

The Seedling Structure of certain Cactaceae.

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With eighteen Diagrams and nineteen Figures in the Text.

CONSIDERABLE importance has of late been attached by some observers¹ to the transition-phenomena in seedlings of Spermophyta, more especially with regard to the help given by them in the elucidation of phylogenetic problems. In view of the value thus assigned to seedling anatomy it seemed desirable to make as complete a study as possible of the seedlings of some well-defined families. The Cactaceae, with their marked adaptations to dry conditions, seemed to offer a profitable field for investigation, particularly as the form of the seedlings of this group bears so evident a relation to that characteristic of the adult.

Ganong,² in his comprehensive account of the morphology of Cactaceous seedlings, states that the progressive condensation of the embryos runs strictly parallel to the condensation in the adults—it has its lowest term in *Pereskia*, and reaches its highest in the almost globular *Mamillarias*; further, this condensation is due to adaptation to a habitat of increasing desert conditions. He suggests that the form of the adults, 'as it becomes more and more fixed and intensified, tends to work back into earlier and earlier stages in the ontogeny of the successive individuals; until, finally, a character adaptively acquired by the adults works back into the epicotyl . . . and finally into the embryo.' This 'working back into the epicotyl' may be comparatively rapid, but the impression of such features on the embryo seems very slow; this is 'due no doubt to the fact that the embryos have a set of activities of their own in their early life which keeps them from being too plastic to other influences working upon them'.

¹ Sargent, E.: *Theory of the origin of Monocotyledons, founded on the structure of their seedlings.* Ann. Bot., xvii, 1903.

Tansley, A. G., and Thomas, E. N.: *The Phylogenetic Value of the Vascular Structure of Spermophytic Hypocotyls.* Report of Brit. Ass., Section K, 1906, p. 761.

² Ganong, W. F.: *Contributions to a Knowledge of the Morphology and Ecology of the Cactaceae.* II. *The Comparative Morphology of the Embryos and Seedlings.* Ann. Bot., xii, 1898.

The present communication forms part of Mr. T. G. Hill's scheme of investigation of seedling-structure, and has been carried out with a view to discovering whether there is any relation between the external morphology of the seedlings and their anatomy; in other words, whether the adult adaptations to physiological conditions, which have impressed themselves on the form of the young seedling, have had a corresponding influence on its internal structure.

The forms of many of the seedling Cactaceae have been figured at various times, but as Ganong¹ has already given a full account of the work done in this direction no detailed reference is required here; so far as has been ascertained, however, no observations on the seedling structure of any member of the family have been recorded.

No details of the colour factors of the seedlings will be given, as this question also has been fully dealt with by Ganong.¹ Owing to the great difficulty experienced in obtaining seeds, and the failure of these in many cases, when procured, to germinate, it has been found impossible to examine representatives of all the genera; in all, forty-seven species belonging to eleven genera have been investigated. I wish, in this connexion, to express my thanks to Professor Trelease of the St. Louis Botanic Gardens and to Dr. Rose of the Smithsonian Institute, both of whom sent me seeds, and also to Mr. Hales, Curator of the Old Physic Gardens, Chelsea, who not only obtained many seeds for me, but kindly undertook the germination of them all.

I should also like to take this opportunity of expressing my thanks to Mr. T. G. Hill, at whose suggestion this investigation was begun, for the encouragement and advice which he has constantly given me throughout its progress.

The methods employed were a slight modification of those described for the Gymnosperm seedlings;² in all cases the seedlings used were microtomed, and longitudinal preparations were frequently made in addition to the transverse series.

THE SEEDLING STRUCTURE OF THE CACTACEAE.

PERESKIA.

Pereskia n. sp., Rose. The seedlings are of an ordinary dicotyledonous type and show no sign of succulence; they have a long slender hypocotyl and two thin leaf-like cotyledons, one very much smaller than the other (Fig. 1).

Fig. 1. *Pereskia n. sp.* × 1.

This asymmetry of the seedling, caused by the difference in size of its

¹ Ganong, W. F. : loc. cit.

² Hill, T. G., and de Fraine, E. : On the Seedling Structure of Gymnosperms, I. Ann. Bot., xxii, 1908.

seed-leaves, is a characteristic feature of the Cactaceae, and may be due to the shape of the seed. The embryo is curved, and has a small quantity of endosperm lying against its concave side; the smaller cotyledon is on this side and is covered by the larger convex one. The seed-leaves have no true petiole, but towards their base they are narrowed off, and are almost oval in transverse section. Each cotyledon has, in its broadest part, from eleven to twelve small vascular strands; these either fuse among themselves or end blindly in the mesophyll, until towards the base of the seed-leaf only the median and two lateral bundles remain. Fairly high up in the seed-leaf the median bundle bifurcates, and the phloem groups rotate until they lie almost in line with the xylem, in which by this time the protoxylem has become exarch. The two lateral bundles (*l*) fuse with the bifurcated main bundle towards the base of the cotyledon in the manner indicated in Diagram 1, Fig. 1.

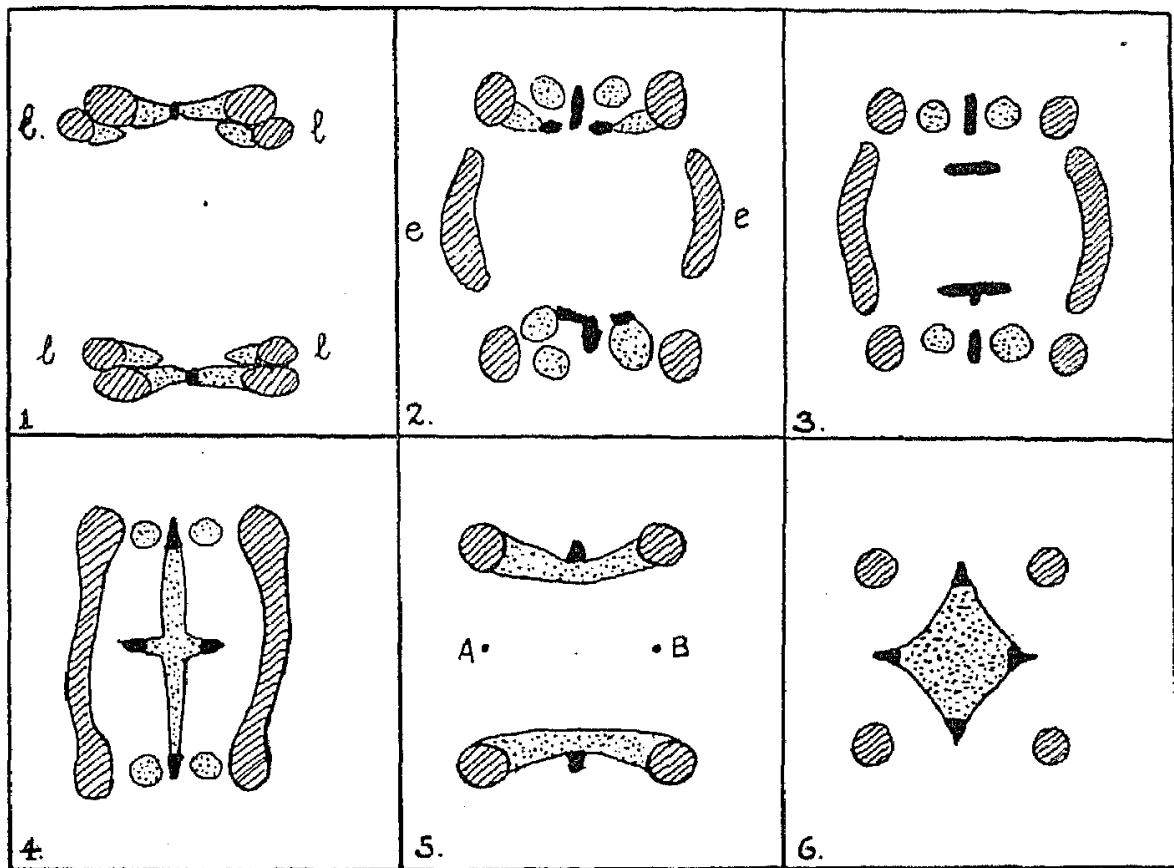


DIAGRAM 1. *Pereskia n. sp.* In this, and in all the following diagrams, the protoxylem is indicated by the black areas, the metaxylem by dots, the phloem by diagonal shading, and the cambium by a broken line.

The xylem elements are much scattered, and it is extremely difficult to make out the position of the protoxylem with any degree of certainty, but it is highly probable that during the passage into the hypocotyl the protoxylem branches in three directions (Diagram 1, Fig. 2). At this stage

a strand of epicotylar phloem bridges the space between the cotyledonary phloem groups. Soon after their separation the protoxylem elements arranged in the tangential position begin to move inwards, leaving the metaxylem and the radially placed protoxylem in an isolated position (Diagram 1, Fig. 3). Before reaching the centre of the axis these lateral branches pass outwards again, and the adjacent ones fuse; thus the two original protoxylem groups have, by branching into three and the subsequent fusion of adjacent lateral arms, given rise to four protoxylem strands in a manner which strongly recalls Miss Sargent's *Anemarrhena* type. The four groups of protoxylem formed in the manner just described very soon become connected, by the differentiation of tracheides, in such a way that a cross-shaped xylem plate is formed (Diagram 1, Fig. 4). This arrangement, however, does not long persist; the first indication of a change is given in the gradual breaking down of the phloem arcs opposite to the last-formed xylem groups; all the epicotylar phloem from this stage slowly dies out. Concurrently with these changes the intercotyledonary xylem arms gradually disappear, until finally only the two cotyledonary 'double' bundles with the protoxylem in the exarch position remain (Diagram 1, Fig. 5). All the details of the transition above described take place very rapidly and are restricted to the upper part of the long hypocotyl; no other changes occur until the root region is almost reached. At the base of the hypocotyl an isolated xylem element then arises in a position similar to that marked *A* (Diagram 1, Fig. 5); a little later this is followed by a second at *B*; new elements are then rapidly formed in the centripetal position until finally a solid core of xylem occupies the centre of the stele (Diagram 1, Fig. 6). The root is thus seen to be typically tetrarch, but two of its protoxylem groups are disconnected from the protoxylem of the higher regions of the hypocotyledonary axis.

The upper part of the root is, for a short distance, very thickly clothed with long root-hairs; below this region a cork cambium appears in the outer layers of the cortex, but at the age at which the seedlings were examined it had not been very active.

Pereskia Pititache, Karw. In general external characteristics the seedlings of this species are extremely like those of *Pereskia n. sp.*, except that the difference in size between the two seed-leaves is much less marked in them than in the latter. The structure of the cotyledons is also similar to that of *Pereskia n. sp.*, and the transition follows the course indicated in Diagram 1, Figs. 1-5. There is, however, no further change after the gradual disappearance of the intercotyledonary xylem arms, and the root structure is of the type which will be described later as characteristic of the genus *Cereus*, for it possesses two xylem-strands and four well-marked phloem-bundles.

In the seedlings of *P. Pititache* there is considerably less metaxylem

developed than in *Pereskia n. sp.*; and there is throughout the whole seedling a great abundance of cluster crystals.

OPUNTIA.

In external features the seedlings of this genus still maintain an almost normal dicotyledonous appearance (Fig. 2), but the hypocotyl has become somewhat more reduced in length as compared with *Pereskia*, while, at the same time, it is slightly more succulent, and the cotyledons though still leafy are distinctly more fleshy. The seed-leaves, as in the other genera, are markedly asymmetrical; they have a network of veins, as many as ten vascular strands being present in the transverse section of the cotyledon at some levels, but towards the base these are usually reduced to one, in which, by this time, bifurcation has generally occurred; there is never any suggestion of a petiole to the cotyledon, such as is indicated in *Pereskia*. The large cortical cells of the hypocotyl frequently contain crystals, e.g. *O. imbricata* and *O. Bergeriana*, and mucilage sacs are a characteristic feature of *O. stricta* and *O. Pseudo-tuna*.



FIG. 2. *Opuntia Tuna*. × 1.

Transition.

Opuntia Ficus-indica, Mill. In this species one 'double' bundle enters the hypocotyl from each seed-leaf; in it the bifurcation and subsequent separation of the phloem have proceeded so far that the xylem, which is composed of protoxylem elements only, is situated between two groups of phloem elements (Fig. 3, A).

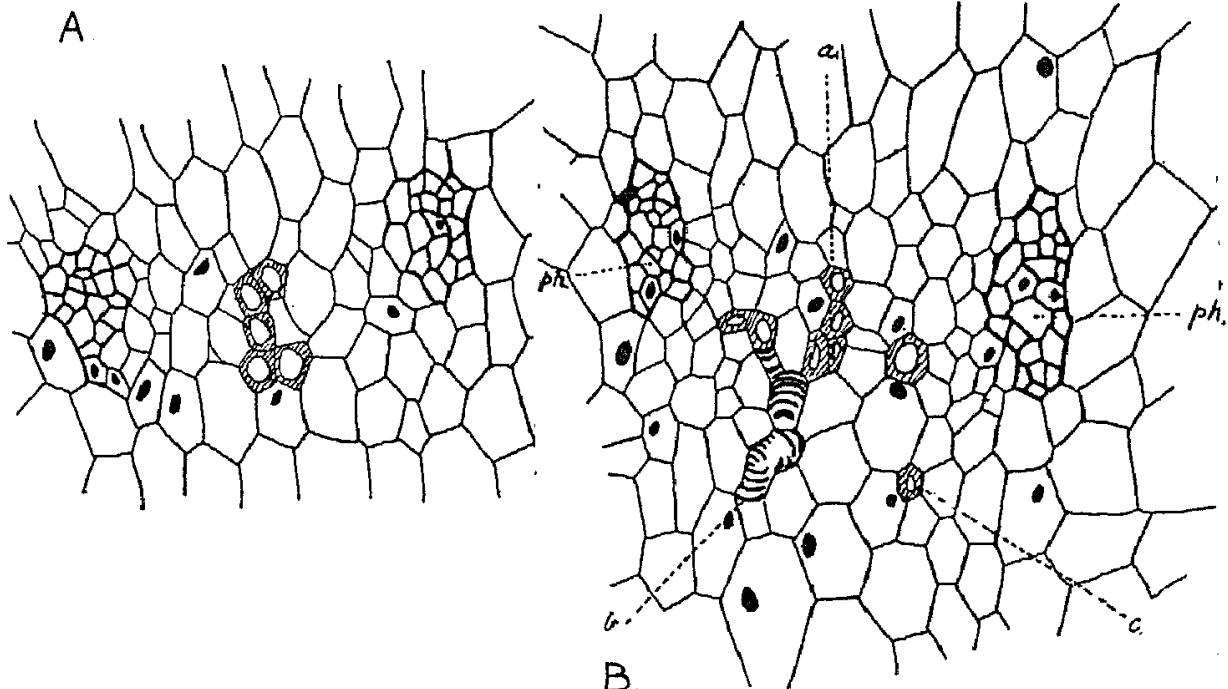


FIG. 3. *Opuntia Ficus-indica*. × 220.

Almost immediately after the entry into the hypocotyl has been made the protoxylem branches in three directions (*a*, *b*, *c*, and *a*₁, *b*₁, *c*₁, in

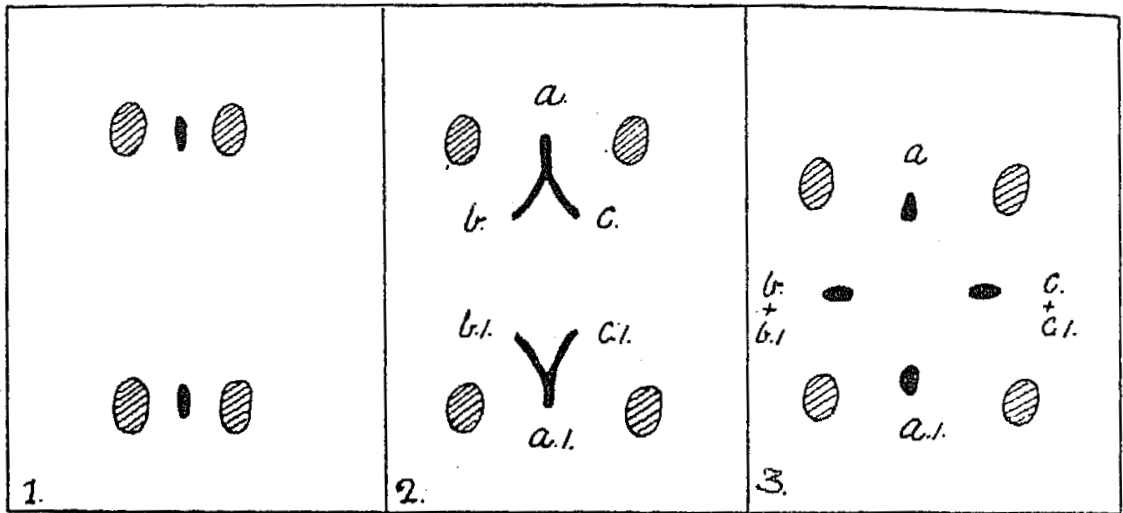


DIAGRAM 2. *Opuntia Ficus-indica.*

Diagram 2, Fig. 2, and Fig. 3, B), the adjacent arms (*b*, *b*₁, and *c*, *c*₁) fuse and give rise to the two intercotyledonary poles of the tetrarch root (Diagram 2,

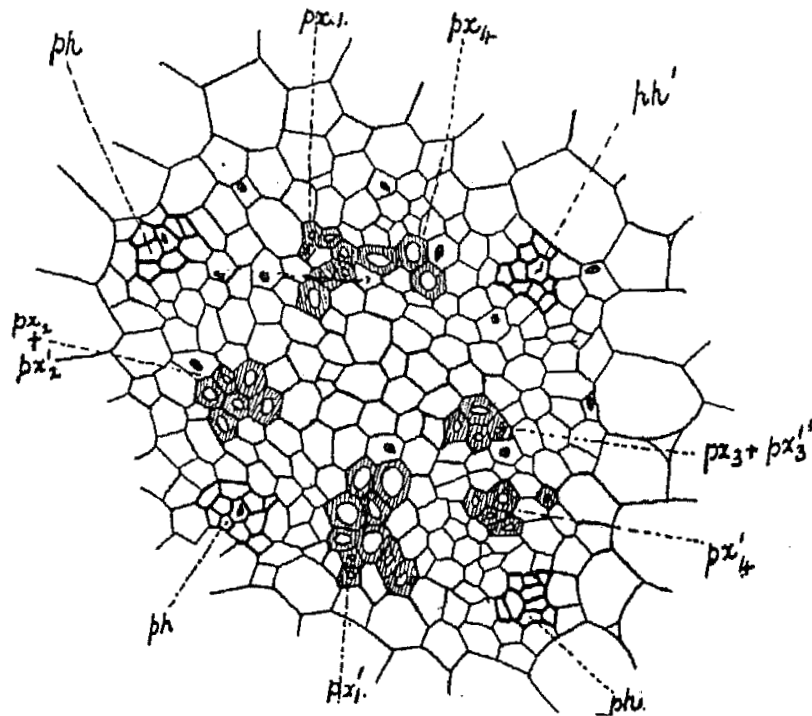


FIG. 4 A. *Opuntia Tuna.* Series B. $\times 220$.

Fig. 3). In this species, and in other of the *Opuntias*, there is thus the formation of a tetrarch root-structure from two cotyledonary traces by means of a transition which is of a type practically identical with *Anemarrhena*,¹ a type which, so far as it has been possible to ascertain, has

¹ Sargent, E. : loc. cit.

hitherto been undescribed among Dicotyledons, with the possible exception of *Eranthis* and *Podophyllum*.

Opuntia imbricata, D.C. In all essential features the transition in this seedling resembles that in *O. Ficus-indica*.

Opuntia Tuna, Mill.

Series A showed a type of transition such as is found in *O. Ficus-indica*.

Series B had at first a tetrarch root, produced in the same way as in Series A; but, at a lower level, this changed to a pentarch structure in the following manner.

