Cosens, Absolom

A contribution to the morphology and biology of insect galls.

A CONTRIBUTION TO THE MORPHOLOGY AND BIOLOGY OF INSECT GALLS

A. COSENS, M.A.

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A CONTRIBUTION TO THE MORPHOLOGY AND BIOLOGY OF INSECT GALLS.

BY

A. COSENS, M.A.

TO THE SENATE OF THE UNIVERSITY OF TORONTO:

Gentlemen:

I certify that the paper presented by Mr. A. Cosens, M.A., entitled "A Contribution to the Morphology and Biology of Insect Galls", is satisfactory as a fulfilment of the thesis requirements exacted of candidates for the Degree of Doctor of Philosophy. It is a distinct contribution to the knowledge of the subject.

(Signed) J. H. FAULL,
Associate Professor of Botany.

January 17th, 1913.

I hereby certify that the thesis above mentioned has been accepted by the Senate of the University of Toronto for the Degree of Doctor of Philosophy, in accordance with the terms of the Statute in that behalf.

(Signed) JAMES BREBNER,
Registrar.

March 29th, 1913.

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A CONTRIBUTION TO THE MORPHOLOGY AND BIOLOGY OF INSECT GALLS.

BY A. COSENS, M.A.

The earliest explanations offered to account for the origin of galls are more or less fanciful, as must needs be, since nothing was known concerning the reciprocal relations of host and parasite involved in their life histories. Some of these theories dating from a less scientific age are crystallized in the popular names attached to certain classes of these structures. Thus the bristling masses of twigs, produced on several species of trees by the stimulation of plant or animal parasites, are known by some as "thunder bushes," a term that implies the expenditure of electrical energy in their origin. Also the more common name, "witches' brooms," indicates an equally imaginative explanation.

With the gradual advances of science much of the mystery surrounding galls has been dispelled, but they still present many interesting problems. Among these are two standing out so prominently that they seem to include all others. The first of these concerns the causes that are operative in producing the gall. It is now generally recognized that its origin is directly ascribable to the stimulation of a parasite, but the problem still remains concerning the nature of the stimulus and the principle governing the response. Concerning the nature of the stimulus, Fockeu and his school ascribe it to mechanical means, while Küster, Küstenmacher and others believe it to be referable to a chemical action. With regard to the response by the host, the conventional view endows the stimulated protoplasm with power to originate something foreign and without a prototype in the normal host. But a view is developed in this paper proposing an entirely different explanation, namely, that the supposedly new types of organs, tissues, etc., are due to the awakening of dormant characteristics in the protoplasm.

The second problem deals with the apparent philanthropy that characterizes the host plant in its care for the parasite. Concerning this, several explanations have been offered. The parasite may be simply taking advantage of structures thrown out by the plant in its own defence, or as Adler[1] figuratively expresses it, the besieger is making use of the water in the moat in pushing forward the attack on the fortifications. Perchance, even what Darwin regarded as impossible has taken place, and the plant is producing the gall entirely for the welfare of the parasite. In opposition to this the theory is proposed by some

investigators that in reality the host does derive benefit from the abnormal swelling since it has been the means of restricting the ravages of the parasite to a limited area.

I have confined the subject-matter of this research to the Zoocecidia including the Insecta and Arachnida. In the Insecta the following orders are dealt with—Hemiptera, Lepidoptera, Diptera and Hymenoptera. No attempt has been made to treat any one order exhaustively, but the work was restricted to the living gall material at hand. As a preliminary to the botanical work, several seasons were spent in rearing the producers in order that unquestioned identification could be assured of the various forms studied.

Concerning the anatomy of our American galls, the only work done previous to this is that by Cook,[22] who must be considered the pioneer in this branch of the subject. The anatomical studies pursued are considered important as forming a foundation for deductions.

The recent investigations of Weidel[45] on the early developmental stages of Neuroterus have added valuable data to the ontogenetic work. It is exceedingly necessary that some of the American species should be worked out in the same manner, but before this can be done with assurance of success, an American Adler must settle the questions concerning the alternate generations of our native forms.

Special attention has been paid to the Sawfly and Lepidopterous galls, since the anatomy of the former has hitherto not been dealt with at all and the ontogeny only very inadequately. The latter have also been neglected to nearly the same extent. The order Diptera and the family Cynipidæ have presented the most interesting biological phenomena, notably concerning the feeding habits and the nature of the gall-producing stimulus, two factors that are closely parallel if not indeed identical in these two sections of the gall producers.

With the exception of *Pachypsylla celtidis-mamma* Riley all the material was collected in the vicinity of Toronto. It was fixed in picro-sublimate or Flemming's weaker fluid and cut in series in paraffin or celloidin. A double stain of safranin and hæmatoxylin was invariably used.

The investigations described in this paper were carried on in the Botanical Laboratories of the University of Toronto under the supervision of Prof. J. H. Faull, who suggested the subject and to whom I wish to acknowledge my indebtedness for invaluable criticism and assistance throughout. To Dr. C. D. Howe I wish to express my obligations for direction in the physiological experiments. My thanks are also due to Mr. W. A. McCubbin, M.A., for valuable assistance in the photography and to Mr. J. H. White, M.A., for normal material.

ORDER ACARINA.

The following species are described in this section:—

Order Acarina.

Fam. Eriophyidæ.

Eriophyes Sp. (*Fagus grandifolia* Ehrh.)

Eriophyes querci. (*Quercus macrocarpa* Michx.)

Eriophyes Sp. (*Acer negundo* L.)

Eriophyes Sp. (*Populus grandidentata* Michx.)

Eriophyes Sp. (*Populus tremuloides* Michx.)

Eriophyes Sp. (*Prunus nigra* Ait.)

Eriophyes abnormis. (*Tilia americana* L.)

Eriophyes serotinæ Beut. (*Prunus serotina* Ehrh.)

The numbers referred to are from "A Catalogue of the Phytoptid Galls of North America," by George H. Chadwick, 23rd Report of the State Entomologist, New York State Museum, 1907.

Eriophyes Sp.

Chadwick's No. 65

Host *Fagus grandifolia* Ehrh.

This gall occurs on the under side of the leaves of the host plant. It is an erineum, white and frost-like at first, turning to a brown colour at a later stage.

The anatomical structure of the interior of the leaf remains perfectly normal, the effect of the stimulation being confined to the epidermis. This produces a large number of unicellular, capitate hairs, resembling miniature mushrooms, the resemblance to which is the more striking since the stalks of the hairs are bulbous at the base, as shown in Fig. 3. The hairs on the normal leaf are long, acicular and unicellular. As this gall is produced with no increase in the number of cells in the leaf, anatomically it stands as a simple type of "hypertrophy", the remaining forms all exhibit the more advanced phenomenon of cell proliferation.

Eriophyes querci (Garman).

Chadwick's No. 112

Host *Quercus macrocarpa* Michx.

In this gall, which is of the "dimple" type, the depression is on the under and the elevation on the upper side of the leaf. The hollow is filled with a dense mass of brown pubescence. In rare cases the elevation is on the under side of the leaf, when the pubescence then covers it.

The leaf blade in this case has become of nearly twice the normal thickness. This has resulted from cell division which has occurred in the tissues of both the palisade and the spongy parenchyma, producing a compact mass of undifferentiated cells, entirely without intervening air spaces. This tissue is shown in Fig. 6.

The epidermis has responded to the stimulation by producing many long, acicular, unicellular hairs, which are narrowed at the base. The hairs are stellate on the normal leaf of the host, but are simple, unicellular and acicular on its reproductive axis. The same feature is true of *Quercus robur var. pedunculata*, and in all probability of the other oaks. This appears to be a clear case, not of the production of a new type of trichome, but of a reversion.

Eriophyes Sp.
Chadwick's No. 2
Host *Acer negundo* L.

A shallow dimple on the under side of the leaf, filled with a white pubescence.

In this gall as in the preceding species, the leaf blade has been very much thickened by proliferation in the mesophyll. The cells produced are circular in outline and of about the same size as those of the normal spongy parenchyma. The hairs produced in this case not infrequently consist of from 2 to 3 cells which are very much convoluted. They are well shown in Fig. 4. The hairs on the normal leaf of the host are straight or only very slightly curved, but the glandular, convoluted type of hair is found on the inflorescence. Both the normal and abnormal hairs are composed of the same number of cells.

Eriophyes Sp.
Chadwick's No. 84
Host *Populus grandidentata* Michx.

A deep dimple gall with the convex part on the upper surface of the leaf. The gall is light green above, with the contents of the depression dark red.

The cells produced by the palisade parenchyma can be distinguished in this case from those arising from the spongy parenchyma. The former are almost square in outline and placed in two very regular rows immediately below the upper epidermis, and parallel with it. This tissue can be seen in Fig. 2. The latter constitute a tissue made up of cells which are circular to elliptical in outline. These cells are much smaller than those produced by the palisade layer. The outgrowths from the lower epidermis described in various ways as trichomes, granules, etc., are in reality produced by a complicated folding, in which only the lower epidermis and the spongy parenchyma participate, as shown in Fig. 2.

A cross section of the gall shows a number of vascular strands, but in my opinion the gall-producing stimulus only enlarges the veins that are already present in the normal leaf; it does not originate a special vascular system for the gall.

Eriophyes Sp.
Chadwick's No. 88.

Chadwick considers this form, first described by Jarvis,[28] the same as his No. 87. But the latter is characterized by a depression on the under side of the leaf, the former by an elevation, so that the two are constantly distinct.

Host *Populus tremuloides* Michx.

A dimple gall with the elevation on the under surface of the leaf. The elevation is a lighter green than the surrounding normal leaf and the folds that occupy the concavity are greenish-yellow or reddish in colour.

In dealing with the anatomical structure it is to be noted that the spongy parenchyma has in this case remained normal. The folds are produced in the same manner as in the preceding species, except that in this form it is the upper epidermis that undergoes the folding process. The nature of this folding can be seen in Fig. 1.

Eriophyes Sp.
Chadwick's No. 93.
Host *Prunus nigra* Ait.

A very much elongated pouch gall, greenish or whitish in colour, found on the upper side of the leaf with the opening on the under side.

All the characteristics of the normal mesophyll have been completely altered in the affected part of the leaf. Its cells, which, with the epidermis, constitute the wall of the gall, are larger than the normal and are elongated parallel to the long axis of the outgrowth. The upper epidermis which forms the epidermis of the gall has not been affected, but the cells of the lower epidermis which line the gall cavity have become much enlarged and in addition have produced a large number of closely set trichomes which project into the gall cavity. The nature of these is shown in the upper part of Fig. 5. These structures are often from 2 to 3 cells in length. Around the opening of the gall a circle of closely set acicular hairs occurs. The hairs on the outside of the gall and on the normal leaf are also of the acicular type. The vascular strands are much larger than those of the normal leaf but appear to be simply the stimulated normal veins.

Eriophyes abnormis (Garman).
Chadwick's No. 144
Host *Tilia americana* L.

A very much lobed pouch-gall, usually on the upper side of the leaf, found rarely on the under side. The opening which is on the opposite side of the leaf to the pouch is surrounded by a dense growth of acicular trichomes.

The anatomical structure of this gall shows it to combine the characteristics of a pouch-gall with a type in which the epidermis lining the larval cavity is thrown into folds, as described in the case of the galls on Populus. The foldings of the lining of the gall cavity often coalesce, and practically divide the cavity into a number of compartments. Morphologically this is one of the most highly differentiated of our Phytoptocecidia. The lining epidermis has produced a large number of acicular, unicellular trichomes; these in some cases almost fill the cavities. The hairs surrounding the gall aperture are of the same type, as are also the normal hairs of the leaf. Glandular cells are much more abundant in the gall tissues than in those of the normal leaf.

Eriophyes serotinæ Beut.

Chadwick's No. 100

Host *Prunus serotina* Ehrh.

This is a club-shaped gall, produced on the upper side of the leaf of the host. The aperture of exit, which is on the lower side, is surrounded by fine white hairs. It varies in length from 5 to 8 mm. and at a distance from the apex of about two-thirds the total length, it is narrowed into a stalk with an average diameter of 1 mm. In color it varies from green to a distinct red.

The stimulation has not produced very marked changes in the structure of the leaf near the origin of the gall. Apart from the fact that the spongy parenchyma has divided more actively, the mesophyll is normal. The upper epidermis of the leaf that forms the outer covering of the gall, has its cell walls abnormally thickened. The lower epidermis that lines the gall cavity has larger cells than the unstimulated epidermis, and from these cells originate elongated, unicellular trichomes with bulbous bases. The hairs on the normal leaf are acicular and unicellular. While the cells in the neck of the gall are arranged in rows parallel to its length, the larger cells that form the main body of the gall are not regularly placed. The vascular strands pass up from the leaf at a distance of about three cell layers from the gall cavity.

Summary.

In some forms the effect of the stimulation does not extend beyond the epidermis, on which the producers are located, but in other species it is transmitted throughout the mesophyll of the leaf.

The abnormal activity of the epidermis is expressed in the curving and folding of the tissue as well as in the production by it of various forms of trichomes.

In general, when the effect of the stimulation extends to the mesophyll the distinction between the palisade and the spongy parenchyma is lost. In place of these tissues a compact mass of uniform cells is produced.

The types of the galls constitute a clear phylogenetic series from the simple erineum to the well developed pouch-gall. The distinction between the different members of this series is largely a difference in degree rather than in kind, and seems to be explainable on the assumption of a gradually increasing intensity of stimulus from the lowest to the highest member of the series.

The literature of this group of galls contains a number of statements, to the effect that the host plant under the influence of the gall stimulus can originate entirely new types of hairs. While it is true, as a general rule, that hairs produced by an organ under such a stimulus differ from those originated by that organ under normal conditions, yet in such cases I have found that the abnormal type of hair is being produced on another part of the host plant. Thus the curiously convoluted, glandular hairs, originating in the dimple galls on the leaves of *Acer negundo* L., are duplicated exactly in the hairs occurring on the reproductive axis of the same plant, and the long acicular hairs composing the brown pubescence that fills the concavities on the leaves of *Quercus macrocarpa* Michx have their exact counterparts in those produced on the flowering axis of that plant. In the former example the normal hairs on the leaves of the host are straight and acicular, in the latter they are of the stellate type.

ORDER HEMIPTERA.

The following Hemipterous galls have been studied:—

Fam. Aphididæ.

Gall on *Populus balsamifera* L. (Unclass.).

Hormaphis hamamelidis Fitch.

Hamamelistes spinosus Shimer.

Aphid Corrugations on Birch.

Pemphigus vagabundus Walsh.

Pemphigus rhois Fitch.

Chermes abietis Chol.

Chermes floccus Patch.

Fam. Psyllidæ.

Pachypsylla celtidis-mamma Riley.

Aphid Gall (Unclassified), Host *Populus balsamifera* L.

A pouch-like gall on the under surface of the leaf, produced by a fold in the blade near the base of the midrib. One edge of the fold is attached along this midrib. The slit-like opening, which is on the upper surface of the leaf, extends the full length of the gall. This species resembles very closely the gall produced by *Cecidomyia majalis* Bass. The general structure is shown in Fig. 7.

Dimensions:—Length along line of attachment to midrib, 10-12 mm.; Width, 4-5 mm.

In the part of the leaf blade that forms the gall all resemblance to the normal mesophyll has disappeared. A compact mass of tissue has taken its place, the cells of which are much larger than normal mesophyll cells. Towards the interior of the gall the cells become smaller and richer in protoplasmic contents. The upper epidermis forming the interior of the gall remains practically normal, except that it produces longer and more abundant trichomes than when unstimulated. These trichomes are usually three cells in length. A cross section of this gall shows two small groups of cells with porous laminated sclerenchymatous walls, one of which is situated near the midrib and the other exactly opposite on the other side of the gall opening. Thus each side of the gall aperture is bordered by a band of sclerified cells, as shown in the transverse section of Fig. 8.

Hormaphis hamamelidis Fitch.
Host *Hamamelis virginiana* L.

The gall formed by this species is found on the upper side of the leaf of the host, but the larvæ escape from an opening on the under side. The mature gall is conoidal in shape with the apex usually slightly bent over. General structure is illustrated in Fig. 12. A circular ring of tissue covered with pubescence surrounds the gall opening which is shown in Fig. 12.

Dimensions:—Average length of gall 10.5 mm.; diameter at base 4 mm.

The gall is composed of small cells placed close together, forming a compact and very uniform tissue. The cells are arranged with their longer diameters pointing in the direction of the gall apex. In a longitudinal section the vascular strands are seen to pass up each side at a depth of about three cells from the gall cavity. The beaks of the larvæ, often found imbedded in the wall of the gall, were inserted far enough to almost reach these vascular strands. The hairs that surround the gall aperture are acicular and unicellular.

Hamamelistes spinosus Shimer.
Host *Hamamelis virginiana* L.

The galls in this species are modified flower buds. These are somewhat elliptical in outline with gradually tapering stalks. They are covered with spines, which are usually curved. The opening is situated at the union of the stalk and the gall proper. This opening is funnel-shaped and is surrounded by a circular ring of tissue as in the preceding species on the same host. The pubescence is absent in this case.

Dimensions:—Average length including stalk 21 mm.; average width 10 mm.

This gall is covered by an unusually small-celled epidermis. The spines that are so noticeable a feature are found to consist of projections of the epidermis, filled with cells in continuity with the mesophyll. The cells of the gall are almost perfectly circular in outline and packed together very closely. This tissue is very uniform except in the four or five layers adjoining the gall cavity. In that zone the cells are smaller and richer in protoplasmic contents, constituting a fairly well marked nutritive layer.

In cross section of the gall about thirty main fibro-vascular bundles are cut; these are comparatively large and situated near the larval cavity. Two of these have been cut in the section shown in Fig. 10. Other smaller strands are cut further out. The gall receives all the fibro-vascular strands that, under normal conditions, would have passed up into the flower. The interior of both this and the preceding species is almost perfectly glabrous.

Aphid Corrugations on Birch.

Hosts { *Betula lenta* L.
Betula alba var. papyrifera (Marsh) Spach.

The primary folds in the leaf that form this gall run parallel to the main veins, with the latter as boundaries between them. Their crests are on the upper side of the leaf, while the hollows which form the larval chambers are on the under side. The primary folds are divided into secondary folds, and these again into depressions resembling minute Acarina dimple-galls. This complex arrangement is conditioned entirely by the veining of the leaf, since each fold, primary or secondary, is supported along its edges by veins. The folding can be seen in Fig. 9.

The anatomical characteristics of these galls show that the folding of the leaf has not entirely changed the structure of its normal mesophyll. Around the gall cavities the spongy parenchyma is nearly normal throughout and the palisade layer is recognizable in different places. The cells, however, are considerably larger than the cells of the normal mesophyll. The cells of the lower epidermis, that form the lining of the gall cavities, are well filled with food materials for the larvæ. The supporting veins on each side of the fold send out branches that supply the gall with an adequate vascular system.

Hormaphis hamamelidis Fitch and *Hamamelistes spinosus* Shimer, as worked out by Pergande,[40] show that they inhabit alternately *Betula nigra* L. and *Hamamelis virginiana* L.

The galls on the birch leaves are produced by the fourth generation of *Hamamelistes spinosus* Shimer. Pergande described them as "pseudo-galls or corrugations".

The witch-hazel galls produced by the stem-mother of this species are plentiful in this locality, but *Betula nigra* L. is not found here. The Aphids have consequently been compelled to extend their list of food plants to include *B. lenta* L. and *B. alba var. papyrifera* Spach.

Pemphigus vagabundus Walsh.
Host *Populus deltoides*, Marsh.

All the leaf rudiments of the terminal bud appear to be concerned in the production of this gall. Yet it is in reality a large pouch-gall with its wall thrown into smaller secondary folds. The apex of the stem, from which the gall originates, is usually swollen to nearly twice its normal diameter. These galls often remain on the host plant until the next season's galls begin to appear.

The cells composing this gall form a compact and fairly uniform tissue and a nutritive layer is not clearly differentiated. About one-third of the thickness of the gall wall, on the side next the larval chamber, however, is composed of cells that are somewhat larger than the remaining cells. The epidermal cells, lining the gall cavity, are elongated into short trichome-like structures. The phyllome origin of this gall is revealed by the presence of well defined stomata on its epidermis. These structures are numerous and appear to be quite normal. Glandular cells are plentifully distributed. Vascular strands pass irregularly throughout the wall of the gall.

Pemphigus rhois, Fitch.
Host *Rhus typhina* L.

A balloon-shaped gall with the regularity of its outline destroyed by the elongated lobes that cover its surface. A gall is shown in Fig. 14. The epidermis is slightly pubescent and coloured red, shading into yellow and green. It originates from the under side of the leaf, and the point of attachment on the upper side is indicated by a small papilla covered with a dense pubescence. These galls vary in size from very short types less than 1 cm. to those that are 4 to 5 cm. in length.

In the part of the leaf blade folded to form the gall, the mesophyll has been entirely changed. The effect of the stimulation has even destroyed the normal characters in the mesophyll for some distance from the point of attachment of the gall. The gall consists of a compact tissue composed of cells considerably larger than the normal cells of the mesophyll. The cells of this tissue are arranged in layers parallel to the epidermis of the gall. The vascular strands are situated about four cell layers in from the gall cavity. In all pouch-galls the tracheary tissue is

composed of the ordinary vascular elements of the normal leaf that have been stimulated to increased activity. There is not a special tracheary system originated for the gall. In the galls the strands occupy a definite position, since in the normal leaf they occupy a definite place in relation to the spongy and the palisade parenchyma. Large glands are present in the gall tissue, as shown in Fig. 14. A gland is found invariably associated with a fibro-vascular strand and seems to have its counterpart in the very small gland that runs through each vein of the normal leaf. In some cases the abnormal glands have acicular trichomes projecting into their cavities.

Chermes abietis Chol.

Hosts { *Picea abies* (L) Karst.
Picea mariana (Mill) B.S.P.

A polythalamous gall produced by the swelling of the base of the young shoots. Since the twigs are not usually killed the galls are surmounted by a variable length of normal stem. The galls in general vary from conoidal to nearly spherical in shape, but in some cases, owing to the stimulation not having affected the entire circumference of the stem, the gall does not extend completely around it and is consequently less regular in outline. The surface of the gall is covered with the enlarged bases of the aborted needles. These give a faceted appearance to the gall and produce a likeness to a miniature pineapple.

Dimensions:—Longer diameter 2-3 cm.; shorter diameter 1-2 cm.

The gall in this case is a joint production of the cortex of the stem and the bases of the leaves of the host. The cells of the epidermis, lining the gall cavities, in some cases have been prolonged to form very short trichome-like structures. The hairs at the aperture of exit, as seen in Fig. 11, are composed of one or two cells.

The resin ducts that occur in the normal cortex are found considerably enlarged in the gall. In addition to these, there are out near the gall periphery numerous smaller resin ducts, as shown near the margin of Fig. 11, that do not have corresponding structures in the unstimulated tissues. These additional ducts pass in from the swollen bases of the aborted leaves. A cross section near the base of these leaves cuts from four to six resin ducts, while a normal leaf does not contain more than two of these structures.

Chermes floccus, Patch.

Host *Picea mariana* (Mill) B.S.P.

In this species the gall is produced by the swelling of the entire shoot. In comparison with the former species, the leaves are little, if any, swollen at the base but are more numerous on the gall than on an equal

length of normal stem, owing to the shortening of the stem axis. The larval cells are in the cortex of the stem at the bases of the needles.

Dimensions:—Average length 2-6 cm.

The abnormal development of the cortex, especially that part contained in the wings on the stem, produces the entire mass of this gall. The stimulation has increased the number of resin ducts in the cortex. Several cross sections of galls were compared with corresponding sections from normal stems. The average number of resin ducts in the abnormal to that in the normal was in the proportion of 20 to 12. The smaller accessory resin ducts are shown in Fig. 13. In every section examined the additional ducts were in an irregular circle outside the normal ducts. The ducts produced under stimulation were larger than the corresponding normal ducts, but those that were found only in the abnormal tissues were smaller than the normal structures.

Fam. Psyllidæ.

Pachypsylla celtidis-mamma Riley.

Host *Celtis occidentalis* L.

A complicated form of pouch-gall produced in the mesophyll of the leaf of the host. On the upper surface of the leaf the gall is indicated by a decided depression in the centre of which is a slight elevation that marks the opening of the gall. The part projecting from the lower surface, is oblate-spheroidal in shape, attached to the leaf by a slightly tapering cylindrical stalk. The average number of galls found on a leaf is usually about ten, but in some cases much higher. The surface of the gall is smooth except for a few fine scattered hairs, glaucous and greenish-yellow in colour.

Dimensions:—Height from point of attachment 6-7 mm.; width 7-8 mm.

The anatomical structure of this gall shows it to be a more complex type than any other of the Hemiptera discussed in this paper.

Besides the folding of the leaf the blade has been further changed in thickness and in the character of the cells. The production of the greater part of the abnormal tissue is due to a wide, well differentiated cambium layer, that extends right across the gall and at its margin passes into the tissues of the normal leaf between the palisade and the spongy parenchyma (Fig. 15). The larval chamber is lined by this cambium sheath which thus functions as a nutritive layer. Bordering this zone is a well developed protective tissue composed of cells with uniformly thickened walls. The sclerenchyma is laminated and penetrated by branched canals, presenting the same character as that found in the galls of the Cynipidæ.

Outside of this protective zone lies the chief mass of the gall, composed of thin-walled irregularly shaped cells, as illustrated in Fig. 15. Typical cells of the protective sheath are also found scattered throughout this tissue. As the gall becomes older these cells increase in number.

Summary.

These galls are characterized by a folding and wrinkling of the leaf when they occur on that organ; in this particular they resemble the Phytoptocecidia. This common characteristic is due to the fact that in the orders Acarina and Hemiptera the stimulation is all from one side. The spherical type of the Cynipidæ is produced by a stimulus equally disseminated in all directions.

The tendency to produce trichome structures from the stimulated surface, so marked a characteristic of the Acarina forms, is in this group practically absent; the only hairs produced are those surrounding the gall apertures.

In most species of both groups there is little differentiation of tissues, so that the protective sclerenchyma zones mentioned in the genus Pachypsylla and the unclassified species on *Populus balsamifera* L. mark a distinct advance on the specialization attained by the Acarina galls and an approximation to the more complex types found in the orders Diptera and Hymenoptera.

The increased number of resin ducts in the tissues of the Coniferæ stimulated by species of the genus Chermes is an important feature of these galls.

ORDER LEPIDOPTERA.

The Lepidopterous producers referred to in this paper occupy the following positions in Dyar's List of North American Lepidoptera, United States National Museum, Washington, 1902.

Fam. Sesiidæ.

Memythrus tricinctus Harris.

Fam. Tortricidæ.

Eucosma scudderiana Clemens.

Fam. Gelechiidæ.

Gnorimoschema gallæsolidaginis Riley.

Gnorimoschema gallæasterella Kellicott.

Fam. Tineidæ.

Stagmatophora ceanothiella Cosens.

The host plants of the various species are:—

Memythrus tricinctus Harris.

Populus tremuloides Michx.

Eucosma scudderiana Clemens.
Solidago canadensis L.
Solidago serotina var. gigantea Gray (seldom).
Gnorimoschema gallæsolidaginis Riley.
Solidago canadensis L.
Solidago serotina var. gigantea Gray.
Solidago rugosa Mill (seldom).
Gnorimoschema gallæasterella Kellicott.
Solidago latifolia L.
Solidago cæsia var. axillaris Gray (seldom).

In speaking of the host plant of this producer Busck[19] makes th following statement: "I have before me specimens from Miss Clark which were unquestionably bred from the white wood-aster, *Aster divar catus* L. (*A. corymbosum* Ait.) near Boston."

Stagmatophora ceanothiella Cosens.
Ceanothus americanus L.

Tucker[43] states that *C. ovatus* Desf. is also a host plant of this specie

The following dates taken from records of specimens represent ap proximately the time of emergence of the moths:

Memythrus tricinctus Harris—July 4 to 8.
Eucosma scudderiana Clemens—June 8 to 20.
Gnorimoschema gallæsolidaginis Riley—August 5 to 15.
Gnorimoschema gallæasterella Kellicott—August 12 to 19.
Stagmatophora ceanothiella Cosens—June 23 to 30.

The two species of the genus Gnorimoschema pass the winter i the imago stage but Eucosma and Stagmatophora in the larval form

Several galls of the Eucosma moth were opened December 1 and the data collected were as follows:—The larva was in a dormar state in the portion of the stem of the plant immediately below the gal Before passing into this inactive condition the larva had carefully pre pared for the emergence of the imago from the gall. The wall of th gall cavity had been eaten through until the part remaining was thi enough to permit the passage of light. The exit thus prepared wa located at the upper end of the gall and was on an average 2 mm. i diameter.

A silk lining covered the whole of the interior of the gall and partition of especially strong silk crossed the cavity just opposite th opening mentioned above. This partition did not pass straight acros the gall but was found always in a slanting direction. It was attache to the gall wall just above the aperture and was always higher on tha side.

