

II. *Studies in the Morphology of Spore-Producing Members.*—III. *Marattiaceæ*.\*

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Received May 27,—Read June 17, 1897.

[PLATES 7–11.]

INTRODUCTION.

IN the two Memoirs of this Series already published, I have dealt with the spore-bearing members of the Equisetineæ, of the Lycopodineæ (including Psilotaceæ and Isoeteæ), and of the Ophioglossaceæ. We must now take up the case of the remaining class of Pteridophyta, viz., the Filicineæ. Of the two sub-classes into which it is divided, I propose to leave the Hydropterideæ for the present on one side, and discuss first the sub-class of homosporous Ferns.

In a previous paper ('Annals of Botany,' vol. 5, p. 109), I have advanced what appear to me to be good reasons for the opinion that the Eusporangiate Ferns represent a more primitive type than the Leptosporangiate. Accordingly, I propose first to take into our detailed consideration the sori of the Marattiaceæ, and it is to them that the present Memoir will be devoted.

I shall assume that those who are interested in this subject will have already made themselves acquainted with the general theoretical position which has been disclosed in the two earlier Memoirs of this series, and I shall not, therefore, recapitulate my views here. But in stating in detail the facts relating to the Marattiaceous sorus, I shall endeavour so to state them as to avoid theory, and reserve the theoretical treatment for separate sections of the text, apart from those which are descriptive.

DANÆA.

Though various writers have contributed to our knowledge of the development of the sori in other genera of the Marattiaceæ, *Danæa* has been left almost untouched: doubtless, this is mainly due to the difficulty of securing suitable material; but it is

\* Part I. of these Studies appeared in 'Phil. Trans.,' B, 1894, pp. 473–572 (Plates 42–52): of Part II. only an Abstract was published by the Society (see 'Roy. Soc. Proceedings,' vol. 59, p. 137); the full paper was published independently by the Author (DULAU & Co., London), 1896.

strange that these difficulties have not sooner been overcome, for on grounds of general comparison it would appear to be an important form. The mature condition, however, has been repeatedly described; and the general characters of the genus are well known.\* I do not propose to discuss the vegetative organs, but merely note that in *D. simplicifolia* (RUDGE), the leaf is simple, and of ovate-lanceolate outline; in other species, however, it is simply pinnate. The fertile leaves resemble the sterile in outline, but are of smaller area, while the greater part of their lower surface is occupied by the large cake-like sori, which lie parallel to one another, and follow the course of the straight nerves from the enlarged midrib towards the margin. In various species it has been noted that the leaf may be only partially fertile, and in these the regular uniformity of outline of the sorus may be departed from, as it is also occasionally in the normal fertile leaf. The sori may be found to be abstricted (Plate 7, fig. 1, *a.*, arrow), and the single sorus may be divided into two or more parts in a somewhat irregular fashion (fig. 1, *b.c.*). This has been noted in various species. The resulting sori are frequently of circular outline, having a single series of sporangia disposed in a ring round a central point. This is virtually identical with the arrangement of the sporangia in the sorus of *Kaulfussia aesculifolia* (BLUME).

The details of structure of the sorus have been represented by KUNZE (*loc. cit.*, Tab. 28) for *D. stenophylla* (KUNZE), and by MARTIUS (*loc. cit.*, vol. 11). More elaborate drawings, though perhaps less correct in detail, are those of FRANCIS BAUER, in HOOKER'S 'Genera Filicum,' vol. 7; the description of them is, however, obscured by the peculiar use of the term "indusium." But the best drawings are those of GREVILLE (HOOKER and GREVILLE, 'Icones Filicum,' vol. 1, p. 18) of *D. alata*, which represent correctly the main points of structure of the mature sorus. From these sources it is apparent that the sorus consists of two rows of confluent sporangia, the loculi of which are separated from one another by complete septa, while they dehisce by distinct pores upon the outer, free surface. Each sorus is inserted above a single nerve, and between the sori, plates of tissue arise from the surface of the leaf; these plates, which have been described as indusia, are enlarged upwards so as partially to cover the sori (compare 'Genera Filicum,' Tab. 7, figs. 2, 4, 6). With insufficient data such as these before us, and without any facts of development, we must begin the investigation of the sori of *Danaea*.

The material used was of *D. elliptica* (SMITH), collected by Mr. ELLIOT, in St. Vincent, and forwarded to me through Mr. GEORGE MURRAY, and *D. alata* (SMITH), sent to me by the late Dr. TRIMEN. The characters of these species are well known; the sori were found to be essentially similar in the two species, except that the number of loculi in *D. alata* is much smaller than in *D. elliptica*. If the sporophyll of the latter species be cut so as to traverse the sori transversely, the outline appears

\* HOOKER, 'Synopsis Filicum,' p. 442; MARTIUS, 'Flora Brasiliensis,' Fascic. 23, p. 154; HOOKER, 'Gen. Filic.,' Tab. 7; PRESL, 'Suppl. Tent. Pterid.,' p. 33; KUNZE, 'Farnkräuter,' pp. 55 and 107, &c., &c.

as in fig. 2, in which are seen inserted on part of the expanded lamina three indusia (*i.*), and alternating with them two sori (*s.*), the latter being seated above respective vascular bundles (*v.b.*). It will be noted how large are the indusia, and how they partially overarch the margins of the sori. The latter each show two loculi, or sporangia, limited by a wall, which consists in the mature state of several layers of cells, of which the outermost is considerably thickened; the sorus to the right has been so cut as to traverse the pores of dehiscence, which are thus seen to lie close to the septum. If sections be cut parallel to the surface of the leaf, so as to traverse the sori, they appear as in fig. 3; three sori are there seen closely fitted round by the indusia. It will be noted that the loculi vary in size, arrangement, and form, those at the end of the sorus deviating far from the ordinary roughly rectangular outline. Lastly, if a section be cut, so as to traverse the length of the sorus, it would appear as in fig. 4, in which the vascular bundle runs below its whole length, while the indusium (*i.*) overlaps the ends in very much the same way as the velum, or indusium of *Isoetes*; in part the section has traversed the pores of dehiscence, but in part of it the loculi appear closed. While we thus recognise the main features of the sorus, it should be at once noted that deviations of detail are frequent; the most noteworthy is the occurrence of incomplete septa (fig. 5), which appear not uncommonly as flanges of tissue running partway across the cavity of a sporangium; they are sometimes found, as in our illustration, running from the outer wall inwards; sometimes they are attached to the sides of the loculus. These incomplete flanges may be compared structurally with those in the sporangium of *Isoetes* (compare 'Phil. Trans.,' B, 1894, fig. 116, *x*), where, instead of free trabeculæ, the sterile tissue projects from the lateral wall as a partial septum into the sporangial cavity.

From these drawings a general idea of the structure of the sorus may be derived. The next step will be to give such details of its development as the material at disposal would allow. It is to be regretted that I have not been able to observe the earliest stages, but as the essential features are found to be very similar to those of *Marattia* and *Kaulfussia*, this is not, perhaps, of so great moment. We will at first discuss the development of normal sporangia, leaving on one side, for the present, those abnormal cases above noted, which have, however, a very special interest.

The earliest condition of the sorus which I have observed is such as is shown in fig. 6, which traverses the sorus vertically, and follows its longer axis; here the sporogenous groups are already of considerable size, while their arrangement is such that, as regards their origin, they are readily referable, together with the superficial cells which cover them, to a single parent cell. This may be called the superficial parent cell; it was doubtless of deep oblong form, with its longer axis perpendicular to the surface, and one of its ends flush with the outer surface. It is, however, impossible to decide from stages so late as this, what the actual succession of segmentations in this parent cell has been, and whether the archesporium is or is not defined finally by the first periclinal wall in the original parent cell. A point, which

is of some interest is the very considerable variety of bulk of the sporogenous groups of successive loculi; this is obvious in fig. 6, which represents three sporangia taken at random. No two of these show the same details of segmentation; the most prominent difference is in their width; the depth of them, however, and the thickness of the tissue which will form the outer wall is almost constant. In figs. 7, *a, b, c*, other cases are shown for comparison; in *c*, the sporogenous group appears only about one-half the size of that in *a*; these differences of bulk have an important bearing, which will be explained below. Though, in the large majority of cases, the sporogenous group, together with the cells of the wall covering it, are thus referable to a single parent cell, examples are to be seen where this cannot be recognised. A case of this is shown in fig. 8, in which it would seem probable that two original parent cells in juxtaposition have been involved. With this should be compared the very regular sporangium in fig. 9, which may be taken as representing the normal type in the same leaf from which fig. 8 was taken. I am not able to state positively that the sporogenous tissue in these sporangia does originate from two parent cells, but, if that be so, as seems probable, in each case it is only a part of the product of such cells which has gone to form the sporogenous mass, the rest contributes to the tissue of tapetum and septum. These considerations will also be found to have an interest in connection with the theory of the sorus.

A transverse section through part of a sorus of the same age as fig. 6 is represented in fig. 10; and again the variation of detail is seen, the form, bulk, and mode of segmentation of neighbouring sporangia not conforming to any strict plan. Again, in fig. 11, extreme cases of difference of the sporogenous groups, all from the same leaf, have been traced in outline, and it will thus be noted that the number of cells of the sporogenous group traversed by the plane of section may vary from 4 to 16, in sporangia of the same age; this is a very considerable margin of difference, which, I think, it would be difficult to match in any other genus of *Pteridophyta*.

Sections, transverse to the axis of the sorus and vertically through the pinna at this stage, appear as fig. 12; here the indusium is seen, as before in fig. 2, overarching the sporangium as a close investment. The sporogenous group, which is shaded, is clearly referable in origin to a single parent cell, together with the region of wall which immediately covers it. It will be readily understood from what has already been said of the variation of detail as seen in other sections, that here also the arrangement and number of the cells is liable to vary, and the fig. 12 must be understood to represent an average sporangium, which shows a segmentation of greater regularity than can always be counted on.

Putting together now the results derived from sections in the three directions described, an idea will be obtained of the sporangium as a solid body. If a section were cut through the sporangium in fig. 12 in a direction X, X, it would correspond, as regards number of cells, with the middle sporangium in fig. 6; while

a section along the line Y, Y, would correspond in all essential points with the left-hand sporangium in fig. 10. These may be considered as normal and regular sporangia. We conclude, therefore, that in an average case the origin of the sporogenous group is, as has been described, by segmentation of a single superficial cell, to be called the superficial parent cell, and that, at the age described, the sporogenous group is a flattened plate of tissue consisting of about 44 cells. This is, however, only an average case, and all the dimensions are subject to variation of detail. The form and segmentation in the sporangia which lie at the end of the sorus depart far from the type thus described; this might have been anticipated from their mature form (fig. 3), and it is illustrated in the outline of the sporogenous group, fig. 11, as well as by fig. 13, which represents the end of a sorus of *D. elliptica*.

As development proceeds, and the sporogenous group undergoes segmentation, it becomes naturally more difficult to trace the genetic relationships of the walls. The cells lying immediately outside the sporogenous tissue now enlarge, sometimes undergoing division, their contents become poor and transparent, and they assume the characters of a tapetum (*x*, figs. 8, 9, 14, 15); at the same time, while the inner limit of the tapetum becomes less regular, owing to the frequent enlargement of some of its cells so as to encroach on the sporogenous group, the outer limit commonly becomes more regular; the result is that the outer limit assumes the appearance of the natural boundary of the loculus; but, notwithstanding this appearance, it must be remembered that the tapetum is not derived from the sporogenous group, but from the tissue surrounding it. Meanwhile, additional divisions will have taken place in the cells which form the wall of the sorus, and these, though irregular, result in some three layers of cells in the lateral region (figs. 14, 15); at the apex of the sporangium, however, it is thicker, as is seen in fig. 14, and also in figs. 8 and 9, which traverse the region where the dehiscence takes place. As regards the division of the spore-mother-cells to form tetrads, and the maturing of the spores, I have nothing of importance to add, as apart from what is known in other Marattiaceæ.

The dehiscence of the sporangia demands a special description; it is well known to be by pores, which are represented in all the old figures; Sir WILLIAM HOOKER, in the letterpress appended to his Plate 7, of the 'Genera Filicum,' describes each pore as "communicating with a number of transverse chambers or cells, and each chamber having two (for there does not appear to be a dissepiment between them) sporangia." This description must have been based on some misconception, for each pore, as a rule, leads into one loculus only.

The wall of the sporangium at maturity consists of a superficial layer of cells with slightly thickened walls, while the subjacent cells remain thin-walled, and are liable to collapse when fully ripe (fig. 18), so that, in parts at least, the wall of the mature sporangium may consist of a single layer of cells. The mechanism of dehiscence is

exceedingly simple : as ripeness approaches, certain cells of the thickened outer layer, situated where the pore will be formed, may be distinguished by their smaller size, both in surface view (fig. 16), and also in section (fig. 17) : the thinner-walled cells below begin to shrivel (fig. 18), forming thus an extension of the cavity of the loculus upwards towards the surface ; as this is approached, the smaller cells above noted come apart (fig. 18), and as they themselves also shrivel, the result is a slit-like pore, which assumes an irregular oval outline, being lined by the persistent remains of the shrivelled cells (fig. 19). The actual rupture is thus seen to occur in the cells immediately above the sporogenous group : these it will be remembered, appear to have a common origin with the sporogenous group from an original parent cell. It will be further noted that there is nothing here of the nature of an annulus ; there are no specially indurated, or hygroscopic cells, not even such as are found in *Angiopteris*. In fact, with the exception of those plants in which the shedding of the spores takes place in water, this mode of dehiscence is probably the simplest of any Filicineæ. And yet, as will be subsequently pointed out, it is fundamentally the same type as holds for all other Marattiaceæ.

From the sections above described of sporangia just before the rounding off and tetrad division, it is possible to estimate the approximate number of spore-mother-cells ; and multiplying the number of these by four, the potential number of spores of each sporangium may be arrived at : but in making estimates it is to be remembered how variable the sporangia are in this genus. In an average example of *D. alata* (fig. 14) there are 108 spore-mother-cells exposed in the single vertical section ; fig. 15 shows that there are about 4 layers of them : the total number of spore-mother-cells is therefore about 432, and the potential output of spores will be about 1728 for an average sporangium.

#### *Abnormalities.*

Having considered the normal sporangium, and traced its development as far as the material at hand would allow, we may turn to the abnormalities, which here present matter of considerable importance. In certain cases the sporangia though varying in size and form, do so within reasonable limits (figs. 3, 4), and frequently whole sori may be found in which there is no case of marked anomaly. In other cases, however, the anomalies are numerous, so much so that it would be difficult to find three or four successive loculi at all nearly similar to one another (fig. 20). Examining the details of outline of the loculi in fig. 20, it will be seen that they vary very greatly in size, some being narrow and compressed, others being elongated in the direction of the longer axis of the sorus ; the largest of these (*x*), show slight lateral extensions of the sterile tissue into the sporogenous mass, these appearing as partial septa : in other cases the septum may be complete, dividing the loculus into two, while it is common to note two equal sporangia side by side, which thus illus-

trate a complete septation by means of a broader wall. It will be necessary, in view of the theoretical interest which attaches to the question of septation, to look more closely into the details of these extraordinary abnormalities, but I shall endeavour first to give a plain statement of the facts, without reference to opinions which may be based upon them.

It is at the period when the difference in character of the tapetal and sporogenous cells becomes clearly marked, both by form and contents, that these anomalies, of which in early stages it is difficult to be sure, may be studied with some degree of certainty. The sporogenous tissue does not appear to be always strictly limited to so regular groups of cells as those previously described: thus in fig. 21, a packet of cells, evidently the result of subdivision of one, projects beyond the neighbouring group, though it shares their characters; this case, which is uncommon, was verified by comparing the whole series of microtome sections through that loculus, and there is no doubt of the fact. We may compare this with what has been described in *Isoetes* in a former Memoir ('Phil. Trans.' B, 1894 p. 531, figs. 106-108), and occasionally in some other plants. A much more common irregularity is the converse: viz., that certain cells, often clearly sister-cells with those of the sporogenous group, remain sterile, and develop as tapetum, or it may be as permanent tissue of a septum. Examples of this are seen in figs. 22, 23, in which the cells (*st*) are clearly sister-cells with those of the sporogenous group, though they develop differently, showing already by the cessation of division, and by the poverty of their protoplasm, that they will be sterile; there is thus a partial sterilisation of the sporogenous group in certain cases.

Another feature, not to be confused with this, though producing similar results, is the encroachment of some of the tapetal cells upon the sporogenous mass; this is well shown in fig. 24, and it is specially a feature in loculi which are larger than the normal; it would appear as though this were a means of enlarging the absorptive surface of the sporogenous group, and leading the nutritive supply into the mass of it. It will be noted how, in fig. 24, many of the tapetal cells (*x*) become convex, and project as rounded sacs inwards, which may even at times undergo division into two or more cells.

Though in such cases as those quoted (figs. 22-24) these two modes of origin of sterile cells in close connection with the sporogenous cells may be distinguished with some degree of certainty, this is not always so, and it is frequently a matter of difficulty to decide of which nature the sterile cells may be which are seen; for instance, in the loculi represented in Plate 8 fig. 25, *a*, *b*, *c*, *d*, the origin of the cells marked (?) is doubtful, whether by ingrowth of tapetum or by sterilisation of cells of the sporogenous groups; the latter interpretation, however, appears in some cases to be the more probable. But whatever their origin, the presence of such sterile cells among the sporogenous cells is not an uncommon factor.

Having thus recognised the two sources of sterile cells, we may now consider them

in their relation to the septation of loculi. As already noted, it is in the larger loculi that sterile cells are most commonly found (fig. 20), and that various conditions of partial septation are seen in them. Thus, in fig. 24, in a loculus which is slightly above the average size, processes are seen opposite to one another, which suggest a median constriction of the large loculus; that is an approach to a condition of septation. This is, however, more pronounced in the much larger loculus shown in fig. 26, in which not only is there a median constriction, but also the cells marked (?), evidently sister-cells with the sporogenous groups, show intermediate characters between tapetum and sporogenous cells. From their position, if sterile and developed as permanent tissue, these would complete the septum; but their cell walls do not show that firmness which is already characteristic of the tissue of the sporangial wall, or of normal septa; probably in such cases the cells we are discussing become disorganised as the loculus approaches maturity. A further example, and a more complex one, is shown in fig. 27, which represents the large, partially trilocular specimen seen in the middle sorus of fig. 20; here the state of things is much the same as in fig. 26, the septa being incomplete, and probably only transitory, while the cells marked (?) show only a slight deviation from the normal. It is noteworthy that a triple partial septation, such as this, may occur; examples of it are not common, but the loculus here figured is not the only one of the sort which has been seen.

It is but a short step from the condition in figs. 26 and 27 to that seen in fig. 28, in which a bridge of tapetal cells, clearly distinguishable as such, extends completely across the loculus; it will be seen that, though in part it is a single row, some of the cells are divided in the plane of the septum, and this leads on to the state shown in fig. 29, where the septum is several layers of cells in thickness, while from either side an extension of tissue, of the nature not of tapetum only, but of permanent tissue of the septum, occupies the central region. Slight extensions of this permanent tissue may be seen also in figs. 26, 28, and 30A, thus illustrating how the permanent tissue extends inwards in rough proportion to the bulk of the septum. It is only a slight step further to the complete and normal septum permanently dividing the two loculi in the mature state; such septa are shown in fig. 30 between the sporangia *a*, *b*, *c*, and may vary in thickness, and in other details of structure, though they commonly consist of two to three layers of cells.

From the above description it will be plain that the sporangia of *Danaea* are by no means constant bodies; they are arranged in two rows, which together constitute the sorus, and this is perhaps their most constant feature. In point of segmentation of the cells which give rise to them, there is very great diversity of detail, though it appears that, as in other Pteridophyta, the essential part of the sporangia is referable in origin to superficial cells. But beyond this, in form and size of the sporangium, in the number of sporogenous cells, in the details of septation, and even in the details of dehiscence, there is an absence of constancy. Though many of the characters provide material for speculation, which will be taken up later, one conclusion may at least be



drawn from the facts (it is, indeed, a mere summary of them), viz., that the sorus and sporangium of *Danaea* are distinctly non-specialised, perhaps more obviously non-specialised than those of any other living Pteridophyte.

*Summary of Data from Study of Danaea.*

(1.) The sori consist of numerous sporangia, arranged in two parallel rows, united into an oblong cake-like mass, partially overarched by indusia, which spring up between the sori, from the surface of the leaf.

(2.) The sori are not always strictly circumscribed, but are liable to abstriction, resulting in shorter, sometimes circular, sori.

(3.) The sporogenous tissue, together with the part of the wall immediately above it, arises by segmentation of superficial cells. Usually one such cell (the superficial parent-cell) supplies the whole sporogenous tissue of each sporangium.

(4.) There is a great variety of detail in the segmentation, and in the size of the resulting groups of sporogenous tissue; hardly any two are exactly alike. Sometimes more than a single parent-cell appears to be involved.

(5.) The tapetum originates from the cells immediately outside the sporogenous group; the tetrad division of the spore-mother-cells and maturing of the spores call for no special remark.

