Galls and Insects Producing Them

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GALLS AND INSECTS PRODUCING THEM.

Melville Thurston Cook.

Part I. The Morphology of Leaf Galls.

The purpose of this study was to contribute to the knowledge of cellular activity of the plant under peculiar animal stimulus; to compare the effects of the two sets of insect organs, mouth parts and ovipositors, and to throw additional light on the classification. The statements made in this paper are based on a large number of collections. The collection of stem galls was too incomplete to draw conclusions and is therefore reserved for a future paper. No attempt was made to follow the development of the galls but rather to make a comparison of the structure of the various forms of galls.

My paper was practically complete before I received the papers of H. Fockeu. After receiving his paper I reviewed my own to determine wherein my results agreed with or varied from his conclusions. Experiments such as are described by H. Fockeu to ascertain the cause of the gall formation were not attempted.

Fockeu's studies were grouped according to the plants affected; my own studies were grouped with reference to the insect producing the galls.

METHODS.

For the killing and fixing, several fluids were used, but the most successful were Chromo-acetic and Picric-alcohol. A number of different stains were used, but Delafields-Haemotoxylon proved very satisfactory for most work.

For the drawings a Bausch & Lomb microscope and camera lucida were used; for the normal leaf, a 1-inch ocular and a $\frac{1}{5}$-inch objective, and for the galls a 1-inch ocular and a $\frac{2}{3}$-inch objective. Since it was unnecessary to make drawings of the entire galls, drawings were made from one or more parts to show the characteristic structure, and this part is indicated on the small diagrammatic drawings. Since the galls were so variable in size, it was practically impossible to make the diagrammatic drawings on a definite scale.

GENERAL CLASSIFICATION.

As a matter of convenience the following temporary classification, based on location of the galls was adopted for this and other

papers now in preparation: A. Stem galls; B. Leaf galls; C. Bud galls, *a*. Terminal buds, *b*. Lateral buds; D. Root galls.

Leaf galls may in many cases be classed as bud galls if we consider that the egg in some orders of insects is deposited while the leaf is in the bud, but in the above classification the term applies to the developed gall, and the 'bud gall' applies to a distortion of the entire bud.

1. The Normal Leaf Structure and Its Variations. The normal leaf structure may be said to consist of a single layer of epidermis on the upper and lower surfaces of the leaf; next to the upper epidermis is the usually single layer of palisade or columnar cells, placed with their long axis at right angles to the surface of the leaf; between the palisade cells and the lower epidermis is the mesophyll, made up of many layers of irregular cells, between which are the large air spaces connected with the outside by the stomata in the lower epidermis; running through the leaf are the fibro-vascular bundles noticable to the naked eye as the venation.

Although the above may be said to be a description of a typical leaf, it must be kept in mind that leaves are subject to great variation and this must be taken into consideration in a discussion of the variation of the gall structure from the normal leaf. The structure of the gall must be compared with the structure of the normal leaf of the plant on which the gall is found, not with the typical leaf.

A brief study of the normal leaves of the plant will serve to emphasize the preceding points. *Hicoria ovata* (Mill.) Britton (Fig. 1), *Ulmus americana* L. (Fig. 4), and *Tilia americana* L. (Fig. 6) may be considered as typical and yet in themselves show minor differences. In *Vitis vulpina* L. (Fig. 3) the palisade is not so pronounced as in the preceding and the mesophyll is more compact. In *Quercus alba* L. (Fig. 7) and in *Acer saccharinum* L. (Fig. 5) the palisade is typical, but the mesophyll is very compact. In *Salix cordata* Muhl. (Fig. 2) the mesophyll while distinct from the palisade has assumed palisade characters.

The differences in structure between the normal leaves of *Hicoria ovata* (Fig. 1) and *Salix cordata* (Fig. 2), members of two related families, are as great as those differences frequently found between a normal leaf and the galls occurring upon it, *e. g.*, H. ovata (Fig. 1) and the simpler Phylloxera galls (Figs. 16–20).

2. Phytoptus Galls. This discussion is based not only on the four galls described below, but from observations of several others. However, the following will illustrate all the points observed:

The Phytoptus galls are small and may extend on either or both sides of the leaf. The outer surface of the galls show the normal epidermis and below this cells which are not palisade but

which are elongated with the surface of the gall, *i. e.*, the direction of growth (Figs. 8, 9, 11). Projecting into the gall cavity are masses of irregular shaped cells (Figs. 8-11). In young galls these cells show a nucleus, take the stain readily and show indications of maturity (Figs. 9, 11). Trichomes are always found extending from the walls of the cavity (Figs. 8-11) of young galls, but disappear as the galls approach maturity. In these galls we evidently have a repeated puncturing of cells by the animal and an increased activity on the part of the plant in its effort to recover from the wound, the wound never being sufficient to cause the death of that part of the plant.

My results on the Phytoptus galls agree with those of H. Fockeu, except in minor points.

3. The Aphididae Galls. In this family we find the simplest form of galls discussed in this paper, of which *Schizoneura americana* Riley (Fig. 12) may be taken as a type. In fact it is a mere curling of the leaf and not what is usually considered a gall. According to E. Perris it would be classed as a galloide. However, the structure is very similar to that of a typical gall of this family of insects and I see no reason why it should not be considered a true gall.

When compared with the normal leaf of U. americana L. (Fig. 4) the palisade cells are observed to have lost their identity and to have assumed mesophyll characters and the mesophyll has become more compact, both distortions being characteristic of true galls of this family (Figs. 13-21).