Galls produced by the Stagmatophora moth were examined a few days later and the larvæ were found to be passing the winter under very similar conditions to those described in the case of the Eucosma species. The Stagmatophora larvæ were not perfectly dormant, however, and soon became quite lively in a warm room. They were found invariably in the gall cavity with their heads a short distance below the prepared exit. This had been constructed as in the preceding case and was situated at the same place. The silk lining covered the interior of the gall but in this case was gradually narrowed to the size of the hole around the edges of which it was attached. As the plant stem was not hollow above the gall, the roof of the gall cavity occupied much the same position as the slanting silk partition in the Eucosma gall.

The silk lining common to both of these galls helps to prevent the loss of moisture and the consequent desiccation of the larva.

The cross partition of the Eucosma gall and the tapering neck found in the lining of the Stagmatophora species seem to have the function in common of guiding the occupant of the gall to the prepared exit.

Memythrus tricinctus Harris.

This form has hitherto never been considered a true gall maker—just why it is difficult to understand. Beutenmüller[3] reports it as a borer in stems of poplar and willow and in galls of *Saperda concolor*. I have repeatedly, however, bred this species from swellings on the smaller branches of young trees of *Populus tremuloides* Michx. These swellings were spindle-shaped, gradually tapering at each end to the size of the normal stem. In external form they were quite typical galls of the Lepidopterous class.

A comparison of the larval chamber of this gall with that of the Eucosma species shows that the two have certain features in common. Thus, although the opening in the stem made by the young larva in entering closes in the Eucosma gall, but not in this one, it can be found in the earlier stages of both. The silk lining in the larval chamber is not present, but the slanting silk partition has a similar structure and position to that found in the Eucosma species. This partition shuts off the permanent larval entrance from the part of the chamber in which pupation takes place. The place of exit has the same relation to this partition as that described in the Eucosma gall. The opening is prepared in the same manner. The larva eats through the wall of the gall until the part remaining is translucent just as in the case of the Eucosma or Stagmatophora forms. The larvæ in the two latter species prepare this opening in the fall, but the Memythrus larva does not complete it until shortly before pupation in the spring.

Dimensions:—As the size of the gall varies with that of the stem, an average of several specimens was taken. Length, 60 mm.; width, 20 mm.; diameter of normal stem at place of location of the gall, 12 mm.

A cross section of this gall, when compared with the normal stem, shows an abnormal thickening of the cortex and an increase in width of the bast and wood. Throughout the annual rings of wood are bast fibres, sometimes arranged irregularly in patches, in other cases forming fairly definite zones on the outside of the annual ring. The fibres are shown in Fig. 16.

Eucosma scudderiana Clemens.

"The galls are at the top of the main stems of the plants, usually within the flowering panicle, rarely on the branches of the panicle; usually but one gall on a plant, occasionally two, rarely three.

"The galls are spindle-form, varying in size from 10×16 mm. to 12×28 mm.; diameter of stem below gall from 4 mm. to 5 mm.; the average of ten galls collected in ten seasons, 100 specimens, was $9\frac{1}{2}\times21\frac{1}{2}$ mm., diameter of stem below gall 5 mm."—Brodie.[17]

The gall mass in this case is produced from the vascular bundles and the intervening parenchymatous strands. When the larva enters the stem it first eats out the pith. After the exhaustion of this source of nourishment, its food is supplied by the radial thickening of the bundles into the gall cavity. The secondary wood elements thus formed remain somewhat parenchymatous and can scarcely be distinguished from the cells of the medullary rays. The cortex is somewhat thicker than that found in the normal stem but this is not a very marked feature in the gall production.

In the normal stem of *Solidago canadensis* L. there is a gland opposite each bundle both on the side of the cortex and on that of the pith. The glands in the cortex of the gall are the same in number but are very much larger (Fig. 21). Likewise they are not regularly arranged but grouped two or three together. This is due to the fact that since some of the bundles have developed much more rapidly than others, their alignment has been destroyed.

The glands corresponding to the normal inner row were not found in the gall. This is accounted for by the early removal of the pith of the stem by the producer larva.

Gnorimoschema gallæsolidaginis Riley.

"Galls usually on the lower third of the stems of *Solidago canadensis* L. occasionally on the upper third, rarely at the summit of the stem. The galls vary in form from spindle-form to prolate and oblate spheroid; and in size from 10×21 mm. to 18×30 mm.

"Some observers say the interior of the gall is lined with silk. I have never found this, but preparatory to the exit, the mature larva before pupating constructs a silken hammock in the upper end of the gall, and opposite the aperture of exit. The larva resting in this hammock bites out a hole to the epidermis of the gall which is carefully left. The hole is bevelled towards the outside, and then neatly filled up with the material gnawed out, mixed with a silk-like substance, doubtless from a gland, which forms a tight-fitting, hard plug which cannot be pushed in from the outside but is easily pushed out from the inside."—Brodie.[17]

The anatomical features of this gall are very similar to those described in the Eucosma species. The gall mass is produced by the radial increase in thickness of the bundles and the growth into the gall cavity of the intervening parenchymatous strands seen in Fig. 20. There is greater proliferation of the cortical tissue in this case than in that of the Eucosma gall and the cells produced are much larger than those found in the normal stem.

The remarks concerning the gland production and distribution of the preceding species are also applicable to this form.

Gnorimoschema gallæasterella Kellicott.

"In a collection of galls made May 29, 1890, a few miles north of Toronto, most of them were at the top of the stem, surmounted by a few leaves, occasionally but one, usually two. The galls at this date seemed to be mature, subtriangular, corresponding to stem of plant; from 20 mm. to 32 mm. long, and from 10 mm. to 15 mm. diameter. In size, form and structure the galls closely resemble the galls of *G. gallæsolidaginis* Riley. Rarely they occur on the middle and lower third of the stem of the plant."—Brodie.[17]

"The gall produced on *Solidago cæsia var. axillaris* Gray by this producer is quite unlike the *S. latifolia* gall in appearance, but as both galls are merely spindle-shaped enlargements of the stems of the host plants, this difference in outward form can easily be explained. The glaucous, terete and slender stem of *S. cæsia* produces a gall with glaucous epidermis, circular in cross section and gradually tapering towards each end. On the other hand, the smooth, angled and comparatively thick stem of *S. latifolia* gives rise to a gall with smooth epidermis, somewhat triangular in cross section. This gall has also a greater diameter and tapers more abruptly than the *S. cæsia* gall."—Cosens.[25]

The anatomy of this gall presents the typical structure of a gall of the Lepidopterous class. The cortex of the stem does not play an important rôle in the production of the abnormal tissue; but when the host plant is *Solidago latifolia* L. the gall cortex is thicker than that of the normal stem. As in the case of the gall produced by *G. gallæsoli-*

daginis Riley, the bundles and the medullary rays are extended into the gall cavity and furnish the principal part of the tissue proliferation. Only a very shallow seam of normal wood is found in the galls produced on *S. cæs a var. axillaris* Gray.

Glands do not occur in the normal stems of either of the host plants and were not found in the tissues of this gall.

A section through the aperture of exit of a gall on *S. cæsia var. axillaris* Gray showed that the edges of the opening had been prepared by the larva for the reception of the "plug" that closed the opening. The sides of this aperture, roughened by the gnawing away of the tissue, would not admit of the "plug" fitting tightly and at the same time slipping out easily when occasion required. Consequently the gnawed surface is smoothed over by a layer of material that presents a perfectly even surface. This levelling-up material is uniform in character and does not show any trace of vegetable débris. At right angles to its free surface, an effect resembling checking takes place, a change that it has probably undergone in drying. This is illustrated in Fig. 22.

The "plugs" of the galls produced by the genus Gnorimoschema have been reported as consisting of silk and material gnawn out by the larvæ in preparing the openings. My observations incline me to the belief that the material, forming the plug and lining the opening, consists entirely of an exudation from the larva. It seems to be a plastic silk-like substance.

Stagmatophora ceanothiella Cosens.

"These abnormal growths are found commonly on a main stem, but rarely on a branch. The flower cluster is sometimes entirely aborted, but usually only partly so, the lower pedicels in the cluster remaining normal. In the majority of cases this gall is terminal, but in a few instances the stem was found to project a short distance beyond it.

"The gall has the relatively simple structure of a spindle-shaped enlargement of the stem. In length it varies from 10 to 15 mm. and in greatest width from 5 to 8 mm. It is roughened on the outside by the stumps of the aborted branches. On account of the shortening of the stem axis and the consequent crowding of the nodes, these branches are more numerous on a gall than on a corresponding length of normal stem. This gives the gall a gnarled surface and forms a strongly protected case for the larva. The gall in some cases is surmounted by a tuft of leaves growing from its apex.

"The aperture through which the moth escapes from the gall is made always near the upper end."—Cosens.[24]

As in the preceding galls described, the principal part of the gall tissues in this species is originated from the vascular bundles and parenchyma strands (Fig. 17). The latter are very wide and the abnormal cell division is more marked in them than in the bundles. The wood elements produced remain undifferentiated and pith-like. The cuticle of the gall epidermis is much stronger than that found in the normal stem. The epidermis itself has responded to the stimulation by the production of an extra layer of cells. The cortex of the gall contains approximately one-third more cell layers than the normal cortex as seen in Fig. 18.

The normal stem of *Ceanothus americanus* L. contains glands in the cortex. These are fairly regularly spaced around the stem but are larger and more numerous at the nodes. Glands occur also in the pith of the stem, the petioles of the leaves and the reproductive axes. But in parts of stems, contiguous with galls, though glands occur in the pith there are none in the cortex, except at the nodes. Glandular cells, however, are plentiful in the cortex of such stems.

A cross section of a gall shows larger and more numerous glands than a corresponding section of the normal stem. The probable explanation of this is that owing to the shortening of the stem axis, nodes are cut more frequently. In the gall cortex there are also narrow, elongated, glandular cavities, that do not seemingly correspond to anything seen in the normal stem. They require further elucidation. They are in groups each containing three or four glands, as illustrated in Fig. 19.

Summary.

The galls are all of a comparatively simple type, for while there is considerable proliferation in the tissues there is little differentiation. The medullary rays and vascular bundles respond the most readily to the gall stimulus, yet cell division takes place in the epidermis of the species *Stagmatophora ceanothiella* Cosens.

The highly specialized habits of the larva, developed in caring for the welfare of the imago, make the group very interesting. Thus in each of the forms studied provision is made by the larva for the emergence of the moth from the gall. These habits are seen at different stages of development. In *Stagmatophora ceanothiella* Cosens and *Eucosma scudderiana* Clemens the gall wall is simply gnawn partly through, while in the Gnorimoschema genus an aperture of exit is carefully prepared and plugged. These different methods of procedure are remarkably suited to the habits of the insects. In the former a plugged exit would not be suitable as the insect winters in the larval condition and the drying of the gall would prevent the plug from slipping out easily. In the latter the galls are still green when the insect becomes mature and the plug mechanism is preferable. It is clear then that in these galls the producer

is much more active in providing for its own welfare than in the higher types and the plant renders a relatively smaller amount of assistance. As the stimulation of the animal participant becomes more effective, the plant is coerced into providing more suitable conditions for the maturing of the producer, which consequently becomes less active on its own behalf and more dependent on the host.

While glands are invariably larger in the gall tissues than in the corresponding normal stems, *Stagmatophora ceanothiella* Cosens furnishes the only example where there is a distinct increase in the number of glands.

An unusual cell division occurs in the species *S. ceanothiella* Cosens and *G. gallæasterella* Kellicott. The daughter cells are in clusters, usually four in number, clearly showing they have originated from a common progenitor. The septations between the cells are always very straight and the elongated nuclei are pressed closely against the division walls. This form of mitosis produces only a very small portion of the gall tissues in these species, but in the Dipterous gall *Neolasioptera perfoliata* Felt (Fig. 23) it originates nearly the whole mass. This form will be referred to again and the cell division illustrated in the part of this paper dealing with Dipterous galls.

As I have repeatedly found the opening through which the larva of *Eucosma scudderiana* Clemens has entered the stem, it is certain that this Lepidopterous producer always oviposits on the outside of the host, and this may prove to be true of the entire group.

ORDER DIPTERA.

The anatomy of the following species is considered:—

Order Diptera,

Fam. Cecidomyidæ.

Cecidomyia bulla Walsh.
Cecidomyia balsamicola Lintner.
Cecidomyia impatientis O.S.
Cecidomyia majalis O.S.
Cecidomyia ocellaris O.S.
Cecidomyia pellex O.S.
Cecidomyia triticoides Walsh.
Lasioptera corni Felt.
Lasioptera impatientifolia Felt.
Neolasioptera perfoliata Felt.
Rhabdophaga batatas Walsh.
Rhabdophaga strobiloides Walsh.

Fam. Trypetidæ.

Eurosta solidaginis Fitch.

The classification is as far as possible in accordance with Aldrich's catalogue of North American Diptera, Smithsonian Institute, Washington, D.C., 1905.

Cecidomyia bulla Walsh.

Hosts { *Helianthus decapetalus* L.
Helianthus divaricatus L.

"Galls found usually on the stem, often from leaf axils, occasionally on petiole and midvein of leaf, rarely on flower disc, protruding from between scales of involucre.

"The galls are attached by an ample base and are very irregular in form and position, usually somewhat compressed, varying from nearly spherical to flask and cone shaped and from equilateral triangular to spur-shaped.

"Dimensions:—The average of twenty galls was, base, 5.5 mm. thick and extending 8 mm. from stem."—Brodie.[16]

On the side of the stem from which the gall originates the vascular bundles are very irregularly arranged and elongated transversely in the direction of the gall axis. From these bundles vascular strands pass out into the gall mass. The principal part of the tissues in this gall originates from the medullary rays, as can be seen in Fig. 39. When the cortex of the stem passes into the abnormal cortex it becomes considerably thicker; this is due chiefly to the increase in size of the cells as the number of rows remains approximately the same as in the normal cortex.

Glands are found in the normal cortex of Helianthus; they are arranged in such a manner that a gland is placed opposite each fibro-vascular bundle. These glands are very much larger in the abnormal cortex of the gall. Besides these glands there are others that have not a counterpart in the normal stem. These are elongated in the direction of the gall axis and are most abundantly produced in the vicinity of the fibro-vascular strands.

There are practically only two zones represented in this gall, the epidermal and the parenchyma. The cells of the latter become slightly smaller towards the larval chamber but a well defined nutritive layer is not differentiated.

Cecidomyia balsamicola Lintner.

Host *Abies balsamea* (L) Mill.

A monothalamous gall formed by a folding of the leaf with the upper surface on the inside (Fig. 29). An enlargement ellipsoidal in shape is thus produced. The needles affected are near the apex of the stem and the galls are situated close to the base of the needles.

Dimensions:—Diameter along the leaf average 2.5 mm.; shorter diameter, average 1.5 mm.

The abnormal part of the leaf differs very markedly from the normal. The cuticle is entirely absent from the upper surface of the leaf that lines the interior of the gall. While the epidermis is uniformly thickened the normal cells have much heavier outer walls. The normal mesophyll cells are circular to widely elliptical in outline (Fig. 28), but the abnormal cells are very much elongated (Figs. 29, 30). Since the endodermis is poorly developed the mesophyll is not clearly separated from the pericycle. In this region the transfusion tissue is well represented, but the non-pitted parenchyma is not so abundant as in the normal (Fig. 31). The abnormal resin ducts are increased in size and have the protective layer irregularly developed.

In tabulated form is given a comparison of the anatomical structure of a normal leaf with one infected by the gall producer *Cecidomyia balsamicola* Lintner and one from a witches' broom produced by *Æcidium elatinum* on *Abies balsamea* (L.) Mill.

The data for the last named were obtained from Anderson.[2]

Leaf Structure.	Normal Leaves.	Affected with *Æcidium elatinum*	Affected with *Cecidomyia balsamicola* Lintner.
Cuticle	Well developed on both surfaces.	Present but less developed.	Abnormally thickened on the lower surface (outside of the gall), not developed on the upper (inside).
Epidermis	The outer are thicker than the inside walls. Both are laminated and perforated by pores.	Epidermal cells more irregular than in normal; less thickened and seldom laminated and provided with pore canals.	On the outside of the gall the epidermal cells are irregular and have uniformly thickened walls; they are not clearly laminated but pore canals are more plentiful than in the normal. The inner epidermis is not thickened.
Stomata	More numerous on the lower than on the upper leaf surface.	Like the normal but fewer on each surface.	The same as the preceding affected by the fungus.
Hypoderm	Well developed at the basal half of the leaf.	Hypodermal cells fewer, but usually larger, thicker walled and more irregular than in normal leaves.	Cells irregularly developed, invariably curved and completely filled with laminated sclerenchyma.

Mesophyll	Usually two layers of palisade parenchyma developed on the upper leaf surface. The remainder of the mesophyll consists of spongy parenchyma (Fig. 28).	No distinction between palisade cells and spongy parenchyma.	The same as the preceding in the fungus, but the cells are very much elongated in a plane perpendicular to the midrib and parallel to the epidermis.
Resin Canals	Two circular canals present. These consist of an outer layer of thick walled cells and an inner epithelial layer of thin walled cells.	Irregular; varying in form and size, on account of the absence of the layer of strengthening cells.	Resemble the normal type in shape and are the same in number, but are considerably larger and the strengthening layer consists of very irregularly shaped cells.
Endodermis	Consists of a single layer of thin-walled elliptical cells that bound the mesophyll on the inside and separate it from the pericycle (Fig. 31).	Endodermis seldom distinguishable. Cells irregular in form and size. No distinct boundary between mesophyll and pericycle.	Only a few cells differentiated and these are irregular in shape and much enlarged (Fig. 30).
Transfusion Tissue of the Pericycle.	Always present: found in two masses, one bordering each phloem area (Fig. 31).	Nearly always present.	Found in from 2-4 layers around the inner side of the endodermis. It comprises the greater part of the pericycle. The cells contain protoplasmic material (Fig. 30).
Non-pitted Parenchyma of the Pericycle	Fills between the two divisions of the bundle and projects on each side but more plentifully on the dorsal (Fig. 31).	More irregular in form and size. Larger and thicker walled than in normal.	Developed only between the bundles and in a single row along the edge of the bast (Fig. 30).
Fibro-vascular Bundle	Phloem and xylem consist of an average of 7 rows of cells. Medullary rays found between the rows.	Phloem and xylem less developed than in normal. The cells are often larger and thicker walled. Medullary rays are absent.	Phloem and xylem better developed than in the normal, the latter is more irregular. The medullary rays are absent.

Cecidomyia impatientis O.S.

Host *Impatiens biflora* Walt.

A spherical, polythalamous gall attached to the host plant by a tapering stalk. Produced by the deformity of a flower bud.

Dimensions:—Diameter at right angles to stalk axis 6 mm.

There are three well differentiated zones. Immediately inside the small celled epidermis is a mass of large thin-walled cells irregularly arranged. The walls of these cells are seldom straight but usually present a wavy outline. They diminish in size progressively, passing in from the periphery of the gall until they merge into quite a well defined nutritive zone. This tissue is illustrated in Fig. 32. In this zone the cells are very much smaller and are arranged in rows radiating out from the larval chamber. Vascular strands pass irregularly throughout the gall. There is no indication of a protective layer separating the two inner zones.

Cecidomyia majalis Bass.

Hosts { *Quercus rubra* L.
Quercus coccinea Muench.

A flat pouch-like gall on the under side of the leaf. The opening which extends the entire length of the gall is on the upper side. It is produced by a folding of the blade of the leaf; this fold is parallel with and very close to the midrib or a main vein.

Dimensions:—Along the line of its attachment to the leaf, diameter 4-7 mm.

The gall has been formed in this case by a folding of the blade of the leaf. The resulting type recalls the pouch-like form usually associated with the Eriophyidæ or more rarely the Aphididæ.

The part of the blade included in the fold has not a well defined palisade and spongy parenchyma, the mesophyll being practically uniform throughout. The cells of this region are much larger than those of the normal leaf and are placed together without intervening air spaces. At the apex of the fold the leaf blade is much thicker than at any other part of it (Fig. 27).

The epidermis that lines the interior of the fold seems to remain intact throughout all the developmental stages of the larva.

Cecidomyia ocellaris O.S.

Host *Acer rubrum* L.

A circular ridge on the under side of the leaf and a slight convexity on the upper surface constitute the chief part of this gall. In the depression the larva rests covered with a viscid fluid secretion. The effect of the stimulation extending out from this centre is shown in the different coloured concentric rings produced in the leaf blade. These colours change in the course of development of the gall through various shades of red, green or yellow.

The slight depression in the leaf blade that constitutes this gall has been produced in the following way. The part of the leaf blade that forms the bottom of the depression has remained practically normal,

but around this the blade of the leaf has become about five times as thick as the normal organ. A circular ridge is thus formed that produces a saucer-shaped hollow in the leaf blade. This can be clearly seen in Fig. 33. The cells that form this ridge are placed at right angles to the blade of the leaf, in nearly the position of the palisade parenchyma. There has been very little increase in the number of the cells, the accretion in thickness of the blade being due principally to the lengthening of the cells already present in the normal leaf.

Wherever a vein occurs in the gall, the cells are arranged in less regular rows and the individual cells are much larger and not nearly so elongated in outline. Intercellular spaces are not found in any part of the gall tissue. The feeding habits of the larvæ are such as do not necessitate the destruction of the epidermis lining the gall.

Cecidomyia pellex O.S.
Host *Fraxinus americana* L.

This gall is formed by a swelling of the blade of a leaflet on each side of the midrib, the cortex of which also undergoes a proliferation that merges insensibly with the mesophyll. Since the production of tissue is unequal on the two sides of the leaf, a folding of the blade occurs with the upper surface on the inside and the midrib at the apex. The depression thus formed constitutes the larval chamber.

Dimensions:—Along the line of the midrib 10-25 mm.

The greater part of the gall mass is produced from the mesophyll of the leaflet but a small part originates from the cortex of the midrib. The epidermal cells have not been stimulated to division. It is possible to determine the origin of the cellular elements from the circumstances that in the gall, as in the normal leaf, the veins mark the boundary between the palisade and the spongy parenchyma. About two-thirds has originated from the spongy parenchyma and the remainder from the palisade layer. The greater amount of tissue thus produced from the lower surface causes the folding of the leaflet with the sinus of the fold above.

The cells produced from the spongy parenchyma are several times larger than the normal. They constitute a tissue in which intercellular air spaces are entirely lacking. On the other hand, the cells that owe their origin to the palisade parenchyma, while larger than the normal cells, are considerably smaller than those originated from the spongy parenchyma. The latter with their epidermal covering constitute the nutritive layer of the gall. Near the surface of this tissue, where the larvæ are feeding, the cells have initiated divisions; here too they show signs of collapsing.

Cecidomyia triticoides Walsh.

"On *Salix cordata* Muhl. A polythalamous woody gall .70-1.23 inch long and .30-.37 inch in diameter, bearing a remote resemblance to a head of wheat with the kernels elongated, naked, pointed and very protuberant, its general outline oval or elongate-oval, and formed by the swelling of a twig to 2 or 3 times its former diameter, the swelled portion being very much contracted longitudinally, so as to bring each kernel-like bud nearly or quite into contact with the base of the one that precedes it in the same row, the whole number being arranged in four irregular rows."—Walsh.[44]

The larval chambers in this gall are placed usually along the line of the fibro-vascular bundles of the stem, and wherever a chamber is situated the vascular tissues are not developed.

An examination of a young stage of this gall shows that nearly the whole of the pith and cortex of the stem consists of a well defined aeriferous tissue. It is absent in only a few cell layers that surround the larval chambers. Represented in Figs 34, 35, 36. At this stage there is a well differentiated protective sheath, of about five cells in depth, around each larval cavity. The cells of this layer have uniformly thickened walls and are arranged in concentric rows around the larval chamber. Each cell of this zone contains either a crystal aggregate or a well defined single crystal of calcium oxalate. Inside of this protective sheath is a nutritive layer which consists of about six rows of thin-walled cells. The cells of this zone have the same tangential arrangement as those of the protective sheath. Many of them are empty, this being especially the case in the innermost row. Likewise, many are commencing to collapse on account of the withdrawal of their contents. These zones are represented in Fig. 38.

A section of a gall at a much more advanced stage of development presents several important differences. The aeriferous tissue is very much compressed in the pith and somewhat in the cortex. The cell walls of the protective zone are now much thicker, and a well defined crystal of calcium oxalate completely fills the lumen of each cell (Fig. 37).

Weidel[45] has recorded a phenomenon similar to this occurring in the gall *Andricus corticis* Hart.

"Oft ist das ganze an sich schon grosse Zellumen durch einen einzigen Kristall ausgefüllt, dem anscheinend so ansehnliche Zellulosemassen späterhin waren sie verholzt, aufgelagert worden sind, dass diese die Wand des Behälters erreicht haben und mit ihr verwachsen sind."

My observations differ in one respect from Weidel's, namely, there is no ensheathing mass of cellulose around the crystals found in the gall dealt with here. In deciding this point tests were made at different stages with Schulze's solution.

There is a cambium layer lying just outside the protective zone in the later stages. The nutritive layer consists of a mass of collapsed cells that stain deeply with hæmatoxylin. These layers are shown in Fig. 37.

Lasioptera corni Felt.

Hosts { *Cornus alternifolia* L.
Cornus paniculata L'Her.

This gall appears on the upper side of the leaf as a circular elevation but does not project on the under side.

The colour is entirely green when young but becomes surrounded by a circle of red at later stages.

In anatomical structure the tissues that compose this gall are the same as those in the normal leaf.

The lower epidermis and the row of mesophyll cells immediately in contact with it remain in the normal position. The upper epidermis and the remainder of the mesophyll become arched and thus separate from the lower epidermis and the part of the mesophyll that adheres to it in the manner shown in Fig. 40. In the space thus formed the larvæ are found.

Lasioptera impatientifolia Felt.

Hosts { *Impatiens biflora* Walt.
Impatiens pallida Nutt.

A monothalamous gall, projecting chiefly from the under side of the leaf. It consists of an elongated, spindle-shaped swelling of the midrib.

Dimensions:—Longer diameter 8-12 mm.
Shorter diameter 3-4.5 mm.

Practically all the abnormal tissue in this case is produced from the cortex of the midrib of the leaf. The stimulation has extended out only a very short distance into the adjoining mesophyll. The general mass of gall tissue consists of large cells with a few small intercellular air spaces. The epidermal cells are larger than those of the normal epidermis, their increased length being particularly noticeable. The features are shown in Fig. 41.

A nutritive layer is not differentiated.

Neolasioptera perfoliata Felt.

Host *Eupatorium perfoliatum* L.

A spindle-shaped swelling of the stem forming a monothalamous gall. It varies in size in proportion to the diameter of the stem or branch from which it originates.

It may be stated as an almost invariable rule, that when a gall and the plant organ from which it originates have a common epidermis the cell walls of that epidermis are thicker in the area covering the gall than

elsewhere. But this gall is an exception to the rule. While the outer walls of the epidermal cells are considerably thickened in the normal they are much less so in the gall. Also the two layers of collenchyma cells underlying the epidermis in the normal stem are absent.

The increase in size of the stem where the gall is situated is due principally to increased cell division in the cortex, since the epidermis produces only two additional layers. The cells produced in the cortex are larger than the normal, but the most peculiar feature to be noted is the mode in which division has taken place and the relative arrangement of the products of division. The location of this tissue is illustrated in Fig. 23. The method of cell division is clearly the same in this species as in the two Lepidopterous types *Stagmatophora ceanothiella* and *Gnorimoschema asterella*. The clusters contain from 2 to 6 members produced from a single cell. The dividing walls are straight, and at the stage examined had the greatly elongated nuclei in close contact with them. These nuclei were seldom exactly opposite but usually diagonally across from one another. These characteristics are represented in Fig. 23. Schürhoff[41] has described the mode of division in callus, contrary to the views in vogue, he states that the nuclei divide mitotically only. There is good reason to believe that the phenomena observed here correspond very closely to those given in his account.

Near the inner edge of the cortex, glands are regularly spaced around the stem. This is a rather remarkable fact as they do not occur normally in this part of the stem. Indeed it was only after a careful search that they were located in the transition region between root and stem. The search was extended to other species with the result that they were found in *Eupatoria purpureum* L. in the roots, the cortex and the reproductive axis, but in *E. urticæfolium* Reichard as in *E. perfoliatum* L. only at the base of the stem.

Rhabdophaga batatas Walsh.

