HYDROCARBON SECRETIONS AND INTERNAL SECRETORY SYSTEMS OF THE CARDUACEAE, AMBROSIACEAE AND CICHORIACEAE.

by

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Historical Introduction

The secretions and secretory systems of the Carduaceae, Ambrosiaceae and Cichoriaceae (Compositae) have been the object of research of many investigators. Some of these have been impelled by the purely scientific aspects of the subject and others by the possibility of finding new sources of products of economic importance.

Early mention of the secretory system of the Compositae in botanical literature was made by Treoul (1862), who distinguished between the secretory canals and latex vessels by the fact that the latter were limited by their own walls while the former were intercellular spaces without any such layer. He also mentioned the occurrence of endodermal secretion canals in the Tubuliferae represented by Vernonia praealta.

Muller (1866-67) confirmed the opinion that the secretory canals were intercellular spaces. In dealing with the Compositae he says of Inula helenium that it is distinguished by large passages in the pith containing ethereal oils and the occurrence of smaller passages in the cortex.

Van Tieghem (1885) has shown that secretory canals are of common occurrence throughout the Compositae and he emphasized the fact that in roots they are formed in close association with the endodermis. Van Tieghem states that in the Compositae the secretory system has three different forms: (1) oil-bearing canals (2) laticiferous cells uniting in a network and (3) isolated, long resiniferous cells; also that, aside from certain transitional forms, "Les Radiees et les Labiatiflores" have only oil-bearing canals, the Liguliflores have only anastomosing latex tubes, while the Tubuliflores, for the most part at least, have both oil-bearing canals and isolated resiniferous cells. Van Tieghem discussed the difference between the secretory canals of the stem and root. He held that the outstanding difference between the two was, that in the stem the canals were surrounded by specialized cells, while in the case of the root they were considered to be merely intercellular spaces formed in close association with the endodermis. He has recorded Ambrosia trifida as having secretion canals at the external border of each vascular bundle at the union of the pericycle with the phloem. These canals are considered by him to belong to the phloem.

Triebel (1885) gave a description of the development of the oil canals in the roots of a few members of the Compositae. He found that the formation of the canals was always preceded by the tangential division of the endodermal cells opposite the phloem, the canals beginning as minute intercellular spaces at the junction of the radial and newly formed tangential walls. These canals became filled with drops of almost colourless oil at a very early stage. The cells surrounding the oil canals had thinner walls and were much shorter than those of the cortex proper, they were meristematic in appearance, being filled with dense protoplasm. He considered that these cells probably played an important part in the secretion of the oil in the canals. The oil was termed an ethereal oil, a conclusion based on the following facts: (1) that most of the plants examined had a characteristic smell (2) that the oil was soluble in alcohol (3) and that it stained with alkanet.

Col (1899-1904) studied the secretory apparatus mainly from the point of view of the classification of the group. He brings to light the following main facts: (1) a survey of the secreting apparatus of the different tribes of the Compositae shows that according to the phyllogenetic progression one finds a gradual replacement of secretion canals by a laticiferous system, however the transition is not an equal gradation in the roots, stems and rhizomes. The transition takes place first in stems, then in rhizomes and roots. (2) Secretion sacs or pockets are simply reduced secretion canals, differing only in longitudinal extent. (3) There are really only two forms of internal secreting apparatus in the Compositae, the canals and anastomosing latex tubes. The occurrence of sacs or pockets and of solitary tubes more or less branching is evidence of either advancing or regressive evolution. Col also distinguished three classes of secreting apparatus (1) anastomosing latex vessels (2) secretory canals (3) isolated cells which secrete latex.

Work by Tschirch (1906-1934) on resins was, for the most part, concerned with the resin and resin ducts of the Coniferae, however, his observations included some on the secretory canals of Compositae. He concluded, as a result of this work that resin formation in the Coniferae took place in what he termed a "resinogener Schicht" which he found lining the canals. He considered that the same layer was present in the secretory canals of the Compositae, but he called this a "Schleimschicht" or mucilage layer, and it was this layer that was supposed to excrete the resin into the canal. He considered that the young resin canals were filled with mucilage before any resin is secreted and that the older secretion canals were lined somewhat evenly with mucilage. In this layer numerous droplets of the secretion were thickly embedded and the cavity surrounded by the mucilage layer contained the most of the secretion. Tschirch was of the opinion that the secretion of resin droplets takes place only in the resin canals and not in the epithele cells.

Moenike's (1924) chief object in his research was to clear up the formation of secretions in the Umbelliferae, Compositae and Araliaceae, and to prove up on Tschirch's idea of there being a resinogenous layer, and that the secretion does not occur in the epithele cells but in the resin canals. He considers that there is no resinogenous layer in any of the above-mentioned families. Moenike did not observe a mucilage layer in the canals of Compositae. He held that the epithele cells do contain resin droplets although extraordinarily minute. By chemical and solubility tests he shows that the droplets in the epithele cells and the resin in the canals are the same substance, and so concludes that the resin is secreted in the epithele cells and then transferred to the canals. Moenike does not know how the droplets get through the wall of the epithele cells when they are excreted into the resin canals. He finds droplets of the secretion adhering to the walls bordering the resin canal just where the droplets accumulate in the epithele cells. Another object of Moenike was to determine the nature of the secretions in the secretion canals of the roots of the Umbelliferae, Compositae and Araliaceae.

Tetley (1925) in more recent work on the roots of the Compositae has discussed the formation of the canals and attempted an interpretation of her observations in the light of work which has been done on the endodermis.

She classifies the secretion canals in the roots into two main groups (1) endodermal, and (2) non-endodermal. The canals are said to be invariably formed opposite the phloem in very early stages. Michrochemical studies of the secretion are discussed. She considers the saponification test which Moenike used as unfeasible due to the minute quantity of substance secreted within the cells. However, she concludes that in developmental stages the secretion is a fatty substance with the nature of an unsaturated drying oil. Various theories of the method of deposition of the secretion in the canals are discussed, and she concludes that the fat is released during the differentiation of the phloem, from which it passes outwards across the endodermis by way of the radial walls to the endodermal canals in which it is deposited.

Lloyd (1932) in an investigation of caoutchouc in Parthenium argentatum discusses possible uses of the secretion to the plant. He feels that very little evidence has been shown for its being used in the metabolic processes of the plant or as an aid to drought resistance.

Whitaker, (1922) in the study of the anatomy of certain golden rods states, "Another point of interest, which is of course a common anatomical character of the Tubuliflorae is the presence of oil canals in the pith and cortex, or in both."

Comparative Anatomy of the Internal Secretory Systems in the Various Species

Agoseris cuspidata.

Root.

Latex tubes are scattered throughout the phloem and cortex.

Stem.

Latex tubes occur in the phloem and on the inside of, and lying in contact with, a slightly suberized endodermis. The suberized endodermal cells are decidedly tangentially flattened.

Latex tubes are also found in the pith in association with isolated groups of phloem.

Leaf.

Latex tubes are found below each of the veins and in the midrib. Those associated with the veins are in contact with the phloem. In the midrib the tubes are next to the group of primary hard bast beneath the phloem.

Ambrosia elatior L.

Root.

Relatively small inconspicuous canals averaging .015 mm. in cross diameter are found in the inner cortex, being more numerous radially opposite the phloem strands.

Stem.

Canals averaging .015 mm. in cross diameter occur within the stem cortex lying alternate with the groups of primary hard bast (Plate III, Fig. 5).

Leaf.

No specialized secretory system is present.

Ambrosia trifida.

Root.

Numerous canals without a differentiated epithele cell layer are found in the inner cortex and phloem which average .015 mm. in cross diameter (Plate I, Fig. 2). Those of the inner cortex of the root are grouped radially opposite the phloem strands.

Stem.

Canals are in the cortex, phloem and pith. Those of the cortex are comparatively few, numbering from four to five as seen in cross section. The average canal is .03 mm. in cross diameter and is surrounded with approximately two rows of secreting cells.

Canals of the phloem are very inconspicuous, as their epithele cells are about the same size and shape as the cells of the surrounding phloem parenchyma. The canals average .007 mm. in cross diameter and there may be from one to several canals within the phloem of each bundle.

In the pith the canals are located near the protoxylem points at the inner margin of the rays and are comparatively small, averaging .009 mm. in cross diameter. They have a definite epithele cell layer composed of from five to eight cells.

Leaf.

Canals are found in the midrib only, one in the ground tissue and several in the phloem. The one occurring in the ground tissue is similar to those in the stem cortex. Its position is below the central vascular bundle. Around this canal are two to three layers of secreting cells which are filled with a dark brown substance. These canals average .02 mm. in cross diameter. The canals of the phloem are quite small and obscure, averaging .01 mm. in cross diameter. There are often several of these canals in the phloem of a single vascular bundle.

Amphiachyris dracunculoides.

Root.

There is a suberized endodermis but no specialized secretory system is present.

Stem.

The canals, averaging .05 mm. in cross diameter, occur within the cortex only and often lie in an indentation of the endodermis. They have a definite epithelium with some cells joined with the suberized endodermis.

Leaf.

One canal occurs beneath each of the larger veins of the leaf blade and one in the ground tissue of the midrib (Plate V, Fig. 3), those below the veins having their epithelium cells in contact with the phloem. An average canal of the midrib is .05 mm. in cross diameter and an average canal of the mesophyll is .03 mm. in cross diameter. The single canal of the midrib has the same position in relation to the phloem as have the canals beneath the veins.

Aster azureus.

Root.

Canals averaging .012 mm. in cross diameter are found located radially opposite the phloem, their epithelium cells lying in contact with the suberized endodermis.

Stem.

There is a suberized endodermis but no specialized secretory system.

Leaf.

Only one canal is found in the leaf, lying in the ground tissue on the lower side of the vascular bundle of the midrib. The average cross diameter was .003 mm.

Aster ericoides.

Root.

There is no specialized secretory system.

Stem.

Canals averaging .03 mm. in cross diameter occur in the stem cortex with their epithelium cells lying in contact with a suberized endodermis.

Leaf.

Canals are present in both midrib and mesophyll, those of the mesophyll always occurring singly below a larger vein. Only one canal is found in the midrib, near the phloem in the ground tissue. Average canals of the leaf are .02 mm. in breadth.

Rhizome.

A specialized secretory system is lacking.

Aster Drummondii.

Root.

No occurrence of a specialized secretory system is found.

Stem.

No specialized secretory system is in evidence.

Leaf.

There is no specialized secretory system.

Rhizome.

There are canals averaging .045 mm. in cross diameter in the cortex, lying in contact with the endodermis.

Bidens frondosa.

Root.

A specialized secretory system does not occur.

Stem.

Canals are found in the cortex and pith. The cortical canals are irregularly dispersed within the inner cortex, and are comparatively numerous but relatively small, averaging .02 mm. in cross diameter. The epithelium cells are not different in shape and size from the other cortical cells; however, from one to three rows of the adjacent cortex cells contain a dark brown substance which marks very conspicuously the position of the canals (Plate II, Fig. 1).

The canals of the pith are very sparce and relatively inconspicuous, excepting for the fact that their epithelium cells also contain a dark brown substance. The canals average .01 mm. in cross diameter and are surrounded with four or five epithele cells. They occur close to the protoxylem points.

Leaf.

