
Oregon Agricultural College Experiment Station

Division of Horticulture

The Pollination of the Pomaceous Fruits

II. Fruit-Bud Development of the Apple

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FOREWORD

This is the second contribution to our series of research bulletins entitled: The Pollination of the Pomaceous Fruits; Bulletin 1, Gross Morphology of the Apple by E. J. Kraus was published in April, 1913.

We are continuing our research studies related to the pollination of pomaceous fruits, and we hope that in the near future we shall have further contributions to this series.

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FRUIT-BUD DEVELOPMENT OF THE APPLE

Introduction

The following pages contain a few brief facts in relation to fruit bud-formation. This work was undertaken originally as part of a series of pollination studies on the apple, and is presented as a part of that investigation. Several articles dealing with this subject in a general way have appeared since the study was begun. It seemed advisable, however, to continue the investigation, not only to confirm the work of other investigators on the subject, but to throw more light on certain points still remaining obscured. In addition, certain facts, by-products, so to speak, of this study, are presented. It is believed that they have a direct fundamental bearing upon the pollination problem which will be discussed in a subsequent paper, as well as a direct application to other horticultural practices.

History

It has long been known that fruit buds are formed in the summer previous to their blossoming. Just when this fact was first recognized cannot be stated and is not of importance. That it was appreciated is suggested by numerous references in early writings. Often these statements are rather vague, yet they indicate a general knowledge of the fact. La Quintinye (1) states definitely, in relation to summer pruning, that it induces the formation of fruit buds for the following year. Passages might be cited from Knight, Lindley, Barry, and numerous other writers indicating the same general knowledge and in all probability it was widely diffused.

Exact investigation of the beginning and progress of fruit-bud formation is, however, comparatively recent. Lazenby (2), Goff (3), and Drinkard (4) have done the most notable work and have, between them, charted out many important facts relating to the time of formation and the development of flower-buds in various fruits.

Methods

In the present investigation Yellow Newtown buds were used entirely, with exceptions to be noted hereafter. They were gathered from the Meeker Orchard, in Corvallis; usually each sample was picked from several trees. Care was exercised to make the material as representative of average conditions as possible.

To save time and thus permit the study of a large number of buds, the technique of the present investigation has been kept very simple. The material has, for the most part, been killed and fixed in Gilson's mixture, as Flemming's solution and 95% alcohol were found to make the tissues brittle. The buds were not dissected, as the scales seemed to give greater rigidity, when imbedded in the celloidin block, and therefore less shattering. They

were, however, shaved down on opposite "faces" until the inner portion was exposed. This permitted the ready access of the killing and fixing solution, facilitated the infiltration with celloidin, and saved much time in sectioning.

Celloidin was the matrix employed throughout. With a sledge microtome sections were cut to 11 microns, on the average, though thicker sections were necessary with flower-buds about to expand. Very little double staining was done. Haematoxylin, both Delafield's and Ehrlich's, has been used throughout most of the work. Safranin was employed on some sections but did not give satisfactory differentiation and is very trying on the eyes, in protracted study. Furthermore, it gives considerable trouble in photography. With haematoxylin the most satisfactory method has been to over-stain, usually over night, sometimes 48 hours; then extract with acid alcohol. Clearing has been done in absolute alcohol and clove oil. Eyclesheimer's Fluid was used in some of the earlier work, and does, perhaps, give somewhat clearer sections, but clove oil dissolves away the celloidin, and it cleared sections sufficiently for the purposes of this investigation.

Results

Fruit-buds are normally formed on one-, two-, or three-year-old wood. Certain exceptions have, however, been found to this rule; these will be considered later in this paper. For the study of the development of the fruit-bud, material from old spurs, that is to say, spurs which had borne in previous years but were not bearing in the current year, was used.

The undifferentiated "crown," or, as it is sometimes loosely called, "growing point," found during the period of active growth, is shown in Figure 1. The location of the growing point is obvious. As growth continues, smaller localized growing points appear, as is shown by the increased activity of the cells at the right of the crown (Figure 1-g). This growth produces a swelling which finally gives rise to a young leaf.

The structure must be regarded as potentially either a leaf-bud or a fruit-bud. Some confusion has arisen from mistaking this for the first stage in fruit-bud formation. This same condition has been found in rapidly growing terminal shoots of one-year-old trees, where there is the least likelihood of fruit-bud formation. It is found in material gathered as late as the fore part of September, though it becomes progressively less common. Long before this time most buds have become differentiated into either leaf-buds or fruit-buds.

