Embryological studies in *Mecardonia procumbens* (Miller) small

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MS received 22 October 1981

Abstract. Sporogeneses, development of gametophytes, endosperm and embryo of *Mecardonia procumbens* (Miller) Small have been described. The wall of the microsporangium consists of an epidermis, an endothecium, a middle layer and a glandular tapetum. The development of the anther conforms to the dicotyledonous type. The tapetal cells become binucleate and the endothelial cells acquire fibrous thickenings in later stages. Quadripartition of the microspore mother cells is simultaneous. Pollen grains are shed at two-celled stage and are tricolpate. Development of the female gametophyte is of *Polygonum* type. Middle part of the gametophyte is surrounded by an endothelium. Endosperm is of *ab initio* cellular type. Chalazal and micropylar haustoria are organised. Both the micropylar and chalazal haustoria are four-celled and this is the first report in the tribe Gratioleae. Embryo development is of *Onagrad* type. The cell 'd' functions as the hypophyseal cell.

Keywords. *Mecardonia procumbens*; embryology; Gratioleae; Antirrhinoideae; Scrophulariaceae.

1. Introduction

Mecardonia procumbens (Miller) Small is a small prostrate herb belonging to the tribe Gratioleae of the subfamily Antirrhinoideae of Scrophulariaceae. Considerable work on the tribe Gratioleae has been done by Krishna Iyengar (1939, 1940a, b, 1941), Yamazaki (1953, 1954), Arekal (1965), Arekal *et al* (1970) and Raju (1976). However, detailed embryological data are available only for about 50% of the members of the tribe. Members of this family have attracted the attention of embryologists because of the diversity in the structure and organisation of endosperm haustoria. The present work deals with the embryology of *M. procumbens*.

2. Material and methods

Buds, flowers and fruits of *M. procumbens* were collected from Srirangapatna and fixed in FAA. The usual methods of dehydration, infiltration and embedding were followed. Sections of 6–12 μ m thickness were cut and stained in Heidenhein's iron-alum haematoxylin with orange-G as the counter stain.

3. Observations

3.1 *Microsporogenesis and development of male gametophyte*

The young anther is four-lobed in cross-section, each lobe representing a microsporangium (figure 1). A plate of 4–8 hypodermal archesporial initials is differentiated

in each microsporangium. The archesporial cells undergo periclinal divisions resulting in the formation of a layer of primary parietal cells towards the outside and a layer of primary sporogenous cells towards the inner side (figure 2). The primary parietal layer, after undergoing a periclinal division, gives rise to two layers of cells, the inner one of which functions directly as a glandular tapetum. The outer layer, by another division forms an endothecium and a middle layer (figure 3). Thus the development of anther conforms to the dictyoledonous type (Davis 1966). The tapetal cells are uninucleate containing two nucleoli to begin with (figure 3) but due to a free nuclear division they become binucleate (figure 4). The nuclei of the tapetal cells subsequently fuse together forming a large irregular nucleus with many nucleoli (figure 5). During the later stages of microsporangial development, the tapetum and the middle layers are consumed and the cells of the endothecium acquire characteristic fibrous thickenings (figures 6,7, 54). These thickenings are found in all cells of the layer except for a few cells between the anther halves.

Simultaneously with the above changes, the cells of the primary sporogenous layer give rise to a group of microspore mother cells by undergoing periclinal and anticlinal divisions (figures 3,4). Microspore mother cells become rounded and undergo simultaneous meiotic division producing tetrahedral tetrad of microspores (figures 8-13). The nucleus of the microspore divides to form a small generative cell and a large vegetative cell (figures 14,15). The pollen grains are shed at this stage (two-celled stage). The mature pollen grain is almost spherical with a thin intine and a thick exine and 3-colpate (figure 15). By the time the pollen grains are mature, the separating layers of cells between the adjacent microsporangia disorganise and the pollen of both sporangia are released through a longitudinal opening (figures 6,54). The generative cell divides to form two male gametes after pollination.

3.2 *Megasporogenesis and the development of female gametophyte*

The ovary is superior, bicarpellary, syncarpous and bilocular with axile placenta. A number of finger-like ovular primordia develop on the placenta and each one of them develops into a tenuinucellate, anatropous and unitegmic ovule.

