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Title   Comparative Anatomical Study of Three Species of Microseris

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Three growth forms of the genus Microseris, of the tribe Cichorieae, family Compositae, were compared with respect to their anatomical structure. The purpose of this study was to clarify lines of evolutionary specialization in the genus. Two of the three species studied, M. laciniata and M. borealis, are perennials, while the third, M. lindleyi is an annual.

Seedling development and primary growth of the root is essentially similar in all three species. There are two groups of initials in the root apex; the upper group giving rise to the stele and the lower group differentiating into the rootcap, epidermis and cortex.

Differences occur in secondary growth of the primary root. The cortex is persistent in all three species. Microseris lindleyi produces a relatively large amount of secondary xylem in relation to secondary phloem. The cambium consists largely of fusiform initials and some non-typical fusiform initials. Definite ray initials were not observed. Outwardly, the cambium derivatives differentiate into

storage parenchyma in which phloem strands are embedded. A phloem strand consists of sieve tubes, companion cells, phloem parenchyma and laticifers. The secondary xylem consists of both tracheids and vessels, both with scalariform to pitted lateral walls and the latter with simple perforated end-walls, thick-walled fibers, appearing only in the later part of secondary growth, and xylem parenchyma. The two perennials, M. laciniata and M. borealis have fleshy roots which consist largely of storage parenchyma, in which the phloem strands are arranged in concentric rings. Here also there are connections between most of the phloem strands of each ring by means of anastomosing laticifers but not between those of different rings. The secondary xylem is scanty, and consists of tracheids, vessels and xylem parenchyma. The vessels are arranged more or less in radiating rows which correspond with the location of phloem strands in the storage parenchyma. Both perennials produce adventitious roots that replace the primary root. Their anatomical structure differs from that of the primary root in that there are more than two protoxylem ridges, and there is a pith present. The adventitious roots show transverse wrinkling in the upper regions as a result of contraction. In the primary root, contraction is indicated primarily by folding of the Casparian strips, and is not obvious externally.

All three species possess a one-layered tunica in the shoot apex. Aerial stem structure was described only for M. lindleyi and

M. laciniata. The rosettes of the perennials form a primary thickening meristem which accounts for much of the increase in diameter of the stem of the rosette stage. In all three species, the stem is a eustele. Vascular bundles are always bordered at their outer margins by laticifers which are the first elements to mature in a procambium strand. In M. laciniata, a ring of phloem strands or medullary bundles develops at the inner periphery of the vascular cylinder. These phloem strands consist of sieve tubes, companion cells, phloem parenchyma and laticifers. Xylem elements may be differentiated at a later stage, and secondary growth may occur also.

This work suggests M. lindleyi as the most advanced species because of its woodiness, alternate leaf position, absence of medullary bundles in addition to morphological and chromosomal features described by previous workers. Among the two perennials, M. borealis is more advanced over M. laciniata because of the horizontal rootstock and the absence of medullary bundles. M. laciniata is considered to be closest to the putative common ancestor than any of the two other species.

COMPARATIVE ANATOMICAL STUDY
OF THREE SPECIES OF MICROSERIS

by

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INTRODUCTION

The family Compositae has for a long time attracted attention

as a well marked plant group with many distinct characters. Its mem-

bers are widely distributed in a variety of habitats and possess a

variety of growth forms. There is a need for a more natural and

phylogenetically accurate classification than the existing one, and

many members of this family have been used in a series of investiga-

tions toward this goal. Newer information from genetics, cytology

and distribution can be combined with the more classical method

based on morphology to produce a natural classification and in this

way give an insight to their relationship and evolution. Babcock (5)

has made a study of the phylogeny in the genus <u>Crepis</u> in which infor-

mation from the above mentioned disciplines was taken into considera-

tion.

The distribution of a plant depends on environmental adaptations,

among which is habit morphology. Knowledge of the growth forms in

closely related taxa, together with information on environmental con-

ditions during the evolutionary history of the taxa, would therefore

contribute to an understanding of the course of evolution in the plants

studied. In the Compositae, many genera exhibit variation in growth

form (11, p. 207; 55), among them the genus Microseris, of the tribe Cichorieae. The species groups in Microseris that have different growth forms were given the rank of subgenera (11, p. 215), i.e. subgenus Scorzonella, subgenus Apargidium and subgenus Microseris. The growth forms represented by these subgenera exhibit varying degrees of specialization in morphological characters. The least specialized species of Microseris are found in the subgenus Scorzonella. They are perennials and have thick biennial adventitious roots from a vertical rootstock. Another relatively little specialized species is the sole member of the subgenus Apargidium. This is a perennial and forms adventitious roots from a short rhizome. The species with more advanced characters are found in subgenus Microseris and are annuals with fibrous roots.

The purpose of this paper is to study the developmental anatomy of three growth forms in the genus Microseris. In this study, the anatomical structures will be compared and correlated with other features, such as cytotaxonomy, necessary for establishing a more accurate natural classification. The three plants studied were selected for two reasons. First, the plants belong to the same genus and are therefore closely related species. Second, the three plants show morphological differences resulting from adaptation to different habitats, and therefore a comparative anatomical study will be useful in clarifying the directions of evolutionary specialization in the genus.

Although the approach of such a problem is both comparative and evolutionary, this work will deal principally with the comparative aspects.

The observations were limited to the anatomical structure of vegetative portions of the plant. No attempts were made to investigate the floral pattern. The main objective of this study was to determine the developmental anatomy of the primary and secondary tissues of the roots and stems. Special reference is made to the laticifers which are an important characteristic for the tribe Cichorieae in general.

All three species grow in Northwestern United States, and are handsome plants with yellow dandelion-like flowers. The morphological characters of the three species of Microseris are listed below, taken from the descriptions by Chambers (12) and Hitchcock, et al. (27, p. 93, p. 260, p. 267).

1. Microseris laciniata (Hook.) Sch. Bip.

This species is a representative of the subgenus Scorzonella. The plants are rather coarse perennial herbs which may become 1-8 dm. tall in the field. The leaves form a rosette and are entire to deeply pinnatifid. The flowers are in solitary heads terminating the naked or subnaked branches. Pale, fleshy, biennial adventitious roots are produced

from the caudex, which forms a vertical rootstock.
The plants grow commonly in moist meadows and some-
times on drier slopes. They are found from Washing-
ton to California, from the east foothills of the Cascade
Mountains to the coast.

2. Microseris borealis. (Bong.) Sch. Bip.

This is the sole member of the subgenus Apar-
gidium. The plants are glabrous perennials growing
1-5 dm. tall in the field. The basal leaves are in a
rosette and are 5-25 cm. long and 2-12 mm. wide. The
flowers are in solitary heads on naked scape-like
peduncles. Adventitious roots produced by the caudex
may persist considerably longer than two years. Each
root arises near the base of an older leaf and is asso-
ciated with a shoot developing in the leaf axil. Roots
and shoots originate from a short, horizontal rhizome.
The plants grow usually in sphagnum bogs and wet
meadows from the coast of southern Alaska to western
California. They do not occur east of the Cascade
Range.

3. Microseris lindleyi. (DC.) Gray

This species belongs to the subgenus Micro-
seris. The plants are villous or sometimes puberulent

annuals. In the field the plants will grow 1-6 dm. tall. The leaves may be 15-20 cm. long, and are entire or linearly lobed. The heads are solitary on naked peduncles that terminate the branches. The root system consists of a short distinct taproot with numerous fibrous lateral roots. The plants grow in dry, open places in the valleys, foothills and plains, in western Idaho and southeastern Washington to southern California, Utah, Arizona and New Mexico.

LITERATURE REVIEW

The previous notes in this paper referring to the three species

of Microseris were concerned with their morphological descriptions

in relation to taxonomical arrangement in the Compositae. Interests

of various taxonomists in this highly variable group of plants resulted

in repeated reclassification as more and more information became

available. According to Chambers (11, p. 209), the genus Microseris,

established by David Don in 1832, was placed by Hooker and Arnott in

Lessing's subtribe Hyoseridae on the basis of its naked receptacle

and a pappus which was either coroniform or of broad paleae. Ben-

tham in 1873 (7), placed Scorzonella in the subtribe Scorzonereae and

Apargidium in the subtribe Hypochoeridae. Hoffmann in 1894 (27),

placed Microseris in his subtribe Cichorieae, based on its paleaceous

pappus, while Apargidium was classified into the subtribe Crepidiinae.

According to Stebbins (49, p. 68), the overemphasis which these

early authors placed on pappus characteristics led to the artificial

separation of genera such as Microseris, Apargidium and Agoseris,

which are similar in many respects. From his chromosome study

(49, p. 47), he concluded that these genera are closely related. A

more natural and phylogenetically significant classification was pro-

vided by Chambers' monograph (11), in which Scorzonella, Apargidi-

um and Microseris are put in a single genus, Microseris, on the

basis of pubescence, growth habit, involucres and fruit. In a later paper, Chambers (12) proposed that Microseris linearifolia replace the name M. lindleyi, but this suggestion need not be followed (Chambers, personal comm.). Peck (36, p. 705, 706) recognized as genera the three subgenera of Chambers' classification.

While the nomenclature has been the object of intensive study, no anatomical descriptions have been published on species of Microseris. A short note concerned with the pappus of M. linearifolia was given by Brandegee (8). The absence of literature pertaining to the anatomical structures of Microseris makes necessary a review of work on anatomical features found in other members of the Cichorieae or in the Compositae in general.

Seedling anatomy has been studied for some members of the Cichorieae, including Tragopogon porrifolius (23), Taraxacum kok-saghyz (3, 43), Lactuca sativa (Port 1937 in 24), and Cichorium intybus (29). Seedling anatomy for other members of the Compositae have been published, such as Cynara scolymus (39) and Parthenium argentatum (2). Description of the transition region has been given for Tragopogon porrifolius (23) of the Cichorieae, and for other Compositae such as Helianthus annuus and Arctium minus (45) and Arctium majus (32). Secondary growth was described for Taraxacum kok-saghyz (3, 45) and Cichorium intybus of the Cichorieae, and also for Parthenium argentatum (2), another member of the Compositae.

The laticifers in the Cichorieae have been described many times in certain plants because their product is commercially important. Dippel (17) described the laticifers of the Cichorieae in general, and Scott (44) gave a literature review on these structures and also described the formation and arrangement of the laticiferous system in Tragopogon and Scorzonera. Many Russian workers concerned themselves with the laticiferous system in Taraxacum kok-saghyz when it became necessary to find a native rubber-producing plant as a substitute for rubber from tropical sources. A review of these studies is given by Krotkov (31). Among others, Savchenko (43) and Artschwager and McGuire (3) were particularly interested in the laticifers in Taraxacum kok-saghyz.

The stem of Scorzonera was studied by Peter (37), while Worsdell (59) was concerned with the origin and significance of medullary phloem which included studies in Tragopogon porrifolius stem. The stem of Cichorium intybus was described by Knobloch (30).

Carlquist (10) studied the woody Cichorieae and found some evidence for the assumption that herbaceous Cichorieae originated from extinct woody ancestors, but that the present woody species have evolved secondarily.

MATERIAL AND METHODS

The main portion of the material used for this investigation was grown in the greenhouse. Field samples of mature plants were collected only at certain times and were used for comparison with the greenhouse material. Seeds of the three species of Microseris studied were kindly provided by Dr. K. L. Chambers, Curator of the Herbarium at Oregon State University. The seeds were sown in a soil mixture composed of equal amounts of soil, sand, peatmoss and pyrrilite. Two or three weeks after germination, seedlings to be used for later development were transplanted into pots 13 cm in diameter where they were grown until the time of collection. For early stages of the seedling, seeds were germinated on moist filter paper in Petri dishes.

Portions of plants of different ages were killed and fixed in Randolph's modified Navaschin fluid (28, p. 45), where they remained for 12 - 24 hours. Air was evacuated from the tissues immediately after immersion in the killing and fixing solution. Material processed in this manner was then washed in running tapwater for two hours, dehydrated in a tertiary butyl alcohol-paraffin oil series according to Johansen's schedule (28, p. 130-132) and embedded in Tissuematt of 54-56°C. melting point. In the later period of investigation, a new embedding medium, Paraplast, of 55-57°C

melting point was used. Prior to sectioning, the paraffin blocks of embedded material were trimmed down, especially at one end close to the material, and left in a softening solution consisting of water, glycerin and Dreft (1) at 38°C. Three to five days were needed to soften tissues with a small amount of lignification, but the fairly woody roots and stems of M. lindleyi were soaked for two weeks. The soaked material was either sectioned immediately or kept in storage in the refrigerator until needed. Sections of the primary root and shoot tissues were cut 7-9 microns in thickness and other sections were cut at 12μ. The sections were stained either by a progressive iron haematoxylin and safranin procedure, or by safranin and chlorosol black E, and mounted in a synthetic resin.

Entire seedlings to be cleared were aspirated in a 5% sodium hydroxide solution, followed by a thorough rinsing in water, and passed through a dehydration series of ethyl alcohol and finally stored in xylene. These cleared seedlings were useful in facilitating recognition of the transition region prior to sectioning.

OBSERVATIONS

The early stages of growth of the seedling, especially early

root development, are very similar in the three species studied.

Therefore, seed germination, primary root histogenesis, develop -

ment of lateral roots, and the manner of transition from a root type

vascular system into that of the cotyledons will be described at the

same time for all three species. Most of these descriptions will

pertain to Microseris borealis in particular. Where minor differ-

ences are present, reference is made to the other species. The

illustrations, also, are taken primarily from M. borealis with a

few additional ones from the other species. The remaining portions

of the plants will be described separately for each species.

Morphological Development

The fruit of Microseris is an achene. Under suitable con-

ditions for germination the primary root breaks through the pericarp

and grows downward. The hypocotyl then elongates and carries the

stem tip and cotyledons upward. The pericarp may remain cover-

ing the cotyledons for a short while. The growth of the hypocotyl

at first exceeds that of the primary root, but this is only temporary

and the root soon becomes longer than the hypocotyl. In appearance,

the hypocotyl of M. lindleyi is longer and more slender than that of

the other species. There is an abrupt increase in diameter of the

hypocotyl at the dividing line between the hypocotyl and the radicle

portion of the seedling. The cotyledons are linear and taper into a

point in M. lindleyi. In M. borealis and M. laciniata they are not

as narrow and are lobed at the tip. The cotyledons function as

photosynthetic organs and have a single layer of short palisade cells.

The cotyledons in M. lindleyi are soon followed by the first true

leaves, whereas in the other species a longer time elapses before

these are developed.

In all species the first true leaves are perpendicular in posi-

tion to the plane through the cotyledons. They are elongate and en-

tire in all species, but subsequent leaves may be lobed. During the

first three or four weeks there is little increase in length of the

slow growing stem in M. lindleyi so that a definite rosette soon de-

velops. Subsequent internodes become longer and an aerial stem is

established (Figure 3). The aerial stem may form as many as

13 internodes prior to flowering. Lateral branches may develop

from some of the nodes after the first flowering, on which terminals

other flowers are produced. Soon after the first flower sets seed,

however, the plant withers and dies. The taproot remains short,

small in diameter and produces many lateral roots, which become

very long and intertwine with each other to form a fibrous root sys -

tem. The taproot may reach two mm. in diameter just below the

hypocotyl, but tapers down rapidly so that most of the primary root appears filiform.

The two other species, which are perennials, formed only a rosette in the greenhouse material studied, with the leaves in a distichous arrangement. An aerial stem was observed in the field material of M. laciniata. The hypocotyl and the upper portion of the root in these perennials increase considerably in diameter and become fleshy. Diameter of specimens grown in the greenhouse may reach six mm. After the first growing season, one or more adventitious roots develop at the base of the stem in the vicinity of an old leaf scar (Figure 2).

In M. borealis (Figures 1A, 1B), additional adventitious roots may develop. All adventitious roots are, in the beginning, slender whitish structures which later become fleshy and function as storage roots. During the subsequent growing periods these replace the primary root. At this stage, the primary root persists at the end of a short, horizontal rhizome as a wrinkled, nonfunctional structure. Meanwhile, buds in the axils of the leaves develop into new shoots. Dormant adventitious root primordia are present that develop when conditions are suitable. An old plant of M. borealis thus will consist primarily of many shoots and adventitious roots on a short horizontal rhizome. In M. laciniata (Figure 2), similar additional adventitious roots may develop but in smaller numbers. Each root

functions for two years, after which reserve foods are withdrawn and the root dies.

For all three species, external evidence for root contraction of the primary root is not distinct. In the two perennials, however, the upper portions of adventitious roots show a definite external wrinkling.

Primary Root

During the first stages of root development, two large initial cells are found at the root apex (Figures 4, 5). During later development, these cells rapidly divide transversely thus giving rise to two somewhat indistinct groups of initials. Cells of the lower group divide transversely, contributing cells to the rootcap immediately below the initials, and also laterally. Their derivatives divide repeatedly to produce the cortex, the protoderm and the lateral flanks of the rootcap. Since the protoderm is established repeatedly by different cells, it appears as a stepped, somewhat irregular layer.

The rootcap is composed of slightly elongated cells that are often filled with many oil droplets, but starch grains are rarely present. The peripheral cells of the rootcap develop an increased amount of oil droplets, the walls become suberized and the cells finally die.

Cells of the innermost layer of the immature cortex undergo

predominantly periclinal divisions resulting in a seven- or eight-layered cortex. Cell divisions occur more frequently adjacent to the protophloem. The cortical cells are isodiametric at the beginning, but, as growth proceeds, the cells elongate and also enlarge tangentially. The formation of the relatively broad cortex by divisions in the innermost layer is largely responsible for the radiate arrangement of the cortical cells. The innermost cell layer then ceases to divide and differentiates into a thin walled endodermis. The endodermis is occasionally biseriate opposite the phloem (Figure 10). Casparian strips are differentiated only after lignification of the first protoxylem elements. The vacuolated cortical cells in the region of elongation are difficult to kill and fix and usually collapse during fixation. The outermost cortical layer, however, appears to be suberized and the cells often retain their shape. This is the only indication of an exodermis in the root.

The meristematic central cylinder is clearly demarcated from the immature cortex close to the initial region (Figure 8). Divisions in this region occur at first in three dimensions, then become predominantly transverse and longitudinal. A one-layered pericycle soon becomes delimited from the remaining cells of the central cylinder (Figure 9). Its cells then divide anticlinally and keep pace with the increasing diameter of the central cylinder. Due to more frequent longitudinal divisions in the stele than in the cortex, the

cells of the central cylinder are of smaller diameter than those in

the cortex. Most of the divisions occur near the periphery of the

central cylinder in the primary phloem region and at the protoxylem

poles. Cells in the narrow strand of differentiating metaxylem

elements begin a rapid enlargement only a few cells back from the

initials. All primary roots observed were diarch.

