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MORPHO-HISTOGENIC STUDIES OF THE FRUIT WALL OF *ARGEMONE MEXICANA* L. (PAPAVERACEAE)

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The spiny capsule of *Argemone mexicana* develops from a unilocular ovary with numerous ovules borne on parietal placentae. The ovary wall comprises a layer of outer epidermis and inner epidermis each with 12 to 14 layered ground parenchyma or mesoderm in between. The epicarp, which develops from the outer epidermis of the developing pericarp, possesses numerous anomocytic type of stomata, but no trichomes. The deep lying mesodermal layers form the mesocarp, which embed pericarpic vascular bundles and their tangentially extended ramifications. The thin walled and highly vacuolated mesocarpic cells undergo disorganisation at the maturity of fruit. The tangentially elongated cells of inner epidermis of ovary form the endocarp, which at maturity of the fruit possesses thick walled cells. The cells of placentum of developing fruit contain abundant starch. Due to the contraction of disorganised parenchyma cells, the dried fruit, leaving the marginal veins and persistent stigma, dehisces at its apical region.

Key words: anatomy, *Argemone mexicana*, dehiscence, fruit, Papaveraceae, pericarp

INTRODUCTION

A perusal of literature manifests that Claudia (1982) studied 20 Papaveraceous genera for their morphology and anatomy, while Sebastian (1994) investigated the structural details of mature fruit of *Argemone mexicana*. Surprisingly, except these investigators and the courtesy reference made on the fruits of Papaveraceae by Roth (1977), no other significant contribution exists in the literature on the morpho-histogenic details of Papaveraceous fruits. Therefore, an investigation has been undertaken to elucidate the structural and developmental details of Papaveraceous fruits so as to fill the lacuna in our knowledge on the fruits of Papaveraceae and the present paper on the morpho-histogenesis of fruit wall of *Argemone mexicana* is first of this endeavour.

MATERIAL AND METHODS

The fruits of *Argemone mexicana* were collected at their sequential developmental stages from local fields. The methods followed for obtaining 8–10 µm thick sections and epidermal peelings and their staining were those described by Dave *et al.* (1977). Histochemical localisation of starch, proteins, insoluble polysaccharides and lipids was done following the methods of Jensen (1962), Mazia *et al.* (1953) and Pearse (1968). Photomicrographs were taken with Carl-Zeiss Photomicroscope-I and AO Spencer's (Phase-Star) Phase-Contrast microscope.

Abbreviations used for Figs 1–28: bc = bundle cap, cu = cuticle, dvb = dorsal vascular bundle, en = endocarp, ep = epicarp, l = laticifer, lvb = lateral vascular bundle, me = mesocarp, mvb = marginal vascular bundle, pl = placenta, sc = sclerenchyma, se = seed, sn = spine, st = stomata.

