

EMBRYOLOGICAL STUDIES IN COMPOSITAE

II. HELENIEAE

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INTRODUCTION

The present paper deals with the embryology of *Tagetes patula*, *Flaveria australasica* and *Gaillardia picta* which belong to the embryologically little investigated tribe Helenieae. Our previous knowledge of the tribe is limited to a few observations on *Tagetes signatus* by Dahlgren (1920) and on *Gaillardia pulchella* and *Gaillardia aristata* by Rosen (1944), who reported Fritillaria type of embryo sac development. In no other member of the tribe Helenieae embryo sac development has been described and Rosen's account of *Gaillardia* is rather meagre and does not include any observations on microsporogenesis, male gametophyte, development of the endosperm and embryo.

The materials of *Tagetes patula* and *Gaillardia picta* were collected from plants cultivated in the Botanical Garden of the Andhra University and that of *Flaveria australasica* was collected at Hyderabad by Mr. N. Ramaiah, College of Science, Osmania University. Formalin-acetic-alcohol or acetic-alcohol was used as fixative. Customary methods of dehydration and infiltration were followed. The sections were stained either with Delafield's haematoxylin or safranin and fast-green.

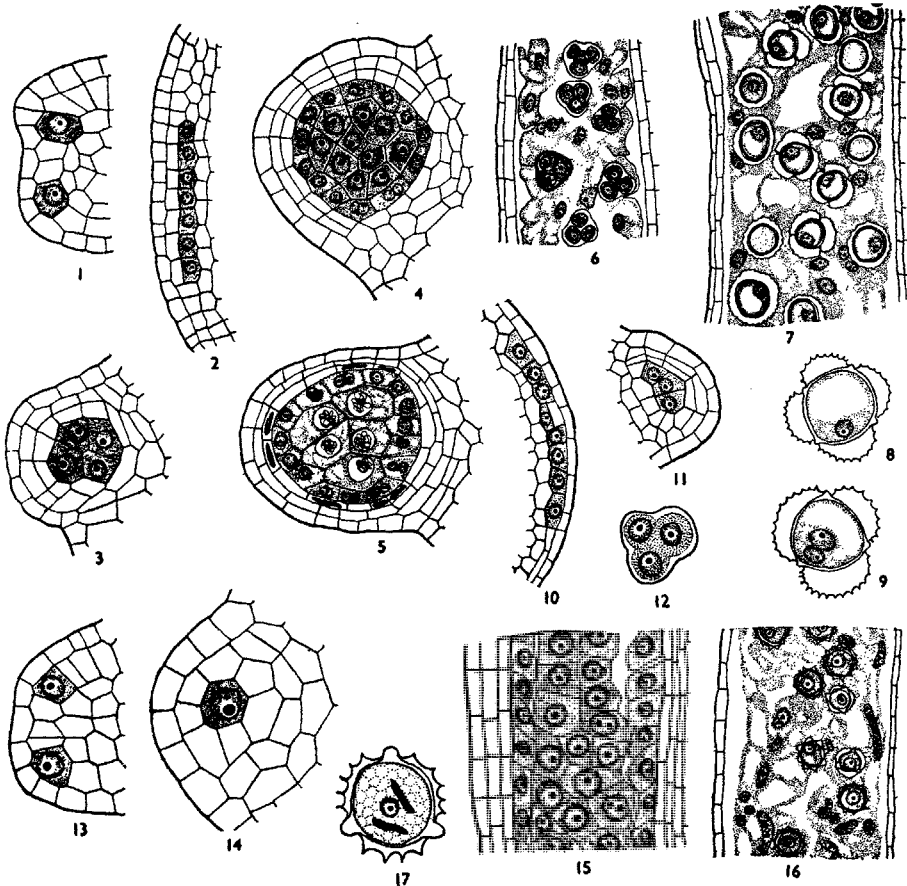
OBSERVATIONS

Organogeny.—Both bisexual and female flowers are found in the same inflorescence. In bisexual flowers the organogeny takes the following sequence: petals, stamens and sepals followed by gynoecium and in the female flowers the sequence is petals, sepals and gynoecium.

Microsporogenesis and Male Gametophyte.—The development of the anther and pollen is closely similar in all the three species investigated and resembles that described in *Launaea pinnatifida* (Venkateswarlu and Maheswari Devi, 1955). The structure of the anther shows the epidermis, two wall layers and tapetum surrounding the sporogenous tissue (Figs. 1-7, 10, 11, 13-16). Here also the fibrous endothecium is not differentiated.

A true periplasmodial type of anther tapetum is found (Figs. 6, 7, 16). Unlike *Launaea pinnatifida* where the nuclei of the periplasmodium degenerate soon, in the three Helenieae studied here they remain healthy for a long time (Figs. 7, 16). The primary sporogenous cells undergo a few mitotic divisions in all directions and give rise to a moderately extensive sporogenous tissue (Figs. 3-5, 11, 15). The pollen mother cells divide in a simultaneous manner. The two meiotic divisions take a normal course and bilateral as well as tetrahedral pollen tetrads are produced. Cytokinesis is by furrowing (Fig. 12).

The mature pollen grains are spherical, echinate and the spines have broad bases (Figs. 9, 17). Usually there are three germ pores, but in *Tagetes patula* a few

