DEVELOPMENT OF THE EMBRYO-SAC IN THE CONVOLVULACEÆ

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THERE are a number of contradictory statements in the literature on the embryology of the Convolvulaceæ, particularly with reference to the presence or absence of parietal cells. Peters (1908) investigated *Cuscuta europea* and *Convolvulus sepium* and reported that the primary archesporial cell in both of them cuts off a wall cell and the embryo-sac develops according to the normal type. Asplund (1920) also reported the formation of a primary wall cell in *Cuscuta lupuliformis*. Svensson (1925), on the other hand, holds the view that the parietal cells described in *Cuscuta* and *Convolvulus* by Peters and Asplund were probably derived from the epidermis and are not true parietal cells. Dahlgren (1927) shares the views of Svensson and states that parietal cells are definitely absent in *Cuscuta lupuliformis* and *C. epithymum*. Macpherson (1921) who studied the embryo-sac of *Cuscuta gronovii* and *Convolvulus sepium* could not observe the early stages of its development. Kenyan (1929) investigated *Ipomea trifida*. He found numerous archesporial cells, formation of the parietal cells and a normal type of embryo-sac. His observations also indicate that the inner cells of the integument are consumed during the growth of the embryo-sac. Mathur (1934) reported the occurrence of a definite primary parietal cell in *Convolvulus arvensis*. Johri (1934) found that in *Cuscuta reflexa* the hypodermal archesporial cell functions directly as the megaspore-mother cell and the wall cells are completely absent. He has further stated that the development of the embryo-sac conforms to the *Scilla*-type. Smith (1934) in several species of *Cuscuta* growing in North Carolina and Tiwary and Rao (1936) in *Evolvulus nummularis* found that the embryo-sac develops according to the normal type. They do not say anything about the parietal tissue. Raghava Rao (1940) in a recent paper describes the development of the embryo-sac in *Ipomea Learii, I. staphylina, I. hederacea, Argyreia speciosa* and *Evolvulus alsinoides*. He reports the formation of a primary wall cell in *Ipomea Learii* and its absence in *I. staphylina* and *Evolvulus alsinoides*. He says nothing about *Ipomea hederacea* and *Argyreia speciosa* in this connection.

The present investigation deals with the development and structure of the embryo-sac in *Jacquemontia violacea* Choisy, *Ipomea pulchella* Roth., *I. Horsfalliae* Hook. *f.*, *I. obscura* Ker-Gawl., *I. sepiaria* Koenig and *Operculina Turpethum* Manso. Material of these was collected from the environs of Bombay and studied according to the customary methods.

