. Also, the heightening of the laesurae is relatively abrupt in Setosisporites, not a gradual increase towards the proximal pole as in Lagenicula.
Setispora Butterworth and Spinner 1967 may appear similar to Lagenicula, particularly in 'dry' specimens. However, any indication of an apical prominence in Setispora is due to sculptural elements on the laesurae.

Some specimens of Cystosporites Schopf 1938 may have an apical prominence similar to Lagenicula (e.g. see Chaloner 1954), but the extremely long polar axis and mesh-like structure of the sue-like spore body clearly distinguish the genus. Isolated abortive specimens of Cystosporites may be confused with small laevigate specimens of Lagenicula, e.g. L. nudata Nowak and Zerdnt 1936.

Lagenoisporites Potonié and Kremp 1954 and Rostratispora Bharadwaj and Venkatachala 1962 are characterized by an apical prominence essentially similar to that of Lagenicula. The former genus was separated by its authors from Lagenicula on the presence of a more or less smooth or laevigate exine. Rostratispora was proposed on the basis of a verrucose rather than 'hair-like' sculptural elements on the exine. Opinion varies considerably on the use of differences in ornamentation to group otherwise similar specimens at a generic level, but I doubt the value of further subdivision at this level on the basis of differences in ornament. Many lageniculate forms are known with very fine elements which are difficult to see on dry specimens. Others when examined by transmitted light reveal elements which vary considerably in form and are difficult to describe in terms of basic element types such as cones, verrucae, pila.

It is proposed that the close similarity in form of apical prominence and original shape of body, suggests that the older name Lagenicula should be retained for the genus, with Lagenoisporites and Rostratispora as junior synonyms; and that the ornament differences are used at a specific level.

Botanical affinities. Lepidodendraceae; Potonié 1962.

Lagenicula subpilosa (Ibrahim) forma major Dijkstra ex Chaloner 1954

Plate 84, figs. 1-4

1950 Trieites subpilosus forma major Dijkstra, p. 871 (nom. nud.).
1954 Trieites subpilosus forma major Chaloner, p. 27, pl. 1, figs. 4-8.
1957 Trieites subpilosus (Ibrahim) S.W. et B. forma major; type 2716 Dijkstra, p. 14, pl. 9, figs. 94-6, pl. 10, figs. 97-103.
1957 Trieites subpilosus (Wicher) S.W. et B. forma major Dijkstra; Dijkstra and Piéart, pp. 12-13, pl. 11, figs. 126-7.
1959 Trieites subpilosus forma major (Dijkstra) ex Chaloner; Winslow, pp. 18-20, pl. 1, figs. 1-9.
1962 Lagenicula subpilosa (Ibrahim) Potonié and Kremp; Ishchenko and Semenova, pars, p. 71, pl. 8, fig. 1.
1967 Lagenicula subpilosa (Ibrahim) forma major Dijkstra ex Chaloner 1954; Butterworth and Spinner, pp. 13-14, pl. 3, figs. 2-4.
1967 Lagenicula subpilosa (Ibrahim 1933) Potonié and Kremp 1955 pars; Karczewka, pp. 286-7, pl. 2, figs. 4-6.


Remarks. The material assigned here to this forma agrees closely with an earlier description (Butterworth and Spinner 1967, pp. 18-20), but an additional feature noted
on several specimens is the presence of a thin, folded layer of exine within the ornamented layer that is generally regarded as the spore wall.

Since there is some disagreement over the value of recognising this *forma* (Karczewska 1967, p. 286), and also in the variation in over-all size of spores, length of sculptural elements etc., which appear to vary with stratigraphic horizon (Winslow 1959, pp. 18–20), the following new results are recorded: Maximum diameter of the spore 960–1760 μ, mean 1280 μ, based on 50 specimens mounted in a hydrous medium; One other specimen measured 640 μ in maximum diameter. The apical prominence ranged between 150 and 300 μ in height, 200–400 μ in basal width (height measured on lateral compressions as from beginning of projection from curved spore outline to apex). The spines on the outer layer of exine, distal to the curvatures, varied between 80 and 250 μ in length, 16–40 μ in basal diameter, 4–10 μ in diameter at the apex or tip.

These figures are in approximate agreement with those previously recorded by Winslow (1959, p. 18) from the Hardingsburg Formation, Kentucky, U.S.A. (low Chester Series, Mississippi) and by Butterworth and Spinner (1967, p. 14) from the Bernician beds, Cementstones, Cumberland, England (Viséan S2). Dijkstra (1952, p. 103) in describing this *forma* for the first time gave a size range of 500–1300 μ, mean 866 μ, based on 50 'dry' specimens.

The species *Lagenicula subpilosa* (Ibrahim) Potonié and Kremp 1955, which characterizes strata of low Westphalian age, has a similar size range (320–1100 μ, mean 652 μ, Dijkstra 1946, p. 46 and 1952a, p. 103, 'dry' specimens; 550–1270 μ, Winslow 1959, p. 17, wet specimens) to *L. subpilosa* *forma major*. This led Karczewska (1967, p. 286) to reject the *forma*. However, as Winslow pointed out (p. 18) the distal spines on *L. subpilosa* are generally less than 100 μ in length, and the maximum length of the spines recorded by Karczewska is 115 μ. It is therefore suggested that on the basis of larger mean diameter of spore, length of spines and different stratigraphic age, that the retention on this *forma* is of value.

The relatively short dimensions of the spines, as given by Karczewska, makes the inclusion of her record in the synonymy questionable. Also Dijkstra (1957, p. 14), Dijkstra and Piérrart (1957, p. 13) describe short elements 10 μ long between the larger distal spines. These were not reported by Winslow (1959) or by the author, either in 1967 (Butterworth and Spinner) or during the present study.