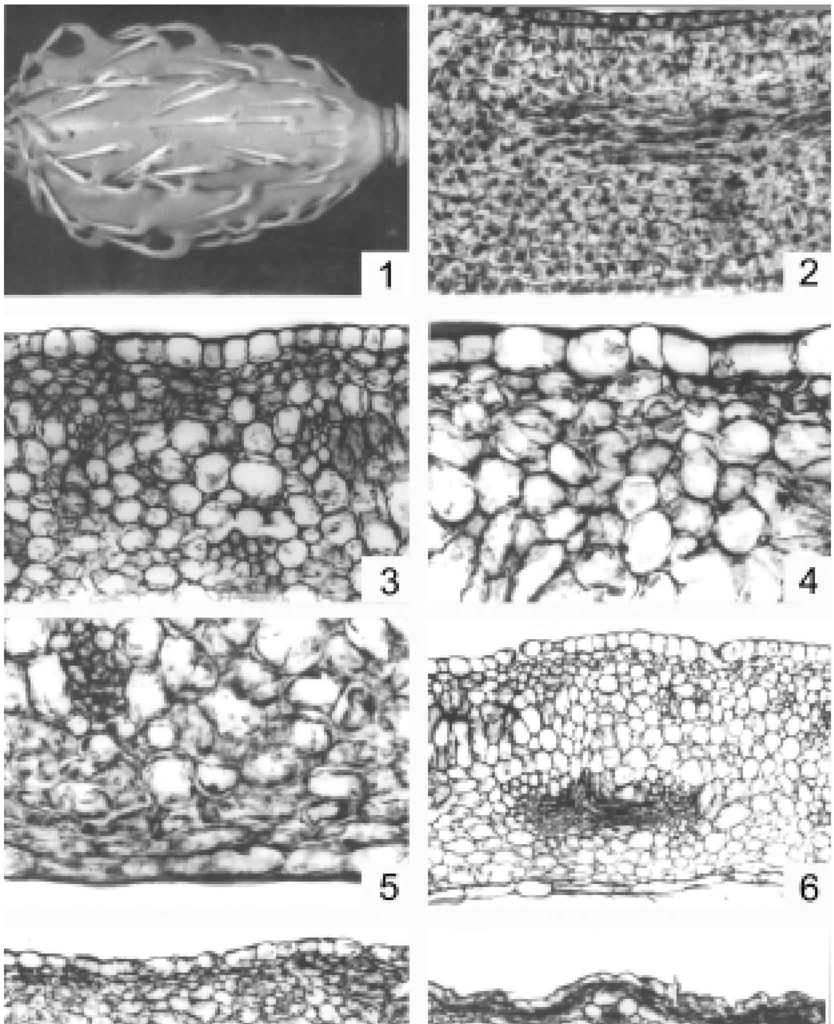
OBSERVATIONS

Argemone mexicana is an armed herb with divaricated branches. Its flowers are solitary and bright yellow in colour. The unilocular ovary is covered with soft spines. Ovules are numerous and arranged on 4–7 parietal placentae. The mature oblong spiny capsule measures 3.5–4.5 cm in length and 1.8–2.0 cm in breadth (Figs 1, 21). The pale greenish fruit dehisces apically into 4–7 valves (Figs 22, 23). The dehisced capsule turns to pale brown in drying stage with its tough spines (Figs 14, 22, 23). Seeds are numerous, rugose, small and brownish-black (Fig. 23). The yellowish latex, which is present in all parts including fruits, is used in scabies and ophthalmic diseases. Seeds yield numerous, bitter non-edible oil, used in skin (cutaneous) troubles. Presence of argemone oil in edible mustard oil is probably responsible for outbreaks of epidemic dropsy. Mixed with drying oils it may be used in soap making and paint industry (Singh *et al.* 1983, Dey 1980).

Ovary wall

It comprises an outer epidermal and an inner epidermal layer, which together encompass 12 to 14 layered ground parenchyma (Fig. 2).

The isodiametric cells of outer epidermis contain scanty cytoplasm and centrally situated spherical and prominent nuclei. These outer epider-



Figs 1–8. Argemone mexicana. – *Fig. 1.* Morphology of the fruit. ×1.2. – *Fig. 2.* Transverse section of the ovary. ×36. – *Figs 3–4.* Portions of the developing fruit wall showing the structural details of epicarp and mesocarp. 3: ×90; 4: ×240. – *Fig. 5.* A portion of the developing fruit wall showing a vascular bundle, mesocarpic part and the endocarp. ×240. – *Fig. 6.* Transverse section of a part of fruit wall with epicarp, mesocarp, sclerosed vascular bundle and endocarp. ×90. – *Figs 7–8.* Mature fruit walls in transverse sections showing the vascular bundle and tangentially elongated mesocarpic cells. ×90

mal cells undergo frequent anticlinal divisions. The anomocytic type of stomata is found to occur occasionally on the outer epidermis, but no trichomes.

The ground parenchyma of ovary wall (*i.e.* mesoderm) comprises thin walled, compactly arranged, isodiametric or spherical cells with scanty cytoplasm. The mesodermal cells situated just beneath the outer epidermis may divide anticlinally and periclinally, but the cells of deep lying mesodermal layers exclusively undergo anticlinal divisions (Fig. 2). The cells in the middle mesodermal layers embed undifferentiated vascular strands. Occasionally these vascular strands may extend their ramifications in tangential direction (*i.e.* they run parallel to the periphery of the ovary wall) (Fig. 2). Moreover, the differentiation of laticiferous canals may take place adjacent to these vascular ramifications. As a result, the cells in the middle mesodermal layers may appear more densely stained than other mesodermal cells (Fig. 2).

