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The Study of Origin of Pericarp Layers in *Solanum melongena*

By

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With 5 figures (3 plates)

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Abstract

The 140—160 cells thick pericarp of *Solanum melongena* is differentiated into three distinct regions — the epicarp, mesocarp and the endocarp. The cells of 4—5 hypodermal layers of the ovary wall divide anticlinally, periclinally and obliquely to produce about 15—18 layers of peripherally elongated cells out of which only outer 4—5 hypodermal layers contribute in the development of the epicarp and the remaining layers contribute to the outer mesocarp. The anomocytic and contiguous stomata are present only on the outer epidermis. The mesocarp is the product of a mesoderm and partly of inner and outer hypodermal layers of the ovary wall. The enlargement of the inner mesocarpic cells is earlier than those of the outer mesocarp. The endocarp is the result of amplification in number of the inner epidermal and 5—6 inner hypodermal layers of the ovary wall. The endocarpic and placental outgrowths join to form small chambers enclosing individual seeds.

Zusammenfassung

Studie über die Entstehung der Perikarpschichten von *Solanum melongena*

Das 140—160 Zellschichten dicke Perikarp von *Solanum melongena* L. ist deutlich in Epikarp, Mesokarp und Endokarp gegliedert. Die Zellen der 4—5 hypodermalen Schichten teilen sich antiklinal, periklinal und schräg, wobei sie 15—18 Schichten peripher gestreckter Zellen liefern. Nur die äußeren 4—5 Hypodermschichten bilden das Epikarp, die übrigen tragen zum äußeren Mesokarp bei. Die anomozytischen, auch paarweis liegenden Stomata finden sich nur in der äußeren Epidermis. Das Mesokarp ist das Produkt der mittleren Zellschichten der Fruchtknotenwand und teilweise auch der inneren und äußeren Hypodermis. Die Vergrößerung der inneren Mesokarpzellen setzt eher ein als die der äußeren. Das Endokarp ist das Produkt aus einer Zellvermehrung

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der inneren Epidermis und der 5—6 inneren Hypodermalschichten der Fruchtknotenwand. Es bildet lappige Auswüchse, die mit Auswüchsen der Plazenta zu kleinen Kammern verschmelzen, die einzelne Samen umschließen.

(Editor)

1. Introduction

The *Solanaceae* are a family of considerable economic importance (LAWRENCE 1960) and are the source of food plants (e. g. Brinjal, Capsicums, Potato and Tomato), the fumitory (e. g. Tobacco), drug plants (e. g. *Datura* sps.) and ornamentals from many genera including *Datura*, *Solanum* sps. and *Cestrum* etc. Brinjal is one of the popular vegetables of India. The fruits are berries with persistent thick green calyx and are of different varieties.

According to ESAU (1965) the terms applied to the different layers of the pericarp have little value for showing the origin of the various tissues of the fruit wall, but they are useful for the description of mature fruits. In the present work the multilayered epicarp, the outer and inner mesocarp and the multilayered endocarp of the fruit are described in relation to their ontogeny. The definite origin of the epicarp, mesocarp and the endocarp have also been traced in various fruit wall studies made by DAVE *et al.* (1974, 1975), KRISHNAKUMAR *et al.* (1975), ZALA *et al.* (1976) and PATEL *et al.* (1976). Although varieties of brinjal are not studied here, the characters from fruit anatomy may provide useful taxonomic traits as in Capsicums (DAVE *et al.* 1979).

2. Materials and Methods

The fruits of *S. melongena* L. were collected from the local fields of Boriyavi—Gujarat state for the developmental and anatomical studies. The

Table 1

The average length and diameter of the ovary and fruits measured at their various developmental stages are as shown in the following table

Stage	Length in cm	Breadth in cm	Remarks
1.	0.2—0.4	0.1—0.2	Ovary (from flower bud and flower)
2.	0.5—0.7	0.4—0.6	Developing fruit stages
3.	1.0—2.0	0.6—0.8	
4.	2.0—3.0	1.0—1.2	
5.	3.0—4.0	1.5—1.8	
6.	5.0—6.0	1.8—2.2	
7.	7.0—8.0	2.4—3.0	
8.	8.0—10.0	3.0—4.1	
9.	13.0—18.0	4.5—6.0	Mature fruit

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rest of the procedures were followed as in Capsicums (DAVE *et al.* 1979). The average length and diameter of the ovary and fruits were measured at their various developmental stages (Table 1).

