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A Determination of Stelar Patterns in Various Root Divisions of Certain Angiosperms

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THE DETERMINATION OF STELAR PATTERNS IN VARIOUS ROOT DIVISIONS OF CERTAIN ANGIOSPERMS

By

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ABSTRACT

A DETERMINATION OF STELAR PATTERNS IN
VARIOUS ROOT DIVISIONS OF CERTAIN ANGIOSPERMS

Root systems from ten species of desert angiosperms were collected and examined histologically to determine the xylem patterns of the primary, secondary, and tertiary roots. The plants used in the study were Cleome serrulata Push, Croton texensis (Klotzch.) Muell. Arg., Franseria acanthicarpa (Hook.) Coville, Gutierrezia microcephala (D. C.) Gray, Mentzelia albicaulis Dougl., Kochia scoparia (L.) Schard., Ratibida columnaris (Sims) D. Don, Salsola kali (S. pestifer A. Nels.), Tribulus terrestris L., and Verbena macdougalii Heller.

Four species, C. serrulata, C. texensis, K. scoparia, and R. columnaris, displayed a reduction in the number of xylem points from primary to secondary to tertiary roots. There were four species (M. albicaulis, S. kali, T. terrestris, and V. macdougalii)whose root systems possessed a constant number of xylem points in all three root divisions. The species, F. acanthicarpa and G. microcephala, were found to have an increase in xylem strands from primary to secondary, however, the tertiary roots had a xylem pattern similar to the primary

ABSTRACT

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roots of the same system. Variations within a given root category were present in three species. Two of these variations occurred in the secondary roots of K. scoparia and R. columnaris and the other occurred in the tertiary roots of V. macdougalii.

Measurements in microns were made on the stele and root diameters of a representative sample of each root division of each species. These figures were used to determine coefficients of correlation, standard deviation, and ratios between the stele and root diameters of the different root categories.

ACKNOWLEDGEMENT

The author wishes to express his appreciation to the National Science Foundation whose grant has made this study possible. He is further especially grateful to his major professor, Dr. Howard J. Dittmer, under whose direction this study was carried out. His advice and suggestions were invaluable. Also, he wishes to acknowledge Dr. William J. Koster and Dr. William C. Martin for their help and criticisms of this report, and to Dr. Harold M. Hefley for his advice and suggestions in taking and developing the photomicrographs used in this study.

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INTRODUCTION

The survival of a plant is controlled in part by the degree of effectiveness its root system maintains in absorbing water and mineral nutrients from the soil. The conducting elements, which transport these essential nutrients to the tissues, of the plant are of interest because of their great diversity in different plants and the possibility that the stele might be of use in taxonomic studies. Investigations of this nature, while not of a direct economic importance, nevertheless contribute to a better understanding of both the anatomy and physiology of plants, and to the root's intimate relationship with its environment.

Many studies dealing with roots of plants are essentially quantitative in character, being concerned with length, and surface area of the various types of root systems (Pavlychenko, 1937; Dittmer, 1937, 1938, 1948). These studies have a very important bearing on an understanding of the absorptive and conductive capacities of plant roots.

There also has been a vast amount of work published on the anatomical and developmental aspects of the

root systems of many species of plants. Nearly all of these, however, have been limited to investigations of the primary root or hypocotyl, Bell, (1934) on soybeans; Goodwin and Stepka, (1945) on timothy; Phillips, (1937) on artichoke; and many others. Histogenesis and the type and occurence of cell divisions responsible for the anatomical features of the roots were of primary interest. Other investigations have considered the origin of lateral roots arising from the primary axis (Lemaire, 1886; Arnold, 1940; Torrey, 1950).

So far as could be determined, the relations (if any) that exist between the xylem points of primary, secondary, and tertiary roots of young angiosperms have not been adequately investigated. Accordingly, an attempt has been made to find out if a progressive reduction in xylem points occurs as roots divide and subdivide laterally and to determine if such reduction follows a regular pattern.

The Problem

A problem of this kind should be of significance in several ways. Developmental patterns of primary xylem in roots should indicate taxonomic affinities particularly in the larger divisions of angiosperms. It would give a clearer understanding of the internal anatomy of roots and

should clarify the relationship of the size of the stele to the root diameter, and the possible influence of the number of xylem points to root diameter.

The histogenesis of a root apex is for the most part constant and generally follows a definite plan in its development. Basically it involves the differentiation of procambial phloem and xylem strands from the plerome, the determination of a fixed vascular pattern and the maturation of these primary elements. Differentiation of phloem and xylem elements usually occurs within the first two millimeters of the root tip. The large size and increased vacuolation of phloem cells make it easy to distinguish these from xylem initials in most species. Comprehensive reviews of root-stem transition and the maturation of tissues are found in Esau (1953) and Eames and McDaniels (1947).

In these accounts xylary cells are described as first becoming noticeable along the outside or periphery of the stele, just inside the endodermis (Plate 1, fig. 1). These protoxylem cells usually are very small with a minimum of vacuolation until after the metaxylem has appeared and has become vacuolated (Plate 2, fig. 1). Thus the development of the primary xylem in roots of higher plants, as in those of this study, are exarch in character. The protoxylem occurs at the outer edges of the rows of xylem cells. The metaxylem elements are

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located just central to these maturing progressively toward the center of the stele as seen on Plate 2, fig. 2, (Eames and McDaniels, 1947).

Esau (1953) states that the number of protoxylem poles or strands in general is specific in the larger taxa of plants, but it is not necessarily a fixed number. The categories referred to are above the family level. Eames and McDaniels (1947) stated that the number of xylem and phloem strands developing just back of the apical meristem is to some extent constant for a species. They also observed that most species show considerable variation as to strand number.

Esau, and Eames and McDaniel agree that the protoxylem strand number can vary in a single root. Preston, (1943) on studies of Lodgepole pine; Bell, (1934) working with soybeans; Hatch and Doak, (1933) working with pines; and Popham, (1955) in studies with Pisum demonstrated that the number of phloem and xylem strands will vary in different regions of a single root system, or even in a single root branch. Esau (1953) contended that phloem and xylem strands can frequently be more numerous at the proximal end than at the distal end of a root. In certain gymnosperms the variation in number of procambial strands in the different roots of a single system has been attributed to the vigor at which these various roots

grow and function (Esau, 1953). Such variations, however, have been toward a reduction in number rather than in an increase.

CHAPTER II

METHODS AND MATERIALS

Plants used in this investigation were obtained in central and north-central New Mexico. The majority of them were collected in the sand dune area near the Santa Ana Indian Pueblo and were taken during the summer and fall of 1958, and in the spring of 1959. Additional material was grown in a greenhouse from seeds collected in the field.

Plants selected for study are as follows:

Cleome serrulata Pursh.
Croton texensis (Klotzch.) Muell. Arg.
Franseria acanthicarpa (Hook.) Coville.
Gutierrezia microcephala (D.C.) Gray.
Mentzelia albicaulis Dougl.
Kochia scoparia (L.) Schrad.
Ratibida columnaris (Sims) D. Don.
Salsola kali L. (S. *pestifer* A. Nels.)
Tribulus terrestris L.
Verbena macdougalii Heller.

In most cases the entire root system was removed by trenching around the plant and lifting intact the ball of soil containing the root system. The soil was then carefully removed with a small pick or probe and the roots were then washed. The cleaned root system was then placed in a container of F.A.A. for fixation and preservation.

At least ten plants of each species were taken as representative samples. Each of these had a practically complete root system. Supplemental material raised in a greenhouse resulted in plants generally not as large as those growing naturally, but with more complete root systems, since they could be more easily harvested. Consequently, the removal of a smaller volume of soil resulted in less damage to the root system.

Seeds of some plants were germinated on moist paper in petri dishes in order to obtain very young root tips. These were fixed and preserved in F.A.A. and later sectioned serially for histological study. Serial sections were made of the primary roots of most species to determine the method of origin of tissues, the type of stele, and the pattern of origin of the lateral roots. Secondary and tertiary roots likewise were sectioned serially for the same reasons.

The sections were all stained first with safranine, to differentiate lignified xylem elements, as

well as nuclei. Light green was used as a counterstain in most cases, although crystal violet and aniline blue were used in a few instances. The primary reason for using various counterstains was to obtain a contrasting stain pattern that would be suitable for photomicrography.

The time of staining the root sections was somewhat shorter than usually recommended (Chamberlain, 1924; Johansen, 1940; Sass, 1940) because of the delicate character of the tissues, and because overstaining frequently was a problem. An outline of the methods used for the preparation of permanently mounted sections follows.

Killing, Fixing, Storage

Root tips and root systems were killed and fixed in standard formalin-acetic acid-alcohol fluid for not less than twenty-four hours. Some were fixed for much longer periods. The time was not critical, since overfixation was not likely with this mixture.

Washing, Dehydration, Clearing

Material to be processed was removed from the formalin-acetic-alcohol, and washed for thirty minutes in running tap water. It was then placed in fifty per cent alcohol for thirty minutes, then in seventy and ninety-

well as nuclei. Light green was used as a counterstain in most cases, although crystal violet and methylene blue were used in a few instances. The primary reason for using various counterstains was to obtain a contrasting stain pattern that would be suitable for photomicrography.

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Root tips and root systems were killed and fixed in standard formalin-acetic acid-alcohol, FAA, for not less than twenty-four hours. Some were left in it for much longer periods. The time was not critical, since overfixation was not likely with this mixture.

Washing, Dehydration, Clearing

Material to be processed was removed from the formalin-acetic-alcohol, and washed for thirty minutes in running tap water. It was then placed in 15 per cent alcohol for thirty minutes, then in [illegible]

five per cent alcohol for thirty minutes each. It was then transferred to absolute alcohol for one hour.

Clearing (replacing the alcohol with xylene) was accomplished by placing the tissue progressively in the following mixtures:

absolute alcohol-xylene	3:1	for one hour
absolute alcohol-xylene	1:1	for one hour
absolute alcohol-xylene	1:3	for one hour
pure xylene		for four hours or more

Infiltration and Embedding

After clearing, the materials were infiltrated with paraffin by using the following schedule. This was carried out in a constant temperature oven, at 53-54 degrees centigrade.

Xylene-paraffin	3:1	for one hour
Xylene-paraffin	1:1	for one hour
Xylene-paraffin	1:3	for one hour
Pure paraffin, three changes, for one hour in each.		

The materials then were embedded and were sectioned at from six to twelve micra depending on the material. Sections were affixed to slides with Mayer's albumin (egg white, filtered, 50 ml., glycerine, c.p. 50 ml.), expanded on a warming table after being flooded with water, oriented on the slide, and allowed to dry thoroughly before staining was attempted.

Sections were deparaffined in xylene, then transferred in order to equal parts of xylene and absolute alcohol, absolute alcohol, ninety-five percent alcohol, and finally to seventy per cent alcohol. They were then stored in this percentage of alcohol until they were to be stained; seldom for more than a few hours.

Staining and Mounting

The xylem elements in the root sections were stained with a one per cent solution of safranin^e in fifty per cent alcohol, having been passed into the stain directly from the seventy per cent alcohol. Staining in safranin^a usually required about six hours. Some were left in safranin^e overnight, which did no harm. The slides were then rinsed briefly in fifty per cent alcohol and counterstained.

Three counterstains were used: crystal violet, light green, and aniline blue. The crystal violet was used first but proved to be no more satisfactory than light green or aniline blue. Its use involved passing the sections progressively through seventy, eighty-five, ninety-five, and one hundred per cent alcohol solutions, then into clove oil saturated with crystal violet for ten minutes. They then were destained in pure clove oil, rinsed in xylene and the coverglass applied over Permount in toluene.

Light green was used as a counterstain in the majority of instances. Its use involved taking the sections from seventy per cent alcohol, rinsing them in fifty per cent alcohol, and then placing a drop or two of a 0.5 per cent solution of light green in fifty per cent alcohol from a dropping bottle. The stain was allowed to react for from five to ten seconds. It was then rinsed from the slide in ninety-five per cent alcohol. The slides were then passed into absolute alcohol and finally into xylene until cleared. The excess xylene was then drained from the slide and the sections mounted in Permount and covered with a No. 1 coverglass.

Aniline blue was used as a counterstain in a few instances. The method of application was precisely the same as for light green. In certain sections it gave a somewhat better contrast between xylem elements stained red with safranin and the other tissues present in the root section.

Photomicroscopy

The illustrative photomicrographs were made on Eastman Plus-X, 35 mm film. The apparatus included a Leitz Ortholu Research microscope equipped with a Berek condenser, 3.5x, 10x, 45x, and 100x oil immersion apochromatic objectives and 6x and 10x periplan oculars.

A Leica III camera was assembled on a sliding copying attachment, to which was attached a bellows and an extension tube. The entire camera assembly was supported above the microscope on a Leitz copying stand. A light tight connection was achieved by lowering the extension tube into an especially constructed collar that fitted over the monocular microscope tube. Various filters were employed to increase particularly the contrast in the xylem elements of root sections. Red and green Wratten color-separation filters were most often used, although a light blue Eastman 85c filter was used on some of the exposures.

The length of exposure was determined by measuring the intensity of the image in foot candles with a Weston Master exposure meter that was checked for accuracy by the U.S. Bureau of Standards and substituting the values so determined into the formula $E = \frac{1}{I_i W}$, where E is the exposure in seconds or fractions thereof, I_i is the image intensity in foot candles, and W is the Weston sensitivity rating of the emulsion being used (Hefley, 1951). This method eliminates all guesswork in arriving at an exposure time, since the intensity value so determined is independent of magnification, lens system, and filters being used. It achieves negatives of uniform density with a gamma of approximately

0.7, considered by most to be of optimal printing density. The Plus-X film was assigned a Weston value of 100.

Developing and Printing

Film was developed in a Leitz tank, using Eastman D-76 developer, at 20°C. and with continuous agitation in a mechanical shaker at 276 oscillations per minute. The film was rinsed in tap water, and fixed with Eastman F5 fixer for approximately 6 minutes. It was then washed in running water for 40 minutes, given a final rinse in a 0.5 per cent aerosol solution and hung up to dry.

The negatives were printed on No. 3 contrast double weight Luminos enlarging paper with engravers matte surface. The paper was then developed in Eastman D-72, diluted 1:3 with distilled water, then rinsed in tap water and placed in an acid fixer for at least 30 minutes. Prints were then washed thoroughly in running water for 3 hours and dried.

Magnification on the negatives varied considerably, from 60X to greater than 450X. The photographs were then magnified approximately 4 times the original negative size.

Some drawings were made from slides at a magnification of 450X. Others were produced by taking

0.7, considered by manufacturer [illegible]
sity. The Plus-X film was [illegible]

Developing and Printing

Film was developed in [illegible] Eastman D-76 developer, at 20°C [illegible] agitation in a mechanical agitator [illegible] per minute. The film was [illegible] fixed with Eastman F-5 [illegible] It was then washed in running water for [illegible] a final rinse in a 0.5 per cent [illegible] up to dry.

