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EMBRYOLOGY OF TWO SPECIES OF *POLYGONUM*[1]

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ABSTRACT

Life history of *Polygonum flaccidum* Meissn. and *P. strigosum* Br. is studied. The anther wall development follows the Monocotyledonous type. Tapetum is of Secretory type. In *P. strigosum* 'Ubisch' bodies are present on the inner walls of the tapetal cells. Simultaneous cytokinesis in pollen mother cells results in tetrahedral tetrads in *P. strigosum* and both tetrahedral and decussate tetrads in *P. flaccidum*. In the latter the pollen grains are shed at 3-celled stage. In *P. strigosum* different sizes of tetrads and mature pollen grains are present even within the same anther locule. Pollen polymorphism is quite common.

The tricarpellary, syncarpous and superior ovary is unilocular with a single orthotropous, bitegmic and crassinucellate basal ovule. Nucellar beak, stylar obturator and hypostase are differentiated. The female archesporium is 2-or 3-celled. Embryo sac development is of the Polygonum type. In *P. strigosum* the embryo sac degenerates at about 2-nucleate stage. Endosperm is *ab initio* Nuclear. A small endosperm pouch is present at the chalazal end. Embryogeny follows polygonum variation of Asterad type.

Seed coat is non-multiplicative and is formed by the outer layer of outer integument. The pericarp is differentiated into an outer epicarp, middle mesocarp and an inner endocarp.

INTRODUCTION

The family Polygonaceae, with 40 genera and 800 species (Willis, 1966) is mainly confined to temperate regions with a few tropical species. The earlier embryological literature on this family pertains to the observations of Hofmeister (1849), Strasburger (1879), Fink (1899), Stevens (1912) Wood Cock (1914), Dudgeon (1918), Souèges (1919a, b; 1920 a, b; 1924), Lonay (1922), Mahony (1935, 1936), Rao (1936), Bhargava and Sawhney (1958), Doida (1960), Periasamy (1964), Guignard (1966), Neubauer (1971), Mukherjee (1972), Rao and Mukherjee (1973), Pausheva (1978) and Agoram and Krishnamurty (1979). In the present investigation embryology of two species of *Polygonum-P. flaccidum* and *P. strigosum* is worked out.

MATERIAL AND METHODS

The material collected from Araku valley and Ooty Botanical gardens, was fixed in Formalin-acetic-alcohol. Customary methods of dehydration, infiltration and embedding in paraffin wax were followed adopting the procedure given by Johansen (1940). The sections were cut between 6-12 μm and stained in Delafield's haematoxylin.

OBSERVATIONS

Microsporangium, microsporogenesis and male gametophyte :

The wall development of the tetras-

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porangiate anther conforms to the Monocotyledonous type. The hypodermal archesporium is single celled (Fig. 1). It undergoes a periclinal division and produces an outer primary parietal layer and an inner primary sporogenous layer. The former divides periclinally and produces two layers of cells, of which the outer directly develops into an endothecium and the inner undergoes one more periclinal division resulting in an outer middle layer and an inner tapetal layer (Figs. 2, 3).

The tapetum is monomorphic and is of Secretory type with uniseriate and uninucleate cells. Later the cells become binucleate in *P. flaccidum* (Fig. 3) and bi-or trinucleate in *P. strigosum*. In *P. strigosum* 'Ubisch' bodies are present on the inner walls of the tapetal cells (Fig. 4). After degeneration of the tapetal cells they tend to lie on the inner walls of the endothecial cells (Fig. 7). Middle layer is ephemeral. Fibrous thickenings are developed in the endothecial cells (Figs. 6, 7). In *P. flaccidum* the outer walls of the epidermal cells show spinous projections (Fig. 6). The epidermis persists in the mature anther.

