IV. DISCUSSION

Professor Puri (1969) commenting upon some of the vital issues confronting the plant morphologists, asserted that, "Morphology is an ever growing discipline of science", and that, "those who consider it as dead, have apparently scooped off all the cream, so to say, from it and think of it in the earliest possible terms". He emphasised that morphogenesis, developmental morphology, causal morphology etc. should not be treated as separate disciplines from morphology. Arber (1950) has aptly remarked that,
"the business of morphologist is to connect into one coherent whole all that may be held to belong to the intrinsic nature of a living thing". Maheshwari and Kapil (1963) in their review on botanical researches in India during the last five decades rightly point out that "carefully prepared descriptions of plant structures will provide the only sound basis upon which (it would be possible) to interpret experimentally induced variations". They visualise "still considerable scope for anatomical studies on tropical crop and drug plants". Of late, morphogenesis has acquired the focal point of morphological investigations. Morphogenesis helps in resolving the major problems that confront morphology. In the present thesis, an attempt has been made through morpho-histogenic investigation to understand some of the morphological problems in the two solanaceous members, brinjal and chilli.

**Ontogeny of shoot apex**

The apical cells of the shoot show certain varying cytological and histological characters. They are expressed with the organization of the shoot apex in the embryo till its varied development and growth through
the various phases of the angiospermic plant. The ontogenetic study of the shoot apex is, therefore, essential for understanding some of the histogenetic characters, with which presumably some aspects of the growth activity of the shoot apex are intimately connected.

In *Amaranthus retroflexus* the distal axial zone and the flanking regions of the apical meristem become distinguishable after 70 hrs of seed hydration. Finally, as a result of the organization of the young leaves, the cytohistological zonation becomes apparent (Nougarède, Gifford and Rondet, 1965). According to Seidlová, Mořavká, Optrná and Krekule (1964), in *Senecio vulgaris*, zonation is little evident immediately after germination. The distinction between the central and peripheral zones appears after two days and is closely related with the initiation of leaf primordia which reach the maximum size. In *S. melongena* and *C. annuum*, the zonation becomes evident after the initiation and early development of the first one or two leaves. I have mentioned that the peripheral regions of the shoot apex of *S. melongena*, during 168 hrs of hydration show heterogeneous staining. At a certain stage it is confined not merely to the axial
and peripheral regions of the apex. In *Amaranthus retroflexus*, at the minimal area phase, the cytological features appear to become uniform throughout the apex, though the cells of the distal axial zone have less dense cytoplasm than those in the peripheral position (Nougarède et al., 1965).

However, the zonation in *S. melongena* and *C. annuum*, according to the present study, differentiates gradually in histological and cytological features. The cells of the central region in *S. melongena* show initial increase followed by reduction and final increase in area, during the first three days of the germination period. It indicates that the cells of the distal axial zone divide but the frequency of mitotic divisions appears to be reduced during the differentiation of the zonation.

In *S. melongena* and *C. annuum*, during the differentiation of the distal axial zone, the degree of vacuolation in its cells increases. The general vacuolation of all the apical meristem cells decreases during the initial period of hydration, but later the cells of the distal axial zone show higher degree of vacuolation than those of the peripheral zone.
In *Glechoma*, the vacuoles in the meristematic cells arise from localized segments of the endoplasmic reticulum by the accumulation of vacuolar material (Bowes, 1965b). According to Whaley, Mollenhauer and Leech (1960) the vacuoles may appear empty or with dense contents depending upon the temperature and the fixative used. In the present light microscopic studies, the vacuoles appear empty. In *Glechoma*, the vacuoles of the meristematic cells show electron-dense contents (Bowes, 1965b), and there is no distinction between the central and the adjacent flank meristem (Bowes, 1965a). According to the French school, the zonation of the apex reflects the plastochronic function of the anneau initial (Cf. Nougarède, 1967). In small apices and where the leaves completely penetrate the meristem during their formation, the zonation is not marked and the apical restoration becomes axial in the minimal area phase (Nougarède, 1967).

*Vegetative and reproductive shoot apex:*

Among the concepts of the shoot apical organization, the one that belongs to the French school is very well debated in the recent literature (Gifford, 1951b, 1954; Nougarède, 1967; Unnikrishnan, 1967; Rao, 1969; Bhar and Radforth, 1969).
The concept of cytobhistological zonation is firmly rooted in the literature (Gifford, 1954). Tolbert (1961) divides the shoot apex into three characteristic zones: I. metameristem, II. flanking meristem, and III. pith rib meristem. Whereas, Esau (1965a) recognizes the distal axial zone, proximal axial zone and peripheral or outer zone. According to Rao (1969) Esau's (1965a) terminology demonstrates morphological loci of the different zones but does not convey the morphogenetic potentialities of the zones concerned. However, I have adopted a modified terminology of Esau (1965a). Accordingly the zones distinguished in the present investigation are central, peripheral, inner axial and sub-central region. Chilli and brinjal, in addition to three common zones, viz., central, peripheral and pith rib meristem (Gifford, 1954; Gifford and Tepper, 1962; Nougarède et al., 1965; Tolbert and Johnson, 1966; Shah and Unnikrishnan, 1969), exhibit a fourth zone, sub-central region below the central region (central meristem). In Senecio vulgaris (Seidlová et al., 1964), sub-central region between central and rib meristem is reported. Trivedi (1969) describes a cambium-like zone below the central mother cell zone in Capparis decidua. Pith mother cell region (Tolbert and Johnson, 1966) with its characteristic orientation of cells in irregular
blocks, situated above the pith rib meristem, corresponds morphologically with the sub-central region in chilli and brinjal.

