CONTRIBUTIONS TO THE ANATOMY OF CHENOPODIACEAE AND AMARANTACEAE II

Primary Vascular System of *Achyranthes aspera* L., *Cyathula prostrata* Blume and *Pupalia lappacea* Juss.

BY

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Introduction.

It has already been stated in the first paper of this series that one point in which the families Chenopodiaceæ and Amarantaceæ differ from the normal dicotyledons, is in the possession of additonal bundles besides those of the normal ring, which from their position in the pith, are called medullary bundles. For this reason, the study of the primary vascular system of these plants is of great interest and has already in recent years attracted the attention of some workers in the field of plant anatomy, as given in the first paper (12). In spite of this, however, our knowledge of these structures is very incomplete, and the structure of many plants still remains to be worked out. Dastur (5) is the only person who has said anything about the structure of the plants described in this paper. He has recorded the occurrence of two medullary bundles, lying opposite to each other in the internodes of the stem and branches of *Achyranthes aspera* and traced their course through a node and the hypocotyl. So far as the knowledge of the writer goes, no work has been done on the primary vascular system of *Cyathula prostrata* and *Pupalia lappacea.*

The material for this investigation has been collected from Punjab and Sikkim,—that of *Pupalia lappacea* from Hoshiarpur, that of *Achyranthes aspera* from Lahore and Hoshiarpur, and that of *Cyathula prostrata* from the neighbourhood of Kurseong, a station on the Darjeeling-Himalayan Railway at an altitude of about 6,000 feet. The habit of all these plants is very similar. These are woody herbs with opposite and decussate leaves and flowers are borne in long spikes which terminate both the main stem and the axillary branches.

The material was fixed, imbedded and microtomed in the usual way. But besides this a large number of hand sections were cut so that an examination of a large amount of material could be carried out.

Achyranthes aspera L.

Structure of the leaf.—The leaves of *Achyranthes aspera*, especially the veins, are covered by long filamentous hair on both the sides. These are multicellular and with the basal cell rather swollen. The walls of the epidermal cells are not wavy. Stomata occur mostly on the lower surface and only a few on the upper surface. The mesophyll is differentiated into spongy and palisade tissues. In the region of the petiole stomata are absent and there are a few layers of collenchyma below the epidermis. The vascular tissue in the midrib of the lamina consists of four collateral bundles, arranged in a ring (fig. 1). Coming down to the petiole, the ventral bundle forks into two, the two halves move apart and give rise to an arc of bundles. The number of the bundles in the arc is five or three due to the union or seven due to the division of the lateral ones on each side.

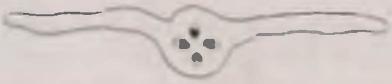

Fig. 1. *Achyranthes aspera.* Transverse section of the leaf, showing the arrangement of bundles in the midrib. Xylem is represented in black and phloem in white. ×25.

Structure of the stem—the internode.—The stem of *Achyranthes aspera* is alternately grooved and ridged due to the presence of ribs of collenchyma below the epidermis. The cells of the epidermis opposite the ridges are greatly elongated, but in the grooves these are not much longer than broad. Hairs similar in structure to those found on the leaves are present all round the very young stem near the apical growing point, both on the ridges and in the grooves. In the older parts, these are shed off from the grooves but persist on the ridges. Stomata are present in the grooves and the cortex in this region shows a chlorenchymatous structure, the cells being separated by inter-cellular spaces and containing chloroplasts. There is no distinct endodermis. The pericycle consists of two or three layers and its outermost layer is differentiated as a more or less broken chain of sclerenchymatous fibres.

A transverse section of the stem just below a node (fig. 2) shows the vascular tissue arranged in the form of a ring just as in ordinary dicotyledons. But in addition to this, there are two more collateral bundles, situated inside the peripheral ring. These lie opposite to each other and in a line with the pair of leaves at the lower node. If two sections are cut, one just below and the other just above a node, the planes of the internal bundles in the two internodes would be found to be at right angles to each other. In fact, the internal bundles in the stem of *Achyranthes aspera* like the leaves of the plant are arranged in an opposite and decussate fashion. An ontogenetic study shows that these internal bundles unlike those of *Alternanthera sessilies* are really medullary, as they are situated opposite to two bundles of primary origin in the peripheral ring and are separated from the peripheral ring by pith cells of primary origin.

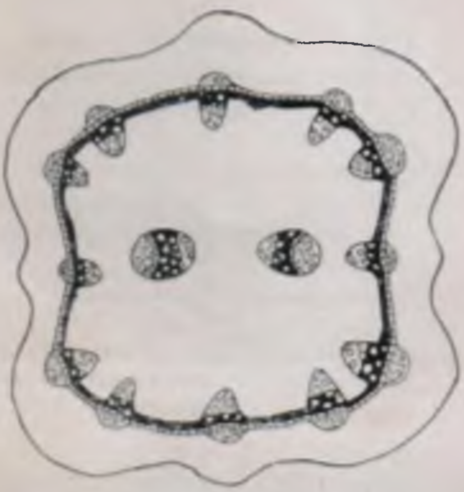

Fig. 2. *Achyranthes aspera*. Transverse section of the stem just below a node, showing two medullary bundles. In this and in figs. 3, 9, 12, & 13, the phloem is shown by dots, cambium by a single line of cells, fibrous elements in black, secondary xylem vessels by spaces in the black and primary xylem vessels by circles on white background. × 25.

In one or two internodes just below the inflorescence the two medullary bundles remain separate throughout the length of the internode. In the other internodes they are separate only just above or below a node. Here these are quite normally orientated and like the primary bundles of the outer ring are collateral, open and endarch. In the greater part of the internode, however, the two bundles fuse together, in a manner described later on, to form a single bundle of an amphixylic type, consisting of a band of phloem with a patch of xylem on each side (figs. 3 and 4). The phloem is rather peculiar in having a big island of parenchyma in the middle of the mature bundle. These parenchymatous cells are somewhat elongated transversely to the plane of the two xylem patches. The protoxylem is situated to the outside and metaxylem and secondary xylem develop centripetally. The cambium keeps its position in between the xylem and the phloem, but also very often extends to the outside of the phloem on the two ends even where there is no xylem. A transverse section through the middle of an

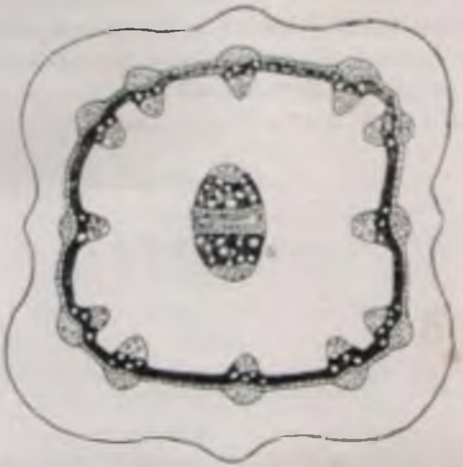

Fig. 3 *Achyranthes aspera.* Transverse section of the stem through the middle of an internode, showing the union of the two collateral medullary bundles to form a single bundle of amphixylic type. × 25.

