Observations on the Seedling Anatomy of Certain Sympetalae.

II. Compositae.

BY

E. LEE, A.R.C.Sc., F.L.S.,

Department of Agriculture, University of Leeds.

With eleven Diagrams and two Figures in the Text.

INTRODUCTION.

SINCE the present investigation was first undertaken two or three years ago, the problem of seedling anatomy has undergone considerable change. The stimulus which investigators received in the first years of the present century has resulted in the detailed examination of hundreds of seedlings from all the great groups of plants. The results obtained are for the most part qualitative, and have been used chiefly as evidence for or against certain phylogenetic theories. Recently, however, Compton (1) has initiated another line of research in connexion with this subject. This author was able to show that in the Leguminosae the type of vascular anatomy in the seedling is correlated with the *size* of the latter, a result which, if it can be applied generally, goes a long way towards destroying any phylogenetic importance which seedling anatomy may have possessed. But in other groups examined by the present writer, while the type of seedling structure is generally correlated with the size of the seedling, there are not infrequently rather disconcerting exceptions, some of which will be noted later.

In the first part of the present investigation (7) it was indicated that the possession of the *Anemarrhena* type of seedling structure does not necessarily involve affinity with the Liliaceae. The discovery of this type in the highly evolved Bignoniaceae appears considerably to weaken the phylogenetic theories of Miss Sargent (8, 9, 10, 11). The physiological aspect of the subject has recently been approached by Hill and de Fraine (6), who have attempted to show that the problem of seedling anatomy is largely, if not wholly, physiological, i. e. that the environment (using the term in its widest sense) is chiefly responsible for the amount of vascular tissue present in the seedling, and therefore, to a certain extent, for the number and kind of strands present and the type of seedling structure.

When the present research was first begun, it was hoped to include a description of the anatomy of seedlings selected, as far as possible, from all the Natural Orders in Engler's *Campanulatae*. But while a considerable amount of work has been accomplished in this direction, little of interest can be reported outside the *Compositae*. The present paper, therefore, is restricted to the latter group.

HISTORICAL.

Considering the large size of the Natural Order *Compositae*, it is a surprising fact that little detailed research has been done on the seedling anatomy of these plants. This is perhaps accounted for by the view that little of phylogenetic importance could be expected in a group which is generally believed to include the most highly evolved plants known. It is hoped, however, that the results here recorded throw some light on the connexion which undoubtedly exists between the different 'types' of seedling structure, if not on the phylogenetic question as a whole.

What are, perhaps, the earliest observations on this subject worth noting were published in 1881. In that year Gérard (5) gave a description of the seedling anatomy of two species belonging to the *Compositae*; this description has been confirmed in the present research. Three years later Vuillemin (12) published a long paper on the anatomy of the *Compositae*. His researches, however, were actuated by a desire to evolve a system of classification, based on the anatomy, which would be of use in the identification of the vegetative parts of medicinal plants. It is not surprising, therefore, to find that, although many seedlings were carefully studied from different points of view, there is only a short general account of the 'transition' phenomena, which, as the author remarks, agrees with the more detailed description given by Gérard and cited above.

For the rest, the very general references by Dangeard (3) and by Thomas (12) to the seedling structure in this group, and the more complete descriptions by Chauveaud (2), should be noted.

METHODS.

The seedlings for this research were grown at Birkbeck College, London, from seeds presented by Mr. W. Hales, A.L.S., Physic Garden, Chelsea, to whom I am deeply indebted for generous assistance. The seeds of upwards of seventy species were selected, of as many shapes and sizes as possible, and of these about fifty germinated. The seedlings were cut and the sections stained according to the methods described in the first part of this report (7).

I would like to take this opportunity of tendering to Miss F. A. Randell, B.Sc., my sincere thanks for the very valuable assistance she has rendered in preparing, cutting, and staining many of the seedlings.

TYPES OF VENATION IN THE COTYLEDONS.

The venation of the cotyledons in the Compositae is perhaps one of the most remarkable features in the seedlings examined. In Diagram I, in which the vascular bundles are represented by dotted lines and crosses, the five types of venation observed are given. It must be remarked that in all cases the smallest bundles have been omitted from the diagram.

Type v, which was seen in only one example—*Cichorium Intybus*—is one of the simplest. Although several bundles are present in the upper portion of each seed-leaf, only a single one enters the hypocotyl, and, as will be seen later, this is associated with the simplest type of transition.

DIAGRAM I. Types of venation in the cotyledons. *a* = apex, *b* = base, and *c* = transverse section of base of cotyledon. Vascular bundles represented thus - - - - and *x*.

Type I, also, is very simple, but here three bundles enter the hypocotyl. The remaining ones are really variants on I and v. In II and III the chief strands are more numerous, but they arise in the same manner as in I and v. At the base of the cotyledon in II (as in I also) there are three vascular strands, but in III five well-marked bundles enter the hypocotyl. Type IV, which is seen in *Arctium majus*, differs from I chiefly because of the peculiar branching of the chief strands near the apex of the cotyledon. This will be described later under the species.

Two rather remarkable facts in connexion with the venation must be noted. The first is that, so far as has been observed, the chief strands never end blindly in the tissue of the mesophyll. The branches which arise near the base of the seed-leaf, whether from the midrib or from the laterals, generally pursue an arcuate or sinuous course and reunite with the bigger

bundles at a higher level. The second fact, which is really only an accentuation of the first, is that the extreme lateral bundles on either side invariably unite with the midrib at the apex of the cotyledon.

To describe this in the reverse way. The first sections at the apex of the seed-leaf show no vascular bundles. Then, in the general case, a broad strand of vascular tissue arises. At first it is indefinite in outline, but lower down it separates into three distinct bundles, one being the midrib, the other two following the outline of the cotyledon and giving rise to the laterals. In the majority of cases, as we pass down the seed-leaf all the bundles branch, but the branches produced always fuse with one or other of the chief bundles before the base is reached, only the midrib and the two laterals persisting. The two exceptions to this are seen in III and V: in the former case four laterals (in addition to the midrib) persist, while in V all the laterals produced unite with the midrib before the latter enters the hypocotyl.