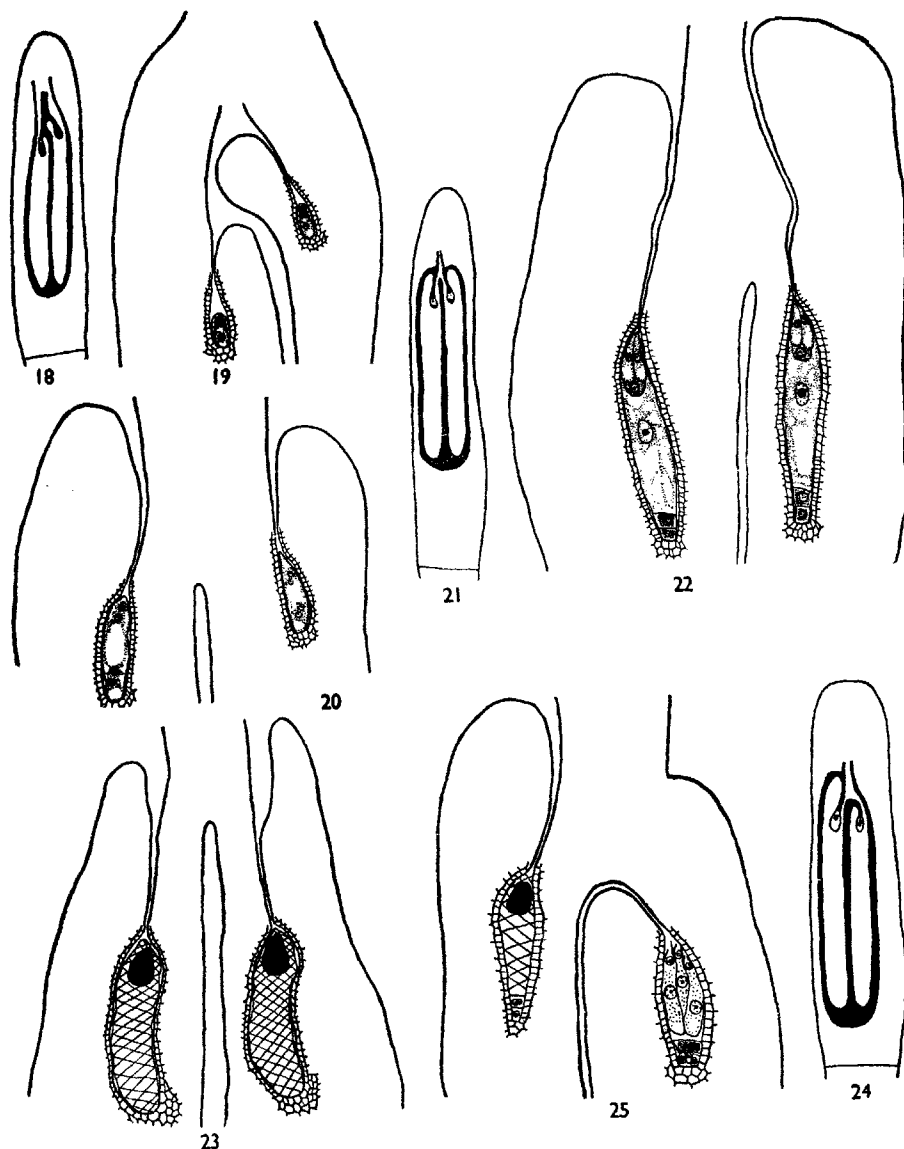


Figs. 1-9—*Tagetes patula*. Fig. 1. T.s. of an anther half showing primary archesporium. $\times 707$. Fig. 2. L.s. anther lobe showing primary parietal layer and the primary sporogenous layer. $\times 527$. Figs. 3-5. Anther lobes at various stages of its development. $\times 707$. Figs. 6, 7. L.s. part of an anther lobe showing the periplasmoidal tapetum surrounding the pollen tetrads and 1-nucleate pollen grains respectively. $\times 340$. Fig. 8. A 1-nucleate pollen grain showing four germ pores. $\times 707$. Fig. 9. A 2-nucleate pollen grain. $\times 707$.

Figs. 10-12—*Flaveria australasica*. Fig. 10. L.s. anther lobe showing primary archesporium. $\times 388$. Fig. 11. T.s. anther lobe showing sporogenous tissue and two wall layers. $\times 527$. Fig. 12. Tetranucleate pollen mother cell showing cytokinesis by furrowing. $\times 707$.

Figs. 13-17—*Gaillardia picta*. Fig. 13. T.s. anther half showing primary archesporium. $\times 527$. Fig. 14. T.s. anther lobe showing primary parietal and sporogenous layers. $\times 707$. Fig. 15. L.s. part of an anther lobe at the stage when the tapetal cells become binucleate. $\times 527$. Fig. 16. L.s. part of anther lobe showing periplasmoidal tapetum surrounding 1-nucleate pollen grains. $\times 340$. Fig. 17. 3-nucleate pollen grain. $\times 707$.

pollen grains with four germ pores such as reported in *Tridax procumbens* and *Blumea laciniata* by Banerji (1940, 1942) were encountered (Fig. 8). However,



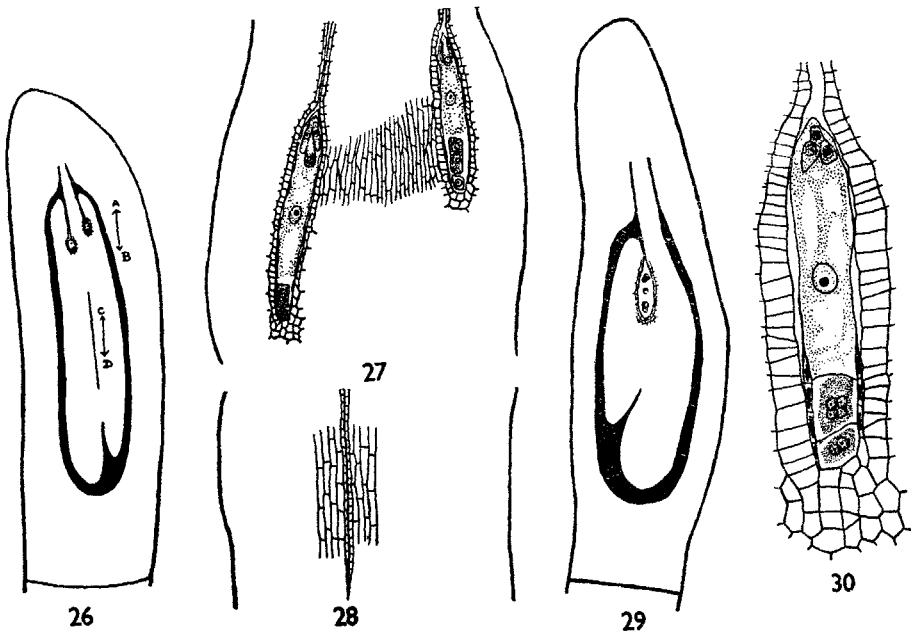
FIGS. 18-25—*Tagetes patula*. L.s. ovaries showing two ovules. Fig. 18. L.s. ovary showing two ovules facing each other. $\times 7$. Fig. 19. Part of ovules from Fig. 18 enlarged, a magaspore tetrad is developed in each of them. $\times 63$. Fig. 20. L.s. part of two ovules contained in the same ovary and showing a 4-nucleate embryo sac in each of them. $\times 107$. Fig. 21. L.s. ovary containing two ovules arranged back to back. $\times 5$. Fig. 22. The two ovules in Fig. 21 enlarged. These show a mature embryo sac in each of them. $\times 107$. Fig. 23. L.s. two ovules contained in the same ovary, both ovules containing cellular endosperm and advanced embryos. $\times 63$. Fig. 24. L.s. ovary with two ovules. The micropylar side of one ovule faces the funicle side of the other. $\times 10$. Fig. 25. The two ovules in Fig. 24 enlarged. One of these shows three embryo sacs in it, while in the other a young embryo and cellular endosperm are already formed. $\times 63$.

none with six germ pores such as reported in *Dahlia* by Wodehouse (1931) has been met with during the present study. The pollen grains are 3-nucleate at the time of shedding (Fig. 17).

