Remarks on the so-called woody and vascular tissues of ferns / by George Ogilvie.

REMARKS

ON THE SO-CALLED

WOODY AND VASCULAR TISSUES

OF

FERNS.

BY

GEORGE OGILVIE, M.D.

[*WITH TWO PLATES.*]

[*From the* ANNALS AND MAGAZINE OF NATURAL HISTORY *for Oct.* 1860.]

LONDON:

PRINTED BY TAYLOR AND FRANCIS,

RED LION COURT, FLEET STREET.

1860.

REMARKS

ON THE SO-CALLED

WOODY AND VASCULAR TISSUES OF FERNS*.

In a former communication (Annals, Dec. 1859) I have referred to a common feature in the rhizomes of Ferns, namely, that the vascular bundles form a curious netted cylinder, dividing the cellular matrix of the stem into a central or medullary, and a peripheral or cortical region. To the dark-coloured tissue which, in dense woody bands or in some other form, is frequently present in the substance of the stem, constituting one of its most remarkable features, I made only a passing allusion, as I found that its arrangement (unlike that of the vascular tissue) varied so much in different species as to require a more particular examination of its modifications than I was able to undertake at the time. Since then, I have re-examined a considerable number of rhizomes with special reference to the disposition of this tissue, as well as of the vascular bundles.

In regard to the former, I have not been able to arrive at any conclusion which could be reduced to the form of a general expression. Still I have thought that a short notice of the actual structure and arrangement of the tissues in the species examined might be worth recording, as I cannot find that any systematic observations have yet been made on these points†. Considering

* Read in part at the Meeting of the British Association at Oxford, June 1860.

† My attention has since been directed by the Rev. W. W. Newbould to some 'Hints on a new Character in Ferns,' with illustrative figures, by the Rev. W. A. Leighton (Phytologist, n. s., i. p. 256). The author confines his remarks to the *petioles* of a few species, and does not always very distinctly state the *part* of the petiole examined, which may account for some apparent differences between his description and that here given

how unsatisfactory all the systems of classification are which have been proposed in this order, these particulars may possibly have a certain value, as increasing the store of facts bearing on the general organography of the group, from which it is to be hoped that some botanist may yet draw materials for a more natural method of arrangement than any which has yet been brought forward. The peculiarities, too, in these points, are in some cases so striking that they appear worth recording as specific characters *.

A brown-coloured principle is very extensively distributed in the organization of Ferns. It is particularly conspicuous in the sporangia and other parts of fructification, and in the epidermis of the stem, and the *ramenta* or scales with which it is clothed; and it is so characteristic of the group, that it communicates a peculiar rusty tint to the vegetation of districts in which (as in some parts of New Zealand) Ferns form a prevailing feature. It is probably identical with the brown principle which occurs in other foliaceous Cryptogamia, particularly in the stems and capsules of Mosses; and, whatever may be its chemical relations —a point on which I can say nothing,—it at least resembles the woody matter of phanerogamic plants in being deposited in the interior of cells, in concentric pitted layers, on the inner aspect of the first-formed wall of cellulose. The tissues in which it is deposited often acquire great hardness, but are deficient in the toughness of true wood; on drying, especially, they become very brittle.

This brown matter is very constantly met with in the epidermic cells of the Fern-stem. The hardening of the cortical layer in these plants, as in arborescent endogens, is even more necessary for the support and defence of the stem than the accumulation of the layers of bark in exogenous trees, on account of the occasional deficiency of hard tissues in the interior of the rhizome. Generally, however, there is a certain limited amount of internal induration also; for we find that particular tracts of the

---

(see a criticism by Mr. Moore, Phytol., n. s., i. p. 378). There is a still greater indefiniteness about the sectional views in Mr. Francis's 'Analysis of the British Ferns.' Another reference given me by the same gentleman (Duval Jouve, 'Etudes sur le Pétiole des Fougères,' in Billot's 'Archives de la Flore de France,' pp. 50–149) I have been unable to verify, though I have made inquiry for the work in the principal libraries in London. I have not had access to the works either of Mohl or others of the German botanists who have discussed the structure of Fern-stems, so that I cannot say how far they may have gone over the same ground.

* In this connexion I may refer to the great similarity in the disposition of the dark tissue in the petioles of *Scolopendrium vulgare* and of *Ceterach officinarum* (*Grammitis Ceterach*), once referred to the first-mentioned genus.

parenchyma become the seat of such a deposit, so that a section commonly shows the pale tissue of the stem relieved by a dark pattern of the indurated cells, as well as by the cut ends of the vascular bundles, which are generally of a whiter colour. This induration of the parenchymatous cells is sometimes not attended by any alteration in their form, the resulting tissue somewhat resembling that of the shells of nuts. In certain cases, however, the cells become elongated into fibres; and we find every variety of brown tissue, from one of short cells like those of the husky structures of the higher plants, to long fusiform fibres, undistinguishable, except in colour, from the wood of the Phanerogamia. The wood-like tissue generally occurs in cords or bands, either surrounding the vascular bundles or interposed between two sets of fasciculi. In the denser fibrous bands the cells become so filled up with brown matter that only a small central cavity is left, as in the duramen fibres of the harder woods; but in the less indurated tracts the cells (both prosenchymatous and parenchymatous) have frequently a large central space filled with starch-grains, like those of the pale-coloured cellular matrix of the stem. Starch-grains, it may be observed, occur in a similar way in the woody fibres of the ivy, and probably in those of *Banksia* and a few other plants, though this arrangement is not usual among Phanerogamia.

The disposition of the tracts of indurated tissue differs very much, as I have already remarked, in different species. There are some instances in which the brown deposit appears to be confined to the layers of cells forming the cuticular investment of the rhizome and of the bases of the petioles near their origin from the rhizome. This is the case, more or less distinctly, in all our Polypodies, in the majority of the species of *Asplenium*, and in *Polystichum aculeatum*, *Lastrea Filix mas*, and *Adiantum Capillus Veneris*.

The deficiency is most marked in the nodulated stems of the common Polypody; their peculiar fragility is due to the soft watery parenchyma in which the minute and straggling vascular bundles are imbedded. In most of the other species there is, more or less, some compensating provision. Thus in *Polypodium Dryopteris*, and still more in *P. Phegopteris*, the parenchyma is much denser, and has a decidedly dark or brownish tinge. In *Asplenium Filix fœmina*, there is no such dark tinge in the fresh parenchyma, but it has a peculiar hardness, from the thickness of the walls of its component cells. In *Lastrea Filix mas*, again, the vascular bundles have a brownish tint, and a degree of tenacity which allows them to be dissected out with more ease than in any other of our Ferns.

We find, too, that in many of these species the brown sub-

stance, which is deficient in the rhizome, makes its appearance in the petioles as sheaths of dark tissue round the vascular fasciculi. In *Asplenium lanceolatum*, in which there is no dark sheath of this kind, the scalariform vessels and cambium-layer of the fasciculi become themselves the seat of a deposit of dark substance, by which they are not merely tinged brown as in *L. Filix mas*, but the cavities of the vessels are more or less filled up. The induration is confined, so far as I have observed, to the fasciculi near the base of the petiole, not extending either upwards towards the frond, or downwards into the rhizome.

