Studies in the Phylogeny of the Filicales.

I. Plagiogyria.

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With Plates XXXII and XXXIII and five Figures in the Text.

FROM very early days the position of the annulus of the sporangium has been held to be a character of the first importance in the comparative treatment of Ferns. In the year 1800 both Bernhardt¹ and Swartz² had introduced features of the annulus as defining the larger divisions of the family, but it remained for Bernhardt³ later to distinguish under the names *Helicogyratae* and *Cathetogyratae* the Ferns respectively with oblique and with vertical annulus. This distinction was adopted by Presl in his 'Tentamen' of 1836 (p. 20), and he made the oblique annulus the character of his first sub-order, while the vertical annulus characterizes the second sub-order of Ferns in his system. Presl's classification was further adopted by Sir William Hooker in his 'Genera Filicum' (1842); it is embodied in the synopsis at the conclusion of that work, with the remark that it is 'the most full and complete that has yet been published'. But, on the other hand, Kunze⁴ criticizes Hooker's neglect of exact detail of position of the annulus in some of his figures, and praises Schott ('Genera Filicum', 1834) for his accuracy in delineation of the annulus; he points out the higher degree of organization of the stomium in the *Cathetogyratae* than that usual in the *Helicogyratae*.

It is in the paper of Kunze just quoted that the first description is given of any species of the genus now recognized under the name of *Plagiogyria*; he found in the Ferns described as *Lomaria niponica* and *euphlebia* a condition different from that of all Polypodiaceae, uniting the type of annulus having a highly organized stomium with the oblique annulus

¹ Bernhardt, J. J.: Schrader, Journal für die Botanik, ii, 1800.

² Swartz, O.: Schrader, Journal für die Botanik, ii, 1890.

³ Dritter Versuch einer Anordnung der Farnkräuter. Schrader, Neues Journal für die Botanik, 1806.

⁴ Pteridologische Studien. Ueber eine noch unbeobachtete Form der Sporangien (*Sporangia plagiogyrata*). Bot. Zeit., 1849, p. 865.

of the *Helicogyratae*. The stock of these Ferns was not examined, but, on other general grounds, he referred them to the genus *Lomaria*, not seeing in the peculiarity of their sporangia any sufficient reason for removing them from that genus. A more full description with careful drawings was given by him in the following year,¹ but again without the axis having been observed. In leaving these species within the genus *Lomaria*, notwithstanding the divergence of structure of their sporangia, Kunze remarks (l. c., p. 62) that in his view the microscopical features will never lead to a natural arrangement, and they can only be used as indications; the species may, however, be designated as a section of the genus under the name of *Plagiogyria*. Next in point of date came the monograph of Mettenius,² in which he separated the sub-genus from *Lomaria* under the generic name of *Plagiogyria*; but Sir William Hooker³ still retained it as *Lomaria*, where it remained in the 'Synopsis Filicum'.⁴ His reasons for this are explicitly stated ('Species Filicum', iii, p. 2); the passage is interesting as illustrating the attitude of a great systematist in the year 1860; he wrote: 'I am not disposed to retain *Plagiogyria* separate from *Lomaria*, although constituted by a botanist by no means addicted to establishing new genera on slight grounds. It has peculiarities in the base of the stipes and in the presence of certain glands called by Mettenius *aerophorae*; but notwithstanding this structure, and even should the capsules in all the species referred to *Plagiogyria* prove to be helicogyrate, yet the habit and sori are so entirely in accordance with true *Lomaria* that, unless the student has the opportunity of examining very perfect specimens, or unless he examines the structure of the annulus of the very minute capsules under the high power of a microscope, the genus cannot be identified. Kunze, who first recognized the physiological differences, only proposed to form a group or section, under the name of *Plagiogyria*, but even that would be inconvenient to retain in a work whose main object is to assist the tyro in the verification of genera or species; and natural habit is often a safer guide than minute microscopic characters.' On this footing convenience of use for purposes of recognition takes precedence over natural affinity in the systematic method.

The monograph of Mettenius above alluded to established *Plagiogyria* as a substantive genus, notwithstanding the divergent opinions of Hooker and of Kunze. Comparisons had been drawn by various writers between the Ferns of the *Plagiogyria* section of *Lomaria*, and other species of *Lomaria*, and of *Stenochlaena* on grounds of external form; but it was pointed out by Mettenius that there were broad differences notwithstanding the superficial similarity; the characters recognized by him as distinguishing

¹ Kunze, G.: *Farnkräuter* (Schkuhr's *Farnkräuter*, Supplement). Zweiter Band, p. 61, Taf. CXXV, and 91, Taf. CXXXVIII.

² Ueber einige Farnngattungen. II. *Plagiogyria*, 1858.

³ *Species Filicum*, iii, p. 2, 1860.

⁴ l. c., p. 182, 2nd ed., 1883.

Plagiogyria were not only the oblique annulus, but also certain peculiarities of the vegetative organs (l. c., p. 7), such as the swelling of the leaf-bases, the spongy tissues (aerophorae) which they bear, and the absence of peltate scales; also he notes that the spores are tetrahedral. This monograph, to which allusion will frequently be made below, gives by far the most complete account yet published of this interesting type of Ferns. Later writers seem to have left the genus severely alone, so far as detailed investigation is concerned. Prantl¹ does not even mention it in his valuable remarks on the systematic importance of the annulus, nor does he place the genus by name in his system of the Polypodiaceae. Of later writers Diels² places *Plagiogyria* as a substantive genus under the Pterideae, and in next proximity to *Cryptogramme*. Christ³ also maintains it as a substantive genus; he places it at the end of the Pterideae (Hook.), and next to *Actiniopteris*, with *Blechnum* as the first genus of the succeeding Blechneae. Raciborski,⁴ on the other hand, follows Hooker's 'Synopsis' in still including the species under *Lomaria*.

It is quite plain from the above notes that the Ferns now grouped in the genus *Plagiogyria* occupy an anomalous position in the whole system; moreover, the knowledge of their characters is still very incomplete; the prothallus has never yet been described, and the anatomy is still very imperfectly known. It thus appears desirable to submit them to a fresh examination, with the object of widening the basis of their comparison with other forms. More especially does this seem necessary in view of the fact that *Plagiogyria* alone of described Ferns appears to combine the distinctly oblique annulus of some Simplices and of the Gradatae with certain general characters of the Mixtae. It will be seen later that this conjunction of features usually distinct gives the genus a special importance in estimating the probable phyletic relations of the Mixtae to other relatively primitive types of Ferns.

As at present described, there are eleven species of the genus *Plagiogyria*; two of these inhabit the Western hemisphere, and one of them, viz. *P. semicordata*, (Pr.) Christ, was collected on Sir John Peak, on my recent visit to Jamaica; living plants and fresh spores were brought to Glasgow, as well as dry specimens and preserved material. The remaining nine species are Eastern, being chiefly represented in China and Japan; the material available was referred to *P. pycnophylla*, (Kze.) Mett., a species native in the north of Hindustan, the Malay Peninsula, and in Java; it was derived partly from Darjeeling, from Mr. Hemsley, and largely from Buitenzorg through the kindness of Dr. M. Treub. From the same source

¹ Das System d. Farne. Arb. aus dem k. bot. Gart. zu Breslau, i, p. 4.

² Engler und Prantl: Pflanzenfam., i. 4, p. 281.

³ Farnkräuter der Erde, p. 175.

⁴ Die Pteridophyten der Flora von Buitenzorg, p. 162.

I also received material of *P. glauca*, (Bl.) Mett. There is also in my hands material apparently of *P. pycnophylla*, collected by Dr. Lang on the Malay Peninsula. It is upon these supplies that the following description is based.

EXTERNAL CHARACTERS.

The stock in all of the species examined was upright and relatively massive, with a habit similar to that of the Osmundaceae; it projects above the soil for some inches to a foot in height, and is entirely covered externally by the persistent bases of the leaves of former seasons, which are enlarged, and coated with dark sclerenchyma. Occasionally the axis bifurcates, the branching being clearly dichotomous; this was specially observed in several examples of *P. semicordata*. In *P. pycnophylla* dichotomy was not seen, but here and there stolons are found attached to the stock; these may be attenuated at their base, taking there a horizontal or oblique course, and bearing at first only stunted scale-leaves; but sooner or later (and in some cases without any attenuated basal region at all) the stolon expands into a massive trunk, bearing numerous and more closely disposed foliage leaves. A formation of stolons was also observed in *P. glauca*, in essentially the same way as in *P. pycnophylla*, while dichotomy was not seen in that species. Stolons were not observed in *P. semicordata*. From the specimens examined it would thus appear that the terminal dichotomy of *P. semicordata*, and the lateral formation of stolons, as in *P. pycnophylla* and *glauca*, are complimentary methods of increasing the complexity of the shoot-system; *P. semicordata* has apparently retained the more direct and primitive, and *P. pycnophylla* has adopted a more indirect and probably a more recent method of carrying this out.

