

# EMBRYOLOGY OF APOCYNACEAE—1. PLUMIEREAE

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## ABSTRACT

Embryology of *Voacanga foetida*, *Catharanthus roseus*, *C. pusillus*, *Rauvolfia tetraphylla*, *R. serpentina* and *Holarrhena antidysenterica*, belonging to the tribe Plumiereae, has been investigated. The anther wall comprises the epidermis, fibrous endothecium, 1 or 2 wall layers and a secretory tapetum in all the members except *V. foetida* where the number of wall layers varies from 10-14 and the fibrous endothecium is multilayered. Division of pollen mother cells is of simultaneous type and cytokinesis is by furrowing. Both bilateral and tetrahedral tetrads are formed. Mature pollen grains are 3-celled and triporate.

The ovary is bicarpellary and bilocular. The ovule is anatropous in *R. tetraphylla* and *R. serpentina* and hemianatropous in *H. antidysenterica*, *V. foetida*, *C. roseus* and *C. pusillus*. The archesporium is hypodermal and single-celled. It functions directly as the megaspore mother cell. Linear and T-shaped tetrads are formed. The chalazal megaspore of the tetrad develops into the 8-nucleate embryo sac of the Polygonum type. 3 uninucleate antipodal cells are formed. Starch grains are present in the 8-nucleate embryo sac. Abnormal embryo sacs with more or less than 8 nuclei have been met with in *H. antidysenterica* and *V. foetida*. Double embryo sacs occur in *R. tetraphylla*, *R. serpentina* and *H. antidysenterica*. Fertilisation is porogamous. The endosperm is Nuclear. It becomes cellular in the later stages. Chalazal endosperm haustorium is present in *C. roseus* and *C. pusillus*.

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The embryogeny conforms to Trifolium variation of Onagrad type in *C. pusillus* and *C. roseus*, Senecio variation of Asterad type in *V. foetida* and Chenopodiad type in *R. tetraphylla*. Polyembryony was observed in a solitary instance in *R. serpentina*. Seed coat is massive in *R. tetraphylla* and *V. foetida*. In *C. pusillus* and *C. roseus* it is formed only by the outer epidermal cells of the integument. The seeds are endospermous.

## INTRODUCTION

The Apocynaceae is a large family 180 genera, 1,500 species, Willis, 1966) of trees, twining shrubs, herbs and lianes. Many members like *Rauvolfia serpentina*, *Catharanthus roseus* (= *Vinca rosea*), *Holarrhena antidysenterica*, *Thevetia peruviana* are medicinally important and a good number of them are grown as garden favourites.

Schnarf (1931) and Davis (1966) summarised the embryological work done in this family upto 1931 and 1966 respectively. Although a good amount of work has been done on the development of ovule and female gametophyte, very little attention has been paid to the development of anther, pollen, endosperm and embryo. Further, there is difference of opinion regarding the nature of the division of pollen mother cells. According to Frye and Blodgett (1905) the pollen mother cells divide by successive method and cytokinesis is by cell plate formation. Täckholm and Söderberg (1918) reported simultaneous type of division of pollen mother cells, while Meyer (1938) reported both successive and simultaneous types of division of pollen mother cells. A few stages of embryo development were traced in *Cerbera odollam*, *Carissa carandas* and *Ichnocarpus frutescens* (Rau, 1940). Murty and Chauhan (1966) studied the embryology of *Lochnera pusilla*.

The present investigation was undertaken with a view to work out the embryology of as many genera as possible in the different tribes of the family. The life

history of *Voacanga foetida* Rolfe, *Catharanthus roseus* (L.) G. Don, *Catharanthus pusillus* (Murr.) G. Don, *Rauvolfia tetraphylla* Linn., *Rauvolfia serpentina* (Linn.) Benth. ex Kurz and *Holarrhena antidysenterica* (L.) Wall. ex A. Dc. belonging to the tribe Plumiereae of the sub-family Plumieroideae has been investigated.

## MATERIALS AND METHODS

The material of *Voacanga foetida* was collected by Sri N. Ganapathy Raju at Yanam and the other materials were collected by the author at various places—*Rauvolfia serpentina* from the hills of Ananthagiri; *R. tetraphylla* at Kakinada and *Holarrhena antidysenterica*, *Catharanthus roseus* and *C. pusillus* at Vizag. The materials were fixed in Formalin-acetic-alcohol and customary methods of dehydration and infiltration were followed. Sections were cut at 10–15 microns thickness and stained with Delafield's Haematoxylin.

## OBSERVATIONS

*Microporangium, microsporogenesis and male gametophyte.*—The hypodermal archesporium in the anther lobe is multicelled (Figs. 1, 2). The archesporial cells undergo periclinal divisions producing an outer primary parietal layer and an inner primary sporogenous layer (Figs. 3, 4). Except in *Voacanga foetida*, in the other numbers studied, the parietal layer undergoes further periclinal divisions and produces a fibrous endo-



thecial layer, 1 or 2 wall layers and a tapetum which is 1 or 2 seriate (Figs. 5-8, 11). In *V. foetida*, 10-14 wall layers and a multiple endothecium are formed as a result of periclinal divisions in the primary prietal layer (Figs. 9, 10). The tapetum is of the secretory type and the cells are uninucleate. In *V. foetida* small granular thickenings develop on the inner wall of the tapetal cells (Fig. 9). As the outer wall layers mature the epidermal cells become prominent. In *V. foetida*, the outer walls of the epidermal cells become very much thickened and make the epidermis even more prominent.

