INTRODUCTION

A study of literature shows that the root apices of gymnosperms have not been worked out in detail in recent years. Van Tieghem (1870, 1891), Strasburger (1872, 1879), Bower (1882), De Bary (1884) and Van Tieghem and Douliot (1889) were among the first to report on gymnosperm roots. Chamberlain (1935) has pictured the development of the primary root from the embryo in some Cycadales. He shows the plerome to have discrete initials. The columella, composed of longitudinal files of cells, is located to its front. Both these are surrounded by a tissue mantle, which has been named by Hanstein (1870) “Keimenhang” and which, according to Guttenberg (1941), corresponds to the coleorhiza of the Gramineae. The cells constituting this outer mantle appear in curving files. The development of the root apical part of the embryo of Ginkgo has been described by Lyon (1904) and Coulter and Chamberlain (1910). In these also the plerome is described as having discrete initials. Recently, Ball (1956a, b) has described the embryo and embryonic root apex of Ginkgo biloba. Two very recent publications (Guttenberg, 1961; Clowes, 1961) have brought the literature on apical meristems into comprehensive shape.

MATERIALS AND TECHNIQUES

The root apical organization of the following species has been studied: Cycas revoluta Bedd., Cycas circinalis L., Zamia latifolia and Ginkgo biloba Linn.

The root tips were fixed on the spot in Buchholz’s variation of F.A.A. (cf. Brownlie, 1953). The usual methods of dehydration and embedding in paraffin were followed. For softening, the blocked materials were trimmed and soaked in water for one to four weeks, the duration depending upon the hardness of the material in each case. Serial longitudinal and transverse
sections were cut at 5 to 8 microns thickness. Tannic acid-iron chloride and safranin schedule with counterstaining in light green was followed (Johansen, 1940).

**Observations**

Though in some previous communications (Pillai and Pillai, 1961 a, b) the histogen terminology in a modified sense was used, here it is avoided and the root apical meristem is divided into zones based mainly on the types of cell complexes observed. By recognizing these cell complexes, the topography and the various cell types, it is possible to get an over-all picture of the general tissue patterns and organization.

The roots of all the four species reported upon here show a similar apical organization. So, a common description is given and the slight differences noticed are mentioned as they come up.

In all the four genera active as well as dormant roots are observed. Although the structural configuration is similar in both, some differences are noticed in the extent of the zones, the levels of tissue differentiation, demarcation between zones, tannin contents, etc.

*Shape of the apex.*—The dormant roots taper rather abruptly forming a blunt or obtuse tip. The active ones have a pointed, elongated and acute tip (Plate XI, Figs. 1 and 3; Plate XII, Fig. 1).

![Text-Fig. 1](image)  
A schematic sketch of the initiating regions of the Cycad type of root apex. The promeristem cup is shown stippled. The brim of the cup swings out to the flanks and forms the initials for the hypodermis proximally.

1 = Zone 1. The common initials for the stele and columella; 2 = Zone 2. The stele; 3 = Zone 3. The columella; 4 = Zone 4. The cortical initials; 5 = Zone 5. The outer cortex and peripheral part of the cap.
Architecture of the root apex.—The cells at the apex radiate from a cyto-
generative centre which is situated at the stelar pole. The cytogen-
enerative centre is composed of a hemispherical or inverted cup-shaped group of cells, with the bottom of the cup at the stelar pole (Text-Fig. 1). The cells comprising this group are densely cytoplasmic and have prominent nuclei. They exhibit a greater frequency of division than the surrounding cells. This group can be termed a promeristem as used by Clowes (1950). This pro-
meristem consists of the initials for all the zones of the root. At the bottom of the promeristem cup and located at the head of the columella rows are the common initials for the stele and the columella. The sides or walls of the cup are formed by the initials for the cortex. The cortical initials at the rim of the promeristem cup swing outwards in an arch and as they reach the periphery of the root extend upwards or proximally (Plate XI, Fig. 1). The lower part of this arch, by Kappe divisions, gives rise to the peripheral region of the cap, while the proximal part by anticlinal divisions, gives rise to the hypodermis (Plate XI, Figs. 1 and 2).

