Observations on the Anatomy of Teratological Seedlings.

IV. Further Studies on the Anatomy of Atypical Seedlings of *Impatiens Roylei*, Walp.

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With ninety-seven Figures in the Text.

THE present paper is the outcome of an attempt to determine the relationships of abnormal seedlings of two types occurring in *Impatiens Roylei*, the anatomy of which has been described in a previous issue of this Journal (18). In the normal seedling each cotyledon possesses a median 'double' bundle with independent laterals, and shows tetrarch symmetry in both hypocotyl and root. The tetrarch condition is reflected in the constant presence of a whorl of four lateral roots at the junction of the hypocotyl and tap-root. In the abnormal seedlings one type¹ described exhibits the characteristic phenomena associated with syncotily, cotyledonary fusion being followed either by a precocious fusion of the laterals on the symphysis side with the midrib, or by their partial or complete suppression. A triarch symmetry is thus produced and is accompanied by other related features, notably the development of three members in the root-whorl and the elimination of the leaf on the symphysis side at the first epicotyledonary node. The second type² apparently possesses a single cotyledon only, and gives rise to a diarch condition in the hypocotyl, this being reflected both in the root-whorl and tap-root. One of the two poles in the hypocotyl is a direct downward continuation of the single median 'double' bundle: the other results from the fusion of the lateral strands on either flank. Only one axillary cotyledonary bud is present, in contrast to the two occurring in the first type. The two types approach each other, as far as

¹ Referred to subsequently in this paper as 'Type 1'.

² Referred to subsequently in this paper as 'Type 2'.

previous investigation has shown, solely in the epicotyledonary modifications, which are strikingly similar. It will be obvious that the mode of origin of seedlings of the second type raises a point of some theoretical interest. If they are produced by cotyledonary suppression, then syncotyly and heterocotyly coexist in the same species: if they represent the ultimate phase in a syncotylous series, then the two cotyledons exhibit so perfect a dovetailing of parts that all traces of double origin are lost.

It was realized that suitable material for the determination of this point would be scarce, and in all some 118 seedlings have been microtomed without yielding absolutely conclusive evidence. As was inevitable, however, collateral problems of interest have arisen, and these have also been followed up and the results included in the present paper.

The direct evidence which bears upon the origin of the seedlings of the second type falls under two heads, namely:

(a) The behaviour of the 'double' bundles in certain undoubted syncotyls.

(b) The variations in the cotyledonary axillary buds.

Two clear cases of complete midrib fusion were obtained (Seedlings A and B), and these will be described in detail. In 'Seedling A' (Fig. 1), in which a closely syncotylous condition obtains, the respective median strands travel down the compound lamina in close proximity and, whilst still separate, develop 'double' bundle structure (Fig. 16). They are inclined slightly to each other, and for some distance subsequent to their union two mesarch protoxylem groups are evident in the common metaxylem, with a phloem group on either flank and one in the plane of junction (Fig. 17). The fate of the median phloem is somewhat curious, the major part passing over to unite with one of the lateral groups, while the remnant dies out. The compound bundle loses all traces of its double origin, and forms a single pole both in the hypocotyl and root. The marginal strand and the lateral of one side fuse and, near the apex of the hypocotyl, unite with the marginal strand only from the opposite side, the composite bundle becoming exarch and constituting a second pole (Fig. 18). The protoxylem of the lateral which remains independent persists in an endarch position for a short distance and then disappears, being followed at a lower level by the metaxylem, so that below this point the hypocotyl is diarch for a period (Fig. 19). The two xylem poles associated with the cotyledonary strands are augmented by two which rise *de novo* in the plane at right angles to them, and a tetrarch condition is thus produced, giving rise to four lateral rootlets in the root-whorl, and below these to a tetrarch tap-root (Fig. 20). In 'Seedling B' the march of events is somewhat different, but is also of interest. The seedling (Figs. 2 a, 2 b) is an obvious syncotyl, but in the bottom third of the compound lamina the midribs, which are represented by collateral bundles at this stage, approach each other at an angle of almost

90° from their normal position, the phloems lying farthest from the line of cotyledonary fusion (Fig. 21). The two bundles unite by their protoxylems and form a mesarch mass almost surrounded by phloem (Fig. 22). At the apex of the hypocotyl the protoxylem is tending to assume an exarch position, and the phloem, which behaves in a curiously anomalous manner

FIGS. 1-15. Fig. 1. 'Seedling A.' A syncotyl combining tetrarchy at the base of the hypocotyl with extremely intimate syncotyly. Figs. 2 a, 2 b. 'Seedling B.' A syncotyl in which the hypocotyl is diarch; Fig. 2 b shows the venation of the compound lamina. Figs. 3, 4. Syncotyls showing tetrarchy. Fig. 5. A syncotyl showing a triarch hypocotyl; the tap-root was pentarch. Figs. 6 a, 6 b. Seedling with markedly unequal cotyledons. Fig. 7. A syncotyl with unequal cotyledons. Fig. 8. Large 'Type 2' seedling in which the epicotyl has not developed. Figs. 9, 10 a, 10 b. Salver-shaped amphisyncotyls, 'Seedlings C and D' respectively. Figs. 11-14. Goblet-shaped amphisyncotyls. Fig. 15. 'Seedling H.'

throughout, is creeping round the inner margin of the composite bundle (Fig. 23). At a slightly lower level it forms a U-shaped system as seen in transverse section, with a gap where the protoxylem is situated (Fig. 24). Meanwhile the marginal bundles of each cotyledon fuse and, after a brief downward course, end blindly. The lateral bundles, which also show

anomalies in their phloem arrangement, after receiving a number of accessory strands, unite in the uppermost third of the hypocotyl (Fig. 25) and, the protoxylem becoming exarch, a diarch condition is produced which persists throughout the hypocotyl and results in the giving off of two stout lateral roots at the point of junction with the tap-root (Fig. 26). Immediately

FIGS. 16-28. Figs. 16-20 'Seedling A', Figs. 21-28 'Seedling B'. Both show a fusion of the cotylar midribs, these behaving in transition like a single normal midrib. These and all subsequent figures are camera lucida drawings reduced to scale.

below the point of origin of the lateral roots the diarch condition is still evident, in spite of a considerable amount of secondary thickening which has produced a tracheide complex with a continuous sheath of phloem. At a slightly lower level the protoxylem, which is continuous with that of the fused laterals, flattens out and bifurcates, the phloem sheath at the same time breaking into four parts (Fig. 27). Three of the gaps in the phloem are opposite the protoxylems derived from the median and lateral bundles

