

THE MORPHOLOGY OF *STAUROPTERIS* *OLDHAMIA* BINNEY

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ABSTRACT

The mode of branching of the frond of *Stauropteris oldhamia* Binney, previously described up to the rachises of the 4th order (BERTRAND, 1907-9) has now been described up to the minute tips, viz. the rachises of the 5th and 6th orders.

The aphyllae are shown to be branched structures, consisting of up to 13 divisions which arise by fundamentally dichotomous branching. The aphyllal divisions have a fibrous structure and are supplied with minute vascular strands. The morphological nature of the aphyllae is discussed.

In the light of the present findings a new reconstruction of a part of the frond of *Stauropteris oldhamia* is given.

INTRODUCTION

THE fossil plants *Stauropteris oldhamia* Binney from the Upper Carboniferous and *Stauropteris burntislandica* P. Bertrand from the Lower Carboniferous consist of a repeatedly branched frond, the daughter branches or rachises of which arise successively in pairs on either side of the rachis. The stem is still unknown in both the species. In 1941 Darrah reported one more species *S. americana* from N. America; the status of this imperfectly known species is uncertain.

The detailed branching of the frond of *S. burntislandica* has been elucidated by Surange (1952) who gave a reconstruction of part of the frond up to the dichotomous ultimate segments. The dichotomous form of the aphyllae has been demonstrated by Lacey *et al.* (1957). The work of Surange (1952), Lacey *et al.* (1957) and Chaloner (1958) has shown that this species was heterosporous. The branching of the frond of *S. oldhamia* was described up to rachises of the 4th order by Bertrand (1907, 1909) but he did not trace the branching up to the ultimate divisions, nor did he describe the form of the aphyllae. The reconstructions of part of the frond published by Hirmer (1927) and Walton (1940) appear to have been based on Bertrand's work, and the

pinnately arranged ultimate segments and simple aphyllae shown in these reconstructions would appear to be hypothetical. There is no evidence that *S. oldhamia* was heterosporous.

In view of the difference in geological age and the possible difference in the mode of reproduction between the two species, coupled with close similarities in anatomy and gross morphology, it was felt desirable to elucidate certain aspects of frond morphology in *S. oldhamia* in order to compare the two species more critically than has so far been done.

The material used in this investigation came mainly from a portion of a coal-ball from the Upper Foot seam, Shore, Littleborough, Lancashire. It contained abundant, well preserved specimens of *Stauropteris oldhamia*. About 180 peel sections were taken by the well known method of Joy, Willis & Lacey (1956). The peels were mounted temporarily in xylol for examination.