3. Observations

3. 1. Ovary wall from flower bud and flower:

The homogenous tissue of ovary wall are mainly polygonal and compactly arranged parenchyma. It is 45—48 cells thick at the base and 20—22 cells thick in the terminal region. Just beneath the outer epidermis of the ovary wall the cells in 14—15 layers are divided anticlinally, obliquely and more frequently periclinally (Fig. 2B). The outer epidermis has small polygonal cells which in later stages show periclinal divisions to form the vertical files which are parallel to the vertical axis of the fruit (Fig. 1 A—C, E, F, P).

The mesodermal cells are slightly larger and more vacuolated. They embed about 27 conjoint and collateral vascular bundles placed more towards the inner epidermis. Some vascular bundles are obliquely cut which is due to the reticulation of the branched vascular system of the ovary wall. The starch is present in the mesoderm cells.

The inner epidermis and its 5—6 hypodermal layers along with the mesoderm of the ovary continue in the thin partition wall of the ovary (Fig. 2C). The placentation is axile but appears to be parietal when the ovary is multilocular (Fig. 2 A). The 2—3 peripheral layers of the placentae are densely stained and meristematic (Fig. 2 G).

3. 2. Developing pericarp:

It increases in thickness upto 140—160 cells in the sixth stage of the fruit and later the cells of outer epidermis (Fig. 1 D), outer mesocarp and endocarp show more enlargement than the increment in cell number (Fig. 5A, B, D).

3. 2. 1. Epicarp:

The outer epidermis shows the presence of anomocytic stomata surrounded by 4—9 epidermal cells (Fig. 1 Q—T, W). At some places contiguous stomata are also observed (Fig. 1 U, V) and trichomes are absent. Figure — 1M—O show the meristemoid and differentiation of guard mother cells. The cuticle on the outer tangential and radial walls of the outer epidermal cells grow thicker (Fig. 4H). Sometimes the outer epidermal cells are found irregularly thickened (Fig. 1G—I). Some cells show the thickening around their cell walls and degenerating nuclei in them; but later they become empty thick walled cells (Fig. 1J—L). Four to five layers of outer hypodermal

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parenchyma show frequent periclinal divisions of their cells which together with the outer epidermis seem to constitute the epicarp (Fig. 2D). In the later stages of the pericarp the deeper layers of the multilayered epicarp also contribute to the mesocarp. The epicarpic cells appear smaller in the extreme basal region of the fruit (Fig. 4B).

3. 2. 2. Mesocarp:

It develops from the mesodermal and partly from the hypodermal regions of the ovary wall. It is 50—55 cells thick at the third stage of the fruit. Many of its parenchyma at the sixth stage are observed separated or with large intercellular spaces (Fig. 4A, B). The vascular bundles and developing strands are found scattered through out the mesocarp due to the furthur branching and anastomosing of the basic vascular system and differentiation of more vascular strands from the mesocarpic parenchyma (Fig. 3A, B, 4A, G). The mature vasuclar bundles are conjoint and collateral or concentric (Fig. 4C, E, F). Figures 3A, B; 4A, C, E—G illustrate the various patterns of the xylem and phloem and indicate the presence of thick and thin or branched veins in the mesocarp.

3. 2. 3. Endocarp:

The inner epidermis of the fruit wall and 6—10 compressed inner hypodermal parenchymatous layers constitute the endocarp of the young fruit (Fig. 2E). The endocarpic cells show the presence of insoluble carbohydrates (Fig. 3C). Some of the deeper layers of the endocarpic cells enlarge, become more vacuolated and contribute to the inner mesocarp of the fruit (Fig. 2E). The endocarp during its development becomes lobed and the lobes outgrow to partly enclose the seed (Fig. 3G). Although the seeds are completly enclosed when the endocarpic outgrowths join with the placental outgrowths (Fig. 3H). The separation occurs in the endocarpic and placental cells and in the cells of their outgrowths (Fig. 3F, H). The endocarpic cells appear more compressed and wavy towards the maturity (Figs. 2E; 4D).