The first primary phloem cells that can be distinguished are

the protophloem mother cells. These are just recognizable, at

approximately 119 μ above the root apex initials as two cells on

opposite sides of the stele adjacent to the pericycle. They are often

pentagonal in cross section (Figure 10). During differentiation the

cell walls become somewhat thicker and a large central vacuole de-

velops in the cytoplasm. The nucleus then degenerates and disappears.

The mature sieve tube element is pentagonal or diamond shaped in

cross section and stains lightly because of the thin, parietal sheet

of cytoplasm. The first sieve tubes mature at approximately 588μ

from the root initials (Figure 11). No companion cells are associated

with the protophloem sieve tube elements and sieve areas are found

only on endwalls. Obliteration of these sieve tubes occurs soon

after maturation by elongation of the surrounding cells.

Metaphloem in the root tip consists of sieve tube elements,

companion cells and phloem parenchyma. Each sieve tube element

is accompanied by a single companion cell of comparable length.

The transverse to oblique end walls of the short sieve tube elements show simple sieve plates, and no sieve areas were observed in the lateral walls. The phloem parenchyma exists as separate cells. Laticifers do not differentiate in the primary phloem region.

Approximately 686 µ above the root initials, a median plate of enlarged and vacuolated cells becomes discernible between the two protophloem regions. This plate is not confined to a single row of cells as adjacent cell series may show vacuolation and form a multiseriate plate with the original layer. The cells in general are graded in diameter from the pericycle toward the center. The first protoxylem cells mature at the terminal ends of the plate and adjacent to the pericycle at approximately 1866 µ above the root initials (Figure 12). The protoxylem elements are tracheids with annular and spiral secondary wall thickenings. The transverse to slightly oblique end walls do not show perforations. The metaxylem elements are vessel elements that generally develop scalariform to reticulate wall thickenings, and the end walls show simple perforations. The central metaxylem elements are still immature at the time vascular cambial activity is initiated, in some cases, but in most cases, maturation of metaxylem occurs prior to secondary growth (Figure 13).

Lateral Root

The first lateral roots of M. lindleyi arise as early as the third

day after germination, and in the perennials, after the second day in

the region immediately beneath the hypocotyl. They arise by cell

divisions in the pericycle opposite or slightly to the lateral sides of

the protoxylem. The divisions are at first periclinal, followed by

both periclinal and anticlinal divisions that expand the root primordi-

um. Cells of the endodermis undergo several anticlinal divisions,

and the new cells thus formed also develop Casparian strips. How-

ever, the endodermis is ruptured before the new root emerges from

the cortex. Penetration of the cortex appears to be primarily by

pressure since the cortical cells become crushed and there is little

evidence of enzymatic activity (Figure 6).

The meristematic cells derived from the pericycle are poten-

tially capable of differentiating the cortex and vascular cylinder of

the root primordium. The cortical tissue thus formed is increased

by repeated periclinal divisions of its innermost cell layer which

afterwards differentiates into an endodermis which becomes contin-

uous with the interrupted endodermis of the parent root, and differ-

entiates similar Casparian strips. By the time the lateral root

emerges from the cortex, an apical meristem similar to that of the

primary root is well organized. Subsequent development of primary

tissues is also similar to that of the primary root. The lateral roots are always diarch, with the protoxylem poles oriented parallel with the axis of the parent root. The epidermis of a lateral root is sloughed off very early and the exodermis becomes suberized. As in the parent root, the lateral root has a radiate arrangement of cortical cells. The endodermis shows Casparian strips and also appears to be biseriate in the regions opposite the phloem. The pericycle persists as a uniseriate layer in all parts of the root. Little or no secondary tissue is produced, and no periderm is differentiated (Figure 7). Thus the diameter of a lateral root is constant throughout its length.

The Transition Region

Transition from the diarch radial protostele of the root to collateral bundles leading to the cotyledons occurs throughout the hypocotyl, especially with regard to the primary phloem. Branching of the xylem plate, however, takes place in the uppermost part of the hypocotyl where the xylem changes rather abruptly from exarch to endarch. The greater portion of the hypocotyl is, therefore, more rootlike in its inner structure. Six day old seedlings were used to study the transition region because primary growth is not yet completed and there is little secondary growth at this stage. The process of transition is diagrammed in Figure 14.

The xylem appears as a continuous median plate at the base of the hypocotyl (Figure 14A). The protoxylem elements are situated immediately next to the pericycle, which is one cell thick in this region. The endodermis shows well developed Casparian strips. At successively higher levels parenchyma cells appear between the endodermis and the protoxylem, establishing a multiseriate pericycle.

Each phloem strand starts to differentiate laterally a short distance above the hypocotyl base and separates into four distinct strands at a somewhat higher level. These strands are arranged parallel to the xylem plate (Figure 14B). Cells at the inner sides of the phloem strands apparently part of the residual meristem, undergo divisions, giving a cross section of this region a square appearance (Figure 14B). Differentiation of the phloem elements takes place as described for those in the root. At this stage, a row of laticiferous cells appears at the outer sides of each phloem strand, followed by maturation of several sieve tubes in each strand. No laticiferous cells are differentiated opposite the protoxylem.

Meanwhile, there is a slight shift in the arrangements of the xylem elements. Parenchyma cells appear at the center of the xylem plate, and the metaxylem elements differentiate laterally from each protoxylem ridge (Figure 14C). This xylem arrangement continues through the greater part of the hypocotyl, in one case through

6-1/2 mm. of the approximately 8 mm. long hypocotyl. The two outermost of the four phloem strands on either side of the xylem plate gradually approach the protoxylem ridge (Figures 14C, D). The metaxylem elements continue to differentiate laterally and finally the xylem is oriented perpendicular to the former median plate (Figure 14D). The xylem ridges thus appear at the former protoxylem poles, leaving a large area of parenchymatous tissue in between. Each of these ridges, together with the approaching phloem strands, forms a "double bundle" as described by Thomas (52) (Figure 14E). Just below the insertion of the cotyledons the two phloem strands of each double bundle merge into one and the xylem ridges merge together somewhat higher up in the cotyledons, thus forming the collateral bundle of the median cotyledonary trace. The two central phloem strands on either side of the xylem plate fuse to form single strands (Figure 14C, D) which, at older stages, will have associated xylem elements differentiated from the residual meristem (Figure 14D). Each vascular bundle thus formed soon divides into two, and each enters a cotyledon as a lateral trace (Figure 14E, G).

The endodermis and the pericycle, which were well differentiated in the lower portion, are not readily discernible in the upper portion of the hypocotyl. Casparian strips are not differentiated in the upper hypocotyl, and the boundaries of the pericycle become less

sharp. Laticiferous cells follow the course of the phloem. These cells always appear first at the outer boundary of a phloem group, although later they are also found in between the metaphloem elements.

Laticiferous cells are especially obvious in the seedling axis at the cotyledonary node. Sections of a one-day-old seedling show laticiferous cells at the outer boundary of the two protophloem ridges (Figures 44, 45, 46). These cells are fairly large, thick-walled, and filled with dense contents. Lateral anastomoses occur, and afterwards, by absorption of end walls between subsequent laticiferous cells, articulated laticifers are established. The laticifers may be followed into the cotyledons where they also exist opposite the protophloem (Figures 15, 16). Downward, they end approximately 1-1/2 mm. from the root initials. Laticifers differentiate later in the metaphloem, and still later from the vascular cambium.

Microseris lindleyi

Secondary Growth of the Primary Root

Secondary growth is initiated by periclinal divisions of parenchyma cells between the xylem plate and the two primary phloem regions. These divisions result in two narrow bands on either side of the xylem plate, appearing like two arcs of an oval shaped cylinder

that is interrupted at the ends. The vascular cambium is established

prior to maturation of the last metaxylem elements. Cells of the

pericycle abutting the protoxylem elements soon undergo periclinal

divisions to complete the cylinder which, at this stage, has become

almost circular. Occasional anticlinal divisions expand the circum-

ference of the cylinder of the vascular cambium.

The cambial initials differentiated along the sides of the pri-

mary xylem plate, between the xylem and primary phloem are typi-

cal fusiform initials. They are relatively short, approximately

140μ in length with oblique end walls as seen in tangential section.

No typical ray initials appear in the primary root of Microseris.

Opposite the protoxylem ridges, especially in the upper portion of

the root, the cambial initials that are differentiated from the peri-

cycle are shorter than the fusiform initials, and variable in shape

as seen in tangential section. There is a progressive gradation in

size and shape between these initials and the typical fusiform initials

on either side of the primary xylem plate. The initials opposite the

protoxylem in the middle and lower portions of the primary root are

the more typical fusiform initials.

During the first two or three months of secondary growth, the

nontypical fusiform initials opposite the protoxylem ridges produce

only parenchyma cells in two broad wedge-shaped zones (Figure 15).

While these superficially resemble rays in cross section, they are

not typical rays. The parenchyma cells are approximately the length of the initials that produced them and show little or no radial elongation. The initials producing the wedge-shaped zones of parenchyma later become transformed into typical fusiform initials and, thereafter, produce only typical vertical elements of the secondary xylem and phloem.

During the period when, in the upper root region, parenchyma cells are being produced opposite the protoxylem poles, the fusiform initials along the sides of the primary xylem plate produce large diameter axial xylem elements primarily of two types. While a few fiber tracheids are produced in this region, most of the cells are vessel elements or similarly appearing tracheids and xylem parenchyma. The vessels occur singly or more frequently in a series of radial clusters usually one vessel wide, separated by large parenchyma cells. Each parenchyma cell was derived from a single xylem initial; i.e., xylem parenchyma strands do not appear (Figure 9). The parenchyma cells remain thin-walled, and the cells are only slightly or not at all lignified. Later, after about three months' growth, a more compact zone of secondary xylem is produced in which thick-walled fiber tracheids occur between the vessels (Figure 16). The diameter of the latter is considerably smaller than those in previous zones. Little or no xylem parenchyma occurs in this zone of dense secondary xylem, and no ray parenchyma is produced.

The vessel elements and tracheids in the first zone of secondary xylem show scalariform to reticulate thickening of the secondary wall. Later formed vessel elements in the second zone have oval to round pits in the walls (Figure 18). The oval pits generally are opposite while the round pits are more or less alternate. No torus was observed in those bordered pits. The end walls are transverse to slightly oblique and have a simple perforation, round to oval in shape. Where the end wall is slanted, the perforation in large elements does not occupy the entire area but is confined to the center or margin; the remainder of the end wall may be pitted or reticulate. The length of the vessel element varies from 140 to 180 μ, but may be much shorter in the vicinity of lateral roots. The large tracheids are approximately the same length as the vessel elements and show similar characteristics except that the end walls are more slanted and nonperforate, and they are usually smaller in diameter. Also, they more frequently have pitted rather than reticulate secondary walls. The fiber tracheids in the compact zone of xylem are elongated cell with tapering ends, and thick heavily lignified cell walls. They vary in length from 140μ to 270μ, and occasionally are septate (Figure 18). The shorter fiber tracheids usually have modified bordered pits with narrow, slit-like inner openings at right angles to each other in adjacent cells. The pits in longer fibers may be reduced to essentially simple pits.

The lower hypocotyl region of the seedling shows the same development as the primary root, with one exception. As secondary growth progresses, the parenchyma cells between the primary xylem elements will undergo occasional division and thus separate the xylem elements more or less from each other while at the same time keeping pace with the enlarging diameter of the root.

The greater portion of the phloem is crushed and obliterated early by the secondary growth of the primary root. The secondary phloem consists of phloem parenchyma, sieve tubes, companion cells and laticifers. The three last elements are present in strands, which occasionally include some phloem parenchyma cells. Such strand will be referred to as a phloem strand, and most of its elements are derived from a single fusiform initial. In the narrow border of secondary tissue formed outwards by the cambium, the phloem strands are arranged in concentric rings. Interconnection between phloem strands of the same ring occurs by the anastomosing laticifers. In between the phloem strands is the phloem parenchyma which is derived from the remaining fusiform initials. The parenchyma cells produced opposite the protoxylem ridges are difficult to distinguish in cross section from other phloem parenchyma because all such cells expand rapidly, both tangentially and radially, as the root becomes older. The phloem parenchyma cells resemble the xylem parenchyma cells except that they expand more in

diameter and have thinner, non-lignified cell walls. The sieve tube elements are narrow thin-walled cells approximately 6.5μ in diameter and vary in length from 140μ to 160μ . The simple sieve plates are thickened and are oriented either transversely or at a slightly oblique angle. Each sieve tube element is accompanied by a single companion cell that extends the full length of the element (Figure 18).

The articulated anastomosing laticifers are difficult to distinguish from phloem parenchyma cells in cross sections. Longitudinal sections show that laticifers are longer than phloem parenchyma cells. Pores are differentiated very early in the side walls to form lateral connections with adjacent laticifers (Figure 20). The end walls also dissolve later to form the articulated laticifer tube. Some of the lateral connections are by means of protuberances from nearby cells, with a pore in the center where the protrusions meet. Similar blind, or nonporous protrusions sometimes occur on adjacent parenchyma cells.

Radial and tangential enlargement of both the cortical and phloem parenchyma cells keeps pace with increase in diameter of the young root. Cells of the outer cortex become stretched tangentially and, in response to these tangential stresses, undergo occasional anticlinal division. At a certain point, however, the cortical cells apparently can stretch no farther and begin to slough

off, starting with the outermost layers. Usually the cell walls of the outer cells become suberized before they are sloughed. Near the end of the first month, weakly developed phellogens differentiate in the deeper layers of the cortex as isolated plates (Figure 15). No phelloderm is formed and only a few cells of phellem are produced at any one point. This cork sloughs off some and new cork cambium differentiates in the deeper layers of the cortex, the location of which may or may not be immediately beneath the preceding one. At six months of growth, there is no indication of development of a cork cambium in the pericycle.

The root of a six-month-old plant retains four or five layers of the original eight or nine layers in the cortex (Figure 16). The endodermis is very much elongated tangentially as are the peripheral cells in general. Both radial and transverse divisions occur in the endodermis during enlargement of the root.

The primary root of <u>Microseris</u> is contractile but not markedly so. Contraction is indicated externally by a slight wrinkling of the cortex that first appears when the seedling is approximately one month old. Internally, the primary evidence of contraction is a gradual shearing of the cortical cells just inside the suberized outer layers, or between the cortex and the phellogen, when present. Also, the Casparian strips of the endodermal cells are thrown into numerous sharp folds or wrinkles (Figure 35).

Shoot Apex

During the first weeks of growth in the greenhouse, Microseris
lindleyi develops a rosette of leaves due to the short growth of the
internodes and spiral leaf arrangement. The number of leaves com-
prising the rosette varies according to environmental conditions.
After three or four weeks, succeeding internodes of the stem grow
rapidly in length and form an aerial stem which later will develop
a terminal capitulum. The leaves of the aerial stem are distichous.
The diameter of the stem remains approximately the same size
throughout since there is little secondary growth.

Figure 24 shows a median longitudinal section of the shoot
apex of a plant which was two months old. The shoot apex has the
shape of a low dome which become modified by the differentiation
of leaf primordia at its margins. Due to its flat dome-shaped struc-
ture, cross sections of the shoot apex always show a continuous
mass of tissue formed by several united leaf buttresses, even at the
highest levels (Figure 27). There is a distinct one-layered tunica
in the apex in which only anticlinal divisions occur (Figure 24). The
corpus consists of three or four cell layers in which both peri-
clinal and anticlinal divisions occur, resulting in a rapid expansion
of this region. In the lower portion of the corpus, the divisions are
predominantly transverse. This region constitutes the rib meristem,

which in this case is very short. Below the rib meristem, the cells elongate and mature rapidly, and develop an extensive pith area. In older portions of the stem, cell enlargements in the outer stem tissues results in stresses which rupture the pith cells and the older stem is hollow (Figure 31). Divisions immediately below the base of a developing leaf primordium result not only in an increase in number of the future procambium cells, but also augment the cortical region. The procambium cells, which are discernible from the surrounding cells because of more densely stained protoplasts and narrower diameters, differentiates acropetally into the developing leaf primordium. Development of vascular tissues in the leaf may be followed by examining successive transverse sections of a young leaf from the apex downward into the stem. Figure 25 shows a transverse section near the apex of a young leaf with a single procambium strand. The number of procambium cells is increased at first by longitudinal divisions occurring in all planes. The first procambium cells to mature are a few cells on the abaxial side of the strand. Along with vacuolization, these cells develop denser staining cell walls and at first resemble sieve tubes (Figure 25). Later, however, these differentiate into laticiferous cells. Still later, additional laticiferous cells appear at the periphery of the vascular bundle in the protophloem region. Protophloem cells without detectable sieve areas, and without companion cells, also

differentiate (Figure 26). Metaphloem consists of sieve tube elements, companion cells and phloem parenchyma. Annular and spiral protoxylem elements differentiate early on the adaxial side of the procambium strand. Later procambial divisions are largely periclinal, and produce radial rows of cells which differentiate into reticulate or pitted metaxylem vessels separated by parenchyma (Figure 27).

The number of leaf traces is generally three, and are considerably larger than the remaining bundles in the leaf. Appendages of the epidermis are found on the young leaves at the shoot apex of an older stem. The most common type of appendage is the glandular multicellular hair. Each hair consists of a basal cell, which may or may not be taller than adjacent epidermal cells, a two-to-five-celled uniseriate stalk, and a multicellular head composed of eight cells all of the same height. In surface view, the head is square in outline (Figure 27). Nonglandular trichomes also are present.

Stem

Similar to the other two species, M. lindleyi will form a rosette during the first three weeks of its growth and then develop an aerial stem bearing leaves which are morphologically similar to those of the rosette. The stem is ridged because of the decurrent leaf bases. The vascular tissue is arranged as a eustele which, in

later stages, develops an interfascicular cambium.

A cross section through the young stem shows the large vascular bundles which will terminate in the leaves at the nodes immediately above (Figure 29). The two largest bundles on opposite sides of the stele reflect the distichous arrangement of the leaves. The young epidermis appears as a layer of isodiametric cell lacking, at this level, any indication of cutinization. Anticlinal divisions result in expansion of the epidermis and also differentiate guard cells of the future stomata. Cells of the subepidermal layer are slightly larger than the epidermal cells and are in turn smaller than the cells of the remaining cortex, which at this stage is five to six cells thick. The inner layer of cortical cells constitutes a starch sheath. Cells of this layer contain starch in the young stem, either of a young plant or the upper portions of an older plant, but this starch disappears as the stem becomes older (Figure 32). No Casparian strips were observed in the cells of the starch sheath.

Laticifers differentiate outside the vascular bundle adjacent to the starch sheath. Additional laticifers appear in the metaphloem which here, as in the primary root, consists of sieve tubes, companion cells and phloem parenchyma.

