

VEGETATIVE AND REPRODUCTIVE DEVELOPMENT OF SHOOT APEX OF BRINJAL (*SOLANUM MELONGENA*) AND CHILLI (*CAPSICUM ANNUUM*)

by J. D. PATEL and J. J. SHAH, *Department of Botany, Sardar Patel University, Vallabh Vidyanagar, 388120*

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The structure and organization of vegetative shoot apex during the vegetative phase of brinjal (*Solanum melongena* L.) and chilli (*Capsicum annuum* L.) have been described. The vegetative shoot apex exhibits one additional cytohistological zone—subcentral region—in addition to central, peripheral and inner-axial regions. The cellular growth has been studied in the cells of the central region of the shoot apex from the germination stage to the mature vegetative apex. It shows that the central region is mitotically active. The main shoot apex of brinjal during reproductive phase remains vegetative but it lacks cytohistological zonation, and its height and width differ from those in the vegetative phase. In chilli the vegetative shoot apex is transformed into a reproductive one. The floral histogenesis for chilli is described. The nuclear diameter and cyto-nuclear ratio are calculated in the reproductive apex of chilli at different phases of its development.

INTRODUCTION

In the previous publication (Shah and Patel 1970 *a*) we have shown how the cytohistological zones in the shoot apex of germinating seeds of *Solanum melongena* L. and *Capsicum annuum* L. differentiate. The cytohistological zonation differentiates gradually histologically and cytologically. After the development of the first 1–3 leaves the cytohistological zonation becomes evident in the shoot apex.

The aim of the present investigation was to extend our earlier studies and to obtain full information on the development and structure of mature vegetative and reproductive apices of the above plants.

MATERIALS AND METHODS

Methods described by Shah and Patel (1970 *a*) were followed in the present study. For the measurements of cells and nuclei the camera lucida drawings were made on a graph paper and the areas of cells and nuclei were calculated in μm^2 .

The length of the cells of the central region of the shoot apex was measured with filar eye-piece. Photomicrographs were taken on the Zeiss Photomicroscope using a yellow filter and ORWO Dokumenten film.

OBSERVATIONS

(A) *Vegetative shoot apex*

The vegetative shoot apex shows two tunica layers (T_1 and T_2) and the corpus. The T_2 cells at the site of leaf initiation divide periclinally. At the maximal phase the shoot apex is dome-shaped (Figs. 1, 25).

Three phases of the plastochrone : leaf initiation, pre-leaf initiation, post-leaf initiation, are distinguished. The formation of a leaf buttress indicates the post-leaf initiation phase (Fig. 2). Till the youngest leaf primordium is about 160 μm , and 125 μm high in brinjal and chilli respectively, the apex is at the post-leaf initiation phase. At this phase the shoot apex is in low convexity. Corpus layers are stratified.

During the pre-leaf initiation phase, the shoot apex gradually becomes convex. The corpus layers appear stratified, and, the youngest leaf primordium is about 160-220 μm and 125-200 μm high in brinjal and chilli respectively (Fig. 3). The width of the shoot apex and the height of the youngest leaf primordium of brinjal and chilli at different plastochronic phases are shown in Table I.

TABLE I

Width of the shoot apex and height of the youngest leaf at different plastochronic phases of the vegetative shoot apex of Solanum melongena and Capsicum annum*

Phase	<i>Solanum melongena</i>		<i>Capsicum annum</i>	
	Width of the shoot apex (μm)	Height of the youngest leaf (μm)	Width of the shoot apex (μm)	Height of the youngest leaf (μm)
Leaf initiation	150-175	220-240	175-200	200-250
Pre-leaf initiation	80-150	160-220	100-175	125-200
Post-leaf initiation	40-80	0-160	70-100	0-125

*Average of 75 shoot apices in all. The sizes are ranges and not absolute figures. It was difficult to measure the length of the youngest leaf in its earliest stage of development soon after its initiation, and so we have considered it as 0 μm height.

Cytohystological zonation—On the basis of differential stainability of the cells, cytohystological zonation is evident when the shoot apex is 150-175 μm in brinjal and, 175-200 μm in chilli. The shoot apex shows only three zones : central, peripheral and inner-axial regions, during its early ontogeny after 192 and 175 hr of seed hydration in brinjal and chilli respectively. A fourth zone, however, differentiates later in the vegetative shoot apex. It is between the central and inner-axial regions and is named the subcentral region (Figs. 1, 25). The cells of this zone stain denser than those of the central and inner-axial regions.

