On the Anatomy of Archangiopteris Henryi and other Marattiaceae.

BY

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With Plate X.

ARCHANGIOPTERIS was established in 1899 by Christ and Giesenhagen as a new genus of the Marattiaceae connecting *Angiopteris* with *Danaea*¹. The plants upon which the genus was founded, as indicated by the specific name, were discovered by Dr. A. Henry in Yunnan in the south-west of China. The Fern was found in one locality only, in a mountain forest to the south-east of Mengtse. The material upon which the following observations were made was a small piece of a stock preserved in spirit which was presented by Dr. Henry to Professor Bower, who handed it over to me for investigation. Dr. Henry informs me that it was only by a lucky accident that this particular material reached Europe at all. It was left behind in a house at Mengtse when Dr. Henry had to retire from that district in consequence of an upheaval among the natives. During his absence the Chinese soldiers who were put on guard to protect European property looted the houses. They forced an entrance into the houses through trap-doors in the floors, which were built on piles some feet above the ground. Luckily in Dr. Henry's house a heavy box had been left accidentally above the trap-door, and in consequence it escaped loot. A year afterwards the bottle containing the material was brought home by Mr. Miller, of the customs service, who returned to Mengtse after the troubles were over.

A detailed account of the morphology and structure of the leaf of *Archangiopteris* is to be found in the original account given by Christ and Giesenhagen, but nothing has yet been published upon the anatomy of the rhizome and petiole save a passing reference to the latter by Brebner²

¹ Flora, Bd. 86, p. 72.

² 'On the Anatomy of *Danaea* and other Marattiaceae,' Annals of Botany, vol. xvi, No. lxxiii, pp. 537 and 538, 1902.

in his paper on the anatomy of *Danaea*. The addition of a new genus to an order so limited in the number of its genera as the Marattiaceae is of sufficient interest to warrant the following supplementary observations upon this the only example of the genus hitherto discovered.

The material at my disposal proved upon examination to consist almost entirely of three large leaf-bases inserted so closely together as to appear to arise one upon the other, as shown by Figs. 1 and 2, Pl. X. Further investigation disclosed a fourth young leaf and a small portion of the apical region of the stem lying between the larger leaf-bases. Unfortunately the specimen had not been cut off from the rest of the stock upon which it grew, but torn away, and in consequence the lower end of the stem was in a very lacerated and fragmentary condition. The tissues, however, were in a fairly satisfactory state of preservation. The portion of stock examined does not appear to have been subterranean, but it was impossible to decide whether it grew erect or not. There was, however, no suggestion of dorsiventrality; on the other hand, the arrangement of the leaves and the structure of the vascular system indicated a radial symmetry.

The two leaves belonging to the petioles, the cut ends of which are shown in the figures, also accompanied the specimen. They were about 28 inches in length, including the terminal pinna. Two pairs of shortly stalked, nearly opposite lateral pinnae are inserted upon the upper third of the rachis in each leaf. The basal region of the petiole is enlarged into a conspicuous pulvinus (Figs. 1 and 2), another occurs about halfway up the free petiole, and the bases of the stalks of the pinnae also show a pulvinar structure. The surface of the basal pulvinus is rough, corrugated, and dark brown in colour. This region is thereby sharply marked off from the rest of the petiole, which is yellowish white in colour and, although bearing a few paleae, is smooth and shining. As stated by Christ and Giesenhagen, the upper part of the petiole shows no articulation with the basal pulvinus. The bend seen in the drawings just above the enlarged bases of the petioles has probably been produced in the collecting.

The characteristic stipular appendages of the order are present at the bases of the leaves, and are produced by the prolongation of the margins of the enlarged leaf-base into two broad wings thinning down towards their edges until they become quite membranous (Figs. 3 and 4). Just above the middle of the basal pulvinus the two lateral wings are united across the adaxial surface of their leaf by a plate of tissue forming a transverse intra-axillary commissure, as described by Sachs in *Angiopteris*, *Marattia* and *Danaea*¹. This cross-piece is abaxially concave, and in the bud it curves over and protects its own leaf, which is circinately coiled up behind it (Fig. 3). The top of the young leaf is covered over by the

¹ Text-book of Botany (English edition), p. 417, 1882.

overlapping upper margins of the wings, which in this region are free from the leaf-base. The lower parts of the stipular wings (below the transverse commissure) enfold the next youngest leaf in front. During the unfolding of the leaf the transverse commissure gets torn across, as shown in Fig. 4. A comparison with the stipular appendages of *Kaulfussia aesculifolia* (represented somewhat diagrammatically by Fig. 5) shows that the protective arrangements in this plant are on a slightly different plan. The upper free portions of the wings are here much larger, and suffice alone for the protection of their own leaf, while the transverse commissure joins the lower parts of the stipular wings in curving over and protecting the next youngest leaf *in front*.