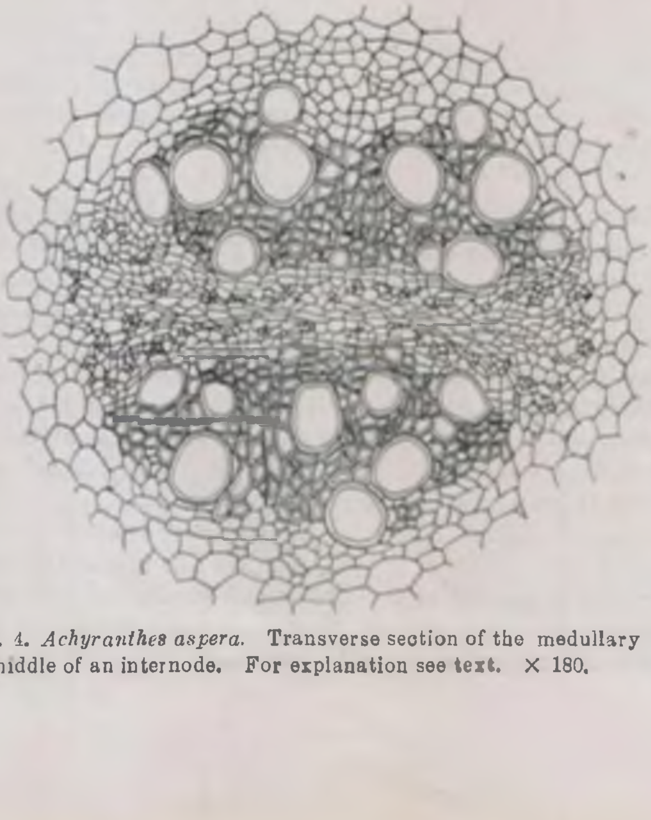

Fig. 4. *Achyranthes aspera.* Transverse section of the medullary bundle in the middle of an internode. For explanation see text. × 180.

internode, a little distance behind the growing apex where the primary bundles are still differentiating, shows that here in the medullary bundle, there is no island of parenchyma in the centre of the phloem and sieve tubes are freely scattered (fig. 5). The formation of a distinct central parenchymatous patch in the mature condition is due to divisions taking place in some of the parenchymatous cells of the original phloem, which push the sieve tubes outwards.

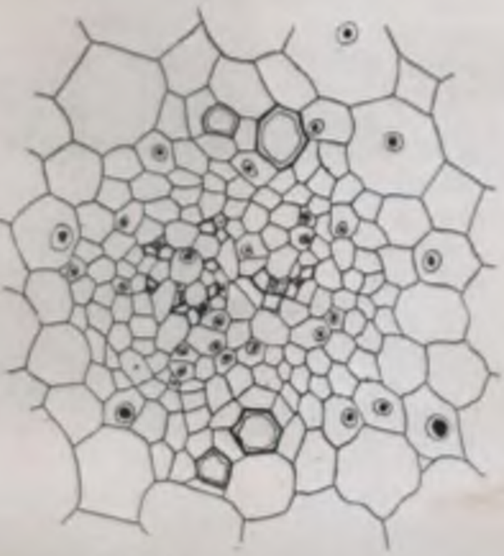

Fig. 5. *Achyranthes aspera.* A young stage of the same as shown in fig. 4. × 400.

The various changes which lead to the formation of a single amphixylic bundle in the internode from two quite free normally orientated collateral bundles near the node are sketched in fig. 6. The two free medullary bundles approach each other (fig. 6a) and meet. The xylem of the two becomes continuous (fig. 6b). The phloem begins to cut into the xylem carrying the cambium before it. islands of parenchyma appear in the middle of the phloem. This invasion of cambium, phloem and parenchyma successively into the xylem continues till those tissues from the opposite sides meet (fig. 5c). This leads to the formation of the structure sketched in fig. 4. It is to be seen that during this change each of the newly formed xylem patches gets one half from one and the other half from the xylem of the second of the two free medullary bundles and the plane of the two xylem patches is at right angles to that of the former medullary bundles. Often this general sequence of events is disturbed by one step preceding another, though in no case does

Fig. 6. (a–d). *Achyranthes aspera.* Transverse sections of the medullary bundles in the internode at various levels, showing the various stages in the union of the two medullary bundles to form a single structure like the one shown in fig. 4. Xylem is shown in black with vessels as spaces, phloem by dots, cambium by a single line of cells, parenchyma is striped. × 60.

it produce any change in the ultimate results. Fig. 6d shows the phloem as having invaded the xylem and separated it into two parts in each bundle even before the two bundles have met. Reverse changes take place when two free medullary bundles are formed from this single amphixylic bundle.

The course of the vascular bundles through a node.— The main problem in tracing the course of the primary vascular bundles through a node, is to find out what connection the medullary bundles have with the leaf traces and how their position changes in every adjacent internode to a different plane. This has been studied by cutting a series of transverse section from the upper part of several nodes downwards. The number of bundles making up each leaf trace has been found to vary from three to seven. In the first few pairs of epicotyledonary leaves the number is three. Generally, it is five and rarely seven. The branch traces are of the same type in transverse section as those of *Alternanthera sessilis.* As the axillary branches approach the parent stem, their two medullary bundles approach the bundles of the outer ring lying opposite to them. Both of these, along with the bundles of the peripheral ring, then fork and their halves move apart. The whole vascular cylinder of the axillary branches becomes divided in this manner into two halves. The bundles of each half come closer, fuse and so give rise to the two bracket-like branch traces.

When the number of bundles in the entering leaf traces at a node is three, the number of primary vascular bundles in the peripheral ring of the lower internode is eight. When each entering leaf trace consists of five bundles, the number of vascular bundles in the outer ring is twelve. The drawings in fig. 7 are from a node where the number of bundles in each leaf trace is five. These represent cross sections of the stem from the various parts of the node above downwards. Fig. 7a shows a transverse section of the stem just above a node. It has got a ring of twelve bundles, with two medullary bundles lying inside. A leaf with an arc of five bundles and its axillary branch is seen on either side of the stem. In fig. 7b the leaves have joined the axis. The medullary bundles of the stem have moved outwards on their respective sides and are approaching the vascular bundles of the outer ring facing them. The latter divide first and then the medullary bundles. One half of each fuses with one half of the other one and these move apart forming the common foliar and ramular gaps. On their outside these receive the branch traces (fig. 7c) and also some branches from the lateral bundles of the leaf traces figs. 7c and d). On their inner side these are joined by the adjacent bundles of the stem one by one. Anastomoses also begin between the different bundles of the entering leaf traces and only the bundles which are directly at right angles to the entering leaf traces remain perfectly free (fig. 7d). At this time, in a cross

Fig. 7. (a–f). *Achyranthes aspera.* · Transverse sections of a node at various levels from above downwards showing the course of bundles in the node. The xylem of the bundles is shown in black and phloem in white. In 7d the dotted lines show the position of the pericyclic cambium. × 25

section of the node no bundles are found lying internal to others, but the position of the first secondary cambium which is indicated in fig. 7d by a dotted line and which develops in the region of the pericycle, shows that some of the bundles are pursuing a medullary course. Lower down the vascular system of the lower internode begins to be differentiated (figs. 7 e and f). The bundles directly at right angles to the entering leaf traces which had remained so far quite free now begin to pass inwards and function as the central point in the formation of the medullary bundles of the lower internode. These receive one branch on either side from the adjacent lying portions of the vascular ring and by their union are formed the medullary bundles of the lower internode but now in a plane at right angles to that of the medullary