A large, densely protoplasmic hypodermal archesporial cell with a prominent nucleus differentiates in the ovular primordium (figure 16). The archesporial cell enlarges in size and elongates considerably and directly functions as the megaspore mother cell (figure 17). The nucleus of the megaspore mother cell undergoes first meiotic division (figure 18) resulting in the formation of a dyad. The second meiotic division in the dyad cells is simultaneous (figure 19), and a linear tetrad of megaspores

Figures 1-15. Development of the Anther in *Mecardonia procumbens*. 1. Transverse section of a young anther showing four microsporangia. 2. TS of anther lobe showing the primary parietal and the primary sporogenous layers 3. TS of anther lobe showing the stages in development of sporogenous tissue and the wall layers 4. TS of a microsporangium showing the microspore mother cells and binucleate tapetal cells 5. TS of part of microsporangium after nuclear fusions in tapetal cells and degeneration of middle layer 6. TS of two mature microsporangia showing the confluence of adjacent microsporangia, the endothelial thickenings and the line of the dehiscence 7. Anther wall showing fibrillar endothecium and pollen grains 8-13. Formation of tetrahedral tetrad of microspores from a microspore mother cell 14. A microspore under division 15. Two-celled pollen grain (1 $\times$ 600; 2,5, 8-15 $\times$ 1500; 3,4,7 $\times$ 1000; 6 $\times$ 270).

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is formed. Usually the chalazal megaspore enlarges and functions further (figure 22). But, occasionally, any one of the remaining megaspores may also enlarge (figures 20,21). However, only the chalazal one forms the female gametophyte and the other three invariably degenerate (figure 22).

The nucleus of the functional megaspore divides to form a two-nucleate female gametophyte (figure 23). The nuclei in the gametophyte move to the opposite poles due to the formation of a central vacuole. The young gametophyte elongates considerably and enlarges. As a result the surrounding nucellar tissue becomes crushed and absorbed. The two-nucleate gametophyte becomes eight-nucleate after undergoing two successive nuclear divisions. At the four-nucleate stage the gametophyte comes in direct contact with the inner most layer of the integument, the cells of which are radially elongated to form a nutritive layer called the endothelium or integumentary tapetum (figure 24). The integumentary tapetum invests the middle part of the gametophyte (figure 25). During organisation of the gametophyte, the micropylar quartet differentiates into a three-celled egg apparatus and the upper polar nucleus and the chalazal quartet into a group of three antipodal cells and the lower polar nucleus. The two polar nuclei fuse near the egg apparatus to form the secondary nucleus. Thus, the development of female gametophyte conforms to Polygonum type (Maheswari 1950).

The mature gametophyte has broad micropylar and a narrow chalazal parts. The egg apparatus consists of a pair of basally vacuolated hook-like synergids and a densely cytoplasmic egg cell (figure 25). The three antipodal cells are comparatively small in size and degenerate before fertilization.

3.3 Fertilization

Entry of the pollen tube is porogamous, one of the male gametes fuses with the egg and the other with the central cell resulting in double fertilization. One of the synergids degenerates during fertilization (figure 26).

3.4 Endosperm

Endosperm is of *ab initio* cellular type. The first division of the primary endosperm nucleus precedes that of the zygote (figure 27) and is transverse resulting in two superposed micropylar and chalazal chambers (figure 28). Vertical divisions take place in both the chambers resulting in the formation of two tiers of two cells each. The micropylar chamber divides earlier than the chalazal chamber (figures 29-31, 55).

The two juxtaposed cells derived from the chalazal chamber divide further at right angles to the first division to form four cells which finally develop into the

Figures 16-25. Megasporogenesis and development of the female gametophyte in *Mecardonia procumbens* ($\times 1,000$). **16.** Young ovule showing the formation of an integument and the megaspore mother cell. **17.** Young ovule with a megaspore mother cell surrounded by the nucellar epidermis and single integument. **18.** Young ovule showing nuclear division in the megaspore mother cell. **19.** Ovule showing nuclear division in the dyad cells. **20.** Ovule showing the degeneration of upper two micropylar megaspores. **21.** Ovule showing degeneration of two middle megaspores in the linear tetrad. **22.** Ovule with functional megaspore and the three micropylar megaspores degenerating. **23.** Two-nucleate female gametophyte. **24.** Four-nucleate gametophyte. **25.** Mature gametophyte.

chalazal haustorium (figures 32,33). The cells of the micropylar chamber divide transversely resulting in the formation of two tiers of four cells each. The derivatives of the upper tier form the micropylar haustorium consisting of four cells (figures 39,57) which remain free throughout and the lower tier forms the initials of the endosperm proper (figure 32). Activity of the micropylar haustorium ceases earlier than that of the chalazal haustorium.

