

VIII.—On the Histology of the Ephedreæ, with Special Reference to the Value of Histology for Systematic Purposes. By R. J. D. Graham, M.A., B.Sc., Carnegie Research Scholar, Botanical Department, The University, St Andrews. *Communicated by* R. A. ROBERTSON, M.A., B.Sc., F.R.S.E., F.L.S. (With Three Plates.)

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PART I.—PRIMARY STRUCTURE OF STEM.

Although a few papers have been published a number of years ago on the genus *Ephedra*, the authors have treated the subject mainly from a systematic standpoint. Thus, while the characters of the floral organs have been carefully examined and described, the structure and character of the vegetative organs have only received passing reference. It is proposed in the following notes to undertake the study of the histology of the vegetative organs, and thereafter to ascertain how far this knowledge applies to the determination of species. The following notes deal with the histology of the primary stem.

The material used, including in all 16 species and varieties, was kindly supplied from the following sources:—11 species from the Director of the Royal Botanic Garden, Kew; 8 species from the Director of the Royal Botanic Garden, Edinburgh; 2 species from Professor TRABUT, Algiers; *E. Helvetica* from Professor SCHROETER, Zurich; *E. altissima Helvetica* from Professor FLAHAULT, Montpellier,—to all of whom I here tender my thanks. Material for the study of 3 species was purchased from the Botanical Supply Association. For permission to examine the living specimens in the Royal Botanic Gardens of Kew and of Edinburgh I have to thank the Directors of these Gardens.

*Æcology*.—The genus *Ephedra*, consisting of some 32 species, belongs to the Gnetaceæ, an order of the Gymnospermæ. The majority of the species are found in the desert parts of both the Old and New Worlds. Correlated with their physiologically dry surroundings, the plants exhibit to a very marked degree various xerophilous adaptations. The leaves in almost every species are reduced to mere scales, while the green colour of the stem shows that the photo-synthetic functions are carried on there. Further reduction of transpiration is effected through the sinking of the stomata in furrows, while each stoma lies in a deep depression of the epidermis. The tender apex is surrounded by many envelopes of leaves, being thus protected from excessive insolation. At the approach of the dry season many species lose a great number of the young branches, thereby leaving only the more mature stems to function through the dangerous period of the year. The erect broom-like habit, so characteristic of many species, exposes a minimum area to the strong light of the noonday sun, while the

position enables full advantage to be taken of the optimum light of the early and the late day.

*Tegumentary System.*—The surface of the stem of the *Ephedreæ* closely resembles that of an ordinary *Equisetum*, in possessing longitudinal ridges and furrows (Plate I., fig. 15), the former corresponding in position with hypodermal stereom strands. The cells of the epidermis are rectangular or slightly hexagonal in shape, being elongated in the direction of the stem axis. The cells at the base of the internode are not usually so much elongated as those in the middle portion of the same. The outer cell walls consist of three strata (Plate I., fig. 1); the most external is a heavily cutinised stratum, bounding a middle layer of mucilage, containing small crystals or granules of calcium oxalate, which tend to have a stratified arrangement. This layer is limited internally by a thick stratum of cellulose. The cells contain the normal cell constituents, with, in some cases, starch grains, while again the cell contents may be stained various shades of yellow. The coloration is apparently due to the presence of tannin, as the cells give a black reaction on treatment with ferric acetate. In some cases the epidermal cells are divided into two by a wall which may be parallel, or nearly so, to any of the three dimensions of the cell. Either of the daughter-cells may further divide by a wall inclined at an angle to the first division wall (Plate I., fig. 2). In some species this division occurs more frequently in the neighbourhood of a stoma, though it may also be shown in independent cells. No trace could be found of the pores recorded by STAPP as passing through the cell wall. The only suggestion of their appearance was the striation in the cellulose layer seen after treating the section with sulphuric acid and methylene blue. These striæ ended at the limit of the cellulose layer.

The epidermal cells covering the ridges are, as a rule, larger than elsewhere; while the external walls are either markedly convex outward, or bear on their outside papillæ into the base of which a blunt protoplasmic protrusion extends (Plate I., fig. 3). The roughness of the surface of the shoot is determined by the number of papillæ (Plate I., fig. 4). The core of the papilla appears to be mucilaginous, and on the addition of water it swells, bursting the cuticle with which it is covered. Owing to the similarity of these papillæ to those found in leaves, and described by HABERLANDT (1) as light-sense organs, an attempt was made to test their optical properties, GRAHAM (2). In this, methods essentially those of HABERLANDT were used. A piece of the young shoot about 1 cm. in length was divided into two. One half was then laid upon a glass slide, while the epidermis was freed from the adjacent tissues by gently scraping with a scalpel. The epidermis was now mounted upside down on a cover-glass, which was then used to roof a moist chamber about 4 mm. deep. The preparation was then placed on the stage of a microscope, extraneous light being shut out by enclosing the stage and tube in a black hood. The sub-stage iris was partly closed, when the whole field appeared darkened, with the exception of certain lighted areas corresponding in position with the papillæ (Plate I., fig. 5). Further, the image of an object, either stationary or in motion, placed before the microscope, could be clearly seen in the light

centres. It was found to be possible to obtain photographs both of the light discs and of the images in them of objects held before the mirror (Plate I., fig. 6). The occurrence of these organs in stems which function to a great extent as leaves is almost to be expected, and the advantage of the erect light position to the desert forms of the Ephedreæ is obvious from an œcological point of view. Any movement of the stem from the normal light position will be followed by a transference of the lighted area to another portion of the cytoplasm of the back wall of the epidermal cell. This transference, accompanied as it must be by a variation in the intensity of the illumination, will act as a stimulus resulting in growth movements, whereby the former light position will be returned to.