The negatives were printed on [illegible] double weight [illegible] matte surface. The paper was then developed in Eastman D-72, diluted 1:2 with distilled water, then [illegible] tap water and placed in an acid fixer [illegible] minutes. Prints were then washed [illegible] in running water for 2 hours and dried.

Magnification [illegible] considerably, from [illegible] The photographs were then [illegible] original negative size.

Some drawings were [illegible] magnification of [illegible]

photomicrographs of sections and then outlining the proto and metaxylem elements with waterproof drawing ink. These were then bleached in a saturated iodine solution in 50 per cent alcohol. When bleaching was complete the photographs were washed briefly in running water, then placed in photographic fixing solution (Hypo) until the iodine stains and faded image were entirely removed. The bleached photographs were washed thoroughly in running water and dried.

Correlation Coefficients and Standard Deviations

Correlation coefficients between root and stele diameters (in microns) were computed from samples of ten different roots in each root category (primary, secondary, and tertiary) for each species of plant studied. They were determined from the following equation, $r = \frac{\frac{\Sigma xy}{N} - \frac{\Sigma x \Sigma y}{N^2}}{\sigma x \sigma y}$.

The standard deviation (σ) of the variates was obtained by assigning the symbols x and y to the diameters of the root and stele respectively, then substituting into the formulae, $\sigma x = \sqrt{\frac{\Sigma x^2}{N} - \frac{(\Sigma x)^2}{N^2}}$ and $\sigma y = \sqrt{\frac{\Sigma y^2}{N} - \frac{(\Sigma y)^2}{N^2}}$. The values of Σx, Σx^2, Σy, Σy^2, Σxy, and $\Sigma x \Sigma y$ were first determined and then substituted into the appropriate formula. The results are recorded in tables I and II.

All formulae were obtained from the booklet, General Statistics by the Monroe Calculating Machine Company, Inc. A Monromatic 8N Calculator was used for all computations.

CHAPTER III

REVIEW OF LITERATURE

The review of literature which follows is divided into three sections. The first presents material that deals with the possibility of a relationship between the size of a root and size of its stele and number of xylem strands present in it. The second section reviews the literature that deals with the progressive reduction in number of vascular strands from the primary, to secondary, to tertiary roots. The third section covers the publications cited in this report that reveal variations within the same root division of a species, and between systems in individual plants within the same species.

Many of the published works, concerning the arrangement of the xylem elements in the stelar portions of plants, have been of an experimental nature: Thimann, 1934, working with indolacetic acid and indole 3 acetic acid; Bond, 1948, using indolacetic, 2, 4, 5 - trichlorophenoxyacetic, and 2, 3, 5, triiodobenzoic acids, also asparagine and tryptophane; Torrey, 1951, 1955, 1957, experimented on peas with the vitamins, thiamin and nicotinic acid, and indolacetic acid; Samantarii and Sinha, 1957, treated

leaves with β indolyl butyric acid, maleic hydrazide, and a solution of sucrose and ammonium sulfate; and others. It was the purpose of these investigations to interrupt normal conditions of growth of certain plants with auxins, and also to study any possible induced change in growth patterns of the vascular tissues resulting from such treatment. These investigators, as well as others, often took into consideration the xylem patterns of but a single plant and did not try to determine if there was any correlation in the pattern of the xylem elements between one root division and another.

Root Size and Vascular Patterns

There are many excellent accounts of the arrangement of stelar patterns in specific plants. The principle concern has been the determination of factors that control, modify, or influence the arrangement of tissues in a radicular stele. Torrey (1955) asserted that there are two concepts of vascular pattern determination: that of Jost (1932-1933), who contended that the mature vascular tissues of the root induce differentiation of the newly formed cells derived from the apical initials into the established pattern of the mature region, and of Thoday (1939), who concluded that vascular patterns of roots are controlled by apical meristem or self-determining power of roots influ-

enced perhaps by the external environment. Torrey (1955) concluded that vascular patterns are determined by the activity of the apical meristem, not by inductive influences from mature vascular tissues of the root claimed by some investigators.

Wardlaw (1928) concluded that there appears to be some relationship between the absorptive capacity of water by roots of plants from the soil and the size of the primary tissues of their vascular cylinders. This idea was later supported by Preston (1943) in his works on juvenile lodgepole pines. He found evidence which supported the belief that the xylem pattern is influenced or controlled by the absorptive power of a root. Wardlaw also suggested that the size of the root is another factor that may influence the stelar make-up of roots. It is presumed in this report that Wardlaw meant the diameter of roots by his term "size". This apparently agrees with the proposed "size factor" hypothesis of Bower (1930) who proposes that the vascular pattern in roots is correlated with their thickness.

Samantarai and Sinha (1957) concluded that the factors chiefly responsible for controlling the vascular patterns in adventitious roots were hormones and foods, mainly sugar. Their experimental material included isolated leaves of Ipomoea batatas Lamk., Impatiens balsamina L., and Daedalacanthus splendens L.

Xylem Point Reduction from Primary to Lateral Roots

Some investigators during recent years have reported a reduction in the number of xylem points in steles of various species of plants. These reductions have occurred from primary to secondary roots and from secondary to tertiary root divisions. In some instances the stelar patterns have exhibited an increase in xylem points with branching while in others xylem patterns have shown an inconsistent variation.

Meyer (1930) noted that the lateral branches of the primary root very often displayed a reduction in the vascular strand number in Maranta. A reduction in xylem strand elements was observed also by Hatch and Doak (1933) in the roots of pine. They found that "long" roots were either diarch or polyarch and that "short" roots exhibited a monarch vascular pattern. This would indicate a definite reduction from the larger root divisions to the smaller lateral branches. The terms long and short roots were differentiated in the following manner. The long roots possessed a root cap and had a diarch or polyarch xylem arrangement. The short roots lacked a root cap and possessed a monarch stele. Also, the diameter quotient of the short roots was significantly lower than the long roots. Hatch and Doak also referred to a third root division which they called pioneers. No mention was made of the xylem pattern of these roots.

The xylem pattern in the juvenile lodgepole pine primary root was found to be tetrarch by Preston (1943). He also found a reduction in xylem points, because the secondaries had diarch steles while tertiaries branching from them had monarch steles. The tetrarch condition in the primary root was found one-half to one inch immediately below the root-stem transition zone. From here to 2.25 inches toward the distal end of the root the xylary pattern was triarch, but below this point a diarch pattern was observed. The xylem pattern of the first laterals or secondaries was diarch throughout. The third division, also exhibited no variation and was monarch in the xylem arrangement.

Bell (1934) concluded that at the completion of the development of the primary tissue the xylem pattern was tetrarch in the primary root of Soja max. The secondaries were either diarch, triarch, or tetrarch. This to some degree indicates that a reduction in xylem points occurs between the primary root and its laterals, at least where a diarch or triarch stele was found in the secondaries. Heimsch (1949), while working on the vascular tissues of maize roots, found that a reduction in xylem points occurred from primary root to the lateral divisions. Similar results were noted by Bottum (1941) in his histological studies on the roots of Melilotus alba. He

The xylem pattern in the juvenile loblolly pine primary root was found to be tetrarch by Preston (1943). He also found a reduction in xylem points, because the secondaries had diarch steles while tertiaries branching from them had monarch steles. The tetrarch condition in the primary root was found one-half to one inch immediately below the root-stem transition zone. From here to 2.25 inches toward the distal end of the root the xylary pattern was triarch, but below this point a diarch pattern was observed. The xylem pattern of the first laterals or secondaries was diarch throughout. The third division, also exhibited no variation and was monarch in the xylem arrangement.

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found some instances of definite reduction in the xylem pattern from primary to secondary root divisions.

The experimental work of Torrey (1951) on the cambial formation in the roots of Pisum revealed that lateral roots produced from triarch primary roots possessed diarch or triarch xylary patterns. The roots referred to here are those used by Torrey as controls in experiments on effects of growth substances on roots of peas.

Variation of Xylem Pattern in Roots

Some investigators, including most of those previously mentioned, noticed variations in the xylem patterns of certain species of plants. These variations have occurred within the root systems of plants of a given species, within the divisions of a root system of a single plant, and even within the length of an individual root or branch root.

Disagreement on the xylem patterns of the pine is evident in the works of Preston (1943) and Hatch and Doak (1933). Preston found the stelar pattern of the primary root in the lodgepole pine to be tetrarch. This was in agreement with Aldrich-Blake (1939) who found the stelar pattern in the Corsican pine to be tetrarch also. Hatch and Doak on the other hand mention, in connection

with mycorrhizal studies, that the xylem patterns in taproots of P. strobus and P. sylvestris are of diarch or polyarch configuration. In Evolution of Land Plants, Campbell (1939[61]) stated that the xylem pattern of the primary root in Coniferales first is tetrarch, but later becomes diarch in structure; indicating that variations occur in this order as well as in higher plants.

Popham's excellent report on root zonation in Pisum sativum (1955) shows that in one instance the xylem pattern varied from its characteristic triarch pattern to a tetrarch pattern. In certain cases Torrey (1957) noticed that in regenerated roots of P. sativum a reduction in vascular strands did occur. This situation, however, could be attributed to the response of the root to wounding.

Variations in the xylem pattern were noted in the secondary roots by Bell (1934) in Soja max. The variations were from diarch to triarch and even tetrarch. Likewise Bottum (1941) found that the secondaries of Melilotus alba exhibited a variation from triarch to a diarch condition. He also observed that the primary root varied from its usual triarch condition to one of a tetrarch pattern. This same condition was also found by Miller (1959) in his studies on Humulus lupulus. He observed that an occasional triarch pattern appeared in

the normally diarch primary root. The laterals, however, did not exhibit this condition.

Eames and McDaniels (1925) expressed the opinion that the number of xylem strands is consistant in some plants, but other species show considerable variation. Xylem poles are characteristic in some plant groups according to Esau (1953) but are capable of considerable variation.

Esau (1953) also observed that sometimes xylem strands are higher in number at the proximal than at the distal end of a root. The change or variation does not, however, have to occur in this direction. The former condition was observed in the primary root of the lodgepole pine by Hatch and Doak (1933). They found that the xylem strands changed from tetrarch at the proximal end (near root-stem transition) to triarch midway between proximal and distal end, to a diarch pattern at the root apex or distal end.

Variations in an individual root were also encountered by Samantarai and Sinha (1957) in adventitious roots of Ipomoea, Impatiens, and Daedalacanthus. The xylem pattern in untreated Ipomoea roots varied from tetrarch to pentarch, to hexarch. Diarch, triarch, and tetrarch patterns were found in the roots of Impatiens. Daedalacanthus displayed a variation from its usual,

hexarch condition to pentarch in some instances, while others had as much as a heptarch pattern. In each of the species cited here the references were taken from the control roots or untreated roots as Samantarai and Sinha were working with growth hormones and other substances.

Torrey (1957) treated vitro cultured pea roots with auxins. This treatment usually increased the number of xylem points in the stelar pattern of the regenerated roots. He noticed that with an increase in the xylem pattern from the triarch to a hexarch condition there was also an increase in the root diameter in auxin treated roots. He stated, however, that the size of the mature root is no absolute guide to the number of vascular strands present in the root.

CHAPTER IV

RESULTS

The results are reported in three parts, under the names of each species investigated, (1) a brief description of a mature root system, (2) the type of xylem patterns present in each division of the root system, (3) the measurements of diameters of roots and steles. The coefficients of correlation between stele and root diameters calculated from their means are recorded in tables 1 and 2.

The xylem patterns of the three divisions for roots of each species are given in table 3. In table 4 the average of root and stele diameters are recorded for each division of each species studied. The figures of stele and root diameters given in the text which follows are all averages of a series of ten cross sections for the particular root division being discussed.

Cleome serrulata Push.

The mature root system of this plant has a single large taproot which usually has a considerable diameter at its proximal end. Secondaries from the

taproot are evenly distributed throughout its length. These were largest within the top 25 cm of soil and were not numerous in the plants studied. The tertiary roots were generally very small and were not numerous.

The xylem patterns of the taproot (Plate 11, fig. 4) in all cases observed were triarch and had an average root diameter of 308 microns. The average diameter of the stele was 132.6 microns. The arrangement of the xylem elements in the secondaries and tertiary roots was diarch (Plate 11, figs. 5 and 6). The secondary roots averaged 213 microns and the third division, 150.3 microns. The stele of secondaries averaged 67.2 microns while the tertiaries averaged 46.2 microns (table 4).

The ratios of stele to root diameter for the three divisions were: primary .4304, secondary .3103, and .3012 for the tertiary roots (table 1).

Croton texensis (Klotzsch) Muell. Arg.

The taproot of this species has numerous secondary roots distributed uniformly along its length. The tertiary roots were also numerous and all were relatively small.

The primary roots exhibited a tetrarch xylem (Plate 10, fig. 1) pattern while the secondary and ter-

tiary roots had a diarch xylem arrangement (Plate 10, figs. 2 and 3). The average diameters for the roots were 294, 241.2, and 234 microns respectively for primary, secondary, and tertiary roots. The stele diameter mean for primary roots was 123.6, for secondary roots, 80.4, and the tertiaries 70.8 microns (See table 4).

The stele-root diameter ratios for primary roots was .4205, for secondary roots .3337, and .3022 for tertiary roots.

Franseria acanthicarpa (Hook.) Corville

The mature root system possesses a very long conspicuous taproot that penetrates deeply into the soil. The secondary roots are numerous and are mostly located in the top 25 to 30 centimeters of soil. A few secondaries, however, arise throughout the length of the taproot. Some of the secondary roots that branch at or just beneath the surface of the soil are extremely long and in some cases produce new plants. The tertiary roots are quite numerous, particularly on the secondary roots arising near the upper end of the taproot.

The stelar pattern of the taproot (Plate 12, fig. 1) was diarch throughout. The secondary roots (Plate 12, fig. 2) observed had an increased number of xylem strands since they were triarch in character.

The tertiary roots, however, reverted to a diarch xylem arrangement (Plate 12, fig. 3). The average root diameters of primary, secondary, and tertiary roots were 303.3, 258.3, and 158.1 microns respectively. The stelar diameters showed a gradual decrease in size from 115.2, to 99.0, and 57.0 microns for the primary, secondary, and tertiary roots respectively. The stele-root diameter ratios were .3901 for primary, .3846 for secondary, and .3609 for tertiary roots (Table 1).

Gutierrezia microcephala (D.C.) Gray.

The perennial root system of G. microcephala is centered around a long, woody, central taproot. The system does not penetrate deeply into the soil or cover a large area. Most of the larger secondary roots are located on the upper 6 to 8 centimeters of the taproot. Shorter and smaller secondaries also are located in this region as well as along the remainder of the taproot. Most of the tertiary roots occur on the secondaries that arise from the upper portion of the taproot. The tertiaries are numerous and give the entire system a fibrous appearance.

