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Morpho-Histogenesis in the Fruit Sculpture of *Datura innoxia*

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With 2 Figures (2 Plates)

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Abstract

The pericarp in *Datura innoxia* MILL. develops from 10—13 cells thick homogenous ovary wall. Epicarp which is 5—7 layered collenchymatous zone of the mature fruit develops from 3—4 outer layers of the smooth ovary wall. A zone beneath the epidermis is 2—3 layered collenchymatous cortex with intercellular spaces. The parenchymatous mesocarp is produced as a result of anticlinal, periclinal and oblique divisions in the mesodermal cells of the ovary wall. In a mature pericarp the mesocarpic cells become enlarged, vacuolated, sinuous and separated. The cambium of hadrocentric vascular bundles show its secondary activity. The whole fruit is well supported because of the scleren-chymatic vascular system of the pericarp and the placenta. The 10—14 layered thick endocarp of a mature capsule results from 5—6 inner layers of the ovary wall which undergo anticlinal, periclinal and oblique divisions. The paren-chymatous placental tissue and the septal tissue are found separated in the mature fruit. The dehiscence of the capsule is the result of shrinkage of the parenchyma of pericarp, placentae and septa and it does not open below the middle region.

Zusammenfassung

Morpho-Histogenese bei der Ausbildung der Früchte von *Datura innoxia*

Das Pericarp von *Datura innoxia* MILL. entsteht aus der einheitlich auf-gebauten, 10—13 Zellagen starken Fruchtknotenwand. Das Epicarp, in der reifen Frucht eine 5—7 Zellen starke kollenchymatische Zone, geht aus den 3—4 äußeren Zellschichten der glatten Fruchtknotenwand hervor. Unterhalb

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der Epidermis liegt ein 2—3 Zellen starkes Interzellularen führendes Hypoderm. Die aus den mittleren Schichten der Fruchtknotenwand hervorgegangenen Mesocarpszellen vergrößeren sich bei der Reifung und vakuolisieren, nehmen gekrümmte Formen an und sondern sich voneinander. Der Kambialring zeigt sekundäre Aktivität. Die Frucht wird durch ein reichlich ausgebildetes sklerenchymreiches Gefäßbündelsystem des Pericarps und der Plazenten versorgt. Das in der reifen Frucht 10—14 Zellagen starke Endocarp geht aus den 5—6 inneren Zellschichten der Fruchtknotenwand hervor. Die parenchymatischen Zellen der Plazenten und der Scheidewände hängen nur lose zusammen oder lösen sich ganz voneinander. Durch Schrumpfen des Parenchyms des Pericarps, der Plazenten und der Septen springen die Kapseln von der weniger sklerosierten Terminalregion ausgehend unregelmäßig auf.

(Editor transl. et. abbrev.)

Introduction

One of the important drug plant *Datura innoxia* MILL. emits a rank, heavy narcotic odour. The fruit is globose, dull green and hairy capsule ornamented with erect and stiff spines of 5—8 mm length. The capsule is 4—5 cm in length and 3.5—4.5 cm in diameter. It bursts at the top exposing a long central column bearing numerous light brown seeds.

DACHYSHYN (1965) and SRIVASTAVA (1969) described the morphology of the fruit and seeds of *Datura* but did not furnish the pericarpic details. NHA & DANERT (1973) although described the development of fruits and centric vascular bundles in the genus *Datura*, they did not concentrate upon the distinct pericarpic tissue zones, their development and the structural details of the dehiscence of the fruit. The present investigation deals with the detailed developmental and structural orientation of the pericarp zones and the dehiscence of the fruit.

Materials and Methods

The different developmental stages of the ovary and fruit of *D. innoxia* growing in the Campus of our University were collected and measured in length and diameter (Table 1). Then to facilitate the studies they were cut into basal, middle and terminal parts and fixed in FAA (BERLYN & MIKSCHE 1976). The paraffin embeded materials were cut into 8—12 μm thick sections and stained with safranin and fastgreen and DELAFIELD's hematoxylin for the study of tissue differenciation. For the detection of insoluble carbohydrates in the fruit at its different developmental stages test was made with the periodic acid-SCHIFF's (PAS) reaction. Photomicrographs of the various preparations were taken on Carl Zeiss photomicroscope.