Ovary and Ovule.—As in all other Compositae the ovary of *Tagetes patula*, *Flaveria australasica* and *Gaillardia picta* is bicarpellary, syncarpous, unilocular and inferior with a single basal ovule which is anatropous, unitegmatic and tenuinucellate.

The integument is massive and about 5–8 celled thick at the sides and 11–16 celled thick in the basal region of the ovule in *Tagetes patula*, 4 or 5 celled thick at the sides and 8–10 celled in the basal region of the ovule in *Flaveria australasica* and 4–7 celled thick towards the sides and 6–9 celled in the basal region of the ovule in *Gaillardia picta* at the time when the archesporial cell is fully differentiated (Figs. 40, 57). In the advanced ovules the thickness of the integument both on the sides as well as in its lower region increases very considerably. In the fully developed seed the integument becomes completely crushed and becomes reduced to a thin membrane.

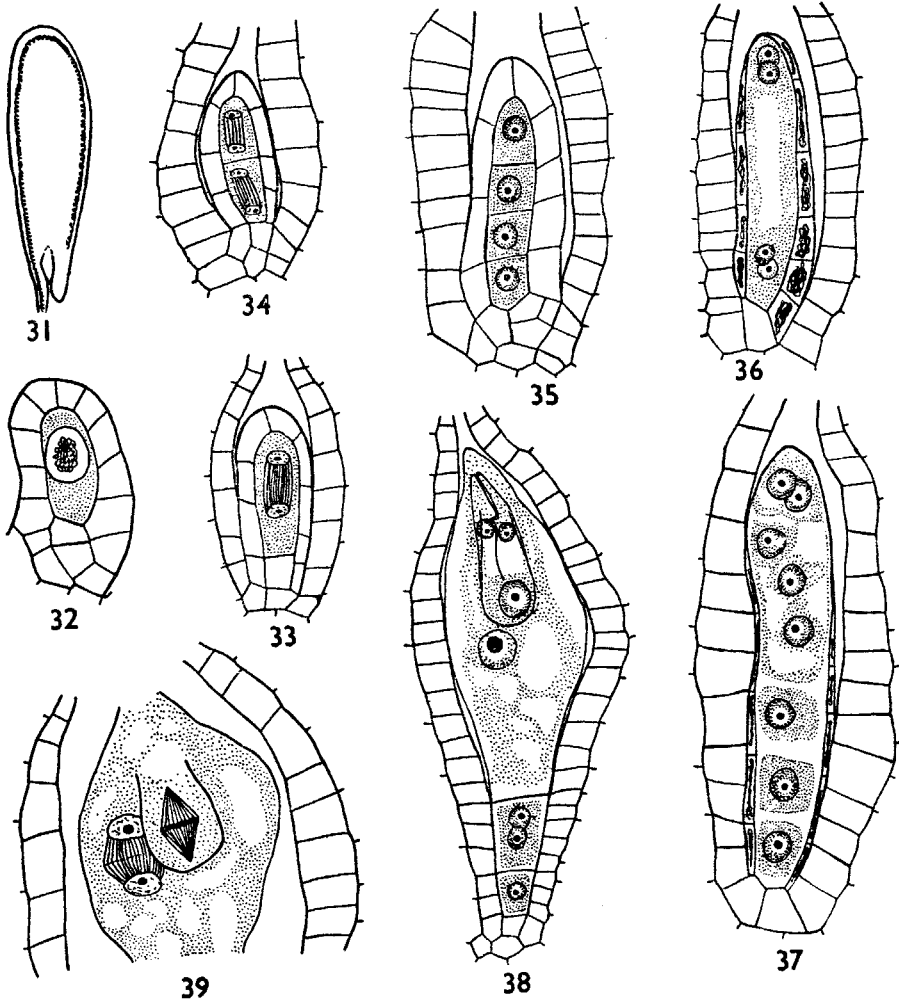
A feature of special interest is the exceptional occurrence of two ovules per ovary encountered in 14 out of 485 ovaries of *Tagetes patula* studied during the course of this investigation. In three of these the two ovules were seen to be partially fused while in the remaining eleven two separate ovules with the funicles fused at the base were found (Figs. 18–25). The two ovules in these cases were



Figs. 26–30—*Tagetes patula*, cases of two ovules contained in the same ovary and showing fusion.

Fig. 26. L.s. ovary with two ovules fused back to back except at the base and a part in the middle. The two ovules, though fused, show one embryo sac in each. $\times 20$. Fig. 27. Part marked A-B in Fig. 26 enlarged to show details. $\times 100$. Fig. 28. Part marked C-D in Fig. 26 enlarged to show details. $\times 100$. Fig. 29. L.s. of ovary containing two ovules fused more intimately than in the case shown in Fig. 26, only one embryo sac is found in the fused structure. $\times 30$. Fig. 30. Embryo sac contained in the fused ovule shown in Fig. 29 enlarged to show details of structure. The egg apparatus is degenerating. $\times 320$.

found situated either back to back (i.e. funicles being adjacent to one other, Figs. 20–23) or face to face (the sides opposite to the funicles being adjacent to one other, Figs. 18, 19) or the funicle side of one ovule is adjacent to the side away from the funicle of the second ovule (Figs. 24, 25). In all these cases the embryo sacs and the embryos were found to develop normally (Figs. 18–23). Usually the stage of development of the embryo sac is the same in both the ovules (Figs. 18–23). However, in one case, one of the two ovules contained in the same ovary showed an embryo with octants, while, in the other, three fully formed embryo sacs were found (Figs. 24, 25).



