BOTRYOPTERIS ELLIPTICA SP. NOV. FROM THE UPPER CARBONIFEROUS OF ENGLAND

K. R. SURANGE
Birbal Sahni Institute of Palaeobotany, Lucknow

INTRODUCTION

DR. H. H. Thomas found a big "petiole" of *Botryopteris* attached to a stem as seen in Text-fig. 1, *f*, in a section prepared from a block (No. 872) from Halifax Coal, Lower Yorkian, England. He thought the specimen interesting and very kindly handed over the block to me for further investigations. In the sections prepared from this block and its counterpart, I have obtained three identical specimens of "petioles", out of which only one showed branching. The "petioles" are distinct in appearance from any so far recorded in tridentate species of *Botryopteris* and show some new and interesting features.

In order to determine the species of my specimen, I examined the slides of Dr. D. H. Scott, kept in the British Museum (Natural History), London. Many of Dr. Scott's slides (SCOTT coll., slide Nos. 58, 158, 729-730, ?820-821, 898, 1157, 1398, 1425, 2167, 2310) showed specimens identical with those of mine. But for one or two exceptions (e.g. on two slides, No. 58 and 1351, the specimens were put down as new with a query mark, but in his notes he assigned them to *B. hirsuta*; similarly for slide Nos. 729 and 730, he does not mention any specific name) Scott included these types in *Botryopteris hirsuta*.

It should, however, be mentioned that in the tridentate species of the British Coal Measures, many a time it becomes difficult to distinguish one species from the other. As regards the two species, *B. ramosa* and *B. hirsuta*, Scott (1920, p. 339) himself wrote that they are "not always easy to distinguish, though it is possible that more than two species are concerned". The specimen under consideration shows a "petiole" distinct in structure from any of the known species of *Botryopteris* and revealed a mode of branching not known in *B. hirsuta*. I have, therefore, described this specimen under a new specific name.

I am thankful to Dr. H. H. Thomas under whose supervision this work was done at the Botany School, Cambridge, England. It was originally assigned to *B. hirsuta*, but my subsequent study convinced me that it is a distinct species. My thanks are also due to Mr. W. N. Edwards for giving me facilities to examine Dr. D. H. Scott's slide collection kept at the British Museum (Natural History), London.

