ON THE ANATOMY OF CHENOPODIUM ALBUM L.

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Introduction

The Chenopodiaceae and related families exhibit a most striking anomalous structure of the stem in that the annual secondary thickenings contain several circles of collateral vascular bundles of limited development which are embedded in lignified so-called "conjunctive tissue."

Gheorghieff (1) in a series of publications gives a detailed review of the early literature on this subject. His own contributions, furthermore, comprise the most comprehensive study of the anatomy of the Chenopodiaceae. He finds that the plants which he examined show greatly varied forms, transitional in structure to many of the Centrospermae.

Sanio (2) in 1863 gives the most complete ontogenetic study of members of the Chenopodiaceae. He attributes the anomalous structure of the stem to the activity of a periodically acting cambium which produces collateral vascular bundles and "conjunctive tissue." At the conclusion of his work Sanio draws a comparison between the anomalous stem structure of the Chenopodiaceae and the stem structure of those monocotyledons which are characterized by growth in thickness.

In his "Comparative Anatomy of the Phanerogams and Ferns," De Bary (3) develops a theory to account for the diverse forms of anomalous growth of the vascular tissue of Chenopodiaceae and related families. He makes four general classes. In the plants of the first group, an extrafascicular cambium appears around the primary ring of leaf-trace bundles. This cambium remains permanently active and forms alternately on its inner side collateral vascular bundles and conjunctive tissue; on its outer face it forms a thin layer of phloem or none at all. The plants of the second type develop a ring of primary vascular bundles with normal cambium. The activity of the latter soon ceases, and on the outer face of the primary ring appear in centrifugal order a succession of cambia each of which forms a distinct ring of vascular bundles and intermediary tissue. Classes three and four are types intermediate between the first two.

Morot (4) points out that the two modes of growth described by De Bary may be reduced to one type. The cambium in each case retains its bipolarity, giving rise to xylem on the inside and phloem on the outside.

Fron (5) subsequently states that the stem of *Chenopodium album* increases in diameter by the activity of a normal and pericyclic cambium, and that this cambium produces to the inside xylem and parenchyma and to the outside phloem tissue.

However, notwithstanding the comparatively large amount of work done on the inner structure of the Chenopodiaceae, the origin of the intraxylary phloem, its relation to the cambium and to the xylem of the bundles, remained obscure. It was therefore the primary object of this investigation to study the relation of cambial activity to the development of the anomalous growth. It was also hoped to extend our knowledge of the histology of the vascular tissue, in particular that of the phloem.

Material and Methods

The work was begun during the summer of 1919 at Ft. Lewis, Colorado, and was completed at the Department of Botany, Cornell University. Material taken from the field was studied while fresh. It was found most satisfactory to use unstained hand sections for both anatomical and ontogenetic studies. This method has an obvious advantage over most modern laboratory practice in that it permits the examination of a large amount of material in all stages of development with the least expenditure of time. But for the purpose of checking results and for use in making photomicrographs, representative material was killed in Flemming's weaker solution, embedded, some in paraffin, some in celloidin, sectioned, and stained in the usual manner.

Anatomy

A transverse section of a young stem shows between pith and cortex a circle of separate bundles—the leaf traces. Their number varies, there being even in very young stems as many as twenty. The largest of these traces belong to the lower leaves, the smallest to the primordia of the leaves near the growing apex.

These primary leaf-trace bundles are collateral. The phloem in cross section is a compact oval or oblong mass of tissue (Pl. XVI, *A*), bounded externally and laterally by parenchyma cells which, when still young, contain chloroplasts. The xylem also is definitely set off from the surrounding fundamental tissue. Its first-formed elements are scattered, and only the later formed metaxylem and the secondary elements show a definite arrangement in radial rows. In older sections we notice the development of an interfascicular cambium uniting individual leaf-trace bundles of the primary cycle, and an extrafascicular cambium from which originates a series of collateral bundles and conjunctive tissue. This tissue later lignifies and, together with the xylem of the bundles, forms a compact woody cylinder in which appear embedded small islands of phloem. The origin of this intraxylary phloem and of the conjunctive tissue, together with changes which take place when the tissues mature, will be discussed under the heading "Ontogeny."

