Studies in the Phylogeny of the Filicales.

V. *Cheiropleuria bicuspis* (Bl.), Presl, and certain other related Ferns.

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With Plates XXIV and XXV and nineteen Figures in the Text.

THE Fern which now passes under the name of *Cheiropleuria bicuspis* (Bl.), Presl, was first noted by Blume in 1828 (Fil. Jav., p. 125, and Fl. Jav. ii. 175, Tab. LXVIII, B). He referred it to *Polypodium*, as *P. bicuspe*, Bl. It was subsequently described and figured by Sir William Hooker in the London Journal of Botany, vol. v, p. 193 (1846), with Plates VII and VIII. His specimens were collected by Thomas Lobb for Mr. Veitch, in the mountain tops of Java, and Sir William Hooker designated it as a splendid new species of an Acrostichoid Fern, ranking it with the genus *Gymnopteris*, Bernhardt, as *G. vespertilio*. But in 1849 it was constituted the sole representative of a new genus, *Cheiropleuria*, by Presl. It will be seen from what follows that it is properly ranked as the only known species of a substantive genus, and that the references to *Acrostichum* and *Polypodium* would only be possible in the older and most extended sense of those genera.

The Fern is rather widely distributed in the Malayan region. It is recorded from Malacca, Java, Sumatra, New Guinea, Borneo, the Philippines, South Annam, Formosa, and it even extends beyond the tropic to Oshima, the northernmost of the Loo Choo Islands (Christ, Geogr. der Farne, p. 164). It is moreover especially worthy of remark that it is commonly associated with *Dipteris conjugata*. This identity of distribution in Ferns which bear such a similarity as will be shown below, may probably be more than a mere coincidence.

After more than one unsuccessful attempt to obtain supplies of material for the examination of this peculiar Fern, which has never yet been submitted to anatomical and developmental study, Professor Bayley Balfour kindly passed on my wish for specimens to the Rajah of Sarawak.

This led to correspondence with the Director of the Museum at Sarawak, and with only very short delay I received from him a plentiful supply of specimens, both dry, and in spirit. They were obtained by him on a collecting trip to Mount Poi, Sarawak, in April, 1913. (See J. C. Moulton, B.Sc., F.R.G.S., Journ. Straits Branch R. A. Soc., No. 65, 1913.) From these it has been possible to ascertain all the essential facts of structure, though naturally certain developmental details must be left aside. In particular the gametophyte is still unknown. My hearty thanks are due to all those who helped in obtaining this material for observation, and especially to Mr. Moulton himself.

The best known of the published figures of the plant is that of Hooker, which is quoted by Diels (E. & P., i. 4, p. 337, Fig. 175). But more recently a photograph has been published by Christ (Geogr. der Farne, p. 18, Fig. 7), which gives a good idea of the appearance of the whole plant. There seems, however, to be some uncertainty as to the habit of this Fern, which probably arises from its being rather variable. The axis is elongated, and the internodes between the alternate leaves of various length (Fig. 1). It is densely clothed with silky yellow hairs, and bears many dark brown roots. Partly from the angles at which the petioles come off, and partly from the absence of soil from some of these rhizomes, it seems probable that some at least of them were climbers, others creeping on the ground. This would accord with the earlier descriptions. For Hooker (Sp. Fil. v, p. 272) mentions that in Java it is found 'on trees'. Diels (E. & P., i. 4, p. 336) describes it as 'epiphytic or terrestrial'; while van Rosenburgh (Malayan Ferns, 1909, p. 732), who probably has had the best opportunities for personal observation of it in nature, describes it as 'creeping or subscandent'. The material I have examined would accord best with this last description.

Dichotomous branching of the rhizome has not been observed. Lateral branches are, however, frequent; they arise on the abaxial face of the bases of certain leaves, but not of all (Pl. XXV, Fig. 2). The position is similar to that of the branches observed in *Lophosoria* and *Metaxya*, and a similar position 'on the hinder side of the stipes of each of the erect fronds' has been ascribed to like buds in *Platynerium alaicorne* (Higher Cryptogamia, p. 252). On the other hand, in *Matonia* (Seward, l.c., pp. 174 and 187, Fig. 6) the branching is dichotomous, as it is also in *Dipteris conjugata* (Seward, l.c., p. 494); and I find the same in *Dipteris Lobbiana*. Other modes of branching have not been observed in these Ferns. These data are in themselves interesting in their relation to the views of Velenovsky and of Schoute. The matter will be considered later, when the anatomical relations of the parts have been described.

The leaves are strongly dimorphic. The sterile have a firm leathery lamina borne on a thin wiry petiole of variable length, up to as much as a foot. The fertile leaves are taller, and bear a narrower lamina;

its under surface is covered by continuous soral masses on either side of the well-marked midrib. It was this feature which Hooker recognized as 'Acrostichoid'. There is a good deal of variety in the outline of the lamina. Hooker was aware of this; he describes the leaves as 'quite entire and tricostate, or sub-orbiculate and deeply bicuspidate' (l. c., p. 271). He notes that specimens from the Loo Choo Islands were mostly with quite entire fronds; and these constituted the var. *b*, *integrifolia*, Eat. Both forms of leaf may be seen on the same plant (Christ, l. c., p. 18, Fig. 7), a point frequently met with among the Bornean specimens, in which also the entire leaves were in the majority. But they also showed examples of greater complexity of form, such as are represented in the photographs Figs. 4, 5. Comparison points towards the conclusion that the more complex outlines are liable to occur in the leaves of the more mature plants, but there is no constant evidence of an ontogenetic progression. Fig. 1 shows to the right a relatively weak plant, with all its leaves simple; to the left is a larger plant with two sterile and one fertile leaf, showing the difference in proportion of the two types. Of the sterile leaves one is ovate with a single cusp, the other is broadly two-lobed. On other plants it was not an uncommon thing to find three distal lobes united below into a broadly ovate lamina. Some plants, however, showed regularly the leaf-form depicted in Hooker's often quoted figure; this is shown in Fig. 3; but these were in a distinct minority in the specimens from Borneo. Hooker's figure, together with the specific name *bicuspe*, has in fact stereotyped much too strongly a form of leaf which is far from being general for the species. Other plants showed still more complex outlines, with irregular dichotomous branching. Thus in Fig. 4, one of the leaves is of the two-cusped type, but in the other both lobes have branched a second time. This condition is shown again in a more complete example in Fig. 5.

Comparing this last leaf with leaves of *Dipteris conjugata* it is at once evident that they conform to the same type, a conclusion which the venation also confirms. On the other hand, a comparison may also be made with the fertile type of leaf of *Platynerium*, and Fig. 6 shows one of these of *P. Hillii*, which corresponds in the number and relation of its dichotomies very closely with that of *Cheiropleuria* in Fig. 5. The chief difference lies in the continuance of the broad expansion downwards, so that there is no distinct petiole. But this is a condition which is still more pronounced in the nest-leaves of *Platynerium*, which have no petiole at all.

The essential features of the venation are already known from the drawings of Hooker, quoted by Diels (E. & P., i. 4, Fig. 175). But their arrangement at the base of the lamina is shown in Text-fig. 1, drawn from a leaf of *Cheiropleuria* made transparent by *eau de Favelle*, and mounted in Canada balsam. The main veins diverge in two groups right and left of the median line, while distally they show bifurcations. An examination of

their mutual relations at the base of the lamina shows that they are on a plan essentially similar to that in *Matonia* (compare Seward, l. c., pp. 175-6, and Fig. 1). It may then be concluded that the leaf in *Cheiropleuria* is a condensed and webbed example of the Matonioid type. When it is further remembered how the stages of progressive webbing are illustrated in the genus *Dipteris*, as well as in the related fossils *Clathropteris* and *Hausmannia*, it becomes clear that this is the true interpretation of the peculiar and variable forms of lamina seen in *Cheiropleuria*. (Com-

TEXT-FIG. 1. Trace of the vascular system at the base of the lamina of a large sterile leaf of *Cheiropleuria*, showing the pedate relation of the main veins, after the manner of *Matonia*. The smaller veins show the 'Venatio Anaxeti'. $\times 4$.

pare Seward, Phil. Trans. 194, Pl. 48, also Land Flora, p. 618. Also Seward, Fossil Plants, ii, pp. 386-94.)

Between the main veins there is a reticulum, which is of the type described as 'Venatio Anaxeti' (Lueresen, Rab. Krypt.-Fl., iii, pp. 17-18, Fig. 22). This is the type also for *Dipteris conjugata* and *Lobbiana* (Text-figs. 2, 2 bis), and the same type, though in a more compact form, is seen in *Platycerium* (Text-figs. 13, 14).

The venation of the leaves of young plants of the Ferns above named would appear to present a promising line for further comparison. Fortunately, among the material of *Dipteris conjugata* collected by Professor Lang on the Malay Peninsula, some plants have been found which were

actually seedlings, or else stunted forms which retained or repeated the juvenile characters. These served for comparison with the youngest leaves available of *Cheiropleuria*, or the seedling leaves of *Platycerium*. Text-figs. 3, *a-d* are from *Dipteris conjugata*. They show that the reticulate

TEXT-FIG. 2. Part of a pinna of *Dipteris Lobbiana*, showing the venation, and its relation to the sori. $\times 6$.

TEXT-FIG. 2 bis. Part of the lamina of *Dipteris conjugata*, including two of the main veins, and showing the venation between them, and its relation to the sori. $\times 6$.

a.

b.

c.

d.