**Affinities.** Lepidodendraceae; Potonié and Kremp 1954.

**Stratigraphic distribution.** Europe: Turkey, Namurian ABC (Dijkstra 1952); Ireland, Lower Carboniferous (Dijkstra 1957, Chaloner 1966); Scotland, Dinantian-Namurian (Chaloner 1954; Dijkstra 1957, Sen 1964); England, Viséan (Butterworth and Spinner 1967); ? Moscow Basin, Lower Carboniferous.

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**EXPLANATION OF PLATE 84**

All specimens by transmitted light.

Figs. 1–4. *Lagenicula subpilosa* (Ibrahim) *forma major* Dijkstra ex Chaloner 1954. 1. Proximal surface, polar compression, × 100; slide D/10. 2. Lateral compression, × 50; slide D/11. 3. Part of specimen to illustrate cones on contact areas, × 100; slide D/12. 4. Part of specimen illustrating spines projecting from distal surface, × 100; slide D/13.

Figs. 5–7. *Setosisporites pseudoreticulatus* sp. nov. 5. Proximal surface, polar compression, × 100; slide D/7. 6. Holotype, oblique compression, × 100; slide D/8. 7. Lateral compression, × 100, slide D/9.
SPINNER, Scottish Viséan megaspores
Genus setosisporites (Ibrahim) Potonié and Kremp 1954 emend.

Type species. Setosisporites hirsutus (Loose 1932) Ibrahim 1933.

Emended diagnosis. Trilete megaspores characterised by an apical prominence at the proximal pole, formed mainly by the expansion of the laesurae at the pole, although the polar part of the contact area may be involved. The greater parts of the contact areas are not involved in the formation of the apical prominence whose size relative to the spore body is such that the polar and equatorial axes are of similar dimensions. There is no preferred type of compression; polar oblique compressions are circular to oval in outline, lateral compressions bottle-shaped. The spore was originally more or less spherical in shape. Distal to the apical prominence the laesurae are low and of variable length. Contact areas are distinct, laevigate, or ornamented with elements similar to those present on the distal surface, but smaller in size. Spore wall when ornamented is covered with basic granae, cones, spines baeulae, capillae or pilae type elements of variable size and density.

Comparison. In their original diagnosis of this genus Potonié and Kremp (1954, p. 152) referred to the exine ornamentation, except the contact areas, as being branched, slightly pointed, short or also relatively long hairs. The emended diagnosis refers to the original shape of the spore body, form of apical prominence and wide variation in exine ornamentation. See also under emendation of Lagenicula above.

Botanical affinities. Porostrobus spp. (Chaloner 1958, Bharadwaj 1958); Bothrodendrostrombus watsoni (Chaloner 1967).

Setosisporites indiannensis (Chaloner 1954) comb. nov.

Plate 85, figs. 1–4

1954 Triletes indiannensis Chaloner, p. 28, pl. 2 figs. 1–2.
1959 Triletes indiannensis; Winslow, p. 26, pl. 6 figs. 1–3.

Size and shape. Trilete megaspores circular to oval in outline varying between 875 and 1615 μ in max. diameter, mean 1195 μ (based on 28 dry specimens). Polar, oblique and lateral compressions are found. Lateral compressions are bottle-shaped due to the projection of an apical prominence. However, the polar axis of the compressed spore is not always larger than the equatorial axis. Originally, the spore body was more or less spherical in shape.

Haptotypic features. An apical prominence is present at the proximal pole. Bluntly pyramidal in shape, this structure is formed by the expansion of the contact areas close to the proximal pole, and in part (?) by the laesurae. Basal diameter of apical prominence varies 200–375 μ, 50–150 μ in height. The laesurae extend as low trilete ridges from the apical prominence to the curvaturae, 30–60 μ high and wide. On the apical prominences of some specimens small ridges occur as (?) extensions of the laesurae.
Contact areas occupy approximately three-quarters of the proximal surface of the compressed spore and ornamented with small grana approximately 6 μ in diameter. The position of the curvature are marked by low arcuate ridges which are only well developed at the junction with the laesurae, 25–50 μ wide, approximately 25 μ high.

Exine structure and sculpture. The spore wall, distal to the contact faces is ornamented with densely placed granulate to conate type elements 10–15 μ up to 20 μ in basal diameter and height. These are generally more densely placed in the region of the curvature. Internal to the granular layer, a thin membrane can be seen on broken specimens. The outer granular layer of exine varies 30–50 μ in thickness.

Comparisons and remarks. Chaloner 1954 and Winslow 1959 both assigned this species to Triletes, sensu Schopf, Wilson, and Benton 1944. An attempt to place this species in one of the narrower genera proposed by Potonié and Kremp 1954, encounters difficulties.

These authors proposed three genera of lageniculate megaspores i.e. Lagenicula (Bennie and Kidston) emend., Lagenoisporites Potonié and Kremp and Setosisporites (Ibrahim) emend. The primary feature used in distinguishing these genera being the structure, form and size of the apical prominence relative to the spore body, and a secondary feature being the type of (or lack of) ornament on the exine. In type of apical prominence T. indianaensis is more similar to Setosisporites e.g. S. praetextus (Zerndt) Potonié and Kremp 1955, than Lagenicula e.g. L. horrida (Zerndt) Potonié and Kremp 1954. However, the exine ornamentation in Setosisporites is ‘hair-like’ e.g. S. hirsutus (Loose) Ibrahim 1932. Comparing with Lagenoisporites T. indianaensis is similar in the small differences in length, between polar and equatorial axes, and in the small size of sculptural elements on some specimens which give an approximately smooth appearance, particularly on specimens not well preserved. The apical prominence in Lagenoisporites is, however, formed by the expansion almost along most of the length of the laesurae and the contact areas.

