CERTAIN ASPECTS OF DEVELOPMENTAL ANATOMY OF AMARANTHUS LEUCOCARPUS S. WATS

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the requirements for the degree of
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Dedicated to the beloved memory of

my father and sister Cissy. .....

who were anxious to see this piece of

work but ..... are not alive.

CONTENTS

SUPERVISOR'S NOTE

The thesis entitled " Certain aspects of developmental anatomy of Amaranthus leucocarpus - S. Wats. submitted by Shri K.T. Sebastian, M.Sc., for the degree of Doctor of Philosophy, embodies the results of the investigations done under my supervision and I certify that the work is original.

(B.D. Deshpande)

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K.T. Sebastian

(K.T. Sebastian)

and root apices.

Root Apex.

The first study on root apical organization came from Nageli (1845), when he postulated the 'Apical cell theory'. The apical cell theory received support from Hofmeister (1851), Nicolai (1865) and others. Later, Hanstein (1868) put forward the 'Histogen theory', which is still used for describing the root apical organization with some modifications. Root apical organization was studied by Janczewski (1874), Eriksson (1878), Haberlandt (1914), Clowes (1950, 1953, 1954, 1956, 1958, 1961a), Guttenberg (1960), Pillai and Pillai (1961 a,b,c), Pillai et.al (1961 a,b). Various types of root apices have been recognised on the basis of the number and arrangement of initials. Janczewski (1874) described five types of root apices.

Eriksson (1878) described only four types of root apical organization. Similarly, Hayward (1938) and Schüepp (1926) have also classified root apices into four types but differently from that of Eriksson, although some types correspond. Popham (1952) modified Janczewski's classification and has described seven types of root apical organization.

Guttenberg (1960) has broadly divided the apical organization of root into two types namely 'closed' and 'open'. He termed the type with discrete initials for

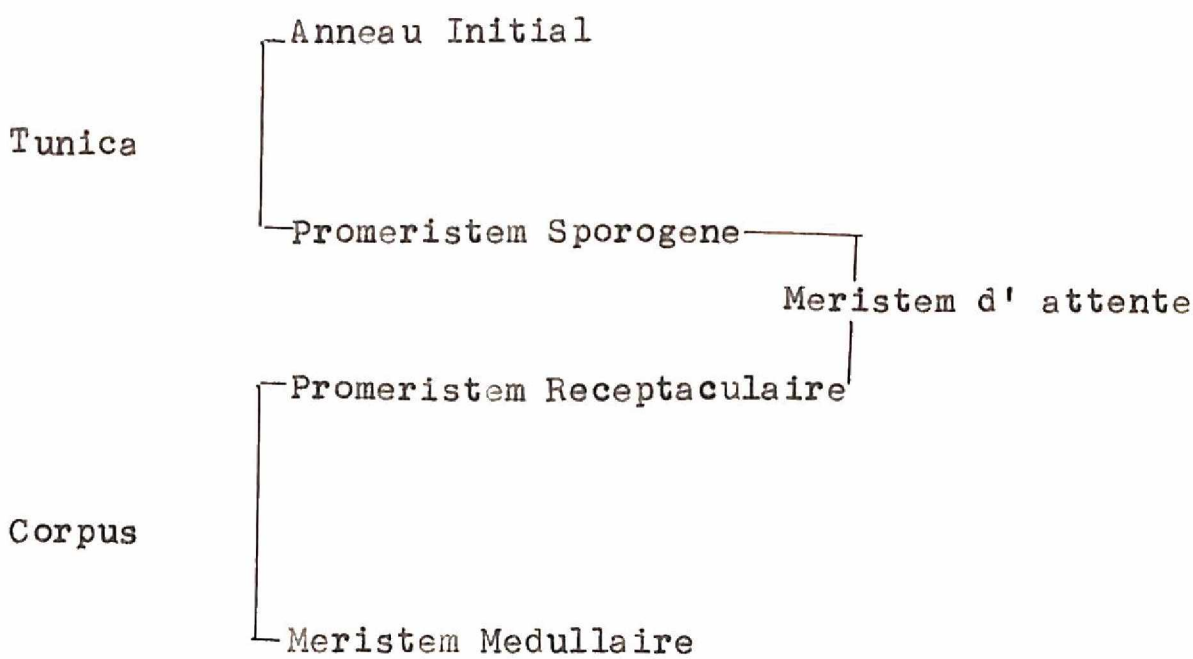
utility in certain cases. With the accumulation of literature both these were found inadequate to explain the diversities of apical configurations.

The large single apical cell of various mosses and algae was discussed in the apical cell theory. Hofmeister (1851) reported a single apical cell in angiosperms. But the applicability of this theory to the apices of higher plants was questioned by some workers even then.

Meanwhile Hanstein (1868) published his 'Histogen theory'. According to Hanstein's theory the shoot apex in angiosperms consists of a central core of irregularly arranged cells covered by a variable number of mantle like layers. According to this theory each layer and core is derived from distinct initial cells which may occur in a superimposed fashion or in groups. The predestination aspect of Hanstien's theory drew a great amount of criticism, which was reviewed and discussed by Schmidt (1924).

Angiosperms as well as gymnosperms were investigated for the shoot apical organization. It was believed that the shoot apex of spermatophtyes was a primordial meristem (promeristem) consisting of undifferentiated cells which are morphologically identical. Recently, however, it has been possible to distinguish cytohistological zones depending upon the plane of divi-

where mitoses are rare and the peripheral part, the 'Anneau initial' with high frequency of mitotic figures corresponds to the tunica. In the same way 'promeristem receptaculaire' and 'meristem medullaire' correspond to the corpus (Gifford, 1954). This correlation can be represented as follows:



In support of this concept of inactive cells the method of counting division figures in various zones has been applied by Lance (1952, 1953, a,b) and Buvat (1953). However, Newman (1956) by direct observations of shoot apex reported the absence of an inactive region. Studies in the culture grown shoot apices by Ball (1960) and application of radio actively labelled precursors of DNA by Gifford (1962 b) and Clowes (1961 a) supported Newman's view.

Dermen's (1947, 1951) studies with improved

techniques on chimeras have yielded valuable information on cyto-histological details of shoot apices. It has been pointed out by many workers (Ball, 1941 ; Boke, 1941; Majumdar, 1942; Philipson, 1949 and Gifford, 1962 a,b) that the dome stains lighter in contrast to the peripheral or flanking zone. The lightly staining feature is found also in tunica. On the basis of cyto-histological pattern Foster (1939 a) has divided the shoot apex into four distinct zones: Zone 1 - Tunica layers, zone II - the corpus mother cells, zone III, the peripheral or flanking zone and zone IV - the pith rib meristem. There are reports of an additional zone between the corpus mother cells and the pith-rib meristem. This zone has been termed as 'Cambium - like' zone (Ball, 1941; Philipson, 1946; Popham and Chan, 1950; Fahn et.al 1963 and Trivedi, 1969). The significance of this zone is differently interpreted. Foster (1938) considered a similar zone in Ginkgo as a transitional stage between low and high mitotic activity, while Gifford (1954) correlated this zone with the size of the shoot apex or to the plastochronic stages. A similar opinion has been expressed by Fahn et.al (1963). Romberger (1963) has stressed the need for a thorough investigation of many more plants to understand the role of this additional zone in the development of the shoot apex.

Primary Vascular Differentiation.

The study of primary vascular differentiation in shoot apices has been a problem for anatomists for the last three decades. Esau (1942, 1943 a,b; 1954, 1965 b) has worked out the primary vascular differentiation of certain angiosperms. Kundu and Dutta (1944) studied the vascular differentiation in Hibiscus sabdarifa, Goodwin and Stepka (1945) in Phleum pratense and James (1950) of Hesperastergus. Wetmore (1947, 1964), and Esau (1965 b) have reviewed the important aspects of primary vascular differentiation. These studies have revealed that the differentiation of procambium takes place in two directions. In some plants it differentiates from the mature structure to developing organs i.e. acropetally, while in others it comes down from the developing organ to the mature structures i.e. 'basipetally'.

The leaf trace procambium is reported to differentiate acropetally. Priestley et.al (1935) have studied this in Alstroemaria, Smith (1941) in Costus, De Sloover (1958) in Anagalis, Coles and Ligestruam and Rohweder (1963) in certain Commelinaceae members. Other studies on this aspect are by Balfour (1957, 1958) in Macropiper, Sharman (1942) and Kumazawa (1961) in maize and Masayuki (1962) in Oryza. Esau (1954, 1965 b) and Gustin and De Sloover (1955) have reviewed the studies on this aspect.

Axillary Bud.

The origin and development of axillary bud have attracted the attention of various workers. Some of the important contributions on this are of Reeve (1943) on Garrya, Miller and Wetmore (1946) on Phlox, Majumdar and Dutta (1946) on Heracleum and Leonurus. Garrison 1949, 1955) and Shah (1960, 1968) have reviewed the various aspects of their development and vascular connection with the mother axis. The vascularization of axillary bud has been investigated by Garrison (1949), Secher (1955), De Sloover (1958) and others.

Reproductive Apex.

Many changes take place as the vegetative bud becomes reproductive. Most of the workers who have studied both vegetative and reproductive apices have observed a change in dimension as well as zonation of the apical dome. Earlier Newman (1936) had worked on certain aspects of floral organs on Acacia longifolia. Brook (1940) investigated the comparative histology of vegetative and floral apices in Amygdalus communis. Philipson (1946, 1947) studied the inflorescence development in Bellis perennis and Succisa pratensis. Boke (1948, 1949) has worked out the initiation and development of floral organs in Vinca. Gifford and Tepper (1962 b) and Anderson and Guard (1964) have studied the comparative structure of vegetative and reproductive apices.

The cyto-histological changes in the shoot apex during the transition from vegetative to reproductive phase must have a biochemical basis. There must be some point at which the biochemical or metabolic characteristics of these two types of apical meristems diverge. The histochemical investigations in shoot apices can reveal the biochemical basis of the transition to a great extent.

The histochemical changes that take place in the shoot apex during floral induction have been studied in several plants (Bernier, 1964; Nouare'de et.al (1964; Knox, 1966 and Corson and Gifford (1969).

Florence (1963) reported the variation in the distribution of starch in the shoot apices of physiologically dwarf peach seedlings. Sadik (1962 a , 1967) studied the histochemical variations in cauliflower apices after cold treatment.

Studies on the shoot apices in Centrospermales are remarkably few. Fuller (1949) studied the photoperiodic responses in the shoot apices of Chenopodium album and Amaranthus caudatus. Zabakia (1961) re-examined Fuller's investigations. Gifford et.al.1961,1962 and Nougarede et.al. (1965) made histochemical investigations in Chenopodium album and Amaranthus retroflexus respectively. Werker and Fahn (1966) studied the development of shoot apex and leaves of articulated Chenopodiaceae.

Seedling Anatomy.

Our knowledge of the seedling anatomy commenced with the intensive studies of plant morphologists who were inspired mainly by the recapitulation concept during the period covering the latter part of the last century.

The transition region represents a connection between an organ with an axial vascular system and one whose vascular system develops in relation to leaves. Study of this region should explain the relation between vascular system of the root and the traces of the cotyledons and epicotyl of the plant. The works of Dangeard (1889) and Van Tieghem (1871, 1891) were mainly descriptive and the emphasis was on the root-shoot transition of the vascular system. They have, however, added much to our knowledge of the orderly sequence of vascular development of the seedlings.

The root-stem transition phenomenon merits a deeper consideration when the subject is approached from the stand point of phylogeny. According to Chauveaud (1911) the root and stem are regarded as fundamentally continuous and differ only in that they represent different phases of vascular evolution. A few theories, such as those of Compton (1912 a,b) and Thomas (1914) were put forward and these were concerned primarily with the transition of the vascular system from root to shoot, especially of the epigeal seedlings.

Holden and Bexon (1918) have studied the structure of some polycotyl seedlings of Centranthus. Holden and Daniel (1921) reported on the anatomy of teratological seedlings of Impatiens roylei. Harris et.al.(1921) gave an account of the dimerous and trimerous seedlings of Phaseolus vulgaris. Holden (1923) has worked on the seedling of Acer pseudoplatanus. Lehmberg (1923) attempted to explain the xylary pattern in the transition zone of Helianthus annuus. Bexon (1925, 1926) worked on the seedling anatomy of Sinapis alba, Brassica oleracea and Althea rosea. Gehlen (1929) has worked on the seedling anatomy of Cicer arietinum Thiel (1931) has also worked on the anatomy of Helianthus annuus seedlings. Murray and Helen (1933) have given a physiological interpretation for the transition in seedlings of Ricinus communis. Malhotra (1935) has worked on the tricotyl seedlings of Boerhaavia repens. Hufford (1938) has worked out the anatomy of watermelon seedlings. Whiting (1938) studied the seedling anatomy of Cucurbita maxima. Havis (1939) and Esau (1940) described the anatomy of the hypocotyl and root of Daucus carota. Miller and Wetmore (1945) have given an account of the seedling anatomy of Phlox drummondii.

Chennaveeriah (1949) has reported tricotyly in Capsicum annuum. Banerjee (1961, 1962 and 1964) has studied the anatomy of teratological seedlings of some compositae members. Deshpande et.al.(1962 and 1968) have worked out the seedling anatomy of certain members

of Umbelliferae and Compositae. Trivedi (1967) studied normal and tetracot seedlings of Prosopis juliflora. Hayat and Canright (1968) have given comparative anatomical data for different members of Annonaceae. Pillai and Sukumaran (1968) have worked out the seedling anatomy of Cyamopsis tetragonoloba.

Seedling anatomy studies in Centrospermales are very few. Hill and De Frine (1912) worked out the seedling structure of certain members of Centrospermae. Bisalputhra (1961) described the seeding anatomy of certain members of Chenopodiaceae. Nair and Nair (1961) investigated the seedling structure of certain members of Nyctaginaceae.

Primary Vascular System.

In Amaranthaceae the number and arrangement of vascular bundles varies considerably. Wilson (1924) has studied the role of medullary bundles in primary vascular system in Chenopodiaceae and Amaranthaceae. Dastur (1925) described the details of the course of vascular bundles in Achyranthus aspera. Joshi (1931, 1934, 1937) has published an excellent account on the phylogenetic significance of vascular cylinder in Chenopodiaceae and Amaranthaceae. According to Joshi (1931) internal bundles in Achyranthus aspera are only apparently medullary. Inouye (1955) studied the vascular system of Celosia cristata and Achyranthus japonica. Shrivastava (1960, 1962) studied the anatomy

of Achyranthus aspera and Achyranthus coynci. Fahn and Sybil (1963) described the primary vascular system in the stem and leaves of Salsola and Sueda (Chenopodiaceae).

Nodal Anatomy.

The anatomy of the node has an important phylogenetic significance. Sinnott (1914) demonstrated that three types of nodes occured in dicotyledons. According to Sinnott the trilacunar node is the primitive type in the angiosperms and the unilacunar node has developed phylogenetically from it by the loss of two lateral gaps together with their respective traces. This view has been refuted by other workers (Gunkel and Wetmore, 1946 a,b; Marsden and Bailey, 1955; Marsden and Steeves, 1955; Bailey, 1956; and Fahn and Bailey, 1957). Swamy (1949) working with Degeneria, came to the conclusion that the complexity of the node might increase as successive leaves are formed in the seedlings. Saha (1952) reported uni-bi-amd tri-lacunar nodes in Citrus. Bailey (1956) also compared the nodes of seedlings and mature shoots and found that while the sequence from the unilacunar to the tri-or multi lacunar conditions was frequent, the reverse transition was not observed. Post (1958) found uni-, tri-. and multilacunar nodes in the genus Frasera, with reduction series upto the appendages of the flowering stem.

Bailey (1956) stated that the unilacunar condition prevails in most of the adult nodes of the Centrospermae. Nair and Nair (1961) also support this view. Bisalputhra (1962) demonstrated evolutionary development from a unilacunar node with two traces to three - or more traces in Chenopodiaceae.

Anomalous Secondary Growth.

Anomalous secondary growth is of common occurrence in members belonging to the families Amaranthaceae, Chenopodiaceae, Basellaceae and Nyctaginaceae of the order Centrospermales and has attracted the attention of botanists since the latter half of the 19th Century, (DeBary, 1884; Pfeiffer, 1926; Wilson, 1924; Artschwager, 1918; 1926; Maheshwari, 1930; Metcalfe and Chalk, 1950 and Esau, 1953 etc.). In the present decade also a few papers have appeared on this aspect (Balfour, 1965; Philipson and Ward, 1965). Balfour (1965) and Philipson et.al (1965, 1966) have shown that the anomalus cambia in stems of Amaranthaceae, Chenopodiaceae and Nyctaginaceae exhibit unidirectional activity, giving off products towards the interior of the stem only. Esau and Cheadle (1969) on the other hand, working on Bougainvillea a member of Nyctaginaceae, have recorded on bidirectional activity.

Considering these two contrasting views on the

activity of cambium it was thought advantageous to work out the details of abnormal secondary growth of Amaranthus leucocarpus to determine which view prevails in this plant.

Leaf Histogenesis and Vasculature.

Important contributions to foliar histogenesis were made by Schüepp (1918, 1926, 1929 and 1931) on Acer pseudoplantanus and Lathyrus. Later, Avery (1933) gave a comprehensive account of the leaf histogenesis in Nicotiana. Foster (1935) compared the histogenesis of cataphyll and foliage leaf of Carya buckleyi. Foster (1936) reviewed the earlier work and pointed out certain problems on differentiation of leaf in angiosperms. Since the publication of Foster's review many workers have studied the development of leaf. The dicotyledonous leaf has received more attention than that of monocotyledons. According to Sharman (1942, 1945) and Thielke (1951) leaf initiation starts with the periclinal divisions in the cells of the surface layer of the apex and the cells of the layer immediately below it. In order to clarify this problem periclinal cytochimeras produced by the application of colchicine, have been used (Satina and Blakeslee, 1941 and Derman, 1947, 1951). With the aid of such cytochimeras it has been possible to show from which layers of the apex various tissues of the leaf have developed. The growth of the leaf is controlled by genetic factors but is also influnced by

internal and external environmental conditions (Allsopp, 1955; Jones, 1956). Werker and Fahn (1966) studied the development of leaf in the articulated Chenopodiaceae. Tucker (1962) investigated the development of leaf in Michelia fuscata. Kaplan (1970) published a comparative account of foliar histogenesis and its bearing on the phyllode theory of Acorus calamus.

The development of vascular system in the leaf has, as yet, been studied only in a small number of plants. In Nicotiana tabacum (Avery, 1933), the procambial strands of the small veins, which arise in a basipetal direction, develop mainly during the intercalary growth of the lamina. In the leaves of Zea (Sharman, 1942) the procambial strands of median and the principal lateral veins develop acropetally while smaller lateral veins develop basipetally. According to Slade (1957, 1959) the blind vein endings occur due to rupture of the minor vascular net work. According to Pray (1963) the vein endings do not result from rupture, but there is a progressive differentiation of procambium from the ground meristem during the expansion of the lamina.

Floral Histogenesis and Embryology.

Joshi and Rao (1934) have published a detailed account of the vascular anatomy of the flower of Digera arvensis Forsk. As a result of this study they have

arrived at certain interesting conclusions regarding the morphology and the early history of the entire family Amaranthaceae. Bakshi (1952) has, however, pointed out that some of these conclusions at least do not appear to be warranted by facts. Besides, some of their observations also need confirmation. Bakshi and Chhajlani (1954) also published excellent account on Digera arvensis, Pupalia lappacea, Achyranthus aspera and Gomphrena globosa.

The embryology of quite a few members of this family have been investigated. Woodcok (1931) studied the seed development of Amaranthus caudatus. Naithani (1938), and Joshi and Rao (1934) investigated the embryology of Digera arvensis, which was later reinvestigated by Puri and Singh (1935). Joshi and Kajale (1937) worked out the embryo development of Digera arvensis, and Alternanthera sessilis. Kajale (1937, 1940) also made a comparative study of the embryology of Alternanthera sessilis (1935), Achyranthes aspera (1937), Celosia argentea, Allmania nodiflora, Amaranthus viridis Cyathula tomentosa, Pupalia lappacea and Aerua lanata (1940). Development of the embryo of Amaranthus caudatus and Amaranthus retroflexus is known through the work of Souèges (1937 c). Dambroise (1947) has given a detailed account of the endosperm development of many members of Centrospermales including Amaranthus retroflexus and Celosia cristata. Bakshi (1952) recorded embryological observations on Psilostachys sericea.

Sachar and Murgai (1958) recorded embryological observations in Aerua tomentosa. Padhye (1962) reported the solanad type of embryo development in Gomphrena - celosioides. Aruna(1968) studied the seed development in Celosia cristata.

In all these works Amaranthus leucocarpus has not figured for detailed embryological studies. Hence this aspect has also been studied.

MATERIALS AND METHODS

The seeds of Amaranthus leucocarpus S. Wats were obtained from the Plant Introduction Division of the Indian Agricultural Research Institute, New Delhi. The plants were raised in the Botanical Garden of the Birla Institute, Pilani, from which the material for the present study was collected.

For the seedling anatomy studies the seeds were sown in small plots. The seeds germinated on the first day only were allowed to grow further. The seedlings were fixed at regular intervals. Second day, 4th day, 6th day, 8th day, and 10th day old seedlings were used in the study of transition. This was supplemented by older seedlings up to 20 days, in which secondary growth was prominent. The seedlings were fixed in Navashin's fixative and Formalin-acetic-alcohol (FAA). The following staining combinations were tried:

i) Safranin - Anilin Blue

ii) Safranin - Light Green

The shoot apices were fixed in five stages from the cotyledonary stage onwards, to study the plastochronic variations and the antomical changes during the transition from vegetative to reproductive phase.

First stage - Just after the emergence of cotyledons.

Second stage - Two leaf condition.

Third stage - Four leaf condition

Fourth stage - Six leaf condition

Fifth stage - Eight leaf condition

Formalin - Acetic - Alcohol (F.A.A.), Formalin Proponic - Alcohol (F.P.A) and Navashin's were the fixatives used for the shoot apical studies. Three staining combinations were employed in this study.

i) Johanson's Safranin - Haematoxylin

ii) Johanson's Safranin - Roselic acid

iii) Safranin O - Light Green

Cytochemical Tests in Shoot Apices.

With the development of new techniques, recent years have witnessed a renewed interest in apical meristems. Histochemical methods have provided a tool for studying both the morphology and chemistry of plant cells at the same time.

To detect starch in fresh tissues, aqueous IKI (Gram's solution) was used, whereas for permanent staining the periodic acid - Schiff's reagent (Hotchkiss, 1948) was used. The brilliant red granules of starch stood out in marked contrast to the lightly stained cells.

Deoxyribonuclic acid (DNA) was stained by the Feulgen method. By dydrolysis with normal HCL, the purine-containing fraction of DNA is separated

from the sugar, unmasking the aldehyde group of the latter. The aldehyde reacts with fuchsin sulphurous acid to yield the typical magenta colour.

Basic nuclear proteins were stained with alkaline fast green (Alfert and Geshwind, 1953) at pH.8 or with 0.1% aqueous solution of bromophenol blue at pH 2.3 as described by Bloch and Hew (1960). Deamination of basic proteins was carried out after removal of DNA by picric acid hydrolysis, by immersing the slides for 15 minutes each in two freshly prepared solutions containing 5% sodium nitrite and 5% trichloroacetic acid.

Summary of cytochemical tests.

Chemical Constituents		Cytochemical test	Fixation	Reference
Starch	(a)	IKI		
	(b)	Periodic acid Schiff's	FPA Mercuric Chloride	Hotchkiss (1948)
DNA	(a)	Feulgen reaction	FAA FPA AA	
Basic protein	(a)	Alkaline Fast Green (pH.8)	FAA FPA	Alfert & Geshwind (1953)
	(b)	Bromophenol Blue (pH. 2.3)		Bloch & Hew (1960)

The seeds were germinated in petri dishes to obtain the root apices. Some seeds were also treated with picric acid to soften the seed coat to obtain the stages of embryo development. Ehrlich's Haematoxylin-Johanson's Safranin combination was adopted for both the root apical and embryological preparations. Wood microtome sections were taken to study the anomalous secondary growth in stems.

The soft materials were dehydrated and cleared through the ethyl alcohol - xylene series. Tert-Butyl alcohol - Liquid paraffin series and Ethyl alcohol - Chloroform series proved better for harder materials. Embedding was dome in paraffin and sections were cut 6 - 10 microns thick.

For the study of venation pattern, the leaves were cleared with 5% KOH and basic fuchsin and dehydrated in Ethyl alcohol series.

OBSERVATIONS

CONTENTS

ROOT APICAL ORGANIZATION

Structurally four histogens can be distinguished which are concerned with the building up of the root body of Amaranthus leucocarpus (Fig.1 and Photomicro.1). They are :-

1. Dermocalyptrogen
2. Columella initials
3. Periblem initials
4. Plerome initials

The root cap is quite prominent. It is about 920 U long and 180 U broad at the region of columella initials. The cap shows two distinct regions, the columella and the peripheral region (Fig.4).

Dermocalyptrogen:

This common initial zone is concerned with the formation of both the dermatogen and the peripheral region of the cap. The cells of this region show lightly stained cytoplasm and prominent nuclei. The exact extent of the initiating region is difficult to trace out. As the protoderm is traced from the root body toward the tip, it is seen to contribute cells to the peripheral region of the root cap. The cells of the protoderm exhibit 'Kappe' type of divisions. The first division of the initial is anticlinal. This is followed by a periclinal division of the * distal

-nent nuclei. The plane of division is transverse but rarely longitudinal division also occurs. The columellogen does not contribute to the peripheral zone. This is supported by the fact that the columella maintains long vertical files. Furthermore, the number of rows that occur across the diameter of the columella is more or less the same at different levels. In Amaranthus leucocarpus the columella does not proceed up to the tip of the root cap but ends blindly (Fig.4).

