The comparative examination of the meristems of Ferns, as a Phylogenetic Study.

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With Plates **XX, XXI, XXII, XXIII, and XXIV.**

INTRODUCTORY REMARKS.

IT is the ultimate aim of all working morphologists who entertain a view of evolution in one form or another, to reconstruct as nearly as possible from the fragmentary records at our disposal the developmental tree. All must however feel that not only is the series too greatly broken to allow of launching out with certainty upon definite views as to the exact relation of existing forms, but also that our knowledge of the details of structure and development of many of the organisms we see living before us is too slight to provide sound ground for argument. At the same time, no details are to be considered as too trivial provided their value be not over-estimated. It is the interest and the duty of investigators at present to attempt to build up short branches of the main tree, rather than to hazard guesses as to the relation of organisms which are but remotely connected; by careful investigation to arrange the more closely related organisms serially according to their characters, in the hope that this may lead to the affinities of such series to others being the more clearly recognised at

[*Annals of Botany*, Vol. III. No. XI. August, 1889.]

either one end or the other. More especially is it desirable that such series should be as strictly defined as possible in those parts of the organic system which obviously lead as connecting links from the lower to the higher, and in no part of the vegetable kingdom is such definition more necessary than in the Vascular Cryptogams. These are admitted to be a transition series from the simpler forms of Algal-Bryophytic affinity to the Phanerogams. It is now generally accepted that there have been at least three series of the Vascular Cryptogams, which after their first origin developed independently of one another: viz. the Lycopodineae, the Equisetineae, and the Filicineae; the more clearly we are able to parcel out the members of these series according to their true affinities among themselves, the less complex will the problem become of recognising the relations of the series one to another, and their connection severally with the forms lower or higher in the main series of plants.

It is reflections such as these which have led me from time to time to devote attention to the Filicineous series of Vascular Cryptogams, and it is the object of the present pages to give a general account of the characters of the meristematic tissues of root, stem, leaf, and sporangium in a number of these plants. Many facts regarding them are already well known, and these, together with freshly acquired facts, will be found sufficient to demonstrate that even in a character so apparently special as the structure of the meristematic tissues, these plants form a natural series.

The distinction between eusporangiate and leptosporangiate forms, according as the sporangium is derived from a single cell or from a group of cells, was first emphasised by Goebel¹, and it has been generally adopted. It will be shown, however, and Goebel himself contemplates this as possible², that this distinction cuts in two what is obviously a natural and continuous series: that though it is useful to recognise the difference between plants in which the sporan-

¹ Bot. Zeit. 1881, p. 717.

² Schenk's Handbuch, III, p. 387.

gium originates only from a single cell, and those in which it has a pluricellular origin, it would be a mistake to accentuate this distinction, for it will be seen below that the Filicineous series leads from the one type to the other by gradual steps, and it is only among Filicineae that leptosporangiate forms are known. Further, it will be shown that as we pass along the series of Ferns from the leptosporangiate to the eusporangiate forms, an increase of complexity of structure more or less marked is to be seen, not only in the sporangium, but in every one of the meristematic tissues: in fact, that the progress in complexity from the leptosporangiate to the eusporangiate Ferns not only involves the increased bulk and robustness of the sporangium, but may be taken as an indication of a more bulky type of development of all the parts of the plant: it will be shown that just as in passing along the series the sporangium of unicellular origin in the Hymenophyllaceae and Polypodiaceae becomes the massive sporangium of *Marattia*, so also as we review the series, we pass from the root with one clearly defined apical cell to that with several initials, while a similar transition from a simple to a more complex construction is to be noted in the apices of stem, and leaf, and even in the mode of origin of the wings of the leaves.

The above remarks will suffice to indicate the general scope of the present memoir: the theoretical considerations which will follow from this comparative study of the meristems of Ferns will be deferred to the concluding paragraphs.

In order to bring out the more clearly the fact that the progress from the simpler to the more complex is exemplified in each of the meristems of root, stem, leaf, wing, and sporangium, each of these parts will be dealt with separately, and their characters traced in a series of examples, and it may be stated that, with few exceptions, the same species have been used for the investigation of each of the above-named parts. So as to preserve some uniformity of treatment, the forms investigated will be taken in regular sequence; the Hymenophyllaceae first, because of their greater simplicity of con-

struction ; then the rest of the leptosporangiate Ferns¹, with the Schizaeaceae as a group leading towards the Osmundaceae, which in turn lead on to the Marattiaceae.

The material necessary for this investigation is for the most part rare : the specimens of *Trichomanes* and *Hymenophyllum*, as well as some others, have been supplied from Kew, and I wish to record my thanks to the Director of the Royal Gardens for this, and for the use of the Jodrell Laboratory, in which much of this work was conducted. Other specimens were derived from the Glasgow Garden, while the specimens of *Marattia* and *Angiopteris* were from my collections made in Ceylon.

APICES OF ROOTS.

I am not aware that any observations of the structure of the apex of the root in any of the Hymenophyllaceae have been recorded, beyond the remark of Prantl² that one conical apical cell is present in *Gonocormus* (*Trichomanes*) *dichotomus*, which he figures in longitudinal optical section in his Plate I, Fig. 8. I have had the opportunity of observing the apex of the roots of *Trichomanes radicans*, and of *Hymenophyllum demissum* : in both of these the structure was found to conform to the normal type for the root of leptosporangiate Ferns, as described by Naegeli and Leitgeb³, and accordingly there is no need here for a special description or for figures : it may, however, be remarked that the structure as shown in Prantl's Fig. 8, above quoted, does not convey the impression of the exact sequence of the cell-divisions being normal ; but as the figure was drawn, not from a section, but from an apex cleared by reagents, and seen in optical section, the slight discrepancy need be no obstacle to the conclusion that the

¹ I do not think it necessary for the present argument to arrange these leptosporangiate Ferns in any definite sequence, since their relation to one another is still uncertain, while the construction of their meristems appears to be almost uniform.

² Unters. z. Morph. d. Gefässkrypt. Heft I, p. 31.

³ Beitr. z. wiss. Bot. Heft IV, 1868.

typical apex of the root of Hymenophyllaceae is coincident in structure with that of other leptosporangiate Ferns.

The apex of the root has been investigated in a large number of other leptosporangiate Ferns: e.g. by Naegeli and Leitgeb (l. c.) in *Asplenium Filix-foemina*, *Pteris aquilina* and *hastata*, *Platyserium alcorni*, *Blechnum occidentale*; by Hofmeister in *Aspidium Filix-mas*¹; by Hanstein in *Marsilia*²; by Strasburger in *Pteris cretica*³, and in *Azolla*⁴, etc., etc. I have also myself investigated the apices of roots of *Cyathea insignis*, Eat., *Gleichenia circinata*, Sw., *Gl. flabellata*, R. Br., *Gl. rupestris*, *Lygodium scandens*, *Aneimia hirta*, and *Phyllitidis*, and *Pilularia globulifera*. It will be seen that among the plants above noted there are representatives of all the families of leptosporangiate Ferns, including the Hydropterideae: in all of them the organic apex of the root conforms in structure to the type laid down by Naegeli and Leitgeb: all have a single, three-sided, pyramidal apical cell, from the sides of which segments are cut off in regular succession by walls parallel to the three sides, and these are formative of the body of the root: after each series of three such segments a fourth is cut off from the base of the pyramidal cell, and such segments are formative of the root-cap. This type of construction has been represented diagrammatically by Sachs⁵ in a figure which is here reproduced (Fig. 1): in this it is to be noted that the centre of construction (*S*) of the whole system of curves lies within the apical cell itself, and that the whole (exclusive of the root-cap) falls under that series of systems of construction which are designated as *confocal*⁶: there may be slight variations in detail of the succession of the segmentations; thus Kny notes

¹ Higher Cryptogamia, Ray Soc. Plate XXVI.

² Pringsh. Jahrb. IV, p. 230.

³ Practicum, p. 278.

⁴ Ueber *Azolla*, p. 45.

⁵ Arbeiten d. Bot. Inst. Würzb. Bd. II, Taf. IV, Fig. 12.

⁶ Compare Sachs' Lectures, Clarendon Press, 1887, p. 451. The term 'confocal' applies properly to the body of the root only, the root-cap being coaxial: but still this type may for brevity be termed confocal to distinguish it from that in which the construction of the body of the root is coaxial.

in *Ceratopteris*¹ that the succession of three segments from the sides and then one from the base is not strictly maintained, but that the number of segments cut off from the sides is considerably greater than three to each segmentation from the base: differences of detail may also be noted in the further subdivision of the segment; but still, putting aside these exceptions, the type for the roots of all the leptosporangiate Ferns, including also the Schizaeaceae, seems to be quite clearly definite, and constant. This uniformity of structure makes those deviations from that type, which will now be described for the roots of the Osmundaceae, more noteworthy than they would otherwise appear.

An examination of the apex of the root of the Osmundaceae has shown that its structure does not conform strictly to this simple type of the leptosporangiate Ferns, while there is considerable variation in detail, even in different roots taken from the same individual plant. Among the many roots of *Osmunda regalis* which I have examined, some few show a certain similarity in the confocal type: thus in transverse sections a single three-sided pyramidal apical cell may occasionally be found; but even when this is the case the structure does not show that diagrammatic regularity which is so characteristic of the roots of the leptosporangiate Ferns (Fig. 2). Other roots of *Osmunda* show in transverse sections other irregularities, such as a single four-sided apical cell, or two such four-sided initial cells, etc.; but of all the aberrant modes of arrangement of the cells of the apical meristem found in the roots of *Osmunda regalis*, that which is most interesting from a theoretical point of view is that represented in the Figs. 3, 4. In these figures it may be seen that the whole tissue is referable in its origin to three initial cells, which are marked (x), while the three walls separating these cells from one another meet at a central point. These three walls are drawn in heavier lines in the figures, and may be traced for some distance from the central point: they may be called the principal walls. In each case the portion of tissue derived from one of these initial cells is

¹ Parkeriaceae, p. 48.

enclosed between two of these principal walls, and thus the whole meristem may be regarded as consisting of three wedge-shaped masses. Taking now those masses singly into consideration, it will be clearly seen that in Fig. 3 each is divided into two unequal parts by walls marked (*s*), which do not proceed to the centre, but on passing towards it curve gradually out of the radial plane, and insert themselves at right angles on the principal walls: these may be called the sextant-walls. A similar arrangement, but less clearly marked, may be seen in such examples as that represented in Fig. 4. In each case the error of regarding sections below the real initial cell or cells as including the initial cells, has been carefully avoided by comparing the whole series of sections cut from each individual root.

For comparison with this arrangement of the initial cells and their derivatives I have quoted as Fig. 5 one of the drawings of Naegeli and Leitgeb, which appeared in their well-known work, 'Entstehung und Wachsthum der Wurzeln,' as Taf. XII, Fig. 8. This represents a view of the structure seen immediately below the apical cell in the root of *Pteris hastata*, and it will be seen that in the most essential points the structure of its central portion is similar to that in Figs. 3 or 4: and if we imagine these principal (*p*) and sextant-walls (*s*) to be continued upwards in *Pteris* or any leptosporangiate Fern, till they reach the root-cap, a structure of the root-apex would result which would correspond to that observed in certain cases in *Osmunda regalis*: in other words, accepting the view of Sachs that the apical cell is a gap in the system of construction, such roots as these of *Osmunda regalis* show the gap less complete, and the three principal walls continued through it, so as to divide it into three parts.

Since the characters of the meristem in the root of *Osmunda* have thus been shown to be subject to variation, and since it is hardly possible to determine with certainty from longitudinal sections what is the actual number and form of the initial cells, a full and exact interpretation of the structure in longitudinal sections cannot be expected. In the majority of

cases, cells of a pyramidal form have been found occupying an approximately central position in median sections: but in no single instance has an apical cell been observed having that regularity of form, and of the arrangement of its segments, together with the central position, which are so characteristic of the roots described by Naegeli and Leitgeb. Taking as the first example (Fig. 6) one of those which approaches most nearly to that type, the pyramidal apical cell (x) can be readily recognised; but a comparison with the figures of Naegeli and Leitgeb, or with Fig. 1, shows certain points of difference. In the first place there is a difference in the form of the cell itself; it is in *Osmunda* proportionately narrower and deeper, that is, more elongated in a longitudinal direction, and consequently the principal walls by which it is bounded laterally are less inclined to the longitudinal axis. Secondly, the arrangement of the cells surrounding the pyramidal cell does not show any definite regularity, and it is thus difficult to ascertain their genetic connections. This irregularity is found not only in the tissue adjoining the sides of the pyramidal cell, but also in those which have been derived from its base, and will go to form tissues of the root-cap. This, it may be stated, is one of the most regular examples of the apex of the root of *Osmunda* which I have observed.

A further point to be noted in Fig. 6, as also in Fig. 7, is that in point of size the wedge-shaped cell is smaller in comparison with the adjoining cells, than is the case in other Ferns: whereas in Naegeli's figures the area of the apical cell equals or exceeds that of any of the surrounding cells, in *Osmunda* it is often smaller than they. In the apex represented in Fig. 7, a central pyramidal cell is clearly seen: here, though there is no marked ascendancy of the neighbouring cells in point of size, still if the genetically connected groups of cells, enclosed between the successive anticlinal walls be taken into consideration as products of successive segments, it is clear that the construction here differs considerably from the ordinary confocal type; the ascendancy of the apical cell is less marked, and periclinal walls predominate, while the anticlinal

walls present a distinctly convex internal surface: thus while in this root a cell is present which may be recognised as a pyramidal apical cell, the whole construction approaches that of the co-axial or fan-like type.

Lastly, the less common, but very interesting arrangement shown in Figs. 8 and 9 must be mentioned. Here no pyramidal cell is to be found; the median longitudinal section shows two cells (x, x) of truncated pyramidal form, from which segments are cut off, (1) from the base, to form tissues of the root-cap; (2) from the sides, and (3) as shown in Fig. 8, from the truncated apex also. In this case the correspondence with Schwendener's description¹ of the apical group in the root of the Marattiaceae is very apparent.

It has been demonstrated repeatedly by various authors that in the cases of *Equisetum* and many Ferns there is a certain order of succession and regularity of position of those walls by which the segments are divided up into smaller cells. A comparison of the drawings above quoted, with those of Naegeli and Leitgeb, will suffice to show that in *Osmunda* the outer limit of the procambial cylinder does not appear to correspond to any definitely recurring wall in the young segments, as is the case in the roots investigated by Naegeli. The same may be said with respect to the limits of the cortex and epidermis; the latter tissue, which can readily be recognised in the older part of the root, and can be traced as entering below the layers of the root-cap, loses its identity at a considerable distance from the actual organic apex of the meristem. This fact is illustrated in the Figs. 6 and 9: in neither of these examples can a clear distinction be drawn between those cells which will develop as tissue of the root-cap and those which will form epidermis or cortex.

The results now detailed have been further supported by observations on young developing lateral roots: in Fig. 10 is shown a young lateral root in median section, and here are seen two oblong initial cells which accord in form and position to those shown in Fig. 8, while the case of Fig. 11 shows a

¹ Sitz. d. K. Preuss. Akad. d. Wiss. 1882.

single pyramidal cell narrower than that of Naegeli's type, and corresponding in many points to that of the older root shown in Fig. 6.

For comparison with *Osmunda regalis* the roots of *Todea barbara*¹ were investigated with the following results: Of a number of apices from which transverse sections were cut not one showed a clearly marked single apical cell. Some, however, showed somewhat irregular arrangements, and in some of these it appeared uncertain whether the meristem be referable to three or to four initial cells. In a majority of the roots observed it is clearly referable to four initial cells (Fig. 12), separated from one another by the four principal walls (ϕ). The meristem in this case appears closely similar to that described by Schwendener in the Marattiaceae. Longitudinal sections, however, do not show so close a correspondence to the structure described by him in this group. Pyramidal cells are not unfrequently to be found, as in Fig. 13, where two are seen (x, x). In other examples, however, the initial cells have the form of truncated pyramids, as in Fig. 14, segments being cut off from the truncated apex, as well as from the sides and base. This arrangement probably corresponds to that shown in transverse section in Fig. 12.

The origin of the lateral roots was also observed in this plant. The root originates from a single cell of the endodermis, situated opposite one of the groups of xylem. Usually the divisions are symmetrical, as in Figs. 15, 16, and these two figures show that from the very first the initial cells of the young root are subject to a certain variation of form, being in some cases pyramidal, in others truncated. Thus, in this respect again, *Todea barbara* resembles *Osmunda regalis*.

The foregoing description of the structure of the apical meristem of the roots of *Osmunda* and *Todea* shows that there is no such strict uniformity in these plants as is found in the meristem of the roots of typically leptosporangiate

¹ See postscript, p. 388.

Ferns. If, on the other hand, a comparison be drawn between the structure in the Osmundaceae, and that described by Schwendener for the Marattiaceae¹ it will be seen that in the character of the meristem the family of the Osmundaceae fluctuates between the two types, and affords intermediate examples between them. In order to make this point clear a comparison may be drawn between Sachs' diagram of the type of the Polypodiaceae (Fig. 1) and a diagram which I have constructed with the intention of representing the Marattiaceous type (Fig. 17). In the former the periclinal walls in the body of the root constitute an interrupted series of confocal paraboloid surfaces, their common focus or centre of construction being situated in the apical cell itself: the periclinal walls in the root-cap constitute a series of similar curves which are however not confocal, though they are coaxial. Since the anticlinal walls cut the periclinals at right angles, those in the body of the root present a concave surface to the axis of growth, while those in the root-cap, cutting the coaxial curves, present a convex surface.

In the Marattiaceous type, according to the description given by Schwendener (and my own observations on the roots of *Marattia fraxinea* and *Angiopteris evecta* bear out his conclusions rather than those of Russow²), the arrangement differs from the above type in certain important points, and a diagram may be drawn to show the scheme of construction as in Fig. 17. In this type of construction there are in the first place walls in two radial planes, which cut one another at right angles, and their line of intersection³ is the organic axis of the root. The periclinal walls are none of them confocal, neither those which lie in the body of the root, nor even those in the procambial cylinder; they are, however, all coaxial, and their common axis is the line of intersection of the radial walls, that is the organic axis. As a necessary consequence

¹ l. c.

² Vergl. Unters. p. 107, Fig. 158. Compare also De Vriese and Harting, Monographie des Marattiacées, Fig. 27.

³ As a matter of fact the two planes do not cut one another accurately along one line; this has been noted by Schwendener.

of this it follows that the anticlinal curves all present a convex surface to the axis of growth, there being no distinction in this respect between the root-cap and the body of the root. In fact the construction of the root is throughout on the coaxial or fan-like plan distinguished by Sachs¹. It is further to be noted in connection with the scheme represented in Fig. 17, that the apparently transverse walls, by which successive segments are cut off from the lower ends of the truncated pyramidal initial cells, form part of the series of periclinal curves; and that the focus of each successive periclinal, by which segments are cut off from the initial cells to form the body of the root, lies at *the time of segmentation at a point below the group of initial cells*. In the former type, however (Fig. 1), it will be readily seen that the focus or centre of construction lies in the apical cell itself (Sachs, l. c.). Thus in passing from the first to the second type of construction, there is a sinking or lowering of the centre of construction; since the anticlinals cut the periclinal curves at right angles, it follows that where the centre of construction is more depressed, the sides of the apical cell or of the initial cells will be less inclined to one another, and more nearly parallel than is the case where the focus lies at a higher point, for instance in the apical cell itself. The figures of Schwendener clearly demonstrate that this is actually the case in the Marattiaceae, in which the initial cells appear almost oblong in longitudinal section. Lastly, it is clear that in our second type the four initial cells may be represented to the mind as being gaps in the system of construction in just the same sense as the idea is applied by Sachs to the single apical cell.

