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The embryology of *Averrhoa* (*Oxalidaceae*)

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Summary. The anther of *Averrhoa* is tetrasporangiate and its wall development is of the Basic type. Cytokinesis in microspore mother cells is simultaneous and results in tetrahedral or decussate tetrads. The mature pollen grains of *A. carambola* are shed at the 2-celled stage whereas those of *A. bilimbi* are at the 3-celled stage. The mature ovule is anatropous, bitegmic, crassinucellate and the micropyle is formed by both the outer and inner integuments. The embryo sac development conforms to the monosporic *Polygonum* type. The development of endosperm follows the *ab initio* Nuclear type and the nuclear endosperm completely turns cellular only after the formation of the heart-shaped embryo. The fruit mesocarp and the combined region of the exocarp and mesocarp are deposited with tannin and calcium oxalate crystals, respectively. The seed coat is formed from the outer and inner integuments.

The Oxalidaceae comprises six genera and 875 species (Airy Shaw 1973). The woody genus *Averrhoa* L., probably of Indomalayan origin, comprises two species, *A. bilimbi* L. (commonly called "belimbing buluh" or "belimbing asam") and *A. carambola* L. (commonly called "belimbing manis", carambola, or starfruit), which are trees up to 15 m tall (Allen 1967; Veldkamp 1971). Both of them are common cultivated fruit tree species in Malaysia. Considering the large number of species in the Oxalidaceae, the number of taxa embryologically investigated is rather few—Davis (1966) and Johri *et al.* (1992) have reviewed the earlier work of Jönsson (1880), Billings (1901), Hammond (1908), Samuelsson (1913), Schürhoff (1924), Mauritzon (1934), Noll (1935), Venkateswarlu (1936), Souéges (1939), Thathachar (1942), Govindappa & Boriah (1956), Narayana (1962), Herr & Dowd (1968), Herr (1972), Kumari & Narayana (1980), Boesewinkel (1985), and Govil & Kaur (1989). Of the six genera, *Oxalis* L. and *Biophytum* DC. engaged the most attention from previous workers, concentrating more on the development of the embryo than the embryo sac.

A perusal of the literature on the embryology of *Averrhoa* reveals that the available information is too inadequate and fragmentary. Therefore, a thorough study is needed to characterise this genus from an embryological standpoint. The previous embryological work on this taxon has been reviewed by Venkateswarlu (1936), Thathachar (1942), Davis (1966), Low (1972), Kumar (1975), Dave, Patel & Rupera (1975), Tan (1977), and Ou Yang (1978). More recently a few brief reports have also appeared (Boesewinkel 1985; Govil & Kaur 1989; Johri *et al.* 1992). The present investigation, dealing with microsporogenesis, megasporogenesis, development of male and female gemetophytes, endosperm and embryo, seed coat and fruit wall in *Averrhoa*, was undertaken with the prime objective of further elucidating the embryology of *Averrhoa*.

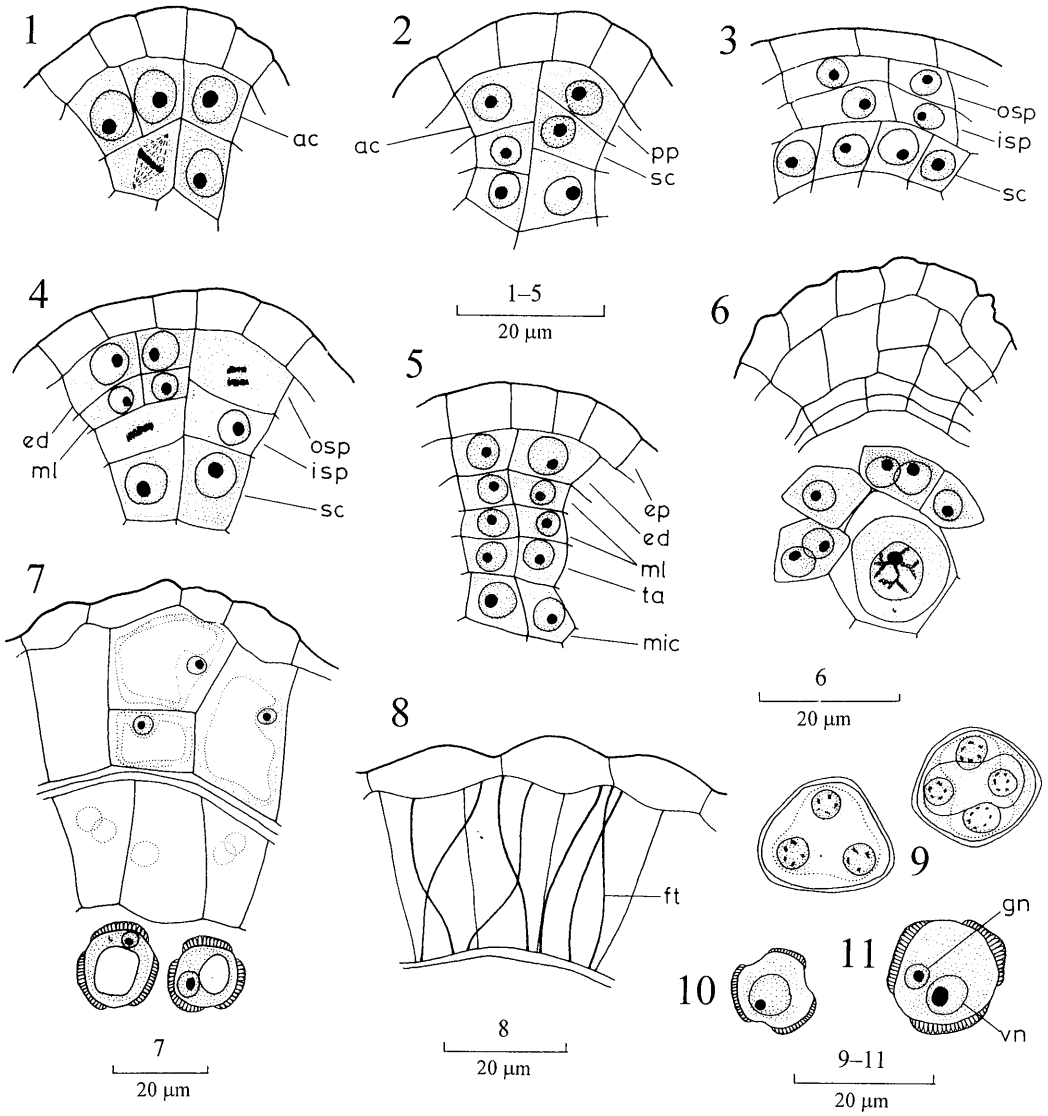
MATERIALS AND METHODS

Buds, flowers and fruits of *A. carambola* and *A. bilimbi* were collected at weekly intervals from the fruit-tree nursery, Institute for Advanced Studies, University of Malaya and the Rimba Ilmu botanical garden, University of Malaya, respectively. Two voucher specimens (KLU 40992 for *A. carambola* and KLU 40993 for *A. bilimbi*) were deposited with the Herbarium of the University of Malaya (KLU). The materials were trimmed to a suitable size and fixed on location in Craf III solution (30 ml 1% chromic acid, 20 ml 10% acetic acid, 10 ml 37% formaldehyde and 40 ml distilled water) at 10°C for at least 48 hours. Customary methods of dehydration and embedding were followed. Microtome sections were cut at 8 μm (for buds and flowers) or 10–12 μm (for fruits) and after dewaxing, were stained in 1% alcoholic (in 50% alcohol) safranin and 0.5% alcoholic (in 95% alcohol) fast green FCF. The sections were mounted in canada balsam.