Figs. 31–39—*Flaveria australasica*. Fig. 31. Ovule showing integumentary vascular trace. $\times 15$. Figs. 32, 33. L.s. nucellus showing megaspore mother cell in meiotic prophase I and telophase I. $\times 790$. Fig. 34. Dyad cells in meiotic telophase II. $\times 790$. Fig. 35. Megaspore tetrad. $\times 790$. Fig. 36. 4-nucleate embryo sac with degenerating nucellar epidermis. $\times 790$. Figs. 37, 38. Young and mature embryo sacs respectively. Fig. 37 $\times 790$ and Fig. 38 $\times 436$. Fig. 39. The integumentary tapetum and the upper part of the embryo sac showing the first division of the fertilized egg and primary endosperm nucleus. $\times 790$.

In one case the two ovules in the same ovary were found in a completely fused state at the apex and the base and also for a considerable length in the middle. In the latter portion, on close examination, it was found that the outermost layer of the cells of the ovules were found to be in very close approximation with each other. The two ovules contained fully developed embryo sacs (Figs. 26-28).

Figs. 29 and 30 show a very interesting case. In the ovary sketched, there is a single structure which represents two ovules as can be seen from the two protrusions in its basal region and only one embryo sac is found in this structure. In this embryo sac the antipodals and the secondary nucleus are in a healthy condition, while the cells of the egg apparatus at the micropylar pole of the embryo sac are in a degenerating stage (Figs. 29, 30).

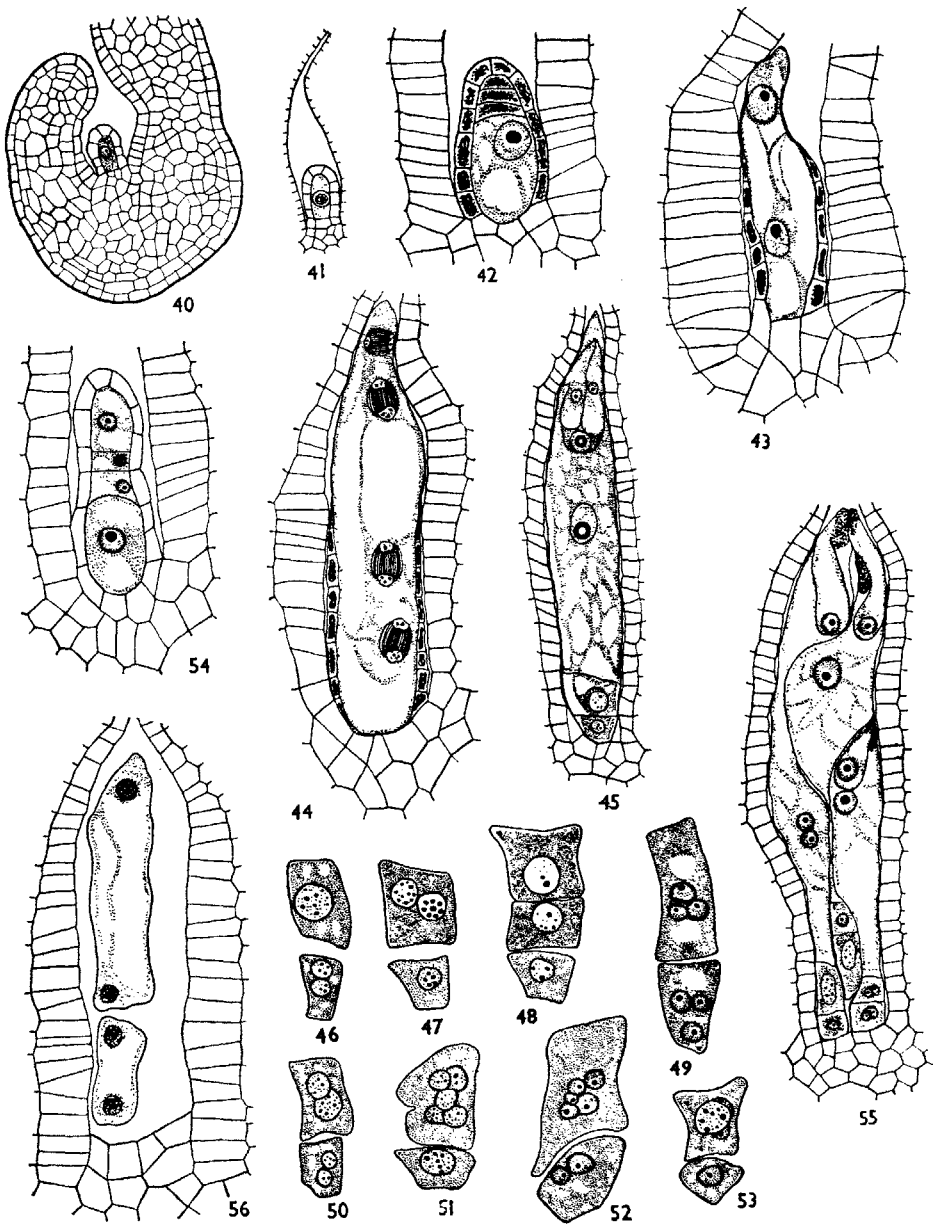
The ovules in the above exceptional cases also show integumentary vascular traces such as recorded in the ovules of the uniovulate ovary of *Tagetes patula* (Venkateswarlu, 1941). In *Gaillardia picta*, however, the ovule does not show an integumentary vascular trace.

