ASPECTS OF THE COMPLEX NODAL ANATOMY OF THE DIOSCOREACEAE [1]

EDWARD S. AYENSU

THIS PAPER IS AN ATTEMPT to explain how the vascular tissue of two successive internodes maintains continuity in the complex nodal structure between them in stems of the Dioscoreaceae, especially in the genera *Dioscorea* and *Tamus*. Because of the economic importance of this family early emphasis (Mason, 1926) was placed on the relation between structure and function. This led physiologists to take a look at the anatomy before they had a full knowledge of how food substances are translocated in the plant.

The Dioscoreaceae is a monocotyledonous family which is distributed throughout the tropics and subtropics of the world. It is, by all standards, one of the most economically important foodstuffs in the diet of most tropical peoples (cf. Coursey, 1967). Attention has recently been focused on this family, especially the genus *Dioscorea*, because a precursor of cortisone and other related steroidal drugs is derived from the tubers of some species.

The unique anatomy of the nodes of the stems of the Dioscoreaceae was brought to attention by Mason (1926) when he studied the rate of sugar transport in *Dioscorea alata* L. Earlier, Falkenberg (1876) had called the glomerulus of the node an imperfect knot in his study of *D. villosa* L. Mason noted that the phloem was of a markedly abnormal type. He further observed that the sieve tubes of the successive internodes did not join with each other directly but through a glomerulus which was composed of a great number of oblong thin-walled parenchymatous cells, each with a distinct nucleus, running fairly parallel with each other. Behnke (1965a) questioned the presence of nuclei in the glomerulus cells. Present studies show that nuclei occur at certain stages in the ontogeny of these cells (FIG. 2).

In his study of the ontogeny of the stem of *Tamus communis* L., Burkill (1949) disproved Mason's claim that glomeruli were absent from the nodes of *T. communis*. Present studies reveal that glomeruli are certainly present in the nodes of *Tamus* (FIG. 12) and, although they cannot be easily overlooked, it should be emphasized that the glomeruli in this genus are not so pronounced as those of most species of *Dioscorea* (FIGS. 4–11).

[1] A full account of the vegetative anatomy of the Dioscoreaceae will be included in the *Anatomy of the Monocotyledons. Dioscoreales*, ed. C. R. Metcalfe, Oxford University Press.

Happ (1950) wrote his thesis on the nodes of the Dioscoreaceae but a copy is not available to me. However, a comment on it appeared in Braun's (1957) work. Essentially, Happ investigated by means of serial sections the interlacing of the xylem-phloem glomeruli in the vascular system of the node.

Brouwer (1953) published his account of the arrangement of the vascular bundles in the nodes of Dioscoreaceae and presented a diagram of the elements of the node. Brouwer concluded that the sieve tubes of two successive internodes were connected in the following manner: sieve tubes, funiculus cells, bast tubulus cells, glomerulus cells, bast tubulus cells, funiculus cells, and sieve tubes. Brouwer, following Mason (1926), concluded that the phloem-glomerulus cells were (a) densely filled with cytoplasm; (b) with a persistent nucleus with nucleolus; and (c) without sieve areas.

A comprehensive study of the nodal anatomy of *Dioscorea batatas* Decne. and *Tamus communis* was conducted by Braun (1957). He concluded that (a) the xylem-glomerulus consists of very numerous short tracheids of various sizes, the orientation of which is difficult to trace; (b) the phloem-glomerulus, which is divided into several partial glomeruli, is composed of a new type of translocatory cell, called phloem-glomerulus cells; and (c) the phloem-glomerulus cells possess thin walls without sieve pores and without visible pitting; they are distinguished from parenchyma cells by their lack of starch. Behnke's (1965c) electron microscopic studies show that sieve areas are, in fact, present in the phloem-glomerulus cells.

The present study, involving more species than were available to earlier investigators, essentially supports and extends their conclusions.

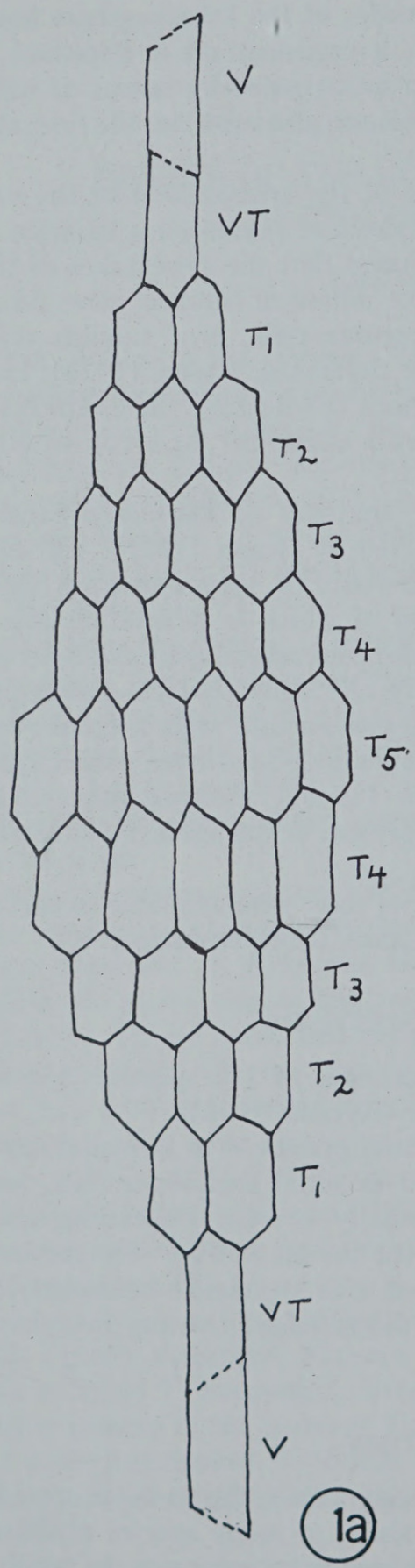
MATERIALS AND METHODS

My observations are based on 180 specimens of 112 species. A complete list and citations are given elsewhere (Ayensu, 1966).