Comparatively small canals averaging .003 mm. in cross diameter occur singly on the lower side of the veins and the midrib. These are made conspicuous by the presence of a dark brown substance found in the epithelium cells. These cells always follow the veins of a leaf, as is plainly apparent in bleached leaves, whether or not a canal is formed.

Bidens involucrata.

Root.

Several relatively inconspicuous canals averaging .015 mm. in cross diameter are found in the inner cortex.

Stem.

Canals occur in cortex and pith. The canals of the cortex are quite similar to those of Bidens frondosa, but occur radially opposite the rays. The canals average .01 mm. in cross diameter and are surrounded with from one to three rows of cells containing a dark brown substance. These cells do not form a well-differentiated epithelium but have the shape and appearance of the other cortical cells.

The pith canals are not so closely associated with the protoxylem points as in Bidens frondosa but do lie in the outer part of the pith cylinder. These have a comparatively definite epithelium of from four to seven somewhat four-sided cells.

Leaf.

Secreting cells with dark brown contents are found conspicuous in the mesophyll and midrib of this species as was the case in Bidens frondosa. The canals of the midrib are dispersed through the ground tissue with a somewhat definite arrangement in relation to the vascular system. Where the secreting cells surround a definite canal they average .005 mm. in cross diameter.

Boltonia latisquama.

Root.

There are all told five canals which average .015 mm. in cross diameter, occurring singly and radially opposite a phloem group, and one to three cells of the suberized endodermis compose a part of the epithelium.

Stem.

The only canals present in the stem are located in the cortex. These are comparatively large, averaging .045 mm. in cross diameter. The epithelium lies in contact with a suberized endodermis. These canals number from one to four in the cortex, alternating tangentially with several large groups of primary bast fibers.

Leaf.

The canals (or pockets) are relatively conspicuous and numerous in the leaf blade (Plate V, Fig. 6). These average .04 mm. in cross diameter and are found singly below a vein in each case, and often are larger than the veins with which they are associated. A single canal averaging .04 mm. in cross diameter is found in the ground tissue on the lower side of the vascular bundle of the midrib.

Rhizome.

Comparatively large secretion pockets averaging .15 mm. in cross diameter are found within the cortical and pith region of the thickened rootstock. These extend longitudinally approximately .15 mm.

Erigeron canadensis.

Root.

Very inconspicuous canals, .015 mm. in cross diameter occur in the root radially opposite the phloem within the inner cortex.

Stem.

Canals occur in both cortex and pith. The epithelium of the cortical canals lies against the suberized endodermis. An average canal is .04 mm. in cross diameter (Plate III, Fig. 1).

Those canals occurring in the pith are comparatively few and are dispersed throughout the entire pith cylinder. Each canal is surrounded by several layers of secreting cells. The canals are relatively small, averaging .012 mm. in breadth.

Leaf.

Very conspicuous canals averaging .09 mm. in cross diameter occur below the veins, where these are located the leaf is decidedly swollen, especially at the margins (Plate V, Fig. 8). A single canal occurs in the ground tissue below the vascular bundle of the midrib.

Erigeron ramosus.

Root.

Canals averaging .018 mm. in cross diameter are found radially opposite the phloem groups. These occur in association with a slightly suberized endodermis, the endodermis furnishing the inside boundary of the intercellular space.

Stem.

Canals are found only in the cortex lying against a suberized endodermis. These canals are often comparatively inconspicuous from being somewhat tangentially flattened. The average canal is .02 mm. in cross diameter. An epithelium surrounds each canal, lying immediately in contact with the endodermis. These canals are usually radially opposite the groups of primary hard bast and vascular bundles.

Leaf.

Canals averaging .015 mm. in cross diameter are associated with the vascular bundle of the midrib and with the larger veins, a single canal occurring on the lower side near the phloem in each case.

Eupatorium altissimum.

Root.

Several comparatively small canals surrounded by four to five epithelium cells are seen in the inner cortex. These average .02 mm. in cross diameter.

Stem.

Fairly conspicuous canals averaging ..05 mm. in diameter, are found only in the cortex alternate with the primary hard bast groups which are opposite the vascular bundles.

Leaf.

There are canals averaging .02 mm. in cross diameter in both mesophyll and midrib, laterally to the veins in each case.

Eupatorium urticaefolium.

Root.

There are two to three relatively small inconspicuous canals averaging .015 mm. in breadth, occurring radially opposite each phloem group.

Stem.

Canals occur in the cortex and pith. The canals of the cortex are found radially opposite the medullary rays and in depressions between the groups of primary hard bast. The canals are relatively inconspicuous because they and their epithelium cells are approximately the same size and shape as the surrounding cortical cells. An average canal is .015 mm. in breadth. The innermost epithelium cells are in contact with a suberized endodermis.

In the pith the canals are located indefinitely through the outer region of the pith and are similar to those of the cortex in size and shape.

Leaf.

Several comparatively inconspicuous canals occur in the ground tissue above and below the vascular bundle of the midrib. These have no well-differentiated epithelium layer and average .01 mm. in breadth; also, canals averaging .01 mm. in breadth are associated with the veins.

Euthamia camporum.

Root.

No specialized secretory system is present.

Stem.

Canals are infrequent and occur only opposite the hard bast in the cortex, with innermost epithelium cells in contact with the definitely suberized endodermis. The average canal is approximately .03 mm. in breadth. In older stems these canals are very hard to find because of the tangentially flattened epithelium cells and canals.

Leaf.

Relatively large and conspicuous canals, averaging .06 mm. in cross diameter, are associated with the veins on the lower side near the phloem. A single canal approximately .03 mm. in breadth is embedded in the ground tissue of the midrib on the lower side.

Rhizome.

Canals averaging .06 mm. in breadth are found lying radially opposite the phloem groups and in contact with a suberized endodermis.

Galinsoga ciliata.

Root.

No specialized secretory system is present.

Stem.

Canals averaging .006 mm. in breadth are found in the cortex. These are relatively inconspicuous because they and their epithelium cells are approximately the same size and shape as the surrounding cortical cells.

Leaf.

Canals averaging .008 mm. in cross diameter occur singly above the veins and midrib.

Grindelia squarrosa.

Root.

No specialized secretory system is to be seen.

Stem.

Canals are found only in the cortex in slight indentations of the suberized endodermis. They are quite inconspicuous, averaging .03 mm. in cross diameter and having no definite epithelium cell-layer. The canals are somewhat tangentially flattened against the endodermis. They occur opposite the primary hard bast which in turn is opposite the vascular bundles.

Leaf.

Canals averaging .04 mm. in cross diameter are located below a few of the larger veins near the phloem. In the midrib a single canal of about the same size as the others is embedded in the ground tissue below the vascular bundle.

Helianthus annuus.

Root.

Tangentially flattened canals averaging .04 mm. in breadth are found in the cortex with their epithelium lying in contact with a suberized endodermis. One or more are found to occur radially opposite the phloem groups.

Stem.

The canals are found in the cortex and pith. Those of the cortex are comparatively large, averaging .08 mm. in cross diameter, and are dispersed through the cortical parenchyma with no definite position in relation to the vascular bundles. The epithelium cells have about the same shape as the surrounding cortical cells.

In the pith the canals are dispersed near its periphery and are much smaller than those of the cortex, averaging .015 mm. in breadth. They have a very definite epithelium layer composed of rectangular cells.

Leaf.

The canals, averaging .04 mm. in diameter, are associated with both the veins and the midrib, occurring singly above the veins, and in the midrib there are eight canals dispersed within the ground tissue of the lower side in definite relation to the five vascular bundles.

Helianthus rigidus.

Root.

Numerous comparatively inconspicuous canals averaging .015 mm. in breadth occur within the inner cortex radially opposite the phloem. These lie in contact with the endodermis.

Stem.

Canals are found in the cortex, phloem and pith. Those of the cortex are relatively large, averaging .09 mm. in breadth, while some are as large as .2 mm. (Plate II, Fig. 3). They are dispersed in the cortex, sometimes opposite the vascular bundles, and again opposite a ray. The epithelium is very pronounced, with comparatively large rectangular cells.

The canals of the phloem also are larger than those in the phloem of most other species, averaging .012 mm. in breadth. Several canals may be found in each phloem group, each with a definite epithelium (Plate II, Figs. 2 and 3).

In the pith the canals are fairly evenly dispersed throughout the entire pith cylinder. These are also relatively large, averaging .04 mm. in cross diameter, and have a definite epithelium layer with decidedly tangentially flattened cells.

Leaf.

Canals are found above the veins and in the ground tissue and phloem of the midrib, those above the veins and in the midrib ground tissue averaging .03 mm. in breadth while in the midrib phloem an average canal is .015 mm. in breadth. In the midrib there are four canals located below the three main vascular bundles, and the phloem of each vascular bundle may have several canals (Plate V, Fig. 7).

Rhizome.

Canals are found in both cortex and pith; those of the cortex are comparatively large, averaging .06 mm. in cross diameter (Plate IV, Fig. 3). The canals of the pith are dispersed throughout the pith cylinder with an average cross diameter of .02 mm.

Helianthus salicifolius.

Root.

There are several tangentially flattened canals in the inner cortex which average .04 mm. in breadth. These do not have a well-defined epithelium.

Stem.

There are numerous comparatively large canals in the cortex of the stem and several smaller canals in the pith. Those located in the pith occur near its periphery but have no particular position in relation to the protoxylem points. These average .015 mm. in breadth, and have from six to eight epithelium cells. The cortical canals average .04 mm. in cross diameter and are surrounded with from twenty to twenty-five rectangular epithelium cells.

Leaf.

Canals occur in the midrib and above the veins, averaging .03 mm. in cross diameter. There are four canals located in the ground tissue of the midrib on the lower side of the vascular bundle (Plate V, Fig. 5). These are conspicuous for their well-differentiated, triangular epithelium cells.

Rhizome.

Numerous canals forming a broken cylinder are found within the inner cortex. The canals group themselves most noticeably radially opposite the phloem strands. These canals average .03 mm. in breadth while canals occurring in the phloem average .05 mm. in breadth.

Helianthus strumosus.

Root.

Numerous comparatively large tangentially flattened canals are found scattered within the inner cortex and phloem averaging .04 mm. in breadth (Plate I, Fig. 4).

The epithelium is not well differentiated.

Stem.

Canals occur in the cortex, phloem and pith. The canals of the cortex have no definite location in respect to the vascular system. An average canal here is .06 mm. in breadth and is usually somewhat tangentially flattened. These canals have a comparatively pronounced epithelium composed of rectangular cells (Plate II, Fig. 5).

The phloem canals are relatively small, averaging .007 mm. in breadth. They each have a definite epithelium.

The canals of the pith are also comparatively small, averaging .008 mm. in cross diameter, but are numerous and scattered throughout the pith cylinder.

Leaf.

Canals averaging .02 mm. in breadth occur above the veins. In the midrib the canals, averaging .04 mm. across, are found in the ground tissue.

Rhizome.

There are numerous canals within the cortical parenchyma and pith of the rhizome. Those of the cortex average .06 mm. in breadth while in the pith the canals average .04 mm. in breadth. Canals averaging .015 mm. are often found in the phloem (Plate IV, Fig. 4).

Helianthus tracheliifolius.

Root.

Several canals averaging .015 mm. in breadth are found immediately opposite the phloem groups and each phloem group has from one to three canals.

Stem.

