Division of Horticulture

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Experiment Station
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The Pollination of the Pomaceous Fruits

I. Gross Morphology of the Apple

By

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GROSS MORPHOLOGY OF THE APPLE.

Introduction.

The subject of pollination of orchard fruits is one which has justly received considerable attention by many workers, both in the United States and foreign countries. The work, for the most part, has been limited to the testing of the different varieties of fruits as to whether they are self-fertile or self-sterile and the determination of the proper pollinizers to be used with such varieties as require them. Waite (1) inaugurated the work in this country, while Fletcher (2) has been one of the most active contributors of valuable data. Ewert (3) and Müller—Thurgau (4) have probably been the most active European contributors to our knowledge of the subject, each having presented several valuable treatises within the last several years. A list of authorities cited will be found at the end of this article. At this time no attempt will be made to give a complete list of authors or articles dealing with the pollination problem. Such a list would certainly be very extended but not of sufficient importance to be given here.

Since many of the results of pollination studies had remained unexplained, the investigation of the entire problem was undertaken by the Division of Horticulture of this Station more than seven years ago. As a result of this work one bulletin by Lewis and Vincent (5) and several shorter articles have appeared. The ground covered by these contributors was similar, in a measure, to that already touched upon by former workers. Several points, especially with reference to the self-fertility of varieties and the relation of color of fruit to variety of pollen used, were presented.

Early in the progress of the studies on the pollination problem, it was recognized that in order to gain any fundamental knowledge and to determine the underlying principles of the subject, a thoroughgoing investigation of all factors which might be concerned was necessary. The apple was selected as the first fruit to be considered. The present paper deals primarily with the gross morphology of this fruit. Subsequent papers dealing with other phases of the problem will be issued from time to time as the work progresses and facts are determined. It seems better to present the knowledge gained on the several phases of the subject as information on them becomes definite, rather than to retain them for publication until the entire problem has been worked over.

Methods.

In following out the investigations, methods of technique already well recognized, were followed, and it scarcely seems necessary to go into detail regarding them in this paper. Material was generally fixed in Flemming's solution, though simple fixation in absolute alcohol serves admirably when the specimens are to be used for dissection only. Material for sectioning was imbedded either in paraffine, or, for the harder material, in celloidin. Delasfield's haematoxylin and erythrosin, gentian-violet, saffranin, and iodine green all proved valuable in bringing out many of the finer details. In the more nearly mature specimens, simple dehydration in alcohol and clearing in cedar oil, will serve to bring out many structures to better advantage than will stains of any kind.

Morphology.

The true nature of any structure can be determined best by the thorough study of the origin of its parts and the arrangement of the same during their
early stages. Parts which appear firmly united in a mature organ are frequently distinctly separated during their early development and even if not, the inter-relation of parts is generally much more clearly defined at such a period than later. The study of the fruit or flower bud in its incipient stages, is absolutely essential. Recently Goff (6), Quaintance (7), and especially Drinkard (8), have given us an insight as to the time that these blossom buds may be expected to form and have pointed out some facts relative to the early development of the young flowers within them. For example, Drinkard has shown that under Virginia conditions, in the case of the Oldenburg apple, the fruit bud can be distinguished from the leaf bud as early as the middle of June preceding the year in which the blossoms would normally expand. In the case of the Yellow Newtown a similar definite differentiation is observable early in July, at Corvallis, Oregon. Of course this early differentiation may depend some-what upon the variety, locality, and probably upon the vigor of the tree and upon the location of the fruit bud on the tree. Many other factors might enter here in the determination of the time when the fruit buds are definitely differentiated, and in the influencing of the rapidity of their further development. In the present paper the origin and development of the several parts of the blossom are considered more in detail.

The following statements, unless otherwise noted, relate to the Yellow Newtown apple. This variety was selected for study because of the frequency with which it is met throughout the orchards of this state and because of an abundance of convenient material, rather than because of any varietal peculiarities.