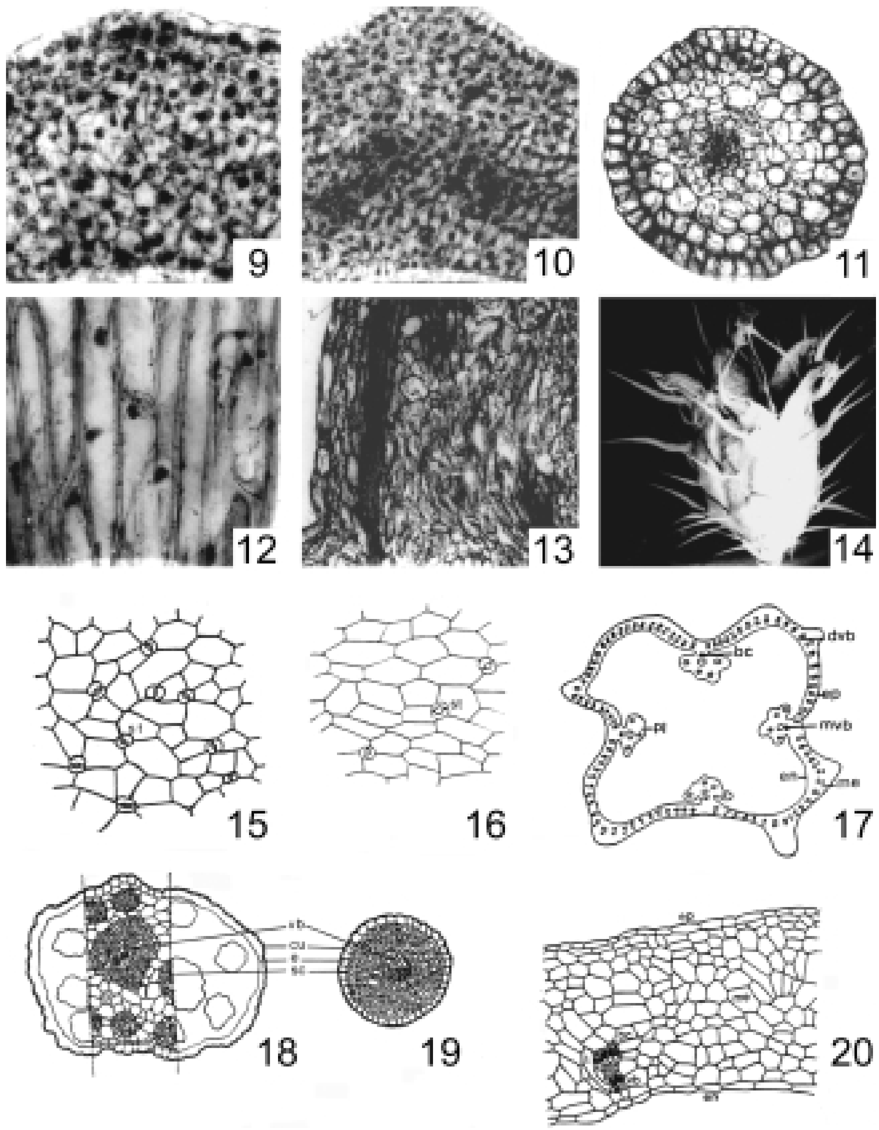
The inner epidermis of ovary wall consists of tangentially elongated cells containing dense cytoplasm and they possess relatively thick tangential walls (Fig. 2). The cell contents of inner epidermal cells resemble with those of outer epidermal cells, as they too possess centrally situated prominent nuclei and undergo anticlinal divisions. Moreover, the inner epidermis of ovary wall also possesses anomocytic type of stomata, but in less frequency, and no trichomes on it (Fig. 2).

Structure of the developing and mature fruit wall

As the ovary develops into a fruit, the pericarp (*i.e.* fruit wall) differentiates into three distinct zones, *viz.* (i) epicarp, (ii) mesocarp and (iii) endocarp. Further, the development of spines on the fruit wall surface (Fig. 1) occurs simultaneously with the fruit development. The spines are arranged in 2 to 3 alternate rows on each valve (Figs 1, 21).