Distinct leaf-buds, well differentiated, were found as early as May. The leaf-buds differ from the undifferentiated in that the crown is flatter and broader, is not raised so high above the level of the embryo leaves, and scale bases, and has no swellings or very young leaves at its periphery. The amount of meristematic tissue is relatively less, and clearly defined tissue occurs closer to the growing point. All in all, the appearance presented strongly suggests a resting stage. Whether the bud can advance from this resting stage again and form a fruit-bud in the same season is a matter for conjecture. If a conjecture is to be hazarded, however, it is that a leaf-bud

is merely a resting stage, or in other words a flower-bud arrested in its development. Any bud, then, is potentially a flower-bud, awaiting only the proper conditions—whatever they may be—for its completion.

The first evidence of fruit-bud formation lies in the rapid elevation of the crown into a narrow conical form, rounded at the apex, with the fibro-vascular connections and pith areas advancing concurrently. In the axils of the young leaves, already noted in connection with the undifferentiated bud, appear other protuberances which soon become blunt at the top, while at the same time other leaf protuberances develop rapidly higher up in the spiral and younger protuberances appear in their axils. The apical protuberance is differentiated last, but when it does take shape it is already larger than those previously laid down, apparently appropriating a larger mass of tissue in its formation. That this succession of changes is gone through with extreme rapidity is to be inferred from the fact that it was shown by a very small number of sections out of a great number examined from material gathered at weekly intervals.

The further development of the fruit cluster has been described by Drinkard (4), and by Kraus (5). Inasmuch, however, as the dates at which the successive stages are reached in the Newtown at Corvallis differ somewhat from those recorded for the Oldenburg in Virginia, a brief outline is presented.

The earliest differentiation is visible during the first ten days of July. It may possibly vary from year to year to a very slight degree. Samples from material gathered throughout a period of three years show very little, if any, difference between the stages reached at a given date in different years, until well toward blossoming time, when the buds apparently become more responsive to external conditions. By the fifth of August the sepals, petals and outermost cycle of stamens are easily recognizable. Sections from material gathered the middle of September show further development in the parts already mentioned; the petals have become longer and wider; the stamens show, frequently, the bi-lobed appearance; in addition, the other two cycles of stamens have appeared and are well differentiated, and in many cases the carpels are already of fair size. The lateral buds of the cluster have, not uncommonly, reached the stage where the second and third cycles of stamens are suggested. Between this time and the last of November the most striking change is in the carpels, which by the latter date have enlarged considerably. Carpels are also beginning in the side buds.

Material gathered the middle of February shows little or no change in the terminal blossom, but pollen mother-cell formation in the side buds is evident. During February and March the pistils begin to push up rapidly and the ovules appear. Petals and stamens appear to have completed their development and to be awaiting the expanding of the blossoms.

Goff recorded the fact that the period of fruit-bud differentiation extends over some considerable time. The present investigation bears out this statement, but it indicates, in addition, that this is more true of buds in some positions than it is in the case of buds in other positions.

Kinds of Buds Considered

The normal condition in the Yellow Newtown is for fruit-buds first to occur on two- or three-year-old wood. Under favorable conditions a bud produced in the axil of a leaf on wood of the current year will produce next year a short spur, with a whorl of leaves and in the following year this spur will bear fruit. Then the normal condition is that the spur, having borne fruit, will during the succeeding year form a fruit-bud, which may be expected to bear again in the following year. These apparently normal conditions are often changed, however; a spur may bear fruit two years in succession and terminal or sometimes even axillary buds produced one year may bear fruit in the following year.

In recognition of these differences, buds were gathered throughout the work in six separate classes, as follows:—(A) axillary buds on the newest wood; (B) terminal buds on the newest wood; (C) buds from young spurs on second-year wood which had not borne fruit but seemed likely to bear in the following year; (D) buds from spurs which were bearing in the current year; (E) buds from spurs which had borne previously but had not blossomed in the current season, in other words, were “resting a year”; (F) buds from spurs which had blossomed but which had not set fruit, or having set fruit, had lost it early through dropping or thinning.