Stomata in single or double rows occur in the furrows between the ridges. Each stoma is sunk in a compartment below the surface of the epidermis (Plate I., fig. 7). The entrance to the ante-chamber is more or less constricted by the encroachment of the walls of the four surrounding cells (Plate I., fig. 8). The encroaching wall contains a central core of mucilage, and in *E. viridis*, where the material had been treated with water, the mucilage had swollen, causing the opposite walls of the chamber to meet. This suggests an adaptation for either narrowing or closing the chamber, and thus limiting transpiration. This is the probable explanation of the closing of the stomatal chambers by resinous masses, referred to by VOLCKENS, and instanced by STAPF (3). The surface shape of the aperture depends upon the degree of encroachment of the projecting walls of the ante-chamber. The guard cells are without the usual ridges of entrance and of exit, as described by DE BARY\* (4).

*The Cortex* is well developed, consisting of chlorenchyma and stereom. The chlorenchyma is differentiated into an outer palisade cortex of radially elongated cells, and an inner spongy cortex of polygonal cells, both having a well-developed aerating system, especially the latter (Plate I., fig. 9). Starch grains occur all through the cortex along with crystals of calcium oxalate, the latter being more abundant in the endocortex, where crystal sacs may occur. Calcium oxalate crystals also occur in the cell walls. In some species a very large proportion of the cortical cells contain tannin, either in the form of mucilage or in the form of small globular masses (Plate I., fig. 2). A sinuous layer of tangentially elongated, closely packed cells, containing large starch grains surrounding the stele, constitutes an endodermis. The innermost layer of the cortex abuts on to this layer at right angles.

In the stem occur typically four series of strengthening fibres. The walls are at first of condensed cellulose, colouring blue only after prolonged treatment with iodine and sulphuric acid; afterwards the walls become lignified, and are coloured red by phloroglucin and hydrochloric acid. Excluding the perimedullary stereom system, reference to which will be made later, the remaining three series of fibres are arranged on a girder principle, that is, a broad flange at either end, the hypodermal and

\* The outer and inner walls of the guard cells are lignified from an early date, a condition found in many of the Coniferae.

pericyclic stereoms, linked radially by an incomplete mesocortical web (Plate II. fig. 10). In all the specimens examined the contours of the hypodermal groups of fibres were fairly uniform, being a flange or triangle with a longer or shorter portion projecting centripetally. The mesocortical and the pericyclic groups of fibres vary considerably, in some cases inversely. The mesocortical web consists of isolated fibres or groups of fibres, usually numerically less than the hypodermal or pericyclic groups. In some cases the mesocortical groups are poorly developed, and in a few cases are almost suppressed; when this occurs the hypodermal is usually well developed. The single mesocortical fibres resemble those of *Welwitschia* in having calcium oxalate deposited in their external membranes (Plate II., fig. 10). This is also the case in the hypodermal fibres of *E. Helvetica*. The pericyclic stereom appears as a series of hard bast crescents or aggregates associated with the primary vascular bundles, one large or a few smaller ones to each (Plate II., fig. 11). Between adjacent crescents occasionally a series of isolated fibres occur.

A perimedullary stereom in the form of a discontinuous ring of sclerenchyma occurs in some species (Plate II., fig. 12); in others it is represented by a few isolated fibres or nests at intervals, while it may be absent altogether.

*Vascular System.*—The vascular system resembles that found in *Equisetum*, with these differences, that in this case the leaf-trace is paired, that it is continued in the cauline part of its course through two internodes, and that in certain species an accessory bundle accompanies each leaf-trace through part of its course, while some species show a fusion of the leaf-traces in part of their course. With these exceptions the bundles in each describe a similar course, alternating in each internode and forming vascular networks at the node. The leaves, reduced to mere scales, are situated in twos or threes at each node. In the former case the arrangement is opposite and decussate, in the latter the whorls alternate. When there are two leaves at the node, the normal shoot shows in cross section a system of six, eight, or ten collateral endarch bundles surrounding a large pith. The structure of the primary bundle is as follows (STRASBURGER, 5). The whole is surrounded by a parenchyma sheath, some of the cells of which may contain chlorophyll. The primary phloem consists of cambiform parenchyma elements and narrow sieve-tubes with oblique plates. The primary xylem consists of spiral elements and bordered pitted elements with parenchyma packing tissue. The bordered pitted elements include both tracheids and vasa, the latter having their end walls steeply inclined and perforated by one or two rows of slightly bordered holes (VON MOHL, 6). Between the bundles medullary rays occur, but soon the bundles are linked up by the completion of a cambium ring. Projecting from the xylem elements of the system in some species isodiametric lignified cells with reticulate thickening occur, and these at an early stage link up the adjacent bundles (Plate II., fig. 11). These cells are the first products of the activity of the cambium. Extending from the xylem to the medullary rays, as they do, they facilitate a rapid lateral distribution of crude sap to the chlorenchyma.