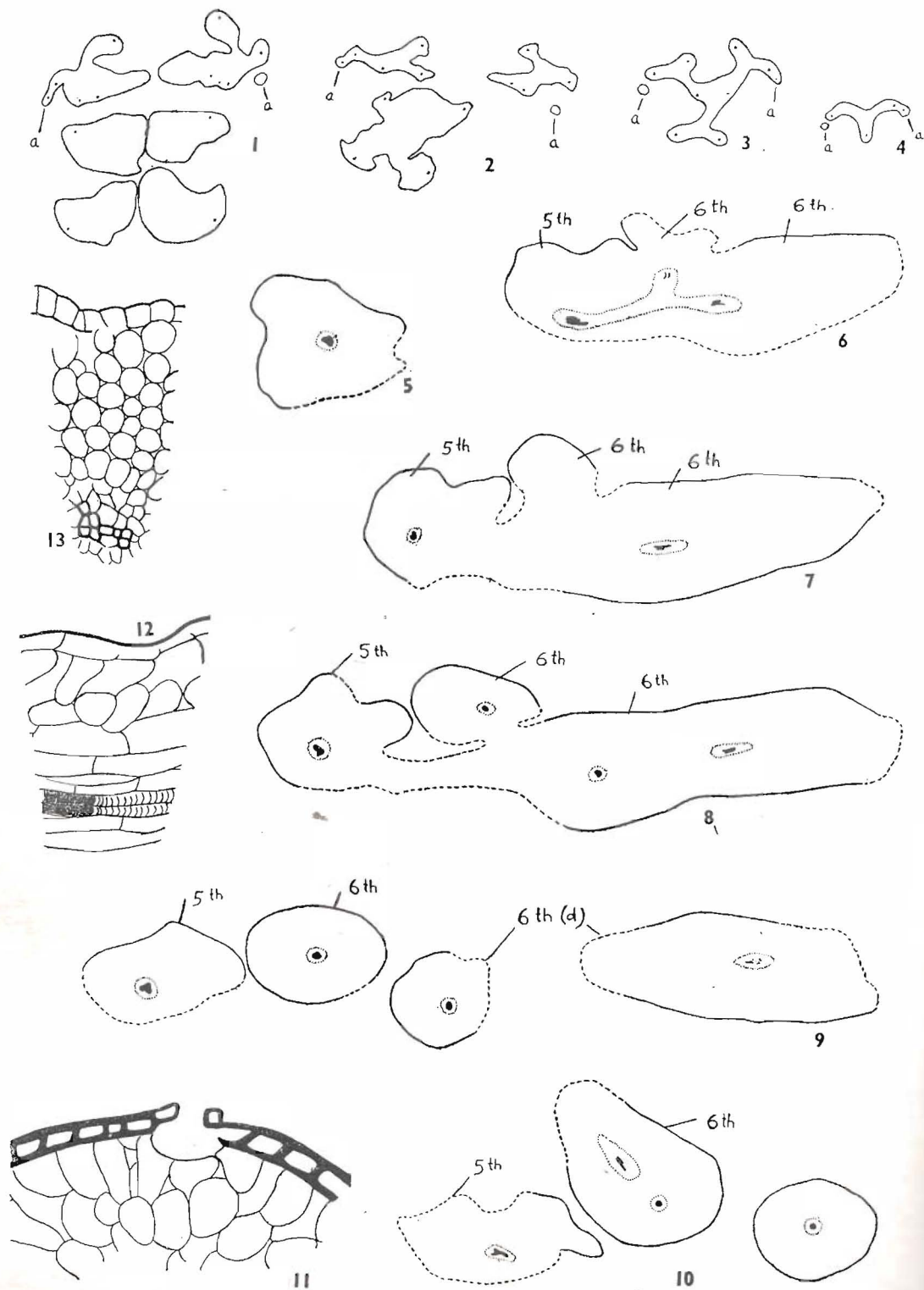
Models of the aphyllae were made by tracing the outlines of the camera lucida drawings on to sheets of wax with a ball pen. The numbered portions were then cut out with a pointed scalpel, stacked in order and sealed.

DESCRIPTION

Observations on the mode of branching and anatomical details of the frond up to the rachises of the 4th order confirm those of Bertrand (1907, 1909).

The rachises of various orders may be recognized chiefly by their size (as shown in Table 1), the characteristic form of the vascular system and to some extent by the mode of emission of lateral rachis traces.

The stages in the branching of the main (1st order) and 2nd order rachises are similar. In both, the aphyllal traces are given out from the pair of branch steles after their separation from the parent stele (FIGS. 1-2). In the branching of the 3rd



TEXT-FIGS. 1-13

TABLE 1

| RACHISES | AVERAGE DIAMETER AND RANGE (BASED ON 8 SPECIMENS) |
|---------------------|---|
| Main rachis | (1.24-) 2.33 (-3.41) mm. |
| Rachis of 2nd order | (0.99-) 1.58 (-2.16) mm. |
| Rachis of 3rd order | (0.66-) 0.83 (-1.00) mm. |
| Rachis of 4th order | (0.41-) 0.45 (-0.49) mm. |
| Rachis of 5th order | (0.33-) 0.37 (-0.41) mm. |
| Rachis of 6th order | (0.16-) 0.20 (-0.24) mm. |

and 4th order rachises, however, the aplebial traces are given out before the separation of the branch steles (Figs. 3-4).

In rachises of 1st, 2nd and 3rd orders the pair of branch traces depart from the parent stele as a "bar", but in the 4th order rachis they arise separately.