THE VASCULAR SYSTEM OF THE STEM.

In order to observe the structure of the stem the larger leaf-bases were first of all removed and the rest of the specimen was then cut up into a series of transverse sections. Unfortunately the insertion of the vascular strands of the first two leaves upon those of the stem could not be satisfactorily followed out on account of the torn and ragged condition of the end of the specimen. The portion of the stem that extended beyond this point was very short and, being so near the meristematic tissues of the apex, it was not very suitable for anatomical purposes. The concrescence of the large leaf-bases with the axis of the stock causes the outline of the latter to be very irregular, and at the same time renders it almost impossible to draw any definite limit between the ground-tissue of the stem itself and that of the adhering leaf-bases. The vascular system of the stem consists of a single dictyostelic ring of two to four small meristeles more or less oval in section. In addition there is usually a small vascular strand lying in the central ground-tissue enclosed by this ring (*int. s.* in Fig. 6). This internal strand may, however, sometimes be absent (Fig. 7). A varying number of entering leaf-traces occur at different levels in the peripheral ground-tissue, which is also traversed by a number of roots passing downwards and outwards. The meristeles of the ring anastomose with each other in a somewhat irregular manner; anastomoses being present other than those which close the leaf-gaps. In one region the meristeles all fuse up to form a single large curved strand.

The small internal strand runs free in the central ground-tissue through the greater part of its course, but from time to time it approaches the dictyostelic ring and fuses with those meristeles that are about to close up the upper ends of a leaf-gap. Soon after it separates off again and passes on across the central ground-tissue to the next leaf-gap above. In one region the central strand ended blindly in the downward direction and for some distance below this point the dictyostelic ring alone was

present (Fig. 7), until another central strand separated off from the inner surface of one of its meristeles.

The roots arise from the external surface and sides of the stem meristeles. A root appears to arise invariably from the point where the central strand fuses with a meristele of the ring. The xylem elements of the root stele spread out over the outer side of the xylem of the stem to form a small attachment-disc of irregular isodiammetric tracheides. These tracheides are differentiated very near the apex—at the same time as the endarch protoxylems of the stem stele itself, and before the intervening metaxylem. The roots have a cortex of their own right up to the stem stele (Fig. 6, *r*), so that there is no 'root-pedicel.' When free from the stem the xylem of the root has seven to ten protoxylem groups, and its centre is occupied by a few cells of thin-walled parenchyma. There is a well-marked endodermis with barred thickenings on its radial walls.

THE VASCULAR SYSTEM OF THE PETIOLE.

The arrangement of the vascular strands in the petiole showed a certain amount of variation in the three leaves in which it was possible to follow their course throughout. On this account it would have been rather difficult to fix with any confidence upon those features which may be held as common to the leaves of the plant in general, were it not for the light thrown upon their interpretation by the structure of the petiole of *Kaulfussia aesculifolia*. Since the number of petioles of *Kaulfussia* examined renders the observations more reliable, it is advisable to describe the arrangement in this plant before going on to that in *Archangiopteris*. Seven vascular strands are given off from the dictyostele of the stem to supply each leaf. They anastomose and divide freely as they pass out, so that a varying number of separate strands are to be found in the base of the petiole. These are arranged in a curve of the form of a widely open arch with its concavity facing directly towards the apex of the rhizome (Fig. 8). The two terminal strands of the arch (marked *x* in all the figures) are somewhat larger than the rest, and as they pass upwards they approach the median plane of the petiole. As they do so they also curve inwards, and at the same time turn round so that their protoxylems face away from each other towards the sides of the petiole (Fig. 9). This rotation is sometimes continued until at a point still further up their protoxylems face almost directly towards the median plane (Fig. 10). At a certain point in the enlarged basal region of the petiole the terminal strands are usually joined together by a transverse suture (*s* in Fig. 9); sometimes, however, it is the two penultimate strands that are thus joined together.

