On Polystely in the Genus *Primula*¹.

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With Plate XIV.

SOME time ago the anomalous variations in structure which are found in the stems of the different species of the genus *Primula* attracted the attention of the French botanist, Van Tieghem, and they received an admirable elucidation at his hands. He showed that while some of the species are monostelic, others, on the other hand, exhibit a polystelic arrangement of their vascular tissue. However, being chiefly intent upon distinguishing between the various types of structure exhibited, and upon arranging the species according to these types, Van Tieghem did not pay much attention to the remarkable variations in structure which may occur within a single species, even in the different regions of one and the same plant, although these facts had already been observed and utilized for the purpose of classification

¹ Van Tieghem, relying chiefly upon anatomical characters, has divided the genus *Primula*, L. into two separate genera, *Primula*, Tourn. and *Auricula*, Tourn. This separation agrees closely with that based upon the external characters which was established by Tournefort himself about 1700. However, it seems best to retain the customary nomenclature.

in a paper written by Kamienski¹. Believing that these variations may also be of some value for the purpose of indicating the manner in which the anomalous *Primulas* came by their remarkable structure, I purpose describing such cases as appeared in the species that I have examined.

To begin with, *P. japonica*, *obtusifolia*, *denticulata*, and *involutrata* are described by Van Tieghem as being gamostelic with a few steles only, and these arranged in a single circle². The steles are two to four in number, elongate or arcuate in form, and they anastomose into a network, the meshes of which correspond to the points of insertion of the leaves. Although it is quite true that such a structure is frequently to be met with in these plants, yet at the same time it is by no means universally present; indeed, in the two first species, it can hardly even be described as generally characteristic. For instance, in the ten or more mature specimens of *P. japonica* that I examined, I did not find a single case in which the so-called steles maintained, throughout the plant, the essential features of true and perfect steles. On the other hand, both in *P. japonica* and in *P. obtusifolia*, the steles present in the stem are usually found to be defective or imperfect. These imperfect steles are at once to be distinguished from perfect ones by the more or less complete absence of those internal vascular bundles which are invariably to be found on the inner side of every perfect stele. In fact, they consist merely of a number of collateral vascular bundles with normal orientation, fused together laterally into so many groups each of which is surrounded by its own endodermis and pericycle (Fig. 1). The endodermis is clearly demonstrable right round the group, on the inner side as well as the outer. The pericycle on the inner side of the group is represented by 1–3 layers of parenchymatous cells directly intervening between the protoxylems of the vascular bundles and the internal endodermis; on the outer side it is greatly complicated by the development of a radiciferous network

¹ Abhandl. der Naturf. Gesellschaft zu Halle, XIV, p. 143, 1878.

² Ann. Sc. Nat. Bot., 7 sér., T. III, pp. 300 and 305.

(*réseau radicifère*), which, both in the perfect and the imperfect steles, not infrequently takes the appearance of an outer series of normally oriented supernumerary bundles. This strange appearance is found wherever the elements of the radiciferous network are cut through transversely. The real nature of these outer bundles becomes at once evident in those sections which pass through the exact point of origin of a root; here it is seen that their position in the pericycle is taken up by horizontally running elements evidently connected with the root-stele, and belonging to the radiciferous network (Fig. 1; cf. also Van Tieghem, l.c., Fig. 31).

In four of the specimens of *P. japonica* examined, the imperfect type of stele alone was present throughout the whole length of the stem. In some it was present in the regions towards the base of the stem only, while the rest of the stem possessed perfect steles. In the remainder, although the imperfect form was present throughout the greater part of the stem, perfect steles also appeared in limited regions variously distributed.

Neither did any of the plants of *P. obtusifolia* that I examined show a perfect gamostelic structure throughout. In one plant the perfect steles did not appear at all; in the others, they were found only in limited regions situated in different parts of the stem.

The only point of difference between the imperfect steles found in *P. obtusifolia* and those in *P. japonica* is that in the former, owing to the strong sclerosis undergone by the cells of the central region of the ground-tissue, the endodermis on the inner side could not always be identified with certainty, although it is distinctly recognizable in young specimens.