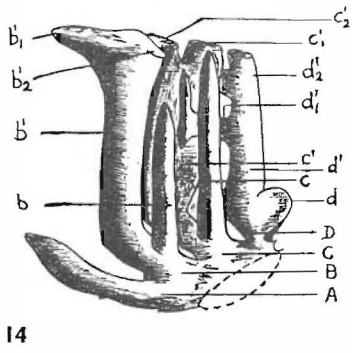
Rachises of 5th and 6th Orders — The branching of the 5th order rachis is basically comparable to that of the rachises of lower orders, but it is simpler and amounts virtually to trichotomy. One division of the trichotomy represents the continuation of the 5th order rachis whilst the other two, somewhat weaker, divisions represent a pair of 6th order branches. One of the specimens studied in detail is illustrated in figures 5-10. This shows the branching of the 5th as well as the 6th order rachises. Figure 5 shows the 5th order rachis below a point of branching. In figures 6 and 7 a pair of branches are seen which represent 6th order rachises. In this particular specimen one of these branches divides into two at the base, in fact before it has separated completely from the parent (5th order) rachis (FIG. 8). The other branch divides only after some distance (about 0.6 mm.) above its insertion (FIG. 10). Judging from other specimens observed, this latter condition is normal. The forked 6th order rachises probably represent the ultimate divisions of the frond, but in all

observed specimens the ends eventually become poorly preserved and fade out. The 5th order rachis in the specimen illustrated after giving off the pair of branches continues for about 1 mm. and then itself fades out in a similar manner. No specimen of a 5th order rachis has been observed to give off more than one pair of laterals.

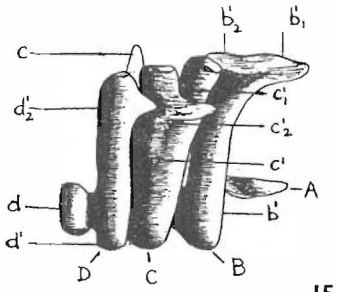
The anatomical structure of the 5th and 6th order rachises is simpler than that of rachises of lower orders. The epidermal cells are comparatively thick walled and the cells of the cortex are isodiametric and thin walled with intercellular spaces. There is no differentiation of the cortex into an inner zone of thick walled cells and an outer region of spongy tissue (parenchyma) which is such a characteristic feature of the rachises up to the 4th order. The stele consists of a few scalariform tracheids surrounded by thin walled compactly arranged cells (Figs. 12 and 13), there is apparently no differentiation into protoxylem and metaxylem. The differences between the 5th and 6th order rachises are slight: the 5th order rachis besides being somewhat larger is slightly lobed in cross section whereas the rachis of the 6th order is characteristically circular; also, the outer cells of the cortex in the 6th order rachis are usually slightly radially elongated and somewhat palisade-like (FIG. 11) whereas in the 5th order rachis there is no such differentiation of cortical cells. Although many sections have been examined only a small number of stomata have been seen (FIG. 11). It is concluded, therefore, that stomata were probably scarce. However, Bertrand figured satisfactorily a few stomata in surface view on what were probably 5th or 6th order rachises.

The Aplebiae — The traces of the aplebiae arise from the steles of the daughter branches and move outwards through the cortex taking a course obliquely backwards away from the daughter steles, so that the aplebiae themselves tend to be inserted on

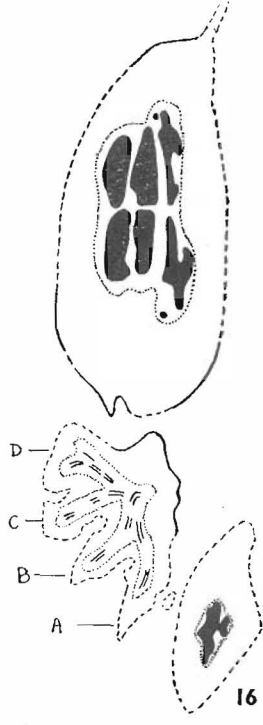
TEXT-FIGS. 1-13 — *Stauropteris oldhamia* Binney. 1-4. Transverse sections through the branching steles of the 1st, 2nd, 3rd & 4th order rachises to show the origin of aplebiae traces (a). 1, peel 85. $\times 20$; 2, peel 74. $\times 29$; 3, peel 66. $\times 50.5$; 4, peel 175. $\times 50.5$; 5-10. Series of transverse sections showing stages in the branching of 5th and 6th order rachises, 6th (d) represents the divisions of the 6th order rachis. 5, peel 142; 6, peel 135; 7, peel 133; 8, peel 130; 9, peel 125; 10, peel 108. All $\times 50.5$. 11. Transverse section of a part of 6th order rachis showing stoma. Peel 144. $\times 210$. 12. Longitudinal section of a part of 6th order rachis. Peel 111. $\times 210$. 13. Transverse section of a part of 5th order rachis. Peel 119. $\times 210$.



