식물학회지 제30권 제3호
Korean J. Bot. 30(3) : 189-199(1987)

Morpho-Histogenesis of Fruit Sculpture and Dehiscence in *Thespesia populnea* (L.) Soland (Malvaceae)

Rao, T.V. Ramana, Yash Dave and J.A. Inamdar

(Department of Biosciences, Sardar Patel University, Gujarat, India)

ABSTRACT

Morpho-histogenesis of fruit sculpture and dehiscence in *Thespesia populnea* is described. The fruit wall is differentiated into epicarp, mesocarp and endocarp. The epicarp is stony, rind-like, 30 to 35 layers thick and derived from outer epidermis, sub-epidermis and ground parenchyma of the ovary wall. The spherical and/of tangentially elongated, thick walled cells of epicarp are interspersed with radial bands of sclereids. The mesocarp is a product of the inner zone of ground parenchyma. At maturity 20 to 25 layers of thin walled parenchyma of mesocarp appear sinuous of disorganized. The innermost 1 to 3 layers of ground parenchyma and sub-epidermis and inner epidermis form 35 to 40 layers thick endocarp. Due to the differentiation of fibrous tissue in the projection of median plane of carpel wall and a complete ring of fibrous zone in the endocarp, the dry capsule of *Thespesia populnea* dehises partially in loculicidal fashion.

INTRODUCTION

The literature concerning growth and development of fruit is meagre(Coombe, 1976;Roth, 1977). It is also true that most of the embryological studies have hardly achieved beyond the structure of the ovary wall in its pre-and post-fertilization stages(Dave *et al.*, 1979). Although Rao(1978) described the structure of pericarp of *Thespesia populnea* fruit, he did not concentrate on the distinct pericarpic tissue zones, their development and the dehiscence mechanism of the dry fruit. For the complete morpho-histogenic studies, one of the Malvaceous members-*Thespesia populnea* is selected with a view to elucidate development and structural orientation of its pericarp zones and the mode of dehiscence in the dry fruit.

MATERIALS AND METHODS

Different sequential stages from young ovaries to dry fruit of *Thespesia populnea* as shown in Table 1 were collected from the Botanical Garden of V.P., R.P.T.P. Science College, Vallabh Vidyanagar. The usual methods employed in the present investigation were those already described by Dave *et al.* (1987). The histochemical techniques were employed for the detection of calcium oxalate crystals(Pizzalato, 1964) and starch (Jensen, 1962).

Table 1. Measurements of ovary and fruit at different developmental stages(mm)

Stage	Length	Diameter	Remark
1	30	40	Ovary before fertilization
2	50	50	Ovary after fertilization
3	80	70	Developing fruit
4	120	100	Developing fruit
5	150	200	Developing fruit
6	200	270	Fully matured or dry fruit

RESULTS

The globose, woody coriaceous capsule of *Thespesia populnea*(Fig. 1A) is a product of syncarpous, 5-chambered superior ovary.

Ovary wall. It is 28 to 35 cells thick in the middle region; 45 to 55 and 20 to 26 cells thick at the base and apical regions of the ovary respectively.

The outer epidermis has single layer of isodiametric cells with dense cytoplasm (Fig. 1B). The peltate scales cover the entire ovary wall as a jacket (Fig. 1B). The frequency of anomocytic stomata is fairly low. The eidermal cells divide anticlinally, whereas the sub-epidermal cells in 1 to 2 layers appear to be anticlinally and periclinally divided (Fig. 1B, at arrow). Below the sub-epidermal tissue, there are 25 to 35 layers of ground parenchyma which can be sub-divided into outer(Fig. 1B) and inner zones(Fig. 1C,D). The compactly arranged cells in the outer zone of 10 to 12 layers appear small, densely cytoplasmic and meristematic (Fig. 1B). The innermost 1 to 3 layers of ground parenchyma, in contact with inner sub-epidermis, consists of tangentially elongated cells with dense cytoplasm(Fig. 1C,D).