Epicarp

It develops from the outer epidermis and two or three mesodermal layers lying beneath the outer epidermis of ovary wall. The development of epicarp starts with the enlargement of its constituent cells followed by their elongation (Fig. 3). However, initially the outer epidermal cells may appear larger and more radially elongated than the other epicarp contributing cells (Fig. 3). In due course, owing to the increment in the circumfer-



Figs 9–20. Argemone mexicana. – Figs 9–10. The initiation and developmental stages of the spine on fruit surface. ×35. – *Fig. 11.* Transverse section of the developing spine from its terminal region with a single central vascular strand. ×350. – *Fig. 12.* The surface cells of the spine. ×240. – *Fig. 13.* The vascular strand in the spine base. ×90. – *Fig. 14.* The mature fruit in dried and dehisced stage. ×1.2. – *Figs 15–16.* The stomata on the outer and inner surfaces of the fruit wall. 15: ×95; 16: ×63. – *Fig. 17.* Schematic diagram of the fruit in cross section. – *Fig. 18.* Transverse section of basal part of spine showing sclerosed vascular bundles embedded in parenchyma. ×170. – *Fig. 19.* Terminal part of the spine in cross section showing single vascular bundle surrounded by sclerenchyma. ×170. – *Fig. 20.* A portion of pericarp from lateral side in transverse section. ×95

ence of fruit, all the epicarpic cells undergo tangential elongation (Figs 2–4). The frequency of divisions in the outer epidermal cells as well as other epicarp contributing cells may continue in the early stages of fruit development but subsequently the frequency of cell divisions ceases and/or it may be replaced by gradual vacuolation. Eventually the epicarpic cells of maturing fruit may attain thick walls (Figs 2–4). The frequency of anomocytic type of stomata also increase during early development of fruit, but later on not only their frequency ceases but also their guard cells become highly vacuolated (Figs 6, 15). As a result of complete loss of cytoplasm and high vacuolation, the epicarpic cells located beneath the outer epidermal layer may get disorganised. The presence of starch, proteins, lipids and insoluble polysaccharides is noticed more in the epicarpic cells of developing fruit, but their quantity may gradually decline towards the maturity of fruit.

Mesocarp

The mesoderm (leaving the epicarp forming cells) of ovary wall forms 14 to 16 layered mesocarp of developing fruit. The compactly arranged and spherical or polygonal cells of developing mesocarp increase in their size, but gradually they undergo tangential elongation. The pericarpic vascular bundles located in the middle layers of mesocarp and the marginal vascular bundles embedded in the placental tissue increase in their size and subsequently undergo sclerefication, while the ramifications of pericarpic vascular bundles may transform into fibrous tissue bundles (Figs 5, 6). Due to this kind of fibrous tissue in the middle layers of mesocarp, its vacuolated cells may get tensile strength even when they are totally disorganised at maturity (Fig. 6). The mature mesocarp is formed of 12 to 14 layers of compactly arranged parenchyma in the lateral sides (Figs 20, 24) and in marginal side it is 20 to 25 layers thick. Laticiferous canals are formed near the vascular bundles (Figs 20, 24). The presence of lipids, proteins insoluble polysaccharides and starch is noticed in the mesocarpic cells.

Endocarp

It develops from the inner epidermis of the ovary wall. The tangentially elongated endocarpic cells do not exhibit much structural variation except their gradual elongation and wall thickening (Figs 5, 6, 24). However, the endocarpic cells of maturing pericarp together with the fibrous tissue of mesocarp protect the thin walled and vacuolated parenchyma cells of mesocarp (Figs 6, 7, 24, 28). Thus the mature pericarp appears to be sandwiched due to inward pulling of mesocarpic layers. There are no starch, insoluble polysaccharides, proteins and lipids in the endocarp. In surface view, endocarpic cells appear tangentially elongated and possess anomocytic type of stomata, but no trichomes (Fig. 16).