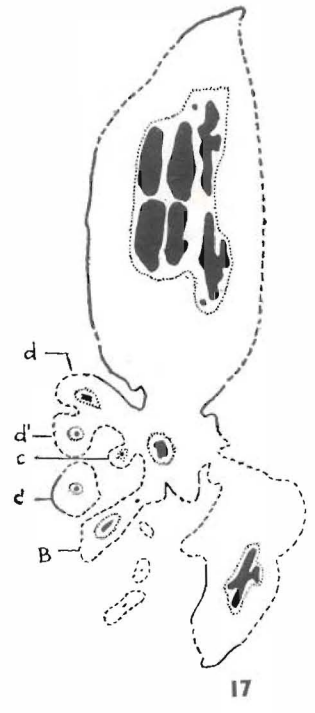
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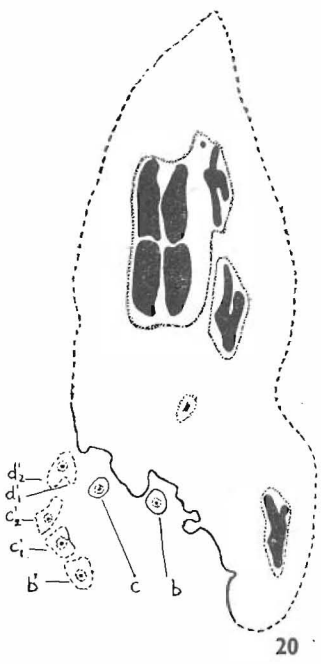
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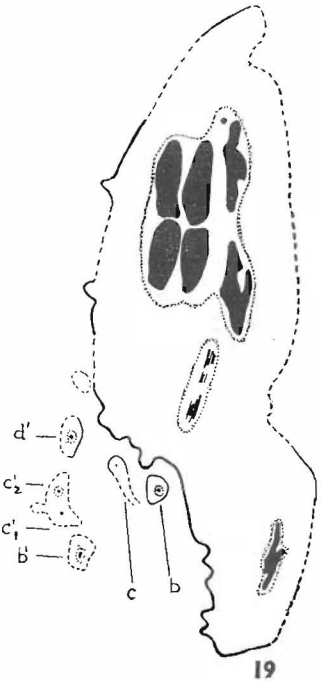
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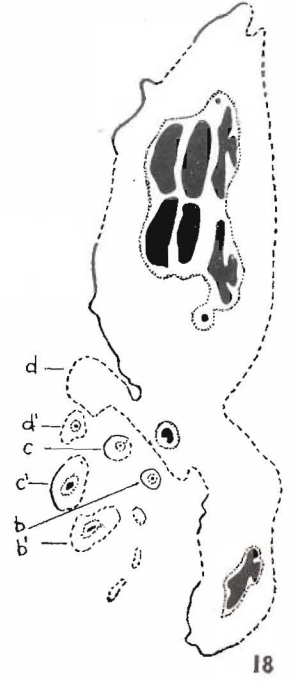
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19



20

TEXT-FIGS. 14-20

the main axis rather than on the bases of the daughter branches (FIG. 26). Surange (1952) noted the same in *S. burntislandica* and explained it by saying that the angle of divergence between the daughter stele and its aphlebial trace was greater than 90°.

A number of branching regions of the rachises of the 1st, 2nd, 3rd and 4th orders have been observed, two examples of each having been studied in detail by carefully following the axes through serial peels.