The leaves are of the simple pinnate type characteristic of the genus *Blechnum*, but they present several points of special interest, for the most part already noted by Mettenius; these are here detailed afresh in order to fill in the picture of the habit of the genus. The leaves form a dense terminal rosette, being arranged on a spiral plan which increases in complexity as the axis enlarges distally. There is a sharp differentiation of the broader sterile from the narrower and often longer fertile fronds. The foliage leaves are of a rather rigid texture in both species, while in *P. semicordata* there is a marked serration at the distal end of the pinnae (compare Mettenius, l.c., Taf. XV, Fig. 1); this is less marked in the leaves of *P. pycnophylla* (compare Kunze, l.c., Taf. CXXV). The leaf-base in both species is enlarged, widening out laterally, and thickening in a marked degree; on the abaxial side it bears a projecting flange, which is specially prominent in *P. pycnophylla*; on either side of this, but not maintaining any degree of regularity in number or in position, are the well-known 'aerophorae' of Mettenius, which appear in the mature leaf as projecting brownish masses of pulverulent tissue leading through the dense

sclerotic covering to the softer tissues within. Passing upwards the enlarged leaf-base tapers gradually without any definite limit into the petiole, which is more or less clearly four-angled, while dwarf wings project slightly from the lateral faces. In the upper region of the leaf the pinnae are inserted upon these wings; in *P. pycnophylla* the pinnae are some little distance apart from one another, and are very shortly stalked, but in *P. semicordata*, especially towards the tip of the leaf, they run together at their bases, so that the rachis is quite continuously winged; these features are repeated in the fertile leaves, though in less pronounced degree (Pl. XXXII, Figs. 1 and 2). The venation is of the sub-Taeniopterid type (Mettenius, l. c., p. 1), and the forking of the veins is inconstant; a considerable number of them run to the margin unbranched, there traversing the minute serrations which are specially prominent in *P. semicordata*.

In the young circinate condition the leaves are completely covered with a dense felt of curly hairs, which are septate, unbranched, and terminated by a single large cell with mucilaginous contents; in essentials they are similar to those of the leaves of the Osmundaceae. Peltate scales are entirely absent, as noted by Mettenius (l. c., p. 1). In this condition the young leaf is completely protected from risks of evaporation from its surface. The felted covering is more strongly developed in *P. pycnophylla* than in *P. semicordata* or *glauc*.

Probably in intimate relation to this is the development of those 'aerophorae' described by Mettenius, or pneumatophores as they would now be called. Their presence on the leaf-base has already been noted, and drawings of them are given in most illustrated treatises; they are here represented as seen on the bases of young leaves of *P. glauca* in Figs. 3 and 4. In the upper region of the leaf they were also recorded by Mettenius as occurring in *P. pycnophylla*, one at the base of each pinnule; here they are clearly to be seen in the mature leaf (Fig. 1); but it is in the young condition, while the leaf is still circinate, that they are most prominent (Figs. 5 and 6). In *P. semicordata*, though the pneumatophores are present on the leaf-base, they are not recognizable on the distal region of the leaf. This may be put in relation with the fact already noted that the hairy investment is less developed in this species than in *P. pycnophylla*.¹

¹ Pneumatophores are well known as prominent objects on the leaf-base in the genera *Alsophila*, *Hemitelia*, and *Cyathea*, where they are often of large size; in the mature state of the leaf they appear as roundish or oval pores traversing the hard sclerotic coat, and are filled with friable and dry tissue (see Mettenius, l. c., pp. 3-5, where are also references to other writers). In the upper leaf of these Ferns there are along the marginal wings, and especially close to the bases of the pinnae and pinnules, pale and slightly turgid spots, which show by the presence of stomata and by the spongy subjacent tissue that they are of importance for ventilation. They do not, however, project beyond the surface to any considerable degree. But occasionally at spots corresponding to these the tissues grow out into processes of considerable size, and the 'aerophorae' or pneumatophores in the upper leaf of *P. pycnophylla* are cases in point. Similar processes are seen also in *Dryopteris* (*Polypodium*) *decussata*, (L.) Urban, and in *Dryopteris* (*Polypodium*) *Thomsonii*, (Jenm.) C. Chr.

The fertile leaves resemble the sterile, except that their pinnae are narrower, and their margins sharply recurved so as to protect the sporangia (Figs. 1 and 2). These are borne in large numbers upon the slightly enlarged receptacles which lie above the distal ends of the veins; the sori are thus slightly elongated between midrib and margin. They seem to be always distinct laterally, and the insertion of sporangia on the leaf-surfaces between the veins, as described by Mettenius (l. c., p. 5), has not been observed.

On the same page of his memoir as that just quoted, Mettenius also describes for *P. scandens* (l. c., Fig. 21) how the neighbouring secondary nerves of the pinnae are joined by intramarginal anastomoses. *P. scandens* from the Khasya hills has since been reduced to *P. pycnophylla*; of this species I have material from Darjeeling and from Java; in neither of these was any evidence found of such anastomoses. So far as my observations go the secondary veins are never united distally, and the sori which they bear are always laterally distinct from one another, except in those cases where there has been a basal forking of the vein.

The roots are of the usual Fern type; they are not so numerous as in some other upright growing Ferns. Judging from the appearance in transverse sections, there are on the average more than two to each leaf; but they do not arise in any definite or constant numerical relation to them (Fig. 6). They spring from the central dictyostele, and usually arise from the margins of the foliar gaps.

ANATOMY.

The anatomy of the genus *Plagiogyria* has received little attention hitherto. Mettenius (l. c., p. 3) has recorded the fact that in *P. semicordata* a single vascular bundle enters each leaf from the stem; this then divides into three as it passes into the swollen region of the leaf-base, but the

It is to be noted that they are associated in these Ferns with a voluminous and slimy secretion completely covering the young circinate leaf; it arises from numerous branched hairs, the distal cells of which are enlarged as in *Osmunda* and *Plagiogyria*, and produce mucilage internally. It appears probable that there is a relation between the existence of the mucilaginous covering over the young part and the formation of the projecting pneumatophores; the latter are longer in the cases quoted than the thickness of the mucilaginous investment of the young part, and therefore project beyond its surface; thus they would readily serve the purpose of gaseous interchange to the tissues within (compare Fig. 5). Moreover, their most important function appears to be past on the development of the leaf, for then they are apt to shrivel. From these facts the conclusion seems justified that they are provisions for the aeration, not of the mature parts, but of the young parts while covered by mucilage, and thus cut off from ready gaseous interchange with the atmosphere. It is to be noted, however, that they are not always present where even a thick mucilaginous felt exists; this is shown by the case of the Osmundaceae. From a morphological point of view they cannot be held as parts of high importance for purposes of comparison, since their inconstancy, even within a genus, indicates that they are opportunist growths, rather than permanent morphological features in any phylum.

Organs similar to those described above have been noted by Kühn (Flora, 1889, p. 486) in *Nephrodium stipellatum*, Hk., and an abstract of his results appears in Haberlandt's Phys. Pflanzen-anat., 4. Aufl., p. 400, where the same function is attributed to them as suggested above.

branches again unite at the upper limit of the swelling into a single strand, and in this form it passes up through the whole length of the leaf. The only statement I know as to the structure of the stock is by Gwynne-Vaughan;¹ he figures a transverse section of a rather small stock (l.c., Fig. 10), with the remark (l.c., p. 697) that it is radially dictyostelic, but still remains very close to solenostely.

A transverse section of a large stock of *P. pycnophylla* accords entirely with this description (Fig. 6); it appears very irregular in outline as a consequence of the closely aggregated leaves with their decurrent insertion. Their arrangement is on a complex spiral, which varies with the size of the stock. Each is plainly served by a single V-shaped vascular strand, which is accompanied on its way by a broad flanking sheet of dark sclerenchyma on its outer side, and a small patch of the same in the fork of the V. Each leaf-base is subtended on its adaxial side by a deep involution of the surface, of semilunar outline convex inwards, and lined by sclerotic tissue. It will be observed, by comparison of the leaf-traces in the section figured, that internally, opposite each leaf-trace at its first separation from the axial stelar ring, there is a patch of sclerenchyma; as the leaf-trace passes outwards this sclerenchyma expands, taking gradually the semilunar form; it is in the middle of these patches that the involutions make their appearance, widening out (as seen in the transverse section) till the leaf-base which each subtends is completely separated from the stock. A similar involution has been noted in other Ferns, and among the Helicogyrate types which show it are *Anemia* and *Onoclea*.²

The middle of the massive axis is occupied by a column of pith, the central region of which is sclerotic, while isolated smaller strands of sclerenchyma about its periphery mark the position where the successive foliar gaps will be formed by passage outwards of the leaf-traces. Surrounding the pith is an almost complete solenostele, interrupted only here and there by the separation of the foliar traces from it: these appear first as outwardly projecting bays opposite to the sclerotic strands already mentioned, and finally they break away from the solenostele by abstriction right and left. The roots, which are seen in large numbers traversing the cortex, spring as a rule from the margins of the gaps thus left by the outgoing traces.