In *P. obtusifolia* and *P. involucrata* those parts of the stem which are formed at the end of one season's growth and the beginning of the next do not attain more than about one-third of the full diameter of the stem, and in these regions the number of steles present is always reduced to three, two, or even a single one, shaped like a horseshoe. Further, they invariably seem to be imperfect, showing a complete absence

of internal bundles. The internal endodermis is readily observed in *P. involucrata*, though not (for reasons mentioned above) in *P. obtusifolia*.

Imperfect steles of a slightly different kind are also to be found in *P. involucrata* and *P. denticulata*, but, although they are constantly to be met with in all regions of the stem, the result is not so far-reaching and disturbing in its effect upon the general anatomy of the plant as in the case just described for *P. japonica*. The chief point of difference between the imperfect steles found in these two plants and that in *P. japonica* is that here the internal vascular bundles are absent only from the median portions of the stele, while they are present for some little distance around each corner. In the median region, where the internal bundles are wanting, the internal endodermis drops in towards the xylem of the external bundles, until it is separated from their protoxylems by one or two layers of pericycle only (Fig. 4).

The existence of this kind of imperfect stele is explained by an examination into the manner in which the leaf-traces take up their place in the ring or circle of vascular tissue in the stem. They do so at the lower angle of each mesh in the network of steles, coming in between two perfect steles as they approach each other towards the lower end of the mesh (Fig. 2). There the leaf-trace fuses laterally, at the same time, with both of these steles (Fig. 3) so as to form a large arc, in which, of necessity, the internal vascular bundles which should be present just within the leaf-trace are wanting, while those on the inner side of the two perfect steles which are connected by the leaf-trace are, of course, present (Fig. 4). However, as this imperfect stele passes down the stem, internal bundles appear in the median region also, on the inner side of those bundles which came in from the leaf-trace, and thus the large arc becomes a perfect stele. Lower down still it divides by constriction into two smaller, but at the same time perfect, steles, which are now ready to undergo a similar process again with a lower leaf-trace (cf. the steles in Fig. 2).

In these several cases, it is certain that the absence of the internal bundles and the consequent production of imperfect steles has nothing whatever to do with the production of the monostelic terminal floral peduncle: for plants have been examined which possess the imperfect type of stele throughout a given year's growth, itself terminating in a floral peduncle, and also exhibiting the same structure again in the next year's growth immediately above the peduncle.

Among the dialystelic species I examined *P. Auricula* and *P. Palinuri*, and as regards their mature structure they agree in every respect with Van Tieghem's description. The steles are perfect throughout, although a slight trace of the phenomena described in connexion with the entrance of the leaf-trace in *P. involucrata* may sometimes be discerned; but only in relation to the median one of the many traces which enter from the leaf.

STRUCTURE OF THE PETIOLE.

In all the species that I examined, the vascular strands which pass off from the stem into the leaves are rather large in size, and take the form of arcs of greater or less curvature. In these plants at any rate, I have obtained a striking confirmation of the opinion so strongly advanced by Strasburger, that the leaf-traces take with them, from the stele of the stem, not only portions of the endodermis and pericycle, but also of the pith and sometimes of the primary medullary rays¹. This fact is particularly well shown in *P. involucrata* and *P. obtusifolia*. The term 'meristele,' therefore, as applied to these vascular strands, is especially appropriate, since they really include portions of each of the constituent parts of the steles from which they arise. The leaf-trace usually takes away several vascular bundles from the stem-stele, although they are not always to be separately distinguished in the meristele itself. The endodermis of the meristele, whenever it is clearly defined, is most certainly continuous throughout

¹ Histol. Beit., Vol. iii, p. 110.

with that of the stem-stele from which the leaf-trace arose. In *P. Auricula* and *P. Palinuri* each leaf is supplied with several meristeles which arise from so many different steles in the stem. In other cases a single meristele arising from one of the stem-steles is given off to each leaf, and this meristele generally branches as it passes outwards so that several are to be found in the petiole. The structure exhibited by such petioles may therefore be fitly termed 'meristelic.' The median meristele is always the largest and the most curved, sometimes forming as much as two-thirds of a complete circle (*P. obtusifolia*). The lateral meristeles become smaller and less curved as they are the more distant from the median one.