The conceptions of the morphology of the pome fruits have been varied. Some have considered the flesh as having been derived from the calyx which has become tubular and fleshy, others as a torus lined by the calyx and enclosing the parchment-like carpels, and still others as a torus surrounding and intimately connected with the five cartilaginous or stony carpels. Strassburger (9), in diagnosing the Pomeae, says, “These are distinguished from the other Rosaceae by their inferior ovary, which usually consists of five carpels which together form the hollow floral receptacle, from which only the styles are free. Each carpel contains one to many ovules. The fruit resembles a berry, the floral receptacle becoming succulent. The boundaries of the separate loculi are formed of parchment-like or stony tissue.” Gray (10), says: The pomes “are fleshy fruits, composed of two to several carpels of parchment-like or bony texture, enclosed in flesh which morphologically belongs to adnate calyx and receptacle. Of the quince the whole flesh is calyx or hypanthium, in the apple and pear, the inner or core-portion of the flesh is of the nature of a disk, investing the carpels. In the fruit of Hawthorns the carpels become bony pyreneae, and so the fruit is drupaceous, is indeed nothing more than a syncarpous drupe.” Bentham and Hooker in characterizing the genus Pyrus, state: “Fruit fleshy, roundish or pyriform, adnate to the calyx or projecting beyond it, two to five loculi, the loculi generally separate, one or two, or occasionally several-seeded, endocarp cartilaginous or occasionally crustaceous or bony.” Decaisne (12) has indicated an independent origin of the carpels within the receptacular envelope, of which they occupy the middle and that with the exception of ‘their inner edges which correspond to the ventral suture,’ the carpels are completely surrounded by parenchymatous tissue which later develops from the walls of the receptacle.

In the light of the present investigations of the matter, these views now seem to be but partially correct. From the study of many specimens it appears, as will be pointed out more in detail later, that the fruit is made up of a fleshy torus intimately surrounding the carpels which are not parchment-like only, but which are more or less fleshy. The parchment-like membrane, which is readily observable in Malus, Pyrus, Amelanchier, etc., constitutes only the endocarp or inner layer of the carpels. The carpels are in part fleshy, the amount of flesh varying greatly, according to the variety, among the several genera and species. In some pomes, such as the fruits of Mespilus and Crataegus, the endocarp has become hard and stony precisely as in the true drupes, and can be readily separated from the fleshy portion (exocarp, meso-
carp) in the same manner as can the stones or "pits" of the drupes. Hence apome
is to be regarded as consisting of one to several drupe-like fruits (drupoids)
more or less intimately connected with a fleshy torus, on and within which
they are borne. The degree to which the torus envelops the carpels is also
variable. In some species and varieties only part of the styles and stigmas
protrude beyond the torus, while in some forms of Crataegus especially, and
to a less marked degree in Sorbus, Mespilus Germanica and others, a con-
siderable portion of the ovary is exposed. Figure 1, of Crataegus oxyacantha,
Linn. (Hort. var.) was taken just before the expansion of the petals. Stamens,
petals, and two of the sepals have been removed in order to afford a clear
view of the carpels, of which at least one-half of each protrudes beyond the
torus. At the right is shown the same blossom in longitudinal section. The
fleshy carpel extends well up out of the torus. That portion which is borne
within the torus and is intimately surrounded by it, is readily distinguishable
from the enveloping tissues. The carpel at the left bears a perfect ovule,
while in the case of the one at the right the placenta has become fleshy and
corrugated and bears no ovule. The mature fruits of this form of Crataegus
are shown in Figure 2. The torus and calyx lobes are fleshy. The three carpels
remain protruding from the torus; their outer flesh is pulpy and colored red,
like the torus and calyx, while the inner portion is stony. The carpellary
flesh is readily distinguishable from that of the torus though the blending
is extremely intimate.

From the study of many sections and dissections it is found that the first
observable indication of the flower is the more or less thickening of the axis.
Minute bracts, in the axils of which are formed blunt protuberances, arise from
it in a very close spiral. The tip of the axis never loses its identity, but on the
contrary enlarges considerably and always develops slightly in advance of
the protuberances immediately below it. Later, these protuberances develop
into definite individual flowers. In Figure 8 are represented the first definite
indications of the fruit bud. The specimen was collected Aug. 5, 1912, though
the stage was readily observable at least a month earlier in other mounts.
At least one or two leaf buds are borne within each fruit bud. They are clearly
distinguishable from the individual flower buds at an early stage by their
smaller size, by the much more pointed apex and by the fact that they are borne
slightly below the flower cluster.