The chalazal haustorium is more prominent than the micropylar haustorium and becomes aggressive. The chalazal haustorium also consists of four cells which remain free throughout (figures 38,58). The haustorium remains active throughout the development of seed and plays an important role in the nutrition of the gametophyte.

Meanwhile the initials of the endosperm proper undergo transverse and vertical divisions resulting in the formation of a massive endosperm tissue (figures 32-37). The endosperm accumulates granular deeply staining reserve food materials (figure 52). Only a part of the endosperm is utilised by the developing embryo and the rest remains in the seed.

3.5 Embryo

The zygote enlarges and elongates considerably during the early stages of endosperm development (figure 40). The first division of the zygote takes place only after the formation of a considerable amount of endosperm tissue. It divides transversely to form a larger basal cell *cb* and a smaller terminal cell *ca* (figures 41,42). The divisions of *ca* and *cb* are simultaneous (figures 43,56). The basal cell divides transversely producing two superposed cells '*m*' and '*ci*' and the terminal cell divides vertically. Thus a 'T'-shaped pro-embryonal tetrad is formed (figure 44). The pro-embryonal tetrad conforms to the A2 category of Souèges (1948). The juxtaposed cells derived from *ca* undergo another vertical division at right angles to the first division resulting in a quadrant, *q* (figure 45). The cells of the quadrant divide transversely resulting in an octant (figure 46). The cells of the octant are disposed in two superposed tiers of four cells each, the upper tier being designated as *l* and lower as *l'*. Meanwhile the cell *ci* divides transversely to give rise to *n* and *n'* (figure 46). The middle cell, *m* produces two cells *d* and *f* (figure 48), after undergoing a transverse division. Periclinal divisions occur in both the tiers *l* and *l'*, delimiting the dermatogen *de* from an inner group of cells (figures 47,48). Subsequent periclinal divisions in the inner group of cells of *l'* initiate the other histogens namely the periblem *pe* and pleiome *pl* (figure 49). By subsequent cell divisions the *l* and *l'* together assume a globular shape. The globular embryo passes through the

Figures 26-33. Development of endosperm in *Mecardonia procumbens* ($\times 1,000$). **26.** Fertilized female gametophyte with the remnants of pollen tube and one of the degenerating synergids. **27.** Zygote and divisions of primary endosperm nucleus. **28.** Zygote and two-celled endosperm. **29.** Zygote and three-celled endosperm. **30.** Zygote and three-celled endosperm showing division of nucleus in the chalazal chamber. **31.** Zygote and three-celled endosperm, showing two nuclei in the chalazal chamber. **32-33.** Delimitation of chalazal and micropylar haustoria.

Zy. Zygote; MC. Micropylar chamber; GC. Chalazal chamber; MH, Micropylar haustorium (four-celled); CH. Chalazal haustorium (four-celled).

heartshaped, and torpedo stages and finally differentiates into a dictyoledonous embryo (figures 48-51,59). After undergoing divisions, the region *l* forms the stem apex *pvt* and cotyledons *cot* of the mature embryo while the region *l* contributes to the hypocotyl *phy*. The cell *d* functions as the hypophyseal cell *h* (figure 49). This cell undergoes transverse division and forms two superposed cells. The upper lenticular cell functions as the initial of the root cortex *iec* and the lower cell acts as the initial of the root cap *ico* (figures 50, 51). The long uniseriate suspensor consisting of cells of *f*, *n* and *n'* degenerates as the embryo matures. The mature embryo is dicotyledonous with two cotyledons, a stem tip, hypocotyl and a radicle (figure 53). Thus the development of the embryo conforms to the Onagrad type (Johansen 1950).

3.6 Seed coat

The seed is endospermous (figure 52). The cells between the endothelium and the outer epidermis of the integument are gradually crushed and absorbed as the endosperm increases in bulk. Later, the wall of the integumentary tapetum is crushed as the embryo grows and little of it remains. The inner tangential and radial walls of the outer epidermis of the integument become thickened. The seed coat in the mature seed consists of the remnants of the endothelium and the outer epidermis of the integument (figures 52,53).