respectively. The fourth gap heralds the formation of a new protoxylem pole which arises laterally and quite independently of the others. It is evident that the tetrarch condition of the main root which characterizes both these seedlings is evolved in a manner which differs fundamentally from that of the normal type. The question of the origin of the root-poles in the abnormal seedlings as a whole will be considered in detail at a later stage, but the chief point for immediate consideration is that provided by the behaviour of the united median strands, which lose all trace of their double origin and act in a manner precisely similar to a normal midrib, forming between them a single root-pole. Dr. E. N. Miles Thomas (31) has recorded a somewhat similar case in an abnormal specimen of *Anemone pulsatilla*, the two fused midribs of which are continuous with one root-pole of a diarch root, the other being in the plane of the first plumular leaf. The same author, jointly with Miss Davey (32), has investigated the seedling anatomy of a number of Pseudo-Monocotyledons, though their results have been up to the present only published in abstract. Material of *Anemone apennina* and *Ranunculus Ficaria*, in which the single member is more or less bifid, and of *Conopodium denudatum*, in which it is undivided, was among that examined. In all the root is diarch, the xylem plane passing through the centre of the first plumular leaf, a feature which they share with the seedling of *Anemone pulsatilla* described above, and in which they differ from their normal dicotyledonous relatives where the diarch plate is at right angles to this plane. In *Ranunculus Ficaria* root structure is initiated *below* the cotyledonary node, the vascular supply of the first epicotyledonary leaf apparently contributing largely to one root-pole. In *Conopodium denudatum* and *Anemone apennina*, on the other hand, root structure is present from the lower half of the cotyledonary 'petiole' downwards, and inferentially, only the cotyledonary vascular strands connect directly with the root-poles. It will be recognized that the two latter forms bear a fairly close resemblance to the 'Type 2' seedlings of *Impatiens Roylei* described here, whilst *Ranunculus Ficaria* is nearer in type to certain Monocotyledons such as *Allium* and *Triglochin*.

Other syncotylous specimens of *I. Roylei* showing a linking of the adjacent half-phloems of the 'double' bundle and occasionally forms with a temporary linking of the xylem also were met with, but these showed the usual triarchy in the hypocotyl with its accompanying three lateral roots.

It seems reasonable from the evidence yielded by Seedlings A and B

FIG. 29. Transverse section of stele, showing the origin of a root-pole, *r*, *de novo*.

and from that provided by other species to suppose that extremely intimate syncotyly may lead to the suppression of all evidence of double origin in the composite petiole, and, if carried farther, in the cotyledon lamina also. The evidence yielded by the behaviour of cotyledonary buds, though different in character, is of no less interest in this connexion. The buds in the axils of the cotyledons are not developed very early, and in much of the material studied they are either not evident or are doubtfully represented by small groups of meristem. In the older syncotylous seedlings an excellent series of forms showing progressively closer fusion of the buds has been secured. In the simplest type the double origin of the bud is very evident, as it consists of a tangentially elongated ovoid mass of meristem which bifurcates near the apex (Fig. 82). Other stages show a rather massive bud with apical splitting, and others again show what to all appearance is a single normal bud (Fig. 35). In addition to this series a solitary specimen was discovered among the 'Type 2' seedlings which showed an axillary bud which was quite evidently of double origin. There was thus in this type of seedling indications of the double nature of the cotyledonary bud, whilst the 'Type 1' series shows that, as is the case with the midribs, a fusion so intimate may occur that all evidence of dual origin is suppressed. When these facts are considered, together with the striking similarity in the modifications of the epicotyl, the view that the whole of the abnormal seedlings must be regarded as syncotylous in origin is materially strengthened. Further collateral evidence is provided by a similarity in the behaviour of the vascular strands during their passage from the cotyledon to the root in the two types of seedling, and also by certain new features in the transition region which exhibit a close parallelism. Considerable numbers of modified seedlings were obtained which, although their appearance would suggest a triarch and diarch condition of the hypocotyl, nevertheless possessed a root-whorl with four members (Figs. 3, 4), and therefore presumably four xylem poles. An investigation of these revealed the fact that the additional poles may arise in one of two ways. One has already been indicated in the previous paper dealing with these seedlings (18), and is due to the combination of two features, namely, the growth in size and importance of the marginal as distinct from the lateral strands, and the remaining independent of the latter so that the marginals alone contribute to the root-pole opposite that formed by the midrib. The independent laterals are often continued into the hypocotyl as endarch strands, which usually soon lose their protoxylem and ultimately die out. Prior to this they may become mesarch and occasionally, near the base of the hypocotyl, exarch, though the position of the protoxylem, where persistent, is inconstant. It is from this type of persistent lateral strand that a new member of the lateral root-whorl and subsequently a root-pole originate. Neither the fact of the protoxylem remaining endarch nor its disappearance at a lower level seem to affect

this, although where the protoxylem is lost high up in the hypocotyl no corresponding lateral root or root-pole is usually formed. The formation of one additional root-pole in this manner is a fairly common feature of both types of seedling, and results in either a triarch or a tetrarch condition. It is due in such cases to the asymmetrical persistence of one lateral only. In the previous paper (18) dealing with these seedlings a comparison of the independent laterals with the 'Zwischenstränge', first described by Dodel (11) and later by Compton (5, 6), was made and the differences between the two types noted. This difference has received emphasis by the discovery of strands showing much closer affinities with true 'Zwischenstränge' in the series of seedlings now described. These strands, each of which normally gives rise to a new member of the lateral root-whorl and subsequently to a root-pole, usually originate in the basal third of the hypocotyl, and at first are represented by an isolated tracheide (Fig. 29) lying in the plane at right angles to the sagittal plane of the seedling. This is augmented at a lower level by metaxylem, and ultimately forms what to all appearances is a normal exarch hypocotyledonary xylem group. In some seedlings the new protoxylems arise at a much lower level, and may be evident only at or near the level at which the whorl of lateral roots is produced. Exceptionally they may not be represented in the hypocotyl at all (Figs. 36, 37, 41, 42), and then are evident only as new root-poles. The fact that a series of stages is present leading from one extreme to the other leaves little doubt, however, as to their being homologous.

The production of a single additional root-pole by this method is the one most commonly occurring in typical syncotylous ('Type 1') seedlings, whilst the development of two such poles, one on either flank of the cotyledonary midrib, is very common in 'Type 2' seedlings, tetrarchy resulting in both cases. The asymmetrical development of one of these accessory strands alone in 'Type 2' seedlings is rare and results in a triarch condition, but it is interesting to note that tetrarchy may be produced by a combination of this type with an independent lateral on the opposite side and is indeed fairly common (Figs. 30-34). Only a single 'Type 1' seedling (Figs. 35-38) has been observed in which this combination of the two methods of additional xylem pole formation has occurred. Of the two poles, the one derived from the independent and persistent lateral alone gives rise to a lateral root (Fig. 37 *c*), whilst the second pole (Fig. 38 *e*) is only differentiated in the tap-root. There are thus four lateral roots in the root-whorl, whilst the tap-root is pentarch. The production of two new poles in 'Type 1' seedlings is extremely rare and has only been met with in two instances. One of these (Seedling A), in which the syncotyl is extremely intimate, has already been described. The second (Fig. 5) is one in which the additional poles only arise in the tap-root, which is thus pentarch, although the root-whorl consists of three members only (Figs. 39-

FIGS. 30-42. Figs. 30-34 show the transition in a 'Type 2' seedling in which tetrarchy has resulted from the production of one *new* pole and the independence of one lateral. The new pole does not give rise to a lateral root at the base of the hypocotyl. Figs. 35-38 show a 'Type 1' seedling with similar transition features, *a, b, c, d* poles, represented in the hypocotyl, *e* pole present from the base of the tap-root onwards. Note the single axillary bud. Figs. 39-42 show the transition in a 'Type 1' seedling, in which the three hypocotyledonary poles, *a, b, c*, are reinforced in the tap-root by two additional ones, *d, e*.