"On *Salix humilis* Marsh. A polythalamous gall of very variable shape and size, pale green when young, the colour of the bark when mature, growing on twigs .06-.19 inch in diameter and always some distance from the tip of the twig. Sometimes it resembles a small kidney-potato pierced lengthways by a twig, and has then most generally a smooth polished surface studded with a few buds, one or two of which occasionally give birth to a shoot, and it then reaches 1.35 inch in length and .6 inch in diameter. Sometimes it resembles a young apple pierced lengthways by a twig and attains a diameter of .3 inch."—Walsh.[44]

In this gall the larval cells are situated in the pith of the host plant, just inside the line of the fibro-vascular bundles. The epidermis has a much thicker cuticle than that borne by a normal stem of corresponding

age. The cortex is approximately four times as thick as the cortex of the normal stem. This is due principally to the increased size of the cells. The cells of the nutritive layer are very similar to those of the surrounding tissues but a well marked protective zone defines its outer limits. This is clearly shown in Fig. 25.

The cells of the protective zone present a characteristic very rare in Dipterous galls, although frequently found in the Cynipid galls, namely, the walls of the cells are not uniformly thickened but are much heavier on the side next the nutritive zone. This unequal sclerification is illustrated in Fig. 26. Crystals of calcium oxalate, that were so characteristic a feature of this zone in *C. triticoides* Walsh, seem to be entirely absent in this gall.

Rhabdophaga strobiloides Walsh.

Host *Salix cordata* Muhl.

"The galls are very uniform in size and form, usually top-shaped, some inclining to spherical, a little oblate below and prolate above, and as the female oviposits but one egg in the terminal bud of the willow shoot, the galls are terminal and monothalamous.

"The gall is a rather tightly and regularly arranged mass of from 70 to 80 aborted leaves, representing perhaps about 1 m. of the leafage of a normal branch.

"The average measurement of 200 galls was 12 mm.×15 mm., and the length of the deformed part of the branch included in the gall around which the aborted leaves were packed was 6 mm."—Brodie.[18]

The leaves that constitute the principal mass of this gall do not take any part in supplying the larva with food. The tissue that has this function is composed of a mass of small, thin-walled cells. It terminates the stem axis and the larva is in immediate contact with it (Fig. 24). This tissue which really furnishes a nutritive layer seems to originate from a cambium-like tissue at the base of the mass of cells.

An important factor in the production of this gall is the practical cessation of growth of the bud axis.

The aborted leaves that compose the gall exhibit very slight anatomical aberrations.

Eurosta solidaginis Fitch.

Host *Solidago canadensis* L.

A monothalamous gall produced by the swelling of the stem of the host plant. Very rarely it is found on a branch of the flowering panicle. A separate gall is almost perfectly spherical in form but occasionally two are produced together forming a common gall, prolate-spheroidal in shape.

Dimensions:—Average diameter of fifteen galls, 23 mm.

The cells that compose the principal mass of this gall are slightly smaller than those of the normal pith but in other respects they resemble them very closely. The irregularity in position of the fibrovascular bundles and their imperfect development are well marked features. Yet a sufficient water supply is ensured to the tissues by vascular strands that are given off from the bundles. These strands extend in a radial direction towards the centre of the gall.

The cortex is considerably thicker than that present in the normal stem. This is due in part to the greater number of cell layers, but also to an increased size.

The glands that are present in the normal stem of *Solidago canadensis* L. occupy certain fixed positions. One gland is present in the cortex outside each bundle and one inside in the region of the pith. The glands found in the cortex of the gall are very much enlarged and have not their characteristically regular arrangement. In the gall pith they are abundant throughout (Fig. 42), but decidedly more plentiful in the vicinity of the fibro-vascular strands. This is the most striking example of gland proliferation found in the galls studied.

The tissues that supply the larva with food are not differentiated into a nutritive zone.

Summary.

The galls produced by this order of insects vary very much in their degree of complexity. Some forms such as *Cecidomyia ocellaris* O.S. are as simple in structure as an Acarina, "Dimple", gall; other species as *Rhabdophaga batatas* Walsh present all the specialized anatomical characteristics of a Cynipid gall.

The abundant production of glands in tissue under stimulation is very clearly exemplified in *Eurosta solidaginis* Fitch. At first sight it appeared as if glands were not present in the host of *Neolasioptera perfoliata* Felt, but they were located at the base of the stem and in other species of Eupatoria.

The unequal thickening of the tangential walls of the sclerenchyma protective layer in *Rhabdophaga batatas* Walsh is a very unusual phenomenon in this group.

Cecidomyia triticoides O.S. is the only gall of this group in which a well defined crystal layer was found. In it each cell lumen is entirely filled with a single crystal of calcium oxalate.

The production of the aeriferous tissue, that occupies practically the entire pith in the gall *Cecidomyia triticoides* Walsh, is one of the most interesting phenomena exhibited in this group. The nature of this will be discussed in the biological section of the paper.

The collapsing of the nutritive zone after the cell contents are withdrawn is well exemplified in *Cecidomyia triticoides* Walsh (Fig. 37).

The unusual type of cell division in the cortex of the hosts infected by certain Lepidopterous forms, e.g. *Stagmatophora ceanothiella* Cosens and *Gnorimoschema gallæasterella* Kellicott and described in that group, is also found in the Dipterous gall *Neolasioptera perfoliata* Felt (Fig. 23). It was not found in any Cynipid form.

A comparison of a leaf of *Abies balsamea* (L.) Mill infected by *Cecidomyia balsamicola* Lintner with one from a witches' broom produced on the same host by *Æcidium elatinum* (*Melampsora Caryophyllacearum*) brings out a number of interesting points. These are given in the tabulated form following the description of the species *C. balsamicola* Lintner.

ORDER HYMENOPTERA.

Following Marlatt's Revision of the Nematinæ of North America, U. S. Dept. of Agriculture, Washington (1896), the species considered in this paper are comprised in the Subfamily Nematinæ, Family Tenthredinidæ. They are included in two genera, Pontania and Euura. The species referred to are:—

Euura S. gemma Walsh.
Euura S. ovum Walsh.
**Euura* (undescribed).
Pontania pisum Walsh.
Pontania pomum Walsh.
Pontania desmodioides Walsh.
Pontania hyalina Norton.
**Pontania* (undescribed).
*Gall on *Salix lucida* (undescribed).
Gall on *Salix humilis* (undescribed).

*Specimens of the first three producers marked (undescribed) were sent to S. A. Rohwer of the Smithsonian Institution.

I have been successful in rearing the producers of all of the undescribed forms except in the case of the one on *S. humilis* Marsh. This was accomplished in the following manner. The galls were collected at the time of the falling of the leaves of the host plants and were placed on earth in breeding jars which were kept under conditions of heat and moisture approximating as closely as possible to that of the natural habitat. Pupation took place at a distance of about a couple of inches below the surface of the soil and the adults emerged the following spring. The dates of emergence were:—

Pontania (undescribed), April 14 to April 24.
Euura (undescribed), May 2 to May 6.
Gall on *S. lucida* (undescribed), April 20 to April 22.

*While this paper was in press, Rohwer[46] published the description of these producers. Following the order above the names assigned are,—*Euura serissimæ* Rohwer, *Pontania crassicornis* Rohwer, *P. lucidæ* Rohwer.

The close restriction of sawfly gall producers to definite species of Salix can be illustrated by means of the forms mentioned in this paper. The host plants of the species are:—

Euura S. gemma Walsh
Pontania desmodioides Walsh
Pontania (undescribed)
found on *Salix humilis* Marsh.
Pontania hyalina Norton
on *S. alba* L.
Pontania pomum Walsh
on *S. cordata* Muhl.
Euura (undescribed)
on *S. serissima* Fernald.
Gall (undescribed)
on *S. lucida* Muhl.
Pontania pisum Walsh
on *S. discolor* Muhl.

In this locality I have not found the above species on any other host than that mentioned. When the type of gall is higher it would seem to be axiomatic that the relations between the host plant and producer would be more intimate than when the gall does not stand so high in the scale and as a consequence the restriction to one host plant would be a necessity. Yet the galls produced by the Cynipidæ are often found on two or three different hosts; as, for example, *Amphibolips inanis* O.S. on both *Quercus rubra* L. and *Q. coccinea* Muench, *Dryophanta palustris* O.S. on *Quercus rubra* L. and *Q. coccinea* Muench. *Aulax nabali* Brodie on *Prenanthes alba* L. and *P. altissima* L.

Euura S. gemma Walsh.

"On *Salix humilis*. The lateral bud of a twig enlarged so as to be twice or thrice as long, wide and thick as the natural bud before it begins to expand in the spring; its external surface otherwise entirely unchanged both in texture and colour. Internally, instead of the normal downy embryo leaves, it contains early in the autumn a homogeneous grass-green fleshy matter, which is afterwards gradually consumed by the larva, leaving nothing at last but a mere shell partly filled with excrement. The gall is monothalamous, sometimes one only on a twig, sometimes two or three or more at irregular intervals, very rarely as many as three or four formed out of three or four consecutive buds.

Length .17 to .36 inch

Breadth .10 to .17 inch.—Walsh.[44]

The anatomy of this gall presents little differentiation of tissue. A cross section shows that the entire mass of the gall consists of small

thin-walled cells, shown in Fig. 68. The bud scales surrounding this group of cells resemble those of the normal bud except that the cuticle of the epidermis is abnormally thickened.

Euura S. ovum Walsh.

"On *Salix cordata*. An oval or roundish, sessile, monothalamous swelling, .30 to .50 inch long, placed lengthways on the side of small twigs, green wherever it is smooth, but mostly covered with shallow longitudinal cracks and irregular rough scales which are pale opaque brown. Its internal substance fleshy in the summer like that of an apple, but with transverse internal fibres. When ripe in the autumn filled with reddish-brown spongy matter, with close-set transverse internal fissures at right angles to the axis of the twig. On cutting down to the twig at any time a longitudinal slit about .20 inch long becomes plainly visible."—Walsh.[44]

As already noted the host of this gall in this locality is *Salix humilis*, it remains to be determined whether there are two distinct species of producers or one species with two hosts. Walsh's description of the gall on *Salix cordata* corresponds to the form occurring here on *S. humilis*.

The ovipositor of the producer has in this case made a longitudinal cut in the stem. A transverse section at the place where the gall is located shows that this wound extends in from the epidermis to the boundary of the pith. The activity of the young tissues, abnormally stimulated, soon fill this fissure with a mass of small, angular parenchyma. The rapid division of these cells forces the exposed edges of the cortex and central cylinder apart so as to form a wedge-shaped opening which is filled up with the gall mass (Fig. 71). It should be stated that the newly formed cells originate mainly from the division of a cambium bordering the pith at the bottom of the fissure. But other tissues also respond to the stimulation initiated by the ovipositor of the insect. Thus a section of the stem at a short distance from the gall shows that the outlying cambium has become abnormally active and has produced a layer of bast nearly one-third thicker than that found in the normal stem. Likewise the activity of a cork-cambium layer has thrown off a strongly cuticularized epidermis present in the earlier developmental stages.

Undescribed Sawfly Gall (*Euura N.S.*) on *Salix serissima* Fernald.

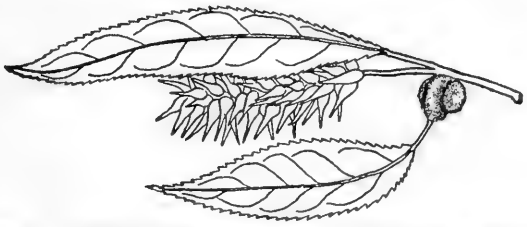

Fig. 1.—A nearly mature gall attached to a leaf of the host plant.

This gall is produced by the abnormal swelling of the petiole of the leaf. The leaves infected are those borne on the branchlets from which spring the pistillate catkins. In the majority of cases, the leaf that bears the gall is the one from the axil of which the peduncle of the catkin arises. The swelling is so close to the branchlet that after the leaves have fallen, the gall appears to have originated from it. This misleading appearance is due to the petiole of the leaf breaking just above the gall. The galls are cone-shaped with the apex towards the blade of the leaf. They are marked deeply by three or four grooves that meet at the tip.

Dimensions:—Height of gall 7-8 mm.; diameter at base 6-7 mm.

The anatomy of this gall presents a very compact tissue, owing to the cells being placed close together without intervening air spaces. The very much thickened cuticle of the epidermis is the greatest departure from the normal tissue. Of the three bundles of the normal petiole two are lacerated by the ovipositor of the insect, as shown in Figs. 69, 70. In the mature gall the halves of these two are found in four widely separated regions (Fig. 69), owing to the abundant production of tissue between them. Indeed practically all the abnormal tissue is produced from the undifferentiated cells stimulated by the cutting of the bundles.

Pontania pisum Walsh.

"On *Salix discolor*. A subspherical, pea-like, hollow, pale yellowish-green gall, always growing on the under side of the leaf and almost always from one of the side veins (in one case from the midrib), and attached to the leaf by only a minute portion of its surface; 0.18 to 0.28 inch in diameter and a few miniature, only 0.08 inch in diameter. Almost invariably there is but one gall to the leaf, but on four leaves there were two, and occasionally two are confluent. Surface in some smooth and even without pubescence; in others a little shriveled, generally studded in the medium-sized ones with four to twelve small, robustly conical nipples, which in the larger ones have burst into a scabrous brown scar. Only in three out of sixty-two was there any rosy cheek as in *P. pomum*. The point of attachment is marked on the upper side of the leaf by a brown sub-hemispherical depression."—Walsh.[44]

Walsh is incorrect in supposing that this gall originates from a midrib or vein. A section shows that it is clearly a product of the mesophyll and is attached to that part of the leaf. The side vein, near which it is always placed, is cut by the ovipositor, however, and vascular strands pass out from it into the gall body.

The mature gall consists of a peripheral layer of thin-walled cells, irregular in outline surrounding a central cavity (Fig. 81). This tissue is clearly derived from the mesophyll and epidermis of the leaf, but a stage was not secured young enough to show the relative amounts

produced from each. The epidermis bears numerous lenticels, organs which Küster[35] mentions as occurring on the gall produced by *Pontania salicis*.

At the point of attachment of the gall the blade of the leaf is strengthened by several rows of cells derived from the upper epidermis and the palisade parenchyma, as shown in Fig. 81. These cells seem to have remained unmodified in any way, since their arrangement in rows is still clear in fairly old stages of the gall. Consequently they differ very markedly from the irregularly arranged cells of the main part of the gall body.

Pontania pomum Walsh.

"On *Salix cordata* (and very rarely on *S. discolor*). A smooth, fleshy, sessile, globular or slightly oval, monothalamous gall, resembling a miniature apple, .30 to .55 inch in diameter, growing on one side of the midrib of a leaf, and extending to its edge or sometimes a little beyond it. The principal part of the gall generally projects from the under side of the leaf, and only about one-sixth of its volume from the upper side, although very rarely it is almost equally bisected by the plane of the leaf. Scarcely ever more than one gall on a leaf and very rarely two of them, more or less confluent so as to seem like one kidney-shaped gall. External colour greenish-yellow, generally with a rosy cheek like an apple especially on the upper surface and often with many dark little dots on its surface."—Walsh.[44]

The ovipositor of the producer of this gall has been thrust laterally through the midrib of the leaf into the mesophyll. The wound has completely severed the bundle of the midrib, as seen in Fig. 76.

The full-grown gall presents an epidermis with a very thick cuticle. The remainder of the gall consists of a complex of thin-walled cells arranged so as to constitute a typical aeriferous tissue (Fig. 77). A similar arrangement of cells is not found in the normal leaf, the mesophyll of which consists of a fairly compact tissue. The vascular strands growing out from the wounded bundle form a complete ring around the gall, situated about half way between the epidermis and the centre.

I was successful in obtaining this gall at such an early stage that the egg membrane was still unbroken (Fig. 76). This phase shows that the epidermis, the palisade and the spongy parenchyma mutually take part in the gall production. Counting along a line passing through the centre, four of the cell layers are seen to have arisen from the lower epidermis and six from the upper, eight from the palisade and fifteen from the spongy parenchyma of the leaf. Hence it is noteworthy that the new tissues are not the product of a cambium but have been contributed to by every morphological region of the leaf. The cells that are

produced at this stage are in rows generally in exact alignment with the cells from which they have arisen. They thus do not have the arrangement of the aeriferous tissue of later stages to which they give rise. The cuticle, so marked a feature of the older stages of the epidermis, is exceedingly thin. The epidermis bears trichomes springing from the bottoms of deep pits (Fig. 76). This condition has arisen through the circumstance that the primary epidermal cells from which hairs have grown out have not experienced the periclinal divisions participated in by their fellows and so have been left far below the general surface as shown in the text fig. below.

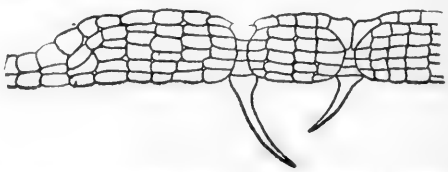

Fig. 2.—Hairs originating from pits in the epidermis of *P. pomum* Walsh.

Pontania desmodioides Walsh.

"On *Salix humilis*. A smooth, flattish, fleshy, sessile, yellowish-green monothalamous gall of a semicircular outline, the chord of the semicircle adjoining the midrib of a leaf; its general shape like the seed of a Desmodium or like the so-called "quarter" of an orange, the thin inside edge of the "quarter" closely hugging the midrib of the leaf, and the robust outer surface not biangulated but rounded off. No rosy cheek. The volume of the gall is generally about equally divided between the upper and lower sides of the leaf but sometimes the lower portion is rather the larger. Usually there is but a single gall on a single leaf, but occasionally there are two of them, either on the same side or on opposite sides of the midrib."—Length .23 to .50 inch Walsh.[44]

When mature this gall shows in cross section a cavity surrounded by a peripheral layer of little differentiated tissue. The epidermis has given rise to a very thick cuticle that is not present in the normal leaf. The bundle of the midrib has been injured only slightly by the ovipositor of the producer. The vascular strands given off from it almost encircle the gall along a line half way in from the epidermis.

A stage of the gall so young that the larva was unhatched shows the gall tissue to have been produced by cell division in the upper epidermis, the spongy parenchyma and the palisade parenchyma of the normal leaf (Fig. 80). At the thickest part of the gall, when it is in this stage, the upper epidermis has produced four layers of cells, the spongy and palisade parenchyma seven layers each. The lower epidermis has not divided as yet, and probably takes no part in the production of the

gall. The abnormal cells from the palisade parenchyma show clearly their origin by their arrangement in rows at right angles to the surface of the leaf. The cells produced by the spongy parenchyma, on the other hand, are not regularly placed but include air spaces. The result is that the abnormal tissue in this case also resembles the normal tissue from which it is derived.

This stage of the gall shows that the cavity present in the mature gall has arisen between the tissue produced by the spongy and that derived from the palisade parenchyma of the normal leaf.

Pontania hyalina Norton.

"Fleshy galls occurring in two parallel rows, one on either side of the midrib, sometimes touching but not originating from the latter, and rarely extending to the edge of the leaf; sometimes as many as twenty on a single leaf; in other cases confined to a row on one side of the leaf or occasionally occurring singly; shape irregular elongate-ovate, projecting equally on both surfaces of the leaf; length 7 to 10 mm.; the abortive ones smaller. Colour on upper side more or less brownish red; beneath white, with slight purplish tinge."—Marlatt.[37]

The anatomy of this gall presents scarcely any differentiation of tissue. When mature it consists of a mass of thin-walled chlorophyll-bearing cells, the innermost of which are arranged in rows almost at right angles to the blade of the leaf, as seen in Fig. 75. Cells are so much alike that they afford no clue as to their origin.

Again I was able to obtain material so young that the larva was still confined within the egg membrane (Figs. 73, 74). It shows that the spongy parenchyma, the palisade parenchyma and the epidermis of the normal leaf were jointly concerned in the production of the abnormal tissue. The spongy parenchyma has contributed nearly half of the entire mass, the epidermes three layers each, and the row of cells immediately overlying the lower epidermis three layers. The remainder has been derived from the palisade parenchyma.

Undescribed Sawfly Gall (*Pontania N.S.*) on *Salix humilis* Marsh.

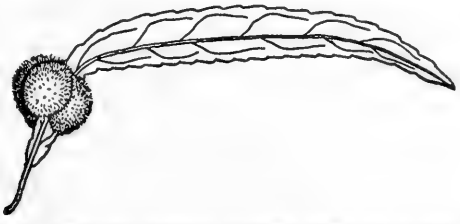

Fig. 3.—Two galls attached on opposite sides of the midrib.

This is a monothalamous gall found on the leaves of *Salix humilis*.

It is spherical in shape and in that feature resembles *P. pomum*, but in other respects it differs very markedly. It extends from the side of the midrib almost out to the margin of the leaf and is divided into two hemispheres by the leaf blade. In consequence the gall protrudes nearly equally from each leaf surface. Usually there are two or three galls on a leaf. When two are present they come in contact with the midrib at the same place but on opposite sides, as illustrated in Fig. 79. In a few cases four and even five galls were found on one leaf. The galls are pubescent but not as densely as the under surface of the leaf.

Dimensions:—Average diameter 1 cm.

The mesophyll of the leaf and the upper epidermis are mutually concerned in the production of this gall. In one, sufficiently immature to show the relative amount of tissue arising from each source, it was found that the upper epidermis had produced two cell layers, while the lower had not responded to stimulation; and that the palisade and spongy parenchyma had each produced one-half of the remaining mass. The hollow in the gall, present from the earliest stages, has been formed between the tissue arising from the palisade and the spongy parenchyma respectively.

When only one gall originates from the midrib at any point, the vascular bundle is cut approximately half through (Fig. 78). But more frequently two galls are located opposite one another, one on each side of the midrib, in which case the two incisions meet and completely sever the bundle, as seen in Fig. 79.

Vascular strands pass almost completely around the gall, along a line half way between the epidermis and the gall cavity. These strands originate from the midrib in the neighborhood of the injury and pass in opposite directions.

Undescribed Sawfly Gall on *S. lucida* Muhl.

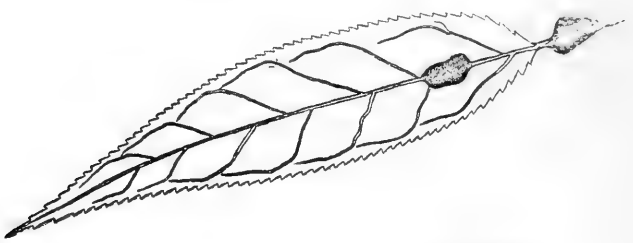

Fig. 4.—Two galls produced on the same leaf of the host.

This gall consists of an enlargement of either the petiole or midrib of *S. lucida*. Neither of these organs bears, as a rule, more than one gall

at a time, but occasionally the petiole of a leaf carries two or even three and the midrib in rare instances two.

The midrib galls are fairly regularly elliptical in outline with the shorter diameter across the leaf. The swellings in most cases are nearly equally divided between the upper and the lower leaf surfaces. The petiole galls vary from spherical to ovoid in shape. In the latter case the smaller end of the gall is towards the apex of the leaf.

Dimensions of the gall:—Longer diameter 6-12 mm.; shorter diameter 3-7 mm.

The very marked proliferation of tissue in this gall is not accompanied by a differentiation that presents many points of interest. The cells are larger than those of the normal leaf and the nuclei are correspondingly larger. The bundle is cut nearly through by the ovipositor (Fig. 82). The free ends of the bundle thus stimulated grow out until in some cases they almost surround the gall. This elongation is produced in part by the increased diameter of the vessels but also by the production of new cellular elements.

The pith, exposed by the cutting of the bundle, produces almost all the abnormal tissue (Figs. 83, 84), but the cortex contributes some. The cells are arranged in curved lines that pass across from one elongated end of the bundle to the other. Between these rows are many air spaces which are elongated in the direction of the lines of cells (Fig. 84).

Undescribed Sawfly Gall on *Salix humilis* Marsh.

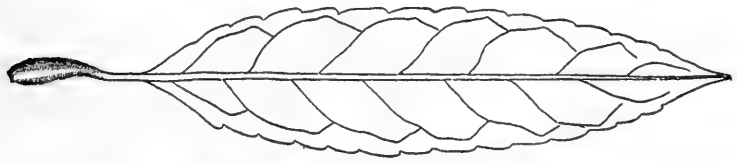

Fig. 5.—Leaf of the host with attached gall.

This is a monothalamous gall produced by the abnormal swelling of the leaf petiole of S. *humilis*. It is conoidal in shape with a long tapering apex which is towards the blade of the leaf. As it is situated at the base of the petiole the uniform enlargement of that organ is often prevented by the axillary bud. This causes the gall to project to a greater extent on the outside of the petiole and produces an irregularity in the outline of the gall. The surface is quite glabrous in spite of the fact that the epidermis of the leaf is decidedly pubescent.

Dimensions:—Length of gall 6-9 mm.; width 3-4 mm.

Nearly the entire mass of this gall originates from the vascular bundle of the petiole which has been stimulated to activity by the insect's ovipositor. The small thin-walled cells of the gall substance

spring from a cambium layer produced in the pith of the bundle near the ovipositor wound. The cells arising from this tissue force the severed ends of the bundle apart until the vascular elements form only a narrow line of cells between the gall proper and the cortex of the petiole; it is shown at this stage in Fig. 85. This cortex is not materially thickened but shows signs of stimulation in that there appears a small amount of aeriferous tissue located near the place of entrance of the ovipositor. This tissue is shown on each side of the wound in Fig. 85. This tissue was not found in the normal cortex of the petiole. The cuticle is very much thickened.

Summary.

Great proliferation of tissue with little differentiation is a common characteristic of all sawfly galls.

All the leaf tissues of the genus Salix appear to be susceptible to stimulation by sawfly producers.

The pith of the bundle produces practically the whole mass of the gall when the place of origin is the petiole or the midrib of the leaf. In the case of a stem gall a layer of cells bordering the pith produces the chief proliferation.

When the gall originates from the mesophyll of the leaf the bundle of the midrib produces relatively only a very small part of the total gall mass.

Of the remaining tissues of the leaf the upper epidermis responds more readily to stimulation than the lower and the spongy parenchyma more actively than the palisade parenchyma.

In some cases the abnormal tissues exhibit the characteristics of the normal from which they have originated. The cells produced to form a solid base of attachment for the gall *Pontania pisum* Walsh never lose their arrangement in vertical rows, and the cells that originate from the same tissue in *P. desmodioides* Walsh are also in vertical series (Figs 80, 81).

Adler[1] secured specimens of *Nematus vallisnierii* in which the larva was still within the egg. I have been equally fortunate with the species *Pontania pomum* Walsh, *Pontania hyalina* Norton and *Pontania desmodioides* Walsh. At this early developmental stage considerable proliferation of tissue had already occurred. Adler even reports that the gall was nearly full grown. My experience has been that the larvæ are invariably found feeding unless the material is secured almost as soon as the galls are visible to the unaided eye. At this time little swelling of the leaf tissues is apparent, but a discoloration of the leaf enables the wound of the ovipositor to be detected. Owing to cell proliferation preceding the emergence of the larva, Adler concluded that the immediate

cause of cell activity, productive of sawfly galls, is the wound caused by the act of ovipositing. But there is a slight possibility that secretions or excretions from the developing larva may be active through the egg membrane.

The protective sclerenchyma sheath of the more advanced types of galls is absent in this group, and the only protective device appears to be the cuticularizing of the epidermis and the presence of tannin in the cells. The cuticle has also a more important function in preventing the desiccation of the underlying thin-walled tissues of the gall.

The possible significance of the aeriferous tissue found in *Pontania pomum* Walsh will be discussed later in this paper.

Lenticels on galls seem to occur very rarely. They were found in this group only in the one species, *Pontania pisum* Walsh, a leaf gall.

The restriction of the various species in many cases to single hosts seems noteworthy when the minor specific differences between the members of the Salicaceæ are considered.

A series of the undescribed species of Euura on *Salix serissima* Fernald furnished undoubted examples of cell proliferation produced by the excrement of the larval producer (Fig. 72). This fact is discussed in the biological section of the paper.

LOCALIZATION OF TANNIN-BEARING TISSUE IN SAWFLY GALLS.

Küstenmacher[33] has discussed the question of tannin in certain Cynipid galls and Cook[22] has detected it in different stages of a number of galls, but no attempt has been made up to the present to work out its distribution in the family Tenthredinidæ.

Pontania pomum Walsh.

Tannin-containing cells are abundant in the epidermis of this gall. They are found also in the "Aeriferous tissue," but are not so numerous there. They are plentiful in the vascular strands, but can scarcely be demonstrated in the tissue next the larva.

In the normal leaf of *Salix cordata* Muhl. these cells are abundant, especially so in the vascular tissue and the epidermis.

Undescribed Pontania Gall on *S. humilis* Marsh.

Tannin-containing cells are very plentiful in the epidermis and in six or seven rows of cells that immediately underlie that tissue. They are also present in the vascular strands and in the tissue next the larva.

In the normal leaf of *S. humilis* Marsh these cells are not present in the epidermis of the midrib but are found in the bundle of the midrib especially in the bast portion.

Pontania hyalina Norton.

Tannin cells are found abundantly in the epidermis and in the gall tissue generally, except the cells on which the larva is feeding.