In a series of transections of the fruit from base upward it is seen that there is no chamber at the extreme base; slightly above the narrow, small chambers lined by thin walled densely stained tissue are observed and there may be no placentae or seeds at that level (Fig. 2F). Then the outgrown placentae and two or more chambers are seen in the middle region of the fruit (Fig. 2H). Sometimes the aborted ovules are observed in these chambers (Fig. 3E). At the extreme terminal region, the cells just above the end of the chamber show concentric cell pattern around the central parenchymatous area (Fig. 3D). From these observations it can be concluded that the fruit locules become multichambered and the placentae bearing seeds become lobed in the middle region of the fruit. But there are no seeds in the extreme basal and terminal chamberless parts of the fruits.

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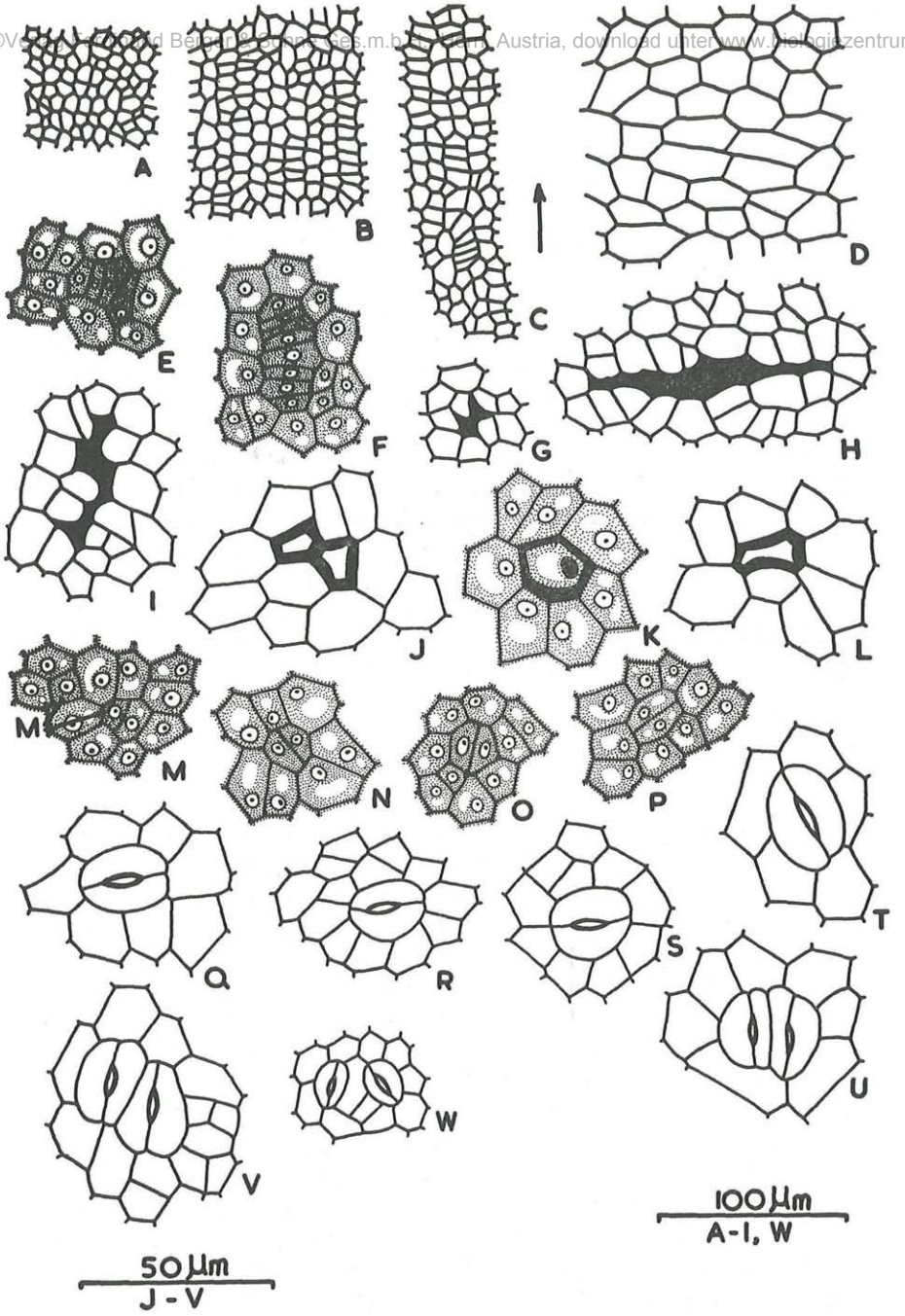