The stelar ring is delimited internally and externally by a brown coloured endodermis, which is continuous through the foliar gaps, and is lined internally by a pericycle of 1–3 layers. The phloem is abundant both

¹ Solenostelic Ferns, II. Ann. Bot., xvii (1903), p. 689. Gwynne-Vaughan names the plant on which he worked *Plagiogyria biserrata* (= *Lomaria semicordata*); but as his material came from the Eastern tropics this cannot be correct; there are no herbarium specimens of the same collection, so it is impossible to check the determination; but all the characters point to the plant having been *P. pycnophylla*.

² Compare Gwynne-Vaughan: On the possible existence of a Fern stem having the form of a lattice-work tube. New Phyt., iv, p. 211.

on the peripheral and central sides of the xylem, but thins off considerably at the foliar gaps. The xylem, which is massive, is composed of tracheides with parenchyma scattered through it; the protoxylem is not clearly defined when seen in the mature condition.

The leaf-trace is initiated in the stelar ring, and may be recognized early by an indentation of the inner limit of the xylem opposite one of the sclerotic groups in the pith, which, as mentioned above, subtend the leaf-trace, and accompany it outwards. As this indentation deepens a group of small tracheides (protoxylem) intermingled with parenchyma becomes apparent at its apex, while opposite it the outer limit of the xylem becomes strongly convex, forming the projecting bay already noted. Subsequently, by abstrictions of the stelar ring at some distance right and left of the indentation, with incurving of the sheaths, the leaf-trace is separated, and passes outwards. Entering the leaf-base, which is deeply keeled so as to be triangular in section, the leaf-trace widens out, and loses its acute shape, the apex of the V expanding and rounding off; the sclerenchyma meanwhile

TEXT-FIG. 1. Transverse sections of the petiole of *P. pycnophylla*. *A* is taken from a point above the basal swelling; *B*, from a point about the middle of the swelling, and it traverses two of the pneumatophores. *C* is from a point near to the insertion of the leaf upon the axis.

spreads out so as to ensheath the whole strand, the periphery of the section being also covered by a hard sclerotic band (Text-fig. 1, *C*). A section higher up shows the leaf-base further enlarged, and the strand widened out still more, especially in its middle part, while the section may often traverse one or more of the large pneumatophores, which are seated on the oblique abaxial faces (Text-fig. 1, *B*). As the upper limit of the swollen region is reached the vascular strand again contracts, and its sclerenchymatous sheath disappears; the adaxial surface of the strand becomes slightly crenate; examination of these crenations shows that they correspond to the groups of cavity-parenchyma (*Lückenparenchym*), which indicate the position of the protoxylem-groups; the number of these is about nine, three on each of the lateral flanges, while of the other three one is median, and the other two are right and left of it at the angles of the sharp curvature of the leaf-trace (Text-fig. 1, *A*). This structure is maintained upwards to the point where the pinnae are borne. The structure of the leaf-base is found to be the same in *P. glauca*.

A curious difference of vascular structure is, however, seen in the leaf-base of *P. semicordata*. It was noted by Mettenius (l. c., p. 3, and Figs. 12 and 13) that the leaf-trace in this species divided into three strands in the

enlarged leaf-base, but that these unite again at its upper limit, traversing the rest of the petiole as a single strand. The main fact is correct, but there seems to be some indefiniteness in the exact point of reconstruction of the single strand. Transverse sections at the base of the leaf show a single vascular strand of V-shape, but very soon the apex of the V widens out, and in place of the single angle there are two, as in the letter W, with a very flattened middle angle (Text-fig. 2, *d*). At each of the lateral angles of the W is a protoxylem-group, while the metaxylem forms a continuous strap-shaped band with a slightly hooked adaxial curve at either of its two margins; then follows a pericycle of several layers, and the endodermis. Thus the structure in essentials is the same as in *P. pycnophylla*, but there is considerable difference in the proportions, while the number of protoxylem-groups is smaller, and the vascular strap much narrower. A little higher up from the base the xylem becomes constricted at a point some distance from its margin, so that a mass about equal to a quarter of the whole is separated off from the rest; the phloem and sheaths also curve inwards, and a marginal strand is thus constricted off; the same happens (but not necessarily at the same level) at the other margin, so that the condition is reached of a larger median strand, which is placed abaxially and has two protoxylems in its concavity, and two smaller marginal strands slightly nearer the adaxial surface of the leaf (Text-fig. 2, *b*, *c*). This state is maintained for some distance upwards, and in one case which was followed out the strands remained separate for some six inches above the enlarged base, and were reconstituted to a single strand only in the last half-inch of the rachis below the lowest pinnae. The reconstitution of the single strand repeats in converse the steps of disintegration which took place below (Text-fig. 2, *a*). The result is that in the upper region of the leaf the strand of the rachis is similar in all essentials to that of *P. pycnophylla*, but the protoxylem-groups are fewer, the median one being absent, while the more pronounced W-shape of the middle region is a curious specific difference, which seems to go along with the absence of the median protoxylem.

In order to verify the position and relations of the protoxylem in the axis and bases of the leaves of a well-grown stock of *Plagiogyria*, serial sections have been cut through the apical region, so that the actual position of those xylem-elements which are earliest lignified may be directly observed (Fig. 7). It is some time after the stelar tube is already defined in the

TEXT-FIG. 2. Transverse sections of the petiole of *P. semicordata*. *a* is from a point below the lowest pinnae, and it shows a single strand. *b* is from a point lower down, and the strand is seen to have divided into three. *c* is in the swollen region of the leaf-base, and the strands are uniting again. *d* shows the strands fully united as they are seen at the base of the petiole before insertion upon the axis.

young stem, as seen in transverse section, that the first lignification of the xylem takes place ; prior to that event it is easy to make out the outlines of the dictyostele, and to recognize where the initiation of the foliar traces will occur ; these are first indicated by the appearance of a group of tracheides in a mesoxylic position. That the position is originally mesoxylic is clearly seen in Figs. 8 and 9, the former of which shows the very first lignification of two tracheides, with the young tracheides of the metaxylem still thin-walled, but easily recognized ; the latter represents an older state with metaxylem surrounding the smaller protoxylem-elements. The reason for being quite explicit on this point is that, on passing upwards from the point where the protoxylem is first recognizable, the mesoxylic position is soon lost ; the indentation of the margin of the stele appears as above described on the side adjoining the pith, and the metaxylem shifts right and left, with the effect that the protoxylem appears as though it were endoxylic ; but that is not its original position : in the first instance it is mesoxylic. Opposite each indentation of the stelar tube the band of sclerenchyma which subtends each leaf-trace may early be recognized, first as a projection from the large central core, and later as a separate band, which passes outwards, taking a position in the angle of the leaf-trace ; these points are readily observed in Fig. 7. The central protoxylem of the leaf is usually a single group (*P. pycnophylla*), though cases have been seen in which two groups are present from the first, separated by a median tract not yet lignified (*P. glauca*). About the same time a discontinuous fringe of protophloem makes its appearance on the abaxial side of the stelar tube. Passing upwards along the stelar tube the indentation opposite each leaf-trace deepens, and the protoxylem widens out ; sooner or later it divides into two strands, disposed right and left, a division which is usually completed before the margins of the V-shaped leaf-trace are abstricted from the stelar tube. These two protoxylem strands diverge further as the leaf-trace passes out, and run directly into the two abaxial angles of the W-shaped meristele of the petiole, as described above (Text-fig. 1). About the same level as this forking of the first protoxylem-group, or a little later, there appear two other protoxylem-groups at some distance right and left of it ; they do not always appear simultaneously, and in point of origin they are quite distinct from the median protoxylems ; they pursue their course upwards into the margins of the foliar strand. In the stelar tube itself meanwhile, apart from the protoxylem-groups thus noted, no definite protoxylem is apparent, but the lignification which begins sporadically, and chiefly towards the exterior of the stelar tube, soon becomes general. (Compare Fig. 7 for the position of the protoxylems in the whole section.)

In *P. semicordata* the two protoxylems at the median region of the leaf-trace continue their separate course upwards into the leaf-base, and occupy the angles of the W-shaped strand ; the abstriction of the strand

upwards into three, peculiar to this species, takes place so that the median protoxylem-groups remain in the central strand of the three, while the lateral protoxylems continue into the two lateral strands; in fact the abstriction is only a temporary interruption of the metaxylem, and of the tissues and sheaths surrounding it. In *P. pycnophylla* and *glauc*a, however, there are usually three protoxylems in the central region of the leaf-strand as it passes into the basal region of the leaf, the third one (and sometimes more) appearing in a median position, but not by branching of the original one. In the lateral arms of the leaf-trace also, as it passes upwards into the leaf, a multiplicity of protoxylem-strands appear on the adaxial face, their position being indicated in the mature state by groups of cavity-parenchyma, as already noted.