(6.) The wall of the sporangium, which consists of several layers of cells when young, may, by their collapse, be reduced in parts to a single layer when ripe. The dehiscence of the sporangium is by a simple rupture, in a radial plane, the resulting slit widening, as the adjoining cells shrink, to an almost circular pore. There is no annulus.

(7.) Where the sporangia are large, imperfect septations are frequently found, and many intermediate conditions have been found between the simple sporangium, and two separate and equal sporangia lying side by side.

(8.) In large sporangia the partial septa may owe their origin partly to encroachment of the tapetum upon the sporogenous tissue, but partly to sterile development of cells belonging to the sporogenous mass.

(9.) The number of spore-mother-cells in an average normal sporangium is estimated at about 432, and the potential number of spores would therefore be about 1728, or, in round numbers, about 1750.

KAULFUSSIA.

The structure of the sorus in this Eastern genus, which, as it were, replaces geographically the Western genus *Danaea*, has been repeatedly depicted and described,\* but I am not aware of any account hitherto published of the develop-

\* By KAULFUSS, in HOOK and GREY., 'Icon. Filicum,' Plate 229; by GRIFFITH, 'Description of *Kaulfussia*,' p. 109; by FRANCIS BAUER, HOOKER'S 'Genera Filicum,' Plate 54; 'Monographie des Marattiacées,' DE VRIESE and HARTING, vol. 5.

ment. The sori, which are circular in outline and without any indusium, are scattered irregularly over the lower surface of the ternate, or quinato-digitate leaf, being inserted upon the smaller nerves. The form of the sorus is like a shallow cup,\* with crenate outer surface, the very slight grooves of the crenation being continued inwards over the margin; on the oblique inner face of each of the sporangia, which naturally correspond to the convexities of the crenation, there is in the mature state a narrow slit-like dimple, which indicates the point of dehiscence; but I do not find the pore to gape widely, as it is represented to do by F. BAUER. The number of the loculi is variable, as is also their size and outline. Further, the sori are not always of the circular form, but sometimes slightly elongated; others again show a median constriction, and it is easy to find examples, which, when placed side by side in series, would appear to illustrate all stages from the usual circular type, to two such sori seated as a pair (fig. 31, *a-e*).

The similarity of general character of this sorus to that of *Danaea* is obvious enough; the chief difference lies in the circular form. But it has been above noted that such circular sori are occasionally found on leaves of *Danaea*, especially on those which show characters intermediate between sporophylls and foliage leaves; in these not only is the distance between the sori often considerable, so that they lie isolated, almost as in *Kaulfussia*, but also the appearance of the sorus itself comes very near to that in the latter genus.

Turning now to the development, I have been able, through the kindness of Dr. M. TREUB, who sent me a large supply of material from Buitenzorg, to follow through the latter stages, though the material did not suffice for showing the earliest.

The youngest condition which I have seen is that represented in fig. 32, in which the sorus appears as a flat upgrowth from the general surface of the leaf, with a slightly raised marginal rim. The segmentation indicates that the whole has arisen by the division, and more active growth of a patch of superficial cells; those at the periphery have grown more actively than those lying centrally. The cells which will give rise to the sporogenous tissue lie immediately within the marginal rim of the young sorus. I have not seen the earliest stages, where the archesporium is represented by a single cell, but the youngest specimens I have seen leave no doubt that this is their mode of origin; thus in fig. 33 the shaded cells of the sporogenous tissue, together with the superficial cells which cover them, are evidently referable in origin to a single parent cell. It would appear doubtful whether the whole of the sporogenous cells are first segmented off by the periclinal wall, *b, b*; from the disposition of the cell walls here, as well as by comparisons of other sections, I am disposed to think that the wall, *a, a*, was formed first, and that a subsequent addition to the sporogenous tissue was made by the later wall, *b, b*; but I have not been able to decide this question by actual observation. The further steps in the

\* I find the cup to be much more shallow than it is depicted by FRANCIS BAUER.

development, as seen in sections radially through the sorus, will be gathered from figs. 34, 35, 36; from these it will be seen how the sporogenous group undergoes further segmentation, while they demonstrate that it is wholly referable in origin to that group already recognised in fig. 33. There is, however, a slower growth of the part involved, so that it is partially overarched by the surrounding tissue; thus the narrow slit-like dimple, already noted in the mature condition, is produced, but, as tangential sections (fig. 40) show, the dimple is very narrow.

Transverse sections (fig. 37) through the sorus of age corresponding to fig. 33, bear out these results; the sporogenous groups are easily distinguished at this stage, as packets of 2 or 4 cells; it is to be noted that neither at this, nor at any later stage, is there any indication that the intervening tissue represents the fused walls of confluent sporangia; the developmental evidence, though it does not directly disprove, does not in any measure contribute to prove any hypothesis of coalescence of distinct sporangia, either in this, or in other genera of Marattiaceæ. Later stages (fig. 38) show that there is no exact type or form of segmentation of the several sporogenous groups, a conclusion which might have been anticipated from comparison of fig. 37, as well as of the mature sporangia, and of the facts relating to *Danaea*.

Tangential sections of the sorus are difficult to obtain so as to give easily intelligible results, owing to the curved form of the sporangium; but if a section be cut in the direction XX, fig. 34, the appearance presented will be as in fig. 39, in which it is easy to see how the several tissues will correspond. An interesting fact which is brought out by such a section is that the groups of cells of the sterile tissue, which forms the septum between two adjoining sporogenous groups, are of similar origin with these, and at first differ in no respect from them, except in the less dense protoplasm, usually smaller nuclei, and in the fact that they do not eventually form spores. Very shortly after the stage shown in fig. 39, the growth of the tissue above the sterile septa becomes more active than that above the sporangia, and the result is the formation of a narrow slit-like depression (fig. 40); but as is shown by figs. 35, 36, 41, this extends only for a short distance in a radial direction, while its position is upon the oblique inner rim of the sorus. It is at the base of this slit that the rupture takes place at maturity, the cells adjoining it, both below and laterally, dry up, and the result is that the pore gapes open in much the same way as that described for *Danaea*. Here again, no mechanical tissue with thickened walls has been seen, which assists in the rupture, or in widening the pore when formed, while the actual rupture takes place in the cells which formed the cap of tissue directly covering the sporogenous group. Though differing in minor details, the dehiscence is thus seen to be essentially similar to that in *Danaea*.

Up to the time of dehiscence the external wall of the sporangia remains of considerable bulk; there is no markedly indurated superficial layer, and the wall maintains its massive character, the inner layers remaining distended without drying

up as in other genera. It may be noted in passing, that the vascular bundle upon which the sorus is seated throws up an irregular extension into the base of the sorus, in the form of tracheids (fig. 42), the physiological importance of which is obvious enough.

Turning now to the sporogenous tissue, it undergoes subdivision in the usual way, till the definitive number of spore-mother cells is attained; these then separate from one another, and round themselves off in the fluid which fills the enlarged cavity of the sporangium. Then follows the tetrad division, all the cells of the sporogenous mass taking part in it in normal sporangia. A tapetum is meanwhile formed from the cells adjoining the sporogenous group, and these may grow and assume irregular form, encroaching on the cavity, as in the case of *Danaea*. In fact all the main features are the same as in other Marattiaceæ.

As in other genera, an estimate has been made of the average number of spores which may be produced from a normal sporangium of *Kaulfussia*. An average number of spore-mother-cells exposed in a single vertical section of a sporangium, radially through the sorus, is found to be 245; transverse or tangential sections show that the whole sporogenous mass is about eight layers in thickness; the total number of spore-mother-cells would therefore be about 1960, and the potential number of spores per sporangium about  $1960 \times 4 = 7840$ .

As regards the septa dividing the loculi, variations in thickness, and even partial septations have been seen. The usual thickness of the septum is of three layers of firm permanent tissue, with a layer of tapetum on either side—from this as normal (though its thickness may be exceeded), various simpler structures have been seen, down to a partial septum; in fact, though I have not thought it necessary to represent the facts by detailed drawings after this has been done so exhaustively for *Danaea*, the main features are similar to those in that genus.

#### *Summary of Results from Study of Kaulfussia.*

(1.) The sori are not strictly circumscribed, but are liable to abstriction, and even apart from such cases, the normal sori are often arranged in pairs on the lower surface of the sporophyll.

(2.) The sorus consists of a number of sporangia arranged almost in a circle, with no indusium.

(3.) The sporogenous tissue, together with the part of the wall immediately above it, arises by segmentation of a single superficial cell for each sporangium.

(4.) The tapetum originates from the cells immediately outside the sporogenous group.

(5.) An average number of spore-mother-cells in a single sporangium is about 1960, and the potential output of spores is therefore about 7840, or in round numbers over 7500.

(6.) The outer wall of the sporangia retains its bulky character up to the period of

dehiscence, and there is no specially indurated superficial layer. The dehiscence is by a narrow slit, which opens by shrinking of the adjoining cells ; there is no annulus.

(7.) Imperfect septations are occasionally found, where sporangia are large.

(8.) The cells which give rise to the sporogenous group, and those which form septa are similar in origin, and at first are indistinguishable from one another.

Though the more general theoretical discussion will be reserved for a later page, it may here be remarked that the similarity of construction of the sorus of *Kaulfussia* to the larger one of *Danaea*, leaves no doubt of their near relationship. The main difference between the two is in size and outline, the absence of indusium, and in their being widely scattered over a large leaf area in *Kaulfussia*, while in *Danaea* they are closely arranged on a smaller leaf surface. But in those leaves of *Danaea* which show an intermediate condition between the sterile and fertile, the sori are frequently circular, and resemble in a remarkable degree those of *Kaulfussia*. Moreover, the similarity extends to the indusium ; for while in *Danaea* this rises between closely placed sori to a height almost equal to that of the sori ; where the sori are further apart the indusium appears only as a slight bank of tissue surrounding it. Thus the indusium is variable even in the genus *Danaea*.

From the above it would thus appear that as regards their sori, *Danaea* and *Kaulfussia* are fundamentally similar types, and that the chief points in which they differ are variable even in the individual of *Danaea*. It is further interesting to note that such variability in *Danaea* is associated with extension of leaf-area, and that the area of leaf of *Kaulfussia* is considerable ; this will be a point of importance in our theoretical consideration to be introduced below.

#### MARATTIA.

The sorus in the genus *Marattia* has been investigated by various writers, and is described more or less fully in the text-books ; this is a natural consequence of the material being readily accessible in Botanic Gardens, as well as in its native habitats. The mature structure of the sorus is thus well known, chiefly through the writings of LUERSSEN ('Beitr. z. Entw. d. Farn-Sporangien,' I.), and STRASBURGER ('Ueber *Scolecopteris elegans*,' p. 93, &c.). The development was examined first by RUSROW ('Vergl. Unters.,' 1871, p. 109, 110), who showed that it arose from superficial cells, and that a number of these are involved in the formation of each sporangium. LUERSSEN followed, in 1872, with a much more complete account, illustrated by numerous drawings, chiefly from *Marattia cicutaefolia* ; but as the sections of the young sorus, which were represented and described by him, were only vertical sections through the sorus, and as the consecutive steps of development were not stringently compared, so as to elicit the mode of progression from one to another, and to show the exact origin of the sporogenous tissue, it is plain that much yet remained

to be done. GOEBEL ('Bot. Zeit.,' 1881, p. 685) briefly notes his own observations on *Marattia cicutaefolia* and *alata*, and states that, as regards the archesporium, there is a complete similarity to that of *Angiopteris*, and that the archesporium is referable in origin to a single cell. He further regards the separate origin of the archesporia as evidence of the whole synangium being a sorus, and not a septate sporangium; in his outlines of classification (Engl. Ed., p. 254) he remarks that the fact of each sporangium having its own archesporium "proves that in *Marattia*, as in *Angiopteris*, we have two rows of distinct sporangia, which have grown together by their lateral faces." We shall inquire subsequently whether the facts are always as stated, and secondly whether this conclusion is really justified.

Since *Marattia* is a middle type of the family, it was thought useful to trace the origin and development of the sorus with the greater care, for purposes of comparison on the one hand with *Danaea* and *Kaulfussia*, and on the other with *Angiopteris*. Moreover, this could be carried out with greater certainty, owing to a plentiful supply of growing material of *Marattia fraxinea* (SMITH), which allowed of the earliest stages being traced.

The locality of the sorus in this species can be very early recognised, in sections which traverse it transversely, by means of the hairs which rise from its margin (fig. 45). The cells which will give rise to the sorus, though not yet projecting beyond the general surface, are deeper than those of the surrounding tissue; they are not constant either in number or form, nor in details of segmentation, as will be seen from figs. 45, 46, 47, 48; and this want of constancy of detail is a feature which is maintained all through the development of the sorus, showing a marked contrast to the regularity of the segmentations involved in the formation of the Leptosporangiate sporangium. Very soon the central region of the sorus is left behind by the more active growth on either side (figs. 46, 47, cells marked *x*), the sorus thus beginning to assume its characteristic form. It might already be concluded, from fig. 46, that there is no strict regularity of segmentation of the cells on either side of the median line, as seen in transverse section of the sorus; but this fact is still more apparent in a tangential section of the pinnule (fig. 47), in which the young sorus is seen in ground plan. In the stage there represented it is impossible to recognise with certainty which cells will ultimately give rise to the essential part of the sporangia, and which will form the sterile septa; all appear alike as regards contents, and equally indefinite as regards their segmentation. Similar results are obtained from a section longitudinally through the region where the sporangia will arise (fig. 47, section along line *b, b*, shown as fig. 48); here again it is impossible to distinguish the future septa from sporogenous cells. In representing the development of the sporangium of *Angiopteris*, GOEBEL ('Bot. Zeit.,' 1881, Plate 6, figs. 4 and 5) enumerates certain anticlinal walls, thereby implying that there is in that genus a constancy in their number and appearance, while he further points out that there is a constant relation of these to the origin of the archesporial cell, which is described as the "hypodermal terminal cell of the central

row of cells" ('Outlines,' p. 254). In *Marattia* I am not able to recognise such constancy; from figs. 45, 46, 47, and 49, but especially from fig. 47, it would be concluded that, while examples could easily be found which would correspond with some approach to exactitude to the plan laid down by GOEBEL for *Angiopteris*, such a plan is not rigidly maintained in *Marattia*, and that it is most conspicuously departed from at the ends of the sorus. Moreover, a comparison of the two opposite halves of the same sorus, as seen in section, shows that they are not strictly dominated by a common plan. A comparison of numerous serial sections, of various ages, leads to a further conclusion that the whole archesporium is not always referable to a single cell, though it seems to be so in most cases. Fig. 50 shows a rather older sporangium in section, and it would appear in that case of a rather undersized sporangium, that the whole sporogenous group may be referable to a single parent cell. In more bulky cases, however (fig. 51), it is difficult to trace such an origin, and it would appear more probable in large sporangia that the sporogenous group originated by the periclinal division of more than a single cell, as is indicated in figs. 46 and 49.

Transverse sections of the sorus have been compared in order to give solidity to the conception of its structure; they again demonstrate the variety of detail. The common type is seen in fig. 52, and it will be noted how this section coincides with what would be seen if the sporangium in fig. 51 were cut in a plane, *cc.* But the subdivision of the archesporium is subject to variation (fig. 53), the extreme cases of which will be considered later. To complete the study sections of the sorus of the same age as figs. 50-53, were cut so as to traverse it longitudinally (compare fig. 48); the result is such as might have been anticipated; it must be remembered in comparing this with the other sections that the anticlinal walls are curved, and that consequently the majority of the cell-rows in fig. 54 will be traversed obliquely; thus their genetic relations are apt to be obscured.

It is not difficult to follow the sporogenous group and its surrounding tissues from the conditions shown in figs. 50-54, to the older stage immediately preceding the tetrad division; this is a condition in which the grouping of the tissues is still sufficiently maintained to serve as evidence of the mode of origin, while on the other hand the cells which will actually form spores can be distinctly recognised by their contents, without any probability of error. Sporangia of such age are represented in figs. 55, 56, 57, respectively, in radial, tangential, and transverse sections. The examples chosen are those which show an average structure, though many deviations from the type occur, which will be discussed later. The tapetum originates outside the sporogenous group, from the cells immediately surrounding it; the latter is at this stage a laterally compressed, disk-shaped mass of approximately cubical cells. The wall of the sporangium in *M. fraxinea* is more massive than is represented in LUERSSEN's figures of *M. cicutaefolia*, while also the number of the sporogenous cells appears to be larger (*loc. cit.*, Plate 21, fig. 7). It will be noted that the wall is narrowest on the flat face where the two sides of the sorus are in contact; it

is here that the dehiscence ultimately takes place, after the two halves of the sorus have gaped apart. The wall here consists of two layers of permanent tissue, within which lies the tapetum. The further details of structure of the sporangium when mature, and of its dehiscence, have been so well treated by LUERSEN and STRASBURGER that there will be no need of a further description here.

Bearing in mind the variations in detail to which the sporangia are liable, we may form an estimate of the output of spores from an average sporangium, as calculated from the number of spore-mother-cells. Proceeding on average examples such as those shown in figs. 55, 56, 57, which were specially selected as examples of a medium type just before separation of the spore-mother-cells, we find in the vertical section (fig. 55) 166 spore-mother-cells. Figs. 56 and 57 show that the laterally compressed sporogenous mass is on the average rather over four layers in thickness, and the total number of spore-mother-cells in an average sporangium may therefore be computed at about  $166 \times 4 = 664$ . The resulting potential output of spores would then be about  $664 \times 4 = 2656$ , say, in round numbers, 2500.

Having so far described the development of sporangia of the type which may be considered the average for *Marattia fraxinea*, it remains to consider the deviations from that type; these, as in other genera, have a special interest in connection with the main lines of this investigation. It has already been shown that it is often difficult in average cases to refer the sporogenous group in origin to a single arche-sporial cell; it will be presently seen that in certain extreme cases more than a single archesporial cell must have been involved.

An examination of any sorus of *Marattia* in which the sporangia are approaching the tetrad division, and in which, accordingly, it is possible on the one hand to note with certainty the cells which will form spores, and on the other to still recognise their genetic relations, shows that the size and structure of the sporogenous groups is very variable. The details are most readily traced in transverse sections of the sorus, and from these the drawings to be discussed have been made. In fig. 57 an average example has been shown; but as a specimen of the differences of detail, which may frequently be seen, the three sporangia shown in fig. 58 will serve; no two of these are alike in size or shape, or in the segmentation; it is, however, possible to refer the sporogenous group in each case to a single parent cell. As extreme examples of small size, the figs. 59, 60 may be quoted, which were drawn from sori of the same age as fig. 58, and to the same scale. But not unfrequently sporangia are found in which the grouping of the sporogenous cells is such that they appear not referable in origin to a single cell; such cases are shown in figs. 61, 62. In the former there are two groups of cells, which are not exactly opposite one another, while the line which separates them is continued on as an obvious line of early cleavage to the anterior and posterior faces. In fig. 62 it would appear probable from their grouping that the sporogenous cells originated from three parent cells. Such cases as these are to be noted in connection with partial septations, which are found to occur in *Marattia* in



somewhat the same forms as in *Danaea*. Two examples are shown in figs. 63 and 64, which represent a rather more advanced stage of development than the preceding drawings. In fig. 63 we see a sporangium of very large area; the sporogenous tissue is encroached upon by ingrowths of the nature of tapetum; in one case these extend completely across the loculus, so as to form a septum; and it was seen, from comparison of the series of sections through this sporangium, that the septum was a complete one, but being only composed of tapetal cells it would not have been apparent in the sporangium in the mature state. In fig. 64 a more complete septation is represented, the sporogenous group being partitioned as before by a plate of tapetum, but, in addition, ingrowths of permanent tissue project on either side into the sporangial cavity. A comparison of such examples as these with those described above for *Danaea* (figs. 26-30) shows that the cases are essentially similar; thus in *Marattia* also the identity of the sporangium is not always strictly defined, a point which will have special interest in connection with the theories which will be subsequently discussed as to the nature and mode of origin of the synangia.

An excellent account of the gaping of the two-lipped sorus, and of the dehiscence of the sporangia having been given by LUERSSEN (*loc. cit.*, p. 21, &c.), it will be unnecessary to enter into the details again. It need only be remarked that, apart from the gaping of the sorus as a whole, the dehiscence of the individual sporangium is of the same type as is seen in *Danaea* or *Kaulfussia*, involving contraction of cells by drying, while the efficiency of this is increased by the fact that the softer dehiscent tissue is set in a firm resistant peripheral frame, which makes it necessary that the process of drying shall widen the fissure. At maturity the wall of the sporangium, apart from the region of dehiscence, consists of a firm superficial layer, with the more or less contracted remains of the inner layers of the wall still visible.

#### *Summary for Marattia.*

- (1.) The segmentation of the young sorus leading to the formation of sporangia is not constant in detail.
- (2.) The sporogenous tissue together with the part of the wall immediately above it arises commonly by segmentation of one superficial cell.
- (3.) But there is frequently a variety in detail of the segmentation and in the size of the sporogenous groups; in some cases the whole group is not referable in origin to a single archesporial cell.
- (4.) The tapetum arises from cells adjoining, and outside the sporogenous groups.
- (5.) There is a mechanical tissue which has the function of making the two sides of the sorus gape apart at maturity; the dehiscence of the individual sporangia is by slits in radial planes, the gaping of which is brought about by contraction of thinner walled cells surrounded by a more firm and resistant frame. The wall at maturity retains evidence of its massive structure.