The dorsal collateral vascular bundles and developing lysigenous ducts are found embedded in the inner zone, but their position is more towards the inner sub-epidermis(Fig. 1C,D). The inner sub-epidermis consists of 5 to 8 layers of isodiametric or radially elongated and vacuolated cells(Fig. 1D). Histochemical tests performed indicate that the cells of outer sub-epidermis, outer zone of ground parenchyma and occassionally inner sub-epidermis, outer zone of ground parenchyma and occssionally inner sub-epidermis show the presence of druses of calcium oxalate crystals and starch. The cells of innermost layer of the ovary wall appear columnar and vacuolated(Fig. 1D).

In the median plane of each carpel wall, a ridge projected into the ovular chamber(Fig. 1E) has 3 to 6 layers of transversely oriented parenchyma(i.e. at right angles to the long axis of the ovary) which contain abundant druses of calcium oxalate cystals. But towards ventral side of the projection cells appear small and spherical or polygonal(Fig. 1E, at arrow).

The structure of developing and mature pericarp. The further growth of the fruit is due to cell

divisions and enlargement and/or elongation of the pericarpic cell layers.

Epicarp. The stony, rind-like epicarp of *Thespesia populnea* is 30 to 35 layers thick. It develops from the outer epidermis, sub-epidermis and outer zone of ground parenchyma. As the ovary develops into a fruit, the cells of sub-epidermis and ground parenchyma undergo frequent anticlinal and periclinal divisions followed by enlargement and/of elongation. The radial elongation in the ground parenchyma(at stage 4) seems to be very regular and is found more frequently in the cells which surround the outward branches of developing vascular bundles(Figg. 1F). Thus, the spherical and/or tangentially elongated cells at stage 5 are found interspersed with bands of radially elongated cells(Fig. 1G).

As the fruit proceeds towards its maturation(i. e. through the stagges 5 and 6), the radially elongated cells may undergo remarkable structural changes like more vacuolation, heavy wall thickening and lignification(Fig. 1H). In contrast to that of radial cells, those changes are moderate and delayed in other epicrpic cells(Fig. 1G). Therefore, at mature stage(i.e. 6th stage) cell of radial bands look like sclereids of diverse sizes wth pit canals(Fig. 1H).

Besides all these structural changes, gradual deposition of cutin in the outer tangential walls of outermost layer and accumulation of tanniniferous contents in the sub-epidermal cells are simultaneous with the fruit development(i.e. stages 3 to 5). Due to development of such a thick and corrugated cuticle, accumulation of tanniniferous contents and differentiation of hard mechanical tissue, the multilayered epicarp of mature fruit(i.e. 6th stage) forms stony, rind-like envelope(Fig. 3H).

Mesocarp. It solely deveops from the inner zone of gound parenchyma. As the fruit grows, the cells of ground parenchyma undergo anticlinal and periclinal divisions. In contrast to that of outer zone, the rate of cell divisions in the inner zone of ground parenchyma is fairly low. Occassionally, the mesocarpic cells situated above the inner sub-epidermis act as meristematic tissue. The derivatives of these cells are seen arranged in the form of groups(Fig. 2E), which subsequently elongate parallel to the long axis of the fruit and become thick walled. As a result sclerenchyma clusters are seen outside the fibrous zone of mature endocarp. In due course, the cells of 20 to 25 layers thick mesocarp enlarge considerably and become vacuolated(Fig. 2A, B). Likewise, the lysigenous ducts of mature mesocarp also become empty. The dorsal vascular bundles of developing fruit(i.e. 4th stage) appear branched and occasionally they are seen surrounded by sclereids(Fig. 2A). At mature stage(i.3. 6th stage) thin walled, vacuolated, parenchymatous mesocarpic cells appear sinuous or disorganized.