In following up the details of dichotomy as seen in the mature stem of *P. semicordata*, by means of serial sections successively from below upwards, the first change is in the division of the central sclerotic core into two by constriction, together with the widening of the dictyostele into an

TEXT-FIG. 3. Five successive sections of the stock of *P. semicordata*, showing the disposition of the vascular tissues at the region of a dichotomy; the lowest section is to the left, and shows the central sclerotic core already divided before the stele itself becomes constricted. ($\times 2\frac{1}{2}$.)

elliptical outline, but without any cessation of the usual formation of foliar gaps where the leaf-traces pass off (Text-fig. 3, *a*). When the two sclerotic cores have separated completely from one another, and have passed to the poles of the ellipse, the stele begins to encroach inwards on either side (Text-fig. 3, *b*); the projecting surfaces meet, and the several tissues successively fuse (Text-fig. 3, *c*); the process is accompanied by involution of the outer surface of the stele (Text-fig. 3, *c, d*), and this is continued till the several tissues separate again, the division being now in a plane transverse to the axis of the ellipse; the xylem separates first, then the phloem, and finally the sheaths. The result is the formation by fission of two equivalent steles (Text-fig. 3, *e*). Throughout the whole process leaf-gaps and foliar strands are formed from both of the steles, even obliquely on the sides of them which face one another. The structure shows plainly that it is a case of true dichotomy, resulting in two initially equivalent shanks.

All the material available for the study of the anatomy of *Plagiogyria* has been of old plants, with the dictyostelic structure fully developed, but it has been seen above that *P. pycnophylla* bears stolons, arising in close

conjunction with the leaves. Since Prof. Gwynne-Vaughan has concluded from the study of the lateral shoots of various Ferns that 'the ontogeny of the vascular system of the plant as a whole is very frequently repeated, although more or less imperfectly, in the development of the lateral shoots' (l. c., p. 724-5), this turns attention with special interest to the stolons of *P. pycnophylla*.

The origin of the stolons appears to be always in connexion with the leaf-base, and from the adaxial side of it; but there is some variety in the proportionate size of the subtending leaf and of the stolon which it bears, and this presents an interesting morphological condition in certain cases. A simple example is seen in Fig. 10, where the subtending leaf has developed to a considerable size, and shows at its apex the circinate curvature; it is in fact normal, but arrested in an early state. From its adaxial side has arisen the stolon, in this case a narrow one, with long internodes. In other cases, however, the stolon is larger in proportion, and the subtending leaf is smaller, being arrested in its growth at an earlier stage; when this is extreme the appearance is as if the leaf-apex were substituted by a stolon, though in face of the former cases this cannot be accepted as the correct interpretation of them. The internal vascular structure accords well with these results of external observation.

The attachment and basal structure of a relatively thin stolon is illustrated by the series of transverse sections in Fig. 11 (I-XIII), while they show also the relation of the stolon to the leaf, the adaxial face of which is constantly turned to the left in these drawings. In (I) the keeled leaf-base is shown traversed by a vascular strand which is, however, more contracted than it is usual for the leaf-trace to be; this becomes crescentic higher up, with the horns directed abaxially (II), and thickens (III); soon a region differentiates in the centre of the xylem (IV), consisting of phloem, pericycle, endodermis, and sclerenchyma in succession inwards from the xylem, which has now opened into a complete ring; except for the slight lateral horns the structure is very similar to that shown in the internode of *Davallia aculeata* by Gwynne-Vaughan (l. c., Pl. XXXIV, Fig. 20); the strand has in fact widened into a solenostele, which still retains, however, the abaxial horns of the original foliar crescent. Presently the ring opens on the abaxial side (VI), and a part of the ring representing its abaxial region between the two horns abstricts first by one margin then by the other, and separating completely (VII, VIII) passes on as the vascular supply of the abortive leaf-apex. The solenostele very shortly closes the gap (IX, X), the point of closure remaining obvious for some time as a thinner region; the ring soon opens again, but now on the adaxial side (XI), to give off the vascular supply of the first scale-leaf of the stolon (XII, XIII).

An example of a typically solenostelic structure is seen in Text-fig. 4,

which is taken from a stolon of considerable thickness, but with long internodes; that is in fact the usual structure in such cases.

The details of relation of the stolon to the subtending leaf do not, however, appear to be constant, as is shown by Fig. 12, I–V. These were taken from a thicker stolon with a closer arrangement of the leaves, and since the leaf-gaps overlap the condition is dictyostelic though of a simple type. A comparison of these with Fig. 6, from a larger stock, shows that the former is constructed on the same plan as the latter, but simpler. It will be noticed that the leaf-trace is a single V-shaped strand, and that as it is given off the stele opens, a portion of its vascular tissue separating off first from one then from the other of the margins of the meristeleles which remain: as in the larger axes a strand of sclerenchyma parts from the central sclerotic core of the axis, and passing outwards inaugurates the involution of surface which finally separates the leaf from the axis. The origination of the leaf is marked externally by the projecting keel, which is apparent even below the level of separation of the leaf-trace. In Fig. 12, I,

TEXT-FIG. 4. A typically solenostelic stolon of *P. pycnophylla*; the dark shading indicates the sclerenchyma, the lighter shading shows the stele. ($\times 4$.)

TEXT-FIG. 5. Three successive sections transversely through a stock of *P. pycnophylla*, of which *a* is the lowest, showing the origin of a stolon (*st*) in place of a leaf; *b* and *c* show its complete separation from the dictyostele of the axis, with a protostelic structure. ($\times 2$.)

which is the lowest of the series, a leaf-trace has passed outwards from the stele, together with its accessory sclerenchyma, which also isolates itself from the central sclerotic core. It may be noted further that roots have arisen right and left from the meristeleles near to the points where the leaf-strand had separated from them. In section II each of the shanks

of the V has put out a process from its inner face, while there is a rounding off of the apex of the V so as to give a circular internal contour; the ends of the divergent shanks of the V then become abstricted (see section III, which, however, shows that to the right still attached); after pursuing a short independent course they both end blindly. Meanwhile, the remainder of the leaf-strand closes into a complete circle, and in fact becomes a solenostele, while the sclerotic strand widens out laterally, and forms a slit centrally (section IV); higher up this widens as in the case of a normal leaf, and thus the secondary stolon passes off from the primary stolon which produced it. Section V of the series shows the parent stolon after the separation is complete.

How nearly a stolon thus produced may in position and in outline correspond to a leaf is shown by a tangential section represented in Fig. 13; here the stolon ranks with the leaves in position and in form; in fact the only feature which distinguishes it is the vascular supply, which has clearly the character of a solenostele. Moreover, if the origin of the 'trace' of such a stolon be examined in a series of sections of the stock, it will be seen that it originates just as a leaf-trace does; but it may be found to differ in form and outline from the very first (Text-fig. 5, *a*), while as it passes outwards it assumes a protostelic structure and circular outline (Text-fig. 5, *b*, *c*).

Clearly this history of origin of a stolon differs from that previously described; here the leaf appears to be completely replaced by the stolon; its vascular supply is mainly taken up in constituting the solenostele, while the remainder terminates in blind endings right and left. In the previous case the leaf has an apex which is traversed by a vascular strand, but early arrested; there is a difference also in the origin of the solenostele of the stolon from it. Without the history of development of the stolon from its first stages, for which the material did not suffice, it is impossible to be sure whether or not the apex of the leaf is ever involved, but certainly in some cases the origin of the stolon is on the adaxial surface at some distance from the apex.¹ Mettenius² has drawn attention to the variation in position of the buds in the Hymenophyllaceae, sometimes on the axis, sometimes axillary, and again sometimes upon the leaf-stalk itself, but always subtended by the leaf. The case of *Plagiogyria* appears to be of the same nature, but it plays in a region further removed from the leaf-base. This latter fact may be related to the closer aggregation of the leaves upon the shoot, and Mettenius has already discussed this point (l. c., p. 625) in the case of the Hymenophyllaceae with crowded leaves, in which also he found the position of the bud to be some distance from the leaf-base.

¹ It is not possible to say how far the case of *Plagiogyria* corresponds to any of those examples worked out developmentally by W. Kuppner, *Flora*, 1906, p. 337.

² Ueber Seitenknospen bei Farnen, p. 615.

The apparent merging of the leaf into the stolon seen in some of the cases in *Plagiogyria* may be compared with the transitions from leaf to stolon described by Goebel in certain species of *Utricularia* ('Organography,' Engl. ed., vol. ii, p. 240). He states that 'we find all transitions between foliage leaves and stolons, for instance in *Utricularia longifolia*, *U. bryophila*, *U. coerulea*, and others'. The stolons of *Plagiogyria* seem similarly to fluctuate between the two types of structure, but here it is a matter of balance between the leaf-primordium and the stolon-primordium, and the resultant structure seems to take the character of the more prominent partner.