Pollen mother cells divide in a simultaneous manner resulting in tetrahedral and isobilateral tetrads (Figs. 12, 13). Cytokinesis is by furrowing. The cytoplasm of the 1-nucleate pollen grain becomes slightly vacuolate and its nucleus moves to the periphery where it divides to form the generative and the vegetative cells (Fig. 14). Later on the lenticular wall disappears and the generative cell moves into the centre of the pollen grain (Fig. 15). The mature pollen grains are triplicate and 3-celled (Fig. 16).

*Megasporangium, megasporogenesis and female gametophyte.*—The ovary is superior, bicarpellary and bilocular. It is apocarpous in *Catharanthus roseus*, *C. pusillus* and *Holarrhena antidysenterica* and connate in *Voacanga foetida*, *Rauwolfia serpentina* and *R. tetraphylla* (Figs. 17, 19, 20). In *C. roseus*, *C. pusillus* and *V. foetida* numerous ovules are borne on the axile placenta (Fig. 18) while in *R. serpentina* and *R. tetraphylla* two ovules are developed in each locule. The ovule is unitegminal and tenuinucellar (Fig. 23). It is anatropous in *R. serpentina* and *R. tetraphylla* and hemi-anatropous in the remaining members (Figs. 23, 24). In *V. foetida*, after ferti-

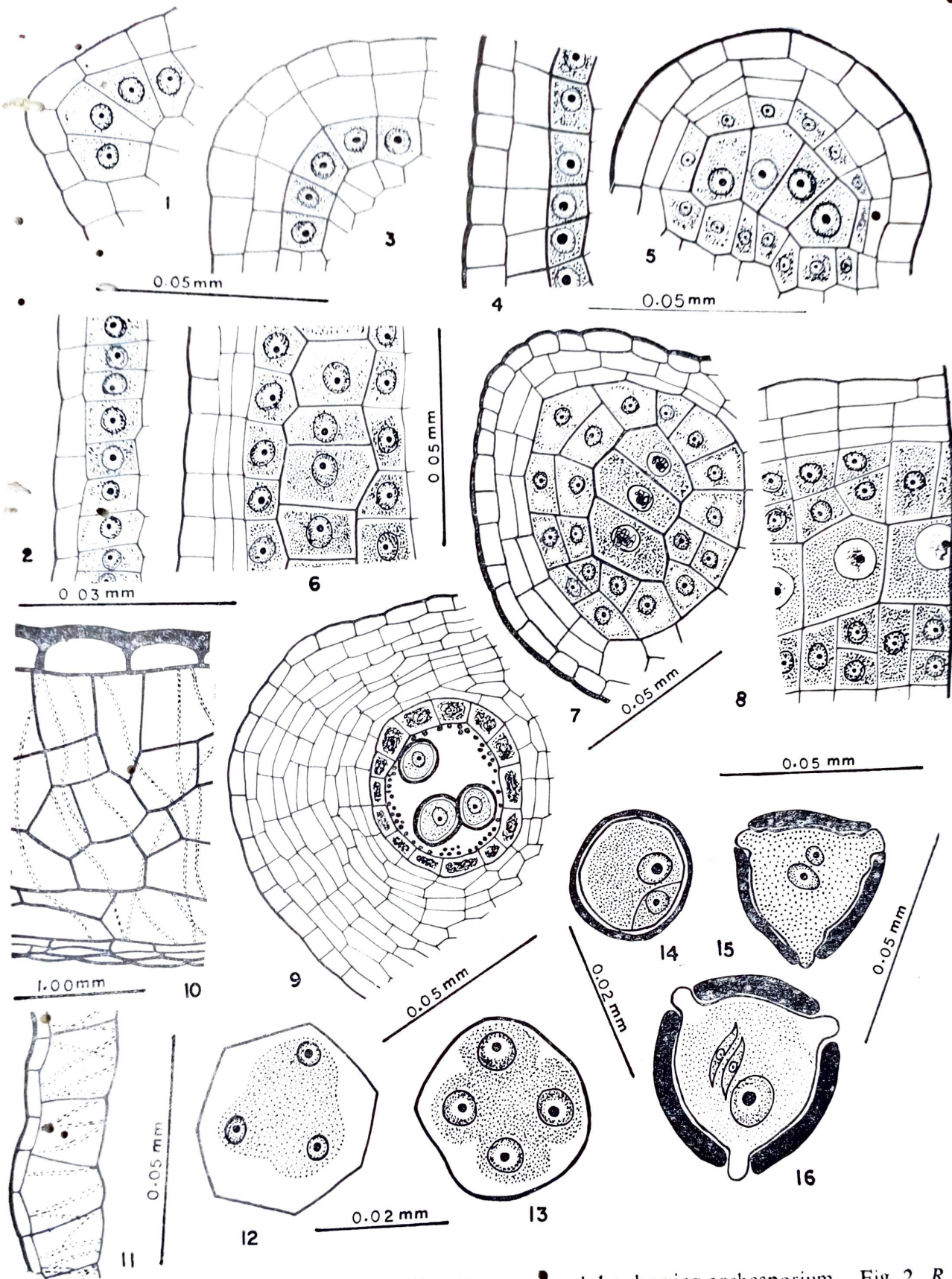
lisation, the placental tissue grows enormously in all directions and forms a massive structure in which the ovules are embedded (Fig. 21). In the older stages due to the growth of the integument on sides the ovule becomes kidney-shaped (Fig. 22).