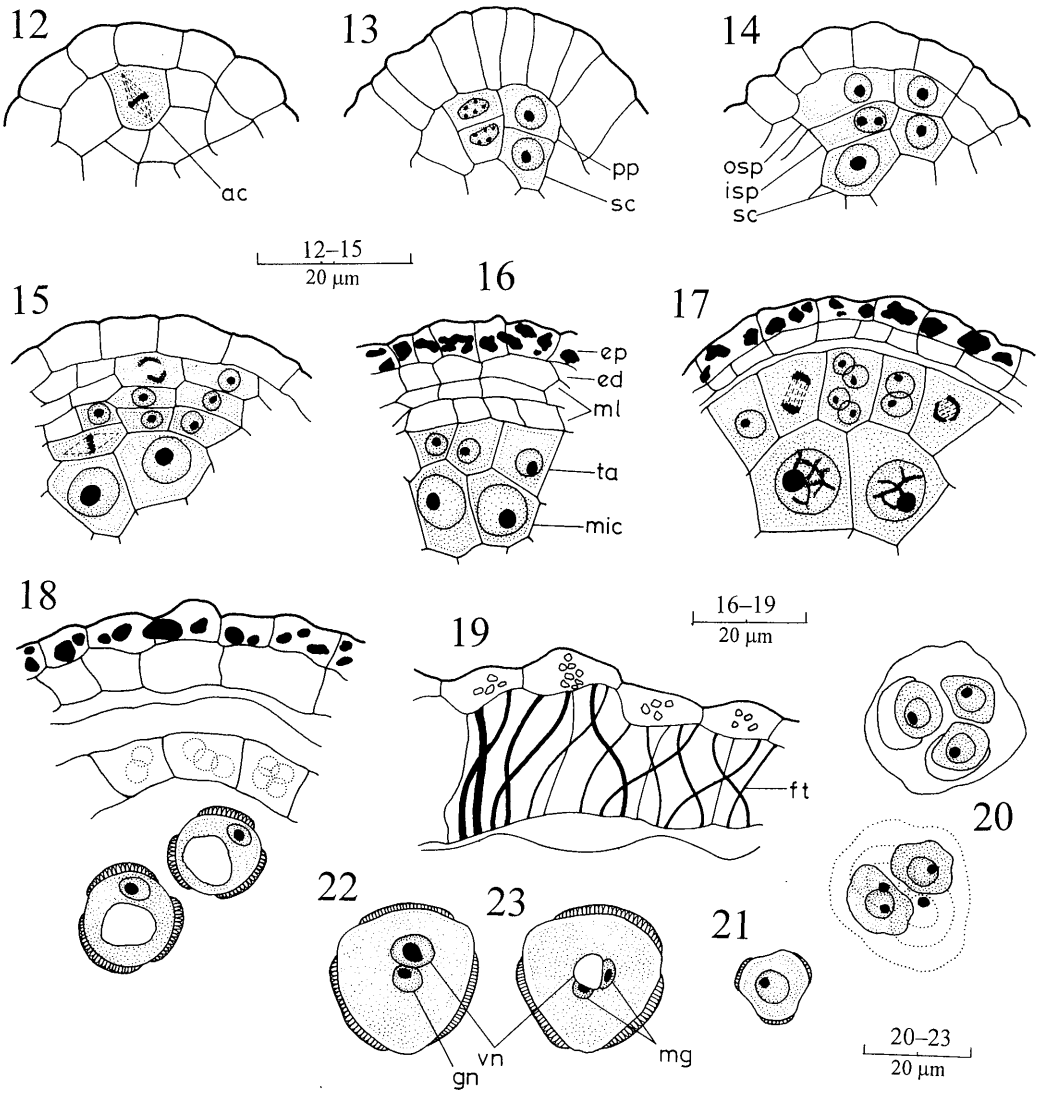
MICROSPORANGIUM, MICROSPOROGENESIS AND MALE GAMETOPHYTE

There are five stamens in a *A. carambola* flower. However, there are ten in *A. bilimbi* and these are arranged in two whorls, i.e., long-whorl and short-whorl anthers. Earlier, Davis (1966) had reported that the number of microsporangia in the anther had not been clearly determined for *Averrhoa*. However, the present study has confirmed the findings of previous work (Thathachar 1942, Low 1972, Tan 1977) that the anther is tetrasporangiate in the two species of *Averrhoa* just as in the other members of Oxalidaceae (Figs. 65, 69).

The unicellular archesporium is hypodermal (Figs. 1, 12). Occasionally, more than one archesporium can be observed in a sporangium of *Averrhoa* and their divisions are not synchronous. The archesporial cells divide periclinally to produce the primary parietal cells and sporogenous cells (Figs. 2, 13). The periclinal division of the parietal cells results in the formation of two secondary parietal layers, i.e., the outer and inner secondary parietal layers (Figs. 3, 14), and the sporogenous cells divide and subsequently differentiate into the microspore mother cells. The secondary parietal layers may divide simultaneously (in *A. carambola*) or the inner parietal divides before the outer (in both species of *Averrhoa*) producing the middle layer and the tapetum (Fig. 15). Rarely, the outer secondary parietal divides before the inner secondary parietal layer (Fig. 4). The sequence of division of



Figs. 1–11. *Averrhoa carambola,* microsporangium, microsporogenesis and male gametophyte. T.S. **Figs 1–5.** Anther wall at different development stages. **Fig. 6.** Anther wall with two to three middle layers. **Fig. 7.** Anther wall at the one-celled microspore stage with degenerating tapetal cells. **Fig. 8.** Anther wall showing fibrous endothecium. **Fig. 9.** Tetrahedral and decussate microspore tetrads. **Fig. 10.** Single microspore. **Fig. 11.** 2-celled pollen grain. ac = archesporial cell; ed = endothecium; ep = epidermis; ft = fibrous thickening; gn = generative nucleus; isp = inner secondary parietal layer; mic = microspore mother cell; ml = middle layer; osp = outer secondary parietal layer; pp = primary parietal cell; sc = sporogenous cell; ta = tapetum; vn = vegetative nucleus.



Figs. 12–23. *Averrhoa bilimbi,* microsporangium, microsporogenesis and male gametophyte. T.S. **Figs. 12–16.** Anther wall at different development stages. **Fig. 17.** Anther locule showing tapetal cells undergoing mitosis. **Fig. 18.** Anther wall at the single-celled microspore stage with degenerating tapetal cells. **Fig. 19.** Wall layers of dehisced anther showing fibrous endothecium and persistent epidermis with crystals. **Fig. 20.** Tetrahedral and decussate microspore tetrads. **Fig. 21.** Single microspores. **Fig. 22.** 2-celled pollen grain. **Fig. 23.** 3-celled pollen grain. ac = archesporial cell; ed = endothecium; ep = epidermis; ft = fibrous thickening; gn = generative nucleus; isp = inner secondary parietal layer; mic = microspore mother cell; ml = middle layer; osp = outer secondary parietal layer; pp = primary parietal cell; sc = sporogenous cell; ta = tapetum; vn = vegetative nucleus.

secondary parietal layers has not been reported in the other members of the Oxalidaceae. In addition, one of the middle layers of *A. carambola* may divide periclinally to form a third middle layer (Fig. 6). Hence, just before meiosis of the microspore mother cells, the anther wall consists of an epidermis, an endothecium, two or rarely (in *A. carambola*) three middle layers and a single-layered multinucleate tapetum (with 2–4 nucleate cells) (Figs. 5, 16). Davis (1966) stated that the anther wall of members of Averrhoaceae and Oxalidaceae (*sensu stricto*) consists of two ephemeral middle layers, as was also shown by Low (1972); Thathachar (1942) and Tan (1977) documented that *Averrhoa* species and *Biophytum sensitivum* (L.) DC. possess either one or two ephemeral middle layers.

The anther wall development of *Averrhoa* conforms to the Basic type, as in *Oxalis*, *Biophytum* (Thathachar 1942, Davis 1966), *A. carambola* (Thathachar 1942, Davis 1966, Low 1972) and *A. bilimbi* (Davis 1966, Tan 1977). At this stage the epidermal cells of *A. bilimbi* accumulate a large number of calcium oxalate crystals and a tannin-like substance (Fig. 18).

