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DEVELOPMENT OF THE FLOWER AND MACROGAMETOPHYTE OF ALLIUM CEPA[1]

H. A. JONES[2] AND S. L. EMSWELLER[3]

IN CENTRAL CALIFORNIA mother bulbs of the onion (*Allium cepa* L.) used for seed production are usually set in the field during late November and December. Subsequently, a number of leaves are formed at each of the several growing points before the inflorescence axis is differentiated fig. 1, *A*). The method of leaf development has been adequately described by Hoffman.[(2)][4] Briefly, the leaves are two-ranked, the blade of each new leaf arising at an angle of 180° from that of the next older. That side of the apical meristem opposite the preceding blade is the first to differentiate; and as this region develops an upward growth of tissue soon completely encircles the growing point of the stem, differentiating the new leaf.

In Maryland, Jones and Boswell[(4)] found that the primordium of the inflorescence axis differentiated in March when mature bulbs were planted in the field in October. In California, bulbs planted in December had floral axes differentiated in February.[(3)] The first stages in the development of the primordium of the leaf and that of the inflorescence axis appear to be very similar. In the latter the single involucral bract is first evident at a point opposite the youngest leaf blade. At the first appearance of the bract, one cannot tell whether the new primordium is that of a leaf or of a bract. Very soon, however, the central axis begins to

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[4] Superscript numbers in parentheses refer to "Literature Cited" at the end of the paper.

