STUDIES IN THE FAMILY SAXIFRAGACEAE—IV*

A Contribution to the Embryology of *Bergenia ciliata* (Royle) Raizada

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ABSTRACT

1. The anther at maturity shows characteristic fibrous thickening of the endothecium expending to the other parts as well. The pollen is shed at 2-celled stage.

2. The ovule is anatropous, bitegmic and crassinucellate. The development of embryo-sac conforms to *Polygonum* type. An abnormal case of twin embryo-sacs has also been recorded.

3. The endosperm is of *Cellular* type and the embryo is of *Caryophyllad* type showing some variations.

INTRODUCTION

The plants of *Bergenia ciliata* are small herbs having a short root-stock and large orbicular or ovate leaves. The scapes bear pentamerous and perigynous flowers in paniculate cymes. Some aspects of embryology of a few species of this genus has been dealt by Mauritzon (1933). The present paper, however, is designed to give detailed account of various aspects of embryology of *B. ciliata*.

The material was collected by Dr. Y. S. Murty from Mussoorie and fixed in formalin-acetic-alcohol. Following customary method of dehydration and embedding, the material was sectioned between 8–12 μ and stained with iron alum-haematoxylin-fast green and safranin-fast green combinations.

OBSERVATIONS

*Microsporangium and male gametophyte.*—The wall of a mature anther consists of an outer epidermis, endothecium, 1–2 middle layers and

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an innermost tapetum. At maturity, however, the endothecium develops characteristic fibrous thickenings (Fig. 1). These thickenings are also observed in some cells around the connective (Fig. 2). The dehiscence of the anther takes place by the confluence of the pollen chambers and subsequent appearance of a slit in the stomial groove (Fig. 2). Early stages of microsporogenesis could not be seen due to lack of young material. The pollen is shed at 2-celled stage (Figs. 3–4). In *Saxifraga diversifolia* (Saxena, 1964a), however, the pollen is shed at 3-celled stage. A few sterile pollen grains are also observed (Fig. 5).

_Megasporogenesis and female gametophyte._—The megaspore mother cell appears in a young ovule primordium capped by two parietal cells even before the differentiated and the ovule begins to bend (Figs. 6, 7). At the binucleate embryo-sac stage the ovule becomes perfectly anatropous (Fig. 8). An orthotropous ovule with a long funiculus is also observed as a case of abnormality (Fig. 9), similar to those reported in *Saxifraga diversifolia* and *Parnassia nubicola* (Saxena, 1964a, b).

Thus the mature ovules are anatropous, bitegmic and crassinucellate. Similar ovules have also been observed in the various species of *Astillbe*, *Saxifraga* and *Heuchera* (see Webb, 1902; Pace, 1912; Chapman, 1933; Wiggins, 1959; Saxena, 1964a). In the latter stages they become tanniferous and the tannins are chiefly distributed in the chalazal region and the outer layer of outer integument (cf. *Astillbe rivularis*—Saxena, 1969). Some vertical and transverse divisions take place in the parietal cells (Figs. 6–8, 10, 13). A transverse division in the megaspore mother cell differentiates the dyads (Figs. 7, 12). The upper dyad divides generally vertically and the lower transversely forming a T-shaped tetrad of megaspores (Figs. 12–13). The two dyads occasionally may divide transversely (Fig. 7). Generally, the lowermost megaspore is functional but the remaining megaspores may also continue up to the binucleate embryo-sac stage.

The nucleus of the functional megaspore divides successively thrice and as a result eight nuclei are formed, four lying at each pole (Figs. 14–17). These eight nuclei organise into the normal *Polygonum* type of embryo-sac (see Maheshwari, 1950). The embryo-sac enlarges in size at the cost of neighbouring nucellar cells. The two polars unite to form a secondary nucleus (Fig. 18). A case of twin embryo-sacs has also been observed (Fig. 19). The two embryo-sacs here lie close to each other. On the contrary, twin embryos have been reported by Lebègue (1949) in _Bergenia delavayi_.
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Presence of pollen tubes in the micropylar region of the ovule suggests the occurrence of porogamy (Fig. 20). The antipodals degenerate after fertilization (Fig. 21).

**Endosperm.**—The primary endosperm nucleus divides prior to zygote. The first division of the primary endosperm nucleus is followed by the divisions of the embryo-sac cavity into a small chalazal and a much bigger micropylar chamber (Fig. 21). The protoplasmic contents of the chalazal cell are denser than that of micropylar. The second and subsequent divisions are also followed by wall formation and thus the development of endosperm conforms to *Cellular* type (Figs. 21–24) Mauritzon (1933) also reports the occurrence of *Cellular* type of endosperm in *Bergenia*. The plane of second division varies in the two cells. The micropylar cell divides by a transverse wall and the septum laid down is slightly towards the egg side thus forming a big cell in the centre (Fig. 22). The chalazal cell, unlike the micropylar one, divides by a vertical wall.