If now the observations above detailed for the roots of the Osmundaceae be compared with the two types of construction thus defined, it will be clearly seen that though subject to considerable variation of detail, they occupy an intermediate position between the two types: thus a single initial cell is but rarely found, the number being variable up to four, which seems to be the usual number for *Todea*; the sides of the

¹ Lectures, Engl. ed., p. 451.

initial cells are less inclined to one another than in the Polypodiaceae, etc., in which the construction is on the confocal type, and the initial cell or cells are thus deeper. Again, the apices of the cells are often truncate, the form of the initial cells being thus not pyramidal but oblong, as is the case in the coaxial type: in both these characters, which are, as above pointed out, to be connected with a *lowering of the centre of construction*, the roots of the Osmundaceae, and more especially of *Todea*, approach the Marattiaceous type.

While drawing this distinction between the two types of construction, and while recognising that the Marattiaceous type is consistently coaxial, it is to be remembered that a pure and consistent coaxial construction is exceptional and is found exemplified in the Marattiaceous type and in the Janczewski's fourth type of Angiospermic roots; the large majority of roots are mixed in the character of their meristem: thus in the leptosporangiate Ferns the construction of the root-cap is coaxial, while that of the body of the root is confocal: in the Gymnosperms the confocal character is limited to the plerome, while all the outer tissues are coaxial: in the Monocotyledons the whole is confocal with the exception of the root-cap. It has, however, been pointed out by Dr. G. Karsten¹ that in the development of certain individual roots there may be a transition from the coaxial type in the early stages, to the confocal in the older root: observations such as these show that too great importance should not be attached to these characters alone as defining natural affinities; but, on the other hand, if there be traceable in a series of forms a sequence of character of the meristems which follows the series as laid out on other grounds, the meristematic characters may well be used as strengthening the systematic conclusion; and this is the way in which such evidence is to be used in the Filicineous series².

From the comparative study of the meristems of roots of

¹ Ueber die Anlage seitlicher Organe. Leipzig, 1886, pp. 6-8.

² See conclusion of this paper.

the series of Filicineae the following conclusions may be drawn:—

(1) That the apices of roots of the leptosporangiate Ferns are of comparatively small bulk, while those of the Osmundaceae are more bulky, and those of the Marattiaceae still more so.

(2) That though the type of structure of the apex of the root in the leptosporangiate Ferns is stereotyped and regular, with one tetrahedral initial cell, in the Osmundaceae this regularity is lost, there being often three or even four initials.

(3) That the initial cells of Osmundaceae and Marattiaceae are narrower and deeper in proportion than in the leptosporangiate Ferns, and are often not pointed but rectangular at the base: this implies a lower position of the centre of construction.

(4) That in respect of the structure of the apex of the root the leptosporangiate Ferns, Osmundaceae, and Marattiaceae constitute a natural series, of which the first named are the simplest, and the last the most complex, while the Osmundaceae occupy an intermediate position¹.

APICES OF STEMS.

As regards the details of structure of the apex of the stem in leptosporangiate Ferns there has been some discrepancy of observation; but there is at least coincidence on this point, that there is present a single initial, or apical cell, the open question having been as to its *form*.

Hofmeister, in his 'Higher Cryptogamia,'² described a two-sided, wedge-shaped, apical cell for *Niphobolus chinensis* and *N. rupestris*, *Polypodium aureum* and *P. punctatum*, and for *Platycerium alcidorne*. He figures³ two apices of *Polypodium vulgare*, which show that the actual form of the cell is variable, and an apex of *Pteris aquilina* in which it is of the form of

¹ For further details and figures relating to the roots of the Osmundaceae, reference may be made to my paper on this subject in Q. J. M. S. 1885.

² Ray. Soc. 1862, p. 248.

³ l. c., Plate XXXIV, Figs. 5, 6; text, p. 248.

a narrow, three-sided pyramid. Sachs¹ figures and describes the apical cell of this plant as a two-sided one, and summarises the knowledge acquired on this point thus:—‘We may for the present take it to be the rule that creeping stems with bilateral structure have a two-sided apical cell, and that in erect or ascending stems with rosettes of leaves radiating in every direction, the apical cell is a three-sided pyramid.’ But the wide observations on the apices of dorsiventral Ferns by Dr. L. Klein² clearly disproved this generalisation: he investigated fifty species, belonging to nineteen genera, with the result that, excepting *Pteris aquilina*, all had a three-sided initial cell at the apex of the stem: further, Klein found that the form of the apical cell is variable in *Pteris* itself. Even in *Ceratopteris*, with its thin and elongated apex, a three-sided initial cell is present³, though it might have been anticipated that in so slender a form the construction might have been simpler: the stem however is upright, and the leaf-arrangement spiral. Passing to the Hydropterideae, in *Azolla*⁴, and in *Salvinia*⁵, the apex of the rhizome has been shown to be occupied by a two-sided cell, with segments alternating on opposite sides; in *Marsilia* however⁶ there is a three-sided cell: the same appears to be also the case in *Pilularia*, according to my own observations, and Campbell⁷ appears to have come to the same conclusion, for though he does not state the fact directly, he allows it to be inferred, since he speaks of a ‘third or ventral segment’: there is in fact a difference in the structure of the apex of the stem between the two sections of the Heterosporous Filicineae, the more distinctly aquatic forms being the simpler. Thus observations on a large number of leptosporangiate Ferns have shown that whether the stems be dorsiventral and creeping, or radial and erect, the apex is occupied by a three-sided pyra-

¹ Textbook, 4th German edition, p. 423.

² Bot. Zeit., 1884, p. 577.

³ Kny, Parkeriaceae, p. 28.

⁴ Strasburger, Ueber *Azolla*, p. 17.

⁵ Pringsheim's Jahrbücher, IV.

⁶ Hanstein in Pringh. Jahrb. IV, Taf. XIV, Figs. 4, 5.

⁷ Annals of Botany, II, p. 260.

midal apical cell; but that this rule is not without exceptions among dorsiventral forms, such as *Pteris aquilina*, *Azolla*, and *Salvinia*, in which a two-sided cell is present.

On various grounds it had seemed to me not improbable that the dorsiventral axes of the Hymenophyllaceae might also prove to be exceptions, and have the simpler construction of the apex: these have, as far as I am aware, never hitherto been thoroughly examined on this point¹: it is true that Prantl² has made some observations on *Trichomanes speciosum* and *T. pyxidiferum*, but he admits that they were insufficient owing to lack of suitable material. Having had access to the fine collection of living specimens in the Royal Gardens, Kew, observations have been made on several of the more robust species of Hymenophyllaceae, in which the difficulties of manipulation are less than in the minute forms, and the security of the observations accordingly greater. The result is constantly to find the apex occupied by a three-sided pyramidal initial cell.

In *Trichomanes radicans* the rhizome is rather bulky, and its apex flat (Fig. 18): upon this rhizome the leaves arise alternately on opposite sides. Seen in surface view (Fig. 19) the apex is occupied by a three-sided cell, of which one side is directed downwards, and one edge upwards. The segments, which are cut off from the successive sides, are relatively bulky, and from the appearance of the whole meristem it would appear that the growth of the segments is much more rapid than that of the apical cell itself. Only a small proportion of the segments take part in the formation of the leaves, and I have been unable to recognise any numerical relation between the segments and the leaves formed. The latter arise from that part of the upper or dorsal segments which adjoins the ventral or lower segments (Fig. 19 *b*). In the axil of each leaf arises an axillary bud, which is constantly present, and may therefore be styled a 'stable bud' in the sense of Strasburger³.

¹ No species of Hymenophyllaceae were examined by Klein.

² Hymenophyllaceae, p. 26; Plate I, Figs. 6, 7, 9.

³ *Azolla*, p. 22.

Longitudinal sections show that the apical cell, both of the main axis (Fig. 20) and of the axillary bud (Fig. 21), is pointed and rather deep: deeper in fact than is usual with the apical cells of the stems of most leptosporangiate Ferns; this is however to be put in relation with the flattened form of the apex, and Prantl's figures¹ seem to indicate that it is not so in the slender forms.

The rhizomes of the following species were also examined; viz. *Trichomanes reniforme*, and *Hymenophyllum caudiculatum* and *demissum*: in each a three-sided pyramidal apical cell was found, but in the two last-named species the further subdivision of the segments was found to be less regular than in *Tr. reniforme* or *radicans*. From these observations it appears that the rhizome of the Hymenophyllaceae corresponds, as regards the essential characters of its apex, to the structure of the apex of the stem in the large majority of other leptosporangiate Ferns.

On the apex of the stem of other leptosporangiate Ferns I have little to add to the excellent observations of Klein. He seems, however, to have had little opportunity of examining the stems of Cytheaceae or Dicksonieae, and though he cites *Dicksonia rubiginosa* and *Hypoderris Brownii* in his list of plants employed, he does not figure either of them, or describe them in the text. As far as I am aware, no observations have hitherto been made on the structure of the apex of the stem of large and well-grown Tree-Ferns, and it would be reasonable to expect that the very large size of the stem might react upon the structure of its apex. Having collected, when in Ceylon, apical buds of large plants of *Amphicosmia* (*Hemitelia*) *Walkerae*, these were investigated with the following result: The apex of the stem is not very broad, and is slightly depressed, while the extreme apex rises from the hollow depression as a central cone: this is terminated by a large and extremely well-defined three-sided pyramidal apical cell, from the sides of which successive segments are cut off; these subdivide with considerable regularity, and the character of the whole is quite as

¹ l. c., Plate I, Figs. 6, 9.

definite and regular as in any of the Polypodiaceae (Fig. 22). Thus it appears that, notwithstanding the size and internal complexity of the mature stem, the character of the apex is essentially similar to that of the smaller forms.

I have but few facts to adduce as to the structure of the apex of the stem of the Schizaeaceae. Klein (l. c.) has investigated those of *Lygodium circinatum* and *scandens*, and appears to have found in them a structure similar to that of other dorsiventral Ferns, for he gives no special description of them¹. I have examined apices of *Lygodium scandens*, and of *Aneimia hirta*, and they both conform to the ordinary type of structure with a three-sided apical cell, while the apical cone is comparatively flat.

Passing on now to *Osmunda regalis*, in a considerable number of well-grown plants, from Ireland and elsewhere, the apex of the upright stem was found to be terminated by a flat apical cone: the meristem is very thin-walled and watery, with greatly vacuolated protoplasm: in transverse sections, cleared with 'eau de Javelle,' in the majority of cases a three-sided apical cell is seen, from which segments are cut off in the ordinary succession (Fig. 23); but the subdivision of the segments often shows irregularities. The size of the segments relatively to that of the initial cell is variable in different cases, and this will be recognised on comparing Figs. 23, 24. In some cases the form of the cell is not regular: thus in Fig. 24 it is four-sided, and the succession of segments is not so readily to be traced as in Fig. 23. In some few apices which were observed it appeared to be impossible to refer all the tissues to any one initial cell (Fig. 25). Now it is to be noted that all these figures were drawn from sections which included the outer wall of the cells: they represent with accuracy what is seen on viewing the apex from above, and no allowance need be made for distortion of the cells in preparation. Taking then Fig. 25 as representing accurately the actual arrangement of the cells, it seems probable that more than one initial is present, but the structure is such as cannot readily be referred

¹ Bot. Zeit. 1884, p. 647.

to any one of the ordinary types of construction. Here we have one of those strangely irregular arrangements analogous to those which have already been observed in the root, and a comparison of this with the apices of stems of the Marattiaceae described below will show the same similarity to the latter as has been traced in the root. It is to be noted however that the large majority of apices of the stems of *Osmunda* conform to the ordinary leptosporangiate type, and such examples as that shown in Fig. 25 are the exception rather than the rule.

The meristem being thus at times irregular, as seen in surface view, and the subdivision of the segments being variable, it is to be expected that the study of it in longitudinal section would present difficulties, and I have not been able to trace any definite and characteristic mode of segmentation. Longitudinal sections cut from a considerable number of stems show that a conical apical cell is usually present (Fig. 26), which is rather deep in proportion to its height: the relations of the surrounding tissues, and their reference to regularly succeeding segments are difficult to recognise. Thus it is seen both from transverse and longitudinal sections that, though the presence of a single initial cell may be ascertained in most cases in the stem of *Osmunda*, it is not always present, and the apical meristem is of a less regular and definite type than in the leptosporangiate Ferns.

Taking next into consideration the apex of the stem in the Marattiaceae, it may be noted that various accounts have from time to time been given of its structure¹. Holle² ascribes to the apex of *Marattia* an elongated, four-sided apical cell: in *Angiopteris* he says that he cannot with certainty track the whole meristem as originating from a single initial cell, though he thinks that such an origin is probable.

Some years since I had the opportunity of examining the apex of one well-grown plant: a conical cell was recognised

¹ Hofmeister, Abhandl. d. K. Sächs. Ges. d. Wiss. 1857. Compare also De Vriese and Harting, Monogr. d. Maratt. pp. 49, 51. The papilla marked (z) which is there regarded as the apex of the stem, appears to be part of a young leaf.

² Bot. Zeit. 1876, p. 218.

in a median longitudinal section of this apex¹, which I took to be the single initial cell, but I was not able to state whether it had two or three edges, or what is the succession of segments cut off from it: further, the question was left open whether the presence of one initial is constant for the species, and the evidence was not considered as by any means conclusive. When in Ceylon, I took the opportunity of collecting apices of well-grown plants both of *Marattia fraxinea*, and of *Angiopteris evecta*, and though even this material has been too scanty for working out all the details of so complicated an apex as this has proved to be, still it has sufficed for acquiring some further knowledge of the meristems of this interesting family.

In large plants the apex of the stem is found to be almost perfectly flat, distinctly more so than in *Osmunda*: the very slightly swelling apical cone is unusually wide, and since the cells composing it are of almost equal size throughout, a careful examination of the tissue as seen in surface view is necessary before the succession of the cell-divisions can be traced. Treatment with 'eau de Javelle' was found useful for distinguishing the older or principal walls from the younger cell-walls, and thus assisting in the recognition of groups of cells of common origin. If a transverse section including the external surface of the apical cone of *Angiopteris* be thus treated, a central point may be recognised where the principal walls meet, and this point is often characterised by a highly refractive thickening of the wall: this is the central point of genesis of the meristem (Fig. 27): around this point are disposed cells which appear to be constant neither in number nor in form: it is true that the four cells marked (*) in Fig. 27 can be regarded as initial cells for the whole meristem, and it is possible to recognise how in this case the whole of the broad area of tissue represented might have been derived from them, the apical structure being thus coincident with that described by Schwendener for the root; but it is to be observed that this was the most favourable and distinct specimen of the

¹ Phil. Trans. 1884, Part II, Plate 37, Fig. 9.

whole number which I had under observation. Accordingly I am not prepared to state that the structure of the apex of the stem always accords to the type of Schwendener, though in some cases it undoubtedly appears to do so: it is possible that Holle's observations having been made on young plants (l. c. p. 216), their apices may have had a more simple structure with a single apical cell, such as he describes.

The apices of several strong stems of *Marattia fraxinea* were also examined, and the results are virtually the same as those for *Angiopteris evecta*; no single initial cell has been found; the meristem is however referable, in some cases at least, to four or five initial cells (Fig. 28), but these are not exactly alike in size or in shape. Whatever the details of the construction may be, there is obviously no single initial cell of definite shape, such as is found in the lower forms.

The study of longitudinal sections through the apex presents greater difficulties, as is always the case where the segmentation is not according to a definite scheme: it is essential at once to recognise that the conical form does not necessarily mark an initial cell, for in the first place undoubted initial cells may have a square base, as in the root of Marattiaceae or the rhizophore of *Selaginella*¹; while conical cells are to be found at points where their character as initial cells is out of the question: thus in longitudinal sections through the leaf of *Angiopteris*, conical cells of considerable depth are to be found at points far removed from the actual apex. Naturally where the apex is very wide and flat, as it is in these plants, it is not easy to be certain which sections are median, and the uncertainty is increased where the character of the meristem is liable to variation: to the best of my belief the section shown in Fig. 29 is a median one; the wall (x, x) corresponds to that central point above recognised in transverse sections. It will be noted, first, that all the superficial cells of this region are unusually narrow and deep; thus, whatever the details of structure of the meristem,

¹ Treub, *Selaginella Martensii*, Plate IV.

the centre of construction must lie relatively low : also that two conical cells are present, one on either side of the wall (x,x); their position relatively to it is however not exactly alike. I am disposed to regard those two cells which are marked (x,x) as the initial cells, notwithstanding their difference in form, and the fact that their size is not greater than that of the surrounding cells. It is interesting at the same time to note the grouping of the cells; clearly the group to the right of the line (x,x) has been derived from a conical cell, which has undergone a T division, while the upper left-hand cell thus derived has divided irregularly to form, among others, the obliquely-based initial (x): the group to the left of the line (x,x) was apparently derived from a cell with a square base, and after somewhat irregular divisions this has resulted in the formation of a conical initial cell (x). These remarks, which are not presumed to give any exhaustive account of the structure of the meristem as seen in longitudinal section, serve at least to indicate this:—that longitudinal sections bear out the conclusions drawn from the study of the meristem in plan, viz. that in strongly grown plants there is no single initial cell at the apex of the stem of the Marattiaceae, and that the series of segmentations of those cells which are believed to be the initials is far from being regular.

I very much regret having to leave the investigation of the structure of these meristems in so unsatisfactory a position, neither being able to reduce the observations upon them to any strict system, nor being able to state directly that a definite system does not exist : such knowledge could only result from the examination of a very large number of specimens. But already my observations on the apex of the root of the Osmundaceae have shown that great irregularity and want of uniformity of construction are to be seen in them, and that irregularity which is found in the apex of the root of Osmundaceae seems to find its parallel in the apex of the stem of the Marattiaceae. But though it is at present impossible to demonstrate a strict type of segmentation for the apices of the stems of these plants, the following general conclusions

may be drawn from the comparative study of the apices of stems in the main series of Filicineae.

(1) That while the apex of the stem of most leptosporangiate Ferns is distinctly conical¹, that of the Osmundaceae and Marattiaceae is flatter, and more bulky.

(2) That, though in the leptosporangiate Ferns a single initial, with definite and regular segmentation, is always present, in *Osmunda* it is not always to be seen, while in well-grown plants of Marattiaceae a single initial is absent, the growth proceeding from a number (4?) of initial cells.

(3) That the initial cells of the Osmundaceae are narrower and deeper than is usual in leptosporangiate Ferns; in the Marattiaceae this is seen in a marked degree, and they are even to be found of rectangular form: these facts imply a lower position of the centre of construction of the meristem.

(4) That in the above respects the leptosporangiate Ferns, Osmundaceae and Marattiaceae, form a natural series, starting from those with a more convex form of the apical cone, and with simpler and more diagrammatic segmentation, and relatively high centre of construction, and proceeding to those with more complicated and less regular segmentation, and relatively deep-seated centre of construction.

(5) That these conclusions as drawn from the comparative study of the apices of stems correspond to the conclusions drawn from the study of the roots.

APICES OF LEAVES.

As we proceed upwards through the same series of Ferns as those above examined for the structure of the apex of root and stem, it will be seen that in the character of the apex of the leaf also a similar increase in complexity of the meristematic tissues is to be traced.

The observations of Kny², of Sadebeck³, and of Prantl⁴,

¹ *Trichomanes* seems to be exceptional in the flatness of its apical cone.

² Parkeriaceae, Taf. XXII-XXIV (= V-VII).

³ Verh. d. bot. Ver. für d. Prov. Brandenburg, XV. 116.

