An Anatomical Study of Syncotyly and Schizocotyly.

BY

R. H. COMPTON.

With forty-one Figures in the Text.

INTRODUCTION.

ONE of the most momentous events in the history of Systematic Botany and Phylogeny was the perception by Andrea Cesalpini (1583) of the fundamental importance of characters of seed and embryo in plant classification. John Ray's division of the Flowering Plants into Dicotyledons and Monocotyledons (1686-1704) has been the basis of the systematic study of Angiosperms ever since. The success of this primary division is perhaps due to the fact that characters which appear early in ontogeny are on the whole more likely to indicate remote ancestral affinities than those which develop later. The same cause has led to the modern reawakening of interest in seedling structure. In the vexed question of the origin of the Monocotyledons seedling characters have been the main point upon which attention has been focused.

The admirable simplicity of the classification of Angiosperms according as they have one cotyledon or two could not in the nature of things but be disturbed at some point. It was found that certain undoubted Dicotyledons had no seed-leaves recognizable as such; others had only one cotyledon; and others again had several; while in the Monocotyledons the question was often—and still is—what form has been taken by the cotyledon which we assume to be present. Moreover, teratologists found that material was provided them by seedlings just as by all other plant structures. Sometimes a seedling of a Dicotyledonous species was found to have but a single seed-leaf; sometimes it had three or four, or the cotyledons were lobed to a greater or less depth.

It is with this last class of variation that I propose to deal in the following paper. The study of teratology is full of intrinsic interest and is often of great value in elucidating obscure morphological problems. The question as to the modes of increase and decrease in number of cotyledons is of such great phylogenetic importance that one is impelled to investigate

cases in which the phenomena in question are taking place, so to speak, before our eyes. Moreover, it is impossible to judge how much theoretical weight to attach to any phenomenon, teratological or otherwise, before it has been adequately investigated; and cases such as the present cannot be dismissed on *a priori* grounds.

The paper will consist of two parts: the first will deal with Syncotyly, the second with Schizocotyly.

SYNCOTYLY.

There exists a small and scattered literature on this subject, for the most part simply recording instances of the anomaly. The most important investigation of the phenomenon is that of de Vries,¹ who dealt with it from the point of view of its heritability. From the morphological and anatomical point of view, however, syncotyly has not been studied, so far as I know: it is from this standpoint that I have approached the subject, partly from its intrinsic interest and partly in the hope that it might shed light upon the origin of the Monocotyledons. The following pages are the results, at present very incomplete, of an examination of some cases of syncotyly: owing to the comparative rarity of the anomaly the research is necessarily prolonged, but the future may furnish fresh material for study and render possible an amplification of what can be written upon the subject at present.

I shall proceed to describe the structures which have been observed in the material available, and shall then enter into a discussion of certain problems arising out of the investigation.

SWAINSONA CADELLI (Leguminosae).

The anatomy of the normal dicotylous seedling of this species is described in my paper on the Leguminosae.² The root is triarch, and each cotyledon takes one whole root xylem united with half of the third intercotyledonary xylem bundle.

A single syncotylous seedling was examined, the two cotyledons being fused to the tips, with only a very shallow apical sinus marking the line of union (Fig. 1): a double system of vascular bundles was evident in the seed-leaf. The root was triarch, as in the dicotyl, and the whole process of transition took place in precisely the same way: the sole difference from the type being that both double bundles entered the single seed-leaf (Fig. 2). The subsequent branching and anastomosing of the bundles took place in the usual fashion.

This is an example of the simplest type of syncotyly, in which there is practically no modification of the vascular anatomy introduced by the lateral union of the two cotyledons, even though this be complete. The simplicity of the bundle system probably accounts for this. When we

¹ de Vries ('95, '11).

² Compton ('12^b), p. 44, and Pl. VI, Fig. 93.

examine other species with more complex vascular anatomy we find that fusion of cotyledons has led to reduction in the total vascular system of the seed-leaves, this being so pronounced in the more advanced cases of syncotyly as to affect the hypocotyl and root.

HELIANTHUS ANNUUS (Compositae).

The material examined was grown from seeds, provided by Professor H. de Vries, of a strain which produced from 50 to 95% of more or less syncotylous seedlings.¹

The seedlings showed a great range of variation from normal dicotyls to syncotyls with completely fused cotyledons and to amphisyncotyls. The syncotylous seedlings were all more or less dwarfed and grew irregularly, the plumule having much difficulty in developing.

The vascular anatomy showed a corresponding range of variation, and several examples must be described.

Dicotyls. The anatomy of very young seedlings has been described by Chauveaud.² The older stages of development were studied by Reinke,³ whose description the present author is able to confirm. For the sake of convenience and completeness the dicotylous structure will here be described, especially as certain new points can be included.

The root is tetrarch, there being a solid four-rayed xylem star without pith, and four phloem groups alternating with the protoxylems. The xylem is usually somewhat irregular, owing to the abundance of lateral roots (Fig. 3). The transition changes begin at a low level in this massive seedling, the pith appearing in the midst of the xylem at about 1 cm. below the collet. The pith rapidly enlarges, and dilates the xylem into the form of a ring which soon opens on one side, the corresponding phloem dividing into two at the same time. Thus at 3 mm. below the collet there is a C-shaped band of xylem with four protoxylems, and five phloem groups (Fig. 4). The xylem-band then begins to break up into detached pieces in the way indicated by the dotted lines in Figs. 4 and 5: the result being the production of two triads, each consisting of a median protoxylem and a pair of lateral metaxylems, and each destined to become the middle vein of one cotyledon; and also of two curious bundles, each consisting of a single metaxylem group with a laterally attached protoxylem, these later dividing and becoming the lateral veins of the two cotyledons. There are now six phloems, one superposed upon each metaxylem (Fig. 6). It is seen that the opening of the xylem-ring on one side only and the formation of a C-shaped band is merely a precocity; and at the level of the collet the vascular system has again become practically symmetrical: this irregularity is, however, of fairly constant occurrence.

¹ de Vries ('95), where a number of seedlings are figured; and ('11), p. 466.

² Chauveaud ('11), p. 414.

³ Reinke ('71), p. 11.

Thus at the base of the hypocotyl there are constituted six collateral bundles of xylem and phloem, and the two small median polar protoxylems (Fig. 6). This condition persists to the summit of the hypocotyl, slight rearrangements in the xylem taking place with the result that each group becomes truly endarch.

In the upper half of the hypocotyl the plumular procambium appears in four tangential bands, each lying between a polar triad and one of the lateral cotyledon traces.

There is a short cotyledon tube, at the base of which the cotyledonary vascular system which has ascended from the root moves outwards, leaving the epicotyledonary procambium behind to pass up into the plumule. The two lateral bundles of the hypocotyl divide radially, and on the cotyledons separating, each takes half of each bundle as well as the main polar triad (Fig. 7).

The base of each cotyledon therefore contains (1) the triad or 'double bundle' (Fig. 8) derived from the whole of a root-xylem; this comprising two collateral bundles of metaxylem and phloem, and a few effete scattered protoxylem elements in between—the latter sometimes accompanied by a tiny detached group of phloem:¹ (2) two collateral bundles, one at each edge of the cotyledon, each derived from half a root xylem.

The cotyledons are slightly asymmetrical, one side being more curved than the other: the venation is shown in Fig. 9.

Syncotyls. There are many degrees of fusion of cotyledons, ranging from seedlings whose cotyledons are united by the petioles alone on one side, to those which have apparently a single broad cotyledon with a barely perceptible apical notch, but with a double vascular supply. Amphisyncotyls, i. e. seedlings whose cotyledons are united by both edges, also occur, but more rarely.

The vascular system varies with the degree of fusion of the cotyledons, and a series of cases will be described in order to illustrate the mode of variation.

Syncotyl A. The two cotyledons were only united for about 5 mm., and the structure was closely similar to that of a dicotyl. The chief differences are illustrated in Fig. 10. There is a slight asymmetry of structure at the node, the lateral strand which is on the open side of the cotyledon dividing radially earlier than the other. The two edges of the seed-leaf have thus a more complex vascular system than the space between the two double bundles at the same level (Fig. 11). Another point of difference, which, however, has no special connexion with the phenomenon of syncotily, is the presence of an additional collateral bundle in between one of the double bundles and a lateral cotyledon trace; this passes out into the cotyledon and divides with the other bundles, forming part of the

¹ Cf. *Lupinus* spp., Compton ('12^b), pp. 29, 79.

FIGS. 1-11. (Xylem cross-hatched, phloem clear.)

FIGS. 1-2. *Swainsona Cadelli*, syncotyl. 1. Syncotyl. 2. Trans. sect. base of seed-leaf.