The cells of the glandular tapetum in both species of *Averrhoa* studied are initially uninucleate, then they become 2–4-nucleate just before meiosis of the microspore mother cells as reported in the present study (Fig. 17) as well as previous work (Thathachar 1942, Low 1972, Tan 1977). At this time, the tapetum layer is pushed towards the microspore mother cells and the middle layers begin to degenerate from the inner layer towards the outer layer. In *A. bilimbi* these middle layers degenerate completely at the microspore tetrad stage. The tapetum reaches maximum development during meiosis of the microspore mother cells and starts to degenerate after the formation of the microspore tetrad (in *A. carambola*) or after the release of microspore tetrads (in *A. bilimbi*) (Figs. 7, 18). There are no ubish granules (present study, Thathachar 1942, Davis 1966, Low 1972, Tan 1977) although these have been found in the tapetal cells of *Oxalis rosea* Jacq. (Davis 1966).

The microspore mother cells enlarge and show a denser cytoplasm before meiosis. The present study as well as previous work (Tan 1977, Davis 1966) has confirmed that cytokinesis in microspore mother cells is simultaneous and the tetrads formed are either tetrahedral or decussate (Figs. 9, 20), whereas *A. carambola* has earlier been reported to have tetrahedral microspore tetrads (Low 1972). Soon after tetrad formation, the microspores separate out and the wall of these microspores gradually differentiate into the exine and intine (Figs. 10, 21).

In *A. carambola,* the anthers within the same flower show synchronous development, but sometimes meiotic division in different locules of the same anther is not synchronous. An example was found of one locule with microspore mother cells at metaphase I while the others are at metaphase II or anaphase II. In *A. bilimbi*, meiotic divisions in the four locules of an anther are synchronous, but the divisions in anthers of the different whorls are not synchronous at all. For example, it was observed that the long-whorl anthers can be at the tetrad-stage while the short-whorl anthers are at the metaphase II stage. However, both whorls of anthers show the same pollen stage during anthesis (Fig. 70).

The nucleus of the one-celled pollen grain will divide mitotically to form a small generative cell and a large vegetative cell (Figs. 11, 22). Both of these cells lie either in the centre or

migrate to the periphery of the pollen grain. However, the generative cell of *A. bilimbi* on division gives rise to two spindle-shaped male gametes (Fig. 23). After gametogenesis the nucleus of the vegetative cell becomes rounded or irregular in shape and shows signs of degeneration. At maturity the pollen grains are tricolpate and shed at the 2-celled (in *A. carambola*) or 3-celled (in *A. bilimbi*) stage. The pollen grains of *Averrhoa* species and *Biophytum* were reported to be shed at the 2-celled stage (Thathachar 1942, Davis 1966, Low 1972, Tan 1977) whereas those of *Oxalis* were reported to be shed at the 3-celled stage (Davis 1966). Brewbaker (1967) points out that as many as 32% of the angiosperm families are characterised by tricellular pollen.

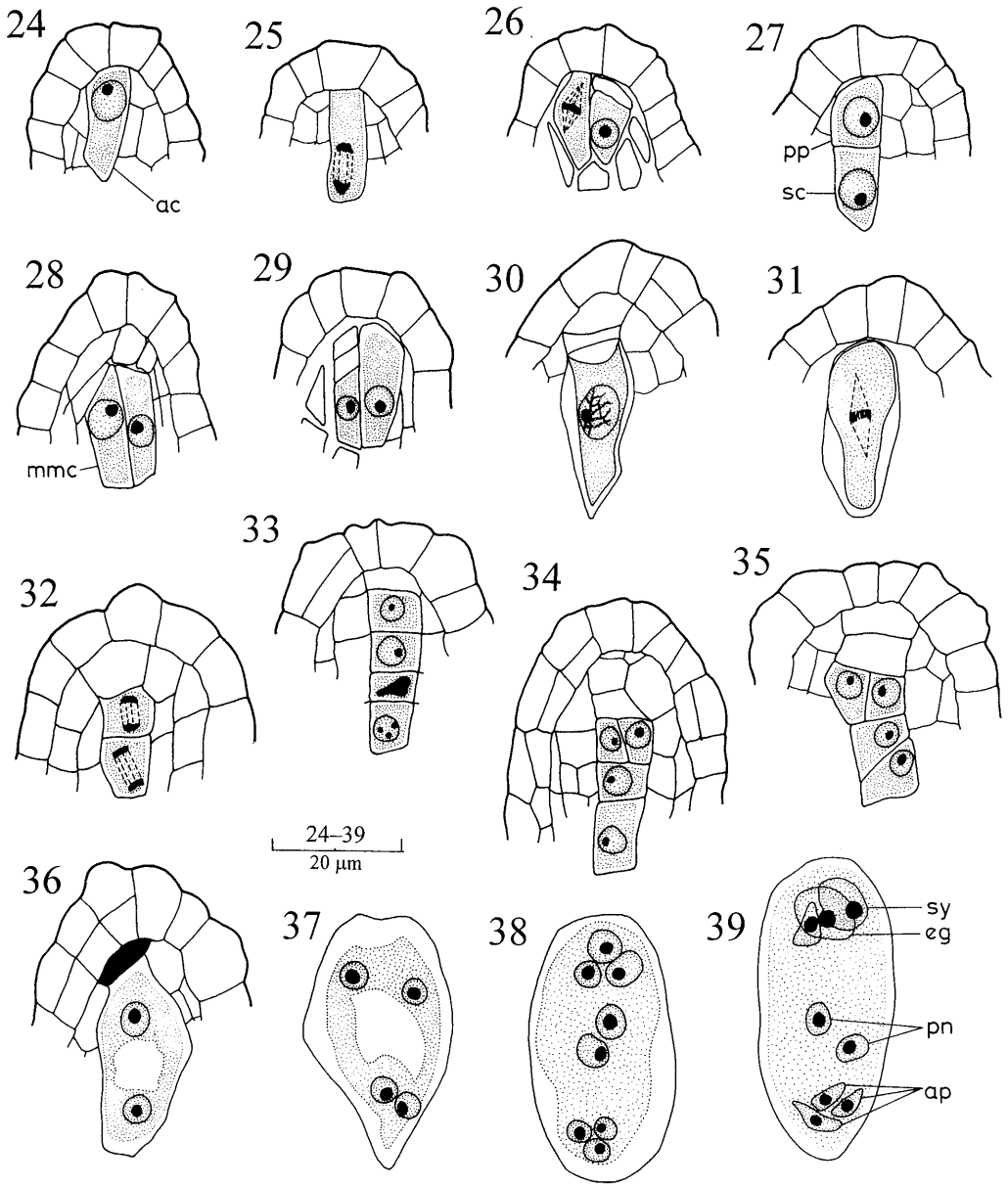
The tapetum completely degenerates and the endothecium develops fibrous thickenings when the anther is at the 1-celled (in *A. carambola*) or 2-celled (in *A. bilimbi*) pollen grain stage. At the time of dehiscence, the anther is extrorse and its wall comprises only the epidermis and the fibrous endothecium (Figs. 8, 19).