The importance of this peculiar venation in connexion with the transition cannot easily be over-estimated. This subject will be referred to again after the seedling anatomy has been described in more detail.

DESCRIPTION OF SPECIES.

The vascular anatomy of most of the species examined will now be described.

A. TUBULIFLORAE.

Tribe III, Astereae.

Solidago ulmifolia, Muhl. Seedlings small (3–7 cm. long), each with two equal cotyledons, which are united along one side for a long distance before fusion occurs on the other margin.

Seedlings A and B. Near the base of each seed-leaf there are three vascular strands, of which the two laterals are very small (Diagram 2, I). On the other side, where the cotyledons first unite, the lateral from one cotyledon fuses with its fellow from the other (Diagram 2, II), and almost immediately the fused bundle, moving round in a clockwise manner (as seen from above), unites with one of the midrib bundles. On the other side, fusion of the laterals is followed by the passage of the double strand into the centre of the hypocotyl, where it remains quite distinct for some distance (Diagram 2, III and IV), finally moving slightly clockwise to join one of the xylem-strands in the cotyledonary plane. In the meantime, the midrib of each cotyledon has passed nearly to the centre of the hypocotyl; the xylem in each case proceeds to undergo rearrangement, and the phloem group bifurcates. A transverse section at this level shows three xylem-masses, of which the intercotyledonary strand near the centre gradually

merges into one of the xylem-masses as described above. In the xylem-strands situated in the cotyledonary plane, the protoxylem becomes exarch, the phloem-groups unite laterally in pairs, and a diarch root-structure results (Diagram 2, V).

DIAGRAM 2. *Solidago ulmifolia*. 'Transition' from base of cotyledons to root. In this and the following diagrams, protoxylem is shown in black, metaxylem dotted, and phloem hatched.

Seedling C is slightly different from the above. Before the first fusion of the cotyledons along one side, each of the laterals on that side fuse with the corresponding midrib, making the whole structure asymmetrical. At

DIAGRAM 3. *Charieis heterophylla*. (For I see Diagram 2, I.)

a lower level, new bundles appear on the same side of the two midribs, fuse together as soon as the cotyledons on that side unite, and immediately disappear without ever having been connected with any of the other vascular strands. The behaviour of the remaining vascular bundles is exactly as in *Seedlings A and B*.

Charieis heterophylla, Cass. Seedlings smaller than in *Solidago ulmifolia*, with anatomy correspondingly simpler, though of the same general type. A fairly conspicuous cotyledonary tube is present, the fusion of the cotyledons taking place as in *Solidago*. Though the vascular strands are very minute, the details of transition are quite clear. The following differences from *Solidago ulmifolia* may be noted: After fusing in pairs in the cotyledonary tube, the laterals pass inwards in the upper part of the hypocotyl, and on reaching the centre (Diagram 3, II and III) they gradually disappear or join on to the midrib bundles. In the latter, the xylem gradually becomes rearranged, so that quite high up in the hypocotyl the two protoxylems are external. The phloem part of each bundle bifurcates, and the halves fuse in pairs on either side of the diarch xylem-plate (Diagram 3, IV).

Aster Amellus, Linn. Seedlings small (about 2.5 cm. long), with long, fleshy seed-leaves and a short cotyledonary tube. The transition, which is not very clearly shown, is like that in *Charieis heterophylla*.

Tribe IV, Inuleae.

Inula Helenium, Linn. Seedlings small and possessing rather long, slender tap-roots. Transition similar to that described for *Charieis heterophylla*.

Buphthalmum speciosum, Schreb. Seedlings small. Hypocotyl slender, but seed-leaves comparatively large and foliaceous, each possessing a distinct petiole.

The transition is exactly as in *Charieis heterophylla*, with the exception that in the hypocotyl the intercotyledonary strands apparently disappear before they reach the centre. The whole of the rearrangement in the xylem takes place in the upper part of the hypocotyl.

Tribe V, Heliantheae.

Silphium perfoliatum, Linn. Seedlings large (7–12 cm. long) and fleshy. Seed-leaves very large, and hypocotyl stout and comparatively short.

As usual in this Order, the single vascular bundle at the apex of the cotyledon first divides into three, after which, in correspondence with the large size of the cotyledons, each main strand gives off a large number of smaller bundles. At a lower level, these begin to re-fuse with the larger strands, and at the base of each cotyledon only five vascular strands remain—a large median one and two smaller laterals on either side (Diagram 4, I). In the pronounced cotyledonary tube, the extreme lateral (and smallest) bundles fuse with the corresponding bundles from the other cotyledon, and the composite structure produced, after decreasing in size, moves round

and joins on to one of the remaining lateral strands (Diagram 4, II). At a still lower level in the cotyledonary tube, the remaining lateral bundles fuse in pairs, so that four equal vascular strands enter the hypocotyl (Diagram 4, III). Almost immediately, the xylem in each case becomes rearranged and the protoxylem assumes an exarch position, while the phloem groups, of which eight have been formed by division of the original four, fuse in pairs, and a tetrarch arrangement is produced (Diagram 4, IV and V).

The root is long and fairly stout, and for the most part a large pith is present. This, however, becomes smaller as the apex is approached, but at no place does it disappear altogether.

DIAGRAM 4. *Silphium perfoliatum*.

It may be observed here that, though the seedling is large, the transition takes place at a high level in the comparatively short hypocotyl.

Xanthium Strumarium, Vahl. Seedlings generally a little larger (never less than 10 cm. long) than in *Silphium perfoliatum*, but possessing the same general characters.

In the upper part of the seed-leaf the behaviour of the vascular bundles is the same as in *Silphium perfoliatum*. After division and subsequent re-fusion of the strands, there are present at the base of each cotyledon a large number of vascular bundles—viz. a large midrib, two smaller laterals near the margin, and, in the intermediate positions, numerous still smaller bundles. In the large cotyledonary tube the midrib bifurcates, its protoxylem becomes exarch, and the whole mass of vascular tissue assumes a form which it retains until the root is reached.