In accordance with the ontogenetic sequence tabulated by Swamy and Parameswaran (1963) the endosperm of *B. ciliata* can be classed under Group I (B).

**Embryogeny.**—The development of embryo in this species closely resembles to that of *Saxifraga diversifolia* (Saxena, 1964 a). As a result of first transverse division a larger basal cell *cb* and a comparatively smaller terminal cell *ca* are differentiated (Fig. 25). Transverse division occurs in the cell *ca* forming cells *cc* and *cd* of which the cell *cd* divides immediately into an upper component *ci* and a lower *m* (Fig. 26). The cell *cc* divides by a vertical wall and the 5-celled proembryo is thus ‘⊥’-shaped (Fig. 27). Another transverse division sets in the cell *m* dividing into a lower cell *d* and an upper *f* (Figs. 28–31). The cell *d* in its further course functions as hypophysis. The cell *cb* generally shows irregular divisions (Figs. 30–39) or it may not divide at all. Another division in the cell *cc* results in differentiation of the quadrants *q* (Fig. 32). Sometimes the nuclei of the cell *cc* do not divide simultaneously (Figs. 33–34). Further division of each quadrant results in the formation of octants, of which the upper tier is designated as *l'* and the lower *l* (Figs. 35–36). Periclinal walls are laid down separating the dermatogen (*de* in Fig. 37). The cells of the tier *l* lying inner to dermatogen are the initials of cotyledons (*cot*) (Figs. 37–38). Similar periclinal walls in the cells of tier *l'* lying inner to dermatogen separate the outer periblem (*pe*) and inner plerome (*pl*) initials (Figs. 38–39). Vertical divisions in the cells *d* and *f* differentiate root-cap initials (*pco*) and initials of root
cortex (*iec*) (Figs. 38–39). Thus, we see that the cell *cb* does not contribute towards the formation of the embryo proper but, on the other hand, it forms a part of the suspensor. As such the development of embryo con-

**FIGS. 25–42**
forms to Caryophyllad type showing similar variations as has been recorded for Saxifraga granulata (Souéges, 1936).

Fate of the integuments.—In an ovule having two-nucleate embryo-sac, the outer and inner integuments are 2-3 and 2-celled thick respectively. The cells of the outer integument have an almost uniformly distributed contents and they are comparatively bigger in size (Fig. 40). At this stage the 4-5-layered nucellus shows smaller cells with comparatively dense contents. At 2-celled embryo stage the cells of the inner integument and nucellus become more radially stretched and the thickness of the nucellus decreases due to the development of endosperm (Fig. 41). At globular embryo stage the structure of the wall is subjected to major changes. The outer layer of the outer integument possesses dense contents and becomes greatly enlarged. The outermost wall becomes very much thickened and papillate (Fig. 42). The remaining two layers of the outer integument remain as such except for that they become tangentially stretched and less denser in contents. The inner integument is reduced to only single layer of empty cells. The bulk of the nucellus is also consumed and now it encloses the endosperm.

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**EXPLANATION OF FIGURES**

Figs. 1-24. Fig. 1. A portion of the anther wall showing fibrous thickening. Fig. 2. T.S. of anther showing extension of the fibrous thickening to other parts. Figs. 3-4. Uni- and bi-nucleate pollen grains. Figs. 5-7. Developmental stages of the ovule. Fig. 8. An abnormal orthotropous ovule. Figs. 9-12. Megaspore mother cell and megasporogenesis. Figs. 13-16. Developmental stages of the embryo-sac. Fig. 17. Organised embryo-sac. Fig. 18. Twin embryo-sacs; the normal embryo-sac is three-nucleate, and the second one is bi-nucleate. Fig. 19. Showing persistent pollen tube. Figs. 20-24. Various stages in the development of endosperm. ant., antipodals; ch.c., chalazal cell; deg. mg., degenerated megaspores; deg. n.c., degenerated nucellar cells; e., egg; emb., embryo; end., endothecium; en., endosperm; fib. th., fibrous thickening; epi., epidermis; i.i., Inner integument; m.c., micropylar cell; m.l., middle layers; meg. m.c., megaspore mother cell; n.e.s., normal embryo-sac; nu., nucellus; o.i., outer integument; p.c., parietal cells; pt., pollen tube; s.e.s., second embryo sac; s.n., secondary nucleus; s.i.g., stomial groove; syn., synergid; zy., zygote.

Figs. 25-42. Figs. 25-36. Early stages in the development of the embryo. Figs. 37-38. Globular embryos. Figs. 39-42. Developmental stages of the seedcoat. ca., terminal cell; c.b., basal cell; ci.cc. (see description); cot., initial of the cotyledons; d. (see description); de., dermatogen; en., endosperm; f. (see description); i.i., inner integument; i.ec., initials of embryonic root cortex; l.l. m. (see description); nu., nucellus; o.i., outer integument; pco., initials of embryonic root-cap; pe., periblem; pl., plerome; q., quadrants.