Periblem:

It is made up of 4-5 layers of cells across in Amaranthus leucocarpus. The cells on the flanks exhibit 'Körper' type of arrangement of Schuepp (1917). These divisions enable the periblem to widen out towards the flanks. The T divisions of the periblem are repeated a few times till the periblem becomes wide enough, after which the cells divide mostly anticlinally (Fig.3 , 4).

An analysis of the cell files towards the dermatogen shows that the adjacent rows are arranged in opposite directions. The cells towards the tip show inverted T - (⊥) pattern. The cell rows towards the inside are arranged in the opposite direction with the T - head directed procimally (T). In the innermost portion of the periblem, the initials exhibit a few T - divisions. After these, the inner most

layer, exhibits only anticlinal divisions and constitutes the endodermis (Fig.4).

Plerome:

About 6-10 rows of cells across constitute the plerome initials of a mature root apex (Fig.3,4 - Photomicro.1,3). Discrete plerome initials can be observed proximal to the periblem initials. In longitudinal sections they appear as a small group of pentagonal or hexagonal cells carranged at right angles. They have prominent nuclei also. These cells generally divide an anticlinal planes but the ' Körper ' divisions are frequent at the periphery. As a result the cells in the centre are broader than those at the periphery. In the region near the initials all the cells are equally cytoplasmic. The cells first to vacuolate within the young stele are those nearer the centre.

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SHOOT APICAL ORGANIZATION

The study of the shoot apical development and organization in Amaranthus leucocarpus was started from the cotyledonary stage (Ist stage). At this stage the apical dome shows distinct zonation (Fig.6 and Photo - micro. 4). The first zone is tunica (Z-1) which consists of one layer, but the number of tunica layers varies in later stages. In tunica the cell size decreases from the summit down the flanks. Beneath the summit of the tunica occurs a group of cells which are isodiametric with prominent nuclei constituting the central mother cells zone (Z-2). The central mother cells on an average are 13 U in diameter. They are vacuolated and the nucleoli in this region are larger with their diameter varying from 2.2 to 3.3 U.

The zone just beneath the central mother cells is the 'pith rib meristem' (Z-3) and on the flanks of pith rib meristem occurs the peripheral meristem (Z-4). The pith rib meristem contains larger cells than the cells of the peripheral meristem which envelop the rib meristem and are comparatively small in size and mitotically active. The zones 2,3 and 4 constitute the corpus of the apex. The diagramatic representation of mature shoot apex is shown in Fig.5.

Plastochronic changes:

The shape of shoot apex of Amaranthus leuco-

carpus changes periodically during plastochronic cycle. The shoot apex at the minimal phase of the plastochron shows well differentiated cyto-histological zonation (Fig.6 and Photomicro.5). All the same the central mother cell zone is reduced; so also is the zone of peripheral meristem. The pith rib meristem, therefore, appears to arise much closer to the top of the apical dome.

The apex at mid-plastochron is more convex (Fig.7 and Photomicro.6). The tunica cells on the flanks divide anticlinally and those at the summit are tangentially stretched. The central mother cells zone becomes more active than at the minimal phase. Gradually the apex attains more height. During mid-plastochron a 'cambium-like' zone arises, the cells of which are tabular. The development of this zone begins first on the flanks, then proceeds to the pith rib meristem, the cells of which are already vacuolated. Because of the formation of this zone the leaf primordium appears cut off from the apex. It is only after the formation of this zone that the shoot apex elevates to enter the maximal phase of the plastochron.

The shoot apex at the maximal phase of the plastochron shows prominent cyto-histological zonation (Fig.8 and Photomicro.7). It has a prominent dome. The flanks of the tunica layer are more active than the apical region with the cells being more deeply stained. These cells undergo repeated anticlinal divisions and

hence appear radially elongated. This greater incidence of anticlinal divisions on the flanks is due to the activity of the cells of the corpus flanks. The cells of the central mother cells zone have larger nuclei than those of the surrounding cells and also of the tunica. The periclinal divisions in the second tunica layer at this stage mark the first step in the initiation of a leaf primordium. After the periclinal divisions in the cells of the second tunica commence the rapidity of the anticlinal divisions in the cells of the first tunica increases and with the appearance of the leaf primordium, the shoot apex passes into the minimal phase of the plastochronic cycle.

The measurements of the height and width of the apical dome were taken from the level of youngest leaf primordium to the apical region and across the youngest primordia respectively. The height and width of the dome at minimal phase are 44 µ and 70µ, at the mid plastochron 66 µ and 72 µ and at the maximal phase 74 µ and 92 U respectively.

Thus during a plastochron the shoot apex of Amaranthus leucocarpus undergoes periodic changes in diameter from the minimal to the maximal phase.

Development of procambium:

The procambial initials are distinguished only after the parenchymatization of pith mother cells on the inner side and the cortical cells on the outer. The

The initiation of leaf primordium:

The leaf primordia are initiated on the flanks of the shoot apex. The first sign of the leaf initiation is the periclinal divisions in the cells of inner tunica layer of the shoot apex. These cells may undergo slight radial elongation before dividing. The periclinal divisions are further observed in the outer layers of corpus flanks. Usually these divisions occur only in one or two layers subjacent to the inner tunica, but seldom in the deeper layers (Fig.9). The inner tunica and the outer flanks of the corpus together form an actively dividing zone for the initiation of the leaf. Further divisions in this zone result in a small protuberance (Fig.10). Meanwhile, the outer tunica also divides anticlinally to maintain the surface growth of the protuberance. At this stage the primordium measures 88 U in height (Fig.12). Following the initial elevation, an apical cell derived from the first tunica layer undergoes periclinal division, the outer cell forming the apical initial and the inner the sub-apical initial (Photomicro.8). The apical initial divides only in anticlinal plane and gives rise to the protoderm of the leaf.

During the apical growth, the primordium gradually curves towards the shoot apex. This apparently

results from more active growth of the abaxial side than that of the adaxial side. The sub-apical initial plays a major role in the elongation of the primordium (Fig.11).

Intercalary elongation of the primordium:

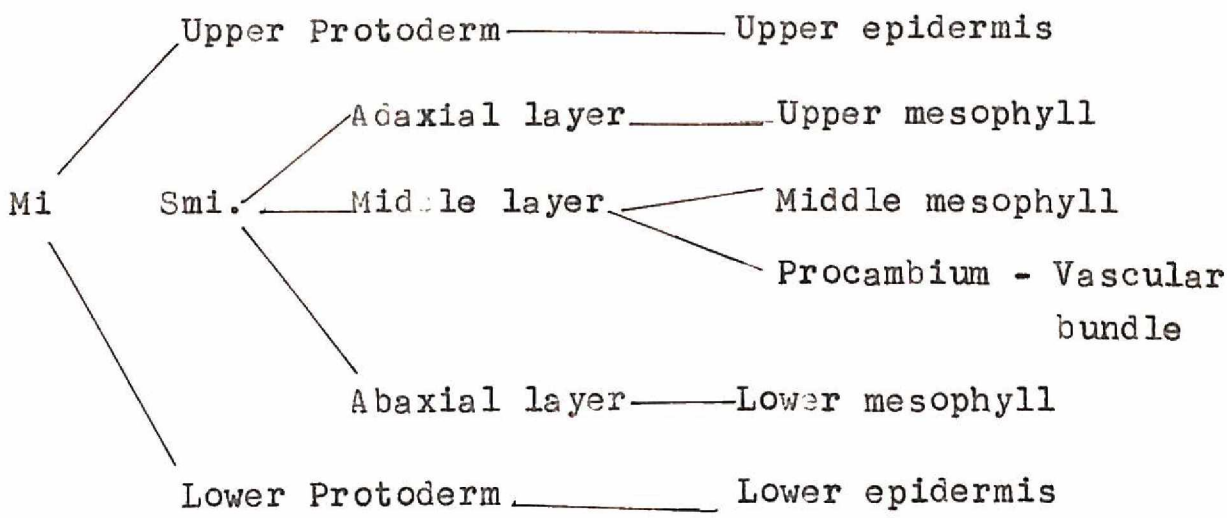
The apical growth alone is not responsible for the total elongation of the leaf. The sub-apical initials were never observed to divide extensively. In later stages the sub-apical cell shows a tendency towards vacuolation with cessation of the division. In the primordium of about 275 μ high (Fig.12), the apical activity has almost ceased. A central procambial strand, vacuolated abaxial cells and comparatively smaller densely stained adaxial cells are evident in a longitudinal section of this stage. Further elongation of the leaf is primarily a result of intercalary cellular division and elongation of cells.

The marginal growth of the primordium:

The initiation of the marginal growth can be recognized by the growth of marginal parts of the flattend primordium. The marginal initials divide only in anticlinal plane to the leaf margin and finally give rise only to the uniseriate upper and lower epidermis (Fig.13). The sub-marginal initial divides in periclinal and anticlinal planes repeatedly. The adaxial and the abaxial layers arise from the sub-marginal initials by their anticlinal divisions with

regard to the leaf margin. The middle layer arises by the periclinal division of the sub-marginal initial (Fig.14 Photomicro.9). Thus the sub-marginal initials give rise directly to three inner layers. The procambium and the middle mesophyll arise from the middle layer, the upper mesophyll and the lower mesophyll form the adaxial and abaxial layers respectively (Photomicro.9).

The marginal growth can be represented diagrammatically in the following fashion:



Youngest leaf primordium is seen without any visible trace of procambium in it. . The leaf trace procambium appears at the base of the second leaf primordium from the apex (Photomicro.10). This indicates that procambium makes its appearance during midphase of the plastochron. From the base, the procambium of leaf trace differentiates acropetally. These procambial strands when traced back join the procambium which develops into medullary strands. This indicates that medu-

lary strands are related to the midrib and that they develop acropetally towards the leaf.

The secondaries which are multiseriate in origin are always continuous with the procambium of the midrib. The procambium of the secondaries differentiates in the early bud stage and the procambium of the tertiaries joining the secondaries differentiates in later bud stage. The tertiaries are initiated continuously from the secondaries. The procambial strands of the tertiaries are uni-or biseriate (Photomicro.11). Differentiation of the xylem elements occurs in the midrib and secondaries in the bud stages, while it occurs in the tertiaries during the expanding stage of the leaf.

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DEVELOPMENT OF AXILLARY BUD

In Amaranthus leucocarpus the first sign of axillary bud is observed in the axil of the second or third leaf primordium. The layers of the shoot apex just adaxial to the leaf primordium first undergo periclinal divisions followed by anticlinal divisions. The periclinal divisions take place in two layers just beneath the tunica layers. The activity of these cells results in the formation of an arc of narrow, elongated 'cambium-like' cells near the axil of leaf. This zone is termed as 'Shell zone' (Photomicro.12). The 'Shell zone' encloses within its arc, a few cells of the flank meristem. These cells are deeply stained with prominent nuclei and form the promeristematic region of the axillary bud. This group of meristematic cells is covered by two layers of tunica which show anticlinal divisions. Further periclinal divisions ~~form a mound~~ form a mound of cells. The characteristic arc of 'shell zone' gradually disappears as the position of the bud is shifted. Since the tunica layers covering the mound do not undergo any change except divide anticlinally, the apex of the axillary bud also comes to possess two tunica layers. The 'shell zone' completely disappears as the dome grows further and the cyto-histological zonation becomes evident.

An axillary bud receives two traces, one from the procambium which supplies the leaf above and another

from the procambium which supplies the leaf subtending it. This aspect becomes clear only in longitudinal sections (Photomicro.12). These two strands show acropetal differentiation towards the apex of the axillary bud. In the transection the two procambial traces form a cylinder which splits up into 4-5 strands. (Photomicro.13).

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MITOTIC ACTIVITY AND HISTOCHEMISTRY OF THE SHOOT APEX DURING TRANSITION FROM THE VEGETATIVE TO THE REPRODUCTIVE PHASE:

In the first and second stages (cotyledonary and two leaf condition) the cyto-histological zonation of the shoot apices in Amaranthus leucocarpus is quite evident. Gradual changes in the shape as well as in cytohistological zonation are evident in fourth and fifth stages (six leaf and eight leaf condition). The shape of the apex changes from the smoothly rounded dome to a flat one with increased dimensions (Photomicro-14.). The mitotic activity also increases at this stage. The central mother cells zone becomes active and the cytohistological zones become indistinct.

Concomitant with the change in the topography of the shoot apices the pith cells also elongate. Only two histological zones are distinguishable in this stage, an outer zone consisting of 2-3 layers of relatively, small cells, whose protoplasts absorb stains intensively and an inner zone of large cells. The latter are highly vacuolated and have weekly staining protoplast. At this stage the loss of apical dominance results in the rapid development of axillary floral primordia (Photomicro.15).

The number of mitoses in the shoot apex increases in the course of ontogeny. The peripheral region of the shoot apex shows more mitoses than the axial region and the greatest concentration of mitotic

figures is located at the sites of leaf buttress formation. The nucleolar volume is observed as an indicator of metabolic activity in cells. The rapid decrease in the nucleolar volume in the second stage (2-3 leaf stage of shoot apex) is followed by a spurt of mitotic activity in the vegetative apex (graph.1).

The histochemical variations during the growth and differentiation has been well established. In Amaranthus leucocarpus variations of starch, DNA and basic proteins were studied in the vegetative and reproductive apices.

Starch:

In stage 1 (cotyledonary stage of apex) prominent starch grains are present only in two or three cells just beneath the tunica layers (Fig.15). The starch grains are usually found surrounding the nucleus. The presence of starch grains only in the central mother cells zone has certain significance in the meristematic activity of the apex. Starch is present only in cells which are meristematically inactive. In the early stages the starch grains are small in size but in later stages there is an increase in the size of starch grains and their staining capacity.

In 2-3 leaf stage (2nd stage) shoot apex shows addition of starch bound cells in the central mother cells region. The starch grains are conspicuous in the apical cell of the tunica also. The accumulation of

starch in these regions indicates the inactivity of the apical cell of tunica and central mother cells(Fig.16). Change in the general topography of shoot apex is evident in the 2nd stage. The smooth rounded apex increases in dimensions. In 3rd stage the central zone of inactive cells also becomes meristematic and as a result of this starch grains disappear entirely from these cells (Fig.17). In 4th and 5th stages the shoot apex elongates and looses its apical dominance; as a result of which axillary floral buds develop rapidly. Accumulation of starch is evident in the mature cells of the apex i.e. at the base of meristematic buds (Fig.18 and Photomicro 16.).

DNA.

In the first stage (cotyledonary apex), with feulgen reaction nuclei in the apical cells of the corpus were lightly stained by the nuclei of the flank cells were stained densely. This demarcation in staining is an additional evidence of the presence of an inactive region (meristem d' attente). Mitotic figures are also remarkably few in the lightly stained region. In the latter stages the apices stain uniformly with fuelgen. This clearly shows that the inactive region becomes meristematic at this stage. During this stage the nucleolar size reduces remarkably. The study of the shoot apex from Ist stage to 5th stage indicates that there is a gradual increase in the concentration of DNA during the transformation of vegetative apex to inflorescence apex (Photmicro. 17).

Basic proteins: Histones.

Basic nuclear proteins stain selectively with alkaline fast green at pH 8. In vegetative apex the histones are restricted to the nuclei (Photomicro.18). The nuclei of the cells of the reproductive apex show weak staining to basic protein but they contain densely stained cytoplasm (Photomicro.19). This difference in the staining capacity indicates the translocation of basic proteins from nucleus to cytoplasm during the floral initiation.

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Inflorescence is apparently a spike which is axillary as well as terminal (photomicro.20,21). Each bract Br-1) on the main axis of inflorescence subtends a short secondary spike, on which occur cymose clusters of flowers. The number of flowers in each cluster varies from nine (maximum number)(Fig.19a & 20); seven (Fig.19b, 20) five (Fig.19c) to three (Fig.19d). In the cluster with five flowers, the extreme lateral flowers appear abortive (Fig.21). This leads to a cluster composed of three flowers only. Each cluster and each flower is subtended by a bract, Br-2 and Br-3 respectively. The cluster is composed of either female or male flowers alone or both male and female flowers. In case a cluster shows both male and female flowers, the central flower is male and lateral flowers are female.

Inflorescence apex:

The material fixed on 19-9-1969 indicates an apex transitional between vegetative and reproductive. The apex shows no zonation except for two distinct tunica layers. The corpus is represented only by the central mother cells zone. Flanking zone and pith rib meristem show vacuolation which is more pronounced in the latter. This apex elongates considerably to form the inflorescence apex as has been observed in the material fixed on 21st and 22nd September, 1969. The

apex fixed on 21st September shows the initiation of only a few axillary reproductive apices and in the material fixed on 22nd September, 1969, there is formation of a considerable number of axillary reproductive apices. The inflorescence apex is tapering with a convex tip (Fig.21 and Photomicro.20). The inner of the two tunica layers shows periclinal division at the point of initiation of bracts. The first axillary shoot arises in the axil of second bract from the apex. The development of this axillary shoot takes place in the same menner as that of the axillary bud which forms vegetative branch. Each reproductive apex initiates the bract Br-2 (Fig.21, 22) in the axil of which occurs the cluster apex. The cluster apex inturn initiates bracts which subtend floral apices. Thus, there occur three categories of apices in addition to the main inflorescence apex: 1, the axillary apex which forms the reproductive shoot, 2, the cluster apex; and 3, the floral apex (Fig.21 and Photomicro.21). All these apices show similar organization as that of the main inflorescence apex, the difference being in size only. The inflorescence is thus a combination of both determinate and indeterminate types. The procambial differentiation is acropetal toward the main as well as the lateral apices (Photomicro.20).

Vasculature of inflorescence:

This could be distinctly followed up in a

series of transections. In the inflorescence axis there occurs a ring of 9-12 medullary bundles and many intermediate strands. From these, two strands from intermediate ring and three from medullary bundles take a cortical course. Inner to these, two strands from medullary bundles become large and differentiate as supply of axillary reproductive shoot which is similar to that of leaf and vegetative branch. The reproductive branches arise in three rows. The two traces to axillary reproductive shoot form a cylinder which breaks into nine to ten strands, nine being the most frequent number. These give rise to intermediate bundles in the form of branches. The strands in bract also may divide further so that each bract, Br-1 comes to possess nine or more strands.

The nine bundles in a reproductive shoot may form a cylinder which becomes three lobed or the axis may become trilobed, each lobe containing three bundles (Fig. 23 & 24). The middle lobe gives out a trace to a bract which subtends the central flower (Fig.23). These lobes further separate into three, each having three bundles. Of these the lateral groups give out a trace each to their bracts (bracteoles according to some authors) and the remaining two bundles join together and resolve to form three bundles (Fig.25,26). In many cases each lateral axis may give rise to more axes in the same way as they are themselves formed (Fig.27). The central part also may produce a cluster of three flowers (Fig.27a).

External morphology of female flower:

The female flower has a uniseriate perianth of five tepals. The aestivation is quincuncial. The anterior tepal is large and outer, and posterior is small and inner. Of the remaining 3 tepals, one is outer, second is inner and the third outer and inner being covered by anterior tepal on one side and covering the posterior tepal on the other. The tepals are pubescent (Fig.28). The ovule is basal and has a long funiculus.

Vascular supply of female flower:

After the bract trace has separated the three bundles join to form a vascular cylinder which becomes five lobed and five traces are given out for the perianth (Fig.29 and Photomicro.22). After the departure of perianth supply the stele again resolves into three bundles, each giving rise to a trace which forms carpellary dorsals (Fig.30). Further up the three strands left in the axis fuse to form a mass in the central region which supplies the ovule (Fig.31).

External morphology of male flower:

The number and arrangement of tepals in male flowers is similar to that of the female flowers, but the tepals of male flowers are larger than those of female flowers. The stamens, five in number, are antitepalous. The anthers are oblong and the attachment

of filaments is dorsal (Fig.32).

Vascular supply to male flower:

It differs from that of the female flower in certain features. The perianth supply is given out in the same way but the stele does not get resolved into three strands; instead it splits into five strands and all proceed to the five antitepalous stamens (Fig.33, 34).

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Microsporogenesis:

The young anther lobe shows a hypodermal archesporium, 6-7 cells across in transverse section and about 9 cells in longitudinal section (Fig.35,36). The archesporial cells enlarge and become richly protoplasmic. They divide periclinally to form outer parietal layer and inner sporogenous layer. The periclinal division does not take place simultaneously in all the cells of the archesporium (Fig.36). The parietal layer divides again giving rise to endothecium and an inner layer which divides again to produce a single middle layer and the tapetum. The middle layer degenerates as early as microspore mother cell stage. Its disintegrated remnants are seen above the tapetum (Fig.37 and Photomicro.23). The separation of tapetal cells from one another commences at microspore tetrad stage (Photomicro.24) and continues till microspores separate from one another (Fig.38 & 39). At a stage when microspore nuclei are ready for the division to form generative nuclei, just beneath the tapetal cells appear a granular matter which becomes denser by the time male cells are formed. As the granular material becomes denser the contents of tapetal cells become less dense. The granular material stains red with safranin. By this time even the endothecium degenerates (Fig.39 , 40). In certain preparations endothecium is observed to remain

intact but the characteristic fibrillar thickenings are not formed. The epidermal cells of microsporangium become large, slightly radially elongated and cutinised (Fig.40). The microspore tetrads are decussate and tetrahedral (Fig.38 and Photomicro.24). Reduction divisions are simultaneous and cytokinesis takes place by furrowing.

Male gametophyte:

The uninucleate pollen grain is full of cytoplasm. No vacuole is formed and hence the microspore nucleus divides in the central region of the microspore to produce a large vegetative cell and small generative cell (Fig.41,42). In between the vegetative and generative cells a small vacuole is formed which increa--ses in size and pushes the generative cell to the periphery (Fig.42,43). The lenticular generative cell divides to give rise to two male cells which are pointed at their distal ends and flat at their proximal sides (Fig.44).

The ovule:

There is a single, bitegmic; crassinucellate ovule attached to the base of the ovary. In certain preparations ovules have been observed to be attached laterally. Initially the ovule is orthotropus with visible integumentary primordia but it curves to attain the anatropous condition. At this stage the inner integument surrounds the nucellus and forms the micropyle

(Fig.45). The inner integument is composed of two cell layers and the tip is slightly club shaped. The outer integument develops slowly and does not reach the level of inner integument. It is also composed of two cell layers with slightly tapering ends (Fig.45). During the embryo sac stage there is more growth on the side opposite to the funiculus resulting in more curvature of the body of the ovule as well as embryo sac (Fig.46). As a result of the pressure due to more growth on opposite side the body of the ovule appears pressed against the funiculus. This is evidenced by the compression of the cells at the chalazal region. Thus the ovule becomes amphitropous (Fig.47 and Photomicro.25). Both the integuments as well as the inner integument and nucellus are separated by distinct spaces running throughout the length of the ovule (Fig.48 and Photomicro.25).

Megasporogenesis:

A hypodermal archesporial cell differentiates in the young nucellus when the ovule is at a stage between orthotropous and anatropous (Fig.49). The archesporial cell divides to form an outer parietal cell and an inner megaspore mother cell. The parietal cell divides anticlinally and periclinally to give rise to a massive parietal tissue, the cells of which are arranged in radiating rows (Fig.48). The megaspore mother cell enlarges considerably and divides resulting in two diad cells which divide once again to form a

linear row of four megaspores (Fig.45). The chalazal megaspore enlarges and gives rise to an embryo sac while the others degenerate.

Female gametophyte:

The functional megaspore becomes vacuolated and its nucleus comes to lie in the centre. It soon divides to give rise to two nucleate embryo sac (Fig.50,51). These nuclei are pushed to the poles by the enlargement of the central vacuole and each of them divides to give rise to four nucleate embryo sac (Fig.51,52). Further divisions of the four nuclei give rise to eight nucleate embryo sac. The synergids become slightly hooked and the two polar nuclei fuse in the middle of the embryo sac(Fig.46,53). The synergids disappear by the time the secondary nucleus comes to lie beneath the egg. It is only after the disappearance of synergids that the flask shaped nature of the egg is revealed. At this stage the antipodals separate from one another and assume triangular shape (Fig.48). The antipodals have been observed to persist till the four-nucleate stage of the endosperm.

By fixing material for embryology at periodic intervals it was possible to find out approximately how many days are involved between the appearance of anther archesporium to pollination. The material fixed on 22nd September, 1969 exhibited the archesporium, that fixed on 23rd September, 1969 showed tetrads and that on 25th September, 1969 showed three-celled pollen. In

the material fixed on 25th September, 1969, some pollen grains were observed on the stigma of the adjacent female flower. Thus, it takes approximately four days from the archesporial stage to the formation of male gametophyte and pollination. The pollen grains are shed at three celled stage.

Embryo development and histogenesis:

In Amaranthus leucocarpus the earliest stage observed during the embryogeny was globular stage.

Early globular stage:

The suspensor is short and the hypophysis is composed of two juxtaposed cells. The terminal part of the developing embryo has a surface layer, the cells of which exhibit mainly anticlinal divisions. This layer, therefore, can be called the protoderm. No tissue differentiation is observed in the central mass of cells. The cells divide in all planes and have deeply stained nuclei and cytoplasm than those of the protoderm layer. This central mass of cells is responsible for the increase in the bulk of the embryo. The width of the embryo at this stage is 35 U and the height including that of the suspensor is 58 U (Fig.54).

Late globular embryo:

The cells of the protoderm are more or less uniform in size and are stained more deeply than the

cells at the centre of the embryo. Anticlinal divisions are seen throughout this layer except at the suspensor end. The embryonic shoot apex is not clearly distinguishable at this stage. At the proximal side, the cells within the protoderm differentiate into an outer embryonic cortex of three to four layers and a central embryonic stele. The central zone contains elongated highly stained cells which are the initials of procambial cells. In an embryo of this stage, the height from suspensor to the embryonic shoot tip is 115 μ and width is 87 μ (measured at the broadest region).