The several strands so far described are all clearly to be regarded as constituting a leaf-trace strictly comparable with the typical leaf-trace of

the Polypodiaceae and Cyatheaceae; the curve that they outline being but a slight variation of the horseshoe design so frequently met with in these two orders. In the enlarged basal region of the petiole, however, a new feature is introduced by the occurrence of one or more internal vascular strands lying within the typical curve (Fig. 8). These internal strands arise as branches from the inside of the median abaxial strands of the curve, but they do not lie in the course of the curve itself, nor can they be considered as forming part of it. Two such strands are usually present (Figs. 9 and 10), but in one case as many as five were observed (*a, b, c, d, e* in Fig. 8). They were arranged in an arc concentric with the abaxial part of the typical curve. Two of them (*a* and *d*) ended blindly above, and two others (*b* and *c*) fused together, so that here also only two internal strands eventually remained. As they pass upwards these internal strands in all cases gradually move across the central ground-tissue towards the adaxial side of the petiole, and before the top of the pulvinus is reached they fuse with the two terminal incurved strands of the typical arc (*xx* in Figs. 9 and 10). In a few cases a single strand alone arose from the abaxial strands of the typical curve, but this soon divided into two which behave as before. The protoxylems of the internal strands first of all face outwards, towards the abaxial surface of the petiole (Fig. 8), but as they advance across the internal ground-tissue they gradually turn round so as to face in the same direction as the terminal strands with which they fuse (Figs. 9 and 10). The internal strands may fuse with either end of the terminal strands according as the protoxylems of the latter face towards the sides of the petiole (Fig. 9) or towards its median plane (Fig. 10). In the region above the pulvinus all the strands present in the petiole belong to the typical curve. The two terminal strands sink in towards the centre of the petiole, and at a point higher up they fuse together across the median plane to form a single large internal strand with the protoxylem on its adaxial side, as described and figured by Bertrand and Cornaille¹.

In *Archangiopteris* two vascular strands only are given off from the dictyostele of the stem to supply each leaf. As they pass outwards they divide up into several (8 or 9) separate strands which are arranged at the base of the leaf in a typical horseshoe-shaped curve, entirely similar to that in *Kaulfussia* (Fig. 11). The terminal strands of the curve (*xx* in all the figures) advance towards the median plane of the petiole, and at one point in the pulvinus they fuse together to form a single broad strand the protoxylems of which face abaxially (Fig. 13). Higher up they become separate again, and curving gradually inwards they turn round at the same time so that their protoxylems face towards the sides of the petiole (Fig. 14).

¹ Études sur quelques caractéristiques de la structure des Filicinées actuelles. Mémoires de l'Université de Lille, tom. x, Mém. 29, pp. 151 et seq., 1902.

All the strands hitherto described belong to the typical leaf-trace curve referred to above, but the additional internal strands that occur in the basal pulvinus of *Kaulfussia* are also to be found in the same region of *Archangiopteris*; they are, however, more feebly developed and less regular in their behaviour. In all the leaves examined, and it probably holds true for the leaves of the plant in general, the internal strands invariably arise as branches on the inside of the strands of the abaxial region of the typical curve, and they always pass upwards across the internal ground-tissue to fuse with the median adaxial strands of the curve before the top of the pulvinar region is reached. Only two of these strands were found in any one petiole, and almost immediately after their origin they fuse together to form a single one with its protoxylems on the abaxial side (cf. Figs. 11 and 12). After passing upwards for a short distance they become separate again, and finally fuse with the two terminal strands of the typical curve (cf. Figs. 13 and 14). In one case a single strand only was given off, which passed obliquely across and fused with the terminal strand on its own side.

The internal strands seem to join on indifferently to either end of the incurved terminal strands. In one case the same internal strand fused first with one end of the terminal strand, and then, after separating off again, finally fused up with the other. Sometimes the internal strands are connected with their respective terminal strands by a short suture before they themselves come into actual contact.

