THE MORPHOLOGY OF *BOTRYOPTERIS ANTIQUA* WITH SOME OBSERVATIONS ON *BOTRYOPTERIS RAMOSA*

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ABSTRACT

In this paper a complete revised description of *B. antiqua* is given. The plant possesses two types of stems, dorsiventral and radial, and the dorsiventral gives rise to the radial at intervals. The radial stem gives rise to roots and petioles in spiral succession. A petiole branches sympodially and produces a frond-like branch system. The morphology of the dorsiventral stem is discussed in detail and it is shown that *B. ramosa* also possesses a similar organ. *B. antiqua* is compared with the Coal Measure species and it is shown how younger species could have been evolved from it and how a triarch leaf trace was developed. A comparison is also made with the leaf impressions from the Lower Carboniferous.

INTRODUCTION

In 1908 Kidston established the species *Botryopteris antiqua* from the Lower Carboniferous rocks of Pettycur, Scotland. Pelourde (1910) recorded the same in France and briefly described petiole and sporangia. In the same year Scott in a short note suggested a connection between such sporangia and a rachis of *B. antiqua*. In 1937 Corsin briefly described branching of a primary petiole. A somewhat detailed account of the species was, however, given by Benson (1911). According to her the plant consisted of an underground rhizome, which bore alternate monarch and diarch petioles in spiral succession. She described the mode of origin of both types of petioles, but that of a diarch one is not explained by her figures.

Recently Long (1943) made an important contribution on the morphology of *B. hirsuta* and *B. antiqua*. As will be seen later, I have interpreted the structures described by Long on rather different lines from those he adopted.

I wish to express my gratitude to Dr. H. H. Thomas, F.R.S., for his help throughout this work and to Professor T. M. Harris, F.R.S., for his criticism and suggestions. Also thanks are due to Mr. W. N. Edwards who so very kindly offered me facilities to go through Dr. D. H. Scott's slide collection at the British Museum (Natural History), London.

MATERIAL AND METHODS

The material was previously collected by Mr. W. Hemingway from Calciferous Sandstone series (Culm), Pettycur, Fife, Scotland, and kindly handed over to me by Dr. H. H. Thomas for further investigations.

A series of sections were prepared from the blocks by the peel method. A block was ground smooth and etched in 5 per cent HCl for 45 seconds. The etched surface was then washed and allowed to dry. Before pouring the cellulose solution it was found useful to wet the etched surface with acetone. It facilitated the spreading of cellulose and avoided the formation of air bubbles. The sections peeled off easily after drying for 8-12 hours. The sections were then treated with dilute HCl and pressed in blotting papers. In this way I have taken four to eight sections in one millimeter.

DESCRIPTION

A. Botryopteris antiqua

The plant of *B. antiqua* consisted of a trailing dorsiventral stem which gave rise to erect or semi-erect radial stems bearing roots and petioles in close spiral succession. When a radial stem is to form, the stele of the dorsiventral stem cuts off a monarch lateral trace, round which are formed small metaxylem tracheides, thus converting it into a radial stem stele. The radial stem then gives off roots and petioles.

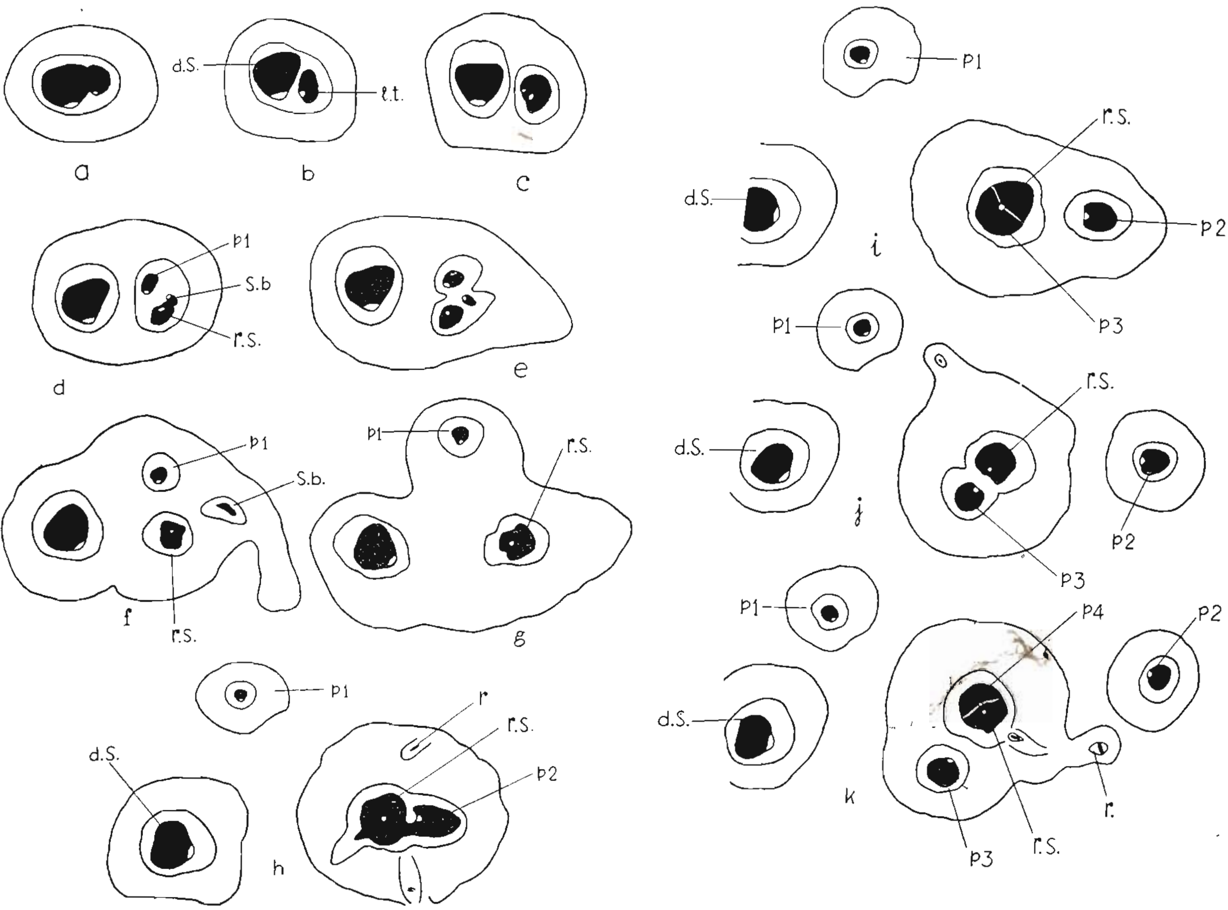
1. Dorsiventral Stem

A dorsiventral stem varies from 1·4 to 2 mm. in diameter and its stele from 0·48 to 0·72 mm. in size (Pl. 1, Fig. 1; Text-fig. 1). The cortex is 0·4 to 0·6 mm. in thickness. The epidermal cells are small and quadrangular and bear sparingly distributed hairs. The outer cortical cells are small, slightly thickened and angular and the inner ones are large and thin walled. The endodermis and pericycle are difficult to distinguish.

The stele is massive in appearance and elliptical in cross-section. The tracheides on its abaxial side are large, often reaching the maximum size of 0·16 mm., and those on the adaxial side are small where one or two protoxylems are situated. The protoxylems are slightly immersed and are not always preserved. The large tracheides have multiseriate pits on their walls and the smaller ones have scalariform and reticulate thickenings. The protoxylem tracheides are spirally thickened.

When a dorsiventral stem is about to branch, a protuberance carrying one slightly immersed protoxylem is formed on one side of the stele (TEXT-FIG. 1, *a*). This is the developing stele of the radial stem. In about 6 to 8 mm. it separates from the parent stele and its protoxylem occupies a position facing the parent stele. Small metaxylem tracheides then begin to form on the outer side of the protoxylem and engulf it completely. The trace thus increases in size and assumes the structure of the radial stem stele (PL. 1, FIGS. 3, 4).

The protoxylem of the radial stem stele now divides into two; one of the two protoxylems supplies the first petiole (TEXT-FIG. 1, *c*, *d*). The size of the radial stem stele varies in different specimens. Where it is small, its first petiole trace is also small.



TEXT-FIG. 1 — Successive stages (*a* to *k*) in the development of the radial stem (*r.s.*) from a dorsiventral stem (*d.s.*) and the origin of petioles (p1 to p4) from radial stem. The xylem is drawn jet black, small clear spaces enclosed by it indicates the position of the protoxylem. This convention is followed in Text-figs. 2 and 3 also. *l.t.*, lateral trace given out by the dorsiventral stem stele which develops into radial stem stele; *r*, root; *s.b.*, small branch. A reconstruction made from this series is shown in Text-fig. 5. × 48.