TEXT-FIGS. 3, *a-d*. Juvenile leaves of *Dipteris conjugata*, showing successive states of complexity of outline, and of venation. $\times 6$.

venation characteristic of the mature plant appears in the young leaves. The chief interest centres in the main veins. There is an apparent bifurcation in each at the upper end of the petiole; the two chief veins thus established may fork again (Figs. *b*, *d*), or their branchings may appear less regular. For purposes of comparison attention should be fixed upon the areolae which lie between the limbs of the first forking. In the smallest leaves (Figs. *a*, *c*) these areolae are less regularly defined, but in the more advanced (Figs. *b*, *d*) they are more definitely of square or polygonal outline, each with a venation within it ending in blind twigs. They present a very regular appearance in Fig. *d*. It may further be noted that as the forkings are repeated, in cases where the lateral lobes are strongly developed, there is a tendency towards a pedate development of the main venation. This is already recognizable in Fig. *d*, and it may become more marked in older leaves.

Comparing with these leaves the youngest leaf available of *Cheiropleuria* (Text-fig. 4), the outline of the lamina is here entire, there being no indication of bifurcation. But as in *D. conjugata* there is an apparent bifurcation of the main vein at the top of the petiole; the areolae between its shanks are of exactly the same type as in Fig. 3, *d*, while the main veins give off further branchings right and left, which correspond essentially to those seen in *Dipteris conjugata*. The similarity of the two is patent, allowing for the difference in outline of the leaves. A further step is to compare the young leaf of *Platynerium*. The young plants of *P. Veitchii* used were probably raised from vegetative budding. One of the youngest leaves (as yet undifferentiated as of the 'nest' or 'fertile' type) was removed. It is sessile, for which fact allowance must be made in the comparison. Its outline is very similar to that of the young lamina of *Cheiropleuria*, and its venation is obviously the same. Two main veins enter the base of the leaf, and behave in all essentials like those in *Cheiropleuria*. Similar areolae lie between them, but the venation within each of the areolae is of a simpler type (Text-fig. 5). This comparison of the young leaves shows that they all conform very closely to one type in their venation. It may be held as supporting the relationship of the three genera, which will be found to be strengthened by various other lines of similarity.

Comparison may be based upon the dermal appendages. Already Seward has noted the multicellular hairs on the rhizome of *Matonia* (l. c., p. 190), and has figured them (Pl. 19, Fig. 32). They appear to be all unbranched, and of the same type; and they form a dense covering. Each has a long setaceous indurated distal part, of two to ten or twelve cells, and a basal region of shorter thinner-walled cells, which suggest an intercalary growth at the base. Seward has also described for all the four species of *Dipteris* how the rhizome is covered by stiff brown scales, forming a dense felt (l. c., p. 493, Pl. 49, Figs. 29, 30, 34, 36). In the young state they are

simple hairs; but later the distal cells elongate and become brown and indurated, while the proximal cells remain short and thin-walled, and divide by longitudinal walls, so as to form a considerable solid base. All the hairs are here again unbranched, but the marginal cells project at their upper ends as blunt bosses, giving the margin a deeply sinuous outline. Thus their structure appears to be an advance upon the simple type of hair seen in *Matonia*. The difference is due to the longitudinal divisions at the base, but still the type of hair is essentially the same. In *Cheiropleuria* the type of hair conforms more nearly to that of *Matonia* than to that of *Dipteris*. Each is long and unbranched, and is always composed of

TEXT-FIG. 4. A juvenile leaf of *Cheiropleuria* showing the venation for comparison with *Dipteris conjugata*. $\times 3$.

TEXT-FIG. 5. A juvenile leaf of *Platycerium Veitchii*, for comparison with Text-Figs. 3 and 4. $\times 3$.

a simple filament of cells. But the induration is much less pronounced than that in either *Matonia* or *Dipteris*. Each may consist of as many as twenty or thirty cells. The type of hair seen in *Cheiropleuria* is thus probably as primitive as in any of these Ferns. On the other hand, in *Platycerium* the leaves, while young, and especially the fertile regions, are very efficiently covered by the well-known 'indumentum' of tufted hairs. Each hair consists of a stalk, with a multicellular distal star of about six rays. Clearly this is a more advanced state than that of any of the Ferns mentioned above.

A more complex type of dermal appendage is seen on the rhizome of *Platycerium*. In *P. alcinorne* the apical bud is densely covered with scales,

which are long and narrow, with a dark brown central rib. The distal end thins out to an acuminate apex, and may be terminated by a glandular cell. The midrib may be more than one layer of cells in thickness, and is composed of oblong cells with thickened brown walls, similar in their character to those forming the whole upper part of the hair in *Dipteris*. Laterally the appendage is flattened out into flaps of thin-walled cells, a single layer in thickness, while at the margins are borne fringes of hairs, each terminated by a glandular cell. At the base of the scale there remains for a time an active formative zone of delicate meristematic cells, a condition which compares with what is seen in *Matonia*, *Dipteris*, and *Cheiropleuria*. The whole scale is thus much more elaborate than in any of the preceding Ferns. But it may be held as a possible derivative of the type seen in *Dipteris*. A widening of the margins into thin lateral flaps, an elongation of the bluntly projecting marginal cells of *Dipteris* into multicellular hairs, and the appearance of terminal glandular cells upon them would convert the type of hair seen in *Dipteris* into the scale of the rhizome of *Platynerium*. And both are possible derivatives of the simple hair of *Matonia*, or of *Cheiropleuria*.

ANATOMY.

I am not aware of any detailed account having yet been given of the internal structure of *Cheiropleuria*. Christ (Farnkräuter, p. 128) makes a statement in his generic description which suggests a solenostelic structure; but none of my specimens confirms this. Sections of the rhizome, at whatever level or age of the specimen, show a protostelic structure. The stele is of considerable size, and in structure and in form it resembles closely that of the protostelic *Gleichenias*, such as *G. flabellata*, or *dichotoma* (Pl. XXIV, Figs. 8–12). It will then be unnecessary to describe it in detail. But it is to be noted that the protoxylem which enters from the leaf as a double strand (Fig. 11) merges at once on entry into a single strand (Figs. 10, 12), and can be traced only for a very short distance downwards below the point of entry. Accordingly, as a rule, only one such strand can be recognized in a given transverse section of the protostele. The xylem consists of rather wide tracheides, interspersed with parenchyma, which is more plentiful towards the centre of the stele. The band of phloem is characterized by narrow sieve-tubes, while the rather prominent proto-phloem is composed of specially small elements, the walls of which appear brown under safranin-haematoxylin. Outside this are about three layers of pericycle, and finally the endodermis. This delimits the stele from the broad peripheral cortex, of which the outermost layers are brown and sclerosed.

The leaf-traces are seen to originate from this protostele alternately right and left of the median line, on the upper side of the creeping or

ascending stele. First a group of small protoxylem tracheides appears some three or four layers below the outer limit of the xylem; opposite it the outer contour of the xylem projects as a rounded hump. Soon parenchyma cells aggregate internally to the protoxylem; the outer xylem then projects still more, and a loop of xylem with the protoxylem lying centrally within it is formed (Figs. 10, 12). This body of tissue continues to move outwards, some of the internally-lying tracheides following it, while laterally a constriction is formed, equally as a rule on both sides. As it deepens, the leaf-trace becomes gradually shut off from the stele by the intruding phloem and sheaths. On the separation of its xylem from that of the stele, it consists of an oval tract of tissue, enclosing within a complete ring of metaxylem a parenchymatous island, and on the peripheral limit of this lies the protoxylem, which has meanwhile divided into two groups (Fig. 11). Subsequently the trace becomes completely abstricted from the stele. It very soon opens out by separation of the metaxylem in a median plane, the lateral portions withdrawing, till the whole leaf-trace takes the form of a crescent, as in the cases of *Matonia* and *Dipteris conjugata*; the differences are that the leaf-trace is here narrower, and the protoxylem groups are only two in number, while the margins of the xylem are less strongly curved; there is also an enlargement of the xylem in the median plane. But this condition is only maintained for a very short distance. A median constriction soon appears (Fig. 13), and the xylem divides through the median enlargement above noted. The whole leaf-trace finally divides into two equal halves, each with its own protoxylem (Fig. 14), and in this state it passes out into the base of the petiole.

In the mere fact that the leaf-trace is at first undivided, *Cheiropteris* corresponds to *Gleichenia*, *Matonia*, and *Dipteris conjugata*. In its origination from a protostele it compares with all the simpler *Gleichenias*, and differs from *Matonia* and *Dipteris*, except in their seedling stage. It has been shown by Tansley and Miss Lulham (Ann. of Bot., vol. xix, p. 496) that the young seedling of *Matonia* has a protostelic axis. The same has been shown to be the case of *Dipteris Lobbiana*, by Miss de Bruyn (Ann. of Bot., vol. xxv, p. 761). The young plants of *D. conjugata* were also examined by her, but the material did not suffice for demonstration of the earliest phases. This deficiency has, however, been supplied by young plants of that species collected by Professor Lang, on the Malay Peninsula, and the section seen in Fig. 15 shows the protostele, from which a leaf-trace is just passing off. It may be taken then as usual for *Matonia* and *Dipteris* that the axis is at first protostelic, and that it passes through a '*Lindsaya* stage' to solenostely of a more or less complicated type. Thus it is only with the youngest stages of these Ferns that the mature condition of *Cheiropleuria* can be compared. It has retained throughout its life the primitive state of *Gleichenia*.