⁴ Hymenophyllaceae, pp. 4-7. Schizaeaceae, p. 3.

have laid the foundation of a knowledge of the mode of development of the fronds of Ferns: also in the Hydropterideae the development of the leaf has been carefully traced in *Marsilia*, *Salvinia*, and *Azolla*: I have also shown that the leaf of *Pilularia* originates in a manner similar to that of typical Ferns¹. Notwithstanding all this there is still an open field for comparative observation on the mode of development of the leaf in different members of the Filicineous series: when it is remembered that the general character of the Fern plant is more closely dependent upon that of its leaves than on any other part, the omission to subject it to a more exact developmental study appears remarkable. The same mode of treatment will be applied here as in the root and stem: the leaf of the Hymenophyllaceae will be first considered, then successively those of other leptosporangiate Ferns, of Osmundaceae, and Marattiaceae. It will be assumed to be unnecessary to recapitulate the general results of other observers, and a reference to the writings above cited, and to the *précis* of the subject given by Sadebeck² will be sufficient.

Only very scanty facts are at present known as regards the origin of the frond of the Hymenophyllaceae, and for these we are chiefly indebted to Prantl³, who has pointed out that in *Trichomanes speciosum* the leaf has a two-sided apical cell, and that from the segments a marginal series of cells is derived on either edge of the leaf. These points I have found to be correct for other species. I have observed early stages of development of the leaves in *Trichomanes radicans*, and find that they arise laterally upon and alternately on opposite sides of the axis: no exact numerical relation has been recognised between the leaves and the segments cut off from the apical cell of the stem, and it would appear that many segments pass without taking part in the formation of leaves. These arise from the lower edges of the obliquely lateral segments (Fig. 19 *l*), and appear as convex projections in

¹ Phil. Trans. Part II, 1884, p. 574.

² Schenk's Handbuch, I, p. 270.

³ Hymenophyllaceae, pp. 4-7.

which segmentation immediately proceeds so as to define a two-sided conical apical cell (Fig. 30); the position of this is such that one of its edges is directed towards the apical cell of the axis, the other away from it, and accordingly a longitudinal tangential section through the axis would, if it traversed a young leaf, show the conical apical cell of the young leaf, and the succession of its segments. I succeeded in obtaining such a preparation of a leaf in a very early stage (Fig. 31), and this shows that the apical cell is defined by the first cell-divisions after the convex projection of the young leaf beyond the surface of the axis; if a median section of the creeping rhizome be cut in a horizontal plane it would traverse the apical cell from edge to edge (Figs. 18, 32). When viewed from above, the segments are seen to be cut off from the apical cell in regular alternate succession (Fig. 30), and they are subsequently sub-divided by cutting off their adaxial and abaxial edges, so that the central part of each segment remains; this divides chiefly by walls parallel to the segmental walls, and the resulting cells are readily recognisable as the marginal cells (*m*, Fig. 30): it is important to note that this marginal series of cells, which plays so prominent a part in the ultimate conformation of the leaf in this as in other Ferns, is thus to be recognised as being initiated in the very first segments cut off from the apical cell; in other words, *the frond is here a typically winged structure to its extreme base*. It is also worthy of note that here, as in most leptosporangiate Ferns, the external area of the segments is relatively small as compared with the apical cell, while in the higher members of the series, if an apical cell be present, the segments appear relatively large (see page 335).

The young frond which thus originates, soon assumes the circinate curvature; it may even be seen in Fig. 30 that the growth is less active on the adaxial than on the abaxial side; but the curvature is very clearly seen in longitudinal sections (Fig. 32), which also demonstrate that cell-division is more active on the convex side, accompanied by occasional forma-

tion of conical cells (*o*). On the circinate phyllopodium¹ thus formed, which has a marginal series of cells continuous on either side to its extreme base, the pinnae begin to make their appearance as monopodial branches, ranged on the lateral flanges or wings which grow out from the marginal series of cells; the first-formed pinnae originate distinctly below the apex of the phyllopodium (Fig. 32), and alternate on opposite sides of it; the marginal series of cells is continuous also over their margins, but no initial cell is to be seen at their apices. On the other hand, the apex of the phyllopodium may be seen to have a clearly defined apical cell, even after a considerable number of pinnae have been formed, and this in itself would preclude the idea of a dichotomous branching; Prantl² has described the branching of the leaves of the Hymenophyllaceae as 'purely dichotomous'; this is certainly not the case for *Trichomanes radicans*.

I have also made observations as to the persistence of the apical cell of the phyllopodium, a point which Prantl left undecided from want of suitable material. In a leaf which had already formed sixteen pinnae the apical cell was still clearly recognised, while in leaves respectively with twenty-three and with thirty-two pinnae no apical cell could be seen. It is probable that there is no strict time when its identity is lost, but that ultimately it undergoes a T division³ (which I was fortunate enough actually to observe in *Trichomanes reniforme*, Fig. 33), and so passes over into the marginal series⁴. It may be added that the monopodial type of branching occurs not only in the phyllopodium, but also in the pinnae, and in one case it was clearly recognised that the eighth pinnule originated in a monopodial manner, distinctly below the extreme apex of the pinna. Subsequently, however, both in the phyllopodium and in the pinna the

¹ This term has been adopted for the rachis or main axis of the leaf, whether branched or not. Phil. Trans. 1884, II, p. 569.

² l. c. p. 14.

³ Compare Sadebeck, Entw. u. Wachstum d. Farnblätter, p. 10, and Fig. 6.

⁴ It is not inconsistent to regard the apical cell itself merely as a special cell of the marginal series.

mode of branching passes over by imperceptible gradations from the monopodial to the dichotomous, the branchings approaching successively nearer and nearer to the extreme apex. It is thus to be clearly understood that, though in *Trichomanes radicans* the ultimate branchings of the frond are of the dichotomous type, the earlier branchings are monopodial, and that the transition is to be seen in the individual frond, as is the case in other leptosporangiate Ferns. Further, though no sharp limit can be drawn between the two, it is to be noted that the monopodial branching is characteristic of that part of the frond where a wedge-shaped apical cell is present, while the dichotomous branching is characteristic rather of that part where T division is found at the extreme apex; the pinnae, however, which have at no time a wedge-shaped apical cell, branch monopodially in their lower parts: the state of matters in *Trichomanes radicans* seems accordingly to be this:—(1) that dichotomous branching occurs only where T division is found at the apex; (2) that where a wedge-shaped apical cell is present only monopodial branching takes place.

The mode of development of the wings will be described later (see p. 342).

Observations were also made on *Trichomanes reniforme*, as being a most markedly different species as regards the character of the leaf: here as before a wedge-shaped apical cell, and marginal series were found, but the identity of the apical cell is lost at a comparatively early period, by the appearance in it of a T division (Fig. 33); since there are no pinnae formed in this species it is difficult to draw a comparison between the period when this division takes place and the disappearance of the apical cell in *Trichomanes radicans*.

Such observations as I have made on *Hymenophyllum Tunbridgense* fall in with those on *Trichomanes*, and putting these together with the observations of Prantl, it may be concluded that a two-sided wedge-shaped apical cell is constantly present at the apex of the young leaf of the Hymenophyllaceae, and that a series of cells derived in the

first instance from the central portion of each segment; occupies the entire margin of the phyllopodium, pinnae, and pinnules.

Such observations as have been made on the development and apex of the leaves of Ferns have been chiefly on the Polypodiaceae; in face of the precise descriptions of Sadebeck¹, Klein², Luerssen³, etc., it seems unnecessary to go further than recapitulate the general conclusion that the apex of the leaf is at first occupied by a two-sided wedge-shaped apical cell, from which segments are cut off alternately on opposite sides; that the central part of each segment contributes to the marginal series of cells, which is continuous up to the apex, and over the apex after the identity of the apical cell is lost: thus in most points there is similarity in the apical meristem to that of the Hymenophyllaceae, though the resulting frond is as a rule more robust. Klein mentions and figures⁴ certain exceptional arrangements of the segmentations in young leaves of the Polypodiaceae. He points out that the apical cell is not always from the first a regular two-sided one, but that sometimes, the second wall only meeting the first on one side, a *three-sided initial* is temporarily present; this form may in some cases be maintained for a considerable time⁵, but always passes over ultimately into the two-sided form. We shall see that this condition, which is only temporary and exceptional in the Polypodiaceae, becomes typical in the Osmundaceae, in which a three-sided initial is constantly present.

Observations were also made on the origin and apex of the leaves of *Amphicosmia* (*Hemitelea*) *Walkerae*, Hk., and it was found that the leaves originate laterally on the apex, in almost simultaneous whorls of three, the successive whorls alternating with one another. The first appearance of the leaf is just as in other leptosporangiate Ferns, by outgrowth of a single superficial cell, which becomes convex, and is

¹ Schenk's Handbuch, I, p. 270.

² Bot. Zeit. 1884, p. 585, etc.

³ Handbuch der Syst. Bot. I, p. 511.

⁴ l. c. p. 486, and Figs. 2, 7, 21, 23, 26, 36.

⁵ l. c. Figs. 11, 22.

divided by alternate walls so as to define at once a two-sided, wedge-shaped apical cell, one edge of which is directed towards the apex of the stem; this apical structure is maintained for a considerable time: thus in its segmentation and the general characters of the apex there is nothing specially worthy of note in *Amphicosmia* as differing from other leptosporangiate Ferns.

For purposes of comparison a few observations have been made on *Lygodium scandens*, and *Aneimia hirta*, with the result that in both the apex of the leaf was seen to be occupied by a two-sided apical cell, from which segments, and a marginal series are derived as usual: in fact, as regards the early development of the leaf they show no advance on the Polypodiaceae. Thus it appears that in the leptosporangiate Ferns there is great uniformity in the segmentation of the young leaf, the only exceptions to the two-sided apical cell hitherto observed among them being those abnormal cases noted by Klein: the type of construction of the apex is that characteristic of flattened growths.

I have already drawn attention to the fact¹ that in the Osmundaceae there is a departure from the more simple type of structure of the apex of the leaf above referred to as characteristic of the Hymenophyllaceae, Polypodiaceae, Hydropterideae, Cyatheaceae, and Schizaeaceae: it has been pointed out that the three-sided type of apical cell which Klein showed to be occasionally found in very young leaves of the Polypodiaceae, is the type for *Osmunda* and *Todea*, though the succession and form of the segments in these plants is much more regular than that shown in Klein's figures. I have recently made fresh observations on *Osmunda regalis*, with the following results. The position of the apical cell which is defined by the first divisions in the young leaf (Fig. 23, *l*), is such that one of the sides faces the apex of the stem, while the opposite angle is directed away from it; this orientation seems to be constant for *O. regalis* and *cinnamomea*, and for *Todea superba*. The sub-division of the

¹ Phil. Trans. 1884, Part II, p. 575.

segments is far from being constant, a fact which has been noted and figured in my former paper (l.c. Fig. 7): it is shown obviously in Fig. 34, in which each segment divides by a sextant wall (*s,s*) into two approximately equal halves, but their further sub-division cannot be reduced to any rule, the resulting cells being triangular, or variously polygonal as seen in surface view from without. Longitudinal sections of the apex show that the apical cell is pointed, and deep in proportion to its width (Fig. 35), in fact very much deeper than the apical cells of the leptosporangiate Ferns¹; in all the Ferns quoted in the foot-note the apical cell of the leaf is proportionately much less deep than it is in *Osmunda*: in other words, the centre of construction in *Osmunda* is more deeply seated than in any of these Ferns, and, coupling this with the more complicated construction of the meristem, which is of a type characteristic of cylindrical rather than flattened structures, the conclusion is that the whole member is of a more robust order than in other leptosporangiate Ferns.

It is obvious from an inspection of apices shown in plan (Fig. 34, also Phil. Trans. 1884, Plate 37, Figs. 4, 6, and 7), that here there can be no marginal series of cells having such relation to the segments of the apical cell on the one hand, and to the wings on the other, as in the leaves of the simpler type; and I have already shown in the paper above quoted, that each of the lateral wings is formed from parts of two of the rows of segments cut off from the apical cell. The structure of the wings will be described later (p. 352). It may further be added that, as far as my observations go, the branching of the frond of *Osmunda* is exclusively monopodial.

It will now be shown that in the Marattiaceae the divergence of the apex of the leaf from the type of the simpler Ferns, as regards the structure of the apical meristem, is even

¹ Compare Fig. 31 above: also Sadebeck's Fig. 33 C. (Schenk's Handbuch, I. p. 271) of *Asplenium Trichomanes*: also Hofmeister, Fig. 2, Plate XXXII. in his Higher Cryptogamia, which is drawn from *Pteris aquilina*: also the beautiful drawings of Kny on Plate XXIV. of his Memoir on *Ceratopteris*: also Prantl's figure of *Aneimia* (Schizaeaceae, Plate III, Fig. 28 B).

more marked than in the Osmundaceae. Holle¹ has investigated the apex of the leaf of the Marattiaceae; but it is not clear from his description whether his observations refer to *Marattia* or to *Angiopteris*, or to both genera. He finds the flattened apex of the leaf to be occupied by a single wedge-shaped apical cell, which is neither two nor three-sided, but of irregular section, and from it segments are cut off without regular order: he states that the identity of the apical cell is maintained till after the origination of the pinnae.

An examination of numerous leaves of well-grown plants of *Marattia fraxinea* has led me to the following results:—When seen in plan, the apical meristem of a young leaf, as yet without pinnae, may show a single three-sided initial cell: from this segments are cut off in regular sequence (Fig. 36); it is, however, to be noted that, as in the case figured, the initial cell is of relatively small size, while the growth of its segments is relatively rapid: thus in Fig. 36, the fourth segment occupies nearly double the area of the other three segments and the apical cell together: comparing this with *Osmunda* (Fig. 34) the difference is obvious, for here the area occupied by the apical cell and the last three segments is distinctly greater than that of the fourth segment: a comparison of the apex of the leaf of *Trichomanes* (Fig. 30) also shows the area of the apical cell in proportion to its segments to be much greater. With this relatively more rapid growth of the segments than of the apical cell itself is associated (as in *Osmunda*) irregularity of sub-division of the segments: each divides, it is true, by a sextant wall into two halves, but the further sub-divisions follow no constant rule. Frequently they present an appearance as though a series of segments were cut off from one triangular cell, which thus acquires the aspect of an initial cell, and may be styled a 'secondary initial': one such is seen in the abaxial half of the fourth segment in Fig. 36, and it will be subsequently shown that forms and arrangements of cells appear in longitudinal sections, which bear out the idea that these cells

¹ Bot. Zeit. 1876, p. 218.

assume in a secondary fashion, and for a short time, those qualities which mark the true initial cells.

But even in young leaves the apex does not always show such regularity as in this first case; thus in Fig. 37 the initial cell, though recognisable, is of less definite form; in Fig. 38 is seen the apex of a rather older leaf, and here the initial cell is still smaller, its segments less regular, and it is even difficult to see how the whole meristem can be referred as regards its origin to the one initial cell: secondary initials (*o*) are also present, but not in so marked a manner as in Fig. 36. Again, in a still older leaf, in which the pinnae were already formed, there was no single initial cell to be seen (Fig. 39): here the meristem has a structure resembling that of the apex of some of the roots of *Osmunda*¹: three principal walls (*p, p*) are present, as in those roots, and the same theoretical interest attaches to that arrangement here as in the case of those roots: in fact, we may represent this condition to the mind as resulting from the continuation of the principal walls upwards, without deflection, so as to divide the apical cell itself, the result being, as in Fig. 39, that three initials would be produced (*x, x*); though 'secondary initials' are also present here, it is possible to refer the whole of this complicated meristem to three initials, each of which is formative of one-third of the meristem lying between two of the principal walls (*p, p*). The arrows in Figs. 36, 37, 38, indicate the direction of the apex of the stem, and a comparison will show that the orientation of the apical cell is not constant as in *Osmunda*, but that sometimes one side, sometimes one angle, is directed towards the apex of the stem.

The above results are borne out by a study of median longitudinal sections: in the young leaf of *Marattia* a single conical cell is found (Fig. 40), from which segments are cut off with considerable regularity; here and there other conical cells are found, which may correspond to the secondary initials above noted in plan: a prominent case of this is

¹ Compare Figs. 3 and 4.

shown in Fig. 41, in which the actual apical cell (x) is seen at the edge of the drawing, while from the conical cell (o) a succession of segments has been cut off. This would support the view that it is a secondary initial comparable to that shown in Fig. 7 of the root of *Osmunda*. Thus in the structure of the apex of the leaf of *Marattia fraxinea* there are many points in common with that of the Osmundaceae, but though a three-sided apical cell is present in the young leaf, neither in its size, form, orientation, or segmentation is it so regular as in the latter.

The apex of the leaf of *Angiopteris evecta* is more complex in structure than that of *Marattia*, and it may be stated at the outset that, though observations have been made on numerous leaves of various ages, including very young ones, no clear case of a single initial cell has been observed. This result falls in with the description given by me some years ago¹, that 'the cells of the apical region may be referred, in some cases at least, to a group of four initial cells; but these cannot always be equally well distinguished, and as seen in surface view from without they exceed the surrounding cells but little if at all in size.' I now find, on the basis of wider observation, that it is difficult to state the actual number of the initial cells, but the arrangement of the meristem seems in some cases to point to the number three: thus Figs. 42, 43, which show good typical examples, have been drawn as accurately as possible, so as to indicate the forms of the cells, and their genetic relations to one another: in neither case is it quite clear what the actual number of the initials is, but comparing these with one another, with Fig. 39 of *Marattia*, and again with Figs. 3 and 4 of the root of *Osmunda*, it would appear probable that we have here further examples of *three* initial cells (x) grouped together in the centre: thus it is possible, on theoretical grounds similar to those already explained in the case of the root, to put this more complicated construction of the apex in relation with the simpler type where one three-sided initial cell is

¹ Phil. Trans. 1884, Part II. p. 580.

present, such as is found sometimes in the leaf of *Marattia*, and constantly in *Osmunda*. It may further be noted that there is usually present a clearly defined longitudinal wall (p, p in the Figs. 42, 43), which runs at right angles to the median plane of the leaf: this divides the whole meristem unequally into adaxial and abaxial halves, and there appear to be as a rule two initials on the adaxial or posterior side of it, but only one on the abaxial or anterior side. Whether such cells as those marked (o) are actually initial cells for the whole of the areas indicated, or not (and such an arrangement has been seen in a number of leaves), I am not in a position to state definitely, but would point out that the arrangement of the cells about them is such as to lend countenance to such a view. Be this as it may, it is evident that the apex of this leaf is more complex than that of *Marattia*, and that there are at least three initial cells present. Inspection of these meristems as seen in plan also show that there is no marginal series of cells present here, having any such relation to the initial cells as that already noted in the leptosporangiate Ferns.

Longitudinal sections of so complex a meristem are naturally difficult of interpretation; the principal wall (p, p) is usually well marked, and cuts the meristem into anterior and posterior halves; this was recognised in my previous paper¹. In a single median section (Fig. 44) several conical cells may be found, but, as already pointed out, the conical form does not necessarily imply that these are initial cells: even in sections which are believed to be exactly median it is very difficult to recognise the initial cells with certainty: the cells marked (x, x) in Figs. 44 and 45 are believed to be the initials, but I should not wish to state this point dogmatically. As regards the branching of the leaves of the Marattiaceae, it is exclusively monopodial, and on this point I have nothing to add to observations already published².

¹ l. c. p. 580, Fig. 12.

² l. c. p. 580, 586.

COMPARISON OF APICES OF LEAVES.

