Seedling Anatomy of Ranales, Rhoeadales, and Rosales.¹

BY

E. N. THOMAS.

Reader in Botany in the University of London.

With Plates L and LI and forty-three Figures in the Text.

THE present century has seen a very vigorous output of work dealing with the anatomical features of the so-called transition between root and shoot structure in Phanerogams. This has, to a large extent, only been possible since the everyday use of the microtome has rendered serial examination of the youngest and slenderest seedlings a matter of ease. Even the most skilful manipulator of hand sections must fail signally to obtain much insight into the anatomical relationships of nine-tenths of the forms during their most illuminating stages.

In comparison with the work of the earlier anatomists in this field (Van Tieghem,² Gérard,³ Dangeard,⁴ &c.) the investigators of the twentieth century have all felt it incumbent upon them to deal with very young seedlings, but some have not been so rigorous as others in this respect, and I wish to associate myself with M. Chauveaud in emphasizing the extreme importance of this precaution. Primary structures are not merely obscured at a later date, but may be obliterated. Chauveaud has laid great stress upon this phenomenon and demonstrated it in many forms, notably in *Mercurialis annua*,⁵ while I discovered it to be the case so early as 1902 in *Cleome sesquiorgialis*, and subsequently in many other species, including the common Wallflower.⁶ Serial sections running through cotyledons, hypocotyl, and primary root of seedlings at different ages prove conclusively the extraordinary changes which take place with age, leading to the disappearance of groups of protoxylem elements. This point has

¹ Thesis approved for the Degree of Doctor of Science in the University of London.

² Van Tieghem, Ph.: *Traité de Botanique*. (Paris, 1891.)

³ Gérard, R.: *Recherches sur le passage de la racine à la tige*. *Ann. Sci. Nat., Bot., sér. vi*, t. xi, 1881.

⁴ Dangeard, P.: *Recherches sur le mode d'union de la tige et de la racine chez les Dicotylédones*. *Le Botaniste, sér. i*, 1889.

⁵ Chauveaud, G.: *L'appareil conducteur des plantes vasculaires et les phases principales de son évolution*. *Ann. Sci. Nat., Bot., sér. ix*, t. xiii, 1911.

⁶ Cf. account of transition in Wallflower in 7th and 8th eds. of Scott's *Structural Botany—Flowering Plants*.

been exhaustively treated by Chauveaud¹ in his 1911 paper, which brings together his work on seedling anatomy, and it forms the pivot of his thesis on the transitional phenomena. Inasmuch as at an early age exarch or, at any rate, 'alterne' protoxylem elements are present throughout the whole seedling, transition, according to this author, is an appearance largely due to subsequent obliteration of these elements in the upper part.

The British work of the last ten years, following upon the presentment by Miss Sargent² of a theory of the origin of Monocotyledons founded upon seedling anatomy, has all had a more or less well-marked phylogenetic aim. In marked contrast to this is the attitude of the earlier anatomists. Thus, in accordance with his bundle concept, de Bary, in the classic 'Comparative Anatomy of Phanerogams and Ferns', treats the hypocotyl merely as the basal internode in which the bundles of the lowest leaves, viz. the cotyledons, fuse and pectinate in a definite manner. Van Tieghem, on the other hand, is chiefly interested in the hypocotyl as the region in which the arrangements characteristic of the root-stele become modified so as to pass into the arrangements characteristic of the stem.

Van Tieghem's investigations led him to lay stress upon two processes, (a) that of the so-called 'rotation' of the protoxylem, which produces the change from endarchy to exarchy, or vice versa, according as the vascular strands are followed from stem to root or root to stem, and (b) that of the splitting and fusion which, together with an alteration in position, produce the change from collateral to radial or radial to collateral. These internal changes correspond to external changes in epidermal characters which take place in a well-defined region termed the *collet*, which is the plane of division between hypocotyl and root. Van Tieghem, however, states that the anatomical transition is frequently drawn out by intercalary growth of hypocotyl, of root, or of both.

Rotation of protoxylem is assumed to take place in all cases, but the methods of change observed under (b) are classified in the 'Traité de Botanique' under three types, depending upon the nature of the strands concerned (i. e. whether xylem or phloem, or both) in the fusions or splittings, and the relative number of such strands as between stem (= hypocotyl) and root.

Thus in Type 1 the xylem changes position; in Type 3 the phloem changes position; while in Type 2 both do so.

In Type 1 the number of collateral strands in the upper part of the hypocotyl is the same as the number of phloem groups in the root; in Type 3 the number is the same as the number of phloem or xylem groups

¹ Loc. cit.

² Sargent, E.: A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings. Ann. Bot., vol. xvii, 1903.

in the root; while in Type 2 the number of collateral strands in the upper part of the hypocotyl is *twice* the number of phloem or xylem strands in the root.

Thus the nature of the 'active' strand (xylem or phloem, or both) and the relation in number of stem to root strands are the distinguishing characters between the types. The determination of these characters, as well as the observation of 'rotation', is bound up with the identification of the first-formed protoxylem elements. Chauveaud¹ maintains that the phenomenon of 'rotation' is an illusion produced by early obliteration of protoxylem in the upper part of the seedling, or, as he terms it, 'accélération basifuge'. However this may be, much confusion has arisen through failure to identify the first-formed protoxylem elements with consequent variations in description of transition phenomena, due largely to difference in age of seedlings examined.

Two changes due to age may be noted now: (a) obliteration of primary tissues, one effect of which is to make a single structure appear to be two (see Scott²); (b) production of secondary tissues, one effect of which is to unify separate strands. As these changes go on together, the net result at any one age will depend upon the relative rates of change of these phenomena. Difference in the level at which the cotyledons were examined has probably also played a considerable part in the divergence of accounts. It is sufficient now to draw attention to one or two concrete instances of discrepancy. Thus Dr. Scott² describes the cotyledons of the Wallflower as having two bundles, while the precisely similar vascular system met with in the cotyledons of many Piperale,³ Centrospermae,⁴ Cactaceae,⁵ and Tubiflorae,⁶ is treated as single by the respective authors, who in consequence regard these as cases of Van Tieghem's Type 3, while Dr. Scott's description would make them examples of Type 2.

The practically identical transitional phenomena seen in *Dipsacus* is instanced by Van Tieghem as an example of Type 1. *Phaseolus* and *Medicago* furnish Van Tieghem with examples of Type 2 and Type 3, respectively, though the course of events is very similar in both.

My own observations on Dicotyledons, begun in 1902, very soon convinced me that there is a common ground plan, if not absolutely for all, for the majority of dicotyledonous species.

(a) The feature of greatest constancy is the existence of two root poles

¹ Loc. cit., 1911.

² Scott, D. H.: Structural Botany, 7th ed., Part I, p. 78.

³ Hill, T. G.: On the Seedling Structure of Certain Piperale. Ann. Bot., vol. xx, 1906.

⁴ Hill, T. G., and de Fraine, E.: On the Seedling Structure of Certain Centrospermae. Ann. Bot., vol. xxvi, 1912.

⁵ De Fraine, E.: Seedling Structure of Certain Cactaceae. Ann. Bot., vol. xxiv, 1910.

⁶ Lee, E.: Seedling Anatomy of Certain Sympetalae. Pt. I, Ann. Bot., vol. xxvi, 1912. Pt. II, id., vol. xxviii, 1914.

in the plane joining the centres of the two cotyledons, which will be referred to as the *cotyledonary plane*. In rather less than one-third of the species chronicled (including those described in this paper) there are two other poles in the plane passing between the cotyledons—the *intercotyledonary plane*.

(b) In a very few cases the poles of the tetrarch root lie in the diagonal planes.

I shall refer to (a) as the *Cruciform* arrangement, of which there are the diarch and the tetrarch varieties, and to (b) as the *Diagonal*, of which there are at least the tetrarch and octarch varieties.

The Cruciform type is accompanied by the peculiar vascular arrangement in the base of the cotyledons, which has been variously interpreted as one bundle or two, and to which the name of 'double bundle' has been applied.

The double bundle essentially consists of two groups of phloem, with one group of protoxylem placed between them. The three groups are always on different radii, so that M. Chauveaud¹ well describes the relative positions as 'alterne'. While maintaining this general arrangement, the details of the strand at any one level are frequently characteristic of systematic groups of greater or less magnitude. The protoxylem groups are continuous with the poles of a diarch root, the xylem plate of which is thus always formed in the planes passing through the centre of the cotyledons. When the primary root is tetrarch, the intercotyledonary poles are represented in the cotyledons by groups of protoxylem, which may be found on the flanks of the 'double bundle' (see *Althaea rosea*, Pl. LI, Figs. 23, 24, 25), or may be more or less detached from it as lateral strands (see *Magnolia tripetala*, Pl. L, Figs. 9–12).

The Diagonal type, judging from my own observations and from the published work of others, is far less common, and may indeed perhaps be regarded as rare. I have observed it in Calycanthaceae, Fagaceae, Euphorbiaceae, and it has been described by Miss W. Smith² in the Sapotaceae and by Mr. Wright³ in the Ebenaceae. Its relation to the Cruciform type is not obvious, but there are some significant features which will be considered later. It may be combined with the Cruciform type to form an octarch root if four of these poles are present, or a hexarch root if only the cotyledonary poles of the cross be present (e.g. *Pyrus communis*, &c.). It is usually accompanied by that wide separation of the halves of the 'double bundle', together with early obliteration of the central

¹ Loc. cit.

² Smith, W.: The Anatomy of some Sapotaceous Seedlings. Trans. Linn. Soc., ser. ii, Bot., vol. vii, 1909.

³ Wright, H.: The Genus *Diospyrus* in Ceylon. Ann. Roy. Bot. Gard., Peradeniya, vol. ii, 1904.

protoxylem group, which gives the most complete appearance of independence at the base. Thus, chance sections of the cotyledonary petiole of *Ricinus communis* certainly do not suggest any connexion between its four widely separated strands and a 'double bundle'; nevertheless, the two central bundles unite higher up, and careful examination at a suitable age reveals the presence of the isolated protoxylem elements in the petiolar base.