The Several Classes Considered

Class A:—This class is intended to include axillary buds on current year wood. Unfortunately, Newtown is not one of the varieties which regularly forms axillary fruit-buds, on new wood, and as this part of the study was confined to this one variety, nothing in relation to the time of formation of such buds can be stated. It was not deemed advisable to substitute axillary buds of another variety which forms fruit in this way rather freely—as, for example, Jonathan, because, as will appear later, the various stages are not strictly comparable in the two varieties.

Class B:—Terminal fruit-buds on one-year-old wood are of this class. They are formed more or less in all varieties, and are numerous enough in some to be considered normal. The condition was so widespread in the College orchard in 1914 that there were only one or two varieties in which this condition was not observed. There is, however, much more of this formation in some varieties than in others; it is very common in Yellow Newtowns, especially on young trees, sometimes their entire first crop resulting from such buds.

On older trees the formation of fruit-buds of this class seems to be an expression, as it were, of superabundance. In other words, if a tree is forming fruit-buds in great abundance, many will be found as terminals on one-year-old wood; if the number of fruit-buds is small, there will be practically none at all formed on the one-year-old wood. This reduction in numbers is so great that it does not seem to be a mere numerical shrinkage, but an actual shifting of the proportions. It is probable, however, that certain varieties are incited to terminal bud formation more readily than others.

In the Newtown, as one might expect in any variety, the actual time of visible differentiation into fruit-buds in this class is somewhat behind that taken as normal. Sections from material taken Aug. 11, 1912, show the terminals considerably less advanced than the "normal" buds at this time; they may be considered as at a stage characteristic of the normal for July 10 or even earlier. Some few, however, have reached the stage where the outermost cycle of stamens is laid down. Strangely enough, by September 16, when other material was taken, they seemed to be fully as advanced as the normal. Sections from material taken as late as March 6, 1912, indicate that there was very little, if any, difference between the buds at that time; the uneven development must arise subsequently. It is well known that the terminal clusters open later in the spring than the others. In the light of these investigations, however, this cannot be attributed to their being formed later, as the present evidence indicates that both kinds go into the winter in substantially the same condition. Perhaps other cultural or weather conditions might change this sequence, but so far as the material studied affords any indication, this condition will hold.

Class C:—Spurs on two- or three-year-old wood which have never borne and are forming fruit-buds for the first time, are here included. The earlier stages of buds of this class are similar to those on spurs bearing fruit during the current year (Class D) in that differentiation into fruit-buds begins at the same time and continues well throughout the summer. In August various stages, from very close to the earliest up to stages representing as much development as the "normal" are observable. The earlier stages are decidedly exceptional, however, and the condition of the average bud of this class is the same as on the older spurs which have borne in previous years (Class E). The fact that late development is so rare suggests that the few cases observed may have been caused by an accidental summer pruning, that is, an earlier removal of sample wood, of which no note had been taken at the time of gathering and that the normal condition for this type of spur is the same as for the old spur. The only difference is that there is a little more variation.

Class D:—Buds on spurs which are bearing in the current year are here included. Possibly the normal sequence of events in the history of a fruit-spur is that it shall bear fruit in alternate years only. This condition is less pronounced in some varieties than in others. In the Newtown, from which the buds studied in this work were taken, many spurs have been found in the course of the work that matured fruit in two successive years. Furthermore, sections of buds from bearing spurs often showed fruit-buds formed for the following year. The interesting point in connection with this occurrence is that the condition of the tree as a whole seems to have considerable influence on it; in a year of a very small crop as was 1912 in the orchard under investigation, those spurs which were bearing were as likely to form fruit-buds for the next year as those not in bearing; on the other hand, when a tree is bearing a very full crop, as was the case with many trees in 1913 in the same orchard, very few, even of the spurs not bearing, will form fruit-buds for next year. In more vigorous trees it is likely that this condition

may be changed. This condition is not set forth as the normal, though it may be; it is cited merely to show the pliability of varieties in this respect.

Buds taken August 5, 1912, showed fruit-bud formation as well advanced on bearing spurs as the "normal" non-bearing spurs. Specimens taken on August 11 showed a considerable range in stages represented; on the one side very early stages, on the other, buds fully up to the normal. Specimens gathered August 27 still show the same range, indicating that fruit-bud differentiation is still going on at this time in bearing spurs.

Class E:—Here are classed those spurs which have borne fruit previously but are out of bearing the current year.