Canals occur in the cortex, phloem and pith of the stem. Those in the cortex have no uniform arrangement in relation to the vascular system. They usually are slightly tangentially flattened and average .04 mm. in breadth. The epithelium is not as pronounced as in other species of this genus, though each canal does have a definite layer.

Canals of the phloem occur often two or three to a vascular bundle and average .007 mm. in breadth. There is a definite epithelium surrounding each canal.

In the pith the canals are also comparatively small, averaging .007 mm. in cross diameter. These canals are located in considerable numbers near the protoxylem points and their epithelium cells average four or five to a canal.

Leaf.

In the midrib canals occur in the ground tissue and in the phloem of the vascular bundle. There are six canals within the ground tissue averaging .04 mm.

in breadth. These have a definite arrangement in relation to the five vascular bundles. The canals in the phloem average .012 mm. in breadth. No canals are with the veins.

Rhizome.

Numerous relatively small canals averaging .018 mm. in breadth are found in the cortex, pith and phloem.

Heliopsis scabra.

Root.

The canals are relatively inconspicuous, appearing as minute intercellular spaces filled with secretion. These average .01 mm. in cross diameter and are located in the inner cortex.

Stem.

Canals averaging .01 mm. in cross diameter occur in cortex and pith. They lie in the cortical parenchyma between the large groups of primary hard bast and opposite a medullary ray in each case. The epithelium is composed of comparatively small cells which have in general the same shape as the surrounding cortical parenchyma cells.

In the pith the canals are similar in shape to those of the cortex and are only slightly smaller in size, averaging .008 mm. in cross diameter. These are close to the protoxylem points and alternate with them.

Leaf.

There are canals below the larger veins and in the midrib. Those with the veins average .015 mm. in cross diameter. In the ground tissue of the midrib the six relatively small canals are dispersed with definite regularity in relation to the five vascular bundles. An average canal of the midrib is .02 mm. in cross diameter.

Iva ciliata.

Root.

No specialized secretory system occurs.

Stem.

The stem of Iva ciliata has canals occurring in the cortex only. They are just outside the groups of primary hard bast. They average .04 mm. in cross diameter and have a definite epithelium layer composed of rectangular cells.

Leaf.

The larger veins of the leaf blade have canals located above them averaging .015 mm. in breadth. A single canal averaging .015 mm. in breadth occurs above the vascular bundle of the midrib.

Lactuca pulchella.

Root.

There are numerous latex tubes occurring in radiating groups opposite the phloem.

Stem.

Latex tubes are found in the cortex and phloem. Those of the cortex form a row lying in contact with each of the groups of primary hard bast (Plate III, Fig. 4).

Leaf.

Latex tubes occur in association with each of the veins and in the ground tissue of the midrib.

Lepachys columnifera.

Root.

Several large secreting pockets are located within the inner cortex. These average .06 mm. in breadth.

Stem.

The stem of Lepachys columnifera has comparatively few and small canals. These occur in the pith only, near the protoxylem points. The average canal is .006 mm. in cross diameter and has relatively small epithelium cells.

Leaf.

Canals averaging .015 mm. in breadth are found in the mesophyll and midrib.

Lepachys pinnata.

Root.

Canals appearing as ordinary intercellular spaces, because of the similarity of the epithelium cells to the cortical cells, are found in groups of three or four radially opposite the phloem. An average breadth is .04 mm.

Stem.

Canals occur in both cortex and pith (Plate III, Fig. 3). The canals in the cortex are not numerous and are opposite the groups of primary hard bast. They are comparatively obscure because they are tangentially flattened against the suberized endodermis. The average canal is .03 mm. in cross diameter. The epithelium layer is composed of relatively small cells.

Leaf.

Two canals averaging .01 mm. in breadth occur in the ground tissue of the midrib, one above and one below the vascular bundle, and canals averaging .008 mm. in cross diameter occur above some of the main veins.

Rhizome.

Tangentially flattened canals averaging .06 mm. in diameter occur in the inner cortex radially opposite each phloem group.

Liatris pycnostachya.

Root.

There is an average of three canals seen in cross section. These lie next to the endodermis and are radially opposite the phloem. An average canal is .03 mm. in breadth.

Stem.

Canals found in the stem occur in the cortex only. They are comparatively inconspicuous, lying against and within an indentation of the undulated primary hard bast. The average canal is .015 mm. in breadth and is surrounded with from five to seven epithelium cells which are not well differentiated from the cortical parenchyma.

Leaf.

Comparatively inconspicuous canals averaging .01 mm. in breadth occur laterally to the veins, while in the midrib there is a canal in the ground tissue on each side of the vascular bundle.

Corm.

The corm has exceptionally large secretion pockets embedded in the parenchymatous tissue, a feature common in this genus (Plate IV, Fig. 5). The pockets, averaging .9 mm. in cross diameter are lined with several rows of tangentially-flattened cells.

Liatris punctata.

Root.

The canals are similar in position and size to those of Liatris pycnostachya.

Stem.

The canals of this species averaging .02 mm. in breadth occur in the cortex only, lying against the primary hard bast, and having about the same location and size as in the species aspera and pycnostachya.

Leaf.

The location and size of the canals of this species are similar to those of Liatris pycnostachya.

Corm.

Secretion pockets occur like those in Liatris pycnostachya.

Liatris aspera.

Root.

The canals have comparatively no difference in size and location from those in Liatris pycnostachya and punctata.

Stem.

Canals are found in the cortex only and average .02 mm. in cross diameter. These have no well-differentiated epithelium layer.

Leaf.

The canals in position and size resemble those of Liatris pycnostachya and punctata.

Corm.

Secretion pockets occur like those in Liatris pycnostachya and punctata.

Mesadenia atriplicifolia.

Root.

Relatively large canals, averaging .12 mm. in cross diameter, one radially opposite each phloem group, are seen in cross section (Plate I, Fig. 6). These are next to a suberized endodermis.

Stem.

Canals with definite epithelium occur in both cortex and pith. The canals of the cortex are comparatively numerous and occur radially opposite a vascular bundle and close to the primary hard bast (Plate II, Fig. 6.). An average canal is .04 mm. in cross diameter.

Canals occurring at the periphery of the pith cylinder are like those of the cortex in size and shape.

Leaf.

Canals occur in both the mesophyll and the midrib, averaging .03 mm. in cross diameter. In the midrib there are usually from two to four canals at the margins of the phloem, and in the mesophyll canals occur singly above and below the veins.

Rhizome (tuberous).

Comparatively large secretion pockets averaging .08 mm. in cross diameter, are found within the cortex of the tuberous underground stem.

Pyrrhopappus carolinianus.

Root.

Numerous latex tubes are found in the cortex and phloem.

Stem.

Latex tubes are in the cortex, phloem and pith. Those of the cortex are in contact with an endodermis, occurring more abundantly radially opposite the vascular bundles (Plate III, Fig. 2).

Those of the pith are in association with isolated groups of phloem.

Leaf.

The latex tubes are beneath the veins and in the midrib.

Senecio plattensis.

Root.

There is no specialized secretory system.

Stem.

No specialized secretory system is present.

Leaf.

No specialized secretory system is present.

Silphium speciosum.

Root.

The canals of young roots averaging .015 mm. in breadth form a broken cylinder around the stele, noticeably grouping opposite the phloem.

Stem.

Canals occur in the cortical parenchyma opposite the medullary rays and in the pith (Plate III, Fig. 6). In the cortex they are relatively large and conspicuous, averaging .08 mm. in breadth. Comparatively small epithelium cells form a single layer about each canal.

The canals of the pith occur in the periphery of the cylinder. They average .04 mm. in diameter and each is surrounded with a definite epithelium.

Leaf.

Comparatively minute canals averaging .006 mm. in cross diameter occur above the veins. In the midrib the canals with triangular epithelium cells are interspersed between the vascular bundles.

Rhizome.

Canals averaging .04 mm. in cross diameter and with a definite epithelium are found dispersed throughout the cortex, phloem and in the outer regions of the pith cylinder (Plate IV, Fig. 2).

Silphium laciniatum.

Root.

Tangentially flattened canals averaging .018 mm. in cross diameter are quite numerous within the inner cortex. They have no well-differentiated epithelium and appear simply as intercellular spaces in contact with the endodermis.

Stem.

In this species also the canals are found in the cortex and pith. Those of the cortex are dispersed throughout the parenchyma without definite relation to the vascular system. They are comparatively numerous and large, averaging .08 mm. in diameter. Each canal has a definite epithelium of rectangular cells.

In the pith the canals are located at the periphery of the cylinder and are much larger than the average of other species, being .08 mm. in breadth. There is a definite epithelium composed of comparatively large cells surrounding each canal.

Leaf.

Outside the midrib, canals averaging .015 mm. in cross diameter are usually found one above and one below the larger veins (Plate V, Fig. 4). Several canals averaging .03 mm. in diameter are located in the ground tissue surrounding the vascular system of the midrib (Plate V, Fig. 2).

Rhizome.

Numerous, large, tangentially-flattened secretion canals occur in the inner cortex averaging .06 mm. in cross diameter.

Solidago canadensis gilvocanescens.

Root.

Quite conspicuous canals with an average diameter of .06 mm. occur singly radially opposite each of the phloem groups and in contact with the suberized endodermis.

Stem.

There are canals in the cortex and pith of this species. The cortical canals lie against the suberized endodermis and are tangentially flattened. The epithelium cells differ from the other cortical cells only by their relatively small size. An average canal is .04 mm. in cross diameter.

The canals in the pith are near the protoxylem points. They average .05 mm. in diameter and have a well-differentiated epithelium.

Leaf.

All canals are comparatively large, averaging .04 mm. in diameter. They occur more often below than above the veins and those in the ground tissue of the midrib are located above and below the vascular bundle (Plate V, Fig. 1).

Rhizome.

Numerous large canals are found in the cortex and pith (Plate IV, Fig. 1). The canals in the cortex lie next to a suberized endodermis and average .07 mm. in breadth. Those of the pith cylinder lie near the xylem and average .09 mm. in diameter.

Solidago Lindheimeriana.

Root.

The canals, ten in number, averaging .06 mm. in diameter, lie within the inner cortex and in association with a slightly suberized endodermis. The epithelium cells are tangentially flattened and relatively small. Each canal occurs radially opposite a phloem group.

Stem.

The canals, found in the cortex only, are very inconspicuous and comparatively few. They are decidedly tangentially flattened against the suberized endodermis bounding the primary hard bast. The epithelium cells are comparatively small and tangentially flattened. An average canal is approximately .03 mm. in diameter radially and .06 mm. tangentially.

Leaf.

The canals are comparatively inconspicuous, averaging .015 mm. in diameter. They occur singly below the veins and in the ground tissue of the midrib below the vascular bundle.

Rhizome.

Numerous large canals averaging .1 mm. in breadth are found located within the inner cortex. The cells composing the epithele layer are quite tangentially flattened.

Solidago rigidiuscula.

Root.

A single canal lying in contact with a suberized endodermis and averaging .08 mm. in diameter is found opposite each phloem group (Plate I, Fig. 1).

Stem.

This species of Solidago also has canals in the cortex only, located against a suberized endodermis and radially opposite the vascular bundles. The average canal is .06 mm. in diameter. Also there are canals associated with the suberized endodermis which surrounds each leaf trace as it traverses the cortex (Plate II, Fig. 4). The epithelium is not well-differentiated.

