

## THREE FRUCTIFICATIONS FROM THE SCOTTISH LOWER CARBONIFEROUS

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**ABSTRACT.** This paper gives descriptions of three fructifications from a Lower Carboniferous horizon in the Kilpatrick Hills, Dunbartonshire. Two new specimens of *Protopitys scotica* Walton provide further information about the structure of the stem and spores of this species. *Staphylotheca kilpatrickensis* gen. et sp. nov., probably the pollen-bearing organ of a pteridosperm, has yielded fertile and abortive spores. *Calathiops trisperma* sp. nov. is a pteridosperm fructification consisting of small cupules, each containing three ovules. The affinities of the three species are discussed briefly.

THE three plants described in this paper were obtained from a Lower Carboniferous exposure near the Loch Humphrey Burn in the Kilpatrick Hills, Dunbartonshire. Several new species have already been described from the bed and a complete list of these is given in Smith (1959). The plant remains were discovered by Professor Walton in a small, lenticular bed of fine sandstone in the series of sedimentary rocks which underlie the Clyde Plateau Lavas. The sandstone of the bed consists largely of volcanic ash which was probably deposited on a land surface and later washed, along with grains of sand and other silty material, into a small pool. The bed has been attributed to the Cementstone Group (Tournaisian) of the Calciferous Sandstone Series, Lower Carboniferous.

With one exception the plant remains used in the investigation were preserved as compressions. The exception, a fragment of a stem of *Protopitys scotica*, was petrified and it was investigated by means of cellulose acetate peel sections. The compressions were examined mainly by means of transfer preparations and cellulose nitrate pulls, some of these being later macerated in Schultze's solution in order to obtain spores. Such treatment did not yield any epidermal cuticles.

Two new specimens of *P. scotica* have been found. One, a stem fragment, was collected by the author; the other, a sporophyll, was collected by Professor Walton. The single specimen of *Staphylotheca kilpatrickensis* and a specimen of *Calathiops trisperma* were also collected by Professor Walton. An additional specimen of *C. trisperma* was collected by the author.

The hand specimens used in the investigation are in the Hunterian Museum Palaeobotanical Collection and the slides prepared from them have been placed in the Figured Slide Collection, both collections being housed in the Botany Department, University of Glasgow.

### THE GENUS *PROTOPITYS* GÖPPERT, 1850

Under the name *Protopytis buchiana*, Göppert described the secondary wood of a stem of Lower Carboniferous age from Silesia. Solms-Laubach (1893) described other specimens of the same species, also from Silesia, and included a description of the medulla and primary xylem. Further descriptions of this species have been given by Seward (1917, p. 210) and Scott (1923, p. 145).

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Walton (1957) described a new species, *P. scotica*, from a fertile specimen which he discovered in the Loch Humphrey Burn bed. According to his description this species is similar to *P. buchiana* in the structure and arrangement of the primary xylem, in the origin of the leaf traces from the primary xylem, and in the structure of the secondary xylem. In both species the medulla is elongated and towards each end there are two primary xylem groups which are slightly mesarch. The leaf traces are derived alternately from each pair of primary xylem strands (Walton 1957, text-fig. 1), and consequently the leaves are arranged distichously. The method of formation of the leaf trace of *P. scotica* has been fully described by Walton (1957, p. 335). In both species the tracheids of the primary xylem are described as having scalariform thickening, those of the secondary xylem as having a single row of transversely elongated bordered pits, with often oblique, elliptical apertures on the radial walls.

A third species, *P. radicans* Kidston ex Scott (nomen nudum), was mentioned by Scott (1923, p. 153) but a description has so far not been validly published.

Because of its possession of both primitive and relatively advanced characters the genus *Protopytis* has been attributed to several widely different plant groups. Göppert (1850), who described only the secondary wood of *P. buchiana*, regarded the plant as a conifer. On the basis of its primary structure Solms-Laubach (1893) concluded that it was related to the pteridosperms. Seward (1917) considered it to be a generalized type with characters of both ferns and the Cordaitales. Scott (1923), on account of its fern-like characters, considered it to be an isolated type of pteridosperm. Most other authors have inclined towards the latter view. Walton (1957), on the basis of the probable pteridophytic method of reproduction of *P. scotica*, placed the genus in a new order of the Pteridophyta, the Protopytiales, though he qualified this by adding that 'it is possible that it may be found to be more closely related to the Pteridospermae, or some other gymnospermous group, than to any phylum of Pteridophyta'. The morphology of the spores and the gymnospermous nature of the bulk of the secondary wood of *P. scotica* suggest that the latter view is most probably the correct one.

A similar case is that of *Archaeopteris*, of which Beck (1960) has found fronds attached to a stem of *Callixylon*; he has thus shown that a plant, previously thought to be a heterosporous fern, had a gymnospermous type of secondary wood. Beck now places *Archaeopteris* in the Pityales, which he groups with the orders Aneurophytales and Protopytiales in a new class, the Progymnospermopsida. He regards this as an ancestral group from which the gymnosperms have evolved. The additional information given below, regarding the spores and secondary wood of *P. scotica*, strongly supports Beck's attribution of the Protopytiales to this new class and also his views regarding the affinities of the class.

#### SYSTEMATIC DESCRIPTIONS AND DISCUSSION

Class PROGYMNOSPERMOPSIDA Beck 1960

Order PROTOPITYALES Walton 1957

Genus PROTOPITYS Göppert 1850

*Type species.* *P. buchiana* Göppert 1850.