The intercotyledonary protoxylem group ($px_3 + px_3'$ in Fig. 4 A)

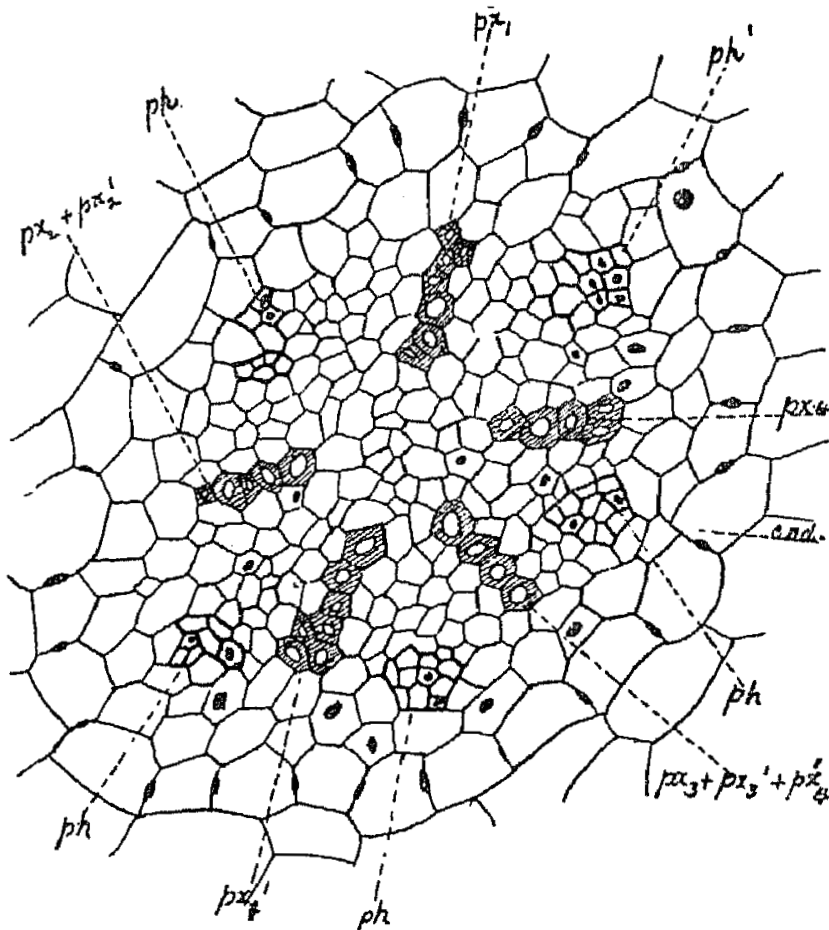


FIG. 4 B. *Opuntia Tuna*. Series B. $\times 220$.

appeared to be about to die out, when it was reinforced by a branch of xylem from px_1' (px_4'); simultaneously px_1 gave off another branch (px_4), and finally a fifth phloem group (ph^1) arose between px_1 and px_4 (Fig. 4 B); in this way the pentarch structure was completed.

Series C had a transition which was a slight modification of the *Anemarrhena* type. Two V-shaped bundles passed into the hypocotyl from the two cotyledons, the arms of the V very rapidly opened out, and the protoxylem which occupied its apex divided; half formed the exarch protoxylem group of the cotyledonary root-pole, the other half passed inwards

towards the centre of the axis, where it fused with the similar protoxylem group from the other cotyledonary bundle; metaxylem elements rapidly formed on either side of the plate thus produced. At a lower level one half of this intercotyledonary protoxylem plate died out, the other half moved rapidly outwards and formed the third root-pole (Fig. 5, $px_3 + px_3'$) and soon became connected by metaxylem elements with the other two protoxylems. The cotyledonary xylem groups (Fig. 5, px_1 and px_1') again branched (px_2 and px_2') and the fourth protoxylem of the tetrarch root was established.

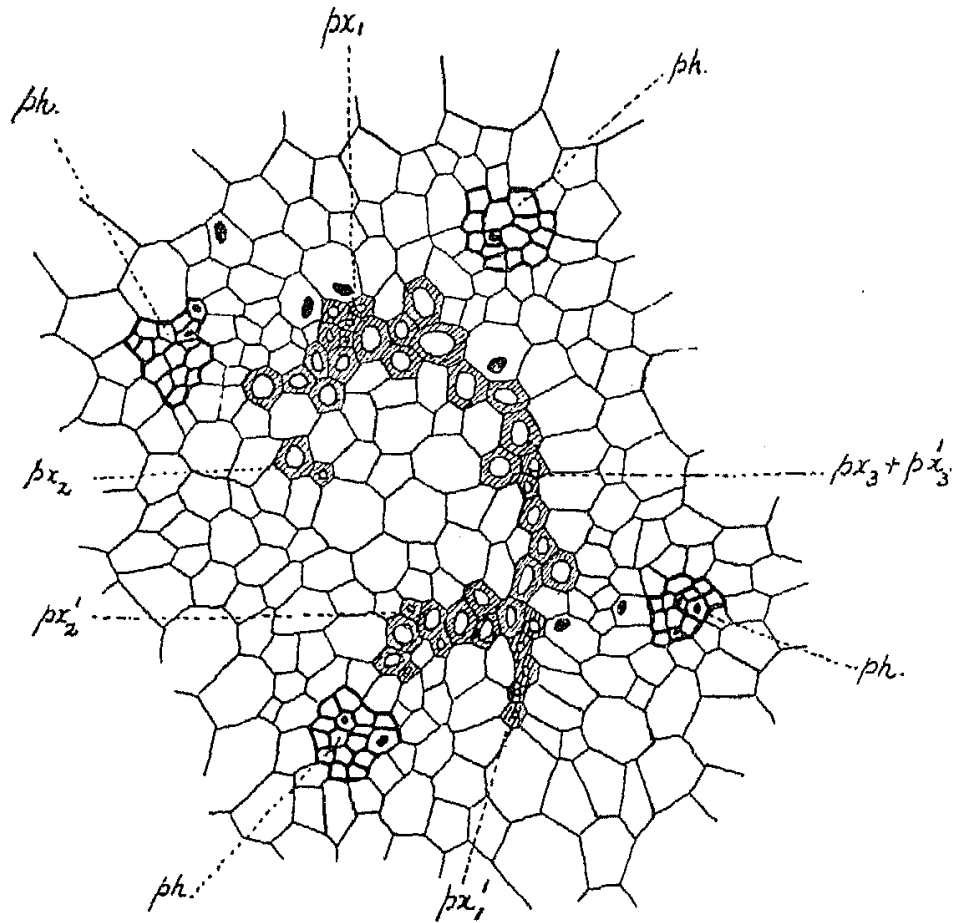


FIG. 5. *Opuntia Tuna*. Series C. x 220.

Two epicotyledonary strands were well developed in the upper part of this seedling and, during the early stages of the transition, they appeared to be about to take part in the root formation; they did not do so, however, and finally gradually died out.

Opuntia polyantha, Haw. Each cotyledon supplies the hypocotyl with one 'double' bundle, in which the xylem is arranged in three groups; very few xylem elements are present and in all probability no metaxylem has as yet developed. The lateral xylem groups of the 'double' bundle pass outwards towards the intercotyledonary plane and there fuse with the similar groups from the other 'double' bundle; the median group remains

in position and forms one of the cotyledonary root-poles. These movements of the wood are somewhat masked by the rapid increase in the number of tracheides which arise in the centre of the axis; they do not long persist and have all disappeared by the time the tetrarch root has become established.

In another example of this same species a modification of this process took place. The cotyledonary bundles were of the normal V-shaped type, part of their protoxylem became exarch by rotation, while the rest passed towards the centre of the hypocotyl and gave rise to a diarch plate; a little later this branched right and left and completed the tetrarch root-structure.

Opuntia Bergeriana, Weber. The transition-phenomena of the single seedling of this species which was examined was of the type found in *O. Ficus-indica*. Epicotyledonary strands were present in the upper part of the hypocotyl; they were well differentiated, and at a lower level fused laterally with the cotyledonary bundles. Cambium was developed in the bundles and contributed a few secondary elements to the metaxylem, and in the tetrarch root secondary thickening had well begun.

Opuntia stricta, Haw.

Series A is in all essential features like *O. Bergeriana*.

Series B is in the first stages of the transition identical with Series A, but the lateral xylem branches gradually die out and the hypocotyl in its middle region possesses only two 'double' bundles. In these features the seedling strongly resembles *Pereskia* (Diagram 1, Fig. 5); further, as in this species, a tracheid arising in the intercotyledonary plane and reinforced by others developed centripetally, once more restores the tetrarch root-structure.

Series C is of interest in that the seedling possessed three cotyledons, each of which contributed one V-shaped bundle to the hypocotyl. Six epicotylar strands were also present, arranged in pairs between the 'double' bundles, with the nearest one of which they almost immediately fused. It was impossible to say which elements represented the protoxylem, for though a considerable quantity of wood was present the elements were practically indistinguishable from one another. Soon after the fusion of the epicotylar strands with the seed-leaf-traces, the xylem of the bundles separated into three parts, so that at this level there were in the hypocotyl six collateral strands of wood and bast and three isolated xylem groups. Towards the base of the hypocotyl the adjacent collateral strands rotated their xylem and fusion took place, new tracheides connected up these xylem groups with the three isolated strands of wood, and so a ring of xylem, with six protoxylems alternating with the six phloem bundles, resulted. 'Barrel' tracheides of the type which will be described later under the genus *Echinopsis*, gradually developed in the centre of the axis until a solid

core of xylem resulted. In this seedling three cotyledonary bundles, by a branching of the xylem into three, have given rise to a hexarch root.

Opuntia albicans, Salm-Dyck. Only two seedlings of this species were obtained for examination, and in all essential characters of the transition they resembled *O. stricta*, Series B.

Opuntia maculacantha, C. F. Foerst. A 'double' bundle passes into the hypocotyl from each cotyledon (Diagram 3, Fig. 1), and during the passage through the cortex the phloems, carrying with them the metaxylem, move further apart and leave the protoxylem more or less isolated. No sign of any branching of the protoxylem occurs, and the remaining two poles of the tetrarch root originate by the development of tracheides at *A* and *B* (Diagram 3, Fig. 2).

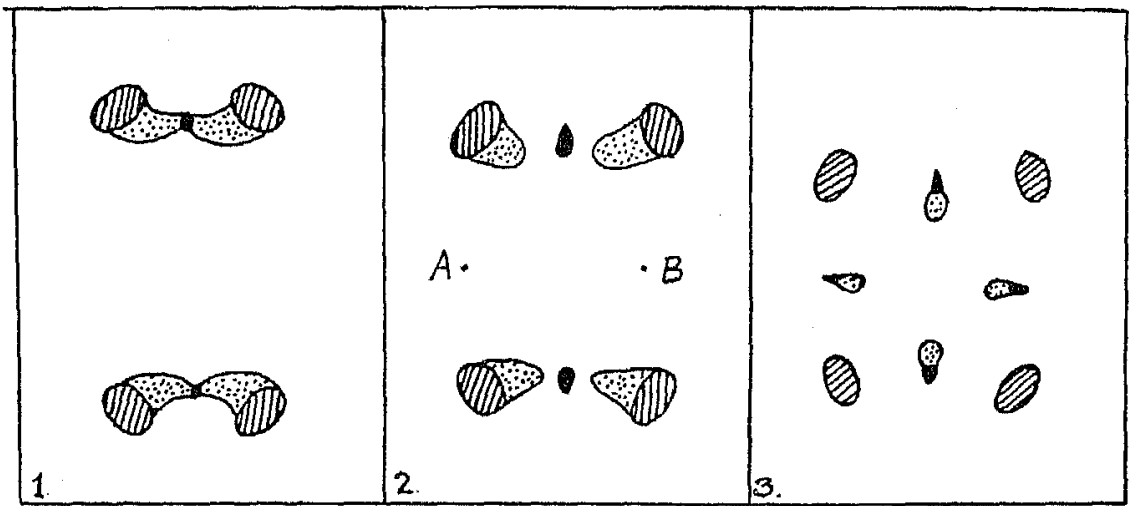


DIAGRAM 3. *Opuntia maculacantha*.

A few metaxylem elements are contributed to these two xylem groups by the cotyledonary metaxylem strands lying on either side. As in *O. stricta*, a few large barrel tracheides develop in the centre of the axis towards the hypocotylar base, but they do not long persist.

Opuntia Pseudo-tuna, Salm-Dyck. The transition in the only seedling of this species available for examination took place as in *O. maculacantha*; it is somewhat complicated, however, by the considerable number of secondary tracheides present, for much secondary thickening had taken place. It further differed from *O. maculacantha* in the complete absence of 'barrel' tracheides.

NOPALEA.

Nopalea n. sp., Rose. Of this genus the seed of only one species germinated, and judging from this example the seedlings bear a very close resemblance to those of the genus *Opuntia*, with the exception that the difference in size of the two cotyledons is much more marked in *Nopalea* than in *Opuntia*, or indeed in any other genus; further, the seedlings show a slight advance in succulence (Fig. 6).

The seed-leaves possess one median and six or seven lateral bundles, which either fuse or end blindly in the tissues of the mesophyll. At the base of the cotyledon only one bundle remains, which, at this level, has bifurcated and rotated (Diagram 4, Fig. 1). Six epicotyledonary bundles (*e*) also enter the hypocotyl; they arrange themselves in two groups between the cotyledonary bundles, and a cambium soon connects them with the phloem of the seed-leaf-traces; no xylem is differentiated in them during any part of their course. The xylem of each cotyledonary strand soon begins to send off a branch towards the centre of the axis (Diagram 4, Fig. 2); this strand almost immediately loses its metaxylem, and then branches right and left; at a later stage, the adjacent arms from the two cotyledonary bundles fuse (Diagram 4, Fig. 3). During these movements of the xylem, the phloem-strands lying next to the cotyledonary phloem groups fuse with them, and the differentiation of the median epicotyledonary phloem-bundle ceases. Metaxylem tracheides develop centripetally and a typical tetrarch structure is attained.



FIG. 6.
Nopalea.
x 1.

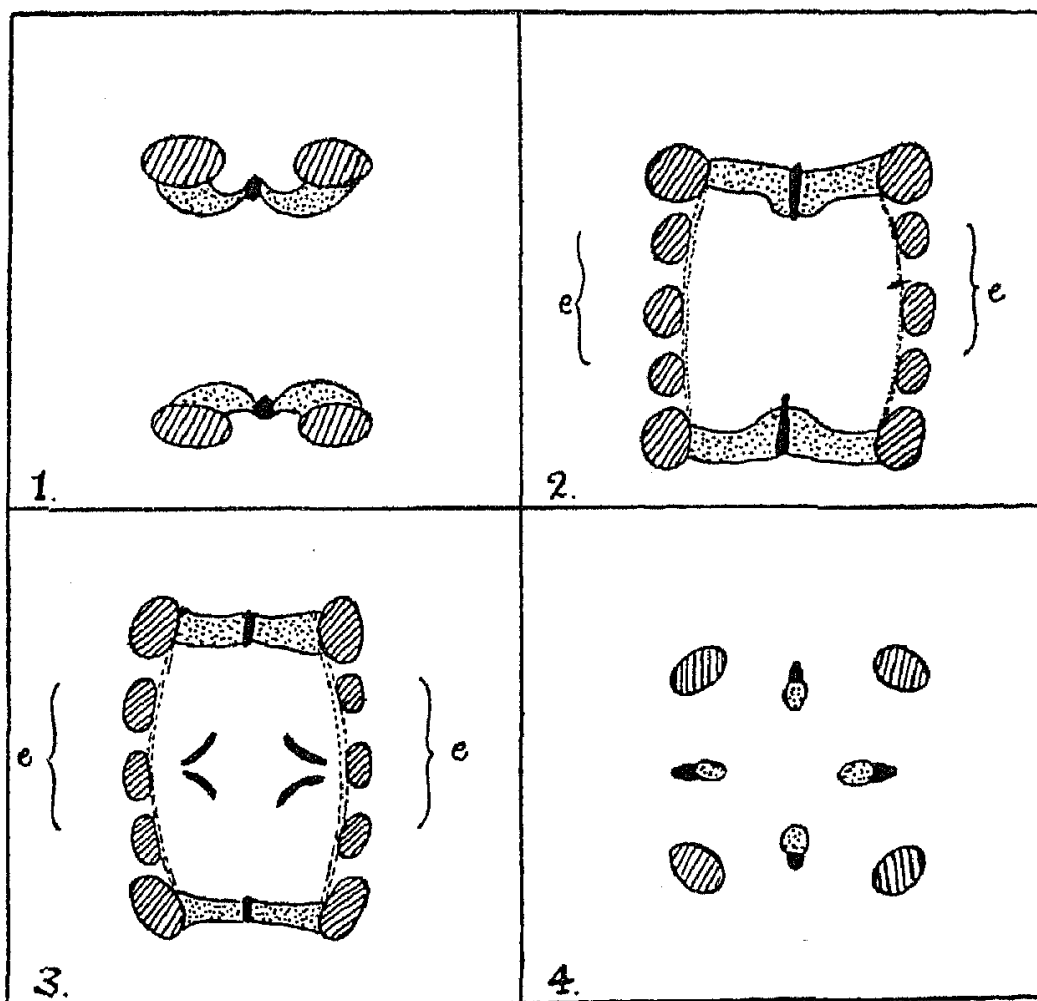


DIAGRAM 4. *Nopalea.*

The seedlings of this species thus show a method of transition from stem to root structure which is essentially of the *Anemarrhena* type, but in the one case the 'double' bundles are derived from two cotyledons, while in the latter they are furnished by a single one.

PHYLLOCACTUS.

Seeds of various species of *Phyllocactus* were planted, but only one set germinated.



FIG. 7.
Phyllocactus
Hookeri. × 2.

Phyllocactus Hookeri, Walp. These seedlings showed a somewhat succulent hypocotyl, with two short cotyledons, which in form and in their degree of fleshiness resembled those of *Cereus tortuosus* (Fig. 7). In general characters the structure of the cotyledon and hypocotyl is very similar to that of species of *Cereus*; and in three of the four seedlings examined, a small cotyledonary bud occupied the base of the cotyledon, although in one case only did this bud possess a vascular supply.

Transition.

1. Series A, B, and C, in which the bundle of the cotyledonary bud was absent.

Each of the cotyledons possessed one small endarch bundle; in one seedling the bifurcation of the phloem took place before the entrance into the hypocotyl, in the others it was delayed for some time, and in no case did any division of the xylem occur. Four very small and ill-differentiated epicotylar strands were present in the upper part of the hypocotyl, but these played no part in the formation of the root, and their differentiation soon ceased. The half-phloems of the cotyledonary bundles separated and left the xylems isolated, the wood consisted of a few somewhat scattered elements, and the protoxylems attained the exarch position rather by a rearrangement of the elements than by a definite rotation. Towards the base of the hypocotyl a loose central strand of wood is produced by the centripetal development of tracheides; at the same time the opposite phloem groups gradually approach as though fusion were about to take place; a junction however is not effected, and the phloems separate again, so that the root-structure is of the type found in *Cereus*, in which there are four phloem- and two xylem-bundles.

2. Series D, in which the bundle of the cotyledonary bud was present.

The cotyledonary bud in this seedling was poorly developed and consisted of a tiny mass of parenchymatous tissue with a few multicellular hairs, but it was provided with a vascular supply. Besides the two cotyledonary bud-bundles and the two endarch cotyledon-strands, there were in the upper part of the hypocotyl four epicotylar traces. The

seed-leaf-bundles showed bifurcation and rotation of their phloem, and the cotyledonary bud-bundles rotated and moved outwards to meet the incoming cotyledon-traces and finally fused laterally with them. The four epicotylar strands played no essential part in the transition, they merely passed outwards and fused with the 'double' bundles. The behaviour of the vascular tissue is thus precisely similar to that illustrated for *Cereus tortuosus* (Diagram 5, Figs. 1 and 2). The phloems and the metaxylems of the 'double' bundles thus produced separate and rotate round the protoxylem, which they thus leave exposed in the exarch position, and the root is again of the *Cereus* type.