In *Colopha ulmicola* Fitch (Fig. 13 a. b.) and *Pemphigus ulmifusus* (Walsh.) Oestlund (Fig. 14 a. b.) both of which are also characteristic galls on the elm, we find practically the same structure as in S. americana. In both the outer (upper) epidermis is much elongated; the same being true of the inner (lower) epidermis of C. ulmicola, but not in P. ulmi-fusus. The identity of the palisade cells is entirely lost, the cells now being slightly elongated parallel to the surface of the gall. The mesophyll cells are more compact than in S. americana and far more compact than in a normal leaf (Fig. 4).

A granular, dark brown, often black substance in the cells was characteristic of the elm and other galls of this group. This was probably tannin, and its presence seemed to depend on the host plant rather than on an insect producing the gall.

The *Hormaphis hamamelis* Fitch (Fig. 15 a. b.) on the Hamamelis virginiana L. showed the same general structure as the preceding galls of this order, except that the epidermal cells were not so much elongated and in the inner (lower) epidermis the cells were much smaller and showed thicker walls, and the dark granular contents of certain cells was restricted to layers near the outer (upper) surface.

The Phylloxera galls show considerable variation from each other. *P. c. avenae* Fitch, *P. c. fallax* Riley, and *P. c. globuli* Walsh. (Figs. 16-18), of Hicoria ovata may be taken as forming a rather well defined group and as showing greatest resemblance to the preceding galls of this family. When compared with the normal leaf (Fig. 1) of the host, H. ovata, they show a reduction in size of the epidermal cells, the palisade cells losing their identity, and the mesophyll becoming very compact. Very little of the dark cell contents characteristic of the preceding galls of this family was present, the greatest amount being formed in P. c. avenae (Fig. 16) where it is restricted to the epidermis and to the cells just below it. The cells are even less elongated and more irregular than in the preceding galls. In general it may be said that in this group the largest cells are midway between the two layers of the epidermis and gradually decrease as we approach the surfaces. This is especially true of P. c. globuli (Fig. 18).

P. c. spinosa Shimer (Fig. 19 a. b.) is a very large gall occurring on leaf, petiole, or young, green twigs of Hicoria ovata and shows considerable variation from the preceding. Two zones are very distinct; the outer is composed of large cells which do not take the stain readily, the inner zone of small cells stained very readily and show great activity. This may, however, have been due to the fact that my specimens of this gall were much younger than of the preceding Phylloxera galls. A long tube for the exit of the insect is formed.

In *P. c. depressa* Shimer (Fig. 20 a. b.) of H. ovata and *P. vastatrix* Planchon (Fig. 21 a. b.) of Vitis vulpina we have still other and more marked variation. The cavity is much smaller, the walls much thicker than in the preceding, and a long tube, especially in P. c. depressa is formed for the exit of the insect. In both cases the size of the epidermal cells is much reduced when compared with the normal (Fig. 1, 3), the palisade cells have not so completely lost their identity as in the preceding and there appears to be a general elongation of the cells with their long axis perpendicular and not parallel to the surface of the gall. A small but definite, deeply staining zone of cells surrounds the cavity in P. c. depressa. Many cells show dark contents similar to that found in the galls on Ulmus and Hamamelis (Fig. 12-15).

P. vastatrix shows a comparatively large number of trichomes, especially near the opening, but this is probably a characteristic of the host plant rather than of the gall.

The presence of the two well defined zones, which may be considered protective and nutritive in P. c. spinosa and P. c. depressa, show a very marked resemblance to the Cynipidae galls (Figs. 25-30).

It may be that all young galls show this arrangement into two or three zones.

In P. c. depressa (Fig. 20) and in P. vastatrix (Fig. 21) the small larval chamber and general arrangement of the cells is very similar to the leaf galls produced by Cecidomyia verrucola (Fig. 2.)

4. The Cecidomyia Galls. This group of galls shows considerable variation. *C. gleditsiae* O. S. (Fig. 22 a. b. c. d.) of Gleditschia triacanthos may be taken as a type of one of the simplest. In this the margins of the leaflets are in contact so as to form a more or less sperical body. To the naked eye it presents no other distortion. Under the microscope the cells show an elongation from midrib to margin, *i. e.*, parallel to the surface of the gall except near the margin, where they are irregular.

C. quercus-pilulae Walsh. (Fig. 23 a. b.) shows a more highly developed gall structure. The epidermal layers are made up of smaller cells than the normal leaf. The mesophyll has lost its identity and assumed the palisade structure, the long axis being perpendicular to the surface of the gall. The larval chamber is large and rather irregular and indefinite, and resembles a large inter-cellular space.

C. verrucola O. S. (Fig. 24 a. b.) on Tilia americana shows a much higher complexity than either of the preceding. The epidermis is made up of small cubical cells. The differentiation into palisade and mesophyll is entirely lost, the cells are very irregular, but show a tendency to elongation at right angles to the surface of the gall. The larval chamber is small and well defined.

C. q.-pilulae (Fig. 23) and C. verrucola (Fig. 24), especially the latter show a striking resemblance to the more highly developed Phylloxera galls such as P. c.-depressa (Fig. 20) and P. vastatrix (Fig. 21).

5. The Cynipidae Galls. This family presents the most striking series of evolutionary development of any family studied and is also apparently the most highly developed.

The general characters presented by these galls are small, cubical epidermal cells; loss of differentiation between palisade and mesophyll cells, all having assumed an irregular character; a differentiation into two well defined zones of cells, the outer made up of large, non-staining cells, the inner made up of smaller, deeply staining cells and surrounding the larval chamber.

Focken divides these into four zones, which he designates as follows: 1. Epidermis; 2. Parenchyma; 3. Protective; 4. Nutritive ("Masse alimentaire"). These four zones may be easily traced in most of our American forms, but in some they show very indistinctly.