Leaf.

A single canal averaging .06 mm. in diameter occurs beneath each of the three vascular bundles of the midrib. Beneath the larger veins is a canal averaging .03 mm. in diameter (Plate V, Fig. 9).

Solidago rigida.

Root.

The canals have the same position as in the other species of Solidago but are smaller, averaging .04 mm. in breadth.

Stem.

The canals of this species are very conspicuous because of their size, an average canal being .15 mm. in diameter. They are found in the cortex only, radially opposite the vascular bundles, with the epithelium in contact with the suberized endodermis.

Leaf.

Canals averaging .05 mm. in diameter occur in the mesophyll and midrib. Those of the mesophyll occur singly below the larger veins. In the midrib a single canal is found in the ground tissue below each of the several vascular bundles.

Vernonia fasciculata.

Root.

The root has both a latex system and canals. It is typical of the above-ground parts to have latex vessels only, but in the root a single canal averaging .03 mm. in diameter is found opposite each phloem group. The latex vessels are quite numerous in the cortex and phloem.

Stem.

Latex vessels occur in the cortex and phloem but there are no canals.

Leaf.

Latex tubes occur in the ground tissue of the midrib and in association with the veins.

Rhizome.

One to three canals averaging .045 mm. in breadth occur within the inner cortex radially opposite each of the primary phloem groups. Scattered throughout the phloem and cortex there are comparatively numerous latex tubes.

Discussion.

The Carduaceae, Ambrosiaceae and Cichoriaceae have been studied by a number of investigators from both anatomical and microchemical view points. Those principally interested in the anatomical investigation of the three families, grouped as one family, the Compositae, were Trecul (1862), Vuillemin (1884), Van Tieghem (1885), and Col (1899). These investigators recognized certain characteristic features of the secretory systems of the Compositae. It was early observed by them that resin canals were widely distributed in the Carduaceae and Ambrosiaceae, while latex systems distinguished the Cichoriaceae. Supplementing these earlier anatomical studies the research embodied in this paper presents a more complete record of a large number of species, especially in the Carduaceae.

Nearly all the species of Carduaceae and Ambrosiaceae that I have studied have resin canals present in roots, stems or leaves; however, Senecio lobatus has no specialized secretory system and Aster Drummondii has canals only in the underground stem. Vuillemin (1884), however, says that Senecio cordatus has a specialized secretory system in the stem.

The roots of species of the Carduaceae present a much more uniform arrangement of the canals than do the stems, as was recognized by Col (1899). The majority of species, indicated in Table I have canals; however none were observed in Amphiachyris dracunculoides, Aster azureus, Aster ericoides, Aster Drummondii, Bidens frondosa, Euthamia camporum, Galinsoga ciliata, Grindelia squarrosa and Senecio plattensis. The resin canals of the roots are found occurring singly or in groups radially opposite the primary phloem. Specialized secreting cells forming an epithelium are not present with the canals of the roots. As stated by Van Tieghem (1885), we do not recognize specialized secreting cells in the roots because each secreting cell has the same form and dimensions as the non-secreting cells and each excretes its products into the canal which it borders. The comparatively small sizes of canals of some species indicated in Table I and the lack of a well-defined epithelium make it difficult at times to locate canals until after treating sections with Scarlet R. The majority of species have relatively small intercellular-space canals in the younger roots, which occur in groups opposite the primary phloem and against the endodermis when this is present, often forming a broken cylinder about the stele. In the genus Solidago the canals are comparatively large (Table I) one occurring radially opposite each primary phloem group (Plate I, Fig. 1). The presence of canals in the roots distant from the endodermis is not common but Helianthus strumosus has canals within the phloem and scattered throughout the cortex (Plate I, Fig. 4). In only one species of the Carduaceae, Vernonia fasciculata, have I found both resin canals and a latex system. Here the canals, averaging .03 mm. in cross diameter, occur singly radially opposite each of the primary phloem groups. The latex tubes in this species are dispersed throughout the cortex and some are found in the phloem.

In the roots of the species of Ambrosiaceae studied by me the canals in the endodermal region are comparable to those of the Carduaceae. Ambrosia trifida has canals in the phloem of the root also. No secretion system was observed in Iva ciliata.

In the Cichoriaceae, a latex system is commonly found in the roots as well as in other parts. The latex tubes here are dispersed somewhat in the cortex, and mostly radially opposite the phloem, with a few in the phloem.

The species of Carduaceae, excepting Senecio plattensis and Aster Drummondii, have canals in some part of the stem (Table II). The canals are relatively more common in the cortex but sometimes they are found in the phloem and pith. Those species having canals in the cortex, as indicated in Table II, may be divided into two groups according to the location of the canals. When an endodermis is present the canals characteristically lie with their epithelium against the endodermis. This characterizes one group, while in the second group the canals are found dispersed in the cortex. Col (1899) says that in the stem the secretion canals are always endodermal in origin. Since my finding a large group of species in which the cortical canals are in no way associated with an endodermis Col's statement needs modification. Van Tieghem (1885) makes the statement that besides the endodermal secretion canals others occur in the cortex of stems beneath the epidermis, and in the parenchyma of the leaves, but he considers these to be rare. Species mentioned by Van Tieghem as having cortical canals not in association with an endodermis were Kleninia neriifolia, Solidago limonifolia, Solidago sempervirens, Solidago laevigata and fuscata. I find Solidago canadensis gilvocanescens, rigidiuscula (Plate II, Fig. 4), Lindheimeriana, and rigida to have cortical canals in contact with an endodermis. There are comparatively great differences in sizes of cortical canals in the various species. The sizes range from .008 mm. in cross diameter in Heliopsis scabra to .05 and .09 mm. in species of Helianthus, Solidago and Silphium (Table II). Position of the canals in relation to the vascular system, whether radially opposite or alternating with the phloem, varies with the different species, but this feature is not stable enough in the various species for their identification although Solereder (1908) refers to it as being the most useful for systematic purposes (mostly as a generic character). The occurrence of well-defined epithelium cells is not consistent in the stem, but is more frequent there than in the root. Species of Helianthus exhibit strikingly well-differentiated secreting cells surrounding canals in the cortex (Plate II, Fig. 5). Solereder (1908) says that the epithelium is probably of little value as a characteristic anatomical character, since resin canals devoid of epithelium and others provided with it occassionally occur side by side in the same plant (Lasthenia glabrata, Cynaria corsica) and that the canals without an epithelium do not always appear in all species of a genus (Cacalia, Senecio). I have observed Mesadenia (Cacalia) atriplicifolia (Plate II, Fig. 6) to have canals in the cortex with an epithelium, while Senecio plattensis has no canals in the stem.

Those species having canals within the phloem of the stem are not numerous in the Carduaceae. Helianthus rigidus (Plate II, Fig. 2), strumosus and trachelifolius were observed to have one or more canals in each phloem group, averaging .012 mm., .007 mm. and .007 mm. in breadth, respectively.

In the Ambrosiaceae, Ambrosia trifida has one or more canals in each phloem group of the stem. Vuillemin (1884) considers it an exception to find canals located within the phloem of the stem.

Canals in the pith are found in a majority of the species of Carduaceae and Ambrosiaceae. These canals are smaller on an average than those of the cortex, as indicated in Table II, ranging from .009 mm. in Ambrosia trifida to .08 mm. in Silphium laciniatum. The characteristic position of the canals in the pith is at the periphery where they usually occur opposite the protoxylem points in the various species (Plate III, Fig. 3). Van Tieghem (1885) observed canals occurring either singly or several together in the pith of species of Ageratum, Carduus, Dahlia, Helianthus, Serratula, Solidago, and

Spilanthes.

Of the Carduaceae I have found only one member, Vernonia fasciculata, to have a latex system in the stem. In this species the latex tubes are scattered within the inner cortex, phloem and more abundantly in the pith. Trecul (1862) speaks of Vernonia praealta as having endodermal secretion canals, and Van Tieghem (1885) has found latex tubes in the phloem of this species.

The stems of species of Cichoriaceae have secretory systems in the form of latex tubes, a feature said by Van Tieghem (1885) and Col (1899) to be typical of the group. I find that these may occur in the cortex, phloem and pith. In the cortex they are most abundant within the inner cortex forming a broken-undulated cylinder (Plate III, Fig. 4). In Pyrrhopappus carolinianus, there are latex tubes in association with isolated phloem groups within the pith (Plate III, Fig. 2).

The perennial species of Carduaceae whose underground stems I have studied have either canals or secretion pockets as typical features. The rhizome may have canals located in the cortex, phloem and pith, as is true for the above-ground stem also (Plate IV, Figs. 1-6). Helianthus strumosus, Helianthus trachelifolius and Silphium speciosum were of this type. The rhizomes of Boltonia latisquama, Helianthus rigidus and Solidago canadensis gilvocanescens have canals in the cortex and pith, while Aster Drummondii, Mesadenia atriplicifolia, Euthamia camporum, Lepachys pinnata, Silphium laciniatum, Solidago Lindheimeriana and Vernonia fasciculata have canals only in the cortex. The species of Liatris I have studied have corms and the secretion systems found here consist of large pockets scattered through the parenchymatous tissues (Plate IV, Fig. 5). The underground stem of Aster ericoides did not seem to have a specialized secretory system.

The presence of a specialized secretion system in the leaves of the various species of Carduaceae and Ambrosiaceae is as typical of the two groups as is its presence in other parts, as indicated in Table III. Senecio plattensis, Ambrosia elatior L. and Aster Drummondii are the only species I studied which do not have a specialized secretion system in some part of the leaf blade. In the leaves, canals may be found, one or more in the ground tissue of the midrib and in association with the veins of the mesophyll (Plate V, Figs. 1-9). In only three species: Ambrosia trifida, Helianthus rigidus (Plate V, Fig. 7), and Helianthus trachelifolius were one or more canals found in the phloem of the midrib. The position of the canals of the leaf is a feature of taxonomic value affording the demarkation of species into groups (See page). The usual position of the canals is above or below the veins; however, cases were found where the canals occur laterally to a vein. The approximate breadth range of the canals is from .003 mm. in Bidens frondosa to .09 mm. in Erigeron canadensis. Only one member of the Carduaceae, Vernonia fasciculata, was observed to have latex tubes in the leaf. These, as was characteristic of the canals were closely associated with the veins of the mesophyll and midrib.

Latex tubes occur characteristically in the leaves of Cichoriaceae, where they are seen to follow the veins.

Table I Summarizing the Cross Diameter in mm. of the Canals of Roots.

Actinomeris alternifolia	.015
Agoseris cuspidata	Latex system.
Ambrosia elatior L.	.015
Ambrosia trifida	.015
Amphiachyris dracunculoides	
Aster azureus	.012
Aster ericoides	
Aster Drummondii	
Bidens frondosa	
Bidens involucrata	.015
Boltonia latisquama	.015
Erigeron canadensis	.015
Erigeron ramosus	.018
Eupatorium altissimum	.02
Eupatorium urticaefolium	.015
Euthamia camporum	
Galinsoga ciliata	
Helianthus annuus	.04
Helianthus salicifolius	.04
Helianthus rigidus	.015
Helianthus strumosus	.05
Helianthus trachelifolius	.015
Heliopsis scabra	.01
Iva ciliata	
Lactuca pulchella	Latex system.
Lepachys columnifera	.05
Lepachys pinnata	.04
Liatris pycnostachya	.03
Liatris punctata	.03
Liatris aspera	.03
Mesadenia atriplicifolia	.12
Pyrrhopappus carolinianus	Latex system.
Senecio plattensis	
Silphium speciosum	.015
Silphium laciniatum	.015
Solidago canadensis gilvocanescens	.06
Solidago Lindheimeriana	.06
Solidago rigidiuscula	.08
Solidago rigida	.04
Vernonia fasciculata	.03 (and latex system)

Table II Summerizing the Location and Diameters in mm. of the Specialized Secretory Systems in the Stem.