The hypodermal archesporium, which is single-celled, directly functions as the megaspore mother cell (Fig. 25). A linear tetrad of megaspores is formed as a result of reduction division in the megaspore mother cell, although T-shaped tetrads are not rare in *C. roseus* and *H. antidysenterica* (Figs. 26, 27). The chalazal megaspore of the tetrad develops into the eight-nucleate embryo sac of the Polygonum type (Figs. 26-31). The synergids are pear shaped in all the species except *R. tetraphylla* in which they are hooked. The fusion of the polar nuclei takes place before fertilisation in all the members except *C. roseus* where it occurs simultaneously with fertilisation. Three uninucleate antipodal cells are formed. In *R. tetraphylla*, *R. serpentina* and *C. pusillus*, the antipodal cells degenerate after fertilisation while in the rest of the forms they are ephemeral. Starch grains occur in the mature embryo sacs (Figs. 31, 32).

*Double embryo sacs.*—In a few cases in *R. serpentina*, *R. tetraphylla* and *H. antidysenterica*, two embryo sacs per ovule have been met with. The two embryo sacs show normal features but for the absence antipodal cells (Fig. 32).

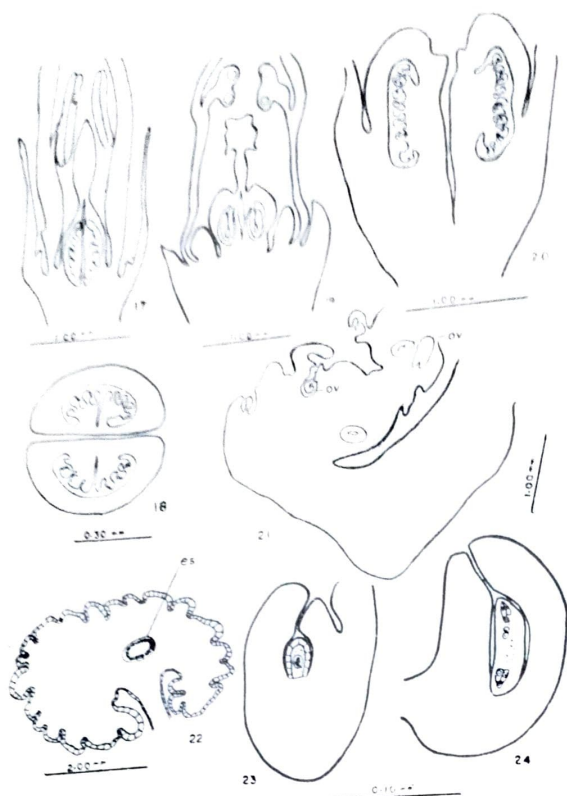
*Embryo sacs with less than eight nuclei.*—A few cases of abnormal embryo sacs containing less than the usual number of nuclei have been met with in *V. foetida* and *H. antidysenterica*. In *H. antidysenterica*, of the 6 nuclei that are formed in the embryo sac, 1 forms the egg cell and the remaining 5 free nuclei lie





FIGS. 1-16. Fig. 1. *Rauvolfia tetraphylla*. T. s. anther lobe showing archesporium. Fig. 2. *R. serpentina*. L. s. part of anther lobe showing archesporium. Fig. 3. *Catharanthus roseus*. T. s. anther lobe showing primary parietal and primary sporogenous layers. Fig. 4. *Voacanga foetida*. L. s. part of anther lobe showing primary parietal and primary sporogenous layers. Figs. 5, 6. *R. tetraphylla*. T. s. and L. s. anther lobes showing wall layers, tapetal layer and pollen mother cells respectively. Figs. 7, 8. *Holarrhena antidysenterica*. T. s. and L. s. anther lobes showing wall layers, tapetum and pollen mother cells in meiotic prophase I. Figs. 9, 10. *V. foetida*. Fig. 9. T. s. anther lobe showing wall layers, tapetum and 1-nucleate pollen grains; note granular thickening on the inner wall of the tapetal cells. Fig. 10. Part of multilayered endothecium. Fig. 11. *C. roseus*. Fibrous wall of the tapetal cells. Fig. 12. *R. tetraphylla*. Tetrahedral tetrad. Figs. 13, 14. *H. antidysenterica*. Fig. 13. Isobilateral tetrad. Fig. 14. Two celled pollen grain showing lenticular generative cell and a large vegetative cell. Fig. 15. *V. foetida*. 2-nucleate pollen grain. Fig. 16. *H. antidysenterica*. 3-nucleate pollen grain.





FIGS. 17-24. Figs. 17, 18. *Holarrhena antidysenterica*. Fig. 17. L. s. flower showing apocarpous ovary. Fig. 18. T. s. ovary. Fig. 19. *Rauwolfia tetraphylla*. L. s. flower. Figs. 20-22. *Voacanga foetida*. Fig. 20. L. s. ovary. Fig. 21. A part of placental tissue enlarged showing ovules embedded in it. Fig. 22. L. s. ovule showing embryo sac. Fig. 23. *R. serpentina*. Anisotropous ovule showing megaspore mother cell in meiotic prophase I. Fig. 24. *Catharanthus roseus*. Hemianisotropous ovule showing 8-nucleate embryo sac.

ov, ovules; es, embryo sac.

close together in the middle of the embryo sac (Fig. 33). In *V. foetida* some of these embryo sacs show 2 synergids, 1 antipodal cell and 3 free nuclei, all lying together near the chalazal end (Fig. 34) and in others, the embryo sacs are 6-nucleate with 2 synergids and 4 free nuclei lying together near the chalazal end.

