CONTRIBUTIONS TO THE EMBRYOLOGY OF STERCULIACEÆ—V

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This paper deals with the embryology of 10 species belonging to 4 tribes of Sterculiaceæ as listed below:

Sterculieæ .. *Sterculia colorata* Roxb. and *S. fœtida* L.

Dombeyeæ .. *Pentapetes phœnicea* L., *Dombeya spectabilis* Bojer. and *D. mastersii* Hook.

Buettnerieæ .. *Abroma augusta* L., *Guazuma tomentosa* Kunth. and *Buettneria herbacea* Roxb.

Helictereæ .. *Klienhovia hospita* L. and *Helicteres isora* L.

Observations on the seed structure of *Pterospermum heyneanum* are also included here. This is followed by a general discussion on the embryological characters of the family.

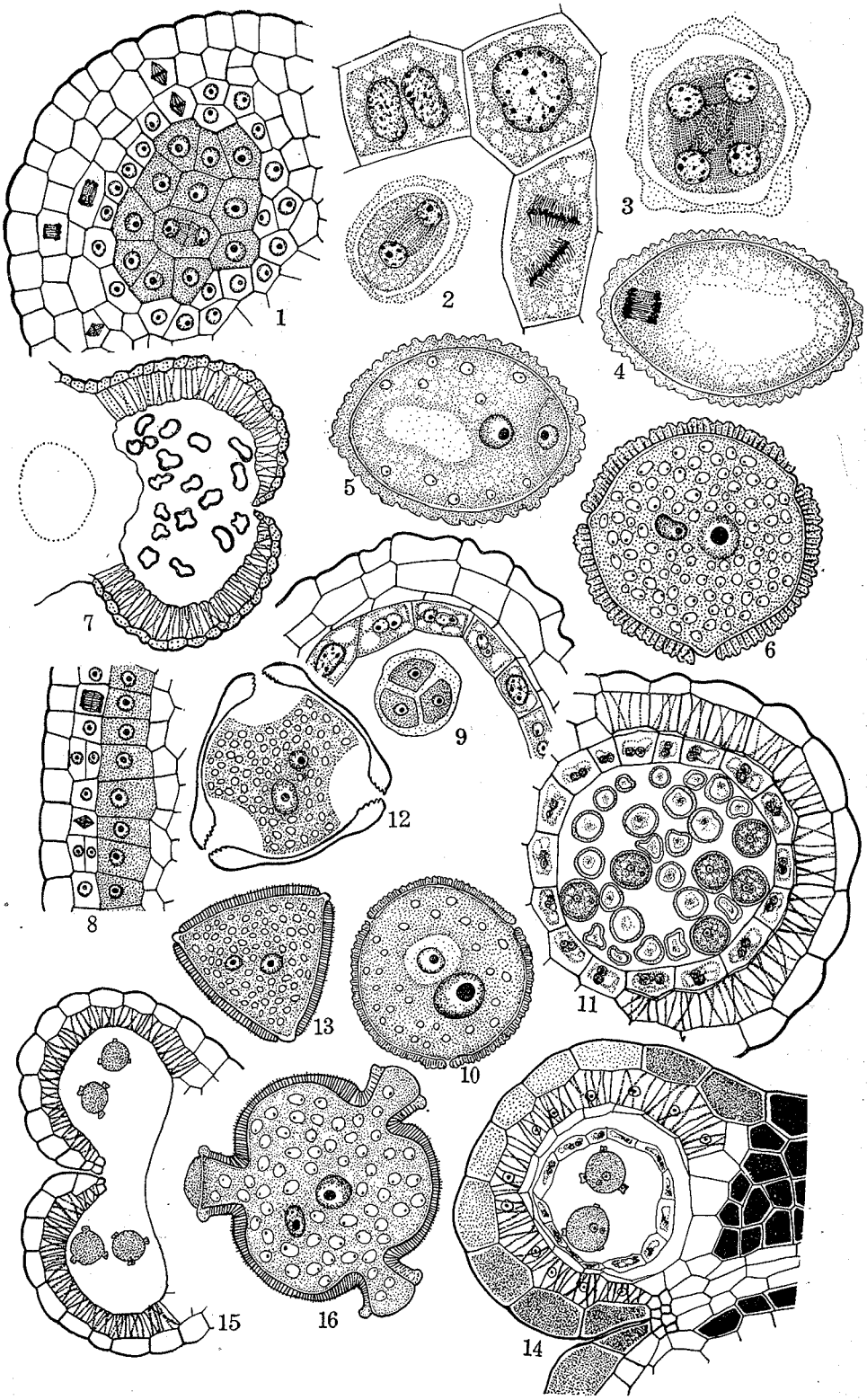
Materials and Methods

The material of *Dombeya spectabilis* was collected from P. R. College Gardens, Kakinada, and that of *D. mastersii* from the Fergusson College, Poona. The material of *Sterculia colorata* was kindly sent by Mr. C. S. Prakasa Rao from Banaras. Material of *Buettneria herbacea* was sent by Dr. K. Subrahmanyam from Bangalore and some of it was collected by the author from Anantagiri Hills. *Klienhovia hospita* and *Abroma augusta* were collected from Kakinada and a part of the material of the latter was also sent by Mr. R. Seshagiri Rao from the Indian Botanic Garden, Calcutta. The materials of the remaining species were obtained locally.

In all cases, formalin-acetic-alcohol was used as the fixative and the material was microtomed according to the customary methods. Delafield's and Heidenhain's Hæmatoxylin and Safranin and Fast Green were used as stains. Fast green, sometimes used as a counter-stain to Heidenhain's Hæmatoxylin, also gave good effect.

Scales and Hairs

In *Pterospermum*, the sepals and ovary wall are covered by brownish scales; in other genera there are several kinds of hairs (Figs. 37, 62, 96). The hairs on the ovary wall may be similar to those on the sepals as in *Guazuma tomentosa* (Figs. 105, 118), or they may be different as in *Helicteres isora* (Figs. 82, 83). The hairs on the ovary wall sometimes differ in shape in different species of the same genus, *e.g.*, *Sterculia*



FIGS. 1-16. Microsporogenesis and development of pollen grains in Sterculiaceæ.

Figs. 1–7. *Sterculia fœtida.*—Fig. 1. T.S. of an anther lobe showing divisions in sporogenous cells and parietal cells, ×425. Fig. 2. Tapetal cells and a sporocyte in telophase I, ×715. Fig. 3. Formation of a bilateral tetrad, ×1065. Fig. 4. First division in microspore, ×1065. Fig. 5. Young male gametophyte, ×1065. Fig. 6. T.S. of mature pollen grain, ×1065. Fig. 7. T.S. of an anther lobe of female flower, ×135. Fig. 8. L.S. of part of an anther lobe of *Pentapetes phœnicea*, ×715. Figs. 9 and 10. *Abroma augusta*—Fig. 9. T.S. of an anther lobe showing tapetum and a microspore tetrad, ×425. Fig. 10. A two-celled pollen grain; note the cytoplasm of the generative cell, ×715. Fig. 11. T.S. of an anther lobe of *Guazuma tomentosa* showing fibrous endothecium, tapetum and pollen grains; note the large proportion of degenerating pollen grains, ×425. Fig. 12. A mature pollen grain of *Helicteres isora*, ×1065. Fig. 13. A mature pollen grain of *Klienhovia hospita*, ×1065. Figs. 14–16. *Buettneria herbacea*—Fig. 14. T.S. of an anther lobe showing stomium, fibrous endothecium, degenerating tapetum and pollen grains, ×285. Fig. 15. Dehisced anther, ×170. Fig. 16. Mature pollen grain, ×1065.

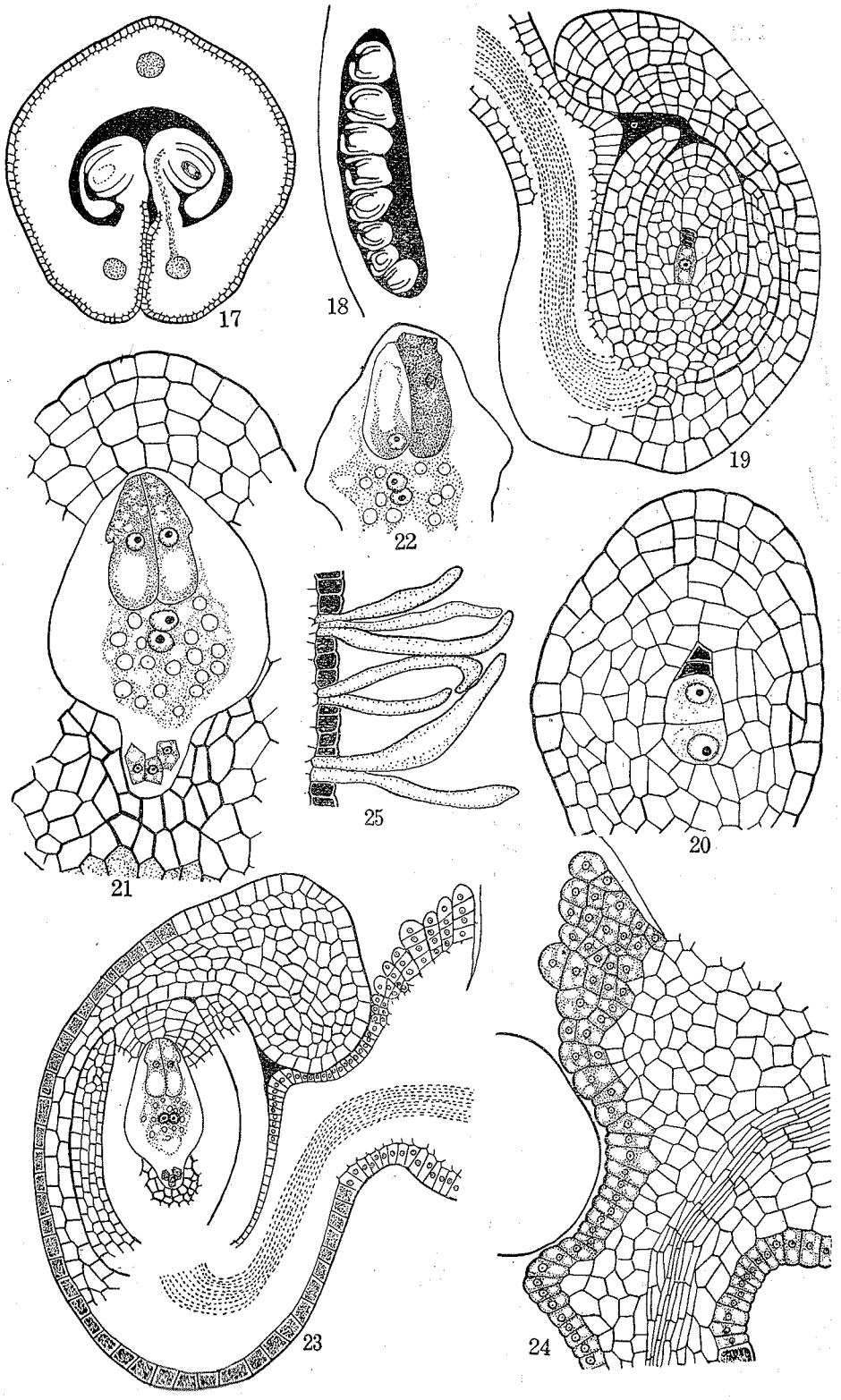
(Figs. 24, 36) and are thus useful as diagnostic characters. In *Buettneria herbacea*, the hairs are slender and glandular on the young ovary (Fig. 106), but after fertilisation, they become large, stiff and spinescent. They develop mucilage sacs and are fed by strands arising from the vascular bundles of the ovary. They probably help in fruit dispersal (Fig. 105). In *Guazuma tomentosa*, the hairs are stellate and are subtended by glandular cells. After fertilisation, these groups of glandular cells grow out into tubercles which are especially conspicuous in the fruit.

Microsporogenesis and Male Gametophyte

The anther wall including the epidermis is 4–5 cells thick. The epidermal layer consists of tangentially flattened tannin-bearing cells (Fig. 14). The hypodermal layer in all species, develops into the fibrous endothecium (Figs. 7, 11, 14, 15) and the innermost layer into the secretory type of tapetum. The cells of the tapetum are usually 2-nucleate but cells showing more than 2 nuclei or with a secondary uninucleate condition are also met with occasionally (Fig. 2). A well-defined stomium is organised in the anther wall (Figs. 7, 15).

The sporogenous cells show secondary increase in number and about 10–15 cells are seen in t.s. of an anther loculus (Fig. 1). In *Sterculia* species, some of the chromosomes in telophase II lag behind. They fail to reach the poles in time and are left out without being incorporated in the daughter nuclei. They, however, perish without forming any micronuclei. In all species some abortive pollen grains occur along with the normal ones. Their percentage is quite high in *Guazuma tomentosa* (Fig. 11). In the female flowers of *Sterculia*, all the pollen grains in the anthers are distorted and sterile. The anther wall, however, shows a stomium and even an endothecium is differentiated (Fig. 7).