MEGASPORANGIUM, MEGASPOROGENESIS AND FEMALE GAMETOPHYTE

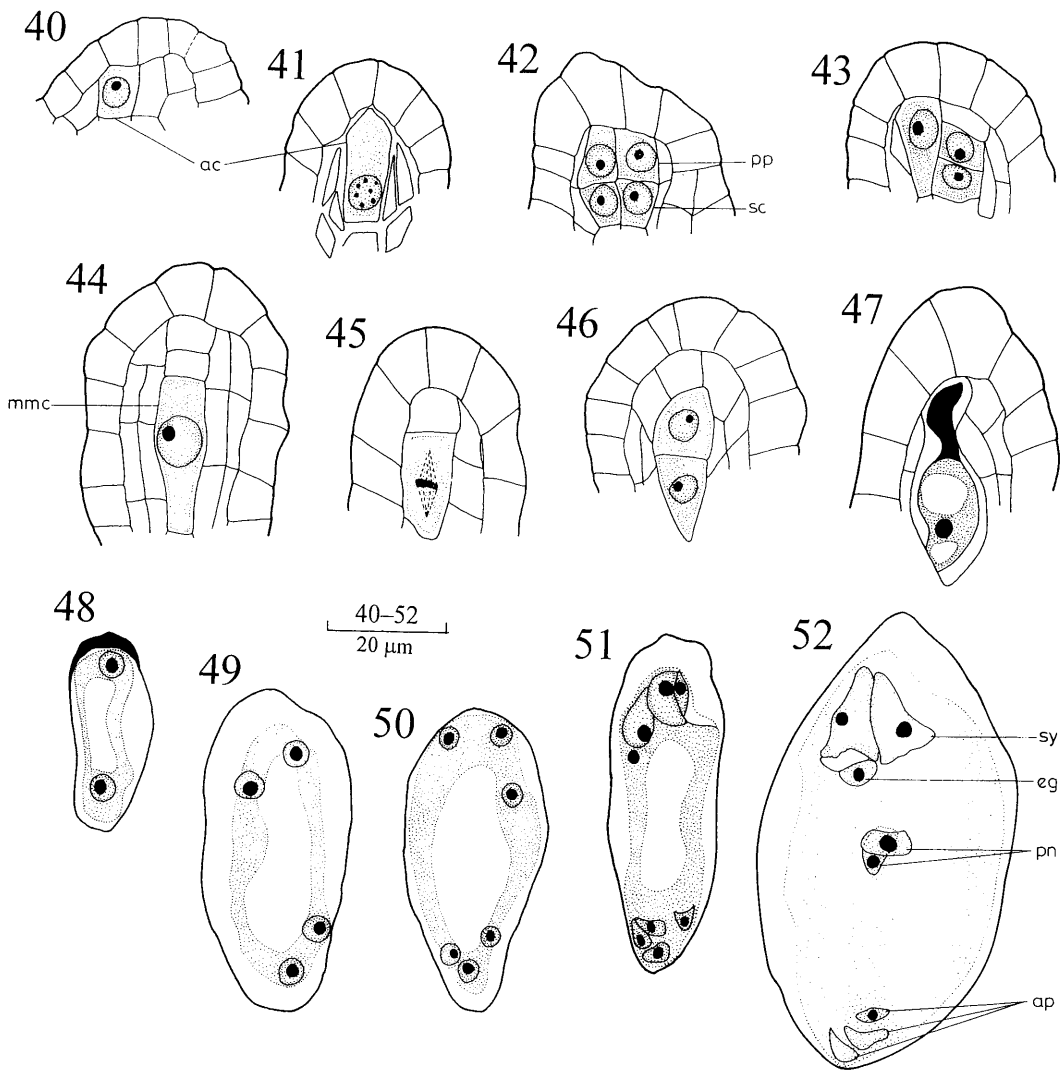
In the *Averrhoa* species studied, the mature ovule is anatropous, bitegmic and crassinucellar (Fig. 66). The micropyle is formed by both the outer and inner integuments (Fig. 67). Similar descriptions of these species have been reported (Davis 1966, Low 1972, Tan 1977). Although the ovule of various members of Oxalidaceae is anatropous and bitegmic, the nucellus is tenuinucellate as reported by Hammond (1908) for *Oxalis corniculata* L., Davis (1966) for *Oxalis* and *Biophytum,* and Bouman (1974) for *Oxalis valdiviensis* Barn. and *B. sensitivum.* Parietal cells are, however, present in both species of *Averrhoa* examined here. According to Thathachar (1942), the primary archesporial cell of *B. sensitivum* functions directly as the megaspore mother cell without cutting off any parietal tissue and therefore the ovule is tenuinucellar. Mauritzon (1934), too, did not mention the presence of parietal cells in *Biophytum* and *Radiola* Hill.

The single archesporium is an enlargement of a hypodermal cell which divides periclinally to form a primary parietal cell and a sporogenous cell that enlarges and differentiates into the megaspore mother cell (Figs. 24–27, 40–43). Both the *Averrhoa* species studied generally show only a single archesporium, though a case of twin archesporia has been observed in an ovular primodium and their divisions are not synchronous in both species (Figs. 28–29, 42–43); an occurrence of twin megaspore mother cells in *A. carambola* was observed in the same nucellus of an ovule (Fig. 28). The twin megaspore mother cells could have been derived from twin archesporia. A single archesporium has been reported in *B. sensitivum, Averrhoa* species (Thathachar 1942), *O. corniculata* (Hammond 1908) and other members of Oxalidaceae (Davis 1966). Nevertheless, twin archesporia were also found in *B. sensitivum* (Govindappa & Boriah 1956).

The primary parietal cell in *A. carambola* may divide to form two to three layers of nucellus at the micropylar end while in *A. bilimbi* it forms two layers of micropylar nucellar tissue (Figs. 30, 34, 44). In certain cases the primary parietal cell does not divide further and it forms



Figs. 24–39. *Averrhoa carambola,* megasporogenesis and female gametophyte. L.S. **Figs. 24–26.** Logitudinal section of hypodermal archesporial cell. **Fig. 27.** Formation of primary parietal cell and sporogenous cell. **Figs. 28–29.** Twin megaspore mother cells. **Fig. 30.** Megaspore mother cell with two layers of nucelli cells. **Fig. 31.** Megaspore mother cell at metaphase. **Figs. 32–33.** Formation of linear tetrads. **Figs. 34–35.** T-shaped tetrad. **Fig. 36.** 2-nucleate embryo sac. **Figs. 37–38.** 4- and 8-nucleate embryo sac. **Fig. 39.** Mature 8-nucleate embryo sac. ac = archesporial cell; ap = antipodal; eg = egg; mmc = megaspore mother cell; pn = polar nucleus; pp = primary parietal cell; sc = sporogenous cell; sy = synergid cells.



Figs. 40–52. *Averrhoa bilimbi,* megasporogenesis and female gametophyte. L.S. **Figs. 40–41.** Longitudinal section of hypodermal archesporial cell. **Fig. 42.** Twin primary parietal cells and sporogenous cells. **Fig. 43.** Archesporial cell, primary parietal cell and sporogenous cell. **Figs. 44–47.** Stages leading to the formation of functional megaspore. **Fig. 45.** Megaspore mother cell at metaphase. **Fig. 46.** Dyad. **Fig. 47.** Functional megaspore. **Figs. 48–52.** Stages in the development of female gametophyte. **Fig. 48.** 2-nucleate embryo sac. **Figs. 49–51.** Formation of 4-, 6- and 8-nucleate embryo sac. **Fig. 52.** Mature 8-nucleate embryo sac. ac = archesporial cell; ap = antipodal; eg = egg; mmc = megaspore mother cell; pn = polar nucleus; pp = primary parietal cell; sc = sporogenous cell; sy = synergid cells.

one layer of micropylar nucellar tissue (Figs. 45–46). However, shortly after the formation of the megaspore mother cell and dyad cells of *A. carambola,* the apical dermal nucellar cells enlarge and divide periclinally to contribute to the formation of the crassinucellar ovule. In one or two cases, the archesporium of *Averrhoa* does not divide but enlarges, elongates and functions directly as the megaspore mother cell. Therefore, the ovule has the tendency to become a tenuinucellar ovule (Figs. 31, 43).