If we pass in general review the characters of the apex of the leaf in the series of Ferns above described, as we proceed from the Hymenophyllaceae to the Marattiaceae, an advance in complexity of structure is to be seen similar to that already noted in root and stem; but it is even more marked here, since in the simpler forms the two-sided apical cell is constantly found. The following general conclusions result from a comparison of the apical meristems of leaves in the Filicineous series:—

(1) That the apex itself is more bulky, and its curvature necessarily less sharp in the Marattiaceae than in the Osmundaceae: while a similar relation holds between the Osmundaceae and the leptosporangiate Ferns.

(2) That in the leptosporangiate Ferns a two-sided apical cell with regular segments is the type for the leaf: that (as occasionally happens as an irregularity in young leaves of the Polypodiaceae) a three-sided apical cell, with three rows of segments is the rule for Osmundaceae: that in *Marattia* also this is often the case (though not always), but the growth of the segments is much greater in proportion to that of the apical cell than in *Osmunda*: that what is the exception in *Marattia* is the rule in *Angiopteris*, viz. that the apex is occupied not by one initial cell, but by a number, apparently three.

(3) That therefore, in respect of the structure of the apex of the leaf, the leptosporangiate Ferns, Osmundaceae and Marattiaceae form a natural and gradual series of which the first are the simplest and the last the most complex.

(4) That on rising through this series of Ferns the apical cells are proportionately narrower and deeper, while in the highest terms of the series the initial cells are often oblong with square base: thus there is a lowering of the centre of construction as we rise in the series.

(5) These results correspond to those already acquired

from a comparison of the apices of the root and the stem in the same series of plants.

THE DEVELOPMENT OF THE WINGS OF THE LEAF.

The leaves of the large majority of Ferns are typically winged structures throughout their length: the wings are, however, variable in their development; in the upper part of the leaf they are usually large and expanded, whereas in the lower part, they may be reduced in size, and only be recognised in the mature state as giving a slightly angular form to the transverse section, or merely as light-coloured and very slightly projecting longitudinal ridges: or they may widen out at the extreme base forming an almost sheath-like, or even stipular development. Though the mode of origin of the wings is known in some few forms, as far as I am aware their morphology and development have never been the subject of comparative study in the whole series of the Ferns, notwithstanding that they are so constant and marked a feature.

As with the stems and leaves of other vascular plants, so the leaves of the Ferns may develop either (1) in a simple cylindrical manner: this is very rare, but is seen in *Pilularia*; (2) as flattened, spathulate structures, without prominent wings or midrib, as in *Drymoglossum*; or (3) with an enlarged midrib, and thin, longitudinally-running wings on either side: this is the type for the very large majority of the Ferns. These wings may not only be traced down the phyllopodium, but may sometimes even be seen to be continuous to the stem itself: this is, however, the case only in Ferns with an elongated, creeping stem, as in *Pteris aquilina*, where they may be recognised as continuous light-brown lines, on either side of the rhizome, or in species of *Acrostichum* (*A. scandens*, Smith, and *A. tenuifolium*, Baker), in which case however they appear as discontinuous white streaks: with this may be compared such examples of winged stems among the Angiosperms as *Symphytum*, or *Vitis pterophora*.

On the leaf, when mature, the more or less largely developed wings may be traced upwards from the extreme base (e.g. various species of *Trichomanes*, *Aspidium*, *Pteris*, *Cyathea*, and in fact the majority of leptosporangiate Ferns), and along the whole margin of the frond, and extending over all the pinnae and pinnules; among the higher terms of the Filicineous series, however, this continuity, as seen in the mature state, appears at first sight to be broken, especially in the lower portions of the frond, where the phyllopodium often appears cylindrical (*Osmunda*, *Todea*, *Marattia*, and *Angiopteris*, etc.), there being only such slight traces of the winged character as those noted as occurring on certain rhizomes. Again, there are formed in connection with the wings, at the base of the leaves of some of the higher Ferns, sheath-like and 'stipular' growths (Osmundaceae, Marattiaceae): these also are more or less clearly continuous with the wings, and are to be regarded as the result of their peculiar development. That these basal growths, as well as those lateral lines, often discontinuous and but slightly marked, which are seen running up the leaf-stalk, are really metamorphosed wings, cannot be doubted, when it is seen that they may be traced upwards, and be seen to merge gradually into the typical wings of the upper portion of the leaf. Here also, as in the leaves of Angiosperms, a certain rough correlation is to be recognised: where the development, be it of leaf or axis, is robust, as a supporting organ; the wings are of a relatively reduced type: where the central phyllopodium is less bulky, there the wings are as a rule more largely developed.

The prevalence of wings on the leaves of Ferns is to be put in relation with what is known of the development: the leaf is a bilateral structure, and these wings are its margins: they are derived in the leptosporangiate Ferns from a marginal series of cells which is continuous over the apex, and thus at least in the simplest Ferns (the Hymenophyllaceae) the leaf is typically but one layer of cells in thickness at its apex: but immediately below the apex begins that thickening which

results in the midrib¹,—a structure which is necessary in order to strengthen and support the thin expansion: this formation of the midrib, which in the Hymenophyllaceae begins below the extreme apex, extends in the higher Ferns to the extreme tip; in other words, the leaf in early stages (Polypodiaceae), or throughout its whole length (Marattiaceae) may be of massive construction; but though this is the case, the wings which are borne laterally upon it are still to be recognised as corresponding to those of the Hymenophyllaceae, and represent the true margins of the bilateral leaf. On this ground, and also on account of the constant presence of the wings on the leaves of Ferns (and as far as I am aware *Pilularia* is the only case of their entire absence), they are parts worthy of more exact study than has yet been conceded to them. Since morphological importance of phenomena is measured chiefly by their constancy of occurrence in long series of organisms, these wings which are so constant and prominent in Ferns, as also in Cycads and many Angiosperms, must rank as parts which cannot be ignored. In studying the development of these wings, a similar series of forms to those above quoted in reference to the apices of root, stem, and leaf will be examined, and I shall show that, as we rise in the series, in point of structure of the young wing, an increase of complexity accompanied by a lowering of the centre of construction is to be traced, similar to that which has been demonstrated in the apices of root, stem, and leaf.

In describing the development of the leaf in the Hymenophyllaceae Prantl has already drawn attention to the early differentiation of marginal cells², and both he and Mettenius have figured and described the wings as consisting of a single layer of cells: this is typically the case for these plants, but as noted by both writers³, it is by no means without exception, an increase in the number of layers being seen near the margin or near the nerves in various species, while in

¹ Compare Prantl, Hymenophyllaceae, Plate III, Figs. 38 A, B, C, and 39.

² Hymenophyllaceae, Plate I, Fig. 1.

³ Mettenius, Hymenophyllaceae, pp. 457–8.

Hymenophyllum dilatatum, and *Trichomanes reniforme* the frond consists throughout of several layers of cells, but without stomata or intercellular spaces.

I have already pointed out that in the leaf of *Trichomanes radicans* a marginal series of cells is to be distinguished even from the very first segmentations (Fig. 30); that the segments divide so that comparatively small parts are cut off from their edges, while the middle part (*m, m*) goes to form the marginal series of cells: thus the leaf is from the very first a winged structure. If transverse sections be cut from the phyllopodium the wings will be seen on either side of it as thin projections, which are smaller below than higher up: whatever be the extent of their surface they appear to be never more than one layer of cells in thickness (Figs. 46, 47, 48). The marginal cells (*m*) retain their identity throughout, and are the cells from which all the others are ultimately derived: the segmentation of these cells is by transverse walls, and each of the marginal cells may, as regards its form and mode of segmentation when seen in section, be compared to the apical cell of certain Algae (e.g. *Chara*, *Polysiphonia*, etc.). An examination of the further developed wing shows that intercalary growth, in addition to the strictly marginal, takes place, as is indicated by division of cells at a distance from the margin (Fig. 48), but this intercalary growth is not specially localised. The development of the wings in the upper parts of the branched frond follow the same rule, and as regards the apices of the pinnae, etc., I can endorse the observations of Prantl on *T. speciosum*¹. When seen in surface view the marginal cells of a young pinna are easily recognised, and their form is then seen to be that of half of a very narrow disc (Fig. 49). This form of the marginal cells, and simple mode of their segmentation by transverse walls seems to be the rule for the Hymenophyllaceae; it remained however to be seen whether those exceptionally thick-leaved forms above quoted would conform to the type: it is well known that the frond of *Trichomanes reniforme* is thicker than that of most other Hy-

¹ l. c. Plate III, Figs. 38, 39.

menophyllaceae, the reniform lamina being composed of four to six layers of cells, though it preserves the filmy character in as much as stomata and intercellular spaces are absent. Prantl conjectures shrewdly enough¹ that the origin of these many layers is by segmentation similar to that described by him for the origin of the nerves, but he had not the necessary material for proving this: the following statement will show that his conjecture was sound. It has been shown how the leaf of *Trichomanes reniforme* is provided with a marginal series of cells (Fig. 33); these give rise to the wings which run down the phyllopodium to its base: upwards the leaf widens out into the broadly reniform lamina. On cutting transverse sections of the lower part of the young leaf, the wings are seen as two round projections, in which the marginal cells do not undergo transverse segmentation, but the segments are cut off obliquely and alternately from opposite sides (Fig. 50): the number of segments thus produced is however small, and the wings of this part of the leaf are never largely developed. Now this mode of segmentation of the marginal cells is characteristic of the Polypodiaceae and other leptosporangiate Ferns, and is, to say the least, extremely rare in the Hymenophyllaceae: even here it is only seen near the base of the leaf, where, as in other Ferns, the structure of the wing is habitually more robust than in the upper parts².

Transverse sections of the reniform lamina of the mature frond of *Trichomanes reniforme* show that in the parts between the nerves it consists of four to six layers of cells, of which the central layers are larger and more watery, while the superficial cells have more protoplasm and chlorophyll: no intercellular spaces nor stomata are present. If transverse sections be cut from the young leaf a marginal cell of large size is seen in each, having a form similar to those found in the thin frond of *Trichomanes radicans*, etc. (Fig. 51)³:

¹ l. c. p. 23.

² See below, p. 350. Compare *Aspidium Filix-mas*, *Osmunda*, *Todea*, and *Marattiaceae*.

³ Compare Fig. 47 of *Trichomanes radicans*, which is drawn to the same scale as Fig. 51.

from the half-disc-shaped marginal cells, successive segments are cut off by transverse walls, and these are subdivided in such a manner that the transverse section of the margin of the frond presents an almost identical appearance with that of a median longitudinal section through the apex of the midrib of other species¹: thus Prantl's conjecture is correct, and though the ultimate bulk and complexity of the leaf in this species is as great as that in many of the Polypodiaceae, the marginal cells retain the form and simple segmentation characteristic of the Hymenophyllaceae.

The parallel case of *Hymenophyllum dilatatum* was also examined: exclusive of the nerves, the wings consist in this species of three to four layers of cells, usually three: of these the cells of the central layer are larger, while the superficial ones are relatively small. The wings extend over all the branches of the leaf, and may be traced down the petiole. In the young state a marginal series of half-disc-shaped cells is to be seen, from which successive segments are cut off by transverse walls, as in other Hymenophyllaceae (Fig. 52): the subdivision of these segments is singular, and seems to follow an almost regular rule: the segment first divides into two unequal parts (Fig. 52, the two youngest segments), by a periclinal wall, the larger cell then again divides, and the three resulting cells contribute to the three layers of which the mature wing is usually composed, and may undergo further divisions by anticlinal walls as in Fig. 54. When the marginal cell is about to cease its activity, irregular divisions appear in it, the walls being variously inclined (Figs. 52, 54), and the result is an appearance which at first sight resembles the segmentation of the marginal cells in the Polypodiaceae; but the same regularity does not hold here, and it is possible in all cases which I have observed to see (as in Figs. 53, 54) that these irregular and oblique segmentations succeed the more regular transverse ones: in fact they are not the type for this plant, any more than the oblique segmentation in the wing of

¹ Compare Prantl's Fig. 39, Plate III of *Trichomanes speciosum*: also Sachs' Lectures, Fig. 295 A.

Tr. reniforme towards the base of the leaf is for that species.

From the above descriptions it would appear that in the Hymenophyllaceae the wings extend from the base of the frond upwards over its whole margin, that (with the two exceptions above noted) the marginal cells have the form of half of a narrow disc: that segments are cut off from these by successive transverse (anticlinal) walls, and the fact that this mode of segmentation is retained, whether the expansions consist of but one layer of cells, or of more, is of special interest as showing that the arrangement of cell-walls is not entirely dependent on bulk, or on the external conformation of the part, but that there is a conservation of the type of segmentation in plants of natural affinity. Since the curvature of the segmental walls is very slight, while the walls by which the segments are further subdivided in *Tr. reniforme* and *H. dilatatum* cut them at right angles, it is clear that the centre of construction lies within the marginal cells themselves, and is situated comparatively near to the extreme margin of the wing.

Passing on now to the other leptosporangiate Ferns, in these, as in the Hymenophyllaceae, the leaf is habitually winged to its extreme base; but the wings of the lower part (petiole) are of a reduced type, and frequently appear there as mere longitudinal, light-coloured streaks. It is in Ferns of this class that the development and segmentation of the marginal series of cells is best known, and chiefly owing to the work of Kny and Sadebeck. It is generally known that a marginal series of cells is present, and that from them segments are cut off successively to form the flattened wings. On examining Kny's figure of *Ceratopteris*¹ it would appear that the segmentation of the marginal cells is similar to that in the Hymenophyllaceae, and this is made clear from a foot-note², in which this is stated to be the case. As far as I am aware, this, and in an obscure manner *Azolla*³, and apparently also

¹ Kny, Parkeriaceae, Taf. XXIV, Fig. 7.

² l. c. p. 40.

³ Strasburger, Ueber *Azolla*, p. 38, Plate I, Fig. 20.

Salvinia, are the only examples among the leptosporangiate Ferns other than the Hymenophyllaceae, which constantly show this mode of segmentation, and it is to be noted that they are all aquatic forms. The prevalent type is that in which segments are cut off by walls obliquely inclined alternately to the upper and lower surfaces of the leaf: this has been described by various writers¹, but it will not, I think, be superfluous to add drawings illustrating the segmentation of the marginal cells, since the drawings hitherto published do not adequately represent the extreme regularity and beauty of segmentation which may be found in certain Ferns. If transverse sections be cut through the young pinna of *Pteris cretica*, and the structure of the young wing be examined, the whole of it will be seen to be referable in its origin to the marginal cell (Fig. 55): it is composed of segments cut off alternately by walls inclined to the lower and upper surfaces, the whole presenting an appearance such as that of a section through an apex with a conical apical cell². In leaves which are unbranched the regularity of segmentation is less liable to be disturbed than in branched leaves: thus, if transverse sections be cut through the young leaf of *Scolopendrium vulgare*, the tissues may not only be seen in the young state to be referable in origin to the marginal cells (Fig. 56), but even when the wing has attained a very considerable size, the derivation of its tissues by segmentation from the marginal cells is still clear enough, and the segments, even to the number of sixteen, may be recognised in sections suitably cleared (Fig. 57). Referring to the segmentation of cells at the margins of flattened members, Prof. Sachs says³:—‘A certain similarity of the cell network with that of a slender growing point with an apical cell impelled the earlier observers to assume in such cases a special type. They regarded cells lying beside one another at the margin as a series of neighbouring apical cells. This,

¹ Sadebeck, Entw. and Wachsth. des Farnblattes, Berlin, 1874; also Schenk's Handb. I. p. 270. Sachs' Lectures, Engl. ed. p. 459.

² Compare Sachs' Lectures, Fig. 295 B.

³ Lectures, Engl. ed. p. 459.

from the purely formal point of view, is of course possible, but it contributes nothing further to the explanation of the processes of growth.' With regard to the wings of the leaves of Ferns, I cannot agree with this statement. If we accept the view that an apical or initial cell represents merely a break in the constructive system of the growing point, then the marginal cell (*m*) in Figs. 55, 56, 57 corresponds in this respect exactly to an initial cell of stem, leaf, or root, and just as from the latter (which may be one or more in number) by segmentation all the fresh tissues of the leaves of the member are derived, so also is all the fresh tissue of the wing derived ultimately by segmentation from the marginal cells: just as in the apices of stems, leaves, or roots, by tracing the origin and subdivisions of the segments we gain a knowledge of the manner of localisation of growth, so also may this be done in the wings. In fact, excepting the difference of form, number, and position, I fail to see that the initial cells of the apex of the stem, leaf, or root can with any reason be regarded in a different light from those initial or marginal cells which are found on the growing margin of the leaves of Ferns.

It is thus to be seen, both from the observations of others, and also from such examples as those above described, that in the leptosporangiate Ferns (exclusive of the Hymenophyllaceae) the type of segmentation of the marginal cells is more complicated than that of the Hymenophyllaceae; from each of the marginal cells two alternating rows of segments are cut off by oblique walls, while in the Hymenophyllaceae only one row of segments is derived from each marginal cell. As shown by a comparison of Sachs' diagrams¹ this latter type is associated with a deeper position of the centre of construction, and is thus characteristic of a more robust type of structure.

But among these Ferns the 'filmy' type of structure is not unknown, and I have had the opportunity of investigating the development of the leaf of *Asplenium resectum* in specimens from the Kew collection². The leaf of this Fern is thin and

¹ Sachs' Lectures, Engl. ed. p. 457, Figs. 295 A and B.

² This Fern was brought under my notice by Mr. Staden, of the Royal Gardens, Kew.

pellucid, and examination of it when mature shows that stomata are absent from the thinner portions of the frond, which consist of but two layers of cells, with no intercellular spaces between them: thus it has the ordinary 'filmy' character. In view of the fact that *Trichomanes reniforme* retains that mode of segmentation of the marginal cells which is characteristic of the Hymenophyllaceae notwithstanding that its leaf is four to six layers of cells in thickness, it was a matter of some interest to ascertain what is the mode of segmentation of this 'filmy' *Asplenium*, and to see whether it would, notwithstanding its 'filmy' character, retain the segmentation characteristic of *Asplenium*¹, or show, in accordance with its texture when mature, the simpler type of segmentation of the Hymenophyllaceae. The result of the examination was to find that the segmentation is according to the more complicated type, two rows of cells being derived from each marginal cell (Fig. 58), and that these remain undivided by periclinal walls, except in the vicinity of the vascular bundles: thus its leaf represents the polypodiaceous type of segmentation reduced to its simplest terms. These observations lead towards the following conclusions:—(1) that the 'filmy' character may be assumed in Ferns of various affinity: this point will be discussed later; (2) that within the circle of affinity of the leptosporangiate Ferns the mode of segmentation is not dominated by the absolute size² or external conformation, but that there is in certain Ferns a conservation of that type of segmentation which is characteristic of the family to which they belong, irrespective of increase (*Trichomanes reniforme*), or decrease (*Asplenium resectum*) of bulk as compared with typical members of the same family.

But the type of segmentation with two rows of segments from each marginal cell is not constant throughout the whole length of the frond in the Polypodiaceae: just as in *Trichomanes reniforme* a more complicated structure is found in the

¹ Compare Sadebeck in Schenk's Handbuch, Vol. I. p. 271, Fig. 36 D.