Cytokinesis occurs by furrowing. Microspore tetrads are usually tetrahedral (Fig. 9) and rarely bilateral (Fig. 3). In *Helicteres* and *Klienhovia*, the pollen grains are triangular and oblately flattened (Figs. 12, 13). In *Sterculia* species, they become ellipsoidal. The nucleus divides at one pole and forms a lenticular generative cell (Figs. 4, 5). After some time this cell migrates into the vegetative



FIGS. 17–25. *Sterculia fœtida.*

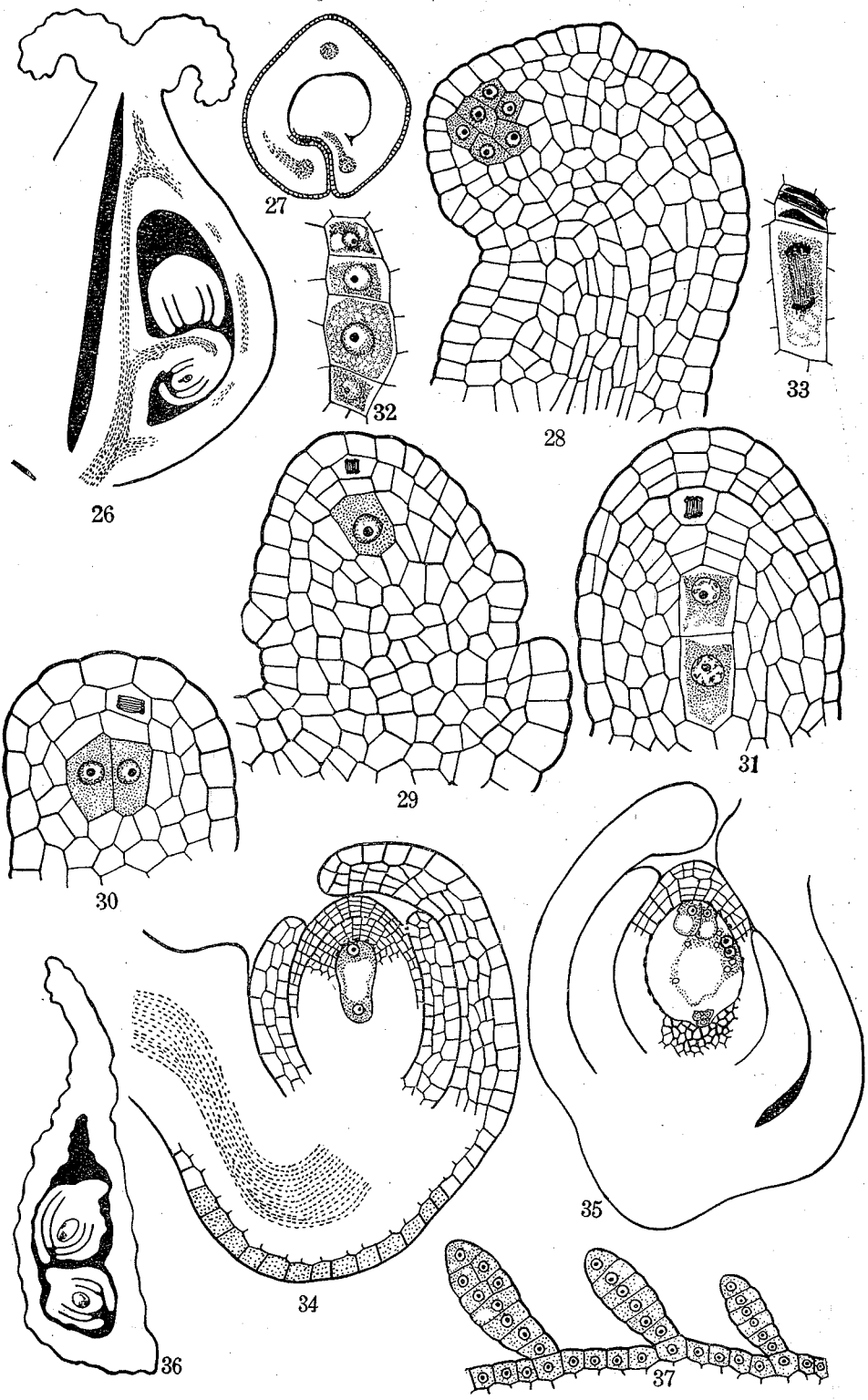
Fig. 17. T.s. of a carpel, ×45. Fig. 18. L.s. of carpel, ×30. Fig. 19. L.s. of young ovule with the lowest megaspore of the linear tetrad enlarging, ×200. Fig. 20. Nucellus with the two chalazal megaspores of the tetrad enlarging, ×425. Fig. 21. Mature embryo-sac with socket of thick-walled cells around its chalazal end, ×425. Fig. 22. Micropylar part of an embryo-sac which has been penetrated by a pollen tube, ×425. Fig. 23. Mature ovule, ×200. Fig. 24. Glandular cells of funicle of a mature ovule magnified, ×335. Fig. 25. Hairs from ovary wall, ×200.

cytoplasm, but its cytoplasm remains distinct as a hyaline sheath around the nucleus (Fig. 10). In the remaining genera, the pollen grains are spherical. In *Pentapetes* and *Dombeya* (Dombeyeæ), the exine is spinescent, while in the rest it is smooth. In all cases, the pollen grains are triporate and 2-nucleate at the time of shedding. In *Buettneria herbacea*, the germ pores are raised on papillate projections of the exine (Fig. 16). Starch grains are found abundantly in the cytoplasm of the mature pollen grains.

Ovule

The ovules which arise as papillæ on the inner wall of the carpels (Figs. 50, 86), closely fill the loculus in *Pentapetes phœnicea*, *Klienhovia hospita* (Fig. 67), *Buettneria herbacea* (Fig. 97) and *Guazuma tomentosa* (Figs. 106, 107), while in *Sterculia* species (Figs. 17, 28) and *Helicteres isora* (Fig. 73), they are not so crowded. In all species, they are anatropous with ventral raphe, bitegmic and crassinucellate. In *Sterculia fœtida* (Fig. 18), *Helicteres isora* (Fig. 74), *Pentapetes phœnicea* (Fig. 38), *Guazuma tomentosa* (Fig. 108) and *Abroma augusta*, the micropyles face the floral axis, while in the rest they are turned towards the top of the loculus. In *Dombeya*, *Klienhovia*, *Abroma* and *Pentapetes*, there is a blunt chalazal outgrowth due to which the ovules appear top-shaped (Figs. 47, 71).

As in other Malvales, the inner integument is more massive and tardy in growth than the outer (Figs. 19, 34, 42, 54, 69, 90). The cells of the outer epidermis of the outer integument and the inner epidermis of the inner integument accumulate tannin (Figs. 23, 54, 71, 80, 100). The micropyle varies in structure in the different species. In *Pentapetes phœnicea* (Fig. 47), *Dombeya* species (Figs. 60, 68) and *Klienhovia hospita* (Fig. 71), the micropyle is zigzag and is formed by both the integuments. In *Sterculia* species (Figs. 23, 35), the pore formed by the inner integument is wider than that formed by the outer. In *Abroma augusta*, the micropyle is formed only by the outer integument. The nucellus of the fertilisable ovule protrudes beyond the inner integument (Fig. 91) so that the description of Banerji (1941) that both the integuments take part in the formation of the micropyle is applicable only to the post-fertilisation stages. In *Guazuma tomentosa*, the micropyle is formed only by the outer integument; the inner covers only about $\frac{3}{4}$ of the nucellus (Figs. 115, 119). In *Buettneria herbacea*, the inner integument grows only to about half the height of the nucellus. The outer integument is developed only on the side opposite to the funicle and stands as high as the nucellus in the upper tier of ovules, but grows much less in the lower ovules (Figs. 100, 102). In the former, the nucellus presses against a hairy placental obturator. In *Helicteres*



FIGS. 26–37. *Sterculia colorata.*

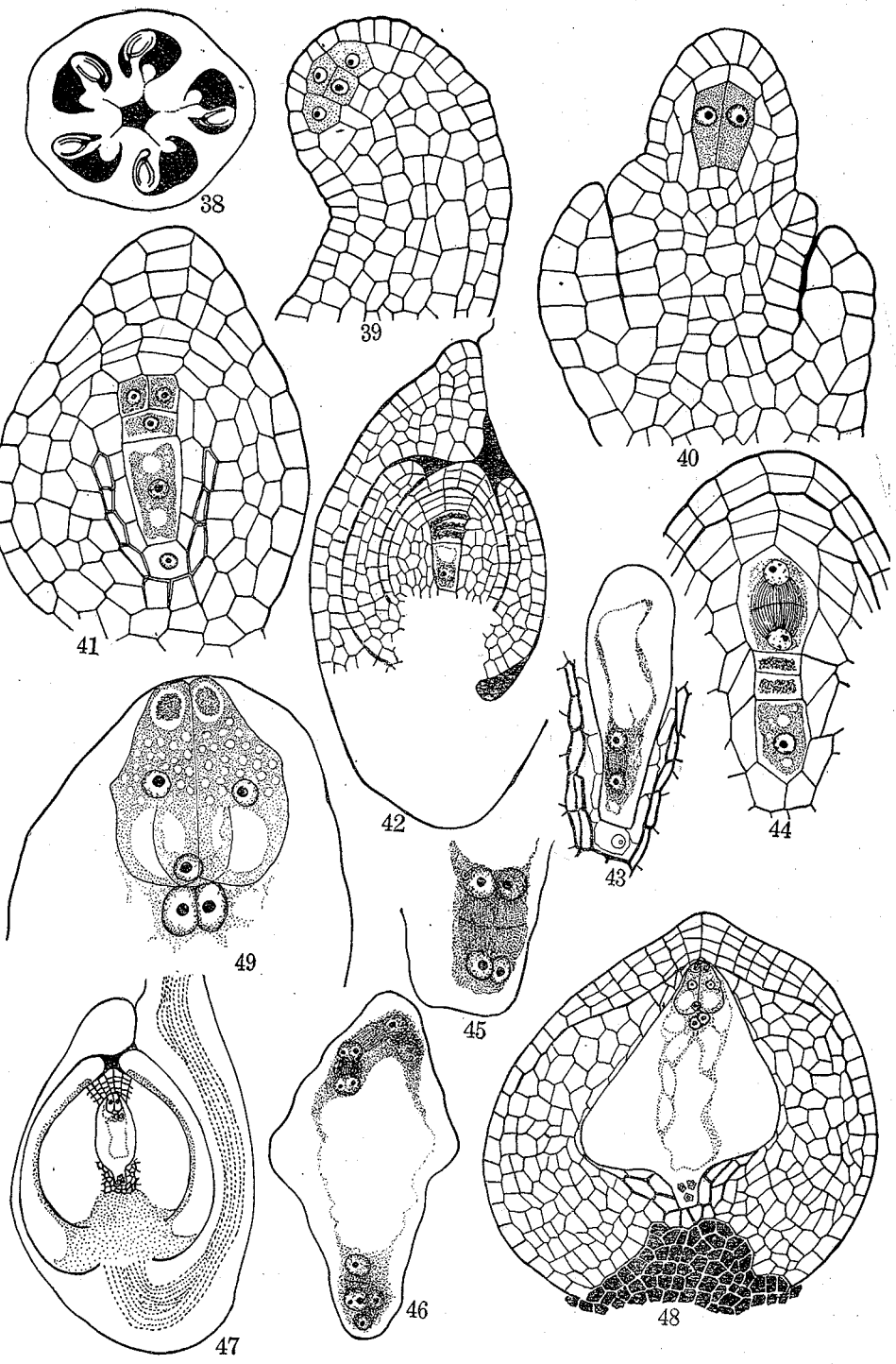
Figs. 26 and 27. L.s. and T.s. of carpel, ×35. Fig. 28. Young ovule showing multicellular archesporium, ×355. Fig. 29. Ovule showing formation of parietal tissue, ×425. Fig. 30. Ovule with two functional megaspore mother cells, ×425. Fig. 31. Nucellus showing dyads, parietal tissue and epidermal cap, ×500. Fig. 32. Linear tetrad with the third megaspore from the micropylar end enlarging, ×500. Fig. 33. First free nuclear division in the functional megaspore, ×500. Fig. 34. Ovule with 2-nucleate embryo-sac, ×185. Fig. 35. Ovule with mature embryo-sac, ×135. Fig. 36. Carpel showing two ovules with degenerating embryo-sacs, ×45. Fig. 37. Glandular hairs from the ovary wall, ×200.

isora, the growth of the integuments ceases practically after the tetrad stage of the ovule and both the integuments cover less than half of the nucellus at the time of fertilisation (Figs. 78, 80). After fertilisation, however, in this species also, a zigzag micropyle is formed as in other species (Fig. 82).

The nucellus is massive and varies from spherical to fusiform shape (Figs. 48, 70, 80, 100, 101). In all species, there is an epidermal cap which ranges in thickness from 2–3 layers in *Guazuma* (Fig. 16) to 5–6 layers in *Dombeya* species (Figs. 59, 65). In several species, *e.g.*, *Dombeya spectabilis* (Fig. 54), *Abroma augusta* (Fig. 89), *Guazuma tomentosa* (Fig. 109), etc., the megaspore mother cell extends to the chalaza. During further growth, several layers of cells are added to the nucellus below the embryo-sac (Figs. 23, 35, 48, 59, 70, 92, 100, 119). In *Pentapetes phœnicea*, the layer of cells immediately surrounding the developing embryo-sac seems to be tapetal in function since the cells are richly protoplasmic. It gets crushed early (Figs. 41, 43). In all species, the cells of the nucellus around the lower half of the embryo-sac become thick-walled so that the embryo-sac in this region is unable to expand and remains much narrower than the micropylar part. These cells surrounding the chalazal end of the embryo-sac also become lignified in *Helicteres isora*. In all species they lose their protoplasmic contents, accumulate tannin and stain deeply. Starch grains also appear in them after fertilisation (Fig. 130). In *Abroma augusta*, the socket of thick-walled cells projects into the embryo-sac as a postament in the developing seed (Fig. 129). While the growth of the embryo-sac keeps pace with the growth of the developing seed in most species, in *Helicteres isora*, the embryo-sac practically remains of the same size after fertilisation (since it is invested by lignified cells), while the nucellus grows comparatively vigorously in the lower region. A hypostase is differentiated in this species and serves to connect the vascular bundle in the funicle with the embryo-sac, thus facilitating rapid transport of food materials (Fig. 82).