The leaf-trace, composed of two bundles, passes down the stem vertically through two internodes. At the third node from that of their entrance to the stem, the bundles fuse right and left with the corresponding bundles of the traces emerging at this node (Plate II., fig. 13). Thus the first internode from an apical bud which has the vascular tissue developed shows in cross section four bundles, while in the second and subsequent internodes eight bundles are seen, two pairs of large bundles forming the traces of the leaves at the second node above, alternating with two pairs of small traces supplying the leaves at the first node above. A similar system is found in those species which have three leaves at each node; the extra trace pairs in this case bring the number of bundles in each internode up to twelve (Plate II., fig. 15). In the internode of species whose phyllotaxis changes from two to three, the internode succeeding the node at which the alterations occur shows ten bundles.

Immediately above each node occurs a region of two or three layers of compressed living cells with thick cellulose walls forming a dehiscence layer (Plate III., fig. 16). This layer, with in some cases a small area of meristematic tissue in the node itself, arises from the remains of the meristematic tissue from which elongation of the internode took place (Plate III., fig. 17). The layer partially cuts through the vascular tissues, the connection of the xylem elements being kept up by means of short reticulate tracheids. In the cortex the layer also appears, and there is a slight ring-like constriction of the surface of the stem corresponding to it in position. The epidermal cells over the constriction are nearly isodiametric. Owing to the stoppage of the stereom systems on approaching this region, the internode is very brittle and readily breaks across at this point. While passing through the area of meristematic tissue the vascular bundles lose their accompanying lateral lignified flanges.

At the node the stelar elements are concentrated into two vascular crescents, through the intercalation of linking tracheids. Spaces are left between the crescents corresponding with the position of the leaves at the node (Plate III., fig. 18). Each crescent is composed of the trace bundles from the leaf at the node above, flanked by a trace bundle from each leaf at the second node above (see Plate II., fig. 13). The leaf-traces of the leaves at the node in question link on to the crescent before passing out to the leaves at the node. Just below the emergence of these leaf-traces the vascular supply for the axillary bud originates as a twig from each leaf-trace (see fig. 13).

*Lateral Branch.*—Each of the bud-traces bifurcates to form the leaf-traces of the first pair of leaves on the side branch. At the first node of the lateral branch vascular crescents are formed. The traces from the leaves at the two next higher nodes unite in pairs during their course in the second internode of the branch. Hence, apparently only two instead of the normal four bundles take part in the formation of each vascular crescent at the first node (Plate III., fig. 19).

*Accessory Bundles* (STRASBURGER'S "complementary bundles" (7)).—Originating from the centre of each vascular crescent, an accessory bundle accompanies each leaf-trace pair in the upper half of its course (Plate II., fig. 14). So far, only in one instance

has the accessory bundle been found accompanying the leaf-trace in the lower half of its course. The accessory bundle, on reaching the node above that at which it originates, bifurcates at the level of the vascular crescents. Each half of the accessory then passes out as an additional pair of traces to the axillary bud (Plate III., fig. 20). The bud supply is hence augmented by two traces; thus in cross section with the first shortened internode of the side branch six bundles appear arranged, two adaxially and four abaxially. Before the bud-traces pass out to the first leaves of the side branch, the accessory bud-traces fuse with them (see fig. 20). Thus the accessory bud supply is shared by the two leaves. In *E. altissima*, *E. intermedia* from Kew, in *E. altissima* from Algiers and from Montpellier, as also in *E. distachya*, *elegantissima*, *lanceolata* from Edinburgh, the leaves of the first node of the lateral branch are in many cases suppressed. This feature has been occasionally observed in other species. In correlation with the absence of leaves, no splitting occurs in the bud supply, while the accessory, when present, ends in the vascular crescents of the main axis.

*Concrescent Bundles.*—This system is derived from the eight-bundle or normal type by the fusion of the adjacent leaf-traces of the opposite leaf-trace pairs in the second half of their course (Plate III., fig. 21, i.). At the end of its course the concrescent trace splits and the two portions link on right and left with the traces on either side (fig. 21, ii.). Thus an incomplete ring is formed, interrupted only between the non-concrescent leaf-traces. At the node through the formation of the girdle of tracheids these non-concrescent traces become joined up (fig. 21, iii.). Thus, through the ultimate splitting of the concrescent bundle vascular crescents are formed composed of the same constituents as the vascular crescents in the normal type (fig. 21, iv.).

Occasionally another type of concrescence occurs through fusion of the leaf-traces in the first half of their course. Exceptionally, concrescence takes place in all the leaf-traces, and the number of the bundles is reduced to four. The leaf-traces in the leaves appear to be very close together in this last case.

When there are three leaves at the node the typical vascular system is still retained. If the leaf-traces be accompanied by an accessory, the number of bundles seen in section is fifteen (Plate III., fig. 22); while if concrescence occur in the latter half of the course of the bundle, the number of bundles seen is nine (Plate III., fig. 23).

These variations due to intercalation and concrescence of bundles may take place at different levels in the course of the trace, and need not be synchronous on the two sides. Hence in different internodes of the same individual four, five, six, seven, eight, nine, and ten bundles may be met with. Similar variations occur in those species which have three leaves at the node.