CEREUS.

The seedlings belonging to this genus show a considerable advance in succulence when compared with *Opuntia*, while at the same time they exhibit a marked diminution in size. The somewhat long and slender hypocotyl characteristic of *Pereskia* and *Opuntia* is replaced by a shorter, swollen structure in the species of *Cereus*. The cotyledons are no longer leaf-like, but are small, pointed and succulent, and are set slightly apart, with the inner line of their broad bases parallel. The two cotyledons of a seedling still show a difference in size, though this feature is not so well marked as in *Opuntia*, *Nopalea*, and *Pereskia*; the whole seedling is indeed slightly asymmetrical (Fig. 8). Towards the base of the cotyledons a small embryonic bud, bearing a few multicellular hairs, appears at the middle of their ventral surface. The structure of the seed-leaf is very simple. It consists of a mass of large, rounded, parenchymatous cells, with extremely small intercellular spaces, and it is traversed by a small vascular bundle, which, towards the base of the cotyledon, may be reinforced by two still smaller lateral strands, and by an inner bundle which formed the vascular supply of the cotyledonary bud. The epidermal cells in some species, such as *C. tortuosus*, *C. triangularis*, and *C. Jamacaru*, show a differentiation into small rectangular cells, which appear in groups consisting of one to six elements in transverse section, and much larger cells in which the outer wall is either convex or somewhat elongated. *C. peruvianus* and *C. Spachianus*, on the other hand, show no such differentiation, and the epidermal system in these species is composed of large cells with a distinctly convex outer wall. As in all the other genera examined, the stomata are of the usual Cactus type; they have subsidiary guard-cells, are on a level with the general epidermal surface, and, where a differentiated epidermis occurs, the stomata are restricted to the areas of the small rectangular elements. The hypocotyl is at first oval, but rapidly becomes circular in transverse section; it is made of very large, rounded, parenchymatous



FIG. 8.
Cereus
tortuosus.
x 2.

cells, practically without intercellular spaces. Towards its base downward growth may occur in two or more regions, resulting in a curious cortical lobing of the upper part of the slender root; a fuller description of this phenomenon will be given later. In other cases the passage from hypocotyl to root is only accompanied by a great diminution in the size of the cortical cells. The short primary root usually possesses a slight development of cork in its outer cortical region.

The transition from stem- to root-structure is remarkably uniform throughout the genus; the phenomena will therefore be described for one species, and only the slight and usually unimportant differences exhibited by those other species which have been examined will be noted.

Transition.

Cereus tortuosus, Forbes. Each cotyledon of the seedlings of this species has one small endarch bundle throughout its length, but towards the base very small lateral strands appear, one on each side of the median

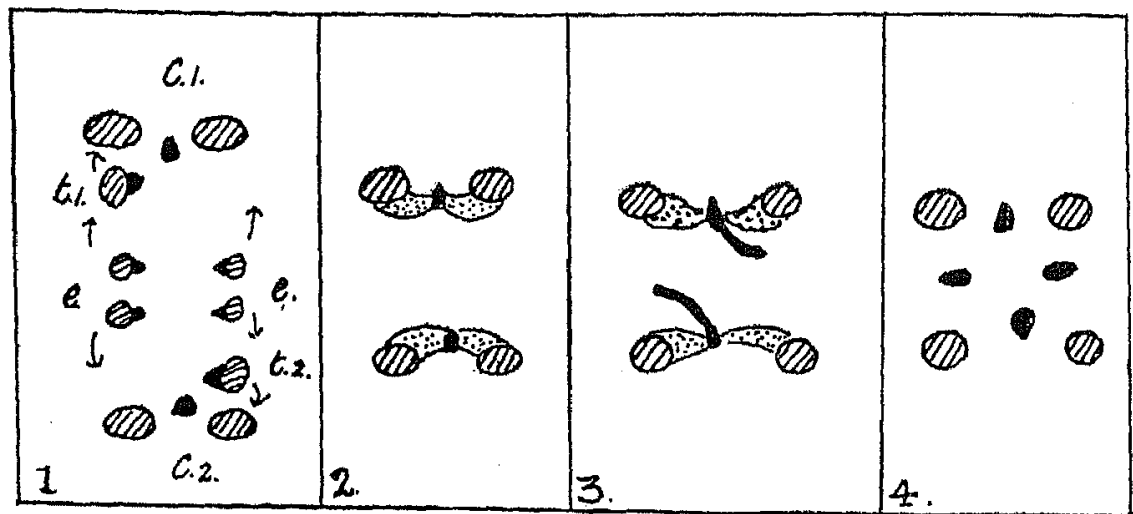


DIAGRAM 5. *Cereus tortuosus*.

one, in which, by this time, the phloem has bifurcated. The lateral bundles run obliquely through the mesophyll and fuse with the median strand. About this level a fourth bundle makes its appearance; it originates in the cotyledonary bud region and evidently provides its vascular supply. This cotyledonary bud bundle moves rapidly outwards, rotating as it does so, and finally fuses laterally with one portion of the cotyledonary bundle (t_1 , t_2 , Diagram 5, Fig. 1).

During these movements the bundles have entered the hypocotyl, where four small epicotylar strands (e) may or may not be present; if they are differentiated they pass outwards and fuse with the seed-leaf-traces (Diagram 5, Fig. 2). With the fusion of the cotyledonary bud-bundle with the seed-leaf-strand the transition is practically effected, for in general no further

change occurs, except for the slight and gradual passing in of the vascular elements towards the centre of the axis. In the usual case, the root possesses four well-marked, though small, phloem groups and only two bundles of xylem. This root arrangement is usually maintained so long as any differentiation of the tissues can be observed, but one seedling examined showed an interesting variation. Towards the base of the root each of the protoxylems sent off a branch, which finally resulted in the formation of a tetrarch root of the normal type (Diagram 5, Figs. 3 and 4).

In all the seedlings of *Cereus tortuosus* examined, the xylem almost entirely consisted of protoxylem; metaxylem tracheides appear just below the cotyledonary node and are situated on either side of the protoxylem group, between it and the phloem (Diagram 5, Fig. 2); occasionally a few elements may appear between the groups of protoxylem. The root, however, rarely possesses any wood except the protoxylem, in the stages examined.

The metaxylem elements are very large in transverse section, and the thickening of the wall projects far into the cavity. They are always sharply defined from the small protoxylem elements (compare with Fig. 19), and consist of the short, broad tracheides with the annular or spiral thickening ridge, which are described by Solereder¹ as occurring in some species of the Cactaceae. According to his observations these 'barrel' tracheides seem to be entirely wanting in the stems of the species of *Cereus*, but however that may be, they are certainly to be found in the seedlings. Van Tieghem's² studies of these cells led him to the conclusion that they were merely a peculiar form of parenchyma, but an examination of well lignified elements in this and in other genera has failed to reveal the presence of cytoplasm and nucleus. It seems probable, therefore, that as Darbishire³ suggested, Van Tieghem's observations were made on very young tracheides, for at the stage when the thickening band is not completely lignified, cytoplasm is usually seen.

Cereus peruvianus, Mill. The seedlings of this species show rather more variation in their cotyledonary bundles than do those of *C. tortuosus*. In one series the small cotyledon had but one lateral strand present, while the larger cotyledon had two; another seedling developed no laterals, while a third had only a median bundle in the smaller cotyledon, but in the larger had two strands, slightly inclined towards one another, which during the transition behaved as a 'double' bundle. The transition phenomena are almost identical with those of *C. tortuosus*, with the single exception to be described.

¹ Solereder: Systematic Anatomy of the Dicotyledons, Vol. i. Trans. by Boodle and Fritsch, Oxford, 1908.

² Van Tieghem: Cell. annelées et spiralées des Cact. Bull. Soc. Bot. de France, 1885.

³ Darbishire, O.: Observations on *Mamillaria elongata*, Ann. Bot., xviii, 1904.

The larger cotyledon (c_2) had two strands which rotated and behaved as the 'double' bundle of the smaller cotyledon (c_1 , Diagram 6, Fig. 1). Fusion of the cotyledonary bud-bundle with the seed-leaf-trace took place as in *C. tortuosus* (t_1, t_2 , Diagram 6, Figs. 2 and 3), and subsequent movements of the vascular elements resulted in a root structure similar to that described above for that genus. Towards the base of the root, however, changes take place, which result in the formation of a pentarch structure (Diagram 6, Figs. 4 and 5). The protoxylem group (x_2) sends off a branch,

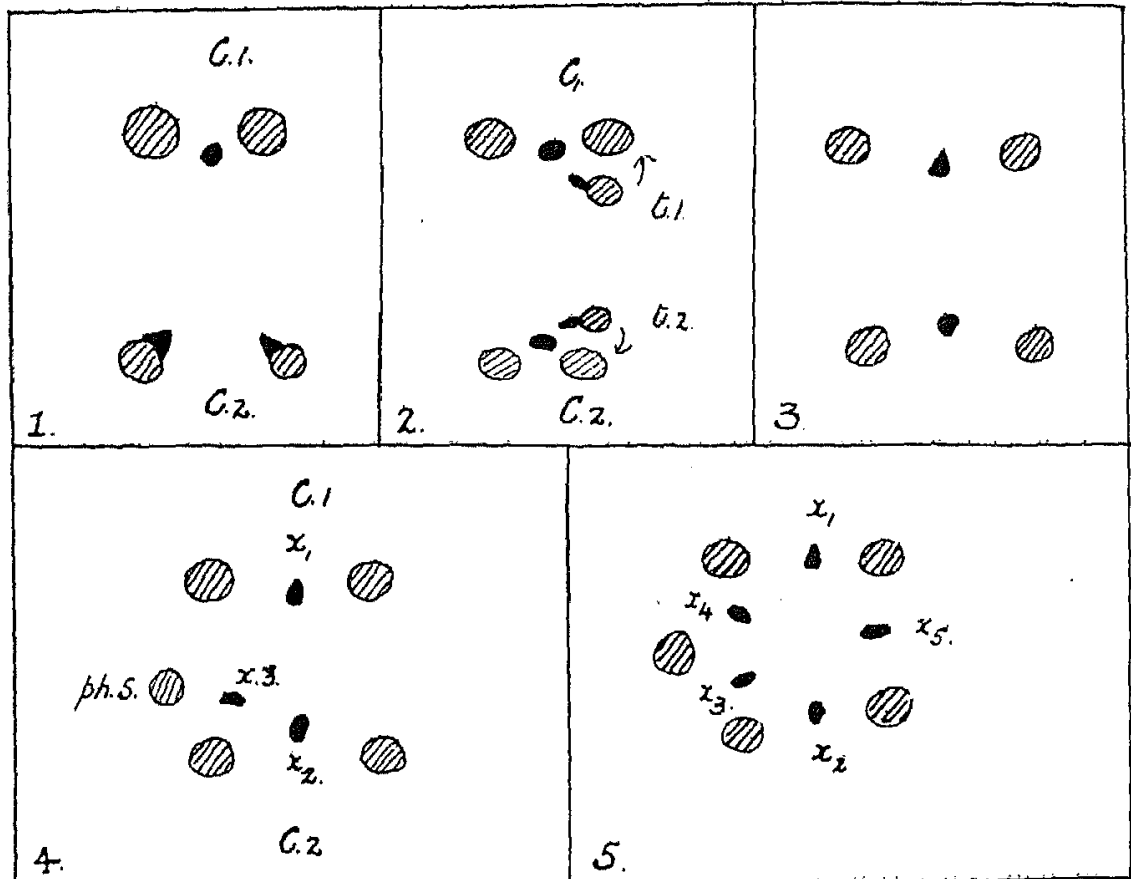


DIAGRAM 6. *Cereus peruvianus*.

consisting of a few elements, between the adjacent phloem groups to its left; very soon a phloem strand (ph_5) arises to the left of this last formed xylem-bundle; no cambium was present, and the phloem arose by the meristematic activity of the cells in this region. At a still lower level the protoxylem (x_1) branches to the right and to the left, and in this way a pentarch root is produced.

The variation just described, taken in connexion with the somewhat similar case figured for *C. tortuosus* (Diagram 5, Fig. 3), appears to indicate the manner in which the simple transition from stem- to root-structure in the genus *Cereus* may have been brought about. A suppression of one xylem branch of each cotyledonary bundle, followed by a total obliteration

tion of the intercotyledonary arms, would result in the curious structure seen in most of the roots of the seedling *Cerei*.

Cereus Jamacaru, D.C. The transition-phenomena of these seedlings were practically identical with those of *C. tortuosus*; there were, however, one or two differences of minor importance. For instance, the seedling had no lateral bundles in the cotyledons, and the strand which supplied the cotyledonary bud was very small, dying out before reaching the seed-leaf-trace. In another seedling four lateral roots arose almost simultaneously, alternating with the phloem groups; in general only two appear, and these opposite the protoxylem.

Cereus Spachianus, Lem. Both in the transition-phenomena, and in other respects, the seedlings of this plant closely resemble those of *C. Jamacaru*.

Cereus triangularis, Mill. With the exception that the cotyledonary bud is but slightly developed, and has no vascular supply, the structure and transition-phenomena in these seedlings are similar to those of *C. tortuosus*.

PILOCEREUS.

The two species of *Pilocereus* which were examined showed a great similarity to *Cereus* in their external appearance; and, as in some species of that genus, small cotyledonary buds were present in the axils of the seed-leaves.

Pilocereus exerens, K. Schum. Each of the two cotyledons has a small endarch bundle throughout its length, and at its base the slightly differentiated tubercle-bundle appears. The seed-leaf-traces and the tubercle-bundles in Series 1 perform differently: in one cotyledon they form the 'double' bundle in exactly the same way as is illustrated for *Cereus peruvianus* (Diagram 6, Figs. 2, 3), in the other cotyledon the seed-leaf-trace shows no bifurcation of its phloem, but rotating slightly, forms one half of the 'double' bundle, the second half being produced by the tubercle-bundle. The two 'double' bundles once formed, the transition is practically completed, since, except for a slight centripetal displacement of the vascular elements, no further changes take place, and the root is of the *Cereus* type. In Series 2 both cotyledon-bundles bifurcate, and the tubercle-strands, in which no xylem is present, fuse laterally with one half of the seed-leaf-phloem; in other respects the transition takes place as in Series 1.

Pilocereus albispinus, Salm-Dyck.

Series 1. Each cotyledon contributes one endarch bundle to the hypocotyl, and also one tubercle-bundle which is composed of phloem only. The tubercle-phloem-strand bifurcates, and the two halves pass outwards until they lie one on either side of the cotyledonary bundle; the phloem of the latter then bifurcates, and the two halves separate slightly and fuse with the adjacent tubercle-phloem groups. Further rotation of

the bast takes place until it occupies the position characteristic of the *Cereus* root-structure, and with these movements the transition is completed. In this series and in all the seedlings of *Pilocereus* examined, only protoxylem was present at the stage observed.

Series 2. In this seedling, towards the base of the cotyledon, four small vascular strands were present, but at the cotyledonary node the number was reduced to one. This bundle soon bifurcated, the tubercle-bundle fused laterally with one half of it, and the remainder of the transition followed the course described for Series 1.

RHIPSALIS.

Seeds belonging to two species only of this genus germinated. The seedlings were very small and resembled those of the genus *Mamillaria* in the possession of a globular hypocotyl; they differed, however, in owning two minute pointed cotyledons. The cuticle was much more strongly developed in these seedlings than in those of any other genus, but in other respects the general characteristics of the cotyledons and hypocotyl are those of such a group as *Echinopsis*.



FIG. 9.
Rhipsalis
dissimilis.
x 1½.

Rhipsalis Warmingiana, K. Schum. One small endarch bundle passes into the hypocotyl from each cotyledon, but during its inward passage bifurcation of the phloem takes place; at this stage, and indeed throughout the whole length of the hypocotyl, only protoxylem is present. Rotation of the phloem groups follows immediately on their bifurcation, and the movement continues round the stationary protoxylem, until they lie at right angles to their former position. A general centripetal displacement of all the vascular elements follows until the opposite groups of phloem lie close together, when fusion of them takes place. New xylem elements develop centripetally to the protoxylem until a central plate is formed; thus the diarch root-structure is arrived at.

Rhipsalis dissimilis, K. Schum. The seedlings of this species are very similar to those of *R. Warmingiana*, but the stem apex is rather more depressed, giving rise to a short cotyledonary tube. Further, bifurcation of the phloem takes place at the base of the cotyledons, and is not delayed until the hypocotyl has been entered, as in the former species.

ECHINOCEREUS.

The seedlings of the species of *Echinocereus* examined show a fairly close resemblance to those of *Cereus*, but there is a slight diminution both in the length of the cotyledons and of the hypocotyl, and the latter is rather more globular than in any of the species of *Cereus*. The epidermal cells of the cotyledons are elongated and almost pointed; but there is no differentiation of these cells as is the case in some of the *Cerei*.

Transition.

Echinocereus Ehrenbergii, Engelm. The cotyledons have at their broadest part five small vascular bundles, which by anastomosing have been reduced, by the time the base of the cotyledon is reached, to two in one cotyledon (c_1) and one in the other (c_2 , Diagram 7, Fig. 1).

During the passage into the hypocotyl the phloem of the bundle c bifurcates and the two halves rotate round the protoxylem ; no metaxylem is present. The two bundles in c_1 rotate slightly until their protoxylems are directed towards one another. Six epicotylar phloem groups (e) are also shown in the hypocotyl at this level (Diagram 7, Fig. 2), but fusion of two of the adjacent bundles soon reduces their number to four. These four groups ultimately join with the cotyledonary phloem next to

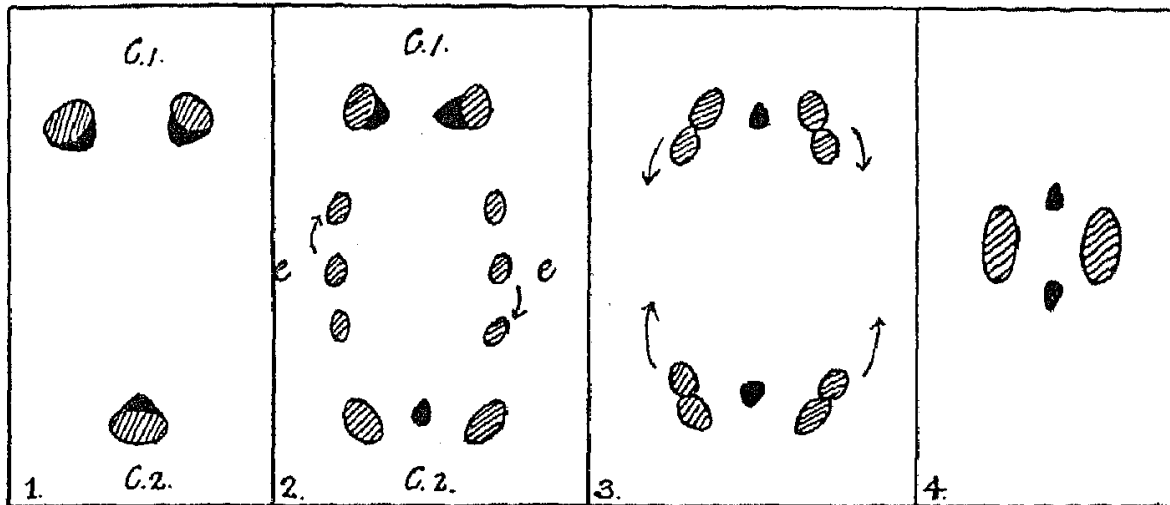


DIAGRAM 7. *Echinocereus Ehrenbergii*.

them, but before this is accomplished the two protoxylems of c_1 have fused. A diarch root finally results by the union of the two adjacent groups of bast (Diagram 7, Figs. 3 and 4).

Series 2 showed two differences from the transition just described : there were fewer bundles in the cotyledons, and the two 'double' bundles of the hypocotyl were both produced as in c_1 (Diagram 7) by the union of two strands, not by the bifurcation of one.