No true secondary phloem develops; the true phloem remains restricted to the bundles in a given cycle. A narrow band of pericycle, sometimes only a ring of fibers, separates the vascular cylinder from the cortex. The cortex itself is of only limited extent and rarely more than two to four cells wide. The outer cortex is differentiated into collenchyma and photosynthetic tissue. The former occupies the ridges of the stem while the latter is found in the intervening spaces. The one-celled epidermis is of two types: the epidermal cells external to the collenchyma are elongated and their tangential walls are thickened; those external to the photosynthetic region are thin-walled and nearly isodiametric.

The collenchyma cells are long, pointed, and thickened at the corners only and communicate with one another by simple pits. The cortex and pith are made up of thin-walled, loosely connected parenchyma cells in which are often found druses of calcium oxalate (Pl. XVII, *B*).

Occupying the periphery of the vascular cylinder is a ring of fibers the elements of which are of the usual type but vary in size and diameter of lumen. They are rarely completely united into a closed ring but rather form short bands one to several cells wide. In places the cells of the phloem elements of the vascular tissue abut directly on the fibers; most often, however, a narrow band of pericyclic tissue intervenes.

The elements of the vascular cylinder are in general of advanced dicotyledonary types. The frequent occurrence of transitional forms in xylem and intermediary tissue makes the study of this group of plants especially interesting.

The xylem is made up of porous vessels, fibers, and wood parenchyma, the last named being vasicentric. The vessels are of two general types (Pl. XVI, *C*). The large type, most commonly arranged in uniseriate radial rows (Pl. XVI, *B*), is rectangular with end walls nearly transverse. The small type of vessel shows less definite arrangement; it is more elongated and its end walls are always more or less oblique. The walls of the vessels are heavily pitted. The pits are small, pentagonal, and arranged in alternate rows (Pl. XVI, *C*, *G*). In the small type of vessel, however, the pits may not show the symmetrical form and regular arrangement.

The fibers approach the libriform type. The elements are long and pointed but comparatively thin-walled. The walls are but sparingly pitted. The longitudinal course of the fibers is not absolutely straight in that the ends of the elements diverge obliquely whereby they become partly interlocked, which arrangement gives the wood an especially great toughness.

In the xylem of the leaf-trace bundles we find in addition to the types of elements just described the typical elements of the protoxylem with transition forms to the pitted vessels. The first formed elements of the protoxylem are narrow; the secondary thickenings of their walls are of the nature of loose spirals and wide rings (Pl. XVI, *E*). Much protoxylem, however, is made up of larger elements with secondary thickenings in the form of close spirals. Gradually the arrangement of the elements becomes more definite. The type of element also changes, and instead of close spirals we now find elements with scalariform and sometimes with reticulate walls. Various types of transitional forms are found between the spiral element on the one hand and the pitted vessel on the other. The meta-xylem, and of course the wood produced by the cambium, contain only pitted vessels.

The xylem, as we have learned, forms a compact woody cylinder made up of a series of concentric, undulate zones of growth (Pl. XVI, *B*), each zone in turn being a circle of collateral vascular bundles united with one another by intermediary or conjunctive tissue. Separating each zone of growth is a tangential band of parenchymatous tissue of varying width. Narrow, or sometimes broad, bands of parenchyma traverse the xylem in radial direction. These bands usually connect radially the individual zones of growth. Often, however, they pass through several zones, and in those instances closely resemble medullary rays.

In cross section the cells of this conjunctive tissue appear like ordinary parenchyma, but in radial and tangential cuts a great variation in form manifests itself. There are groups of cells made up of the common substitute fiber—a tracheidal element with simple pits. Other elements of this tissue are comparatively short or even isodiametric. Morphologically, then, this tissue is not homologous with rays, though it may function as such.

The phloem is made up of three types of elements: the sieve tube, the companion cell, and the phloem parenchyma. Contrary to the conclusion of earlier investigators (1, 4), the sieve tube is the principal element of this tissue. The tubes form longitudinal series (Pl. XVI, *D*) with occasional anastomosing of the elements of closely connected groups. On the whole, however, the course of the phloem groups is radial-perpendicular, with connections of the elements of the groups taking place only through the leaf gaps formed by the branching of the leaf-trace bundles and their subsequent fusion.