*Emended diagnosis.* Woody axis with parenchymatous medulla; two pairs of distinct primary xylem strands with protoxylem elements, at opposite ends of medulla; metaxy-

lem more or less continuous round medulla. Leaves alternate, distichous. Below a node each of the two strands of primary xylem at one side divides and supplies a strand which passes outwards. The two strands combine to form the leaf trace. Metaxylem tracheids with scalariform thickening. At least the first formed tracheids of the secondary xylem with a single series of transversely elongated bordered pits on radial walls.

*Protopitys scotica* Walton 1957

Plate 34, figs. 1-5; plate 35, figs. 1-3; text-fig. 1, 2

*Syntypes.* Specimens Pb 3320 and Pb 2256, in the Hunterian Museum Palaeobotanical Collection, and the slides prepared from them, F.S.C. 921-1060, 1368-77, in the Figured Slide Collection.

*Horizon.* Cementstone Group (Tournaisian) of the Calciferous Sandstone Series, Lower Carboniferous.

*Locality.* Tributary on south side of Loch Humphrey Burn, Kilpatrick Hills, Dunbartonshire.

*Emended diagnosis.* Fertile shoot with sporophylls alternate, distichous. Leaf trace curved, adaxially concave, with protoxylem elements on adaxial face. Protoxylem tracheids with spiral thickening, metaxylem scalariform. First-formed secondary tracheids scalariform to pitted with a single series of transversely elongated, bordered pits on radial walls. Later-formed secondary xylem tracheids with irregularly multi-seriate pitting on radial walls. Pits with oblique, elliptical, crossed apertures. Vascular rays uniseriate, 1-2 (-3) cells high. Sporophyll dichotomously and pinnately branched; sporangia borne terminally on ultimate divisions. Sporangia beaked, *c.* 3 mm. long, dehiscing by one longitudinal slit. No distinct annulus.

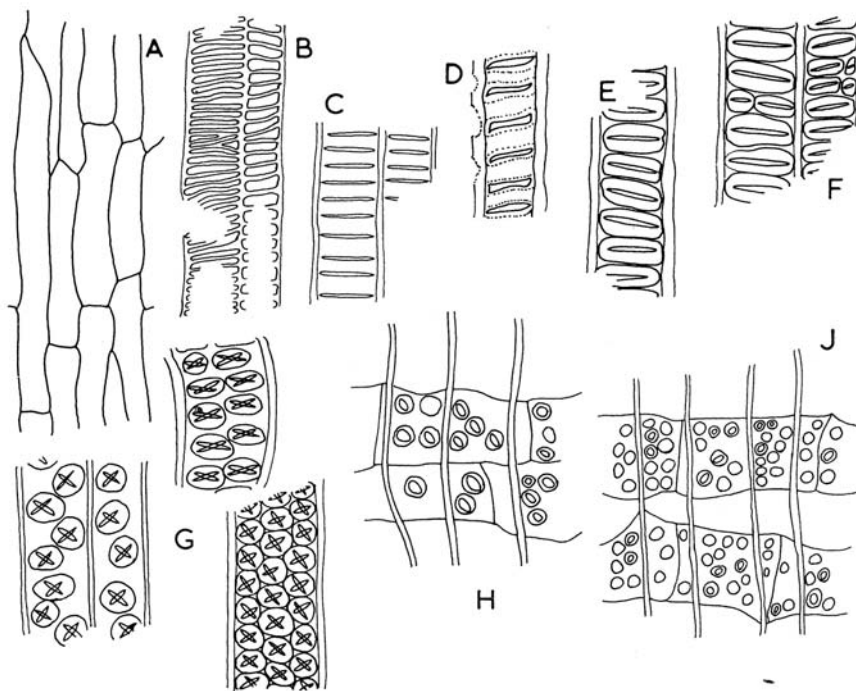
Spores rounded in equatorial outline, approximately 75 to 355  $\mu$  in diameter. Spore coat thin, laevigate, usually folded. Trilete mark prominently raised; suture narrow and simple. Each spore at least initially enclosed in thin, cutinized membrane.

*Description and Discussion*

*The stem.* The fragment of stem is about 10 mm. long. It is elliptical in transverse section, the greatest diameter being 11 mm., the shortest 7 mm. The medulla is elliptical, 2.5 mm. long and 1 mm. broad. The secondary xylem is unevenly developed, being 2.5 mm. broad at one end of the ellipse but 6.0 mm. at the other. Two growth-rings are present in the secondary xylem. The outer is very conspicuous and extends completely round the stem; the inner is much less conspicuous and is incomplete. The primary xylem has the same arrangement as in Walton's type specimen, with two slightly mesarch groups projecting into each end of the elliptical medulla (Plate 34, fig. 1). There are no leaf traces in the new specimen. It differs from the original type specimen in possessing a well-developed ring of secondary xylem and in the absence of leaf traces.

The cells of the medulla have been compressed laterally and are rather distorted (Plate 34, fig. 1). The average measurements of twenty cells from the centre of the medulla are: maximum diameter 79  $\mu$ , minimum diameter 33  $\mu$ , i.e. the cells are now approximately 2.4 times as long as they are broad. As already mentioned, the maximum diameter of the elliptical pith is about 2.5 mm., the minimum 1 mm. Therefore, if the pith cells were originally isodiametric (in transverse section) the pith, and consequently the stem, must originally have been more or less circular in section. The cells are arranged in longitudinal files and are commonly four to twelve times as long as they are broad (text-fig. 1A).

The protoxylem tracheids have spiral thickening; those of the metaxylem have scalariform thickening with occasional reticulation (text-fig. 1B). It is impossible to decide whether there is a continuous single layer of metaxylem elements in contact with the secondary wood, as described in the original type specimen. The innermost, i.e.



