The Embryology of Melilotus Alba.

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In the space assigned to this paper it will be possible to give but a brief outline of the development and nutrition of the flower, embryo sac and embryo, trusting to the plates to make clear the points not sufficiently explained in the text.

In the flower of Melilotus alba, the common white sweet clover, there are two factors which interfere with the orderly successive development of the floral organs; the one is mechanical and is due to the crowding of the flowers on the side of a stem axis, the other is physiological and ecological and depends upon the relative use of parts at different times in the development of the flower; the one interferes with the simultaneous appearance of the parts of the same cycle, the other with the acropetal succession.

Melilotus forms an exception to most of Leguminosae so far examined, since the megaspore mother cell develops into the embryo sac without first undergoing tetrad division. The development of the latter differs from typical cases only in details. When the eight-celled stage is reached, the embryo sac elongates rapidly toward the chalaza at the same time curving strongly, and the three antipodal cells disappear. The egg cell occupies a position lateral to the synergids. The polar nuclei lie close together near the egg apparatus. Their fusion takes place just prior to fertilization, before the pollen tube reaches the ovule.

After fertilization the primary endosperm nucleus undergoes several divisions before the egg cell begins to divide. The latter then undergoes two transverse divisions, resulting in a terminal cell which develops into the embryo and two other cells which give rise to a conspicuous suspensor. The embryo follows in the main the Capsella type of development, but with two important differences, viz., much later differentiation of the dermatogen, plerome, and periblem, and the absence of a hypophysis derived from the terminal cell of the suspensor.

Lack of space prevents more than the merest glance at the facts observed regarding the nutrition of the embryo sac and embryo. In its earliest stages, the embryo sac grows at the expense of the tissue of the nucellus. As it becomes mature it is surrounded by a definite layer of active looking cells, derived from the inner integument, forming a nutritive jacket. This stage is characterized by the storage of reserve food to supply the rapid growth which follows fertilization. Starch is deposited in the placenta and very abundantly in the micropylar region of both integuments. The funiculus contains no starch, since it is the path by which food material enters the ovule and it is important that it should not be blocked by a store of reserve food.

After fertilization the nutritive jacket becomes even more strongly developed, especially in the chalazal region on the side of the sac nearest the funiculus. The cells of the inner layer have a characteristic appearance. They are rounded and turgid, their protoplasm is vacuolated and forms a thick layer lining the inner ends of the cells. They give evidence of great activity which would seem to justify the conclusion that they are the cells most concerned at this time in the nutrition of the embryo sac. Later there appears in this region a thick mass of endosperm which, acting as an haustorium, rapidly digests and absorbs all tissue with which it comes in contact, and the nutritive jacket is naturally the first part destroyed. The location of the starch-bearing and non-starch-bearing areas at this stage seems to justify the following conclusions: Food material enters the ovule in solution and is partly stored up and partly passed on to the chalazal region of the embryo sac. Moreover the stored-up food supply is drawn upon by the nutritive jacket in the chalazal region. Starch does not appear in the embryo until just before the cotyledons appear, when a small quantity is found in the base of the embryo and also in the suspensor. In later stages there is a scanty supply of starch in the periblem.

In the latest stages examined starch was found in varying quantities in all parts of the tissue outside the embryo sac. The ovule, which might now be called the seed, was surrounded by a thick membrane of columnar cells extending even across the funiculus. Inside this columnar layer in the region of the funiculus is a flattened, fan-shaped mass of tracheid-like cells of irregular form having reticulate markings on their walls. These absorb food material through the funiculus and pass it on to the surrounding tissues, and especially through a vascular bundle, the raphe, to the chalazal region of the embryo sac. Surrounding the tracheid-like cells in the later stages are large cells separated by intercellular spaces, which contain, besides starch, rather large granules which give the test for proteids.

Summary and Conclusion.