Throughout the course of this study it has become increasingly evident that there is less variation in time of differentiation and more uniformity of development—so far, at least, as Yellow Newtown is concerned—of fruit-buds on spurs that have borne in previous years. There is, even in these buds, some late development, early stages being occasionally found in late August, but less than was found in buds of other kinds. Because of this relative stability, the development of the various organs was studied in these buds and this is the class of buds whose development has been already detailed. It is here considered as the "normal" and other classes of buds referred to it.

Material from the other kinds of buds was taken as often as the "normal" but enough only was sectioned to indicate the comparative development. It is believed, however, that the material was ample and sufficiently representative to be indicative of conditions for this variety.

Class F:—Buds from spurs which have borne blossoms in the spring of the current year, but which have failed to set or to carry the fruit for any considerable period are of this class. They show throughout the summer every possible range of variation from the first differentiation to stages even slightly in advance of the normal. This may be more or less related to the period at which the fruit has fallen, the most advanced, possibly, occurring on spurs where the blossoms failed to set fruit and the earliest stages appearing where the fruit hung for some time.

There has thus been shown some difference in the time of fruit-bud formation in buds in different positions. This is observable until late in the fall, when all fruit-buds seem to be retarded measurably in their progress, and develop equally from then on, until very near the time of blossoming in the spring.

A Consideration of Variation of Varieties

A rather hurried and incomplete attempt was made to ascertain whether there is any difference, among varieties, in the time of fruit-bud formation. On August 7, 1913, buds were taken from trees in the College orchard, representing the following varieties: Shiawassee, Grimes, Jewett, Jonathan, Oldenburg, Tetofski, Northern Spy, Stark, and Red Astrachan. This selection afforded an opportunity for the comparison of varieties differing rather widely in time of blossoming and of ripening. The buds examined were taken

rom spurs which had borne in previous years but were not bearing in the current year. Buds of this class had shown greater uniformity of development in Newtown, and presumably afford the best basis for a comparison of varieties in this respect. Between 20 and 30 buds of each variety were examined.

Though no extended or final conclusion can be drawn from such limited study, the work, as far as it went, showed beyond probability that there is some little difference between varieties in their respective times of fruit-bud formation, or, at least in the development of the bud at the time when the samples were taken. As may be seen readily enough from the accompanying cuts, which represent fair samples of the material studied, there is a considerable range of stages, from the Stark at one end to the Jonathan and Spy at the other. This difference extends to the side buds as well as to those in the apical position.

In relation to the periods of ripening or to the times of blossoming, the relative development in August has no exact correspondence. There is, however, rather more agreement with the times of blossoming than with the periods of ripening.

Material was gathered from the same trees in December, 1913, but unfortunately this material has not been studied far enough to warrant even the generalizations made from the buds gathered in August. A hasty examination of dissection of this material seemed, however, to indicate an approach to a uniform winter stage for the different varieties.

The writer wishes to acknowledge the suggestions of Professor C. I. Lewis, and the valuable advice and substantial help afforded by Professor E. J. Kraus, under whose direction the work was conducted.

Literature Cited

1. Quintinye, Jean de la. Instructions pour les Jardins fruitiers et Potagers; Pt. 2; p. 579; 1746.
2. Lazenby, W. R. The Development of the Buds in some of our Common Orchard Fruits. Proceedings of the American Pomological Society; p. 40; 1899.
3. Goff, E. S. The Origin and Early Development of the Flowers in the Cherry, Plum, Apple and Pear. Sixteenth Annual Rept. of the Wisconsin Agric. Exp. Sta.; pp. 290-303; 1899.
— Investigation of Flower Buds. Seventeenth Annual Rept. of the Wisconsin Agric. Exp. Sta.; pp. 266-285; 1900.
— Investigation of Flower Buds. Eighteenth Annual Rept. of the Wisconsin Agric. Exp. Sta.; pp. 304-316; 1901.
— Origin and Development of the Apple Blossom. American Gardening; Vol. 22; p. 330 and 346-7; 1901.
4. Drinkard, A. W. Fruit-bud Formation and Development. Report Virginia Agric. Exp. Sta., 1909-1910; pp. 159-205; 1911.
5. Kraus, E. J. The Pollination of the Pomaceous Fruits. 1. Gross Morphology of the Apple. Research Bulletin No. 1, Part 1, Oregon Agric. Col. Exp. Sta., 1913.

Explanation of Plates

Plate I. Spitzenberg. Aug., 1914. Uppersections, terminals from actively growing shoots; lower, from shoots having terminal buds well developed.

