Development of the flower and embryo-sac in Aster and Solidago.

G. W. MARTIN.

(WITH PLATES XIX AND XX.)

Before entering directly upon the subject it may be well to recount the primitive conditions of the leaf-shoot and its growing point as found in Compositæ. The point of growth of the shoot-axis becomes very much retarded, and as a result, the growing-point is transformed into a broad, somewhat elevated disc, on which are to appear flowering capitula with centripetal inflorescence (fig. 1). The first structure indicating an individual, embryonic flower on the receptacle is a hemispherical outgrowth almost perfect in outline, and becoming obconical as growth takes place (figs. 2a and 3a).[1] This embryonic tissue, standing on a lateral axis, constitutes the foundation from which arises a differentiation of tissue into special organs (fig. 4). Thus far the path of embryonic development remains the same for all organs, even those of the most various kinds. From this condition of things on a new departure is made; the apex of the broad flower-axis ceases to grow, while the peripheral portion continues to develop; and here we have the first hint of the initial growth of true floral organs (fig. 5). A tubular ring is thus formed, and on its peripheral wall small papillæ arise, giving the structure a cup-shaped appearance with a shallow depression and scalloped margin (fig. 5a). This so-called cup elongates; its sinus grows deeper, and the five corolla lobes become sharply defined and are known at once by their shape (fig. 6). Simultaneously with the development of the floral organs in the rising ring, in which there is a complete fusion of all flower parts till liberated a deep, central depression is forming, when ultimately the ovule-bearing portion is placed beneath the rest of the flower-parts (figs. 6–10). Thus we have an epigynous flower with an inferior ovary.[2] However, there are some who would substitute the word hypogynous for epigynous, basing their argument on the theory that all the floral organs in their initial state are coalesced in the annular

[1] Just here may be stated that this rudimentary, sessile floret is the firstindication of plant subdivision.

[2] Gray's Structural Botany, p. 183.

wall; that the appearance of each is due to the liberation of their uppermost parts; that each whorl may appear either in acropetal or certain whorls seemingly in basipetal order.[3] The real origin and behavior of the floral organs in their younger stages of development as correlated with the inferior ovary has attracted but little attention, and therefore, no definite statement can be made as to the true relationship existing between the floral organs in their embryonic condition.

Turning now to the order of development of flower parts, the first foliar structure that appears is a petal. At first they appear as small papillæ on the annular wall (fig. 5a). In their further development the tissue thickens and the epidermal cells with their rather heavy cell walls become quite large; in later growth the tissue becomes more uniform, and the tips of the five marginal teeth of the corolla-tube turn inward, thus furnishing a splendid protection to the andrœcium and gynæcium (figs. 7–10). The petals forming the flower tube are not simply contiguous but united, and as the tube elongates it assumes the form of a funnel whose upper margin has five spreading teeth. The tubular corolla is not composed of parts originally separate and subsequently united by their lateral margins; for the parts set free are the marginal teeth arising from a common, basal tissue; and this tissue develops and elongates *pari passu* with the growth of the nascent organs within.

Almost immediately following the visible corolla, appearing on its inner basal margin, are five minute elevations, the rudimentary stamens (fig. 7a). These develop with remarkable rapidity, and their primitive oval form is soon exchanged for one that is oblong (fig. 8a). The histological structure of the stamen in its early growth is a mass of uniform parenchyma. Presently a new condition arises; a differentiation of tissue into anther-lobes and a connective takes place. The fibro-vascular bundle, which is a continuation of that of the flower-axis, though very much reduced, differentiates in the upper part of the stamen and forms the so-called connective. At the same time there is a modification of tissue which develops into anther-lobes; these are connected and yet separated by the connective. In the early process of growth there appear two longitudinal ridges

[3] Coulter on the Dandelion, Amer. Naturalist, xvii, No. 12, p. 1212.

