Observations on the Anatomy of Teratological Seedlings.

III. On the Anatomy of some Atypical Seedlings of *Impatiens Roylei*, Walp.

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With one hundred and thirteen Figures in the Text.

IMPATIENS ROYLEI is an annual of Indian origin which has become naturalized in England, and which, when once introduced, rapidly colonizes patches of bare ground unless thoroughly eradicated. A plot of ground in the garden of the University College, Nottingham, is completely covered with the plant in question, and it is from this source that much of the material for the present investigation has been derived. A further supply of seedlings has been obtained from the gardens of friends in Plymouth, the total number examined being sixty-one. It is proposed first of all to give some account of the vascular anatomy of the normal seedling and the young epicotyl, and then to show how these have been modified in the atypical specimens studied.

1. *The hypocotyl of the seedling*, at the time that the first epicotyledonary leaves become obvious, is about five centimetres in length and bears two somewhat fleshy, heart-shaped cotyledons with stout petioles which occasionally unite basally to form a very short cotyledonary tube. At the junction of the hypocotyl and root is a whorl of four stout rootlets below which the main root thins considerably (Figs. 1, 2, and 3). This whorl of roots, which is initiated at a relatively early stage in the development of the embryo, is very characteristic and forms a useful basis of comparison in studying the abnormal seedlings. A similar root whorl has also been described in *Impatiens Balsamina* by Chauveaud (1, p. 334).

In most seedlings the vascular supply of each cotyledon consists, at the proximal end of the blade, of a median endarch xylem group with a mass of phloem on either flank, and a pair of lateral bundles; this system giving rise to a tetrarch hypocotyledonary grouping, and in the root to a solid tetrarch xylem star with the usual radial arrangement of the phloem. In the very young seedling (Fig. 1) exarchy is evident a little way

FIGS. 1-8. Figs. 1, 2, 3, successive stages in the growth of the normal seedling, showing the whorl of four lateral roots at the junction of hypocotyl and tap-root. Fig. 4 *a*, older seedling viewed in plan, showing the relationship of the cotyledons and the epicotyledonary leaves at the first two nodes. Fig. 4 *b*, the same in lateral view, one cotyledon removed. Figs. 5 *a*, *b*, *c*, different aspects of a typical syncotyl for comparison with Figs. 4 *a*, *b*. Fig. 6, side view of a Group II seedling. Figs. 7 *a*, *b*, two views of a Group II seedling with peltate cotyledon. Figs. 8 *a*, *b*, *c*, seedling with unequal cotyledons and a whorl of three asymmetrically placed rootlets.

FIGS. 9-22. Figs. 9-19, typical examples of syncotyls showing modification of general habit and venation. Figs. 20, 21 *a*, *b*, typical Group II seedlings. Note the two rows of hypocotyledonary roots arising from the protoxylem poles in Fig. 21 *a*. Figs. 22 *a*, *b*, Group II seedling with a whorl of four roots and a tetrarch symmetry.

below the apex of the hypocotyl, so that four exarch xylem groups, with alternating phloem, traverse the hypocotyl until the base is approached. This primary structure becomes very considerably modified in older seedlings, owing to secondary changes. Prior to the giving off of the whorl of lateral roots, to which reference has been made earlier, the typical vascular structure of the hypocotyl is obscured, even in the youngest seedlings examined, by the development of a solid plug of xylem consisting of short tracheidal elements, and this persists until it is gradually replaced by the tetrarch xylem star characterizing the main root (cf. Fig. 99).

2. *The vascular system of the young epicotyl.* In the normal seedling the leaves borne at the first two epicotyledonary nodes are decussate and opposite, the lower pair being in the intercotyledonary plane: those produced at subsequent nodes are usually in whorls of three. Although the anatomy is subject to minor variations the essential features are stereotyped, and it is proposed to describe the course of the vascular strands from above downwards in a typical specimen at a stage in which two *whorls* of leaves are developed. For the sake of brevity the leaves will be referred to as the upper and lower whorls and the upper and lower pairs respectively. The petiolar vascular supply consists of three collateral bundles, one median and two lateral, the latter often being somewhat flattened transversely. There is thus at the apex of the young stem a ring of nine bundles (Fig. 23). This number becomes doubled by the entry of the three bundle-systems of the lower whorl, the eighteen bundles thus produced being reduced, first to twelve by the fusion of the laterals (Fig. 24), and then to nine again by the subsequent union of the median bundles of the upper whorl with one of the adjacent compound laterals (Fig. 28). This fusion of the median bundles is generally regular in either a clockwise or a counter-clockwise direction, but in some specimens it is irregular, two fusing in a clockwise direction whilst the third fuses in the opposite direction, or vice versa. The insertion of this trimerous system on to that of the members of the upper and lower pairs¹ gives rise to an interesting disturbance of symmetry. The bundle-systems of the upper pair do not enter the stem exactly in the cotyledonary plane, but slightly obliquely, forming with those of the whorl above an irregular ring of fifteen bundles (Figs. 24, 25). This number is ultimately reduced by the fusion of the adjacent laterals, but often before this occurs an additional complication arises owing to the insertion of the components from both nodes on to the vascular bundles of the lower pair.¹ The latter enter the stem in the intercotyledonary plane, but one group shows a retarded rate of entry compared with its fellow, a feature which is to be correlated with the difference in the methods of insertion of the vascular strands from