This relation in size between these two is well marked.

The first petiole trace eventually separates from the radial stem stele. Immediately afterwards, the stem stele gives out a still smaller monarch trace, which occupies a position between the stem stele and its first petiole (TEXT-FIG. 1, *d, c*). Benson (1911) interpreted this trace as an aphlebia. Its formation may be delayed in some specimens or it may remain adnate to the first petiole. In any case it (" aphlebia " of Benson) passes out of the stem first. Benson mentioned (1911, p. 1050), " There is no evidence that the vascular bundle supplying an aphlebia ever branched "; but I have found in one case that it divides by an equal dichotomy.

Within 1 mm. from this stage, the first petiole passes out of the radial stem which simultaneously separates from the dorsiventral stem (TEXT-FIG. 1, *g, h*).

2. Radial Stem

A radial stem varies from 1·4 to 2 mm. in diameter (PL. 2, FIGS. 7, 8). The epidermal cells are small and bear numerous uniseriate hairs, which are not always preserved in connection with the stem. The hairs are from one to a few cells in height, with expanded bases and attenuating apical cells. The cortical cells appear thick walled and somewhat uniform in size. The endodermis could not be determined with certainty. The pericycle and phloem are not preserved.

The stele varies in size from 0·32 to 0·62 mm. It is somewhat circular in cross-section and consists of small, and more or less uniform tracheides. The protoxylem is not distinguishable, but, as indicated by the history of development of the radial stem, it should be monarch. Small tracheides, as in other species of *Botryopteris*, are taken to denote the protoxylem. The metaxylem tracheides are scalariform or reticulate (cf. pitted tracheides of the dorsiventral stem).

One point of interest should be mentioned here. It is surprising how much structural variation a stem stele may undergo at different levels in the same plant. For example, the stem stele in Pl. 2, Fig. 7 shrinks in size and assumes a somewhat dorsiventral form a little higher up, as shown in Pl. 3, Figs. 9 and 10. Further up, the same stele divides by equal dichotomy (*see* p. 423). Incidentally, this is the only example on record of the dichotomy of the radial stem in *B. antiqua*. Similar dorsiventrality of a radial stem stele is seen in Pl. 3, Figs. 11 and 12, where it bears a circinately coiled young ' leaf '.

The radial stem, after coming out of the dorsiventral one, moves away from it. This is clearly seen in two reconstructions shown in Text-figs. 5 and 6. It gives out petiolar traces in quick spiral succession. Text-fig. 5 shows the origin of four petioles. I have traced the maximum number of six in other specimens and the stem was in no way diminished in size.

The radial stem gives out further petioles in the same manner as the first. The tracheides supplying a petiole become large in size (PL. 2, FIGS. 6, 7). At the junction of the small and large tracheides one protoxylem is situated. The latter divides into two, one of which remains behind in the stem, while the other accompanies the developing petiole. The protoxylem occupies a position on the adaxial side of the petiolar trace.

The petioles pass out gradually through the cortex of the radial stem, with their protoxylem side facing the stem stele. A radial stem has been observed to give out five petioles in quick spiral succession without diminishing in size. In some the first petiole of a radial stem may be larger than the second, but all the petioles of the radial stem are *always* monarch. I believe Dr. Benson is mistaken in her view that *monarch* petioles are preceded and followed by *diarch* petioles. She appears to have confused a dorsiventral stem, which looks like a petiole and shows two protoxylems, with a diarch petiole. The figures she gave for the serial sections observed by her illustrate the region of a dorsiventral stem in connection with a radial stem which has given out its first petiole. She appears to have missed the first stages in the development of a radial stem from a dorsiventral stem and emission of more than one petiole from one and the same stem.

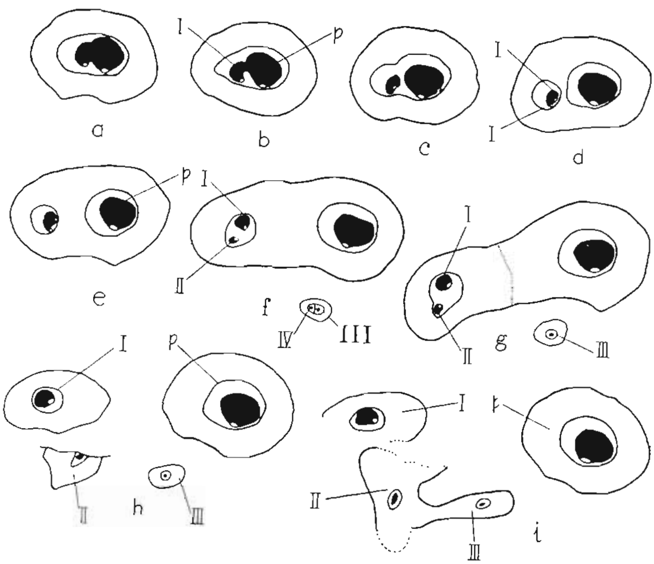
It has now been shown that all petioles of *B. antiqua* are monarch, and what Benson thought as a diarch petiole was in reality a dorsiventral stem.

Roots — Roots come out from radial stem at irregular intervals. When no petioles are developing, the roots radiate out from all round the stem. In other cases, the part of the stem which is free from developing petioles, gives out roots. In Text-fig. 1, *i* and *h*, three roots are seen radiating out of the stem, one of the three is situated opposite the developing branch trace, while the other two flank on its right and left. The roots appear to form roughly in the same position in relation to the developing petiolar trace.

Equal Dichotomy of a Radial Stem — The radial stem shown in Pls. 1, 2 and 3, Figs. 1 to 10 shows equal dichotomy. About 1½ mm. after giving out its second petiole the stem stele decreases rapidly in size and assumes a somewhat dorsiventral form as shown in Pl. 3, Fig. 9. In another millimeter an indentation is formed on the side where the protoxylem is situated (PL. 3, FIG. 10). Eventually, two almost equal xylem lobes, presumably each carrying one protoxylem, are formed. In the next section, two xylem lobes are seen to have separated from one another. Unfortunately, the preservation becomes poor at this stage. One of the xylem lobes looks very much like a stele of a small petiole. It, however, disappears within one millimeter.

This, in my opinion, represents an equal dichotomy of the radial stem. It is interesting to recall that Dr. Kidston also mentioned a case of dichotomy in *B. antiqua*, which, however, he interpreted as a dichotomy of a petiole (KIDSTON, 1908, PL. 45, FIGS. 11, 12). Benson (1911, p. 1048) regarded the specimen as a node of the stem which seems to be correct. Fig. 7 of Kidston is not unlike Fig. 9, Pl. 3 in this paper. After dividing, however, neither looks at all like a petiolar stele. On the other hand, they can very well be two radial stem steles.

Another interesting specimen shows a circinately coiled young frond on a stem (PL. 3, FIG. 11). This radial stem is somewhat dorsiventral at this stage. The tissue of the coiled branch, being very young, is poorly preserved, but small tracheides from the stem stele are seen supplying the young branch. In the next section the young branch disappears, and a mantle of hairs (PL. 3, FIG. 12) appears in its place, which must have served as protective ramenta for the young branch. Although the frond of *B. antiqua* does not possess a flattened lamina (TEXT-FIG. 7), the presence of such a circinately coiled young branch is not without interest. It shows clearly that a coiled young branch like this has nothing to do with a flattened lamina. Besides, it provides one additional point in favour of regarding this plant as a fern.



TEXT-FIG. 2 — The lateral division of the petiole (*p*) I to IV are the branches of the 1st, 2nd, 3rd and 4th orders. In *a* and *b* the petiolar stele gives out a lateral trace (I) which separates from it in *C* and divides in *d*, *e*, *f* to produce a trace for the branch of the II order. In *f* the branch of the III order, which is seen in *g*, *h* and *i*, is seen dividing to produce a branch of the IV order. × 11½.

3. Frond

(a) *Petiole*

I have not been able to trace petioles much further after they left the radial stem. The maximum length traced was 1 cm. in which they showed no sign of branching. The following description is based on detached petioles which could easily be identified by their size and structure.

General Structure — A petiole varies from 1 to 1·4 mm. in diameter and the steles from 0·32 to 0·42 mm. in size. The epidermal cells are small, quadrangular and sometimes bear short hairs. The outer cortex consists of a few layers of somewhat thickened cells, which in longitudinal section are longer than broad. The difference between inner and outer cortex is not so well marked.