In the normal leaf of *S. alba* L. on which this gall is found, these cells are not present in the epidermis of the midrib but are plentiful in the wood and bast of the bundle.

Pontania desmodioides Walsh.

Tannin cells are plentiful in the epidermis and in the underlying tissue, but gradually diminish in number in the tissues nearer the larva.

This gall also is found on *S. humilis* Marsh.

Undescribed gall on petiole of *Salix lucida* Muhl.

Tannin cells are found practically all through the tissues of the gall, but tannin is most plentiful in the epidermis and in the petiole that is involved in the gall swelling.

Tannin cells are found throughout the normal petiole except in the parenchyma tissue immediately underlying the epidermis.

Conclusions concerning Tannin-bearing Tissue.

(1) Tannin is more plentiful in gall tissue than in the normal tissue from which it originates.

(2) In gall tissues it is most abundant in the epidermis and the bast.

(3) It is more abundant in the older than the younger stages of galls.

(4) It does not appear to function as food for the larvæ as the tannin cells are less abundant in the tissue on which the larvæ feed.

(5) As tannin is always plentiful in the gall epidermis it may serve for protection by rendering the gall tissues unpalatable.

Technique used in Testing for Tannin.

The test substance used was a saturated solution of ammonium chloride saturated with ammonium molybdate.

Razor sections of the galls were used for testing.

NOTES ON OVIPOSITING BY SAWFLY GALL PRODUCERS.

Pontania hyalina Norton.

The leaves of *Salix alba* L. are folded in the bud with the under surfaces towards the outside. The ovipositing takes place before the leaf selected has separated from the others in the same bud. As a consequence of this the ovipositor is inserted from the ventral surface of the leaf (Fig. 74).

May 27th, 1911.—On this date a producer was observed ovipositing in young leaves, but other leaves on the same stem lower down bore galls that were almost full size.

June 3rd and 4th.—On these dates producers were seen ovipositing.

June 18th.—Producers ovipositing.

August 11th.—Galls were found in which the ovipositing could have taken place only a few hours before. The ovipositing in this species must continue over a period of at least two months.

Pontania pomum Walsh.
Pontania desmodioides Walsh.

These producers begin to oviposit at about the same date as the above species. The period of ovipositing must comprise a comparatively short space of time as the galls of these species are all at about the same stage of development on the same date.

The galls produced respectively on *Salix cordata* Muhl. and *Salix humilis* Marsh. by these producers are not found near the tips of the young stems, but the galls on *Salix alba* L. produced by *Pontania hyalina* Norton are found on leaves along the whole length of the young stems. This difference in the location of the galls is caused by the period of ovipositing being much longer in *Pontania hyalina* Norton than in the other two species.

The first effect of ovipositing by *Pontania pomum* Walsh, visible to the unaided eye, is a dark red colour produced in the leaf blade surrounding the spot where the ovipositor has entered. This colour is also visible for a short distance along the midrib of the leaf. When the gall is opened at this stage the egg of the producer can be found with the aid of a lens. It is elliptical in outline and of pearly lustre. The membrane is translucent and the egg contents can be distinguished through it.

ORDER HYMENOPTERA.

Whenever possible the specific names have been selected from the monographs by Wm. Beutenmuller,[5-14] that are now being issued from the American Museum of Natural History, New York. These publications give full synonymy and bibliography of the different species.

The following species are here described:—

Fam. Cynipidæ.

Holcaspis globulus Fitch.
Holcaspis bassetti Gillette.
Philonix erinacei Beut.
Philonix hirta Bassett.
Philonix nigra Gillette.
Amphibolips confluens Harris.
Amphibolips inanis O.S.
Dryophanta palustris O.S.
Andricus imbricariæ Ashmead.
Andricus singularis Bassett.

Andricus piger Bassett.
Andricus petiolicola Bassett.
Andricus (undescribed).
Rhodites multispinosus Gillette.
Rhodites lenticularis Bassett.
Rhodites ignotus O.S.
Rhodites bicolor Harr.
Rhodites gracilis Ashm.
Rhodites nebulosus Bassett.
Cynips? constricta Stebbins.
Solenozopheria vaccinii Ashm.
Aulacidea nabali Brodie.
Neuroterus majalis Bassett.
Aylax glechomæ Linné (referred to the section on Cytology).

Holcaspis globulus Fitch.
Host *Quercus alba* L.

A monothalamous, spherical gall produced at the nodes of the stem of the host.

It occurs singly or in groups of from two to four. The colour is yellowish-green usually with a reddish tinge. When mature the oval larval chamber is free from the remainder of the gall. The aperture of exit of the producer is placed at the end of this larval cell.

Dimensions:—Average diameter 13 mm.

When this gall is so young that it is still soft, it has the following anatomical characteristics. The larval chamber is in organic continuity with the remainder of the gall. Beneath the small celled epidermis are four or five layers of cells with their long axes parallel to the periphery of the gall. Inside this tissue is the more typical part of the parenchyma zone. Here the cells are in radial rows forming a fairly compact tissue with only a few small air spaces. Their radial walls are more elongated the nearer they are to the larval chamber. Inside of the parenchyma zone is a poorly defined cambium tissue that passes gradually into a crystal layer. Each cell of this zone contains a large crystal mass. A second cambium tissue, in this case well defined, bounds the crystal layer on the inside. From this cambium the nutritive layer is produced. This consists of cells, almost square in outline, arranged in radial rows (Fig. 65).

The protective zone is differentiated only in the later stages of development. It is found, however, when the gall is mature, forming the entire wall of the free larval chamber and extending a short distance beyond it. Its cells are of the usual sclerenchyma type with uniformly thickened, laminated walls perforated by branched simple pores.

Holcaspis bassetti Gillette.

Host *Quercus macrocarpa* Michx.

A monothalamous gall occurring singly or in clusters around the stems of the host. When grouped the galls often cover completely 4 to 5 inches of the stem.

When the gall is not deformed by crowding, it is irregularly circular in outline at the base, gradually tapering to a distinct point that is recurved in most cases. The gall is attached to the host by a small stalk at the centre of the base. Colour green, often tinged with pink when young; becoming brown when more mature. The larval chamber resembles closely that found in the former species in being oval and free at maturity, but it differs in being placed nearer the base of the gall and in tapering to a point at the end nearer the twig.

Dimensions:—Diameter at base, average, 16 mm.

Except in a few details the anatomical structure of this gall is the same as that found in the species just described. In this species the outer part of the parenchyma zone is composed of cells almost square in outline, but towards the larval chamber the cells become more elongated and arranged in distinctly radial lines. Rays of from one to three cells in width pass in radial lines throughout this zone. The cells composing them are much smaller than the ordinary cells of the zone. The cells of the nutritive layer are much more elongated radially than those of *H. globulus* Fitch (Figs. 58, 65). The cambial layers and the crystal-bearing tissue hold the same relative positions as in the preceding species. The relation of the crystal layer to the nutritive zone is shown in Fig. 58. The protective sheath in the mature gall extends out almost to the epidermis. Except in its distribution it cannot be distinguished from the corresponding zone in *H. globulus* Fitch.

Philonix erinacei Beut.

Host *Quercus alba* L.

A polythalamous gall springing usually from the midrib but rarely from a principal vein of the leaf. It originates from the under or occasionally the upper surface of the leaf.

The gall is spherical or ellipsoidal and slightly flattened on the surface in contact with the leaf. The point of attachment is narrow and elongated in the direction of the vein. The epidermis of the gall is divided up into numerous facets, each of which is drawn out at the centre into a trichome structure that becomes more spiny as the gall approaches maturity. The colour of the surface of the gall is yellowish with occasional red tints. The trichomes vary in shade from pink to red.

Dimensions:—Longer diameter 10-15 mm.; shorter diameter 5-10 mm.

In the earliest stage examined the gall was 2 mm. in diameter. At this time none of the cell walls are sclerenchymatous and the nutritive zone is only about four narrow cells in width. Outside of this layer is a part of the parenchyma zone in which each cell contains a large crystal mass.

At a stage in which the gall is full grown but still soft, all the zones are differentiated. The epidermis is thrown into folds and is covered with a heavy cuticle (Fig. 64). This is absent in the sinuses of the folds and on the epidermis covering the spines. The parenchyma zone is gradually converted into a protective tissue of porous sclerenchyma. The thicker deposit is usually on the walls of the cells nearer the periphery of the gall. Along the outside of the nutritive zone and throughout the protective layer generally are lines of small cells almost square in outline. The walls of these cells are very thick and the lumen of each is filled with a single crystal or a mass of crystals. In galls that had become hard all the cells of the parenchyma zone were found to have sclerified. The sclerification is partially complete in Fig. 64.

The nutritive layer of this gall differs very little in appearance from the parenchyma zone. Its cells do not contain the rich protoplasmic contents common to the nutritive zones of typical Cynipid galls.

Philonix hirta Bassett.

Host *Quercus macrocarpa* Michx.

A monothalamous, spherical gall originating from a principal vein of the leaf. Found somewhat irregularly spaced along the vein and about equally distributed between the upper and lower surfaces of the leaves.

The epidermis has the same faceted appearance found in the preceding species, but in this form the trichomes are represented only by short points. Colour greenish yellow. When the leaves become tinted in the autumn the galls assume a reddish brown colour.

Dimensions:—Diameter 2-3 mm.

The anatomical structure of this gall differs from *P. erinacei* Beut. only in the distribution and nature of the protective zone. This tissue is limited to a layer 3 to 4 cells in thickness, just outside the nutritive zone. The sclerifying deposits are limited almost entirely to the outside tangential walls of these cells and gradually entirely fill them. As a result of this the pores pass completely across the cells in the older stages. The small square crystal-bearing cells are, in this species, just outside the regular protective sheath.

Philonix nigra Gillette.

Host *Quercus alba* L.

A monothalamous gall attached to the principal veins on the under side of the leaf.

This species is spherical in form and has an epidermis covered with a short dense pubescence that gives a felty appearance to the exterior of the gall. A fibrous mass of cells surrounds the centrally placed larval chamber. Colour gray turning darker when dry. Individuals of this species are so numerous that the ground, under the trees infested by them, is often covered thickly with galls.

Dimensions:—Average diameter 8 mm.

Outside the nutritive zone is a wide crystal layer, each cell of which is completely filled with a crystal mass. The sclerenchyma of the protective zone is formed in a very unusual manner. The sides of contiguous cells are thickened in such a way that there is an almost spherical deposit at the points where the cells are in contact.

Radiating out from the protective layer are long narrow cells which form the minor part of the parenchyma zone. The remainder of this zone consists of irregularly elliptical, thin-walled cells. The epidermis is covered with a dense growth of trichomes with thick laminated and sclerified walls.

Amphibolips confluens Harris.
Host *Quercus coccinea* Muench.

A monothalamous gall attached to the petiole or midrib of the leaf. The midrib is never continued beyond the point of origin of the gall.

Globular to prolate spheroidal in shape and invariably terminating in a minute point. The thick walled larval cell at the centre of the gall is surrounded by a sponge-like mass of fibres that is at first white but becomes dark brown when the gall is dry. At a very early stage of development the epidermis of the gall is pubescent but later it becomes smooth. The colour is at first green but this changes to a lustrous light brown when the gall is old.

Dimensions:—Average diameter 40 mm.

(*a*) Stage in which the gall is 2 mm. in diameter.

Almost the entire gall consists of a compact tissue, which is composed of small uniform cells. Lines of narrow elongated cells, however, pass in a radial direction throughout this tissue. These cells do not extend into the gall cavity nor out to the epidermis, they traverse about two-thirds of the gall radius. As they approach the epidermis the lines curve around and run parallel to its surface. Spiral vessels are in some cases differentiated in these rays and the elements are more numerous near the point of attachment of the gall.

(*b*) Older stage 9 mm. in diameter.

The gall wall can now be divided roughly into three sections. That part lying next the larval cell resembles closely the compact tissue described in the preceding stage, except that immediately adjoining the

cavity a typical nutritive layer has been formed by the elongation of the cells in a radial direction. In the centre zone the lines of cells containing the vessels are much more apparent at this stage, since the intervening tissue has become loose and skeleton-like. The cells composing it are long, very narrow and frequently branched. In many cases a branch is attached to the main cell without the formation of an intersecting partition between the two. The outside zone of the three is composed of somewhat elliptical cells. These form a fairly firm tissue constituting the rind of the gall.

(*c*) Mature stage.

The protective zone is now the most characteristic feature of the anatomical structure. The part of the protective sheath adjoining the larval cavity consists of a few layers of elliptical cells arranged in tangential rows. The sclerenchymatous deposits on the outside walls of these cells are much heavier than those on the inside. Further out the protective cells are formed in radial rows and their walls are uniformly thickened. This protective strengthening of the cell walls extends even into the loosely arranged filament-like cells, some of which are heavily sclerified.

Amphibolips inanis O.S.

Hosts *Quercus coccinea* Muench.
Quercus rubra L.

Resembles the preceding species in external appearance and in its attachment to the midrib or the petiole of the leaf.

In shape it is more nearly spherical than *A. confluens* Harr. and it has a much thinner rind than is found in that species. The epidermis of the gall, which is at first green with dark spots, becomes light brown with darker patches at a later stage. The larval cell in this case is held in position by a number of fine radiating fibres.

Dimensions:—Average diameter 35 mm.

In the earlier stages the anatomical structure of this gall is practically the same as *A. confluens* Harr. The vascular strands surrounded by elongated cells are present, but as the gall becomes older the connecting tissue from between the strands disappears.

In the mature gall the protective zone is very apparent. It consists of 8 to 10 rows of comparatively small elliptical cells. The walls of these cells are uniformly thickened, constituting a porous sclerenchyma.

Dryophanta palustris O.S.

Hosts { *Quercus rubra* L.
Quercus coccinea Muench.

A monothalamous gall produced singly or in groups of two or more on the leaves of the host plant. It is spherical in form and extends almost

equally on each side of the leaf. In the majority of cases the gall extends out almost to the margin of the leaf and only the edge of the blade rims its outer side. Rarely this gall is found originating from the peduncle of the staminate catkin of the host.

The very young gall of this species is densely pubescent, while the well-grown specimens are usually quite smooth. In galls collected when the leaves are just beginning to unfold from the bud the larval cell and the outer zones of the gall are united, but very soon a separation occurs and the larval cell is left rolling freely around in the outer gall. Colour of mature gall green with patches of red in some places.

An average of about three weeks elapses from the time of the opening of the buds until the producers emerge from the galls. After another week the galls are wrinkled, dried up and brown. About ten days before the time of emergence of the producers the larval chambers were removed from several galls and placed under dry conditions. While the time of emergence of these producers was not appreciably changed, the insects in almost every case had difficulty in freeing themselves from the larval cells and one wing usually remained shrunken. It would appear that the outer gall during the later stages of development functions only as a moist chamber for the prevention of the desiccation of the larval cell.

The youngest galls examined were obtained from leaves that were just breaking out of the bud. At this stage the larval chamber still has organic connection with the remainder of the gall (Fig. 49). A well-defined cambium zone, in which mitosis is taking place, divides the gall wall into nearly equal parts. The parenchyma layer on the outside extends from the cambium to the epidermis. It consists of small cells that resemble closely those of the cambial zone. The inner half of the gall, forming the nutritive layer, is composed of much larger cells arranged in rows radial to the larva. A canal passes from the outside into the larval chamber. The epidermal lining of this canal is continuous with that of the epidermis of the gall and is covered with the same class of trichomes (Fig. 49). It gradually passes over into the innermost layer of the nutritive zone.

In a very short time after the opening of the buds, the larval chamber is severed from the remainder of the gall. The break occurs near the outside of the cambium zone, and separation has commenced in Fig. 50. At this stage the protective layer is not yet differentiated. Soon after the separation occurs it is produced, however, and the four zones of a typical Cynipid gall are complete.

The cells of the protective sheath are placed tangential to the larva. There are two layers of these cells, both of which have one tangential wall thicker than the other. In the outer row the thicker wall is towards

the larval chamber, but in the inner row the reverse is the case. On the outside of the protective zone are about two layers of round, loosely connected parenchyma cells (Fig. 51). The canal mentioned in the early stage is still visible, penetrating the outer wall of the gall and that of the larval chamber. A layer of collapsed tissue is now clearly defined around the inside of the nutritive zone (Fig. 51). The inner layer of the parenchyma zone is also showing this same tendency to collapse.

In the mature gall the nutritive zone is represented by only a narrow layer of shrunken tissue (Fig. 52), the individual cells of which cannot be distinguished. The inner layer of the parenchyma zone is now almost completely collapsed and the cell walls of the whole zone are wrinkled.

Andricus imbricariæ Ashmead.

Host *Quercus coccinea* Muench.

A globular gall issuing from the stem of the host plant. Several galls are found near each other on the stem but they are never crowded.

It is usually monothalamous, but occasionally dithalamous forms are found, the larval cells are closely connected with the remainder of the gall. When the gall drops off its point of attachment is marked by a small, elliptical, depressed area surrounded by thin scales of tissue. These scales represent tissue forced aside by the emergence of the young gall.

Dimensions:—Diameter 6-9 mm.

This species has the four zones well differentiated. The most striking features of the anatomical structures are the following:—

The cells of the protective layer contain large crystal masses and have their walls uniformly thickened. Radiating lines of cells pass out from this protective zone (Fig. 48), through the parenchyma sheath and end near the epidermis. These bands are composed of narrow, elongated cells and are from 1 to 3 cells in width. These rows of cells contain a great deal of starch and a substance that takes a very deep stain with saffranin. Large cells of the parenchyma zone separate these bands of cells from each other, as seen in Fig. 48.

Andricus singularis Bassett.

Host *Quercus rubra* L.

In the majority of cases this gall originates from the mesophyll of the leaf blade but rarely it is found attached to the petiole. It is situated near the margin of the blade of the leaf and projects about equally from the upper and lower surface.

It is a monothalamous gall closely resembling in external form *Dryophanta palustris* O.S., but its outer wall is much firmer and it does not wither so quickly after the producer emerges. The ellipsoidal, larval chamber is suspended at the centre of the gall by radiating bands of

tissue which pass inwards from the gall rind; this gives the species a superficial resemblance to small specimens of *Amphibolips inanis* O.S.

Dimensions:—Diameter 10-15 mm.

The larval chamber in this species is suspended at the centre of the gall by fine strands of tissue. These are composed of long, narrow, filament-like cells interspersed with spiral vessels. These fibres represent the inner part of the parenchyma zone. The outer part of this zone resembles closely that found in the gall produced by *Dryophanta palustris* O.S. The cell walls of the epidermis are strongly thickened and this is the case also in the underlying layer of cells of the parenchyma sheath. The protective zone, when the gall is full grown, consists of two rows of porous, laminated sclerenchyma cells. The outside tangential walls of these cells are much more thickened than the inside walls. The cells of the nutritive layer are unusually large and almost square in outline. By the time the gall is nearly mature many of them have been emptied of their contents and a wrinkling in the radial walls shows that the whole tissue is collapsing (Fig. 59).

Andricus piger Bassett.

Host *Quercus coccinea* Muench.

A polythalamous gall produced by the swelling of the petiole or midrib of the leaf. It is situated always near the distal end of the petiole or the proximal end of the midrib.

It is an irregular, elongated structure, somewhat triangular in cross section. When it originates from the midrib the projection is almost entirely from the under surface of the leaf, the broad flattened part of the midrib above rising very little above the general surface of the blade. On the under surface of the leaf along each side of the gall is a row of small openings. The larval cells are in two rows following the line of the openings. The total number in the gall varies from 20 to 30.

Dimensions:—Length of longer diameter 20-25 mm.

A nearly mature specimen shows the following anatomical characteristics. The four typical zones are well defined. Surrounding the nutritive zone are three rows of cells that form the protective zone. The walls of these cells are porous laminated and uniformly thickened. Outside of the protective sheath is a zone of tissue of about the same width, each cell of which contains a large crystal aggregate. These masses of crystals alone distinguish this tissue from that of the parenchyma zone into which it gradually passes by the crystal groups becoming less plentiful.

Connected with the openings mentioned in the macroscopic description are remarkably straight canals that extend in as far as the protective sheath. At this point they are closed by cone-shaped plugs of sclerenchyma (Figs. 43, 44), that extend out from the protective zones of the

larval cells towards which the canals are passing. The cells of this tissue are identical with those of the ordinary protective zones.

From analogy with *Dryophanta palustris* O.S. (Fig. 49), and with other species of Andricus it would seem safe to infer that this canal opens into the larval chamber at earlier stages in the development of this gall. This also appears more likely to be the case since the protective zone that blocks the way, is differentiated only in the later stages.

Andricus petiolicola Bassett.

Host *Quercus alba* L.

This gall is produced in the same manner as *A. piger* Bassett by the swelling of the petiole or midrib. It is also located at the same place on the leaf as that species.

It has an irregular, spherical shape drawn out at some place on its surface into a short tapering projection. At the summit of this elongated part of the gall is an opening surrounded by a dense ring of coarse, brown trichomes. The larval cells are numerous and very variable in number. They are arranged around the axis of the gall at about the same distance from the epidermis.

Dimensions:—Diameter of the swollen basal part 10-12 mm.

In this species the protective layer is much thicker than in *A. piger* Bassett, but the individual cells composing it are the same in both species. The galls sectioned were nearly mature but the crystal layer of the former species was not found.

In this species also there is a canal passing towards each larval chamber (Fig. 46). These canals do not open directly to the outside but into a main canal of larger bore that extends a considerable distance into the mass of the gall (Figs. 45, 46). The branch canals are blocked by the protective sheath as in the preceding species. All of the canals are lined with a cuticularized epidermis, continuous with the gall epidermis (Fig. 45). The lining of the main canal produces abundant trichomes but these structures do not appear to be present in the tributaries. A tubular outgrowth of the protective zone surrounds the main canal. This sclerenchymatous sheath is separated from the canal by several layers of parenchyma cells. Outside of this protective tube a cork cambium is differentiated.

Andricus (Undescribed).

Host *Quercus macrocarpa* Michx.

The swelling of the midrib of the leaf produces this gall. It resembles closely *A. piger* Bassett, but is always found within the blade of the leaf, although close to its base in most cases.

The openings mentioned in the two preceding species are in this case found on the surface of the gall which appears on the upper side of

the leaf. They correspond to the larval cells, varying from 3 to 7 in number.

Dimensions:—Length parallel to axis of midrib 10-15 mm.

Although nearly mature specimens of this gall were sectioned, a protective zone was not found.

In this species each larval chamber has a canal related to it. In this respect it resembles *A. piger* Bassett. A section of the gall at a very early stage of development shows that the canals open into the larval chambers. When the gall becomes older, each canal is blocked by two plugs of sclerenchyma. One of these occupies the same position relative to the larval chamber as in the two preceding species; the other is formed near the external opening. These masses of sclerenchyma are shown in Fig. 47. Trichomes do not appear to be produced in the canals.

Rhodites multispinosus Gillette.

Host *Rosa blanda* Ait.

A globular to ovoid polythalamous gall produced by the swelling of the stem or branches of the host plant. Since the larval cells are arranged around the stem axis at about the same distance from the periphery of the gall, the abnormal swelling completely encircles the stem.

The gall is reddish brown in colour and has its surface usually densely covered with fairly stout prickles.

Dimensions:—Average diameter 25 mm.

The principal mass of this gall is formed from the cortex of the stem. The larval cells are embedded in it and a common parenchyma zone is thus formed. A well-marked protective tissue, composed of cells with porous, sclerenchymatous walls, separates this parenchyma zone from the nutritive tissue that lines each larval cell.

The response of the gall epidermis to stimulation is shown in the production of the numerous prickles that are so marked a characteristic of this gall. Since the stem of the host is usually unarmed this feature appears the more remarkable.

Rhodites lenticularis Bass.

Host *Rosa blanda* Ait.

A monothalamous, lens-shaped, thin-walled gall produced in the mesophyll of the leaf of the host. They sometimes occur singly but usually several are located on one leaflet. They often are so crowded that they lose their circular outlines.

This gall projects chiefly from the under side of the leaflet.

Dimensions:—Longer diameter 2-3 mm.; shorter diameter 1-2 mm.

Since it is possible to trace a considerable part of the unaltered mesophyll of the leaf along the upper surface of this gall, proliferation must have commenced in the spongy parenchyma of the leaf. The

normal epidermis of the leaf passes over the surface of the gall without modification. On the upper surface of the leaf a protective layer of about five cells in depth separates the normal part of the leaf from the gall tissue. On the under surface a corresponding protective layer occurs at a distance of three rows of cells below the epidermis. The cells of this protective zone have uniformly thickened sclerenchymatous walls. The general structure of the gall is shown in Fig. 63. Inside this layer a cambial tissue is differentiated, from which the cells of the nutritive zone are produced directly. The nutritive cells are rectangular in outline and arranged in radial lines, presenting very much the same appearance as the cambium from which they have originated.

Rhodites bicolor Harr.

Hosts { *Rosa blanda* Ait.
Rosa carolina L.

A monothalamous, spherical, hollow gall with a wall 1 to 2 mm. in thickness.

They originate singly or several close together from the upper surface of the leaf.

The gall bears numerous stiff prickles that average about the same length as the diameter of the gall. Colour green with red tints, turning brown at maturity.

Dimensions:—Average diameter 11.5 mm.

The anatomical structure of this gall presents very little differentiation of tissue. The parenchyma zone consists of large irregularly shaped cells. This tissue passes into the nutritive layer with little change in the shape or size of the cells. The protective zone is entirely absent.

Rhodites ignotus O.S.

Host *Rosa blanda* Ait.

A polythalamous or occasionally monothalamous gall attached to the under side of the leaves by a small extent of surface. These galls are generally found clustered together and often deform the entire leaf.

Dimensions:—Average longer diameter 11 mm.; average shorter diameter 3-5 mm.

While somewhat variable, the shape approximates usually to an irregular oblate-spheroid. At the apex of the gall is a shallow depression containing a small scale-like patch of tissue. The epidermis is glaucous and light brown in colour.

The anatomical structure of this species presents the rare feature of two protective layers. These are each of about five cells in thickness in the full-grown gall. One of them is found in the usual position separating the parenchyma and the nutritive zones. The other is situated in the

parenchyma just beneath the small-celled epidermis. This outside protective sheath gradually passes into the parenchyma zone by the constituent cell walls becoming thinner. The large size of the cells in the parenchyma layer marks them out from the rounder and smaller cells of the nutritive zone.

Below the depressed area, mentioned in the macroscopic description, is a small patch of sclerenchymatous cells. In position and character these cells appear to be homologous to the groups of cells that block the canals in different species of Andricus. Only the mature stage of this gall was examined, but in all probability the depression at the top is the remains of a canal that connected the gall cavity with the outside in the early stages of development. A part of the normal epidermis of the leaf was held fast by the closing of this canal, and when the gall was forced out beyond the leaf tissues a small patch of the epidermis of the leaf was carried out on it. This persists in the later stages of development as the scale of tissue in the depression.

Rhodites gracilis Ashm.
Host *Rosa blanda* Ait.

A thin-walled, monothalamous gall produced from the mesophyll of the under surface of the leaf of the host. Occurs singly or in clusters on the leaflets.

It is irregularly spherical with a broadened top, in the centre of which is the same shallow depression and scale-like patch found in *R. ignotus* O.S. Numerous ridges radiate out from the point of attachment of the gall, pass up its sides and project as short blunt tubercles around the top.

Dimensions:—Diameter 5-6 mm.

This species resembles closely *R. bicolor* Harr. in anatomical structure. It presents little differentiation of tissue. The protective sheath is not present, and the parenchyma and nutritive zones are marked out from each other only by the cells of the latter being slightly smaller and more circular in outline. The observations on the preceding species concerning the depression at the summit of the gall and the discussion of them also apply to this species.

Rhodites nebulosus Bass.
Host *Rosa blanda* Ait.

This species, as the preceding, is monothalamous and thin-walled. It also originates from the mesophyll of the leaf of the host. It occurs usually in dense clusters deforming the entire leaflet.

The gall is spherical in form, bearing at the summit the depressed area and scale-like patch characteristic of the two preceding species.

The surface of the gall is smooth or covered with short weak spines. Colour green, tinted strongly with red.

Dimensions:—Diameter 5-6 mm.

This gall resembles closely the preceding species in anatomical structure. The cells of the nutritive and parenchyma layers differ in much the same way and to the same extent. Further, the protective zone is again absent. The explanation given in the two preceding forms, to account for the scale in the depression at the summit of the galls, is applicable also in this case.

Cynips? constricta (Stebbins).

Host *Quercus coccinea* Muench.

A monothalamous gall originating from the midrib or a principal vein of the leaf. Its origin from a vein is shown in Fig. 53. It is usually found on the under side of the leaf but occurs occasionally on the upper side.

This gall has the form of a sphere surmounted by a short cylindrical neck, which is slightly constricted at the base. The general form is shown in Fig. 54. A very small portion of its surface attaches it to the leaf. The epidermis on the main body of the gall is smooth, shiny and green in colour. The neck is red at the tip.