A number of angiosperm shoot apices (Ball, 1949; Steinberg, 1950; Sussex, 1955) do not exhibit zonation on the basis of staining. The shoot apex in chilli and brinjal, in its juvenile stages does not exhibit zonation; nevertheless, it produces first one or two leaves. Hence, the cytohistological zonation is apparently not necessarily related to this functional activity of the shoot apex. *Solanum tuberosum* and other species of *Solanum* lack cytohistological zonation (Sussex, 1955). But mature shoot apices of chilli and brinjal do show cytohistological zonation.

According to the French school, the central meristem (central region) of the shoot apex is inactive during the vegetative phase (see Nougarede, 1967). But experimental data have proved otherwise (Soma, 1958; Soma and Ball, 1963). Tolbert (1961) and Tolbert and Johnson (1966) consider the central region as the focal point of the zoned apices and call it "metrameristem". The cell size fluctuates in region - S (central region) during
various plastochronic phases (Denne, 1966). The fluctuation in the length of the cells of the central region during the various stages of the shoot apex of brinjal and chilli, from a germinating seed to a mature plant is suggestive of the activity of the cells in this region.

In chilli, at post-leaf-initiation phase, the peripheral region is composed of only a few cells. It indicates that the peripheral region is consumed in the formation of a leaf primordium. But during the late post-leaf-initiation and pre-leaf-initiation phases, the peripheral region shows an increase in volume because of the derivatives contributed from the central region.

In brinjal, as in Trigonella (Unnikrishnan, 1967) and Cuminum (Shah and Unnikrishnan, 1969) where the flowers are axillary, the main vegetative shoot apex lacks zonation even during the onset of anthesis. In the vegetative phase these plants exhibit cytohistological zonation.

Grégoire (1938) and his followers maintained that the floral meristem is fundamentally different from the vegetative meristem. Buvat (1952, 1955) and his associates suggested that the flower arises exclusively from the central.
zone of the vegetative apex, which, according to Buvat is inactive during the vegetative period and forms the waiting meristem or "méristème d'attente". Findings of Wetmore et al. show that the flower is a modified (metamorphosed) shoot and not a structure sui generis (see Lang, 1965). In chilli, the vegetative shoot apex during its transformation into a floral apex loses cytohistological zonation as evidenced by staining and shows an inner axial region and an outer region - formed by central and peripheral regions. The sepals arise at the periphery of the apex, in contrast to the observations of Buvat (1952, 1955). Floral appendages develop centripetally, hence, the diameter of the apex gets reduced gradually. It manifests that the méristème d'attente is not only involved in floral histogenesis, but the flanking region too has a role.

A floral part or a flower as a whole in many plants has been reported to undergo various degrees of reversion to the vegetative habit, a phenomenon known as virescences (Lang, 1965). The causal factors underlying are both genetical and environmental such as day length, attack by pests: parasites and change in culture media (Lang, 1965; Mohan Ram and Wadhi, 1966, 1969;
Krishnamoorthy and Nanda, 1968). In brinjal, the reversion to vegetative condition is a consequence of virus attack. Hence, the process of floral induction is not always an all-or-none phenomenon (Bernier, 1966). The differentiation of an internode between two whorls of the floral appendages, i.e., sepals and petals or between two appendages of the same whorl, i.e., between the sepals or two petals in the flowers of virus affected brinjal also recalls the vegetative characters of a shoot. The presence of axillary bud in the axil of a sepal in a diseased flower, and marginal and apical growth of floral appendages are further evidences towards homology between a flower and a vegetative shoot.

In chilli, as in Frasera carolinensis (McCoy, 1940), Downingia bacigalupii (Kaplan, 1968), Portulaca grandiflora (Soetiarto and Ball, 1969), the inception of the carpels occurs laterally in the periphery, leaving a small depression in the center of the floral apex.

Satina and Blakeslee (1941) reported that in Datura the stamen is more like an axis than a leaf. On the other hand, Kaplan (1968) attributes foliar nature to the stamen on the basis of its apical growth and the filament arises later by intercalary growth of a constricted,
non-sporogenous region at the base (as in petiole in a leaf). The present investigation is in accordance with these observations.

Effect of Gamma irradiation on shoot apex:

At different dose rates of irradiation, a particular plant species or a variety $x^2$ may be inhibited in its growth or even killed or, less often, may show growth stimulation (Gunckel, 1965). Medium and heavy doses on seed germination are injurious and light doses are considered stimulatory by some authors, while others report lack of change or retardation (Cf. Gunckel, 1965). In the present investigation both the species show retardation in seed germination and development of seedling to the mature plant.