The following conclusions result from the above observations:

1. The order of appearance of the primordia of the floral organs is sepals, stamens, carpel, petals, although the last three may appear simultaneously.
2. The energy of the plant is directed at first to the development of the stamens and carpel at the expense of the petals.
3. The archesporium becomes differentiated at a rather late stage.
4. The tapetum divides but a limited number of times.
5. The megaspore mother cell gives rise to the embryo sac directly.
6. The early development of the embryo sac is typical.
7. The antipodals disappear at a very early stage.
8. The embryo sac increases much in size before fertilization and replaces all the tissue within the integuments.
9. The egg cell is placed laterally to the synergids. The latter have striated tips.
10. The polar nuclei do not fuse until just before fertilization. The latter is a rapid process.
11. The ovule is at first anatropous, later campylotropous.
12. The fertilized egg does not divide until there are several endosperm nuclei in the embryo sac.
13. In the three-celled proembryo the terminal cell gives rise to the entire embryo and the second cell to the mass of the suspensor.
14. The early stages in the development of the embryo are of the Capsella type. The dermatogen, however, appears at a later stage.
15. There is no hypophysis.
16. The embryo sac is nourished by means of a nutritive jacket derived from the inner integument.
17. The food material which enters the ovule through the funiculus is partly deposited in the surrounding tissues and partly passed on to the chalazal region of the embryo sac.
18. A mass of endosperm in the chalazal region of the embryo sac acts as an haustorium in the later stages and digests the surrounding tissue.

19. After the formation of the seed coat nutritive material passes from the parenchyma of the funiculus by diffusion through the columnar cells of the seed coat into the tracheid-like cells, which partly distribute it to the surrounding tissue and partly pass it on through a vascular bundle to the chalazal region of the embryo sac.

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Explanation of Figures.

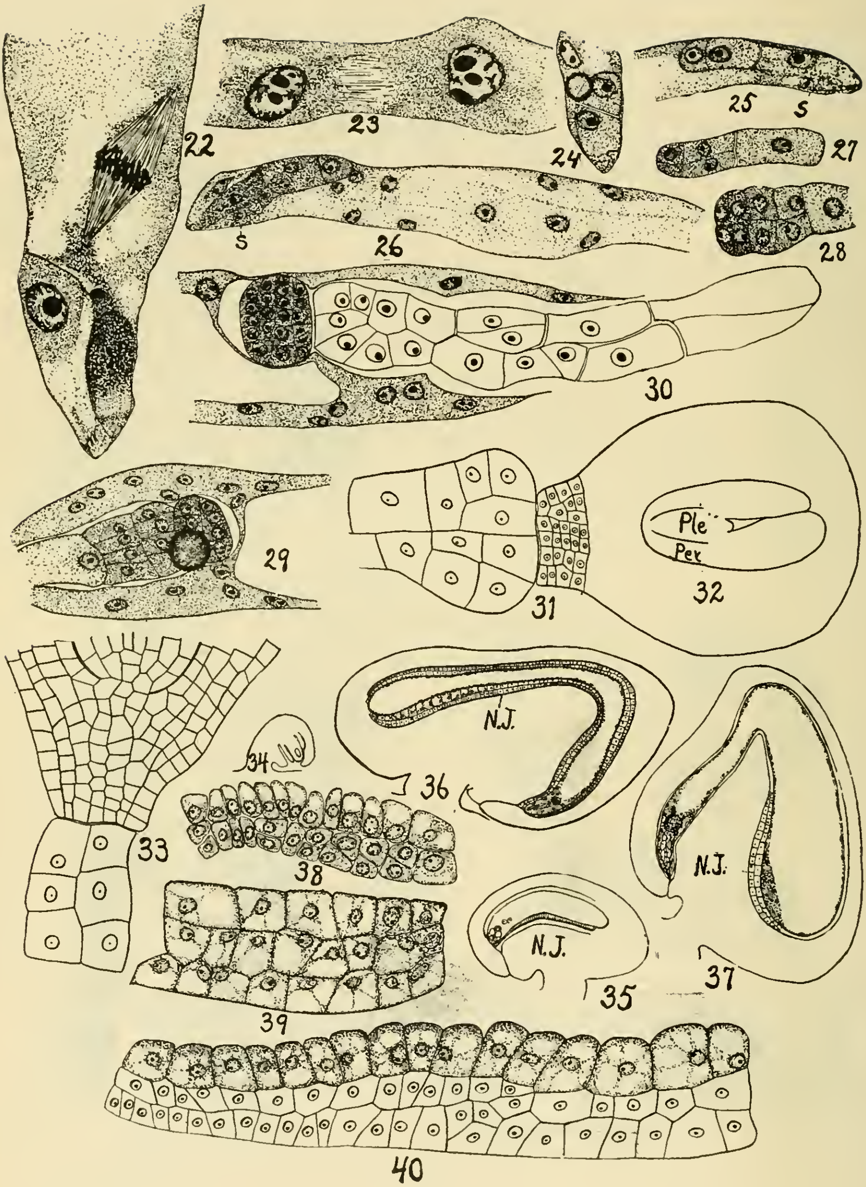
1. Stem tip (a) showing origin of flowers (f) in axils of bracts (B) X 125.
2. Stem tip, later stage, showing origin of flowers and the primordia of the floral organs; (f) flower, (B) bract, (S) sepal, (St) stamen, (c) carpel. X 125.
3. Single flower at a slightly later stage when the petal (P) appears. X 125.
4. Still later stage, indexed as above. The stamens and carpel are enlarging while the petals remain small. X 125.
5. Later stage, the cavity of the ovary appearing; (M) microsporangium. X 125.