¹ The level at which the fusion of the adjacent laterals occurs is somewhat variable. It may occur soon after the entry of the bundles of the upper and lower pairs into the stem (Fig. 26), or it may be delayed until a relatively late stage (Fig. 27).

above. It will be perceived that *two* of the *lateral* bundles of the lower whorl (*a* and *b*, Figs. 27, 28) have of necessity no part in the bundle fusions occurring at the second epicotyledonary node, and it is these which unite

FIGS. 23-27. The distribution of the vascular strands in the young epicotyl. Fig. 27 is from an older seedling than the rest. In Fig. 26 the laterals of the lower whorl have, with the exception of the upper one on the right, fused with the adjacent laterals of the upper and lower pairs respectively. Bundles from the lower whorl are indicated in outline, from the upper pair cross-hatched, from the lower pair dotted. The dotted lines in Fig. 27 indicate the bundles which first unite. These and all subsequent figures, except Fig. 28, are camera lucida drawings reduced to scale.

with the lateral bundles of that one of the basal pair which first enters the stem (Figs. 25, 27, 28). The laterals of the other member of the basal pair each unite with a half-bundle derived from the midrib of that leaf in the lower whorl standing vertically above it, this bifurcating to produce the

necessary gap (Figs. 26, 27, 28). A transverse section of the epicotyl at this point will therefore, if no prior lateral fusions have occurred, reveal a system of twenty-two bundles comprised as follows:

- (a) Two sets of three from the lower pair of leaves;
- (b) Two sets of three from the upper pair of leaves;
- (c) Two sets of three from two of the leaves of the lower whorl;
- (d) Four bundles from the remaining leaf of the lower whorl;

namely, the laterals and bifurcated midrib (Fig. 27), this number being reduced to fourteen by the lateral fusions to which reference has already

been made. A further reduction to twelve bundles is next produced by the fusion of each of the two undivided median bundles from the lower whorl with one of the laterals of the adjacent leaf of the basal pair (Fig. 28). The twelve bundles are reduced to six by the unequal fusion of those of the upper pair of leaves with those of the lower pair, the median bundle and one of its laterals fusing with one set of lower pair laterals, whilst the remaining laterals of the upper pair fuse with the other set of lower pair laterals. A certain compensatory principle is observable in this unequal fusion, the two *pairs* of bundles fusing with the laterals which received the products of the bifurcating strand, whilst the remaining bundle fuses with the laterals which received two bundles each at the previous node. The six bundles so formed enter the apex of the hypocotyl in the intercotyledonary plane and eventually fuse to form two xylem

FIG. 28. Diagram indicating the course of the bundles in the young epicotyl.

masses which, in fairly old seedlings, are continuous with a patch of secondary xylem immediately below them. The relationship of the epicotyledonary strands to the vascular strands of the cotyledons is also a feature of some interest, especially in mature seedlings.¹ As the latter approach the former they appear in transverse section as bow-shaped systems, the ends of which extend beyond the laterals from the epicotyl. At the same time connexion is established between the two by the phloem

¹ By mature seedlings is meant those in which vigorous epicotyledonary growth has begun and in which the cotyledons have attained their full development.

of the cotyledonary laterals travelling round the outer ends of the bundles and uniting with that of the epicotyledonary laterals. At a slightly later stage the phloem, in some seedlings, forms locally a ring broken only opposite the median cotyledonary bundles. Simultaneously the epicotyledonary and cotyledonary xylems are brought into close contact by a collar of transfusion tracheides extending across the inner faces of each of the latter. The identity of the epicotyledonary xylem is ultimately lost in the previously mentioned patch of secondary xylem.

3. *The atypical seedlings*, with one exception, fall into two well-defined groups. The first of these comprises forty-three seedlings and forms a very complete series illustrating the development of a closely syncotylous condition from the normal.

Accompanying this development there has been a compression modification of the epicotyl, though the two processes have not proceeded with absolute uniformity. In all cases but one the syncotyl is essentially unilateral, although a short cotyledonary tube is very commonly formed. The exceptional specimen shows a fusion of the proximal third of the cotyledonary laminae and the distal parts of the petioles by their upper surfaces (Figs. 18 *a*, 18 *b*). The resultant modifications in this instance have been relatively slight, consisting of a lateral displacement of the epicotyl and a distortion of one of the lateral cotyledonary bundles which is involved in the fusion and which appears to have lost its phloem locally. Of the remainder the simplest case is one in which the cotyledonary fusion is purely laminar (Fig. 12) although the petioles are closely apposed throughout. Both in this and in such cases as those in which the petioles only are completely fused and in which the major portions of the laminae are free (Figs. 16 *a*, 16 *b*) the normal tetrarch symmetry of the vascular system remains undisturbed. In one seedling of this type, however, a curious condition is brought about by the persistence of the epicotyledonary xylem, which, lying in the intercotyledonary plane, constitutes a barrier between the apposed lateral bundles, preventing their fusion at the apex of the hypocotyl. The separation is maintained for quite a third of the way down the hypocotyl, and during that time the lateral bundles are endarch and offer a striking contrast to the exarch median bundles. Ultimately they unite, coming together at a very acute angle and thus differing from the sharp, almost horizontal fusion which is normal for the species. With regard to the modifications in the epicotyl, beyond a slight and variable reduction in the size of the leaf on the fusion side at the first node, these are usually negligible. One very definite tendency must, however, be noted, and that is that the vascular systems from the second epicotyledonary node incline to a precocious fusion with that of the reduced leaf, this often occurring prior to the entry into the stem of the vascular system of the unaffected leaf. As the laminae become more closely implicated in the