FIGS. 3-11. *Helianthus annuus syncotyleus*. 3-9. *Dicotyl*. 3. Trans. sect. root. 4. Trans. sect. root 3 mm. below collet. 5. Trans. sect. at collet. 6. Trans. sect. 4 mm. above collet. 7. Trans. sect. just above cotyledonary node. 8. Trans. sect. cotyledon : the double bundle (triad). 9. Venation of one of the cotyledons. 10-11. *Syncotyl A*. 10. Trans. sect. at cotyledonary node (plumular xylems line-shaded). 11. Trans. sect. base of seed-leaf.

vascular supply of the lamina (Figs. 10 and 11). It is the same kind of accessory vascular strand which is of such frequent occurrence in *Phaseolus* spp., and which was called a 'Zwischenstrang' by Dodel:¹ these structures are often present in *Helianthus* also, and usually take their origin at a higher or lower level in the hypocotyl—frequently in the collet region.

Syncotyl B. In this seedling the cotyledons were fused together for about half their length (Fig. 12). The root was found to be triarch in the main, though towards the apex it became practically diarch by the disappearance of the protoxylem in the intercotyledonary plane. The triarch star became medullated in the usual way below the collet, and the xylem-ring opened out into the C-shape recorded for dicotyls, but with only three protoxylems: two of the phloems also dividing radially so as to produce five groups (Fig. 13). Just below the collet the xylem-ring broke into pieces as indicated by the dotted lines in Fig. 13, with the production of two ordinary triads (or double bundles) and a single asymmetrical lateral cotyledon trace (Fig. 14). That is to say, we have the dicotylous structure with the omission of one of the lateral cotyledon traces, viz. the one on the side of the axis on which the cotyledons had united. The condition of Fig. 15 was reached about 2 mm. above the collet and persisted through the greater part of the hypocotyl. In the upper part of the axis plumular bundles appeared, but no 'Zwischenstränge' were present in this seedling (Fig. 16). The single lateral cotyledon trace behaved in the same way, dividing between the two edges of the seed-leaf (Fig. 17).

Thus the first marked effect of syncotily on anatomy is simply the elimination of one of the two lateral cotyledon traces, and the corresponding reduction of the root stele from tetrarchy to triarchy.

Syncotyl C. The cotyledons were fused for about three-quarters of their whole length. The root was triarch and the general structure was very similar to that of Syncotyl B, except that through the greater part of the hypocotyl the adjacent metaxylems of the two double bundles were almost in contact with one another, their phloem groups not separating until just below the cotyledonary node. A further difference was the presence of an accessory cotyledon strand (cf. Syncotyl A).

Syncotyl D. The cotyledons were united to the tip, there being a scarcely perceptible sinus to mark the line of fusion. This seedling carried further the modification foreshadowed in Syncotyl C. The two adjacent metaxylems of the triads lay practically in contact from the root to some distance up the cotyledon lamina, and the superjacent phloem group remained entire throughout the axis (Fig. 18). The lateral cotyledon trace on the side away from the fusion occurred and behaved as usual.

Advanced syncotily thus results in considerable compression of the vascular system towards the line of fusion.

¹ Dodel ('72), p. 156; Compton ('12^b), p. 61.

Syncotyl E. Complete syncotyly obtained here, as in Syncotyl D, accompanied, however, by a further reduction. One of the triads had here lost the metaxylem group towards the line of fusion. Thus the seed-leaf traces consisted of (i) a normal 'double bundle'; (ii) a 'double bundle' with only one metaxylem group and a protoxylem; (iii) a lateral bundle; (iv) an accessory cotyledon trace (Fig. 19). The root was triarch, as usual in all except slight degrees of syncotyly. It is doubtful whether this asymmetrical elimination of a single metaxylem should be considered as a stage in the series of reductions and compressions following upon syncotyly; this was the only example of the kind seen, most of the advanced syncotyls approximating to type D.

Other Types of Structure. The syncotyls are frequently misshapen and twisted owing to difficulties in the process of extraction from the testa, growth inequalities, and, later, obstruction to the plumule. The anatomy often reflects these deformations, and examples were studied whose structure it was found impossible to relate to the normal syncotylous series. No useful purpose would be served by describing these seedlings, whose whole appearance was rather pathological than teratological.

In one seedling an accessory bundle ('Zwischenstrang') was prolonged downwards into the root, there giving rise to an additional xylem pole. This was in an example of advanced syncotyly whose root would normally have been triarch, but that the addition of the accessory strand rendered it tetrarch. A similar occurrence in a dicotyl would produce a pentarch root, and pentarchy has actually been recorded in *Helianthus annuus* by Kattein;¹ but in this case it appears that the accessory strand was fused with the adjacent lateral cotyledon trace.

The effects of syncotyly in *Helianthus annuus* are therefore as follows, according to the degree of fusion:

- (i) Retardation of division of the lateral cotyledon trace on the side of fusion.
- (ii) Elimination of this lateral cotyledon trace, reduction to triarchy.
- (iii) Compression of the triads towards the line of fusion.
- (iv) Partial union of adjacent triad metaxylems.
- (v) ? Elimination of one of the triad metaxylems towards the symphysis.

PRUNUS DOMESTICA.

Examples of dicotyls and syncotyls of certain cultivated Plums were given me by Mr. W. O. Backhouse, of the John Innes Horticultural Institute: these exhibit a state of affairs much the same as in *Helianthus annuus syncotyleus*. The dicotyl is tetrarch, and each cotyledon takes a median

¹ Kattein ('97), p. 129. The structure of tetrarch seedlings is also described, but no notice is taken of the median polar protoxylems of the triads.

triad and two edge-veins, each derived from half one of the intercotyledonary root-poles. Syncotyly results in a reduction to triarchy and the elimination of one of the lateral cotyledon traces, just as in *Helianthus*.

GENERAL REMARKS ON SYNCOTYLY.

A great number of dicotylous seedlings normally exhibit a small degree of syncotyly. This is a common occurrence in the Papilionatae, where the cotyledons are frequently united for a millimetre or two along the straighter edges—i. e. the edges against the accumbent radicle in the seed and opposite the first leaf (when unpaired). It is noteworthy that in many such cases among the Leguminosae the seedlings are triarch, and the vascular system is thus roughly similar in plan to that of a moderately syncotylous *Helianthus* such as Seedling B.¹ In the syncotyl of *Swainsona Cadelli*, indeed, we have a normally triarch structure remaining practically unaltered by the fusion. But we can hardly attribute triarchy to syncotyly in the Leguminosae, for the real problem in the case of small triarch seedlings is not the disappearance of one intercotyledonary bundle but the retention of the other; and this, as I have endeavoured to show elsewhere, is related to the useful supplementary function performed by the retained bundle in relation to the first primordial leaf.²

The chief interest of syncotyly is in relation to the vexed question of the origin of Monocotyledons. It is widely admitted that the forms with one seed-leaf have been derived from ancestors with two, and the problem is the method or methods by which this reduction in number has occurred. The two possible methods by which one seed-leaf may be derived from two are (1) by lateral fusion or syncotyly; (2) by the elimination or change in function of one cotyledon, or heterocotyly. Both these methods have been supposed to have taken place in various instances, and the rival schools, assuming monophyly of the Monocotyledons, have warmly debated the alternatives. One of the most recent presentments of the problem, however, is that of Lotsy,³ who considers that the Monocotyledons are at least diphyletic, and that both methods may have been adopted in different groups. Lotsy considers that the syncotylous origin of monocotyly is less well established than the heterocotylous, but that the former view derives support from the occurrence of syncotyly among undoubted Dicotyledons. He, indeed, regards the theory that the epiblast and the scutellum in the Gramineae are respectively equivalent to reduced and suctorial cotyledons as better supported than the syncotylous theory of the origin of monocotyledony. Here the present writer cannot follow Lotsy, having regard to the great diversity of opinion which still exists as to the morphology of the Grass embryo. But leaving this point on one side, if we accept the view

¹ Compton ('12^b).

² Compton ('12^b), p. 101.

³ Lotsy ('11), p. 624.

that the Spadicifloreae are derived from Dicotyledons of the Piperalean alliance, we may agree that monocotyly has here arisen in the heterocotylous fashion, as illustrated by certain geophilous species of *Peperomia*.¹ There remains the question of the origin of monocotyly in all the other Monocotyledonous orders, and here it appears that the theory of syncotyly has much to recommend it.

On the side of the Dicotyledons a large number of species are known in which fusion of cotyledons for a greater or less distance has undoubtedly occurred, and is a constant feature of the seedlings. The theory of syncotyly, as expounded by Miss Sargent,² is largely based on the resemblances in anatomy between such normally syncotylous Ranunculaceae and *Aemarrhena asphodeloides* among the Liliaceae. The syncotyly usually takes the form of the production of a long cotyledonary tube, through the base of which the plumule breaks; but in *Ranunculus chius* the fusion is along one margin only.