A model (FIGS. 14, 15) based on a series of camera lucida drawings of the aphlebia of one side on the 1st order rachis was prepared to illustrate the form of the aphlebia. In this example the aphlebia divides very near the base (FIG. 16) to give rise to four main divisions A, B, C and D by dichotomous branching in the horizontal plane. The division A appeared to remain undivided as far as it could be traced, but this portion was rather poorly preserved. The division B almost at once dichotomises in a vertical plane to give rise to divisions *b* and *b'* (FIG. 17). Of these the division *b'* finally dichotomises again after a distance of about 2 mm. to give rise to *b'₁* and *b'₂* (FIG. 22), while *b* remains undivided. The behaviour of the division C is somewhat similar to B (i.e. it dichotomises to give rise to divisions *c* and *c'* at about the same level as B), but in this case the dichotomy of the outer member *c'* occurs at a lower level (after a distance of 0.3 mm.) as seen in figure 19, and one of its forks *c'₂* forks again after a distance of 1 mm. (FIG. 22). The division D also dichotomises at the base to give branches *d* and *d'* (FIG. 17), but the branches lie in the horizontal plane instead of a vertical one. Branch *d* does not appear to divide further but like division A at the other side of the aphlebia, it is not well preserved. Branch *d'* forks at about the same level as *c'* to give rise to *d'₁* and *d'₂* (FIG. 20) and these each fork again near the tips (FIG. 21).

Thus this aphlebia shows altogether 13 distinct divisions which are a result of up to

TABLE 2

| RACHISES | EX. | NO. OF DIVISIONS | | NO. OF DICHOTOMIES | AVERAGE DIAMETER OF DIVISIONS |
|-----------|-----|------------------|----------------|--------------------|-------------------------------|
| | | Aph. 1 | Aph. 2 | | |
| 1st order | 1 | 13 | 5 | 3, 4 or 5 | 0.49 mm. |
| | 2 | 6 | not determined | 5 | |
| 2nd order | 1 | 7 | 3 | 2 or 3 | 0.33 mm. |
| | 2 | 4 | 2 | | |
| 3rd order | 1 | 3 | 2 | 1 or 2 | 0.16 mm. |
| | 2 | 2 | 2 | | |
| 4th order | 1 | 2 | 2 | 1 | 0.12 mm. |
| | 2 | 2 | 2 | | |

5 dichotomies, a 5th dichotomy occurring in one case.