Echinocereus cinerascens, Lem. These seedlings had only three bundles in the cotyledons, which fused towards the base into a single strand, bifurcation of which took place during the passage into the hypocotyl. With the exception that no epicotylar phloem was developed, the transition was essentially like that in *E. Ehrenbergii*.

ECHINOPSIS.

The seedlings belonging to the *Echinopsis* group are distinctly smaller than those of the genus *Cereus*. They are characterized by an almost

globular hypocotyl, which terminates in a short, slender root (Fig. 10). The marked increase in succulence in the hypocotyl is correlated with a decrease in the size of the cotyledons, which in some species of the genus show extreme reduction. In the seedlings in which the cotyledons attain their maximum development, they consist of small pointed structures with an almost circular base of insertion; while, on the other hand, the almost complete suppression of the pointed apex in *Echinopsis multiplex* results in the diminution of the seed-leaves to such an extent that they are merely represented by two papillae. In every case, however, no matter how reduced the cotyledons may be, a difference in size between those of any one plant can always be observed.



FIG. 10.
Echinopsis
Lagermannii.
x 2.

THE TUBERCLE.

The tubercles with their tufts of spines, which are so characteristic a feature in so many of the Cactaceae, have received attention from several observers with a view to the elucidation of their morphology; and Darbishire¹ very briefly summarizes the principal views which have been put forward. The appearance of the cotyledonary buds at the extreme base of the seed-leaves has been already noted above for some species of *Cereus*, *Pilocereus*, and *Phyllocactus*, e.g. *C. tortuosus*, *C. Famacaru*, *Pilocereus exerens*, *P. albispinus*, and *Phyllocactus Hookeri*, and in the following species of *Echinopsis* precisely similar buds appear: *E. oxygona*, *E. Eyriesii*, and *E. Zuccarinii*. In other species, e.g. *E. multiplex*, *E. tubiflora*, and *E. Lagermannii*, these cotyledonary buds attain comparatively large dimensions, and where their development is most complete they closely resemble the tubercles which arise on the epicotyl. In some species of *Mamillaria*, to be described later, the cotyledonary bud is absolutely indistinguishable from the epicotyledonary tubercle, and can only be identified by its subsequent fusion with the seed-leaf. A well developed cotyledonary bud consists of a mass of tissue composed of large, parenchymatous cells, and throughout its length runs a single vascular bundle; at the apex of the bud is a cushion of tissue on which the ends of the spines are inserted, and a cork cambium separates this cushion from the underlying tissues (Fig. 11). When a comparison is made between the anatomy of a 'cotyledonary bud' and that of the tubercle of an adult plant, such as is described by Darbishire,² there is seen to be a very close resemblance in structural details between the two. From these considerations it is concluded that the 'cotyledonary buds' of the seedling are morphologically identical with the tubercles of the mature plant.

¹ Darbishire, O. : loc. cit.

² Loc. cit.

Owing to the greatly depressed stem apex, which often results in the appearance of a short apparent cotyledonary tube, the tubercles may seem in some cases to be situated on the cotyledon itself, instead of in its axil; but longitudinal sections through the seedlings indicate that the tubercles are really auxiliary structures and are not outgrowths from the cotyledon.

With regard to the morphological nature of the tubercle and spines it has been stated by Goebel¹ that in many Cactaceae, 'the spines are transformed leaves which arise upon very much reduced lateral shoots standing in the axils of the leaves.' In another connexion he remarks² that in many Cacti, 'the thorns are here usually arranged in tufts on very short shoots,'

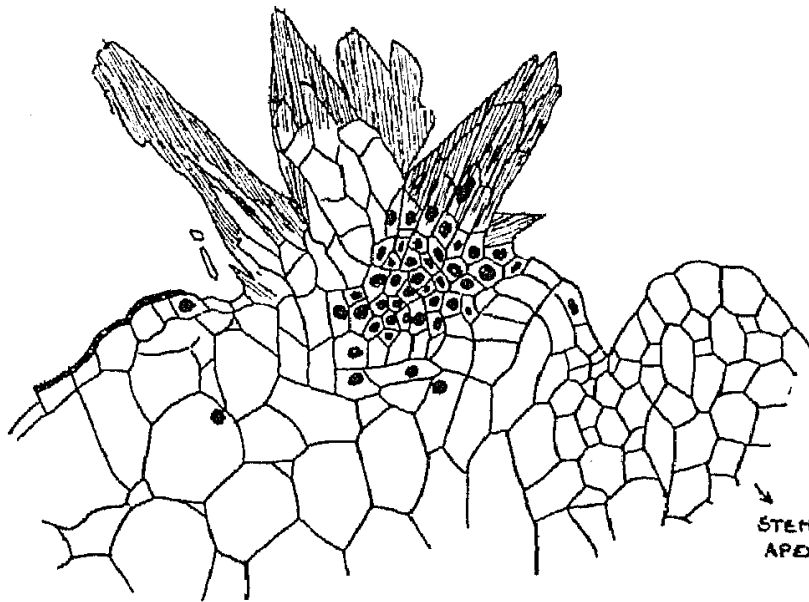


FIG. 11. *Echinopsis Lagermannii*. Group of thorns on the cotyledonary tubercle. L. S. $\times 109$.

and that 'the thorns are transformed leaves'. He further observes³ that in many Cactaceae, especially in the Mamillarieae, 'the axillary shoot "grows up upon" its subtending leaf—that is to say, the common base of the two is elongated.' Darbishire,⁴ however, 'can see in the mature tubercle only the highly developed leaf-base. The spines together represent the leaf-blade, the leaf-stalk being absent.'

The development of tubercles in the axils of the cotyledons appears to support Goebel's view that the tubercles represent short shoots, but it is desired to carry out further investigation along experimental lines before expressing any very definite opinion as to their morphological nature.

The tubercles in the *Echinopsis* group show a very well marked rise in importance when compared with the cotyledons; increase in size of the

¹ Goebel, K.: *Organography of Plants*, Oxford, 1905, Part I, p. 168.

² *Loc. cit.*, Part II, p. 429.

³ *Loc. cit.*, Part II, p. 436.

⁴ *Loc. cit.*

one is usually accompanied by decrease in size of the other. In *R. Eyriesii*, *E. oxygona*, and *E. Zuccarinii* they closely resemble the 'cotyledonary buds' of the *Cereus* group, but in *E. Lagermannii* and *E. multiplex* the cotyledons are, comparatively speaking, small, and the tubercles are well developed, tufted with spines, and have a vascular bundle running to the base of the cushion.

VASCULAR RELATIONSHIPS BETWEEN THE COTYLEDONS AND THE TUBERCLES.

The behaviour of the cotyledon- and tubercle-bundles is extremely erratic, and varies not only within the species but even in the opposing pairs of bundles of a single seedling.

The simplest case was that found in *E. multiplex*, Series 1 (Diagram 8,

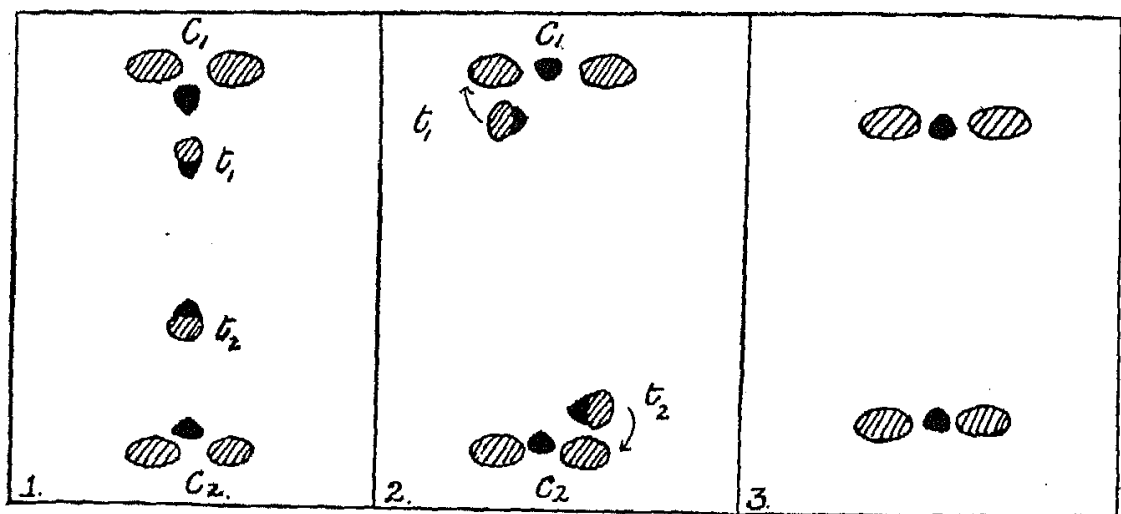


DIAGRAM 8. *Echinopsis multiplex*, Series 1. Behaviour of cotyledonary and tubercle bundles.

Fig. 1), in which the cotyledonary bundles (c_1, c_2) both showed bifurcation of the phloem by the time the tubercle-bundles (t_1, t_2) appeared. The strand t_1 rotated through an angle of 90° , moving outwards as it did so to meet the incoming cotyledonary trace (c_1), and t_1 finally fused laterally with c_1 (Diagram 8, Fig. 2); in a similar manner t_2 fused with c_2 . By this means two bundles, such as are shown in Diagram 8, Fig. 3, are produced. This is a parallel case to what occurs in *Cereus tortuosus*.

Echinopsis multiplex, Series 2, showed a similar sequence of events as far as the larger cotyledon was concerned, but in the smaller seed-leaf the two strands behaved differently. In this case the tubercle-trace rotated and moved outwards to meet the seed-leaf-trace; this latter also rotated slightly but did not bifurcate, and the two strands together formed one bundle by the fusion of their protoxylems. In this cotyledon the tubercle-

and the cotyledon-strands were of equal importance in effecting the formation of one of the root-poles. In a third series of *Echinopsis multiplex* yet another variation was seen. The two strands derived from the larger cotyledon and the corresponding tubercle rotated towards one another and the xylems fused (c_2, t_2 , Diagram 9, Figs. 1 and 2); when the junction was almost completed the cotyledonary phloem (c_2) showed a belated bifurcation, one half immediately joining with the tubercle phloem (t_2) lying near it (Diagram 9, Fig. 3). In the smaller cotyledon (c_1) the tubercle bundle (t_1) soon lost its xylem, and its phloem bifurcated. The cotyledonary trace (c_1) remained *in situ*, and the two phloem groups (t_1) passed outwards on either

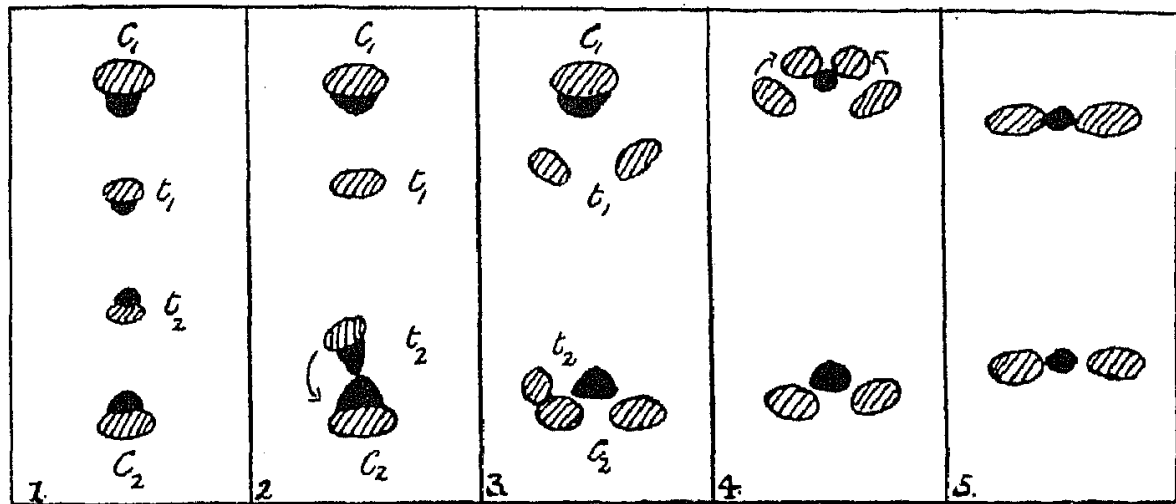


DIAGRAM 9. *Echinopsis multiplex*, Series 3.

side of it, and fused with the cotyledonary phloem (c_1), which by this time had bifurcated (Diagram 9, Figs 1 to 5).

It is thus seen that a tubercle-trace may act in a manner usually associated with the vascular strand of a cotyledon.

Echinopsis Lagermannii. Two vascular strands are present in each cotyledon. These two strands rotate towards one another, their protoxylems fuse, but the phloems remain separated, one mass on either side of the wood; thus a bundle is produced exactly like that figured in Diagram 8, Fig. 1 (c_1); it is derived, however, by the fusion of two bundles, and not, as in *Echinopsis multiplex*, by the bifurcation of one. The behaviour of the cotyledon- and tubercle-traces in all other respects resembles that described in *E. multiplex*, Series 1.

Echinopsis tubiflora, Series 3, is essentially similar to *E. multiplex*, Series 1.

In Series 2 the behaviour of the cotyledon- and tubercle-bundle of one seed-leaf is like that of Series 3; in the other seed-leaf two equal bundles replace the median cotyledon-bundle, and these two strands, together with the tubercle-bundle, act as in *Echinopsis Lagermannii*.

One cotyledon in Series 3 is also similar to *E. Lagermannii*, but in the second cotyledon there are three equal bundles present; two of these fuse and later form one half of the 'double' bundle, while the second half is produced by the fusion-product of the third cotyledonary bundle and the tubercle-trace.

A study of the various methods of formation of the two bundles always found towards the upper part of the hypocotyl in the species of *Echinopsis* examined, leads to the conclusion that the behaviour of the cotyledon-bundle depends almost entirely upon the stage of development of the vascular supply of the tubercle; where the latter is absent or is poorly differentiated, the former dominates the transition; on the other hand, where it is well developed it shares equally with the seed-leaf-trace, and may even play the more important part.

A further detail in connexion with *E. multiplex* assumes interest when compared with the Mamillarias to be described later. In this species the epicotylar strands contribute a fair share to the root-structure, while in the other species of *Echinopsis* examined, the bundles, even when fairly well developed, play no part in the formation of the root.

THE HYPOCOTYL.

The globular hypocotyl in *Echinopsis* is remarkable for the enormous development of its large parenchymatous cells; the vascular tissue appears but of slight dimensions when compared with the non-vascular tissue.

The curious cortical lobing of the hypocotylar base, which was mentioned above as occasionally occurring in some members of the *Cereus* group, is an almost constant feature of *Echinopsis* species. Towards the base of the hypocotyl the outer layers of the cortex grow downwards for a short distance, very closely enveloping the upper part of the root. The growth may take place in a complete circle around the axis, so that a transverse section, at a level towards the base of the region of downward growth, shows a remarkable zoned structure, the primary root having the appearance usually associated with an adventitious root embedded in the cortex of a rhizome. More usually, however, it occurs only at two or more places, so that at a lower level the cortex is lobed. This growth rarely attains an equal depth all round the axis, hence it often appears, in transverse section, as though an outer layer of cortex were being gradually peeled off.

The upper part of the root, as in most of the other genera, just below the region of exfoliation of the cortex, is closely invested with long root-hairs; below this, again, there is a more or less well marked superficial cork formation.

Transition.

- A. *Species in which the vascular symmetry of the root is attained by the cotyledonary bundles only.*

Echinopsis Eyriesii, Pfeiff. and Otto. Each cotyledon supplies the hypocotyl with one endarch collateral bundle, approximately equal in size to a single mesophyll cell. Soon after entering the node the phloem bifurcates, and its two halves rotate until they lie almost in a straight line with the protoxylem; no metaxylem is present. The four strands thus produced show no further change beyond a slight centripetal displacement, and the root structure is of the typical *Cereus* type (Fig. 12).

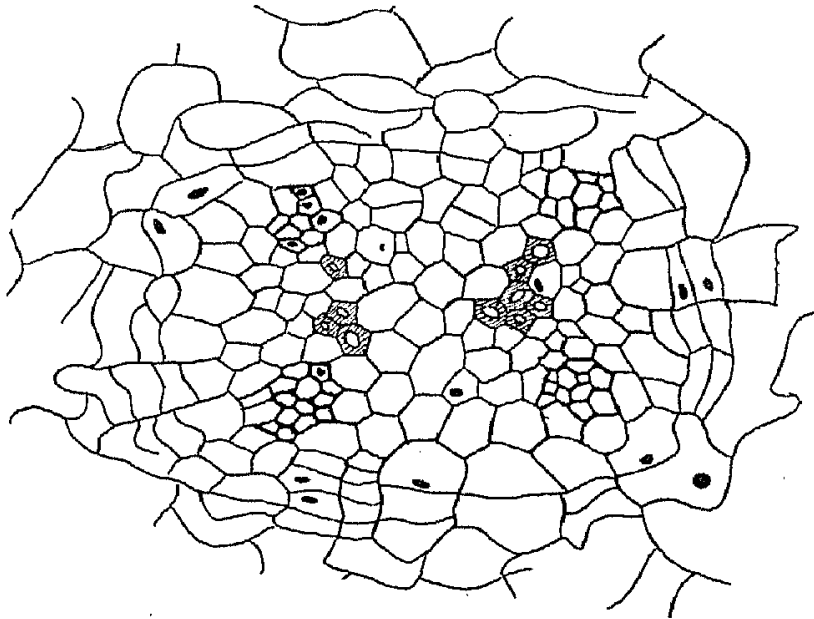


FIG. 12. *Echinopsis Eyriesii*. × 220.

Echinopsis Zuccarinii, Pfeiff. and Otto. These seedlings differ from those of *E. Eyriesii* in but one respect; in one series the root-structure gives place towards the root-tip to a completely diarch arrangement by the fusion of the opposing groups of phloem.

Echinopsis oxygona, Pfeiff. and Otto. In this species the bifurcation of the phloem in the cotyledonary bundles takes place before the node is reached; in other respects the transition-phenomena resemble those of *E. Eyriesii*. The *Cereus* type of root is not maintained, however, for just as differentiation is about to cease the opposing phloem groups fuse, giving rise to a diarch root.

- B. *Species in which the vascular symmetry of the root is attained by means of tubercle and cotyledonary bundles.*

The upper region of the hypocotyl in all the seedlings examined showed two vascular strands, in which the phloem groups appeared on either side of a centrally placed group of protoxylem elements, which often

consisted of one or two tracheides only. The formation of these two strands from the tubercle and cotyledonary traces has already been described in the account of the tubercle, so that no further description is necessary, and only the subsequent transition features will be given.

Echinopsis multiplex, Pfeiff. and Otto. In the upper region of the hypocotyl there are present only the two 'double' bundles (Fig. 13), but very soon six epicotylar bundles appear; they are grouped in threes on either side and occupy the intercotyledonary plane.

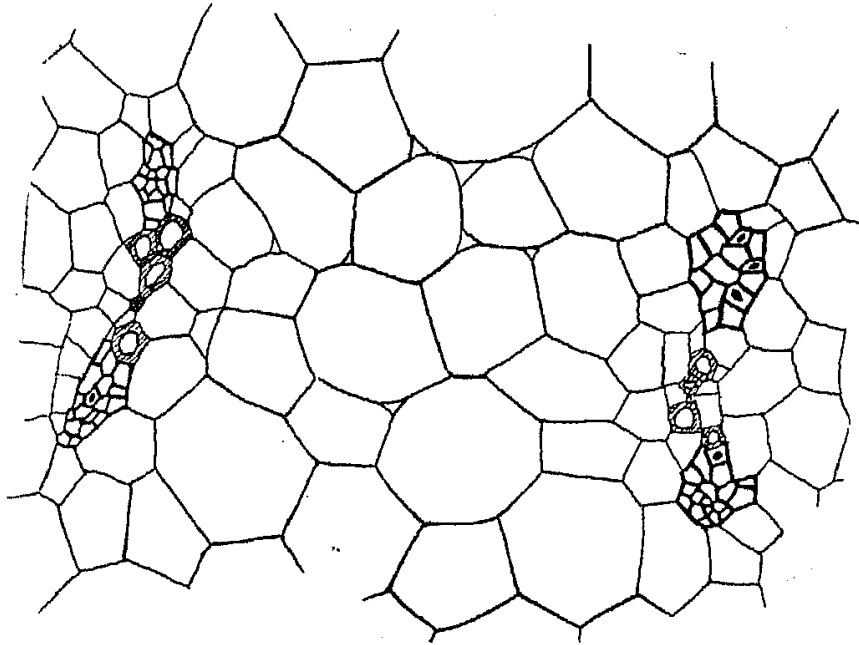


FIG. 13. *Echinopsis multiplex*. Upper part of the hypocotyl. $\times 109$.