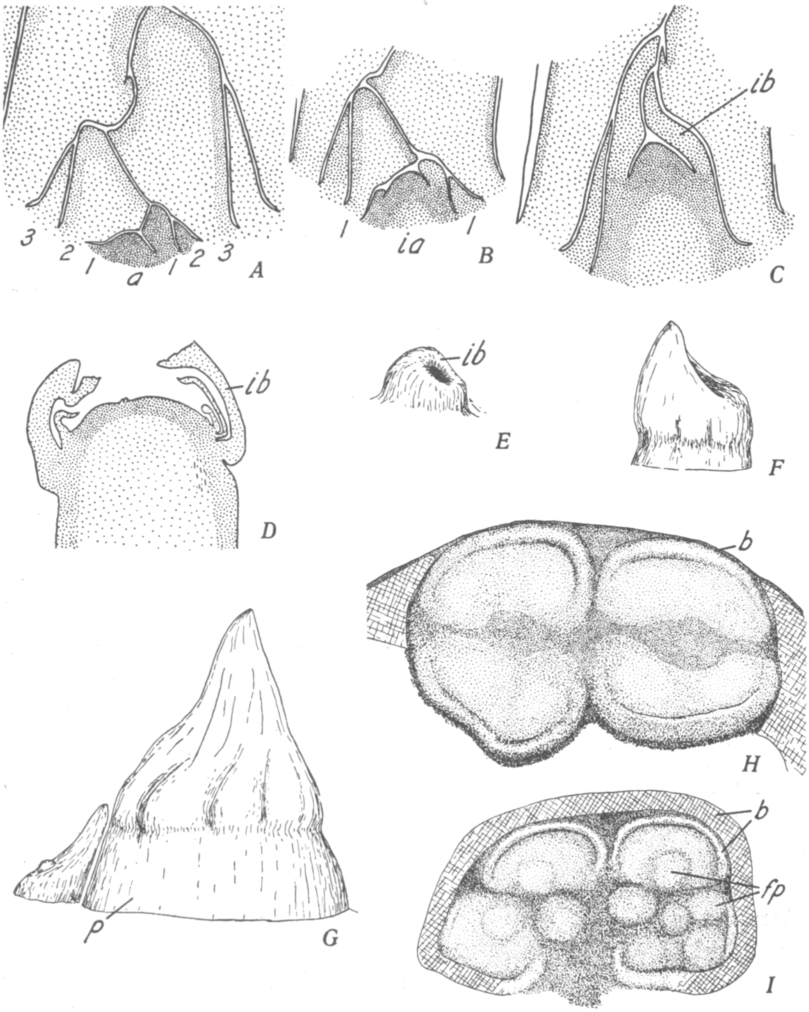

Fig. 1.—*A*, Longitudinal section through the growing point of onion bulb: 1, 1; 2, 2; 3, 3, are opposite portions of the same leaf that encloses the central axis *a*. *B*, Primordium of the inflorescence axis. Involucral bract just arising; 1, 1 are opposite sides of the same leaf encircling the inflorescence axis, *ia*. *C*, Elongating peduncle of the inflorescence axis. The involucral bract, *ib*, completely covers the central region. *D*, Apex of inflorescence axis somewhat flattened; additional bracts arising within the involucre. *E*, Inflorescence axis is in about the same stage of development as in *B*, showing the unilateral development of the involucre. *F*, *G*, Developing flower stalks. At the base of the peduncle in *G* another shoot has differentiated. *H*, Within the young bracts are slightly raised kidney-shaped areas from which most of the flowers develop; *b*, bracts. (× about 32.) *I*, The primordia of the first flowers are being differentiated: *b*, bracts; *fp*, flower primordia. The bract covering four kidney-shaped areas has been cut away. (× about 32.)

elongate to form the peduncle or scape of the inflorescence (fig. 1, *B* and *C*), and the involucral bract covers the meristematic region from which the flowers develop (fig. 1, *C, F,* and *G*). Within the involucre and over the broad surface of the stem tip, numerous membraneous bracts develop, which cover the cluster of young flowers in their first stages (plate 2, *A*). In other words, during their early development, the flowers are protected by the involucre as well as by another series of bracts within. Figure 1, *E* shows how the single involucral bract in a very early stage completely encircles the growing point.

FLOWER DEVELOPMENT

The individual florets are preceded by a varying number of slightly elevated kidney-shaped meristematic regions (fig. 1, *H*) over the surface of the stem apex. It is mainly from these kidney-shaped areas that the flower primordia are differentiated. The plan or order of differentiation seems fairly definite but the exact sequence of development was not determined.

In the onion there are three members in each of the five whorls of floral organs; these whorls are outer perianth, inner perianth, outer stamens, inner stamens, and carpels. The flower primordium develops at first as a slight projection (fig. 1, *I*), then becomes globose. Later it is slightly elongated with a convex summit and is circular in cross section (fig. 2, *A* and *B*). By marginal growth just below the summit the primordia become somewhat flattened and when viewed from above distinctly triangular (plate 2, *B* and plate 3, *A*). The outer perianth whorl and the outer stamen whorl are the first to be formed. At each angle of the triangle there is differentiated a primordium of an outer perianth segment, and in its axil a primordium of one of the stamens of the outer whorl. Occasionally the first lobe of the perianth is well developed before the primordium of the stamen which it subtends is evident. Usually, however, these two appear to arise simultaneously from a single growing region, an outer primordium giving rise to the perianth segment and an inner to the stamen. The second perianth segment with its subtended stamen, as a rule, arises counterclockwise to the first (fig. 2, *G*). The remaining apex of the triangle also develops a rounded protuberance (fig. 2, *C*), which in turn develops two rapidly growing regions, the primordia of the third perianth segment and its subtended stamen.

The inner whorls of perianth and stamens are formed after the outer. The first of the inner perianth segments with its subtended anther appears between the oldest and second oldest segments of the outer whorl