Rostratispora Bharadwaj and Venkatachala 1962 another lageniculate genus of megaspore is similar to T. indianaensis in the type of ornamentation (verrucose) but has an apical prominence similar in form to Lagenicula and Lagenoisporites. Although lateral compressions of Setispora Butterworth and Spinnier 1967 appear lageniculate, the height of laesurae is a result of capillate type ornamentation, and is not comparable with T. indianaensis. Triletes indianaensis Chaloner is therefore recombined to the genus

EXPLANATION OF PLATE 85

All specimens by reflected light, ×40, unless stated otherwise.

Figs. 1–4. Setosisporites indianaensis (Chaloner 1954) comb. nov. 1. Proximal surface, polar compression, illustrating typical Setosisporites type apical prominence and large contact areas; slide D/6. 2. Lateral-oblique compression; slide D/6.

Figs. 5–7. Setosisporites splendida (Zerndt 1937) comb. nov. 5. Proximal surface, polar compression; slide D/5. 6. Distal surface, polar compression; slide D/5. 7, 10. Part of specimen illustrating ornament at spore margin, ×120, by transmitted light; slide D/5.

Figs. 8. Setosisporites sp. A, oblique compression; slide D/4.

Fig. 9. Setosisporites sp. B, lateral compression; slide D/3.
Setosisporites as emended above in the characteristics of original shape of spore body, form of apical prominence and type of ornamentation.

Stratigraphic distribution. North America, Beaver Bend Limestone, Indiana, Low Chester Series, Mississippian (Chaloner 1954); Bethel Formation, Kentucky, Low Chester Series, Mississippian (Winnslow 1959).

Setosisporites pseudoreticulatus sp. nov.

Plate 84, figs. 5-7

?1937 Type 13a, Trilete tespinosus var. brevispinosus Zerbit pars, p. 6, pl. 3, figs. 1, 2, 5-7.
?1955 Trilete tetratus (Loose) var. brevispinosus Schoff, Wilson and Bentall forma I Dijkstra pars, p. 13, pl. 7 figs. 67-71.
?1959 Trilete globosus Arnold var. A Winnlow, pl. 4, figs. 1-3.

Holotype. Plate 84, fig. 6.

Diagnosis. Trilete megaspores approximately circular to rounded triangular in outline varying 420–800 μ in maximum diameter. Apical prominence varies 60–120 μ in height, 90–150 μ in basal width, rounded at apex. Contact areas are ornamented with cones 4–6 μ high. Distal to the contact areas, baculate to pilate elements, 10–30 μ in length, up to 6 μ in basal diameter with small cone-like terminals, form an irregular reticulate pattern of ornamentation. These elements are densely placed in the region of curvaturae and may be partly fused to form a small flange-like structure 20–30 μ in width.

Description: Size and shape. Trilete megaspores, approximately circular to rounded triangular in outline, carrying between 420 and 800 μ in maximum diameter, mean 620 μ (based on 50 specimens in a hydrous medium). Polar, oblique and lateral compressions are all commonly found, there being no apparent preferred direction of compression. On lateral compressions the curved outline of the spore body is interrupted by a small 'neck-like' protuberance from the proximal pole. Originally, the spore body was of approximately spherical shape, the polar and equatorial axes being of similar dimensions.

Haptotypic features. Lascureae are straight to slightly sinuous in outline, approximately two thirds the radius of the spore body in length. The line of commissure may be ruptured, and is bounded by narrow (approximately 10 μ wide) tecta raised 20 μ high near the junction with the curvaturae. The height of the lascureae increases gradually 20–40 μ from the curvaturae towards the proximal pole, where there is a marked expansion forming an apical prominence. This structure varies 60–120 μ in height (measured in lateral compressions as projections from spore margin), 90–150 μ in basal diameter (measured perpendicular to height). The apex of the apical prominence is smoothly curved.

Contact areas are distinct occupying one-half to two-thirds of the proximal surface of the compressed spore, and ornamented with small cones, approximately 4 μ basal width, up to 6 μ high. On some specimens the contact areas have irregular areas of thickened exine, which tend to be arranged radially from the proximal pole. The curvaturae are represented by narrow thickenings on the exine.

Exine structure and sculpture. The spore wall excluding the contact areas, is covered by what are basically baculate to pilate type elements. These vary 10–30 μ in length, up to 6 μ in basal diameter, slightly swollen at the apex, where one or more small, pointed, cone-like projections may occur. The elements may be curved or straight-sided
and are often joined at the bases. This feature, in addition to the elements being adpressed to the spore exine, gives the appearance of an irregular interrupted reticulum. On many specimens the elements are densely placed in the region of the curvaturae so as to form a small flange-like structure 20–30 µ wide.

Two layers of exine can easily be distinguished forming the spore wall. The outer layer appears infrapunctate, approximately 20 µ thick, lightened in optical section, yellow-brown in colour. The inner layer, distinguished under transmitted light, is attached to the laesurae, thin and folded. In some specimens it is shrunken, but in others it is in close proximity to the thick outer layer.

Under reflected light, the exine is yellow-brown in colour, the apical prominence is not always clearly visible, and the sculptural elements appear more or less granular. The pseudoreticulate nature of the ornament is not clearly distinguishable.

Comparisons and remarks. This type of spore illustrates some of the difficulties that arise, when descriptions are given based on only one type of examination, i.e. reflected or transmitted light.