The anatomical arrangements found in hypocotyl, primary leaves (cotyledonary and plumular), and primary root, together with their inter-relationships, have proved very difficult of description, and there is not a little danger of being led astray by our own conventional even though quite necessary terminology.

Perhaps the greater number of investigators, beginning with Van Tieghem, and including Sargent, Wright, Tansley and Thomas, Hill and de Fraine, and Lee, have described the transition features from above downwards, but not a few, including Smith, Chauveaud, and Compton, have described them in the reverse direction. Although I have been in the habit of describing the course of the vascular strands proceeding from leaves to root, in view of the many pitfalls involved, the reverse procedure is perhaps less open to objection. In both cases the hypocotyl is treated solely as a 'transitional'¹ region, and the inevitable impression of motion or change of position is exaggerated. From many points of view I am inclined to think that a truer concept is obtained by considering the hypocotyl as an axis with an anatomical structure of its own, having relation to that of leaves on the one hand and primary root on the other.

The hypocotyl may be taken to be the region between the *collet* and the cotyledonary node. This region may be short or long, and at either end it will be influenced by its relationships with the other members. The most independent and uninfluenced part will be roughly half-way between these points. The cotyledonary node is always well defined morphologically, the collet far less so. The internal changes do not necessarily correspond in level with the external changes. This is true in general of the insertion of leaf-traces for fossil (e. g. *Lyginodendron* and *Palaeostachya*), and recent forms, as witnessed by de Bary's twenty-three types of leaf-trace insertion, varying in distance from point of entry (i. e. node) and mode of union.

In 1904 Mr. Tansley² and I drew attention to the phenomenon of root structure in the central cylinder of the hypocotyl of a number of forms. I think it is safe to say that a more or less *root-like* anatomy is characteristic of the hypocotyl of by far the great majority of the forms now known to us, that in short it is the rule and not the exception. Nevertheless, the

¹ This finds its most extreme expression in the work of Sterckx.

Tansley, A. G., and Thomas, E. N. : Root Structure in the Central Cylinder of the Hypocotyl. New Phytol., vol. iii, 1904.

structure is by no means the same as that of the root. When the hypocotyledonary region is long enough for its structure to appear uninfluenced by the changes associated with the cotyledonary node and collet respectively, it is seen to consist essentially of a more or less pithed xylem mass with a varying number of practically exarch protoxylem groups, the whole sometimes almost completely surrounded by phloem, but more often with the phloem broken into groups alternating with the protoxylem groups.

All the conducting tissue present at a very early age is directly continuous with that in the cotyledons in an upward direction, and with that in the primary root in a downward direction.

In Text-fig. 42 (p. 730) the phloem breaks away along the line indicated, and a xylem group, together with the two phloem groups thus produced, passes into the base of one cotyledon (*a*, *b*), constituting the curious 'double bundle' described above, the other cotyledon being supplied in a similar manner. At the other end of the hypocotyl the extended phloem groups of the latter are continued by the much smaller and more compact ones of the root (*c*), while the rather scattered xylem is continuous with the definite diarch plate of the same, the pith having disappeared. The ill-defined endodermis of the hypocotyl passes into the well-defined endodermis of the root.

In Text-fig. 43 (p. 731) a similar process takes place, but in addition to the central protoxylem of the 'double bundle', groups of protoxylem on the flanks continue the intercotyledonary groups of the hypocotyl (*a*, *b*). (See also Pl. LI, Figs. 24, 25 of *Althaea rosea*.) In other forms these groups are separated from the double strand as distinct laterals, e. g. *Magnolia tripetala*, and the double bundle itself may be represented by what appears at first sight, particularly at some ages and at some levels, to be two perfectly distinct strands. (See Text-fig. 38, p. 722, of *Prunus persica*.) Following the strands downwards through the hypocotyl, the intercotyledonary protoxylem groups are seen to pass into the intercotyledonary poles of the tetrarch root (*c*).

The most marked 'transition' takes place somewhere in the cotyledon, where the double bundle becomes continued upwards as a single collateral strand. Most authors speak of this as the delayed fusion or precocious splitting of phloem groups, according to direction of description, but none, so far as I am aware, have suggested any reason for the delay, or, in other words, for preparation for root formation in the cotyledons. The double bundle, moreover, is met with in its most extreme form in those species in which root structure is furthest from the cotyledonary node (Euphorbiaceae, Calycanthaceae). The homology with the double bundle of the widely separated central strands of these forms is proved by their union in the upper part of the cotyledon, and by the identification of isolated central protoxylem elements in the lower part.

THE FORMS DESCRIBED.

The species to be described in this paper form part of an investigation on seedling anatomy which has been proceeding for some years. It was begun in 1902 at the instigation of Mr. A. G. Tansley, and some of the work was carried on while acting as his research assistant. I take pleasure in expressing my extreme indebtedness to him for the very kind permission to include the work done at that period.

Quite recently I have been greatly assisted in the matter of preparations, &c., by my Demonstrator and former student, Miss A. J. Davey, B.Sc. Some of the data included have been taken from preparations made by Miss K. Blackburn, B.Sc., in connexion with another investigation now in progress.

In all, some 150 species belonging to the cohorts Ranales, Rhoadales, and Rosales have been examined, about half of which are Ranalean forms.

Much of the material has been grown at Bedford College, a little at University College, while seedlings for this investigation were raised some years ago at University College, Reading, and also by Miss Strudwick at Cambridge.

RANALES.

More than seventy species have been examined, fifty-two of which are members of the Natural Order Ranunculaceae, seven of Berberidaceae, and one of Lardizabalaceae. In the Magnoliaceae six species have been examined, in the Calycanthaceae four, in Anonaceae two, and in Lauraceae two.

The Ranunculaceae are very uniformly diarch; the Magnoliaceae, Calycanthaceae, and Lauraceae are very largely tetrarch; while the Berberidaceae have tetrarch species. The Calycanthaceae present the most outstanding features, and show the rare Diagonal type in a very interesting form.

Ranunculaceae.

The Ranunculaceae are characterized by a tendency to form cotyledonary tubes, which, as was noted by Darwin, seems to be associated with a tendency to form tubers. The lateral bundles of the cotyledon usually unite with the central high up, so that the base of the cotyledon shows only one bundle which is not usually markedly double. These bundles connect in many forms with the vascular system of the hypocotyl through a very sharp angle, rearrangements in the tissues taking place at the same time, so that the hypocotyl has a root-like structure from very near the node.

Anemoneae.

Anemone coronaria. This species has a marked cotyledonary tube in which two small collateral strands, corresponding to the midribs of the respective cotyledons, face each other across the central cavity. Immediately below the cotyledonary node the strands close into the centre of the axis through a sharp bend, so that the tissues are almost longitudinal in the transverse section, and this may be sometimes more marked on one side than on the other. As the strands enter the axis, the readjustments take place which produce a diarch root very near the top of the hypocotyl. These readjustments are obscured by the fact that, to a large extent, they take place in the bend, but in the section shown in Pl. L, Fig. 3, the bifurcation of the phloem can be seen very plainly in the strand to the south. The aggregation of the phloem in two alternating patches is the root character which appears highest in the hypocotyl, while the absence of pith and formation of a definite xylem plate with exarch protoxylem groups are characters only to be found at a lower level. Although each cotyledonary bundle consists of only three or four xylem elements, one or two of these are usually secondary in formation, judging from the radial arrangement found.

Anemone fulgens forms a cotyledonary tube of considerable length, which in the upper part becomes a solid cylindrical structure through the interlocking of cells of the cavity (Text-fig. 1). The cotyledon strands pass more steeply into the hypocotyl, so that the transition can be followed with greater ease than in *A. coronaria*.

Anemone rivularis is very similar to *A. fulgens*.

Anemone sylvestris. In this a very short cotyledonary tube or sheath is found, which in some individuals is asymmetrical through union of the cotyledons at a slightly higher level on the south side away from the first leaf, and through displacement of the cotyledonary strands to this side.

The transition features are similar to those of *A. coronaria*.

Anemone virginiana. In this species the cotyledons fuse quite at the base as in *A. sylvestris* (Text-fig. 2). In this region the cotyledon strands are very slightly double groups. The features of transition are like those of the above-described species.

Anemone pulsatilla. There is a very slight cotyledonary tube at the base, in which the cotyledon bundles show a double structure.

In one individual the most remarkable asymmetry was found, resulting in the formation of a diarch root, one of the poles of which is continuous with the vascular system of the first plumular leaf, while the other is continuous with the two asymmetrically placed cotyledonary strands.

Anemone vitifolia also possesses a short cotyledonary tube, which is

somewhat asymmetrical through union at a higher level on one side than on the other. The vascular bundles are slightly displaced towards this side, but the transition is normal.

Anemone vernalis has a distinct cotyledonary tube, in which union of the cotyledons takes place on one side first, and rearrangements occur as the bundles turn inwards at the node. This species shows very markedly the early (i. e. high) union of the phloem groups, together with the wide and indeterminate grouping of the protoxylem elements in the upper part of the hypocotyl.

Anemone montana shows the usual features very distinctly. The early

TEXT-FIGS. 1-5. 1, *Anemone fulgens*; 2, *A. virginiana*; 3, *A. alpina*; 4, *A. nemorosa*; 5, *A. apennina*. All nat. size.

phloem grouping and late protoxylem aggregation of *A. vernalis* is seen in this species also.

Anemone alpina possesses a short cotyledonary tube or sheath, in which the strands are markedly double (Text-fig. 3). As the individual examined was rather older than the members of other species, it is possible that the doubleness may be, to some extent, an age phenomenon. The result is a much closer resemblance to members of the Rhoeadales cohort than is seen in other species.

Anemone nemorosa. In the quite young stage the seedlings of this species are normal (Text-fig. 4), but very soon become swollen up in a tuberous manner, so that the conducting tissues in some cases become

separated by parenchyma. Thus the two phloem groups are separated from the somewhat distorted diarch plate by parenchymatous cells. In the middle line, however, of these cells, at right angles to the plate, there is to be found one row of secondary xylem elements, giving a curious tetrarch appearance. (Cf. *Eranthis*.)