Fig. 1. A. Outer epidermis from ovary wall in surface view; B. Outer epidermis in surface view from stage-4; C. Outer epidermis in surface view from basal region of stage-5 showing the cell divisions (arrow indicates the vertical orientation of cells from basal to middle); D. Outer epidermis in surface view from stage-7; E, F. Group of cells showing cell divisions; G—I. Epidermal cells showing the thickening of walls; J—L. Thick walled epidermal cells (Note degenerating nucleus in K); M—O. Developmental stages of anomocytic stomata; P. Some of the guard mother cells are becoming normal epidermal cells instead of forming guard cells (Note vacuolation in them); Q—T; W. Anomocytic stomata surrounded by 4—9 epidermal cells; U—V. Contiguous stomata. (M = Meristemoid)

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3. 3. Growth patterns:

The cell areas of the different zones of the pericarp and placentae when plotted against the various stages of the developing fruit (Fig. 5A—E) revealed that: (1) The cell areas from different zones are different at the maturity of the fruit. (2) The largest cells are of the inner mesocarp and the placentae, and the smallest cells are of the outer epidermis. (3) The outer epidermal cells of 2—4 stages do not show rapid increment in their size but after the sixth stage they are more enlarged. At the ninth stage of the fruit their cell area is maximum (Fig. 5A). (4) The growth pattern of the outer mesocarpic cells appears to be a simple sigmoid type as the growth appears slow during the second to sixth stage period (Fig. 5B). (5) The inner mesocarpic cells are slow in their growth during first to third stages. Then they show rapid increment in their area. It is also evident here that the parenchyma of inner mesocarp start their enlargement earlier than those of the outer mesocarp. The maximum growth of the inner mesocarpic cells is found from eighth to ninth stages (Fig. 5C). (6) The inner epidermal cells show maximum growth from stage sixth to seventh (Fig. 5D). (7) The placental cell areas increase rapidly from stage three onward (Fig. 5E).

4. Discussion

The pericarp starts its development from about 20—50 cells thick ovary wall and attains the thickness of 140—160 cells during the sixth stage of the fruit development, which is due to the rapid divisions of its cells; but after the sixth stage the cells do not increase much in number and show more enlargement towards the maturity of the fruit. The epicarp of the fruit can be said to be originated from the outer epidermis and some of the hypodermal layers, as their cells simulate each other at the maturity of the fruit. This is mostly due to the frequent periclinal divisions in the hypodermal zone. The deeply situated epicarpic cells enlarge, become more vacuolated and appear similar to the cells of the outer mesocarp.

The mesocarpic large and vacuolated parenchyma which become separated towards the maturity of the fruit have their ontogeny in the mesoderm and partly from the outer and inner hypodermal layers of the ovary wall. The mesocarp of *S. tuberosum* develops from the mesoderm and partly from the outer hypodermal layers, while in *S. indicum* it develops only from the mesoderm of the ovary wall (Patel 1977).

The number and nature of the vasuclar bundles found scattered throughout the mesocarp reveal the further branching and anastomosing of the vascular system. The occurrence of various developmental stages and patterns of xylem and phloem strands in the developing mesocarp also show the capacity of mesocarpic parenchyma to divide and differentiate into vascular strands. Some large vascular bundles show the presence of 3—4