Van Tieghem describes the petioles of all the species of the genus *Primula* as being astelic throughout their whole length¹; that is to say, they contain either a single meristele or several separate and distinct ones. The only exceptions to this statement that I found were in the petioles of *P. japonica* and *P. denticulata*, where certain structures are invariably present, which in all essential respects are entirely similar to normal and perfect steles. These steles were found in all the specimens examined of both species, and they extended from a point near its base throughout the petiole, and often for a long distance along the midrib of the lamina also. Of the several vascular strands in the petiole, only the three median ones form steles, the lateral strands being meristeles similar to those described above.

These petiolar steles are circular in transverse section, and consist of a ring of phloëm surrounding a ring of xylem. A considerable amount of parenchyma is scattered among the elements of the xylem, but separate vascular bundles are not distinguishable either here or in the phloëm (Fig. 6; cf. Fig. 5). The centre of the stele is occupied by a sclerotic parenchyma, scattered among the peripheral cells of which are the elements of the protoxylem, generally rather crushed

¹ Ann. d. Sc. Nat. Bot., 7 sér., T. III, p. 294; and also Bull. Bot. Soc. de Fr., XXXIII, p. 95.

and flattened. The central parenchyma is, in the median stele, generally marked off as a distinct medulla, but in the smaller steles it is either scanty or absent. Both in *P. japonica* and in *P. denticulata* the whole stele is surrounded by an exceptionally well-marked endodermis enclosing a collenchymatous pericycle, the latter consisting of about three or four layers towards the lower surface of the leaf, and rather less towards the upper.

In order to account for the appearance of these steles in the petiole, I will now describe the changes that the leaf-trace undergoes during its course. In these two plants the leaf-trace invariably arises from one of the steles in the stem as a single large meristele. It is at first curved into the shape of a horseshoe, open towards the interior of the stem, and is completely surrounded by the endodermis, which is folded round the corners of the horseshoe, following the concavity of the inner side. Within the endodermis lies the pericycle, and the concavity between the latter and the xylem is occupied by a few conjunctive cells continuous with the pith of the stem-stele. As the meristele passes through the cortex of the stem it branches so as to form several strands, the extreme lateral branches remaining meristeles throughout the petiole. As the three median strands (to which alone I now refer) are followed in their outward course, the endodermis is seen to straighten out across the gap between the arms of the horseshoe, gradually falling less and less into its concavity (Fig. 5). At the same time, the vascular tissue at each corner gradually extends itself across the gap so as to meet that approaching from the other side, and thus to complete the circle, so that finally a complete stele is the result. Again, towards the tip of the lamina the steles gradually lose their internal bundles in an inverse but perfectly analogous manner, becoming meristeles once more.

Although I do not wish to lay too much stress upon the value or necessity of a strict continuity of tissues, yet it should be noted that these steles are essentially different from the single central stele described by Van Tieghem in

the petioles of the Cucurbitaceae and Solanaceae. In the latter, as Strasburger points out, the tissue which Van Tieghem regards as pith is really only enclosed cortical tissue, and is not continuous with the pith of the stem at all.

In spite of the discovery of these polystelic petioles in the Primulas, the fact that the Gunneras are more deeply imbued with the phenomenon of polystely still holds good; for they possess polystelic floral peduncles also, while those of the Primulas are monostelic. As regards the possession of polystelic petioles, I was at first under the impression that these two genera stood alone among the Phanerogams. But, from an interesting paper recently published by M. Casimir de Candolle¹, I gather that in certain species of *Alchemilla* (*A. vulgaris*, &c.) the petioles contain structures precisely similar to those described above, and which I take to be steles also. This resemblance becomes the more remarkable on account of the fact that another feature, cited by M. de Candolle as characteristic of the Alchemillas, is also excellently demonstrated in certain Primulas (*P. involucrata*, *obtusifolia*, and *japonica*), namely, that in these plants the vascular system of the axillary shoot is not directly connected with one of the stem-steles, *but with the leaf-trace itself*, joining on to the latter some distance before it takes its place in the central ring of vascular tissue in the stem.