Unlike the embryonic shoot apex, the root apical region becomes more clearly delineated at this stage. Periblem and plerome initials are clearly distinguishable at this stage. These initials are arranged in two superimposed tiers and are hexagonal in shape. The cells towards the flanks of these tiers exhibit Körper type of division (Fig.55). Thus the radicle is the first to be clearly distinguished in the embryo.

Heart shaped embryo:

The protoderm becomes elaborate by further anticlinal divisions. Kappe type of division is observed on the flanks of the suspensor. The protoderm cells are stained more clearly than those of the inner zones. The cells at the distal half of the embryo do not appear to be uniformly active. The shoot apex is represented by a small dome in between the cotyledonary shoulders.

These cells are more densely stained than the central cells. The tunica of the shoot apex is prominent at this stage. The cells on either side of this embryonic apex become more active, dividing in all planes and leading to two projections which are the primordia of the cotyledons. In these projections a subapical initial is conspicuous. An embryonic cortex of four cells across is observed at this stage. The embryonic pith is composed of large vacuolated cells, surrounded by procambial initials. The embryo now attains a size of 105 μ in width (in the region just below cotyledonary primordium) and 120 μ in height from the suspensor to the end of the cotyledon. Root organization is more clearly visible at this stage (Fig.56, Photomicro.26).

Torpedo shaped embryo:

The protoderm is single layered. The cotyledons have grown more in size by the activity of the sub-apical initials. The cells of the protoderm keep pace with the increase in size of the embryo by anticlinal divisions. The height of the embryo at this stage including that of cotyledons is 160 μ and width (just below the cotyledons) is 135 μ (Fig.57).

The shoot apex is represented by a dome in the inner space between the two cotyledons. The tunica layer is distinct but the corpus meristem is not clearly made out. The embryonic cortex is composed of about five rows of cells across. This zone is followed by a narrow

zone composed of long, elongated cells, constituting the procambium.

The radicular apex becomes more extensive at this stage. Kappe type of divisions are seen at the suspensor end. These divisions lead to two to three layers of cells which constitute the periphery of the root cap. Körper type of divisions in periblem and plerome initials result in the formation of periblem and plerome of the root.

Mature embryo:

The cotyledons are well developed at this stage. The shoot apex is dome shaped (Fig.58 and Photomicro.27). The cells of the dome are comparatively smaller than the cells below. The outer most layer of the shoot apex is differentiated into a single layered tunica. The cells of this layer divide only in anticlinal plane. The inner cells divide in all planes and constitute the corpus.

At the suspensor end the embryonic root apex attains clear zonation. The plerome dome is more discrete. The periblem is about four to five layers in thickness. The dermocalyptrogen is also clearly seen. The structure of the embryonic root apex, therefore is similar to that of mature root apex. (Photomicro.28).

The height of the embryo from the distal end of the root cap to the dome shaped embryonic shoot apex is 315 μ. The height including the cotyledons is

about 507 μ. The width of the embryo measured at the level of origin of the cotyledons is 165 μ.

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SEEDLING ANATOMY

4th day seedling:

Root shows typical diarch condition with two patches of procambial cells on either side of the xylem elements. The xylem forms a solid core (Fig.59). With the widening of the axis xylem core elongates and each of the procambial patches divides into two (Fig.60). Concomitantly the pith develops and due to the rapid intrusion of the pith cells the centripetal xylem separates into two portions. Each portion later forms two strands associated with the procambium on its side. As a result of these changes four collateral bundles A are formed at a distance 5 mm from the root apex (Fig.61).

In the strands A the evidence of phloem differentiation appears at this stage. The sieve elements differentiating at the outer layers of the procambial strand are conspicuous due to their deep staining capacity. A bundles are continuous through the whole length of the hypocotyl and then diverge into cotyledons as medians. Before they go as medians, they give rise to central strands in the following manner. Each procambial strand gives out a branch B on the intercotyledonary plane with the result the axis comes to possess 8 strands (4A and 4B) (Fig.62). The B strands of either side fuse to form B '1 (Fig.63). Each of the

B'1 bundles at 8 mm level resolves into 3 strands B'1 (Fig.64). As a result of this reorganization the total number of the strands becomes ten (4A + 6 B'1). At 11 mm level the A bundles are in the process of fusing in pairs.

Due to the considerable increase in vascular tissue and the cell enlargement the diameter of the stele also increases. In the paired A bundles the tracheary elements show thick secondary walls. At this stage each of the xylem pole is flanked by two phloem patches. The centripetal xylem shows signs of obliteration (Fig.65). It is difficult to distinguish the centripetal from lateral xylem on the basis of size alone. Yet the relative location of these elements can be used as a criterion to differentiate the tracheary elements. The centripetal xylem now disappears and two collateral bundles are formed, each consisting of centrifugal xylem and centripetal phloem.

Just at the base of the cotyledonary node bundles B'1 give out branches B'' 1 which go to the cotyledons as lateral strands (Fig.65). The B'1 which occurs on the intercotyledonary plane also divide once again and thus 8 central strands are formed in the 4th day seedling. The differentiation of vascular elements in these strands takes place during this stage. The inner procambial cells differentiate into centrifugal xylem and the outer into phloem. These 8 strands (B'1)

extend to the epicotyl.

In subsequent discription the strands extending into the epicotyl are designated as central strands.

8th day seedling:

The number of central bundles varies from 8-12. Three bundles go to each leaf, two as laterals and one as median (Fig.66). In this seedling buds appear in the axil of the cotyledon for the first time.

12th day seedling:

12-16 central bundles are present. In addition four procambial strands also appear outside these bundles. At this level the central bundles (12-16) become medullary due to the appearance of procambial strands. Axillary buds are also present in the axis of young leaves (Fig.67).

15th and 20th day seedlings:

In these seedlings the pattern of central bundle formation differ from the earlier seedlings. Fusion and reorganization of B and B'1 strands as in the case of 4th and 8th and 12th day seedlings is not observed in 15th and 20th day seedlings. The number of peripheral bundles varies from 10-15 (P). The formation of the peripheral bundles is as follows:

The outer ring of procambium arises in vacuolated cortical cells by tangential division. Which initiates

the normal cylinder of peripheral bundles in a ring. At the point where the future vascular bundle is situated, the procambium undergoes more tangential divisions to form a group of cells. The outer cells of this form protophloem and the lower most cells further undergo tangential divisions and give rise to protoxylem (Photomicro.29). The cells in between the protoxylem and protophloem give a seriated appearance and these cells could be mistaken to be cambial initials, but proceeding further the cells subjacent to protophloem give rise to fascicular cambium. Bundles of peripheral cylinder do not differentiate at the same level but at subsequent levels.

Diarch root gives rise to two endarch bundles (A) (Fig.68 Photomicro.30). They divides to form four bundles (A) (Fig.69 Photomicro.31). In addition, peripheral bundles are also present. Each of the A' bundles gives rise to 3 strands out of which two functions as the medullary strands (B 1 and B 2), so that 8 medullary bundles are formed (Fig.70 Photomicro.32). The remaining strands (C) fuse with adjacent peripheral bundles to form the laterals of the cotyledons (C + P), (Fig.71). Even after giving rise to branches bundles A maintain their identity. These bundles fuse in pairs and form A+A further gives out a branch D towards the centre just below the cotyledonary node. This forms the supply to the axillary bud (Photomicro.33). The medullary bundles which are already formed divide further to form to 12-16 strands (Fig.73,74).

The medullary bundles continue into the shoot in addition to the peripheral strands formed from procambium. Cotyledonary node in a seedling of two days and eight days is unilacunar with four traces which join to form two and then again split and branch further. In a seedling of 15 and 20 days each cotyledon receives two lar e pairs of strands (medians), and two laterals. This vascular supply of cotyledons is very much similar to that of the leaf supply. Thus cotyledonary node is unilacunar multistranded.

Formation of intermediate bundles and nodal structure:

The supply for a particular leaf differentiates atleast at two or more internodes below the node of its insertion. Thus the leaf traces traverse through more than two internodes before they depart for the leaf. At about the 8th plastochron, the central strands divide to give rise to additional strands external to them (Fig.75). These strands form intermediate bundles. From 8th plastochron upwards, each leaf receives two more strands in addition to the bundles given out for earlier leaves by the central strands. Thus each leaf after 8th plastochron receives two traces, which branch into three and then five, from the central strands as already mentioned and two from outer branches of procambium, making the number seven (Fig.75). The formation of peripheral bundles changes the nodal aspect also in the sense that these bundles give out two additional lateral

traces to leaves. Thus at subsequent nodes the leaves receive as many as 9-11 strands of which two upper ones are from the intermediate bundles, inner 5-7 (after branching, initially they are three) from central strands and other two from the bundles of the peripheral ring (Fig.76).

The axillary bud during early stages received only two strands but at this stage each axillary bud receives about eight strands (Photomicro.34). In axillary bud also the intermediate bundles are formed in the same way as that of the main.

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LEAF HISTOLOGY AND VENATION PATTERN

Stomata occur on both abaxial and adaxial sur-faces of the dorsiventral leaf, but usually more on the abaxial surface. The upper epidermis is followed by a single layer of compact palisade cells (Photo-micro.35). Lower epidermis is followed by spongy parenchyma. Vascular bundles of both large and small veins are surrounded by sheaths of parenchymatous cells containing chloroplast (Photomicro.36). Sphaero-raphides commonly occur in the ground parenchyma.

Development of trichomes:

The epidermal cell which initiates a trichome becomes papillose and possesses dense protoplasmic con-tents. The tip of the cell is broad and lower portion is narrow (Photomicro.37). The narrow part remains embedded in the epidermis and protoplasmic contents move to the tip leaving the narrow portion vacuolated. The nucleus undergoes a division followed by septation resulting in two cells. In this two celled condition the upper cell has again a rounded tip. A vacuole is formed in the lower part of the upper cell and as a result of this the nucleus moves to the upper part. Similar is the position of nucleus in the lower cell where it lies just beneath the newly formed wall between upper and lower cells. It is always the upper cell that divides. This sequence of division continues until a uniseriate trichome of 6 to 8 cells is formed (Photomicro-38.).

The ultimate cell of the trichome also has a rounded tip but the position of the vacuole is contrary to its position during earlier stages. Thus once a terminal cell with vacuole above and nucleus beneath is formed it should be regarded as the ultimate cell of the trichome.

There is an interesting sequence in nuclear degeneration also. By the time the third cell in a trichome is formed the nucleus in the lower most cell starts degenerating. At four celled stage the nucleus in the second cell degenerates and that in the first cell almost disappears at the fifth celled stage and nucleus in the third cell shows degeneration. This sequence is maintained and the ultimate cell is the last to loose the contents.

The anatomy of petiole:

The transverse section through the distal end of the petiole exhibits an arc of separate bundles. The trichomes are present on the petiole also. The abaxial ground tissue has loosely arranged parenchymatous cells which become compact towards the margins.

Gradual variation in the number of bundles is observed while tracing from the axis towards the leaf blade. At lower region of the petiole seven endarch bundles are arranged in an arch (Photomicro.39). In the middle region of petiole the number of bundles increases to twelve as a result of the division of central

bundles (Photomicro.40). Towards the upper petiolar region the adjacent bundles fuse in pairs to form five bundles (Photomicro.41), of which the central three bundles function as the medians. The marginals on either side give out brahches towards the centre. These two strands fuse to form an additional central strand (Photomicro.42). The branches of this central strands proceed to the margin of the leaf blade.

Venation pattern:

Leaf margin is entire. Epidermal cells in the surface view are sinuous. The mid rib terminates with a pointed tip and secondary veins branch out from the primary veins. The secondary veins do not terminate at the margin, but curve acroscopically to form a series of loops of variable distinctness, with adjacent secondaries or their branches. This type of venation was termed 'Camptodromous' type by Ettinghausen (1861). The leaf used here for illustration shows five secondaries on the left and seven secondaries on the right (Photo - micro.43). The large vein on left side which is counterpart of the third secondary on right (from the base) is regarded as an intermediate vein (Foster 1950). It parallels the course of adjacent secondaries but is completely enclosed within the panel delimited by the secondaries. Variation in the number of secondaries is recorded and that is due to variable strength in one or both of the intermediate veins. Secondary veins branch off to give rise to the tertiary veins. The tertiary

veins may roughly be divided into two groups, namely those connecting adjacent secondaries more or less distinctly and those producing series of rather prominent loops along the margins. Tertiary veins joining adjacent secondaries traverse the inter-secondary panel directly or follow an oblique course. Branches of the tertiaries are known as quarternaries. Prominent bundle sheath is present around the vein. The major venation of leaf is formed by medians, secondaries and tertiaries. The quarternaries and their branches form a reticulum of regular meshwork constituting the minor venation. The reticuli show free vein endings in the ultimate vein areoles. Smaller areoles lack the vein endings. Vein endings are broad and sometimes forked (Photomicro.44).

Average number of vein islet in 10 x fields = 12. Palisade ratio = 5.

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ANOMALOUS SECONDARY GROWTH

Secondary growth in stem:

It has already been pointed out in account on seedling anatomy that a young stem of ten days or so does not show any secondary growth.

In twenty days old seedling the central bundles (medullary) are scattered in the parenchymatous ground tissue. The procambium has become active at certain loci. As a result of this localised activity of the procambium the peripheral bundles are formed (Photo-micro.45). Strips of cambium develop outside the phloem patches of the peripheral bundles. The cambial cells of these anomalous strips can be identified easily due to their densely staining nature. The cambial strips extend to form a ring. This cambial ring is bidirectional in its activity, since it gives rise to xylem inside and phloem outside. The first inner derivatives formed by the activity of this cambium are a few xylem elements which can be recognised due to the deposition of lignin in them. This cambium appears to be more active on its inner side than on its outer. As a result of this cambial ring formation, the peripheral bundles are displaced inwardly (Photomicro.45), and the phloem patches associated with these peripheral bundles are crushed.

The 'phloem islands' are of usual occurence in

the secondary xylem of mature and thick stems of Amaranthus leucocarpus (Photomicro.46). This feature also needs an explanation. As the cambial rings develop in close succession the phloem platches formed by lower cambia become embedded in the secondary xylem formed by next upper ring of cambium. This embedded patch can be distinguished as the inter - xylary phloem or phloem islands.

Secondary growth in roots:

The initial secondary growth in the roots of Amaranthus leucocarpus is normal. A normal cambium develops outside the diarch primary xylem plate. It cuts off secondary xylem centripetally and secondary phloem centrifugally. The diarch primary xylem plate thus become embedded in the first increment of secondary xylem. Two patches of parenchyma tissues are observed opposite the protoxylem poles (Photomicro.47). Much of the phloem associated with the normal secondary xylem increment is crushed. The parenchyma cells which are associated to the crushed phloem are larger than the rest.

The second layer of cambium develops in the cortex. This cambium at places forms secondary phloem externally, but in between such patches the cambium forms parenchymatous tissues on both sides. As a result of this cambium, wedge shaped vascular bundles are formed. The bundles are separated by broad layers of parenchyma

(Photomicro.48). In addition to this 2-3 rings of cambia are developing in the cortex. These cambial rings are also bidirectional in their activity, forming secondary xylem and conjuctive tissue on their inner side and secondary phloem and parenchymatous tissue towards the cortex. Interxylary phloem is observed in Amaranthus leucocarpus roots also. Its mode of development is similar to that in stem.

DISCUSSION

Root Apical Organization:

The structural configuration of *Amaranthus leucocarpus* with a common initiating zone for dermatogen and Calyptrogen and discrete periblem, plerome and columella initials, falls under type-3 of Janczewski (1974) and Hayward (1938), type-1 of Haberlandt (1914) and type-4 of Popham (1952). This type has not been mentioned by Treub (1876) and Flahault (1878). According to Popham (1952) this is the most common type of structural organization in roots of dicotyledons and has been reported from *Isoetes* among the Pteridophytes, *Hibiscus* sp. among the more primitive dicotyledons and *Helianthus annuus* among the highly evolved.

The common initial layer for the epidermis and root cap has been designated as 'Dermo-Calyptrogen' by Eriksson (1878). However, Hanstein (1868) interprets the relation between the root cap and dermatogen in a different way. According to him the root cap is a proliferation of the dermatogen. Haberlandt (1914) feels that this view of Hanstein agrees more with the probable phylogeny of root cap than Eriksson's dermocalyptrogen.

In *Amaranthus leucocarpus* two distinct regions can be distinguished in the root cap on the basis of

the origin and arrangement of cells. The central region is composed of superimposed vertical files of cells, the columella. This region is surrounded on all its sides by oblique rows of cells which widen from the flanks towards the columella i.e. the peripheral region. These two regions have different initials, where as the peripheral region has common origin with the dermatogen. The origin of columella has not been mentioned by many of the earlier authors. Pillai et.al (1961 b) have pointed out distinct initials for columella which they have designated as 'Columellogen'.

Clowes (1956, 1958 a,b and 1961) and Jensen and Kavaljan (1958) have shown that the cells of the central part of the promeristem of the root apex have very low mitotic activity. This part is termed the 'quiescent centre'. Pillai and Pillai (1961 a,b,c) have also reported such a quiescent centre. The quiescent centre could not be distinguished in Amaranthus leucocarpus. On the other hand, the cells at the region corresponding to the quiescent centre are quite active. Clowes (1956, 1958 a) and Pillai and Pillai et.al (1961 a,b,c) have reported that the quiescent centre is not found in thin and immature roots. The material for the present investigation was collected from the elongating radicle of the germinating seeds. Probably the quiescent centre has not yet developed in these roots and all the cells are found to be active,

though in some roots the cells at the tip show vacuolation, indicating that they may go into quiescence in time. Wimber et.al (1960) used H^3 thymidine as a nuclear label to study the percentage of divisions in the root apex of Tradescantia paludosa. The studies on the small roots of Euphorbia (Raju, Steeves and Naylor 1964) also supports the above view. They came to the conclusion that if it is present it will be of only a few cells in size.

The Körper - Kappe theory (Schüepp, 1917) is found to be of great help here in interpreting the root apical organization. Clowes has explained the utility as well as limitations of this theory. In interpreting the root apex of Fagus sylvatica Clowes (1950, 1961a) has used the Korper - Kappe concept in combination with histogen concept.

Shoot apex.

The early research works on shoot apices were greatly influenced by the 'apical cell' and histogen theories (Nageli, 1845, Hanstein 1868). More recent researches have brought out the inadequacy of these theories in explaining shoot apical structures. The various theories of shoot apex organization have been adequately discussed by Schmidt (1924), Schuepp (1926) Foster (1939 b, 1941), Wardlaw (1945) Philipson (1949), Esau (1953) , Gifford (1954). The 'zonation theory' of Foster (1939) is based on cytohistological demarcation

between tunica and corpus in the shoot apex. Popham (1951) classified the shoot apical organization of seed plants into seven types describing two types as organization among angiosperms. The one with four zones is the most common and is referred as 'normal angiosperm type'. Another described for a few angiosperms as 'Opuntia type' shows five zones.

Philipson (1946) attributed specific importance to the 'cambium-like transitional zone' in the elongation of the shoot apex. Fahn (1963) also supports Philipson's view but considers it as a temporary phase. The development of this zone in Dwarf cavendish banana always depend on plastochronic changes. In Amaranthus leucocarpus the 'Cambium' like transitional zone becomes apparent during the midplastochronic phase and is short lived.

On the basis of apical size, Schmidt (1924) divided the plastochron into two phases viz. 'maximal phase' a stage of maximal apical area with the beginning of leaf initiation; and 'minimal phase' - a stage of reduced apical area after the appearance of the leaf primordium. Abbe, Phinney and Baer (1951) divided shoot apex of maize into three plastochronic stages viz. early stage, mid stage and late stage. Paolillo and Gifford (1961) divided Ephedra apex into five stages viz. (1) minimal (2) early postminimal (3) late postminimal (4) premaximal (5) maximal. Cohen (1965) described 5 phases of plastochron in the inflo-

rescence apex of Areceuthobium viz. phase of maximal area stage, minimal area stage, early post minimal area stage, late post minimal area stage and pre-maximal area stage. Trivedi (1968) reported three phases of plastochron in Capparis decidua. In Amaranthus leucocarpus also three phases of plastochron can be recognized viz. maximal, mid-plastochron and minimal.

Flemon and Topping (1963) investigated the accumulation and deposition of starch in the shoot apices with the onset of dormancy. In the present study the accumulation of starch is observed in the central mother cells zone during the early phase of shoot apical development. The accumulation of starch indicates inactivity of this region. The starch grains disappear from the central mother cells when they become meristematically active. The same phenomenon has been reported in Chenopodium album (Gifford, 1962).

A positive correlation between nucleolar size and number with metabolic activity has been observed in cells of Citrus tissue cultures by Kordan and Morgenstrum (1962). Buvat (1952) and Lance (1957) have used relative nucleolar dimensions as a measure of metabolic activity, but Gifford and Tepper (1962) have indicated that total nucleolar volume is more significant in assessing the synthetic activity of cells. The present observations are in full agreement with Buvat (1952) who reported that reduced nucleolar volumes indicated cells in the process of different action.

Sadik and Ozbun (1967) reported denser and more granular feulgen staining in vegetative shoot apex than the reproductive apex in cauliflower. In Amaranthus leucocarpus feulgen staining is prominent in reproductive phase also. The histone distribution followed closely the DNA distribution as determined by Feulgen reaction. Gifford and Tepper (1962) also reported the same pattern of histone/DNA distribution in Chenopodium album. The experiments of Huang and Bonner (1964) have indicated that basic proteins (histones) may play more important role in growth and differentiation than most other proteins by providing the cell with a mechanism of genetic expression and consequent morphological differentiation.

Translocation of basic protein from nucleus to cytoplasm is observed during the floral initiation. Usually the basic proteins are considered to occur as nucleo-histone, but there are reports of their occurence in the cytoplasm of animal cells. Taleporos (1959) identified basic protein in the cytoplasm of the sea urchin egg. Gifford (1963) also reported the presence of basic protein in the cytoplasm of Xanthium shoot apex 3 days after the inductive night.

In Amaranthus leucocarpus, the central mother cells are inactive during the vegetative phase as in the case of Chenopodium album (Gifford 1962) and become active during the transitional phase. As a result of this meristematic activity in the central mother cell

region the cyto-histological zonation of the shoot apex becomes indistinct.

The disappearance of cytohistological zonation and the disappearance of starch from the central mother cells appear to be the cardinal events in the transition from vegetative to reproductive phase. General increase in DNA and cytoplasmic histones in all regions of the shoot apex during transition to flowering would indicate that the entire apex is involved in the floral production.

Axillary bud.

There are two opinions about the origin of the axillary bud. Schmidt (1924) and some others believe that axillary bud arises from a detached meristem whereas Priestley and Swingle (1924), Majumdar (1942), Majumdar and Dutta (1946) are of the opinion that the axillary bud arises by the meristematic activity of the parenchymatous cells in shoot at the base of the leaf. Their former view was supported by Garrison (1949) in Syringa, Gifford (1951) in Drimys and Trivedi (1969) in Capparis. Esau (1965 a), reviewing the work on this aspect, feels the possibility of bud being initiated by both methods because the initiation of bud is associated with early leaf primordia in some cases and in others with later ones.

In the formation of axillary bud usually both tunica and corpus take part, although the extent to which each zone contributes differs. Champagnat (1955)

reported epidermal origin of axillary bud in Linaria. In Amaranthus leucocarpus both tunica and corpus take part. The corpus forms the promeristem region while both tunica layers cover this region. A similar observation was recorded by Gifford (1951) in Drimys and Shah (1960, 1969) in Cayratia and Cuminum respectively. Normally, axillary buds are described as exogenous in origin but this expression is commonly used only for comparing it with lateral root initiation. True exogenous buds should be those which are initiated by the outer tunica alone.

Procambium differentiates in the axillary bud in various directions. Schmidt (1924) and Miller and Wetmore (1946) reported acropetal differentiation while Majumdar (1942) and Gifford (1951) reported bidirectional differentiation. Shah (1968) also reported the acropetal differentiation of procambium in axillary bud. In Amaranthus leucocarpus acropetal differentiation of procambium is observed.

Initiation of leaf:

The form of the mature leaf of Amaranthus leucocarpus results from the correlated processes of cellular divisions and cellular enlargement in the primordium. The growth in length is achieved by the combined activities of apical, sub-apical and inter-calary dividing cells. As in most of the angiosperms, in Amaranthus leucocarpus also the apical and sub-apical initials mature at a relatively early stage and the

final height is acquired by intercalary cellular elongation.

The initiation of leaf primordium is first recognizable by periclinal divisions in the hypodermal layer at the uppermost part of the peripheral merisistem, irrespective of the number of tunica layers. In case the shoot apex has more than one tunica layer, all the tunical layers except the outermost, take part in the initiation of leaf primordium. The flanking zone may or may not take part in the initiation of leaf primordium if the number of tunica exceeds two, while in plants with a single tunica the flanking layers also take part in the formation of leaf primordium. In Veronica myrtifolia and Carya buckleyi (Foster, 1935, 1936) the leaf is initiated from the inner tunica and flanks of the corpus. In Tradescantia and Vanilla (cited by Sun, 1957) only the tunica layer forms the leaf primordium. In plants like Capparis decidua (Trivedi 1969) and Clematis lingustifolium (Tepper, 1969) the inner tunica and flanks of the corpus take part in the formation of leaf primordium. In Amaranthus leucocarpus also a similar type of development is observed. In the developing primordium the first division of the apical initial is periclinal. This type of division is not frequent in dicotyledons. Hara (1958) reported periclinal division in the apical cell of Triperaleia paniculata

Marginal growth of dicotyledonous leaves can

be divided into two types viz. marginal and sub-marginal types (Hara, 1957, 1958). According to the origin of procambium, the sub-marginal type can further be divided into three: The adaxial; abaxial and middle types. The procambium arises from the adaxial layer in the first type, from the abaxial in the second type, and in the third type, from the middle layer which arises from sub-marginal initial directly as observed in the leaves of Amaranthus leucocarpus.