In all the species, indeed, now mentioned, the dark tracts stop short just above the origin of the petioles from the root-stock; but there are others in which they pass some way into the substance of the latter, accompanying the vascular bundles to their junction with the netted cylinder, and even bordering some of the anastomosing fasciculi by whose interlacement the cylinder is formed, so that they appear as dark spots in a transverse section of the rhizome.

Thus in *Scolopendrium vulgare*, in which we find in each petiole two vascular fasciculi, running into one above in the midrib of the frond, these are accompanied, from their origin in the rhizome, by dark lines on their outer margins. In the petiole itself, a little above the base, other dark lines appear on the inner margins of the fasciculi, gradually expanding, as they ascend, into two half-sheaths, which become united by their convexities as the fasciculi approach, and finally stop short at the point of junction of the latter, while the outer marginal lines run far on, along the midrib of the frond. The general arrangement of these parts is illustrated in Plate VI. figs. 1, 2, 3.

In *Ceterach officinarum* (*Scolopendrium Ceterach*, *Grammitis Ceterach*) the two fasciculi of the petiole are accompanied, from their origin in the netted cylinder, by three dark lines—two on the outer margins, and one median, the latter at first somewhat on the upper or inner aspect of the petiole, but gradually insinuating itself between the fasciculi, so as to form two half-sheaths united by their convexities, as in the last species. Higher up in the petiole, where the fasciculi unite into a single vascular cord in the midrib of the frond, the median tract of dark tissue comes to lie on its upper surface, the others continuing to run along its lateral margins.

In *Lastrea Oreopteris* the petiole has two fasciculi of scalariform vessels, and on the inner margin of each (that lying next to the axis of the stalk) a chain of dark-coloured cells—sometimes continuous, sometimes interrupted. The two chains unite below, like the sides of the letter V, just above the junction of the vascular bundles of the petiole with those of the netted cylinder.

of the rhizome. A horizontal section of the rhizome shows these tracts in section as dark spots on the contiguous margins of such of the vascular bundles as have been divided a little above the point of convergence (Pl. V. fig. 6).

In *Asplenium Ruta muraria*, instead of these dark lines, we have, near the base of the petiole, a complete sheath of brown tissue surrounding the single central vascular fasciculus (Pl. V. fig. 8). In the rhizome, the sheaths of the petiolar fasciculi become reduced to dark lines on the outer and inner margins of the vascular bundles which go to join the netted cylinder; and on a horizontal section, they are represented by a series of black spots on each side of the interrupted circle formed by the cut extremities of these bundles, but most distinctly on the inside. In *Asplenium Trichomanes* the arrangement is somewhat similar, but the dark sheaths round the petiolar fasciculi appear to be mainly derived from the brown cortex or tegumentary investment of the bases of the petioles.

But the darker spots seen in a horizontal section of the rhizome are not always due to the prolongation downwards of the lines of brown tissue belonging to the petioles. In *Lastrea dilatata* there occur in the medullary parenchyma (that is, inside the circle formed by the netted vascular cylinder) numerous isolated fusiform nodules, with their long diameter parallel to the axis of the rhizome. Each nodule consists of a few short cells placed end to end and filled with a very dark, almost black deposit (Pl. V. fig. 7)*. This species has its petiolar fasciculi ensheathed with dark tissue, as in its congener *L. Filix mas*; but these sheaths disappear near the base of the petiole, and there is no connexion between them and the nodules in the centre of the rhizome.

The nodules in *L. dilatata* may be considered as an example of the first degree of induration in the rhizome; in the species which remain to be noticed the amount of dark tissue is much more considerable. In *Pteris aquilina* and *Allosorus crispus* there are continuous bands or cords running the whole length of the stems; and in *Blechnum boreale*, *Osmunda regalis*, and *Hymenophyllum*, the dark tissue really makes up the principal mass of the rhizome.

In *Pteris aquilina* the creeping rhizome is invested by a villose integument of a hard leathery consistence, formed of rounded cells indurated by the dark deposit. In the pulpy and lubricous parenchyma immediately underneath, there is a series of vascular

* The allied species or variety *L. Fœnisecii*, which, I am informed by Prof. Balfour of Edinburgh, is remarkable for the dark colour of the central part of the rhizome, probably owes this peculiarity to the great development of these dark nodules.

bundles corresponding to the netted cylinder of other Ferns, though, from the way in which the stem is drawn out longitudinally, the reticulations are represented only by long wide slits formed by the irregular anastomosis of the bundles. Inside the more external layer of parenchyma containing these bundles are two dark bands, of a hard woody nature, running the whole length of the rhizome,—one on its upper, and the other on its under aspect. The former is flat; the latter, which is broader, is turned at the edges, like the sides of a boat; so that the two together partially enclose the axis or central portion of the stem, consisting of soft white parenchyma, like that on their exterior. But the great peculiarity of the rhizome of *P. aquilina*, in which it differs from all our other Ferns, is the occurrence of a second vascular system in this central region, consisting of two bands or broad fasciculi lying immediately on the inner aspect of the woody tracts (Pl. VI. fig. 7). The fasciculi are in the main distinct from each other, and from those of the outer series, though there is an occasional communication by anastomosing fibres. In the same way the two woody bands are generally quite distinct, though here and there they may become fused together for a space, on one or both sides, so as in the latter case to form a complete ring round the medullary parenchyma and the vascular fasciculi imbedded in it. This occurs at points where several fronds are given off in close proximity—a circumstance which affects the disposition of the tissues of the stem, both woody and vascular, in consequence of these branching out to form the corresponding tissues of the petioles. In the petiole the main tract of dark tissue forms a plaited band, having a T-shaped section,—the perpendicular lamina, which lies towards the inner aspect of the petiole, arising mainly from the upper band of the rhizome, and the fluted transverse lamina from the lower. These central plates, along with subsidiary and more superficial tracts, arising in the petiole itself, serve partially to ensheath the numerous fasciculi of vessels which are derived from both the vascular systems of the rhizome, outer and inner (Pl. VI. fig. 8). The brown tint and woody character of the plates disappear in the upper part of the petiole, their tissue merging into the general parenchyma of the part. The parenchyma of the rhizome, both medullary and cortical, is also marked occasionally with interrupted striæ of brown tissue, like those occurring in the medullary parenchyma of *Lastrea dilatata*, but much more attenuated, and of very considerable length.

In *Allosorus crispus* (*Cryptogramma crispa*) there is a perceptible tracery of dark tissue round the several fasciculi of the netted cylinder; but the principal accumulation is along the axis of the

stem, nearly the whole of the parenchyma within the vascular circle being converted into a hard woody core, of a deep brown colour, which is continued through all the ramifications of the rhizome (Pl. VI. fig. 6). It is as if the two longitudinal tracts of the Braken stem were fused into a solid central cord, to the obliteration of the intervening parenchyma and vascular bands.