Neuroterus irregularis O. S. (Fig. 25 a. b.) is a small, fleshy, solid, irregular gall projecting from both sides of the leaf. It is covered with dense growth of trichomes and contains several larval chambers. In structure it does not correspond to the preceding description, as well as the galls described in the latter part

of this paper. The parenchyma is divided into two very distinct zones, the larval chamber occupying the lower part of the inner zone. The inner zone cells have much thinner walls than those of the outer cells. Surrounding the larval chamber is a zone of cells which stain very deeply and probably furnish nourishment to the larva. The epidermal cells are small.

Callirhytis tumifica O. S. (Fig. 26 a. b.) is a small, fleshy, solid gall projecting on both sides of the leaf and resembles N. irregularis (Fig. 25), except that it is a little larger, does not have so many larval chambers and is smooth. It presents the simplest characters studied, showing the characteristic small, more or less cubical epithelial cells, the lack of differentiation into palisade and mesophyll, and the two zones. The outer zone is very thick and is in contact with the inner zone. The inner zone is narrow and lies near the large larval chamber. At the point of union of the two zones the cells are very small. The outer zone can be readily subdivided into epidermis and parenchyma, but the inner zone cannot be subdivided into two sub-zones unless we consider the layer of small cells as the protective sub-zone. However, this sub-zone of small cells does not possess the sclerenchyma character described by Fockeu for the Cynipidae galls.

Holcaspis centricola O. S. (Fig. 27 a. b. c.) is a large, spherical gall projecting both above and below the leaf. In this we have the two zones, but each retaining the characters previously described; the cells of the inner zone, however, being smaller than in C. tumifica. The epidermal cells have thicker walls than in any other Cynipidae gall examined. The two zones are connected by fibro-vascular bundles. In this the four zones of Fockeu are quite well defined: The outer zone forming the very distinct epidermis and parenchyma; the inner zone showing a fairly well defined protective and nutritive part.

Amphibolips inanis O. S. (Fig. 28 a. b.) shows a very striking resemblance to H. centricola (Fig. 27), except that it is much larger. The epidermal cells do not have such thick walls as in H. centricola and are much longer and narrower. The inner zone is readily subdivided into the protective and nutritive sub-zones described by Fockeu. The inner or nutritive sub-zone is made up of thin-walled cells with prominent nuclei, the outer or protective sub-zone of sclerenchyma cells. The connection between the two main zones is by means of fibro-vascular bundles, the same as in H. centricola.

Dryophanta palustris O. S. (Fig. 29 a. b. c.) presents a condition very similar to the two preceding galls, H. centricola (Fig. 27) and A. inanis (Fig. 28), except that the fibro-vascular bundle connection between the two zones is not present; the inner zone containing the larva forms a sphere which is free in the large chamber formed by the outer zone.

The inner zone shows a marked resemblance to H. centricola (Fig. 27). The subdivision into protective and nutritive parts in my specimens was not like the characteristic zones described by Fockeu; the inner cells were apparently much thicker walled and more indefinite. However, I believe that younger galls would have shown the typical characters. The outer zone is thicker than in either H. centricola (Fig. 27) or A. inanis (Fig. 28), but not so thick as in C. tumifica (Fig. 26). It can be readily subdivided into epidermis and parenchyma and it also shows a fairly well defined endodermis, and in that respect differs from either H. centricola or A. inanis.

Callirhytis papillatus O. S. (Fig. 30 a. b. c.), which is similar to the preceding Cynipidae galls, but shows considerable variation from them. It is smaller than any of the preceding and is embedded in the leaf very similar to C. tumifica (Fig. 26). The two zones are separated, the outer being similar to A. inanis (Fig. 28), the inner zone surrounding two or three larval chambers instead of one. Next to the larva the cells are very large and thin and may be considered nutritive; outside these we have well defined parenchyma or protective cells, and outside these we have two or three layers of cells well filled with protoplasm. The connection between the outer and inner zones is by single elongated cells, which are very rich in protoplasm.

The evolutionary development of the preceding Cynipidae galls is evident. All show the two well defined zones, the outer nonstaining made up of epidermis and parenchyma and the inner which takes the stain readily and is made up of two subdivisions, protective (or sclerenchyma cells) and nutritive (or parenchyma cells). In C. tumifica (Fig. 26) we have the two zones in contact; in H. centricola (Fig. 27) and in A. inanis (Fig. 28) we have a separation of the two zones which are now connected by fibro-vascular bundles; in C. papillatus (Fig. 30) the two zones are connected by long, undivided cells; in D. palustris (Fig. 29) we have a complete separation of the two zones.

With the exception of N. irregularis (Fig. 25) and C. tumifica (Fig. 26) they all show a division into four zones as described by Fockeu. However, Fockeu does not describe a separation between the parenchyma and protective zones which is so characteristic of some of our American galls. I am inclined to consider our American Cynipidae galls as having reached a higher stage of development than the European forms.

The larva in all species evidently draws its nourishment directly from the inner zone. In H. centricola (Fig. 27) and A. inanis (Fig. 28) the inner zone evidently gets its nourishment through the fibro-vascular bundles; in C. papillatus (Fig. 30) the supply of nourishment comes through the long filamentous cells; in D. palustris (Fig. 29) it is probable that the larva is far advanced

in its development before the separation of the two zones and the nourishment remaining in the inner zone at the time of the separation is sufficient to complete its development.