*Embryo sacs with more than eight nuclei.*—In *H. antidysenterica*, in a few cases, embryo sacs with more than 8 nuclei have been met with. Figure 35 shows an embryo sac which contains 8

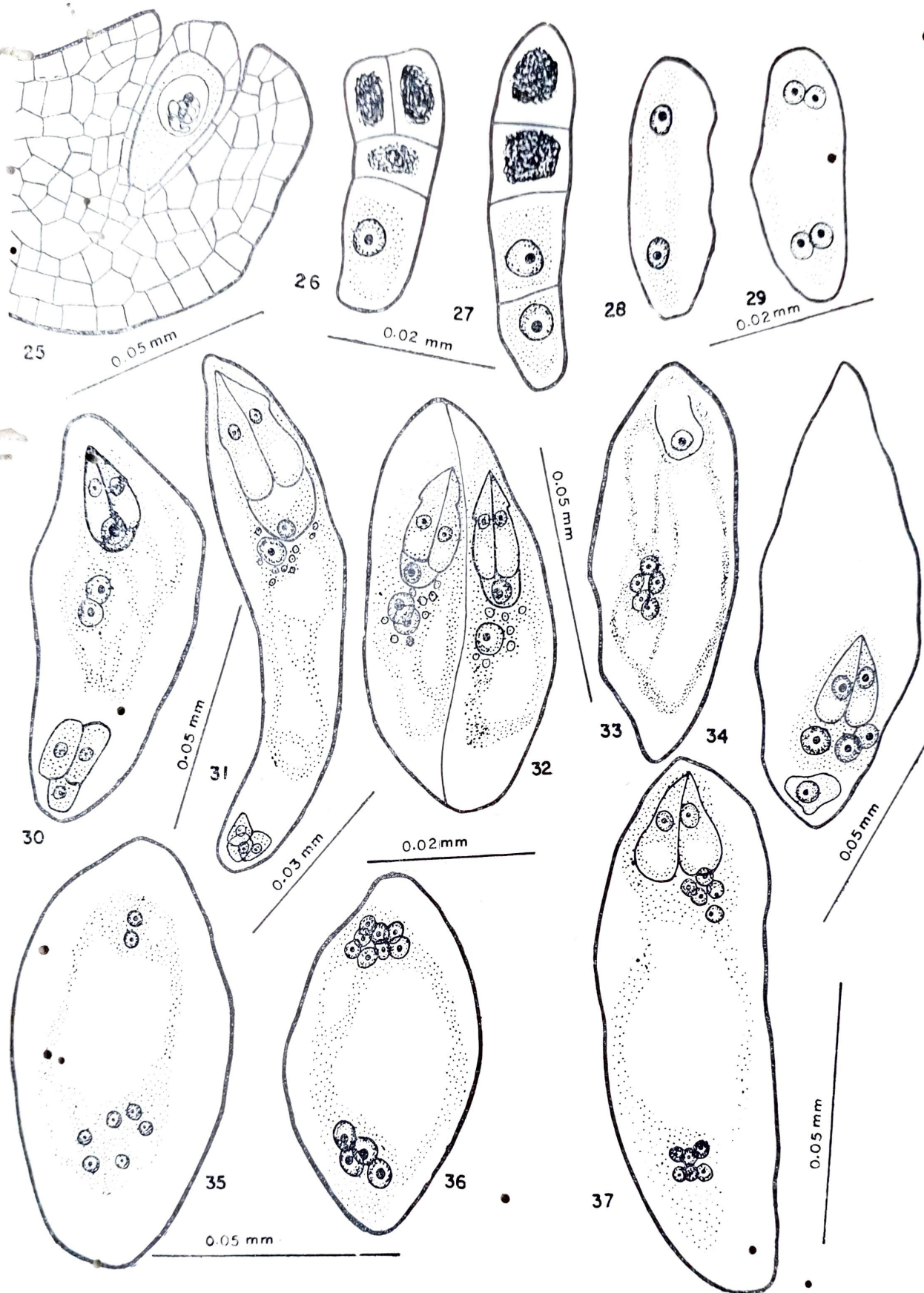
free nuclei without organising into cells. In other cases there are 12 nuclei, of which 8 are situated in the micropylar region and 4 at the chalazal end (Fig. 36). In another case in *H. antidysenterica*, the embryo sac contains 2 synergids and 5 free nuclei in the micropylar region and 6 nuclei in the chalazal region (Fig. 37).

*Fertilisation.*—Is porogamous. In *C. pusillus* and *C. roseus*, the pollen tube is stout and almost plugs the micropyle (Fig. 39). Syngamy and triple fusion take place more or less simultaneously (Figs. 38, 39). The pollen remains persistent until a few free endosperm nuclei are formed in the embryo sac.

*Endosperm.*—The endosperm is Nuclear and the division of the primary endosperm nucleus precedes that of the zygote (Fig. 40). After a few free nuclear divisions the endosperm nuclei become distributed in the periphery of the embryo sac and a large central vacuole is formed (Fig. 41). Cell wall formation commences at the periphery and extends into the interior of the embryo sac ultimately filling the entire embryo sac with cellular tissue (Figs. 42, 44). In a very late stage, protein bodies develop in the endosperm cells as reserve food (Fig. 45).