(6.) Imperfect septations are found in some sporangia, similar in their main features to those already described in detail for *Danaea*.

(7.) The potential number of spores initiated in an average sporangium, reckoned from the number of spore-mother-cells, is  $(4 \times 664) = 2656$ , or in round numbers 2500.

### *Angiopteris.*

The sori of this genus have been more thoroughly investigated than those of any of the preceding genera of Marattiaceæ. Their mature structure, as seen from above, has been illustrated in many systematic works with varying success: the best drawings are those by STRASBURGER in his memoir on *Scolecopteris* ('Jenaische Zeitschrift,' 1874, Taf. 3). The general nature of the sorus, with its separate sporangia, is so well known as to require no description of its external characters here.

The development was traced by TCHISTIAKOFF ('Ann. Sci. Nat.', 1874, Ser. 5, vol. 19, p. 219, &c.): he found that each sporangium originates from several cells, while he refers the sporogenous tissue to a single parent cell; but the drawings, which are only of radial sections, do not exactly demonstrate the relations of this cell to the rest. LUERSSEN ('Handbuch der Syst. Bot.', 1879, p. 578), also examined young sori of *Angiopteris*, and gave a drawing of a sorus cut longitudinally: but he specially notes that the cell-group which gives rise to the mother-cells of the spores is never referable in origin to a single central cell. GOEBEL ('Bot. Zeit.', 1881, p. 681, &c.), on the other hand, found the case of *Angiopteris* to be similar to that of *Botrychium*, and recognised as the archesporium the hypodermal cell of the axile row of cells of the young sporangium: this he asserts gives rise to the whole sporogenous tissue. He notes how the sporangium grows more strongly on its outer side, thus acquiring an unsymmetrical form; in his figures (Taf. 6, figs. 4 and 5) he numbers certain anticlinal walls in sporangia of successive ages, and indicates the relation of the archesporium to these; thereby giving the impression that there is a certain constancy in the occurrence of these walls. The tapetum originates from the cells outside of and surrounding the archesporium, but he states that it is not of long duration, being soon disorganised. This statement is however corrected by CAMPBELL ('Mosses and Ferns,' p. 272), who points out that the cells of the tapetum, which often have numerous nuclei, do not break down early, but remain at least up to the tetrad division of the spore-mother-cells. He gives also a figure (fig. 143) of a sporangium approaching maturity in median section, and this together with the drawings of STRASBURGER, *loc. cit.*, Taf. 3, figs. 14-18, are hitherto the best illustrations of the structure of the whole sporangium: STRASBURGER's figures and description show especially the mode of dehiscence by a slit on the inner face, while a group of indurated cells, occupying the apex of the sporangium, act as a sort of annulus, performing an essential part in the mechanism of the dehiscence. The

structure of these indurated cells, and their relation to the rest of the wall has also been described and figured by ZELLER ('Bassin Houiller et Permien d'Autun et d'Epinae,' Fasc. 2, p. 19, figs. 12 and 13). It will be seen that his statements and drawings will harmonize with the description given below.

Using in part specimens from the Royal Gardens, Kew, partly material from the Glasgow Botanic Garden, I have followed the development of the sorus in *Angiopteris* from the earliest stages, and find that there is a general similarity at first to that of *Marattia*, as above described; the same want of constancy in details of segmentation is apparent. At an early stage the individual sporangia begin to project as separate upgrowths, but I find it impossible, from a study of superficial sections, to detect any regular system of segmentation which is maintained in all sporangia; a comparison of the four sporangia, shown in fig. 65 in surface view from above (in which the sporangia are indicated by shading), discloses no regular sequence of segmentations, and the cell-groups which will develop into the sporangia appear consequently ill-defined. I do not propose to attempt an exhaustive description of the variations of detail which may be found in organs which are thus variable from their earliest stages, but to give an account of the most central and frequent type of development. Of the sporangia *a*, *b*, *c*, *d*, shown in fig. 65, that marked (*b*) is believed to be the most regular and usual type; and the cells shaded in it are evidently sister cells, derived from a single parent cell which, as we shall see, gives rise to the central and essential part of the sporangium; we may call this, as in the other genera, the superficial parent cell. If a section were taken along a line  $x - x$  through such a sporangium, after it had grown more convex, it would appear as fig. 66, in which the cells shaded are believed to correspond to those shaded in fig. 65. It becomes apparent from such sections as these that a single cell, the central cell, had divided periclinally to form an inner cell and a superficial one; the former is the archesporium, and has in fig. 66 already divided into two; the superficial cell has also divided repeatedly. Tangential sections (*i.e.*, vertical sections at right angles to  $x - x$ , fig. 65) do not greatly aid our idea of the developing sporangium, and are unsatisfactory owing to the inward curve which it assumes as a consequence of the stronger growth on the peripheral side of the sorus: such a section is shown in fig. 67. Though we may thus select sections so as to represent a reasonably regular and typical structure of the young sporangium, it is clear, from fig. 65, that what has been described is only a central type, and as a matter of fact hardly any two sporangia show exactly the same details of segmentation. A comparison of our central type, as illustrated in fig. 66, shows substantial correspondence with the drawing of GOEBEL ('Bot. Zeit.', 1881, Plate 6, fig. 4), while even the walls which he numbered 1-5 may be compared with the principal walls in our fig. 66; but since we find that these are not constant, this correspondence in detail cannot be considered of material importance. An older sporangium of typical structure is shown in fig. 68, and it is an easy matter to see how such a younger sporangium as fig. 66 might develop into it; the correspondence again with GOEBEL'S

fig. 5 is sufficiently close to confirm the accuracy of his observations for certain average cases. Transverse sections of sporangia of this age show the great variability of segmentation, even in sporangia of approximately equal size. A common type is, however, that of fig. 69, which corresponds in essentials with a section along the line  $x - x$  through fig. 68; the sporogenous group is of the same construction, but the tissue on the peripheral side of the sporangium is rather more bulky; in this matter, however, variations are common. Finally, tangential sections at this stage confirm the results hitherto obtained: one of the most regular, though from a bulky sporangium, is shown in fig. 70; a comparison with fig. 68, if we imagine it cut through along the line  $y - y$ , will sufficiently explain itself. From these three sections of typical sporangia, of an age to show the sporogenous group already recognisable, a good idea of it as a solid body will be gathered. The sporogenous group is clearly referable in origin to a single cell, while the portion of the wall included in the bracket in figs. 66, 68, was derived from its superficial sister cell. The essential part of the sporangia is thus referable in ultimate origin to a single superficial parent cell, as has been found to be the case typically for other Marattiaceæ, and for *Botrychium*, *Helminthostachys*, and *Equisetum*. The wall of the sporangium, as yet undifferentiated, consists of a tissue of variable thickness, being thinnest on the side next the centre of the sorus, and thickest on the peripheral side. I do not find constancy either in position or number of the segmentations in the wall of the sporangium, on comparison of numerous sporangia one with another. Continuing the development of the most regular type of sporangium, growth and cell-division often continue with sufficient regularity to allow the genetic grouping of the tissues to be clearly followed (fig. 71). Meanwhile, a group of cells at the apex enlarge to form the crest-like annulus. The relation of this to the main lines limiting the product of the superficial parent cell is variable; a common case is that in fig. 71, where the middle line ( $x$ ) coincides with the limit of the annulus; but this is by no means constant: from this point ( $x$ ) downwards, on the central side of the sporangium, the dehiscence will take place. The sporogenous group is now clearly defined by the character of its protoplasmic body, and it forms a definite block of cells, referable to a single parent. Next follows the change of the cells immediately surrounding the sporogenous group, to the character of tapetum (fig. 72), and it may be stated that though questionable cases are frequently seen, the type appears to be that the whole tapetum is extra-archesporial in its origin. The figs. 72, 73, 74, represent respectively in radial, transverse, and tangential sections, sporangia which have arrived at the stage of complete division of the sporogenous mass, and in which the spore-mother-cells are about to separate and round themselves off, prior to the tetrad division.

From such sporangia it is possible to compute the average number of spore-mother-cells, and for this purpose a number of countings have been made. In radial sections the average of the countings gave 59, say in round numbers 60, spore-mother-cells traversed. Tangential sections show, on the average, about 6 such layers of cells to

be present, and the average number of spore-mother-cells in each sporangium would thus be  $6 \times 60 = 360$ , while the average potential output of spores per sporangium would be  $360 \times 4 = 1440$  spores. I have no details to add to what is already known of the tetrad divisions of the spore-mother-cells, and their progress to the maturing of the spores. It may be noted that, in the cases observed, all the spore-mother-cells undergo the tetrad division, and none have been seen to be disorganised, though this, doubtless, may occur in some cases.

Reverting to the tissues outside the sporogenous group, the tapetum is not a strictly defined layer, and is often irregularly doubled by periclinal divisions; but this is by no means always the case, as will be seen from a comparison of figs. 72-74. It remains recognisable as distinct, enlarged, glandular cells, often with several nuclei, up to the period of the tetrad division. This has been noted by CAMPBELL ('Mosses and Ferns,' p. 273); but, as the spores become mature, the tapetal cells lose their definite outline, till all that remains of them is a peripheral granular residuum lining the sporangial cavity (fig. 75). The wall of the sporangium outside the tapetum consists of two or more layers, commonly three, of which the outermost is the firmest and most differentiated; the inner layers are less regular, and are composed of more or less tabular cells. I have never seen the tapetum in direct juxtaposition with the superficial layer, as it has been figured and described by CAMPBELL (*loc. cit.*, p. 273, and fig. 143, C.). Of the external wall three essential parts may be recognised, and they will be best seen in fig. 76, which represents the apex of the sporangium, cut off in such a plane as *x, x* in fig. 72. The first part (*a*, fig. 72) is found on the dorsal (peripheral) side of the sporangium, and consists of large turgid cells, with moderately thin walls, and granular contents, which stain deeply with Bismarck brown. A second region (*b*) consists of deep prismatic cells with thick lignified walls, which may be recognised as the annulus; it extends as a narrow bridge across the apex of the sporangium (fig. 72), and widens out on either side, as the apex is left, into a broader band of cells with lignified walls (fig. 77). The third region (*c*) consists of thinner walled cells, of elongated form, which constitute a narrow band (fig. 75) running down the anterior (ventral) side of the sporangium. This is the tissue adjoining the fissure of dehiscence, and the structure which thus determines it is comparable to that seen in *Gleichenia* (CAMPBELL, fig. 185, B), or *Osmunda* (CAMPBELL, fig. 184). The above description corresponds in all essentials to the account given by STRASBURGER ('Ueber *Scolecopteris*,' p. 91).

The structure of the sporangial wall being as thus described, we may now consider how it works in connection with dehiscence. The annulus, together with the two broader lateral extensions of it, constitute a firm resistant arch, of which the apex is the narrowest part, being only about three cells wide (figs. 72, 76). If the thinner-walled posterior region (*a*) were to contract, as we may presume it does by drying as the sporangium matures, the two sides would be pulled backwards, while the thin bridge of the annulus at the apex would act as a sort of semi-rigid hinge; the line

of dehiscence on the ventral face, having been structurally defined, would thus, on fission, be caused to gape widely. It is not probable, however, that this hinge-like action is very considerable, and the gaping of the slit may be mainly due, as in other *Marattiaceæ*, to mere drying up of the cells in the neighbourhood of the rupture.

At maturity the more or less indurated superficial layer of cells of the sporangial wall is the most conspicuous part, but the thinner-walled cells lying within, though they may shrink, do not entirely disappear.

#### Angiopteris.—*Irregularities.*

It has been repeatedly noted that there is no definite strictness of segmentation in the sporangium of *Angiopteris*, though it is possible to fix upon a central type which is reasonably definite. It remains now to mention some of the more marked deviations from that type, but the attempt will not be made to follow out the less obvious variations.

As regards size of the sporangium, there is certainly a greater uniformity than in *Danaea* or *Marattia*, and very many sori may be examined without finding marked differences; but such differences do occur, and fig. 78*a, b, c*, will serve as a sufficient illustration; the large terminal sporangium in (*c*) is specially worthy of note as being a synangium, which is distinctly uncommon, though the terminal sporangia are frequently larger than the rest.

The series, figs. 79, 80, 81, illustrate what is perhaps the most interesting deviation from the normal. Fig. 79 shows a normal sporangium from the same pinnule as the others, with the usual structure, and a well-defined sporogenous group already segmented. Fig. 80 shows an unusually large sporangium, in which the sporogenous group is not regular, nor clearly defined; in the region where this should be, a number of cells with characteristic large nuclei are seen, not constituting a regular group, but spread over a considerable area. Fig. 81 shows a still more peculiar case, the structure of which at once suggests the synangial condition; the size of the whole sporangium is approximately double that of the normal (fig. 78*c*.); the sporogenous tissue, again ill-defined and rather irregular, appears to constitute two groups, which thus support the view of this as a synangium. A comparison of such cases, which are however by no means common, with those above described for *Danaea* and *Marattia*, shows such close similarity, that the conclusion is justified that the phenomenon is really one of partial septation of an enlarged sporangium such as occurs much more commonly in those genera than in *Angiopteris*.

#### *Summary.*

(1.) The segmentation of the young sorus, leading to the formation of sporangia, is not constant in detail.

(2.) The sporogenous tissue, together with the part of the wall immediately above it, arises commonly by segmentation of one superficial parent cell; but irregularities may be found.

(3.) The sporogenous group is commonly referable in origin to a single archesporial cell, but the segmentation is variable, and exceptions do occur.

(4.) The tapetum is an ill-defined band, one or two layers in thickness; it originates outside the archesporium, and remains till after the tetrad division, but is absorbed before maturity of the spores.

(5.) The annulus is a crest of cells at the apex of the sporangium, and is continuous with two lateral bands of indurated cells to form an arch: the rupture is determined, on the ventral face, by special thin-walled cells.

(6.) Abnormally large sporangia, and even synangia, though rare, are occasionally found.

(7.) The potential number of spores initiated in an average sporangium, reckoned from the number of sporogoneum-cells, is  $(4 \times 360) = 1440$ , or in round numbers about 1450.

#### GENERAL COMPARISON OF RESULTS FOR SORI OF LIVING MARATTIACEÆ.

In the above pages details have been given of the development and mature structure of the sorus in each of the four living genera of the Marattiaceæ. Ferns allied to these constituted a prominent feature in the early fossil Flora. It will be our duty presently to compare these with our living genera as regards their fructifications. But as the fossils are only known to us imperfectly, and in the mature state, while we have the advantage of being able to study the living forms developmentally, it would seem most satisfactory first to consider these more completely known modern survivors.

On comparing the mature structure of the sorus as a whole, and that of the constituent sporangia, and taking in also the facts of development, it will be apparent that the four living genera follow one type, and that they form, notwithstanding certain external differences, a very natural family. The genus which appears externally to be most aberrant is *Kaulfussia*; but a comparison of the sorus, and especially its development, shows that in all essential features the sporangium and sorus are of the same type as in the other genera; the apparent peculiarity depends on the outline of the leaf, which is not a dependable character.

The sorus in all the living genera shows the sporangia disposed in a peripheral series, each sporangium being developed with reference to a radial plane, which at maturity coincides with its more or less elongated fissure of dehiscence. As this type of sorus is not found exclusively in the Marattiaceæ, and seems an important one from a theoretical point of view, I propose to designate it by a definite term, such as "*the radiate uniseriate sorus.*" The outline of the sorus may be almost

circular, as in *Kaulfussia*, or more elongated, as in *Marattia* or *Angiopteris*, or greatly elongated, as in *Danaea*; but in all these the uniseriate arrangement of the sporangia is maintained, and the line of dehiscence, whether it be an elongated slit as in *Angiopteris*, or a short slit which widens on drying into an almost circular pore as in *Danaea*, is included in a plane running radially towards the central point, or towards the median line in those cases where the sorus is elongated.

As to the relation of the sporangia to one another, the living genera show important differences. In *Danaea* and *Marattia* the individuality of the sporangia is barely indicated by a slight convexity of the outer surface of each sporangium when mature, while the young sorus appears as a smooth upgrowth. In *Kaulfussia* the individual sporangia are not much more clearly marked externally, but in *Angiopteris* they project at an early stage as separate convexities, and in the mature state, though slightly united at the base, they rise upwards as almost separate rounded bodies. These facts may be taken as representative stages in a morphological series, and the similarity of development in the four genera would support that idea. Moreover, as we shall see, the fossils provide other examples which amplify the series. As in other morphological series, however, the facts may be taken as illustrating either of two views; in this case either a progression from a coherent to a separate condition of the sporangia, or a progressive fusion of them. This question will be considered again later, when the fossils have also been brought into the comparison.

The existence of a specialised mechanism for dehiscence of the individual sporangium appears to run parallel with the separate projection of the individual sporangia. In *Danaea* and *Kaulfussia*, in which the sporangia are closely united laterally, no indurated tissues have been found which can be held to act as an annulus for the mechanical widening of the slit of dehiscence. In these genera the slit, once formed, gapes merely by reason of the collapse of the neighbouring cells. Nor would it be possible, by any simple use of mechanical tissue, to improve upon this method, where the loculi are merely separated from one another by thin septa. In the sorus of *Marattia*, as has been fully described by LUERSSEN (*loc. cit.*, pp. 21-26), there are mechanical tissues, but their chief function appears to be that of bringing about the wide gaping of the two lips of the sorus, which precedes the dehiscence of the individual loculi; this change of form is a necessary prelude, since in earlier stages the two faces, upon which the dehiscence will take place, are in close contact, facing one another. The well-known change of form and wide gaping of the two lips of the sorus is brought about by certain masses of mechanical tissue lying about the base of the sorus. But for the actual dehiscence of the loculi themselves, the mechanism is of the simplest, and compares closely with that in *Danaea*. In *Marattia*, while the greater part of the sporangial walls, and even the septa are more or less indurated, the region of the wall where dehiscence takes place is composed of thin-walled cells; these rupture by a somewhat irregular slit, and the



fissure widens by the drying and contraction of the adjoining cells. The firmer tissues of the remainder of the wall constitute a resistant framework, so that any such contraction widens the slit once formed. The simple arrangement is, as regards the individual sporangium, quite like that in *Danaea*, though complicated by the change of form of the whole sorus as it ripens; and together with the simple structure goes the absence of individual projection of the sporangia.

But in *Angiopteris*, where the sporangia are freely projecting bodies which do not exercise a controlling influence upon one another at the time of dehiscence, and thus leave free scope for change of their form, a more elaborate mechanical system is present, and I have endeavoured above to explain how it works.

When we place the above facts in connection with those familiarly known in the Gleicheniaceæ, Osmundaceæ, and the main body of Leptosporangiate Ferns, we see that *the presence of an annulus, and its elaborateness, are to be correlated with the freedom of the sporangia from mutual relations with others*; it is a mechanism—and in the Leptosporangiates a most wonderfully specialised mechanism—which is produced only in those forms where it has an opportunity of working; its office is to induce a change of form of the sporangium on rupture, and this can only be carried out when the single sporangium is free from its neighbours. As regards its presence or absence, *Danaea* and *Kaulfussia* may be cited as the least specialised of Ferns, excepting, perhaps, the Hydropterideæ.

It has been shown, in the detailed description given above, that in all the four genera the typical mode of origin of the sporogenous group, together with the group of cells lying immediately above it, is from a single superficial cell, with a square base, which I have designated *the superficial parent cell*. It is true that examples occur where it is impossible to refer the whole sporogenous group to so simple a source, but, though these are of peculiar interest from a theoretical point of view, the simpler origin is undoubtedly the type for the Marattiaceæ. The more superficial products of this cell develop into that part of the wall which covers the locus, including the greater part, though perhaps not always the whole of the tissue of dehiscence. According to the unequal intercalary growth of the sporangium, this region of dehiscence may face directly upwards, as in *Danaea*; or it may, owing to stronger growth of the peripheral side of the sporangium, face obliquely inwards, as in *Kaulfussia*, or *Angiopteris*; or, finally, the surface of dehiscence may, owing to strong growth on the peripheral side, be turned into a vertical plane, as in *Marattia*. Here the two sides of the sorus are closely appressed till nearly mature, when they gape apart, owing to the mechanism above alluded to, and the dehiscence takes place on the faces thus exposed. All these are to be regarded as secondary differences, and, in all cases, the surface of dehiscence is similar in origin, the tissues involved originating mainly, if not always exclusively, from the outer products of the superficial parent cell.