41). It will be noted that in no instance does the root-whorl consist of five members, although one 'Type 1' specimen was obtained which, on macroscopic evidence, was thought to provide evidence of such a condition. In this seedling the hypocotyl is symmetrically triarch (Fig. 44), and a lateral root arises from each of the three poles (Fig. 45, *a*, *b*, *c*). Two additional roots (Fig. 45, *adv*, *adv*¹) arise at the same level which are not referable to any protoxylem, and sections at a lower level show that the main root has been broken off and is replaced by a healed stump, on either side of which are two heptarch adventitious roots (Fig. 46). The two lateral roots arising at the level of the root-whorl are evidently adventitious also, and conform to the description given by Miss McClatchie (23), who has shown that the production of adventitious roots of this type at or near the surface

FIGS. 43-46. A 'Type 1' seedling in which the tap-root has been destroyed. Note the adventitious roots, *adv*, *adv*¹, at the base of the hypocotyl, and the two heptarch ones arising to either side of the healed stump at a lower level.

of the soil is a characteristic traumatic response in *Impatiens Roylei*. The results with regard to the derivation of the root-poles may be summarized as follows:

	'Type 1' Seedlings.	'Type 2' Seedlings.
(a) One additional pole arising <i>de novo</i> in the hypocotyl or tap-root	Common	Somewhat rare
(b) One additional pole arising by the persistence of an independent lateral	Fairly common	Fairly common
(c) Two additional poles by the combination of (a) and (b)	Very rare.	Common
(d) Two additional poles arising <i>de novo</i> in the hypocotyl or tap-root	Very rare	Common
(e) Two additional poles arising by the persistence of <i>both</i> independent laterals	Unknown	Very rare
(f) One new pole arising by the bifurcation of the protoxylem	Very rare	Unknown

It is obvious that a series of modifications so suggestively similar in the two types of seedling points to community of origin, especially when, as is the case here, extremely intimate syncotyly leads to the type of modification found commonly in 'Type 2' seedlings. We can thus say that points of

contact between the two types of seedling have been established in four respects, namely :

1. The proof that the coalescence of midribs is possible.
2. The proof that a coalescence of cotyledonary axillary buds is possible.
3. The fact that hypocotyl and root show similar types of vascular modification.
4. The fact that the modifications in the epicotyl are identical.

Quite apart from their significance as links between the two types of seedling, the vascular modifications have an additional interest as illustrating how such seedlings, whilst retaining certain ancestral features, may modify these and add to them. Syncotyl has inevitably brought with it a suppression of certain of the vascular strands, and it would seem that this modification of the normal symmetry has evoked a response in many cases consisting of either the modification in relative importance of the persistent lateral vascular components or the introduction of entirely new strands into the hypocotyl and root. It seems impossible to assign any phyletic significance to these modifications, and one is compelled to assume that the impetus to change is physiological. If we make that assumption we are confronted with the difficulty that seedlings below the average in size may show a new complexity far in advance of that shown by seedlings above the average size which have retained the simplified vascular features imposed upon them as a result of compression. It is possible that accurate measurements of the total bulk of the vascular system and of the transpiring and assimilatory areas would show that there is a definite relationship between these, but the whole problem only serves to stress our profound ignorance of many of the fundamental features of seedling physiology.

The literature of seedling anatomy contains a number of references to an increase in the number of root-poles from above downwards, and in some of these a physiological explanation of the phenomenon is suggested. Thus Sargent (26), speaking of the development of new poles in *Fritillaria alpina* and *F. imperialis*, regards this as 'due to the persistence of the primary root and its physiological activity, which renders a considerable girth necessary'; whilst Hill and de Fraine (16), referring to a similar phenomenon in the Cycadaceae, believe that the probable cause is 'that the swollen axis requires a greater dispersal of the vascular tissues'. There is, however, no obvious reason to account for the increase in the number of root-poles in cases such as that of *Opuntia Tuna*, Series B, described by de Fraine (10). While the general trend of the present investigation has been to show that the two types of seedling have a syncotylous origin, a careful search has been made for seedlings showing marked inequality of the cotyledons, and of these two have been obtained, one of which is syncotylous in addition. Neither shows any affinity with the seedlings

previously described, but both exhibit features of some interest and will be described in detail. The first seedling (Figs. 6 *a*, 6 *b*) exhibits no striking anatomical peculiarity in either the cotyledons or petioles, except that the

FIGS. 47-58. Figs. 47-52 show the transition phenomena in a seedling (Figs. 6 *a*, 6 *b*) in which the cotyledons are markedly unequal. Figs. 53-58 show the transition in a seedling (Fig. 7) in which cotyledonary inequality and syncotyle are combined.

vascular bundles are smaller and more feebly differentiated in the reduced member (Figs. 47, 48). This difference in size is faithfully reflected in the hypocotyl (Fig. 49), though the transition is normal until the base of the hypocotyl is approached. In this region the intercotyledonary xylems appear to lose their protoxylem and unite with the xylem from the midrib

of the smaller cotyledon to form a large mass (Fig. 50). Only a single root is produced at the point normally occupied by the root-whorl, and this is continuous with the pole which forms the midrib of the larger cotyledon (Figs. 51, 52). The tap-root is tetrarch. It is obvious that the reduction in the size of the cotyledon exercises an appreciable effect on the vascular symmetry even at the base of the hypocotyl, and the seedling suggests comparison with *Abronia umbellata* and *A. villosa*, in which a difference in the size of the cotyledons is a normal feature. Hill and de Fraine (17), who have investigated the seedling anatomy of these two species, show that here also the vascular strands of the reduced cotyledon play a smaller part in the transition phenomena than those of the larger one, though the details of transition differ widely from those of *Impatiens Roylei*. The second specimen is remarkable in that it combines inequality in the size of the cotyledons with syncotyly, this being unilateral as regards the laminae but involving both petiole margins (Fig. 7). The bundle system of the smaller cotyledon consists of a series of collateral strands, one of which occupies the position of the midrib (Fig. 53). At the apex of the hypocotyl these bundles have been reduced to two laterally situated pairs, a phloem group marking the site occupied by the 'double' bundle in the normal cotyledon (Fig. 54). Of these, one pair, after the union of its constituent bundles, fuses with the adjacent lateral from the larger cotyledon, the vascular system of which is normal (Fig. 55). The strands of the other pair, after union, form an endarch xylem group which remains independent of the adjacent lateral and forms a pole. The lateral thus left continues down the hypocotyl for some distance (Fig. 56), but ultimately dies out, so that the hypocotyl develops a triarch symmetry and produces three lateral roots at its base (Fig. 57). Subsequently a fourth pole is developed by the tap-root in the plane corresponding to that passing through the independent lateral to which reference has just been made. The behaviour of the strands in the second seedling recalls that described for a somewhat similar case by one of us (18), in which a seedling with unequal cotyledons developed an asymmetrical triarchy in the hypocotyl owing to the absence of a 'double' bundle midrib in a smaller cotyledon. It is difficult to say whether the replacing of the normal median symmetry by a lateral bundle concentration is to be correlated with the reduction of the cotyledon or not, but this is doubtful. The available material is quite inadequate for the determination of the homologies of the bundles involved, but it is worthy of note that Davey (9), in her description of the seedling anatomy of certain Amentiferae (e.g. *Fuglans cinerea*, *Pterocarya rhoifolia*), records a loss in the relative importance of the median cotyledonary strand and a corresponding increase in the transition value of the laterals, though the similarity between these forms and *Impatiens* is not a close one.