The later procambial divisions are largely periclinal, so that the primary vascular tissues, especially the primary xylem, show a definite radial arrangement of cells. The primary xylem matures

in a centrifugal direction, and consists of radial rows of annular and spiral protoxylem elements and larger reticulate to pitted metaxylem elements. One or two tiers of nonlignified cells, primary xylem rays, alternate with the single series of the lignified elements (Figure 28). The pith cells at the inner periphery of the xylem are elongated cells with tapering ends, and may best be designated as prosenchyma. The remaining pith consists of thinwalled, more or less isodiametric cells which are slightly larger than those of the cortex in cross section (Figure 32).

During later development, the epidermal cells elongate in a tangential direction. The outer tangential wall and the radial walls become cutinized. The guard cells may protrude somewhat above the epidermis (Figure 28), and ledges occur along the upper sides of the guard cells that delimit a front cavity. Cortical cells adjacent to the stomata are generally thin-walled and contain chloroplasts. Between the patches of chlorenchyma there is a layer, one or more cells in thickness, of somewhat smaller, thicker-walled collenchyma cells lacking chlorophyll but containing tanniniferous materials. The remainder of the cortex is five to six cells thick and consists of large parenchyma cells which undergo considerable enlargement and tangential stretching. The inner layer loses the abundant starch that characterized the young stem. The outer cortical cells do not undergo anticlinal divisions as was the case in the

root cortex. Collenchyma occurs as small strands located at the angles or ridges of the stem immediately adjacent to the epidermis.

The laticifers outside the vascular bundle adjacent to the starch sheath, and also those in the metaphloem, do not collapse as the stem develops secondary tissues. The protophloem sieve elements are crushed early, followed by collapse of the metaphloem elements and companion cells. Areas of obliteration are recognizable by the densely staining remnants of the cell walls. Phloem parenchyma, as well as the laticifers within the primary phloem, enlarge and stretch tangentially followed by some thickening of the walls. Part of the protophloem differentiates into thin-walled fibers, which remain as a cap on the vascular bundle.

The secondary phloem consists of the same elements as the metaphloem, i.e., sieve tube elements, companion cells, phloem parenchyma, and laticifers. During the differentiation of a sieve tube element the "nacre" wall thickens irregularly and appears as a crenulated surface. The mature element has relatively thin side walls and a thick transverse to oblique end wall with a simple sieve plate. Sieve tube elements average 272μ in length, while the width is relatively constant at approximately 5μ . Spindle shaped slime bodies are present in many sieve tube elements. A sieve tube member is accompanied by a single companion cell, which is generally of the same length, but in some cases may be only two

thirds the length of the mother cell. When similar in length, the ends of the companion cells terminate just before the sieve plates. The companion cells are living nucleated cells with thin walls.

The phloem parenchyma cells are thin-walled, somewhat elongated cells that do not undergo transverse division after being derived from a fusiform initial. They are similar in diameter to the laticifers which have thicker walls. Anastomoses between adjacent laticifers are readily observed and it may be assumed that through these anastomoses an intricate laticifer system is established. Laticifers may occur in close association with sieve tube elements and openings through the adjacent walls of these cell types has been observed (Figure 39). Frequency of this type of association has not been determined.

Anastomoses between laticifers occur very early in the differentiation of the cells. The lateral cell walls first become thin at places of contact, and the thin membrane is then absorbed completely so that no remnants of this structure persist. Anastomoses through end walls of laticifers in longitudinal series also occur, although later than those through lateral walls. Hence the end walls are in a more advanced stage of differentiation, and connections between cells in longitudinal series appears to take place by rupture of the end walls. Remnants of these walls were often observed in the lumen of laticifers. The formation of secondary tissues exerts

pressure and tensions on the laticifer system. Adjacent cells may

be forced apart by enlargement of phloem parenchyma cells except

at the location of anastomoses. At this point, the adjacent cell walls

are drawn out into connecting protrusions, with an open pore at the

point of contact. Because of the narrow band of secondary phloem

in the stem, the laticifer system is more restricted than it is in

the other two species studied.

The vascular cambium, both fascicular and interfascicular,

consists largely of nonstoried fusiform initials. Distinct ray initials

were not observed. The interfascicular cambium produces only

phloem parenchyma cells outwardly, and mostly fiber tracheids to

the inside, interspersed with short radial rows of vessels (Figures

31, 32). The fascicular cambium produces all cell types found in

the secondary phloem and secondary xylem. Both vessel elements

and similarly appearing tracheids are present in the secondary xy-

lem. The secondary walls of both cell types are reticulate to pitted.

The bordered pits may be opposite in some vessels but in most

cases they are alternate. The vessel elements and tracheids are

longer than corresponding elements found in the primary root,

averaging approximately 302 μ in length and 9 μ in width. The end

walls are transverse to oblique and the perforation is simple.

Where the end wall is very oblique, the perforation occupies only

a portion of the end wall and may be located in the center or toward

the margin. The vessels are arranged in radiate series, often
times as a continuation of the rows of vessels in the primary xylem.
Vessel elements produced by the interfascicular cambium are simi-
lar to those produced by the fascicular cambium.

The fiber tracheids of the secondary xylem are long, narrow
cells with tapered ends and thicker walls. The bordered pits have
reduced borders and slitlike inner openings, with the openings of
the pitpair at right angles to each other. The average length and
width is 524 and 3µ, respectively. The modified bordered pits
may be reduced to essentially simple pits. This is usually accom-
panied by production of transverse septa, usually one but sometimes
two per cell.

The xylem parenchyma consists of living, nucleated cells
with transverse to oblique end walls with simple pits. The xylem
parenchyma cells lack starch and mostly undergo lignification in
older secondary xylem. The prosenchyma cells immediately to the
inner side of the primary xylem become lignified in older stems.
In some instances a few of these cells develop a very thick wall and
tapered ends and become fibers. The remaining pith cells are thin
walled and large in diameter. A hollow pith is established by rup-
ture of the centrally located cells (Figure 31).

<u>Microseris borealis</u>

<u>Secondary growth of the Primary Root</u>

The upper region of the primary root and the hypocotyl of <u>M.</u> <u>borealis</u> develops into a large, white to yellowish storage organ. Initiation of cambial activity occurs after all the primary xylem has matured. Periclinal divisions at first occur in the parenchyma tissue between the diarch xylem plate and the primary phloem, then appear progressively outward into the pericycle opposite the proto-xylem poles, thus completing the oval cylinder of vascular cambium. A similar sequence occurs in the hypocotyl portion of the seedling where the pericycle is several cells in thickness. The vascular cambium in both hypocotyl and radicle produces much more secon-dary phloem than xylem. More secondary tissues are produced in the hypocotyl than in the upper portion of the root, and the xylem produced in the radicle is more centralized than in the hypocotyl. In the hypocotyl, the cambium opposite the protoxylem poles pro-duces a considerable amount of parenchymatous tissue to the inside before any lignified xylem elements are formed (Figure 33). In cross section, this will appear as two parenchymatous zones fan-ning out from the protoxylem poles. In the radicle, lignified ele-ments are produced immediately adjacent to the protoxylem poles (Figure 34). The cambial initials producing the parenchymatous

tissue opposite the protoxylem poles are not typical ray initials, but resemble the irregularly shaped initials that produce corresponding tissues in the primary root of M. lindleyi (Figure 36). Much of the active cambium in the older root consists of initials of this type. These initials produce storage parenchyma in both secondary xylem and phloem, especially the latter. The parenchyma cells do not elongate radially and hence are not typical rays. The fusiform initials are narrower, spindle-shaped cells arranged in a network of interconnected strands. These initials produce the conducting elements of the secondary xylem and phloem (Figure 35).

The major portion of the secondary phloem consists of storage parenchyma derived from the fusiform initials. These parenchyma cells are thin-walled and are comparable in length to the initials although frequently a transverse division may occur. Primary pitfields are abundant in the cell walls. The cells divide radially and enlarge in the older portion of the root (Figures 37A, 37B).

The fusiform initials produce interconnected longitudinal strands consisting of sieve tubes, companion cells, phloem parenchyma cells and laticifers. All of the elements in small strands, and many of those in large strands, are derived from a single phloem initial by repeated longitudinal divisions that occur in the region adjacent to the cambium and may also occur in older regions.

Because of these divisions, the elements in the strands are much
smaller in diameter than the surrounding storage parenchyma cells
(Figures 38, 39). The fusiform initials do not form phloem strands
continuously. After the production of a strand, the fusiform initials
will form storage parenchyma cells for a time, thus leaving large
gaps between successive phloem strands. In cross sections, the
strands thus appear in rows which radiate out from the cambial re-
gion (Figure 37A). The production of phloem strands occurs more
or less simultaneously at different points in the vascular cambium.
Each ring of phloem strands, as seen in cross sections, thus con-
sists of an interconnected net but there are no connections from
ring to ring. In cross section, the outermost ring of phloem strands
is frequently seen to be continuous (Figure 37). The sieve tube
elements are similar to others observed in this study. They are
slender, elongated cells with thin lateral walls and horizontal to
oblique end walls which are penetrated by many pores. No sieve
areas were observed in the lateral walls. There is a single com-
panion cell usually of the same length as the corresponding sieve
tube element (Figure 40).

Laticifers in the secondary phloem occur only within the
strands containing the sieve tubes. Lateral anastomoses between
the laticiferous cells differentiate very early. In close proximity
to the cambium, round to oval-shaped areas of the lateral walls

remain thin and, as growth proceeds, the thin areas are absorbed and pores are established between the cells involved. As the cells enlarge in the older phloem, and are pushed apart by enlargement of adjacent parenchyma cells, walls around the pores undergo local growth and form protrusions that maintain the connections between adjacent cells. These protrusions range from small elevations of the lateral wall, to bulges to tubular protrusions in old secondary phloem. The lateral walls of the laticifers become very thick, especially in older phloem. Anastomoses between cells in longitudinal series are established later than the lateral anastomoses. Parts of the end walls, or more rarely entire end walls, are ruptured and the remnants often persist in the cell. The nuclei of laticifers remain functional for a long period, but were not observed in the laticifers of the older phloem. Because the laticifers are restricted to the phloem strands, the intricate network of laticifers involves only a single ring, and there are no connections between laticifers of different rings of strands.

The phloem parenchyma located within a phloem strand appears as elongated cells with blunt or rounded ends. The diameter is often similar to that of the laticifers and the walls attain a similar thickness. In cross section, these cells are difficult to distinguish from the laticifers at levels where no anastomoses occur. In older secondary phloem, these phloem parenchyma cells as well

as the storage parenchyma cells in which the phloem strands are

embedded, are stretched tangentially and occasional anticlinal divis-

ions occur. Functional sieve tubes and companion cells are not found

in the outermost secondary phloem. Where they are not crushed by

the stretching and enlargement of adjacent cells, they may become

incorporated into the laticiferous system.

The amount of secondary xylem produced in the primary root

is very limited. A large portion of the secondary xylem consists of

parenchyma produced by the irregular ray initials. The fusiform

initials produce radiating rows of vessels that are usually located

opposite the phloem strands but may also occur in the regions be-

tween (Figure 37A). As growth proceeds, the parenchyma cells be-

tween the earliest formed vessels may divide occasionally, form-

ing more parenchymatous tissue, and in this manner keeping pace

with the increasing diameter of the root. The only lignified cells

of the secondary xylem are vessel elements with secondary wall

thickening of the scalariform to reticulate type. The end walls are

transverse or oblique and possess a simple perforation. No trach-

eids or fiber tracheids are differentiated in the primary root.

The epidermis of the root is sloughed off at a very early

stage. Periclinal divisions in the outermost cortical cells of both

the lower hypocotyl and radicle give rise to a phellogen (Figures

33, 34, 48). When all cells of the first cork layer are suberized,

deeper cortical cells undergo periclinal divisions and differentiate

a new phellogen. The cortical cells undergo some tangential stretch-

ing followed by anticlinal divisions as the root enlarges.

In approximately the fifth or sixth month of growth, lysigenous

cavities appear in the endodermal region. These cavities develop

mostly between the endodermis and adjacent cortical layers, but

may also occur between the endodermis and pericycle (Figures 41,

42, 43). Absorption of cells adjacent to these cavities may occur,

followed by divisions of some cells bordering the lumen. Oil drop-

lets are observed within these cells, the walls of which undergo a

light brown discoloration. The cavities occur locally and are not

interconnected. During their development, the endodermal cells

divide radially and keep pace with the enlargement of the cavity.

Shoot Apex

M. borealis is a perennial with a short horizontal rhizome

and slender adventitious roots. A rosette is formed in which the

leaves are in a distichous arrangement. A peduncle bearing one

terminal capitulum develops at the time of flowering.

The cotyledons of the seedling remain functional photosyn-

thetically for more than a month, and true leaves are not initiated

at the apex until after the cotyledons have become fully differentiated.

Hence, in a young seedling, the apex of the epicotyl is elevated above

the base of the cotyledons and shows no leaf primordia (Figure 44).

There is a single-layered tunica which gives rise to the protoderm.

It consists of small isodiametric cells which cover the apex. The

corpus consists of more or less vacuolated cells in the center sur-

rounded by a peripheral region of smaller, more densely staining

cells. The apex of a two-month-old shoot appears as a flattened

dome from which will differentiate usually many leaf primordia in

a distichous arrangement. The stem is thus very short and is con-

fluent with the leafless hypocotyl and radicle at the base (Figure 47).

The one-layered tunica overlays a four- to five-layered cor-

pus, the uppermost two or three layers of which are regularly

placed and may appear to be part of the tunica. Occasional peri-

clinal divisions do occur, however, in this outer zone. Cells of

the regularly layered zone of the corpus stain densely and are of

the same appearance as those of the tunica. Leaf primordia are

initiated in this region. The remainder of the corpus consists of

larger, more vacuolated cells which undergo both longitudinal and

transverse divisions to increase rapidly the diameter of the stem.

The lowermost cells of the corpus are confluent with the rib meri-

stem, which consists of a layer three to four cells thick of trans-

versely dividing cells across the base of the apex. Thus a broad

pith region is differentiated a short distance below the stem apex.

Procambium differentiates acropetally into a developing leaf

primordium, appearing first as a narrow strand of more densely staining cells. As development proceeds, divisions become predominantly longitudinal and the cells assume the characteristic shape of procambium cells. The cells adjacent to the procambium also undergo divisions in periclinal direction, resulting in the formation of anticlinal rows of cells. This meristem is referred to as a primary thickening meristem (21, p. 387) which forms a considerable part of the stem of caudex of the rosette stage in M. borealis (Figure 47). Meanwhile, the vascular cambium becomes active shortly beneath the shoot apex, producing secondary tissues. In a longisection the two types of lateral meristems can be readily distinguished. The primary thickening meristem is responsible for the formation of a broad cortex. Its derivatives will elongate and afterwards differentiate into the parenchyma of the cortex. Further increase in thickness occurs by enlargement and division of these cells. The cortex thus formed possesses many air spaces, and resembles the mesophyll of a leaf.

Development of vascular tissue in the leaf was by examination of serial cross sections through a young leaf and downward until the leaf trace reaches the vascular cylinder of the stem. The vascular system of a leaf consists of a median trace and two lateral traces at either side. Simple trichomes develop on the leaves but none of the glandular hairs found in M. lindleyi were observed.

Development of the vascular tissue is essentially similar to that in M. lindleyi. The procambium strand entering a young leaf is enlarged by longitudinal divisions within the procambium group and also by divisions of adjacent cells. The first cells to differentiate in the procambium are the laticifers which appear on the abaxial side. Walls of these cells become thicker but anastomoses do not develop until later. Walls of the protophloem also thicken somewhat, but become thinner after degeneration of the nucleus. No companion cells are associated with the protophloem, but each of the metaphloem sieve tube elements is associated with a single companion cell. The adaxial portion of the procambium undergoes predominantly periclinal divisions so that the primary xylem differentiates in radial rows. The protoxylem matures soon after the protophloem. The primary xylem here is essentially similar to that of M. lindleyi in structure and composition, but is much less in amount. Also, no prosenchymatous tissue is present at the inner border of a vascular bundle. The vascular cambium becomes active early in the development of the vascular bundle.

Stem

The stem of M. borealis has a eustele in which interfascicular cambia develop very early. Primary growth is confined to a small region immediately beneath the shoot apex. The very short

stem or caudex of the rosette stage becomes confluent with the hypocotyl and upper root, all of which develop approximately the same amount of secondary tissues and attain similar diameters (Figure 51).

Cells of the young epidermis are isodiametric but will elongate slightly tangentially as growth proceeds. The epidermis is sloughed early. Cells of the young cortex are capable of dividing tangentially and thereby increasing the stem diameter. The cortex of a two-month-old stem is wide and composed of rounded cells with large intercellular spaces. The cells are not stretched tangentially by secondary growth, as in the root, but adjust to increasing diameter by developing large intercellular spaces (Figure 49, 50). The cortex finally assumes the appearance of aerenchyma. The cells become rounded and occasionally resemble the spongy mesophyl of a leaf. Chloroplasts, however, are found only in the young stem. There is no indication of a starch sheath at the innermost boundary of the cortex of a young stem. In older stems, an endodermis is readily recognizable by the appearance of Casparian strips. In the two-month-old plant, an endodermis is mature at 1100μ beneath the shoot apex. The Casparian strip often become very broad and occupies half the area of the radial and transverse cell walls. Frequently the outer and inner margins of each strip appear thicker than the middle portion, which sometimes appears to have short, radial folds. The walls of still older endodermal cells are light

brown in color, and many oil droplets appear in the cytoplasm.

The primary phloem is similar in structure and development to that of M. lindleyi. The protophloem elements become crushed very soon after the differentiation of the metaphloem, and sieve tubes and companion cells of the metaphloem in turn are crushed when the vascular cambium becomes active. Cells of the primary phloem which persist are mostly the laticifers, some of the phloem parenchyma cells and thin walled fibers which differentiate later. The laticifers at this stage are thick walled cells connected with one another by anastomoses. As in M. lindleyi, the outer boundary of the phloem strand is delimited by a single layer of laticifers. The cells are, however, very short as is the case for all the cells in the caudex of M. borealis (Figures 40, 52). The tangential stretching causes the sieve tubes to diverge out of their usual course. Some sieve plates are occasionally seen to be situated almost vertically instead of in a horizontal plane. No sieve plates were observed on the lateral walls.

The vascular cambium consists largely of typical fusiform initials, which produce conducting elements, laticifers, and storage parenchyma. No typical ray initials are present. All cells produced are approximately of a similar length, and only slight elongation occurs during differentiation. Outwards the majority of the cambium initials produces storage parenchyma in which groups of

conducting elements and laticifers are embedded. The interfascicular

cambium, however, produces largely parenchymatous tissue and

therefore the vascular bundles remain distinct from each other,

whereas no continuous rings of isolated phloem strands are estab-

lished.