The leaf trace procambium is reported to differentiate acropetally. Studies on this aspect have been made on certain angiosperms like Alstroemeria (Priestly et.al 1935), Costus (Smith, 1941), Anagallis, Coleus and Ligustrum (De Sloover, 1958). Rohweder (1963) has explained the basipetal differentiation of procambium in certain members of Commelinaceae. Some interesting cases have been described where the procambium differentiates in both acropetal and basipetal directions. According to Sharman (1942) and Kumazawa (1961) the median trace differentiates acropetally in maize leaf, while the lateral trace differentiates basipetally in stem from leaf base, downwards.

In Amaranthus leucocarpus the youngest leaf primordia are without any visible trace of procambium. The leaf trace procambium appears at the base of the second leaf primordium from the apex. This indicates that the procambium makes its appearance during midphase of the plastochron. From the base it differentiates acropetally

towards the leaf primordium. These procambial strands when traced back join the procambium which develops into medullary strands. This indicates that medullary strands are related to midrib and that they develop acropetally towards the leaf. In a leaf primordium abaxial parenchymatization commences earlier than the adaxial parenchymatization.

Inflorescence:

Bakshi and Chajlani (1954) discussed the nature of inflorescence in Amaranthaceae at length. According to these authors the original form of inflorescence appears to have been a raceme of dichasia in which the axis of each dichasium ends in a flower and subsequent growth continues through a bud in the axil of each bractole. They have stated that the reduction process continued to attain a condition observed in Pupalia lappacea where each dichasium has one fertile flower surrounded by the remains of others. Further reduction and transformation of the arms of dichasium into scales, has resulted in a condition as seen in Digera arvensis. Ultimately a stage was reached where the scale also disappeared. This stage is observed in Psilostachys sericea (Bakshi, 1952), Pupalia lappacea, Achyranthus aspera and Gomphrena globosa (Bakshi and Chhajlani 1954)

To this series of reduction it would be interesting to add Amaranthus leucocarpus. Here also the inflorescence has a raceme of dichasia in which the axis of

dichasium ends in a flower and further growth continues by means of buds in the axils of bractoles. The cymose cluster developing from a cluster apex bears a maximum of nine flowers composed of three dichasia. From this there is a regular reduction series; first by the suppression of two lateral flowers in the central dichasium leading to seven flowers; by further reduction of lateral members (only one each) a stage with five flowers is attained; with further reduction two surviving lateral members of lateral dichasia disappear leading to a cluster with three flowers. This reduced cluster of three flowers does not represent a single dichasium but three dichasia representing the central flower of each dichasium. These three flowers approximate and by condensation of the axis of the dichasia it appears as though the three flowers belong to the same dichasium.

Rao (1963) has indicated an interesting parallelism between Proteaceae and Amaranthaceae. According to him the single flower in Amaranthaceae represents a surviving member of a lateral branch system just like the flower pair in Proteaceae. In Amaranthus leucocarpus the surviving member is the central flower of the dichasium and three such flowers in a reduced cluster are three central members of three dichasia. Rao (1963) further adds that flower in Amaranthaceae represents the results of phylogenetic fusion of the primordia of an ancestral flower pair such as that of Proteaceae. Developmental study of the inflorescence in Amaranthus leuco

carpus does not give any such indication. Psilostachys sericea (Bakshi, 1952) and Achyranthus aspera (Bakshi and Chhajlani, 1954) show three traced vascular supply to tepals. In Digera arvensis Joshi and Rao (1934) reported univeined tepals in a few flowers; while Bakshi and Chhajlani (1954) observed univeined uppermost perianth leaves and three veined lower most perianth leaves. In Amaranthus leucocarpus tepals and stamens receive one trace each and gynoecium has three dorsals and ventral (formed by fusion of three strands). It appears, therefore, that Digera indicates a transition stage in reduction of tepal supply and Amaranthus shows further reduction.

Gametogenesis:

The presence of globular bodies just beneath the tapetal cells has been recorded in Digera arvensis (Puri and Singh, 1935; Kajale, 1940) and Psilostachys sericea (Bakshi, 1952). Such deeply staining globular, rather granular, matter appears in Amaranthus leucocarpus, also. The exact nature and function of these globules are not properly understood but it is beleived that these globu--les have a role in the formation of exine of micros--pores. Well developed endothecium with fibillar thick--enings has been reported for many of Amaranthaceae (Puri and Singh, 1935, Kajale, 1940; Bakshi, 1952), however, in Amaranthus leucocarpus endothecium is short lived. It degenerated by microspore stage and till then the cells do not develop any fibrillar thickening .

The epidermal cells are slightly elongated and get cutinised. A some what similar situation has been reported for Ditepalanthus (Fagerlind, 1938) and Balanophora (Fagerlind, 1945). Generally, prior to the division of microspore nucleus to give rise to generative cell, the nucleus is pushed to the periphery by the formation of a vacuole (Maheshwari, 1950). In Amaranthus leucocarpus, however, the nucleus divides in the centre to form generative and vegetative nuclei and vacuole appears between the two pushing the generative nucleus to the periphery.

The ovule in Amaranthus leucocarpus is amphitropous, bitegmic and crassinucellate. Bakshi (1952) and Padhye (1962) have reported circinotropous ovules in Psilostachys sericea and Gomphrena celocioides respectively. The ovule in Amaranthaceae is basal but in Amaranthus leucocarpus in addition to usual basal ovule, certain sections revealed lateral (peripheral) position. Does this indicate that basal placentation is derived from perietal? There is a clear space between the two integuments and also between inner integument and nucellus. Similar observation has been recorded for Psilostachys sericea (Bakshi, 1952). However, Digera arvensis does not show any such space (Joshi and Rao 1934; Puri and Singh, 1935). The behaviour of antipodal cells is variable in the members of Amaranthaceae. In Amaranthus leucocarpus the antipodals persist till about four nucleate stage of endosperm. The persistence

of antipodals has been recorded for other members of Amaranthaceae (Joshi 1936; Kajale, 1935, 1937, 1940). In Pupalia lappacea the antipodals divide to form a mass of 30 - 40 cells (Kajale, 1940). Bakshi (1952) reported ephemeral antipodals in Psilostachya sericea.

The development of embryo and histogenesis:

Only a few studies on histogenesis of embryo have emphasised the ontogeny of apical meristems. Schleiden (1849) who was among the first to describe embryogeny, gave the histogenic sequence of embryo as root tip, stem tip and cotyledons. Strasburger (1879) corrected Schleiden's error concerning one feature, viz. that it is the plerome histogen of the root which is the first part of embryo to become differentiated and not the root tip. The studies of Schoff (1943), Allen (1947) and Spurr (1949) on gymnosperms and of Boke (1944), Miller and Wetmore (1946), Reeve (1948) and Guttenberg et.al (1944 a,b, 1955, 1960) on angiosperms also bring out that the first to become distinct is the region of the root pole. In contrast, Meyer (1958) and Mahlberg (1960) have put forward the view that the shoot pole is the first to become distinct in the embryo of McIntosh apple and Nerium respectively. Similar observation has been recorded by Padmanabhan (1964, 1967) for Avicenia and Epithema and Swamy and Padmanabhan (1962) for Sphenoclea. In Amaranthus leucocarpus the radicle initials become distinct at the globular stage of the embryo.

The protoderm exhibits the Kappe type of divisions around the hypophysis leading to the formation of root cap. Simultaneously, the stelar pole also becomes delimited and a file of one or two cells outside the stelar pole form the initials for the embryonic cortex or periblem, exhibiting Korper type of divisions.

As a result of the study of embryogeny Guttenberg et.al (1954 a,b, 1955, 1960) concluded that single central cell may be present in very young embryos, but this is transitory and gives place to a plate composed of a larger number of cells. This per-haps has been the basis for Guttenberg (1960) to classify root apical structure into two types: (i) the 'closed' type, where the histogens for various tissues are distinct and (ii) the'open' type, where there is a common group of initials for all the tissues. In their study of the embryology of Helianthus, Guttenberg et.al (1955) reported closed type of organization in the early stages of development at the radicular end. But this closed organization was found to give place to an open type as the embryo grow. According to Guttenberg (1960), this does not happen in every case. In Amaranthus leucocarpus discrete initials are present from the late globular stage of the embryo itself.

Epicotyl apex:

A study of the developmental stages in

Amaranthus leucocarpus embryo clearly indicates that the appearance of the epicotyl apex is quite late in the ontogeny. When the cotyledons have grown to a considerable extent in torpedo stage, it is possible to distinguish the epicotyl apex on cytohistological grounds though the zonation is not marked. It is therefore, not possible to agree with Mahlberg (1960) and Padmanabhan (1967) who stated that the epicotyl apex is the first to be delimited in the embryo.

The morphology of cotyledons:

There is a controversy regarding the entity of cotyledons. Brown (1960) has expressed the view that the cotyledons are embryonic organs, its resemblance to a foliage leaf being superficial. On the basis of comparative observations on form, function and ontogeny, Doak (1935) considered the cotyledons as the first leaves. The terminal part of the globular embryo is regarded as the shoot apex by Mahlberg (1960) in Nerium. Padmanabhan (1967) in Epithema and Kaplan (1969) in Downingia have regarded cotyledons as first foliage leaves. The method of origin, development and vascularization of the cotyledons tend to support the view that the cotyledons are the first foliage leaves. In addition the presence of the buds in the axil of cotyledons in Amaranthus leucocarpus strongly suggests the foliar nature of the cotyledons.

Seedling anatomy:

The term transition region refers generally to that part of the seedling in which top of the primary root is confluent with the bottom of the primary shoot axis. It has also been used to refer to a specific portion in which there is transition from radial arrangement of phloem and exarch xylem to the eustelic cylinder of the collateral endarch bundles in the shoot.

Chauveaud (1911) explained different regions in the seedlings as follows: in a root and lower hypocotyl there is an alternate arrangement; at a higher level there is an addition of the xylem elements on the flanks - intermediate arrangement, and in the upper hypocotyl region or just below the cotyledons there is an extrusion of xylary bundles from the root with half strands of phloem abaxially superimposed. Lehmberg (1923-1924) recognizes two centres of differentiation of xylem in Helianthus seedlings: one in the upper part of the root and the other in the cotyledons. In the former the xylem elements develop in centripetal direction i.e. exarch and in the latter in centrifugal direction i.e. endarch. The point where the two meet and become a functional water conducting system , is the transition region. Gehlen (1929) defines 'transitional zone' as the zone in which we find neither true exarch nor true endarch arrangement but in which xylem and phloem areas are more or less disturbed. Thus if tran-

sition means the change from exarch to endarch and radial to collaterel, the general designation of any particular region of the hypocotyl as the transition region would be erroneous.

The transition in Amaranthus leucocarpus does not take place by splitting, rotation and fusion. The centripetal xylem shows obliteration and therefore, the question of torsion does not arise here. New centrifugal xylem develops from the inner part of procambial strands, the outer part of which differentiates into phloem. Obliteration of centripetal xylem and formation of centrifugal xylem clearly indicate a shift in pole of differentiation of xylem and therefore, go in support of Bonnier's (1900) view. Hill and de Fraine (1912) observed isolation of protoxylem of root in many families belonging to Centrospermae. Murray (1933) has given a physiological interpretation for the obliteration of centripetal xylem. Gradual alteration in position of the food conduction results in the change of focus of lignification of xylem vessels. This results in the gradual disappearence of the original xylem. Nair and Nair (1961) have also observed degeneration of root protoxylem in Boerhaavia diffusa and Boerhaavia verticillata.

Vascular system:

The development of procambium in shoot indicates that the central strands are first to differentiate. In young nodes i.e. second to seventh node from the youngest visible leaf primordium the leaf traces are formed from these central strands and only three traces (median strands of the leaf) diverge to the leaf. From seventh node onwards leaf receives more strands since intermediate strands are formed at this level and take part in leaf supply. These intermediate strands are formed many nodes below the node of their departure in the form of leaf traces as deflections from central strands and continue to have cortical course through many internodes and thus have intermediate position. The peripheral ring of bundles (belated bundles, Maheshwari, 1930) develops from procambium arising late in the ontogeny. After peripheral bundles are formed the leaf receives still more traces, at least two, so that a leaf at this stage possesses as many as seven traces, of these seven traces three are median strands connected with central bundles (medullary bundles), two are from intermediate bundles and the other two from peripheral ring. Thus the intermediate and peripheral ringsare connected with lateral traces. That the median traces are related to central strands has also been pointed out by Nair and Nair (1961), Philipson and Balfour (1963).

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Seedling anatomy reveals very interesting for-

-mation of central and intermediate strands. The central strands are formed as downward branches of cotyledonary traces. The four cotyledonary strands fuse in pairs just below the cotyledonary node and give out downward branches. Further divisions of these branches result in the formation of central strands. These can be considered as 'medullary' only after the formation of the peripheral bundles. There are four central strands in the middle hypocotyl region and by the level of cotyledonary node they become 8,9,10, nine being the most common number. The buds in the axil of cotyledons receive supply from the central strands. The traces take a form of V or Y, the lower part of these traces, towards the axis, forms a bundle which descends to add to the central strands, the middle part givesrise to intermediate strands (in a 20th day seedling) and the upper part supplies the axillary bud. Thus seedling study also shows that intermediate strands are in a way deflections of central strands. The differentiation of peripheral strands commences from 12th day seedling onwards. Maheshwari (1930) considered the two large strands as medullary in Boerhaavia. Nair and Nair (1961) favour the term primary instead of medullary for these strands, since these strands are the first to develop in the seedling vasculature and are related to median traces of leaf. Pant and Mehra (1963) on the other hand support Maheshwari's view on the basis that the term 'medullary' can be justified while considering the centripetally shifted position of these bundles in

relation to the bundles of the inner ring.

In any case vasculature of Amaranthus leucocarpus has two systems: cone of the central strands related to median leaf traces; second the peripheral or belated strands related to lateral leaf traces, the intermediate bundles being regarded as deflected branches of central strands.

Venation pattern:

The size and number of bundle changes from level to level in the petiole of Amaranthus leucocarpus. Five strands enter the leaf blade, and these strands make up the entire venation pattern by branching. Pray (1954) divided the venation pattern into two major categories: major venation and minor venation. Major venation consists of primary, secondary and intermediate veins. Primary vein may be defined as the one that has independent origin from the axis and maintains its identity through the petiole and the leaf lamina. Minor venation consists of tertiary, quarternary and their branches which form areoles. In Amaranthus leucocarpus mostly the quaternaries constitute the areoles and the vein ends are the branches of quaternaries i.e. the veins of fifth category. Minor venation formed of polygonal areoles is of widespread occurrence among the angiosperms.

The tendency of minor venation to the formation of rectangular, elongated areoles is interpreted by Pray (1959) as a week expression of 'lineolate' type of

venation. This is well pronounced in some members of Rubiaceae. Foster (1950) observed that minor venation in Quiina consists of loose reticulation, the areoles of which are narrowly linear or elliptical in shape. According to Pray (1959) minor venation with polygonal areoles is a basic type from which other types could be derived. Amaranthus leucocarpus display the common dicotyledonous type of venation pattern i.e. polygonal areoles.

Anomalous secondary growth:

Philipson and Ward (1965) in their excellent review on cambium have mentioned abnormal cambia of different types:

(a) Medullary cambium.

(b) Accessory or extra fascicular cambium.

In the latter these authors have mentioned bidirectional cambium as observed in plants like Cocculus, Boscia, Gnetum and Cycas, where the cambium gives rise to xylem internally and phloem externally. According to these authors families Nyctaginaceae, Amaranthaceae and Chenopodiaceae also show supernumerary cambia but these cambia are unidirectional that is the formation of both xylem and phloem is centripetal. Recently, however, Esau and Cheadle (1969) have observed bidirectional cambium in Bougainvillea. These authors have criticised the observations of Philipson and Ward (1965).

With this context in view it will be worthwhile considering some of the earlier important views on the initiation and activity of abnormal cambium in these three families. According to Artschwager (1926) in Beta, the cambial initials divide and the inner cells resulting from this division continue to divide a number of times before they undergo differentiation into xylem and phloem elements, while the outer cells form the initials of the next outer cambium, which replaces the former one. The initials of this cambium divide similarly to those of the cambium which it replaces and this feature is repeated many times.

In Boerhaavia (Maheshwari, 1930), the bundles of the outer ring are initially separate, very minute and each provided with its own fascicular cambium. The fascicular cambial regions of the bundle subsequently become interconnected by interfascicular cambium, thus producing cylindrical meristem, which gives rise internally to xylem and to interfascicular parenchymatous tissue between the bundles. After a time cambium ceases to be active, and a new meristem arises in the secondary parenchymatous tissue to which the first has given rise on the outside. This process is repeated at intervals.

Eames and MacDaniels (1947) have given the following details regarding the formation of accessory

cambium and its activity. The secondary cambial zones commonly develop in the pericycle and function as does a normal cambium or, when the first cambium has functioned in an unusual manner, repeat this peculiar behaviour such secondary cambial activity follows the cessation of function of the first layer, one or even many additional layers successively appearing and ceasing to function. Thus a cylinder of alternate concentric layers of xylem and phloem is formed. In the Chenopodiaceae, Amaranthaceae and allied families a somewhat different type of unusual growth is present. Here there is first formed a hollow cylinder of vascular tissue or a ring of irregularly arranged bundles. These bundles are partly of secondary nature, but cambial activity soon ceases and a new, secondary cambium arises in the pericycle just outside the bundles. In some species the cambium forms tissues centripetally, consisting of bundles embedded in non-vascular tissue. Centrifugally the cambium forms a very little parenchyma or no cells at all. In Chenopodium the cambial activity is bidirectional the phloem is formed centrifugally and later buried by the development of an arc of new cambium formed without it.

The underlined part of the statements of Artschwager (1926) and Maheshwari (1930) clearly indicate unidirectional activity of cambium. Eames and MacDaniels (1947) mentioned both the types in

general but unidirectional for members of families Chenopodiaceae and Amaranthaceae.

In Amaranthus leucocarpus the activity of fascicular and interfascicular cambium of the peripheral bundle ceases within a short span of time. Strips of cambium develop outside the phloem patches of the peripheral bundles. These anomalous cambial strips are bidirectional in their activity.

There are different views regarding the formation of interxylary phloem. In genera like Combretum (Pfeifer, 1926), Salvadora and Leptadenia (Singh, 1944) small segments of the cambium produce phloem cells towards the inside for a brief period in place of xylem cells which are normally produced. After a brief period of such activity these cambium segments resume normal activity and thus bury the inwardly formed phloem with xylem.

In Trianthema and Strychnos (Eames and MacDaniels, 1947) the interxylary phloem strands are formed by the cambium toward the outside as a part of the external phloem. New segments of cambium then arise, as secondary meristem, in the outer periphery of the phloem or in the pericycle. These unite with the edges of the segments of the general cambium cylinder and continue their normal activity and thus enclose a strand of phloem cells. This process is repeated in other segments of the cambium

also. As a result of this activity, the secondary xylem possesses numerous scattered strands of embedded phloem.

According to Metcalfe and Chalk (1950) the successive cambial strips or arches are responsible for the inclusion of phloem in most of the members of Amaranthaceae. In Amaranthus leucocarpus also the 'phloem islands' are of usual occurrence in the secondary xylem of mature stem and roots

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SUMMARY AND CONCLUSIONS

Structurally the following histogens viz: plerome, periblem and dermocalyptrogen can be distinguished, which are concerned with the building up of the root body in Amaranthus leucocarpus. Dermocalyptrogen is concerned with the formation of both the dermatogen and the peripheral region of the cap. Columella arises from 'Columellogen' and is independent of the periphery of the cap. A quiescent centre has not been observed in the root apex.

Four cytohistological zones can be distinguished in the shoot apex. A fifth zone - the 'cambium-like zone' arises in relation to plastochronic changes and is short lived.

The inner tunica and the outer flanks of the corpus together initiate the leaf primordium. The apical and subapical initials are distinct. The marginal growth of the primordium is due to the activity of marginal and submarginal initials. Marginal growth conforms to submarginal middle type as described by Hara (1957). The procambial differentiation is acropetal towards the leaf.

The axillary bud develops from detached - meristem. During the development of axillary bud, an arc of narrow elongated cells is formed near the

axil of the leaf. This zone is termed as 'shell zone' which gradually disappears as the position of the bud is shifted. In axillary bud also the procambial differentiation is acropetal.

The variation in the nucleolar volume is observed as an indication of metabolic activity in shoot apex. The rapid decrease in the nucleolar volume in the second stage (2-3 leaf stage) is followed by a spurt of mitotic activity.

Specific importance has been given to the presence of starch grains in the central mother cells. This indicates the inactivity of this region during that particular phase. The gradual increase in DNA concentration and the translocation of basic protein (histone) from nucleus to cytoplasm during the reproductive phase is discussed.

Development of vascular system in Amaranthus leucocarpus indicates that the central strands arise first and are related to midrib traces of the leaf. The intermediate traces arise as deflected branches from central strands, as inner lateral traces and have cortical course through many internodes and thus appear intermediate in position. The peripheral vascular strands arise very late in the ontogeny. Seedling studies indicate that the central strands are related to cotyledonary traces.

Inflorescence is a raceme of dichasia. There

is a regular reduction in number of flowers in a cluster composed of three dichasia developing from a single cluster apex. The manimum number of flowers in a cluster is 9 and reduction continues in steps of 7-5 and ultimately three flowers representing three central flowers of three dichasia are observed.

Embryological observations indicate absence of distinct endothecium. Small globules occur beneath the tapetal cells. The pollen are shed at three celled stage. The ovule is amphitropous, clear space is present between the two integuments and between inner integument and nucleus. Embryo sac development is of polygonum type. Antipodals persist till about 4 celled stage of endosperm.

The radicular apex is established by late globular stage of the embryo. The shoot apex differentiation commences by torpedo stage of the embryo.

In leaf, the vascular bundles are surrounded by parenchymatous sheath. Venation pattern indicates 'camptodromons' type. The development of trichome is studied. Gradual variation in the number of vascular bundles is observed in the petiole at different levels.

The anomalous cambium is bidirectional in its activity in stem as well as in root. As a result of the formation of cambia in close succession the interxylary phloem patches are formed.

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* Original not referred.

Figs. 1 - 4. Root apical organization

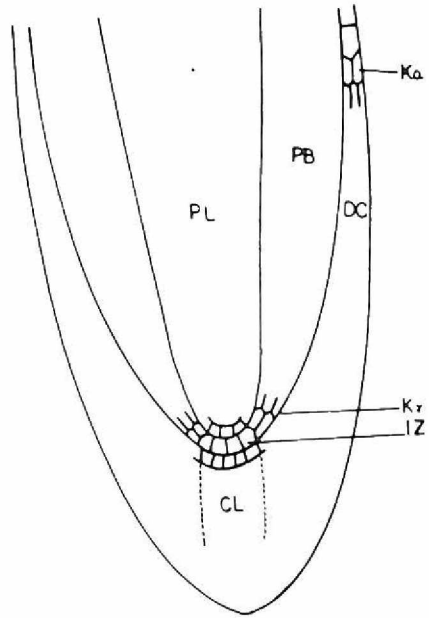
Fig. 1 Diagrammatic representation showing various zones of root apex.

Fig. 2 Showing discrete initials for plerome, periblem and columella.

Fig. 3 L.S. Root apex. Showing developing columella

Fig. 4 L.S. Root apex showing well developed columella

PL	Plerome, PB. Periblem
DC	Dermo-calyptrogen
	CL = Columella
IZ	Initial zone. Kr - Körper division
Ka	Kappe division
PLI	Plerome initial
PBI	Periblem initial
COG	Columellogen



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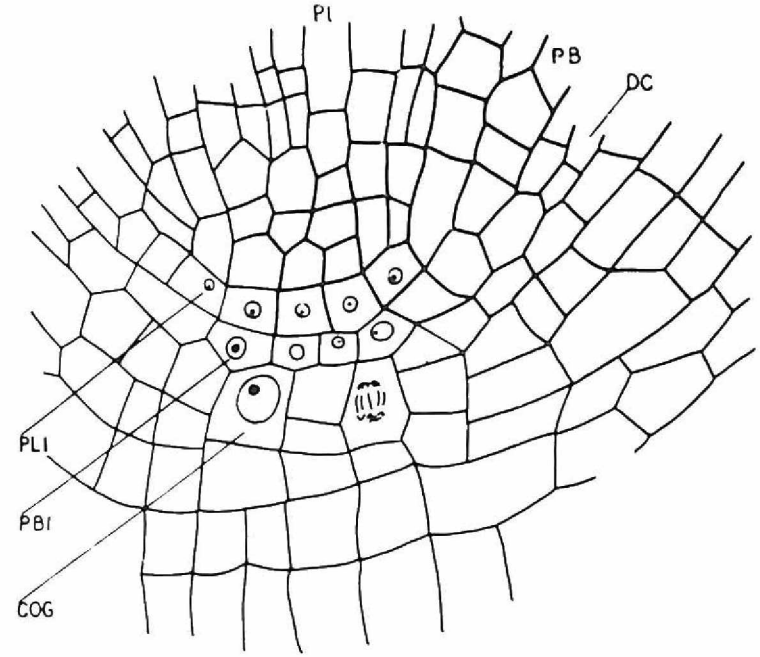

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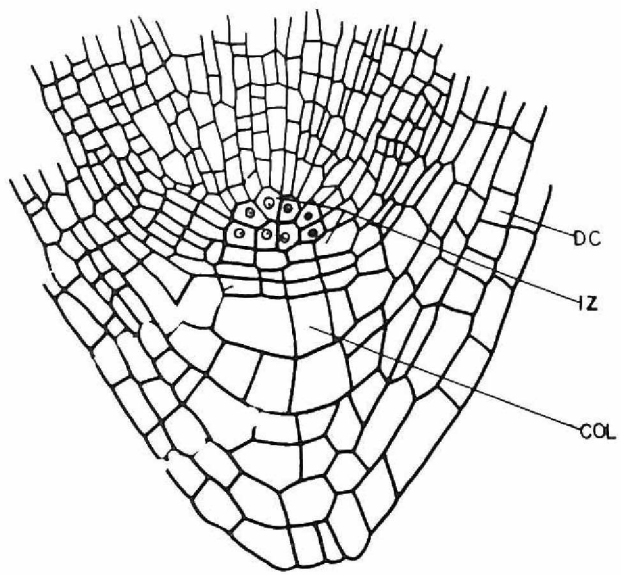

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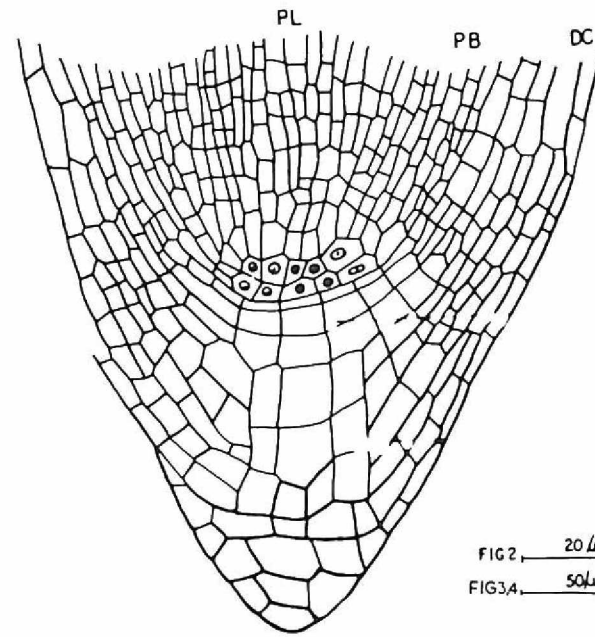


FIG 2 — 20 μ

FIG 3,4 — 50 μ

4

Figs. 5 - 8 Shoot apical organization

Fig. 5 Diagrammatic representation of shoot apex. Showing various zones.