The *Pith* consists of large and small cells, whose walls from an early stage are lignified, except around the intercellular spaces. Lignification is centripetal, being found in the fourth internode of *E. fragilis*, v. *campylopoda*. The perimedullary stereom (Plate II., fig. 12) has already been noticed. Cells containing tannin mucilage occur in many species, though they may be entirely absent from others (Plate III.,

fig. 22). Certain of the pith cells in the neighbourhood of the protoxylems show greenish-coloured contents, which seem to be chlorophyll. The cells of the pith have pitting on all their walls, especially on the end walls (Plate III., fig. 23).

*Meristematic Tissues.*—The stem apex, enclosed in several whorls of leaves, consists of a small conically-shaped mass of tissue. According to DINGLER (8), growth is from a tetrahedral apical cell. In all the material examined the meristem has been found to be stratified. Different records in regard to the nature of the apex have, however, been made, and DE BARY (9) mentions that both forms of apex occur in the same species. In the first internode after the apical the stelar elements have begun to differentiate, while in the second internode they are well developed. In this internode elongation of the stem has set in, but is more pronounced in the succeeding two or three internodes. At first the whole internode is meristematic (Plate III., fig. 17), but later elongation comes from a meristem situated at the base of the internode. This basal meristem remains functional for some considerable time, eventually passing over into permanent tissue, with the exception of a layer of from two to three cells in thickness, situated just above the node. This layer functions as a dehiscence layer (Plate III., fig. 16).

## PART II.—HISTOLOGY APPLIED TO THE DETERMINATION OF SPECIES.

Considerable attention has recently been paid to the use of the internal structure of the vegetative organs of plants in the diagnosis of orders, genera, and species. The genus *Ephedra*, consisting as it does of a uniform oecological group of species, seems to furnish a fair test of the value of such diagnostic characters. In his paper on Gnetaceæ and Coniferæ, BERTRAND (10) was of opinion that the histological features of stem and leaf were insufficient, and not thoroughly trustworthy for specific distinctions. This opinion is also held by Dr STAPF in his monograph, "Die Gattung der Ephedreæ," in which he constantly emphasises the extreme variability of the histology of the vegetative organs. While the tendency to variation in the histology is admitted, it has yet been possible, as a result of the above-mentioned notes, to divide the genus into sub-generic groups. Further, the additional evidence furnished from the internal structure, when taken with the ordinary external morphological characters, greatly facilitates diagnosis. The idea with which this part of the work was undertaken was to work from some definite level, and thereafter to include such other features from other parts of the stem as might seem to be of value. The second elongated internode from an apical bud was taken to start with, as being the youngest in which the complete primary stelar structure is attained. A general division of the group can be made, basing the evidence on the vascular supply of this internode. The number of bundles is very constant in some species (eight in *foliata*, *Helvetica*, *procera*, *distachya*; ten in *viridis*); while in a few there is a slight tendency to vary (*nebrodensis* and *gerardiana*), and in even fewer variations actually occur (*trifurca*). These variations are never of such an extent that they interfere with the value of the classification, for

they never interfere with the average number of bundles, and hence the type can always be determined. Two other important features for distinction of species are mentioned by FRITSCH (11). These are the occurrence of isolated groups of sclerenchyma in pith and cortex, and the distribution of secretory organs. Both of these can be applied to the genus *Ephedra*. The development of the mesocortical stereom web, as already mentioned, is much better in some species than in others. A division can, therefore, be made into species which have a well-developed mesocortical stereom (*foliata*, *distachya*, *viridis*), and those in which the stereom is poorly developed (*trifurca*, *fragilis*, *Helvetica*, *procera*). Again, the extent to which the perimedullary stereom is developed furnishes a basis for another threefold division. The perimedullary stereom is represented in two stages of development—as a discontinuous ring (*nebrodensis*), as a series of isolated fibres (*trifurca*, *foliata*, *distachya*, *viridis*), or as absent altogether (*fragilis*, *Helvetica*, *gerardiana*, *procera*). The presence of tannin sacs in the pith of many species (*Helvetica*, *distachya*, *procera*) furnishes another basis for division.

In determining the value of varieties, histology plays an important part. Thus *E. nebrodensis* differs from *E. procera*, not only in the former having a roughened epidermis while the latter is smooth, but *E. nebrodensis* has ten vascular bundles, while *E. procera* has only eight. A striking instance occurred in regard to three specimens received from Edinburgh. The names borne by the plants were apparently synonyms for *E. altissima*. Their identity was established by a study of their histology, and by a subsequent examination of the plants with regard to external morphology the identity was confirmed.

TABLE OF SPECIFIC DISTINCTIONS, BASED ON THE CHARACTER OF THE VASCULAR SYSTEM OF THE SECOND INTERNODE, STEREOM GROUPS, AND PITH.

1. *E. trifurca* (TORR). Primary bundles, 12 or 15. Mesocortical stereom web poorly developed. Perimedullary stereom isolated fibres. No pith tannin sacs.
2. *E. foliata* (C. A. MEYER). Primary bundles, 8. Mesocortical stereom web well developed. Perimedullary stereom isolated fibres.
3. *E. fragilis* (DESF.). Primary bundles, 8. Mesocortical web poorly developed. Perimedullary stereom absent. No pith tannin sacs.
4. *E. Helvetica* (C. A. MEYER). Primary bundles, 8. Mesocortical stereom web poorly developed. Perimedullary stereom absent. Pith tannin sacs.
5. *E. distachya* (LIN.). Primary bundles, 8. Mesocortical stereom web well developed. Perimedullary stereom isolated fibres. Pith tannin sacs.
6. *E. gerardiana* (WALL). Primary bundles, 10. Perimedullary stereom absent. Pith tannin sacs.
7. *E. nebrodensis* (TINEO). Primary bundles, 10 or 15. Perimedullary stereom discontinuous ring. No pith tannin sacs.
8. *E. procera* (C. A. MEYER). Primary bundles, 8. Mesocortical stereom web poorly developed. Perimedullary stereom absent. No pith tannin sacs.
9. *E. viridis* (COVILLE). Primary bundles, 10. Mesocortical stereom web well developed. Perimedullary stereom isolated fibres. Pith tannin sacs.