Megasporogenesis and Embryo-Sac

The primary archesporium in the ovule consists of a group of cells (Figs. 28, 39, 51, 75, 87), but usually only one axially placed hypodermal cell functions and the rest merge into the nucellus (Figs. 29, 52, 54, 63, 68, 76, 89, 109). Occasionally, two collaterally placed cells were seen to function till the megaspore mother cell stage (Figs. 30, 40, 55, 88). In one ovule of *Dombeya spectabilis*, two 2-nucleate embryo-sacs were noticed (Fig. 58). In this species, sometimes two superposed archesporial cells were seen to function. The upper cell



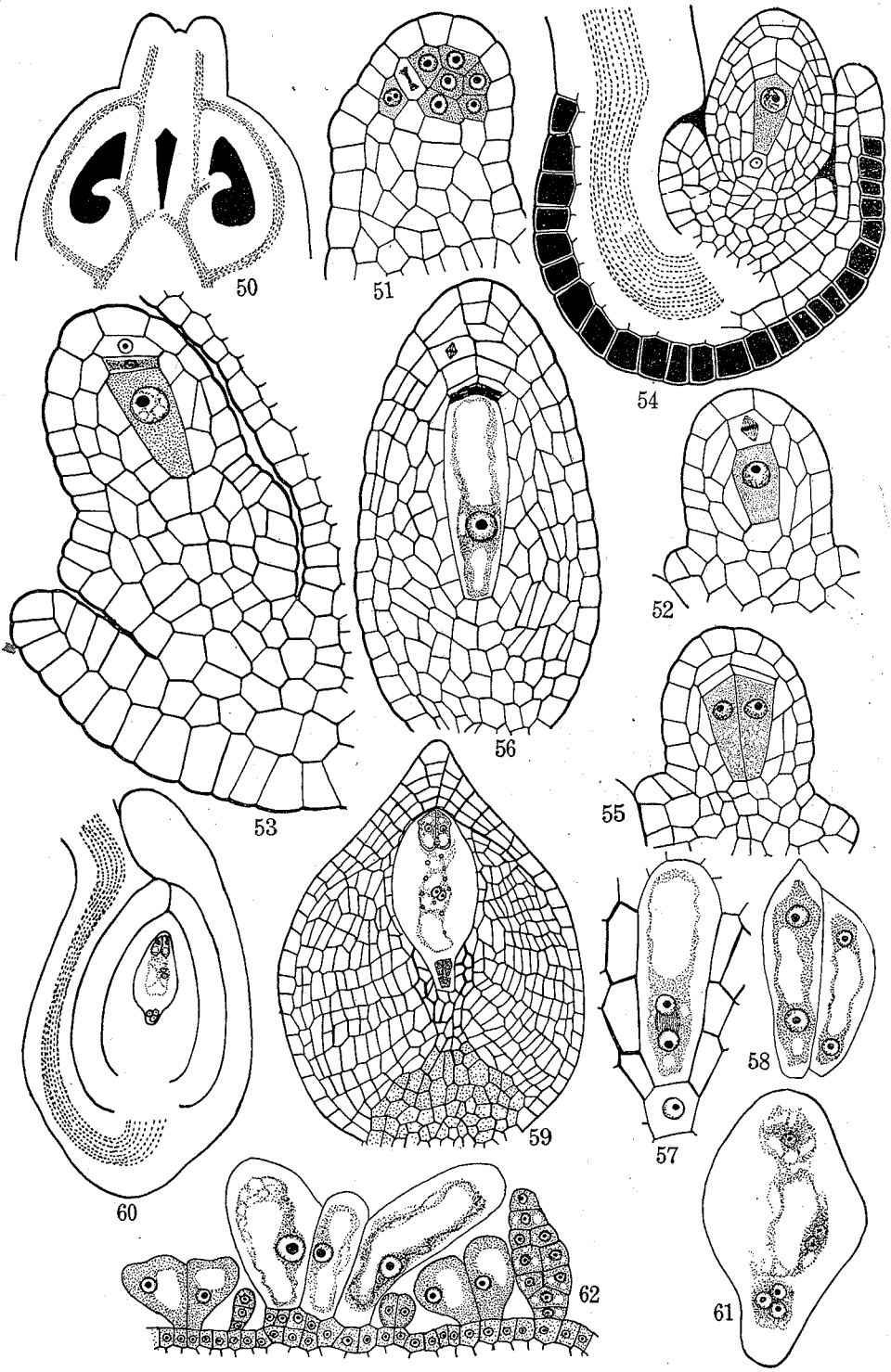
FIGS. 38–49. *Pentapetes phœnicea.*

Fig. 38. T.s. ovary, ×15. Fig. 39. Ovule primordium showing multicellular archesporium, ×425. Fig. 40. Ovule with two functional megaspore mother cells, ×425. Fig. 41. Nucellus with T-shaped tetrad, ×425. Fig. 42. Ovule with linear tetrad of which the lowest megaspore is enlarging, ×200. Fig. 43. First free nuclear division in embryo-sac; note the tapetal layer of cells around the enlarging embryo-sac and the thick-walled cells, ×425. Fig. 44. A linear tetrad with both the terminal megaspores forming embryo-sacs, ×425. Figs. 45 and 46. Nuclear divisions in the embryo-sac; note the secondary spindle fibres and cell plates, ×425. Fig. 47. L.s. fertilisable ovule, ×90. Fig. 48. Nucellus of fertilisable ovule with nucellar cap embryo-sac, zone of thick-walled cells around its lower end and the tannin-bearing cells, ×335. Fig. 49. Upper part of the embryo-sac showing the egg apparatus and polar nuclei; note the starch grains and ring-like patches in synergids, ×715.

in such cases cuts off the primary parietal cell and then gets crushed by the lower which functions directly as the megaspore mother-cell (Fig. 53). Such an archesporium appears as a very much reduced form of the one seen in *Pterospermum* species (C. V. Rao, 1949, 1952).

After cutting off the primary parietal cell to the outside, the megaspore mother cell grows for some time and undergoes the two meiotic divisions which usually result in a linear tetrad of megaspores (Figs. 20, 31–33, 42, 69, 78, 90, 99, 110, 111, 113, 114) and occasionally T-shaped tetrad (Figs. 41, 64, 112). The lowest megaspore of the tetrad functions and gives rise to the embryo-sac according to the *Normal*-type. In one case, the second megaspore from the micropylar end in *Guazuma* (Fig. 114) and in another the third in *Sterculia colorata* (Fig. 32), were seen to be enlarging, while others were showing signs of degeneration. In one ovule of *Sterculia fœtida* (Fig. 20), the two chalazal megaspores of a tetrad were enlarging. Figure 44 shows a megaspore tetrad of *Pentapetes phœnicea* in which the micropylar and chalazal megaspores are forming the embryo-sacs while the median ones are degenerating. The chalazal megaspore has formed a 1-nucleate embryo-sac, while the micropylar one which is more precocious, is showing the first free nuclear division. On the spindle can be seen an evanescent cell plate. In this species such cell plates are noticed in the telophase of the second and third divisions (Figs. 45, 46). Nuclei placed close together get connected by secondary spindle fibres.

The embryo-sac presents normal features. The synergids are hooked (Fig. 79). In *Pentapetes phœnicea* starch grains are present in the cytoplasm of the synergids (Fig. 49). In *Pentapetes phœnicea* (Fig. 49) and *Abroma augusta* (Fig. 92), each synergid shows near its micropylar end, an oval or rounded deep-staining patch with frilled rim. This is probably analogous to the filiform apparatus. A similar structure has been noticed in the synergids of *Pachira rosea* of Bombacaceæ (C. V. Rao, 1954). In *Buettneria herbacea*, in one ovule, one of the synergids showed egg-like vacuolation (Fig. 103). The polar nuclei do not fuse till the time of fertilisation (Fig. 22). The antipodals are 3 in number, 1-nucleate and ephemeral. Starch is seen in the embryo-sac. It is especially abundant in *Klienhovia hospita* in which the nucellar cells also store it (Figs. 69, 70). A case of an embryo-sac with reversed polarity was noticed in *Helicteres isora*; this has been described elsewhere (C. V. Rao, 1952 *a*).



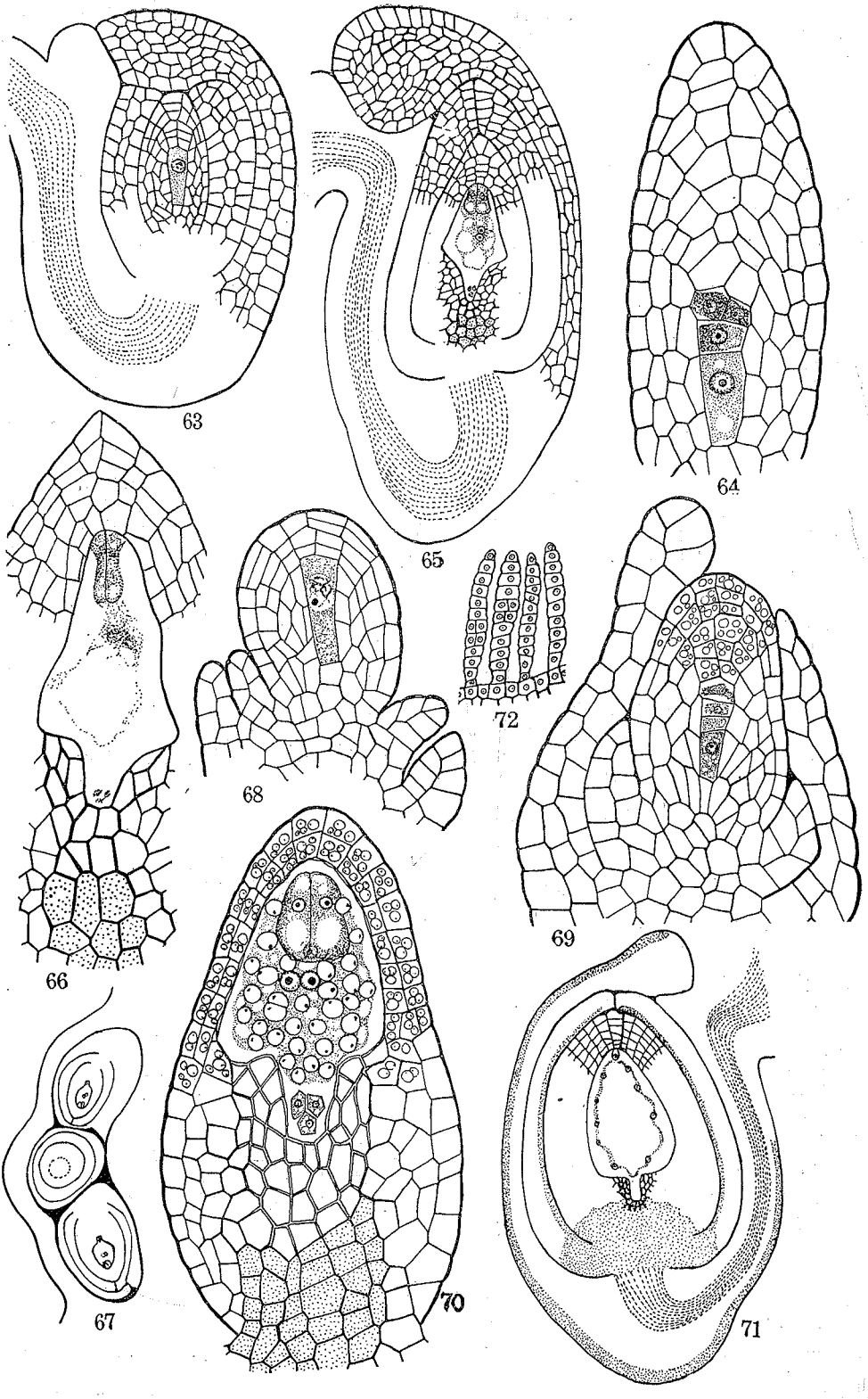
FIGS. 50–62. *Dombeya spectabilis.*

Fig. 50. L.s. ovary showing ovule primordia, ×45. Fig. 51. Ovule primordium with multicellular archesporium; note the degenerating cell, ×425. Fig. 52. First division of primary parietal cell, ×425. Fig. 53. Ovule showing development of integuments and parietal layers, ×425. Fig. 54. Ovule with two superposed megaspore mother cells of which the upper is degenerating, ×715. Fig. 55. Ovule with two megaspore mother cells, ×425. Fig. 56. Nucellus with enlarging functional megaspore, ×425. Fig. 57. First free nuclear division in functional megaspore, ×1065. Fig. 58. Two 2-nucleate embryo-sacs in one ovule, ×715. Fig. 59. Nucellus of fertilisable ovule showing nucellar cap, embryo-sac, thick-walled cells around it and the tannin-bearing cells in the chalaza, ×200. Fig. 61. A degenerating embryo-sac, ×285. Fig. 62. Glandular hairs from the ovary wall, ×200.