The formation of a very short cotyledonary tube at the base of the

petioles is a common feature of normal seedlings and occurs in many of the abnormal seedlings also (Fig. 43). Occasionally, as in the seedling just described, the whole of the petiole is involved and leads to an asymmetrical amphisyncotyly. This condition may exceptionally cause a partial roofing-in of the plumular bud owing to secondary fusions of the apposed cotyledonary tissues. The effect of this roofing-in is apparently in many cases to cause a partial arrest of plumular development, since, as a general rule, the plumule is ill developed compared with that of other seedlings of similar size and age in which the cotyledonary tube is rudimentary or absent. The seedling illustrated in Fig. 8 is a case in point. Both from the standpoint of size and the amount of secondary thickening present this seedling should have possessed a partially expanded epicotyl, but as a matter of fact it shows a stage of development very little in advance of that possessed by quite young seedlings. Its position is indicated by a large swelling in the basal portion of the tubular petiole, and some idea of the relatively enormous size of this region may be gleaned from a comparison of Fig. 60 with that of the same region in other seedlings. The cotyledonary tube communicates with the exterior only by a small pore (Fig. 60, *p.*), and the adjoining tissues show evidences of compression in the rows of flattened cells which are indicated by dotted lines in the diagram. The vascular details of this seedling also serve to illustrate one or two points of interest. The midrib forms one xylem pole in the hypocotyl and the marginals constitute another, *both* laterals remaining independent and showing an endarch position of the protoxylem (Fig. 61). One of the independent laterals persists throughout the hypocotyl but loses its protoxylem, whilst the other soon dies out completely, its position being represented for a short distance by a small patch of secondary xylem (Fig. 61). Towards the base of the hypocotyl a new bundle appears in the same relative position (Fig. 62), and though it does not give rise to a root at the root-whorl, which consists of three members, it is continued downwards and forms a root-pole. It will be noticed that the history of this particular root-pole is capable of two interpretations, since it may be derivable either from the independent lateral, which died out after a brief course in the upper part of the hypocotyl and has subsequently been restored, or it may be an entirely new structure. The second view seems the more probable, since in all other cases observed, with the exception of 'Seedling A', and of the syncotyl with unequal cotyledons previously described, where an independent lateral dies out in the upper hypocotyl, no root-pole of any kind is formed in the corresponding position. Hill and de Fraine (16) record a case in *Pinus sylvestris* in which there is a local disappearance of a vascular strand, and similar cases have been noted by other investigators; but these are hardly comparable with the case under discussion, in which a distance of over three centimetres separates the termination of the one strand from the initiation of the other. Amphisyncotyly involving both

laminae was not found so commonly, but where it does occur the fused blades have either a salver-like appearance (Figs. 9, 10 *a*, 10 *b*, 11), in which case the upper portions of the laminae are free, or are goblet-shaped with the whole length of the blade margins united (Figs. 13 *a*, 13 *b*, 13 *c*). The effect

FIGS. 59-63. Transition in a 'Type 2' seedling (Fig. 8). Fig. 60 shows the effect of partial roofing-in of the plumule on the side of the base of the petiole. The dotted lines - - - - indicate irregular lines of crushed cells; *p*. = the pore-like communication with the plumular bud.

on the anatomy is exceedingly variable, but in nearly every case a more or less complete roofing-in of the plumular bud is evident (Fig. 64). The two-sided fusion of the cotyledons evidently imposes considerable strain on the tissues, as in some cases a tearing has occurred down one side (Fig. 14), whilst in others lacunae are developed in the mesophyll, which can only be

ascribed to the conflicting internal tensions set up (Fig. 65). In some cases the transition features show no noteworthy variation from those of normal dicotyls (Fig. 66), but several show rather remarkable modifications, and some of the most clearly defined of these are described below.

'Seedling C' (Fig. 9) is an amphisyncotyl showing a salver-shaped condition. The marginals and laterals of both cotyledons on one flank unite with their respective midribs at a fairly high level, thus causing the latter to appear to have undergone displacement to one side (Fig. 67). The midribs themselves are mesarch and are almost enclosed by their phloems, which form strongly incurved arcs (Fig. 67). The bundle systems of the other side gradually unite until they form a large mesarch xylem mass, the phloems of which are linked locally with the adjacent half-phloems of the midribs (Fig. 68). This xylem mass loses its protoxylem and gradually becomes very much reduced, being represented at the base of the hypocotyl by a little metaxylem only. The midribs alone contribute to the root-whorl, which thus consists of two members (Figs. 9, 69), and below these a protoxylem is developed in the plane of the third hypocotyledonary xylem group, the tap-root being triarch.

'Seedling D' (Figs. 10 *a*, 10 *b*) is externally a seedling of similar type to the previous one, but its vascular arrangements are somewhat different. The midribs are well defined, as are the marginals of one side, but generally speaking the lateral systems of both cotyledons consist of an elaborate anastomosing series of small veins which may locally extend into the solid basal tissue formed by the secondary ingrowths from the adaxial petiolar surfaces. The well-defined marginals after a temporary union diverge, and the whole of the bundle complex gradually concentrates upon the two midribs, uniting with these adaxially so that a pair of mesarch xylem groups, completely surrounded by phloem, enters the hypocotyl (Fig. 73). Traversing the hypocotyl the xylem becomes exarch and the sheaths of phloem open at the protoxylem (Fig. 74, *b*), so that for a time they are U-shaped in transverse section. A little lower down they divide into two parts which unite laterally, the xylems becoming united at the same level, so that a diarch plate results (Fig. 74, *c*, *d*). Two lateral roots are given off at the base of the hypocotyl, and the tap-root is diarch.

FIGS. 64-66. An amphisyncotyl (Fig. 11) in which partial roofing-in of the plumule has occurred, and in which the cortex shows splits due to tissue tensions.

FIGS. 67-74. Figs. 67-70 illustrate the transition phenomena in 'Seedling C' and Figs. 71-74 those in 'Seedling D'.

'Seedling E' (Fig. 12) is a goblet-shaped amphisyncotyl. The vascular system shows no apparent abnormality in the upper part of the fused laminae, but at the base neither midrib develops 'double' structure. A concentration of the majority of the lateral strands upon one collateral

midrib occurs, leading to the formation of a pseudo-concentric bundle. The other also becomes pseudo-concentric. A minor concentration also takes place on one of the laterals (Fig. 78, *b*), so that three mesarch bundles pass into the apex of the hypocotyl. Each of these is for a time completely invested by phloem, but as the bundles move towards the axis of the seedling the phloems open on the inner side and their free margins unite so that a common ring surrounding the whole of the xylem is formed. The continuity of this ring is permanently broken opposite the now exarch protoxylems and also locally throughout, but otherwise there is no further change until the formation of the solid xylem core, which heralds the formation of

FIGS. 75-80. A goblet-shaped amphisyncotyl, showing an abnormal type of transition.

the lateral roots, is well forward. At this stage a new protoxylem pole arises between the strand continuous with the permanent lateral and one of the midrib strands. This pole gives rise to a lateral root, as does one of the midribs (Fig. 80), and the third lateral root of the series appears to be derived from the lateral and the second midrib jointly, a most unusual state of affairs. The tap-root is tetrarch, the four poles represented in the base of the hypocotyl persisting unchanged.