on each half-anther-lobe; these answer to the future pollen-sacs, and give rise to the archesporium cells, which, usually having but one row of cells in each pollen-sac, again give rise to the squarish mother-cells; in turn the latter yield four pollen grains each. The developmental path pursued by all pollen grains is so common that it needs no special description. To give a more complete account of stamineal tissue, mention also should be made of the anther-tube. At first the filament develops slowly and the stamens are distinct from one another, but just preceding the unfolding of the flower-bud the filament gains length at a very rapid rate by the elongation of its cells; finally, the lateral margins of the anthers become coalescent, thus forming a tube, which, when the flower is fully developed, projects beyond the tubular-corolla. The anthers do not simply cohere but unite, for cross-sections show the blending of epidermal tissue; this makes the union complete. Simultaneously with the origin and development of the stamen another structure comes into view, the calyx (fig. 7b). When first observed there is a bulging-out of the epidermal layer in the region of the seeming insertion of the other floral parts. The tube of this outgrowth is not distinguishable from the ovarian wall, but its limb is visible as a tuft of hairs. Primitively, it consists of a short delicate bunch of hairs, arranged in a circle at the upper extremity of the young ovary. Later, the hairs by rapid growth develop into long appendages, made up of several rows of narrow but extremely elongated cells, the lower ends of which splice into the upper ends of the cells below at the point where the upper end of the cell below turns away from the main trunk, and rapidly tapers into an acuminate tip; hence, the hair has the appearance of a barbed spear. By its late appearance in development, and its epidermal structure, some do not regard pappus as a calyx, while on the other hand others so consider it, though very much reduced in form and structure, caused by the pressure of surrounding parts.

A little previous to the formation of the pistil another structure may be seen to arise from the receptacle between the individual florets (fig. 9b). These foliar bodies, or bracteoles, very much resemble the scale-like leaves of poorly developed vegetative branches. They project quite far between

the individual flowers. Their epidermal tissue consists of very thick walled, elongated cells surrounding several layers of smaller parenchyma cells.

The next and last set of floral organs to appear is the pistil. About the time when the stamens begin to assume an oval outline and form a constriction near their bases, thereby separating the stamineal tissue into anther and filament, there is detected on the inner border of the primitive ring, in the region of stamineal insertion, an inward growth of cells (fig. 9a). This cell tissue gradually develops inward around a common axis till all sides meet, and at the same time elongates in the direction of the flower axis, thus forming the style above, and completely overarching the once oval cavity below, changing it into a flask-shaped cavity which is the true ovarian cell (fig. 10a). Just at this stage of development it may be mentioned that from now on, the flower parts develop with remarkable rapidity, and finally the flower axis is very much elongated, the gynœcium forming the terminal structure of the flower. The growth of the pistil is somewhat analogous to that of the stamen. As before stated, stamineal growth is partially retarded up to a certain point, from whence it makes rapid strides by the elongation of the cells of the filament; and for a time the stamen crowns the summit of the flower. So there is a similar phase of growth which characterizes the style; there is a slight cessation of its growth until the anthers begin to shed their pollen, when the style by rapid development pushes its way up through the syngenesious stamens. The lengthening of the style is due to the growth and elongation of the carpellary cells above the ovary. In this case is found a good example of protandry, which suggests cross-pollination. After the opening of the flower, the style lengthens and the pollen is pushed out of the anther-tube by the brush-like upper portion of the style as the anthers dehisce. The lines of the stigmatic receptive surfaces remain intact till that portion of the two-branched style is shoved above the anther-tube, whence the two branches separate, curving far back, and expose the stigmatic papillæ on their inner faces; thus the style is made the instrument for disseminating the pollen which it cannot use for itself; as a result, cross-pollination, with almost absolute certainty, is insured. To speak further of the two-branched style: Two kinds of

hairs are detected; these comprise stigmatic papillæ and brush hairs. The former are usually short, being either acutely or obtusely tipped, and are confined to the inner faces of the style-branches. The latter are cylindrical, epidermal outgrowths, having various arrangements both on the inner and outer faces of the style-branches. In the *Aster* the style-branches are flattened, and linear from their bases to the ends of the two lines of papillæ which line each stigmatic surface. Above the termination of the stigmatic lines are seen brush hairs which cover both faces of the style branches. In the *Solidago* the style-branches very much resemble in outline those of the *Aster*. Two stigmatic lines are observed which extend from the base of the branch to a point about one-half the distance to its tip. The brush hairs usually cover the whole outer surface of the branch, and the edges and the tip of the inner face above the termination of the stigmatic lines.