Iqbal (1969, 1970) records irrevocable damages in the irradiated shoot apex of Capsicum annuum. Both the species of the present study show that the apical meristem cells are more susceptible to radiation damage than "resting cells" as suggested by Guckel (1957). The cellular contents of tunica and a few corpus cells below it degenerate in irradiated shoot apices.
Cuttings from the irradiated plants of *Tradescantia paludosa* eventually grow indicating that the abnormalities are due to physiological disturbances rather than to mutation (Gunckel, Sparrow, Morrow and Christensen, 1953). The morphohistogenetical sterility of the irradiated shoot apex is attributed to the disturbances in the morphological and physiological zonation. The formation of the leaf primordium in the central region after the vacuolation of cells in the peripheral region indicates the range of disturbance and overlapping of physiological functions of various zones in chilli and brinjal. The shoot apex from treated seeds of brinjal and chilli does not attain even the minimal width of the normal shoot apex. Sometimes after forming one or two leaves, the apex becomes histogenically inert. Similar results are reported for *Kalanchoe* (Stein, 1957-'60) and grape vine (Pratt, 1959). Increasing vacuolation in the shoot apices of chilli and brinjal in high doses is similar to that of *Zea mays* (Stein and Steffensen, 1959). Pratt (1959) reports that the morphohistogenetic activity of the irradiated shoot apex is arrested and the shoot apex culminates in a single leaf in grape vine. In brinjal, the shoot apex forms a leaf leaving a small inactive residue of apical meristem and in chilli, the shoot apex
forms a leaf primordium leaving a dead line of shoot apex as in certain instances of grape vine (Pratt 1959). Observations of Stein and Steffenson (1959) on Zea mays are also on similar lines.

Periclinal divisions in T₄ (as a result of irradiation) reported in G. annuum (Iqbal, 1969), Nicotiana tabacum, Coleus, apple and tomato (Cf. Iqbal, 1969), could not be confirmed in the varieties of chilli and brinjal of this investigation. Iqbal (1970) reports the origin of adventitious meristem and meristematic centers in the irradiated apices of chilli. But this feature is not observed.

Normally, in both the plants, the phyllotaxy is alternate but sometimes, in treated ones, it is found to be opposite or sub-opposite. The leaf initiation in the control shoot apex occurs after the previous leaf is 220 - 240 μ and 200 - 250 μ high in S. melongena and G. annuum respectively. However, in treated apices, the leaf initiates and develops even when the earlier formed leaf is only 10 μ high.

Vegetative and reproductive axillary buds:

Gifford (1951b) identified the early bud meristem as a "shell zone". The early axillary bud of Dioscorea alata (Shah, Poulose and Unnikrishnan, 1969) and Clerodendrum phlomoidis (Shah and Unnikrishnan, 1969a) is lightly stained.
On the contrary, in *C. annuum* and *S. melongena* it is densely stained.

In *Syringa vulgaris* (Garrison, 1959) the 'shell zone' is of narrow cells delimiting the bud meristem from the surrounding cells. Floral and vegetative axillary buds develop from a "shell zone" (Reeve, 1948). 'Shell zone' is also termed as 'cambiform zone' (Shah and Unnikrishnan, 1969b). Two possibilities of origin of shell zone are reported (Unnikrishnan, 1967); either from the parenchymatized cells that detach the bud meristem from the main apex as in *Syzygium* and *Mentha*, or by the differentiation of a part of bud meristem at its early inception as in *Duranta*. The shell zone is absent in foliar axillary bud and accessory bud of brinjal and accessory bud in chilli. But it is present in cotyledonary bud and floral or inflorescence bud of brinjal and foliar bud in chilli. Its origin is from the derivatives of the axillary bud.

In most of the reported cases the bud originates at 3rd or 4th node from the shoot apex (Gifford, 1951b; Kundu and Rao, 1955; Esau, 1965a; Marr and Blaser, 1967). But in the floral apex, buds appear soon after the
foliar primordia are initiated and their development is more conspicuous than that of the axillant leaves (Miller and Wetmore, 1946). Chilli and brinjal partly confirm this observation.

Positional readjustments of the buds have been reported in Corchorus and Boehmeria (Kundu, Rao and Saha, 1954; Kundu and Rao, 1957) and in Syzygium cumini (Shah and Unnikrishnan, 1969c). During reproductive phase, brinjal shows pronounced shifting of the floral or inflorescence bud from its axillary to extra-axillary position.

Different theories regarding the morphology of vitaceous and solanaceous shoot have been discussed (Bugnon (Caldwell, 1930; Hayward, 1938; Venning, 1949; Willis, 1951; Rendle, 1952; Bugnon, 1953; Shah, 1960; Millington, 1966; Shah and Dave, 1970). The family Solanaceae has been reported to have a sympodial type of growth with the successive principal internodes developing from the axillary buds, and the terminal buds producing inflorescence or short rudimentary branches (Venning, 1949). The present study does not substantiate this view. Monopodial and dichotomous branching have been reported for tomato shoot (Caldwell, 1930; Hayward, 1938). Venning (1949) states that the
growth in the stem during vegetative period in tomato is monopodial but all flower-bearing branches arise from the dichotomous division of the main stem. Brinjal, like tomato has flower or inflorescence in an internodal position. The stem in brinjal is monopodial in the vegetative and reproductive phase. No evidence of dichotomy of the axis is observed in brinjal.