All the vascular strands in the petiole above the basal pulvinus belong to the typical horseshoe-shaped curve. The ends of the horseshoe are curved deeply inwards so that the two terminal strands take up a more or less internal position (Fig. 15). They remain separate from each other throughout the greater part of the petiole, but in certain regions they fuse together to form a single large internal strand with the protoxylem facing adaxially (Fig. 16), just as in *Kaulfussia*. In these two plants, therefore, an important distinction has to be made between these more or less included strands of the typical curve and the internal strands that occur in the basal pulvinus which have quite a different origin. In other Marattiaceae, however, the internal strands of the pulvinus are continued into the upper part of the petiole. For instance, in a form of *Marattia fraxinea* that I examined there were, at a point just above the basal pulvinus, two separate concentric rings of internal strands, and also a single strand occupying the centre of the ground-tissue. In the upward direction these strands gradually disappear in precisely the manner that might have been anticipated from the behaviour of the internal strands in the basal pulvinus of *Kaulfussia* and *Archangiopteris*. First of all the central strand fuses with one of the median adaxial strands of the inmost ring. Then those of the inmost ring successively fuse with the adaxial strands of the ring next without, which

in turn disappears by fusing in a similar manner with the outermost ring, or typical curve. All this takes place so slowly that a number of the internal strands continue their course from the pulvinus far up into the region of the rachis. According to Bertrand and Cornaille (l. c.), the same holds true for the internal strands in the petiole of *Angiopteris*.

It is known also that the vascular system of the petiole of *Helminthostachys* is characterized by the presence of an internal strand, and in the light of these facts it becomes necessary to determine the exact manner in which it arises. In this plant the leaf-trace departs from the stem stele as a single circular or elliptic strand with a mesarch protoxylem. In the free petiole the protoxylem becomes endarch, the endodermis disappears, and the leaf-trace divides up into several strands which arrange themselves along a curve almost completely closed adaxially. Then in all the petioles examined I was astonished to find that the terminal strand of one arm of the curve, *and of one arm only*, sinks inwards towards the centre of the petiole, and turns round so that its protoxylem faces adaxially. This internal strand has, therefore, a different origin from those in the basal pulvinus of the *Marattiaceae*, and can only be compared with the internal strands in the upper part of the petiole of *Kaulfussia* and *Archangiopteris*, the surprising feature about it being that it represents the adaxial terminal strand of one arm only of the curve.

To return again to *Archangiopteris*; the manner in which the pinnae obtain their vascular supply from the rachis is worthy of especial notice. The terminal strands of the petiolar curve are always separate from each other in the neighbourhood of the insertion of the pinnae, and each pinna receives two strands from the rachis. One of them is comparatively large, and comes from the side of the curve (Fig. 17, *p. tr.*); the other is small, and comes from the extremity of the incurved terminal strand on the same side. This small strand travels right across the *central ground-tissue within the curve* to fuse with the adaxial end of the large strand (Fig. 17, *st.*). In my examples the small strand never became quite free from the terminal strand, but moved along in contact with its inner surface.

In the petiole of *Kaulfussia*, also, a strand passes across the internal ground-tissue from the extremity of the incurved terminal strand of the curve to join those that depart from its sides into the branch. Again, Bertrand and Cornaille (l. c.) describe a similar procedure in the petioles of *Marattia fraxinea* and *Angiopteris*. They find that the primary branches are supplied with vascular strands from the internal system (which is continued from the basal pulvinus far up into the rachis) in addition to those they obtain from the outer ring, and this is also confirmed in the *Marattia* that I myself examined.

I believe, with these authors, that this method of vascular supply to the

petiolar branches will probably prove to be characteristic of the Marattiaceae as an order, and I agree with them in regarding it as a distinction between this order and the leptosporangiate Filicineae. As regards the Ophioglossaceae, *Helminthostachys* seems to present a parallel case; for each of the first pair of pinnae certainly receives branches from the internal strand, although the greater portion of it passes out into the fertile spike.

THE STRUCTURE OF THE STIPULE.

The wings of the stipule of *Archangiopteris* contain a number of small anastomosing vascular strands arranged in a row with their protoxylems facing adaxially towards the median plane of the petiole. There are also a few additional strands in the upper part of the stipule lying on the adaxial side of the main row, and facing in the opposite direction. They are all derived from about three main branches which arise from the strands at the adaxial corners of the petiolar curve. The transverse commissure has no vascular supply at all in *Archangiopteris*, but in *Kaulfussia* it contains a row of strands facing away from the petiole.