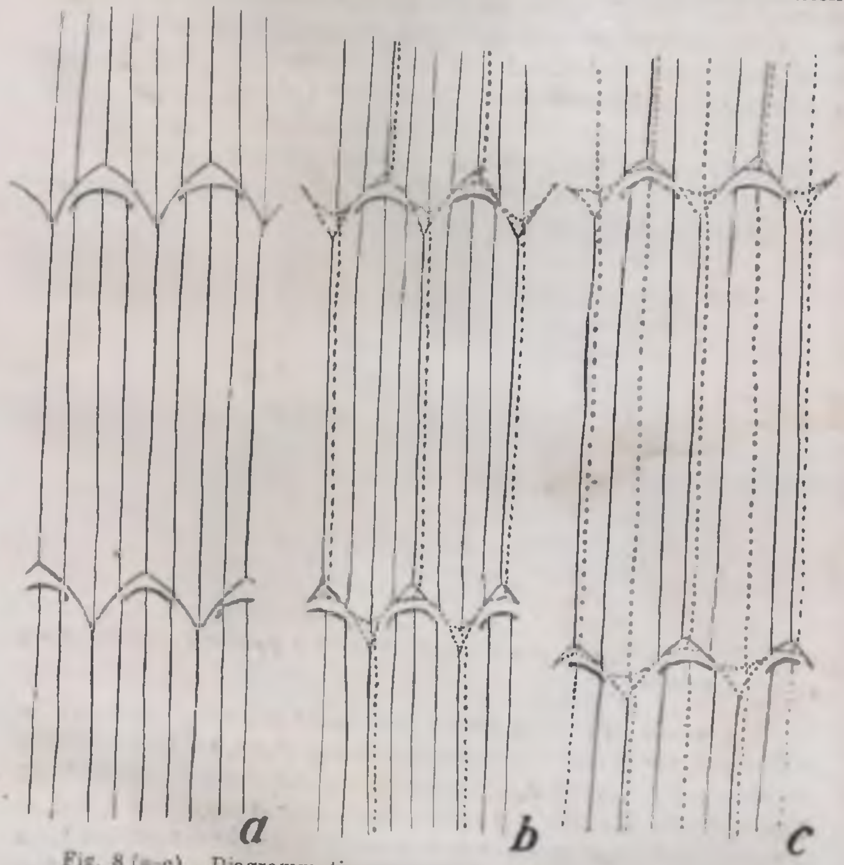

Fig. 8 (a-c). Diagrammatic representation of the course of bundles in the stems of (a) *Pupalia lappacea*, (b) *Achyranthes aspera* and (c) *Cyathula prostrata*, as split down on one side and spread out in one plane. The dotted lines represent the medullary bundles.

bundles of the upper internode. The leaf traces have by this time given off the various branches which they were destined to do and the anastomoses which take place between the different bundles of the leaf traces, come to an end. These begin to separate and become distinct. The remaining of the vascular elements, leaving aside the incoming leaf traces, after giving off the branches which go to form the medullary bundles, unite to form one bundle on either side to the outside of the two medullary bundles. These are the bundles which along with the medullary bundles will fork and form the leaf gaps at the next lower node, where similar changes as described above will again take place and result in the formation of two new medullary bundles of the next lower internode again in a different plane.

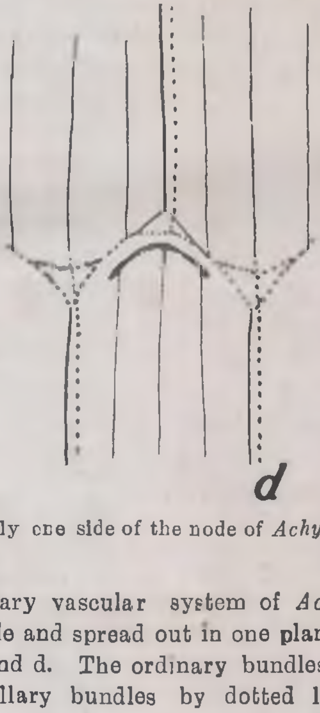

Fig 8 d. In (d) only one side of the node of *Achyranthes aspera* is shown on a larger scale.

The whole primary vascular system of *Achyranthes aspera*, as split down on one side and spread out in one plane, is diagramatically sketched in figs. 8b and d. The ordinary bundles are shown by black lines and the medullary bundles by dotted lines. The point of entrance of the leaf traces into the central cylinder is shown by a curved black line. The large number of anastomoses which take place at the node are obviously omitted and to avoid further complication, each leaf trace is shown to consist only of three bundles and the two medullary bundles have been shown to run quite separately which they do but in a few internodes, just below the inflorescence. The figure shows that each medullary bundle of *Achyranthes aspera* is formed by the inward progression and union of the median bundle of the arc of bundles that entered as leaf traces at the next higher node and certain branches received from the bundles lateral to it. And since the median bundles of the next higher pair of leaf traces always lie in a plane at right angles to the plane of the medullary bundles of an internode and these serve as the central point in the formation of the medullary bundles of the next lower internode, it will be clear how the medullary bundles change their position in every adjacent internode through an angle of 90°.

At the base of the inflorescence there are always four medullary bundles. The only point in which the node just below the inflorescence differs from the other nodes, is that the medullary bundles here do not divide, since they are already four. The rest of the changes take place just as at the other nodes.

Vascular system of the inflorescence.—Like the vegetative stem the inflorescence axis is also characterised by the possession of medullary bundles (fig. 9). Their number, however, is greater here. At the base of the inflorescence there are always four medullary bundles but higher up their number increases still further and may go up to eight or nine. These here form a definite ring inside the outer vascular ring. The two rings are, however, connected at several places. At intervals, the bundles of the outer ring pass inwards into the pith

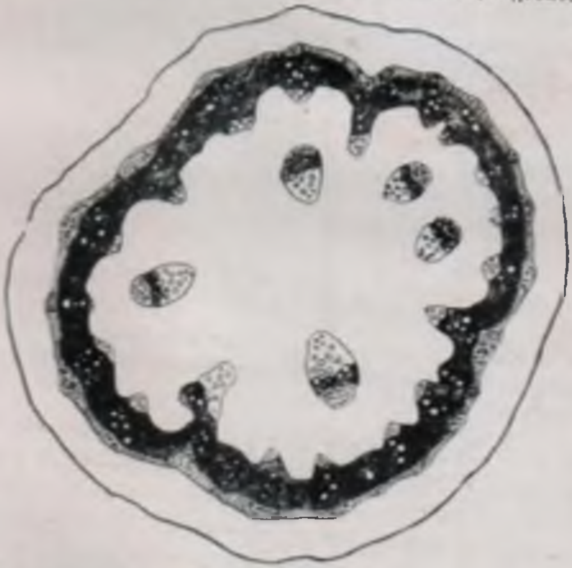

Fig. 9. *Achyranthes aspera.* Transverse section of the inflorescence. For explanation of the various parts see fig. 2. The striped tissue to the outside of the cambium is secondary parenchyma formed from it. × 40.

and unite with the medullary bundles. Sometimes, the union fails to occur, these remain quite free and so the number of medullary bundles in a cross section increases.

Study of the cross sections from the apex of the inflorescence downwards shows that the medullary bundles develop earlier than the bundles of the outer ring which are always somewhat belated in their development. Fig. 10 is a part of the cross section of the inflorescence axis, a little distance behind the apex. It shows the medullary bundles to be well developed, while in the outer ring the vascular elements are just beginning to differentiate.