Under reflected light examination *S. pseudoreticulatus* is similar in shape, size, and ornamentation to *S. hirsutus var. brevispinosa form 1* (Zerny) Potonié and Kremp 1955 as described by Zerny (1937, p. 6) and Dijkstra (1957, p. 13). Zerny noted that it was difficult to distinguish a regular form of the sculptural elements present on his specimens, but that he regarded the elements as small spines, up to 6 µ in length, 4 µ in basal width. He also reported much smaller elements on the contact areas of his material. On most specimens of *S. pseudoreticulatus* the elements are adpressed to the spore wall, and appear under reflected light as small projections of the size given by Zerny. However, both Zerny and Dijkstra emphasize the radial thickenings of the exine on the contact areas as being the characteristic feature of *S. hirsutus var. brevispinosa form 1*. Although some specimens of *S. pseudoreticulatus* were found with thickenings on the contact areas, these were not common as distinct as suggested by Zerny. It may be noted that Dijkstra (1957) using reflected light found *S. hirsutus var. brevispinosa form 1* to be common in the coals of the Limestone Coal Group of Scotland, slightly younger (E1) in age than the horizon studied here. Thus, there is evidence which suggests that some of the material referred by earlier workers to *S. hirsutus var. brevispinosa* could be assigned to *S. pseudoreticulatus* and this is indicated in the synonymy given above. The major argument against such an assignment is the prominence of the radial thickenings on the contact areas, and the size of ornament.

Under transmitted light many more of the details of morphology of *S. pseudoreticulatus* are seen, and similarities can be seen with *S. globosus* (Arnold) Potonié and Kremp 1955 in shape and general morphology. However, *S. globosus* has a smaller size range (390–570 µ Arnold 1950, p. 80; 385–640 µ Winslow 1959, p. 42), and the sculptural elements are larger (35–50 µ length, up to 12 µ diameter; Arnold p. 80), straight-sided with terminal clefts. The sculptural elements are not joined to form a reticulate type pattern which characterizes *S. pseudoreticulatus*, but are discrete and widely spaced.

Winslow (1959, pp. 43–5) described three varieties of *S. globosus*. Of these varieties, *S. pseudoreticulatus* is very similar to *S. globosus var. A* in length and height of laesurae, size of apical prominence, type and size of sculptural elements forming an irregular reticulate pattern (catenulate ornament of Winslow, p. 43). The size range of var. *A* is
smaller (330–630 μ; mean 515 μ; Winslow, p. 43) than S. pseudoreticulatus (420–800 μ, mean 620 μ). Winslow (p. 43) also noted the similarities of var. A with S. hirsutus var. brevispinosus when compared under reflected light examination, but did not consider the two as being the same due to the absence of radial thickenings on the contact faces of variety A.

The differences in ornamentation between S. globosus and S. pseudoreticulatus (including Winslow’s var. A, see synonymy) are considered here to warrant separation at specific level. No specimens with the type of ornamentation present on S. globosus were found associated with S. pseudoreticulatus during the present study.

Winslow’s other two varieties of S. globosus can be distinguished from S. pseudoreticulatus by the larger size of the sculptural elements (15–57 μ, generally more than 35 μ, var. B) and the type of element (tubercles 5–26 μ length, 5–52 μ basal diameter, var. C).

S. pseudoreticulatus also resembles S. reticulatus Karczewski 1967 in size, shape, and ornament pattern. However, on S. reticulatus the outer layer of exine forms a uniform fused reticulum on the distal surface. Small projections 3–7 μ in length, are situated between the lumina of the reticulum.

S. pseudoreticulatus Spiner 1965 and S. pilatus Spiner 1965 are similar in shape and size of the spore body to S. pseudoreticulatus, but these species have smaller, discrete, sculptural elements which do not form a reticulate type pattern.

Triletes ceterulatus Winslow 1962 can be distinguished from S. pseudoreticulatus by the presence of highly developed laesurae (200 μ or more high).

In my opinion many of the specimens previously assigned to S. hirsutus var. brevispinosus forma 1 could be placed in S. pseudoreticulatus. However, rather than raise the varietal name to species rank, a new name is proposed for the following reasons. Zernndt (1937) recognised two forms (varieties 1, 2; Zernndt 1937, p. 7) within var. brevispinosus. These forms are markedly different in type and size of ornamentation (form 1, appendices up to 6 μ long; form 2, spines 39–96 μ wide at the base, decreasing to approximately 12 μ near the tip). However, Zernndt emphasized the folding, thickening on the contact areas as the common feature of both forms grouped within the named variety brevispinosus. Later Schopf, Wilson, and Bentall (1944, p. 26) in dealing with the problem of Zernndt’s varieties with a variety regarded variety 1 of Zernndt as being var. brevispinosus and proposed a new varietal name secundus for variety 2 of Zernndt; whereas Dijkstra (1946, 1956) interpreted varieties 1, 2 of Zernndt as forms within var. brevispinosus. Due to the different interpretation of Zernndt’s work, the emphasis on folding and thickening in his description of the variety, and the small size of the appendices on his form 1, a new name pseudoreticulatus is proposed for the species.

Botanical affinities. Unknown.

Stratigraphic distribution. Limestone Coal Group, Scotland, Namurian E (Dijkstra 1957); Lower Carboniferous, Ireland (Chaloner 1966); Upper Carboniferous, Kentucky, Wattersburg Formation, Illinois, Chester series, Low Mississippian (Winslow 1959).

Seatosipites splendidus (Zernndt) comb. nov.