Plate II. Newtown. Development of buds of "E Group". Reading from left to right: June 24; June 24; July 21; July 21; Aug. 5; Aug. 11.

Plate III. Newtown. Development of buds of the "E Group". Reading from left to right: Aug. 19; Sept. 10; Sept. 16; Nov. 25; Feb. 14; Mar. 6.

Plate IV. Newtown. Development of buds of the "C Group" and showing variation of development on same date. Reading from left to right: Aug. 11; Aug. 11; Aug. 11; Aug. 11; Aug. 19; Aug. 27; Sept. 16; Jan. 31.

Plate V. Newtown. Development of buds of the "F Group" all on same date, Aug. 5, 1912. Lower right hand section more enlarged.

Plate VI. To show variation in fruit-bud development according to variety. Buds all taken Aug. 7, 1913. Reading from left to right: Jonathan, Spy, Grimes, Shiawassee, Jewett, Red Astrachan, Stark, Tetofski, Oldenburg.

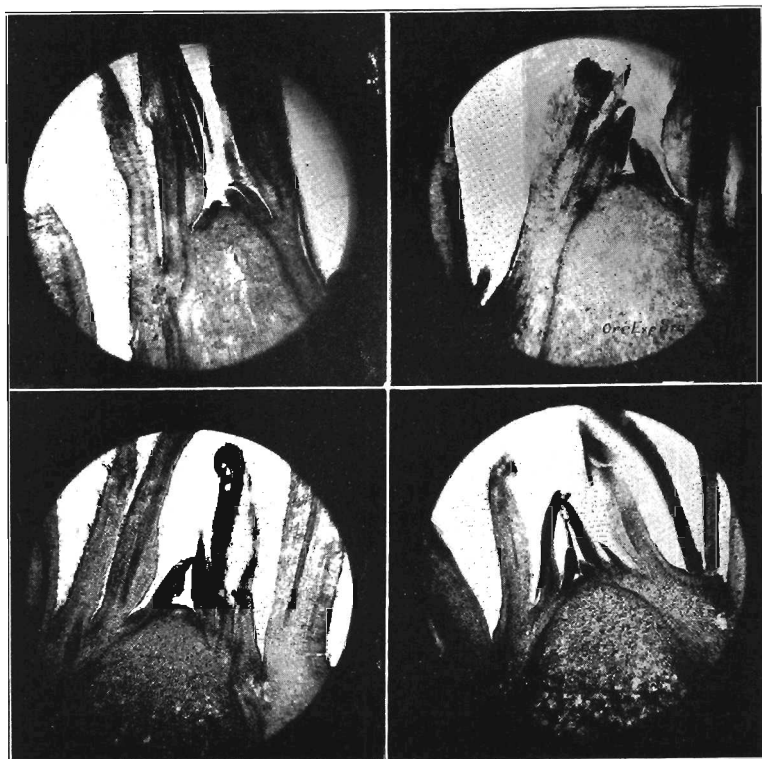


Plate I.