In respect to its further development, the center protuberance which ends
the axis may be selected as typical of all the flowers in the cluster. When
sufficiently differentiated from the remainder of the cluster to be recognizable,
it resembles to a marked degree a short cylinder with the plane surface upper-
most and the base more or less rounded. The plane surface represents the
broadened and flattened axis. A section through this very young bud, for
such it really is, reveals at the upper surface and a short way down the sides
one or more layers of actively growing cells. Beneath these layers this tissue
has become differentiated into pith cells which occupy the center of the area
and at either side of the pith is a large vascular bundle. Exterior to the latter
is the cortex, a layer of tissue somewhat resembling the pith except that the
cells are comparatively smaller and possessed of heavier walls, and still ex-
terior to this layer is the epidermis.

Sepals.—The further development of this bud consists first, in the rapid
multiplication of the cells at the outer edge of the plane, upper surface, result-
ing in the formation of a blunt, slightly elevated ridge. Very soon, growth
takes place more rapidly at five points on this ridge around the circumference,
with the result that five blunt protuberances, the primordia of the sepals, are
produced.

The torus, as stated, has also been undergoing development meanwhile,
especially toward the outer edge, as a result of the increase in cells below the
calyx. This development results in an arching up of the outermost parts of the
torus and elevates at the same time the rapidly forming calyx lobes to a notice-
able degree. This uprising of the torus continues during the laying down of the
primordia of petals and stamens as will be described later, in such a manner
that while these latter structures apparently arise from the calyx tube they
actually arise from the concave torus. The meristematic tissue which gives rise to these latter structures as well as the carpels is clearly observable, lining this entire cup.

Development of the sepals proceeds with great rapidity. Almost immediately after the laying down of the sepal primordia, those of the petals appear. During further development the calyx lobes strongly incline toward one another at the apex and interlap in a sort of tent-like arrangement, thus roofing over, in a manner, the cavity below them. They are densely clothed without and within with long, fine, septate hairs. When the fruit bud goes into the winter rest, the sepals are proportionally the most advanced structures of the flower. Their development is practically complete and when growth is resumed in the early spring, their enlargement is due largely to the expansion of cells already formed.

Petals.—The primordia of the petals are laid down in a cycle within the sepals and alternate with them. Like the sepals, the primordia of the petals appear as blunt, more or less rounded protuberances. Development is less rapid than in the case of the sepals but each outgrowth gradually assumes a thin scale-like appearance, more or less sickle-shaped in longitudinal section, and narrowly attached at the base. Each petal finally assumes an acute angle with the calyx and together they roof over the cup-shaped torus. The space intervening beneath the tips of the calyx lobes and above the upper surface of the petals is filled almost entirely by the hairs coming from the calyx. The petals are without hairs except at the base. At the resumption of active growth in the spring, there is probably some further formation of new cells in the petals, especially at the base, where they are attached to the torus. However, enlargement is largely a matter of cell expansion.

Stamens.—Directly after, or in some instances even at the same time that the primordia of the petals are being laid down, those for the stamens appear. They occur in three cycles. Those of the outermost cycle, directly within the petals, are laid down first, though they are immediately followed by the other two, in fact in some cases all three apparently form at the same time though the outermost cycle always develops the most rapidly. The outermost cycle arises so near to the primordia of the petals that in some sections they appear almost if not quite connected, though as a rule they are very distinct. This cycle consists of five pairs of primordia, each primordium appearing at first as a blunt, broad protuberance scarcely to be distinguished from a petal primordium. The middle and innermost cycles each consist of but five primordia. It is a difficult matter to decide whether there are actually three or but two cycles of stamens inasmuch as the two inner cycles are extremely close together. From an examination of many sections and dissections, however, the conclusion that there are actually three, seems to be well founded. The young stamen rapidly assumes a distinctly bi-lobed appearance; the basal lobe is short and slender while the apical broadens out, and it in turn becomes distinctly four-lobed, each lobe representing a distinct microsporangium. The microsporangia pass the winter in the mother cell stage. Only slight changes take place during the early part of the winter up to the middle of February or the middle of March, when more active growth again takes place.*

