

# HILGARDIA

*A Journal of Agricultural Science Published by  
the California Agricultural Experiment Station*

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VOLUME 13

AUGUST, 1940

NUMBER 5

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REID M. BROOKS

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UNIVERSITY OF CALIFORNIA • BERKELEY, CALIFORNIA

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# COMPARATIVE HISTOGENESIS OF VEGETATIVE AND FLORAL APICES IN AMYGDALUS COMMUNIS, WITH SPECIAL REFERENCE TO THE CARPEL<sup>1</sup>

REID M. BROOKS<sup>2</sup>

## INTRODUCTION

THE INTERPRETATION of the carpel<sup>3</sup> as a foliar structure has been criticized both favorably and adversely. Evidence for and against Goethe's classical theory of metamorphosis in reference to the flower has been presented from a study of the vascular system of floral organs, paleobotanical material, and ontogeny. Thus far, however, no one has made a comparative histogenetic study of the mode of initiation of the foliage leaf and floral organs within the same species, together with an interpretation of the homologous or analogous nature of these structures.

Since, however, reproduction should be treated as a function of the entire plant, the reproductive shoot cannot be understood except in relation to the vegetative body (Arber, 1937).<sup>4</sup> As a background, accordingly, for the interpretation of the carpel, the vegetative apex and the production of foliage-leaf primordia have been studied, by the present author, within the same species in order to permit a comparison with the floral apex and initiation of floral organs, with particular emphasis on the carpel.

In attempting to compare the carpel and the vegetative leaf, the histogenetic method of attack attempts to do more than merely describe the expected anatomical differences between the two types of structures. This method seeks to explain the nature of the organs in terms of their origin from an initial cell or region and to show the distribution of growth in each. The general morphological development of an organ may be known; but the histological method associates these modes of growth and development with the localization, the type, and the duration of the different kinds of meristematic phenomena. At present there is an increasing interest in the morphogenetic significance of the early phases

<sup>1</sup> Received for publication August 8, 1939.

<sup>2</sup> Instructor in Pomology and Junior Pomologist in the Experiment Station.

<sup>3</sup> In this paper, *carpel* refers not only to a single, simple, closed macrosporophyll, but also to each individual macrosporophyll unit of a compound pistil.

<sup>4</sup> See "Literature Cited" for complete data on citations, which are referred to in the text by author and date of publication.



of form development that results from the activity of primary meristems.

The research here reported is confined to *Amygdalus communis* L., horticultural variety Nonpareil, a commercial paper-shell almond. The purpose is two-fold: (1) to compare the development of the flower bud with that of the leaf bud, especially foliage-leaf initiation with the origin of floral organs; (2) to trace the development of the flower, particularly the initiation and early development of the carpel. The presentation of such evidence may suggest a new mode of attacking a problem of considerable morphological interest. The general applicability of the inferences drawn must await broad comparative studies of a similar character.

### REVIEW OF LITERATURE

The idea of the homology of plant parts, especially leaf and flower, had been recognized before Goethe's time by Linnaeus (1759, cited by Lindley, 1832; 1760, cited by Lindley, 1832, and also by Schleiden, 1849) and by Caspar Friedrich Wolff in 1759 (cited by Bower, 1935, by Green, 1909, and by Sachs, 1890). According to Worsdell (1916), however, the views of Wolff and Goethe were probably founded on teratological data; evidence of the sort has been brought to bear upon this problem (cf. Goebel, 1895; Bancroft, 1935; and Kausik, 1938), but will not be discussed here. Goethe not only recognized these affinities but attempted to explain them in a theory of metamorphosis published in 1790 (at Gotha) in his *Versuch die Metamorphose der Pflanzen zu erklären*. According to Goethe the metamorphosis of plants is the phenomenon by which one and the same organ appears to us under numerous diverse forms. He called this original organ or prototype, whence arise all appendages of the stem, the "leaf" (*Blatt*), although the term never quite satisfied him and today causes much discussion because of its varied interpretations. Thus Goethe, in recognizing "the fertility which lies hidden in a leaf," developed, more or less abstractly, the idea that floral organs are homologous with foliage leaves. This *literal* interpretation of the theory is at present rather prevalent (Eames and MacDaniels, 1925; Hutchinson, 1926; Robbins and Rickett, 1929; Wilson and Haber, 1935; and Newman, 1936).

Goethe's theory of the foliar nature of the flower has been interpreted *figuratively* by Gray, A. Arber, and others (James and Clapham, 1935). Gray (1845) stated that the term *metamorphosis*, as applied to the floral organs, is figurative: foliage and floral leaves do not develop one from the other, although they may have the same underlying nature. This

same idea was expressed verbatim in the fifth edition of his *Botanical Textbook* (1871); yet, in another text of more recent date, he remarked that a pistil "consists of a leaf with its margins curved inwards till they meet and unite to form a closed cavity, the ovary, while the tip is prolonged to form the style and bear the stigma" (Gray, 1878). Recently A. Arber (1937) has discussed this question in detail, suggesting the term *parallelism* (within the development of the individual) in place of *equivalence*, *correspondence*, or even *homology*, whereby one compares the carpel to an infolded foliage leaf instead of calling it such a leaf.

Initiated by Goethe, the theory came to full fruition with A. P. de Candolle (1827, 1841), who placed it upon a much firmer and more definite basis and directed general attention to this conception. Basing his investigations upon external form-relations (as did Goethe), de Candolle (1841) considers the flower "an assemblage of several (usually four) verticils of leaves, variously transformed." Referring to the carpel he states, "Each carpel may be considered as a leaf folded longitudinally upon itself." Also, he gives many characteristics such as texture, color, presence of stomata and hairs, vascular system, and degeneration that aid in showing a similarity between carpel and leaf.

Brown (1840), a contemporary of de Candolle, in laying the foundation of floral anatomy and in using the microscope for the first time as mentioned in an earlier publication (1833) in such work, wrote: "The simple ovary . . . consists of the modification of a leaf folded inwards and united by its margins, which in most cases are the only parts of the organ producing ovula . . . ." To Lindley the metamorphosis of the organs is synonymous with the study of morphology (1832); further, "the ovary itself is a convolute leaf, with its coats elongated into a style, and the extremity of its vascular system denuded under the form of a stigma . . . ." Braun (1851) also supported this theory of metamorphosis, interpreting the sporophylls as modifications of Goethe's hypothetical leaf, although he did not put forward a definite conception of this "ideal leaf." Thomas (1932) has remarked that present conceptions of the morphological relations of the higher plants, as expressed by such investigators as Velenovsky (1905) and Troll (1928), closely resemble those ideas noted by Goethe, Lindley, and de Candolle.

After this formal and abstract treatment of the problem (primarily from the organographical viewpoint), studies diverged along two general lines—morphology and physiology. The former point of view will be emphasized here, the physiological viewpoint being concerned primarily with the influence of internal and external factors on the structure of the shoot apex. As Klebs (1914) has shown experimentally, flower

formation is related to quantitative seasonal differences in the substances supplied to the growing apex. In *Scrophularia*, Schmidt (1924) found that there are more meristematic layers at the apex at the time of flower formation than before this stage. Priestley (1929) discovered that at the time of flower formation, the meristematic layers at the apex occur at a greater depth because of a greater thickness of cell walls and a consequent increased water supply through the walls to the protoplasts.

In morphology the different interpretations of the carpel may be based upon three main trends of thought—namely, on the vascular anatomy of the flower, on paleobotany, and on ontogeny. Necessarily, in any comparative morphological investigation, the facts arising from these sources cannot be divorced from one another in a true analysis of a structure such as the carpel; all are related to phylogeny. No doubt the “full problem of morphology is,” as Bower (1908) noted three decades ago, “to explain . . . how in the past plants came to be such as we now see them.”

Brown (1822) had pointed the way in research on the vascular system when he wrote: “In the ovarium . . . the vascularity, compared with that of the leaf, is in general rather modified than diminished; the principal vessels occupying the margins or lines of production, and giving off branches toward the axis (midrib), whose vascularity is frequently reduced.” Payer (1857, cited by Hunt, 1937) asserted that the carpel “is formed by an appendicular part, the carpellary leaf, inserted by its base on the two branches of a bifurcated axis which carries the ovules.” Van Tieghem (1868) saw in the vascular system of the flower a main point on which the interpretation of the carpel may be based, and in 1875 (cited by Hunt, 1937) he “established the appendicular nature of the entire carpel (in the sense that the leaf is appendicular).” Earlier, though, Cave (1869) had stated: “La majorité des savants considèrent ces organes (les carpelles) comme exclusivement appendiculaires.” Eichler's (1875) contribution was his *Blüthendiagramme* with a discussion of floral morphology from the viewpoint of the evolutionist. Henslow (1891), greatly influenced by the writings of van Tieghem, believed that the vascular strands of the floral whorls are fundamentally alike and that this similarity enabled the different parts of the flower to interchange their structure and function. E. A. N. Arber and Parkin (1907), following the dictum of Goethe, regarded the carpel as a fertile leaf, more or less modified.

New impetus, which has carried to the present time, was given to research in floral morphology in 1923 when Saunders reopened this subject by publishing a theory of carpel polymorphism. She (1937) in-

interprets the gynoeceium in accordance with the view that in true apocarpy the individual ovary is formed of a single carpel, which arises as a separate structure, but that in syncarpous and pseudo-apocarpous forms it is composed of two kinds of carpels, sterile and fertile. She (1931) conceives of the polymorphism of carpels as arising simultaneously with syncarpy. Further, these two kinds of carpels differ markedly in form as well as function and compose two alternating whorls. Authors (among them A. Arber, 1933; Eames and Wilson, 1928; but cf. Wilson, 1937, noted below) preferring the classical interpretation of the flower have held that the vigor of vascular development has shifted from the midrib to the marginal bundles and that "normally, in the majority of Angiosperm families, a carpel receives three traces, a dorsal or midrib bundle and two ventral or marginal bundles" (Eames and Wilson, 1928). But Saunders (1934), holding to the theory of carpel polymorphism, views "the *vigorous marginal* veins as the *main* bundles of intervening consolidated carpels" and declares that "the vascular supply of the valve carpel is *in its origin* precisely similar to that of the members of the other floral whorls . . . . Whether a carpel has one trace or three *at the level of exsertion* is merely a question of whether the midrib happens to give off its first laterals before or after exsertion."

Eames (1931), using the vascular anatomy of flowers as Saunders has done, concluded that "the theory of polymorphism is clearly unsound." For him the flower is a specialized stem, all the floral organs being homologues of leaves; polymorphism has erred in interpreting the anatomy of the flower, especially as regards the carpellary vascular system. From a study of the vascular supply to sepal, petal, stamen, but not carpel, Wilson (1937) concludes: "The modern stamen is not homologous with the entire leaf, as stated under the classical theory of the nature of the sporophylls of the flower; it is rather homologous with only a part of a leaf, and the term sporophyll may no longer be applied." As concerns the stamen, therefore, he has modified his viewpoint on the classical interpretation of the flower as noted above (Eames and Wilson, 1928).

Significant facts unearthed by paleobotany have assisted in determining the nature of the carpel even though it be static, rather than growing and changing in form and structure. According to Thomas (1934) the angiospermic flower is not the homologue of a vegetative bud. From studies on the reproductive bodies of the Caytoniales, a Lower Jurassic group of fossil plants, he concluded that certain structures originally fertile have been sterilized. Further, he states, this transition is much more likely to have taken place in almost all the higher plants than is the derivation of anthers, carpels, and ovules from expanded foliar

structures with fertile edges (Thomas, 1931; cf. Bancroft, 1935). According to this interpretation, expressed by Thomas (1936), the carpel of a flowering plant is composed of two fused cupules rather than of a single foliar structure.

Parallel with these studies on paleobotany and floral vascular systems, there has developed an extensive literature dealing with the comparative anatomy of the various foliar organs in angiosperms. Contributions, however, to the problem of foliar histogenesis and floral ontogeny have been made only recently. No doubt Schuepp (1926) has made one of the most important of these in his review of meristems and their relation to growth processes. This work has been greatly furthered by Foster (in *Carya Buckleyi*, 1935*a*, 1935*b*, and *Rhododendron* spp., 1937*a*, 1937*b*) by studying histologically the shoot apex and the development of various foliar organs, and by discovering the differences between cataphyll and foliage-leaf primordia. Opposing the ontogenetic method is the "typological method" advanced by Troll (1935), whereby the comparative study of a wide range of adult forms is considered far more important than studies pertaining to the ontogeny of such structures. Conclusions based on observations of mature structures cannot be depended upon alone unless accompanied by and correlated to comparative results concerning the developmental phases of the organs themselves (Cross, 1937*b*).

Of the recent interpretations of the carpel based on ontogeny, three important ones have been promulgated by Grégoire, Newman, and J. McLean Thompson. Grégoire (1931) was among the first to investigate histogenetically the floral and vegetative apices of angiospermous plants and review comprehensively (1938) the comparative nature of these apices. Through these earlier studies he found two essential differences between the development of the flower and of the vegetative shoot.

In the structure of the vegetative "cone" Grégoire finds that a "tunica," consisting of several self-perpetuating cell layers, envelops an inner mass of cells, the "corpus," furnished with an initial region that produces growth in length. The floral apex, however, possessing no particular initial region, has only a meristematic "hood" or "mantle" covering a raised parenchymatous mass, which cannot become longer. Thus the floral meristem contains no tissue corresponding to the tunica and corpus of the vegetative cone (Grégoire, 1935). A corollary of this conception forms another point of difference between floral and vegetative shoots; the floral apex as thus constituted gives rise only to the petals, stamens, and pistil; "the sepals begin development *as leaves on a vegetative cone*." Only after having produced the sepals does this vegetative



cone modify its divisions and its parenchymatous differentiation in such a manner as to become a floral axis.

From these observations that the meristematic origin of a carpel is not the same as that of a leaf, Grégoire (1931) reaches a conclusion opposed to the classical theory: "*Carpels do not represent modified leaves, but are organs 'sui generis,' without homology among organs of vegetative equipment.*" Also, the dimensions of the apex may influence the type of structure to be produced, for he states that if the vegetative cone were larger, it apparently would have become a carpel itself. Unfortunately, in this earlier work, he compared the vegetative cone of one genus with the floral apex of another genus in securing and interpreting his results. This difficulty has been overcome to a certain extent in his most recent paper (Grégoire, 1938), whereby, at least in some instances, he figures and discusses the two types of apices in the same species (for example, *Aconitum napellus*). In this last paper Grégoire has emphasized further, by discussion and numerous illustrations, his original conception of the difference between vegetative and reproductive apices. No tunica is found in the floral apex corresponding to that in the vegetative cone; it is replaced by a homogeneous meristematic mantle, which represents "*à lui seule, tout le meristème du sommet floral*" (Grégoire, 1938). Because of its innate structure this floral summit cannot increase its axis: it is a determinate structure. Thus the meristematic mantle is but a simple producer of the floral organs alone; the floral apex and the vegetative cone consequently belong to two entirely separate and distinct morphological categories.

