FERTILE RHYNIOPHYTINA FROM THE LOWER DEVONIAN OF BRITAIN

by DIANNE EDWARDS

ABSTRACT. A new genus *Steganotheca* is erected to include plants from the Downtonian of South Wales with naked dichotomously branching axes and terminal sporangia, which are longer than wide, sharply truncated apically, and with tapering bases. Comparison is made with other members of the Rhyniophytina (Banks 1968). Sterile Silurian axes probably belonging to the same genus are briefly mentioned. The first occurrence of *Cooksonia* in the Lower Old Red Sandstone of Scotland, consisting of naked dichotomously branching axes terminating in oval to circular sporangia, is described from the Cairnconnan Group of the Lower Devonian in Angus; it is placed in a new species.

THE fossils described in the first part of this paper were collected from the Capel Horeb Quarry, Breconshire. Although the majority, including all the fertile ones, were found at the eastern end of the quarry in the lowest of the Long Quarry Beds in the grey Downtonian of the Lower Old Red Sandstone (Potter and Price 1965), some were collected from the older Ludlovian rocks (Lower Whitcliffian). The plants are preserved as heavily carbonized compressions in which little structure can be detected. They were treated in the way described by Edwards (1968), but bulk maceration of the rock was relatively unsuccessful. All the fossils and preparations have been deposited at the National Museum of Wales, Cardiff.

Although *Cooksonia* is commonly found in the Downtonian and Breconian rocks of South Wales and the Welsh Borderland, it has hitherto not been recorded from Scotland. The fertile specimens described in the second part of this paper were all collected at Aberlemno quarry near Turin Hill, Angus. Two of the specimens are in my possession while the third, which is designated the holotype is housed in the Royal Scottish Museum. Also found in this Quarry are *Zosterophyllum myretonianum*, *Prototaxites*, and *Parka*. The plants, associated with occasional fish and eurypterid fragments, are preserved as pinkish-red impressions in a fine-grained, grey sandstone. Very occasionally casts of axes are present or a film of granular carbon covers the specimen. In neither case does structure remain, and the account presented here is merely a description of the fossils immersed in 70% alcohol and examined using a hand lens or binocular microscope. Some of the plants have been developed by removing the covering rock layer with tungsten steel needles.

Most of the rock was collected from the tips on the floor of the quarry, but some fossils were also visible on the quarry face where a hard jointed sandstone is interbedded with the shale and softer fissile sandstone layers in which the plants are found. The rocks form part of the Cairnconnan Group of the Dittonian of the Lower Old Red Sandstone of Angus, probably equivalent to the Gedinnian of Europe (Waterston 1965).

SYSTEMATIC DESCRIPTION

Family RHYNIACEAE Kidston and Lang 1919

Genus STEGANOTHECA gen. nov.

Type species. Steganotheca striata sp. nov.

[Palaeontology, Vol. 13, Part 3, 1970, pp. 451–61, pl. 84–87.]

Diagnosis. Naked dichotomously branching axes with erect terminal sporangia. Sporangia longer than wide with tapering bases and truncated apices; apices formed by terminal lens-shaped structure of coaly material; sporangia with almost parallel sides.

Steganotheca striata sp. nov.

Plate 84, figs. 1–6, Plate 85, figs. 1–8

Diagnosis. Axes with at least four dichotomies, 0·4–0·8 mm. wide, with central line. Surface longitudinally striated. Sporangia 1·8–2·7 mm. long and 1·0–1·5 mm. wide; tapering at base; apex truncated; apex formed by terminal lens-shaped structure of coaly material, up to 0·25 mm. thick; surface of sporangium obliquely striated; parallel sides.

Locality. Capel Horeb Quarry, abandoned quarry on the A40 between Trecastle and Llandovery Nat. Grid. Ref. SN 844323.

Horizon. Long Quarry Beds, Grey Downtonian, Lower Old Red Sandstone of South Wales.

Holotype. Specimen 69·64 G32a and counterpart; Department of Geology, National Museum of Wales, Cardiff; Plate 84, figs. 1, 2, 5, 6, Plate 85, fig. 1.

Description of specimens. Most information was obtained from three fertile specimens found in a fine-grained grey sandstone, interbedded with micaceous layers.

(*a*) Specimen 69.64.30a and b (Pl. 84, figs. 3, 4). This fossil consists of a slightly flexuous branching system of over-all length 5·0 cm. The width of the axes remains almost constant through three successive dichotomies ranging between 0·7 mm. at the base and 0·5 mm. distally, where each axis widens into the base of a sporangium. The axis surface is striated, representing perhaps the outlines of epidermal or cortical cells. A faint central line is sometimes seen when the rock is held at a suitable angle to the incident light. The reconstruction given in text-fig. 1 is derived from part and counterpart. The sporangia are cup-shaped, 2·5 mm. high and 1·5 mm. wide on average. The coaly residue in the truncated sporangium apex is much thicker than that in the rest of the sporangium wall, forming a terminal lens-shaped structure (Pl. 85, fig. 4). The coaly residue from the axes, sporangia, and distal thickened region was macerated in Schulze's solution for several days, but no structure was discernible.