Considering these facts as a whole, it appears that in *P. japonica* and *P. denticulata* a leaf-trace is capable of transforming itself into a stele at any point in its course whenever it may be advantageous to do so. Thus, if such a leaf-trace be followed throughout its downward course, at first, in the upper part of the lamina, it is found to be a perfectly collateral meristele. Towards the base of the lamina, or at any rate throughout the petiole, it exercises the capability which it possesses of producing internal bundles on its upper side, and thereby converts itself into a perfect stele. On arriving at the periphery of the stem it again

¹ Bull. de l'Herbier Boissier, T. I, No. 10.

returns to its collateral structure, and enters into the vascular circle as a horseshoe-like meristele. Later, passing down the stem, the now cauline portion of the leaf-trace once more develops internal bundles, and in connexion with the cauline portions of other leaf-traces with which it has fused, it becomes once more a complete and perfect stele. Finally, it divides into two branches, which eventually fuse with the leaf-traces of the lower leaves as they take their places in the vascular circle.

Bearing in mind the manner in which the leaf-trace enters the vascular ring between two steles already present, as described for *P. denticulata* and *P. involucrata*, and also the general course of a leaf-trace as followed out above, it seems possible to regard the whole vascular system of these plants as consisting of the cauline portions of the leaf-traces. They pass in, arrange themselves in a circle, and having passed some distance down the stem, divide into two branches, which insert themselves on the entering leaf-traces of the lower leaves. The fact that the leaf-trace has become a stele during the cauline portion of its course may be regarded as incidental only. For such an incident may, and does, take place at other points of its course where no very great importance can be attached to its occurrence. Moreover, the examination of *P. japonica* and *P. obtusifolia* has shown that whether the trace becomes a stele or not, *even in the stem itself*, is just as much a matter of chance, or rather of convenience.

Regarded in this light, the existence of the imperfect steles in *P. japonica*, *obtusifolia*, *involucrata*, and *denticulata* is easily understood. For the appearance of the internal bundles on the inside of the cauline portion of the leaf-trace may either be more or less delayed (*P. involucrata*, *P. denticulata*), or they may sometimes be altogether dispensed with (*P. japonica*, *P. obtusifolia*). Again, in the two latter plants their presence in certain varying regions of the stem, and their absence in others, is also to be expected, for the leaf-trace may be regarded as potentially capable of producing internal vascular tissue at any point throughout its course. Their actual

existence in any particular region would thus depend upon the physiological conditions to which that region is exposed.

In *P. Auricula* and *P. Palinuri*, although the leaf-trace produces no internal vascular bundles at any point in its foliar course, yet they are invariably present in the cauline portion, appearing as soon as the leaf-trace turns downward in the stem.

THE LEAVES OF THE SEEDLING.

The leaves of the seedlings of these plants exhibit, as regards their structure, an interesting series of gradations through which the leaf-traces become gradually less and less complex as the cotyledons are approached. In those species in which the petiole of the adult form of leaf is polystelic (*P. japonica*, *P. denticulata*), the first step that takes place is the reduction of the steles to meristeles throughout the whole length of the petiole, which takes place at about the seventh leaf. Then the leaf-trace ceases to give off lateral branches, so that the petiole contains one meristele only. Finally, this meristele itself diminishes in size until it appears simply as a single small collateral bundle. In *P. involucrata* and *P. Auricula* similar changes take place: but since the traces in the adult form of leaf itself are only meristeles, the first step that takes place in descending to the earlier leaves in the former is a reduction in the number of branches given off by the median trace, and in the latter a reduction of the leaf-traces given off from the steles of the stem. In *P. Auricula* the traces are at first reduced to three, and then, at the first or second leaf above the cotyledons, the leaf-trace in both species is represented by a single small bundle only.