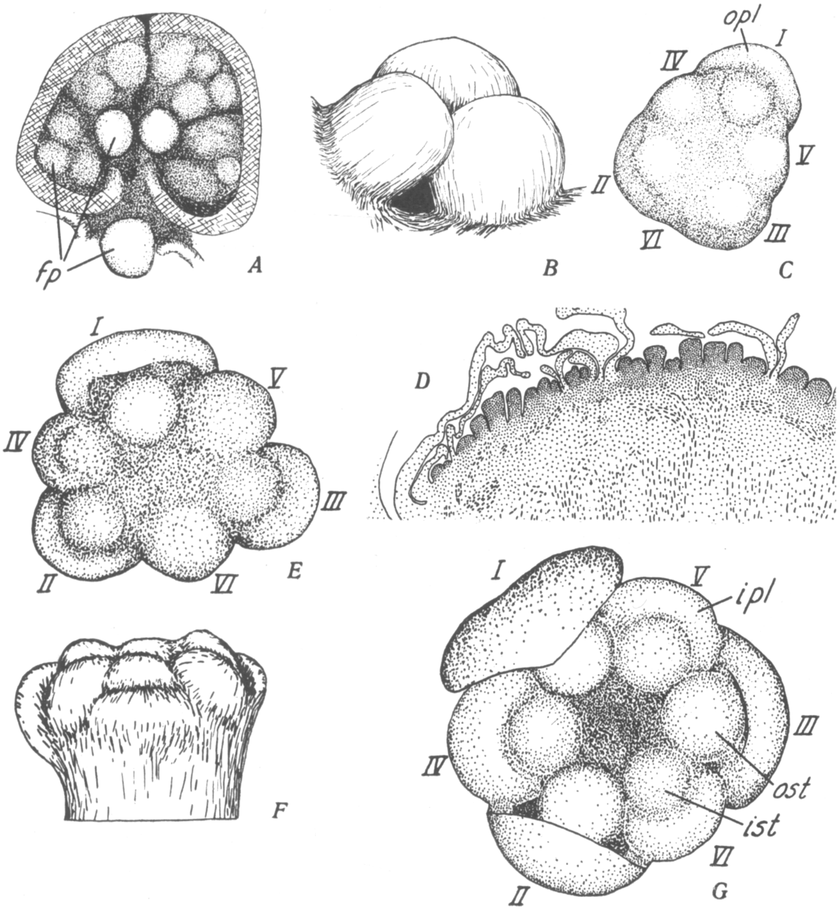

Fig. 2.—*A*, Slightly older stage than figure 1, *I*; *fp*, flower primordia. (× about 32.) *B*, Side view of three flower primordia. (× about 85.) *C*, Top view of a young flower showing counterclockwise differentiation of outer perianth lobes and outer whorl of stamens. The youngest primordium (VI) will appear opposite the oldest perianth segment (*I*); *opl*, outer perianth lobe. (× about 85.) *D*, Longitudinal section of a portion of inflorescence at about the time the floral organs of the oldest flowers are beginning to differentiate. *E*, Top view of a young flower showing outer whorls of perianth and stamens differentiated; the inner whorls are just beginning to differentiate. The Roman numerals indicate the sequence of origin of the different segments. (× about 85.) *F*, Side view of a young flower slightly younger than the one shown in *E*. (× about 85.) *G*, Top view of a young flower in which primordia of all perianth segments and stamens have been differentiated: *ipl*, inner perianth lobe, *ost*, outer stamen, *ist*, inner stamen. (× about 85.)

(fig. 2, *E*). The next members appear between the oldest and youngest segments of the outer whorl. Occasionally this sequence is reversed. As a rule the last segments to arise are opposite the oldest (figs. 2, *C*; 2, *E*; and 3, *B*). Sometimes segments of the inner whorls lying both clockwise and counterclockwise to the oldest segments of the flower appear to arise simultaneously. Even though the inner stamens are the last to arise, they are the first to shed their pollen.