The stamens in the outermost cycle are borne in pairs side to side at an acute angle to the sepals, while the two inner cycles are borne at nearly right angles to the calyx lobes. Furthermore, of each pair of stamens in the outermost cycle one stands at either side the middle line of each calyx lobe, each stamen in the next cycle of five stands opposite each petal, while each stamen in the innermost cycle of five stands opposite the middle axis of each sepal, thus alternating with the middle cycle of stamens by which they are partially overlapped in the bud. The arrangement of the three cycles is shown in Figure 14 and the floral diagram. The outermost series stands more or less erect and after the expansion of the petals are the first to dehisce, the two inner cycles remaining incurved and bent down for a varying length of time, depending on environmental conditions. They soon become erect, however, and shortly thereafter dehiscence of the anthers and discharge of pollen occurs.

*The cytological changes will be discussed in a later publication.
Carpels.—The five primordia for the carpels are the last to appear, doing so immediately after the primordia of the proximal cycle of stamens have been laid down. They are borne immediately within the innermost cycle of stamens and some distance from the center of the torus, which is now apparently lower than the outer edges which have been undergoing elevation continuously; the torus, accordingly, has become distinctly cup shaped at this time.

The primordia of the carpels like all other structures previously mentioned, appear first as short blunt protuberances arising directly from the torus. Directly after this very early beginning, growth does not proceed equally in all directions from the center and form a solid cone-like or spherical structure, but instead, about the circumference of a circle which is not quite closed, thus forming as further growth takes place, a narrow hood-like scale with infolded edges.

Actual elevation above the surface of the torus takes place slowly at first; but growth and elevation proceed very rapidly across the entire remainder of the torus except at the center. This central portion becomes elevated very slightly, however, and its level is raised a trifle above the level of the bases of the concavities of the several carpels, thus resulting in the formation, at the center of the torus, of a tube or cavity around which the five carpels are arranged, their inner edges forming the wall of this cavity. Drinkard evidently is in error concerning the manner in which the "pistil" is formed. The several carpels, to be sure, do appear to be arranged about a cavity, but this cavity is not an ovary, it is simply the result of a lack of growth at the center of the torus. And furthermore there is no common placenta. Each carpel is furnished with two placentae which are the result of the infolding of the edges of the carpels.

In the case of so-called "open cored" pomes the cavities of the carpels open directly into the center cavity and the placentae then do appear to be parietal about the common center. The ovary becomes one-loculed instead of five-loculed and the placentae of adjoining carpels are more intimately connected than are the placentae of any single carpel.

Goebel (13) has already shown that in the case of inferior ovaries "the carpels share in the construction of the ovarian cavity, and the ovules have no other origin than that which is found in the superior ovary." He has pointed out that the inferior ovary such as is found in the pomes, results from a common growth of the carpels and torus, the former keeping pace with the latter and remaining united with it. If soon after the laying down of the primordia of the floral parts there were a strong intercalary growth on the part of the carpels, and a similar growth in that part of the urn-shaped torus which bears the sepals, petals and stamens, a perigynous flower, in which the carpels alone produce the ovary, would be the result.

The carpellary tissue, while intimately connected with that of the torus, is very readily distinguishable from the tissues which immediately surround it. In a median cross-section of the immature fruit, taken when the flower is in full bloom, the carpellary tissue can be recognized at once by the unaided eye, because of its appearance as a band of lighter colored, slightly more dense tissue surrounding each cavity or locule. This tissue, furthermore, is well supplied with a net-work of fine vascular bundles especially at the periphery where it comes into intimate contact with the pith. The large primary dorsal bundle of each carpel always stands out very distinctly, and two smaller bundles, one in each of the infolded edges, are prominently noticeable. Frequently a small bundle is traceable extending entirely around the periphery of the carpel. A thick cross-section of the mature apple, dehydrated and cleared in cedar oil, demonstrates these finer bundles much more clearly. Microscopically the carpellary tissue and the pith appear much the same; the cells of the former are generally smaller, and fine vascular bundles are traceable among them, while the pith is absolutely without such network. These tissues also differ in their reaction to stains. For example, in material fixed either in alcohol or Flemming's solution and stained in alcoholic safranin (1% in 50% alc.), the pith takes on a bright vermillion, the carpels a rose pink. The resemblance of each carpel to a true drupe is very striking. The vascular system of the flesh is nearly the same in both cases: the endocarp in the one is cartilagenous; in the
other, stony; the infolded carpellary edges correspond to the suture of the drupe.