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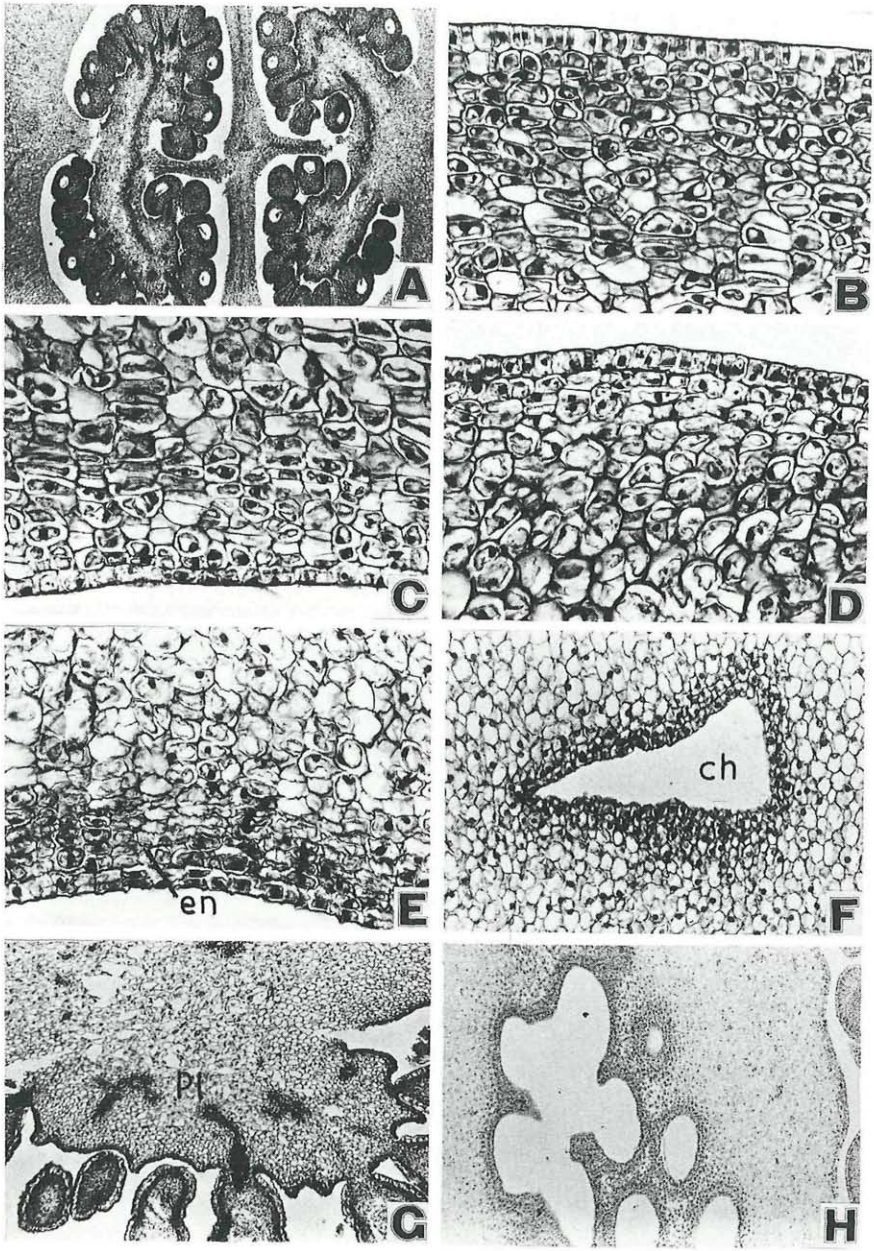


Fig. 2. A. T. S. of ovary showing the arrangement of placentae (× 30); B. Cellular details of ovary wall showing anti- and periclinally divided cells in the outer hypodermis (× 290); C. Cellular details of inner epidermis and inner hypodermis showing anti- and periclinally divided cells (× 290); D. Cellular details of epicarp from stage-2 (× 290); E. Cellular details of endocarp showing anticlinally divided cells in inner hypodermis and inner epidermis (× 270); F. T. S. of fruit from the base showing narrow chamber (× 140); G. Cellular details of placental region (× 42); H. L. S. of fruit showing the placental region and seed chambers (× 30); (ch, Chamber; en, Endocarp; pl, Placentae)