The xylary patterns of the primary (Plate 10, fig. 6) and tertiary (Plate 10, fig. 4) roots were diarch. The secondary roots exhibited an increase in xylem

points to a triarch pattern (Plate 10, fig. 5). The average diameters of the roots were 310.2 microns for the primary, 258.3 for the secondary, and 213 microns for the tertiary roots. Average stelar diameters followed the same trend with primary roots having an average diameter of 66 microns, the secondaries of 91.2 microns, and the tertiaries 61.2 microns.

The stele-root diameter ratios reflected the diarch, triarch, diarch condition. The primary root ratio was .2132, for the secondary roots .3433, and for the tertiary roots was .2839.

Kochia scoparia (L.) Schrad.

The mature system is characterized by a single, large, long taproot. Secondary roots branching from it are longest near its upper end. Those arising from more distal portions of the primary root show a progressive decrease in length as the tip is approached. In the plants examined, secondary roots were most numerous immediately beneath the surface of the soil. Tertiary roots were quite abundant, giving the secondaries a fuzzy appearance in many places.

The xylem patterns of the three root divisions exhibited a progressive reduction (Plate 12, figs. 4, 5, and 6). The primary roots were tetrarch and the second-

aries were triarch in all cases except for roots that had a diarch arrangement. The tertiary roots had a diarch pattern throughout. The average root and stele diameters were as follows: primary, 149.8 and 72.6 microns; triarch secondaries, 211 and 88.5 microns; the one diarch secondary, 133.5 and 69 microns; and the tertiaries, 125.4 and 54 microns (See table 4).

The stele-root diameter ratios were .4871 for the primary, .4418 for the secondary, and .4282 for the tertiary roots.

Mentzelia albicaulis Dougl.

The root system of M. albicaulis is characterized by a very long, conspicuous taproot which penetrates deeply into the soil. Only a few secondary roots are present and these occur at wide intervals along the taproot. Tertiary roots are present, but are very few, small, and widely scattered.

All root divisions of M. albicaulis (Plate 3, fig. 1 and 2, Plate 4, fig. 1) had a diarch xylem pattern. The average diameter for primary roots was 167.4 microns, 140.7 microns for secondary roots, and 151.8 microns for tertiary roots. The average diameter of the stele was 68.4, 58.2, and 52.8 microns in the primary, secondary, and tertiary roots respectively.

The stele root diameter ratios for the primary roots and the secondary roots were almost identical, being .4120 and .4132 respectively. The tertiary roots had a ratio of .3508.

Ratibida columnaris (Sims) D. Don.

The root system of R. columnaris is shallow and has a single large taproot which is extremely broad at its upper end. The secondary roots arising from it are evenly distributed along its length. Those leaving the taproot near the surface of the soil are the longest. The remaining secondary roots become progressively shorter near the distal portion of the taproot. Tertiary roots are not numerous and are small and widely scattered on the secondary roots.

The primary root (taproot) of this species (Plate 4, fig. 2) has a tetrarch xylem arrangement. The secondary roots generally had a diarch pattern (Plate 5, fig. 2), however, two roots examined had a triarch pattern (Plate 5, fig. 1). A diarch condition was present in the tertiary roots (Plate 6, fig. 1). No measurements were taken on the primary roots of this species because the material examined was older than those of the other plants studied. The secondary roots possessing diarch steles averaged 288 microns in diameter.

Those with triarch stelar averaged 351 microns in diameter. The average stele diameter for the secondaries was 88.2 in the diarch roots and 121.5 microns in the triarch roots. The tertiary roots averaged 234.4 microns in diameter while the stele averaged 75.6 microns.

Salsola kali L. (S. pestifer A. Nel.)

The primary root of this plant is typically long and slender with some secondary roots borne in two locations on it. The largest group of secondary roots is located just below the soil surface. These roots are short and possess small tertiary roots. The second mass of secondaries is located approximately 10 centimeters back of the root tip. These roots are not numerous but are considerably larger in diameter and longer than those found at the upper end of the taproot. Tertiary roots either are absent from these, or are extremely small.

The stelar patterns of the primary, secondary, and tertiary roots of S. kali were all diarch in arrangement in the specimens examined (Plate 11, figs. 1, 2, and 3). The average diameter of the taproot was 256.5 microns with the stele averaging 108 microns. The secondary roots averaged 184 microns in diameter with the stele averaging 60 microns. The tertiary

roots averaged 134.7 microns in diameter and the stele 44.4 microns (Table 4).

The stele-root diameter ratios for the secondaries and the tertiary roots were very similar being .3229 and .3282 respectively. The primary root gave a much larger ratio, .4212 (Table 1).

Tribulus terrestris L.

The primary root (taproot) of T. terrestris is completely devoid of lateral branches for the first 2 to 3 centimeters below the soil surface. Below this point a few secondary roots are produced. Some of the secondary roots are as long as the primary while others are small, hairlike structures. Extremely small tertiary roots occur on most secondaries and in some instances clusters of quaternary roots were also formed.

The xylem arrangement of the primary, secondary, and tertiary roots was diarch (Plate 6, fig. 1); (Plate 7, figs. 1 and 2). The average root diameters of these divisions were as follows; 428.7 microns for the primaries; 215.1 microns for the secondaries; and 256.6 microns for the tertiaries, while the steles measured 130.8, 67.8, and 78.0 microns respectively as seen in table 4.

The stele-root diameter ratios for the three root divisions all were within 0.01 per cent of each

other being, .3066, .3172, and .3054 respectively (See table 1).

Verbena macdougalii Heller.

This species possesses a rather shallow root system, which possibly is an adaptation to the hard caliche soil, which is its usual habitat. The taproot is broad in diameter at its upper end and does not penetrate straight into the soil. V. macdougalii possessed the most numerous secondary roots of any species studied. They formed a fibrous-like mass at or just below the surface of the soil. Many also were found along the total length of the taproot. Tertiary roots were also numerous and long and hair-like.

The primary and secondary roots possessed a diarch xylem pattern (Plate 8, figs. 1 and 2). The tertiary roots, however, exhibited a variation in xylem points. Most of the tertiaries had the diarch pattern (Plate 9, fig. 1) with two roots showing an increase to a triarch condition (Plate 9, fig. 2). The average diameters of the roots were 272.4 microns and 193.8 microns for the primary and secondary roots respectively. The steles for these roots were 107.4 and 70.2 microns in average diameter. The triarch, tertiary roots averaged 303 microns and the stele averaging 102 microns.

other being, .3065, .1772, and .2698 respectively (see table 1).

<u>Verbena macdougalii</u> Heller.

This species possesses a rather shallow root system, which possibly is an adaptation to the hard caliche soil, which is its usual habitat. The taproot is broad in diameter at the upper end and does not penetrate straight into the soil. *V. macdougalii* possessed the most numerous secondary roots of any species studied. They formed a fibrous-like mass at or just below the surface of the soil. Many also were found along the total length of the taproot. Tertiary roots were also numerous and long and hair-like.

The primary and secondary roots constituted a diarch xylem pattern (Plate 9, Figs. 1 and 2). The tertiary roots, however, exhibited a variation in these points. Most of the tertiaries had the diarch pattern (Plate 9, Fig. 1) with two roots showing an increase to a triarch condition (Plate 9, Fig. 2). The average diameters of the roots were 272.1 microns and 273.8 microns for the primary and secondary roots respectively. The steles for these roots were 137.1 and 74.2 microns in average diameter. The primary tertiary roots averaged 303 microns and the stele averaging 132 microns.

The diarch tertiaries had an average root diameter of 167.5 microns with a stele diameter of 56.2 microns (Table 4).

The ratios for stele-root diameters were as follows, primary, .3641, secondary, .3627, and the tertiary, .3277 for diarch roots, .3363 for the triarch roots (Table 1).

CHAPTER V

DISCUSSION

There are a number of factors that may influence or modify the findings revealed by an investigation such as the one reported here. The extrinsic environment surrounding a root system has a modifying influence over development and extent of growth of the entire plant although the genes probably play a more dominant role.

Most of the plants whose root systems were used in this work were taken from their native habitats. The one exception was Gutierrezia microcephala which was grown in a greenhouse. Since the plants grew mainly under natural conditions no attempt was made to determine which essential elements required for growth were present or in what concentrations. Differences in essential elements in the several habitats might affect the growth of roots and in some cases may have caused some to be a bit stunted. This in turn would affect the size of roots and possibly the stelar patterns.

The period of active growth in different root systems probably would vary. The time when a root system of an individual plant initiates growth in spring after

the winter dormant period depends upon its location, altitude, soil, temperature, available water, and root competition for space to mention only a few of the more obvious factors of the environment. Plants would begin to grow at different times of the year because of different values of physical, chemical, biotic, and meteorologic factors influencing plants in different habitats or in different portions of the same habitat. Such varying environmental factors probably affect the growth in different root systems and might give the roots quite different peaks of activity. The majority of the plants used, were growing in a characteristic sandy desert soil.

Some evidence does exist to show that the water holding capacities of different soil strata, varying amounts of available water, and the growth of the roots in this environment may exert some influence on the structure and character of a developing stelar pattern (Wardlaw, 1928; Preston, 1943; Weaver and Clements, 1938). This possibly lends support to the "size factor" hypothesis of Bower (1930), the conclusions of Wardlaw (1928), and of Preston (1943), that the absorptive ability of plant roots possibly influences the xylem pattern in them. It might be argued that a root located in a stratum of soil amply supplied with available water and dissolved nutrients would not become as large, or need to have as much

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conducting tissue to supply a plant of given size with nutrients as a root located in a stratum not having these attributes.

The general picture of root structure, indeed the overall growth form and structure of any species of plant apparently is genetically determined. But the fluctuations of environment may either enhance, suppress or modify the expression of a particular plant's genetically determined capacity to develop in a given fashion (Sinnott, Dunn, and Dobzhansky, 1950).

This statement seems to be confirmed by the findings presented here. Some species of plants apparently were quite consistent in the pattern of primary xylem points in the steles of their primary, secondary, and tertiary roots. But in some cases plants whose secondary roots had steles usually triarch in structure, occasionally had secondary roots with diarch steles.

In the ten species of plants considered, four displayed a reduction in number of primary xylem points from primary to secondary to tertiary divisions. Cleome serrulata exhibited a reduction from a triarch primary root to diarch secondary and tertiary roots (Plate 11, figs. 4, 5, and 6), Kochia scoparia generally displayed a reduction from a tetrarch primary root, to triarch secondary roots, to diarch tertiary roots (Plate 12,

figs. 4, 5, and 6). Ratibida columnaris had a tetrarch stele in the primary roots (Plate 4, fig. 2), a diarch stele in the secondary roots (Plate 5, fig. 2), and a diarch stele (Plate 6, fig. 1) in the tertiary roots (Table 3).

Such reductions were constant in the four species except for two diarch secondary roots observed in Kochia scoparia whose secondary roots normally are triarch in character (Table 3). Two secondary roots in Ratibida columnaris likewise were found to be triarch in structure (Plate 5, fig. 1) while the majority were diarch. These variations are similar to those found by Bell (1934) in soybeans, Preston (1943) in lodgepole pine, and Popham (1955) in Pisum sativum. Similar variations were described by Torrey (1951) who found that lateral branches of primary roots often show a reduction in vascular strands from the usual number.

Two species (Gutierrezia microcephala and Franseria acanthicarpa) exhibited an increase in xylem points from diarch, primary roots to a triarch condition in secondary roots (Table 3). This increase was not shown in average stele and root diameters (Table 4). It was reflected in the ratio of stele-root diameters in Gutierrezia microcephala (Table 2). Franseria acanthicarpa did not reflect an increase in number of xylem points in stele-root

diameter ratios (Table 2). Torrey (1955) found that in peas diameters of a number of roots and their steles showed little or no relationship. Monarch stele diameters were inconsistent, varying between 57 and 103 microns. Root diameters ranged between 507 and 780 microns. Secondary and tertiary roots were found to have similar variations (Torrey, 1955).

Mentzelia albicaulis, Salsola kali, and Tribulus terrestris possessed a constant diarch, primary xylem pattern in the stele of the three root divisions. The ratio of the stele-root diameters ranged from .4212 in primary roots of S. kali to .3054 in tertiary roots of T. terrestris (Table 2). Six of the nine root divisions fell between .3054 to .3508. Of the diarch roots one failed to have a coefficient of correlation not significant at the 1 per cent level and two were not significant at the 5 per cent level. Only two root categories in the entire group were not significant at the 5 per cent level (Table 1).

In the twenty-three root divisions with a diarch xylem arrangement, seventeen of these had an average stele-root ratio that fell between .3000 and .3999 (Tables 2 and 3). Two of the remaining six had ratios below, and four above these averages. All tertiary roots examined had diarch steles, with exceptions found in Verbena macdougalii, where two triarch roots were found. The stele-

root diameter ratios of tertiary roots fell between .2839 and .3508 except in Kochia scoparia which had a ratio of .4295.

Six different root categories displayed roots that had triarch steles. These include the primary roots of Cleome serrulata, and the secondary roots of Franseria acanthicarpa, Gutierrezia microcephala, and Kochia scoparia. Two triarch steles were found in normally diarch secondary roots of Ratibida columnaris and tertiary roots of Verbena macdougalii (Table 3). The stele-root diameter ratios of tertiary roots show a range of .3366 to .4418 (Table 2). This shows a statistical error of just over one per cent from the mean stele-root diameter ratio for the tertiary roots.

Three root divisions in the plants studied possessed tetrarch xylem pattern. Measurements were able to be made only on the primary roots of Croton texensis and Kochia scoparia. The stele-root diameter ratios in both instances were high being .4205 and .4871, respectively. This would average .4538 compared with .3803 mean for triarch roots and .3382 mean for diarch roots.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Ten species of desert angiosperms were examined to determine the stelar patterns of their primary, secondary, and tertiary roots. Before the roots were sectioned for histological examination the general pattern of each root system was observed. Most of the species possessed long taproots that penetrated deeply into the soil. The taproots usually possessed two regions of lateral branching, one immediately beneath the surface of the soil and the other below the characteristically hard-packed clay layer.

The steles of four species exhibited a decrease in number of xylem points from the primary to secondary and tertiary, or primary to secondary to tertiary root divisions. Cleome serrulata had a decrease in xylem strands from a triarch primary root to diarch secondary and tertiary branches. Croton texensis and Ratibida columnaris displayed a reduction, from a tetrarch primary pattern to a diarch stele in the secondary and tertiary roots. Kochia scoparia was the only plant that showed a progressive reduction in xylem strands

in the secondary and tertiary divisions. The primary root had a tetrarch pattern, the secondary roots basically had a triarch stele, while the tertiary roots possessed a diarch stelar condition.

The roots of four plants examined showed no reduction in number of xylem strands with branching and possessed steles that were constant in number of xylem points. These were Mentzelia albicaulis, Salsola kali, Tribulus terrestris, and Verbena macdougalii, the steles were diarch in all root divisions of these plants.

Franseria acanthicarpa and Gutierrezia microcephala exhibited an increase in xylem points with branching from diarch primary roots to secondary roots that were triarch in structure. Their tertiary roots reverted to the diarch pattern of the primary roots.