Most of the specimens examined were fluid-preserved in formalin acetic alcohol. Microscopic details were studied in serial sections at 10μ, and those produced on a sliding microtome usually at 16μ. Depending upon the nature of some specimens, sections were cut up to 90μ. The sections were stained in safranin and counterstained with Delafield's haematoxylin followed by conventional differentiation, dehydration, clearing in xylene, and mounting in Canada balsam.

NODAL ANATOMY

As pointed out in an earlier paper (Ayensu, 1965), the vascular strands between the petiole and the stem at the nodes of many species of Dioscoreaceae are highly distinctive and are believed to be unique in the family. Longitudinal serial sections of the node reveal two groups of interlacing vascular elements, each forming a plexus close to the petiole insertion.



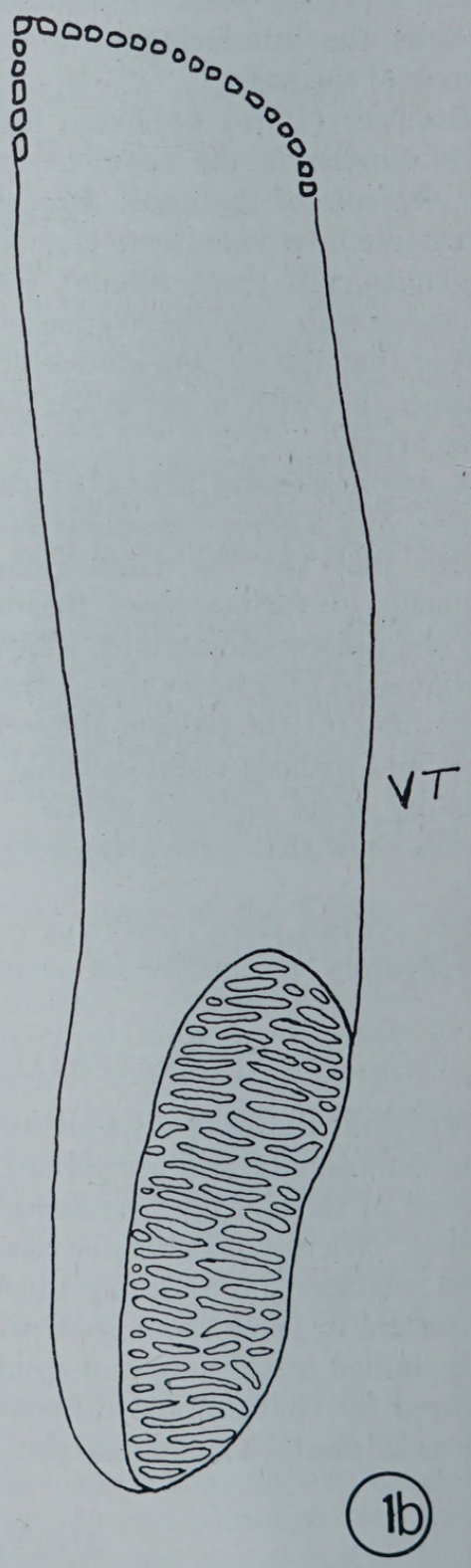


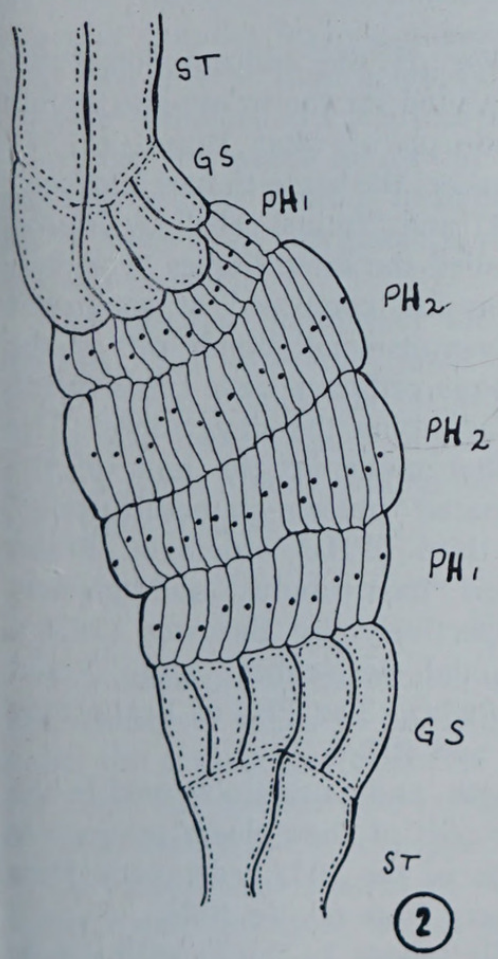
FIG. 1a (LEFT). Schematic diagram illustrating the arrangement of the elements of xylem-glomerulus in the nodal region of stems of *Dioscorea* and *Tamus*.