6. Still later, the ovules (O) have appeared. X 125.
7. Transverse section of a bud at about the time the embryo sac begins to enlarge; (S) calyx, (P) petals, (St)) stamens, (c) carpel, (Pl) placenta, (V) vascular bundle. X 75.
8. Longitudinal section of carpel, same stage as Fig. 9. The microtome section included about the area between the lines a'b'. X 345.
9. Section of carpel along the line ab, Fig. 8. The folding together of the sides is nearly completed. X 345.
10. Young flower showing nearly simultaneous appearance of petals, stamens and carpel. X 125.
11. Young ovule, sporagenous tissue not yet differentiated. X 1460.
12. Archesporial cell. X 1460.
13. Spore mother cell and tapetum. X 1460.
15. Embryo sac, two-cell stage. X 1460.
16. Embryo sac, four-cell stage. X 1460.
17. Embryo sac, eight-cell stage. Cells of egg apparatus cut from the remainder of the sac. Antipodals beginning to degenerate. X 1460.
18. Young egg apparatus before differentiation of egg. X 1460.
19. Mature embryo sac. The egg cell lies back of the synergids. Polar nuclei fusing. X 1460.
20. Same stage as Fig. 19 but showing the position of the egg lateral to the synergids. X 1460.
21. Embryo sac immediately after fertilization. Neither the egg cell nor the primary endosperm nucleus has divided. (S) synergid. X 610.
22. First division of primary endosperm nucleus. Egg cell still undivided. X 1460.
23. First division of primary endosperm nucleus. Telephase. X 1460.
24. Proembryo of two cells. X 610.
25. Proembryo of three cells; (s) synergid. X 610.
26. Same stage as Fig. 25 showing endosperm with radiating character of the protoplasm surrounding the nuclei. X 610.
27. Embryo of two cells. X 610.
28. Embryo of eight cells. X 610.
29. Embryo composed of two layers of cells. X 610.
30. Embryo at a little later stage when the dermatogen begins to be distinguished. X 610.

31. Embryo just before appearance of cotyledons. X 610.
32. Embryo after appearance of cotlyedons; (Ple) plerome. (Per) periblem. X 125.
33. Base of embryo of about the same stage as Fig. 32 showing plerome, periblem and relation of embryo to suspensor. X 610.
34. Young ovule of anatropous type. X 125.
35. Ovule at time of fertilization, campylotropous type; (N. J.) nutritive jacket. X 125.
36. Ovule a short time after fertilization, showing the curvature of the embryo sac and the extensive development of the nutritive jacket. X 125.
37. Later stage, embryo sac much curved, with mass of endosperm in chalazal region. X 75.
38. Nutritive jacket, same stage as Fig. 35. X 610.
39. Nutritive jacket, same stage as Fig. 36, micropylar region. X 610.
40. Nutritive jacket, same stage as Fig. 36, chalazal region. X 610.
41. Mass of endosperm serving as an haustorium in chalazal region of embryo sac. Same stage as Fig. 37. X 610.
42. Section in region of the funiculus in the plane of the mass of tracheid-like cells; (T) tracheid-like cells, (V) raphe, (c) columnar cells of seed coat. The section is in the plane indicated by the line a'b'; Fig. 43 X 345.
43. Same as Fig. 42 but slightly earlier and in a plane perpendicular to it as indicated by the line ab, (T) tracheid-like cells, (C) columnar cells of seed coat, (C') columnar cells of funiculus, (E) parenchyma of funiculus in path of food supply. X 610.