Results

I Ovary

The ovary from the small flower bud is smooth walled and slightly lobed. It is four chambered at the basal and middle regions but two cham-

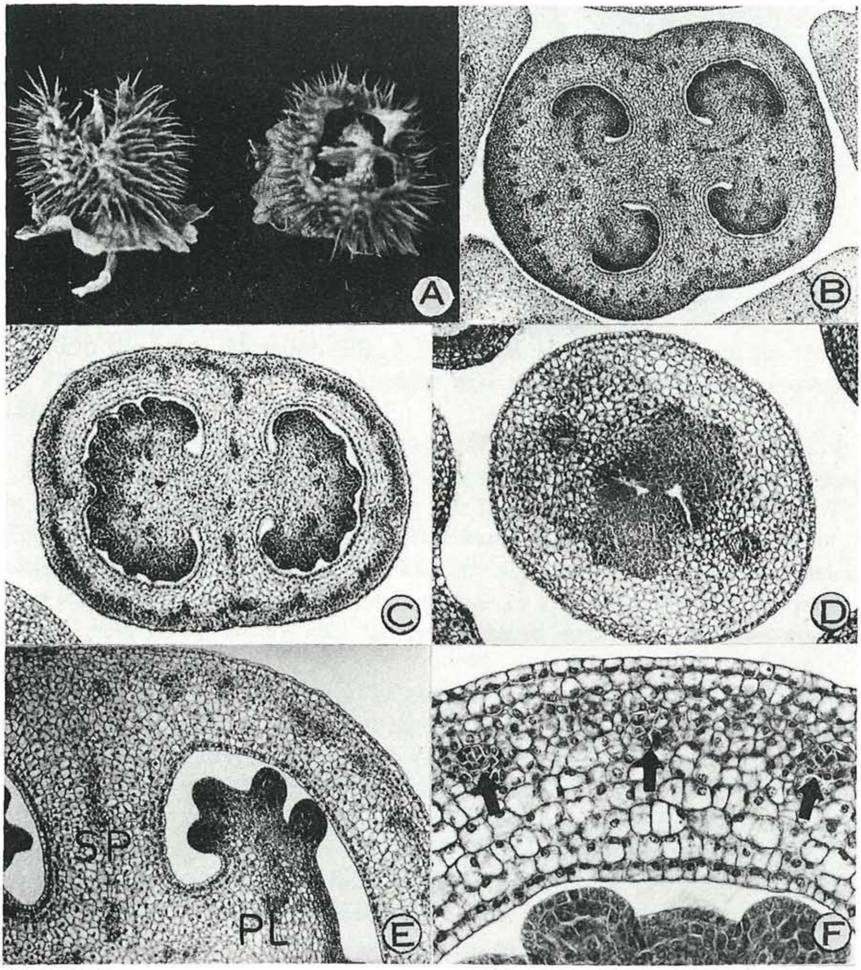

Fig. 1 A—F (plate 1)

A. Mature fruit showing the bursting of pericarp; × ½. — B—D. Transections of ovary from base to terminal region showing vasculature and placentation; B: × 38; C: × 60; D: × 96. — E. Part of ovary in transverse section; × 96. — F. Cellular details of ovary wall from dorsal side with developing vascular bundles (at arrows); × 240

Table 1

The measurements of the ovary and fruit at its various developmental stages

Stage	Length in cm	Diameter in cm	Remarks
1	0.2—0.3	0.1—0.15	Ovary (from flower bud)
2	0.3—0.4	0.2—0.3	Ovary (from flower)
3	0.6—1.0	0.4—0.6	Developing fruit
4	1.0—1.5	0.6—1.0	
5	1.5—3.0	1.5—2.5	
6	3.0—4.0	2.5—3.5	
7	4.0—5.0	3.5—4.5	Mature fruit

bered in the terminal region (Fig. 1 B—D). In the extreme tip of the ovary or beneath the style it is unilocular and without placentae and ovules (Fig. 1 D).

Ovary wall: It is 10—13 cells thick and homogenous in nature (Fig. 1 E, F). Its outer epidermal cells in transection appear tabular or rectangular in shape with their nuclei placed at the inner tangential walls (Fig. 1 F). There is a thin cuticle on their outer tangential walls. The mesodermal cells are large polygonal and vacuolated with distinctly spherical nuclei. The nuclei are sometimes spherical, elliptic or spindle shaped in the mesodermal cells of the ovary wall. There are small intercullular spaces among them.