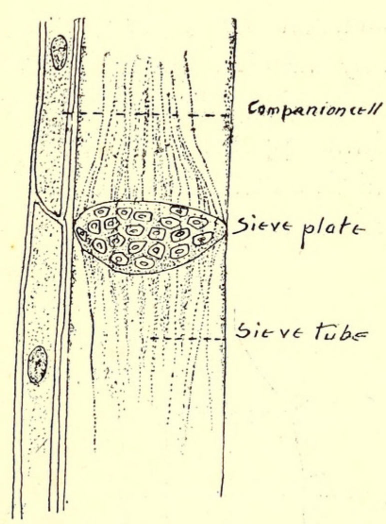

FIG. 1. *Chenopodium album:* Diagrammatic drawing of sieve tube and companion cell.

The sieve tube is of medium size with an average diameter of 14 μ. The end walls are usually slightly oblique, which makes it difficult to observe the sieve plates in strictly transverse sections. There are no sieve plates in the radial walls. The latter, however, are extensively pitted with the companion cells, which, as is usually the case, are connected by simple pits with the neighboring parenchyma cells of the conjunctive tissue. Late in the season the plates of many sieve tubes become covered with callus; this callus formation is most often observed in the phloem of the primary bundles.

Ontogeny

Almost immediately below the growing point the procambium becomes distinct, forming a concentric band of tissue between cortex and pith. At certain points in this procambium the primordia of vascular strands appear recognizable as such by the small size of the elements and by their granular content. The smallest primordia contain only elements of the phloem. Slightly older groups also contain elements of the protoxylem. The first formed phloem cells are thin-walled, very narrow, and take the typical haematoxylin stain. Sieve tubes become distinct in maturer sections only. The protoxylem elements are also narrow and of the loose spiral type (Pl. XVI, *E*). The groups of phloem and xylem are at first separated by undifferentiated procambium. With enlargement of the group, a cambium develops which later initiates secondary growth.

The procambium surrounding the strands of vascular tissue undergoes active division, causing the primary bundles to become separated and initiating the formation of new bundles in the widening spaces. These new bundles naturally do not extend so far into the pith (Pl. XVII, *D*), and, like the primary bundles, they increase in size through the activity of a cambium.

Gradually the procambium cells between the vascular groups cease dividing. All the elements mature except a single layer which remains meristematic, and which, as an interfascicular cambium, unites the separate bundles into a vascular ring. This cambium layer appears at first only between the larger groups, while later the smaller and more distant groups may also become united to form a part of the primary cylinder.

During the enlargement of the primary bundles an extrafascicular cambium appears (Pl. XVII, *A*, *C*) in the still undifferentiated procambium on the outer face of the primary bundles. This layer of meristematic cells is not formed simultaneously in a given circle, and as a consequence,

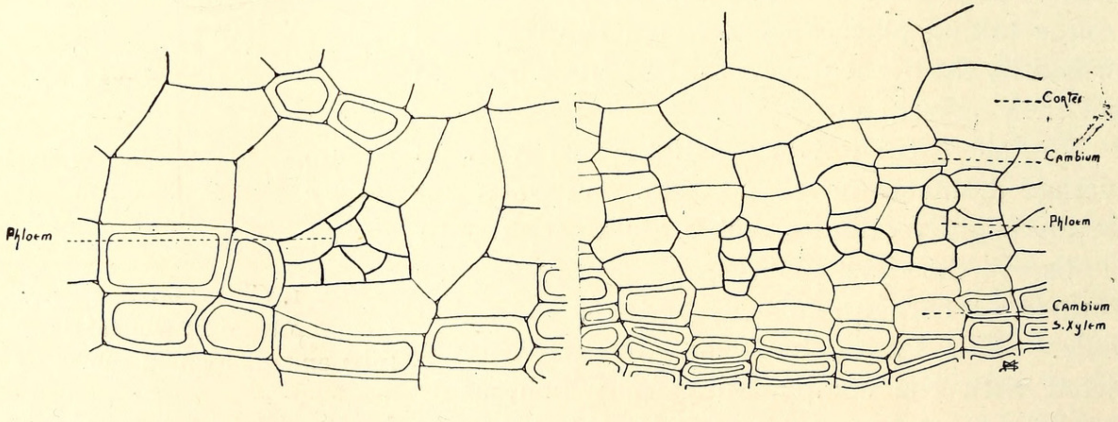

Fig. 2. *Chenopodium album:* Drawings illustrating the mode of origin of the intraxylary phloem. *A*, transverse section of stem showing cambium cells dividing in different planes, forming eight cells which become the phloem of the vascular ring. *B*, transverse section of stem showing the appearance of a new cambium in the parenchyma adjacent to the newly formed phloem groups.

different parts of the ring are found in different stages of development. This condition results in the formation of an undulate circle of cambium. In this cambium, cell division takes place only centripetally, resulting in the formation of a cylinder of tissue consisting of alternate radial segments of xylem and of conjunctive tissue. The cells of this secondary xylem, the large vessels in particular, are arranged in radial rows, differing therein from the primary tissue in which the elements are without any definite arrangement.