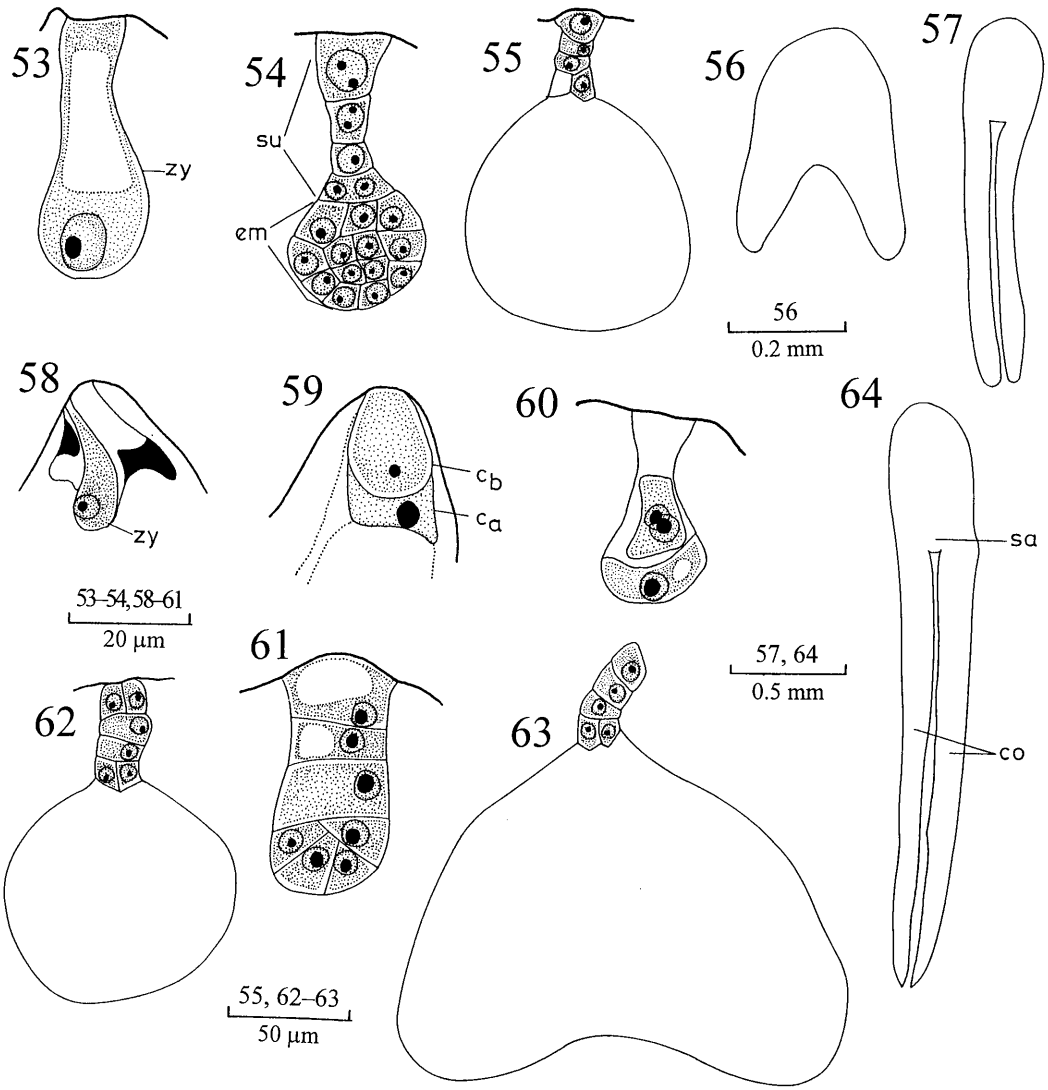
The megaspore mother cell "rests" for a long time then begins to undergo meiosis to form a dyad, followed by a tetrad through synchronous division (Fig. 32). Investigations of *Averrhoa* so far show that the megasporogenesis develops a linear tetrad of megaspores (Thathachar 1942). This is true in *A. bilimbi*, but *A. carambola* produces both linear and T-shaped tetrads (Figs. 33–35) in present study. In *B. sensitivum* (Govindappa & Boriah 1956), the dyad may divide to form a T-shaped megaspore tetrad. According to Davis (1966), linear and T-shaped megaspore tetrads have also been observed in various members of Oxalidaceae. The formation of tetrads in *A. bilimbi* is rapid and this is followed by an immediate degeneration of three micropylar megaspores (Fig. 47). At this stage the anther has produced pollen tetrads or uninucleate microspores.

The chalazal megaspore is functional and divides mitotically to form a 2-, 4- and finally 8-nucleate embryo sac (Figs. 36–39, 48–52). The mature embryo sac consists of two synergids, an egg cell, two polar nuclei and three ephemeral antipodals (Figs. 39, 52). The present study has confirmed that the embryo sac development in *Averrhoa* conforms to the monosporic *Polygonum* type (Maheshwari 1950) as reported in *A. carambola* (Thathachar 1942, Low 1972, Davis 1966), *A. bilimbi* (Thathachar 1942, Davis 1966, Tan 1977), *O. corniculata* (Hammond 1908) and *B. sensitivum* (Mauritzon 1934, Govindappa & Boriah 1956). The early work of Thathachar (1942) also revealed that the sequential formation of the embryo sac in *B. sensitivum* followed that of the 8-nucleate embryo sac of the bisporic *Allium* type.

No pyriform synergids were observed and the polar nuclei fuse close to the egg cell. The three ephemeral antipodal cells degenerate before fertilization (in *A. carambola*) or after the formation of the secondary nucleus (in *A. bilimbi*). Actual pollen tube growth and fertilization have not been observed. However, degeneration of one of the synergids followed by the fusion of the polar nuclei to form a secondary nucleus and the increase in size of the egg nucleus indicate that fertilization has taken place.

ENDOSPERM AND EMBRYO

Soon after fertilization, the primary endosperm nucleus divides to form two free nuclei that subsequently divide repeatedly to produce more nuclei to fill the enlarging embryo sac. The development of the endosperm follows the *ab initio* Nuclear type (Davis 1966). The divisions in the nuclear endosperm are not synchronous. In *A. bilimbi*, the free endosperm nuclei are uninucleolate or sometimes clearly visible as having two nucleoli, while those of *A. carambola* have only one. As the number of endosperm nuclei increases, the nuclei tend to concentrate around the micropylar and chalazal regions and also at the periphery of the



Figs. 53–64. *Averrhoa* species, embryo development. L.S. **Figs. 53–57.** *A. carambola.* **Figs. 58–64**, *A. bilimbi.* **Figs. 53, 58.** Zygote. **Figs. 54–55.** Globular embryo. **Fig. 56.** Heart-shaped embryo. **Fig. 57.** Mature straight embryo. **Figs. 59–62.** Stages leading to the formation of globular embryo. **Fig. 63.** Initiation of the cotyledons. **Fig. 64.** Mature, staight embryo. Ca = terminal cell; C_b= basal cell; em = embryo; co = cotyledon; sa = shoot apex; su = suspensor; zy = zygote.

embryo sac while the centre of the embryo sac is occupied by a large vacuole. At the globular embryo stage (with a 5-celled suspensor in *A. carambola* or a 4–6-celled suspensor in *A. bilimbi*), the nuclear endosperm turns cellular from the micropylar towards the chalazal region (in *A. carambola*) or from the chalazal and peripheral regions to the micropylar region (in *A. bilimbi*). These endosperm cells are irregular in size and shape, with large vacuoles. These cells become homogenous only after the embryo reaches the heart-shaped stage. At the late globular embryo stage, the cellular endosperm concentrates around the developing embryo, which consumes food from these cells, resulting in a region of degenerating endosperm in this area (Figs. 68, 71).

Thathachar (1942) stated that in *A. carambola* and *A. bilimbi,* the wall formation which proceeded from the periphery towards the centre of the embryo sac began only after the number of endosperm nuclei had exceeded 32. Similar observations had been made for *Averrhoa* (Davis 1966). According to Low (1972) and Ou Yang (1978), the endosperm became cellular most probably after the 64-nuclei stage and by this time the embryo had reached the 8-celled proembryo stage. Ou Yang (1978) further noted that when the endosperm reached the 32-nuclei stage, the embryo was only at the 3-celled proembryo stage.

The zygote undergoes a short resting period (Figs. 53, 58). The first division of the zygote occurs at about 7 to 10 days after fertilization. The division of the zygote is transverse, giving rise to a basal cell (C_b) and a terminal cell (C_a). The basal cell of *A. bilimbi* divides transversely first before the terminal cell, resulting in the formation of a 3-celled proembryo, while the terminal proembryo divides longitudinally to form a T-shaped 4-celled proembryo (Figs. 59–61). Subsequent divisions in this proembryo give rise to an octant proembryo followed by a globular embryo with a 2–6-celled (in *A. carambola*) or 4–6-celled (in *A. bilimbi*) suspensor (Figs. 54–55, 62). Later, it develops into a heart-shaped embryo and then a mature, straight dicotyledonous embryo with a radicle, plumule and two thin, leaf-like and equal cotyledons (Figs. 56–57, 63–64, 68, 71–73).