² As regards absolute size compare Fig. 51 of *Trichomanes reniforme* with Fig. 58 of *Asplenium resectum*: they are both drawn to the same scale.

young wings towards the base of the leaf, so also here the structure of the wing at the base of the frond is more complicated than above. If transverse sections be cut from a young frond of *Scolopendrium* near to its base, the internal structure of the wings does not admit of their tissues being referred in origin to marginal cells similar to those typically found in the upper part of the leaf: they appear to correspond rather in structure and development to that more robust form to be presently described as typical for the Osmundaceae and Marattiaceae, in which no single series of marginal cells is present. Similar results are to be obtained from *Asplenium nidus*, *Aspidium Filix-mas*, etc.; in fact, it seems to be a common character among the Polypodiaceae that the wings are more bulky towards the base of the frond, and that their construction is there on a more complex type. There is thus, roughly speaking, a proportion between the greater bulk of the phyllopodium and that of the wings towards the base of the leaf, while both are less bulky and simpler in construction above. This corresponds to similar observations above noted in the leaf of *Trichomanes reniforme*.

Examination of the leaves of *Amphicosmia* (*Hemitelia*) *Walkeræ*, Hk., shows that the type of the Polypodiaceae holds also for this representative of the Cyatheaceae. In the mature leaves of this plant the wings are but slightly indicated towards the base, appearing there as discontinuous longitudinal streaks, and in the young state a definite series of marginal cells is not to be recognised there; but transverse sections of the upper parts of the pinnae and pinnules show the marginal series of cells clearly defined, and with that regular alternate segmentation above described for the Polypodiaceae.

In connection with the 'filmy' development of Ferns an interesting question arises as to the nature of those strange growths called *Aphlebiae*, which are found attached to the base of the leaf of *Hemitelia* (*Alsophila*) *capensis*¹: such

¹ I owe it to Prof. Bayley Balfour that my attention was drawn to this Fern, and it was on specimens supplied by him from the Edinburgh Botanic Garden

developments appear to have been frequent on the Ferns of earlier geological periods¹, though they are rare on living species. Dissection of the bases of the leaves of this plant shows that the profusely branched 'Aphlebiae' are inserted above the extreme base, and, like the normal pinnae, alternately along the marginal lines or wings: they vary in number, two, three, or four being found on each leaf: their branching is irregular at the base, but higher up they produce alternate branches of a higher order (pinnules), which are inserted on the reduced marginal wings. The higher branches widen out into thin, meagre expansions, which correspond in general conformation to the normal pinnae, but are of a much more reduced type.

Comparing their microscopic structure with that of the normal pinnae, it is seen that they show the same characters but on a reduced scale; e.g. the normal pinna is five layers of cells in thickness, the aphlebia only three to four; while stomata and intercellular spaces are present in both: thus the comparison of these aphlebiae to 'filmy' Ferns is based on slender grounds. All the facts above adduced point to the conclusion that the 'aphlebiae' of *Hemitelia capensis* are nothing more than peculiarly developed basal pinnae, and when the fact is added that on one of the Edinburgh plants a pinna was found showing intermediate characters between the normal and the aphlebiae, this conclusion is greatly strengthened. But what circumstances they are which have led to so strange a development of certain pinnae, and the question whether in all the cases in which such growths have been described for fossil forms a like explanation is possible, must remain for the present undecided.

Material could not be obtained for working the actual development of the aphlebiae.

From Prantl's account of the Schizaeaceae² it would appear that these observations were made. Compare also Hofmeister, Higher Cryptogamia, notes on pp. 212, 243.

¹ Solms-Laubach, Palaeophytologie, p. 136.

² Schizaeaceae, p. 4. Compare his Plate VII., Figs. 109, 110, 111; Plate VIII, Fig. 133.

that the structure of the wings in these plants conforms, at least in the upper parts of the frond, to that of the Polypodiaceae. I have also noted that in *Aneimia* the wings of the basal part of the leaf are of the more bulky type: thus the Schizaeaceae appear, as regards the wings, to show no advance of complexity upon the Polypodiaceae.

Passing on now to the Osmundaceae, the structure of the young wings has been most exactly observed in *Todea barbara*, but observations have also been made on *Todea superba* and *T. hymenophylloides* (= *pellucida*), and on *Osmunda regalis*: it may be stated at once that (excluding the 'filmy' *Todeas*) the result is to find the wings in this family more complex than those of the true leptosporangiate Ferns.

Taking first *Osmunda regalis*, it has been stated by Kny¹ that marginal cells are present on the wings, from which, as in the Polypodiaceae, segments are cut off obliquely and alternately. This may be the case in young plants, but numerous sections which I have made from various parts of the leaf of this species fail to bear out the statement for well-grown plants: the construction of the young wing is found in old plants to be essentially similar to that to be described for *Todea barbara*; sometimes it is true that a series of larger cells may be seen from without to occupy the margin, while in section a wedge-shaped cell may be seen to lie at the extreme outer edge of the wing, but this is not constant, and when so found it is of relatively small size, while the segments never show that regularity of arrangement which is so characteristic of the Polypodiaceae. Knowing as we do that the apex of the leaf of *Osmunda* is occupied by a three-sided apical cell, and that the position of the wings corresponds to two of the angles of that cell², and that the edges of two rows of segments contribute to the formation of each wing, it would be contrary to all expectation that a definite marginal series should be found. In fact, I look upon the absence of

¹ Parkeriaceae, p. 40, footnote.

² Compare Phil. Trans., 1884, Plate 37, Figs. 4, 5, 6.

a definite marginal series as a very natural concomitant of the more complex construction of the apex of this leaf.

The base of the phyllopodium of *Osmunda* is considerably enlarged, so as to form a wide sheath, and the wings are here laterally extended: in the young leaf their margins are bluntly rounded, but later they run out into thin and membranous lateral flaps, consisting in part of but a single layer of cells: none the less are these to be recognised as developments of the wings, and a comparison may fairly be drawn between this thinning out of the wings, and that which is found in the upper parts of the leaves of *Todea superba* and *hymenophylloides*, and lends to them that 'filmy' character which will be discussed later. Above the sheath the phyllopodium of *Osmunda* is almost cylindrical, the wings being reduced (as in the petioles of the higher vascular plants), while in the upper part of the leaf, and especially the pinnae and pinnules, they are more extended. The leaf of *Osmunda* is thus winged throughout, but shows in its lower portion varieties of development which might be compared with such as are seen among the higher plants.

But it is in *Todea barbara* that the structure of the young wings, and the nature of the segmentations of the margins have been most carefully examined. I have already described the base of the leaf of *Todea superba*¹, and that of *T. barbara* is similar to it. In early stages of development the base of the leaf resembles that of *Osmunda*, being furnished with massive wings: later the activity of growth extends transversely across the face of the phyllopodium, resulting in such a development as may be compared to the axillary stipule which is not uncommon among Angiosperms, and also finds its homologue in the commissure of the Marattiaceae and in *Stangeria*. Here also the margins, which are at first blunt and rounded, extend as the leaf develops into membranous flaps, which consist at their extreme edge of only one layer of cells. The conformation of the upper parts is generally

¹ Phil. Trans., 1884, p. 578, Plate 37, Figs. 8 a, b, c.

similar to *Osmunda*, the wings being massive, and consisting of about nine layers of cells.

Now the question is how are these massive wings produced? If the margins of young wings be examined externally, no marginal series of cells is seen; they appear to be composed of a complicated net of relatively small cells, which are arranged more or less definitely in transverse rows (Fig. 59). Examining these rows individually¹ there is no single cell in each which can readily be fixed upon as a single initial for the whole row; in fact no marginal series of cells is present here, such as is found in the simpler Ferns. This conclusion is borne out by transverse sections through the young wing (Fig. 60), in which no single cell is obviously larger than the rest, and the segmentation is not by inclined and alternate walls, but there is a T division, the bases of the individual cells being not pointed, but approximately rectangular. It may frequently be seen, as in Fig. 60, that a clearly defined wall (x, x) divides the wing into two almost equal halves: in such a case the idea of a single marginal cell is clearly out of the question, and it appears probable that at least two initials are present in each transverse layer; if this were regularly the case the margin of the wing would be occupied by two longitudinal rows of initials placed side by side, which would take up the function performed in the leptosporangiate Ferns by a single row. It is clear enough that the origin of the tissues in Fig. 60 might be traced to the two cells marked (x, x): but though such a definite arrangement of the meristem may be found in some sections, it does not appear to be constant, nor does the surface view from without (Fig. 59) clearly point to such a conclusion. Accordingly, without actually defining the exact order of segmentation of the cells at the margin of the wing of *Todea barbara*, or even assuming that a fixed and definite rule exists, we may conclude (1) that no single series of initial cells is present; (2) that the superficial cells of the wing are of oblong form,

¹ It can hardly be doubted that these rows of cells correspond to one marginal cell together with its segments, in the Polypodiaceous type.

having rectangular bases ; (3) that they undergo T division, and therefore (4) the whole segmentation of the wing is of a more complicated type than in the typical leptosporangiate Ferns : the whole wing is more massive, and the centre of construction more deeply seated.

These being the results of examination of *Todea barbara*, a peculiar interest attaches to the examination of similar points in the 'filmy' species of *Todea* (= *Leptopteris*, Presl.), and to the question whether the filmy character is to be taken as any indication of an affinity to the Hymenophyllaceae. I have already described the conformation of the base of the leaf of *Todea superba*¹, and in this respect, as also in the structure of its apex, it is essentially similar to the more robust *T. barbara* ; but the pinnae and pinnules with their wings are more delicate : stomata and intercellular spaces are absent from the wings, which consist of but few layers of cells, and accordingly they have that delicate pellucid character which is described as 'filmy.'

The wings on the lower part of the phyllopodium are not largely developed, and appear when mature to be about three layers of cells in thickness : similarly, the wings of the mature pinnae and pinnules are three layers in thickness near to the midrib, but tail off towards the margin to a single layer : thus it is only at the margin that the wings actually attain the character of the simpler Hymenophyllaceae. As regards their development, *no marginal series is to be seen on any part of the leaf when young* ; it is only subsequently that a rather irregular marginal series appears, and in their first segmentations the marginal cells follow the polypodiaceous type (Figs. 61, 62) ; but in some cases (Figs. 63, 64) the segmentation is rather that of wings of a more bulky character : later, however, as the wings grow more extended, they become thinner at the margin, and transverse segmentation such as is seen in the Hymenophyllaceae becomes the rule (Figs. 65, 66, 67) ; thus, as regards their development, these filmy wings of *Todea superba* show first, though imperfectly, the characters of the

¹ Phil. Trans. 1884. Part II, p. 578.

more robust Osmundaceae, and it is only as the filmy character becomes pronounced that the segmentation as in the Hymenophyllaceae appears. The points of most importance are (1) that no clearly marked series of marginal cells is present from the first; (2) that both the contour of the wing as seen in section, and its internal structure are variable; and (3) that though the segmentation is finally that seen in the *Hymenophyllaceae*, still where the whole structure when mature is but one layer of cells in thickness, no other mode of segmentation is possible but that by transverse walls.

Todea hymenophylloides (= *T. pellucida*) occupies an intermediate position between *T. barbara* and *T. superba* as regards the texture of the leaf: the thin expanded wings of the pinnae and pinnules have no stomata or intercellular spaces, and consist of three to four layers of cells, of which the superficial cells are relatively small, while the central are large, the margins do not run out to a thin edge as in *T. superba*: in fact, the structure of the wings resembles that of *Hymenophyllum dilatatum*, and accordingly the question of their mode of development is an interesting one for comparison. Transverse sections of the pinnules show that the wings do bear marginal cells, but that these are not large or prominent, nor is their segmentation very regular: in the large majority of sections the segments appear to be cut off alternately from the marginal cell, according to the polypodiaceous type, but the segments divide up according to no fixed rule (Figs. 68, 69): the cells which constitute the central layer are formed by periclinal walls, which apparently do not appear in all the segments. Thus it is seen that, though certain species of *Todea* assume in the wings of the upper parts of their leaves the 'filmy' structure which is characteristic especially of the Hymenophyllaceae, they do not at the same time assume the stereotyped mode of segmentation of marginal cells of the latter; and indeed a marginal series of cells seems not to be formed till a comparatively late period. When it is also remembered that the conformation of the base of the leaf and of its apical meristem corresponds to that of the robust *T. barbara*, the conclusion

naturally follows that the 'filmy' character is not a safe index of affinity, but that it is rather to be regarded as the result of adaptation. The general discussion of the filmy character in Ferns will be taken up later (page 378).

Passing on to *Angiopteris evecta* as a type of the Marattiaceae, the thick coriaceous wings may be traced in the mature leaf as extending, with varied development, over the upper part of the phyllopodium, pinnae, and pinnules: passing down the phyllopodium the wings become gradually reduced, till above the 'stipules' they are lost, and the base of the phyllopodium is almost perfectly cylindrical: at the base are the massive stipules, joined transversely by the fleshy commissure, and containing a well-developed system of vascular bundles. The development of these basal parts has already been described elsewhere¹, their first appearance being as a thick and massive weal, in which the component cells undergo repeated T divisions, and on comparative grounds it has been concluded that notwithstanding their size, massive character, and the presence of vascular bundles in them, they are to be regarded as peculiarly metamorphosed wings, and as comparable to the somewhat similar, though smaller growths in *Todea* and *Osmunda*². It is well known that these stipules as they develop run out to a thin edge, which is almost transparent, with uneven margin, and consists at the extreme edge of but a single layer of cells; this we may I think rightly compare with the thinning out of the wings of the pinnae in *Todea hymenophylloides* and *superba*, and in this sense even the massive stipules of *Angiopteris* may be said to have 'filmy' margins.

The development of the wings of the pinnules was traced with

¹ Phil. Trans. 1884, Part II, p. 582; Plate 37, Figs. 10, 11.

² The presence of vascular bundles in the stipules of *Angiopteris*, while the corresponding outgrowths in *Todea* have none, need be no obstacle, since wings in different plants are very variable in this respect, e.g. bundles are absent in the wings of the pinnae of *Cycas*, while they are present in those of *Stangeria*. Again, the occurrence of vascular bundles is very irregular in the wings of the leaf of *Angiopteris* itself: it would appear rather that the presence of vascular bundles, here as in other parts of the shoot, depends roughly upon the area and bulk of the wings. In the stipular growths of *Stangeria* no vascular bundles are present.

the following results: the apex of the young pinnule appears rounded, so that transverse sections of it are circular, the formation of the wings not having begun; but lower down the wings appear as a rounded weal on either side: here (Fig. 70, *x*) the superficial cells increase in size, and are more densely filled with protoplasm than the rest: the projecting wing which thus originates does not spring from a single row of cells; the transverse section clearly shows that a number of cells take part in its initial formation, and these continue to grow and divide, while the rest of the pinnule, which finally constitutes the midrib, passes over into the quiescent condition. The cells forming the wing are of rectangular form (Fig. 70) and undergo repeated T divisions (Figs. 71, 72, 73); pyramidal cells are absent with the exception of those which form the hairs. As to the exact sequence of segmentation in the growing wing, I have not been able, any more than in *Todea barbara*, to recognise any invariable rule: sometimes (Figs. 71, 73) a group of cells, having obviously a common origin, occupy the centre of the transverse section, and in such cases it might be possible to recognise a certain cell as the permanent initial: in other cases (Fig. 72) the wing obviously originated from the outgrowth and repeated divisions of several cells, and the whole section of the wing may be seen to be composed of a number of groups of cells, each having apparently a distinct origin. I conclude that here, as in *Todea barbara*, though T division is the universal rule, there is no definite arrangement of the groups of cells composing each transverse section, so as to indicate their origin from any single initial. This mode of growth and segmentation of the wing is maintained throughout its development¹, the result being a massive structure of the wing, consisting of ten or more layers of cells.

The results of the above observations on the characters and mode of development of the wings of the leaves of Ferns may now be drawn together, and compared: the following are the chief points to be noted:—

¹ Phil. Trans. 1884, Part II, Plate 38, Fig. 19.

(1) That the leaves of the large majority of Ferns are winged, and that the wings may be traced, more or less distinctly, as continuous from the apex to the base of the leaf.

(2) That the wings are typically delicate and thin in the Hymenophyllaceae, that those of the Polypodiaceae are more robust, while in the Osmundaceae (excluding the filmy *Todeas*) and Marattiaceae the wings are thick and almost coriaceous.

(3) That the type of the Hymenophyllaceae is that each cell of the marginal series has the form of half a disc, and the segmentation is transverse (Fig. 47): in the Polypodiaceae the form of the marginal cell is a sector of a disc, and the segmentation is alternately from the upper and lower margins (Fig. 56): that in the Osmundaceae (excluding the filmy *Todeas*) and Marattiaceae there is no marginal series, but the cells forming the wing have square bases, and undergo a T division (Figs. 60, 72).

(4) That the Hymenophyllaceae, Polypodiaceae and other leptosporangiate Ferns, Osmundaceae, and Marattiaceae form a natural series as regards the complexity of structure of the young wing, the first-named being the simplest, and the last the most complex.

(5) That as we rise in this series, the centre of construction becomes more and more deeply seated, the progression in this respect being closely comparable to that above noted for the apical meristems of root, stem, and leaf.

(6) That in the Ferns observed (and it may be stated also for Ferns generally) the wing is of a more robust character near to the base of the frond than in its upper portions, there being thus some relation of bulk of the wing to that of the phyllopodium which bears it.

(7) That the wings may undergo various metamorphoses, being in some parts reduced, so as to be barely recognisable (petiole), in other parts being developed as broad flanges, or as the massive 'stipules.'

(8) That the 'filmy' character which depends upon thinness of the wings, and absence of stomata and intercellular spaces, is found to occur at three distinct points in the series, and

that filmy wings may be produced by various modes of marginal segmentation.

SPORANGIA.

Much more attention had been paid to the comparative investigation of the origin and development of the sporangia of Ferns, than to the other meristematic tissues, and I have but little to add to the facts already published elsewhere on this subject: nevertheless, in order to bring observations on the sporangia in line with the facts above detailed, and to show that the progress of other meristems from the simpler to the more complex as we pass along our series, runs parallel with a similar increase of complexity in the origin and construction of the sporangium, it will be necessary briefly to sketch out the characters of the young sporangium in the series of Ferns above cited.

On the ground of the mode of origination of the sporangium from a single superficial cell, or from a number of cells, Goebel has distinguished leptosporangiate from eusporangiate forms: and I shall show that this distinction, which divides a very natural series of plants, is in itself by no means a sharp line of demarcation. In drawing this distinction, however, Goebel has laid his finger upon a far-reaching difference of character, which finds its reflection in every meristematic tissue of the plants in question: in roots, stems, leaves, and wings, as well as in the sporangia, an increase of complexity of construction is to be seen as we pass upwards through the series of Ferns.

Without entering on details as to the exact succession of segmentations of the young sporangia, it will suffice for our present purpose to note that the sporangium of the Hymenophyllaceae¹, and Polypodiaceae², and other leptosporangiate Ferns arises typically as an outgrowth of a superficial cell. The first division in this cell is transverse in the Polypodiaceae³,

¹ Prantl, l. c. p. 39: also Plate VI.

² Reess, Pringsh. Jahrb. v, p. 222. Kny, Parkeriaceae, p. 49.

³ Reess, l. c. Plate XXI, Figs. 4, 5, 7.

dividing a basal or stalk cell from the cell which will form the head of the sporangium (compare diagram Fig. 88 *a*, *x,x*): this I take to be the simplest segmentation of all. In the Hymenophyllaceae¹, in *Ceratopteris*², and in *Marsilia*³ the first segmentation is frequently not transverse, but oblique, and this type I take to be nearer to the more complicated eusporangiate forms (compare diagram Fig. 88, *b*). This is, however, only a slight difference of detail; the main point is, that in all these Ferns the sporangium ultimately springs from a single superficial cell: in all of them it has been demonstrated by the writers above quoted that the position and order of succession of the divisions in the head of the sporangium show quite a diagrammatic regularity, and it will be remembered in connection with this that the structure of their apical meristems is comparatively simple and precise, a single apical cell with definite mode of segmentation being present; thus in these plants there is a parallelism between the structure of the apical meristems and that of the young sporangium.