FIG. 1b (RIGHT). Vessel-like tracheid showing a reticulate perforation plate (lower) and bordered pits (upper).

Xylem-glomerulus. Serial sections and macerations reveal that the mature xylem glomerulus is mainly composed of short tracheids of variable shape closely fitted together, thus resembling the distinct parts of a composite jig-saw puzzle. These peculiar tracheids are confined to the node and have large bordered pits. Presumably in the internodes water moves freely from vessel element to vessel element through the scalariform perforation plates. Exactly how materials are translocated through the nodal region is not clearly understood.

The phyllotaxy determines the width of the glomerulus in the nodes. In the species having simple, alternate leaves, a single glomerulus occupies about one-third of the area of the node. In an opposite (or decussate) arrangement, the glomerulus occupies about two-thirds of the nodal area. In species that exhibit a whorled arrangement, the glomerulus occupies almost all the nodal area.

The tracheids vary in width and length within species. The widths varying from 40μ to 110μ, and lengths from 80μ to 260μ have been recorded for different species. These tracheids are closely fitted together, and have numerous pit-pairs on their common walls. The exact pathway of the contiguous tracheids between successive internodes is very complicated and variable within a species. (See Figs. 4–12.) Longitudinal



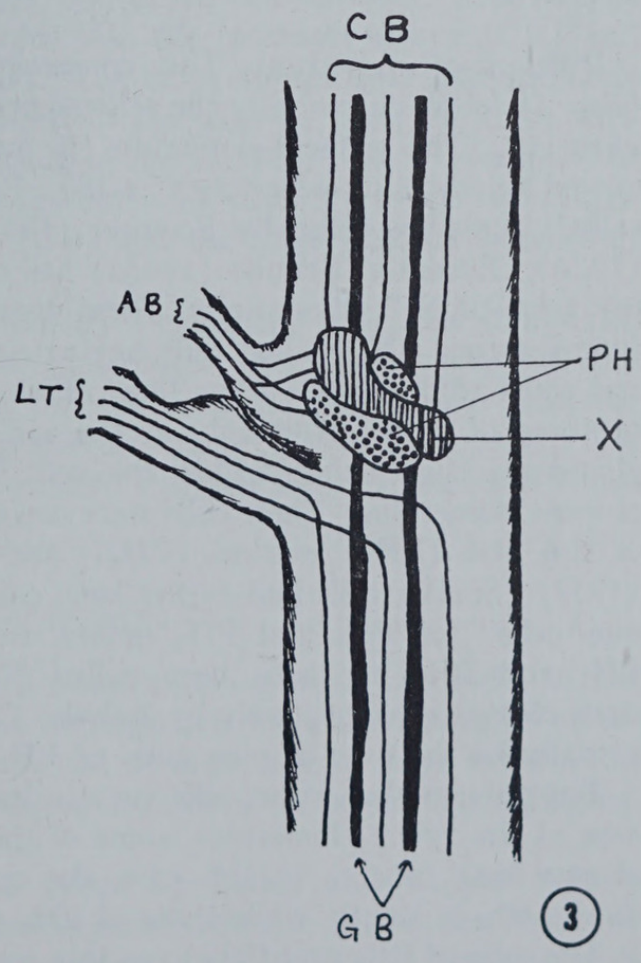


Fig. 2 (left). Schematic diagram of the phloem glomerulus.

Fig. 3 (right). Schematic representation of the stem showing the relationship of and the position of the xylem and phloem glomeruli in the region of the leaf insertion.

sections and macerations of the node give a partial elucidation of the complicated sequence of the tissue structures. As Braun (1957) interpreted *D. batatas* and *Tamus communis*, a vessel just about to enter a node is attached to 1, 2, or 3 cells which Braun referred to as "vessel-like tracheids." The end wall of the vessel-like tracheid (VT) facing the vessel (v) has a reticulate perforation plate, while the other end wall has bordered pits (FIGS. 1a, b). The elements that constitute the bulk of the xylem-glomerulus lie between the vessel-like tracheids. The tracheids of the first group (T_1) are closely fitted to those of the second group (T_2) and to other successive tracheid groups, thus establishing the normal communication between them. The lengths of the tracheids vary from one node to the other within a species. In this respect variation in tracheid length does not have any taxonomic value. Those of the first few groups (T_1 — T_3) are shorter than those of T_4 and T_5. It is also observed that the tracheid groups increase in number from T_1 to T_5, presumably for enlarging the water conducting tissues in the node. The surface area of the water conducting tissues is further increased by the complex arrangement of many xylem-glomeruli at a node. Each glomerulus is S-shaped and longitudinally orientated. A xylem-glomerulus diagram (FIG. 1) is presented for the sake of simplicity, but the full complexity of it is demonstrated by FIGS. 4–12.