The inner-lying products of this cell form the sporogenous group, of which all the

spore-mother-cells appear normally to undergo the tetrad division. A point of special interest is the number of spore-mother-cells produced, and, in estimating this, it is hardly necessary to reiterate how variable the individual sporangia are, and that the estimates are based upon such as appeared to be normal average specimens. The numbers, as above stated, are :—

	Spore-Mother Cells.	Output of spores in round numbers.
<i>Angiopteris</i> . . . . .	360	1450
<i>Dancea</i> . . . . .	432	1750
<i>Marattia</i> . . . . .	664	2500
<i>Kaulfussia</i> . . . . .	1960	7850

Now, these numbers are in great excess of those hitherto stated for any ferns. The estimates for Leptosporangiate ferns involve commonly such numbers as 48–64 spores per sporangium, while certain genera (*Aneimia*, *Osmunda*, &c.), have been described as producing a larger output, rising in the case of the latter genus to about 500; even this number is considerably exceeded by species of *Gleichenia*. But still there is a wide margin in favour of the Marattiaceæ. Beyond drawing attention to this fact I do not propose to go at present, but reserve the whole question of output of spores for discussion in a later paper, which will embody facts derived from the Leptosporangiate ferns. It may, however, be remarked that the large output of spores gives a physiological justification for the deeply-seated sporangia, and their broad base—in fact, the Eusporangiate condition is that best adapted for maturing large numbers of spores from the individual loculus.

The tissues which surrounded the superficial parent cell provide the rest of the wall of the sporangium and the tapetum; this latter tissue arises outside of, and genetically distinct from the sporogenous group. There are, however, occasional abnormalities of origin of the tapetum, and of the sporogenous cells, which will be discussed later. As a general rule, all the Marattiaceæ show this difference from Leptosporangiate ferns, that in the latter the tapetum is cut off from the sporogenous parent cell itself, but, in the Marattiaceæ, it originates from the tissues outside the sporogenous cell, or group of cells.

If we compare the Marattiaceous sporangium with that of the Leptosporangiate Ferns, the chief differences are seen to be :—

- (1.) The broader base of insertion, and origin from a bulky group of cells.
- (2.) The closer relation of the sporangia to one another.
- (3.) The thicker sporangial wall, consisting at maturity usually of more than a single layer of cells.
- (4.) The less specialisation of the mechanism of dehiscence.

- (5.) The larger number of spore-mother-cells produced.
- (6.) The cubical or prismatic, in place of the conical archesporial cell.
- (7.) The origin of the tapetum from cells outside the sporogenous group.

It will be a matter of interest later to see how far these characters are absolute and distinctive. There are, in fact, certain ferns (Gleicheniaceæ, Osmundaceæ, and Schizæaceæ) which provide important material for comparison, and they show that the Marattiaceous type is not so isolated among ferns as it is often assumed to be.

#### NOTES ON FOSSIL MARATTIACEÆ AND ALLIED FORMS.

Having now seen that, though differing in certain features of the mature sorus, the four genera of living Marattiaceæ conform to one type as regards their development, and so would appear to constitute a very natural family, we may turn to the consideration of allied fossils. But I shall not attempt to give an exhaustive account of fossil ferns of presumable Marattiaceous affinity. This would bring with it little advantage, since so many are merely known by impressions, and the interpretation of these may often be doubtful. I shall only cite such examples as are reasonably well preserved, and are accordingly reliable for purposes of comparison.

Among the four living genera, notwithstanding the differences in form of the sporangium, in the number of sporangia in the sorus, and in the degree of their lateral connection with one another, there are essential points of similarity, such as the position of the sorus on a nerve, the uniseriate radial type of its construction, the relatively thick sporangial wall, and introrse dehiscence by a slit in a radial plane, and the deficient or absent annulus. Among the fossils there are various genera which conform to the modern Marattiaceæ in all these particulars. We shall first take those which are best known, and conform most completely to the modern types: of these *Scolecopteris* naturally takes the first place.

This genus, founded by ZENKER, has been extended by STUR\* so as to include certain ferns previously described as species of *Pecopteris*. This author gives also very full references to the literature, and especially to the writings of STRASBURGER† and RENAULT.‡ As extended by STUR, the genus includes plants with sessile or shortly pedunculate sori, of three to six sporangia; they are united below, but separate above, and extend into a more or less elongated beak. The Marattiaceous characters are unmistakable, and it has been pointed out by STRASBURGER (*loc. cit.*, p. 87) that *Sc. elegans* (ZENK.) shows features connecting it with *Marattia* as regards the form of the sporangia, and with *Kaulfussia* in their circular disposition in the

\* 'Sitz. d. Wiener Akad.,' Vol. 88 (1885), pp. 720-757.

† STRASBURGER, 'Jenaische Zeitschrift,' 1874, p. 81.

‡ RENAULT, 'Cours de Bot. Foss.,' III. p. 116, Plate 20. &c.

sorus, while the outline of their upper free portion would point to *Angiopteris*: in dehiscence it compares with all three, but especially with *Marattia*. In fact, *Scolecopteris elegans* is a type which unites in itself characters of various living genera. Other species of STUR's genus show differences of detail, such as greater or less length of the receptacle; this is what is seen among living species of *Marattia*: or the varying length of the terminal beak, of which *Sc. polymorpha* (BGT.) is an extreme case: this, though peculiar in being an extension of individual sporangia, may be compared with the differences of upward extension of the tip of the sorus in various types within the genus *Marattia*: so that this variability is not without its parallel among modern ferns of a single genus (compare LUERSEN, *loc. cit.*, Plate 21). It may be noted that the number of sporangia in the sorus of *Scolecopteris*, which we thus on other grounds regard as a central type, is small and variable, but that 4 and 5 seem to be the most frequent numbers.

The fossil ascribed by STUR\* to the genus *Scolecopteris*, under the name of *Scolecopteris cyathea* (SCHL., *sp.*), with its sporangia united below, but with free acuminations, leads on towards the genus *Asterotheca* (PRESL).† Here the circular sori consist of 3-8 sporangia, which are united almost up to the apex, they have the peripheral wall strongly convex, and show no annulus. The mode of dehiscence has not been directly observed, but it seems highly probable that it is by radial slits, which opened upon the small dimple-like depression at the apex. The whole sorus is strongly suggestive of that of a *Kaulfussia*, with a smaller number of loculi, and much narrowed apical depression, while the obscure slits of dehiscence of the modern genus, and the absence of any annulus would correspond to the condition of this fossil. PRESL has grouped this genus with *Kaulfussia*, but STUR (*loc. cit.*, p. 720) rejects this on the ground of the form of the leaf, which is closely similar to that of *Marattia Kaulfussii* (J. SM.); and he accordingly founded the special group *Asterotheceæ*. But to those who fully recognise how greatly the outline and character of the leaves of modern living ferns may vary within the single genus, this point would seem to be over estimated. I see in it no sufficient reason for separating the *Asterotheceæ* from *Kaulfussia*. In any case the correspondence between the sori seems to be a peculiarly close one. It may be noted that *Asterotheca* is a relatively early form,‡ a fact which has its importance.

*Ptychocarpus* (= *Diplazites*, GOPP.) *hexastichus* appears to have sori of a similar type to *Asterotheca*,§ but the sori are placed "in several rows on both sides of the median nerve in each pinna,"|| a condition which has its interest for comparison with *Kaulfussia*.

\* *Loc. cit.*, p. 752.

† STUR, *loc. cit.*, p. 704.

‡ *Ibid.*, p. 720.

§ *Ibid.*, p. 763.

|| SOLMS, *loc. cit.*, p. 144.

A very important fossil for comparison with *Kaulfussia* is that recently described, with new drawings, by RENAULT ('Gîtes Minéraux Fasc.,' 4, pp. 9-11), as *Pecopteris* (*Goniopteris*) *unita* (BRONGT). It is found throughout the whole thickness of the Upper Coal Measures (*loc. cit.*, p. 5). The synangium figured in transverse section consists of seven loculi, completely fused to a circular form, with an outer wall consisting of several layers of cells, while the septa are relatively thin. The central mass of tissue is occupied by a vascular axis of star-like appearance in transverse section. The large number of spores which the loculi still contain, is quite in keeping with what is seen in *Kaulfussia*, while the detachment of the whole synangium in one piece, which is specially noted by RENAULT, is also a point for suggestive comparison. In comparing the fossil with the modern genus RENAULT remarks that their synangia differ considerably; he notes the cup-like form of the synangium of *Kaulfussia*, and that the dehiscence is obliquely inwards, while in the fossil the synangium is not hollowed at the apex, and the dehiscence does not take place obliquely inwards, but is apical: moreover, the vascular tissue is extended even to the upper part of the synangium: he concludes, "it appears, therefore, that these fructifications were of a more complex structure than that of the living Marattiaceæ of the genus *Kaulfussia*." But the differences thus noted do not appear to me to be so great as they are deemed to be by RENAULT. A comparison of my fig. 32 shows that the cup-like depression of *Kaulfussia* is very slight when young, and even in the mature state (fig. 43) it is not so great as the often-quoted drawings in the 'Genera Filicum' (Plate 59A) would indicate. Secondly, as shown by fig. 43, the oblique inward direction of the slit is only slight. Again, we see in *Kaulfussia* that the vascular tissue is extended upwards into the synangium (fig. 42), though not so far as in *Pecopteris unita*, nor is it so coherent a strand. All these are differences of degree, not of kind, and involve characters which, on comparison with other living Marattiaceæ, we regard as of secondary importance. The conclusion which I draw is that there is a substantial and striking similarity between the sorus of this fossil and that of the modern *Kaulfussia*.

Another interesting genus of Marattiaceous fossils, with circular sori consisting of 3-6 sporangia, united in their lower part, and accordingly coming away in one piece, is that described by RENAULT (*loc. cit.*, pp. 11-19), under the name of *Diplolabis*. The walls of the sporangia at maturity are only one layer of cells in thickness, and there is no differentiated annulus. As regards the number of spores in each loculus seen in section, this fossil would accord with modern Marattiaceæ, but the correspondence in general characters is not specially close with any living genus.

The genus *Renaultia* created by STUR to receive the fossil described by RENAULT,\* and ascribed by him† undoubtedly to the Marattiaceæ, includes a form of sorus which again combines characters in an interesting way. The sorus, consisting of five

\* 'Cours,' III., p. 122, Plate 22, figs. 9-11.

† STUR, *loc. cit.*, p. 760.

sporangia is of the uniseriate radiate type, with introrse dehiscence ; the sporangia are united below upon a common receptacle, so that the whole sorus may come away in one piece. The peculiarity is the presence of a rudimentary apical annulus, which suggests an affinity with *Angiopteris*; but it would appear that though there are undoubted points of correspondence, the sporangium of *Renaultia* was a less massive one than that of *Angiopteris evecta*; a comparison of RENAULT's drawing\* with my own drawing of the apex of the sporangium of *A. evecta*, fig. 76, demonstrates this. It is highly probable that *Renaultia* has Marattiaceous affinities; but it would appear that the sporangium is of a more attenuated type than that of any living Marattiaceous Fern.

The genus *Hawlea* (CORDA)† shows a circular uniseriate, radial sorus of 3-6 sporangia, which are separate from one another, but seated on a short circular receptacle. They diverge radially from one another when mature, and dehisce by a radial introrse slit, which is directed obliquely upwards. STUR‡ describes a "rudimentary apical annulus," but it is not clearly shown in his figures. The character of the leaf is compared by him with that of *Marattia*. CORDA referred it to the Gleicheniaceæ; BERTRAND§ gives only partial assent to this, and STUR repudiates that affinity, both on ground of the form of the leaf and of the sporangium, the latter having no circular annulus. He assigns to it|| a middle position among living forms, recognising in the leaf a similarity to *Marattia*, in the circular form of the sorus to *Kaulfussia*, and in the details of the sporangium to *Angiopteris*; and this is probably its true position, though it would be accepted with greater confidence if the microscopic details were better known by a study of sections.

The genus *Oligocarpia* (GOEPPERT) has been the subject of some divergence of opinion, and offers certain points of considerable interest. The genus as founded by GOEPPERT, has been considerably extended by the observations of STUR.¶ The species first made known (*O. Gutbieri*, GOEPP.) has a uniseriate sorus of 3-5 sporangia; later described species show 6-7 sporangia, with one of these in a central position surrounded by the rest; these lead to the case of *O. Brongniarti* (STUR),\*\* where there are usually seven sporangia, of which one is central; there are, however, others with as many as twelve sporangia, of which 8-9 are peripheral, and 2-3 occupy a central position. This arrangement of the sporangia finds no parallel among living Marattiaceæ, in which the sorus is always radiate and uniseriate, the central region being always unoccupied by sporangia. But in the genus *Gleichenia* the case can be exactly

\* *Loc. cit.*, Plate 22, fig. 9.

† STUR, *loc. cit.*, p. 681, &c.

‡ *Ibid.*, p. 684.

§ 'Cours,' III., p. 83.

|| *Loc. cit.*, p. 685.

¶ *Ibid.*, p. 687.

\*\* *Ibid.*, p. 688, fig. 16.

matched. While most *Gleichenias* have a strictly uniseriate and radiate type of sorus, with relatively few sporangia, *Gleichenia dichotoma* (WILLD) shows a sorus with more sporangia, which are disposed in a peripheral series, with a variable number placed centrally. Sometimes there is a single central sporangium, sometimes two, three, or even four. STUR remarks\* that in *Oligocarpia* the sori with most numerous sporangia are seated where nerves are so close together as not to allow space for development of the two sori individually; this is precisely what may be observed in *Gleichenia dichotoma*. It is certainly interesting to note this correspondence of the modern *Gleichenia* with the ancient *Oligocarpia*, and specially so since some authors† have referred the fossil to a Gleicheniaceous affinity. But it must not be assumed that the similarity of arrangement of the sorus will demonstrate an affinity in face of differences of detail of the sporangia. We shall therefore turn to the examination of the latter.

The sporangia are closely arranged on a relatively broad receptacle, and are of pear-like form, and quite separate from one another. The comparison with *Gleichenia* turns upon the presence of an annulus, and fissure-like dehiscence. As against the statement of ZEILLER‡ that a transverse annulus exists, as in the Gleicheniaceæ, SOLMS§ supports STUR's denial that such an annulus is to be seen, though the upper part appears to be occupied by strongly-thickened cells. Moreover STUR states that though he has examined hundreds of sporangia he has never seen one with a gaping dehiscence; he describes a terminal hole or depression, and compares this with the porous dehiscence of *Danaea*. While we reserve an opinion as to the correctness of this comparison till details are better known, the absence or at least the great rarity of dehiscence suggests the question: what use would there be for an annulus such as ZEILLER postulates if dehiscence by a slit does not take place? The view which I am disposed to entertain is that *Oligocarpia*, which is but incompletely known, is not necessarily to be ranked either with Marattiaceæ or with Gleicheniaceæ, but it is probably one of those intermediate forms, showing affinities with both, which on general grounds we should naturally expect to have existed. We know as yet of no other fern type with porous dehiscence of an exannulate free sporangium; these characters in themselves, if established, should suffice to indicate an independent position, though probably with Eusporangiate affinities.

And if such an uncertain view is to be entertained for *Oligocarpia*, much more will the element of uncertainty enter into discussions of other fossils attributed with more or less certainty to the Marattiaceæ, such as *Saccopteris*, *Discopteris*, &c. I do not think that any good morphological purpose can as yet be served by instituting strict comparisons of living forms with ferns known so imperfectly by impressions,

\* *Loc. cit.*, p. 689.

† ZEILLER, 'Ann. Sci. Nat.,' 6, XVI., pp. 190-192; RENAULT, 'Cours,' III., p. 67.

‡ *Loc. cit.*, p. 191-192.

§ 'Fossil Botany,' p. 146.

and not by internal structure. Still *Saccopteris* (STUR) shows us a radiate though not simply uniseriate sorus, of separate sporangia, with oblique slit-like dehiscence; a type of which the pollen sacs of Cycads are suggested by STUR as the nearest living representatives. The number of sporangia in the sorus is about fifteen, but in *Discopteris* (STUR) the number of the free sporangia may be 70 to 100; in the sorus. Whether or not these ferns are rightly attributed to the Marattiaceæ (a matter on which I feel some doubt) they show at all events that ferns existed at the coal period, with sori not simply uniseriate, and composed of numerous relatively small free sporangia, which did not conform to the annulate Leptosporangiate type.

From examples such as those above noted, and they have been selected as those in which the details are best known, the similarity of the sori of certain early ferns to the modern Marattiaceæ is sufficiently clear. But while modern Marattiaceæ show differences of cohesion of the sporangia, this is still more obvious in the fossils, which range between the complete coherence of *Asterotheca*, and the entirely separate state of those of *Hawlea*. One striking feature which is shared by all the best known of these Marattiaceous types is the almost circular, rosette-like form of the sorus, but all the living genera show a more or less elongated form of sorus, while in *Danaea* the sorus is commonly much longer than broad. The question then arises as to the existence of fossil types having a similar form of sorus.

Under the names *Danaïtes* and *Danaopsis* certain ferns are described, which, so far as can be judged from a study of impressions, appear to conform to the *Danaea* type of sorus;\* it is, however, an open question whether the relation of the sporangia to one another, and the mode of dehiscence, were exactly as in the modern *Danaeas*. At least the ferns appear to be Marattiaceous, and have elongated sori. They are found in the Coal Measures, Keuper, and Lias.

On the other hand, there are certain fossils of probable Marattiaceous affinity, known from well-preserved specimens, which show a disposition of the sporangia with less clear definition of the sori. Among these may be cited STUR's *Grand' Eurya Renaulti* and *G. Autumnensis*. In these STUR† specially notes the arrangement of the sporangia, and his use of the terms "general sorus" and "special sorus" is a consequence of their indefinite grouping: for the individual sorus does not seem here to be definitely circumscribed, though the sporangia are often grouped together by fours. This arrangement may find its nearest parallel in that of the pollen-sacs of certain modern Cycads.

Other early fossil ferns with a possible Marattiaceous affinity show even less definiteness of the sorus. Such is the case in the fragment named *Myriotheca* by ZEILLER,‡ in which the whole lower surface of the pinnule is covered by sporangia,

\* See STUR, *loc. cit.*, p. 778; SOLMS, *loc. cit.*, p. 149. The earlier references to these fossils are quoted by these authors.

† *Loc. cit.*, p. 677, &c.

‡ 'Ann. Sci. Nat.,' Ser. 6, vol. 16, p. 186.



without apparent order. ZEILLER'S description and figures point to a Marattiaceous affinity for this fern, in which case it would be to those Marattiaceæ with circumscribed sori, as *Acrostichum* is to most Polypodiaceous ferns. With such types that of *Senftenbergia* might also be compared, though the true affinity of this fossil may be questioned; here the large sporangia appear to be solitary.

We have so far considered cases where the sori are on the under surface of the leaf; there remain to be noted those fossil ferns of probable Eusporangiate affinity, in which the sori or sporangia are marginal. Prominently among these are *Grand' Eurya*, ZEILLER,\* with its massive, apparently marginal sori, and the curious family of the Botryopterideæ, described by RENAULT.† Such fossils as *Calymmotheca* and *Crossotheca* have also marginal fructifications, but it is impossible in the present fragmentary state of our knowledge to make much use of these for purposes of comparison. One point at least they serve to illustrate—that whatever may have been the nature of their fructifications, they were seated in a marginal position, and the sporangia in certain of them were of size comparable to that of living Eusporangiate ferns.

From the fossils above cited it is plain that in the earlier fern flora there was a greater variety of position, and of detail in the fructifications, than in the Marattiaceæ of the present day. The latter illustrate one main type, upon which the four genera show certain variations. The fossil ferns, which we believe to have been more or less allied to them, were more varied. Nevertheless, there were among them certain plants which correspond in a remarkable degree, even in the details, with modern Marattiaceæ, and the most closely comparable types yet known are those in which the details are in best condition for microscopic study, viz., *Scoleopteris elegans* and *Pecopteris unita*.

#### THEORETICAL CONSIDERATIONS BASED UPON COMPARISON OF FOSSIL AND MODERN MARATTIACEÆ.

Certain theoretical questions may now be discussed on the basis of such data as have been collected in the preceding pages. But in so very ancient a family it will be readily believed that finality of opinion will be difficult to attain, and we can hardly look for actual demonstration; it will be necessary to be satisfied with a consideration of probabilities.

As regards the *distribution of the sori* on the sporophyll we note as facts of interest, among the fossils described as belonging to the Marattiaceæ, that in certain cases the sori appear not to be segregated (*Myriotheca*), in others they are not clearly defined (*Grand' Eurya*), while in all the living genera they are commonly isolated on the under surface of the leaf. But even here they are not always strictly defined, for

\* 'Ann. Sci. Nat.,' Ser. 6, vol. 16, p. 303.

† 'Cours.,' III., p. 100, &c., originally described in 'Ann. Sci. Nat.,' Ser. 6, vol. 1, p. 220.

they show occasional abstractions. These facts plainly correspond to those well known in Leptosporangiate ferns; as in them, so here, it should be recognised that the circumscribed sorus is only the prevalent, not the exclusive type, while in the Marattiaceæ it is the fossils which supply the less definite examples. On the question of origin of the definite sorus, STUR (*loc. cit.*, p. 792), after remarking that types with solitary sporangia lived simultaneously with those in which sporangia are united into true sori, proceeds (p. 793) to state that "*Hapalopteris* is more recent than *Senftenbergia*," that is, "the species with solitary sporangia are older than those in which the sporangia appear gathered in irregular groups." I do not think that this can be accepted as a general statement of a morphological progression. It appears to be based upon observation of two genera only, important and early though they certainly are. Before it can be considered as established on palæontological grounds alone, the absence of ferns with clearly defined sori of prior date and of reasonably close affinity would need to be demonstrated; but it is to be remarked that various genera with definite sori (*e.g.*, *Oligocarpia*, *Saccopteris*) are recorded by STUR himself from the same strata as *Hapalopteris*, and even *Danaëtes*, which has a most compact and circumscribed type of sorus, is accepted by him as simultaneous with that genus. The question of time and mode of origin of the definite sorus would thus appear to be still an open one; the palæontological facts are not sufficient to justify a general statement on the point, in view specially of the fact that there is evidence of ferns with considerable variety of structure having existed at the time of the Culm and in the Devonian period.