But though *Gleichenia*, *Matonia*, and *Cheiropleuria* all agree in having an undivided leaf-trace, that is not a constant character of the genus *Dipteris*. It is so in *D. conjugata*, as has been shown by Seward (Phil. Trans., vol. 194, p. 498, Pl. 47, Fig. 4). But already Miss de Bruyn has observed that in the young plant of *D. Lobbiana* the leaf-trace comes off as two separate strands (l. c., p. 769, Pl. 57, Figs. 9–12). In mature plants it may be more complex still, and Text-figs. 6, *a–f* show by a succession of sections from below upwards how the trace arises. In *a*, the solenostele is about to open to form the foliar gap; *b* shows how, after opening, the margins are deflected outwards, while *c* shows how two strands have separated from the stele, and one of them has already divided;

TEXT-FIGS. 6, *a–f*. Successive transverse sections, from below upwards, showing the separation of the leaf-trace from the solenostele in *Dipteris Lobbiana*. $\times 3$.

in *d* and *e*, both have divided, and the leaf-trace consists of four strands, in which state it passes out into the petiole: very shortly the solenostele again closes, as shown in *f*.

These facts are here adduced because they have an interesting relation to what is seen in *Cheiropleuria* on the one hand, and in *Platycerium* on the other. In the former the leaf-trace comes off, it is true, as a single strand; but it divides almost at once, in fact before it has traversed the cortex of the axis. In this respect it is in advance of the condition seen in *Gleichenia*, *Matonia*, and *Dipteris conjugata*. But *Dipteris Lobbiana* is again more advanced, since the trace originates as two separate strands, which divide again before the trace leaves the cortex of the axis. On the other hand, in the young plant of *Platycerium* Miss Allison has shown that the leaf-trace arises as two strands; but in the case of the mature leaf it is much more complex, consisting from the first, it may be, of a large number of separate strands (compare Text-fig. 9, below, p. 508). Thus in the matter of

complexity of the leaf-trace these Ferns may be held as forming a series, progressive from the simple condition seen in the simpler *Gleichenias*, and leading to the state seen in *Platyserium*. It will be seen later how far this runs parallel with seriation of them according to other characters.

It has been seen that branches are given off from the bases of many of the leaves, on the abaxial side (Fig. 1). In resolving the question of the nature of the branching, it is important to know the vascular connexions of the bud. This is shown for a given case of *Cheiropleuria* by the sections *a-e* of Text-fig. 7, which read from below upwards. The related leaf-trace originates from the axial stele in the normal way, and the protoxylem divides as usual as it enters the leaf-trace into two strands, which take the usual position. But the proportions of the leaf-trace strand are different from the normal. (Compare *a*, which is normal, with *b*, which bears a bud.) Its outline is

TEXT-FIG. 7. Transverse section of the rhizome of *Cheiropleuria*, to show the relations of the leaf-trace and the lateral bud to the stele of the axis. *a* shows the relation of two normal leaf-traces, where no bud is formed. *b-e* show successive sections from below upwards, in the case of a leaf-trace where a lateral bud is borne on the abaxial side of the leaf-trace. $\times 3$.

nearly circular (*b*), owing to an enlargement of the xylem on the abaxial side. Later the trace opens out, as in the normal leaf, on its adaxial face; then, first on the one side and then on the other, lateral hook-like processes are formed (*b*, *c*). These soon become detached as the two components of the leaf-trace, and as such enter the petiole. The large residuum of vascular tissue, lying in the median position with regard to the leaf, passes out directly as the stele of the lateral axis (*d*, *e*). The vascular relations are here essentially the same as those seen in *Lophosoria*, or *Metaxya*. As in those Ferns, so here in *Cheiropleuria*, the vascular connexions indicate that the lateral axis is an accessory appendage to the leaf. It would be difficult to see in them any evidence supporting the view that such branches are a result of some modified bifurcation. The conclusion will then be that dichotomous branching is in abeyance in *Cheiropleuria*, and that a formation of adventitious buds at the leaf-bases is the rule. This conclusion is, however, provisional, pending a searching examination of the ultimate

genesis of the bud, whether it be in relation to the apex of the shoot, or is really adventitious.

We have seen that in *Cheiropleuria* two strands of the leaf-trace enter the petiole: they maintain their identity for some distance (Text-fig. 8, i). The following details relate to a special case, and may be open to variation. About 3 inches above the base of the petiole the two strands divide, each into two (ii, iii); the four resulting strands pursue their course thus for about 2–3 inches further (iii), when those nearest the median line fuse (iv); this takes place about 2–3 inches from the base of the lamina. Later they again separate, the former arrangement of the four strands being resumed (v). The marginal strands then bifurcate (vi), to give six strands, the further course of which may be followed in the superficial views of the base of the lamina.

TEXT-FIGS. 8, i-vi. Successive transverse sections of the petiole of a sterile leaf of *Cheiropleuria*—i, at the base; ii, about 3 inches up; iii, 4 inches; iv, 6 inches; v, 8 inches; vi, 9 inches from base. Figs. vii, viii, are from a fertile leaf, at levels corresponding to Figs. v, vi of the sterile leaf. $\times 8$.

A comparison may be drawn with the petiole of *Dipteris Lobbiana*, as regards this behaviour of the strands of the petiole. It has been seen that the leaf-trace there also originates as two strands, which at once divide; so that four strands pass up the petiole (Text-fig. 6); thus the condition comes to be virtually the same as that seen in Text-fig. 8, iii. But at some point about two-thirds the distance up the petiole, the pairs of strands fuse again, and the two resulting strands have an obvious relation to the bifurcation of the lamina.

Such division of strands as this in the petiole of *Dipteris Lobbiana*, and in *Cheiropleuria*, and the subsequent fusion of the strands so as to close the gap formed, is only a special case of those arrangements commonly occurring in the petioles of Ferns, and giving the character of a divided leaf-trace. The point is most obvious in those cases where the leaf-trace is in other species of the genus an undivided strand, as in *Dipteris Lobbiana* and *Plagiogyria semicordata* (Ann. of Bot., xxiv, p. 431, Text-fig. 2). Such cases as these, occurring as they do without any relation to the pinnae or their pinna-traces, may be held to be 'perforations' of the petiolar supply, comparable in their nature to the 'perforations' so often seen in relatively advanced

Ferns in the axial stele.¹ Their occurrence in the Dipterid affinity has a special interest, in connexion with the comparisons with *Platycerium* to be instituted below.

In the case of the fertile leaf of *Cheiropleuria*, the outline of which is simple and narrow, the fertile region has as a rule a marked midrib, while two thickened ridges mark the margins. The extensive soral area covers the more or less extensive tracts within these, right and left of the midrib. A transverse section of the fertile lamina then shows in outline as in Text-fig. 8, viii. The difference between this and the sterile lamina is more apparent than real, as is seen if the vascular system is followed from below upwards. The petiole of a sporophyll shows at a middle level a condition as in (iii), and (iv) of the sterile; but above that level, instead of the fused median strand dividing again, as in the sterile petiole, it continues its fused course directly into the fertile lamina, where it forms the midrib (Text-fig. 8, vii, viii). A comparison of the result may be drawn between this condition of the fertile lamina and that of the leaf-segments in *Dipteris quinquefurcata*, or *Lobbiana* (Seward, l.c., Figs. 18, 24; or Land-Flora, Figs. 343-5). If we imagine the branched sporophyll of either of these species represented only by a single segment, it would have substantially the vascular structure of the fertile lamina of *Cheiropleuria*.

The venation of the distal end of the sporophyll is worthy of note, as in some degree harmonizing the difference between that of the sterile and fertile leaves. The soral areas frequently stop short of the extreme tip, which may then extend for some distance as a narrow beak. It may be traversed by a midrib with lateral reticulate branchings; or it may show two marginal ribs, with reticulations between them. Or, again, various other irregularities may be seen, including loops of the main veins quite comparable with those often found in *Dipteris*. All these facts appear to harmonize with the idea of the leaf of *Cheiropleuria* being a webbed and simplified example of the fundamental type seen in *Matonia* and *Dipteris*.

Platycerium.

As it will be necessary later to draw comparisons between *Cheiropleuria* and *Platycerium*, genera which have already been placed in near relation to one another by various writers, it will be convenient to introduce here certain facts relating especially to the vascular system of the latter genus. The similarity of the venation of the young leaves of *Platycerium* to that of *Cheiropleuria* and *Dipteris* has already been noted. Putting aside the remarkable dimorphism of the leaves in the genus, which is related to its epiphytic habit, the outline of the fertile leaves of *Platycerium* is often very closely conformable to that seen in the genera named. As an

¹ Compare Tansley, *The Filicinean Vascular System*, p. 65.

example, the leaf of *P. Hillii* shown in Fig. 6 might be very nearly matched by the more complex leaves of *Cheiropleuria*; at the same time it is impossible to miss the resemblance which they also show to so distant a type as *Ophioglossum palmatum* (compare Land-Flora, Fig. 238, p. 436). It is also to be noted that the leaves, both of *Platycerium* and of *Cheiropleuria* and of *Dipteris*, show the 'Venatio Anaxeti'. Accordingly, a comparison of the vascular system of their shoots should present points of interest.

Miss Allison has lately described the vascular system in the rhizome of certain species of *Platycerium* (New Phyt., vol. xii, p. 311, &c.). It was found that in *Pl. alcorni*, one of the less robust species, the vascular

TEXT-FIG. 9. A. Sections of rhizome of *Platycerium alcorni*, showing relation of two leaf-traces to the ring of meristemes of the axis. B. similar sections from *Platycerium aethiopicum*, showing the greater complexity with numerous medullary strands. After Miss Allison, New Phytologist, 1914.

system of the axis is a simple dictyostele, but very highly perforated (Text-fig. 9, A); on the other hand, in *Pl. aethiopicum*, one of the most robust species, there is in addition a very complex medullary system (Text-fig. 9, B). As Miss Allison has pointed out, a comparison may be drawn with *Matonia* and *Dipteris* thus: 'Anatomically *Dipteris* is relatively simple; its simple solenostele is replaced by several concentric solenostelic cylinders in *Matonia*. In many other phyletic lines it may be seen how the solenostele becomes broken up into a dictyostele. It would be quite consistent with the structural facts here described, if we were to consider *Platycerium* with its complicated dictyostele as the dictyostelic type of a series of which *Dipteris* and *Matonia* are the solenostelic types' (l. c., p. 321). This seems to be a very reasonable interpretation of the facts so far as known; widespread 'perforation' would be an important factor in leading to the conditions described for *Platycerium*. Moreover, the fact that such perforations do occur in the petiole of *Dipteris Lobbiana* and of *Cheiropleuria* have a special

interest in this connexion. If the modifications there seen were extended into the solenosteles of the type of *Dipteris*, the state seen in the axis of *Pl. alcicorne* would be the result; or into the axis of the type of *Matonia*, something like what is seen in *Pl. aethiopicum* would appear.