FERTILISATION

In *Pentapetes phœnicea*, *Buettneria herbacea* and *Abroma augusta* the style shows a stylar canal which is lined by narrow elongated and richly protoplasmic cells. In *Abroma*, it is occluded at the base of the style by large radially elongated cells (Fig. 122). The axial space of the ovary is also lined by richly protoplasmic cells. In this species, these cells grow out into elongated hairs after fertilisation (Figs. 93, 95). In *Pentapetes phœnicea*, in which the ovules have short funicles, the micropyles stand close to or almost in contact with the placenta. In others, there are various contrivances which facilitate the progress of pollen tubes towards the micropyles. In *Sterculia fœtida* and *Abroma augusta* in which the funicles are pretty long, the latter are lined by radially elongated glandular cells (Figs. 23, 24, 91, 94). In *Abroma*, these cells also contain starch grains and seem to be well adapted to nourish the pollen tubes which pass along them towards the micropyles. In *Helicteres isora*, the naked nucellus lies in contact with some glandular cells of the placenta (Fig. 80). In *Buettneria herbacea*, the upper ovules have their nucelli in contact with a hairy placental obturator (Fig. 100). The lower ones have no such contrivance and their nucelli lie wedged in between the loculus and the chalaza of the upper ovules (Fig. 101). It is probably due to this difference that the upper ovules as a rule develop into seeds, while the lower ones abort (Figs. 103, 106).

In *Abroma augusta*, the pollen grains germinate in the stigmatic furrows (Fig. 122). Though there is a well marked stylar canal, the pollen tubes penetrate through the tissue of the style and enter the axial space of the ovary. Creeping along the funicles they enter the ovules in a porogamous manner. They penetrate the nucellar cap and enter a synergid (Figs. 81, 122, 123) or pass by it and destroy it (Fig. 101). In *Helicteres isora* and *Klienhovia hospita* the track made by the pollen tube in the nucellus can be seen for a long time in the developing seed, although the pollen tube itself perishes quite early (Figs. 82, 157). The tube nucleus seems to degenerate inside the pollen tube itself. One male nucleus fuses with a polar nucleus first (Fig. 124) and then the triploid primary endosperm nucleus is formed. The process of syngamy is very much slower. By the time it is completed, some endosperm nuclei are already formed (Figs. 132, 157, 173). In *Klienhovia*, *Pentapetes* and *Abroma* both the ovule and embryo-sac grow considerably after fertilisation. The starch reserve of the embryo-sac appears to be completely used up during this process, but accumulations of starch grains are seen in the chalaza and integuments.



FIGS. 63–72.

FIGS. 63–66. *Dombeya mastersii.* Fig. 63. Ovule with full grown megaspore mother cell, ×200. Fig. 64. Nucellus with a T-shaped tetrad of megaspores, ×425. Fig. 65. L.s. fertilisable ovule, ×170. Fig. 66. Nucellus showing a degenerating embryo-sac, ×355. Figs. 67–72. *Klienhovia hospita.* Fig. 67. L.s. loculus of ovary, ×75. Fig. 68. Ovule with full-grown megaspore mother cell, ×425. Fig. 69. Ovule with linear tetrad; note the sarch grains in cells of the parietal tissue, ×425. Fig. 70. Nucellus of mature ovule showing nucellar cap, embryo-sac and zone of thick-walled cells; note the large starch grains in the cytoplasm of the embryo-sac, ×425. Fig. 71. Young seed with a few endosperm nuclei, ×330. Fig. 72. Hairs from sepals, ×200.

ENDOSPERM

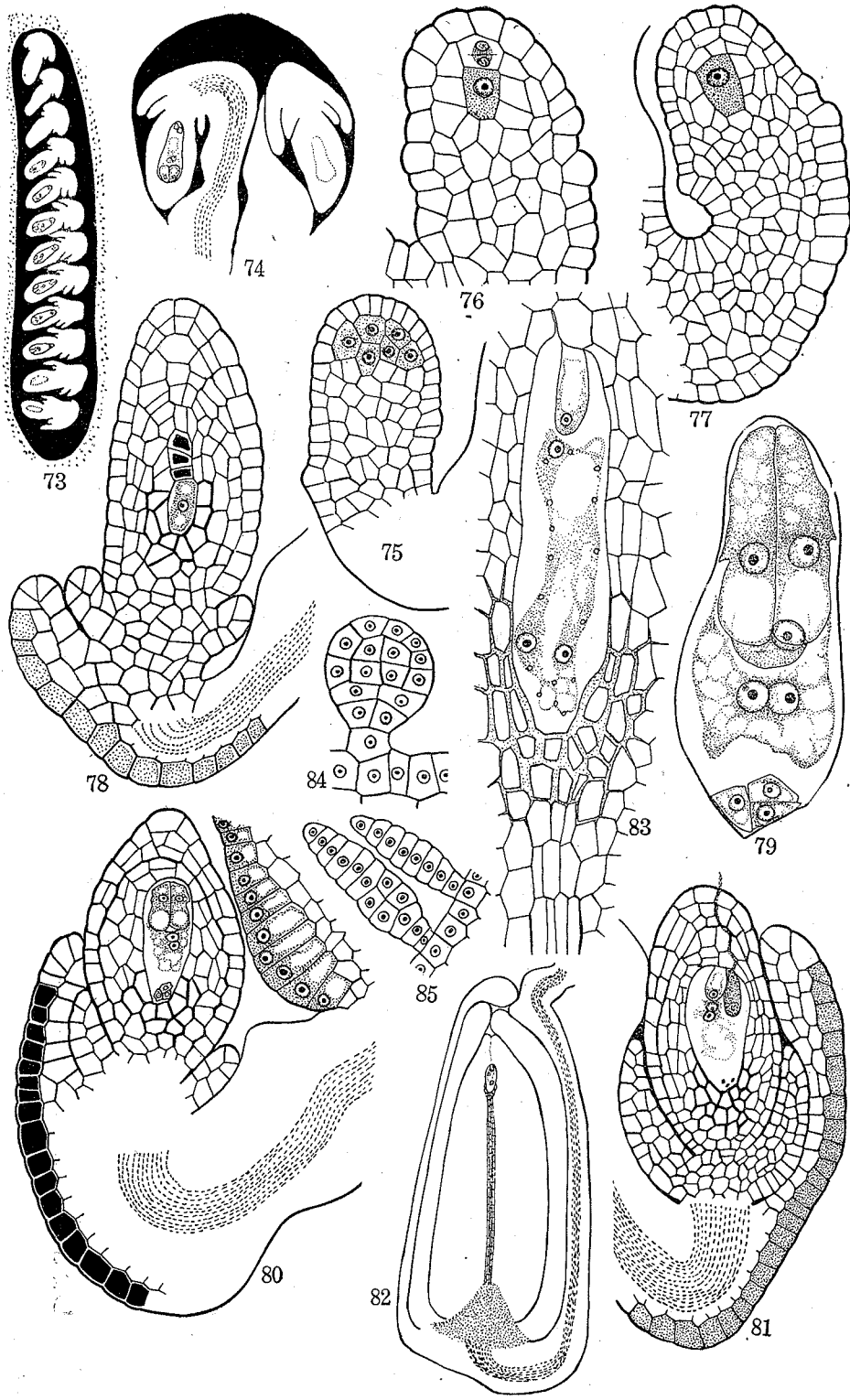
The endosperm is formed according to the nuclear type. It shows both micropylar and antipodal aggregations in which the nuclei are more closely crowded. In the tubular antipodal end of the embryo-sac, the nuclei often fuse together to form large polyploid nuclei. The nucleus situated right at the antipodal end of the embryo-sac is especially conspicuous by its size and number of nucleoli. In *Abroma* and *Pentapetes*, while the normal nuclei measure 8–10 μ in diameter, the gigantic endosperm nuclei at the antipodal end of the sac measure 30-40 μ. In *Pentapetes phœnicea*, these polyplolid nuclei are seen to divide, forming large mitotic figures (Fig. 128). Nuclear fusions are not noticed in the micropylar part of the endosperm.

The endosperm becomes cellular at a relatively late stage in seed development. By this time more than a hundred endosperm nuclei are already formed and the embryo shows cotyledon primordia. The cell formation occurs by the process of cleavage or indentation (Figs. 125, 126). First the protoplasm around the nuclei becomes vacuolated. The zones of contact between the protoplasts are now marked by regions of denser cytoplasm and shortly afterwards cleavage furrows develop along them and the protoplasts become separated. Cell walls are secreted later. Cell formation occurs simultaneously in the micropylar and antipodal regions in *Abroma augusta*. At first the cells in the antipodal region are larger than those in the micropylar part. The former contain one large polyploid or 2–3 triploid nuclei. By further divisions they become smaller and uninucleate. After the endosperm in this region has become cellular, the gigantic nucleus begins to degenerate. It becomes more and more chromatic and develops a central vacuole. Finally it collapses and disappears. The endosperm completely crushes the nucellus so that there is no perisperm in the mature seed.

In all species, the endosperm formation commences soon after fertilisation. In *Helicteres isora*, on the other hand, it is suspended after 3–4 endosperm nuclei are formed and during this period the seed grows considerably.

EMBRYO

The development of the embryo and seed have been studied *i* *Abroma augusta* (Figs. 132–156), *Klienhovia hospita* (Figs. 157–172) and *Pentapetes phœnicea* (Figs. 173–189) and seed development alone



FIGS. 73–85. *Helicteres isora.*

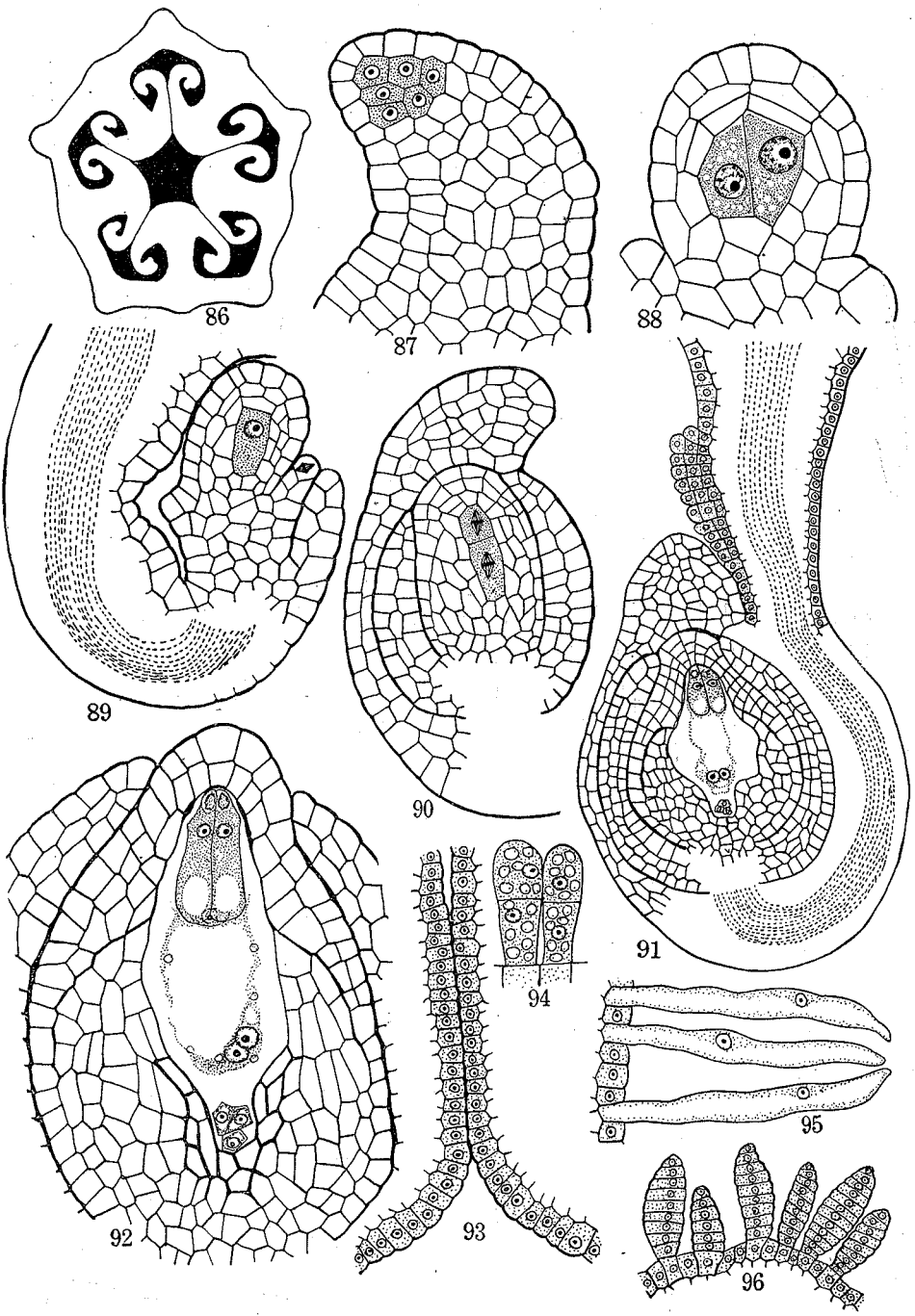
Fig. 73. L.s. loculus of ovary, ×80. Fig. 74. T.s. loculus of ovary, ×155. Fig. 75. Ovule primordium with multicellular archesporium, ×500. Fig. 76. Ovule showing first division of primary parietal cell, ×715. Fig. 77. Ovule with integument initials and parietal layers, ×645. Fig. 78. Ovule with a linear tetrad, ×500. Fig. 79. Mature embryo-sac, ×1065. Fig. 80. Mature ovule: note the glandular cells at the base of the funicle, ×500. Fig. 81. Ovule penetrated by a pollen tube, ×500. Fig. 82. Young seed showing hypostase, ×40. Fig. 83. Part of the above magnified, ×500. Figs. 84 and 85. Hairs from ovary wall and sepals respectively, ×355.

has been studied in *Helicteres isora* (Figs. 82, 83). The development of the embryo keys out to *Urtica* variation of the Asterad Type.