TEXT-FIG. 1. *Protopitys scotica*. A, Longitudinal section of cells of the medulla; B, metaxylem tracheids with scalariform thickening; C, secondary xylem tracheids with scalariform thickening; D, secondary xylem tracheid with scalariform pitting; E, secondary xylem tracheid with uniseriate pitting; F, secondary xylem tracheids with partly biseriate pitting; G, secondary xylem tracheids with pits having crossed apertures; H, radial section of the first formed secondary xylem showing the ray cells and the cross-field pitting; J, radial section of the later formed secondary xylem showing the more numerous pits of the cross-field areas. A-F and H drawn from slide F.S.C. 1375; G and J drawn from slide F.S.C. 1376; all magnifications  $\times 400$ .

the first-formed, tracheids of the secondary xylem also have scalariform thickening with some reticulation (text-fig. 1C). The secondary scalariform tracheids differ from the primary in that they are distinctly bordered. There is a rapid transition to scalariform pitting (text-fig. 1D) and then to tracheids with a single series of transversely elongated bordered pits with transverse or slightly oblique elliptical apertures on the radial walls (text-fig. 1E). The latter is the pitting described by Walton in the original specimen. Partially biseriate pitting is also present, probably as a development from reticulation

(text-fig. 1F). The above types of tracheid are confined to the 1 to 2 mm. of secondary xylem nearest to the medulla. Most of the secondary xylem tracheids have multiseriate pitting on the radial walls. Usually there are up to three irregular vertical rows of pits (Plate 34, 1, figs. 2, and 3; text-fig. 1G). The pits are slightly oval to circular and have elliptical apertures. The two apertures of the pit are crossed. The pits are not usually crowded. Pitting of this type is probably present in the outermost tracheids of the secondary xylem of Walton's specimen, though owing to the state of preservation of the outer regions of the stem and the plane of the sections, this is not certain. Pits of this type do occur occasionally, however, on the tangential walls of the secondary xylem tracheids in his specimen (Plate 34, fig. 4).

The rays are small and numerous. Most are one cell high but a few two or three cells high are present. All the rays are uniseriate. The ray cells may be up to twice as long as they are high (text-fig. 1H, J). They are thin-walled. In the cross-field areas there are normally from one to twelve circular to oval pits. At about 2 mm. from the medulla, in the broadest zone of secondary wood, there are most commonly one to four large round pits per cross-field area (text-fig. 1H). The pits appear to be of the cupressoid type, with a narrow border and an oblique, elliptical aperture. Towards the periphery of the secondary wood the pits are more numerous (text-fig. 1J), being most commonly six to twelve per cross-field area, though up to twenty-one have been counted. The pits here are smaller. Some of them are apparently bordered but the aperture is often almost circular. Many of the pits in this region appear to be simple, without a border, though this may be due to poor preservation.

The tissues outside the secondary xylem have not been preserved.

*The sporophyll and sporangia.* The original specimen of *Protopitys scotica* was apparently immature since the sporophylls had not unfolded and the sporangia had not dehisced. From the evidence available Walton (1957, p. 355) concluded that the sporophylls were arranged alternately on opposite sides of the stem and that the branching of the sporophyll was mainly dichotomous, but the smaller rachides which bore the sporangia were branched in a pinnate manner. Apparently the sporophylls were entirely fertile.

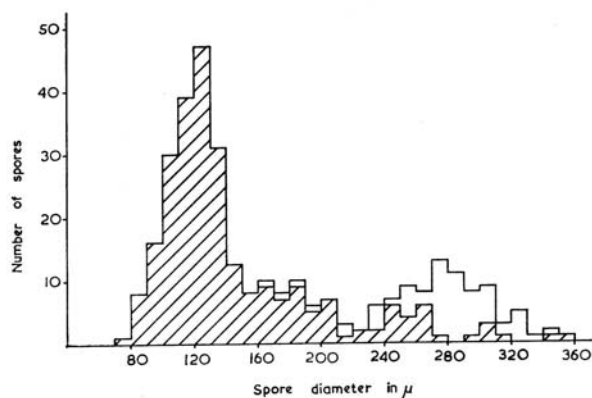
The new specimen collected by Professor Walton is a compression of a plant fragment fitting the above description of a sporophyll of *P. scotica* (Plate 34, fig. 5). It consists of a dichotomizing rachis bearing at the tips of its four main branches a number of irregular branches arranged more or less pinnately. This pinnate arrangement is clearly derived from a dichotomous system.

Several nitrocellulose pulls were prepared from this specimen. Two of these were mounted on slides; one was macerated in Schulze's solution and the residue mounted. From an examination of the mounted pulls it was obvious that the ultimate divisions of the rachis bore sporangia, but unfortunately dehiscence had occurred before fossilization and very few spores were present in them. The sporangium wall was reasonably well preserved and does not appear to differ from that of *P. scotica* described and figured by Walton (1957, pl. iii, fig. 19). Two stomata were also observed on a sporangium wall and these too agreed with that of *P. scotica* figured by Walton (1957, pl. iii, fig. 18).

The residue of the macerated pull contained fifty-one spores of which forty-six were of one type. The latter group, although morphologically similar, showed an enormous size range of about 150  $\mu$ , from about 80 to 230  $\mu$ . Many of them were enclosed,

individually, in a discrete, cutinized membrane. The remainder had apparently shed their membranes since detached membranes were present in the residue.

In order to carry out a complete comparison and to establish definitely that the new specimen was attributable to *P. scotica*, spores were isolated from the original type specimen. A small fragment was detached, treated first with dilute hydrochloric acid and then with concentrated hydrofluoric acid. Half the residue was mounted directly in glycerine jelly; the other half was first macerated in Schulze's solution and then mounted. There was no appreciable difference between the two batches of spores so obtained, and, more important, they were identical with the forty-six spores isolated from the



TEXT-FIG. 2. Histogram of spore size in *Protopytis scotica*. The shaded part represents the complete spores measured. The unshaded part represents the damaged spores whose size was estimated by measuring the trilete mark.

new specimen. It was concluded, therefore, that the new specimen is specifically identical with *P. scotica* and that it confirms Walton's deductions regarding the morphology of the sporophyll.