The induration of the stem reaches its maximum in the genera *Blechnum* and *Osmunda*. In the former, even in the petioles, near their origin from the rootstocks, the dark cortical layer becomes so much thickened at the expense of the pale parenchyma, that the latter is reduced to a thin sheath investing the vascular fasciculi; and the same arrangement prevails throughout the whole rhizome, which consists, from its exterior to its centre, of hard tissue, formed of dark fusiform cells, except only a thin stratum of pale parenchyma surrounding the cambium-layer of the fasciculi of the netted cylinder (Pl. V. fig. 5). Even the interstices of the latter are occupied in the centre by the dark material; so that, as compared with some of the rhizomes which have been described, the white and dark substances seem to have changed places: instead of the vascular bundles and their sheaths forming a dark network on a pale field, we have here a general dark ground marked by a pattern of light reticulations. This great development of the indurated brown tissue gives to the rootstock of *Blechnum* a very remarkable hardness as compared with others in which the pale parenchyma is the sole or preponderating element. In this respect *Blechnum* and *Osmunda* are peculiar among our Ferns, though at the same time they differ from each other in one or two important points.

In *Osmunda* the vessels of the petiole are all collected into a single voluminous bundle, crescentic in horizontal section, with the concavity towards the common axis of the plant. A band of parenchymatous brown tissue, with a similar crescentic curve, lies in the concavity of the vascular bundle, separated from the scalariform vessels by the cambium-layer of the fasciculus. The general parenchyma of the petiole is also marked on all sides with fusiform striæ of brown tissue, like those before described as occurring in the rhizome of *Pteris aquilina* (Pl. V. fig. 2). The cuticular layers of cells form a very tough investment —green above, but passing at the lower part of the petiole into a dark brown. Towards the base it is covered on the exterior with a soft whitish film, forming lateral wings, by which the bases of the petioles overlap each other, as they become crowded upon the rhizome. This film becomes brown and chaffy whenever it is left exposed. The bases of the petioles are at first somewhat dilated, and then taper away to their connexion with

the rhizome, and their *internal* dark tissue disappears, while the *cortical* is much thickened and, by fusion with that of the neighbouring petioles, forms a mass of dark-brown prosenchyma on the exterior of the rhizome, very hard and tough, and of such thickness as to make up the great bulk of the stem,—the only other constituents being a slender medullary tract of pale tissue, in which the vascular cylinder is imbedded, and a cuticular film of white spongy substance, derived from that investing the bases of the petioles (Pl. V. fig. 1). It is the thick and tough cortical layer of dark indurated tissue that gives the tenacity to the stem which is so remarkable in this species, and is probably connected with the great age and size it occasionally attains.

In this toughness of texture, and in the preponderance of dark tissue on which it depends, there is a great resemblance between the stems of *Osmunda* and *Blechnum*, notwithstanding the larger dimensions of the former; but they differ in this—that the induration extends to the medullary region of *Blechnum*, where we find a dense axial column of dark tissue; while in *Osmunda* the axis, though reduced to slender dimensions, is distinctly formed of a pale parenchyma consisting of delicate cells with less than the usual amount of starchy deposit in their interior. The thick cortical layer of dark substance which surrounds it is marked on a horizontal section with white spots, indicating the points of passage of the vascular bundles of the petioles and rootlets.

Another point of difference is, that in *Osmunda* the vascular cylinder has not (at least to the naked eye) the beautiful netted appearance so common in the rhizomes of Ferns, from the closeness with which the component fasciculi are set together. Each fasciculus has the same crescentic section as in the petiole; and a transverse division of the stem shows about eight crescents placed in a circle near the outer margin of the pale medulla, with their concavities all turned inwards, and encircled in turn by the thick cortical layer of dark tissue. The vascular cylinder as a whole forms a cord of some thickness, cellular within, where the medullary parenchyma is not separated from the vessels by any cambium-layer, and fibrous externally, without any apparent interstices, but imbricated with the fasciculi given off to the petioles. On microscopical examination, a real interlacement of the vascular bundles may be detected; but it may be observed at the same time that the whole cord is surrounded by one continuous cambium-layer on its exterior, which dips partially between the several fasciculi, but never passes through the vascular circle to form an internal investment to the component bundles, as in other Ferns. Hence, while it is not difficult to dissect off from the vessels the stratum of pale parenchyma in-

terposed between them and the dark cortical portion of the stem, it is hardly possible to separate the vascular coat in the same way from the delicate cellular tissue of the medulla which it invests. (Pl. V. fig. 3; compare with fig. 4.)

The rhizomes of *Hymenophyllum Tunbridgense* and *H. Wilsoni* are of interest from presenting a transition to the type of stem characteristic of the Lycopodiaceæ, as there is but a single vascular bundle, lying in the axis of the bristle-like rhizome (Pl. VI. fig. 5). This central fasciculus contains four or five scalariform vessels, surrounded by a cambium-layer. Round this, again, there is a thin stratum of pale parenchyma, and a cortical layer of brown tissue, fibrous and much indurated internally, but loose and chaffy on the exterior. The transition-character of the stem is of the more interest that we have in it all the essentials of the rhizome of *Osmunda*. We have only to conceive the stout caudex of the latter drawn out till it is reduced to the thread-like dimensions of the rhizome of *Hymenophyllum*, to have a complete transformation of the one into the other; for when the vascular cord of *Osmunda* is reduced to the dimensions of that of *Hymenophyllum*, its cellular pith necessarily disappears, as a single series of vessels of the ordinary thickness must come to occupy its whole diameter.

In all the stems noticed above, with the dark tissue much developed, and particularly in *Osmunda regalis*, *Blechnum boreale*, *Pteris aquilina*, and *Allosorus crispus*, there is a very remarkable contrast between the hardness of the coloured tracts and the great softness and delicacy of the pale parenchyma and of the vascular bundles (especially in their cambium-layer). The close juxtaposition of tissues of such different powers of resistance adds much to the difficulty of obtaining thin sections for microscopical purposes. The permanency of these tissues is in proportion to their hardness. Thus in the rhizomes of the common Braken, after long exposure the cortical layer and the two internal bands of dark substance are sometimes the only parts left, the pale parenchyma and the vascular bundles having all disappeared by the process of natural decay. And when this dark substance forms the main element, as in *Osmunda* and *Blechnum*, the whole rootstock has a like protracted duration, as has been already observed of the former species.

In connexion with this subject, the question suggests itself, whether the hard brown tissue now referred to (or *phæenchyma*, as it might be called) corresponds to the proper wood of the higher or phanerogamic plants? There is some difficulty in answering this question, arising principally out of the ambiguity of the term "woody tissue." I do not see any reason to doubt that in many of the higher plants there are hard parts, commonly called

woody, which may in all essential points be compared with those of Ferns, and which really owe their induration to a deposit in the cells of ligneous matter undistinguishable from that of the true wood of the stem—such as the veins of leaves, nut-shells, and various husky tissues. But between the dark tracts of the rhizomes of Ferns and the proper wood of the stems of Phanerogamia, there are at least two points of difference, both of considerable importance:—

1st. Unlike the woody tissue of the stems of the higher plants, the cells of the dark-coloured tracts of the Fern, even when they assume a distinctly fibrous character, never occur in the same fasciculus or layer with the vascular tissue, but are always separated from the ducts by the cambium-layer which encircles each vascular bundle,—and this even when in the closest relation, as in the sheath of dark tissue round a fasciculus.