Even though all the cells of the root can be traced back to the promeristem, it is being divided into five zones for descriptive purposes.

Zone 1: The common group of initials for the stele and the columella.—This is an irregular group of cells forming the bottom of the promeristem cup. In dormant roots this group shows 1 to 3 cells (in L.S.) which are bigger than the cells surrounding them on the proximal side (Text-Fig. 2). In active roots this zone is much broader and is composed of many cells of almost equal size (Text-Fig. 3). The cells towards the distal side show trans-
verse divisions and form the beginnings of the columella. Those at the proximal side exhibit T-divisions of the Körper type and give rise to the stele by further activity.

Zone 2: The stele.—Allen (1947 a) designates the immediate derivatives of the “apical initials” as the “ stelar mother cell zone”. Here, this zone and the maturing stele are together being referred to as stele. The Körper type of divisions of the initials and their derivatives result in the broadening of the stele proximally while there is no appreciable increase in the size of the initial group. Such divisions almost stop a little distance proximal to the initials (when the stele is about 150 to 250 μ wide). This results in a stele which is narrow as compared to the total width of the root. In Cycas and Ginkgo the stele in the active root is about 1/3 of the total width of the root and in Zamia it is only 1/6 or less.
Text-Fig. 2. *Cycas revoluta*. A median L.S. of the apex of a dormant root with a few big cells at the columella head. The cells shown with nuclei mark the approximate boundary of the procambium cup. The regularity of the columella files has become disorganized. The secretory cells are shown black.

Text-Fig. 3. *Ginkgo biloba*. A median L.S. of the apex of a semi-dormant root with the regular files intact. The cells shown with nuclei mark the approximate boundary of the procambium cup. The secretory cells are shown black.
In actively growing roots the endodermis, pericycle and the vascular elements are not discernible in the neighbourhood of the promeristem. These are noticed closer to the cytogenerative centre in dormant roots (Table I).

**Table 1**

*The distance of mature xylem and vacuolated cortical cells from the bottom of the promeristem cup and the width of the columella at its head, in active and dormant roots*

(Mean of 10 to 12 measurements in μ)

<table>
<thead>
<tr>
<th>Name of the species</th>
<th>Mature xylem</th>
<th>Vacuolated cortical cells</th>
<th>Width of columella</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Active</td>
<td>Dormant*</td>
<td>Active</td>
</tr>
<tr>
<td><em>Cycas revoluta</em></td>
<td>1930</td>
<td>105-126</td>
<td>160</td>
</tr>
<tr>
<td><em>Cycas circinalis</em></td>
<td>2170</td>
<td>350-560</td>
<td>175</td>
</tr>
<tr>
<td><em>Zamia latifolia</em></td>
<td>1120</td>
<td>119-420</td>
<td>98</td>
</tr>
<tr>
<td><em>Ginkgo biloba</em></td>
<td>1820</td>
<td>280-525</td>
<td>210</td>
</tr>
</tbody>
</table>

*The values are from roots in different stages of dormancy and hence the range.

However, secretory elements (tubes sécrétateurs of Dangeard, 1892) are found close to the promeristem in dormant as well as active roots and this may be regarded as the first sign of stelar differentiation. The secretory cells are long and their brownish contents are not uniformly distributed. These cells occur as irregular arcs mainly outside the phloem groups (Plate XI, Fig. 4; Plate XII, Fig. 2).