Endocarp. It is 35 to 40 cells thick consisting of innermost 1 to 3 layes of ground parenchyma and underlying inner sub-epidermis and innermost epidermis. In the course of fruit development(i.e. stages 3 and 4), the tangentially elongated cells of ground parenchyma, bordering the sub-epidermis, appear periclinally divided(Fig. 2C,D) and arranged in 25 to 30 layers(Fig. 2E,F). The derivatives of these cells eventually become vacuolated and attain maximum tangential elongation and wall thickening. As the fruit proceeds towards maturation(i.e. through the stages 5 and 6) these layers are transformed into fibrous zone(Figg. 2E,F) which form a complete ring parallel to the periphery of the fruit. Occassionally, the fiber cells

are found crossing each other and producing interwoven pattern(Fig. 2F).

The vacuolated cells of inner sub-epidermis and inner epidermis of developing fruit do not exhibit any noteworthy structural changes except having well-developed spaces among them (Fig. 2E). Occassionally, the sub-epidermal cells situated just beneath the developing fibrous zone form sclerenchyma clusters(Fig. 2E,F). The differentiation of these clusters is similar to that of the development of sclerenchyma clusters outside the fibrous zone of endocarp(Fig. 2E). The thin walled, loosely arranged cells of inner layer of endocarp are found disintegrated at mature stage(i.e. stage 6) (Fig. 2F). Thus, 25 to 30 cells thick fibrous zone of endocarp at stage 6 comprises only sclerenchymatic clusters on either side of it.

Similar structural changes have been noticed in the projection of median plane of carpel wall, where the transversely oriented cells(Fig. 3E) become thin walled and vacuolated;while that of the spherical cells, located in the ventral side of the projection, undergo rapid multiplication, vacuolation and wall thickening, and establish fibrous tissue as in the endocarp(Fig. 3F,G). The cells of boundary layers of the projection also disintegrate at maturity(Fig. 3G).

Septum. The septum in the ovary has 12 to 14 layers of isodiametric or transversely elongated and compactly arranged parenchym which embed 2 to 3 developing lateral vascular bundles(Fig. 2G.) As the cells of developing septum(i.e. stagges 3 to 5) undergo structural changes like multiplication followed by vacuolation and wall thickening, the central cells of mature septum(i.e. stage 6) are transformed into sclerenchyma(Fig. 2H).

Placenta and central column. The compactly arranged, spherical or polygonal and tangentially elongated parenchyma of the placenta embed the branches of placental vascular bundles. The elongation and vacuolation of the cells of placenta are simultaneous with the fruit development. The ramifications of placental bundles in the placentae, consequently appear well-differentiated(Fig. 3D).

The presence of wide gap or cleavage in the basal region(Fig. 3A) and fusion of ventral sides of the adjacent septae in the middle and apical regions(Fig. 3B) show that the central column of the *Thespesia populnea* fruit is not a true proliferation of the pedicel, but merely a fusion product of the ventral sides of the adjacent carpels. Thus, at middle region the central column appears segmented. The spherical and compactly arranged parenchyma of central column show the presence of tanniniferous contents and lysigenous ducts and embed 10 placental vascular bundles(Fig. 3B,C) which extend far up. The central column of the fruit at stage 6 has five vertically elongated sclerenchymatic strands which differentiate from the parenchyma situated just below the fused walls of ventral sides. As a result the central column of mature fruit may get tensile strength from the axis side also.

Mode of dehiscence of dry fruit. The splitting of he dry fruit wall is partial and it occurs in the median plne of each carpel wall. The partial splitting of wall is due to the differentiation of a complete ring of fibrous zone in the pericarp. When the splitting of wall reaches the fibrous zone from stony, rind-like epicarp through thin walled cells of median plane, the tensile strength of fibrous zone of endocarp and fibrous tissue of projection do not allow the splitting to proceed inward. Thus, the dry capsule wall may open partially(Fig. 3H). When the fruit is

soaked in water for long period, probably, the fibrous cells become soft and allow the seedlings to come out. Therefore, the present investigation reveals that the *Thespesia populnea* fruit is partially dehiscent in loculicidal fashion.