In *C. annum*, cytohystological zonation is evident at leaf initiation and post-leaf initiation phases (Figs. 25, 26). But in post-leaf initiation phase only a few apical cells towards the older leaf primordium (L_2 in Fig. 26) appear darkly stained, whereas towards the younger leaf (L_1 in Fig. 26) more cells of the peripheral region appear dense. Similar zonation is not evident in *S. melongena* at post-leaf initiation phase.

The central region includes cells of tunica and one or two outer layers of the corpus. Its cells are lightly stained and bigger than those of the peripheral region.

The peripheral cells are densely stained and stratified except at the time of leaf initiation (Fig. 1). The subcentral region shows densely stained cells (Figs. 1, 25). It is evident in chilli at the leaf-initiation phase as well as post-leaf initiation phase, whereas in brinjal it is evident only at the leaf initiation phase (Fig. 1). Below the subcentral region, the inner-axial region shows vacuolated cells which differentiate as pith cells. The diameter of nuclei and cytonuclear ratios in the cells of different zones of shoot apex of brinjal and chilli are given in Table II.

TABLE II
Diameter of the nuclei and cyto-nuclear ratio in different zones or areas of shoot apex in chilli and brinjal

Area of Shoot apart	<i>Solanum melongena</i>		<i>Capsicum annum</i>	
	Diameter of nucleus (μ)	Cyto-nuclear ratio	Diameter of nucleus (μ)	Cyto-nuclear ratio
Central region	4.38	3.3	7.92	3.0
Peripheral region	3.42	3.3	7.40	3.5
Shoot apex	3.82	4.5	6.78	3.8
Inner-axial region	4.68	6.2	7.16	5.0
Pith	4.62	7.8	6.76	6.7
Tunica I	4.20	—	6.48	—
Tunica II	5.02	—	7.40	—

Cellular growth in the shoot apex—Some aspects of cellular growth were studied in the shoot apices at the following stages of development :

- Stage I* : Shoot apex from the germinating seeds of chilli and brinjal after soaking the seeds for one hour in water*.
- Stage II* : Shoot apex from the germinating seeds of brinjal and chilli after 15 and 50 hr of seed hydration respectively*.
- Stage III* : Shoot after 144 and 100 hr of seed hydration in brinjal and chilli respectively.*
- Stage IV* : Shoot apex after 168 and 175 hr of seed hydration in brinjal and chilli respectively.*
- Stage V* : Shoot apex after 192 hr of seed hydration in brinjal* and shoot apex of mature vegetative plant in chilli (Fig. 25).
- Stage VI* : Shoot apex of mature vegetative plant in brinjal (Fig. 1).

A row of cells in the central region of the median section of the shoot apex was selected as shown in Fig. 4. Twenty cells from tunica downwards were measured in three successive sections, pre-median, median and post-median. Sixty apices

*For Figures see Shah and Patel (1970 a)

were taken for measurement, i.e. 180 sections were examined. The length of 20 cells was taken for each stage of development of the shoot apex. The average length of each cell was taken and plotted (Figs. 5-15 and Tables III, IV), and following conclusions are drawn therefrom :

- (a) In the early stages of germination, shoot apices show a large number of elongated cells in the median row.
- (b) During later stages of germination more cells appear to have divided (outer cells in the row). This is evident by the increased number of shorter cells.
- (c) At maturity, short cells increase in number indicating involvement of more cells in mitotic divisions.
- (d) The cells of the central region of shoot apex show, during different stages, decrease in length (Fig. 6) indicating mitotic activity; increase in length (Fig. 7) indicating elongation and again decrease in length (Figs. 9, 10) indicating renewed mitotic activity. It is also evident that this region of the shoot apex is histologically active.

Shoot apex during reproductive phase in brinjal—Unlike in chilli, the vegetative shoot apex of brinjal is not transformed into a floral apex. The shoot apex of the main and lateral axes, though vegetative, lacks cytohistological zonation during reproductive phase of the plant. Compared to the vegetative period, the width of the vegetative shoot apex is less and its height is more in the reproductive period.

(B) *Floral histogenesis in chilli*

Transformation of vegetative shoot apex into floral shoot apex and initiation of sepal and petal—During vegetative period 20-25 leaves are produced. There is a loss of cytohistological zonation (Fig. 27) in the transitional stage of the apex. At transition, two successive leaves arise at the shoot apex without any differentiation of the intervening internode. Each of these apparently opposite leaves bears a vegetative axillary bud (Shah and Patel 1970 *b*).