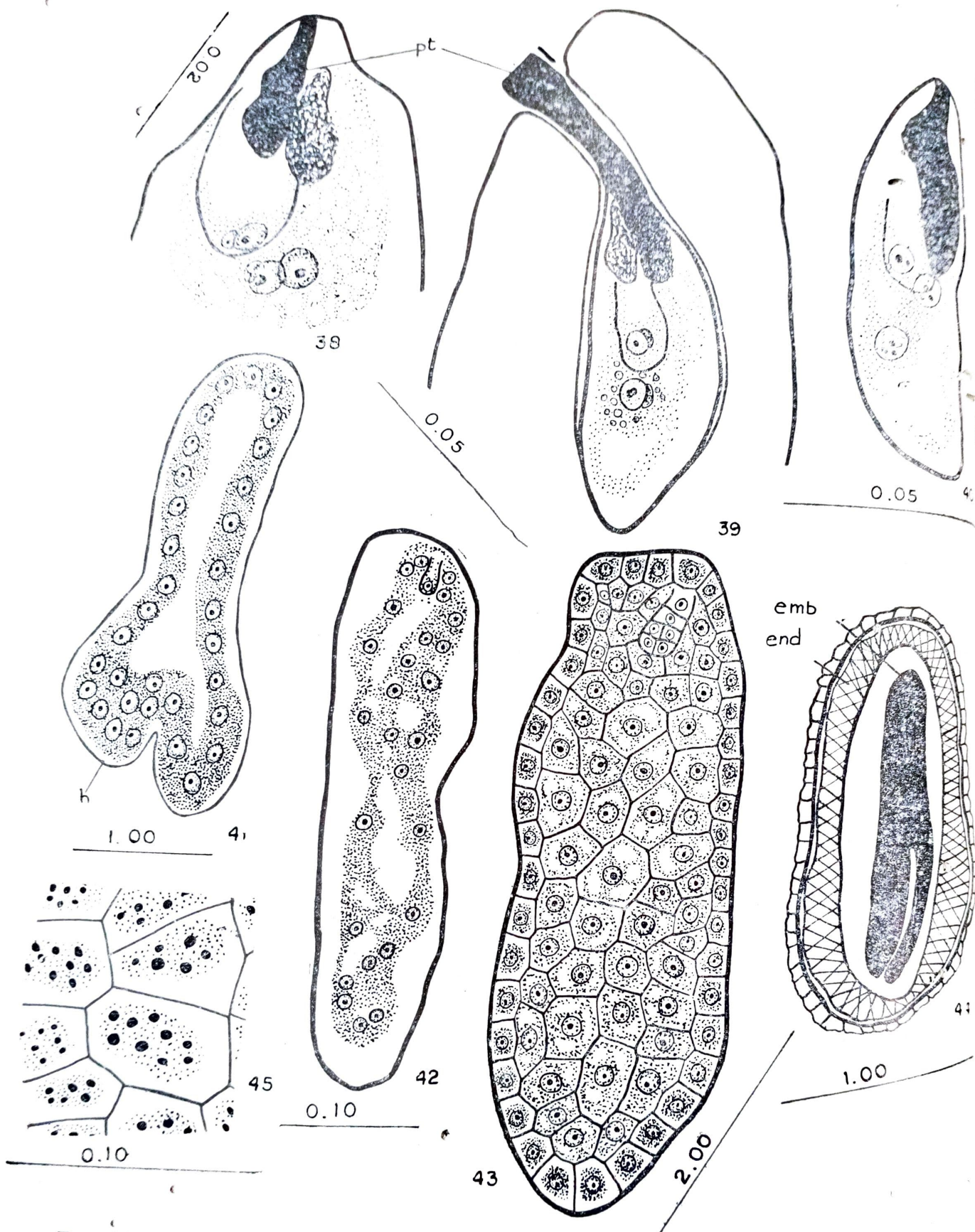
Although the development of the endosperm in *Catharanthus roseus* and *C. pusillus* is essentially similar to the rest of the members, in the 2 members it differs in the formation of a chalazal haustorium. The endosperm, at the chalazal region produces a lobed structure into which accumulation of dense cytoplasm with a large number of nuclei is seen (Fig. 41).

*Embryo.*—The development of the embryo differs in the different genera and hence a separate account is given for each of the genera. In *Voacanga foetida*



FIGS. 25-37. Figs. 25-28, *Catharanthus roseus*. Fig. 25. L. s. C. ule showing megaspore mother cell in meiotic prophase I. Fig. 26. T-shaped megaspore tetrad. Fig. 27. Linear megaspore tetrad. Fig. 28. 2-nucleate embryo sac. Figs. 29, 30. *C. pusillus*. 4 and 8-nucleate embryo sacs respectively. Figs. 31, 32. *Rauvolfia tetraphylla*. Fig. 31. 8-nucleate embryo sac showing starch grains. Fig. 32. Double embryo sacs. Fig. 33. *Holarrhena antidysenterica*. 6-nucleate embryo sac showing 1 egg cell and 5 free nuclei. Fig. 34. *Voacanga foetida*. 6-nucleate embryo sac showing 2 synergids, 1 antipodal cell and 3 free nuclei. Figs. 35-37. *H. antidysenterica*. Fig. 35. 8-nucleate embryo sac showing 2 micropylar and 4 chalazal free nuclei. Fig. 36. 12-nucleate embryo sac with 8-micropylar and 4 chalazal free nuclei. Fig. 37. 13-nucleate embryo sac showing 2 synergids and 11 free nuclei.