FIGS. 29-34. Syncotyl showing the suppression of one lateral bundle on the symphysis side and the compression of the leaves at the second epicotyledonary node. Note the modification of the bundle distribution in the epicotyl.

fusion the effect of the ensuing compression on the laterals on that side becomes plainly evident (cf. Figs. 10 *b*, 11 *b*, 13 *b*, 14, 15, 16 *b*, 17 *a*, and 19). In one or two instances both persist in a much reduced condition, but do not form a root pole, and end blindly in the hypocotyl. More usually only one persists, and, though in one instance (Figs. 29–34) it remains prominent through the greater part of the hypocotyl and becomes mesarch, it ultimately dies out. Generally the persistent lateral is represented in the hypocotyl by a few metaxylem elements which have no effect on the trimerous symmetry which has resulted from syncotyly. In the lamina it is usually well-developed and often receives bundles from both cotyledons (Figs. 13 *b*, 15, 19). The result of the further stages in syncotyly is to cause its complete suppression (Figs. 35–39), this being compensated to some extent by

FIGS. 35–39. Typical advanced syncotyl showing suppression of both laterals on the symphysis side and delay in the fusion of the lateral and marginal bundles. Note the two cotyledonary buds in Fig. 36.

a slight elaboration of the lateral bundle-system of both cotyledons on the side remote from the symphysis (Figs. 35, 36). The other points common to the whole series are that where the seedling is sufficiently developed two cotyledonary buds are always present, and also that a short cotyledonary tube is practically a constant feature (Fig. 36).

Reference has already been made to the precocious epicotyledonary vascular fusions incidental to the less extreme cases of syncotyly. This stage is followed by one showing a displacement of the vascular supply of the leaf of the first epicotyledonary node situated on the symphysis side, which, instead of retaining its normal position in the intercotyledonary plane, divides into two parts, one consisting of the midrib and one lateral bundle, and the other of a lateral bundle only. These fuse with the right and left laterals of the other leaf from the same node, so that the vascular supply of

the epicotyl below that point resembles an open gutter with its concavity towards the point of cotyledonary symphysis (Figs. 40–43). This condition characterizes the majority of those syncotyls in which there is partial suppression of the involved lateral cotyledonary bundles, and where the suppression is complete this is accompanied in many cases by a corresponding suppression of the first epicotyledonary leaf on the same side. As has been stated, however, the cotyledonary and epicotyledonary modifications do not synchronize exactly, so that complete suppression of the epicotyl leaf on the symphysis side may occur with a still persistent cotyledonary lateral, whilst a retention of the leaf in a reduced state may characterize a seedling in which the laterals have disappeared. Only one instance was observed in which compression affected the paired leaves of the second epicotyledonary node, and in this seedling, which was one with a single persistent lateral, the leaves of the first epicotyledonary node were practically normal in size, whilst the affected leaves were markedly reduced (Fig. 29). The behaviour of the vascular strands of the symphysis leaf was curiously aberrant, one of its lateral strands bifurcating and half fusing with the median strand to form a compound bundle situated close to one of the cotyledonary strands. This persisted for some time independently and ultimately died out, whilst the other half-lateral and the lateral on the opposite side formed the extreme members of the usual gutter-shaped system (Figs. 30–32).

What may possibly represent the ultimate effect of compression on the epicotyledonary leaves is seen in some of the seedlings in which the cotyledonary laterals on the symphysis side are completely suppressed. In these seedlings the number of leaves at the third cotyledonary node is reduced to two lying in what is normally the intercotyledonary plane (Fig. 49; cf. also Fig. 54). The vascular system of the one standing vertically above the persistent leaf from the first node behaves similarly to that occupying the same position in typical dicotyls, its median bundle bifurcating and the constituent halves uniting with the laterals of the basal leaf, whilst its laterals unite with the adjacent bundles from the leaves of the second node. The bundles of the other leaf from the third node unite with the adjacent laterals of the leaves of the second node, its midrib and one lateral fusing with one second node lateral, and its remaining lateral with the other. Their behaviour thus resembles that of the bundles of the leaf of the first node on the symphysis side in those seedlings in which it persists in a reduced condition (Figs. 51, 52; cf. also Figs. 54–59).