Three species displayed a variation in xylem points within a given root division. Kochia scoparia basically had triarch steles in secondary roots, although in two instances diarch steles were present in this root category. Ratibida columnaris characteristically possessed diarch secondary roots, however, in two cases a triarch stelar structure was present. Among diarch tertiary roots of Verbena macdougalii, two roots were found to have triarch steles. The variation in xylem strands in all of these cases was directly

reflected in the average diameters of the roots and steles in the particular divisions (Table 4).

Conclusions

1. All plants in this investigation possessed moderately long to long taproots which usually branched into secondary and tertiary divisions.
2. The xylem pattern of a root system is apparently genetically determined but the possibility exists that this pattern may be modified by severe variations in extrinsic environmental factors.
3. The xylem pattern, differentiated in the root apex, is maintained throughout the length of the root prior to pronounced secondary thickening for the plants in this study.
4. The size (diameter) of a developing root apex could possibly influence the number of xylem points of a root stele.
5. Generally, if the number of xylem points in the stele of a root system show a decrease it will be from primary to secondary to tertiary roots.
6. The ratios of stele-root diameters of diarch and triarch roots studied show that a relationship probably exists between this ratio and the number of xylem points in the stele of a root.

7. Standard deviations of each root category were less than one third of the mean.

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TABLE 1

Coefficients of correlation (r) between diameters of root and stele of primary, secondary, and tertiary roots for each species studied and the five per cent and one per cent levels of significance.

plant species	root division	(r)	level of significance	
			5 %	1 %
C. serrulata	primary	.8503	S	S
	secondary	.6024	NS	NS
	tertiary	.7949	S	S
C. texensis	primary	.8414	S	S
	secondary	.7884	S	S
	tertiary	.9868	S	S
F. acanthicarpa	primary	.8293	S	S
	secondary	.2895	NS	NS
	tertiary	.5878	NS	NS
G. microcephala	primary	.8336	S	S
	secondary	.9444	S	S
	tertiary	.8333	S	S
K. scoparia	primary	.5483	NS	NS
	secondary	.7371	S	NS
	tertiary	.9159	S	S

TABLE 1--Continued

plant species	root division	(r)	level of significance	
			5 %	1%
M. albicaulis	primary	.5714	NS	NS
	secondary	.9047	S	S
	tertiary	.2207	NS	NS
R. columnaris	primary	--	--	--
	secondary	.8982	S	S
	tertiary	.8756	S	S
S. kali	primary	.6975	S	NS
	secondary	.8530	S	S
	tertiary	.9017	S	S
T. terrestris	primary	.8890	S	S
	secondary	.8149	S	S
	tertiary	.6730	S	NS
V. macdougalii	primary	.7469	S	NS
	secondary	.2207	NS	NS
	tertiary	.6911	S	NS

TABLE 1--Continued

Plant species	Root division	(r)	Level of significance	
			5 %	1%
M. alkalensis	primary	.5714	NS	NS
	secondary	.9047	S	S
	tertiary	.2207	NS	NS
B. polymorpha	primary	--	--	--
	secondary	.5988	S	S
	tertiary	.8756	S	S
S. Nuttallii	primary	.6975	S	NS
	secondary	.8530	S	S
	tertiary	.9017	S	S
T. torreyensis	primary	.8890	S	S
	secondary	.8149	S	S
	tertiary	.6730	S	NS
V. macdougalii	primary	.7409	S	NS
	secondary	.2207	NS	NS
	tertiary	.6913	S	NS

TABLE 2

Standard deviations (6) of stele and root diameters and mean ratios of stele- root diameters (sd/rd).

plant species	root division	(6) of stele dia.	(6) of root dia.	mean ratio of sd/rd
C. serrulata	primary	10.54	21.75	.4304
	secondary	9.95	15.41	.3103
	tertiary	7.12	18.99	.3012
C. texensis	primary	8.89	21.21	.4205
	secondary	15.59	32.12	.3337
	tertiary	7.80	18.00	.3022
F. acanthicarpa	primary	3.67	9.01	.3801
	secondary	7.22	18.51	.3846
	tertiary	6.70	12.55	.3609
G. microcephala	primary	8.89	40.34	.2132
	secondary	15.59	32.12	.3433
	tertiary	7.80	18.00	.2839
K. scoparia	primary	6.81	12.64	.4871
	secondary	5.81	17.03	.4418
	tertiary	8.48	6.39	.4295

TABLE 2--Continued

plant species	root division	(σ) of stele dia.	(σ) of root dia.	mean ratio of sd/rd
M. albicaulis	primary	5.49	19.93	.4120
	secondary	6.60	13.77	.4132
	tertiary	3.60	14.95	.3508
R. columnaris	primary	--	--	--
	secondary	10.39	31.60	.3006
	tertiary	10.81	33.92	.3214
S. kali	primary	10.39	19.68	.4212
	secondary	12.58	20.39	.3229
	tertiary	6.68	12.33	.3282
T. terrestris	primary	11.92	24.42	.3066
	secondary	36.36	25.24	.3172
	tertiary	4.64	23.01	.3054
V. macdougalii	primary	8.67	15.22	.3941
	secondary	7.12	10.08	.3627
	tertiary	7.90	18.70	.3277

TABLE 3

Xylem pattern or patterns for each root division of ten studied angiosperms.

plant species	primary	secondary	tertiary
C. serrulata	triarch	diarch	diarch
C. texensis	tetrarch	diarch	diarch
F. acanthicarpa	diarch	triarch	diarch
G. microcephala	diarch	triarch	diarch
K. scoparia	tetrarch	triarch *	diarch
M. albicaulis	diarch	diarch	diarch
R. columnaris	tetrarch	diarch #	diarch
S. kali	diarch	diarch	diarch
T. terrestris	diarch	diarch	diarch
V. macdougalii	diarch	diarch	diarch #

* two roots were diarch

two roots were triarch

TABLE 4

Average diameters in microns of roots and root steles.

plant species	primary		secondary		tertiary	
	stele	root	stele	root	stele	root
C. serrulata	132.6	308.0	67.2	213.0	46.2	150.3
C. texensis	123.6	294.0	80.4	241.2	70.8	234.0
F. acanthicarpa	115.2	303.3	99.0	257.5	57.0	158.1
G. microcephala	66.0	310.2	91.2	258.3	61.2	213.0
K. scoparia	72.6	149.8	88.5 69.0*	211.0 133.5*	54.0	125.4
M. albicaulis	68.4	167.4	58.2	140.7	52.8	151.8
R. columnaris	---	---	88.2 121.5#	288.0 351.0#	75.6	233.6
S. kali	108.0	256.5	60.0	184.8	44.4	134.7
T. terrestris	130.8	428.7	67.8	215.1	78.0	256.6
V. macdougalii	107.4	272.4	70.2	193.8	56.2 102#	167.5 303#

* two roots were diarch
\# Two roots were triarch

TABLE 5

Measurements in microns for each root of each division for plants studied and their stele-root diameter ratios.

primary			secondary			tertiary		
root dia.	stele dia.	sd/rd	root dia.	stele dia.	sd/rd	root dia.	stele dia.	sd/rd
C. serrulata								
345	150.	.4347	240	78	.3250	186	54	.2903
336	138	.4107	234	60	.2820	174	60	.2873
330	144	.4363	222	72	.3243	162	48	.2962
312	138	.4423	219	78	.3052	156	42	.2692
306	132	.4313	216	60	.2777	150	48	.3200
303	138	.4554	210	72	.3428	144	48	.3333
300	126	.4200	204	60	.2941	144	48	.3333
291	114	.3917	198	72	.3636	138	42	.3042
282	120	.4255	195	60	.3076	129	36	.2790
276	126	.4565	192	54	.2812	120	36	.3000
C. texensis								
336	138	.4107	264	84	.3181	258	78	.3023
312	126	.4038	258	90	.3488	246	78	.3170
306	132	.4313	252	84	.3333	246	78	.3170
306	120	.3921	252	78	.3095	246	72	.2926
297	132	.4444	246	78	.3170	240	72	.3000
291	126	.4329	243	84	.3456	231	72	.3116
282	120	.4255	234	78	.3333	225	66	.2933
279	120	.4301	228	78	.3421	222	66	.2972
273	120	.4395	225	78	.3466	246	72	.2926
258	102	.3953	210	72	.3428	204	60	.2941
F. acanthicarpa								
342	132	.3860	282	102	.3617	180	72	.4000
336	126	.3750	282	108	.3829	171	60	.3508
324	114	.3518	276	102	.3695	168	60	.3571
318	132	.4150	270	102	.3777	162	60	.3703
312	108	.3461	264	90	.3409	162	48	.2962
303	114	.3762	258	102	.3953	159	54	.3396
294	108	.3672	246	84	.3414	150	54	.3600
291	120	.4123	240	96	.4000	147	54	.3673
267	102	.3820	234	96	.4102	144	48	.3333
246	96	.3902	231	108	.4675	138	60	.4347

TABLE 5--Continued

primary			secondary			tertiary		
root dia.	stele dia.	sd/rd	root dia.	stele dia.	sd/rd	root dia.	stele dia.	sd/rd
G. microcephala								
402	84	.2089	330	126	.3818	288	66	.2894
342	72	.2105	288	96	.3333	240	78	.3250
330	72	.2181	276	108	.3913	231	60	.2597
327	66	.2018	270	102	.3777	222	66	.2972
306	60	.1960	255	84	.3294	216	60	.2777
294	54	.1836	252	84	.3333	216	60	.2777
291	66	.2268	237	78	.3291	210	60	.2857
288	72	.2500	228	78	.3421	195	48	.2461
270	60	.2222	225	78	.3466	192	54	.2812
252	54	.2142	222	78	.3513	180	54	.3000
K. scoparia								
171	72	.4210	225	96	.4266	156	72	.4615
162	78	.4814	216	90	.4166	144	60	.4166
159	78	.4905	210	90	.4285	138	60	.4247
159	78	.4905	207	84	.4057	129	54	.4186
150	66	.4400	204	96	.4705	123	48	.3902
147	84	.5714	192	90	.4687	120	54	.4500
144	72	.5000	186	78	.4193	117	54	.4615
138	66	.4782	168	84	.5000	114	54	.4736
135	72	.5333	141*	72*	.5106	108	42	.3888
129	60	.4651	126*	66*	.5238	105	42	.4000
M. albicaulis								
198	66	.3333	162	66	.4074	180	60	.3333
192	78	.4062	153	60	.3921	168	54	.3214
189	72	.3809	150	60	.4000	162	48	.2962
180	72	.4000	150	66	.4400	156	48	.3076
168	72	.4285	144	60	.4166	153	54	.3529
156	68	.4230	141	60	.4255	150	54	.3600
156	66	.4230	138	60	.4347	147	48	.3265
150	60	.4000	132	54	.4090	141	54	.3829
144	72	.5000	123	54	.4390	132	54	.4090
141	60	.4255	114	42	.3684	129	54	.4186

* diarch roots

TABLE 5--Continued

primary			secondary			tertiary		
root dia.	stele dia.	sd rd	root dia.	stele dia.	sd rd	root dia.	stele dia.	sd rd
R. columnaris								
			366#	129#	.3524	300	78	.3611
			360	108	.3000	288	84	.2916
			336#	114#	.3392	246	72	.2962
			303	96	.3168	243	84	.3456
			300	84	.2800	219	72	.3276
			288	84	.2916	222	72	.3243
			276	78	.2826	216	78	.3611
			273	90	.3296	216	72	.3333
			270	84	.3113	198	66	.3333
			246	72	.2926	192	54	.2812
S. kali								
288	108	.3750	216	72	.3333	144	48	.3333
276	132	.4782	210	66	.3142	150	54	.3600
270	108	.4000	204	72	.3529	147	48	.3265
267	108	.4044	192	72	.3750	144	48	.3333
264	108	.4090	192	78	.4062	138	42	.3043
258	114	.4418	180	54	.3000	132	48	.3636
246	108	.4390	174	48	.2758	126	36	.2857
246	108	.4390	168	48	.2857	126	42	.3333
228	96	.4210	156	42	.2692	120	36	.3000
222	90	.4054	156	48	.3076	114	36	.3157
T. terrestris								
492	156	.3170	240	78	.3250	288	84	.2916
441	138	.3129	240	78	.3250	282	84	.2978
438	132	.3013	228	72	.3157	276	72	.2608
432	144	.3333	228	66	.2894	273	84	.3076
426	132	.3098	228	66	.2894	264	78	.2954
423	126	.2978	225	66	.2933	258	78	.3025
414	114	.2753	216	66	.3055	240	78	.3250
411	120	.2919	210	66	.3142	237	78	.3291
408	126	.3088	174	60	.3448	231	72	.3116
402	120	.2985	162	60	.3703	216	72	.3333

triarch roots

TABLE 5--Continued

Primary			Secondary			Tertiary	
root dia.	stele dia.	No. of rd	root dia.	stele dia.	No. of rd	root dia.	stele dia.	No. of rd
B. Polyarchs								
.3664	.1259	300	.3584	.1259	300	.3621		76
.3600	.1188	300	.3600	.1188	289	.3716		84
.3764	.1114	300	.3752	.1114	284	.3682		74
.3702	.1196	300	.3768	.1196	283	.3684		84
.3600	.1184	300	.3680	.1184	219	.3672		72
.3684	.1184	284	.3640	.1184	222	.3684		72
.3676	.1176	278	.3688	.1176	216	.3684		70
.3672	.1172	270	.3676	.1172	216	.3672		72
.3672	.1172	270	.3672	.1172	198	.3672		66
.3684	.1172	264	.3684	.1172	192	.3684		54
B. Diarchs								
.3684	.1196	288	.3684	.1196	144	.3684		48
.3676	.1184	276	.3672	.1184	138	.3684		48
.3672	.1184	270	.3672	.1184	138	.3672		48
.3672	.1184	264	.3672	.1184	138	.3672		48
.3672	.1184	258	.3672	.1184	138	.3672		48
.3672	.1184	252	.3672	.1184	138	.3672		48
.3672	.1184	246	.3672	.1184	138	.3672		48
.3672	.1184	240	.3672	.1184	138	.3672		48
.3672	.1184	234	.3672	.1184	138	.3672		48
.3672	.1184	228	.3672	.1184	138	.3672		48
.3672	.1184	222	.3672	.1184	138	.3672		48
.3672	.1184	216	.3672	.1184	138	.3672		48
.3672	.1184	210	.3672	.1184	138	.3672		48
.3672	.1184	204	.3672	.1184	138	.3672		48
.3672	.1184	198	.3672	.1184	138	.3672		48
.3672	.1184	192	.3672	.1184	138	.3672		48
C. Tetrarchs								
.3672	.1184	276	.3672	.1184	138	.3672		48
.3672	.1184	270	.3672	.1184	138	.3672		48
.3672	.1184	264	.3672	.1184	138	.3672		48
.3672	.1184	258	.3672	.1184	138	.3672		48
.3672	.1184	252	.3672	.1184	138	.3672		48
.3672	.1184	246	.3672	.1184	138	.3672		48
.3672	.1184	240	.3672	.1184	138	.3672		48
.3672	.1184	234	.3672	.1184	138	.3672		48
.3672	.1184	228	.3672	.1184	138	.3672		48
.3672	.1184	222	.3672	.1184	138	.3672		48
.3672	.1184	216	.3672	.1184	138	.3672		48
.3672	.1184	210	.3672	.1184	138	.3672		48
.3672	.1184	204	.3672	.1184	138	.3672		48
.3672	.1184	198	.3672	.1184	138	.3672		48
.3672	.1184	192	.3672	.1184	138	.3672		48

* Triarch roots

TABLE 5--Continued

primary			secondary			tertiary		
root dia.	stele dia.	sd/rd	root dia.	stele dia.	sd/rd	root dia.	stele dia.	sd/rd
V. macdougalii								
294	126	.4285	210	78	.3714	312#	108#	.3461
294	120	.4081	201	72	.3582	294#	96#	.3265
288	102	.3541	204	72	.3529	183	66	.3606
276	108	.3913	198	60	.3030	180	66	.3666
276	108	.3913	195	66	.3384	180	60	.3333
270	102	.3777	195	72	.3692	177	54	.3050
264	102	.3863	192	66	.3437	174	54	.3103
258	108	.4186	186	72	.3871	168	60	.3571
252	96	.3809	183	84	.4590	156	42	.2692
252	102	.4047	174	60	.3445	123	48	.3200

triarch roots

PLATE 1

Figures 1-2. Differentiation of an exarch diarch stele: Figure 1. A partial transection of a young root of Mentzelia albicaulis with the initial cambial cells barely beginning differentiation. The first protoxylem elements (px) and the first protophloem cells (pp) are distinguishable. The vascular elements are forming just inside the pericycle. End.= endodermis. Figure 2. Later development with two, almost three, protoxylem elements visible at the poles. The same condition is evident in the protophloem.