44-50. Distribution of starch in ovule. Amount of starch is indicated by the thickness of stippling.

44. At about the megaspore stage. 345.
45. At the time when the embryo sac begins to enlarge. X 345.
46. At the time of fertilization. X 125.
47. Soon after fertilization. X 125.
48. At a considerably later stage. X 125.
49. In embryo just before formation of cotyledons. X 75.
50. In ovule and embryo at a much later stage; (C) columnar cells of seed coat, (V) raphe, (T) tracheid-like cells, (P) reserve proteid. X 75.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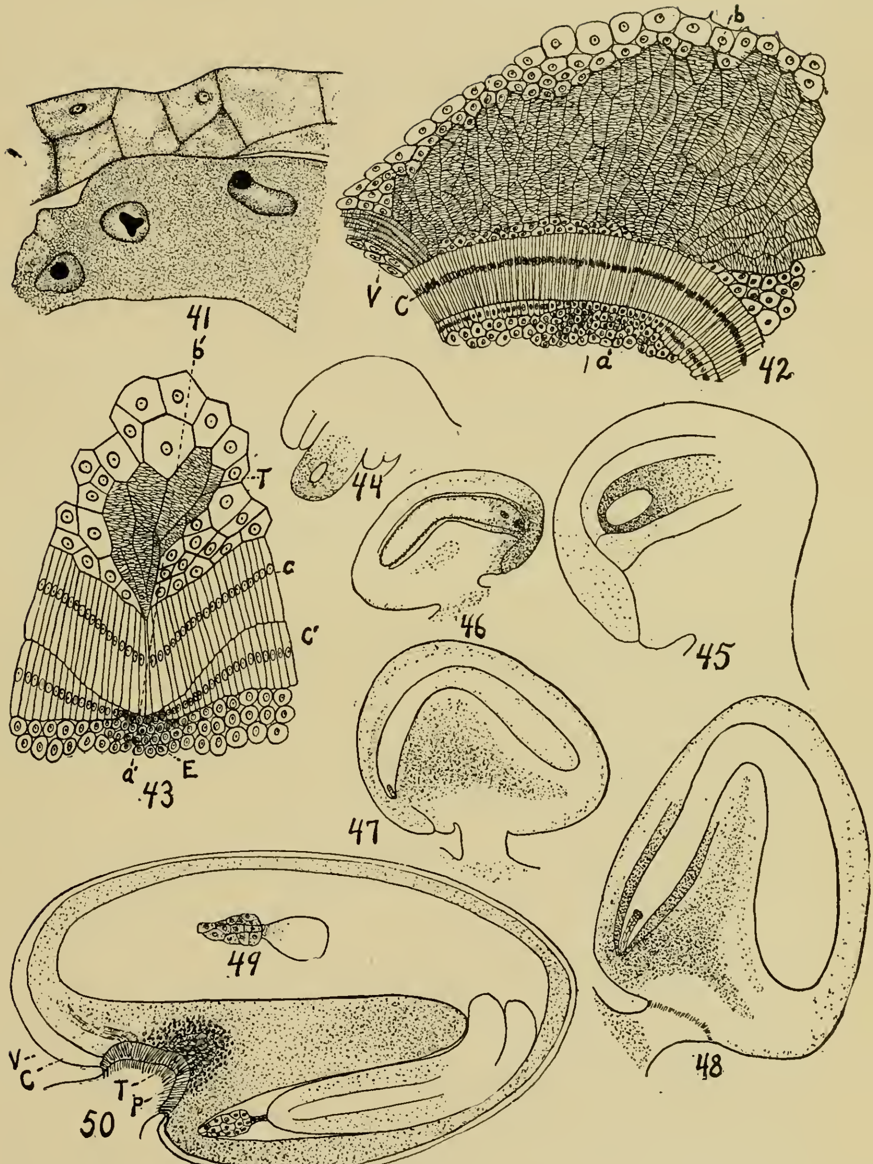
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