The effects of progressively closer syncotily may therefore be summarized as follows:

A. Cotyledonary vascular system.

(i) Modification of the lateral bundles on the symphysis side leading to their reduction, either simultaneously or otherwise, and their ultimate suppression.

(ii) Reduction in the hypocotyl and root of the tetrarch to triarch symmetry.

B. Young epicotyl.

(i) Precocious fusion of the bundle-systems of the leaves of the second node on to that of the leaf of the basal node on the symphysis side.

(ii) Reduction of the leaf of the basal node on the symphysis side and the division and lateral displacement of its vascular system.

(iii) Complete suppression of this leaf, and possibly

(iv) Reduction in the number of leaves at the third node from three to two with modification of the vascular relationships of one of the persistent members.

FIGS. 40-48. Figs. 40-43, young epicotyl in syncotyl showing reduction of one leaf of the basal pair and the modification of its bundle distribution. Figs. 44-48, young epicotyl of seedling with unequal cotyledons (Fig. 8) showing bundle distribution. Note the trimerous whorl at the second node and the precocious fusion of two of its members.

Comparing these results as regards the cotyledon with those obtained by Compton (3) in his study of syncotyls, it will be seen that up to a point the correspondence between the two is very close, but that the ultimate stages recorded by him for *Helianthus annuus syncotyleus*, namely, partial union of the median bundles and, more doubtfully, partial suppression of one of the median bundles, are absent in the material of *Impatiens Roylei*. Compton apparently made no attempt to study the effect of advanced syncotily on the young epicotyl.

The second group of seedlings, seventeen in number, also form a very completely graded series. All the members of this group show what is apparently a single cotyledon with no macroscopic evidence of syncotylous origin (Fig. 20). The first epicotyledonary node bears a single leaf

occupying what in a normal seedling would be the place of a second cotyledon (Fig. 6). In the simplest case the anatomy of the cotyledon is identical with that of one cotyledon of a typical dicotyl, its vascular supply consisting of a median 'double' bundle with a lateral on either flank. The behaviour

FIGS. 49-62. Figs. 49-52, epicotyl of syncotyl showing total suppression of first epicotyledonary leaf on the symphysis side and two leaves only at the third node. Note the trimerous whorl at the fourth node. Figs. 53-57, a similar type of epicotyl in a Group II seedling. Figs. 58-62, cotyledon bundles from the same seedling, showing anomalously situated bundle in the same vertical plane as the double bundle. Note the development of diarchy by the concentration of the lateral and marginal bundles on the anomalously situated bundle.

of the median bundle is perfectly regular and it forms a root pole in the usual way. The two lateral bundles on entering the hypocotyl rapidly approach each other and unite to form a second root pole, so that a diarch condition obtains throughout the hypocotyl and root (Figs. 63-69). As a consequence the root whorl at the base of the hypocotyl is reduced to two

members, and it is of interest to note that the hypocotyledonary adventitious roots which characterize this plant, and which arise from the protoxylems, also develop in two vertical series instead of the usual four (Fig. 21 a). Starting from this basal type there has been a progressive elaboration of the

FIGS. 63-77. Figs. 63-69, simple type of Group II seedling, the cotyledon showing the structure of a single normal cotyledon and developing a diarch root-plate. Figs. 70-77, Group II seedling showing on the left delayed fusion of lateral and marginal bundles and on the right independence of the two.

lateral vascular system. This seems to be due in a measure to an increase in the relative importance of the marginal veins from the lamina, which, instead of uniting with the laterals at the distal end of the cotyledonary petiole, show a progressively delayed fusion until in many cases they only unite near the apex of the hypocotyl. This delay in fusion has inevitably

led to the entry into the petiole of smaller veins of secondary rank which normally would fuse with the marginal or lateral veins within the cotyledonary lamina. There is little doubt that the increase in the complexity of the petiolar vascular supply is to be correlated, in part at least, with the increase in the area of cross-section of that organ, this having become U- or C-shaped with the concavity on the adaxial side. One seedling of this type shows a curious anomaly in the arrangement of its petiolar vascular system, a presumably lateral strand lying in the same plane as, and immediately ventral to, the median strand. It retains this position throughout (Figs. 53 and 58-62), and the second pole of the diarch hypocotyl is produced by a concentration of the more distal lateral strands upon it, thus contrasting with the usual condition in which the concentration is bilateral and away from the middle line rather than towards it. There is also a further peculiarity in that the extreme marginal strand of one side is locally pseudoconcentric in character owing to the xylem being at that point completely surrounded by phloem (Fig. 59). From the stage in which the fusion of the lateral and marginal strands only occurs at the base of the petiole, further progress is inaugurated by this union being delayed until their entry into the hypocotyl. This is followed by the two becoming entirely independent (Figs. 81-83), and in one case the two strands of one side show delayed fusion, whilst on the other the marginal constituents alone take part in the formation of a root pole (Figs. 73-75). In such cases the strands representing the laminar laterals traverse the greater part of the hypocotyl, but ultimately their protoxylem disappears and their identity is lost in the xylem complex associated with the production of the root whorl to which reference has already been made. As long as the protoxylem persists it retains an endarch position, the only exception noted in the eight cases of this type being one in which it became mesarch towards its lower end. In one seedling both laterals are independent and persistent, and each forms a root pole so that a tetrarch condition is once more established (Figs. 84-90).