After a limited period of activity, certain areas in the cambium, chiefly opposite the large primary bundles, undergo a change of function. One or two cambium cells divide rapidly in different planes forming from two or three to ten cells (fig. 2, *A*, *B*; Pl. XVII, *E*, *F*).

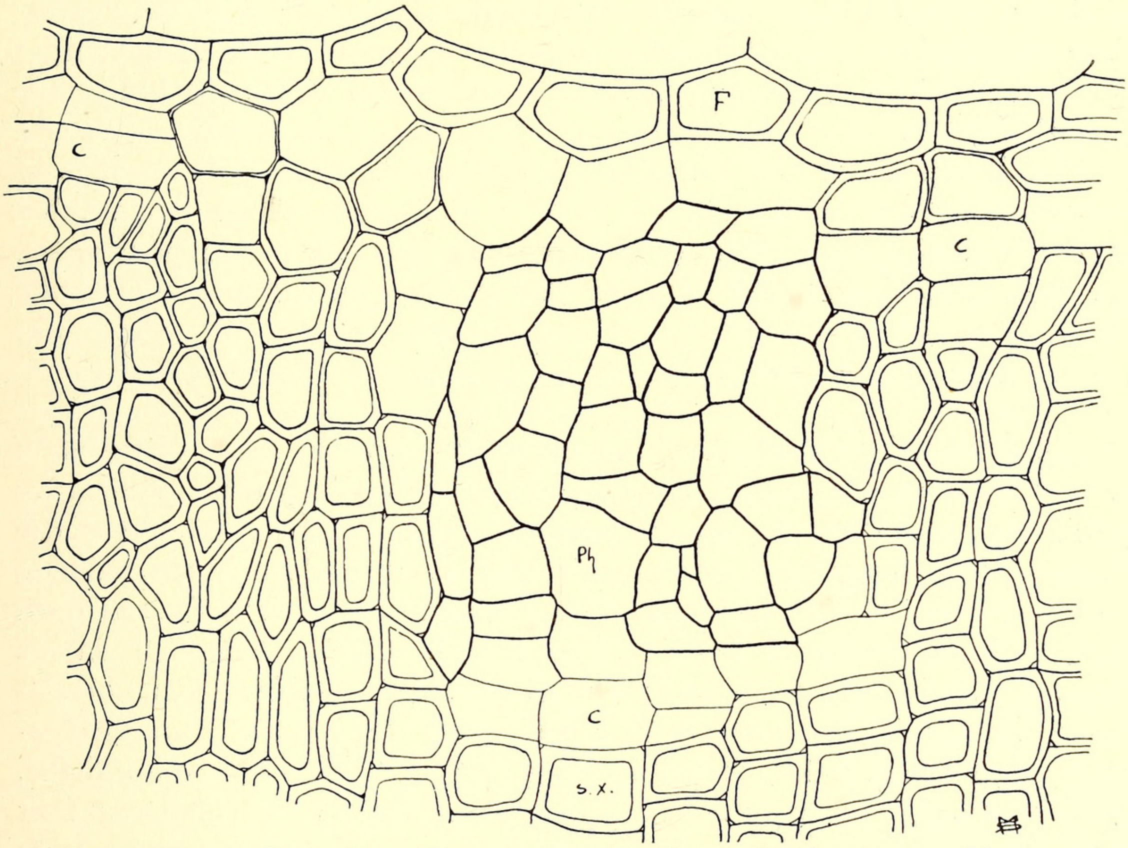

FIG. 3. *Chenopodium album:* Transverse section of stem showing mature phloem group. The appearance of the new cambium segment above the group is belated. The cambium at either side of the phloem group has divided very actively and has thus caused the phloem to be completely embedded in xylem. (*C*, cambium; *F*, fibers; *Ph*, phloem; *s.x.*, secondary xylem.)