The remaining strands pass unchanged into the hypocotyl. In the

upper part of the latter, the extreme lateral bundle on either side fuses with its fellow from the other cotyledon, and in pursuing its way down the hypocotyl the resulting strand bifurcates, the protoxylem becoming external during the process.

Thus a tetrarch root is formed in which, as one might expect in so large a seedling, there is at first a large pith. The smaller lateral bundles of the cotyledon continue unchanged for a long distance in the hypocotyl. Finally, however, owing to the decrease in size of the latter as it passes into the root, the whole of the vascular tissue becomes arranged nearer the centre, and the bundles, fusing laterally, form a continuous ring of xylem

DIAGRAM 5. *Heliopsis laevis*. Seedling A.

and a ring of phloem which is only broken where it passes the protoxylem groups.

The rearrangements are thus initiated in the seed-leaves, and the region of transition is very elongated.

Heliopsis laevis, Pers. The seedlings were of the small, slender type, but the seed-leaves were long and rather fleshy, and also were unequal in size.

Seedling A. In the cotyledons there is the usual branching and re-fusion of the vascular bundles, as a result of which six strands (three from each seed-leaf) pass into the short cotyledonary tube (Diagram 5, I). The two in the cotyledonary plane are very large. Each of these bifurcates, the xylem assuming the form of a flat ribbon with the small protoxylem elements

in a median position. In this condition, the midrib strand traverses the greater portion of the hypocotyl. The lateral strands pass inwards, and each pair, after fusing completely, separate again, and, moving laterally, join on to the strands in the median plane (Diagram 5, II, III, and IV). There are thus formed two broad ribbons, each consisting of almost continuous masses of xylem and phloem. Near the base of the hypocotyl the median protoxylem strands become really exarch, and about the same time the original lateral strands separate once more, and, fusing in pairs with the protoxylem exarch, form the intercotyledonary strand of the tetrarch root (Diagram 5, V).

At this stage the tetrarch arrangement is radially symmetrical, but changes now occur which result in a reduction of the symmetry. The intercotyledonary xylem strands become gradually smaller and the four phloem masses fuse in pairs, forming two large phloem groups situate in the cotyledonary plane. The stele is now bisymmetrical, a symmetry which it retains to the root-tip. Gradually the two intercotyledonary xylem masses disappear, or, as in one case, they pass inwards and form the core of the diarch root (Diagram 5, VI).

Seedling B. The above is the usual course of events in this species, but in one case the tetrarch stage, so clearly shown in all the other examples, is entirely omitted. From the 'ribbon' stage, in which the vascular tissue is enormously elongated laterally, one passes straight to the diarch root by a simple closing in of the vascular tissue followed by fusion in pairs of the phloem groups. It is noteworthy that in this case no two seedlings were exactly the same in all details.

Zinnia pauciflora, Linn. Seedlings 4-6 cm. long, each with an elongated hypocotyl and a definite cotyledonary tube.

The transition, though not very clear, is, so far as can be determined, almost exactly the same as in *Bidens pilosa*.¹ At the base of each seed-leaf, however, there are five vascular bundles, of which the very small ones near the margin fuse with their fellows from the other cotyledon as soon as the cotyledonary tube is reached. At a lower level, the fused bundles unite with the other laterals on the same side, so that four strands enter the hypocotyl. Thenceforward the transition is like that in *Bidens pilosa*. Rearrangements in the midrib are always initiated in the lamina, and the region of transition is very elongated.

Rudbeckia amplexicaulis, Vahl. Seedlings about 3 cm. long, and possessing petiolate seed-leaves which fuse to form a cotyledonary tube.

The transition, which takes place at a high level, is very similar to that in *Charieis heterophylla*, the chief difference being that here the fused lateral strands generally disappear before they reach the centre of the hypocotyl.

Leptosyne Douglasii, D. C. Seedlings 2-4 cm. long, very slender, and

¹ See p. 313.

possessing linear seed-leaves which unite at the base to form a very short cotyledonary tube.

In each seed-leaf there are three principal strands present, the two laterals fusing with their fellows in the upper part of the hypocotyl (Diagram 6, I, II). The fused bundles immediately pass inwards, but remain at some distance from the centre throughout the hypocotyl. The larger midrib strands undergo slight rearrangement, the protoxylem becoming exarch, but the phloem remaining more or less in position. Near the base of the hypocotyl, the four midrib strands approach nearer the centre, and the xylem elements (the number of which fluctuates) now become loosely

DIAGRAM 6. *Leptosyne Douglasii*.

arranged and tend to intermix. At this level (Diagram 6, III), though the structure simulates a tetrarch arrangement, it does not form an ordinary tetrarch root. The xylem is four-angled, but the angles consist, on the whole, of larger elements than the rest, although all the lignified tracheides and vessels are spirally thickened. In addition the phloem groups are situated *outside* and *not between* the angles. This condition obtains not only in the greater part of the hypocotyl, but also nearly to the root-tip. Finally, a gradual rearrangement occurs: some of the lignified elements disappear and the rest become more closely arranged to form a regular triarch root. Similarly with the phloem, three groups being formed which take up positions between the xylem angles (Diagram 6, IV, V).

In one or two cases there were indications near the root-apex of further reduction to a diarch arrangement.

Bidens pilosa, Linn. Seedlings 5–7 cm. long, slender, and each possessing two equal, linear seed-leaves which unite at the base to form a cotyledonary tube.

Near the apex of the seed-leaf there are three vascular bundles—the usual median strand and two smaller laterals—formed by division of

DIAGRAM 7. *Bidens pilosa*.

a single large strand. At a lower level, small median bundles occur which subsequently unite with the median strand. In the upper part of the hypocotyl the median bundle divides, and the branches pass to the corners of the almost square stele, leaving behind a small strand of protoxylem in the cotyledonary plane (Diagram 7, I, II). The metaxylem branches thus formed consist in each case of 1–3 lignified elements, the protoxylem of only a single vessel. The lateral strands from the two seed-leaves fuse in pairs in the cotyledonary tube. At a lower level, the metaxylem in each case disappears, leaving behind a single, more or less lignified, protoxylem

element (Diagram 7, III). The stele is therefore perfectly symmetrical at this stage and in all the succeeding sections to the root-tip. Lower down, the metaxylem of the corner bundles becomes reduced to a single strand which passes inwards towards the centre, where new lignified elements arise in such large numbers that the pith disappears. The groups of phloem and protoxylem having closed in also, a typical tetrarch stele results (Diagram 7, IV).