The development of the embryo in the family Oxalidaceae was studied by Mauritzon (1934), Noll (1935), Souéges (1939), Johansen (1950) and Narayana (1962), and classified under the *Oxalis* variation of the *Asterad* type. According to Davis (1966), the embryogeny of both the Averrhoaceae and Oxalidaceae conformed to the *Asterad* type. Thathachar (1942) reported the *Geum* variation in *A. carambola* and *A. bilimbi*, while Ou Yang (1978) observed the *Asterad* type in *A. carambola*. Hammond (1908) reported the formation of a multicellular suspensor in *O. corniculata*. He observed a multicellular haustorial-like organ formed from the basal cells of the suspensor, which forced its way through the integuments until it reached the testa.

SEED COAT

The inner integument ultimately becomes about 6–8 cell layers in thickness. The cells of the outer and middle layers are soon crushed. The inner layer of the inner integument develops into its endothelial character lining the outer side of the endosperm. These cells are

tangentially flat and thin-walled. In *A. bilimbi*, these cells contain tannins while the outer layer forms a fibrous exotegmen with reticulate wall thickenings.

The outer integument is multiplicative and may thicken up to 20 cell (in *A. bilimbi*) or 25 cell (in *A. carambola*) layers. The outer layer of the outer integument is tanniniferous. The inner layer of the outer integument of *A. carambola* develops into collenchymatous tissue, while the outer layer becomes more lignified. The middle layer is parenchymatous with tannin deposition in these cells. The cells of the inner layer of the outer integument in *A. bilimbi* contain crystals and show some slight wall thickenings (Figs. 77–78, 82–83).

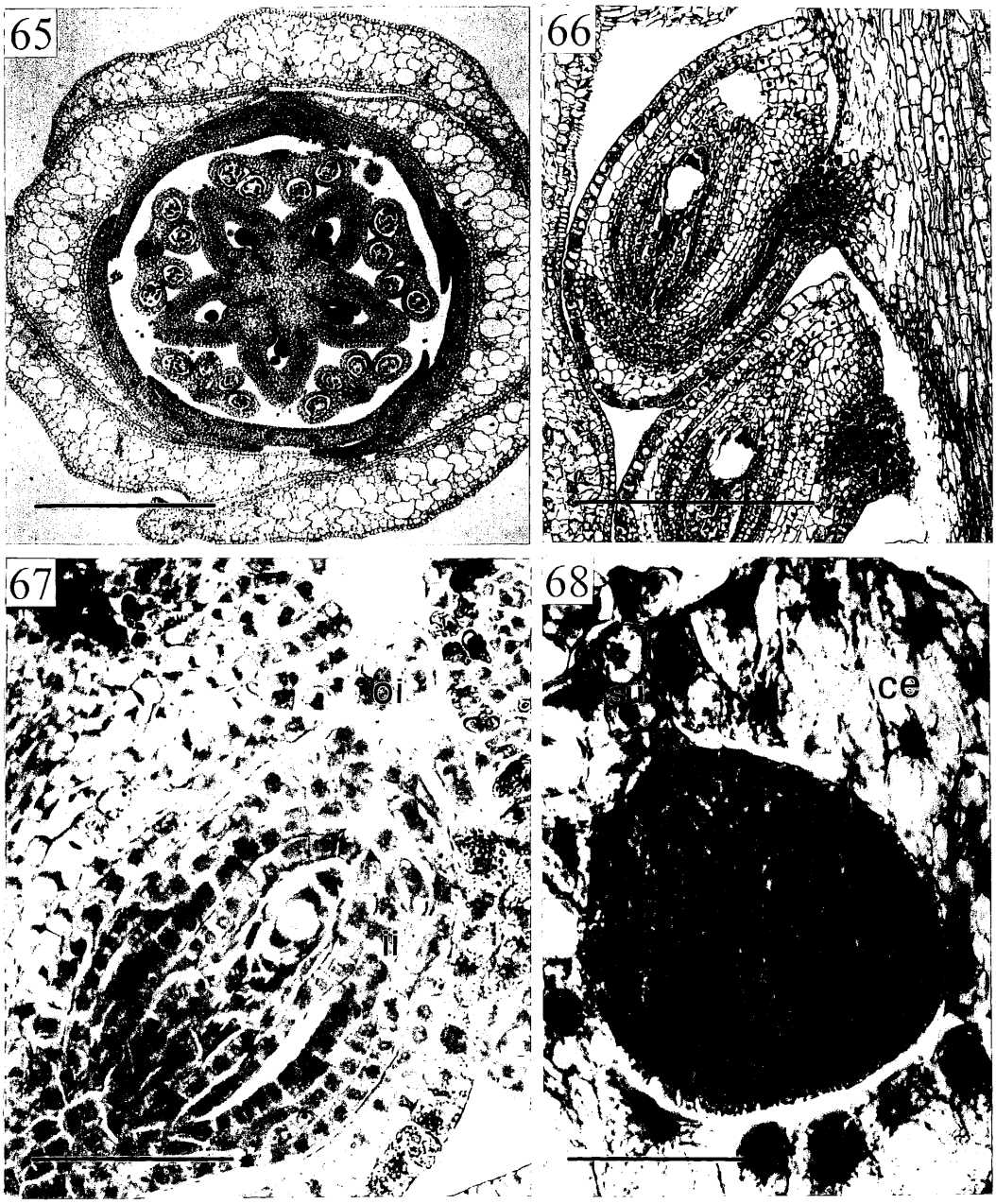
The present study confirms the observation of Boesewinkel (1985) that the inner integument of *Averrhoa* is initially 2-layered and later becomes 4–5-layered. The endothelium develops into an inner pigment layer while the middle layer is crushed and the exotegmen becomes fibrous. The outer integument becomes multiplicative by division in the inner layer, while the endotestal is deposited with crystals. This is generally similar to the seed coat of *Oxalis* and *Biophytum* (Bouman 1974), which is of simpler construction, the inner integument remaining 3-layered and the inner layer of the outer integument without so many divisions.

As the embryo develops and the endosperm becomes cellular, the inner integument becomes slightly ruminate and the outer integument becomes thinner and tanniniferous. In a mature seed, the seed coat consists of a thin layer of the outer integument densely filled with tannin substances and a thin layer of ruminate inner integuments. The rumination of the seed coat in *Biophytum* was exclusively caused by the differential, radial stretching of the cells of the middle layer of the outer integument. However, the ruminations in *Oxalis* and *Averrhoa* were caused by an increased mitotic activity of groups of cells in the middle layers of the outer integument (Boesewinkel 1985). According to Boesewinkel (1985), the mature seeds of *Averrhoa* were hardly or not ruminated in contrast to those of *Oxalis* and *Biophytum* (Bahadur, Bhaskar & Farooqui 1983).