Megasporogenesis and Female Gametophyte.—In *Tagetes patula* and *Flaveria australasica* the primary archesporium consists of a single hypodermal cell. It enlarges and becomes the megaspore mother cell without cutting off a parietal cell. A linear tetrad is formed after two meiotic divisions and the chalazal megaspore develops into the 8-nucleate embryo sac (Figs. 31-38, 40-45). The synergids are hooked (Figs. 38, 45). There is a great variation in the number of the antipodal cells and in the number of nuclei in an antipodal cell, a feature met with in many other members of Compositae such as *Eclipta erecta* (Bhargava, 1935), *Bidens leucanthus* (Dahlgren, 1920), *Zinnia grandiflorum* (Palm, 1931), *Xanthium spinosum* (Dahlgren, 1920), *Helianthus annuus* (Tackholm, 1916; Dahlgren, 1924), *Blumea laciniata* (Banerji, 1942), *Antennaria* and *Gnaphalium* (Schnarf, 1931), *Mikania scandens*, *Ageratum conyzoides* (Mitra, 1947), *Eupatorium cannabinum*, *Ageratum mexicanum*, *Erigeron*, *Solidago* and *Aster* (Schnarf, 1931). The number of the antipodal cells in *Tagetes patula* and *Flaveria australasica* varies from two to three. Where three antipodals occur, each of them is uninucleate (Figs. 37, 48). In such cases of *Flaveria australasica* when only two antipodal cells are present, one of them is binucleate. In *Tagetes patula*, when two antipodal cells are present, the number of nuclei in each cell varies from one to six (Figs. 46-53). Usually the antipodals persist even up to the formation of a mature embryo (Figs. 73, 74).

Usually only one embryo sac is developed in each ovule of *Tagetes patula*, but in a few cases two or three embryo sacs were found. No cases of ovules with more than one archesporial cell or megaspore mother cell were met with but sometimes megaspore tetrads with more than one megaspore developing further were encountered (Fig. 54). Therefore it is probable that the extra embryo sacs are formed due to further development of more than one megaspore of a tetrad. These double and triple embryo sacs show normal structure characteristic of the species and are found to be in a perfectly healthy condition (Figs. 54, 55). In one case with two binucleate embryo sacs in an ovule both the embryo sacs were found in a degenerating condition (Fig. 56).

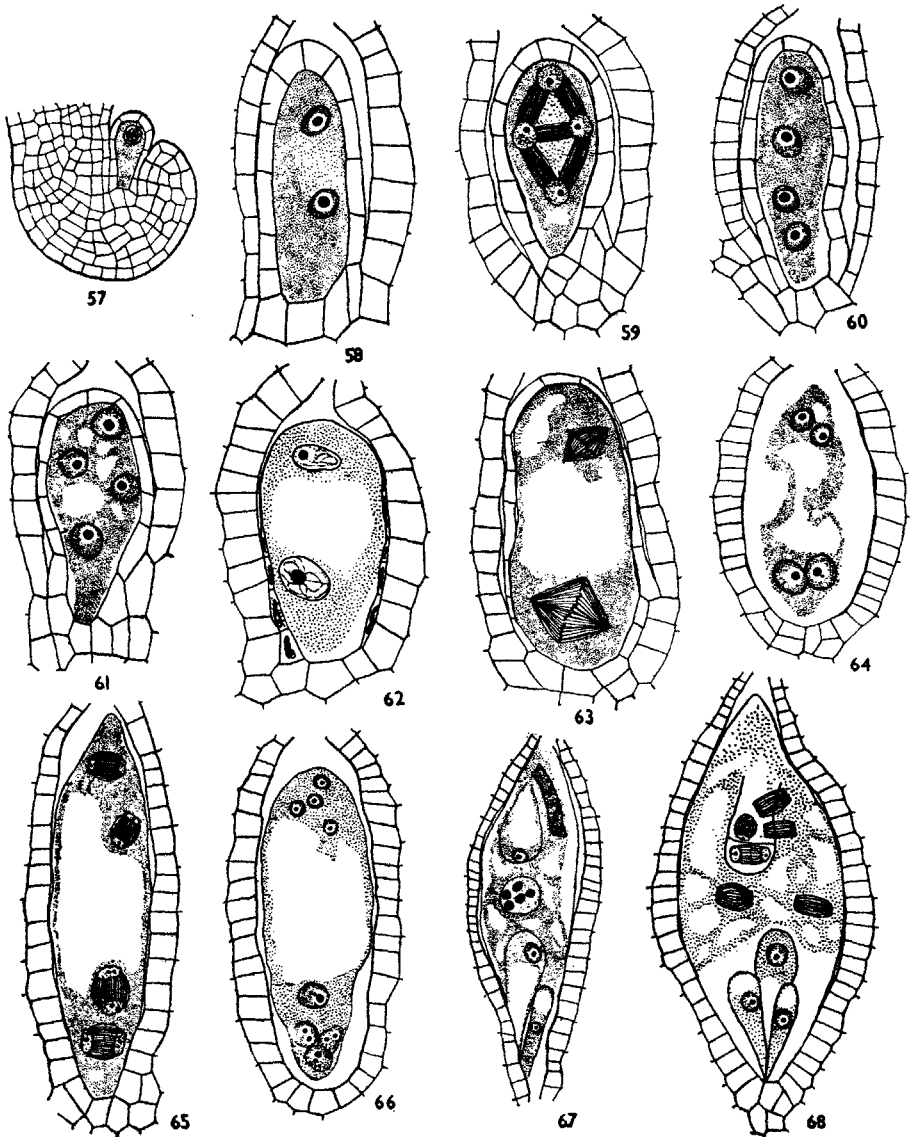
In *Gaillardia picta* the embryo sac develops according to the *Fritillaria* type. The megaspore mother cell undergoes the usual meiotic divisions unaccompanied by any wall formation and becomes tetranucleate. In some cases the four nuclei are arranged one at either pole and one on each side while in other cases they form a linear row (Figs. 57-61). Whatever may be the initial position they ultimately take 1+3 arrangement, three at the chalazal end and one at the micropylar end. These two groups are separated by vacuoles. All the four nuclei take part in the formation of the embryo sac.

The three nuclei at the chalazal end fuse together thus resulting in a secondary 2-nucleate embryo sac with a single large-sized triploid chalazal nucleus and a smaller haploid micropylar nucleus. The two nuclei then divide to give rise to the



Figs. 40-56—*Tagetes patula*. Figs. 40, 41. L.s. young ovules showing primary archesporial cell and megaspore mother cell respectively. $\times 213$. Fig. 42. L.s. ovule showing a linear tetrad. The nucellar epidermal cells begin to degenerate. $\times 527$. Figs. 43-45. Stages in embryo sac development. Figs. 43, 44. $\times 527$ and Fig. 45. $\times 213$. Figs. 46-53. Variations in the antipodals. $\times 527$. Fig. 54. A linear tetrad with chalazal and micropylar megaspores developing further. $\times 527$. Fig. 55. Two 2-nucleate embryo sacs in the same ovule, both are degenerating. $\times 527$. Fig. 56. Three fully formed embryo sacs in an ovule. $\times 213$.