PLATE 1

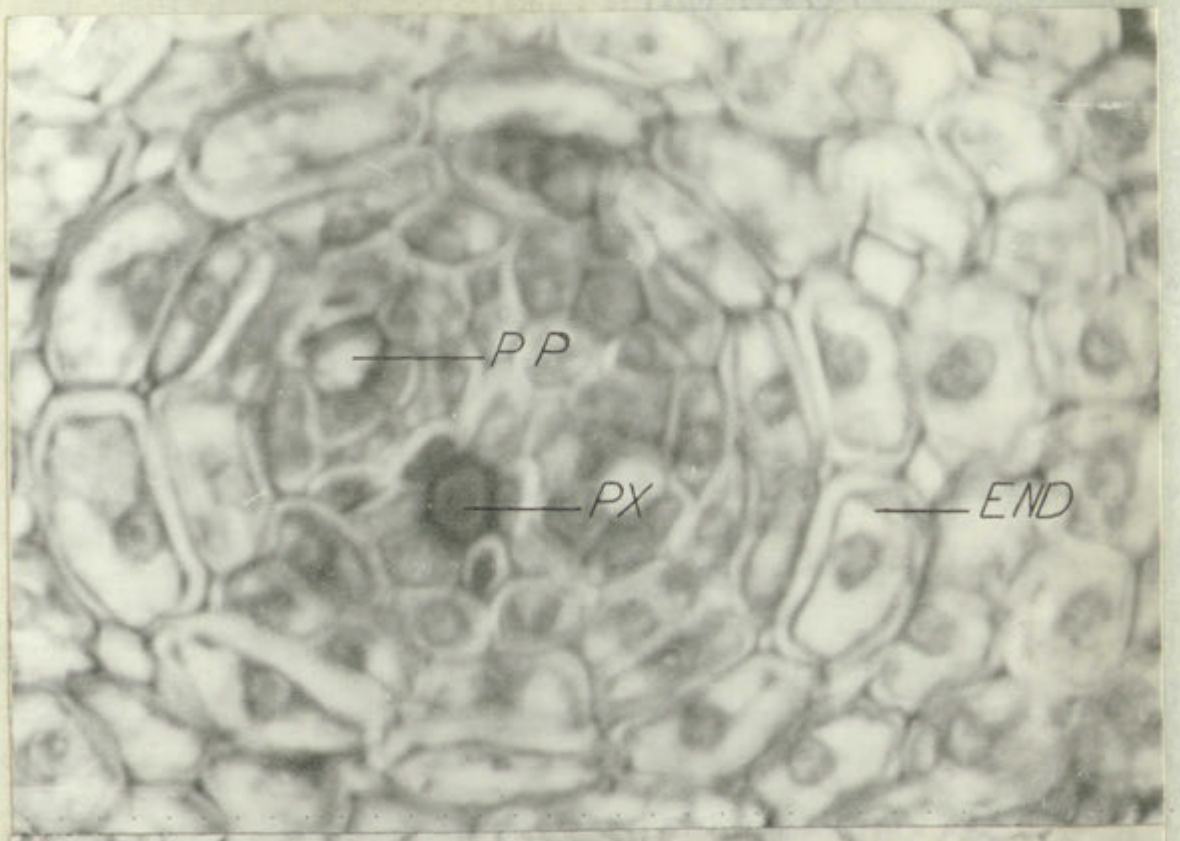


Fig. 1

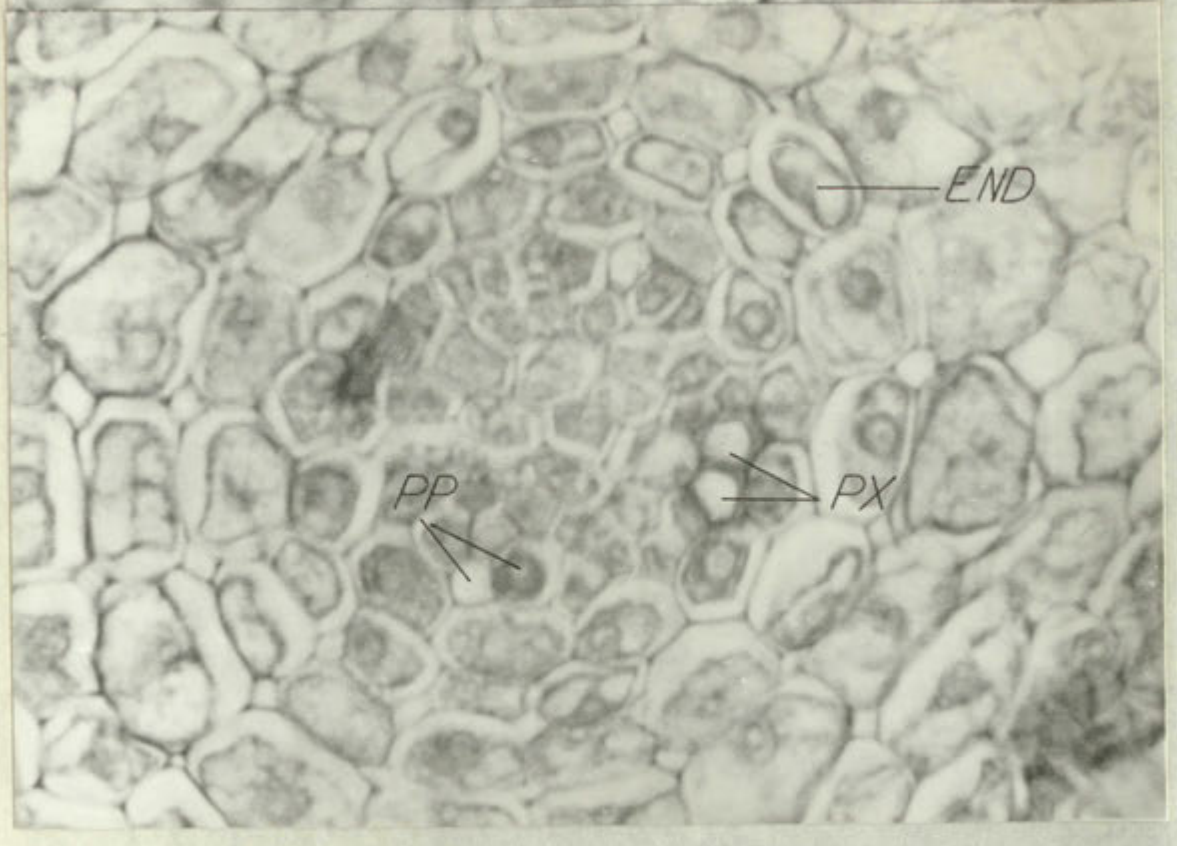
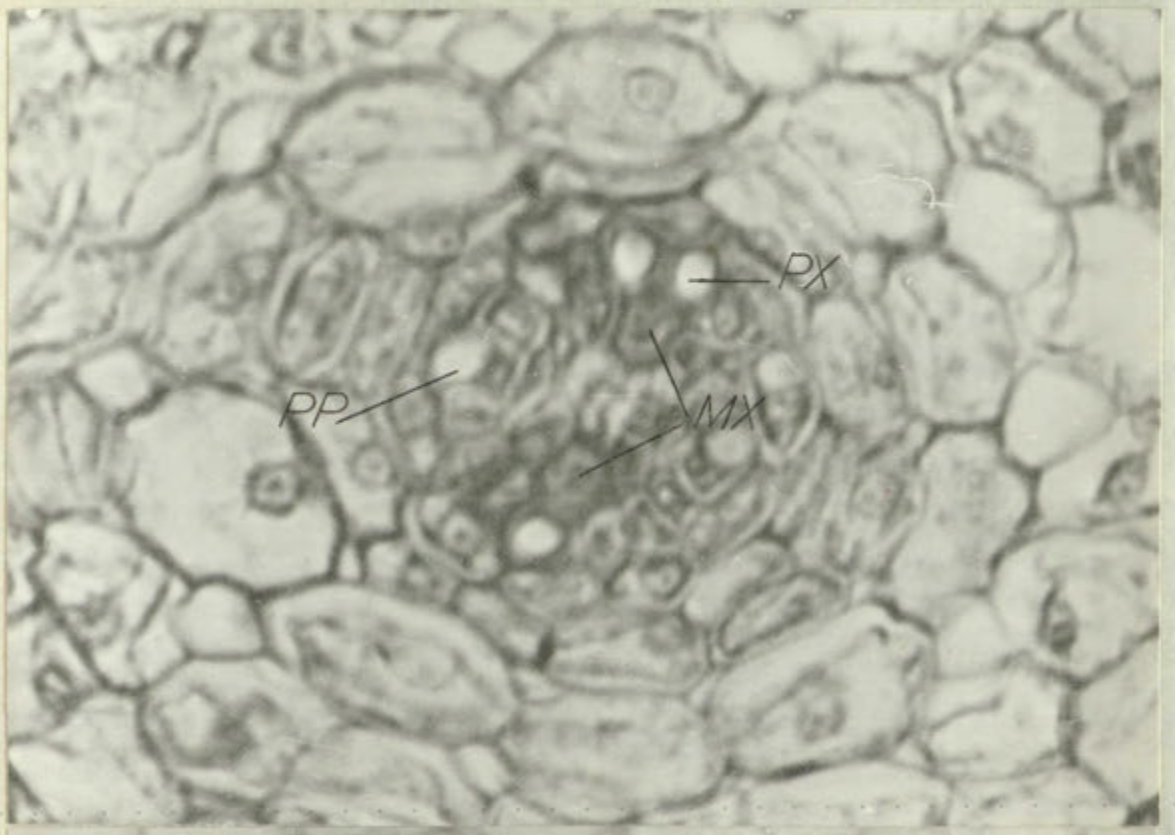


Fig. 2

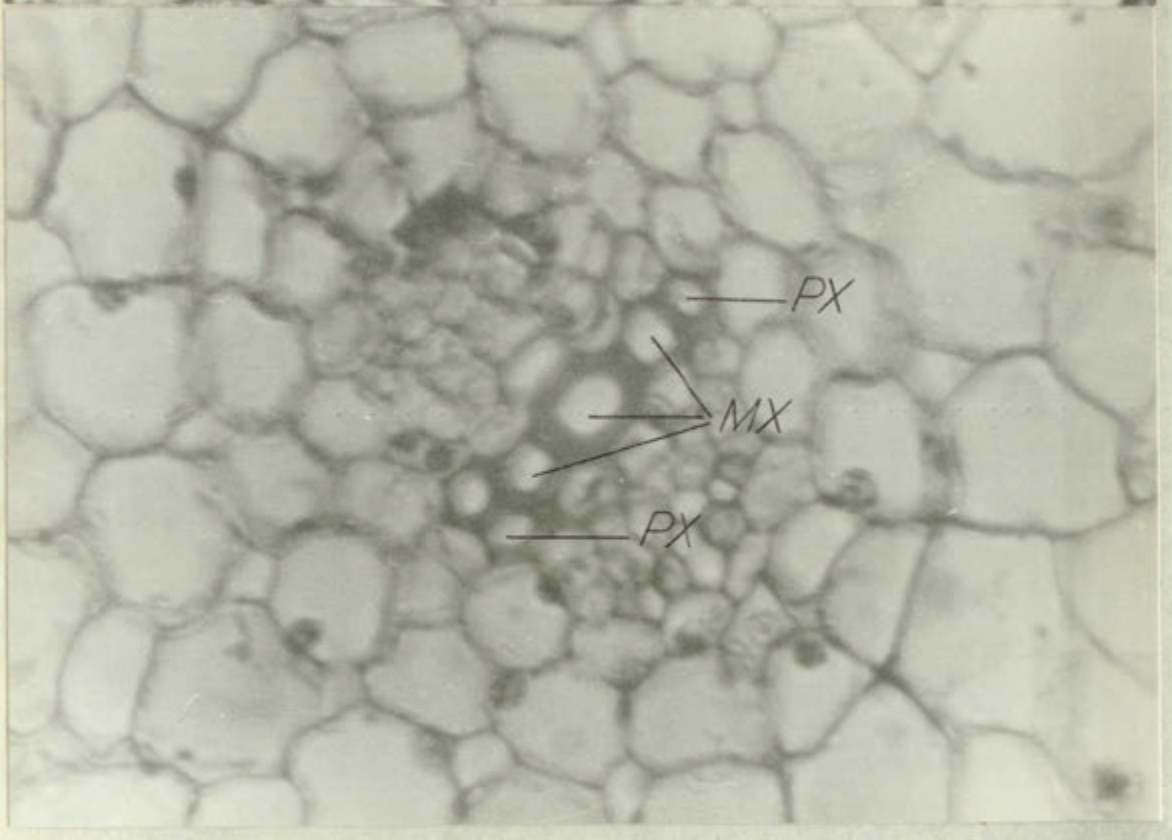
PLATE 2

Figures 1-2. Differentiation of an exarch diarch stele: Figure 1. Last stage in the development of the vascular cylinder in Mentzelia albicaulis Dougl. Metaxylem cells (mx) have appeared inside the protoxylem elements. Figure 2. A fully formed diarch stele, protoxylem elements are toward the outside with larger metaxylem cells located central to them.