(*b*) Specimen 69.64.G31a and b (Pl. 85, figs. 2, 3). This specimen consists of an axis 0·4–0·5 mm. wide and 18 mm. long which dichotomises once. One of the branches ends

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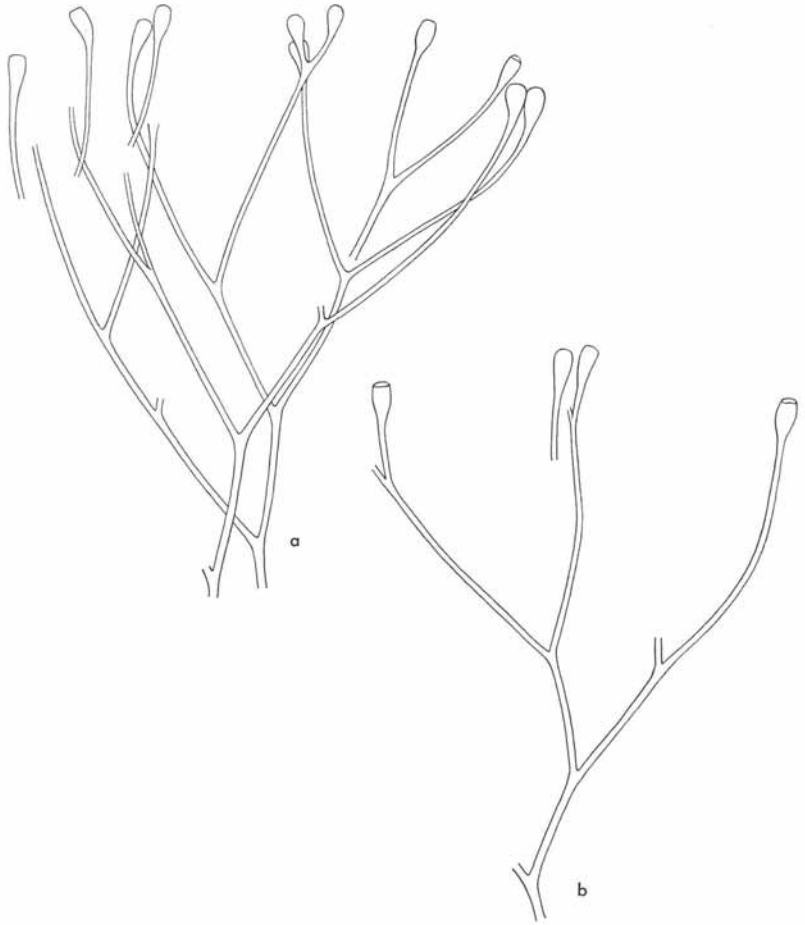
EXPLANATION OF PLATE 84

Figs. 1–6. *Steganotheca striata* sp. nov. 1, 2, Dichotomously branching fertile axes, 69.64.G32a and b; ×1·2. 3, 4, 69.64.G30a and b; ×1·2. 5, 6, Sporangia from 69.64.G32a; ×7·7.

EXPLANATION OF PLATE 85

Figs. 1–8. *Steganotheca striata* sp. nov. 1, Sporangia from 69.64.G32a; ×7·7. 2, 3, Sporangium and counterpart, 69.64.G31a and b; ×8; note the conspicuous striations in fig. 2 and the thickened apical region in fig. 3. 4, Cup-shaped sporangium with apical thickening, 69.64.G30a; ×8. 5, 6, Sterile Downtonian axes from Capel Horeb, 69.64.G33, ×1·2; 69.64.G34, ×7·5. 7, Cells from Downtonian axis recovered after maceration, 69.64.G35; ×430. 8, Film pull of Downtonian axis showing cell walls, 69.64.G36; ×126.



TEXT-FIG. 1. Reconstructions of *Steganotheca striata* sp. nov. *a*, Drawn from 69.64.G32a and b; ×1·8 *b*, Drawn from 69.64.G30a and b; ×1·8.

in a sporangium 1·8 mm. high and 1·0 mm. wide. The axis surface is longitudinally striated. The sporangial features described above are again clearly seen here (Pl. 85, fig. 3). In addition, the sporangium surface is striated, with the lines running diagonally across the sporangium. This is most clearly seen in the counterpart (Pl. 85, fig. 2). The heavily carbonized distal region is not present on the latter.

(*c*) Specimen 69.64.G32a and b (Pl. 84, figs. 1, 2). A reconstruction of the plant is given in text-fig. 1. It consists of a 'bushy' three-dimensional branching system in which at least ten of the axes end in sporangia. Branching is dichotomous with a wide angle

(*c.* 60°) at each branching point. The axes vary between 0·5 and 0·8 mm. in diameter. The sporangia are, on average, 2·4 mm. high (ranging between 2·0 and 2·7 mm.) and 1·2 mm. wide (1·0–1·5 mm.). The majority have truncated tips (Pl. 84, figs. 5, 6) with heavily carbonized areas similar to those already described. A few, however, are rounded at the apices (Pl. 85, fig. 1). These are also unusual in that they terminate very short lengths of axis above the ultimate dichotomy. It is therefore suggested that these oval sporangia are immature ones, though it should be noted that they are no smaller than the others.

Summary of description. Steganotheca striata is a small bushy plant, at least 5·0 cm. high, consisting of naked, dichotomously branching axes with terminal sporangia. Its basal parts are unknown. Branching is strictly dichotomous, with the angle at the branching point ranging between 45° and 75°. The length of axis above a branching point is approximately the same in both arms, and the branches terminating in sporangia are of equal length. The distance between the sporangium and last branching point is usually long compared with the distances between successive dichotomies. The sporangia themselves are almost twice as long as wide. Their apices are truncated and terminate with a heavily carbonized lens-shaped region. The base of each sporangium is not clearly defined. No spores have been isolated and very little is known of the structure of the sporangium wall.

Associated with the fertile specimens are numerous short lengths of axis, the majority being Y-shaped, but some unbranched and some with two successive dichotomies. These axes are approximately the same width as the fertile ones (average 0·55 mm. in the former, 0·6 mm. in the latter) and the angles at branching points are similar. It is therefore probable that these fragments belong to the same genus as the fertile ones (Pl. 85, figs. 5, 6).