Anemone apennina is a pseudo-monocotyledonous form in which the single cotyledonary member has a long petiolar region, bearing a more or less bifid blade. The root has the customary diarch structure; this structure is not only found throughout the hypocotyl, but also above the cotyledonary node in the lower part of the cotyledonary petiole. Thus the transition takes place *wholly* in the cotyledon, and more or less in the region marked by a collet (Text-fig. 5), half-way between blade and insertion. This species will be more fully described in a subsequent paper.

The twelve species of *Anemone* examined indicate the prevalence of cotyledonary tubes within the genus and the tendency to form tubers. *A. apennina* is extreme in both characters. The cotyledonary member appears to be absolutely single, and none of the individuals examined show the bisymmetrical anatomy figured by Sterckx.¹

Twelve species of the genus *Ranunculus* have been examined. With the exception of *R. Ficaria*, which is a pseudo-Monocotyledon and wholly peculiar, the species do not differ from one another in any important respect, and are generally characterized by the sharp angle of entry of the cotyledon strands, rearrangements occurring at the entry, so that a diarch structure is met with just below the node. Secondary roots are produced almost at the node, and in some species, e. g. in *R. sceleratus*, there is a tendency for the primary root to abort as in Monocotyledons. Most of the species have a slight cotyledonary tube, and some form tubers.

Ranunculus acris, *R. gramineus*, *R. parviflorus* show very perfectly the features of the genus. They are slender forms, but with a tendency to the suppression of internodes. The small diarch root structure is found just below the cotyledonary node. As the strands pass from the hypocotyl into the base of the cotyledonary tube, they usually become single and collateral. Each is continued into the free portion of a cotyledon as its single central collateral strand, which only gives off laterals in the lamina (Text-figs. 6 and 7).

R. bulbosus, *R. arvensis*, *R. auricomus*, and *R. repens* are quite similar, and call for no comment.

R. hederaceus shows great development of secondary roots at the node (Text-fig. 8).

R. sceleratus has not only plentiful secondary roots at the node, but the primary root dies out at an early age.

¹ Sterckx, R.: Recherches anatomiques sur l'embryon et les plantules dans la famille des Rénonculacées. Mém. Soc. roy. Sci., Liège, sér. iii, t. ii, 1900.

R. flammula conforms to the general features of the genus, with some peculiarities obviously due to the water habit.

Chauveaud has described half a dozen additional species which do not appear to differ from those described above.

R. Ficaria (Text-fig. 9). The morphology of this species has given rise to much discussion. The cotyledonary member appears to be quite single, and it is traversed by a single strand. As in the other species the primary root is diarch. At the cotyledonary node the greater part of the vascular tissue passes upwards into the cotyledon and is continued as its central strand. From the same region the vascular strand of the first leaf has its connexion. The exact relationship of these vascular strands will be discussed in a subsequent paper.

TEXT-FIGS. 6-9. 6, *Ranunculus acris*; 7, *R. gramineus*; 8, *R. hederaceus*; 9, *R. Ficaria*.
6, 7, and 8 $\frac{2}{3}$ nat. size; 9 $\times 2\frac{1}{2}$.

The seedlings of the genus *Clematis* are distinctly more robust than those of *Ranunculus* and *Anemone*. Nine species have been examined, and the chief interest lies in the two species *C. viticella* and *C. Hendersoni*, in which there are vascular strands in the intercotyledonary plane of the hypocotyl, which are continued upwards as the lateral bundles of the cotyledon. (See Pl. L, Fig. 6, *Liriodendron tulipifera*.)

Clematis vitalba. The transition is high, and the vascular bundle of the cotyledon is double at the node. The diarch plate is found at a short distance below the node, and consists of a radial file of vessels.

Clematis flammula (Text-fig. 10). This species forms a short cotyledonary tube. The bundles of the cotyledons are double for some distance above the cotyledonary node, and connect with the diarch root in the usual

manner. The plumule is noticeably late in differentiation. In seedlings which show plentiful metaxylem and crushed protoxylem, there is no sign of lignification in the plumular rudiments.¹

Clematis recta possesses a short cotyledonary tube, and presents the usual type of anatomy.

Clematis orientalis (Text-fig. 11). The cotyledonary strands are double in the cotyledons of this form, as in *C. flammula*. The transition is quite normal; the xylem of the root does not meet in the centre of the diarch plate but is present in two pegtop-shaped clumps, the broad ends of which are directed towards one another, but do not touch.

Clematis glauca and *Clematis alpina* call for no remark.

TEXT-FIGS. 10-14. 10, *Clematis flammula*; 11, *C. orientalis*; 12, *C. Davidiana*; 13, *C. Hendersoni*; 14, *C. viticella*. All reduced about $\frac{1}{2}$.

Clematis Davidiana. An interesting peculiarity was met with in one individual of this species (Text-fig. 12), which showed a single cotyledonary member evidently produced by marginal fusion of the pair. The two vascular strands of this member approached each other at the node, and it would seem that the diarch plate is formed in the normal plane, i. e. that passing through the supposed centres of the cotyledons. Comparison with similar anomalies in *Anemone sylvestris* and *A. pulsatilla* adds interest to this occurrence.

C. Hendersoni and *C. viticella* (Text-figs. 13 and 14). These species stand out from the others by virtue of the possession of lateral strands in the base of the cotyledon. These strands pass into the hypocotyl independently of the double bundle and unite with the corresponding bundle from the other cotyledon. There may be said to be practically a tetrarch stage, inasmuch as the small phloem groups of the laterals divide in the hypocotyl, so that the intercotyledonary protoxylem elements are exarch, although through their disappearance the root in its final form is diarch. The tetrarch appearance is enhanced in older seedlings by the production of four masses of secondary xylem, leaving rays in the intercotyledonary plane which are almost as marked as those in the cotyledonary plane.

Thalictrum flavum, *T. glaucum*, *T. javanicum*, and *T. adiantifolium*. This genus presents many histological peculiarities which will not be considered in this paper. The transitional features of the four species examined are quite alike, and similar to those of the genera described above.

¹ The terms protoxylem and metaxylem are applied in a purely relative sense throughout this paper and no precise or histological meaning is to be attached to them.

Adonis annua. The seedling anatomy is of the ordinary type, but the doubleness is more marked in the cotyledon than in many of the Ranunculaceous forms.

Myosurus minimus, although absurdly reduced, seems to form its minute diarch root in the usual way.

Helleboreae.

Nigella aristata and *N. hispanica*. The hypocotyl has the usual four phloem groups, with the four metaxylems connected in the cotyledonary plane by a thin bridge of crushed protoxylem. At the node the xylem and two phloem groups pass out to form the double bundle of the cotyledon, which gives off laterals at this point. Further down the hypocotyl the fusion of the phloem groups and approximation of metaxylem to form a plate results in the usual diarch root.

Nigella sativa, described by Gérard,¹ and *N. damascena*, described by Chauveaud, appear to resemble the above species.

Helleborus foetidus shows similar features.

Aquilegia vulgaris, *A. alpina*, and *A. canadensis*. This genus very closely resembles *Thalictrum*, and has the same histological peculiarities. The transition features seem to be quite normal, but the seedlings examined were rather old. As in *Thalictrum*, the cotyledonary bundle is markedly double.

Delphinium formosum, *D. luzulinum*, and *D. sp.* (annual form). The seedling anatomy is quite normal. The double bundle is extremely marked, and the genus resembles *Aquilegia* even in some of the histological details.

Trollius asiaticus and *Caltha palustris*. These species conform in some measure to the general type, but present special features which will be dealt with in a subsequent paper.

Paeonieae.

Paeonia herbacea and *P. arborea* show two Y-shaped xylem groups in the cotyledonary plane of the hypocotyl, alternating with two extended phloem groups in the hypocotyledonary plane, which, in combination with the lateral extension of the xylem arms, is slightly suggestive of the tetrarch condition. At the node the half of each phloem group passes out with a xylem Y into each cotyledon, where they form a large extended double bundle, which in *P. arborea* gives off laterals at the base of the petiole. When the strands are followed downwards, it is seen that as the diarch root structure is attained by aggregation of phloem

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TEXT-FIG. 15.
Paeonia herbacea.
 $\frac{2}{3}$ nat. size.

¹ Loc. cit.

groups, &c., the xylem decreases in quantity until only the two small protoxylem strands remain.

Berberidaceae.

The genus *Berberis* is of great interest, inasmuch as both the tetrarch and the diarch condition are to be found within the genus, and even within the species, as in *B. macrophylla*.

Berberis Lycium. The hypocotyl shows four diagonal strands of phloem with some metaxylem to the inside, and with obvious exarch protoxylem elements in the cotyledonary plane, and somewhat less obvious ones in the intercotyledonary plane. At the node the usual double strand passes out into the base of the cotyledon, and is continued up the petiole.

17 At the base of the hypocotyl the slight adjustments take place which convert the structure into that of a typical tetrarch root. (See Pl. LI, Figs. 21-6 of *Althaea rosea*.)

B. aristata shows similar features, but may reduce to triarch, while *B. macrophylla* reduces rapidly to a triarch, and sometimes later to a diarch condition.

B. vulgaris, *B. aquifolium*, *B. nervosa*, *B. heteropoda* show early fusion of the phloem groups and a diarch root.

TEXT-FIGS. 16-18. 16, *Berberis Lycium*; 17, *B. aristata*; 18, *B. vulgaris*. All $\frac{2}{3}$ nat. size.

Comparison of seedlings at different stages in these species shows very clearly the changes produced by age. Thus in *B. aquifolium*, at an age when the first leaf is just visible, the halves of the double bundle appear to be very widely separated at the cotyledonary node on account of the obliteration of the central protoxylem group and the semi-obliteration of the two tangentially produced wings, while inside the four phloem groups are to be found masses of metaxylem not to be found at an earlier age.