The boundary between the stele and the surrounding zone (Zone 4) is not easily distinguishable near the promeristem because of the absence of any stratification. However, a close scrutiny of the cell lineages brings out the *Körper* type of divisions in the stele whereas the cells of Zone 4 show predominantly transverse divisions. Furthermore, the stelar cells at the periphery retain their cytoplasmic contents to a greater distance proximal to the promeristem than the cells of Zone 4 immediately surrounding them (Plate XI, Fig. 1; Plate XII, Fig. 1).

**Zone 3:** The *columella* is made up of regular vertical files of cells in the actively growing roots. The regularity of the vertical files is disturbed, especially in the distal half, when the root becomes dormant (Plate XI, Fig. 1).
The width of the columella is also reduced in dormant roots (Table I). In the columella cells the main plane of division is at right angles to the long axis of the root, but occasional T-divisions add to its width.

The columella is demarcated from the peripheral region of the root-cap and the pericolumnar cortical initials by the greater staining density of the inner proximal cells of the former and the cells of the latter around the columella head. This demarcation is clear in actively growing and semi-dormant roots (Plate XI, Fig. 1; Plate XII, Fig. 1). The columella cells as a rule, are not very deeply staining, but the intensity of staining is greatest at the head of the columella. The cells become highly vacuolate a short distance distally (Plate XI, Fig. 1; Plate XII, Figs. 1 and 3).

Zone 4: The cortical initials.—These constitute the sides or walls of the promeristem cup and so they lie obliquely to the root axis (Text-Figs. 1, 2 and 3). These initials can be distinguished from the columella on account of their dense cytoplasm and prominent nuclei (Plate XI, Fig. 1).

The cortical initials divide mainly by transverse or oblique walls and so more or less continuous, unbroken chains of cells can be traced from the initiating zone into the mature cortical region. However, a few Körper type of divisions are also noticed. The rarity of such divisions may be attributed to the fact that the initiating zone itself is broad enough and hence, the necessity to widen the cortex by such divisions is reduced. Proximally the cells mature into the vacuolate cortical cells. This changeover from the densely cytoplasmic initials to the vacuolate mature cortical cells is rather abrupt in dormant roots and gradual in active ones (Table I, Plate XI, Figs. 1 and 3).

Zone 5: Outer cortex and peripheral part of the cap.—The cortical initials at the rim of the promeristem cup appear to swing out in an arch as seen in L.S. (Plate XI, Fig. 1). These cells contribute to the peripheral part of the cap distally by Kappe divisions. Proximally, they divide mainly anticlinally and contribute to the cortex. The arch swings upwards or proximally near the periphery of the root. The cells of this arch remain meristematic and densely cytoplasmic to a much greater distance proximally than do the cortical cells. The former give rise to three to five layers of hypodermal cells in the older regions of the root. This is observed in both the species of Cycas and Zamia while in Ginkgo biloba a hypodermis is absent (Plate XII, Fig. 3). The hypodermis is bounded on the outside by a single layer of cells which forms the covering layer of the root. Plaut (1910) had reported a multi-layered hypodermal tissue in Cycad roots. Guttenberg (1941) designates this tissue
as “exodermis” and adds that in the Cycad roots he investigated there is a one-layered, distinct “rhizodermis” over a many-layered “exodermis.” In Ginkgo also he reports an “exodermis”.

Thus, the Kappe divisions in the lateral derivatives of the cortical initials give rise to the peripheral region of the cap. Such divisions are more frequent in the region around the proximal half of the columella where the cell rows of the peripheral region curve inwards and abut around the columella cylinder. The sloughing off of the outer cap cells and the loss of meristematic activity in the more distal cells seem to counterbalance the increase in the number of cell rows in the peripheral region of the cap.

Plaut (1910) has described two types of “rhizodermis” in Cycad roots, viz., ‘primitive epiblema’ and ‘diffused’. The roots of the two species of Cycas and Zamia latifolia show the first type and that of Ginkgo the latter.