The pith of the stem or fruit spur is clearly traceable through the very short pedicel into the torus itself and up to the base of the calyx. It is most readily observable in very young specimens fixed in alcohol and stained in alcoholic safranin. The pith takes on a bright vermillion, the other structures, a rose pink. It is clearly visible filling the spaces between the carpels themselves and extending outward to the circle of primary vascular bundles. It is without vascular fibers, except for the large bundle masses which pass through it to supply the carpels. The cells composing it are large, thin-walled, approaching spherical, and blend intimately with those composing the carpels and with those which make up the cortex.

As previously mentioned, growth and elevation at the center of the torus take place very slowly, whereas there is practically a cessation of growth at the middle of the base of the carpels. This results, as is clearly seen in the diagram, in the base of the carpels being below the level of the center of the torus. Later, growth of the carpel takes place most rapidly at the upper surface of the torus involving at the same time a portion of the latter, thus resulting in the elongation of the five styles as a solid column at some distance below their apices. A careful examination of a median longitudinal section through the fruit and styles will reveal the presence of the tissue of the torus extending for a short distance up the styles. In the mature fruit of many varieties these united style bases persist and are known as a "pistil point or style point." Still later growth, shortly before the expansion of the flower, produces an elongation of that part of the styles between the apex (stigma) and the united portion. A tiny groove, the remnant of infolding, persists on the inner face of each style. The conductive tissue is traceable from the stigma, at which point it is not covered by the epidermis, down through the style into the placentae of the carpels to the ovules. In a cross-section of the style, the conductive tissue appears as a narrow curved band completely surrounded by epidermis.

The infolding of the edges of the carpels takes place very early in their development; in fact, it is observable almost immediately after the laying down of their primordia. These infolded edges are clearly traceable throughout the entire length of the pistil to the stigma. These edges form the placentae of the carpels and from them the ovules arise.

There are no traces of the ovule evident at the beginning of the winter rest, nor do they appear until active growth has been resumed in the spring. A small protuberance, slightly below the middle of the carpel, first becomes evident, about the time the winter fruit buds are swelling and almost immediately a second blunter protuberance appears directly below it. This latter protuberance, called by Péchoutre (14) the obturator, is made up largely of parenchymatous tissue and enlarges very unevenly, thereby assuming a tuberculated form. It soon practically ceases to enlarge, though this cessation is not complete. The upper protuberance which becomes the ovule develops very rapidly. At first it stands at nearly right angles to the placenta from which it arises. Very soon thereafter, as growth progresses, it begins to assume a slightly downward and outward movement away from the middle line of the carpel toward the side walls. At this time the initial development of the integuments, of which there are two, begins. They develop at practically the same time though the inner may be slightly in advance of the outer. At this time the axis of the ovule no longer remains at right angles to the placenta, but now forms an acute angle with it, the distal end of the ovule pointing downward and outward toward the sides of the carpels. Thus the two ovules in each locule stand back to back, so to speak, their tips pointing toward the base of the carpel. At the time the flower is in full bloom the integuments entirely cover the nucellus, the ovule has become completely anatropous and the micropylar end rests against the obturator below it. The embryo sack and its contents are completely formed at this time and are ready for fertilization.*

*The detailed cytological changes which take place are reserved to be treated in another publication.
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The maturing of the structures outside of the seed itself consists mainly in the enlargement of cells already formed, the change of the chemical contents of the cells, and the storing of food. Undoubtedly further cell division takes place, possibly in some such manner as pointed out by Farmer (15) for Crataegus.