DISCUSSION

The syncarpous, 5 chambered, superior ovary of *Thespesia populnea* with axile placentation develops into a globose, woody coriaceous capsule. The outer epidermis, sub-epidermis and outer zone of ground parenchyma of the ovary wall collectively form the picarp. The mesocarp is a product of the innerzone of ground parenchyma, while the endocarp comprises the derivatives of innermost layer/s of ground parenchyma and following inner sub-epidermal and inner epidermal layers.

The peltate scales cover the entire outer epidermis of the ovary wall and also during subsequent developmental stages of the fruit. The development of peltate scales in the vegetative and floral organs of *Thespesia populnea* has been studied by Inamdar *et al.* (1983). According to Ramayya and Rao (1976) peltate scales may reduce transpiratory losses by its microcanopy effect. Due to gradual deposition of cutin, thick and corrugated cuticle is noticed on the outer tangential walls of mature epicarpic cells of *Thespesia populnea* fruit. Such heavy cutinization and corrugated cuticles are reported in the mature capsules of *Moringa*(Dave *et al.*, 1974), capsicums(Dave *et al.*, 1979), *Gossypium*(Rao, 1985) and *Hibiscus* spp.(Dave *et al.*, 1987;Rao *et al.*, 1987). According to Roth(1977) the cuticle plays a more important part as protective layer in berries and drupes. It may impede in elevated water loss in capsular fruits also.

Rao (1978) observed that the outer region of ground tissue of *Thespesia populnea* fruit wall is about 80 cells thick with parenchymatous, thin walled, loosely agrranged fleshy cells interspersed with stone cells. The present investigation reveals that the sclereids of radially elongated cells differentiate 5 to 35 layers deep from the outer periphery of the fruit and no thin walled or loosely arranged fleshy cells are seen among 30 tro 35 layers thick epicarpic cells. The epicarpic cells, on the contrary, appear compactly packed without and intercellular spaces. The mesocarp of developing fruit comprises 20 to 25 lyers of thin walled, vacuolated parenchyma, which appear sinuous or disorganised at mature stage.

The endocarp of *Thespesia populnea* fruit is heterogenous in nature. The differentiation of fibrous zone in the endocarp show close similarity with that of hard layer in the pericarp of legume(Roth, 1977). The tangentially elongated fibers of *Thespesa populnea* occassionally cross with each other and show an interwoven pattern. This type of cell arrangement gives more tensile strength to the tissue(Roth, 1977). Furthermore, the differentiation of vertically elongated sclerenchyma clusters on either side of fibrous zone may act as buffers between the fibrous tissue and the seed. Due to the separation of thin walled parenchyma of endocarp from each other, loose mesh work of cells is noticed in the innermost layers of developing *Thespesia populnea* fruit. Roth and Lindorf observed such a conspicuous perforated inner epidermis and they attributed that the formation of intercellular spaces may be partly due to the action of

dilation growth(c.f. Roth, 1977). The loosely arranged parenchyma of *Thespesia populnea*, however, disintegrate at mature stage of fruit.

The circumstances which form a cleavage or gap and segmentation of central column in *Thespesia populnea* differ from that of *Hibiscus* spp. (Dave *et al.*, 1987;Rao *et al.*, 1987). The cleavage and segmentation in the central column of *Thespesia populnea* is found because of acropetal fusion of ventral sides of adjacent carpels, whereas the separation layers make the central column of *Hibiscus sabdariffa* segmented(Dave *et al.*, 1987). The formation of cleavage in *Hibiscus* spp. is due to either increment in the circumference of fruit(Dave *et al.*, 1987) or due to schizolysigenous activity(Rao *et al.*, 1987).