Podophyllum Emodi. This species has a very long cotyledonary tube with a small central cavity, which becomes occluded in the upper part and widens out round the plumule near the base. The root is typically diarch, but the plate in the hypocotyledonary region develops intercotyledonary xylem arms between the phloem groups, which produce a tetrarch appearance reminiscent of the tetrarch species of *Berberis*. These groups are continued upwards into the plumular leaves, and the main strands are continuous above with the double bundles of the cotyledons in the usual manner. The double bundles are remarkable for the extremely exarch position of the xylem, which constitutes the apex of an outwardly directed V

throughout the petiole. Lateral strands are given off as these enter the free laminae. Apart from this special feature *P. Emodi* would seem to resemble *Eranthis hiemalis*, judging from Miss Sargent's¹ description and figures of that species.

Lardizabalaceae.

Decaisnea Fargesii. The hypocotyl of this species is long and stem-like. It shows the usual four groups of phloem with metaxylem within, and somewhat crushed protoxylem outlining the inner border. At the cotyledonary node four small strands are detached which pass independently into the base of the cotyledons. The main portion of the four diagonal bundles of the hypocotyl is continued upwards as the very widely divergent halves of the double bundle, only identifiable as such by the sporadic appearance of isolated central protoxylem elements. (Cf. Calycanthaceae below.) The four apparently collateral strands of the lower part of the hypocotyl gradually pass into the tissues of a diarch root by approximation of the phloems in the intercotyledonary and of the xylems in the cotyledonary planes, respectively.

TEXT-FIG. 19. *Decaisnea Fargesii*. $\frac{2}{3}$ nat. size.

The behaviour of the lateral strands is somewhat similar to that of the corresponding bundles of *Liriodendron tulipifera* (Pl. L, Fig. 6), while the central double bundle is very like that of *Calycanthus* (Text-fig. 22).

Magnoliaceae.

Magnolia tripetala (see Pl. L, Figs. 9-12). The hypocotyl shows as its most characteristic arrangement eight groups of phloem with metaxylem within each, and four groups of protoxylem situated in the cotyledonary and intercotyledonary planes, so that phloem and metaxylem are found in twin pairs in the diagonal planes. The aggregation first of the phloem pairs to form four masses in the diagonal planes, and then of the metaxylem so as to form a quadrangular mass of wood which is nearly solid (see Pl. L, Figs. 10-12), gradually changes the hypocotyledonary arrangement to that of a root as we follow it downwards. In passing upwards from the structure described for the hypocotyl, the phloem and xylem groups nearest to the intercotyledonary plane are seen to fuse a short distance below the node, so that a single collateral strand is formed in this plane, thus sharply distinguishing it from the double bundles in the cotyledonary plane which are continued as such into the petioles of the cotyledons. The collateral intercotyledonary strands bifurcate at the node just after leaving

¹ Loc. cit.

the central cylinder, and the halves thus produced pass into the cotyledons as the lateral bundles of the petiole. Thus a tetrarch root is formed from the 'doubles' and two laterals of the cotyledons.

It is to be noted that if the 'double' be regarded as one bundle, the laterals, coming as they do one from each cotyledon, cannot but be considered as two strands, and we have therefore a condition which does not fall into either of Van Tieghem's types, but is partly conformable with Type 3, and partly with Type 2.

Magnolia Soulangiana (Text-fig. 20) has the same mode of transition and general features as *M. tripetala*, with the exception that the lateral bundles do not form a collateral strand just below the node, but pass out as two separate bundles, one going to each cotyledon as in *M. tripetala*.

TEXT-FIGS. 20, 21. 20, *Magnolia Soulangiana*; 21, *M. acuminata*. $\frac{1}{2}$ nat. size.

Magnolia acuminata (Text-fig. 21) resembles *M. Soulangiana*, and forms a tetrarch root in a similar manner. Sections from an older seedling of this species show how completely age masks the primary structure. In this individual a complete ring of secondary tissues is found just below the cotyledonary node, which take the place of the obliterated protoxylem groups of the 'doubles' so obvious at an earlier age.

The transition phenomena of these three species are thus precisely similar.

Magnolia Yulan differs markedly from the preceding species in the possession of a diarch primary root, and also in the absence of free lateral strands in the base of the cotyledons.

Liriodendron tulipifera (Pl. L, Figs. 5-8). The upper part of the hypocotyl resembles that of *M. tripetala* in essential features, but the vascular system in the intercotyledonary plane is smaller, so that the stele forms a rectangle of which the intercotyledonary sides are shorter than the cotyledonary sides. As the intercotyledonary strands pass upwards to the cotyledonary node, they unite to form a single collateral strand as in *M. tripetala*, which only bifurcates to form the laterals of the cotyledon petioles as the latter diverge from the axis. As the strands of the hypocotyl are followed downwards towards the root, the intercotyledonary ones gradually disappear, inserting themselves on the more robust cotyledonary strands. This leads to the formation of a diarch root.

Illicium religiosum. This species has not been fully worked out, but it would seem to resemble *Magnolia Yulan* in the absence of lateral bundles and formation of a diarch root.

Calycanthaceae.

Calycanthus floridus, *C. praecox*, *C. occidentalis*, and *C. (Chimonanthus) fragrans*. The very long hypocotyl shows an elliptical stele with four collateral bundles at the corners. At the cotyledonary node the two at the same end of the ellipse pass out into the base of a cotyledonary petiole, where they approach each other slowly, to form a very widely separated 'double bundle', the halves of which are, as it were, linked together by a few scattered and disorganizing protoxylem elements (Text-fig. 22, A). These protoxylem elements can be identified occasionally here and there in the hypocotyl isolated in the cotyledonary plane. (Cf. *Decaisnea*, described above.) A short distance from the base of the petiole lateral bundles become distinct from the central 'double', but remain in close connexion nearly to the top of the petiole.

TEXT-FIG. 22. *Calycanthus floridus*. A, Cotyledonary node; B, Root of abnormal specimen. Diagrammatic.

Outlining the inner margin of the four cotyledonary strands of the hypocotyl is a fringe of crushed protoxylem elements at an age when no plumular tissue is lignified. At the base of the hypocotyl the protoxylem in the four strands becomes exarch, and with the exception of certain individuals of *C. floridus*, a tetrarch root is formed through the production of a phloem group in the cotyledonary plane. I have not satisfied myself with regard to the origin of this phloem strand, but Chauveaud¹ describes it as taking its origin in the hypocotyl, or, considering the strand from root upwards as ending blindly in the hypocotyl, having no connexion with the upper part of the seedling. Older seedlings of *C. praecox* show small 'secondary' bundles between the halves of the double bundle, as the result of cambial activity near the cotyledonary node. It is possible that these may connect with the cotyledonary phloem groups just described.

The exceptional individuals of *C. floridus* possessed a diarch root with the poles in the customary cotyledonary planes (Text-fig. 22, B). (Cf. *Decaisnea*.)

Anonaceae.

Anona triloba. The stele of the hypocotyl is somewhat similar to that of *Calycanthus* in the upper part, but the double bundle forms much more of a unit with central exarch protoxylem obvious up to the cotyledonary node and present in a rather more mesarch position in the base of the

¹ Loc. cit.

petioles. Proceeding downwards, root structure which in *Anona* is diarch is attained at a higher level than in *Calycanthus*.

A. reticulata presents similar features.

Lauraceae.

Laurus Sassafras. The top of the hypocotyl shows four groups of phloem and xylem in the diagonal planes, with two or three very small crushed and almost obliterated protoxylem elements isolated in the cotyledonary plane. As these tissues are followed upwards they are seen to pass into the cotyledons, as in the previous families forming a double bundle which at the base of the petiole detaches two main laterals. In other words, the main lateral strands which in *Magnolia tripetala*, *M. acuminata*, and *M. Soulangiana* pass into the hypocotyledonary axis independently, sweeping round so as to enter the stele in the intercotyledonary plane, in *L. Sassafras* merge with the double bundle at the cotyledonary node and thus enter the stele as one unit. Downwards the hypocotyledonary arrangements merge into those of a tetrarch root as the intercotyledonary protoxylem poles become defined.

TEXT-FIGS. 23, 24. 23, *Laurus Sassafras*; 24, *L. nobilis*. $\frac{2}{3}$ nat. size.

Laurus nobilis presents an octarch stage in the seedlings examined, which were, however, too old.

Cassyltha is described by Mirande as tetrarch.

Laurus and the species *Lycium* and *aristata* of *Berberis* present the so-called 'Anemarrhena' type reported by de Fraine as occurring in Cactaceae and by Lee in Compositae, in which it

may be said that the xylem of the cotyledonary strand divides into three and the phloem into two to form a tetrarch root.

I have been familiar with this type for many years and *Althaea Rosea* (Pl. LI, Figs. 23-6) presents a very good instance of it. In this case the lateral strands are only independent in the lamina and are merged with the central one throughout the petiole, which thus possesses an extended kidney-bean-shaped 'double' bundle, the central protoxylem of which is external at the cotyledonary node (Pl. LI, Fig. 24). *Althaea* differs from *Laurus Sassafras* only with regard to the degree of independence of the laterals, or, in other words, with regard to the exact point of approximation with the double bundle in the cotyledon.

The constancy of the Ranunculaceous type is in contrast to the variation met with in the few members examined of the other Ranalean families.

They furnish, in addition to the 'Anemarrhena' type of *Berberis* and *Laurus*, the series in the Magnoliaceae (Text-fig. 25, 1, 3, and 4) in which *Liriodendron* links the tetrarch and diarch forms. *Liriodendron* and *Decaisnea* couple presence of laterals with a diarch root (Text-fig. 25, 3), while

RANALES

TEXT-FIG. 25.

Diagrams illustrating principal types of vascular arrangement in cotyledons, hypocotyl, and root of Ranalean forms.

Berberis and *Laurus* form a tetrarch root in the absence of laterals (Text-fig. 25, 2). *Calycanthus* presents that wide separation of the halves of the double bundle with almost complete obliteration of the central protoxylem which is one of the most puzzling aspects of seedling anatomy, and it is coupled with two forms of root.

RHOEADALES.