Newman (1936), on the other hand, surveying the primordia of *Acacia longifolia* and *A. suaveolens*, favors the classical interpretation of the carpel as a modified fertile leaf; specifically he concludes that the fruit of these species, a legume, is a single, folded, foliar structure. He is among the first, if not the first, to describe floral meristems and the initiation of floral organs, especially of the carpel, in a truly ontogenetic manner, even though he based his descriptions on the generalized aspect of apical meristems and on their activity rather than on precise demarcation of tissue-areas. According to him there is no fundamental difference between vegetative and floral apices; and therefore the legume is initiated in the same manner as the other parts of the flower *and of vegetative leaves*, the ovules being found on the margins of the lamina of the legume. Newman's knowledge of the vegetative apex is obtained, however, only from the recent literature of other authors; he gives no information, either in text or figures, on the shoot apex or on the origin of the phyllode of *Acacia*. Yet he compares the carpel with the vegetative leaf

from the histological viewpoint, concluding that "there is no reason for doubting that the legumes of *Acacia longifolia* and *Acacia suaveolens* are of foliar nature, and that it is reasonable to interpret the flower of these species as modified leafy shoots." The carpel is thus homologous with foliar structures—a totally different conclusion from the one Grégoire reached by following virtually similar histological methods and also from the one J. McLean Thompson reached by using the same species of *Acacia* and similar histological methods.

J. McLean Thompson (1934, 1936*a*, 1937) conceives of the flower as a heterosporous sporogenous axis, with limitation of growth in one dominant direction and of continued growth in others, leading to the creation of one or a series of fertile style-bearing structures of axial origin, on which ovules may be formed. Although this sporogenous axis alone is essential to flowering, its base is sterile, marking the transition from the vegetative body to the spore-bearing organ. Bracts, bracteoles, and sepals are products of this sterile base. The lower portion of the sporogenous tissue is potential microsporangium, of which the lower emergences from this area are commonly sterilized and mature as either petals or staminodes. Further, says Thompson, if toral growth is dominant over apical growth from an early stage of development, the maturing axis is cup-shaped, lined with potential sporogenous tissue; and an inferior ovary is thus initiated. If, however, apical growth predominates, a flower with an hypogynous ovary results. Concerning the ontogenetic approach to the study of the morphology of the flower, Thompson (1934) states: "On the present view ontogenetic study of flowering is the only form of morphological enquiry which needs no apology. It is the basis of all comparison."

After Newman (1936) had published his paper on *Acacia*, J. McLean Thompson (1936*b*) wrote an article using the same species as did Newman but completely refuting Newman's conclusions. Instead of considering the legume of these species of *Acacia* as foliar in nature and the flower as a modified leafy shoot, Thompson believes: "There are no grounds for either of the above conclusions. They are merely in conformity with an historical interpretation which is not in accord with established facts. The carpellary theory of gynoeceal construction has been a veil obscuring the true issues. Spore-production is the only fundamental feature in flowering, and the floral apex, whatever be its final form, is the seat of origin of megaspores and is the gynoeceum."

Contributions in floral histology have been made in other lines of endeavor as well as in the realm of "pure botany." In the field of horticulture particularly, numerous papers such as those of Bradford

(1915), Tufts and Morrow (1925), Abbott (1935), Bonnett (1935), Aaron (1936), Winkler and Shemsettin (1937), and Barnard (1938) have reported the formation and differentiation of flower buds, especially as regards the time at which floral primordia are produced, and have attempted to correlate environmental conditions to this production. Unfortunately for the present problem, these investigations do not deal with the ontogenetical aspects of floral apices.

Judging from the review of literature pertaining to the interpretation of the carpel, the eventual clarification of this complex problem of the carpel and its developmental history must involve some reconciliation of all lines of attack—that is, a judicial application of data of ontogeny, vascular anatomy, paleobotany, and comparative morphology. At present this reconciliation is impossible because of the incomplete evidence, particularly with respect to the comparative histogenesis of the development of the vegetative and floral shoots. The present paper attempts to throw light on this aspect of the problem.

Investigations of the almond have been concerned, for the most part, with horticultural problems, whereas few have studied the histology of the almond flower and fruit. Brief reports have been made on certain of these structural features. Pease (1930) and Young (1912) have discussed the histological features of the almond seed coats. Campbell (1915) has briefly discussed the relation of stamens to insects in pollination of the species. Bonne (1928, cited by Ragland, 1934) has described the vascular system of the pedicel and receptacle of both the almond and the peach. Cave (1869) has given certain features of the vascular and anatomical structure of the fruit. The most comprehensive treatise on the histology of the almond was that wherein Garcin (1890) discussed minutely the tissues concerned in the mature fruit rather than the buds or flowers.

## MATERIALS AND METHODS

The material of *Amygdalus communis* L., horticultural variety Nonpareil, used in this investigation was collected from a single tree growing on the University of California Farm, Davis. Leaf buds were collected semiweekly from their time of formation through differentiation of the floral organs. Flower buds, flowers, and fruits were collected also at semiweekly intervals throughout the growing seasons of 1936 and 1937. Spurs with the buds were brought to the laboratory, where, in the case of the mature buds, the outer foliar structures were removed and the buds were placed directly either in Navaschin's fluid (Derman's Harvard modifica-

tion)<sup>5</sup> or in a formalin-acetic-alcohol fluid<sup>6</sup> for killing and fixing. The material was evacuated while in the killing reagent. Flowers and fruit were preserved in the formalin-acetic-alcohol fluid.

The usual alcohol-xylol-paraffin schedule was followed, serial sections being cut 6–10 microns in thickness. Transverse serial sections were cut from the base upwards. A tannic acid-iron chloride method (Foster, 1934) and a modified safranin-fast green FCF staining schedule (Moore, 1936) were used. As the former schedule showed well the cytological features of the meristematic region of buds together with cellular detail of carpel development, it was relied upon for the greater part of the work.

All drawings were made with the aid of a microprojector, using an oil-immersion lens wherever cell structure is shown. Primordia were measured (1) by using an ocular micrometer in conjunction with a calibrated glass slide, (2) by measuring the drawing directly with a slide micrometer in the microprojector, and (3) by multiplying the number of serial sections by their thickness in microns.

## GENERAL MORPHOLOGY OF THE SHOOT SYSTEM

The majority of the almond flower buds are borne laterally on short shoots (spurs) of the past season (fig. 1, *A* and *B*), only a few occurring on comparatively long shoots of the past season (one-year-old shoots, fig. 1, *D*). To be certain of securing flower buds they were selected only from spurs, where they appear as a rosette of axillary buds around a single terminal leaf bud. Flower buds on a spur and on a long shoot are distributed in a similar manner. On a spur, flower buds are produced only at the nodes nearest the terminal bud (which is always vegetative). The number of flower buds per spur varied from one to six, with an average of three in the rosette. On a long shoot (fig. 1, *B* and *D*), especially on one-year-old shoots 6 inches or more in length, most of the flower buds occur near the apex, involving as many nodes as there are on an individual spur, but of course not arranged in a rosette. Below these three-to-six apical flower buds, on the remainder of the long shoot, flower and leaf buds are arranged in no definite sequence at the nodes, although the number of leaf buds predominates. Thus, below the terminal leaf bud of both spur and long shoot, the apical one-to-six flower buds are usually distributed in a similar manner. Gourley (1938) has noted the existing confusion regarding the terms *flower bud* and *fruit bud*. Since abundant

<sup>5</sup> Solution A: 1.5 grams chromic acid, 12 cc glacial acetic acid, and 86.5 cc water. Solution B: 50 cc commercial (40 per cent) formalin, and 50 cc water.

<sup>6</sup> 5 cc formalin, 5 cc glacial acetic acid, and 90 cc 70 per cent ethyl alcohol.

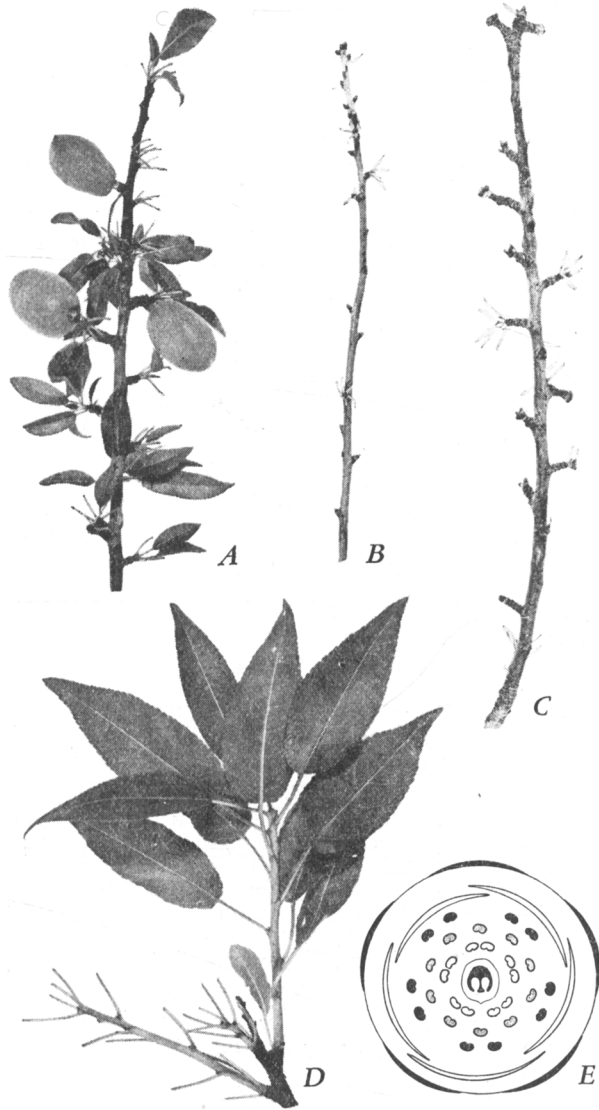


Fig. 1.—*A*, Four-year-old shoot (June 8, 1938) showing the growth habit. The upper fruit shows the ventral suture and remnant of the style; the lower fruits show the dorsal side. *B*, Two-year-old shoot (September 14, 1938) showing the formation of the spur type of growth; a long shoot was produced also during the current season. *C*, Four-year-old shoot (September 14, 1938), farther advanced than that in *B*. Leaves or leaf blades have been removed to show the rosette of buds on a spur. *D*, Current shoot (June 8, 1938) showing growth habit, axillary, and terminal buds. *E*, Diagram of the almond flower, showing the sympetalous calyx, the arrangement of the corolla, the three whorls of stamens, and the unilocular carpel containing two ovules. (*A–D*,  $\times \frac{1}{5}$ .)



flower production is no guarantee of fruit production, *flower bud* is considered the better term and is used in this paper (cf. Loehwing, 1938).

The leaf bud is triangular in longitudinal section, the basal portion being extremely woody—much more so than in the flower bud. Flower buds are longer, narrower, and more pointed than the other type. Both kinds are covered with deep-brown cataphylls (bud scales); those of flower buds, however, bear a distinct whitish fringe along the margin of each scale. The cataphylls on both bud types exhibit imbricated vernations, those of the leaf bud being much tighter.

Noticeable swelling of the flower buds began nine weeks before the first flowers opened on the tree and continued during that period of time even though temperatures ranged down to 14° F during January of one year (1937). Six weeks after swelling began, the inner bud scales were a light green and the calyx a darker green, although none of the structures was exposed to light; the scales were removed very easily for fixation. Two weeks later the petals were pink; but not until four days later did they protrude through the scales.

Leaf buds began to enlarge some eight weeks after the flower buds. The tree was in full bloom (fig. 11, *A*) about five days before the leaf buds began to open. Within ten days after bloom, most of the petals had fallen.

The form or design of the flower is shown in the floral formula,  $\frac{\text{Ca}^5\text{Co}^5\text{S}^{30}\text{P}^1}{\text{Dr}}$ . The general structure of this perigynous flower is shown

in a floral diagram (fig. 1, *E*). Ten stamens are borne in each of the three whorls. The outer whorl is arranged in five antepetalous pairs; the innermost whorl in five antesepalous pairs. The stamens of the center whorl are located opposite each pair of stamens of the outer rows: each central filament is subtended by a U-shaped structure, the nectary. Viewed differently, all stamens except five antepetalous stamens of the second whorl are opposite the calyx lobes, five in each group. Each of the thirty stamens is located on a different radius. The stamens of the innermost (adaxial row) are shorter than the others, being 6.0 mm long; those of the central whorl range from 7.5 to 10.0 mm; those of the outer (abaxial row) from 10.0 to 12.0 mm (fig. 11, *A*).

The petals of this cultivated variety exhibit three types of estivation, of which the most common is illustrated in figure 1, *E*: several authors, among them Small (1921), term this "the cochlear descending imbricate type." Petals are borne on the rim of the floral tube between the calyx lobes. The single carpel contains two ovules, of which only one usually matures (fig. 11, *B*).

After fertilization the calyx persists for some four weeks; during the

latter part of this time an abscission layer forms on the receptacle near the base of the carpel. Growth of the fruit ruptures the floral tube, which then falls off, bearing the withered stamens. After elongation of the peduncle, cataphylls fall about ten days after full bloom. The style withers shortly after fertilization, although it may persist almost until fruit maturity. Leaves remain on the tree until November or December under normal conditions.

## SUCCESSIVE STAGES IN THE HISTOGENESIS OF THE LEAF BUD

Although the flower may be compared to a vegetative shoot, the two structures show important differences. These dissimilarities, together with the likenesses, have been aptly pointed out by A. Arber (1933, 1937) for the general form of the organs involved. To view further the homologies and analogies of the vegetative and floral axes, the histological and (as far as possible) the cytological aspects of the apices of both leaf and flower buds have been investigated. The early ontogenetic development of the leaf bud will be described first.

*Organization of the Apex.*—Organization is concerned with the architecture of the apex<sup>7</sup> and with the precise demarcation of the tissue areas that give rise to the cataphylls and foliage leaves in the bud. The term *histogenesis* has often been used to refer exclusively to cell destiny, but such usage is not correct. Problems of growth in surface and volume in a meristem are quite apart from the destiny or fate of the cells themselves; thus arise two viewpoints, exemplified by Hanstein and by Schmidt.

Hanstein (1868) was concerned with the destiny of cells. He divided the meristem into three different histogens: the "dermatogen," which produced the epidermis; the "plerome," which produced the central cylinder; and the "periblem," a region lying between these, which usually formed the cortex and sometimes the pericycle and vascular tissue also. But Hanstein's divisions have been discarded by several recent workers—Schmidt (1924), Rösler (1928), Zimmermann (1928), Kühl (1933), Foster (1935*a*), and Cross (1936). The publications of de Bary (1884), Schoute (1902), and Strasburger (1908) show that the Hanstein conception is not applicable to the apices of all plants. Foster (1935*a*), Cross (1936), and others (Eames and MacDaniels, 1925) have demonstrated

<sup>7</sup> The term *apex* seems preferable to the ambiguous though common *growing point*. Considering the complex character of *growth* and the impossibility of localizing it to a point, it seems preferable to substitute the expressions *vegetative apex* and *floral apex*, respectively, in speaking of the entire embryonic terminal region of a leafy and a floral shoot.

that the three classic histogens, even when present, have little morphological significance.