The petiolar stele is oval and not so massive as that of a dorsiventral stem (Pl. 4, Figs. 15, 16). The metaxylem tracheides are large and the protoxylem, which, however, is slightly immersed, is not always preserved. The protoxylem tracheides are spirally thickened, smaller metaxylem tracheides are scalariform and the larger ones are pitted.

Branching — The stages in the division of a petiole or rachis are shown in Text-fig. 2.

At the commencement of branching the protoxylem of the petiolar stele divides into two, one of which goes to a protuberance formed laterally on the stele (Text-fig. 2, *a*) and which becomes the stele of the primary branch. Within two millimeters the primary branch stele separates and on its outward course its protoxylem faces the parent stele (Text-fig. 2, *b*, *c*, *d*).

When still enclosed in the cortex of the rachis, the primary branch stele may also begin to divide, exactly in the same way as the petiolar stele and gives out a trace for the tertiary branch (Text-fig. 2, *e*, *f*).

After about 1 to 2 mm. from this stage the primary branch separates from the rachis and simultaneously the secondary branch also comes out of the primary (Pl. 6, Figs. 15, 16; Text-fig. 2, *g*, *h*, *i*). Further up, the primary branch is seen moving obliquely upwards.

All primary branches I have observed produced secondary branches before or immediately after they left the petioles. Detached petioles did not show branching at two places within the distance of 1·8 cm. One petiole was, however, traced through 3·8 cm. and it produced two primary branches at a distance of about 3·2 cm.

(b) *Primary Branch (I Order)*

A primary branch measures nearly 0·48 to 0·7 mm. in diameter and the stele 0·16 to 0·24 mm. in size (Pl. 4, Fig. 16). The cortical cells are large, thin walled and more or less uniform in size. The outer and inner cortical cells do not differ much in size. The stele is somewhat oval and monarch. A primary branch gives out alternate and opposite branches of the II order (Text-fig. 2, *d-h*). The one shown in Pl. 4, Figs. 15 and 16 was traced through 9 mm. right from its separation from the rachis. One secondary branch is seen in Fig. 16. After 5 mm. it gave out its second secondary branch, opposite to the first and continued further for another 2 mm. without branching. It was then lost.

Many detached branches of the same size and appearance as the primary branch showed division at two places. One gave off two alternate and opposite branches at a distance of 8 mm. and continued further for 3 mm. without branching. Another one produced two secondary branches in the same manner at a distance of 7 mm.

Although a primary branch is observed to divide only at two places, there is little doubt that it produced a few more branches before attenuating, because a primary branch hardly diminishes in size after producing two lateral branches.

(c) *Secondary Branch and Further Branches up to V Order*

The epidermis and a part of the cortex was generally missing in my sections. The secondary branches are probably 0·48 to 0·32 mm. in diameter. The cortical cells are thin walled and slightly angular. The stele is nearly 0·08 mm. in size and probably carries one protoxylem. The size of the stele helps considerably in the identification of detached secondary branches.

Text-fig. 2, *i* shows a branch of the III order given out by the secondary branch. In *g* and *h* the former is seen detached and lying on the lower side of the rachis. The branch of the III order is seen divided a little further up into two branches of IV order.

A more complete lateral branching of a secondary branch is shown in Text-fig. 3.

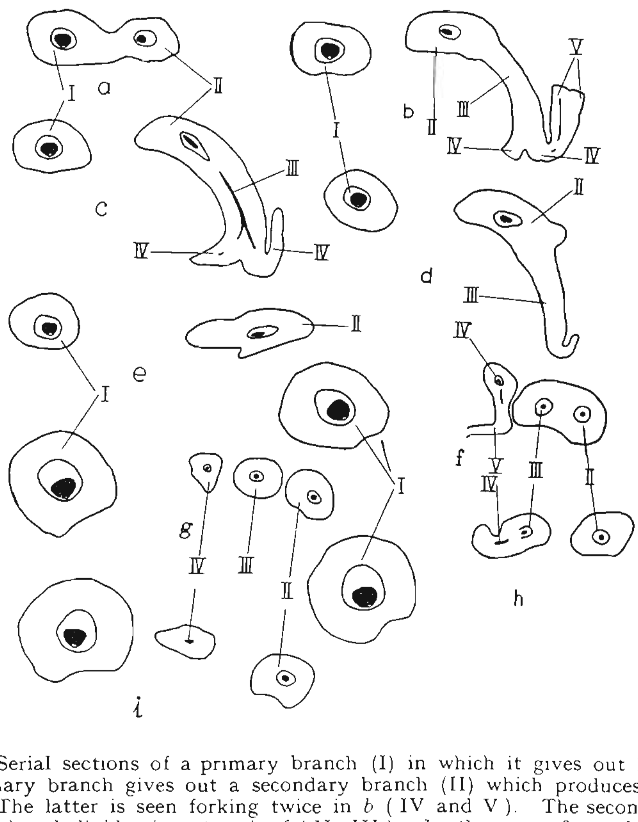
This branch was traced through 9 mm. in which it forked twice and probably ended itself in a bifid lobe.

In Text-fig. 3, *a*, a branch of the I order (with 0·16 mm. stele) is seen giving out a branch of the II order (about 0·48 mm. in diameter). The secondary branch separates from the primary (TEXT-FIG. 3, *d*, *e*) and divides almost equally into two branches. The one which is pushed laterally (*b*, *c*) measures only 0·4 mm. at the base. This is the branch of the III order. Then it bifurcates into two branches of IV order (*c*) and each fork measures 0·3 mm. in diameter. In *b* there is an indication that one branch of the IV order again forked at a distance of 1 mm. from the previous dichotomy.

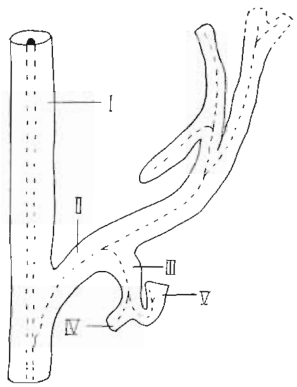
The branch of the II order then proceeds further (*e*), moving away from the primary branch. At a distance of 4 mm. from the latter the secondary branch divides into two by equal dichotomy, each measuring about 0·3 mm. in size (*f*, *g*). Within 1 mm. the branch of the III order gives out a branch of the IV order (*h*). The latter is seen detached in *f* and *g*. The branch of the IV order measured about 2 mm. in length and 0·2 to 0·16 mm. in diameter. The main branch then tapered to about 0·16 mm. and disappeared.

The main branch of the II order continued further for nearly 4 mm. without any change, after which it probably again forked. This fact could not be ascertained because the preservation became poor. However, judging from its size, it appears that its apex was not very far from here.

A reconstruction based on Text-fig. 3 is shown in Text-fig. 4. This specimen showed the ultimate branchlets of a secondary branch in an almost complete form.



TEXT-FIG. 3 — Serial sections of a primary branch (I) in which it gives out lateral branches up to V order. In *a* primary branch gives out a secondary branch (II) which produces a branch of the III order in *b* and *c*. The latter is seen forking twice in *b* (IV and V). The secondary branch (II) then travels forward (*d*, *e*) and divides into two in *f* (II, III). In the same figure branches of IV and V orders are seen. In *g* branch of the III order separates from the II, and in *h*, branch of the IV order is seen fusing with the tertiary branch III. A reconstruction based on this series is shown in Text-fig. 4. ×16½.



TEXT-FIG. 4 — A reconstruction of the lateral branching of a primary branch made from Text-fig. 3. The xylem is shown by broken lines. I to V are the branches from second to fifth orders.

The description given in preceding pages shows a complete sequence of lateral branching of a petiole measuring 1·4 mm. to a smallest branchlet 0·16 mm. in diameter. There is no indication of flattening in any of these branches. The frond of *B. antiqua* (if we may call it by that name), therefore, consisted of a branch system, a diagrammatic reconstruction of which is shown in Text-fig. 7.

The maximum length of a smallest branch observed is nearly 2 mm. and the diameter 0·16 mm. The epidermal cells were not preserved completely. The cortex is only 3-4 cells in thickness and the cells are comparatively large and thin walled. These must have served as a photosynthetic tissue. A few small scalariform tracheides are present in the centre.

Pl. 4, Fig. 18 shows a part of small fragment of epidermis I have obtained from a petiole. What looks like stomata are present rather sparingly and parallel to the epidermal cells.

4. SPORANGIA

In my material I have found sporangia similar to those attributed by Scott (1910) to *B. antiqua*.

The sporangia occur either singly or are preserved close to one another (PL. 3, FIG. 13). In some cases four sporangia are seen lying close to one another, but they do not show any fixed arrangement or attachment to a branchlet or with one another. Scott (1910) in his text-figure showed four sporangia with their annulus inside. I have, however, not found any uniformity in their arrangement and, therefore, I feel a detailed study should be made before one can conclude that the sporangia are borne in groups of four.