Adler and Stratton after describing similar modifications in the European Cynipidae galls, say: "Besides these histological differences, the outward characters are also of varying complexity; each infinitesimal improvement, which has been of service as a protection against parasites, or has been successful in securing natural conditions favorable to the life and growth of the larva, has been preserved, and has formed the starting point of further beneficial variation. It is always that larva which has been able to induce successful morphological abnormalition, which is reproduced to continue the race; the unsuccessful perish. The ruling force is natural selection; it is impossible that intelligence or memory can be of any use in guiding the Cynipidae; no Cynips ever sees its young, and none ever pricks a bud the second season, or lives to know the results that follow the act. Natural selection alone has preserved an impulse which is released by seasonally recurring feelings, sights, or smells,* and by the simultaneus ripening of the eggs within the fly. These set the whole physiological apparatus in motion, and secure the insertion of eggs at the right time and in the right place. The number of eggs is instinctively proportionate to the space suitable for oviposition, to the size of the fully grown galls, and to the food supplies available for their nutrition."

CONCLUSIONS.

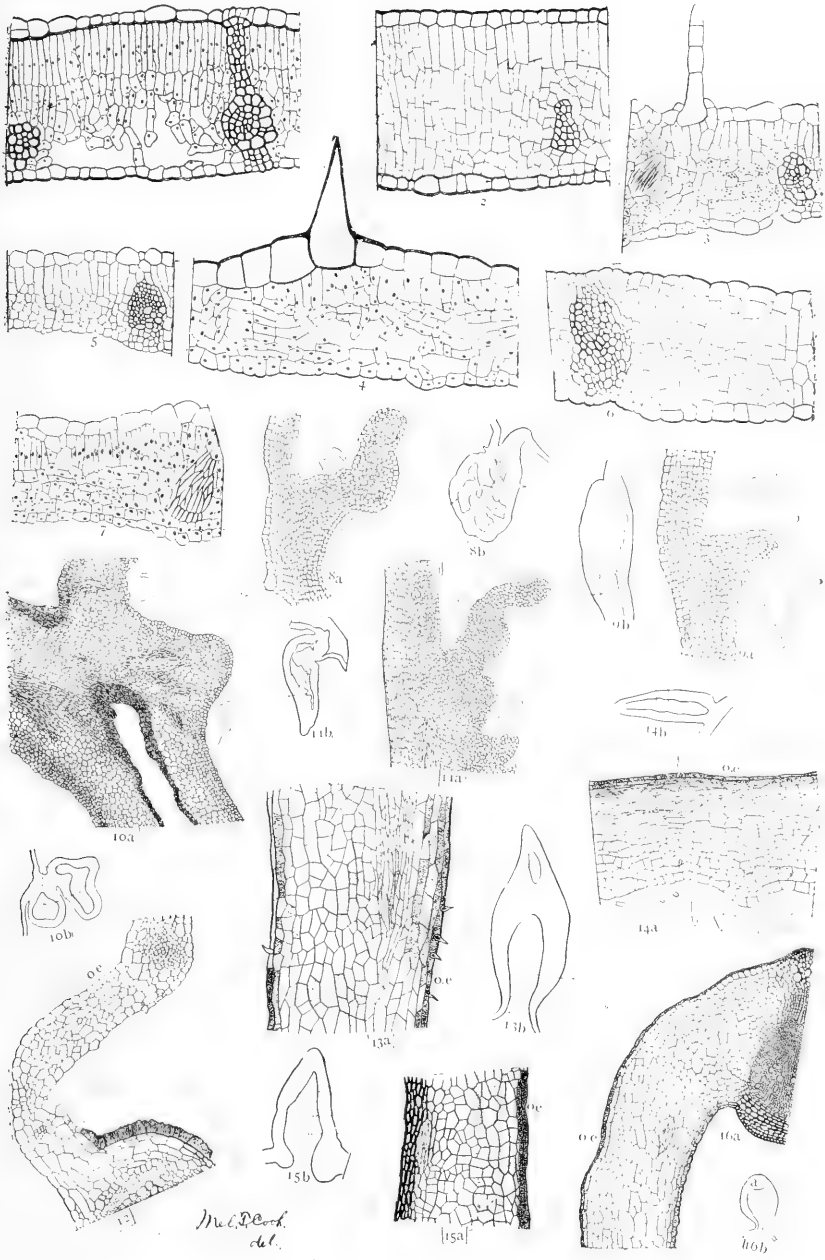
1. Galls may be classified into two general groups, viz., those produced by mouth parts and those produced by oviposition. Those produced by oviposition may be considered the more highly developed.

2. The family Cynipidae shows by far the highest development of gall structures.

3. The morphological character of the gall depends upon the genus of the insect producing it rather than upon the plant on which it is produced; *i. e.*, galls produced by insects of a particular genus show great similarity of structure even though on plants widely separated; while galls on a particular genus of plants and produced by insects of different genera show great differences. This seems to indicate that the stimulus of a particular genus of insect is given to a particular part of the host plant or is of a peculiar kind, characteristic of that genus. However, if the stimulus of two different genera of insects be applied to the same part of the plant the results may be similar. (See Part II.)

4. Within each family we find certain morphological resemblances; *e. g.*, Aphididae.

* Weismann, Essays on Heredity, Vol. I, p. 95.



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5. The families show parallel lines of development from a low form of gall structure up to a high form. *e. g.*, Aphididae and Cynipidae.

6. I am inclined to believe that the modification of the plant tissue is purely mechanical. The loss of differentiation between palisade and mesophyll and the closing up of the intercellular spaces would be a natural result of rapid cell division. The elongation of cells in certain directions would be a natural result of mechanical tension arising from rapid growth. In the family Aphididae where the gall is primarily a folding of the leaf the elongation of the cells is parallel with the surface of the gall. In those galls where the formation is a thickening of the leaf the long axis of the cells is perpendicular to surface of the formation.