About thirty species have been examined belonging to the Rhoeadales cohort. They show very great constancy of feature and present good typical examples of the diarch type. They include members of the Cruciferae, Papaveraceae, Resedaceae, and Capparidaceae. They are for the most part herbaceous forms, but the shrubby *Capparis* and *Cleome* are very similar in their anatomy. The species here described include *Papaver*, instanced by de Bary¹ as a form with one bundle to the cotyledonary trace, and *Cheiranthus*, stated by Scott² to have two. *Corydalis* and *Fumaria*, in common with the other members of the group, present the features which have been described by all recent authors as illustrative of Van Tieghem's Type 3, but Van Tieghem³ himself gives *Fumaria* as an example of Type 1.

Cruciferae.

This order shows very uniform structure and it is only in the neighbourhood of *Lunaria* that there is any departure from type.

Hesperideae.

Cheiranthus Cheiri. The hypocotyl shows a somewhat elliptical vascular cylinder consisting of the usual diagonal strands of phloem and metaxylem. The pairs at each end of the ellipse are connected by the more or less "crushed" protoxylem of the cotyledonary plane. Near the cotyledonary node the ellipse widens out and the vascular tissue at each end is continued into the cotyledons as the double bundles of the petioles, while the tissue in the intercotyledonary plane ultimately connects with the vascular system of the first plumular leaves. Proceeding towards the collet, the hypocotyledonary tissues become continuous with those of a diarch root (similar to that shown in Pl. LI, Fig. 16) by the following stages: (1) disappearance of the pith, (2) aggregation of the alternate phloem masses, and (3) reduction of the xylem to a single file of elements constituting the diarch plate. The epidermis and endodermis also change in character, but usually at a lower level. In the upper part of the cotyledon the double bundle is continued by a single strand. This is the now familiar diarch type (Pl. LI, Figs. 17–20). The examination of a form with three cotyledons revealed a triarch root.

¹ de Bary, A. : Comparative Anatomy of the Phanerogams and Ferns, p. 236, (Oxford) 1884.

² Loc. cit.

³ Loc. cit., p. 782.

The extreme simplicity of this arrangement is due to the continuity of two strands of alternately placed exarch protoxylem throughout the seedling from the diarch root to some region in the cotyledons where more or less gradually the collateral arrangement is assumed. These strands are continuous with the central bundle of the series of collateral strands of the lamina, all of which are massed with the central at some point usually in the blade, but one independent lateral bundle may be met with in the petiole on each side of the central strand (e. g. *Lunaria biennis*). The existence of the alternate exarch or mesarch protoxylem group is frequently almost or quite non-identifiable on account of the degeneration changes which take place in these elements, leading to their obliteration in cotyledons and top of hypocotyl at an early age.

Cheiranthus maritimus. The structure is in essentials quite similar to that of *C. Cheiri*. No laterals were seen in the petiole.

At an early age the primary protoxylem is degenerated but usually still discernible as crushed streaks, while a few cambial divisions are to be observed. The first plumular leaves are opposite each other and alternate with the cotyledons. Their single central strands are essentially similar to those of the cotyledons, in that they are markedly double, consisting of a central group of protoxylem alternating with two centres of phloem formation. One lignified element which is continuous with the strand of the rudimentary first leaf may be found in the upper part of the hypocotyl at an age when the plumule is not obvious to the naked eye.

Erysimum pulchellum. The transition features in this species are very similar to those in *Cheiranthus*.

Alyssum rostratum. In the seedlings examined there are slight deviations from type in detail. Thus the protoxylem is scattered and not very obvious in the upper part of the hypocotyl, and even in the diarch plate it is crushed and degenerate-looking. This is no doubt only an extreme case of early degeneration of the protoxylem, as it is more marked in the older seedlings and is correlated with very precocious development of the cambium, the activities of which are very manifest even in the youngest seedlings.

Alyssum maritimum, as described by Chauveaud,¹ seems to be quite similar.

Anastatica hierochuntina. The anatomical arrangements are those characteristic of the group, and show the usual features of the diarch type.

Malcolmia littorea presents a good example of the common arrangement. Degeneration of the protoxylem takes place at an extremely early age, as was far advanced in the seedlings examined, which were still very young as judged by internal as well as external marks.

Matthiola tricuspidata (Text-fig. 26). Normal seedlings show the

¹ Loc. cit., 1911.

usual structure. An individual having three cotyledons was examined (Text-fig. 27). Two of these cotyledons united near the base and their confluent vascular systems became continuous in the hypocotyl with one of the groups forming the quite normal elliptical stele, and through this with a pole of the diarch root. Thus, contrary to what was recorded of a tricotyledonary specimen of *Cheiranthus Cheiri*, two cotyledons form between them only one pole, so that the root is diarch and not triarch. It is of interest to note that in the free portion of these cotyledons the vascular strand is quite distinctly double, and this not in preparation for the root arrangement but contrary to it, as in the lower united portion the strand becomes single so as to form with that of the other cotyledon or half-cotyledon a double bundle. This would seem to have some bearing on our conception of the meaning of 'doubleness'.

Hesperis tristis. The cotyledons insert themselves by broad flat bases which unite on one side for a very short distance before fusing with the

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TEXT-FIGS. 26, 27. *Matthiola tricuspidata*. 26, Normal seedling; 27, Seedling with three cotyledons. Nat. size.

TEXT-FIG. 28. *Draba Aizoon*: vascular system of plumular leaf. *ph*, phloem; *xy*, xylem. $\times 800$.

hypocotyl. One minute lateral on either side of the central double bundle remains free until quite near the cotyledonary node, when it unites with the central. The protoxylem is in a somewhat degenerate condition throughout, but persistent and obvious.

Draba Aizoon. While the main features are entirely according to type there are several distinctive subordinate characteristics in this species. Thus the hypocotyl shows a very definite central region that may perhaps be termed a 'stele', which approaches protostelic appearance by early (i. e. high up) loss of pith and somewhat cylindrical disposition of phloem.

This appearance is enhanced by the extremely early activity of the cambium, which is perhaps most active in the position corresponding to the two protoxylem poles of the root. The appearance suggests that there is probably no interval of time, i. e. stage of quiescence, between the cell-divisions of the primary desmogen and those more definite radial divisions termed 'secondary'.

While the cotyledon strands are not markedly double above the

cotyledonary node the first plumular leaves show very well the 'double-ness' often seen in the leaves immediately succeeding the cotyledons (Text-fig. 28).

Arabis rosea presents a very perfect example of the diarch type in which complete root structure is present very high up in the hypocotyl. This structure bears no relation to the apparent collet.

Aubretia Antilibani shows a detailed likeness to *Arabis rosea*.

Sinapeae.

Teesdalia nudicaulis is very similar to the preceding genera.

Iberis tenerea (Pl. LI, Figs. 13-16) is a good example of the general features of the type. One seedling shows particularly well the way in which the doubleness of the cotyledonary strand may be masked by early appearance of cambium, which by its activity between the two primary groups of phloem links these together with secondary phloem, with the result that the two original centres of phloem production are so obscured that they may be overlooked at this stage. At the base of the cotyledons the cambium is confined to the wings—that is, to the inside of the phloem groups, so that the bundle is obviously double. At this level in still older seedlings a further age effect is very well seen, namely, the obliteration of the central alternate protoxylem group, which gives the appearance of two separate bundles described by many writers (see de Bary and more recently Scott).

Iberis sempervirens resembles *Iberis tenerea* very closely.

Aethionema persicum. The transitional phenomena are similar to those of the preceding genera. The top of the hypocotyl shows very definite strands in the intercotyledonary plane, each having two or three lignified elements. These are continuous with the plumular midribs, which however are as yet in the undifferentiated desmogen state. The central protoxylem of the cotyledonary strands is obviously degenerating in the cotyledons, hypocotyl, and root. Secondary thickening has begun early, and partly on this account a rectangular-looking stele is found in the top of the hypocotyl which is slightly more elongated in the intercotyledonary than in the cotyledonary direction, and has four phloem groups arranged in pairs.

Peltaria alliacea is characterized by the presence of root structure very close to the cotyledonary node. Very early production of cambium masks the degenerating protoxylem elements of the central position in the cotyledons except quite at the base, where cambium is not formed in the middle line. (Compare *Iberis*, &c.)

Sisymbrium carpaticum conforms completely to the general type. Degenerating protoxylem is obvious throughout the seedling. One tricotylous specimen was examined which formed a triarch root as in *Cheiranthus Cheiri*.

Lunaria biennis is of interest on account of the very different habit of the seedling with its comparatively large thick cotyledons. The base

TEXT-FIGS. 29, 30. 29, *Lunaria biennis*. $\frac{1}{2}$ nat. size. 30. Outline of cotyledonary node of same.

of the cotyledons shows in addition to the central double strand a small lateral on each side. These maintain their independence above the cotyledonary node, indeed in some cases may be said to pass into the hypocotyl independently. There are no differentiated plumular strands as in *Aethionema*, &c., although the presence of a robust cambium and the half-obliterated condition of the protoxylem show that the seedling is past the primary stage. The most noticeable feature of the transition is the

presence of four phloem groups throughout the hypocotyl arranged so as to form two elongated bands of phloem, the middle of which is probably chiefly secondary.

Lunaria annua is described by Chauveaud¹ as showing free laterals in the upper part of the hypocotyl.

Cardamine hirsuta seems to be quite normal, but only a rather old stage has been examined.

Barbarea vulgaris. It is interesting to note in this form, which is placed by Engler not far from *Lunaria*, that there seems to be the same somewhat leisurely manner of completing root structure, although the habit of the seedling is quite different and laterals are not found so low. It differs from *Lunaria* in the presence of a strand already lignified in the hypocotyl, which corresponds to the midrib of the first leaf. In Bismarck brown and gentian violet preparations the red-brown half-obliterated protoxylem elements, which are quite exarch in the cotyledonary node, present a marked contrast to the brilliant blue of the later-formed xylem elements.

Crambe tartarica differs from the other members of the Cruciferae examined in the wide separation of the halves of the double bundle in the hypocotyl. The laterals are free near the base of the cotyledon, and as in *Lunaria* may enter the hypocotyl independently.

Chauveaud² reports lateral strands in the hypocotyl of *Brassica oleracea*, and at the base of the cotyledons in *Ricotia lunaria*.

Raphanus sativa is the species in which Chauveaud³ first observed 'resorption' of protoxylem.