In *Archangiopteris* a small group of cells having the appearance of an arrested meristem is to be found at the bottom of a little pit situated at the base of the stipule near the margin of the wing, but slightly over on to the adaxial surface (about the point *x* in Figs. 3 and 4). A similar group occupying the same position is also present in *Kaulfussia* (*x* in Fig. 5). It is here rather more highly developed, and sometimes forms a definite projection into the bottom of the pit. In both genera there is a broad curved vascular strand in the stipule which is derived from the corner strands of the petiolar curve and terminates just below this meristematic group. The whole structure clearly belongs to the petiole and not to the stem. These structures are to be found on all the leaves, even the young ones, and they are no doubt to be regarded as arrested apices of dormant adventitious buds, and the 'stipular budding' that is well known to occur in the Marattiaceae is probably to be accounted for by their belated development.

HISTOLOGY.

Archangiopteris, as regards the minute structure of its tissues, agrees almost exactly with the descriptions given for the related genera by Miss Shove, Farmer and Hill, and Brebner¹. The protoxylem elements

¹ R. F. Shove, 'On the Structure of the Stem of *Angiopteris evecta*,' *Annals of Botany*, vol. xiv, No. lv, p. 497, 1900. Farmer and Hill, 'On the Development and Structure of the vascular strands in *Angiopteris evecta*, and some other Marattiaceae,' *Annals of Botany*, vol. xvi, No. lxii, p. 371, 1902. Brebner, l. c.

are endarch in both stem and petiole. The phloem extends all round the meristemes of the stem, but protophloem occurs only on the outer side of the xylem, and there, as described by Miss Shove in *Angiopteris*, it lies between the xylem and the metaphloem. This extraordinary fact can be observed with perfect clearness in all the strands, external or internal, of both stem and petiole, and even in those of the stipule. The cells of phloem-parenchyma in immediate contact with the sieve-tubes are small and have albuminoid contents. A layer of large cells usually containing starch intervenes between the protophloem and the metaphloem, and two or three layers of similar cells separate the former from the xylem. The two cell-layers immediately surrounding the phloem are slightly different from the rest of the ground-tissue of the stem both in their form and in their reactions towards staining reagents. They might, perhaps, be regarded as a pericycle, but since neither an external nor an internal endodermis could be demonstrated in either stem or petiole, it is impossible to set any definite limit to the vascular strands. As in the rest of the order, there is no sclerotic tissue of any sort in the stem, but in the petiole there is a layer of fibres with colourless lignified walls situated a few layers below the epidermis. In the pulvini this fibrous layer is replaced by a zone of collenchyma. It is, perhaps, also worth mentioning that a certain amount of sclerotic tissue, quite different in nature from that of the fibrous zone, is to be found in the upper part of the rachis in the form of *Marattia fraxinea* that I examined. It consists of short rectangular elements with very thick pitted walls; something like stone cells. They form a very irregular and incomplete sheath around the vascular strands, separated from the phloem by two or three layers of thin-walled parenchyma.

Mucilage canals occur irregularly distributed in the stem, root, and petiole. In the latter they are confined to the tissue within the fibrous zone, except in the pulvini, where they also occur between the collenchyma and the epidermis. Tannin sacs are present in the petiole, but not in the stem. The paleae which occur at the base of the petiole arise from the bottom of deep pits. They are lanceolate in form, with a toothed margin, and run out into a long narrow point.

GENERAL CONCLUSIONS.

In forming any conclusions based upon this account of the structure of *Archangiopteris* it is necessary to bear in mind that a small portion of a single plant only has been examined, and that, since a comparatively small specimen would naturally recommend itself to a collector as convenient for manipulation and transport, it may quite well be that this particular specimen does not represent the full size attainable by the species. It is possible, therefore, that other specimens may disclose a structure considerably more

complex than that described above. With this reservation the mature stem of *Archangiopteris* may be said to present a simpler structure than that of any of the other Marattiaceae. In fact it still retains at maturity a stage rapidly passed through by the young plants of the other genera. It has been shown that in young plants of *Angiopteris*, *Marattia*, and *Danaea*¹ there is a stage with a single internal strand only, which itself fuses with each leaf-gap margin; just as in the mature stem of *Archangiopteris*. The mature stem of *Kaulfussia*, although it only contains a single internal strand, is a stage in advance of *Archangiopteris*, for here the internal strand runs freely and continuously through the central ground-tissue, and is only connected with the leaf-gap margin by means of branches.