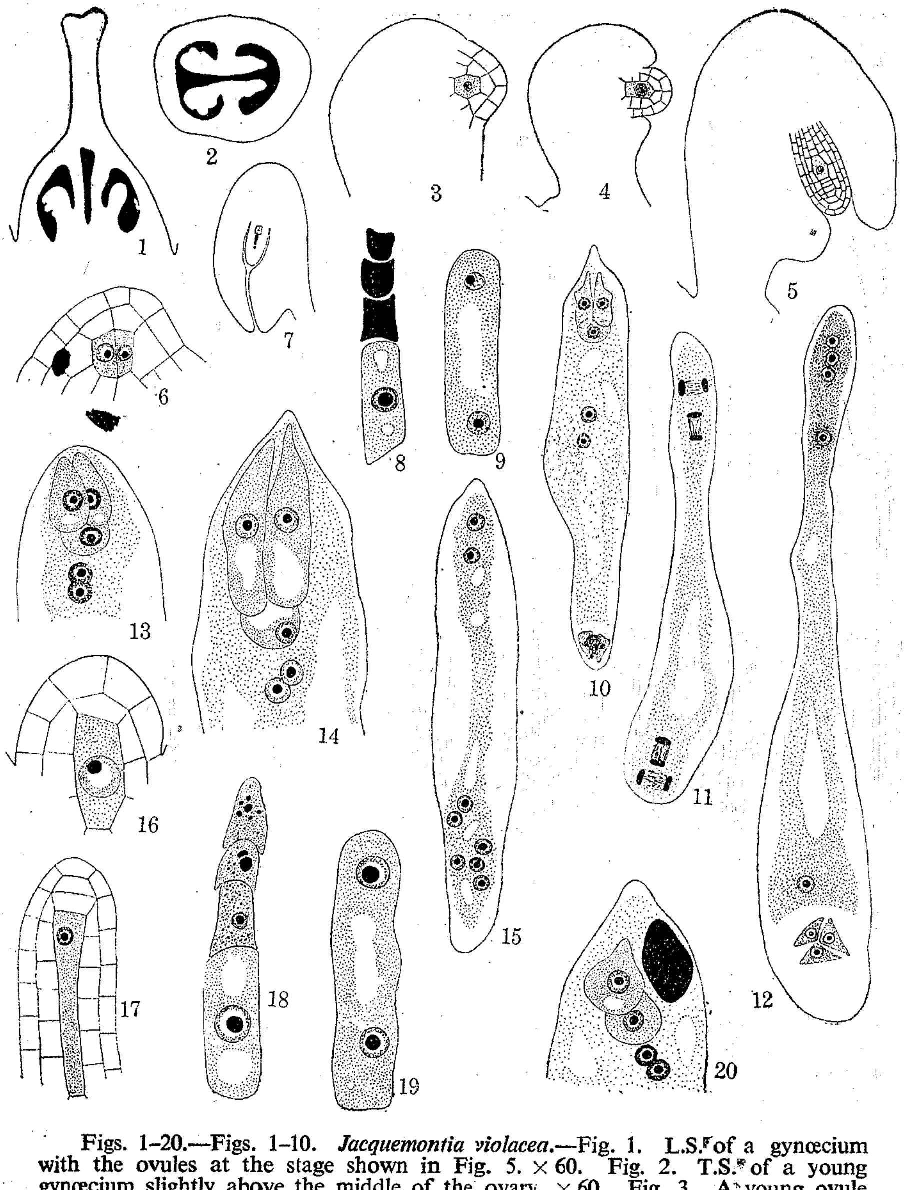
Observations

Ovary and Ovule.—The ovary of the Convulvulaceæ is generally described as bilocular, with two axile ovules in each loculus arising from near the base as shown in Fig. 1. Such a description however is not true for all the stages. Serial transverse sections of young ovaries, as illustrated in Fig. 2 for *Jacquemontia violacea*, reveal that the ovule-bearing carpel margins do not meet in the centre. The ovary therefore is at first unilocular and the placentation marginal and parietal. The two placentas are separated near the base of the ovary by a narrow channel. Near the top of the ovary the margins of the carpels become even more clear and those of the opposite sides are seen to be quite free. The line of fusion between the two carpels is quite clear even in the style. Thus the microscopical examination of the young stages of the ovary shows that the union of the carpels is not so thorough as might appear from the outside. These stages also clearly bring out the bicarpellary nature of the gynoecium.

The ovule initials as usual arise as papilla-like outgrowths from the placenta (Fig. 3). Soon the terminal part of the initial curves so as to make an angle of 90 degrees with the basal part, which forms the funicle of the ovule. It is about this stage that the single integument arises from the base of the nucellus (Fig. 4). The bending of the ovule continues until the adult anatropous form is attained. The funicle is very short. The nucellus is very small as compared with the thick integument. The micropyle is long and extremely narrow as described by Kenyan (1929) in *Ipomea trifida*. This is clear from Figs. 5 and 7, which illustrate the structure of the ovules of *Jacquemontia violacea*.

Development of the Embryo-sac.—The archesporium is hypodermal and differentiates very early, even before the origin of the integument. In *Jacquemontia violacea* sometimes two or three archesporial cells are seen to occur side by side in the same nucellus (Fig. 6). In all other species in every case only one archesporial cell was noted.

The archesporial cell cuts off a parietal cell immediately after its formation (Figs. 3 and 16), which divides further to form a distinct, parietal tissue (Figs. 4, 5 and 17). The first division wall formed in the parietal cell is periclinal (Fig. 17) or anticlinal (Fig. 4). The second division may be either anticlinal or periclinal, and the later divisions occur irregularly. As the result of these divisions in the primary wall cell, the megaspore-mother cell is covered by about 4–7 layers of cells (Fig. 5). Raghava Rao (1940) states that the first division of the primary wall cell in *Ipomea Learii* is anticlinal and a similar behaviour has been observed by Mathur (1934) in *Convolvulus arvensis*. From the occurrence of primary wall cell in every one of the six species investigated during the course of the present work, it appears, in spite of Dahlgren's (1927) strong criticism, that Peters (1908) was correct in his assertion about the occurrence of parietal cells in the Convolvulaceæ investigated by him. Also, therefore, many of the observations on the Convolvulaceæ, where the presence of the parietal cells has been denied, appear to be doubtful and deserve reinvestigation.