7. The presence of at least two zones, of which the inner may be considered nutritive, is very common.

8. The formation of the gall is probably an effort on the part of the plant to protect itself from an injury which is not sufficient to cause death. Both Adler and Fockeu consider that after the first stages of formation the gall becomes an independent organism growing upon the host plant.

9. Trichomes are far more prominent in galls produced by mouth parts than in those produced by oviposition.

10. It appears from these studies that the histological characters of the gall will prove very important in determining the characters of the species.

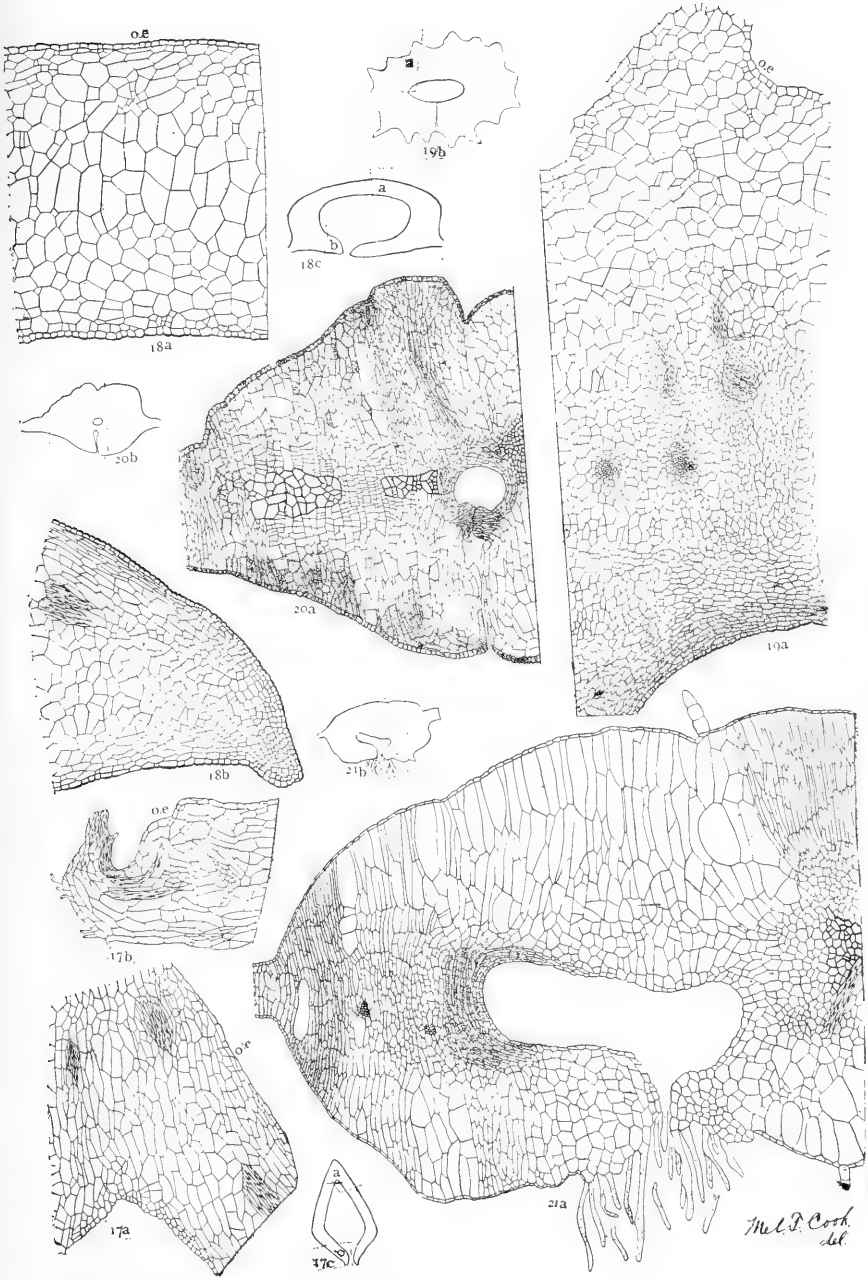
Part II. Apical Bud Galls.

In my third conclusion in the preceding paper I have expressed a belief that galls produced by the same genus of insects show a decided resemblance even though produced on widely different plants. Furthermore, this similarity seemed to be due to the particular part of the host plant to which the stimulus was applied.

The following study of the apical bud galls seem to indicate that when corresponding parts of different plants are stimulated by insects of different genera that the galls produced have characters in common.

The gall produced by *Cecidomyia solidaginis* Lw. (Fig. 31) is merely a large bunch of leaves at the end of the stem of Solidago. The cone-shaped gall of *Cecidomyia salicis-strobiloides* O. S. (Fig. 32) at the tip of the twigs of Salix is a bunch of leaves reduced in size and so compactly arranged as to produce the peculiar cone effect. A further examination of these two galls shows that the tips of the stems are enlarged and that the larval chamber is in the apex.

A superficial examination of the gall of *Callirhytis clavula* Fitch (Fig. 33 a. b. c. d.) shows no resemblance to the preceding galls except in location at the tip of the stem. The gall is apparently



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a mere enlargement of the tip of the stem, and containing one or more larval chambers. Examination of section under a compound microscope, however, reveals a condition similar to that described for C. solidaginis and C. s.-strobiloides. Each larval chamber is in reality the apex of a bud. The young leaves of the bud are closely applied to each other and their structure unaffected by the insect. As the gall developes the leaves do not unfold but assume a corky texture and in the fully mature gall their identity is almost lost.