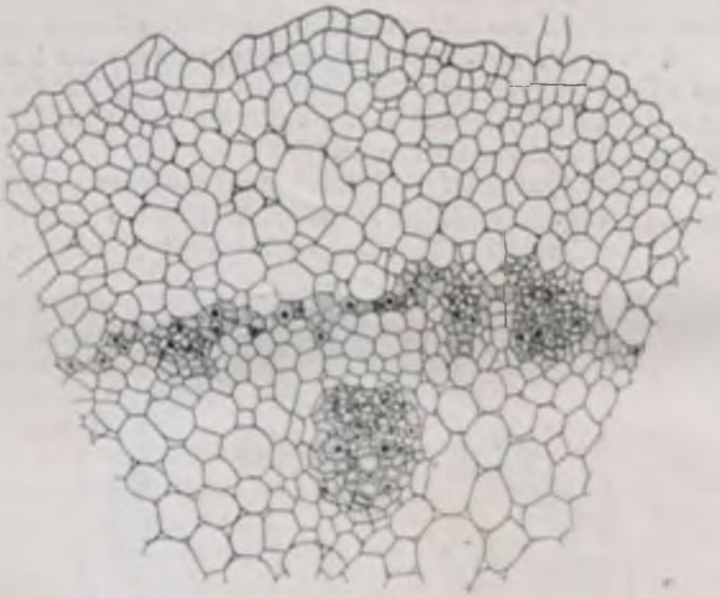

Fig. 10. *Achyranthes aspera.* A part of the transverse section of the inflorescence near the apex. The medullary bundle is better developed than the peripheral ring. ×180.

The medullary bundles of the inflorescence are always collateral and except for unions here and there with the outer vascular ring and among themselves, they always remain perfectly free. They never come together and unite to form any amphixylic type of bundle as is the condition in the internodes of the vegetative axis, though these always more or less turn outwards when going to receive a bundle from the outer ring.

An a cessory cambium to the outside of the medullary bundles has been seen in one inflorescence axis (fig 11). All the medullary bundles at the base of that inflorescence showed this anomaly. The cells lying in the outer region of the phloem of the collateral bundles had become meristematic and given rise to secondary cambium which formed wood consisting of vessels and fibres, to the inside, as any cambium would do. To the outside, however, no phloem was formed, but only some thick-walled elements which take the same stain as the lignified structures. This type of growth further resulted in crushing the outer portions of the pre-existing phloem.

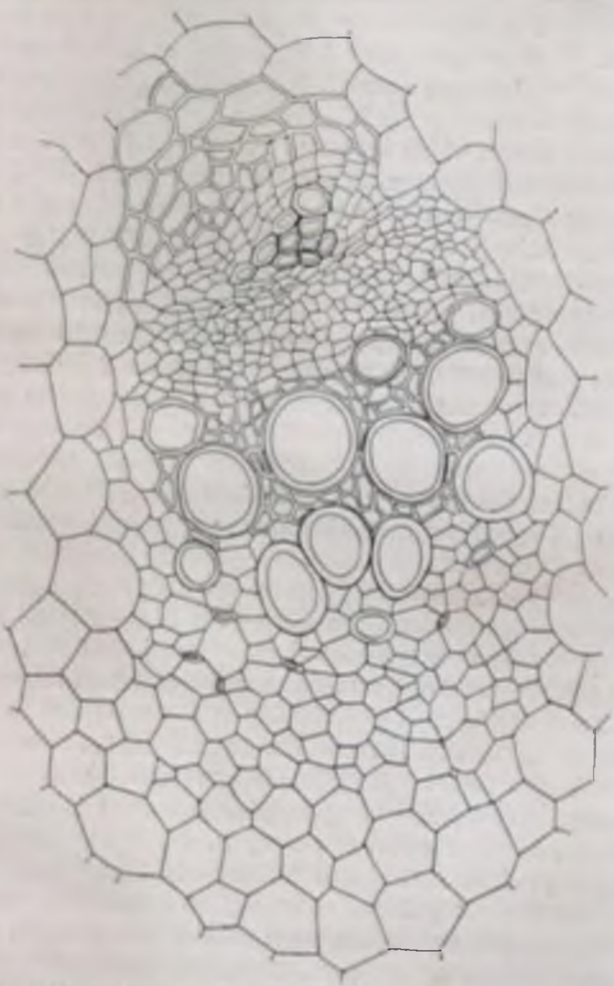

Fig. 11. *Achyranthes aspera.* A medullary bundle at the base of the inflorescence in transverse section showing growth by an accessory cambium. ×400.

Stem-root transition.—At the cotyledonary node, the medullary bundles approach the outer ring and divide along with the bundles to their outside to form the common foliar and ramular gaps as at the other nodes (fig. 15) and join the adjacent epicotyledonary traces (fig. 16). A single bundle comes from each cotyledon (fig. 15). At its entrance into the stem, it is considerably flattened. The phloem is very small in amount or almost absent, and it has on the outside at two corners two patches of sclerenchyma. These cotyledonary bundles now approach the epicotyledonary ones which are at this time going in the opposite direction. Each cotyledonary bundle divides into two and the adjacent epicotyledonary traces join their bifurcations (fig. 16). But the epicotyledonary bundles directly at right angles to the entering cotyledonary traces which represent the median bundles of the leaf traces that enter at the next higher node and which would have at other nodes formed a part of the medullary bundles of the lower internode, remain free for a long time. This leads to the formation in the upper region of the hypocotyl of six bundles arranged in a sort of rectangle (fig. 17). The four bundles at the corners here are the branches of the cotyledonary traces and the two in between them on two sides of the rectangle only, are the aforesaid epicotyledonary bundles. The primary cambial ring at this point has a rather peculiar course. It is quite normal so far as the four cotyledonary bundles are concerned but in the region of the two epicotyledonary traces the interfascicular cambium does not join the fascicular cambium. The primary cambial ring in this region is extrafascicular. Lower down the two epicotyledonary bundles fork and their branches join the adjacent cotyledonary traces. In this way, a ring of four collateral bundles is formed (fig. 18). This is the general structure of the hypocotyl and may be found in more than half an inch of the hypocotyl when the seedling is only one inch long. Further changes take place at the base of the seedling where transition to the root structure takes place. The seedling in this region often shows a slight swelling. The four bundles move towards the centre and the first or the primary cambial ring which was normal in the hypocotyl becomes extra-fascicular and secondary in this region (fig. 19). The protoxylem portions of the two bundles derived from the forking of the same cotyledonary trace, swing to the outside and meet each other, forming the protoxylem poles of the root (figs. 20 and 21). These bundles continue to come closer and closer and ultimately meet in the centre to form a diarch xylem plate (fig. 22). The phloem of each bundle swings in a direction opposite to that of its protoxylem and union takes place between the phloem groups coming from different cotyledons. In this way, two patches of phloem alternating with the diarch xylem plate are formed and complete the diarch structure of the primary root. The transition resembles exactly the third type of Van Tieghem (16).

The secondary and the adventitious roots differ from the primary root in being triarch instead of diarch.

Comparison with Professor R. H. Dastur's account.— The account of the vascular system of *Achyranthes aspera* as given here differs from the account of Dastur (5) in several respects. Dastur says that " the position of the two medullary bundles in the stem of *Achyranthes aspera* remains the same throughout the length of an internode as they traverse it with a radially perpendicular course". This condition, however, is found only in a few internodes just below the inflorescence in the Panjab plants. In the great majority of the internodes, the two medullary bundles are free only for a short distance just above or below a node. Through its greater length they run together and fuse to form in the centre of the stem a single bundle of an amphixylic type, as described above.

As regards the origin of the medullary bundles at a node he says that these are formed by the union of forked arcs of bundles entering at the upper node, branch traces, forked halves of the pre-existing medullary bundles and some branches received from the entering leaf traces. The present investigation shows that these are formed only by the inward progression and union of the median bundles of the leaf traces that enter at the next higher node and some branches received from the bundles adjacent to these. The medullary bundles of the upper internode, branch traces and the branches received from the entering leaf traces have no connection except an indirect one in the formation of the medullary bundles of the lower internode. The various constituents which Dastur mentions to take part in the formation of the medullary bundles of an internode, form not only the two medullary bundles but also the two bundles of the peripheral ring situated to the outside of the medullary bundles.