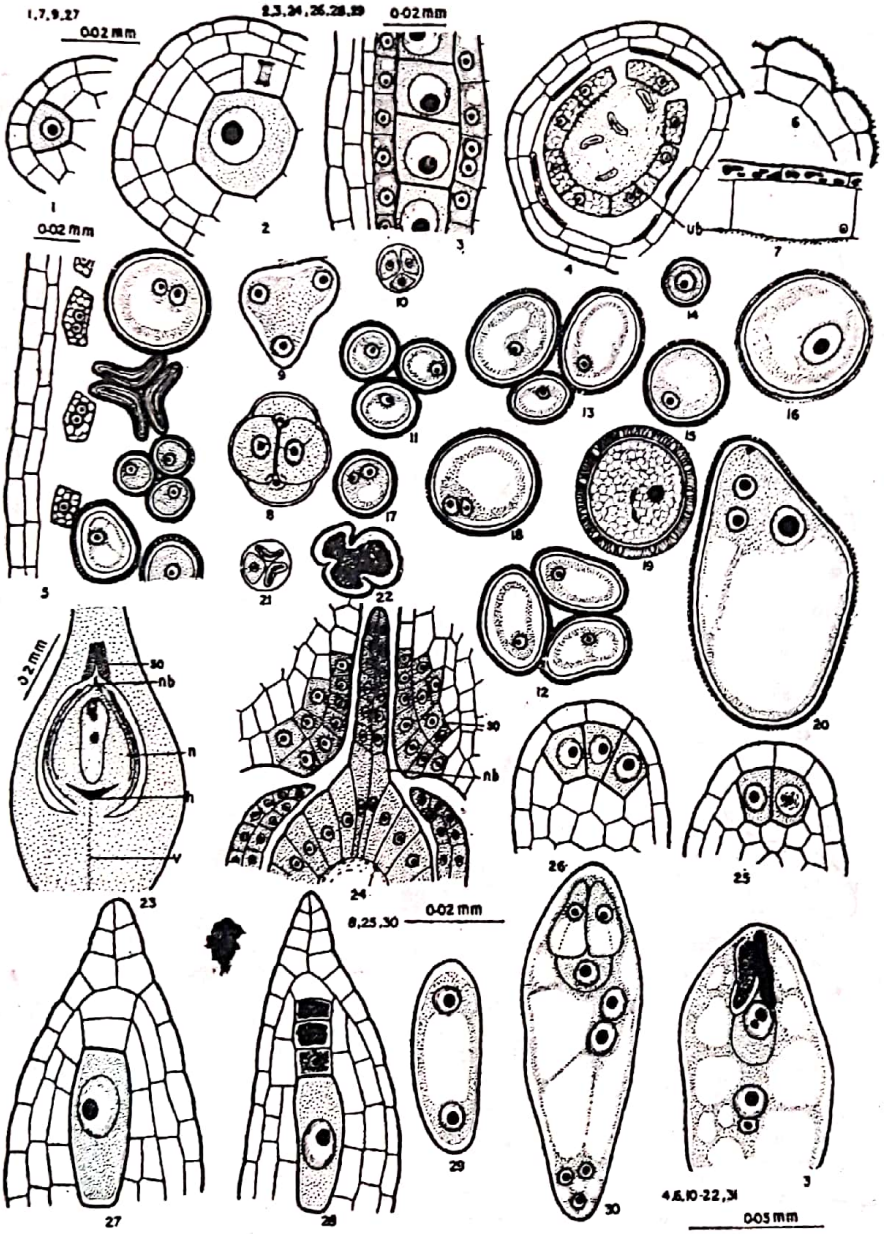
The primary sporogenous cells under go a few transverse divisions resulting in a single row of pollen mother cells which on simultaneous cytokinesis results in the formation of pollen tetrads. They are tetrahedral and decussate in *P. flaccidum* (Figs. 8, 9) and only tetrahedral in *P. strigosum* (Figs. 10-13). In the former the pollen grains are shed at 3-celled stage (Fig. 19). The exine shows reticulate ornamentation.

In *P. strigosum* a number of interesting variations both in the tetrads as well as in pollen grains are recorded. In some cases the microspores of the tetrad remain intact and all the microspores are of the same size (Figs. 10-12), while in other cases the tetrads show different sizes of microspores (Fig. 13). In a few cases the microspores become free from the tetrad condition and show pollen polymorphism. The size of the pollen grain ranges from 18 μm $\times$ 16 μm to 104 μm $\times$ 60 μm (Figs. 14-18, 20). The largest pollen grain simulate the embryosac in its size and shape. However, they are 3-nucleate with a large vegetative and two small generative nuclei (Fig. 20). All these variations are observed even within the same anther locule besides some degenerating tetrads (Fig. 5). Tetrad and pollen degenerations are quite common (Figs. 21, 22).