FIGS. 38-45. Fig. 38. *Catheranthus roseus*. Upper part of embryo sac showing syngamy and triple fusion. (Figs. 39, 40. *C. pusillus*. Fig. 39. Embryo sac showing double fertilisation; note the pollen tube plugging the micropyle. Fig. 40. Embryo sac showing the zygote, persistent pollen tube and the endosperm nucleus in its first division. Fig. 41. *C. roseus*. Endosperm haustorium. Figs. 42, 43. *Rauvolfia tetraphylla*. Fig. 42. Nuclear endosperm. Fig. 43. Cellular endosperm. Figs. 44, 45. *C. roseus*. Fig. 44. Embryo sac showing cellular endosperm and well developed embryo. Fig. 45. A part of endosperm showing reserve food.  
 end, endosperm; emb, embryo; h, haustorium; pt, pollen tube.  
 (Numerals given over magnifications are mm.)

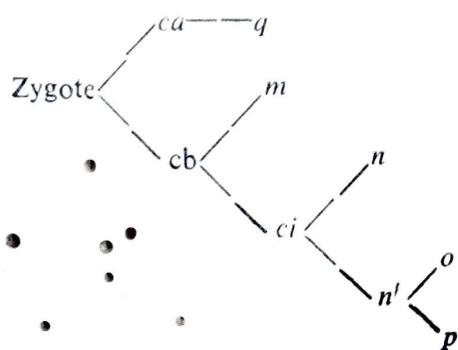


first division of the zygote is transverse and a 2-celled proembryo is formed (Figs. 46, 47). The terminal cell, *ca*, divides vertically and the basal cell, *cb*, divides transversely to engender a 4-celled proembryo which is T-shaped (Figs. 48–50). The two derivatives of the cell, *cb*, are termed as, *m*, and *ci*. The cell *ci* divides transversely resulting in 2 superposed cells, *n* and *n'* (Fig. 51). The cell *n'* divides by transverse wall to form *o* and *p* (Figs. 52, 53).

Due to vertical divisions at right angles to one another in the two tiers, *ca* and *m*, quadrants are formed (Fig. 52). The 4 cells of the tier *q* divide to form octants, the walls being oriented obliquely (Fig. 53). The derivatives of the tier *q* contribute to the formation of the cotyledons and stem tip, while the derivatives of the tier *m* contribute to the formation of hypocotyledonary region and plerome initials of the root.

The cells *n* and *o* undergo 2 vertical divisions at right angles to each other. Their derivatives contribute to the formation of the root tip, root cap and dermatogen of the root. The cell *p* undergoes 1 or 2 transverse divisions to form a short uniseriate suspensor (Figs. 53–55).

Details of the development of the elements of the proembryonic tetrad into various organs of the mature embryo are shown in the following schematic representation :



In *V. foetida*, the terminal cell of the 2-celled proembryo divides vertically and both the terminal cell, *ca*, and the basal cell, *cb*, contribute to the development of the embryo. Thus the embryo development conforms to the Asterad type. The cell *m* gives rise to the entire hypocotyledonary region and plerome initials of the root and thus keys out to the Senecio variation.

In *Catharanthus roseus* and *C. pusillus* the zygote divides transversely and 2 superposed cells, *ca* and *cb* are formed (Fig. 56). The terminal cell, *ca*, divides vertically and the basal cell, *cb*, divides transversely resulting in a 4-celled, T-shaped proembryo (Fig. 57). The derivatives of the cell *cb*, are termed as, *m* and *ci*.

The vertical wall in the cell *ca* is slightly oblique and two dissimilar juxtaposed cells are formed (Fig. 57). The larger cell, *a* divides by another oblique wall which is perpendicular to the first wall and two cells are formed (Figs. 58–60). The upper cell, *e*, is differentiated as the epiphyseal initial. The larger cell, *a*, and the smaller cell, *b*, divide by transverse walls and two tiers of cells, the upper, *pc*, and the lower, *pc'*, are formed (Figs. 59, 60). The epiphyseal initial undergoes further divisions and gives rise to the cortical initials of the stem (Figs. 61, 62). The cells of the tier *pc*, after undergoing further trans-

...Cotyledons and stem tip.

...Hypocotyledonary region and plerome initials of root.

... { Root tip, root cap and dermatogen of root.

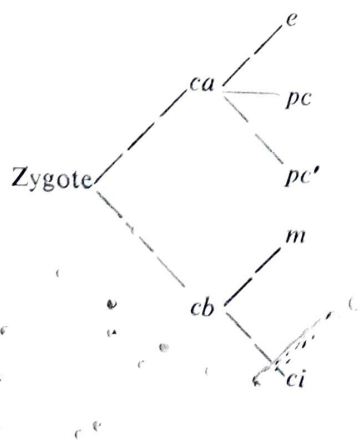
...Suspensor



verse and vertical divisions followed by periclinal divisions produce an outer dermatogen layer and an inner layer of cells which after undergoing a few more divisions give rise to the central cylinder of the stem and the two cotyledons (Figs. 62-65). The derivatives of the tier *pc'* contribute to the formation of the hypocotyledonary region.