In these seedlings there is a good deal of variation in the level at which transition first begins. In the midrib, for example, in some cases, the phloem bifurcates and the xylem divides into three before entering the hypocotyl.

Seedling with three cotyledons. In this case one of the cotyledons was much larger than the other two. In the upper part of the hypocotyl the strands from each cotyledon behave as in the ordinary seedlings; consequently, for some distance there are six protoxylem groups, and six other masses each consisting of xylem and phloem. Finally, the protoxylem and the metaxylem bundles from the smallest cotyledon die out, and rearrangements occur which result in the production of a tetrarch root.

Tridax procumbens, Linn. Seedlings small (generally less than 4 cm. in length), each possessing two unequal cotyledons which unite at the base to form a very short cotyledonary tube.

In the sessile cotyledons the vascular bundles are of the type, and follow the course, characteristic of the Compositae. A noteworthy feature is the early preparation for transition in the median bundle. As soon as the numerous vascular strands of the upper part of the cotyledon have given place, by fusion, to the usual midrib and two lateral bundles, the former bifurcates (Diagram 8, I). The two xylem portions thus produced remain in continuity by means of the protoxylem (which moves slightly to take up an exarch position), but the phloem halves diverge and become widely separated. Lower down, in the short cotyledonary tube, the lateral strands fuse in pairs, and the resulting bundles pass inwards nearly to the centre, where for a time they remain symmetrically disposed in the intercotyledonary plane. In the upper part of the hypocotyl, these bundles move round in an anti-clockwise direction (as seen from above), and finally come into contact with the two branches of the bifurcated midrib bundles situated at diametrically opposite corners of the square stele. This is the condition characteristic of the hypocotyl (Diagram 8, II).

Near the base of the hypocotyl the symmetry is restored by the disappearance of part of the original intercotyledonary strands, and the complete fusion of the remainder with the corner bundles (Diagram 8, III). In the latter, at this level, no protoxylem can be distinguished. In the root most of the pith becomes replaced by vessels, and in the almost solid xylem core there are occasionally four narrow angles simulating a tetrarch structure. Finally, the xylem narrows considerably in the intercotyledonary plane, the

four phloem groups fuse in pairs, and near the root-tip there is a typical diarch stele (Diagram 8, IV).

In one seedling in which the cotyledons were comparatively thick, the bundles in them showed less division and re-fusion. A further point of difference concerns the intercotyledonary bundles; these moved to the same side in the hypocotyl, instead of assuming the diagonal position.

Galinsoga parviflora, Cav. Seedling about 2.5 cm. long, with a very slender hypocotyl. The transition region is elongated, and the rearrangements are like those in *Heliopsis laevis*, Seedling B.

DIAGRAM 8. *Tridax procumbens*.

Madia sativa, Molina. Seedlings slender, over 12 cm. long, and possessing comparatively large, foliaceous cotyledons.

The details of transition are exactly like those in *Heliopsis laevis*, Seedling B, and it is worth noting that though these seedlings were twice the size of Seedling A in the species just referred to, there was only the slightest trace of a tetrarch structure.

Tribe VI. Helenieae.

Baeria coronaria, A. Gray. Seedlings about 3 cm. long and extremely slender.

Little vascular tissue is present. The two laterals in each seed-leaf fuse with the midrib before they reach the short cotyledonary tube, and the details of transition conform to Van Tieghem's Type 3.

Gaillardia aristata, Pursh. Seedlings 4–6 cm. long, with prominent cotyledons and very short hypocotyls. Transition exactly as in *Charieis heterophylla*.

Tagetes erecta, Linn. Seedlings 5–6 cm. long with narrow, rather fleshy cotyledons.

The transition, first described by Gérard (5, p. 369), is similar to that described for *Heliopsis laevis*, *Seedling A*, the following being the chief points of difference: the strands produced by fusion of the laterals from the cotyledons gradually die out while still some distance from the centre of the hypocotyl. Near the base of the latter they reappear internally to the lateral phloem groups, only to disappear finally in the root, which then possesses a diarch arrangement. Thus, a semi-tetrarch structure, with four protoxylem groups and two or four phloem masses, is present for a long distance.

T. patula, Linn. Seedlings externally like those of *T. erecta*.

Transition similar in all details to that in *Heliopsis laevis*, *Seedling B*.

Tribe VII. Anthemideae.

Anacyclus Pyrethrum, DC. Seedlings about 6 cm. long. Transition as in *Tridax procumbens*, a diarch root being produced.

Achillea pyrenaica, Sibth. Seedlings about 3 cm. long, each with two equal cotyledons, which, uniting at the base, produce a cotyledonary tube. The transition is almost exactly as in *Charieis heterophylla*.

Matricaria eximia? Seedlings about 2 cm. long. Vascular strands very minute, with transition as in *Charieis heterophylla*.

Tanacetum vulgare, Linn. Seedlings generally 4–5 cm. long, with comparatively large seed-leaves, and a very long cotyledonary tube.

Transition is similar to that in *Charieis heterophylla*, but the fused laterals disappear in the cotyledonary tube. In one seedling which was larger than the rest, however, the lateral (cotyledonary) strands persisted for a considerable distance in the hypocotyl.

Chrysanthemum carinatum, Schousb.

C. Sibthorpii?

} Seedlings slender, 4–6 cm. long; cotyledons equal in size and comparatively fleshy. Transition almost exactly as in *Charieis heterophylla*, except that the intercotyledonary bundles may join those in the cotyledonary plane by moving in a clockwise direction, or may disappear before they reach the centre of the hypocotyl.