MATERIAL

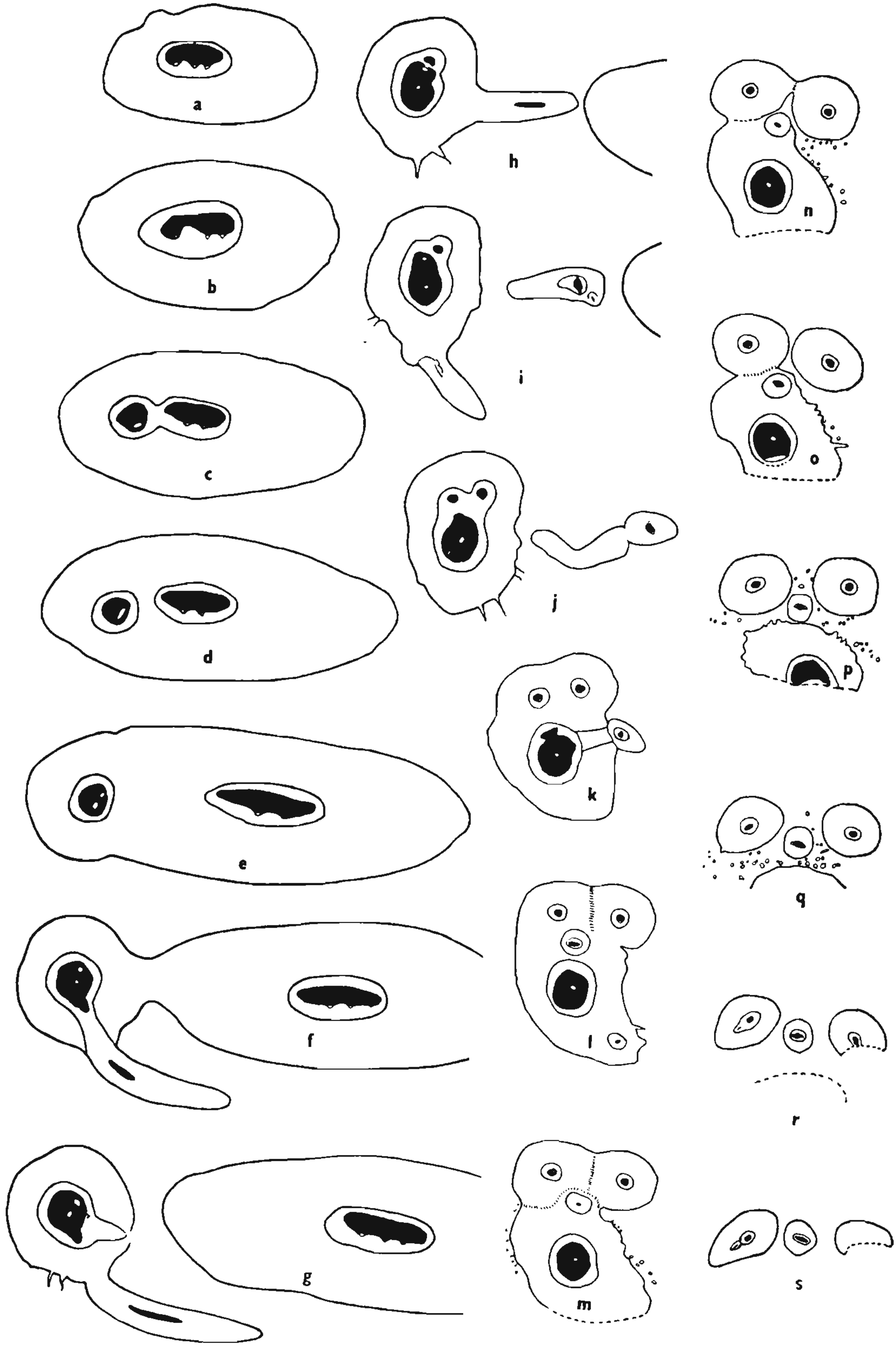
The present description is based upon a series of peel sections taken from a coal ball in Mr. Hemingway's collection from Halifax Coal, Lower Yorkian Shore, Lancashire, England, at present kept at the Botany School, Cambridge. The coal ball was already cut by Mr. Hemingway into more than two blocks to which he gave different numbers. Two of these blocks (one being the counterpart of the other) were numbered 872 and 874. Block 874 was 1·2 cm. thick, from which 22 sections were prepared in 8 mm. thickness. Block 872 was 1 cm. thick, from which 25 sections were prepared in 7 mm. thickness. Text-fig. 1, *a-e*, shows the stages in the branching of a dorsiventral shoot (petiole) observed in sections from block No. 874. Text-fig. 1, *f-s*, shows the stem and its branching observed in sections from block No. 872. The specimen under consideration, however, disappeared within 4 mm. in block No. 872. The total length traced is, therefore, nearly 1·2 cm.

Besides, two more dorsiventral shoots, identical with the one which showed branching, were observed, one in each block. They showed no branching.

DESCRIPTION

Botryopteris elliptica sp. nov.

In the following description, I have called the so-called petiole a "dorsiventral shoot" as I have done in *B. antiqua* (SURANGE, 1952), since it gave rise to a stem and not a secondary branch.



Text-fig. 1

In *B. elliptica* the dorsiventral shoot gives out a stem in the same manner as in *B. antiqua*. The stages in the origin of stem are as follows:

The stele of the dorsiventral shoot is tridentate, the three small teeth marking the positions of the protoxylems. From the lateral side of this stele a few metaxylem tracheids, together with one protoxylem group situated on one of the outer teeth, separate as a lateral trace. On the outward passage of the trace, new metaxylem tracheids are added on the outer side of the protoxylem. As a result, the protoxylem becomes mesarch and the lateral trace begins to assume the terete structure of a stem stele. The stem then separates from the dorsiventral shoot without undergoing any change and immediately gives out roots. As in other species of *Botryopteris*, it is difficult here also to count exact number of protoxylem groups. However, at this stage at least two protoxylems are clearly distinguishable. One is situated in the centre and the other near the periphery on one side which is abaxial to the dorsiventral shoot. From this side the stem stele now gives off a small trace, followed immediately by another one, which is given off very near to the first and is exactly similar to it. The two traces follow the same course outwards through the cortex of the stem and look like twin branches coming out of the stem. The twin branches eventually separate from one another and the stem. Immediately after this the stem and the branches disappear and further observations, therefore, could not be made.

After this summary a detailed description is given below.