Sepal initiation occurs by periclinal divisions in the second layer. Its trace procambium is present (Fig. 28). The cells subjacent to the site of sepal initiation divide periclinally and anticlinally whereas cell layers in the central region remain stratified (Fig. 17). No periclinal divisions occur in cells of the first 3-4 layers in the central region of shoot apex (Fig. 17). Due to periclinal divisions and anticlines the peripheral region elevates the sepal primordium and due to anticlines only the central apical region appears flat (Figs. 18, 28).

Petals are initiated by periclinal divisions in the 2nd or the 3rd layer in the peripheral region of the floral apex. Petal primordia are formed at the flanking region of the apex above the sepal primordia (Fig. 29).

Sepal and petal primordia elongate due to apical growth. When the petal primordium is about 25-30 μm high, an apical initial is recognized (Fig. 23). Its anticlines contribute to the formation of the protoderm (Figs. 23, 24). The sub-apical initial divides periclinally to form the middle layers and anticlinally to give rise to abaxial and adaxial derivatives (Figs. 23, 24). The surface cells on the abaxial side of the sepal and petal are more vacuolated and enlarged than those on the adaxial surface. Cell enlargement is greater on the abaxial side as compared to that

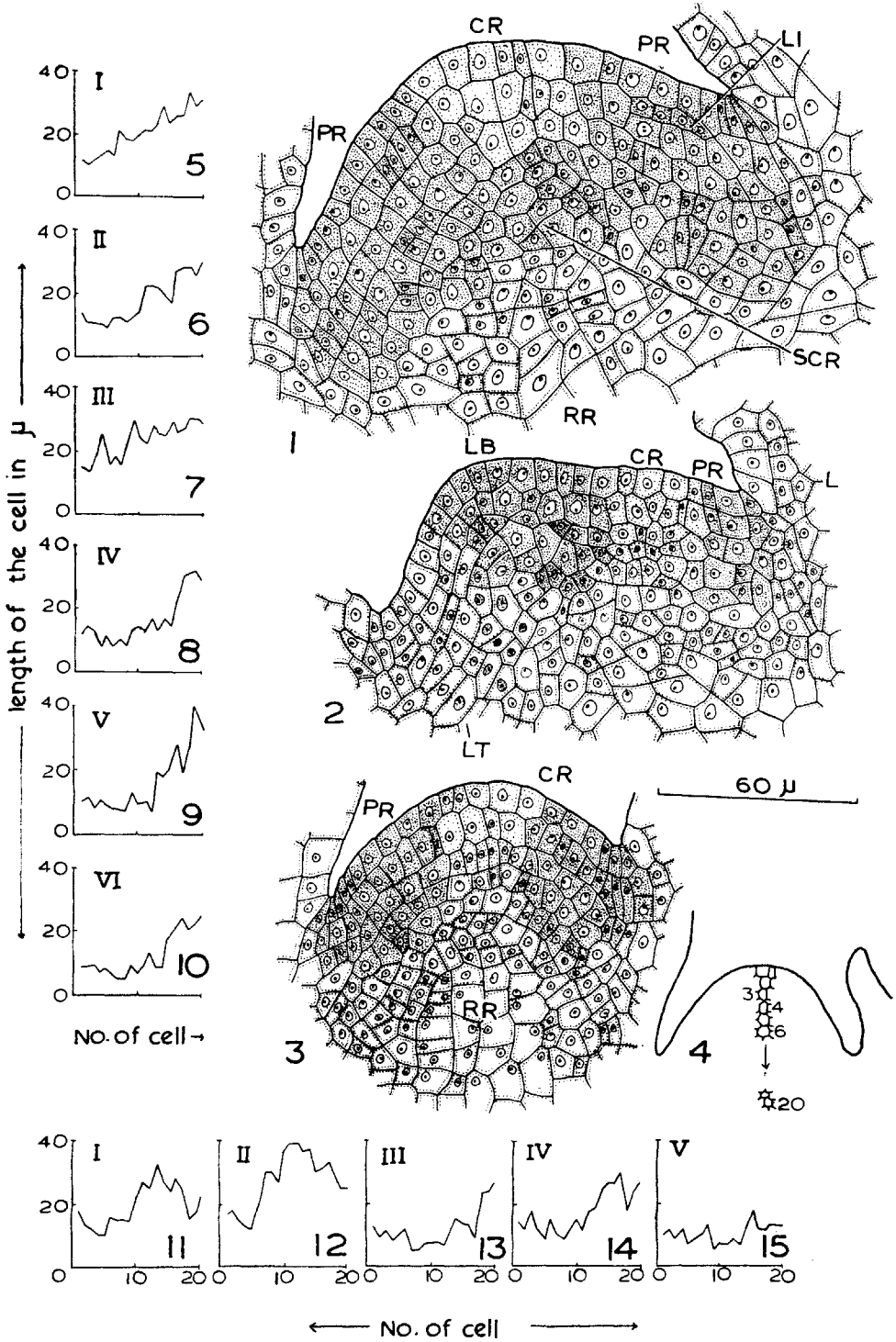


TABLE III

Avg. height of cells in the shoot apex at different stages of its development in S. melongena

No. of cell	Height (in μm)						
	Stage of development						
	I	II	III	IV	V	VI	VII
1	12	14	15	12	10	9	7
2	10	11	14	14	11	9	7
3	12	11	19	13	8	10	7
