A STUDY OF ROOT APEX ORGANIZATION IN SOME MONOCOTYLEDONS

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(G.S.Nathawat)

C O N T E N T S

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INTRODUCTION

Science is like a river. It has its unostentatious beginnings, its quiet stretches as well as its rapids. Periods of fullness alternate with those of drought. Its progress is maintained by contributions from many investigators. Thus, fed by varied streams of thought, it gets deepened and widened by the gradual evolution of newer concepts. Other disciplines add to it, resulting ultimately in a large and comprehensive body of thought.

Foster and Gifford (1959) observe, "The science of plant morphology attempts by rigorous techniques and meticulous observations, to probe beneath the surface aspects of plants --- in short, to explore and compare those hidden aspects of form, structure and reproduction, which constitute the basis for the interpretation of similarities and differences among plants". The enquiring mind accepts this broad concept and strives towards its realisation. The importance of anatomical studies in this broad perspective cannot be overstressed.

All the organs of plants develop from apical meristems and so a study of these is of primary importance. Modern histological techniques and interpretations have proved that many early observations on apical meristems have only historical value and cannot be accepted as very reliable from the stand-point of descriptive anatomy.

Consequently, there has been a revival of interest in apical ontogeny. During the last two or three decades an enormous amount of work has been carried out on apical meristems and we have come closer to an understanding of how they originate and behave (cf. Gardner, 1945; Philipson, 1949; Gifford, 1954; Clowes, 1959b, 1961; Guttenberg, 1960, 1961). Although investigations on shoot apices are numerous (cf. Hanstein, 1868; Schmidt, 1924; Dermen, 1947; Guttenberg, 1960; Gifford, 1943, 1954; Foster, 1939a,b, 1940, 1941 a,b, 1949) those on root apices are comparatively less. Studies on the root apices of monocotyledons in particular seem to be few.

The pioneering investigations of Hofmeister (1850), Hanstein (1868) and Radlkofer (1875) established plant anatomy as a science and a discipline. After this, although a good deal of attention was paid to the study of the developmental aspects of stems, leaves and flowers, the root apex has been sadly neglected. Even in recent years there has been considerable activity in the study of cell lineages and growth in meristems of shoots but not of roots. Eames and MacDaniels (1947) point out that the root apex is in need of broad and critical study. Esau (1953) deplores the dearth of attention paid to root apices when compared to shoot apices. Foster (1949) has stated *inter alia* that investigations on a wide variety of plants should aid in clarifying the present confused state of terminology and interpretations with reference

to root apices. The need to undertake detailed investigations on the root apices of as many plants as possible with a view to study their structures and to arrive at comprehensive ideas on the subject have been felt by a team of workers in this laboratory and this is a part of an exhaustive investigation which is underway more.

In recent years Guttenberg and his students (Guttenberg, 1960, 1961; Guttenberg et al., 1954 a,b, 1955, 1957a) have reported that changes may occur in the structural configuration of the root apical initials. This interesting feature has yet to be confirmed by others and this has been one of the objects of the present study.

Chapter I

REVIEW OF THE LITERATURE

Wolff (1759) seems to be the first to have studied the origin and organization of the shoot and he is considered, the father of developmental plant anatomy. The investigations on the organization of the shoot apex of cryptogams by Nägeli (1845) about a century later led to the postulation of the apical cell theory which was supported by Hofmeister (1860).

Much of the work of the nineteenth century was centred upon the determination of the number of "apical cells" in apices and the origin of the tissues from them. Nicolai (1865), who was the pioneer in studying the root apex, found the growing point to be composed of a group of cells. Nageli and Leitgeb (1868) also made some investigations and observed an irregular meristem at the root apex of higher plants which they attempted to correlate with the apical cell theory, propounded earlier by Nägeli (1845). They stated that the root-let started in the early stages with a single cell, which later gives rise to an irregular meristem. This led to the recognition of the difference between the root apices of Phanerogams and those of Cryptogams. An exhaustive investigation on the development of lateral roots was undertaken by Van Tieghem and Douliot (1888).

The most important contribution of the nineteenth century is Hanstein's Histogen theory (1868) which superseded the apical cell theory. This was originally postulated as based on an exhaustive study of shoot apices and their organization. Nevertheless, this theory was often seen, and is still being applied to root apices with some modifications. Meanwhile, other ideas like that of the "tunica-corpus" concept of Schmidt (1924), the "Körper-kappe" concept of Schuepp (1917) and the "Mantle-core" concept of Popham and Chan (1950) developed for interpreting the organization of shoot apices.

While such ideas were developing about the organization of the shoot apices, only sporadic efforts were being made by some investigators to unravel the organization of the root apices. The latter half of the last century was a period when the root apices attracted the attention of a few investigators like Janczewski (1874), Treub (1876), Flahault (1878), Eriksson (1878) and Schwendener (1882). All of them tried to understand and classify the organization of root apices. Janczewski (1874) added a fourth histogen, the calyptrogen, as far as the roots are concerned, to the three already postulated by Hanstein (1868).

For nearly another two decades the root apex was not the object of any worthwhile attention. It was again investigated in the second decade of this century by Kroll (1912) and Haberlandt (1914). More recently, Schuepp (1917, 1926), Hayward (1938), Guttenberg (1940,

1941, 1947) and Guttenberg et al. (1955) and studied root apices and attempted to interpret their organization.

However, the fourth decade of this century showed a resurgence of interest in the study of root apices when a number of papers began to appear. Wagner (1939) took interest in the ontogeny of the root tip and cap of several plants and established the pattern of growth of cells by T-wall formation, revealing the diversity of structure involved. Goodwin and Stopka (1945) and Wojnowicz (1956) have contributed to this field by studying the growth and differentiation of the root tip of Phleum pretense L.

The interest in root apices seems to have gathered momentum from this time onwards as revealed by contributions from different parts of the world. Guttenberg (1941) postulated that there is a single "central" cell at the root tip for which further support is adduced by Clim (1943, 1947), and Schade and Guttenberg (1951) recalling the Nagelian hypothesis. Meyer (1940) and Krauss (1949) in their studies of the roots of the Bromeliaceous plants have also supported the apical cell theory. Brumfield (1943) proposed that there is a small group of three cells which behave like the apical cell of Nageli and the central cell of Guttenberg, which he designated as the "initial group". Reeve (1948) had studied the late embryogeny and histogenesis of Pisum and reported that no zonation on the basis of histogens

could be distinguished. Popham (1955) on the other hand, reported that there was a transversal meristem which is concerned with the production of the various tissues. Clowes (1950) after investigating the apex of the root tip of Fagus sylvatica and on the basis of surgical experiments (1953, 1954) hypothesised that the cytogenerative centre is a broad promeristem and that in the middle of this is a smaller group of cells, which he calls the minimal constructional centre. Further studies by Clowes (1956 a,b) on the distribution of nucleic acids and with labelled compounds (1958 a,b; 1959a) led him to the identification of a group of cells in a state of repose which he named as the 'quiescent centre'. Mulay et al. (1956, a,b) have studied the apical organization in the roots of some terrestrial orchids while Despande (1960, 1961) investigated that of a number of members of the Liliaceae and Amaryllidaceae. Sun (1957) studied on the apical meristem of the root of soya bean. Guttenberg et al. (1954,a,b,1955, 1957a,b) have investigated the root apical organization and its development in the embryonic stages of some monocotyledons and dicotyledons.

Another line of investigation on root apices is the effort at correlating and comparing the growth rates of the various regions of the root apex (Hejnowicz, 1959; Clowes, 1962). This promises to help in arriving at a better understanding of the relative growth rates of the various regions of the organ.

Very recently some papers have appeared from this laboratory on the root apical organization of monocotyledons. Pillai & Pillai (1960 a,b, 1961 a,b,c) and Pillai et al. (1961) described the organization of the root apex of some members of Musaceae, Cannaceae, Marantaceae, Zingiberaceae, Palmae and Xyridaceae. Pillai & Pillai (1960 a) observed that in the case of roots with a common group of initials, a ~~group of~~ a few cells at the centre of this group appears to be the site of histogenesis from a structural point of view. They have named it "central group". However, on the basis of the reaction to cytoplasmic stains and on the cytonuclear and nucleolus/nucleus ratios of cells, and on the frequency of mitoses, they also reported the occurrence of a quiescent centre in apices of mature roots, proximal to which is the real histogenetic region, the "meristematic region". They have attempted to show the characteristics of the cells of the quiescent centre and meristematic zone in the roots by performing some surgical experiments (Pillai & Sachdeva, 1960; Pillai & Pillai 1961 d).

In the meantime, reports have appeared (Guttenberg, 1960; Guttenberg et al., 1954 a,b, 1956, 1957 a,b) which show that there is no fixity in the structural organization of root apical meristems, at least in some plants. They report two types of structural organization. One is the "closed" type with discrete initials and the other is the "open" one having a common group of initials.

Guttenberg (1960) describes that an organization with discrete initials, i.e. the closed type, may change into one without them, i.e. the open type, during the course of development. This indicates that we have to reorientate our ideas if this is substantiated.

Recent reviews have brought into a comprehensive shape, the literature on apical meristems of seed-bearing plants in general, and that on root apical meristems in particular (Guttenberg, 1960, 1961; Clowes, 1961; Romberger, 1963; Newman, 1965).

Chapter II

MATERIAL, METHODS AND TECHNIQUES

The root apical organization of the following species has been investigated : -

Blyxa auberti Rich. Syn. B. ceylanica Hook.f.	Hydrocharitaceae	from Kerala
Hydrilla verticillata (L.)Royle	-do-	Jaipur
Nechamandra alternifolia (Roxb.) Thw	-do-	Annamalainagar
Ottelia alismoides Pers.	-do-	-do-
Vallisneria spiralis Linn.	-do-	-do-
Acorus calamus Linn.	Araceae	Dehradun
Alocasia indica Schott	-do-	Jaipur
Colocasia esculenta (L.) Schott	-do-	Kerala
Pothos scandens Linn.	-do-	Jaipur
Typhonium trilobatum Schott	-do-	Kerala
Caladium sp.	-do-	Jaipur
Dieffenbachia sp.	-do-	Jaipur
Cyperus diffusus Vahl	Cyperaceae	Jaipur
Frimbristylis dichotoma (L.)Vahl	-do-	Dehradun
Scirpus grossus Linn.	-do-	Dehradun
Tinantia fugax Scheidw.	Commelinaceae	Mussorie
Canna humilis Bouche	Cannaceae	Argentina
Calthea bella Rogel.	Marantaceae	Lucknow
Thalia geniculata Linn.	-do-	Argentiana
Canna glauca Linn.	Cannaceae	Argentina
Ensete superba (Roxb.) Cheesm.	Musaceae	Kerala

Strelitzia reginae Banks	Musaceae	Argentina
Typha angustata Bory & Chaub.	Typaceae	Jaipur
Monochoria vaginalis (Burm.f.) Presl.	-do-	Annamalainagar
Najas minor Allione	Najadaceae	-do-
Alisma plantago L.	Alismataceae	-do-
Aponogeton monostachyon L.F. Syn.A.natans (L) Engl.& Krau.	Aponogetonaceae	-do-
Potamogeton lucens L.	Potamogetonaceae	Jaipur & Dehradun
Cautleya lutea Royle	Zingiberaceae	Dehradun
Phoenix humilis Royle	Palmae	Kerala
Paspalum vaginatum Swartz.	Gramineae	Dehradun

The root tips were fixed on the spot in F.A.A.; Randolph's modified Navaschin's fluid (CRAF) was also used as a killing and fixing agent. The fixed materials were later preserved in 70% alcohol, till required for processing. The materials were washed, four to five times and each time for 15 to 20 minutes in 70% alcohol. They were dehydrated with alcohol, cleared in xylol, and embedded in paraffin wax.

Softening was necessary in some cases to secure good sections. For this, the embedded materials were trimmed and soaked in water for one to four weeks - ~~the duration~~ depending on the hardness of the material.

Serial longisections and transections were cut at 5 to 8 micron thickness on a Spencer's or Reichert's rotary microtome. Haupt's adhesive (Johanson, 1940) was

used as an adhesive for affixing the paraffin ribbons to the slides.

Haidenhain's iron-alum haematoxylin (with 7.5% glacial acetic acid added to the haematoxylin for hastening maturity) destained with saturated picric acid solution; safranin and fast green; tannic acid-iron chloride-safranin (Foster, 1934) and Northen's variation of Foster's method (Johansen, 1940) were used for staining. The last schedule proved to be the most satisfactory as the cell walls also of the meristematic cells were nicely stained. This helped in obtaining good photomicrographs.

The tannic acid and iron chloride used were 2% and 3% respectively and were added to the 50% alcohol. Fifteen minutes' staining each in tannic acid, and iron chloride was adequate enough. After this the slides were stained for ½ to 1 hour in safranin. The safranin was prepared according to Johansen (1940), by dissolving 4 gm of the dye in 200 cc. of methyl cellosolve to which 100 cc each of 95% alcohol and distilled water were added, followed by 4 gm of sodium acetate and 8 cc of formalin. Counter-staining with 0.5% light green in 100% alcohol helped to give sharp and brilliant contrast. The meristematic cell walls were stained black, cytoplasm bluish green, nuclei, nucleoli and chromosomes red.

Slides were cleared in xylol and mounted in Canada balsam. Drawings were made with the aid of a camera lucida. Photomicrographs were taken using a Zeiss Photomicroscope.

Chapter III

TERMINOLOGY

Hanstein (1868) studied the shoot meristems and put forward the well known "histogen theory". He reported the presence of well-marked layers of cells and distinguished three regions of histogens, each of which he believed gave rise to a particular tissue or tissues of the stem. The Dermatogen, the outer-most layer, is single-layered and produces the epidermis. This is followed by the several-layered thick periblem which gives rise to the cortex. The innermost region - the plerome forms the vascular cylinder and the pith.

Such a differentiation of the primordial meristem is quite evident in the shoot apex of most plants.

A study of the literature shows that from the early days, the histogen terminology has been used as such or after augmenting it with new terms or combinations for interpreting apical organization (Schacht, 1853; Strasburger, 1872, 1879; Buchholz & Old, 1933; Schopf, 1943). Clowes (1959, 1961) follows the histogen terminology. He states, however, that in work on shoot apices the histogen theory is now of the historical interest only. Nevertheless, it retains some usefulness in work on root apices (Clowes, 1961). Guttenberg (1940, 1941, 1960, 1961) has also used the histogen terminology in interpreting his observations

and reviewing the literature on apical meristems in angiosperms and gymnosperms.

There is now ample evidence to show that there is no constant relation between the histogens and the structures formed by them which may be valid for all plants. Some of this evidence comes from direct observations as in Schoute's (1903) studies on the origin of the vascular cylinder and Some evidence is derived from the structure of periclinal chimeras. Evidence from these sources shows that a particular tissue may arise from a meristematic layer in one species and from a different histogen in another species.

In many roots the dermatogen and periblem have a common genetic origin and hence can in no sense be regarded as two separate histogenetic layers. Secondly, the concept of histogens involves the assignment of exact destinies to regions of the meristems from their very origin which is not always the case.

Haberlandt's (1914) topographic division recognises three primary meristems which he named as the "protoderm", the "procambium" and the "ground meristem".

In view of the variations in the usage of the terms used by different authors for describing the structure of the root apices, it is desirable to clearly state the terminology used in the present study. The following terminology is being used :-

Promeristem :

This term is used in the present study in the same sense in which it is used by Clowes (1950), "The promeristem consists of the initials of all the histogens together and can be considered as comparable to the apical cell of some of the pteridophytes. It is that group of cells at the apex from which all future cells are derived..". Although for purposes of description the promeristem is treated as a discrete unit, its boundaries are considered to be vague and changeable. Subsequent to the postulation of the quiescent centre in roots, Clowes (1961) slightly changed his ideas regarding the promeristem, as follows : "the promeristem is considered as the layer of cells on the surface of the quiescent centre but fluctuating in position" (p.152).

Kaspligil (1954) describes the promeristem as the "central region" or the "initial zone of the root tip which produces other histogens of the apical meristems". Esau (1960) defines promeristem as "the initiating cells and their most recent derivatives".

The Protoderm-Periblem Complex :

This term is used for the initiating region present between the calyptra and the stele or the central cylinder. This is usually a single tier of cells. The cells in the centre of the tier divide anticlinally. After a few such divisions the outer most daughter cells continue to divide only anticlinally whereas the inner ones may exhibit

further T-divisions. Thus, the epidermis, hypodermis, cortex and endodermis arise from this tier.

Van Tieghem and Douliot (1888) named these initials as the epistele, while Schade and Guttenberg (1951) and Clowes (1954) refer it as the "Periblem-Dermatogen complex", and Kaapligil (1954) calls it the "Protoderm-Periblem complex".

The Protoderm :

The term "Protoderm" is being used in the original sense (Haberlandt, 1914) to designate the surface meristem which will give rise to the epidermis only, or to the epidermal as well as the subepidermal layers. It becomes distinct some distance from the promeristem because of its common origin with the cortex. According to Haberlandt (1914) dermatogen and protoderm are not synonymous terms. Protoderm refers to the outermost layer of the apical meristem and may give rise to epidermis only, or to the epidermal plus subepidermal layers, whereas the dermatogen has its own initials and generates only the epidermis. According to this, therefore, the protoderm is a term which comprehends something more than the dermatogen. Schade and Guttenberg (1951) call the dermatogen formed from the periblem as the "pseudo-dermatogen". Guttenberg (1960) however, calls it as the "secondary dermatogen".

The Stele :

As conceived by Van Tieghem (1875) it is a morphological unit comprising the vascular system and

the associated ground tissue (pericycle, interfascicular regions and pith). It is equivalent to the "central cylinder" of Esau (1960); "procambium" of Haberlandt (1914) and "plerome" of Hanstein (1868). The expression has been used in the same sense as used by Van Tieghem and Douliot (1886).

The Columella :

It is the cylindrical portion in the middle of the root cap and consists of vertical rows of cells which may extend to the tip of the cap, or may be overarched by the cap flanks. Its cells show only transverse divisions. Holle (1876) and Eriksson (1878) called it the "Saule" and "Kolonne" respectively. Schüepp (1926) also calls it the "Saule"; Zirkle (1932) calls it the "core". Neumann (1939) and Guttenberg (1941) call it the "kolumella". Johansen (1941) proposed a new term, the "stalace" for this region. Recent investigators like Schopf (1943), Allen (1947 a,b), Spurr (1949), Kasapligil (1954), Pillai & Pillai (1960 a,b, 1961 a,b,c) and others have recognized a columella in the root cap.

The Cap Flanks :

It is the peripheral part of the root cap which shows kappe type of divisions i.e. the tangential division of a single row of cells to form two rows which are towards the centre of the root (Schüepp, 1917). The maturing outer cells of the flanks degenerate and are compensated by the cap initials on the inner side. This

zone is closely applied to the protoderm due to the mechanical pressure exerted by the growing root tip, while in free-floating or aquatic plants it may be free from the latter, as is the case of Eichhornia, Lemna etc. Such a condition is referred to, as the peripheral region by Spurr (1949), Kanapligil (1954), and Pillai & Pillai (1960 a,b, 1961 a,b,c). In the present study the columella is not distinct upto the tip of the root cap in most of the cases and as such calling it as peripheral zone does not seem advisable. The expression cap-flanks is being used for designating the topographical region and does not refer to the mode of its origin.

The Korper pattern of division :

This expression is used here in its original sense, as put forward by Schüepp (1917, 1926). Korper pattern is formed when a single row of cells dividesmore actively into two rows in a tangential plane, away from the cytogenerative centre, increasing the number of cell rows in a radial plane. Wagner (1939) has related the patterns of cell rows to cell-complexes, i.e. groups of cells of relatively recent origin. The Korper complex is derived from a single initial cell by the formation of T-walls. The first division of the initial is transversely oriented, followed by a longitudinal division of the daughter cell which continues to be in the position of the initial, relative to the rest of the meristem. This

pattern is repeated in the Korper complex. In this case the capital of the T is directed towards the initials as it is the proximal daughter cells of the initials which divide longitudinally and not the initials themselves (Plate I).

The Kappe pattern of division :

This expression has also been used in its original sense as used by Schüepp (1917, 1926). In this pattern the tangential division of a single row of cells to form two rows is towards the centre of the root. Here also cell complexes are formed by T-divisions with one important difference that the capital of the T is pointing toward the flanks, away from the root tip. Here the orientation of the T is opposed to that of the Korper complex or pattern.

The T-wall pattern looks more like a Y pattern in the mature cell-groups. When newly formed, however, it appears as T and so it is designated by this letter. The Korper and Kappe are not histogens and histologically their boundaries meet in different histological regions of the roots depending on the species.

Proximal :

The side towards the root body is referred to as the proximal side.

Distal :

The side towards the root tip is referred to as the distal side.

Chapter IV

OBSERVATIONS

Type I - Discrete initials for cap and stele, the cortex and protoderm arising from the common initials - the protoderm-periblem complex.

This structural configuration is exhibited by the root apices of :-

Vallisneria spiralis Linn., Blyxa ceylanica Hook.f., Nechamandra alternifolia (Roxb.) Thw., Colocasia esculenta (Linn.) Schott., Typhonium trilobatum Schoot., Fimbristylis dichotoma (Linn.) Vahl., Tinantia fugax Scheidw., Canna glauca Linn., Canna humilis Bouche, Thalia geniculata Linn. Calathea bella Regel., Calathea splendens Hort., Strelitzia reginae Banks., Typha angustata Bory at Chaub., Monochoria vaginalis (Burm.f.) Presl., Eichhornia crassipes (Mart.) Solms., Alisma plantago Linn., Aponogeton monostachyon Linn.f., Potamogeton lucens Linn., Cutleya lutea Royle, Paspalum vaginatum Swartz.

The Root Cap :

The root cap is distinct from the root-body and has its own initials. The developmental studies of the lateral roots in Eichhornia (Fig. 29, Plate 32),

Monochoria (Fig. 28, Plate 31 a) and Canna (Fig. 30) show that the cap originates from the endodermis and the root-body from the pericycle (see p. 40), thus showing no histogenetic connection between them as is the case in dicotyledons. The cap is separated from the root-body by a thick mucilaginous layer that extends proximally. In Eichhornia crassipes (Fig. 13, Plate 13) it extends far behind the apical meristem and does not have any organic connection with the root-body on the proximal side. The only attachment in this root is at the root tip.

The root cap shows Kappe type of division, the capital of the T being towards the base of the root. Such divisions are common in the peripheral zone while in the central columella region these are predominantly transverse.

Though the majority of these plants are aquatic, there is a distinct well developed root cap. Guttenberg (1960) has stated that there is an extreme reduction in the organisation of the root cap in aquatics to fit in the aquatic life in which the formation of a cap is superfluous. On the other hand Esau (1953) has stated, "In the water plants, root caps are usually prominently developed". It appears that the root caps in aquatic plants may have functions other than those in terrestrial plants.

Columella :

The columella can be clearly recognised in Colocasia (Fig. 9, Plate 9), Typhonium (Fig. 15), Tinantia (Fig.11), Canna spp. (Figs. 7 & 8), Thalia (Fig. 14), Typha (Fig.10), Potamogeton (Fig. 20; Plate 18) and Paspalum (Fig.5; Plate 6) while in the rest of the plants it is not sharply delimited. It consists of regular longitudinal rows of cells having their initials on the proximal side i.e. just distal to the tip of the root body and show transverse divisions like a rib meristem. Its derivatives elongate towards the tip of the cap and become vacuolated. Some of these files may occasionally show vertical divisions towards the distal side, thus enabling the columella to become wider. This helps to keep pace with the transverse expansion of the central region.

The cell rows of the columella do not extend right upto the tip of the root cap in all the plants studied herein but are over-arched by the cap flanks, where their bounderies ~~thus~~ are being lost. The columella cells grow practically at the same rate as that of the peripheral part of the cap but when there is a difference in the rate of division between the two, it causes distortion and their boundaries become indistinct. The columella cells get vacuolated from the proximal to the distal end, much earlier than those of the cap flanks and the root body.

The cap flanks show cell complexes of the Kappe type. At the tip of the columella, the number of rows of cap flanks is large and oriented in oblique files showing T-divisions with the capital of the T pointing proximally. The flanks widen out towards the distal side by such divisions while on the proximal side they can be traced to a single row of cells. In the root cap, the whole of the complex is never to be seen because the outer cells are rubbed off. The increase in the number of files on the distal side of the cap, counterbalances the sloughing off of the cap cells. The first division of the cap initial is transverse to its long axis and is followed by the longitudinal division of the inner daughter cell which functions as the initial. Thus, a single initial gives rise to three cells, two of which behave as initials and are capable of repeating the pattern.