Structure of the Dorsiventral Shoot

The dorsiventral shoot is somewhat flattened and measures 4·5 × 2·5 mm. (PL. 1, FIG. 1). What strikes the eye most in the dorsiventral shoot is the wideness of the cortex and small size of the vascular bundle. The vascular bundle measures only 1·1 × 0·4 mm. and is also flattened dorsiventrally.

Cortex — The cells of the epidermis are comparatively big, four-sided and occasionally bear multicellular hairs. The epidermis is followed by a dark-coloured zone (PL. 1, FIGS. 1, 2) of small cells, which are rather badly preserved. It is difficult to make out what these cells are, but most probably they represent slightly thickened cells of the mechanical tissue. This dark zone is followed by big, slightly angular, thin-walled cells of the inner cortex. These cells appear rectangular in oblique section and show a strikingly regular arrangement (PL. 1, FIG. 2). The two zones of the cortex are distinct, as it is in *B. hirsuta*, but its appearance as a whole is different from *B. hirsuta* as described by Long (1943), and also from *B. ramosa*. This difference in appearance is further emphasized by the fact that the transverse section of the dorsiventral shoot in my material is neither circular as in *B. hirsuta* (LONG, 1943) nor D-shaped as in *B. ramosa*, but it is always somewhat flattened.

The Stele — The stele is elliptical (PL. 1, FIG. 1) and is unlike that of *B. hirsuta*. Big and pitted metaxylem tracheids form a long plate, on the adaxial side of which project three very small teeth, marking the positions of the three protoxylem groups. These three small teeth are in contrast with the more pronounced teeth of *B. hirsuta*. After the protoxylem on one of the two outer teeth had supplied the lateral trace, the stele of the dorsiventral shoot is left with only two protoxylems. But at a higher level the stele again becomes triarch. It is perhaps the central protoxylem which restores the triarch condition of the stele.

It thus appears that the central protoxylem group is the main protoxylem of the stele, the two other protoxylems on its right and left are probably derived from it and are only awaiting their release into the lateral

←—

TEXT-FIG. 1 — *a-e* shows the stages in the branching of a dorsiventral shoot, producing the radial stem and the branching of the radial stem. *a-e*, branch trace is given off by the tridentate stele of the dorsiventral shoot. In *e* the branch trace has developed into the radial stem stele and gives off roots in *f*, *g*, *h* and *i*. The dorsiventral shoot then disappears. The radial stem first gives out one primary branch (? petiole) trace in *h* and then the second one in *j* and a root in *l*. The primary branches then separate from one another in *o* and from the radial stem in *p*. The primary branch on the left side gives out a lateral trace for the secondary branch in *r* and *s*. After this no trace was left of the stem or branches in the block.

branches. Looking from this angle, it becomes easy to compare such a triarch bundle with a monarch one in *B. antiqua* shoot. The main central protoxylem of *B. elliptica* can be compared with the single protoxylem of the *B. antiqua*. The single protoxylem of *B. antiqua* shoot gives off branch protoxylems right and left, but only when division is to occur. The two branch protoxylems have not yet acquired a permanent place on the stele in the Lower Carbonifeours species. It, nevertheless, shows clearly a trend of evolution, which appears to have been realized in the Lower Coal Measure species. In *B. hirsuta* and probably other tridentate species the central protoxylem gives off branch protoxylems right and left, which remain attached to the stele, until one of them is released into the lateral trace. It is then very soon replaced by a new one from the central protoxylem. Thus, in *B. hirsuta* two branch protoxylems have acquired a permanent place on the stele, the stele consequently becomes permanently triarch.

The phloem is not well preserved.

Branching of the Dorsiventral Shoot and Origin of the Stem

When a dorsiventral shoot branches, a few metaxylem tracheids, together with one protoxylem group from one of the outer teeth of the stele, separate as a lateral trace (Text-fig. 1, *a-c*). As a result, the stele of the dorsiventral shoot is left with two, instead of three, protoxylems. The detached lateral trace at first is somewhat oval in shape, but very soon small metaxylem tracheids appear on the adaxial side of the protoxylem, thus engulfing it and giving the trace a terete shape. This is the stele of the stem in formation. The small tracheids are formed on that side of the stem stele which faces the stele of the dorsiventral shoot (Pl. 1, Fig. 2; Text-fig. 1, *d*). At this stage the protoxylem of the stem has already divided into at least two groups (Pl. 1, Fig. 3), which are clearly discernible. The addition of small metaxylem tracheids to the stem stele continues and as a result the stele increases in size (Text-fig. 1, *e*). The stele consists of small and large tracheids.