Figs. 1–20.—Figs. 1–10. *Jacquemontia violacea*.—Fig. 1. L.S. of a gynœcium with the ovules at the stage shown in Fig. 5. × 60. Fig. 2. T.S. of a young gynœcium slightly above the middle of the ovary. × 60. Fig. 3. A young ovule showing the formation of the primary wall cell. × 440. Figs. 4 and 5. Two ovules showing the megaspore-mother cell and the development of the nucellus. × 260. Fig. 6. An ovule showing two megaspore-mother cells. × 570. Fig. 7. An ovule at the tetrad stage showing the thick integument and the long narrow micropyle. × 260. Fig. 8. A linear tetrad of megaspores with the three micropylar megaspores degenerating. The chalazal one is developing into the embryo-sac. × 950. Fig. 9. A 2-nucleate embryo-sac. × 950. Fig. 10. A mature embryo-sac. × 570. Figs. 11–13. *Ipomea pulchella*.—Figs. 11 and 12. Two stages in the development of the

8-nucleate embryo-sac. × 570. Fig. 13. Micropylar region of a mature embryo-sac, showing the egg-apparatus and the polar nuclei. × 260. Figs. 14–15. *Ipomea Horsfalliæ*.—Fig. 14. Micropylar portion of an embryo-sac showing the egg-apparatus and the polar nuclei. Fig. 15. An abnormal embryo-sac showing 6 nuclei at the chalazal end and 2 at the micropylar end. × 570. Figs. 16–20. *Operculina Turpethum*.—Fig. 16. An ovule showing the megaspore-mother cell and the formation of the primary wall cell. × 950. Fig. 17. An ovule showing a later stage in the development of the megaspore-mother cell. × 570. Fig. 18. A linear tetrad of megaspores. × 950. Fig. 19. A binucleate embryo-sac. × 950. Fig. 20. Micropylar portion of a mature embryo-sac with one of the synergids degenerating. × 440.

The megaspore-mother cell forms a linear tetrad of megaspores by two successive divisions,—*cf.* Fig. 8 for *Jacquemontia violacea* and Fig. 18 for *Operculina Turpethum*. Similar stages have been observed also in the other investigated species belonging to the genus *Ipomea*. The chalazal megaspore functions in every case and develops into the 8-nucleate embryo-sac according to the normal type (Figs. 9–10, 11–13 and 18–20). One or two prominent vacuoles can be discerned in the cytoplasm of the functional chalazal megaspore even before the first division of the nucleus (Figs. 8 and 18). In the 2-nucleate stage of the embryo-sac they are replaced by a prominent central vacuole (Figs. 9 and 19). The enlargement of the embryo-sac at first takes place at the expense of the surrounding nucellus cells. In *Jacquemontia*, most of the nucellus except the outermost layer is absorbed by the 2-nucleate stage. The integument at this stage is 12–15 cells thick. During the course of further development the inner layers of the integument are also absorbed. The 4-nucleate stage of the embryo-sac calls for no remarks. During the mitotic divisions preceding the 8-nucleate stage, of the two spindles at each end, one is placed parallel, the other at right angles to the long axis of the embryo-sac (Fig. 11).

The mature embryo-sac is long and narrow, its length being generally about six times the width (Fig. 16). In *Ipomea pulchella*, it is even longer, and the micropylar end is narrower than the chalazal (Fig. 13). This species is characterised by a very much smaller nucellus and comparatively thicker integument than the rest.

The synergids of *Operculina Turpethum* are nearly as long as broad (Fig. 20); of other species they are generally about three times as long as broad (Figs. 10, 13 and 14). The apex of the synergids except in *Operculina* is usually drawn out. Hooks of a small size have been observed on the synergids of *Jacquemontia violacea* (Fig. 10) and *Ipomea pulchella*.

Definite antipodal cells are always formed (Figs. 10 and 12). They are organized generally even before the cells of the egg-apparatus (Fig. 12), but are quite ephemeral and begin to degenerate as soon as they are formed.

The two polar nuclei travel towards the micropylar end of the embryo-sac and stay near the egg-apparatus (Figs. 13 and 20). A fusion of the polar nuclei has not been observed even in those embryo-sacs, where the egg-apparatus appears to be fully ripe. Their fusion, as pointed out by Raghava Rao (1940), is perhaps delayed until the second male nucleus approaches them.

Macpherson (1921) stated that the cells of the nucellus are rich in starch. Dahlgren (1927) pointed out that these cells may really belong to the integument. The writer's observations as regards the distribution of starch agree with those of Dahlgren. Starch is present in the cells of the integument, but not in the nucellus.

An abnormal embryo-sac has been observed in *Ipomea Horsfalliæ* (Fig. 15). It shows six nuclei at the chalazal end and only two at the micropylar end. Probably one of the micropylar nuclei at the 4-nucleate stage of the embryo-sac was here pushed towards the chalazal end.

SUMMARY

Development of the embryo-sac has been studied in six species of Convolvulaceæ belonging to three genera, namely, *Jacquemontia violacea, Ipomea pulchella, I. Horsfalliæ, I. obscura, I. sepiaria* and *Operculina Turpethum.* Two or three primary archesporial cells are occasionally present in *Jacquemontia.* Otherwise there is always only one hypodermal archesporial cell, which differentiates much before the origin of the integument. Parietal tissue is formed in all the species, the archesporial cell cutting off a primary wall cell in every case. The development of the embryo-sac corresponds to the normal type. The antipodals are short-lived. The fusion of the polar nuclei is long delayed.

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