Protoderm-Periblem complex :

It is present as a single tier of initials outside the stelar dome and gives rise to the epidermis and cortex.

It is one to two cells across in the median longi-section in Aponogeton (Fig. 2), Fimbristylis (Fig. 3; Plate 4), Paspalum (Fig. 5; Plate 6), Canna glauca (Fig.7; Plate 8), Typha (Fig. 10), Tinantia (Fig.11), Strelitzia (Fig.12), Eichhornia (Fig. 13), Typhonium (Fig.15),

Elyxa (Fig.16; Plate 15), Alocasia (Fig.17), Alisma (Fig. 18), Hydrocharis (Fig. 4) and Vallisneria (Fig.1, Plate 2). However, in the broad roots such as Thalia (Fig.14), Colocasia (Fig.9; Plate 9), Canna humilis (Fig.8) and Monochoria (Fig. 6; Plate 7) this tier is several cells broad and slightly curved to overarch the broad stelar dome.

T-divisions occur on the flanks of protoderm-periblem initials. In this case the capital of the T is directed towards the initials as it is the proximal daughter cell on the flanks of the initials which divides periclinally, not the initials themselves. The first division of the initials is transverse and the cells towards the centre function as the initials i.e. they continue to divide only transversely. The increase in the number of rows of cells is due to the periclinal division of some of the cells of the initials toward the flanks and also due to their further derivatives which produce secondary T patterns. In such a type of division more than one transverse division of the daughter cells may take place before the periclinal division occurs.

The division of the initials and their derivatives results in the widening of the cortex away from the apex. These files run in the opposite direction to those of the Kappe.

Protoderm :

The protoderm initial is the sister cell of the cortical initial which gives rise to the epidermis by anticlinal divisions, e.g., in Vallisneria (Fig. 1, P), Aponogeton (Fig. 2,P), Fimbristylis (Fig. 3, P; Plate 4). In the case of Colocasia (Fig. 17), [illegible] (Fig. 5) and Paspalum (Fig. 5; Plate 6) the epiderm initials and hypodermis initials are sister cells i.e. cells arising from the protoderm-periblem complex divide periclinally. Of these the distal ones form the initials for the epidermis while the inner ones form those of the hypodermis. The latter may exhibit Korper divisions to form a two-to three-layered hypodermis. The epidermis, however, is single-layered and shows only anticlinal divisions. These anticlinal divisions take place so rapidly as to keep pace with the developing cortex. The epidermal cells, therefore, appear radially elongated, and look like a stack of coins, e.g. Alisma (Fig. 18 P), Potamogeton (Fig. 20, Plate 18), Hydrilla (Fig. 21; Plate 20). In Potamogeton (Plate 29) the protodermal cells of the proximal portion mature into the epidermis by dividing unequally and give rise to short cells with dense cytoplasm (trichoblasts) and long cells with scanty cytoplasm (atrichoblasts). The former give rise to root hairs and alternate with the latter. In Vallisneria (Plate 30) the trichoblasts alternate with two atrichoblasts. In other plants, however, such a differentiation

does not exist. The epidermal cells get vacuolated later than the hypodermal and cortical cells.

Hypodermis :

This is composed of a few layers of cells. The hypodermal initials originate either as sister cells of the cortical initials as in Canna (Fig. 7), Nechemandra (Fig. 4), Aponogeton (Fig.2) or as sister cells of the protoderm from the protoderm-periblem complex as in Alocasia (Fig. 17), & Monochoria (Fig.6). In some cases the hypodermal initials appear behind the tip of the root-body e.g. Acorus (Fig. 23).

The hypodermal initials, like those of the protoderm, show anticlinal divisions, but unlike the latter they may exhibit one or two korper divisions also, depending upon the number of hypodermal layers, which are 1 to 3 in the plants studied.

The hypodermal cells stain densely as compared to the rest of the cortical cells and get vacuolated earlier than the other cells of the cortex. In the proximal region these cells become elongated and show thickenings on their walls.

It is observed that in aquatic plants the air-spaces arise very close to the meristems but even in these plants the hypodermal cells remain closely applied to one another showing no air spaces between them even in the mature regions.

Stele :

Immediately proximal to the "protoderm-periblem complex" lie the initials for the stele. They are irregularly arranged but may be marked out from the former due to the stratification of their walls. The stelar initials are pentagonal or hexagonal in shape.

In those plants where the protoderm-periblem complex is one or two cells broad in median longisections, the stelar pole is narrow and pointed, but where the protoderm-periblem complex is many-celled broad, the stelar initials form a dome several cells broad.

The stelar initials divide transversely and their derivatives by further transverse and vertical divisions form a cell complex which can be regarded as the Körper complex of Schüepp (1917). By these divisions the size of the initial group of the stele does not increase but results in the widening of the stele away from the apex. The stele does not continue to widen far behind but becomes cylindrical. The pericycle forms the outer limit of the stele and it becomes distinct even very close to the stelar pole. Its cells retain their meristematic activity to a considerable distance behind, whereas, other cells have already lost it.

The pericycle is composed of a single layer of cells which divide only anticlinally and have densely staining cytoplasm. As mentioned above it is also characterised by the cells retaining their meristematic activity long after theother cells have lost it

The initials for the metaxylem vessels can be distinguished very close to the stelar pole. These have wider lumen and start vacuolation earlier.

Endodermis :

Near the stelar pole all the cells of the cortex are found to exhibit T-divisions (Korper Type) enabling the region to become wider. After some T-divisions, the innermost of these initials stop further T-divisions and divide only anticlinally to form the endodermis. Thus, the endodermis is the innermost layer of the cortex derived from the common initials for the endodermis and cortex. Same is the case for development of the epidermis and cortex.

Cortex :

The cortex is limited by the hypodermis on the outside and endodermis on the inside, between them are present the cells complexes of the Korper pattern. These consist of vertical rows of cells at the proximal side. These cell rows bend outward from the stelar pole and gradually increase in number due to the T-divisions of the Korper type.

Type II : Discrete initials for the stele, cap, and protoderm-periblem complex in the early stages but change later from the "closed" to the "open" type.

The change from the "closed" to "open" type is exhibited by the root apices of Pinete superba, Caladium sp. and Ottelia alismoides, among the species studied herein.

In Pinete superba (Fig. 26a; Plate 27a), Ottelia alismoides (Fig. 27a; Plate 26a) and Caladium sp. (Plate 28a) the apical organization of the young roots is the same as described in the type one, having discrete initials for the stele, cap, and the protoderm-periblem complex. However, the outer boundaries of the protoderm-periblem complex in Ottelia (Fig. 27a; Plate 26a) are slightly vague and show signs of opening out. In some of the younger roots of this species a discrete stele and a protoderm-periblem complex may be observed. The layer next to the protoderm shows oblique divisions ~~at or~~ surrounding the stelar dome (Fig.27b; Plate 26b,c). The cells thus added, press the part of the protoderm near the columella head and bend it distally. Due to this the discreteness of the protoderm-periblem complex is disturbed or lost at these places & an open joint between the cortex and the cap is formed. The lower or distal daughter cell resulting from the oblique division of the outer cortical cell is added to the periphery of the columella. As such an activity is continued, more and more cells are added to the columella periphery; the cells

themselves divide transversely. This results in the formation of new cell-rows penetrating between the outer columella files and the cap flanks. The curve like areas which are formed at places which establish a connection between the outer cortical layers and the cap are termed as the 'knees' (Guttenberg, 1960; Fig. a & b). The new files of columella cells added as a result of knee formation are called the "secondary columella". The cells of the cap flanks surrounding this secondary columella show an increased meristematic activity and add more cells possibly in order to keep pace with the increase in girth inside due to the formation of the secondary columella files (Fig. 26b, 27b,c; Plates 26b, c; 27b; 28b). The knees form an important meristematic zone which add cells to the root body as well as to the root cap around the columella. The cortical layer just inner to the one that has already opened may also show a similar activity and a second knee may be formed (Fig. 27c; Plate 26c,d; 27b). As a result of the knees adding cells to the root cap distally and root body proximally, gradually the discreteness of the protoderm-periblem complex as well as the stele gets lost. Thus, the ultimate result of this "opening out" is the formation of a common group of initials for all the zones of the root (Figs. 26b, 27c; Plates 26D, 27B).

In the early stages of opening out of the cortical files, the columella cells on the flanks are subjected to pressure by the protoderm layer which grows distally. Its

files are, therefore, gradually pushed outwardly. With the formation of further secondary files inwards, the initials for the primary columella are displaced and the cells in the middle of the root body contribute to it. The initials at the distal end of the stelar dome thus start contributing to the columella and the discreteness of the stelar dome also is lost.

Cap :

The cap initials are discrete in the young roots of Ensete and Caladium (Fig. 26A; Plate 28A) and show the Kappe type of division in the peripheral region. The columella shows characteristic transverse divisions. These cell files are distinct in the proximal region of the columella but at the distal end their boundaries are lost due to the pressure of the cap flanks.

On opening out, the cortical files add more cells to the peripheral region of the primary columella and make it wider. The secondary columella and the cap flanks gradually merge with one another on the distal side. In the cap region the oblique cell files straighten out due to the pressure of the secondary columella files and the usual T-pattern of the cells is lost (Fig. 27c; Plate 26D).

In Ensete superba there is the formation of 'metakutis' layer, a layer of cells with lignified and suberised walls in the outer cap cells and become continuous with the epidermis. The 'metakutis' extends upto

the central files of the columella (Plate 27a, c) and indicate the dormancy of the root. Such layers are reported by Philipp (1923) in Musa sapientum and by Riopel and Steeves in Musa acuminata (1964).

Protoderm Periblem complex :

This tier is two cells across in the longisections (Fig. 26a, 27a; Plate 28A) and gives rise to the cortex and epidermis. The derivatives of these initials show Korper division and add to the bulk of the cortex in the initial stages. As the roots open out, the discreteness of this group is lost and the epidermis and the cortex appear to arise from the peripheral region of the promeristem (Fig.26B, 27C, Plate 26B, 27B,28B). The central cells in the promeristem show lesser mitotic activity as compared to the peripheral region and seem to coincide with the 'quiescent centre' (Clowes, 1959). The study of cell lineages reveal that the specific initials for these regions can not be traced back to their initials and the boundaries are more apparent than real. The disposition of a derivative from any initial to any one of these regions is primarily determined by its proximity to that region. If it is marginal in position the initial may contribute to both the regions.

Endodermis :

The differentiation of endodermis follows the completion of periclinal divisions associated with the

development of the inner cortex. It is thus the innermost cortical layer which does not divide further. Subsequently the cells of the endodermis become vacuolated and ~~some~~ a little proximally they are characterised by increased radial and longitudinal dimensions.

Stele :

It is formed by the transverse division of the promeristem cells in the central region. The proximal daughter cells thus formed divide and redivide to form the steler elements while the distal daughter cells continue to be initials. The metaxylem elements originate very close to the promeristem while the seive tubes differentiate farther behind the apex.

Epidermis :

It is the outermost layer of the cortex and is differentiated very close to the promeristem. It shows only anticlinal divisions. In Ensete the epidermal cells get suberized and add to the 'metakutis' layer. In Ottelia and Caladium the epidermal cells develop normally. In these plants the epidermal cells are not differentiated into trichoblasts and atrichoblasts.

Type III : Common initials for the stele, cortex, protoderm and root cap.

This type is exhibited by Hydrilla verticillata Royle, Acorus calamus Linn., Cyperus diffusus Vahl., Scirpus grossus Linn., and Phoenix humilis Royle.

In all these plants, there is a common group of initials which gives rise to the stele on the proximal side, columella on the distal side, and the root cap, protoderm, and cortex peripherally (Figs. 21-25; Plates 20-25).

Promeristem :

It consists of a common group of initials for all the histogens. Its boundaries are undefined and indefinite. It is like a plano-convex disc, whose flat distal side gives rise to the columella, the convexity to the stele, while the cortex, protoderm and cap initials arise from its rim or periphery. The more central cells of this disc though potentially meristematic, rarely divide and are in quiescence. These cells are stained lightly and have less prominent nuclei and nucleoli with low cytonuclear ratio.

Columella and root cap :

The columella forms the core of the root cap and extends upto its tip (Figs. 21, 22, 24, 25; Plates 21, 23, 24). However, it is not distinct in Acorus (Fig. 23;

Plate 22). The columella initials arise from the flat face of the promeristem disc and by transverse divisions give rise to the vertical files of the columella cells. Thus, it is the distal daughter cells which give rise to the columella cells.

Though the root cap is not quite distinct from the root-body, in the central region, however, its boundaries may be marked out by the analysis of the cell lineages in the central and peripheral regions. In the peripheral portion they show the Kappe complex where the cell-files curve distally, while in the centre the files show transverse divisions and form vertical files of the columella.

Protoderm:

It originates from the margin of the promeristem in Hydrilla (Fig. 24) and Cyperus (Fig. 22; Plate 21). In the latter the protodermal cells exhibit a 'knee' bend distally. This permits the cortical files to add to the files of cells at the periphery of the columella. This "opening out" has already been described.

In Acorus (Fig. 23), Najas (Fig. 21) and Scirpus (Fig. 25) the protoderm can be distinguished quite far away from the promeristem. Once the protoderm initials become distinct, they divide only anticlinally and mature into the epidermis. Due to repeated anticlinal divisions, the epidermal cells look like stack of coins as in Najas (Plate 20).

Cortex :

The cortical initials develop from the peripheral region of the promeristem. Periclinal and anticlinal divisions form the Körper complex of cells. In Acorus the formation of cortex is different from the rest of the plants. In this case the initials, instead of exhibiting the Körper type of divisions more profusely around the stele as is the case in most other roots, do so towards the outer half of the cortex. This may be due to the appearance of air spaces in the inner cortex, very close to the promeristem.

The stele :

The stelar initials appear by to the transverse division of the promeristem cells and by further Körper divisions, giving rise to the stelar tissue. Unlike columella, the stelar tissue is differentiated from the proximal daughter cells while the distal daughter cell remains as an initial.

Cyto-histological state of the root apices :

In the root apices with stabilized structural configuration as in Type I, two zones can be distinguished on cytohistological characters - (i) At the tip of the root body, except the root cap, a group of cells with ~~(a)~~ lightly staining cytoplasm (Plates 3, 10, 13, 21, 23 and 25), and ~~(i)~~ ~~cells with~~ less prominent nuclei and nucleoli, and smaller cytonuclear and nucleolus/nucleus

ratios (Table I). This group of cells is like the frustum of a spheroid with the flat surface towards the calyptra. Surrounding this zone proximally and appearing like an arch is; (ii) a zone of cells with more densely staining cytoplasm, and more prominent nuclei and nucleoli (Table I).

Clowes (1956 a, b) has named the former zone as the quiescent centre and the latter, the promeristem. However, Clowes earlier to the postulation of the quiescent centre, used the expression promeristem to include the quiescent centre also and later used it for designating the cells surrounding it. The confusion, however has been clarified (Clowes, 1961). Pillai & Pillai (1960 a, b, 1961 a, b, c) named this region, viz. promeristem as the meristematic zone.

Comparison of the quiescent centre and the meristematic zone :

The corresponding areas of the cell, nucleus and nucleolus were measured from some cells of the quiescent centre and the promeristem respectively, in the root tips of some of the plants studied herein (Table I). Care was taken to select cells containing only one nucleolus in their nuclei. In the cells of the quiescent centre, the nucleoli are found to be smaller than in those of the promeristem. The ratios of the areas of the nucleolus/nucleus, and nucleus/cell in these two regions were also

Species	Quiescent centre Cell	Nucleus	Nucleolus	Nucleus/Cell %	Nucleolus/Nucleus %	Promeristem Cell	Nucleus	Nucleolus	Nucleus/Cell %	Nucleolus/Nucleus %
ichhornia crassipes	37.7	27.5	0.52	73.2	1.9	9.5	32.7	2.57	32.8	7.8
nna glauca	95.0	30.3	2.3	31.5	2.3	100.0	34.0	3.17	34.0	9.3
phonium trilobatum	114.0	42.7	0.63	47.4	1.4	105.4	44.0	3.14	41.9	4.5
yxa auberti	121.7	17.1	0.31	5.9	4.3	108.0	16.8	1.54	15.5	9.1
spalum vaginatum	59.1	25.7	0.14	43.5	0.54	71.0	28.8	4.49	40.3	15.6
[illegible]	162.6	71.9	2.18	44.2	3.03	131.6	62.3	5.15	47.4	9.26
nochoria vaginalis	100.6	32.3	0.6	20.0	2.14	81.6	29.4	3.04	36.1	10.3
onogeton natans	112.9	2.26	0.97	1.06	42.9	135.1	44.0	8.04	32.4	15.3
orus calamus	100.6	31.0	1.13	19.0	3.6	144.2	50.9	4.68	35.3	9.19
tamogeton lucens	80.9	28.3	1.41	34.9	4.9	79.9	38.3	5.97	48.2	15.5
llisneria spiralis	139.2	49.0	1.28	35.2	2.6	127.0	61.3	5.0	48.3	9.15
relitzia reginae	140.0	33.6	0.90	23.0	2.06	135.5	51.8	17.05	38.3	32.9
mbristylis dichotoma	53.9	23.5	1.06	43.5	7.00	85.7	26.0	4.74	30.6	18.2
isma plantago	106.0	29.0	1.03	27.3	5.6	171.0	62.5	7.44	36.7	10.9
effenbachia sp.	212.0	88.0	2.07	41.5	2.3	423.0	153.9	8.45	36.3	5.5
oenix humilis	86.6	20.7	0.44	24.0	2.1	86.0	33.3	2.76	38.7	8.2
locasia indica	121.0	40.0	1.54	33.0	3.85	242.0	71.0	6.15	29.0	8.6
locasia esculenta	369.0	35.2	0.72	9.5	2.0	221.4	39.2	2.2	18.0	5.6
ttelia alismoides-I-closed	379.0	142.0	4.08	37.3	3.3	296.0	153.9	3.92	52.0	2.5
-do- II-Opening out	143.6	63.4	3.64	43.6	5.7	133.9	59.0	3.27	42.0	5.5
-do- III- open	183.6	85.1	3.93	40.5	4.6	169.6	86.7	6.5	51.0	7.5
lodium sp. - closed	155.0	51.8	1.19	33.9	2.3	131.3	57.8	1.91	44.1	3.3
-do- - open	161.6	52.7	1.26	32.6	3.9	108.4	66.6	3.45	39.6.	5.1

Note: The measurements have no statistical value but they serve to indicate the changes in cells of the two regions of the root at and after the development of the quiescent centre.

calculated. The ratios work out to be smaller for the cells of the quiescent centre than those of the promeristem. These, and the reactions to stains, indicate that the cells of the quiescent centre are not synthesizing as much nucleic acids as the cells of the promeristem. They are, therefore, in an inactive state and are not preparing themselves for division unlike those of the promeristem. Brachet (1952), Caspersson & Schulz (1939) and Clowes (1956 a, b) have shown by some other methods and Pillai & Pillai (1960 a, b; 1961 a, b, c) by a method similar to the one described herein, that there is lesser synthesis of nucleic acids in the cells of the quiescent centre than in those of the promeristem.

One interesting feature of the quiescent centre is that it is not a definite structural zone but a cyto-histological one which embraces the cells of all the structural zones of the root body. There is no clear demarcation between the quiescent centre and the promeristem, and the cells of the former gradually merge with the latter.

Under type II, where the closed type of the structure in the young root opens out as they grow older, there is no quiescent centre in the young stages. Even just after opening out, quiescence does not occur and there is very little difference in the nucleus/cell and

nucleolus/nucleus ratios (Table I). It may develop as the opening out becomes stabilized and the root grows older.

Dormancy and attendant phenomena :

Some roots of Typha angustata (Plate 10), Ensete superba (Plate 27 a & c), Alisma plantago (Plate 17) and Tinantia fugax (Plate 11) exhibit the presence of tanniferous cells in the root cap region. In Ensete superba root, a zone of a few layers of thick-walled cells with deeply staining contents more or less completely encircles the apex of the root body. This zone embraces the epidermal and a few hypodermal layers in the region proximal to the apical initials. It extends distally progressively involving 2 or 3 layers of root cap cells in a zone lying 8 to 10 cell-layers outside the meristematic region (Plate 27 a). Kroemer (1903-4) was the first to report the development of such a layer. Busgen (1905), Muller (1906), Plaut (1910), and Noelle (1910) have all noted this phenomenon in roots of different plants. Muller (1906) named it metacutis. Plaut (1918) has given a classification of 'metacutis' development. Cossman (1933) and Hayward & Blair (1942) have reported that the 'metacutis' in citrus roots is of a simple type, as is observed here in Ensete, where 2 to 3 rows of cells in the root cap adjacent to the growing point are suberized.

The outer derivatives of the first periclinal division of the pericycle cells form the protoderm-periblem initials (Plates 31a, b, 32b). The inner ones form the stelar initials.

The endodermal cells at the apex of the 'bulge' become meristematic and divide periclinally to form the root cap or 'Tasche' (Figs. 28c,d, 29c,d, 30c,d; Plate 32c).

The outer daughter cells formed by the periclinal divisions of the pericycle show the Körper division and give rise to the protoderm, which shows only anticlinal divisions, and to the bulk of the cortex which exhibit further Körper divisions (Figs. 28d, 29d, 30d; Plates 31 d & 32 c).

The stelar initials by Körper and anticlinal divisions form the bulk of the stele.

The structure of the lateral root while still enclosed by the cortex of the mother root resembles that of the mature root, except in cases like Ensete, which have a transition from the 'closed' to the 'open' type.

The lateral root grows in length pushing its way through the cortex by further division and elongation of its cells. Elongation of the cells is more prominent at the base of ~~the root~~.

In the roots of the other species investigated herein, such a complete covering to the meristematic region has not been observed. The development of the deeply staining cells in the root cap region may probably be the earliest step leading to the formation of such a covering of 'metacutis'.

Origin and development of lateral roots :

In aquatic plants the lateral roots arise at an early stage when the mother root is still passing through the cell elongation stage. The endodermis and the pericycle of the mother root take part in their formation (Figs. 28 a, 29 a, & 30 a; Plates 31 a, 32 a). They arise 150 to 350 u behind the stelar pole in Eichhornia, 450 to 600 µ in Monochoria, 700 to 950 u in Canna, and 800 to 1050 µ in Ensete.

The lateral roots arise from the pericycle opposite the xylem bundle (Plate 31). About 4 to 10 cells of the pericycle, in a single layer initiate the lateral root by expanding radially. These cells have dense cytoplasm and large nuclei. The endodermal cells in contact with these cells also become densely cytoplasmic and divide anticlinally (Figs. 28a, 29a, 30a; Plates 31 & 32). The radially elongated pericycle cells divide periclinally; also anticlinally (Figs. 28b, 29b, 30b), pushing the endodermis outwards.

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It is noteworthy that in these plants the root cap originates from the endodermis and it has no histogenetic connection with the main root body since it arises from the pericycle of the mother root.

The derivatives of the endodermis coalesce with those of the pericycle in the formation of the lateral root. This may be due to the fact that the lateral roots arise at a very early stage when the immature endodermal cells have not even developed the casparian strips.

Nägeli and Leitgeb (1868) reported that in Oryza sativa the cells of the endodermis form the cap in the initial stages of lateral root development, but to this are also added toward the inside, some cells derived from the division products of the pericycle. This type of cap formation has been recorded by Janczewski (1874) and Van Tieghem & Douliot (1888). The latter authors found that the endodermis with or without the assistance of adjacent cortical layers produces the outer apical envelope of the lateral root which they termed as the "poche digestive". The "poche digestive", however, is cast off at a later stage. The pericycle is the place of origin of all tissues of the lateral root, including the root cap, according to them. Schade and Guttenberg (1951) and Guttenberg (1960) report variations in the mode of formation of the lateral roots. In Liliaceae and Gramineae they found that the 'poche' is reinforced by cap cells developing from calyptrogen but in aquatic plants like Hydrocharis, Lemna, Pistia, there

is no [illegible] but there is a permanent "poche digestive". Such a poche, called here 'trosche', is found in the [illegible] among the species investigated in this study.