2nd. The hard tissues of Ferns, even when they put on most distinctly a woody character, do not seem to be formed out of a superincumbent layer of cambium-cells, like the true wood of the phanerogamic stem, but simply by an induration of the parenchyma, with occasional elongation of its cells. Hence, while the vascular bundles—lubricated, as it were, by their cambium-coat—may with a little pains be dissected clean out of the cellular tissue of the stem, the coloured tracts adhere so intimately to the surrounding parenchyma, that, with every care, the denuded surface has a rough or villose appearance, from adhering particles.

I have found these points constant in all the British Ferns I have examined; and I have reason to believe that they hold also in Tree-ferns, though my opportunities of examining the latter have been too limited to allow me to speak very positively on this point.

It may be observed, further, that while the woody fibres of the ribs of leaves and of their footstalks in all Phanerogamic plants are continuous with those of the stem or trunk, the dark lines of the petioles of Ferns are rarely to be traced into those of the rhizome. Among our native species, the Braken (*Pteris aquilina*) is perhaps the only instance.

The variability in the development and disposition of these dark tissues seems of itself an argument in the same direction, as tending to assimilate them rather to the capsular indurations and the husky tissues generally of the higher plants, which we observe to vary much, even in allied species*, than to the true stem-wood, which possesses so constant and uniform a structure.

Mr. Berkeley takes the same view of the relations of the

* Compare, for instance, the fruit of the Apple, Pear, and Mountain Ash, and, more strikingly, of the different suborders of Rosaceæ.

masses of dark tissue. In his remarks on the structure of the stems of Ferns, in his 'Introduction to Cryptogamic Botany' (p. 515), he states distinctly that the hard tracts belong to the parenchyma, and do not correspond to the proper wood of the Phanerogamia. The latter he considers to be represented by certain pale fibres, occurring in the substance of the vascular bundles. I have recognized such fibres distinctly enough in two species of Tree-fern which I have lately examined. They form a sort of surface-coating to the fasciculi, exterior to the scalariform vessels, and immediately within the cambium-layer. This is just the position occupied by the pleurenchyma of the Endogenous stem; but in themselves these fibres have none of the characters of woody tissue. They appear to be portions of the cambium-layer which have undergone an imperfect conversion into vascular tissue. The transformation seems to take place by the clustering of the minute cambium-cells into long fusiform masses, which then become invested by a cell-wall, on whose inner surface the scalariform markings are developed, by a deposit of cellulose at particular points, *pari passu* with the disappearance of the original cells of the cluster enclosed by it. I think I have observed all stages of this transition—fusiform masses of cellules, pale granular fibres, and tubules or elongated cells, differing from the scalariform vessels of the fasciculus only in their smaller diameter and fainter markings.

In most of our indigenous species I have been unable to recognize any distinct fibrous coating to the vascular bundles, though the inner stratum of the cambium-layer has certainly at times an appearance of faint longitudinal striation, and the scalariform vessels on the exterior of the fasciculus are generally of smaller diameter and less distinctly marked than those within. The striated layer comes nearest to the characters of a real fibrous tissue in the netted cylinder of *Polystichum Lonchitis* and *Cystopteris fragilis*, and in the indurated petiolar fasciculi of *Trichomanes radicans* and *Asplenium lanceolatum*. In *P. Lonchitis* and *A. lanceolatum* some of these cambium-fibres make a still closer approach to those of woody tissue, by the deposit of a brown sclerogenous matter in their interior. In *Botrychium Lunaria* similar fibres occur, and the vessels are rather annular than scalariform.

That the woody fibres of plants generally differ from the ducts or vessels only in being a less-differentiated form of cambium-tissue, is a view which was very distinctly laid down by Schleiden*, and one which derives some support from the replacement of ducts by punctated woody tissue in the Coniferæ, and from the occurrence in some species of various intermediate forms, such

* Principles of Botany, bk. 2. c. 2. § 26.

as the woody fibres of the Lime and the Yew, which are marked in the interior with a spiral thread.

Not that woody fibres of any kind are themselves to be regarded as elements in progress of conversion into vessels or ducts, or as in any sense in a transition state. Both fibres and vessels are equally ultimate forms, though it may be surmised that, according to the energy of the developmental process, the result is either simple woody fibre or some of the varieties of vascular tissue. The transformation, according to Schleiden, takes place progressively from within outwards in the fasciculi of Endogenous plants, but in Ferns simultaneously throughout the whole of that portion of the cambium-tissue which is to undergo conversion.

A summary is here subjoined of the more prominent characters of the petiole and rhizome in the species which have been enumerated, and a few others. It was my wish to have included all the well-defined species of our flora; but in a few cases I have not been successful, after every exertion, in obtaining rhizomes in a state fit for examination. The notice could not have been made even so complete as it is, but for the kind assistance of some friends, among whom I have especially to tender my thanks to Professors Balfour of Edinburgh and Dickie of Belfast, Mr. L. Squire of Falmouth, the Rev. W. Gregor of Macduff, and Mr. Beverley and Mr. Roy, Sen., of Aberdeen. All the descriptions have been verified by the examination of fresh specimens.

Polypodium vulgare.

The petiole has three or more fasciculi, derived from the netted cylinder of the creeping rhizome, which acquire sheaths of dark tissue, and finally run into one central bundle as they ascend towards the frond.

The rhizome consists of pale tissue, invested by a brown cuticular layer.

Polypodium Dryopteris.

The petiole has two fasciculi running the whole length of the frond, with sheaths of dark tissue.

The rhizome as in the last species, though less tortuous and much more attenuated.

Polypodium Phegopteris.

The petiole has two fasciculi running into one above the base, and without dark sheaths.

The rhizome as in the former species, except that the general tissue (as well as that of the lower part of the petiole) has its cells somewhat elongated, and of a decided brown tint.

Polypodium alpestre.

The petiole has two flattened fasciculi, without dark sheaths, which, as they pass upwards, run into one of a horseshoe section, with the convexity towards the back of the stalk.

The rhizome is of pale tissue, with a brown cuticular layer, and occasionally with a faintly-marked stratum of darker cells surrounding the fasciculi of the netted cylinder*.

Polystichum Lonchitis.

The petiole has two large lateral fasciculi, and one or more intermediate, of smaller size, sparingly anastomosing with each other and with the former; all without dark sheaths.

The rhizome has the fasciculi of the netted cylinder indurated in places by the conversion of part of the cambium-coat into fibres with an internal brown deposit; but there are no dark tracts in the general parenchyma.

Polystichum aculeatum.

The petiole has numerous fasciculi invested with dark sheaths, and sparingly connected by slender transverse branches.

The rhizome, at the origins of the petioles, has deep indentations running into the interstices of the netted cylinder. The whole substance is of pale tissue, except the cuticular layer.

Lastrea Filix mas.

The petioles as in the last species.

The rhizome is of pale tissue (except a brown cuticular layer), thick and fleshy, with the netted cylinder deeply imbedded in its substance; the vascular fasciculi and their cambium-coat have a brownish tint.