Thus there has arisen another viewpoint of histogenesis, as expressed above, which is concerned primarily with the genesis and growth of cells in the meristem region itself. Following this trend, Schmidt (1924) proposed the terms *tunica* and *corpus* as substitutes for those used by Hanstein; Lund (1872) expressed a similar conception some fifty years earlier in his idea of perinome and pynome (Foster, 1936*b*, 1937*a*). In the present paper *tunica* and *corpus* will be used. Schmidt defined them as follows: "The tunica is the apical external layer or layers of cells which do not ordinarily divide in the periclinal plane except during leaf or bud initiation. The corpus includes all the remaining internal tissue in which divisions commonly occur in diverse planes." As Foster (1935*a*) has reported occasional periclinal divisions in the tunica of *Carya Buckleyi*, evidently these zones are not sharply demarcated. In this paper Foster has discussed the general applicability and validity of Schmidt's conception: namely, it is applicable to certain cases in which there is no distinction between periblem and plerome; by avoiding the implication that cortex and stele are always derived from independent histogens, it allows for the wide variability known to occur; and finally, it unites Hanstein's dermatogen and periblem under the collective term of tunica.

The apex during cataphyll and leaf formation exhibits a broad, dome-like, slightly convex appearance in median longitudinal section, its width being about 125 microns. The apical meristematic region of the leaf bud consists of a distinct four-layered tunica and an extensive corpus (fig. 2, *D*; plate 1). This condition may be observed at all times in differentiation in the almond (fig. 2, *A*, *B*, and *C*; plate 1, *B*). Cross (1937*b*), however, noted in *Viburnum rufidulum* that the four-layered condition was easily shown only at the end of the production of an organ, when the apex had attained its greatest surface area. For convenience in description, the layers of the tunica are numbered inwardly and designated as *t-1*, *t-2*, *t-3*, and *t-4*.

The outer row of cells of the tunica, *t-1*, always forms a definite and discrete layer over the apex, keeping its identity in the developing primordium. This layer corresponds to the dermatogen of Hanstein and is characterized solely by anticlinal divisions in the almond; it forms the epidermis of both the foliar and floral organs and of the stem. The subepidermal region, consisting of *t-2*, *t-3*, and *t-4*, constitutes an individual zone over the entire apex, dividing periclinally only during foliar initiation (fig. 3, *A*). This cell division is limited, however, to that region from

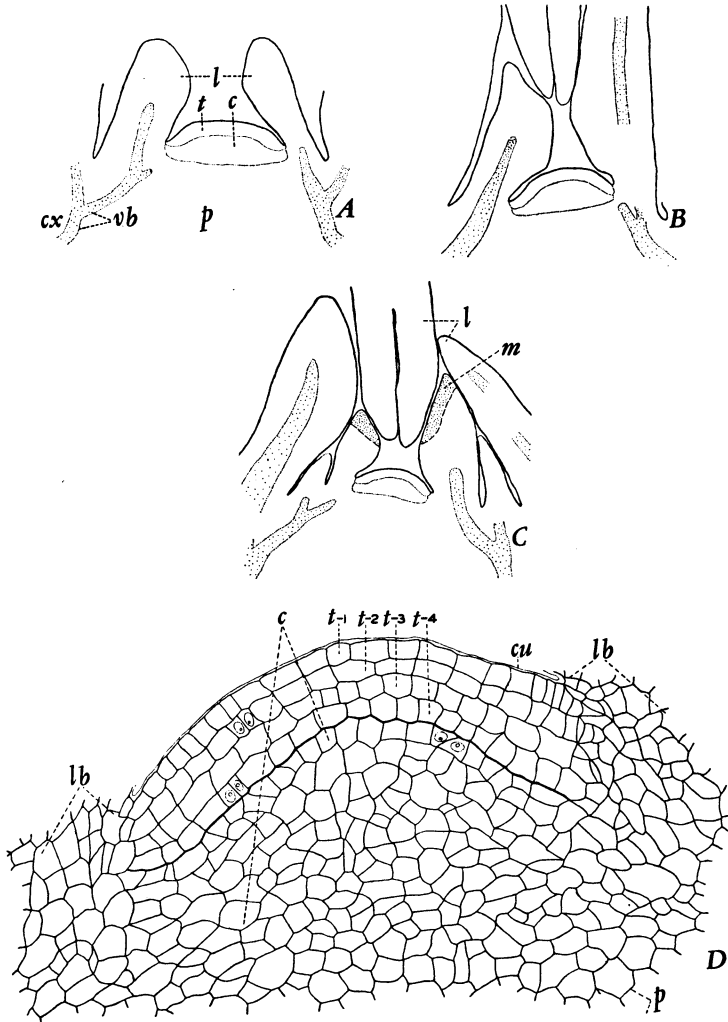


Fig. 2.—A–C, Outlines of median longitudinal sections of the apices of leaf buds collected, respectively, May 18, July 11, and December 7, 1936. D, Apex of the leaf bud showing the four cell layers of the tunica and the large corpus, and the mode of cell division in each region. Details are: *c*, corpus; *cu*, cuticle; *cx*, cortex; *l*, leaf; *lb*, leaf base; *m*, meristematic zone; *p*, pith; *t*, tunica; *t-1*, *t-2*, *t-3*, *t-4*, rows of cells in the tunica; *vb*, vascular bundle. The dotted lines at the apex in A–C demarcate the tunica and corpus regions in this and all similar figures which follow. The heavy line in D delimits the tunica and corpus regions of the apex in this and all similar figures which follow. The nuclei indicate the type of division in the various regions. (A–C,  $\times 82$ ; D,  $\times 436$ .)

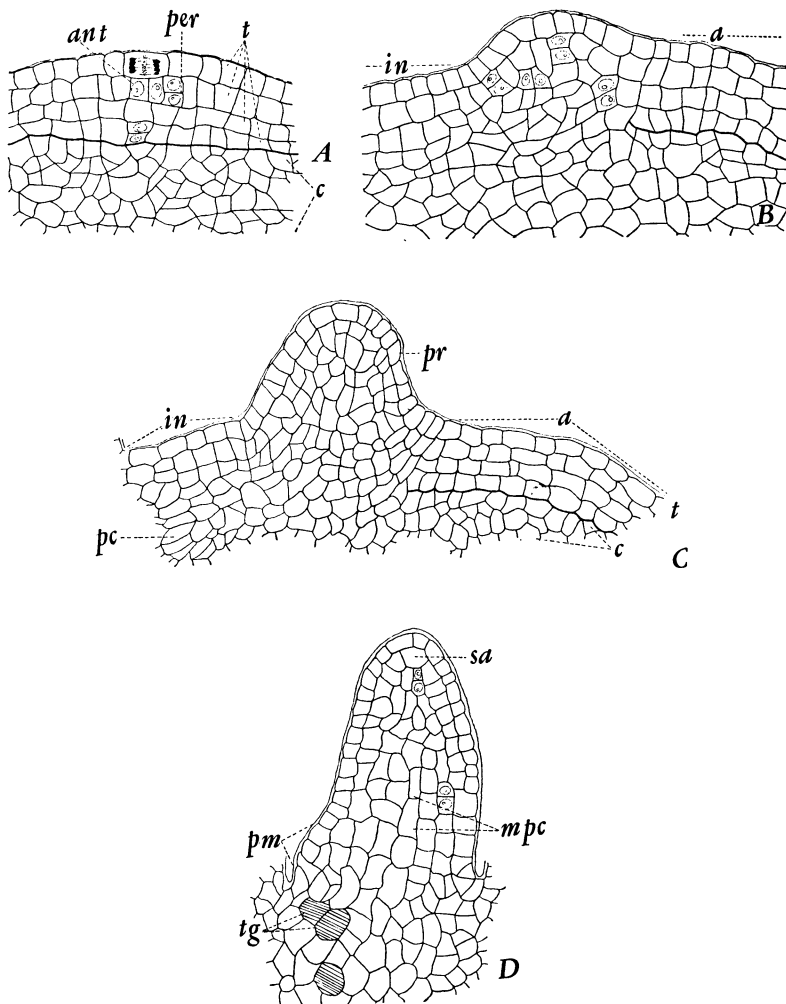


Fig. 3.—*A*, Side of the apex of a leaf bud, showing initiation of a leaf by periclinal divisions in the tunica region. *B*, Primordium of a leaf shortly after the stage shown in *A*. The tunica has now lost its identity in this initiating region. *C*, A developing leaf primordium, showing its relation to the apex and the internode. The tunica and corpus are clearly demarcated in the apex which has not given rise to the leaf. *D*, Leaf primordium in an advanced stage of development, 90 microns in height. Procambium and petiolar-midrib region are being initiated. Details are: *a*, apex; *ant*, anticlinal division; *c*, corpus; *in*, internode; *mpc*, median procambial strand; *pc*, procambium; *per*, periclinal division; *pm*, petiolar-midrib region; *pr*, primordium; *sa*, subapical cell; *t*, tunica; *tg*, tannin globules. (*A* and *B*,  $\times 465$ ; *C* and *D*,  $\times 372$ .)



which the primordium arises, not being found below the immediate summit of the apex. The corpus tissue extends vertically for some thirteen to fifteen layers of cells, until the pith of the stem is reached. Laterally the corpus extends to the toral procambial strands. No vascular strands have appeared as yet in this region (fig. 2).

Since bud scales of the leaf and flower buds are morphologically similar, no attempt has been made to compare cataphyll initiation in the two bud types.

*Mode of Initiation of the Foliage Leaf.*—Initiation of the leaf is first evidenced by rapid anticlinal divisions in the surface layer, *t-1*; as few as two or three cells may start this initiation (figs. 2, *D*, and 3, *A*). Vertical elongation produces a perceptible swelling on the surface of the apex, followed immediately by periclinal divisions in two or more cells of *t-2* which then elongate vertically also, giving the characteristic raised portion of a primordium. Division then ensues in *t-3-4*, so that shortly the identity of the subepidermal cells (*t-2-3-4*) as part of the tunica is lost (fig. 3, *B*). Cells of the corpus do not divide at this time, for the highly meristematic region extends only through the tunica at this stage of development; hence the corpus does not enter into leaf initiation at this point. In the primordium itself, after several divisions have taken place, there is no evidence of a discrete tunica and corpus (fig. 3, *B* and *C*). It may be noted, therefore, as Foster (1936a) did for *Carya Buckleyi* var. *arkansana* and Cross (1937a) for *Morus alba*, that there is no clear demarcation between the derivatives of the inner tunica layer in the apical region of a primordium. Thus the tunica does not maintain its individuality in the leaf, except for the epidermal layer.

At a height of 90 microns the foliar primordium differentiates a median procambial strand by periclinal divisions in the cells of the central region. These cells elongate parallel to the length of the primordium so that a distinct procambial region is delimited some 6 to 15 cells below the apex, forming an area 1 to 4 cells in length (fig. 3, *D*). It then develops both acropetally and basipetally until it joins the vascular system of the stem axis. Evidence of differentiation in this median procambial strand is first noted considerably after the vascular system is continuous into this axis.

Viewed transversely instead of longitudinally, the young leaf exhibits no marginal meristem—that is, the surface divides anticlinally only, preserving its identity; nor is there indication of any apical meristem cell, although the tip of the leaf blade is characteristically more meristematic than the remainder of the cells (fig. 2, *C*). A large subapical initial has been observed several times, however, directly below the apical epider-

mis; from this initial, apparently, arise all the rest of the cells of the mesophyll tissue (fig. 3, *D*). The subapical cell, when seen in longitudinal sections, cuts off cells periclinally, which then become greatly elongated as the base is approached. How long this cell functions was not determined.

The young leaf increases in length by divisions throughout its entirety until a height of 90 to 120 microns is reached. Then the cells of the adaxial surface become highly meristematic, producing a slight swelling (Cross, 1937*b* and 1938); this is the early differentiation of the petiolar-midrib region (figs. 2, *B*, and 3, *D*). Differentiation of the embryonic leaf into the characteristic mesophyll tissue of the mature leaf takes place exceedingly late—often as late as twenty days before the bud opens.

At the time of procambial formation, scattered cells in the hypodermal layers of the embryonic leaf begin to fill with what appear to be minute globules of tannin, which later coalesce into a solid mass completely filling the cell (fig. 3, *D*). Also, at a somewhat later stage, several tannin-filled cells are around the median vascular strand. As the leaf grows, cells containing tannin are more prevalent around the vascular elements than elsewhere, until, in a leaf several months old, as viewed transversely, the midrib area is characterized principally by such cells surrounding a small vascular bundle. In addition, at this stage more of the subepidermal cells of the lamina are filled with the red globules as stained by the safranin; but they are still relatively few. In the cataphyll, however, there is a preponderance of these tannin cells throughout its entirety; they do not seem to be localized as in the foliage leaf.

Throughout the growing period of the leaf bud, the meristematic region of the apex maintains its characteristic four-layered tunica and central corpus. The corpus adds cells basipetally to the stem region, as evidenced by the proportionate increase in larger vacuolated cells with thicker cell walls found below the dense, closely packed cells of the corpus. Here the corpus gives rise to the pith, procambium, and part of the cortex. Corpus cells divide anticleinally, pericleinally, and obliquely in order to keep pace with the ever expanding apex as it continually gives rise to additional primordia.

Unicellular epidermal hairs arise early on the foliage leaf, soon becoming vacuolated and enormously long; these persist during the life of the organ. No druses are present except those found in the cataphylls.

Specific differences between foliage leaf and cataphyll initiation are difficult to determine because their early formative periods are essentially similar; but characteristics have been found that aid in delineating the two types of structures. The embryonic leaf is characterized by the

development of a median procambial strand early in the primordial stage when the primordium is less than 100 microns high; this strand develops at a height of 175 microns in the cataphyll. The foliage leaf shows less rapid and less extensive cell vacuolization during the early embryonic period than does the scale leaf (Foster, 1931) and is more meristematic in its staining reaction. In the cataphyll, many cells contain tannin, others contain druses; but in the foliar structure, few cells are filled with tannin, and none with druses. Judging from the present study, leaf differentiation, as apart from bud-scale initiation, begins shortly after the formation of the bud. True leaves were present in the leaf bud on May 4, 1936; these would unfold the following February (in 1937).

### SUCCESSIVE STAGES IN THE HISTOGENESIS OF THE FLOWER BUD

In the entire history of flower-bud development, structures appear and differentiate in definite phases or cycles; each phase during which a certain structure arises may be termed a "stage." Floral histogenesis, as noted here, will be described as a series of successive stages. Such histogenetic development is concerned with the production of bud scales by the promeristem before differentiation of floral parts; with the change in form of the primordial meristem at the time of sepal differentiation; and finally with the acropetal succession of calyx, corolla, androecium, and gynoecium.

*Stage 1, Ontogeny of the Apex up to Floral Differentiation.*—The earliest phase in the history of the apex is distinguished by the characteristic structure and shape of the meristematic apex and by the production of cataphylls. At the time the flower bud is initiated, the surface of the apex covers an exceedingly small area (fig. 4, *A*) in comparison with that of the leaf bud (fig. 2, *A*) in a similar stage of development, for the width of the flower-bud apex between the bud-scale primordia is only 50 microns, whereas the leaf-bud type is 150 microns, or three times as great in width. The apices from which figures 2, *A*, and 4, *A*, were drawn are from serial sections of the same spur, in which one bud was terminal, the other lateral. The width of this floral apex, however, becomes progressively greater as more scales are produced, until, several weeks later, a width is reached (fig. 4, *B*) comparable with that of the leaf apex.