Phloem-glomerulus. The construction of the phloem-glomerulus (FIG. 2) follows essentially the scheme presented for the xylem-glomerulus (FIG. 1). The phloem-glomerulus is made up of what Braun (1957) named "glomerulus sieve-tubes" (GS). Earlier, the same tissues had been called "funiculus cells" by Brouwer (1953) and "funnel-cells" by Mason (1926). Recently, Behnke (1965a) has called the same tissues "connecting sieve-tubes." Essentially, these tissues are composed of somewhat funnel-shaped, thin-walled cells having numerous small simple pits at the end walls adjoining the PH. They differ from ordinary sieve tubes in the presence of sieve plates only at the end adjoining the sieve tubes. The glomerulus sieve-tubes adjoin the cells that make up the bulk of the phloem glomerulus. These cells were designated "phloem-glomerulus cells" of the first (PH_1), second (PH_2), and third (PH_3) orders by Braun (1957). Similar cells had earlier been called "bast tubulus" and "glomerulus cells" for PH_1 and PH_2 orders, respectively, by Brouwer (1953). PH_1 and PH_2 had also been called "Nodal sieve-tubes" and "Nodal sieve-elements" respectively by Behnke (1965a). The PH_3 of Braun may actually be the over-lapping ends of PH_2 and PH_21.

The phloem-glomerulus cells vary in length, and as was observed in the case of the xylem-glomerulus, some of the cells of the phloem groups are shorter than others. In this case, the cells of the PH_1 order vary from 20μ to 60μ in length, while those of PH_2 vary from 60μ to 140μ.

The cells of PH_1 and PH_2 have thin walls (about 1μ thick) with simple pits that can hardly be seen with a light microscope. Whether the walls are interconnected by cytoplasmic threads (plasmodesmata) or by any

other mechanism has not been demonstrated with the light microscope. Dr. Behnke of Bonn University informed me that his electron microscope studies show that plasmodesmata are indeed present in the cells of PH_1 and PH_2. His recent publications (Behnke, 1965a, b, c) support his findings. It is, however, certain that these phloem cells are specialized and differ from sieve tubes and sieve cells of ordinary phloem tissue. Microchemical tests reveal the absence of starch-grains from the phloem-glomerulus cells; the surrounding parenchyma cells possess starch. The histochemistry of the phloem will have to await critical studies.

Cleared and stained portions of young and old stems reveal that at the node (FIG. 3) three major vascular bundles (LT) enter the petiole from the stem through the node without joining other vascular bundles, coming through the underlying internode as peripheral vascular bundles. These leaf-trace bundles are V-shaped.

The vascular bundles of the stem axis lying in front of the point of entry of the leaf traces, and those of the inner and outer circles become enlarged and join to form the xylem and phloem glomeruli (X, PH). These glomeruli lie obliquely above each leaf insertion at the same height as the axillary bud (AB). Opposite the outer circle of the vascular bundles in the internode they appear somewhat towards the outside and project into the base of the axillary bud or the lateral shoot. Five cauline vascular bundles leave a glomerulus into the internode above (CB), but only two enter it from below (GB). The latter are the characteristic large vascular bundles which are arranged in the gaps between the three leaf-trace bundles, which lie on the inside of the stem furrows. Hence the five cauline vascular bundles forming the circle are made up of the two vascular bundles from the glomerulus (GB) and the three vascular bundles of the leaf-trace (LT).

The vascular bundles of the axillary buds come from the glomerulus directly. Just after they leave the glomerulus, each divides into two (an upper xylem branch and a lower phloem branch), which come from the upper and lower regions of the glomerulus respectively. Occasionally the lower phloem branch subdivides into two with one establishing itself above the xylem branch.

DISCUSSION

The structure of the xylem and phloem glomeruli in the nodes of the Dioscoreaceae seems to be unique amongst the monocotyledons. Futhermore, the presence of tracheids and the distinct type of sieve elements in the node has considerable implications regarding the evolutionary history of these tissues in the angiosperms.

The anatomical studies of the xylem by Bailey and Tupper (1918) showed that the most logical phylogenetic sequence is the derivation of vessels from tracheids in the angiosperms. Cheadle (1943) working with the xylem of monocotyledons confirmed Bailey's work. In the light of the above theory it is interesting to examine the developmental aspects

of the tracheal elements in the node of the Dioscoreaceae. The bulk of the xylem glomerulus is made up of tracheids which are considered primitive in the phylogenetic sense. Similarly, the cells of the phloem glomerulus are considered to be of a relatively primitive type (cf. Braun, 1957, and the papers he quotes).

It is significant that such a difference can occur in a stem with primitive structures in the nodes and more advanced structures in the internodes. Bailey (1956) stated that "It is now clearly demonstrated that evolutionary modification of the xylem of stems and roots is *not necessarily* closely synchronized with phylogenetic trends in the specialization of the angiospermic flower. Either trend of evolution may be accelerated or retarded in relation to the other." The above can be extended with a statement that vessel development in an individual part of an organ can be delayed or advanced within that particular part as demonstrated in the node and internode of the Dioscoreaceae respectively.

This study demonstrates that in the midst of the complex nodal vascular system lies an orderly and systematic mechanism that permits the transport of assimilatory materials through the stems of the Dioscoreaceae. However, any attempt to gain full understanding of the exact pathway, and therefore, the movement of material through the phloem glomerulus must first confirm the present observations which are based on a reconstruction from serial microtome sections. A more reliable understanding of the pathway will hopefully be gained when the writer is able to study the vascular system of the Dioscoreaceae using the motion-picture analysis technique employed by Zimmermann and Tomlinson (1965, 1967).