'Seedling F' (Figs. 13 *a*, 13 *b*, 13 *c*) is also goblet shaped, and sections reveal the fact that it possesses three fused cotyledons, that is to say, it is an amphotrisyncotyl. A trisyncotylous seedling of *Centranthus ruber* has been described by Miss Bexon (1), and a somewhat similar seedling of *Acer pseudoplatanus* has been collected by one of us, but neither of these exhibits

the symmetrical amphisyncotyly of the subject of the present observations. A section towards the base of the cotyledons shows three somewhat flattened mesarch double bundles with which the laterals have either united or are converging to do so (Fig. 81). At a slightly lower level the flattening of the double bundles is more pronounced, and the cotyledonary axillary buds are

FIGS. 81-88. Figs. 81-83 illustrate the earlier stages of transition in an amphitrisyncotyl (Figs. 13 *a*, 13 *b*, 13 *c*); Figs. 84-88, the earlier stages of transition in a tricotyl.

evident, two of the three showing partial union to form a tangentially elongated structure (Fig. 82). One pair of laterals (Figs. 81, 82, *l*, *l'*), after uniting with their respective midribs, separates again and unites in the intercotyledonary plane to form a collateral endarch group, which, however, dies out in the hypocotyl. The three main bundles, which at this level are

exarch, are continued downwards without any striking modification, and a triarch condition characterizes the remainder of the seedling. The evidence provided by the study of a relatively small number of amphisyncotyls hardly justifies the putting forward of any decided views as to the effects of this type of cotyledonary fusion, but there does seem to be a definite tendency towards the modification of the lateral strands, this taking the form of relatively early union of these with the midrib instead of their pursuing an entirely independent course.

Two other seedlings remain to be described which show special anatomical peculiarities and which constitute at present more or less isolated records. The first of these, 'Seedling G', is a tricotyl, and exhibits trimerous symmetry in the epicotyl (Fig. 84). The general vascular features of each cotyledon are apparently quite normal, but the midrib of one retains its collateral structure to the base of the petiole when that of the other two is distinctly 'double' (Fig. 84). As the node is approached the petioles fuse, but the adjacent margins of two show delay compared with the remainder (Fig. 85). At this level the vascular strands of that cotyledon possessing a collateral midrib coalesce to form a tangentially elongated group (Fig. 85), which later loses all trace of its triple origin and forms an endarch xylem group almost surrounded by phloem (Fig. 86). This type of structure has been regarded as an 'Anemarrhena' condition by Lee (21), Thomas (31), and others, but it is a far cry from a temporary union such as we have here, even where it leads to local loss of identity, to the condition recorded by Sargent (24) for *Anemarrhena*. The subsequent history of the aberrant vascular structure is peculiar. It will be perceived that the transition in the other two cotyledons is normal, the adjacent laterals of these members uniting to form a xylem group in the intercotyledonary plane, and each leaving a free lateral on the side adjoining the remaining cotyledon. Near the apex of the hypocotyl the bulk of the large strand turns almost horizontally to unite with one of the free laterals (Fig. 87), whilst at a slightly lower level a smaller portion unites with the free lateral of the other cotyledon, a small remnant thus being left. A section at this level would therefore show the following strands:

1. A pair of exarch strands derived from the midribs of two of the cotyledons (Fig. 88).
2. A pair of exarch strands derived from the laterals and parts of the vascular system of the aberrant cotyledon (Fig. 88).
3. A strand produced by the union of the adjacent laterals (Fig. 88).
4. A small strand representing the remnant of the vascular system of the aberrant cotyledon.

Of these, the strand produced by the union of the laterals remains endarch and dies out in the upper part of the hypocotyl, the small strand, which consists of metaxylem only, sharing the same fate. The four exarch

strands thus left continue throughout the remainder of the seedling, producing a root-whorl of four members and a tetrarch tap-root.

'Seedling H' is a 'Type 2' seedling in which the anatomy of the major portion of the blade shows no striking difference from its fellows (Fig. 89). Towards the base of the lamina, however, the midrib becomes hour-glass shaped in transverse section (Fig. 90), and the protoxylem, which is mesarch at this stage, elongates and separates into two, half supplying the adaxial

FIGS. 89-97. A 'Type 1' seedling, showing an abnormal type of transition.

portion of the bundle and the other half supplying the outer portion. The adaxial portion then separates off as a separate mesarch strand (Fig. 91) which soon becomes endarch, whilst the outer portion becomes exarch and forms a typical 'double' bundle. The endarch portion then assumes a slightly lateral position and is joined successively, first by two lateral strands (Fig. 92) from the side to which it is inclined, and then by one from the opposite side (Fig. 93). Finally the marginals from both flanks (Fig. 94) unite and together join the xylem complex previously formed, the

whole forming a mesarch xylem completely surrounded by phloem (Fig. 95). Meanwhile the phloem of the double bundle has bent inward and the two halves have united adaxially (Fig. 95). The two strands thus formed traverse the greater part of the hypocotyl unchanged, but near the base the phloems open out on the inner side and unite laterally, the mesarch bundle at the same time becoming exarch and causing a break in the phloem at this point also (Fig. 96). Two lateral roots are developed and a new proto-xylem originates in the plane at right angles to these (Fig. 97), so that the tap-root is triarch. The interpretation of the singular vascular behaviour of this seedling is distinctly difficult, though it shows points of considerable resemblance, especially in the concentration towards the middle line of the lateral strands, to a similarly odd seedling previously described by one of us (18). The division of the midrib as the petiole is approached suggests that not only have the two phyletically distinct midribs merged their identity, but that one of the lateral strands has also become involved in the intimate union. In the absence of further supporting evidence, however, such an explanation must be regarded as purely tentative, and the chief interest of the seedling is that it provides a further instance of the plastic nature of juvenile vascular structures.

DISCUSSION.

The investigation of the structure of seedlings, such as those described in the present paper in which a pseudo-monocotyledonous condition is a relatively common teratological feature, provides a tempting starting-point for a consideration of the possible origins of the Monocotyledons proper. Theoretically the seedling possessing a single leaf is derivable from the dicotyledonous type in a variety of ways. These may be briefly tabulated as follows:

1. By syncotyly involving both cotyledonary margins (amphisyncotyly) so that a cotyledonary tube, often more or less solid secondarily, results. This condition is occasionally realized in *Impatiens Roylei*.
2. By syncotyly involving one margin only of the originally separate cotyledons. This is the condition most frequently found in the syncotylys of *I. Roylei*.
3. By a specialization in function of the cotyledons, one of which becomes purely suctorial, the other undergoing retardation in development and subsequently appearing as the first leaf.
4. By a total suppression of one cotyledon.
5. By the suppression during embryogeny of the meristematic activity of the cotyledonary apex, the other cotyledon, with the basal sheath common to both, continuing to develop and producing the typical sheathing structure which characterizes the majority of Monocotyledons.