It has been noted that in the Hymenophyllaceae the basal wall (*x,x*, diagram Fig. 88, *b*) is oblique: its position is apparently not quite uniform, but it appears usually to meet one of the lateral walls of the initial cell⁴; in the Schizaeaceae, however⁵, this basal wall appears to be inserted actually on the periclinal (basal) wall of the initial cell (compare *x,x*, diagram Fig. 88, *c*), and is accordingly more inclined than in the previous cases. Though this may appear a trivial detail, it is to be noted as an indication of a lowering of the centre of construction of the sporangium, and of the assumption of a more robust and massive character. Though the sporangium of the Schizaeaceae is wholly derived from a single initial cell, it is, when mature, relatively large as compared with the other leptosporangiate Ferns, and it is seated on a short thick

¹ Prantl, l. c. Plate VI, Figs. 103-105, etc.

² Kny, Parkeriaceae, Plate XXV, Figs. 2, 3, 5.

³ Russow, Vergl. Unters. Taf. VI, Figs. 62, 71, etc.

⁴ Prantl, Hymenophyllaceae, p. 39, Taf. VI, Figs. 100, 104.

⁵ Prantl, Schizaeaceae, p. 49.

stalk, and this character is foreshadowed by the first segmentations. In all the plants hitherto cited the wall of the sporangium consists of a single layer of cells, while a tapetum of not more than two layers intervenes between it and the spore-mother-cells.

Taking next the Osmundaceae, here as in the Schizaeaceae the sporangia are of relatively large size, and have short and thick stalks, and so they approach the Marattiaceae in these respects. The origin of the sporangium has been investigated by Prantl¹, and by Goebel²: the latter leaves the point still open whether or not the sporangium of *Osmunda* be referable in its origin to a single cell, as in the true leptosporangiate Ferns; and this is just one of those questions which, when dealing with transitional forms is so difficult to answer with certainty. If the origin be traced far enough back, doubtless the whole sporangium could be referred to a single cell, just as the whole plant may be ultimately referred in origin to the ovum; but without straining the point in such a way as that, it is often difficult to trace back the sporangium of *Osmunda* to a single cell, and in any case, a single initial cell does not project obviously outwards before segmentation, as is the case in the true leptosporangiate Ferns.

In *Osmunda regalis* the sporangia first appear as rather broad and very slightly convex projections on the wings of the pinnae and pinnules (Fig. 74); more than a single cell may take part, and though such cells often bear an obvious relation to one another, still it cannot be said in the same sense as in the leptosporangiate Ferns that the sporangium results from the outgrowth of a single superficial cell. In all cases, however, one cell distinctly takes the lead, and this we may call the initial cell (Fig. 75); but the arrangement of its division-walls does not, as in the true leptosporangiate Ferns, conform to any strict plan; the initial cells are oblong as seen in vertical section, and the first divisions are longitudinal, so as to meet the basal wall (Fig. 74): both in the segment thus cut off and in the central cell, periclinal, or sometimes oblique

¹ Bot. Zeit., 1877, p. 64.

² Schenk's Handbuch, III, p. 387.

divisions may take place (Fig. 75), so that a considerable bulk of tissue is formed, in the projecting apex of which a single large cell occupies a central position. This ultimately divides by a periclinal wall (Fig. 76), and the inner of the two resulting cells is the archesporium¹, which is completely surrounded by a single layer of other cells, and these, as in other Ferns, develop into the wall of the sporangium. The form of the archesporium is not definite and uniform as in other Ferns; and in most cases, instead of being pointed, its base is irregularly oblique; but the subsequent divisions, by which the layer of tapetal cells is cut off from it, follow with somewhat greater regularity (Figs. 77, 78), and the most common result is that the sporogenous cell (the true archesporium) has a tetrahedral form: nevertheless exceptions even to this are by no means uncommon (Figs. 79, 80). The whole sporangium, of which Fig. 77 may be taken as a good typical example, thus comes to consist of a short and massive stalk, a median longitudinal section of which shows four rows of cells; this bears the head, which is composed of a superficial layer which forms the wall of the sporangium, a tapetal layer, which is shaded obliquely in Fig. 77, and consists as yet of a single layer of cells. Towards the base of the sporangium, cells which have been cut off by extra oblique walls intervene between the tapetum and the superficial layer of the wall, giving the sporangium a more massive character than in the leptosporangiate Ferns (Figs. 77, 78, 80): there is thus a considerable bulk of internal tissue which takes no part in the formation of the spores (Figs. 81, 82). Subsequently anti-clinal divisions appear in the cells forming the wall of the sporangium, but as no periclinals are formed the wall remains a single layer of cells in thickness even to the period of maturity; towards the base, however, it is supported internally by the cells above mentioned (Fig. 82). The tapetum divides

¹ I use the term archesporium for this cell before the tapetum is separated from it, because this is customary, and notwithstanding the inconsistency of so using the term, while in the higher plants it is applied to the cell from which the spore-mother-cells are directly derived.

first by anticlinal and later by periclinal walls, the result being two, or even three layers, the latter condition showing a greater complexity than in the leptosporangiate Ferns ; but opposite the point where dehiscence takes place these divisions are delayed (x , Fig. 82). Meanwhile the sporogenous cell has grown, and divided repeatedly, and formed numerous spore-mother-cells, of which the number is much larger than in the Polypodiaceae ; their number may be judged from the fact that more than twenty appear in a single section (Fig. 82). Each of these divides into four, the inner tapetal layer becomes glandular and disorganised, the outer however persists for a time, but dries up before maturity without becoming glandular.

I have already published a preliminary account of the origin of the sporangium in *Todea barbara*¹, and am now able to give a more full account with figures. This plant shows a structure and development of the sporangium which corresponds in all essential points to that of *Osmunda*, and there is a like irregularity as to the exact position and sequence of the segmentations. The essential parts of the sporangium appear to originate from a single cell with a square base, and deeply sunk in the tissue : having divided by a periclinal wall, the outer of the resulting cells undergoes anticlinal divisions (Fig. 83), by which three peripheral cells are cut off from a central cell (Figs. 84, 85) : the whole group is still deeply sunk in the surrounding tissue, and the young sporangium projects as yet but slightly beyond the surface ; it is clear from observation from without (Figs. 84, 85) that the disposition of the three lateral cells round the central one is similar to that in the Polypodiaceae, though the base of the central cell is often square. Then follows a periclinal division (Figs. 86, 87), by which the archesporium is cut off from a superficial cell : the form of the archesporium is variable, sometimes (Fig. 87) it is pointed below, and tetrahedral in form, as in the leptosporangiate Ferns ; but this is the less common case : more frequently (Fig. 86) it has a square base ; but even when this is so, the

¹ Q. J. M. S. Vol. XXV, p. 100, 1885.

subsequent divisions to form the tapetum may be inclined to one another, so that the sporogenous cell is ultimately tetrahedral, as in *Osmunda* (Fig. 77). In its further development the sporangium of *Todea* corresponds closely to that of *Osmunda* (compare the diagrammatic Figs. 88, *d*, *e*).

Observations have also been made on the filmy Todeas (*T. superba*, and *T. hymenophylloides*): in both of these the sporangia are seated only on the more massive nerves, and do not arise from the filmy part of the pinnules. In these species the first stages of development were not noted, but sporangia were seen corresponding closely in structure to those of *Osmunda* (Fig. 77), and all observations I have made point to the conclusion that the development of the sporangium is in these species essentially similar to that in *Todea barbara*, or *Osmunda regalis*.

The mode of origin of the sporangium in the Marattiaceae is well known through the researches of various writers, but especially of Goebel¹: for our present purpose the most notable points with regard to it are (1) that the sporangium is not directly referable in its origin to a single cell, i. e. it is eusporangiate; (2) that the archesporium is the hypodermal cell of the axile row of those cells which grow out to form the sporangium; (3) that it has a cubical form, and is deeply sunk in the tissue of the sporangium; (4) that the tapetum is derived from the cells surrounding the archesporium; (5) that the wall of the mature sporangium consists of more than a single layer of cells; and (6) that the sporangia which individually produce a relatively large number of spores, are massed together into bulky confluent sori (compare Figs. 88, *f*, *g*).

From a comparison of the characters of the young sporangia above noted, and of the diagrammatic figures (Figs. 88, *a-g*) which embody them, the following conclusions may be drawn:—

(1) That as regards the complication of the mode of origin, and the complexity of structure of their sporangia, the Hymenophyllaceae and Polypodiaceae, the Schizaeaceae, *Osmun-*

¹ Bot. Zeit., 1881, p. 681, etc.

daceae, and Marattiaceae form a natural series, the last named being the most complex.

(2) That in respect of reference of the sporangium to one or to more than one initial, the Osmundaceae are intermediate between the leptosporangiate and eusporangiate types, and that therefore this distinction cuts through a natural series of plants.

(3) That the increase of complexity is accompanied by a sinking of the centre of construction, similar to that already noted in the apices of root, stem, leaf, and wings of the leaf of the above series.

(4) That the change in form of the archesporium (from the conical in the leptosporangiate Ferns to the cubical in the eusporangiate) is similar to the change of form of the initial cells of root, stem, leaf, and wing, observed as we rise in the above-named series.

(5) That the structure of the wall and tapetum is more complex in the eusporangiate Ferns, and the number of spores in each sporangium is larger, while the sporangia themselves are fewer.

(6) That no difference of importance in the sporangium is to be found between the filmy and the robust types of the Osmundaceae.

CONCLUSION.

A comparative study has now been made of each of those meristematic tissues which contribute to the formation of the sporophyte of the Fern, viz. of Root, Stem, Leaf, Wing, and Sporangium. Each of these has been examined in representatives of various divisions of the Filicineous series, viz. in the Hymenophyllaceae, Polypodiaceae, Cyatheaceae (in part), Schizaeaceae, Osmundaceae, and Marattiaceae. The main result is to demonstrate a singular parallelism in character of all the meristems in these several divisions, and to show that in the divisions first named the meristems are relatively simple in construction, and exhibit definite regularity of segmentation, one initial cell of definite form being present in

each¹. Passing upwards through the series this simplicity and regularity is gradually departed from in each and all of these meristems; the structure becomes more complex, the identity of the single initial is lost, and the regular sequence of segmentations becomes less definite: this is associated in each case with a sinking of the centre of construction. The first-named divisions of the Filicineous series have a typically more delicate structure of their mature organs than those named later in the series, and this character comes out clearly also in the construction of the meristems. Taking into consideration for the moment the relative complexity of their meristems alone, the above list may be accepted as representing a natural series which graduates by gentle steps from the simpler to the more complex.

It may at first sight be felt that to use as a basis for arrangement of a series the detailed characters of the meristematic tissues, is to proceed on insufficient ground, and to approach too nearly to that cellular morphology which, if pursued universally and consistently into detail, would lead to unsound results; and those who are disposed to object will doubtless point out that there is not always a parallelism between all the meristematic tissues of a given plant. Thus in typically eusporangiate forms, such as *Ophioglossum* or *Equisetum*, a single initial cell with definite segmentation is found in stem and root: these exceptional cases will be again referred to below. In support of the main conclusion of this paper, however, it will be sufficient to point out that on the ground of comparative study of the external form and internal structure of both the sporophyte and the oophyte, the relative positions of certain families is already agreed upon: the main series of Ferns is recognised by recent writers as extending between two extreme types—the Hymenophyllaceae, which are considered to be of Algal-Bryophytic affinity,

¹ The results of the detailed examination *Onoclea Struthiopteris* by D. H. Campbell (The development of the Ostrich Fern; Mem. of the Boston Soc. of Nat. Hist. Vol. IV. No. II) fall in for the most part with those of other observers. I regret that this memoir only came to my hands after these pages had been set up in type.

and the Marattiaceae and Ophioglossaceae, which approach the Cycadaceae at least in the characters of the sporophyte. The evidence adduced in this paper is to be taken as materially strengthening this view, while it is also intended as a contribution to that knowledge which will be necessary for the final arrangement of the several sub-divisions of Ferns in sequence between these two extremes: thus the close relation of the meristems of the Osmundaceae, and especially of *Todea barbara* to the Marattiaceae, is clearly brought out. It is also seen that *Amphicosmia* (as an example of the Cyatheaceae), though so much larger than the ordinary Polypodiaceae, does not differ materially from them in the character of its meristems; and again, judging from the evidence adduced, the relation of the Schizaeaceae appears to be closer to the true leptosporangiate Ferns than to the Osmundaceae, notwithstanding that on various grounds they may be regarded as more nearly connected with the Osmundaceae than are the Polypodiaceae or Cyatheaceae.

As regards the sequence of the various groups of homosporous Ferns, various authors have arranged them in different ways—sometimes arbitrarily, sometimes with definite purpose. In the Synopsis Filicum¹ the order is:—

- I. Gleicheniaceae.
- II. Polypodiaceae [including Cyatheaceae and Hy-menophyllaceae]
- III. Osmundaceae.
- IV. Schizaeaceae.
- V. Marattiaceae.
- VI. Ophioglossaceae.

Russow² speaks of the leptosporangiate Ferns as constituting six equivalent branches of the phylogenetic tree, and does not distinguish any one of them as specially approaching the Marattiaceae. Luerssen³ gives the series thus:—

¹ Synopsis Filicum, Sir W. Hooker.

² Vergl. Unters. 1872, pp. 194, etc.

³ Handbuch d. syst. Botanik, 1879.

- I. Hymenophyllaceae.
- II. Cyatheaceae.
- III. Polypodiaceae.
- IV. Gleicheniaceae.
- V. Schizaeaceae.
- VI. Osmundaceae.
- VII. Marattiaceae.
- VIII. Ophioglossaceae.

This arrangement is also observed by Goebel¹; though, oddly enough, the position of the Schizaeaceae and Osmundaceae is reversed where the special description of the groups is given (l. c. p. 228). This same reversed position is adopted also by Van Tieghem²; and from these facts I conclude that these authors had not recognised the near affinity of the Osmundaceae to the Marattiaceae. Prantl³ suggests that the isosporous Ferns may be arranged, in respect of their general characters, in three groups, as follows :—

I.	II.	III.
Hymenophyllaceae.	Schizaeaceae.	Osmundaceae.
Polypodiaceae.	Gleicheniaceae.	Ophioglossaceae.
Cyatheaceae.	Parkeriaceae.	Marattiaceae.

He recognises the affinity more especially of the Schizaeaceae to the third group, and, on grounds which appear to me to be insufficient, especially to the Ophioglossaceae, rather than to the Osmundaceae or Marattiaceae.

It is thus seen that of the intermediate divisions of isosporous Ferns, the close relation of the Polypodiaceae and Cyatheaceae has been recognised by all the authors above quoted, and these two groups are placed by them next to the Hymenophyllaceae; this I believe to be their true position, and this conclusion is also borne out by the study of their meristems. The details of structure and development of the Gleicheniaceae are too imperfectly known to allow of their

¹ Outlines, p. 194, Engl. ed.

² Traité de botanique, p. 1256.

³ Schizaeaceae, 1881, p. 151.

position being definitely fixed at present: at the same time I may state that, as far as my observations on the meristems extend, they appear to correspond to the Polypodiaceae. The Schizaeaceae are recognised as those among the truly leptosporangiate Ferns which show affinities to the eusporangiate Ferns, while the Osmundaceae show that affinity much more distinctly, and most recent writers admit more or less fully that they form a connecting link between the leptosporangiate and eusporangiate members of the series.

But these conclusions, based chiefly upon the comparison of the sporophyte, are also borne out by the characters of the oophyte: thus the filamentous, protonema-like character of the oophyte of the Hymenophyllaceae is the simplest in structure of all the prothalli of Ferns, and indicates their relation to the Bryophyta¹. The prothallus of the Polypodiaceae, after a short filamentous growth, widens out into the cordate expansion with circular 'cushion'; the Cyatheaceae resemble them in these respects²; the Schizaeaceae also appear to correspond to the Polypodiaceae in the characters of the prothallus³, and this, as well as other grounds of comparison, lead me to conclude that their affinity to the true leptosporangiate Ferns is nearer than to the Osmundaceae. In the Osmundaceae the result of germination may be directly a massive prothallus, the filamentous stage being here lost⁴; often, however, the prothallus of these plants may first assume a flattened form. In the Marattiaceae the first result of germination may occasionally be a short filament, or more frequently a flattened expansion; but often the direct result is a massive body which, when the prothallus is mature, is thicker than that of the Osmundaceae⁵. Lastly, as far as it is known, the oophyte of the Ophioglossaceae is a solid, massive body. Though in comparison of the oophyte it is not

¹ See Bower, *Annals of Botany*, Vol. I, p. 270, where the most important literature on this subject is quoted.

² Bauke, *Pringsh. Jahrb.* Bd. X, pp. 49, etc.

³ Sadebeck, in *Schenk's Handbuch*, I, p. 170.

⁴ Luerssen, *Zur Keimungsgeschichte der Osmundaceen*.

⁵ Jonkman, *La Génération Séxuée des Marattiacées*.

advisable to lay much stress upon details of conformation, the general progress of the oophyte in our series is shown to be from the filamentous type to that of a solid mass of tissue, that is, from the simpler type of construction to the more complex; and in this a parallel is seen to the observations above detailed on the meristems of the sporophyte in the same series. Again, if the antheridia and archegonia be compared in this same series, it will be seen that there is a progression in their mode of insertion. In the Hymenophyllaceae the antheridia are seated on stalks, which appear lateral or terminal on the filamentous oophyte¹, and the length of the stalk is often as great as the whole depth of the antheridium. In the other leptosporangiate Ferns the stalk, if present, is usually short, or the antheridium may even be sunk in the margin of the thallus²; in the Osmundaceae there is but little difference from these, but in the Marattiaceae and Ophioglossaceae the antheridium is deeply sunk in the tissue of the massive prothallus³. In the case of the archegonia also it is to be noted that in the Hymenophyllaceae the archegonia are exposed in groups on the relatively small archegoniophores and have projecting necks⁴, while in the Marattiaceae⁵ they are immersed in the tissue of the thallus and their necks project only slightly. Thus in the simpler terms of our series the sexual organs are exposed and project, while in the most complex forms they are protected by being sunk in the tissue of the oophyte.

Accordingly, whether the general character of the sporophyte or of the oophyte be considered, the divisions of the Filicineae would range themselves serially, according to their characters, in the same sequence as that indicated as the result of comparative study of their meristems; and since that is so, I think that no further answer is necessary to those who might at first feel an objection to the use of such apparently special

¹ Compare *Annals of Botany*, I, Plate XIV, Fig. 9; Plate XVI, Figs. 45-50.

² Kny, *Monatsber. d. K. Acad. der Wiss. Berlin*, 1869.

³ Jonkman, l. c. Plate VII, Figs. 87-90.

⁴ *Annals of Botany*, I, Plate XIV, Figs. 10, 16.

⁵ Jonkman, l. c. Figs. 100-105.

characters as the details of meristematic structure as a ground for phylogenetic argument with respect to the series of Ferns.