These cells become the phloem of the just-formed vascular ring. We thus have a ring of xylem with segments of parenchymatous conjunctive tissue with a number of separated phloem strands on the outside. Occasionally the portions of cambium behaving in this manner are not used up in this process but may form a small amount of xylem toward the inside after the completion of phloem formation. These segments of cambium disappear, as such, since they mature into vascular tissue. The ring of cambium is thus broken up.

The cells of the cambium which are not concerned with the formation of these phloem groups are dividing very actively meanwhile, so that the cambium ring becomes undulate, the phloem groups occupying the depressions. Very soon after the initials of these phloem groups appear, a cambium forms in the parenchyma adjacent to the outer face of these groups (fig. 2, *B*). This new cambium becomes connected laterally with the cambium ring of the vascular cylinder. Sometimes the appearance of these new cambium segments is belated, and not until the unequal activity of the cambium ring has produced the undulate appearance and the depressions does a cambium layer appear at the outer face of each new group (fig. 3). In such a case the cambium formation begins at the margin of the depression, advances laterally, and when united undergoes reciprocal tangential division, thus giving rise to xylem and parenchyma which mature in the normal manner.

The formation of new cambium initials which mature into groups of phloem completes the growth of a zone of thickening which is succeeded by a new similar zone. The same process is repeated, and thus arise the undulate zones of vascular tissue so characteristic of the members of the Chenopodiaceae.

Conclusions

The study of the anatomical features of the vascular tissue of the stem in part confirms and in part modifies and extends the results obtained by earlier investigations. In the discussion of the histological features of the phloem it was shown that sieve tubes and not phloem parenchyma make up the larger portion of that tissue. Why earlier investigations limit or even deny their occurrence is hard to understand. Even Gheorghieff in his detailed anatomical researches of the group simply states: "Die Phloempartie ist vorwiegend aus parenchymatischen Elementen zusammengesetzt. Siebröhren habe ich nur selten gefunden." It must be admitted, however, that the elements of the phloem are comparatively small, and that the sieve tubes especially are narrow and easily mistaken for plasma-rich cambiform elements unless staining reactions show the sieve plates or the callus deposits over the plates. The typical staining reaction of this substance is a further aid in identifying the sieve tubes.

The elements making up the conjunctive tissue exhibit such a variety in form and arrangement that they could not be conceived of as ray cells in the morphological sense. That they may function, however, as rays is not at all unlikely.

Above all, however, this study has shown that the anomalous growth of the stem is produced by a periodically acting cambium which is progressively renewed at places where new phloem groups originate. In the development of each individual zone of growth, the xylem of the bundle is formed first, its formation being followed by a change in the activity of the initial strand on the outer face of the cambium; from the active division of this strand the phloem is produced. There is little if any new xylem added to the vascular ring in those places where phloem initials originate, for the xylem of the bundles, as has already been shown, is developed before any of the phloem matures. The cambium then does not exhibit the unipolarity which De Bary claimed for the group to which *Chenopodium album* belongs; it is always bipolar in restricted regions in that it gives rise to normal tissue elements on either side.

Summary

1. The anomalous stem structure of *Chenopodium album* is produced by a periodically active cambium which forms xylem centripetally throughout its extent and phloem centrifugally in restricted regions. Where phloem is formed the cambium is "used up." The continuity of the cambium ring is maintained by the formation of new portions outside the phloem groups.

2. The phloem of a secondary zone of growth is produced after all or most of the xylem has been formed. It is the normal product of the cambium and only belated in its development.

3. The intermediary or conjunctive tissue is not ray tissue in the morphological sense though it may function as such.

4. The chief element of the phloem is the sieve tube with its companion cell. Phloem parenchyma is of only secondary importance.

5. The stem structure shows in its ontogeny a striking similarity to the structure of the root of the sugar beet, a developmental study of which is contained in De Bary's "Comparative Anatomy."

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EXPLANATION OF PLATES

Plate XVI

A. Cross section of a large primary bundle showing arrangement of primary and secondary xylem; position and extent of phloem groups.

B. Cross section of part of mature stem showing undulate appearance of the zones of growth; extent and position of the conjunctive tissue and the radial arrangement of the large vessels.