The stages described above are observed in block No. 874. Further stages are seen in block No. 872, the counterpart of block No. 874. Text-fig. 1, *e*, shows the last section prepared from block No. 874 and *f* the first from block No. 872. In the latter the radial stem is seen still attached to dorsiventral shoot by a layer of a few cells, but now the former has developed into its adult form (Pl. 1, Fig. 3).

Structure of the Radial Stem

The radial stem measures 2 mm. in diameter. Its stele at this level has increased considerably in size and measures $0{\cdot}8 \times 0{\cdot}5$ mm.

The cells of the epidermis are comparatively big and prominent (Pls. 1, 2, Figs. 3, 6, 7). Some of them bear multicellular hairs. In my specimen the hairs are few and not always fully preserved. The hairs do not possess long, somewhat curved ultimate cells (unless it is a fault of preservation) which are so characteristic of *B. hirsuta* as figured by Williamson (1889).

In the lower region of the stem the epidermis is followed by a comparatively broad zone of thick-walled cells. A little higher up, however, only a few thick-walled cells remain in this zone, the rest being replaced by small thin-walled cells. Other cortical cells are large, angular and thin-walled. In Pl. 2, Figs. 7, 8, the cortex is no longer divided sharply into outer and the inner zones (cf. Pl. 1, Fig. 3).

Immediately after the separation from the dorsiventral shoot, the stem stele consists of small and large tracheids (Pl. 1, Fig. 3), and is somewhat irregular in shape. Two protoxylems can be detected at this stage. One is situated in the centre, the other near the periphery (Pl. 1, Fig. 5). The latter is not preserved and is presumably indicated by a cavity. This protoxylem supplies the two branches. After the emission of these branches, the structure of the stem stele changes slightly as can be seen in Pls. 1, 2, Figs. 5, 8. The stele has assumed a round shape and the tracheids have become more uniform in size. In the centre of the stele a small cavity is present which represents the position of the protoxylem group. This, I believe, is the permanent adult form of the stem. Unfortunately the stem disappears immediately after this (Pl. 1, Fig. 4) and further changes, therefore, could not be observed.

The phloem is not well preserved.

Primary Branches

As soon as the stem separates from the dorsiventral shoot, it gives out two roots (TEXT-FIG. 1, *f*). The root seen in Pl. 1, Fig. 3, measures 0·48 mm. in diameter. In the same section the root has given out two lateral branches, one of them is seen in Text-fig. 1, *f*. The roots are diarch and similar to those in other *Botryopteris* species. A root receives its vascular supply from the periphery of the stem stele (PLS. 1, 2, FIGS. 3, 7).

Within one millimetre after its separation from the dorsiventral shoot, the stem stele gives out a small branch trace from the periphery where the cavity representing the protoxylem is situated (PL. 2, FIG. 6; TEXT-FIG. 1, *h*). The trace occupies an abaxial position in relation to the dorsiventral shoot. This is exactly the position from where the first branch trace of *B. antiqua* is given out. Could this trace then be compared with the first branch trace of *B. antiqua* ? The branch trace is very small in size and does not exceed 0·16 mm. in diameter. It is difficult to locate the protoxylem, but judging from the small xylem elements in the trace, a single protoxylem appears to be situated on the side of the trace facing the stem stele (PL. 2, FIG. 6). One protoxylem remains behind in the stem stele for supplying the second and perhaps subsequent traces.

At this level the stele of the dorsiventral shoot has already acquired its triarch condition. The new protoxylem is most probably supplied by the central protoxylem. The dorsiventral shoot is moving obliquely away from the stem. It eventually disappeared from the sections.

Immediately after the separation of the first branch trace, a second branch trace, very similar to it, is given out by the stem stele, near the place from where the first trace came out (TEXT-FIG. 1, *j*; PL. 2, FIG. 7). The protoxylem which remained behind supplied the second trace, which is also monarch.

Small peripheral clear space in the stem stele, which presumably marked the position of the protoxylem, has disappeared at this level (PL. 2, FIGS. 7, 8). There now remains probably one protoxylem in the centre of the stele (TEXT-FIG. 1, *j*).

Now a diarch root trace comes off from the side of the stele from where the two branch traces were given out (TEXT-FIG. 1, *k*, *l*; PL. 2, FIG. 8). The root occupies a middle position between the two branch traces.