The seedling in which this phenomenon occurred was very short and stout (Figs. 22 *a*, 22 *b*), but whether this had any bearing on the development of tetrarchy it is impossible to say. A condition of secondary triarchy would obviously arise in a similar way granted an asymmetrical independence and persistence of one of the lateral strands. The median strand of this particular plant is remarkable in assuming a pseudoconcentric structure at the base of the petiole, though this is not persistent (Figs. 84-86), and a similar feature also characterizes the two lateral and to a certain extent the marginal strands immediately before and subsequent to their entry into the hypocotyl (Figs. 85-86). There is a distinct similarity between these strands and the 'Zwischenstränge' recorded by Dodel (5) in *Phaseolus* spp. and by Compton (2) in *P. Hernandezii*, *Abrus precatorius*, and in

(3) *Helianthus annuus syncotyleus*, but the two do not seem exactly homologous, since the latter appear to be primarily hypocotyledonary in character and, although they occasionally contribute a root pole, they only exception-

FIGS. 78-90. Figs. 78-83, Group II seedling showing a further advance on that shown in Figs. 70-77, but still producing only a diarch root. Figs. 84-90, Group II seedling showing a still further advance leading to tetrarchy in the root.

ally constitute a part of the laminar vascular supply, whilst in *Impatiens* the additional vascular complexity of the hypocotyl is the result of the modification and increase in importance of certain of the chief laminar strands.

A subsidiary line of evolution is exhibited by three seedlings in which a very complete cotyledonary tube is formed. Two of these show no special departure from the group as a whole in their vascular arrangements, but the third specimen is unique. In it there is no line of demarcation between cotyledonary petiole and hypocotyl, and the former consists of a more or less peltate basin-shaped structure, the floor of which is thrown into a number of wrinkles surrounding what looks like a small median pore (Figs. 7 *a*, 7 *b*). The vascular supply consists of the usual median, lateral, and marginal strands, but the two latter unite well inside the lamina, the resultant compound strands also fusing and becoming exarch very rapidly (Fig. 91). As a result the vascular system consists, immediately below the lamina, of two

FIGS. 91-96. Anomalous Group II seedling with peltate cotyledon (Fig. 7), showing abnormal bundle behaviour.

bundles, the one derived from the laterals showing for a time the curious pseudoconcentric structure to which reference has been made in the other seedlings (Fig. 92). During their passage down the hypocotyl their behaviour is somewhat anomalous, that from the median strand remaining endarch, and turning outwards through 90° , whilst its exarch fellow also turns outwards through 90° to the same side (Fig. 93). The latter then swings back through 180° , whilst the endarch bundle becomes mesarch and finally exarch and in so doing comes to occupy its normal position. The result is that the two lateral roots representing the root whorl lie at right angles to each other (Figs. 94, 95), and it is not until these have been given off that the normal diarch plate is evident. At no stage is there any evidence, apart from the pore in the floor of the lamina, of the median cavity which the epicotyl would occupy. This may be due either to occlusion by the ingrowth of the walls of the tube, or possibly to the suppression of the petiole, a view which is supported by the early union of

the lateral strands and by the absence of any line of demarcation between cotyledon and petiole.

The modification of the epicotyl is along the same general lines as those indicated in the first group, but in the series now under consideration there is, with two possible exceptions, no trace of a second leaf at the first node,

FIGS. 97-100. Figs. 97, 98 illustrate the details of xylem and phloem distribution of Figs. 93 and 95. Fig. 99, tracheidal hypocotyledonary complex developed prior to the giving off of the basal root whorl from a syncotyl. Fig. 100, typical diarch plate in a Group II seedling.

though the second node is normal and bears two leaves. Where the seedlings are old enough the leaves of the third node are also two in number as in the first group. The evidence of epicotyledonary compression in the second group is thus as great as that found only in the extreme cases of the undoubted syncotyls. The exceptional cases referred to above were seedlings which were not discovered until the epicotyl had developed to a greater extent than that of the remainder of the series. Their salient features are illustrated in Figs. 101-106, and, as may be seen from these,

the arrangement of the leaves diverges very widely from the normal, so much indeed that it is impossible to correlate it at all closely with that of the remaining seedlings studied. Whether this divergence is an extreme expression of the effect of compression it is impossible, on such limited evidence, to say, but leaf *A* and, judging from the behaviour of its vascular strands, leaf *A* 1 in both seedlings arise at the first epicotyledonary node, and leaves *B* and *B* 1 at the second epicotyledonary node. Beyond these it is difficult to assign values, and little useful purpose would be served by the attempt.

FIGS. 101-106. Epicotyls of two Group II seedlings showing considerable modification of the leaf arrangements. Figs. 101-105 are from one seedling and Fig. 106 from a second.