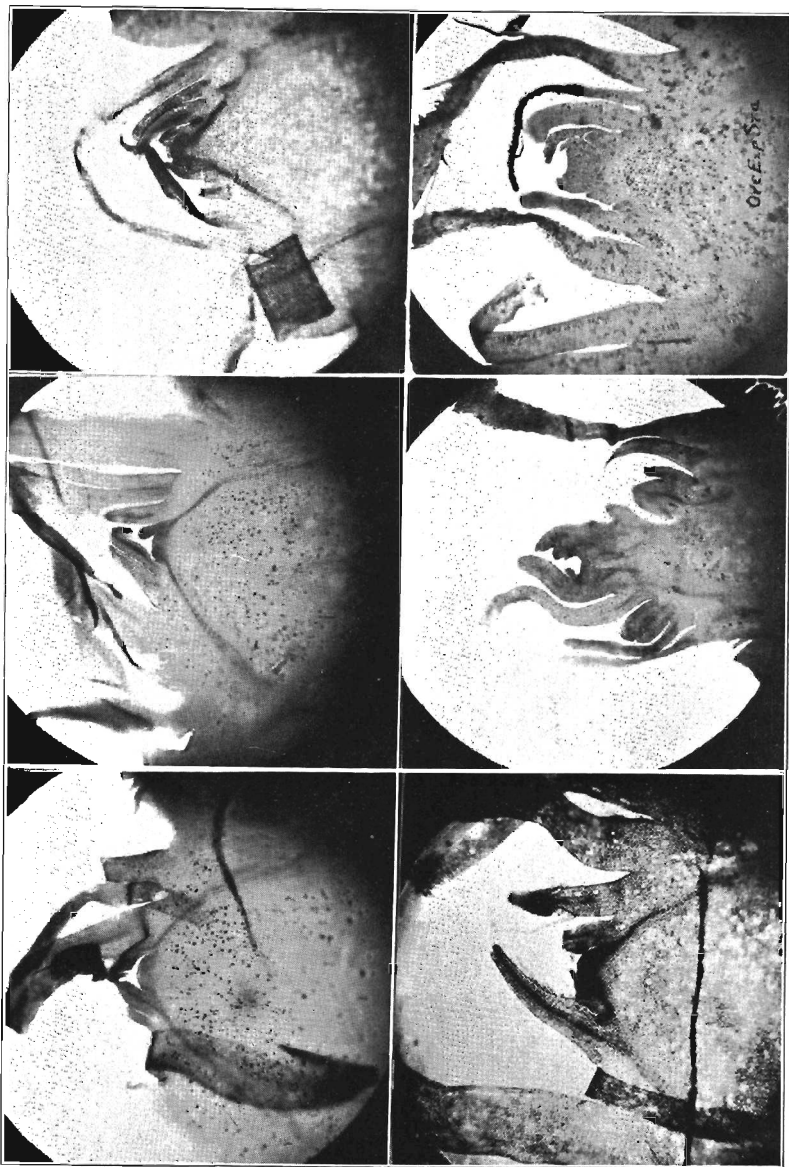


Plate II.

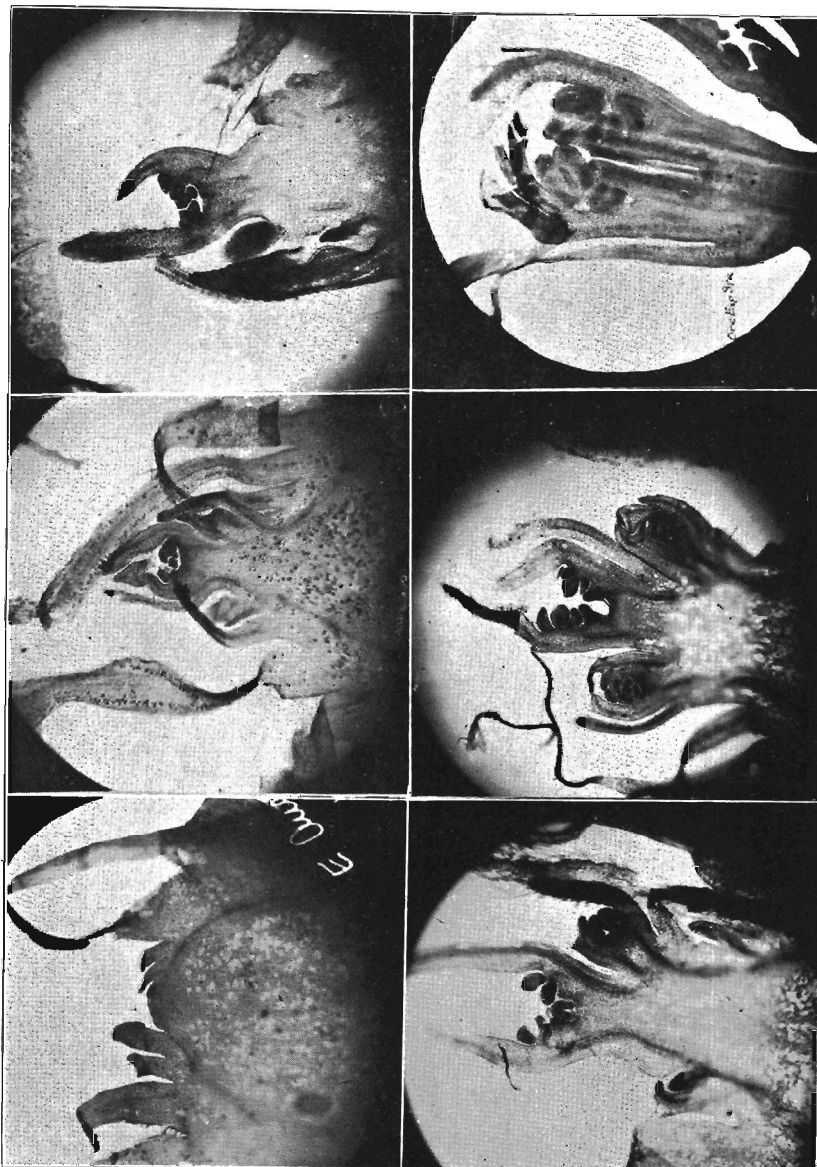


Plate III.