secondary 4-nucleate and then the 8-nucleate stage. Here we have four haploid nuclei at the micropylar end and four triploid nuclei at the chalazal end (Figs. 62-67). The nuclei of the micropylar quartet are smaller in size than those of the chalazal. Three of them form the egg apparatus while the fourth becomes the upper polar nucleus. The egg shows the characteristic basal nucleus and a terminal vacuole. The two synergids are pear-shaped and show a basal vacuole with the nucleus situated above it. From the lower quartet one of the nuclei migrates to the



Figs. 57-68—*Gaillardia picta*. Figs. 57-67. Various stages in the development of the Fritillaria type of embryo sac. Fig. 68. L.s. embryo sac showing young embryo, dividing endosperm nuclei and persistent antipodals. Fig. 57, $\times 194$; Figs. 58-63, $\times 527$; Figs. 64-67, $\times 536$ and Fig. 68. $\times 172$.

centre and forms the lower polar nucleus which later fuses with the upper polar nucleus resulting in a tetraploid secondary nucleus. The remaining three nuclei at the chalazal end form the antipodals. The central antipodal cell is egg-like in appearance while the other two resemble the synergids in their form. Thus the antipodals simulate the egg apparatus in appearance (Figs. 67, 68). Two of the antipodals persist till a few endosperm nuclei are formed, while the third, usually the centrally placed one, persists till even an advanced embryo is formed. Owing to insufficient material, Rosen described the structure and behaviour of the antipodals in *Gaillardia pulchella* and *Gaillardia aristata* in early stages only and most probably in these two species also they persist as in *Gaillardia picta*.

Fertilization.—In *Tagetes patula*, *Flaveria australasica* and *Gaillardia picta* fertilization is porogamous. The pollen tube passes between the egg and one of the synergids. The contents of the pollen tube are discharged into one of the synergids through a terminal pore. Details of the process are followed only in *Tagetes patula*. In the embryo sac the male gametes lose their rod-shaped form. They show a somewhat coiled thread-like structure surrounding a nucleolus-like body when they are within the egg cell and within the secondary nucleus (Fig. 69). The same has been recorded previously in *Crepis capillaris* by Gerassimova (1933). The nucleolus-like structure increases in size and gradually becomes applied to the egg nucleus (Fig. 70). Gradually the male and female nuclei fuse with each other and become indistinguishable as separate entities. Triple fusion and syngamy take place more or less simultaneously. In one case, however, triple fusion was completed earlier than syngamy (Fig. 70). After fertilization the embryo sac increases in size, while the synergids become more and more vacuolated.

In *Gaillardia picta* the secondary nucleus is tetraploid and after fusion with the male gamete it becomes pentaploid (Fig. 67). The pollen tube in *Tagetes patula* and *Gaillardia picta* persists till the first division of the fertilized egg is completed, while in *Flaveria australasica* it is not persistent and disappears.

Endosperm.—The first division of the primary endosperm nucleus is completed slightly earlier than that in the fertilized egg and is not accompanied by the formation of a cell wall.

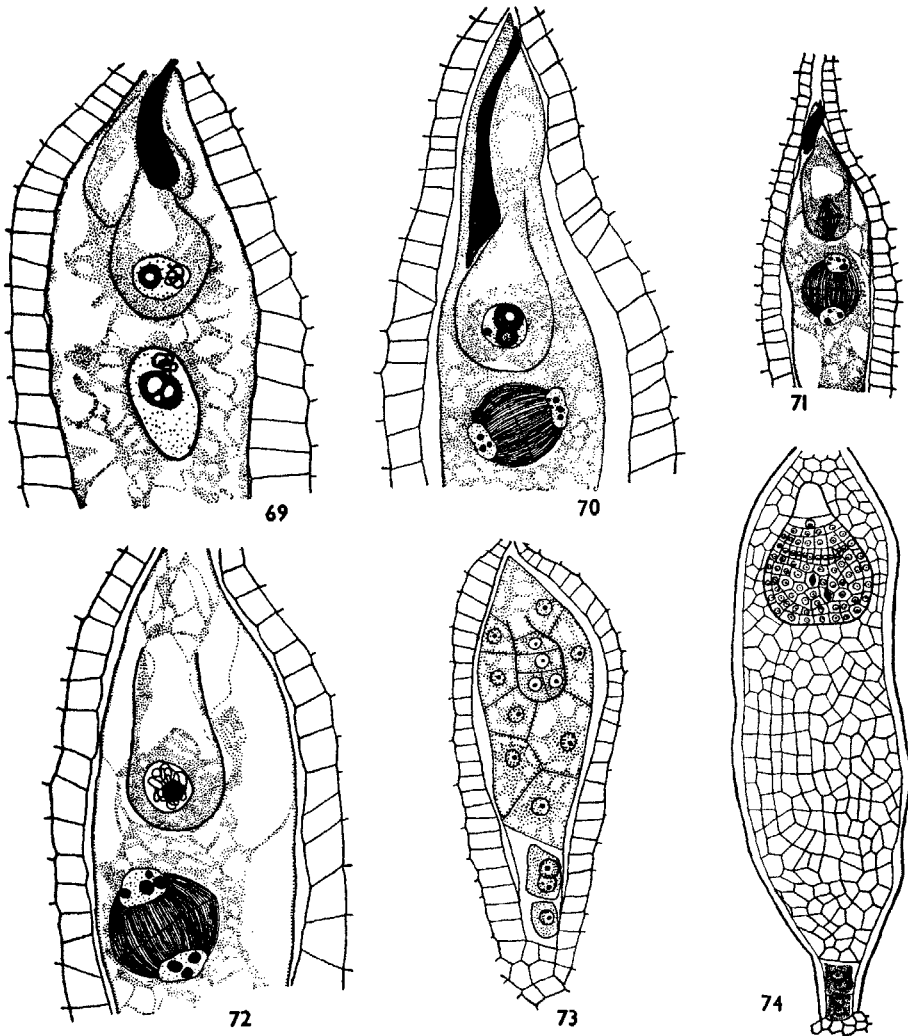
In *Tagetes patula* the orientation of the spindle of the first division of the primary endosperm nucleus is not constant. In some cases it is transverse and in others it is oblique, sometimes being very nearly vertical (Figs. 70–72). In *Flaveria australasica* the long axis of the spindle is parallel with that of the embryo sac and no variation in its orientation has been found (Fig. 39).