It is very evident that the larval chamber occupies a corresponding position in each of these galls. The insect prevents the elongation of the stem, thus causing the leaves of the apical bud to be bunched and reduced in size. The fact that the leaves of the Solidago reach the greatest development and those of the Quercus the least development is probably due to the character of the plants. Of these three plants the growth of the Solidago is the most rapid while that of the Quercus is the slowest. In Solidago the rapid growth may be sufficient to overcome the injury and cause the bunch of leaves; in the Salix where the growth is not so rapid the leaves are smaller and more compact; in the Quercus where the growth is slowest the bud never opens but becomes corky and the leaves gradually lose their identity.

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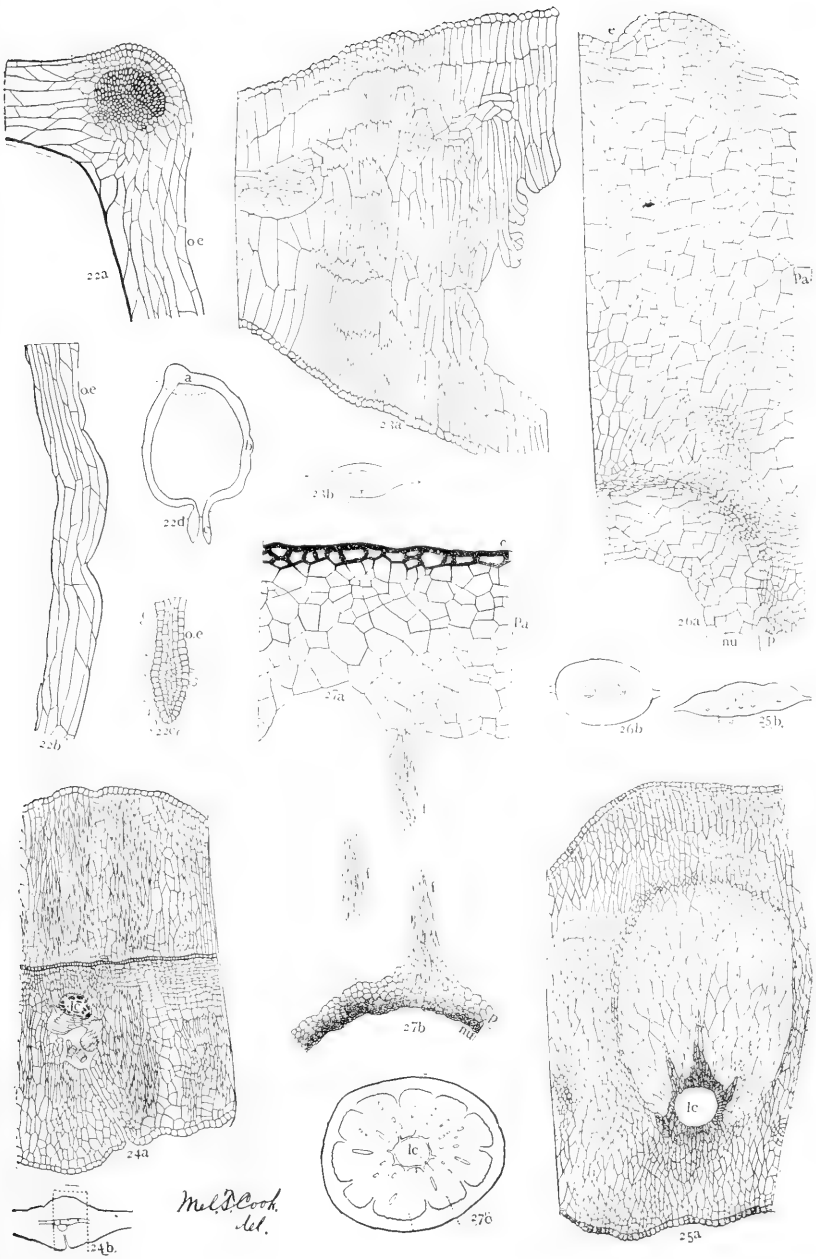