Nearly all the axes have faint surface striations which probably represent the outlines of elongate cells of the epidermis or cortex. A thin central strand is seen on some of the sterile axes, but this is more obvious on film pulls of axes, because the coaly residue of the central area forms a continuous band, while that of the remainder of the axis is cracked and often incomplete. Pieces of rock-bearing axes have been macerated and the carbon recovered cleared with Schulze's solution. Fragments of carbon have also been picked off the rock and film pulls and cleared in the same way. No tracheids have been seen. Very occasionally film pulls bear the remains of cell walls, those running parallel to the long axis of the branch being most often preserved. They are 9–20 μ apart, the distance tending to vary proportionally with the width of the axis. Very narrow axes are 10–12 cells wide. Occasionally transverse end walls are seen. These are perpendicular or oblique to the longitudinally running walls (Pl. 85, fig. 8).

Little or no cuticle is recovered on maceration. Some fragments of a 'stringy' nature are sometimes found. These are most probably the longitudinal walls described above. There is no definite cellular structure visible, but occasionally two walls meet suggesting tapering cells (Pl. 85, fig. 7).

Other material. Plant fragments in the Silurian (Ludlovian) part of the quarry are surprisingly abundant. They are found in a very fine-grained, grey sandstone, but unlike the Downtonian plants are not associated with micaceous layers. The remains fall into

three categories: (*a*) Some bedding planes are almost completely covered with small pieces of axis and patches of coaly residue (Pl. 86, fig. 2). (*b*) Slightly longer axes are concentrated sporadically, sometimes in the depressions of ripple marks, and are again associated with patches of coaly residue (Pl. 86, fig. 1). (*c*) Isolated fragments sometimes over 2·0 cm. long with one or two dichotomies are found scattered throughout the deposit (Pl. 86, fig. 3).

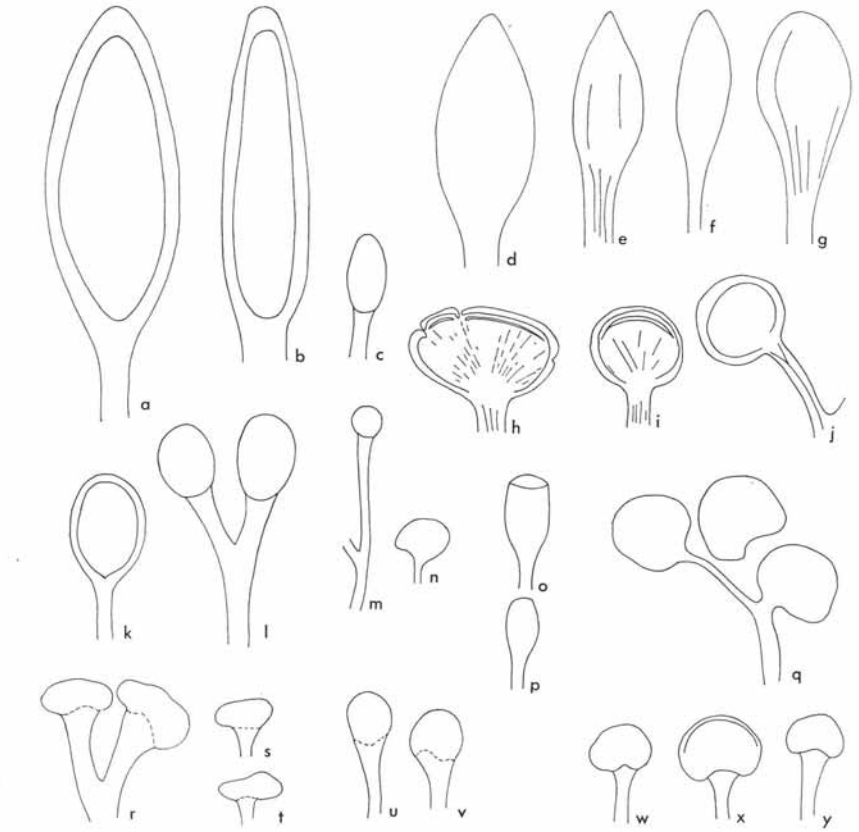
These Silurian axes look very similar to the Downtonian ones. They range from 0·7 to 0·1 mm. in width (on average 0·4 mm.). Surface striations and central strands are often seen. Film pulls and maceration products showed similar cellular organization (Pl. 86, figs. 4–7). No tracheids have been found. In the absence of fertile specimens it cannot be determined with certainty that these axes belong to *Steganotheca*.

Discussion. Banks (1968), in his new classification of the psilophytes, divided the group into three subdivisions. The one relevant to this discussion is the Rhyniophytina in which plants with terminal sporangia (*sensu* Kidston and Lang 1917) are placed. Banks has included two families in a single order, the Rhyniales. In the Rhyniaceae, the terminal sporangia are 'usually fusiform and may dehisce longitudinally' (Banks 1968, p. 76) while in the Cooksoniaceae they are globose. Because there is considerable variation in sporangial shape within both the families recognized by Banks, in this paper I prefer to compare all the genera with solitary terminal sporangia included in the Rhyniophytina, with the plants from Capel Horeb.

In the Rhynie Chert flora (Kidston and Lang 1917, 1919), *Rhynia major* and *R. gwynne-vaughanii* both have terminal sporangia which are longer than they are wide on dichotomously branching naked axes. The sporangia of *R. major* are considerably larger than those in *Steganotheca* but those in *R. gwynne-vaughanii* are of comparable size. *Horneophyton lignieri* sporangia are columellate, while the sporangia are branched. Since the Rhynie plants are petrifactions and unknown in the compressed state, comparison is difficult. It seems probable however that, if preserved as compressions, the two *Rhynia* species, at least, would have well-defined sporangia with good distinction between sporangium and axis, and rounded apices.

The genus *Sporogonites* (Halle 1916), although investigated by a number of workers, is still somewhat of an enigma. On present evidence, it is unlikely that it is a vascular plant. The elongate, obovoid sporangia, terminating long, unbranched axes are larger than those in the Welsh plant. The sporangium apex is rounded and the tapering base merges into the thick upper part of the stalk. The sporangium is longitudinally grooved and columellate. It may be difficult to understand why *Sporogonites*, with its clearly defined sporangial characters, should not be eliminated immediately from this discussion. Cookson (1949) pointed out that, in heavily compressed fossils, the columella and ridges are unlikely to be preserved, and concluded that the critical character is whether or not the axis is branched. The Capel Horeb specimens have branched axes and none of the distinctive characters seen in *Sporogonites*.