*The spores.* The two interesting features of *P. scotica* arising from this further investigation, using maceration techniques, are the morphology and size range of its spores. Walton (1957, p. 337) stated that three sizes of spores were present, in separate sporangia. Most sporangia had small spores (diameter 82 μ); some had large spores (147 μ); while some had spores of an intermediate size (98 μ). An examination of the type slides by the author has confirmed this observation, but it is obvious that the spore samples obtained by maceration strongly contradict it. The histogram in text-fig. 2 shows the size range of the spores isolated from the original type specimen by maceration. It shows an almost continuous variation in size. Two hundred and sixty-one complete spores were measured; they showed a size range from 75 to 355 μ, with a mean of 125 μ. About 70 per cent. of the spores were in the range 90 to 150 μ.

An attempt was made to isolate the spores from a single sporangium but it was unsuccessful. As far as can be determined from peel sections the range in size of the spores within any one sporangium is very small. This is what would be expected. In one



sporangium twenty spores measured had a mean size of  $102\ \mu$ , the range being from  $95$  to  $107\ \mu$ . In another sporangium twenty spores had a mean size of  $147\ \mu$ , the range being  $137$  to  $160\ \mu$ .

It was thought that the count obtained for the larger spores, i.e. above  $200\ \mu$ , was inaccurate. Many of the spores measured were damaged and the number of fragments present suggested a rather higher number of large spores than was shown by the counts. Since repeated attempts to isolate more undamaged large spores were unsuccessful an estimate of their numbers was made by measuring the rays of the trilete mark present on spore fragments. Only those showing at least two of the three rays were measured. The average length of the rays multiplied by  $4.4$  gives the approximate diameter of the spore, since the ratio of the length of the ray to the spore diameter is constant throughout the size range. The emended histogram (text-fig. 2) gives a second peak at about  $280\ \mu$ .

Often the spore is surrounded by a discrete, cutinized membrane (Plate 35, fig. 2). It could be a sort of perispore or it could be a true air-bladder or saccus such as is found in species of *Glomospora* B. & W. or *Remysporites* B. & W. In many cases the spore is free inside this membrane, though occasionally it appears to be attached to the spore along the rays of the trilete mark. Detached membranes are quite common in the maceration and many of them show the trilete mark quite clearly (Plate 35, fig. 3). Even so it is likely that they functioned as air bladders in spore dispersal since spores with the membrane still attached have been found among the dispersed spores in the bed. The membrane has many small folds so that it is usually irregular in outline. The surface is smooth to microreticulate.

The spore itself (Plate 35, fig. 1) is more or less circular in equatorial outline. The margin is smooth. The spore coat is fairly thin and usually folded. It is usually perfectly smooth though occasionally it appears to be slightly roughened. The trilete mark is prominent. The rays, which are straight, extend for about half the length of the radius. The ratio of the length of the trilete mark to the diameter of the spore is fairly constant and is independent of the size of the spore. The suture is narrow and simple. The lips are prominently raised.

*Discussion.* The new stem fragment of *Protopytis scotica* differs significantly from that of the original type specimen and from those of *P. buchiana* and *P. radicans* in the structure of its secondary xylem. The first-formed secondary xylem of *P. scotica* (and that of Walton's specimen is almost entirely in this category) consists of radially seriate tracheids with uniseriate, transversely elongated, bordered pits and is in this respect similar to the secondary xylem of the other two species. The multiseriate pitting of the later wood of *P. scotica* is entirely different from anything found in the other two species. A further difference is in the structure of the vascular rays. Those of *P. buchiana* may be up to fifteen cells high and occasionally they are biseriate. There are from one to six pits per cross-field area. These differences are not considered sufficient to remove *P. scotica* from the genus *Protopytis*, since the structure of the first-formed secondary xylem and the arrangement and structure of the primary xylem are probably more important characters. The wood of *P. scotica* is most probably representative of a more advanced type of organization within the group. The later-formed secondary xylem is similar to that of some stems at present attributed to the Cordaitales, e.g. *Endoxylon zonatum* Scott (Lacey 1953).

The spores of *P. scotica*, as obtained by maceration, are of considerable interest. The two most outstanding features are the range in size and the possession of an enclosing cutinized membrane. The nature of this membrane is uncertain but it is similar to the perispore of some modern ferns. As defined by Bower (1923, p. 259) the perispore is a tapetal deposit on the outside of the spore wall, appearing like a loose sac. It is laid down after the division of the spore-mother cell. It is possible that in the present case the membrane is homologous with the air sac or saccus of some monosaccate spores and pollen, which is derived from the exine. In the absence of any information regarding its origin the non-committal term 'perine', as used by Erdtman (1952), should perhaps be used.

Walton (1957, p. 338) has suggested that *P. scotica* probably represents a stage in the evolution of heterospory. Though, as the histogram in text-fig. 2 shows, the spores do not fall into three distinct size categories, as he thought, the fact that they tend to fall into two broad, indistinct size groups provides stronger support for his views. There is no morphological difference between the two groups and there is no way of telling whether they did, in fact, function as microspores and megaspores.