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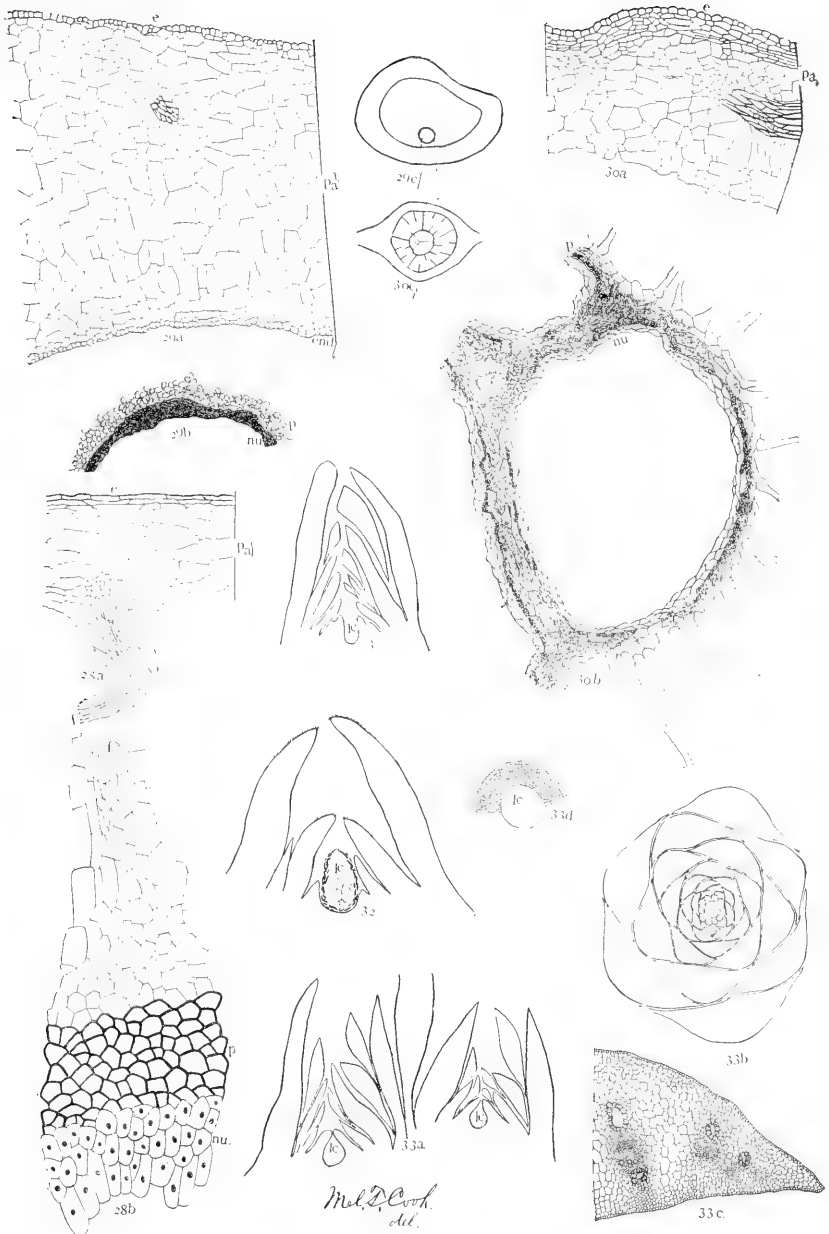

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22. Walsh, B. D. "On Insects, Coleopterous, Hymenopterous, and Dipterous, inhabiting the Galls of certain species of Willows." Proc. Ent. Soc. of Phil. Vol. III. pp. 543–644; id. Vol. VI. pp. 223–288.

EXPLANATION OF PLATES.

In making the drawings, a Bausch and Lomb microscope and camera lucida were used. Figs. 1–7 were made with 1-inch ocular and 1–5-inch objective. The diagrams of the galls were not made upon a definite scale. All other drawings were made with 1-inch ocular and ⅔-inch objective.

Abbreviations: e.—epidermis. end.—endodermis. f.—fibro-vascular bundle. l. c.—larval chamber. nu.—nutritive zone. o. e.—outer epidermis. p.—protective zone. pa.—parenchyma.

1. Cross section of leaf of Hicoria ovata.
2. " " Salix cordata.
3. " " Vitis vulpina.
4. " " Ulmus americana.
5. " " Acer saccharinum.
6. " " Tilia americana.
7. " " Quercus alba.
8. a. b. Phytoptus ulmi on Ulmus americana.
9. a. b. " abnormis on Tilia americana.
10. a. b. " quadripes on Acer saccharinum.
11. a. b. " acericola " "
12. Schizoneura americana on Ulmus americana.
13. a. b. Colopha ulmicola on Ulmus americana.
14. a. b. Pemphigus ulmi-fusus on Ulmus americana.
15. a. b. Hormaphis Hamamelis on Hamamelis virginiana.
16. a. b. Phylloxera carya-avena on Hicoria ovata.
17. a. b. c. " " fallax " "
18. a. b. c. " " globuli " "
19. a. b. " " spinosa " "
20. a. b. " " depressa " "
21. a. b. " vastatrix on Vitis vulpina.
22. a. b. c. d. Cecidomyia gleditsiae on Gleditschia triacanthos.
23. a. b. " pilulae on Quercus alba.
24. a. b. " verrucola on Tilia americana.
25. a. b. Neuroterus irregularis on Quercus macrocarpa.
26. a. b. Callirhytis tumifica " alba.
27. a. b. c. Holcaspis centricola " palustris.
28. a. b. Amphibolips inanis " rubra.
29. a. b. c. Dryophanta palustris " palustris.
30. a. b. c. Callirhytis papillatus " sp.
31. Longitudinal section of Cecidomyia Solidaginis on Solidago.
32. " " " salicis-strobiloides on Salix cordata.
33. Callirhytis clavula on Quercus alba.
    a. Longitudinal section.
    b. Cross section.
    c. " " of leaf from b.
    d. " " of larval chamber from b.

NOTE:—P. vastatrix was also collected on V. bicolor; C. pilulae was also collected on Q. rubra and Q. palustris.

GALLS AND INSECTS PRODUCING THEM.

MELVILLE THURSTON COOK.

PART III. LATERAL BUD GALLS.

In Part II of this series of papers I gave a discussion of apical bud galls. The lateral bud galls differ from the apical only in point of location; therefore, this (Part III) may be considered a continuation of Part II. There is, however, considerable difference in the galls dependent upon the order and genus to which the insect belongs and to the part of the plant which is attacked by the enemy. These differences may be summed up briefly as follows:

(1) Affection of the tip of the stem causing it to remain in its incipient condition and the leaves to remain aborted, instead of lengthening. This is well illustrated by the apical bud galls of *Cecidomyia solidaginis* Lw. on Solidago; *Cecidomyia salicis strobiloides* O. S. on Salix; and *Callirhytis clavula* Fitch on Quercus alba. (Part II, Figs. 31, 32, 33.) In these cases we have two orders of insects represented but producing similar galls: this, as previously explained, is no doubt due to the fact that the insects affect corresponding parts of the host plant.