These gradations indicate progressively the various arrangements employed by the individual plant to provide the amount of vascular tissue necessary for the steadily increasing needs of the leaves. And, as far at least as the later steps are concerned, they probably represent phylogenetically the several devices by which the ancestors of the plants en-

deavoured to attain a similar end. We may therefore suppose that, as a first resort, the original vascular bundle was enlarged to the greatest size that such a collateral structure could possibly attain compatible, at the same time, with economy of space. This point reached, it became subdivided into several strands. Then, in *P. japonica* and *P. denticulata*, a still further increase in the amount of vascular tissue present was obtained by the production of bundles on the inner side of certain of the traces, thus converting them into perfect steles.

TRANSITIONAL PHENOMENA IN THE SEEDLING.

The epicotyledonary region of the stem in these plants is monostelic, with a narrow pithless central cylinder, in which no separate vascular bundles can be clearly distinguished. The structure remains the same also for some little distance up the stem, except that the central cylinder increases slightly in diameter owing to the appearance of a few pith-cells at its centre. Two different types of development are to be found in the seedlings of *P. japonica* which are parallel to the two types of structure present in the mature stem. Seedlings exhibiting the first type would no doubt grow into those mature plants in which the imperfect form of stele is at least greatly predominant, if not exclusively present. In these the central cylinder of the epicotyl is retained in a perfectly normal condition until the departure of the seventh or eighth leaf-trace at least; in fact, so far as the differentiation of the tissues renders any decision possible. The first three or four traces in passing out leave a small gap of two or three cells only; and although the higher traces may leave a somewhat wider gap, still the endodermis invariably passes directly across the opening, and does not become folded into the interior of the cylinder (Fig. 7). Thus the gap does not really affect the stele as a whole, but only the ring of vascular bundles. In fact, it is only an unusually large medullary ray which becomes filled up again by the more or less rapid

growth of the vascular tissues on either side to meet each other across it. This type is by far the most prevalent; the other, which probably corresponds to those plants in the mature structure of which the perfect stele predominates, was present in two cases only out of fourteen examined.

In the second type of seedling the central cylinder is, as before, maintained intact until the third or fourth leaf, but the gap formed by the departure of the fourth or fifth trace becomes an actual gap or break in the cylinder itself. The endodermis, instead of passing straight across, falls in around the margins of the gap, and passes right round the periphery of the medulla, just within the xylems of the vascular ring (Fig. 8); so that when this gap becomes closed up by the approximation of its margins, the endodermal layers first meet and fuse (Fig. 9), then the pericycles, and finally the ring of vascular tissue again becomes continuous. But now that portion of the endodermis which has been invaginated into the medulla, in consequence of the process just described, has become cut off and separated from the external endodermis, and forms a distinct internal endodermis, which often also extends into the internode below the gap at which it was actually invaginated (cf. Fig. 10). When the next leaf-trace departs, the internal endodermis is once more put into continuity with the external endodermis around the corners of the gap. Further up the stem they become separate again in exactly the same way as before. The seedling has therefore attained at this point exactly the same structure as that termed (for the sake of convenience) imperfect gamostely in the mature plant.

According to Van Tieghem, almost identical processes are gone through in the seedling of *Botrychium Lunaria*¹, resulting in an exactly similar structure, which, however, he here speaks of as 'gamodesmy.' If it be held necessary to retain Van Tieghem's terminology throughout, I see no alternative to calling the imperfect steles 'gamodesmic groups,' both in the

¹ Journ. de Bot., Vol. iv, No. 23, p. 405.

seedling and also in the mature plant of *P. japonica* (cf. Van Tieghem, l. c., No. 24, p. 483).

From one point of view the chief peculiarities of this type of structure may at the same time be epitomized and explained by considering that the leaf-trace, when it enters into the circle of vascular tissues, carries the endodermis of its upper surface straight in with it through the breadth of the vascular ring, where this endodermis then turns down at the inner border of the trace and runs down the stem, spreading laterally at the same time so as to form the internal endodermis of the vascular ring or stele, as the case may be (Fig. 10).