Dimensions:—Diameter of spherical part 2.5-3.5 mm.

At an immature stage of the gall the parenchyma zone in the spherical part consists of a mass of cells that gradually decrease in size from the epidermis to the inner limit of the layer. At the epidermis the cells are nearly circular in outline but become square or rectangular in proportion to their proximity to the centre.

Bounding this zone on the inside is a crystal layer of about three cells in thickness, each cell containing a large crystal mass. Around the inside of this tissue is a nutritive zone, the cells of which are regularly rectangular.

At the top of the main part of the gall is a well-defined cambium tissue which produces the cylindrical projection that caps the spherical portion (Fig. 54). The anatomical structure of this part shows clearly that it functions as an outer nutritive zone. Its walls are thin and the cell contents take the same stain as those in the nutritive zone surrounding the larva. Large starch grains are also scattered throughout the cells. This zone is separated from the cambium tissue in the later developmental stages by a protective layer of typical porous sclerenchyma. These cells are filled with protoplasmic material, and the system of canals between the individual cells is very complete and clearly defined. This feature is very important since the nourishment from the outlying nutritive zone has to pass through this tissue to reach the larva.

Solenozopheria vaccinii Ashmead.

Hosts { *Vaccinium pennsylvanicum* Lam.
Vaccinium canadense Kalm.

A polythalamous gall originating from the lower part of the stem of the host plant.

In the majority of cases this gall is reniform in shape but rarely it is irregularly spherical. The surface is depressed where it is attached to the stem, which is almost invariably bent at that point. The colour is green, often with red tints turning to brown as the gall becomes older.

Dimensions:—Longer diameter 10-30 mm.

At an early stage, while the tissues are still soft, the anatomical structure of this gall presents practically no differentiation. It consists of a mass of dense tissue, the cells of which are small and placed very close together. The small-celled epidermis is covered with an exceedingly heavy cuticle. At regular intervals small papillæ occur on the epidermis which seem to secrete a glandular material from small openings at their tips.

When the gall is mature all the cells, except a few layers below the epidermis, have sclerified walls. The thickenings are decidedly heavier on one wall than on the opposite.

Aulacidea nabali Brodie.

Hosts { *Prenanthes alba* L.
Prenanthes altissima L.

A polythalamous gall originating from the stem or the main root of the host plant. It occurs at or near the base of the stem, usually just below the surface of the ground but in some cases it is situated some distance above the ground.

The single galls are irregularly spherical, but these are generally clustered in such a way as to form roughly cylindrical masses. In some cases these completely surround the stem, but in others they only partly encircle it.

Dimensions:—Diameter of single gall 5-10 mm.

The cambium of the stem stimulated to unusual activity produces the abnormal tissues in this case (Fig. 66). Along the line of contact of the gall with the normal stem, the cambium produces wood and bast, but in abnormally large amounts, as can be seen in Fig. 66. In the gall tissue proper, in place of wood, radial lines of nucleated thin-walled cells occur. A few rows of vessels are interspersed among these cells. The stimulated cambium produces these parenchyma cells also on the side where the bast would normally occur. In the gall tissue on the outside of the line of the cambium, small patches of vessels are found. These have arisen from clumps of cells detached from the original cambium.

Associated with these isolated masses of vessels, often occurs a small amount of bast that appears normal. When the detached cambium is curved, wood is almost invariably produced on the inside of the curve and bast on the outside, giving rise in some cases to almost perfect concentric bundles.

The club-shaped cells of the nutritive zone do not follow the general rule and radiate out from the larval cell, but are oriented with their long axes at right angles to the cambium. The nuclei of the cells in this zone are abnormally large and often present good examples of amitosis (Text Fig. 6).

The normal cortex passes over the gall with little alteration during the early stages of development, but later a cork cambium is differentiated that throws off the cortex and covers the gall with its characteristic corky layer.

Neuroterus majalis Bassett.

Host *Quercus alba* L.

A polythalamous gall originating in the mesophyll of the leaf and divided into two nearly equal parts by the blade. The galls are found usually in contact with the side of the midrib and extending out to the margin of the leaf.

This gall is characterized by a flat, irregular shape and a finely granular epidermis. It is translucent and of a light green colour until the producers emerge when it becomes light brown and opaque.

The apertures of exit of the mature insects seem to occur invariably on the upper surface of the gall.

Dimensions:—Diameter parallel to leaf blade 12-24 mm.; diameter at right angles to leaf blade 7-9 mm.

Only the mature gall was examined. At this stage the nutritive zone consists merely of a narrow line of collapsed tissue (Fig. 67). From two to three rows of cells constitute a protective layer. The tangential walls of these sclerified cells are unequally thickened, the heavier deposit being on the wall nearer the larval chamber. The parenchyma zone consists of large thin-walled cells, the majority of which are empty and devoid of nuclei. A small-celled epidermis continuous with that on the normal leaf passes over the gall.

Summary.

All the galls in this group have three tissue zones developed and only very seldom is the fourth absent. The three always present are the epidermal, the parenchyma or tannin and the nutritive. The parenchyma zone, as shown by Cook[23] is subject to a great amount of variation. The fourth, not always present, is the protective or sclerenchyma zone.

Even in one genus there may be considerable variation in the degree of development of the protective zone. It is entirely absent in *Rhodites gracilis* Ashm. and *R. bicolor* Harr., but two distinct layers are found in *R. ignotus* O.S.

In several species of the genus Andricus canals were found passing from the exterior towards the larval chambers. In the early developmental stages these opened into the gall cavity, but later were blocked by outgrowths of sclerenchyma from the protective zone. They were located in the species *Andricus piger* Bassett, *A. petiolicola* Bassett and *Andricus* N.S. (Figs 43-47).

A canal similar to those in the Andricus genus was found also in *Dryophanta palustris* O.S. In this species the plug of sclerenchyma is not developed (Fig. 49).

An epidermal scale was found in the bottom of a depression at the apex of the galls produced by certain species of Rhodites. Below each scale a small mass of sclerenchyma is differentiated. These structures seem to be homologous to the canals in the genus Andricus. They are present in the following species: *Rhodites ignotus* O.S., *R. gracilis* Ashm. and *R. nebulosus* Bassett.

The gall *Solenozopheria vaccinii* Ashmead has the sclerified tangential walls of its protective zone much thicker on one side than on the opposite. This is very unusual in stem galls, although a common feature in leaf galls.

The collapsing of the cells of the nutritive zone after the withdrawal of the contents is exemplified in almost any gall studied. It is, however, particularly noticeable in *Dryophanta palustris* O.S. (Fig. 52).

Empty cells were found throughout the nutritive zones in the later stages of nearly all the galls examined. Good examples of this phenomenon are furnished by *Andricus singularis* Bassett and *Aylax glechomæ* Linné.

The separation of the tissues so as to produce a free larval chamber gall is shown in the species *Holcaspis globulus* Fitch and *H. bassetti* Gillette; also in *Dryophanta palustris* O.S. (Fig. 50). In the last species, as Cook[23] has shown, the separation of the larval chamber takes place at a very early developmental stage.

Mitotic phenomena were observed in the cambium and near it in the adjoining parenchyma zone of *Dryophanta palustris* O.S. The number of chromosomes remains as in the normal. Good examples of amitosis were located in the nutritive tissues of *Aylax glechomæ* Linné, and *Aulacidea nabali* Brodie (Text Fig. 6).

The parenchyma zone of *Amphibolips confluens* Harris furnishes an example of a tissue consisting of long filamentous cells from which

branches are given off without the formation of intercepting walls. It seems to represent an exaggerated form of the spongy parenchyma.

Proliferation of glandular tissue is shown in *Aulacidea nabali* Brodie.

Cynips? constricta Stebbins furnishes an example of an outer accessory nutritive zone that clearly assists in supplying the larva with nourishment (Fig. 54).

NOTES ON THE PROTECTIVE ZONE.

This zone is typical for the Cynipid galls, but as already stated it is differentiated in certain Dipterous forms, such as *Rhabdophaga batatas* Walsh (Figs. 25, 26) and *Cecidomyia triticoides* Walsh (Figs. 37, 38), and also in the Hemipterous gall *Pachypsylla celtidis-mamma* Riley (Fig. 15).

In the Cynipidæ it usually bounds the nutritive zone on the outside, but it does not invariably occupy that location. When two layers are present the inner occupies that position, but the outer is situated nearer the periphery of the gall.

The term, "protective," has been applied to this tissue without a very clear idea as to what it protects from. The common notion appears to be that it forms an inner line of defence against parasites and small animals other than insects. The latter class of enemies appears to interfere very seldom with galls. Cook[23] mentions one example—he found birds tearing open the galls of *Pemphigus vagabundus* Walsh. Very few examples of such cases have come under my notice. Galls of *Holcaspis bassetti* Gillette are occasionally opened by woodpeckers, and the larvæ of *Eurosta solidaginis* Fitch are sometimes taken from the galls by field mice. Chipmunks will also tear open the galls of *Pemphigus rhois* Walsh to get at the inhabitants. Not only are galls seldom attacked by such animals but a sclerenchymatous tissue would be a very poor defensive device against them.

Adler[1] has advanced the idea that this zone protects against insects that are parasitic on the producer-larva. This appears very unlikely since the parasites oviposit at a comparatively early stage, and the sclerenchyma is differentiated relatively late in the development of the gall. The same writer cites the large size of the gall and the thickened epidermis as other protective devices against parasites. The same argument is applicable in this case; the gall is not large nor is the epidermis abnormally thick at the time the parasites are ovipositing. Were Adler correct the gall *Amphibolips confluens* Harris should be almost immune against parasites, as it is large, has a thick epidermis and a well-developed protective sheath. In spite of all these apparent advantages this gall has a heavy casualty list owing to parasitism. During last season hundreds of this species were opened and on an average about 75% were found to

be parasitized. In some cases a tree would not yield a single perfect producer, although a couple of dozen galls were examined.

It seems safe to conclude that if this zone has ever functioned as a means of defence against parasites, it is no longer operative. Apparently the only protective function that can be ascribed to this tissue is the prevention of injury to the producer by desiccation during its later larval and pupal stages of development. A thick or cuticularized epidermis would also afford protection in the same manner.

Concerning the form of the elements comprising this zone, Weidel[45] has recently made some interesting observations. He makes the following too sweeping statement in his summary,—

"Auch das gallentragende Organ der Mutterpflanze hat einem Einfluss auf die Gestaltung der Elemente in der Galle, denn die blattbürtigen Gallen führen in der Schutzschicht einseitig verdickte, die übrigen allseitig gleichmässig verdickte Zellen."

That this can be accepted only as a general rule, and at least requires further study, is indicated by the fact that our American galls furnish undoubted exceptions. Thus the gall produced on the stem of *Vaccinium pennsylvanicum* Lam. by *Solenozopheria vaccinii* Ashmead has cells that have a much thicker deposit of sclerenchyma on one tangential wall than on the other. In some cases practically the entire cell lumen is filled with sclerenchyma and the deposit has grown entirely from one side of the cell. Also a number of leaf galls have their protective zones composed entirely of cells with uniformly thickened walls. The following species furnish examples of this: *Amphibolips inanis* O.S., *Rhodites lenticularis* Bass. and *Neuroterus majalis* Bassett. The statement quoted is true, however, in the majority of cases and is important as indicating a possible effect of environmental conditions on the elements composing the gall.

CYTOLOGY OF GALLS.

Cell division in the Cynipid galls was not found to present any unusual phenomena. In the cambial layer of *Dryophanta palustris* O.S. in which mitosis was taking place the chromosomes were found to be eight in number. They are slightly curved and show a decided tendency to group in pairs when moving out from the equatorial plate. The root tips of the host *Quercus coccinea* Muench. were found to give the same chromatic count and the chromosomes present the same feature of moving out to the poles of the spindle in groups of two.

In several galls amitosis was noted and very marked examples in the nutritive zones of the galls *Aulacidea nabali* Brodie (Text Fig. 6) and *Aylax glechomæ* Linné. Cell division did not appear to accompany the phenomenon in any of the cases examined.

In galls other than the Cynipidæ, the only cytological phenomen that presented unusual features were found in the orders Diptera an Lepidoptera. An unusual type of cell division was observed in the corte and epidermis of *Neolasioptera perfoliata* Felt (Text Fig. 7) and in th cortex of *Gnorimoschema gallæasterella* Kellicott and *Stagmatophor ceanothiella* Cosens. This has been already referred to in the descriptiv part of the paper and only the main features will be noted here. Th mother cells produce from 2 to 5 daughter cells and these remain i groups that are easily recognizable. The elongated nuclei are found i contact with the septating walls but not exactly opposite each othe In the Dipterous genus Neolasioptera this was the only form of ce division that occurred in the gall, but in the Lepidopterous genera was found only in a limited area of the abnormal tissue.

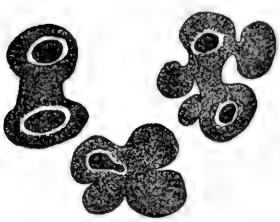

Fig. 6.—Nuclei from the nutritive layer of *Aulacidea nabali* Brodie.

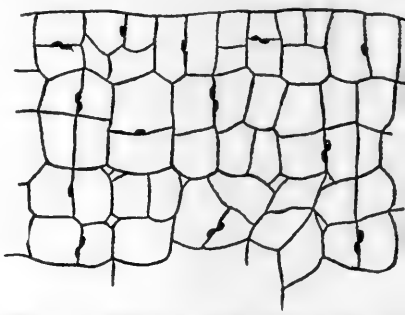

Fig. 7.—Cell division in the epidermis and corte of *Neolasioptera perfoliata* Felt.

THE BEGINNING OF GALL DEVELOPMENT.

In some species of galls that originate from stems, veins or petiole the eggs of the producer are deposited within the tissues of the host i or near the cambium zone. Adler and Küstenmacher have detecte eggs actually placed in that region, and while my own observations i the case of *Cynips? constricta* Stebbins were made on older develop mental stages, yet the nature and arrangement of the tissues were suc as would seem to preclude any other conclusion. The origin of this ga from the vein is shown in Fig. 53. In leaf galls that are produced in th blade as *Rhodites lenticularis* Bass. (Fig. 63), a cambium is differentiate in the mesophyll into which, in this case, the egg is inserted. Two inde pendent observers, Beyerinck and Weidel, have demonstrated beyond doubt, however, that the egg is in some cases placed on the epidermi of the host, and consequently there are at least two distinct methods o ovipositing.

The two observers, who deal with the development of galls from eggs deposited on the outside of the host, hold entirely different opinions concerning the early stages. Beyerinck[15] supposes that after the egg is placed at the selected spot, the tissues under it grow very little, if at all, but those immediately adjacent undergo rapid proliferation until the egg is completely enclosed, forming a gall of the "Umwallung" type. According to his view the larva possesses the power to stimulate the tissues through the egg membrane without rupturing it.

Weidel, on the other hand, holds an entirely different opinion concerning the enclosing of the larva by the tissues of the host. He has been able to convincingly demonstrate that in the gall *Neuroterus vesicator* Schlecht, the cuticle of the leaf is punctured before the larva is completely free from the egg membrane. "Die in der Eihaut noch vollständig eingeschlossene Larve durchbricht diese an einer Stelle und senkt in die Epidermis des Blattes ein Organ ein durch das die Cuticula durchbrochen und das pflanzliche Gewebe verletzt wird."—Weidel.[45] The influence of the larva[45] soon produces proliferation in the tissues of the leaf, and following this a degeneration commences at the epidermis and extending quickly forms a cavity of sufficient size to hold the larva. Into the larval chamber thus prepared the producer gradually passes, and the opening through which it entered is soon closed by the growth of the stimulated tissues.

While the excellent work of Weidel cannot be questioned concerning this particular gall, it is not necessary to assume that this is the only method by which a larval cavity is formed. In my opinion the method as described by Beyerinck is found in some of our American species of Andricus and Dryophanta, reference to which will be made later. Weidel's objections contained in the following quotation do not seem serious enough to warrant the setting aside entirely of the "Umwallung" type of development. "Gerade diese Stelle war es, die mich zu meinen Untersuchungen anregte, denn eine grosse Anzahl von Fragen bleibt bei diesen Ausführungen Beyerinck's unaufgeklärt: Wie kommt es, dass an der Stelle, wo das von der Larve abgesonderte Enzym am stärksten wirken muss, keine Vergrösserung der Zellen stattfinden soll, sondern nur in einiger Entfernung? Was wird aus Epidermis unmittelbar unter dem Ei? Aus Beyerinck's Figuren muss man annehmen, dass sie in Nährgewebe umgewandelt wird, da sie die Larve unmittelbar berührt. Wie kommt das, "Sinken," oder, "Vergraben," zustande, Vorgänge, für die ihn seine Erklärungen selbst nicht befriedigen?"—Weidel.[45]

Concerning the first question, as to why the proliferation is more pronounced around the larva than in immediate contact with it, it may be stated that this is a usual occurrence in the lower groups of galls in

which the stimulus is applied in one direction only. The stem mother of the genus Chermes thus become surrounded by a ring of tissue tha grows out around the point of attachment of the insect (Fig. 11). Th Dipterous gall *Cecidomyia ocellaris* O.S. also furnishes a very strikin example of this phenomenon. In this species the leaf is scarcely at a thickened under the larva, but the proliferation is so marked around i that the producer ultimately lies in a concavity, not formed by the lea becoming depressed, but by the outgrowth of the circular ridge of tissu (Fig. 33). Any explanations offered to account for these facts are merel conjectural, but it seems likely that the enzyme content requires a certai degree of concentration in order to exhibit its maximum activity, an that immediately in contact with the larva it has not the requisite dilutio to cause the greatest proliferation. It is a well-known fact that th amount of growth of plants in culture solutions varies with the degree c concentration of the nutrient substance in the medium; thus there is a optimum quantity and as this is exceeded growth is more and mor inhibited. An example of this is furnished by the checking of the growt of Penicillium when the culture solutions are too concentrated.

With regard to the question, "What becomes of the epidermis unde the egg?" I agree with Weidel that there is little likelihood of abnorma cell production until the larva punctures the egg membrane, but whe this occurs the epidermis becomes part of a nutritive zone and wi undergo such rapid changes that its epidermal characteristics will soo disappear. The chief alterations will be expressed in the much riche contents of the cells and in their steady collapsing as these contents ar withdrawn (Figs. 49, 51, 52). The latter change makes it extremel difficult to follow the normal into the abnormal epidermis unless at a extremely early stage. While the enclosing of the larva is due chiefly t the growth of the surrounding tissues, yet the collapsing of the nutritiv layer will assist it to a certain extent.

Weidel's photographs show that in Neuroterus there is not at an stage an opening into the larval cavity that is lined with the epidermis c the leaf, and that after the larva enters its prepared chamber the openin is very soon closed. In the method of development as stated by Beye rinck we would expect to find such an opening persisting for some time and if we do, that must be accepted as confirmatory evidence of th truth of his hypothesis. In two different genera, namely Dryophant and Andricus, I have found canals leading into the gall cavity in th early developmental stages (Figs. 43-49). The epidermis of these struc tures is continuous with the gall epidermis and it bears the same class c trichomes as the latter. The canal is very marked in *Dryophanta palu tris* O.S., and its lining which is the same as the gall epidermis, can b

traced until it passes over into the inside layer of the nutritive zone (Fig. 49). This canal can still be detected in well-grown specimens.

Only mature material of *Andricus piger* Bassett and *Andricus petiolicola* Bassett was obtained, and while the canals with the epidermal lining are well marked, they are shut off from the larval cavity by outgrowths of sclerenchyma from the protective sheath (Figs. 43, 44). There is little doubt, however, but that in early developmental stages they open into the gall cavity as in the genus Dryophanta. This view, indeed, I have practically confirmed in the examination of an undescribed species of Andricus on *Quercus macrocarpa* Michx. In this form the canal is blocked at maturity by sclerenchyma (Fig. 47) as in the former species, but at an early stage I have found it extending into the larval chamber.

Summary.

The evidence seems conclusive that there are two types of early developmental stages of galls when the egg is deposited on the epidermis of the host. The method of formation of the larval chamber as described by Beyerinck is found in certain genera, as Dryophanta and Andricus, while the method worked out by Weidel occurs in Neuroterus and in all probability other forms.

FEEDING HABITS OF THE LARVÆ OF GALL PRODUCERS.

With the exception of the family Tenthredinidæ, all gall-producing larvæ have started to feed before the abnormal production of tissue commences. The narrowing of the problem of gall production to the influence of the larvæ on the tissues of the host has given additional importance to the problems dealing with the feeding habits of these larval producers.

Order Arachnida.

Fam. Eriophyidæ.

The members of this family have mouth parts of the sucking type. With their cone-shaped beaks they pierce the cell walls and withdraw the liquid contents. The cell walls are not used as food.

Order Hemiptera.

Fam. Aphididæ.

Fam. Psyllidæ.

The feeding habits of these families are similar to the preceding. The possession of a suctorial proboscis makes it possible for them to obtain the liquid contents of the cells by merely puncturing the walls.

Order Lepidoptera.

The larvæ in this case consume the entire cells that line the interior of the galls.

Order Coleoptera.

Feeding habits as in the preceding order.

Order Diptera.

Fam. Cecidomyidæ.

Fam. Trypetidæ.

Concerning the feeding habits of this order, Packard[38] states that the Cecidomyia larvæ must absorb their nourishment through the skin or suck it in at the mouth. He bases his conclusion on the facts that the larvæ are devoid of jaws and that excrement is not found in the mature galls.

Walsh[44] from the same data has come to the conclusion that the larvæ abrade the interior of the galls with the chitinous structure, the so-called breast bone, on the ventral surfaces of their bodies. The irritation produces a flow of liquid from the cells and upon this the larvæ feed. He further states that the mouth of the larva of *Eurosta solidaginis* Fitch possesses a horny, black termination that probably serves the same purpose of abrasion as the breast bone of the Cecidomyidæ.

Both of these observers have concluded that the nourishment is obtained by the larvæ without the destruction of the cell walls, and that these do not form a part of the food of the larvæ. My observations confirm this view. In several species such as *Lasioptera corni* Felt and *Cecidomyia ocellaris* O.S. (Figs. 33, 40), the walls of the cells, through which the larvæ were obtaining food, were apparently uninjured. In other forms as *Cecidomyia triticoides* Walsh (Fig. 37), and *Cecidomyia pellex* O.S., the cells of the nutritive zone had collapsed as the contents were withdrawn.

Order Hymenoptera.

Fam. Tenthredinidæ.

By the time the larvæ in this family are full fed, nothing remains of the galls but a thin rind on the outside of each. Both the cell walls and contents are swallowed indiscriminately.

Fam. Cynipidæ.

In this family the larvæ are invariably surrounded by a layer of thin-walled cells which usually present a radial elongation especially in the innermost rows (Fig. 58). The cells of this nutritive zone contain sugar, starch, oil emulsion and albumen. The amount of starch varies directly and the sugar inversely with the distance of the cells from the larvæ.

With regard to the manner in which this zone is used as food by the larva at least two views are current. The following statement of Kerner[3] may be presented as an adequate expression of one of these theories. "The larva when hatched finds the inner wall of the chamber which has been fitted for its temporary abode always provided with the necessary

food, and it immediately attacks and devours the juicy tissue with great avidity. The cells which are demolished, wonderful to relate, are replaced almost at once. The cells of the gall pith remain capable of division as long as the larva in the chamber requires food, and the surface cells which have been devoured in the gall chamber are soon replaced by new cells."

Küstenmacher[33] has advanced an entirely different view and his opinion may be taken as representing the theory of the other school of observers.

He states,—"Die im Innern entschlüpfte Larve, welche ihren Tisch reichlich gedeckt findet, beisst die innern Zellen des Nahrungsgewebes, welche lose, von der Eiweiss-Zucker-Oel-Emulsion strotzend, hervorragen, an und saugt dieselben regelmässig ringsherum aus, während die sehr dünnen Wandungen schmal schlauchartig übrig bleiben."

In deciding between these two theories the question to be answered is, does the larva eat both the walls and contents of the cells as stated by Kerner, or does it extract in some way the contents of the cells, leaving the walls practically intact? Several different points are involved in the discussion of this question. (*a*) The absence of frass in the larval chamber. (*b*) The completeness of the alimentary canal in the larva. (*c*) The nature of the stomach contents. (*d*) The presence of collapsed tissue and empty cells in the nutritive zone.

When a mature Cynipid gall is examined the larval chamber, in which the producer has passed through its early stages, is found unsoiled by excrement. Concerning this matter my observations agree with those made by Walsh in respect to the Cecidomyia larvæ. By way of comparison, if a mature gall is examined, the larva of which is known to eat the entire cells, a comparatively large quantity of excreted material is found (Fig. 68). The mature larva and its frass from a gall of *Pontania pomum* Walsh were dried in a desiccator and weighed. The following result was obtained:

Larva .0115 gm.
Frass .0319 gm.

In view of the comparatively large amount of frass in the sawfly gall, its absence in those of the Cynipidæ appears significant.

This fact concerning the larvæ of the Cynipidæ has not received attention since it has been supposed that the intestine of the Cynipid larva ends blindly. Comstock[21] makes the following statement on this point: "The larvæ are maggot-like and without a caudal opening to the alimentary canal." Serial sections were made of the larvæ of the producers *Philonix nigra* Gill (Fig. 61), and *Amphibolips confluens* Harris (Fig. 62). These sections prove conclusively the completeness of the

intestinal tract throughout, and that therefore if Kerner's theory be correct frass should be found as in the sawfly galls.

Further evidence in favor of Küstenmacher's view is furnished by a comparison of the stomach contents of a Cynipid and an inquiline larva. The former consists of a mass of extremely fine particles, among which can be detected nothing that is recognizable as having formed a part of a cell (Fig. 55). As this material passes along the digestive tract it becomes less dense the nearer it is to the posterior opening, and is entirely absent in the last part of the canal (Figs. 61, 62). The latter consists of much coarser material in which crystals, similar to those in the surrounding cells, and parts of cell walls can be easily detected. These contents are shown in Fig. 56, and at a higher magnification in Fig. 57. So characteristic is this difference between these two classes of stomach contents that by means of it alone a Cynipid can be easily distinguished from an inquiline larva.

The data already presented furnish indirect proof that only the contents of the cells form the food of the Cynipid larva. An examination of the walls of the cells immediately surrounding the larva gives direct evidence in favour of this hypothesis. The nutritive layers of a large number of Cynipid galls were examined at different stages of development, and in none of the examples did the walls of the cells appear to have been eaten away by the larva. A layer of collapsed tissue (Figs. 52, 59, 60), especially in the older specimens, is often found around the inside of the larval chamber and there are also many empty cells throughout the nutritive zone. These are shown in the inner row of cells in Figs. 59, 60. In some cases the radial walls of the cells are wrinkled, indicating that these cells are gradually contracting. This can be seen with the aid of a lens in Fig. 59. The folds are not found in the tangential walls of the cells. The majority of the empty cells are found in the row that lines the interior of the larval chamber (Fig. 60), but others are distributed irregularly throughout the entire nutritive zone. These can be seen in Figs. 59, 60. There does not seem to be the slightest possibility of doubt that the larva withdraws the contents from the cells of the nutritive zone without destroying the walls, and that in consequence the cells surrounding the larva gradually collapse.

If an inquiline larva is feeding in the gall, a ragged, broken edge of tissue is found lining the cavity in which it is living, a marked contrast to the smooth interior of the Cynipid larval chamber. This uneven edge is shown in Fig. 56, compare with Fig. 55. Neither of these views takes into account the possibility of enzyme action in rendering more soluble the contents of the nutritive zone.

A number of investigators have suggested that some form of enzyme is secreted by the larvæ of the Cynipidæ. Küstenmacher[33] indeed states in this connection that he could detect a distinctive odor from these larvæ, but enzyme action has always been considered in relation to the gall-producing stimulus and never with the feeding habits. The gradual decrease in the proportion of sugar to that of starch, in the contents of the cells, from the inside of the nutritive zone to the outside, would seem to indicate a relation between the relative amount of sugar and the proximity of the larva. Experiments were accordingly undertaken with the purpose of deciding whether the larva was capable of producing this change and of thus rendering the cell contents more easily soluble.

FIRST SERIES OF EXPERIMENTS.

Forty larvæ of *Amphibolips confluens* Harris just removed from the galls were placed in about 7 c.c. of starch solution made of corn meal. The test tube containing the larvæ was placed in a bath at 50° C., along with a control.

This starch was tested for sugar with Fehling's solution. No sugar was found at the end of 2 hrs. but after 20 hrs. a test for sugar was readily obtained.

SECOND SERIES OF EXPERIMENTS.

Forty-two larvæ were placed in the same quantity of starch solution and treated as in preceding case.

No sugar was found at the end of 8 hrs. but after 12 hrs. from the beginning of the experiment sugar was detected, and again at the end of 24 hrs.