As in the root, the typical fusiform initials produce vascular

strands consisting of sieve tubes, companion cells, phloem paren-

chyma and laticifers. In cross sections these cells are arranged

in radial rows, with each strand along a radius being part of a ring.

In tangential sections, the strands of each ring form an interconnect-

ed network. There are no connections between strands of different

rings. The cell types differentiate in very much the same way as

corresponding phloem strands in the root. The storage parenchyma

cells between the phloem strands are in radial rows, remain thin

walled, and are interconnected by simple primary pitfields.

The secondary xylem also consists primarily of storage paren-

chyma, with only a relatively few scattered vessels (Figure 52).

The vessel elements have secondary wall thickenings of the scalari-

form to reticulate to pitted type, and are shorter than in M. lindleyi,

although close to the hypocotyl longer elements can be found. In the

stem they average 46μ in length and 15μ in width. The

end walls are horizontal or slightly oblique and possess simple per-

forations. The vessel elements are even shorter in the upper portion

of the stem. No prosenchymatous elements are present at the inner boundary of the primary xylem. The large pith is composed of thin walled parenchyma cells that are not disrupted by increase in stem diameter.

Cork formation occurs, similar to the root, during the third or fourth week of growth (Figure 48). Cells of the outermost cortex layer enlarge somewhat prior to undergoing periclinal division. The inner cell thus produced becomes the phellogen. A several layered cork zone is established, but no phelloderm is produced. In contrast with the root, cork formation in the stem is regular and results in a continuous layer of phellem at the outer boundary (Figure 49, 50). The periderm is four to five cells thick at the base of the caudex and gradually diminishes in thickness towards the shoot apex.

Adventitious Root

In the greenhouse, M. borealis produces the first adventitious root at approximately the fifth month of growth. After it has attained a considerable diameter, more adventitious roots originate at the stem base somewhat above the first. These roots appear to be initiated in the cambium region of the stem (Figure 53). The tips of these roots are larger than those of either primary or lateral roots. They emerge almost at right angles and then turn downward and

grow parallel to the primary root. They are similar to the primary root in that they are white or yellowish in color, but have a more spongy appearance. As growth proceeds, the upper portion enlarges more in diameter than the lower portion, and finally an adventitious root resembles very closely the primary root. At this stage, however, the primary root starts to wither and will gradually decay.

Contraction of the adventitious roots apparently causes the short stem of the plant to be pulled down toward one side into a more or less horizontal position, thus establishing the horizontal rhizome typical for M. borealis. Later in the growth period after flowering, shoots develop from the axils of the older leaves while additional adventitious root primordia are formed at other places on the rhizome. These primordia, however, remain dormant and will resume growth only under suitable conditions. Until then, they appear as brown, cone-like structures at the base of the stem or rhizome (Figure 1A).

The root initials are organized prior to the emergence of the adventitious root from the cortex. There are two groups of initials (Figure 56) functioning in the same manner as those of the primary and lateral roots of all three species studied. Similarly thickness of the cortex is increased by periclinal divisions in the endodermis (Figure 57). Later, large intercellular spaces develop in the cortex, giving the root a spongy external appearance. The endodermis is

occasionally biseriate in the regions opposite the protophloem poles and Casparian strips differentiate after the first protoxylem elements are matured. The pericycle is uniseriate and the first vascular elements mature adjacent to this layer. In contrast with the primary root, the stele of the adventitious root may be triarch, tetrarch (Figure 56, 57), or pentarch (Figure 59). Also, instead of metaxylem vessels differentiating to the center of the root, there is a pith-like region of parenchyma cells with small intercellular spaces (Figure 58, 59). Aside from these differences, differentiation of the primary vascular tissues is similar to that in the primary root. Also, the structure of the vascular cambium and secondary tissues produced are similar to those in the primary root.

Similar to the primary root, cork formation is subepidermal and regular. Microscopic wrinkles appear in the Casparian strips of the endodermis (Figure 55).

Root contraction, so obvious externally, does not have a strong influence on the anatomical structure of the organ. In the stele, the cells are stretched radially and tangentially. More pronounced influence is found in the cortex, where the outer layers remain passive during contraction of the inner tissues, and therefore are thrown in folds responsible for the external wrinkled appearance (Figure 54).

The adventitious roots also produce lateral roots, especially in the lower portions. These are initiated in the pericycle opposite

a protoxylem ridge, are diarch, and develop very little secondary growth.

Microseris laciniata

Secondary Growth of the Primary Root

The taproot develops into a large storage root which is derived from the hypocotyl and the upper portion of the radicle. Secondary growth in the primary root of M. laciniata proceeds essentially as in M. borealis, and is initiated when the seedling is about seven days old. At this stage the metaxylem is not yet fully matured and the large metaxylem vessels of the diarch xylem plate are still devoid of secondary thickenings. As in M. borealis, only a small amount of secondary xylem is produced. This consists of vessels embedded in storage parenchyma, which constitutes the major portion of the secondary xylem. The vessels in older roots are usually arranged in radial rows which frequently are opposite the strands containing sieve tubes in the phloem. The storage parenchyma cells in the secondary xylem, and also phloem, are produced largely by fusiform initials as in the other two species. Nontypical fusiform initials produce shorter parenchyma cells. During early secondary growth, the vascular cambium opposite the protoxylem poles produces only parenchyma. Vessel elements usually develop scalariform

to reticulate wall thickenings but occasionally pitted elements are differentiated. They vary in size and may be as much as 220μ in length, although shorter vessels are not rare. As in the other species, the end walls are horizontal to oblique and possess a simple perforation. The storage parenchyma consists of vertically elongated cells with blunt ends and thin walls. These cells are capable of dividing as are the primary xylem parenchyma cells. As growth proceeds these cells may divide longitudinally, especially in the hypocotyl, thereby forcing the vessels farther apart. Thus , in the hypocotyl portion of an old plant, the scanty vessel elements appear scattered in the central region.

A relatively large amount of secondary phloem is produced, again consisting mostly of storage parenchyma. Phloem strands, consisting of sieve tubes, companion cells, phloem parenchyma cells and laticifers are produced in an almost continuous ring adjacent to the vascular cambium. Later formation of storage parenchyma cells by the cambium, and enlargement of all parenchyma cells in the older phloem, moves the phloem strands farther apart, so that strands of the same ring appear to be isolated. As the sieve tubes and companion cells become nonfunctional and are crushed and obliterated by the adjacent parenchyma cells, the laticifers enlarge to a certain extent in the growing root. The laticifers show anastomoses very early in differentiation, first on the lateral

walls and later on the end walls. In general, the degree of anasto-

moses in M. laciniata is more pronounced than in the other two spe-

cies. Bulging out of the cell walls at the site of anastomoses, fol-

lowed by protrusions in later stages, also occurs. Laticifers in

this species are also capable of forming protrusions into regions

where no other laticifers are present. Whenever this occurs, and

when the laticifer is still isolated and devoid of anastomoses, the

cells resemble nonarticulated laticifers. Occasionally, laticifers

from phloem strands of the same ring form interconnections, thus

establishing an intricate system. This is especially obvious in the

outermost ring of phloem strands. No connections were observed

between laticifers of different rings. Laticifers of the outermost

rings undergo tangential stretching and are seen to diverge from

their original position, due to enlargement and stretching of neigh-

boring cells. The storage parenchyma cells, in keeping pace with

the enlarging diameter of the root, divide anticlinally and also trans-

versely.

The epidermis dies and is sloughed off early in development

of the root. Cells of the cortex undergo tangential stretching as do

the storage parenchyma cells of the outer secondary phloem. The

subepidermal cells may or may not form a distinct cork cambium

which, when present, produces only phellem cells for a short per-

iod before it too is sloughed. Sloughing of the cortex takes place

very gradually, and the endodermis persists for over a year, be-coming suberized and filled with oil droplets. Formation of inter-cellular cavities in the pericycle or endodermis, as in M. borealis was not observed in M. laciniata.

Both primary root and subsequent adventitious roots are con-tractile. As in the other species, the outer cortex of the adventi-tious root becomes wrinkled and shows a tendency to separate from the inner cortex. The outer part of the cortex thus appears as a loose jacket around the remainder of the root and is connected to it by a narrow zone of loose cortical cells with many intercellular spaces in between.

Primary adventitious roots of M. laciniata are so similar to those of M. borealis that description of their structure and develop-ment is omitted.

Stem

The structure and differentiation of the shoot apex is essentially similar to that in M. borealis. It is elevated above the cotyledon bases in the epicotyl stages and later becomes concave at the time of leaf initiation. The shoot apex possesses a one-layered tunica and a several layered corpus, of which the two or three outermost layers resemble the tunica. In the rosette plant, a short broad caudex continuous with the hypocotyl and primary root are developed

in the same manner as in M. borealis. The thickness of this caudex is also due in part to a primary thickening meristem found at the inner periphery of the differentiating cortex. Activity of this meristem ceases where the stem has attained a diameter similar to that of the hypocotyl. The resulting cortex appears as a broad tissue in which many intercellular spaces occur.

Differentiation of the vascular elements is also as in M. borealis. The cambium originates very close to the root apex and at the inner periphery of the primary thickening meristem.

The stem of M. laciniata is a eustele. In the rosette plant, the endodermis develops into a typical endodermis shortly below the shoot apex. The Casparian strips become wide, and in older plants the entire cell wall becomes light in color. Interfascicular cambia develop a short distance from the shoot apex of the rosette and usually produce vascular tissue but may form parenchyma and extend the pith rays. The secondary vascular tissues are similar in structure and distribution to M. borealis. The amount of storage parenchyma is less than in the root.

Young field grown aerial stems have a eustele, and an interfascicular cambium develops early (Figure 60). The stomata are similar to those described for M. lindleyi. The hairs are uniseriate. The cortex consists of at least six layers of cells containing chlorophyll. One or two outermost layers show collenchymatous

thickenings at irregular isolated places, mostly on ridges or longi-

tudinal elevations of the stem. No starch sheath was observed and

no indication of an endodermis was detected in this field grown ma-

terial. As in the two other species, the cell layer immediately ad-

jacent to the primary phloem consists largely of laticifers. Later,

these laticifers may connect laterally with other laticifers arising

in the secondary phloem produced by an interfascicular cambium.

In the primary vascular bundles the outermost cells of the phloem

are distinct from the inner layers by their more or less diamond

shape in cross section and larger size. This portion consists large-

ly of laticifers, thin walled fibers, and phloem parenchyma, which

remain after most of the sieve tubes are obliterated. The primary

xylem elements are arranged in radial rows as in the two other

species. In the field material, small medullary strands consisting

of phloem elements and laticifers are found at a short distance from

the vascular ring (Figures 60, 61). These strands are composed of

sieve tubes and companion cells and usually a marginal layer of

laticifers which may or may not be in connection with each other.

In the young stem of this field material, no primary xylem elements

are differentiated in these strands, and there are no connections be-

tween these strands and the primary xylem in the larger vascular

bundles.

The stem at ground level of such field material at the end of

the growing season shows a considerable amount of secondary growth. The fascicular cambium consists largely of typical fusiform initials. The secondary phloem is composed of phloem strands embedded in storage parenchyma. The storage parenchyma produced, is, however, much less than in the primary root and is confined to the vascular bundle. The structure and shape of the phloem elements is similar to those in the two previous species. Thin walled fibers occur within the primary phloem. The secondary xylem consists of elements similar to those of M. lindleyi. The amount of fibers, however, is much less, and tyloses are formed which often fill the entire vessel lumina. The interfascicular cambium consists largely of non-typical fusiform initials, which differentiate into parenchymatous tissue which continue the pith rays. At certain places, the initials divide longitudinally and form phloem strands (Figure 64).

The medullary strands in the caudex show some secondary growth, obvious from the regular cell arrangement (Figure 65). Xylem is differentiated in association with the medullary strands, usually to the inside. Most of the medullary strands are connected with each other by means of anastomosing laticifers at their borders. In longitudinal sections, the laticifers are shown to form an intricate network between the irregularly placed medullary bundles. The xylem consists of rather short vessels, generally with reticulate to pitted lateral walls, and simple perforate end walls. The vessels

have a narrow lumen.

Observation of the leaf structure shows that M. laciniata pos-
sesses phloem strands on the adaxial sides of the major leaf traces,
the median leaf trace in particular (Figure 66). Interconnection be-
tween laticifers of the leaf trace and those of the phloem strand was
observed, but the extent of this laticifer network was not studied.

Cork is formed irregularly in the subepidermal layers. Cork
cambia are also formed inside the many leaf scars at the caudex
region, finally causing them to slough. The remaining cells of the
cortex undergo proliferation as the stem increases in diameter.
Vascular strands composed either of phloem elements and laticifers
or with additional xylem are present in the cortex as well as obvious
leaf traces (Figure 62). No definite endodermis was observed in
the aerial portion of the field material.

DISCUSSION AND CONCLUSIONS

In this chapter, the developmental anatomy of the three species will be compared and discussed. Since no previous anatomical studies have been made of these species, the results will be compared with other members of the Compositae, the tribe Cichorieae in particular, of which the anatomical structure is well known. On the basis of this discussion, conclusions will be drawn whenever possible from the anatomical information obtained which might aid in clarifying lines of evolutionary specialization in the genus Microseris.

Seed germination, primary root histogenesis and the manner of transition from the protostele in the root to the collateral bundles found in the cotyledons are very similar in all three species. Transition occurs in the upper half of the hypocotyl. Havis (23, p. 645) observed the abrupt rearrangement of vascular tissues in Tragopogon porrifolius and stated that this phenomenon is common in plants with fleshy roots. In all three species, the median vascular bundle of the cotyledon is connected with the vascular system in the root by the double bundle described by Thomas (52, p. 79), which consists of two xylem plates centrifugal to the protoxylem region, capped by two adjacent phloem groups occurring at this level. The double bundle is common in plants with diarch roots.

The organization of apical initials is the same in primary,

lateral, and adventitious roots, is similar in all three species, and approaches that described by Guttenberg (22, p. 57) for <u>Helianthus</u> <u>annuus</u>. Port (see 24, p. 636) reported that three layers of initials were present in <u>Lactuca sativa</u>, giving rise to the central cylinder, cortex and rootcap-epidermis.

The radiate arrangement of the cortical cells, with the differentiating endodermis often appearing as biseriate opposite the protophloem, is also present in <u>Calendula officinalis</u> and <u>Zinnia</u> <u>elegans</u> (14, p. 410), <u>Lactuca sativa</u> (24, p. 638), <u>Cynara scolymus</u> (39, p. 715), Helianthus annuus (45, p. 428) and <u>Parthenium argen-tatum</u> (2, p. 8) but is not found in <u>Taraxacum kok-saghyz</u> (3, p. 5). The phenomenon is a functional reflection of the phloem (25) and is common in Compositae (57).

All three species have diarch primary roots, as in <u>Arctium</u> <u>minus</u> (45, p. 444) and <u>Cichorium intybus</u> (29). Other Composites may possess tetrarch roots (45, p. 428). Di- and tetrarch roots are common in the Compositae (32, p. 328).

Lateral roots originate in the uniseriate pericycle opposite the protoxylem poles, or slightly off these points, in all three species. In <u>Cichorium intybus</u> (29) and <u>Arctium minus</u> (45, p. 444) they originate typically from the region opposite the protoxylem poles, whereas in <u>Lactuca sativa</u> (24, p. 636) they arise slightly lateral to this position. The lateral roots are also diarch except

for one case in M. borealis where a triarch lateral root was en-
countered. Parthenium argentatum has triarch lateral roots (2, p. 8),
as does Taraxacum kok-saghyz (3, p. 20).

Secondary growth in the primary root may be initiated either
before metaxylem is completely differentiated, as usually occurs in
the perennial species, or after differentiation of metaxylem is com-
pleted, as in M. lindleyi. The cambium usually consists of typical
fusiform initials and irregularly shaped ray initials. The fusiform
initials produce the vascular elements, laticiferous cells and, in
the perennials, a large amount of storage parenchyma. Rays de-
rived from the irregular ray initials are not distinct in M. lindleyi
but occur infrequently in the storage root of the perennials. Ana-
tomical differences among the three species of Microseris are par-
ticularly evident in the development of secondary tissues. Micro-
seris lindleyi, which is an annual, produces an abundance of secon-
dary xylem in the primary root and a comparatively small amount
of secondary phloem. On the contrary, the perennials M. laciniata
and M. borealis produce a broad zone of secondary phloem consist-
ing largely of storage parenchyma, and only a small amount of
secondary xylem. The fleshy roots of both perennials consist pri-
marily of storage parenchyma in which are embedded strands com-
posed of phloem elements and laticifers. These strands appear in
continuous or discontinuous rings in cross sections. A decreased

number of these strands occurs in the innermost rings, as in Taraxa-cum kok-saghyz (3, p. 19) and Cichorium intybus (29). This arrange-ment of tissues is similar to that of fleshy roots in other Compositae such as Parthenium argentatum (2). The number of phloem strands in Microseris, however, does not correspond to the number of leaves as it does in Taraxacum kok-saghyz according to Savchenko (43).

In all three species, laticifers are in close association with sieve tubes as described for other Cichorieae (3, p. 13 and 29). Anastomoses between sieve tubes and laticifers were observed in all three species of Microseris. In M. lindleyi, round areas appear in the lateral walls of a sieve tube element adjacent to a laticifer, which may or may not be traversed by pores. Sieve tubes thus ap-pear to serve as extensions of the laticifer system. Dippel (17, p. 105) reported a similar situation in other Cichorieae which he stu-died but his findings were denied by subsequent workers (3, p. 19; 44, p. 141). In all cases, observed anastomoses in Microseris were between nonfunctional sieve tubes and adjacent laticiferous cells.

The ability of laticifers to produce bulges or protrusions, which may end blindly or anastomose with each other at the point of contact, is common in all three species and other members of the Cichorieae (3, 29, 37, 38). Microseris laciniata shows a remark-ably pronounced development of laticifers and protrusions ending

blindly in parenchymatous tissue of the root are frequent, whereas

in the other two species the phenomenon is confined to the leaf re-

gions.

Initiation of the articulated laticifer system in the seedling oc-

curs in all likelyhood in the cotyledonary node and from there ex-

tends to the cotyledons and the root. This pattern of development is

characteristic of the non-articulated laticiferous system in Nerium

oleander (33). In Scorzonera hispanica and Tragopogon eriospermus,

the laticifers develop first in the root and from there advance to-

ward the opposite end of the embryo (Schmallhausen in 44, p. 142).

In all three Microseris species, two systems of laticifers are present

in the primary tissues; the first originates in the region immediately

outside the protophloem in the cotyledonary node of the embryo,

abutting the endodermis as is described for the Cichorieae in gener-

al (47, p. 463), and the second system develops later in the primary

phloem. Additional laticifers differentiate in the secondary phloem

in association with the strands embedded in the storage parenchyma.