DORMANCY AND METACUTIZATION

Many changes occur when the root becomes dormant. In the Cycad roots the hypodermis extends distally and cuts through the cap at about half its length (Plate XI, Fig. 1). The outer portions of the cap thus cut off are sloughed off. The covering layer of cells as well as some of the outer layers of the hypodermis become metacutized. Müller (1906) has described this phenomenon as “Metakutisierung” to denote the special chemical process occurring in certain cells of the cortex and the dormant root-cap, wherein lignification of the walls of these cells occurs with simultaneous suberization throughout the cell-walls and cell contents. The term metacutization is used in this study as has been used by Wilcox (1954). Guttenberg (1941) states that the “exodermis” extends and stretches over the root apex during metacutization and that this type of metacutization is present in Ginkgo, Cycadales and Gnetales.

Concomitant with these external changes, there is a dwindling in the number and size of the cells constituting the promeristem (Plate XI, Fig. 3; Plate XII, Fig. 4). In dormant roots mature xylem elements are found nearer to promeristem. There is a gradation in this distance depending on the state of activity of the root (Table I). Wilcox (1954) has also reported a similar occurrence in Abies procera and concludes “The acropetal maturation of elements continues even after cessation of divisions of the apical meristem and the concomitant cessation of elongation” (p. 280).

During reactivation after dormancy, there is no collar formation in the Cycas species and Zamia latifolia. The wavy outline of the root with ridges
and furrows and the outer metacutized cells getting torn off, indicate the alternating active and dormant periods (Plate XI, Figs. 3 and 4). In Ginkgo, due probably to the absence of a hypodermis, the mode of metacutization varies slightly. At dormancy the apex is covered by a single-layered metacutis (Plate XII, Fig. 4). At resumption of activity, the initials increase in size and number and this widened apical portion breaks through the metacutis and has the narrower older cortex as a collar on its proximal side (Plate XII, Fig. 4).

In both Ginkgo and the Cycads no secretory cells were observed inside the cap formed by metacutization as mentioned by Guttenberg (1941).

Plaut (1910) includes Cycas revoluta in type 1 in his classification of types of metacutization.

**DISCUSSION**

In older literature on root apical organization, the type with a discrete "plerome" covered on the outside by a common initiating zone for all the other tissues, is designated as the "gymnospermous" type. Recent investigations of Allen (1947 a, b) and Wilcox (1954) go to show that this is not universally applicable to all gymnosperms. Guttenberg (1941) mentions a discrete plerome in the root apex of Ginkgo. Ball (1956 a), however, describes a common group of initials giving rise to all the tissues of the root in this plant.

The present findings agree in general with those of Ball (1956 a, b) on Ginkgo biloba in so far as the presence of a common initiating zone is concerned. It is to be made clear that in the present study the promeristem is being divided into zones for descriptive purposes and that there are no definite boundaries between the various zones. The extent of the promeristem and the number of initials also are variable. There is no predetermined destiny for the derivatives of the initial cells. On the other hand, they produce tissues according to the position in which they happen to be. Ball (1956 a) has also expressed a similar view based on the results of surgical experiments on embryonal roots of Ginkgo.

It does appear significant that the root apical organization of the Cycads and Ginkgo, representatives of the two most primitive groups of seed bearing plants, shows a close similarity. Furthermore, it is interesting to note that this finds a parallel in the similarity reported in the zonal structure of the shoot apex of the Cycads and Ginkgo (cf. Foster, 1939).

This type of organization is designated here as the Cycad type.
The histogen theory is not applicable here as the derivatives of the generative meristem do not have a fixed or unchangeable destiny as was originally proposed by Hanstein (1868). The apical cell theory, Guttenberg's (1940) central cell theory, and Brumfield's (1943) initial group hypothesis are also not applicable here because the number of initials seem to be large. Clowes' (1953) surgical experiments on roots as well as Ball's (1956 b) work on Ginkgo embryos point to the conclusion that a large number of initials are required for a root apex to be viable. Clowes (1961) has discussed these theories in the light of the concept of the promeristem and quiescent centre.