	Cortex	Cortex'	Phloem	Pith
Actinomeris alternifolia		.015		
Agoseris cuspidata	Latex system in all parts.			
Ambrosia elatior L.	.015			
Ambrosia trifida	.025		.007	.009
Aster azureus				
Aster ericoides		.03		
Aster Drummondii				
Bidens frondosa	.02			.01
Bidens involucrata	.01			.02
Boltonia latisquama		.045		
Erigeron canadensis		.04		.012
Erigeron ramosus		.02		
Eupatorium altissimum	.05			
Eupatorium urticaefolium		.015		.015
Euthamia camporum		.03		
Galinsoga ciliata	.006			
Grindelia squarrosa		.03		
Helianthus annuus	.08			.015
Helianthus salicifolius	.06			.015
Helianthus rigidus	.09		.012	.04
Helianthus strumosus	.06		.007	.008
Helianthus trachelifolius	.04		.007	.007
Heliopsis scabra	.008			.01
Iva ciliata	.04			
Lactuca pulchella	Latex system in all parts.			
Lepachys columnifera				.006
Lepachys pinnata		.03		.012
Liatris pycnostachya	.015			
Liatris punctata	.02			
Liatris aspera	.02			
Mesadenia atriplicifolia	.04			.04
Pyrrhopappus carolinianus	Latex system in all parts.			
Senecio plattensis				

	Cortex	Cortex'	Phloem	Pith
Silphium speciosum	.08			.04
Silphium laciniatum	.08			.08
Solidago canadensis gilvocanescens		.04		
Solidago Lindheimeriana		.05		
Solidago rigidiuscula		.06		
Solidago rigida		.15		
Vernonia fasciculata	Latex system in all parts.			
Amphiachyris dracunculoides		.05		

Secretory system in the cortex with epithelium in contact with an endodermis.

Table III Summarizing the Location
and Sizes in mm. of the
Specialized Secretory Systems
of the Leaf.

	Midrib	Midrib (phloem)	Mesophyll
Actinomeris alternifolia	.008		
Agoseris cuspidata	Latex system in all parts.		
Ambrosia elatior L.			
Ambrosia trifida	.02	.01	
Amphiachyris dracunculoides	.05		.03
Aster azureus	.003		
Aster ericoides	.02		.02
Aster Drummondii			
Bidens frondosa	.003		.003
Bidens involucrata	.005		.005
Boltonia latisquama	.04		.04
Erigeron canadensis	.09		.09
Erigeron ramosus	.015		.015
Eupatorium altissimum	.02		.02
Eupatorium urticaefolium	.01		.01
Euthamia camporum	.03		.06
Galinsoga ciliata	.008		.008
Grindelia squarrosa	.04		.04
Helianthus annuus	.04		.04
Helianthus salicifolius	.03		.03
Helianthus rigidus	.03	.015	.03
Helianthus strumosus	.04		.02
Helianthus trachelifolius	.04	.012	
Heliopsis scabra	.02		.015
Iva ciliata	.015		.015
Lactuca pulchella	Latex system in all parts.		
Lepachys columnifera	.015		.015
Lepachys pinnata	.01		.008
Liatris pycnostachya	.01		.01
Liatris punctata	.008		.01
Liatris aspera	.008		.01
Mesadenia atriplicifolia	.03		.03
Pyrrhopappus carolinianus	Latex system in all parts.		
Senecio plattensis			
Silphium speciosum	.006		.006

	Midrib	Midrib (phloem)	Mesophyll
Silphium laciniatum	.03		.015
Solidago canadensis gilvocanescens	.04		.04
Solidago Lindheimeriana	.015		.015
Solidago rigidiuscula	.06		.03
Solidago rigida	.05		.05
Vernonia fasciculata	Latex system in all parts.		

Key to Species Based on Location, Size, and Characteristics of Epithelial Cells of the Internal Secretory System

I. No specialized secretory system present.
Senecio lobatus.
Aster Drummondii.

II. Secretory system present (canals) in roots, stems, and leaves.

A. In the stem the canals are present in cortex, phloem and pith.

1. Canals of the leaf in the mesophyll and midrib.

a. Canals in the phloem of the midrib.
Helianthus rigidus.

b. No canals in the phloem of the midrib.
Helianthus strumosus.

2. Canals of the leaf in the midrib only.

a. One canal in the ground tissue below the midrib vascular bundle.
Ambrosia trifida.

b. Six canals in the ground tissue around the midrib vascular bundles.
Helianthus trachelifolius.

B. In the stem the canals are present in the cortex and pith only.

1. Canals in the stem cortex with epithelium in contact with an endodermis.

a. Canals of the leaf with cavities not over .015 mm. in cross diameter.

(1) Midrib with two canals; one above and the other below the central vascular bundle.
Lepachys pinnata.

(2) Midrib with several canals; occurring above and below the central vascular bundle.
Eupatorium urticaefolium.

b. Canals of the leaf with cavities ranging from .04 mm. to .09 mm. in cross diameter.

(1) Canals of the mesophyll sometimes above, sometimes below the veins.
Solidago canadensis gilvocanescens.

(2) Canals of the mesophyll always below the veins.
Erigeron canadensis.

2. Canals in the stem cortex with epithelium cells apart from the endodermis.

a. Canals of the stem cortex averaging .08 mm. or over in cross diameter.

(1) Canals of the leaf midrib averaging .03 mm. in cross diameter.
Silphium speciosum.

(2) Canals of the leaf midrib averaging .04 mm. in cross diameter.

(a) Canals of the mesophyll occurring above and below the veins.
Silphium laciniatum.

(b) Canals of the mesophyll occurring above the veins only.
Helianthus annuus.

b. Canals of the stem cortex averaging .06 mm. or less in cross diameter.

(1) Epithelium cells of the canals well defined; composed of rectangular cells.
Helianthus salicifolius.

(2) Epithelium cells of the canals not well defined nor rectangular.

(a) Epithelium cells of the canals containing a dark brown mass.
Bidens involucrata.

(b) Epithelium cells not as above.

1' Canals of the stem cortex average .008 mm. in cross diameter.
Heliopsis scabra.

2' Canals of the stem cortex average .04 mm. in cross diameter.
Mesadenia atriplicifolia.

C. In the stem the canals are present in the cortex only.

1. Canals of the stem not in contact with an endodermis.

a. Underground stem in the form of a corm with large secretion pockets.
Liatris aspera.
Liatris pycnostachya.
Liatris punctata.

b. Underground stem not in the form of a corm.
Eupatorium altissimum.
Actinameris alternifolia.

2. Canals of the stem cortex with epithelium in contact with an endodermis.

a. Canals of the stem averaging .05 mm. or over in cross diameter.
Solidago Lindheimeriana.
Solidago rigidiuscula.
Solidago rigida.
Boltonia latisquama.

b. Canals of the stem averaging .04 mm. or less in cross diameter.
Erigeron ramosus.

D. In the stem the canals are present in the pith only.
Lepachys columnifera.

III. Canals present in stems and leaves only.

A. Canals in stem cortex with epithelium cells in contact with an endodermis.

Aster ericoides.
Amphiachyris dracunculoides.
Euthamia camporum.
Grindelia squarrosa.

B. Canals in the stem cortex not having epithelium cells in contact with an endodermis.

1. Canals in both cortex and pith.

Bidens frondosa.

2. Canals in cortex only.

Galinsoga ciliata.
Iva ciliata.

IV. Canals present in the roots and stems only.

Ambrosia eliatior L.

V. Canals present in the roots and leaves only.

Aster azureus.

VI. Canals in the roots only; latex system in other parts as well as in the roots.

Vernonia fasciculata.

VII. Only a latex system present.

Agoseris cuspidata.
Lactuca pulchella.
Pyrrhopappus carolinianus.

The Occurrence and Identification of Secretions Stained Red with Scarlet R.

Secretions which stain red with Scarlet R are found in abundance in the Carduaceae, Ambrosiaceae and Cichoriaceae. Sections taken from various parts of the plant show as a rule numerous globules of these secretions dispersed in the parenchymatous tissues, and in masses in specialized secretory systems. In many species which have large-cavitied canals the secretion exudes easily from the fresh-cut surfaces.

The tissue of the plant which contains the greatest number of dispersed globules is the mesophyll of the leaf. Cross sections of leaves of such species as Solidago canadensis gilvocanescens (Plate V, Fig. 1), Amphiachyris dracunculoides (Plate V, Fig. 3), Mesadenia atriplicifolia and Boltonia latisquama treated with Scarlet R present a striking appearance due to the great quantity of dispersed globules.

The quantity of secretion in the mesophyll varies among the species observed but in each some secretion was present. The following table gives a comparison of the species based upon the relative amounts of dispersed globules within the mesophyll of the leaf:

The Symbol (#) in Table IV Indicates Comparative Amounts of Secretion in the Leaves.

Agoseris cuspidata	##
Ambrosia elatior L.	#
Ambrosia trifida	#
Amphiachyris dracunculoides	####
Aster azureus	###
Aster ericoides	###
Aster Drummondii	###
Bidens frondosa	#
Bidens involucrata	#
Boltonia latisquama	####
Erigeron canadensis	##
Erigeron ramosus	##
Eupatorium altissimum	##
Eupatorium urticaefolium	##
Euthamia camporum	####
Galinsoga ciliata	#
Grindelia squarrosa	####
Helianthus annuus	###
Helianthus salicifolius	###
Helianthus rigidus	###
Helianthus strumosus	###
Helianthus trachelifolius	###
Heliopsis scabra	###
Iva ciliata	###
Lactuca pulchella	##
Lepachys columnifera	##
Lepachys pinnata	##
Liatris pycnostachya	####
Liatris punctata	####
Liatris aspera	####
Mesadenia atriplicifolia	####
Pyrrhopappus carolinianus	##
Senecio plattensis	##
Silphium speciosum	####
Silphium laciniatum	####
Solidago canadensis gilvocanescens	#####
Solidago Lindheimeriana	####
Solidago rigidiuscula	####
Solidago rigida	####
Vernonia fasciculata	###
Actinomeris alternifolia	###

The secretions of the above-and below-ground stems are principally in the canals, but small globules are found dispersed in all of the living tissues. If the stem has chlorenchyma the globules are abundant, as in the leaf. The frequency and size of the canals in the stems of the different species indicate the relative amounts of secretion.

Roots have the least amount of the secretion of any of the plant parts. Certain species are outstanding for their large canals and abundant secretions, such as species of Solidago and Helianthus.

Evidence of the nature of the secreted materials within the various parts of the plants has been sought for by various microchemical tests. The microchemical tests have been found altogether satisfactory on account of the relatively small size of the globules present.