Three views seem to be possible as to the origin of this group, and these may be briefly stated as follows :

- (i) That the monocotylous condition is due to the suppression of one of the cotyledons, that is, the condition is heterocotylous in origin.
- (ii) That the monocotylous condition is due to a degree of syncotyl of so extreme a character that there is no anatomical evidence of the double origin of the resultant cotyledon remaining.
- (iii) That one of the cotyledons has retained its normal characteristics, whilst the other has become entirely leaf-like and is represented by the first epicotyledonary leaf.

The points in favour of the first hypothesis are based chiefly on the character of the cotyledon. The simplest member of the series exhibits

a cotylar anatomy which is indistinguishable in essentials from that of a single cotyledon of a normal dicotyl, and possesses, in common with the remaining members of the group, a single median axillary bud. Moreover, the group as a whole exhibits an admirably graded series of forms of progressively greater complexity, the final member of which is tetrarch owing to the increase in importance of the lateral and marginal strands respectively. If these seedlings were the ultimate products of a reduction series it would be reasonable to anticipate the development of a relatively stable type, whereas the reverse, as we have seen, is the case. A further point is that between the most extreme member of the undoubted syncotyls and the group under consideration there is a wide gap unbridged by any transitional forms whatever. It is recognized that negative evidence of this type is always liable to be shaken by subsequent discoveries, but it is fair to expect that some at least of the specimens studied would have furnished evidence of a double origin, since it is difficult to conceive of a cotyledonary union so intimate that no part of the seedling anatomy would reveal it, especially in view of the fact that syncotyly is not normal for the species.

The facts which tell against the above interpretation are three in number, namely:

- (i) The absence of material showing any trace of suppression of one of the cotyledons. (This, as negative evidence, is of course open to similar objections to those indicated in the previous paragraph.)
- (ii) The position of the first epicotyledonary leaf.
- (iii) The character of the modifications of the epicotyl.

The second and third of these points will be dealt with subsequently. With regard to the first, although a careful search was made and a number of seedlings exhibiting a difference in the size of the cotyledons were examined, no evidence of a convincing character was obtained. Where the discrepancy in the size of the cotyledons was not very pronounced the vascular structure was not affected, and where the cotyledon had remained very small this was due, with one exception, to traumatic causes. The injury responsible for the arrested growth as a rule involved a more or less complete severance of the median petiolar bundle, and often of one of the lateral bundles as well. The result was that, though the cotyledon became green, it retained its intraseminal form and size and was packed with starch grains owing to the interference with the channels of translocation. The one exceptional case, although not bearing directly on the origin of the group under discussion, is of sufficient interest to merit description. Of the two cotyledons, one was normal in size, whilst the other was small and was flexed downwards by the petiole (Figs. 8 *a, b, c*). Serial sections revealed a curious anomaly in the vascular supply of the reduced cotyledon, the midrib consisting of a collateral bundle flanked, in the petiole, by three smaller bundles on either side (Fig. 107). At the apex of the hypocotyl

these bundles unite to form two groups which become widely separated and ultimately unite with the lateral bundles of the normal cotyledon, thus producing an asymmetrically triarch condition of the hypocotyl which is reflected in the development of three members only in the root whorl (Figs. 110-113). Below the point of origin of these roots the main root is tetrarch as in normal dicotyls. We have evidently to deal in this instance with a cotyledon in which the midrib is entirely lacking, its place being taken, in the lamina and petiole, by one of the laterals. With regard to the epicotyl this is chiefly remarkable from the fact that a whorl of three

FIGS. 107-113. Transverse sections of seedling with two unequal cotyledons (Fig. 8), showing suppression of the median double bundle in one cotyledon and the development of asymmetrical triarchy in the hypocotyl. R i, R ii, R iii, lateral roots; AX., tetrarch axis.

leaves is produced at the second epicotyledonary node instead of the usual pair. The resultant modification in the grouping of the foliar traces in the epicotyl is indicated in Figs. 44-48. It is noteworthy that one of the compound epicotyledonary bundles (Fig. 109, *a*) is interposed between, and unites with, the approaching cotyledonary laterals on the same side, and that towards the base of the epicotyl the remaining strands form a shallow open gutter in the intercotyledonary plane.

The positive evidence in support of the origin of the second group of seedlings by syncotyl rests chiefly on the leaf position and the type of modification found in the epicotyl. The first epicotyledonary leaf stands in the position normally occupied by the second cotyledon, and if the cotyledon

is of dual origin this position represents what would be, in typical dicotyls, the intercotyledonary plane. If, on the other hand, the single cotyledon is heterocotylous in origin it is obvious that there has been an increase of ninety degrees in the angle of divergence between that structure and the first epicotyledonary leaf. There is no evidence in support of this change, though, in view of the fact that the epicotyledonary primordia originate much later than the cotyledons, it is conceivable that the modification in the latter may have induced an alteration in the orientation of the former.

The character of the epicotyledonary modifications themselves is wholly in favour of a syncotylous derivation, since the compression modifications typical of the more advanced syncotyls are reproduced faithfully in the seedlings comprising the second group.