From the description thus given of the vascular structure at the base of the stolon in *P. pycnophylla*, it appears that there may be a short basal region which is technically protostelic; this is followed by a region which is solenostelic with leaf-gaps at intervals, a structure which is characteristic of the lower part with long internodes; it is succeeded by a dictyostelic region, where the leaves are more closely disposed and the leaf-gaps overlap, this being the condition of the mature stock. Similar results were obtained from *P. glauca*; the bases of the stolons were there found to be clearly protostelic, but the stele widened out rapidly to the solenostelic and dictyostelic state, the stolons in the material available being short, and expanding at once into leafy buds. These observations are of interest in showing the primitive vascular condition of the stolons at their base, which has its special bearing where, as in *Plagiogyria*, the adult structure is not far removed from solenostely.

The structure of the root is diarch, and calls for no special remark.

It has been pointed out elsewhere ('Land Flora,' p. 659) that in Eusporangiate types the segmentation of the apex of the stem, root, leaf, and of the wings of the leaf, is more complex than that seen in the Leptosporangiate Ferns, and that this is shared in some degree by the Osmundaceae; in fact that there is some accord between the segmentation of the sporangium and that seen in the embryonic condition of the tissues of the several vegetative parts. It becomes then an interesting question to see what is the state in *Plagiogyria*, a genus in which some analogy has been recognized with the Osmundaceae.

It may be said briefly, and without entering into unnecessary detail, that the segmentation of stem, leaf, and root of *Plagiogyria* has not been found to depart from the usual Leptosporangiate type; the wings of the leaf also show the usual marginal series, with a regular segmentation (Fig. 14), a condition shared by all other Leptosporangiate Ferns, as far as is known, with the exception of the Osmundaceae, which latter occupy a peculiar primitive position.

SORUS AND SPORANGIUM.

The mature sorus and sporangium of *Plagiogyria* have been described by Mettenius (l. c.), and his figures have been quoted by Diels (Engler and Prantl, i, 4, p. 281). But hitherto no account has been given of the development which would make it possible to enter on an exact comparison with other Ferns. The drawing of Mettenius, quoted by Diels as his Fig. 149, F, gives a very fair idea of the disposition of the sporangia upon the forked veins; this is shown also in our Figs. 1 and 2, respectively for *P. pycnophylla* and *P. semicordata*, while it is in the former species that the development has been traced. Sections of the young pinna show that the veins cause a convex swelling of the surface, and it is upon the receptacle thus formed that the sporangia make their appearance (Fig. 15, *c*). Those first formed are almost simultaneous in their origin, but they are followed later by others which are interspersed amongst them; and thus sporangia of various ages are in juxtaposition, giving the sorus the well-known character of the Mixtae. Fig. 18, *c*, shows the outline of such a sorus in a section traversing it transversely, while the sections shown in Fig. 15, *a*, *b*, represent what is seen when cut in a direction following the course of the vein: these two latter sections were cut from the same pinna, and a comparison of them with Fig. 15, *c*, shows that there is no fixed succession of the sporangia such as is seen in the Gradatae. A comparison of numerous sections has disclosed no regular seriation in time of appearance of the sporangia; in fact the sorus is a mixed one, but the formation of the interpolated sporangia is not long continued.

The sporangium originates from a single cell, which has a square, or more commonly an obliquely wedge-shaped base; it soon projects convexly, and segmentation begins by a wall inclined downwards so as to impinge upon one of the sloping sides of the wedge-like base (Fig. 16, *a*); this is according to the type of segmentation seen in *Alsophila* and *Cyathea* (see 'Land Flora', p. 637, Fig. 349, *c*). This wall is succeeded by others inclined to the first (Fig. 16, *b*, *c*) in the usual manner of Fern-sporangia, followed by a cap-cell (Fig. 16, *d*). A comparison of these drawings, together, and with Fig. 16, *e*, *h*, shows that there is some variation of detail in the basal region of the sporangium, and in the first segmentations; but they all result in a relatively massive stalk, which is a natural consequence of the deep inclination of the first segment-wall. It may be remarked that in the case of the larger sporangium shown in Fig. 16, *d*, the first segment-wall must have impinged directly upon the periclinal basal wall, after the manner characteristic of the Schizaeaceae, *Thyrsopteris*, and *Trichomanes* ('Land Flora', p. 637, Fig. 349, *d*). In older sporangia the cells of the stalk subdivide so that when mature it is commonly composed of six rows of cells in the distal region just below the sporangial head (Fig. 17, *a*, *b*);

the structure may, however, be simpler in the lower region of the stalk. In the sporangial head the segmentation to form the tapetum follows the usual plan (Fig. 16, *f*, *g*), and it later divides into two layers (Fig. 16, *h*), and becomes disorganized in the usual way (Fig. 17, *c*, *d*). Meanwhile, the cell remaining at the centre divides to form the spore-mother-cells, apparently twelve in number, and the further development proceeds in the usual way. The total output of spores per sporangium appears to be forty-eight. This is a feature which *Plagiogyria* shares with many of the *Gradatae* and *Mixtae*, but it is to be noted that a limited spore-number (48–64) is also seen in *Matonia*, while in the *Schizaeaceae* the spore-numbers are not high as compared with what is seen in others of the *Simplices*. The spores themselves are tetrahedral, and when fully ripe numerous highly refractive globules are found attached to their external walls; the attachment is not a very close one, as is shown by the fact that they are easily separated in the mounting, and may be found lying in the mounting medium apart from the spores; they are formed just before the maturity of the spore. Apart from the globules the wall of the spore has no very distinctive markings; in general character it shows some similarity to that of *Lygodium* (Engler and Prantl, i, 4, Fig. 192, J), but the spore-characters cannot be held to be altogether trustworthy for comparison among the *Simplices*, as both in *Schizaeaceae* and *Gleicheniaceae* they are variable within the order. The tetrahedral type is, however, the prevalent one among the early *Filicales*.

The mature sporangium has been depicted by Mettenius (l. c., Figs. 2 and 3), and his drawings have been copied by various later authors; they do not, however, give all the detail for necessary comparison with those of other Ferns, especially when it is remembered how important a part the sporangial structure plays in arriving at conclusions as to phyletic relationships.

The mature sporangium is long-stalked (Fig. 18, *a*, *b*), in fact quite unusually so among Ferns with oblique annulus, in which the sporangia are as a rule short-stalked, or sessile. A comparison in this respect may be made, on the one hand, with the *Osmundaceae*, and ultimately with some *Botryopterideae*; on the other, with *Gleichenia* § *Mertensia*, and especially with *G. dichotoma* ('Land Flora,' Fig. 310, and text, p. 556); with the latter there is also correspondence in the absence of any central cell or cells in the transverse section of the stalk, which is an indication of the less massive structure of the sporangium. There is a gradual transition from the sporangial stalk to the head, giving the whole body that pear-like form which is so conspicuous in *G. dichotoma*; it appears also in *Loxsonia* ('Land Flora,' Fig. 320, p. 572), and in certain species of *Dicksonia* ('Land Flora,' Fig. 330, p. 593). The head is traversed obliquely by the annulus, which is a complete ring, as recognized by the sequence of the cells, though there is variety in the manner of their induration; there is also some irregularity in their form and number—thirty being about the average; there is also some variability in

their sequence, while occasionally single cells of the sporangial wall quite distinct from the annulus may be indurated. But putting these irregularities aside, the annulus of about thirty cells takes an oblique course round the sporangium, being quite continuous past the insertion of the stalk. The obliquely distal area of the sporangial wall surrounded by the annulus, seen in surface view in Fig. 18, *b*, clearly corresponds to the 'peripheral' face in the Gleicheniaceae type, and is here, as in *Gleichenia*, only slightly convex; while the rest of the thinner part of the wall to which the stalk is attached is strongly convex, and corresponds to the 'central' face of *Gleichenia* (Fig. 18, *a*). A similar comparison may be drawn also with *Dicksonia*. Comparing with the Schizaeaceae, the differences appear at first sight more striking than the resemblances, for in most of them the 'peripheral' face is greatly reduced; but it has been seen that the nearest anatomical correspondence is with *Anemia*, and in this genus the 'peripheral' face is larger than in any other genus of the Schizaeaceae; in fact, notwithstanding its short stalk, its apparently transverse annulus, and its peculiar form, the type of sporangium is essentially the same in *Anemia* as in *Plagiogyria*. It is not desirable to press such comparisons too much into detail but it is worthy of remark that on the side of the annulus nearest to the stalk in the sporangia shown in Fig. 18, *b* and *d*, the series of cells is duplicated; this corresponds exactly in position to that extension of the annulus down the side of the sporangium in *Anemia* which is related to the function of dehiscence (compare Engler and Prantl, i, 4, Fig. 192, *g*). Turning to the mechanism of dehiscence as seen in *Plagiogyria*, this leads to the formation of a lateral slit, as in *Dicksonia* and most other Gradatae; but the structural provision for it shows some variability, which may be held to suggest the sort of changes which would be involved in a shifting of position of the dehiscence. In the sporangia of the Simplices there is no highly organized 'stomium'; and this applies equally for *Anemia*, with which comparison has above been drawn. In *Plagiogyria* the dehiscence is localized laterally by a well-organized mechanism; but a comparison of various sporangia of this plant shows that there is uniformity neither in the exact position nor in the size or number of the cells which determine it. There is usually a well-defined group of four sister cells, which constitute the actual stomium (Fig. 18, *a*, *b*); on either side of it (sometimes in immediate juxtaposition with these, or sometimes not) is a group of thin-walled cells, which, however, vary in number; thus on the distal side of the stomium there may be only one of these cells (Fig. 18, *d*), or two (Fig. 18, *c*), or three (Fig. 18, *a*, *b*); on the proximal side there may be two (Fig. 18, *c*), three (Fig. 18, *a*), or four (Fig. 18, *d*), while they may be in direct juxtaposition with the group of cells of the stomium (Fig. 18, *a*), or removed from them on either side by the intervention of a variable number of indurated cells (Fig. 18, *b*, *c*). This variability, so different from what

is seen commonly in the sporangia of the Leptosporangiatae, is so marked that it again indicates that *Plagiogyria* occupies a position distinct from other Ferns with a 'mixed' sorus; nor is it apparent that the same variability holds in any of the Gradatae. It suggests that sort of plasticity which might have accompanied the shifting of the point of dehiscence from a median to a lateral position—a change which comparison indicates to have actually taken place in the phyletic transition from the Simplicies to the Gradatae and Mixtae.