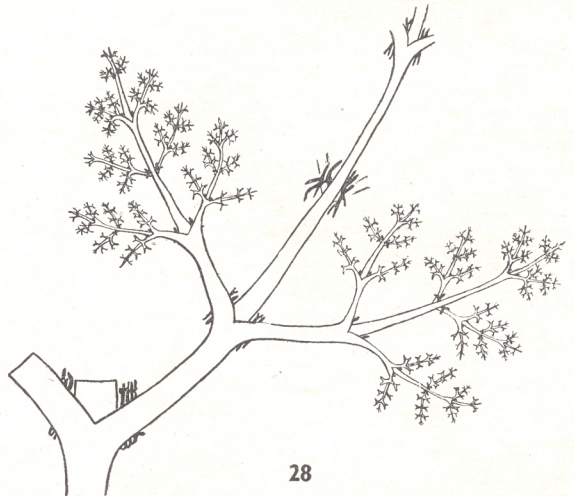
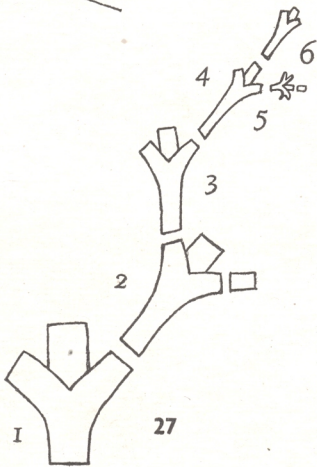
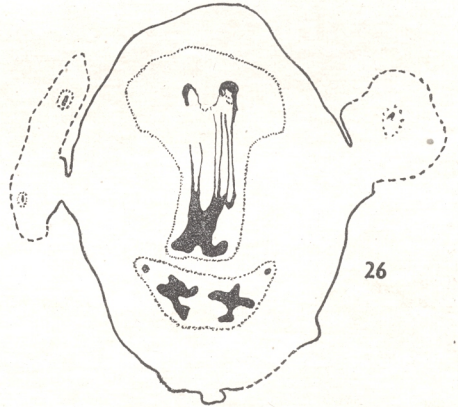
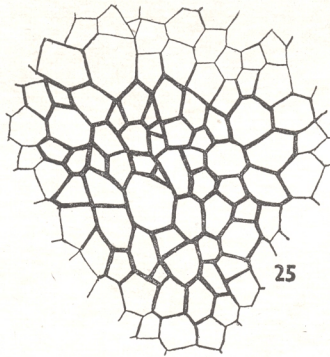
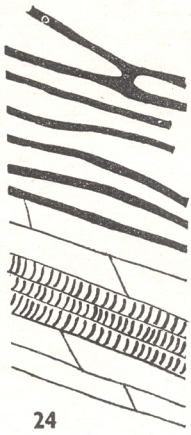
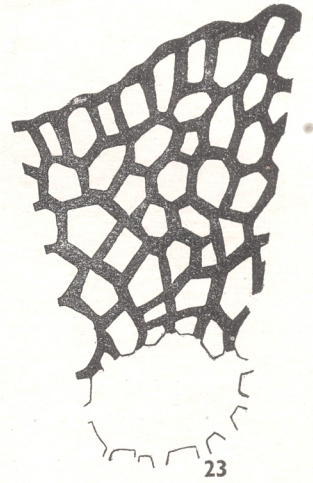
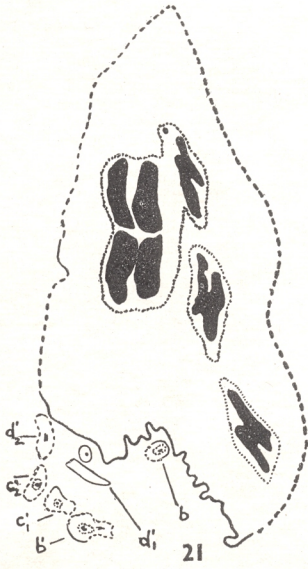
The other member of the same aphlebial pair appears to bear only 5 divisions, but it is not so well preserved. Variations in the form of the aphlebiae of other rachises are recorded in Table 2.

The aphlebiae are thus complex structures with 2-13 divisions which appear to represent a dichotomous system. The vascular system also branches in a dichotomous fashion and supplies each division of the aphlebiae with a small strand of tracheids.

Table 2 indicates a gradual reduction in the size and complexity of the aphlebiae from the rachises of the 1st order up to the rachises of the 4th order. The rachises of the 5th and 6th orders do not possess any aphlebiae.

The aphlebiae traces at the time when they have separated from the daughter steles consist of a small mass of protoxylem and metaxylem tracheids surrounded by thin walled cells (FIG. 25). However, the protoxylem is not recognizable after a short distance. The divisions of the aphlebiae are circular in cross section. The epidermal cells are comparatively thick walled. The cells of the cortex are thick walled, angular

TEXT-FIGS. 14-20 — *Stauropteris oldhamia* Binney. 14, 15. Diagrammatic representation of a model of the aphlebia of one side of the 1st order rachis to show the abaxial (14) and adaxial (15) view of the form of the aphlebia. 16-20. Series of transverse sections through a branching region of the 1st order rachis to show the origin, mode of departure and branched nature of the aphlebia of lower side. The vascular tissues of the main axis, its branches and aphlebia traces are all shown in solid black. 16, peel 29; 17, peel 31; 18, peel 32; 19, peel 35; 20, peel 38. All × 8.5.



TEXT-FIGS. 21-28

and compactly arranged without intercellular spaces (FIG. 23). In longitudinal section (FIG. 24) the cells of the cortex are elongated. The vascular supply consists of a few strands of small scalariform elements surrounded by thin walled cells elongated longitudinally.