The summit of the floral apex shortly after initiation is but slightly rounded, extending only about the width of 1 to 3 cells above a line drawn between the bases of two opposite cataphyll primordia. It can hardly be

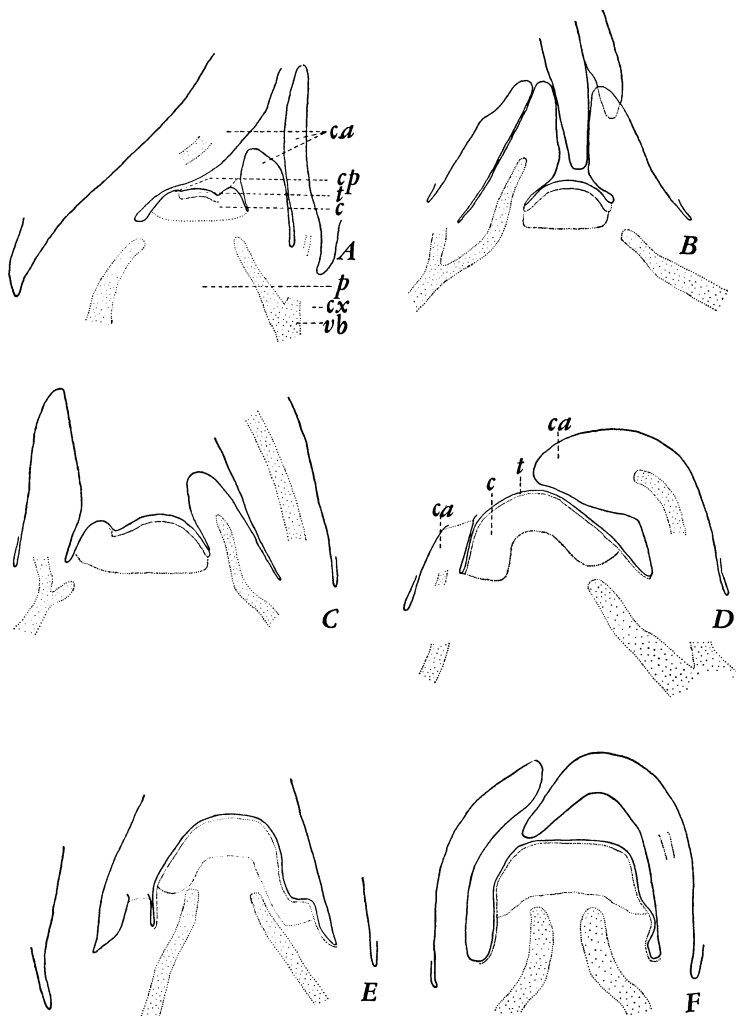


Fig. 4.—*A*, Very young flower bud (May 18) showing apical region, formation of cataphylls, and relation of tunica and corpus. *B*, Apex of flower bud (July 16) showing the type of growth in the developing cataphylls. *C*, Apex of flower bud (August 3) showing the origin of a cataphyll three weeks prior to the transitional stage. A two-layered tunica is present. *D*, Apex of flower bud (August 21) showing the transition from the vegetative type to the floral type of apex. The tunica is now uniseriate. *E*, Apex of flower bud (August 27) showing an advanced stage in the transition to the floral type of apex. *F*, Apical region of the flower bud (August 31) in the transition stage, just prior to sepal initiation. This stage shows the axis with a broad flat plateau and nearly vertical sides. The procambium is developing in the lower part of this region. Details are: *c*, corpus; *ca*, cataphyll; *cp*, cataphyll primordium; *cx*, cortex; *p*, pith; *t*, tunica; *vb*, vascular bundle. (All  $\times 82$ .)

termed dome-shaped, like the leaf bud on the same date; yet before long the apex does begin to assume this shape. Thenceforth the apex becomes more convex, being higher above the bases of the bud scales, until it begins to assume the form and structure peculiar to the "transition" apex of stage 2. The floral apex during stage 1 is, then, much more pronouncedly dome-shaped than that of the vegetative apex (fig. 2, *C*, and 4, *B*; plates 1 and 2, *A*).

In contradistinction to the four-layered tunica of a foliar bud, a distinct two-layered tunica is always present in the apex of a floral bud (fig. 5, *A*; plate 2, *A*). Cells of the corpus that lie below *t-1-2* show periclinal and oblique divisions and form an area relatively as large as that of the leaf bud. Grégoire (1935), however, found no central corpus in the floral apices of *Magnolia* and *Ranunculus*. The type of cell divisions characteristic of each zone in the almond may be seen clearly in figure 5, *A*. Cytologically, the tunica cells are square and large in longitudinal section, containing a large nucleus characteristic of meristematic tissue. Epidermal cells are prominently cuticularized—more so than are the cells of the foliar apex.

In the corpus of the young bud, cells have the same uniform appearance for a depth of about 15 cells from the apex, where they are slightly larger and decidedly vacuolated and begin to form a rib meristem (fig. 5, *A*). Throughout the corpus, periclinal divisions (in relation to the apex) predominate, followed by oblique divisions; there are few if any anticlinal divisions, for apparently the oblique ones take care of the growth in width. In the lower part of the corpus very few cells contain tannin; it is noticeably lacking.

Apparently, therefore, elongation of the receptacle results from divisions in the corpus near the apex.

As the base of the bud is reached, the corpus tissue merges with the mature basal cells of the area that will become the peduncle. These cells, though not much larger than those of the corpus, are vacuolated, contain considerable amounts of what appears to be tannin, and are somewhat elongated in a horizontal direction. No evidence was noted of any of the mature tannin-filled cells' dividing. Tannin occurs in globular form.

Cataphylls are found almost immediately after initiation of the bud itself, and they cease to be produced only ten days before actual differentiation of floral organs takes place (fig. 4, *E*). As the apex is less advanced than that of the leaf bud in its initial stage, there are correspondingly fewer scales at a given time in the flower bud than in the other type during the early period, although this discrepancy is not noticed in mature buds.



Cells of the apex that give rise to bud-scale primordia contain much cytoplasm, for they stain more deeply than the surrounding tissues; these cells include both tunica and corpus. The formation of a cataphyll

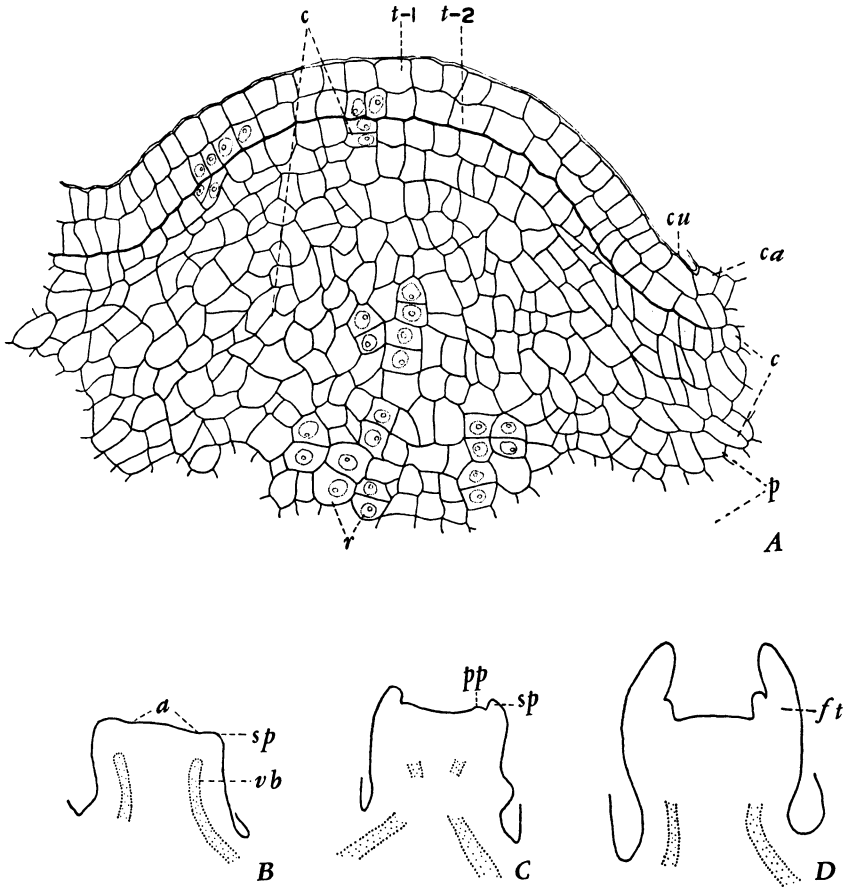


Fig. 5.—*A*, Apex of flower bud showing the two-layered tunica and location of corpus between the tunica and the rib meristem. The apex shows a prominent cuticle. *B*, Initiation of the sepal (stage 3) from the side of the apex at the end of the transition stage (stage 2). The vascular system is very near the primordium. *C*, Initiation of the petal (stage 4) from the sides of the apex between the sepal primordia. *D*, Formation of the floral tube by growth of the sepal and petal primordia. Details are: *a*, apex; *c*, corpus; *ca*, cataphyll; *cu*, cuticle; *ft*, floral tube; *p*, pith; *pp*, petal primordium; *r*, rib meristem; *sp*, sepal primordium; *t-1*, *t-2*, first and second cell layers, respectively, of the tunica; *vb*, vascular bundle. (*A*,  $\times 607$ ; *B-D*,  $\times 75$ .)

primordium resembles that of a foliage leaf: the tunica divides anticlinally, then periclinally; but its individuality soon becomes lost, although *t-1* always maintains its identity. There is evidence that the mature mesophyll of the cataphyll originates, at least in part, from the corpus.

Noticed in some of the cataphyll primordia is a definite subapical cell that cuts off cells obliquely and thus gives increase in height and width. The epidermal layer divides only anticlinal. Growth in length is accompanied by rapid cell divisions at and near the apex and base of the cataphyll; growth in width is caused by divisions in the corpus near the base. Cell enlargement follows the cell divisions, but is more evident nearer the base. The median procambial strand of the cataphyll usually differentiates early in the primordium.

Tannin appears early in the growth of the scale, being present in large amounts within two weeks after initiation. It appears first on the adaxial side in one or two cells of the subepidermal layer, and later appears in the epidermal layer. Subsequently it fills the same type of cells on the abaxial side. Finally, contiguous cells from the base upwards are filled, but none over the apex until the cataphyll approaches maturity. Tannin is in a solid mass in the scales, whereas it appears as globules in the corpus of the bud. In many cataphyll cells, tannin surrounds the nucleus, leaving a translucent area in each cell. Druses appear later than the tannin and always in cells other than those of the epidermis. Numerous hairs arise from the epidermal layer of the cataphyll.

At the end of this stage the number of cataphylls formed around the floral apex corresponds to the number (ranging from 10 to 18, with an average of 12.5) found on a mature bud at full bloom.

*Stage 2, Transition from Vegetative to Floral Type of Apex.*—A week before floral differentiation is noticeable in the formation of sepal primordia, there is an abrupt transition from the architecture typical of the apex which thus far has produced only vegetative structures, to the architecture typical of the apex which is to produce floral organs. This meristematic region is characterized first by becoming greatly elongated and broadened; and the dome-shaped form noted above in early stages is emphasized (fig. 4, *D* and *E*).

The striking histological feature accompanying this change in shape and size is the reduction in number of the tunica layers from two to one, so that the apex at the time of producing floral primordia is composed of a single-layered tunica and a massive corpus, larger than heretofore (fig. 4, *C* and *D*; plate 2). In all regions except the tunica, cell divisions are periclinal and oblique as well as anticlinal. Since cataphyll primordia have ceased to be produced, "*t-2*" is not dividing to form any such primordia, nor any floral primordia, as these appear several days later. The tunica, therefore, has lost its identity except for the one-celled surface layer, *t-1*. Thus, the cells of the corpus build up this apical region that becomes so typical of the floral-differentiation period.

Immediately before the production of floral primordia the apical surface undergoes a further change: it becomes flattened, and forms a broad plateau, slightly obovate in longitudinal section, but with its sides nearly vertical (fig. 4, *F*; plate 2, *B*). Its height has now been increased by growth in the toral region to 0.19 mm above the bases of the two innermost scale primordia. If an imaginary line is drawn between the bases of any two cataphylls, all the cells enclosed by that line and by *t-1* are derivatives of the corpus; all are similar in structure; and all are like the typical corpus of the preceding developmental stage. Those cells nearer the apex, however, take a deeper stain and are thus more meristematic than the basal ones, which are slightly vacuolated; yet they nevertheless retain meristematic properties. Few of these cells contain any tannin, and those only toward the base. The cuticle is thick and uniform over the epidermis.

A vascular system is well defined in the peduncle and extends upward into the lower portion of the receptacle (fig. 4, *F*; plate 2, *B*). Differentiation into xylem is beginning, as witnessed by the presence of spiral vessels.

The end of this transition period was September 1 in 1935 but came five days earlier in 1936. This stage is followed immediately by the production of floral organs in acropetal succession.

*Stage 3, Initiation and Early Development of the Sepal.*—The apex, preparatory to the initiation of floral organs, is thus greatly elongated in contrast to prior apices, either floral or vegetative, extending some 0.19 mm above the bases of the surrounding cataphylls. The tunica is reduced to a uniseriate surface layer, which covers a large corpus; and the internal tissue of the floral organs is derived, consequently, from this region, as the tunica maintains its identity only as a surface layer, maturing later into the epidermis (fig. 4, *F*; plate 2, *B*).

The first indication of a sepal primordium is the division in an anticlinal plane of the tunica cells located at the uppermost periphery of the apex. These divisions are accompanied in this area by periclinal ones in the subepidermal layer, the uppermost layer of the corpus; as a result, a slightly raised protuberance appears (fig. 5, *B*). The tunica cells maintain their original shape and do not elongate; in the vegetative primordia described above, they always elongate radially or anticlinally before cell division in the corpus. The meristematic region of this primordium extends basipetally to a greater extent than the cell divisions indicate, for the cells covering an area four rows deep show the characteristic deeper-staining qualities of such tissue. Because of the simultaneous initiation of the five sepal primordia, the apex is now slightly bowl-shaped, al-

though its center remains significantly convex. The surface of the entire summit is uniformly clothed with a heavy cuticle.

Cells of the corpus are meristematic, dividing anticleinally, pericleinally, and tangentially; they extend downward some 12 cells until the vacuolated cells of the pith and cortex are reached. Boundaries of pith and cortex are indicated by elongated cells that form about 8 to 15 cells below the apex and 5 to 8 cells in from the surface layer; these cells constitute the procambium. The pith thus forms much of the receptacle, whereas the cortex remains small. The surface layer of the cortex apparently retains its meristematic nature, for the cells are square (viewed longitudinally) and contain a large nucleus surrounded by dense cytoplasm; the subepidermal layers are composed of vacuolated cells. The lower portion of this enlarged apex is the young peduncle, whereas it grades into toral tissue in the upper part of this massive axis tissue; differentiation has not proceeded far enough for exact structures to be demarcated.

In the basal portion of the axis and in the torus (but not in the corpus), tannin-filled cells occur, notably around the vascular system and epidermis; as tannin appears only in vacuolated cells, it is not present in the corpus. Some cells have only a few globules of tannin, whereas others are filled with one solid mass.

During the production of sepal primordia around the periphery of the apex, periclinal divisions continue in the remainder of the corpus, especially in the outer layer, which results in further growth in height of the entire axis. Continued periclinal divisions of the corpus within the initiated sepal give added length and, to a certain extent, added width. Basal cells of the sepal soon become vacuolated, and a procambial strand differentiates early in its ontogeny. In these respects the origin of the sepal closely resembles that of a foliage leaf.