Had the spores been encountered only as *spora dispersae* those which had shed their 'perines' would without doubt have been placed in the genus *Calamospora* S., W. & B., species of which, as the name implies, are thought to be the spores of calamites. Many species are distinguished solely by their size and the spores of *P. scotica* would probably be placed in one or other of the following species, according to their size:

<i>C. liquida</i> Kosanke	76-94 $\mu$
<i>C. ferrugosa</i> (S., W. & B.) Loose	130-160 $\mu$
<i>C. laevigata</i> (S., W. & B.) Ibrahim	250-500 $\mu$

Had the 'perine' still been present the classification of the spores would have been doubtful. They would probably have been compared to a monosaccate type such as *Glomospora* B. & W. or *Remysporites* B. & W., a genus whose only known species, *R. magnificus* (Horst) B. & W., is the pollen of a pteridosperm, *Paracalathiops stachei* Remy (Butterworth and Williams 1958).

Class PTERIDOSPERMEAE Oliver & Scott 1904

Genus STAPHYLOTHECA gen. nov.

*Type species.* *S. kilpatrickensis* sp. nov.

*Diagnosis.* Dichotomizing rachides with undulate margins; having on undersurface bunches of linear organs among which or on which sporangia are borne.

EXPLANATION OF PLATE 34

Figs. 1-5. *P. scotica*. 1, Transverse section of part of stem, showing medulla, two primary xylem groups and secondary xylem,  $\times 50$  (F.S.C. 1370). 2, Radial longitudinal section of secondary xylem, showing pitting and rays,  $\times 150$  (F.S.C. 1376). 3, Radial wall of secondary tracheid, showing pits with crossed apertures,  $\times 500$  (F.S.C. 1376). 4, Tangential wall of secondary tracheid showing pitting,  $\times 500$  (F.S.C. 953). 5, Compression of a sporophyll,  $\times 1$  (Pb 2696).

Fig. 6. *S. kilpatrickensis*, compression of fructification,  $\times 2$  (Pb 335).

Fig. 7. *C. trisperma*, compression of group of ovulate cupules,  $\times 2$  (Pb 3326).



*Staphylotheca kilpatrickensis* sp. nov.

Plate 34, fig. 6; plate 35, figs. 4, 5; text-fig. 3

*Holotype.* Specimen Pb335 in the Hunterian Museum Palaeobotanical Collection, and the slides prepared from it, F.S.C. 1387-9, in the Figured Slide Collection.

*Horizon and locality.* As for *Protopitys scotica*.

*Diagnosis.* Rachides bearing linear organs in bunches of ten to twenty; up to 10 mm. long, 0.5 mm. broad. Sporangia borne among these organs ovoid, about 1 mm. long, 0.7 mm. in diameter.

Spores round, 78 to 100  $\mu$  in diameter, mean 87  $\mu$ . Spore coat up to 5  $\mu$  thick distally, 2  $\mu$  thick proximally. Ornamentation round to linear depressions, 4 to 10  $\mu$  long, up to 3  $\mu$  deep. Rays of trilete mark straight, extending for over half radius; suture with simple margins; lips not raised.

*Description.* The specimen, as collected, consisted of a rather irregular rachis with a single dichotomy. A second rachis of similar appearance arose from under one of the branches but was separated from it by about 1 mm. of rock. The rachis has undulate margins and varies from about 3 to 5 mm. in width (Plate 34, fig. 6). Whether it was flattened or rounded in nature is impossible to decide but as the film of coal now representing the rachis is almost 1 mm. thick in parts it must have been a fairly massive structure.

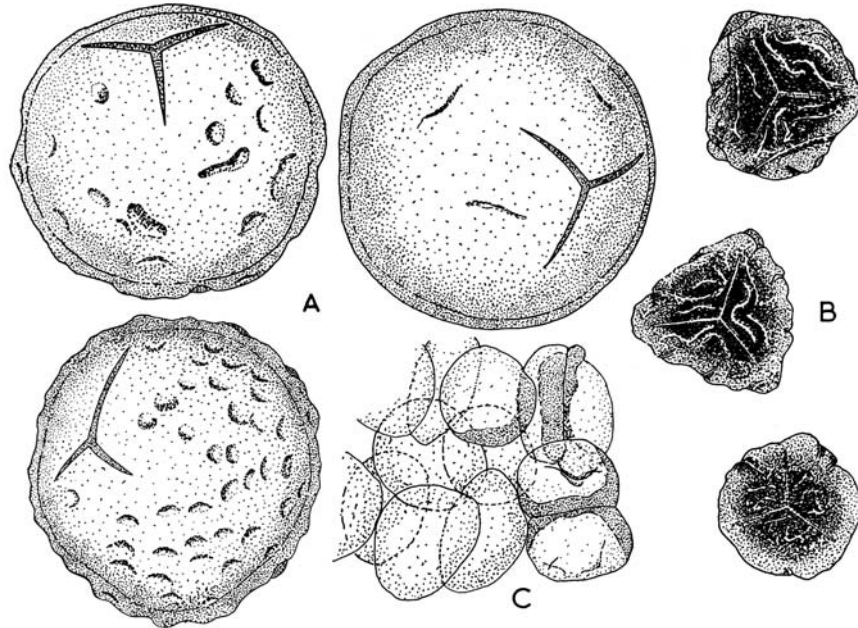
Two saw cuts were made across part of the fructification (Plate 34, fig. 6) and the intervening rock was chipped away. Transfers were made from the fragments removed; these were later macerated to yield large numbers of spores. During the chipping it was found that the second rachis was actually a branch of the right-hand fork of the main rachis. Transfers and pulls of the rachides have yielded very little detail of its structure. The only tissue preserved was the xylem where a few fragments of scalariform, reticulate and irregularly pitted tracheids were found. They were similar to those of *Geminitheca scotica* (Smith 1959). The pits are transversely elongated and have transverse elliptical apertures. They are not crowded.