It is worthy of note that in the monocotylous *Ranunculus Ficaria* and in all Monocotyledons proper¹ the seedling anatomy of which has been investigated, the insertion of the first epicotyledonary leaf is opposite that of the cotyledon. If this insertion is to be regarded as decisive in demonstrating a syncotylous origin of an apparently single cotyledon, then the Monocotyledons are undoubtedly of dicotylous origin. It must be remembered, however, that in embryonic tissues, such as are characteristic of an intraseminal stem apex, one is dealing, as Miss Sargent rightly emphasized, with extremely plastic material, and it is readily conceivable that the explanation of such an insertion is to be sought along physiological rather than phyletic lines. The third alternative need not be discussed at length. If the material investigated had been represented by apparent heterocotyls only, the conception might have been possible, although it would have involved a suppression of the vascular continuity between the modified cotyledon and the radicle. In the face of the evidence supplied by obvious syncotyls in which a gradual suppression of one leaf of the basal epicotyledonary pair can be demonstrated the idea becomes untenable.

It is of course realized that the evidence afforded by an anatomical study of teratological seedlings in a single species provides much too insecure a peg to hang a comprehensive theory upon, but one is perhaps justified in pointing out that, whichever view is adopted with regard to the origin of the second group of seedlings described, the result gives food for thought. If syncotily is invoked, then we have, in a species normally dicotylous, teratological syncotyls in which all trace of double origin is lost: if, on the other hand, a heterocotylous origin is regarded as more probable we are faced with the fact that syncotily and heterocotily are possible within the limits of a single species. A comparison of the cotyledonary anatomy of the second group of seedlings with that of *Ranunculus Ficaria* reveals

¹ E.g. *Albuca Nelsoni*, *Allium* spp., *Anemarrhena asphodeloides*, *Anthericum Liliago*, *Arisaema dracontium*, *Arthropodium cirrhatum*, *Arum maculatum*, *A. italicum*, *Chlorogalum pomeridianum*, *Fritillaria imperialis*, *Hyacinthus romanus*, *Triglochin palustre*, *Zygadenus elegans*.

one interesting point of similarity, this being the increase in the relative importance of the marginal strands in some of the specimens figured by Sterckx (15). Thus his Fig. 178 shows the marginal strands deferring their fusion with the median strand until well down the cotyledonary petiole, and Figs. 173 and 176 illustrate cases in which the strands are apparently independent throughout the petiole. A similar increase in the relative importance of the lateral strands is also characteristic of many monocotyledonous seedlings, although further complications are produced in many of these by the vascular system of the first epicotyledonary leaf contributing to that of the hypocotyl. Thus independent laterals characterize both *Arum maculatum* (14) and *A. italicum* (1), and Sargent (12) has described a number of species in the Scilleae (Liliaceae) in which all stages are shown, varying from a condition in which the contributions to the vascular symmetry of the radicle by the cotyledonary lateral strands are more or less capricious (e.g. *Galtonia candicans*, *Dipcadi serotinum*) to forms in which the lateral bundles of the cotyledon take a perfectly regular share in the formation of the root stele. 'The species *Hyacinthus romanus*, *Muscari atlanticum*, *M. armeniacum*, and *M. neglectum*, for example, form a series in which the lateral traces become more and more important until they supply a full half of the root stele.'

Special mention must be made of the condition characterizing *Anemarrhena asphodeloides* (10), in which extreme compression of the median and lateral bundles has resulted in their fusion to form two massive bundles situated one on either side of the sagittal plane of the seedling. The protoxylem of these bundles divides into three, the median portions each constituting a root pole situated in the intercotyledonary plane, whilst the others unite in pairs in the cotyledonary plane, so that a tetrarch root is formed. Sargent (12) regards the massive cotyledonary bundles as homologous with the 'double bundle' characterizing the cotyledon of such forms as *Allium*, and there is little doubt that this is true, though of a portion only, of each of the *Anemarrhena* bundles. Chauveaud (1) has shown, however, that the widely separated halves of the double bundle of *Allium* originate as a radial file of protoxylem elements flanked by primary phloem, and that the wide separation of the two xylem segments in the maturer condition of the cotyledon is due to the successive resorption first of the radial file of vessels (Chauveaud's 'vaisseaux alternes') and then of the intermediate vessels succeeding it on either side. The three stages are admirably illustrated in Chauveaud's figures (1, pp. 177-179, Figs. 20-25). A further point of interest in this connexion is provided by a comparison of Chauveaud's Fig. 25, illustrating the last remnants of the crushed and partly resorbed intermediate vessels in *Allium*, with Sargent's figure of a section across the cotyledon of *Anemarrhena* (10, Pl. XXXIII, Fig. 2). The latter exhibits evidence for the resorption of intermediate vessels lying