C. Longitudinal section of xylem showing both types of vessel.

D. Radial section of stem showing size and longitudinal course of the phloem.

E. Radial section of primary xylem showing spiral and ringed elements.

F. Radial section of phloem showing the sieve tubes with companion cells and phloem parenchyma.

G. Radial section of xylem showing (from left to right) fibers, vessels, and conjunctive tissue.

PLATE XVII

A. Cross section of part of young stem showing the appearance of an extrafascicular cambium above a phloem group.

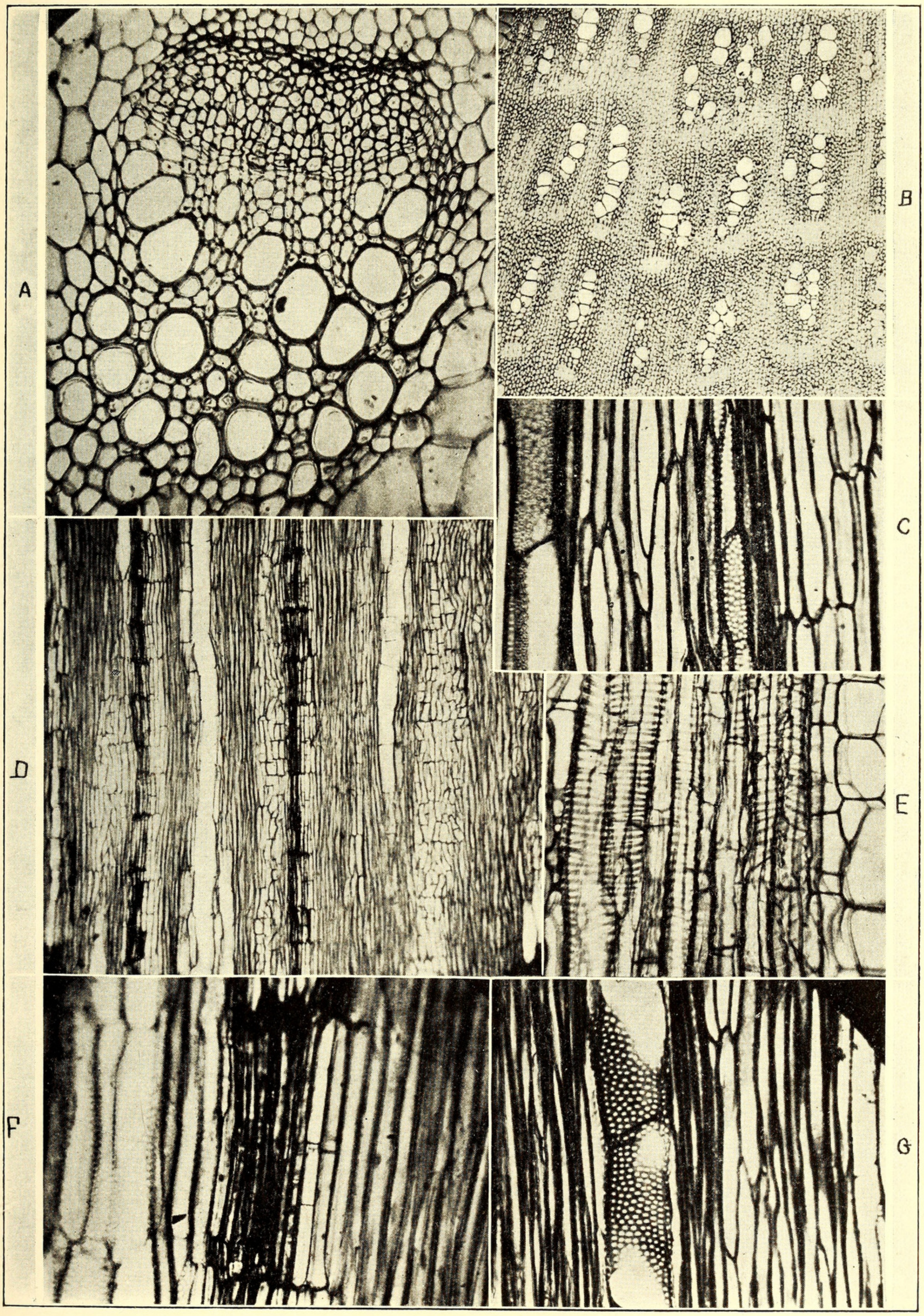
B. Cross section of a more mature stem showing the same condition as in *A*. Druse of calcium oxalate in cell of cortex.