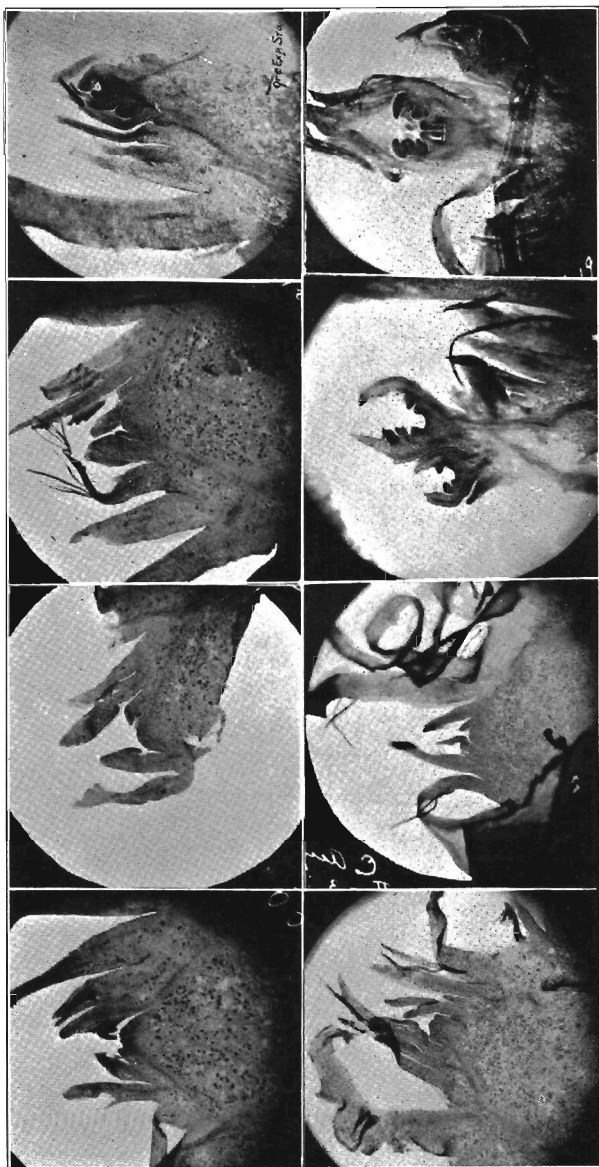


Plate IV.