Hicklingia edwardii (Kidston and Lang 1923) from the Middle Old Red Sandstone of Scotland with its almost spherical sporangia differs from the older plant in sporangial shape and arrangement. In *Taeniocrada decheniana* (Kräusel and Weyland 1930) the terminal sporangia are larger, and borne in clusters on flat ribbon-shaped axes. The dimensions of the Lower Devonian genus *Eogaspesiea* (Daber 1960) are similar to those



TEXT-FIG. 2. Diagrams to show variation in sporangium shape and size in certain Rhyniophytina; ×4. *a*, *b*, *Rhynia major* (Kidston and Lang 1919); inner line shows extent of spore cavity and is not a thickened border. *c*, *R. gwynne-vaughani* (Kidston and Lang 1917, 1919). *d–g*, *Sporogonites exuberans* (Halle 1916). *h–j*, *Cooksonia crassiparietilis* (Yurina 1964). *k*, *l*, *Cooksonia* sp. (Croft and Lang 1942). *m*, *n*, *Cooksonia* sp. (Obrhel 1962). *o*, *p*, *Steganotheca striata* sp. nov. *q*, *C. rusanovii* (Ananiev 1959, 1960). *r–t*, *C. pertonii* (Lang 1937). *u*, *v*, *C. hemisphaerica* (Lang 1937). *w–y*, *C. caledonica* sp. nov.

in *Steganotheca*, but the sporangia are oval. *Hedeia corymbosa* (Cookson 1935), another Lower Devonian genus, resembles *Steganotheca* because the dichotomously branching axes terminate in elongate sporangia with their tips all at the same level forming a corymb-like arrangement. In *Hedeia*, however, the whole system is compacted to form a definite fructification. In addition, it differs in sporangial shape and size.

When Lang erected the genus *Cooksonia* in 1937, he distinguished it from early genera on the basis of sporangial shape. From his diagnosis, any plant assigned to the genus should have a combination of the following characters: (1) terminal, short, wid

sporangia, (2) dichotomously branched, naked axes, (3) central vascular cylinder composed of annular tracheids. Of these, in my opinion, the most significant and definitive are the short and wide sporangia. There has been a tendency to place any poorly preserved Lower Devonian fossils, where the sporangia are terminal and few anatomical details are known, in the genus *Cooksonia*. The variation in sporangial shape and size is illustrated in text-fig. 2. On the basis of sporangial shape, the Capel Horeb fossils are clearly not assignable to the genus *Cooksonia*. Heard (1939), however, described a single fertile specimen from the Downtonian of the Capel Horeb locality, in which dichotomously branching axes terminated in 'capsule-like' sporangia (5 mm. long by 2 mm. wide). There is little doubt in my mind that this fossil, named *Cooksonia downtonensis* by Heard, should be transferred to the new genus, *Steganotheca*. The lack of distinction between sporangium and stalk might account for the discrepancy in sporangial length. The impression of the plant gained from Heard's illustrations supports my conclusion. In addition, in the line-drawing of the fertile specimen, published by Høeg (1967) at the tip of the left-hand sporangium is a lens-shaped region, limited by a dotted line, which corresponds to the apical feature described above. Heard, however, did not mention this apical feature, nor the oblique striations on the sporangium wall. The morphological nature of this apical thickening is questionable. It is possible that it was similar to the operculum of a bryophyte, but it is unlikely that it could ever be stated with certainty that it was concerned with dehiscence. It is equally possible that the thickness of coaly residue is a preservation feature produced by compression of the flat top of the sporangium. Oxidation of various parts of the sporangia have yielded nothing.

In conclusion the fossils described above present a new combination of characters, not seen in any of the above genera. The new genus *Steganotheca* is therefore erected to include fragments of plants which possess the following characteristics: (*a*) Dichotomously branched, naked axes; (*b*) Erect terminal sporangia, longer than wide with parallel sides, truncated apices and bases tapering into the axes beneath; (*c*) Fine striations running obliquely across the sporangium wall; (*d*) Thick, heavily carbonised, lens-shaped region at sporangium apex.

Heard's specimen has not been made the type of this new taxon, because his material is missing and, secondly, because the new fossils show the distinctive sporangial characters not mentioned in Heard's specific diagnosis.

Genus COOKSONIA Lang 1937

Type species. Cooksonia pertonii.

Original diagnosis. Dichotomously branched, slender, leafless stems with terminal sporangia that are short and wide. Epidermis composed of elongated, thick-walled cells. Central vascular cylinder consisting of annular tracheids.

Cooksonia caledonica sp. nov.

Plate 87, figs. 1–10

Diagnosis. Incomplete plant at least 6·7 cm. high. Naked dichotomously branching axes 0·4–1·8 mm. wide (average 0·65 mm.). Terminal spherical to oval sporangia, some

also reniform. Border (0·1–0·2 mm. wide) sometimes present. Globose sporangia 1·2–2·0 mm. high (average 1·7 mm.) by 1·3–2·2 mm. wide (average 1·8 mm.). Oval ones 1·1–1·8 mm. high (average 1·6 mm.) by 1·8–3·0 mm. wide (average 2·4 mm.). Axis widens slightly below sporangium.

Locality. Aberlemno Quarry, Aberlemno, approximately 1½ miles north-north-west of Turin Hill, Angus; Nat. Grid Ref. 527551.

Horizon. Cairnconnan Group, Dittonian Stage Lower Old Red Sandstone of Scotland.

Holotype. Specimen R.S.M. 1967. 30. 2P and C; Royal Scottish Museum, Edinburgh.