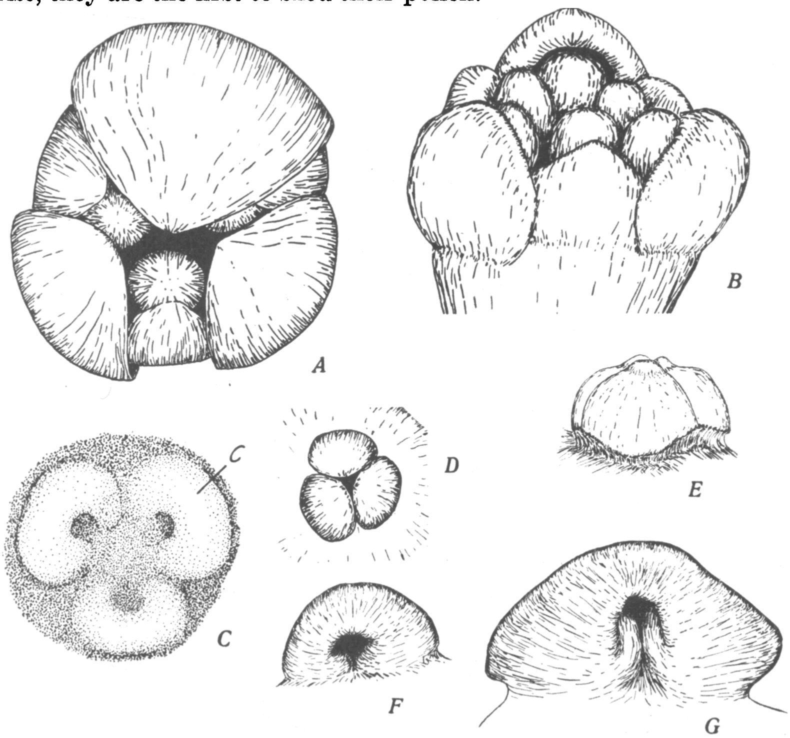

Fig. 3.—*A*, Top view of a young flower. The outer perianth lobes almost cover the stamens. At about this time the carpels are differentiated. (× about 85.) *B*, Side view of a young flower, slightly younger than *A*. (× about 85.) *C*, Early differentiation of the three carpels. (× about 85.) *D*, Carpels have grown upward until they nearly meet at the center. (× about 32.) *E*, Carpels with the style just beginning to form. All carpels play a part in the formation of the style. (× about 32.) *F*, Inturned edges of a single carpel, showing origin of the two ovules. (× about 85.) *G*, Slightly older carpel than *F*. (× about 85.)

The carpels are differentiated at about the time the outer perianth segments overarch the stamens (fig. 3, *A*). Three horseshoe-shaped areas of meristematic tissue begin to project on the flattened surface within the three inner stamens and alternate with them. These areas, growing upward and toward the center (fig. 3, *C*), soon meet along their inturned edges (fig. 3, *D*). The style is formed by the apical growth of the three carpels (fig. 3, *E*). When the three carpels begin to elongate to form the style, the primordia of the ovules have already been differentiated on the inner edges of the carpels (fig. 3, *F* and *G*). In figures 4, *D* and 4, *E* a

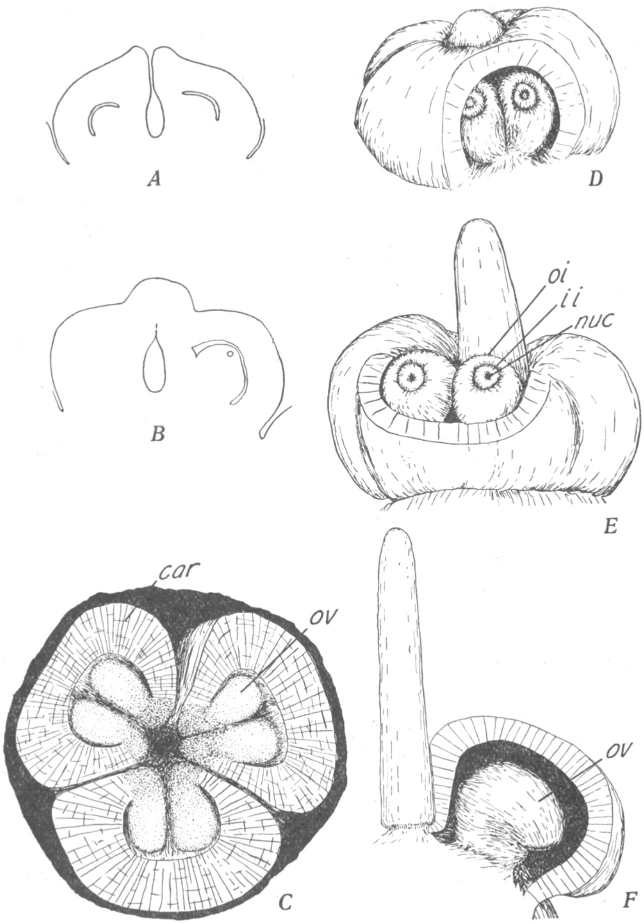

Fig. 4.—*A*, Longitudinal section through two carpels about the same age as in figure 3, *E*. *B*, Stage of development at which the archesporial cell is differentiated. *C*, Upper portion of carpels (*car*) removed, showing young ovules (*ov*). (× about 85.) *D, E*, Portion of a carpel removed to show the two ovules, outer (*oi*) and inner (*ii*) integuments, and nucellar (*nuc*) tissue. (× about 32.) *F*, Longitudinal section through one of the locules at time of anthesis.

section of the ovary wall has been removed, exposing the two ovules within the carpel. Figure 4, *F*, the pistil of an open flower, shows the almost complete inversion of the ovule.