According to Rendle (1952), in Solanaceae, the leaves are generally alternate in the vegetative parts, but often opposite in the flowering regions, an arrangement which like the extra-axillary position of the flowers or cymes, is the result of congenital union of axes. In Datura (Fig. 4. 3.A) where the branching is dichasial, the leaf at any given node really belongs to the node below, but has become adnate to, or raised upon, its axillary shoot as far as the next node (Rendle, 1952; Willis, 1951). Capsicum resembles Datura in similar morphological features. If the leaf really belongs to the node below, the leaf trace for that particular leaf should depart from the axial vasculature at the node below. But it is not so in Capsicum. The leaf traces of the young and mature leaves depart at the node to which they belong. No intermediate stage which shows the shifting of the leaf to the node
above is found. In chilli, the opposite leaves at the node below the terminal flower are ontogenetically alternate. However, due to lack of the intervening internode between the two leaves, they appear to be opposite. The apparently opposite arrangement of a leaf and tendril results when the intervening internode between the paired leaf and tendril, in *Vitis vinifera*, fails to elongate (Tucker and Hoefert, 1968).

Rendle (1952) illustrates *Solanum nigrum* (Fig. 4. 3.A) to show the union of the floral axis and the internode for some distance above the position of its axillant leaf. Brinjal shows a similar morphological situation. The flower or inflorescence in the middle of an internode, in brinjal, is due to the elongation of the internodal region between, the flower or inflorescence and accessory bud, and vegetative shoot apex. The development of the floral trace along with the differentiation and consequent development of the internode does not support the idea of flower-internode fusion. The vascular inter-relationship between leaf, accessory bud and flower or inflorescence axis also shows that flower or inflorescence does not show any kind of flower-internode fusion. Its position is due to a specialized type of internodal differentiation and
development. Similarly in the family Vitaceae, Millington (1966) reports that it is due to the internodal elongation that axillary tendril meristem later occupies extra-axillary position in *Parthenocissus inserta*. However, Shah and Dave (1970), from their developmental studies in Vitaceae conclude that no such internodal elongation occurs.

Leaf:

In brinjal and chilli, the periclinal divisions in $T_2$ at the flank of the shoot apex initiates the leaf as in *Drimys* (Gifford, 1951a). Outer tunica retains its identity as protoderm of the leaf in brinjal and chilli.

Hara (1957) reviewed and illustrated types of marginal growth in dicotyledonous foliage leaves.

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Marginal growth
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  | Adaxial type            |
  | Abaxial type            |
  | Middle type             |
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*Nicotiana tabacum* (Avery, 1933b) shows middle, submarginal type of foliar growth. Bhandari (1969) reports one more type of marginal growth in *Eubrachion ambiguum* wherein marginal initial gives rise to upper protoderm, inner layers and lower protoderm. His (Bhandari, 1969) illustrations for *Daphne odora* of Hara (1957) gives an impression that upper and lower protoderm do not take part in the formation of inner layers. However, the original illustrations of Hara (1957) show that upper and lower protoderm takes part in the formation of inner layers.

In chilli, the marginal growth of leaf is similar to that of *Nicotiana tabacum* (Avery, 1933b). Middle, submarginal type has not been correlated with apical growth in tobacco (Avery, 1933b).
The complete schematic diagram representing the development of leaf in chilli and brinjal is given below.

In brinjal, occasionally the derivatives of the marginal initial also divide periclinaly contributing derivatives to the upper hypodermis (see text for schematic diagram). The marginal type is considered primitive (Bhandari, 1969). In brinjal, a member of a fairly advanced family, rarely marginal type is found along with the predominant advanced type - submarginal type. As far as I am aware, there is no report of occurrence of marginal as well as submarginal growth of leaf in the same species. This is hitherto a new report. In addition to the known types of marginal growth (Hara, 1957) we can add one more type, mixed type of marginal and submarginal types.
Venation:

The minor or small veins are closely related to the photosynthetic tissue, and are particularly concerned with the exchange of materials with this tissue (Esau, 1967). As suggested by Esau (1967) for Beta leaves, in chilli half the distance of 1 in figure 5.3.A and 2 in figure 5.3.C, D is the farthest distance that water has to travel from xylem to photosynthetic tissue and photosynthates to phloem. If the areoles are very big and distance between two veins is more, the free veins occur in the areole, to help in translocation of water and photosynthates.

As in Beta (Esau, 1967), the free veins are directed towards the bigger veins in brinjal and chilli (Cf. Figs. 5.2.F, G) where anastomoses of smaller veins are absent.

Fischer distinguished two types of vein endings: principal endings which are branched and secondary endings which are short (see: Pray, 1954). According to him almost all vein endings are principal ones. Both types of vein endings are found in chilli and brinjal.

The tracheids that terminate in the ultimate tips show an increase in cell diameter and/or thickness.
become isodiametric (Pray, 1954; Esau, 1967). In the present study similar tracheids at the vein endings are observed. But sometimes a longer tracheid is also found followed by a short and wide tracheid in chilli.