The complexity of the phloem glomerulus in the Dioscoreaceae raises some fundamental questions about the current hypotheses on transport mechanisms in plants. Esau, Currier and Cheadle (1957) summarized the hypotheses as (a) mass or pressure flow; (b) mass flow together with activities of parenchyma cells associated with the phloem that account for the turgor gradients necessary for mass flow; (c) transport of solutes in the sieve tube along protoplasmic interfaces; (d) accelerated solute movements in sieve tubes resulting apparently from some special kind of cytoplasmic movement or flow; (e) independent solute movement resulting from one or more as yet unknown active transfer processes that occur in the sieve element cytoplasm.

The unique anatomical characteristics of the phloem glomerulus in this family seem to suggest that perhaps more than one of the above methods is responsible for the movement of assimilatory substances in the Dioscoreaceae. Arisz's (1952) suggestion that every substance moves its own way, and that different mechanisms may be involved in translocation should be considered in the light of the anatomical variation in the phloem of this family.

Although I have no proof as to the exact function of the phloem glomerulus, it seems likely that rapid translocation is achieved by the numerous cells that form the bulk of the nodal region.

SUMMARY

The complex nodal anatomy which is unique and basically uniform in the Dioscoreaceae, especially in *Dioscorea* and *Tamus*, is described. The width of the two masses of tissues referred to as glomeruli is correlated with the phyllotaxy in each species. The xylem-glomerulus is composed of numerous short tracheids of various sizes and shapes which are closely fitted together. The phloem glomerulus, whose construction is essentially that of the xylem-glomerulus, consists of thin-walled cells without visible pitting and sieve areas. Because of the presence of primitive xylem and phloem structures in the nodes in contrast to more advanced structures in the internodes, it is postulated that vessel development in an individual part of an organ can be delayed or advanced within that particular part as shown in the node and internode of the Dioscoreaceae respectively. The peculiar nature of the vascular bundle glomeruli is presumed to have some effect on the rate of fluid transport in the stem. It is suggested that another technique, such as the motion-picture analysis method, should be employed to study further the nodal structure and its relation to translocation.

ACKNOWLEDGMENTS

I am very grateful to Drs. P. B. Tomlinson, R. H. Eyde, and H. Robinson for reading the manuscript.

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DEPARTMENT OF BOTANY
SMITHSONIAN INSTITUTION
WASHINGTON, D.C. 20560

EXPLANATION OF PLATES

FIGS. 4–12. Longitudinal sections of the stem nodal region illustrating the complexity of the xylem and phloem glomeruli, × 80.

PLATE I

FIG. 4. *Dioscorea hirtiflora* Benth., showing an example of the meeting point between the phloem glomerulus cells (PH_2) of the second order, and a transverse section of a sieve tube (ST).

FIG. 5. *Dioscorea discolor* Kunth, interlacing of xylem glomerulus cells. Arrow points to a transverse section of a vessel (V) just entering the node.

PLATE II

FIG. 6. *Dioscorea schimperiana* Hochst., exhibiting general orientation of xylem and phloem glomeruli. Vessel element (V); phloem glomerulus of the first (PH_1) and second (PH_2) orders. Xylem glomerulus cells (XG), phloem glomerulus cells (PHG).

FIG. 7. *Dioscorea multiflora* Mart., showing a vessel element (V) and xylem glomerulus cells (XG).

PLATE III

FIG. 8. *Dioscorea luzonensis* Schauer, showing transverse sections of phloem glomerulus cells (PHG).

FIG. 9. *Dioscorea composita* Hemsl. (*D. tepinapensis* Uline ex Knuth). Arrows pointing to vessel (V), vessel-tracheid (VT) and xylem glomerulus in transverse section (XG).