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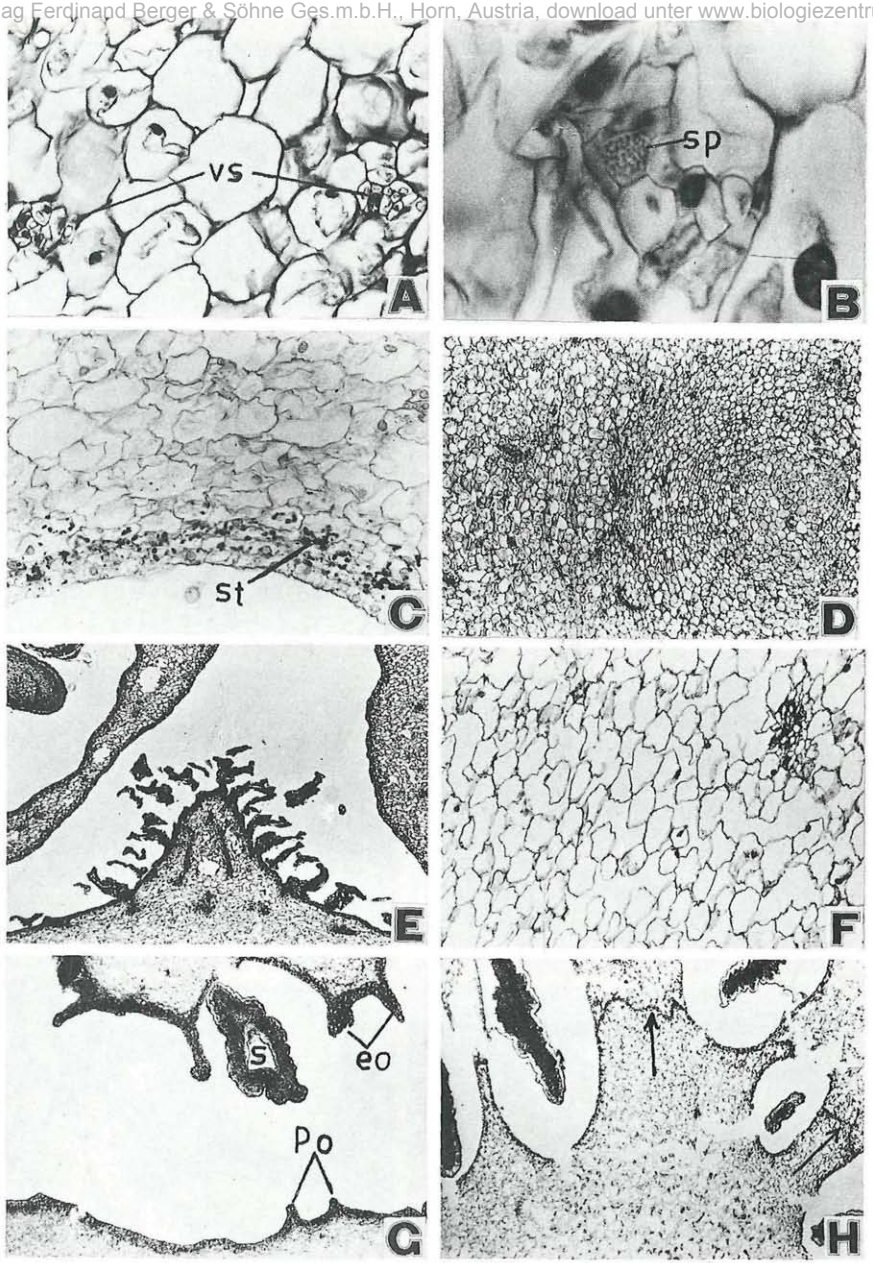


Fig. 3. A. Cellular details of mesocarp with developing procambial strands (×310); B. Small vascular strand showing only phloem (×1160); C. Pericarp stained with PAS showing the presence of insoluble carbohydrates only in the endocarpic cells (×290); D. Part of fruit from extreme tip (note the cells arrangement in the centre) (×30); E. T. S. of fruit from basal region showing aborted ovules in the central chambers (×30); F. Cellular details of endocarpic outgrowth showing separated cells (×116); G. Portion from endocarp and placenta showing the development of outgrowths (×30); H. Single seeded chambers and fusion of endocarpic and placental outgrowths (at arrow) (×30); (eo, Endocarpic outgrowth; po, Placental outgrowth; s, Seed; sp, Sieve plate; st, Starch; vs, Vascular strand)