Chemically different substances have been demonstrated: fats, ethereal oils, resins and caoutchouc, all staining red with Scarlet R. A fat is an ester of glycerol with one or more of the higher fatty acids. Essential, or ethereal, oils consist of a mixture of hydrocarbons, mostly terpenes, together with alcohols such as terpeneol and camphors. The chemistry of resins is not nearly as well known as that of fats and ethereal oils. Resin according to Tschirch (1934) is neither a chemical nor a physical term applied to any specific substance but is one of common usage, as is the term tannin, being applied to a group of similar substances. Wiesner (1927) considers resins as an excreted product resulting from the plant's metabolism. Chemically, resins are considered very complex substances formed by a combination of linkages of various kinds, the majority of which contain phenol groups, aliphatic acids, aldehydes and terpenes.

The microchemical tests have been carried on only with fresh materials. After using Scarlet R for the differentiation of the contents occurring in the canals and other parts, relative solubility tests were employed. These alone may not be considered sufficient to distinguish between fats, resins, ethereal oils and caoutchouc but do serve for a major part in making this distinction possible. The solvents used were alcohol, acetone, chloroform, acetic acid, carbon disulphide and benzene. Any of these solvents may dissolve various resins, alcohol is a solvent for but very few fats while chloroform and carbon disulphide are well known fat solvents. Caoutchouc is insoluble in acetone but soluble in benzene. Wiesner

(1927) speaks of "Harze" as being distinguished from caoutchouc and guttapercha through the fact that resin and resin-like materials are soluble in alcohol and acetone while the other two are insoluble. For further distinction between fats and resins I have used the saponification test for fats. Moenike (1924) considered this to be the most critical test for fats. For this test I used a concentrated solution of KOH in methyl alcohol which has been found to produce myelin bodies within five to ten minutes with any of the more common plant oils, such as castor bean seed oil, cocoanut oil, palm oil and others. This reagent taken from Tunmann (1913) is superior to other saponification tests in the speed of the reaction. This test has been carried on with sections first treated with Scarlet R to increase the visability of the secretions and also with exuded "juice" carrying dispersed globules which were stained red with Scarlet R. Ethereal oils have been tested for, in addition to the solubility test of acetic acid, by using micro-distillation. These tests, in conjunction with the tabulated solubility tests point to the fact that the secretions are resinous in their chemical nature. The presence of caoutchouc which has been found to occur in a number of the examined plants was made certain by observing the solubility. That is, when the substance was stained red with Scarlet R and was non-saponifiable but was insoluble in acetone, but soluble in benzene, chloroform, alcohol or carbon disulphide, it was considered to be caoutchouc. A complete list of the plants with the solubility of their secretion follows:

Table V Showing Solubility of
Secretions Which Stain
Red with Scarlet R.

	Acetone	Benzene	Chloroform	Alcohol	Carbon disulphide	Acetic acid
Agoseris cuspidata (globules)	sol.	sol.	sol.	sol.	sol.	sol.
(latex)	insol.	sol.	sol.	insol.	sol.	insol.
Ambrosia trifida	sol.	insol.	sol.	insol.	sol.	insol.
Amphiachyris dracunculoides	insol.	sol.	insol.	insol.	sol.	insol.
Aster azureus	insol.	sol.	insol.	insol.	insol.	insol.
Aster Drummondii.	insol.	sol.	insol.	sol.	sol.	insol.
Aster ericoides	insol.	sol.	insol.	insol.	insol.	insol.
Bidens frondosa	insol.	insol.	insol.	sol.	insol.	insol.
Bidens involucrata	insol.	insol.	insol.	sol.	insol.	insol.
Boltonia latisquama	insol.	sol.	insol.	insol.	sol.	insol.
Erigeron ramosus	insol.	sol.	sol.	insol.	sol.	insol.
Erigeron canadensis	insol.	insol.	sol.	insol.	sol.	insol.
Eupatorium altissimum	sol.	sol.	p. sol.	sol.	p. sol.	insol.
Eupatorium urticaefolium	sol.	sol.	sol.	sol.	sol.	insol.
Euthamia camporum	sol.	sol.	sol.	sol.	sol.	insol.
Grindelia squarrosa.	sol.	insol.	sol.	sol.	sol.	insol.

	Acetone	Benzene	Chloroform	Alcohol	Carbon disulphide	Acetic acid
Helianthus annuus	sol.	insol.	sol.	sol.	sol.	insol.
Helianthus salicifolius	insol.	sol.	insol.	insol.	sol.	insol.
Helianthus strumosus	sol.	sol.	p. sol.	sol.	sol.	insol.
Helianthus trachelifolius	sol.	insol.	sol.	sol.	sol.	sol.
Heliopsis scabra	sol.	sol.	sol.	sol.	sol.	insol.
Iva ciliata	insol.	insol.	sol.	insol.	sol.	insol.
Lactuca pulchella (globules)	sol.	insol.	sol.	sol.	sol.	sol.
Lactuca pulchella (latex)	insol.	sol.	sol.	insol.	sol.	insol.
Lepachys pinnata	Insol.	sol.	p. sol.	insol.	sol.	insol.
Liatris pycnostachya	sol.	insol.	p. sol.	insol.	insol.	insol.
Liatris aspera	sol.	insol.	sol.	sol.	sol.	sol.
Mesadenia atriplicifolia	insol.	sol.	insol.	insol.	sol.	insol.
Pyrrhopappus carolinianus (globules)	insol.	sol.	sol.	sol.	sol.	insol.
Pyrrhopappus carolinianus (latex)	sol.	insol.	sol.	sol.	sol.	sol.
Senecio plattensis	sol.	insol.	sol.	insol.	p. sol.	insol.

	Acetone	Benzene	Chloroform	Alcohol	Carbon disulphide	Acetic acid
Silphium speciosum	sol.	insol.	insol.	insol.	sol.	insol.
Silphium laciniatum	sol.	insol.	sol.	sol.	insol.	insol.
Solidago canadensis gilvocanescens	insol.	sol.	p. sol.	insol.	sol.	insol.
Solidago Lindheimeriana	insol.	sol.	p. sol.	insol.	sol.	insol.
Solidago rigidiuscula	insol.	sol.	p. sol.	insol.	sol.	insol.
Vernonia fasciculata	sol.	sol.	insol.	sol.	insol.	sol.

Table VI

Chemical Nature of Secretion Based upon Solubility Tests.

Agoseris cuspidata	(globules)	Resinous
	(latex)	Caoutchouc
Ambrosia trifida		Resinous
Amphiachyris dracunculoides		Caoutchouc
Aster azureus		Caoutchouc
Aster Drummondii		Caoutchouc
Aster ericoides		Caoutchouc
Bidens frondosa		Resinous
Bidens involucrata		Resinous
Boltonia latisquama		Caoutchouc
Erigeron canadensis		Resinous
Erigeron ramosus		Caoutchouc
Eupatorium altissimum		Resinous
Eupatorium urticaefolium		Resinous
Euthamia camporum		Resinous
Grindelia squarrosa		Resinous
Helianthus annuus		Resinous
Helianthus salicifolius		Caoutchouc
Helianthus strumosus		Resinous
Helianthus trachelifolius		Resinous
Heliopsis scabra		Resinous
Iva ciliata		Resinous
Lactuca pulchella	(globules)	Resinous
	(latex)	Caoutchouc
Lepachys pinnata		Caoutchouc
Liatris aspera		Resinous
Liatris pycnostachya		Resinous
Mesadenia atriplicifolia		Caoutchouc
Pyrrhopappus carolinianus		Resinous
Senecio plattensis		Resinous
Silphium speciosum		Resinous
Silphium laciniatum		Resinous
Solidago canadensis gilvocanescens		Caoutchouc
Solidago rigidiuscula		Caoutchouc
Solidago rigida		Caoutchouc
Vernonia fasciculata		Resinous

In following the development of a number of species in their primary permanent tissue stages it has been observed that the majority of the young plants do not contain the dispersed globules in their parenchymatous tissues typical of the more mature plants. However, the canals did contain secretion during the formation of the primary meristematic tissues.

Considerable difference in time of formation of the dispersed globules so typical of the mature leaf mesophyll has been noted for several species. For this purpose plants of Silphium laciniatum and speciosum, Chrysanthemum leucanthemum and Helianthus strumosus were grown in the greenhouse. The plant of Chrysanthemum leucanthemum when brought in from the field had a large group of basal leaves, but these contained no globules. Formation of globules occurred soon after the plant had produced its first flowers. The plant of Helianthus strumosus grew to a height of five feet and was ready to produce flowers when globules began to appear in the leaf mesophyll. Silphium laciniatum produced a number of large basal leaves without having the dispersed globules until after three weeks. Silphium speciosum grew approximately two feet tall before globules were observed. In each of the latter two cases globule formation occurred considerably ahead of flower formation.

Similar observations were made of these species when they grew in the field which gave comparable results.

Possible functions of these secretions in the plant are not evident. To consider that they actually serve as a reserve substance later used in the plant's metabolism might seem justified by the large quantities formed. However, dead parts, especially the leaves of certain species, when examined microchemically exhibit an abundance of the secretion remaining. Species showing this were Solidago canadensis gilvocanescens, Boltonia latisquama, Helianthus salicifolius, Solidago rigida, Euthamia camporum, Mesadenia atriplicifolia, Liatris aspera and pycnostachya. Lloyd (1932) in discussing possible uses of caoutchouc to the plant says that whether the hydrocarbon in question is, in the case of the guayule, actually a reserve substance and is actually made use of in metabolism requires proof which has not yet appeared. That the presence of the globules in the leaves might serve in drought resistance has been suggested by Transeau (1904). Lloyd (1932) says that the view which has been advanced from time to time, that caoutchouc in the guayule confers on the plant some ability to withstand drought, has no convincing evidence.

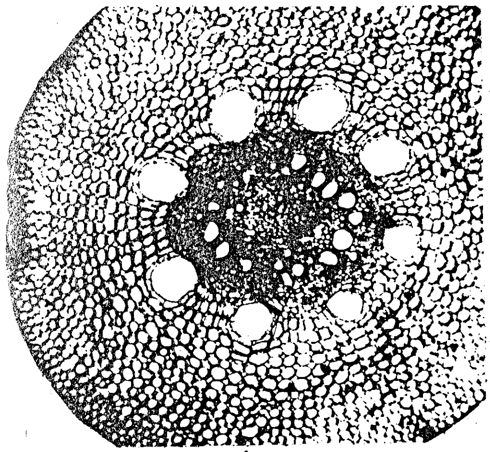
In an attempt to determine if the globules would disappear when the plant was starved indicating their being used in metabolism, young and old plants were brought in and placed in the dark. The young plants were taken from the field just after the first evident globule formation. The globules remained in the older plants but disappeared from the younger plants. Plants showing this were Mesadenia atriplicifolia, Liatris aspera, Helianthus strumosus, rigidus and Solidago canadensis gilvocanescens.

PLATE I

Photomicrographs of Root Cross Sections.

X76

1. Solidago rigidiuscula.
2. Ambrosia trifida.
3. Actinomeris alternifolia.
4. Helianthus strumosus.
5. Silphium speciosum (old root).
6. Mesadenia atriplicifolia.