The conjoint and collateral or bicollateral and the developing vascular bundles are situated in the outer mesodermal region which is just beneath the 3—4 layered hypodermal zone (Fig. 1 F). They are cut transversely, obliquely or longitudinally due to the branched and anastomosing pattern of the vascular system. The basic vascular system below the level of ovary is in the form of a ring. From this ring two arcs separate at the base of the ovary from whose two free ends two placental bundles are given off. Little higher up in the ovary two dorsals, two ventrals from the two free ends of each arc and about 8—12 laterals between each dorsal and ventral bundles become distinct in the ovary wall (Fig. 1 B, C). The placentals and their short branches end in the terminal region. The laterals and ventrals also end obliquely in the extreme terminal region and finally only two dorsals extend towards the style (Fig. 1 D). There are no distinct meristematic inner hypodermal layers.

The innermost layer of the ovary wall is made up of tabular, vacuolated cells with their nuclei mostly placed on their inner tangential walls (Fig. 1 F). The stomata are present in the inner epidermis but trichomes are absent. The inner epidermis continue over the septa of the ovary (Fig. 1 E).

Placentae: There are four placentae in the basal and middle regions of the ovary (Fig. 1 B), but towards the terminal region only two large placentae are seen because the dorsally borne false partitions or the septa of the ovary wall end in the terminal region (Fig. 1 C). In the extreme terminal region no placentae and ovules are seen but densely stained meristematic zone on both the sides of the slit like single chamber are observed (Fig. 1 D). The peripheral tissue of the placenta is meristematic which partly contributes in the further growth of the placenta (Fig. 1 E). The inner or central tissue of the placenta is parenchymatous and largely vacuolated and with intercellular spaces. The placental vascular bundles embeded in this tissue are conjoint and bicollateral.

II. Developing Pericarp

The trichomes on the developing pericarp of *D. innoxia* can be described as eglandular conical unicellular and uniseriate types; glandular capitate stalked (with unicellular and multicellular heads) and long stalked (with multicellular head), according to the classification of trichome types of Polemoniales by Inamdar & Patel (1973). The ornamentations called spines of *Datura* pericarp originate from the local active meristems of the subhypodermal tissue of the ovary wall (Dave *et al.* 1979).

Epicarp: The epicarp develops from 2—3 outer hypodermal layers of the smooth ovary wall of small flower bud. The outer epidermal cells in the early stages of developing pericarp are slightly vacuolated with spherical nuclei, thin cuticle on their outer tangential walls and are compactly arranged in the epidermis. Later they become cutinized on their outer and inner tangential walls and appear separated from the first hypodermal layers (Fig. 2 F).

The outer hypodermal layers later increase due to the periclinal divisions of their cells to form 5—7 layered thick epicarp. Their cells appear almost empty or with scanty cytoplasm towards the maturity of the pericarp. They appear to be collenchymatous with little thickening with large intercellular spaces and separated or loosely arranged (Fig. 2 F).

Mesocarp: The mesodermal cells of the ovary wall undergo transverse, vertical and/or oblique divisions to increase the layers of mesocarp in the developing fruit. In their later stages of development they become enlarged, more vacuolated, roundish or sinuous and show the presence of starch. Towards the maturity of the fruit the mesocarpic cells are separated or loosely arranged with large intercellular spaces (Fig. 2 B). The pericarpic vascular bundles embeded in the mesocarp are conjoint and collateral, bicollateral or hadrocentric (Fig. 2 D). During the further development of the vascular bundles a complete cambium ring is formed and secondary xylem and secondary phloem are produced due to its meristematic activity. The other tissues produced with the secondary xylem are lignified sclerenchymatic cells. Thus the pericarpic vascular bundles are also sclerenchymatic. The xylem is acentrically borne in the hadrocentric bundles (Fig. 2 D).