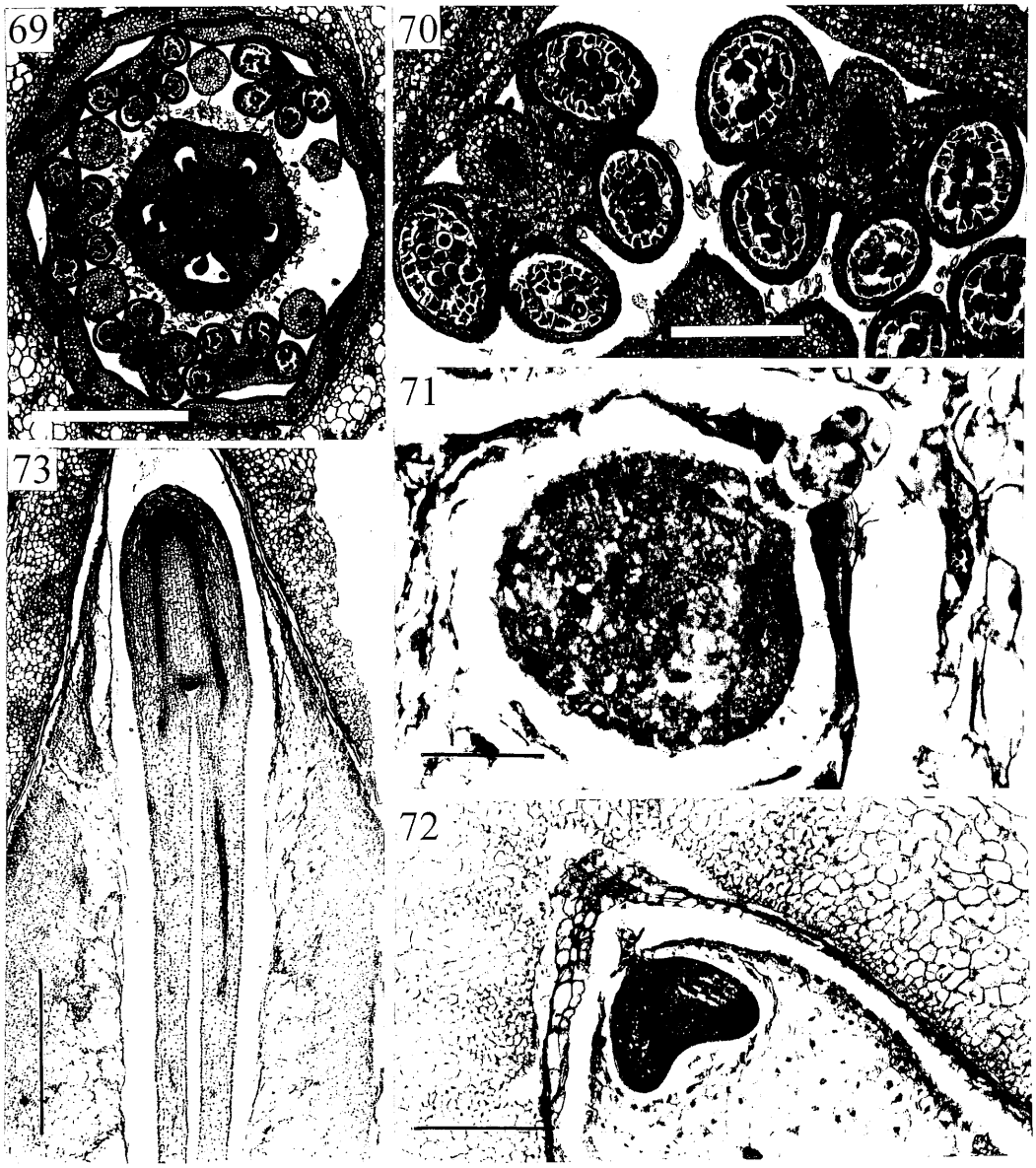
FRUIT WALL

The *Averrhoa* fruit is a fleshy berry developed from a 5-chambered, superior ovary with axile placentation. Fahn (1967) described a berry as a fruit with thick and juicy pericarp in which the following three strata can be distinguished, i.e., exocarp, mesocarp and endocarp. The pericarp of *Averrhoa* is distinguished into three layers, i.e., the outer epidermis with hypodermal layers as exocarp; the middle parenchymatous zone comprising the great bulk of the berry wall including its vasculature as mesocarp; and the inner epidermis with a few layers of parenchyma constituting a parenchymatous zone as endocarp (Kumar 1975, Lim 1975, Dave, Patel & Rupera 1975 and present study).

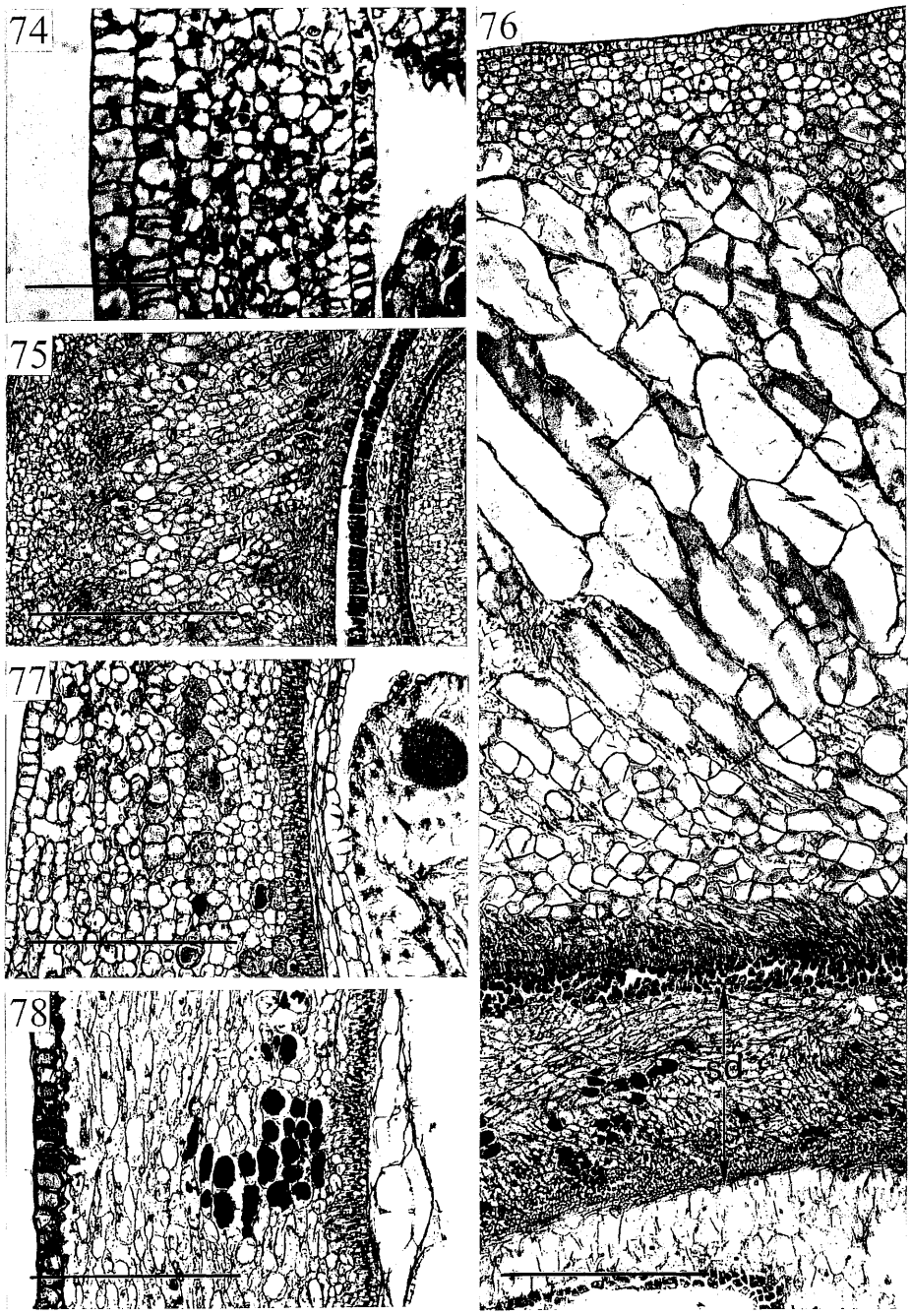
Although the anatomy of Oxalidaceae has been surveyed by Metcalfe & Chalk (1950), anatomical studies of the fleshy pericarp in *Averrhoa* are few (Kumar 1975, Dave, Patel & Rupera 1975, Tan 1977, Ou Yang 1978). The present investigation shows that at the mature embryo sac stage, the exocarp consists of two cell layers, the mesocarp has 10–12 parenchyma