A hypodermal system, as occurs in Tragopogon eriospermus and

Scorzonera hispanica (44) was not observed in Microseris. Anasto-

moses between lateral walls of adjacent laticiferous cells occur

prior to anastomoses of end walls as in Tragopogon and Scorzonera

(44, p. 148). In Parthenium argentatum (2), Taraxacum officinale

and Lactuca virosa (17, p. 14), Taraxacum kok-saghyz (3, p. 19)

and Cichorium intybus (29), end wall anastomoses occur prior to lateral wall anastomoses. Secretory ducts as described by Tetley (50) for other Compositae are not present. In M. borealis, however, secretory cavities are formed in the endodermal region of the root of five-month-old plants, although less regularly than those present in Senecio (58). Similar cavities in the endodermal region along with laticifers was reported by Van Tieghem for Scorzonera (53).

The sieve tubes have been discussed together with the laticifers. In all three species, one companion cell is associated with a sieve tube element and is often of the same length, as in Taraxacum kok-saghyz (3, p. 13) and Cichorium intybus (29). The phloem parenchyma exists as individual cells which may divide transversely later.

An abundance of secondary xylem is found only in the annual species, M. lindleyi, and there is a greater variety of xylem elements than in the two perennial species. The scalariform to reticulate lateral wall thickenings of the vessel elements, and the simple perforated end walls observed in M. lindleyi are common in the Compositae (16, p. 74), but the Cichorieae may exhibit multi perforate plates also. Scalariform perforation plates were not observed except where vessel elements had long tapering ends that overlapped. Bordered pits on the lateral walls are tangentially elongated and opposite in the first formed secondary xylem but are round and

alternate in the later xylem. Taraxacum kok-saghyz (3, p. 13) shows

scalariform pitting similar to that in the early xylem of Microseris,

but in Cichorium intybus (29) the vessel elements usually have oval,

opposite pits. The number of vessels in each group in the primary

root does not correspond to the average given by Carlquist (10, p. 75)

for woody Cichorieae, although there is a definite tendency toward

arrangement of vessels in radial rows. The libriform fibers are

thick walled. Carlquist described several species with thin walled

fibers in the woody Cichorieae. In M. lindleyi, elements with a

gradation in the degree of pitting were observed. The pits ranged

from those with a distinct border to those with less border to those

with slitlike inner openings with the two slits of a pit pair perpendi-

cular to each other. The simplest form is a simple pit, which is

found in the thick walled fibers. Tracheids occur in all three spe-

cies, although sporadically. Xylem parenchyma is found as indivi-

dual cells, but these may divide at a later stage. In the two peren-

nials, lignified xylem elements are scanty and consist of the scalari-

form to reticulate vessel elements and a few pitted elements. The

xylem parenchyma in these perennials also exists as individual cells

which may divide transversely at a later stage. Typical ray paren-

chyma was not observed in any of the three species. The irregular

fusiform initials, which appear as short structures with fusiform

shape in tangential section, are not obviously elongated radially,

and they produce parenchymatous cells as seen in transverse section.
The presence of parenchyma rays opposite the protoxylem poles dur-
ing early secondary growth in all three species was also observed
for Cichorium intybus (29).

The three species of Microseris possess a persistent cortex,
as does Parthenium argentatum (2, p. 24). On the contrary, early
sloughing of the cortex occurs in Taraxacum kok-saghyz (3, p. 12;
43), Lactuca sativa (24) and Cichorium intybus (29). The cortical
cells as well as the outer layers of storage parenchyma cells pos-
sess radial septa, which were also observed in the chicory (29). In
all three species the first cork cambium arises in the subepidermal
layers.

Organization of the shoot apex was determined from relatively
young seedlings grown in the greenhouse. The apices of all three
species show a one-layered tunica. The shoot apex of chicory (29)
has a two-layered tunica, and Gifford (21, p. 521) stated that a two-
layered tunica is common in the Compositae. Fitchia speciosa was
reported to possess a two-layered tunica (9, p. 43).

Differentiation of the primary vascular system in the shoot is
similar in all three species and follows the pattern of differentiation
described for Helianthus annuus (18). The laticifers are always the
first cells to mature at the abaxial side of a leaf trace. Only M.
lindleyi developed an aerial stem in the greenhouse, but in the

field both the perennials also develop aerial stems or peduncles.

Under certain conditions all three species develop an aerial stem

(Chambers, personal comm.). Internally, the two perennials show

a primary thickening meristem very close below the shoot apex of

the stem of the rosette stage. This tissue, which accounts for a con-

siderable growth in diameter of the caudex, is also found in

Taraxacum officinalis (40, p. 328). The aerial stems of M.

laciniata and M. lindleyi lack an endodermis, a phenomenon

considered by Esau (19, p. 362) to be common. An endodermis is

differentiated a short distance below the shoot apex in the rosette

stages of M. laciniata and M. borealis. Arrangement of the vascu-

lar tissues is similar in all three species in that all possess a

eustele. The bundle cap of primary phloem fibers, which is com-

mon for the Compositae in general and is found in Cichorium intybus

(30), is present in all three species studied. Lignified prosenchyma

occurs in the pith region immediately adjacent to the primary xylem

in the aerial stem of M. lindleyi. This characteristic has not been

mentioned for other Cichorieae, except for Scorzonera (37) where

lignification of the pith cells occur.

Medullary bundles occur only in the aerial stem of M. laciniata

and are arranged in a pattern similar to type III of Peter (37, p. 11).

In this type, in addition to the regular ring of vascular bundles

there are scattered phloem strands in the pith. The latter strands

may or may not have xylem elements associated with them. In M. laciniata, however, the phloem strands form a more or less regular ring at the inner periphery of the primary vascular bundles. In older stems, the regular arrangement is somewhat disrupted by the differentiation of additional strands and the phloem strands form a more or less regular ring at the inner periphery and sometimes also at the outer periphery of the primary vascular ring. In the stem of M. lindleyi and the rosette of M. borealis, the laticifer system is confined to the region adjacent to the protophloem, to the metaphloem and secondary phloem. Because of the presence of medullary bundles, laticifers are found also in the pith of M. laciniata, in association with the medullary phloem strands. This was also found in other Cichorieae such as Helminthia echinoides (38, p. 398). There are also cortical strands of phloem, with laticifers which may be associated with leaf traces in that region. Dippel (17, p. 67) found similar phloem strands with associated laticifers in Lactuca, Sonchus, Tragopogon and Scorzonera, whereas Trecul (54) did not find laticifers in the pith. The presence of medullary bundles was thought to be a primitive feature (59) and they were assumed to represent leaf traces (16, 59).

Root contraction occurs in the primary roots of all three species and in the adventitious roots of the two perennials. In the primary roots, however, contraction is not distinct and is detected

primarily by microscopic folding of the Casparian strip. This characteristic was recognized first by Rimbach (41, p. 113) in the monocots that he studied; later it was also observed in <u>Brodiaea</u> <u>lactea</u> (46) and in <u>Taraxacum</u> (42). In the adventitious roots, there is a radial enlargement and shearing of the outer cells of the cortex accompanied by a shortening of the innermost cells, and later also of the stele. This results in a transverse wrinkling of the passive outer cortex. This manner of contraction is common for the dico-tyledons (De Vries, in 51, p. 571) and is also exemplified by <u>Tarax-</u> <u>acum</u> and <u>Heracleum</u> (42). No extreme tissue rearrangement as described by Thoday (51) for <u>Oxalis</u> <u>incarnata</u> in which the vascular strands become distorted was observed. The contraction of the root draws the plant down to a suitable level for growth (42, p. 182). <u>Microseris</u> <u>laciniata</u> develops a vertical rootstock and <u>M.</u> <u>borealis</u> produces a short horizontal rhizome.

In discussing the significance of the differences in the develop-mental anatomy of the three species studied for clarification of evo-lutionary lines, several findings may be mentioned. The various xylem elements of <u>M.</u> <u>lindleyi</u> show resemblance to those of the woody Cichorieae described by Carlquist (10, p. 89), who suggested that woodiness of the insular species was secondarily acquired from herbaceous species. The alternate leaf arrangement in <u>M.</u> <u>lindleyi,</u> as compared to the distichous leaf position in the rosettes

of the two perennials, is another advanced character (15, p. 480).

The absence of medullary bundles in the aerial stem of M. lindleyi

is advanced in Worsdell's view (59, p. 480), which is, however,

questioned by Davis (16) who stated that medullary strands are

formed in connection with leaf traces. Evidence from a study of

climatic evolution in western North America (4) used to explain

evolution in Microseris (13) points to M. lindleyi as an annual which

evolved later than the two perennials. The fleshy roots of M. lacini-

ata and M. borealis represent a more specialized condition than

those of the annual species. This character, however, has develop-

ed in relation to a moist habitat and is thus an ecological specializa-

tion. On the other hand, M. lindleyi has adapted to the dry habitat

resulting from the increased aridity in earlier periods in Northwest

America by assuming a short and rapid life cycle (13, p. 127). Also,

morphological features (10) and chromosomal evidence (49), in addi-

tion to anatomical factors described in this paper, point toward an

evolutionally more advanced position for M. lindleyi as compared

with that of the perennials.

Of the two perennials, M. laciniata is assumed to have evolved

earlier than M. borealis, due to the fact that a vertical rootstock of

the former species resembles putatively the primitive or original

condition more than does the horizontal rhizome of M. borealis

(5, p. 160; 6, 34). Also, the presence of medullary bundles in M.

laciniata and the absence of those structures in M. borealis is

another factor suggesting a more primitive condition in M. laciniata.

With regard to the original purpose of this paper, it may
therefore be concluded that anatomical studies of the three growth
forms of Microseris confirm findings of previous workers, in so
far as evolutionary lines are concerned. M. laciniata possesses
more primitive characters and may have evolved earlier than the
two other species. It is followed by the somewhat more advanced
M. borealis, and the species with the most advanced characters is
M. lindleyi.

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APPENDIX

Figure 1A. Microseris borealis, approximately eight months.
Primary root in the center flanked by three ad-
ventitious roots. Arrow points toward a dormant
adventitious root. X 1/2.

Figure 1B. Microseris borealis, approximately 1-1/2 year.
Many slender adventitious roots originating from
a short, horizontal rhizome. X 1/2.

Figure 2. Microseris laciniata, approximately nine months.
Two stout adventitious roots originating from a
vertical rootstock. X 1/2.

Figure 3. Microseris lindleyi, approximately four months.
Small, short taproot. An aerial stem of which
the lowermost leaves whither. X 1/2.

Figures 1-3

Morphological habit of the three species of Microseris.
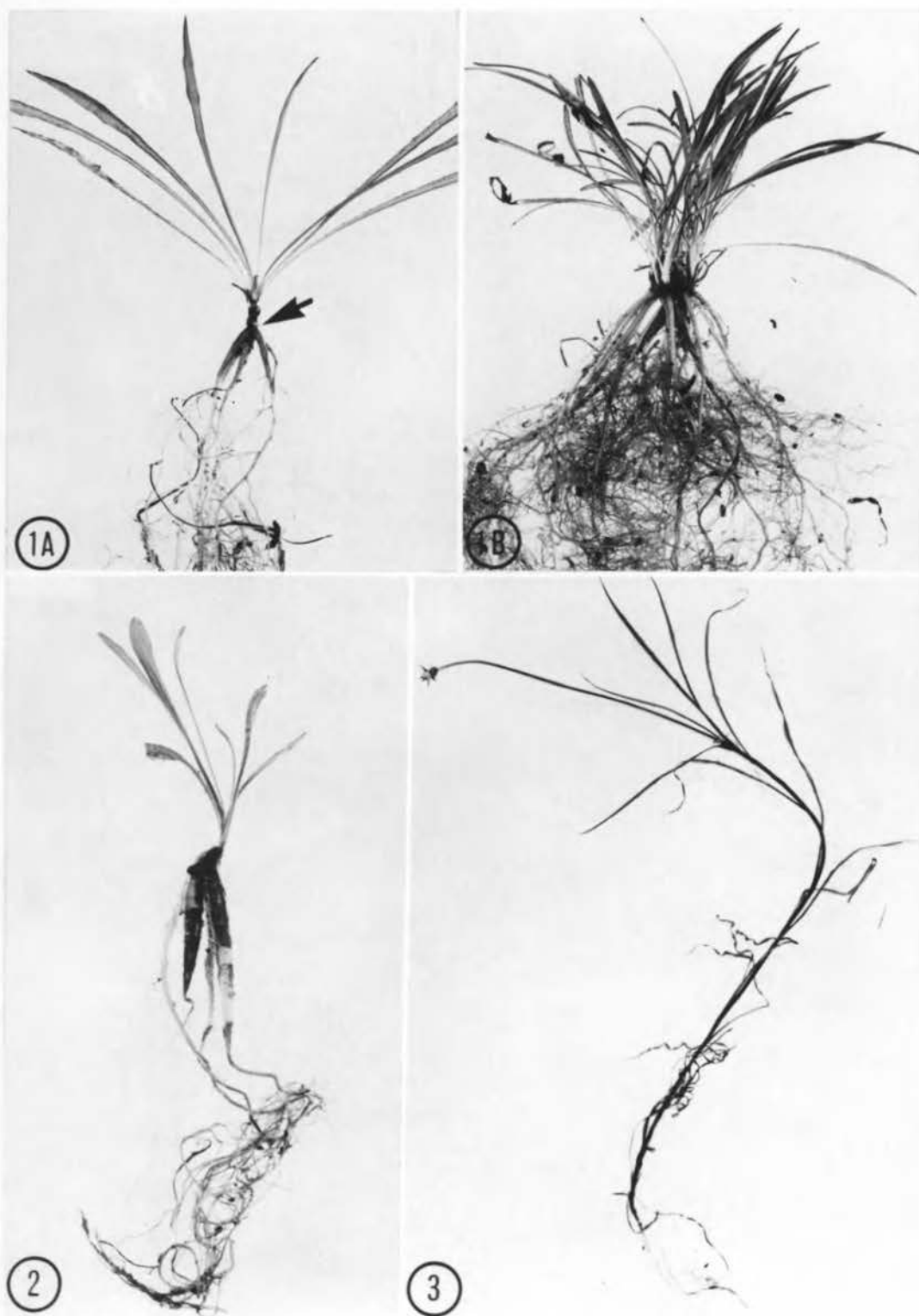
Figure 4. Median longitudinal section through the pri-
            mary root apex. X100.

Figure 5. Detail of the initial region in Figure 4. X430.

            r c - root cap
            p d - protoderm
            c o - cortex
            c c - central cylinder

Figure 6. Cross section through primary root of six day
            old seedling showing differentiating lateral root.
            X100.

Figure 7. Cross section through diarch lateral root. En-
            dodermis biseriate opposite the protophloem
            poles. No pronounced cambial activity. X100.

                    Figures 4 - 7

                  Microseris borealis

        Primary root tip and the lateral root.
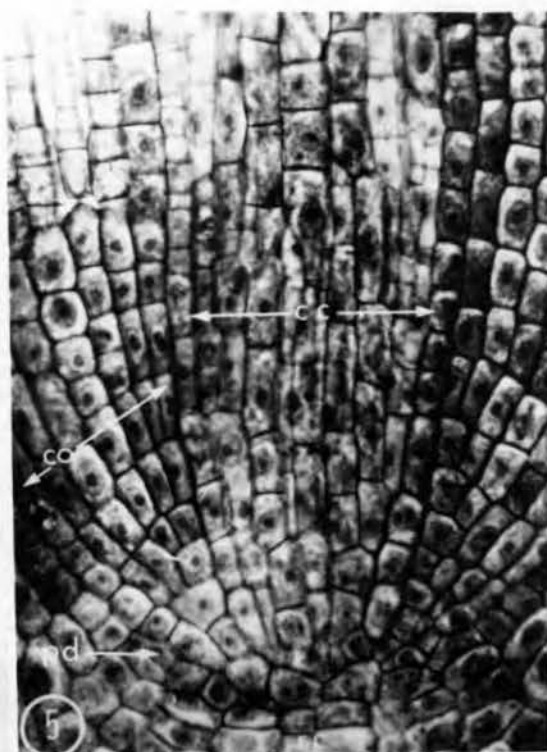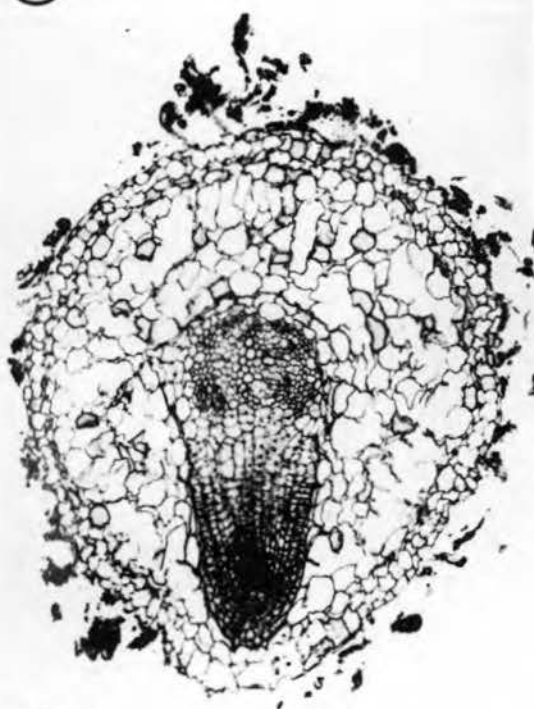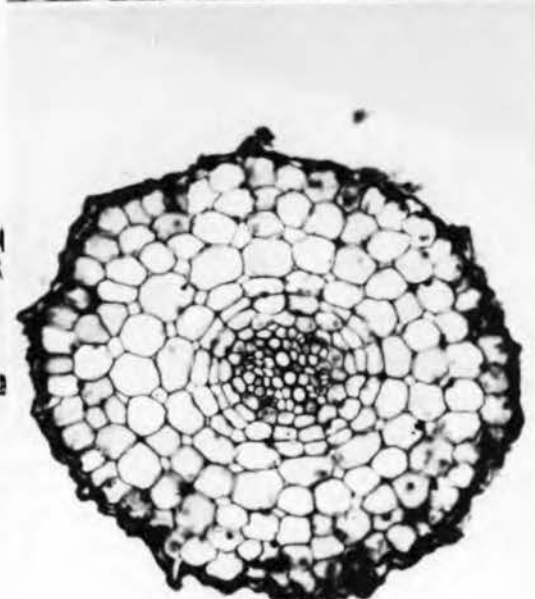
Figure 8.   Immediately above the root initials.
             Arrow points toward root initials.

Figure 9.   Delimitation of the one layered pericycle; peri-
             clinal divisions in endodermis.
             p - pericycle

Figure 10.   Differentiation of protophloem sieve tube ele-
             ments.   The two arrows point to differentiat-
             ing sieve tubes which at this stage have
             thickened walls.   Innermost layer of the cor-
             tex divides periclinally.