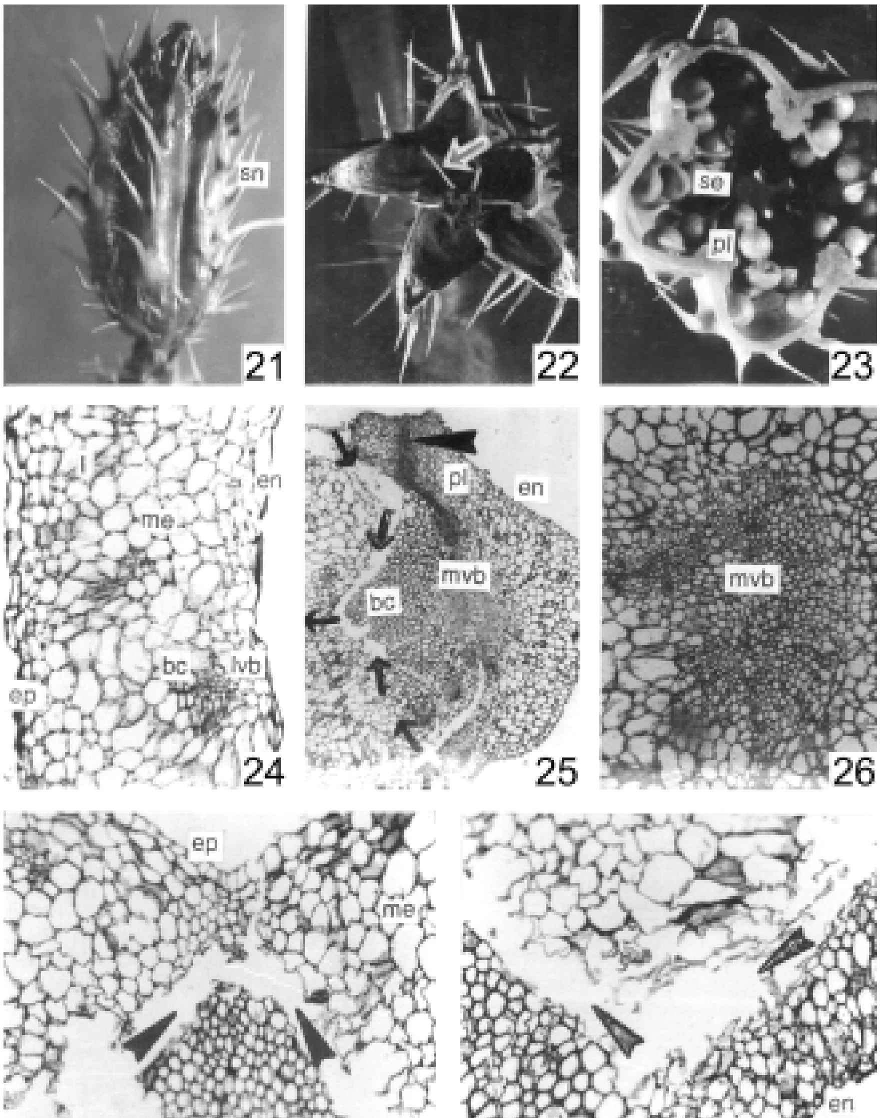
Placentum

The inwardly extended hood-shaped placentum occurs in the marginal portions of locule. It consists of small and compactly arranged cells, which embed a vascular bundle (Figs 17, 23, 25). As the fruit grows, the cells in the placentum increase in their size. Besides, a considerable amount of starch deposition occurs in these cells. The marginal vascular bundle, which extends vascular supply to the growing seeds, increases in its size and differentiates into clear xylem and phloem strands. In concurrence with the differentiation of marginal vascular bundle, a sheath development occurs on dorsal side of this bundle, which eventually transforms into a sclerenchymatous sheath (Figs 8, 25, 26).

Origin of spines on the surface of ovary wall and their development

The ovary wall of *Argemone mexicana* possesses thin and delicate spines on its surface. They develop from spine primordia consisting of 2 to 3 outer epidermal cells and 2 to 3 cells lying below to it (Fig. 9). These cells of deep lying layers are meristematic (Fig. 10) and they undergo frequent anticlinal and periclinal divisions, while the outer epidermal cells divide anticlinally. The daughter cells formed due to divisions in the cells of deep lying layers start elongating in radial direction. Thus these cells function as cortical cells of developing spine. During this kind of radial elongation, the ramifications of vascular bundles occurring in the middle mesocarp also extend into cortical cells of developing spine (Figs 10, 13). However, these vascular extensions in the spines acropetally become narrow. The basal portion of spine is composed of parenchyma as well as sclerenchyma cells with 7 to 9 conjoint collateral vascular bundles (Fig. 18). The tip portion of the spine is composed of compactly arranged sclerenchymatous cells with a single vascular bundle embedded in the centre (Figs 11, 19).