Description of specimens. Very occasionally scattered among the long, relatively unbranched axes of *Zosterophyllum myretonianum* were found narrower dichotomously branching axes, which in the absence of fertile parts, would be assigned to the form genus, *Hostimella*. One piece of rock and its counterpart (R.S.M. 1967.30. 2P and C), found by Dr. C. D. Waterston, was completely covered with these axes lying parallel to each other (Pl. 87, figs. 1, 3). The longest exposed axis was 4·0 cm. long. The slightly flexuous axes branch dichotomously, with an angle of 55–60° at the branching point. Longitudinal striations are sometimes visible on the surfaces of the axes, but what could definitely be called a central strand has not been seen.

A slightly asymmetrical positioning of the branches above a dichotomy indicates a tendency to pseudomonopodial branching, but there is no inequality of axis diameter.

Scattered in the matrix and sometimes attached to short lengths of axis are circular to oval bodies, presumably sporangia (Pl. 87, figs. 5, 6–10). The globose ones measure, on average, 1·8 mm. wide and 1·7 mm. high, while the oval sporangia are 2·4 mm. wide and 1·6 mm. high on average. The height of all the sporangia is slightly less than the width. Occasionally a narrow border less than 0·1 mm. wide extends around the convex margin of the sporangium (Pl. 87, fig. 8). In profile, this is either apparent as a ridge separated from the rest of the sporangium by a sharp depression, or as a groove (Pl. 87, fig. 8). This border could be removed easily.

One specimen (Pl. 87, fig. 10) appears to represent two sporangia almost superimposed, but only one subtending axis is visible. It is possible that this is in fact a dehisced

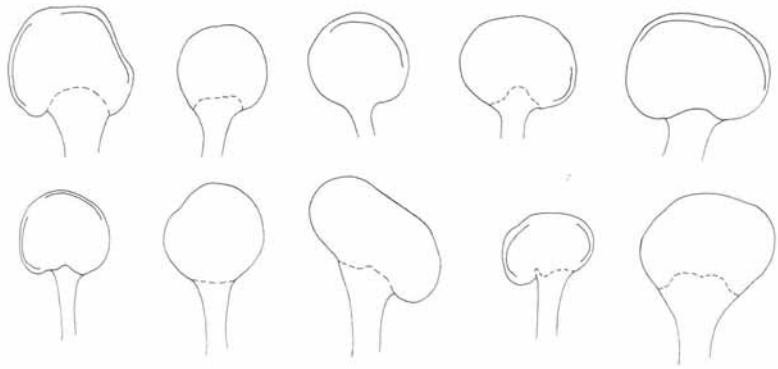
EXPLANATION OF PLATE 86

Figs. 1–7. Sterile axes from Silurian at Capel Horeb. 69.64.G37; ×2·3. 2, 69.64.G38; ×5. 3, 69.64.G39; ×7·7. 4, Axis recovered on film pull, central strand indicated by arrow; 69.64.G40, ×126. 5, Film pull of axis with longitudinal cell walls and transverse banding (indicated by arrows), the latter are formed because the carbon tears when the film pull is removed and are not tracheidal thickenings; 69.64.G41, ×430. 6, 7, Film pulls from axes showing cell walls, 69.64.G42 and G43; ×126.

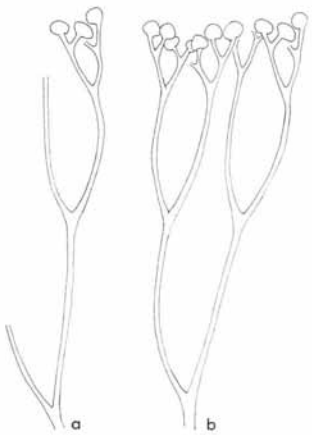
EXPLANATION OF PLATE 87

Figs. 1–10. *Cooksonia caledonica* sp. nov. 1, R.S.M. 1967.30.2P before uncovering; ×1·1. 2, Specimen illustrated in fig. 1 showing dichotomously branching axes with terminal sporangia; ×1·1. 3, R.S.M. 1967.30.2C; Sterile axes with isolated sporangia indicated by arrows; ×0·9. 4, Sporangium from specimen DE 33/22; note pad of tissue in base of sporangium; ×7·7. 5, Isolated almost circular sporangium (R.S.M. 1967.2C); ×8. 6, Sporangia as in fig. 2; ×8. 7–10, Isolated sporangia (R.S.M. 1967.30.2P and C); ×8: 7, Oval sporangium with axis entering its base. 8, Oval sporangium with border, here represented by a depression. 9, Globose sporangium. 10, Two superimposed sporangia or single dehisced sporangium.

sporangium, split into two valves, although the original assumption should not be ignored. The variation in sporangial shape is illustrated in text-fig. 3. In some cases, the tip of the axis extends a short way into the base of the sporangium.



TEXT-FIG. 3. Diagrams showing variation in size and shape of sporangia of *Cooksonia caledonica* sp. nov.; ×9.



TEXT-FIG. 4. *a*, Drawing of *Cooksonia caledonica* sp. nov. from R.S.M. 1967.30. 2P; ×1. *b*, Reconstruction on the plant; ×1.

One branching system, on uncovering, was found to exhibit four orders of branching with a distinct decrease in axis diameter from base to apex. The most complete part terminated in three relatively large sporangia (Pl. 87, figs. 1, 2, 6). Text-fig. 4*a* shows what has actually been seen, but text-fig. 4*b* is a probable reconstruction of the plant assuming that the branching pattern seen in text-fig. 4*a* is repeated. This assumption is supported

by the fact that a row of sporangia, of which the attached ones form one end, is visible on the specimen.