Plate 85, figs. 5–8, 11–12

1937 Type 28; Lagenicula splendidid Zernndt, p. 13–14, pl. 18, figs. 1, 2; pl. 19, figs. 1–3, 5; pl. 20, figs. 2, 3, 4.
1944 *Triletes splendida* (Zernndt) Schopf, Wilson, and Bentall, p. 25.
1946 *Triletes splendida* (Zernndt) Dijkstra, p. 50, pl. 16, figs. 173-5.
1955 *Lagenicula splendida* Zernndt; Potonié and Kremp, p. 119.
1957 *Triletes splendida* (Zernndt) S.W. et B.; Dijkstra, p. 14, pl. 8, figs. 85; pl. 9, figs. 86-8.
1959 *Triletes splendida* (Zernndt) Schopf, Wilson, and Bentall; Winslow, p. 27, pl. 5, fig. 8.
1962 *Lagenicula splendida* Zernndt; Ishchenko and Semenova, pp. 72-3, pl. 8.
1962 *Lagenicula verrucosa* Ishchenko and Semenova, p. 74, pl. 9, fig. 3.

**Description:** *Size and shape.* Trilete megaspores more or less circular in equatorial outline. Lateral compressions are most commonly found which have a marked ‘bottle-shaped’ outline, the ‘neck’ being formed by an apical prominence at the proximal pole of spore. The difference between the polar and equatorial axes is not large, and on some lateral compressed specimens the polar axis is the smaller. Polar and oblique compressions also occur. Maximum diameter of the spore body including apical prominence on lateral compressions varies 935–1625 μ, mean 1225 μ based on 35 dry specimens. Originally, the spore body was more or less spherical in shape.

**Hapotypic features.** The characteristic feature here is the bluntly pyramidal apical prominence at the proximal pole, varying 200–300 μ in basal diameter, 150–270 μ high on lateral compressions, and may appear slightly constricted at the base. This structure is probably formed by an expansion of the exine of the immediate polar part of the contact areas, and in part by the laesurae. On some specimens, small ridge-like continuations of the laesurae can be traced on to the prominence. In some specimens the laesurae are ruptured, but the ruptures have not been observed extending on to the prominence, whilst in other damaged specimens the prominence has been completely removed. Distal to the apical prominence, the laesurae form low ridges 250–400 μ long.

The contact areas occupy approximately three-quarters of the proximal half of the compressed spore. These are delimited from the remainder of the spore body by the smaller cone-like sculptural elements, generally less than 12 μ in diameter, but occasionally up to 30 μ on some specimens. Arcuate ridges representing the curvatures are not well developed except at the junction with the laesurae i.e. curvatures imperfectae.

**Exine structure and sculpture.** In the region of, and distal to the curvatureae the spore wall is ornamented with cones and granular type elements. These are most densely placed in the region of the curvatureae. Two groups of elements can be recognized based on size. The most prominent group consists of relatively large cones 30–75 μ in basal diameter (generally larger than 50 μ), 12–35 μ high, and often mammillate in form. Interspersed with these elements are smaller cone and granular type forms generally 20 μ or less in basal diameter, 5–15 μ high.

Broken specimens reveal a thin layer of exine, internal to the heavily ornamented layer which is approximately 50 μ thick.

**Comparisons and remarks.** The limits of this species are ill defined. Both Zernndt (1937, pp. 13–14, pls. 18–20) and Dijkstra (1946, p. 50, pl. 16, 1957, p. 14, pl. 8) allow considerable range in spore diameter (700–1700 μ; Dijkstra 1957) and in size of sculptural elements (16–97 μ diameter, Zernndt 1937; 10–150 μ diameter, Dijkstra 1957). At the same time both authors recognised other species e.g. *Lagenicula subtilinodulata* Nowak and Zernndt 1936, which could be placed within the limits they described for *L. splendida*. Chaloner (1954, p. 28) proposed *Triletes indiesensis* for specimens having a distal ornamentation
of elements of up to, but generally less than, 20 μ in length. These specimens could, on the basis of the limits given by Zerndt and Dijkstra, be assigned to *L. splendidida*. Winslow (1959, pp. 26–7) recognizes *S. splendidus* (Triletes splendidus of Winslow) as being larger in size of spore and ornamentation, than *L. subtilinodulata* and *Triletes indiamentis*. Reference to the holotype is of no assistance for, as far as I am aware, neither Zerndt nor any other worker has designated a holotype for this species.

I do not think that any particular value should be placed on relatively small differences in the size of the spore body, but suggest that a useful character for distinguishing this species is the two types of sculptural element. This character is seen on Zerndt's specimens illustrating the species, and plate 18, fig. 2 is designated here as the lectotype of the species.

*Triletes indiamentis* Chaloner 1954 differs from *S. splendidus* in the small size (generally less than 20 μ in basal diameter and height) of the elements forming the ornamentation on the spore wall.

*LAGENICULA AGNINA* Zerndt 1937 can be distinguished from *S. splendidus* by the type of apical prominence (laesurae expanding along most of the length), small contact areas, and close verrucose ornament on the distal surface.

*LAGENICULA VERRUCA* Ishchenko and Semenova 1962 can according to its authors be distinguished from *S. splendidus* by its smaller size (1360 × 1325 μ) and 'barbate' sculpture. Judging from the drawings produced as illustrations of the two species, *L. verrucosa* appears more similar to the specimens described here than does *L. splendidida sensu* Ishchenko and Semenova and this is indicated in the synonymy given above.