Origin and development of air spaces :

The origin and development of air spaces have been studied in the roots of the following species : - Acorus calamus, Alisma plantago, Blyxa auberti, Canna spp., Eichhornia crassipes, Fimbristylis dichotoma, Lydrilla verticillata, Monochoria vaginalis, Najas minor, Ottelia alismoides, Potamogeton lucens and Vallisneria spiralis.

The distance from the apex of the generative centre at which the air spaces first appear in each species is given in the following table : -

S.No.	Species	Level of origin in μ	Nature
1.	Acorus calamus	100 to 150	Schizogenous
2.	Alisma plantago	300 to 400	-do-
3.	Blyxa auberti	150 to 200	Both Schizogenous and Lysigenous
4.	Canna spp.	600 to 900	-do-
5.	Eichhornia crassipes	800 to 950	-do-
6.	Fimbristylis dichotoma	900 to 1200	-do-
7.	Hydrilla verticillata	75 to 120	Schizogenous
8.	Monochoria vaginalis	400 to 500	-do-
9.	Najas minor	120 to 200	-do-
10.	Ottelia alismoides	150 to 300	-do-
11.	Potamogeton lucens	200 to 300	-do-
12.	Vallisneria spiralis	400 to 600	-do-

Sachs (1882) classified the air spaces into two groups, the one formed due to the "splitting of the partition wall between cells and the growth of its now-separated lamellae", and the other due to "the cessation of growth of inner masses of tissue and their drying and disintegration while the surrounding tissues continue to grow". De Bary (1884) named the former schizogenous and the latter, lysigenous lacunae. Martens (1937) has pointed out that the schizogenous lacunae are formed where the new cell wall of the daughter cells come in contact with that of the mother cell and that the pectic substances rupture or disintegrate at these corners. Mangin (1888), in his chemical studies of cell walls, found that pectins between cells were soon changed into pectates. The development of air spaces was studied in the stems of Elodea densa (Hulbary, 1944) and Elodea canadensis (Dale, 1957).

Sifton (1945, 1957) has carefully reviewed the work on air space tissue in plants. Mulay & Saluja (1957) reported the formation of air spaces in the roots of some desert grasses and Pillai & Pillai (1962) have described their formation and development in some monocotyledonous roots.

In the present study the schizogenous air spaces appear to begin with as intercellular spaces at the corners of the cells (Plates 34, 35). In the majority of these roots, the cortical cells are arranged in radial

roots and the development of air spaces can be traced easily. The young cortical cells are rectangular in cross section and there are incipient intercellular spaces at their corners. When the cells enlarge, they become oval or elliptical and the size of the original small intercellular space increases. The rounding up of the cells releases tension along the corners and intercellular spaces enlarge to form air spaces. They are diamond-shaped to begin with, but in the mature stage they may be quadrangular as in Ottelia (Plate 33), polygonal as in Hydrilla, Vallisneria and Acorus (Plates 34, 35) or of irregular shape as in Eichhornia (Plate 36b). The shape of the air space in Hydrilla and Acorus remains constant though its size varies with the age and the environmental conditions of the plant.

In Acorus and Hydrilla the air spaces are polygonal surrounded by 3 or 4 cells. Later on, however, they are converted into large air canals bordered by many cells (Plates 34 and 35). This enlargement is accompanied by and is dependent upon numerous cell divisions in a plane parallel to the long axis of the root. Thus, the increase in the diameter of the developing lacunae is the result of cell enlargement plus cell division in a vertical plane in the cells encircling them.

The formation of lysigenous lacunae in the root cortex has been reported by many authors (Newcombe, 1894; Norris, 1913; Henrici, 1929; McPherson, 1929; Beckel, 1956, etc).

Newcombe (1894) concluded that the tension within tissues is a factor in limiting the life span of cells which normally break down in cavity formation. Tobler (1943), in his studies on the stem of Pragmites communis, reports that the occurrence of lysigenous lacunae is comparatively more in submerged parts than the aerial ones. Yamasaki (1952) describes the breakdown of root cells in Japanese upland crops due to "excess moisture injury". Norris (1913) reported that Zea mays roots from water culture had more air spaces than those from the soil and concluded : "the development of air spaces appears to depend largely upon the quantity of air available in the medium surrounding the roots".

In Eichhornia, Canna, Alpxa and Fimbristylis, the intercellular spaces arise schizogenously but later on they also increase in size lysigenously (Plates 36a and b, 37a and b, 38 and 39).

Chapter V

DISCUSSION

Literature abounds in attempts at explaining root apical structures on the basis of the theories interpreting shoot apices. Thus, the workers on root apices appear to depend upon the theories of shoot apical organization for interpreting the structure of root apices.

Hanstein (1868), in his classical "histogen" theory, postulated that there are three sources of permanent tissues in shoots : the plerome, composed of cells extended axially and longitudinally; the periblem, a shell of concentric layers of isodiametric cells covering the plerome; and, the dermatogen, the outermost meristematic layer. Each of these cell-groups originates from a cell called the "initial", which divides into two; one daughter cell of which continues cell division while the other daughter cell differentiates into the permanent tissues after several mitoses. This theory was applied to root apices also. Janczewski (1874), Treub (1876), Flahault (1878), Kroll (1912) and others have interpreted and classified root meristems on the basis of this theory. Though their interpretations were not realistic, nevertheless, these were based on real differences in ontogeny, as shown by Schuepp (1926).

The structural organization in the root apices studied here can be brought under three different types : -

Type I - With discrete initials for the stele inside and root cap outside, and between them with a common initiating zone for the epidermis and cortex, named here as the "protoderm-Periblem Complex". This is exhibited by the following species : -

Vallisneria spiralis Linn., Blyxa auberti Rich., Hedyosmandra alternifolia (Roxb.) Thw., Colocasia esculenta (linn.) Schott, Typhonium trilobatum Schott., Fimbristylis dichotoma (Linn.) Vahl, Timentia fugax Scheidw., Canna glauca Linn., Canna humilis Bouche, Thalia geniculata Linn., Calathea bella Regel., Strelitzia reginae Banks, Typha angustata Bory & Chaub., Monochoria vaginalis (Burm.f.) Presl., Eichhornia crassipes (Mart.) Solms, Alisma plantago Linn., Aponogeton natans (Linn.), Engl. & Krause, Potamogeton lucens Linn., Cautleya lutea Royle, Paspalum vaginatum Swartz.

In older literature this type is reported in grasses (Janczewski, 1874; Treub, 1876; Flahault, 1878). Haberlandt (1914) and Hayward (1938) mention this as their type 2 which is commonly found in Gramineae, Cyperaceae, Juncaceae and Cannaceae. Esau (1953) has described such a type as her type four. Popham (1952) on the other hand, mentions it as the principal monocotyledonous type,

although the examples cited are only from the members of the Gramineae. Pillai & Pillai (1960b, 1961a, c) and Pillai et al (1961) have, however, found this type of organization in the root apices of the members of the families Cannaceae, Marantaceae, Xyridaceae and Zingiberaceae. In the present study, the apices of the majority of the species exhibit this type of organization.

Many authors describe "the common monocotyledonous type" of organization as having a discrete plerome and common initials for all the other regions. The more recent investigators on root apices of monocotyledons (Guttenberg, 1960; Krauss, 1949; Pillai & Pillai, 1960a, b, 1961a, b,c; Pillai et al., 1961; Deshpande, 1960, 1961), however, show that such an organization is not at all common among monocotyledons. The present study supports this observation. Such an expression viz. "the common monocotyledons type", therefore, leaves an erroneous idea of the root apical organization of the monocotyledons.

Type II - With discrete initials for the stele inside and root cap outside & with a common tier of initials for the epidermis and cortex in the young roots, which open out as the root grows older giving place to a common group of initials for all the regions of the root.

This transitional type is exhibited by the roots of Caladium sp., Ottelia alismoides and Thgeta superba (Figs. 27, 26; Plates 26, 27, 28).

Some investigators have taken for granted the idea of fixity of the structural configurations in root apices and they have, therefore, not recorded any such transitions. Guttenberg et al (1958) report such transitions in the root apices of Helianthus annuus, Anoda triangularis and Cucurbita sp. On the basis of his studies, Guttenberg (1960) has classified the structural organization of root apices into two main types, viz., (i) the "closed" type, having discrete initials as described under Type I, and (ii) the "open" type, where the initials for all the regions of the root merge to become a common one, as in the roots mentioned under Type III. He further states that the "closed" type of the young roots changes to the "open" type in older ones due to the formation of "cell-joints" between the periblem and the columella. "Die wichtigaste Bildungszone liegt in den" Knieen" Und deren Verlängerung in die Haube hinen; hier herrscht die grösste Teilungsaktivität"(Guttenberg, 1960, P. 62-63). These cell-joints open the 'dermatogen' and add 'cell-packets' both to the root body and the root cap.

Guttenberg (1960) describes that in the process of opening out the outermost layer of the cortical initials, located just inside the protoderm and distal to the stelar pole, undergo oblique divisions. As a consequence, daughter cells arise distally which press the protoderm downward and the cortical file then bends forward to form a 'Knee'. The cells of the 'knee' which arise distally

are interposed between the columella files and the cap flanks. These files are referred to by Guttenberg (1960) as the "secondary columella".

This phenomenon may be repeated by the inner cortical files so that more than one 'knee' and more than one secondary columella file may be formed.

In the present study, the opening out of the protoderm-periblem initials is similar to that described by Guttenberg (1960). The stelar initials lose their discreteness and 'open out' in the roots. This may be due to the original columella files being pushed forward by the opening protoderm file. The gap thus produced may be filled up by cells being cut off distally by the stelar initials. Thus, the "opening out" of the 'closed' initials is complete in the roots. Guttenberg and Jakuzeit (1957a) and Heydel & Guttenberg (1957) have described similar coalescence of all the initials in Galtonia and Allium giganteum respectively.

A point of difference in this connection is that Guttenberg (1960) and his students found such changes mainly in the developing embryos and the radicular tip of the germinating seed. In the present studies, however, the embryonic root tips were not studied as most of the plants do not set seeds and are vegetatively propagated. Therefore, fibrous and lateral roots of different ages were studied and similar changes observed in them.

One remarkable feature which is noticed during the process of opening out is that the initials which were very close together in the early "closed" stage, spread out in the form of a sphere of a bigger diameter. This shifting naturally leaves the cells in the centre of the sphere without the function of initiation and they may gradually undergo a stage of quiescence. In such roots, therefore, a quiescent centre (Clowes, 1956a,1958a) may arise in the above described manner.

Type III - With a common generating centre from around which differentiates the various zones, viz., the root cap distally, stele proximally and cortex and protoderm on the flanks.

This type is exhibited by Majas minor, Cyperus diffusus, Acorus calamus, Hydrilla verticillata and Scirpus grossus.

Older literature does not contain a type like this (Janczewski, 1874; Treub, 1876; Flahault, 1878). However, Haberlandt (1914) and Hayward (1938) mention that this type of organization is of common occurrence in dicotyledons. Popham (1952), in his modification of Janczewski's classification, mentions this type of organization as common among dicotyledons, and is thought not to occur among monocotyledons. However, Pillai & Pillai (1960a, 1961b) have reported such a type among members of Musaceae and Palmeae and Deshpande (1960, 1961) in some members of Liliaceae and Amaryllidaceae.

According to the present study of Type II described above, and those of Guttenberg and co-workers (1955, 1957a, 1960) this is the "open" type and it could arise by the "opening out" of a previously "closed" type. Since it has not been possible to get root tips of different ages and study their organization from this point of view, it is not definite whether the organization in all these roots arises by this method. It, however, appears to be so in the root apex of Cyperus where knees can be made out around the columella.

The other possibility that some of these root apices may possess such an "open" type of organization from the beginning cannot be denied. Since most of these plants do not set seeds, their development during embryogeny could not be studied. The only course open is to study this aspect during the development of lateral roots.

This study shows that (i) the "closed" type of organization in a young root may "open" out, (ii) that three types of organization can be identified from the ontogenetic studies: (a) the "closed" type, (b) the "open" type, and (c) the "closed" to the "open" type.

Application of the theories of apical organization

Nageli's (1845) apical cell theory does not find any support whatsoever, from the apical organization studied herein. The apical cell theory fully established

In regard to apical organization of lower plants does not seem to be substantiated from the data available so far in case of the flowering plants and Gymnosperms. It is interesting to note, however, that some peridophytes show the occurrence of a group of apical cells at more older stages (Ogura, 1938).

Hanstein (1868) in his histogen theory of the apical meristems recognizes three distinct histogens, namely, plerome, periblem and dermatogen corresponding to the stele, cortex and epidermis of the developed organ. Janczewski (1874) proposed calyptrogen as the fourth histogen which forms the root cap. Much of the early work on root apices was orientated towards the classification of plants, based on the destiny of the histogens. Ample evidence has now accumulated to show that a correlation between the histogens and the regions developing from them does not always exist as Hanstein (1868) believed, and the histogens may not invariably be discrete from their very origin.

Hanstein's histogen theory (1868) though obsolete for the interpretation of the shoot apices, still retains some usefulness in interpreting the root apical meristem. This has been emphasized by Foster (1941b) and recently by Clowes (1961). Guttenberg (1960) and his students also have used the histogen terminology in explaining the root apical organization. The present author feels that with a suitable modification the histogen theory may be used in

the interpretation of roots that show a 'closed' type of organisation.

Guttenberg (1940, 1947) postulates the presence of a central initial cell which not only gives rise to the cortex and the root cap but also initiates the formation of the stele. He combines the features of the Apical Cell Theory and the Histogen Theory and draws homologies between the apical cell of pteridophytes and the central cells of the Angiosperms. It is suggested that the histogen initials are replaced by the derivatives of the central cell. The place of the single apical cell at the pole of the stele, is taken over by these central cells and they form the generative centre. The central cells themselves divide and the subsequent divisions of their derivatives are responsible for the development of the rest of the root. Steffen (1952) has criticized the central cell hypothesis as he could not corroborate the occurrence of such a cell even during the embryo development. The present study also does not lend any support to Guttenberg's observation as at no stage such a cell could be identified, not even at the initial stages of the lateral root primordia. The developmental studies of lateral roots in Eichhornia, Monochoria etc. reveal that the root body and root cap, originate from the pericycle and the endodermis of the mother root respectively. In majority of the plants studied, cap, cortex and the stele arise independently and cannot, therefore, be ontogenetically traced back to a single central cell.

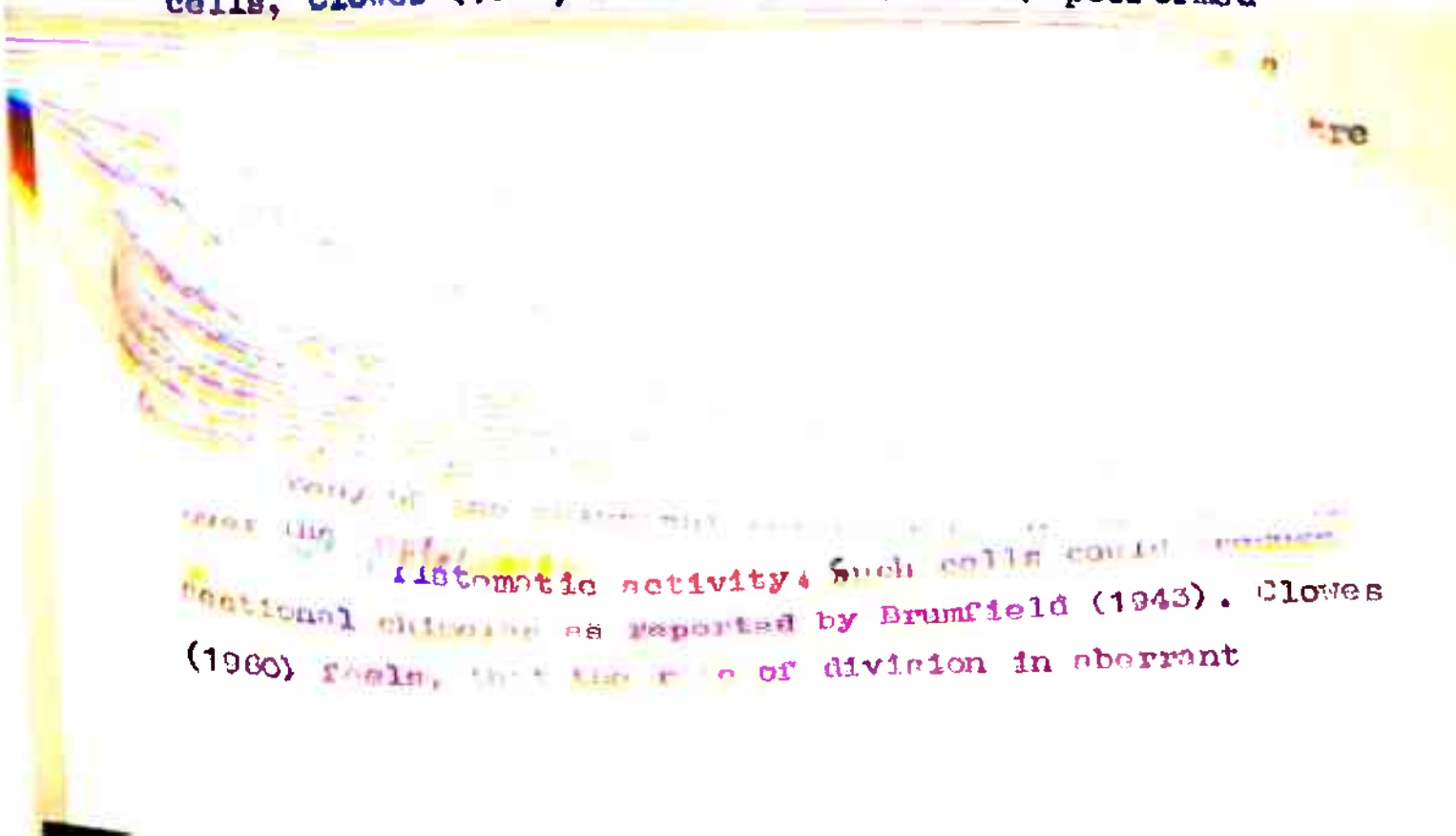
Brumfield (1943) has suggested a group of three initials at the root tip. These three initials lie around the axis of the root in the same transverse plane, each covering one third of the root area and giving rise to stele, cortex and the root cap in the corresponding sector. His conclusions are based on the study of chromosome aberrations, caused by X-radiation in the growing roots (1943).

Brumfield's hypothesis differs from Guttenberg's (1940) in the increase of the number of initials from one to three, but resembles with it in considering the region of initiation of promeristem as very small, capable of producing all the regions of the root. His conclusions,

chromosomes may be different from the normal ones and the viability of the chromosomes may be changed after irradiation and the meristems may behave abnormally.

Richards (1952) repeated Brumfields (1943) experiments on the roots of Crepis and instead of sectorial chimeras found periclinal one in the irradiated roots. He concluded that the promeristem in Crepis consists of three superposed tiers of three initials each. The proximal tier produces stele, the middle one cortex, and the distal root cap and the epidermis. In the closed type of root apices met with heroin, the initials also lie in three superposed tiers, the proximal forms the stele, the central forms the epidermis and cortex, and the distal forms the root cap. The number of initials in each tier varies with the species.

In order to ascertain the actual number of initial cells, Clowes (1953, 1954) and Kadej (1956) performed



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Clowes (1959) took the same material as that of Brumfield's (1943) and reinvestigated it by feeding the roots with labelled adenine after irradiation. By autoradiographic studies he could show that the promeristem cells being in an active stage of division could be damaged by X-rays.

Many of the quiescent cells could survive and take over the meristematic activity. Such cells

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In order to ascertain the actual number of initial cells, Clowes (1953, 1954) and Kadej (1956) performed microsurgical experiments. They could conclude that a large number of initials, the minimal constructural centre unlike the central cell of Guttenberg (1940), three cell promeristem of Brumfield (1943), the nine cell promeristem of Richards (1952) comprises a large number of initials which can regenerate even in a mechanically removed sector of the root. This could not have been possible had the promeristem been small. With the discovery of quiscent centre Clowes (1956) further clarified that in the minimal constructional centre, the rate of cell

division is less as compared to the surrounding promeristem.

Gautenberg (1960) does not accept the regeneration of cut roots as having any bearing upon the number of initials in the root tip. He believes, that the regeneration after wounding is only an indication of great powers of restitution inherent in the apical tissue. He agrees with others that the roots can grow without the division of the central cells but claims that the few central cells are the normal formative centre in the unmolested roots.

The results of regeneration of angiospermic roots after micro-surgery, therefore, could neither clearly indicate the nature of the active promeristem nor could they support the old concept of apical cell or discrete histogens.

Ball (1956) suggests that the behaviour of the remaining cells is changed, when some cells are cut or in any way injured. A large number of cells at the root apex are potential initials and their activity is controlled by the micro-environment of the root. This is in cognizance of the fact, that the fate of the cell is the function of its position (Driesch quoted by Sinnott, 1960).

In longisections of root apices, certain groups of cells or even individual cells, appear to be initials by virtue of their position in relation to the total structural pattern. Cloves (1960) feels that the arrangement of cells

freeze dried roots. He noted the lowest content of DNA, RNA and protein nitrogen in the apical initials. Howard & Pelc (1951) and Clowes (1956) noticed that when the roots are fed with radioactive isotopes of adenine or thymidine these initials do not incorporate them in DNA while the surrounding meristematic cells make liberal use of these compounds in doubling the amount of DNA prior to their division.

The quiscent centre has been identified in several root apices studied herein especially in the closed type. The cells of this region stain less heavily than the surrounding cells. The lesser affinity for the basic dyes may be due to the smaller amount of RNA in the cytoplasm. It shows smaller cytomuclear or nucleus/ nucleolus ratios. There are low counts of mitoses in quiscent as compared to the surrounding tissue (promeristem). The boundary between the quiscent cells and the actively dividing cells is ill defined and is rather fluctuating on the proximal side but on the distal side it is anatomically well defined and it coincides with the boundary between the root cap and the root body (Plates 7, 9, 13).

Popham (1958), Partanen and Gifford (1958) and Clowes (1959) could not demonstrate 'quiscent centre' in case of shoot apices fed with radioactively labelled precursors of DNA. Popham (1958), therefore, does not accept it for the roots also, and Shimabuku (1960) finds

no evidence of the occurrence of quiescent centre in the root apices of Oryza sativa. Clowes (1960) believes that the small roots without columella may not have quiescent centre but as the roots grow broader the degree of quiscence gradually increases. There is a great variation in the extent of quiscence development. In pteridophytes the roots are without any quiscent centre, whereas, in angiosperms it may be composed of several thousand cells.

As regards the significance of the quiscent centre, it may be stated that all the previous theories speaking about the occurrence of initials or histogens at the meristematic root apex may well be rejected, as they fail to take into account the difference in the rates of mitoses in the cells of this region. The assumption that all the cells at the root apex are meristematic has not been supported by any experimental evidence.

Although the quiscent cells do not contribute cells to the growth of the root apex, their importance can not be underestimated as they may be responsible for the synthesis of hormones or in regulating the geometry of the large meristems. The behaviour of meristematic cells surrounding the non-dividing cells has a great significance in the study of root growth and development.

Popham's (1955) transversal meristem is not applicable in the root apex organisation in Type I and II but it can be applied to Type III having a common group of initials. According to Popham (1955) the central

reflects the past history of the root and not the present behaviour of the meristem. The assumption that the cells at the root tip divide at approximately similar rates was challenged by Clowes (1954, 1959, 1961), Jensen (1958), Wejnowicz (1959) and others. With the cytohistological and radio-isotopic studies they could prove that the so called histogens or the cells that appear to be initials are not meristematic. Clowes (1954) designated such cells as the quiscent cells and proposed the concept of a hemispherical quiscent centre in root apices. He could demonstrate by autoradiographic technique such a quiscent centre at the root apices comprising of cells with smaller nucleoli, low ribonucleic acid (RNA) content and no synthesis of deoxyribonucleic acid (DNA). Clowes (1959, 1961) believes that leaving aside very slender or young roots the 'quiscent centre' is of general occurrence in roots. The promeristem consists of a layer of meristematic cells surrounding the quiscent centre with fluctuating boundaries. According to Clowes (1961) with the forward growth of the root the quiscent centre is carried passively by the growth of the cells surrounding it. The cells of the quiscent centre are inactive only because of their relative position with respect to the active cells. In case the active cells are cut or injured, the quiscent cells take over the meristematic activity.