The median bundle of each group of three gradually dies out, the remaining two move slowly outwards towards the cotyledonary bundles and fuse laterally with them. Towards the base of the hypocotyl 'barrel' tracheides are developed; at first they bridge the gap which exists between the protoxylem and its phloems, but they gradually extend inwards, until they occupy most of the central part of the axis. The four phloems do not fuse, thus the root shows the arrangement characteristic of the species of *Cereus*.

Echinopsis Lagermannii. The transition-phenomena in this species resemble very closely those just described for *E. multiplex*, with the exception that the phloems fuse in pairs, so that the root is diarch.

Echinopsis tubiflora, Zucc., is similar to *E. multiplex*.

ECHINOCACTUS.

The seedling *Echinocacti* show a close resemblance to those of *Echinopsis* in their external features, but their cotyledons are usually very unequal in size; in *E. Ottonis* they are reduced to microscopic papillae,

which fuse with the well developed tubercle at the cotyledonary node (Fig. 14). A small cotyledonary bud is developed in *E. denudatus* and *E. bicolor*, which in one seedling of the latter species possesses a vascular bundle; *E. hexaedrophorus* and *E. Wislizeni* show no sign of this structure.

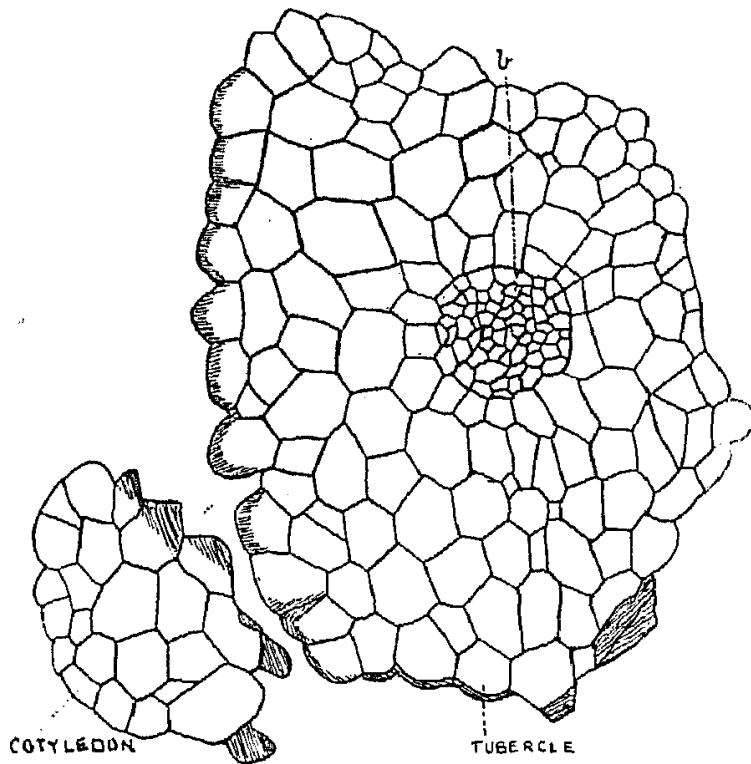


FIG. 14. *Echinocactus Ottonis*. Base of cotyledon and its tubercle. *b* = base of spine group. $\times 109$.

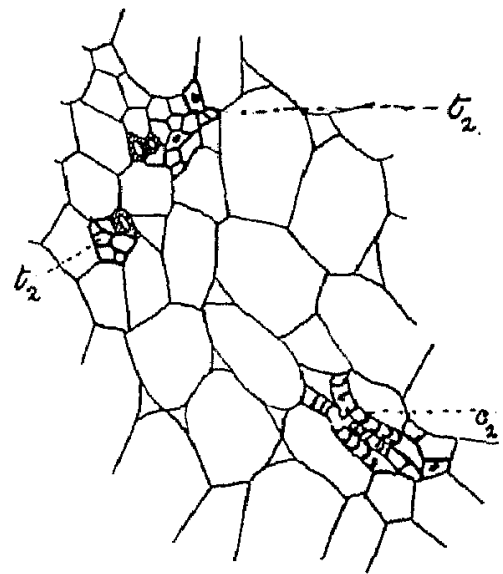


FIG. 15. *Echinocactus Ottonis*. Cotyledon- and tubercle-bundles. $\times 109$.

Transition.

Echinocactus hexaedrophorus, Lem. Each cotyledon supplies the hypocotyl with one small endarch bundle, in which the phloem bifurcates during the passage through the cortex; protoxylem only is present in the bundles and the phloem groups move round this as round a pivot, until they lie one on either side of it. About the central region of the hypocotyl new xylem elements arise between the two protoxylem groups until the two become connected; this diarch plate, however, does not long persist, for new tracheides arise to the right and left of its central region until a cross-shaped xylem mass results. Towards the base of the hypocotyl the central elements of the cross disappear and leave four xylem groups alternating with the four phloem-bundles of a tetrarch root.

Echinocactus Wislizeni, Engelm. The bifurcation of the single bundle of the cotyledons in this species takes place in the cotyledon. The phloem, accompanied by a small quantity of metaxylem, rotates and separates from the protoxylem, which it thus leaves exposed in the exarch position. Four

well developed epicotylar bundles are present in the upper part of the hypocotyl; these move towards the adjacent halves of the cotyledonary 'double' bundles and fuse with them. Towards the base of the hypocotyl the four phloem groups have lost their accompanying metaxylem elements, and the root-structure is thus of the type characteristic of species of *Cereus*.

Echinocactus denudatus, Link and Otto. Each of the cotyledons of this seedling has a median bundle and two small lateral ones, which at the base of the seed-leaf fuse with the central strand. Bifurcation and rotation of the phloem take place as in *E. hexaedrophorus*, but, at a later stage, two of the phloem groups fuse ($ph_4 + ph_1$, Fig. 16, A).

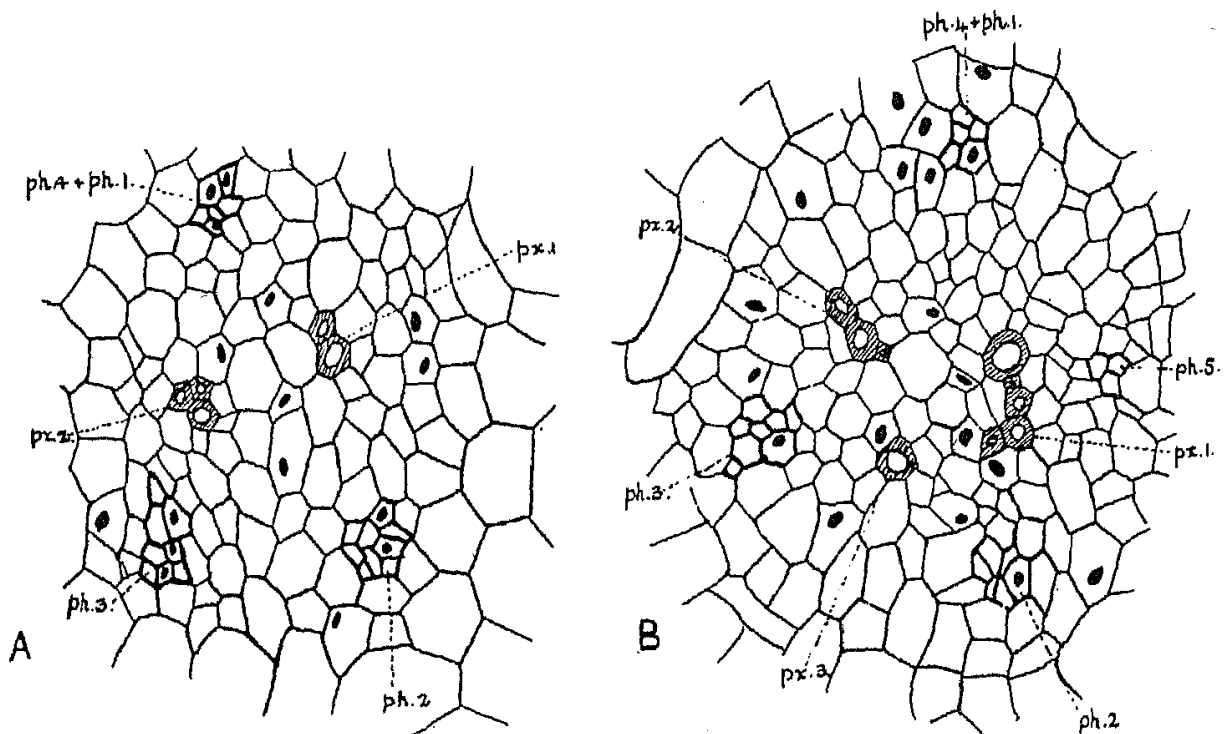


FIG. 16. *Echinocactus denudatus*. Formation of the tetrarch root. $\times 220$.

At a still lower level new xylem elements are differentiated on either side of px_1 , producing a slightly elongated strand of tracheides. Opposite to the middle of this xylem arc a phloem group arises (ph_5 , Fig. 16, B), and between ph_2 and ph_3 (Fig. 16, B) the appearance of a new xylem element shows the origin of a third xylem-bundle. The fourth bundle results from the breaking of the protoxylem group px_1 , one branch passing between the phloem groups $ph_4 + ph_1$ and ph_5 , the other remaining *in situ*; by means of these changes a tetrarch root is produced.

Echinocactus bicolor, G. The top of the hypocotyl is occupied by two endarch cotyledonary bundles and six epicotyledonary strands; the latter arrange themselves in two groups of three, alternating with the seed-leaf-traces, and, at a slightly lower level, two of each group fuse. The phloem

of each cotyledonary bundle bifurcates and rotates round the xylem, which consists only of protoxylem tracheides; as soon as this is completed the epicotyledonary strands, which have been moving outwards, fuse with the cotyledonary bundles. This *Cereus* arrangement persists almost to the apex of the root, but finally the phloems fuse and a diarch root results.

E. tricolor, Series 2, shows a slight difference from the above in its possession of a cotyledonary bud-bundle, in addition to the six epicotyledonary strands. These bud-bundles (t_1 and t_2 , Diagram 10, Fig. 1) pass obliquely to one side and fuse with one of the epicotyledonary bundles, the remaining two strands (e) also fuse (Diagram 10, Fig. 1). The four strands thus produced (t_1+e , e , t_2+e , and e , Diagram 10, Fig. 2) move outwards and join on to the cotyledonary strands, which have by this time bifurcated. The remaining details of the transition are essentially similar to those of the other seedlings of the genus.

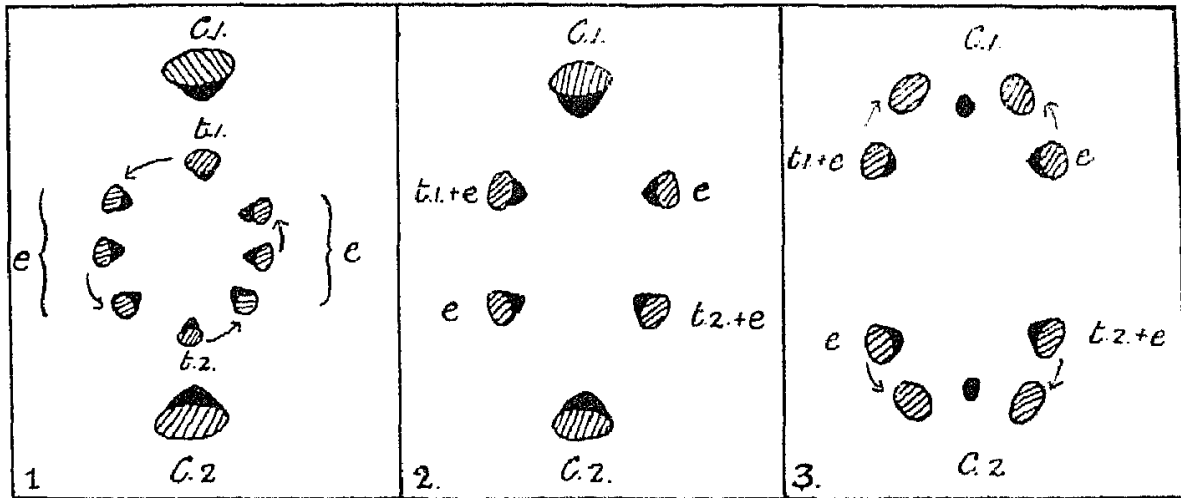


DIAGRAM 10. *Echinocactus bicolor*, Series 2.

Echinocactus Ottonis, Link and Otto. The seedlings of this species differ very considerably from those of the other members of the genus in their possession of well-marked cotyledonary tubercles, which far surpass in importance the seed-leaves themselves, for the latter are reduced to mere papillae. This increasing importance of the tubercle over the cotyledon is shown in the behaviour of the vascular strands. In all the seedlings examined, the tubercle-traces (t_1 , t_2 , Diagram 11, Fig. 1) appeared some time before those which supplied the cotyledons, but this would naturally be expected from the greater comparative development of the tubercle.

Echinocactus Ottonis, Series 3, illustrates the simplest course of events. In its larger cotyledon the two traces (c_1 , t_1 , Diagram 11, Fig. 2) rotate and fuse, thus producing one bundle, as in *Echinopsis multiplex*, Series 2; in the smaller seed-leaf the cotyledonary strand c_2 remains *in situ* while the

tubercle-strand t_2 bifurcates; its halves pass outwards and fuse with the seed-leaf-trace, forming the second bundle (Fig. 15, and Diagram II,

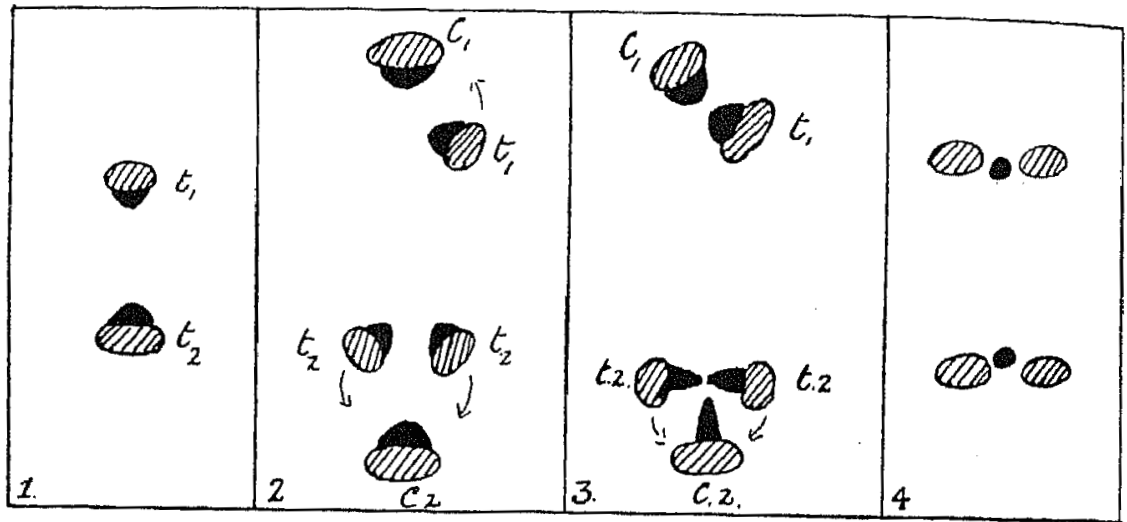


DIAGRAM II. *Echinocactus Ottonis*, Series 3.

Figs. 1-4). In this seedling we thus have a further example of a tubercle-trace acting in the manner usually associated with a cotyledonary bundle.

Echinocactus Ottonis, Series I, shows an interesting feature in its

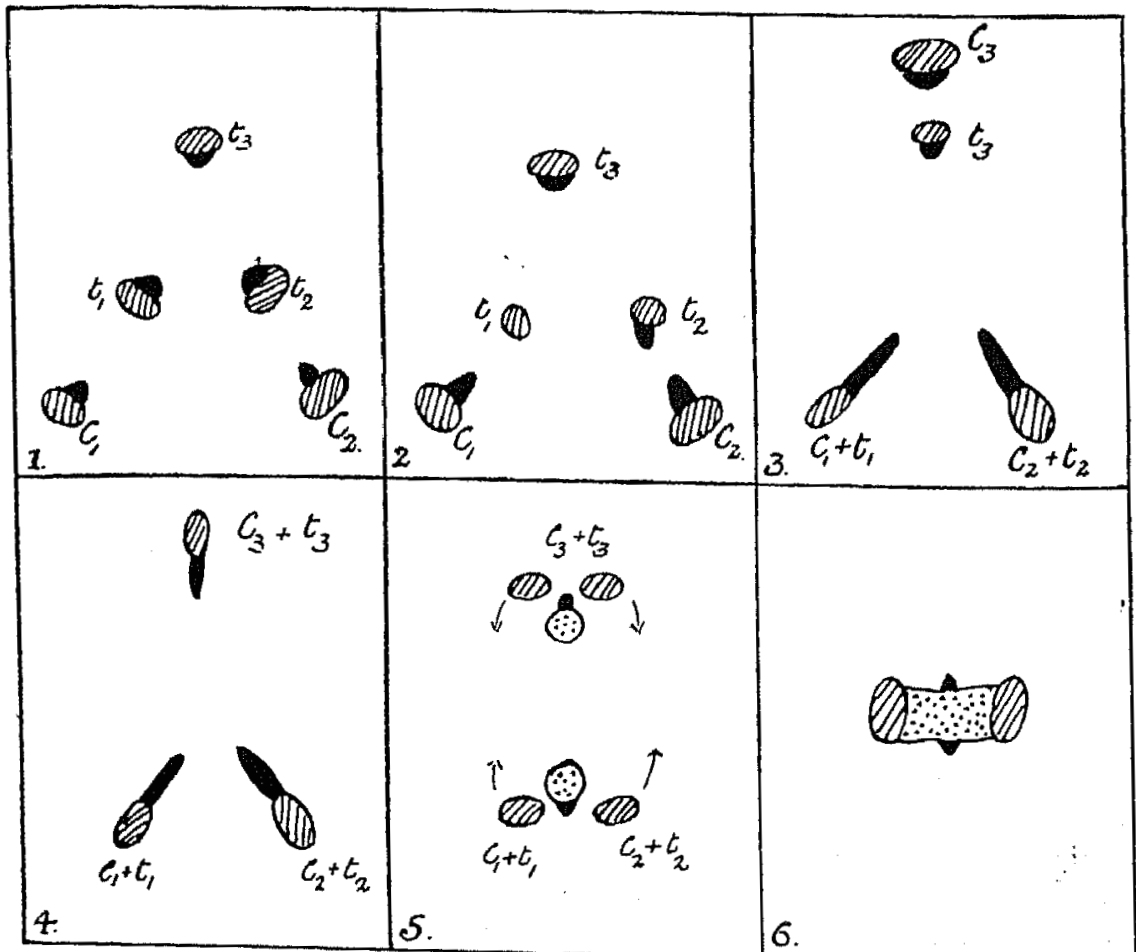


DIAGRAM 12. *Echinocactus Ottonis*, Series I.