There is some reason to doubt the correctness of assigning this species to *Lagenicula* as described by Potonie and Kremp (1955, p. 118). In their diagnosis these authors maintain: 'a long polar axis, an apical prominence larger than the part of the contact areas not involved in its formation, and unornamented contact areas.' These features are not applicable to this species. The type and size of the apical prominence relative to the other haptotypic features is more typical of *Setosisporites* e.g. *S. praetextus* (Zerndt) Potonie and Kremp 1955. Consequently this species is assigned to *Setosisporites* as emended above.


*Setosisporites* sp. A

Plate 85, fig. 9

*Description.* Trilete megaspores circular to oval in outline, approximately 1250 μ in maximum diameter (only two specimens found, 1310 and 1180 μ in maximum diameter). Apical prominence at proximal pole, blunt pyramidal shaped, 300 μ maximum diameter. Laesurae relatively low, 25–60 μ wide at junction with curvaturae. Contact areas approximately 650 μ in radius ornamented small cones 25 μ diameter. Spore wall distal to contact faces, ornamented with large cones 65–80 μ basal diameter, 60–70 μ high, smaller cones approximately 40 μ diameter in region of curvaturae.

*Remarks.* These megaspores closely resemble *Setosisporites splendidus* as described
here, but have more typical conate ornamentation in which the elements are higher, approximately equal to basal diameter, and not mammilate in form as in S. splendidus. The elements are also not so densely placed on the contact areas or distal surface. Lagionicula agnina Zerndt 1937 has larger sculptural elements on the distal surface (97–225 μ width, 48–160 μ high; Zerndt 1937, p. 14). L. subtilinodulata Nowak and Zerndt 1936 is smaller in size of spore body and distal ornamentation, and the contact areas are laevigate.

Setosisporites sp. B
Plate 85, fig. 10

Description. Trilete megaspores 912–1500 μ maximum diameter, mean 1300 μ based on six dry specimens. Apical prominence is bluntly pyramidal, 150–225 μ high, 250–375 μ
basal diameter. Laesurae, distal to apical prominence, are approximately 50–60 μ high and wide, best developed near the junction with the curvatures. Contact areas 
occupy three-quarters proximal surface, smooth bounded by arcuate ridges 35–50 μ high, 50–80 μ wide, most pronounced at junction with the laesurae. Distal surface 
ornamented with irregularly scattered cones, 25–40 μ high, and wide, 60–300 μ apart.

Remarks. In type of apical prominence this species resembles S. splendidus and S. indanensis.

Genus Zonalessporites (Ibrahim) Potonié and Kremp emend. Spinner 1965

Type species. Zonalessporites brasserti (Stach and Zerndt) Potonié and Kremp 1956.

Zonalessporites fusinatus sp. nov.

Plate 86, figs. 1–4

?1957  Triletes brasserti Stach and Zerndt, type 20; Dijkstra pars. p. 13, pl. 7, figs. 73–6.

Holotype. Plate 86, fig. 1.

Diagnosis. Trilete megaspores composed of spore body with a subequatorial corona. Spore body varies 1300–2160 μ in maximum diameter. Corona varies 415–700 μ width, composed of a number of layers of baculate type elements, 10–30 μ width, with rounded tips. Elements are more fused distally to form a rim with some dissections and ornamented with small baculate processes. Margin of rim generally smooth, lacking ornamentation.

EXPLANATION OF PLATE 86

All specimens by transmitted light, ×40, unless stated otherwise.

Figs. 1–4. Zonalessporites fusinatus sp. nov. 1. Holotype, proximal surface, polar compression, by reflected light; slide D/1. 2. Distal surface, polar compression, by reflected light; slide D/2. 3. 4. Parts of corona, ×120; slide D/17.

SPINNER, Scottish Viséan megaspores
Description: Size and shape. Trilete megaspores approximately circular to rounded, triangular in outline consisting of a spore body with an equatorial corona. The spore body varies between 1300 and 2160 μ in maximum diameter, mean 1440 μ (based on 36 ‘wet’ specimens). Entire specimens are not common, 10 such specimens measured 1550-2300 μ in maximum diameter, mean 1950 μ. Polar compressions are most common, due to the longer equatorial axis of the entire spore. The spore body was originally more or less spheroidal in shape.

Hapiotypic features. Laesurae are straight or sinuous in outline, half to three-quarters the spore body radius in length. Broadly based, the laesurae are raised 100–250 μ at the proximal pole. On most specimens the laesurae decrease slightly in height from the proximal pole before attaining the greatest height at the position of the curvaturae, 150–290 μ. Also on some denuded specimens the laesurae are seen projecting beyond the spore body margin. An apical prominence is not present. Contact areas are laevigate and occupy half to three-quarters of the proximal surface of the compressed spore body. The positions of the curvaturae are marked by the bases of the elements forming the corona.

Exine structure and sculpture. The corona is attached in a region slightly proximal to the geometrical equator of the compressed spore body. The width of the corona varies 415–750 μ, greatest width in line with the laesurae, hence the subtriangular outline of the entire spore. The overlap of the corona onto the proximal surface of the spore body approximately equals one third of the width of the corona. The corona is formed by several layers of elements (five or more). These are approximately 30 μ wide at the base, densely spaced, and partly fixed to form a loose type of reticulum. The proximal elements are most distinct 10–25 μ width, baculate in form, with smoothly rounded tips. Distally the layers are more completely fused and form an almost continuous rim to the corona. Small baculate elements with rounded tips 10–30 μ in width project from the fused part of the corona, but only rarely from the rim (small dissections occur in the corona approximately 100 μ in diameter). On some small specimens the fused outer part of the corona is not so clearly distinguishable and the rim has a crenulate appearance.