In studying such anomalous Dicotyledons comparison can only be made with other related species with two seed-leaves. The advantage of an examination of teratological syncotyls lies in the facts that we can compare them with normal dicotyls of the *same* species, and that a series of degrees of syncotyly can be studied. Unfortunately the material is necessarily scanty, except in such a case as de Vries's *Helianthus annuus syncotyleus*, which throws a high percentage of syncotyls. The criticism that such abnormalities are of no significance will be dismissed by serious students of teratology.

It is hoped that as time goes by it will be possible to obtain further examples of syncotyly to supplement the present account. Imperfect though this is, it throws a certain amount of light on the main problem.

In the first place, syncotyly, when it occurs, is a symmetrical process, both cotyledons taking an equal part in the production of the single seed-leaf. The vascular system, as would be expected, is also symmetrical about the plane in which the fusion takes place, i. e. the intercotyledonary plane, though in no other. In *Swainsona Cadelli* the fusion has no marked effect on the vascular system. This is also the case apparently in *Ranunculus chius*, a normally syncotylous species, as compared with other Ranunculaceae;³ but it is noteworthy that *Ranunculus Ficaria*, which Miss Sargent regards as a syncotyl, differs markedly from *R. chius*, the only other syncotylous species of the genus examined. In *R. chius* the two cotyledons each send a double bundle into the diarch root, the two cotyledonary systems being independent of one another. In *R. Ficaria*, on the other hand, the bilobed seed-leaf only sends one double bundle⁴ into the root, this

¹ A. W. Hill ('06).

² Sargent ('03), p. 66; and ('08).

³ Sargent ('03), p. 65.

⁴ Some of Sterckx's specimens also had lateral petiolar bundles in addition to the midrib (Sterckx ('99), p. 45).

being derived equally from the two similar lobes of the seed-leaf and from its midrib; the second xylem pole of the diarch root is plumular. The conclusion seems to be that the single seed-leaf of *R. Ficaria* represents a single cotyledon; the fact that it is bilobed cannot by itself be held to indicate syncotyly, for this phenomenon normally occurs in both cotyledons of other species of dicotyls, though there is nothing to suggest their derivation from tetracotylous ancestors (e.g. *Raphanus sativus*, *Eucalyptus orientalis*, *Eschscholtzia californica*,¹ *Schizopetalon* spp., &c.). Moreover, the venation of the seed-leaf of *R. Ficaria*, on which Sterckx lays such stress as being distinct from that of the forked cotyledon of *Raphanus sativus*, is not characteristic of syncotyls; indeed, it can be closely paralleled among hemitri- and hemitetracotyls such as those of *Cannabis sativa* and other species described in another part of the present paper. The presence of a median commissural nerve in the great majority of the seedlings of *R. Ficaria* which I have examined and some of those figured is no argument for either theory, for this may occur in both syncotyls² and in schizocotyls;³ but in specimens of *R. Ficaria*, in which there is scarcely any lobing, the midrib is conspicuous and the venation is on the same general plan as that of the foliage leaves, allowing for differences of shape. There is nothing in the embryogeny of *R. Ficaria* to indicate which method of reduction was adopted; and, as a matter of fact, Hegelmaier⁴ and Schmid⁵ assume the heterocotylous, Sterckx⁶ the syncotylous theory, without entertaining the other alternative.

On the whole the tendency of the evidence seems to be in favour of the view that the seed-leaf of *R. Ficaria* represents a single cotyledon; whether the second ancestral cotyledon has been completely aborted, as contemplated by previous authors, or whether it has been retarded in development and now appears as the first foliage leaf⁷ are subsidiary questions which cannot be considered further here.

If we therefore omit *R. Ficaria* from the list of normal syncotyls we are left with two species only, in which there is pronounced cotyledonary fusion along one edge alone. These are *Ranunculus chiensis*, of which Miss Sargent saw three specimens; and perhaps *Anemone apennina*, as to which, however, the contradictory statements of Sterckx⁸ leave the facts in some doubt. The production of a long cotyledonary tube and its rupture by the plumule are frequent, and may perhaps be compared to

¹ Kerner and Oliver ('02), p. 621.

² Winkler ('84), p. 39.

³ e.g. in some specimens of *Cannabis sativa*.

⁴ Hegelmaier ('78).

⁵ Schmid ('02), p. 211.

⁶ Sterckx ('99), p. 42.

⁷ The second alternative is supported by the facts that (i) 180° separates seed-leaf and first foliage leaf—an argument used by Miss Sargent ('08, p. 157) for syncotyly. (ii) The first foliage leaf trace forms one protoxylem pole of the diarch root, the seed-leaf trace forming the other. (iii) Retardation of development is a marked feature of the embryogeny of *R. Ficaria*, as of the other pseudo-monocotyledons *Corydalis cava* and *Carum Bulbocastanum*.

⁸ Sterckx ('99), pp. 34, 80.

teratological amphisyncotyly; but the ordinary form of syncotyly occurring as an abnormality in apocotylous species appears to be extremely rare as a normal feature.

A noteworthy feature of practically all the tube-forming species on record is that the seeds are 'albuminous'; the embryo is small, usually straight, and develops in a homogeneous medium, the endosperm.¹ Embryogeny is likely to be symmetrical under such conditions; and whether or no the presence of endosperm is conducive to concrescence of cotyledons, it seems probable that if such concrescence occurred at all it would affect both edges of the cotyledons equally. The rarity of one-sided syncotyly as a normal feature is therefore intelligible.

On the other hand, a remarkable feature of the species which are normally apocotylous, but occasionally produce syncotylys, is that the great majority of them have 'exalbuminous' seeds.² The normally monocotylous Dicotyledons, about which there is doubt as to the means of reduction, are largely exalbuminous, and in many of these the probabilities are apparently in favour of a heterocotylous origin.³

The conclusions which may be drawn from these facts are—

1. Syncotyly occurs in a great variety of species, normally or teratologically.
2. In species with albuminous seeds syncotyly usually gives rise to a symmetrical cotyledonary tube.
3. In species with exalbuminous seeds syncotyly is usually asymmetrical, the cotyledons uniting along one edge only.
4. The reason for (2) is probably the homogeneity of the surroundings of the embryo before germination, for (3) the asymmetry of its environment which produces accumbency and other irregularities.

Leaving on one side the Spadicifloreae whose monocotyly is very possibly heterocotylous, there can be little doubt that the Helobieae include those Monocotyledons which are most closely allied to such admittedly

¹ The only exceptions to this rule in the long lists of tube-forming Dicotyledons given by Holm ('99, p. 422) and Miss Sargent ('03, p. 73) are *Serratula radiata*, *Limnanthes Douglasii*, *Cardamine* spp., and perhaps *Megarrhiza californica*. (See Sargent, ('03), p. 83.)

² An examination of the species mentioned by de Vries ('11, p. 457 et seq.) and other authors as yielding occasional syncotylys reveals the fact that out of about *thirty-seven* species in which the anomaly is known to occur only the following six have the embryo surrounded by endosperm in the seeds: *Silene hirsuta*, *Phacelia tanacetifolia*, *Anagallis grandiflora*, *Polygonum Fagopyrum*, *Mercurialis annua*, *Urtica dioica*.

Syncotyly is also recorded in Coniferae, often accompanying polycotyly. The most striking example was observed by T. G. Hill and de Fraine ('08, p. 706) in a seedling of *Widdringtonia Whytei*, whose two cotyledons were fused nearly to their tips—a feature which the authors compare with the double needle of *Sciadopitys*. The anatomy was unaffected.

³ See Miss Sargent's list ('03, p. 76). Abortion or displacement of a cotyledon seems to have been the probable cause in the *Corydalis* spp., *Ranunculus Ficaria*, *Carum Bulbocastanum*, *Pinguicula* spp., and *Abronia* spp.

primitive Dicotyledonous families as the Ranales, and are most probably, therefore, themselves primitive as compared with other Monocotyledonous families. The Helobieae are, however, remarkable among Monocotyledons in possessing exalbuminous seeds. The Ranales, on the other hand, are typically albuminous. No order of Dicotyledons yields so many tube-forming syncotyls as the Ranales, and we may perhaps expect a similar tendency to apply all through the Ranales-Helobieae alliance. Now we have seen that syncotyly in albuminous species usually produces a cotyledonary tube, but that in exalbuminous species the cotyledons tend to fuse on one side only. It is therefore probable that if the Helobieae are descended by syncotyly from exalbuminous dicotyls, the fusion of cotyledons would take place along one edge, and we should obtain an embryo symmetrical about one plane only, and not about two, as in the tube-forming Ranales. This form of embryo is what we actually find in the Helobieae—and, indeed, in the more advanced Monocotyledons generally, where the asymmetric condition may well persist in spite of endosperm in the seeds.