If we regard the sporangium of *Plagiogyria* from the biological point of view, it will appear that it is not highly specialized in accordance with its requirements. There is no regular sequence of the sporangia in the sorus, consequently the oblique position of the annulus is not a feature of high moment. The induration shows a considerable interruption, the thin-walled region including the stomium; it extends down to, or even sometimes across the insertion of the stalk, so that a condition is arrived at which is not unlike that of the Polypodiaceous type; it has, however, the mechanical disadvantage in the case of *Plagiogyria* as compared with these that the end of the indurated annulus is not directed straight to the stalk itself, but obliquely towards it. The sorus not being a crowded one this point is probably immaterial. The retention of the oblique annulus, as in the Gleicheniaceae for instance, with only the modification of the dehiscence having been swung into a lateral position, is in no way surprising when it is remembered that there is only a slight departure here from the primitive sorus of the Simplicies.

There has been some difficulty in obtaining germination of the spores; the cultures of spores of *P. semicordata* from Jamaica came on very slowly, and prothalli are only sporadic, many spores failing to germinate. This may raise some doubt of the identification, though the prothalli observed appear in close relation to undoubted sporangia of *Plagiogyria*, and the form and character of the spores from which the individual prothalli arise are those above described. The difficulty of identification lies in the fact that, in the absence of the highly refractive globules above noted (which were seen not to be firmly attached to the mature spore, and seem to disappear on germination), no marked features remain beyond the tetrahedral form. Final certainty of identification must be awaited when the prothalli have produced young sporophytes.

The character of the prothalli observed are, in general, those usual for Leptosporangiate Ferns, being commonly symmetrical in form, and without any distinctive hairs or glands. The interesting feature is in the antheridia, of which the distinctive modes of dehiscence have been pointed out by Heim ('Flora,' 1896, p. 349); the one type characteristic of the Osmundaceae, Gleicheniaceae, *Lygodium*, Hymenophyllaceae, Cyatheaceae, and Dicksonieae, shows dehiscence by throwing off a lid-like cell, which

type may be held to be the more primitive ; the other is generally characteristic of the Polypodiaceae, together with *Anemia* and *Mohria* ; here the rupture is by breaking down of a distal cell, with the formation of a rosette-like aperture. The latter is the type seen in the antheridia of the prothalli attributed to *Plagiogyria* ; the process has been carefully watched ; first an increased convexity of the antheridial wall appears near to the distal end ; this gradually protrudes more and more, till rupture of the wall begins at one side of the cell ; the convex part of the wall is then turned back as on a hinge, and the spermatozoids come out of the opening ; there is no extrusion of a complete cell, but the wall of the distal cell is ruptured, and fragments of it remain attached to the antheridium, forming the star-like outline of the aperture.

COMPARISONS.

Comparisons may now be instituted between the characters of *Plagiogyria* as above described, and those of other Ferns, with a view to assigning to it an approximate position in the system.

In the bulky upright stock, with closely aggregated leaves and persistent leaf-bases, and showing at least in *P. semicordata* occasional dichotomy of the axis, characters are seen which are shared by such primitive types as the Osmundaceae ; this comparison is accentuated by the densely sclerotic tissues which compose it, and cover it externally. The deep involutions of surface which subtend the leaf-bases are closely similar to those seen in *Anemia* (compare Prantl, 'Schizaeaceen,' Pl. III, Fig. 27, *b*), a comparison which is further supported by the similarity in structure of the leaf-trace. The enlarged base of the leaf reminds us again of that in the Osmundaceae, but the details of its structure do not correspond with any exactitude. The pneumatophores which it bears (which are present also in the upper leaf of the Eastern species) are striking objects, and might be expected to give a valuable basis for comparison ; this is, however, in some degree discounted by the fact that they are not constant within the genus itself, being absent from the upper leaf in *P. semicordata*. But, putting this aside as not entirely depriving the comparison of value, the existence of similar organs in the Cyatheaceae is a matter for remark. Closely related causally with them, as already suggested above, are the very numerous glandular hairs which secrete mucilage ; such hairs are found plentifully in the Osmundaceae of the present day, and in other relatively primitive Ferns, while somewhat similar hairs were characteristic also of the ancient Botryopterideae. The absence of flattened scales is a feature of importance for comparison ; it differentiates *Plagiogyria* from the Cyatheaceae, as well as from the genus *Lomaria*, and when taken together with other primitive characters which the genus shows, indicates a relation with the lower rather than with the higher forms of Ferns.

Passing to the leaf itself, the simply pinnate form gives no distinctive point for comparison, but the serration suggests that it has been condensed from some more complex prototype. The simply forked venation points clearly to a primitive position, though, as is well known, many Ferns of advanced affinities still show it.

The existence of buds and stolons is a widespread feature in Ferns, but the peculiar relation which they bear to the leaf in *Plagiogyria pycnophylla* and *glaucæ* resembles in near degree that seen in the Hymenophyllaceae; in them, as has been seen, the bud is subtended by the leaf, but there is some variation in the position of the bud relatively to the leaf-base, and in some cases it appears to be borne upon the leaf; the condition of *Plagiogyria* would then be only a case of the further removal of the axillary bud from the basal position; as already suggested, this may be a consequence of the close aggregation of the leaves upon the axis, which would necessitate a more distal position for the accessory bud. It is true many other Ferns have buds associated with their leaf-bases, but none of them seem so nearly to correspond to what is seen in *Plagiogyria* as do the Hymenophyllaceae.

Turning to the anatomical features, it has been seen that the stolons show at their base a structure that is solenostelic, or even protostelic; in the absence of young plants this may be taken as evidence of a primary structure of the axis, such as is seen in various primitive types of Ferns. The mature axis shows a condition of dictyostely, though this is not of a high grade; the foliar gaps overlap, so that there is technically a dictyostelic state, but, as Professor Gwynne-Vaughan remarked, it is not far removed from solenostely, and it corresponds in fact to that seen in *Anemia*. The leaf-trace itself consists of a single strap-shaped strand, which again is a primitive feature, though shared by some Ferns which have progressed to higher differentiation; it is characteristic especially of the Simplices and Gradatae, and among them it is a feature of those types which are regarded as being anatomically the more primitive. In actual detail of structure the leaf-trace of *Plagiogyria* corresponds very closely with that of *Anemia* (compare Prantl's Figs. 30, 32, Taf. III of his 'Schizaeaceen'), while the whole vascular system of the axis corresponds also in its main features to that shown by him for the same genus (compare Prantl's Fig. 27, *a*, *b*, Taf. III, l. c.); there is, however, in *Anemia* only a single central protoxylem-group in the leaf-trace, while in *Plagiogyria* there are two or sometimes more; but, as has been seen, there is only one at the extreme base, so that the correspondence with *Anemia* is the closest at this point, where the leaf-trace originates (compare Boodle, 'Ann. of Bot.', vol. xv, p. 382). The mesoxyle origin of the protoxylem of the leaf is a character shared with many Ferns; its quick fading out as it enters the axial system is matched by what is seen in *Anemia* (Boodlè, l. c., p. 384). The general character of the vascular

system of *Plagiogyria* is thus relatively primitive, but with distinct advance beyond what is seen in the earliest types; the closest correspondence being with *Anemia*, which, though it belongs to the primitive Schizaeaceae, is one of the most advanced members of that anatomically variable family.

Turning to the fertile leaf and sorus as seen in *Plagiogyria*, the general habit, with narrow pinnae having their margins reflexed like an indusium over the superficial sori, at once suggests the old comparison with *Lomaria*, or stated more generally, with the Pterideae as a whole. But it is to be remembered that the same holds, though with less closeness of the parallel, for the fertile leaves of *Gleichenia* & *Mertensia*; for though here the margins are not thinned off in the membranous fashion of the Pterideae, the venation corresponds in point of the absence of fusions with that of *Plagiogyria*. On the other hand, though *Lomaria* and *Pteris* habitually show fusions of the venation, many of the simpler Pterideae show a complete absence of vein-fusions; this is conspicuously the case with *Cryptogramme* and *Llavea*, genera with which *Plagiogyria* has been specially related by Diels (Engler and Prantl, i, 4, p. 281).