Of these the first alternative has received strong support from Sargent (26) as the result of an extensive series of comparative observations on the seedling anatomy of the Monocotyledons and of certain Dicotyledons, in which an amphisyncotylous condition obtains. This worker considers that the type of seedling anatomy characterizing *Anemarrhena asphodeloides* provides the clue to the source of the monocotyledonous condition. In this species the major portion of the cotyledon is traversed by two separate symmetrically placed strands, each of which, at the level of transition to the primary root, branches into three, the marginal portions uniting in pairs and constituting two of the root-poles, whilst the median portions also each form a root-pole, so that tetrarchy results. The 'Anemarrhena' condition is believed to have given rise in other Monocotyledons to that type of cotyledonary vascular supply in which there is a single median cotyledonary bundle (e. g. *Allium*, *Zygadenus*) by the intimate fusion of the two originally independent strands. The 'Anemarrhena' condition is further compared with the type of vascular symmetry shown by a dicotyledonous species, *Eranthis hiemalis*, in which the seedling is amphisyncotylous. In this species each cotyledon is supplied with a median bundle flanked by lateral strands, the latter uniting with the midrib at the base of the lamina. Each midrib bifurcates in the hypocotyl so that two pairs of independent collateral bundles result. From these what is interpreted by Sargent as a fugitive tetrarch condition ultimately results, diarchy following on the loss of the two intercotyledonary protoxylems. The development of an Anemarrhena-like phase in the hypocotyl and root of a geophilous dicotyledon is considered to support the view that Monocotyledons have arisen by a method approximating to this. De Fraine (10) criticizes this interpretation and points out that the occurrence of an Anemarrhena-like phase is not confined to geophilous Dicotyledons. (It has been recorded, for example, by Thomas (31) in *Althaea*, by Lee (21) in *Incarvillea*, and by de Fraine (10) in *Opuntia* spp.) It is noted also that amphisyncotily does not necessarily lead to the type of anatomy characterizing *Anemarrhena* (e. g. *Delphinium* sp., *Anemone coronaria*). A further criticism is put forward by Thomas (31), who considers that the xylem elements regarded by Sargent as constituting the intercotyledonary poles in *Eranthis hiemalis* are probably of secondary character, and if this view is correct the species is diarch throughout and the resemblance to *Anemarrhena* is illusory. Much obviously depends upon the correct interpretation of the two independent strands which traverse the cotyledon in *Anemarrhena*. If each represents the products of an intimate fusion of a median strand with a lateral on either flank, then the resemblance to Dicotyledons of the *Althaea* type is plain. There is, however, a possible alternative, namely, that each represents the widely separated half of a 'double' bundle which has fused with a lateral and a marginal strand on the distal flank only. That a condition analogous to this is possible is

shown by Chauveaud (4) for *Cordyline indivisa*. Moreover, the same author has also shown that typically the lower portion of the cotyledonary midrib, or the hypocotyledonary strand derived from it, is initiated as a radial file of xylem elements flanked by the phloem groups, this arrangement giving place with advancing age to two separate collateral strands, that is, to an *Anemarrhena*-like condition. Further, a number of cases are on record in which the earlier phases (Chauveaud's 'Alterne' and 'Intermédiaire' groupings) do not occur in ontogeny, this being notably the case in *Podocarpus chinensis* and *Ephedra distachya* (16), in which the half-bundles are separate throughout the cotyledon and hypocotyl. Sporadic cases also occur in which one of the cotyledonary midribs is represented by a 'double' bundle, while the other is represented by two wholly independent half-bundles (e.g. *Echinocereus Ehrenbergii* (10)). We have no information as to the very early vascular phases of the majority of the seedlings with which Sargent worked, but it seems plain that the widely separated strands characterizing *Anemarrhena* may be as readily regarded as the ultimate derivatives of a series starting from a compact 'double' bundle (that is, one consisting of a central xylem group flanked by phloems) as the initial member of a series which has evolved the compact 'double' bundle as a result of fusion. Which of these alternatives is the correct one cannot be stated with confidence, but the probabilities appear to lie with the former. The special type produced by the merging of the identity of the lateral strands in that of the main bundles does not appear to have the phyletic significance which Sargent would attach to it, but it serves to illustrate the fact that members of widely different groups (e.g. *Anemarrhena*, *Opuntia*, *Althaea*, *Incarvillea*) may show a common type of vascular evolution. De Fraine (10) further, as a result of her studies of the seedling anatomy in the Cactaceae, also casts doubt on the phyletic significance of the 'double' bundle, pointing out that this structure, in the hypocotyl, may be the product of widely different contributing strands. It must be borne in mind, however, that it is only in the more specialized cactaceous seedlings, forms in which the cotyledons are vestigial and in which the hypocotyl is short and much thickened, that the hypocotyledonary strands are produced in this exceptional manner, and it is very doubtful whether evidence derived from the study of such forms should be regarded as invalidating a view which is supported by the large series of facts derived from the investigation of more normal seedlings.

However, while it is perhaps justifiable to say that the grounds upon which Sargent has based her conception of the *amphisyncotylous* origin of the Monocotyledons are open to somewhat damaging criticism, there is a certain amount of evidence which seems to support the view that a *one-sided syncotily* may have given rise to a monocotylous condition. Sargent indeed accepts this view of the origin of the pseudo-monocotyledonous

Dicotyledons, and Compton (6), whilst apparently favouring the derivation of the *Anemarrhena* type through amphisyncotyly, considers that the exalbuminous Helobieae may have arisen by unilateral syncotyly. It is noteworthy that in *Impatiens Roylei*, which possesses an exalbuminous seed with a perfectly straight embryo, both amphisyncotyly and unilateral syncotyly occur, the latter predominating. The evidence as to the origin of the 'Type 2' seedlings of *Impatiens Roylei* brought forward in the present paper points strongly to their being derived from a dicotyledonous type by a close unilateral syncotyly, yet a study of a typical member of this group shows no sign whatever of the dual origin of the cotyledonary structure. If this evidence is accepted, then we are bound to admit that a midrib phyletically the product of *two* 'double' bundles behaves throughout in a manner identical with that of one of the ancestral midribs. The evidence put forward by Thomas and Davey (32) in the cases of *Anemone apennina*, *Ranunculus Ficaria*, and *Conopodium denudatum*, as far as can be judged from the published abstract, also seems to point in the same direction. A further point in favour of unilateral syncotyly, and one again the significance of which Davey and Thomas seem to recognize, lies in the position of the first epicotyledonary leaf relative to the median plane of the cotyledons. It is extremely rare to find the first epicotyledonary leaf, in Dicotyledons, lying in any other plane than that at right angles to the median cotyledonary plane. The position of the first leaf in Monocotyledons, granted unilateral syncotyly, is strictly conformable with that typical with the vast majority of Dicotyledons. On the other hand, unless it is assumed that in the Monocotyledons there has been a shifting through 90° of the position of this leaf, it must remain a stumbling-block to all theories in which differentiation of cotylar function or partial or total suppression of the second cotyledon is considered as the source of Monocotyledony. The support of the theory of the differentiation of cotyledonary function is largely due to A. W. Hill (14), and has resulted from his investigation of the seedling anatomy of a number of geophilous species of *Peperomia* which yield a series of forms commencing with a normal dicotylous type and ending in one in which one cotyledon is purely suctorial in function whilst the other is purely assimilatory. Hill considers that monocotyledony has arisen as a result of specialization of this kind, the assimilatory cotyledon having delayed its development until carried outside the seed, when it appears as the first leaf. Hill regards the monocotyledonous seedling of the Araceae as conforming more nearly to the primitive condition, and would group Sargent's *Anemarrhena-Zygadenus* series in the reverse order to that adopted by her. De Fraine (10) supports this view, considering that the continued separation of the components of the 'double' bundle into two independent portions would, on physiological grounds, be advantageous in an absorbing cotyledon and would thus lead to the condition charac-