Ovary, megasporangium, megasporogenesis and female gametophyte :

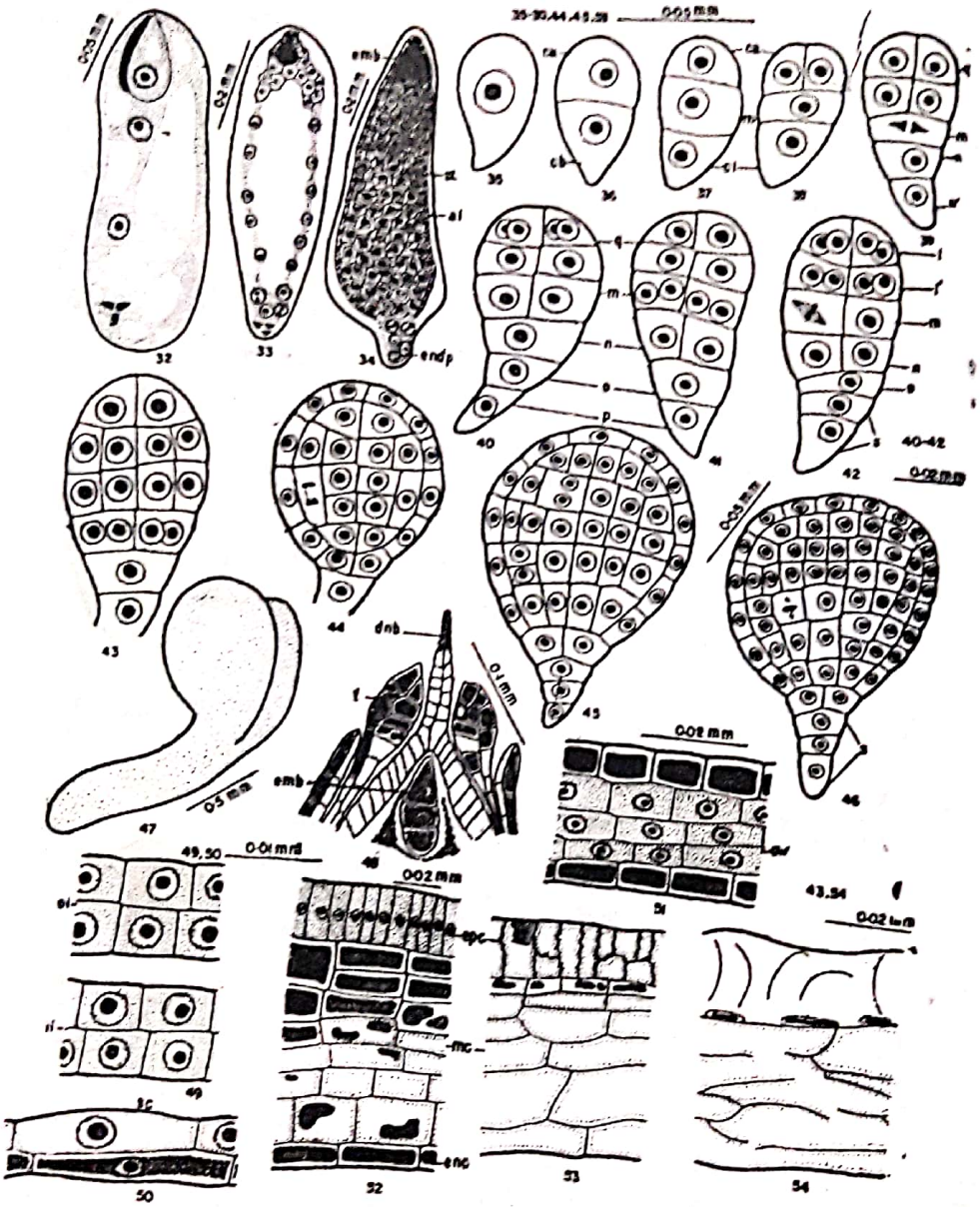
The ovary is superior, tricarpellary, syncarpous and unilocular with a single orthotropous, bitegmic and crassinucellate ovule on basal placentation (Fig. 23).