The two branch traces move out of the cortex of the stem simultaneously (TEXT-FIG. 1, *m*, *n*). They remind one of the twin branches in *Stauropteris burntislandica* and other similar Zygopteridean fronds. The first primary branch (? petiole) separates first from the stem and then from the second primary branch (TEXT-FIG. 1, *n*, *o*). The latter then separates from the stem (TEXT-FIG. 1, *p*, *q*; PL. 1, FIG. 4).

The stem disappears completely in the next section. The two branches also disappear within 1 mm., but before that the second branch had given out a small lateral trace, a secondary branch (TEXT-FIG. 1, *r*, *s*).

Structure of the Primary Branches

Each primary branch measures 1 mm. in diameter and its vascular bundle does not occupy more space than 0·16-0·2 mm. in the centre (PLS. 1, 2, FIGS. 4, 9).

The epidermal cells are comparatively big and distinct. They also bear occasionally multicellular hairs. The cells of the cortex vary slightly in size and tend to become smaller towards outside. A few thick-walled cells are present in the outer part of the cortex.

The primary branches were still young when preserved, for the metaxylem tracheids had not developed thickenings (PL. 2, FIG. 9). A few small tracheids, which represent the protoxylem are, however, thickened. The rest of the vascular tissue is not well preserved.

The second primary branch gives out a small secondary branch trace immediately after separating from the stem (TEXT-FIG. 1, *r*, *s*). It is interesting to note that this behaviour of the second primary branch is exactly similar to the small trace in *B. antiqua* (also second in the sequence), separating from the stem.

The primary branches disappear in the next two sections after the stage shown in Text-fig. 1, *s*. Further observations, therefore, could not be made.

On account of the disappearance of stem in my material, it is not known what really is the normal structure of a primary branch or a petiole in this plant. One can reasonably expect that it would be tridentate and triarch as in other species of *Botryopteris*, unless, of course, this plant possesses only monarch petioles. This point will have to be left open until we know more about this plant. At present, however, I can only compare these two monarch branches with the first two primary branches (petioles) of *B. antiqua* stem (cf. TEXT-FIG. 1, *d-f*).

Diagnosis — Dorsiventral shoot elliptical, wide cortex and comparatively small flattened vascular bundle with three very small teeth marking the positions of protoxylems. It gives rise to a stem bearing roots. Stem 2 mm. in diameter with hairs. Stele terete, mesarch or endarch with one or two protoxylem groups. Stem gives off monarch branches (? petioles). Petiole and further branching not definitely known.

COMPARISON AND DISCUSSION

B. elliptica does not correspond closely with any of the known eleven species of *Botryopteris*.

B. elliptica possesses a stem about 2 mm. in diameter, with mesarch or endarch stele. This distinguishes it from *B. trisecta* Mamay & Andrews (1950), *B. forensis* Renault, *B. Fraiponti* Leclercq, and *B. radiata* Darrah, which have much bigger stems. The last two species have recently been merged with a new lycopsid genus *Paurodendron* Fry (FRY, 1954).

B. cylindrica Williamson differs from *B. elliptica* in possessing two types of stems, and petioles which are semi-lunar in cross-section and are monarch or diarch.

In *B. mucilaginosa* Kraentzel the stem is much bigger in size, 6-7 mm. in diameter, and the structure of the cortex and stele is also quite different. Besides, it possesses " gum " canals which are absent in *B. elliptica*.

B. elliptica can also be distinguished from *B. antiqua* Kidston, *B. tridentata* Felix, *B. americana* Grahm, *B. Renaulti* Bertrand & Cornaille and *B. minor* Corsin by the structure and size of the " petioles ".

Lastly, *B. elliptica* differs from *B. hirsuta* Williamson and *B. ramosa* Williamson in several respects. In *B. ramosa* the stem is much bigger in size, 5-6 mm. in diameter. In *B. hirsuta* and also in *B. ramosa* the " petiole " is round or shows a depression on the adaxial surface. In *B. elliptica* the " petiole " (dorsiventral shoot) is flattened and elliptical. That this flattening is not accidental is shown by the fact that the other "petioles" in my material as well as in Scott's slides are all invariably elliptical in cross-section. Similarly the vascular bundle of the "petiole" is also elliptical and does not possess three so well-developed arms carrying protoxylems as in *B. hirsuta* and *B. ramosa*. Instead, in *B. elliptica* there are three minute projecting points which indicate the positions of the protoxylems. Also, the mechanical tissue system appears to be inadequate in *B. elliptica* as compared to its size. On the other hand, the " petiole " of *B. ramosa* and *B. hirsuta* are stronger and have better developed mechanical tissues.