In conclusion, I wish to thank Mr R. A. Robertson, at whose suggestion the work was undertaken, for his great help throughout its course.



## DESCRIPTION OF PLATES.

## PLATE I.

Fig. 1. Transverse section of *E. Helve'ica*, showing epidermal cells with thickened external wall. (a) Cuticle; (b) calcium oxalate layer; (c) cellulose stratum.  $\times 360$ .

Fig. 2. Transverse section of *E. fragilis* (Algiers). (a) Division of epidermal cell into two; (b) division of one of the daughter-cells by a wall at right angles to the first division wall; (c) cortical tannin sacs.  $\times 160$ .

Fig. 3. Transverse section of *E. viridis*, showing large epidermal cells over ridge, one having a papilla on the external wall. (a) Cuticle; (b) calcium oxalate layer; (c) cellulose stratum.  $\times 360$ .

Fig. 4. Surface view of *E. viridis*, showing papillæ and stomata in alternating rows.  $\times 42$ .

Fig. 5. Photomicrograph of preparation of the epidermis of *E. altissima*, showing position of light spots.  $\times 160$ .

Fig. 6. Photomicrograph as above of *E. altissima*, showing image of St Andrew's cross in each light spot.  $\times 160$ .

Fig. 7. Transverse section of *E. nebrodensis*, showing sunk stoma, guard cells, respiratory chamber, ante-chamber. (a) Mucilaginous core of wall of cells forming ante-chamber.  $\times 360$ .

Fig. 8. Longitudinal section of *E. distachya*, showing stoma, respiratory chamber, ante-chamber. (a) Mucilage core of cell wall.  $\times 360$ .

Fig. 9. Transverse section of *E. nebrodensis*, showing hypodermal stereom, and differentiation of cortex into palisade and spongy cortical cells containing starch grains and crystals of calcium oxalate.  $\times 160$ .

## PLATE II.

Fig. 10. Transverse section of *E. distachya*, showing stereom systems well developed. (a) Welwitschia-like fibres; (b) division of epidermal cell.  $\times 160$ .

Fig. 11. Transverse section of *E. distachya*, showing pericyclic stereom crescent and vascular flange projecting from xylem. (a) Pericyclic stereom crescent; (b) vascular flange.  $\times 160$ .

Fig. 12. Transverse section of *E. nebrodensis*, showing perimedullary stereom (a).  $\times 160$ .

Fig. 13. Diagram of eight or normal bundle system, showing the entrance of the trace at  $a^i$ , the parallel course of the bundles, the behaviour of the trace at the first node ( $a^{ii}$ ), the continuation through a second internode and the linking on of the traces to the bundles passing out at the third node ( $a^{iii}$ ). Vascular crescents (a) with their component parts are diagrammatically indicated. The bud-trace (b) is indicated in position below the passing out of the trace at  $a^i$ . The splitting of the bud-trace is indicated.

Fig. 14. Diagram of the ten or accessory bundle system. Explanation as in last. The accessory (c) is indicated splitting in the region of the vascular crescent at  $a^i$ , where it passes out to form an extra pair of bud-traces.

Fig. 15. Transverse section of *E. trifurca*, showing twelve bundles due to the presence of three leaves at the node.  $\times 42$ .

## PLATE III.

Fig. 16. Longitudinal section of *E. nebrodensis*, showing dehiscence layer.  $\times 42$ .

Fig. 17. Longitudinal section of apex of *E. foliata*, showing development of young internode.  $\times 42$ .

Fig. 18. Transverse section of *E. fragilis*, v. *campylopoda*, showing vascular crescents with accessory splitting in between.  $\times 42$ .

Fig. 19. Diagram of junction of lateral branch with main stem, showing the bifurcation of the bud-trace (b) and its course into the leaves; the fusion of the traces of the higher leaves of the lateral branch before their arrival at the first node (a), thereby making the crescent have the appearance of being made up of only two bundles.

Fig. 20. Diagram of the junction of lateral branch in the accessory system. The main features are as above, while the splitting of the accessory bundle to augment the bud-supply is indicated (c); also the fusion

of the twigs of the accessory with the normal bud-trace before they pass to the leaves is shown (f). The accessory is represented as being absent from the first two internodes of the side branch.

Fig. 21. Diagram of the behaviour of the concrescent bundle at the end of its course. (i.) represents the six bundles after the disappearance of the lateral flanges; (ii.) represents the concrescent bundle linking on to the traces on either side; (iii.) represents the concrescent bundle as split, while the non-concrescent bundles have become united by the formation of intercalary tracheids; (iv.) represents the true vascular crescents formed equally of the traces from the first node above, flanked on either side by half the concrescent bundle.