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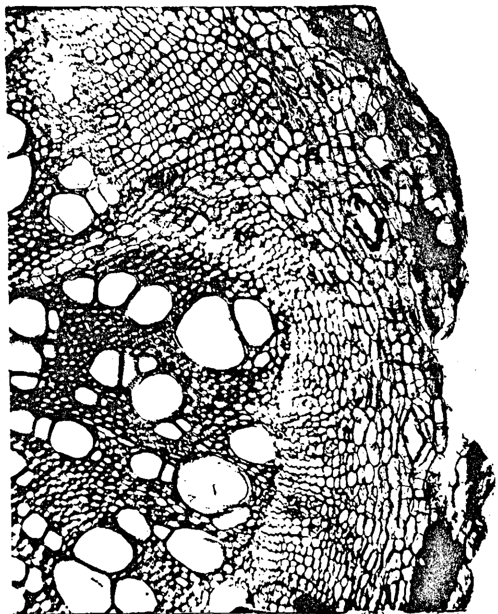

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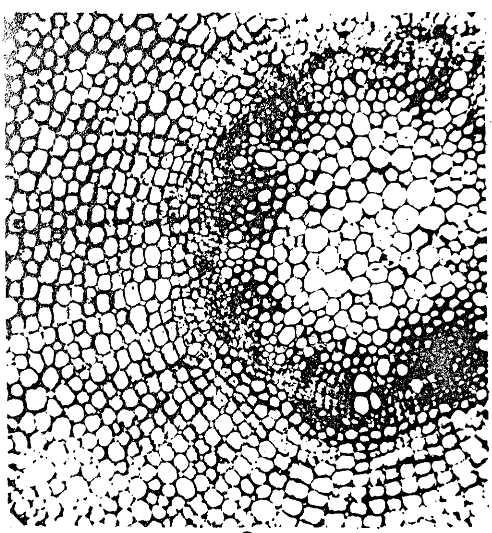

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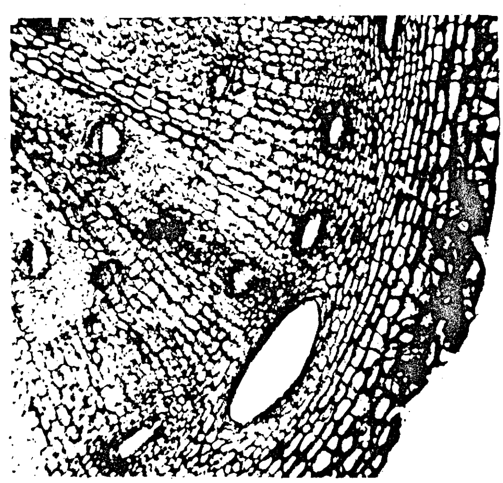

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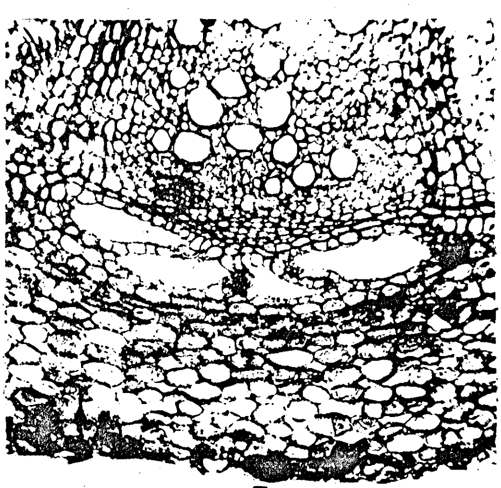

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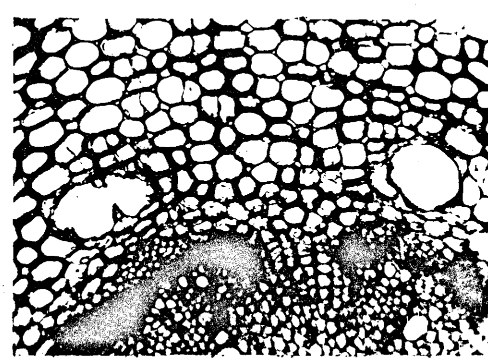

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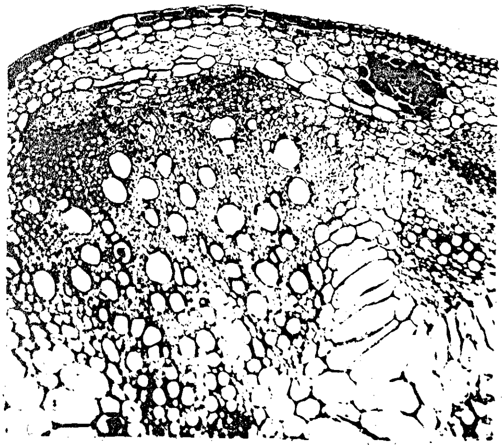
PLATE II

Photomicrographs of Stem Cross Sections.

1. Bidens frondosa X 76.
2. Helianthus rigidus X 150.
3. Helianthus rigidus X 76.
4. Solidago rigidiuscula X 76.
5. Helianthus strumosus X 76.
6. Mesadenia atriplicifolia X 76.



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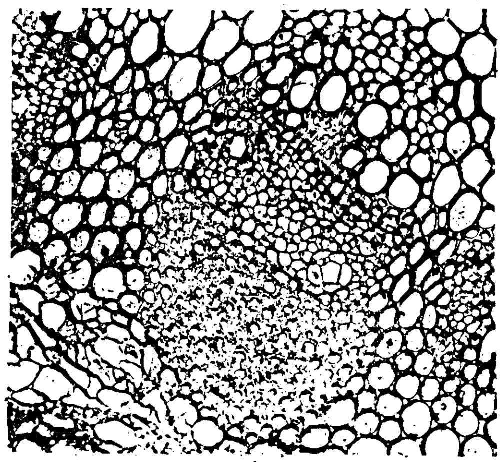

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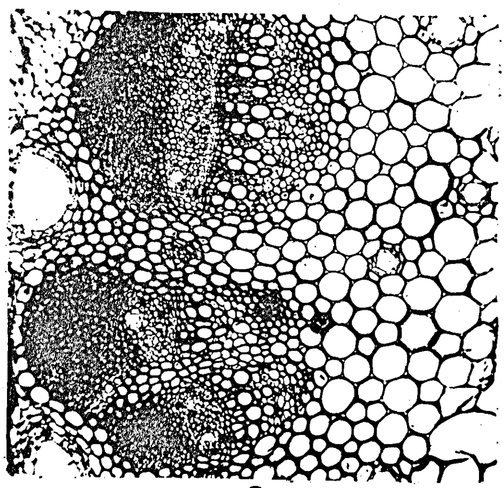

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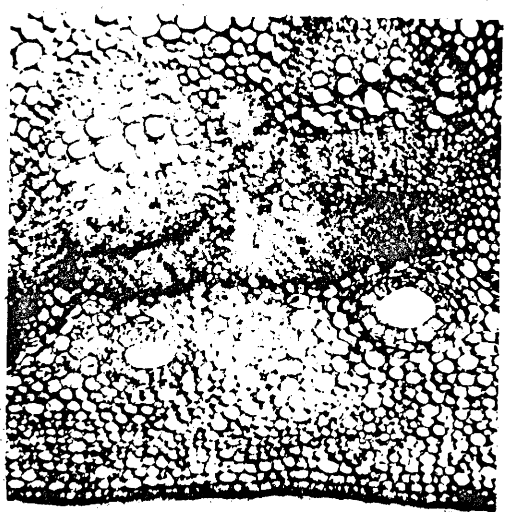

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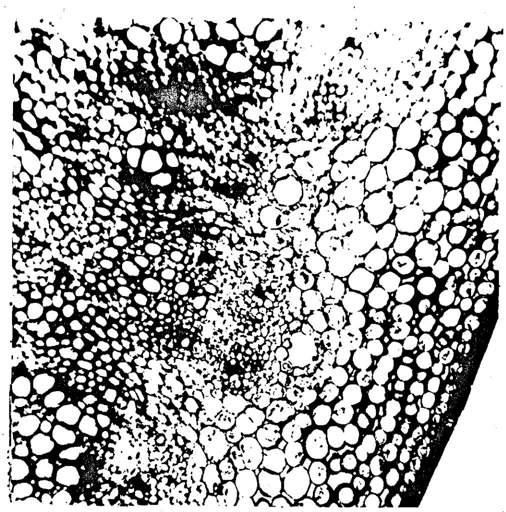

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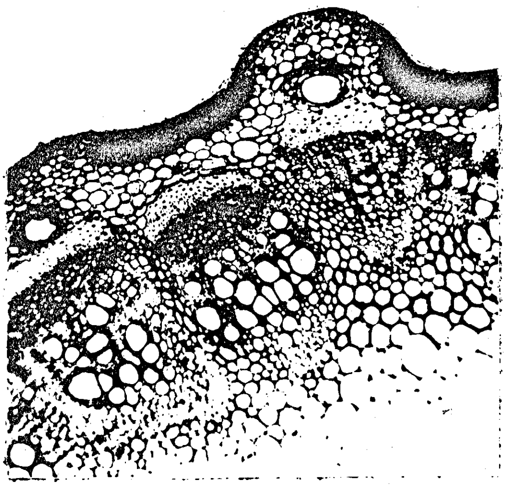
PLATE III

Photomicrographs of Stem Cross Sections.

X76

1. Erigeron canadensis.
2. Pyrrhopappus carolinianus.
3. Lepachys pinnata.
4. Lactuca pulchella.
5. Ambrosia elatior L.
6. Silphium speciosum.



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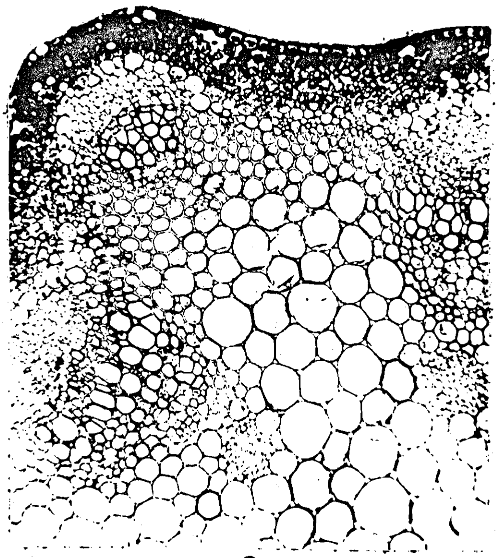

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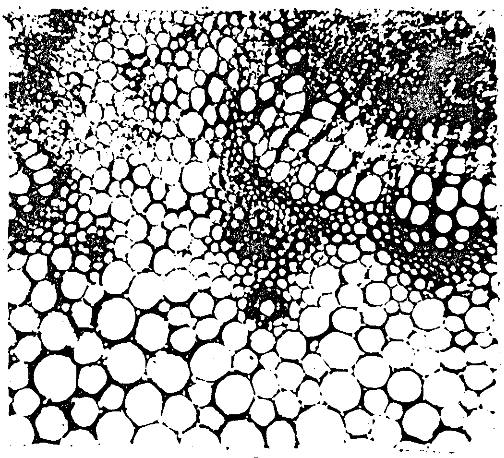