The *form of the sorus* in the Marattiaceæ when it is circumscribed, varies considerably, though, as above noted, its plan of construction is remarkably uniform, being of the radiate uniseriate type. It may be almost perfectly circular (*Asterotheca*, *Scolecopteris*), or more or less elongated (*Kaulfussia*, *Marattia*, *Angiopteris*), or elongated to a very considerable extent (*Danaë*, *Danaëtes*). It would appear that very much the same extreme variations of form of the sorus are found among the early fossil Marattiaceæ as in those of the present day: but there is not sufficient evidence to show on palæontological grounds how far the two types are related by descent, and if they be so, which type, the circular or the elongated, was the prior, and which the derivative; for both types appear in the lower Coal Measures, though *Saccopteris* with a circular sorus is believed to occur in the Culm. On comparative and developmental grounds, however, the question may be approached.

There is among the early fossil ferns a distinct prevalence of the type with sori arranged with regularity in a single row on either side of the midrib of the leaf-segment, an arrangement which is maintained in our modern *Gleichenias*, in *Angiopteris*, *Marattia*, and *Danaë* (with occasional exceptions), but not in *Kaulfussia*. In many of the fossils the form of the sorus is circular, and the number of sporangia small (*Scolecopteris*, *Asterotheca*, *Hawlea*, *Oligocarpia*); and partly on the ground of its early prevalence, partly on developmental grounds which will be explained in con-

nection with the details of septation, I think it reasonable to regard the circular sorus with few sporangia as a central type from which others were derived, especially such an extreme condition as that seen in *Danaea*, though it is to be remembered that this type is recorded so early as the Carboniferous period. But whatever view may be taken on this point, the extremes are connected by intermediate examples, and it is no difficult matter to see that a slight modification of a pinna with circular sori, by extension of the sori along the veins, might result in a type like *Danaea*, while in *Danaea* itself, the sori when abstricted (fig. 1) take a form very much like that normal for *Kaulfussia*. The instability of form in the individual serves thus to connect the more divergent types; it suggests that the condition in *Kaulfussia*, where the numerous circular sori are spread over a large leaf-area, may have arisen by extreme lateral extension of the wings of the pinna, accompanied by repeated abstriction of the sori during the process, after the manner shown in *Danaea* in fig. 1, *a*, *b*, *c*: signs of such abstriction are still to be seen in *Kaulfussia* as shown in fig. 31. Such extension of sori following on the broader development of the leaf, will harmonise with the facts stated by ZEILLER ('Bassin Houiller et Permien d'Autun,' pp. 23-4, also pp. 57-8), in the case of *Pecopteris densifolia* (GOEPPERT), *Grand' Eurya Autunensis* (STUR), and *Pecopteris Platoni* (GRAND' EURY) (*loc. cit.*, pp. 3 and 53, and plate 8, fig. 7). If a widening of the pinnule were followed by an extension of the sori and their final abstriction, just such difficulties in definition of the individual sorus as he mentions in the former species would probably present themselves. Accordingly, while admitting that the matter is not susceptible of present proof, my own opinion is that in *Danaea* and *Kaulfussia*, which are the extreme examples of extension of leaf-area, while the leaves themselves are simply pinnate, or even unbranched (*D. simplicifolia*), extension was accompanied in the former genus by elongation of the individual sorus, in the latter by abstriction of sori, and that both were derived from the circular type of sorus so prevalent in early times, as exemplified by *Asterotheca* or *Scolecopteris*; *Marattia* and *Angiopteris*, with their slightly elongated sori, would occupy a middle position. It will be shown that the facts relating to irregular and partial septations in the Marattiaceous sorus will accord with these views.

A further point for discussion is the *relation of the sporangia to one another in the sorus*. Among fossil and modern *Marattiaceæ* various gradations may be seen between such as have their sporangia quite separate, and those in which they are united from base to apex. Certain of those best known may be placed in series as follows, starting from those with separate sporangia:—*Hawlea*, *Angiopteris*, *Scolecopteris*, *Asterotheca*, *Kaulfussia*, *Danaea*. Without for a moment suggesting that such plants as those named ever constituted an evolutionary sequence, they at least show, within the limits of the *Marattiaceæ*, steps between the condition with separate sporangia, which is common for all *Leptosporangiate* ferns, and that syngangial state which is one of the most marked characters of certain *Marattiaceæ*—

a peculiarity which they share, however, with various other Pteridophytes. It will be necessary, then, to consider upon all the evidence, whether the synangial state was the more primitive, or whether it resulted from the coalescence of parts originally distinct.

The latter view has been commonly held by writers on the subject, but more often, perhaps, as an assumption following from the belief that the Leptosporangiate ferns with their separate sporangia, were the more primitive, than as the result of comparative and developmental study; this opinion is reflected with varying distinctness in the works of the earlier descriptive writers, by the use of such terms as "synangia," composed of "connate sporangia," &c. As long as it is held that the Leptosporangiates are a relatively primitive type, and that the Marattiaceæ, if not themselves derived from them, must have their morphology explained from the Leptosporangiate point of view, the assumption that their synangia are a result of fusion is a convenient, if not even a necessary consequence. But in recent years the relatively primitive character of the Eusporangiate ferns has been repeatedly insisted upon,\* and I think the present position should be that they are to be taken on their own merits, and their morphology discussed independently of any question whether or not the results arrived at will harmonise with views as to descent from any Leptosporangiate ancestry.

In his paper on the development of the sorus of *Marattia*, LUERSSEN (1872), upheld, as against the prevalent theory of coalescence, that the sorus of *Marattia* is really a multilocular sporangium ("vielfächeriges Sporangium"), and not a sorus. He rejects (*loc. cit.*, p. 4) the analogy of *Angiopteris*, remarking: "It is not clear why the organ of fructification of *Marattia* should be looked upon as a 'sorus,' and the single loculi as 'sporangia.' To do so only on account of the analogy with the genus *Angiopteris*—leaving out of account the rest of the ferns—does not seem advisable." LUERSSEN was evidently struck by the probability of septation as accounting for the condition of the sorus of *Marattia*, and it will be seen that his view of the sorus as a single partitioned body, rather than a body resulting from the fusion of sporangia originally distinct, has some affinity with the opinions expressed below; but it is necessary that I should at once dissociate my own views from his as regards the comparison with *Angiopteris*: the error which he made, was in underrating the true similarity of the sorus in those obviously related ferns. And subsequent writers were not slow to take up this point. In SACHS'S 'Lehrbuch,' which reflects so admirably the current botanical opinion up to 1874, it is stated (p. 413) that the analogy with *Angiopteris* "clearly determines that in *Marattia* we have not to deal with a plurilocular sporangium, but with a sorus of which the single sporangia have fused one with another." Fresh developmental work was used as evidence in the same direction, and GOEBEL ('Bot. Zeit.,' 1881, p. 685) remarks

\* CAMPBELL, 'Bot. Gazette,' January, 1890. BOWER, 'Annals of Botany,' vol. 5, p. 109. CAMPBELL, 'Mosses and Ferns,' p. 302, &c.

that "It is hardly necessary to state again that the fused sporangia of *Marattia* are a sorus, and not, as they had sometimes been held to be, a plurilocular sporangium; this follows from the fact that each sporangium, as in *Angiopteris*, has its own special archesporium."

We shall naturally accept the position that what is usually styled the sorus in *Marattia* is a true sorus, comparable with that of *Angiopteris*, and of various other ferns; but the further point included in the above quotation from GOEBEL does not necessarily follow. Even if the fact were always as he states, that each sporangium has its own special archesporium, this does not by any means prove that it was separate by descent from its neighbours. And it has been shown above that, as a matter of fact, occasionally in *Marattia*, and much more frequently in *Danaea*, each sporangium has not always its own distinct archesporium. Moreover, while using developmental evidence, little account has been taken by other writers of the structure of the septa which separate the loculi; whereas their variable thickness and occasional incompleteness are matters very material to the question before us. It will thus be seen that the real nature of the sorus, and its mode of origin by descent, cannot be settled simply by brief allusion to the usually separate archesporia; as regards the developmental evidence, the question must be considered as still an open one.

STUR, having in view chiefly the data derived from the study of fossils, has also expressed his opinion as to the relative time of origin of the synangial condition in certain Marattiaceæ.\* Having summarised into a table† those fossils of the Culm, Coal Measures, and present periods, which he attributes to the Marattiaceæ, he argues on the point in question from the data in the table as follows‡:—

"*Danaites* and *Oligocarpia*, both with sporangia dehiscing at the apex, are present alike in the lower Coal Measures (Unter-Carbon), while *Saccopteris* with sporangia resembling pollen sacs dehiscing at the apex, is believed to have existed in the Culm ("schon im Culm zu vermuthen ist"). Accordingly the flask shaped coalescent § (*sic*) sporangium would be earlier, having appeared at the time of the Culm, while its coalescence first appeared in *Danaites* in the lower Coal Measures (Unter-Carbon)."

"Accordingly the *coalescence* of sporangia to a star-shaped (*Scolecopteris*) or linear (*Danaites*) sorus was more recent than the first appearance of the correlative non-coalescent sporangia."

"The types of *Senftenbergia* in the Culm, of *Scolecopteris* and *Renaultia* in the upper Coal-Measures (Ober-Carbon), and of *Marattia* at the present time, indicate three different stages of the Marattiaceous fructification attained by modification."

From the above quotations it is plain that STUR contemplated a progressive

\* 'Sitz. d. Wien. Akad.,' 1883, Abth. 1, p. 633, &c.

† STUR, *loc. cit.*, p. 791.

‡ *Loc. cit.*, p. 793.

§ The word "verwachsene" in the text must, I think, be a mistake for "unverwachsene," for *Saccopteris*, to which it is applied, has non-coalescent, separate sporangia.

coalescence of sporangia to form synangia, and read the palæophytological record as establishing this opinion. I do not think that this conclusion is sufficiently justified by the facts. We may put aside *Senftenbergia* on the double ground that its affinity with the Marattiaceæ is uncertain, and that, its sporangia being isolated, and not associated into sori, it cannot be used in argument as to the progressive changes within the sorus itself at that early period. The argument of STUR as to the later appearance of coalescence of sporangia within the sorus, turns then upon the case of *Saccopteris*; but even STUR himself does not go further than saying that this plant is believed to have existed in the Culm ("im Culm zu vermuthen ist"): it is present, certainly, he states, in the lower Coal Measures; but he admits that *Danaëites* is also present in the lower Coal Measures, and that is a type in which the synangial condition is seen in its most pronounced form. So that, as far as there is really secure evidence from forms admitted to be Marattiaceous, it would seem that the geological record shows a simultaneous appearance of the two types in the lower Coal Measures, and therefore will not serve to decide the priority either of those with sporangia distinct in the sorus, or with the sporangia united in a synangium.

In this connection the recently expressed opinion of RENAULT is of especial interest ('Gîtes Minéraux,' vol. 4, p. 5). Speaking of the true "*Pecopteris*," by which name he designates those with "sporangia grouped in a sorus," he remarks that "hitherto the true *Pecopteris* appeared peculiar to the upper Coal Measures, we therefore think it interesting to indicate their presence in the quartzes of Esnost; these quartzes enclose, as is known, the remains of *Bornia*, of stems and branches of *Lepidodendron*, the anthracites which accompany them have yielded impressions of *Cardiopteris*, and of *Bornia*; all this leads to the supposition that they belonged to an epoch much more ancient than that of the upper Coal Measures, for instance, to the Culm."

The last passage above quoted from STUR, in which he selects *Senftenbergia*, *Scolecopteris*, *Renaultia*, and *Marattia*, as indicating stages in the progress of the Marattiaceous sorus, cannot be accepted as cogent, when it is remembered that *Senftenbergia* is of doubtful affinity, and that *Danaëites* with its synangial sorus is recorded from older strata than any of the other three. My own opinion is that, even without urging strongly the inherent weakness of negative evidence, which would lay stress on the fact that certain types are not yet recorded from certain strata, the question of the time and mode of origin of the synangial sori cannot be settled on the ground of present palæophytological knowledge; as regards the facts available from the study of fossils the question should be regarded as still open.

The most that can be said with certainty is that the earliest ferns of which the sporangia are at all accurately known have separate sporangia; but on the other hand, both the type with coalescent sporangia, and that with separate sporangia associated in a sorus, are very ancient, and have been recognised as having existed already in Marattiaceous ferns from the lower Coal Measures. In arriving at these

conclusions I do not ignore the possibility that ferns interesting for comparison, or even of truly Marattiaceous character, may have existed earlier. I would on the contrary suppose that very important links in the chain of evolution existed before those taken by STUR as the basis of his argument. It is true that *Senftenbergia* is recorded from earlier rocks than well authenticated Marattiaceæ; but its affinities seem to be with the Schizæaceæ rather than the Marattiaceæ. In the fact that it is perhaps the earliest recorded fern in which the details of the sporangia are well enough preserved to form a basis for comparison, I see no sufficient reason for regarding it as a Marattiaceous ancestor, or even as representing a condition ever passed through in the evolution of the Marattiaceæ. Moreover, it is not the earliest known fern; those of the Devonian period have also to be remembered, while in the Culm there is evidence of a considerable and varied fern flora; this has been brought into prominence afresh by SOLMS-LAUBACH'S recent revision of the fossil plants described by UNGER from the Unter-Culm ('Abhandl. d. k. Pr. Geol. Landesanstalt,' Neue Folge, part 23). The variety of structure of fern petioles there described is considerable; it is reasonable to suppose that this variety of vegetative structure was accompanied by variety of the sorus, and it should at least be a warning against generalisation in such a case as this from few facts. It is quite possible that the differentiation both of synangial sori, and of those with separate sporangia, either grouped in sori or solitary, may have been of much earlier date than those used as the basis of his argument by STUR.

Another consideration will make the conclusion of STUR seem questionable; perhaps no feature in the Marattiaceæ is more remarkable than the persistence of type from the remote past to the present day. STUR himself points this out (*loc. cit.*, p. 796). Are we to believe that this type which has virtually stood still through so many successive geological periods, was so quickly plastic at the Carboniferous period as to show a progression from a type with entirely separate sporangia, as seen in *Senftenbergia*, to the completely synangial condition seen in *Danaëites*, between the Culm and the lower Coal Measures? I think such a suggestion is improbable, though, of course, it is not impossible.

Accordingly, whether we discuss the form of the Marattiaceous sorus, or the relations of the sporangia composing it, it appears desirable to return to comparative and developmental considerations derived from living Marattiaceæ, and see how far the facts detailed above may serve as a basis for views such as shall not be incompatible with the fossil evidence.

It cannot fail to strike even a superficial observer how great is the similarity of the sorus of *Danaëa* to the fertile spike in *Ophioglossum*. Notwithstanding that the former is applied throughout its length to the lower surface of the leaf, while the latter is a body which rises free and erect from the upper, still they resemble one another in being composed essentially of two parallel rows of laterally flattened sporangia, which are of approximately uniform size, project only slightly at the surface, are separated

from one another by septa of variable thickness, and produce numerous homosporous spores. The difference of position of the two bodies would be sufficient to preclude any suggestion of homology; but as I have elsewhere explained, the mere search after homologies is not the main feature in our morphological study: it is a matter of deeper interest to inquire after the probable method by which parts so different in position, but so similar in structure and function as the spike of *Ophioglossum* and the sorus of *Danaea*, may have come into existence.

In a former Memoir (Studies II., Ophioglossaceæ) I have discussed the morphology of the spike of *Ophioglossum*, and found that the details of development are compatible with a view of its origin by septation from a simpler non-septate body. It was seen, moreover, that such a process of septation, producing somewhat similar results, has occurred not uncommonly in the Anthers of Angiosperms. Comparative evidence was also adduced which supported the view of septation for *Ophioglossum*. Having thus the analogy of anthers of Angiosperms, and (on my view) that of the spike of *Ophioglossum* before us, it may be inquired what bearing the developmental facts have upon the origin of the sorus in *Danaea*; do they support a theory of fusion or of septation as explaining the present structure?

It has been seen that in the synangial genera of Marattiaceæ a "superficial parent cell" commonly gives rise to the sporogenous group, together with the cap of tissue covering it, while a band of tissue, which develops into the septum together with the tapetal layer on either side of it, separates the sporogenous groups one from another. Such a structure of the young synangium would be compatible either with a view of progressive septation or of sporangial fusion, if the septa were of uniform thickness, and the archesporia all distinct from one another. GOEBEL has already used the developmental evidence in favour of the theory of fusion, assuming, in accordance with his own observations on *Marattia*, that there is this uniformity.

But it has been a matter of special description and remark in the above pages, that in *Danaea* there are palpable departures from regularity, also though less commonly in *Marattia* and *Kaulfussia*, and occasionally in *Angiopteris*. The chief points material to the present question are the following:—

(1.) The great variability of size and shape of the single loculus. A glance at fig. 20, or fig. 58 shows this very clearly; or if the comparison be based upon enumeration of the sporogenous cells, the extreme cases shown in fig. 11, which were drawn from the same leaf and are of similar age, may be quoted; extreme variability of the loculi is seen at the ends of the sori in *Danaea* (fig. 13). Such differences are certainly rare in ferns with separate sporangia, and would not be probable if the synangium were the result simply of lateral fusion of such sporangia. A special interest attaches to those cases where the sporogenous group is not referable to a single parent cell; it is difficult, on a view of coalescence of sporangia, to understand how such a condition would have come into existence.

(2.) The occurrence of incomplete septa, and of sporangia in equal pairs suggesting



a process of septation, is a feature which is by no means uncommon in *Danaea* (fig. 20), especially where the sori are long; it occurs also, though less frequently, in *Kaulfussia* and *Marattia*, but is rare in *Angiopteris*. It may, therefore, be taken to be a special feature of the synangial forms, and is most prominent when the sori are longest. This is a point of the greatest importance as bearing on the theory of the sorus.

(3.) Closely connected with the occurrence of incomplete septa is their variable thickness, and this has been described in detail. From the usual septum, consisting of some two or three layers of permanent tissue, with transitory layers of tapetum on either side, all gradations of thinning off of the septum may be found in *Danaea*, to the condition of a simple tapetal layer (fig. 28), and even onwards to the mere encroachment of tapetal cells into the simple sporogenous group.

(4.) The occasional development in *Danaea* of cells outside the definite sporogenous group as fertile cells (fig. 21), and conversely of cells of the sporogenous group as sterile cells (figs. 22, 23), shows that the fertile tissue is not so strictly defined in this genus as it is usually found to be in other ferns.

Now it is possible to read these facts as consistent with either a view of progressive coalescence of sporangia originally separate, or of a progressive septation of a less completely septate sorus. If the former view be taken, then the sorus of *Danaea*, which shows the features mentioned more commonly than other genera, would be held to have been descended from a type with sori even more elongated than those of the present day. But *Danaea* is the genus of Marattiaceæ which has the longest sori known in the family. I am not aware that any genus of Eusporangiate ferns, fossil or modern, has been described with sori longer than *Danaea*, and with separate sporangia. In the absence of evidence that any such supposititious ancestor ever existed, the view that the above phenomena in the sorus of *Danaea* imply coalescence of sporangia previously distinct appears to me to be without proper foundation.

But if we contemplate the converse view, that the characters described are evidence of septation of a body originally of less complex structure, some important considerations may be brought forward in support of it. *Danaea* is a broad-leaved type; the outline of its sori, which are the longest in the family, suggest that they have followed the broadening of the leaf or pinna, and that they are the result of extension rather than contraction. If derived from some average Marattiaceous type, with less elongated synangial sori (such as is represented in early rocks by *Asterotheca* or *Pecopteris unita*), an increase of septation as the sorus elongated would be a physiological advantage, if not even a necessity. There is thus a reasonableness in the suggestion that the present condition of the sorus has been the result of progressive septation, following on elongation of the sorus. Strong support of this is to be found in the analogy of septate anthers of certain Angiosperms, which show a close structural parallel to the details described for the sorus of *Danaea*. I have elsewhere

dealt with septate anthers,\* and it cannot be doubted, I think, for those genera of Onagraceæ in which the anthers are septate, that they were derived by septation from the ordinary Angiospermic type, the anthers, for instance, of *Gaura*, *Clarkia*, and *Eucharidium* being in other respects normal. But in these not only are the loculi of unequal size, as are the sporangia of *Danæa*, but the septa also vary in thickness, being sometimes composed of a band of permanent tissue with tapetum on either side [compare fig. 15 of *Danæa* with fig. 54 (Plate 4, *loc. cit.*) of *Clarkia*]; sometimes they are thinner, and may even consist of only a single layer of tapetum [compare fig. 28 of *Danæa* with fig. 53 (Plate 4, *loc. cit.*) of *Gaura*]. Moreover, in the mature anther of various Angiosperms, which show such septations, partial septa similar to those of *Danæa* may be seen. I do not think that these are merely fortuitous resemblances; it seems much more probable that this similarity of detail, in plants so far apart systematically, is a consequence of a similar morphological advance, in either case by subdivision of loculi previously less completely septate. The analogy of the septate anthers of Angiosperms shows, in any case, that the similar details of structure in *Danæa* are consistent with a theory of progressive septation of the sorus; this again is in accord with the results of comparison with other Marattiaceæ, on which ground it seems probable that the sorus of *Danæa* has been subject to elongation.