Jensen (1958) confirmed the existence of the quiscent centre by measuring nucleic acid and protein content of

freeze dried roots. He noted the lowest content of DNA, RNA and protein nitrogen in the apical initials. Howard & Pelc (1951) and Clowes (1956) noticed that when the roots are fed with radioactive isotopes of adenine or thymidine these initials do not incorporate them in DNA while the surrounding meristematic cells make liberal use of these compounds in doubling the amount of DNA prior to their division.

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Popham's (1955) transversal meristem is not applicable in the root apex organisation in Type I and II but it can be applied to Type III having a common group of initials. According to Popham (1955) the central

region of the transversal meristem gives rise to continuous rows of cells extending from the columella into the stele, while the peripheral region of the transversal meristem forms cells which differentiate into root cap on the distal side and cortical cells on the proximal side.

The broad roots of Acorus show meristems as extending transversely in the median longisection, but a careful examination reveals, that the columella files do not extend into the stelar files. A clear anatomical boundary exists between the two. In the peripheral region the cortical files are in continuation with the secondary columella files and the root cap files. In Hydrilla, Cyperus and Scirpus the promeristem forms a group of common initials somewhat spheroidal in shape and cuts stelar cells proximally, columella cells distally, and the cap and the cortex along the periphery.

According to Popham's (1955) belief of 'transversal meristem' it is essential that all the tissues initiating a lateral root must belong to a single source i.e. the pericycle of the mother root. A careful study of the development of lateral roots in above referred plants reveals that the endodermis of the mother root forms the root cap and the pericycle forms the main body of the lateral root. Thus the possibility of the occurrence of a transversal meristem is totally ruled out in these cases.

Guttenberg (1960) has recently described the root apex organisation in angiosperms, to be of two types, geschlorsener or closed and 'offener' or 'open' type. The closed type as seen in Type I possesses discrete and independent initials for various zones whereas, in the open type, which is represented by Type III, the initials are not discrete and there is ~~a~~ merging of cells of ~~one~~ one region into the other. Guttenberg (1960) also states that there is no stability in the root apex organisation, so much so that during post embryonic growth the discrete initials may lose their identity. The roots under Type II represent a transition between the discrete and common group of initials. A succession of columella complexes are formed due to continued division of the cortical initials. According to Clowes (1961) the quiscent centre in such cases develops only when the final set of columella initials is initiated.

Recently Newman (1965) has revieved the literature on apical meristem and designates the apical meristem as 'the continuing meristematic resique'. According to his concept more importance is given to the behaviour of the apical initials rather than their structure and continued identity. The concept of 'the continuing meristematic residue' was developed from Prat (1948), who stated that when a cell divides it ceases to exist, being replaced by two sister cells, neither of which can be regarded as derived from the

other. Thus, the parent cell or the initial cell is impermanent. Therefore, according to Newman (1965), the apical initials at any stage are the 'temporary occupants of a permanent office'. As seen at a particular time they are the momentary representatives of the 'continuing meristematic residue' at the apex of the relevant layer or the zone. They have always been so regarded and named as apical meristems not because of their form but because of their function. "The search for the apical cell as a permanent entity in the apex has had its day. I think we should look for apical cell characteristics rather than an apical cell". (Newman, 1965, P. 208). The present author feels that the choice of the term 'meristematic residue' is rather inappropriate since the term 'residue' conveys the sense of something not functioning further.

In Newman's scheme (1965) there is no provision for 'quiescent centre' and the 'promeristem'. Although in his earlier paper Newman (1961) did report the difference in the mitotic division at the apical centre, round about the apical cells, and a little distance away from it. However, this is attributed by him due to the passing of raw materials around and through the unrubbed-off mature cap cells in an encircling movement. The apical region, therefore,

The central region, therefore, receives only small insufficient amount of raw materials. "Thus the infrequency of cell division at the apical centre could be incidental and need not deny the concept of the continuing meristematic residue ...". (Newman, 1965, pp. 202-203).

The quiescent centre has been proved by experimental evidences and is claimed to be of universal occurrence in roots (Clowes, 1961). It is a matter of relativity rather than of reality and only further researches with isotopes can solve the problem decisively. The 'continued meristematic residue' is divided into three basic types, viz., monoplex, simplex and duplex, based on the plane of division in the initial cells and the number of their layers (Newman, 1965). The root apex organization described in the present study under Type I can very well fit into the sub-type 5 of duplex and Type III under sub-type 1 of monoplex of Newman's scheme (1965). Type II of the present study cannot be classified according to Newman's classification.

Whatever may be the implications of the older concepts, the great usefulness of the Korper-Kappe theory (Schuepp, 1917, 1926) in interpreting root apical organization cannot be ignored. This theory is as useful for roots as the tunica-corpus theory (Schmidt, 1924) is for shoots. Clowes (1961) points out that this theory, "ought to have led to a better understanding of root organization, but for various reasons, the theory has never received the support it deserves". Wagner (1939) first applied this theory successfully and his work is an example of how it can be applied for the analysis of the pattern of cell growth and division. Though meant primarily for interpretation of root apical meristems, Guttenberg (1961) has used it in analysing the cell lineages in gymnosperm embryos as well.

The Körper and Kappe are not histogens and the theory simply describes the differences in planes of division and does not ascribe any definite destiny to the two regions. It has an advantage over the tunica-corpus theory in that it can be applied to all kinds of roots, whereas, the latter can be applied to only the shoot apices of angiosperms and some gymnosperms. Clowes (1961) is of the opinion that the histogen theory and the Korper-Kappe theory are not mutually incompatible as is evident from Schuepp's (1926) classification of plants based on the Korper-Kappe boundary in the histogens.

The Kappe complex is external and forms the cap flanks, and the protoderm between the cortex and cap flanks divides only anticlinally. In such roots, therefore, the boundary between the Korper and Kappe does not fluctuate.

Formation of root cap :

The root cap is a structure which is peculiar to the root. Its presence makes the actual tip of the root subterminal. As a consequence, the study of the root apex is made more complicated, particularly in such plants where the cap is not having independent initials. Eames and Macdaniels (1947), Schade & Guttenberg (1951) and Esau (1953) state that the root cap is independent organ in monocotyledons. It is separated from the root body by mucilaginous walls.

Hanstein (1868) and Haberlandt (1914) considered the cap as a proliferation of the dermatogen and they do not attribute it the activity of any separate histogen. Nolle (1876) assigned roots of all plants to two categories on the basis of the mode of root cap origin (i) where root cap originates from an apical cell, and (ii) where root cap originates from the "periblem". The possibility of an independent initiating region for the cap is not visualised by Nolle (1876).

Based on the present study, the root cap may be formed in three different ways : (i) where the cap is independent of the root body, (ii) where the cap is independent of the root body in the young root, but as the root grows older, the root body opens out and coalesces with the cap, and (iii) where the root cap and root body are common from the early stages.

Haberlandt (1914) has put forward a phylogenetic scheme of the root apical structures based on the development of the root cap and its relation to the root body in different plants. According to this, the most primitive and also the most ancient and simplest, is the type with discrete initials. In more advanced types, the protoderm, ground meristom and finally the procambial initials also become merged with the root cap initials, so that the root apex with a common generative centre for all the regions of the root is considered as the most advanced.

Clowes (1959b, 1961) gives a detailed exposition of the utility as well as limitations of this theory.

This concept has been used in the present study in interpreting the development of the cortex and stele proximally and the cap flanks distally. Clowes (1961) mentions that though some roots have an indefinite boundary between the Korper and the Kappe, some others have a boundary which is quite constant in relation to the "histogens". In all the roots studied herein, the cortex and stele belong to the Körper complex; the pericycle between them exhibiting only anticlinal divisions. The Kappe complex is external and forms the cap flanks, and the protoderm between the cortex and cap flanks divides only anticlinally. In such roots, therefore, the boundary between the Körper and Kappe does not fluctuate.

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The root cap is a structure which is peculiar to the root. Its presence makes the actual tip of the root subterminal. As a consequence, the study of the root apex is made more complicated, particularly in such plants where the cap is not having independent initials. Eames and Macdaniels (1947), Schnde & Guttenberg (1951) and Esau (1953) state that the root cap is independent organ in monocotyledons. It is separated from the root body by mucilaginous walls.

In the present study these various steps in the evolutionary scheme are exhibited by some root apices during their ontogeny. Such ontogenetic developmental stages have been worked out in greater details by Guttenberg and Co-workers (1954a, b, 1955, 1957a,b) from the young embryo to the mature root. Whether ontogeny recapitulates phylogeny cannot be asserted at the moment because of insufficient data. More exhaustive studies may enable us to substantiate or repudiate this view.

Columella and cap flanks :

In many roots of Types I and II described herein, a columella is more or less distinct while in others it is indistinct. This region is characterised by vertical files of cells which have arisen by the transverse division of the initials. Occasional T-divisions, with the capital of the T directed distally, add to the width of the columella in the closed types. In the "transition" type, mentioned already, the width of the columella increases by the 'knee' formation and the consequent formation of secondary columella files.

The region of the cap surrounding the columella named here as cap flanks, is characterised by a different type of cell lineage. The cells exhibit the same type of division by which the cell files increase in number distally and abut round the columella. In many roots

In monocotyledonous roots the columella and cap flanks are not very distinct, though in some cases the two regions can be distinguished by the cell lineages. Pillai (1962) has recently brought out the demarcations between these two regions in coniferous roots. According to Tiegs (193), Schopf (1943), Allen (1947a, b), Spurr (1949), Kanapligil (1954) and Wilcox (1954), the columella initials are distinct from those for the cap flanks. Pillai & Pillai (1960b) have named these initials as "columellogen" in roots with distinct columella. In the present studies also the initials of the columella are distinct from those of the cap flanks in roots with a distinct columella. The term columellogen, however, has not been used here since the histogen terminology is altogether avoided. This becomes clearer in such roots where transition occurs and the secondary columella files augment the primary ones.

In their studies of gymnosperm embryos and root apices, Schopf (1943) and Allen (1947 a, b) consider that the cells of the columella contribute to the cap flanks, "due to the more lateral cells of the column shifting polarity abruptly and growing out obliquely upward and radially from the axis alignment". On the other hand, Spurr (1949), Clowes (1953, 1954, 1959b, 1961), Pillai & Pillai (1960 b, 1961 a) and Pillai (1962) find that the columella initials do not contribute

to the cap flanks. In the present study also where the columella is distinct, it appears that its initials are separate from those of the cap flanks.

The protoderm :

As mentioned already, this expression is preferred because the initials give rise not only to the epidermis but also to the subepidermal tissues (Haberlandt, 1914). Such a protoderm, differentiating from initials which gives rise to the "periblem" also, has been called by Schade & Guttenberg (1951) as "pseudo-dermatogen". Esau (1953) says, "the dermatogen is supposed to be the outermost layer of the cortex". In these roots this layer separates out from the initials which give rise to the cortex also. Clowes (1950, 1953) considers such a protoderm as arising from the cortex complex in contrast to that in dicotyledons where it arises from the cap complex. Eriksson (1878) has termed the latter type "Dermocalyptrogen".

Recently, Guttenberg (1960) has clarified these usages. He calls a discrete initial layer from which the epidermis arises as the "primary dermatogen" and an initiating region, from which both epidermis and cortex arise, as the "secondary dermatogen" as this is arising secondarily.

Hypodermis or Exodermis :

Confusion exists in the use of these two terms. Jorgensen (1878), Sachs (1882) and De Bary (1884)

described the outermost cortical layer next to the epidermis as the "hypodermis". Fielder (1892) also used this term to designate the 2-5 layers beneath the epidermis in roots of Bromelia sp. Kroemer (1903) calls it the "intercutis". Holm (1915) calls these cell layers as exodermis, and was followed by Meyer (1940); Guttenberg (1943), Krauss (1949) and Foster (1949); whereas, Eames & MacDaniels (1947) call it the hypodermis. Mulay et al.(1956 a,b, 1959) found a layer of cells which is the mirror image of the endodermis inner to the velamen tissue which they call the "exodermis". According to them. the "hypodermis" is the multilayered tissue inner to the epidermis, though Van Fleet (1950) uses this expression for the exodermis of Mulay et al. (1956a,b).

In this discussion the term "hypodermis" is used for the multilayered subepidermal tissue, as has been used by Mulay et al. and Pillai & Pillai (1960a, b, 1961a, b, c). In the present studies there is, of course, no root with a single layered tissue which is the mirror image of the endodermis.

Endodermis :

Haberlandt (1914,pp.391-392) has stated, "the ontogenetic origin of the endodermis is quite as variable as its phylogenetic development". He describes the procambial origin of the endodermal layers in Juncaceae and cyperaceae. However, in the root of Cyperus diffusus studied herein, the endodermis does not have any relation with the procambial initials. Eames and MacDaniels (1947

p.160) also mention, "the endodermis has been considered both the innermost layer of the cortex and the outermost layer of the stele". However, they further state (p.285), "limiting the cortex on the inside and frequently considered part of it is the endodermis". But, Williams (1947) and Beckel (1956) think that the endodermis is also meristematic in the early stages. The roots studied herein show common initials for the cortex and endodermis around the stelar dome. The initials for the endodermis become distinct only later as in the case of the protoderm-periblem complex from which the protoderm differentiates later. Pillai & Pillai (1960a, b, 1961 a,b,c) are of the opinion that it will be more appropriate to consider the endodermis as arising from an endodermis-periblem complex. I am in agreement with their view.

Origin and development of lateral roots :

There is difference of opinion about the origin of the tissues of the lateral roots. As already mentioned Nageli and Leitgeb (1868) reported that in Oryza sativa the cap is of endodermal origin in the initial stages but this is supplemented by derivatives from the pericycle during lateral root development. Janczewski (1874) recorded similar observations.

Van Tieghem & Douliot (1888), in their exhaustive studies on the origin and development of lateral roots, found that their structure is similar to that of the mother roots. The endodermis, with or without the

derivatives from the adjoining cortical cells, produced an envelope which they termed the "poche digestive". This is cast off at a later stage. The pericycle is alone concerned with the origin of all the tissues of the lateral root including the root cap. Schade & Guttenberg (1951) report variations in the mode of formation of lateral roots in the materials they studied. In aquatic plants they consider the pouch, which is cast off later on, as endodermal in origin and the cap as arising from pericyclic cells. In terrestrial plants, they report the body and cap of the lateral root to arise from the pericycle. In graminaceous members alone, they report the cap to have an endodermal origin.

In the species where the lateral root development could be studied, the cap is entirely endodermal in origin. As the cap increases in size, the Kappe type of divisions increase on the cap flanks while in the middle portion of the cap, transverse divisions are found. The pericyclic cells divide once periclinally and the outer daughter cells form the common initials for the protoderm and periblem. These initials, by Körper divisions, give rise to both these tissues. The inner daughter cells differentiate into the stelar initials (Figs. 28. 29; Plates 31, 32).

Formation of root hairs :

As the epidermis is traced proximally, the cells differentiate into two types : one, which vacuolate early

and elongate, ——, theothers do not elongate and are with dense protoplasm (Plates 29, 30). These cells are called trichoblasts and trichoblasts respectively. The root hairs originate from cells of the latter type. The trichoblasts may be separated from one another by one or more atrichoblasts.

Quiescent centre :

There are reports regarding some features or the other suggesting that meristematic cells may be inactive. Zirkle (1932) and Foster (1939a) have reported vacuolation in such cells and lighter staining of the cytoplasm. Clowes (1956a, b), Jensen (1956, 1957) and Jenson & Kavaljian (1958) mention that there is reduced synthesis of nucleic acids at the quiescent centre. However, it was not realised that some cells of the root apical meristem may become quiescent till this feature was pointed out by Clowes (1956 b). Although, some authors like Esau (1953) mentioned that sometimes the cells further removed from the initial region of an apical meristem are more densely cytoplasmic than the initials themselves, it was not felt that such initials may be quiescent. Further studies by Clowes (1959, 1961), Jensen (1958), and Davidson (1960) with radioactive compounds have clearly indicated that there is a reduced

and elongate, [illegible], theothers do not elongate and are with dense protoplasm (Plates 29, 30). These cells are called atrichoblasts and trichoblasts respectively. The root hairs originate from cells of the latter type. The trichoblasts may be separated from one another by one or more atrichoblasts.

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Pillai (1960 a,b, 1961 a,b,c) and Rejnowicz (1956, 1959) have also studied this aspect using other criteria like nucleic acid-specific stains, and a study of cytonuclear and nucleolus/nucleus ratios and found a quiescent centre arising in roots as they grow older and broader. The present author studied this phenomenon using the variations in cytonuclear and nucleolus/nucleus ratios. A quiescent centre is found in older roots whatever be their structural configuration.

In roots showing a transition of the structural organization from the closed to the open type, there are also indications that such a quiescent centre develops. As has been pointed out earlier, in such roots it is easy to visualize the shifting of the meristematic activity from the initials at the centre to the circumference of the spheroid. In the other types, however, this shifting of activity can be explained as due to the much larger number of cells which become meristematic and hence, the ones at the distal end losing their function. Pillai & Pillai (1960 a,b, 1961 a,b,c) have suggested that this may be due to the non-availability of food materials owing to the greater distance of these initials from the phloem elements which conduct them.

Dormancy and metacutisation :

Numerous investigators have observed that the extent of the absorbing zone of a root will vary with changes in the environmental conditions such as soil

moisture, temperature and aeration. In some roots a metacutis is developed and this covers the meristematic tip for a longer or shorter distance. All these authors ascribe to the metacutis the function of protection of the absorbing zone. Cossman (1939), Maynard & Blair (1942) and Wilcox (1954) have described experiments where this layer arises as a result of unfavourable external conditions. Cossman (1939) and Pillai (1962) have also reported that the development of 'metacutis' is simple in the roots of citrus,&some cycads and Ginkgo biloba respectively, as has been reported here for Ensete.

Air Chambers :

There is an increase in the size of the air chambers from the inner part of the cortex towards the periphery. This is clear in the roots of Acorus, Hydrilla and Ottelia (Plates 34, 35, 33). Further enlargement of the small air spaces into large air lacunae is caused by the tension created in the rounding up of the rectangular cells which become oval or elliptical. This is the case in roots where the air chambers originate and enlarge schizogenously. Schizogenous development is usually exhibited by aquatic plants (Stover, 1951, p.22). Stover also mentions that when roots of land plants grow in water, the air spaces begin schizogenously and quickly enlarge lysigenously. In Hydrilla, Elodea, Monochoria, Aponogeton, Ottelia, and Alisma

the chambers arise and enlarge schizogenously. In Canna, Oryza, Fimbristylis and Eichhornia they arise schizogenously but enlarge lysigenously.

According to Martens (1937), the spaces arise at the point of contact of the new cell wall of the dividing cell and the older wall of the mother cell. The pectic substances rupture or disintegrate at the corners where the new and the old cell walls abut at right angles. Mulbery (1944) found a similar process of air space formation in Elodea stem. In the present study the schizogenous air spaces arise as mentioned above. The enlargement of air spaces into air canals as revealed in cross sections of Acorus and Hydrilla, is accompanied by and is dependent upon numerous cell divisions in a plane approximately parallel to the long axis of the root. By such repeated divisions a system of rounded or polygonal air canals is formed which are separated from one another by one layer of cells. Their general shape usually remains the same despite the enormous increase in size.

Regarding the causes leading to the formation of air chambers, different views have been put forward. Lewcombe (1894) suggested tension of the surrounding cells as a probable cause; Stover (1951) also supports it. Norris (1913) and Bryant (1934) observed that air space development probably depends upon the availability of oxygen. Lack of oxygen, according to McPherson (1939) Hooke (1940) and Beckel (1956) cause rapid deletion of

SUMMARY

The root apical organization of a large number of monocotyledons belonging to 16 families was studied. Ontogenetically they fall under three types :-

(i) With discrete initials for the cap and the stele, the cortex and protoderm arising from common initials — the 'protoderm-periblem complex' — referred to as the 'closed' type.

(ii) With discrete initials for the cap and the stele, the cortex and the protoderm having a common tier of initials in the young roots which open out as the root grows older giving place to a common group of initials for all regions, named here as 'transition' type.

(iii) With a common generative centre around which differentiate the root cap distally, stele proximally, and the cortex and protoderm on the periphery referred to as the 'open' type.

The quiescent centre was studied based on the basis of nucleic-acid specific stains and the variations in cytonuclear and nucleolus/nucleus ratios. The quiescent centre is found in older roots irrespective of their structural configuration.

food supplies by anaerobic respiration and death of the cells which result in the formation of air chambers. Dale (1957), while working on Elodea canadensis, has pointed out that the production of schizogenous lacunae is connected with an abundant supply of oxygen during photosynthesis and that of lysigenous ones with scarcity of oxygen.

Conway (1936-37), while working on Caladium esculus, has pointed out that the aquatics derive benefits from air spaces formed by the disintegration of cells in the stock-cortex and root-cortex. Her experimental work (1937) led her to conclude that, "the roots growing in unaerated mud are dependent on oxygen supplies upon the bases of leaves already dead and on leaves which though still green are not growing".

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The quiescent centre was studied on the basis of nucleic-acid specific stains and the variations in cytonuclear and nucleolus/nucleus ratios. The quiescent centre is found in older roots.

The root cap may be :

(i) Independent of the root body, or,

(ii) Independent in young roots but as they grow older the root body opens out and coalesces with the cap, or,

(iii) Common with the root body even from the early stages.

The ontogenetic studies of the lateral roots in Eichhornia, Monochoria and Canna reveal that there is no histogenetic connections between the root cap and the root body. The former arises from the endodermis and the latter from the pericycle of the mother root.

The origin and development of air spaces was studied in the roots of the following plants :-

Acorus calamus; Alisma plantago; Blyxa auberti; Canna; Eichhornia crassipes; Fimbristylis dichotoma; Hydrilla verticillata; Monochoria vaginalis; Oryza minor; Ottelia alismoides; Potamogeton lucens; Vallisneria spiralis. In aquatic plants the air spaces arise very close to the growing point of the roots. They first appear as tiny intercellular spaces at the point of contact of the new cell wall of the dividing cell and the older wall of the mother cell. Further enlargement of these spaces into large air canals may be schizogenous or lysigenous. In Canna, Blyxa, Fimbristylis and Eichhornia they arise schizogenously but enlarge lysigenously.

The roots of Typha, Phragmites, Alisma and Sagittaria exhibit dormancy. The metacutization is of the simple type and covers 2 to 3 rows of cells but completely encircles the growing point, while in others the formation of tomiferous cells precedes metacutization.

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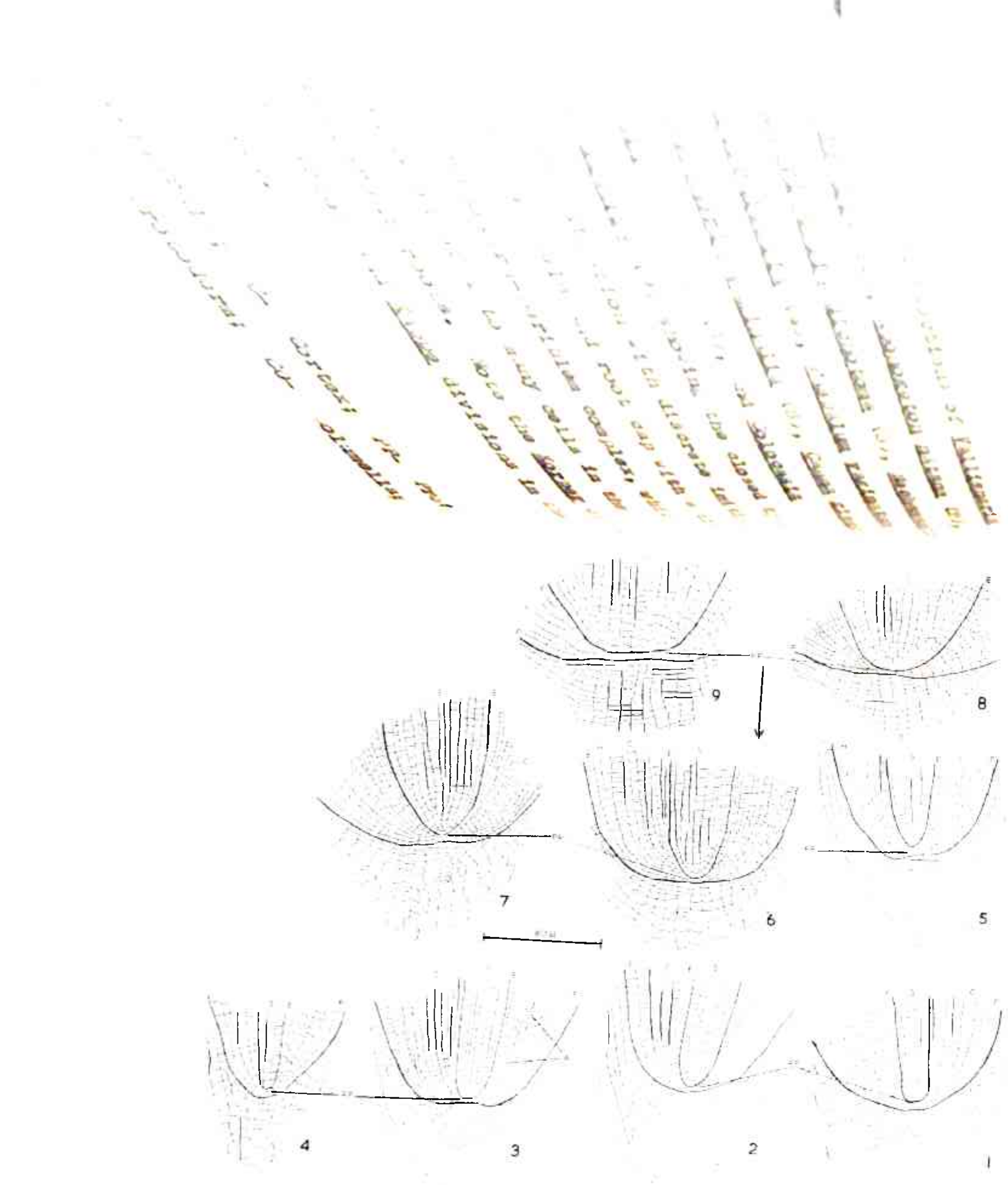
* Not read in original.