terizing forms like *Anemarrhena*. There is no evidence, however, of any connexion between the absorptive cotyledonary function and the separation of the halves of the 'double' bundle, and in the absence of such evidence this idea can only be regarded as purely speculative. It has been pointed out already that the orientation of the epicotyledonary leaves presents a difficulty against which this theory has to contend, and it is noteworthy that in *Impatiens Roylei* undoubtedly syncotylous seedlings exhibit that balance of cotyledonary structures and first epicotyledonary leaf which Hill has laid stress upon in certain Aroids (e.g. *Arisaema dracontium*). Apart from this, however, there seems to be no reason to consider Hill's view as unlikely, nor does its acceptance automatically eliminate the possibility of a syncotylous origin for some groups of Monocotyledons. Certain systematists, notably Lotsy, would regard the Monocotyledons as at least diphyletic in origin, deriving the Spadiciflorae from an ancestral dicotyledonous group approximating to the Piperales, and the remaining forms from a hypothetical pro-ranalean stock which has also given rise to the modern Ranales. The derivation of the Monocotyledons from the Dicotyledons by the complete suppression of one cotyledon depends for support largely on indirect evidence. Many undoubted Dicotyledons are known in which there occur seedlings showing a marked dissimilarity in size between the two cotyledons (e.g. *Abronia* spp., *Citrus Aurantium*, *Pachira aquatica*). Occasionally a similar phenomenon occurs in *Impatiens Roylei*, and the anatomy of three such seedlings has already been described, two in the present and one in the previous paper (18). Other Dicotyledons, again, are known in which only a single cotyledonary member is produced normally (e.g. *Cyclamen persicum*, *Ranunculus Ficaria*, *Carum bulbocastanum*, *Corydalis tuberosa*). Of the first group *Abronia umbellata*, *A. villosa* (17), and *Impatiens Roylei* are, as far as can be ascertained, the only species in which the anatomy has been investigated. These undoubtedly show that where a pronounced inequality in the size of the cotyledons exists this exercises a marked effect on the vascular symmetry of the hypocotyl and, in a measure, of the root, the strands contributed from the smaller cotyledon being less important than those of the larger one. With regard to the pseudo-monocotyledonous types the available evidence, though as yet somewhat meagre, points to their being syncotylous in origin in many cases (32). The all-important cases which link the species with unequal cotyledons with those which are apparently pseudo-monocotyledonous are thus lacking, and in their absence the 'suppression' hypothesis must be regarded as not proven.

The most recent theory as to the origin of the Monocotyledons is that put forward by Coulter and Land (8), who consider that there exists both in the Monocotyledons and Dicotyledons a peripheral cotyledonary zone which gives rise to two or more growing points or primordia, this being followed by a general zonal development and resulting in a cotyledonary ring or

sheath of varying length. If both growing points continue to develop equally the dicotyledonous condition is attained. If one of the growing points ceases to develop, the growth of the whole cotyledonary zone is associated with that of the other growing point and the monocotyledonous condition is reached. Monocotyledony is thus due neither to syncotylly nor to cotylar suppression, but is simply the result of the continued development of one growing point of the cotyledonary ring rather than a division of the growth between two growing points. Cotyledons are thus invariably lateral structures. The variation in the cotyledon number which has led to the separation of the two great Angiosperm series is considered to have arisen, in all probability, in those forms which possessed a massive proembryo of a type similar to that of the Liliales, Arales, and many Ranales among the modern groups. The massive proembryo is therefore held to represent the primitive proembryonic condition, the filamentous type of *Alisma* and *Capsella* being derived from this.

The evidence marshalled in support of this theory lies chiefly in the interpretation placed upon the intermediate stages of embryonic development in certain Monocotyledons, notably *Agapanthus umbellatus* and *Cyrtanthus sanguineus*, but also on the comparative morphology of monocotyledonous and dicotyledonous seedlings of the former. The fact that *Agapanthus* produces, though apparently rarely, dicotyls as well as monocotyls is considered to be significant, since, it is argued, if this is the case there must be some evident relationship between the two conditions.

The vascular system of the normal seedlings of *Agapanthus* is simple. The cotyledonary vascular supply consists of a median bundle with a lateral on either flank. These unite at the node, where they are joined by the midrib of the first plumular leaf. The strand from the latter forms a root-pole, whilst the cotyledonary strands between them form two poles so that a triarch root is organized. At a lower level a tetrarch condition arises owing to the bifurcation of the pole derived from the first leaf-strand. From the fact that the primordia of the cotyledon and first plumular leaf are developed first and the vascular strands subsequently laid down in these, it is inferred that the vascular features are determined by the primordia rather than the reverse. The vascular strands, in fact, are held to be 'secondary structures whose appearance is dependent upon the character of the primary structures and therefore of no phylogenetic significance'.

The dicotylous specimen described shows two epicotyledonary leaves also. Each cotyledon is supplied with *two* strands in lateral positions 'as if the middle one present in the monocotyledonous seedling has not been laid down'. Each epicotyledonary leaf has a single median strand. Six strands thus unite at the cotyledonary node, and from these, as in the monocotylous seedlings, three root-poles are organized, an additional pole being developed by the bifurcation of that continuous with the midrib of

the first plumular leaf. The possibility of the dicotyledonous embryo being a fusion twin is rejected on the vascular evidence which shows that 'it is merely a slight modification of the monocotyledonous one and gives no suggestion of the fusion of two embryos'.

In *Cyrtanthus sanguineus* (8, 12) the embryo, prior to maturation, passes through a phase in which the cotyledonary tube shows division into four shallow apical lobes, each of which is supplied by an independent procambial strand. The lobes are obviously in pairs, one of which is slightly smaller than the other. This stage Coulter and Land regard as representing a tetracotylous condition. It is followed by a stage in which, owing to a more active growth of the cells of the cotyledonary zone lying between the growing points of each pair, a union in twos occurs, this being accompanied by an elongation of the sheath. This stage is interpreted as a dicotyledonous condition. Subsequently one 'cotyledon' develops rapidly whilst the growth of the other ceases, so that a monocotyledonous mature embryo is produced in which the originally independent vascular strands from the shorter side bend sharply to unite with those supplying the elongated portion. In a further contribution Coulter (7) extends the theory to the Gramineae, homologizing the epiblast with the second reduced cotyledon, and the scutellum with the dominant one. A series is described ranging from species such as *Zizania aquatica* and *Oryza sativa*, in which the epiblast is well developed, through those showing a small epiblast (e.g. *Triticum vulgare*), to species like *Zea Mays*, in which it is absent. These are interpreted as illustrating the progressive stages in the abortion of the second cotyledon.

It will be noticed that Coulter and Land's theory rests upon three assumptions, namely that—

- (a) The massive proembryo is more primitive than the filamentous one.
- (b) The earlier and intermediate stages in embryogeny have a profound phyletic significance.
- (c) The phyletic value of the vascular structures is negligible.