PLATE 2



g. 1

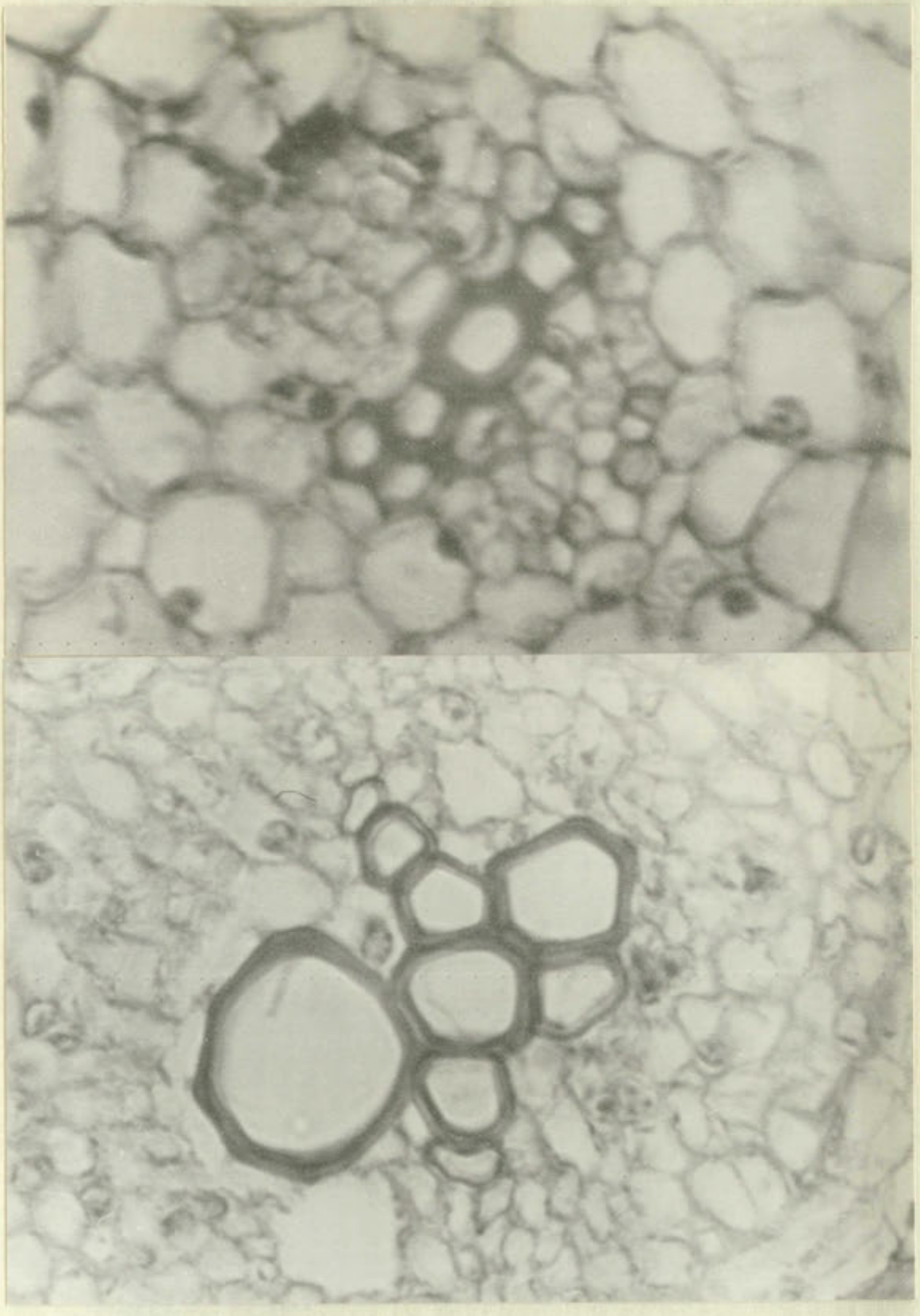


g. 2

PLATE 3

Figures 1-2. Stelar patterns of primary and secondary roots of Mentzelia albicaulis. Figure 1. Diarch xylem arrangement exhibited in the primary roots of Mentzelia. Figure 2. Diarch xylem arrangement present in the secondary roots of the same species.

PLATE 3



1

2

PLATE 4

Figures 1-2. Stelar patterns in tertiary roots of Mentzelia albicaulis and the primary roots of Ratibida columnaris. Figure 1. Outlined ink tracing from photomicrograph of the diarch pattern of tertiary roots of Mentzelia. Figure 2. Outlined ink tracing from a photomicrograph of the tetrarch xylem arrangement in the primary root of Ratibida.

PLATE 4

Fig. 1

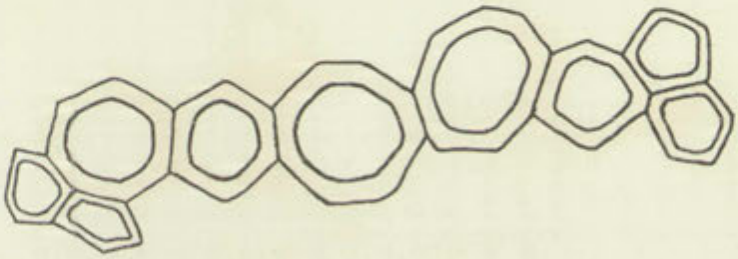


Fig. 2

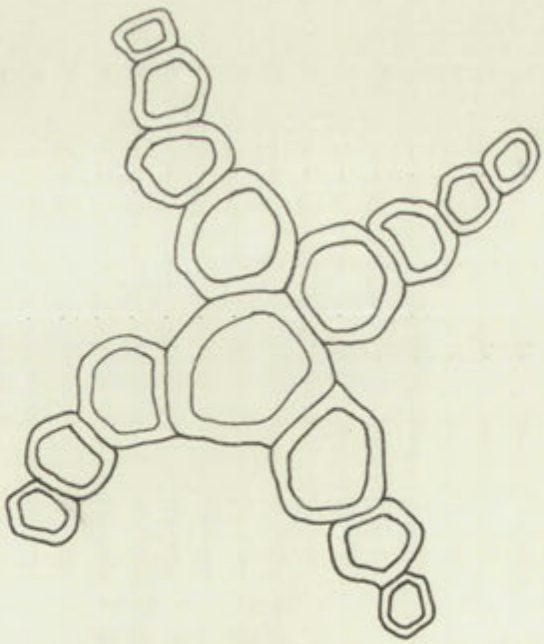


PLATE 5

Figure 1-2. Stelar patterns of triarch secondary and diarch secondary roots of Ratibida columnaris. Figure 1. The triarch xylem pattern that was found in two secondary roots. Figure 2. The diarch pattern, which was the characteristic pattern in secondary roots, with two exceptions.

PLATE 5

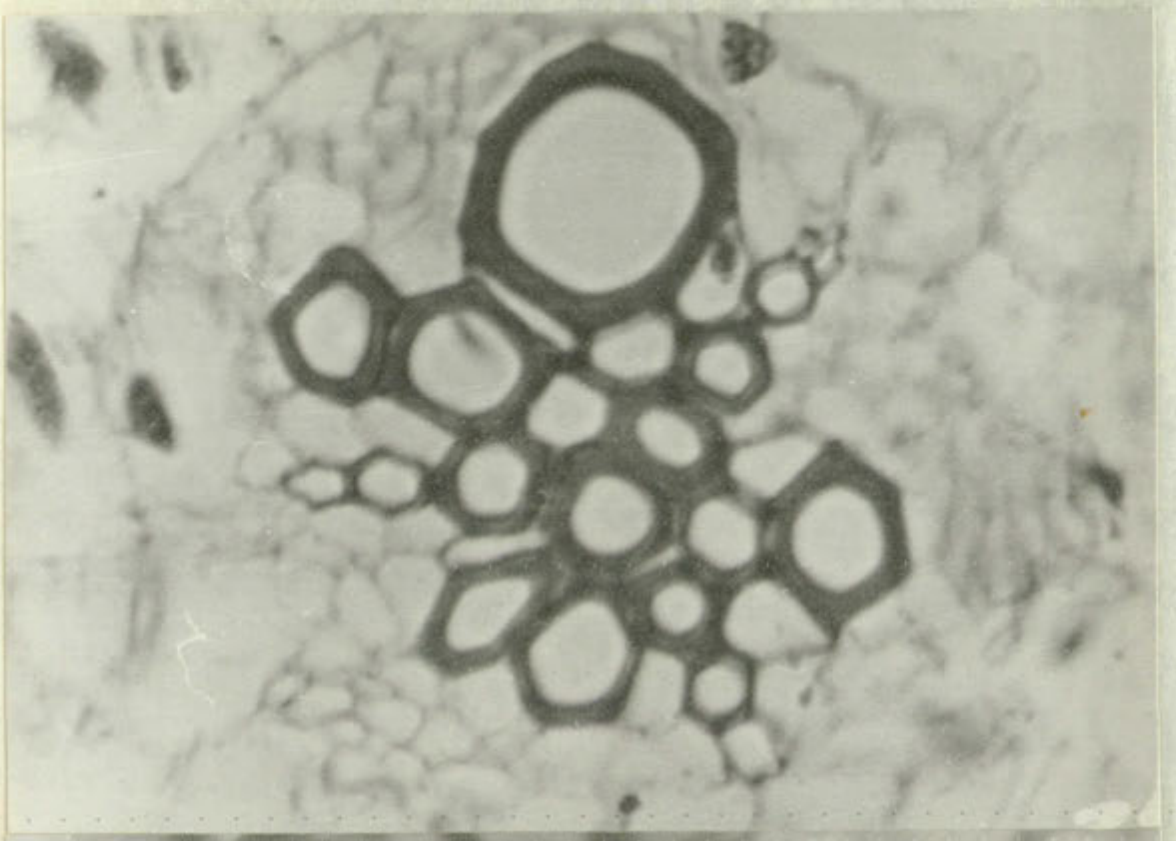


Fig. 1

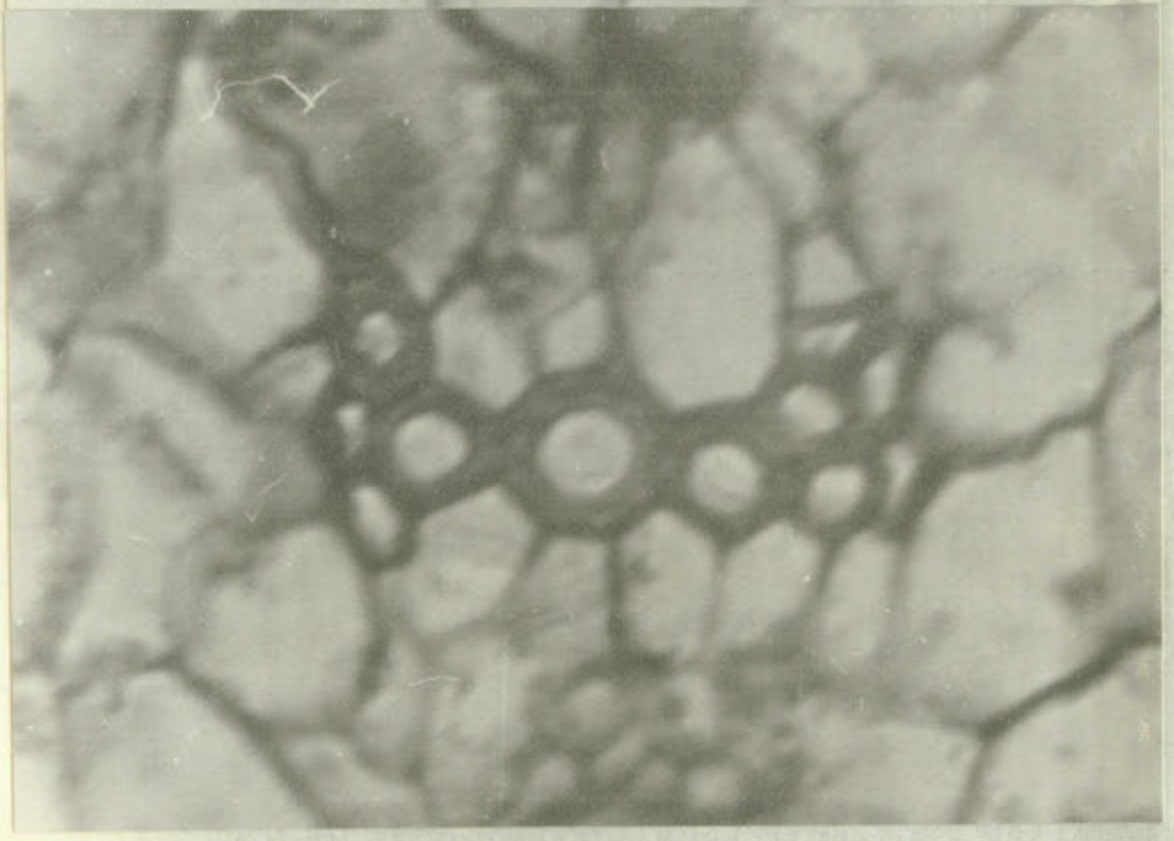


Fig. 2

PLATE 6

Figures 1-2. Stelar patterns in tertiary roots of Ratibida columnaris and the primary roots of Tribulus terrestris, showing the development of a lateral root. Figure 1. Outlined ink tracing from a photomicrograph of the diarch pattern in the tertiary roots of Ratibida. Figure 2. Diarch stelar condition in the primary roots of Tribulus. Also shown is the early stage of a developing lateral root. The lateral root has its origin directly opposite a xylem pole, which condition is typical in developing lateral roots studied whether of primary, secondary, or tertiary rank.