On the question of stem-root transition, Dastur writes: " At the base of the stem the two medullary bundles curve inwards and meet in the centre of the stem. The phloem disappears before the fusion takes place. The fused mass of xylem elements ends in the woody cylinder of the root ". According to the present investigation, however, it is absolutely clear that the medullary bundles of the stem do not take any part in the formation of the root structure, nor even any other epicotyledonary traces. There are no medullary bundles below the cotyledonary node in the region of the hypocotyl. The transition to root structure is essentially affected in between the cotyledonary traces.

Dastur did not investigate to any great extent the structure of the inflorescence axis, but his statement,—"Medullary bundles similary developed could also be made out in the lower part of the inflorescence but towards the apex they could not be distinguished as the tissues are not differentiated"—, can, however, be brought into conformity with the description given here that the medullary bundles in the inflorescence develop earlier than those of the outer ring which are somewhat late in their development.

Cyathula prostrata Blume.

The structure of *Cyathula prostrata* agrees in main with that of *Achyranthes aspera*, except in the fact that the medullary condition of some of the primary vascular bundles is here more marked. There are two more medullary bundles as compared with the former plant. A section of the internode just above or below a node shows four collateral medullary bundles, two of which are in a line with the pair of leaves at the lower node and correspond to the medullary bundles of *Achyranthes aspera* and two are in line with the pair of leaves at the upper node (fig. 12). In the middle of the internode (fig. 13) the two medullary bundles corresponding to those of *Achyranthes aspera* join to form a single amphixylic bundle in the centre of the stem (figs. 13 and 14), and all the medullary bundles become arranged in a single line.

Fig. 12. *Cyathula prostrata.* Transverse section of the stem just below a node, showing 4 medullary bundles. For explanation of the various parts see fig 2. ×25.

The course of the bundles of this plant is sketched in fig. 8*c* in the same manner as that of *Achyranthes aspera* is sketched in fig. 8*b*.

Fig. 13. *Cyathula prostrata.* Transverse section of the stem through the middle of an internode. Two of the medullary bundles have united to form a single bundle of an amphixylic type. For explanation of the various parts see fig. 2. × 25.

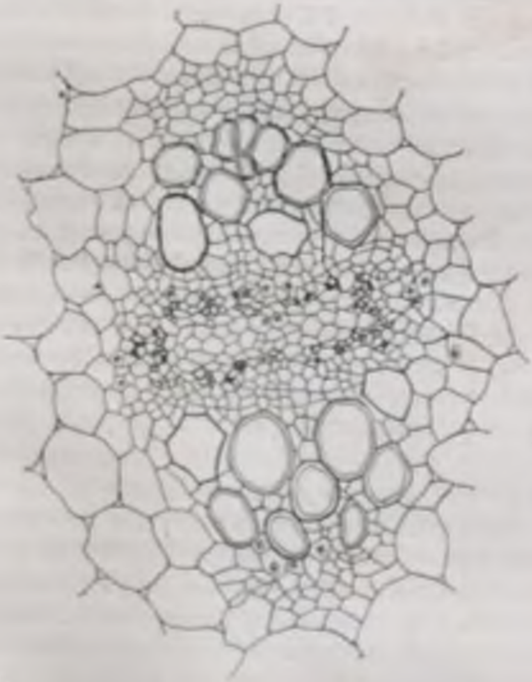

Fig. 14. *Cyathula prostrata.* The amphixylic medullary bundle of the internode in transverse section. × 180.

It agrees with that of *Achyranthes aspera* in all respects, except that two additional medullary bundles are formed here due to the median bundles of the leaf traces becoming medullary on their very entrance into the central cylinder. Both in *Achyranthes aspera* and *Cyathula prostrata*, the median bundles of the leaf traces run for two internodes. In *Achyranthes aspera* these remain in the peripheral ring in the upper internode and become medullary in the lower and so there are only two medullary bundles in an internode. In *Cyathula prostrata* the median bundles of the leaf traces are medullary in both the internodes and consequently there are four medullary bundles in each internode.

The structure of the infloresence and the phenomenon of root-stem transition have not been studied in this plant due to lack of material.

Pupalia lappacea Juss.

Pupalia lappacea resembles *Achyranthes aspera* in almost all respects except in the absence of medullary bundles. It has got the same habit, the same arrangement of leaves and the same type of hair. The stem is grooved and ridged, the epidermal cells are elongated on the ridges and the cortex is differentiated into collenchymatous ribs below these external ridges and into assimilatory tissue opposite the grooves in the same manner. There is no distinct endodermis and the outer cells of the pericycle are differentiated into a more or less broken chain of sclerenchymatous fibres. The midrib of the leaf contains a ring of four collateral vascular bundles formed from an arc of bundles in the petiole just as in *Achyranthes aspera*. The phenomenon of root-stem transition is exactly similar to that of the same plant. In the hypocotyl there are four collateral bundles formed by the division of the cotyledonary traces and these in the same way give rise lower down to a diarch stele of the primary root. The secondary and the adventitious roots are triarch. The only difference from *'chyranthes aspera* is that both in the stem and the inflorescence all the primary vascular bundles are arranged in the same ring and there are no medullary bundles.

The course of vascular bundles is again similar to that of *Achyranthes* except for the fact that these bundles always remain in the peripheral ring and never pass into the pith. It is sketched in fig. 8a. The number of leaf trace bundles is fundamentally three and those of the primary vascular ring of the stem eight. At a node, the bundles opposite the entering leaf traces fork to form the common foliar and ramular gaps. Their branches receive the branch traces and some branches from the lateral bundles of the entering leaf traces and further receive on each side the rest of the vascular bundles of the upper internode. All these converge to form two bundles, one on either side, in a line with the pair of leaves at the lower node and in between the leaf traces, coming from a pair of opposite leaves. In this way of the eight primary vascular bundles of an internode six are leaf traces coming from the pair of leaves above and the rest two, in a line with the pair of leaves at the lower node, are formed by the union of all the vascular bundles of the upper internode, the branch traces and certain branches received from lateral bundles of the leaf traces entering at the node above.

Discussion.

The three Amarantaceous plants, namely, *Achyranthes aspera*, *Cyathula prostrata* and *Pupalia lappacea*, the primary vascular system of which has been described in the foregoing pages are very closely related. The three genera occupy very close positions both in Engler and Prantl's (8) and in Bentham and Hooker's, (3) systems, all being included in the subtribe Amarantoideae—Amaranteae—Achyranthineae of the Englerian system. *Alternanthera sessilis*, the arrangement of the primary vascular bundles of which, has been described in the first paper, is a little more separated from these three genera. It is put in the tribe Gomphreneæ which differs from the tribe Amarantoideæ in the structure of the anthers. In the Amarantoideæ. the anther-halves are two-celled, but in the Gomphreneae, these ultimately become single-celled.

In internal structure also, *Achyranthes*, *Cyathula* and *Pupalia* resemble each other more than with *Alternanthera*. In *Alternanthera sessilis* each leaf trace consists of three bundles and in the midrib of the leaf as well there is an arc of three bundles. In *Achyranthes* *Cyathula* and *Pupalia* the number of bundles in each trace in the first few pairs of leaves above the cotyledonary node is three; in the later formed leaves, this number increases to five or seven due to the division of the lateral bundles of the leaf trace. But what is most characteristic in these three genera is, that in the midrib of the leaf, the vascular tissue consists of a ring of four bundles. The phenomenon of root-stem-transition in *Pupalia lappacea* and *Achyranthes aspera* is also exactly similar, while in *Alternanthera sessilis* the cotyledonary bundles divide into two and the exarch protoxylem poles of the root are differentiated even at the base of the cotyledons. Resemblances in several other characters, such as the structure of the hair, epidermis, cortex and pericycle, are more pronounced between *Pupalia*, *Achyranthes* and *Cyathula* than with *Alternanthera sessilis*.