¹ Loc. cit., 1911.

² Loc. cit., 1911.

³ Chauveaud, G.: Compt. Rend. Acad. des Sc., 1901.

Braya supina and *Biscutella ciliata* are described by Chauveaud as having the same general features.

Resedaceae.

Reseda alba presents a good example of the familiar diarch type of the Rhoadales.

Reseda odorata and *Caylussa abyssinica*, according to Chauveaud's² descriptions, are similar, except that he comments upon the separateness of the halves of the double bundle in the latter.

Papaveraceae.

Papaver paeniflorum and *P. Dan.* The transition features are quite characteristic of the cohort. Older seedlings of *P. Dan* show semi-obliteration of all the primary xylem, including that of the diarch plate. The cotyledons in *P. paeniflorum* are nearly cylindrical, and the small central bundle is not markedly double in the upper part.

Glaucium serpiei. The comparison of seedlings of different ages shows that this is a form in which age causes the almost complete dis-

TEXT-FIGS. 31, 32. 31, *Glaucium serpiei*; 32, *Chelidonium majus*. Nat. size.

appearance of the primary elements, which are resorbed at an early stage, only a few isolated rings and portions of rings of wall thickening occasionally remaining. It is therefore very easy to overlook the central exarch proto-xylem elements in the upper part of the seedling. The plumular strands lignify late.

Glaucium flavum, described by Chauveaud, seems to be quite similar.

Chelidonium majus. The cotyledons form a well-marked tube. The double bundle is of the extended secant form at the base of the cotyledons, as in *Glaucium*, &c. The primary elements disappear later, and a fragmentary appearance is given by the scattered rings of thickening. The transition phenomena are quite normal.

Bocconia japonica is a slender seedling showing the same general features as the preceding genera. Evidences of resorption were seen.

Platystemon californicus. The cotyledons are centric in structure. At

¹ Loc. cit., 1911.

² Loc. cit., 1911.

the apex they possess a large double bundle which lower down gives off a lateral on each side. The laterals unite with the central strand again some distance above the base of the cotyledon. The minute diarch root is formed very high up in the hypocotyl.

Corydalis aura and *C. lutea*. The anatomical arrangements are very typical and call for no comment. *C. lutea* shows slight asymmetry in the fusion of its cotyledons.

Capparidaceae.

Cleome sesquiorgialis. This is an interesting form because it shows a much slower root formation than is characteristic of the cohort, or, in other words, complete root structure is only found lower in the hypocotyl than in most of the members of the Rhoeadales, and this is particularly true of the phloem arrangements—four phloem groups existing quite low in the hypocotyl. Examination of this species at different ages is very instructive as it shows that persistence of the degenerate resinous-looking remains of the protoxylem which enables the observer to determine its primary position in a comparatively old seedling.

Cleome arborea is described by Chauveaud¹ as having *fused* phloem groups high in the hypocotyl. His figures show that the double bundle possesses three groups of primary xylem at an early age—the central alternate group and a group at the most remote point of each wing. This feature of *C. arborea* and the persistence of the four phloem groups in *C. sesquiorgialis* suggest the possibility of tetrarch allies.

Capparis inermis and *C. rupestris*. These species are good examples of the type.

The cohort of the Rhoeadales as judged by some thirty-five species thus presents very uniform features in its seedling anatomy. The only suggestions met with of departure from this uniformity are in the neighbourhood of the Brassicas and in the Cleomes. In the first a tendency to the formation of lateral strands in the hypocotyl recalls forms in which a tetrarch root obtains (e.g. *Magnolia*), as also does the long separation of the phloem groups in the hypocotyl of *Cleome sesquiorgialis* and the marked production of protoxylem groups on the flanks of the double bundles of *Cleome arborea*.

TEXT-FIGS. 33, 34. 33, *Cleome sesquiorgialis*.
Nat. size. 34, *Capparis inermis*. $\times 2$.

¹ Loc. cit., 1911.

ROSALES.

The seedling anatomy of some forty species has been worked out, of which more than half belong to the Natural Order Rosaceae, while members of the Crassulaceae, Saxifragaceae, Pittosporaceae, Hamamelidaceae, and Platanaceae are included, together with a few species of the Leguminosae not recorded by Compton.

So far as our information goes, the Crassulaceae and Saxifragaceae are diarch, the Pittosporaceae and Hamamelidaceae tetrarch, while the Rosaceae

TEXT-FIGS. 35-37. 35, *Prunus spinosa*; 36, *Prunus avium*; 37, A and B, *Prunus persica*.
All nat. size.

and Leguminosae show both varieties of the cruciform type. The cohort also includes forms which are suggestive with regard to the possible relationships of the cruciform and diagonal types.

Rosaceae.

The members of the Spiraeoideae and Rosoideae, so far as examined, are diarch, the Prunoideae tetrarch, while within the Pomoideae both tetrarch and diarch forms are found, as well as hexarch and even octarch arrangements, which suggest a possible connexion with the diagonal type.

Prunoideae.

Prunus persica, *P. spinosa*, *P. Cerasus*, *P. avium*, and *P. amygdalus* var. *amara*. The five species of *Prunus* examined show the same hypocotyledonary structure, but with an interesting variant in connexion with the

cotyledon strands. The hypocotyl presents four protoxylem groups with or without tangentially developed metaxylem wings, according to age.

Alternating with the four protoxylem groups are four extended phloem masses, which in the upper part of the hypocotyl are twin groups. At the node the usual triad of xylem and two phloem groups pass out to form the double bundle of the cotyledon. In *Prunus amygdalus*, *P. amara*, *P. persica* (see Text-fig. 38), and *P. spinosa*, the intercotyledonary strands are continued upwards as the independent lateral bundles of the cotyledons (see Pl. L, Fig. 11 of *Magnolia*), but in *P. Cerasus* these are continuous with the flanks of the double bundle (see Pl. LI, Fig. 23 of *Althaea*).

TEXT-FIG. 38. *Prunus persica*. A, cotyledonary node; B, hypocotyl; C, root, enlarged. *cot*, *intercot* = protoxylem in cotyledonary and intercotyledonary planes, respectively.

Rosoideae.

Rosa rubiginosa and *R. polyantha*. The transition in these forms is of the simple diarch type. The insertion of the cotyledons at the node is slightly asymmetrical, being delayed on the side of the production of the first leaf. This asymmetry is reflected in that of the hypocotyledonary stele, which shows vascular elements continuous with those of the first leaf on one side of the emerging diarch plate. Complete root structure is present a short distance below the node, as in the members of the Rhoeadales and Ranunculaceae.

Rubus vestitus and *R. xanthocarpus*. The two species of *Rubus* examined show the usual formation of a diarch plate, with rather low insertion of plumular traces. The diarch plate has a characteristic form, being lignified in two bowed lines connected by the protoxylem groups. Lower down in the older seedlings the centre lignifies, so that the stele presents a curious protostelic xylem body, upon the periphery of which the two small protoxylem groups are scarcely visible. One individual of *R. vestitus* possessed intercotyledonary strands in the upper part of the hypocotyl which were continued into the cotyledons as single strands, one passing into the left side of one cotyledon, and the other into the right side of the opposite cotyledon. That is to say, each cotyledon has, in addition

to the central double bundle, *one* lateral which is on opposite sides in the two cotyledons. These laterals pass into the hypocotyl, where they persist lower down than the plumular tissue, but ultimately die out, and the root is diarch. This phenomenon is suggestive of tetrarch relationship.

Potentilla chrysantha and *P. fruticosa*. These species show the usual arrangement associated with the diarch type. The plumular traces, which are distinctly double, are inserted rather low down, and in *P. chrysantha* the cotyledon strands pass out asymmetrically into the base of the fused cotyledons.

Fragaria indica. The very slender seedlings of this species show similar features to those in the *Potentillas* described.

Geum canadense, *G. urbanum*, *G. coccineum*, *G. japonicum*, and *G. montanum*. Very slender seedlings possessing high transition and diarch root. In one individual of *G. canadense* an interesting variant was provided by the presence of a small strand in the intercotyledonary plane, which passed out as a single cotyledonary lateral.

Rhodotypus kerrioides. This seedling has a more robust habit, but it conforms in a general way to the diarch type. The process of root formation is, however, very much delayed throughout the long hypocotyl, and even much below the collet the root has a large central pith. The hypocotyl is characterized by four widely separated metaxylem masses lightly bridged in the cotyledonary plane by the protoxylem strands, and the general form is reminiscent of *Rubus*.

Spiraeoideae.

Spiraea callosa is an extremely minute form, showing the simplest possible production of a diarch root by the fusion of the double bundles at the cotyledonary node.

Exochorda grandiflora and *E. Albertii* possess far more robust seedlings than the *Spiraeas*, but the transition features are essentially the same. The details, however, recall slightly those of *Rubus* and *Rhodotypus*.

Pomoideae.

Pyrus communis, *P. Malus*, *P. Aria*, *P. Aucuparia*. These species present considerable variation, and furnish proof of the unimportance of the independence or non-independence of the laterals, since not only do both conditions occur within the genus as in *Prunus*, but even within the species, e. g. *P. communis*. The hypocotyl possesses four or six protoxylem groups with alternating phloem strands arranged in the usual triad manner. The group in the cotyledonary plane is continuous with the double bundle of the petiole as always, and the one intercotyledonary or two diagonal groups

are continuous either with the flanks of the double bundle (e. g. *P. Malus*, *P. Aucuparia*, and some individuals of *P. communis*), as in Pl. LI, Fig. 25 of *Althaea rosea*, or with independent laterals (e. g. *P. Aria*, and some individuals of *P. communis*), as in Pl. L, Fig. 10 of *Magnolia tripetala*.

The forms which have four groups of protoxylem in the hypocotyl possess a tetrarch root, e. g. *P. Aria*, while those which show six protoxylem groups in the hypocotyl may, or may not, reduce lower down. In one individual of *P. communis* both the intercotyledonary protoxylem group and the diagonal groups were present, and the root was heptarch, obviously through suppression of one diagonal pole of an octarch condition. It is noteworthy that these differences bear no obvious relation to habit of seedling, but would appear to depend upon some inner cause as to the nature of which one can, in the present state of knowledge, only speculate. *Pyrus communis* would seem to be by far the most variable species, but fewer individuals of the other forms have been examined.