DEVELOPMENT OF THE MACROGAMETOPHYTE

The archesporial cell, which is subepidermal, functions directly as the macrospore mother cell. This cell can be distinguished among the other nucellar cells at a very early stage, even before the integuments begin

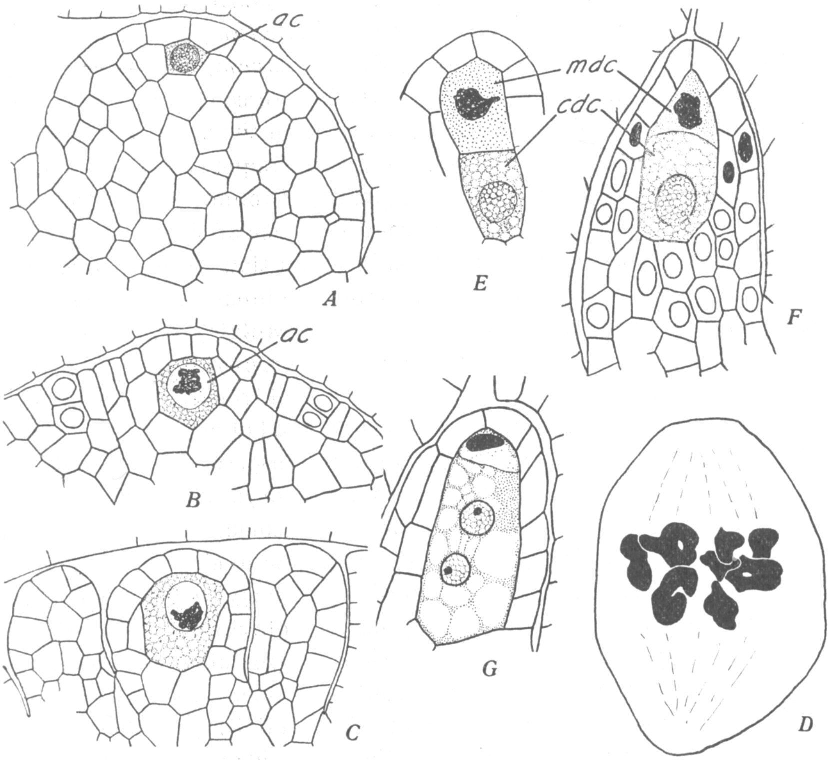

Fig. 5.—*A,* Ovule with differentiating archesporial cell (*ac*) which in this case is the macrospore mother cell. (× about 375.) *B,* Mother cell in early prophase. The inner integuments are being initiated by periclinal division in the epidermis. (× about 375.) *C,* Enlarging mother cell still in prophase. The integuments have made considerable development. (× about 375.) *D,* Heterotypic division of the mother cell. (× about 1,250.) *E,* Two daughter cells: the micropylar daughter cell (*mdc*) begins to disorganize shortly after division; the chalazal daughter cell (*cdc*) forms the embryo sac. *F,* Enlarging of the inner daughter cell to form the embryo sac. (× about 375.) *G,* Two-nucleate embryo sac. (× about 375.)

to form. When the inner integument first begins to differentiate (fig. 5, *B*), the prophase has already begun. Immediately following the first metaphase (fig. 5, *D*), the micropylar daughter cell begins to disorganize but persists for some time (figs. 5, *E* and *F*) ; the other forms the embryo sac. This degeneration of the micropylar daughter cell in *Allium* *cepa* is characteristic of many species of *Allium* and occurs in other genera as well.

The origin of the embryo sac from the chalazal daughter cell has also been described by Strasburger[8] for *Allium fistulosum;* by Weber[9] for *A. porrum, A. victoriale, A. paniculatum, A. flavum, A. ursinum, A. zebdanense, A. uniflorum, A. rotundum,* and *A. sphaerocephalum.* These have only flowers in the inflorescence. In *A. carinatum, A. oleraceum, A. scorodoprasum, A. moly bulbiferum, A. paradoxum,* and *A. sativum,* which have both bulblets and flowers in the inflorescence, Weber[9] states that the embryo sac is also formed directly from the chalazal daughter cell; but aberrations from this type are more frequent than in species with only flowers in the inflorescence. Heatley[1] found that in *Trillium cernuum* the embryo sac developed from the inner of the two daughter cells. In *Streptopus roseus,* McAllister[5] writes that in most cases the eight-nucleate embryo sac was derived from the inner daughter cell. In *Scilla hyacinthoides* var. *caerulea* and *S. campanulata,* McKenney[6] reports that the embryo sac develops from the micropylar daughter cell. In *Cypripedium,* Pace[7] found that it was derived from the inner daughter cell, but the mature sac had four nuclei instead of eight.