Lastrea dilatata.

Petiole and rhizome as in the last species, except that the rhizome has numerous isolated fusiform nodules, of a very dark tissue, in the parenchyma within the netted cylinder.

Lastrea Oreopteris.

The petiole has two fasciculi, and a tract of dark tissue on the inner margin of each, meeting its fellow at the point where the fasciculi are connected with the netted cylinder of the rhizome.

The rhizome is of pale substance, with a cuticular layer of brown tissue; and a transverse section shows dark spots in the line of the netted cylinder, at the points of convergence of the tracts of the petioles.

* These characters apply in some degree to all the specimens which have been shown me as of this species, though differing considerably in the general appearance of the fronds.

Lastrea cristata.

The petiole has two large lateral fasciculi, and three smaller intermediate, the latter running into one upwards; all with dark sheaths.

Lastrea Thelypteris.

The petiole has two flattened and plaited fasciculi, somewhat resembling those of *Athyrium Filix fœmina*, but with dark sheaths. They unite above into one of a horseshoe section, as in *Polypodium alpestre*.

The rhizome is long, and creeps horizontally. The fasciculi of the vascular cylinder which lie towards the upper surface are thicker than those on the lower. The substance is of pale tissue, with a brown cuticular layer.

Athyrium Filix fœmina.

The petiole tapers from a swelling near the base to its point of connexion with the rhizome; it has two fasciculi, without dark sheaths, which acquire the form of fluted bands, in the dilated portion of the petiole.

The rhizome is indented as in *Polystichum aculeatum*, and is formed of pale but dense and thick-walled cells, with a cuticular layer of brown tissue.

Athyrium fontanum.

The petiole has two fasciculi running on into the midrib of the frond, without dark sheaths.

The rhizome has no dark deposit in the parenchyma, but the scalariform vessels have a decided brown tint.

Asplenium marinum.

The petiole has a single central fasciculus, without a dark sheath.

The rhizome is of pale tissue, except the cuticular layer.

Asplenium Adiantum nigrum.

Petiole and rhizome as in the last species, except that the former has two fasciculi at the base, which coalesce as they ascend towards the frond.

Asplenium lanceolatum.

The petiole has two (or sometimes three) fasciculi, uniting above, as in the last species, without dark sheaths, but with the vessels themselves and the cambium-layer of a brown colour, most decided at the base of the petiole, and disappearing upwards.

The rhizome is of pale tissue, as in the last species, except

that the cells immediately surrounding the fasciculi of the netted cylinder have a light-brown tint.

Asplenium viride.

The petiole has a single central fasciculus, without a dark sheath.

The rhizome shows no dark tissue in its interior.

Asplenium Trichomanes.

The petiole has a single central fasciculus and a cortical layer of dark substance, much thickened at the base.

The rhizome has the general parenchyma of a brownish tinge, with a darker tissue (continuous with that of the petioles) forming a cortical layer, and also partially ensheathing the vascular bundles. The anastomosis of the fasciculi of the netted cylinder is very close.

Asplenium Ruta muraria.

The petiole has a single central fasciculus, containing a double vascular cord, and surrounded near the base with a sheath of dark tissue.

The rhizome has the same general arrangement as in the last species; only the dark tissue about the netted cylinder is less marked, and is mainly derived from the sheaths of the petiolar fasciculi.

Asplenium septentrionale.

The petiole has a single fasciculus, with a dark sheath at the base.

The rhizome has also a thin stratum of dark tissue round the fasciculi of the netted cylinder, as in the last species,—especially on their outer side*.

Woodsia ilvensis.

The petiole has a single fasciculus, without a dark sheath.

The rhizome shows no dark tissue in its interior.

Cystopteris fragilis.

The petiole has two fasciculi, running into one about the middle of the frond, without dark sheaths.

The rhizome shows no dark tissue internally, but the outer stratum of the vascular bundles of the netted cylinder has a distinctly fibrous character.

Adiantum Capillus Veneris.

The petiole has a dark glossy cortical layer, and a single fas-

* In decaying parts of the rhizome, the central parenchyma becomes brown, presenting somewhat the appearance of the dark central tract of *Allosorus crispus*.

ciculus with a double origin from the netted cylinder, but without any dark sheath.

The rhizome is of pale tissue, except the cuticular layer, and one of brownish cells round the fasciculi of the netted cylinder.

Scolopendrium vulgare.

The petiole has two fasciculi uniting above in the midrib of the frond, and separated below by two half-sheaths of dark tissue, united by their convexities. Externally also the fasciculi are bordered by dark lines, which run down into the rhizome.

The rhizome is of pale tissue, except the cuticular layer and the lower ends of the outer dark lines of the petioles just mentioned.

Ceterach officinarum.

The petiole has two fasciculi, which unite above in the midrib of the frond, and three lines of dark tissue, which run down into the rhizome—two lateral, on the outer margins of the fasciculi, the other median, forming two half-sheaths, united by their convexities.

The rhizome is of pale tissue, except the cuticular layer and the inferior extremities of the petiolar lines just noticed.

Pteris aquilina.

The petiole has numerous anastomosing fasciculi derived from the outer and inner systems of the rhizome, also a main central plaited band of dark fibrous tissue (connected with those of the rhizome), and some subsidiary tracts arising within the petiole.

The rhizome has a white pulpy parenchyma, with a hard cortical shell of dark tissue, and two longitudinal dark bands within, separating an inner vascular system of two flat bundles from a more external, which consists of numerous small fasciculi anastomosing sparingly to form an irregular wide-meshed cylinder.

Allosorus crispus.

The petiole has a single fasciculus without a dark sheath, and a double vascular cord.

The rhizome consists in part of pale tissue, with a brown cuticular layer, but it contains also dark tissue internally—as a central cord along the axis, and as faintly-marked sheaths round the fasciculi of the netted cylinder.

Blechnum boreale.

The petiole has two fasciculi, imbedded in the pale tissue of the interior, which towards the base is reduced to a mere sheath

by the thickening of the dark cortical layer continuous with the substance of the rhizome.

The rhizome is almost wholly composed of dark substance, both externally and internally, the pale tissue forming only thin sheaths round the several fasciculi of the netted cylinder.

Trichomanes radicans.

The petiole has a single fasciculus, without a dark sheath, but with a fibrous development in the cambium-coat.

Hymenophyllum Tunbridgense and *Wilsoni.*

The petiole has a central fasciculus, surrounded by a dark cortical fibrous layer, continuous with that on the exterior of the rhizome.

The rhizome consists of a cortical coat of dark tissue (dense and fibrous internally, loose and chaffy on its outer surface), and of a layer of pale tissue surrounding the cambium-coat of the single central fasciculus or vascular cord.

Osmunda regalis.

The petiole has a crescentic fasciculus, with a dark band on its concavity, which looks towards the axis of the rhizome. These structures are imbedded in a pale parenchyma. As the petiole tapers to its connexion with the rhizome, the dark band disappears, and the pale tissue is reduced to a mere sheath, by the thickening of the dark cortical layer.