It has already been noted that in the young leaves of *Platyserium* the leaf-trace consists of only two strands. But in the mature state the trace comes off from the dictyostele of the axis as a number of distinct strands (*Pl. alcicorne*), while in the more complex case where there is a medullary system in the axis, this also takes its share in the organization of the trace (*Pl. aethiopicum*) [New Phyt., vol. xii, p. 317]. The constitution and further

TEXT-FIG. 10, i-xiii. Successive transverse sections of the petiole of *Platyserium Hillii*, showing the disposition of the vascular strands. After the stage shown in xiii, the midrib settles down to three strong strands disposed in the plane of the leaf-expansion. $\times 3$.

behaviour of the trace as it passes upwards into the leaf has been followed in the case of *Pl. Hillii*, a form nearly related to *Pl. alcicorne*. The actual leaf examined was one of the fertile type, as shown in Fig. 6. Externally there is in the stalk an appearance as of a single central strand, or midrib, which throws off smaller veins right and left. But transverse sections show that the midrib is traversed not by one strand, but by a number of them, disposed in a circle (Text-fig. 10); and the condition is not unlike that seen in transverse sections of the leaf-stalk of *Ophioglossum palmatum* (Land Flora, p. 463, Fig. 259).

Starting from the base of the petiole, the strands are seen at first to be disposed in a simple circle (Text-fig. 10, i); their number varies, owing to splittings and fusions, which extend even across the adaxial face of the

circle (iii-iv, v-vi, vii-viii). From this circle come off at intervals strands of varying size, right and left. A comparison of Text-fig. 10, i-xiii, illustrates the method, and the way in which these spread, with further branchings and fusions, to form the reticulum of the flattened wings. As these wings expand upwards, the midrib gradually diminishes, and its strands simplify in number and arrangement, till with final fusions of abaxial and adaxial strands (xii) the circle is reduced to a single plane. After this the reticulum follows the course easily seen from the surface view. There is some similarity between this arrangement and what is seen in *Ophioglossum palmatum*, in the fact that in both there is a circle of strands, with fusions across the frontal face. But the correspondence does not extend into detail, and there is no correlative in *Ophioglossum* for the antero-posterior fusion of the strands of the circle itself seen in *Platynerium*. The facts point to an interesting homoplasy in two quite distinct epiphytic types.

THE SPOROPHYLL IN *Matonia*, *Dipteris*, *Cheiropleuria*, AND *Platynerium*.

A comparative examination will now be made of the venation of the sporophylls in the Ferns in question, and its relation to their soral developments. It will be found that they form in a general sense a series, leading from simpler to more complex states; and that so far as this comparison is concerned, they form a rough sequence in the order in which they have been named in the above heading.

TEXT-FIG. 11. Portion of a pinna of *Matonia* to show the venation, and its relation to the sorus. x 6.

The venation of the fertile leaf of *Matonia* is known from the observations of Seward (Phil. Trans., vol. 191, Series B, p. 175, Pl. 18, Fig. 23). The pinnules have a midrib, from which veins come off at a wide angle. They show frequent, but irregular anastomoses. But the most notable of these, as they are also the most regular, are those associated with the isolated sori. Each of the latter is seated at the centre of an areola formed by the lateral fusion of veins, while branches run radially in to the centre, where the receptacle is attached. At the base of the receptacle a few tracheides may be seen, but they do not extend conspicuously into it (Text-fig. 11).

The condition of the fertile leaf of *Dipteris* is also known from the description given by Seward and Dale (Phil. Trans., Series B, vol. 194. See also Land Flora, Figs. 344-6). In *D. Lobbiana* the bifurcating lamina is narrower, and the sori are arranged in a more or less regular single row on each side of the midrib, as in *Gleichenia*. The venation is reticulate,

with two lines of areolae, and partially a third one, on either side of the midrib. Smaller twigs of vascular tissue extend into the areolae. Text-fig. 1 shows this, and the relation to it of the sori which remain on the one side of the drawing, but have been removed on the other. Each sorus is seated near to the centre of its areola, upon a vein connected with its margin. The vascular tissue does not show any characteristic extension into the receptacle, which in its position and in its vascular relations is similar to that in *Matonia*.

Much the same is the case with *Dipteris conjugata*, which is the broadly webbed species (compare Land Flora, Fig. 346). Through *D. quinquefurcata*, as explained elsewhere (Land Flora, p. 618), the transition is seen from the simple arrangement of sori on a narrow leaf to the webbed condition with very numerous sori scattered over its enlarged surface. But in *D. conjugata* the relation of the sori to the venation remains the same (Text-fig. 2); each is seated at the centre of its areola, above a branched vein which is connected with the boundary of its own areola. Thus whatever may be the differences of the sporangia in size, number, construction, or development, the relation of the sori to the venation is substantially uniform, so far as observation goes, in the genus *Dipteris*.

But when we pass to *Cheiropleuria*, while the relation to the venation is still essentially as in *Dipteris*, it will be seen that an extension occurs which is important in facilitating a comparison further with *Platycerium*. The fertile leaf differs from the sterile in being long and narrow, and upright in position. Its venation is the same as that of the sterile leaf in essentials, but upon a contracted plan; so that the areolae are much less numerous. If an examination be made of the thinner area of the fertile leaf, right and left of the midrib, which the soral area seems to cover entirely, and the venation be traced, it will appear as in Text-fig. 12. Clearly the method of venation is as in the fertile leaf of *Dipteris*, as would indeed have been expected from its similarity in the sterile leaves, old and young. But the important difference appears, that whereas in *Dipteris* the terminal twigs do not appear distended as wider storage tracheides, this is a marked feature in *Cheiropleuria*. Here the endings form considerable tracts of xylem, composed of tracheides with a high proportion of breadth to length, and these tracts may themselves be considerably elongated, while they extend so markedly towards the lower surface of the leaf, on which the sporangia and paraphyses are seated, that the distal tracheides lie very closely below the sporangial stalks. Further, it may occasionally be seen (as at 'x' in Text-fig. 12) that these receptacular extensions are not limited to a single areola, but pass in a lower plane than the limiting vein into the next areola, actually crossing the course of the vein limiting the areola, but in a lower plane. This is not a very marked or frequent feature in *Cheiro-*

pleuria, though it may happen repeatedly in near juxtaposition, as is seen in the case represented in Text-fig. 12. But it provides the explanation of that state of the fertile leaves of *Platycerium*, which, though described long ago by Hofmeister, and by Mettenius, has not yet been brought into line with other observations in Ferns. Mettenius, in his *Filices Horti Lipsiensis* (p. 26, Pl. IV, Figs. 1–3), described the double vascular system which occurs in *Platycerium*. He showed how in the fertile region of this Fern fine branches spring from the vascular network of the normal leaf; these anastomose to a superficial network immediately within the lower surface: its meshes are elongated, and always much narrower than those of the sterile region, and only seldom give off free twigs. It is only this superficial

TEXT-FIG. 12. Part of lamina of *Cheiropleuria* with two large veins, showing the relation of the smaller veins to the patches of receptacular storage-xylem. x, x, are points where the receptacular storage-xylem, in a lower plane, has crossed the limits of an areola of the venation which lies in a higher plane. $\times 6$.

network which bears the sporangia. Hofmeister, in his *Higher Cryptogamia* (Engl. edn., p. 252), described a similar condition in the circular or reniform nest-leaves of *P. alcidorne*. 'Their vascular bundles lie, not in one, but in two planes parallel to the surface of the frond. These bundles form two many-meshed nets, one close under the upper side, the other immediately above the lower side of the frond; the two networks are united in many places by frequent ramifications, which pass through the mass of the frond in a transverse direction.' In my *Studies on Spore-producing Members*, No. IV (Phil. Trans., Series B, vol. 192, p. 86) the main results of these observers are confirmed as regards the fertile leaves, by examination of those of *P. alcidorne*, Desv. The double vascular system was thus known to exist in the leaves,

and especially in the fertile areas of *Platycerium*. Also that the soral areas were not indiscriminately spread over the leaf-surface, but restricted to more or less parallel lines. This comes out most clearly in those cases where the fertile area is less prolific, and the leaf has the appearance of being only half fertile. Occasionally in these the sori appear quite isolated, and relatively short. It is such leaves as these which give a ready basis for comparison with what has just been described for *Cheiropleuria*.

A semi-fertile area of *Platycerium aethiopicum* of this character is shown in Text-fig. 13. The venation is of the *Dipteris*-type, as it is in *Platycerium* generally. The free twigs of the venation are elongated, though more greatly than they are usually in *Cheiropleuria*, and they bore downwards so that their distal ends approach the lower surface of the leaf. Often each is restricted to its own areola; but in not a few cases, on arriving

at that lower level in the mesophyll of the leaf, it extends past the limiting vein of its own areola, thus crossing into the next. This is what has been seen to happen occasionally in *Cheiropleuria*; but it is a much more pronounced feature here in the partially fertile leaf of *Platycerium*. Still more is it so in the normal fertile area, as is shown in Fig. 14. Here the receptacles are much more elongated, and occasionally branched, and follow a distinctly parallel course. Their connexion with the main venation is as

TEXT-FIG. 13. Part of a lamina of *Platycerium aethiopicum*, which is only half-fertile, i. e. with the sori isolated and small: for comparison with Fig. 12. $\times 3$.