In *P. involucrata* the epicotyledonary central cylinder is maintained until the seventh leaf, or even higher. The first two or three leaf-traces, including those of the cotyledons, produce a gap of about two or three cells wide, the higher ones of about six cells. In the latter the endodermis, in passing over the gap, becomes slightly concave; however, this infolding is not deep, and the endodermis soon straightens out again as the gap fills up (Fig. 11). When the seventh or eighth leaf-trace comes off, this infolding of the endodermis is carried on to a much greater extent, and at the same time the gap remains open for an unusually long distance; so long, indeed, that the next leaf-trace above is given off from the opposite side of the stem before it becomes closed (Fig. 12). Around the margins of this gap also the endodermis is very deeply infolded, so much so, in fact, that it meets and fuses with the endodermis infolded from the other side through the still unclosed gap of the seventh or eighth leaf-trace (Fig. 13). Later on they separate completely, thus dividing the vascular ring into two separate groups, each completely surrounded by its own endodermis and forming an incomplete stele or gamodesmic group. Proceeding upwards, these fuse across the earlier gap left by the seventh or eighth leaf-trace, to form a horseshoe-like group which remains open on the opposite side of the stem (eighth or ninth leaf-gap) until the next leaf-trace above comes off (Fig. 14), which divides it in an exactly similar manner into two new groups, and so on.

Sometimes the transition takes place in *P. involucrata* much in the same way as in *P. japonica*, the endodermis at the seventh or eighth leaf-gap being completely invaginated, and cut off by the closing of the gap. As in *P. japonica*, the departure of the next leaf-trace establishes a horseshoe of vascular tissue. But here the gap between the arms of the horseshoe remains open until the departure of a still higher leaf-trace, which divides it into two groups, and then it proceeds as above described. In either case the vascular groups are at first imperfect steles, but after some time they develop internal vascular bundles, and assume the form found in the mature stem.

In *P. Auricula* the fact that even the earlier leaves are supplied with more than one leaf-trace from the stem serves to complicate matters considerably, but the median trace has such a paramount influence on the transitional phenomena that it alone is alluded to below.

The epicotyledonary stele is maintained intact until the fourth or fifth leaf (cotyledons included) is reached. Until this point a very small gap only is left by the outgoing traces, but at the departure of the fourth or fifth leaf-trace a gap of considerable width is formed, around the margins of which the endodermis is invaginated into the medulla, just as in *P. japonica*. Thus a horseshoe of vascular tissue is produced which remains open on one side until the next leaf-trace is given off on the opposite side of the stem, dividing it into two separate groups, just as in *P. involucrata*. These two groups are almost always of unequal size, and they appear to become perfect steles even before the next leaf-trace comes off from the largest of the two. So we see that *P. Auricula* becomes completely and typically polystelic at a very early stage. The lateral leaf-traces arise on either side of the median trace from the steles that have just been formed by the departure of the latter, or, in the case of the formation of the horseshoe, from its corners, whereby the gap between its two arms becomes much widened.

Van Tieghem seems to have entirely overlooked the all-

important influence of the leaf-traces on the phenomena of the transition, and, indeed, on the vascular system throughout the whole plant. On this account he regards the polystely, when present, as having originated by the continued bifurcation of the central cylinder found in the lower part of the stem. He speaks of it as flattening itself out and constricting itself in the middle until it becomes nipped into two¹. I have not seen anything that would lead to a similar conclusion. The transitional phenomena in the seedling, and also the extreme variability in certain species, of the most important characteristics of polystely, give strong support to the opinion that polystely is not a primitive feature of the group of *Primulas* in which it is found, but a comparatively recent modification. Monostely is undoubtedly to be regarded as the fundamental type, and Van Tieghem appears to be correct in laying so much stress upon the incapacity of the narrow epicotyledonary stele, in the polystelic section of the genus, to expand itself sufficiently to satisfy the needs of the plant, an inability which he regards as the ultimate cause of their polystely (l. c., p. 304).