Fig. 6 Shoot apex. L.S. Minimal plastochronic phase.

Fig. 7 Shoot apex L.S. Midplastochronic phase.

Fig. 8 L.S. Shoot apex maximal phase of the plastochron.

T_1 Tunica 1 ; T_2 Tunica -2.

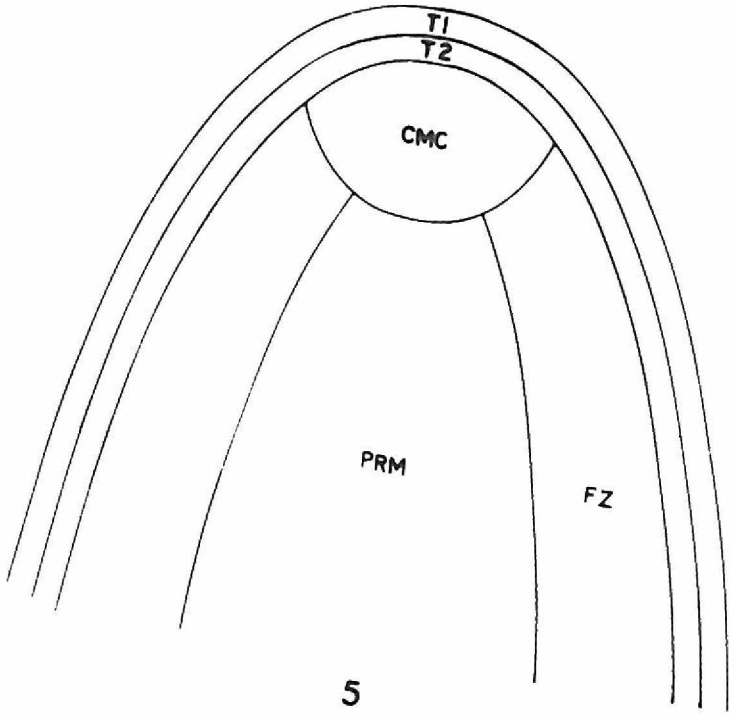
CMC Central mother cells

PRM Pithrib-t meristem

FZ Flanking zone(Peripheral zone)

CZ Cambium like zone

LP Leaf primordium



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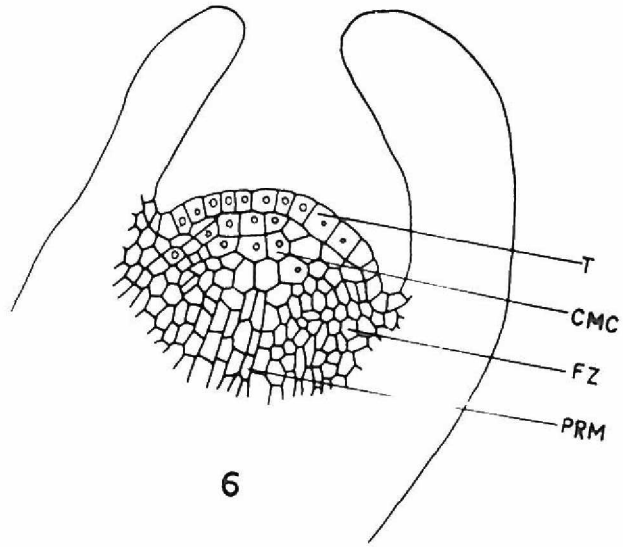

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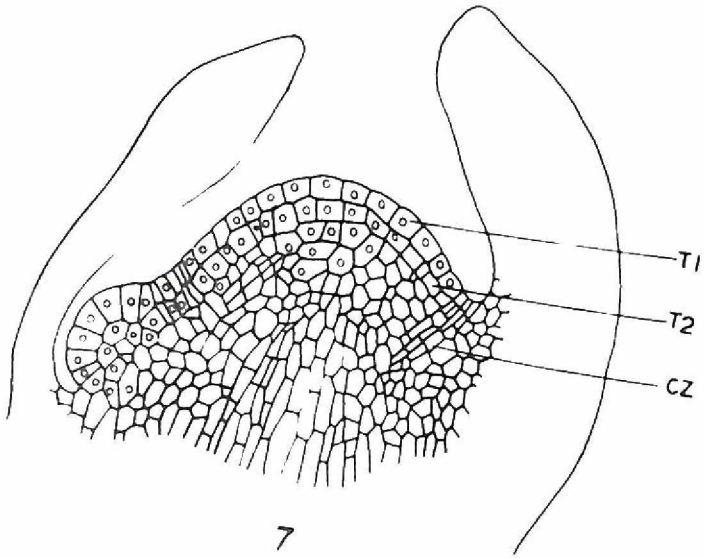

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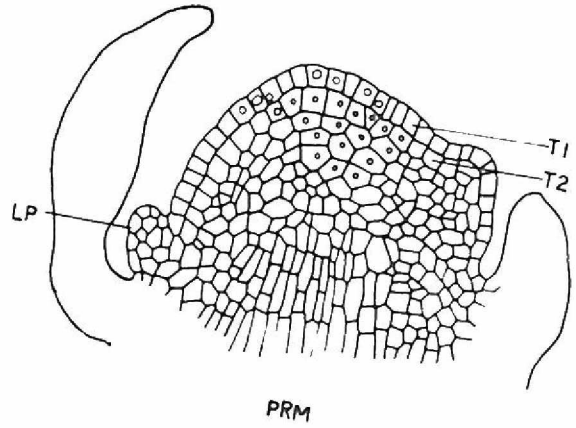


8

Figs. 9 - 14 Development of leaf.

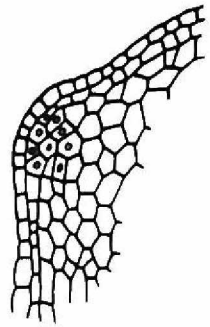
Figs. 9 and 10 L.S. Shoot apex showing initiation of leaf buttress.

Fig. 11 L.S. Leaf primordium with sub-apical initial.

Fig. 12 L.S. Leaf primordium showing acropetal development of procambium.

Figs. 13 - 14 T.S. Leaf primordium showing marginal growth.

SAI	Sub-apical initial
MI	Marginal initial
SMI	Sub-marginal initial
PC	Procambium



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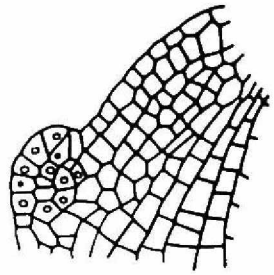

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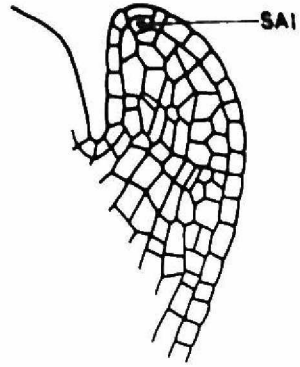

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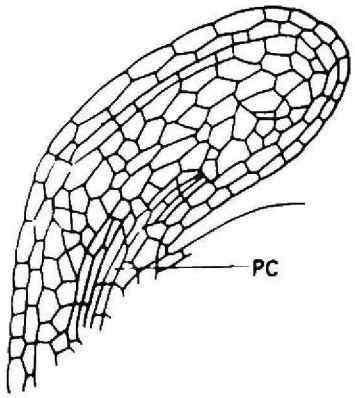

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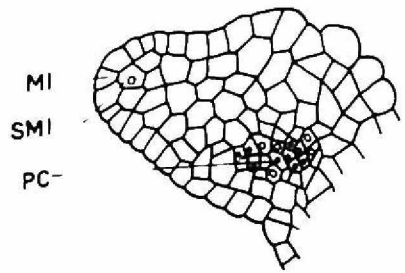

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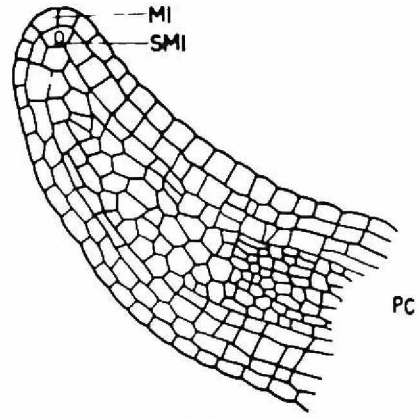


14

FIG 9 14 — 50 h

Figs. 15 - 18 Variation in starch concentration in various stages of shoot apex.

Fig. 15 L.S. Shoot apex at cotyledonary stage showing starch bound cells in the central mother cell.

Fig. 16 L.S. Shoot apex at 2-3 leaf stage showing addition of starch bound cells in the central mother cell region.

Fig. 17 L.S. 3rd stage. Disappearence of starch grains from central mother cell region.

Fig. 18 L.S. Infloresence apex, Showing accumulation of starch in mature cells

SG Starch grains.

FIG 15-18

Figs. 19 - 26 Inflorescence.

Figs. 19 and 20 Diagrammatic representation of flower clusters in L.S. and T.S. respectively.

Fig. 21 Cluster of five flowers indicating lateral flowers abortive

Fig. 22 Inflorescence L.S.

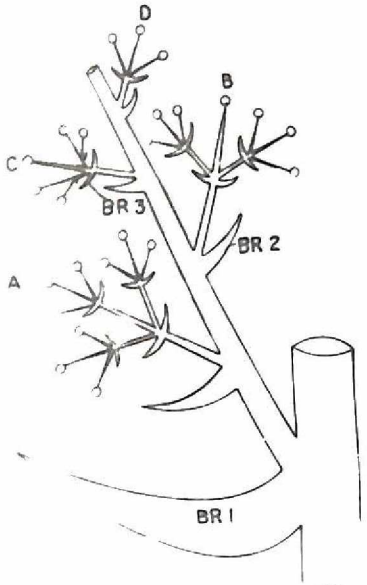
Figs. 23 - 26 Transections showing vasculature of the inflorescence axis.

BR-1 and BR-2 Bracts

RS Reproductive shoot

CA Cluster apex

BRT Bract traces.



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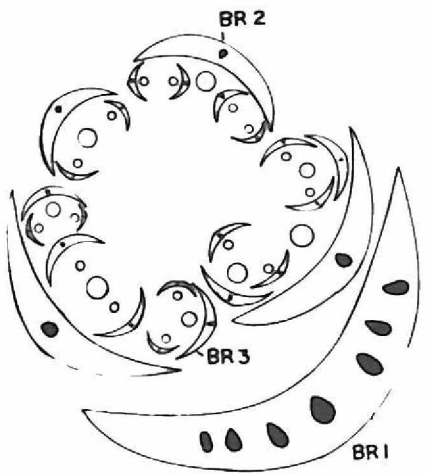

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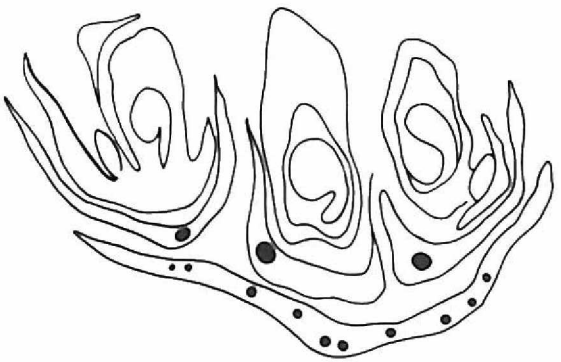

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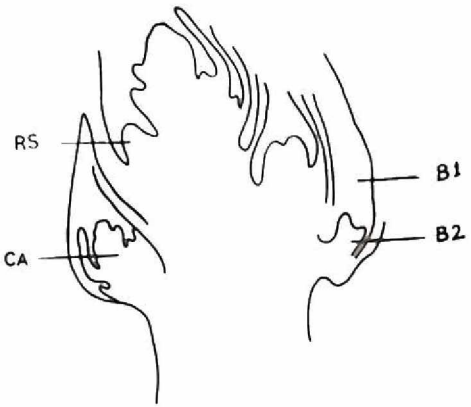

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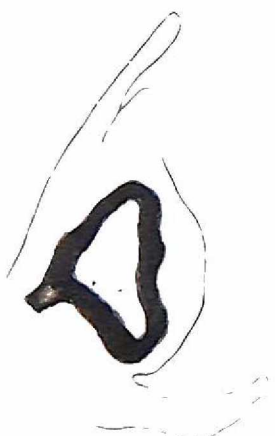

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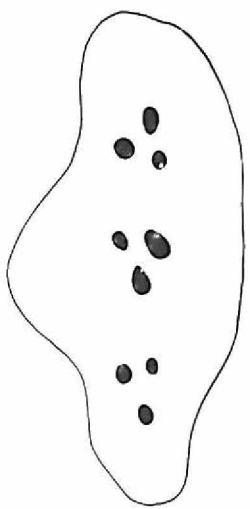

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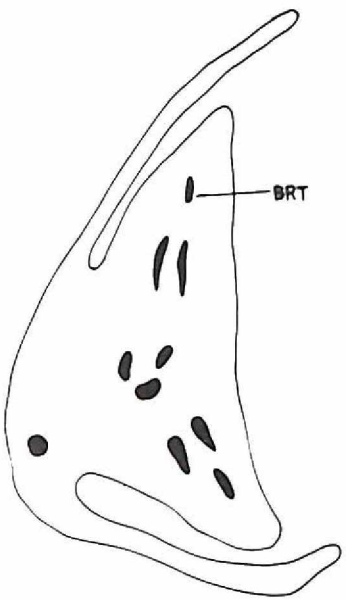

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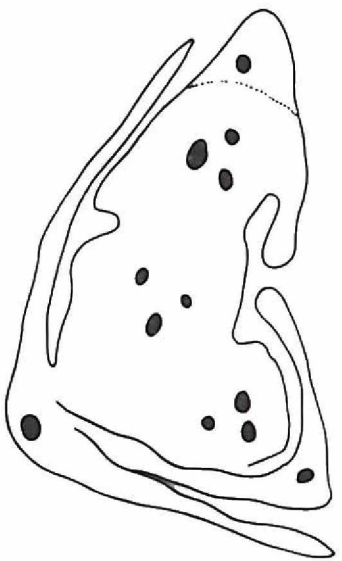


26

FIG 21,22 — 200μ
23-26 — 50μ

Fig. 27 Transection showing vasculature of the cluster.

Fig. 28 Female flower

Figs. 29 - 31 Vasculature of female flower

Fig. 32 Male flower

Figs 33 and 34 Vasculature of male flower

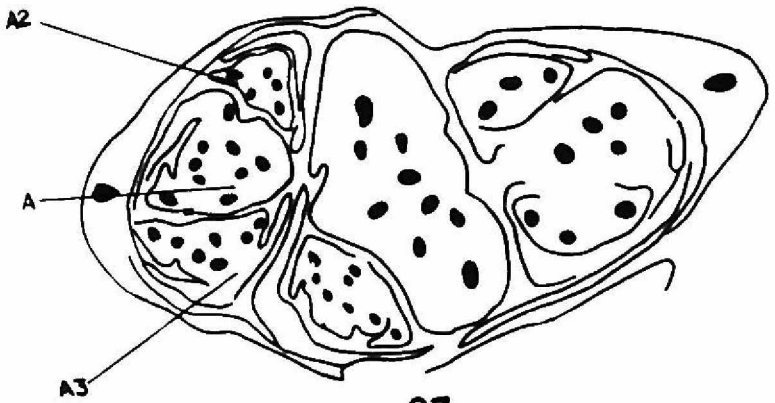
A, A2, A3 Three lateral clusters

TT Tepal trace

CD Carpellary dorsals

V Ventral

ST Staminal trace



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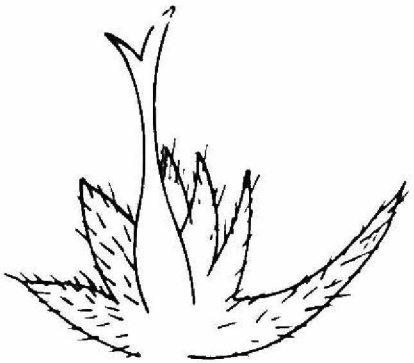

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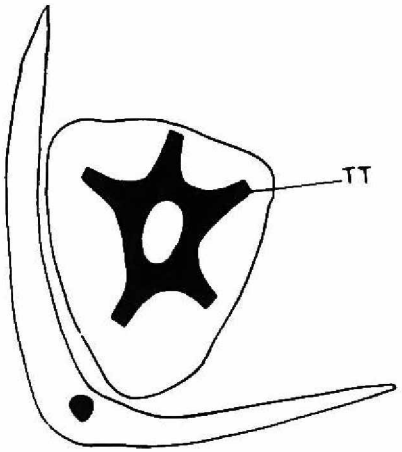

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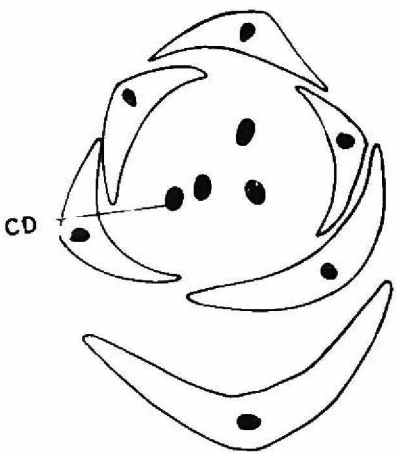

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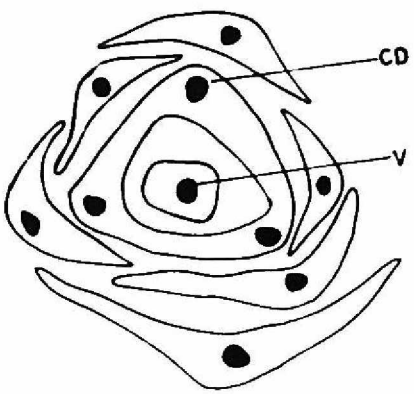

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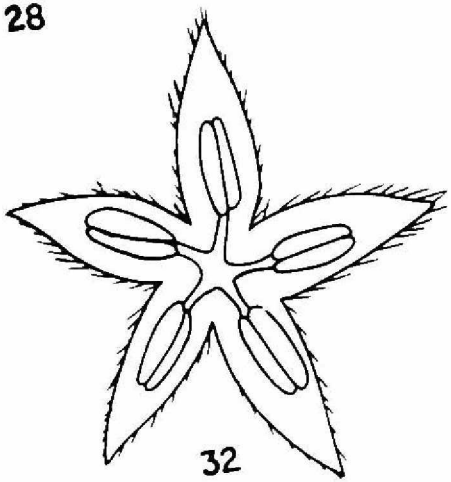

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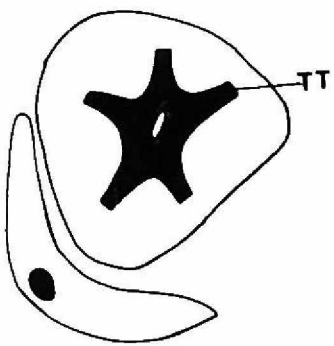

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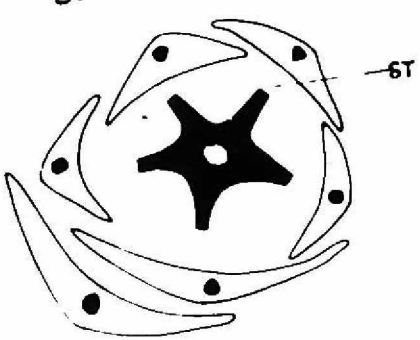


34

FIG 27 —— 200μ
29, 31-34 —— 50μ
33,34

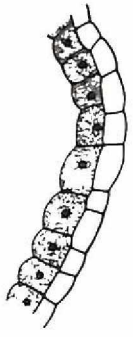
Figs. 35 - 44 Microsporogenesis

Fig. 35 and 36 Young anther lobe showing hypodermal archesporium

Fig. 37 L.S. Microsporangium showing microspore mother cells, remnants of middle layer and conspicuous tapetum.

Figs. 38 - 40 L.S. Portion of microsporangium showing the separation of tapetal cells and the degenerating endothecium.

Figs. 41 - 44 Development of male gametophyte



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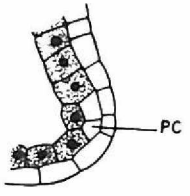

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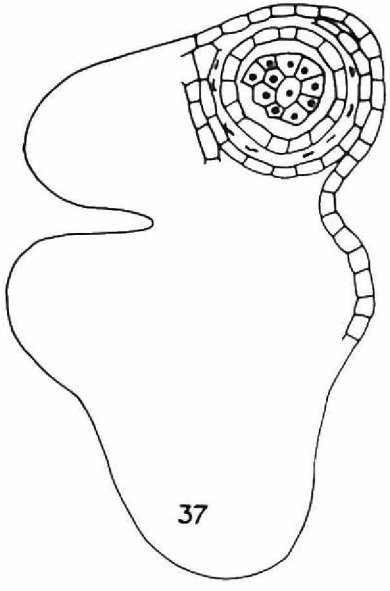

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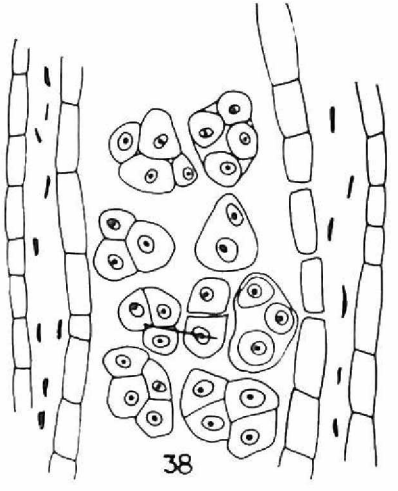

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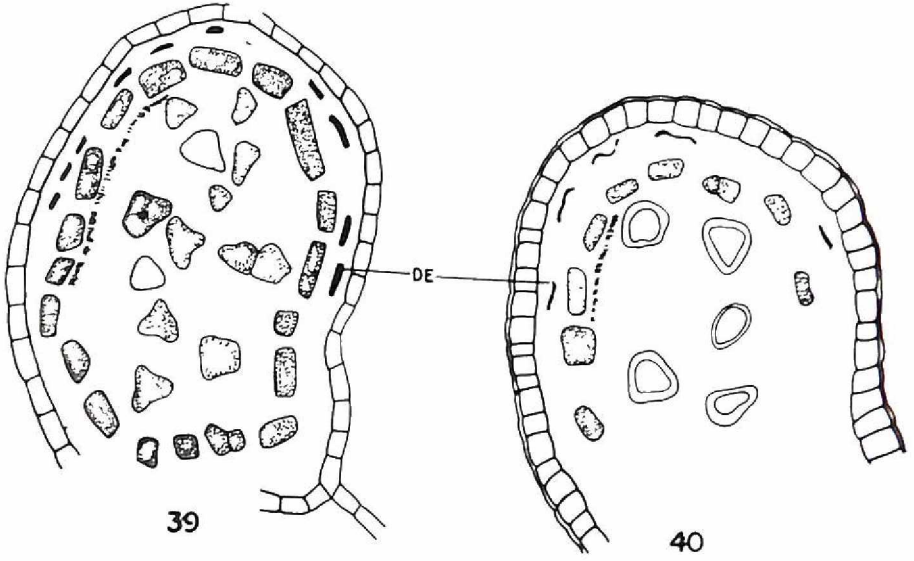

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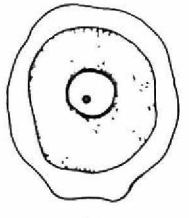

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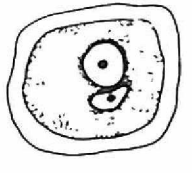

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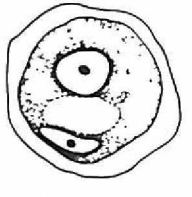

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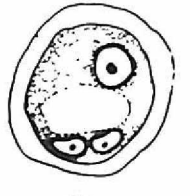


44

FIG 35.36 100μ
37-40 200μ
41-44 20μ

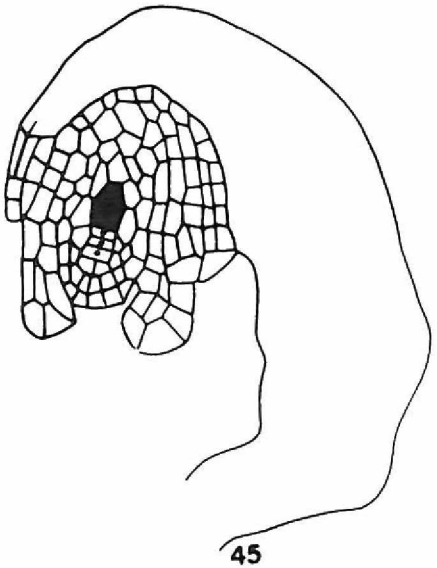
Figs. 45 - 53 Megasporagenesis

Figs. 45 - 48 Showing the change of the ovular position from orthotropous to anatropous condition

NOTE: The linear row of four megaspores in Fig.45.