Attached to short slender pedicels on the underside of the rachis are several bunches of linear organs which were at first thought to be sporangia. There are at least ten in each bunch, possibly twice that number. It is impossible to decide whether they are entirely free from one another or whether they are fused at the base. Most of them are 7 to 10 mm. long and about 0.5 mm. broad. Pulls and transfers revealed very little of their structure; they appear to have consisted largely of thin-walled, elongated cells. It is possible that they were sporophylls since the sporangia are borne among them. They are, however, more numerous than the sporangia. Alternatively, they may have formed a rudimentary cupule.

The sporangia are ovoid, up to 1 mm. long and 0.7 mm. in diameter. There is no indication whether or how they were attached to the organs among which they were borne. No structural details of the sporangial wall have been observed. Several spore masses have been isolated from individual sporangia and in addition several thousand isolated spores have been obtained by macerating the transfers. In addition to obviously immature spores there are two types of apparently fully developed spores which occur in the same sporangia. For convenience they are referred to here as types A and B.

Spores of type A (Plate 35, fig. 4) are by far the commoner. They are more or less

circular in equatorial outline. They vary from 78 to 100  $\mu$  in diameter, mean 87  $\mu$ . At the distal end the spore coat is 4 to 5  $\mu$  thick but at the proximal end it is only about 2  $\mu$ . A number of depressions or large punctations is present over most of the spore surface, though they tend to be absent from the contact faces. They are usually 4 to 10  $\mu$  in diameter and up to 3  $\mu$  deep; most are circular to subcircular in outline but in some



TEXT-FIG. 3. *Staphylothecha kilpatrickensis*. A, Three type A spores showing the range in ornamentation; B, three type B spores showing the range in shape and ornamentation; C, part of a group of immature spores showing both types. A and B drawn from slide F.S.C. 1388; C drawn from slide F.S.C. 1389; all magnifications  $\times 500$ .

spores they are elongated or irregular. Text-fig. 3A shows several spores isolated from the same sporangium. They illustrate the range of variation which occurs. The rays of the trilete mark extend for slightly over half the radius of the spore. The lips are not raised; the suture has simple margins.

Type B spores (Plate 35, fig. 5) are much smaller than those of type A. They are rounded-triangular to sub-circular in equatorial outline. The margin is irregular. They vary from 42 to 57  $\mu$ , mean 45  $\mu$ . The spore coat is very thick. The ornamentation is rather irregular, consisting of a number of narrow, elongated depressions separated by more or less convolute ridges. The trilete mark is very narrow and in some spores is barely distinguishable. The rays extend for over three-quarters of the radius. Text-fig. 3B shows the variation in this type within a single sporangium. All the spores in text-fig. 3A and B came from one sporangium.

Very few well-preserved immature spores have been found. Since they are only partially cutinized they are damaged or destroyed by maceration. They were obtained by dissolving a small fragment of rock, containing sporangia, in dilute hydrochloric acid followed by concentrated hydrofluoric acid. Most are 25 to 35  $\mu$  in diameter. Even at this stage it is possible to distinguish two types, thin-walled and thick-walled, which would presumably develop into types A and B respectively (text-fig. 3C). The walls of the young spores of type A are featureless and the spore is often folded; the walls of the young type B spores, on the other hand, show the beginnings of the ornamentation by the irregular development of thickening, particularly on the contact faces. They are usually pale yellow-brown in colour while the immature type A spores are colourless or pale yellow.

*Discussion.* There can be little doubt, from their heavily cutinized walls, that type B spores are abortive. That both types of spore occur in the same sporangia and that both are recognizable at a very early stage in their development supports this conclusion.

As *spora dispersa* type B spores would probably have been placed in the genus *Convolutispora* H., S. & M. Type A spores do not appear to resemble any previously described spore type. Certainly the two types would have been widely separated in any classification. Both would probably have been regarded as fern spores. It is possible that type A would have been split into two or more species.

In its dichotomizing rachis bearing bunches of linear appendages the fructification of *S. kilpatrickensis* bears a superficial resemblance to *Alcicornopteris hallei* Walton (Walton 1949). They differ in the shape of the rachis and in the nature of the bunches of appendages, which in *A. hallei* are sporangia. The spores of the two species differ markedly. The bunches of appendages of *S. kilpatrickensis* are also similar to species of *Calathiops* Göppert and *Scheutzia* Geinitz. The distinctive rachis and the presence of sporangia exclude it from the former genus, which was emended by Benson (1935) to include only ovulate cupules borne on simple rachides. The genus *Scheutzia* is ill defined and may possibly include both ovulate cupules and microsporangia.

As regards the affinities of *Staphylotheca* nothing definite can be decided owing to an incomplete knowledge of the reproductive organs and of the vegetative parts. Fructifications of this type are usually considered to be the pollen-bearing organs of pteridosperms but in many cases there is no direct evidence in support of this view and some of them may have belonged to plants superficially similar to the pteridosperms but with a pteridophytic method of reproduction. In *S. kilpatrickensis* the only positive evidence suggestive of a pteridospermous affinity is the nature of the pitting of the tracheids in the rachis.

Genus CALATHIOPS Göppert 1865 emend. Benson 1935

*Calathiops trisperma* sp. nov.

Plate 34, fig. 7; plate 35, fig. 6

*Holotype.* Pb 3326 in the Hunterian Museum Palaeobotanical Collection, and the slides prepared from it, F.S.C. 1374-6 in the Figured Slide Collection.

*Horizon and locality.* As for *Protopitys scotica*.

*Diagnosis.* Ovulate cupules borne singly at the tips of naked, dichotomizing stalks.