It yet remains to speak of the tissue and its modifications that make up the structure of the style. It consists, chiefly, of ordinary parenchyma, the central portion of which is modified, while the upper stigmatic portion is a differentiation of the epidermis into a soft mucilaginous tissue, thus forming a loose conducting mass for the penetration of the pollen-tube.[4] In the center of the conducting tissue is also seen a very narrow tubular opening, indicating that it is a continuation of the ovarian cavity. This seems to be constant throughout the species examined. Before concluding, however, the description of the different floral organs, let the following order of succession as observed in their sequence of development be noted, viz., corolla, calyx, androecium and gynoecium; although this order of parts does not correspond to Gœbel's generalizations on Compositæ.[5] There may be evidences showing a disturbance in the acropetal order of development of whorls, but of necessity the calyx is developed first, and its late appearance without doubt is due to the late liberation of its upper portion.

Simultaneously with the development of the ovule as far advanced as fig. 12, appear small, fleshy glands above the ovary at the base of the style these form a disk and are supposed to represent an inner row of imperfectly formed stamens.

[TO BE CONCLUDED.]

[4] From all observations made I could not satisfactorily make out the descent of a pollen-tube.

[5] Gœbel's Outlines of Classification and Special Morphology, p. 422.

EXPLANATION OF PLATES XIX AND XX.

(All figures on Plate XIX are magnified 450 diameters; all on Plate XX 600 diameters).

Figs. 1, 2 and 3, receptacle of the flower axis, with individual florets appearing in Figs. 2 and 3*a*. Fig. 4, a single floret before the appearance of flower parts. Fig. 5*a*, the first floral whorl, the corolla. Fig. 6, further development of corolla. Fig. 7, the corolla, the appearance of the androecium *a* and the calyx *b*. Fig. 8, a later stage of fig. 7. Fig. 9*a*, the formation of the ovary; *b*, the bracteole. Fig. 10, a further development of fig. 9, showing the flask-shaped ovary *a*. Fig. 11, the formation of the ovule with all other parts eliminated. Fig. 12*a*, the nucellus of the ovule; *b*, appearance of the integument. Fig. 13, later development of fig. 12; *a*, the nucellus; *b*, the embryo-sac. Fig. 14, a further development of fig. 13. Fig. 15, the mother-cell divided once. Fig. 16, the cells divided again. Fig. 17*a*, the true mother-cell of the embryo-sac, the upper three cells becoming disorganized. Fig. 18, disappearance of the upper cells, the mother cell occupying a central position, the nucellus breaking up and showing signs of disappearance. Fig. 19, a further development of Fig. 18; the nucellus almost gone and the appearance of vacuoles. From fig. 20 to fig. 23, inclusive, are shown the division of the mother-cell and its further divisions, culminating in the formation of the egg-apparatus, the antipodal cells and the endosperm nucleus; the vacuoles and the expansion of the embryo-sac.

A study of some anatomical characters of North-American Gramineæ. IV.

THEO. HOLM.

The genus Leersia.

(WITH PLATE XXI.)

In previously published papers[1] the anatomical characters of Uniola, Distichlis and Pleuropogon have been discussed, and it is the purpose of this, and a following paper, to show how the species of Leersia may be distinguished anatomically.

It would, of course, have been more proper to proceed from Uniola to the genera allied to it. This was done when the comparison was drawn between Uniola, Distichlis, and Pleuropogon; but the lack of sufficient material has necessitated a change in the order of treatment. Some groups, at least, of closely related genera may be considered at once, so as to give a broader view of their anatomical divergencies.

[1] Botanical Gazette, June, August and October, 1891.