Partial septa are also found in *Kaulfussia* and *Marattia*, though less commonly. These are genera with slightly elongated sori, and if they have been derived from a type with a circular form of sorus, such as that of *Asterotheca*, the partial septations might be regarded as related to the elongation of the sorus, just as in *Danæa*, though in a less prominent degree.

The facts and arguments contained in the above pages are not put forward as leading to any definite demonstration as to the mode of origin of the Marattiaceous sorus, or as to the relations by descent of any of its various types. The contention which I do press, however, with some persistence, is that these questions are still open, notwithstanding that writers of authority have treated them as already decided, whether by evidence from fossils, or from development of living forms. I have above pointed out how in my opinion the palæophytological evidence is insufficient to prove the priority in the Marattiaceæ either of the type with separate sporangia, or of the synangial type. As far as I can see, the facts from fossils would be consistent with either view. Nor does the argument from comparison and development of living forms lead to any definite conclusion, so long as we treat the Marattiaceæ on their own merits, and do not proceed on the assumption that they were descended from Leptosporangiate ferns. Comparing them, *inter se*, it would be possible to interpret all the facts as consistent either with a progression from a synangial state to sori with separate sporangia, or as consistent with a progressive coalescence. This conclusion will I think be admitted by those who follow all the

\* 'Studies,' II., pp. 1-6.

details above described, and I consider it to be the most important result of this investigation.

But it is our duty not only to contemplate *possible* views, but to decide which is, in our own opinion, the more *probable*. Having in view, in addition to the facts from palæontology and from the study of development, the comparison with other Pteridophyta and the facts from septate anthers of Angiosperms, it seems to me probable that a progressive septation has taken place in certain types of Marattiaceæ, where the sori are elongated, such as *Danaea*, and in a less degree *Marattia* and *Kaulfussia*. It may be a question how far a similar septation may be accountable for the origin in the first instance of a sorus with a plurality of sporangia united together, as in *Asterotheca*, though I think this not improbably the mode of their origin. I am disposed to regard such synangial types as being probably the more primitive, and to think that a progressive separation of the individual sporangia has led from these to such a type as *Angiopteris* or *Hawlea*. This view is at least consistent with the facts, so far as I understand them, though it is not put forward as in any way demonstrated. A full discussion of this matter will, however, be deferred for the present; it will find its best place when the Leptosporangiate ferns have been examined, and it is to them that the next part of these Studies will be largely devoted, while it will also include a discussion of the morphology of the spore-producing members of Pteridophytes at large.

Certain of the facts brought forward in this Memoir have a general bearing. It follows from the occurrence of partial septa, and of gradual steps in septation, that in the cases where this occurs the identity of the individual sporangium is not maintained. Seeing, in the Leptosporangiate ferns, the wonderful specialisation of the sporangium, and the regularity of its segmentation, the mind is disposed to accord to it a definite individuality; but this is only a character of this highly-specialised series, and is in itself one of the most clear marks of their specialisation. In such a leaf as that illustrated in fig. 30, the identity of the single sporangium seems quite lost, and it may be left as an interesting matter for reflection whether or not such a condition is to be considered as more primitive than the highly-individualised sporangia of a *Polypodium*.

Again, it is a matter of general interest to note any further example of the want of a definite limit of sporogenous tissue. In *Danaea* each sporogenous group is commonly derived from a single parent cell, and forms a clearly-defined body of cells, but, occasionally, a cell-packet outside the definite group becomes sporogenous (fig. 21), while conversely, certain cells of the definite group do not develop as spores, but as tapetum (figs. 22, 23, 26, 27). Such cases show, as has already been remarked elsewhere,\* that the limits of spore-producing tissues are not constant in the individual plant, and that normally vegetative tissues may at times be sporogenous, and normally sporogenous tissues may be diverted to a vegetative function.

\* 'Phil. Trans.,' B, 1894, p. 553.

## DESCRIPTION OF FIGURES.

*Danaea*. Figs. 1-30.

## PLATE 7.

- Fig. 1. *Danaea alata* (SMITH). *a*, a fertile pinna, with many normal sori; the arrow indicates an abnormal fission. *b*, *c*, show more numerous abnormal fissions, resulting in irregularly-formed sori distributed over a slightly enlarged leaf-surface. ( $\times 2$ )
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*Figures illustrating Partial Septations.*

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- Fig. 25, *a, b, c, d*. Ditto, in some cases it is doubtful whether the sterile cells are the result of encroachment or of conversion of sporogenous cells. ( $\times 150$ .)
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*Kaulfussia æsculifolia* (BLUME). Figs. 31-44.

- Fig. 31. Sori of *Kaulfussia*, showing states of partial to complete abstriction; *f, g*, are seen from below; *st* is the common stalk of the double sorus.
- Fig. 32. Young condition of the sorus, which is but slightly raised above the surface of the leaf, as seen in vertical section; the position of the two sporangia is indicated by shading. ( $\times 20$ .)

- Fig. 33. Part of a similar section on a larger scale, showing a sporogenous group (shaded). ( $\times 150$ .)
- Fig. 34. Ditto, more advanced. ( $\times 150$ .)
- Fig. 35. Ditto, still further developed. ( $\times 150$ .)
- Fig. 36. Ditto, the apex of the sporangium is now overarched by the more active surrounding tissue, the section having traversed the slit-like dimple, at the base of which the sporangium lies. ( $\times 150$ .)
- Fig. 37. Transverse section through a sorus traversing four young sporogenous groups. ( $\times 150$ .)
- Fig. 38. Similar section of part of an older sorus. ( $\times 150$ .)
- Fig. 39. Tangential section (such as along the line  $x, x$ , fig. 34), traversing two sporogenous groups, and illustrating the similarity of origin of the sporogenous groups, and of the septum. ( $\times 150$ .)
- Fig. 40. The slit-like dimple shown in tangential section is very narrow. ( $\times 150$ .)
- Fig. 41. The slit-like dimple in transverse section. ( $\times 150$ .)
- Fig. 42. Extension of irregular tracheides from the vascular bundle upwards into the base of the sorus. ( $\times 150$ .)

## PLATE 9.

- Fig. 43. Vertical section of mature sorus. ( $\times 20$ .)
- Fig. 44. Ground plan of mature sorus. ( $\times 20$ .)

*Marattia fraxinea* (SMITH). Figs. 45-64.

- Fig. 45. Very young sorus in vertical section. ( $\times 300$ .)
- Fig. 46. Ditto, older. ( $\times 300$ .) Compare line of section  $a, a$ , in fig. 47.
- Fig. 47. Tangential section, showing a sorus of the same age as fig. 46, in ground plan. ( $\times 300$ .)
- Fig. 48. A section through the young sorus corresponding to the line  $b, b$ , in fig. 47. ( $\times 300$ .)
- Fig. 49. Vertical section of rather older sorus ( $\times 300$ ), sporogenous group shaded.
- Figs. 50, 51. Ditto, still further advanced. ( $\times 300$ .)
- Figs. 52, 53. Transverse sections showing the common type of sporangium of age corresponding to fig. 51.
- Fig. 54. Transverse section rather older. ( $\times 300$ .)
- Figs. 55, 56, 57. Sections radial, tangential and transverse through a sporangium with sporogenous group ready to undergo separation, and tetrad division of the sporogenous cells. ( $\times 150$ .)

## PLATE 10.

- Fig. 58. Three sporangia of similar age to the above, showing how variable the size, form, and segmentation of the sporogenous groups may be. ( $\times 300$ .)

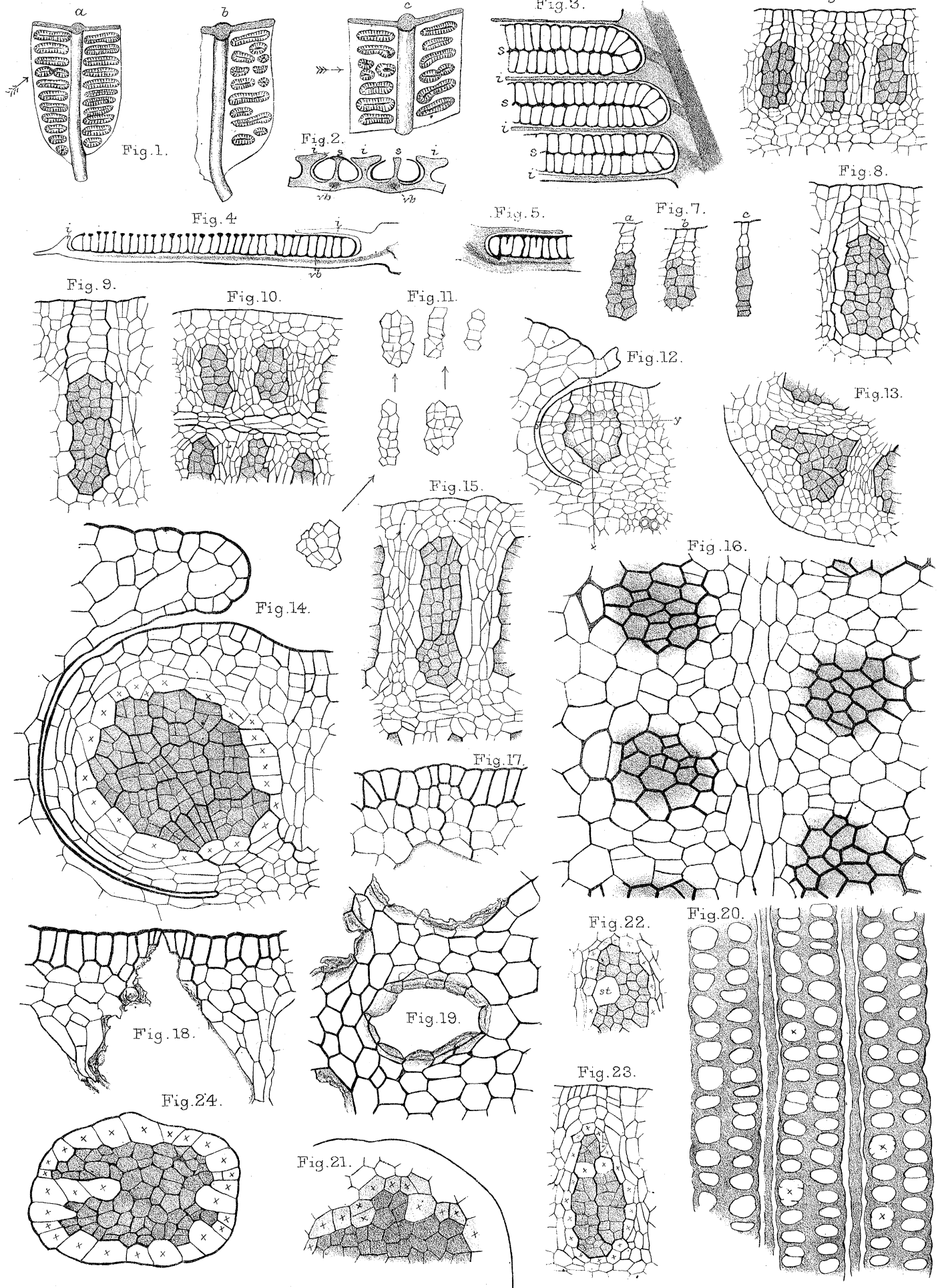
- Figs. 59, 60. Outlines of other sporogenous groups. ( $\times 300$ .)  
 Figs. 61, 62. Examples of sporogenous groups which appear referable in origin to more than a single parent cell. ( $\times 300$ .)  
 Fig. 63. Unusually large sporangium, showing ingrowth of tapetal cells, so as to encroach largely upon the sporogenous tissue. ( $\times 150$ .)  
 Fig. 64. Partial septation of a sporangium; the tapetal septum is complete, but there is only a slight indication of encroachment of permanent tissue on the loculus. Compare figs. 29, 30 of *Danæa*. ( $\times 150$ .)

*Angiopteris evecta* (HOFFM.). Figs. 65–81.

- Fig. 65. Part of a young sorus, seen in surface view from without. ( $\times 300$ .)  
 Fig. 66. Vertical (radial) section of a sporangium, such as would be seen on cutting the sporangium (*b*) of fig. 65, along a line *x, x*. ( $\times 300$ .)  
 Fig. 67. Tangential section through a similar sporangium. ( $\times 300$ .)  
 Fig. 68. An older sporangium in vertical (radial) section. ( $\times 300$ .)  
 Fig. 69. Transverse section of a similar sporangium along the line *x, x*, in fig. 68. ( $\times 300$ .)  
 Fig. 70. Tangential section of a rather bulky sporangium showing such structure as might be seen if fig. 68 were cut in a plane *y, y*. ( $\times 300$ .)

PLATE 11.

- Fig. 71. Vertical (radial) section of an older sporangium, which still shows the genetic grouping of the cells. ( $\times 300$ .)  
 Fig. 72. A similar section of an older sporangium. ( $\times 300$ .)  
 Fig. 73. Transverse section of a similar sporangium, such as along a line *z, z*, in fig. 72. ( $\times 300$ .)  
 Fig. 74. Tangential section of a similar sporangium, such as along a line *y, y*, in fig. 72. ( $\times 300$ .)  
 Fig. 75. Apical region of an almost mature sporangium in tangential section, showing the thin-walled cells which define the line of dehiscence. ( $\times 300$ .)  
 Fig. 76. Apex of an almost mature sporangium, seen from above; such a section as along the line *x, x*, in fig. 72. ( $\times 150$ .)  
 Fig. 77. Transverse section of an almost mature sporangium. ( $\times 300$ .)  
 Fig. 78. *a, b, c*, irregularities of sori. ( $\times 35$ .)  
 Figs. 79, 80, 81. Sporangia from the same pinnule, cut transversely. Fig. 79 is normal. Figs. 80, 81 show very large sporangia, with indications of a partial septation in fig. 81. ( $\times 300$ .)

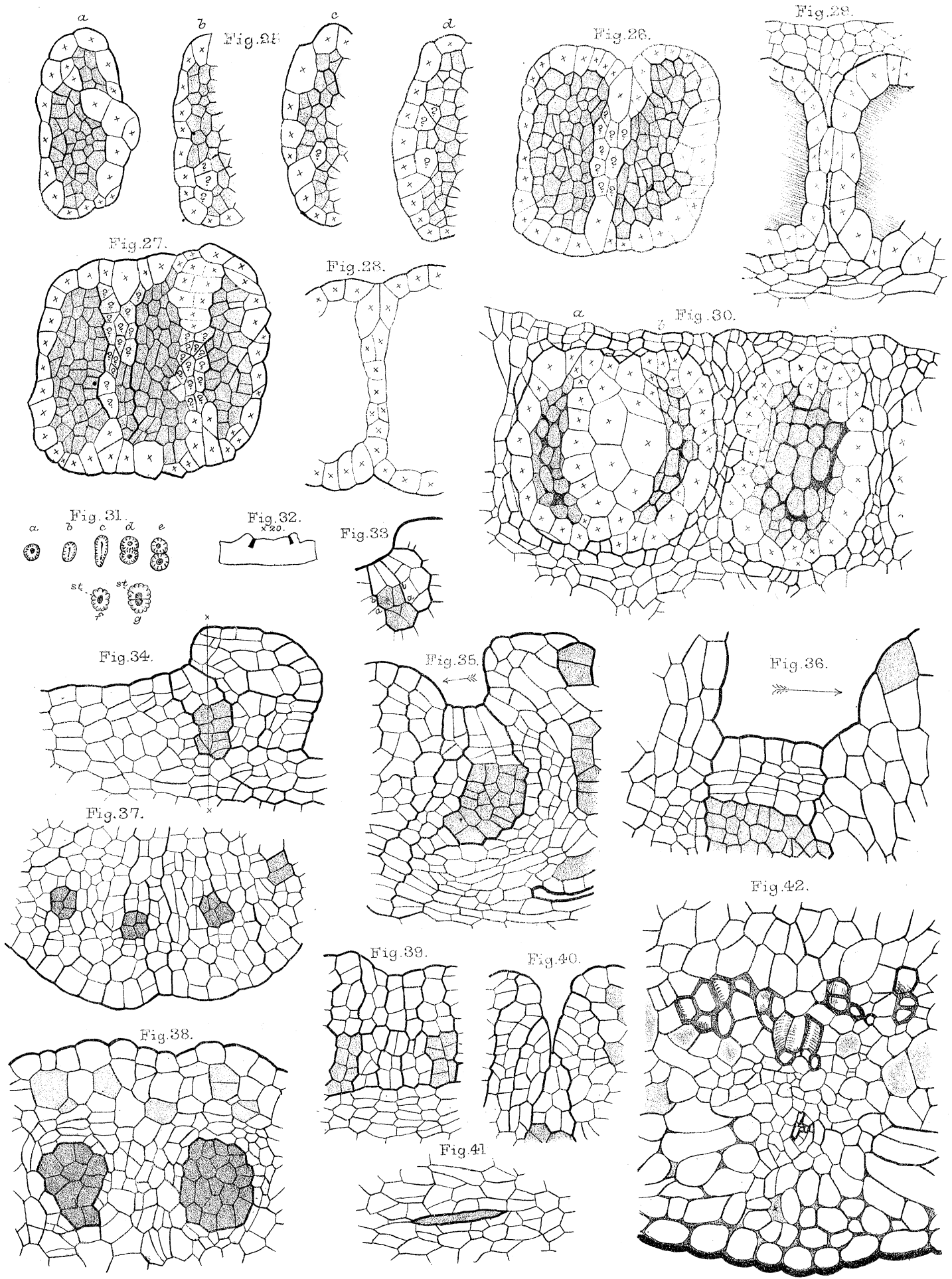


F.O. Bower del.

West, Newman lit

Figs. 1-24. Danæa





Figs. 25-30. *Danaea elliptica*, Sm.  
Figs. 31-42. *Kaulfussia aesculifolia*, Blume.

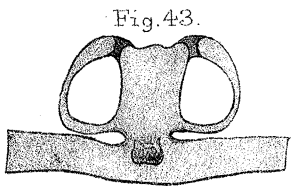


Fig. 43.

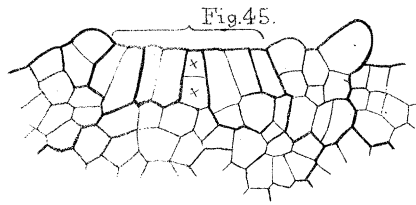


Fig. 45.

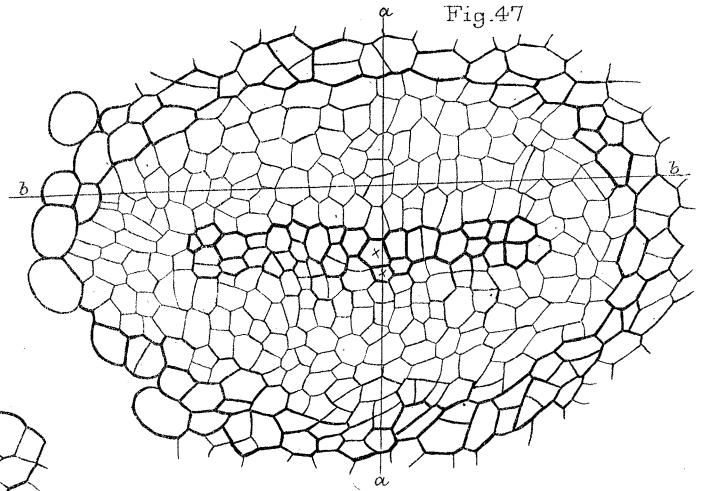


Fig. 47

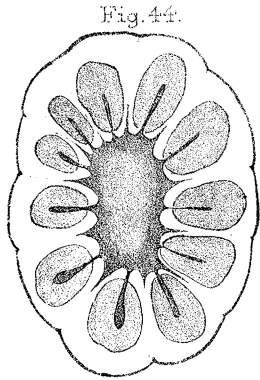


Fig. 44.