Distal to the corona the spore body is generally laevigate, but small verrucate type elements 20–50 μ in diameter may occur scattered on the distal surface. These tend to become more elongate near the spore body margin and merge into the corona. The spore body wall appears infrapunctate, approximately 40 μ thick, as measured in optical section. Within this layer a further thin folded layer of exine can be distinguished (transmitted light) in most specimens.

Under reflected light the corona appears almost completely fused, with some striations, lighter in colour than the spore body. Dissections can be distinguished.

Comparison and remarks. Under reflected light both Zonalesporites brasserti (Stach and Zerdit) Potonié and Kremp 1956 and Z. fusinatus sp. nov. appear very similar, and the differences in corona structure are not easily seen. Dijkstra (1952, 56, 57) recognizes wide variation in size of spores and some variation in the corona of this species, but does not consider these differences to warrant distinction at species level, but he distinguishes several forms within the species. Potonié and Kremp (1956, p. 122) give no details of the structure of the corona (cingulum of P. and K.) in their description. However, Winslow
(1959) using transmitted light, restricted *Z. brasserii* to those forms with a corona (flange of Winslow) formed by layers of elements, fused laterally except at the point of attachment to spore body and at the terminals. The outer layer forms 'bar-like' processes (Winslow, p. 36) projecting at the margin. Only rarely are small dissections seen in the corona.

I agree with this interpretation of *Z. brasserii* and separate the specimens described here into a new species *Z. fusinatus*. The two species are similar in general appearance, especially under reflected light. However, in *Z. fusinatus* the corona is less compact, the elements are baculate processes with smoothly rounded tips, are only partly fused, and the rim of the corona is generally smooth, lacking any projections. The lacerae and contact areas are usually ornamented in *Z. brasserii* with verrucate type processes, generally laevigate in *Z. fusinatus*.

*Z. conacies* Butterworth and Spinner 1967 can be distinguished from *Z. fusinatus* by the elongate cones which characterize the corona (Pl. 86, fig. 5). *Z. radiatus* (Zernitz) Spinner 1965 lacks the fused margin of the corona, and the elements are spaced on the spore body. *Z. fusinatus* differs from *Z. rotatus* (Bartlett) Spinner 1965 by the larger spore body and the corona formed by several layers of elements. *Z. ramosus* (Arnold) Spinner 1965 although having a corona formed by several layers of elements as in *Z. fusinatus*, characteristically has relatively large projections (up to 52 μ long, Winslow 1959, p. 33) from the rim of the corona (Pl. 86, fig. 7).

The comparisons made above are based on transmitted light studies. Under reflected light examination it is difficult to distinguish *Z. brasserii* from *Z. conacies* and *Z. fusinatus*. However, the author considers the differences (see Pl. 86, figs. 3–8) to be distinctive and worthy of recognition at a specific level.


**Stratigraphic distribution.** *Namurian*, Scotland (Dijkstra 1957).

**THE MEGASPORE ASSEMBLAGES**

Both coal seams yielded well preserved megaspores of considerable variety. A count of 500 specimens from each seam indicated the composition of the assemblage as follows:

<table>
<thead>
<tr>
<th>Coal samples</th>
<th>Skateraw</th>
<th>Longraig</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lagenicula subpilosa forma major</em></td>
<td>176</td>
<td>132</td>
</tr>
<tr>
<td><em>Setosporites pseudorotundatus</em></td>
<td>145</td>
<td>101</td>
</tr>
<tr>
<td><em>Setosporites splendidus</em></td>
<td>53</td>
<td>30</td>
</tr>
<tr>
<td><em>Setosporites influenus</em></td>
<td>0</td>
<td>22</td>
</tr>
<tr>
<td><em>Setosporites sp.</em></td>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td><em>Cystosporites sp.</em></td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td><em>Zonalosporites fusinatus</em></td>
<td>34</td>
<td>194</td>
</tr>
<tr>
<td><em>Zonalosporites rotatus</em></td>
<td>78</td>
<td>0</td>
</tr>
</tbody>
</table>

At generic and specific level the two assemblages are closely similar in over-all content and proportional representation. However, the differences may be of significance in correlation with other areas in northern Britain, in that the Longerraig and Skateraw coals are stratigraphically almost immediately below and above the upper Longerraig
limestone; these are the records of *S. indiannensis* and *Z. rotatus*, and the dominance of *Z. justnatus* in the Longcrag coal. Accepting the suggested correlation of this limestone with the Hurlet limestone of the Midland valley of Scotland by Wilson, the differences between these assemblages may contribute further to the subdivision and correlation of Lower Carboniferous deposits in the Midland valley of Scotland and northern England. Although no plant megaspores have been recorded from the area, some indication of the types of plant forming the forests at this time can be obtained from the megaspore assemblages. Chaloner (1954, p. 31) and Winslow (1959, p. 94) commented on the importance of the Lepidodendrid-Lepidocarpon elements in the forests during the Mississippian (Chesterian) of central U.S.A. The same comment may be made here, based on the occurrence of *Lagenicula* and *Cystosporites*. Probably a more important element was the plant producing the *Zonalesporites*. This type of spore is known from *Sporangiostrobus* Bode (Chaloner 1962). The plant bearing *Sporangiostrobus* is unknown, but the large size and structure of the cones suggests a large arborescent form. Néméc (1946, p. 7) suggested that the most probable parent plants of *Sporangiostrobus* are among the lycopsids with long leaves, such as *Ulodendron* Lindley and Hutton. The recorded species of *Setosisporites* are unknown from fructifications, although spores assignable to the type species of this megaspore genus, *S. hirsutus*, are known from the small *?*herbaceous lycopod *Porostrobus canoniensi*ss Chaloner (Chaloner 1962).