We may conclude that (i) syncotyly is a single phenomenon wherever it occurs, whether affecting one or both edges of the cotyledons; the differences being due to space and symmetry relationships within the developing seed. (ii) Since one-sided syncotyly is the form produced in exalbuminous seeds, this is what would be expected to occur in the primitive and exalbuminous Helobieae if that family had adopted syncotyly. (iii) The Liliifloreae, which according to modern views are very possibly derived from plants sharing many characters of the Helobieae, have retained certain primitive features, and among them tetrarchy and a seed-leaf with two equal vascular bundles as in *Anemarrhena*, though not in the majority of species.

Syncotyly has a more or less pronounced influence upon the vascular structure according as the typical anatomy is complex or simple. In the Ranunculaceae the structure of apocotylous and syncotylous species is closely similar, the diarch root and two double-bundles in the cotyledon occurring throughout; this is so whether a tube be present, as in most syncotylous species,¹ or whether syncotyly be one-sided, as in *Ranunculus chius*.² The same is true of the relatively simple *Swainsona Cadelli*, where, be it noticed, the base of the seed-leaf only contains two vascular strands, though the root is triarch. In the larger species, such as *Helianthus annuus* and *Prunus domestica*, where lateral cotyledon traces are present, syncotyly leads to elimination and compression of vascular bundles, together with reduction in the type of symmetry in the root.

The '*Anemarrhena* type' of vascular structure is characterized by the

¹ Sterckx ('99).

² Sargent ('03), p. 65.

possession of two vascular strands in the single seed-leaf giving rise to tetrarchy in the root. This type has also been found (with slight modifications) in certain Dicotyledons—viz. *Eranthis hiemalis*¹ and several Cactaceae.² The derivation of this type of structure from the stable tetrarch type found in large seedlings seems to have taken place by the crowding together of the double bundle and the two lateral bundles of each cotyledon into a single median vascular strand, the tetrarchy of the root remaining unaltered.³ If the hypothetical dicotylous ancestors of *Anemarrhena* had such a compressed vascular system we should expect that syncotyly would not modify it greatly; the fact that other tetrarch seedlings show a reduction to triarchy through syncotyly cannot be maintained as an argument against the structure of the tetrarch *Anemarrhena* being produced by these means. In *Helianthus* and *Prunus* syncotyly is superposed on a complex cotyledonary vascular system, and reduction follows. In *Anemarrhena* (as in the instructive Leguminous *Swainsona Cadelli*) simplification of structure had occurred prior to syncotyly, and no further reduction is produced by fusion.

A feature of syncotylous anatomy which may be mentioned here is its similarity in some respects to the structures produced by longitudinal splitting of cotyledons. This parallelism between fusion and fission will be further discussed under Schizocotyly (p. 819).

Finally, there is evidence of the hereditary nature of syncotyly in *Helianthus annuus*, of which de Vries⁴ cultivated an intermediate race (or ever-sporting variety) yielding from 50 to 95 per cent. of syncotylys. It appeared probable that similar races could have been isolated from *Mercurialis annua* and *Centranthus macrosiphon*, and also, perhaps, from some other species. A pure-breeding syncotylous variety, however, was not obtained, even after selection through ten generations. Thus there remains some doubt as to whether this teratological syncotyly can be considered as a parallel with that which occurs as a normal feature in so many Dicotyledons, and which it is thought gave rise to monocotyly in *Anemarrhena* and its allies.

SCHIZOCOTYLY.

Seedlings with more than two cotyledons are a normal feature in many Gymnospermae, and the question as to the primitiveness or the reverse of polycotyly has given rise to much discussion.⁵ In the Angiosperms the phenomenon of polycotyly is extremely rare, being apparently confined to

¹ Sargent ('03).

² de Fraine ('10).

³ An intermediate condition is very frequent among Leguminosae (Compton ('12^b)).

⁴ de Vries ('95); ('11), p. 466.

⁵ Duchartre ('48), Dangeard ('92), T. G. Hill and de Fraine ('08-10) taking the view that dicotyly is primitive; Sachs ('82), p. 507, Masters ('91), Dorety ('10) holding the reverse view; Coulter and Chamberlain ('10) considering that 'the question is an open one'.

certain species of *Perseonia* (Proteaceae), *Nuytsia*, and *Loranthus* (Loranthaceae).¹ Other reputed examples have proved to be instances of deeply bifid cotyledons. The view that dicotyly is primitive in Gymnosperms and Angiosperms alike attaches much importance to the occurrence of bilobed seed-leaves; thus Hill and de Fraine² consider that in Conifers 'the polycotyledonous condition has been derived from the dicotyledonous condition, in the vast majority of cases by the splitting of the seed-leaves and by the promotion of cotyledons from a lower to a higher rank'. Fletcher also takes the same view for *Perseonia* and *Nuytsia*.³ The reverse view either takes no account of these abnormalities or regards them as stages in fusion rather than fission.

The cases of teratological schizo- and polycotyly, which will be considered below, are of interest from whichever point of view we regard the phylogenetic problem. If dicotyly be primitive they afford an instructive parallel to the course of evolution of polycotyly; if dicotyly be a derived condition these teratological seedlings may be regarded as reversions to a more primitive type.⁴

A few examples of polycotyly among normally dicotylous species have been studied anatomically, the investigators relying on chance specimens. I have been so fortunate as to receive from Professor H. de Vries a number of packets of seed of several of his schizocotylous races; and although this seed was mostly harvested in 1894, the year when he discontinued his breeding experiments on these races, a large percentage of most of the species germinated and yielded abundant material, exhibiting all degrees of the abnormality. It is mainly on this material, for which, as well as for seed of *Helianthus annuus syncotyleus*, my warm thanks are due to Professor de Vries, that the following statements are founded.

I shall proceed to give some details of the structure of certain schizocotyls, following this by a discussion of the problems of polycotyly.

CANNABIS SATIVA (Urticaceae, or Moraceae).

Dicotyls. The hypocotyl is from 6 to 9 cm. long and 0.9 mm. in diameter throughout: the cotyledons are oblong-ovate, 11 by 5 mm.; their venation varies considerably, but usually there is a well-marked midrib in the basal half which may or may not be prolonged to the apex (Fig. 20).

The root has a continuous diarch xylem-plate flanked by two bands of phloem (Fig. 21). The xylem-plate begins to divide transversely at the collet and the phloems divide simultaneously: half-way up the hypocotyl the condition shown in Fig. 22 is attained. This slowly changes, triads being formed about three-quarters up the hypocotyl (Fig. 23), and each

¹ Duchartre ('48), von Müller ('82), Fletcher ('09), Hill and de Fraine ('12).

² Hill and de Fraine ('09a), p. 225.

³ Fletcher ('09), p. 878.

⁴ Dorety ('10), p. 428.

FIGS. 12-24. (Xylem cross-hatched, phloem clear.)

FIGS. 12-19. *Helianthus annuus syncotyleus* (continua). 12-17. *Syncotyl B*. 12. The seed-leaf, showing course of bundles. 13. Trans. sect. 3 mm. below collet. 14. Trans. sect. 2 mm. below collet. 15. Trans. sect. 2 mm. above collet. 16. Trans. sect. $\frac{3}{4}$ up hypocotyl. 17. Trans. sect. base of cotyledon tube. 18. *Syncotyl D*. Trans. sect. at summit of hypocotyl. 19. *Syncotyl E*. Trans. sect. at summit of hypocotyl.

FIGS. 20-24. *Cannabis sativa*. 20-24. *Dicotyl*. 20. Cotyledon showing venation. 21. Trans. sect. root. 22. Trans. sect. $\frac{1}{2}$ up hypocotyl (dotted areas = plumular procambia). 23. Trans. sect. $\frac{3}{4}$ up hypocotyl. 24. Trans. sect. just above cotyledonary node.

cotyledon takes one of these triads. There is a short cotyledonary tube (Fig. 24). The two main plumular traces appear in the intercotyledonary plane. Thus the transition is of a normal intermediate type, as might be expected in a seedling of this diameter¹.

The transition has also been described by Gérard,² with whose description my own observations agree, except that he says that 'the vascular bundles of the root do not meet in the centre'.

Schizocotyls. Numerous examples were seen in which one or both of the cotyledons were more or less deeply bifid. In some cases there was a slight notch of 1 or 2 mm., in others the half-cotyledons were only united by a few millimetres at the base: and intermediate degrees of fission were abundant.