Figures 1 to 9: Median longisections of Vallisneria spiralis (1), Aponogeton [illegible] (2), Fimbristylis dichotoma (3), Hechamandra alternifolia (4), Paspalum vaginatum (5), Monochoria vaginalis (6), Canna glauca (7), Canna [illegible] (8), and Colocasia esculenta (9) showing the closed type of organization with discrete initials for the stele and root cap with a tier of protoderm-periblem complex, which is composed of 1 to many cells in the different roots. Note the Körper divisions in cortex and Kappe divisions in the cap flanks.

S- Stele; E- Endodermis; C- Cortex; PP- Protoderm-periblem complex; P- Protoderm; CO- Columella; A- Air space.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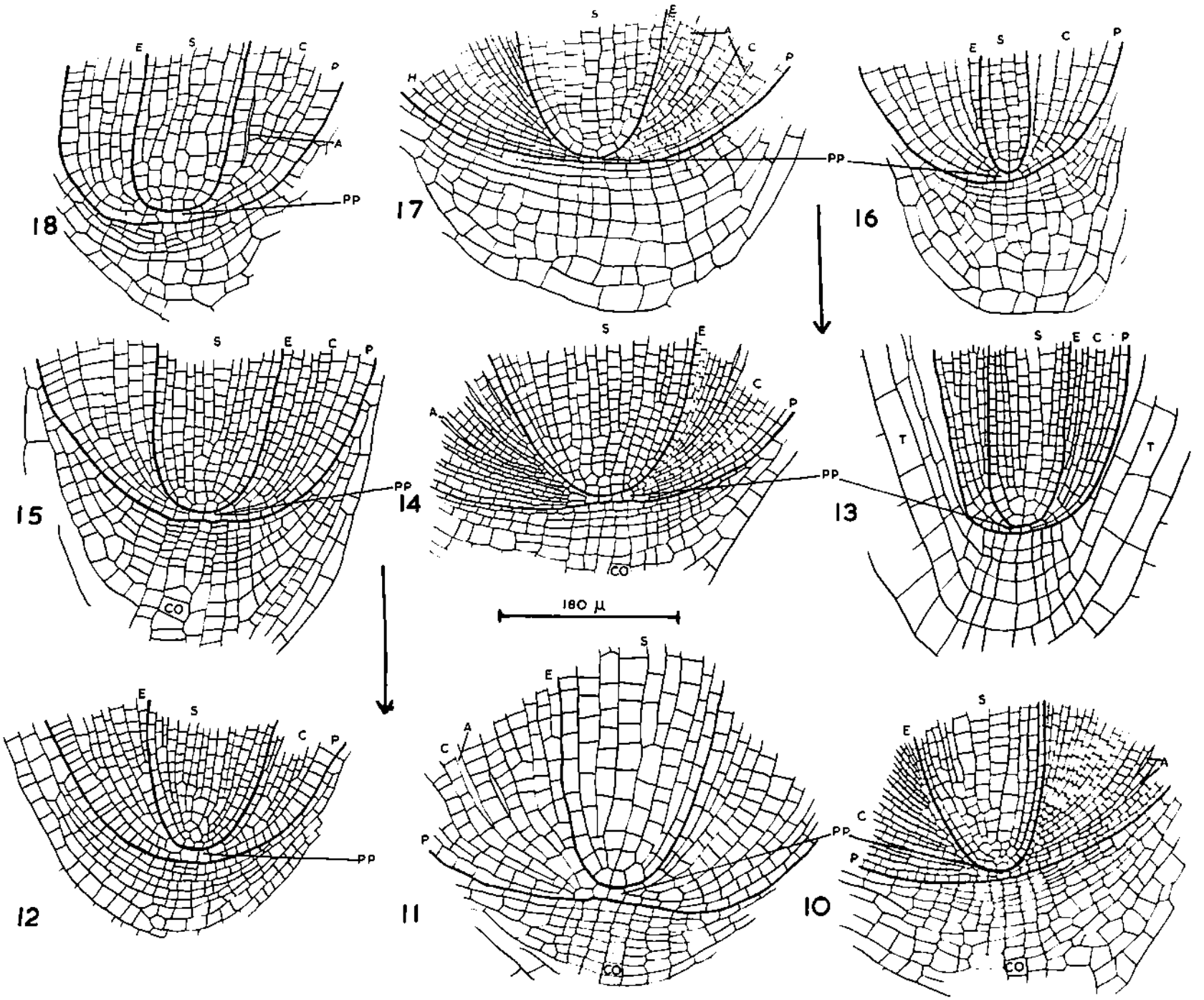
Figures 10 to 18: Median longisections of the closed type of root apex of Typha angustata (10), Tinantia fugax (11), Stratiotes aloides (12), Eichhornia crassipes (13), Limnocharis emarginata (14), Typhonium trilobatum (15), Alyxia ruscifolia (16), Alocasia indica (17) and Alisma plantago (18) with discrete initials for the root cap and stele and a protoderm-periblem complex of one to many cells. Note the T-divisions of the Körper and Kappe types in the cortex and cap respectively.

S- Stele; E- Endodermis; C- Cortex; PP- Protoderm-periblem complex; P- Protoderm; CO- Columella; A- Air space.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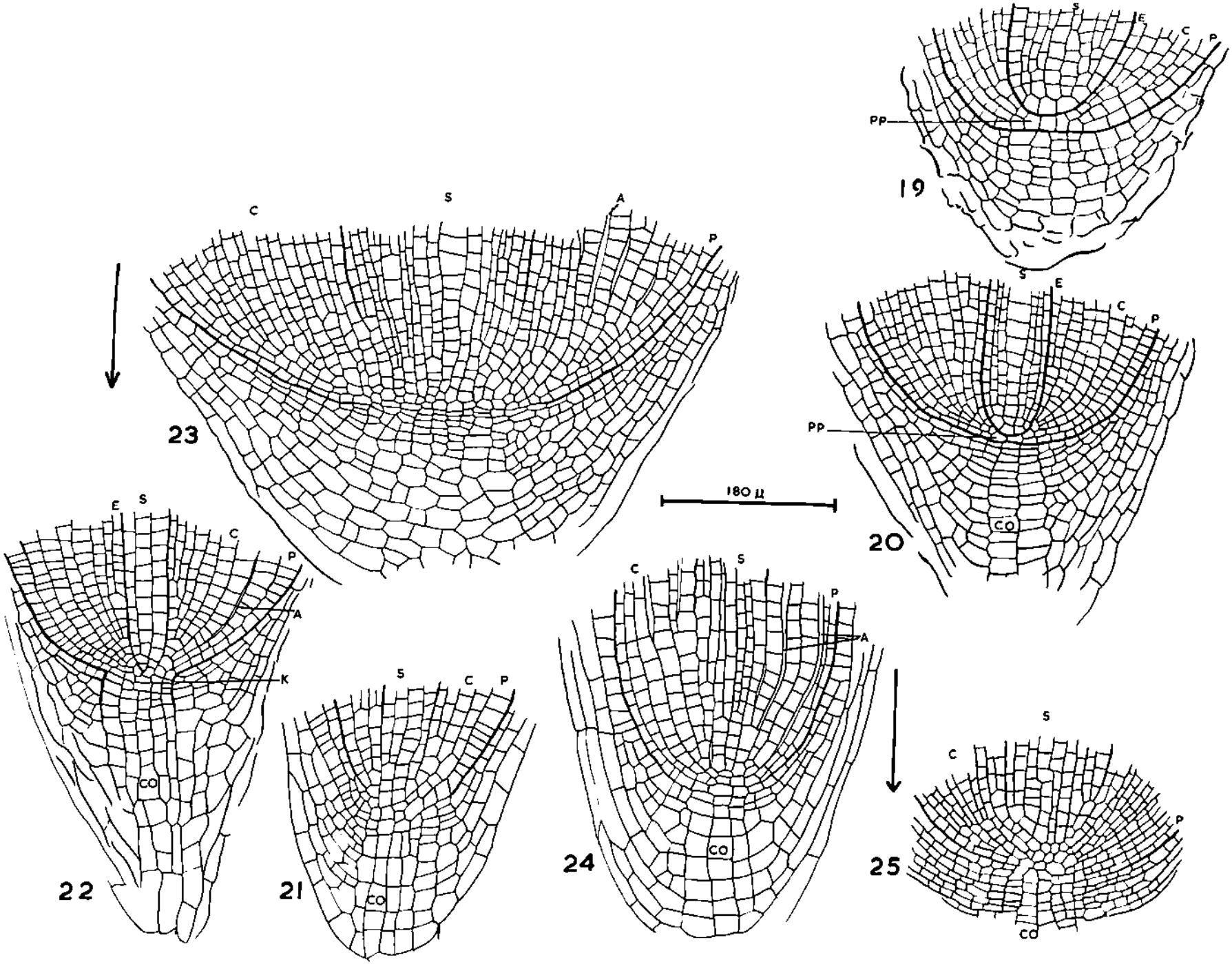
CO
180 μ

Figures 19 & 20: Median longisections of the root apices of Cattleya lutea (19) and Potamogeton [illegible] (20) showing the closed type of organization with discrete initials for the stele and root cap and with a single tier of initials for the epidermis and cortex, the Protoderm-periblem complex.

Figures 21 to 25: Median longisections of the root apices of Najas minor (21), Cyperus diffusus (22), Acorus calamus (23), Hydrilla verticillata (24) and Scirpus [illegible] (25) showing the open type of configuration with a common group of initials from which arise the stele proximally, root cap distally, and the epidermis and cortex on the flanks. Note the knee formation connecting the cortex and columella in 22 and the formation of more [illegible] divisions to the periphery than near the stele in 23.

S- Stele; E- Endodermis; C- Cortex; P- Protoderm; PP- Protoderm-periblem complex; CO- Columella; K- Knee joint; A- Air spaces.


S
E
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CO
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P
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24
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C
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25

Fig.26a. Ensete superba. Median L.S. of apex of young root apex with discrete initials for the stele and root cap and the protoderm-periblem complex for the epidermis and cortex, i.e., the closed type.

Fig.26b. Ensete superba. Median L.S. of apex of an older root showing the opening out of the closed type of organization and now exhibiting common initials for all portions, with knee joints connecting the cortex with the root cap.

Fig.27a. Ottelia alismoides. Median L.S. of young root showing partially closed type having discrete initials for the stele but with those of the cap and cortex merging.

Fig.27b. Ottelia alismoides. Median L.S. of older roots. The stelar initials have also merged and the knee joints and secondary columella files can be seen clearly.

Fig.27C. Ottelia alismoides. Median L.S. of a fully open root apex with common group of initials for all tissues, the columella having become broader by more knees and secondary columella files.

P- Protoderm; C- Cortex; S- Stele; Co- primary columella; S.Co- Secondary columella; K- Knee joints; PP- Protoderm-periblem complex; A- Air space.

Figs.A & B. Schematic representation of the opening out of the closed type by the formation of knee joints and secondary columella files.

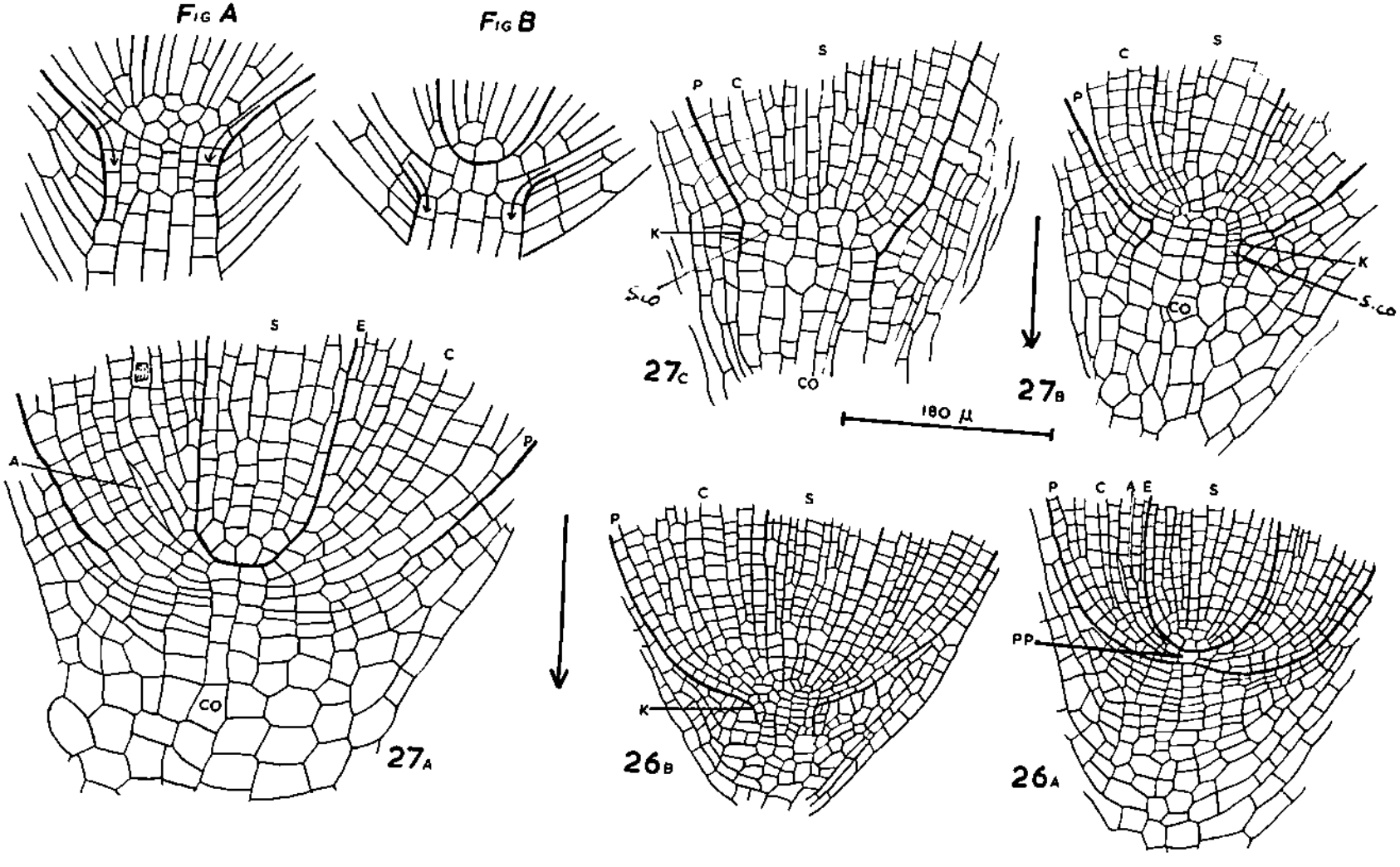


FIG A
FIG B
S
P
C
K
S.CO
CO
27C
27B
180 μ
E
A
27A
PP
26B
26A

Stages in the development of lateral roots.

Figures 23a,b,c,d. Monochoria vaginalis.

Figures [illegible]. Eichhornia crassipes.

Figures 30a,b,c,d. Canna glauca.

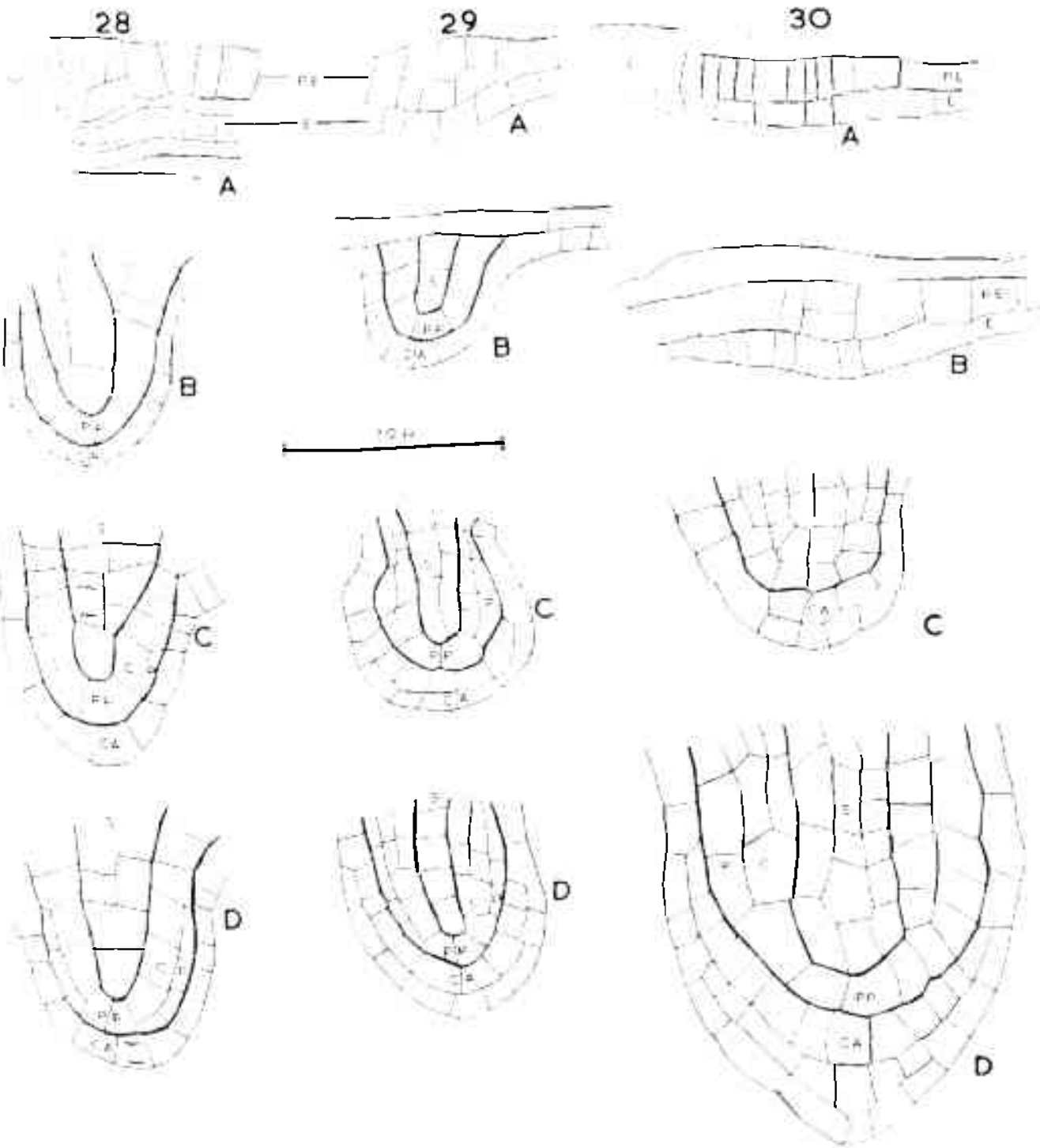
a- Cells of the pericycle and endodermis of the mother root enlarging and those of the former dividing periclinally.

b- Further segmentation resulting in two discrete regions of which the inner forms the stelar initials. The endodermal cells dividing anticlinally and keeping pace with the growing hump.

c- The outer layer of cells derived from the pericyclic cells dividing periclinally on the flanks to give rise to the initials for the protoderm and cortex, leaving a few cells at the tip. The endodermal cells at the tip of the hump also exhibiting periclinal divisions resulting in the Kappe complex formation.

d- A more advanced stage of development of the lateral root where the Kappe complex is more advanced. The protoderm-periblem initials are seen distinctly from which the protoderm and cortex initials arise to the sides. The former retains its single layered condition by anticlinal divisions whereas the cortical initials exhibit more T-divisions of the Körper type and become wider.

P- Pericycle; E- Endodermis; S- Stele; PP- Protoderm periblem complex; C- Cortex; P- Protoderm; Ca- Cap initials.


28
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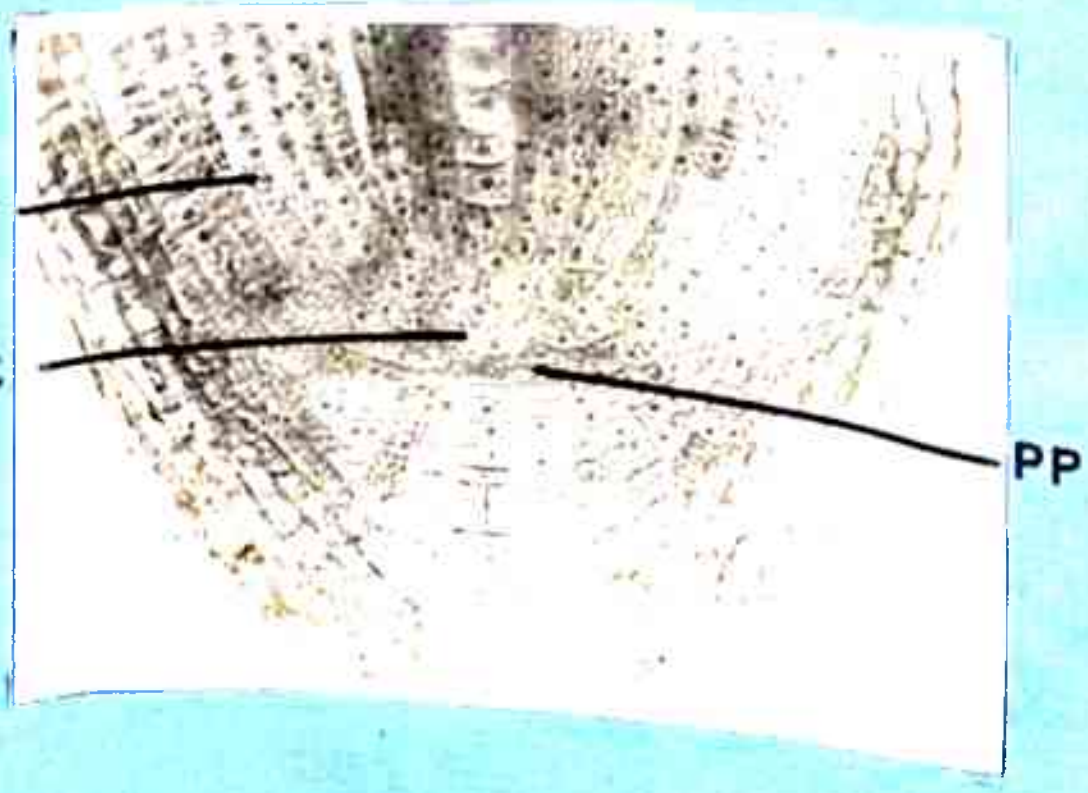
1. Typha angustata. An oblique section through the root apex showing the T-division (T) of the Grass type (x 400)

2. Vallisneria spiralis. Median L.S. of the 'closed' type of root apex with discrete initials for the root cap, the stele and the protoderm-periblem complex (pr). Note the lightly staining cells of the quiescent centre (QC) and the deeply staining ones of the promeristem (pm) lining it proximally. (x 400).