THIRD SERIES OF EXPERIMENTS.

Thirty-five larvæ were placed in 7 c.c. of water and left for about 3 hrs. This water was then placed in an equal quantity of starch solution and kept at about 50° C. as before. The water was tested before it was poured into the starch and found to give an acid reaction. In this case sugar was detected in 50 hrs. and a very decided reaction was obtained after 70 hrs. The larvæ that had been washed were placed in starch and kept at 50° C. as before but sugar could not be detected.

In all the cases cited above, as a control experiment, starch without the larvæ was kept in the bath under the same conditions as that which contained the larvæ. This starch did not give the slightest indication of sugar at any time. From these experiments we conclude that the Cynipid larvæ must secrete an enzyme that has the property of changing starch to sugar. It seems quite possible that other ferments may be employed by the larva for similar purposes. To my knowledge

no tests have been made, but the observations of Weidel[45] point conclusively in this direction. He noted that the walls of the protective sheath become delignified; this is strongly suggestive of the presence of a hadromase or allied ferment.

With the purpose of discovering the source of the enzyme a number of species of Cynipid larvæ were examined for glandular structures. An enlargement of the first two segments immediately below the mouth was found to be a common characteristic of all these specimens. Regularly arranged on these projections are two pairs of openings as shown in Text Fig. 8. Longitudinal serial sections of *Philonix nigra* Gillette and *Amphibolips confluens* Harris show that these openings are connected by ducts with cavities lined by a glandular epithelium composed of large cells. From these cells the enzyme containing material passes into the cavity and from thence to the outside by means of the duct. There seems little reason to doubt but that these structures are salivary glands opening externally, and that they are the source of the enzyme. A gland with the connecting duct is shown in Text Fig. 9. Only the two species mentioned have been examined by serial longitudinal sections, but the external openings were noted in several forms and in all probability these glands are a characteristic common to all the Cynipidæ.

Fig. 8.—Head of Cynipid larva showing external openings of the salivary glands just below the mouth.

Fig. 9.—Longitudinal section of the larva of *Philonix nigra* Gillette, passing through a salivary gland and its associated duct.

Concerning the feeding habits of the larvæ of the Cynipidæ, we can state positively that the cell contents alone furnish the nourishment and that these are withdrawn from the cells without destroying the walls. An enzyme secreted by the salivary glands of the larva partially predigests this food. This ferment must act through the *cell membrane

*I have found that the froth on plants in which the "Spittle Insects" of the Family Cercopidæ develop, also contains an enzyme that rapidly changes starch to sugar. Experiments by Miss J. McFarlane that are not yet fully completed seem to indicate a larger amount of sugar in the stems surrounded by the froth than in corresponding parts of unaffected stems.

lining the interior of the larval chamber. None of the nourishment, taken into the alimentary canal, passes from it as excrement; it is either completely absorbed or remains in the digestive tract until the completion of the larval stage.

The invariable inert appearance and partially coiled condition of the larva would seem to indicate inactive feeding habits, but the theory of food absorption through the body wall is quite untenable; since the complete digestive tract, containing often large quantities of nourishment, as in Fig. 62, shows conclusively that the food enters the canal through the mouth.

GALL-PRODUCING STIMULUS

All actively growing tissues are capable of responding to a gall-producing stimulus: the growth energy already present in them is controlled and compelled to expend itself in a definite direction. These abnormal tissues that result have the common characteristic of remaining longer in a plastic state than if they had been produced under normal conditions of growth.

The stimulating influence produces an effect on tissues at a considerable distance from the centre of application. Thus in the Acarina galls this influence extends to tissues other than the epidermis on which the mites are located, and in such a case as *Stagmatophora cearothella* Cosens the epidermis of the stem undergoes division, although the larva is feeding in the pith (Fig. 17).

The power to stimulate tissues to abnormal activity is not confined to gall-producing larvæ. Certain inquilines likewise exhibit this ability to a limited extent. By a fortunate chance I have been able to establish this fact in the case of an inquiline larva found in the gall of *Holocnipis globulus* Fitch. Reference to Fig. 65 will show that a nutritive layer has been developed around the inquiline. That it possesses the power of stimulation to a less extent than the producer is obvious from the fact that it was unable to originate a cambium of its own, and in consequence the nutritive zone is incomplete on the side opposite to the producer-larva. This is shown in Fig. 65. Yet it is equally obvious that, feeding as it was in proximity to the cambium of the producer, it was able to excite that zone to the production of typical nutritive cells instead of the parenchyma zone cells that would have resulted had the producer alone been in control. Küster[15] records a similar instance of inquiline-produced galls in *Rhodites eglanteriæ*.

Küster[15] states that the excrement of the larval *Pontania vallisi* is capable of producing cell division. I have found this phenomenon occurring also in *Pontania pomum* Walsh and particularly good examples

in the undescribed sawfly gall on *Salix serissima* (Bailey) Fernald (Fig. 72). While I have made no attempt to determine by experiment the cause of this unusual example of cell proliferation, yet it would seem highly probable that the enzymes, introduced into the protoplasm by the ovipositor of the producer and swallowed by the larva, have not entirely lost their power by passing through the digestive tract but are still able to excite cell division.

The gall producer's influence works remarkable changes in the affected part of the host; even apparently new tissues, glands, trichomes, etc., make their appearance. The activity of its protoplasm is so much increased that hypertrophy or hyperplasia is an invariable accompaniment of gall production. The conventional view to account for these phenomena is that the protoplasm has been endowed with entirely new characteristics and power to produce something foreign to the normal host. But this is probably true only in a very limited sense, for according to my experience at least the prototypes of such apparently new tissues, etc., have been found elsewhere in the host or its relatives. Seemingly the correct explanation is that not only are dominant characteristics in the protoplasm stimulated but also in certain cases latent properties are called into activity, and thus apparently new structures appear in the host. Attention has already been drawn to examples confirming this opinion, but the evidence will now be more fully elaborated in the case of glands, trichomes and aeriferous tissue.

It may be stated as an unvarying rule, that when glands are present in the normal tissue they are always more plentiful or larger in the gall originating from that tissue. This is exemplified in the galls produced by *Eurosta solidaginis* Fitch (Fig. 42), *Aulacidea nabali* Brodie (Fig. 66), and numerous other species to which attention has been directed in the descriptive part of this paper.

But glands also occur in certain galls on parts of the host that are normally glandless; thus they are plentiful in the gall produced by *Neolasioptera perfoliata* Felt on *Eupatoria perfoliatum* L. (Fig. 23), but are not found at the same location in the normal. At first sight they appeared to be new structures, but were finally discovered in the normal host at the base of the stem. In *E. urticæfolium* Reichard they likewise occur in the transitional region between stem and root, while in *E. purpureum* L. they are present in the roots, petioles, and flowering axes as well as in the cortex and pith of the stem. In the case of gland production it is clear that not only have active characteristics of the protoplasm in that direction been stimulated to an activity greater than the normal maximum but nearly dormant properties have sometimes been aroused into action.

The trichomes worked out in a manner very similar to the glands. When the gall produced types different from the normal they were searched for successfully on the reproductive axes of the host. The unicellular, acicular hairs of *Eriophyes querci* Garman (Fig. 6) are totally unlike the stellate hairs of the leaf, but their exact counterparts are found on the reproductive axes of the host *Quercus macrocarpa* Michx. The much convoluted type of hair present in the Acarina dimple gall on the leaves of *Acer negundo* L. (Fig. 4) are found plentifully distributed over the reproductive axes, although the normal leaf hairs are straight.

The production of aeriferous tissue in certain Salicaceous galls substantiates in quite as striking a manner the view I have advanced. These galls contain examples of a typical aeriferous tissue, comparable indeed to that found in such aquatics as Nymphæa, Potamogeton or Saururus, while in the corresponding part of the host it does not occur. Indeed, this statement may be extended to include all the species of the host genus. A cross section of the gall originated on *S. cordata* Muhl. by *Cecidomyia triticoides* Walsh shows this tissue surrounding each larval cell. It is present throughout the cortex of the stem and extends entirely across the pith (Figs. 34, 35, 36). This tissue is found also in the gall originated on the leaf of the same willow by *Pontania pomum* Walsh (Fig. 77), but is not found in the normal tissues; indeed, the mesophyll of the leaf of *S. cordata* Muhl. is peculiarly compact in structure. It is figured by Cook[22] in the cortex of the stem gall produced on *S. discolor* Muhl. by *Cecidomyia rigidæ* O.S.

With the purpose of determining the distribution of this tissue in the normal stem a number of species of Salicaceæ were examined by Mr. T. A. Sinclair and myself with the following results, a detailed description of which will be published later. It was found in the primary cortex of the stems of the following species and invariably more plentiful at the nodes,—*Salix humilis* Marsh., *S. alba* L., *S. rostrata* Richards, *S. lucida* Muhl., *S. discolor* Muhl., *S. nigra* Marsh., *S. longifolia* Muhl., *S. serissima* (Bailey) Fernald, *S. cordata* Muhl., *Populus deltoides* Marsh., *P. balsamifera* L., P. *tremuloides* Michx. and *P. grandidentata* Michx. It was also differentiated to some extent in the pith of the stems of *P. balsamifera* L. and *P. deltoides* Marsh., *P. grandidentata* Michx. and *P. tremuloides* Michx. The only indication of this tissue found in the stem pith of Salix was in sections through the bases of branches of *S. cordata* Muhl. and *S. alba* L. Possibly it may be present in the corresponding region in other species. It can be traced a greater distance from the growing tip in the cortex of Populus than in Salix before it becomes unrecognizable owing to compression. It is apparently nearly always present in the pith and cortex of the reproductive axes of Populus and

Salix. The leaf petioles of the following species were found to contain it,—*Populus balsamifera* L., *P. deltoides* Marsh., *Salix humilis* Marsh., *S. alba* L. and *S. cordata* Muhl. The tissue is developed much more plentifully on the side adjacent to the stem.

In general then this tissue is indicated in the pith of the stem of Populus but is restricted in Salix to the bases of the branches. It is well represented in the primary cortex of the stems of both Populus and Salix, rather better so in the case of the former genus. It is abundant in such primitive regions as the reproductive axes, nodes and leaf traces. Thus the unexpected appearance of this tissue in the galls cited is readily explainable on the same grounds as in the case of glands and trichomes, namely, the power to produce this tissue is latent in the protoplasm of the host and it becomes sufficiently active to reinstate the tissue only when the gall-producing stimulus gives rise to unusual conditions.

Concerning the nature of this powerful stimulating agent there is at present a growing tendency to ascribe it to enzymatic action. It is difficult to say just how wide the application of this method of stimulus may be, but as plants present so many features in common in their reactions to produce the different types of galls, universal enzyme action would seem to be at least a safe working hypothesis. It is only, however, in the case of the Cynipidæ that we have any experimental evidence concerning enzymatic action. As described in a previous part of this section, I have been able to prove, in the case of the gall *Amphibolips confluens* Harris, that the larva secretes an enzyme capable of changing starch to sugar. It is now my purpose to discuss this fact in its relation to gall production.

Küster,[34] after experimenting with Cynipid galls in culture solutions, arrived at a conclusion that furnishes some experimental data on the subject. "Bei normaler Entwickelung wird der Inhalt der Nährgewebe von den Gallentieren verzehrt; unter abnormalen Verhältnissen kann aber das Nährmaterial von den Pflanzenzellen selbst verbraucht werden. Gallen von Pediaspis Aceris (Cynipide), die von ihren Bwohnern befreit und auf nährstoffarmen Lösungen oder auf gewöhnlichem Leitungswasser belassen werden, bleiben wochenlang am Leben; der Inhalt der Nährgewebe schwindet dabei. Werden Gallen gelicher Art ceteris paribus auf Zuckerlösung verbracht, so bleibt der Inhalt der Nährgewebe unverbraucht oder erfährt noch eine geringe Vermehrung."

These experiments prove that a gall is able to extract nourishment from the nutritive zone to assist in its growth in general. It appears axiomatic then that the greater the quantity of soluble food there is in the nutritive layer, in excess of what the larva requires, the larger is the supply the gall has at its command and the more marked will be the

proliferation of gall tissue. The larva consequently by accelerating the rate of change from starch to sugar is indirectly stimulating the protoplasm and thus controlling the growth of the gall. The general principle is applicable here that the available food supply governs very largely the size of an organ and consequently must influence the activity of its protoplasm. It is interesting to note in this connection that the size of the gall and the contained larva are directly proportional to each other. The relations between the two are reciprocal. The larger larva ensures a greater enzyme production and hence a more abundant food supply and presumably a larger excess for the stimulation to cell proliferation. The amount of enzyme action appears clearly to be proportional to the size of the larva. The evidence seems conclusive that the nutritive zone functions as an organ for preparing soluble food materials for both the larva and the gall. This evidence receives further confirmation from the fact that in addition to the empty cells lining the larval chamber there are others scattered throughout the nutritive zone often to its outermost layers (Fig. 59). This also seems to point to the conclusion that the contents of these cells have been used in supplying food for the proliferation of tissue in the other parts of the gall.

Summing briefly, the larva secretes an enzyme, capable of changing starch to sugar, which acts on the starchy constituents of the nutritive zone and accelerates the rate of their change to sugar. The material thus prepared supplies nourishment for both the larva and the gall. The protoplasm of the latter is thus rendered unusually active since it receives an abnormal quantity of available food material in a limited area. The hypertrophy and cell proliferation and probably also the appearance of vestigial tissue or other primary characters are the response of the protoplasm of the host to the additional food supply.

Attempts were made to substantiate this theory by further and more direct experiment. Diastase in solution was injected into seedling Windsor beans at different points with the purpose of stimulating the tissues to increased cell proliferation. When the place selected was just below the arch of the hypocotyl, a decidedly large callus was obtained in some of the experiments. These were not conclusive, however, owing to the variation in size of the normal plant in that region and the very great if not insurmountable difficulty of detecting increased callus formation when only differences in amount are to be expected. It is further very difficult to simulate the action of the producer-larva in bringing the diastase into contact with the proper tissue.

The discovery of an enzyme as an exudation from gall-producer larvæ recalls the statement of Laboulbène[36] that he had induced cell proliferation by injecting into plant tissue the water in which larvæ had been washed.

The theory, just stated, furnishes an explanation intended to account only for the stimulation of the protoplasm expressed in cell proliferation, hypertrophy and the production of unusual structures. There are other gall characteristics, however, that can scarcely owe their origin to the action of enzymes alone on the protoplasm of the host. For example, the colour of galls appears to be controlled partly at least by the intensity of the illumination. Thus the galls produced on *Salix cordata* Muhl. by *Pontania pomum* Walsh are little, if at all, coloured when the host is growing in deeply shaded stations. Besides this environmental effect, however, there is another factor that may also have an influence on the colour of this gall. De Vries[26] states that the red colour in plants is a dormant characteristic in the protoplasm that can be reinstated by stimulation. As a distinct confirmation of his view he found that red tints were produced in the leaves of *Viburnum opulus* L. as a consequence of bruising. This experiment seems to be closely paralleled in the sawfly gall *Pontania pomum* Walsh, where a red colour is apparent in the leaf of *Salix cordata* Muhl. in a very short time after oviposition. It seems very probable that in this case as in that of Viburnum the dormant red characteristic has been reinstated by the mere mechanical injury. It is noteworthy in this connection that shades of red are the predominating tints in gall structures, so that in the production of colour enzymatic action may frequently be operative in reinstating the dormant character red, especially in the case of galls in which the mechanical injury is negligible.

Further, the shape of the gall and the relation of the various zones to each other are not explainable by reference to any one factor. They doubtless result from a combination of factors. Just what all of these may be is yet not apparent but this much is certain that there appears to be an entire lack of evidence supporting the view that the protoplasm of the host has become endowed with a property that enables it to produce a fairly definitely shaped but withal abnormal structure. Such a pronounced change would surely be expressed in the hereditary characteristics, yet there is not a vestige of proof tending to show that insect galls ever produce the slightest variation in the descendants of the host. Not only so, but in the case of stems growing beyond the gall, there is no certainty that the prolongations are abnormal except for the slight dwarfing which is possibly explainable on the basis of an interrupted food supply. Examples of such stems are furnished by *Cecidomyia triticoides* Walsh on Salix, *Chermes abietis* Linn. on Picea, or *Eurosta solidaginis* Fitch on Solidago. Küster also found in his regeneration experiments that the roots produced from specimens of *Pontania salicis* were perfectly normal. There is still another argument to be cited in opposition to this view, in the fact that one gall may be parasitic on another. Thus when

Biorhiza forticornis Walsh is produced on *Neuroterus batatus* Fitch the stimuli from the different producers are exerted on nearly the same region of the host at the same time, as both these species are stem galls and commence to develop just as the buds are opening. In such a case as this if we assume that the protoplasm of the host has acquired characteristics necessary to the production of a certain form of gall, it seems unlikely that it could also possess the characteristics that would enable it to originate an entirely different type at the same time.

With the exclusion of the likelihood that the genetic characteristics of the protoplasm have been modified in any way, we must turn to the environmental factors to account for the shape of the gall and the relations of its various zones. Among these one feature that must have a certain amount of controlling effect is the direction in which the stimulus is applied. The various types of dimple and pouch galls, in which a curving of the affected organ is a very marked feature, are originated by stimuli disseminated in one direction only, while a Cynipid gall with its characteristic, spherical inner gall arises when the influence is about equally distributed in all directions. In some species it is also clear that the location of the egg has produced an effect on the external form of the gall. If the egg is deposited on the epidermis of the host and the tissues grow up around it, a gall of the type produced by *Cecidomyia ocellaris* O.S. results (Fig. 33). Even in the Cynipidæ this factor has been in operation. In species of Andricus the openings of the canals give a characteristic appearance to the galls, and in *A. petiolicola* Bassett the gall is drawn out to a decided tip in the region of the canal. These canals owe their origin to the fact that the galls are of the "Umwallung" type, and the larvæ have been enclosed by the growth of the surrounding tissues.

In some galls such as *Dryophanta palustris* O.S. a cambium is differentiated at a very early developmental stage, and has a very marked influence on the general relation of the zones in the gall. This cambium layer is shown in Fig. 49. The cells produced from the inside of this cambial tissue constitute the nutritive and sclerenchyma zones, while those given off from the outside form the parenchyma zone and epidermis. The former that are under the immediate control of the larva and less exposed to external conditions come to differ more markedly from the normal than do the latter that are nearer the outside limit of the larva's sphere of influence.

Summary.

The idea that the gall-producing stimulus must of necessity be applied directly to the cambium layer is not true in all cases, as any actively growing tissue will respond to a producer's influence.

The effect of this stimulus is operative on tissue at a considerable distance from the centre of application.

Certain inquilines in Cynipid galls possess the gall-producing power but to a less extent than the real producer.

Cynipid producers and probably others secrete an amylalytic ferment that pre-digests food for the larva and may indirectly stimulate cell proliferation by storing the nutritive zone with an unusually large quantity of available nourishment which can diffuse to all parts of the gall.

The gall-producing stimulus renders the protoplasm of the host more active and awakens in it dormant characteristics, but apparently does not endow it with power to produce entirely new structures. This has been demonstrated in the case of glands, trichomes and aeriferous tissue.

The red colour of galls is perhaps a dormant characteristic that may be reinstated by enzymatic action but there are other possible inducing factors such as the light relations and in sawfly galls mechanical injury by the act of oviposition.

The shape of galls is controlled partly at least by the direction of the stimulus and the location of the egg of the producer. In galls such as the Lepidopterous types, where the larva burrows into the tissues after leaving the egg, this feature has no effect.

The relation of the various zones in the Cynipid galls is influenced in some cases by the early differentiation of a cambium layer.

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EXPLANATION OF PLATES.

PLATE I.

Fig. 1. *Eriophyes Sp.* (*Populus tremuloides* Michx.). Section showing the folding of the upper epidermis of the leaf. ×50.

Fig. 2. *Eriophyes Sp.* (*Populus grandidentata* Michx.). Section showing the nature of the folding produced on the lower surface of the leaf. ×60.

Fig. 3. *Eriophyes Sp.* (*Fagus grandifolia* Ehrh.). Section through a number of capitate trichomes. The almost normal character of the leaf is shown. ×50.

Fig. 4. *Eriophyes Sp.* (*Acer negundo* L.). Section through the gall, showing a large number of convoluted trichomes. ×35.

Fig. 5. *Eriophyes Sp.* (*Prunus nigra* Ait.). Longitudinal section in which is shown the elongation of the cells in the direction of the long axis of the gall. The peculiar nature of the trichomes is also shown. ×30.

Fig. 6. *Eriophyes querci* Garman (*Quercus macrocarpa* Michx.). Section in which the long acicular trichomes are shown, as also the thickening of the leaf blade. ×30.

Fig. 7. Unclassified gall on the leaf of *Populus balsamifera* L. The uniform nature of the abnormal cells is apparent. The gall cavity is occupied by the mycelium of a fungus. ×10.

Fig. 8. Transverse section of band of sclerenchyma from the preceding gall, showing the pores that traverse the tissue. ×120.

PLATE II.

Fig. 9. Aphid corrugations on the leaf of *Betula lenta* L. produced by the fourth generation of *Hamamelistes spinosus* Shimer. The formation of the larval chambers by the closing of the folds is shown. ×22.

Fig. 10. *Hamamelistes spinosus* Shimer on the leaf of *Hamamelis virginiana* L. Transverse section that passes through a spine, cross sections of two bundles are shown. ×35.

Fig. 11. *Chermes abietis* Chol. on the stem of *Picea abies* (L) Karst. Longitudinal section, showing two larval chambers with their apertures of exit. A number of resin ducts are cut near the margin of the section. ×30.

Fig. 12. *Hormaphis hamamelidis* Fitch on the leaf of *Hamamelis virginiana* L. Longitudinal section passing through the aperture of exit. ×10.

Fig. 13. *Chermes floccus* Patch on the stem of *Picea mariana* (Mill.) B.S.P. Transverse section, showing the smaller accessory resin ducts. ×25.

Fig. 14. *Pemphigus rhois* Walsh on the leaf of *Rhus typhina* L. Longitudinal section of a young gall, showing a number of glands. ×15.

PLATE III.

Fig. 15. *Pachypsylla celtidis-mamma* Riley on the leaf of *Celtis occidentalis* L. Section through the larval cavity, showing the cambium tissue and the sclerenchyma sheath bordering it on the outside. ×15.

Fig. 16. *Memythrus tricinctus* Harris on the stem of *Populus tremuloides* Michx. Cross section through the thickened annual rings, showing the clumps of bast fibres. ×20.

Fig. 17. *Stagmatophora ceanothiella* Cosens on the stem of *Ceanothus americanus* L. Cross section, showing secondary growth in the wood and the abnormal glands in the cortex. ×50.

Fig. 18. Normal stem of the host of the preceding species. Section taken near the gall; glands are not present in the cortex. ×50.

Fig. 19. Glands found in the cortex of *S. ceanothiella* Cosens; these correspond to those shown in Fig. 17. ×150.

Fig. 20. *Gnorimoschema gallæsolidaginis* Riley on the stem of *Solidago canadensis* L. Transverse section showing an abnormally large gland in the cortex. ×45.

PLATE IV.

Fig. 21. *Eucosma scudderiana* Clemens on the stem of *Solidago canadensis* L. Transverse section showing the proliferation in the bundles and the medullary rays and also the enlarged glands in the cortex. ×75.

Fig. 22. *Gnorimoschema gallæasterella* Kellicott on the stem of *Solidago latifolia* L. A transverse section through one side of the aperture of exit, the material used by the larva in smoothing the sides of the hole for the reception of the plug is shown. The cross checking in this material can also be seen. ×120.

Fig. 23. *Neolasioptera perfoliata* Felt on the stem of *Eupatorium perfoliatum* L. Transverse section showing an unusual type of cell division in the cortex and epidermis of this gall. The glands shown near the inner boundary of the cortex are not found in the normal stem at the same height. ×55.

Fig. 24. *Rhabdophaga strobiloides* Walsh on the stem of *Salix cordata* Muhl. Longitudinal section showing the larva in contact with the small celled tissue at the apex of the stem. ×25.

Fig. 25. *Rhabdophaga batatas* Walsh on the stem of *Salix humilis* Marsh. A transverse section that shows the larval chamber surrounded by a nutritive zone which is bounded on the outside by a well defined protective sheath. ×22.

Fig. 26. A part of the protective sheath of the preceding species enlarged to show the unequal thickening of the tangential walls. ×200.

Fig. 27. *Cecidomyia majalis* O.S. on the leaf of *Quercus coccinea* Muench. Section at right angles to the midrib. The folding of the leaf is shown and the uniform character of the mesophyll of the gall. The epidermis lining the gall cavity is shown intact. ×15

PLATE V.

Fig. 28. *Abies balsamea* (L.) Mill. Transverse section of normal leaf. ×35.

Fig. 29. *Cecidomyia balsamicola* Lintner on the leaf of *A. balsamea* (L.) Mill. Transverse section showing the folding of the leaf and the elongation of the mesophyll cells. The irregularity of the cells in the strengthening layer of the resin ducts can also be seen. ×35.

Fig. 30. *C. balsamicola* Lintner on the leaf of *A. balsamea* (L.) Mill. Transverse section through the midrib. The chief points shown are the irregularity in the development of the endodermis, the large amount of the transfusion tissue and the relatively small amount of the non-pitted parenchyma. ×100.

Fig. 31. *Abies balsamea* (L.) Mill. A section, through the midrib of a normal leaf, corresponding to the preceding section (Fig. 30). ×100.

Fig. 32. *Cecidomyia impatientis* O.S. on *Impatiens biflora* Walt. Section through a larval chamber, showing the general nature of the cells of the gall and the smaller cells of the nutritive layer. The two dark masses attached to the nutritive tissue in the lower part of the gall cavity consist of the mycelium of a fungus. ×30.

Fig. 33. *Cecidomyia ocellaris* O.S. on the leaf of *Acer rubrum* L., showing the almost unchanged character of the leaf immediately below the larva and the great amount of proliferation in the region surrounding it. The general arrangement of the cells at right angles to the leaf blade is also shown. ×30.

Fig. 34. *Cecidomyia triticoides* Walsh on the stem of *Salix cordata* Muhl. Transverse section in which is shown the general arrangement of the larval chambers and the distribution of aeriferous tissue throughout the cortex and pith of the gall. ×10.

PLATE VI.

Fig. 35. *Cecidomyia triticoides* Walsh on the stem of *Salix cordata* Muhl. Transverse section showing the character of the aeriferous tissue. ×50.

Fig. 36. *Cecidomyia triticoides* Walsh on the stem of *S. cordata* Muhl. Transverse section of a young gall, showing the well defined nutritive layer lining the larval cavity and the protective zone bounding this tissue on the outside. The aeriferous tissue is also shown. ×60.

Fig. 37. *Cecidomyia triticoides* Walsh on the stem of *S. cordata* Muhl. Transverse section through the nutritive and protective zones of a mature gall. At the top of the figure is a dark band of collapsed nutritive cells; below that a lighter coloured and wider band of sclerenchymatous cells, the lumen of each filled with a crystal of calcium oxalate; and below that again a layer of cambium of nearly the same width as the preceding zone. ×150.

Fig. 38. *Cecidomyia triticoides* Walsh on the stem of *S. cordata* Muhl. Transverse section of a young gall, corresponding to the preceding mature form. The nutritive zone is at the top of the figure, its cells are filled with rich protoplasmic contents, with the exception of those in the upper row and a few scattered ones throughout the zone. The protective zone is shown below this tissue, but the cambium layer is not differentiated in the early stages. ×150.

Fig. 39. *Cecidomyia bulla* Walsh on the stem of *Helianthus divaricatus* L. Transverse section through stem of host and attached gall, showing the elongation of the fibro-vascular bundles in the direction of the gall axis and the very marked proliferation in the medullary rays. At the upper part of the figure, in the gall cortex, an enlarged gland is partly shown and also other glands at the junction of the gall and the stem of the host. ×18.

Fig. 40. *Lasioptera corni* Felt. on the leaf of *Cornus alternifolia* L. The section shows the lower epidermis and one row of mesophyll cells in normal position and also the strongly curved character of the upper epidermis and the remaining mesophyll cells. The normal appearance of all the cells is also apparent. ×18.

Fig. 41. *Lasioptera impatientifolia* Felt. on the leaf of *Impatiens biflora* Walt. Section at right angles to the midrib, showing the generally uniform character of the cells. Cells containing the mycelium of a fungus are shown a short distance in from the

gall cavity and above it. These cells give a false appearance of a protective zone. ×20.

Fig. 42. *Eurosta solidaginis* Fitch on the stem of *Solidago canadensis* L. Transverse section, showing the proliferation of glandular tissue and the general arrangement of the glands along the lines of the fibro-vascular bundles. ×25.

PLATE VII.