Rathke(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 observations". A definite zone of dehiscence is found in the capsules of *Moringa*(Dave *et al.*, 1974), *Catharanthus*(Zala *et al.*, 1976), *Abelmoschus* and *Gossypium*(Rao, 1985), *Hibiscus* spp.(Dave *et al.*, 1987;Rao *et al.*, 1987) and some other fruits as described by Roth(1977). According to Rao(1978) *Thespesia populnea* fruit is a hard dehiscent capsule. The present detailed morphohistogenic study of *Thespesia populnea* fruit wall reveals that a definite zone of dehiscence is formed in the early stages of fruit development, but the differentiation of fibrous tissue in the projection of median plane of carpel wall and a complete ring of fibrous endocarp does not allow the dry fruit wall to dehisce and expose the seeds. Thus, the dry capsule of *Thespesia populnea* dehisces partially in loulicidal fashion.

ACKNOWLEDGEMENT

The first author(TV) is grateful to the University Grants Commission, New Delhi for financial assistance.

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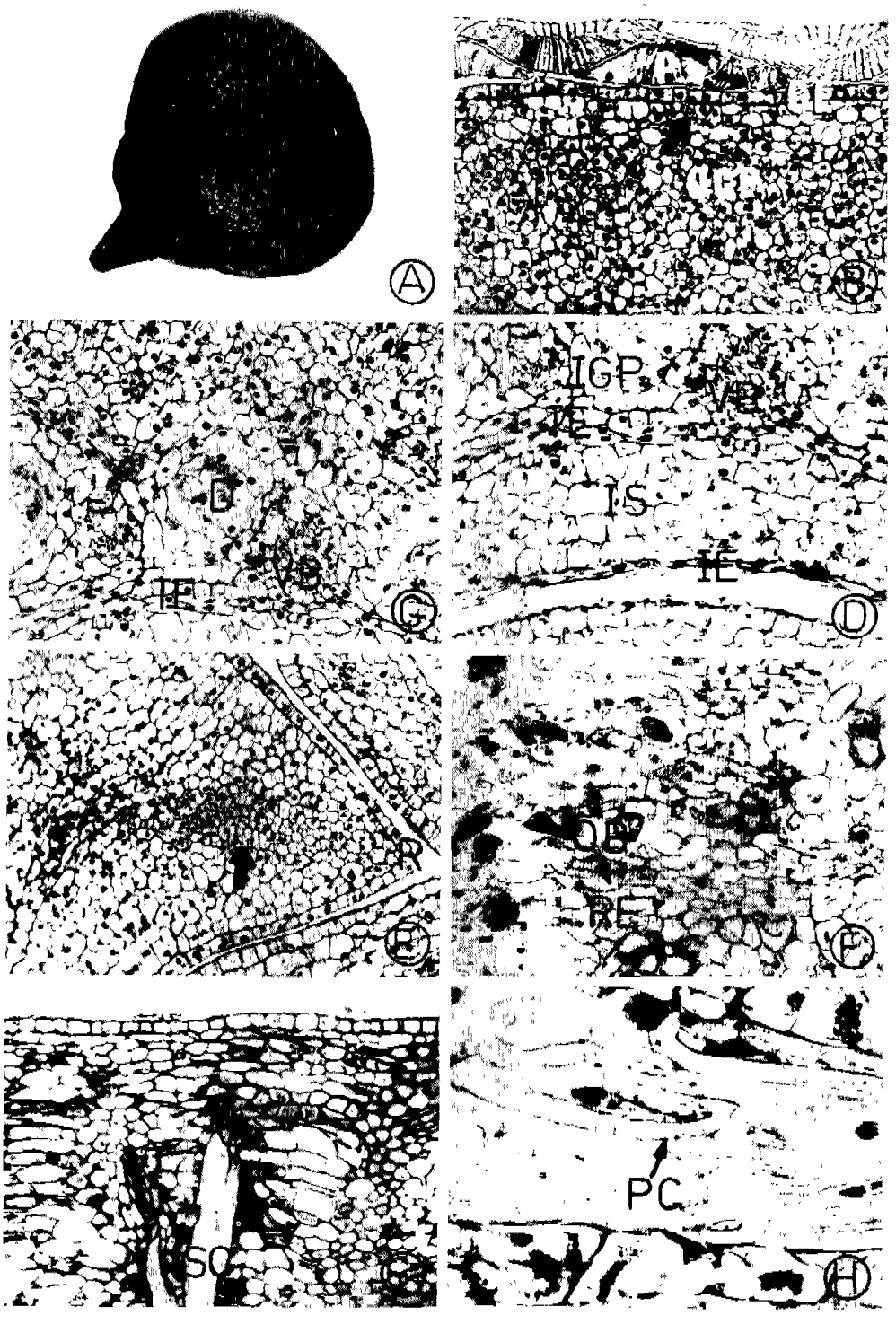
(Received August 5, 1987)