4	14	10	25	8	10	7	6
5	15	9	16	11	9	8	6
6	13	12	18	8	8	6	9
7	21	13	16	10	8	5	6
8	19	11	22	8	7	5	7
9	18	13	30	13	13	9	8
10	20	14	24	14	10	7	6
11	21	22	23	13	10	9	7
12	21	22	28	16	7	13	7
13	22	21	26	13	19	9	9
14	29	19	25	19	18	9	11
15	24	17	29	14	21	18	10
16	25	27	26	24	28	21	11
17	26	28	27	30	19	24	13
18	33	28	30	31	27	21	11
19	29	25	30	32	40	22	16
20	30	30	28	29	33	23	15

on the adaxial side. This results in the characteristic adaxial curvature (Figs. 23, 24). Marginal growth causes formation of the blades (lobes) of sepal and petal. The marginal initial divides anticlinally contributing to abaxial and adaxial protoderm (Figs. 19, 20, 22). The submarginal initial divides anticlinally (Figs. 19, 22) or periclinally. Rarely a marginal initial may divide periclinally in a petal (Fig. 21).

Stamen development—Five stamens arise in antisepalous position shortly after the initiation and early development of the petals. In longisection the early

FIGS. 1-15. 1-3, longisections of shoot apices of *Solanum melongena*; 1, leaf initiation phase; 2, post-leaf initiation phase; 3, pre-leaf initiation phase; 4, schematic representation of a row of cell of the shoot apex, selected for measurements; 5-15, graphical representation of length of the cells in the shoot apex (as shown in 4) during different stages of the development of the shoot apex; 5-10, *S. melongena*; 11-15, *C. annuum*.

(CR, central region; L, leaf; LB, leaf buttress; LI, leaf initiation; LT, leaf trace; PR, peripheral region; RR—inner-axial region, SCR, subcentral region; I-VI, different stages of development of shoot apex; 1-20, number of cells.)