Sometimes a number of sporangia are preserved in groups at one place. Is it accidental or does it show that a particular region of a frond was fertile and bore only sporangia ?

A sporangium is oval in cross-section with a maximum diameter of 0·28 mm. When the section passes through the spore cavity, the sporangial wall is seen to consist of some uniformly thickened big cells, tapering rather abruptly towards the end. In a tangential section the big cells are rather hexagonal. These big cells, which Scott (1910) described as " multicellular annulus", appear to extend right round the sporangium, perhaps covering half of its area. A sporangium opens by a stomium at its narrow end (PL. 4, FIG. 17). The spores are smooth walled and show a tetrad scar.

I have not been able to observe a definite connection between a branchlet of *B. antiqua* and a sporangium. The sporangia, however, occur in constant association with small branchlets of *B. antiqua*. Some sporangia suggest connections with badly preserved axes as shown in Pl. 4, Fig. 17, but it is difficult to say definitely whether such branchlets belong to *B. antiqua* or not. However, this suggestion of attachment is always found at the junction of big and small cells of the sporangium wall. In some of these badly preserved ultimate leaf branchlets small tracheides could be made out. From the type of preservation found in some recognizable small branchlets of *B. antiqua* lying near these sporangia, it seems very likely that the badly preserved axes might also belong to the same species. If this connection is true, then it appears that each sporangium had its own short stalk.

Scott (1910) figured a flat plate of cells between two sporangia which he regarded as probable indusium. I have not been able to obtain any evidence in support of this interpretation. In Pl. 3, Fig. 13 some cells are seen lying between some sporangia, but these cells represent badly preserved remains of some finer axes, for in some tracheides are still preserved. Perhaps a sporangium assigned to *B. antiqua* did not possess an indusium.

5. Reconstructions

(*a*) *Reconstructions of Dorsiventral Stems and Radial Stems* — Two semi-diagrammatic reconstructions of dorsiventral and radial stems and some of the petioles are shown in Text-figs. 5 and 6. Text-fig. 5 shows a reconstruction of the specimen from which Text-fig. 1 is made.

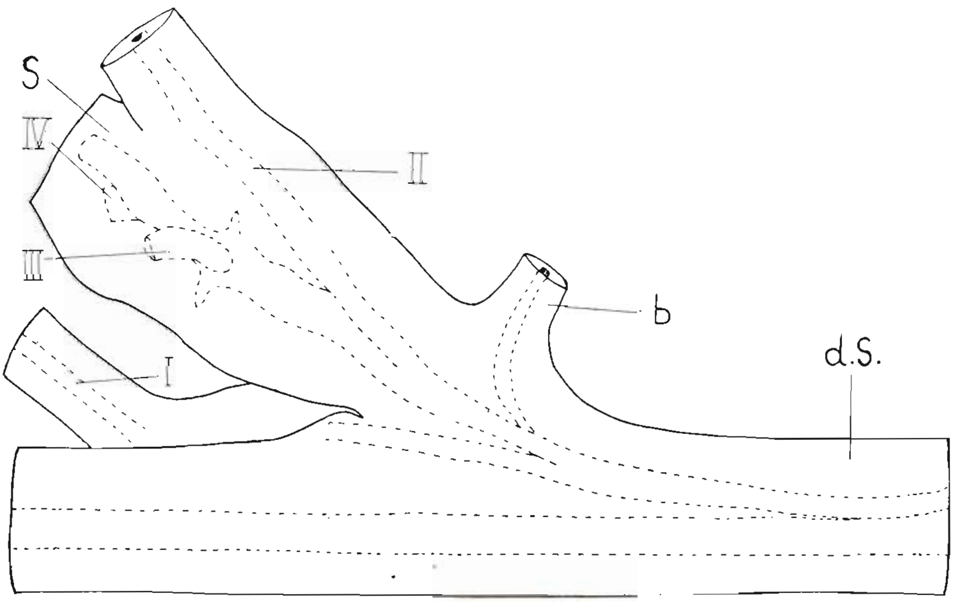
The reconstructions are made by superimposing the sections at levels where they were cut and by joining their outlines. In order to show the deviation of radial stems from the dorsiventral stems, I have drawn the latter straight in my figures. The steles are indicated by broken lines. Roots and hairs are omitted to avoid complications.

In Text-fig. 5, the first petiole (I) is seen coming out from behind the stem (*s*). The small branch (*b*) is attached to the radial stem when the latter was still connected with its first petiole and the dorsiventral stem (*d.s.*). The second petiole (II) comes out from the right side of the stem. In this series, however, only traces of III and IV petioles are seen. The radial stem is moving away from the dorsiventral stem but has not yet assumed erect position.

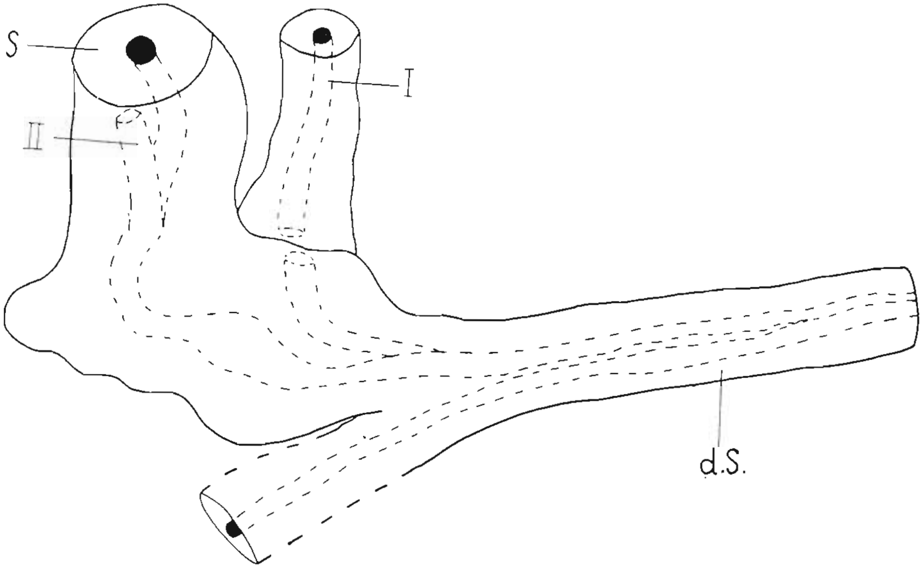
In Text-fig. 6, a dorsiventral stem (*d.s.*) which was giving out a radial stem (*s*) was seen cut obliquely in the series. The radial stem, when it comes out, turns sharply away and assumes an erect position. It is then seen cut transversely in the series. The dorsiventral stem, which was still moving obliquely, disappears soon. The sharp turning of the radial stem from the shoot is seen very clearly in this specimen. The radial stem gives out two petioles. It could not be traced further.

Thus these specimens seem to provide definite evidence that the radial stem turns away from the dorsiventral stem without, in any way, diminishing in size. Obviously, they must have continued their growth further. Does this indicate that these dorsiventral stems were some sort of trailing organs which gave off short, erect or semi-erect radial stems at intervals?

(*b*) *Diagrammatic Reconstruction of the Plant* — A diagrammatic reconstruction of the plant, based on the observations made



Text-fig. 5 — A reconstruction made from Text-fig. 1 The dorsiventral stem (*d.s.*) is drawn straight in order to show clearly the deviation of the radial stem (*s*) I to IV are the petioles given out by the radial stem. The traces of the III and IV petioles are still enclosed in the cortex of the stem. *b*, small branch. × *ca*. 10.



TEXT-FIG. 6 — A reconstruction made from a specimen in 34 series. The dorsiventral stem (*d.s.*) is seen obliquely cut in the series. It gave rise to a radial stem (*s*) which turned sharply away from the dorsiventral stem and then was seen cut in a transverse plane. It produced two petioles (I, II) up to the end of the series. The stem did not diminish in size. × *ca.* 9.

from the material as a whole, is shown in Text-fig. 7.

A dorsiventral stem (*d.s.*) is shown here to have given out a radial stem (*s*) which produces petioles (I). It is not known at what distance from the stem a petiole begins to give out branches, and hence a break is shown. Only two alternate and opposite primary branches are shown on the petiole and similarly two secondary branches are shown on the primary. An almost complete lateral branching, as shown in Text-fig. 4, is drawn here on the first primary branch. The roman figures indicate the order of the branches.