After a period of rest, the fertilised egg undergoes a transverse division and gives rise to the basal cell *cb* and a terminal cell *ca* (Figs. 134, 160, 175). Usually the terminal cell divides vertically and the basal cell transversely at about the same time forming a T-shaped proembryo of which the lower two cells are designated *m* and *ci* (Figs. 135, 163, 176). Occasionally the division in one cell precedes that in the other so that a 3-celled proembryo results. In case the basal cell divides earlier, the embryo is linear (Fig. 162). If the terminal cell divides earlier, a T-shaped embryo results (Fig. 161). In the latter case, the segmentation gives definite evidence for the derivation of *m* from *cb*. The two juxtaposed cells of the terminal tier undergo a vertical division forming circumaxially arranged quadrants designated *q*. *M* divides vertically and *ci* transversely forming *n* and *n'*. The next divisions in cells of *q* are obliquely vertical and result in two layers of cells *a* and *b*. *n* divides vertically and *n'* transversely forming *o* and *p*. Now the embryo is 5-tiered and the destination of the tiers is as follows: *q* forms the stem tip and cotyledons; *m* develops into the hypocotyl; *n* gives rise to the root tip and *o* functions as the hypophysis and fills out the dermatogen of the root tip and root cap; *p* forms the suspensor which is usually short.

In *Klienhovia hospita*, sometimes the divisions in *cb* or its derivatives are irregular. The basal cell may undergo a vertical instead of a transverse division (Fig. 164), or *ci* may undergo first a vertical division (Fig. 166). But as the later divisions are transverse, the number of tiers and their destination remain unchanged. Such irregularities in behaviour of the derivatives of the basal cell were also noticed in *Tilia platyphyllos* by Souèges (1941), but Johansen (1950) feels that they are not of such significance as to necessitate the erection of a separate variation.

The dermatogen initials are demarcated first in *m* and then in *q* and *n*. One of the inner group of cells (*b*) may sometimes divide in an oblique manner giving rise to what looks like an epiphyseal cell, but by further divisions the derivatives of this cell get mixed up with those of the remaining cells. The number of root cap initiating layers varies from one to two. The suspensor remains 1-celled for a pretty long time in *Pentapetes* and *Klienhovia* but in *Abroma augusta* it divides early and becomes several celled. In the mature seed, the cotyledons are large and foliaceous. They may be straight as in *Abroma augusta* (Figs. 154–156) or variously folded as in *Klienhovia hospita* (Fig. 172)



FIGS. 86-96. *Abroma augusta*

Fig. 86. T.s. ovary, ×30. Fig. 87. Ovule primordium with multicellular archesporium, ×500. Fig. 88. Ovule with two functional megaspore mother cells, ×715. Fig. 89. Ovule showing development of integuments and parietal layers, ×425. Fig. 90. Formation of linear tetrad, ×285. Fig. 91. Mature ovule; note glandular cells on the funicle, ×200. Fig. 92. Nucellus of mature ovule; note the circular patches on the synergids, ×425. Fig. 93. Glandular epidermal cells of carpellary wall which function as transmitting tissue, ×285. Fig. 94. Glandular cells of the funicle rich in cytoplasm and starch grains, ×285. Fig. 95. Cells of carpellary wall grown into hairs after fertilisation, ×285. Fig. 96. Glandular hairs from the sepals, ×285.

and *Pentapetes phœnicea* (Figs. 185–187). The cells of the embryo are laden with starch and other food materials. In *Klienhovia hospita* some of the cells of the radicle become papillate (Fig. 171).

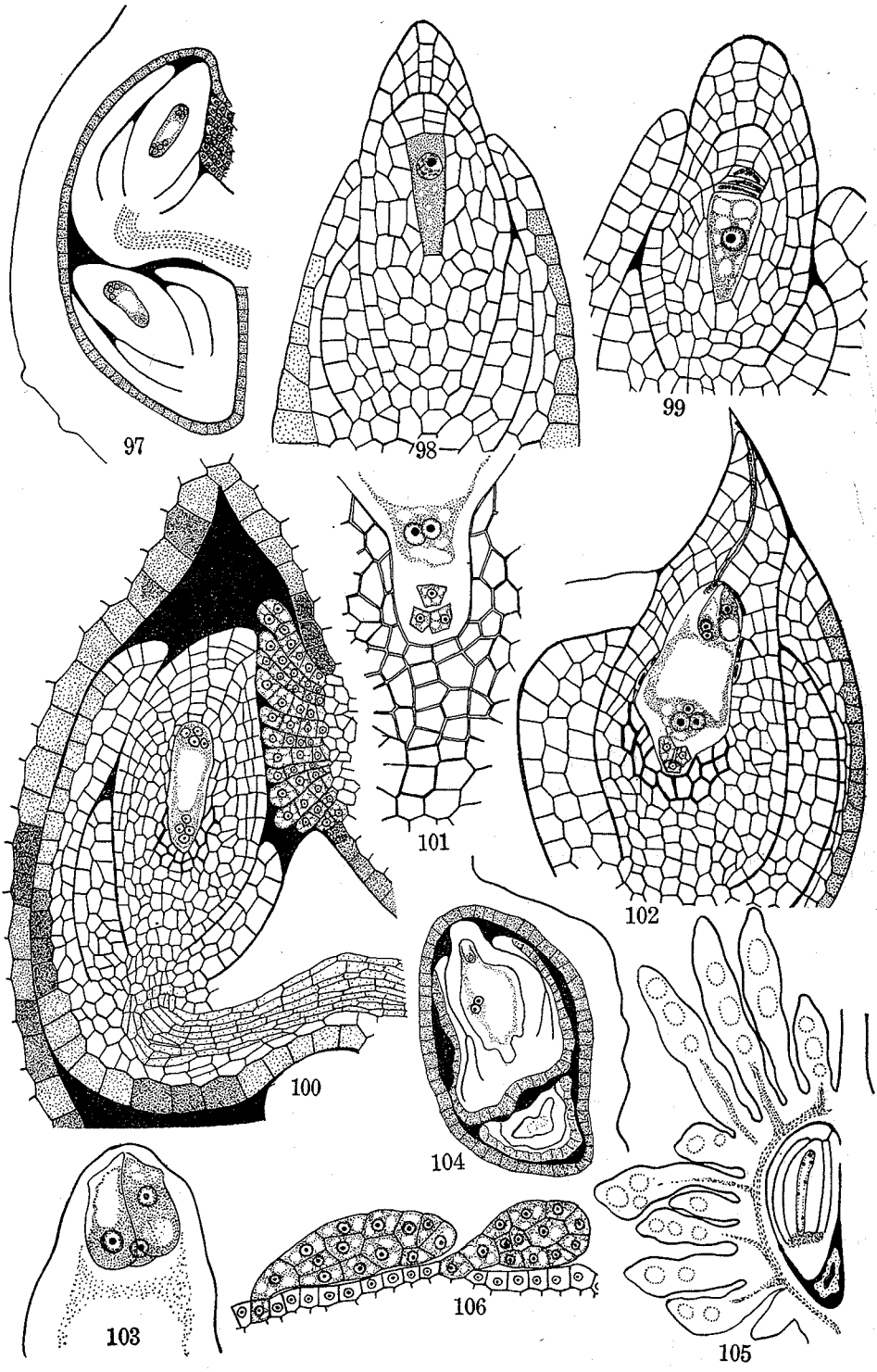
Seed Coats

The post-fertilisation growth in the integuments is shown in the following table:

Name of plant	Layers in outer integument	Layers in inner integument	Layers in testa	Layers in tegmen
Sterculia colorata ..	3	4	10–12	25–30
Pterospermum heyneanum ..	3	4	6–12	8–10
Pentapetes phœnicea ..	3	4	3–5	6–8
Buettneria herbacea ..	2	3	3–4	8–10
Abroma augusta ..	2	5	2	8–10
Helicteres isora ..	2	2	2	8–10
Klienhovia hospita ..	3	4	6–10	10–12

After fertilisation, the integuments increase in thickness, the tegmen becoming more massive than the testa. Starch grains appear in the cells of the seed coats in *Abroma*. The integuments are thicker in the chalazal region than in the region of the micropyle. They show the maximum thickness at about the time when the embryo has the shape of a large globular mass. The thickness of the coats given above was observed about the middle of the seed.

The testa in general is smooth. Its outer epidermis consists of tangentially flattened cells filled with tannin. In *Abroma augusta*, in which the testa does not increase in thickness after fertilisation, the 2 layers of the testa are loosely attached and the outer epidermis does not accumulate tannin (Fig. 208). Sometimes tannin is seen in isolated groups of cells which give a speckled appearance to the surface view of the testa (Fig. 197). In *Klienhovia hospita* some of the epidermal cells grow out into short spinescent processes (Fig. 207). The inner epidermis of the outer integument consists of tangentially flattened cells except in *Buettneria herbacea* in which they are somewhat



FIGS. 97–106. *Buettneria herbacea*

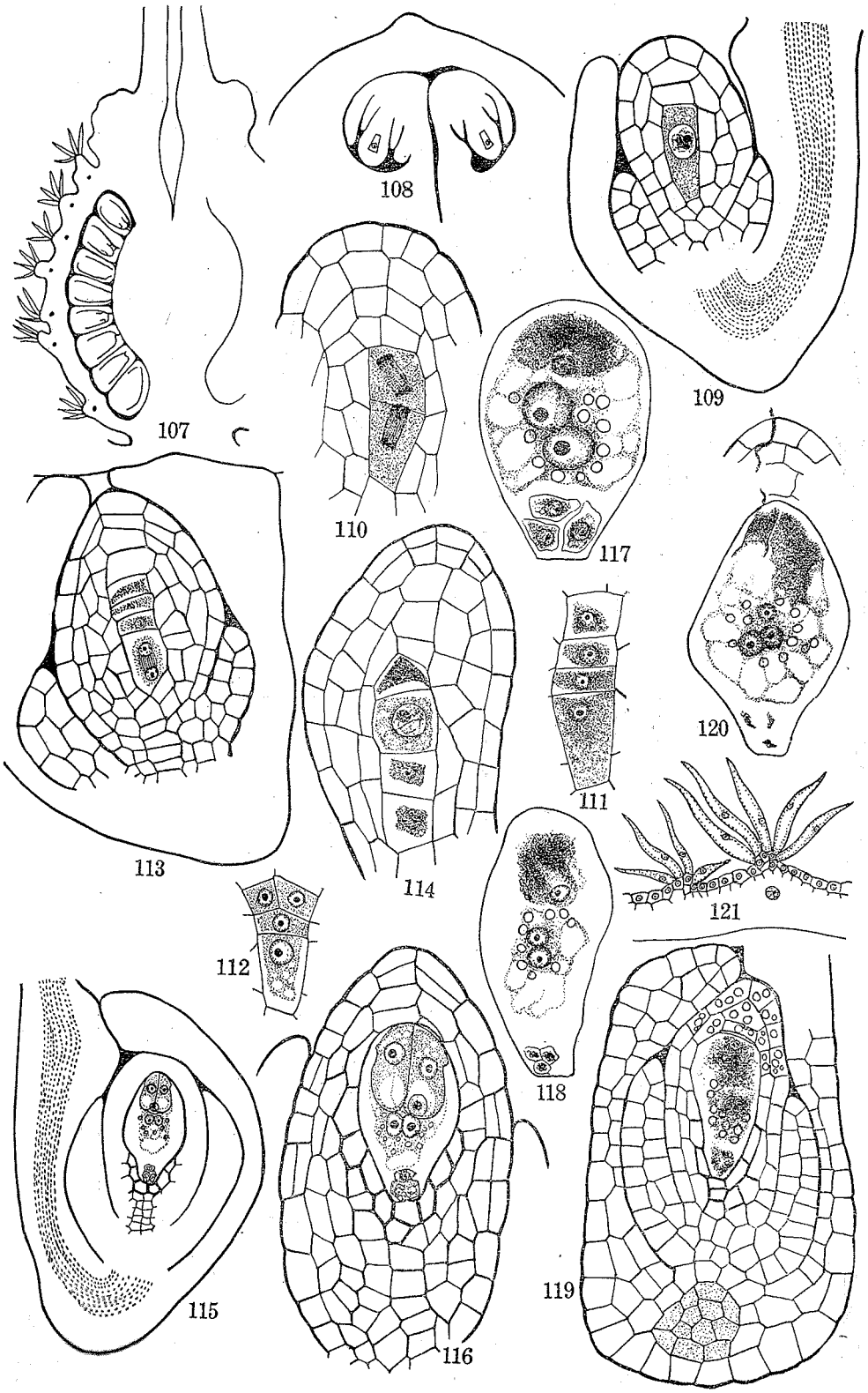
Fig. 97. L.s. loculus of ovary showing the two superposed ovules, ×200. Fig. 98. Ovule showing full grown megaspore mother-cell, ×425. Fig. 99. Ovule with 1-nucleate embryo-sac, ×425. Fig. 100. Upper ovule of the loculus with 8-nucleate embryo-sac, in contact with the placental obturator, ×355. Fig. 101. Lower part of the embryo-sac invested by thick-walled cells, ×715. Fig. 102. Ovule of the lower tier showing entry of pollen tube, ×355. Fig. 103. Micropylar part of the embryo-sac showing one egg-like synergid, ×855. Fig. 104. A loculus of ovary showing degeneration of ovules, ×170. Fig. 105. Loculus of a fruit with one developing seed; note the spinescent outgrowths on the fruit wall, ×30. Fig. 106. Glandular hairs on the ovary wall, ×285.

radially elongated (Fig. 199). Sometimes these cells also contain tannin.