Explanation of Figures

Fig. 1. A. A developing fruit of *Thespesia populnea* photographed at 5 stage(2 X). B-D. A portion of ovary wall in transverse section showing its outer, middle and inner layers respectively. Note anticlinal and periclinal divisions in sub-epidermal cells at arrow in Fig. B. (B,205 X; C,220 X; D,243 X). E. Structure of inner ridge in the median plane of ovary wall. Note that the ventral side of the ridge is consisting of small polygonal cells at arrow(177 X). F. The radial elongation of epicarpic cells at stage 4(225 X). G. Structural details of epicarp at stage 5(100 X). H. Sclereid cells of radial bands in the epicarp of mature fruit at stage 5(100 X). D: Duct; IE:Inner epidermis; IGP:Inner zone of ground parenchyma; IS:Inner sub-epidermis; OB:Outward branches of vascular bundles; OE:Outer epidermis; OGP:Outer zone of ground parenchyma; P:Peltate scale; PC:Pit canal; R:Ridge; RE:Radial elongation; SC:Sclereid; TE:Tangentially elongated cells; VB:Dorsal vascular bundle.

Fig. 2. A-B. The structure of mesocarp at stages 4 and 5 in Fig. A and B respectively.(A,130 X;B,102 X). C-F. A portion of endocarp at different developmental stages(3 to 6). Note the disintegration of thin walled cells of innermost layers of mature pericarp at stage 6.(C,530 X; D,225 X, E,90 X; F,80 X). G-H. Structural details of septum in the ovary(stage 1) and mature fruit(stagge 6) in Figs. G and H respectively.(G,133 X; H,220 X). DV:Developing bundle; FZ:Fibrous zone; ICS:Inter-cellular spaces; ILE:Inner layers of endocarp; IS:Inner sub-epidermis; IW:Interwoven pattern; MS:Mesocarp; S:Sclerenchyma; SC:Sclereid; SCL:Sclerenchyma cluster; TE:Tangentially elongated cells.