The rhizome has a thick layer of dark tissue externally, continuous with the cortex of the petioles, and a thin sheath of pale tissue within, round the vascular cylinder and the fasciculi connecting it with the petioles. The vascular cylinder is solid, having no obvious reticulations in its walls, from the closeness of the fasciculi, and the absence of any cambium-layer between their inner surface and the cellular tissue of the axis which they enclose.

Botrychium Lunaria.

The petiole has two fasciculi, united at the base, without dark sheaths.

The rhizome has a vascular cylinder with very few openings or reticulations, and with a cambium-layer only on its exterior. There is no dark tissue, except the cuticular investment.

Ophioglossum vulgatum.

Stem fistulose, with eight or nine fasciculi in the wall, without dark sheaths.

In the following Table the species are arranged with reference

to the external characters of the rhizomes, as explained in my former communication on this subject (Ann. Nat. Hist. Dec. 1859).

Rootstock a stoloniferous rhizome.

Polypodium vulgare.
—— Dryopteris.
—— Phegopteris.
Lastrea Thelypteris.
Pteris aquilina.
Adiantum Capillus Veneris.
Hymenophyllum Tunbridgense.
—— Wilsoni.
Trichomanes radicans.

Rootstock a dichotomous caudex.

Polypodium alpestre.
Polystichum Lonchitis.
Lastrea Oreopteris.
—— rigida.
Cystopteris fragilis *.
Athyrium Filix fœmina.
—— fontanum.
Asplenium Adiantum nigrum.
—— lanceolatum.
—— marinum.
Asplenium viride.
—— trichomanes.
—— Ruta muraria.
—— septentrionale.
Woodsia Ilvensis.
Allosorus crispus.
Scolopendrium vulgare.
Ceterach officinarum.
Blechnum boreale.
Osmunda regalis.

Rootstock a right caudex (*extending by a single terminal bud*).

Polystichum aculeatum.
Lastrea Filix mas.
—— dilatata.
Lastrea cristata.
Botrychium Lunaria.
Ophioglossum vulgatum.

EXPLANATION OF THE PLATES.

Plate V.

Fig. 1. Cross section of the rhizome of *Osmunda regalis*, showing the brown cortical substance and the pale tissue within, surrounding the central vascular cylinder with its cellular pith, and a cambium-layer only on its exterior: *a a*, origins of the petioles; *b b*, rootlets. (The outer tissue has been partially pared away, to fit the specimen into the section instrument.)

Fig. 2. Cross section of a petiole near the base, showing the cut extremities of the longitudinal filaments and of the crescentic fasciculus and dark band. The asterisk in this and the other sections of petioles marks the side next the rhizome—that which is uppermost when the frond is laid on its back.

Fig. 3. The central vascular cylinder of the rhizome of *O. regalis* dissected out, showing the imbricated fasciculi going to the petioles.

Fig. 4. A portion of the netted cylinder of *Lastrea dilatata* opened out, showing the origin of the petiolar fasciculi.

Fig. 5. Cross section of the rhizome of *Blechnum boreale*, showing the great development of dark tissue in this stem. The outer series of fasciculi (in pairs), *a a a*, belong to the origins of the petioles;

---

* The other British forms of *Cystopteris* are questionable species; but if Mr. Newman is correct in assigning to *C. montana* a "stoloniferous rhizome" (History of British Ferns, p. 97), this may perhaps be a good species.

the inner, *c c c*, represent the section of the netted cylinder; *b*, origin of a rootlet.

Fig. 6. Cross section of the rhizome of *Lastrea Oreopteris*, somewhat foreshortened, with a portion of a petiole attached, showing the converging tracts of dark tissue, *a*.

Fig. 7. Section of the rhizome of *Lastrea dilatata* along the axis, showing the fusiform dark nodules in the medullary tissue: *a a*, fasciculi of the netted cylinder in section.

Fig. 8. Cross section of a petiole of *Asplenium Ruta muraria* near the base.

PLATE VI.

Fig. 1. Section of the petiole of *Scolopendrium vulgare*, along the axis, showing the course of the dark tracts, like two converging lines of railway.

Fig. 2. Cross section of the same, a little above the base.

Fig. 3. Cross section of the same, about the commencement of the lamina of the frond. In the small fronds of *Ceterach officinarum* the arrangement is somewhat similar.

Fig. 4. Cross section of the petiole of *Athyrium Filix fœmina* at the base.

Fig. 5. Cross section of the rhizome of *Hymenophyllum Wilsoni*, showing the brown cortical and pale medullary tissue, with the single vascular fasciculus imbedded in the latter.

Fig. 6. Cross section of the rhizome of *Allosorus crispus*, showing the central dark cord, and the sheaths round the fasciculi of the netted cylinder.

Fig. 7. Cross section of the rhizome of *Pteris aquilina*, showing the outer and inner series of vascular fasciculi, the two intermediate dark bands, and the extremities of some of the longitudinal dark filaments.

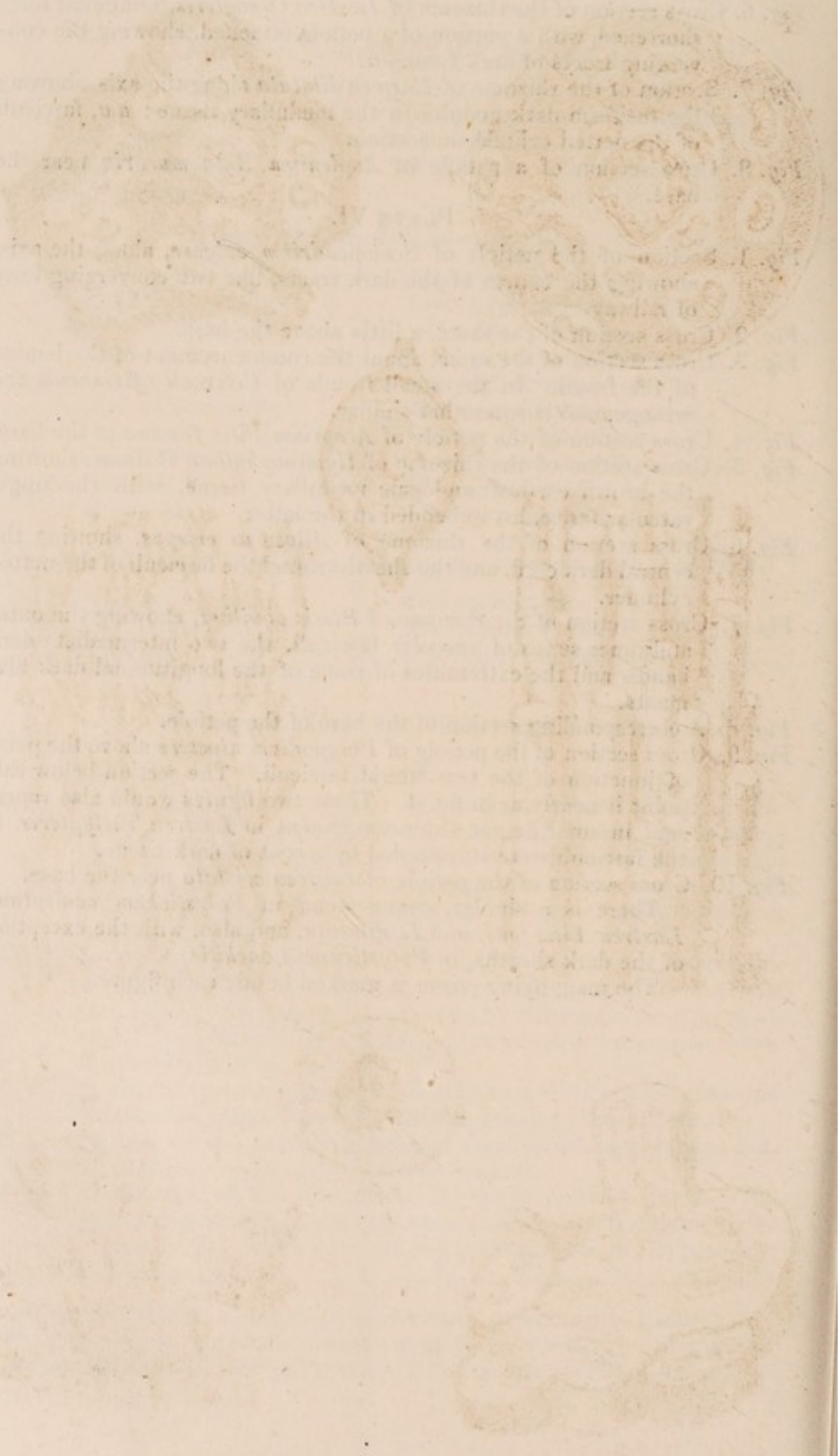
Fig. 8. A corresponding section of the base of the petiole.