The micropyle is endostomial and is formed by the inner integument which projects slightly beyond the outer integument (Fig. 23). The epidermal cells at the apex of the nucellus divide transversely several times and produce a 2-celled thick nucellar beak which extends into the stylar canal (Fig. 24). The nucellar beak degenerates after fertilization. Less frequently, a cell or two of the adjacent nucellar epidermis may also divide periclinally. The adjacent nucellar cells along with the parietals begin to degenerate at about 2-nucleate embryo sac stage and hence the mature embryo sac comes to lie in direct contact with the nucellar epidermis (Fig. 23) which persists for a long time even after fertilization. The cells of the style near the micropylar region elongate radially, accumulate dense cytoplasm and protrude towards the micropyle and func-



Figs. 1-31. 1-5, 7, 10-18, 20-22, 25, 29: *P. strigosum* Figs. 6 & 9, 19, 23, 24, 26-28, 30, 31: *P. flaccidum*. Figs. 1-3. T. S. and L. S. of part of anther lobes showing development of wall layers. Fig. 4. T.s. of anther lobe showing meiosis II in pollen mother cells, note degenerating middle layer. Fig. 5. L.s. of an anther lobe showing tetrads, degenerating tetrads and pollen grains of different sizes. Fig. 6, 7. Fibrous endothecium. Figs. 8-13. Tetrahedral and decussate tetrads. Figs. 14-20. Pollen grains of various sizes. Figs. 21, 22. Degenerating tetrads and Pollen grains. Fig. 23. L.s. of ovary Fig. 24. Upper part of ovule showing nucellar beak and stylar obturator. Figs. 25, 26. 2-and 3-celled female archesporium. Fig. 27. Megaspore mother cell. Figs. 28-30. Stages in the development of embryo sac. Fig. 31. Embryo sac showing syngamy and triple fusion with degenerating synergid and pollen tube.

h-hypostase, n-nucellus, nb-nucellar beak, so-stylar obturator, ub-'Ubish' bodies, v-vascular bundle.



Figs. 32-54. 32-47, 49-54 : *P. flaccidum*. Fig. 48: *P. strigosum*. Fig. 32. Em—bryosac showing zygote and two free endosperm nuclei with degenerating antipodals. Fig. 33. Embryo sac showing cellularisation of endosperm. Fig. 34. Embryo sac showing cellular endosperm with an endosperm pouch. Figs. 35-47. Stages in the development of embryo. Fig. 48. L. S. of an ovule showing degenerating 3-celled embryo and Nucellar beak. Figs. 49 & 50. L.s. part of integument showing development of testa. Figs. 51-54. Stages in the development of pericarp.

al-aleuronelayer, dnb-de-generating nucellar beak, emb-embryo, enc-endocarp, endp-endosperm pouch epc-epicarp, ii-innerintegument, mc-mesocarp, oi-outer integument, ow-ovary wall, st-starch, sc-seed coat, t-tannin.

tion as stylar obturator (Fig. 24). It is, however, feebly developed in *P. flaccidum* and well developed in *P. strigosum*. The stylar obturator directs the pollen tube into the embryo sac. The hypostase consists of a well defined group of tannin filled cells which constitute a plate-like structure (Fig. 23). The vascular bundle terminates near the hypostase (Fig. 23).

The female archesporium is hypodermal and 2 or 3-celled (Figs. 25, 26). Usually one of them develops further and after undergoing a periclinal division produces an outer parietal and an inner megaspore mother cell. The former undergoes periclinal divisions to form a two layered parietal tissue (Fig. 27). As a result of meiotic divisions in the megaspore mother cell a linear tetrad of megaspores is formed (Fig. 28). The chalazal megaspore after undergoing three mitotic divisions produces an 8--nucleate embryo sac of the Polygonum type (Figs. 28-30). The mature embryo sac consists of an egg apparatus, secondary nucleus and three antipodals.