Morphology of the " Petiole " — The morphology of a typically well-developed botryopterid petiole, or " the dorsiventral shoot " as I have called it, presents a perplexing morphological problem. In at least four out of eleven species of *Botryopteris*, namely *B. antiqua*, *B. ramosa* (SURANGE, 1952), *B. hirsuta* (LONG, 1943) and *B. elliptica*, it has been shown that the so-called " petiole " gave rise to a stem, bearing fronds and roots. And when it is so, why call it a petiole ? The problem is whether this organ is foliar or cauline in nature. It appears that it is cauline.

The evidence is furnished by *B. trisecta* Mamay & Andrews, which is the most completely known species of *Botryopteris* so far. A different interpretation, rather than the conventional one as given by Mamay and Andrews (1950), has to be given to the branch system of *B. trisecta*. Thus, the petiole of *B. trisecta* could be regarded as a dorsiventral shoot (as in *B. elliptica*) and the product of its division — the " primary pinna " and the " proximal secondary pinna " — which appears to be one and the same (for, the " proximal secondary pinna " could easily be regarded as the continuation of the " primary pinna "), as a stem. In both the so-called stele is terete and just like that of a stem. "The proximal secondary pinna " gives off *adventitious rocts* after giving rise to two branches (" distal and median secondary pinnae "), or divides again by dichotomy like a normal stem (*see* " the proximal secondary pinna ", MAMAY & ANDREWS, 1950, pp. 476-478). This further explains why there is a " striking difference in size and form between the vascular tracts of the proximal secondary pinna (which, I think, is a stem) and its two associated branches " (MAMAY & ANDREWS, 1950, p. 485). This type of branching of a big " petiole " is exactly similar to that of a dorsiventral shoot in *B. elliptica* (cf. FIG. 7, and MAMAY & ANDREWS, 1950, PL. V, FIG. 14, P2C, P2B, P2A).

The reason for considering the so-called " petiole " as cauline in nature is that, as far as we know, it gave rise to stems only. Nothing contrary to this has been found so far in *B. antiqua*, *B. hirsuta*, *B. ramosa* and *B. elliptica*. In *B. trisecta* also in no case the " petiole " has been observed to give off appendages beyond the first pair of pinnae (which can be regarded as stems as explained above), which depart near its base (MAMAY & ANDREWS, 1950, p. 473).

Further, it has been shown in *B. trisecta* that in its initial departure the " petiolar trace " is actually a simple branch segment of the stem with terete, stem-like stele which is retained for at least some distance. When the terete stele divides, it gives off two " stems " (" primary pinnae ") and then itself becomes W-shaped. In *Botryopteris* the organ with a dorsiventral, W-shaped stele is regarded as a petiole, which, I think, is not always correct. In *B. trisecta* itself Mamay and Andrews (1950, p. 474) have observed that the terete stele of the " proximal secondary pinna " (which can be interpreted as a stem) have assumed a W-shape. It, therefore, appears that in *B. trisecta* and most probably in other species of *Botryopteris* also the stem is an extremely plastic entity and its stele may become terete as in a normal stem, or assume a W-shape like that of a petiole. Hence, the so-called " petiole " with a W-shaped stele and producing a stem may be just another form of the stem, rather than that of a petiole.

It is not intended here to convey that all the organs with W-shaped stele are not real petioles. They should be put under the category of stem or petiole only when their branching is known. The petiolar traces of *B. trisecta* and other similar species could be W-shaped, but they would perhaps be smaller in size than the stems which bear them and also from the dorsiventral shoots. The stem stele which assumes W-shape appears to be generally bigger in size. Why the terete stem stele assumes petiole-like dorsiventral W-shape, it is difficult to say.

Perhaps this extreme plasticity of the stem in *Botryopteris* has something to do with the habit of the plant. The stem with a terete stele might have been the upright organ, giving off roots and branches (frond). It would sometimes dichotomize and one of the branches would have a dorsiventral stele, which would act like a runner and perhaps at a considerable distance and at favourable spots would again produce erect, radial stems giving out roots and " fronds ".

REFERENCES

FRY, W. L. (1954). A study of the Carboniferous lycopod, *Paurodendron*, gen. nov. *Amer. Jour. Bot.* **41**(5): 415-428.