All three assumptions are at least debatable, and the third seems open to serious objections. It is plain that the denial of the phyletic value of vascular structures in phanerogamic seedlings carries with it the onus of supplying an adequate alternative explanation for certain well-defined anatomical characters. Two examples of this kind may be cited. It is a matter of common knowledge that the hypocotyl in its young stages usually shows an exarch position of the protoxylem elements and a radial grouping of the xylem and phloem, this being subsequently replaced by a collateral grouping of the vascular tissues owing to the resorption of the first-formed elements and the substitution for them of others with a different orientation. The remarkable constancy with which this cycle is repeated in all phanerogamic groups (4) creates a strong *prima facie* case

for regarding it as of phyletic importance. That it is occasionally of very brief duration or that in a few species it may be altogether omitted is only to be expected, and in no wise affects the conclusions drawn from its general occurrence.

A further illustration of the value of vascular evidence of a somewhat different type is furnished by the varying behaviour of the cotyledonary strands in teratological polycotyls. In some such the midrib retains its collateral structure and, with a similar strand from a neighbouring cotyledon, constitutes a single root-pole. Such cotyledons are held by us to have been primarily produced by the qualitative division of the growing apex of the seed-leaf. In other cases the cotyledonary strand develops 'double' structure, and may either unite with a similar strand at varying levels in the hypocotyl or root or remain entirely separate and constitute an additional root-pole. These types are interpreted by us as having arisen by the quantitative division of the cotyledonary apex, and have led to absolutely symmetrical triarchy and tetrarchy in normally diarch species. Such an hypothesis provides a perfectly logical and consistent explanation of the origin of teratological polycotyly, and appears to be equally applicable to the case of those Gymnosperms which possess polycotyledonous seedlings. If this hypothesis is rejected it remains to be explained why growing points which, according to Coulter and Land's theory, are presumably equivalent should capriciously produce strands which behave in transition in such varying ways.

Moreover, it is surely illogical to confine the argument to the special case of seed-bearing plants, and its absurdity is evident when we attempt to apply it to the vascular Cryptogams. As an example we may take the ontogenetic sequence in the Filicales, which is familiar enough to need no detailed description and the phyletic value of which is undoubted. Evidence of yet another kind is provided by the discovery of petrified plant remains from the Old Red Sandstone (of Middle or Lower Devonian age) of Aberdeenshire. The aerial parts of these plants, the anatomy and morphology of which have recently been described by Kidston and Lang (20), are, with one exception, entirely devoid of leaves and consist of dichotomizing assimilatory branch systems with apical sporangia. The existence of such types, which represent the oldest known vegetable petrifications, would seem to lend support to the contention that vascular differentiation phyletically antedated differentiation into stem and leaf.

Proceeding, however, from general criticism to an examination of the special evidence upon which Coulter and Land's theory rests, it will be seen that much depends on the interpretation placed upon the dicotyledonous seedling of *Agapanthus*. It seems to us that the weakness of Coulter and Land's interpretation lies chiefly in the facts which it does not attempt to explain. It is not clear, for example, why one of the two growing points,

which normally produces three strands, should only produce two, and the other, which normally produces none, should also produce two, and further why the bundles of the two 'cotyledons' should together produce a vascular condition essentially similar to that of the normal monocotyl. Another difficulty is encountered in the position of the first epicotyledonary leaf, which, in the dicotyl, lies in the plane at right angles to the median plane of the two 'cotyledons'.

Now where only one cotyledon elongates the median plane of the first epicotyledonary leaf *corresponds* to that of the two 'cotyledons'. If therefore the dicotyledonous condition is the result of the equal development of the two growing points which, according to Coulter and Land, are normally present in Monocotyledons, it has been accompanied by a shifting through 90° of the insertion of the first leaf, a phenomenon which seems somewhat unlikely. The alternative explanation is that the dicotyledonous seedling has arisen by the qualitative fission of a normally single cotyledon. In such a case each half-cotyledon would contain two bundles, namely one lateral and half the midrib bundle, and these would behave in transition like the bundle system of the undivided cotyledon, precisely as they do in the seedling under discussion. It is noteworthy in this connexion that the median cotyledonary bundle normally produces two widely divergent half-bundles prior to the constitution of the cotyledonary plate, so that complete division would only be an extension of such a process. Granted the accuracy of this interpretation the orientation of the first epicotyledonary leaf is seen to be perfectly normal, a view which is confirmed by the relationship of its vascular strands with those of the two cotyledonary members. With regard to the theoretical construction placed upon the embryonic structure of *Cyrtanthus sanguineus* it would appear that some knowledge of the earlier phases of embryogeny is desirable, since the shallow apical lobing of the younger of the two stages figured by Miss Farrell (12) may be interpreted with equal plausibility as the *result* of the development of four procambial strands rather than as the cause of their development. Finally, with regard to the conception of the epiblast of the grass embryo as a cotyledon, one would expect, if this were the case, to find at least some evidence of vascular tissue where this structure is well developed. Actually there is no trace of such tissue, unless the small meristematic group of cells opposite the scutellum in the maize, a form in which the epiblast is absent, be interpreted as such. Here too, as in previous cases, the position of the first epicotyledonary leaf offers a difficulty which Coulter does not attempt to explain. It seems to us, therefore, that, taken as a whole, the evidence submitted in support of this theory is of too flimsy and too equivocal a character to be entirely trustworthy, and certainly does not appear to provide an adequate foundation upon which to erect the imposing superstructure for which its authors have intended it.

It finally remains to state the conclusions to which our investigations have brought us. Briefly we consider that, whilst in the present state of knowledge dogmatism as to the origin of monocotyledony would be most unwise, the view that it is the result of unilateral syncotyl has much to recommend it. It is not claimed that it is necessarily the sole method by which the monocotyledonous condition may have been attained, but it is held that it provides a consistent explanation of the observed facts in Monocotyledons proper and that it is one the evolution of which is well illustrated by both normal and teratological Pseudo-Monocotyledons.

SUMMARY.

1. *Impatiens Roylei* produces two main types of abnormal seedling, one of which is obviously syncotylous (Type 1) and the other, judged by morphological standards, heterocotylous (Type 2).

2. The apparently heterocotylous type is in all probability the product of extremely close syncotyl.

3. This conclusion is supported by the following facts:

(a) Undoubted syncotyls occur in which the midrib bundles unite and behave in transition in a manner indistinguishable from that of a single normal midrib.

(b) Syncotyls occur in which there is a progressively closer fusion of the originally separate cotyledonary axillary buds.

(c) 'Type 2' seedlings occur in which the double origin of the bud is evident.

(d) The modifications found in the epicotyl are very similar in both types of seedling.

(e) The modification of the existing vascular components and the introduction of new vascular strands are fundamentally the same in both.

4. The production of new vascular strands or the modification of existing ones is believed to be a reaction against the elimination of certain strands on the symphysis side, and to be explicable on physiological grounds.

5. Amphisyncotylous seedlings occur, and these show in many cases a retardation in the development of the plumular bud which is held to be due to the partial roofing-in of this structure by the secondary tissue fusions occurring between the adaxial cotyledonary surfaces.

6. Many amphisyncotyls show vascular modifications which appear to be related to their morphological conditions.

7. The anatomy of a tricotyl and of an amphitrisyncotyl is also described.

8. It is considered that the evidence submitted as to the origin of the 'Type 2' seedlings of *I. Roylei*, combined with that derived from the studies

of other workers on the anatomy of teratological syncotyls and of species normally pseudo-monocotyledonous, renders probable the view that many Monocotyledons have arisen from Dicotyledons by a process of unilateral syncotyly.

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