possession of three cotyledons subtending three tubercles. The behaviour of the vascular tissue points to the fact that two of the cotyledons (c_1, c_2 , Diagram 12, Fig. 1) have been derived from the splitting of one larger one to its extreme base. The three pairs of vascular strands run into the hypocotyl so very obliquely that it is impossible to say definitely exactly what occurs, but fusion of the members of a pair takes place, resulting in the formation of three bundles, as shown in Diagram 12, Figs. 1-3.¹ The strand ($c_3 + t_3$) which supplied the smaller cotyledon and its tubercle

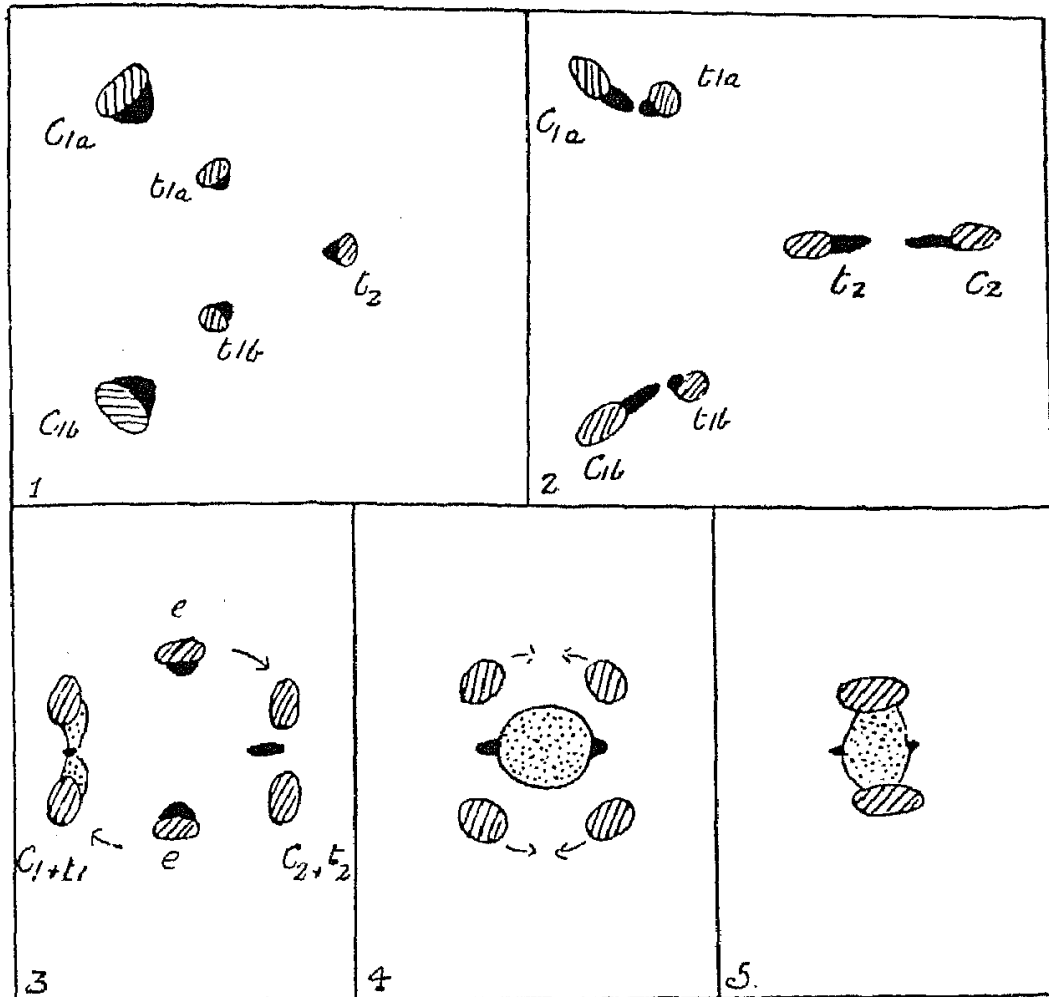


DIAGRAM 13. *Echinocactus Ottonis*, Series 2.

soon showed a bifurcation of the phloem (Diagram 12, Fig. 5), while the other two bundles rotated towards one another and together formed a V-shaped strand in which the protoxylem occupied the apex of the V. Large metaxylem tracheides were enclosed by the arms of the V; these, however, soon died out and others differentiated centripetally, as is shown in Diagram 12, Fig. 5.

¹ The elongation of the bundles shown in Diagram 12, Figs. 3 and 4, and in Diagram 13, Figs. 2 and 3, is intended to represent their appearance in almost longitudinal section. This is due to the rapidity of their centripetal displacement.

Echinocactus Ottonis, Series 2, shows a seedling in which the splitting of the larger cotyledon has not completely taken place, for while it possesses three seed-leaves, there are only two tubercles. Two of the cotyledons subtend one tubercle, and these two may be considered to represent one which has split nearly to its base. The tubercle (t_1) belonging to the split cotyledon is, however, supplied with two vascular bundles instead of the usual one (t_{1a} , t_{1b} , Diagram 13, Fig. 1). These two strands pass outwards and fuse with those of the cotyledons (c_{1a} , c_{1b} , Diagram 13, Fig. 2); the two strands thus produced undergo rapid centripetal displacement, rotate slightly towards one another, fuse as regards their protoxylems, and finally together form one bundle (Diagram 13, Fig. 3). The second bundle is formed by the union of the remaining cotyledon- and tubercle-traces (c_2 , t_2 , Diagram 13, Figs. 2-4).

Transition.

In Series 2 there were present in the upper part of the hypocotyl two 'double' bundles, produced in the manner described above, and two epicotyledonary bundles (e , Diagram 13, Fig. 3). The behaviour of these bundles in the transition is indicated in Diagram 13, Figs. 3-5. Extraordinarily large 'barrel' tracheides are developed in the central region of the axis.

In Series 1 and Series 3 the formation of the diarch root takes place in a similar manner by the fusion of the opposite pairs of phloem-strands, but in these seedlings there is no development of epicotylar bundles.

MAMILLARIA.

The Mamillarias have reached the ultimate stage in the development of a succulent habit in the seedling, which, in this group, consists of a tiny globular structure ending in a short, thread-like root (Fig. 17).

Cotyledons are practically absent, for even in the species in which they attain their maximum size they merely appear as two minute swellings at the apex of the spherical hypocotyl (Figs. 17 and 18). In spite of the extreme reduction of the cotyledons, a reduction to microscopic papillae in most of the species examined, a difference in size between the two can always be observed. In general the stem apex is very much depressed (Fig. 18).

Tubercles are well developed in those members of the genus in which the cotyledons attain their greatest size, e. g. *M. multiceps*, *M. rodantha*, *M. centricirrha*, *M. polyëdra*, and *M. meiacantha*; in these species it is only possible to differentiate cotyledonary from epicotyledonary tubercles by the position of the former in the axils of the cotyledons. The tubercle

possesses a vascular strand which traverses its tissue to the base of the spine group, but the cotyledon is usually without a vascular supply. In some cases a bundle may reach the base of the seed-leaf papilla, but more usually it does not do so, but ends blindly in the hypocotyl; the name cotyledonary bundle will still be applied to these strands, however, for, from their position, they obviously represent the seed-leaf-traces of the other genera. The behaviour of the tubercle- and cotyledon-bundles will be described later, in the account of the transition-phenomena.

The still further reduction of the cotyledons shown by *M. pentacantha*, *M. hexacantha*, and *M. eriacantha* is accompanied by the partial suppression of the tubercles, which are here represented by cotyledonary buds, such as were described as occurring in some species of *Cereus*; these buds may



FIG. 17.
Mamillaria
rhodantha.
× 3.

Fig. 18. *Mamillaria multiceps*. L.S. through upper part of seedling.
s = group of spines, t = tubercle, c = cotyledon, a = stem apex, v = vascular strands. × 62.

or may not possess vascular tissue. *M. spinosissima* and *M. Donatii* have neither tubercles nor buds, and the cotyledonary papillae are almost entirely suppressed; while, finally, *M. pusilla* has reached the stage in which the seedling consists of hypocotyl and root only; cotyledons are entirely absent.

The structural details of the hypocotyl and the root so closely resemble those described in *Echinopsis* that any further account of them is quite unnecessary.

Transition.

The details of the transition-phenomena in the different species of *Mamillaria* examined differ considerably, so that it is quite impossible to give any general description; for this reason the account of the various species will be given separately.

A. *Species in which tubercle- and cotyledon-bundles play a part in root formation.*

Mamillaria multiceps, Salm-Dyck. The upper part of the hypocotyl contains four vascular bundles, two of which are supplied by the cotyledon and two by the epicotyledonary tubercles (Diagram 14, Fig. 1).

Very soon four smaller epicotylar bundles make their appearance, alternating with the other four (Diagram 14, Fig. 2), and the eight bundles almost immediately fuse into two groups ($e+t_1$, $e+t_2$), which take up

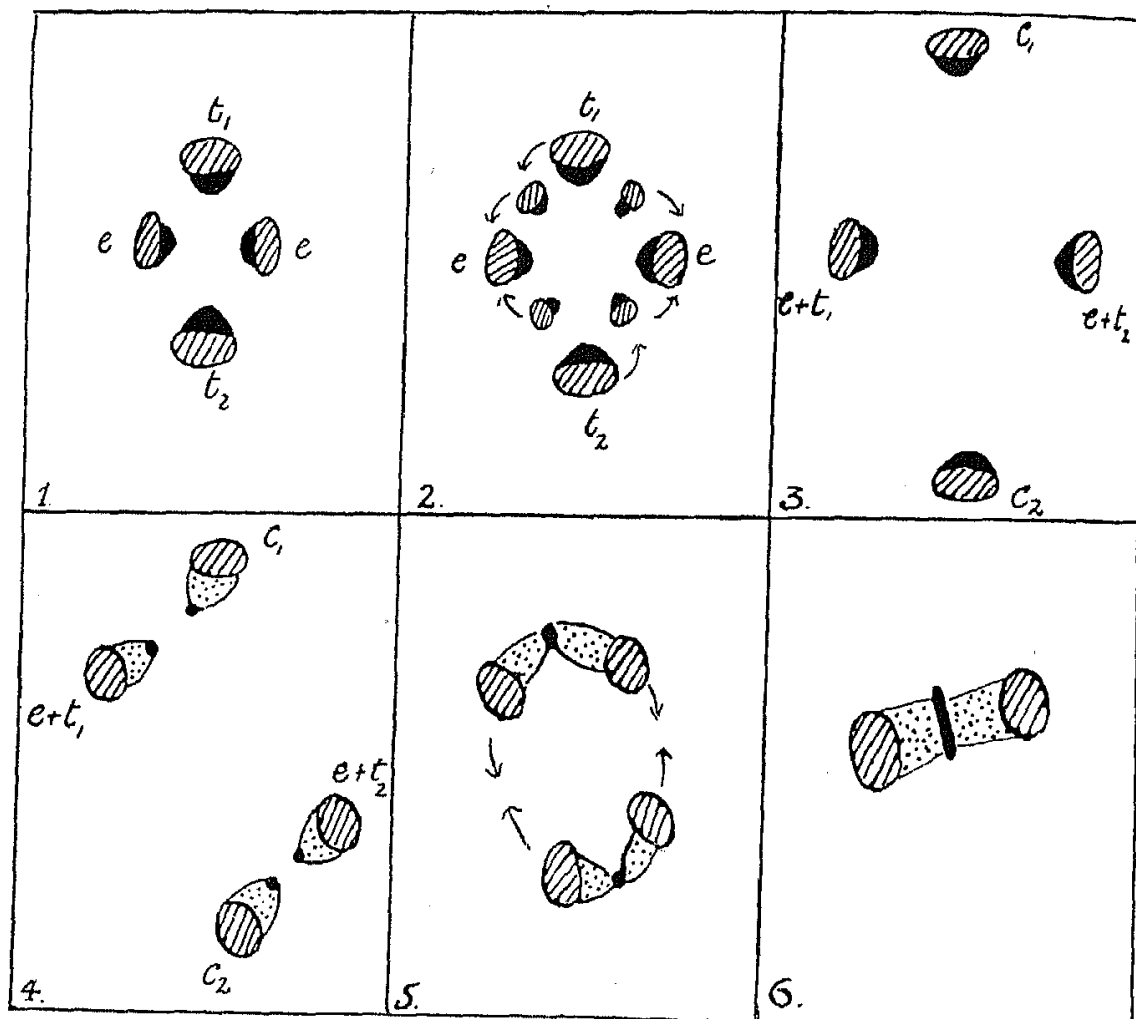


DIAGRAM 14. *Mamillaria multiceps*.

a position in the intercotyledonary plane alternating with the two cotyledon-bundles (c_1 , c_2), which have by this time differentiated (Diagram 14, Fig. 3). The two strands (c_1 , c_2) rotate slightly and pass inwards to meet the two rotating bundles $e+t_1$ and $e+t_2$ (Diagram 14, Fig. 4). The protoxylems of the adjacent bundles fuse, and by the continued movements of the phloems they are left in the exarch position (Diagram 14, Fig. 5). The opposite phloem groups finally fuse, resulting in the formation of a diarch root (Diagram 14, Figs. 5 and 6). In this species the metaxylem elements, which make their appearance towards the middle region of the

hypocotyl, are of the 'barrel' or spindle type, and are very sharply marked off from the protoxylem (Fig. 19).

Mamillaria rhodantha, Link and Otto. One of the seedlings examined showed a transition almost precisely similar to that described in *M. multiceps*, but the others differed.

In these last the cotyledonary bundles (c_1, c_2) appeared at the node ;

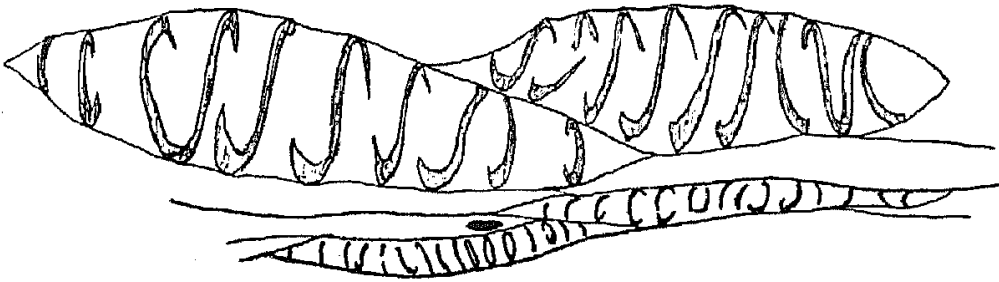


Fig. 19. *Mamillaria multiceps*. Protoxylem elements and 'barrel' tracheides. $\times 420$.

in addition to them were two tubercle-strands (t_1, t_2) and two epicotyledonary traces (e), and, very shortly, four smaller epicotyledonary strands were differentiated. Fusion of these bundles took place in the manner indicated in Diagram 15, Figs. 1 and 2. At this stage the cotyledonary phloem bifurcated, and rotated through an angle of 90° , thus leaving the

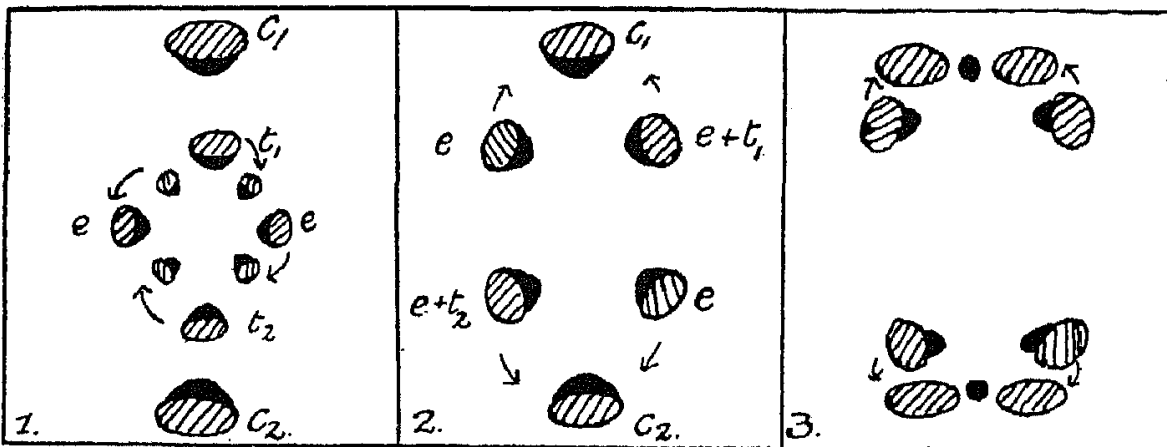


DIAGRAM 15. *Mamillaria rhodantha*.

protoxylem exposed. The remaining four bundles present in the hypocotyl moved outwards and fused laterally with the cotyledonary bundles (Diagram 15, Figs. 2 and 3). A few large metaxylem elements begin to develop at this stage between the protoxylem and the phloem, so that there are present two strands similar to those figured in Diagram 14, Fig. 5. The remaining details of the transition are similar to those of *M. multiceps*.

Mamillaria meiacantha, Engelm. These seedlings showed a transition which in all essential features resembled that of the last described individuals of *M. rhodantha*.

Mamillaria centricirra, Lem. This species showed some slight

variation when compared with the seedlings of *M. rhodantha* described above. The upper region of the hypocotyl possessed, in addition to the tubercle- and cotyledon-traces, four epicotylar bundles; these four strands together with the tubercle-bundles (t_1 , t_2 , Diagram 16, Fig. 1) by their movements finally occupy the intercotyledonary plane.

The adjacent epicotyledonary bundles soon fuse, and at about the same level cotyledonary bundle c_1 bifurcates (Diagram 16, Fig. 2), the tubercle-strand (t_1) and the epicotyledonary bundle (e) pass outwards and fuse with the bifurcated bundle (c_1 , Diagram 16, Fig. 2). The second cotyledonary bundle (c_2) shows no sign of bifurcation, it simply rotates as a whole towards e and fuses laterally with it; this fusion bundle ($e+c_2$) then fuses as regards its protoxylem with the tubercle-bundle (t_2), in the

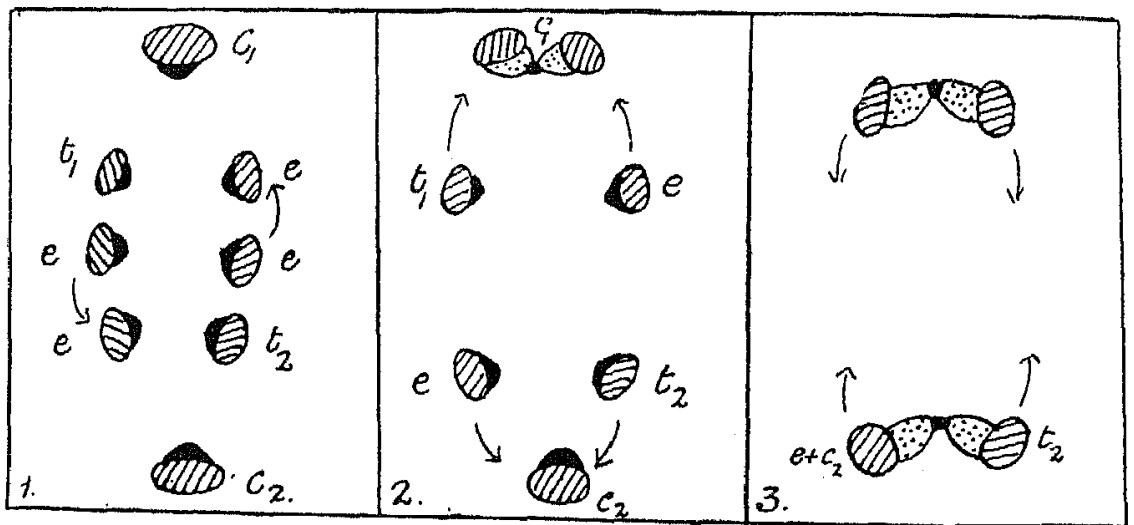


DIAGRAM 16. *Mamillaria centricirrha.*

manner shown in Diagram 16, Fig. 3. The remaining details of the transition resemble those described in *M. multiceps*.