TEXT-FIG. 14. A similar drawing from a fertile leaf of *Platycerium angolense*. The position of the sori is upon the distal ends of blind veins; these elongate and enlarge as in *Cheiropleuria*, and pass to a lower level in the mesophyll: they extend frequently across the limits of the areola of the main venation which lies in a higher plane. $\times 3$.

before; but once they have passed into the lower plane in the thick and fleshy leaf, they may extend to great length, and cross not one only, but several areolae, and branch in their course. And thus there is constituted that second vascular system of the fertile area recognized by Mettenius. The appearance in transverse section is shown in Pl. XXV, Fig. 16, in *P. Willinkii*, from which it is seen that the two vascular systems extend in quite different planes, and that the receptacular strands are in close relation to the insertion of the sporangia.

While we may thus feel a special interest in this elaborate extension of the receptacle, and in the prolongation of its tracheidal system to form a sort of vascular system of its own, it may be recalled that such a development does not stand alone. In various types of Ferns the vascular system of the receptacle is liable to spread beyond the restricted area of the primitive sorus. It has been seen how in *Saccoloma* the marginal sori are isolated;

but in *Lindsaya* they are laterally confluent; the vascular system of their receptacles is there linked by commissures, so as to form a continuous strand. The origin of this state is by lateral spreading of the isolated sori of the *Saccoloma*-type (Studies, III, Figs. 20, 21). Similarly in the Pterideae, as was long ago pointed out by Prantl (Engler's Bot. Jahrb. iii, p. 403, &c.), while *Pellaea* has the sori separate, at the distal ends of veins, in *Pteris* they are confluent. The veins are linked by vascular commissures, which are really lateral extensions of the vascular supply of the receptacle. Again, in Studies, IV, a strong probability has been advanced that the primitive condition from which the Blechnoid Ferns have been derived was that with isolated sori, such as are seen in *Matteuccia intermedia*. By lateral extension of their receptacles, and especially of their vascular systems, the fusion-sori typical of the Blechnoids was produced. It has also been shown (Ann. of Bot., vol. xxviii, Pl. XXIX, Fig. 20*f*), that occasionally the tracheidal system of the receptacle in these Ferns may extend separately from the conducting venation of the leaf, and pursue a course of its own in a slightly different (lower) plane. This, though slight in extent in the case quoted, is similar in essential character to the larger receptacular extensions described for *Platyserium*. And thus it appears that in a number of distinct phyla of Ferns, the receptacle, and very markedly the vascular system of the receptacle, is liable to extension. This may result in a mere linking together of isolated sori, as suggested by comparison of *Matteuccia* with *Blechnum*, or of *Pellaea* with *Pteris*; or it may lead to an extensive vascular system with elongated sori attached, as in *Cheiropleuria* and *Platyserium*. However peculiar the latter case may itself appear, the above comparisons indicate that it cannot be held to stand absolutely alone. It may be held to be a specially pronounced example of a widespread phenomenon, viz., the extension of the individual sorus.

The sori of the series of Ferns at present under discussion show a forward progression in several features. The most important are, (i) the number of the sporangia, (ii) the order and time of their appearance, and (iii) the extent of the receptacle which bears them. The number of the sporangia in the sorus of *Gleichenia* is small, though it rises in certain species, which are on that and other grounds held to be in advance of the rest (Studies, II, Ann. of Bot., xxvi, pp. 274-5). In *Matonia* also the number is only from six to nine, and they are individually large, and are produced simultaneously. In *Dipteris* the number may be larger, and the individual sporangia small. In point of order and time of appearance of the sporangia, the simpler species correspond to the type of *Gleichenia*, or *Matonia*; this is so for *D. Lobbiana*, where the sori are disposed as in these Ferns in a simple series on either side of the mid-rib, and the sporangia arise simultaneously. But in *D. conjugata*, with its broad-webbed leaf, the sori are scattered over the enlarged surface, and

show a mixed condition, as regards the order of appearance of the sporangia (Land Flora, p. 621). But this is not actually an 'Acrostichoid' condition, for the sori are still circumscribed, and the receptacles are quite distinct, as is shown in Text-fig. 2; and individual sporangia do not occur as a rule upon the areas between the receptacles. In *Cheiropleuria* the venation is the same as that in *D. conjugata*; but the sori are not circumscribed. They are merged into a continuous mass of sporangia and paraphyses, which covers the whole surface, the identity of the sori being completely lost. The sporangia are borne indiscriminately over the whole surface, and not only at points above the vascular receptacles. Further, sporangia of very various ages are found in juxtaposition, giving a pronounced 'mixed' character to the whole mass (Text-fig. 15). Thus *Cheiropleuria* is fully 'Acrostichoid', and non-soral, and shows a marked advance upon the other types as regards these characters.

Platynerium, on the other hand, is not truly 'Acrostichoid', though it has often been assumed to be so. It has already been shown that the fertile patches of this genus are not continuous, but that the sporangia are disposed along definite lines, which are really extended sori (Phil. Trans., B, vol. 192, p. 86). They lie above those vascular strands, which constitute in each case an elongated

TEXT-FIG. 15. Transverse section of part of a fertile lamina of *Cheiropleuria*. $\times 50$.

receptacle, and form collectively the lower vascular reticulum (see Text-fig. 15). The sporangia are disposed upon these in two more or less definite rows, one on either side of these elongated receptacles. Moreover, they originate for the most part, if not wholly, simultaneously. Thus the fertile patches of *Platynerium* are really composed of closely placed aggregates of greatly extended sori, themselves essentially of the type of the Simplicies, so far as the origin of their sporangia is concerned.

It thus appears from the facts adduced that the soral condition of the Ferns under discussion is referable in origin to a primitive state seen typically in *Gleichenia*, with a single row of circumscribed sori on either side of the relative midrib; and with few sporangia produced simultaneously in the sorus. It has been shown (Studies, II, Ann. of Bot., xxvi, p. 275) that in *G. pectinata*, by crowding of the sorus, it had become mechanically inefficient, since there is not sufficient room for median dehiscence of its sporangia. From this relief might be found (1) by increasing the length of the sporangial stalk, (2) by adopting lateral dehiscence, (3) by extending

the area of the sorus, or (4) by elongating the receptacle. *Gleichenia* did not adopt any of these devices, but other Ferns did, and have succeeded. The *Matonia-Dipteris-Cheiropleuria* Series has adopted the three first named, but not the last, for none of them have developed as Gradate types.

Matonia itself retained the circumscribed sorus, but adopted a lateral dehiscence of its short-stalked, but large and few sporangia. In *Dipteris* the number of the laterally dehiscent sporangia is larger, their size smaller, their stalks longer, and the area of the sorus larger, especially as seen in *D. Lobbiana*, and *quinquefurcata*. In *D. conjugata* the less size of the sorus is balanced against their much greater number spread over the webbed lamina. In *Cheiropleuria* the laterally dehiscent sporangia are still longer-stalked, and the confluent sori are spread continuously over the leaf-surface, giving a fully 'Acrostichoid' character. In *Platyserium*, however, the sori are merely elongated, not confluent, the large number of the sporangia being accommodated by the extension of the area of their elongated receptacles. The latter types appear to have diverged far from the simple Gleichenioid source, which would hardly be recognized in them were it not for the intermediate states which some of them show, and also the comparisons which may be based on other characters.

THE SPORANGIA.

The sporangia of *Matonia* are well known, and need no fresh description (see Seward, Phil. Trans., vol. 191, p. 171; Studies, IV, Phil. Trans., B, vol. 129, Pl. 4, Figs. 59-62, and Land Flora, p. 565). But those of *Dipteris* are less fully investigated. They have been figured and described by Seward (Phil. Trans., vol. cxciv, Pl. 48, Figs. 11-16) and by Miss Armour (New Phyt., 1907). But these analyses were not exhaustive, and their development has never been fully traced. It will be seen that their segmentation gives an important line of comparison with *Cheiropleuria*. The sporangia of *Dipteris Lobbiana* are shown from their 'peripheral' side in Text-fig. 16, *a*, *b*, and it is apparent that the annulus is a complete ring of cells, though the induration of those opposite the stalk is incompletely carried out. A comparison may be made with a similar view of the sporangium of *Gleichenia lineata* (= *Gl. dichotoma*) (Land Flora, p. 555, Fig. 310), which shows similarity of form and of position of the annulus; but there the induration is complete, and the dehiscence distal and median. In *Dipteris Lobbiana* the dehiscence is obliquely lateral and, as the Text-figs. 16, *a*, *b* show, either right or left of the median line. The stomium is not well defined, a character shown also in *Matonia* and *Gleichenia*. The stalk is short, and shows two rows of cells, as seen from the peripheral side. Fig. *c* shows a similar view of a sporangium already dehiscent. In Fig. *d* is a view from the 'central' side, but with the annulus hidden on the dehiscent margin. Again the stalk appears as two rows of cells. Since

this appearance is shown from both sides, it follows that the stalk has the unusual composition of four rows of cells, a point definitely demonstrated by transverse sections. Text-figs. 16, *e* and *f*, show sporangia seen obliquely from the side, the first from the side of the stomium, the other from the completely indurated side. From these various views the structure of the sporangium will be fully realized. The similarity of form, and in certain features of the annulus, to that of *G. lineata* is obvious; but though the annulus remains oblique, as in that Fern, its induration is incomplete,

TEXT-FIGS. 16, *a-f*. Various aspects of the sporangia of *Dipteris Lobbiana*. For description see Text. $\times 50$.

while the stomium has swung into a lateral position; and the stalk is of a less complex construction.