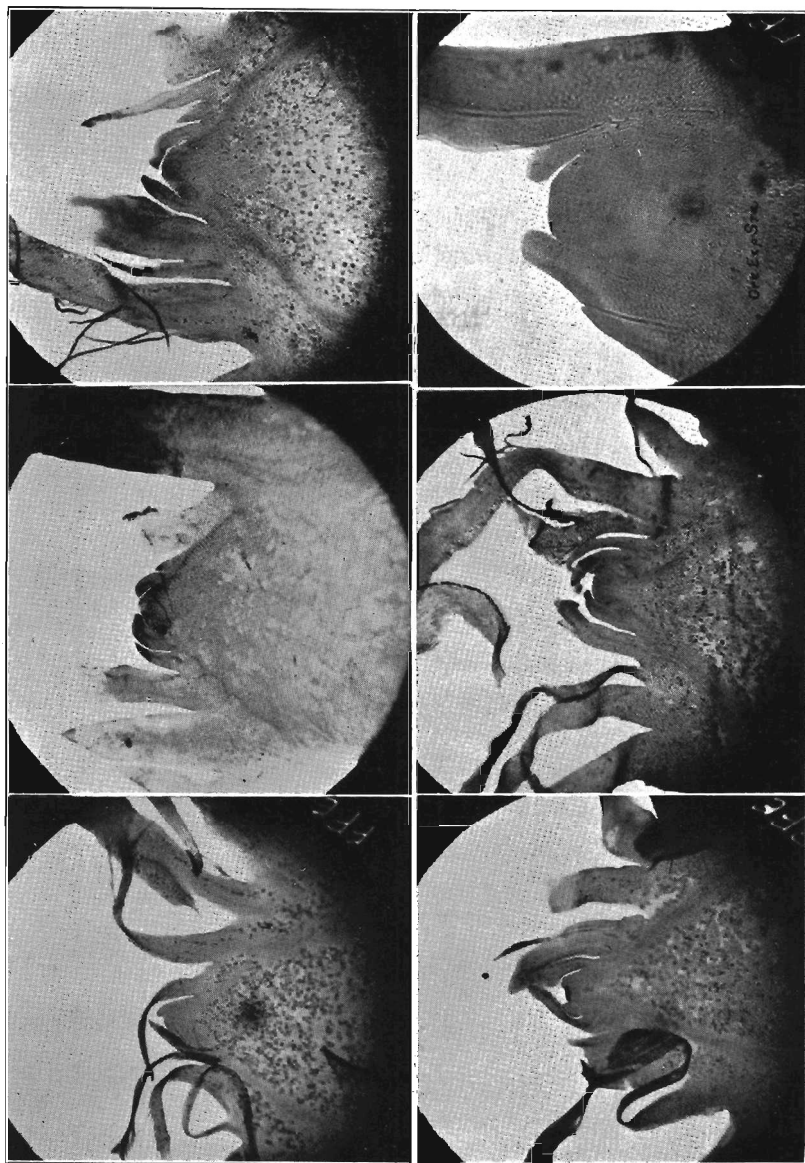


Plate V.

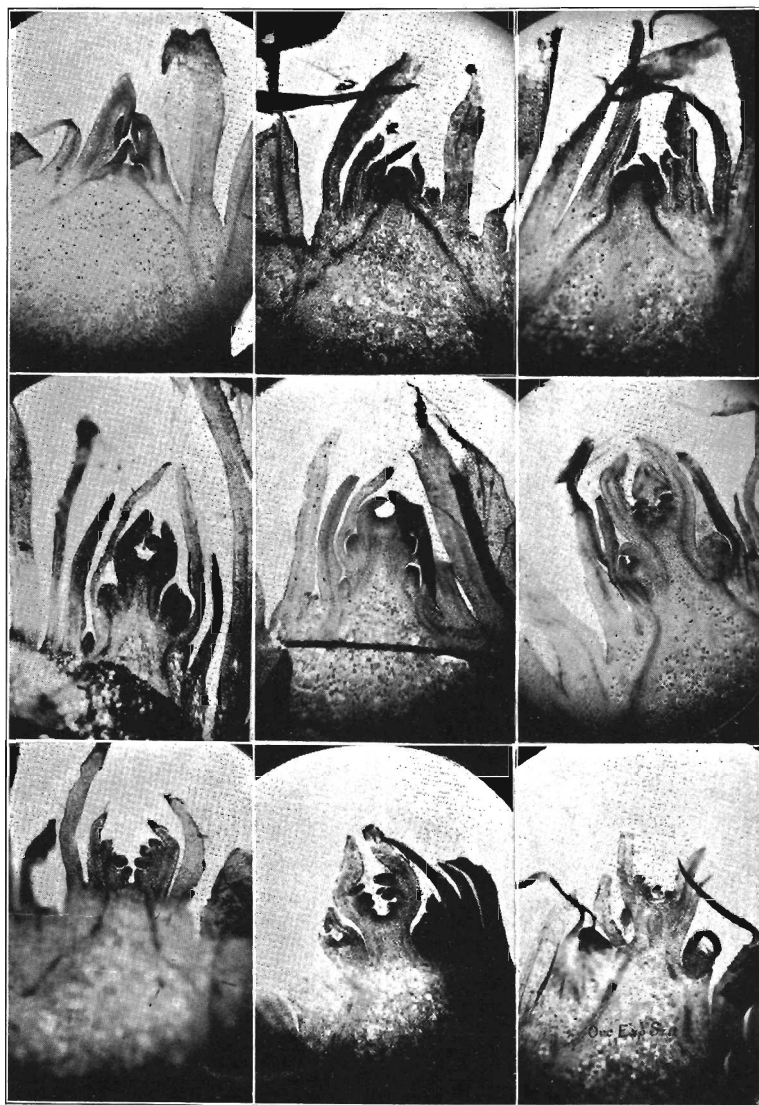


Plate VI.