C. Parthenium, Bernh.

C. viscosum, Desf.

} In these seedlings, which are slightly larger than in the last species, the general course of events is the same, but the intercotyledonary strands generally travel to the centre of the hypocotyl, where the xylem portion forms the core of the diarch plate. In all the

species of *Chrysanthemum* the arrangement of the median strand begins in the long cotyledonary tube, and is soon completed.

Artemisia annua, Linn. } Seedlings very short (2-3 cm. long) and
A. Absinthium, Linn. } slender; the vascular strands throughout are correspondingly small, and the transition is exactly similar to that in *Chrysanthemum Parthenium*, the root being diarch in structure.

Tribe VIII. Senecioneae.

Senecio clivorum, Maxim. In all the seedlings, which varied in length from 7-10 cm., the hypocotyl was comparatively short (less than 1 cm.), and the seed-leaves, which were spatulate in shape and were furnished with long petioles, were distinctly unequal in size.

The venation of the cotyledons is not peculiar. The numerous bundles present in the leaf-blade fuse in various ways to give rise to a large midrib and two small laterals, all of which run down the petiole and enter the hypocotyl almost unchanged. In the upper part of the latter each midrib bundle undergoes modification: the phloem bifurcates, and the two halves travel laterally, while in the wood portion the protoxylem begins to take up an exarch position. The intercotyledonary strands produced by the fusion of the laterals in pairs pass to the centre of the hypocotyl, and after a longer or shorter distance has been traversed, they gradually die out. The phloem groups having previously assumed a lateral position and fused in pairs, the midrib xylem masses meet at the centre, and a typical diarch root is produced. Altogether the transition is like that in *Charieis heterophylla*.

In the region of the root-tip, after the pith has completely disappeared, there is often a return to an almost tetrarch condition: this is brought about by the enlargement of the xylem in the intercotyledonary plane, and the subsequent more or less complete division of the phloem masses.

Tribe IX. Calenduleae.

Silybium Marianum, Gaertn. Seedlings 8-10 cm. long, and rather massive.

The course of the vascular strands in the cotyledon is the same as in *Silphium perfoliatum* (p. 308). The bundles formed by the fusion of the four laterals on either side of the midrib are smaller than the latter, and their protoxylem groups never become exarch. With the decrease in size of the hypocotyl in passing downwards, the intercotyledonary strands travel centrewards, then dwindling in size, they move laterally in a clockwise manner (as seen from above), and fuse with the flattened midrib. There is no real tetrarch arrangement, but at the base of the hypocotyl the midrib xylem groups, each of which by this time has a definite protoxylem, meet

at the centre, the phloem groups unite laterally, and the diarch root is complete.

Dimorphotheca pluvialis, Moench. This species is interesting in that the small crop of seedlings grown included many tricotyledonary examples, while the rest showed all stages between these and seedlings with the normal number of cotyledons. Reference to Text-Fig. 1 (p. 319) will show that the larger number is due to the splitting of one of the two original cotyledons.

DIAGRAM 9. *Silybium Marianum*. (For I, II, and III see Diagram 4.)

The seedlings are generally about 4.5 cm. long, and

are very slender. There is no cotyledonary tube, and the transition is very similar to that described for *Tridax procumbens*, but of a much reduced type, the vascular bundles being very small.

DIAGRAM 10. *Dimorphotheca pluvialis*. 'Transition' in seedling with 3 cotyledons. (For description see text.)

Seedlings with three cotyledons. A comparison of Diagram 8 with Diagram 10 will reveal the peculiar features of the transition in the

tricotyledonary seedlings. Working from root to cotyledons, the diarch stele gives place in the hypocotyl to four collateral strands—the two large ones in the plane of the diarch plate (corresponding to the plane of the cotyledons in an ordinary seedling), and two small ones in a plane at right angles to the diarch (intercotyledonary plane in an ordinary seedling), (Diagram 10, IV and V). If two of the cotyledons really correspond to one in the dicotyledonous seedling, it follows that half the vascular tissue should supply one of the three cotyledons, while the other half should do duty for the remaining two cotyledons; which is what actually happens. One of the large bundles (y) and half of each small one (x and z) pass to a single cotyledon, while the remaining halves of the small strands form one of the lateral bundles in each of the other cotyledons. The other large strand divides into three—two large bundles, each forming a midrib, and a small bundle which bifurcates so as to supply the two lateral strands required (compare with Diagram 10, I, II, and III).

Thus the anatomy, also, supports the view that two of the seed-leaves are homologous with one in the dicotyledonous seedling.

Tribe X. Arctotideae.

Arctotis calendacea, Linn. (*Cryptostema calendulaceum*, R. Br.). Although the seedlings are much larger than those of *Charieis heterophylla*, the transition is similar, the lateral strands of the cotyledon, after fusing in the hypocotyl, passing to the centre to form the core of the diarch root. The transition, which is completed at a high level, begins in the cotyledonary tube.

Tribe XI. Cynareae.

Arctium majus, Bernh. In this species the seedlings, which are generally about 6–8 cm. long, are each provided with two rather fleshy, equal cotyledons, which possess a peculiar venation. Near the base of each seed-leaf there are the usual three bundles—a large midrib and two small laterals. The latter follow the margins of the cotyledon to the apex, where they are joined by the midrib and its chief branches, which arise in the following manner. In the upper half of the seed-leaf the midrib gives off its branches, which run outwards at an acute angle and join the laterals somewhat nearer the apex; but before doing so each gives rise to a branch which runs

TEXT-FIG. 1. *Dimorphotheca pluvialis*. A and B represent seedlings showing two stages in the production of the tricotyledonous condition. a, b, c (from actual specimens) show stages in division of one cotyledon into two.

approximately parallel with the midrib, and like the latter joins the lateral strands at the apex. Smaller branches are also given off by all these bundles. The character seen in most of the Compositae examined, i. e. fusion of the chief bundles at the apex of the cotyledon, is easily demonstrated in this species.

The transition is much like that seen in *Charlieis heterophylla*. The xylem of the lateral strands remains distinct in the centre of the hypocotyl for a long distance before finally merging into the xylem of the midrib bundles to form the diarch plate.