between the two xylem masses strikingly like that given by Chauveaud in *Allium*. There is little doubt that an examination of younger seedling material of *Anemarrhena* would reveal both 'alterne' and intermediate elements situated in the region separating the two divergent bundles characterizing the older cotyledon. If this interpretation of the structure of the *Anemarrhena* be the correct one, it follows that each xylem 'massif' really represents the fused constituents, not of a median bundle with a lateral on either flank, but of half a median bundle with both a lateral and a marginal strand on the distal side only. A certain amount of collateral support for this interpretation is provided by Chauveaud's description of the seedling anatomy of *Cordyline indivisa* (1, pp. 421-425). This seedling has a tetrarch root, but in the young state only one xylem is differentiated in the hypocotyl, the remainder of the root poles being represented by their phloem only. The phloem groups coalesce to form two larger composite groups flanking the persistent xylem, which becomes the cotyledonary midrib. It is evident that in *C. indivisa* there is an *Anemarrhena* condition in which the lateral and marginal xylem elements are not differentiated in the hypocotyl till a relatively late stage. There is thus in *Cordyline indivisa*, and probably in *Anemarrhena asphodeloides* also, a close parallel to the condition found in the tetrarch seedling of the second group described in this paper, the only essential difference being that consequent on the crowding together of the lateral and marginal and median strands in the two monocotyledonous species. The evidence for regarding the vascular system of *Anemarrhena* in this way is admittedly somewhat sketchy and incomplete, but it serves to emphasize the urgent need for a reinvestigation of the very young stages of the seedling anatomy of Monocotyledons, a task which it is hoped to proceed with during the coming summer.

SUMMARY.

1. The bundle-system of each normal cotyledon of *Impatiens Roylei* consists of a median double bundle with a lateral bundle on either flank, these producing tetrarch symmetry in the hypocotyl and root.

2. The young epicotyl produces paired leaves at the first two nodes and whorls of three members at subsequent nodes. The vascular anatomy of these leaf-systems and their interrelationships is described.

3. The atypical seedlings fall into two main groups, the first of which is undoubtedly syncotylous in origin.

4. The seedlings of this first group show a graded series in which the syncotily becomes progressively more intimate, this resulting in the suppression of the lateral bundles, and consequently of the root pole, on the symphysis side.

5. The effect of syncotily on the epicotyl is shown in the reduction and

ultimate disappearance of the first epicotyledonary leaf on the symphysis side, and possibly, in extreme cases, the modification of the leaves at the third node. The leaves of the second node are usually not affected.

6. The seedlings of the second group may be either syncotylous or heterocotylous. In favour of the first alternative there is the position of the first epicotyledonary leaf and the character of the epicotyledonary modifications as a whole: in favour of the second alternative is the cotyledonary morphology, its anatomy, and the possession of a single axillary bud.

7. The seedlings of the second group show certain anatomical tendencies due to the increase in the relative importance of the lateral and marginal strands, which are paralleled to some extent by the lateral strands in many seedling Monocotyledons.

BIBLIOGRAPHY.

1. CHAUEAUD, G. : L'appareil conducteur des plantes vasculaires. *Ann. Sci. Nat. (Bot.)*, 9^e sér., t. xiii, 1911.
2. COMPTON, R. H. : An Investigation of the Seedling Structure in the Leguminosae. *Journ. Linn. Soc. (Botany)*, vol. xli, No. 279.
3. ————— : An Anatomical Study of Syncotyly and Schizocotyly. *Ann. Bot.*, vol. xxviii, 1919.
4. COULTER, J. M., and CHAMBERLAIN, C. J. : Morphology of the Angiosperms, pp. 206-10.
5. DODEL, A. : Der Uebergang des Dicotyledonen-Stengels in die Pfahl-Wurzel. *Pringsh. Jahrb.*, viii, 1872.
6. HENSLow, G. : A Theoretical Origin of Endogens from Exogens by Self-adaptation to an Aquatic Habit. *Journ. Linn. Soc.*, vol. xxix, 1892.
7. HILL, A. W. : The Morphology and Seedling Structure of the Geophilous Species of *Peperomia*. *Ann. Bot.*, vol. xx, 1906.
8. LUBBOCK, SIR J. (Lord Avebury) : On Seedlings, vol. i, p. 12, pp. 314-16.
9. LYON, H. L. : The Phylogeny of the Cotyledon. *Postelsia*, 1901.
10. SARGANT, E. : A New Type of Transition from Stem to Root in the Vascular System of Seedlings. *Ann. Bot.*, vol. xiv, 1900.
11. ————— : The Origin of the Seed-leaf in Monocotyledons. *N. Phyt.*, vol. i, 1902.
12. ————— : A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings. *Ann. Bot.*, vol. xvii, 1903.
13. ————— : The Reconstruction of a Race of Primitive Angiosperms. *Ann. Bot.*, vol. xxii, 1908.
14. SARGANT, E. A., and SCOTT, R. : On the Development of *Arum maculatum* from the Seed. *Ann. Bot.*, vol. xii, 1898.
15. STERCKX, R. : Recherches anatomiques sur l'embryon et les plantules dans la famille des Renonculacées. *Mém. Soc. Roy. Sci. Liège*, 3^e sér., t. ii.

Holden, Henry Smith. 1920. "Observations on the anatomy of teratological seedlings. III. On the anatomy of some atypical seedlings of *Impatiens roylei*, Walp." *Annals of botany* 34, 321–344. <https://doi.org/10.1093/aob/os-34.3.321>.

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DOI: <https://doi.org/10.1093/aob/os-34.3.321>

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