In the inset figure a diagrammatic drawing of a part of the frond is shown on a reduced scale. Only two primary branches are shown on the petiole. A primary branch is presumed to taper upwards. The number of secondary branches drawn on it is purely arbitrary. In any case it gave off more than two. The sequence of lateral branching, as shown in Text-figs. 3 and 4, is taken as a basic unit and is drawn repeatedly on the primary branches. It is, however, presumed that as the primary branch diminished in size, the branches of further orders also became simplified. With these assumptions a branch system or a frond, as shown in the inset figure, is obtained.

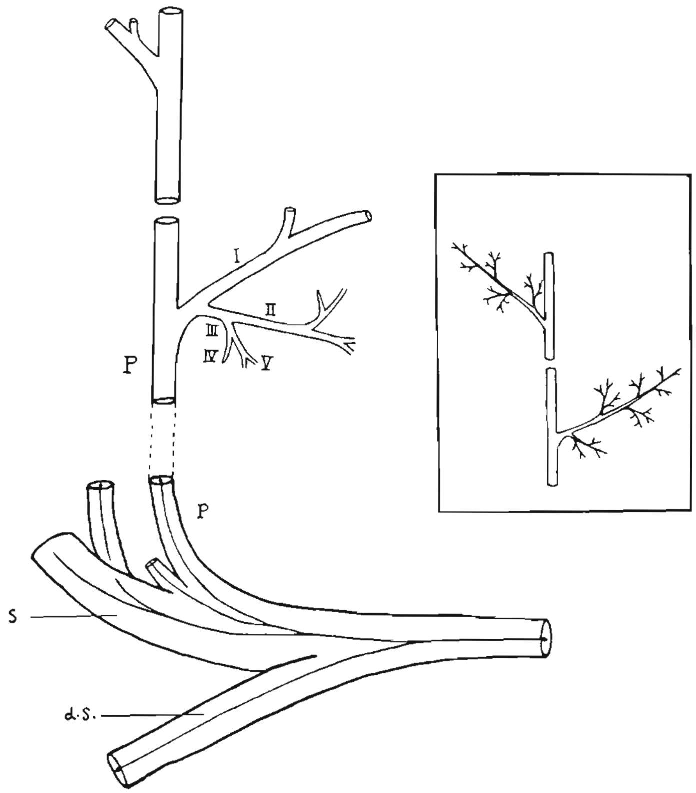
This figure shows that if a branch system of *B. antiqua*, as revealed in Text-figs. 3 and 4, is carried further, it gives an appearance of a frond the like of which is not uncommon among the Lower Carboniferous impressions.

B. Botryopteris ramosa

The origin of radial stem from a dorsiventral stem agrees even in close details. From Dr. Scott's figure (1920, p. 339, FIG. 150) I suspected a similar origin for the radial stem of *B. ramosa*. The following observations are based on the examination of Dr. Scott's slides kept in the British Museum.

The Fig. 150 of *B. ramosa* in Dr. Scott's book (1920) is drawn from slide No. 2314. Here the stem is seen to have given off a number of roots and, according to Dr. Scott, two leaf traces ; lt_1 is directed differently from the leaf trace lt_2 (which faces the stem stele). The leaf trace lt_1 shows the orientation of a dorsiventral stem in a similar condition, in *B. antiqua* and *B. hirsuta*.

This is supported by what is seen in slide No. 2313, which shows an earlier stage than the one in Fig. 150. In slide 2313 the so-called leaf trace lt_1 is seen giving off a lateral trace, which is formed from one of the outer



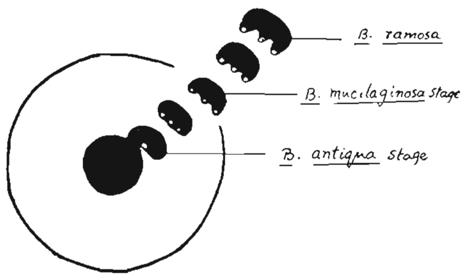
TEXT-FIG. 7 — A diagrammatic reconstruction of a part of *B. antiqua* plant. The dorsiventral stem (*d.s.*) is shown as a trailing organ which gives rise to a radial stem (*s*) turning up slowly. The roots and hairs are omitted. On one petiole (*p*) branches up to V orders are drawn as observed in serial sections and shown in Text-fig. 4. In the inset figure a diagrammatic reconstruction of a part of frond is shown on a reduced scale (*ca.* nat. size). $\times 2\frac{1}{2}$.

xylem teeth of the stele, and this lateral trace developed into the stem stele, as seen in Fig. 150 (slide No. 2314). This is what happens in *B. antiqua* and *B. hirsuta*. Therefore, what Scott called the " leaf trace " lt_1 is really a dorsiventral stem, which produced the radial stem seen in Fig. 150 (SCOTT, 1920, p. 339).

Another interesting point is shown by Dr. Scott's slides of *B. ramosa*. Out of the three protoxylems of the dorsiventral stem (leaf trace lt_1) the central one is the main protoxylem, which appears to have supplied the two protoxylems to its right and left. This is exactly how a dorsiventral stem behaves in *B. antiqua* and *B. hirsuta*. In Scott's slide No. 2314, so far as I can see, the " leaf trace " lt_1 (SCOTT, 1920, FIG. 150) has only two protoxylems — the third one, as seen in slide No. 2313, had supplied the stem to which it had given rise. In slide No. 2315, which is cut at a higher level than the slide No. 2314, the stem is seen to have separated from the dorsiventral stem (" leaf trace " lt_2) and has produced another leaf trace. In slide No. 2316, the main protoxylem of the dorsiventral stem (" leaf trace " lt_1) is seen to have divided and produced a protoxylem, obviously to take the position of the one which supplied the stem. It is, thus, the main protoxylem on the central arm of the " leaf trace " lt_1 which restored its triarch condition. This is what happens in *B. hirsuta* also.

Thus, the origin of a radial stem from a dorsiventral stem is almost similar in *B. antiqua*, *B. hirsuta* and *B. ramosa*.

One more point of interest shown by Dr. Scott's slides on *B. ramosa* is the origin of a triarch leaf trace (petiole). I have illus-



TEXT-FIG. 8 — A diagrammatic representation of the development of a leaf trace in *B. ramosa* showing the evolution of a tridentate leaf trace of the Coal Measure species from a monarch trace as that of *B. antiqua*.

trated this point diagrammatically in Text-fig. 8. In *B. ramosa* a leaf trace possesses a single, median, endarch protoxylem at the time of its separation from the stem stele. The leaf trace at this stage resembles the one in *B. antiqua*, where this condition remains permanent (" *B. antiqua* stage " in TEXT-FIG. 8). A little higher up the median protoxylem gives off two protoxylems right and left and the trace thus becomes triarch. Then the three protoxylems protrude gradually on three small teeth, a stage which becomes permanent in *B. mucilaginosa* (KRAENTZEL, 1933). Three teeth of the trace then become more prominent and it assumes the adult form of the petiole of *B. ramosa*.

Thus, a trace of *B. ramosa* perhaps repeats in its development the stages of its own evolution.

COMPARISONS

1. COMPARISON WITH THE IMPRESSIONS FROM THE LOWER CARBONIFEROUS

The frond of *B. antiqua*, as reconstructed in Text-fig. 7, is not complete enough to be identified with any of the Lower Carboniferous impressions.

One of the genus with which the frond of *B. antiqua* shows resemblance is *Rhodea* (KIDSTON, 1923). This genus consists of fern-like leaves with capillary segments. One of the most comparable species is *R. Smithi*, in which the manner of branching, particularly in distant segments, seems very similar to *B. antiqua*. Both bear ramuli of up to about the fifth order. However, *R. Smithi* appears to be a bigger leaf with a petiole up to 4 mm. wide, while that of *B. antiqua* only reaches 2 mm. in diameter.

2. COMPARISON OF *Botryopteris* SPECIES

The stem of *B. antiqua* is the smallest in size as Table I shows.

TABLE I

NAME OF SPECIES	NORMAL SIZE OF STEM	NORMAL SIZE OF PETIOLE	NORMAL SIZE OF PETIOLAR STELE
	mm.	mm.	mm.
L. Carboniferous			
B. antiqua	1·4–2·0	1·0–1·4	0·3–0·42
Lower Coal Measure			
B. cylindrica	2·0–2·5	1·5–1·3	0·45×0·3
B. hirsuta	2·0–3·0	2·0–3·0	0·8 ×0·5
B. ramosa	3·0–6·0	2·0–3·0	?
B. mucilaginosa	6·0–7·0	3·5×3·0	0·63×0·48
Upper Coal Measure			
B. Renaulti	Unknown	7·0×4·5	3·3×1·8
B. forensis	7·5	5·0–8·0	2·4

Although the stems of *Botryopteris* species show a progression in size, it cannot be said that they show progression in structure as well. The stems are protostelic with central protoxylems. The tracheide pittings vary from scalariform to reticulate. In the stem of *B. antiqua* the scalariform tracheides predominate; in *B. cylindrica*, *B. hirsuta* and *B. ramosa* a mixture of scalariform and reticulate tracheides occur.