Fig. 49 Orthotropous ovule with an archesporial cell.

Figs. 50 - 53 Development of female gametophyte.



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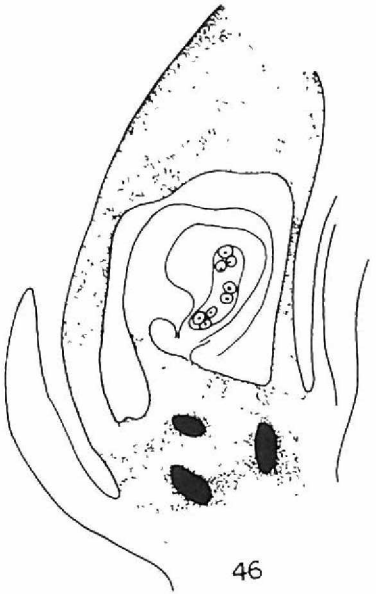

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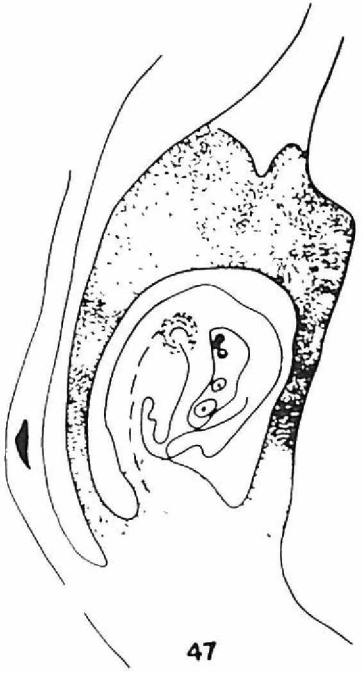

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50

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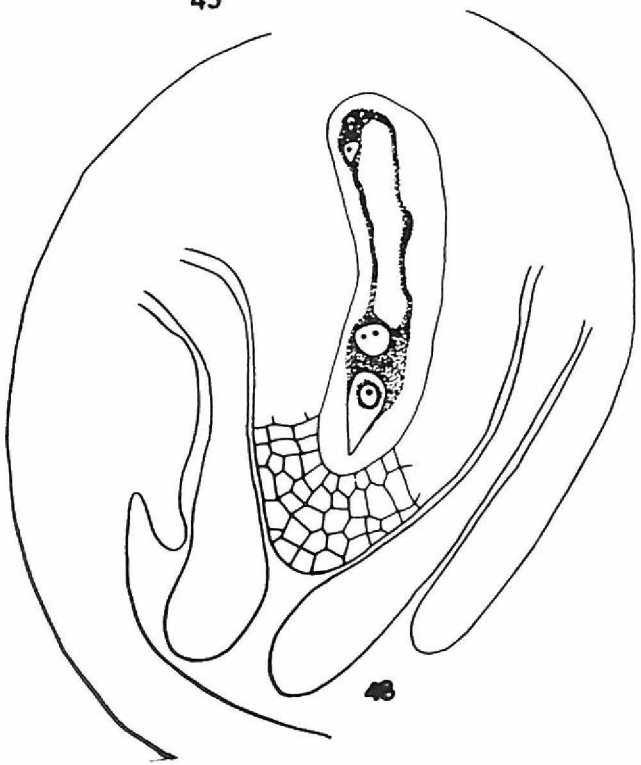

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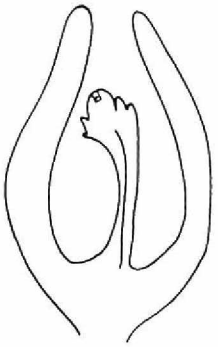

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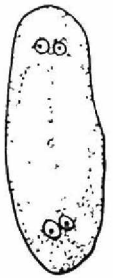

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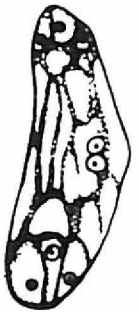


53

FIG. 45-48 — 50μ
49 — 200μ
50-53 — 20μ

Figs. 54 - 58 Development of embryo.

Fig. 54 Early globular stage

Fig. 55 Late globular stage

Fig. 56 Heart shaped stage

Fig. 57 Torpedo stage

Fig. 58 Mature embryo.

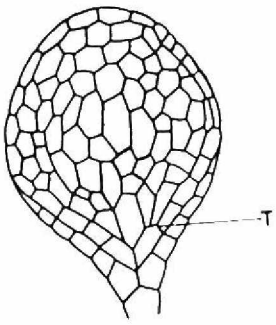
T T-division

PLI Plerome initials

PBI Periblem initials

SA Shoot apex

SAI Sub-apical initials of cotyledons.



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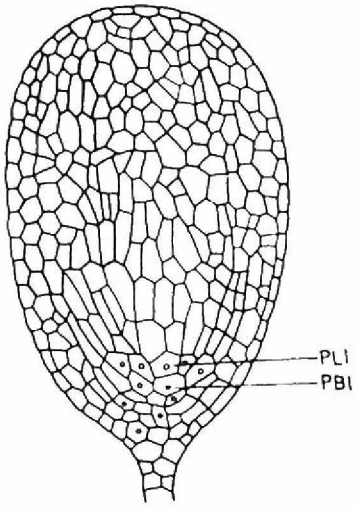

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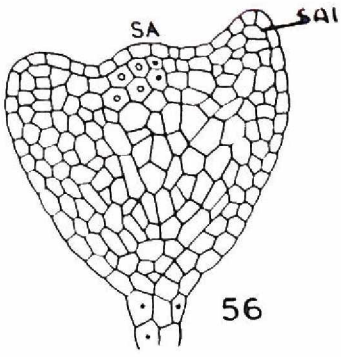

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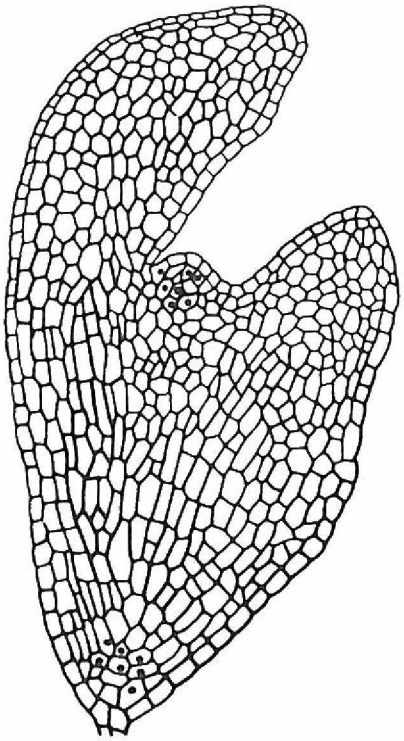

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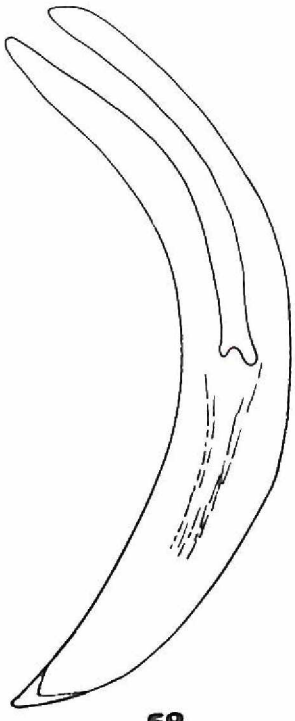


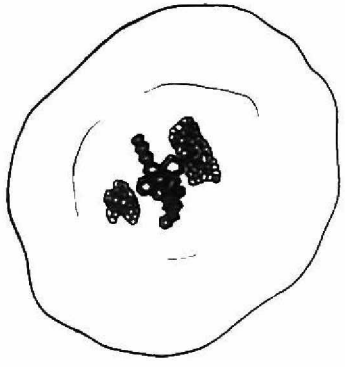
58

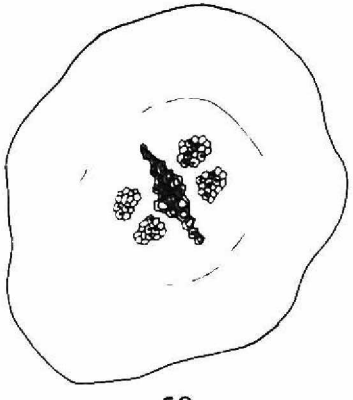
FIG.54 — 20µ
56-57 — 50µ
58 — 200µ

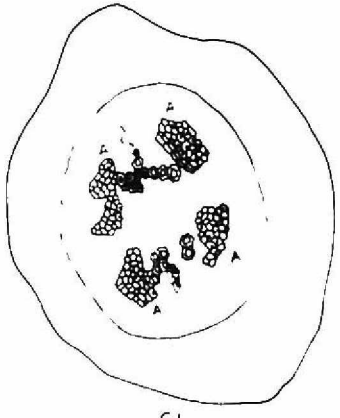
Figs. 59 - 65 Series of transections of stem. 4 day old seedling, Showing the formation of central bundles

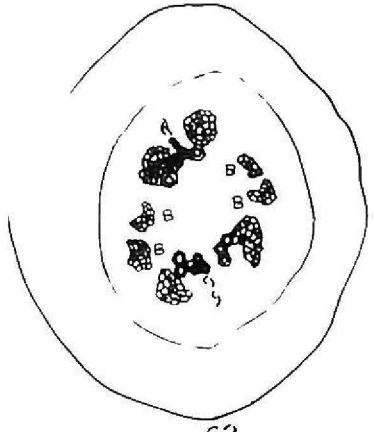
NOTE: The obliteration of centripetal xylem

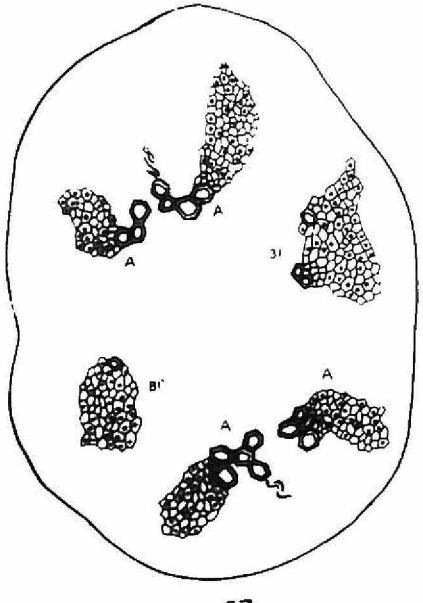
CP Centripetal xylem

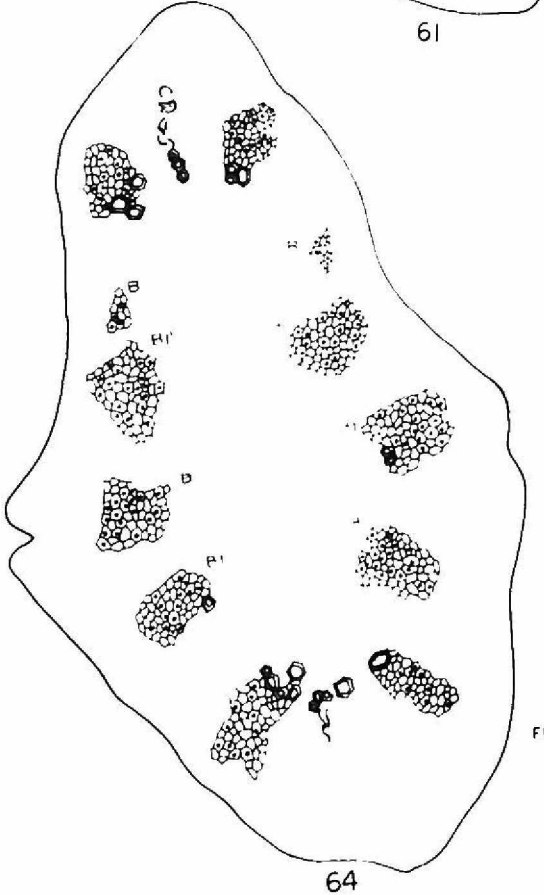












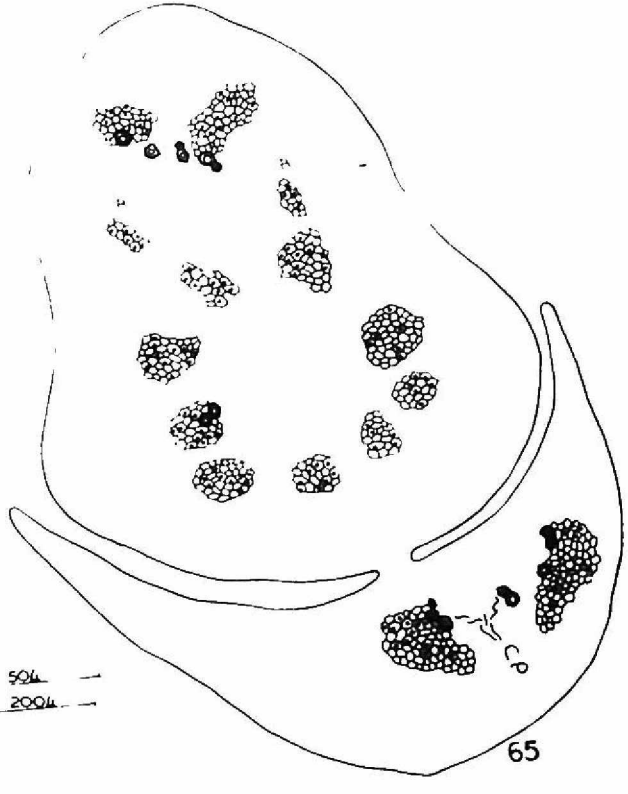


FIG 59 62 - 50μ
63 65 - 200μ

Figs. 66 - 76 Serial transections of 8, 12, 15 and 20 days old seedlings.

Figs. 66 and 67 Transection of 8 and 12 days old seedlings, showing buds in the axil of cotyledons.

Figs. 68 - 74 Series of transection of 15 days old seedlings showing formation of central bundles.

A, A1, B1, B2, C, D and P explained in the text.

Figs. 75 - 76 Transections, 20 days old seedling showing formation of intermediate bundles and the vascular supply to the axillay bud.

CB	Central bundle
IB	Intermediate bundle
LT	Leaf trace
BTR	Bud trace

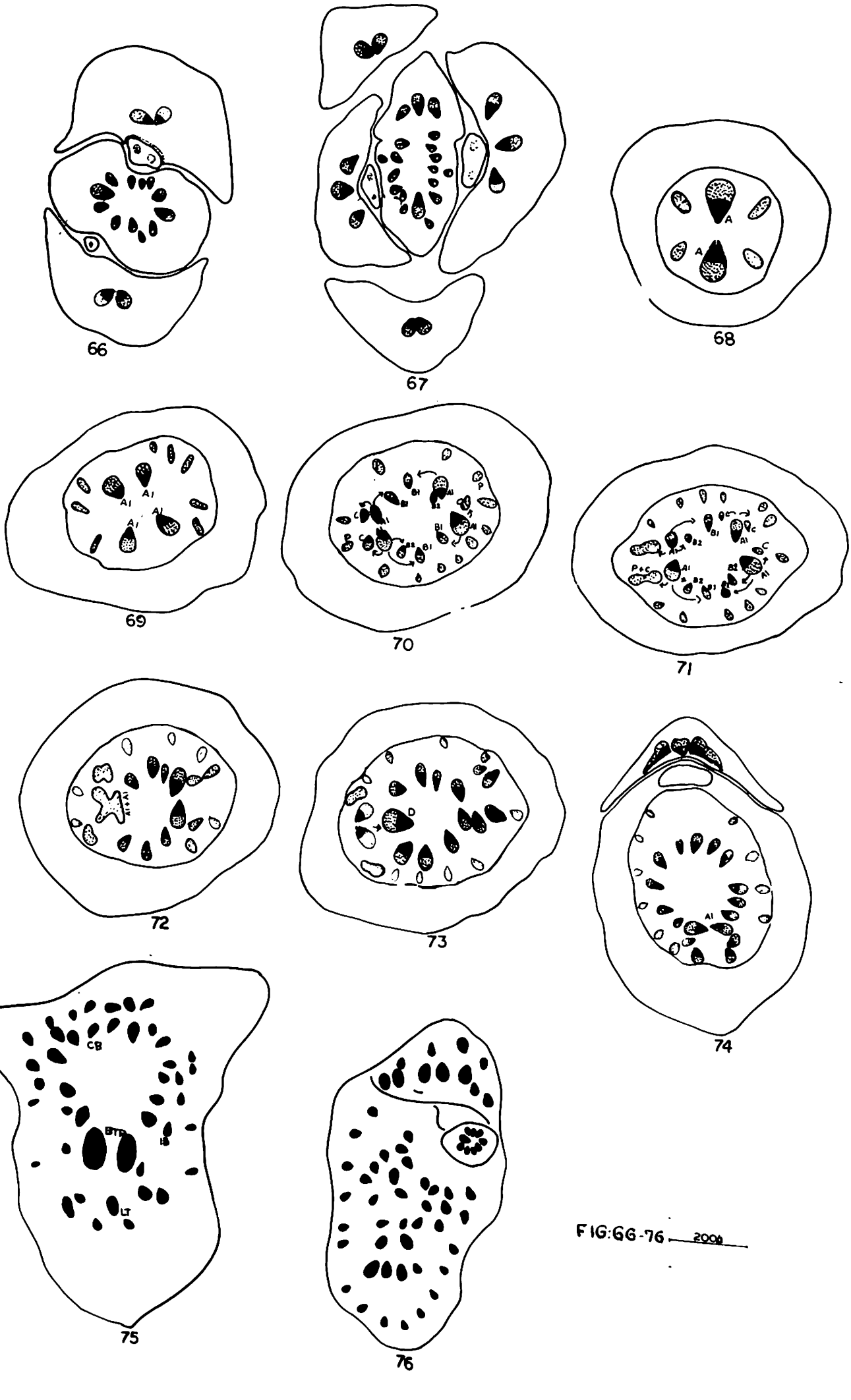
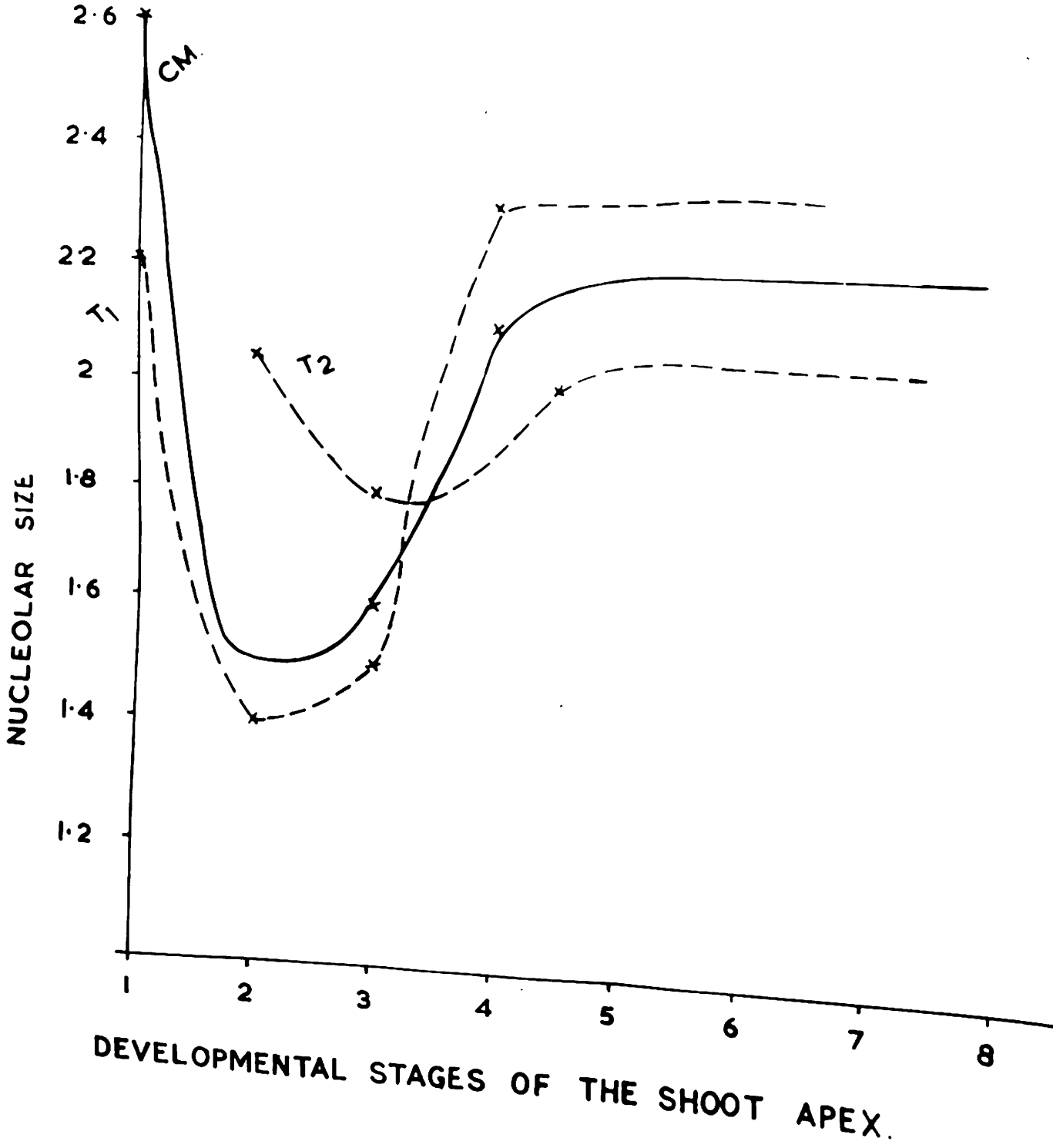


FIG:66-76 2004


2·6
2·4
2·2
2
1·8
1·6
1·4
1·2
CM
T1
T2
NUCLEOLAR SIZE
1
2
3
4
5
6
7
8
DEVELOPMENTAL STAGES OF THE SHOOT APEX.

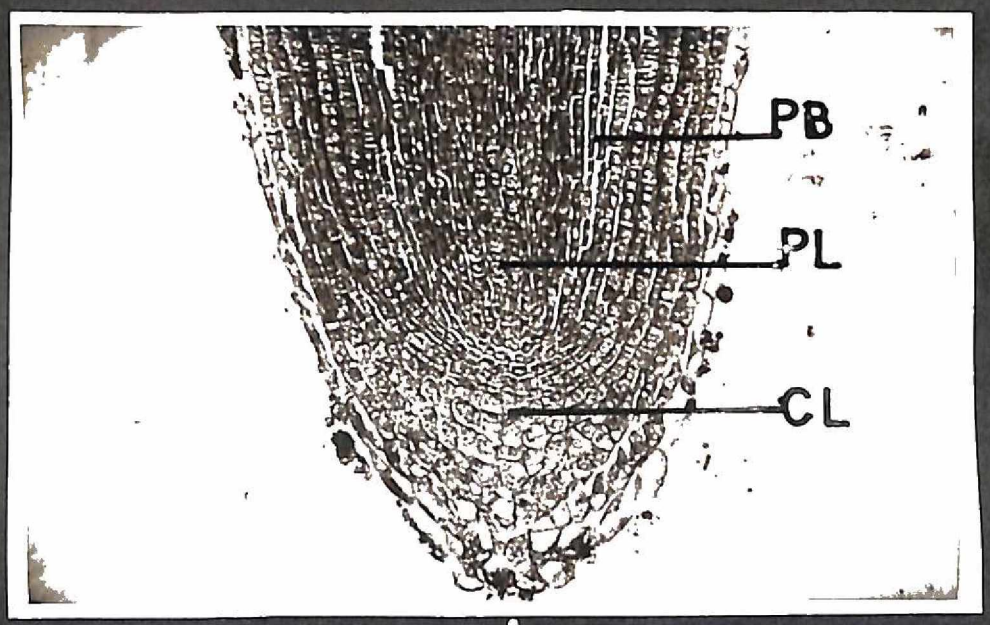
Photomicrograph. 1. L.S. Median of root apex showing plerome, periblem and developing columella.

PL = Plerome; PC = Periblem;
CL = Columella.

Photomicrograph 2. L.S. Median of root apex showing columellogen.

NOTE: The curved peripheral layers.
COG = Columellogen.

Photomicrograph. 3. L.S. Median of root apex showing well developed columella.