In any median cross-section of a Newtown apple a short time after fertilization there is observable at the center a more or less circular cavity, the result of the upright growth of the carpels and the lack of axial growth on the part of the central portion of the torus. The five carpellar cavities are clearly defined. The inner walls of the carpels are somewhat parchment-like, and liberally supplied with vascular bundles. To the casual observer this seems to constitute the entire carpel, but such is far from the case. Actually these carpels are drupe-like, and careful inspection of the fruit even in this immature condition, reveals the outlines of the carpels clearly defined by rather firm vascular bundles, and between this outline and the parchment-like inner lining lies the flesh derived from the carpellar tissue. This flesh is composed of cells considerably more elongated than those of the pith immediately surrounding it and well supplied with fine anastomosing vascular bundles in the same manner as is the exocarp of the true drupes of Prunus. Completely enfolding the carpels on all sides, is a mass of large-celled, thin-walled tissue entirely without vascular tissue except for a few definitely defined bundles which pass through it to reach other structures. On careful examination, its resemblance to the pith of the stem and its close connection with the same is readily observable. This "core" or pith tissue has been frequently confused with the carpellar tissue and by some included with it. Such, evidently, was the standpoint recently taken by McAlpine (16). He indicated that the carpel consisted of all the tissue from the center of the fruit out to the prominent circle of (normally) ten vascular bundles always readily observable in any median cross-section. These bundles actually mark the limits of the pith, and exterior to them the tissue is largely cortical in nature. Figure 4 represents the stage just described.

Figure 5 is from a photograph of a thick section of a mature Baldwin apple dehydrated and cleared in cedar oil. The carpel boundaries are clearly defined, appearing more or less cuneate in general outline. The primary dorsal bundle of the carpel lies at about the center of the line forming the base of the triangle. What appears to be a vascular connection between it and the primary bundle of the torus is merely a denser area in the pith, caused by a crowding together of cells at these points. The complete vascular system is complex, and a full discussion of it will be presented in a forthcoming article.

The only wood to be found in the fruit lies in the vascular bundles. The study of these reveals xylem, cambium and phloem regions. Near and within the pedicel these bundles are confluent and form a continuous ring.

The cortex region is liberally supplied with a fine network of vascular bundles, which branch and anastomose in all directions, becoming finer and finer toward the circumference of the fruit until they finally blend with the cells of the hypodermal parenchyma, as pointed out by Brooks (17). The branchlets from one main bundle unite with those from another and form a mat of interlacing strands between which are large, thin-walled, spherical cells very closely resembling in this respect those which make up the pith.

Summary.

1. A pome is to be regarded as consisting of one to several drupe-like fruits more or less intimately connected with a fleshy torus, on and within which they are borne.
2. In the apple, the carpels are composed of a fleshy exocarp and mesocarp, and a parchment-like endocarp.
3. All floral parts are borne on the torus, none on a so-called fleshy calyx.
4. All parts of the flower are cyclic in arrangement; the succession of cycles is acropetal.
5. The initial development of an epigynous fruit as typified by the apple (Malus), and of a perigynous fruit such as the plum (Prunus), are the same. Subsequent growth, in the former, proceeds across the entire torus and carpels conjointly; in the latter, such growth is intercalary; the carpels and that part of the torus which bears the sepals, petals and stamens, maintain an independent growth.

6. Parenchymatous tissue, homologous to the pith of the stem, immediately surrounds the carpels and is firmly united with them. This tissue is without vascular bundles.

7. The primary vascular bundles of the fruit are similar in make-up to those found in many annual exogenous stems.

8. The region exterior to the primary vascular bundles is homologous to the cortex of an annual exogenous stem. It is liberally supplied with a network of anastomosing bundles which arise from the primaries.

Literature Cited.


EXPLANATION OF PLATES.

PLATE I.

Fig. 1. *Crataegus oxyacantha* L.—Young fruits shortly before the expanding of the petals. Stamens, petals and two sepals have been removed. At the left, part of each of the young carpels, of which there are two, protrudes above the torus. At the right, the same in longitudinal section. X about 15.

Fig. 2. *C. oxyacantha* L.—Mature fruits. In the specimen at the right three calyx lobes have been removed. At least one-half of each carpel protrudes above the level of the torus.

Fig. 3. Diagram showing development of apple. Not drawn to scale.

PLATE II.