The sporangium of *Cheiropleuria* is larger, and longer-stalked than that of *Dipteris*, but the general type of it is the same, a very distinctive point of similarity being the four-rowed structure of the stalk. This is clearly shown by tangential sections of the soral area, in which the sporangial stalks appear densely surrounded by paraphyses (Text-fig. 17, *e*). Seen from the 'peripheral' side the sporangium appears as in Text-fig. 17, *a*, associated with paraphyses, which are longer than itself until maturity is reached. The stalk shows two rows of cells, which become slightly constricted below

the insertion of the head. The latter has a continuous series of cells of the annulus, but the induration is not continued past the stalk; moreover, the cells opposite the stalk, which are thus thin-walled, are less regular in outline than the rest. Laterally there is a stomium which is in a position unusually near to the insertion of the stalk, that is, distinctly below the equator of the sporangial head. It is more regularly constructed here than in *Dipteris*, being usually composed of four cells; this point is best seen in Text-fig. 17, *c*, which represents an oblique view, with the stomium facing

TEXT-FIGS. 17, *a-e*. Various aspects of the sporangia of *Cheiropleuria*. For description see text. $\times 80$.

the eye. The 'central' side of the sporangium is shown in Text-fig. 17, *b*, where the constriction of the stalk just below the head is very marked. Here also the relation of the continuous annulus to the stalk is seen, but it is best understood from Text-fig. 17, *d*, which shows from below the insertion of the stalk (shaded), and the way in which the series of cells of the annulus extends, though with modified form and without full induration, continuously past it. The details of the sporangia are, however, not rigidly constant; thus the number of the cells of the annulus may vary; such numbers as thirty-six, thirty, and twenty-six have been counted.

Moreover, it is not always equally clear that the annulus is continuous past the stalk. Such differences are natural, and are even to be anticipated in cases like the present, where, *ex hypothesi*, the sporangium has undergone modification from a more primitive type.

For comparison with the above, the sporangia of *Platycerium* have been examined, and a typical example is shown in Text-fig. 18, *a*, for *P. aethiopicum*. One point of difference is in the stalk, which here consists of only three rows of cells, as is clearly indicated by transverse sections (Text-fig. 18, *b*). The form of the sporangial head is more pear-shaped, and the annulus less clearly oblique, while it retains the lateral position of the stomium distinctly below the equatorial line. Opposite the insertion of the stalk the annulus is drawn down into an acute angle, in accordance with the pear-like form of the sporangium, and it is almost interrupted, but not actually so; for the rather elongated cells on either side do, as a matter of fact, retain contact, as is shown by the dotted lines in Text-fig. 18, *a*. Comparing this sporangium with that of *Dipteris* or *Cheiropleuria*, it is seen to be of a more advanced type, as shown by the thinner stalk, the more vertical annulus, and the almost completed interruption of it at the insertion of the stalk.

TEXT-FIG. 18. *a*, sporangium of *Platycerium aethiopicum* as seen from the side. *b*, transverse sections of its stalk. $\times 80$.

DEVELOPMENT OF THE SPORANGIUM.

Unfortunately the material of *Cheiropleuria* did not, in age or in preservation, suffice for tracing the development of the sporangium fully. But the essential features have been observed, and a comparison may be drawn with the very similar development in *Dipteris conjugata*. The general features of the fertile leaf have been described above. If sections of the fertile region be examined, the flattened expansion is found to be relatively thick, and it has a spongy texture of the mesophyll towards the upper surface. The mesophyll is traversed by two distinct types of vascular tissue; first, the normal venation, lying in a median plane, and with the small and compact strands clearly circumscribed by parenchymatous sheaths. Two of these strands are shown, right and left, in Text-fig. 15. Secondly, there are found lying between these, and closer to the lower surface, more lax strands composed of larger tracheides of the storage type, and without parenchymatous sheaths. These are the receptacular endings of veins, which, as seen in surface view, are liable to be greatly enlarged and elongated (Text-fig. 12).

The lower surface of the leaf is covered by the dense sorus, which is not limited to any position above the veins, but is spread uniformly over the whole area. It consists of (*a*) very numerous paraphyses, simple unbranched hairs, each terminating in a glandular cell; (*b*) isolated sporangia disposed with no definite regularity among them. The relations of these are shown in transverse section in Text-fig. 17, *e*, and in vertical section in Text-fig. 15. The sporangia are seen in the latter to be sometimes seated over the vascular tracts; but they appear to be equally common in the areas between them. Further, as they are not disposed in any order of age, the soral areas are of the 'mixed' type. Thus there is a definite 'Acrostichoid' condition of the sorus in *Cheiropleuria*.

While young, the sporangia are efficiently covered by the paraphyses, which are taller than they. But as maturity approaches, the sporangial stalk elongates, so that the sporangial head comes to be level with their ends, and can discharge its spores freely, while those which are younger are still protected below. This arrangement is closely parallel with that of the *asci* in any of the Discomycetous Fungi.

The sporangium originates from a single superficial cell. In a large number which have been examined, the segmentation appears to show a regular cleavage of the segments *in two opposite rows*. Naturally, those selected for drawing show these right and left, for thus they present the most definite appearance. The first of such segment-walls cuts obliquely down to the base of the square mother-cell (Fig. 17, *a*). The number of the cleavages does not appear to be constant (compare Fig. 17, *b-e*). After the number of the cells in each row, either by primary cleavage or by subdivision, has reached four to six, the wedge-shaped cell which occupies the apex undergoes periclinal division (*d*), which is followed by further segmentations parallel to the last, giving rise to the tapetum, and the central sporogenous cell (*f*). Later development follows the course usual in Leptosporangiate sporangia. Meanwhile, subdivision of the two rows of segments of the stalk by walls in the plane of the drawings has given rise to the four rows of cells of the stalk, as seen in the later stages (Text-fig. 17, *d*).

The cleavages thus described are so peculiar and exceptional among Leptosporangiate Ferns that it was thought well to compare them with those seen in *Dipteris*, in which a like structure of the sporangial stalk has been seen. Here again the storage tracheides of the receptacle lie closely below the surface where the sporangia are borne (Fig. 18, *a*). The sporangia arise from single cells, which may here have an oblique base, and the first oblique segment-wall impinges upon that oblique face; thus the type of sporangium is from the first less robust than that of *Cheiropleuria*. Alternate segments in two rows then follow, as in *Cheiropleuria*. In order to check the fact of this alternate segmentation, sporangia were examined

also from the side facing one of the rows of segments, instead of taking them in profile. Such a view is shown in Fig. 18, *b*, the appearance of which is consistent with the segmentation by two alternate rows of cleavages. Transverse sections also bear out the correctness of the conclusion (Fig. 18, *c*). Miss Armour has already shown (*New Phytologist*, 1907) that in these sori the sporangia are not all of the same age, and Fig. 18, *a* and *c*, confirm this. Some are found to show only two cells, corresponding to the two rows of segments; others have undergone subdivision of the segments, and show as the result the four rows of the mature stalk.

It is clear from these observations that 'Dipteris' and 'Cheiropleuria' provide a new and distinct type of segmentation of the Fern-Sporangium. The similarity which these genera show in other features, when taken to-

TEXT-FIGS. 19, *a-g*. Segmentation of young sporangium of *Metaxya*. *a, b* are two lateral views, at right angles to one another: *c, d* show the sporangial head in transverse section: *e* is a transverse section of the sporangial stalk; *f*, a transverse section of an older sporangial head: *g* shows a sporangium of the age of *c, d*, seen laterally. $\times 300$.

gether with their similarity in this rare feature, forms a convincing body of evidence of their real affinity.

The only other type of Fern which has been described as having constantly four rows of cells of the sporangial stalk is *Metaxya* (*Ann. of Bot.*, xxvii, p. 447, Pl. XXXII, Fig. 8). The detail of segmentation of the young sporangium, as viewed from above, was not looked into when the plant was being investigated; but it will be seen at once that Figs. 5, 6, on the plate quoted, show numerous segmentations, as seen from the side, which would accord with a two-sided segmentation. Fresh observations were therefore made with the results shown in Text-figs. 19, *a-g*. The drawings *a, b* show sporangia in which the cap-cell has not yet been formed, from points of view at right angles to one another; in *a*, the

wedge-shaped cell from which segments have been cut off right and left, is seen on edge; in *b* it is seen from the side, and the segments themselves have divided into equal halves, thus giving the four-rowed structure of the stalk, as seen in *e* when cut transversely. In *c*, *d*, which show views from above, the two-sided segmentation is clearly demonstrated; while in *g* the cap-cell has been cut off, and has already divided. Thus the segmentation of the sporangium in *Metaxya* accords with that of *Cheiropleuria* and *Dipteris*. It has been shown that *Metaxya* on comparative grounds may be held as related to *Lophosoria*, and be regarded as a Gleichenioid derivative. *Dipteris* and *Cheiropleuria* have probably a similar relation, and all the three genera correspond in this uncommon feature of the two-rowed segmentation of the sporangial primordium.

Lastly, for purposes of comparison, a section of the fertile region of the leaf of *Platycerium* is represented in Pl. XXV, Fig. 16. Here the leaf is thicker than in *Cheiropleuria*, and the sori are localized above the receptacular strands. It is clear from the section that the latter run here in a plane much nearer to the lower surface than the strands of the regular venation. In *Cheiropleuria* (Text-fig. 15) the difference of level between the receptacular strand and the true venation is only slight; but here, in Fig. 16, strands of the two systems are seen directly superposed, and several layers of cells intervene between them. This is in accordance with what has been stated above (p. 512), and with the drawing of Mettenius (*Filices*, Hort. Lips., Pl. 4, Figs. 1-3). It may also be noted that the three sporangia shown in Fig. 16 are at approximately the same stage of development, though that which is median is slightly in advance of the others. This is characteristic for *Platycerium*. The origin of the sporangia is almost simultaneous, but slight differences of time may be observed in them.