In *Daphne pseudo-mezereum* (Hara, 1962) some elongated cells are found between one vein and vein ending of the another vein. Hara (1962) gave them the term "extension cells". Similar cells are found in chilli and brinjal. In the way in which they are associated with veins, it seems that they probably could also play a role in translocation.

**Trichomes:**

In addition to the types recognized by Metcalf and Chalk (1950), the clavate, capitate, cylindrical glandular, capitate filiform glandular and conical types of trichomes in brinjal and chilli are recorded. But I have not come across simple, unicellular trichomes and uniseriate hairs described for Solanaceae by Metcalf and Chalk (1950). In chilli, the trichomes are only glandular. However, brinjal shows both glandular and eglandular trichomes where stellate type is predominant.

**Stomata:**

That the stomata of solanaceous plants lack
subsidiary cells (Paliwal, 1969) seems to be utenable for Inamdar and Patel (1969) report four kinds of stomata in Solanaceae. However, diacytic stomata are not observed in the cultivars of chilli and brinjal investigated by me.

Ahmad (1964) believes that the abnormalities like stomata with one guard cell and stomata that are represented by pores are due to degeneration of the guard cells. We confirm this observation in chilli and brinjal. But, an incompletely differentiated meristemoid, contiguous to a normal stoma, in chilli and brinjal is a developmental abnormality. During degeneration of the guard cells in chilli, the nucleus elongates or becomes lobed followed by degeneration of cytoplasm. The degeneration of nucleus, cytoplasm and obliteration of guard cells overlap.

 Normally contiguous stomata develop from two meristemoids (Shah and Gopal, 1969). One meristemoid divides to form two initials which give rise to two contiguous stomata (Inamdar, Gopal and Chohan, 1969), or 'budding' of guard cells also gives rise to superposed contiguous stomata (Shah and Gopal, 1969). In our study we have not come across 'budding' of guard cells. Our observations show the following additional possibilities for development of contiguous stomata.
(a) A subsidiary cell cuts off a meristemoid near the pole of one stoma, which gives rise to a superposed contiguous stoma.

(b) An incompletely differentiated meristemoid adjacent to the normal stoma cuts off a meristemoid.

(c) A cell between two stomata is obliterated making the two adjacent stomata contiguous.

Gertz, Kuster and Guttenberg (see Dehnel, 1960) have discussed at length guard cell divisions under plant- and animal-induced pathological conditions. Gertz (see Dehnel, 1960) has reported divided guard cells in ovaries and seeds. In chilli and brinjal, the divisions of guard cells occur in a normal leaf.

In Araliaceae (Inamdar, Gopal and Chohan, 1969) and Asparagus (Gopal and Shah, 1970) cytoplasmic connections between the guard cells of nearby stomata are reported. In chilli, similar cytoplasmic connections are found between the guard cells of adjacent and contiguous stomata.

As far as I am aware, there is no report of an extruded nucleolus in the guard cell.
Dehnel (1960) has shown that the epidermal cells near the wound undergo divisions. Degeneration of one or both the guard cells is also reported. We confirm these observations in chilli. The contour of epidermal cell walls changes near the wound.

**Internodal elongation, cortex and pith:** The detailed studies on internodal elongation are few (Wetmore and Garrison, 1959; Gunckel and Thimann, 1949; Gunckel and Wetmore, 1946). In *Helianthus annus* (Wetmore and Garrison, 1959) the span of the first internodal elongation is three or four weeks. The initial growth is more vigorous and later stabilizes uniformly. In chilli and brinjal, 15th and 13th internode respectively from the cotyledonary node takes about 30 - 33 days to grow 1.5 cm long. The rate of growth increases gradually.

In the shoot as a whole and in each internode, in *Ginkgo biloba*, elongation occurs to the maximum at the apical end and decreases progressively towards the base (Gunckel and Thimann, 1949). However, growth first occurs in the basal portion of a young internode and it becomes progressively localized towards the upper end of the internodes in *Helianthus annus* (Wetmore and Garrison, 1959). In brinjal and chilli, in the plant as a whole, the part towards the
apical and elongates more than the part towards the base, i.e., the first formed internodes are shorter than the later formed ones. Also in each internode the lower part elongates less than the upper part (in vegetative phase).

In tomato the prominent branch arises in the leaf axis, in the node below the inflorescence (Thompson and Heimsch, 1964). Growth of this branch is so rapid that it more or less equals to that of the main axis. The length of the internode is always more if it bears an inflorescence in tomato (Thompson and Heimsch, 1964). Similarly, in brinjal the internodes bearing flowers or inflorescences grow more rapidly in length than the vegetative internodes. The part of an internode between the extra-axillary flower or inflorescence and the upper node is shorter than the internodal portion between the flower and lower node in most of the cases in brinjal. However, the basal region of both the portions of the internode above and below the flower or inflorescence is shorter than the upper part.