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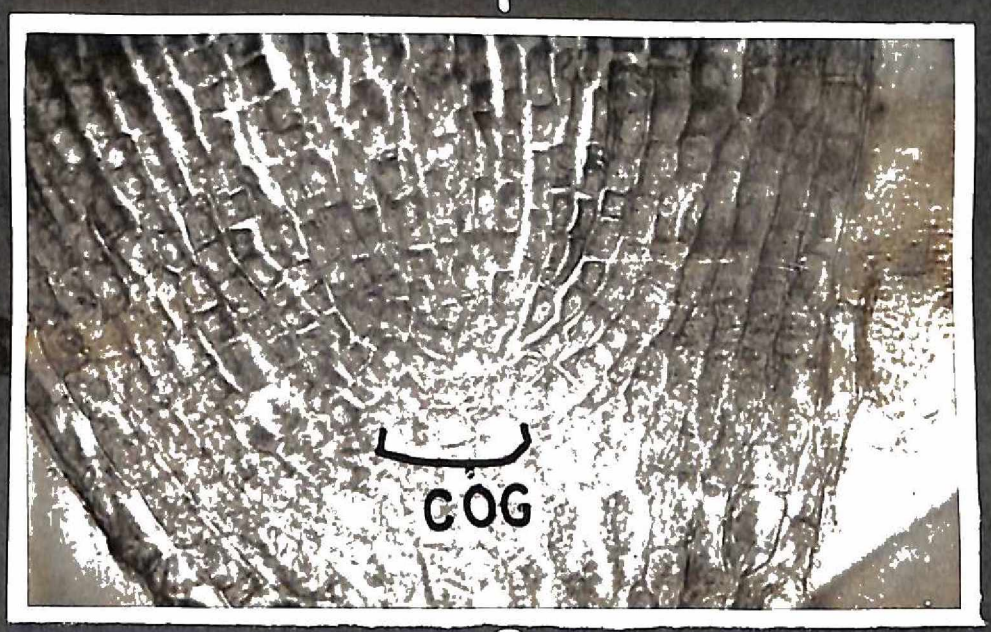


2

3

Photomicrograph. 7. L.S. Shoot apex showing the maximal phase of plastochron

Photomicrograph. 8. L.S. Leaf primordium

AI. = Apical initial

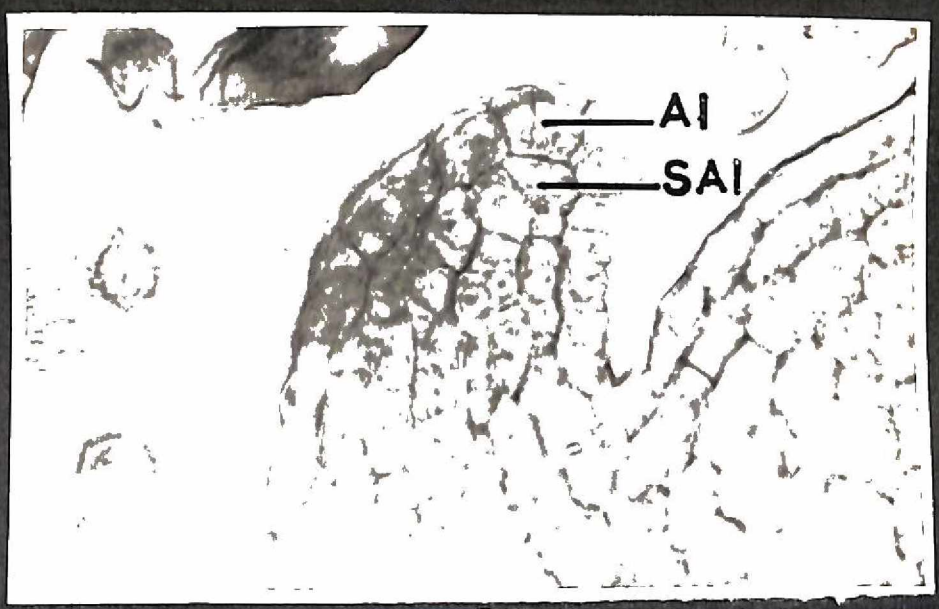
S AI = Sub-apical initial

Photomicrograph. 9. T.S. Leaf primordium showing marginal growth.

NOTE: The sub-marginal initials directly giving rise to the inner layers.

SMI = Sub-marginal initial.

7



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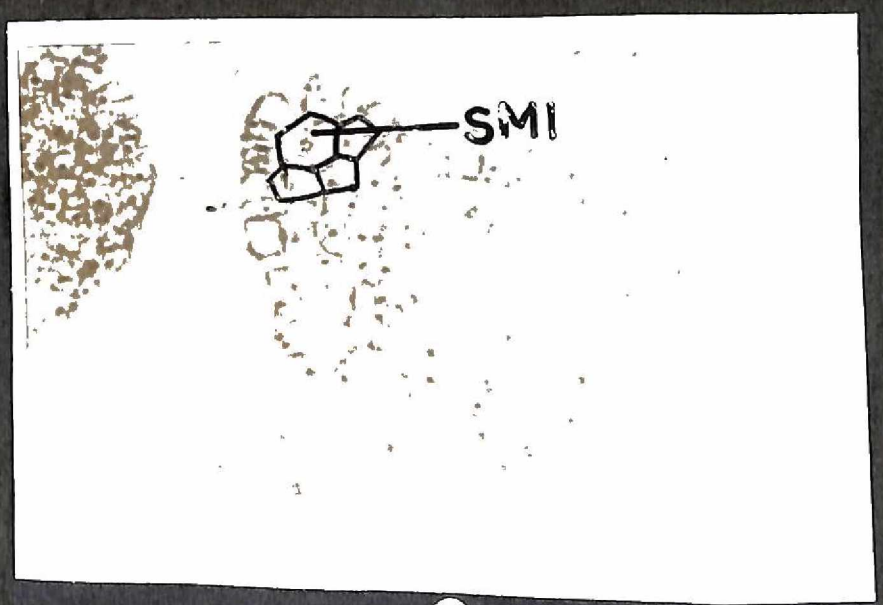


9

Photomicrograph. 10. L.S. of shoot apex showing the procambial differentiation towards the leaf primordium.

NOTE: The youngest leaf primordium is without any trace of procambium.

Photomicrograph. 11. Paradermal section of foliage leaf showing the multistranded secondaries and biseriate tertiaries.

NOTE: The bundle sheath all along the vascular strands.

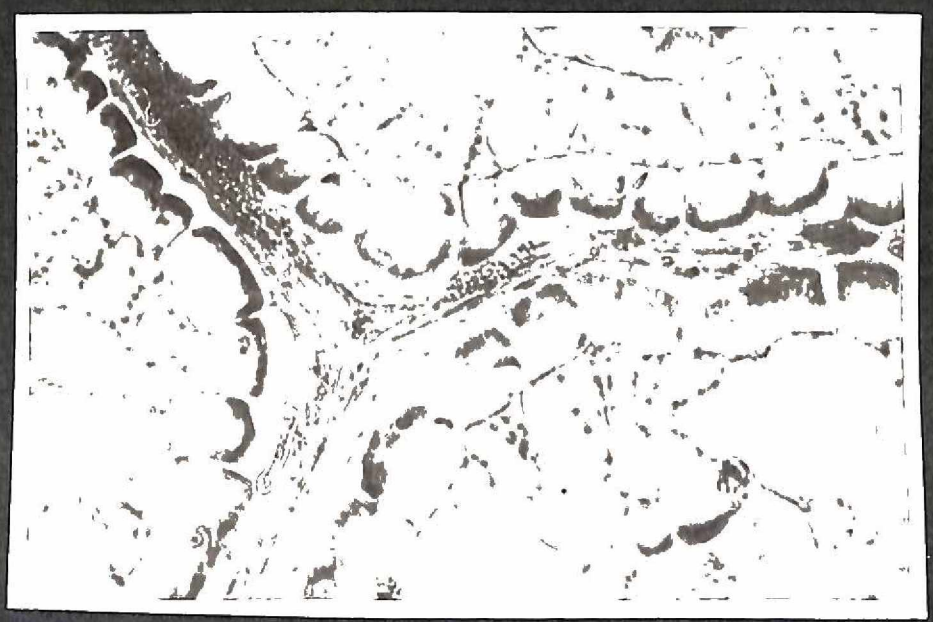
Photomicrograph. 12. L.S. showing the development of axillary bud.

NOTE: The acropetal differentiation of procambial strands towards the axillary bud.

AXM. = Axillary bud meristem

SZ. = Shell zone.

10



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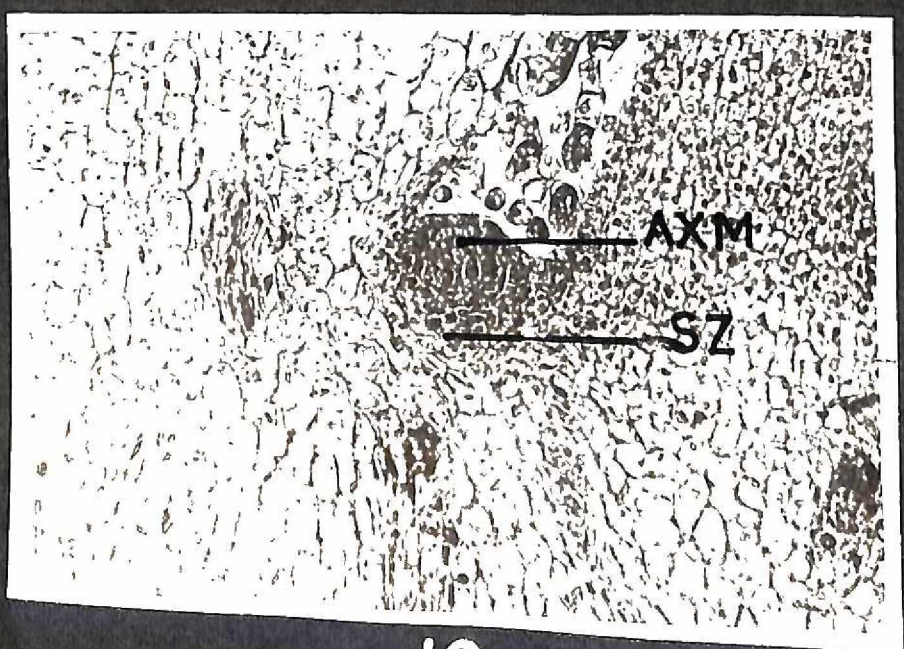


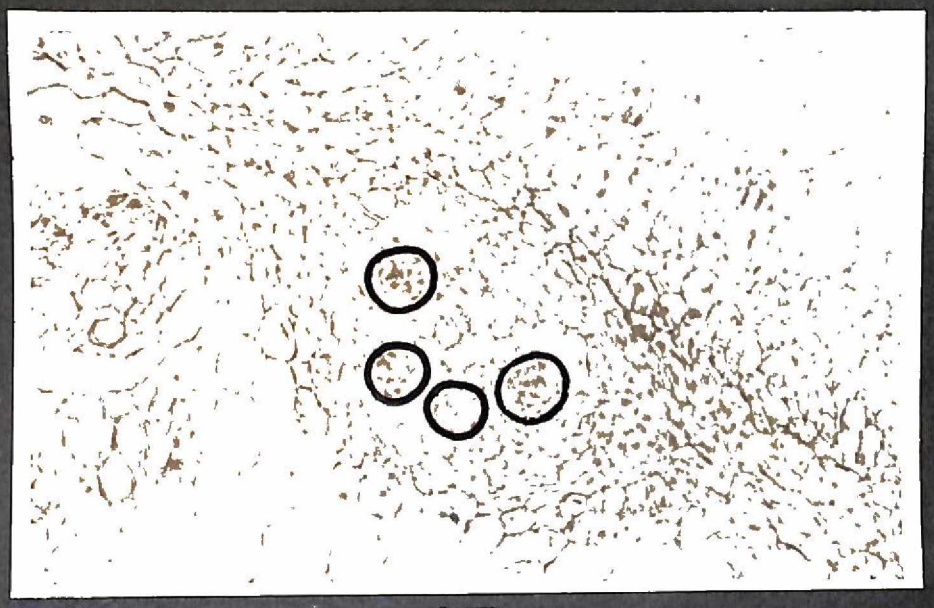
12

Photomicrograph. 13. T.S. showing the supply of procambial strands to the axillary bud.

Photomicrograph. 14. L.S. shoot apex showing the transition from vegetative to reproductive phase.

Photomicrograph. 15. L.S. Inflorescence apex in the early stage.

NOTE: The formation of axillary floral primordia.



13

14

Photomicrograph. 16. L.S. showing the accumulation of starch in the mature tissues of the inflorescence.

NOTE: The absence of starch grains in meristematically active regions.

Photomicrograph. 17. L.S. Inflorescence apex stained for DNA with Feulgen.

Photomicrograph. 18. L.S. Vegetative apex stained for basic protein with alkaline fast green at pH 8.

16

17

18

Photomicrograph. 25. L.S. Amphitropous ovule.

NOTE: The space between the integuments as well as between the nucallus and inner integument.

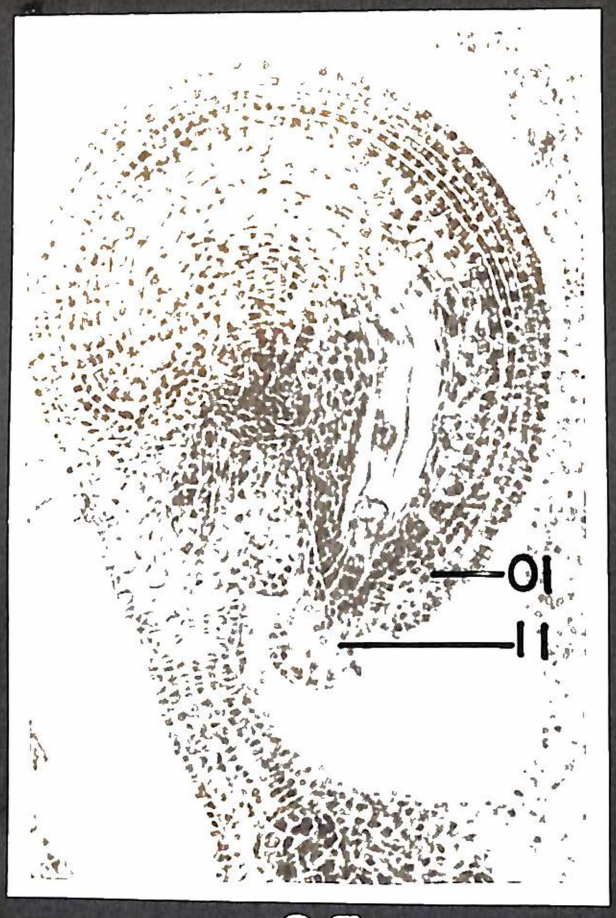
II = Inner integument

OI = Outer integument

Photomicrograph. 26. L.S. Heart shaped embryo.

CP = Cotyledonary primordium

S = Suspensor.



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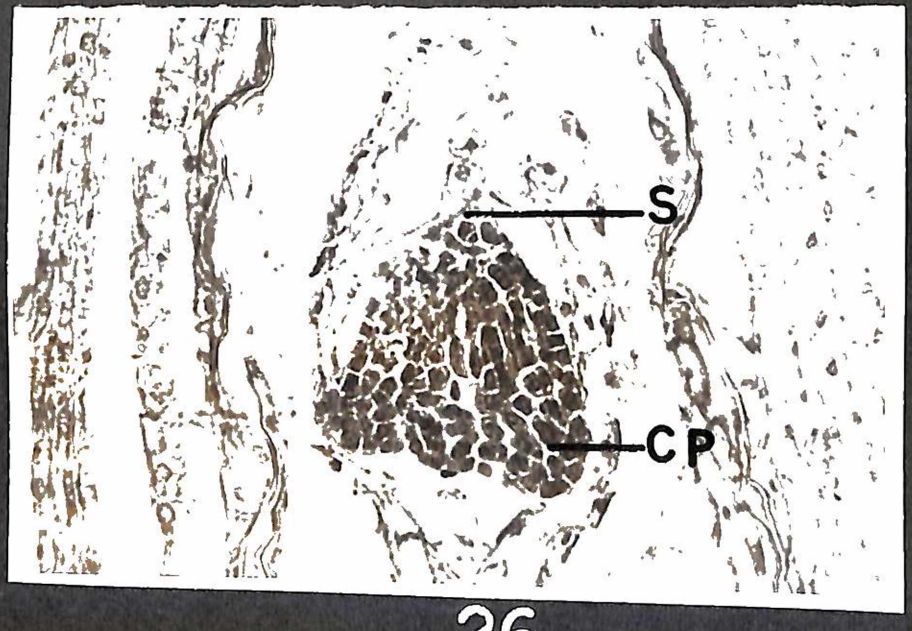


26

Photomicrograph. 27. L.S. Mature embryo showing shoot apex.

NOTE: The well developed procambium

PC = Procambium

Photomicrograph. 28. L.S. Embryonic root apex.

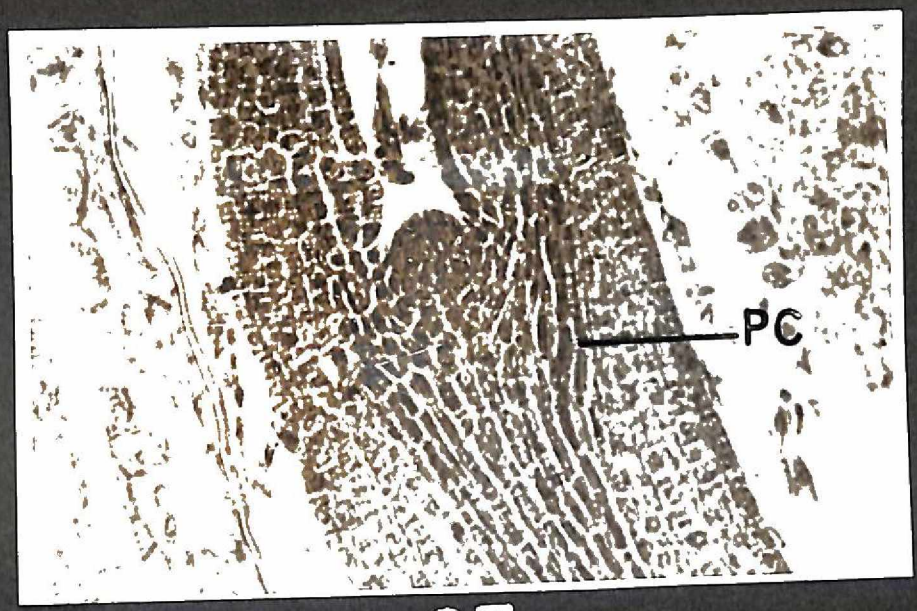
IZ. = Initial Zone.

Photomicrograph. 29. T.S. Stem of twenty days old seedling.

NOTE: The formation of peripheral bundles.

PC = Procambium

PB = Peripheral bundles



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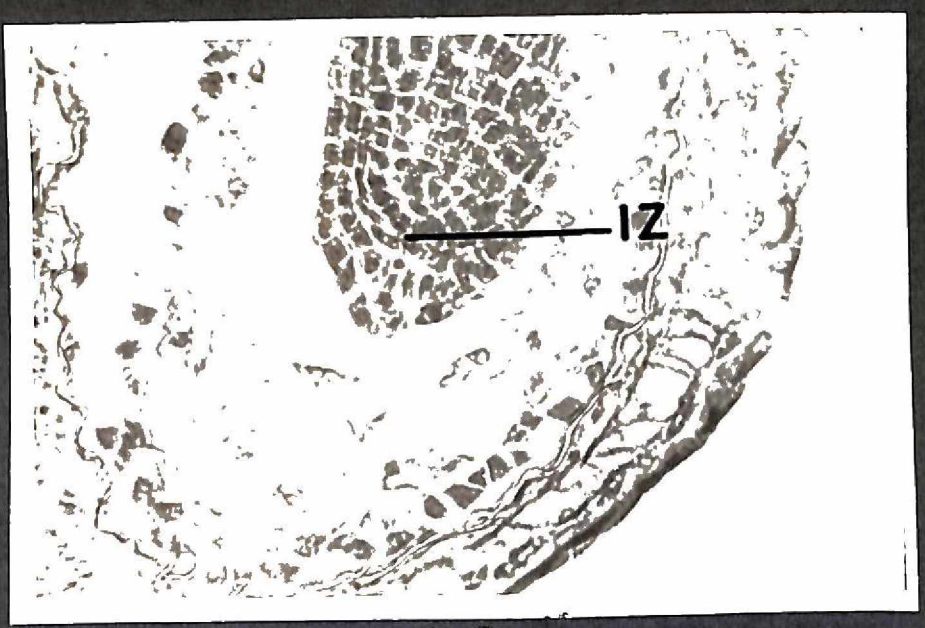

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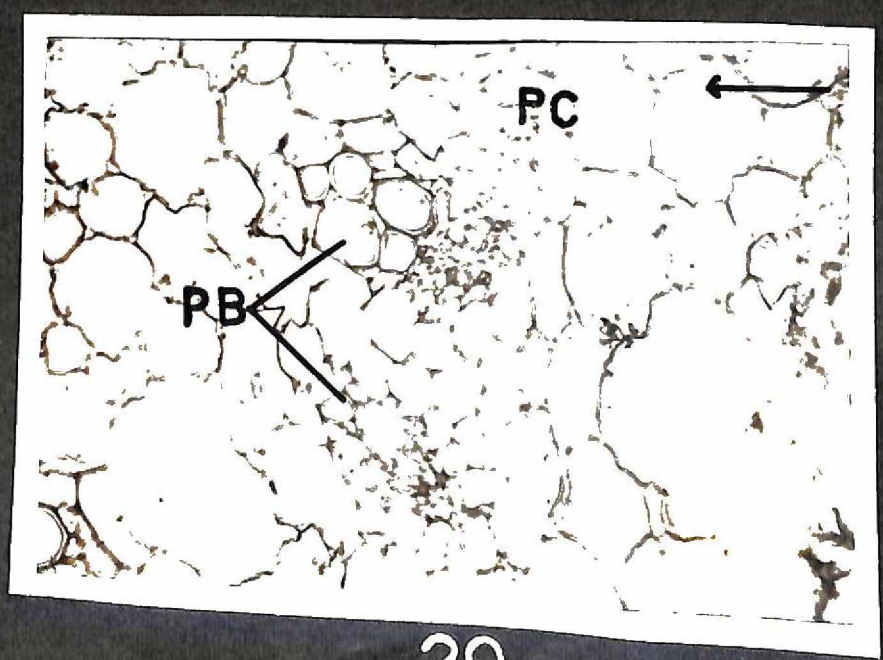
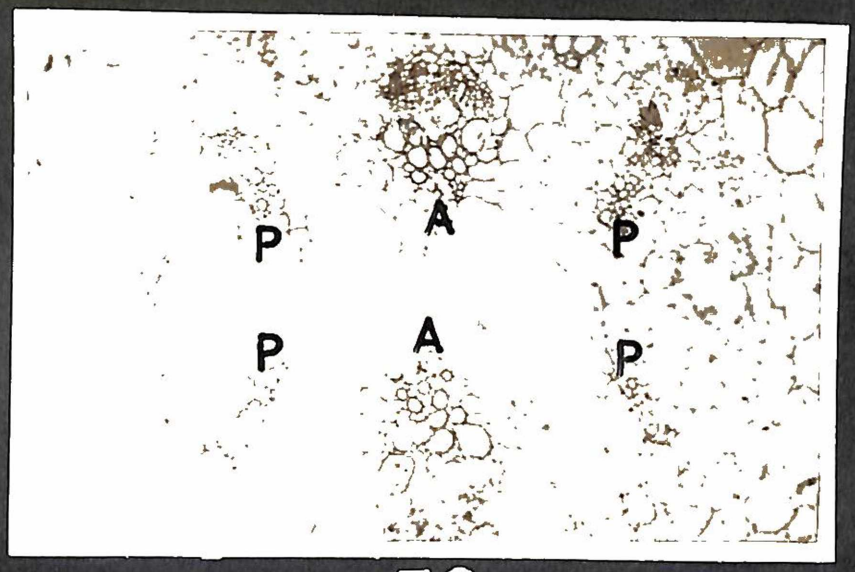


29

Photomicrograph. 30. T.S. Stem of 15 days old seedling showing two endarch bundles (A).

Photomicrograph. 31. T.S. Stem of 15 days old seedling showing four endarch bundles (A')

Photomicrograph. 32. T.S. Stem of 15 days old seedling showing the formation of central strands B1, B2 C, P, explained in the text.