In the meanwhile, in the cell *m*, a transverse wall is laid down cutting off a lenticular cell towards the apical side and a watch glass shaped cell towards the basal side (Figs. 59-61). In this division, the wall is curved and both the ends are attached to the transverse wall, originally separating the cell *ca* from *cb*. These form the initials of the hypophysis. In the lower daughter cell of the cell *m*, the first division is vertical and two juxtaposed cells are formed (Figs. 60, 61). Later on, the derivatives of the upper daughter cell of the cell *m*, form the initials of the root cortex and the derivatives of the lower daughter cell form the initials of the root cap (Figs. 62-65). The cell *ci* divides transversely and forms an uniseriate suspensor of 4 or 5 cells.

The development of the mature organs of the embryo in specific relation to the proembryonic tetrad is represented below in the schematic representation :



...Epiphysis.

...Cotyledons and central cylinder of the stem.

...Hypocotyledonary region.

...Hypophysis.

...Suspensor.

From the above, it can be seen that the terminal cell, *ca*, of the 2-celled proembryo alone contributes to the formation of embryo proper and the suspensor and hypophyseal region are derived from the basal cell, *cb*. The above features are characteristic of the *Onagrad* type while the presence of an epiphyseal initial is characteristic of the *Trifolium* variation. Thus the embryo development in *C. roseus* and *C. pusillus* conforms to the *Trifolium* variation of *Onagrad* type.

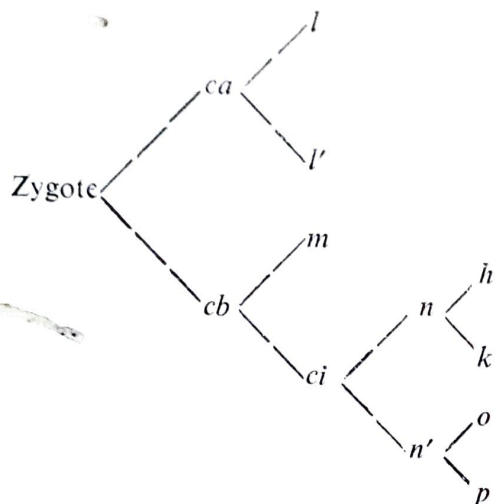
In *Rauvolfia tetraphylla* the first division of the fertilised egg is transverse and a 2-celled proembryo is formed (Fig. 66). Both the cells, the basal cell, *cb*, and the terminal cell, *ca*, undergo one more transverse division each resulting in the formation of a 4-celled linear proembryo. The cells are termed as *l*, *l'*, *m* and *ci* (Fig. 67). Due to further vertical divisions in the two tiers, *l* and *l'*, quadrants are formed in each of the tiers (Figs. 69-71). The derivatives of the tier *l*, after undergoing further divisions contribute to the formation of cotyledons and those of tier *l'*, to the upper part of hypocotyledonary region (Figs. 71-73). In the meanwhile, the cell *m* also undergoes further divisions and contributes to the formation of lower part of the hypocotyledonary region.

The cell *ci* divides transversely to form



$n$  and  $n'$  (Figs. 68–70). These, after undergoing each a transverse division, form 4 cells which are termed as  $h$ ,  $k$ ,  $o$  and  $p$  (Fig. 71). Of these cells,  $h$  func-

that the derivatives of  $cb$  also contribute to the formation of embryo proper. The embryo development in *R. tetraphylla* conforms to the Chenopodiad type.



tions as hypophyseal cell and contributes to the formation of root tip. The 3 cells,  $k$ ,  $o$ , and  $p$ , form a short suspensor.

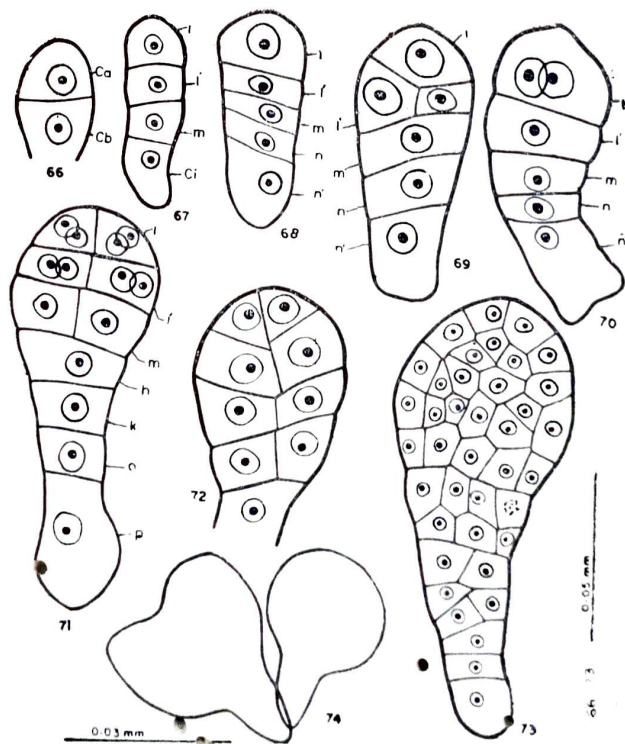
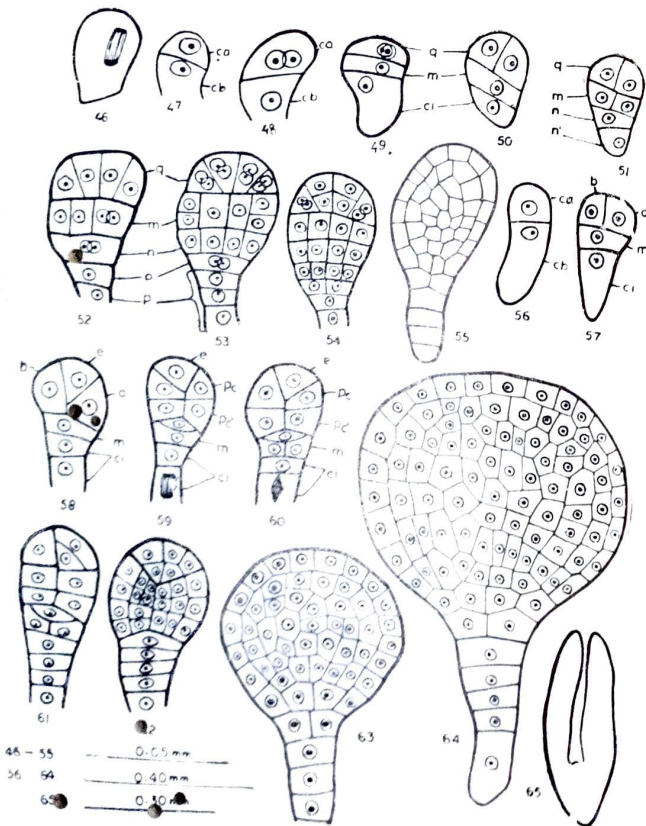
From the above it can be concluded that the proembryo is a linear tetrad and