Specimen DE 33/22 in my own collection is again fertile. Here an axis, 0·6 mm. wide at its base, dichotomises once and one branch terminates in an oval to reniform sporangium 1·7 mm. wide and 1·2 mm. high. The axis increases in width just below the sporangium and forms a pad of tissue (1·0 mm. wide) in its base (Pl. 87, fig. 4). This is particularly noticeable on the counterpart where the sporangium itself is fainter. In another specimen (DE 33/19) a dichotomously branching system bears a single, here almost spherical sporangium, 1·5 mm. high and 1·6 mm. wide. The axis widens into the sporangium base. No border is present.

Discussion. This Scottish plant is clearly a member of the genus *Cooksonia* and comparison with the four species already placed in the genus shows that it differs sufficiently to be a new species (text-fig. 2).

In *C. pertonii* (Lang 1937) the sporangia are more irregularly shaped than in the Scottish plant and a border has not been seen. The latter differs from *C. hemisphaerica* (Lang 1937) and the plants designated *Cooksonia* sp. by Croft and Lang in 1942, both in sporangial shape and size. Not enough is known about Ananiev's *Cooksonia rusanovii* (Ananiev 1959, 1960) described from rather fragmentary remains. Although sporangial shape is similar to that in the new plant, the arrangement of sporangia in the Russian specimens is different and even suggests that the plants belong to another genus.

In sporangial characters the Scottish plant most closely resembles *C. crassiparietilis* described by Yurina (1964) from the Lower Devonian of Karaganda, U.S.S.R. One of her specimens consists of a naked dichotomously branching axis about 2 cm. long, varying in width between 1·5 mm. and 4·0 mm., the latter below a branching point. The terminal sporangia are reniform to circular in shape, and are 3·5–5·67 mm. wide and 2·75–4·50 mm. high. Each sporangium has a thickened border and the surface is ornamented by fine ribs diverging from the point of attachment. The wall itself is three-layered. Spiny spores have been isolated. These sporangia, although much larger, are similar in shape to those in the Scottish plant. An odd feature of the Russian specimens is that more than one, presumably vascular, strand is visible in the axis immediately below a sporangium. There is no indication of this in the Aberlemno specimens.

In conclusion, it is considered that the new Scottish *Cooksonia* differs sufficiently from the existing species to warrant the erection of a new species.

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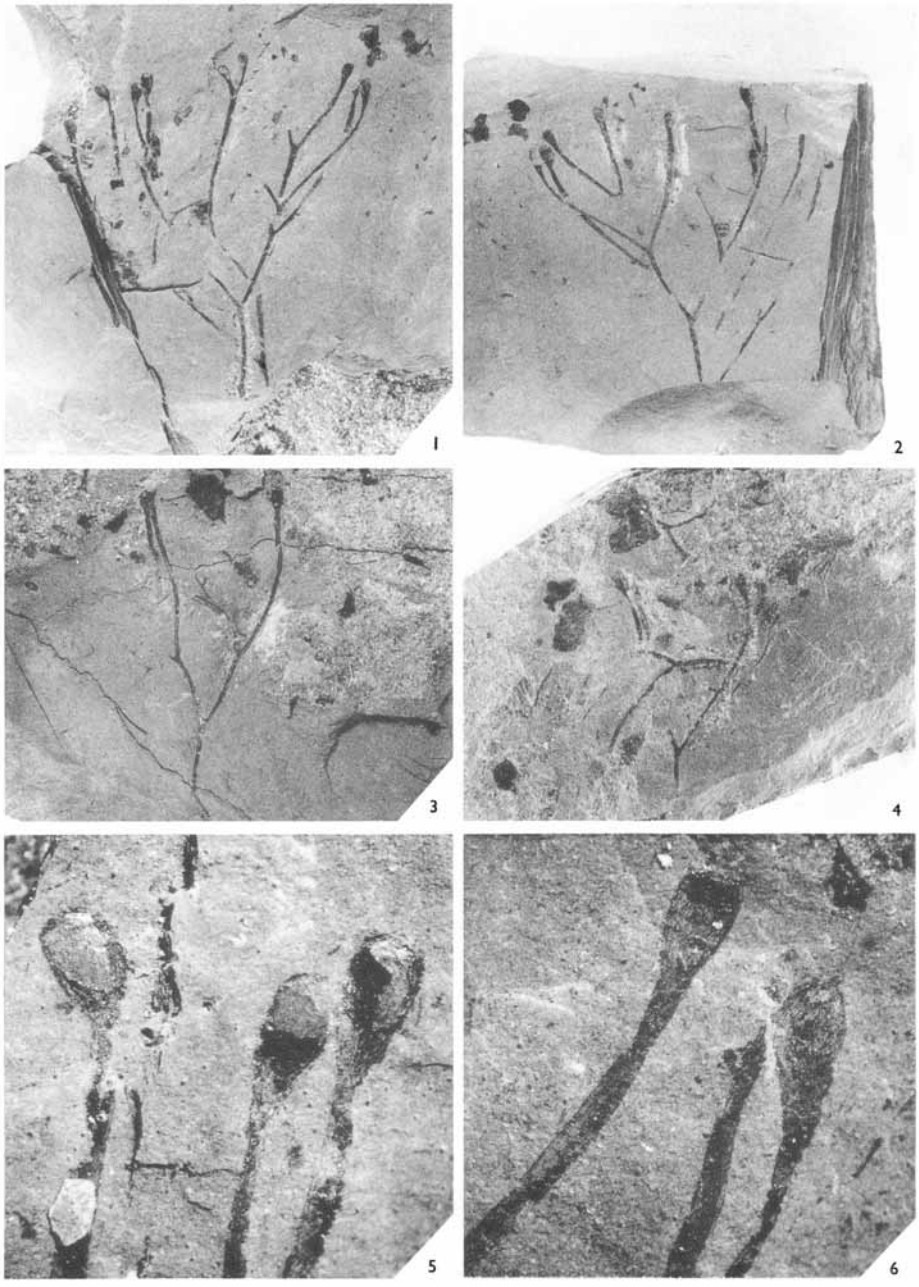