Fig. 43. *Andricus piger* Bassett on the leaf of *Quercus coccinea* Muench. At the lower part of the figure a thick nutritive layer is shown, bordering the larval chamber; outside of this tissue is the protective zone from which a cone-shaped projection originates that blocks the canal leading in from the outside. The epidermis lining this canal is shown continuous with the general epidermis of the gall. ×25.

Fig. 44. *Andricus piger* Bassett on the leaf of *Q. coccinea* Muench. Section showing a nearly complete larval chamber. The other parts correspond to those in the preceding figure. The epidermis lining the canal is not shown so well in this case, as the section passes along the edge of the canal. ×25.

Fig. 45. *Andricus petiolicola* Bassett on the leaf of *Q. alba* L. Section passing through the main canal. The epidermis of the gall is shown passing into the trichome bearing lining of the gall. ×25.

Fig. 46. *Andricus petiolicola* Bassett on the leaf of *Q. alba* L. Section passing through the termination of the main canal, showing a number of trichomes and two larval chambers blocked by masses of sclerenchyma. ×45.

Fig. 47. *Andricus* (undescribed) on the leaf of *Quercus macrocarpa* Michx. Section passing through the edge of a canal and showing the two masses of sclerenchyma almost united. ×35.

Fig. 48. *Andricus imbricariæ* Ashmead on the stem of *Q. coccinea* Muench. Section showing the numerous bands of cells radiating out from the boundary of the protective sheath, the light coloured layer in the figure. The darker coloured nutritive zone bounds the protective layer and lines the gall cavity. ×20.

PLATE VIII.

Fig. 49. *Dryophanta palustris* O.S. on the leaf of *Quercus coccinea* Muench. Section of a very early stage in which the inner and outer galls are still in contact. The following points are shown, a canal passing from the outside into the larval chamber, the

trichome bearing epidermis of the gall continuous with the lining of this canal and passing into the inner row of cells of the nutritive zone, the bay-like depression in this zone where the canal enters. ×30.

Fig. 50. *Dryophanta palustris* O.S. on the leaf of *Q. coccinea* Muench. Section of a somewhat more mature stage than the preceding, showing the commencement of the separation of the inner gall from the outer in the region of the cambium layer. ×12.

Fig. 51. *Dryophanta palustris* O.S. on the leaf of *Q. coccinea* Muench. Section of the wall of the inner gall, showing the nutritive zone with a line of collapsed cells next the larval chamber and a row of empty cells just inside the collapsed tissue. The protective layer borders the nutritive on the outside and a few round cells of the parenchyma adhere to the protective zone. ×70.

Fig. 52. *Dryophanta palustris* O.S. on the leaf of *Q. coccinea* Muench. Section of the larval chamber of a mature specimen, showing the insect breaking out of the inner gall. At this stage the nutritive layer has entirely collapsed. ×15.

Fig. 53. *Cynips ? constricta* Stebbins on the leaf of *Q. coccinea* Muench. Longitudinal section showing the origin of the gall from the midrib of the host in the region of the cambium layer. ×100.

Fig. 54. *Cynips ? constricta* Stebbins on the leaf of *Quercus coccinea* Muench. Longitudinal section of an early developmental stage showing the general structure of the gall. The dark mass at the top of the figure represents the supplemental nutritive zone of the gall; it is separated from the spherical part of the gall by a cambium tissue. The protective sheath that separates the nutritive from the cambium in later stages is not yet differentiated. A nutritive zone is also shown lining the larval chamber. ×40.

PLATE IX.

Fig. 55. *Holcaspis bassetti* Gillette on the stem of *Quercus macrocarpa* Michx. Section through the gall cavity with enclosed larva. The character of the cells of the nutritive zone is shown and the unbroken edge of its inside boundary. The finely divided material of the stomach contents of the larva is also shown. ×60.

Fig. 56. Section of a larval inquiline from the gall *Holcaspis bassetti* Gillette. The broken edge of the tissue on which the larva has been feeding is shown, also the comparatively coarse material of the stomach contents. ×60.

Fig. 57. Contents of the stomach of the preceding inquiline. The black masses are parts of cell walls, while the lighter roundish particles are crystals. ×300.

Fig. 58. *Holcaspis bassetti* Gillette on the stem of *Q. macrocarpa* Michx. Section through the nutritive zone of a nearly full grown specimen. The nutritive zone is shown to consist of elongated cells next the larval chamber and elliptical further out. The dark zone is a crystal layer that bounds the nutritive zone on the outside. A cambium is differentiated between the nutritive and the parenchyma layers but it is not well shown in the figure. ×60.

Fig. 59. *Andricus singularis* Bassett on the leaf of *Quercus rubra L.* Section through the nutritive and protective zones, showing empty cells throughout the nutritive layer and the wrinkling of the radial walls of its cells in general. ×100.

Fig. 60. *Aylax glechomæ* Linné on the leaf of *Nepeta hederacea* (L.) Trevisan. Section through the nutritive and protective zones, showing the unbroken lining of the gall cavity and the row of empty cells that borders the larval chambers. ×80.

PLATE X.

Fig. 61. *Philonix nigra* Gillette. Longitudinal section of the larva, showing the external opening of the alimentary canal. ×15.

Fig. 62. *Amphibolips confluens* Harris. Longitudinal section of the larva, showing the completeness of the digestive tract. ×15.

Fig. 63. *Rhodites lenticularis* Bassett on the leaf of *Rosa blanda* Ait. Section through the larval chamber, showing the nutritive layer lining it. Bordering this tissue on the outside is the cambium zone from which practically the entire gall is originated. The dark band shown plainly at the right of the figure is the protective sheath. ×20.

Fig. 64. *Philonix erinacei* Beut. on the leaf of *Q. alba* L. Section in which the four typical zones of a cynipid gall are shown, namely nutritive, protective, parenchyma or tannin, and epidermal. The sclerification can be seen to have passed out into the parenchyma zone. ×25.

Fig. 65. *Holcaspis globulus* Fitch on the stem of *Q. alba* L. Section through adjoining larval chambers of a producer and an inquiline, a complete section of the latter is shown. The nutritive tissue that supplies the inquiline with nourishment can

be seen to have originated entirely from the cambium differentiated by the producer of the gall. Its irregularity on the side opposite to the producer is very marked. ×30.

Fig. 66. *Aulacidea nabali* Brodie on the stem of *Prenanthes alba* L. Section through the stem of the host and the attached gall. The relation of the cambium of the host to the cells of the gall tissue is shown. ×30.

PLATE XI.

Fig. 67. *Neuroterus majalis* Bassett on the leaf of *Quercus alba* L. Section through a larval chamber containing the pupa of the producer. The dark band around the inside of the gall cavity consists of the collapsed nutritive zone and the protective layer. At the upper right of the figure the general nature of the cells of the parenchyma zone is shown. ×50.

Fig. 68. *Euura S. gemma* Walsh on *Salix humilis* Marsh. Section through a mature gall, showing a larval chamber containing a pupal producer and several large masses of excrement. The general nature of the small celled tissue of the gall is also shown. ×30.

Fig. 69. *Euura* (N.S.) on the leaf of *Salix serissima* Fernald. Transverse section, showing one uninjured bundle of the petiole and the parts of two others widely separated by the proliferation of the tissue stimulated by the laceration of the bundles. ×35.

Fig. 70. *Euura* (N.S.) on the leaf of *Salix serissima* Fernald. Section of a younger stage than the preceding, showing as before one uninjured and two injured bundles. ×35.

Fig. 71. *Euura ovum* Walsh on the stem of *Salix humilis* Marsh. Transverse section through the stem of the host and the gall originated from it. It shows the wedge-shaped cavity occupied by the gall mass and the origin of the latter from a cambium tissue at the boundary of the pith of the host. ×18.

Fig. 72. *Euura* (N.S.) on the leaf of *Salix serissima* Fernald. Section of the gall showing proliferation induced by the excrement of a larval producer. ×18.

PLATE XII.

Fig. 73. *Pontania hyalina* Norton on the leaf of *Salix alba* L. Section of gall with larva still within the egg membrane. Proliferation is shown well advanced in all the tissues of the leaf. ×35.

Fig. 74. *Pontania hyalina* Norton on *Salix alba* L. Section showing the wound of the ovipositor. ×25.

Fig. 75. *Pontania hyalina* Norton on the leaf of *Salix alba* L. Section of a more mature stage than numbers 73 and 74. The amount of gall tissue derived from the various sources can no longer be distinguished. The uniformity of the tissue is very marked. ×25.

Fig. 76. *Pontania pomum* Walsh of the leaf of *Salix cordata* Muhl. Section through an early developmental stage in which the larva had not freed itself from the egg membrane. There is shown the laceration of the bundle of the midrib by the ovipositor and the proliferation in the various tissues of the leaf. ×20.

Fig. 77. *Pontania pomum* Walsh on *Salix cordata* Muhl. Section of a nearly full-grown gall, showing the distribution of the aeriferous tissue and the location of the vascular strands. ×18.

Fig. 78. *Pontania* (N.S.) on the leaf of *Salix humilis Marsh.* Section at right angles to the midrib of the leaf to which the gall is attached. The general character of the gall tissue is shown and the distribution of the vascular strands from the wounded bundle. ×20.

Fig. 79. *Pontania* (N.S.) on the leaf of *Salix humilis* Marsh. Section through the midrib from which two galls had originated. The bundle is shown completely severed. ×8.

PLATE XIII.

Fig. 80. *Pontania desmodioides* Walsh on the leaf of *Salix humilis* Marsh. Section through a chamber containing an unhatched larva. Proliferation is well marked in all the tissues of the leaf. ×40.

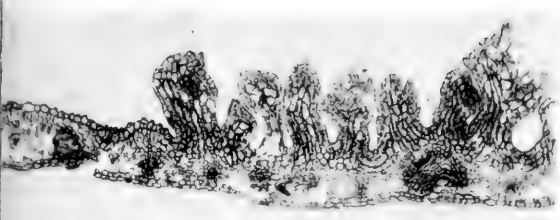
Fig. 81. *Pontania pisum* Walsh on the leaf of *Salix discolor* Muhl. Section of a mature gall, showing the general character of the tissues. The dark band at the upper right of the figure marks the line of attachment of the gall to the blade of the leaf. Just beneath this line the proliferation in the palisade parenchyma is shown. .×20.

Fig. 82. Undescribed gall on the leaf of *Salix lucida* Muhl. Section of a young gall on the midrib, showing the commencement of the proliferation in the pith of the bundle. ×20.

Fig. 83. Normal leaf of *S. lucida* Muhl. Section through midrib for comparison with the preceding. ×25.

Fig. 84. Undescribed gall on the leaf of *Salix lucida* Muhl. Section of a well-grown gall on the leaf petiole. The two arms of the bundle are shown widely separated by proliferation set up in the pith. The arrangement of the cells of the gall tissue in curved rows is shown and the presence of elongated air spaces between these. ×15.

Fig. 85. Undescribed gall on the leaf petiole of *Salix humilis* Marsh. Section showing the ovipositor wound. Around the edge of the incision is shown the cambium tissue from which the greater part of the gall tissue has been produced. ×18.



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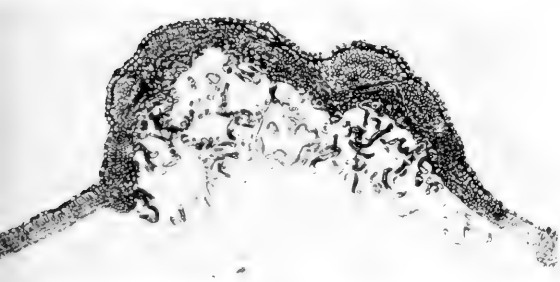

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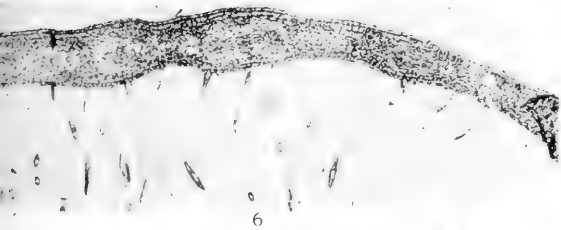

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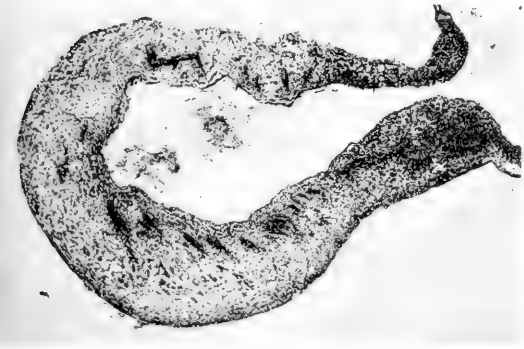

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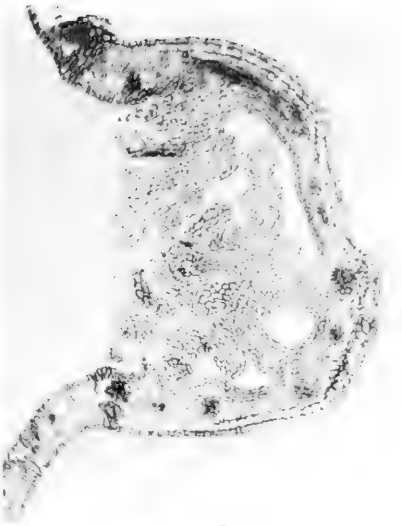

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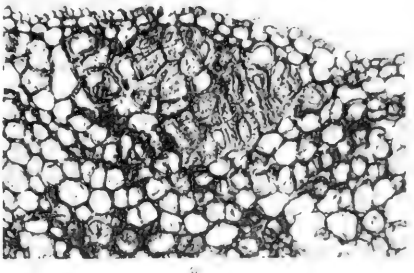

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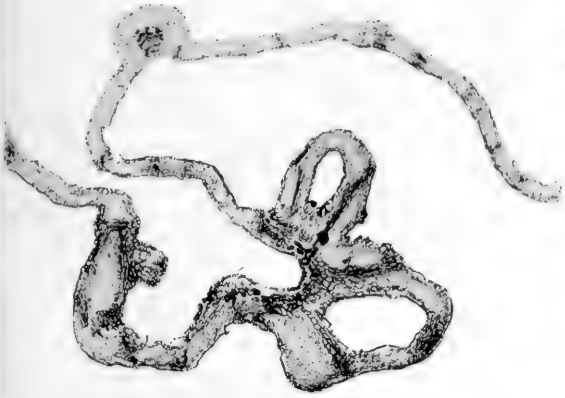

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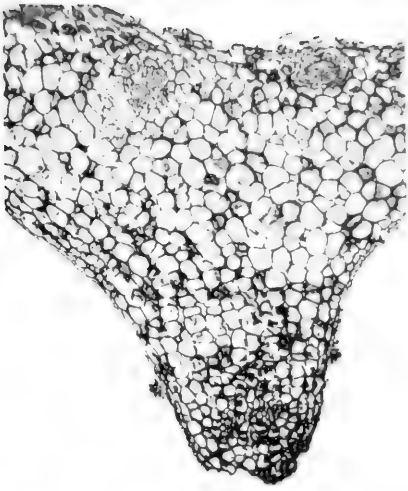

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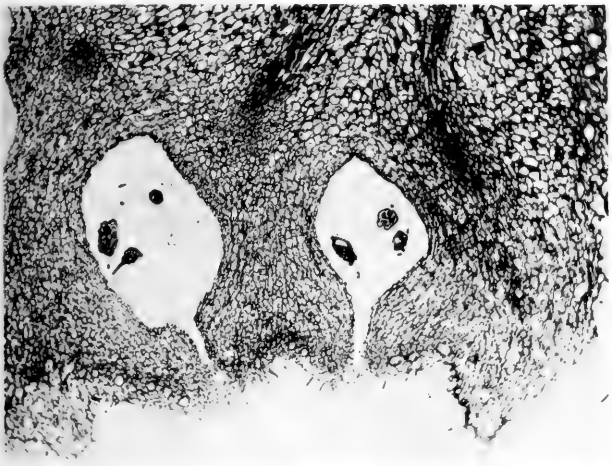

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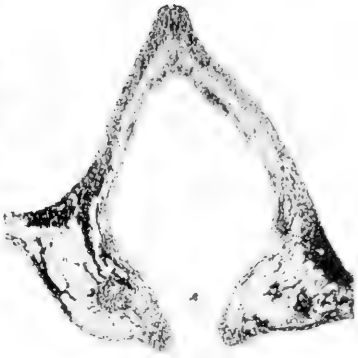

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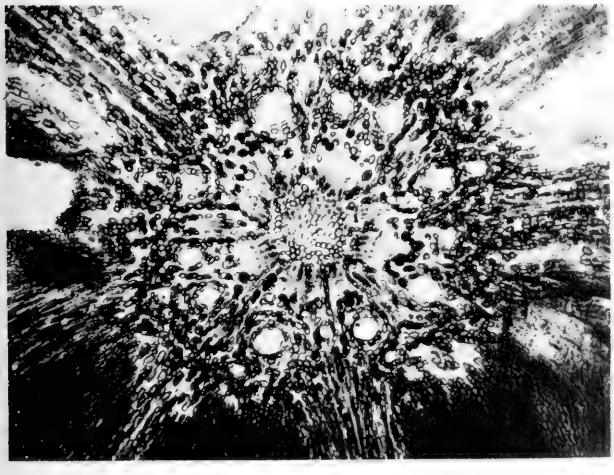

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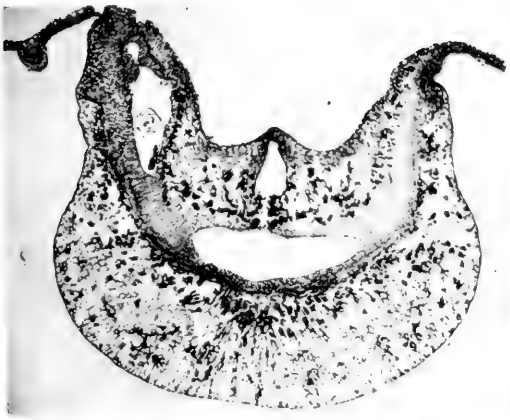

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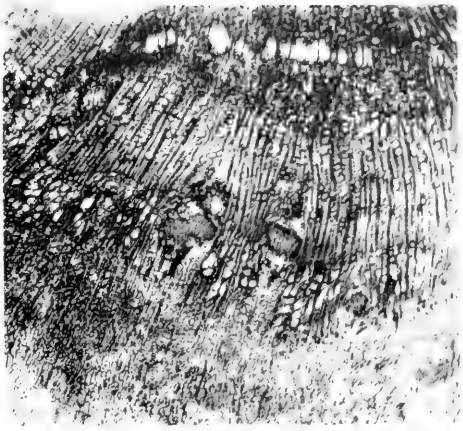

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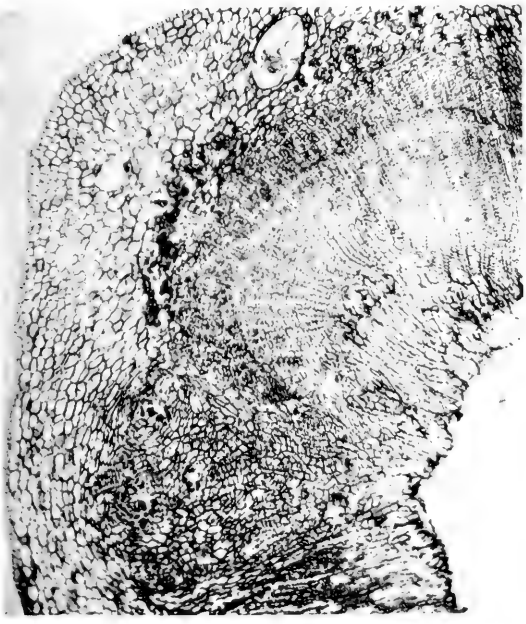

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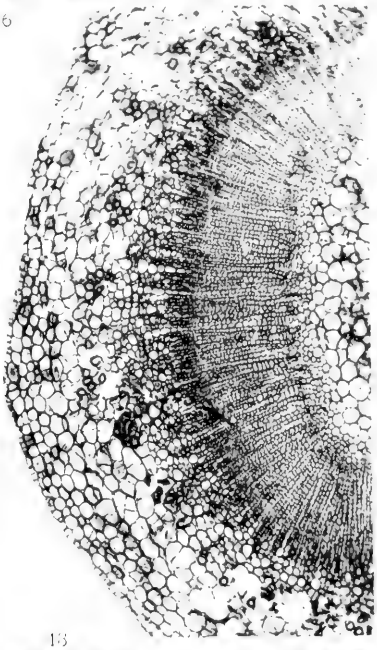

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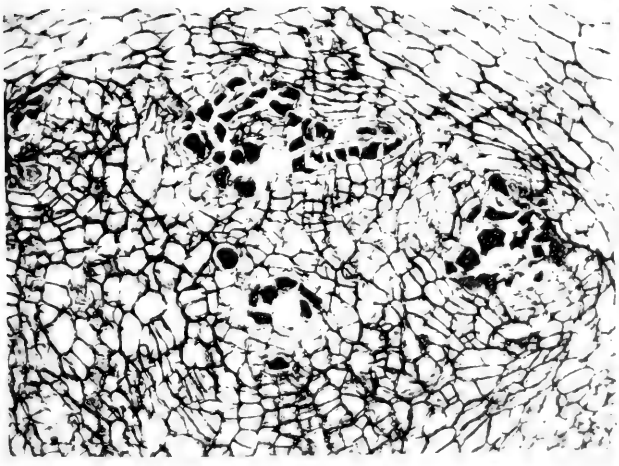

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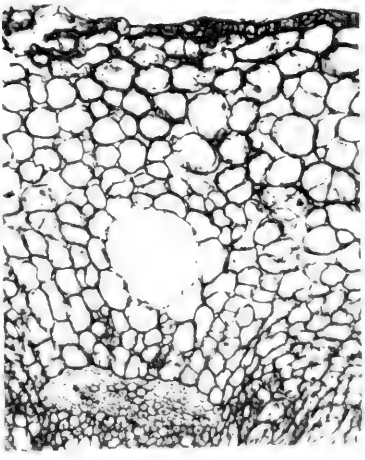

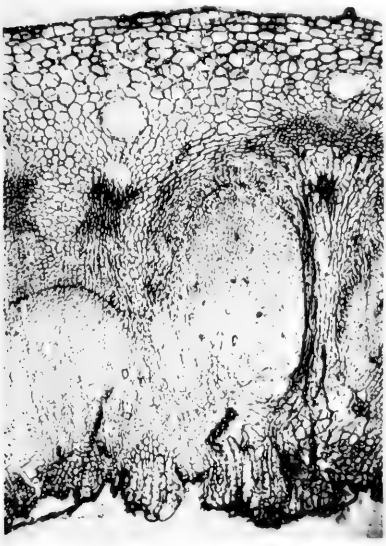

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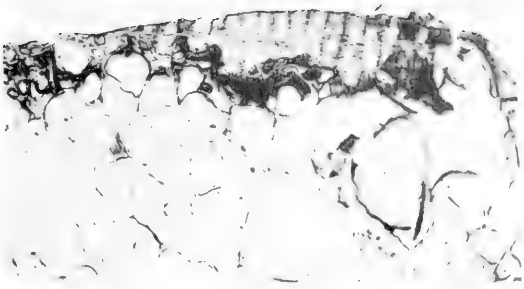

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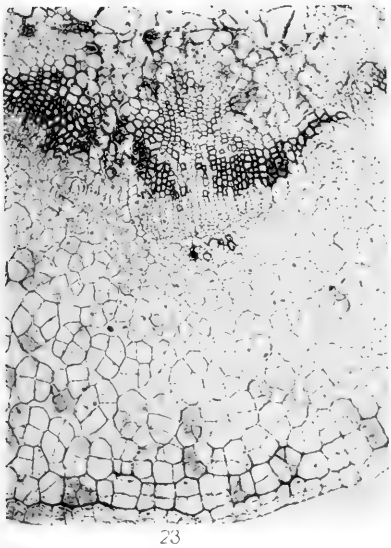

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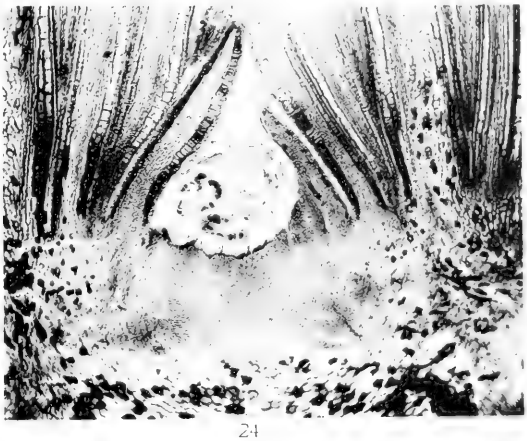

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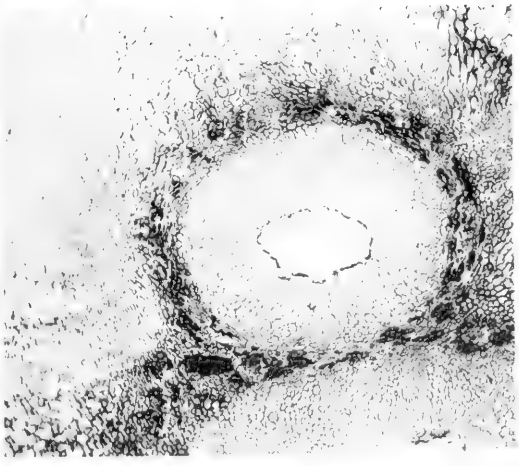

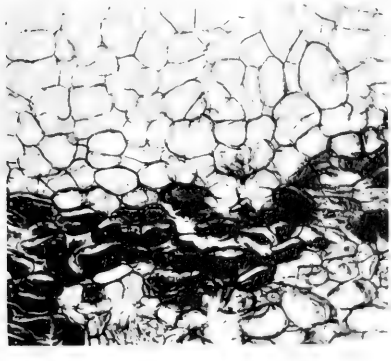

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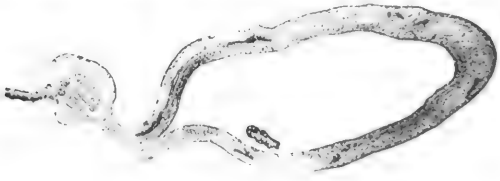

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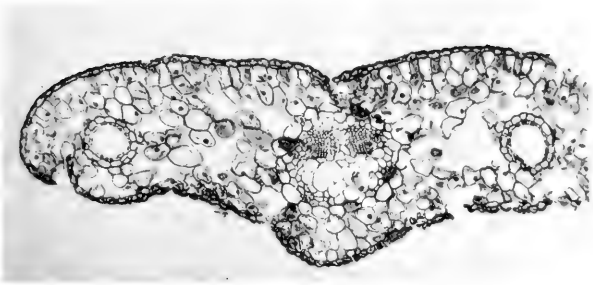

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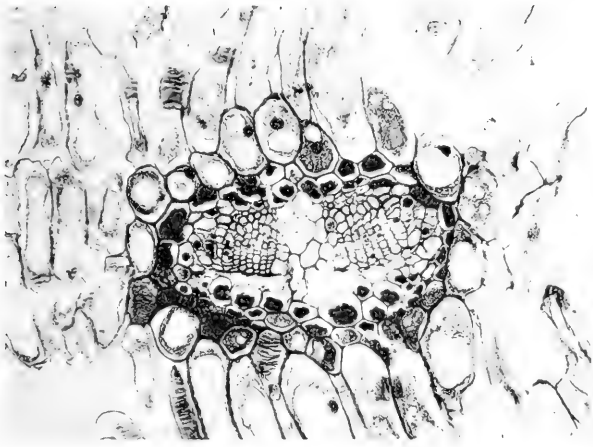

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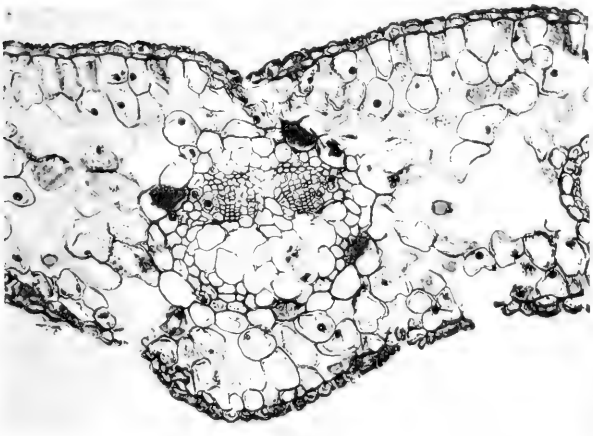

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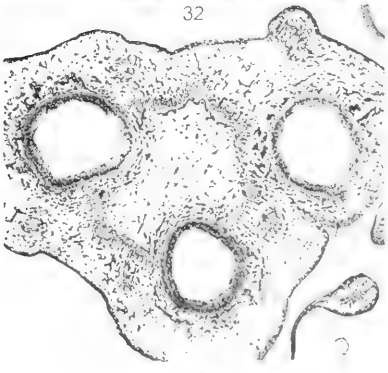