In Ginkgo biloba, the cortex differentiates only when abaxially vacuolated leaf primordia and their subjacent vacuolated buttresses surround the stem apex (Gunckel and Wetmore, 1946). Abbe and Pollock (1946) have
shown that in *Anacharis* the cells of cortical parenchyma are arranged in longitudinal files. Each file is derived ontogenetically from a rib meristem initial which is first recognizable in the 7th to 13th stem unit. Sussex (1955), on the other hand reports the origin of the cortical tissue from the inner tunica and outer corpus layers of the apical meristem in *Solanum tuberosum*. However, Barthelmes (1935) could not recognize the vacuolated cortex at a level higher than the buttresses of the 4th to the 7th primordia in some gymnosperms. The present investigation reveals that the early internode and cortex are discernible as soon as the youngest leaf buttress is formed at the flank of the shoot apex. The cells on the abaxial side of the leaf buttress become vacuolated and differentiate as an early cortical ground meristem. Early cortical ground meristem is delimited from the pith ground meristem tissue by vascular meristem.

The pith is derived from the cells of the lowest layer of the corpus which undergoes periclinal divisions in *Solanum tuberosum* (Sussex, 1955). In *Ginkgo biloba* (Gunckel and Wetmore, 1946), the derivatives of actively dividing rib meristem cells soon develop into a rapidly maturing pith. Pith is derived from the inner axial
region or rib meristem in chilli and brinjal where progressive changes in the rib meristem cells and their derivatives are followed right from the apex. Barthelmess (1935) has shown an early differentiation of the pith above the origin of the first leaf primordium in gymnosperms. Gunckel and Wetmore (1946) observed that in no case did the pith appear higher than the first leaf in Ginkgo. In the two plants investigated here, pith never develops at or above the level of the youngest leaf primordium. The differentiation of cortical pattern, as suggested by Wetmore (1943) in a number of gymnosperms and angiosperms is generally correlated with the formation of leaves at the apex. The development of pith is independent of the leaf development and it belongs to the central ground meristem.

Primary vasculature:

The vascular meristem is blocked out from the apical meristem in the form of a ring of densely stained cells (Clowes, 1961; Esau, 1965b; Thompson and Heimsch, 1964; Sussex, 1955) by the differential parenchymatization of adjacent tissues (Esau, 1965b). This ring till it gives rise to the strands of elongated cells has been named by different authors as, "meristem ring", "prodesmogen" and "residual meristem" (Cf. Clowes, 1961). The term "residual meristem" has been used here to describe the vascular meristem.
in its initial stage of differentiation, since, it implies that it is a region which continues to be meristematic after the other regions at the same level have stopped or slowed down their meristematic activity.

Procambium gradually differentiates from the residual meristem. In early stages of procambial differentiation, the elongation is attained primarily by longitudinal divisions in the cells of the residual meristem followed by elongation. The level of the first stage of procambial differentiation can not be determined exactly (Esau, 1965b). In the present investigation, as soon as the residual meristem cells, in longisection, appear slightly elongated, they are considered procambial cells. The determination of procambial strand required knowledge of phyllotaxis, leaf trace relationships and plastochronic steps in the development of leaf primordia (Esau, 1965b). It can, usually, be identified by the small cross-sectional area of its cells and its position in the axis (Clowes, 1961). As there is no single reliable criterion of identifying procambium strand (Clowes, 1961), I have used leaf-trace relationships, ontogenetic stage of the leaf primordia, stainability, cross-sectional size of the cells and longitudinal length of the vascular meristem cell, and position of the vascular meristem in the axis as key positions points to identify the procambial strands.
The procambial strands differentiate in relation to the leaf (Esau, 1965b). In chilli at the 2nd node, three procambial strands, one for each are observed in relation to first, second and third leaf. At the fifth node, all the five procambial strands appear in the stem axis. The procambial strands expand laterally (Esau, 1965b). In tomato (Thompson and Heimsch, 1964) and Nicotiana tabacum (Esau, 1938), the procambium assumes a practically continuous appearance as the leaf traces become contiguous during their lateral expansion. However, as in chilli the common pattern in dicotyledons is the discrete strands of procambium which alternate with the interfascicular regions.

Some of the procambial cells remain undifferentiated during vascular tissue differentiation, between primary xylem and primary phloem. In early stage, it is unstratified in chilli as in Nicotiana (Esau, 1938). Later, when more vascular tissues differentiate, the residual procambium shows stratification in Nicotiana (Esau, 1938). This is an indication towards the differentiation of fascicular cambium in chilli as in Nicotiana.

The following is the scheme of primary vascular differentiation in chilli.
Apical meristem

Residual meristem

Ground meristem

Procambium

Outer phloem Fascicular cambium Primary xylem Inner phloem

Interfascicular parenchyma

_Cambium:

Two types of cambial cell arrangements, viz., storied and monstoried, occur in angiosperms (Esau, 1960; Cumbie, 1963, 1967). Brinjal shows monstoried cambium. The circumference of the fascicular cambium in brinjal increases by anticlinal divisions, cell elongation, elimination of initials, and formation of ray initials from fusiform initials as in _Leitneria_ (Cumbie, 1967), _Hibiscus_ (Cumbie, 1963) and other seed plants (Esau, 1960).