In *Sterculia*, *Pterospermum* and *Klienhovia*, vascular bundles are given off into the testa from the chalazal end of the ovular trace. In *Klienhovia hospita*, these strands form a plexus in the lower third of the seed. In *Sterculia colorata* (Figs. 190–192) 6–9 prominent strands arise and extend nearly to the micropyle giving off a few branches on the way. In *Pterospermum heyneanum*, the strands are more numerous and their branches form an anastomosing system throughout the testa (Figs. 194–196). Similar integumentary vascular bundles have been reported in *Thespesia*, *Gossypium* and *Ingenhousia* (Reeves, 1936) of Malvaceæ and *Pachira aquatica* of Bombacaceæ (C. V. Rao, 1954).

The cells of the outer epidermis of the outer integument become radially elongated and form the palisade layer as in other Malvales. The inner tangential and radial walls become thickened so that the lumens of the cells are seen only in the outer halves. The palisade layer shows a prominent light line (Fig. 209). The inner half of the cell wall stains deeply with phloroglucinol showing thereby that it is lignified while the outer non-stainable zone is made of cellulose. Except in *Helecteres isora*, 1–3 layers of cells immediately below the palisade layer accumulate tannin and constitute the 'inner pigment layer'. In *Sterculia colorata* in which the tegmen is much thicker than in others, this layer is of greater thickness (Fig. 192). In *Helicteres isora*, the pigment layer develops in the median region of the tegmen and is separated from the epidermal layers by 1–3 layers of colourless cells (Figs. 201, 202). The inner epidermis of the tegmen consists of tangentially flattened tannin-filled cells, called 'the fringe tissue', and the median layers are composed of thin-walled parenchyma which are resorbed in the seed. In *Sterculia colorata*, where the nucellus is crushed and absorbed much earlier than in others, these parenchymatous cells seem to constitute an important nutritive tissue for the growing embryo. The cells of the fringe tissue stain deeply and their cell walls are lignified. The structure of this layer in *Sterculia colorata* differs from that of others in that they do not show tannin nor do their cell walls stain deeply. They show reticulate thickenings, the presence of which is considered by Netolitzsky (1926) to be a primitive feature.

The seed coat structure of *Pentapetes phœnicea* deserves special mention. The cells of the inner integument in the region of the micropyle become much elongated; their cell walls become lignified and they develop reticulate thickenings characteristic of tracheids (Figs. 188,



FIGS. 107–121. *Guazuma tomentosa*

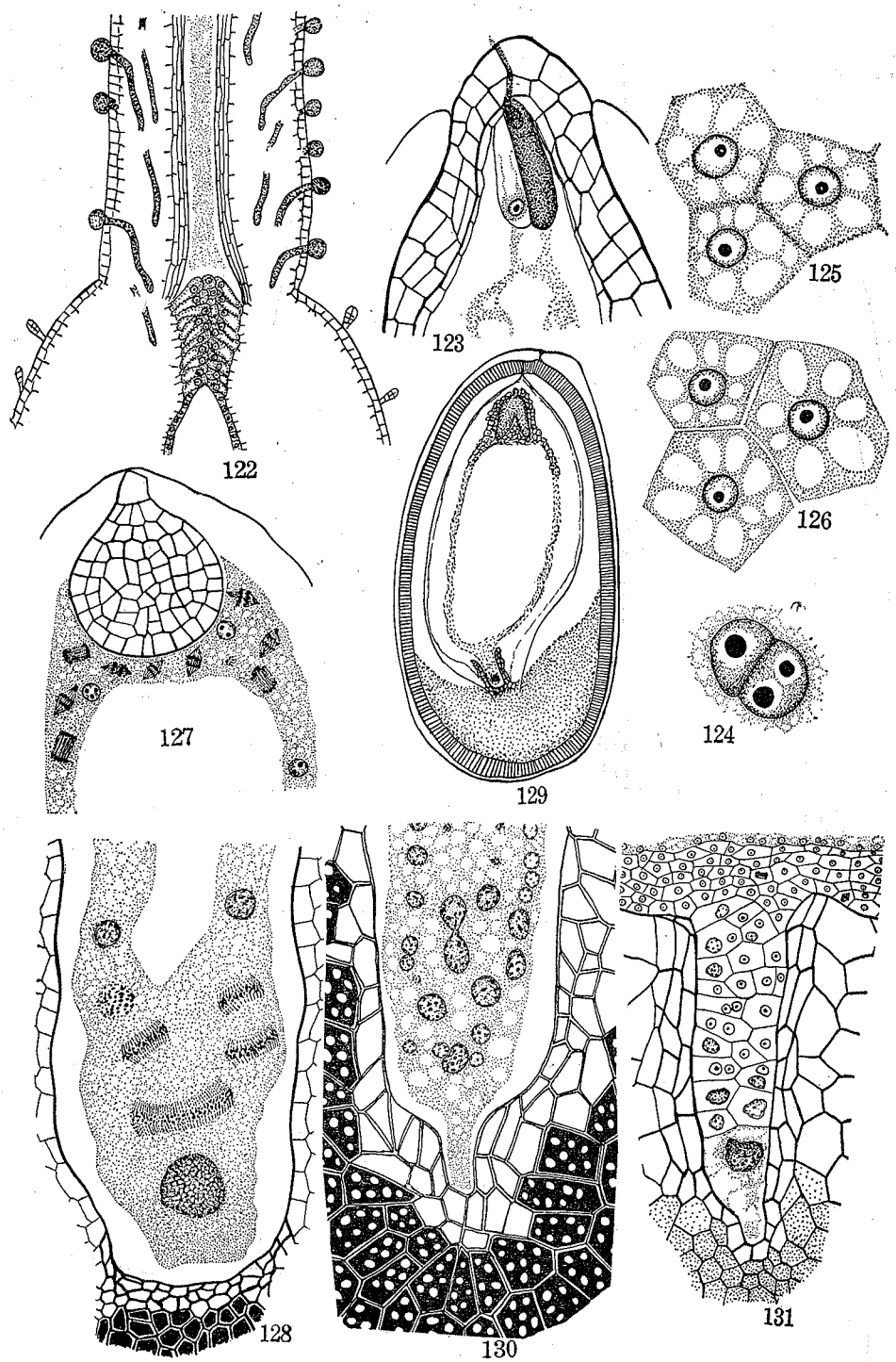
Fig. 107. L.s. ovary, ×50. Fig. 108. T.s. loculus of ovary, ×135. Fig. 109. Ovule with full grown megaspore mother cell, ×425. Fig. 110. Nucellus showing formation of linear tetrad, ×715. Fig. 111. A linear tetrad, ×715. Fig. 112. A T-shaped tetrad of megaspores, ×425. Fig. 113. Ovule showing first free nuclear division in the functional megaspore, ×425. Fig. 114. Nucellus with linear tetrad in which the second megaspore from the micropylar end is enlarging, ×715. Fig. 115. Mature ovule, ×355. Fig. 116. Nucellus of fertilisable ovule showing embryo-sac and socket of thick-walled cells, ×715. Figs. 117 and 118. Degenerating embryo-sacs, ×500. Fig. 119. Ovule with degenerating embryo-sac; note the starch grains in parietal cells, ×425. Fig. 120. A degenerating embryo-sac being penetrated by a pollen tube, ×715. Fig. 121. Glandular hairs from the ovary wall, ×135.

189). These cells might serve in the quick transport of water during the germination of seed. Similar cells were reported by Venkateswarlu (1937) in *Sonneratia*. Guilford and Fisk (1952) described that in *Mimulus*, the cells of the placenta and funicle by the side of the embryo become tracheidal. In the mature seed, the testa remains membranous. The tegmen consists of the palisade layer, the fringe tissue and the crushed remnants of the pigment layer.

Sterility

Sterility is common in species of *Dombeya*, *Sterculia* and *Guazuma*. This is ascribable to both infertile pollen grains as well as to degeneration of embryo-sacs. In *Guazuma tomentosa*, sometimes all the flowers of an inflorescence drop off without forming a single fruit. In *Dombeya spectabilis*, the flowers wither with all their parts in tact. The ovaries form conical woody 'fruits', 1–1½ cm. long, but only with abortive seeds. In *Sterculia* species also, very few fruits are developed. In all these species, the embryo-sacs in many ovules degenerate after reaching the 8-nucleate stage (Figs. 36, 61, 104, 117–120). In *Dombeya mastersii*, occasionally all the megaspores of a tetrad degenerate. Still the ovules continue to develop for some time and occur alongside with the normal ones in ovaries ready for pollination. In the process of degeneration of an embryo-sac, the synergids seem to be affected first, then the egg and lastly the polar nuclei. After all the cells have degenerated, the cytoplasm forms a deep staining mass and finally the ovule collapses.

In *Guazuma tomentosa*, sometimes degeneration of the embryo-sac commences before the flowers open. In a few cases, the pollen tubes were seen penetrating ovules in which the egg apparatus was already showing signs of degeneration (Fig. 120). In one case, a male nucleus was found in contact with the polar nuclei which alone were persisting in the embryo-sac. In such cases, the penetration of the pollen tube might stimulate the ovary to form the 'fruit' and the the ovule to develop into the 'seed' but since the egg had already degenerated, there would be no embryo and the seeds would be exembryonate. The presence of the male nucleus in contact with the polar nuclei makes probable the formation of some endosperm. An examination of a number of seeds from mature fruits of *Sterculia colorata* and *Pterospermum heyneanum* revealed that associated with seeds containing large embryos there were some as large as the normal seeds, with seed



FIGS. 122–131. Fertilisation, endosperm and seed development in Sterculiaceæ

Fig. 122. L.s. top of the ovary and part of the style of *Abroma augusta* showing stylar canal and germinating pollen grains. Note that the stylar canal is occluded by glandular cells at its base, ×45. Fig. 123. Micropylar part of nucellus and embryo-sac of *Abroma augusta*, showing entry of pollen tube, ×425. Fig. 124. Fusion of a male gamete with a polar nucleus in *Pentapetes phœnicea*, ×855. Figs. 125 and 126. Cell formation in endosperm of *Klienhovia hospita* by indentation, ×425. Fig. 127. Upper part of embryo-sac of *Pentapetes phœnicea* showing globular embryo, endosperm aggregation and free nuclear divisions, ×285. Fig. 128. Lower part of embryo-sac of young seed of *Pentapetes phœnicea* showing polyploid endosperm nuclei and their divisions, ×285. Fig. 129. L.s. developing seed of *Abroma augusta*, note the postament, ×15. Fig. 130. Lower part of embryo-sac of *Abroma augusta* surrounded by thick-walled tannin and starch-bearing cells; note the nuclear fusions in endosperm, ×355. Fig. 131. Same as above but from older seed; endosperm has become cellular; note the degenerating gigantic nucleus at lower end, ×135.

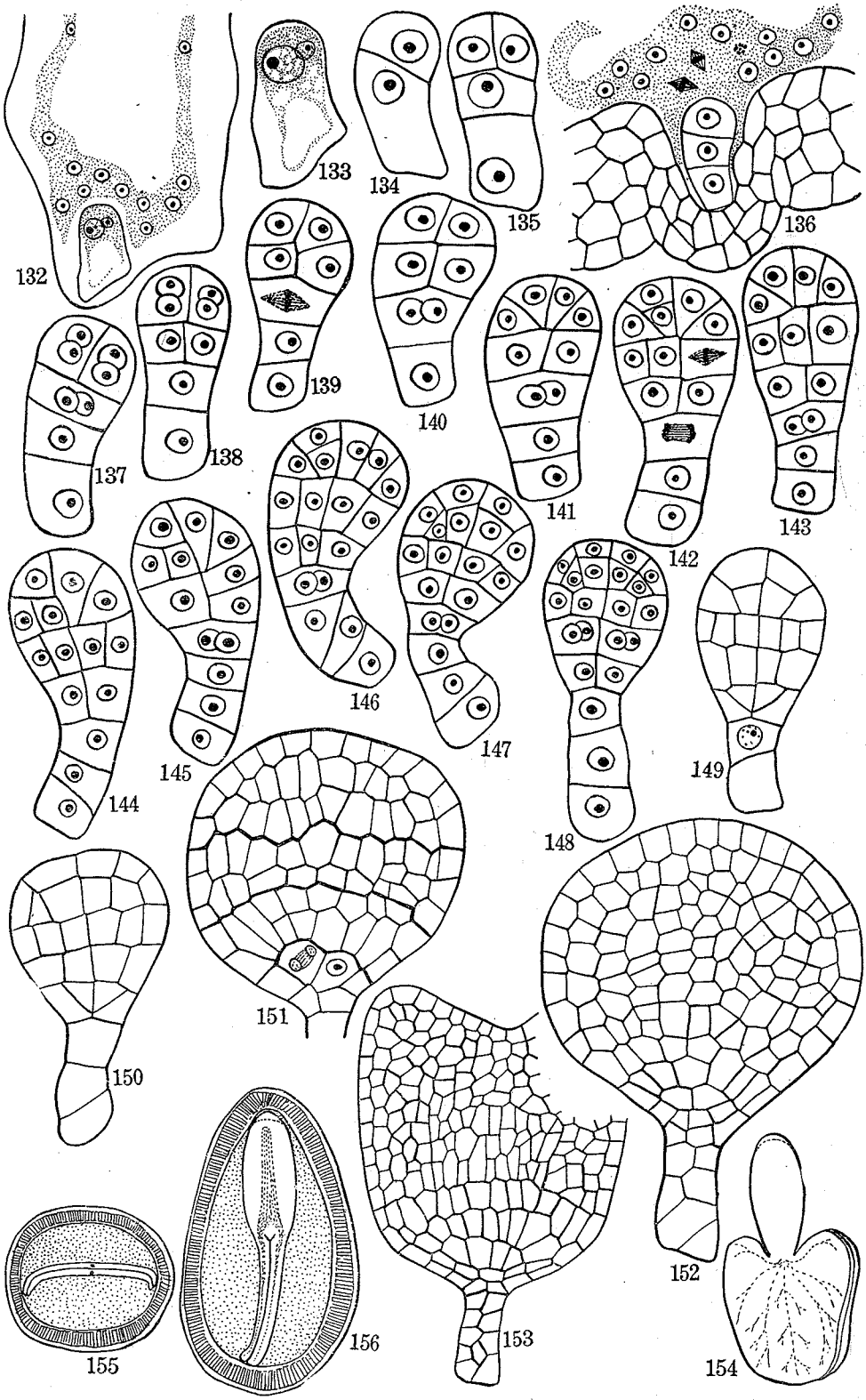
coats normally formed, which had only a large cavity inside and showed no trace of an embryo. In some cases, however, they showed a little endosperm.