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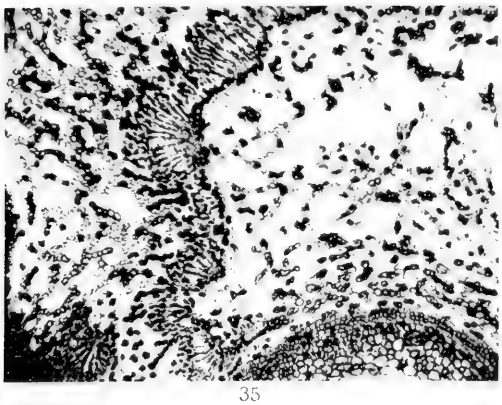

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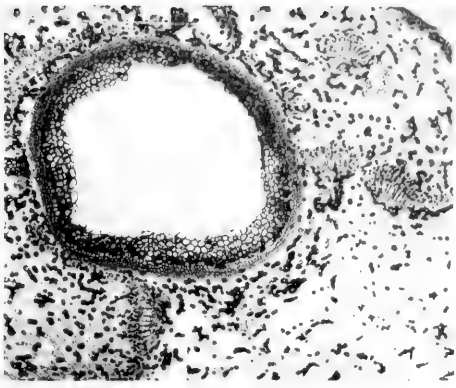

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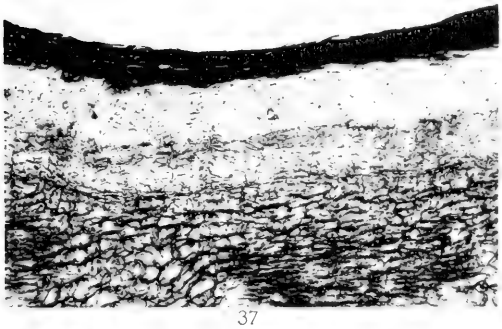

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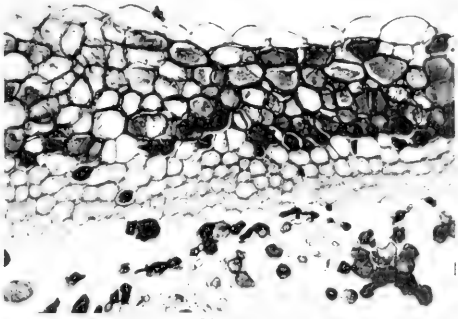

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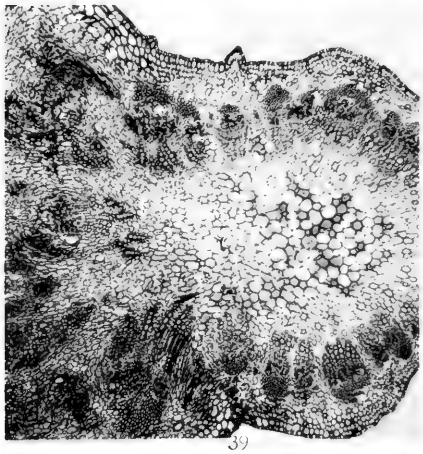

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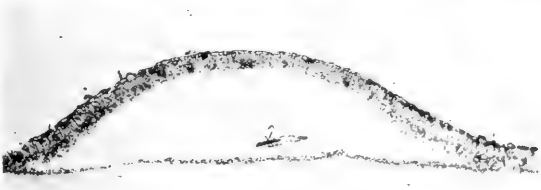

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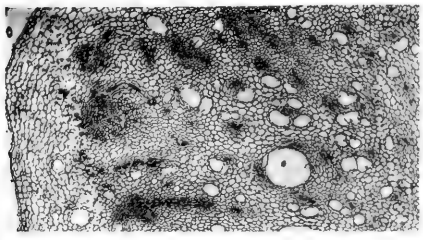

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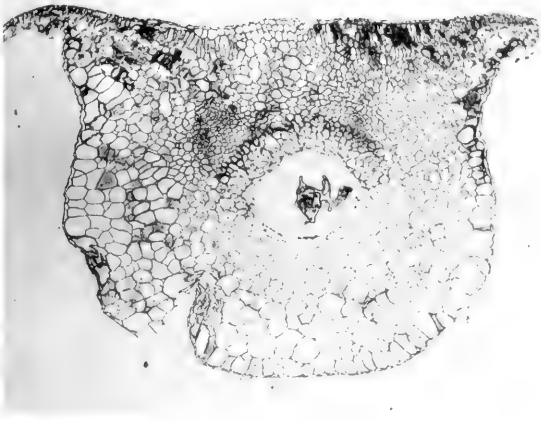

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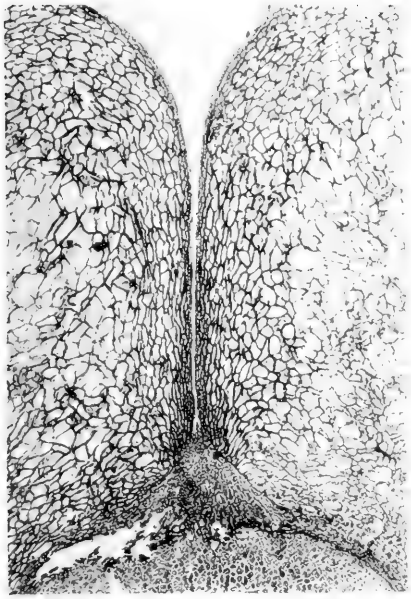

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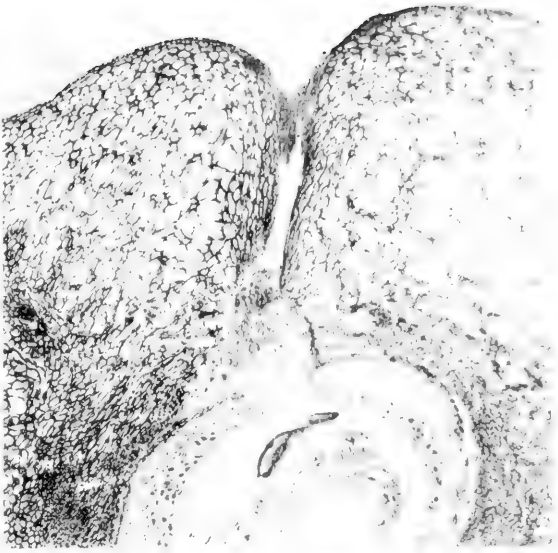

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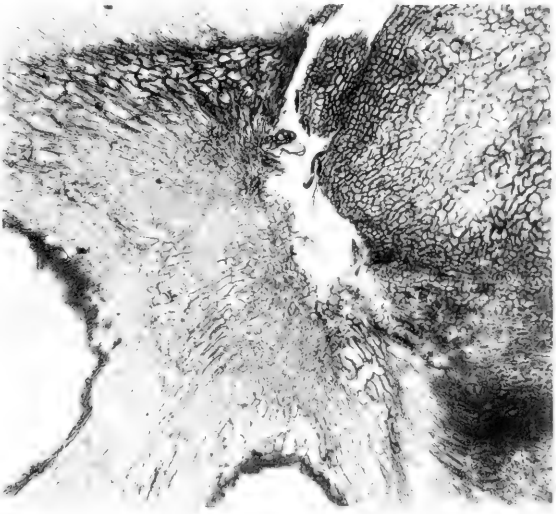

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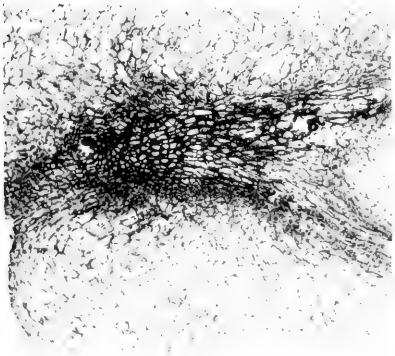

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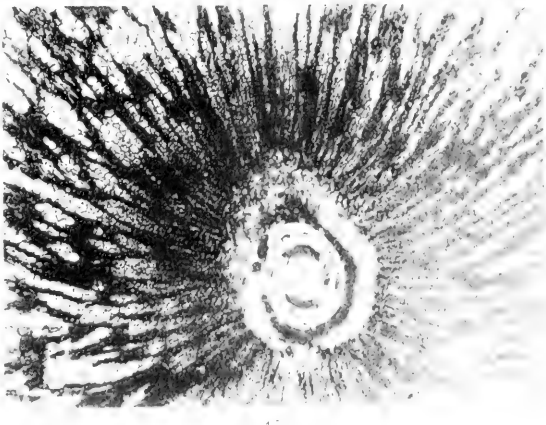

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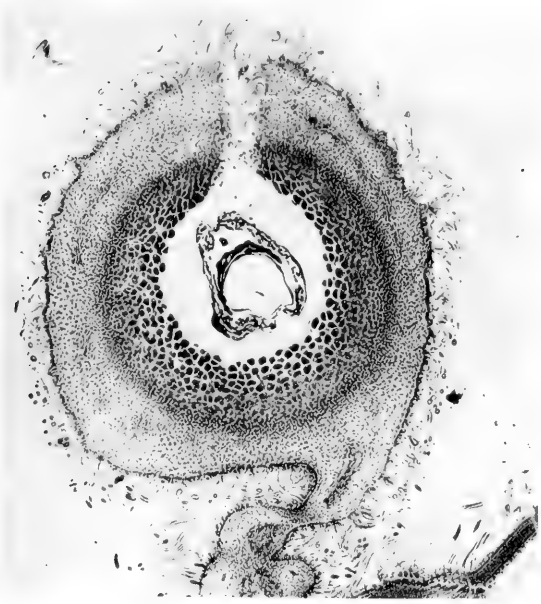

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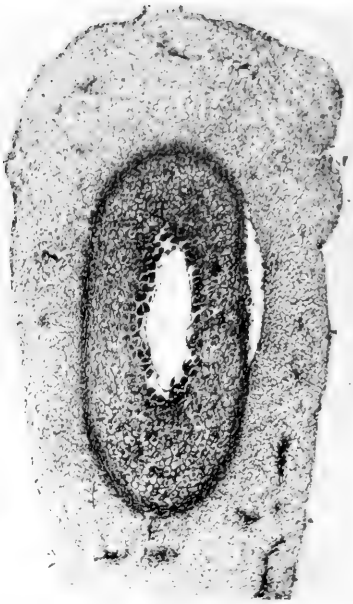

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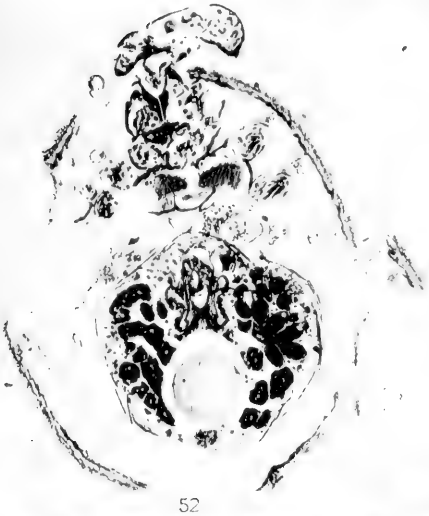

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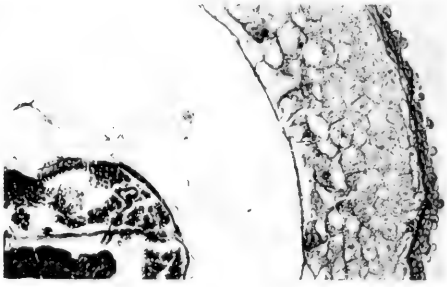

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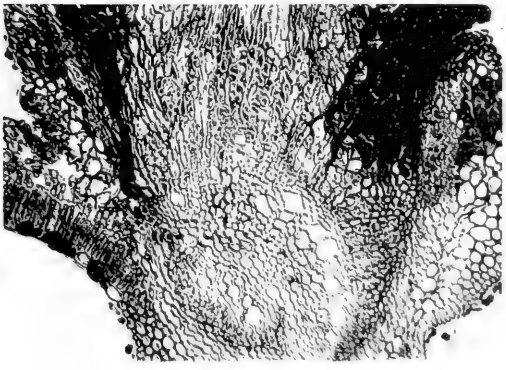

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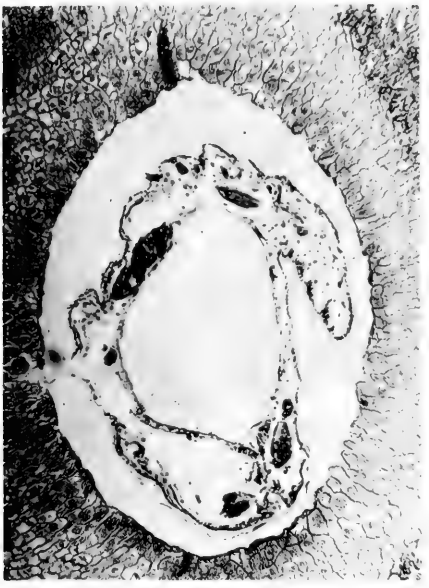

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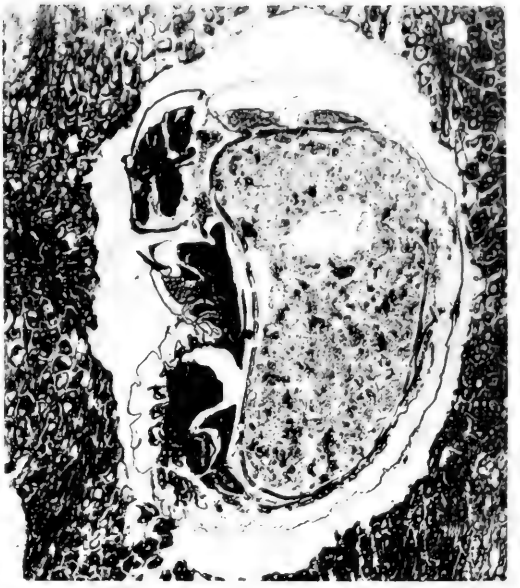

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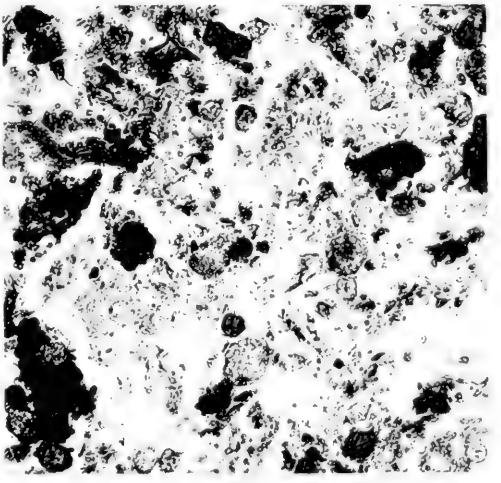

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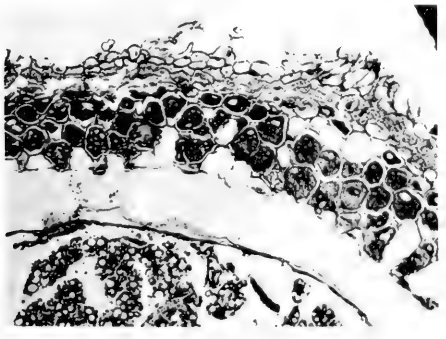

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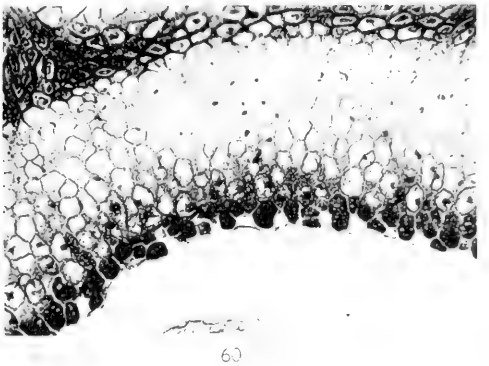

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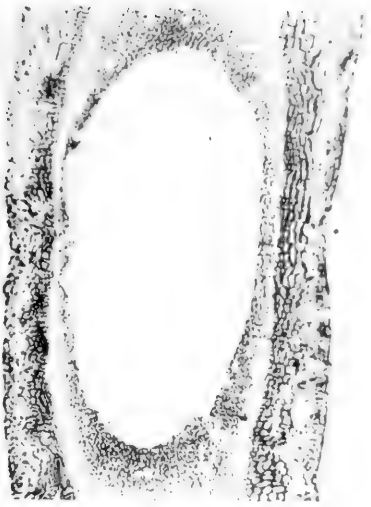

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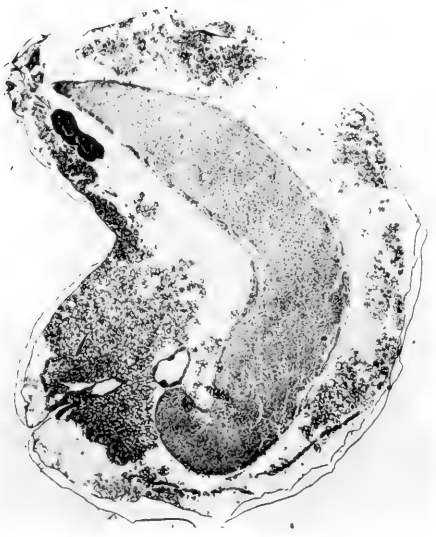

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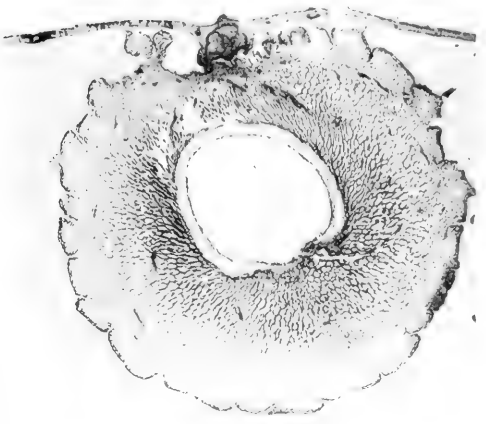

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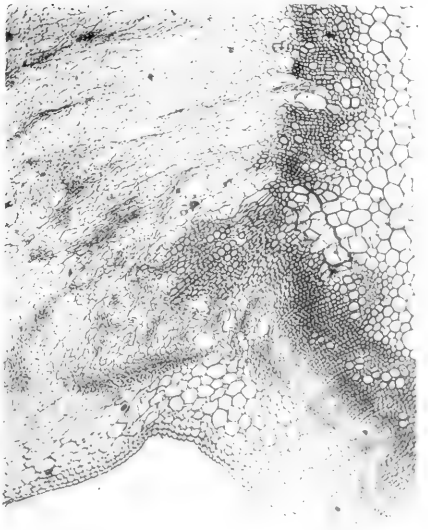

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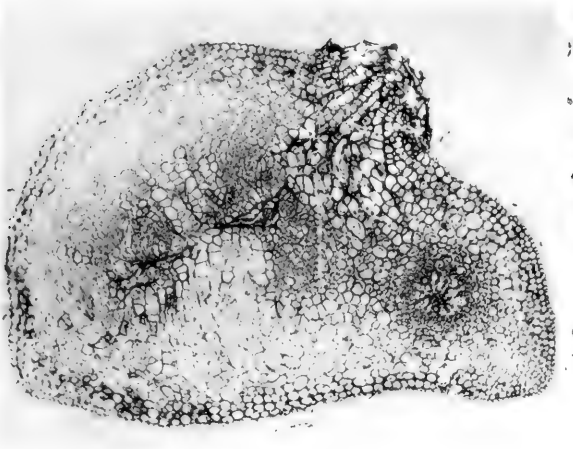

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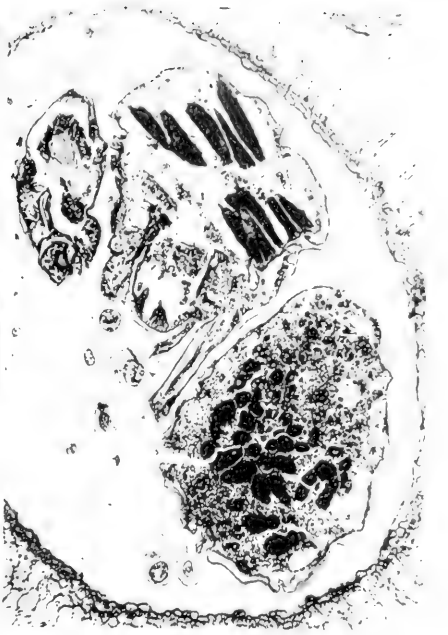

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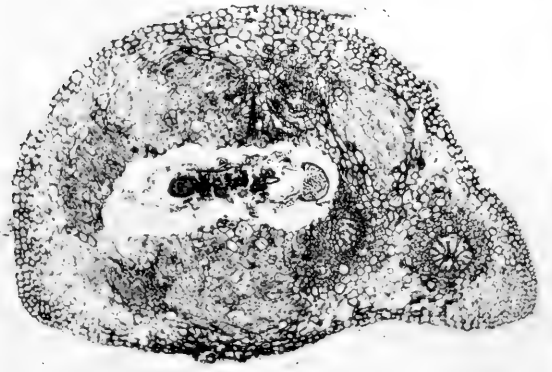

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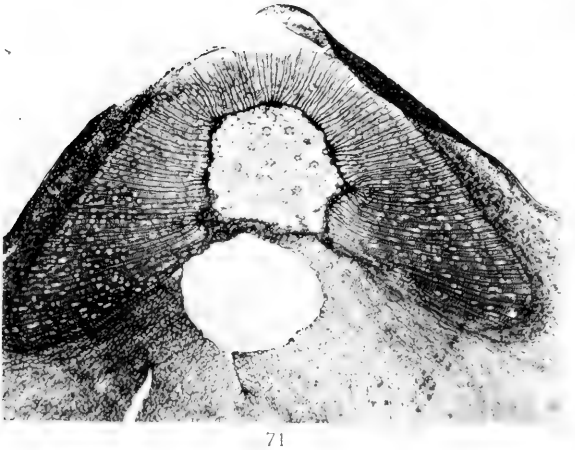

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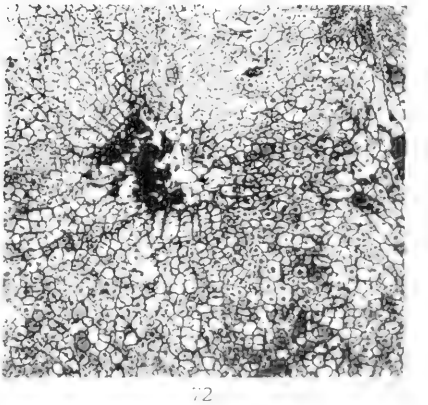

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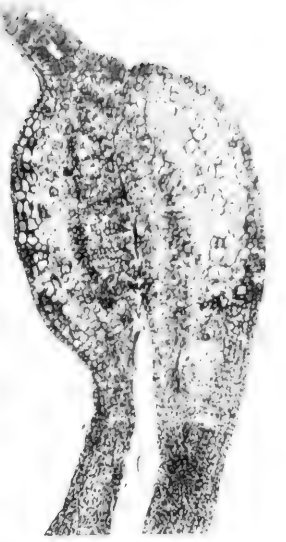

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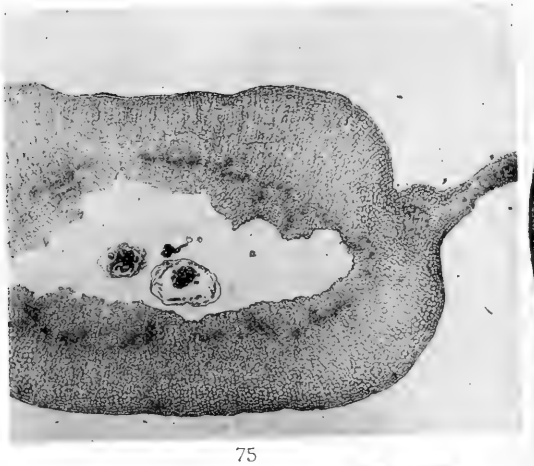

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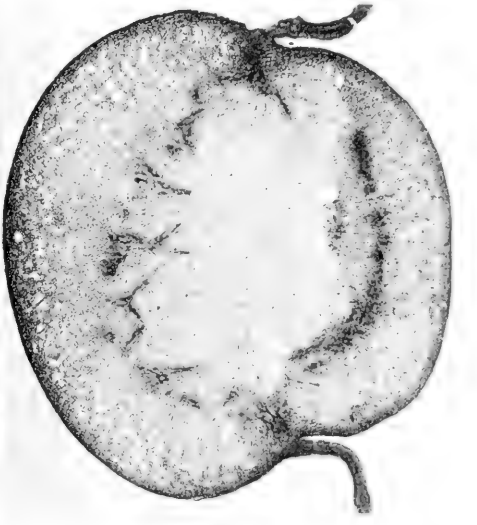

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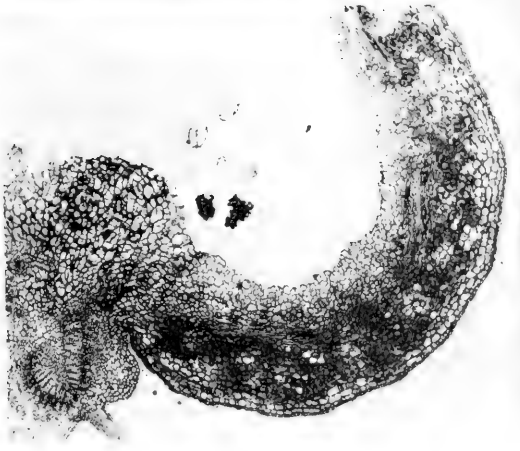

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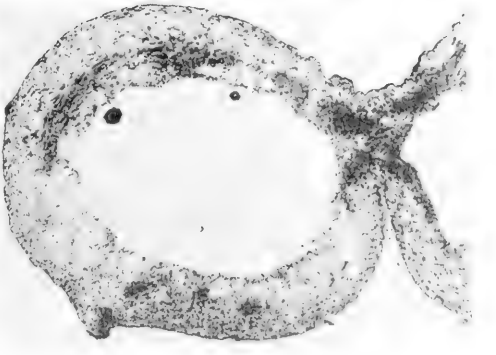

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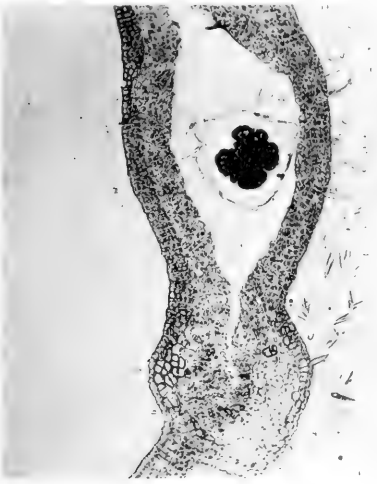
COSENS ON CALLS



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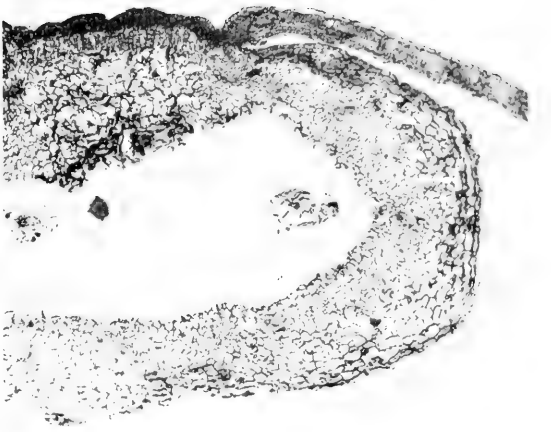

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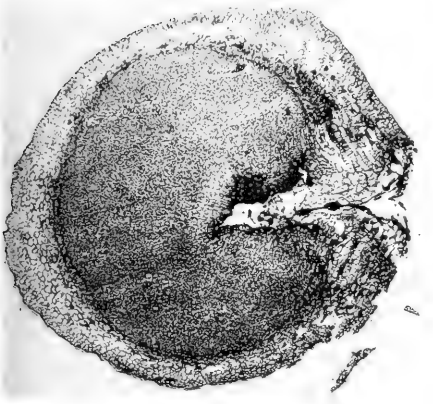

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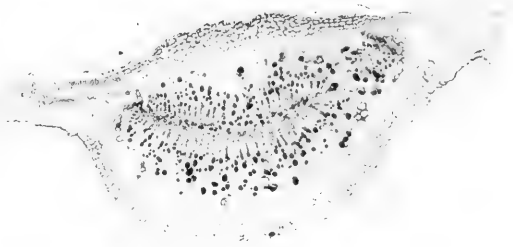

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