C. Section of primary bundles of stem. Above the bundles an extrafascicular cambium has developed which is several rows wide.

D. Cross section of young stem showing several primary bundles and the first zone of thickening.

E. Section of vascular strand initial. Extrafascicular cambium has developed above the newly formed phloem group.

F. Section through annual zone of growth showing the development of an initial strand of phloem.



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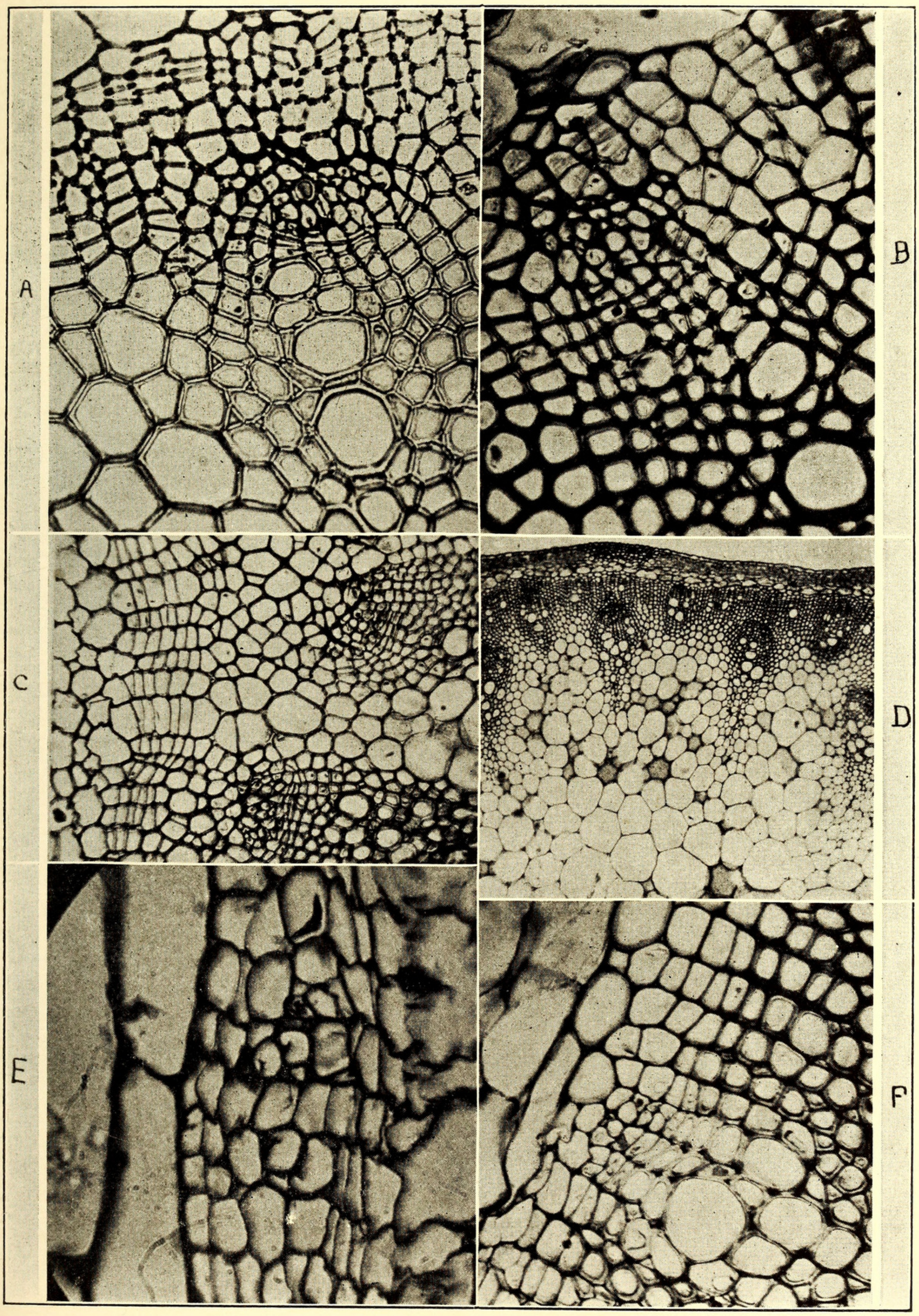

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