Medullary bundles, their origin and relation to the primary vascular system.—Medullary bundles are of universal occurrence in the monocotyledonous stems but are also found in about twenty-five dicotyledonous families which apparently have no relation to each other, such as the families Piperaceæ and Compositæ and are formed according to De Bary (6) either due to "an oblique radial course of the bundles of the leaf trace" or due to "the appearance of the cauline bundles besides the bundles of the trace which are arranged in the typical ring". At the present time there may be said to be two views about their phylo-genetic significance. According to Worsdell (20, 21) the scattered arrangement of the primary vascular bundles in the stem is an ancestral character of the angiosperms which the monocotyledons have retained and the dicotyledons have mostly left behind. He thinks the monocotyledonous axis to be more primitive than the dicotyledonous.

The second view, which is the more widely accepted of the two, regards the medullary bundles to be a new formation (Scott and Brebner (15)), to have developed in response to greater needs of translocation (Westermaier (18), Alexandrov and Alexandrova (1)). Col (4) believes such a condition to have been caused by a large number of leaf trace bundles entering at a node and the lack of space there. He thinks these bundles to have been forced to run into the pith. Views similar to these have been put forward by Jeffrey (11). He says, "The multiplication of the conducting strands, due to the higher efficiency of the leaves in the elaboration of the food stuffs, brings with it complications of arrangement in the stem, for the number is too large to be accommodated on the periphery. As a consequence of the necessities which have thus arisen leaf traces are displaced from the margin of the central cylinder into the pith or medulla".

Wilson (19) has very recently discussed in detail the question of the origin of medullary bundles in the families Chenopodiaceæ and Amarantaceæ and since his views are mainly based on the study of the families under consideration here, these may be more fully considered. Based chiefly on the wide distribution of the medullary bundles, he calls attention to the belief that this bundle arrangement has probably had an independent evolution in the various groups in which it is found "by the gradual advance of bundles from the peripheral circle of bundles into the pith". Next he presents a series of diagrams of the longitudinal course of the primary bundles of a number of plants belonging to these families which according to him set forth in an ascending series a probable method of evolution of the medullary arrangement of bundles as found in its best developed form in *Amaranthus*. The various steps in this development according to him, are: (i) the cauline bundles on either side of an entering leaf trace pass into the pith for a short distance probably due to the influence of the node and return quickly to the normal position; (ii) this condition becomes exaggerated; the cauline bundles abandon their temporary course in the pith and become medullary throughout their course in the stem; (iii) the bundles of the leaf trace behave in a similar manner. In the earlier stages of such a development they are also members of the peripheral ring of bundles; their later course in the stem becomes more and more extended, until they are finally completely medullary.

A final decision cannot be taken at the present time on such views for the obvious reason of our ignorance of the primary vascular system of the majority of the flowering plants. But so far as the anatomy of the four plants considered during the course of the present investigation goes, it lends a general support to his views. The primary vascular system of these four plants is very uniform and similar in plan to that of *Iresine*, described by Wilson. The various differences from the primary vascular system of the other plants described by Wilson are to be regarded to be caused by the different arrangement of leaves in the different plants. There are no fundamental differences between them and the use of such a word as 'novel' for the vascular system of *Achyranthes aspera* by Dastur (5) is highly questionable. Further, these four plants may be arranged in an ascending series just as Wilson has arranged his plants. In all of them, the various bundles of an internode, except those in a line with the pair of leaves at the lower node, whether medullary or in the peripheral ring, are the leaf trace bundles entering at the node above, while those, in a line with the pair of leaves at the lower node, are formed by the union of all the bundles of the upper internode, branch traces and some branches received from the lateral bundles of the leaf traces and according to Wilson's use of the word these bundles would be called cauline. In *Pupalia lappacea* there are only two such bundles and these remain in the peripheral ring both in the internode and at the nodes. In *Alternanthera sessilis* there are again only two such bundles and these are the groove-opposed ones. In the internode they remain in the peripheral ring, though they differ from the rest of the bundles in the fact that they are situated slightly nearer the centre than the rest of the bundles and the cambium in this region is extra-fascicular. At the node these fork to form the leaf gaps and their branches pursue a medullary course. In *Achyranthes aspera* two bundles running parallel to each other are formed in place of each groove-opposed bundle of *Alternanthera sessilis* in the region of the internode. One of these is situated in the peripheral ring and the other runs in the pith and is medullary. At the node, the two unite, and their branches take a common medullary course. In *Cyathula prostrata* the medullary disposition of the bundles is still further accentuated. The median bundles of the leaf trace here become medullary on their very entrance into the central cylinder. The only difference from Wilson's series is in a small detail. The cauline bundles of *Achyranthes*, and *Cyathula*, if we may so call them, do not become completely medullary, but each divides into two, an outer and an inner half and only one half takes a medullary course and the other half remains in the peripheral ring.

One of the chief drawbacks in such views which regard medullary bundles of Amarantaceæ as a new formation is that there is no evidence that the series has been a progressive one. It is assumed that the medullary bundles are a new formation and such forms as *Amaranthus* are the highest in the scale of evolution. The series is complete but there is no evidence that it should be read in this direction or that direction, whether it is an ascending or a descending series. In the anatomy of the plants described here, however, there is a little point which shows that this series has been a progressive one. Medullary bundles are absent in the axis of *Achyranthes aspera* below the cotyledonary node. But in the upper region of the hypocotyl when the vascular tissue consists of six bundles (fig. 17), the primary cambial ring is extra-fascicular in the region of the two bundles, which are the median ones of the leaf traces, entering at the first epicotyledonary node and which would have at other nodes served as the central point in the formation of the medullary bundles of the lower internode, while it is quite normal and joins with the intrafascicular cambium of the other bundles. This condition exactly corresponds to that of the groove-opposed bundles of *Alternanthera sessilis.* The occurrence of this condition in the hypocotyl of *Achyranthes aspera* is some proof that the medullary bundles of this plant may have developed from the *Alternanthera sessilis* condition.