Mamillaria polyëdra, Mart. The two bundles supplied to the hypocotyl by the two cotyledons bifurcate early, and the transition takes place in the manner shown in Diagram 16, Fig. 2 (c_1); unlike *M. centricirrha*, however, both cotyledonary bundles behave in a similar way. A slight variation was shown by one seedling of the species, in that the two halves of the seed-leaf-trace separated widely after bifurcation, and remained some distance apart throughout the greater part of the passage through the hypocotyl.

Mamillaria pentacantha, Pfeiff. In this species the tubercles were present in the form of cotyledonary buds, which in two of the seedlings examined were supplied with a vascular bundle, while in the third no such bundle was present; the transition-phenomena varied in the two cases.

In the seedlings belonging to the first category, viz. those with a tubercle-bundle, the upper part of the hypocotyl possessed four epicotyledonary, two cotyledonary, and two tubercle strands. By the gradual

movement of the tubercle and epicotyledonary strands until they occupied a position similar to that indicated in Diagram 16, Fig. 1, and by the subsequent fusion of the three bundles lying between the cotyledon-traces, the eight bundles originally present were reduced to four, which performed during the remainder of the transition in the manner indicated for *M. multiceps* in Diagram 14, Figs. 3-6.

The seedling in which no tubercle-bundles appeared showed a transition very closely resembling that described for *M. rhodantha*, but the four bundles occupying the intercotyledonary plane in the latter species and shown in Diagram 15, Fig. 3, were, in *M. pentacantha*, all epicotylar in origin.

Mamillaria eriacantha, Hort. As in *M. pentacantha*, a tubercle-bundle supplying the cotyledonary bud may or may not be present; but, unlike that

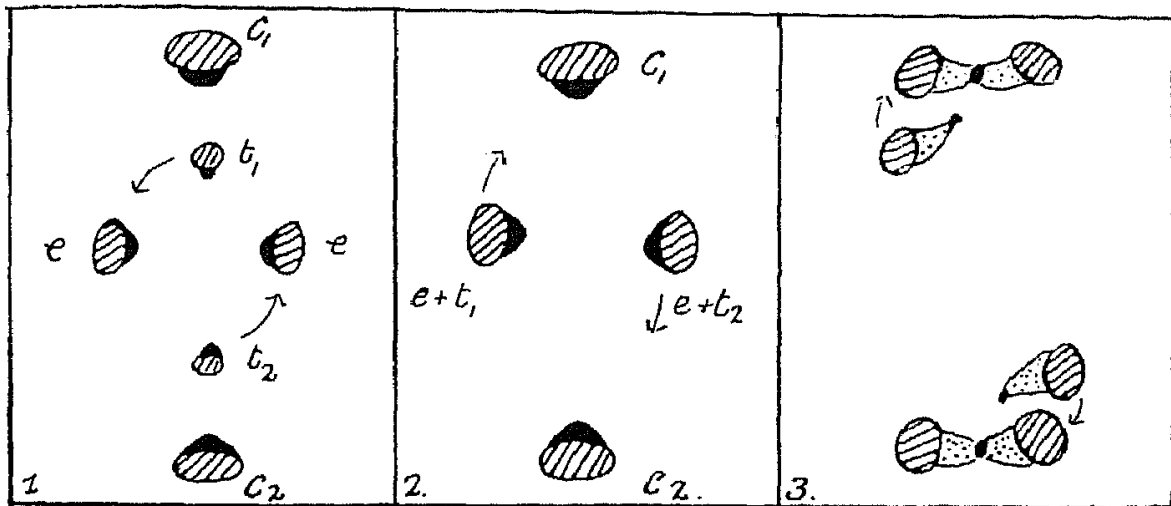


DIAGRAM 17. *Mamillaria eriacantha*.

species, the transition takes place in essentially the same manner in both cases. Two cotyledonary and two epicotyledonary bundles are present at the top of the hypocotyl; when the tubercle-bundles are developed they simply move outwards and fuse with the epicotyledonary strands (Diagram 17, Figs. 1 and 2). Almost concurrently with this fusion the cotyledonary bundles bifurcate, their phloems separate and rotate until they lie on either side of the protoxylem, which by this means is left exposed; during this change large metaxylem elements appear, in the position indicated in Diagram 17, Fig. 3. The epicotyledonary strands have by this time moved laterally towards the cotyledon-traces, fusion with them takes place, and the resulting bundles give rise to a diarch root in a precisely similar way to that indicated in Diagram 14, Figs. 5 and 6.

B. *Species in which only cotyledon-bundles play a part in root formation.*

(Strictly speaking some seedlings of *M. pentacantha* and *M. eriacantha* fall into this category and not into Group A, but for the sake of simplicity they have been described above.)

Mamillaria hexacantha, Salm-Dyck. The transition-features in these seedlings are practically identical with those of *M. eriacantha*, in which cotyledonary bud-bundles are absent.

Mamillaria spinosissima, Lem. The transition-phenomena of most of the seedlings of this species which were examined were practically identical with those of *M. eriacantha*, in which the tubercle-bundle was absent; one, however, showed a somewhat different method of procedure. In this seedling the upper hypocotylar region possessed six epicotyledon-traces lying in two groups of three, in alternation with the cotyledonary bundles. At a lower level each of the two groups fused into one strand, which, unlike what usually obtains, remained in position during the remainder of the transition. Concurrently with the fusion of the three bundles, the cotyledonary phloem bifurcated; the two halves thus produced rotated and at the same time moved gradually inwards; thus towards the middle region of the hypocotyl the epicotyledonary bundles each showed a phloem group derived from the cotyledon-bundles lying on either side of it; these phloem groups soon fuse laterally with epicotyledonary phloem; the epicotyledonary xylem dies out, but this is probably to be attributed to the age of the seedlings. During these changes the protoxylems of the cotyledon-strands, which by the movement of the phloems had been left exposed, undergo centripetal displacement; finally large metaxylem elements bridge the space between them and the diarch root is completed.

Mamillaria Donatii, Berge. The transition-phenomena in these seedlings very closely resemble those which are found in the seedlings of *M. pentacantha* which possess no cotyledonary tubercle-trace. The bundles are, however, very small, and the xylem is composed of very few elements.

Mamillaria missouriensis, Sweet. The seedlings of this species differ in one respect from all of the above described Mamillarias. The papillate cotyledons possess at first one median vascular strand, which almost immediately branches into three. In one of the two seedlings available for examination two of these strands (*b* and *c*, and *d* and *e*, Diagram 18, Fig. 1) fused in the upper part of the hypocotyl, so that there were present four cotyledonary and four epicotyledonary bundles.

The pairs of cotyledonary strands rotated towards each other as is shown in Diagram 18, Fig. 2, and at a lower level one epicotyledonary bundle (*e*) fused with each seed-leaf-trace (Diagram 18, Fig. 3), but this fusion does not take place simultaneously. After it has been accomplished the four phloem-strands separate; accompanied by the metaxylem tracheides, which from this stage gradually die out, they finally take up a position such as is shown in Diagram 18, Fig. 4. Towards the base of the hypocotyl each of the protoxylems branch, and as a result a tetrarch root is produced (Diagram 18, Figs. 5 and 6).

The other seedling of this species behaved as did the preceding one as regards the branching of the cotyledonary traces ; the branches, however, soon fused again, leaving only one cotyledon-bundle for each papillate seed-leaf. This bundle bifurcated at a lower level and the divided bundle played

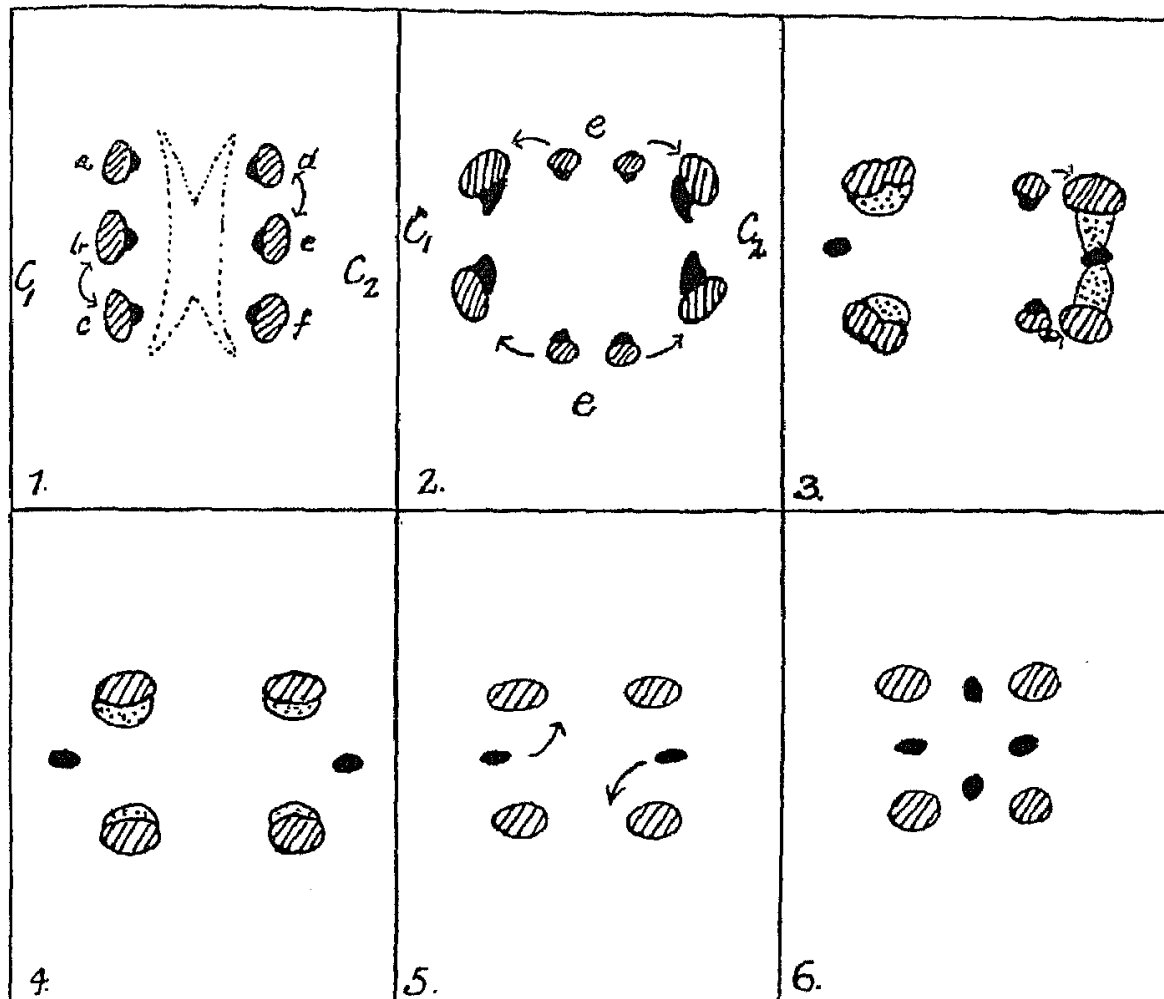


DIAGRAM 18. *Mamillaria missouriensis*.

the same part in the transition as did the paired bundle of the first described seedling. In all other respects the two seedlings were precisely similar.

The belated formation of a tetrarch root by the branching of the xylem arms recalls the similar feature described in *Cereus tortuosus*.

C. *Species in which cotyledons are absent, and epicotyledonary bundles alone produce the root structure.*

Mamillaria pusilla, Sweet. The hypocotyl of these seedlings possesses in its upper region four vascular strands. These bundles move gradually towards the centre, and at the same time rotate slightly towards one another in pairs; finally the protoxylems of a pair fuse and metaxylem elements begin to appear centripetally, until a solid mass of large 'barrel' tracheides results. During this development the phloem-strands have been gradually

moving laterally, until the opposite groups finally fuse, and a diarch root results. The transition is thus seen to be very similar to that illustrated in Diagram 14, Figs. 3-6, but the four groups are in *M. pusilla* all epicotylar in origin.

VALUE OF SEEDLING ANATOMY IN CLASSIFICATION.

The Cactaceous seedlings examined can be classified into two groups so far as their external morphology is concerned. The first of these groups includes those seedlings which bear a more or less close resemblance to those of an ordinary Dicotyledon, having a long hypocotyl and distinctly leafy cotyledons. Three genera are included in this division, namely, *Pereskia*, *Opuntia* and *Nopalea*; the seedlings of the first show no sign of a succulent habit, but in the last two genera evidence of it is given in the somewhat swollen hypocotyl and in the thick seed-leaves.

The second group is composed of all the other genera which have been examined, viz. *Phyllocactus*, *Cereus*, *Pilocereus*, *Rhipsalis*, *Echinocereus*, *Echinopsis*, *Echinocactus* and *Mamillaria*. The members of this group show a considerable diminution in length and a marked increase in succulence as compared with the seedlings of the first group; in them the hypocotyl is always short and is ovoid or globular in shape, while the cotyledons are small, pointed structures often microscopic in size.

Generally speaking, two types of transition are found in the order; the *Anemarrhena* type of Miss Sargent is characteristic of the seedlings of Group I, while Van Tieghem's Type 3 forms the ground-plan of the transition phenomena of the members of Group II; in this respect the seedling anatomy follows the morphology.

GROUP I.

In the seedlings of this group the transition in the upper part of the hypocotyl follows closely the *Anemarrhena* type, with the exception of *Opuntia maculacantha* and *O. Pseudo-tuna*. The type is maintained and a tetrarch root is established in the usual way in *Nopalea n. sp.*, *Opuntia Ficus-indica*, *O. Tuna*, *O. polyantha*, *O. imbricata*, *O. Bergeriana*, and *O. stricta* Series A and C, but a modification of it occurs in *O. stricta* Series B, *O. albicans*, *Pereskia n. sp.*, and *P. Pititache*. The seedling structure is, however, of very little use in delimiting the genera in the group, for the resemblance between two species of the same genus is sometimes much less close than between species of different genera; thus *Nopalea n. sp.* and *Opuntia Ficus-indica*, or *Opuntia albicans* and *Pereskia n. sp.*, would appear from their seedling anatomy to be much more closely related than *Opuntia Ficus-indica* and *O. albicans*.

GROUP II.

The transition in the majority of the species examined in this group was of Van Tieghem's Type 3; many variations on it occurred, of which the following were the most important:—

(a) In *Phyllocactus*, *Cereus*, *Pilocereus*, *Echinocereus*, sp. of *Echinopsis*, and certain species of *Echinocactus*, the root is not of the typical diarch nature, but possesses four phloem- and two xylem-bundles; this is due to the fact that the opposing groups of bast remain apart in the hypocotyl instead of fusing.

(b) In many seedlings a cotyledonary tubercle-bundle is developed; it usually merely fuses laterally with a portion of the cotyledon-strand, but in *Echinocactus Ottonis*, *Echinopsis multiplex* Series 2, *Pilocereus exerens* Series 1, *Mamillaria multiceps*, *M. rhodantha* (one seedling), and *M. pentacantha*, it played an essential part in the root formation, forming half of each of the 'double' bundles.

(c) In *Echinocactus hexaedrophorus* and *Mamillaria missouriensis* a tetrarch root is formed in a manner which recalls the similar feature in *Opuntia maculacantha*.

In Group II, as in Group I, the transition-phenomena afford little assistance in the delimiting of genera within the group, for the details of the seedling anatomy are not always constant in a single species, and much less in a particular genus; this is well seen in *Echinopsis multiplex*, *Pilocereus exerens*, *Mamillaria rhodantha*, and *M. pentacantha*. Further, although in some cases, as for example in the genus *Cereus*, the seedling anatomy of the species is a fairly constant feature, yet individuals of other genera bear so close a resemblance to them that it is impossible by this means to separate one genus from the other; in other words, it is impossible to define a genus in terms of its seedling structure.

On the other hand, just as the seedlings of Group I are distinctly marked off by their external appearance from those of Group II,¹ so the transition-phenomena of the members of Group I are fairly constant and are sharply marked off from the type of transition characteristic of Group II. From this it would seem that the physiological factors which have ultimately resulted in the specialized seedlings of Group II have reacted on the seedling anatomy, producing a transition very different from that of the less reduced members of Group I.

RELATION OF THE SEEDLING ANATOMY TO SOME PHYLOGENETIC PROBLEMS.

One of the most interesting features in the seedling anatomy of the Cactaceae is the occurrence in some genera, e. g. *Opuntia* and *Nopalea*, of the type of transition shown by Miss Sargent to be characteristic of

¹ Compare Figs. 1, 2, and 6 with Figs. 7, 8, 9, 16, and 17.

Anemarrhena asphodeloides. So far as has been ascertained this formation of a tetrarch root-stele from two cotyledonary traces has been previously described in only two other dicotyledonous seedlings, *Eranthis hiemalis*¹ and *Podophyllum peltatum*,² in both of which the tetrarch arrangement is fugitive and the root is really a diarch structure. In the Cactaceae, on the other hand, the resemblance to *Anemarrhena* is more complete, for the tetrarch structure persists to the root-tip; indeed, the only important difference between the two seems to lie in the fact that the two cotyledonary bundles are derived in the Cactaceae from two seed-leaves and in *Anemarrhena* from one.

The occurrence of the *Anemarrhena* type in a modified form in a member of the natural order Ranunculaceae which, on other grounds, has been considered to bear a somewhat close relation to the Monocotyledons, has been used as a reason for formulating an hypothesis as to the origin of the monocotyledonous condition, namely, a theory that 'the two cotyledons of Primitive Angiosperms have united to form the single member in Monocotyledons'.³ The close resemblance between *Eranthis* and *Anemarrhena* led to the conclusion that there is probably 'a real genetic connection between *Eranthis* and *Anemarrhena*; that they are descended from a common ancestor with two distinct seed-leaves, each represented by a single trace in the hypocotyl'.⁴ Now the cotyledons of *Eranthis* are united as regards their petioles, and this led to the statement that even if there were no historical connexion between them, 'the structure of *Eranthis* may nevertheless illustrate the double origin of the *Anemarrhena* cotyledon. For without the analogy of *Eranthis*, the assumption that each trace in the cotyledon of *Anemarrhena* represented a distinct seed-leaf was groundless. Not only was direct evidence of such a double origin absent, but there was nothing to show that the union of two cotyledons, if it did take place, would actually give rise to such a type of vascular symmetry.' The second Dicotyledon in which the *Anemarrhena* type was found was also a geophilous seedling in which the petiolar tube was well developed; hence the 'fusion' hypothesis appeared to receive additional support, for the known facts seemed to show that union of cotyledons might bring about such a vascular arrangement as was found in *Anemarrhena*. But at the same time it must be observed that the formation of a cotyledonary tube does not necessarily produce this *Anemarrhena* type of structure, for in two other Ranunculaceous seedlings, *Delphinium* sp. (probably *nudicaule*) and

¹ Sargent, E. : The Origin of the Seed-Leaf in Monocotyledons. *New Phyt.*, i, 1902, p. 112.

² Sargent, E. : Reconstruction of a Race of Primitive Angiosperms. *Ann. Bot.*, xxii, 1908, p. 170.

³ *Loc. cit.*, p. 183.

⁴ Sargent, E. : A Theory of the Origin of Monocotyledons, founded on the Structure of their Seedlings. *Ann. Bot.*, xvii, 1903.

Anemone coronaria,¹ a cotyledonary tube is present, but the transition is of the ordinary Ranunculaceous type in which there is a diarch root and no hint of tetrarchy. Thus it is seen that the development of a cotyledonary tube may or may not give rise, even in seedlings of the same family, to the *Anemarrhena*-type of vascular rearrangement; while this same type may occur, as has been shown above, in seedlings in which there is not the slightest sign of cotyledonary fusion.