Hemitricotyl A. Fig. 25 shows the degree of lobing of the one bifid cotyledon and the venation of the two seed-leaves. Diarchy persisted till after the two root-xylems had separated. Just above the collet one of the protoxylems divided radially and equally, and the distance between the two halves gradually widened: the position at 5 mm. above the collet being shown in Fig. 26. A little higher up a new group of phloem appeared in the segment between the two half-protoxylems, these separating still further, the result being the formation of a middle collateral strand lying between the two half-protoxylems (Fig. 27, at half-way up the hypocotyl). This middle strand then divides radially, and so three triads are organized (Fig. 28); the two arising from one pole of the root entered the bifid seed-leaf, the third entering the entire one. The plumular vascular strands were two in number as in the dicotyl, and lay in the corresponding plane; two primordial leaves were present at the first epicotyledonary node.

Hemitricotyl B. The abnormal seed-leaf was divided nearly to the base. The chief difference from *Hemitricotyl A* was that the second pole of the diarch root divided radially 5 mm. below the collet; i. e. below where the transverse division of the two xylems took place (Fig. 29). Corresponding with this, the separation of the two triads serving the split cotyledon took place lower down in the hypocotyl.

Hemitetracotyl C. Two cotyledons were present, each being divided to about the same extent as the single split one of *Hemitricotyl A*, and the transition was essentially similar in all three cases; the main difference being that the division of the protoxylems was deferred to a much higher level, to three-quarters up the hypocotyl on one side and to the base of the seed-leaf on the other. Similar instances of slight lack of parallelism between the division of cotyledons and vascular system were frequently observed in other cases.

Tricotyl D. The three cotyledons were not exactly equal, one being distinctly larger than the other two. This is a general feature of terato-

¹ Compton ('12), pp. 67, 96.

² Gérard ('81), p. 396.

logical tricotyls, and in the present species at least is connected with their origin, the two smaller cotyledons representing the products of fission, as indicated by the anatomy. The mode of folding of the three cotyledons in the seed helps to explain their persistent differences in size and shape; this is shown in transverse section in Fig. 30, the ventral surfaces of the cotyledons being indicated by thicker lines. The two smaller cotyledons are also slightly falcate when unfolded, as shown in Fig. 31 (taken, however, from Tricotyl E): and the venation differs somewhat from that of the whole and symmetrical cotyledon; the two smaller seed-leaves being practically related to one another as object and mirror image.

The root was diarch, but began to become triarch at the collet: the mode in which this was effected was somewhat different from that seen in the above hemitri- and hemitetra-cotyls. The protoxylem, instead of dividing equally, did not divide at all: a protrusion of metaxylem appeared just below the collet (Fig. 32), and just above the collet this metaxylem acquired a new protoxylem having no connexion with any group lower in the axis (Fig. 33). Corresponding with the protrusion of metaxylem, the superjacent phloem group divided radially. A normal triarch stele was thus organized just above the collet, and this behaved in a precisely analogous fashion to the diarch stele in a dicotyl: three triads being produced, one serving each of the three seed-leaves.

It is noteworthy that this exceptional mode of origin of the third protoxylem is that considered as characteristic of what Hill and de Fraine term a 'subsidiary' cotyledon.¹ I shall return to this later.

Tricotyl E. The root was triarch (Fig. 34), and the whole transition was perfectly symmetrical, each cotyledon taking a triad derived from a single root-pole. The first whorl of plumular leaves was also trimerous; and there were three main plumular traces in the upper part of the hypocotyl alternating with the three triads (Fig. 35).

This seedling shows the anomaly in its most complete form: there is nothing to indicate its relations with dicotily, save possibly the slight inequality of the cotyledons (Fig. 31).

Other Tricotyls. Nine other completely tricotylous seedlings were examined: of these, four had diarch, five triarch roots; no corresponding differences being noticed in the cotyledons. One triarch seedling had only two primordial leaves, but the others, diarch and triarch alike, had a trimerous plumule.

Hemitetracotyl F. This seedling bore two whole cotyledons and a third divided below half-way. The root was diarch, becoming triarch by division of one protoxylem 2 cm. below the collet; the three protoxylems thus formed supply the three seed-leaves. The other original root-pole forked about one-eighth up the hypocotyl and behaved just like the dividing strand

¹ T. G. Hill and de Fraine ('08), p. 708.

in Hemitricotyl A, forming two triads which enter the split cotyledon. There were three leaves in the first whorl.

Hemitricotyl G. A curious example, only observed once, in which the vascular system derived from one root-pole began to fork in the way typical of schizocotyly (cf. Seedling A), although there was no sign of a split in the cotyledon it supplied. It thus appears that the tendency to fork may be manifested in the vascular structure, though not in the external form. The other cotyledon was forked in the usual way.

We may summarize the main features of these anomalous seedlings of *Cannabis sativa* as follows:

- (i) The dicotyl is diarch with an intermediate level of transition.
- (ii) The fission of a cotyledon leads to a fission of the corresponding root-pole or its connexions, at a higher or lower level in the axis roughly according to the degree of splitting. This applies alike to the splitting of one or both cotyledons.
- (iii) There is a continuous series of stages from scarcely perceptible fission to deep lobing and complete tricotyly.¹
- (iv) The vascular structure seems to lag behind the degree of splitting of the cotyledons to some extent (except in Hemitricotyl G), for several examples were seen of complete tricotylys with diarch roots; others, however, had triarch roots and the whole structure was symmetrical about three diameters.
- (v) An instance of a 'subsidiary' cotyledon was observed in Seedling D; the validity of this category is doubtful, for we can hardly assume any phenomenon beyond schizocotyly in this case, whatever we may do in the Conifers.
- (vi) The plumular symmetry lags behind the cotyledonary: we do not find trimery in the epicotyl unless at least three distinct cotyledons are present, and occasionally not even then.

ULEX EUROPAEUS (Leguminosae).

The dicotylous anatomy has been described recently.² Mr. Bolland, of the Cambridge Agricultural Laboratory, gave me a single hemitricotyl whose lobed cotyledon was divided to within 1 mm. of the base. The structure of this seedling corresponded to some extent with that of *Cannabis sativa* and may be taken next in order.

The root was diarch, and the two polar protoxylems remained undivided to three-quarters up the hypocotyl: the usual processes found in the dicotylous transition taking place, so that two polar bands of xylem are formed each with two phloems. At three-quarters up the hypocotyl one of these phloems gives off a branch towards the cotyledonary plane, and at

¹ And probably tetracotyly, which, however, I have not observed.

² Compton ('12), p. 28.

the same time the corresponding protoxylem divides: the phloem branch coming to lie between the two half-protoxylems. A radial division then occurs along the cotyledonary plane on this side, separating the median xylem and phloem into two halves and thus producing two triads which enter the split cotyledon (cf. *Cannabis*, Figs. 27, 28). The other undivided polar protoxylem serves the unsplit cotyledon.

Thus the chief differences from *Cannabis* are (i) the mode of origin of the new phloem group by a branch instead of *de novo* (but cf. *Cannabis*, Seedling D); (ii) the high level at which the xylem forks.

PHACELIA TANACETIFOLIA (Hydrophyllaceae).

Abundant schizocotyls were obtained from Professor de Vries's seed: his 'intermediate race' yielding an average of 57 % of schizocotyls.¹

Dicotyls. The root is diarch, with a continuous one to two-seriate xylem-plate. In this slender seedling the transition is a high one, the cotyledon xylem-trace being widely V-shaped at the node, with two phloem groups on its flanks; shortly after entering the lamina the phloems fuse dorsally, and the midrib branches. No exceptional features worth recording were observed.

Schizocotyls.

Hemitricotyl A. The structure was diarch throughout the hypocotyl and in transition; after entering the deeply-split cotyledon the 'double bundle' began to divide equally, each half taking one of the two phloems and passing into the cotyledon lobe.

Tricotyl B. The root was diarch. About a quarter up the hypocotyl a new detached protoxylem appeared, dividing the adjacent phloem into two groups: this new xylem gradually increased in size, and joined on to the original diarch xylem-plate half-way up the hypocotyl. Thus a triarch 'root-like' structure was produced. Towards the cotyledonary node the three xylems developed into double bundles, one of which entered each of the three sub-similar seed-leaves.

This 'diarch-triarch' structure is common in tricotyls: there being much variety, however, in the level at which the new protoxylem appears. This method of increase in the number of protoxylems is the one generally adopted in *Phacelia*: *Hemitricotyl A* being the only instance observed of radial division such as is typical of *Cannabis sativa*. It is the method followed by the vascular bundles of so-called 'subsidiary cotyledons' in *Coniferae*.²

Tricotyl C. The whole seedling was constructed on the triarch plan, from root-tip upwards. The behaviour of the vascular system was strictly analogous with that of the dicotyl. Trimery continues in the epicotyl also.

This symmetrical type of structure is frequent, though perhaps not quite so abundant as varieties of the type of *Tricotyl B*. In seedlings which

¹ de Vries ('11), p. 436.