COMPARISONS AND CONCLUSIONS.

It will be evident from this detailed description of *Cheiropleuria*, incomplete as it is, and entirely deficient as regards the gametophyte, that the genus is one which has a special comparative interest; and that the interest lies, not only in the location of the Fern in its own probable phyletic position, but also in the demonstration that it brings of the divergences from strict parallelism, in respect of the various characters which are used as criteria in such comparisons. It is only when such divergences are fully taken into account that a correct valuation can be set upon the method of phyletic study, based upon such comparisons, and of the conclusions which follow from them.

The first question will be as to the probable phyletic position of *Cheiropleuria*, and especially its connexions *downwards* in the scale. Then may follow the question of its probable relations *upwards*, with forms still

more advanced than itself. There can now be little question of the relations of *Cheiropleuria* downwards. Its nearest affinity is with *Dipteris*, and less closely with *Matonia*. This is shown by the similarity of form of the shoot, and of the dermal appendages. The form of the lamina, and especially of those variants of it which have more than two cusps, and the venation also, link it clearly with *Dipteris*. The steps towards a webbed character of the lamina seen in *D. Lobbiana*, *quinquefurcata*, and *conjugata* lead, in a manner which cannot be overlooked, to the more complete integration of the lamina as it is seen in the one-cusped type so frequent in *Cheiropleuria*. This conclusion is also borne out by comparison of the outline and venation of the leaves of young plants of *Dipteris*.

In venation, the types of *Gleichenia*, *Matonia*, *Dipteris*, and *Cheiropleuria* form an interesting sequence. In *Gleichenia* the venation is open throughout, thus showing a state which is usually held to be primitive. In *Matonia* there are occasional vein-fusions, especially in relation to the sorus. But in the narrow-leaved species of *Dipteris* such fusions are so frequent as to form a reticulum, while in the webbed species *D. conjugata*, the type is that of 'Venatio Anaxeti'. This venation is characteristic also of *Cheiropleuria*, as it was also of the fossil genera, *Dictyophyllum*, *Clathropteris*, and *Hausmannia* (see Seward, *Fossil Plants*, vol. ii, p. 380, &c.), which have been referred to the Dipteridinae. Thus, as regards the venation, *Gleichenia* corresponds to the type prevalent in the Palaeozoic Period; *Matonia* takes a middle position, and the Dipteridinae show a venation characteristic of Mesozoic or later periods. *Cheiropleuria* is, as regards this character, as recent as any of them, notwithstanding the primitive structure seen in its axis.

The Matonioid Ferns, including the Dipterids, have been habitually regarded as *Gleichenioid* derivatives (Land Flora, pp. 622, 623). But hitherto the anatomical conditions have not materially helped this comparison, for in the mature state both *Matonia* and *Dipteris* have advanced solenosteles, while *Gleichenia* shows in most of its species a protostelic state. It is here that *Cheiropleuria* comes in as a synthetic link. The comparison of its protostelic axis with that of *Gleichenia* (Figs. 8–12) is very striking. Similarly its leaf-trace comes off at first as an undivided strand, though its early division into two indicates a state advanced beyond that of any *Gleichenia*, or indeed of *Matonia*. But it shows some similarity to what is seen in *Dipteris Lobbiana*, which is even more advanced in the division of its leaf-trace; for it there arises as two or even four distinct strands (Text-fig. 6).

As regards the protostelic state of *Cheiropleuria*, it may be noted that a similar protostely has been found in the young plant of all of the related Ferns which have been examined. Thus *Cheiropleuria* maintains to maturity that primitive anatomical state which others have departed from early.

A minor character which also indicates a primitive state is that the dermal appendages are all hairs. Flattenedramenta are absent, though they may be found even in some *Gleichenias*. As compared with the hairs of *Matonia* and *Dipteris*, those of *Cheiropleuria* are simpler, and suggest that in this feature it is the most primitive of them all.

The comparisons given in detail above have shown that, as regards the sorus, *Cheiropleuria* is an advanced type. This is seen from its 'Acrostichoid' soral areas, and from the 'mixed' condition of the sporangia. But the comparison instituted through examination of the vascular supply shows that the state seen in *Cheiropleuria* is relatively primitive compared with that seen in *Dipteris* and *Matonia*, though closely resembling that seen in *Gleichenia*. The sori of all of these are superficial, and *Dipteris*, with its variable soral conditions, gives the connecting clue between the simple state in *Gleichenia* and *Matonia*, and the 'Acrostichoid' state of *Cheiropleuria*. The arrangement in *D. Lobbiana* is clearly conformable to that of *Matonia* and *Gleichenia*. The advance seen in *D. quinquefurcata* leads, with the addition of the webbing of the frond, to that seen in *D. conjugata*, with its enlarged leaf-surface. Upon this the numerous sori retain their identity; but in *Cheiropleuria* that identity is lost, and the result is seen in the large continuous fertile patches. Such progression from a state with discrete sori to the merged, 'Acrostichoid' state finds its parallel in several other phyletic lines in Ferns. (Compare *Annals of Botany*, 1914, p. 427.)

In their sporangial characters *Cheiropleuria* and *Dipteris* are closely alike. The most striking point of that similarity lies in the four-rowed stalk, which so readily results from the peculiar cleavage of the sporangial primordium by alternate segments ranging in two rows. The resemblance of the genera in a character so remarkable is the strongest possible evidence of correctness of the comparisons based upon other features.

Taking all the characters together, the conclusion seems fully justified that *Cheiropleuria* is a Fern of Matonioid-Dipterid affinity. That while it has retained a primitive type of dermal appendages, and a vascular structure of its axis such as is seen in the presumable Gleichenioid ancestry, it has adopted a type of leaf and of sorus which are seen in the relatively advanced species of *Dipteris*, but has carried these features to a still more advanced state than is seen in any member of that genus. It is a striking example of the absence of strict parallelism of advance in the several criteria of comparison. But at the same time the incongruity of its characters marks it out as one of the most interesting synthetic types to be found among living Ferns.

Turning now to the relation of *Cheiropleuria* upwards in the scale, that is to forms which, though probably related, show collectively characters of still further advance than *Cheiropleuria* itself does, these are found

especially in the curiously modified epiphytes of the genus *Platynerium*. In *Cheiropleuria* a scandent tendency has been seen, though it does not appear to have led to any definitely climbing or epiphytic state. But *Platynerium* has its shoot strongly modified in relation to epiphytic life, as shown particularly in its peculiar leaves. Nevertheless, externally a similarity to *Dipteris* and *Cheiropleuria* may be traced, not only in the outline of the erect or pendent leaves, with their regular bifurcation, but also in the venation; and this may be traced even in the highly modified nest-leaves. Perhaps it is in the newly-described species, *P. Sumbawense* n. sp. Christ (Warburg, Monsunia, i, 1900), that the similarity between the fertile leaves and those of *Dipteris* is the most marked. For there the narrow lamina is repeatedly furcate, so that the lacineae may number twenty on a single frond, and all are soriferous; this is reminiscent of the simpler species of *Dipteris*, such as *D. Lobbiana*. The comparison already made of the juvenile leaves of *Cheiropleuria* with those of young plants of *Dipteris* and of *Platynerium* supports the similarity still further, and it is apparent also in the mature leaves of *D. conjugata*, of *Cheiropleuria*, and even in some measure in the nest-leaves of *Platynerium*.

But the anatomical comparison of the axis shows marked divergence of character in *Platynerium* from what is seen in *Cheiropleuria* or *Dipteris*. As Mettenius has shown, and Tansley has quoted in his Lectures on the Filicinean Vascular System (p. 62), the axis of *P. alcorni* is highly dictyostelic, and perforated. There is, as a result, an almost simple ring of meristeles, while the leaf-trace, with certain complications at its origin, comes off *ab initio* as a number of detached strands (Text-fig. 9, A). Miss Allison (New Phyt., 1913, p. 311) has recently published a description of this with figures, and has also described the vascular system for *P. aethiopicum*. In the latter the structure is still more complex, for the leaf-trace consists of still more numerous strands, while a large number of medullary strands are present at the centre of the axis (Text-fig. 9, B). A comparison of the structure of these species with the states seen in *Matonia* and *Dipteris* suggests that the relatively simple ring of meristeles seen in *P. alcorni* finds its correlative in the simple solenostele of *Dipteris*; while the more complex system in *P. aethiopicum*, with the numerous medullary strands in addition, finds its correlative in the polycyclcy of *Matonia*. Imagine these genera with their solenosteles profusely 'perforated', and something very like the stem structure of the species of *Platynerium* would be the result. Clearly *Platynerium*, on such an interpretation, takes anatomically a more advanced position than *Dipteris*, or *Matonia*, and a still more decidedly advanced position than *Cheiropleuria*.¹

¹ See The Genus *Alcornium* of Gaudichaud, by L. Underwood. Bull. Torrey Club, vol. xxxii, 1906, p. 587, &c. Underwood desires to retain the name *Alcornium*, Gaud., in place of *Platynerium*, Desv. But I follow Christensen's Index in retaining *Platynerium* as the generic name.