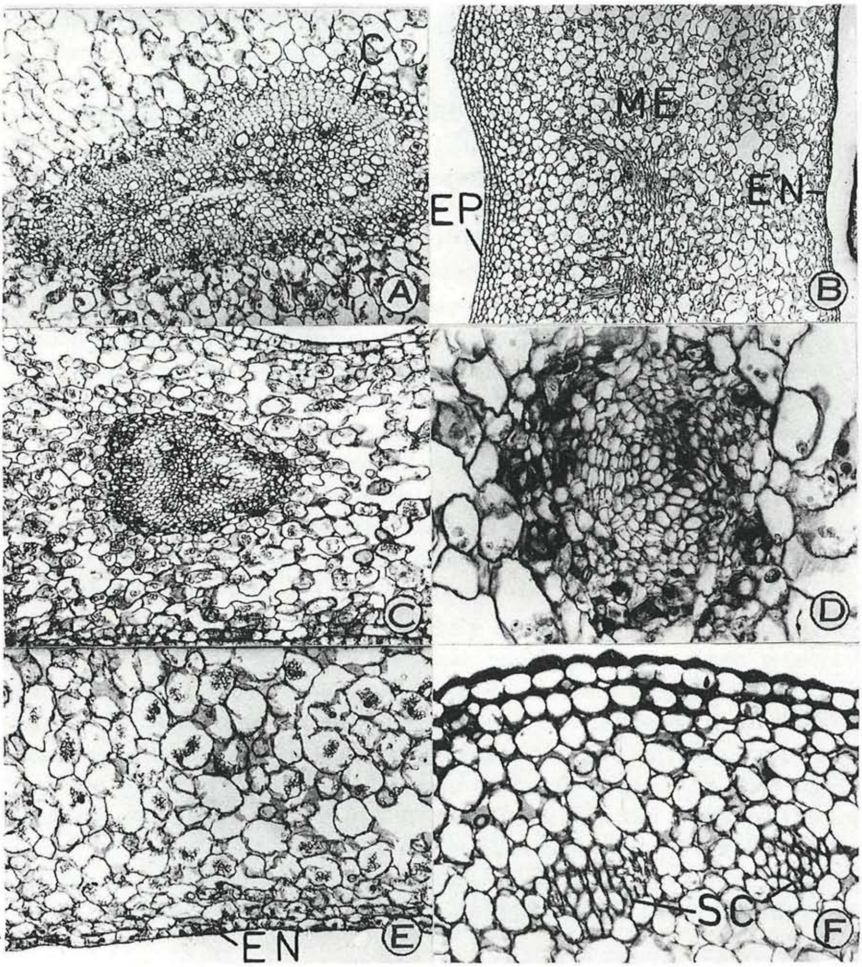

Fig. 2. A—F (plate 2)

A. Vascular bundles from placental region; × 96. — B. Part of pericarp showing separated mesocarpic and endocarpic cells; × 38. — C. Cellular details of septum with a vascular bundle. Note the separated cells with starch; × 96. — D. Vascular bundle from pericarp; × 290. — E. Cellular details of mesocarp and endocarp; × 116. — F. Cellular details of epicarp and mesocarp from mature fruit. Note small patches of sclerenchyma in mesocarp; × 116

Key to labelling; C, cambium; EP, epicarp; EN, endocarp; ME mesocrap; PL, placentae; SC, sclerenchyma; SP, septum

Endocarp: It is 10—14 layers thick including inner epidermis. It has its origin from an inner epidermis and the inner 4—5 hypodermal layers of the ovary wall. The hypodermal cells divide transversely, obliquely and vertically to increase the number of layers towards the maturity of the pericarp. Later these cells become much vacuolated, sinuous and separated; they also contain starch (Fig. 2 E). The inner epidermal cells are small, tabular or rectangular as seen in transection of the ovary and early stages of the pericarp. They have thin cuticle on their outer and inner tangential walls (Fig. 2 E). Patel & Dave (1976) have reported he anomocytic stomata in the inner epidermis of *D. innoxia* and *D. metel.*

Placentae: The placental tissue consists of much vacuolated, thin walled parenchyma containing starch (Fig. 2 A). In the later stages of the developing fruit the placentae and septa show loosely arranged or separated cells among which hadrocentric vascular bundles are embeded (Fig. 2 C). The cambium reveals its meristematic activity due to which secondary xylem (xylem parenchyma) and secondary phloem are produced (Fig. 2 A). The two or three subepidermal layers of the septa appear rectangular and the middle cells appear roundish and with intercellular spaces in the early stages. The septa of the fruit later show loosely arranged or separated parenchyma (Fig. 2 C).