LONG, A. G. (1943). On the occurrence of buds on the leaves of *Botryopteris hirsuta*. *Ann. Bot.* **7**: 133-146.

MAMAY, S. H. & ANDREWS, A. N. (1950). A contribution to our knowledge of the anatomy of *Botryopteris*. *Bull. Torr. Bot. Club.* **77**(6): 462-494.

SCOTT, D. H. (1920). Studies in fossil botany. 1. *London*.

SURANGE, K. R. (1952). The morphology of *Botryopteris antiqua* with some observations on *Botryopteris ramosa*. *The Palaeobotanist* (Birbal Sahni Memorial Volume). **1**: 420-434.

WILLIAMSON, W. C. (1878-1891). On the organization of the fossil plants from the Coal Measures. Pts. 9, 15 and 18. *Phil. Trans. Roy. Soc. London*. Series B.

EXPLANATION OF PLATES

Plate 1

1. A dorsiventral shoot in cross-section. Note the structure of the cortex. The stele is somewhat flattened and possesses three protoxylems. The one on the left side supplies the lateral trace, which has been initiated. × 22.

2. The same dorsiventral shoot cut at a higher level. The lateral trace is moving out of the cortex of the dorsiventral shoot. The stele of the former consists of large and small tracheids (situated on the inner side) as in *B. antiqua*. × 16.

3. Further up the stem is now fully formed and is almost completely detached from the dorsiventral shoot, a few cells of which are seen at the right-hand bottom side. The stele consists of small and large tracheids and possesses two protoxylems, one of which is situated near the edge (indicated by a clear space). This supplies the two branches at a higher level. One root is also seen in connection with the stem. × 30.

4. The stem cut at a higher level than in Fig. 8. Half of the stem had disappeared. Its two branches have completely separated from each other. One diarch root is seen between the two branches. × 26.

5. The stem stele from Fig. 3 enlarged. It shows only one protoxylem in the centre. × 70.

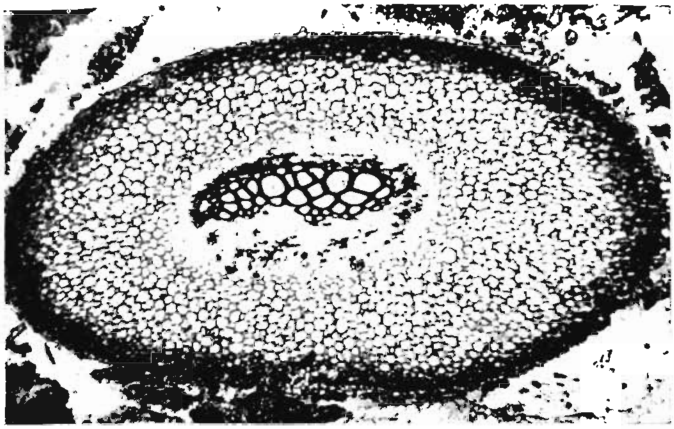
Plate 2

6. The stem seen in Fig. 3 cut at a higher level. Note the structure of the stem and the hairs. From the peripheral protoxylem one small trace is formed. × 32.

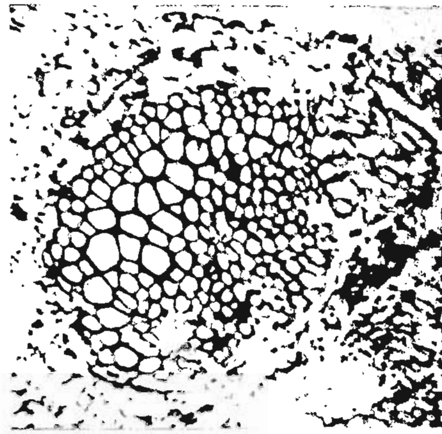
7. Further up the same peripheral protoxylem supplied another small trace. The stem stele is left with only one protoxylem in the centre. × 30.

8. The two small branches are separating from the stem. A diarch root is seen between the two branches. The large tracheids have disappeared from the stele, which now consists of only small tracheids with one protoxylem in the centre. × 31.