² T. G. Hill and de Fraine ('08), p. 708, &c.

possess it there is absolutely nothing to indicate that tricotyly is derived from dicotyly by splitting.

Hemitetracotyl D. There were three cotyledons, one of them being split about half-way. The root and hypocotyl were triarch throughout, the double bundle supplying the split cotyledon not dividing till after it entered the lamina. There were three leaves at the first epicotyledonary node.

Tetracotyl E. The root was diarch, with two lateral phloems. A third protoxylem appeared laterally about a quarter up the hypocotyl, this dividing the adjoining phloem into two equal halves; about half-way up the hypocotyl another protoxylem arose *de novo* on the opposite side of the original xylem-plate, this dividing the other phloem. A tetrarch root-structure was thus produced, and the upper half of the hypocotyl had a symmetrical structure, each xylem-pole producing a double bundle which supplied one of the four cotyledons.

The majority of the tetracotyls examined had diarch roots, but there was much variety in the level at which the new protoxylems were added. In one case the stele did not become triarch till three-quarters, and tetrarch till seven-eighths up the hypocotyl. It was general to find one of the new protoxylems appearing at a lower level than the other, though no more than a quarter of the hypocotyl separated them in any case. One seedling was seen which possessed a triarch root, and no instance of tetrarchy occurred in the root.

Tetracotyls have four leaves in their first epicotyledonary whorl.

The most striking feature in the schizocotyls of *Phacelia* is the fact that the vascular strands do not split to correspond with the split of the cotyledons. In all cases (except two, where the division occurred in the lamina) the number of xylem bundles is increased by the addition of new ones, not by the division of old. On tracing the strands from above downwards, we may say that in these cases the traces of certain cotyledons or half-cotyledons do not contribute to the structure of the root, but die out in the hypocotyl. This is the characteristic of 'subsidiary cotyledons'—a category of plant-members which apparently cannot be maintained.

Other Species with Diarch Dicotyls.

ANTIRRHINUM MAJUS (Scrophulariaceae).

SCROPHULARIA NODOSA (Scrophulariaceae).

AMARANTHUS SPECIOSUS (Amarantaceae).

CLARKIA PULCHELLA (Onagraceae).

PAPAVER RHOEAS (Double and Shirley) (Papaveraceae).

Seeds of schizocotylous races of the first four species were received from Professor de Vries:¹ the Papaver material was derived from trades-

¹ de Vries ('11), pp. 429, 432, &c.

men's seed. A considerable number of seedlings of each species was examined, the specimens ranging from dicotyls to tetracotyls, through all intermediate stages. The structures are very uniform for all the species, and closely resemble those described for *Phacelia*, so that I need not enter into details. The following is a summary of results.

In all the species the root is diarch in the dicotyl, and, since the seedlings are very small and slender, the transition is high, root-structure being found to within one or two millimetres of the cotyledons. Each cotyledon takes the strand derived from a single root-pole and a pair of half-phloems.

Splitting of a cotyledon or an increase in number of cotyledons involves the increase of the number of xylem-poles, this being almost always accomplished by the addition of one or more *de novo*.

Triarchy is frequent in tricotyls and seedlings of higher grades of schizocotyly. Tetrarchy is occasionally found in tetracotyls.

LEPIDIUM SATIVUM (Cruciferae).

The cotyledons of Cress are pinnately three-lobed (Fig. 36). It was thus of interest to ascertain if schizocotyly occurs in this species, and, if so, what effect it has. Large sowings were made, and among them were found three tricotylous seedlings. Each of these seedlings had three equal and similar trilobed cotyledons. One of these was pickled and microtomed; the other two were grown to maturity in pots, and their seeds (self-pollinated or crossed by one another) were sown. The offspring were almost entirely dicotylous, but after some search four complete tricotyls were found—about 0.5 per cent. of the whole number of seedlings.¹ These four seedlings were also studied anatomically. No other abnormalities of the class we are at present concerned with appeared in the seed-pans.

Dicotyls. The root is diarch, and the transition is high. At the cotyledonary node the 'double bundle' is practically tangential. On entering the cotyledon petiole it becomes a single collateral strand, giving off a pair of lateral bundles which pass into the lateral pinnae (Fig. 36).

Tricotyls. Three of the five tricotyls (A, B, C) were triarch throughout, the behaviour of the vascular strands being strictly analogous to that found in dicotyls.

One tricotyl (D) showed a diarch xylem in the root; just above the collet a third protoxylem appeared laterally but towards one end, thus not dividing the phloem; the new xylem gradually increased in size until it equalled the two original ones, and a new phloem appeared. The upper part of the hypocotyl was constructed on the triarch plan.

The fifth seedling (E) showed near the root-tip a xylem-plate with one protoxylem at one end, and two somewhat unequal ones at the opposite

¹ It therefore seemed clear that a rich 'intermediate race' was not obtained, and the experiment was discontinued.

end; two phloem bands were present. The xylem gradually became symmetrically triarch, a new phloem appearing in between the two adjoining protoxylems. Doubtless, if the seedling had been a little older, diarchy would have been found at the root-tip; but as it was there was no means of knowing the manner in which the three protoxylems could have joined on to the diarch plate—whether both or only one of the neighbouring ones would be prolonged downwards.

There is nothing in the external morphology of these seedlings to suggest schizocotyly: the vascular system, too, is either trimerous, or the third xylem arises in the 'subsidiary' manner (in D and perhaps also in E). It may be that this is an instance of true meristic variation—'absolute Vermehrung', as Winkler¹ calls it. Winkler, indeed, remarks that this mode of increase in the number of cotyledons is most obvious in seedlings with divided cotyledons; but the argument appears to be fallacious, and at present, owing to the small numbers observed, the question must remain unanswered.

LOTUS CORNICULATUS (Leguminosae).

The anatomy of dicotyls of these species has recently been described.² The root is normally triarch, each cotyledon receiving an equal share of the root xylem, viz. one whole protoxylem and half of the intercotyledonary protoxylem—the latter, however, being somewhat reduced in bulk. It is therefore a curious problem as to what will be the structure of tricotylous and hemitricotylous seedlings. One of each class was found and studied, with the following results:

Tricotyl. The root was triarch, as in dicotyls, and the whole transition was carried out on this plan of symmetry. Each cotyledon took a single triad derived from one root-pole. Thus the behaviour of one of the three root xylems was changed; instead of dividing itself between two cotyledons, as in a dicotyl, it served a single cotyledon.

Hemitricotyl. One cotyledon was split for about one-third of its length. The root was triarch, and the whole transition was carried out exactly as in the dicotyl. The base of the split cotyledon contained the usual 'double bundle' with two phloems (Fig. 37). A little distance along the petiole one of these phloems gave off a branch towards the median plane, so that a xylem bundle with three dorsal phloems was produced (Fig. 38). Further along the lamina this vascular complex divided into two equal halves, each consisting of a xylem with two phloem groups—in fact a 'double bundle' (Fig. 39). These two double bundles supplied the two lobes of the bifid cotyledon.

Thus the hemitricotyl yielded no hint as to the mode of origin of the tricotylous type of anatomy.

¹ Winkler ('84), p. 39.

² Compton ('12), p. 38.

FIGS. 25-41. (Xylem cross-hatched, phloem clear.)

FIGS. 25-35. *Cannabis sativa* (continued). 25-28. *Schizocotyl A*. 25. Two seed-leaves, showing venation. 26. Trans. sect. 5 mm. above collet. 27. Trans. sect. $\frac{1}{2}$ up hypocotyl. 28. Trans. sect. at summit of hypocotyl. 29. *Schizocotyl B*. Trans. sect. root 5 mm. below collet. 30. Diagram showing mode of folding of the cotyledons of a tricotyl in the seed; upper surface indicated by thick line. 31. *Tricotyl E*. The three cotyledons. 32, 33. *Tricotyl D*. 32. Trans. sect. just below collet. 33. Trans. sect. just above collet. 34-35. *Tricotyl E*. 34. Trans. sect. root. 35. Trans. sect. at summit of hypocotyl.

FIG. 36. *Lepidium sativum*. A cotyledon.

FIGS. 37-39. *Lotus corniculatus*, hemitricotyl. 37. Trans. sect. midrib at base of split cotyledon. 38. Trans. sect. further along petiole. 39. Trans. sect. further still along cotyledon.

FIGS. 40-41. *Helichrysum bracteatum*. 40. *Dicotyl*. Plan of the behaviour of the vascular system. 41. *Tricotyl* (second example): Trans. sect. just above node showing veins of the three cotyledons.

CARMICHAELIA AUSTRALIS (Leguminosae).

A somewhat similar case to that of Lotus. The root of the dicotyl is triarch,¹ the xylem being equally shared between the two cotyledons. In a single tricotyl the root was also triarch, each cotyledon being supplied by one root-pole.