Saussurea albens, Hook. Seedlings 6-9 cm. long, and rather massive. The internal morphology is very similar to that in *Silybium Marianum*, the chief difference being that here the transition begins at a high level. In the midrib bundles the phloem bifurcates, and the protoxylem becomes exarch while still in the cotyledons.

Onopordon tauricum, Willd. Seedlings very large, with ovate and equal cotyledons which join at the base to form a large cotyledonary tube. The transition is almost exactly as in *Tridax procumbens*, a diarch root being produced:

Crupina Crupinastrum, Vis. In this species the seedling is similar in size and external morphology to that of *Silybium Marianum*, and differs from the latter only in a few particulars with regard to transition. In both there are five strands at the base of the cotyledon. The extreme laterals from one cotyledon fuse with the corresponding bundles from the other as soon as the cotyledonary tube is reached. The fused structure, instead of moving round in a clockwise manner as in *Silybium Marianum*, passes inwards, and is joined by the remaining lateral strands on the same side, the three fusing together. All this occurs in the cotyledonary tube, so that only two bundles in addition to the two midribs enter the hypocotyl. These four strands, of which the intercotyledonary ones are the smaller, are symmetrically arranged. In the midrib the bundles become tangentially flattened, and gradually the protoxylem takes up an exarch position. In the intercotyledonary bundles the phloem, also, spreads out and is joined by the bifurcations of the midrib phloem. At a lower level, the xylem of these bundles gradually decreases in size and passes inwards. Near the centre it is joined by the xylem from the cotyledonary plane, with which it fuses, producing a diarch root.

It should be noted that here, though the arrangement in the hypocotyl suggests a tetrarch root-structure, the latter is never attained. In the intercotyledonary strands the xylem never becomes exarch, and the phloem, though assuming a flat ribbon-like form, never bifurcates.

Amberboa (Volutarella) muricata, DC. Seedlings 4-6 cm. long, and with comparatively fleshy seed-leaves. The transition is similar to that in *Crepis rubra*.

Serratula tinctoria, Linn. Seedlings 9–12 cm. in length, with long, almost linear cotyledons, and a very extended cotyledonary tube. The main features of the cotyledons and of the rearrangement of the vascular bundles are very similar to those in *Charieis heterophylla*, but the region of transition is much longer. In some cases the intercotyledonary strands are retained in the centre almost to the root-tip.

Centaurea macrocephala, Puschk. Seedlings both externally and internally similar to those of *Silphium perfoliatum*. A tetrarch root with a large pith is first produced, which lower down decreases in area in transverse section, so that the pith becomes smaller and the vascular tissue takes up a position nearer the centre. The xylem in the intercotyledonary plane now becomes reduced. One by one the lignified elements disappear, the phloem groups fuse in pairs laterally, and a diarch root is produced.

C. babylonica, Linn. Seedlings not so large as in the last species, and vascular strands correspondingly smaller. The chief features of the transition are similar to those in *Crupina Crupinastrum*. The intercotyledonary bundles decrease immediately after their formation by fusion of the four lateral strands, and when only slightly rearranged they pass inwards and fuse with the cotyledonary bundles. At quite a high level, a diarch root-structure obtains.

Carthamus tinctorius, Linn. In all essentials the seedling of this species (which was also examined by Gérard (5, p. 367), is like a much reduced one of *Centaurea macrocephala*, exhibiting exactly the same features as *Centaurea babylonica*. The seedling is not nearly so massive as that of the former species, and the vascular bundles are very much smaller. In the very long cotyledonary tube the extreme lateral strands fuse in pairs, and almost immediately die out or fuse with the other lateral bundles. The latter next fuse in the same order, and of the four strands which enter the hypocotyl, the two very small ones in the intercotyledonary plane immediately pass to the centre to form the core of the diarch root. Thus there is only the slightest trace of a tetrarch structure. At a fairly high level the midrib strands undergo rearrangements which result in the production of a diarch stele.

Tribe XIII. Cichorieae.

Cichorium Intybus, Linn. (garden variety). Seedlings short (not more than 5 cm. long) and rather stout. The cotyledons are broad and ovate in shape, and fuse at the base to form a fairly long cotyledonary tube. In each seed-leaf there is a definite midrib with smaller veins which run more or less parallel with the margin. These join on to the midrib very gradually, the last fusion occurring in the cotyledonary tube. Only two bundles enter the hypocotyl, and these become rearranged according to Van Tieghem's Type 3.

Picris echioides, Linn. Seedlings 5–6 cm. long, with slender hypocotyl and large foliaceous cotyledons. Transition as in *Charieis heterophylla*, with only slight variations on the latter.

Tragopogon dubius, Scop. Seedlings 10–12 cm. in length, with short hypocotyl and long, linear cotyledons.

Though the seedlings differ so much externally from those of *Centaurea macrocephala*, the transition is almost exactly similar. In the upper part of each cotyledon, there are three main vascular bundles with numerous smaller ones. At the base these give place to five strands which in most seedlings follow the course described for *Centaurea macrocephala*. An almost perfect tetrarch root is formed, which becomes diarch at a lower level.

DIAGRAM II. *Hieracium alpinum*.

In one seedling the outermost bundles in the cotyledons disappeared soon after fusion. In the same specimen there were two extra small bundles, one on either side of the midrib, which persisted for some distance in the hypocotyl. It was not clear whether these small strands finally died out or fused with some of the other bundles.

Lactuca sagittata, Waldst. Seedlings small (less than 5 cm. long); cotyledons equal in size and rather fleshy. Transition almost exactly as in *Charieis heterophylla*.

Crepis rubra, Linn. Seedlings about 4 cm. long, each with a distinct cotyledonary tube. Transition as in *Charieis heterophylla*, with the exception that the intercotyledonary strands, instead of passing directly

to the centre of the hypocotyl, travel obliquely and fuse with the midrib bundles. By further rearrangement a solid diarch xylem-plate is formed.

Hieracium alpinum, Linn. Seedlings 7-9 cm. long, with comparatively large, more or less lanceolate seed-leaves which join the hypocotyl without forming a cotyledonary tube.