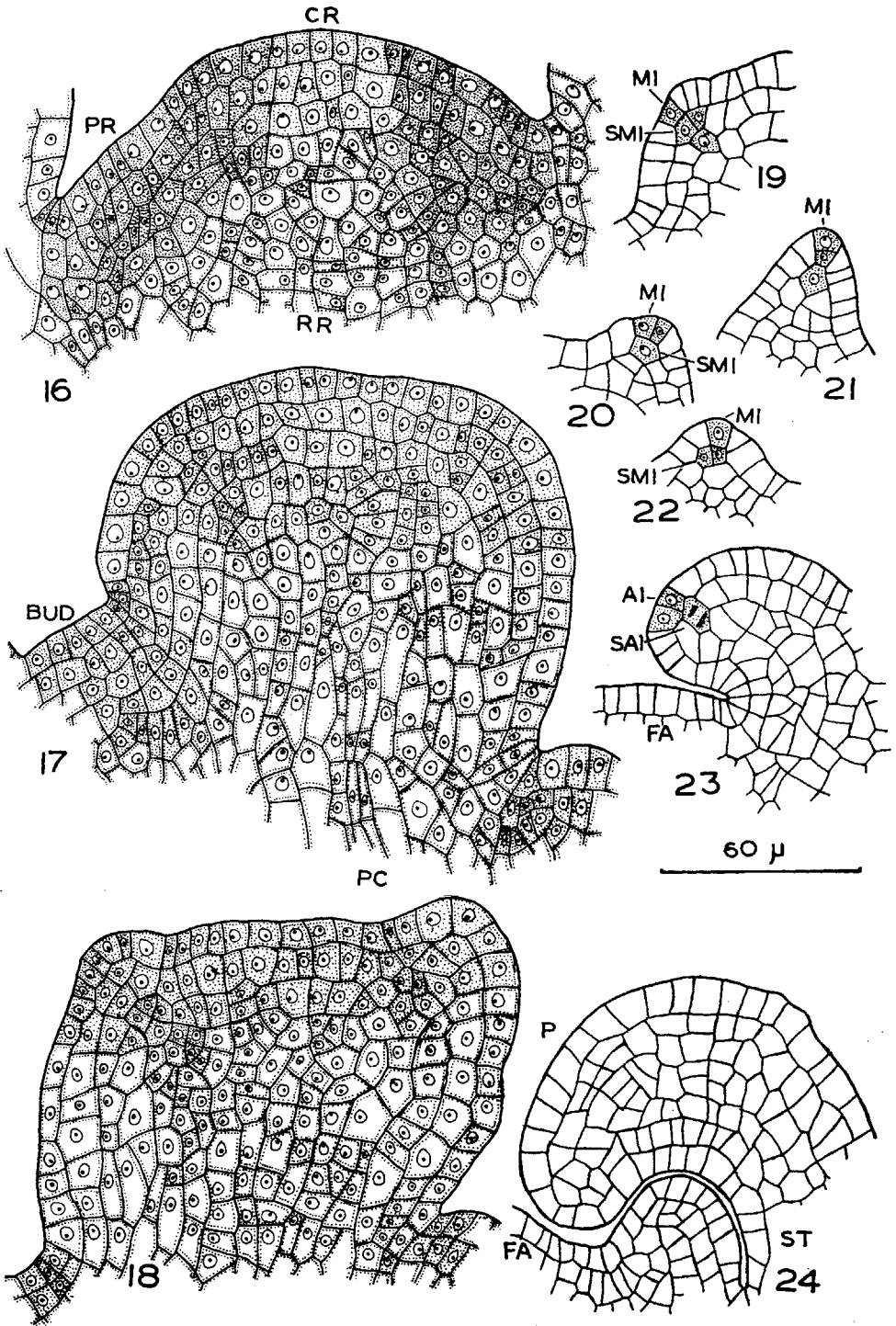


TABLE IV
Average height of cells in the shoot apex at different stages of its development in *Capsicum annuum*

No of cell	Height (in μm)				
	Stages of development				
	I	II	III	IV	V
1	19	16	13	15	11
2	13	18	10	12	12
3	12	15	12	18	10
4	11	13	9	12	12
5	11	12	10	9	8
6	16	19	12	13	9
7	15	30	6	11	11
8	15	30	6	9	14
9	15	27	7	12	6
10	22	36	8	15	8
11	27	39	8	12	7
12	26	39	7	18	9
13	33	36	11	19	7
14	27	37	15	25	13
15	25	30	14	27	18
16	28	32	13	27	12
17	25	34	10	30	12
18	15	29	24	18	13
19	18	25	24	24	13
20	22	25	26	27	13

stamen primordium differs from the sepal and petal primordia in its thick, broad and clavate apex. It is erect without adaxial curvature (Figs 24, 33, 34). The trace procambium is absent in the young primordium. Its growth in height is intercalary.

The early primordium is almost oval having its adaxial surface broad (Fig. 30). It later becomes almost trapezoidal (Fig. 32, only one corner is shown). The centrally located cells of the young primordium are lightly stained and vacuolated (Fig. 30).

FIGS. 16-24. 16-18, *C. annuum*; 16, longisection of the shoot apex in vegetative state; 17, longisection showing the transformation of vegetative apex to reproductive one; 18, longisection of the floral apex; 19-24, *S. melongena*; 19, transection of sepal primordium showing marginal growth; 20-22, transections of petal primordium showing marginal growth; 23, longisection of petal showing apical growth; 24, longisection of petal and stamen primordia.