Medullary bundles are very poorly differentiated in the family Chenopodiaceæ except in *Acroglochin persicarioides*, the stem of which according to Volkens (17) possesses eight cauline medullary bundles. Fron (9) has been the chief investigator on the subject and he has separated the Chenopodiaceæ into two groups on the basis of their primary vascular system. The first group includes such forms as *Salicornia herbacea*, *Haloxylon articulatum*, *Camphorosma monspeliacum*, *Kochia hirsuta*, *Corispermum canescens*, *Sueda fruticosa*, *Salsola soda*, *Obione portulacoides* and several species of *Rhagodia*, in which the primary bundles are always at an equal distance from the centre of the central cylinder and medullary bundles are entirely absent. This arrangement he terms *rectilinear.* In his second group are included such forms as *Atriplex*, *Chenopodium*, *Beta*, *Spinacia*, *Blitum* and *Roubieva*, in which a certain number of bundles reach nearer the centre than other bundles and pursue a medullary course through a shorter or longer distance. This arrangement he terms *undulate.*

From the examples given by Fron, the first or the rectilinear arrangement seems to prevail in the Spirolobeæ and the second undulate arrangement in the Cyclolobeæ. There is a good deal of evidence from the highly specialised character, absence of perisperm and spirally coiled embryo of the spirolobeæ that this tribe is more advanced and of recent origin than the Cyclolobeæ in which the embryo is simply curved, perisperm is present and which is neither so specialised in habit and structure as the former. The prevalence of the rectilinear type in the first and of the undulate type in the second indicates that the rectilinear type has been derived from an undulate arrangement of the primary vascular bundles. In other words, in the family Chenopodiaceæ, medullary bundles were formerly present and are now disappearing, a conclusion exactly opposite to the one derived from the consideration of the arrangement of the primary bundles in the Amarantaceæ. The two different conclusions can, however, be reconciled on the supposition that the evolution of the medullary bundles has been quite independent in the two families, a hypothesis supported by the occurrence of homologous stages in the evolution of medullary bundles in both the families, as Wilson puts it. The next stages may be explained in two ways. First by supposing that the evolution of the medullary bundles continued in the Chenopodiaceæ for some time and gave rise to an undulate arrangement of the primary bundles such as is found in the Cyclolobeæ and then reversion took place to the rectilinear type probably due to the reduction in the number of leaf trace bundles – in the majority of the Spiroloceæ the leaf trace consists of but one bundle. This reduction may have been brought about by these plants leading their lives under extremely unfavourable conditions such as are found in extremely saline soils and deserts, reduction in the assimilatory leaf surface and consequent decrease in the elaborative efficiency of the leaves. The second method by which the occurrence of undulate arrangement of the primary vascular system in the Cyclolobeae and of the rectilinear arrangement in the Spirolobeæ, may be explained, is that the evolution of the medullary bundles set in after the two tribes had become separately established. The medullary bundles were formed only in the Cyclolobeæ, as only in this the number of the leaf trace bundles was fairly large to necessitate such a change.

The complexity of all evolutionary problems is unique and it has driven even such veteran students of plant evolution as Lotsy (13) into despair. In the writer's opinion before any adequate idea about the evolution of the medullary bundles in the axis of the flowering plants can be formed, the primary vascular system of every family and tribe should be thoroughly investigated. It is impossible from the study of a single family or tribe to draw conclusions, applicable to the whole group of angiosperms. Further, the hypothesis cannot be ruled out, that the different families of flowering plants may have started with a different structure. In some cases there may have been no medullary bundles to begin with but these may be differentiating at the present time. Other families may have started with a medullary disposition of bundles and these may be disappearing now. In this way alone the divergent evidence from different groups about the phylogenetic significance of medullary bundles can be brought into harmony. Any definite answer, however, to such questions can only be given when our knowledge has progressed much beyond the present stage.

Another point of great interest in the anatomy of *Achyranthes aspera* is the differentiation of the primary vascular system in the vegetative and the flowering axis. In the vegetative stem of this plant, the medullary bundles develop simultaneously with the bundles of the peripheral ring but in the inflorescence the medullary bundles develop earlier than those of the peripheral ring. This feature has been shown in the vegetative axis of the Nyctaginaceae by De Bary (6) in *Mirabilis jalapa* and by Maheshwari (14) in *Boerhaavia diffusa*. If the inflorescence of *Achyranthes aspera* be taken as a conservative organ, *Achyranthes* would appear to be derived from some Nyctaginaceae like forms. Some authors like Jeffrey (12), however, do not believe, rightly or wrongly, in the conservative character of the inflorescence of angiospersms. For this reason, the writer does not want to press the point further at this stage. He soon hopes himself to investigate the structure of some Nyctaginaceæ and if any thing interesting is found about this point, it shall be taken up later on. Giving any detailed consideration to it here, may lead us too far into speculation.

The Structure of the medullary bundles.—In the various families of flowering plants, the medullary bundles are usually only of three types. These may consist of phloem alone and then are usually associated with the bundles of the peripheral ring and are known under such names as 'internal phloem' and 'intraxylary phloem or these may be collateral or amphivasal concentric. Many people believe that the first condition has originated by reduction from collateral or concentric condition of the bundles. As regards the concentric medullary bundles Worsdell (20, 21) believes these to be the most primitive condition of the bundles of the flowering plants and to have given rise by reduction to collateral bundles. But there is an overwhelming opinion in favour of the view that these have been derived from collateral bundles. Mrs. Arber (2), dealing with the monocotyledons in which group amphivasal bundles are more common than in the dicotyledons, thinks that the amphivasal condition has arisen from the extreme V-type of bundle in which the arms of the xylem-V have simply enclosed the phloem. Jeffrey (11) on the other hand believes these amphivasal concentric bundles to have been formed as a result of the crowding and fusion of foliar strands at the nodes. This view he supports by the fact that it is in the nodal region that these are best developed.

The amphixylic medullary bundle such as has been described above in the stem of *Achyranthes aspera* and *Cyathula prostrata* is probably a very rare thing in the axis of flowering plants and such books on plant anatomy as those of De Bary (6) and of Eames and MacDaniel (7) make no reference to such a structure.* There can, however, be little doubt that it has developed from the collateral bundles and by their fusion. The occurrence of free collateral bundles in the inflorescence axis, in a few internodes just below the inflorescence, just above or below a node and in the rest of the Amarantaceæ, the structure of which has been investigated so far, is a conclusive proof about the matter.

Further, this amphixylic bundle is very near an amphivasal concentric bundle. Both in *Achyranthes* and *Cyathula*, the cambium is often present on all sides of the phloem, and only if the xylem were to develop on those two ends as well, where it is absent, it would be a completely concentric bundle. If any value is to be attached to analogical evidence in plant morphology, it would appear that in some cases at least the amphivasal type of concentric bundle in the stem of the angiosperms has originated by the fusion of the collateral bundles. Such conclusions, however, derived from the consideration of the structure of *Achyranthes* and *Cyathula* differ from Jeffrey's views about the origin of the concentric bundles in the fact, that the fusion of the two collateral bundles here does not take place at the nodes but on the contrary in the internodes, where in no case can it be explained as due to any such mechanical cause

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* Hoffstadt describes such bundles in the stem of *Piper methysticum* under the name of "double bundles" (Bot. Gaz. 62: 115 132, 1916).

as crowding. What other cause has been responsible for such a change it is also impossible to suggest. All that can be said is that in some plants, the concentric type of bundle may have originated by the fusion of two collateral bundles and that also without any reference to such causes as crowding.

Growth by an accessory cambium developed in the periphery of the medullary bundles in the inflorescence of *Achyranthes aspera*, is a very peculiar feature and it seems impossible to find any parallel for such a structure in the medullary bundles of any other flowering plants. It has been seen in one axis only and may be a malformation but its presence in all the medullary bundles is definitely against such a supposition.

Summary.

1. In the stem of *Achyranthes aspera* there are two free medullary bundles only in a few internodes just below the inflorescence and just above or below a node in other places. In the latter case through the greater length of the internodes, these unite to form a single bundle of an amphixylic type.

2. At a node, the medullary bundles of the upper internode move out towards the peripheral ring and divide along with the bundles of the peripheral ring, exactly opposite to them, to form the common foliar and ramular gaps. New medullary bundles of the lower internode are formed, in a plane at right angles to that of the medullary bundles of the upper internode, by inward progression into the pith of the median bundles of the leaf traces entering at the node above and certain branches received from the adjacent bundles. The rest of the vascular tissue, of the upper internode, the branch traces and a few branches received from the lateral bundles of the leaf traces, fuse to form a single bundle on either side to the outside of the medullary bundles. The rest of the vascular bundles of an internode are the leaf trace bundles.