Figure 11.   The two first sieve tubes matured.   In the cen-
             ter of the central cylinder, differentiation of
             the first metaxylem element is shown by the
             vacuolated cell.

Figure 12.   Maturation of the first protoxylem elements.
             p x - protoxylem
             p   - pericycle
             c   - Casparian strip

Figure 13.   The primary xylem and phloem matured.

Figures 8-13

Cross sections through root tip of Microseris
borealis showing successive stages of root de-
velopment.   X430.
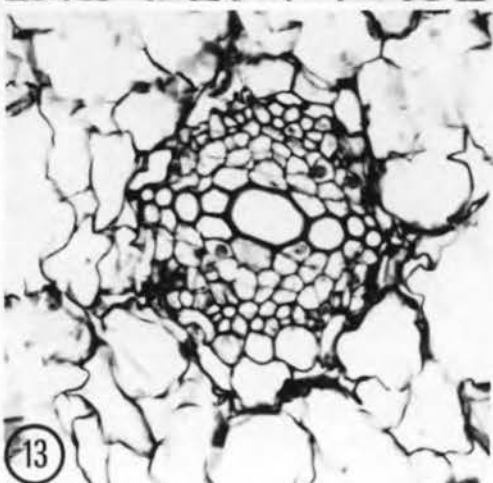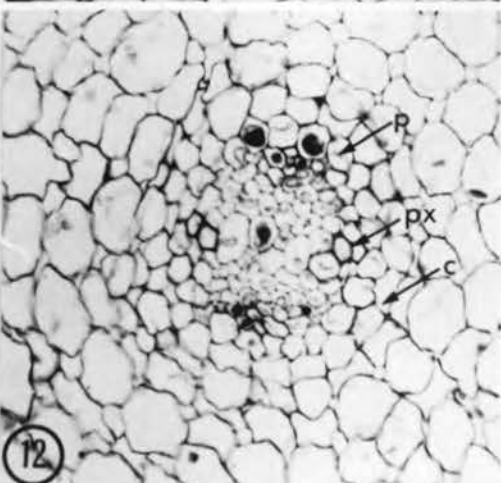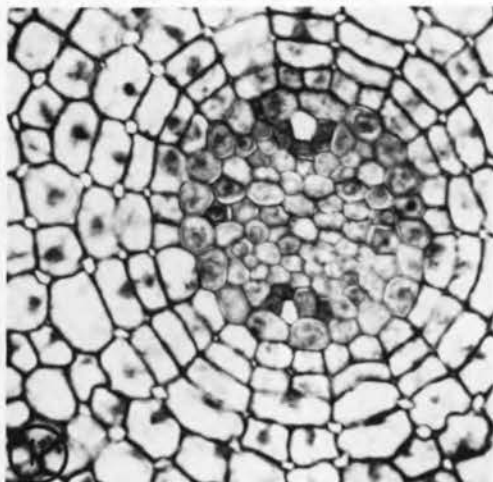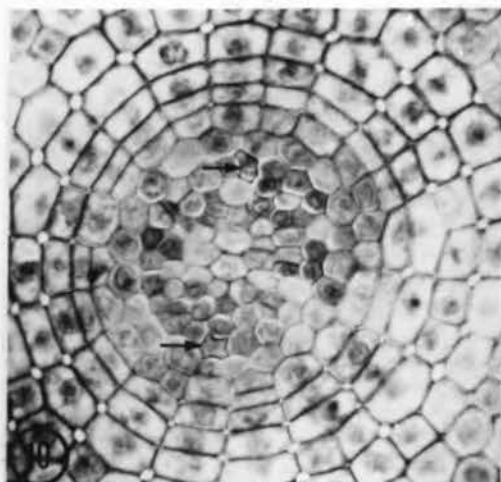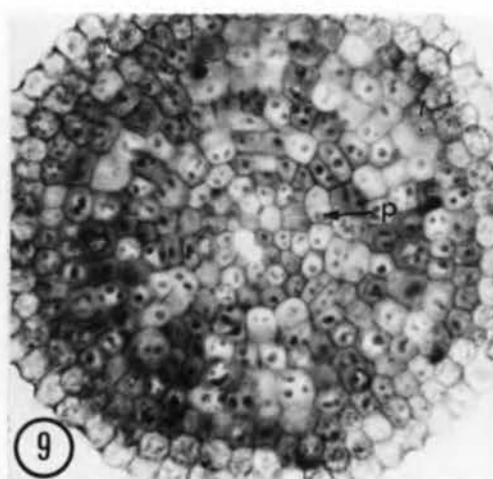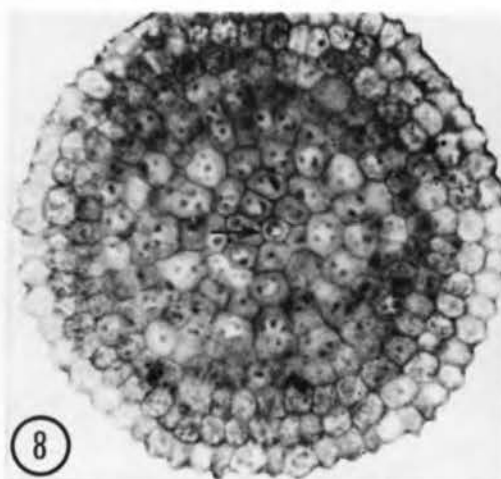
Figure 14. A - G Diagram of seedling to show
transition. Xylem drawn in
three dimensions. Phloem
drawn in two dimensions.
Explanations in the text.

Figure 14

Transition in <u>Microseris</u>

D

C

B

A

(14)

G

F

E
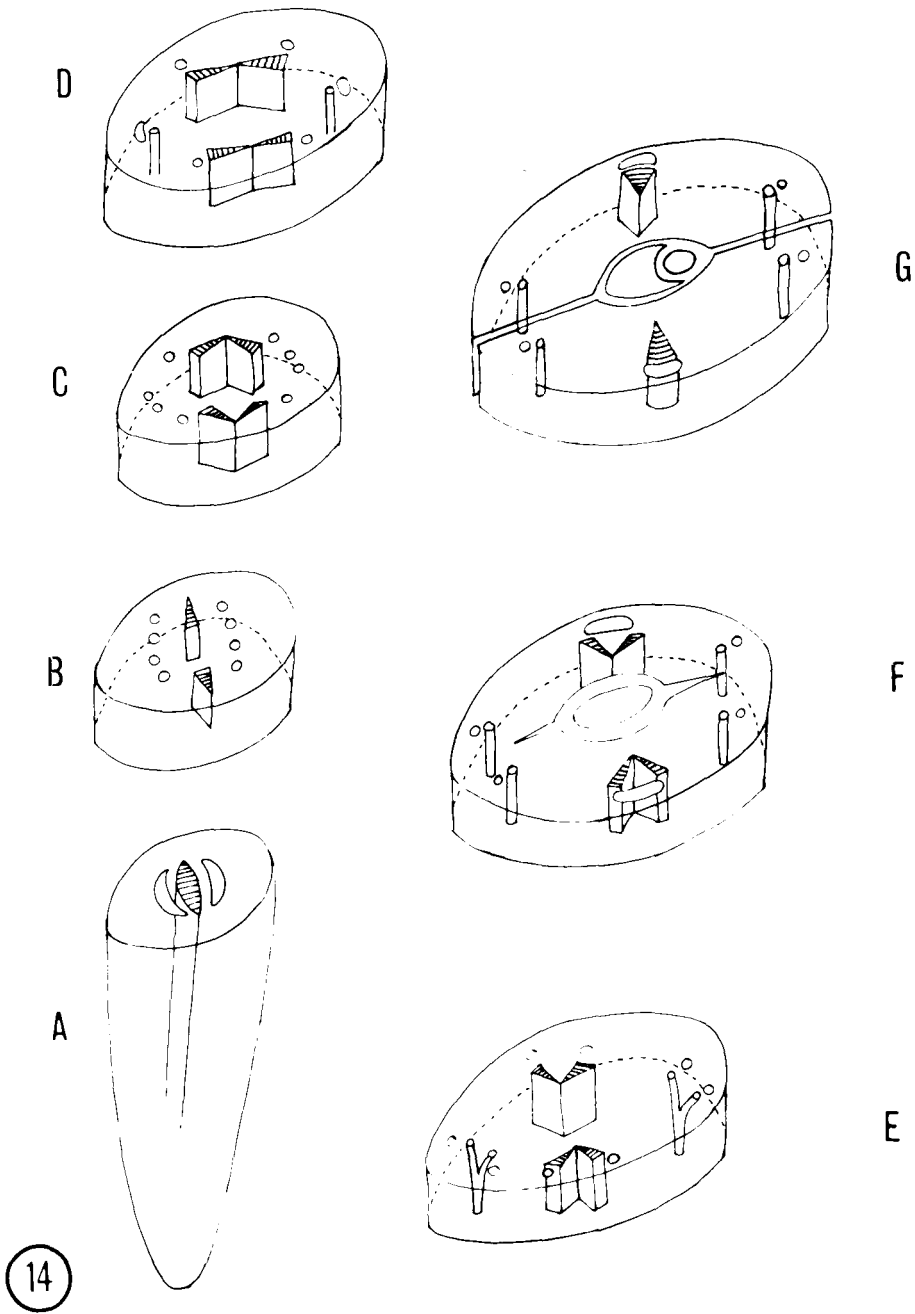
Figure 15. Cross section through primary root of two-month-old plant. An irregular cork is formed in the persistent cortex. X100.

p w - parenchyma wedges opposite the protoxylem.

Figure 16. Portion of a cross section through a six-month-old primary root. X100.

e n - endodermis

p s - phloem strand

Figure 17. Tangential section through the inner zone of zylem of primary root of a six-month-old plant. X210. Arrow points toward scalariform thickening of the lateral wall.

Figure 18. Radial section through outer zone of xylem and phloem of primary root. X210.

s t - sieve tube

c m - companion cell

s - septum of septate fiber

Figures 15-18

Microseris lindleyi

Secondary growth in the primary root.
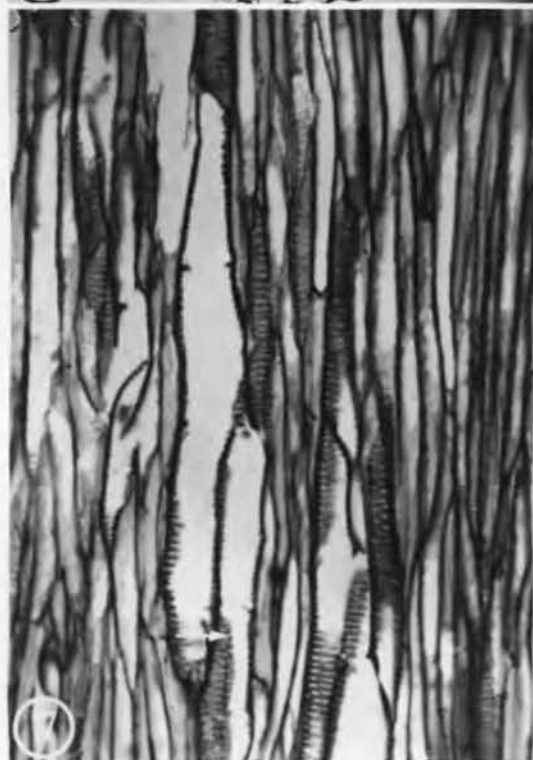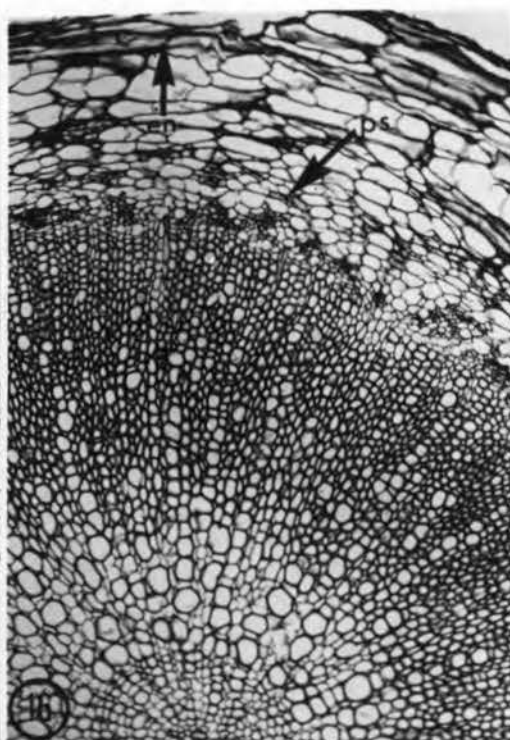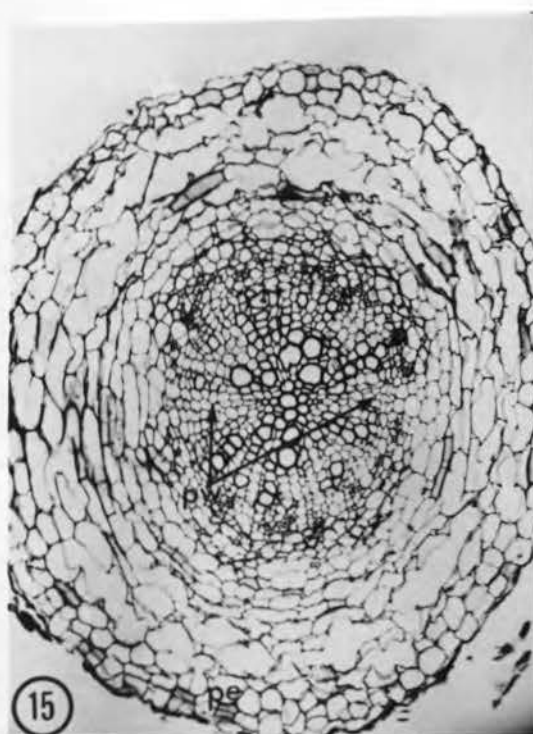
Figure 19. Radial section of xylem of primary root. X210.
White arrow points to a xylem parenchyma cell.

Figure 20. Radial section through cambial region of the
primary root of a six-month-old plant. At the
right: a differentiating phloem strand. White
arrow points toward thin region in the lateral
walls of laticiferous cells, prior to anastomes.
X210.

Figure 21. Tangential section through phloem region of a
six-month-old primary root, showing phloem
strands with anastomosing laticifers. X100.

Figure 22. Detail anastomoses as in Figure 21. Arrow
points toward protrusions produced by cell walls
which anastomose of point of contact. X430.

Figure 23. Longitudinal section through phloem of six-
month stem. Arrow points toward opening be-
tween laticifer (right) and sieve tube (left). At
the left hand side of the two circles are thick-
ened areas of the lateral wall. X210.

Figures 19-23

Microseris lindleyi

Laticiferous System.
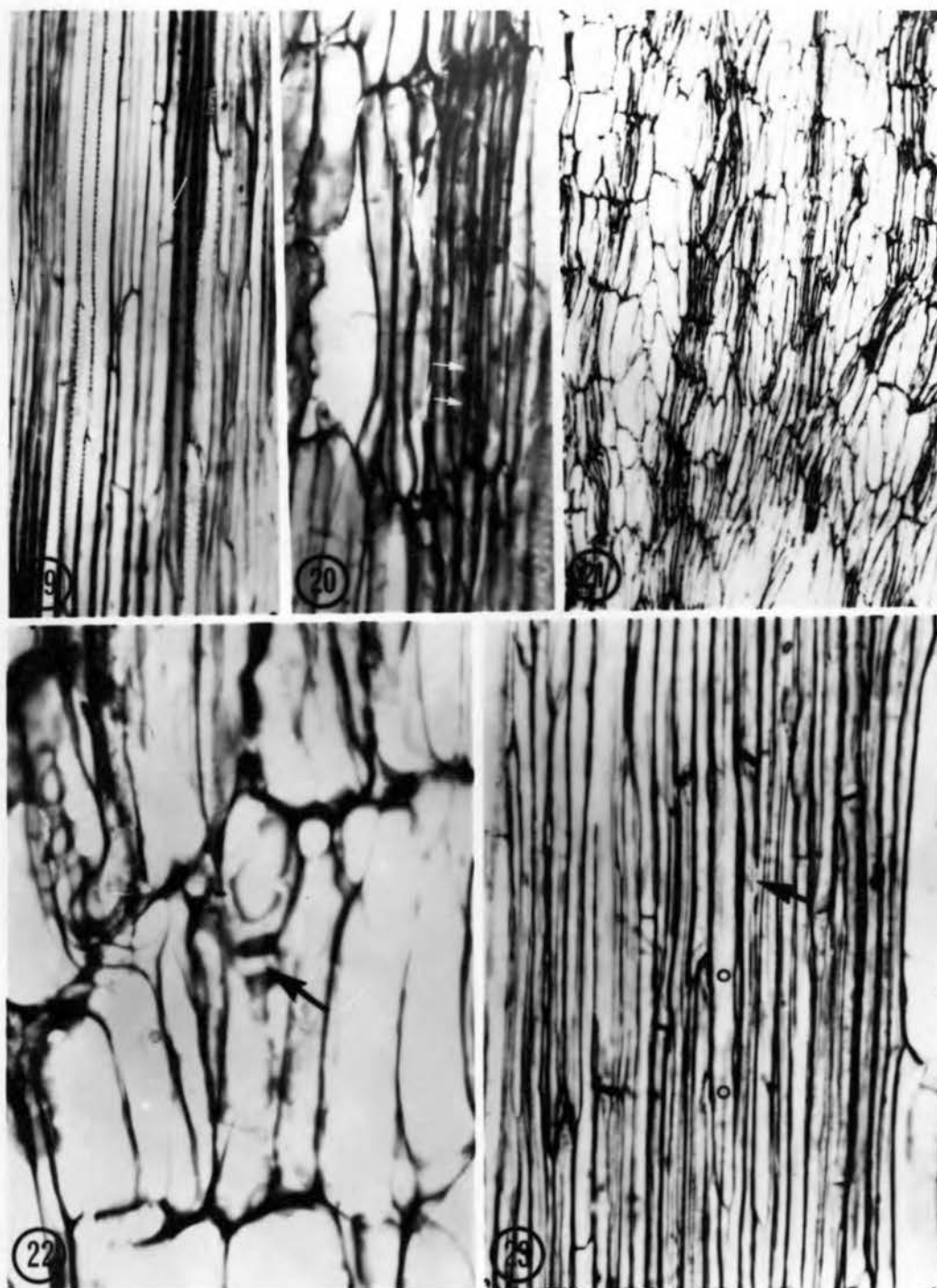
Figure 24. Longitudinal section through shoot apex of two-month-old plant. X430.

Figure 25. Cross section through young leaf. At left: the many celled head of a glandular hair. X430.

    p c - procambium
    l - maturing laticifer at abaxial side of the procambial strand.

