

EMBRYOLOGY AND SYSTEMATIC POSITION OF *CROSSOSOMA CALIFORNICUM* NUTT.

R. N. KAPIL AND R. S. VANI

Department of Botany, University of Delhi, Delhi-6

DIVERSE opinions have been expressed regarding the systematic position of the genus *Crossosoma*. Bentham and Hooker¹ included it in the Dilleniaceæ; Engler and Prantl³ raised this taxon to the rank of a family, the Crossosomataceæ, and placed it near the Rosaceæ in the Geraniales and Hutchinson⁴ and Eames² in the Dilleniales. Lawrence⁵ has included the Crossosomataceæ in the Rosales. Lemesle^{6,7} studied the wood anatomy of *Crossosoma californicum* and assigned the family to the Ranales between the Pæoniaceæ and the Ranunculaceæ. He derived it from the Pæoniaceæ. In view of the above controversy, and lack of embryological data on this family, the present investigation was undertaken. The material of *Crossosoma californicum* was obtained from Dr. Sherwin Carlquist of Claremont, California, U.S.A., through the courtesy of Professor P. Maheshwari.

The flowers are solitary and terminal, and are borne on short shoots. They are bisexual and regular with a long pedicel (Figs. 1, 2). The calyx consists of five, connate, persistent sepals forming a turbinate tube. There are five free orbicular petals. The stamens are numerous, free and inserted on the rim of the hypanthium. The gynoecium is tricarpellary (rarely tetracarpellary) and apocarpous, although sometimes two of the carpels are fused (Figs. 3-5). The ovary bears a number of ovules which are arranged in two rows on a marginal placenta. Small rosettes of acicular crystals are present in all the floral parts.

In a young anther, the sporogenous cells are surrounded by a glandular tapetum, three middle layers, an endothecium, and an epidermis (Fig. 6). Initially the tapetum is single-layered and the cells are uninucleate. However, it becomes irregularly 2- or 3-layered and the nuclei become polyploid due to repeated divisions and fusions (Figs. 7-10). The pollen grains are tricolporate (Fig. 11) and are shed at the 2-celled stage.

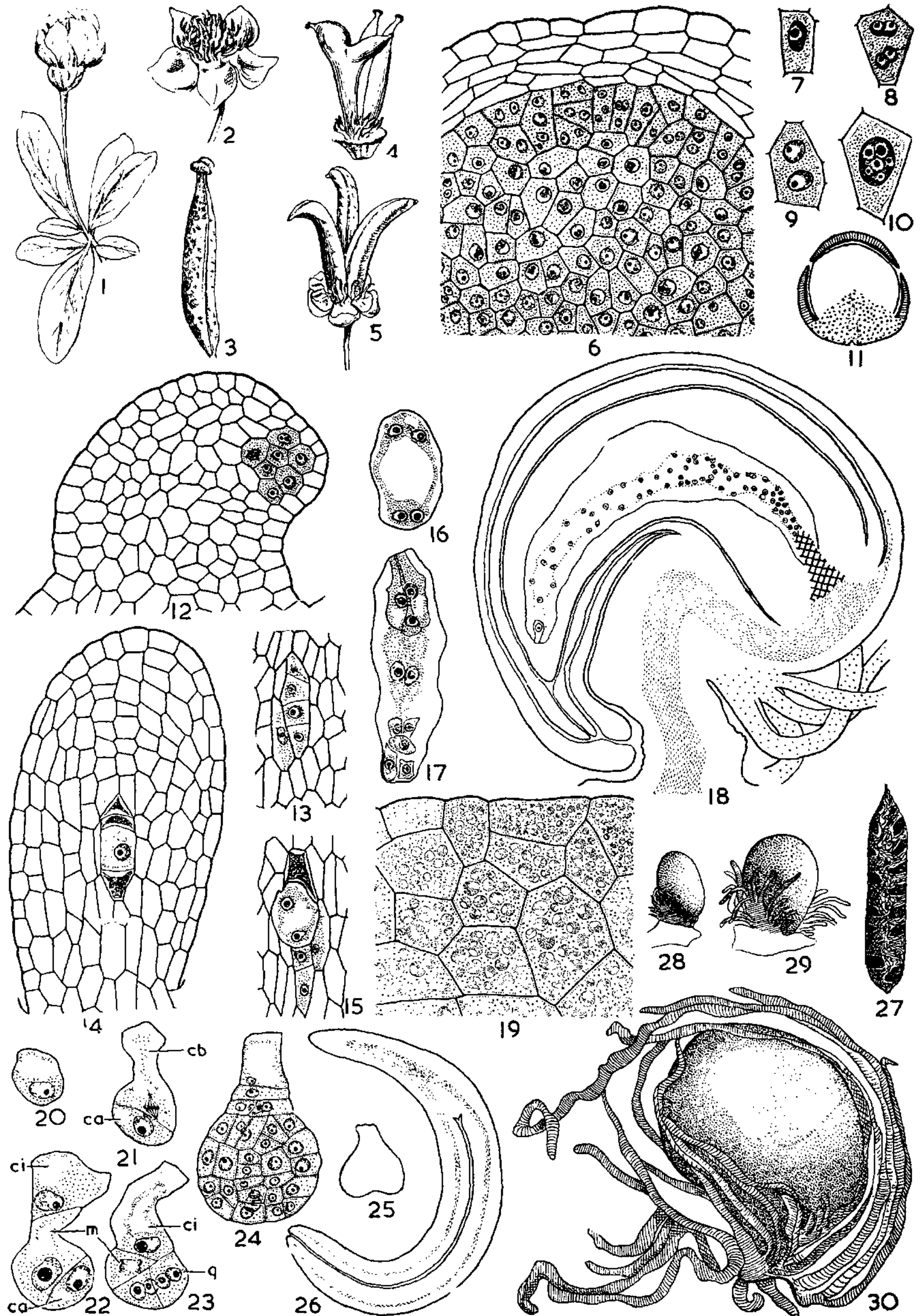
The ovules are campylotropous, bitegminal and crassinucellar. A multicelled hypodermal archesporium differentiates in the young nucellus (Fig. 12). The subepidermal cells of the archesporium cut off the primary parietal cells which by further divisions produce a massive 6- or 7-layered parietal tissue (Fig. 14).