Dichotomy irregular. Cupules up to 5 mm. long, consisting of five to nine linear lobes. Each cupule containing usually three ovules. Ovules elongated, about 2.5 mm. long.

*Description.* The fructification consists of small ovulate cupules which are borne on naked dichotomizing stalks. The stalk forks fairly regularly and the cupules are borne singly at the tips (Plate 34, fig. 7). The number of cupule lobes is not constant but varies in the two specimens found from five to nine. The lobes are represented merely by a structureless film of coal. They are 4 to 5 mm. long and about 0.5 mm. broad at the base. Transfers were prepared from the two counterparts of one cupule and both were macerated on a slide, under a coverslip. No structure was revealed in the cupular lobes but two halves of megaspore membrane were isolated from one counterpart, and one from the other. The maceration was stopped when traces of cell outline appeared on the surface of the megaspore membranes.

The half membranes vary from 1.2 to 1.5 mm. in length and are 0.7 mm. broad near the break. Since all three membranes were orientated in the same direction it is assumed that they belonged to three different ovules. The complete membrane must have been about 2.5 mm. long. The best-preserved half (Plate 35, fig. 6) has three prominent longitudinal folds. These may indicate that the ovule was three-ridged or they may be an effect of compression. On the surface of the membrane there are traces of several layers of small elongated cells which must be the remains of the nucellus and integument. A few narrow, scalariform tracheids are also present, presumably in the integument. The membrane is very thick at its apex, 25  $\mu$  in one case. At the thinnest part, near the break, it is only 5 to 6  $\mu$  thick. Although it has not been sectioned it seems to be similar in fine structure to that of *Geminitheca scotica* (Smith 1959), in having a homogeneous inner and an outer granular layer.

There is no indication as to whether the integument was fused to or free from the nucellus. Maceration of other cupules failed to yield more megaspore membranes or additional structural details.

*Discussion.* The genus *Calathiops* was instituted by Göppert (1865) for fructifications of Lower Carboniferous age from Silesia. The fructifications included in the genus were described as consisting of small bunches of scale-like appendages borne on the ends of naked, dichotomizing stalks. Göppert did not demonstrate whether they were ovulate cupules or microsporangia. Benson (1935) emended the genus to include only ovulate fructifications and her view is followed here.

*C. trisperma* is certainly the ovulate organ of a pteridosperm but its affinities are not clear. It probably represents some hitherto unknown group within the pteridosperms and provides some evidence in favour of the theory that the seed habit has evolved separately in a number of perhaps unrelated plants. It does not resemble any of the

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EXPLANATION OF PLATE 35

Figs. 1-3. *P. scotica*. 1, Spore without 'perine',  $\times 500$  (F.S.C. 1371). 2, Complete spore,  $\times 500$  (F.S.C. 1372). 3, Detached 'perine' showing trilete mark,  $\times 500$  (F.S.C. 1371).

Figs. 4, 5. *S. kilpatrickensis*. 4, Fertile spore,  $\times 500$  (F.S.C. 1377). 5, Abortive spore,  $\times 500$  (F.S.C. 1377).

Fig. 6. *C. trisperma*. Upper half of megaspore membrane,  $\times 40$  (F.S.C. 1374).

structurally preserved species described so far. Of the species described from compressions it resembles most closely *Calathiops bernhardtii* Benson (Benson 1935). This species differs from *C. trisperma* in that it is larger and contains many more ovules which are approximately the same length as, but are broader than, those of *C. trisperma*. In both species the cupular lobes are more or less linear.