Fig. 22. Transverse section of *E. trifurca*, showing fifteen bundles due to three leaves at the node, each leaf-trace pair being accompanied by an accessory.  $\times 42$ .

Fig. 23. Transverse section of *E. elegantissima*, showing nine bundles due to three leaves at each node, the leaf-traces being concrescent in the second half of their course.  $\times 42$ .

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R. J. D. GRAHAM: "Histology of the Ephedreæ."—PLATE I.

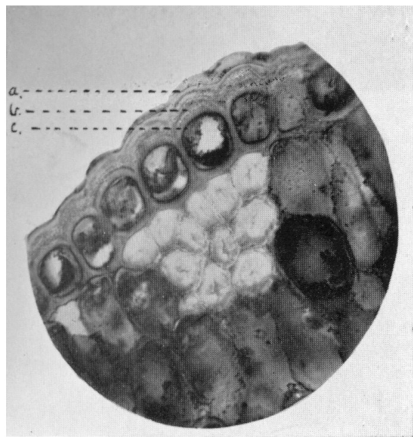


FIG. 1.

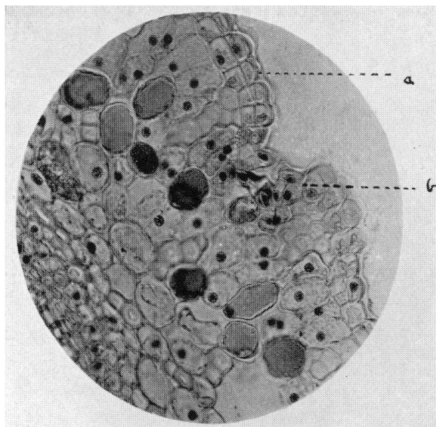


FIG. 2.

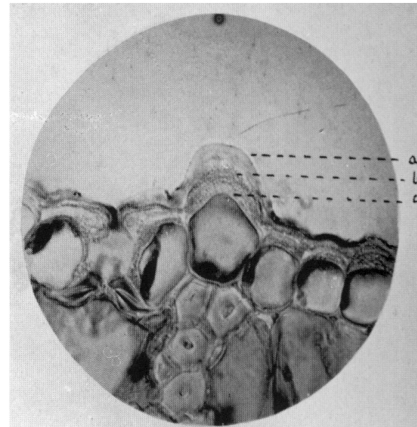


FIG. 3.

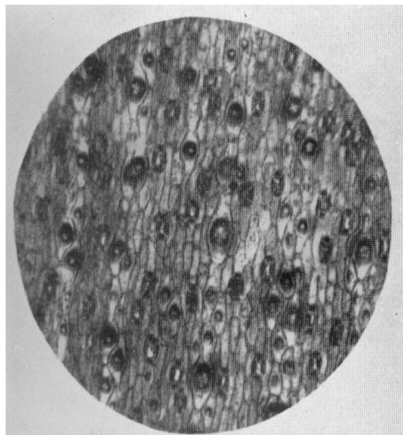


FIG. 4.

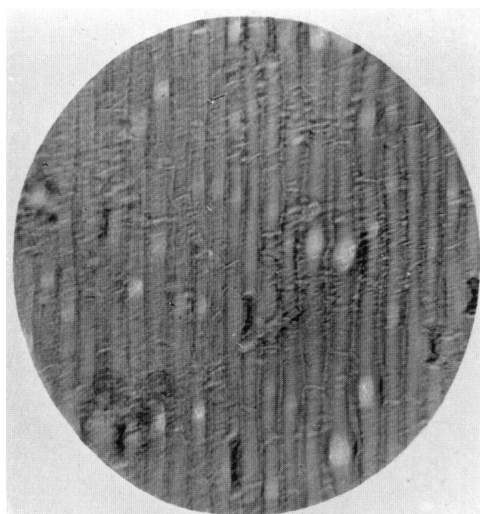


FIG. 5.

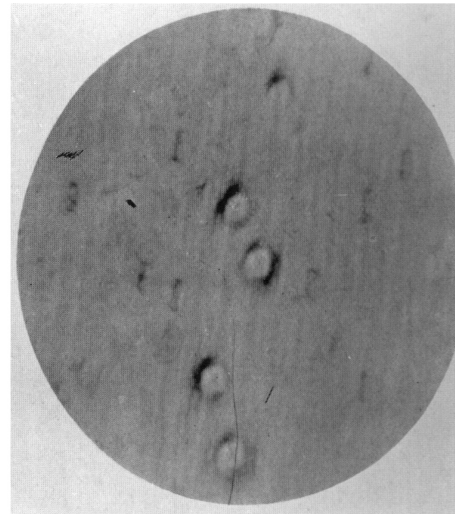


FIG. 6.

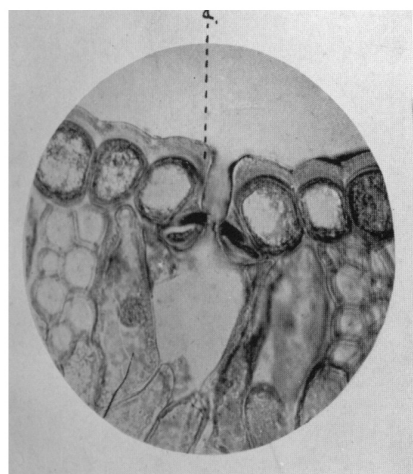


FIG. 7.