The vascular system of the petiole is also comparatively simple both in *Archangiopteris* and *Kaulfussia*, the arrangement of the strands being based upon a simple horseshoe-shaped curve comparable to that typical for the Cyatheaceae and Polypodiaceae. It is clear also that the further increase in complexity that occurs is not due to any alterations in the outline of this curve, but to the formation of an altogether new system of internal strands which arise from the inside of those of the original curve.

Miss Shove (l. c.) has stated that in the base of the petiole of *Angiopteris* the internal strands are seen to arise from the outer ring, and the same thing has been said of *Marattia fraxinea* by MM. Bertrand and Cornaille (l. c.). There is very little doubt, therefore, that in these genera also the outer ring of strands represents the same original curve, which remains comparatively simple throughout the order. It is certain also that the internal petiolar strands have no direct connexion with those in the stem. The initial appearance of these strands probably took place in the basal region of the petiole, and it is suggested that *Archangiopteris* and *Kaulfussia* represent an early stage in which they are still confined to the basal pulvinus. The more or less internal strands that occur in the upper part of the petiole of these two plants really belong to the original horseshoe-shaped curve, and are not to be confused with those found in the basal pulvinus, nor with those that occur practically throughout the petiole in *Marattia* and *Angiopteris*. With this exception my observations are thoroughly in accord with the conclusion arrived at by Bertrand and Cornaille—that these internal petiolar strands of the Marattiaceae are not strictly comparable with anything to be found in the petioles of the leptosporangiate Ferns, nor, in my opinion, are they comparable with the internal strand found in the petiole of *Helminthostachys*.

There is no essential difference between the Marattiales and the Filicales as regards the origin and final distribution of the vascular strands

¹ Farmer and Hill, l. c., p. 376. Brebner, l. c., p. 530. Jeffrey, 'The Structure and Development of the stem in the Pteridophyta and Gymnosperms,' Phil. Trans., vol. 195, p. 120, 1902.

in the stem, nor as regards the primitive vascular arrangement in the petiole. At the same time the Marattiales possess a number of distinctive anatomical features of considerable value; such as (1) the centrifugal differentiation of the protophloem, (2) the exceptional nature of the internal vascular strands in the petiole, (3) the special method by which the petiolar branches are supplied with vascular tissue, and (4) the fact that roots arise upon the internal strands in the stem. The first of these characters is quite without parallel in either the Ophioglossales or the Filicales. It is true that a centrifugal development has been observed in the phloem of *Todea* by Seward and Ford¹; I have also seen the same thing in *Osmunda regalis*, where it is quite clear that the so-called protophloem is still undifferentiated when the sieve-tubes of the rest of the phloem lying within it are fully formed. But this state of affairs is not really comparable with that in the Marattiaceae, because the 'protophloem' in the Osmundaceae is clearly derived from the same layer of meristematic cells which also gives rise to the pericycle; and further, its elements, even when mature, are not vertically elongated like sieve-tubes, but tangentially, like the cells of the pericycle. In fact these elements may be regarded as specialized inner layers of the pericycle, and it may be said that the Osmundaceae have no true protophloem at all. Again, in the phloem of *Aneimia* and *Schizaea* there is no clear distinction into protophloem and metaphloem, but all the sieve-tubes remain functional throughout; in this case, however, the whole phloem has more the appearance of protophloem than of metaphloem. In relation to this it is suggestive to note that Boodle² is of the opinion that in *Schizaea digitata*, the whole of the phloem is derived from the same meristematic layer that also gives rise to the pericycle and endodermis. From some observations that I made on *Aneimia hirta* it appears that the same view holds good for this plant also. It is, indeed, hardly possible at present to decide upon the proper morphological value to be given to these differences in the constitution of the phloem, but at the same time the unique position of the protophloem in the Marattiaceae seems to me to be of so great importance that, until some idea of its real meaning has been obtained, the other anatomical evidence cannot with advantage be brought to bear upon the question of the relationship of the order.