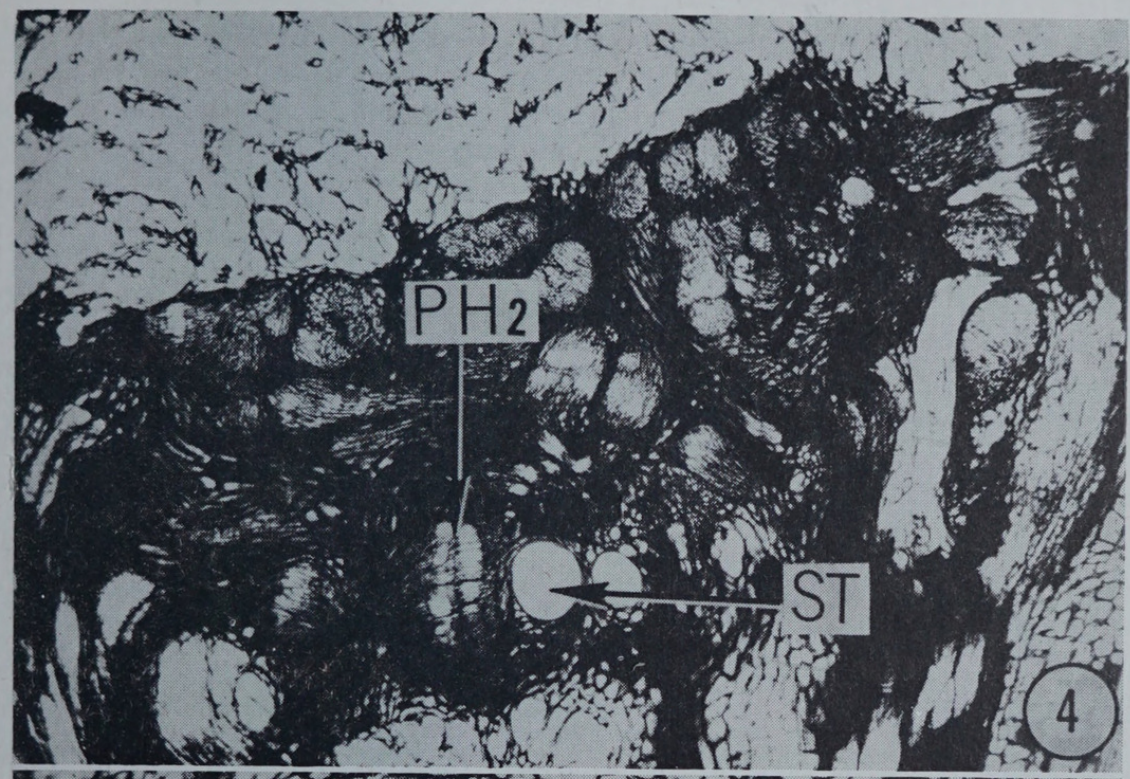
PLATE IV

FIG. 10. *Dioscorea pentaphylla* L., end plates of a vessel-tracheid (VT) and a vessel element (V).

FIG. 11. *Dioscorea dregeana* (Kunth) Th. Dur. & Schinz, end plate of vessel-tracheid (VT) and phloem glomerulus cells (PHG).

PLATE V

FIG. 12. *Tamus communis* L., exhibiting the presence of xylem (XG) and phloem (PHG) glomeruli.



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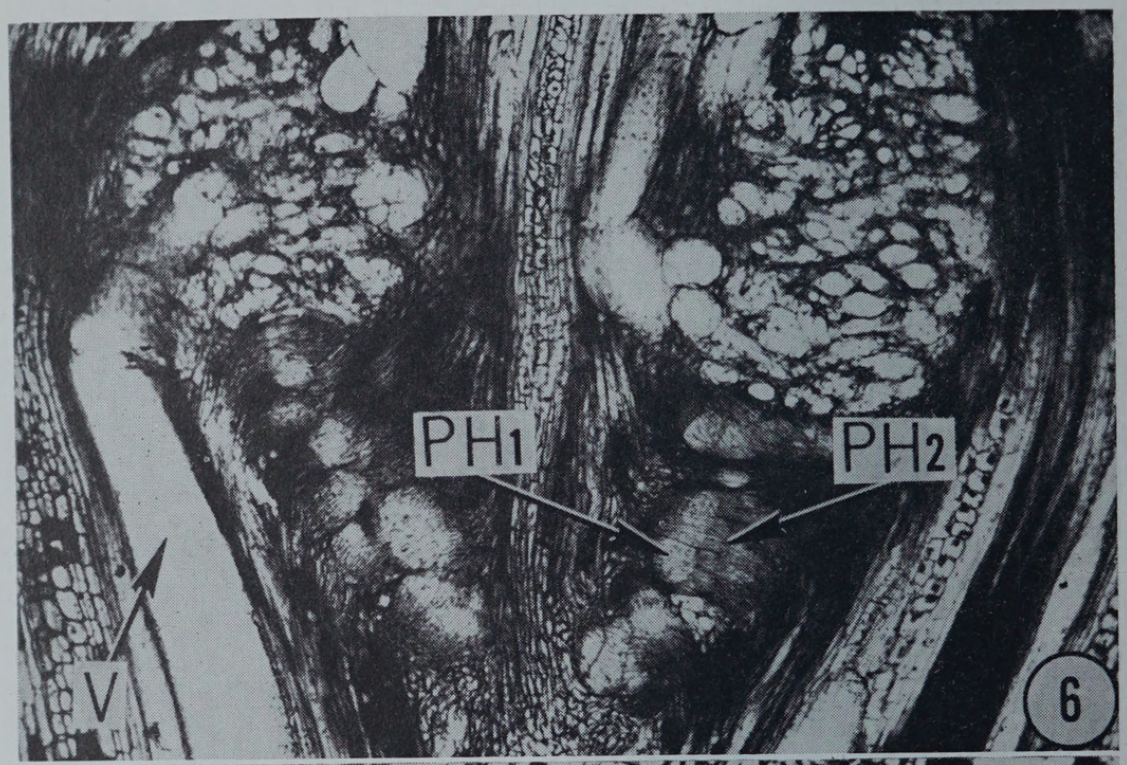