The numerous vascular strands which occupy the upper part of the cotyledon give place at the base to three, the two lateral bundles being very small (Diagram 11, I). The rearrangement in the midrib strand begins at the base of the cotyledon, but the protoxylem does not become really exarch until the root is reached. In the upper part of the hypocotyl the corresponding laterals fuse in pairs, the resulting bundles passing inwards towards the centre (Diagram 11, II and III). During its passage, the protoxylem becomes exarch, and the metaxylem gradually disappears. At a lower level there is a bisymmetrical tetrarch arrangement, the protoxylem groups being devoid of metaxylem, and the phloem being disposed in two flattened masses in the intercotyledonary plane (Diagram 11, III). Finally, the protoxylem elements enlarge, merge into the metaxylem at the centre, and give rise to a diarch root (Diagram 11, IV).

In other seedlings examined the same sequence was found, but owing to the extreme smallness of the lateral bundles, the features were not exhibited with the same diagrammatic clearness in all cases.

THEORETICAL CONSIDERATIONS.

In a former paper on the seedling structure of the Tubiflorae (7) certain theoretical conclusions were put forward, to one of which allusion has already been made (vol. xxvi, p. 742). It was also shown that in the matter of classification no assistance is to be derived from seedling anatomy. In the Tubiflorae, genera, which on other grounds are held to be nearly related, differ markedly in the vascular anatomy of their seedlings, e.g. *Incarvillea* and *Eccremocarpus* (N. O. Bignoniaceae).

The present case is rather different. In the fairly large number of seedlings examined, it cannot with reason be held that more than one type of transition has been discovered: for, although there are two extremes—diarch and tetrarch—all stages from the one to the other have been described in the preceding pages. The diarch type seen in *Cichorium Intybus* and *Baeria coronaria* passes by way of *Solidago ulmifolia*, *Charlieis heterophylla*, and others (in which the laterals persist for a longer or a shorter distance without giving more than the slightest indication of tetrarchy) to *Hieracium alpinum*, *Heliopsis laevis*, and others (in which the laterals persist to form the weak intercotyledonary poles of a tetrarch root); and thence to such plants as *Silphium perfoliatum* (in which a fully symmetrical, tetrarch root is invariably present). That these are essentially stages of the same

type is also indicated by the variations not uncommonly found in the seedlings of certain species. To take a single instance, in one seedling of *Heliopsis laevis*, the tetrarch stage present in the others was entirely omitted. Many smaller variations were noted in other cases, all of which unite in giving the observer the impression that even the extreme 'types' are only variations on one method of transition. Throughout the group this sense of similarity is apparent, and, as in other cases where evolution has been at work, it is impossible to draw hard and fast lines between the two extremes. The case of *Heliopsis laevis* again demonstrates the uselessness of seedling structure as an indicator of affinity.

It is very difficult to determine the cause or causes of such variations; and it is equally difficult to determine which type—diarch or tetrarch—of seedling structure is primitive and which derived. Many authors have discussed the general question of the evolution of seedling structure. In her 'Theory of the Double Leaf-trace' Miss Thomas (12) examines the evidence and concludes that the tetrarch type is primitive, and has given rise to the diarch by reduction. To the present writer this conclusion seems to require extreme conservatism on the part of the seedling: for, unless we assume that the first seedling had a certain type of structure, and that in the ages that have passed since it existed, either the structure has remained unaltered or has changed once and once only, the term 'primitive' becomes meaningless and the discussion futile.

But is such an assumption justified? Are we at liberty to assume that while the mature parts of plants have varied enormously, the young parts have suffered little or no structural alteration? Comparatively little work has been published on the physiology of seedlings, but sufficient has been done to indicate that seedlings can easily be altered artificially. Evans (4), working on *Luzula*, showed that by sowing the seeds at different depths in the soil a hypocotyl of corresponding length could be produced; and when other methods are used and other species experimented with, it will probably be shown that within certain limits the size of the seedling organs can be regulated. Apart, however, from mere speculation, Evans's work indicates that seedlings can be made to vary by artificially altering the environment. There is no doubt that great changes have occurred on the earth's surface during even recent geological times, and if this be so, it is highly probable that seedlings also have altered in accordance with the changed conditions. The different sizes and shapes which seeds have assumed, and the various functions adopted by seedling organs (in connexion with storage, transference of food material, &c.), indicate that the seedling is the reverse of conservative, and that it is really very susceptible to changes of all kinds. There seems, therefore, a high degree of probability that not only have seedlings not been more or less at a standstill during recent geological times, but that they have been continually evolving.

Several writers have emphasized the fact that in general seedlings have either a diarch or a tetrarch root. The connexion between these two types has been shown above. Only in exceptional cases is some other arrangement found to hold, e.g. in the Liliaceae (10). If, in the general case, evolution of the seedling anatomy has not been an extremely slow process, it is quite possible that diarchy and tetrarchy have been gained and lost many times during the evolution of the Angiosperms. This may help to explain the presence of the two types of seedling structure in the Compositae, which by universal consent is the most highly organized Natural Order in the Plant Kingdom. In this group, if there are cases, as Miss Thomas assumes, where the tetrarch structure is becoming reduced to diarch, there are as certainly seedlings in which the diarch structure is giving place to tetrarch.

In the general description of the venation of the seed-leaves (p. 305) it was shown that there are always present more or less numerous laterals in the cotyledon. On a first consideration it appears that the conditions which regulate these laterals determine the type of root to be produced; that is, that the *size* of the laterals and the *level* at which they unite with the bundles in the cotyledonary plane might well determine the type of root structure. But the problem is not so easily solved. Compared with the respective midrib bundles, the lateral strands in the species which possess fully symmetrical tetrarch roots are often no larger than the laterals which form the core of the diarch root in the diarch species; while in such examples as *Bidens pilosa* and *Zinnia pauciflora*, both of which are strongly tetrarch, they are much smaller and are more or less insignificant.