1

2



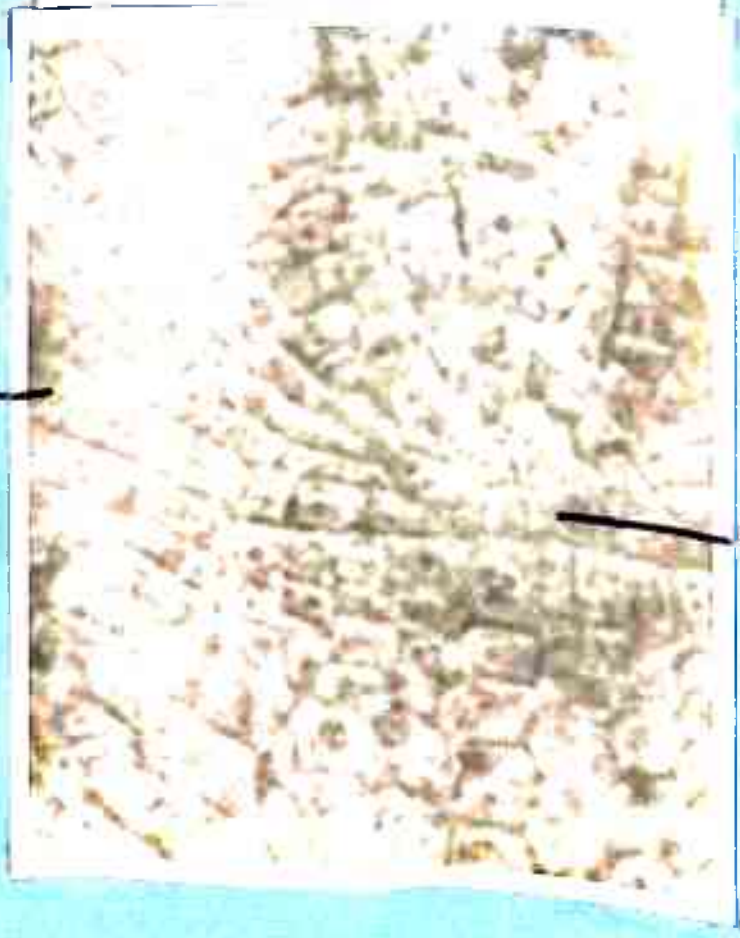
3 & 4. *Aponogeton natans* and *Fimbristylis dichotoma*.

Median longisections through the closed type of root apices showing discrete initials for the root cap & the stele; the protoderm-periblem complex between them (PP). (x 300 & 600 respectively).

P- Protoderm.

3

4



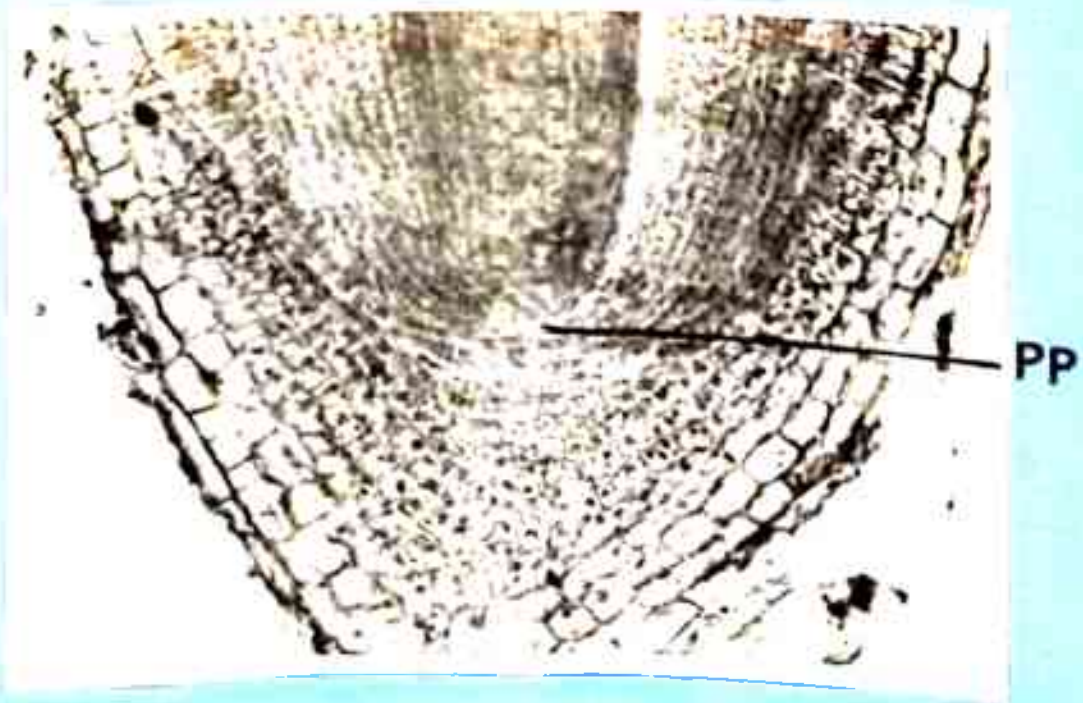
5 & 6. Calathea bella and Pandanus vaginatum.

Median longisections through the closed type of root apices showing discrete initials for the root cap and the stele; the protoderm-periblem complex (PP) between them. (x 400 & 650 respectively).

P- Protoderm.

H- Hypodermis.

5

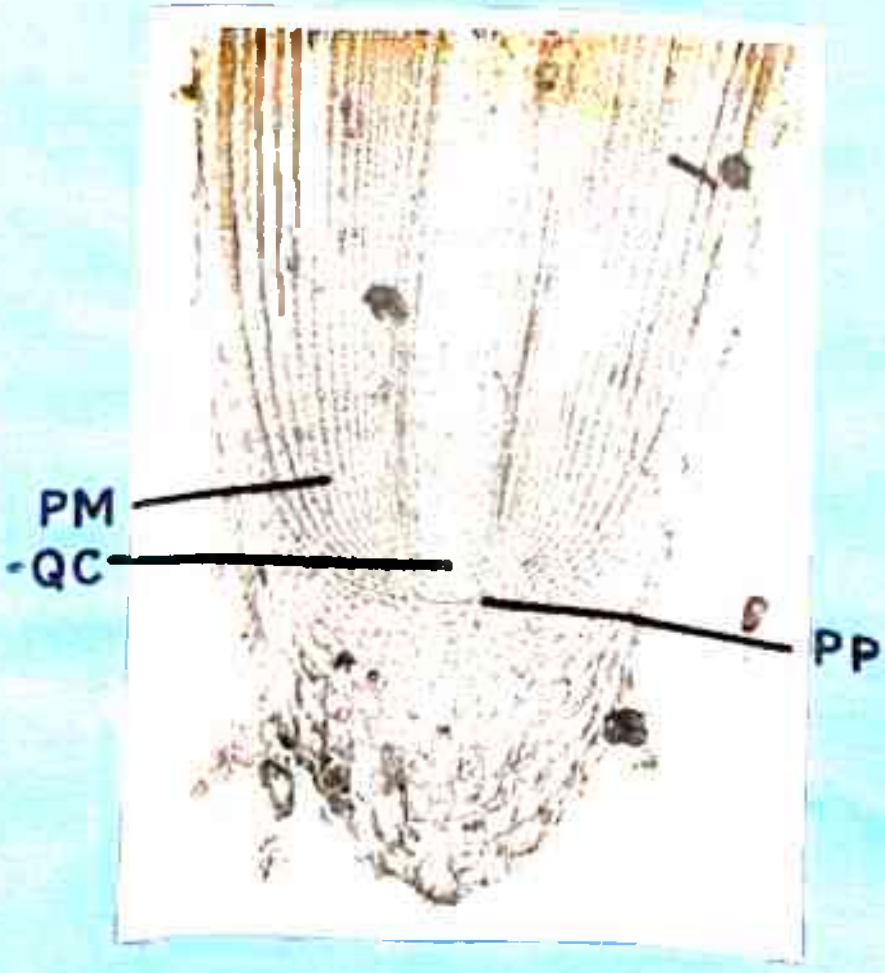


6

7 & 8. *Mompesoria vaginalis* and *Canna glauca*.

Median longisections of closed type of root apices with discrete initials for the root cap and the stele; the protoderm-periblem complex(PP) between them. Note the lightly stained cells of the quiescent centre (QC) and the deeply stained cells of the promeristem (PM) lining it proximally. (x 160 & 250 respectively).

7

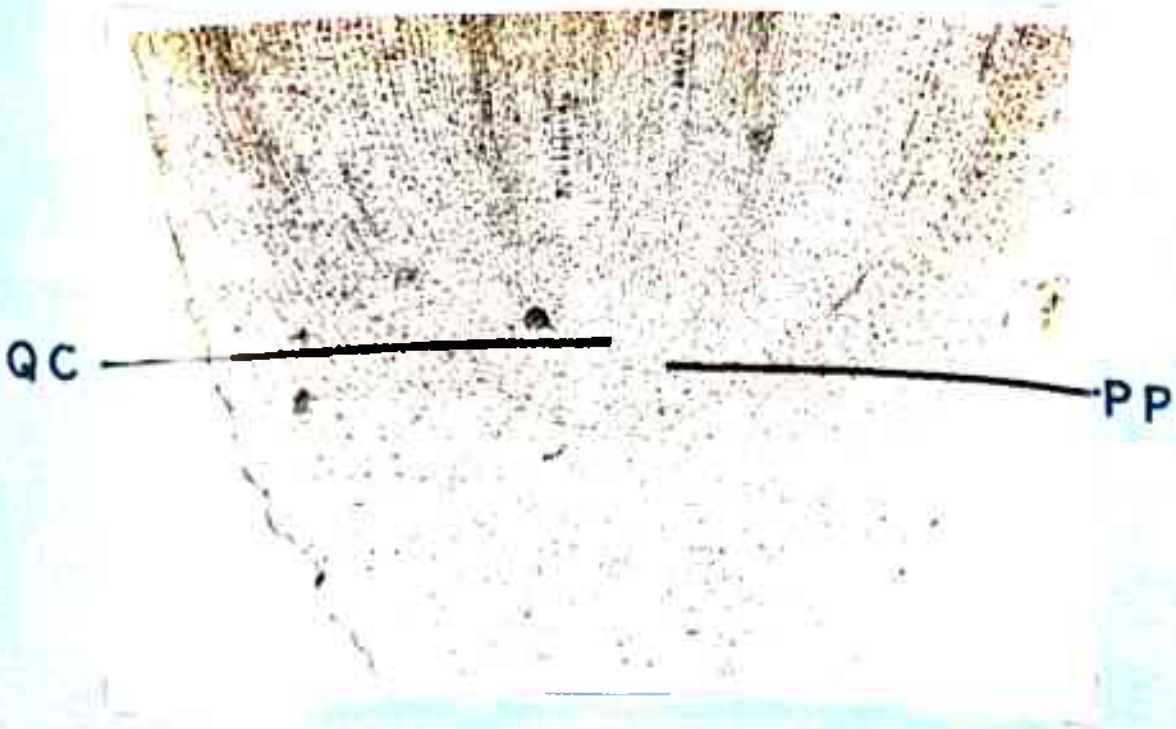


8

9 & 10. *Colocasia esculenta* and *Typha angustata*.

Median longisections of closed type of root apices with discrete stelar and root cap initials and the protoderm-periblem complex (PP) between them. Note the root cap cells with darkly staining contents (M) in *Typha* which may be the beginning of metacutis development. Note also the lightly staining cells of the quiescent centre (QC) and the deeply staining cells of the promeristem lining them proximally. (x 130 each).

9



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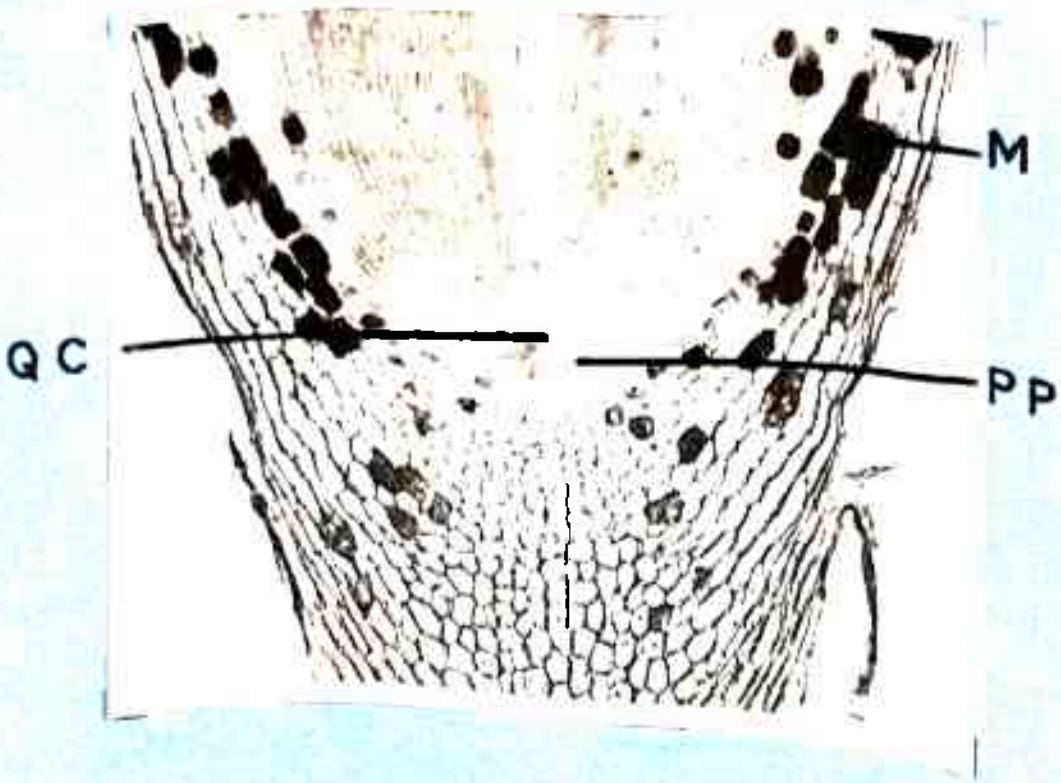
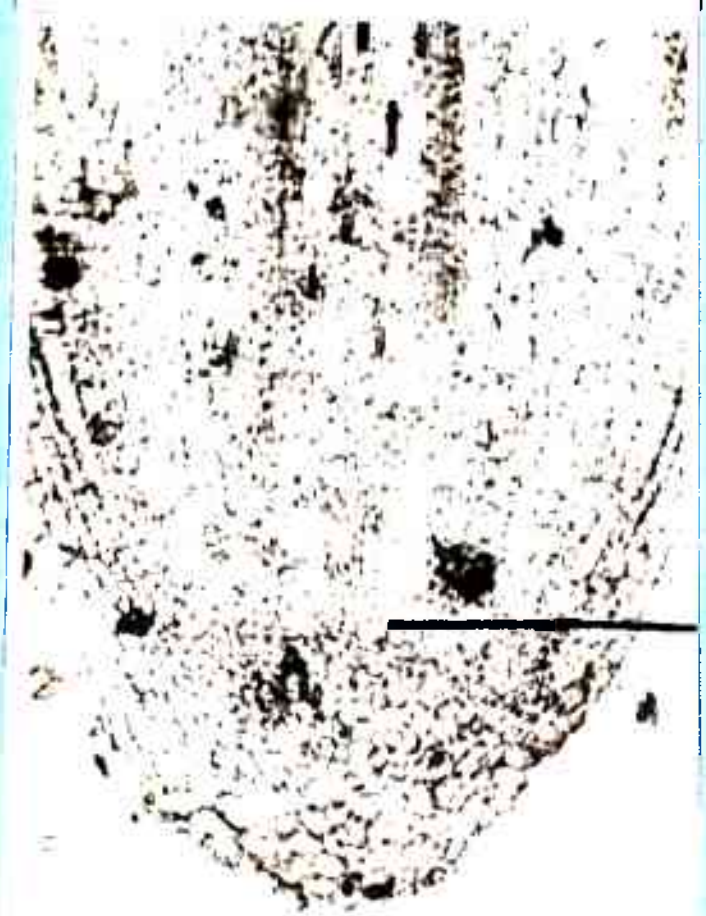


11 & 12. *Tinantia fugax* and *Streptolirion [illegible].*

Median longisections of closed type of root apices with discrete initials for the stele and the root cap; the protoderm-periblem complex (PP) between them. Note the deeply stained cells of the metacutis (M) more or less covering the root apex. (x 160 & 200 respectively).

11

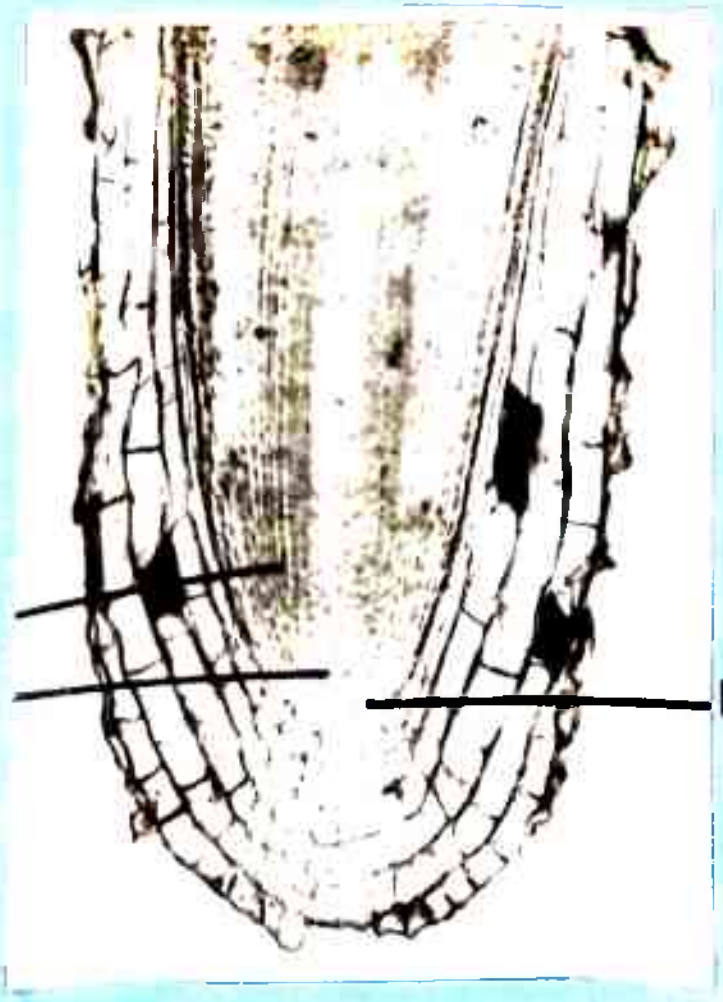
12



13 & 14. Eichhornia crassipes and Dieffenbachia sp.

Median longisections of closed types of root apices with discrete initials for the stele and the root cap; the protoderm-periblem complex (P.) between them. Note the lightly stained cells of the quiescent centre (QC) and the deeply stained cells of the promeristem (Pm) lining it proximally. (x 160 & 200 respectively).

13



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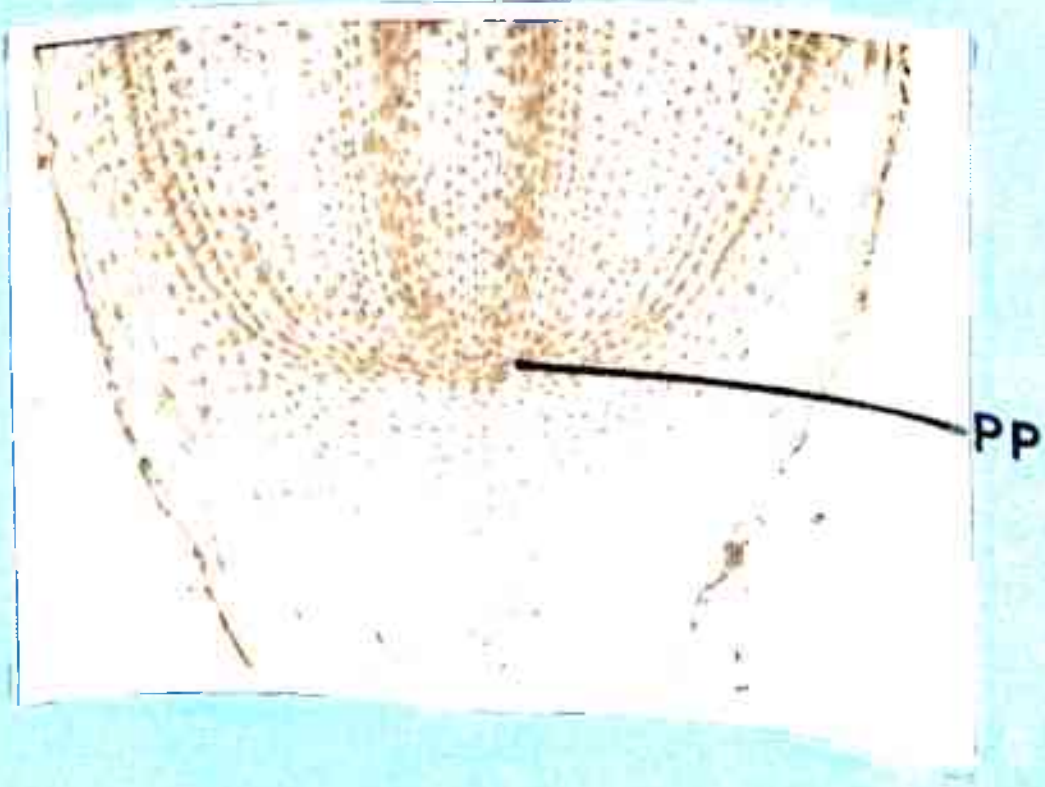
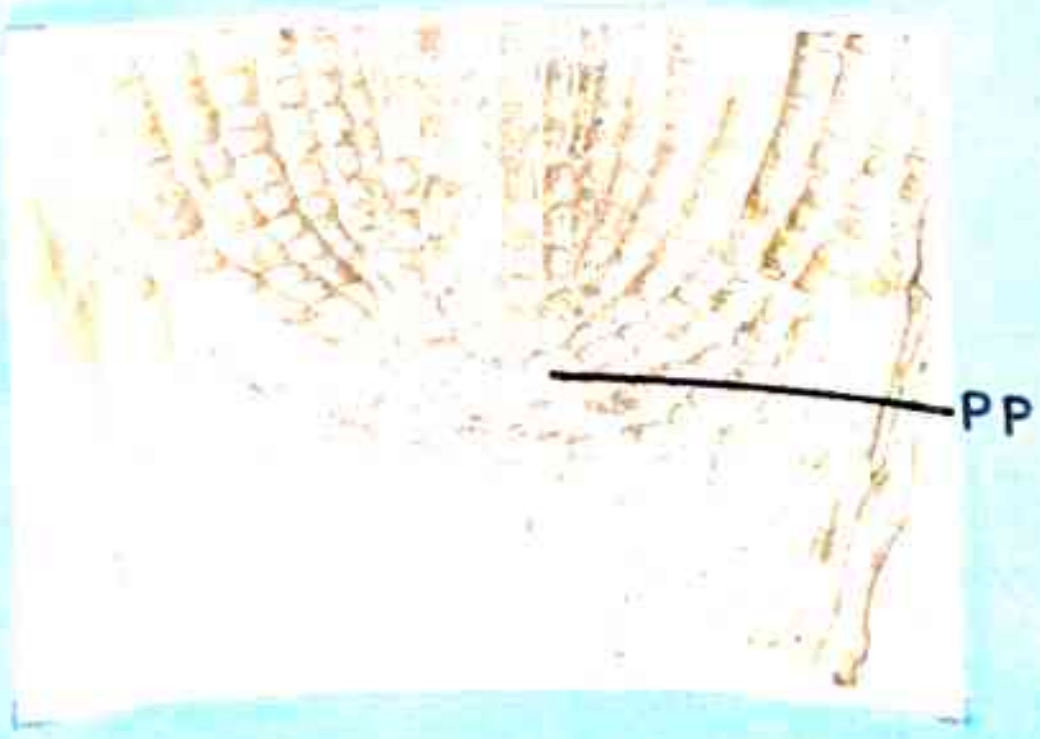


15 & 16. Alyxia subarti and Alexandia indica.

Median longisections of closed type of root apices with discrete initials for the stele and the root cap; the protoderm-periblem complex (PP) between them. (x 400 & 200 respectively).