In *B. cylindrica* there are two types of stems called *a* and *b* types; the *a* type is larger and more complex than the *b* type which resembles the stem of *B. antiqua*. In type *a* the inner tracheides are smaller and in this respect is more advanced than *B. antiqua*.

In the production of a petiole only one protoxylem of the stem stele is concerned. In *B. antiqua* this protoxylem remains as it started and hence the trace remains monarch. In *B. cylindrica* it is at least in part similar to *B. antiqua*. Bancroft mentions diarch petioles in *B. cylindrica*, but I have not been able to detect a clear sign of diarchy in the figures given by her for petioles. This point needs confirmation.

Benson (1911, p. 1051) postulated that Botryopteridean leaf trace passed through a diarch stage in its evolution from a monarch to triarch condition. I do not think so. Diarch petioles did not exist in *B. antiqua*, nor most probably in *B. cylindrica*. I believe that the triarch leaf trace was evolved directly from the monarch leaf trace as that of *B. antiqua*. Text-fig. 8 gives an idea how this could have happened. The single median protoxylem was simply split into three and were protruded out on three arms, thus producing the triarch leaf trace of Coal Measure species of *Botryopteris*. A similar thing might have happened with dorsiventral stems also.

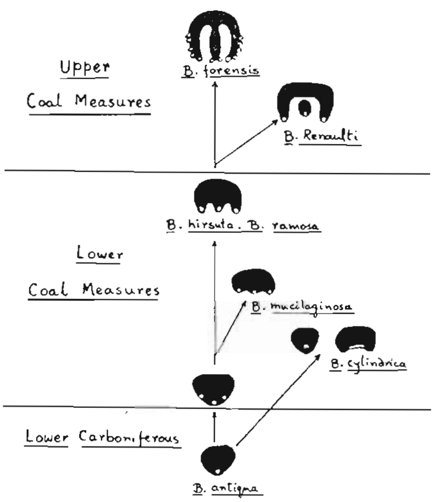
I believe this is how Coal Measure species of *Botryopteris* could have evolved from their ancestral type, *B. antiqua* of the Lower Carboniferous age. Thus *B. antiqua*, *B. mucilaginosa*, *B. hirsuta* and *B. ramosa* form a progressive evolutionary series (TEXT-FIG. 9).

There is evidence that *B. antiqua*, *B. cylindrica* and *B. hirsuta* have no flattened lamina. In *B. forensis*, however, a flat lamina exists.

The sporangia attributed to *B. antiqua* are very much like those of *B. ramosa*, *B. hirsuta*, *B. cylindrica* and *B. forensis*.

I have not investigated *B. forensis* and *B. Renaulti* (CORSIN, 1937), but I have included them in Text-fig. 9 for the sake of completeness. It seems to me that these occupy natural positions in the evolutionary series of the genus.

My work does not, however, throw any new light on the relation of *Botryopteris* to other families. The classification of *Botryopteris* has changed from time to time. I consider that the classification of Bertrand (1941) fits the facts known to me.



TEXT-FIG. 9 — The evolution in the genus *Botryopteris* as indicated by the form and structure of the leaf traces.

MORPHOLOGY AND HABIT OF THE PLANT

1. RADIAL STEM AND ITS BRANCH SYSTEM

While studying *B. antiqua* I always encountered the difficulty of classifying some of its organs into distinct morphological categories as we understand them in modern plants. The radial stem offers no difficulty, but the frond is difficult because it has no flattened part that can be called a lamina and the dorsiventral stem is peculiar.

The rachis of the frond produces branchlets of successive orders which are better designated by numbers rather than as " pinnae " and so on. In *B. antiqua* terminal forking is confined only to the higher region of the frond, whereas in its lower parts, lateral and unequal dichotomy has prevailed. As a result, a branch system in one plane, similar in appearance to a frond, is formed. Such a branch system should be viewed as one of those showing transitional forms between an indeterminate, dichotomous branch system of more primitive types, such as that of Psilophytales, and fully evolved, expanded, dorsiventral leaf of more advanced types.

2. DORSIVENTRAL STEM

This is an organ somewhat similar in appearance to a petiole of the radial stem, but different in function, for it gives rise to a radial stem and nothing else. This behaviour of the organ was not known to Kidston or to Benson. Kidston, therefore, described it as a petiole and Benson as a " diarch petiole ", since she found that it possessed two protoxylems. As in the preceding pages it is clearly shown that, although looking like a petiole, it gives rise to a stem, the question then arises, what is its real morphology ?

I believe a dorsiventral stem was regarded as a petiole by previous authors for two reasons:

(1) A petiole seemed the only available category of organ once the radial stem was clearly recognized. It was studied in isolated sections and when found in connection with a radial stem, the dorsiventral stem was regarded as a large petiole.

(2) Its similarity in appearance to the petiole of the same plant.

As for the first reason, we now know the complete history of the branching of a dorsiventral stem. In my material I have found that it invariably gives rise to a radial stem and to no other structure. If it were a petiole giving rise to adventitious buds, it should have shown pinnae in some of the many specimens examined.

Again, a dorsiventral stem produces a radial stem laterally, and, therefore, its protoxylem is always directed away from the stem stele; whereas the protoxylem of a petiole always faces the stem stele. This different orientation of the dorsiventral stem from the normal petioles of the stem was explained as due to its swinging round (SCOTT, 1920) and was consequently confused with the normal petioles. In *B. hirsuta* also the so-called " main petiole " (LONG, 1943), which produces a stem laterally, has its protoxylems directed away from the stem while those of the petioles face the stem stele as in *B. antiqua*.

The second reason for regarding a dorsiventral stem as a petiole is the resemblance of its stele with a petiolar stele which, no doubt, is a strong one. But even here on close examination the differences between them become evident.

The stele of a dorsiventral stem is massive in appearance (0·48 to 0·72 mm. in size as against 0·4 to 0·32 mm. of a petiole) and possesses wide tracheides. I have not found a single radial stem which produces petioles as massive as dorsiventral stems. Long (1943) mentions the same for *B. hirsuta*.

In *B. antiqua* the dorsiventral stems are sometimes found to possess two or three protoxylems when dividing. Benson mistook such a stem with two protoxylem for a " diarch petiole ". The dorsiventral stem, however, is essentially monarch though it may possess one or two accessory protoxylems (" pôles sortants " of Corsin). They can be interpreted as belonging to the lateral traces, which would develop into radial stems. This is actually seen in one of my series of sections.

The products of division of a petiole and a dorsiventral stem are again quite different as shown in Text-figs. 1, 2 and 3. The petiole gives out only pinnae, whereas the dorsiventral stem produces a radial stem bearing petioles and roots. Such differences in behaviour and structure in these two organs (dorsiventral stem and petiole) do not permit us to regard them as being one and the same.

The equivalent of a dorsiventral stem in *B. antiqua* is designated by Long (1943) as a main rachis in *B. hirsuta*. This is the fundamental difference in our interpretations and other differences follow necessarily from this. In *B. hirsuta* a lateral trace given out by the " main rachis " is called a " common trace ", because it supplied a " pinna " as well as " bud ". The " bud " is equivalent to a radial stem and the " pinna " to the first petiolar trace of the stem in *B. antiqua*. In *B. hirsuta*, Long interprets the stem as a " bud " occupying a subaxillary position between the main rachis and the pinna.

It should be borne in mind that all the radial stems observed in *B. antiqua* (as well as in *B. hirsuta*) have been found to originate from organs like a dorsiventral stem. This was, therefore, a normal mode of growth in the plants concerned. It is rather difficult to imagine that a branch system like the one shown in Text-fig. 7 could support the weight of " buds ", roots and their entire branch systems. In my opinion, it is more likely that a dorsiventral stem, whatever may be its nature, acted as a trailing organ, which gave rise to radial stems (bearing fronds and roots) at favourable intervals.

The fact that the radial stem bears its petioles in a $\frac{2}{5}$ phyllotaxis from the beginning makes it natural to regard it as a stem bearing a series of equivalent leaves. I do not think anyone knowing these facts would regard the first of these leaves as a pinna of the dorsiventral stem. The same appears to be true of *B. ramosa*.

For these reasons I could not regard what looks like the first petiole of a radial stem as a " pinna " of the dorsiventral stem and consequently the dorsiventral stem as a " rachis ". Unless its petiolar nature is decisively proved, it will be better to keep the organ producing a radial stem under the category of " stem ".