The level at which the laterals unite with the midrib strand varies greatly. In the extreme cases it is true that in the diarch seedlings this union occurs in the cotyledon or in the upper part of the hypocotyl; while in the extreme tetrarch seedlings the union occurs near the base of the hypocotyl. But between these two extremes there is every gradation, as will be seen from the descriptions in the preceding pages. To the present writer it seems obvious that there must have been some other factor at work in addition to the size of the laterals and the level at which these unite with the midrib bundles.

According to Hill and de Fraine (6), 'size of seedlings almost, if not quite, determines whether or not the laterals shall penetrate the hypocotyl or fuse with the main cotyledonary strand before its entrance,' i.e. size of seedling determines whether a diarch or a tetrarch arrangement shall be produced. A similar conclusion was reached by Compton in studying the Leguminosae (1). In the Compositae, as well as in the Tubiflorae, it is generally true that large seedlings are tetrarch and small seedlings diarch, but there are many conspicuous exceptions. An inspection of the outline-drawings given in Text-fig. 2 will save discussion. The drawings are all

to scale. The roots of those marked (1) are diarch throughout, those distinguished (2) are tetrarch throughout, while those marked ($\frac{2}{1}$) are first tetrarch, but finally become diarch. The difference in size between *Arctium majus* or *Crupina Crupinastrum* and *Baeria coronaria* need not be emphasized, but it must be noted that all these possess the same type of seedling structure. Again, compare *Arctium majus* or *Crupina Crupinastrum* with *Silphium perfoliatum*; the first two are diarch, the last tetrarch throughout, though one can hardly say that the difference in size warrants such a difference in vascular anatomy. An examination of the seedling of *Bidens pilosa* serves not only to emphasize this point, but also to throw light on another, i. e. the relation between the amount of vascular tissue present and the type of seedling structure.

If, as has been cautiously advanced by Hill and de Fraine (6), there is a real relation between the size of the organ and the amount of vascular tissue present, it follows that organs of the same size should (if the vascular tissue be arranged in the same way) possess the same amount of vascular tissue, not in a transverse section, but in the whole organ; and further, that in an organ like the hypocotyl, which presumably, in the ordinary case, everywhere performs the same function, the vascular tissue present in any transverse section should equal in amount the vascular tissue in any other transverse section of the same area.

To take the first case. In the seedling of *Fagus sylvatica*, Hill and de Fraine appear to pit the area of vascular bundles in a transverse section of the seed-leaf against the surface area of the cotyledon. Now, as the vascular bundles decrease in size towards the apex of the seed-leaf, the area of the bundles depends very much on the position of the transverse section, and it is improbable that one would be able to select the corresponding section in a large number of seedlings. Furthermore, the relation between the amount of vascular tissue in a transverse section and the surface area of the leaf is not at all obvious. It appears, on the other hand, that the total amount of vascular tissue present in the organ should be taken into account, and should be correlated either with the cubic contents of the leaf or with the surface area. Here again, it is almost impossible to make precise measurements. A cursory examination, however, of almost any species will reveal the fact that while the type of venation remains the same, the number and extent of the smaller bundles vary greatly, even when the leaves are of the same size.

With regard to the second point raised above, in most hypocotyls, measurements show that in successive transverse sections of the hypocotyl the amount of vascular tissue is approximately the same, or it decreases slightly towards the base of the hypocotyl. This is what one would expect on any theory postulating a definite connexion between size of organ and the amount of vascular tissue present. In the hypocotyl of *Bidens pilosa*,

TEXT-FIG. 2. Some of the seedlings used in the present paper (drawn to scale). (1) indicates that the root is diarch throughout; (2) indicates that the root is tetrarch throughout; (2/1) indicates that the root is first tetrarch, but becomes diarch at a lower level.

however, there is much variation; near the top of the hypocotyl the vascular bundles enlarge, while a little lower down they decrease to a very small number of elements in each case before finally increasing at a still lower level and attaining a comparatively large size. This is only one out of several instances where fluctuations occur in the size of the bundle in the hypocotyl. Everywhere in the latter organ, apparently, the vascular bundles do the same work, yet fluctuate in size.

Finally, from a careful study of a large number of seedlings, and after making measurements into which it seems impossible to read anything like constancy or uniformity, the present writer is forced to the conclusion that other factors are at work in addition to those which are purely physiological. It is possible that two sets of factors are constantly influencing the seedling: (1) those factors which are purely physiological, and which are concerned with changes in the environment; and (2) factors which are connected with the nature of the organism.

It seems impossible to avoid the impression that changes occur in the seedling which cannot be correlated with changes in the environment. These changes in the seedling, due to the nature of the organism, occur continuously, and are probably to a certain extent guided by the first set, or physiological factors. But even when the latter are quiescent—as they must be when there are no changes in the environment—the innate factors are probably always active, and are constantly producing morphological changes in the various seedling-organs. The two sets of factors will sometimes be antagonistic, in which case the physiological factors, which are based on the immediate needs of the plant, will be dominant and will determine the changes which occur. When the physiological factors are quiescent, and new structures are produced by the innate factors, so long as these new structures do not unfit the seedling, they will persist; but when a new structure begins to clash with the environment the physiological factors will be brought into play.

In general, seedlings are limited to two extremes of vascular structure, the diarch and the tetrarch. The course of evolution is probably not to be represented by a straight, nor by a zigzag line, but by a spiral with a large number of turns, the spiral representing the fluctuations between the diarch and tetrarch structure, the axis the general line of advance of the seedling.

SUMMARY.

1. The present paper deals with the seedling structure of about fifty species belonging to the Compositae.
2. All the seedlings belong either to the diarch or to the tetrarch type.
3. Variations in vascular structure occur not only in nearly related species, but in different examples of the same species, indicating that seedling anatomy is of no value in questions of affinity.

4. It is held (*a*) that the evolution of the vascular structures of seedlings is probably not an extremely slow process; but that (*b*) tetrarchy and diarchy have probably been interchanged several times during the evolution of Angiosperms.

5. It seems probable that physiological factors are not sufficient to account for all the structures found in seedlings.

6. There are many exceptions to the rule that size of seedling is correlated with the type of structure.

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(A more complete list will be found in the previous paper (7).)

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