Discussion

On the basis of several morphological and anatomical features like the predominance of pentacyclic flowers, presence of 3-bundled staminal traces, hood-like outgrowths for stamens, gynophore, cortical vascular system in the receptacle (*Pterospermum*) and apocarpy (*Sterculia*), the writer (C. V. Rao, 1952) regards Sterculiaceæ to be the most primitive family among the Malvales. This conclusion is supported by embryological findings. Smooth-walled pollen grains which are regarded by Wodehouse (1936) as more primitive than spinescent ones are found in 4 out of the 5 tribes of the family studied so far. Other features which indicate its primitiveness are: secondary increase in the sporogenous tissue of the anther, secondary increase in the sporogenous tissue of the ovule (*Pterospermum suberifolium*), multicellular archesporium with several functional cells, etc. The following seed characters exhibited by the family are also to be considered primitive according to the criteria of Netolitzsky (1926): crassinucellate ovules, 2–3 layered integuments which cover the straight nucellus and are separated from each other and from the nucellus by a cuticle, the unbranched vascular bundle of the raphe, early resorption of the nucellus, smooth testa, copious endosperm and embryo laden with food.

Among Sterculiaceæ, Sterculieæ stands apart from the rest of the tribes by its apetalous and unisexual flowers and apocarpous pistil. The nucellus of the developing seed in *Sterculia colorata* is consumed much earlier than in other genera and reticulate thickenings are seen on the inner epidermis of the inner integument. Netolitzsky (1926) remarks " delicate markings on the cell walls of the inner epidermis of the inner integument designate the seed as primitive within larger or smaller groups".

Among the remaining tribes, the genus *Pterospermum* seems to be the most primitive anatomically, morphologically and embryologically. The flowers are pentacyclic and floral parts other than the carpels do not show connation. The presence of hood-like outgrowths of the



FIGS. 132–156. *Abroma augusta*

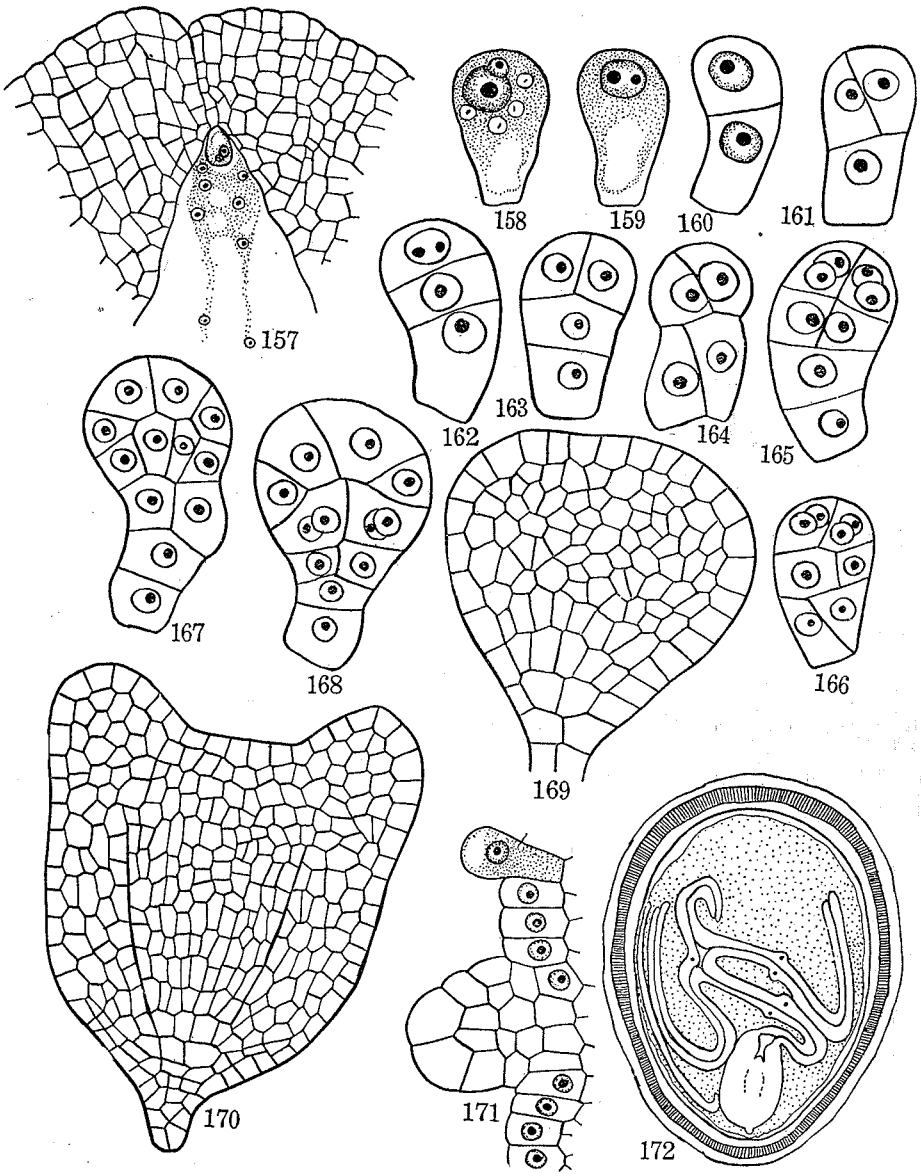
Fig. 132. Micropylar part of the embryo-sac with a few endosperm nuclei and egg in the process of fertilisation, ×355. Figs. 133–153. Various stages in the development of the embryo. Figs. 136 and 153, ×355; the rest, ×425. Fig. 154. Mature embryo, ×8. Figs. 155 and 156. T.s. and L.s. of mature seed, ×9.

connectives of stamens and the cortical vascular system of the gynophore are regarded as very primitive features (Parkin, 1951; Ozenda, 1952). Embryologically, the presence of multicellular archesporium in the ovule with a secondary increase of sporogenous tissue, several functional cells and development of double and triple embryo-sacs in an ovule, secondary increase in sporogenous tissue of the anther, etc., are primitive features. In other genera of Dombeyeæ (*Dombeya*, *Pentapetes*) and *Guazuma*, etc., the archesporium of the ovule is 1-celled. In *Buettneria*, the lateral stamens of the triplets of the outer whorl (present in the above genera) are suppressed. Embryologically also the presence of a placental obturator in this genus can be considered as a specialised feature. Helictereæ (*Helicteres* and *Klienhovia*) shows some advanced morphological and embryological features. The flowers are zygomorphic and in *Helicteres* they are not only tetracyclic but also the median stamens of the triplets of the outer whorl are suppressed. The pollen grains are triangular and flattened. The integuments cover the nucellus incompletely and glandular cells are present on the placenta which help in nourishing the pollen tubes. A hypostase is found in the nucellus of the developing seed. Netolitzsky (1926) considers smooth testa as more primitive than one with outgrowths. While the testa in all other genera is smooth, that of *Klienhovia* shows spinescent outgrowths from some of its epidermal cells. The Hermannieæ (*Melochia* and *Waltheria*) seems to be the most highly evolved tribe of the family. The flowers are typically tetracyclic and pentamerous in *Melochia*, while in *Waltheria* there is the reduction of carpels to one. The embryological features which support such a conclusion are: the direct functioning of the sporogenous cells of the anther (*Melochia*) and presence of plasmodial tapetum, both features being found in Malvaceæ, which is considered to be the most highly evolved family of Malvales.

Summary

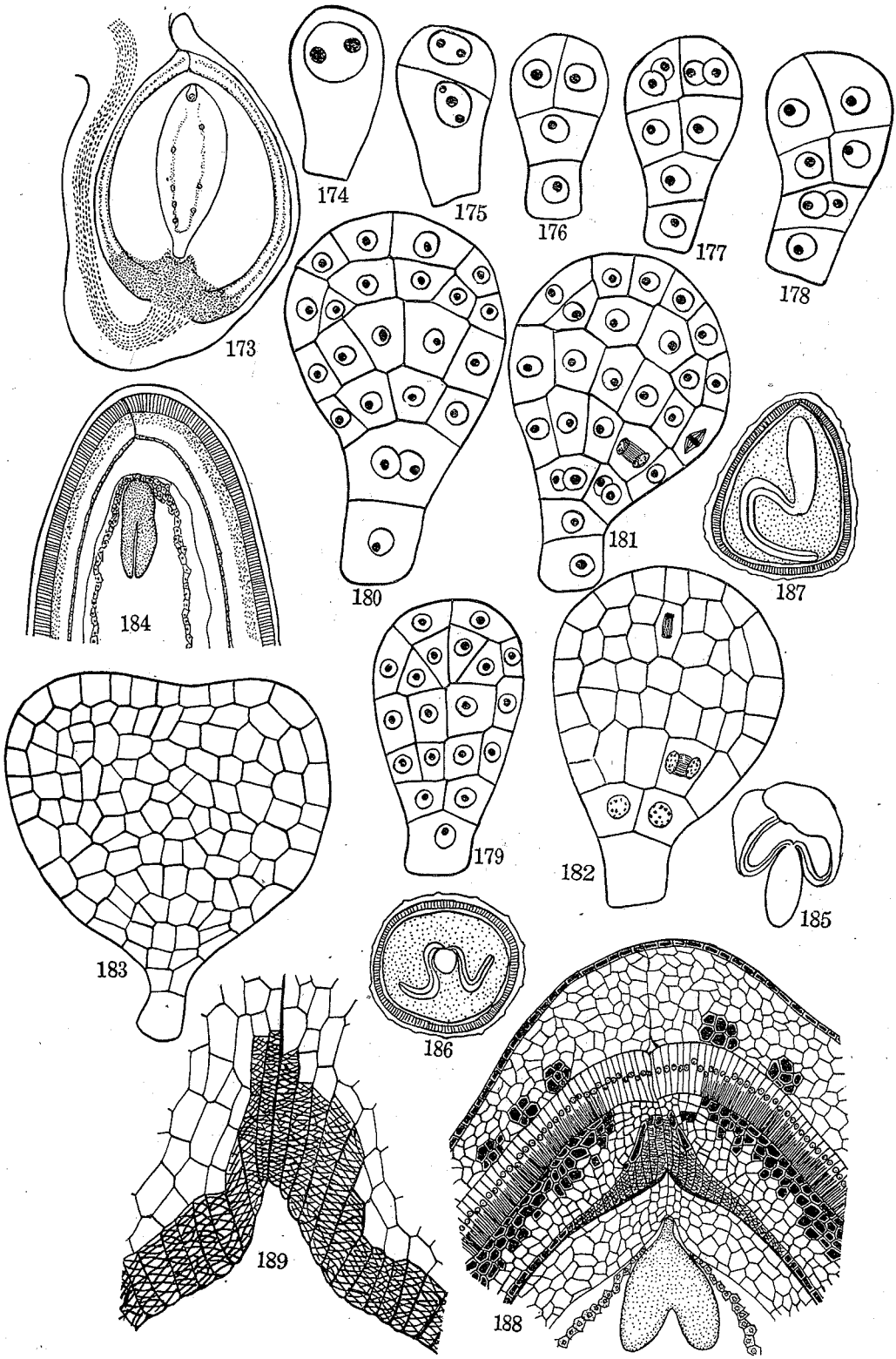
Development of the anther, pollen, ovule and embryo-sac has been studied in the following 10 species: *Sterculia colorata* Roxb., *S. fœtida* L., *Pentapetes phœnicea* L., *Dombeya spectabilis* Bojer., *D. mastersii* Hook., *Abroma augusta* L., *Guazuma tomentosa* Kunth., *Buettneria herbacea* Roxb., *Klienhovia hospita* L., and *Helicteres isora* L. Development of embryo was followed in *Pentapetes phœnicea*, *Abroma augusta* and *Klienhovia hospita* and seed development in *Buettneria herbacea* and *Helicteres isora*. Seed structure of *Sterculia colorata* and *Pterospermum heyneanum* is described and finally, the embryological features of the family are discussed.