The lower portion of this lateral floral structure differentiates later into a tube to which are attached the free floral parts (sepals, petals, and stamens); the result is a perigynous condition. Evidence from ontogeny in the almond apparently substantiates the view that this tube is floral, not receptacular. Hence the term *floral tube*, suggested by Jackson (1934) for other members of the Rosaceae, is used in place of *hypanthium*, *calyx tube*, or *receptacular tube*, which may imply toral origin.

When the calyx primordia reach a height of some 5 to 8 cells above the apex, petals are initiated; thus, petals are produced very shortly after the origin of the calyx.

*Stage 4, Initiation and Early Development of the Petal.*—Petal primordia arise alternately with the now-expanded sepal primordia (fig. 5, C). In the initiation of the petal the epidermal cells, after anticleinal

divisions, elongate anticlinally to almost twice the length of cells on either side; this elongation gives the slightly raised protuberance indicative of a primordium, although shortly the corpus divides periclinally. Divisions, mostly at right angles to the long axis, then proceed, as indicated for the sepal, to give height and width to the corolla primordia.

The meristematic apex between the petal primordia is flat (fig. 5, *C*), but soon becomes slightly rounded again (fig. 5, *D*). Further growth involves the floral tube, not the apex. During the growth of the petals the sepals elongate, show prominent procambial strands, and begin to arch over the apex slightly; growth is thus predominantly abaxial.

*Stage 5, Initiation and Early Development of the Stamens.*—Stamen initiation follows immediately upon the production of the corolla lobes. The floral apex is slightly dome-shaped, being raised some 3 to 4 cells, and is about 25 cells wide (fig. 6, *A*). The sepal and petal primordia have grown to form the visible beginnings of a floral tube, with the calyx growing inwardly over the other structures. It is upon the basal portion of the petal primordium, upon the structure which may be termed floral tube (although there is no line of demarcation between petal base and toral region), that the first evidence of a stamen appears. Thus the origin of the androecium is not from the apex, as in the other floral structures, but from the lowest point of the adaxial surface of the floral tube. As will be discussed later, this raised apical region is the first indication of the carpel; since such a structure as the carpel cannot give rise to other floral organs, the zone of growth and of initiation has shifted, in consequence, to a toral structure which produces the perigynous condition typical of the almond flower and which bears the matured stamens.

The stamen is initiated by anticlinal division in the surface layer, followed by periclinal and anticlinal divisions in the subepidermal row of cells of the floral tube. Growth of the newly divided tunica and corpus cells results in a slight protuberance, pushed out the width of a cell above the surface. Since there is no apical or subapical cell that may give rise to the inner tissues of the stamen, growth results from periclinal and anticlinal divisions of this central corpus tissue, although activity is greater in the subepidermal cells than in any others. In the apical layer of the corpus, adjacent cells may be dividing periclinally and anticlinally; this is the only cell row of the corpus that maintains its identity for any length of time. The meristematic region extends basipetally some 10 cells to the developing vascular system that leads from the petal.

As growth ensues, the cells of the tunica become much larger than those over the summit; yet they are not elongated. Covering the stamens is a definite cuticle like that over the other bud structures. As in all pre-

viously described primordia, the tunica divides only anticlinally; but the major part of the tissue comprising the stamen is cut off by successive

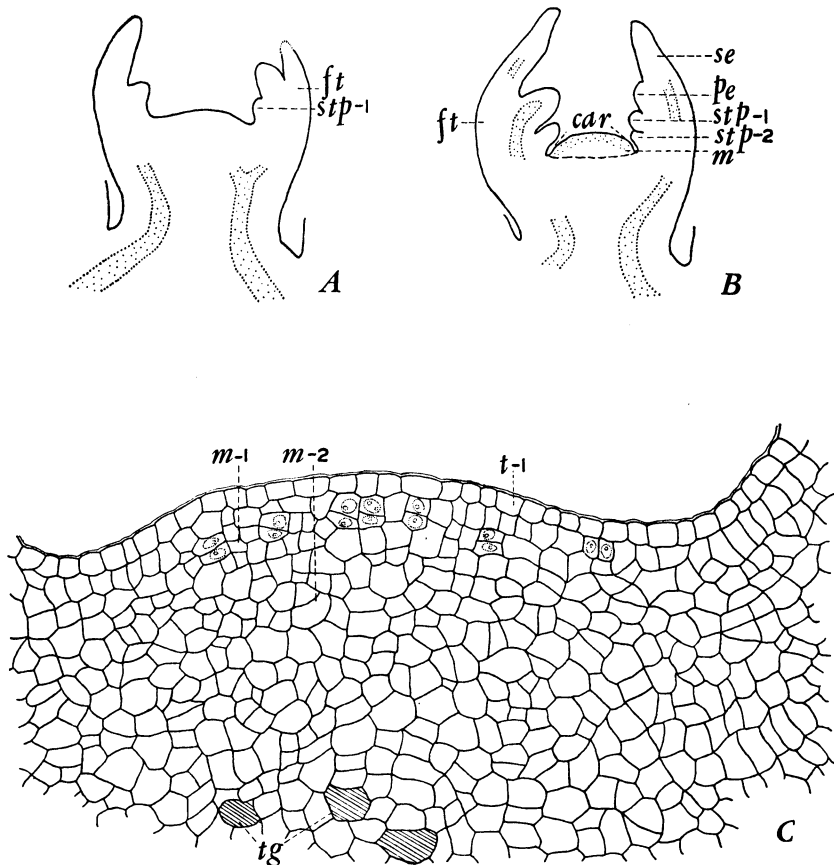


Fig. 6.—*A*, Flower bud showing initiation of the stamens of the outermost or abaxial whorl from the basal portion of the floral tube. *B*, Initiation of the carpel from the apex of the bud. The meristematic region is composed of two distinct types of cells, *m-1* and *m-2*. Procambial tissue is appearing in the petal primordium. *C*, Apex of the bud showing the initiation and emergence of the carpel from the entire width of the apex. Cell divisions, primarily in a periclinal plane, are localized in the uppermost four rows of cells. Cell division is also taking place in *m-2*, but to a lesser degree. The tunica is uniseriate. Details are: *car.*, carpel primordium; *ft*, floral tube; *m*, highly meristematic zone; *m-1*, meristematic area of small cells containing a great deal of cytoplasm; *m-2*, meristematic area of large, vacuolated cells; *pe*, petal; *se*, sepal; *stp-1*, stamen primordium of first whorl; *stp-2*, stamen primordium of second whorl; *tg*, tannin globules; *t-1*, uniseriate tunica. (*A* and *B*,  $\times 63$ ; *C*,  $\times 430$ .)

divisions, principally in the upper layer of the corpus. When the primordium is about 7 cells high, procambial cells appear 5 cells from the apex and at the base of the primordium.

The mature width of the filament is soon reached, for no periclinal divisions are observed. Very shortly all cells except about the six uppermost apical ones, as seen in longitudinal section, become vacuolated, including the surface layer. This condition does not, however, preclude cell division, for anticlinal divisions still proceed, giving increase in length. Tannin is soon found in the adaxial subepidermal layer and very near the apex of the stamen. The initiation of the stamen in each of the three whorls is similar.

The uppermost (abaxial) whorl of stamens arises first and opposite the calyx lobes (fig. 6, *A*). When this whorl is some 20 microns high, the second whorl is initiated, with every other filament opposite a petal primordium. Lastly, the short stamens of the innermost (adaxial) whorl arise. This sequence is in accord with the acropetal succession of floral organs and is substantiated, not only by an examination of serial sections showing this phase, but by macroscopic observation of the flower at the time of anthesis.

From observation of cell divisions in the calyx and corolla during this developmental period of the androecium, corpus tissue and its derivatives produce the mesophyll and the enclosed network of veins, although the mesophyll does not begin its differentiation until much later. Cell enlargement, accompanied by continued cell division, gives added growth in the floral tube, so that the sepals are beginning to touch overhead, resulting in an imbricated condition. Similar growth in the toral region (below the apex) produces height, with eventual delineation of a peduncle. The pith region is extremely large and contains much tannin. Outside the vascular system, in the cortex, cells are greatly vacuolated, including the surface layer.

*Stage 6, Initiation of the Carpel.*—The carpel originates on one side of the apex and begins by producing a slightly convex surface (fig. 6, *B*). As growth ensues, it becomes evident that this initial margin is the dorsal side of the carpel. The structure then forms in the shape of a horseshoe, with its two ventral (and open) edges or rims eventually uniting to form the adaxial suture. Thus this stage describes the changes occurring primarily in the dorsal portion of the apex, as nearly in a median plane as possible. Initiation of the carpel begins within three to five weeks (according to environmental conditions) after the transition of the vegetative apex to that characteristic of the floral apex.

The uniseriate tunica and upper subepidermal layers of the corpus of the apex show no localized meristematic activity during the formation of petals. But as soon as cells have divided in the basal portion of the floral tube to form the stamens, active cell division is observed in the

apex—first indication of carpel initiation (fig. 2, *A*). As in all preceding structures, the anticlinal divisions of the tunica maintain its identity throughout development, finally producing the pubescence characteristic of the epicarp of the fruit. The apex is some 25 to 30 cells (175 to 190 microns) wide when the carpel primordium is formed, the entire apical surface being used for its production.

The meristem that initiates the carpel is composed of a definite layer of small cells, deeply stained, which extend from the uniseriate tunica to a depth of only 4 to 6 cells (*m-1* in fig. 6, *C*; fig. 5, *A*). These contain large nuclei and much cytoplasm. Cell division is predominantly periclinal throughout the entire uppermost layer of four cells, although with more divisions localized toward the center of the apex; as a result, the summit becomes slightly convex. At the time the second stamen whorl is initiated, the carpel primordium is some 4 to 7 cells high (fig. 6, *B*). Below these four to six rows of meristematic initials is a second region of meristematic cells, distinguished from the others by being larger and slightly vacuolated (*m-2* in fig. 6, *C*; fig. 5, *A*). These are immature and meristematic, are capable of extensive cell division, and extend basally some 4 to 8 cells, until the large and highly vacuolated cells of the pith are reached. Thus the corpus is composed of these two types of meristematic zones (*m* in fig. 6, *B*, and *m-1*, *m-2* in fig. 6, *C*; fig. 5, *A*); these areas maintain their identity in the developing carpel until exceedingly late.

As shown by serial sections, the apex on the side away from the initiating carpel is perfectly flat, with no meristematic tissue present in any part of the flat summit; carpel initiation is localized, therefore, on but one side of the apex. Below these meristematic areas are the more highly vacuolated and larger cells of the pith of the receptacle. In these cells a substance is found that apparently is tannin, for it stains a brilliant red and is comparable with the tannin of bud scales and leaves (fig. 6, *C*; fig. 5, *A*).

*Stage 7, Development Prior to Union of the Carpel Edges.*—As cell growth by division and enlargement proceeds on the dorsal side, cell division is initiated in two parallel lines running towards the ventral side; this is the beginning of the rims or edges that will finally unite to give the ventral suture. Cooper (1932) observed this same type of development in *Bougainvillea glabra*. Such growth results in a slope, as seen in longitudinal section, from the top of the dorsal side to the bottom of the ventral side (figs. 7, *A* and *B*, and 8, *A*). The dorsal margin tends to become vertical as growth ensues (fig. 7). Here, as in previous stages, the uniseriate tunica divides only by anticlinal divisions. The two meri-



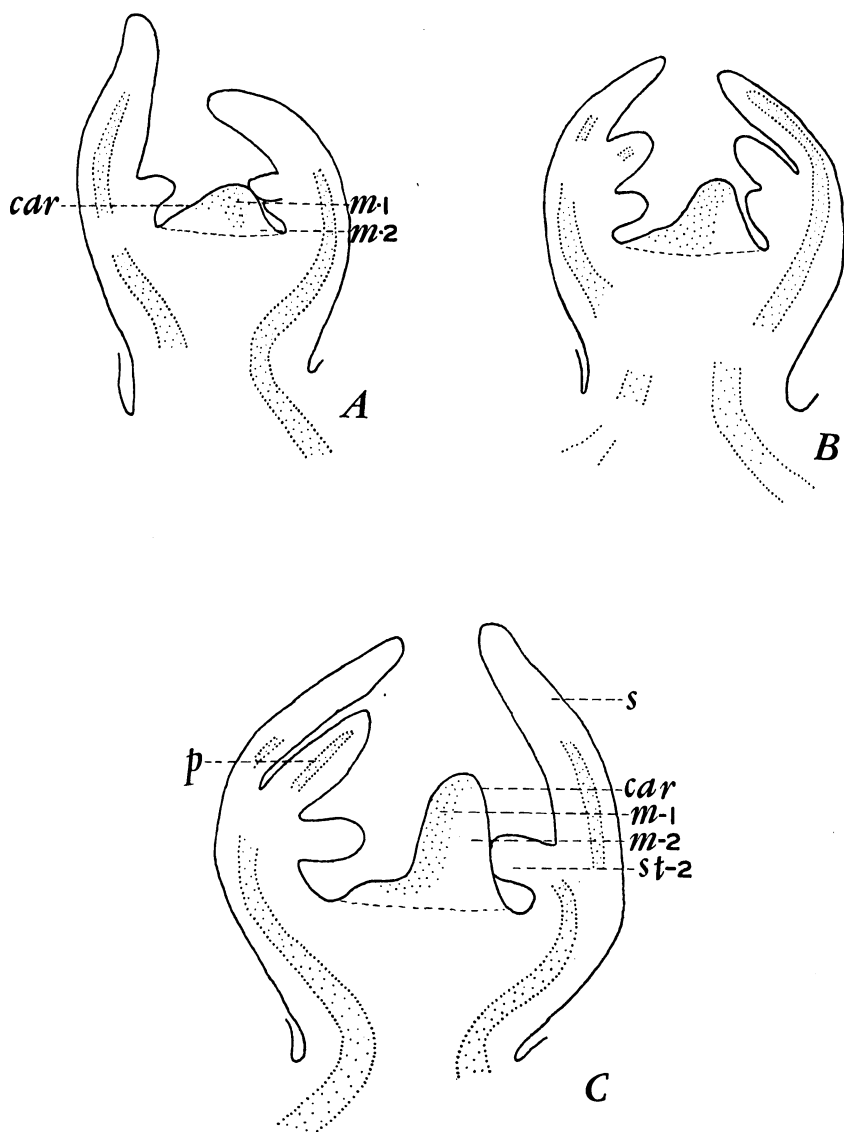


Fig. 7.—A-C, Longitudinal sections of the flower bud showing the emergence and successive stages in the growth of the carpel. The meristematic regions and persistent slope of the ventral edge (to the left in each drawing) are shown. Details are: *car*, carpel; *m-1*, meristematic area of small cells containing much cytoplasm; *m-2*, meristematic area of large, vacuolated cells; *p*, petal; *s*, sepal; *st-2*, stamen primordium of the second whorl. (All  $\times 63$ .)

stematic zones noted in stage 6 are exceedingly noticeable at this point in development (fig. 8, *A*; plate 3, *B*).

The region noted by the symbol *m-1* in figure 7 is located primarily along the sloping ventral side, with a dip downwards toward the base of the carpel primordium. The center of this area is localized at the tip of the primordium (figs. 8, *A*, and 9; and plates 3, *B*, and 4); rapid periclinal, and to a certain degree anticlinal, divisions are characteristic of this region. The apex is covered with a heavy cuticle.