The difference between tetrarchy and hexarchy is of the same order as the difference between fused and free laterals in the base of the cotyledon, since in the first case the lateral strands unite to form one pole of the root, as in *P. Aria* and some individuals of *P. communis* (cf. Pl. LI, Fig. 26 of *Althaea rosea*), or remain apart, as in other individuals of *P. communis*. This union or separation in the root, however, is not correlated with the union or separation of the strands in the base of the cotyledons, since all combinations occur, as will be seen by reference to examples and diagrams (Text-fig. 41).

Cotoneaster affinis. The hypocotyl shows the four groups of phloem with more or less metaxylem within, according to age. In the cotyledonary plane are the protoxylem strands. The usual triad passes out to the cotyledons, constituting the double bundle which at the node differentiates lateral strands on the flanks, that in some cases do not separate from the central bundle until some distance up the cotyledons. The diarch root is produced in a somewhat leisurely manner.

Crataegus Oxyacantha is very similar to *Cotoneaster*.

Saxifragaceae.

Saxifraga muscoides, *S. Aizoon*, *Heuchera alba*, *Philadelphus grandiflorus*. These are very slender seedlings with a very high transition to a diarch root.

Crassulaceae.

Sedum glaucum is a very swollen seedling with high transition to a diarch root.

Cotyledon orbiculare is another very globose form with extremely minute vascular strands which form a diarch root just below the node.

Pittosporaceae.

Sollya heterophylla presents in the main the usual features of the diarch form, but with very characteristic details. Thus the primary xylem is distributed in the double bundle at the base of the cotyledons in an unusually definite T-shaped manner. The protoxylem is completely exarch, and the arm of the T composed of a single file of centripetally developed elements which spread out left and right inside the phloem groups.

Pittosporum crassifolium. This species is noted for its polycotyledony. In the lower part of the hypocotyl are to be found four triad groups, which in the upper part pass out into the four cotyledons as their respective double bundles. The radial files of primary xylem are noticeable, but are not so marked as in *Sollya heterophylla*. The hypocotyledonary strands are continued downwards into those of a tetrarch root. On the periphery of the bundles opposite the protoxylems large secretory sacs are to be found.

In the tricotyledonary forms there is apparently fusion between two of the four vascular triads in the upper part of the hypocotyl, so that three double bundles pass out into the three cotyledons.

TEXT-FIGS. 39, 40. 39, *Sollya heterophylla*. $1\frac{1}{3}$ nat. size. 40, *Pittosporum crassifolium*. $\frac{1}{2}$ nat. size.

Hamamelidaceae.

Liquidambar styraciflua. The hypocotyl possesses the customary four strands. In the position usually occupied by the central protoxylem of the double bundle there is to be found a large secretory canal, so that the halves are completely separated from one another. In each cotyledon they form a double bundle only, differing from the usual arrangement in the presence of the large secretory canal in its centre, on either side of which a streak of crushed protoxylem is obvious. In the root the four xylem strands assume an even greater independence, each with a well-defined completely exarch protoxylem pole. Two phloem groups are present in the customary position, viz. in the intercotyledonary plane, and if it were not for the secretory canal in the cotyledonary plane the root would doubtless be diarch.

Platanaceae.

Platanus occidentalis and *P. orientalis*. The seedlings are remarkable for their slightness, in view of the habit of the adult plant. Although the root is ultimately diarch, the hypocotyl is characterized by the presence of

four phloem groups, which may probably be taken as an indication of tetrarch relationship.

Leguminosae.

Ceratonia siliqua, *Acacia dealbata* (see Compton¹), *Medicago marginata*, and *M. rutitexta*. These species show hypocotyledonary structure which is essentially similar to that of *Prunus persica*, that is to say, four protoxylem strands are present alternating with four phloem groups with metaxylem to the inside. These strands of phloem and metaxylem are more or less twin structures according to the individual. This difference corresponds to some extent to the degree of freedom of the lateral strands in the base of the cotyledon. Thus in *Ceratonia siliqua* they become independent at the node, while in the other species they are massed together at the node, so that these species conform to the 'Althaea' or 'Anemarrhena' type (see Pl. LI, Fig. 23). The root is tetrarch, as in so many Leguminosae.

The cohort of the Rosales may perhaps be said to present the widest range of seedling anatomy of the three cohorts considered in this paper.

It is impossible to assign a position to the tetrarchy of the Pittosporaceae without some knowledge of the origin of the four cotyledons.

If they are derived from the dicotyledonous condition, two methods are possible: (1) bifurcation of two original cotyledons; (2) suppression of internode between cotyledons and plumular leaves which, in the language of Hill and de Fraine,² have been thus 'promoted' to be cotyledons.

In the first case the tetrarchy would necessarily be a modification of diarchy, in the second case probably of tetrarchy.

I know of no morphological evidence bearing upon this question. So far as collateral evidence goes, the only other member of the Pittosporaceae examined, namely *Sollya*, is diarch, and the neighbouring order of the Hamamelidaceae shows in *Liquidambar* the curious separation of the halves of the cotyledonary strand by means of a secretory canal; it is probable therefore that *Pittosporum* shows that modification which leads to the production of poles in the diagonal planes (see *Calycanthus*).

Within the Rosaceae it is the Pomoideae section which includes the greatest range of type, the diarch forms of which might be accountable for on the habit hypothesis, but the variations in the genus *Pyrus* do not lend themselves to this interpretation. They illustrate very well the comparative constancy of the hypocotyl, which may be associated with very different arrangements in cotyledons and root.

¹ Compton, R. H.: An Investigation of the Seedling Structure in the Leguminosae. Journ. Linn. Soc. Bot., vol. xli, 1912.

² Hill and de Fraine: On the Seedling Structure of Gymnosperms, II. Ann. Bot., 1909, vol. xxiii.

TEXT-FIG. 41.
Diagrams illustrating principal types of vascular arrangement in cotyledons, hypocotyl,
and root of Rosalean forms.

DISCUSSION OF RESULTS.

No attempt will be made in this paper to discuss at length the various aspects of seedling anatomy, but I shall rather concern myself with pointing out the immediate problems suggested by a consideration of the forms herein described.

A review of these species alone would of necessity raise several very pertinent questions.

The universality of the vascular unit of the hypocotyl, which in the cotyledonary plane is continued upwards as the 'double bundle' and in the intercotyledonary plane as two separate strands, forces itself upon one's attention.

If the position in the hypocotyl be regarded as an inevitable stage of transition from leaf to root, to which view the examination of the strands from above downwards predisposes us, we are confronted with the necessity of accounting for the difference in behaviour between the central and lateral strands. Why do not the lateral strands of the cotyledons behave in the same way as the central strand, i. e. each 'form' or relate to a root pole, instead of combining with another to do so, and if root structure is 'carried up' in the central bundle, why not in the lateral strands also?

If with Chauveaud we regard the root as of paramount importance, to which I cannot but think the examination from root upwards inclines us, we tend to become overpowered by conceptions gained from a consideration of root structure, and while these offer a very plausible explanation of the arrangements met with in the diarch type, many difficulties arise in connexion with the tetrarch type. For instance, M. Chauveaud's¹ very happy suggestion (abundantly supported in his own work) that there is a primary phase of the young seedling characterized by alternate or, as he regards it, 'root' structure throughout the plant, while doubtless largely true of diarch forms, breaks down according to his own showing in connexion with tetrarch forms, the intercotyledonary root poles of which are, according to M. Chauveaud, continuous with the 'éléments superposés' of the lateral strands of the cotyledon. M. Chauveaud does not discuss this type in relation to his interesting hypothesis, but it presents the stumbling-block here, as also in connexion with the views of Lee, Hill and de Fraine, &c. By implication Chauveaud would seem to agree with these latter authors in regarding the diarch condition as the more primitive.

Sargent and Compton, on the other hand, as the result of their investigations of monocotyledonous and dicotyledonous forms respectively, sum up in favour of the tetrarch condition as being the more primitive, at any rate for the forms examined. As Compton associates tetrarchy with the arboreal and diarchy with the herbaceous habit, and holds that the arboreal

¹ Loc. cit., 1911.

habit is primitive for Angiosperms, he may be said to be in favour of tetrarchy in general as being more primitive than diarchy. Miss Sargent¹ in 1903 presented a well-reasoned statement in support of her view that the varieties of seedling anatomy met with in the Monocotyledons were derived from a tetrarch condition, and pointed out that there were suggestions of this condition in the Ranunculaceae, which also furnished so many other points of similarity with the Monocotyledons. I agree with Mr. Tansley, who pointed this out in his criticism of the hypothesis that the elements instanced in *Eranthis* in support of the presence of tetrarchy are probably secondary. Nevertheless the work of the last ten years has shown that the tetrarch condition is to be found very widely in the Dicotyledons, forming about 50 per cent. of the Leguminosae and about the same of all known forms of the Rosales. Similar very rough calculations reveal some 30 per cent. in the Cactaceae and in the Compositae, 15 per cent. in the Ranales, 11 per cent. in the Tubiflorae, 6 per cent. in the Centrospermae, while none at all have been recorded either in the Piperales or in Rhoeadales.

As the total percentage of tetrarch forms recorded in these groups taken together is about 30 per cent., we see that the Cactaceae and Compositae present about the average distribution of the types, the Rosales have an excess of tetrarch forms, the Ranales, Tubiflorae, and Centrospermae an excess of diarch, while the Piperales and Rhoeadales so far as known are exclusively diarch.

These figures of course count for very little in view of the comparatively few forms described (about five hundred in the cohorts enumerated) and their unequal representation of groups, due to the practical difficulties of obtaining the most desirable forms. Thus the preponderance of Ranunculaceae in the Ranalean species recorded in this paper and the comparative fewness of the representatives of the other families probably account for the low percentage of tetrarch forms.