The aplebiae therefore appear to have been non-photosynthetic and, judging from their fibrous structure, strong and rigid, perhaps like thorns or spines in present day plants. In structure the aplebiae are markedly unlike the ultimate divisions of the frond with which they are comparable in size.

Reconstruction of the Frond — The reconstruction of the frond as shown in figure 27 is based on the observations made on the detached rachises of various sizes. The rachises of different orders show a fine graduation in size which suggests that the frond tapered gradually. The various rachises show a definite relationship with one another.

The distance between the two alternate pairs of branches on the main rachis has not been determined but judging from a specimen which ran obliquely through the block and which has been traced through the series of peels, this internodal length was probably in excess of 5 cm. This specimen had a pair of 2nd order rachises attached at one end, but at the other (approximately 5 cm. distant) its anatomy still showed no indication of the approach of another point of branching.

The second, partly hypothetical, reconstruction (FIG. 28) implies that the various rachises, as they branch, diminish in size continuously until they end as ultimate forking divisions, so that even the main rachises terminate as simple axes equivalent in size, and presumably structure, to 6th order rachises. No rachis has been traced far enough to demonstrate this progressive diminution in size and simplification of structure. If the frond was however, of limited apical growth, like the frond of most living ferns, it is difficult to envisage how the morphology could have been otherwise.

Comparison with S. burntislandica — Surange (1952) gave a detailed comparison of the two species up to the 4th order rachises.

The 5th order rachises in both species are similar. The stele consists merely of a few tracheids surrounded by thin walled cells. The only difference is that in *S. oldhamia* the cortex is thicker than in *S. burntislandica*.

As regards the 6th order rachis the outermost cortical cells in *S. oldhamia* are slightly elongated radially and form a kind of palisade layer, whereas in *S. burntislandica* the cortical cells are all round.

In both species the aplebiae are dichotomous axis-systems. In *S. oldhamia* there occurs a gradual reduction in the form and size of the aplebiae from rachises of the 1st order up to the rachises of the 4th order.

DISCUSSION

The new observations on *S. oldhamia* have strengthened the view that this species is closely similar in general morphology and anatomy to the older species *S. burntislandica*. No further information has been obtained concerning the reproductive organs. Many sporangia associated with the vegetative remains have been observed during the course of the work, but all the sporangia were of the same kind, although some contained spores and others had dehiscence. Some were attached to stalks having the typical structure of ultimate divisions of the frond.

A number of views have been expressed regarding the morphological nature of the aplebiae of *Stauropteris*. According to Scott (1920), Bower (1935) and Surange (1952), the aplebiae are emergences or enations, the morphological equivalent of the 'leaves' of *Asteroxylon* or *Psilophyton*. According to Browne (1935) although aplebiae may be branched with a dichotomous vascular supply (now demonstrated in *S. burntislandica* and *S. oldhamia*) they may still represent merely the microphyllous emergences comparable to those of *Asteroxylon*

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TEXT-FIGS. 21-28 — *Stauropteris oldhamia* Binney. 21, 22. Continuation of the transverse sections commencing from Fig. 16. 21, peel 42; 22, peel 47. $\times 8.5$. 23. Transverse section of a part of an aplebial division showing thick-walled angular cortex cells. Peel 32. $\times 210$. 24. Longitudinal section of a part of an aplebial division showing scalariform tracheids surrounded by thin-walled cells. Peel 29, $\times 210$. 25. Transverse section of aplebia trace after its departure from the branch stele. Peel 175, $\times 210$. 26. Transverse section through a branching region of 2nd order rachis to show insertion of aplebiae. Peel 23. $\times 20$. 27. Diagrammatic drawing to illustrate the successive orders of rachises. 28. Diagrammatic reconstruction of a part of the frond.

and *Psilophyton*. Zimmermann (1938) and Lam (1948) on the other hand believe aplebieae to be of telome character. In 1957 Lacey, Joy and Willis interpreted the aplebieae in *S. burntislandica* as condensed and overtopped dichotomies.