The superficial sorus of *Plagiogyria*, so far as the observations here recorded are concerned, is restricted to the vein, but extended along it, borne on a slightly enlarged receptacle; it is not unlike what would result from an elongation of a sorus of the type of *Gleichenia pectinata* or *dichotoma*, or, on the other hand, it may be directly compared with that of *Cryptogramme* or *Llavea*, to which it corresponds very closely. As regards the composition of the sorus, it has been noted that most of its sporangia arise simultaneously, as is the case in the Simplices; but that subsequently others are interpolated between those first formed, giving the sorus the character of the Mixtae. This character is also shown by *Cryptogramme* and *Llavea*, but it is worthy of note that it is only arrived at as a late and subsequent condition in *Plagiogyria*.

It is, however, the character of the sporangium itself which has always been held as distinctive for *Plagiogyria* among those Ferns with which on ground of habit it has hitherto been classed. The oblique annulus, continuously indurated as it passes the insertion of the sporangial stalk, is a feature unknown elsewhere among Ferns having a mixed sorus, with the solitary exception of *Dipteris conjugata*.¹ The usual comparison of *Plagiogyria* on this point has been with those prominent families of the Gradatae, the Cyatheaceae, and Dicksoniaceae, which share with *Plagiogyria* the features of lateral dehiscence and small spore-output. But it ought to be borne in mind that there is in *Plagiogyria* no basipetal

¹ The peculiar case of *Dipteris conjugata*, of which a phyletic explanation was offered by the discoverer of the fact of its having a mixed sorus, may be held as an example of the adoption of a mixed condition of the sorus by a single species, in a genus having the soral character of the Simplices. (See Miss Armour, *New Phyt.*, vol. vi, p. 238.)

succession of sporangia in the sorus; also that the obliquity of the annulus is equally shared with *Gleichenia*, while in § *Mertensia* the form and size of the sporangium is not unlike that of *Plagiogyria*; it differs, however, in the important features of the much larger spore-output, and the median dehiscence shown by *Gleichenia*. The comparison has also been instituted above with the sporangium of *Anemia*, to which the sporangium of *Plagiogyria* shows similarity in the essentials of construction, and in the indefiniteness of the stomium; but it differs in the important point of number of the spores produced; in these respects there is perhaps a closer comparison with the condition seen in the Matonineae, where also there is an oblique annulus and lateral dehiscence, together with a small spore-output.

These comparisons, all of which place *Plagiogyria* in relation with relatively primitive Ferns as regards the characters of the mature sporangium, raise also the comparison on the basis of segmentation of the young sporangium, as well as of the apices of the various parts (compare 'Land Flora,' p. 650). It has been seen above that the details of segmentation of the young sporangium conform to that type which appears in the more primitive Leptosporangiateae, such as the Cyatheaceae and Dicksonieae: also that the segmentation of the apices is according to that common to Leptosporangiateae at large, while in the segmentation of the wings of the leaf there is nothing to strengthen the comparison with the Osmundaceae, which therefore rests rather on external features than upon internal structure or details of development. This is in fact the position which might have been anticipated.

In this place it is only right to express the regret that the prothalli available for study have been open to some doubt as to identity. Pending the clearing up of this uncertainty it may be remarked that the antheridia observed showed dehiscence of the type characteristic of the more advanced Leptosporangiate Ferns; but in view of the uncertainty that exists it is unavoidable that our comparisons shall at present be confined to the sporophyte generation, and any conclusions must in so far be held to be provisional, pending the facts relating to the sexual generation.

But, subject to this proviso, the facts relating to the sporophyte are distinctive, and they indicate clearly that the affinities of the genus are relatively primitive; this follows from (1) the entire absence of flattened scales, the young parts being protected by filamentous hairs only; (2) the occasional dichotomy of the shoot; (3) the simple venation of the leaves, with absence of connecting commissures; (4) the stelar structure, not far removed from solenostely; (5) the undivided leaf-trace; (6) the absence of a 'true' indusium, the sori being covered by the recurved leaf-margin; (7) the type of sorus with initially simultaneous sporangia, among which others are intercalated later; (8) the structure of the sporangium with oblique annulus and indeterminate stomium; (9) its mode of initial segmentation

leading to a relatively thick stalk ; (10) the tetrahedral form of the spores. All these characters indicate for the genus a relatively primitive position, and the strength of that conclusion lies in the number of the facts upon which it is based.

From the comparisons detailed in the above pages it will be apparent that *Plagiogyria* does not naturally fall into any of the families of Ferns which have an oblique annulus ; it is a type of which the cross characters indicate some intermediate position, with affinities in various directions ; in fact it is a 'synthetic' type. But though the bulk of the indications are clearly towards the Simplicies, they do not relate the genus specially with any family of them ; thus the habit suggests the Osmundaceae, the anatomy the Schizaeaceae, and the sorus the Gleicheniaceae or Matonineae, while the venation would compare reasonably with any of these. But it is plainly a primitive type which has broken away from its original characters, as is seen in the dictyostelic structure of the mature stem following on solenostely and even protostely, and in the mixed character of the sorus. It would seem probable that the mixed character of the sorus was acquired directly from the simple state ; from the entire absence of any indication of basipetal sequence of the sporangia it is probable that this took place without the intervention of any gradate condition, as in the case of the *Dennstaedtia-Davallia* series ;¹ it has here been achieved by the simple interpolation of new sporangia between those formed in the first instance. There is a precedent for this already recognized within the genus *Dipteris* ; for while in *Dipteris Lobbiana* the sori show simultaneous origin of the sporangia, *D. conjugata*, which on other grounds may be held to be a more advanced type, has a mixed character of the sorus. It was concluded in that case that a direct progression had been effected from the simple to the mixed condition of the sorus within the limits of a very natural genus ; and the conclusion appears probable that a like direct progression has produced what is seen in the sorus of *Plagiogyria* ; this conclusion eliminates any near relationship with the Gradatae.

In the dictyostelic structure of the axis, as well as in the mixed sorus, *Plagiogyria* compares with the Mixtae, and especially, as indicated by the characters of position and protection of the sorus, with that relatively primitive group of them, the Pterideae ; but it differs from them in its oblique annulus ; the question will therefore be whether in any of the Pterideae there is indication of a like feature. Without entering here into details, which must be reserved for a future paper of this series, it may be stated that there is evidence among the Pterideae of the existence of an oblique annulus, and that it is found in the genus *Cryptogramme*, which has already been placed by Diels in near systematic relation to *Plagiogyria*.²

¹ See Studies in the Morphology of Spore-producing Members. IV. Leptosporangiate Ferns. Phil. Trans., B., vol. 192, p. 91.

² Engler and Prantl, i, 4, pp. 279-81.

But the position of the annulus in *Cryptogramme* is more nearly vertical, and its induration is interrupted opposite the insertion of the stalk; these are steps which lead towards the condition of the annulus common in Ferns with a mixed sorus, and seen in other Pterideae. Such facts indicate the correctness of the conclusion that *Plagiogyria*, though independent of near relation to any of the families of the Simplices, is a form which has broken away from the primitive state in certain features, and that, as a synthetic type, it serves as an indication of the probable origin of those features which characterize a certain group of the Mixtae, viz. the Pterideae, to which it has already been held by systematists to be akin.

The attempt must now be made to locate this synthetic type, *Plagiogyria*, in the system of the Filicales. In the first place the generic separation of it from *Lomaria* cannot be for a moment in doubt; *Plagiogyria* must certainly be held to be a substantive genus; the question will be whether a higher degree of systematic separation is not required for a form which combines such distinct features. It might at first sight seem desirable to found a new order of Ferns to accommodate it; and my first impulse was to establish it as the only genus of a new order, the Plagiogyriaceae. But reflection upon the facts which point to its natural alliance with the simpler Pterideae, and especially the fact that traces of an oblique annulus exist in *Cryptogramme*, indicates that a separation is not desirable. A natural order should be as nearly as possible a phyletic unity. Our conclusion from the comparison of the facts must be that *Plagiogyria* gives the key to certain changes which have accrued in the descent of the Pterideae, such as the progression anatomically towards the dictyostelic state though maintaining the united leaf-trace, and the progression from the simple to the mixed sorus with the swinging of the oblique annulus to the vertical position, together with its interruption at the insertion of the stalk. If, within the Pterideae, there were no forms which shared in any degree the peculiar characters of *Plagiogyria*, then a separate systematic position might be desirable for the genus. But as it now appears that anatomically, as well as in the characters of the annulus, it does not stand entirely apart, the conclusion seems justified that its natural place is within the Pterideae. But of these it must be ranked as the most primitive form, while its affinity in character with the various groups of the Simplices, but not especially with any one of them, indicates a probability that the Pterideae sprang directly from such a source, though not from any one of the families of them at present known. Accordingly no change from the definition of the sub-families or of genera of the Pterideae as arranged by Diels¹ is proposed as a consequence of the new facts; but as regards phyletic grouping, which will be worked into further detail in subsequent papers of this series, *Plagiogyria* will be placed in the lowest

¹ l. c., p. 255.

position, as their oldest type, while *Cryptogramme* will retain the position in near relation to it, as has been correctly recognized by Diels.