In *Allium cepa* the chalazal daughter cell undergoes successive mitosis to form the eight-nucleate embryo sac. In an embryo sac, from material collected four days after the stigma had first become receptive, the egg was still unfertilized (plate 1, *B*), and the polar nuclei were separate (plate 1, *C*). The small synergid (plate 1, *D*) and egg were of about the same size. The volume of the large synergid (plate 1, *E*) was several times that of the small one; both were richly supplied with food. Even when the stigma is first receptive the contents of the two synergids are much denser than those of the egg (plate 4, *A* and *B*).

In the genus *Allium* the behavior of the synergids is not the same for all species. Weber[9] reports that in *A. senescens* and *A. victoriale* the synergids disappear immediately after fertilization; *A. flavum, A. paniculatum, A. ursinum,* and *A. zebdanense* have slight hypertrophy of the synergids, and these probably provide food until the embryo reaches the two to three-celled stage. Weber states that in *A. unifolium* and *A. rotundum* one of the synergids acts as a nutritive cell and does not disintegrate until the embryo has developed a large number of cells. Strasburger[8] pictures one of the synergids of *A. fistulosum* as much hypertrophied and filled with granular protoplasm. In *A. cepa* the persistence of the synergids was not determined. No doubt the large synergid functions, for a short time at least, as a nutrition organ.

SUMMARY

The outer perianth whorl and the outer stamen whorl are the first floral organs to differentiate in the onion. These are followed by the inner perianth whorl and inner stamens, and lastly by the carpels.

The outer perianth segments and their subtended anthers usually arise counterclockwise. The sequence of development of the members of the inner whorls of perianth and anthers is usually clockwise. The first segments of the inner whorls usually arise between the oldest and second oldest segments of the outer whorls.

The embryo sac is formed from the chalazal daughter cell.

One of the synergids is distinctly hypertrophied; both appear to be well supplied with reserve food.

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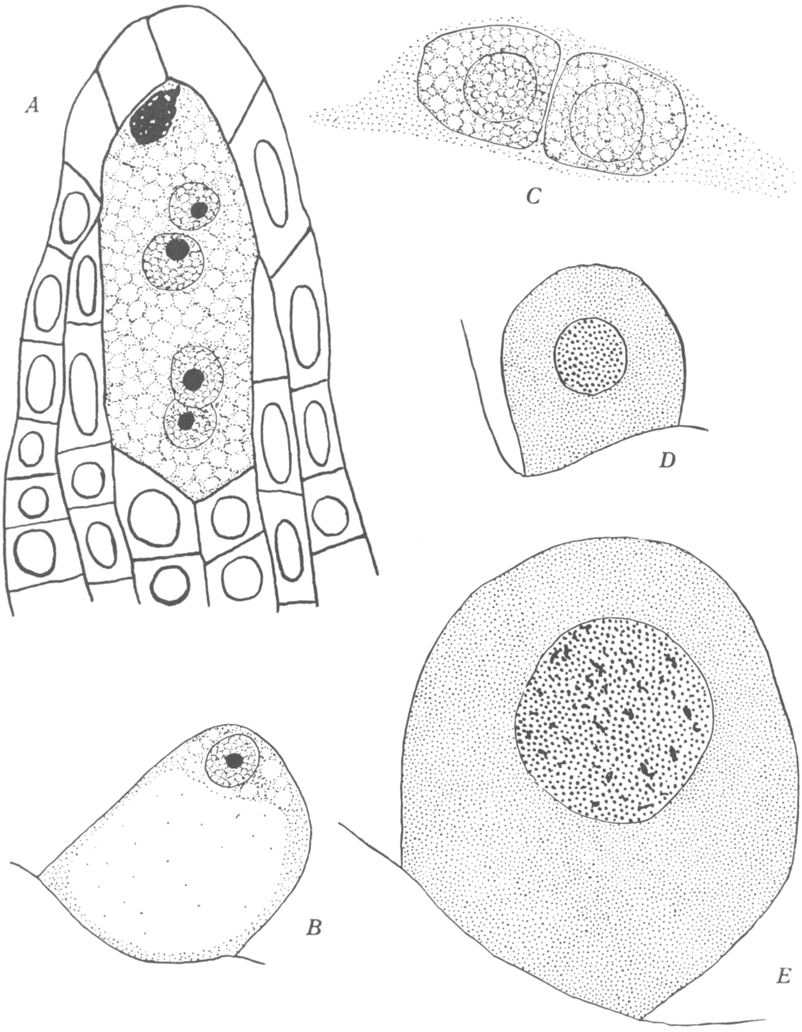