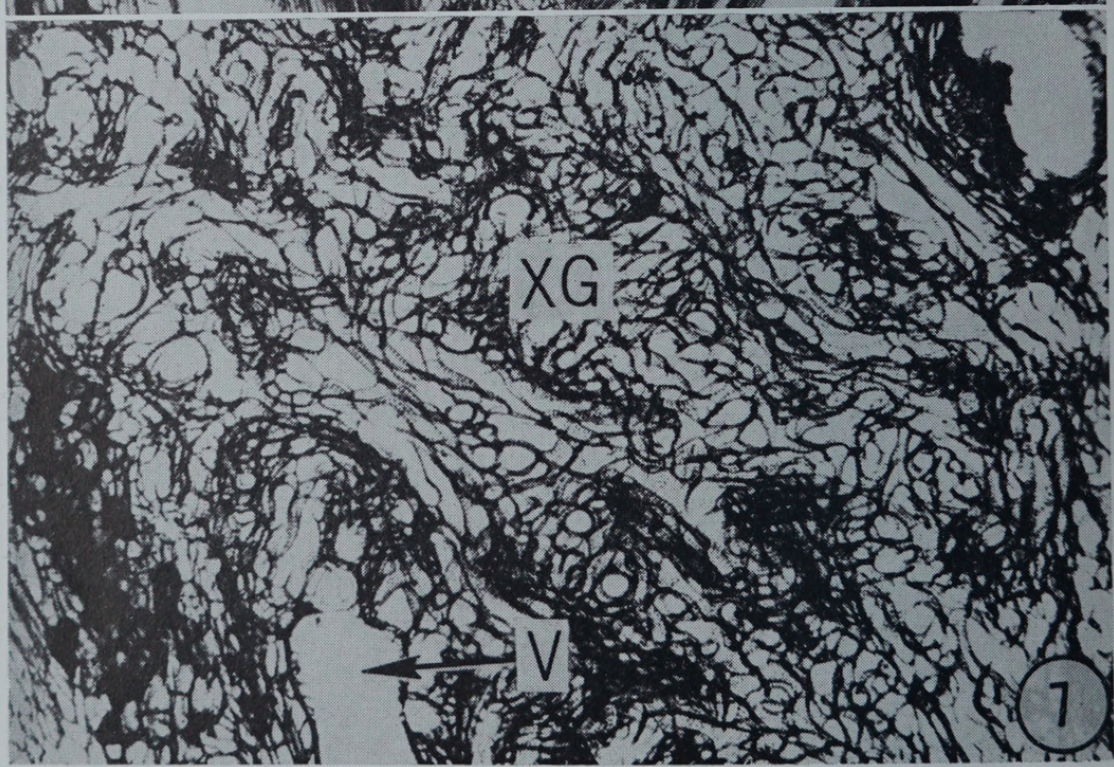

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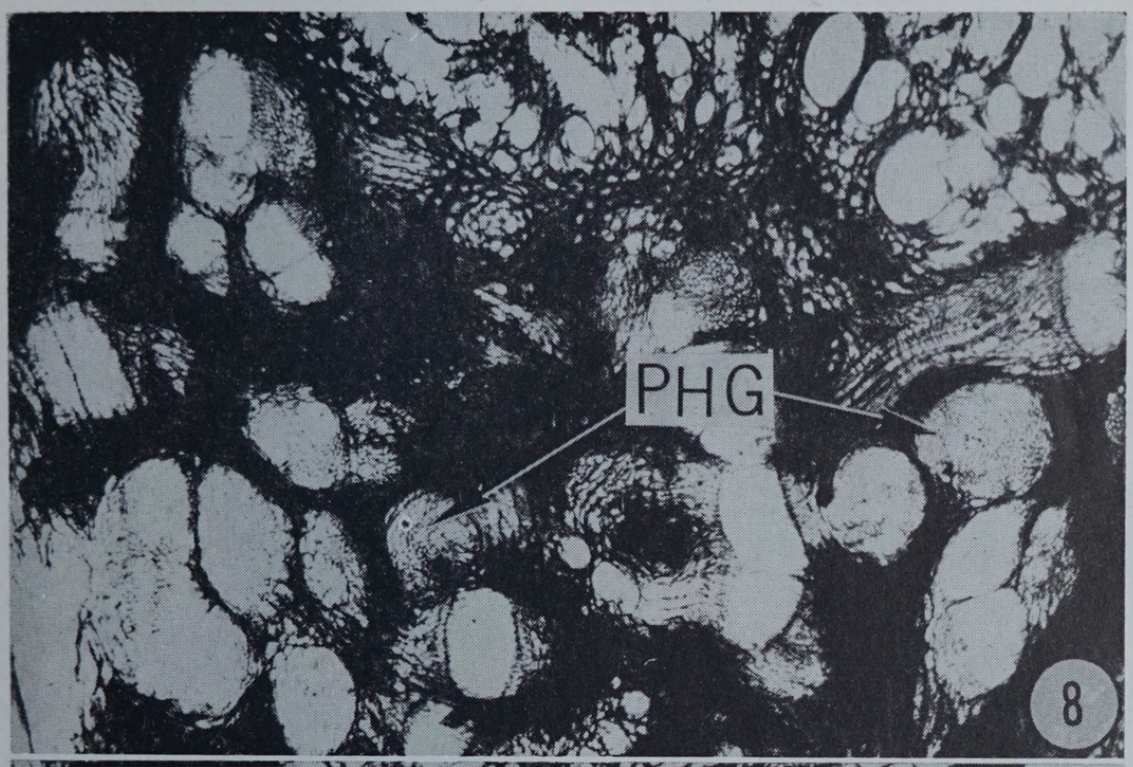