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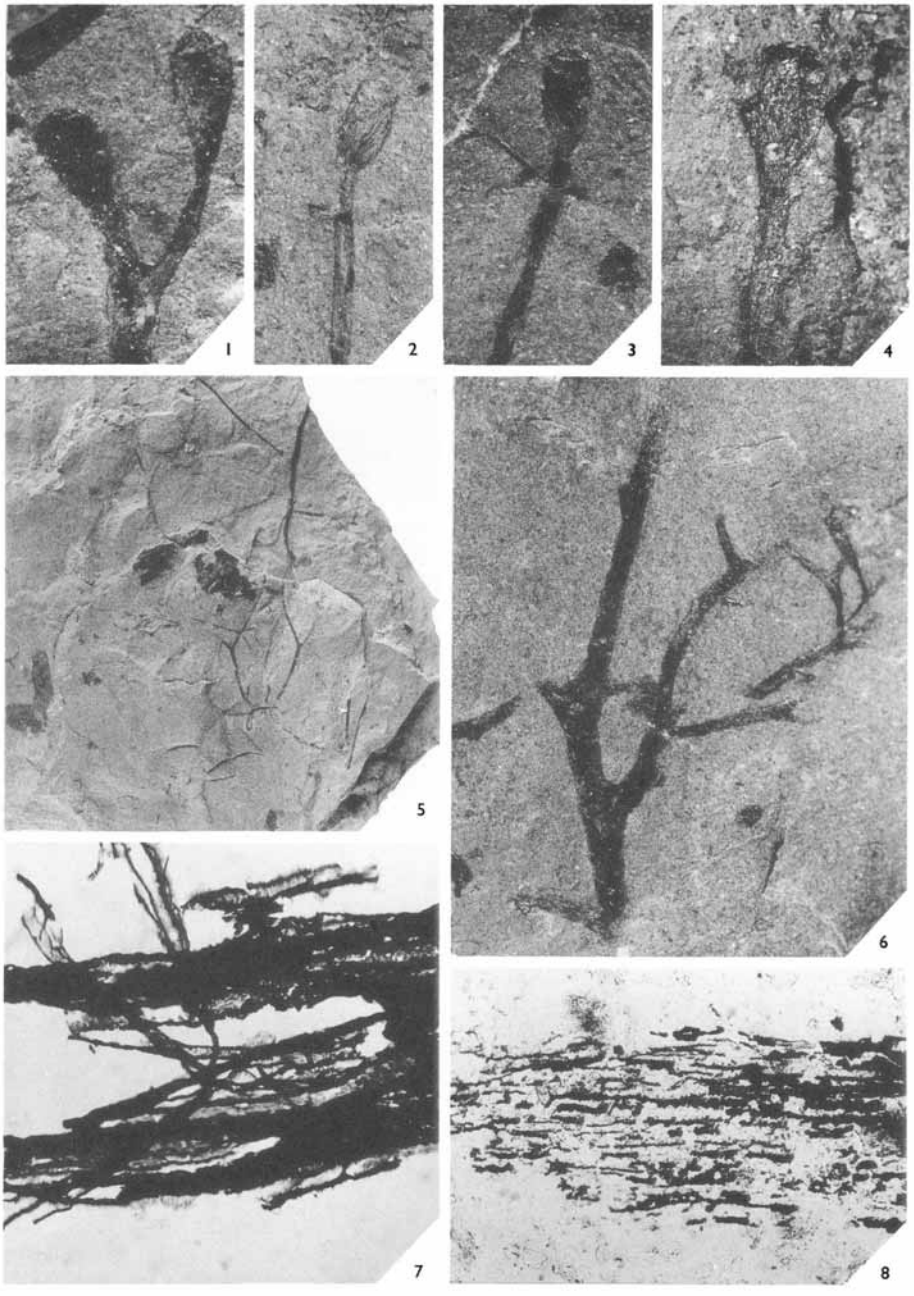