(AI, apical initial; BUD, dichasial bud; CR, central region; FA, floral apex, MI, marginal initial, P, petal, PC, procambium, PR, peripheral region, RR, inner-axial-region, SAI, subapical initial, SMI, submarginal initial; ST, stamen)

TABLE V
*Diameter of the nuclei and cyto-nuclear ratio in reproductive apex of
 Capsicum annuum at different phases of its development*

Developmental stage	Diameter of nucleus (μm)	Cyto-nuclear ratio
Shoot apex in transition	6.40	2.78
Apex at sepal differentiation	7.20	2.30
Apex at carpel differentiation	6.32	2.85
Ovule primordium	5.86	2.80

Later, they increase in size and become progressively more vacuolated, except the procambial tissue in the centre. The cells at the corners of the primordium remain densely cytoplasmic (Fig. 31). The outer periclinally dividing layers form the anther tapetum and inner cells form the sporogenous tissue (Fig. 32). The young stamen is sessile (Figs. 33, 34) and the filament is formed by the general intercalary growth of the basal cells of the stamen.

Carpel development—Following the early development of stamen, two carpel primordia arise separately on the flanks of the apex (Fig. 34). They elongate due to apical growth (Fig. 35) which is of short duration. Intercalary growth is also present.

In the early development, a carpel primordium is erect and short with a broad apex (Fig. 34) but later, due to differential growth, it bends adaxially (Fig. 35). By further bending the two free primordia come in contact with each other at their adaxial margins and fuse (Fig. 36).

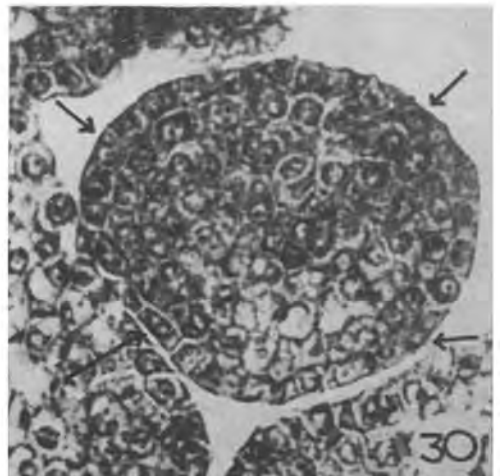
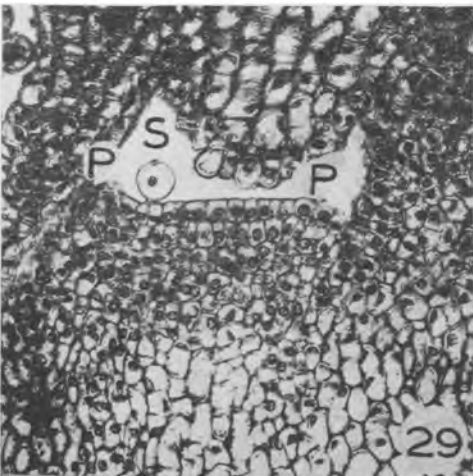
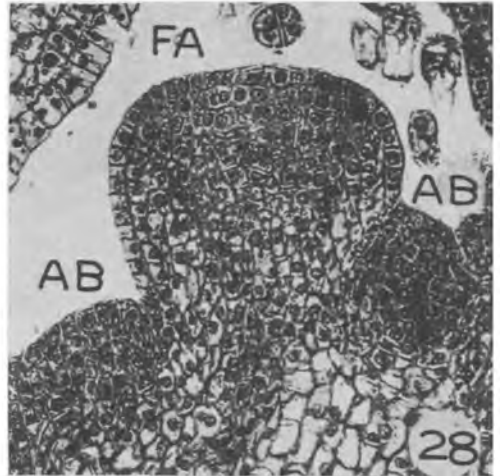
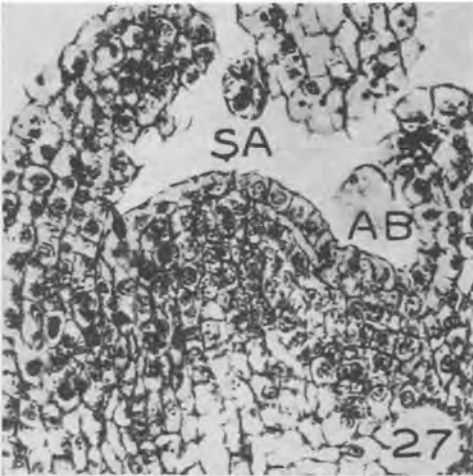
A part of the floral apex remains distinct after the initiation of the carpels (Figs. 34, 35). This residual apex (R) is flat in the beginning (Fig. 34) but later becomes convex and subsequently elongated as the carpel primordia elongate (Fig. 35) and fuse (Fig. 36).