PLATE 6

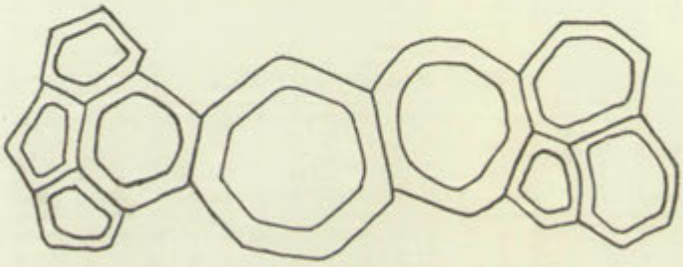


Fig. 1

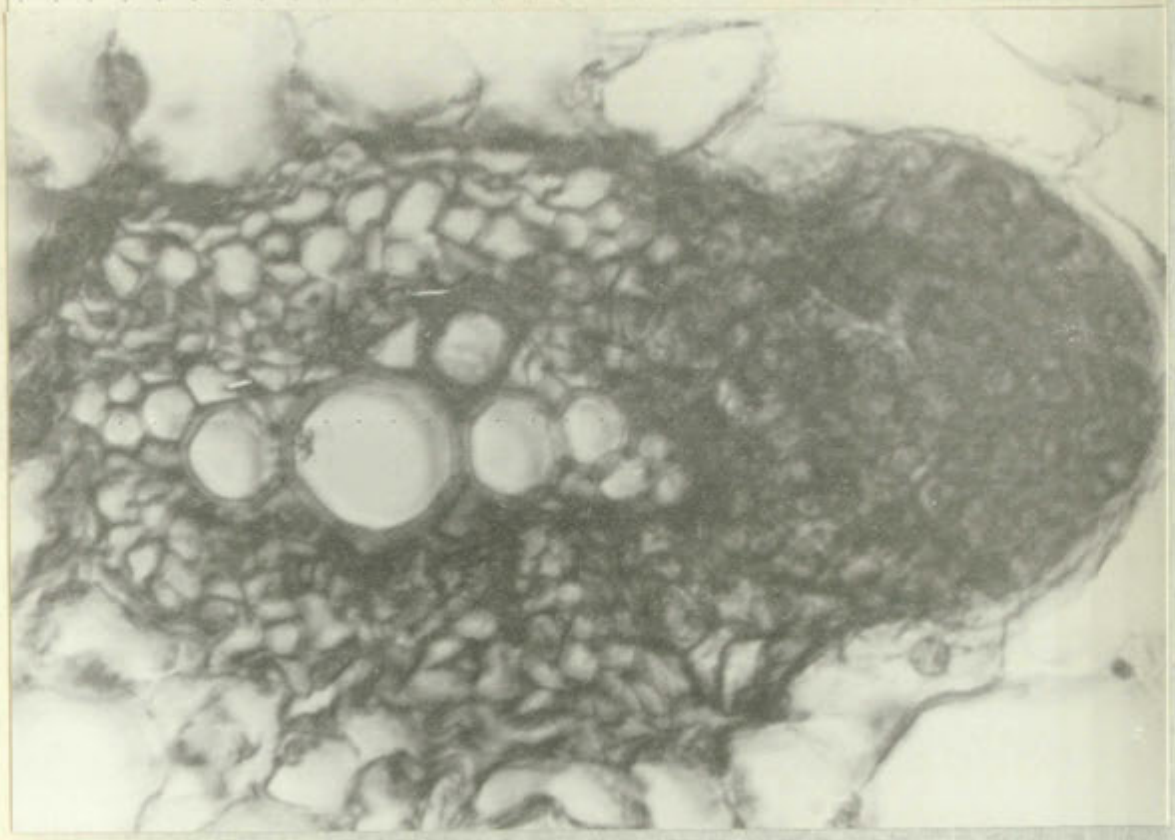


Fig. 2

PLATE 7

Figures 1-2. Stelar patterns of secondary and tertiary roots of Tribulus terrestris. Figure 1. Diarch xylem arrangement was found in all secondary roots of Tribulus. Figure 2. Outlined ink tracing from a photomicrograph of the characteristic diarch pattern found in tertiary roots of Tribulus terrestris.

PLATE 7

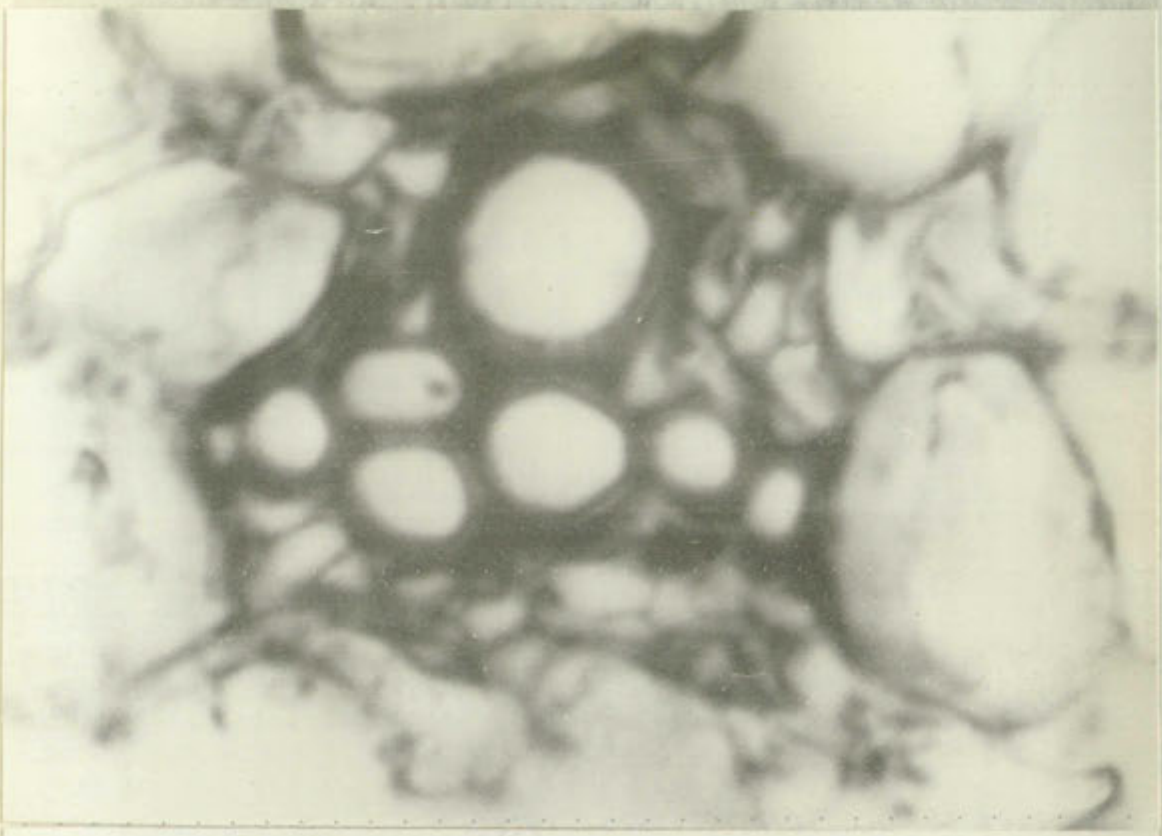


Fig. 1

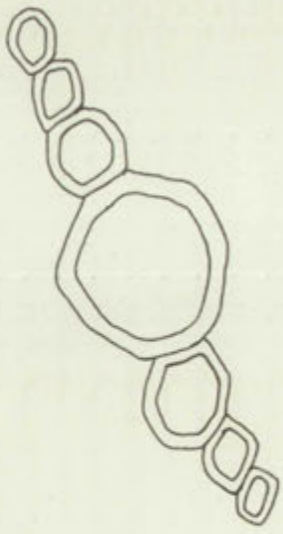


Fig. 2

PLATE 8

Figures 1-2. Stelar patterns of primary and secondary roots of Verbena macdougalii. Figure 1. Outlined ink tracing from a photomicrograph of the diarch pattern of the primary root. Figure 2. Diarch pattern for a secondary root. In both pictures there are extra large metaxylem cells in the center of the xylem strands.

PLATE 8

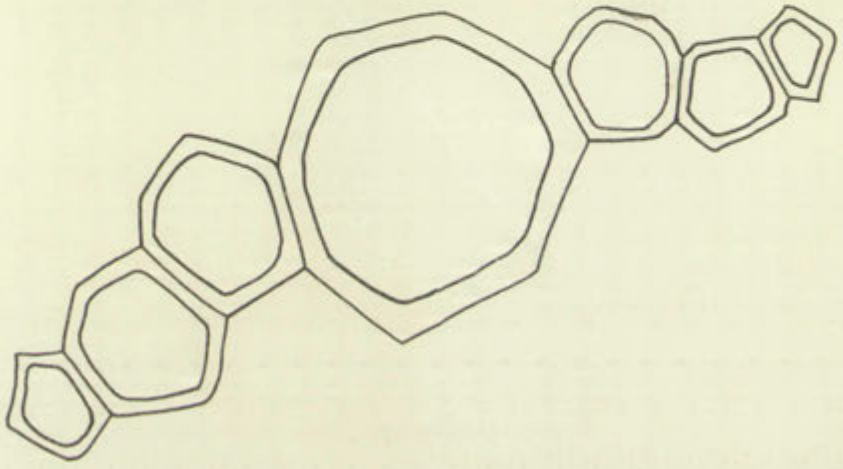


Fig. 1

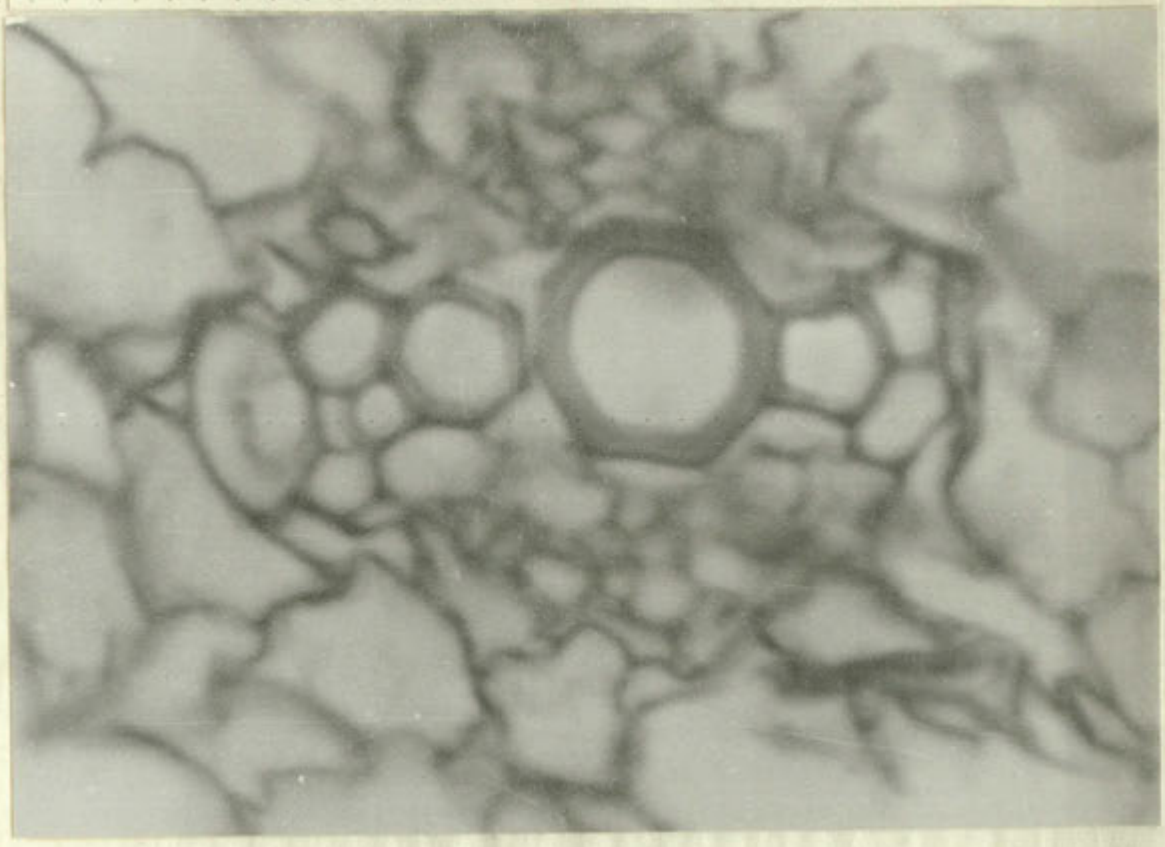


Fig. 2

PLATE 9

Figures 1-2. Stelar patterns of tertiary roots of Verbena macdougalii. Figure 1. Diarch stele characteristic of most of the tertiary roots examined. Figure 2. The triarch condition that was found in two roots.