Viewing the carpel primordium transversely (fig. 8, *B*), its meristematic nature is obvious, particularly in the ventral edges, as would be expected from the location of these cells viewed in longitudinal section. The large, vacuolated cells (*m-2*) are about three to four times the size of the small cells near the periphery (*m-1*); this distinguishing feature is evident throughout development (figs. 7-9; plates 3 and 4). Many vacuolated cells show recent indications of cell division (fig. 9, *A*); the majority are periclinal, giving increase in height to the primordium. Cells typical of the pith are found several rows below the base of the carpel primordium. As is evident from the many divisions taking place in both types of meristem tissue, this region (the corpus) is responsible for producing the entire carpel. There is no indication of any procambium or any inorganic cell inclusions. The carpel shows its horse-shoe-shaped structure almost throughout its height, as observed in transverse section (fig. 10, *J* and *K*).

If the carpel primordium is cut at right angles to the abaxial side, the nature of the groove that will form the locule may be observed, as in figure 10, *C*. The small meristematic cells characteristic of *m-1* are located at the tip of the primordium and around the groove; the vacuolated cells of *m-2* are around the periphery. The abaxial side is now practically vertical, for the serial section (not shown) next to figure 10, *A* shows no primordium at all, but only the flat surface of the receptacle directly against the raised floral tube on which are borne the stamens, petals, and sepals. At this time, the carpel is 185 microns wide—that is, from the vertical abaxial side to the flattened adaxial margin (fig. 10, *A-E*).

The ventral edges of the carpel have now developed (by October) considerably in height and, more significantly, in width, so that the open groove is beginning to be enclosed to form the locule. This growth in width is due primarily to cell division of the meristematic zone (*m-1*) which lines the central adaxial portion of the carpel. The abaxial tip of the carpel is beginning to assume the characteristic lobed shape of the stigma, for the edges have come together sufficiently at that point.

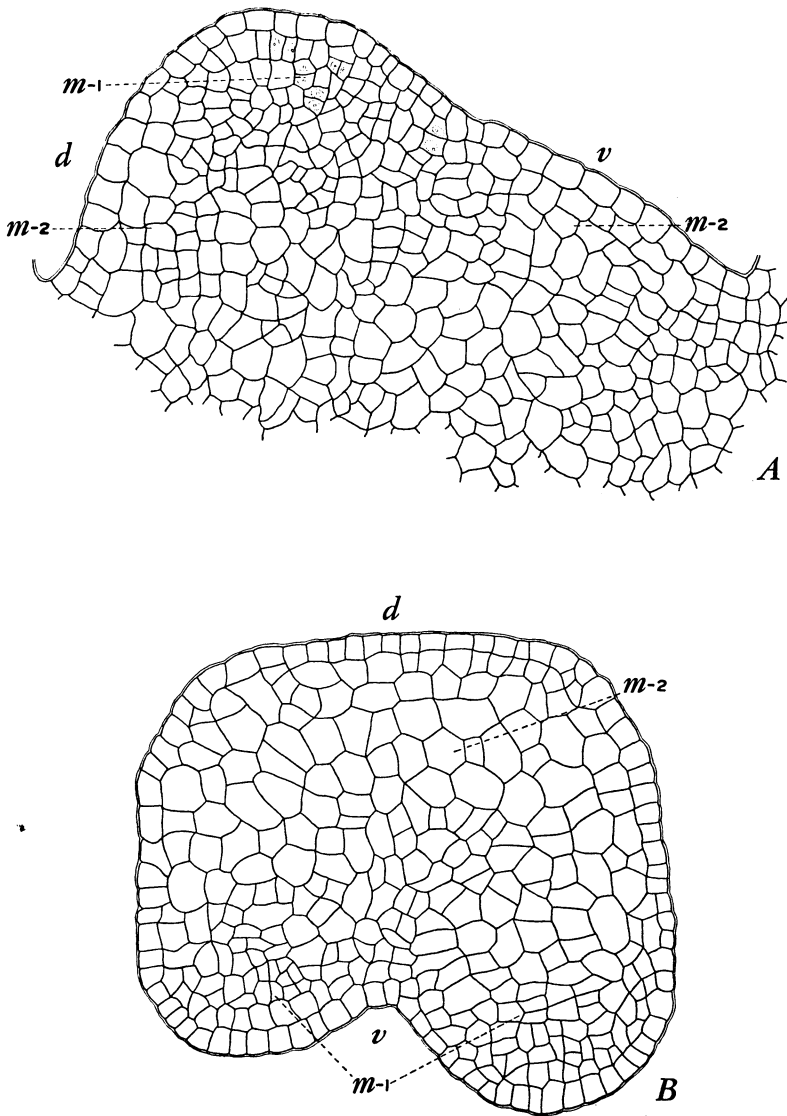


Fig. 8.—*A*, Longitudinal section of the carpel primordium showing the small cells characteristic of the apex and ventral side (*m-1*) and the large, vacuolated cells characteristic of the remainder of the primordium (*m-2*). *B*, Transverse section of the carpel primordium showing the highly meristematic area (*m-1*) of the two ventral margins, and the large cells of the dorsal side (*m-2*). The structures in this figure and in *A* were found in buds collected during the same week in October. Details are: *d*, dorsal side; *m-1*, meristematic area of small cells containing a great deal of cytoplasm; *m-2*, meristematic area of large, vacuolated cells; *v*, ventral side. (Both  $\times 400$ .)

A procambium in the developing carpel is first noticeable about the middle of October. It appears in the central part of the primordium, on the abaxial side, and later connects with the vascular system of the torus. What seems to be tannin is found at the base of the primordium, in the receptacle (figs. 8 and 9, *B*; plate 4).

At the same stage of development as the carpel, the sepal, petal, and stamen whorls have developed considerably. The procambium is about to become differentiated. Tannin is abundant in the subepidermal layers and around the vascular strands in these organs; it is found in the epidermis of the sepal but not in the petal. Stamen attachment is already characteristic of that found in the mature flower (fig. 11, *A*), whereby there are three whorls of stamens alternating in a manner best shown by a floral diagram (fig. 1, *E*). The anther shows no differentiation into sporogenous tissue.

*Stage 8, Development of the Carpel to Anthesis.*—The ventral edges of the carpel come together to form the locule during the first week in November (two weeks after the preceding stage). The locule in longitudinal section is a narrow, elongated “slit” (fig. 10, *G*; plate 4, *B*). Union of the carpel edges to form the ventral suture does not involve cell growth nor true cell union across the suture; rather, the inner edges of the carpel mechanically touch each other more or less throughout the region (fig. 10, *I*). This loose condition of the ventral suture may last until the time of anthesis; the same condition has been observed in the peach by Ragland (1934). Soon after the formation of the ventral suture the locule enlarges considerably, preparatory to the production of the two ovules from placentae on the ventral margins (fig. 10, *G*, *H*, *I*, *L*, *M*, and *N*).

The carpel has developed considerably into definite regions—namely, ovary, style, and stigma (fig. 10, *H*). In the ovary a procambium has now arisen in each of the adaxial sides (fig. 10, *I*). The inner margins of the carpel, around the locule, maintain their characteristic meristematic activity (fig. 10, *I*; plate 4, *B*), as has been noted in much younger stages (fig. 7, *C*). This area gives rise to the ovule primordia. The remainder of the carpel shows the large, vacuolated cells of the other meristematic type (namely, *m-1* except for the vascular areas).

During this time (the latter part of November), there is no indication of any differentiation of the ovary wall into the three distinctive regions of the pericarp—epicarp, mesocarp, and endocarp (fig. 10, *M*). The earliest evidence of this differentiation comes in the latter part of January (two to three weeks before full bloom), when darkly stained cells form a “border” around the locule some 6 to 8 cells in from the epider-

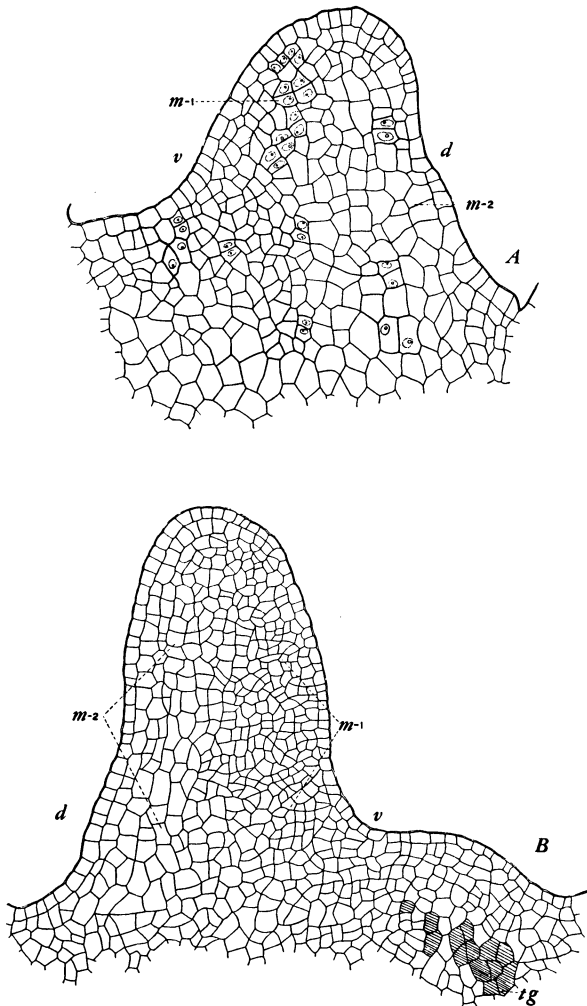


Fig. 9.—*A*, Longitudinal section of the developing carpel, showing cell divisions in both meristematic areas (*m-1* and *m-2*). The more highly meristematic region (*m-1*) is now found the full length of the ventral side. *B*, Longitudinal section of the carpel at a later date than that shown in *A*. The dorsal side is almost vertical, and is still composed of large vacuolated cells. Rapid cell division is occurring on the ventral side. Inclusions are found in the ventral basal cells. Details are: *d*, dorsal side; *m-1*, meristematic area of small cells containing much cytoplasm; *m-2*, meristematic area of large, vacuolated cells; *tg*, tannin globules; *v*, ventral side. (*A*,  $\times 327$ ; *B*,  $\times 235$ .)

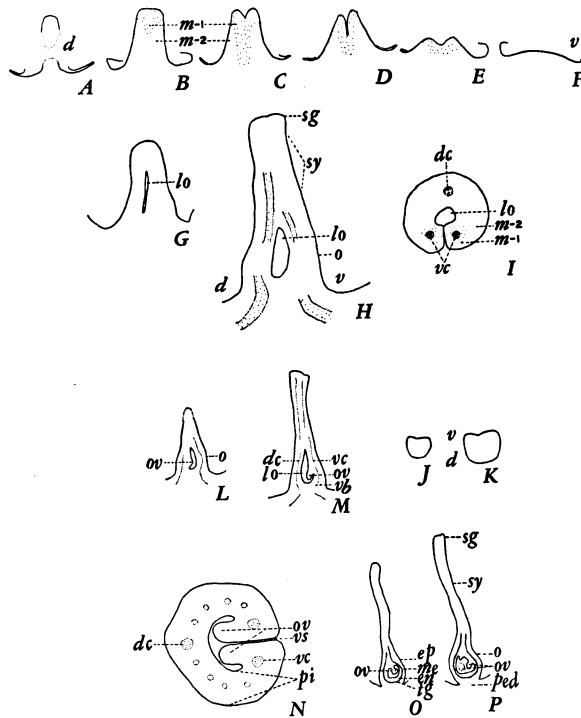


Fig. 10.—*A–F*, Consecutive longitudinal sections through the carpel (November 1, 1936) at right angles to the dorsal side, showing the groove and slope of the ventral margin and approximately in the same stage of development as the carpel in figures 7, *C*, and 9, *B*. The series represents 29 sections cut at 7 microns, of which numbers 1, 6, 12, 15, 22, and 29 are shown. *G*, Longitudinal section of the carpel in which the ventral margins have come together to produce the locule of the ovary. *H*, Longitudinal section of the carpel (November 26, 1936) showing its differentiation into stigma, style, and ovary. Dorsal and ventral bundles are present. *I*, Transverse section of the carpel (November 26, 1936) showing the enlarged locule and the ventral suture which is formed by the touching of its two margins. The ventral edges are highly meristematic. *J*, *K*, Transverse sections of the same carpel. *J* is 40 microns below the tip of the stigma and 80 microns above the receptacle; *K* is 48 microns below *J*. The cellular detail of *K* is shown in figure 8, *B*. *L*, Longitudinal section of the carpel (December 10, 1936) showing the initiation of the ovule from the basal ventral margin. *M*, Longitudinal section of the carpel (December 31, 1936) showing growth of the ovule. *N*, Transverse section of the carpel (February 8, 1937) showing the origin of the two ovules from the ventral margins, which are not yet closely united. *O*, *P*, Longitudinal sections of the carpel, showing the differentiation of the pericarp into endocarp and mesocarp. Growth has resulted in the orientation of the ovules at the stylar end of the locule. Two macrospores are present in the ovule in *O*. Details are: *d*, dorsal side; *dc*, dorsal carpellary bundle; *ep*, epicarp; *en*, endocarp; *lo*, locule; *m-1*, meristematic area of small cells; *m-2*, meristematic area of large, vacuolated cells; *me*, mesocarp; *o*, ovary; *ov*, ovule; *ped*, peduncle; *pi*, pericarp; *sg*, stigma; *sy*, style; *tg*, tannin globules; *v*, ventral side; *vb*, vascular bundle; *vc*, ventral carpellary bundle; *vs*, ventral suture. (*A–K* and *N*,  $\times 34$ ; *L* and *M*,  $\times 12$ ; *O* and *P*,  $\times 3\frac{1}{2}$ .)

mis that bounds the locule (fig. 10, *O* and *P*). This area and the light-colored area toward the inside constitute the endocarp; the mesocarp extends from this region of darkly stained cells to the outermost three or more subepidermal cell layers composing the epicarp. These deeply stained cells apparently contain tannin, or precursors of the material composing the shell; they are found in cells between the primary bundles of the ovary wall (fig. 10, *N*). Most of the vascular bundles, therefore, are embedded in the endocarp (shell of the mature fruit) or in the "transition" tissue between endocarp and mesocarp (hull of the mature fruit). This latter condition is shown clearly at fruit maturity, when the hull particularly splits from the shell (fig. 11, *C*), leaving remnants of vascular tissue at random in the space thus formed. The ovary and style are exceedingly pubescent (fig. 11, *A*).

In the latter part of November the stigmatic lobes become well developed (fig. 10, *H*). During the last of December and all of January the style elongates so much that it is bent to one side by the pressure of the enveloping floral organs (fig. 10, *L*). In this stylar region the five or so cells next to the epidermis are large and vacuolated; the inner cells, found between the vacuolated ones as a central core, are small, full of cytoplasm, and deeply stained. In this latter region the vascular system develops, and what appears to be tannin is found.