In *P. strigosum* the embryo sac begins to degenerate at about 2-nucleate stage.

Fertilization and Endosperm :

In *P. flaccidum* the path of the pollen tube into the embryo sac is porogamous. One of the synergids is destroyed during this process. Syngamy and triple fusion occur more or less simultaneously (Fig. 31). In *P. strigosum* though a well developed nucellar beak and stylar obturator are formed the chances of fertilization are very rare as the embryo sac degenerates at an early stage.

Endosperm is *ab initio* nuclear. After syngamy has established the triploid primary endosperm nucleus originally situated at the centre moves towards the chalazal end and undergoes a free division resulting in two nuclei (Fig. 32). They undergo further free nuclear divisions resulting in a number of nuclei which are arranged along the periphery of the embryo sac enclosing a central vacuole. At about globular embryo stage, cell wall formation commences at the micropylar end and progresses towards the chalazal end (Fig. 33) finally filling the entire embryo sac with cellular tissue (Fig. 34). The endosperm at the chalazal region produces a small pouch in which the nuclei remain free with dense cytoplasm (Fig. 34). The degenerating antipodals are seen persisting even at this stage. The entire endosperm is starchy, but the peripheral aleurone layer (Fig. 34).

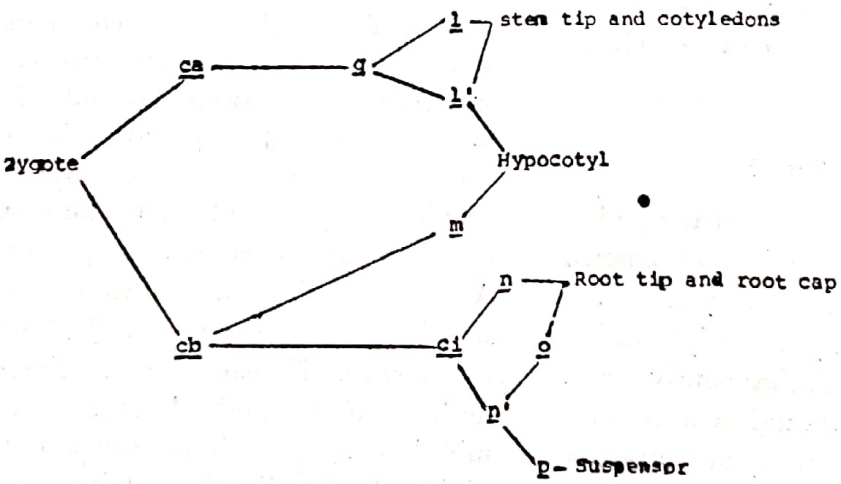
Embryogeny :

The zygote (Fig. 35) undergoes a transverse division resulting in a terminal cell *ca* and a basal cell *cb* (Fig. 36). The former divides longitudinally and the latter transversely resulting in a 4-celled T-shaped proembryo (Figs. 37, 38). The cell *cb* divides transversely producing two superposed cells *ci* and *m*. The two juxtaposed cells of *ca* undergo one more division by a wall oriented perpendicularly to the first wall to form quadrant of cells *q* (Fig. 39). As a result of one more transverse division in these two tiers of cells, four cells are formed in each tier. These are designated as 1 and 1′ (Fig. 42). The middle cell *m* at about the same time divides longitudinally forming two juxtaposed cells (Fig. 39). The proximal cell *ci* divides transversely forming two superposed cells *n* and *n* (Fig. 39). During further development the cell *n* undergoes a transverse division to form two cells *o* and *p* (Figs. 40, 41). Later

the cell *n* also undergoes two vertical divisions at right angles to each other resulting in quadrant (Figs. 41-43). In the two tiers 1 and 1 periclinal divisions occur resulting in dermatogen layer towards outside and periblem and plerome initials towards inside. Due to similar periclinal divisions in tier *m* and *n* also dermatogen, periblem and plerome initials are differentiated (Figs. 43, 44).