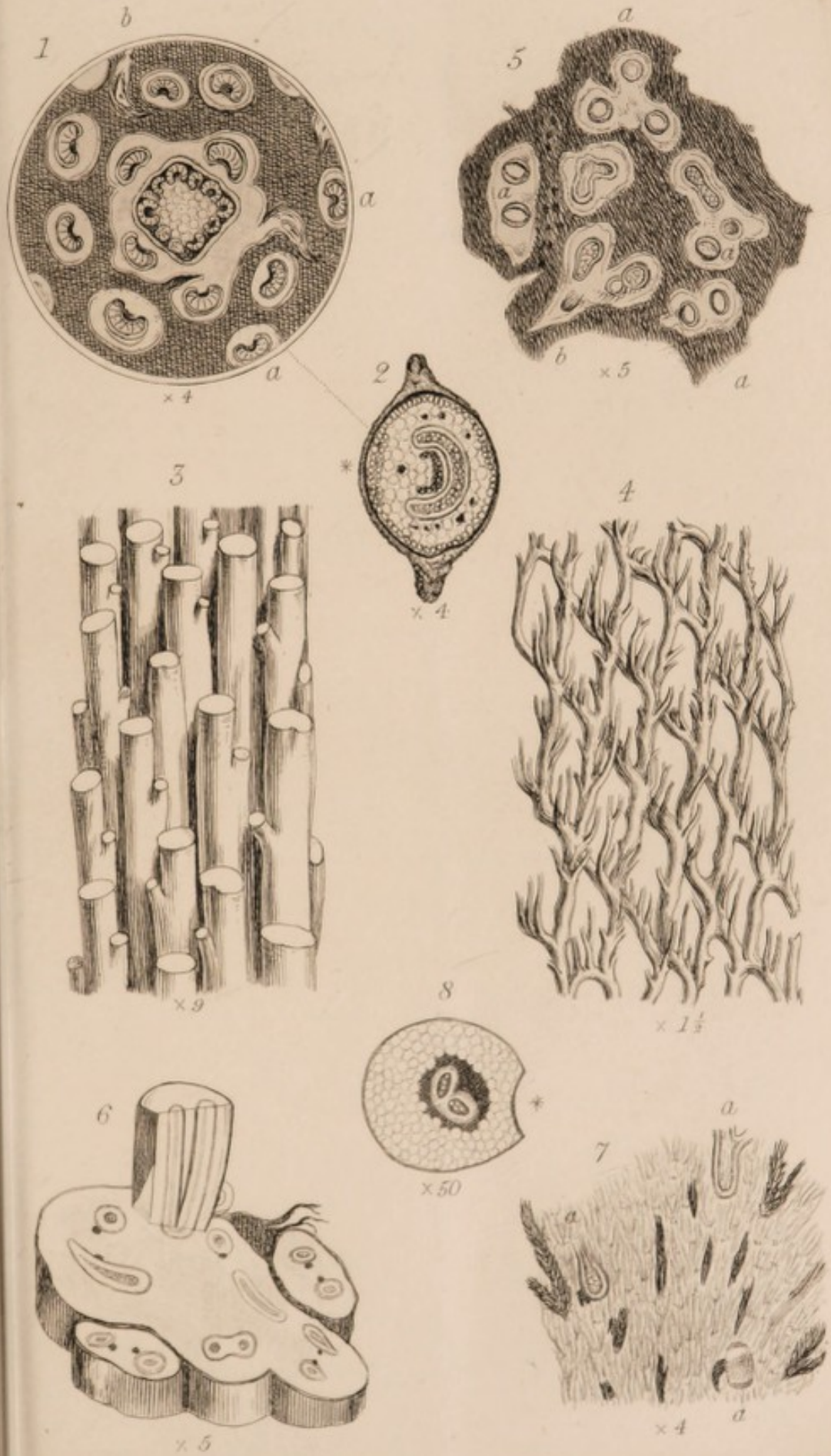
Fig. 9. Cross section of the petiole of *Polypodium alpestre* above the point of junction of the two lateral fasciculi. The section below this point is nearly as in fig. 4. These two figures would also represent in some degree the arrangement in *Lastrea Thelypteris*, if the fasciculi were surrounded by a coat of dark tissue.