A fusiform initial may divide by oblique anticlinal or by lateral wall formation. It may either give rise to new fusiform initial or a small segment. Such a segment sometimes becomes a ray initial and forms an uniseriate ray (see, Esau, 1960).
Apical intrusive growth of the fusiform initial is well known (Bailey, 1923; Bannan, 1950; Cumbie, 1963, 1967). As a result of this growth, nonstoried type of arrangement is brought about in cambium of brinjal and chilli. A small segment of a fusiform initial becomes long by intrusive growth. In brinjal, sometimes, the fusiform initial during its apical intrusive growth forks as in Juglans and Liriodendron (Cf. Esau, 1960). Multiseriate rays are divided into two or more groups of initials by intrusive growth in brinjal. Rarely, a cell at the end of the multiseriate row shows intrusive growth and becomes a fusiform initial.

Fusiform initials in brinjal show multinucleate condition. Later, all but one nucleus degenerate before the fusiform initial differentiates into a vascular element. Russow also reported multinucleate cambial cells in pine (Cf. Esau, 1939).

Vascular inter-relationships:

Usually two branch traces are present in many dicotyledons. But one or more branch traces are also reported (Esau, 1965; Ezalarab and Dormer, 1963; Poulose, 1968). Ezalarab and Dormer (1963) classify bud trace connections into five patterns in the family Ranunculaceae.
The normal, *Petasites* and *Lepidium* conditions are described for trilacunar nodes, and *Berberis* and *Thalictrum* conditions for the plants where branch traces arise from the leaf trace or traces (Ezelarab and Dormer, 1963). Since in brinjal and chilli the node is unilacunar and branch traces arise from the strands flanking the leaf gap, they do not fit into this classification. The origin of the bud traces from the strands flanking the leaf gap appears to be correlated with either absence of branching of these strands or their branching oriented away from the subtending leaf (Shah and Patel, 1969). Brinjal and chilli agree with the generalization of Shah and Patel (1969). Nodal condition does not affect the nature of bud trace connection with the axial vasculature (Shah and Patel, 1969).

**Phloem:**

The solanaceous plants, excepting *Nicotiana tabacum* (Avery, 1933a; Crafts, 1934; Esau, 1938; Esau and Cronshaw, 1967) and a few other species (Fukuda, 1967), have not been studied for phloem.

As in *Mimosa pudica* (Esau, 1970) and many reported dicotyledons, in brinjal and chilli, the protophloem sieve elements differentiate in the outer layers of procambium when the adjacent cells are denser. The internal phloem
differentiates from the procambium as reported for other species of Solanaceae (Fukuda, 1967; Esau, 1969) and hence, the vascular bundles are truly bicollateral (Esau, 1969). But later the inner phloem gets widely separated from the protoxylem by parenchymatization of the procambial cells between the inner phloem and early formed xylem. Similar observations are made by Sussex (1955) and De Bary (Cf. Esau, 1969). Venning (1949) reported the inner phloem of the tomato shoot to be medullary.

Artschwager (1918) reports that the inner sieve elements differentiate before the external and that the protoxylem matures before the protophloem in potato stem. However, Esau (1938, 1969) doubts this observation. Protoxylem elements differentiate first, then the protophloem elements and then the development of the inner phloem follows in the stem of chilli and brinjal.

The slime or P-protein bodies of the solanaceous plants are sinuous, elongated and become fibrous as they grow in size (Esau, 1938, 1939; Crafts, 1934). They occur singly in each cell (Esau and Cronshaw, 1967; Esau, 1939) as in chilli and brinjal. The P-protein body is long but does not become fibrous at any stage. Its ends are more or less tapering. As in Nicotiana tabacum, chilli and brinjal, the P-protein body is comparable in width to the nucleus.
(Esau and Cronshaw, 1967). P-protein body disintegrates with the nucleus in Solanaceae (Esau, 1939). In the present investigation, it is found that the P-protein body disperses before the nucleus degenerates. No limiting membrane is observed around the P-protein body in chilli or brinjal, a report similar to that of tobacco (Esau and Cronshaw, 1967).

Slime plugs with various morphological configurations are found in the sieve elements. They are artifacts induced by injury to sieve elements (Esau, 1939).

P-protein strands are present in the sieve elements of both chilli and brinjal. Crafts (1969) believes that slime is a dead decomposition residue from breakdown of slime bodies, nuclei, tonoplast and dictyosomes and that the fibrillar meshwork of Northcote and Wooding (1966), the plasmatic filaments of Behnke and Dörr (1967) and the striated P2-protein of Cronshaw and Esau (1967) are not slime.

The dispersal of slime bodies and the disorganization of the nucleus occur more or less concomitantly in many angiosperms (Esau, 1939; Shah and Jacob, 1969a, b;
Esau, 1969). However, in brinjal and chilli
the nucleus remains in a sieve element even after the
dispersal of P-protein body. In *Neptunia oleracea*
(Shah and James, 1968), *Nelumbo nucifera* (Shah and James,
1969) and *Mimosa pudica* (Kundu and Saha, 1967) the nucleus
is reported to be present in a sieve element for a brief
time even after the formation of the sieve plate.
Nevertheless, the observations of Kundu and Saha (1967)
for *Mimosa pudica* could not be corroborated by Esau (1970).
The nucleus is retained in a sieve element even after the
formation of sieve plate and formation of slime plug in
chilli and brinjal. The nucleate sieve elements are found
in elongating internodes. Their retention in sieve element
for a long time suggests that the nucleate elements could
also be functional (as suggested by Shah and Daniel, 1970a)
and enucleate ones must be functional.