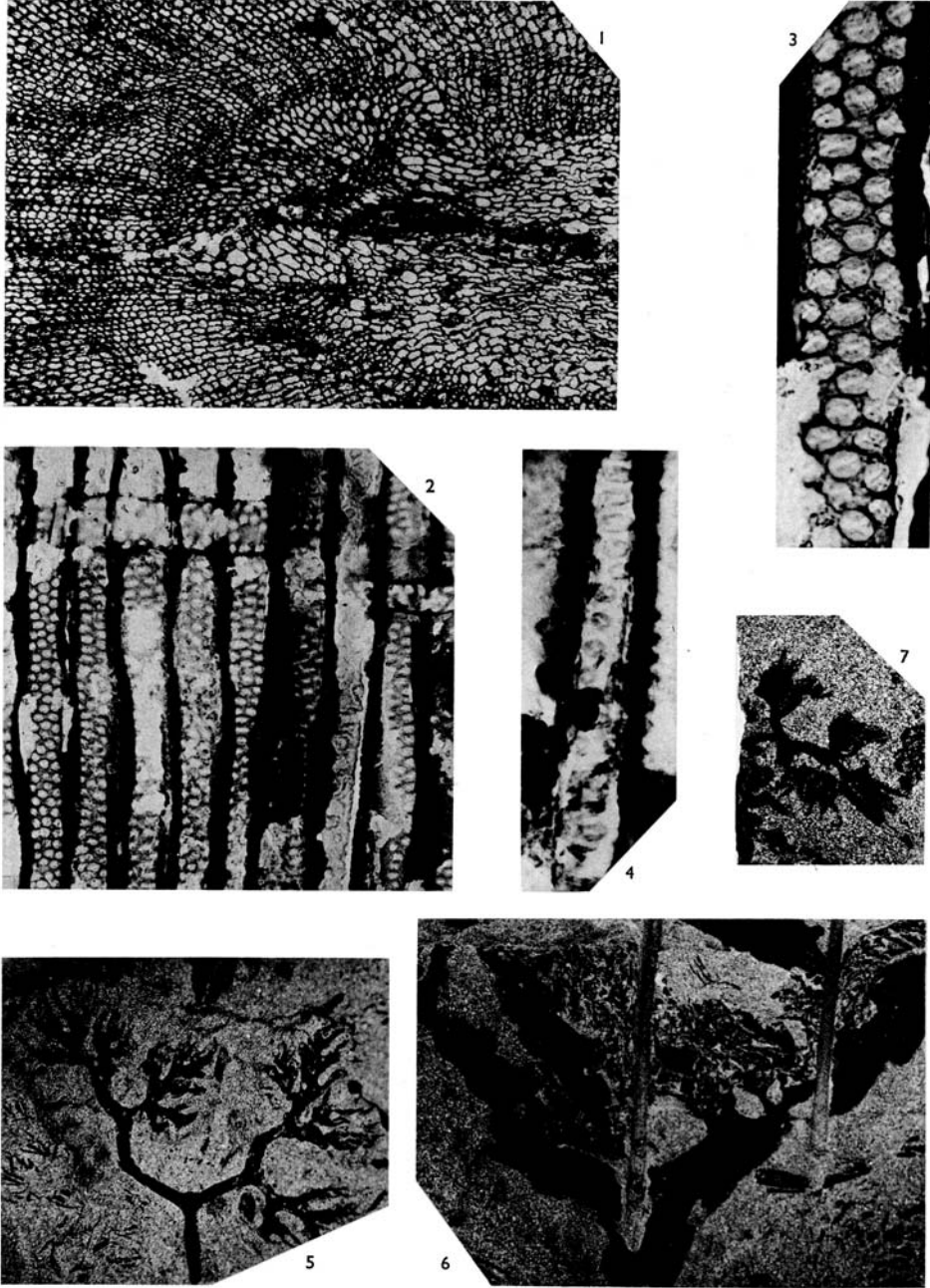
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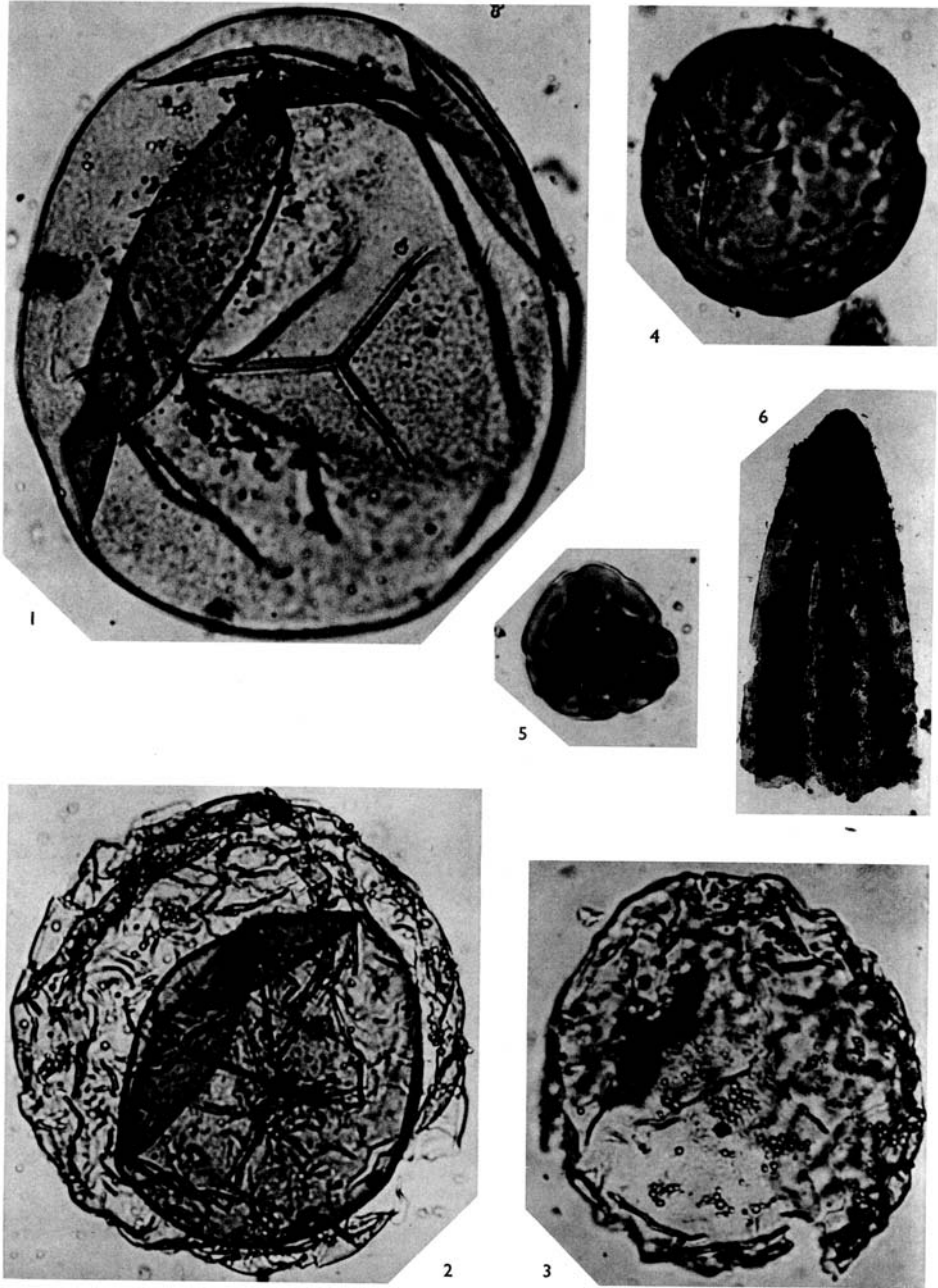
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SMITH, Carboniferous fructifications





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