Plate 1. ***A,*** **Four-nucleate embryo sac. (× about 375.)** ***B–E,*** **Polars, synergids, and egg from** the same sac, four days after stigma is first receptive: *B,* egg; *C,* polars; *D,* small synergid; ***E,*** **large synergid. (× about 375.)**

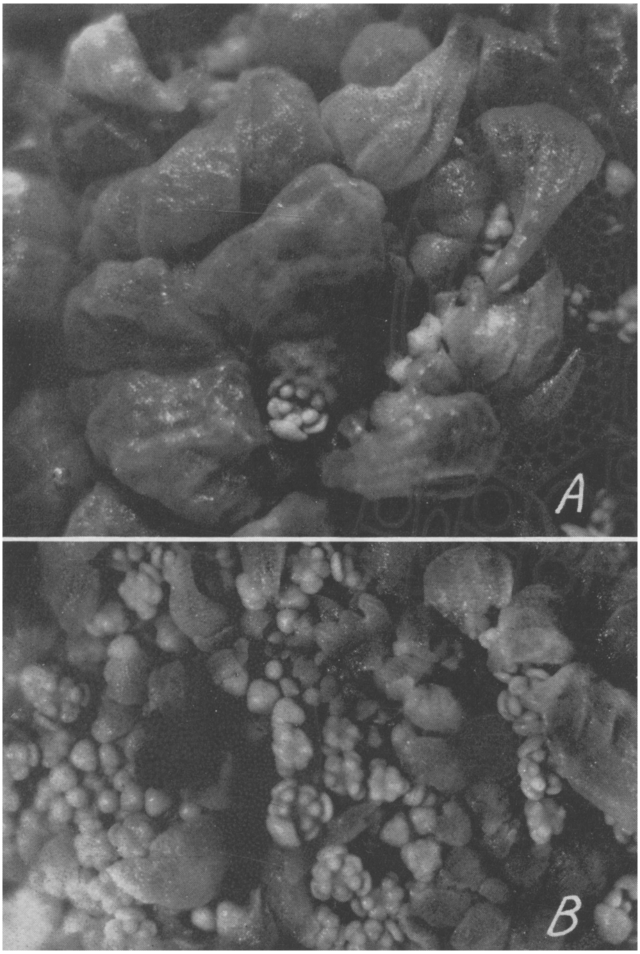

Plate 2. *A*, Photomicrograph of a portion of young inflorescence, involucre removed, young flowers covered with membranous bracts. *B*, Young inflorescence with portion of membranous bracts removed to show the developing flowers.