Figure 26. Section through lower part of the leaf in Figure 25. X430.

    s t - sieve tube.

Figure 27. Cross section through upper portion of the shoot of a two-month-old plant. X100.

Figure 28. Cross section of a young stem. X210.

Figures 24-28

Microseris lindleyi

Shoot apex and differentiation of vascular tissue.
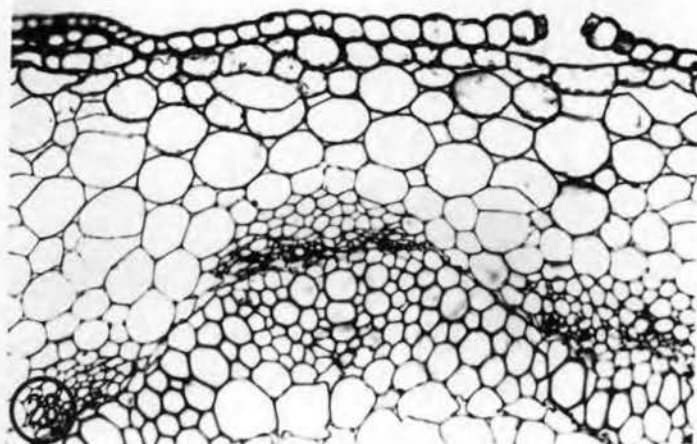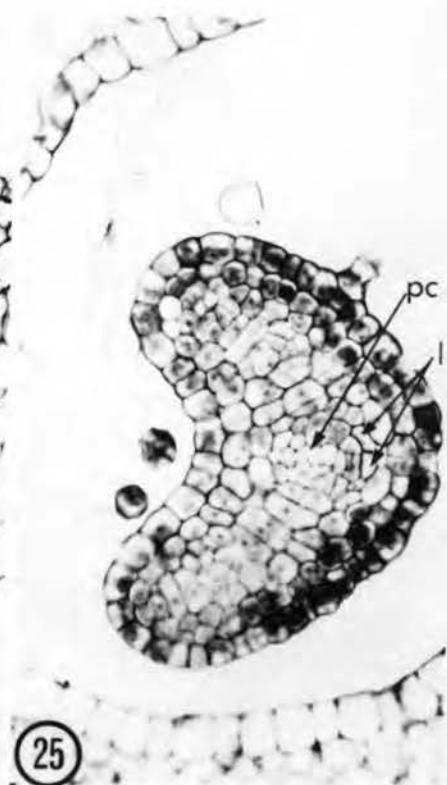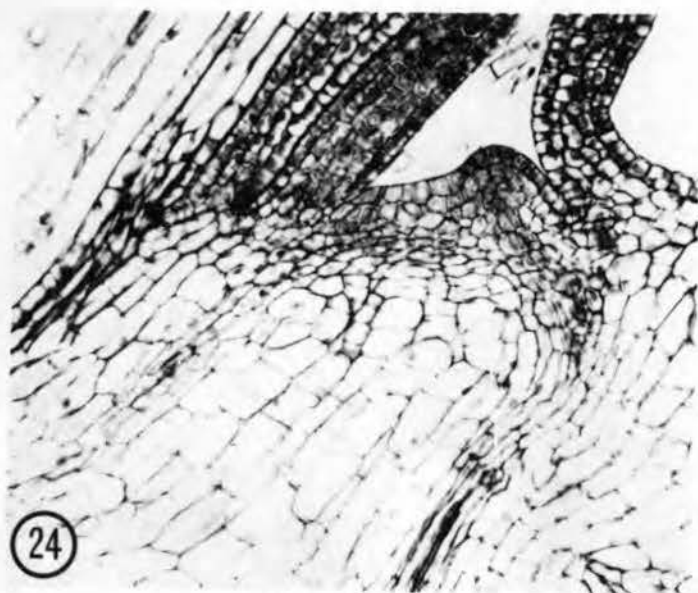
Figure 29. Cross section through a young portion of
the stem. X100.

Figure 30. Sector of Figure 29 in detail. X210.

1 - laticifer.

Figure 31. Cross section through older stem of six-
month-old plant. X27.

Figure 32. Detail of a portion of the stem in Figure 31.
X210.

p r - prosenchyma.

Figures 29-32

Microseris lindleyi

Cross sections through young and
old stem.

(29)

(30)

(31)

(32)
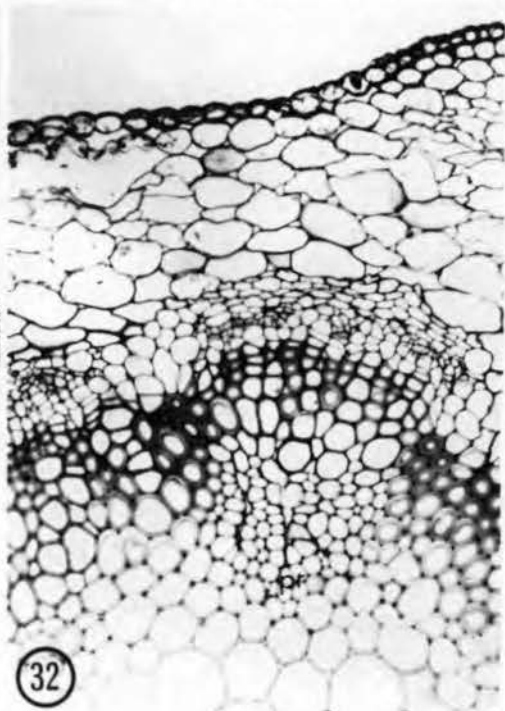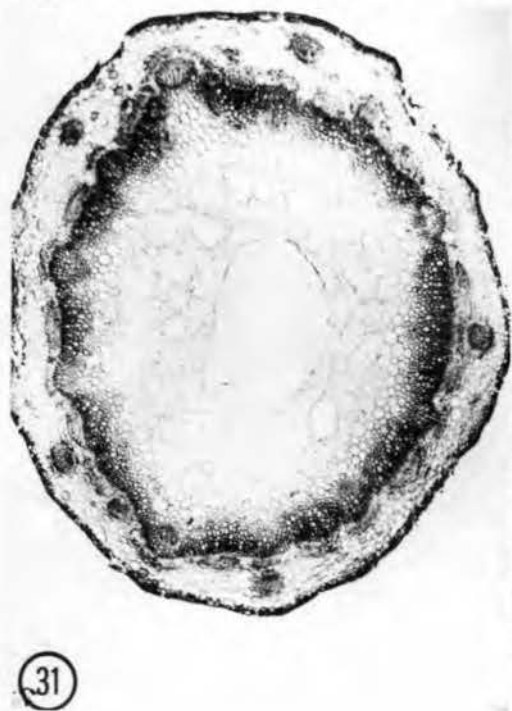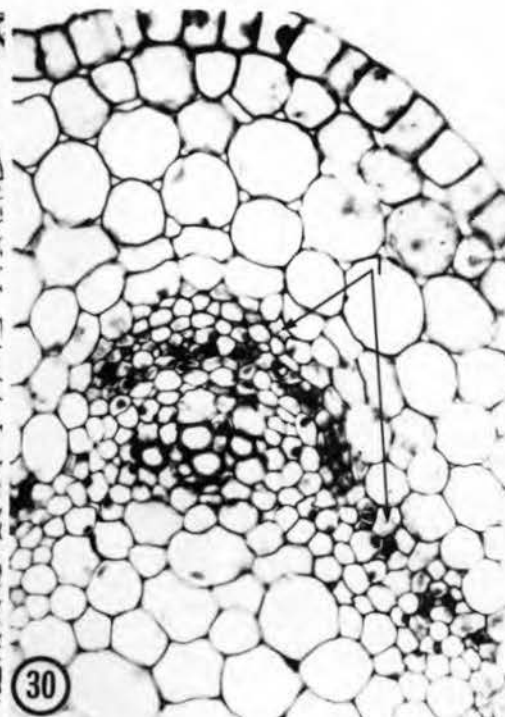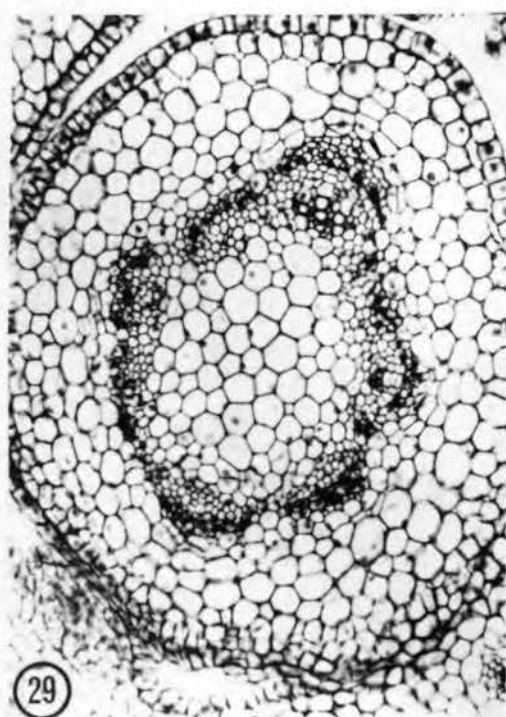
Figure 33. Cross section through base of hypocotyl of a one-month-old plant. X100.

Figure 34. Cross section through primary root of a two-month-old plant. X35.

Figure 35. Tangential section through the vascular cambium of an old primary root. Note the regular tiers of storage parenchyma at the lateral sides. X60.

f - fusiform initials

Figure 36. Tangential section through old root, to show the irregular fusiform initials here flanked by phloem strands. X60.

n f - non-typical fusiform initials.

Figures 33-36

Microseris borealis

Cross sections through hypocotyl, primary root and tangential sections of the cambium initials.
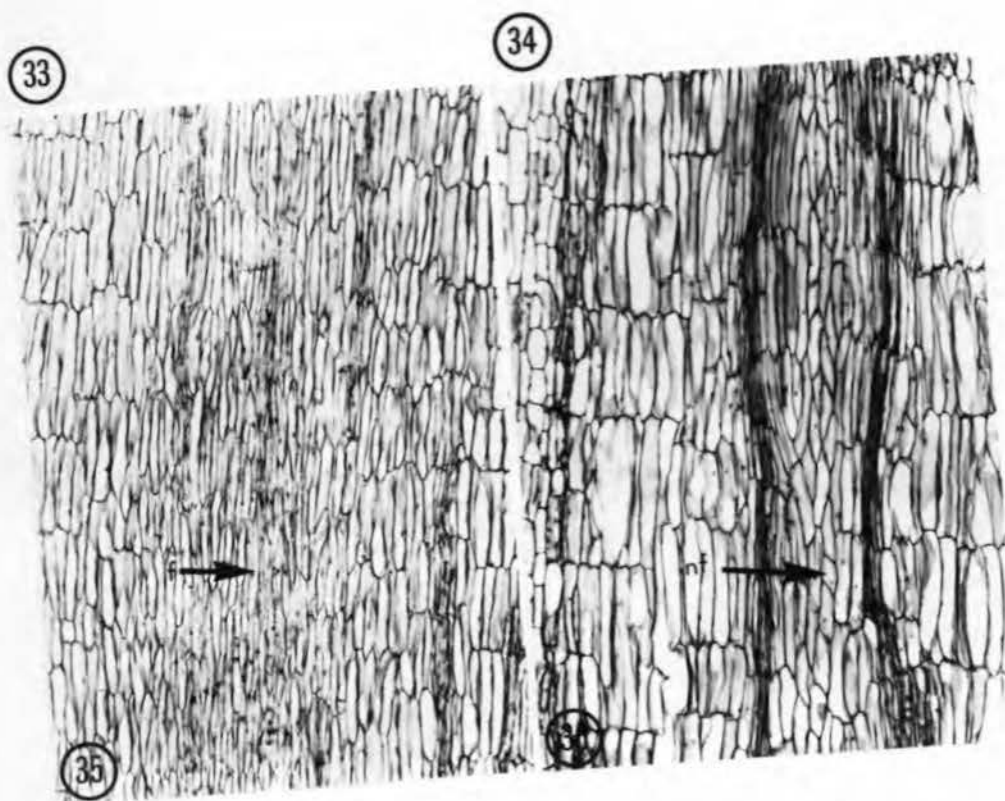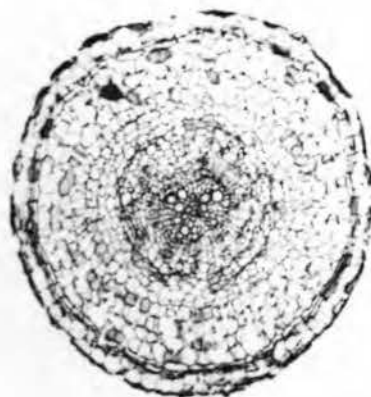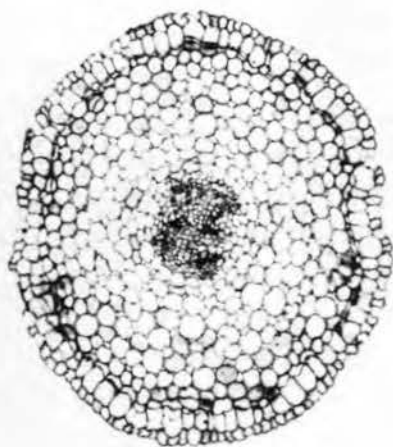
Figure 37A.   Cross section of a sector of a five-month-old
              primary root.   X60.
              Arrow points toward phloem strand.

Figure 37B.   Radial section of an older primary root.   X60.

Figure 38.   Detail of phloem strand in cross section.   X430.

              s t - sieve tube, with a companion cell at the
                  right hand side.
              p p - phloem parenchyma.
              l - laticifer.

Figure 39.   Detail of phloem strand in longitudinal section.
              X430.

Figure 40.   Detail of a phloem strand in the caudex of
              rosette stage, in longitudinal section.   X430.

              s t - sieve tube
              c m - companion cell

                      Figures 37-40

                    Microseris borealis

        Arrangement of phloem strands and phloem elements.
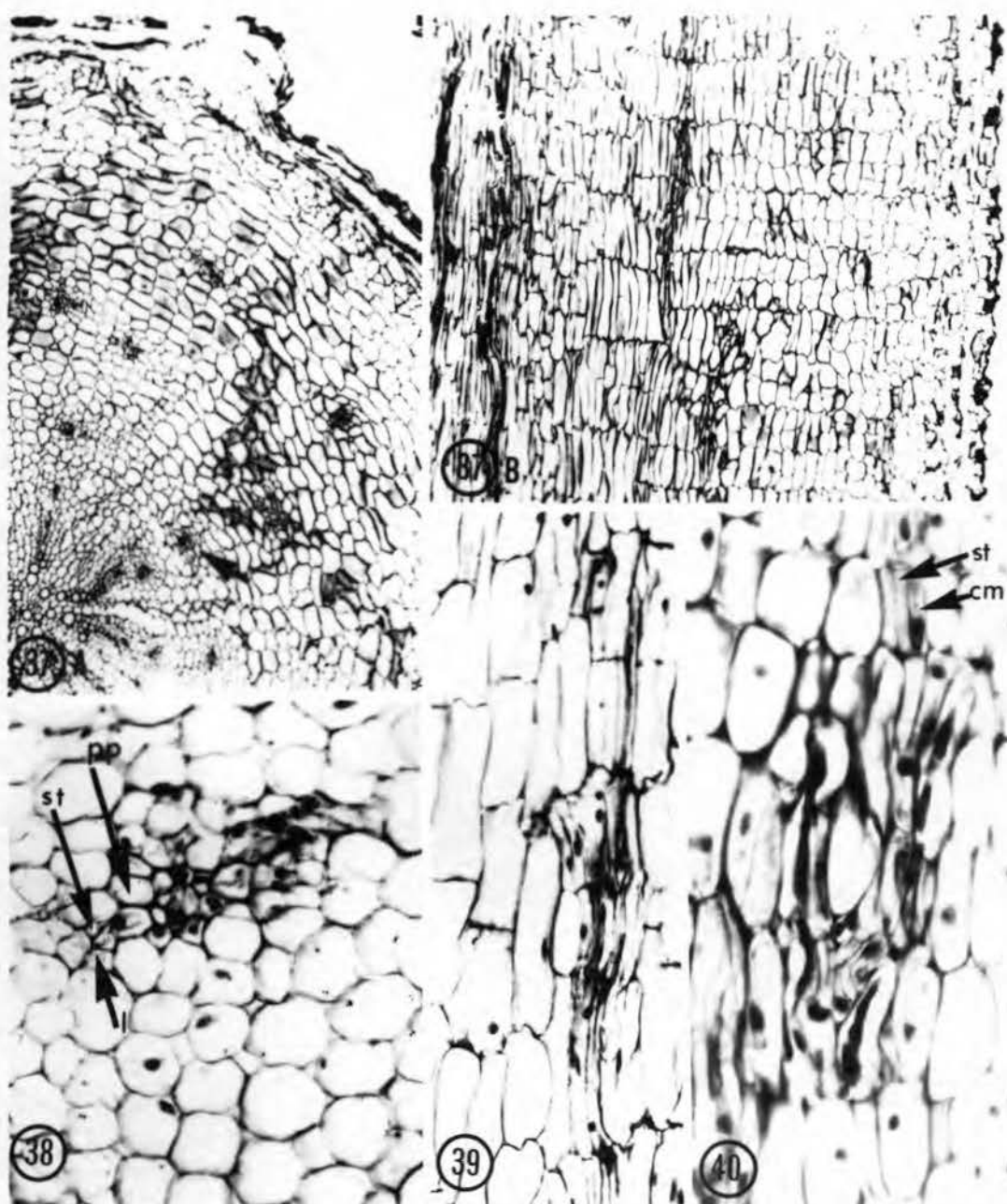
Figure 41. Cross section through a six-month-old
primary root. Arrow points toward
secretory cavity in the endodermal
region. X36.

Figure 42. Detail secretory cavity. X430.

e n - endodermis

Figure 43. Longitudinal section through six-month-
old primary root. The arrow points
toward a secretory cavity. X100.