The ovules are initiated about the second week in December, some eight weeks before full bloom; in the closely related peach (*Amygdalus Persica*), the initiation begins six weeks before full bloom (Ragland, 1934). The ovules originate as two small protuberances from the two highly meristematic adaxial margins, toward the base of the locule (fig. 10, *L* and *M*). Figure 10, *N*, shows their origin from the ventral margins; a space is still visible between the margins of the carpel. One ovule is usually somewhat higher than the other as regards attachment to the endocarp (fig. 10, *P*). After the production of these protuberances into the ovarian cavity, the ovules apparently remain dormant in this embryonic stage for several weeks until about January 1, when they mature rapidly by producing two integuments and sporogenous tissue. Two macrospores were visible in the macrosporangium in material collected January 31, 1936 (fig. 10, *O*). The gametophyte is formed and matured shortly thereafter, for the tree was in full bloom on February 15 of that year.

Growth in the base of the ovary wall orients the ovules so that their point of attachment to the pericarp is on the apical side of the locule, toward the style (figs. 10, *O* and *P*, and 11, *B*). The micropyle of each anatropous ovule points toward the style.

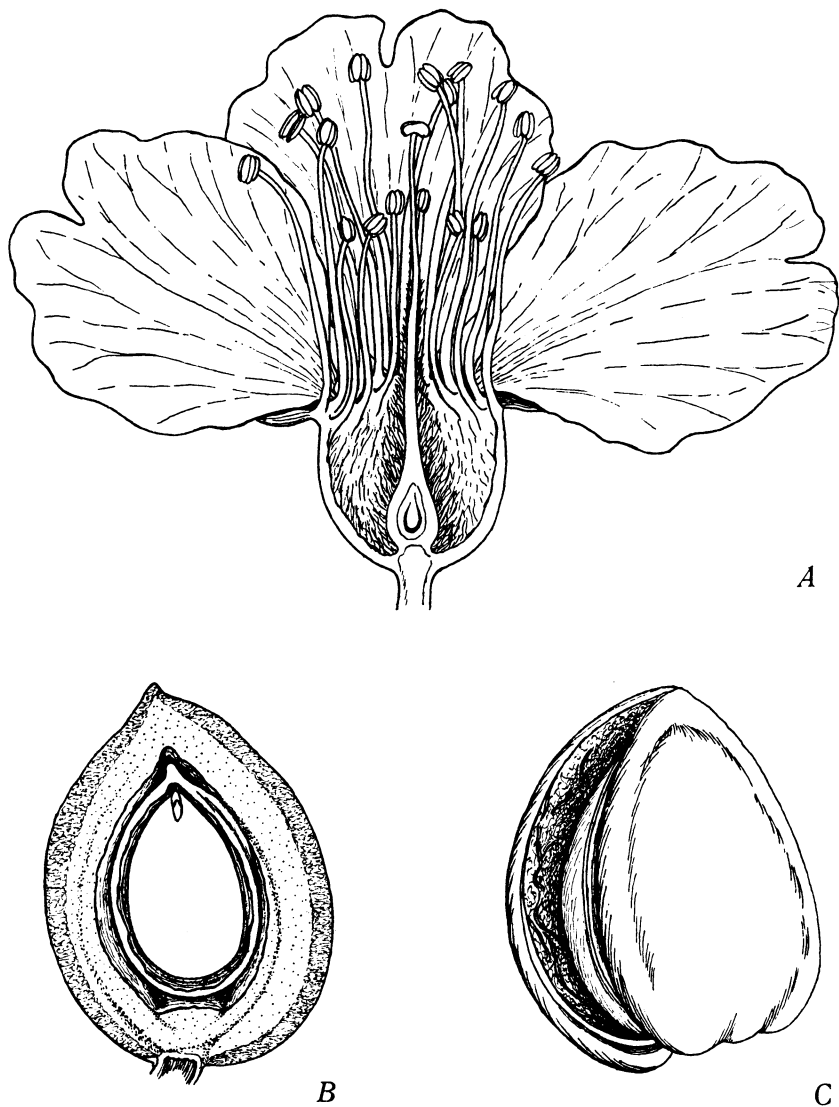


Fig. 11.—*A*, Longitudinal section of the perigynous flower of the almond at time of anthesis, showing the structure and location of the calyx, the corolla, the insertion and height of the stamen whorls, and the relation of the carpel to these other floral structures and to the floral tube. *B*, Median longitudinal section of a semimature fruit cut parallel to the sutures. This shows the differentiated pericarp, the locule, and the parts of the seed. *C*, Surface view of a mature fruit, showing the splitting of the mesocarp (hull) along the ventral suture which exposes the endocarp (shell). (*A*,  $\times 7$ ; *B*,  $\times 1$ ; *C*,  $\times 1\frac{1}{4}$ .)



Stamens continue their development so that by the latter part of November the sporogenous tissue has differentiated into pollen mother cells, and the primary parietal tissue into tapetal and connective tissue. Within two weeks tetrads appear, and by December 15 (1935) pollen grains are present in the anther sac; these are shed at the time of anthesis, two months later.

Ten months elapse between initiation of the carpel and its maturation at the time of harvest the following year; initiation took place from September 28 to October 1 in the years studied, and the fruit matures approximately the first few days in August.

### DISCUSSION

In comparing histogenetically the vegetative and floral apices in the almond, it has been demonstrated that there are distinct differences in the initiation and early growth of foliage-leaf and floral organs, particularly with reference to the carpel. In the leaf bud the foliage leaf originates from a surface tissue, the tunica; the corpus does not enter into its formation in the early stages. In the flower bud the floral organs originate from tissues that had their origin deep in the bud and have "emerged" to the surface through progressive reduction of the tunica, from four layers in the leaf bud to two in the flower bud and then to one layer at the time of floral-organ formation. The question arises, therefore, should this progressive structural change be regarded as a "transformation" of a vegetative apex into a floral apex during its ontogeny? The idea that the plant forms but one type of apex from which arise foliage leaves, cataphylls, and floral organs, as maintained by Goebel (1933), is not supported by the present investigation (Foster, 1928; Sinnott, 1938; for physiological implications, see Loehwing, 1938).

In going from the vegetative to the reproductive phase in the almond flower bud, there is a definite "emergence" of tissue located at the surface of the apex. Accompanying this change is the reduction of the tunica from two layers to one layer, together with a modification of the architecture of the entire apical region. The tissues, therefore, and the direction of growth have been modified.

During the growth of the bud the cells of the corpus region divide in various planes, whereas tunica cells divide only anticleinally except at the time of initiation of primordia, and then only distal to the apex, next to the cataphyll or the foliage leaf bases as the case may be. Nowhere in either type of bud does the tunica in the median axial plane of the apex show periclinal cell division. Cataphylls, of both leaf and flower buds, and foliage leaves originate in the tunica at the periphery of the

apical meristematic area, although the corpus becomes involved *earlier* in the formation of the foliar structures of the flower bud than in that of the leaf bud. Formation of the floral organs involves corpus tissue exclusively (except for the surface layer), even though all floral structures except the carpel originate on the periphery of the apex, as noted for the foliar organs. The corpus, therefore, has an increasingly important rôle when a comparison is made of tissues involved in the formation of vegetative and reproductive organs.

In discussing the formation of the legume, J. McLean Thompson (1936*b*), together with Grégoire, holds that "the apex of the flower itself is the true primordium of the legume." Judging from the present investigation, the floral apex before carpel formation differs slightly from the apex at the time of carpel initiation. Before carpel formation the apex shows no localized meristematic zone and may be almost flat; but with initiation of this primordium the four apical layers of cells (fig. 6, *C*; fig. 5, *A*) become highly meristematic, giving rise to the protuberance that is the beginning of the carpel. To go back beyond this point: the apex of the flower bud during the formation of the other floral organs is histologically different from the apex at the time of carpel formation or carpel development. And before sepal initiation there is, of course, no trace of similarity. Although, at carpel initiation, the meristematic activity of the apex becomes more pronounced and the form of the apex slightly more dome-shaped, apparently the actual apex of the carpel has been present since the time of transition from vegetative to floral phase, though its development has been held in abeyance until the other organs have formed.

Newman (1936), in his work on the fruit of the *Acacia*, concluded that the legume was a lateral structure, not terminal as has generally been held. In his photomicrographs he indicates that cells "flow" away from the apex in the formation of the ovule-bearing organ, leaving behind a "residue" of the original apex. This residue, he found to be present at least until a stage immediately before the formation of ovule primordia, when it is then located at the base of the locule; the carpel wall has grown up and around it. Thompson (1936*b*) has raised the point that it is arbitrary where the "residue" of the original apex is indicated: the apex may or may not "remain" there, because meristems are not static.

According to the present study the entire apex becomes meristematic in producing the carpel. Similar stages in development are shown in *Amygdalus* (plate 3; figs. 6 and 7) and in *Acacia* (Newman, 1936, plate III, fig. 32); in figure 7, *A*, the label (*car*) indicating the carpel points directly to an area that Newman might call the residue of the

apex. In the almond, however, it is interpreted not as a residual portion of the apex, but as a stage of growth in the formation of the two adaxial edges of the carpel. Viewed transversely (fig. 8, *B*) and longitudinally at right angles to the dorsal side (fig. 10, *A*), the region in question is but one side of the ventral rim; the almond carpel starts its growth on the margin that is later noted to be the dorsal side, then extends immediately toward the ventral side by producing these two rims, all in the shape of a horseshoe. Thus the carpel may be interpreted as a terminal floral organ, in which no residual apex remains.

Grégoire (1936) remarks in criticizing Newman's study: "Nous croyons donc pouvoir conclure, sans aucune reserve, que l'origine du carpelle, dans les *Acacia*, est parfaitement terminale. Loin de contredire notre argumentation en faveur de l'autonomie morphologique du carpelle et du sommet floral dans les Angiospermes, les photographies de Newman ne font que la confirmer."

According to Grégoire (1931, 1938) the floral apex is entirely used up in the formation of the carpel; but A. Arber (1937) holds the contrary view. In the almond there is direct evidence that the apex is used up completely in the formation and development of the carpel. The entire apex enters directly into the initiation of the ovule-bearing structure, first on its future dorsal side, then with growth proceeding immediately toward the ventral side. The flower is truly a determinate structure, in contrast to the indeterminate leaf bud where, as far as was investigated, an apex was always present during production of cataphylls or leaves, throughout an entire year. Certain characteristics of the apex of the flower bud make it sporogenous in contrast to the purely vegetative axis of the leaf bud; growth of the sporogenous apex, at the time of carpel initiation, thus becomes limited in contrast to the unlimited growth of the leafy shoot, which continues to be meristematic throughout the life of the plant.

The apices of leaf and flower buds, at the same date, are of approximately the same relative size (fig. 2, *B*, and 4, *B*). A comparison of the apex of a flower bud in its vegetative (fig. 4, *B*) and reproductive state (figs. 4, *D* and *E*, and 5, *B*) shows a remarkable difference in the position and distribution of the meristematic tissue present. In comparing the limits of the various tissue areas in flower and leaf bud, one notes distinct differences. It seems reasonable to consider, as others do (Zimmermann, 1928; Newman, 1936), that the corpus region functions in increasing the volume of a vegetative apex, which is expressed mainly as increase in length. The tunica, by dividing anticlinally, produces increase only in surface. In the almond the surface layers diminish from

vegetative to floral condition, until at the time of floral initiation only a single discrete surface layer is maintained. The corpus, then, is found directly beneath the single surface layer and gives rise to all the *inner* tissues of the carpel. This fact supports the idea that the floral apex is of limited growth and that it leaves no residual axis behind.

In such meristematic regions as the embryo, Dixon (1936) and D'Arcy Thompson (1917) have shown that cell divisions do not control the growth of the parts. Actual observation, as indicated by these two men and by the present study, shows that growth precedes cell division, though the direction of growth may or may not control cell division. Dixon and D'Arcy Thompson conclude that the direction of growth controls cell division; but in the tunica layers of the almond this view does not appear to be correct.

In the initiation of any vegetative primordium the cells of *t-1* are the first to enlarge, elongating parallel to the longitudinal axis of the bud. These cells divide in such a direction as to give a daughter cell similar in length to the mother cell. Hence the succeeding cell division is not transverse to the elongation, as would be expected, possibly because of the mechanical rigidity of the elongated cell. The epidermal layer of the tunica is thus characterized solely by anticlinal divisions. In *t-2*, however, during the initiation of primordia, cell division is controlled by growth, as explained by Dixon (1936), for the division is periclinal in the elongated cell and transverse to this elongation. The apparent contradiction in relation between the direction of cell enlargement and the plane of cell division in the two outer tunica layers illustrates our lack of understanding of the mechanics of growth.

In reviewing the literature on the carpel, one finds two existing views concerning its interpretation: (1) the carpel is a modified or transformed foliage leaf (the classical Goethean Theory of Metamorphosis) and (2) the carpel is a distinct organ, in no way related to the foliage leaf except by analogy. As to the first interpretation, one main contribution that this theory has made to morphological studies through the years has been its use in correlating all the descriptions in floral morphology, especially in the field of taxonomy. Many taxonomists themselves hold to this viewpoint. Engler (1926), after more than fifty years of work, stated definitely that he adopted the foliar carpel interpretation for all angiosperms. Hutchinson (1926) clearly pronounced his own system to be a logical interpretation of the theory that the parts of an angiospermous flower are modified leaves.

From histological evidence Newman (1936) concludes that the carpel is homologous with the foliage leaf, although he did not compare the

floral apex to the vegetative apex of the two species of *Acacia* that he investigated. Grégoire (1935), in his earlier work, compared vegetative and floral apices taken, unfortunately, from plants of different genera (*Lonicera periclymenon* and *Ranunculus sceleratus*), and found characteristic differences between these apices. But in a more recent study of numerous species, in some of which he studied both vegetative and floral apices, Grégoire (1938) has considered the entire floral apex, in its production of all organs, as being distinctly different from the vegetative phase. According to him the apices of foliar and floral axes are "irreducible," and the tunica-corpus aspect is not applicable in the interpretation of the structure and growth of a floral apex. This concept agrees, in general, with the results of the present study. In the almond, however, to some extent, the presence of a uniseriate surface layer is suggestive of a tunica; also, the highly meristematic area found immediately below this layer implies a corpus as well as it does a mantle or hood, a conception which fits Grégoire's description of the floral apex. Grégoire naturally concludes that carpels do not represent modified leaves, but are organs without homology among vegetative organs.

In a similar vein, J. McLean Thompson has stated that sepals belong to the vegetative or sterile phase of the sporogenous axis (the flower), whereas the remaining portion pertains to the reproductive phase. According to him, furthermore, the carpel is not a leaf, but rather a phylloclade; as Clapham (1934) observes, to call it thus does not seem to help appreciably. Thompson (1935) also concludes that no carpels are involved in the organization of an inferior ovary—that it is acarpous.