4. Discussion

Development of the anther in *M. procumbens* is essentially similar to that of *Mimulus ringens* (Arekal 1965) and *Lindernia hyssopioides* (Arekal *et al* 1970) of the tribe Gratiroleae. As in other members of the tribe in *M. procumbens* also the tapetal cells fuse during the later stages of development. Occasional occurrence of two-layered tapetum recorded for *Mimulus ringens* (Arekal 1965) has not been observed in the present study. Pollen grains are two-celled at the time of shedding as in other members of Gratiroleae investigated so far and also the dehiscence of anther is by longitudinal slits.

Development of the female gametophyte in *M. procumbens* is of Polygonum type (Maheswari 1950) as in other investigated species of Gratiroleae. Occasional occurrence of T-shaped megaspore as reported for *Microcarpaea muscosa* (Raju 1976) has not been observed in the present study. The mature female gametophyte has a narrow chalazal part and a broad micropylar part as in *M. muscosa* (Raju 1976), *L. hyssopioides* (Arekal *et al* 1970) and other members of the tribe. The three antipodal cells in *M. procumbens* are smaller and ephemeral as in *L. hyssopioides* (Arekal *et al* 1970) and *M. muscosa* (Raju 1976). On the other hand in *Gratiola*

Figures 34-39. Development of endosperm in *Mecardonia procumbens* ($\times 1,000$). **34.** Longitudinal section of seed showing the zygote and developing endosperm. **35-36.** Longitudinal section of seed showing the proembryo and cellular endosperm. Note the division of *ca* and *cb* in (35). **37.** Micropylar part of the seed showing the proembryo and developed endosperm. **38.** Transverse section of chalazal haustorium showing four-celled condition. **39.** Transverse section of micropylar haustorium showing four-celled condition.

ZY, Zygote; Cb, basal cell; Ca, terminal cell.

officinalis (Glišić 1933) the antipodal cells are large and persist for a long time during seed development. Unlike other members of Gratioleae, *M. ringens* (Arekal 1965) has only two superposed antipodal cells, the upper being larger and binucleate and they persist for a long time during seed development. As in *G. officinalis* (Glišić 1933) *Limnophila heterophylla* and *Stemodia viscosa* (Krishna Iyengar 1939) *M. ringens* (Arekal 1965) *L. hyssopioides* (Arekal et al 1970) and *M. muscosa* (Raju 1976) the gametophyte in the present species remains within the ovule. On the other hand in *Vandellia hirsuta*, *Torenia cordifolia*, *T. hirsuta* (Krishna Iyengar 1940a, 1941) *Vandellia angustifolia*, *V. crustacea* and *Torenia japonica* (Yamazaki 1954) the gametophyte grows out of the micropyle and comes in contact with the funiculus, the extraovular part apparently functioning as a haustorium.

The endosperm in this species is of *ab initio* cellular type as in other members of Gratioleae so far studied. The first division of the primary endosperm nucleus is transverse. However, the pattern of further divisions and sequence of wall formation during early stages of development are different in the various species of the tribe. In *M. procumbens*, the micropylar chamber undergoes a vertical division as in *Limosella aquatica* (Svensson 1928), *M. tigrinus* (Guilford and Fisk 1952), *Dopatrium lobelioides* (Srinivasan 1940), *Bacopa hamiltoniana* (Safeeulla and Govindu 1950), *Torenia japonica* (Yamazaki 1954), *Lindenbergia indica* (Pal 1958), *M. ringens* (Arekal 1965), *Ilysanthes hyssopioides* (Arekal et al 1970) and *M. muscosa* (Raju 1976).

According to Raju (1976), reports on the occurrence of a transverse division in the micropylar chamber in *Vandellia hirsuta*, *V. scabra*, *Bonnaya tenuifolia*, *I. hyssopioides* (Krishna Iyengar 1940a, b) and *M. tigrinus* (Guilford and Fisk 1952) leading to the formation of a linear row of three cells in the young endosperm, appear to be doubtful. Some of these reports have been contradicted by later workers (Arekal et al 1970; Yamazaki 1954; Glišić 1933). In all the cases reinvestigated the division in micropylar chamber is found to be vertical.

In *M. procumbens* the chalazal chamber undergoes a vertical division as in *D. lobelioides* (Srinivasan 1940), *L. pyxidaria* (Yamazaki 1954), *M. tigrinus* (Guilford and Fisk 1952), *I. hyssopioides* (Arekal et al 1970), *I. parviflora* (Raghavan and Srinivasan 1941), *M. ringens* (Arekal 1965) and *M. muscosa* (Raju 1976).