Dehiscence: The seeds are tightly enclosed by the mature pericarp of *D. innoxia.* The pericarp, placentae and septa have much separated parenchymatous tissue which are highly vacuolated or with scanty cytoplasm. In the absence of any definite zone of dehiscence in the mature pericarp, when the parenchymatous tissue undergoes shrinkage, septa and pericarp break irregularly and expose the seeds (Fig. 1 A). The tightly enclosed growing seeds may also exert pressure over the pericarp. The terminal portion of the fruit has only few mechanical tissue to resist this force of growing seeds and the placentae also do not extend upto the tip of the fruit. Thus the irregular bursting of the fruit is from the terminal region.

Discussion

According to Nha & Danert (1973) the fruits in the genus *Datura* are capsules (sect. *Datura*) or dry berries (sect. *Brugmansia*) or the seeds are lost by bursting of the pericarp (sect. *Datura* which includes *D. innoxia*; sect. *Ceratocaulis*). The smooth walled ovary of the small flower bud is slightly lobed and four chambered at the base and middle regions, two chambered in the terminal region but one chambered and without placenta or seeds beneath the style. The entire pericarp develops from 10—13 cells thick homogenous ovary wall.

Epicarp: The 5—7 layered thick epicarp which develops from the outer epidermis and 2—3 hypodermal layers of the smooth ovary wall is ornamented with spines and trichomes. The outer and inner tangential walls of the outer epidermis gradually become thickened and as the fruit matures the epidermal cells and the collenchymatous hypodermal cells become separated.

Mesocarp: It is the product of the mesoderm in the ovary wall whose cells have undergone periclinal, anticlinal and oblique divisions. These cells towards the maturity of the pericarp become enlarged, more vacuolated, sinuous and later separated. The mesocarp embeds conjoint, collateral, bicollateral and hadrocentric vascular bundles of which the latter show the meristematic activity of the cambium to produce secondary xylem, phloem and sclerenchymatic tissue. According to NHA and DANERT (1973) the centric vascular bundles with secondary growth originate from bicollateral vascular bundles. KAPOOR (1973) observed that ascending towards the distal end of the *Papaver* capsule the amphicribal bundles bend and become progressively reduced from an amphicribal to a collateral type of vascular bundles. In the sections *Datura* (which include *D. innoxia*) and *Ceratocaulis* the primary phloem bundles are mainly arranged in centripetal and centrifugal direction of the primary xylem. In both these ways secondary growth is concentrated, laterally the production of secondary tissue is very low (radiocentric vascular bundles). The cells of secondary xylem are only low lignified and are similar to parenchymatic cells (NHA & DANERT 1973).

Endocarp: The 10—14 layered thick endocarp develops from an inner epidermis and 4—5 layers of the inner hypodermis of the ovary wall. The hypodermal cells divide transversely, obliquely and vertically to increase the thickness of the endocarp. Towards the maturity of the fruit the endocarpic cells become vacuolated, sinuous and separated and contain starch.

Placentae: The thin walled parenchyma of the placentae and septa become separated towards the maturity of the fruit. The placental hadrocentric vascular bundles show secondary growth as described by NHA & DANERT (1973). They mentioned that in all the sections of *Datura* the vascular bundles of placenta coincide in the structure of secondary growth, it is a tissue of sclerenchymatic cells with high lignified walls.

Dehiscense: RETHKE (1946) wrote "Comparatively little is known about the mechanism of dehiscence in dry fruits of the angiosperms ... and little of that is more than gross observation". A definite zone of dehiscense is found in the capsules of *Moringa* (DAVE *et al.* 1974), *Tecoma* (KRISHNAKUMAR *et al.* 1975), *Catharanthus* (ZALA *et al.* 1976), Mustard (RAO 1976) and in some other fruits as described by FAHN (1967), RETHKE (1946), SUBRAMANYAM & RAJU (1953), PATEL *et al.* (1976) and SWAMY (1976). According to McLEAN & IVIMEY-COOK (1967) in the capsule of *Datura* the dishiscence is truely septifragal but each carpel (valve) splits secondarily along its midrib, opposite the false septum formed by the placentae. They also state that the dehiscence of the fruits is generally brought about by the shrinkage of the pericarp in drying. In the absence of any definite zone of dehiscence in the mature fruit of *D. innoxia*, it is believed that the parenchyma of the pericarp, placentae and septa undergo shrinkage so the septa and pericarp break irregularly to expose the seeds. The fruit hardly opens below the middle region as the parenchyma of basal region remain less separated. The exposure of seeds is first from the terminal portion of the fruit and that is because of the presence of less mechanical tissue and short placentae which prove weak against the pressure exerted by the tightly enclosed growing seeds.

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