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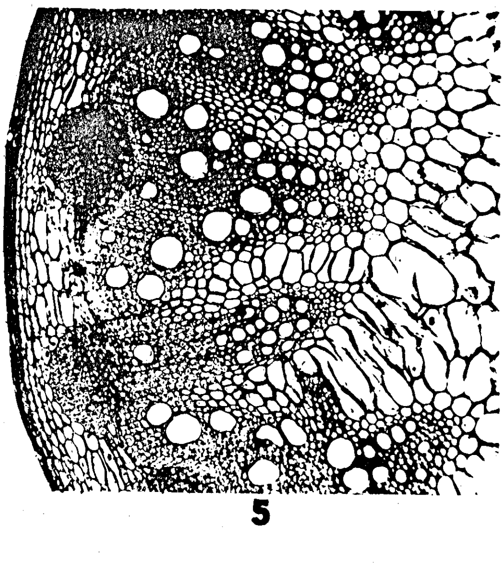

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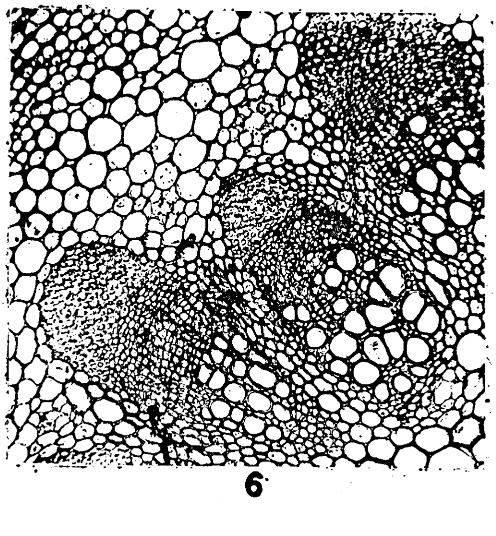

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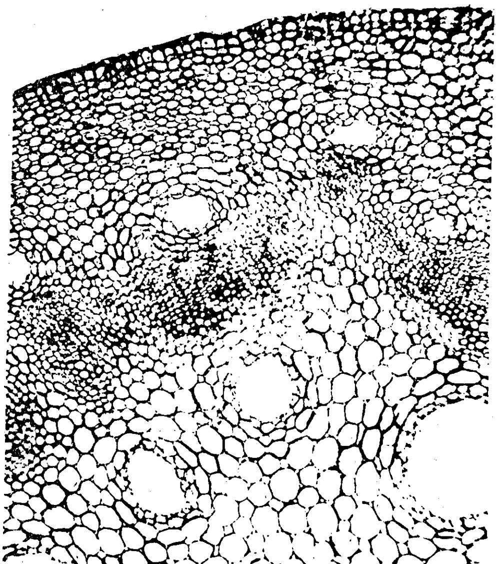
PLATE IV

Photomicrographs of Rhizome Cross Sections.

X76

1. Solidago canadensis gilvocanescens.
2. Silphium speciosum.
3. Helianthus rigidus.
4. Helianthus strumosus.
5. Liatris pycnostachya (corm).
6. Actinomeris alternifolia.



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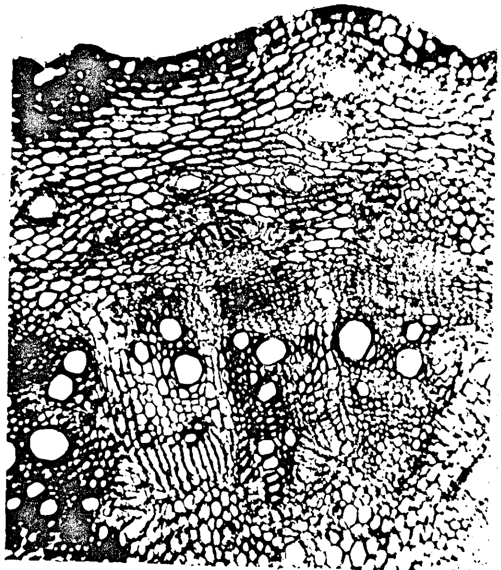

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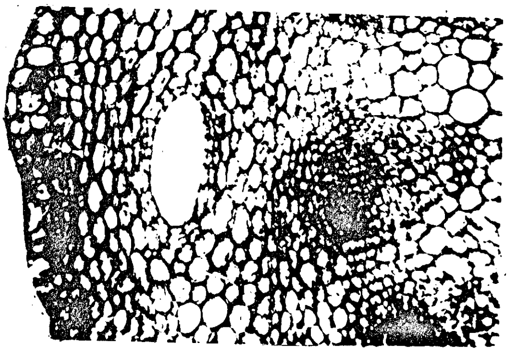

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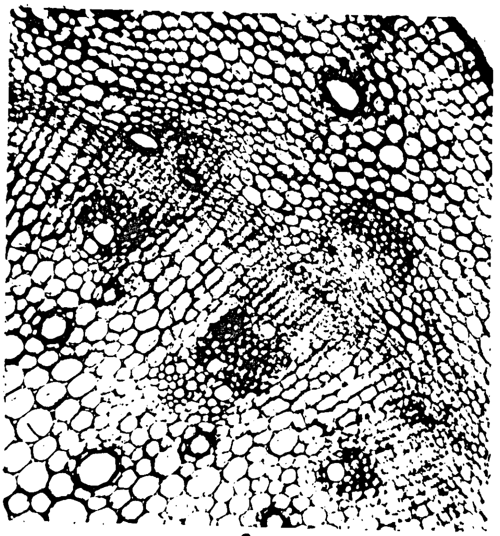

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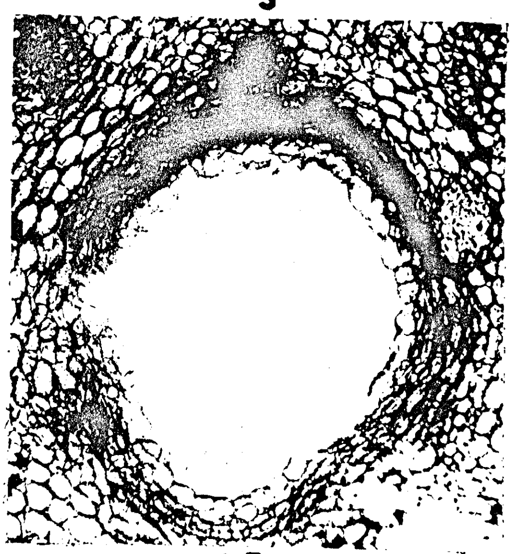

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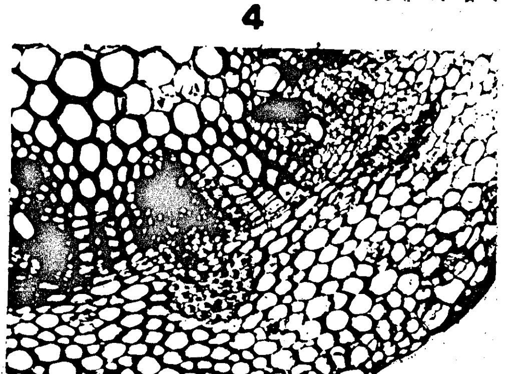

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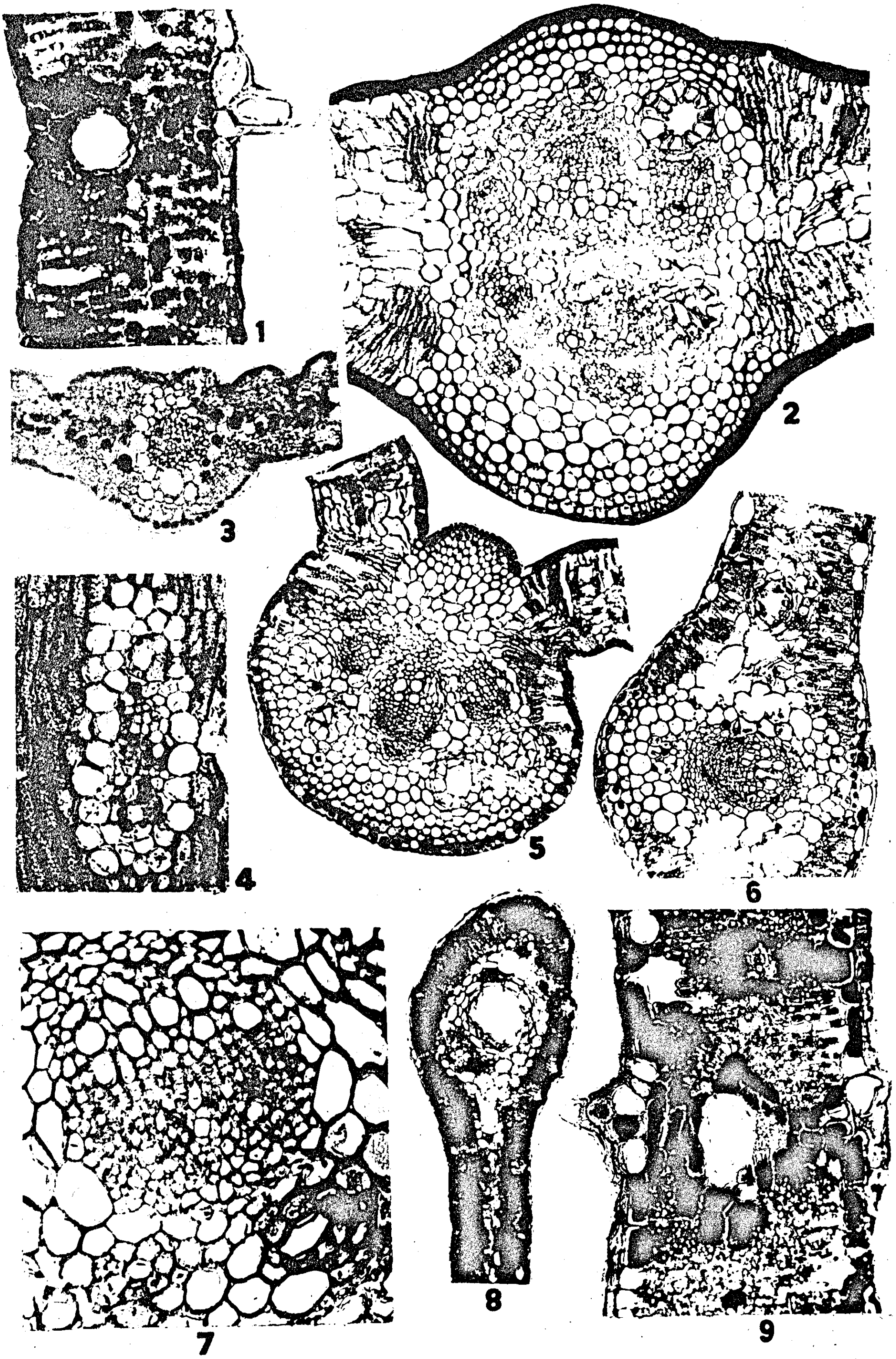
PLATE V

Photomicrographs of Leaf Cross Sections.

1. Solidago canadensis gilvocanescens X 76.
2. Silphium laciniatum X 76.
3. Amphiachyris dracunculoides X 76.
4. Silphium laciniatum X 150.
5. Helianthus salicifolius X 76.
6. Boltonia latisquama X 76.
7. Helianthus rigidus X 76.
8. Erigeron canadensis X 76.
9. Solidago rigidiuscula X 76.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