The endosperm becomes cellular in later stages (Figs. 73, 74) and is completely consumed by the embryo in the fully developed seeds in all three species studied.

Embryo.—The embryo development in *Tagetes patula*, *Flaveria australasica* and *Gaillardia picta* is essentially similar except for some differences in detail.

The first division of the fertilized egg is transverse (Figs. 39, 75, 86, 87, 95) and a two celled proembryo is formed. The terminal cell of the two celled proembryo, *ca*, divides vertically resulting in two juxtaposed cells while the basal cell, *cb*, divides transversely forming two cells which are arranged in a superposed manner. The upper of these is termed as *m* and the lower, i.e. the one towards the micropylar side, as *ci* (Figs. 76, 96, 97). In *Gaillardia picta*, *ca* divides slightly earlier than *cb* (Figs. 86, 87).

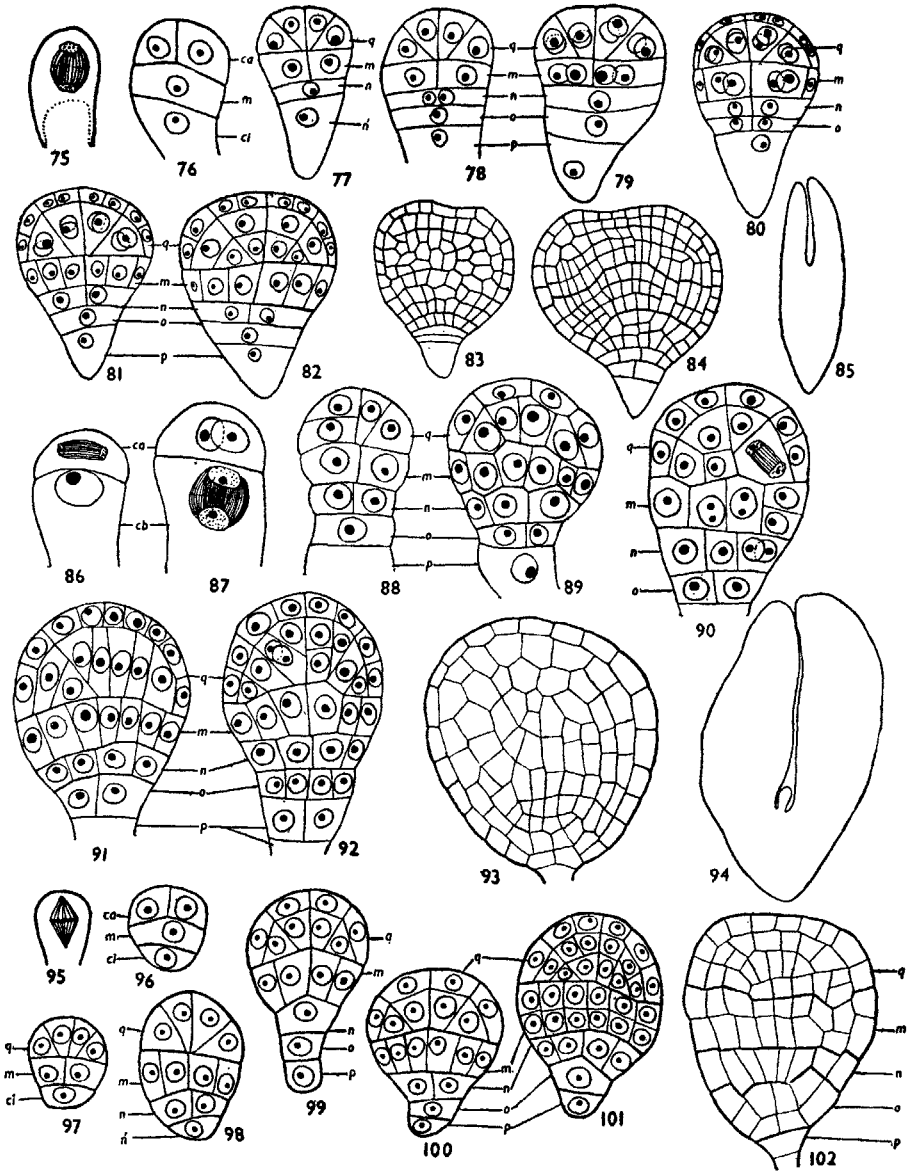
The two cells derived from *ca* undergo a vertical division each, the walls being laid at right angles to that formed in the preceding division. The four circum-axially arranged cells derived from *ca* form the tier *q*. The next division in this tier results in the formation of octants and walls are obliquely oriented (Figs. 77, 88, 98). In *Gaillardia picta*, however, occasionally the walls in one of the quadrants may be transverse (Fig. 88). Periclinal divisions take place in the octants resulting in the demarkation of a single layer of dermatogen cells (Figs. 80, 89, 99). The cells inner to the dermatogen divide further in all directions and the derivatives



FIGS. 69-74—*Tagetes patula*. Fig. 69. Syngamy and triple fusion. $\times 527$. Fig. 70. A section of upper part of embryo sac at the time of syngamy and at the time of the first division of the primary endosperm nucleus. $\times 527$. Figs. 71, 72. L.s. part of the embryo sacs at about the time of the first division of the fertilized egg and the endosperm primordium. $\times 231$ and $\times 527$ respectively. Fig. 73. L.s. embryo sac showing young embryo and cellular endosperm and persistent antipodals. $\times 231$. Fig. 74. Same as Fig. 73 but at an advanced stage. $\times 150$.

later on give rise to periblem and plerome. The dermatogen cells, however, divide further only in an anticlinal manner. The derivatives of the tier *q* give rise to the two cotyledons and the stem tip (Figs. 82-85, 92-94, 99-102).

The cell *m* divides into two juxtaposed cells by the time octants are formed in the tier *q* (Figs. 77, 88, 97). By another vertical division at right angles to the first one, quadrants are formed in this tier also. Close upon the differentiation of dermatogen in the tier *q*, periclinal divisions result in the formation of dermatogen in the tier *m* also (Figs. 80-82, 89-92, 98-100). In *Gaillardia picta*, however,



FIGS. 75-85—*Togetes patula*.

FIGS. 86-94—*Gaillardia picta*.

FIGS. 95-102—*Flaveria australasica*.