The aplebieae of the Zygopteridaceae borne on the 'phyllophore' or main rachis of the frond, may be compared, especially in their position in relation to the main branches or pinnae, to the aplebieae on the repeatedly branched frond of *Stauropteris*. In the Zygopteridaceae the aplebieae are vascularized and their traces always depart from the pinna trace and not from the parent (phyllophore) stele; here they have been interpreted (e.g. SAHNI, 1928) as the 1st pair of pinnules borne on the pinna. Further, in *Rhacophyton zygopteroides* Leclercq (1954) the lowest pair of secondary pinnae on the fertile frond are inserted in a position comparable to that of the aplebieae in other Zygopterids, and are at the same time different in form and branching from the succeeding secondary pinnae. These organs may well be compared with the aplebieae in other zygopterids. In *Stauropteris*, however, there are no organs that can be called pinnae, as the frond is not pinnately branched. The aplebieae therefore can hardly be regarded as pinnae, unless it is supposed that the frond form in *Stauropteris* has been secondarily derived from a pinnate organization. There is no evidence that

this is so. If the aplebieae is to be interpreted therefore as a telome system, it can be regarded as representing one shank of a dichotomy, the other of which is represented by one of the branch rachises. This interpretation implies that much morphological 'telescoping' has occurred in the phylogeny of the *Stauropteris* frond, as the paired arrangement of the branch rachises must already represent one basal dichotomy. It is surprising that in the older species (*S. burntislandica*) the aplebieae traces of the 1st and 2nd order rachises arise not from the daughter branch steles but from the parent stele, a condition which, if this telomic interpretation is correct, would appear to be more advanced than that found in *S. oldhamia* where the aplebieae traces always arise from the daughter rachis steles.

Surange (1952) has discussed the systematic position and probable affinities of *Stauropteris*.

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The peels are preserved in the Botany Department, Imperial College, London.

REFERENCES

- BERTRAND, P. (1907). Principaux caractères de la frond du *Stauropteris oldhamia* Binney. *C.R. Acad. Sci. Paris*. **145**: 147-9.
- Idem (1909). Etudes sur la fronde des Zygopteridées. Texte et Atlas. *Lille. Danel*.
- BOWER, F. O. (1935). Primitive Land Plants. *London*.
- BROWNE, I. M. P. (1935). Some views on the Morphology and Phylogeny of the leafy vascular sporophyte (cond.). *Bot. Rev.* **1**: 427-47.
- CHALONER, W. G. (1958). Isolated Megaspore tetrads of *Stauropteris burntislandica*. *Ann. Bot. (Lond.) N.S.* **22**: 197-204.
- DARRAH, W. C. (1941). The coenopterid ferns in American coal balls. *Amer. Mid. Nat.* **25**: (2); 233-269.
- HIRMER, M. (1927). Handbuch der Paläobotanik; I. *München und Berlin*.
- JOY, K. W., & WILLIS, A. J. & LACEY, W. S. (1956). A Rapid Cellulose Peel Technique in Palaeobotany. *Ann. Bot. (Lond.) N.S.* **20**: 635-37.
- LACEY, W. S., JOY, K. W. & WILLIS, A. J. (1957). Observations on the Aplebieae and Megaspore tetrads of *Stauropteris burntislandica*, P. Bertrand. *Ann. Bot. (Lond.) N.S.* **21**: 621-25.
- LAM, H. J. (1948). Classification and the New Morphology. *Acta Biotheor.* **8**: 107-54.
- LECLERCQ, S. (1954). An Upper Devonian zygopterid showing clepsidropsid and eptapteroid features. *Am. Jour. Bot.* **41**: 488-92.
- SAHNI, B. (1928). On *Clepsydropsis australis*. A Zygopterid Tree Fern. etc. *Phil. Trans. R. Soc. B.* **217**: 1.
- SCOTT, D. H. (1920). Studies in Fossil Botany. I. *London*.
- SURANGE, K. R. (1952). The Morphology of *Stauropteris burntislandica* P. Bertrand and its Megaspore tetrads *Bensonites fusiformis* R. Scott. *Phil. Trans. Roy. Soc. B.* **237**: 73-91.
- WALTON, J. (1940). Introduction to the study of Fossil Plants. *London*.
- ZIMMERMANN, W. (1938). Phylogenie. In Manual of Pteridology. Ed. F. Verdoorn. *The Hague*.