The anther wall is 4–5 layered. The cells of the epidermis and connective accumulate tannin and sometimes starch grains. Dehiscence of the anther is brought about by fibrous endothecium and a



FIGS. 157–172. Embryo and seed development in *Klienhovia hospita*

Fig. 157. Upper part of nucellus with fertilised egg and micropylar aggregation of endosperm, ×200. Figs. 158–170. Various stages in the embryo development, ×425. Fig. 171. Suspensor and epidermal cells of root tip; note the papillate cells, ×355. Fig. 172. L.s. seed, ×30.



FIGS. 173–189. Development of embryo and seed in *Pentapetes phœnicea*

Fig. 173. L.s. young seed with fertilised egg and a few endosperm nuclei, ×50. Figs. 174–183. Various stages in development of embryo, ×425. Fig. 184. L.s. upper part of seed, ×30. Fig. 185. Entire embryo, ×8. Figs. 186 and 187. T.s. and L.s. mature seed, ×8. Fig. 188. L.s. upper part of the seed; note the tracheidal cells in the micropylar region, ×200. Fig. 189. Part of the above magnified, ×255.

well-defined stomium. The innermost layer of wall cells forms the tapetum of the secretory type. The sporogenous cells of the anther show a secondary increase. Microspore tetrads are mostly tetrahedral and cytokinesis takes places by furrowing. The pollen grains are shed in the 2-nucleate condition and their cytoplasm is packed with starch grains. The pollen grains are triangular and oblately flattened in Helictereæ, ellipsoidal in *Sterculia* and spherical in the rest. In the Dombeyeæ they are spinescent. They are triporate in all species and in *Buettneria* the germ pores are raised on papillate projections of the exine.

The ovules are crassinucellate, bitegmic and anatropous. A zig-zag micropyle is formed by both the integuments in *Dombeya*, *Pentapetes*, *Sterculia* and *Klienhovia*. In *Guazuma*, *Buettneria* and *Abroma* it is formed only by the outer integument, the inner covering less than half of the nucellus. In *Helicteres*, both the integuments stand low and the nucellus of the fertilisable ovule protrudes nakedly. A nucellar cap is formed in all species. Cells in the chalaza accumulate tannin and starch and develop thick walls. In *Abroma* a postament develops in the seed and in *Helicteres* a hypostase is organised in the nucellus of the young seed.

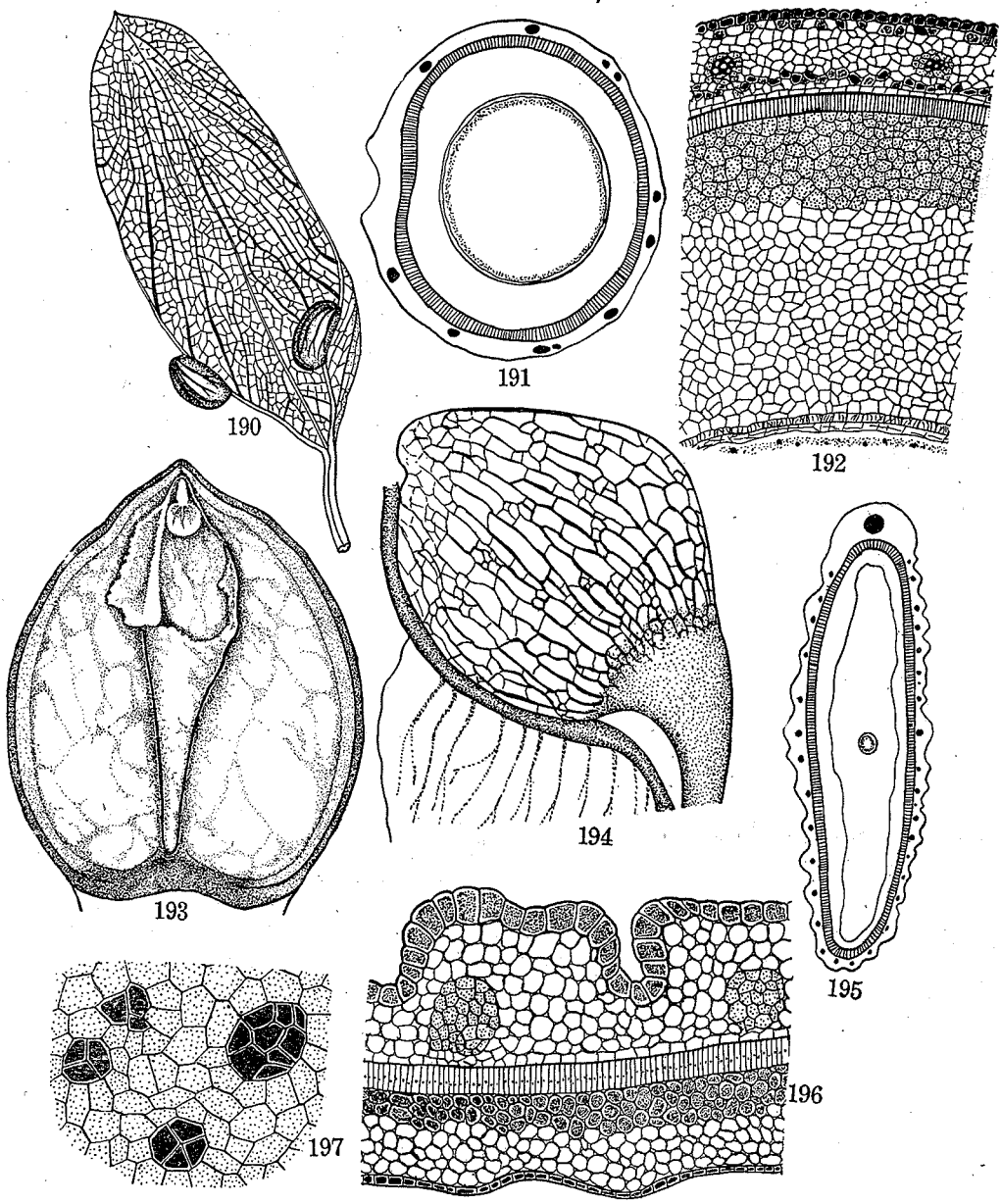
The archesporium of the ovule is multicellular, but only one cell functions. Megaspore tetrads are mostly linear and embryo-sac develops according to *Normal*-type. The synergids are hooked and in *Pentapetes* and *Abroma* they show circular deep staining patches near the micropylar ends which may be analogous to filiform apparatus. Polar nuclei remain separate till the time of fertilisation. The three antipodals are ephemeral. A case of an embryo-sac with reversed polarity was noticed in *Helicteres isora*.

In *Buettneria herbacea* there is a hairy placental obturator for the upper tier of ovules. The cells of the funicle in *Sterculia colorata* and *Abroma augusta* are radially elongated and richly protoplasmic and seem to serve in nourishing the pollen tubes. Similar cells are seen at the base of the funicle in *Helicteres*.

Fertilisation is porogamous. The endosperm is nuclear and becomes cellular at a late stage in seed development by the process of indentation. Large polyploid nuclei are found in the antipodal part of the endopserm in *Pentapetes* and *Abroma*. The mature seeds are endospermic but devoid of perisperm.

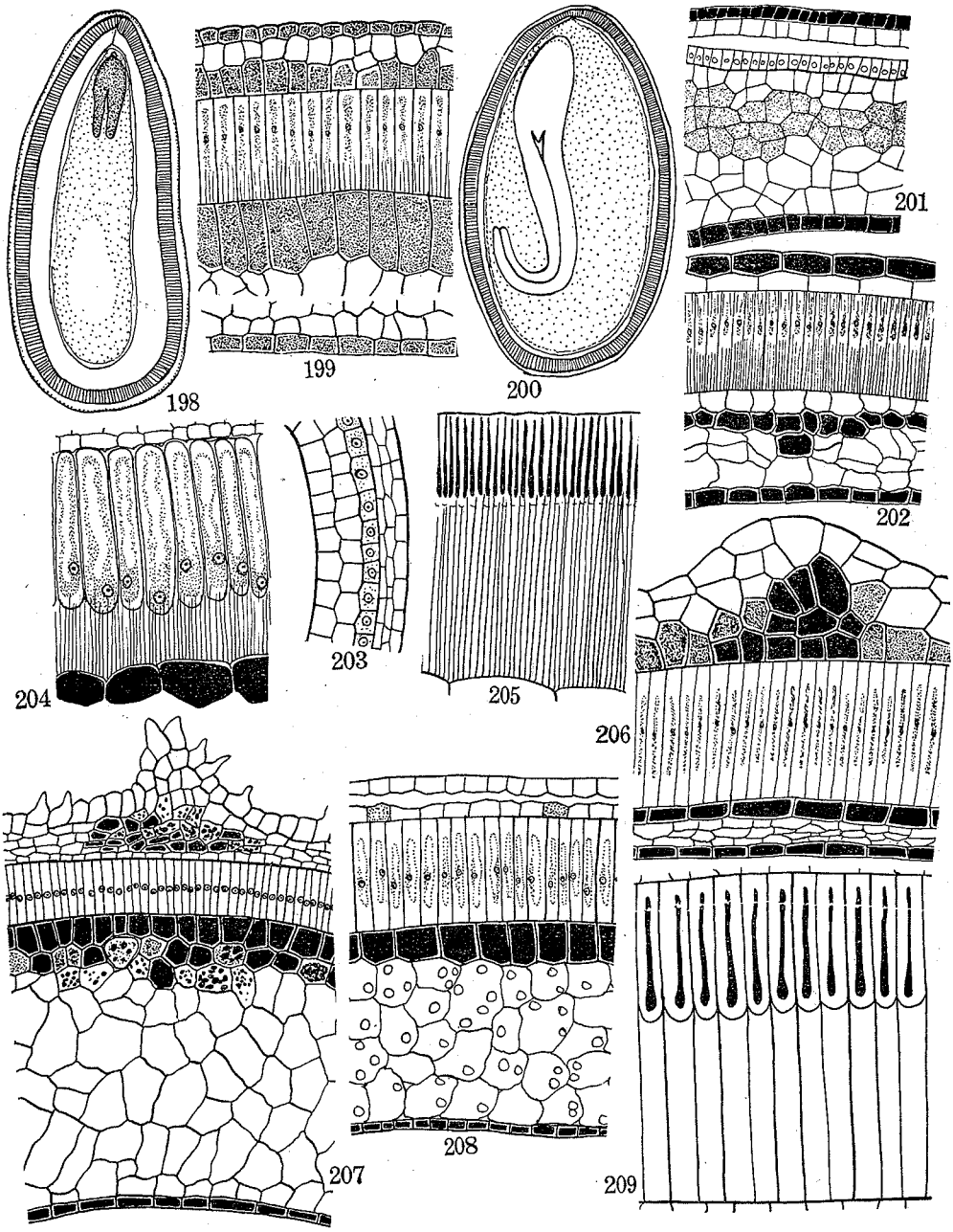
Development of the embryo conforms to the *Urtica* variation of the Asterad Type. The suspensor is small.

The outer integument develops into a membraneous testa. In *Pterospermum* and *Sterculia* it is thicker than in others and shows



FIGS. 190–197. Seed and seed coat structure in Sterculiaceæ

Fig. 190. A dehisced fruitlet of *Sterculia colorata*, ×1. Fig. 191. T.s. seed of *Sterculia colorata*, ×5. Fig. 192. Seed coats of *Sterculia colorata*; note the delicate markings on the inner epidermis of the inner integument, ×75. Fig. 193. L.s. seed of *Pterospermum heyneanum*, ×3. Fig. 194. Surface view of the seed of *Pterospermum heyneanum*; note the integumentary vascular bundles, ×3. Fig. 195. T.s. seed of *P. heyneanum*, ×6. Fig. 196. Seed coats of the same in sectional view, ×75. Fig. 197. Surface view of the testa of *Pentapetes phœnicea* showing groups of tannin-bearing cells, ×135.



FIGS. 198–209. Seed and seed coat structure in Sterculiaceæ

Fig. 198. L.s. seed of *Buettneria herbacea*, ×10. Fig. 199. Seed coats of *Buettneria herbacea*, ×135. Fig. 200. L.s. seed of *Helicteres isora*, ×30. Figs. 201 and 202. Seed coats of *Helicteres isora* from young and somewhat old seeds. Fig. 201, ×535; Fig. 202, ×135. Figs. 203–206. Integuments and seed coats of *Pentapetes phœnicea*, ×355. Fig. 207. Seed coats of *Klienhovia hospita*, ×75. Figs. 208 and 209. Seed coats from young and old seeds of *Abroma augusta*. Fig. 208, ×135; Fig. 209, ×235.

integumentary vascular bundles. In *Klienhovia* some of the cells of the testa become papillate. The outer epidermis of the inner integument develops into the palisade layer and 1 or 2 layers of cells below it into the pigment layer. The next few layers of parenchymatous cells become crushed in seed and the innermost layer persists in the form of fringe tissue.

The embryological features of the family, like those of floral anatomy, show that the family is the most primitive among Malvales. On these data the tribes of the family can be arranged in the following evolutionary sequence: Sterculieæ, Dombeyeæ, Buettnerieæ, Helictereæ and Hermannieæ.

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