Results of the present study indicate that the floral organs are all produced in a separate and distinct phase from that which produces foliar structures. Furthermore, just prior to formation of the characteristic floral apex, there is even a histological difference between apices that will become leaf buds and flower buds. The leaf arises from the tunica as a single primordium, continuing as a single linear structure and not as a "folded lamina" until a very late stage. The apocarpous almond carpel arises from the corpus as a primordium with two lateral (ventral) protuberances, all in the form of a horseshoe, which will come together later to form the ventral suture and the ovarian cavity; this type of primordium is never observed in the formation of a foliar primordium. The almond carpel is not considered homologous with a foliage leaf. The mode of initiation and the areas from which leaf and carpel arise are distinctly and characteristically different (cf. fig. 3, C, and 9, A). This conception is directly opposed to that recently expressed by Just (Wilson and Just, 1939)—namely, "The origin of carpels on the

apex of the floral axis differs in no way from that of vegetative leaves, despite the fact that the growing point is frequently used up in their formation." These two organs may be analogous, but they are not homologous histogenetically in the almond. Likewise in a comparison of the mode and location of initiation of foliage leaf and floral organs other than carpel (sepals, petals, and stamens), all arise from a similar locus of the apex (on the periphery); but the tissue from which foliage and floral organs arise is distinctly different. Foliage leaves and cataphylls arise from a definite four-layered tunica. Sepals, petals, and stamens arise from superficial tissue; but, except perhaps the surface layer, this cannot be viewed as a tunica. Since homology implies a likeness in origin as well as in position (Cross, 1939), these two types of structures (vegetative and floral apices) are considered to be ontogenetically dissimilar.

Schmidt's (1924) tunica-carpus concept is evidently fundamental at the present time; let us hope that it rests upon sound premises. But if there is no such condition as tunica and corpus in floral apices, as Grégoire states, then our conception of apical structure must surely undergo revision. The almond may be a case intermediate between these two points of view.

The present study emphasizes Grégoire's contention that there is no histogenetic similarity between vegetative and reproductive apices. But, on the other hand, one cannot definitely state that no tunica and corpus are present in the floral apex of almond as in the vegetative apex.

Thus, certain evidence given here may aid in a true delineation of the nature of the carpel. Obviously, even the developmental history of an organ is not the "whole and sole 'way of salvation,'" as Goebel (1926) has stated; but, together with evidence from other sources, the histogenetic method is valuable in determining the present state of growth and development of structures, especially in their immature stages. In conclusion, it must be emphasized that the histogenetic approach to the problem of carpel morphology may be expected to yield more general results only when carried out along broad *comparative* lines. Such work should involve the detailed investigation and comparison of vegetative and floral apices in the same species in a wide series of angiospermous types.

## SUMMARY

Marked histogenetic differences between leaf and flower buds in the almond (*Amygdalus communis* L., horticultural variety Nonpareil) apparently shed light upon the general problem of carpel morphology in the Angiospermae.

The apex of the leaf bud exhibits a four-layered tunica in contrast to the two tunica layers characteristic of the floral apex. The structure of the corpus is similar in both types of buds.

A week before the formation of the calyx, the form of the apex of the flower bud changes gradually from a broad dome to an elongated structure with a flat top and vertical flanks. During this change in external form the biseriate tunica is reduced to a single layer.

The foliage leaf primordium is derived from cells in the tunica, whereas all internal tissue of the floral organs originates from the corpus.

Cataphylls, foliage leaves, sepals, petals, and stamens originate as lateral members at the sides of the apex. In contrast, the entire apical region of the flower bud produces the carpel primordium.

Histogenetic evidence fails to support the classical interpretation that the carpel is homologous with a foliage leaf. It is concluded that from a developmental standpoint, the carpel is a distinct and unique organ among living angiospermous plants. Broad comparative histogenetic studies are urgent in order to test this interpretation.

#### ACKNOWLEDGMENTS

I wish to express my appreciation to Dr. A. S. Foster, under whose direction this investigation was carried on, for valuable advice and suggestions; and to Dr. W. P. Tufts, for giving advice and encouragement and for placing at my disposal the facilities needed. I am indebted to my wife, Doris Fender Brooks, who assisted with the drawings.

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## PLATES





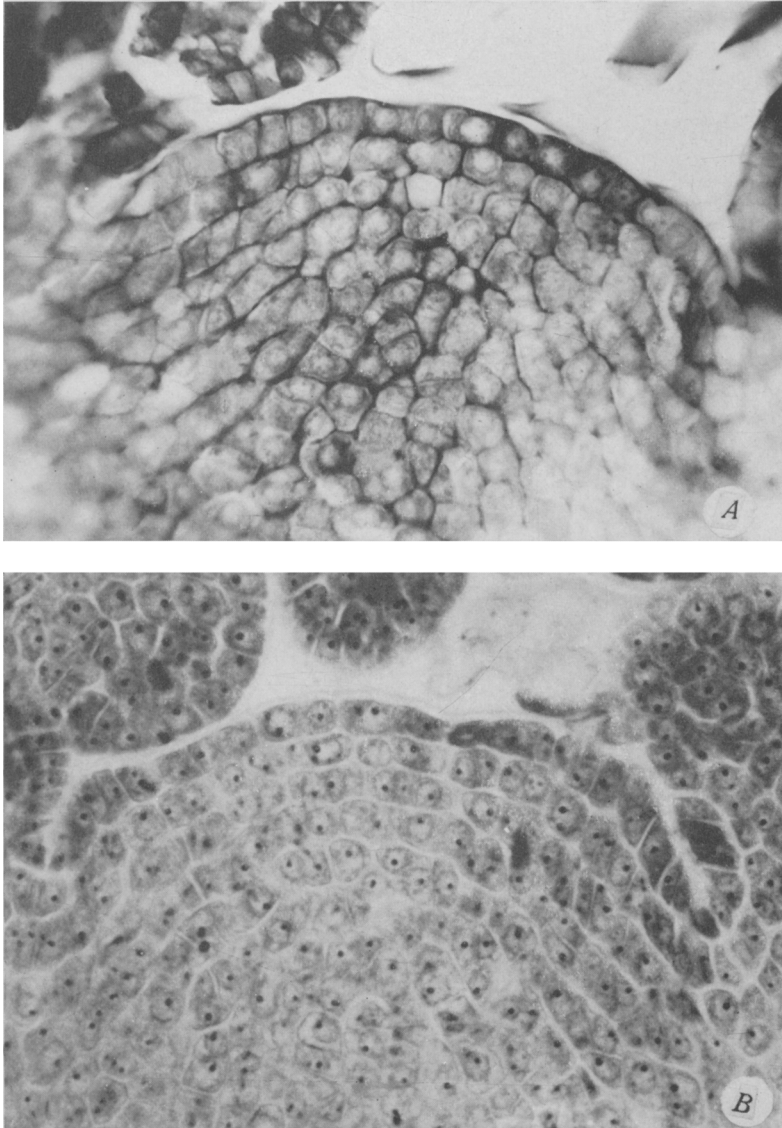


Plate 1.—Longitudinal sections of the apex of the leaf bud, showing the four tunica layers which surmount the corpus. *A*, Apex just before leaf arises. *B*, Apex showing the initiation of leaves on its periphery. Notice the elongated cells of the outer layer of the tunica (*t-I*), especially in the primordium at the left. (Both  $\times 720$ .)

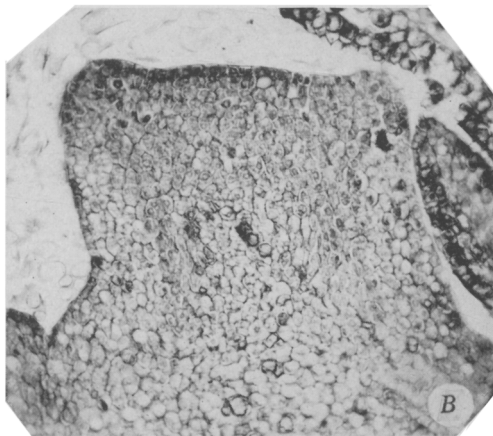
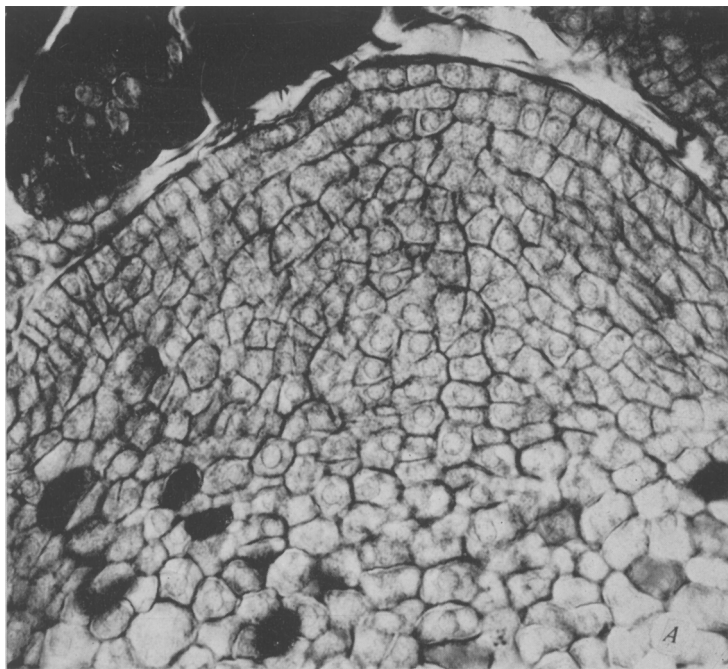


Plate 2.—Longitudinal sections of the flower bud. *A*, Apex showing the two layers of the tunica which surmount the corpus. Note the periclinal and oblique cell divisions in the first row of the corpus. Anticlinal divisions are characteristic of the tunica except during initiation of the cataphylls. *B*, The floral apex following transition from the purely vegetative apex in *A*. The tunica is now uniseriate. A procambial tissue is particularly noticeable on the left side of this massive axis. (*A*,  $\times 565$ ; *B*,  $\times 275$ .)

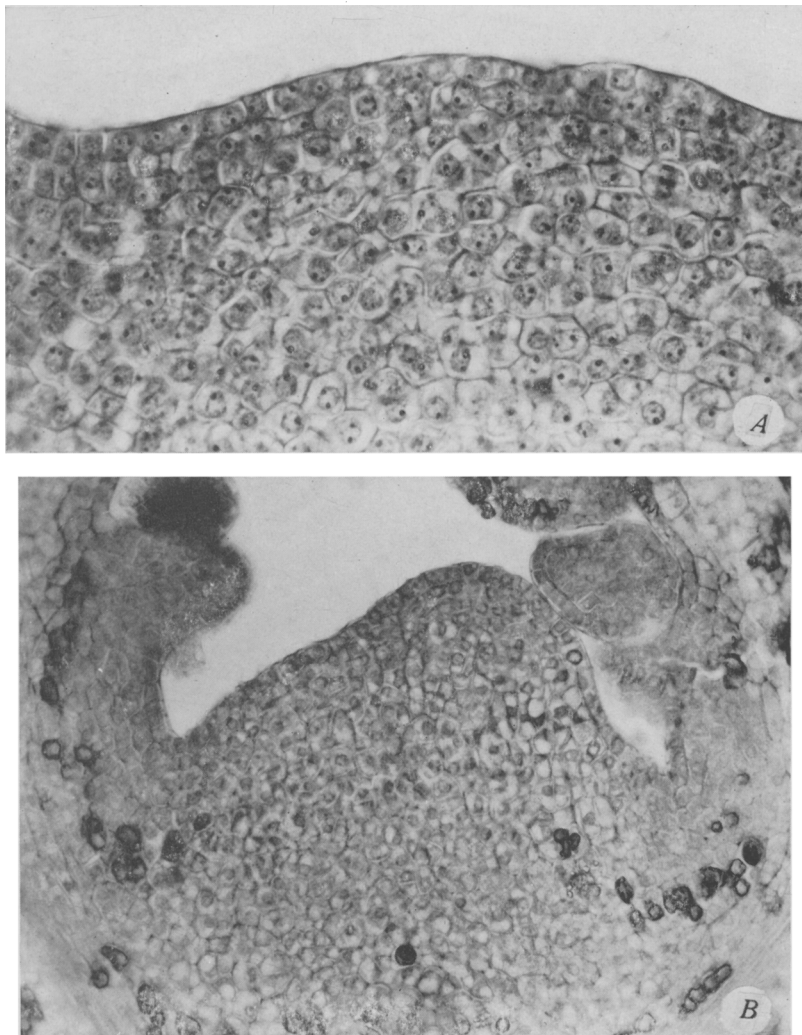


Plate 3.—Longitudinal sections of the flower bud, showing carpel initiation and development. *A*, Initiation of the carpel from the entire apex of the bud. Periclinal divisions are especially prevalent in the four layers of cells beneath the surface layer; below these layers are large, vacuolated cells which are also meristematic. At either side of the apex is the basal portion of the floral tube. *B*, The developing carpel, showing the rapid divisions in the tip and along the ventral margin. Large, vacuolated meristematic cells comprise the rest of this structure. The uniseriate tunica maintains its identity. The deeply stained cell inclusions are masses of tannin. (*A*,  $\times 510$ ; *B*,  $\times 310$ ).

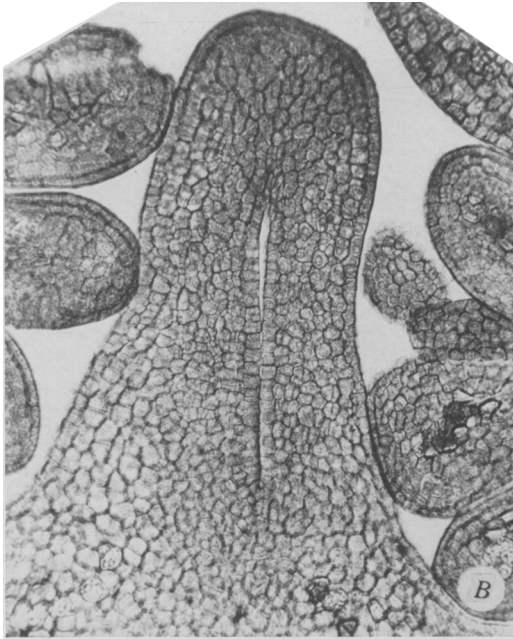
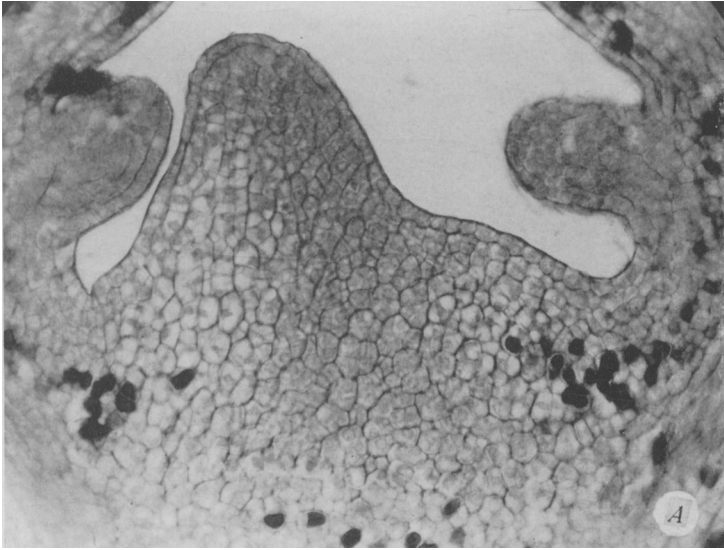


Plate 4.—Longitudinal sections of the carpel in more advanced stages. *A*, Carpel showing clearly the two different types of cells on the ventral (right) and dorsal sides of the structure; large vacuolated cells are characteristic of the dorsal side. Stamen primordia are found on either side arising from the floral tube. The deeply stained cell inclusions apparently are masses of tannin. *B*, The carpel showing the enclosed locule. Meristematic activity is centered around the locule. (*A*,  $\times 275$ ; *B*,  $\times 185$ .)