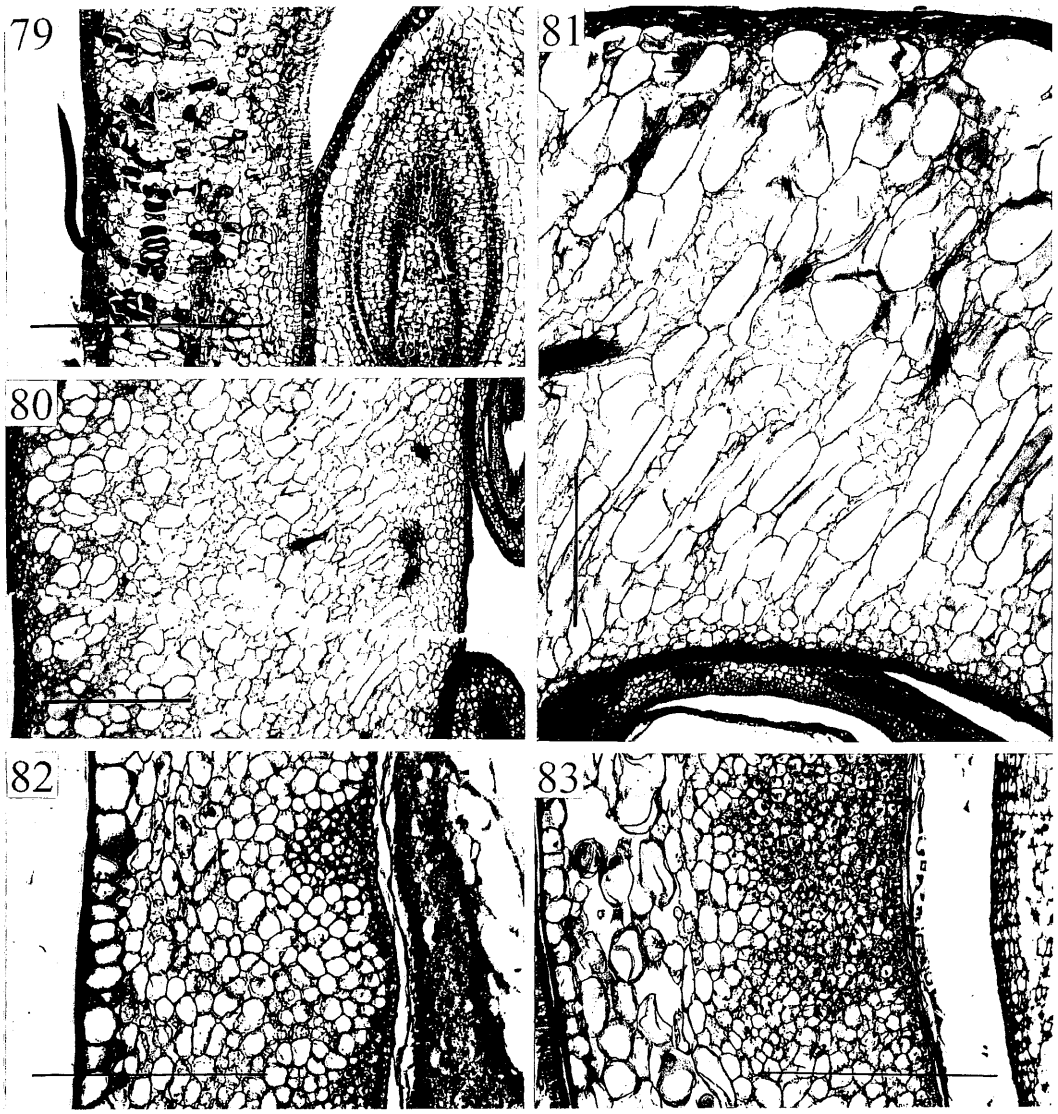
Figs. 65–68. *Averrhoa carambola.* **Fig. 65.** T.S. flower bud. Scale bar = 0.4 mm. **Fig. 66.** L.S. anatropous ovule at mature embryo sac stage showing the vascular bundle. vb = vascular bundle, scale bar = 0.25 mm. **Fig. 67.** L.S. micropyle is formed by the inner and outer integuments at the 2-nucleate embryo sac stage. ii = inner integument; oi = outer integument, scale bar = 50 mm. **Fig. 68.** L.S. globular embryo with suspensor surrounded with cellular endosperm. ce = cellular endosperm; su = suspensor, scale bar = 50 mm.



Figs. 69–73. *Averrhoa bilimbi.* **Fig. 69.** T.S. flower bud. Scale bar = 1 mm. **Fig. 70.** T.S. division of the two whorls of anthers are not synchronous, e.g. long-whorl anther at meiosis I and II while short-whorl anther at microspore mother cell stage. la = long-whorl anther; sa = short-whorl anther, scale bar = 0.4 mm. **Fig. 71.** L.S. globular embryo with suspensor surrounded with cellular endosperm. Scale bar = 75 mm. **Fig. 72.** L.S. initiation of the cotyledons. Scale bar = 0.4 mm. **Fig. 73.** L.S. mature straight embryo. Scale bar = 1 mm.



Figs. 74–78. *Averrhoa carambola.* **Fig. 74.** L.S. ovary wall at mature embryo sac stage. Scale bar = 50 mm. **Fig. 75.** L.S. fruit wall at zygote stage. Scale bar = 0.25 mm. **Fig. 76.** L.S. fruit wall at young globular embryo stage (15 cells thick). sd = seed coat, scale bar = 0.25 mm. **Fig. 77.** L.S. seed coat at globular embryo stage. Scale bar = 0.25 mm. **Fig. 78.** L.S. seed coat at heart-shaped embryo stage. Scale bar = 0.25 mm.



Figs. 79–83. *Averrhoa bilimbi.* **Fig. 79.** L.S. ovary wall at mature embryo stage. Scale bar = 0.25 mm. **Fig. 80.** L.S. fruit wall at zygote stage. Scale bar = 0.4 mm. **Fig. 81.** L.S. fruit wall at young globular embryo stage. Scale bar = 0.4 mm. **Fig. 82.** L.S. seed coat at globular embryo stage. Scale bar = 0.25 mm. **Fig. 83.** L.S. seed coat at young heart-shaped embryo stage. Scale bar = 0.25 mm.

cell layers and the endocarp is only 1–2 cells thick (Figs. 74, 79). After fertilization, the outer epidermal cells and the 2–3 layers of hypodermal cells show periclinal division and contribute to exocarp development. The mesocarp cells enlarge and their nuclei degenerate simultaneously with the nuclei of the endocarp. These cells have large vacuoles and thin walls. At this stage, the cells above the endocarp towards the centre are filled with tanniniferous material and oxalate-crystals, while the endocarp cells become thin and elongated (Figs. 75, 80). Dave, Patel & Rupera (1975) recognised the fruit wall of *Averrhoa* as the parenchymatous fleshy type with many cells containing tannin and calcium oxalate.

As the embryo sac enlarges, the cell of the exocarp and mesocarp continue to increase as well as enlarge and finally their nuclei disappear completely. However, the cells of the endocarp, in 7 to 10 cell layers, become compressed and elongated. These cells are filled with tannins and oxalate crystals. When the embryo reaches the globular stage, the cells of the outer epidermis become smaller with the outer wall cuticularized. The cuticle layer thickens at the heart-shaped embryo stage (Figs. 76, 81). Crystals of calcium oxalate are deposited in the combined region of the exocarp and mesocarp. The mesocarp cells are parenchymatous and enlarge tremendously, filled with juice. The cells with tannins are larger than the surrounding parenchyma cells. The tannin deposition in the cells are denser towards the central axis but the contents are thinner towards the exocarp of the ridges. When the fruit reaches maturity, it becomes yellow or yellowish-green while the texture of the fruit wall is softer. The exocarp cells, which are compressed by the mesocarp cells, become elongated. The mesocarp cells are filled with juice, thin-walled, irregular in shape with the intercellular binding of these cells loosened. In the *A. carambola* fruit, only a few inner epidermal cells towards the ridge are slightly thickened on their outer walls and thinly cutinised. The young immature pericarp has a firm texture but becomes softer as the fruit ripens. Such softening may be due to the chemical changes in cell content and in the structure of the cell (Esau 1953).

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