We see then that on comparing a series of forms which on independent grounds marks itself off, and ranges itself in order as a natural series, there is in every one of the meristems of the plant to be recognised a progression, as we pass along the series, from the simpler to the more complex, from a definite type of meristem, characteristic of lower organised plants, such as Bryophyta and Algae, to a less definite and more complex type characteristic of higher organisation, such as that of the Gymnosperms and Angiosperms. It may with confidence be stated that at no point in the vegetable kingdom is such a transition so clear and so marked as in the Ferns. The significance of this transition is not far to seek: the lowest terms of our series, the Hymenophyllaceae, have probably a joint alliance to the Algae and Bryophyta, and are plants of characteristically semi-aquatic habit, living for the most part in air saturated with moisture, and in accordance with this habitat they have thin extended rhizomes, membranous fronds, thin roots, projecting sporangia, and a delicate usually filamentous prothallus with antheridia and archegonia freely exposed: here is seen in every part a relatively great exposure of surface in proportion to bulk, and accordingly, were it not for the wetness of the habitat, there would be danger of drying up on exposure to the air. Passing upwards along the series to the Marattiaceae, we see the transition by successive steps to plants capable of enduring without harm an exposure to considerable drought: we see, instead of the thin rhizome with scattered leaves, the thick upright stock with a terminal bud of leaves which protect its apex¹; instead of the membranous frond, the thick, almost coriaceous leaf with massive wings; the roots instead of being thin become bulky: the sporangia do not project on a thin stalk, and so run the risk of drying up before maturity, but

¹ Here I speak in general terms: the majority (though not all) of the Hymenophyllaceae have creeping stems: the majority of the Marattiaceae have short, upright stems with crowded leaves; but species of *Danaea* are exceptions to this.

originate deeply in the tissue of the leaf, and are sessile and massive, or are even coherent together in masses when mature. Finally, in place of the filamentous, Alga-like oophyte, we find the fleshy and massive prothallus with its antheridia and archegonia not projecting and exposed, but protected from drying up by being sunk in the tissue. Every one of these characters points in the same direction: and if we once grant that the Hymenophyllaceae are phylogenetically the lowest members of the Filicineous series (a view which is held by all recent writers), then the Ferns illustrate in a most remarkable way the emergence of this branch of the Vascular Cryptogams from a semi-aquatic to a truly aerial habit. This is to me the real meaning of the lowering of the centre of construction, and consequent increase of robustness in all these meristems as we pass from the Hymenophyllaceae to the Marattiaceae: in it I believe that we see the expression of the fact that the higher plants of this series, by their more bulky habit, are the better adapted to an existence under circumstances of exposure to air which is not saturated with moisture. Regarding the series of green plants as a whole, those lowest in the scale are characteristically dependent upon water for their life, and especially for their fertilisation, and in this latter respect at least they betray their aquatic origin: in vascular plants it is seen that those which we regard as the higher in the scale are as a whole those best adapted to living in the air and in comparatively dry situations, and they are independent of external water as regards their fertilisation¹. Among the Vascular Cryptogams, however, we see a series in a transition state, emerging from the semi-aquatic habit: the differentiation and construction of the vegetative organs of the sporophyte here shows a general similarity to that of the highest forms, but the sexual process, which is still dependent for its completion upon external water, is a clear index of their position lower in

¹ It is hardly necessary to point out that the aquatic Phanerogams are not typical Phanerogams, but that their simplicity of structure is to be regarded as a degradation: their fertilisation is, even in so extreme a case as *Vallisneria*, characteristically that of an aerial habit, i. e. siphonogamic.

the scale. Accordingly, while we rightly regard aquatic Phanerogams, which in many respects show similarities in detail of structure to the filmy Ferns, as exhibiting degeneration in accordance with their aquatic habit, I think that considering their position in the scale of Vascular Plants, we are justified in recognising the series of Ferns from the Hymenophyllaceae to the Marattiaceae, as an ascending series, and that this series illustrates the emergence of one phylum of the Vascular Cryptogams from the semi-aquatic to the aerial habit¹: it is this which seems to me to give a special interest to the singular parallelism of characters of the meristems which I have demonstrated in this paper.

But in our series of Ferns the progressive adaptation of structure to external circumstances is especially to be recognised in the characters of the sporangia: in the Hymenophyllaceae these are aggregated in sori protected by a cup-like indusium from drying up while young, the youngest sporangia being nearest the base of the sorus, and accordingly most completely protected: in the Cyatheaceae the arrangement is similar, though the protection is somewhat less close and complete: in the Polypodiaceae the indusium serves as a protective cover during early stages: in all these Ferns the sporangia are stalked, and of small size, and each produces a limited number of spores, the sporangia being relatively numerous. In the Schizaeaceae the sporangia have shorter stalks and are of relatively larger size; they are not aggregated in so large numbers as in the Polypodiaceae, but (to judge from Prantl's figures²) this is compensated for by the larger number of the spore-mother-cells, and spores produced by the single sporangium. These characters become still more pronounced in the Osmundaceae:

¹ Obviously the converse view is capable of defence: it might be held that the Hymenophyllaceae owe their simple construction to their adaptation to a semi-aquatic habit, and that the Marattiaceae are the original type, from which the simpler Ferns have degenerated: general considerations of comparison of both generations, and of their position in the whole system lead me to think this view improbable.

² Schizaeaceae, Plate VIII, Figs. 120, 121.

here, the sporangia being of a still more bulky type, and massively but shortly stalked, the protection from evaporation from their surface when young is less necessary, and the indusium is no longer present: though the wall of the sporangium when mature is still only one layer of cells in thickness, it is more robust in early stages than in the proceeding types. I have pointed out (Figs. 77-78, 82) that extra oblique segmentations occur in the basal part of the sporangium, and that the tapetum may divide into more than two layers (Fig. 82), though this is the typical number for the simpler Ferns¹. The number of spores produced from each sporangium is also very large²: thus the sporangia are relatively fewer, but more bulky and shorter stalked, and produce individually a larger number of spores: these are all characters leading towards the Marattiaceae. Finally, I have observed occasionally in *Todea barbara* a coalescence of two sporangia together. But this which is exceptional in the Osmundaceae is the rule in the Marattiaceae; not only are the sporangia sessile, large, and massive, with thick walls, and producing very numerous spores, but they are aggregated together in confluent masses, while an indusium is absent. These characters I regard as further indications of adaptation for protection against drying up while young, the lateral coalescence especially would well qualify the Marattiaceae for successfully developing their sporangia in exposed situations.

A comparison of these coalescent sori of the Marattiaceae, on the one hand with the sori of *Marsilia*, and on the other with the large and deeply sunk sporangia of *Ophioglossum*, led Strasburger³ to conclude that the latter are not simple sporangia but 'sporocysts,' which, resulting from a coalescence of sporangia more complete than that of the Marattiaceae, really are, according to him, not homologous with the sporangia of the true Ferns, but with sori: this view he

¹ Compare Goebel's Fig. 103 D; Schenk's Handbuch, III, p. 388.

² Twenty-three spore-mother-cells are seen in the section shown in Fig. 82, while thirty are seen in section in Goebel's figure above quoted.

³ Bot. Zeit. 1873, p. 84.

extends to the sporangia of *Equisetum* and to *Lycopodium*, and *Selaginella*, and it is still maintained by him in comparatively recent writings¹. Now we have seen that the transition from leptosporangiate to eusporangiate forms is effected with the transitional step of the Osmundaceae within the Filicineous series, and without any lateral coalescence of simpler sporangia being necessary to bring it about; therefore, the eusporangiate sporangium is not in all cases a 'sporocyst.' To me the view that it ever is seems to be quite unnecessary and improbable: it is a much more simple interpretation of the deeply seated sporangia of *Ophioglossum* to regard each as a true sporangium, in which the shortening of the stalk, widening of the insertion, thickening of the wall, and increase in number of spores, are all carried to a still higher degree than in the Marattiaceae. To argue on such a point across from the Filicineae to the Lycopodineae and Equisetineae appears to me to proceed on the assumption of a much nearer relationship of these series than a comparison of their characters will justify: again, in their case I think that the view of their sporangia as coalescent 'sporocysts' is ill-founded.

On comparing the different vegetative members of the plant as seen in the series of Ferns, it will be found that as we rise in the series certain members retain the single initial more persistently than others. This will be seen from the following table, in which the numbers refer to the number of initial cells observed in each case:—

	Root.	Stem.	Leaf.
Hymenophyllaceae . . .	1	1	1
Polypodiaceae, etc. . . .	1	1	1
Schizaeaceae	1	1	1
Osmundaceae { (1) Osmunda . . .	1-3	1 (rarely more)	1
{ (2) Todea	usually 4	—	1
Marattiaceae { (1) Marattia . . .	apparently 4	4 (or more)	1 (or more)
{ (2) Angiopteris.	4	4 (or more)	3 (or more)

From this it will be gathered that in the series of plants named,

¹ Angiospermen und Gymnospermen, p. 53, footnote 4.

the root is the first to depart from the simpler growth with a single initial, and even in *Todea* it appears to settle down into a definite type. The stem is the next to depart from the definite type of the simpler Ferns, while the apex of the leaf is most conservative in its characters, and even in *Marattia*, which shows greater complexity of apical construction both in root and stem, the leaf still shows, at least while young, a fairly regular segmentation from a single initial. This is, however, finally lost in *Angiopteris*. Thus there is not a strict parallelism of progression from the simpler to the more complex type of construction of the meristems, of a single species or individual, even within the series of plants specially examined.

Turning to other members of the Vascular Cryptogams, further exceptions are to be found, such as the Ophioglossaceae¹: these being members of the Filicineous series, are for us at present the most important exceptions, and may be considered first. Here the apex both of root and stem appears to have a single initial; it is to be noted, however, that both these members are buried deeply underground in the living plant, and are so protected by their habit; but the leaf bearing the sporangia is aerial and exposed, and it is to be noted that its structure is comparatively bulky, and that in its early stages no single initial is found, while the sporangium is typically eusporangiate. Accordingly, it would appear that here there is a correlation even in the parts of an individual plant between exposure to dry air and a greater complexity of meristems on the one hand, and on the other between protection from evaporation and simplicity of structure of the meristems. But while recognising these facts, care must be taken that they be not overestimated. A comparison of the table above given will show that the case of the Ophioglossaceae is the exact converse of that for the Osmundaceae and Marattiaceae: in these the leaf which is aerial and exposed is the most conservative of the structure typical of

¹ See Holle, Bot. Zeit. 1875; as far as my own observations go, they bear out those of Holle.

the simpler forms, while in the Ophioglossaceae it is rather the root and stem which retain the simpler construction. This would therefore warn us of the danger of applying too closely in detail the correlation of exposed habit with increased meristematic complexity.

Again, in *Equisetum*, which is eusporangiate, the roots and stems have a single initial, with diagrammatically regular segmentation: it is to be noted that in these plants underground rhizomes are the rule, and it is only in their later stages of growth that the stems arise above ground. In many species of *Selaginella*, on the other hand, a single initial cell is formed in the sub-aerial stem; in other species there is a more complex structure of the meristem, while in *Lycopodium* three initials have been observed, though the general habit is similar to that of the allied Selaginellas. These notes will suffice to show that speaking of the Vascular Cryptogams as a whole, we are not in a position to state that there is any strict, invariable, and definite correlation of structure of meristems with exposed habit, or that there is any exact parallelism of progression in complexity in all the members of a given individual, species, or family. Still, I do not think that such exceptions as those above quoted invalidate my general conclusion that in the Filicineous series, taken as a whole, the progression of complexity of meristematic structure is to be taken as one index among others of the rise of the series from a semi-aquatic to a more distinctively sub-aerial habit, a conclusion which is borne out by comparison of the texture of the mature parts, and of the oophytes and sexual organs.

The texture of the leaves of the Ferns above studied, and their wings, present characters which deserve further remark, and especially we may draw a comparison between the 'filmy' Ferns, and their more robust neighbours. It has been repeatedly pointed out that the characters of submerged leaves of the higher plants, as distinct from subaerial leaves, are that they are thin, being composed of only few layers of cells; that stomata are absent; that there is no distinction of palisade and spongy parenchyma; and that the chlorophyll is

specially located in the superficial tissues, and much less plentiful within¹. The chief differences of external condition between submerged and subaerial plants are, that transpiration is in the former impossible, and that they are less exposed to direct sunlight. Now these are also the conditions of plants which grow in shade, where the air is constantly near to the point of saturation with water; in them transpiration is at a minimum, while they receive only diffused sunlight. Accordingly a similarity of construction to that of water-plants may be expected, and it is clear that the leaves of the Hymenophyllaceae show more or less distinctly all the characters above noted, some of them even in a more marked degree than those of submerged Phanerogams. Further, while intercellular spaces are often large in submerged Phanerogams, they are entirely absent from the wings even of those filmy Ferns which are several layers in thickness. The 'filmy' texture is then to be regarded as an adaptive character, suited to life in a moist and shaded habitat.

But it is not found exclusively in the Hymenophyllaceae; *Asplenium resectum* and the *Leptopteris* section of the genus *Todea* show a similar texture of the frond, with absence of stomata and intercellular spaces, and with special location of the chlorophyll near the surface. I have shown that in the development of these filmy wings the segmentation of *Asplenium resectum* is that of the Polypodiaceae; also that that of the 'filmy' *Todeas* (which in every other respect correspond to other Osmundaceae) is at first like the latter, and that it is only in the later stages that a mode of segmentation is assumed which corresponds, and even then imperfectly, to that characteristic of the Hymenophyllaceae. Taking all the facts together, the general conclusion may be drawn that the 'filmy' texture is an adaptive character assumed by plants which live in shady and damp situations, and that it is not a safe indication of affinity; that while its most characteristic representatives are found among the Hymenophyllaceae, it has probably originated independently in at least three dis-

¹ Schenk, Vergl. Anat. d. subm. Gewächse, p. 3, and various other writers.

tinct divisions of the Ferns; viz. in the Hymenophyllaceae in which it is probably the typical structure; in species of *Asplenium* and of *Todea*, in which it is rather to be regarded as the result of a retrogressive adaptation.

An attempt has also been made in the above pages to make a comparative study of those wings which are so commonly found on the leaves of Ferns. It has generally been assumed that because those wing-structures which are continued, or decurrent from the leaf to the stem, are of irregular occurrence, therefore wings, whether on stem or on leaf, are of little morphological moment. This is an entirely fallacious conclusion. It is a matter of common observation that such wings are very constant in appearance and position on leaves of large classes of plants, more especially of the Ferns and Dicotyledons. Now one of the most important factors in stamping the morphological importance of any part is its constancy of occurrence and character in considerable series of organisms, and on this ground the wings deserve special attention. It may be objected, however, that wings are merely a natural consequence of the flattened development of leaves, and that an elongated and flattened structure must have two marginal lines of greatest curvature. This is true, but it does not diminish the interest of tracing those margins, comparing them in different plants, and noting their various modes of development in the different parts of the same leaf.

I have repeatedly dwelt upon the fact that though the leaves of the Filicineae may develop occasionally in a cylindrical form (*Pilularia*), or as spatulate structures without a midrib (*Drymoglossum*), those of the vast majority of them have a robust midrib, which is traversed longitudinally by two more or less developed lateral flanges or wings. These originate in the lowest Ferns from definite parts of the segments cut off from the apical cell, while in the higher, though their position is the same, the segmentation is less definite. In the mature state they usually show more robust and massive characters in the lower part of the leaf. This has been recognised both in external form, and in the internal struc-

ture in *Trichomanes reniforme*, in *Scolopendrium vulgare*, *Aspidium Filix mas*, *Asplenium nidus*, *Pteris aquilina*, and may be verified in most Ferns: more especially however is it to be noted in the higher Ferns of the series; and I have elsewhere pointed out¹ that the bulky developments which are found at the base of the leaf of *Osmunda* and *Todea*, and even the 'stipular' growths of the Marattiaceae are to be regarded as the result of metamorphosis, or special conformation of these wings, or of the extension of the growth across the face of the phyllopodium, so as to form the well-known commissure. There is thus a certain relation between the greater bulk of the base of the leaf, and that of the wings which it bears; but the wings of the lower part, though of bulky development, are but little expanded in area. In that part of the phyllopodium which is usually distinguished as the petiole, the wings are of a reduced type, and are seen merely as pale streaks, often discontinuous, which run down the sides of the petiole, and, though they may not project at all, these streaks show where the morphological margin of the leaf lies; sometimes, however, the wings project even here as distinct flanges (many Hymenophyllaceae). It is, however, in the upper part of the leaf that the wings attain their typical development, and there they constitute the large proportion of the expanded surface, whether of the simple or the branched leaf. Thus the wings are subject to great differences of development in different parts of the leaf, and indeed the general conformation of the different parts of the leaf depends more closely upon this than upon differences of development of the thickened midrib. It is also a matter of common experience that from them arise the branchings of the leaf.

It will be recognised that this mode of viewing the leaf throughout its length as a whole, and avoiding at the outset those horizontal distinctions into 'foliar base' and 'upper leaf,' which are habitual with other writers, naturally leads to a more coherent view of the real nature of the leaf. It is typically a flattened structure, of which the longitudinal lines

¹ Phil. Trans. 1884, Part II, pp. 578, etc.

of greatest curvature, or margins, are subject to various development in different parts, and are the seat of the branchings of a higher order.

The meristems of the various parts having been investigated in a series of plants which bridges over the transition from growth with a single initial to growth with several, it is to be expected that some light may have been thrown upon the problem of the real nature of the apical cell, and of the causes which bring about so remarkable a construction as that where there is a regular segmentation from an initial of definite form. Though the solution of the problem is not yet to hand, certain interesting conclusions may be drawn from a comparison of the plants studied¹.

The comparison of Figs. 3 and 4 of roots, and of Figs. 39 and 43 of leaves, shows, in place of a single three-sided initial, three initials so arranged, together with their segments, as to correspond to what is seen in transverse section through segments immediately below a typical three-sided apical cell. Thus both in certain roots and in certain leaves there may be seen a construction which is the equivalent of the continuation of the typical system of construction upwards into that space (the apical cell), which is usually unsegmented. This I take to be evidence supporting the view of Sachs that the apical cell is but a gap in the system of construction: though in other cases (Figs. 12, 25, 27, 28) the arrangement of the walls is not according to the exact type, still I think the conclusion is justified that the difference between growth with one initial and with several initials is due to the greater completeness in the latter case of the system of walls.

It is obvious that not only the apex of the average root, but also those of stem and leaf are more bulky in the higher terms of our series than in the more slender, lower terms:

¹ Sachs, in his well-known paper 'Ueber Zellanordnung und Wachstum' (Arbeiten, Vol. II, p. 200), writes in connection with the partitioning off of the interior of plants by cell-divisions and its relation to growth as follows:—'The acquisition of a cellular character of the interior is accordingly an independent phenomenon, the cause of which we are as little aware of as that of growth itself: but from what has been said, it must necessarily be subordinated to growth.'

and the suggestion appears ready to hand that the greater complexity of structure depends directly upon, or is at least closely connected with, the greater bulk. This point I have already discussed elsewhere as regards the root¹, and the conclusion there arrived at for the root is equally applicable to stems, leaves, and wings of the leaf of the Ferns examined. That conclusion is this:—That greater size of a member does not entail greater complexity of meristem in members of the same individual plant, or of plants of the same species; for instance, roots, etc. of smaller size may have a more complex meristem than larger roots (*Osmunda*): but such a correlation may be traced to some degree in different species of the same genus (stems of *Selaginella*), and it is plainly to be seen on comparison of the corresponding parts of plants less closely related. In comparing corresponding parts of plants not in the same genus or division of Ferns, a certain relation between bulk and complexity of meristematic structure is obviously seen, and this has been referred to so constantly throughout this paper that it need not be farther dwelt upon here. On the other hand, the comparison of the mode of development of the wings plainly shows that actual size does not directly dominate the mode of segmentation within narrow limits of affinity: the bulky leaf of *Trichomanes reniforme* (Fig. 51), notwithstanding its thickness, retains the simple mode of segmentation of its genus: the thin filmy leaf of *Asplenium resectum* (Fig. 58), notwithstanding that it is actually much less bulky than the above, retains the more complicated segmentation of the Polypodiaceae. Both of these show, independently of actual size, a conservatism of their family type of segmentation, and though I would not be prepared, on the narrow ground of observation as yet before us, to state as a general principle that such conservatism or hereditary character is of common occurrence, such examples as these are sufficient to show that those who state that the arrangement of cell-walls has

¹ Quart. Journ. Micr. Sci. 1885, pp. 88, 98-99.

actually no systematic importance have gone too far¹. The whole argument of this paper is based on comparison of meristems: it has been shown that the progressive characters of the meristems run parallel with other systematic characters of the Filicineous series, and accordingly they must themselves be recognised as having a systematic value. The fault in dealing with meristems as systematic evidence has been the abuse of them: that is, however, no sufficient reason for ignoring entirely their systematic value.