Crafts (1934) reports multinucleate sieve elements
in tobacco. Esau (1938) was unable to confirm this observation.
Multinucleate sieve elements are not found in chilli and
brinjal. The degeneration of nucleus in the sieve elements
of many investigated angiosperms occurs by loss of contents
and disintegration of the membrane (Esau and Cheadle, 1965;
Ervin and Evert, 1967; Shah and Jacob, 1969a,b). In *Neptunia*
oleracea (Shah and James, 1968) the nuclear membrane
disappears first and then the nuclear material. In Pennisetum typhoides (Shah and Daniel, 1970b) the elongation of nucleus followed by its degeneration in various ways is interesting. In the present investigation the nuclear degeneration occurs in three ways. (a) The nuclear membrane disappears followed by the loss of nuclear material. (b) The nuclear material loses its chromophilic nature and then the nuclear membrane breaks down. (c) The nucleus decreases in size without losing its chromophilic nature and nuclear membrane, and it ultimately disappears.

Xylem:

There exists controversy regarding the ontogeny and early development of vessel elements and perforation plate formation (Priestley, Scott and Malins, 1935; Esau, 1936; Majumdar, 1940, Esau and Hewitt, 1940). Priestley et al. (1935) and Majumdar (1940) believe that perforation occurs during very early development of vessel mother cell, before the secondary wall thickening takes place on the lateral walls. At a certain stage of expansion of the vessel segment, the cross walls become stretched to their fullest extent, so that any further expansion will cause their rupture (Majumdar, 1940). On the other hand, continuity between the vessel elements is established after the
development of the secondary thickening on the lateral walls (Esau, 1936; Esau and Hewitt, 1940). In brinjal, the perforation is formed only after the vessel element expands and its lateral walls are deposited with secondary wall materials. In brinjal as in celery (Esau, 1936) the perforation occurs by dissolution of the end wall rather than by its rupture (Priestly et al., 1935; Majumdar, 1940). In the present study, the broken end walls (which are due to microtomy) are seen in the form of segments. No coiling is observed in any case. The rim formation takes place before the perforation in brinjal as in celery (Esau, 1938).

In celery, first the end wall becomes thickened and appear lenticular and is primary (Esau, 1936). However, in brinjal the end wall is not lenticular. It gets thickened, especially the middle lamella appears thick and sharp.

Cytoplasmic contents degenerate when the perforation occurs at the transverse end walls of the vessel mother cell. The prominent nuclei elongate as the cells enlarge (Cronshaw and Bouck, 1965). In cross-section, nuclei often have lobed appearance as illustrated by Cronshaw and Bouck (1965). Nucleus is also retained till the perforation plate formation.
It may be found near the end wall where the perforation is to occur as illustrated by Eames and MacDaniels (1925, p 364).

**Root apex:**

The root cap is composed of columella and calyptra. Calyptra is otherwise known as peripheral zone (Pillai, Pillai and Girijamma, 1961). The term columellogen for the meristem which forms the columella was coined by Pillai and Pillai (1961). The same terminology has been adopted here.

The root apex falls in type II of Pillai et al. (1961) with a common initiating zone for the epidermis and calyptra, i.e., dermo-calyptrogen and another group of initials for the periblem and plerome. However, in addition to this, columellogen is also present.

Kappe-type T-divisions cause an increase in the number of rows of cells near the root tip in brinjal and chilli. Whereas, Körper-type T-divisions help in increasing the number of cortical cell layers. The calyptra cells divide by Kappe-type T-divisions whereas, the columella cells by transverse divisions only.

Sinnott and Bloch recognized two main types of primary tissue arrangement, i.e., opposite and alternate (Cormack, 1947). The cortex of tomato root shows the second
type (Cormack, 1947). In the present study, the
cortex of brinjal and chilli exhibits a mixed type,
i.e., outer cortical layers are alternate and the inner
ones opposite in the young root. As in chilli and brinjal,
the intercellular spaces are larger in the inner cortical
layers than in the outer ones in tomato (Cormack, 1947)
and chicory (Knobloch, 1954).

The cortex, in many investigated root apices
appears to be formed by a sort of cambial activity of a
single layer of cells which surrounds the periblem and later
differentiates to become the typical endodermis (Williams,
1947). Cortex develops in two stages in chilli and
brinjal. During the first stage, the outer cortical
layers are formed from the periblem. During the second
stage, the cells of the innermost periblem layer become
large and divide periclinally to form an outer layer and
inner layer. The inner layer later becomes endodermis,
whereas, the outer one divides periclinally forming inner
cortical layers. Thus, the innermost periblem layer forms
an endodermis-periblem complex. The outer cortical
layers increase in number by Körper-type T-divisions
whereas the inner ones by periclinal divisions as seen in
transection.
A quiescent center is not found in the embryonic apices investigated by me. Pillai et al. (1961) and Clowes (1956; 1958a, b) have recorded that the quiescent center is absent in thin and immature roots.