Various stages in the development of the embryo. Figs. 75-82. $\times 527$; Figs. 83-84. $\times 213$; Fig. 85. $\times 47$; Figs. 86-92. $\times 527$; Fig. 93. $\times 258$; Fig. 94. $\times 50$; Figs. 95-101. $\times 527$ and Fig. 102. $\times 388$.

dermatogen in tier *m* is differentiated slightly later (Fig. 89). Periclinal divisions take place in the cells inner to dermatogen in the tier *m* ultimately resulting in the differentiation of periblem and plerome in it (Figs. 82-85, 89-94, 100-102). These periclinal divisions are followed by anticlinal divisions. The derivatives of the

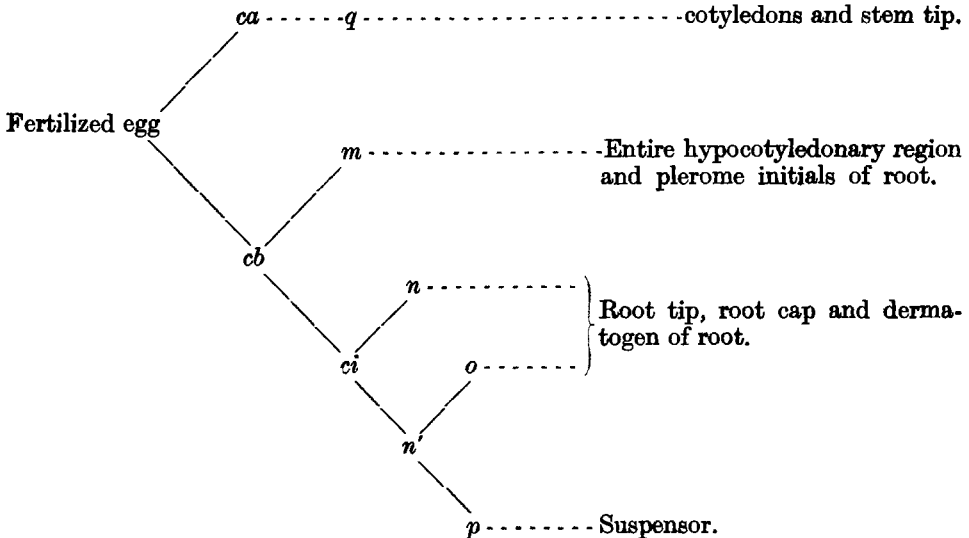
tier *m* give rise not only to the entire hypocotyledonary region but also to the plerome initials of the root.

The cell *ci* divides transversely and gives rise to two superposed cells *n* and *n'* (Figs. 77, 98). Of these the former undergoes two vertical divisions at right angles to each other and the derivatives contribute to the formation of the root cortex and lateral portions of the root cap (Figs. 80–84, 89–93, 100–102). The cell *n'* divides by a transverse wall and forms two superposed cells, namely *o* and *p* (Figs. 78–83, 88–92, 99–102). The cell *o* (forming the tier *o*) at first undergoes two vertical divisions at right angles to each other (Figs. 80, 89–92). The derivatives from the cells of this tier contribute to the formation of the root cap and completion of the dermatogen of the root.

The cell *p* undergoes one or two transverse divisions resulting in a short suspensor. These cells sometimes divide vertically (Figs. 84, 90–93). The suspensor is short in all the species studied.

From the foregoing it can be made out that both *ca* and *cb* contribute to the development of the embryo proper and that the embryo development in *Tagetes patula*, *Flaveria australasica* and *Gaillardia picta* conforms to the Asterad type. The cell *m* (superior daughter cell of *cb*) gives rise to the entire hypocotyledonary region and also to plerome initials of the root and therefore the embryogeny in the three species keys out to the Senecio variation of the Asterad type (Johansen, 1950).

The relation of the individual cells of the proembryo to the organs of the mature embryo is shown in the following schematic representation:



Seed.—In fully developed seeds of *Tagetes patula*, *Flaveria australasica* and *Gaillardia picta* the endosperm and almost all layers of the integuments are consumed and the embryo lies within a thin membrane closely appressed to the pericarp. The innermost layer of cells of the pericarp in *Gaillardia picta* as also the cells of the outer layer of the integument contain prismatic crystals, but as pointed out already the latter is completely crushed in mature seeds.

SUMMARY

Three members of the tribe Helenieae, namely *Tagetes patula*, *Flaveria australasica* and *Gaillardia picta*, have been studied.

The sequence of development of the floral whorls is corolla, androecium, calyx and gynoecium.

The anther shows an epidermis, two wall layers, amoeboid anther tapetum of parietal origin and moderately extensive sporogenous tissue. No fibrous endothecium is differentiated. The pollen mother cells divide in a simultaneous manner and cytokinesis is by furrowing. The pollen grains are shed in the 3-nucleate stage. The exine is echinate and shows three germ pores. A few cases of pollen grains with four germ pores have been encountered in *Tagetes patula*.

Usually there is a single, unitegmic, tenuinucellate, anatropous ovule in an ovary but about 3 per cent of the ovaries of *Tagetes patula* examined showed two ovules which sometimes showed various degrees of fusion. An integumentary vascular trace occurs in the ovules of *Tagetes patula* and *Flaveria australasica*.

In *Tagetes patula* and *Flaveria australasica* the female archesporium is 1-celled. A linear tetrad is formed and the chalazal megaspore develops into an 8-nucleate embryo sac. The number of antipodals varies from two to three and the number of nuclei in an antipodal varies from one to six in *Tagetes patula* and one to two in *Flaveria australasica*. Double and triple embryo sacs occur in *Tagetes patula*, probably owing to the further development of more than one megaspore of a tetrad.

In *Gaillardia picta* the development of the embryo sac is of the *Fritillaria* type. There is a secondary 2-nucleate stage followed by a secondary 4-nucleate stage. The antipodals are persistent.

Fertilization is porogamous. Syngamy and triple fusion take place more or less simultaneously. Pollen tubes are persistent in *Tagetes patula* and *Gaillardia picta*.

Endosperm is of the nuclear type. It later becomes cellular and is completely consumed in the mature seed.

Embryo development conforms to the Asterad type and keys out to the Senecio variation.

In fully developed seeds the endosperm and the integument are completely consumed except for a thin membrane.

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* Publication not seen in original by the authors.