15



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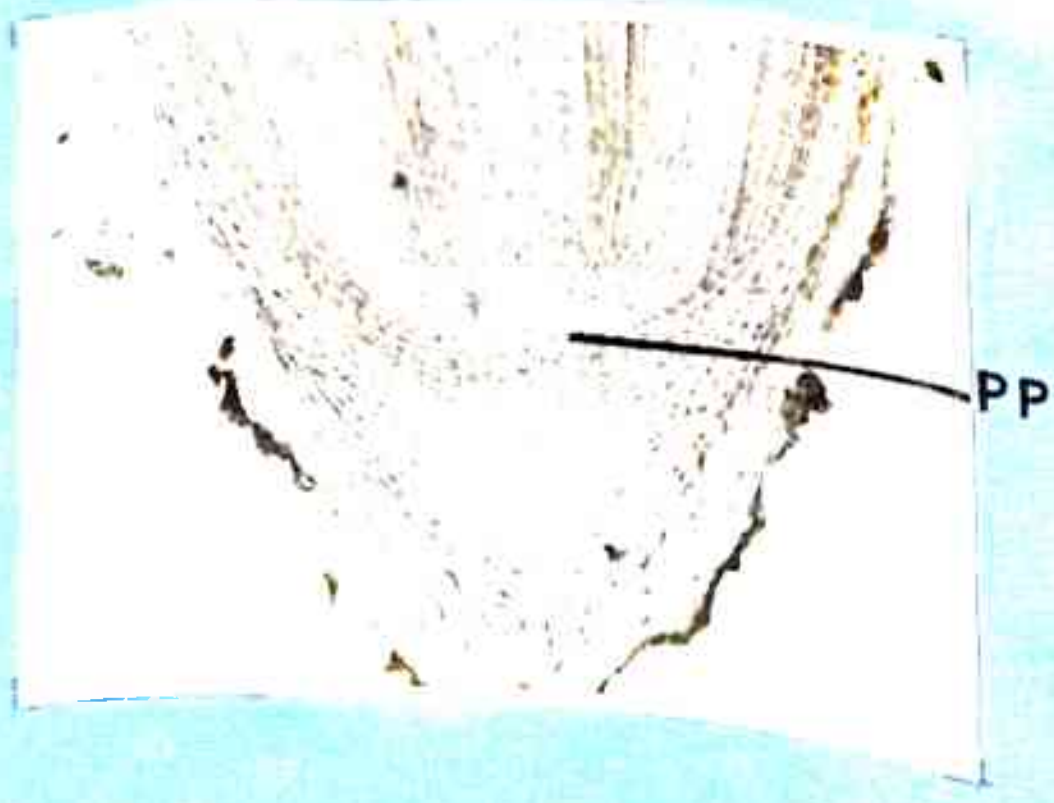
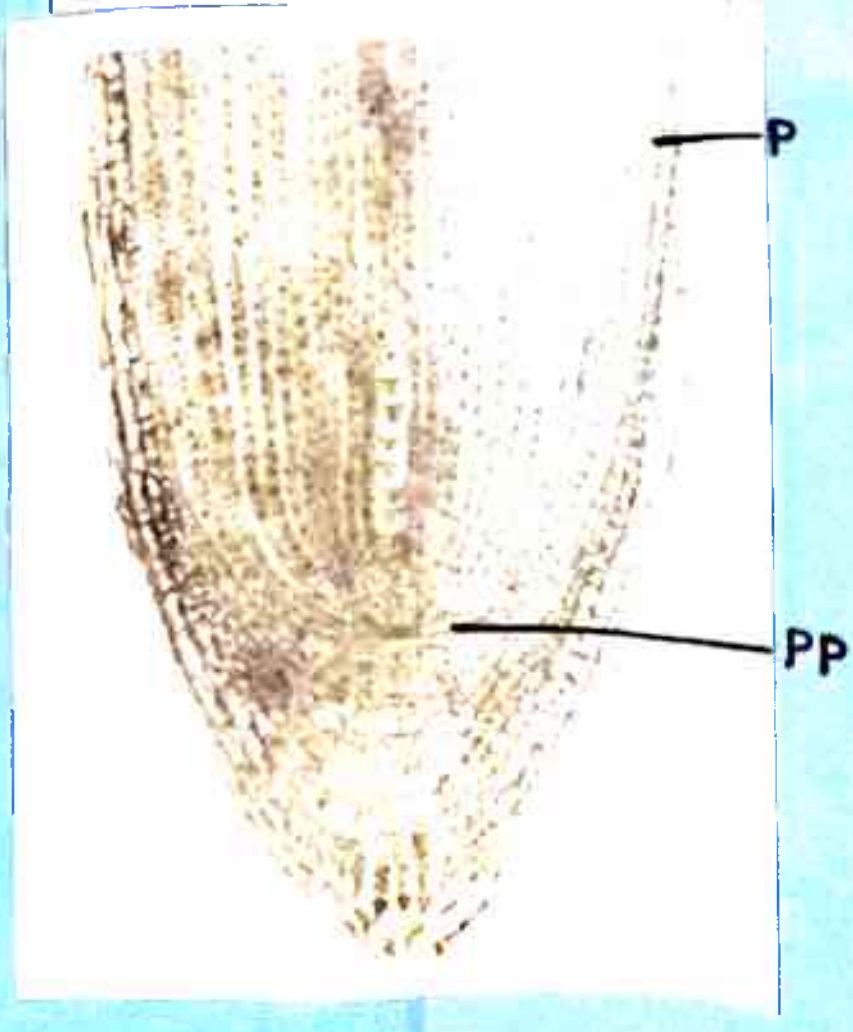


17 & 18. *Alisma plantago* and *Potamogeton lucens*.

Median longisections of closed type of root apices with discrete initials for the stele and the root cap; the protoderm-periblem complex (PP) between them. Note the darkly stained metacutis cells (M) in the root cap region of *Alisma*.
(x 200 & 250 respectively).
P. Protoderm.

17

18



19. Hocquandra alternifolia.

Median longisection of the closed type of root apex with discrete initials for the root cap; the stele; the protoderm-periblem complex (pp). (x 400).

20. Nyssa minor.

Median longisection of the open type with common group of initials. (x 200).

P- Protoderm.

19

20

21 & 22. Cyperus diffusus and Acorus Calamus.

Median longisections of open type of root apices with common group of initials for all tissues. Note the knee (K) in Cyperus and the preponderance of Korper type of divisions to the periphery of the cortex in Acorus. (x 400 & 150 respectively).

21

22

23 & 24. Hydrilla verticillata and Scirpus grossus.

Median longisections of root apices showing the open type of configuration with common group of initials for all tissues. Note the cells of the quiescent centre (QC) with lightly stained cytoplasm and the deeply stained cells of the promeristem lining it proximally. (x 400 & 250 respectively.)

23

24

25. Phoenix humilis.

Median longisection of open type of root apex with common group of initials for all the tissues. Note the lightly stained cells of the quiescent centre (QC) lined by the deeply stained cells of the promeristem proximally. (x 300).

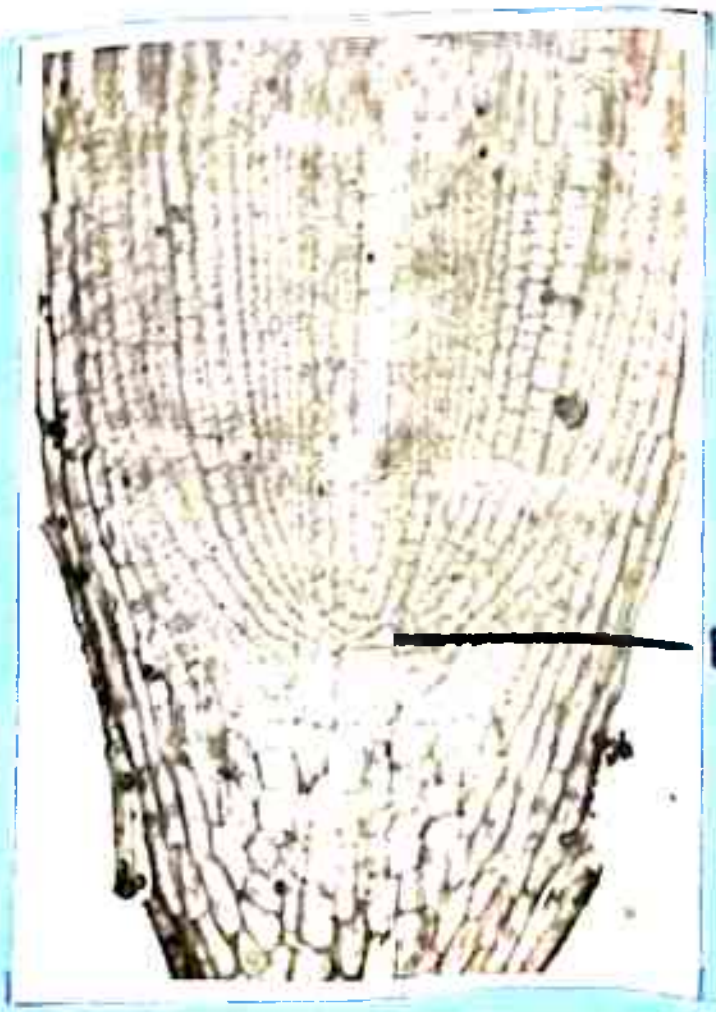
26a. Ottelia alismoides.

Median L.S. of young root apex with discrete stelar initials and the cortex initials opening out. (x 160).

Pr- Protoderm-periblem.

25

26
A



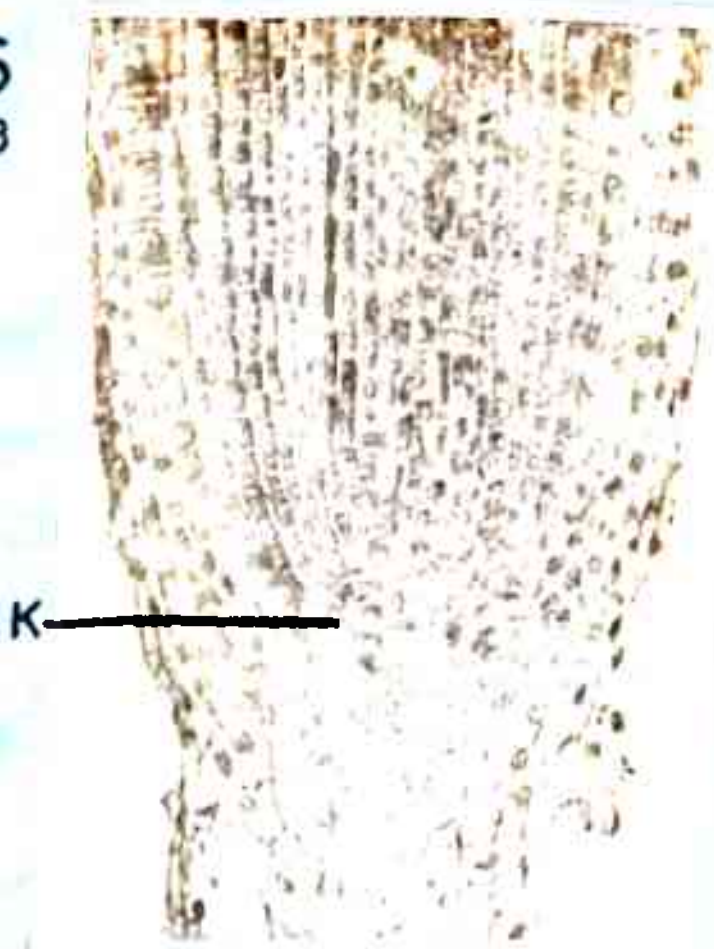
26b. Ottelia alismoides.

Median L.S. of root apex with open configuration. Note the knees (K) connecting cortex and columella. (x 160).

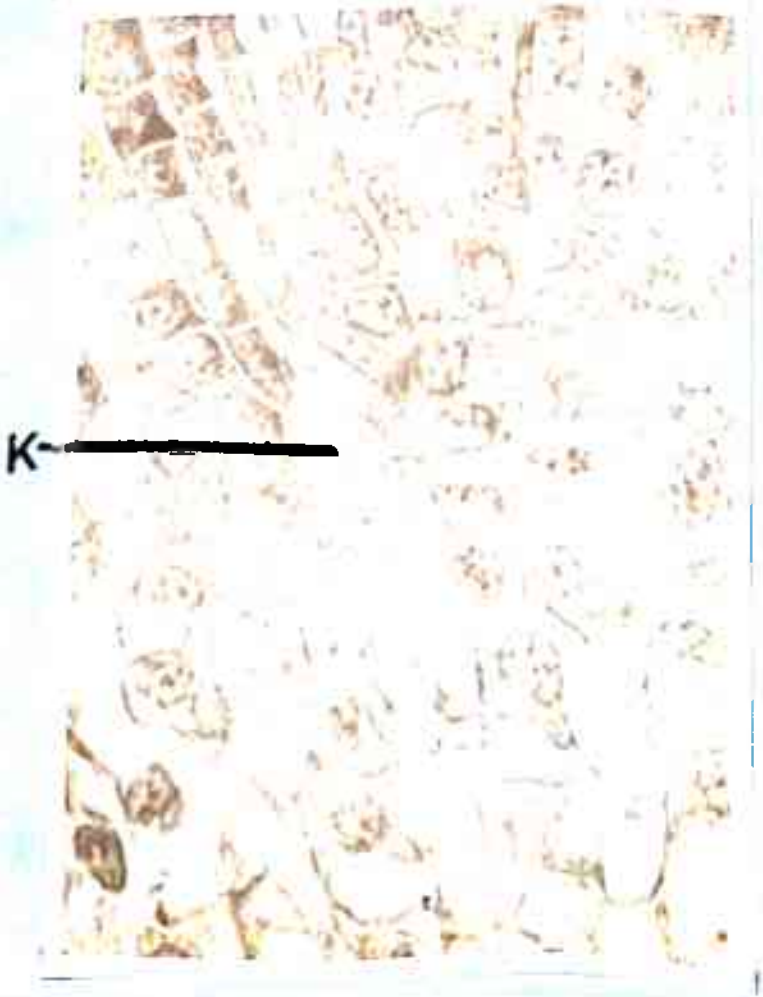
26c. Ottelia alismoides.

Portion of root in 26b enlarged to show knee joints (K). (x 600).

26
B



26
C



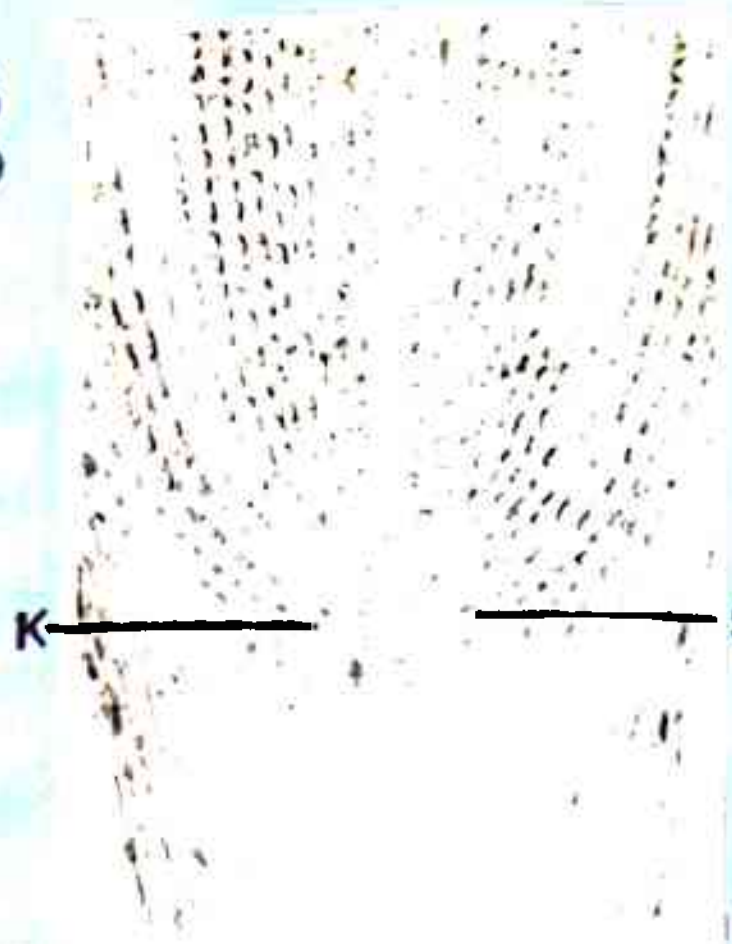
26a. Stele elaborated.

Median L.S. of apex of old root with fully open configuration. Note knees and secondary columella files (S.CO). (x 200).

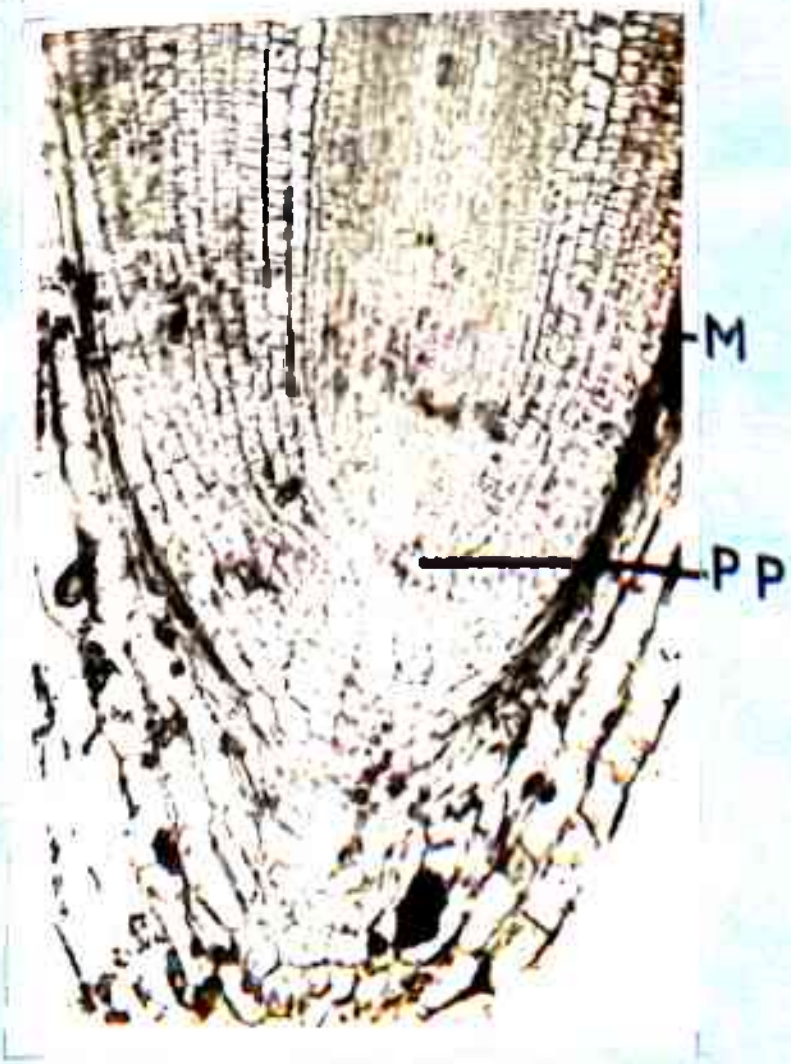
27a. Stele young.

Median L.S. of young root with close type of configuration showing discre initials for the stele and the root the protoderm-periblem complex (PP) them. Note the development of meta in root cap. (x 160).

26
D



27
A



27b. Ornata superba.

Median L.S. of apex of older root with open configuration. Note the knob (K) connecting cortex with cap and secondary columella files (S.CO). (x 300).

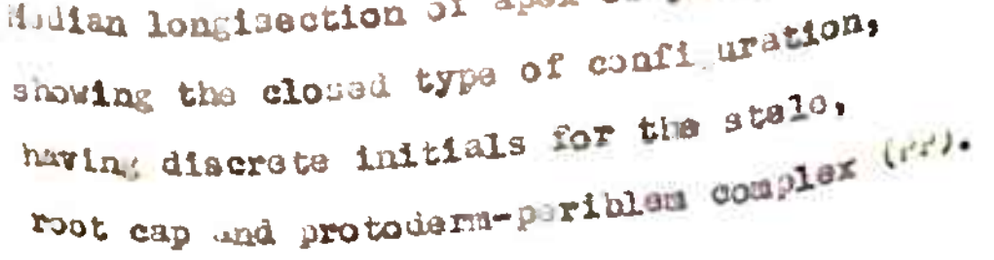
27c. Ornata superba.

Non-median longisection of root apex to show the development of metacutis (M). (x 160).

27B

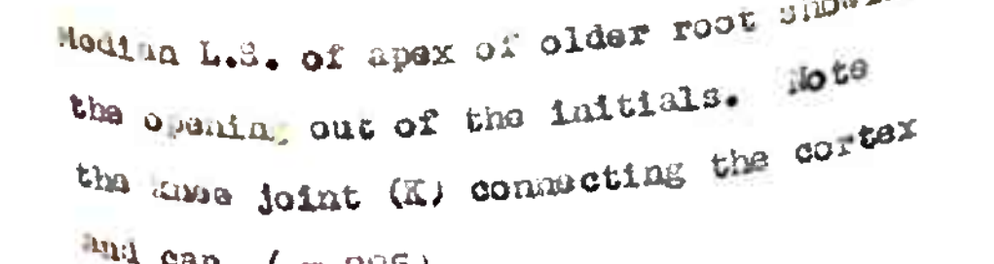
27C

28a. Caladium sp.



Median longisection of apex of young root showing the closed type of configuration, having discrete initials for the stele, root cap and protoderm-periblem complex (*r*). (x 325).

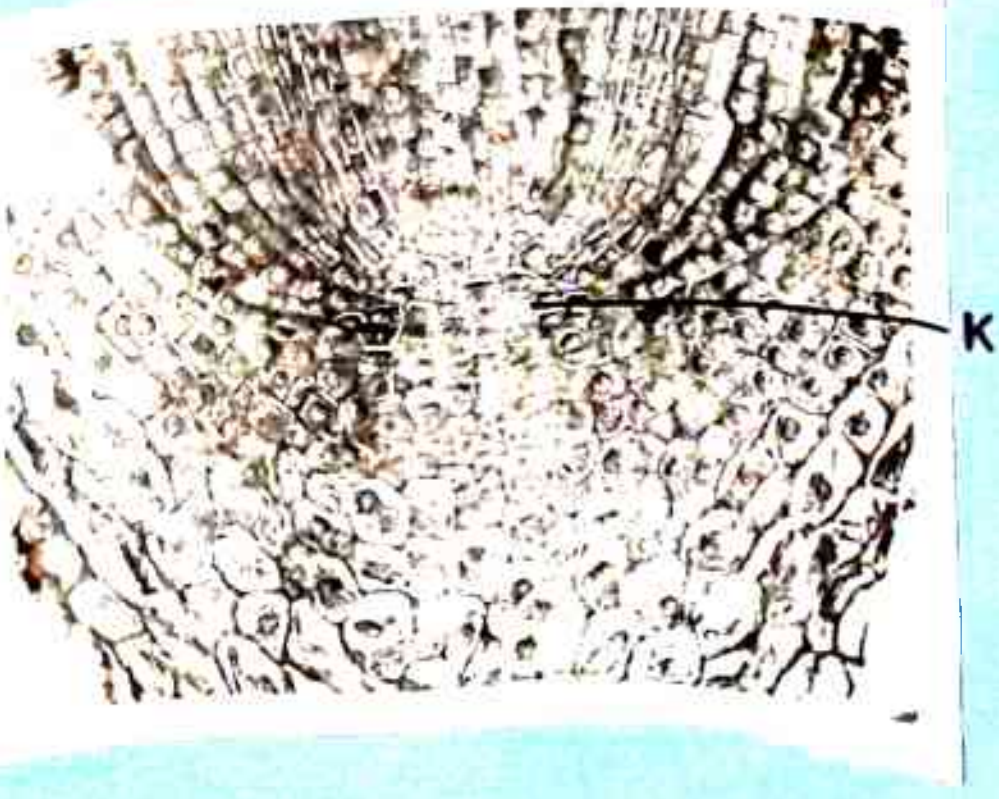
28b. Caladium sp.



Median L.S. of apex of older root showing the opening out of the initials. Note the knee joint (K) connecting the cortex and cap. (x 325).

28A

28B



29 & 30. Potamogeton lucens and Vallisneria spiralis.