HELICHRYSUM BRACTEATUM (Compositae).

It is unfortunate that schizocotyls have not been obtained of species with normally a tetrarch symmetry. The nearest approach to this is the above plant, the seed of a schizocotylous race being received from Professor de Vries.²

The root in dicotyls is diarch, but about half-way up the hypocotyl two new protoxylem groups appear, one on each side of the xylem-plate, these dividing the original two phloems into four, so that what is apparently a tetrarch structure results. The original root xylems pass out as the midribs of the two cotyledons; the new xylem groups divide, and half of each enters each cotyledon as a lateral nerve, there being no preliminary fusion with the midrib (Fig. 40).

Tricotyls. Material was unfortunately scarce, and only two seedlings can be described. These were both complete tricotyls, and their structure was on the whole similar. The root was diarch. A third xylem group appeared about half-way up the hypocotyl, metaxylem first, protoxylem higher up. The lateral cotyledonary traces appeared as usual, these being three in number and alternating with the three root-poles. The upper part of the hypocotyl was constructed on the triarch plan. In one seedling each of the three cotyledons received a whole root-pole and halves of the two adjacent lateral cotyledon traces. In the other seedling two of the lateral cotyledon traces did not divide, but each passed entire to one of the cotyledons; thus two of the cotyledons possessed only a midrib and one lateral bundle (Fig. 41).³

THE LITERATURE OF SCHIZOCOTYLY.

The occurrence of Angiosperm seedlings with an abnormal number of cotyledons has attracted the attention of several writers; and numerous notes have been published dealing with the external features of such seedlings. Reference may be made to the work of Duchartre ('48), Junger ('69-'71), Krause ('80), Winkler ('84, '94), Gain ('00), Thiselton-Dyer ('02), Guillaumin ('11), and Lutz ('11). From the standpoint of Genetics a systematic study of the inheritance of seedling anomalies has been made by de Vries

¹ Compton ('12), p. 43. A rudimentary fourth protoxylem appears at the summit of the hypocotyl.

² de Vries ('11), p. 430.

³ A similar variation was noticed in seedlings of *Lepidium sativum*, where the midrib typically gives off a pair of lateral bundles near its base.

('02, '11). No pure-breeding races of tricotylys were obtained, but 'intermediate races' were frequent.

On the anatomical side schizocotylys have been examined by Léger ('90), in *Acer platanoides*, Gain ('00), in *Phaseolus*, Guillaumin ('11), in *Ruta montana*, and *Schinus terebintifolius*, Lutz ('11), in *Dianthus margaritae*. Notes on their writings will not be out of place here.

Dianthus margaritae. A single tricotyl examined by Lutz ('11) showed a triarch structure throughout. No mention is made of the anatomy of dicotylys.

Ruta montana. The hypocotyl of a tricotyl showed a triarch symmetry, but Guillaumin ('11) does not mention the root structure nor the dicotylous anatomy.¹

Schinus terebintifolius. A few diagrams are given by Guillaumin ('11), but these throw no light on the structure of the root, nor the transition in dicotylys nor in schizocotylys.

Acer platanoides. A full and careful study of a series of schizocotylys has been made by Léger ('90) in this species, which regularly produces a relatively high percentage of abnormal seedlings.² The dicotyl is tetrarch, so that Léger's work is complementary to my own, in which no tetrarch seedling is included.

The mode in which the gradual increase in number of cotyledons through schizocotyly is reflected in the structure is somewhat complicated, and reference must be made to Léger's paper for details. The anatomical anomaly may be described as a gradual increase in the importance of the vascular system in the margins of the half-cotyledons adjoining the line of fission. When the fission is deep enough these internal marginal systems produce an augmentation in the number of bundles in the hypocotyl, and finally in the root: complete tricotyly produces pentarchy and hexarchy; tetracotyly produces heptarchy (and octarchy is to be expected).

Phaseolus sp. The variety known as 'Haricot beurré nain Mont-d'Or' produces a high percentage of tricotylys, which were studied anatomically by

¹ The genus *Ruta* (like other Rutaceae) is of special interest in this connexion. Gérard (('71), p. 341) states that seedlings of *R. graveolens* are either tricotylous, or else possess one small and one large forked cotyledon: in the latter case the large cotyledon takes two, the small one of the three root-poles; in the former each cotyledon takes one root-xylem. Duchartre ('48) mentions that *R. montana* and *R. graveolens* are always dicotylous. The only two seedlings of *R. graveolens* I have seen were both dicotylys with practically equal seed-leaves.

² I am permitted by Dr. Ethel de Fraine to include here the results of an examination of a great number of *Acer* seedlings growing wild or in gardens. In all 7,190 seedlings were collected, and among these 143 showed some abnormality: this being 1.98 per cent. of the whole. The numbers of the different classes were as follows: 2 complete syncotylys, 2 hemisyncotylys, 44 hemitricotylys, 72 tricotylys, 18 hemitetracotylys with two split seed-leaves, 2 hemitetracotylys with one split and two entire seed-leaves, 3 tetracotylys. A higher percentage of schizocotylys occurred among the offspring of cultivated than among that of wild trees. Schizocotylous seedlings of *Acer pseudo-platanus* have also been figured and described from the morphological point of view by Thiselton-Dyer ('02), who draws attention to the importance of an anatomical study.

Gain ('00). The dicotyl is tetrarch (occasionally pentarch); tricotylys are either pentarch or hexarch. The behaviour of the individual vascular strands was not followed accurately; the author remarks that the structure of the upper part of the hypocotyl of tricotylys 'rappelle tout à fait la structure de la région correspondante des plantules dicotylées' (p. 383). Hemitricotylys were also observed, and exhibited a pentarch symmetry (p. 388).

GENERAL REMARKS ON SCHIZOCOTYLY.

In the case of syncotyly it was remarked that all degrees of the anomaly occur, from slightly attached cotyledons to complete fusion. The same is the case in schizocotyly, as has been emphasized by all writers on the subject. There can be scarcely any doubt that polycotyly and schizocotyly in the Angiosperms are one and the same phenomenon. The possession of three equidistant and equal cotyledons is the culmination of a series beginning with a slightly forked cotyledon; there is probably not so much difference between complete tricotyly and advanced hemitricotyly in fact as there is in thought and speech. There is no warrant for assuming more than one process or tendency in schizocotylous races; though certain cases, perhaps owing to lack of adequate knowledge, may invite a meristic explanation (e. g. *Lepidium sativum*).

At one time I expected that the differences in genetic properties between different tricotylous races might be due to differences in the morphological nature of the anomaly; but no real support for such a view has been obtained. It seems reasonable to think that schizocotyly is the mode of increase of the number of cotyledons in all the above cases.

T. G. Hill and de Fraine ('08-'10), as a result of their extensive study of the seedlings of Gymnosperms, also see in schizocotyly the chief method by which the number of cotyledons has been increased from the primitive dicotylous condition. But two other methods are also supposed to have been employed. One of these is the shifting of a plumular leaf downwards into the cotyledonary whorl. The other method is of more interest in the present connexion; certain seed-leaves were termed 'subsidiary cotyledons', the criterion of this class of members being the fact that their vascular supply 'plays no important part in the formation of the root structure'.¹

I have found some difficulty in understanding how far Hill and de Fraine's subsidiary cotyledons constitute a morphological category: they say, for instance, that 'a subsidiary cotyledon may be promoted, as it were, to the rank of a half-cotyledon'²—a remark which appears to be unthinkable if taken in connexion with their further statement that 'the seed-leaves, as judged by the behaviour of their bundles in the transition region, naturally fall into three categories, viz. (a) whole cotyledons,

¹ Hill and de Fraine ('08), p. 708.

² Loc. cit. ('09), p. 222.

characterized by the bundle of each forming one pole of the root ; (b) half-cotyledons, which are recognized by the bundles of two of them being required to form one pole of the root structure ; and (c) subsidiary cotyledons, the strands of which have no influence on the number of bundles in the root structure'.¹

The fact appears to be that Hill and de Fraine are not justified in arguing from anatomy to morphology in this matter. Their categories apply only to the behaviour of vascular strands (and even here not by any means strictly²) ; they cannot be transferred to the cotyledons.³

This may be illustrated by reference to the cases of polycotyly here described. As stated above, everything points to schizocotyly being the explanation of teratological polycotyly ; and yet in a great many cases the two vascular strands of the split cotyledon (or of two equal half-cotyledons) do not behave alike, but one of them has the characteristic upon which Hill and de Fraine define a subsidiary cotyledon. (See, for example, *Phacelia tanacetifolia*.) In other cases (e. g. *Cannabis sativa*), the vascular strands of the half-cotyledons are strictly equivalent, and unite to form jointly a single root-pole. It seems quite clear that the distinction between subsidiary cotyledons on the one hand, and half- and whole cotyledons on the other, cannot be maintained. The term 'subsidiary cotyledon' should be restricted to the other use which Hill and de Fraine make of it, viz. to denote a displaced plumular leaf.