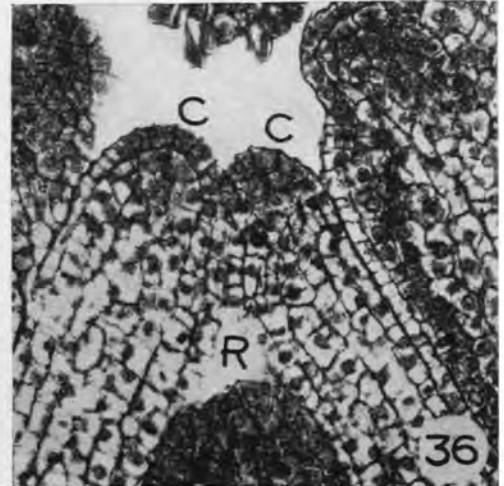
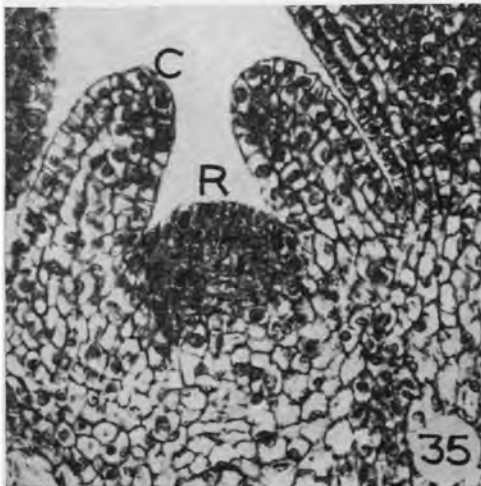
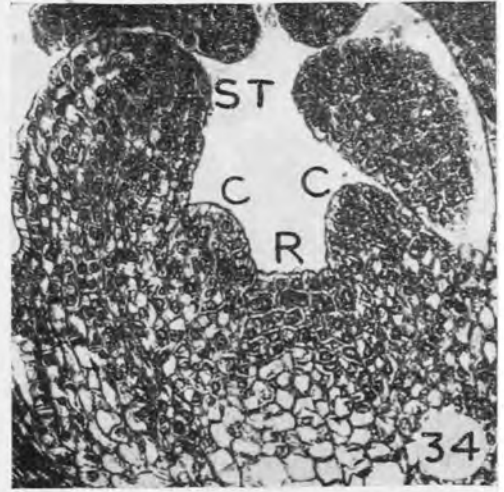
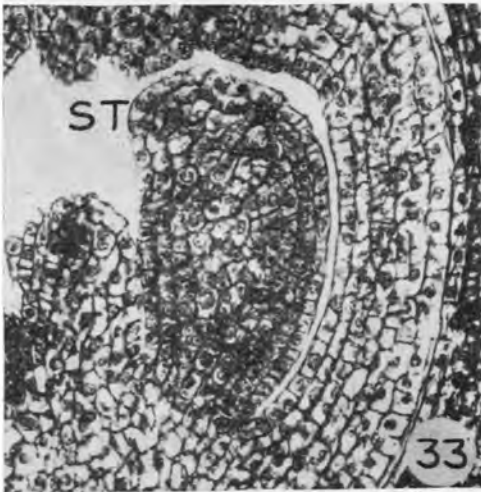
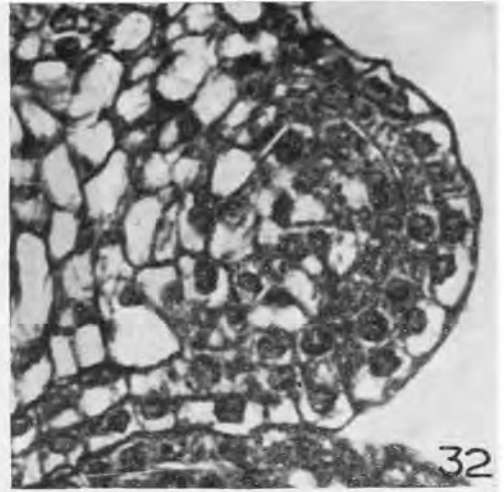
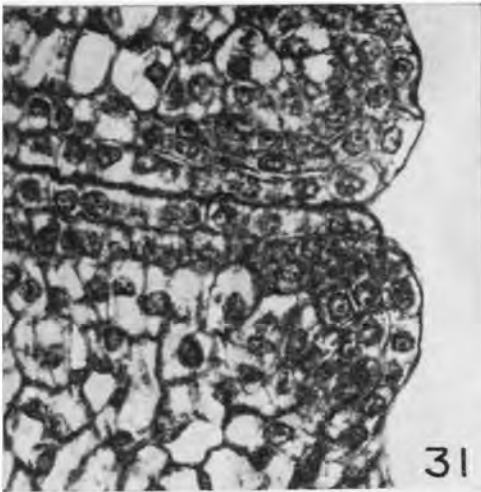
DISCUSSION