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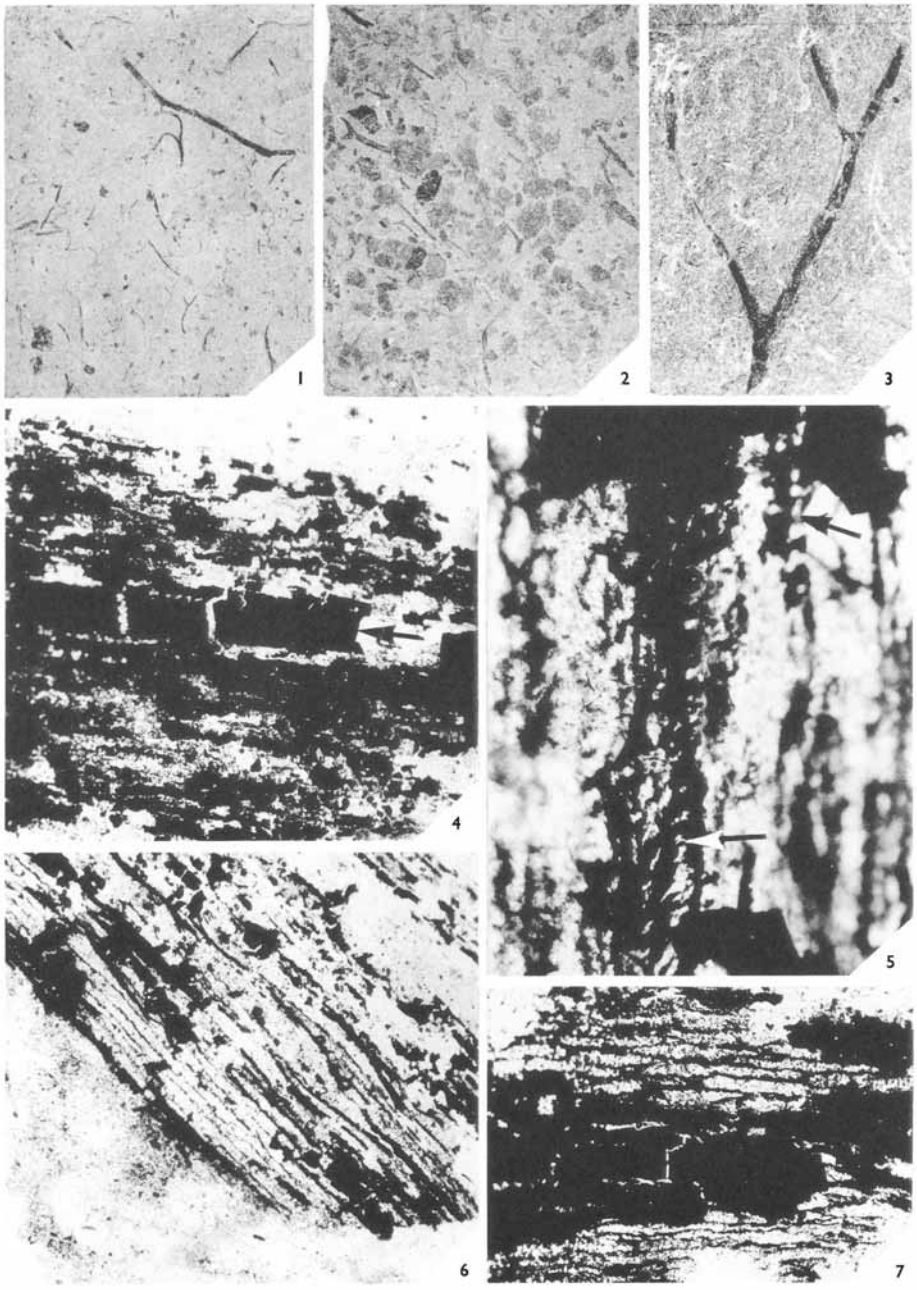
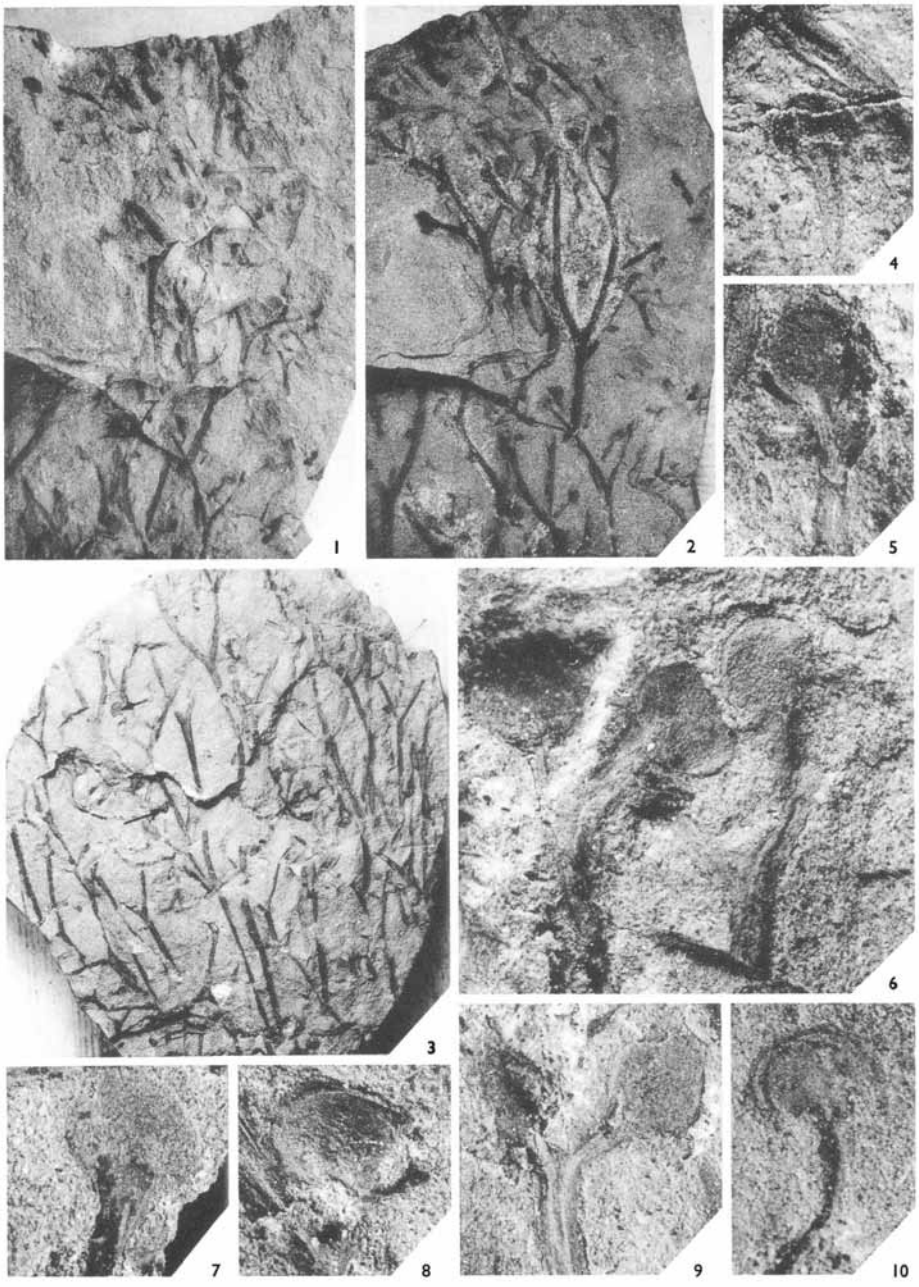


EDWARDS, Silurian (Ludlovian) plants



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