With the general conclusions of Hill and de Fraine's work I am in agreement, considering that the evidence for the derivation of polycotylous types from dicotylous ancestors is supported by highly cogent evidence. In addition to the arguments which have previously been brought forward in support of this view we have now the evidence that an increase in number of cotyledons by fission does take place as a more or less heritable anomaly in a great number of Dicotyledons, and that the anatomy of such schizocotyls shows features of close similarity with those described in normally polycotylous Gymnosperms.

Moreover, in the relatively advanced Dicotylous families Proteaceae and Loranthaceae we find a few species whose seedlings are polycotylous and show remarkable resemblances to Coniferous polycotyls ; and here, as Fletcher⁴ and Hill and de Fraine⁵ have recently maintained, there can be practically no doubt that the ancestry was dicotylous.

¹ Hill and de Fraine ('09), p. 221.

² This becomes clear from a comparison of the different ways in which they explain the structure of, for instance, *Cupressus torulosa*, series C, *Abies sibirica*, series B, and *Abies amabilis* (('08) p. 699, ('09) pp. 191, 195.

³ It is clear that the term 'half-cotyledon' implies that the structures in question have arisen by the fission of 'whole-cotyledons'. This, in itself, makes the idea that they can arise by 'promotion' of 'subsidiary cotyledons' unthinkable.

⁴ Fletcher ('09), p. 877.

⁵ Hill and de Fraine ('12).

It has already been remarked that there is a close similarity between the structure of a seed-leaf produced by fusion and one undergoing fission. This opens the door to the view that dicotyly may have been derived from polycotyly by a series of fusions. It is only possible to decide between the opposing views on the basis of other classes of evidence and on comparative studies.

The only recent argument in favour of a polycotylous origin of dicotyly in Gymnospermae is that brought forward by Coulter and Chamberlain,¹ who remark that 'it must be remembered that probably our oldest group of Coniferales, older even than the Cycadales and Bennettitales with which we are acquainted, is the extreme illustration of polycotyledony, while the youngest of the Coniferales are dicotyledonous or nearly so'. With the implication of primitiveness in the word 'oldest' I cannot agree, for the argument is founded on our ignorance and the imperfection of the geological record: and almost the whole of modern morphological work tends to the conclusion that it is the dicotylous Podocarpeae and Araucarieae which must be regarded as the most primitive Coniferales; the polycotylous Abietineae, old as they are, being a relatively advanced family.

The earliest known embryo, that of *Bennettites*, was dicotylous; the cotyledon-bearing Pteridophyte, *Selaginella*, is dicotylous; and numerous lines of investigation have led to the conclusion that dicotyly is a primitive character—whether for the Monocotyledons, or for teratological syncotyls and schizocotyls, for polycotylous Proteaceae and Lorantheae, or for Gymnospermae.

BOTANY SCHOOL,
CAMBRIDGE.

BIBLIOGRAPHY.

- CESALPINI, A. (1583): De plantis libri XVI. Florence.
 CHAUVEAUD, G. ('11): L'appareil conducteur des plantes vasculaires. Ann. Sci. Nat. (Bot.), 9^e sér., t. xiii, p. 113.
 COMPTON, R. H. ('12^a): Theories of the Anatomical Transition from Root to Stem. New Phyt., xi, p. 13.
 ——— ('12^b): An Investigation of the Seedling Structure in the Leguminosae. Journ. Linn. Soc. (Bot.), xli, p. 1.
 COULTER, J. M., and CHAMBERLAIN, C. J. ('10): Morphology of Gymnosperms. Chicago, p. 297.
 DODEL, A. ('72): Der Uebergang des Dicotyledonen-Stengels in der Pfahlwurzel. Pringsh. Jahrb., viii, p. 149.
 DORETY, H. A. ('10): In J. M. Coulter and C. J. Chamberlain, Morphology of Gymnosperms. Chicago, p. 427.
 DUCHARTRE, P. ('48): Sur les embryons dits polycotylés. Ann. Sci. Nat. (Bot.), 3^e sér., t. x, p. 207.

¹ Coulter and Chamberlain ('10), p. 300. See also Dorety ('10), p. 428.

- FLETCHER, J. J. ('09): Illustrations of Polycotyledony in the Genus *Persoonia*, with some reference to *Nuytsia*. Proc. Linn. Soc. New South Wales, xxxiii, p. 867.
- DE FRAINE, E. ('10): The Seedling Structure of certain Cactaceae. Ann. Bot., xxiv, p. 125.
- GÉRARD, R. ('81): Recherches sur le passage de la racine à la tige. Ann. Sci. Nat. (Bot.), 6^e sér., t. xi, p. 279.
- GUILLAUMIN, A. ('11): Germinations anormales. Bull. de la Soc. Bot. de France, lviii, p. 481.
- HEGELMAIER, F. ('78): Vergleichende Untersuchungen über Entwicklung dikotyledoner Keime. Stuttgart.
- HILL, A. W. ('06): Morphology and Seedling Structure of the Geophilous Species of *Peperomia*. Ann. Bot., xx, p. 395.
- HILL, T. G., and DE FRAINE, E. ('08-'10): On the Seedling Structure of Gymnosperms. Ann. Bot., xxii, p. 689; xxiii, pp. 189, 433; xxiv, p. 319.
- ('12): On the Influence of the Structure of the Adult Plant upon the Seedling. New Phyt., xi, p. 319.
- HOLM, T. ('99): *Podophyllum peltatum*, a Morphological Study. Bot. Gaz., xxvii, p. 419.
- JUNGER, E. ('69-'71): Ueber tricotyledone Embryonen. Jahresb. d. Schles. Ges., t. xli-xlviii.
- KATTEIN, A. ('97): Der morphologische Werth des Centralcylinders der Wurzel. Bot. Centralbl., lxxii, p. 91.
- KERNER, A., and OLIVER, F. W. ('02): The Natural History of Plants, i.
- KRAUSE, K. E. H. ('80): Drei Kotyledonen. Arch. d. Ver. d. Freunde d. Naturg., Mecklenburg, p. 236.
- LÉGER, L. J. ('90): Note sur les germinations anormales d'*Acer platanoides*. Bull. Soc. Linn. de Normandie, 4^e sér., t. iii, p. 199.
- LOTSY, J. P. ('11): Vorlesungen über botanische Stammesgeschichte. iii, 1.
- LUTZ, L. ('11): Germinations à trois cotylédons. Bull. de la Soc. Bot. de France, lviii, p. 488.
- MASTERS, M. T. ('91): Comparative Morphology, Anatomy, and Life-history of the Coniferae. Journ. Linn. Soc. (Bot.), xxvii, p. 226.
- VON MÜLLER, F. ('82): Plurality of Cotyledons in the Genus *Persoonia*. New Zealand Journ. of Sci., p. 115.
- RAY, J. (1686-1704): Historia plantarum.
- REINKE, J. ('71): Untersuchungen über Wachsthumsgeschichte und Morphologie der Phanerogamen-Wurzel. Hanstein's Bot. Abhandl., i. 3.
- SARGANT, E. ('03): A Theory of the Origin of Monocotyledons founded on the Structure of their Seedlings. Ann. Bot., xvii, p. 1.
- ('08): The Reconstruction of a Race of Primitive Angiosperms. Ann. Bot., xxii, p. 121.
- SCHMID, B. ('02): Beiträge zur Embryo-Entwicklung einiger Dikotylen. Bot. Zeit. lx, i, p. 207.
- STERCKX, R. ('99): Recherches anatomiques sur l'embryon et les plantules dans la famille des Renonculacées. Mém. Soc. Roy. Sci., Liège, 3^e sér., t. ii.
- THISELTON-DYER, W. T. ('02): Morphological Notes. VIII. On Polycotyledony. Ann. Bot., xvi, p. 553.
- DE VRIES, H. ('95): Over de Erfelijkheid van Synfisen. Bot. Jaarboek, 1895, p. 129.
- ('02): Ueber tricotyle Rassen. Ber. d. deutsch. bot. Ges., xx, p. 45.
- ('11): The Mutation Theory. Vol. ii, London (Engl. transl.).
- WINKLER, A. ('84): Die Keimblätter der deutschen Dicotylen. Abhandl. d. bot. Ver. Brandenburg, xxvi, p. 30.
- ('94): Anomale Keimungen. Ibid., xxxvi, p. 127.

Compton, R. H. 1913. "An anatomical study of syncotyly and schizocotyly."
Annals of botany 27, 793–821.

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