PLATE 9

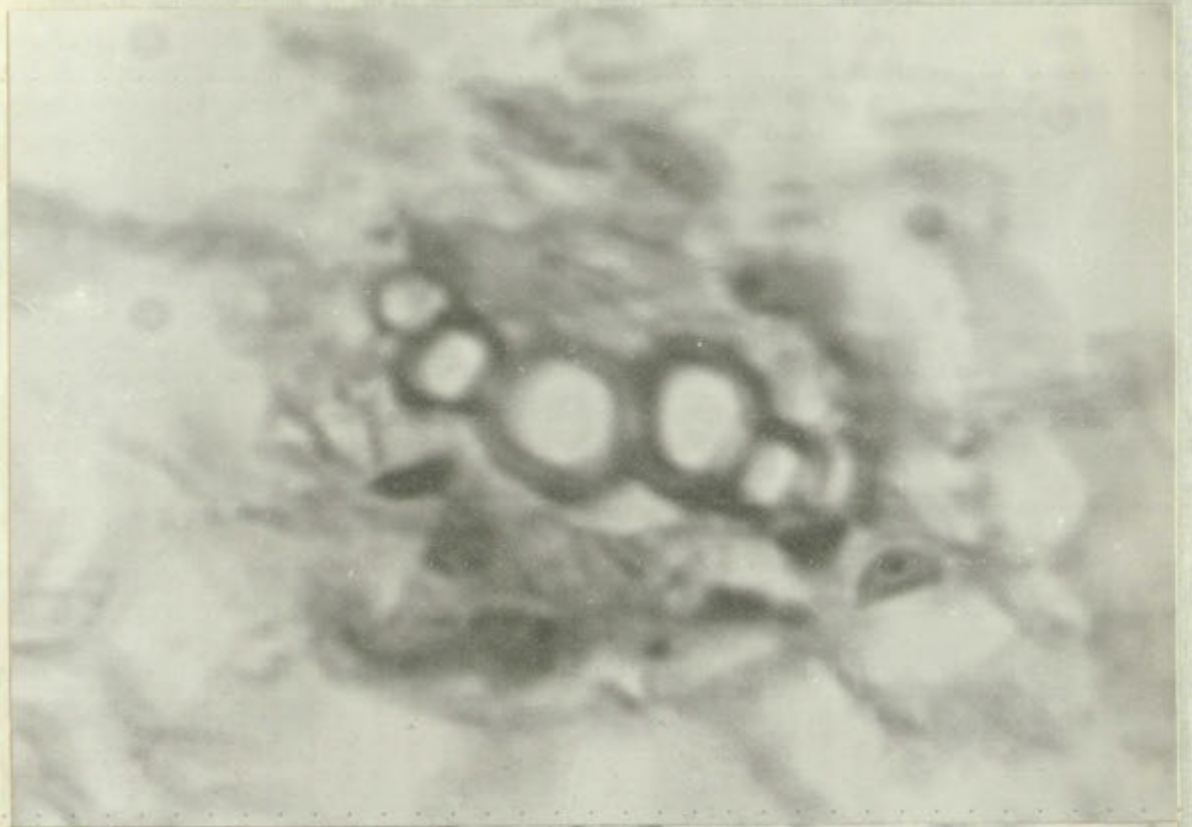


Fig. 1

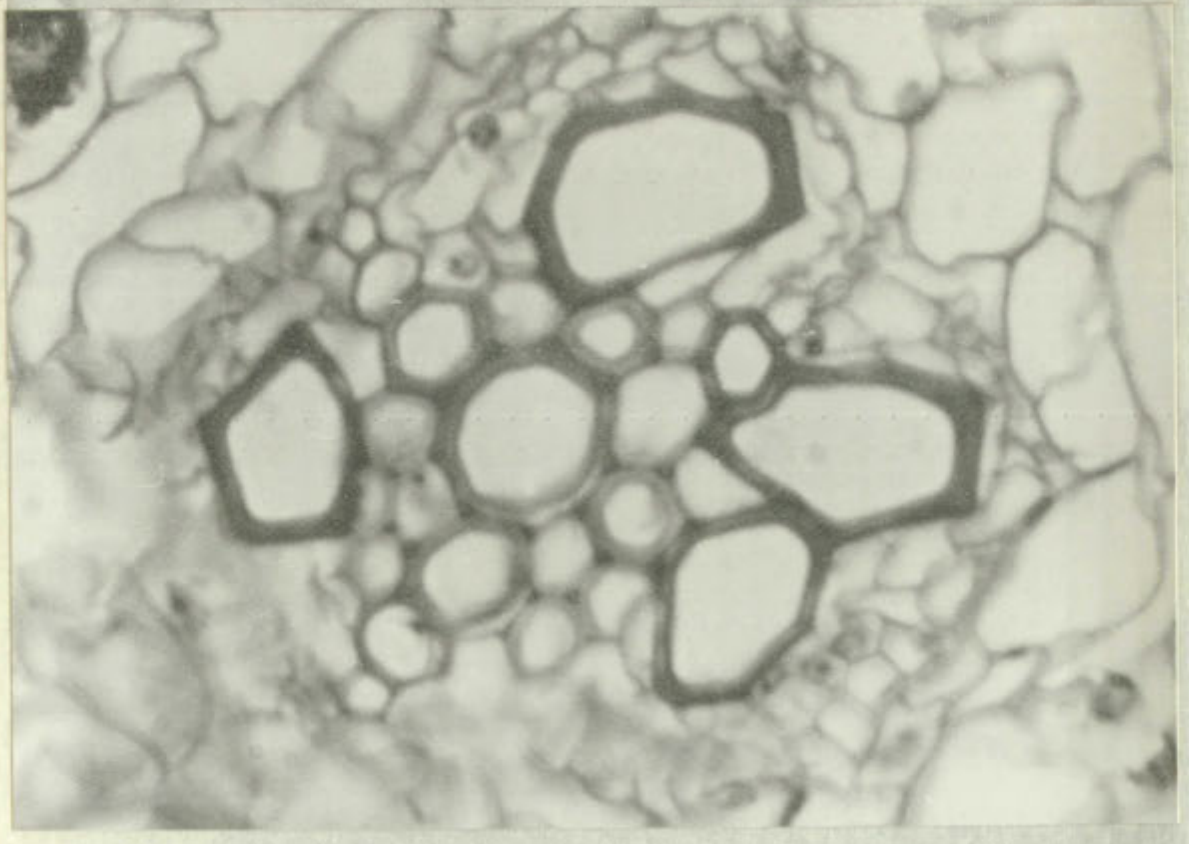


Fig. 2

PLATE 10

Figures 1-6. Stelar patterns in primary, secondary, and tertiary roots of Croton texensis and Gutierrezia microcephala. Figure 1. Tetrarch xylem arrangement in the primary roots of Croton texensis. Figures 2 and 3. Diarch pattern in secondary and tertiary roots of Croton texensis. Figures 4 and 6. Diarch xylem patterns in tertiary and primary roots of Gutierrezia microcephala, respectively. Figure 5. Increase in xylem points in secondary roots to the triarch xylem pattern from the primary diarch condition.

PLATE 10

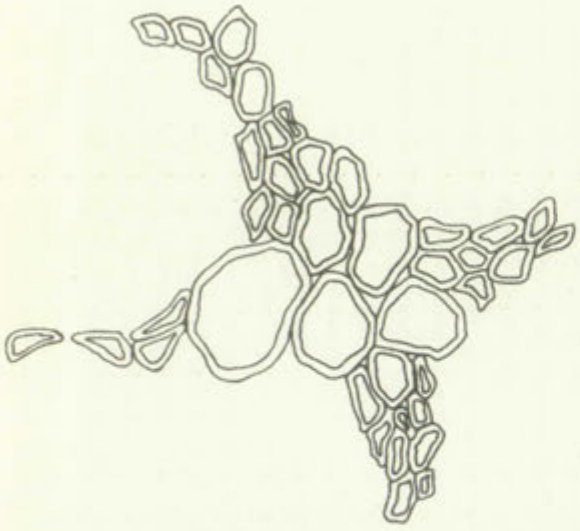


FIG. 1

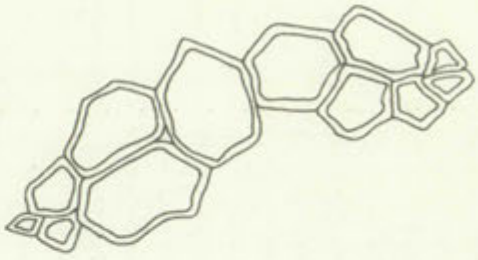


FIG. 2

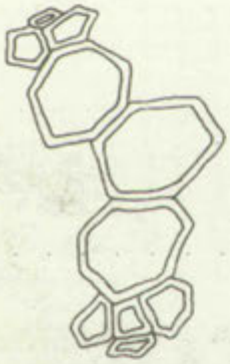


FIG. 3

FIG. 4

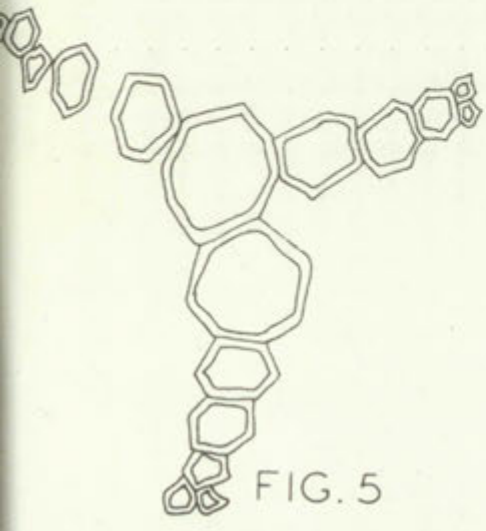


FIG. 5

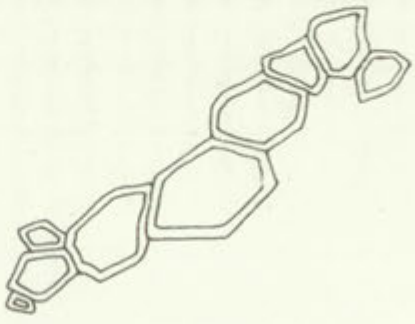


FIG. 6

PLATE 11

Figures 1-6. Stelar patterns of primary, secondary, and tertiary roots of Salsola kali and Cleome serrulata. Figures 1, 2, and 3. Diarch xylem patterns found in primary, secondary, and tertiary roots respectively of Salsola kali. Figure 4. Tetrarch pattern present in all primary roots of Cleome serrulata. Figures 5 and 6. Characteristic diarch condition in the secondary (fig. 5) and tertiary (fig. 6) roots of Cleome.

PLATE II

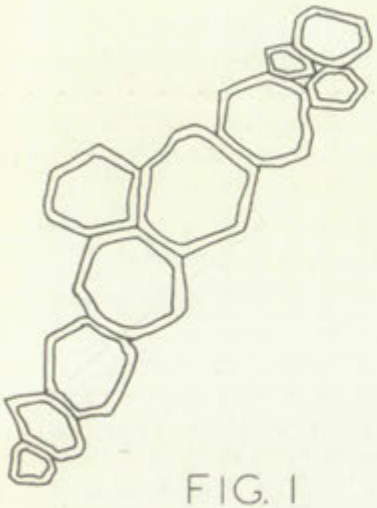


FIG. 1

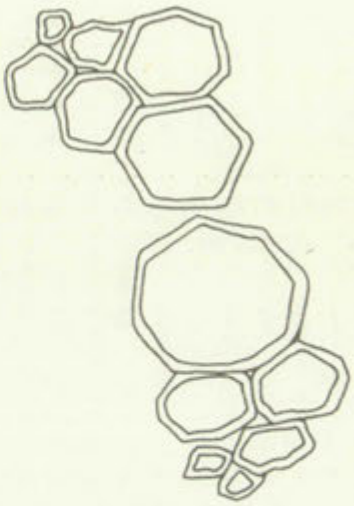


FIG. 2

FIG. 3

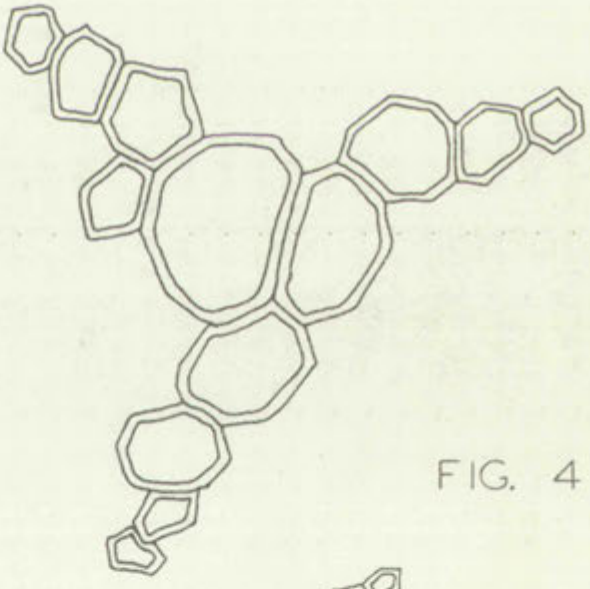


FIG. 4

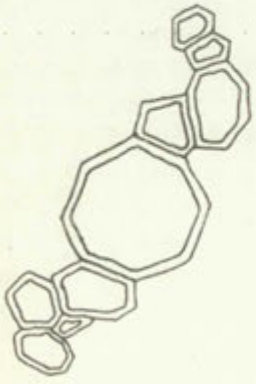


FIG. 5

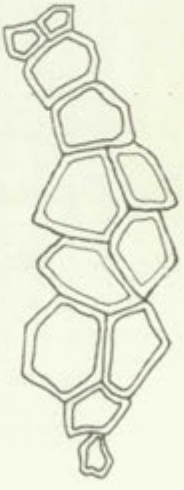


FIG. 6

PLATE 12

Figures 1-6. Stelar patterns of primary, secondary, and tertiary roots of Franseria acanthicarpa and Kochia scoparia. Figures 1 and 3. Diarch xylem pattern in the primary and tertiary roots, respectively, of Franseria acanthicarpa. Figure 2. Triarch xylem arrangement in secondary roots of Franseria. Figures 4, 5, and 6. Tetrarch condition of primary roots (fig. 4), triarch pattern of secondary roots (fig. 5), and the diarch xylem arrangement of tertiary roots of Kochia scoparia (fig. 6).

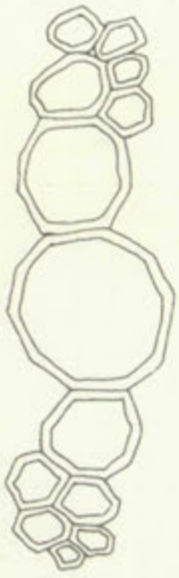


FIG. 1

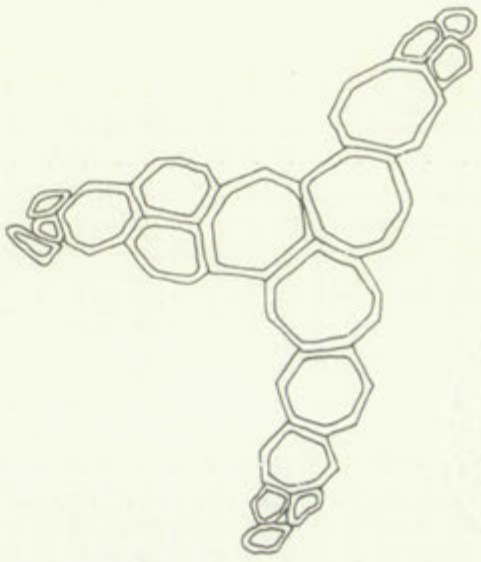


FIG. 2

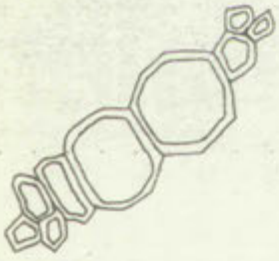


FIG. 3

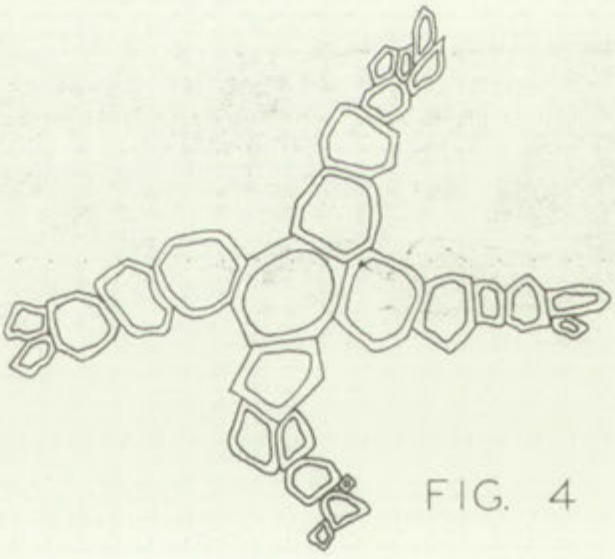


FIG. 4

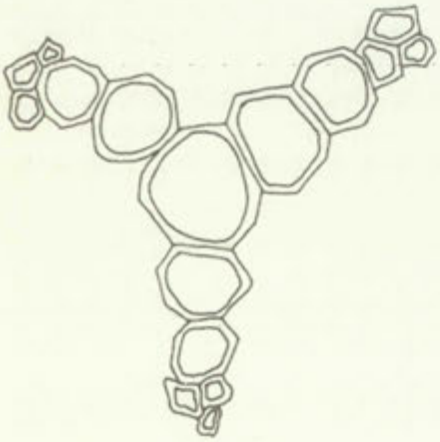


FIG. 5

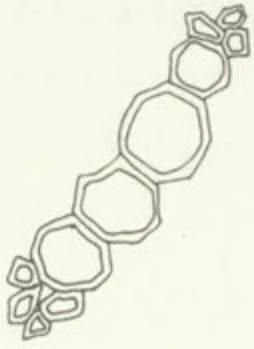


FIG. 6

IMPORTANT!

Special care should be taken to prevent loss or damage of this volume. If lost or damaged, it must be paid for at the current rate of typing.