The existence of the tetrarch condition within the Ranales—as recorded in this paper—as well as the prevalence of the type in other parts of the Natural System, notably in the Rosales, removes any special importance that may seem to have attached to *Eranthis* and places the connexion between the seedling anatomy of Monocotyledons and Dicotyledons on a broader basis. Furthermore, the ‘Anemarrhena’ variety of the tetrarch form is quite common in Dicotyledons (witness *Berberis Lycium* and *B. aristata*, *Laurus*, *Prunus Cerasus*, *Pyrus Malus*, *Medicago*, &c., described in this paper), and no special significance such as has been claimed by de Fraine and Lee attaches to its existence in the Cactaceae and Tubiflorae.

In addition to these definitely diarch and tetrarch forms there are a number of intermediate conditions recognized as such by Compton in the

¹ Loc. cit.

Leguminosae and by Lee in the Compositae. Such forms are to be found in the groups described in this paper (e. g. *Liriodendron*, *Decaisnea*, &c.), even in the Ranunculaceae, and I am in complete agreement with Lee when he says, 'Although there are two extremes—diarch and tetrarch—all stages from the one to the other have been described in the preceding pages,'¹ and what is true of the Compositae is true, I think, in general. It is interesting, however, to note that while Compton and Lee agree as to the close connexion between what I have termed the diarch and tetrarch varieties of the cruciform type, they differ fundamentally as to the relative primitiveness of these conditions. While Compton pronounces in favour of the primitiveness of tetrarchy, Lee regards the seedling anatomy of the Composites as founded upon the diarch condition, the tetrarch and the intermediate forms being produced in relation to size of seedling and other factors.

It should be clearly borne in mind that the intermediate cases instanced

Cruciform Type – Diarch variety

TEXT-FIG. 42.

by me in 1907—of which Mr. Lee says, 'If there are cases, as Miss Thomas assumes, where the tetrarch structure is becoming reduced to diarch'—fall within precisely the same category of phenomena as those of which he remarks, 'There are as certainly seedlings in which the diarch structure is giving place to tetrarch'.² It is important that it should be fully realized that there is only one set of phenomena in question, but of these there are two distinct interpretations.

Mr. Lee's conclusion that 'tetrarchy and diarchy have probably been interchanged several times during the evolution of Angiosperms' is quite unnecessary if, as seems indicated, he suggests it to account for different phenomena, but it may well take its place as a useful and suggestive contribution to the theory of the subject. His view would seem to be that the process of evolution of the diarch and tetrarch forms is a 'reversible one'. This is a tenable hypothesis if we can with any measure of plausibility deduce a reasonable concept of the components, even though the factors directing the action $\rightarrow$ or $\leftarrow$ await discovery. One thing is certain, that we

¹ Loc. cit., p. 323.

² Loc. cit., p. 325.

cannot regard the cotyledonary strands as the fixed quantity which, when present, will produce a certain type of root. That is to say, there is no inevitable connexion between the presence or absence of lateral strands and the possession of a tetrarch or diarch root respectively. The figures and diagrams in this paper demonstrate this point. When absence of free laterals is correlated with tetrarchy we have the so-called 'Anemarrhena type'; when laterals are present, although the root is diarch, they may perhaps be regarded as an indication of tetrarch affinity, since this feature is most commonly found in the allies of tetrarch species.

The factors which control the freedom or aggregation of the lateral strands of the cotyledon petiole are probably capable of elucidation, and there is a fairly obvious correlation between this anatomical feature and the morphology of the cotyledons, particularly with regard to their insertion. The factors which control the production of a tetrarch or of a diarch root are more difficult of analysis. It is probably true that there is a broad correlation between habit of seedling and root anatomy, but the

Cruciform Type - Tetrarch variety

TEXT-FIG. 43.

connexion is by no means close or universal. Thus comparison of the habit of the seedlings of the tetrarch and diarch species of *Berberis* and of the *Magnolias* reveals no obvious difference and it is interesting to note that among the *Cactaceae* the normal and comparatively slender seedlings are tetrarch, while the swollen much modified forms are diarch. Lee remarks upon this lack of direct correlation in the *Compositae*, and numerous other instances could be furnished.

The root symmetry is undoubtedly affected by local as well as by more fundamental causes. Thus many authors have recorded cases of reduction from the tetrarch to the diarch condition in the apical region of the individual, and an increase in poles may also occur, but not so commonly. (See Hill and de Fraine on Classification of Seed-leaves.¹)

The anatomy of the hypocotyl, however, is frequently practically

¹ Ann. Bot., vol. xxviii, 1914.

identical in closely allied tetrarch and diarch forms, and has more in common in the majority of seedlings than has the anatomy of the cotyledons or of the roots (compare *Magnolias* and *Liriodendron*, *Berberis* sps.). The hypocotyl shows a varying number of primary centres of xylem which alternate with two phloem groups and from which differentiation proceeds in a more or less tangential direction on either side. These triads¹ recall the 'divergeant' of Bertrand and Cornaille,² and they seem to constitute the units upon which the vascular system of hypocotyl, cotyledons, and root (perhaps also that of the plumular leaves, example *Draba*) is built up. They may pass out into the leaves practically unaltered and downwards into the root with very little change, but they may be very seriously modified by more or less unknown causes. The arrangement in the hypocotyl does not suggest to my mind *root* anatomy as it does apparently to M. Chauveaud, but rather a stele of a less specialized character more comparable to the structure of the stem axis of primitive cryptogams both living and extinct. Thus it has the essentials of the exarch to mesarch solid or hollow steles of the Osmundaceae, &c., and the leaf-traces passing off from it are also suggestive of those of the primitive forms. The three centres of xylem differentiation so often seen in the 'double bundle' of Phanerogams render this leaf-trace remarkably like the leaf-trace of *Osmunda regalis* (see Bertrand),³ if we neglect the internal phloem of the latter.

Our knowledge of the more primitive Spermatophytes, living and extinct, points to the probability of the ancestral Spermatophyte having been a plant of robust organization with large seeds.

This inclines one to the view that not only is the tetrarch condition probably relatively primitive, but that it is very possibly itself derived from a larger plan such as we see in some of the *Pyrus* forms, in *Laurus nobilis*, and in certain Amentiferae. The suggestive Cryptogamic characters of the hypocotyl are, however, independent of number and size, and are seen in the slenderest forms, the larger ones possessing a greater number of units which are the triads similar to the 'divergeants' of Bertrand and Cornaille.⁴

Several authors have decided that seedling anatomy is of no phylogenetic importance, by which apparently they mean that it does not furnish sharp taxonomic characters. The phenomena upon which they have fixed their attention, namely, the broad features of transition and particularly the polarity of the root, are not, I think, likely to do so; but there are small characters indicative of relationship which become familiar to the worker,

¹ The presence of isolated protoxylem elements in the upper part of the hypocotyl of *Calycanthus*, *Ricinus*, and other forms in which the hypocotyl appears to have a modern stem structure points to the derivation of this form from the structure described.

² Bertrand, E. C., and Cornaille, F.: *La masse libéro-ligneuse élémentaire des Filicinées actuelles*. Trav. et Mém. de l'Univ. de Lille, vol. lx, 1902.

³ Bertrand, P.: *Progressus*, Bd. 4, Heft 2, 1912.

⁴ Loc. cit.

and which, when subjected to a careful analysis, might prove of some taxonomic value. The phylogenetic aim of recent work I conceive to be something much broader, and I think the results already obtained, which I will not attempt now to summarize or analyse, fully justify the labours and the hopes of the earlier workers. It seems possible that data such as that supplied by Lee on the Composites may one day be enhanced in value by statistical and experimental work, the need for which is so rightly laid stress upon by Compton and by Hill and de Fraine.

BEDFORD COLLEGE,
LONDON.

EXPLANATION OF PLATES L AND LI.

Illustrating Miss E. N. Thomas's paper on Seedling Anatomy of Ranales, Rhoadales, and Rosales.

PLATE L.

Anemone coronaria.

- Fig. 1. Outline of seedling. Natural size.
- Fig. 2. Base of cotyledonary tube of same. $\times 167$.
- Fig. 3. Hypocotyl. $\times 427$.
- Fig. 4. Root. $\times 427$.

Liriodendron tulipifera.

- Fig. 5. Outline of seedling. Natural size.
- Fig. 6. Outline of transverse section of base of cotyledons. $\times 50$.
- Fig. 7. Hypocotyl. $\times 300$.
- Fig. 8. Root. $\times 427$.

Magnolia tripetala.

- Fig. 9. Outline of seedling. $\times \frac{2}{3}$.
- Fig. 10. Outline of transverse section of cotyledonary node. $\times 30$.
- Fig. 11. Hypocotyl showing crushed protoxylem. $\times 167$.
- Fig. 12. Root. $\times 200$.

PLATE LI.

Iberis tenerea.

- Fig. 13. Outlines of bases of cotyledons. $\times 50$.
- Fig. 14. Details of bundle of 'north' cotyledon of same. $\times 253$.
- Fig. 15. Hypocotyl showing disorganizing protoxylem. $\times 253$.
- Fig. 16. Root of same. $\times 253$.

Cheiranthus Cheiri.

- Fig. 17. Seedling. Natural size.
- Fig. 18. Outlines of cotyledon bases. $\times 50$.
- Fig. 19. Bundle of 'south' cotyledon showing crushed protoxylem. $\times 427$.
- Fig. 20. Hypocotyl with crushed protoxylem. On the left is one lignified plumular element (*p.*). $\times 427$.

Althaea rosea.

- Figs. 21 and 22. Seedlings. Natural size.
- Fig. 23. Outline of cotyledon bases. $\times 30$.
- Fig. 24. Details of bundle of 'north' cotyledon of same. $\times 253$.
- Fig. 25. Hypocotyl with median (*cot.*) and lateral (*int.*) protoxylem groups. $\times 253$.
- Fig. 26. Root. $\times 253$.

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Figs 13-16, *Iberis tenerea*: 17-20, *Cheiranthus cheiri*: 21-26, *Althaea rosea*.

Thomas, Ethel N. 1914. "Seedling anatomy of Ranales, Rhoeadales, and Rosales." *Annals of botany* 28, 695–733.

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