Portion of root epidermis in L.s. showing short, highly cytoplasmic trichoblasts with prominent nuclei and nucleoli alternating with longer, vacuolated cells having small, dwindling nuclei. (x 600 & 400. respectively).

29

30

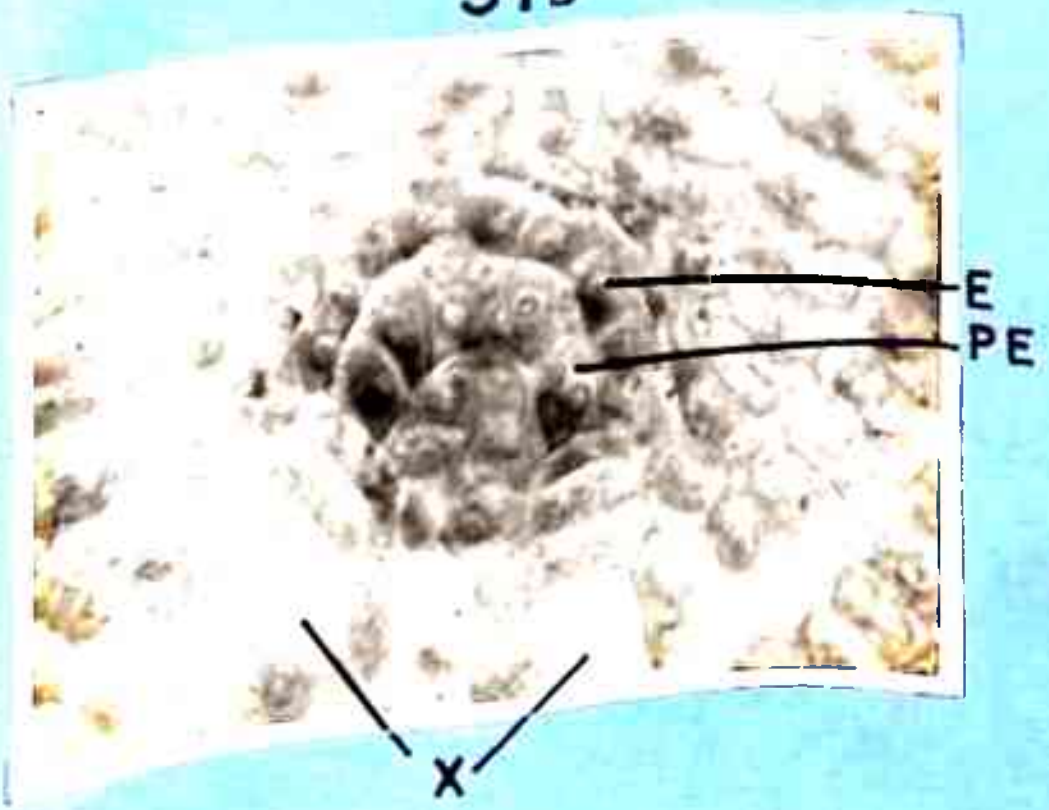
31a,b. <u>Monochoria vaginalis</u>.

Section of root showing development of lateral root. Note pericycle (Pc) and endodermis (E) taking part. The pericyclic cells dividing periclinally, the outer layer of which becomes distinct from the inner. (x 1000 each).

X- Xylem.

31A

31B

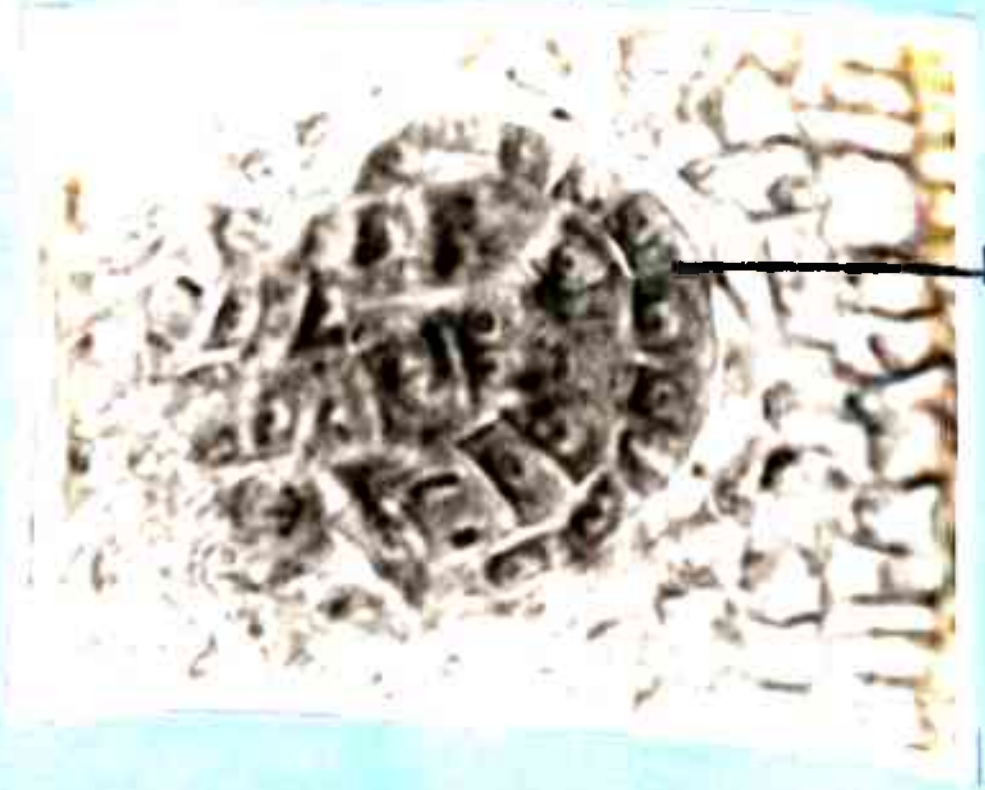


31c,d. Monoceria vaginalis.

Section of root showing development of lateral root. Note the outer layer of cells derived from the pericycle dividing periclinally to form the Körper complex of which the outer layer forms the protoderm (P) and the inner layers, the cortex (C). The inner layer derived from the pericycle forms the stelar initials. (x 1000 & x 1000).

RC Root cap.

31C



C P 31D

32a. Eichhornia crassipes.

L.S. of root showing lateral formation, in which both pericycle (PE) and endodermis (E) of mother root are taking part. (x 400).

32b. Eichhornia crassipes.

L.S. of developing lateral root showing three layers, the outer derived from the endodermis and the inner two from the pericycle of the mother root. (x 1000).

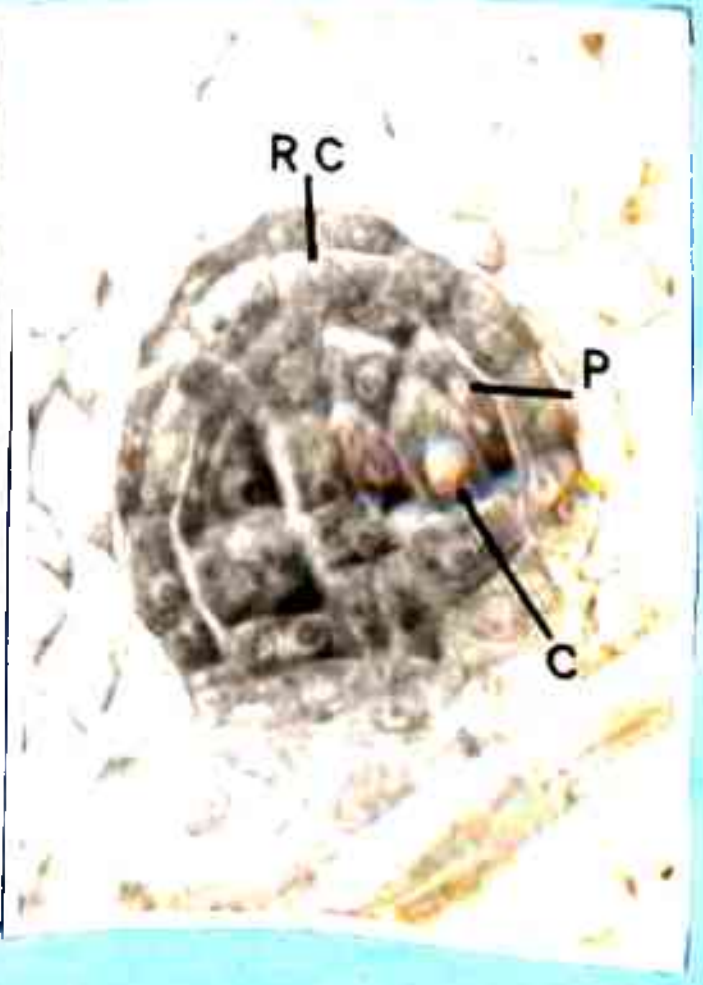
32c. Eichhornia crassipes.

L.S. of developing lateral root showing the periclinal divisions in the outer layer of endodermal origin forming Kappe complex of the root cap (RC). The periclinal divisions in the middle layer result in the Korper complex leading to the formation of protoderm (P) outside and cortex (C) inside. The innermost layer forms the stele. (x 1000).

32A

32B

32C

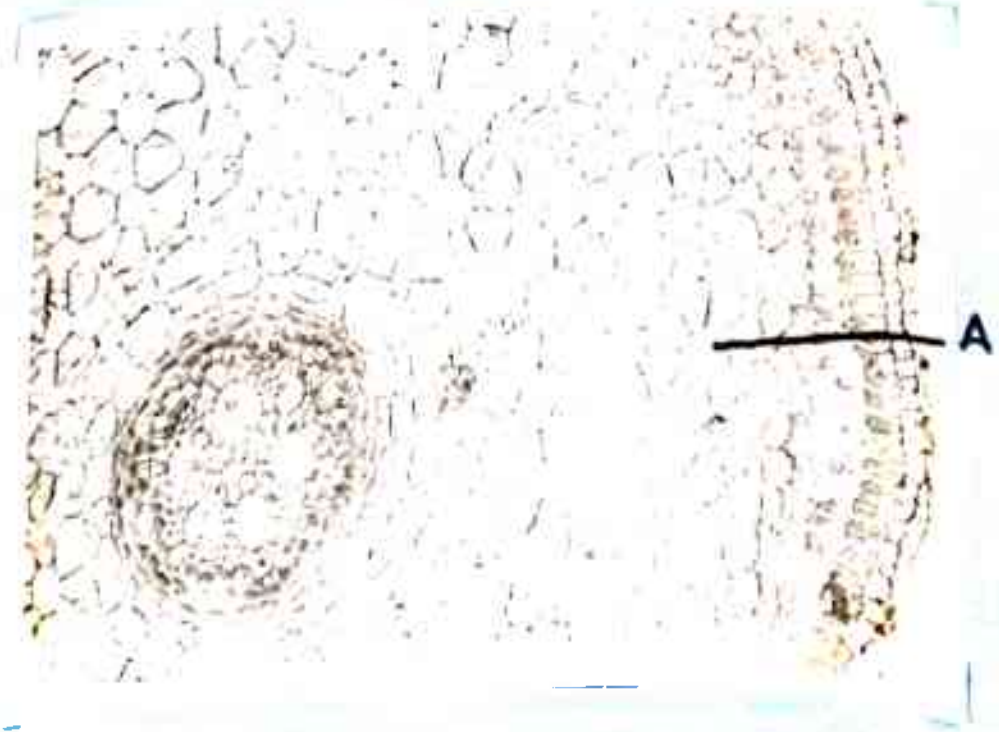


33 & 34. *Ottelia alismoides* & *Acorus calamus*.

T.S. of root showing schizogenous development of air spaces (A). Note the smaller spaces around the stele becoming bigger towards the periphery, with cross- shaped cells around diamond-shaped spaces in *Ottelia* and polygonal cells and spaces in *Acorus*. (x 250 each).

33

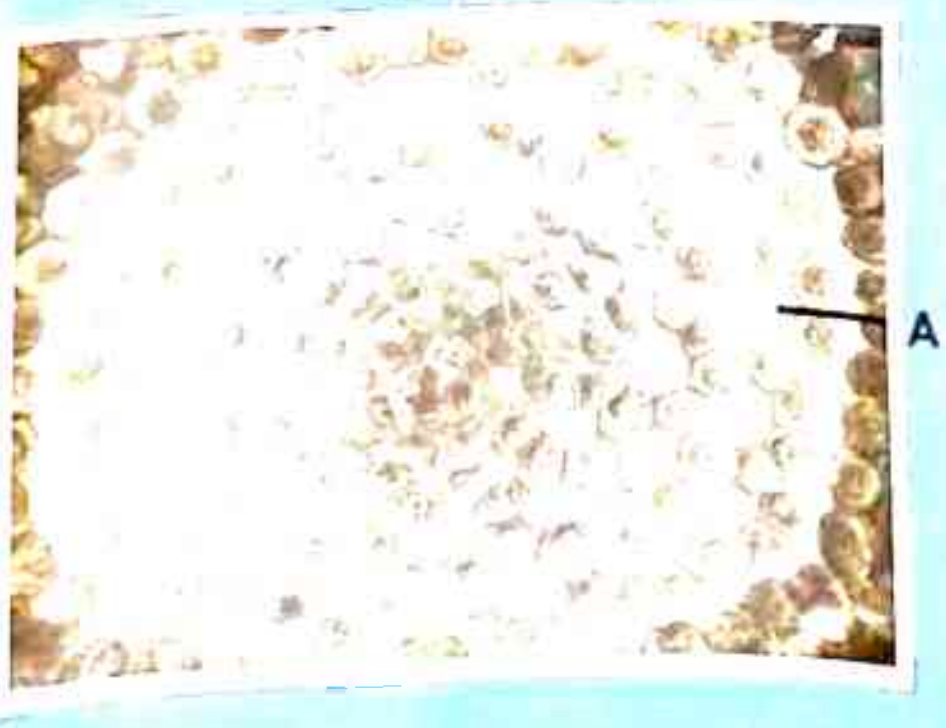
34


A

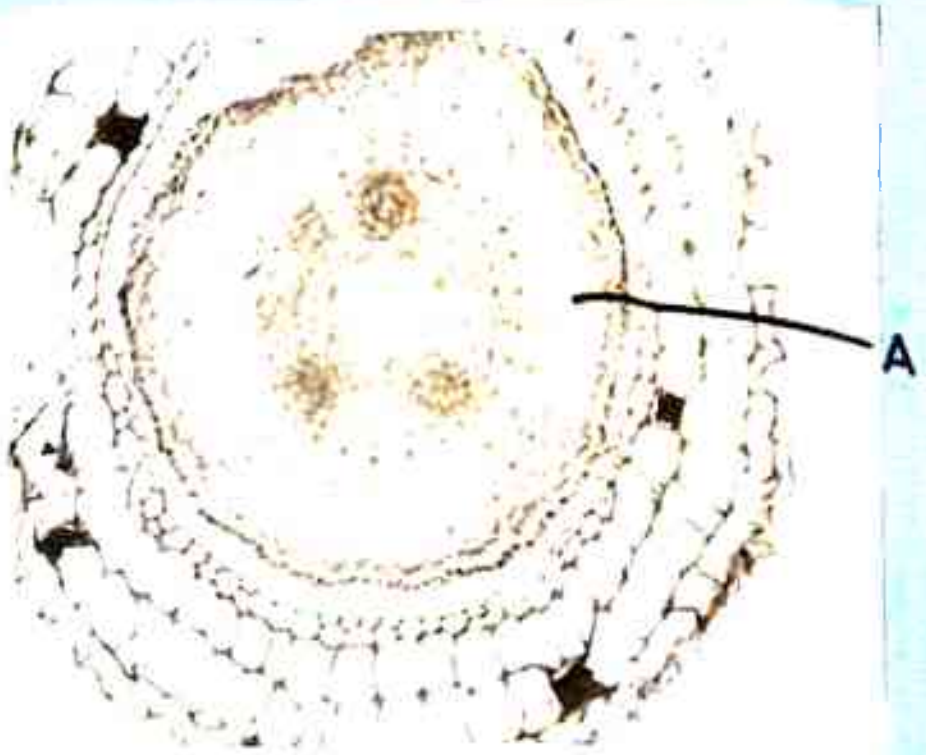
35, 35a. <u>Hydrilla verticillata</u> & <u>Eichhornia crassipes</u>.

T.S. of root with schizogenous air spaces (A), the smaller ones around the stele and bigger ones farther away. Note the polygonal spaces surrounded by polygonal cells in <u>Hydrilla</u>. In <u>Eichhornia</u> no connection between the root pocket cells and the root proper in the proximal region. (x 400 & 100 respectively).

35



36A



36b. Eichornia crassipes.

T.s. of root cortex of older portion of root enlarged to show the lysigenous enlargement of air spaces (A). (x 1000).

37a. Canna indica.

T.s. of root to show (i) schizogenous development of air spaces (A), and (ii) origin of lateral root involving both the endodermis and pericycle. (x 300).

36B

37A

37b. Canna humilis.

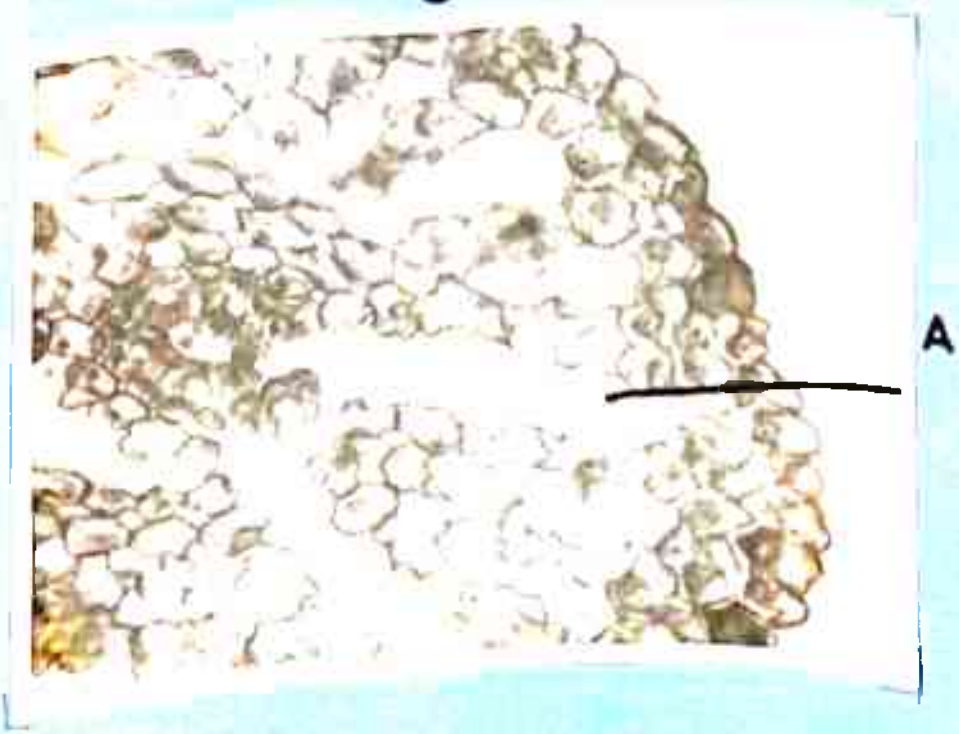
T.S. of cortex of older portion of root showing lysigenous enlargement of air spaces (A). (x 600).

38. Oryza sativa.

T.S. of cortex of older portion of root showing lysigenous enlargement of air spaces (A). (x 600).

37B

38



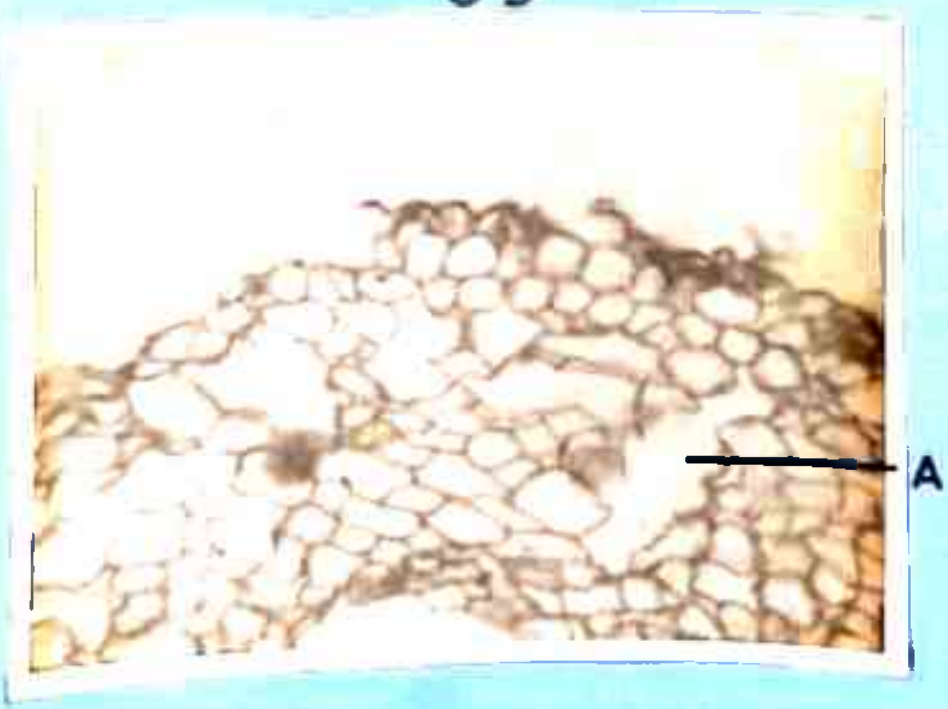
39. Fimbristylis dichotoma.

T.S. of cortex of older portion of root showing lysigenous enlargement of air spaces- A. (x 400).

40. Alisma plantago.

T.S. of cortex of older root showing schizogenous development and enlargement of air spaces (A). (x 400).

39



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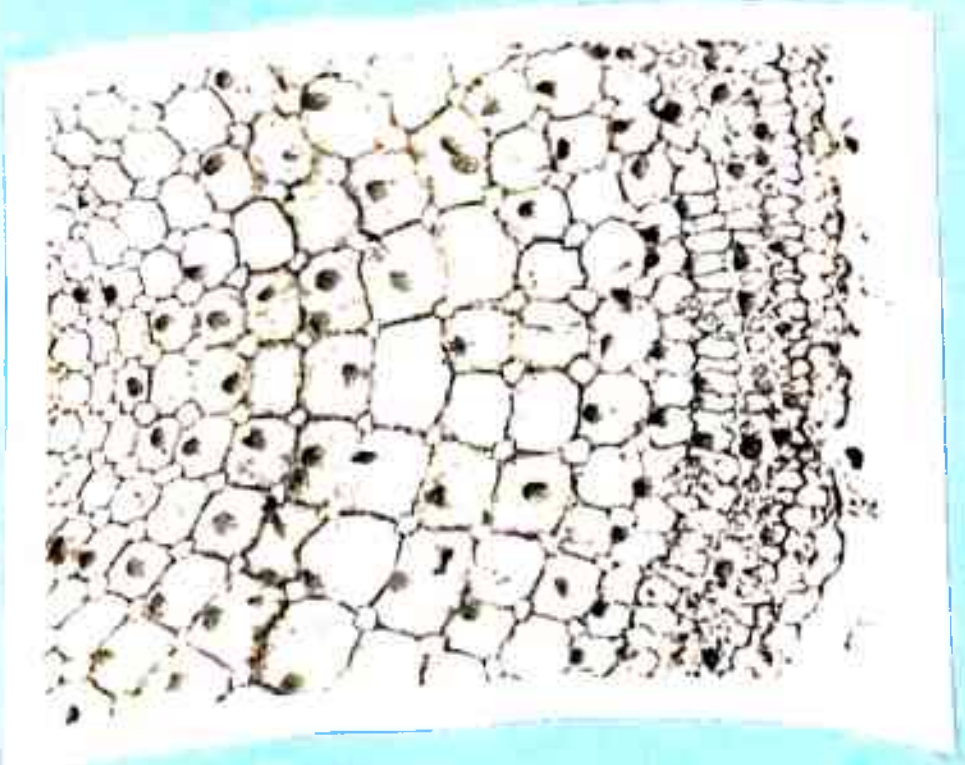

41. Maize shoot.

T.s. of root cortex showing schizogenous air spaces (A). (x 600).

42. Jussiaea vaginalis.

T.s. of root cortex showing schizogenous development and enlargement of air spaces (A). (x 600).

41

42