As regards the arrangement of the species within the genus, though there are no quite distinctive features of priority, it appears that *P. semicordata* is in certain characters more primitive than *P. pycnophylla* and its closely allied species (or forms), *P. scandens* and *P. glauca*. This is indicated by the prevalence of dichotomy of the axis in the former, while it is, as far as observed, absent in the latter, its place as a method of amplification of the shoot being taken by stolons in the Eastern species. The more marked serration of the leaves in *P. semicordata*, while in the Eastern species they are more nearly entire, may be held to be a nearer condition to a more richly branched ancestry, while the leaf-form of the Eastern species is more completely condensed; the Eastern species show a fuller development of the pneumatophores, which are a special adaptation extended here to the upper leaf, while they are present only on the leaf-base in *P. semicordata*; and this goes along with the more highly developed covering of mucilaginous hairs in the Eastern and Western species. These are only indications it is true, but they all point to *P. semicordata* as being the more primitive species. On the other hand, the division of the leaf-trace in *P. semicordata* into three strands in the basal region of the leaf must be borne in mind, though the bearing of the fact is obscured by their subsequent junction below the lowest pinnae into a single strand again. There is also the fact of the absence of the median protoxylem-strand, which is present in *P. pycnophylla* and *glauca*, but again it is not clear what interpretation is to be put upon this fact.

Lastly, the observations on *Plagiogyria* have their bearing on the relations of those three grades of soral condition characteristic of the Simplices, Gradatae, and Mixtae. When these types were first recognized by me, it was clearly laid down that the three divisions illustrate steps in the evolution of the Filicales, but that they were arrived at not by progression along a single line of descent, but by similar adaptations making their appearance in more than one evolutionary sequence, and the results were grouped according to their common adaptation ('Studies,' v, p. 123). It was specially insisted on that, though at that time no evidence was available to show that the 'mixed' condition of the sorus had been acquired by modification of the 'gradate' condition, 'it is possible that a mixed condition of the sorus may have arisen also by interpolation of successive sporangia without order in a typical simultaneous sorus, such as that of *Angiopteris* or *Gleichenia*; but evidence of this has not come to hand' (l. c., p. 124). Since this was written in 1899 such evidence has been acquired in the case of the genus *Dipteris*, already quoted; here in the broad-leaved *D. conjugata* sporangia of different ages are found side by side in the same sorus, though in other species of the genus, having the more primitive

narrow type of leaf, the sporangia of the same sorus are simultaneous in their origin; there has in fact been a progression from the simple to the mixed type of sorus within the genus. A parallel progression is now suggested as having resulted in the mixed condition seen in the sorus of *Plagiogyria*; from a superficial sorus such as that of *Gleichenia dichotoma* or *pectinata* it would be produced by a slight elongation along the vein, together with an irregular interpolation of younger sporangia between those first formed, but with the characters of the individual sporangium for the most part maintained. Whether or not the *Gleichenia* type was the actual source, it seems probable that there has been here another direct progression from a simple sorus to one of a mixed character. The natural affinity already recognized by Diels and discussed above, between *Plagiogyria* and the simpler genera of the Pterideae, indicates that this direct progression has probably given rise to one of the greatest phyla of Leptosporangiate Ferns. The further discussion of this, and the marshalling of the evidence to support it, must be deferred for the present, but the facts already in hand are sufficient to give the main conclusion a reasonably degree of probability.

The general effect of such a conclusion will be to condense the brush of phyletic lines of the Leptosporangiate Ferns, for, in the case of a very considerable sequence of forms with a 'mixed' sorus, it removes any necessity for the idea that they were arrived at through a stage such as is seen in the Gradatae, and it refers them in origin directly back to the more primitive Simplicies.

CONCLUSIONS.

1. The genus *Plagiogyria*, merged by Sir W. Hooker in *Lomaria*, is a substantive genus, quite distinct from any other.

2. It shows its relatively primitive character in the stelar structure, the undivided leaf-trace, the simple forked venation, occasional dichotomy of the axis, the absence of flattened scales, absence of a 'true' indusium, the sorus initially simple but later showing mixed character, the segmentation of sporangium, its thick stalk, oblique annulus, and indeterminate stomium, and the tetrahedral spores.

3. It shows resemblances, more or less marked, to all the great series of the Simplicies, but not to any one of them so clearly as to point to close affinity.

4. On the other hand its characters indicate that it is rightly allied with the Pterideae, of which it may be held to be the most primitive type.

5. Its 'mixed' character of sorus, without any indication of a gradate sequence of sporangia, combined with its primitive characters and its probable affinity to the Pterideae, shows that a great phylum of Mixtae has probably been derived directly from the Simplicies.

DESCRIPTION OF PLATES XXXII AND XXXIII.

Illustrating Professor Bower's Paper on *Plagiogyria*.

Fig. 1. *Plagiogyria pycnophylla*. Parts of two pinnae seen from below, with a pneumatophore at the base of each; on one side of the right-hand pinna the indusial margin and the sporangia have been removed, so as to show the venation and the absence of distal connexions of the veins. ($\times 4$.)

Fig. 2. *Plagiogyria semicordata*. Parts of two pinnae seen from below, from near to the apex of the leaf; on the right-hand side the indusial margin and the sporangia have been removed, so as to show the venation; note the winged character of the rachis, which is specially developed at the apical region of the leaf. ($\times 4$.)

Fig. 3. Apical bud of *Plagiogyria glauca*, showing leaves still circinate and bearing the pneumatophores projecting from the enlarged leaf-bases. ($\times 2$.)

Fig. 4. *P. glauca*. The persistent base of an old leaf, showing a row of pneumatophores on either side of the midrib. (Enlarged.)

Fig. 5. Circinate apex of leaf of *P. pycnophylla*, showing the pneumatophores projecting through the covering of mucilaginous hairs. ($\times 2$.)

Fig. 6. Transverse section through a well-developed stock of *P. pycnophylla*, showing the central sclerotic core (*sc*), the stele (*st*), the leaf-traces (*lt*), and their subtending sclerotic patches (*sp*), which as they pass outwards become hollowed by surface involutions (*inv*). To the left is a solenostelic stolon in place of a normal leaf (*sol*). ($\times 2$.)

Fig. 7. Transverse section of the stem of a well-grown plant of *P. pycnophylla* at a point close below the apex, to show the position of the protoxylem-groups, which are indicated as dark dots in the meristemes; note that the first indication of the formation of a leaf-trace is by an outgrowth of the central sclerotic core, and that a mesoxylem protoxylem-group appears opposite it in the meristeme of the axis. ($\times 6$.)

Fig. 8. Part of a meristeme of *P. glauca*, showing the first protoxylem-elements already lignified, lying in a distinctly mesoxylem position. ($\times 100$.)

Fig. 9. Part of a meristeme of *P. pycnophylla*, showing mesoxylem protoxylem. ($\times 250$.)

Fig. 10. A leaf of *P. pycnophylla*, itself arrested in its growth, and bearing on its adaxial face a stolon (*st*); *pn* indicates the pneumatophores.

Fig. 11. A succession of transverse sections through a leaf bearing a stolon, the lowest being placed first; see text. ($\times 4$.)

Fig. 12. I-V. Successive sections through a stolon of *P. pycnophylla*, showing a structure not far removed from solenostely; on the right-hand side of the drawings a stolon, which replaces a leaf, is originating, and in IV it shows a stolon structure (*st*). (Natural size.)

Fig. 13. Tangential section through the leaf-bases of *P. pycnophylla*, showing how one of them is structurally replaced by a stolon (*st*) having a stele which is almost protostelic. (Natural size.)

Fig. 14. Transverse section through a young pinna of *P. pycnophylla*, showing marginal segmentation of the usual Leptosporangiate type. ($\times 300$.)

Fig. 15 (*bis*). Sections through the sorus of *P. pycnophylla*, in an advanced state, but not mature; *a* and *b* show the 'mixed' character of the sorus, which is covered by the attenuated margin of the pinna, these sections being transverse through the pinna, and following the course of the veins; *c* is at right angles to these, and cuts the vein transversely. ($\times 30$.)

Fig. 16, *a-h*. Sections through sporangia of *P. pycnophylla* in early stages of development; for details see text. ($\times 225$.)

Fig. 17. Older stages of the same; *a, b*, transverse sections through the sporangial stalk; *c* and *d*, sections longitudinally and transversely through the sporangial head. ($\times 225$.)

Fig. 18, *a-e*. Mature sporangia of *P. semicordata*; for details see text. ($\times 80$.)

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