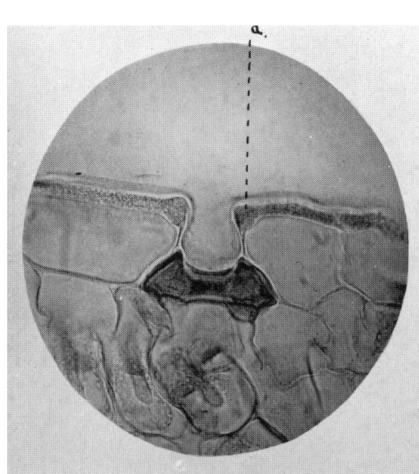


FIG. 8.

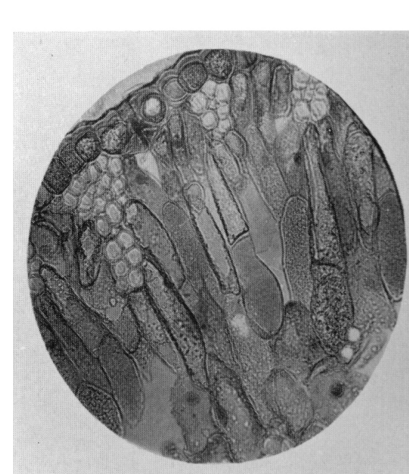


FIG. 9.

R. J. D. GRAHAM: "Histology of the Ephedrea."—PLATE II.

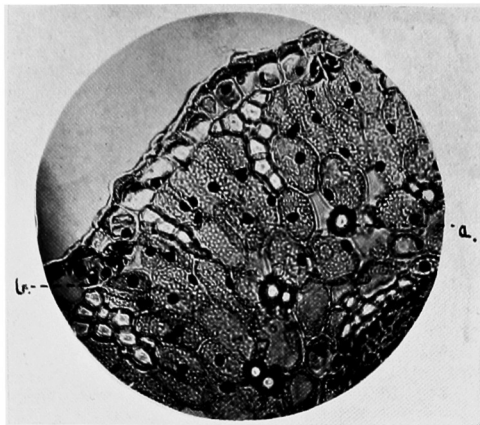


FIG. 10.

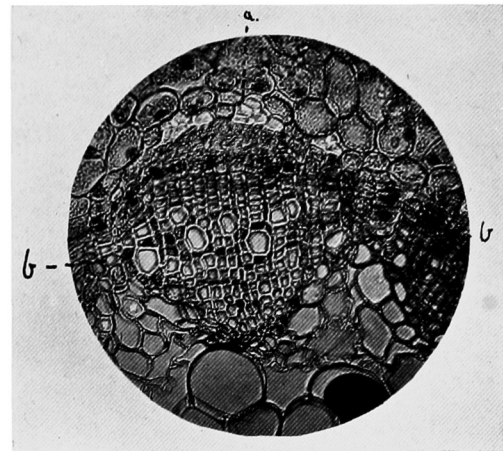


FIG. 11.

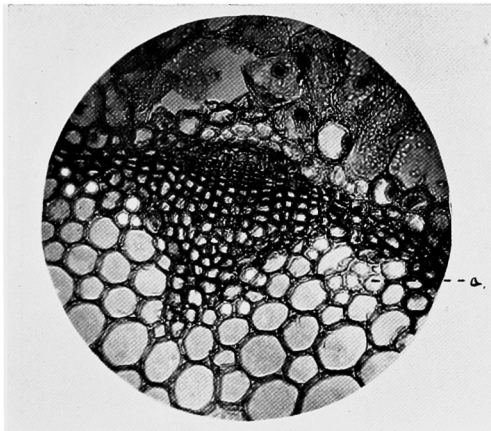


FIG. 12.

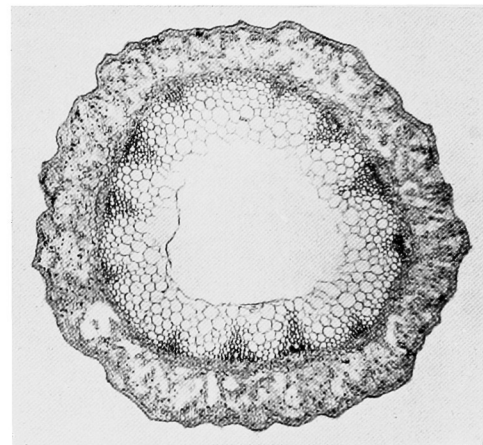


FIG. 15.

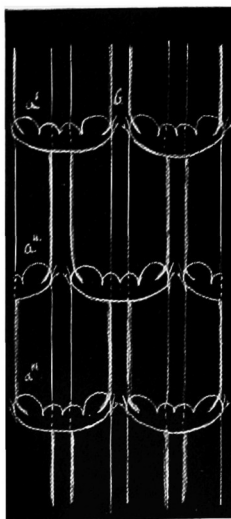


FIG. 13.

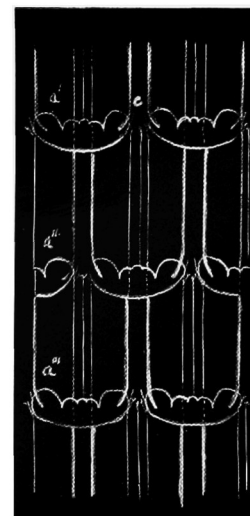


FIG. 14.