Fig. 4. Cross section of Newtown apple taken a short time after fertilization, stained with safranin. c, carpel; *p*eb primary vascular bundle; *dp*b, dorsal vascular bundle of carpel; p, pith region; co, cortex region; s, seeds. X about 10.

Fig. 5. Cross section of mature Baldwin apple dehydrated in alcohol, cleared in cedar oil. *p*eb, primary vascular bundle; p, pith region; c, carpel; co, cortex region. Nat. size.

PLATE III.

Fig. 6. Longitudinal section of winter bud of Newtown taken when the winter buds are beginning to swell. f, flower bud; l, leaf bud. Bud scales have been removed. X25.

Fig. 7. Longitudinal section of Newtown bud taken March 21, 1912, showing relation of parts. The calyx lobes have been removed. One carpel is shown in longitudinal section. Note the infolded edge (placenta) and the beginning of the ovule arising therefrom. X8.

Fig. 8. Early stage of fruit bud. Longitudinal section taken Aug. 5, 1912. Balsam preparation by F. C. Bradford. a, growing axis; b, incipient lateral
flower bud; c, beginning of a bract in the axil of which a flower bud may develop; d, a bract or leaf; e, surrounding bracts and bud scales; f, vascular bundles; g, pith. X90.

**PLATE IV.**

Fig. 9. Stages in development of the fruit. Sepals, petals, stamens and part of the torus and carpel wall have been removed in order to show the ovules. Reading from left to right the stages represented were collected as follows: Top row, March 16, March 21, March 30, April 2. X90. Lower row, April 6, April 15, April 20, April 25, April 30 (full bloom). X3.

**PLATE V.**

Fig. 10. *Pyrus communis* L.—Development of the integuments and first division of the primordial mother cell. ti, inner integument; te, outer integument; ob, obturator. X375. (After Péchoutre).

Fig. 11. *Pyrus communis* L.—Young ovule in longitudinal section. The two integumentary papillae (the inner [ti] and the outer [te]) are distinct. The "calotte" cal is represented by two layers of cells, and two distinct mother cells of the embryo sac (ms) are in the course of evolution. X375. (After Péchoutre.)

Fig. 12. *Pyrus communis* L.—Longitudinal section of the ovary, showing the relation of the funiculus, the micropyle and the obturator (ob). f, rows of cells subjacent to the embryo sac and in course of degeneration. X50. (After Péchoutre.)

Fig. 13. Floral diagram of the apple flower.

**PLATE VI.**

Fig. 14. Apple flower bud taken April 4, 1912, showing the relation of the three cycles of stamens and the styles. Note in left hand figure the outermost cycle of five pairs of stamens borne upright; in the middle figure is shown the middle cycle of five stamens each of which is borne before a petal; in the right hand figure is shown the innermost cycle of five stamens, which alternate with the petals and are overlapped by the middle cycle of stamens.

Fig. 15. The development of the ovule. At the left the mature ovule ready for fertilization, at the right the very young ovule showing the seed coats in process of growing over the nucellus. Note the very slight enlargement on the part of the obturator as compared with that of the ovule. X50.

**PLATE VII.**

Fig. 16. Cross section of primary vascular bundle of Newtown taken when flower is in full bloom. Section taken near middle of fruit. X315.

Fig. 17. Median cross sections of apples showing two types of core. At left, York Imperial, core axile and closed; at right Lawver core abaxile and open.
GROSS MORPHOLOGY OF THE APPLE.

PLATE I.

Fig. 1.

Fig. 2.

Fig. 3.
GROSS MORPHOLOGY OF THE APPLE.

PLATE II.

Fig. 4.

Fig. 5.
GROSS MORPHOLOGY OF THE APPLE.

PLATE III.

Fig. 6.

Fig. 7.

Fig. 8.
GROSS MORPHOLOGY OF THE APPLE.

PLATE IV.
GROSS MORPHOLOGY OF THE APPLE.

PLATE V.

Fig. 12.

Fig. 10.

Fig. 11.

Fig. 13.
GROSS MORPHOLOGY OF THE APPLE.

PLATE VI.

Fig. 14.

Fig. 15.
Fig. 16.

Fig. 17.