Since the epicotyledonary stele of the monostelic section of the *Primulas* has retained its ability to expand with the growth of the plant, that of the polystelic section must have lost this same power, which at one time it also possessed, and it must have done so at a period anterior to the first appearance of polystely in the section. The only way in which this could have come about is by the prototypes of the polystelic section having been at one time subjected to very different conditions from those of the monostelic section, those conditions being such as were unfavourable to the production of much vascular tissue, and therefore favourable to the establishment of a very narrow central cylinder throughout the plant. Now a recurrence to those conditions, in which an increased amount of vascular tissue would be advantageous, could be met, as regards the leaf-traces, by an increase in their size or in their number. But if such an increase actually

¹ Ann. des Sc. Nat. Bot., 7 sér., T. III, pp. 282 and 295.

took place, it would appear that the epicotyledonary cylinder, having lost the faculty of adequate expansion, and being no longer able to enclose these leaf-traces within its slender circumference, would have to accommodate them in some other manner.

Now, we may reasonably regard the manner in which the epicotyledonary stele of the seedling becomes converted into the mature structure of the stem as a reminiscence of the phylogenetic progress of the race itself, though, of course, with the earlier incidents blurred by subsequent adaptation to the surroundings. It therefore appears probable that the narrow central cylinder, being unable to expand, became broken up, in connexion with its constituent leaf-traces, into so many vascular arcs, and that these arranged themselves in a ring of suitable diameter around the centre of the stem, fusing with each other laterally at intervals, and opening out again. In fact, a structure was produced similar to that found in some specimens of *P. japonica* and *P. obtusifolia* at the present time.

Again, it is evident that even such a ring as this might at length reach a limit of expansion, relative to the size of the stem, while room could still be found for more vascular tissue on the inner side of the cauline portions of the leaf-traces, thus converting them into steles, and at the same time without breaking up the ring. The various gamostelic species may be cited as exhibiting such a structure.

If, however, we suppose that a continual increase in the number or size of the leaf-traces entering the stem necessitated a still further increase in the amount of vascular tissue contained in the latter, there appears to have been no alternative but to break up the ring and to scatter the steles throughout the ground tissue, as is to be observed in many dialystelic species.

However that may be, one result appears clear—that, in the *Primulas*, the gamostelic condition is more primitive and nearer normal monostely than is the dialystelic type, and that probably a gamodesmic condition preceded either.

STRUCTURE OF THE APEX.

I found that in the apical region of these plants the vascular system undergoes no simplification whatever, but presents precisely the same arrangement as it does in the fully differentiated stem. Therefore, if in the fully differentiated regions there are several steles arranged in a slightly interrupted ring, as in *P. japonica* and *P. involucrata*, they will also be represented in the apex by a similar ring of desmogen-strands, which may be followed up as far as any differentiation can be distinguished in the meristem. Whether this apparent plerome extends past the youngest leaf, into the apical cone itself, is somewhat doubtful, but, on the whole, the probability is that it does so.

Again, if in the differentiated regions of the stem the steles are irregularly scattered and widely separated, as in *P. Auricula*, the desmogen-strands which correspond to them are also found to be scattered in the merismatic regions of the apex; and further, in this case it appears tolerably certain that no plerome is to be found in the apical cone itself. Therefore in these plants the study of the apical meristem throws no light upon the phylogenetic origin of the various types of structure; such light can only be obtained from the ontogeny of the whole plant, as exhibited in the development of the seedling.

The most striking feature in the apical region is the extreme insignificance of the development of the apical cone itself compared to that of the youngest leaf produced by it. The latter, immediately after its first formation, grows with great rapidity, completely overshadowing and pushing aside the minute apex which often becomes a mere lateral protuberance at the base of the precocious leaf. Correlated with this early and excessive development of the young leaves, the leaf-traces also play a predominant part in the first appearance of the desmogen-strands in the meristem of the apical regions, especially in *P. japonica* and *P. involucrata*, where by

far the greater portion of the ring of desmogen is formed by the leaf-trace that has latest entered it, a fact completely in accordance with the manner in which the leaf-traces regulate the arrangement of the vascular system in the fully differentiated stem.