The early ontogeny and structure of the micropylar and chalazal haustoria differ in different members of Gratioleae. In *M. procumbens* the micropylar haustorium consists of four uninucleate cells as in *I. hyssopioides*, *Torenia cordifolia*, *T. hirsuta* (Krishna Iyengar 1940b, 1941), *I. parviflora* (Raghavan and Srinivasan 1941), *L. pyxidaria*, *B. verbenaeifolia*, *B. ruellioides*, *Vandellia setulosa* (Yamazaki 1954) and

Figures 40-53. Stages in the development of embryo in *Mecardonia procumbens*. 40. Zygote. 41. Nuclear division in the zygote. 42. Two-celled proembryo. 43. Nuclear division in the two-celled proembryo. 44. Proembryonal tetrad. 45-51. Stages in the development of the embryo. 53. Longitudinal section of mature seed showing dicotyledonary embryo. 52. Portion marked 'X' in 'n' enlarged to show details of the seed coat and the endosperm.

ca, terminal cell; cb, basal cell; q, quadrant; pe, periblem; pl, plerome; de, dermatogen; d, hypophyseal cell; ice, root cortex; ico, root cap; int, integument; end, endosperm. (40-51 $\times$ 1,500; 52 $\times$ 270; 53 $\times$ 600).

Figures 54-57. 54. TS of part of microsporangium showing endothelial thickenings. 55. Three-celled endosperm. 56. Longitudinal section of young seed showing the cellular endosperm and division of *ca* and *cb*. 57. TS of micropylar haustorium showing four-celled condition. (54, 56 $\times 625$; 55, 57 $\times 1000$).

Figures 58 and 59. 58. TS of chalazal haustorium showing four-celled condition. 59. Vertical section of seed showing globular embryo. (58 $\times$ 1000; 59 $\times$ 625).

L. hyssopioides (Arekal *et al* 1970). In *Deinostema violacea* (Yamazaki 1953) the four cells fuse only partially but in *S. viscosa*, *Limnophila heterophylla*, *V. hirsuta*, *V. scabra*, *Torenia cordifolia*, *T. hirsuta* (Krishna Iyengar 1939, 1940a, 1941), *T. fournieri* (Guilford and Fisk 1952) and *D. junceum* (Yamazaki 1953) they fuse to form a four-nucleate haustorium. Such a condition has not been observed in the present study. A two-celled micropylar haustorium has been observed in *V. angustifolia* and *I. violacea* (Yamazaki 1951), *M. ringens* (Arekal 1965) and *M. muscosa* (Raju 1976). Many-celled haustorium is reported in *G. officinalis* (Glišić 1933). In *V. angustifolia* and *T. violacea* (Yamazaki 1954) the micropylar haustorium is bicelled and binucleate.

In *M. procumbens* the chalazal haustorium consists of four uninucleate cells as in *M. ringens* (Arekal 1965) and *M. muscosa* (Raju 1976). A two-celled chalazal haustorium has been recorded in *M. tigrinus* (Guilford and Fisk 1952), *I. hyssopioides* (Krishna Iyengar 1940b; Arekal *et al* 1970), *I. parviflora* (Raghavan and Srinivasan 1941), *S. viscosa* (Srinivasan 1940) and *Majus japonicus* (Pal 1958). However, the wall between the two cells degenerates making it unicellular and binucleate. In *D. lobelioides* (Srinivasan 1940) the two cells of the chalazal haustorium give rise to protruberances which grow sideways towards the middle part of the ovule. In majority of the species of Gratiroleae like *T. cordifolia*, *T. hirsuta* (Krishna Iyengar 1941), *B. verbenaeifolia*, *B. ruellioides* (Yamazaki 1954), *Bacopa hamiltoniana* (Safeeulla and Govindu 1950) and *L. indica* (Pal 1958), the chalazal haustorium is generally unicellular and uninucleate. It is worthwhile to note that in *M. procumbens* both the micropylar and chalazal haustoria are four-celled and such a feature has not been reported in any member of the Gratiroleae so far.

The development of the embryo conforms to Onagrad type (Johansen 1950) as in other species of Gratioleae so far investigated.

The mature seed in *M. procumbens* is endospermous. The seed coat in the mature seed is made up of epidermis and remnants of the endothelium. It resembles that of *M. ringens* (Arekal 1965) and *M. muscosa* (Raju 1976).

Acknowledgements

One of the authors (KG) is grateful to the UGC for the award of a Teacher fellowship.

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