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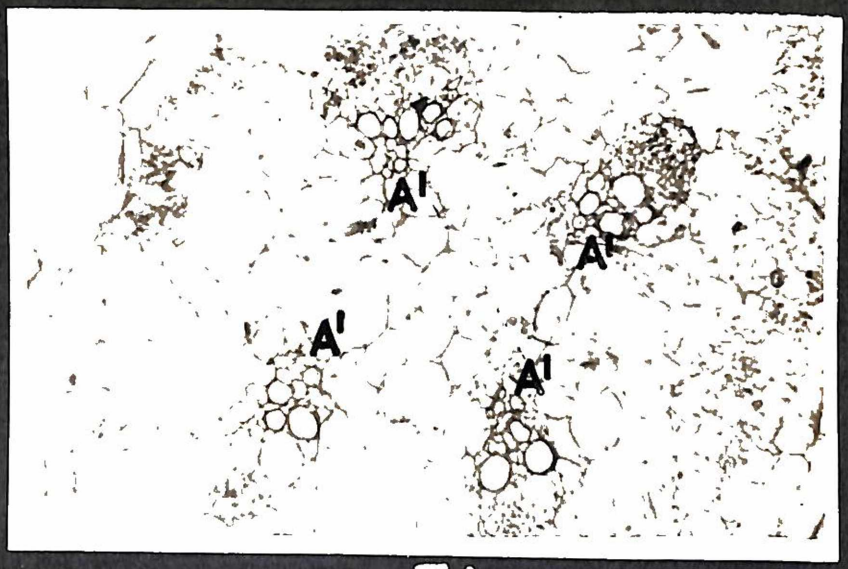

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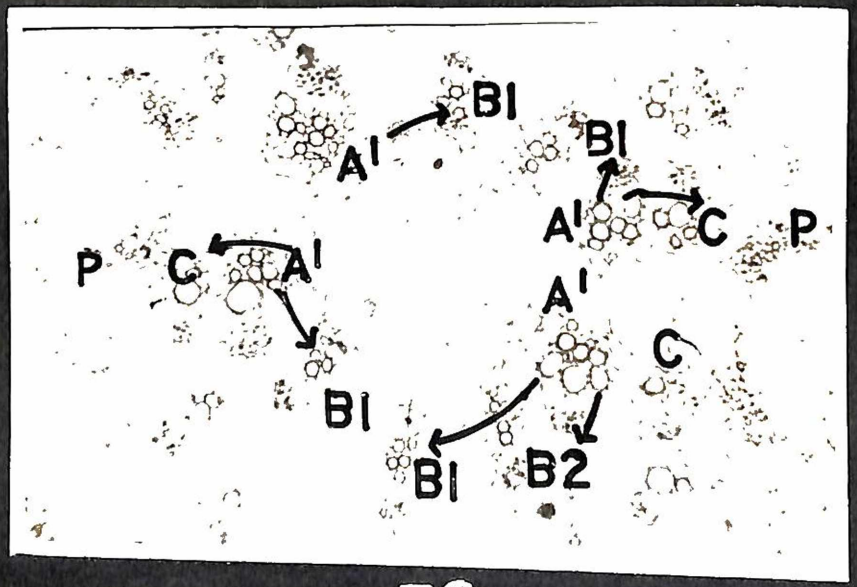


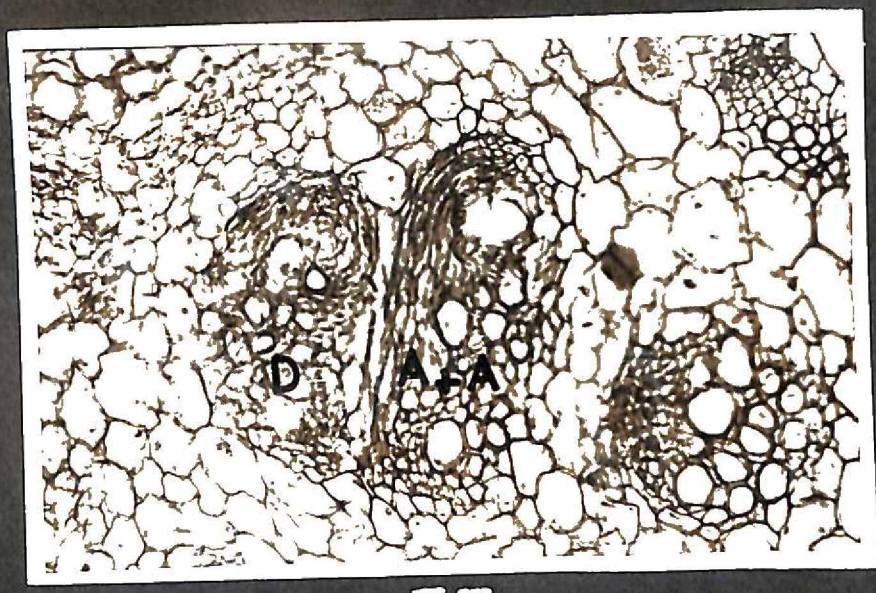
32

Photomicrograph. 33. T.S. Stem of 15 days old seedling showing the formation of vascular strand to the axillary bud.

A + A and D explained in the text.

Photomicrograph. 34. T.S. Nodal region showing the vascular supply to axillary bud and formation of intermediate strands

Photomicrograph. 35. T.S. of the leaf.



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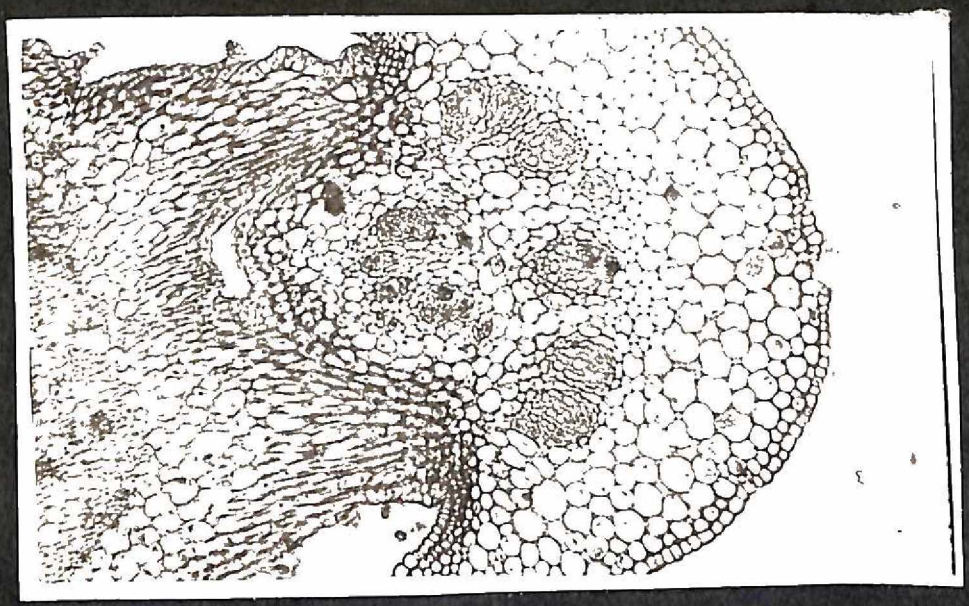

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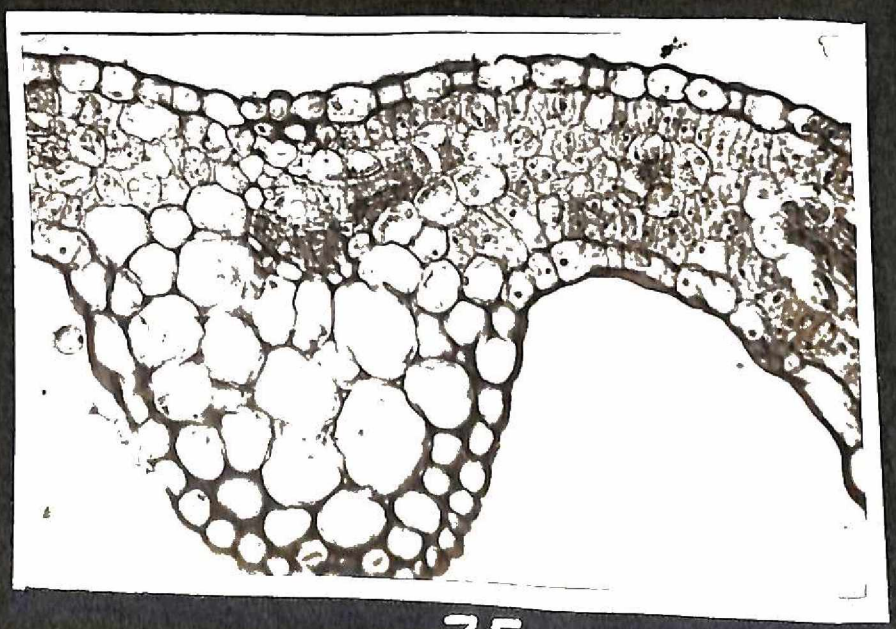
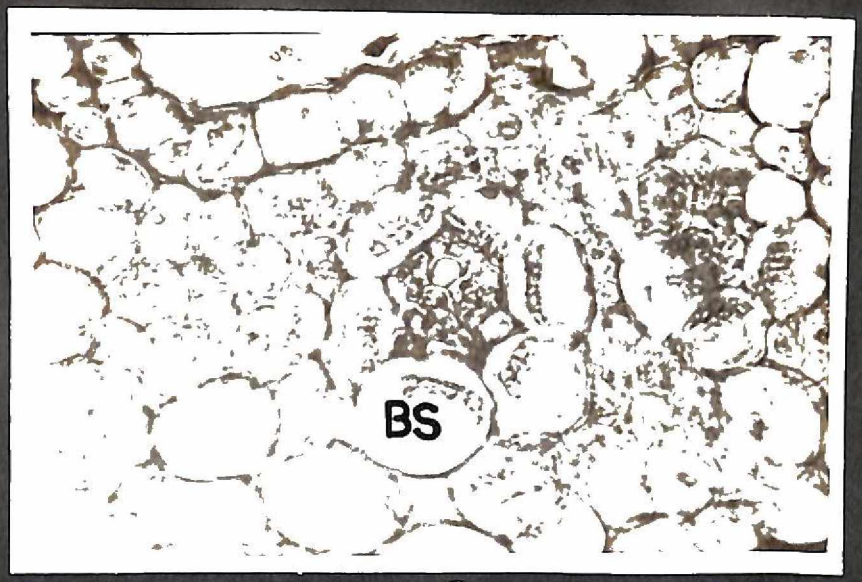


35

Photomicrograph. 36. T.S. of leaf showing well developed bundle sheath around the vascular bundle.

BS = Bundle sheath.

Photomicrograph. 37 and 38. Stages in trichome development.



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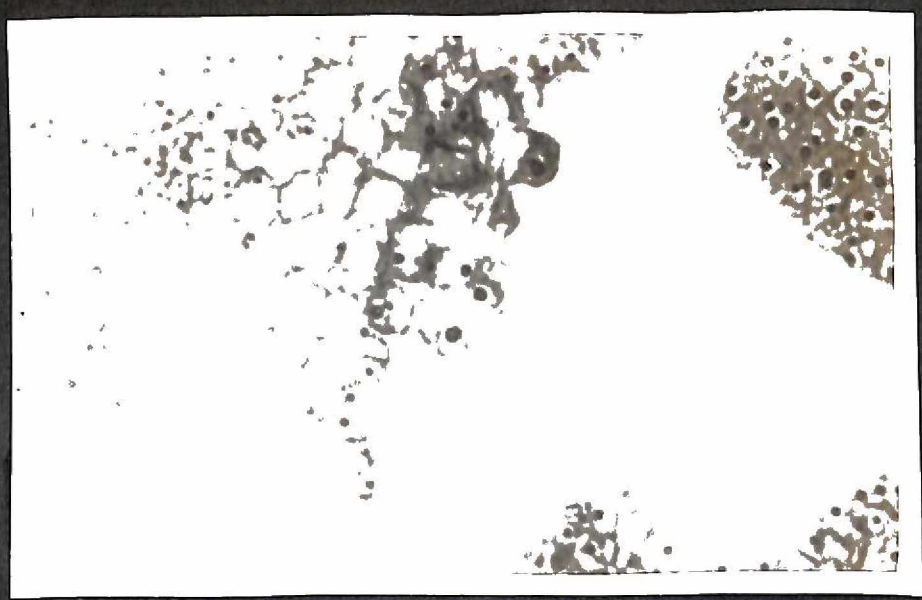


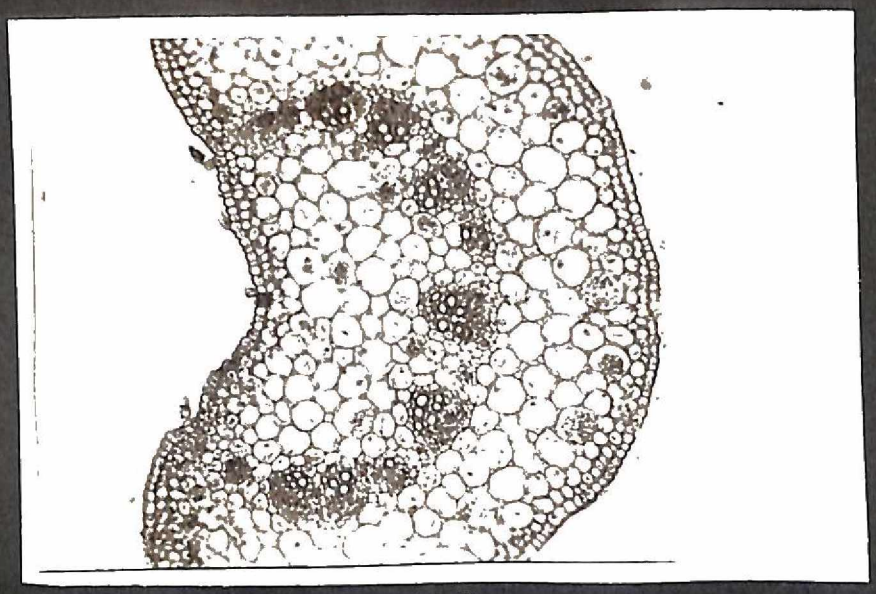
37

38

Photomicrograph. 39. T.S. of petiole at basal region.

Photomicrograph. 40. T.S. of petiole at middle region.

Photomicrograph. 41. T.S. of petiole at the upper region.



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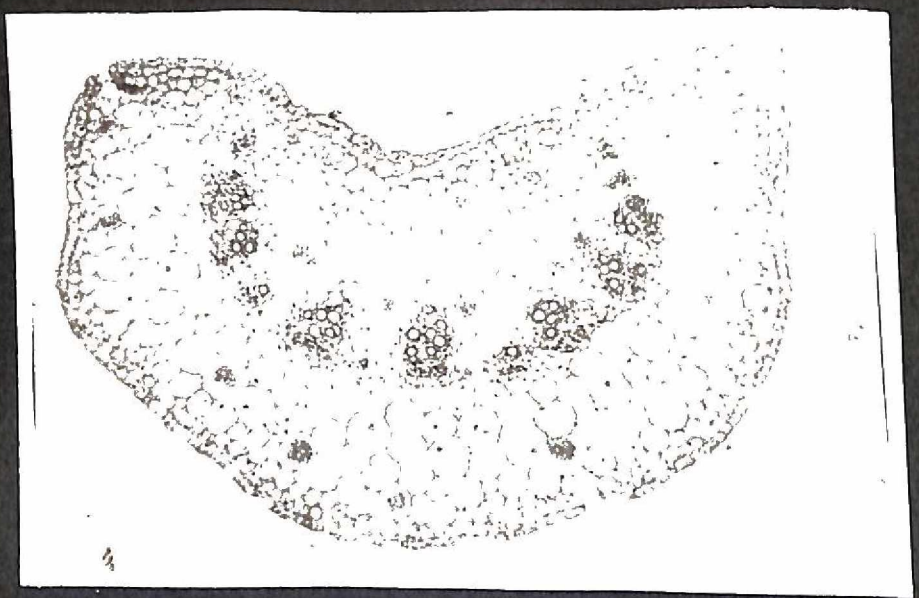

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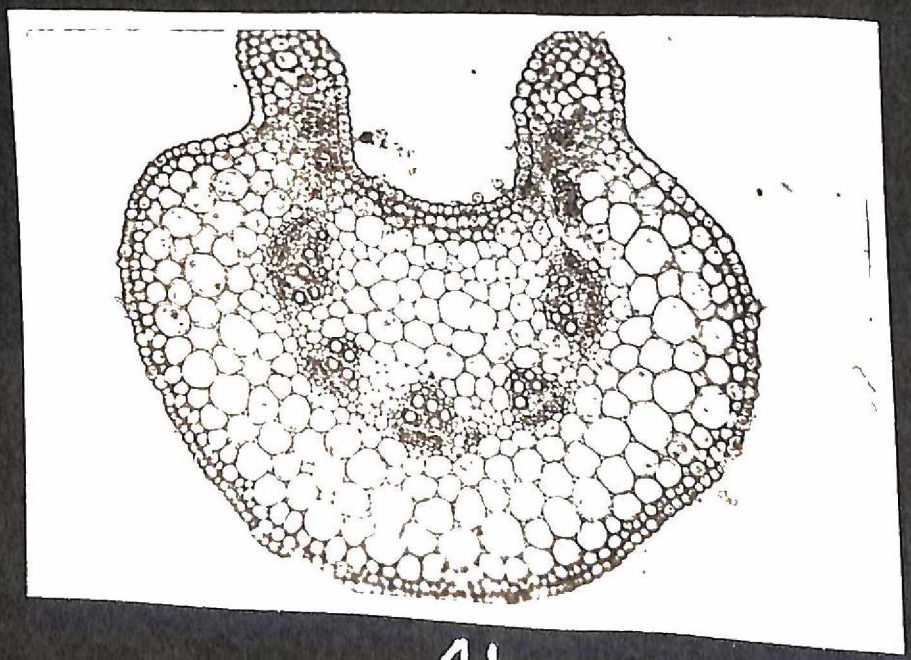


41

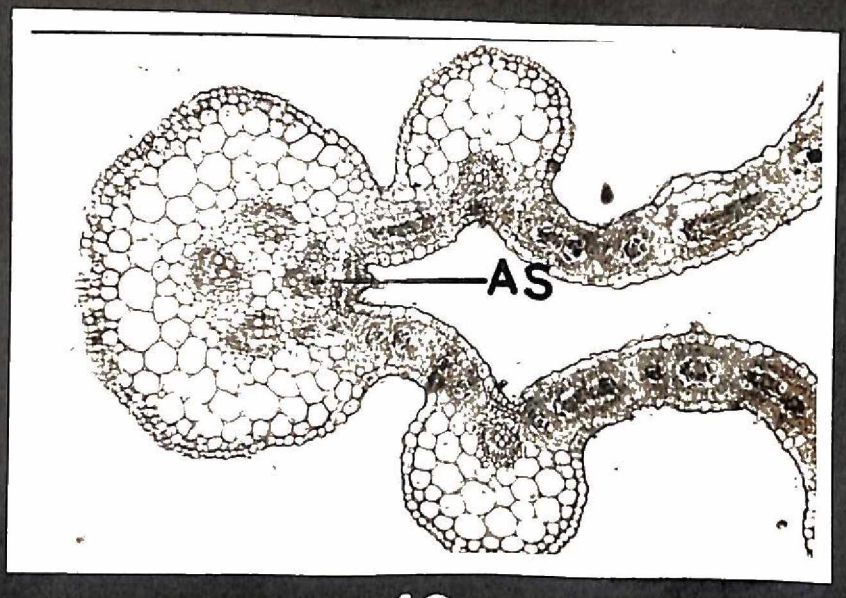
Photomicrograph. 42. T.S. of petiole at the upper petiolar region - approaching leaf lamina.

NOTE: The additional central strand.

AS = Additional central strand.

Photomicrograph. 43. Portion of cleared leaf showing the median, secondary and tertiary veins.

Photomicrograph. 44. Portion of cleared leaf showing vein endings in areoles.



42

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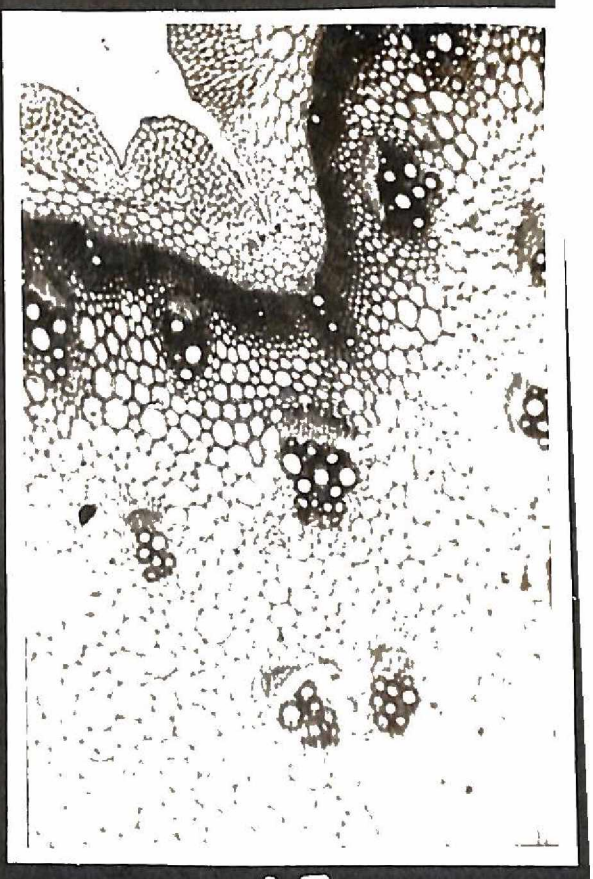
44

Photomicrograph. 45. T.S. Stem of 20 days old seedling showing the formation of peripheral bundles.

NOTE: Displaced peripheral bundles

Photomicrograph. 46. T.S. of stem showing the formation of phloem islands



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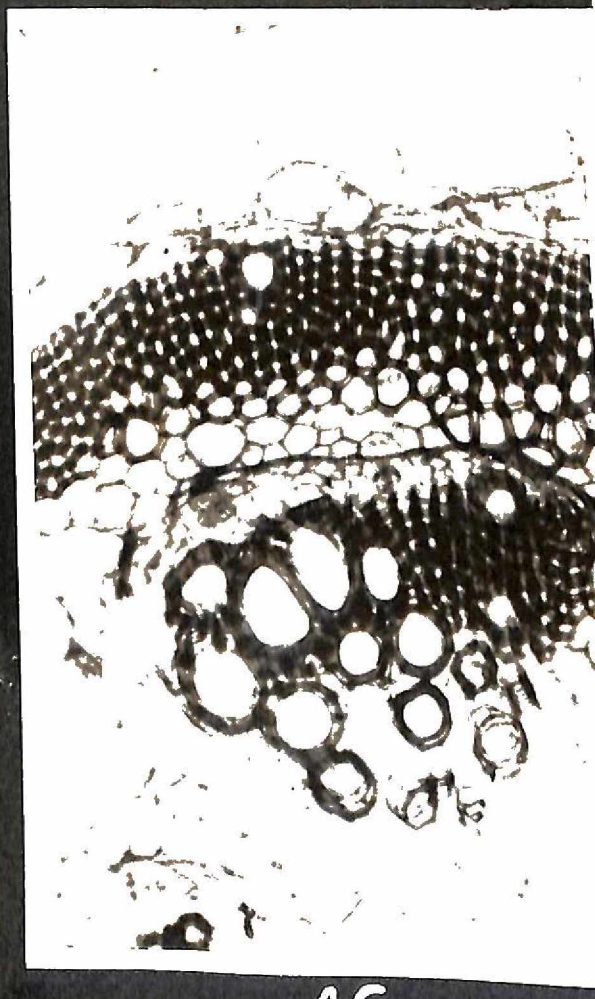
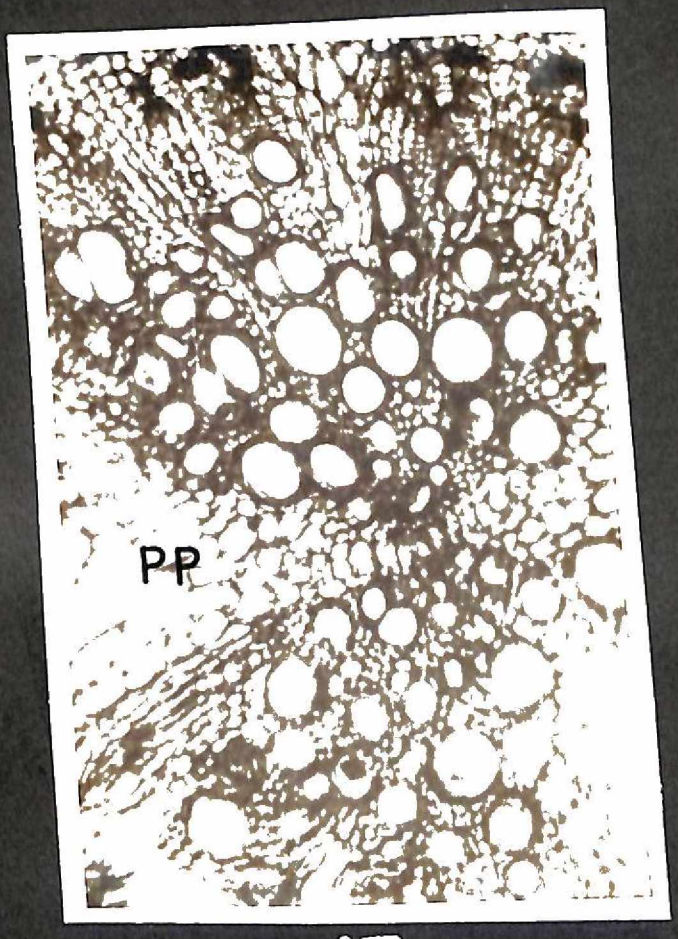


46

Photomicrograph. 47 and 48. T.S. of root showing anomalous secondary growth.

NOTE: The parenchyma patches opposite the protoxylem poles.



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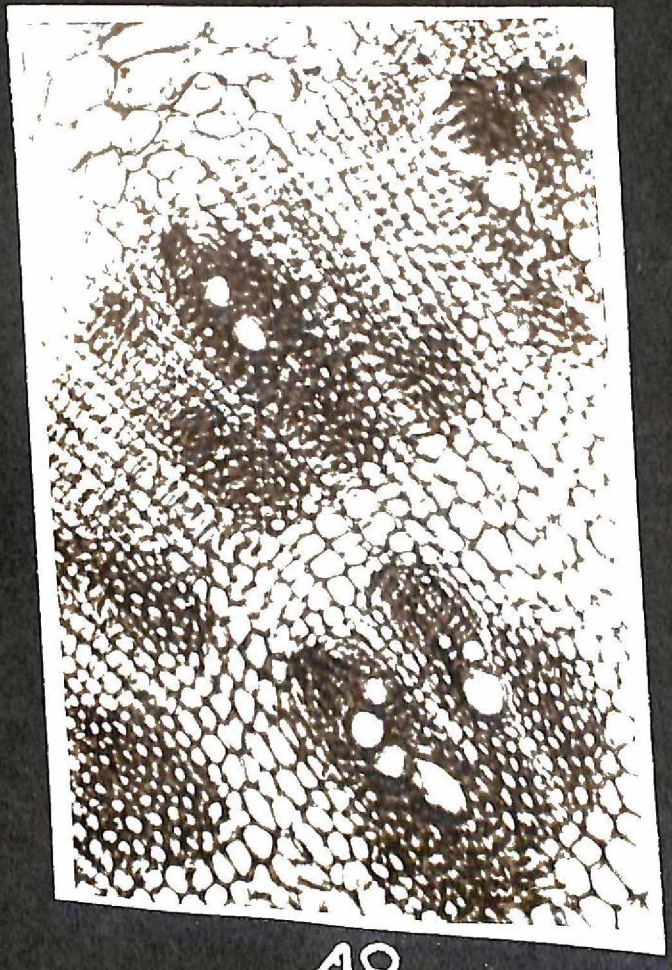

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