Among the concepts of the shoot apical organization, put forth by the French School has been much debated in the recent literature (Gifford 1951, 1954; Nougarede 1967; Unnikrishnan 1967; Rao 1969; Bhar and Radforth 1969; Cutter 1971; Gifford and Corson 1971). The concept of cytohistological zonation is firmly rooted in the literature (Gifford 1954; Gifford and Corson 1971). Tolbert (1961) divided the shoot apex into three characteristic zones (i) metrameristem, (ii) flanking

FIGS. 25-30. *Capsicum annuum*. 25-26, longisections of the vegetative shoot apices; 27, longisection of the vegetative shoot apex during its transformation into floral apex, 28-29, longisections of the floral apices; 30, Transection of stamen in its early development stage. $\times 240$.

[*AB*, dichasial bud, *FA*, floral apex, *MI*, marginal initial, *P*, petal primordium, *S*, sepal primordium, *SA*, shoot apex; arrow (in Fig. 26)—peripheral region of the shoot apex, arrow (in Fig. 30)—loci of marginal growth in stamen primordium]





meristem, and (iii) pith rib meristem. Esau (1965) recognized the distal axial zone, proximal axial zone and the peripheral or outer zone. According to Rao (1969), Esau's (1965) terminology demonstrates morphological loci of the different zones but does not convey the morphogenic potentialities of the zones concerned. However, we have adopted a modified terminology of Esau (1965). Accordingly, the zones distinguished in the present investigation are central, peripheral, inner-axial and subcentral regions. In *Senecio vulgaris* (Seidlova *et al.* 1964), the subcentral region between the central and the rib meristem was reported. Trivedi (1969) described a cambium-like zone below the central mother-cell zone in *Capparis decidua*. The pith mother-cell region (Tolbert and Johnson 1966) with its characteristic orientation of cells in irregular blocks, situated above the pith rib meristem, and central zone between the summit zone and the pith rib meristem in *Datura stramonium* (Corson 1969; Cutter 1971) correspond topographically with the subcentral region in chilli and brinjal.

In many angiosperm shoot apices (Ball 1949; Steinberg 1950; Sussex 1955; Shah and Dave 1970), distinct zones cannot be demarcated on the basis of staining reaction. The shoot apex in chilli and brinjal does not exhibit zonation in its juvenile stage, nevertheless, it produces one or two leaves (Shah and Patel 1970 *a*). Hence, the cytohistological zonation is apparently not related to the functional activity of the shoot apex. Mature shoot apices, however, show cytohistological zonation in brinjal and chilli. *Solanum tuberosum* and other species of *Solanum* lack cytohistological zonation (Sussex 1955).

According to the French School, the central meristem (central region) of the 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 regions (central region) during various plastochronic phases (Denne 1966). Corson (1969) concludes that in *Datura stramonium* since the number of cells in the summit zone (referred as central region in this paper) remains constant, the daughter cells (of central region) must be contributing to outer zones of the apex and, therefore, cannot be considered passive. The fluctuation in length of the cells of central region during various stages of shoot apex of brinjal and chilli, from germinating seed to a mature plant, is suggestive of the activity of the cells in this region.

At post-leaf initiation phase, the peripheral region of the shoot apex of chilli 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 by 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

FIGS. 31-36. 31-32, transections of stamen at different phases of its development. $\times 350$; 33, longisection of the young stamen. $\times 240$; 34, longisection of the floral apex showing stamen and carpel primordia $\times 240$. 35-36, longisections showing the carpel primordia and residual apex. 33-36, $\times 240$. CC, carpel primordium; R, residual floral apex; ST, stamen)

lacks zonation even during the onset of anthesis. In the vegetative phase these plants exhibit cytohistological zonation.

In chilli, as in *Frasera carolinensis* (McCoy 1940), *Downingia bacigalpii* (Kaplan 1968), *Portulaca grandiflora* (Soetiarlo and Ball 1969), inception of the carpels occurs laterally in the periphery, leaving a small depression in the centre 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 also because the filament arises by the 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.

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