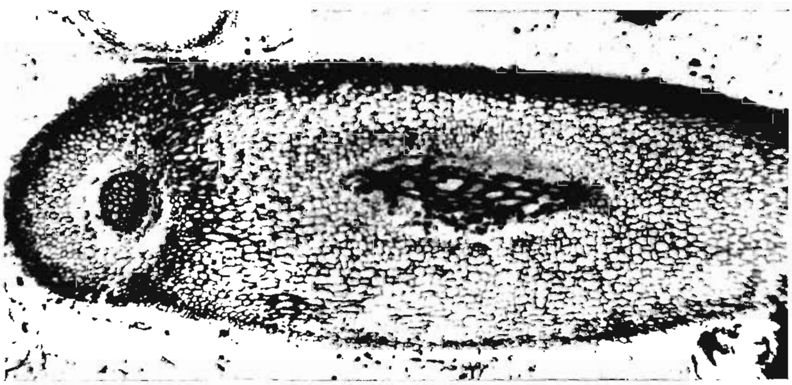
9. A small branch enlarged to show its structure. × 60.



1

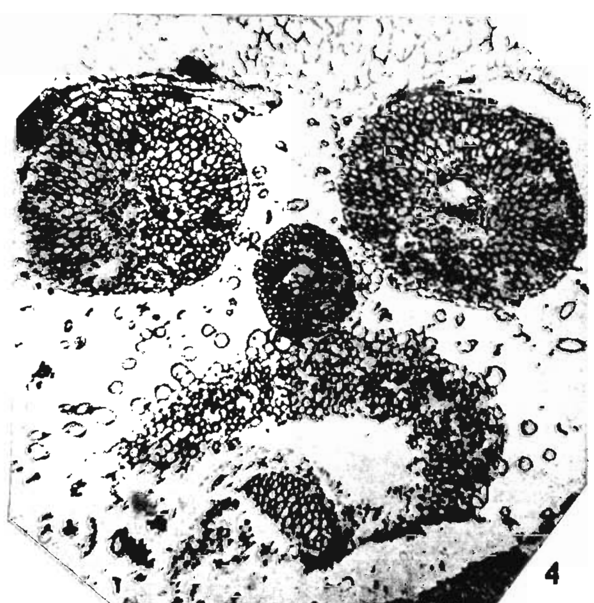


5

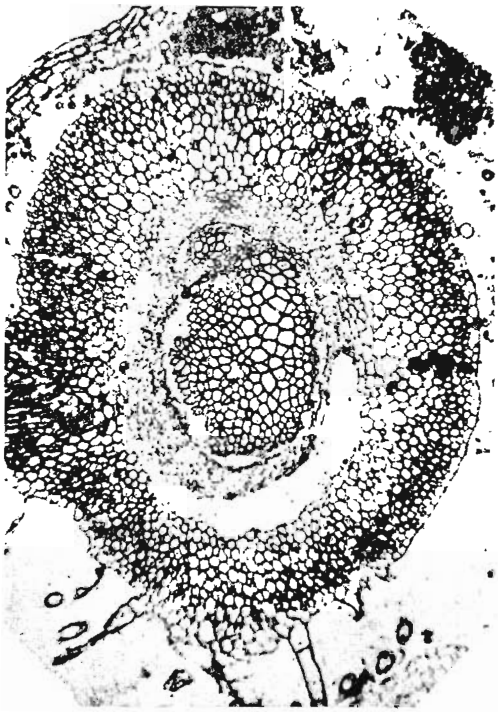


2

3



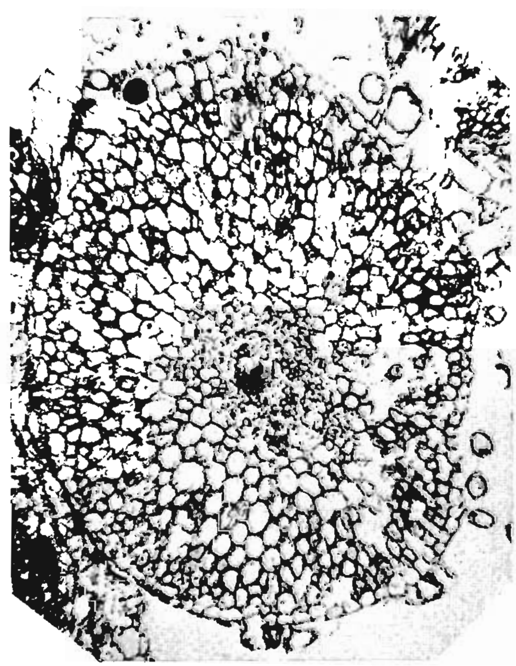
4



6

7

8



9