But in respect of the venation in the fertile region of the sporophyll, *Cheiropleuria* is in closer relation to *Platynerium*. It has been shown above how the receptacular strand in *Cheiropleuria* may pass, in a lower plane, out of its own vascular areola, thus initiating an independent course of its own. The same may be found in *Platynerium*, though here it is on a larger scale; and it leads to the formation of that second vascular system described by Mettenius, which spreads in a lower plane, between the main system of the leaf and the sori themselves. This condition is so exceptional among Ferns that the degree of correspondence demonstrated between *Cheiropleuria* and *Platynerium*, in this respect, gains thereby additional weight. It may therefore be held that the points of similarity seen in their leaves go far to outweigh the differences of stelar structure in the stem between these two genera.

In its dermal appendages—whether the flattened scales of its rhizome, or the stellate hairs which cover the young sori—*Platynerium* shows an advanced condition. But the sorus itself, though the receptacles are greatly elongated, are still not typically 'Acrostichoid', as in *Cheiropleuria*; each, though prolonged, maintains its individuality, while the sporangia originate almost simultaneously. The sporangia themselves have the usual three-rowed stalk, and the annulus is more definitely interrupted than in *Dipteris* or *Cheiropleuria*. Thus sorally *Platynerium* shows a curious mixture of characters, some in advance of those of *Cheiropleuria*, others, and especially the distinctness of the sori, being more primitive.

The sum of the features noted in the above paragraphs appears to place *Platynerium* definitely in phyletic relation to the *Matonia-Dipteris* Series, as a form probably derived from such types, but curiously specialized; and perhaps its high degree of specialization to an epiphytic habit may account for the strange mixture of its characters. The anatomy of its stem relates it rather to *Matonia* and *Dipteris*; but its leaf, and its soral state points to *Cheiropleuria*. It may probably be held not to have been actually derived from any one of the living genera, but rather as a curiously specialized form, sprung from some extinct Matonioid or Dipterid which had a relatively advanced vascular structure; and that the soral system became specially enlarged, thereby giving a high spore-output, advantageous as an offset to the difficulties of an epiphytic habit.

The question remains whether any other Matonioid-Dipterid derivatives may be recognized among living genera. This question cannot be answered satisfactorily without much further comparative study. But it seems probable that others may actually be related. For instance, *Leptochilus tricuspidis* was placed close to *Cheiropleuria* by Sir W. Hooker. *Neocheiropteris* also is probably related, as well as some others ranked at present as species of '*Polypodium*'. A careful comparative study of such types, upon which I have already entered, would go far to decide what

can be at present no more than a suggestion of a possible relation of other living Ferns to the group under consideration.

It would thus appear that we may have in some measure to revise the current view of the Matonioid-Dipterid phylum. They are commonly held to have been a series of Gleichenioid origin, which was prevalent in the Mesozoic Period, but struggled on to the present time only in the surviving genera *Matonia* and *Dipteris*. There can now be little doubt that *Cheiropleuria* must be added to these surviving types, while *Platycerium* can hardly be anything else than a highly specialized Dipterid, related especially to *Cheiropleuria*, and adapted to modern life under the peculiar conditions of epiphytism. And it is possible that other derivative forms may be ultimately added to those modern representatives of a very ancient sequence.

Finally, if the position ascribed be accepted, the case of *Cheiropleuria* will have its value in showing that, in special cases, a want of parallelism of the several criteria is to be recognized and even expected. Many cases are already known. For instance, the single initial cells in stem and root of the Eu-sporangiate Ophioglossaceae, and the massive dermal appendages on the leaf-base of the primitive Gleichenias; the reticulate venation of the Eu-sporangiate *Kaulfussia*; the high subdivision of the vascular tracts in the living Marattiaceae; the protostelic structure combined with advanced gradate sori of the Hymenophyllaceae. But such instances of the absence of parallelism in the several criteria are relatively slight compared with the glaring fact of the primitive protostely, and simple hairs accompanying in *Cheiropleuria* a mixed sorus of an advanced 'Acrostichoid' type. It is this strange collocation of characters, which comparison marks out as incompatible elsewhere, that gives to *Cheiropleuria* its special interest and value in relation to the phyletic study of the Filicales.

SUMMARY.

1. *Cheiropleuria bicuspis* (Bl.), Presl, is the only known species of a substantive genus.
2. It shows an uncommon mixture of primitive and advanced characters, by which it takes a place phyletically as a synthetic form.
3. Its characters, external and internal, connect it downwards most clearly with *Dipteris*; and upwards, that is in the direction of more advanced specialization, with *Platycerium*.
4. Its simple hairy investment, protostelic axis, undivided leaf-trace, and its frequently bifurcate form of leaf, are relatively primitive characters.
5. Its reticulate venation and its 'Acrostichoid' and 'mixed' sorus are characters of relative advance.
6. The occasional extension of the receptacular vascular supply of the individual sorus beyond the single vascular areola gives the clue to the

state of the sporophyll in *Platycerium*, with its double vascular system in the fertile region.

7. Its slightly oblique annulus, four-rowed sporangial stalk, and alternate segmentation of the primordium, form a peculiar link with *Dipteris*, which is shared also by *Metaxya*.

8. The mixed characters which this Fern shows are one of the clearest examples of non-parallelism of progression in the several criteria used for comparison among Ferns.

9. The outcome of its comparative examination is to strengthen the relation of *Dipteris* and *Matonia* to some Gleicheniacious source.

10. It shows that probably *Platycerium* is also a Dipterid derivative, specialized for an epiphytic habit.

11. Probably other Dipterid derivatives will also be found on detailed study, in such forms as *Leptochilus*, *Neocheiropteris*, and some others.

12. Thus the representation of Matonioid-Dipterid derivatives among living Ferns appears to be more extensive than had been hitherto appreciated.

EXPLANATION OF FIGURES IN PLATES XXIV AND XXV.

Illustrating Professor Bower's Paper on *Cheiropleuria bicuspis* (Bl.) Presl, and allied genera.

PLATE XXIV.

Fig. 1. Specimens of *Cheiropleuria bicuspis* (Bl.) Presl, from the Lingga Mountains, Borneo, showing the general habit, the one-cusped and two-cusped sterile leaves, and one narrow fertile leaf. Reduced to $\frac{1}{4}$.

Fig. 2 has been placed at the top of Plate XXV.

Fig. 3. Two sterile leaves of the bi-cusped type, as shown in Hooker's Figure. Journ. of Botany, 1846; also one fertile leaf. Reduced to $\frac{1}{4}$.

Figs. 4, 5. Specimens with irregularly furcate leaves. Reduced to $\frac{1}{4}$.

Fig. 6. A leaf of *Platycerium Hillii*, Moore, for comparison with Figs. 4 and 5. Reduced to $\frac{1}{2}$.

Fig. 7. Instead of this there has been substituted Text-fig. 1, which see.

Fig. 8. Transverse section of the protostele of *Gleichenia linearis*, Clarke (= *G. dichotoma*, Hk.), from a section by Professor Gwynne-Vaughan. $\times 30$.

Fig. 9. Transverse section of the protostele of *Gleichenia flabellata*, R. Br., from a section by Professor Gwynne-Vaughan, taken at a point where a leaf-trace is being given off. ($\times 30$).

Fig. 10. Transverse section of a protostele of *Cheiropleuria*, showing a leaf-trace being given off from it. $\times 45$.

Fig. 11. A similar section of *Cheiropleuria*, showing the leaf-trace completely separated. It has two internal protoxylem-groups, with the metaxylem surrounding them completely—a condition which holds only for a short distance. $\times 30$.

Fig. 12. Transverse section of a young stele of *Cheiropleuria*, showing the absence of protoxylems, except in the young leaf-trace, while metaxylem tracheides are developing simultaneously, scattered through the whole area. $\times 45$.

Figs. 13, 14. Transverse sections showing the leaf-trace on its outward course, and beginning to bifurcate. $\times 30$.

Fig. 15. Transverse section of the stem of a seedling of *Dipteris conjugata*, Reinw, showing a protostelic state. $\times 45$.

PLATE XXV.

Fig. 2. Drawing by Mr. J. M. Thompson of a rhizome with the superficial hairs removed, so as to expose the successive leaf-bases, which are numbered L.-i to L.-viii, and the lateral axes which spring from their bases (*ax. i.*, to *ax. iv.*). But the leaves iii, vi, vii, viii have no associated axes. The leaf-arrangement is alternate, and the shoot is seen from the side facing away from the support. $\times 2$.

Fig. 16. Transverse section of a fertile leaf of *Platynerium Willinkii*, Moore, showing strands belonging to the two vascular systems: the strand nearer to the upper surface belongs to the main system of the lamina, that nearer the lower surface is a receptacular strand. $\times 100$.

Fig. 17, *a-e*. Stages in the development of the sporangium of *Cheiropleuria*. *a*, *b*, *c* show the alternate cleavages of the primordium to form two rows of cells of the stalk: *d* shows the formation of the cap-cell: *e* shows the beginning of formation of the tapetum: *f* shows the tapetum complete, as two layers surrounding the sporogenous cell. $\times 250$.

Fig. 18, *a-c*. Stages in development of the sporangium of *Dipteris*. *a* shows a young sorus of *D. Lobbiana*, bearing two hairs, and two sporangia. The receptacular tracheides are closely below the surface, and are of the large storage type. *b* shows a sporangium of *D. conjugata* seen from the side facing one of the rows of segments, and demonstrating how each segment divides into two cells, which together with the results of division of the segments of the other row form the four rows of cells of the sporangial stalk. *c* represents transverse sections of similar sporangia of *D. conjugata*, showing some stalks—the younger, with only two cells; others, the older, with four cells. In one sporangium there are only three, one segment having divided and the other not. $\times 325$.

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Bower, F. O. 1915. "Studies in the phylogeny of the Filicales. V. Cheiropleuria bicuspis (Bl.), Presl, and certain other related ferns." *Annals of botany* 29, 495–529. <https://doi.org/10.1093/oxfordjournals.aob.a089562>.

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