It should be mentioned here that its dorsiventral stele is not against this interpretation, for dorsiventrality in fern stems is not unknown (VERDOORN, 1938, p. 25). It is, for example, found in *Hymenophyllum serecium* of the Hymenophyllaceae, which shows striking similarity in many structural respects to the Botryopterideae (BOWER, 1928, Vol. II, p. 248; TANSLEY, 1907, p. 112). Moreover, a radial stem of *B. antiqua* sometimes assumes dorsiventrality in the same plant, as seen in Pl. 3, Figs. 9 and 10, which shows that a step from a radial to a dorsiventral structure is not a great one in this plant. However, it should be noted that a dorsiventral stem has not been observed to give out roots or petioles as an ordinary stem would be expected to do. Neither it has been established yet (and which is more important) that it gives rise exclusively to radial stems. It has been observed to branch only once in *B. antiqua* as well as in *B. hirsuta* (LONG, 1943).

In conclusion we may say that for the present our knowledge about this organ still remains incomplete. It is not known how it originates, nor do we know whether it gave rise to stems exclusively, or behaved in some different way, although I believe that all radial stems in *B. antiqua* as well as in *B. hirsuta* originated from this organ. Long traced the organ (in *B. hirsuta*) for 6 cm., but even then it did not divide for the second time. In *B. antiqua* I have observed it to branch only once. These are the gaps in our knowledge which must be closed before any definite conclusion is reached about the real morphology of this organ. For the present, however, I thought it better to include this organ under the term "*dorsiventral stem*".

3. HABIT OF THE PLANT

The tiny plant of *B. antiqua* appears to have flourished in humid, shady places as an epiphyte on other plants or a creeper on the ground of a thick forest. The dorsiventral stem probably served as a runner. At favourable spots it gave rise to a short radial stem which was erect or semi-erect. The radial stem bore crowded petioles in spiral succession and roots. The radial stem sometimes underwent equal dichotomy. The bulk of the stem remained larger than the leaves it bore because of the crowded petiolar traces developing in the stem cortex. The leaves branched repeatedly in a pinnate manner, the ultimate branchlets being almost as thin as hair's ends with no flat lamina. The sporangia were borne at the tips of these branchlets.

The dorsiventral stem in *B. antiqua* appears to be an organ leading to vegetative spread of the plant in a manner analogous to the small plants of today in the undergrowth of forests.

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EXPLANATION OF PLATES

PLATE 1

1. Figs. 1 to 10 show the development and further branching of radial stem from a dorsiventral stem. The specimen is from 58 series. In this figure the dorsiventral stem stele (*d*) has given out a lateral trace consisting of bigger (*p*1) and smaller (s) tracheides. × 55.

2. Small tracheides which belong to the developing radial stem (*s*) have increased in number and have engulfed the protoxylem. × 36.

3. The tracheides of the radial stem as well as that of the petiole have increased further. × 30.

4. The first petiolar trace (*p*1) is separating from the radial stem (*s*) stele which is still enclosed in the cortex of the dorsiventral stem. × 30.

PLATE 2

5. The first petiolar stele (*p*1) has separated from the radial stem stele (*s*) and has also given out a small branch trace (*b*). × 20.

6. Further up the petiole and the radial and dorsiventral stems have separated from one another. Second petiole (*p*2) is seen developing at $\frac{2}{3}$ angular divergence. × 20.

7. Shows further development of the second petiole (*p*2) which is nearly of the same size as the first. The radial stem has given off some roots. × 18.

8. A radial stem of a small variety of *B. antiqua*. It had given out its first petiole seen on its right side. The second petiolar stele is coming out from the stem stele and shows immersed position of the protoxylem. × 38.

PLATE 3

9. Shows the condition of the radial stem stele after it has given out second petiole as shown in Fig. 7. The stele is somewhat flattened with the protoxylem occupying asymmetrical position. × 30.

10. The radial stem stele at a higher level than in Fig. 9. It is dividing by equal dichotomy as shown by the arrow. The radial stem stele eventually divides into two small somewhat dorsiventral steles. × 43.

11. An oblique section through a radial stem (*s*) bearing circinately coiled young 'leaf' (*Y.l.*). The radial stem developed from a dorsiventral stem at the lower level. × 41.

12. Shows a mantle of hairs on the radial stem (*s*) which formed a protective ramenta over the circinately coiled young 'leaf' shown in Fig. 11. × 55.

13. A group of sporangia attributed to *B. antiqua*. × 60.

PLATE 4

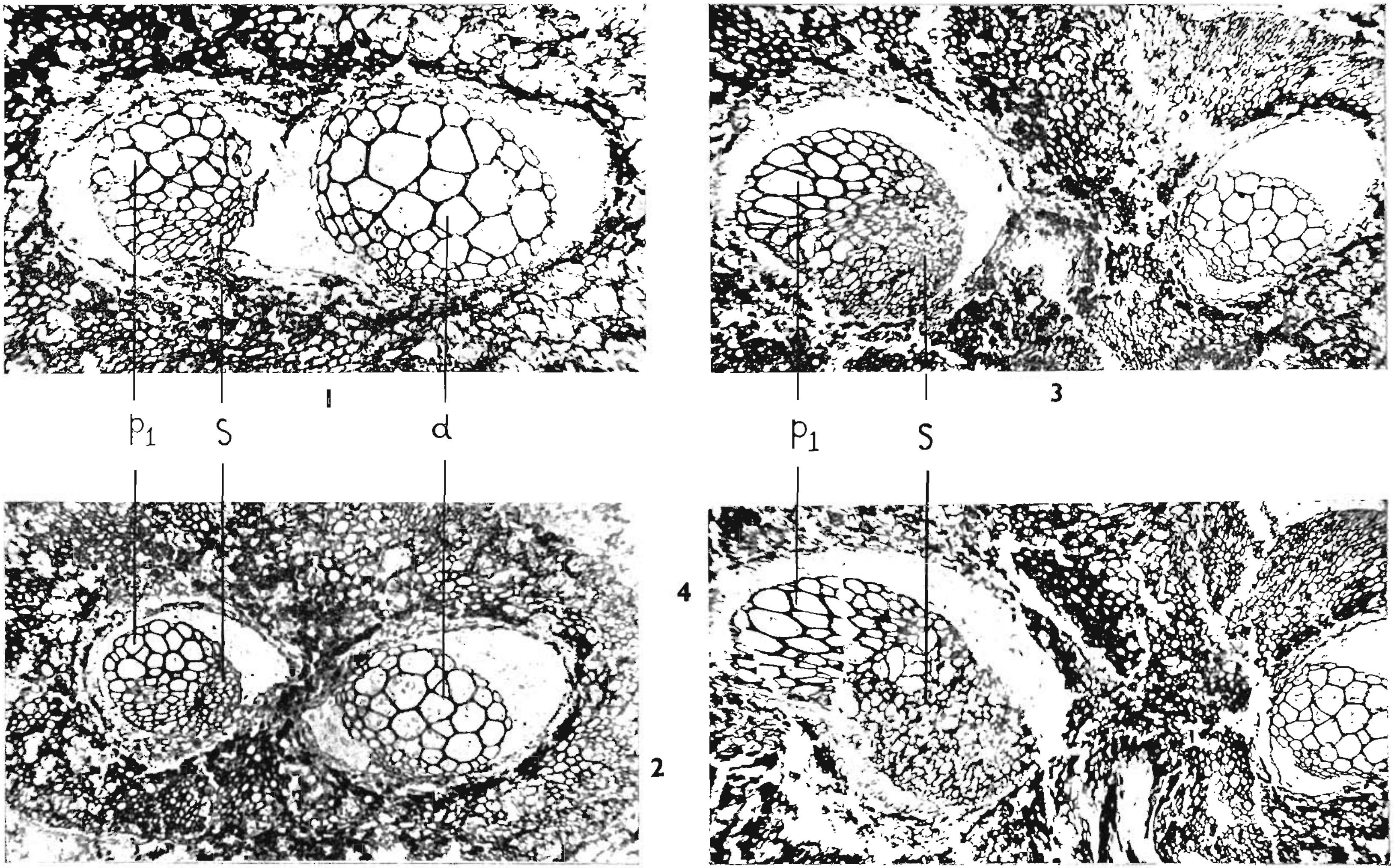
14. The stele of a dorsiventral stem which is giving out a lateral trace (*s*) magnified to show three protoxylem groups (1, 2, 3). × 116.

15. A petiole (*p*) which has given out a primary branch (*sb*). × 35.

16. The petiole shown in Fig. 15 cut at a higher level. The secondary branch (*sb*) while passing out of the petiole has given out a tertiary branch (*t*). × 48.