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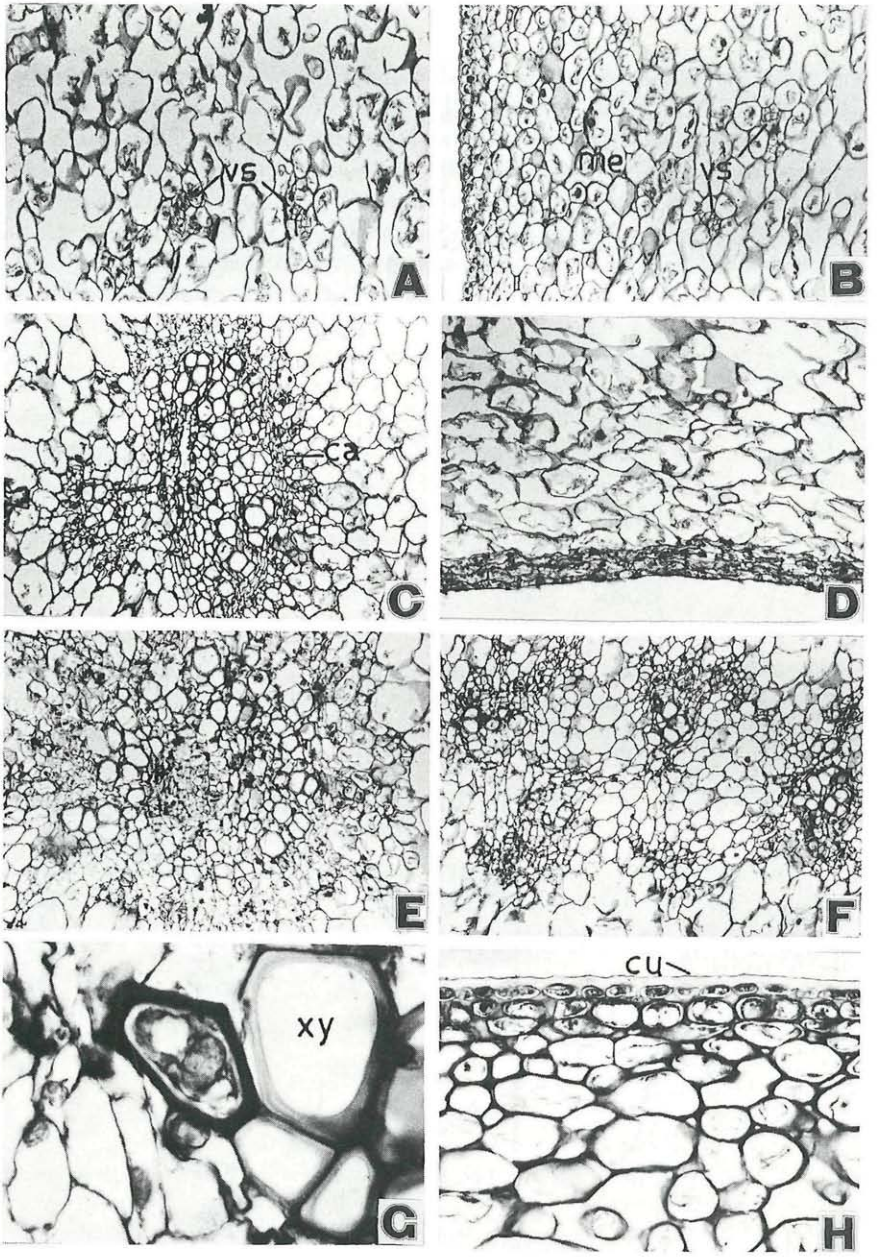


Fig. 4. A. Cellular details of mesocarp (× 116); B. Cellular details of fruit from basal region showing the separation of cells in mesocarp (× 116); C. Vascular bundle from mesocarp showing cambium between xylem and phloem (× 116); D. Cellular details of endocarp showing compressed cells (× 120); E—F. Vascular bundles from pericarp showing different arrangement of xylem and phloem (× 270); G. Part of vascular bundle showing the developing xylem vessel (× 960); H. Cellular details of epicarp from stage-9 showing the thick cuticle on the outer epidermal cells (× 240); (ca, Çambium; cu, Cuticle; me, Mesocarp; vs, Vascular strand; xy, Xylem)

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celled thick cambium which seems to indicate the possibility of the origin of secondary tissue as in the fruit wall of Datura (NHA & DANERT 1973).

The endocarpic and placental outgrowths join each other in large locules of the fruit to form single seeded chambers in *S. melongena* and also in *S. indicum* (PATEL 1977). Thus the multichambered condition in brinjal is due to the union of the endocarpic and placental outgrowths. There are no endocarpic outgrowths in *S. tuberosum* but only the placental outgrowths surround the seeds (PATEL 1977).