Not only are the meristems of the higher members of this series more bulky, and the external surface less strongly curved, but they are also notable for their extremely watery character, their very thin cell-walls, and the relatively large size of the individual cells. These characters mark the meristems out as badly nourished, and they present a most striking contrast to the small-celled, densely-protoplasmic and largely-nucleated meristems of the Phanerogams, notwithstanding that in respect of their segmentation they approach them. It may even be suggested that the poverty of the tissue and the size of the cells composing it may have a connection as cause and effect, the substance necessary for the formation of more numerous walls and nuclei not being at hand: and reflections such as these would lead us on to consider whether the presence of an apical cell with a regular segmentation may not have its origin in some phenomena of nutrition not yet clearly recognised. We might with some show of probability assume that the regularity of segmentation depended upon the regularity of supply of wall-forming substance from the several sides of the meristems. Such regularity of supply would be most easily maintained where the whole apex is of small size, while in the larger apices the stream of nourishment would be less likely to converge equally from all sides upon the central point, and irregularity of construction would be the result: this is in accordance with experience, for, speaking generally, the smaller apices of the Filicineous series have as a rule a single initial, while the

¹ Compare Goebel. Sachs' Arbeiten II, p. 451.

larger are less regular in their segmentation. I do not consider that this suggestion is by any means established by my observations on the Ferns, but the result of the examination of a very considerable number of meristems makes me think that some such connection between nutrition and meristematic construction is not improbable.

In this connection two other points deserve notice: the first is, that where a single initial is found in the relatively bulky meristems of the plants higher in the series, the segments cut off from it increase more rapidly in size as compared with the apical cell itself than in the lower terms of the series. (Compare Figs 22, 23, 24, of stems, and Figs. 35, 36, 37, 38, of leaves). The second is, that in the course of this growth, the subdivisions of the segments are far from being regular: often cells which I have styled 'secondary initials' make their appearance in the segments, and appear to undergo subdivisions which show some similarity to those of the apical cell itself (compare Figs. 34, 36, 38, 41, the cells marked *o*; also Fig. 7). If, as above suggested, the regularity of segmentation depend upon the regularity of the nutritive supply, these irregularities of subdivision of the segments and the appearance of the 'secondary initials' point to such want of uniformity of supply as may be expected to have its effect also upon the initial cell itself. With regard to these 'secondary initials' a comparison may be drawn to the meristematic arrangements of *Psilotum* as represented by Graf. Solms¹; his account of the appearance, disappearance, and renewal of initial cells goes far to break down too formal ideas as to the importance and supremacy of the apical cell itself.

The general results of these investigations as regards phylogeny are to demonstrate, more clearly than before, that the Filicineae constitute a natural series, illustrating an adaptive sequence from plants of semi-aquatic to those of a more dry habit; to show that additional evidence only tends to fix the Osmundaceae still more firmly than before in the position of a link bridging over the gap between the leptosporangiate and

¹ Ann. d. Jard. Bot. d. Buitenzorg, Vol. IV, 1884, Plate XXI, Figs. 1, etc.

eusporangiate Ferns; and to strengthen the bond between them and the Marattiaceae. A reference to the table of meristems given above (p. 376) shows further that in these characters *Todea* stands nearer to the latter than *Osmunda*, and this conclusion is further borne out by the presence of the commissure at the base of the leaf. On the other hand, as regards the meristems, *Marattia* appears to be nearer to the Osmundaceae than is *Angiopteris*; thus on the basis of the meristems the series of genera would be *Osmunda*, *Todea*, *Marattia*, *Angiopteris*. It is, however, to be noted that the coalescence of the sporangia is less complete in *Angiopteris* than in *Marattia*.

It remains to remark on the probable relation of this Filicineous series to other forms. There is, I think, every reason to believe that the Hymenophyllaceae are of Algal-Bryophytic origin, and they probably arose from some forms intermediate between our present green Algae and the Bryophyta, but not directly from either as we now see them; the position of the Hydropterideae (the only heterosporous Ferns) is probably in relation rather to the lower terms of the homosporous series than to the higher ones. Then, as regards the vegetative organs of the sporophyte, whether we take external form, internal structure, or development into account, the relation of the highest Pteridophyta (Marattiaceae and Ophioglossaceae) to the Cyadaceae is undeniable; but between these, as regards reproduction, there is the vital difference between the homosporous zooidogam and the heterosporous siphonogam. Though there is no reason to assume that progress in vegetative structure and in sexual differentiation has necessarily taken place simultaneously, still, this is a very serious gap, and from the point of view of phylogeny it is very desirable to find some heterosporous form allied to the Marattiaceae, which should serve as a connecting link. Approaching the matter from the point of view of the characters of the leaf, I appended the following note to a paper written in 1884¹:—‘The leaf of *Isoetes* shows intermediate characters between those of *Angiopteris*

¹ Phil. Tran. 1884, Part II, p. 610.

and of the Cycadaceae. There is no apical cell, and apical growth is not strongly defined; periclinal divisions of the superficial cells are frequent throughout the leaf, from apex to base, but especially on the ventral side; intercalary growth is strongest at first below the ligule, and then diminishes in that part and extends to the upper part of the leaf. These characters, as well as others, suggest that *Isoetes* may be a form intermediate between Marattiaceae and Cycadaceae, in which the vegetative organs have been reduced in structure and external form in accordance with aqueous habit.¹ Since then, Vines¹ has on various grounds arrived at the conclusion that the true relation of *Isoetes* is rather to the Filicineae than to the Lycopodineae. Without at present entering upon the discussion of this matter at large, it will be well to point out the bearing of the observations contained in this paper upon this debateable question. So far as they affect the point, they strengthen rather than invalidate the suggested grounds of affinity of *Isoetes* to the Marattiaceae. It has been shown by Bruchmann that the apices of the roots of *Isoetes* have a stratified structure, similar to that which is seen in certain Angiosperms, there being present no clearly defined initial cells. The same writer, and also Hegelmaier², point out that the apex of the stem is occupied by a small number of initial cells, which appear to correspond to the structure found in the Marattiaceae. I have also indicated that the characters of the leaf are not inconsistent with the suggested position, and Hegelmaier³ also points out that there is no apical cell. As regards the form of the leaf, when it is remembered that the leaves of the *Danaeas* are relatively simple in conformation, while in *D. simplicifolia*, Rudge, the leaf is actually unbranched⁴, it will be seen that comparatively slight simplification of the type of leaf would result in such a one as that of *Isoetes*. Taking all the meristematic characters together (and it is with them that we are now more especially concerned), the evidence offers no serious barrier to assigning to *Isoetes* the position

¹ Annals of Botany, II, pp. 117, 223.

² Bot. Zeit. 1875, pp. 485-6.

³ l. c. p. 499.

⁴ Kunze, Die Farnkräuter, Plate 50.

suggested by Vines. But, on the other hand, it may be argued that such evidence would be equally strongly in favour of a Lycopodinous affinity; and I anticipate that a knowledge even of minutest details of the meristems will not suffice to decide this interesting question. A final conclusion will have to be based on the broadest possible comparative grounds.

POSTSCRIPT.

Since the above was in type, the comprehensive work by MM. Van Tieghem and Doulist has come to my hands, in which the authors state (footnote, page 379) that there is only one initial cell at the apex of the root in *Todea* 'as in other ferns.' It will be no surprise to me to find that in certain cases *Todea barbare* has a structure at the apex of the root more closely resembling that of the typical ferns than that which I have described. It will be noticed that I lay down no type of structure in *Todea* and *Osmunda*, but point out rather that 'there is no such strict uniformity in these plants as is found in the roots of typically leptosporangiate ferns (above, p. 284); thus the reference of the whole meristem of *Todea* in certain cases to a single initial cell does not affect the general argument, so long as it is recognised that a system of construction occurs not infrequently in these plants, such as I have described and figured, which is more complex than that which is so regular and prevalent in the Leptosporangiate Ferns.

DESCRIPTION OF FIGURES IN PLATES XX,
XXI, XXII, XXIII, & XXIV.

Illustrating Professor F. O. Bower's paper on the Comparative Examination of the Meristems of Ferns as a Phylogenetic Study.

ROOTS.

Fig. 1. Scheme of construction of the apex of the root with a three-sided pyramidal apical cell, quoted from Sachs's Arbeiten, Bd. II, Taf. III, Fig. 12.

Roots of *Osmunda regalis*, Figs. 2-4, and 6-11 ($\times 216$).

Fig. 2. Transverse section of apex of root with a three-sided initial, but the segments not regular.

Fig. 3. Ditto. Three initial cells (x) separated by principal walls p, p . The sextant walls are marked s, s .

Fig. 4. Transverse section immediately below the root-cap, showing three initials (x): the dotted line is a cell-division in the root-cap, seen on focussing deeply, and this shows that the section has passed through the initials, and is not below them.

Fig. 5. Quoted from Naegeli and Leitgeb, Taf. XIV, Fig. 5, a transverse section of the apex of the root of *Pteris hastata*, as seen by focussing below the apical cell. p, p , the principal walls. s, s , the sextant walls. Compare this, which is an optical section through the segments below the initial, with Figs. 3, 4, which are sections through the initials of *Osmunda*.

Fig. 6. Median longitudinal section, with pyramidal apical cell. tr , cells developing as tracheides.

Fig. 7. A very irregular meristem, with a pyramidal apical cell (x). Segments undergoing repeated periclinal division.

Fig. 8. Two oblong initial cells (x, x): segments are cut off by periclinal walls from both ends of them, and by anticlinals from their sides.

Fig. 9. Two similar initials with their segments.

Fig. 10. Young lateral root with two oblong initials. xy , the xylem of the main root. p , the pericambium.

Fig. 11. Apex of a young lateral root in longitudinal section.

Roots of *Todea barbara*, Figs. 12-16 ($\times 216$).

Fig. 12. A very regular meristem in transverse section, showing four initials (x, x).

Fig. 13. Apex of root in longitudinal section, showing two pyramidal initials.

Fig. 14. Ditto, with two oblong initials.

Fig. 15. Group of cells derived from one rhizogenic cell of the endodermis showing two oblong initials (x, x).

Fig. 16. Apex of a rather older lateral root with two pyramidal initials (x, x).

Fig. 17. Scheme of construction of a root of the Marattiaceous or coaxial type. AA , axis; aa , anticlinals; p, p , periclinals; xx , initial cells.

STEMS.

Trichomanes radicans, Figs. 18-21.

Fig. 18. Longitudinal section through the apex ($\times 35$): *ap*, the apex. *ax*, the axillary bud. *l*, the leaf.

Fig. 19. Transverse section showing apical meristem in plan: *l*, young leaf. The arrows indicate the vertical direction as the plant grew ($\times 130$).

Fig. 20. Longitudinal section of the apex of the stem ($\times 130$).

Fig. 21. A very young axillary bud in longitudinal section: the arrow indicates the direction of the apex of the main axis ($\times 130$).

Amphicosmia Walkerae.

Fig. 22. Apical meristem of stem seen in plan ($\times 130$).

Osmunda regalis, Figs. 23-26 ($\times 130$).

Fig. 23. Apex of stem seen in plan. *l*, young leaf. *l'*, *l''*, older leaves. Initial (*x*) of regular form, segmentation regular.

Fig. 24. Ditto, initial less regular in form, and segmentation less regular.

Fig. 25. Ditto, apparently no single initial.

Fig. 26. Apex in median longitudinal section: the succession of segments is not clearly to be seen.

Angiopteris evecta, Figs. 27-29 ($\times 130$).

Fig. 27. Apex of stem seen in plan ($\times 130$): apparently four initials (*x*, *x*).

Fig. 29. Apex of stem in median longitudinal section.

Marattia fraxinea.

Fig. 28. Apex of stem as seen in plan: the number of initials is uncertain ($\times 130$).

LEAVES.

Trichomanes radicans, Figs. 30-32.

Fig. 30. Young leaf as seen from above when projecting only slightly from the surface of the stem: the arrow points to the apex of the stem: *m*, *m*=marginal cells. ($\times 163$).

Fig. 31. Part of a tangential section of the stem, passing vertically through a young leaf, and showing its first segmentations ($\times 130$).

Fig. 32. Median longitudinal section of leaf: the arrow indicates the direction of the apex of the stem ($\times 130$).

Trichomanes reniforme.

Fig. 33. Apex of the leaf showing the T division of the initial cell, the identity of which is thus lost. ($\times 130$).

Osmunda regalis, Figs. 34-35.

Fig. 34. Apex of leaf seen in plan. *s*, sextant walls. *o*, partial initial. The arrow shows in this and subsequent figures the direction of the apex of the stem.

Fig. 35. Median longitudinal section of the apex of a leaf.

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Marattia fraxinea, Figs. 36-41 ($\times 130$).

- Fig. 36. Apex of leaf seen in plan : *o*, *o*, partial initials.
Fig. 37. Ditto, from a young leaf with no pinnae.
Fig. 38. Ditto, from a young leaf.
Fig. 39. Ditto, but no single initial cell is to be seen : from a leaf on which some pinnae were already formed.
Fig. 40. Apex of a young leaf in median longitudinal section. *o*, a partial initial.
Fig. 41. Ditto, the segmentation of the partial initial (*o*) has shown some regularity. *x*, is the apical cell.

Angiopteris evecta, Figs. 42-45 ($\times 130$).

- Fig. 42. Apex of leaf seen in plan. *p*, principal wall.
Fig. 43. Ditto. *o*, partial initials. *p*, principal wall.
Fig. 44. Apex of leaf in median longitudinal section. *p*, principal wall.
Fig. 45. Ditto.

WINGS OF THE LEAF.

Trichomanes radicans, Figs. 46-49 ($\times 325$).

- Fig. 46. Young wing as seen in a transverse section of the phyllopodium. *m*, the marginal cell.
Fig. 47. Ditto, rather older.
Fig. 48. Ditto, more advanced.
Fig. 49. Marginal series of cells (*m*, *m*) seen from without. *h*, *h*, hairs.

Trichomanes reniforme, Figs. 50-51 ($\times 325$).

- Fig. 50. Wing as seen in a transverse section near to the base of the leaf: segmentation of the marginal cell (*m*) of the polypodiaceous type.
Fig. 51. Transverse section through the young lamina, showing the large marginal cell (*m*) with regular transverse segmentation (compare Figs. 46-48).

Hymenophyllum dilatatum, Figs. 52-54 ($\times 325$).

- Fig. 52. Wing as seen in transverse section of the young petiole: compare Fig. 51.
Figs. 53-54. Irregular segmentations at the close of the functional activity of the marginal cells.

Pteris cretica.

- Fig. 55. Wing as seen in a transverse section of a pinna. ($\times 325$.)

Scolopendrium vulgare.

- Fig. 56. Wing as seen in a transverse section of the young leaf near its apex. *m*, marginal cell. ($\times 325$.)
Fig. 57. Ditto, more advanced. ($\times 325$.)

Asplenium resectum.

- Fig. 58. Transverse section through a young pinna, showing, notwithstanding the filmy character of the frond, the same marginal segmentation as in *Pteris* and *Scolopendrium*. ($\times 325$.)

Todea barbara.

Fig. 59. Surface view of the margin of a pinnule: the arrow points to the apex of the pinnule. ($\times 325$.)

Fig. 60. Young wing as seen in transverse section ($\times 325$).

Todea superba, Figs. 61–67 ($\times 325$).

Figs. 61, 63, 65. Young wings as seen in the transverse sections of very young pinnules.

Figs. 62, 64, 66, 67. Wings as seen in transverse sections of pinnules, and showing the variability of segmentation.

Todea hymenophylloides, Figs. 68–69.

Figs. 68, 69. Young wings as seen in transverse sections of the pinnules ($\times 325$).

Angiopteris evecta, Figs. 70–73 ($\times 325$).

Fig. 70. Transverse section of a very young pinnule, showing the first origin of a wing at *.

Figs. 71, 72, 73. Older wings as seen in transverse section, and illustrating their mode of segmentation, and the absence of definite marginal cells.

SPORANGIA.

Osmunda regalis, Figs. 74–82.

Fig. 74. First origin of a sporangium as seen in a transverse section of a young pinnule ($\times 550$).

Fig. 75. Three sporangia rather more advanced ($\times 325$).

Figs. 76–82. A series of sporangia cut in longitudinal section, illustrating the development, and also those irregularities of segmentation, which are commonly found. The most frequent type is that shown in Fig. 77 ($\times 325$).

Todea barbara, Figs. 83–87.

Fig. 83. Early stages of development of two sporangia as seen in transverse section of a pinnule ($\times 550$).

Figs. 84, 85. Young sporangia as seen in surface view ($\times 550$).

Figs. 86, 87. Sporangia in longitudinal section, showing different modes of segmentation. Fig. 86 is the commoner type ($\times 550$).

Fig. 88, *a-g*. A series of diagrammatic figures, constructed from drawings of the sporangia of different members of the Filicineous series.

a. Sporangium of the *Polypodiaceae* (compare Reess, Pringsh. Jahrb. Tom. V, Taf. XXI, XXII).

b. Sporangium of the *Hymenophyllaceae* (compare Prantl, Hymenophyllaceae, Taf. VI, Figs. 100 *c*, 104).

c. Sporangium of *Schizaeaceae* (compare Prantl, Schizaeaceae, Taf. VI, Fig. 91).

d. Sporangium of *Osmundaceae*: diagram constructed from comparison of a number of specimens (compare Fig. 87 of *Todea*, and Fig. 75 of *Osmunda*).

e. Sporangium of *Todea barbara*, in which the archesporium has a square base (compare Figs. 83, 86).

f and *g*. Sporangia of *Angiopteris* (compare Goebel, Bot. Zeit. 1877, Taf. VI, Figs. 3, 4).

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 6.

Fig. 8.

Fig. 7.

Fig. 16.

Fig. 15.

Fig. 17.

Fig. 13.

Fig. 14.

F. O. Bower del.

Fig. 4.

Fig. 5.

Fig. 9.

Fig. 11.

Fig. 12.

Fig. 10.

Fig. 18.

Fig. 19.

Fig. 21.

Fig. 20.

Fig. 22.

Fig. 23.

Fig. 27.

Fig. 30.

Fig. 28.

Fig. 29.

F.O. Bower del.

Fig. 26.

Fig. 25.

Fig. 24.

Fig. 32.

Fig. 31.

Fig. 35.

Fig. 33.

Fig. 34.

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Fig.

Fig. 43.

Fig. 40.

Fig. 49.

Fig. 45.

Fig. 47.

Fig. 46.

F.O. Bower del.

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Fig. 42.

Fig. 41.

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Fig. 64.

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Fig. 68.

F.O. Bower del.

Fig. 57.

Fig. 56.

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Fig. 77.

Fig. 75.

Fig. 81.

Fig. 82.

Fig. 85.

F.O. Bower del.

Fig. 78

Fig. 79.

Fig. 80.

Fig. 83.

Fig. 86.

Fig. 87.

Fig. 84.

Fig. 88.