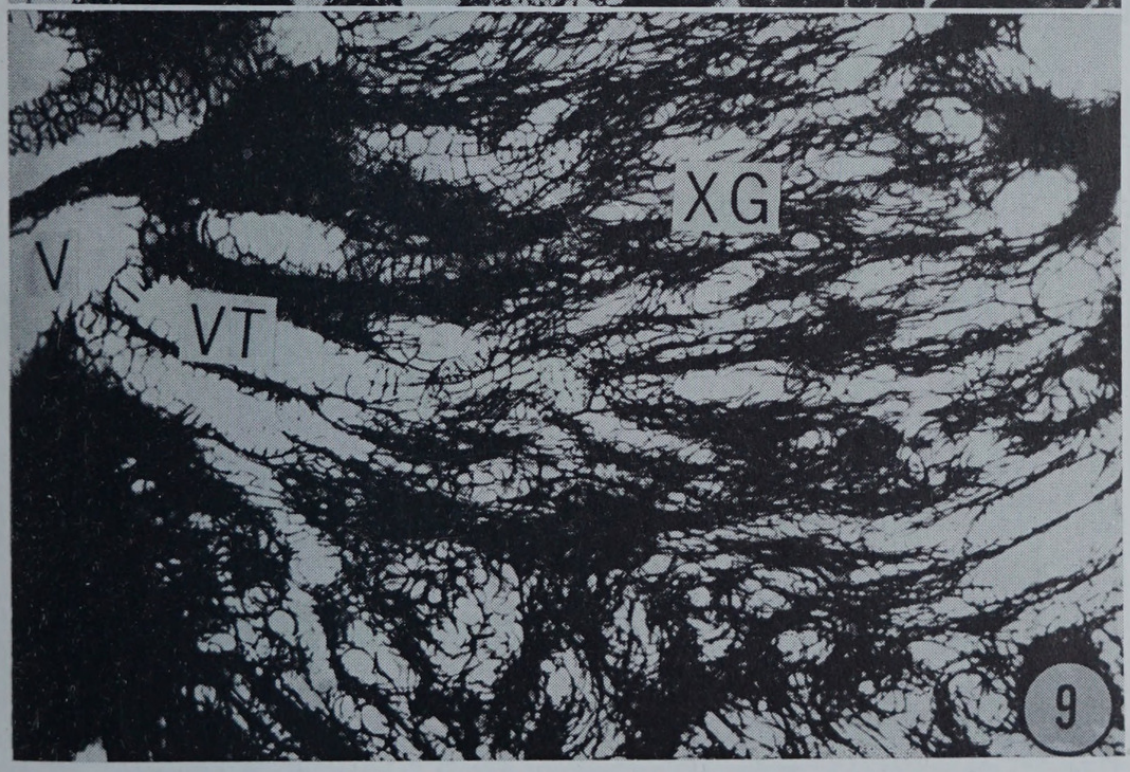

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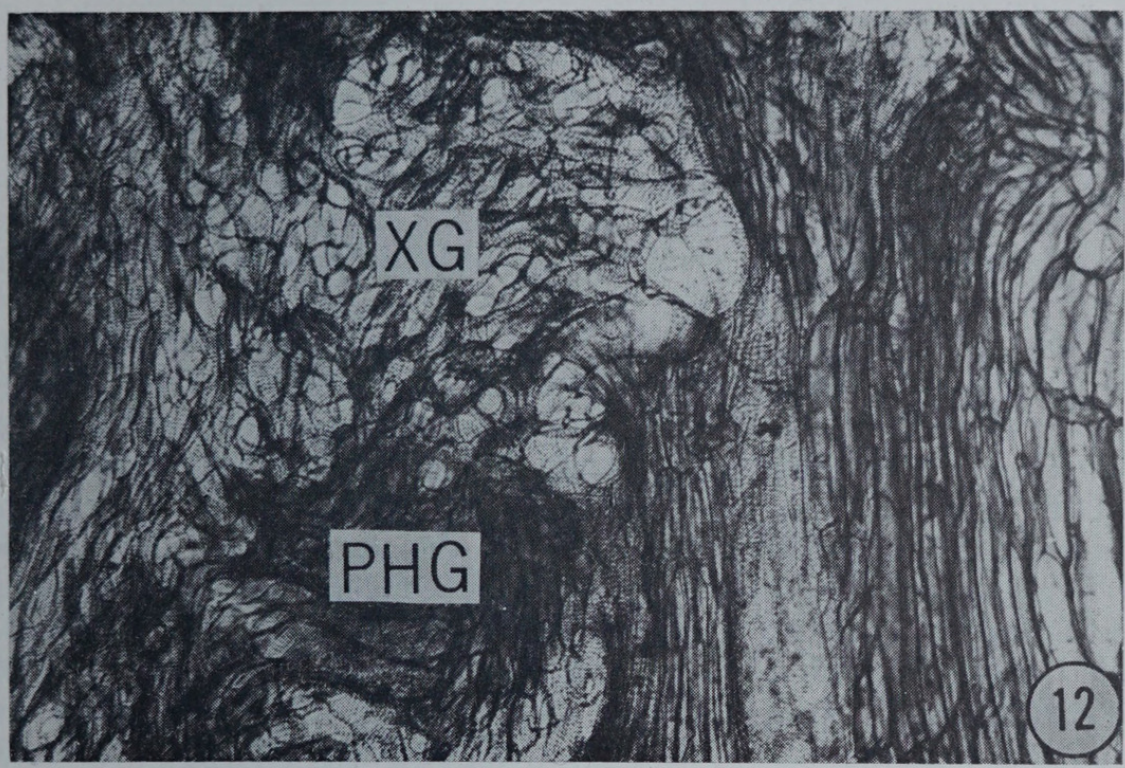

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