The sori and sporangia on the one fertile leaf of the specimen were examined by Professor Bower, who permits me to add the following account.

'The sporangia correspond very closely to those of *Angiopteris*; they are somewhat more elongated and pointed. Cut transversely, they show the same differentiation of the three- to four-layered wall. Comparing my

¹ 'The Anatomy of *Todea*,' &c., Trans. Linn. Soc., 2nd Series, vol. vi, p. 237, 1903.

² 'Comparative Anatomy of the Hymenophyllaceae,' &c., Annals of Botany, vol. xiv, No. lviii, p. 377, 1901.

figure of *Angiopteris* (Studies, III, Pl. II, Fig. 77) and the description (p. 55), there are the same large, turgid, thin-walled brown cells on the peripheral side; laterally the same bands of deep prismatic lignified cells; while the central face, which is thin-walled, bears in a median position the fissure of dehiscence. A transverse section from the distal end of the sporangium shows the narrow bridge of indurated tissue extending from the lateral bands just described across the apex (compare l. c., Fig. 76); and thus the arch of indurated tissue or "annulus" is complete over the apex, as it is in *Angiopteris*, and the mechanism of dehiscence will be the same. Longitudinal sections, i. e. vertically through the sorus, show a structure similar to that seen (l. c., Fig. 72) for *Angiopteris*, with a slight difference of outline, *Archangiopteris* being more pointed at the apex.

'There can be no doubt of the near affinity to *Angiopteris*. There may, however, be some difference of opinion as to the phyletic relations of these two Ferns. So far as a conclusion can be drawn from the outline of the sorus, I should be disposed to look upon the long sorus of *Archangiopteris* as a derivative and secondary condition; while the compact, almost circular sorus of *Angiopteris*, corresponding as it does with most of the modern Marattiaceae, and with the very large majority of Palaeozoic Ferns, would seem to be the more primitive type. It may be that the extension of the sorus to the dimensions now seen in *Archangiopteris* was an incident of relatively late occurrence.'

EXPLANATION OF FIGURES IN PLATE X.

Illustrating Mr. Gwynne-Vaughan's paper on '*Archangiopteris* and other Marattiaceae.'

Figs. 1 and 2. Views of the specimen of *Archangiopteris Henryi* seen from opposite sides (Natural size.)

Fig. 3. Adaxial aspect of the youngest leaf seen in Fig. 2, showing the stipular appendages. *w.*, wings of stipule; *com.*, transverse commissure; the mark *x* indicates the points at which the arrested apices may be found.

Fig. 4. Adaxial aspect of the base of the upper leaf seen in Figs. 1 and 2. Lettering as in Fig. 3.

Fig. 5. Diagrammatic representation of the end of a rhizome of *Kaulfussia*, showing stipular appendages. Lettering as in Fig. 3.

Fig. 6. *Archangiopteris*. Transverse section of stem; the departing traces of two leaves are shown. *s. s.*, meristeles of stem; *int. s.*, internal strand; *l. t.*, leaf-trace; *r.*, root stele. The dotted line indicates the limit of the root cortex.

Fig. 7. *Archangiopteris*. Transverse section of the stem in a region where no internal strand is present. Lettering as in Fig. 6.

Fig. 8. *Kaulfussia*. Represents the vascular system at the very base of a petiole. The letters *a. b. c. d. e.* indicate the internal strands. In this and in all succeeding figures the courses traversed by these strands are indicated by the fine continuous lines. The dotted line joins up the strands that form the typical curve, the terminal strands of which are marked with an *x*. The arrow-heads show the direction of the protoxylems.

Fig. 9. *Kaulfussia*. The vascular system in the lower part of another petiole. *s.* is the transverse suture passing across between the two terminal strands.

Fig. 10. *Kaulfussia*. The vascular system in the upper part of a third petiole.

Figs. 11-14. *Archangiopteris*. The vascular system at successively higher levels in the basal pulvinus of the same petiole. *a. b.*, internal strands.

Figs. 15 and 16. *Archangiopteris*. The vascular system at two succeeding levels in the petiole above the basal pulvinus.

Fig. 17. *Archangiopteris*. The vascular system in the rachis just below the insertion of a pinna. *p. tr.*, main strand for the pinna; *st.*, strand which passes out into pinna from end of terminal incurved strand.

D.T.G.V. del.

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