R. J. D. GRAHAM: "Histology of the Ephedreæ."—PLATE III.

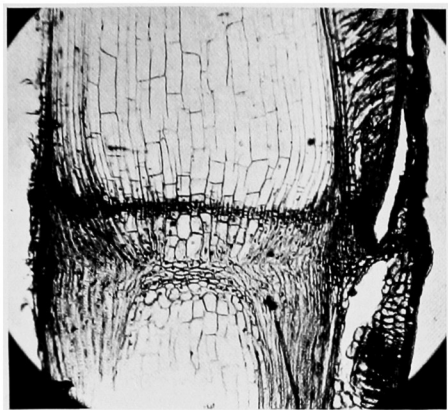


FIG. 16.

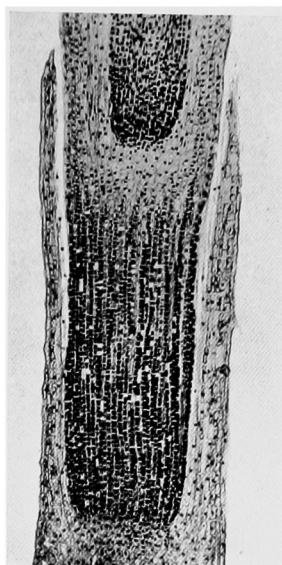


FIG. 17.

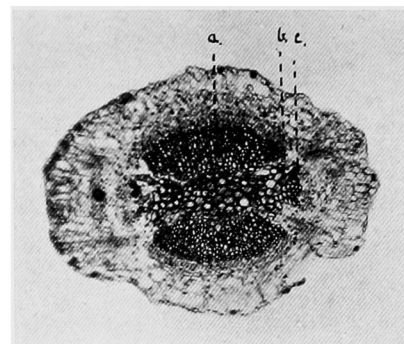


FIG. 18.

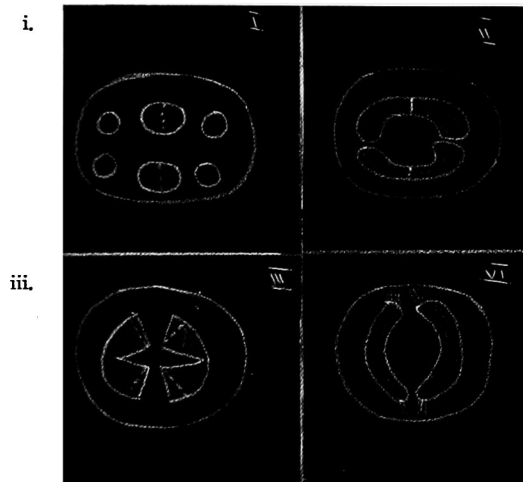


FIG. 21.

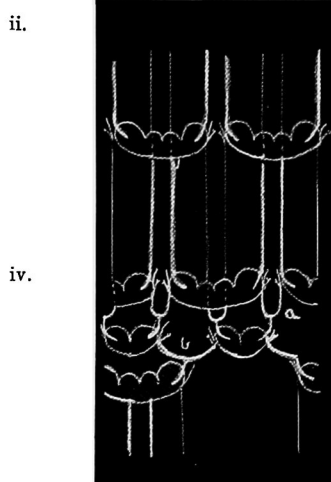


FIG. 19.

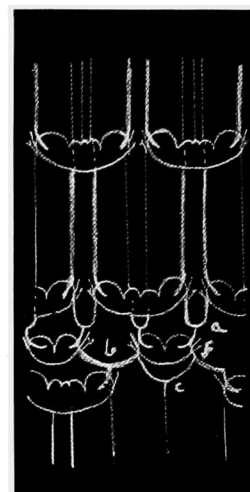


FIG. 20.

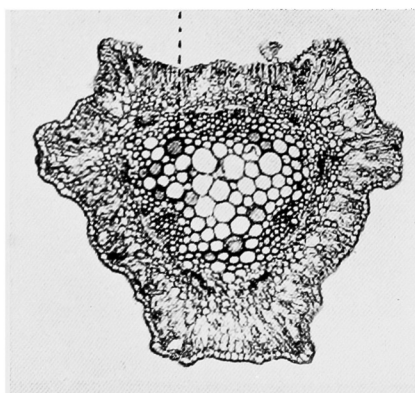


FIG. 23.

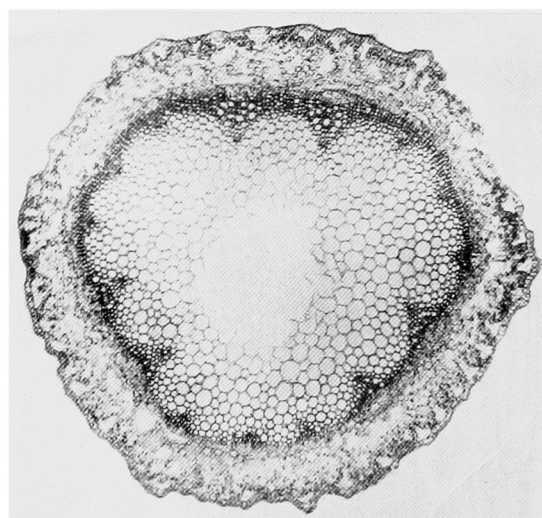


FIG. 22.