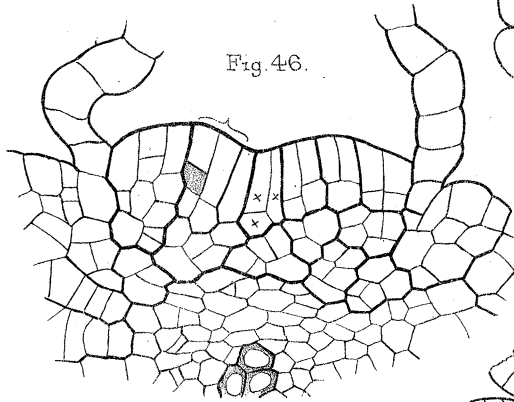


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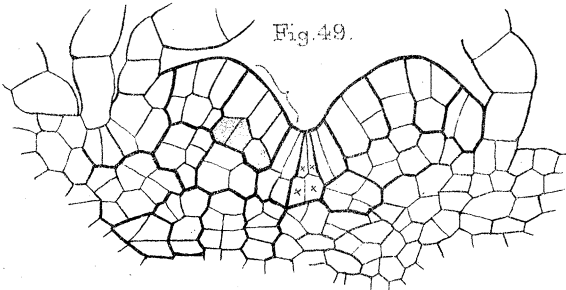


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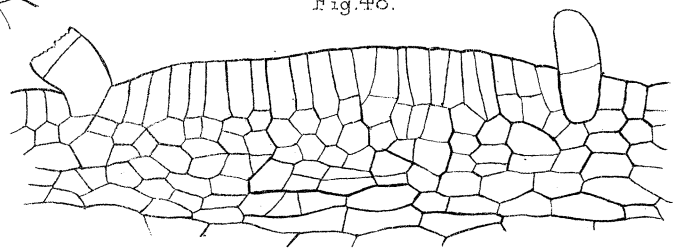


Fig. 48.

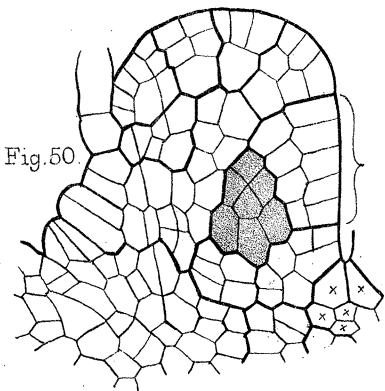


Fig. 50

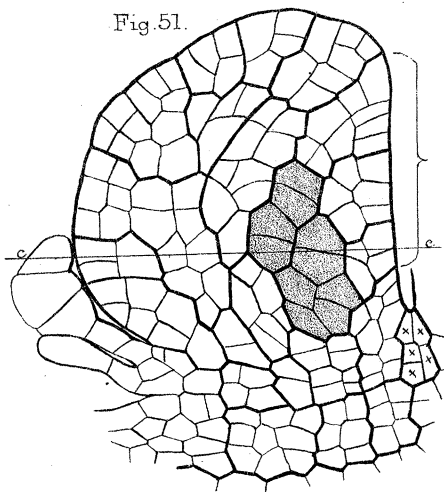


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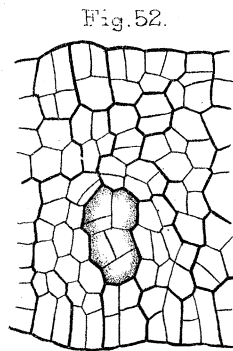


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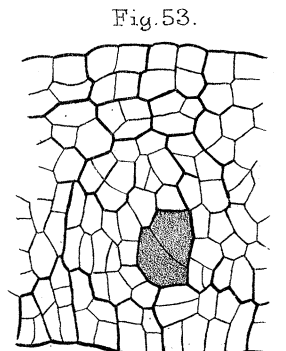


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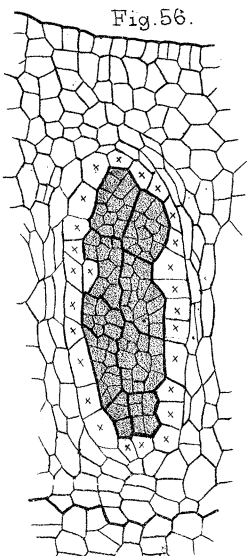


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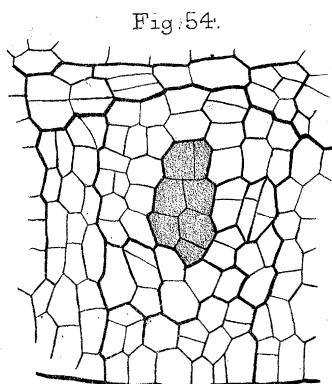


Fig. 54.

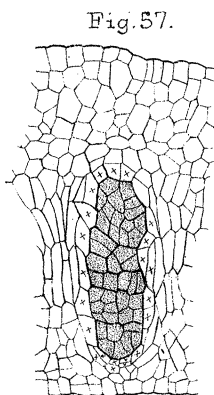


Fig. 57.

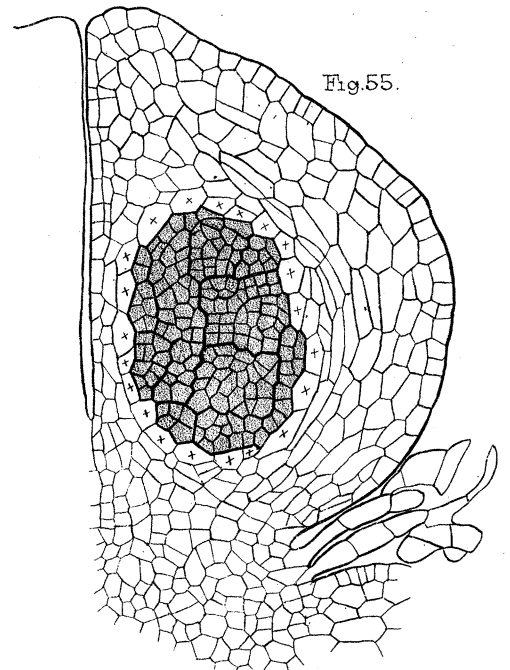


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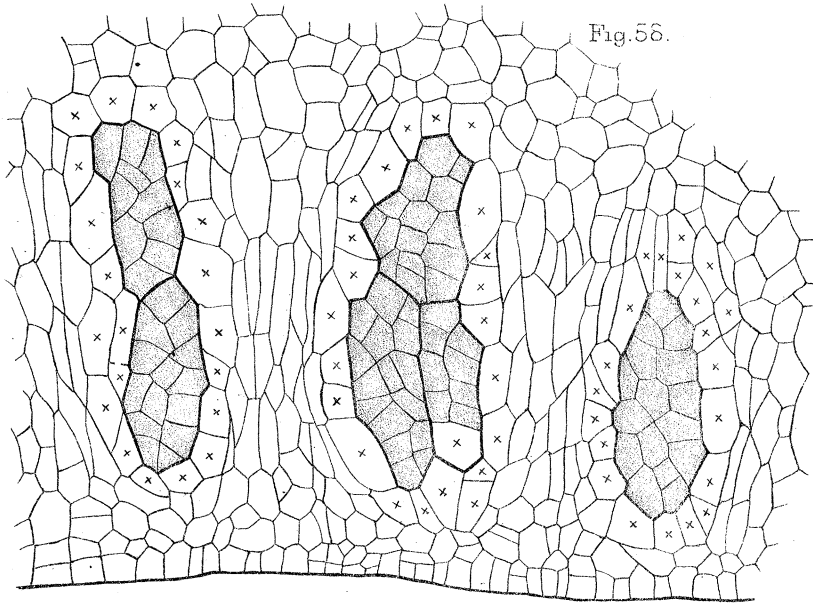


Fig. 58.

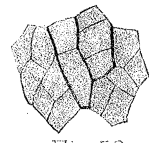


Fig. 59.

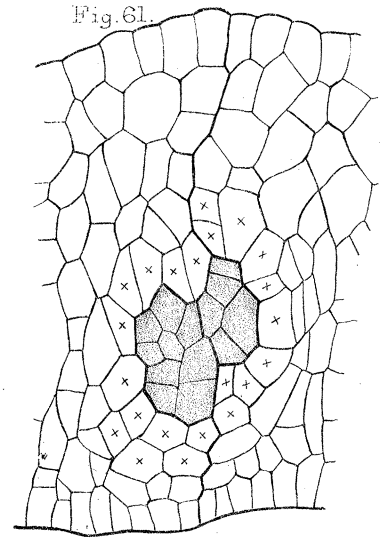


Fig. 61.



Fig. 60.

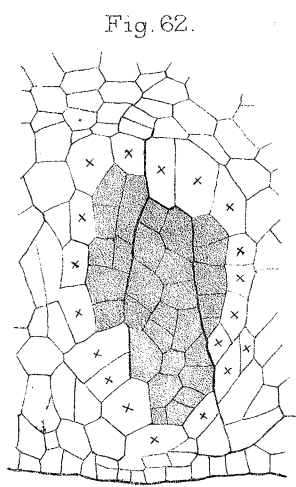


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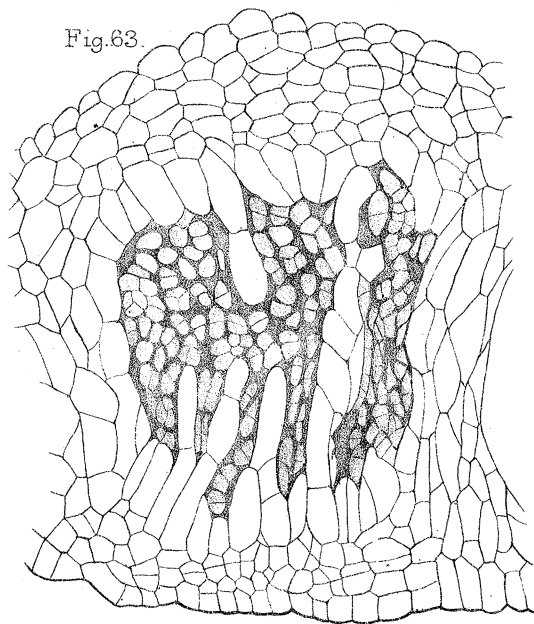


Fig. 63.

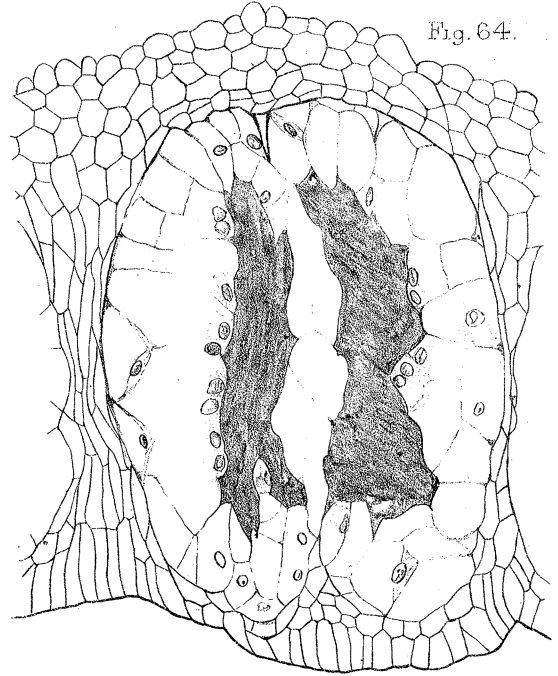


Fig. 64.

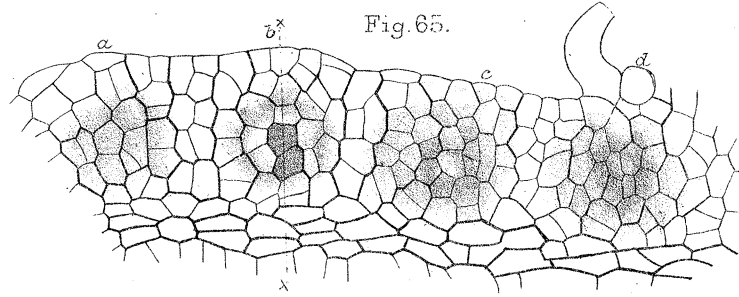


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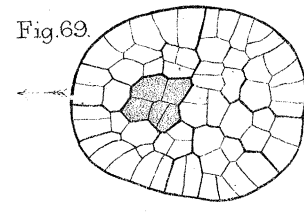


Fig. 69.

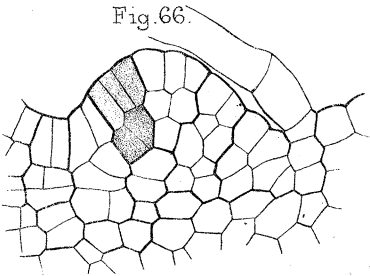


Fig. 66.

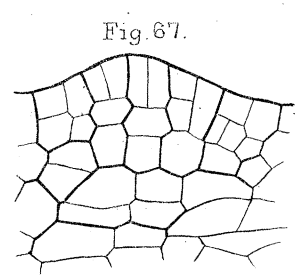


Fig. 67.

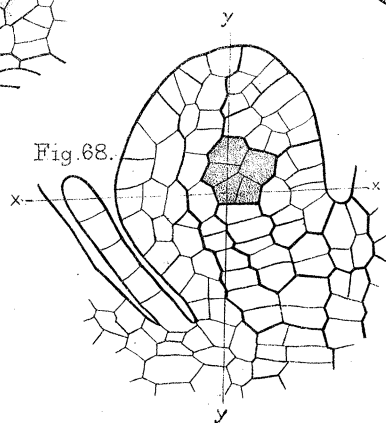


Fig. 68.

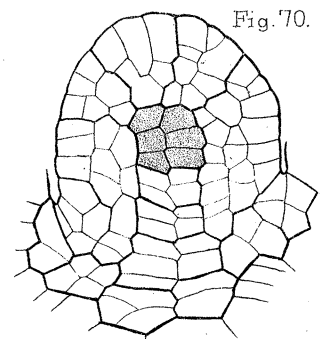
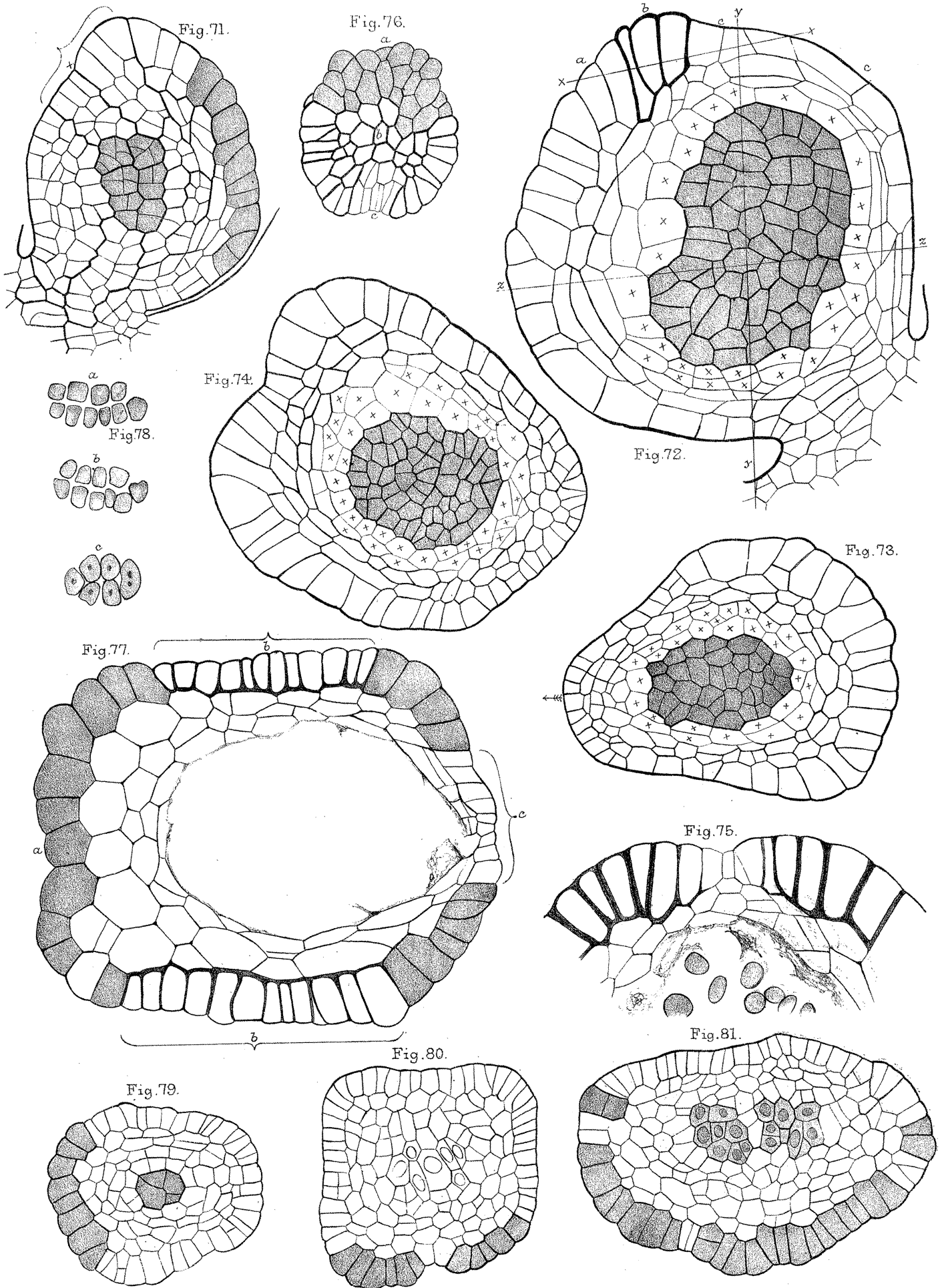


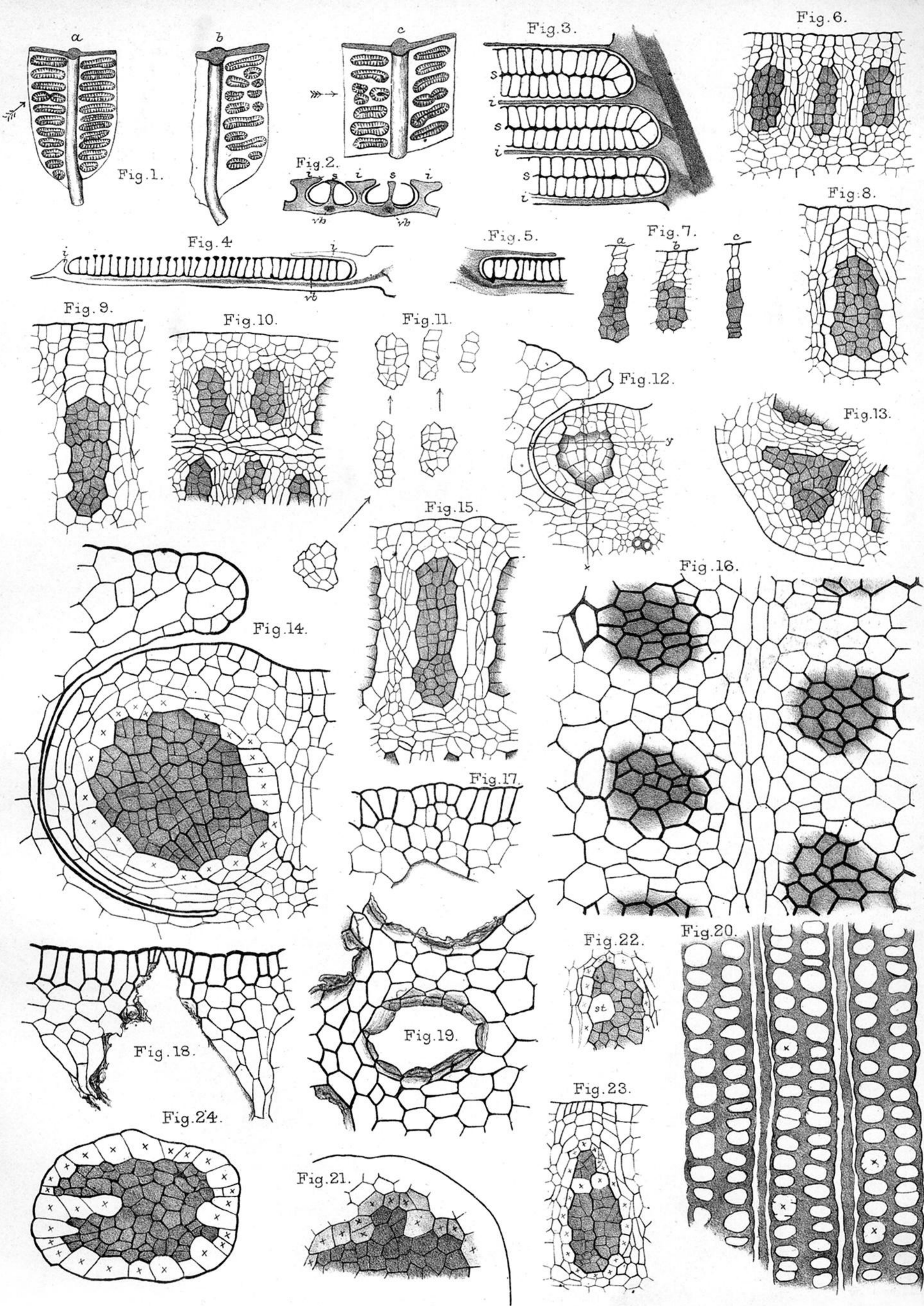
Fig. 70.