3. In the inflorescence of *Achyranthes aspera* the number of medullary bundles is greater, varying from four to eight or nine. These develop earlier than the bundles of the peripheral ring, while in the vegetative axis both the medullary bundles and the bundles of the peripheral ring develop simultaneously. Accessory cambiums have been seen to the outside of the medullary bundles of the inflorescence in one instance.

4. The medullary bundles of the stem or any other epicotyledonary traces take no essential part in the stem-root transition. The change is affected essentially in between the cotyledonary traces and according to the III scheme of Van Tieghem (15).

5. In *Cyathula prostrata* there are two more medullary bundles, as compared with *Achyranthes aspera*, formed by the median bundles of the leaf traces taking a medullary course on their very entrance into the central cylinder.

6. There are no medullary bundles in *Pupalia lappacea*, otherwise the structure is very similar to that of *Achyranthes aspera*.

7. From a comparison of the various forms described in this paper, medullary bundles in the family Amarantaceæ appear to be a new formation, and the amphixylic and amphivasal bundles to have developed by the fusion of collateral bundles.

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Literature Cited.

1. ALEXANDROV, W. G., and ALEXANDROVA, O. G.—Uber konrentrische Gefassbündel in stengel von *Ricinus communis*. Bot. Arch. 14 : 455-460, 1926.
2. ARBER, A.—Monocotyledons, A Morphological study. Cambridge 1925.
3. BENTHAM, G. and HOOKER, J. D.—Genera Plantarum. London, 1862-1883.
4. COL, A.—Recherches sur la disposition des faisceaux dans la tige et les feuilles de quelques dicotyledones. Ann. Sci. Nat. Ser. 8. Bot. 20 . 1-285. 1904.
5. DÁSTUR, R. H.—The origin and course of vascular bundles in *Achyranthes aspera*, L. Ann. Bot. XXXIX : 539-545, 1925.
6. DE BARY, A.—Comparative Anatomy of the vegetative organs of Phanerogams and Ferns. Eng. Transl., Oxford, 1884.
7. EAMES, A. J , and MACDANIEL, L. H.—Introduction to Plant Anatomy, New York, 1925.
8. ENGLER, and PRANTL, K.—Die naturlichen Pflanzenfamilien, Teil III, Leipzig, 1893.
9. FRON, M G —Recherches anatomiques sur, la racine et la tige des Chenopodiacees. Ann. Sci. Nat. Ser. 8 Bot. 9 : 157-240, 1899.
10. HOOKER, J. D.—The Flora of British India, Vol. IV, London, 1885.
11. JEFFREY, E. C.—The Anatomy of Woody Plants. Chicago, 1917.

12. JOSHI, A. C.—Contributions to the Anatomy of Chenopodiaceæ and Amarantaceæ I. Anatomy of *Alternanthera sessilis* R. Br. Jour. Ind. Bot. Soc. X: 212–231, 1931.

13. LOTSY, J. B.—Evolution by means of Hybridisation. The Hague, 1916.

14. MAHESHWARI, P.—Contributions to the Morphology of *Boerhaavia diffusa* (II) Jour. Ind. Bot. Soc. IX: 42–62, 1930.

15. SCOTT, D. H. and BREBNER, G.—On the secondary tissues in certain Monocotyledons. Ann. Bot. VII: 21–62, 1893.

16. VAN TIEGHEM, P.—Traite de Botanique, Paris, 1891.

17. VOLKENS, G.—Chenopodiaceae. In Engler and Prantl's "Die naturlichen Pflanzenfamilien", Teil III, pages 36–61.

18. WESTERMAIER, M.—Über das markstaudige Bundel system der Begoniaceen. Flora 62: 117–168, 193–201, 1879.

19. WILSON, C. L.—Medullary bundle in relation to primary vascular system in Chenopodiaceæ and Amarantaceæ. Bot. Gaz. 78: 175–199, 1924.

20. WORSDELL, W. C.—The origin and meaning of medullary (intraxylary) phloem in the stems of dicotyledons. I. Cucurbitaceae. Ann. Bot. 29: 567–590, 1915.

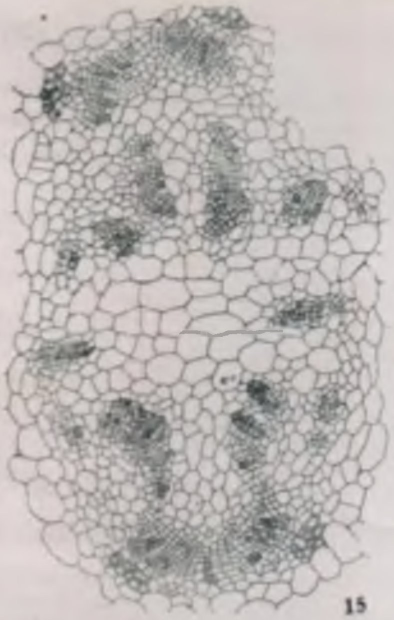
21. WORSDELL, W. C.—The origin and meaning of medullary (intraxylary) phloem in the stems dicotyledons. II. Compositæ. Ann. Bot. 33: 421–458, 1919.

Explanation of the Plate.

All these figures, 15–22, represent cross sections of a seedling of *Achyranthes aspera* about 1.5 ins. long, at various levels, from the cotyledonary node (fig. 15) downwards to the primary root (fig. 22), showing the various transition stages between stem and root structure In figs. 15, 16, 19, 20, 21 and 22, only the central cylinder or a part of it is represented. Figs. 17 and 18 are rather complete sections.

For further explanation see text—*Achyranthus aspera*, stem—root-transition.

Figs. 15–19 are magnified about 75 times, while figs 20–22 are magnified about 90 times.



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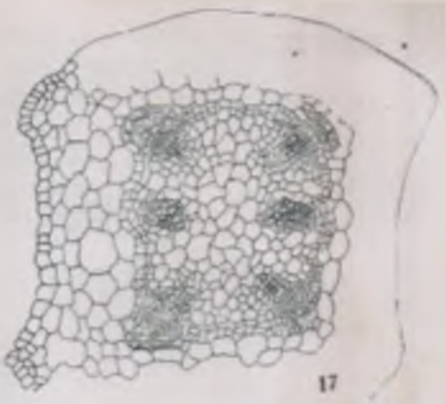

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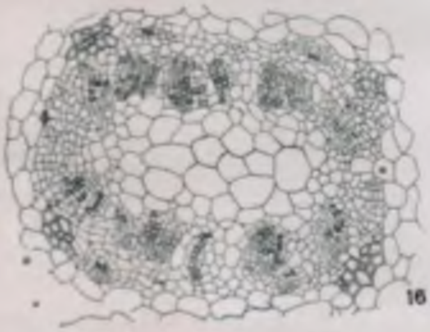

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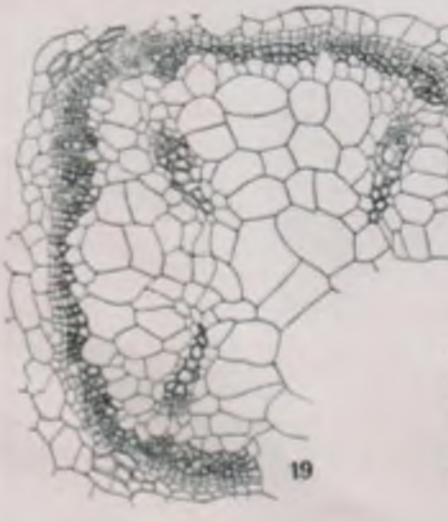

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