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EXPLANATION OF FIGURES IN PLATE XIV.

Illustrating Mr. Gwynne-Vaughan's paper on Polystely in the Genus *Primula*.

Note.—Figs. 1, 5, and 6 only are to be regarded as accurate drawings. The insertion of the leaf-traces and adventitious roots, and also the presence of the radiferous network, cause so much confusion among the vascular elements that I was obliged, for the sake of clearness, to make the other figures somewhat diagrammatic, although in every case I follow the actual sections as closely as possible.

Abbreviations: *m.* medulla; *x.* xylem; *ph.* phloëm; *p.* pericycle; *e.* external endodermis; *i.* internal endodermis; *c.* cortical tissue; *l. t.* leaf-trace; *l. g.* leaf-gap; *s.* a stele of the stem.

Fig. 1. *Primula japonica*; portion of transverse section of an imperfect stele; *r.* the elements of the radiferous network; *ext. b.* external bundles. The internal bundles are completely absent. $\times 130$.

Figs. 2, 3, 4. *Primula involucrata*; portion of transverse section of the stem, showing a leaf-trace entering between two perfect stem-steles. $\times 40$. In Fig. 2 the leaf-trace is seen approaching the steles; in Fig. 3 it has become fused with both of them. Fig. 4 shows the imperfect stele thus produced, which has no internal bundles in its median region.

Fig. 5. *Primula denticulata*; transverse section of the median leaf-trace in the petiole. The stele is not yet perfect, but the vascular ring is open towards the upper surface. $\times 90$.

Fig. 6. *Primula japonica*; transverse section of the median leaf-trace in the petiole. The stele is here quite perfect, having passed through a stage similar to Fig. 5 lower down in the petiole. $\times 90$.

Fig. 7. *Primula japonica*; transverse section of central cylinder of a seedling. The leaf-trace departs in a normal manner, leaving the stele intact. $\times 100$.

Figs. 8 and 9. *Primula involucrata*; transverse sections of central cylinder of a seedling. The leaf-trace departs in such a manner as to leave an internal endodermis. (*P. japonica* also makes use of this method of transition.) Fig. 8, the endodermis is invaginated through the leaf-gap. $\times 70$. Fig. 9, the leaf-gap becomes closed in such a manner as to include a portion of the endodermis which becomes internal. $\times 100$.

Fig. 10. *Primula japonica*; diagrammatic longitudinal section through the central cylinder of a seedling. The endodermis passes into the interior of the stele through the leaf-gaps. The dark regions indicate xylem: the light, phloëm; and the dotted line, endodermis.

Fig. 11. *Primula involucrata*; transverse section of the central cylinder of a seedling after the departure of one of the earlier leaf-traces. The stele is still intact. $\times 100$.

Figs. 12-14. Transverse sections of the same, showing how the stele eventually becomes broken up. *l. t.*² the eighth leaf-trace; *l. t.*³ the ninth leaf-trace; *l. g.*¹ the seventh leaf-gap; *l. g.*² the eighth leaf-gap. Fig. 12 shows the invagination of the endodermis through the seventh leaf-gap. $\times 100$. Fig. 13 shows that the seventh leaf-gap is still open, while the eighth leaf-gap is almost free; its final departure will break up the stele into two portions. $\times 70$. Fig. 14, the two portions are fused across the seventh leaf-gap, the eighth leaf-gap is still open, and the ninth leaf-trace is about to pass off. $\times 90$.

Fig. 1.

Fig. 2.

Fig. 6.

Fig. 5.

Fig. 7.

Fig. 11.

Fig. 12.

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Fig. 10.

Fig. 8.

Fig. 13.

Fig. 14.

Gwynne-Vaughan, D. T. 1897. "On polystely in the genus *Primula*." *Annals of botany* 11, 307–325. <https://doi.org/10.1093/oxfordjournals.aob.a088651>.

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