F.O. Bower del.

West, Newman lith.

Figs. 58-64. *Marattia fraxinea*. Smith.  
Figs. 65-70. *Angiopteris evecta*. Hoffm.





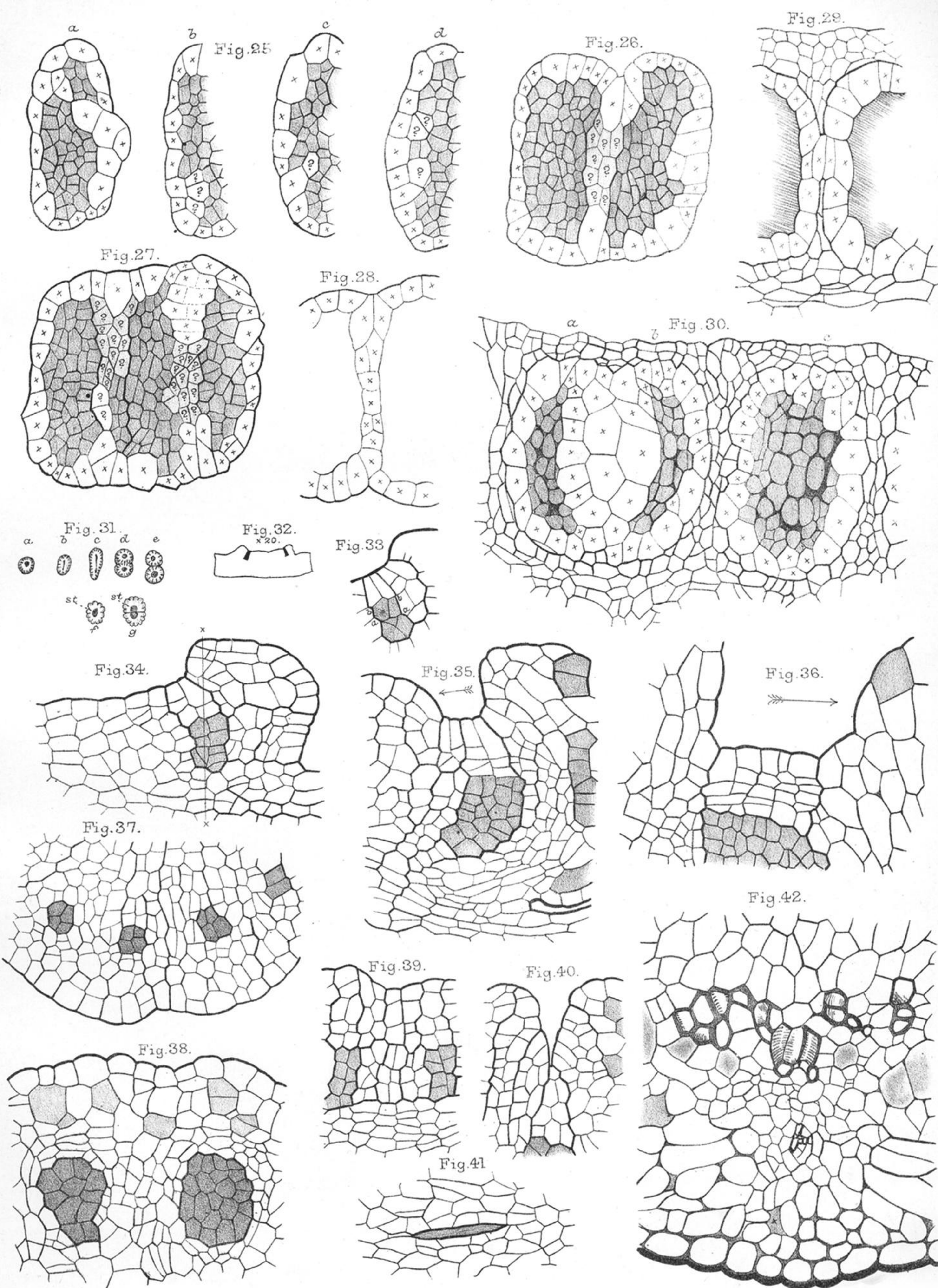
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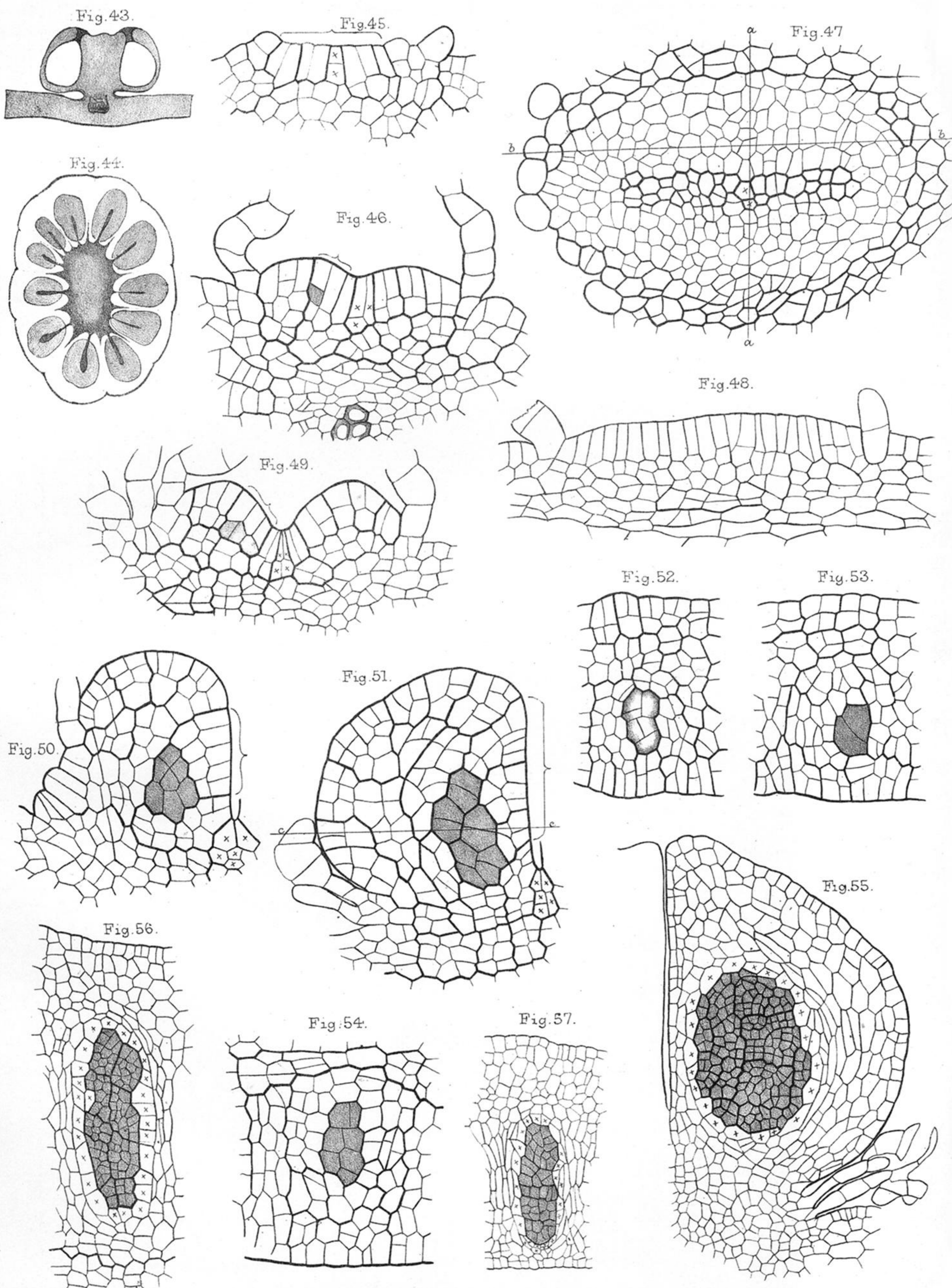
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 Figs. 31-42. *Kaultussia æsculifolia*, Blume.

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*Kaultussia æsculifolia* (BLUME). Figs. 31-44.

- Fig. 31. Sori of *Kaultussia*, showing states of partial to complete abstriction; *f, g*, are seen from below; *st* is the common stalk of the double sorus.
- Fig. 32. Young condition of the sorus, which is but slightly raised above the surface of the leaf, as seen in vertical section; the position of the two sporangia is indicated by shading. ( $\times 20$ )
- Fig. 33. Part of a similar section on a larger scale, showing a sporogenous group (shaded). ( $\times 150$ )
- Fig. 34. Ditto, more advanced. ( $\times 150$ )
- Fig. 35. Ditto, still further developed. ( $\times 150$ )
- Fig. 36. Ditto, the apex of the sporangium is now overarched by the more active surrounding tissue, the section having traversed the slit-like dimple, at the base of which the sporangium lies. ( $\times 150$ )
- Fig. 37. Transverse section through a sorus traversing four young sporogenous groups. ( $\times 150$ )
- Fig. 38. Similar section of part of an older sorus. ( $\times 150$ )
- Fig. 39. Tangential section (such as along the line *x, x*, fig. 34), traversing two sporogenous groups, and illustrating the similarity of origin of the sporogenous groups, and of the septum. ( $\times 150$ )
- Fig. 40. The slit-like dimple shown in tangential section is very narrow. ( $\times 150$ )
- Fig. 41. The slit-like dimple in transverse section. ( $\times 150$ )
- Fig. 42. Extension of irregular tracheides from the vascular bundle upwards into the base of the sorus. ( $\times 150$ )



Figs. 43-44. *Kaulfussia æsculifolia*. Blume.  
 Figs. 45-57. *Marattia fraxinea*. Smith.

PLATE 9.

Fig. 43. Vertical section of mature sorus. ( $\times 20$ .)

Fig. 44. Ground plan of mature sorus. ( $\times 20$ .)

*Marattia fraxinea* (SMITH). Figs. 45-64.

Fig. 45. Very young sorus in vertical section. ( $\times 300$ .)

Fig. 46. Ditto, older. ( $\times 300$ .) Compare line of section  $a, a$ , in fig. 47.

Fig. 47. Tangential section, showing a sorus of the same age as fig. 46, in ground plan. ( $\times 300$ .)

Fig. 48. A section through the young sorus corresponding to the line  $b, b$ , in fig. 47. ( $\times 300$ .)

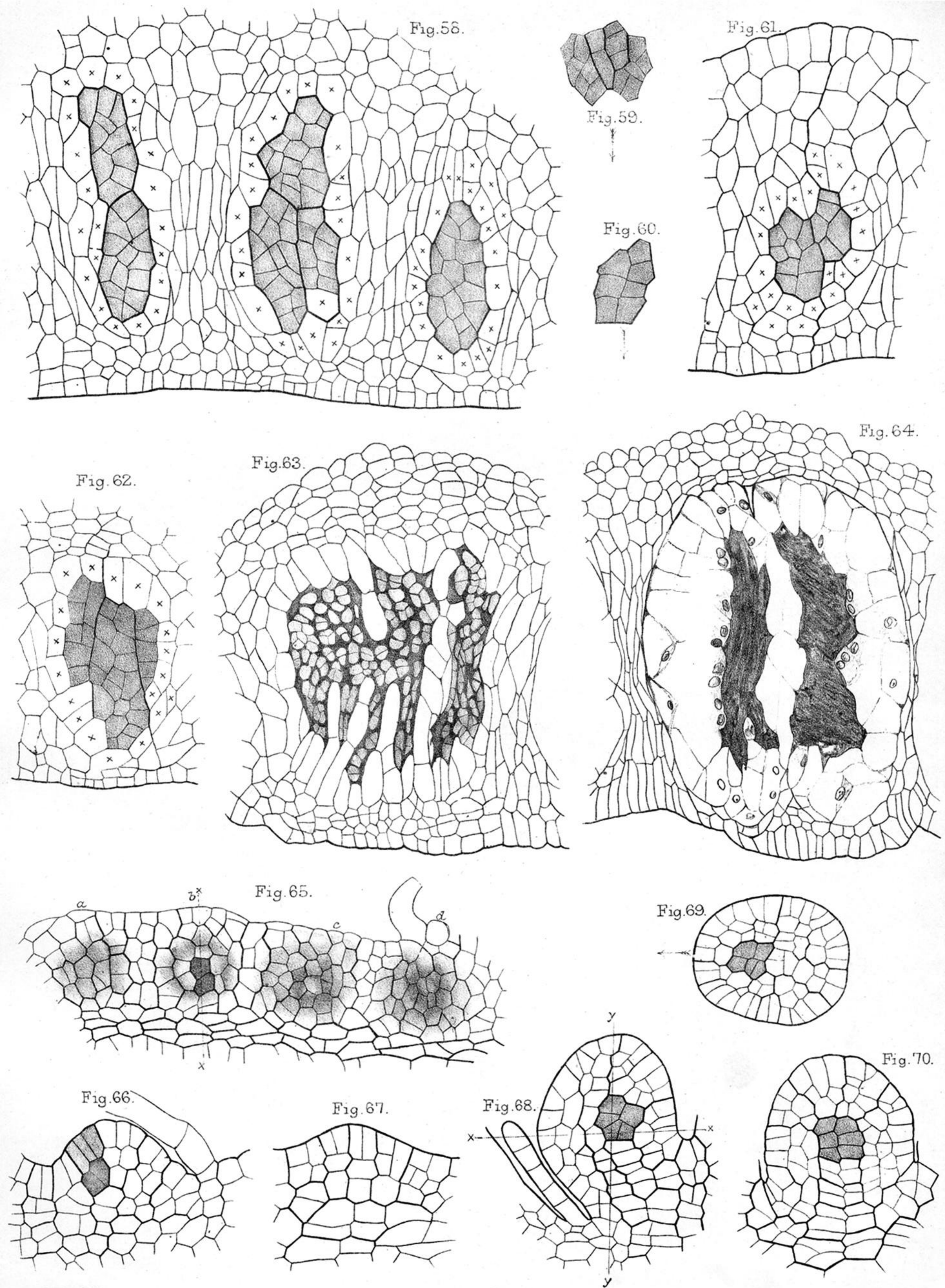
Fig. 49. Vertical section of rather older sorus ( $\times 300$ ), sporogenous group shaded.

Figs. 50, 51. Ditto, still further advanced. ( $\times 300$ .)

Figs. 52, 53. Transverse sections showing the common type of sporangium of age corresponding to fig. 51.

Fig. 54. Transverse section rather older. ( $\times 300$ .)

Figs. 55, 56, 57. Sections radial, tangential and transverse through a sporangium with sporogenous group ready to undergo separation, and tetrad division of the sporogenous cells. ( $\times 150$ .)



Figs. 58-64. *Marattia fraxinea*. Smith.  
 Figs. 65-70. *Angiopteris evecta*. Hoffm.

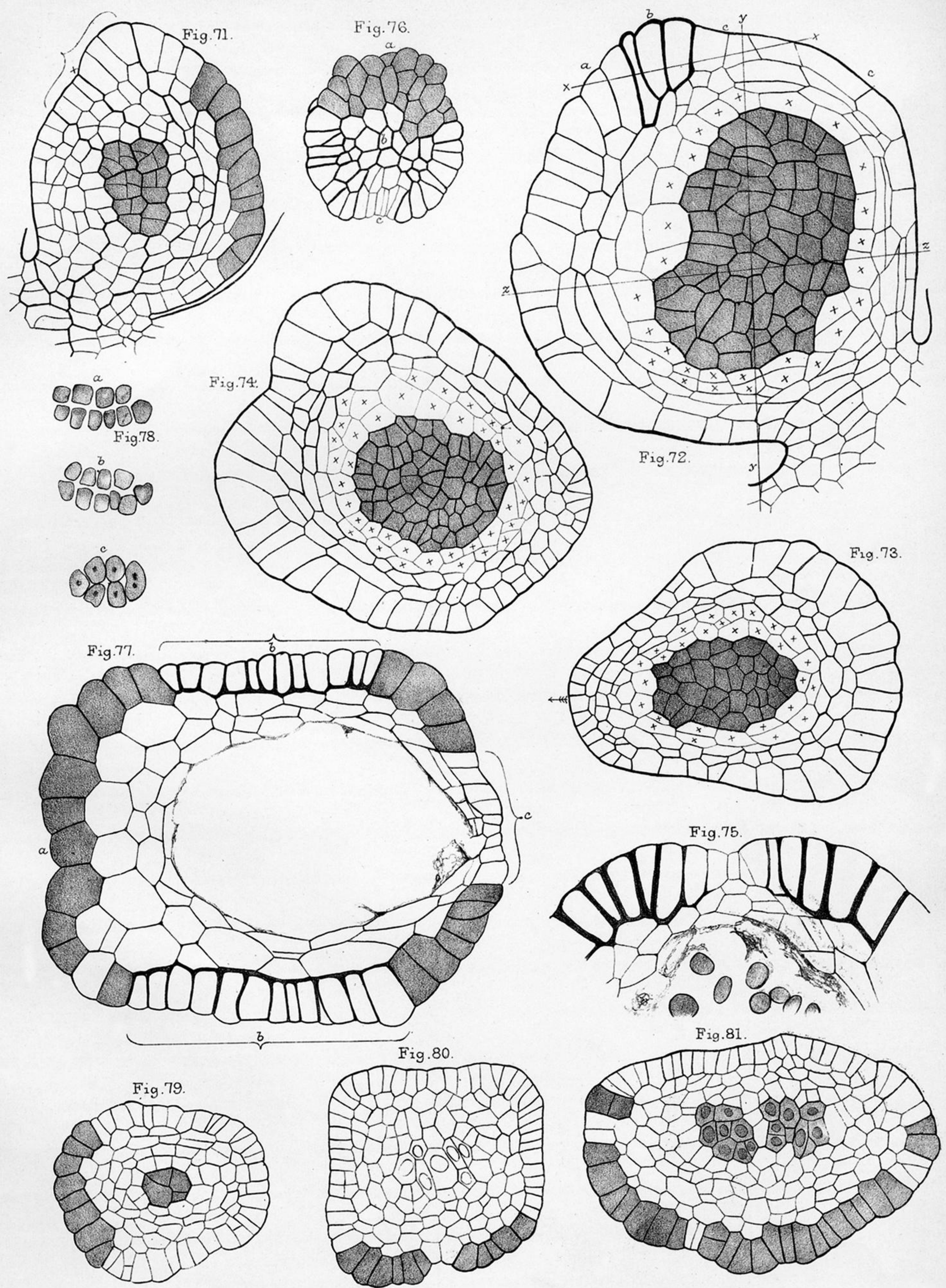
PLATE 10.

- Fig. 58. Three sporangia of similar age to the above, showing how variable the size, form, and segmentation of the sporogenous groups may be. (× 300.)
- Figs. 59, 60. Outlines of other sporogenous groups. (× 300.)
- Figs. 61, 62. Examples of sporogenous groups which appear referable in origin to more than a single parent cell. (× 300.)
- Fig. 63. Unusually large sporangium, showing ingrowth of tapetal cells, so as to encroach largely upon the sporogenous tissue. (× 150.)
- Fig. 64. Partial septation of a sporangium; the tapetal septum is complete, but there is only a slight indication of encroachment of permanent tissue on the loculus. Compare figs. 29, 30 of *Danaea*. (× 150.)

*Angiopteris evecta* (HOFFM.). Figs. 65-81.

- Fig. 65. Part of a young sorus, seen in surface view from without. (× 300.)
- Fig. 66. Vertical (radial) section of a sporangium, such as would be seen on cutting the sporangium (b) of fig. 65, along a line x, x. (× 300.)
- Fig. 67. Tangential section through a similar sporangium. (× 300.)
- Fig. 68. An older sporangium in vertical (radial) section. (× 300.)
- Fig. 69. Transverse section of a similar sporangium along the line x, x, in fig. 68. (× 300.)
- Fig. 70. Tangential section of a rather bulky sporangium showing such structure as might be seen if fig. 68 were cut in a plane y, y. (× 300.)





Figs.71-81. *Angiopteris evecta* Hoffm.

PLATE 11.

Fig. 71. Vertical (radial) section of an older sporangium, which still shows the genetic grouping of the cells. ( $\times 300$ .)

Fig. 72. A similar section of an older sporangium. ( $\times 300$ .)

Fig. 73. Transverse section of a similar sporangium, such as along a line  $z, z$ , in fig. 72. ( $\times 300$ .)

Fig. 74. Tangential section of a similar sporangium, such as along a line  $y, y$ , in fig. 72. ( $\times 300$ .)

Fig. 75. Apical region of an almost mature sporangium in tangential section, showing the thin-walled cells which define the line of dehiscence. ( $\times 300$ .)

Fig. 76. Apex of an almost mature sporangium, seen from above; such a section as along the line  $x, x$ , in fig. 72. ( $\times 150$ .)

Fig. 77. Transverse section of an almost mature sporangium. ( $\times 300$ .)

Fig. 78.  $a, b, c$ , irregularities of sori. ( $\times 35$ .)

Figs. 79, 80, 81. Sporangia from the same pinnule, cut transversely. Fig. 79 is normal. Figs. 80, 81 show very large spores, with indications of a partial septation in fig. 81. ( $\times 300$ .)