From the known broad association of *Zonalesporites* and *Setosisporites* with the *Cristatisporites/Densosporites* group of microspores (Chaloner 1962, pp. 82–3) it may be suggested that the *Zonalesporites* and *Setosisporites* of the assemblages recorded here represent elements of the open moor of Kremp (1952) or the densosporale phase of Smith (1957). Similarly, *Lagenicula subpilosa* forma *major* and *Cystosporites* sp. represent the forest moor or lycospore phase.

The absence of the megaspore genera *Tuberculatisporites* (Ibrahim) Spinner 1968, *Lavignatisporites* (Ibrahim) Potonié and Kremp 1954, or similar forms, suggests an absence of Sigillarians in the lycopod flora. A similar comment may be made regarding the Selaginellales since there is an absence of any spores of *Triangulatisporites* Potonié and Kremp 1954. In general, the megaspore assemblages indicate a flora in which large arborescent lycopsids with long leaves were important together with some more diminutive forms.

**Comparisons with records from other areas**

The relatively little published research on Lower Carboniferous has been largely concerned with records of occurrence, discussion on the value of broad or narrow species definitions, and the relationship of megaspores to fructifications. Consequently, it is not yet possible to reach firm conclusions on the stratigraphic value of these megaspores.

In one of the earliest papers dealing with dispersed megaspores (Bennie and Kidston 1886), three forms were described and recorded from localities in the ‘Carboniferous Limestone Series’ of Scotland: *Tritelites IV, Lagenicula I*, and *Lagenicula II* of Bennie and Kidston are very similar to *S. pseudoreticulatus*, *L. subpilosa* forma *major* and *Cystosporites* sp (*?*igameus) recorded here. Much later, Dijkstra (1956) recorded the same forms as well as *Tritelites rotatus*, *T. splendidus*, *T. brasseri* (a form very similar
(to *Z. fusinatus*) from the Limestone Coal Group, which overlies the Lower Limestone Group in Scotland. Dijkstra's records were confirmed by Sen (1964) who studied the Limestone Coal Group in Ayrshire, west Scotland. Also, Chaloner (1968, p. 79) recorded megaspores closely similar to those reported by Dijkstra from part of the Ballycastle coalfield, Northern Ireland. The present work extends the stratigraphic record of these species into the Lower Limestone Group of the Carboniferous Limestone Series and records for the first time the presence of *S. indianensis* outside North America. In addition, Dijkstra and Sen reported *Triletes praetextus* Zernndt forma minor Dijkstra 1952, *T. simplex* (Zernndt) Schopf, Wilson, and Bentall 1944, *T. mcroronatus* Nowak and Zernndt 1936, *T. horridus* (Zernndt) Schopf, Wilson, and Bentall 1944, *T. subsimplex* Dijkstra 1957, *T. hirsutoides* Dijkstra 1957 in the Limestone Coal Group. None of these species have been recorded from either the Lower Limestone Group or older deposits in Scotland.

Butterworth and Spinner 1967 described megaspores from coals and shales of the Cementstones and Lewis Burn (Scremerston) Coal Group of Cumberland, north-west England, which are C2 to S4 in age (coral-brachiopod zonation, Garwood 1931) and equivalent to part of the Calciferous Sandstone of Scotland. The megaspores obtained were not so abundant, nor were the assemblages as varied (Butterworth and Spinner 1967, p. 21, table 1) as those obtained here. Of the seven species of megaspores recorded, only one, *L. subpilosa* forma major has also been recorded here.

Summarizing, it appears that the megaspore assemblages from the Dunbar area (upper P1 to basal P2 in age) are different in content from those reported from the underlying Calciferous Sandstone formations (C1–S1 age) below and the Limestone Coal Group above (E1 in age) in the Midland Valley of Scotland and northern England respectively.

Studies of megaspores from Lower Carboniferous deposits in areas outside Great Britain are also few in number. Chaloner 1954 recorded *L. subpilosa* forma major, and *S. indianensis* from the Beaver Band limestone (low Chesterian), Indiana, U.S.A. Two species, *Setiptora echinoides* (Chaloner) Butterworth and Spinner 1967, *S. palaeocristata* (Chaloner) Butterworth and Spinner 1967 were also first described by Chaloner from this formation. Although these species were not found during the present study, the only other record of this genus is of three similar species, *S. pseudoreticulata* Butterworth and Spinner 1967, *Triletes pamosus* Alvin 1966, *T. subpalaecocristatus* Alvin 1965; all reported from the underlying Calciferous Sandstone Series of this region.

Winslow (1959) published on the distribution of megaspores in the Mississippian (Chester series; Winslow, p. 74) deposits of central U.S.A. In this work Winslow commented (p. 77) that although megaspores were often abundant, there was little variety within an assemblage. Most of the species recorded during the present study were also reported by Winslow, a notable exception being the *Zonalesporites*. Winslow reported (p. 80) this type of spore appearing for the first time in the Pennsylvania (Caseyville Group).

A markedly different impression of the variety of Lower Carboniferous megaspores is given by workers in continental Europe. Dijkstra 1956 described twelve new species from samples obtained from Egypt considered by Dijkstra to be older than the Limestone Coal Group of Scotland, and later (1957) with Piéart proposed 29 new taxa from the Moscow Basin.
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From our present knowledge it appears that the megaspore assemblages described here are more comparable with those of approximately equivalent age in North America than in continental Europe and Asia. Further work may produce more evidence for Sullivan’s (1965, 67) suggestion of regional differentiation of Mississippian floras, and may answer the question as to whether the similarities and differences noted above have stratigraphic value.

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REFERENCES


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