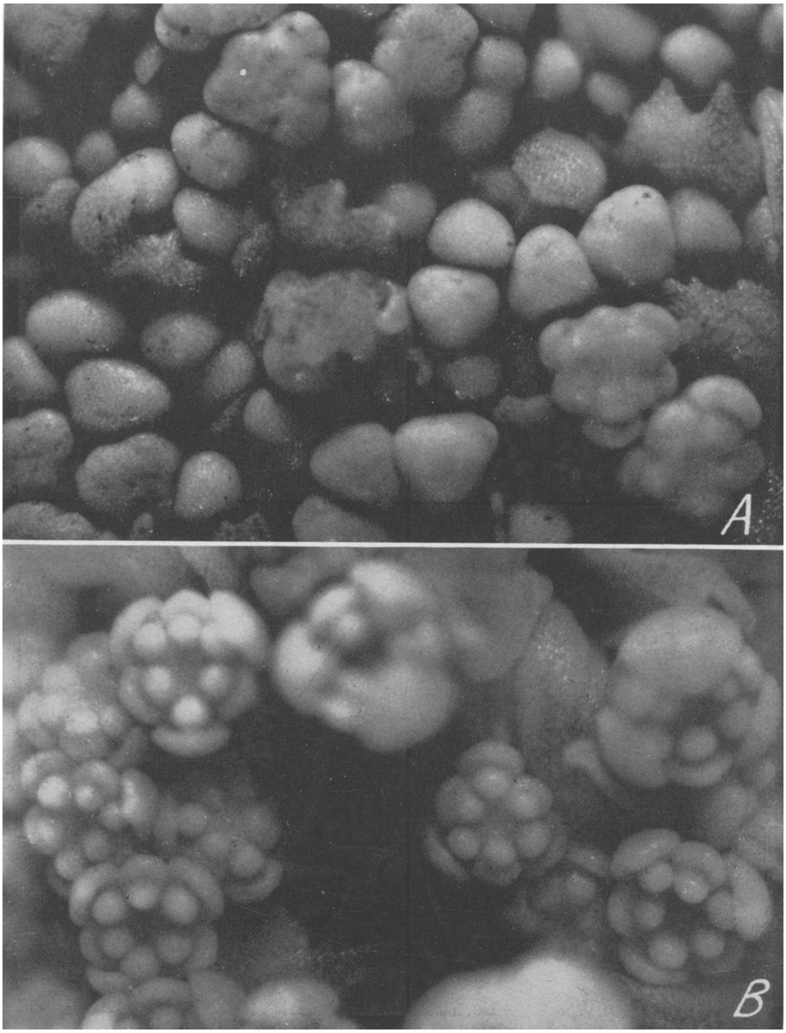

Plate 3. *A*, Flower primordia at the time the floral organs are beginning to differentiate. *B*, Perianth segments and stamens have differentiated.

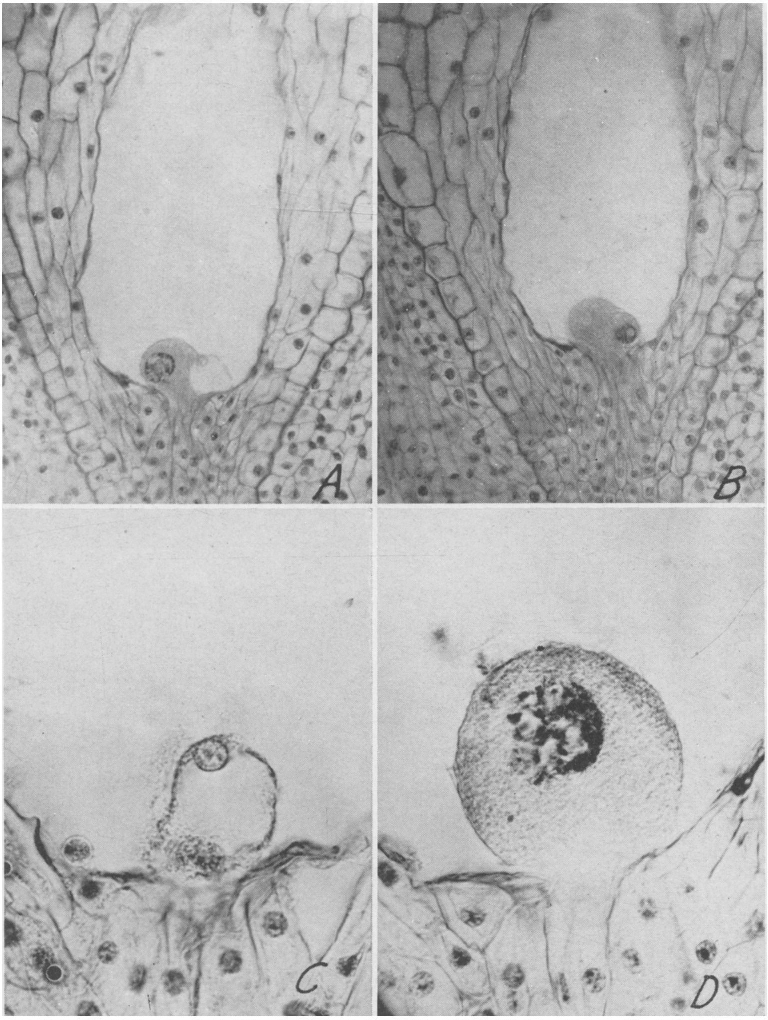

Plate 4. *A*, *B*, Two sections of the same sac at the time the stigma is first receptive: *A*, large synergid and egg; *B*, two synergids. *C*, *D*, Two sections of the same sac four days after the stigma was first receptive: *C*, egg; *D*, large synergid.