...Cotyledons.

{ ...  
...Hypocotyledonar region.  
...Hypophysts.

{ ...  
... Suspensor.  
...

**Polyembryony.**—In one case of *Rauvolfia serpentina*, however, two embryos were seen developing. These embryos lie close to one another (Fig. 74) and probably the extra embryo is developed from one of the synergids.



FIGS. 46–65. Various stages in the development of the embryo. Figs. 46–55. *Voacanga foetida*. Figs. 56–65. *Catharanthus roseus*.

FIGS. 66–74. Figs. 66–73. *Rauvolfia tetraphylla*. Stages in the development of the embryo. Fig. 74. *Rauvolfia serpentina*. Polyembryony.



*Seed coat.*—The seed coat is massive and consists of many layers of cells in *R. tetraphylla* and *V. foetida*. In *V. foetida* the mature seed is irregular in outline and in the cells of the outer epidermis brown contents are seen. In *C. roseus* and *C. pusillus* all the wall layers of the integument, but for the outer epidermis, are destroyed during the development of the embryo and endosperm. The outer epidermis alone develops into the seed coat.

### DISCUSSION

The development of the anther wall in the tribe Plumiereae of the sub-family Plumioideae, conforms to the Dicotyledonous type (Davis 1966). The anther tapetum in the family Apocynaceae shows some variation. It is either parietal or sporogenous in its origin. All the members investigated in the tribe Plumiereae (present study) show an anther tapetum, which is parietal in origin as in the other investigated members of the tribe like *Thevetia nerifolia*, *Alstonia scholaris* (Meyer, 1938), *Cerbera odollam* (Rau, 1940) and *Lochnera pusilla* (Murty and Chauhan, 1966).

Meyer (1938) reported simultaneous type of division of pollen mother cells and cytokinesis by cell plate formation in *Alstonia scholaris* and *Thevetia nerifolia* and both successive and simultaneous types of division of pollen mother cells in *Rauvolfia canescens*. The present observations on *Rauvolfia tetraphylla* (= *R. canescens*) and *R. serpentina* and substitute by as well as other members investigated show simultaneous cytokinesis as in *Cerbera odollam* (Ray, 1940). The pollen grains are shed at the 3 celled stage.

A tendency for the reduction of the

nucellus to a few cells prevails in the family. According to Meyer (1938), *R. canescens*, the nucellar epidermal cells on the sides merge with the integumentary tissue. But the members investigated in the tribe Plumiereae including *R. tetraphylla*, show a well developed nucellar epidermis which is distinct from the integumentary tissue. A similar report was made in *Cerbera* and *Amazonia* (Guignard, 1917).

The archesporial cell develops directly into the megaspore mother cell without cutting off a parietal cell as in the other investigated members of the tribe (Rau, 1940; Murty and Chauhan, 1966). The chalazal megaspore of the tetrad develops into the Polygonum type of embryo sac.

Endosperm development is of the Nuclear type as in the other members of the tribe Plumiereae. However, in *Catharanthus roseus* and *C. pusillus* development of chalazal endosperm haustorium is seen. A similar report was made by Murty and Chauhan (1966) in *Lochnera pusilla*.

Though a few developmental stages of embryo were traced by Andersson (1931) in *Lochnera rosea* and *Vinca minor*, they are not of any help in enabling one to assign the embryo development to a particular type. Murty and Chauhan (1966) reported 'Crucifer type' (Onagrad type of Johansen, 1950) of embryo development in *Lochnera pusilla*. In the present study the development of the embryo has been followed in some detail and from the results obtained in the 3 genera—*Catharanthus*, *Voacanga* and *Rauvolfia*—it is interesting to note that the type of embryo development differs in them. It conforms to the Trifolium variation of Onagrad type in *C. roseus* and *C. pusillus*, Senecio variation of Asterad type in *V. foetida* and Chenopodiad type in *R. tetraphylla*.



As in *Voacanga grandiflora* (Periasamy, 1963) the seed coat in *Voacanga foetida* is irregular in outline and the cells

of the outer epidermis contain brown contents.

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