Fig. 3. A. A cleavage in the central column of the ovary(stage 1) at its base(92 X). B. Fusion of ventral sides of the adjacent septae in the middle region of the ovary(stage 1) (104 X). C. The structure of central column and placental bundles in the ovary(stage 2) (104 X). D. structure of mature placentum(stage 6). Note the occurrence of ramifications of placental bundles(200 X). E-G. Structural details of ridge at its different developmental stages(stages 3, 5 and 6 in Figs. E, F and G respectively). (E-F,90 X: G,46 X). H. Partially dehisced dry capsule of *Thespesia populnea*(stage 6). (2 X). BL:Boundary layers; C:Cleavage; D:Duct; EP:Epicarp; FT:Fibrous tissue; FZ:Fibrous zone; PB:Placental bundle; R:Ramifications; TC:Tanniniferous contents; TOC:Transversely oriented cells; VS:Ventral side of the septae.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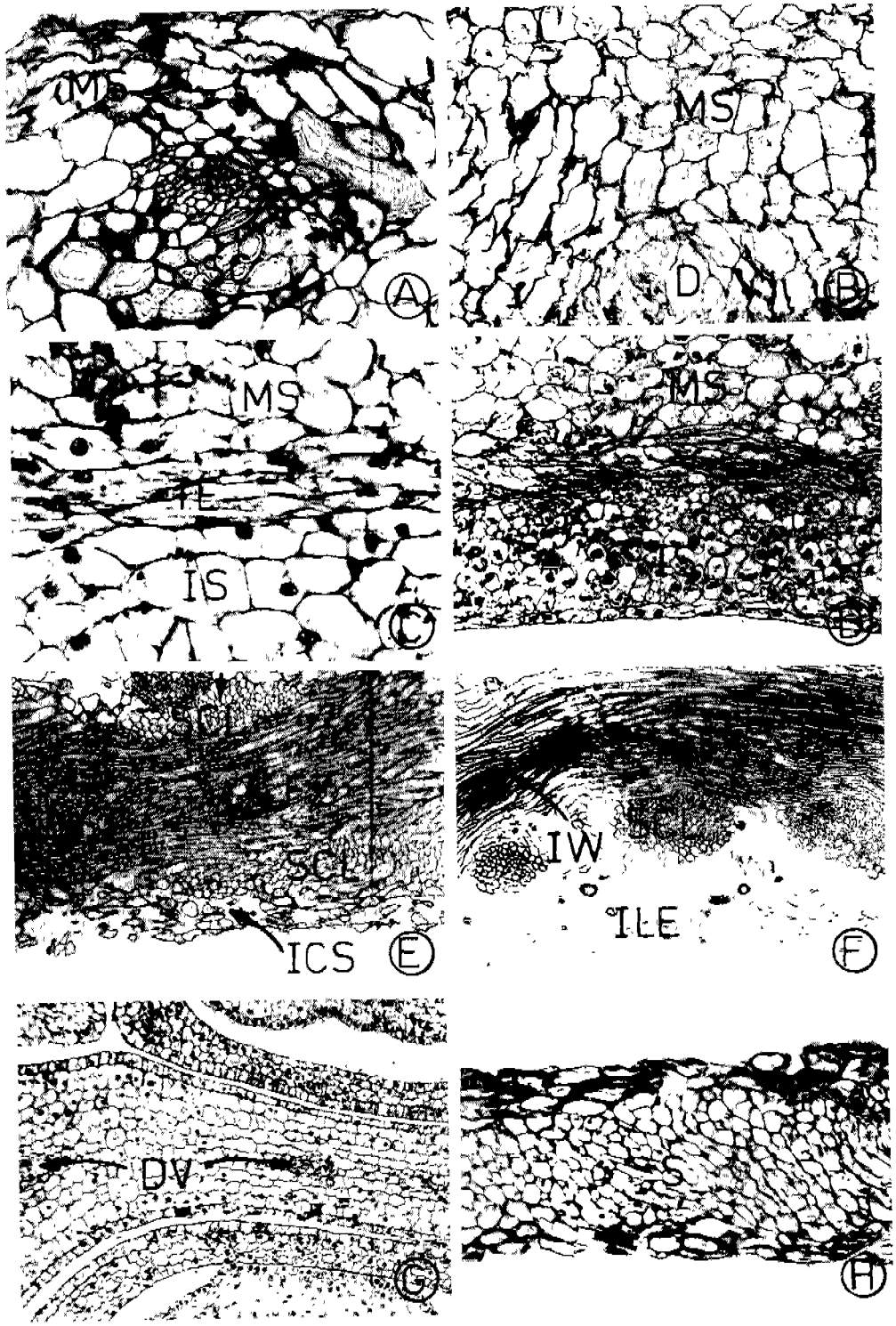
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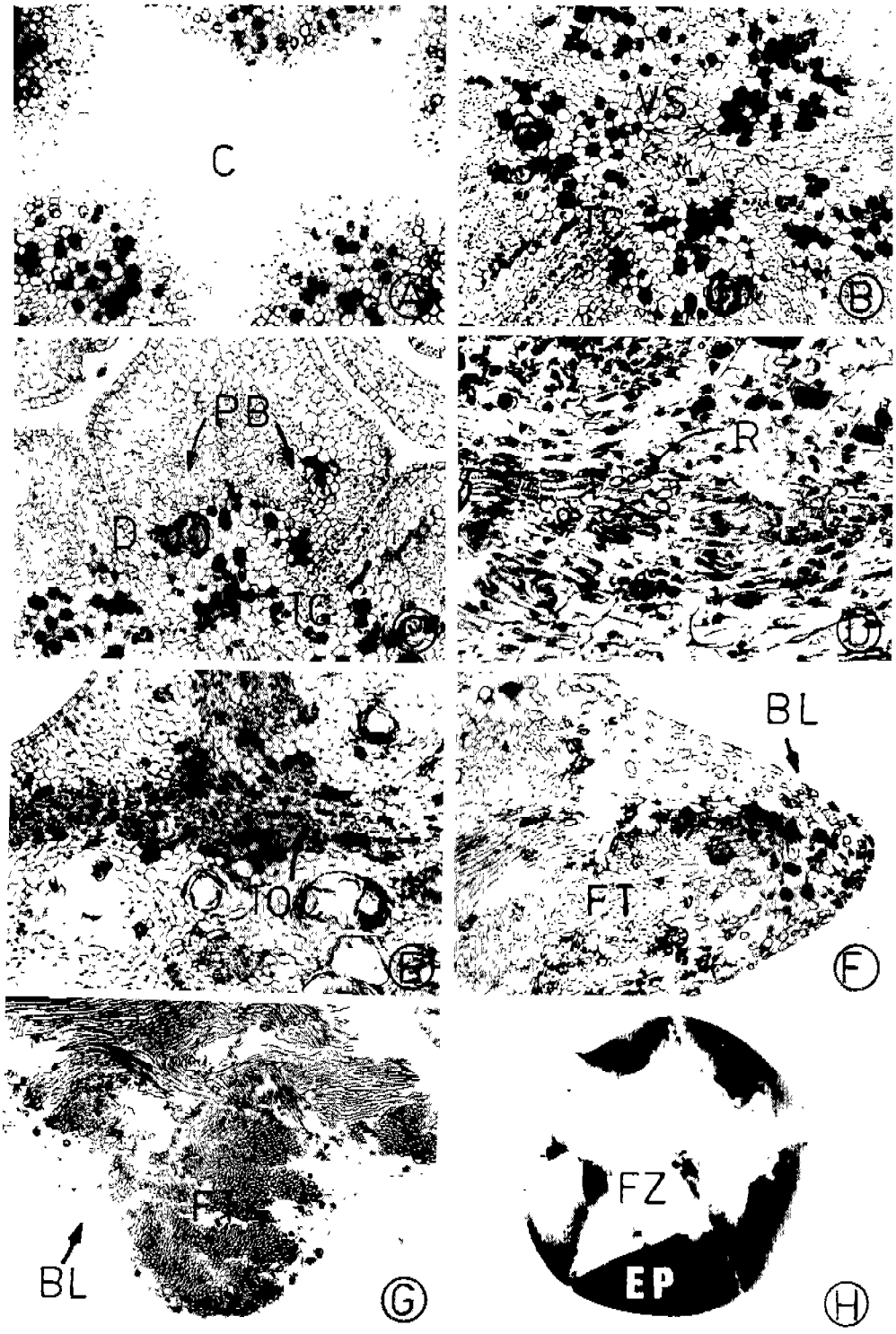
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