The derivatives of the tiers 1 and a part of 1′ contribute to stem tip and cotyledons and the remaining part of 1′ and *m* contribute to the hypocotyledonary region. The derivatives of cells *n* and *o* contribute to all parts of root. The cell *p* after undergoing one or two transverse divisions produces a suspensor of 3 cells (Figs. 45, 46). The mature embryo is somewhat curved (Fig. 47).

The relationship of the derivatives of the proembryonic tetrad to specific organs of mature embryo is shown below in the schematic manner :



From the above, it is evident that the 4-celled proembryo is T-shaped and the derivatives of both the cells *ca* and *cb* contribute to the embryo proper. Thus the embryogeny conforms to the Asterad type. Further the hypocotyledonary region is formed from the lower portion of tier 1′ (derivatives of *ca*) and from the derivatives of *m* and this keys out to polygonum variation.

Testa and Pericarp :

The integuments are two layered (Fig. 49). In *P. flaccidum*, as a consequence of fertilization both the layers of the inner integument along with the inner layer of the outer integument degenerate and the testa is formed by the outer layer of the outer integument alone (Fig. 50). Thus the seed coat is non-multiplicative.

The ovary wall at the megaspore mother cell stage consists of 4 or 5 layers of parenchymatous cells (Fig. 51). At mature embryo sac stage, cells of the inner and outer epidermal layers enlarge and the number of layers in the ovary wall increases upto 6. At the time of fertilization the outermost layer of the ovary, the epicarp consists of a single layer of palisade cells which are thin walled. The mesocarp consists of an outer region of 3 or 4 layers of elongated tannin filled cells and an inner region of 3 or 4 layers of parenchyama-

tous cells. The endocarp consists of single layered tannin filled cells (Fig. 52). In the later stage the cells of the epicarp become much convoluted and thick walled (Fig. 53). At maturity the pericarp consists of convoluted cells of the epicarp and crushed remnants of mesocarp (Fig. 54).

In *P. strigosum* though the fruit develops into a perfect nutlet with differentiation of epicarp, mesocarp and endocarp, the fruit does not necessarily contain a seed or an embryo but rather an accumulation of degenerating cells and the fruits develop parthenocarpically. In a rare instance of *P. strigosum* a three celled degenerating embryo is recorded (Fig. 48).

DISCUSSION

The family Polygonaceae is embryologically characterised by the presence of Monocotyledonous anther wall development, Secretory type of anther tapetum, 3-celled pollen grains, orthotropous, bitegmic and crassinucellate ovule on basal placentation, nucellar beak, periclinal divisions of the nucellar epidermis, hypostase, Nuclear type of endosperm development with a small endosperm pouch and Asterad type of embryogeny (Hofmeister, 1849; Strasburger, 1879; Fink, 1899; Stevens, 1912; Wood Cock, 1914; Dudgeon, 1918; Soueges, 1919a, b; 1920a, b; 1924; Lonay, 1922; Mahony, 1935, 1936; Rao, 1936; Bhargava and Sawhney, 1958; Doida, 1960; Periasamy, 1964; Guignard, 1966; Neubauer, 1971; Mukherjee, 1972; Rao and Mukherjee, 1973; Pausheva, 1978 and Agoram and Krishnamurty, 1979).

P. flaccidum, the presently investigated member, identifies itself with the rest of the hitherto investigated members of the family in its embryological features. However, Agoram and Krishnamurty (1979) reported Dicotyledonous type of anther wall development in *Antigonon leptopus*.

A stylar obturator was reported for the first time in *P. flaccidum* and *P. strigosum* (present data). Similarly in *Coccoloba uvifera* Periasamy (1964) and in *A. leptopus* Agoram and Krishnamurty (1979) reported ruminate endosperm as an exceptional case. The crucifer type of embryogeny in *Fagopyrum esculentum* (Stevens, 1912; Mahony, 1936) may also be taken as the exception to the family Polygonaceae. *P. strigosum* is unique in showing microspores remaining united in tetrads in certain cases, pollen polymorphism, pollen and embryo sac degenerations and parthenocarpic development of fruits.

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