Only one mother cell divides to give rise to a linear tetrad of megaspores. However, a few cells of the nucellus adjacent to it contain dense cytoplasm and prominent nuclei (Figs. 13-15). They may possibly be interpreted as unreduced embryo sac initials but we have not found them to develop any further. Often the second megaspore from the chalazal end functions (Fig. 14), but any of the other three megaspores may engender an embryo sac. Subsequent mitoses of the functioning megaspore result in 2-, 4- and 8-nucleate embryo sacs (Figs. 15-17). The development, thus, conforms to the *Polygonum* type. The synergids start degenerating soon after fertilization but occasionally one of them may persist for some time. The polar nuclei fuse before fertilization. There are three antipodal cells which frequently divide to form five or six cells (Fig. 17).

Fertilization is porogamous and the endosperm is Nuclear (Fig. 18). Centripetal wall formation sets in at the micropylar end at the globular stage of the proembryo and the endosperm becomes completely cellular by the time the embryo is heart-shaped and contains fatty food reserves (Fig. 19).

The zygote (Fig. 20) divides only after a large number of endosperm nuclei are formed. The first division is transverse resulting in a small apical cell *ca* and a large basal cell *cb* (Fig. 21). The cell *cb* divides earlier than *ca* by an obliquely transverse wall, forming the tiers *m* and *ci* (Fig. 22). The cell *ci* remains undivided while *m* undergoes a transverse division to form the cells *d* and *f*. The apical cell divides vertically and then transversely to give rise to the quadrant and the octant stages. Further divisions proceed in all planes resulting in a globular and later a heart-shaped proembryo (Figs. 23-25). The mature embryo is large, dicotyledonous and curved, and occupies a major portion of the seed (Fig. 26).

The fruit is a follicle and contains several fertile seeds which are reniform and black. The seed coat consists of 4 or 5 layers of highly sclerified cells of the outer integument and a single fibrous layer contributed by the inner epidermis of the inner integument. A well developed fimbriate aril partially envelope the seeds (Fig. 27). It differentiates as a small