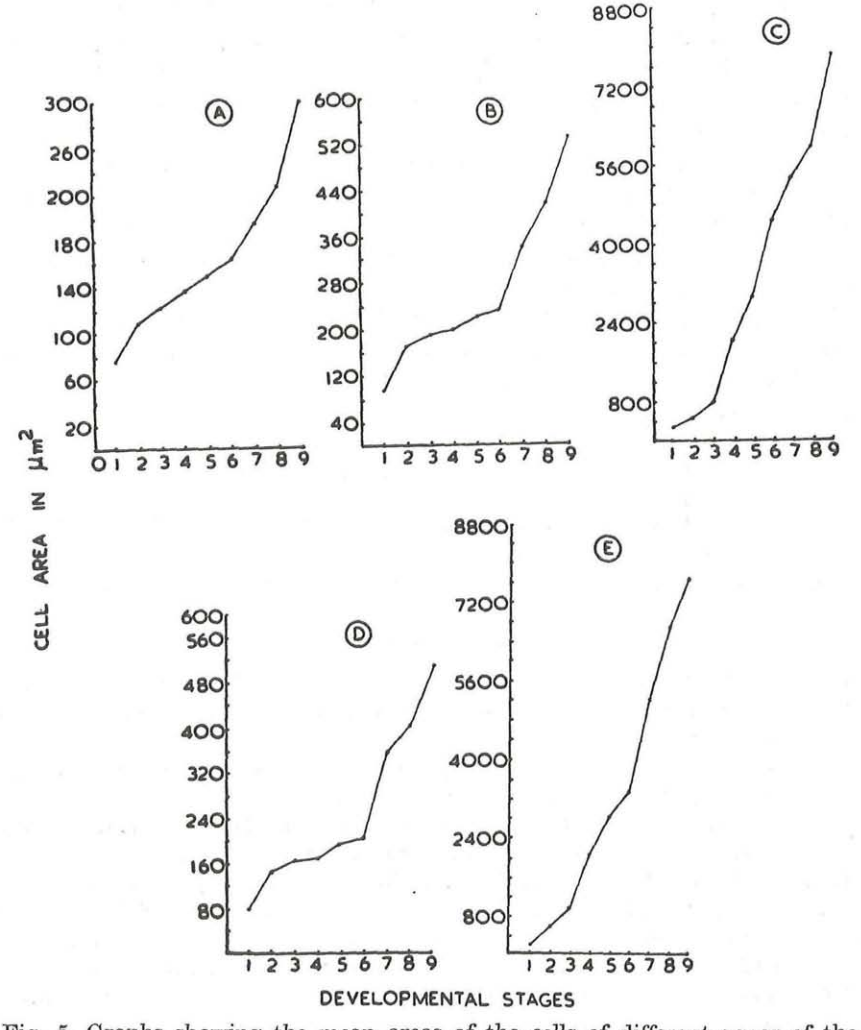


Fig. 5. Graphs showing the mean areas of the cells of different zones of the fruit at its different developmental stages.
(Explanations from the Text)

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It is evident from the developmental studies in brinjal pericarp that the multilayered epicarp has been derived from the outer epidermis and its hypodermal layers; the outer mesocarp is developed from the mesoderm and partly from the deeply situated layers of the outer hypodermis of the ovary wall; the inner mesocarp is also derived from the mesoderm and partly from the inner hypodermal layers borne towards it and the endocarp is originated from the inner epidermis and few inner hypodermal layers of the ovary wall. Thus the origin of the various tissue zones of the fruit wall lies in difinite tissue layers of the ovary wall. This will be also emphasised in our subsequent papers on the studies of some more Solanaceous fruits.

Many fruits have growth patterns of the simple sigmoid type common to most cells, tissues and organisms, starting with an exponential increase in size and then slowing in sigmoid fashion and this kind of growth curve is common to the apple, pineapple, strawberry, pea tomato and many other fruits (Leopold & Kriedemann 1964). The almost simple sigmoid type of growth patterns of the cells of different zones of the pericarp and the placentae of Chillie (Dave *et al.* 1979) and brinjal are obtained. In chillie only the inner mesocarpic cells and the giant cells have the largest cell areas of 4042 μm^2 and 44710 μm^2 respectively but the endocarpic cell areas are the smallest, i. e. 415 μm^2 (Dave *et al.* 1979). In case of brinjal the inner mesocarpic cells and the placental cells show largest cell areas of 7969 μm^2 and 7706 μm^2 respectively. In brinjal the epicarpic cells have the smallest cell areas of 300 μm^2.

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