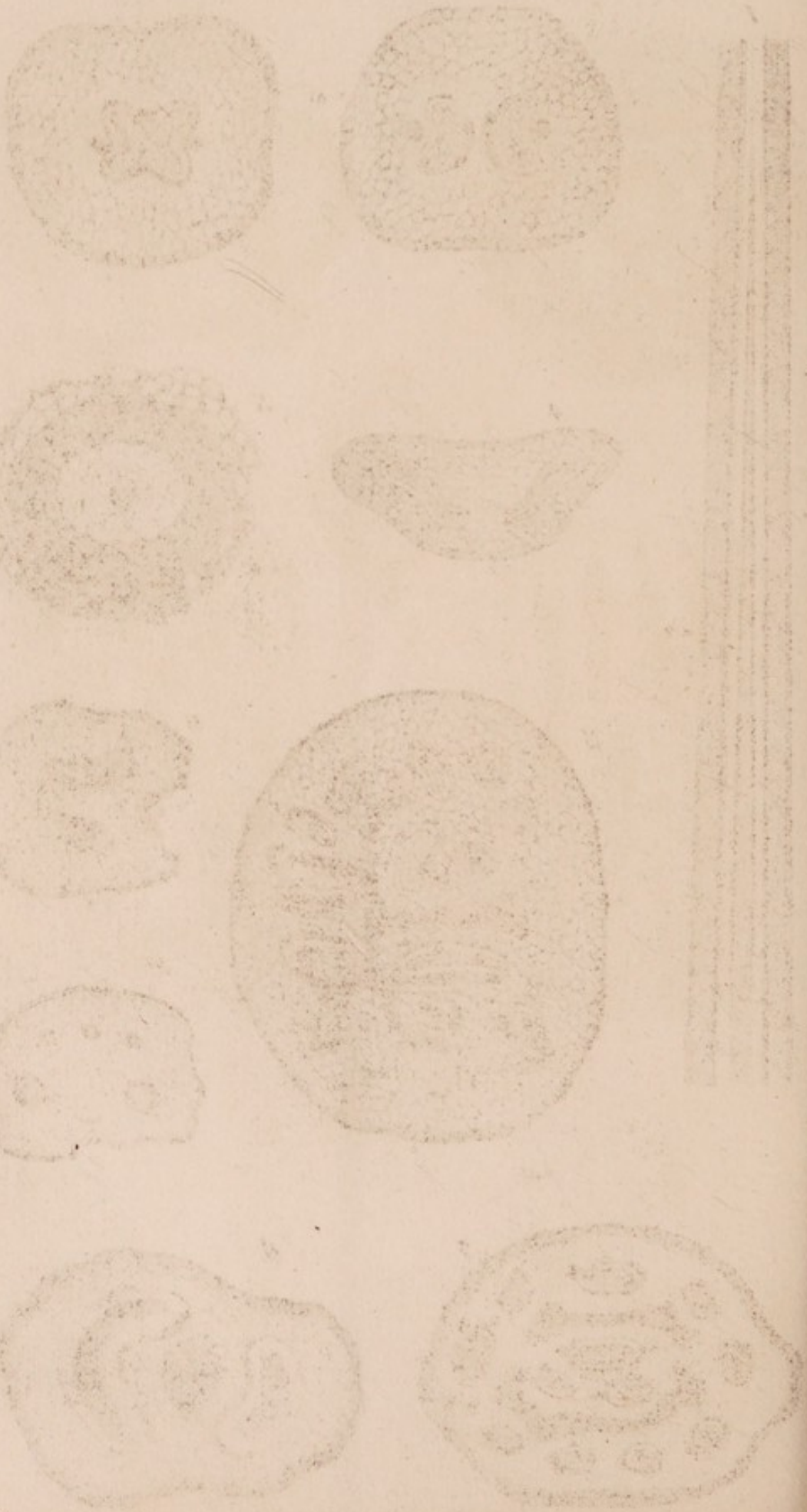
Fig. 10. Cross section of the petiole of *Lastrea cristata* near the base.

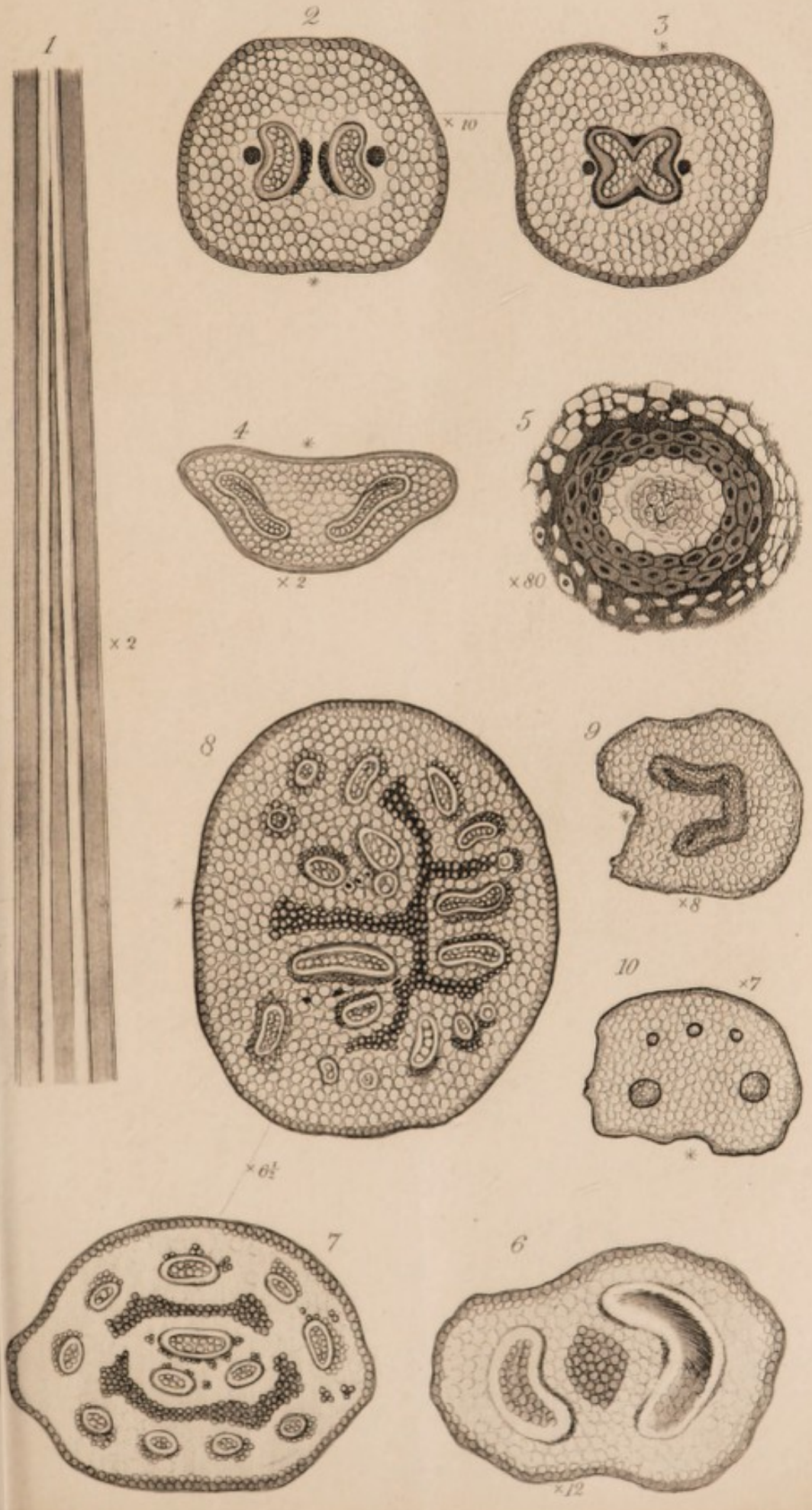
There is a similar arrangement in *Polystichum aculeatum*, *Lastrea Filix mas*, and *L. dilatata*, and also, with the exception of the dark sheaths, in *Polystichum Lonchitis*.

The magnifying power is marked beside each figure.




1
b
a
a
×4
5
a
a
a
b
×5
a
2
*
×4
3
×9
4
×1½
8
*
×50
6
×5
7
a
a
a
×4




1
×2
2
×10
3
4
×2
5
×80
8
×6½
9
×8
10
×7
7
6
×12