Figures 41-43

Microseris borealis

Secretory cavities.
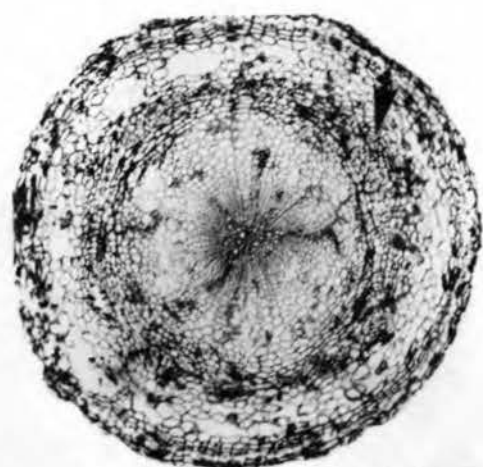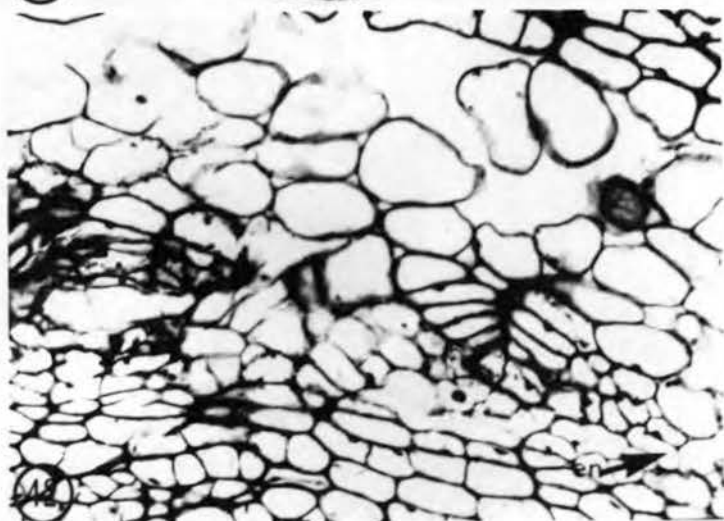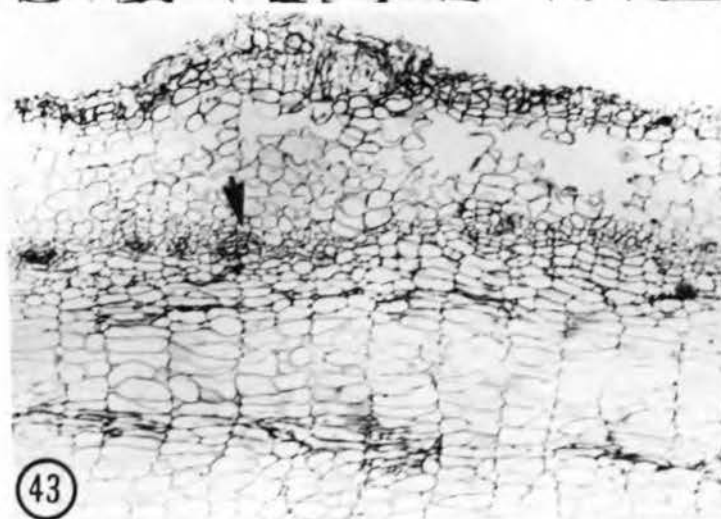
Figure 44.   Longitudinal section through epicotyl of a
              one-day-old seedling.   X210.

Figure 45.   Detail of laticifers in Figure 44.   Arrow
              points toward lateral anastomoses.   X430.

Figure 46.   Cross section through cotyledonary node of
              one-day-old seedling,   showing laticifers at
              the outer margins of the protophloem and
              also within the phloem region.   White arrow
              points toward a matured sieve tube.   X430.

Figure 47.   Longitudinal section through the stem apex
              of a two-month-old rosette.   X210.

              p t m - primary thickening meristem
              p c - procambium

Figure 48.   Cross section through the upper hypocotyl
              of a one-month-old plant.   X100.

                        Figures 44-48

                      Microseris borealis

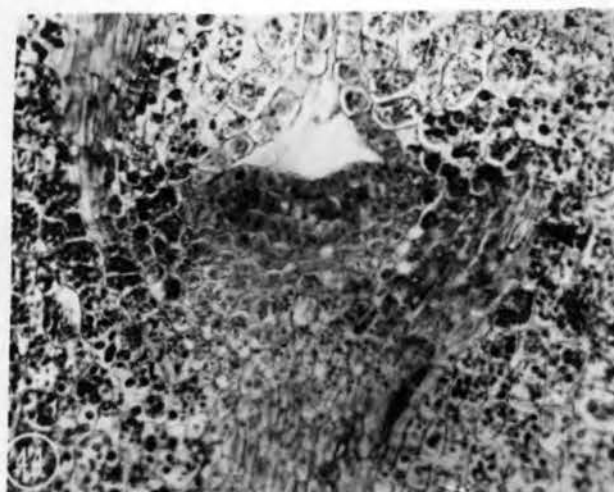   Shoot apices of seedling and rosette stages.
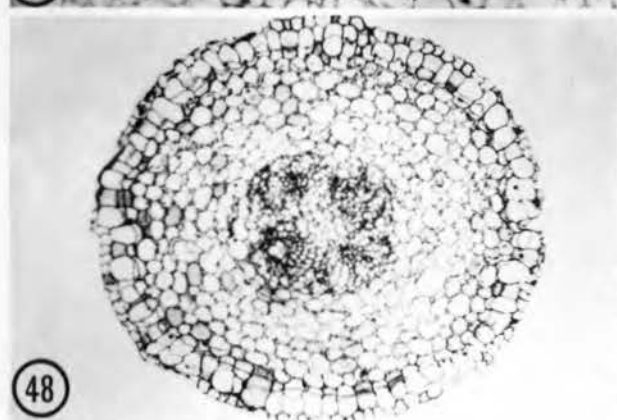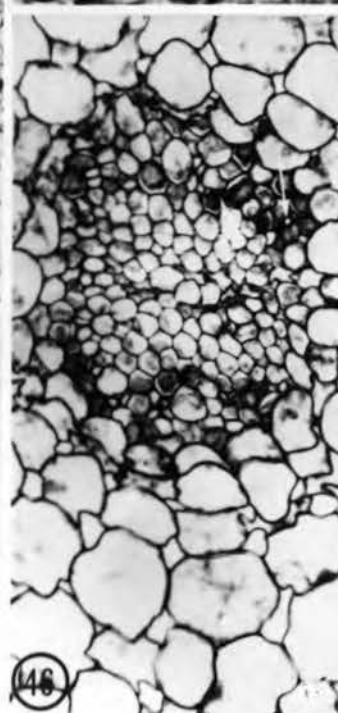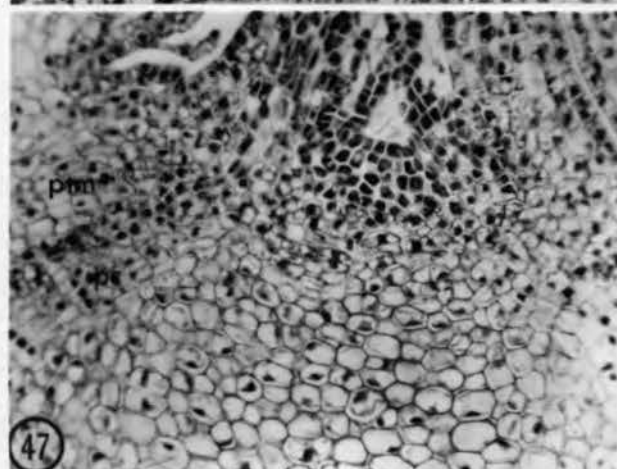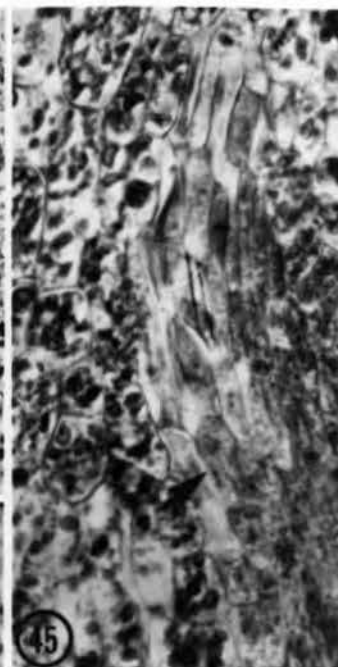
Figure 49. Cross section through caudex of a rosette.
X27.

Figure 50. Detail sector of section in Figure 49. X100.

Figure 51. Longitudinal section through caudex of a
rosette. X27.

p t m - primary thickening meristem
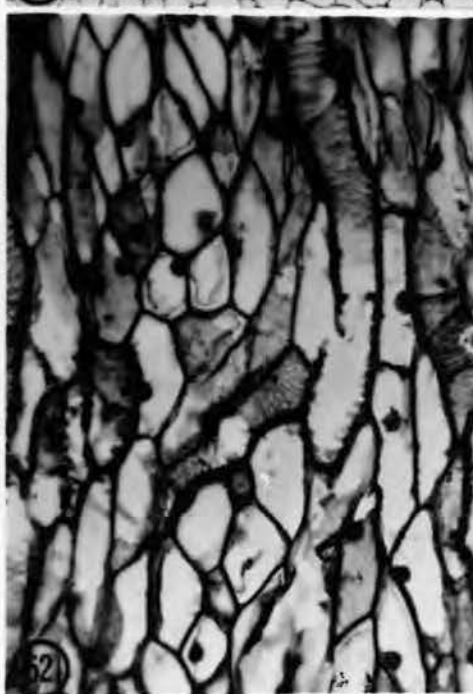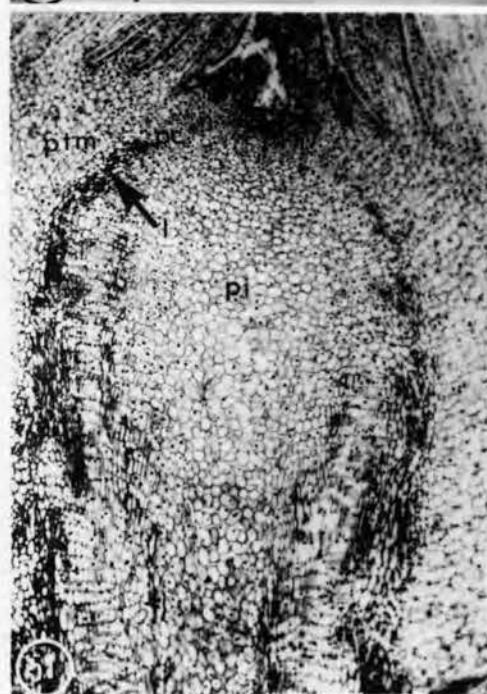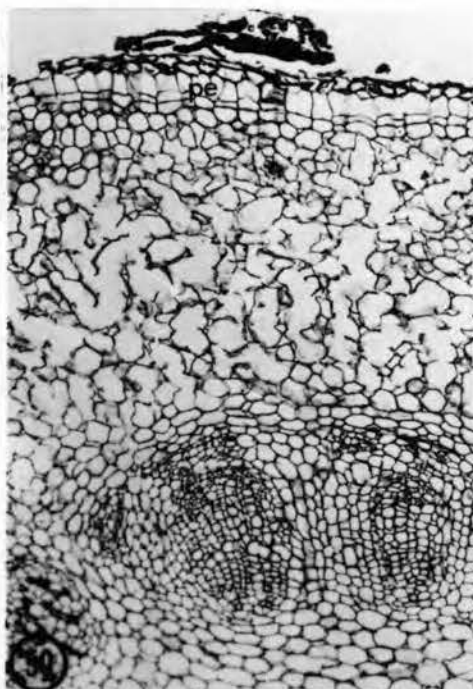l - laticifers in the phloem strands
p i - pith

Figure 52. Detail of the xylem elements in a longitudinal
section of the caudex. X430.

Figures 49-52

Microseris borealis

Cross and longitudinal sections through
rosette stage.

Figure 53. Longitudinal section through an old rosette
            showing initiation of an adventitious root. X27.

Figure 54. Longitudinal section through an adventitious
            root. X27.
            Arrow points to the endodermal region.

Figure 55. Detail of endodermis of the section in Figure 54.
            X430.
            Arrow points to folded Casparian strip.

                    Figures 53-55

                  Microseris borealis

         Initiation of adventitious root and internal
              indication of root contraction.

Figure 56.   Median section through adventitious root tip.
             The two white arrows point to two cell layers
             which constitute the two groups of initials.
             X210.

Figure 57.   Cross section close to adventitious root tip
             showing immature tetrarch stele.   X430.

Figure 58.   Cross section through older portion of an
             adventitious root.   Arrow points to endoder-
             mis which divide radially.   X100.

Figure 59.   Cross section through an old adventitious root.
             Arrow points to endodermis.   X100.

                    Figures 56-59

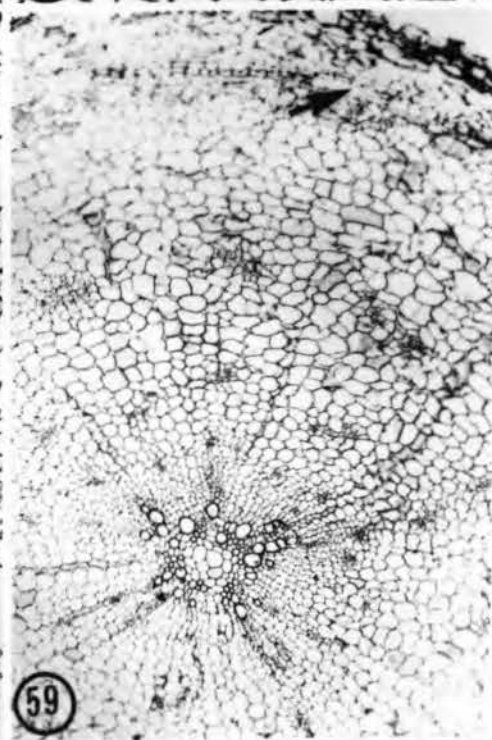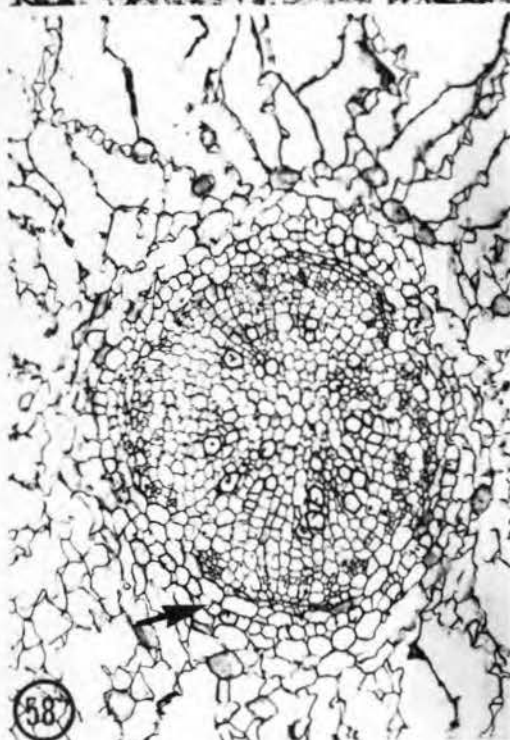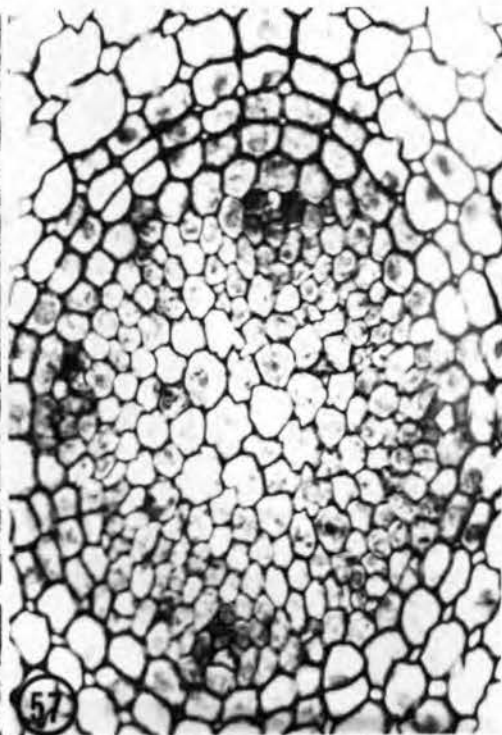   Microseris borealis

                 The adventitious root.

Figure 60. Cross section through young aerial stem. X60.

Figure 61. Detail sector of the section in Figure 60, show-
ing medullary phloem strands. X100.

s - phloem strand

Figure 62. Longitudinal section through stem at ground
level, at the end of growing season. X60.

s - phloem strand

Figure 63. Cross section through stem at ground level,
at the end of growing season. X60.

c o - cortex

Figures 60-63

Microseris laciniata

Medullary phloem strands in young and
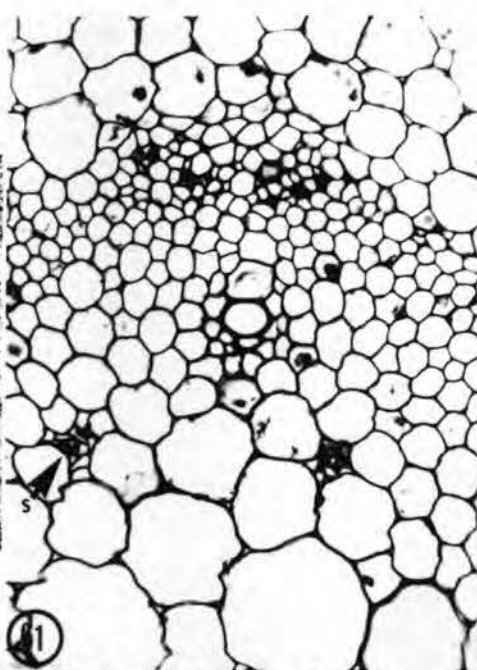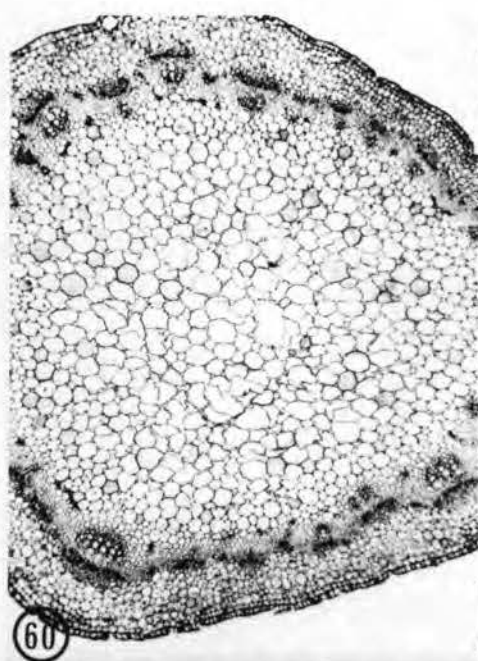old stems.

Figure 64. Portion of cross section of stem at ground
            level at end of growing season. X27.

            p s - phloem strand

Figure 65. Detail of medullary bundles in Figure 64.
            X210.

Figure 66. Detail of median leaf trace. Phloem strand
            at adaxial side, not connected with primary
            xylem. X210,

                    Figures 64-66

                 Microseris laciniata

            Medullary phloem strand in stem
                      and leaf.