The outer epidermis of spine neither possesses stomata nor trichomes. During the course of spine development the outer epidermal and cortical



Figs 21–28. Argemone mexicana. – *Fig. 21.* The undehisced mature fruit showing spines over its surface. ×1.2. – *Fig. 22.* Mature dry dehisced fruit showing the persistent stigma and marginal veins intact. ×2. – *Fig. 23.* Cross section of the whole fruit showing the seeds attached with placenta. ×3. – *Fig. 24.* A transactional view of a portion of pericarp from lateral side. ×90. – *Fig. 25.* The marginal vascular bundle and placenta in transverse section. ×35. – *Fig. 26.* An enlarged view of marginal vascular bundle. ×90. – *Figs. 27–28.* Arrow heads indicate the line of separation of marginal vein from the pericarp as seen in transverse sections. ×120

cells of spines also become highly vacuolated and attain thick walls (Fig. 12). The wall thickening is, especially, more in the outer epidermal cells of spine (Figs 11, 12, 18, 19). The centrally situated vascular bundle in the spine becomes completely sclerosed at maturity (Figs 9, 18). Due to the occurrence of thick walled epidermal and cortical cells and sclerosed vascular bundle in the centre of spine, the stiffened spine remains persistent on the surface of dried *Argemone mexicana* fruit (Figs 14, 20, 23).

Dehiscence of the mature fruit

When the fruit attains maturity, it turns to pale green in colour and dehisces in basipetal direction, but dehiscence occurs only in its apical region, leaving the persistent stigma and marginal veins intact (Figs 14, 22). The separation of pericarpic tissue from marginal veins (Figs 25, 27, 28) is due to the fact that the increment in the circumference of the developing fruit is more in its apical region than in middle or basal regions. Thus the pericarpic tissues in the apical region stretches more, but due to disorganisation of their constituent cells at maturity, pericarpic tissues get refluxed, which causes the separation of dried pericarp from marginal veins (Figs 14, 22). More or less a similar phenomenon takes place for causing the separation of pericarpic tissues from persistent stigma, wherein constituent tissues are highly sclerosed. Thus they do not stretch or contract, while the contraction of dried pericarpic tissues cause their separation from stigma (Figs 14, 22).

DISCUSSION

The capsular fruit of *Argemone mexicana* is a product of a unilocular ovary. Its pericarp differentiates into two- or three-layered epicarp, 14 to 16 cells thick mesocarp and a single layered endocarp. In accordance with the observation by Claudia (1982) the outer epidermis and the endocarp of the developing fruit possess anomocytic type of stomata, but their frequency is more in the outer epidermis. Roth (1977) stated that stomata in Papaveraceae might occur in the outer as well as inner epidermis. Moreover, she also stated that stomata formation in *Papaver* begins very early (during fruit development), *i.e.* in the flower bud stage. The present observations of stomata in the outer epidermis of ovary wall of *Argemone mexicana* support this view.

The development of spines occurring on the outer surface of *A. mexicana* fruit is due to periclinal divisions in the cells of local primordia formed in the sub-epidermal layers. The structural details of developing spine reveal that the epicarp and the mesocarp of developing fruit, together with pericarpic vascular bundles take part in the formation of spine. Thus the spine of *A. mexicana* shows developmental similarity with the spines of *Xanthium* (Trivedi and Sharma 1964), *Datura* (Dave *et al.* 1980) and glochids of *Urena lobata* (Rao *et al.* 1985) and of *Triumfetta* spp. (Dali and Dave 1999).

Like in *Xanthium* and *Datura*, the spines of *Argemone mexicana* also possess vascular strand, but it tapers towards the tip of the spine. Trivedi and Sharma (1964) equated the spine of *Xanthium* to a bract due to the presence of vascular traces in it, while Dave *et al.* (1980) recognised the emergences present on *Datura* fruit as multicellular heterogeneous spiny projections. According to Roth (1977) emergences produce certain sculpturing on the fruit surface. The persistent and hard spines of *Argemone mexicana*, besides producing sculpture, may also protect the fruit from biological and physical forces.

The dehiscence of capsular fruit of *Argemone mexicana* also exhibits quite interesting phenomenon as the dehisced valves of dried fruit in its apical region leave the marginal veins and persistent stigma intact. Thus the dehiscence of *A. mexicana* fruit is incompletely basipetal, as also observed by Claudia (1982). Moreover, the mode of apical dehiscence in *A. mexicana* shows resemblance with the porocidal dehiscence in *Papaver* and some other Papaveraceous members.

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