It cannot be considered that the resemblance of *Opuntia*, for example, to *Anemarrhena* is the result of a close genetic relation between the two; nor can it be conceded that it is due to a response of two unrelated forms to similar conditions; hence we cannot but conclude that the resemblance is accidental. This being so, then it is quite possible that the similarity of *Eranthis* and *Podophyllum* to *Anemarrhena* is also accidental, more especially as the other two related seedlings, *Delphinium* and *Anemone*, do not diverge from the normal Ranalian type, though they might naturally be expected to do so, on analogy with *Eranthis*.

The theoretical importance of the anatomical resemblance of *Eranthis* to *Anemarrhena* has already been denied on other grounds by Tansley.² Miss Sargent, in her paper on the 'Reconstruction of a Race of Primitive Angiosperms',³ has put forward many reasons for the probability of a dicotyledonous Proangiosperm; she concludes that the monocotyledonous condition arose by a fusion of the cotyledons in adaptation to a geophilous habit, the fusion taking place on account of the need for strict economy which must be observed by the seedling. But, as has been already pointed out, the evidence on which the 'fusion' hypothesis was based has been considerably weakened by the discovery of the *Anemarrhena* type in seedlings of such a specialized order as the Cactaceae; moreover, the economizing of time and material may have taken place in at least two other ways without necessitating any theory of fusion. It may have occurred:—

1. By the gradual suppression of one cotyledon of an ancestral pair, or,
2. By the assumption of different functions by the two cotyledons.

The first of these views, the 'suppression' hypothesis, was supported by Prof. Henslow,⁴ and Miss Sargent⁵ has summarized the most important evidence given by him in support of his views.

Charles and Francis Darwin⁶ have shown that dicotyledonous plants

¹ Sargent, E.: loc. cit.

² Tansley, A. G.: Reduction in Descent. New Phyt., i, p. 132.

³ Loc. cit.

⁴ Henslow, G.: A Theoretical Origin of Endogens from Exogens by Adaptation to an Aquatic Habit. Linn. Soc. Journ., xxix, 1892.

⁵ Sargent, E.: Reconstruction of a Race of Primitive Angiosperms. Ann. Bot., xxii, 1908, p. 175.

⁶ Darwin, C. and F.: Power of Movement in Plants, 1880, p. 94.

may possess cotyledons in which one shows signs of reduction, or even of complete abortion, and they cite as instances of this *Citrus Aurantium*, in which the cotyledons differ in size and are not necessarily placed opposite to one another; *Pachira aquatica*, which shows similar features; species of *Abronia*, in which one of the cotyledons is quite rudimentary; and *Chaerophyllum* and *Corydalis*, where only one cotyledon is present. They infer that 'there is some close connection between the reduced size of one or both cotyledons and the formation by the enlargement of the hypocotyl or of the radicle of a so-called bulb . . . and that one or both cotyledons, from being superfluous, decreased in size'. A further illustration of this reduction in size of the cotyledons is afforded by the Cactaceae seedlings.

Additional evidence of this suppression is given by Goebel¹ for *Trapa*, in which not only is there a difference in the size of the cotyledons, but the larger one arises as a terminal structure upon the embryo, while the smaller is lateral to the stem-bud.

Finally, the experimental work of A. W. Hill² on the genus *Cyclamen* has shown that normally only one cotyledon is developed, which first serves as an absorbing organ, and, later, as an assimilating one; the rudiment of the second cotyledon is always present, and should anything happen to the first cotyledon this rudiment develops into a normal green leaf. Further, in some species the second cotyledon may closely resemble the first one, while in others it is more like a foliage leaf.

Thus there is no lack of evidence to show that the partial or complete suppression of one of the seed-leaves may occur in the Dicotyledons when the necessity for economy occurs; and it is possible that a similar suppression, owing to the adoption of a geophilous habit, may have taken place in the ancestors of Monocotyledons.

For these reasons it does not appear necessary to postulate a theory of fusion to account for the occurrence of the monocotyledonous condition.

The second theory relating to the evolution of the Monocotyledons has been put forward by A. W. Hill,³ as the result of his observations on the germination of apparently monocotyledonous species of *Peperomia*, in which one cotyledon is hypogeal, and acts as a sucker, while the other has assumed the appearance and functions of a foliage leaf. He suggests that evolution along similar lines may have produced the normal seedling habit of such monocotyledonous orders as Araceae, and that the cotyledon and

¹ Goebel, K.: *Organography of Plants*, Part II, Oxford, 1905, p. 257.

² Hill, A. W.: *The Seedlings of certain Pseudo-monocotyledons*. Section K, Brit. Ass., York, 1906.

³ Hill, A. W.: *Morphology and Seedling Structure of the Geophilous species of Peperomia, together with some Views on the Origin of Monocotyledons*. *Ann. Bot.*, xx, 1906, p. 395.

so-called 'first leaf' which are directly opposite to each other in the seedlings of some species of *Arum* and *Arisaema* may be the equivalent of the two cotyledons of *Peperomia*. He has further shown¹ that in *Arisarum vulgare* the 'first leaf' can perform the function of a cotyledon when the latter has become aborted or been torn off.

Among the Monocotyledons the Araceae have been considered to be most nearly related to the Piperaceae. 'The affinities between two such simple orders as the Piperaceae and Araceae appear to be much more close and definite than between the anomalous Ranunculaceae and the highly specialized Liliaceae, and in the former case the modified pseudo-monocotyledonous *Peperomias* show definite homologies in their adult condition with the Monocotyledons.' It seems probable that in some of the Monocotyledons, at any rate, the monocotyledonous condition has arisen from the dicotyledonous one along similar lines to those followed by the *Peperomias* in their development of the geophilous habit.

In this connexion it may be noted that there has always been much difference of opinion as to the interpretation of the organs present in the grass embryo, and the view has been put forward that the scutellum and the germ-sheath represent highly differentiated parts of a single cotyledon;² in view of A. W. Hill's work it is possible that they represent two cotyledons which have each taken on a separate function. A similar explanation may serve to explain the complicated structure of those monocotyledonous seedlings in which the seed-leaf is differentiated into an haustorium, a middle portion, and a sheath, e. g. *Tradescantia*, *Cyperus*, &c. In other monocotyledonous families, e. g. Juncagineae, Butomeae, and Alismaceae, the cotyledon becomes green, and according to Goebel³ does not differ in form and structure from the first foliage leaves in any essential feature, though its anatomical differentiation is somewhat simpler.

According to Miss Sargent,⁴ however, the seedling anatomy of the Monocotyledons does not support A. W. Hill's view, for the first leaf is characterized by a midrib and usually has lateral bundles in addition to it, while the cotyledon usually has no midrib; it has instead a double bundle or two single and quite distinct bundles, while in the cases in which a midrib is present it usually shows its double character during the transition.

The presence or absence of a midrib seems then to be the chief difference between the cotyledon and the first leaf, and the question as to the possibility of the first leaf being a second cotyledon really rests upon the importance which can be attached to the 'double' bundle.

¹ Hill, A. W. : The Origin of Monocotyledons. Ann. Bot., xxii, 1908.

² Rendell, A. B. : The Classification of Flowering Plants, i, p. 235.

³ Goebel, K. : loc. cit., p. 408.

⁴ Loc. cit., p. 178.

On this point the seedling structure of the Cactaceae can throw some light. In general the upper part of the hypocotyl of these seedlings is occupied by two 'double' bundles, which may have been formed in one of the following ways:—

1. By the bifurcation of the cotyledonary bundle, e.g. *Echinopsis multiplex*.
2. By the fusion of separate vascular strands.

The strands which fuse may be:—

- (a) The two separate bundles present in a cotyledon, e.g. *Echinopsis Lagermannii*, *Cereus peruvianus*, and *Echinocereus Ehrenbergii*.
- (b) The cotyledon-bundle and its tubercle-bundle, e.g. *Echinocactus Ottonis*, Series 3.
- (c) The fused cotyledon- and tubercle-bundles to form one half of the double bundle, the other half being similarly produced, e.g. *Echinocactus Ottonis*, Series 1, *Mamillaria multiceps*.
- (d) The fused cotyledon- and tubercle-bundles to form one half of the double bundle, the other half being formed by the fusion of the other two cotyledonary strands, e.g. *Echinopsis tubiflora*.
- (e) The epicotyledonary strands only, e.g. *Mamillaria pusilla*.

Further, in *Mamillaria missouriensis* the 'double' bundle may be produced either by bifurcation of a single strand or by the fusion of the separate ones; while in *Mamillaria centricirrha* one 'double' bundle is derived by the splitting of the cotyledon-trace, and the other by the interaction of a tubercle- and a cotyledon-strand.

A consideration of these various methods of formation of the 'double' bundle in the Cactaceae points to the fact that it is unsafe to formulate any theory on the homology of such variable structures;¹ for they would appear to be nothing more than an arrangement of the vascular elements in such a way that the change from stem to root structure may take place as conveniently as possible; they would certainly not appear to have any definite morphological value. If then the 'double' bundle, which appears to be a fairly constant feature of the cotyledon of Monocotyledons, is not necessarily the homologue of two separate bundles, that is, if the 'double' bundle has no definite morphological significance, it is quite possible to account for the distinction between the vascular symmetry of the cotyledon and of the 'first leaf' in the Monocotyledons. Thus, supposing that the ancestor of the group was a seedling with two equivalent cotyledons, adaptation to a geophilous habit led to these cotyledons assuming different functions; one serving as an organ for the absorption of the endosperm, the other retaining its assimilating function. Since the need for economizing

¹ Thomas, E. N.: A Theory of the Double Leaf-trace founded on Seedling Structure. *New Phyt.*, vi, p. 88.

time was urgent, one seed-leaf delayed its appearance more and more until finally the symmetry of the root-stele of the seedling had to be attained without its aid, and the second cotyledon became practically the first leaf. We may consider that, since the cotyledons originally were equivalent in function, their vascular structure would be similar, each of them would contribute equally to the root-structure, and each would furnish a strand opening out somewhere in its course as a 'double' bundle. In the 'sucking' cotyledon it would obviously be an advantage to delay the closing up of the 'double' bundle and to separate its parts, producing the appearance of two distinct bundles, especially where much endosperm had to be absorbed. In these cases the structure of the first cotyledon and the second would be different, but the second might still, although its appearance was delayed, contribute to the root formation. Finally, when the second seed-leaf did not develop until very late, the first would necessarily carry out the transition unaided; its two strands, formed as indicated above, would now each act as a 'double' bundle, and the difference between the two originally equivalent cotyledons would be still further increased. In this connexion it is important to remember that 'seedlings are thrown on their own resources at so early a period in their life history that the struggle for existence, repeated through many generations, often transforms their whole structure. At the time of germination this structure is still so little differentiated as to be extraordinarily plastic.'¹

It is, therefore, quite conceivable that the difference in structure between the cotyledon and the so-called 'first leaf' in Monocotyledons can be explained as due to the physiological needs of the young plant, and if so, A. W. Hill's theory is still left without any serious objection against it.

In conclusion, of the three hypotheses which have been put forward in explanation of the evolution of Monocotyledons from a dicotyledonous ancestry:—

1. The *fusion* hypothesis is seriously weakened by the discovery of the facts described above.

2. The *suppression* hypothesis is but slightly affected.

3. The *first leaf* hypothesis is supported, for the chief objection which has been urged against it has been shown to be no longer valid.

In regard to the transition-phenomena of the seedlings of the Cactaceae, much variation is to be found throughout the group; it does not always appear to be uniform even in the members of a single genus, as is seen in *Opuntia* and *Mamillaria*, although it may be fairly constant, as for example in *Cereus*. Ganong² has already pointed out that in all probability the adaptations to physiological needs in the adults have worked back into the

¹ Sargent, E.: The Origin of the Seed-Leaf in Monocotyledons. *New Phyt.*, i, p. 108.

² Ganong, W. F.: *loc. cit.*

embryo, for the form of the seedlings corresponds very closely with that of the adults. A study of the seedling anatomy shows that not only the form but also the structure has been so influenced; this is seen, for example, in the appearance of tubercles and of 'barrel' tracheides in seedlings of those plants in which similar features are characteristic of the adults.

Miss Sargent has shown that much variation in the transition-phenomena occurs in the Liliaceae, and T. G. Hill¹ has found that 'the details of the transition in the Piperaceae are anything but rigid', while there is probably 'much variation in the Centrospermae'.

Since, then, there is such variation in small groups of plants, and since seedling structure can be influenced by physiological factors working on the adults, to me it does not appear justifiable to use such characters as indicators of phylogenetic connexions.

SUMMARY.

Cotyledons.

1. There is a gradual increase in succulence combined with a marked decrease in size in the seedlings from *Pereskia*, which is normally dicotyledonous in form, through *Opuntia*, *Nopalea*, *Phyllocactus*, *Cereus*, *Pilocereus*, *Echinocereus*, *Rhipsalis*, *Echinopsis*, *Echinocactus* to *Mamillaria*, in which the seed-leaves are either microscopic or absent.

2. In general the cotyledons are two in number; they are always unequal in size, the difference being most marked in *Nopalea*. Seed-leaves are absent in *Mamillaria pusilla*.

Three cotyledons were found in *Opuntia stricta*, Series C. In *Echinocactus Ottonis*, Series 1, one of the two cotyledons was split to its base, giving the seedling the appearance of possessing three distinct seed-leaves, and three cotyledonary tubercles were also present.

In *Echinocactus Ottonis*, Series 3, one of the two cotyledons was bifurcated almost to its base and the split cotyledon subtended one tubercle which was laterally elongated.

3. Cotyledonary buds have been observed in *Cereus triangularis*, *Echinopsis Eyriesii*, *E. Zuccarinii*, *E. Oxygona*, *Echinocactus bicolor*, *E. denudatus* and *Mamillaria hexacantha*.

There is an increase in the size of the buds, and a vascular bundle to supply them in *Phyllocactus Hookeri*, *Cereus tortuosus*, *C. peruvianus*, *C. Jamacaru*, *C. Spachianus*, *Pilocereus exerens*, *P. albispinus*, *Echinocactus bicolor* (one seedling), *Mamillaria pentacantha* and *M. eriacantha*.

Tubercles with spines of the form found in the mature plant occur in *Echinopsis multiplex*, *E. Lagermannii*, *E. tubiflora*, *Echinocactus Ottonis*,

¹ Hill, T. G.: On the Seedling Structure of certain Piperales. *Ann. Bot.*, xx, 1906, p. 174.

Mamillaria multiceps, *M. rhodantha*, *M. centricirra*, *M. meiacantha* and *M. polyëdra*.

4. The cotyledonary bud-bundles behave in various ways. They may or may not be essential to the formation of the root-structure.

In the following species they are essential in the transition, forming one half of a 'double' bundle: *Echinopsis multiplex*, Series 2, *Echinocactus Ottonis*, *Mamillaria multiceps*, *M. rhodantha* (some seedlings), and *Pilocereus exerens*, Series 1.

In the following species they are not essential in the root formation. They may:—

(a) Fuse laterally with one half of the double bundle, e.g. *Phyllocactus Hookeri*, *Cereus tortuosus*, *C. peruvianus*, *Pilocereus*, *Echinopsis multiplex*, Series 1, *E. Lagermannii*, *E. tubiflora*, and *Mamillaria polyëdra*, Series 1.

(b) Fuse with an epicotyledon-strand, and the fusion product unite laterally with the cotyledon-trace, *Echinocactus bicolor*, Series 2, *Mamillaria rhodantha* (some seedlings), and *M. polyëdra*, Series 2.

(c) Bifurcate and rotate, each half bundle fusing with the cotyledon-bundle, e.g. *Echinocactus Ottonis*. In *Pilocereus albispinus*, Series 1, and in one cotyledon of *Echinopsis multiplex*, Series 3, the tubercle-bundle which bifurcated consisted of phloem only.

Transition-Phenomena.

5. The transition-phenomena are of the *Anemarrhena* type in *Opuntia Ficus-indica*, *O. imbricata*, *O. Tuna*, *O. polyantha*, *O. Bergeriana*, *O. stricta* and *Nopalea n. sp.* This type is slightly modified in *O. Tuna*, Series C, and in one seedling of *O. polyantha*, and is considerably modified in *Echinocactus hexaedrophorus* and *E. denudatus*.

The following species show a branching into three of the cotyledonary xylem, but the lateral arms die out again at a later stage, and the two intercotyledonary root-poles arise independently of the cotyledonary xylem:—

Pereskia n. sp., *Opuntia stricta*, *O. albicans*. In *P. Pititache* the two intercotyledonary root-poles do not arise, so the root-structure is of the *Cereus* type. In *O. maculacantha* and *O. Pseudo-tuna* the tetrarch root arises in a similar way to *O. stricta*, but there is no previous suggestion of the *Anemarrhena* type.

In all the remaining Cactaceae seedlings examined the two 'double' bundles which are found in the hypocotyl follow a somewhat similar course, and the transition is of Van Tieghem's Type 3. The bundles rotate until the phloems lie on either side of the xylem in which the protoxylem has become exarch; the phloems then either fuse in pairs to form a diarch root, or else remain isolated, when the *Cereus* root type results.

6. The epicotyledonary vascular tissue plays no essential part in the transition-phenomena in any of the species examined except *Mamillaria pusilla*, in which seedling no cotyledons are present; it is, however, differentiated very early, especially in the *Mamillarias*, and supplements the existing vascular supply.

7. There are differences in the method of transition between seedlings of the same species, in the case of *Opuntia stricta*, *Echinopsis multiplex*, *Mamillaria rhodantha* and *M. pentacantha*.

8. The two 'double' bundles of the hypocotyl show a very great variation in their method of formation. They may arise:—

(a) By the bifurcation of the cotyledonary bundle, e.g. *Echinopsis multiplex*, *Opuntia sp.*, &c.

(b) By the fusion of separate vascular strands. The strands which fuse may be:—

(1) The two separate bundles present in the cotyledon, e.g. *Echinopsis Lagermannii*, *Cereus peruvianus* and *Echinocereus Ehrenbergii*.

(2) The cotyledon-bundle and its tubercle-bundle, e.g. *Echinocactus Ottonis*, Series 3, *Mamillaria multiceps* and *M. centricirrho*.

(3) The fusion product of a cotyledon- and a tubercle-bundle to form one half of the 'double' bundle, the other half being produced by another similar fusion, e.g. *Echinocactus Ottonis*, Series 1.

(4) The fusion product of a cotyledon- and a tubercle-bundle to form one half of the 'double' bundle, the other half being produced by the fusion of two cotyledon-strands, e.g. *Echinopsis tubiflora*.

(5) The epicotyledonary bundles, e.g. *Mamillaria pusilla*.

9. 'Barrel' tracheides are present in the hypocotyl and root of *Opuntia stricta*, *O. maculacantha*, *Cereus tortuosus*, *C. peruvianus*, *Echinopsis multiplex*, *E. tubiflora*, *E. Lagermannii*, *Echinocactus Ottonis*, and all the species of *Mamillaria* examined.

ROOT.

10. A tetrarch root is characteristic of *Pereskia n. sp.*, the *Opuntias*, *Nopalea n. sp.*, *Echinocactus hexaedrophorus*, *E. denudatus* and *Mamillaria missouriensis*.

A 'Cereus' type of arrangement, with four phloem and two xylem bundles, is found in the roots of *Pereskia Pititache*, *Phyllocactus Hookeri*, *Cereus tortuosus*, *C. peruvianus*, *C. Famacaru*, *C. Spachianus*, *C. triangularis*, *Pilocereus exerens*, *P. albispinus*, *Echinopsis Eyriesii*, *E. multiplex*, *E. tubiflora* and *Echinocactus Wislezeni*.

A normal diarch root is produced in *Rhipsalis Warmingiana*, *R. dissimilis*, *Echinocereus Ehrenbergii*, *E. cinerascens*, *Echinopsis oxygona*, *E. Lagermannii*, *E. Zuccarini*, *Echinocactus bicolor*, *E. Ottonis*, and the species of *Mamillaria* with the exception of *M. missouriensis*.

THEORETICAL.

11. The adaptations shown by adult plants in response to their environment, which have been impressed on the *form* of the young seedling, have had a corresponding influence on their internal structure.

12. It is not justifiable to use the seedling structure as an indicator of phylogenetic connexions.