FIGS. 1-30. Fig. 1. Twig bearing a flower, $\times 1$. Fig. 2. Open flower showing free stamens, $\times 1.5$. Fig. 3. Carpel, $\times 3$. Fig. 4. Abnormal pistil with two free and two fused carpels, $\times 1.5$. Fig. 5. Mature fruits, $\times 1$. Fig. 6. T.s. portion of anther at the microspore mother cell stage showing epidermis, endothecium, three middle layers and an irregularly 2- or 3-layer red tapetum, $\times 453$. Figs. 7-10. Nuclear divisions and fusions in tapetal cells, $\times 741$. Fig. 11. Palynogram, $\times 453$. Fig. 12. L.s. young nucellus with multicelled archesporium, $\times 412$. Fig. 13. Linear tetrad of megaspores; a possible unreduced embryo sac initial is also seen, $\times 412$. Fig. 14. Functioning megaspore, $\times 412$. Figs. 15-17. 2-, 4-, and 8-nucleate embryo sacs, $\times 412$. Fig. 18. L.s. young seed showing zygote and free nuclear endosperm, $\times 67$. Fig. 19. Cells of mature endosperm packed with fatty food reserves, $\times 453$. Figs. 20-25. Stages in development of embryo, Figs. 20-24, $\times 412$; Fig. 25, $\times 67$. Fig. 26. Mature embryo, $\times 25$. Fig. 27. Fruit with pericarp removed; note seeds partly covered by aril, $\times 1.5$. Figs. 28-29. Young ovules showing initiation and branching of aril, $\times 58$. Fig. 30. Mature seed enveloped by fimbriate aril, $\times 29$.

annular structure at the base of the funiculus (Fig. 28). As it grows it becomes lacinate and surrounds the seed on the sides (Figs. 29, 30). It is devoid of any vascular supply. Its cells have scanty cytoplasm and remain uninucleate throughout.

Crossosoma resembles the peonies in having perigynous, bracteate, and bisexual flowers; numerous stamens; an apocarpous gynoecium; multicelled archesporium; and a Polygonum type of embryo sac. However, it stands apart from them in possessing simple leaves; vessels with simple perforations; rosettes of small acicular crystals in all the floral and vegetative parts; a whorled perianth; free and cyclic stamens; campylotropous ovules; a non-vascularized aril; single embryo sac; and a large, curved embryo. A more significant difference lies in the presence of a coenocytic phase in the proembryo of *Paeonia* which is conspicuously absent in *Crossosoma*. Hence any close relationship between *Crossosoma* and *Paeonia* is unwarranted.

Morphologically and embryologically the Ranunculaceae differ from *Crossosoma* in the presence of hypogynous flowers, centripetal development of the stamens, a single-layered tapetum, anatropous ovules, a parietal tissue partly formed by the periclinal divisions of the nucellar epidermis, occurrence of both Allium and Polygonum types of embryo sacs, persistent and polyploid antipodal cells, a minute and straight embryo, and non-arillate seeds. Thus a position intermediate between the Ranunculaceae and Paeoniaceae is not justified for *Crossosoma*.

No doubt there are striking similarities in the flowers of *Crossosoma* and the Rosaceae like perigyny, numerous free stamens, and apocarpous gynoecium but this family has several characteristic features which have no parallel in the Crossosomataceae. For example, in the Rosaceae the leaves are usually compound, the vessels are in small groups, crystals are either solitary or clustered, the stamens are centripetal, the pollen grains are united in loose tetrads, the ovules are anatropous (sometimes uni-

tegminal), the seeds are non-arillate with a small and straight embryo with hardly any endosperm, and apomixis is common. Therefore, the assignment of the Crossosomataceae to the Rosales near the Rosaceae must also be rejected.

Crossosoma differs from the Dilleniaceae in having free, perigynous stamens (Hutchinson⁴); tapetal cells with polyploid nuclei; a multicelled female archesporium; a large, curved embryo; and rosettes of small acicular crystals. The absence of tubes or sacs filled with raphides and crystal sand also indicates that the genus has no affinities with the Dilleniaceae (Metcalf and Chalk⁸). However, the two families show several common features: (1) simple leaves; (2) isolated vessels; (3) secretory tapetum; (4) tricolporate pollen grains; (5) campylotropous, bitegminal, crassinucellar ovules; (6) Polygonum type of embryo sac; (7) Nuclear endosperm; and (8) reniform and arillate seeds.

It is concluded that although *Crossosoma* appears to be more appropriately allied to the Dilleniaceae than to the other families mentioned earlier, it is necessary to investigate more genera of the Dilleniaceae before a final word can be said about its relationships.

It is a pleasure to thank Professor P. Maheshwari for his generous counsel and Dr. N. N. Bhandari for suggestions. Acknowledgements are expressed to the Government of India for the award of a Junior Research Fellowship to one of us (R. S. V.).

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