Schüepp's (1917) Körper-Kappe theory is found to be useful in interpreting the relation between the different cell complexes observed in the present study. Clowes (1961) is of the opinion that though some roots have an indefinite boundary between the Körper and Kappe, some others have a boundary which is quite constant in relation to the ‘histogens’. The Cycad type of organization described here presents a case where the boundary between the Körper and the Kappe fluctuates to some extent. The outer files of the cortical initials by Kappe divisions contribute to the peripheral region of the cap. The Körper-Kappe concept, combined with a study of the cytohistological state of the cells at the apex, helped to arrive at a more or less satisfactory interpretation of the apical organization.

Guttenberg (1941) states that the process of metacutization is alike in Cycadales, Ginkgo and Gnetales. Basing on the present study it seems that metacutization in the roots of Ginkgo and the Cycads has only a superficial resemblance. In Ginkgo the metacutis develops by the suberization of the outer cell layers of the root-cap (Plate XII, Fig. 4). But, in the Cycas spp. metacutis develops first on the hypodermal cell layers (Plate XI, Fig. 4). At the time of renewal of activity a collar is formed in Ginkgo whereas in the Cycas species there is no collar formation (Plate XI, Fig. 3; Plate XII, Fig. 4).

SUMMARY AND CONCLUSION

The root apices of three species of Cycadales and Ginkgo show a cup-shaped common promeristem. From the bottom of the cup arise the stele proximally and the columella distally. The cells at the sides of the cup give rise to the cortex. The initials swing out and up from the brim of the cup giving rise to the peripheral part of the cap by Kappe divisions. Those initials near the periphery of the root give rise, by anticlinal divisions, to a multi-layered hypodermis. A hypodermis is absent in Ginkgo root.

Both active and dormant roots are found. The changes accompanying dormancy are described. The hypodermis is also involved in the metacutiza-
tion in Cycad roots. In Ginkgo, due probably to the absence of a hypodermis, metacutization occurs only in the outermost cell layer.

During reactivation Ginkgo roots exhibit a collar, which is absent in the Cycad roots.

The similarity in root apical organization of the Cycads and Ginkgo is stressed especially in the light of the similarity these show in shoot apical organization as well.

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Root Apical Organization in Gymnosperms

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EXPLANATION OF PLATES

PLATE XI

Fig. 1. Cycas revoluta. Median L.S. of root apex in the early stages of dormancy. Note the cup-shaped group of initials in the centre, the brim of which swings out and gives rise to the hypodermis (Hy) proximally. At M the metacutised hypodermis is seen cutting through the cap at about half its length, ×190.

Fig. 2. Cycas revoluta. A portion of the hypodermis in Fig. 1 shown enlarged. Note the multi-layered hypodermis, ×610.

Fig. 3. Cycas circinalis. Median L.S. of dormant root apex. Note the obtuse and blunt tip and the small group of initials, obliteration of the columella files, metacutised hypodermis (Hy) and the wavy outline of the root with ridges and furrows, ×45. M = Metacutis.

Fig. 4. Cycas circinalis. T.S. of older portion of root. Note the multi-layered metacutis (M) which gets torn off at places, ×100.

PLATE XII

Fig. 1. Zamia latifolia. Median L.S. of apex of an active root showing the cup-shaped promeristem and regularly arranged columella files, ×95.

Fig. 2. Zamia latifolia. T.S. through an older portion of the root showing the secretory cells (S.C.) situated outside the phloem groups, ×310.

Fig. 3. Ginkgo biloba. Median L.S. of a semi-dormant root. Note the cup-shaped promeristem, a secretory cell (S.C.) and Kappe division at K, ×240.

Fig. 4. Ginkgo biloba. L.S. through a root showing collar (CO). Note the single-layered metacutis (M), reduced group of initials and the absence of a hypodermis, ×45.
FIGS. 1-4