17. A sporangium attributed to *B. antiqua* attached at the apex of the stalk which is very badly preserved. The opening of the sporangium is seen on the left-hand side. × 225.

18. A part of epidermis showing a stoma. × 488.



1
2
3
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p_1
S
d
p_1
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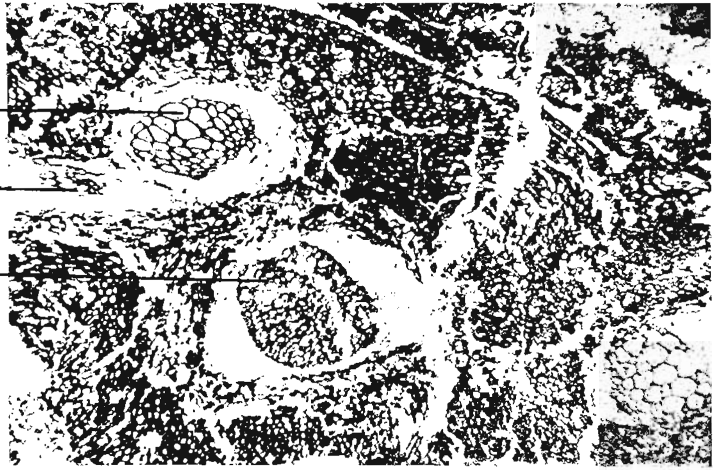
6



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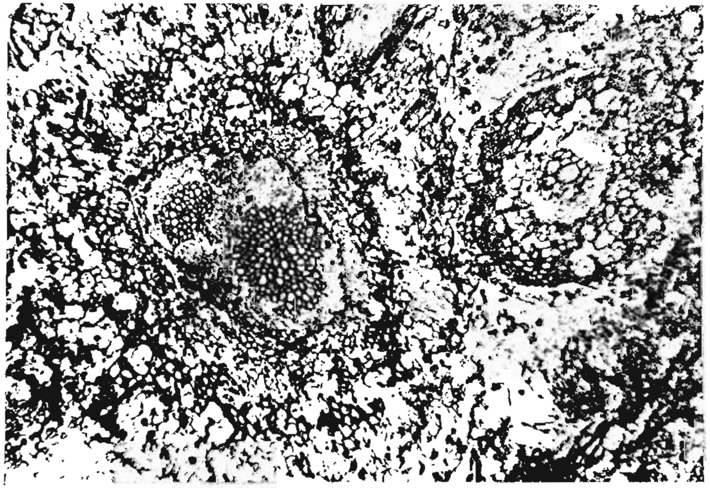

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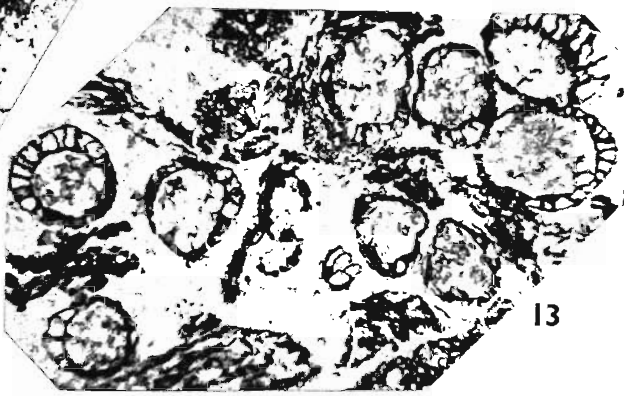

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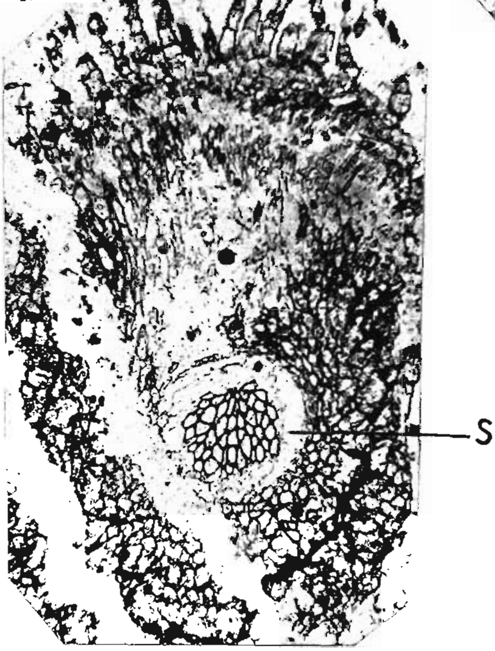

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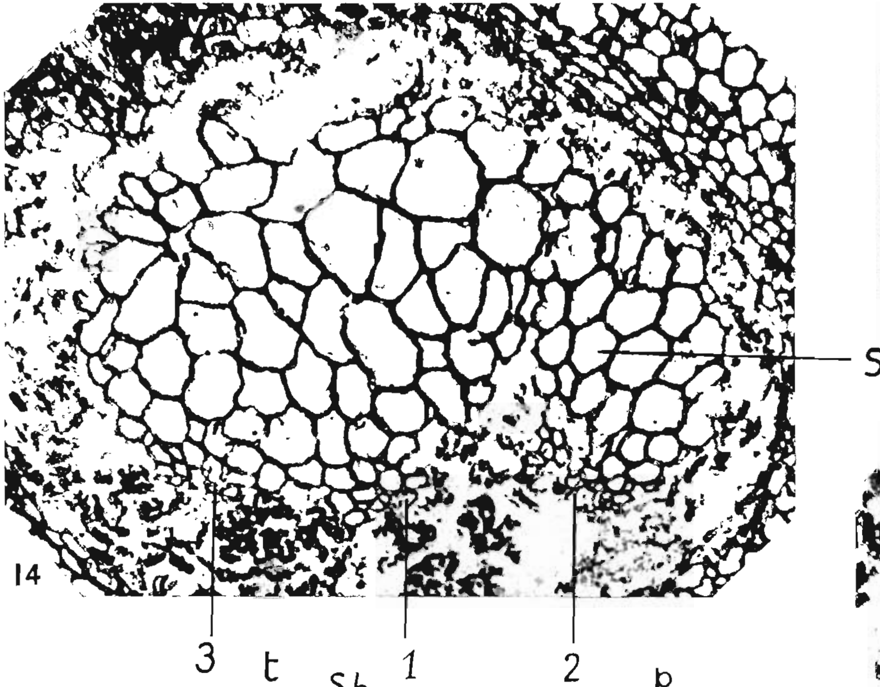

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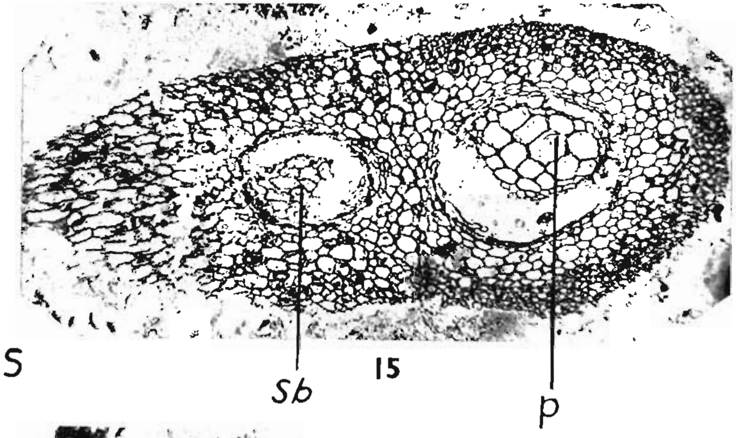

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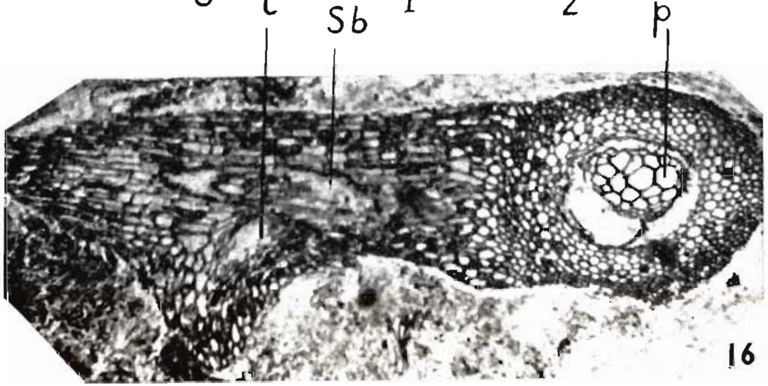

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