(2) Affection of the tip of the bud causing it to remain short but to become large and globular. This is well illustrated by *Holcaspis globulus* Fitch (Fig. 34, a, b, c.) By collecting specimens of this gall in April or early part of May it is easy to demonstrate that the gall is in reality an enlargement of the stem part of the bud. The insect evidently deposits the egg in the apical part of the incipient stem. This causes the stem to enlarge, forming a globular body, but to remain so short as to form a sessile gall on the main stem. The bud scales are at first very prominent but gradually shrivel up and are lost, leaving a naked,

globular gall. At this late stage the only evidence that we have of its bud origin is its location at the node of the main stem. The transition from bud to gall occurs very early, before there is any differentiation of the parenchyma tissue ; examination of the structure of the gall fails to show any stem characters but does show the Cynipidous gall character described in Part I of this series.

(3) The third type of the bud gall is illustrated in *Andricus seminator* Harris (Figs. 35, a, b, and 36, a, b.) Ashmead* refers to this as a flower gall. It is not difficult to demonstate that this gall is a true, compound bud gall, but whether it is a flower or leaf gall is not so easily determined. The strongest evidence of its bud character is its location at the node of the stem and the presence of the leaf scales at its base. The writer gathered and dissected a large number of galls of various ages and is confident that this is a true compound bud gall. In Figure 35 a, we have a short twig with three buds, one of which was attacked by the insect ; the other two buds remained unaffected. Around the base of the gall are four well-defined bud scales. In Figure 35 b, two buds were affected ; one of these has been removed showing the scar where it was attached and also exposing the back side of the compound gall formed from the other bud. A great many galls of various ages were dissected ; the younger ones showing the bud scales and the older ones showing the well-defined scars by which it was easy to trace the number of buds affected. Careful observations were made in hopes of finding a gall which would show whether this was a leaf or flower bud, but without success. However, from a careful microscropic examination of a number of galls I am inclined to consider it a leaf bud, in which each leaf becomes a single gall of the large cluster and in which the incipient stem remains short. The microscopic examination of the single galls (Fig. 36, a, b) shows that each gall contains at least one (and usually only one) fibro-vascular bundle which in most cases is very much atrophied and in some cases so much reduced as to be very indistinct. The writer considers the fibro-vascular bundle as the mid-rib of the modified leaf and the cottony part of the gall as the mesophyll part of the leaf. This gall does not show the four zones which are characteristic of the cynipodous galls as pronounced as other galls which we have examined, but this point will be discussed in a later paper.

(4) The fourth type of gall is illustrated by a cecidomyid gall (Fig 37) found upon Acer negundo in which the bases of the petioles of a number of leaves from the same bud are enlarged,

*Ashmead, Wm. H.: "On the Cynipidous Galls of Florida, with descriptions of new species and synopses of the described species of North America." Trans. Amer. Ent. Soc. Vol. XIV, pp. 125–128.

thus forming a bulb-like compound gall. On the inner surface of the base of each petiole is a cavity containing the larva. The stem remains short but the outer leaves are fully developed in most cases.

(5) *Pachypsylla celtidis-gemma* Riley (Fig. 38) is evidently a bud gall very similar to the preceding. Only advanced stages of this gall were collected, and therefore its development could not be observed. From the specimens collected it appeared that each scale and undeveloped bud formed a pocket for the insect, there being a single insect under each scale.

CONCLUSIONS.

Bud galls are subject to considerable variation due to the fact that they are produced by insects of different orders and that these insects attack different parts of the buds and different tissues in these parts. In all cases except the fourth the demands of the insect are so great as to cause a very pronounced change in the bud. In the fourth the modifications are not so pronounced as in the other four types.

PART IV. STEM GALLS.

Stem galls, according to my definition, include only those galls which cause a swelling of the stem and with the larva placed in or near the center, thus affecting the stelar and fibro-vascular parts of the stem. This definition may not be as broad as it should be, but I hesitate to make it include other forms until I have had an opportunity to make a more careful examination of the questionable forms. The fact that such galls as H. globulus (Fig. 34, a, b, c), which is frequently mentioned as a stem gall, are in reality bud galls, leads me to be doubtful of the origin of galls which have similar locations. Many of the so-called stem galls may be in reality bud galls and this point can be determined only by a study of their development and structure.

Some galls occur on both leaves and stem, but in these cases the gall affects only the outer layers of the cells of very young twigs and these cells at this time resemble the leaf cells in both structure and functions. *Phylloxera carya-spinosa* Shimer (Part I, Fig. 19) and *Phylloxera caryae-caulis* Fitch (referred to in Part V) are good examples of leaf galls affecting stems.

The Lepidopterous galls are usually stem galls and may be either solid or hollow and are most common on Solidago. In studying such galls it is necessary to examine first a normal stem.

The stem of Solidago (Fig. 39) shows the ordinary dicotyledonous character. The epidermal cells (e p) are firm and rather hard. Just below these cells is the parenchyma zone (p a) of closely-fitted cells and few intercellular spaces. Below the parenchyma zone are the fibro-vascular bundles (p. v. b.), which

contain a large amount of woody, fibrous tissue. Inside the zone of fibro-vascular bundles and forming the axis of the stem, is the stelar (st) made up of large parenchyma cells.

In *Trypeta solidaginis* (Fig. 40) a solid globular gall on the stem of Solidago, we find the walls of the outer parenchymatous cells much thickened and numerous large intercellular spaces which are not characteristic of the unaffected stem (Fig. 39). The fibro-vascular bundles (f. v. b.) are spread out and flattened, the sclerenchyma tissue and tracheary tissue being reduced and the fibrous tissue increased in amount. The parenchyma tissue of the stelar (st) part of the gall is increased in amount and the size of the cells reduced. This tissue is undoubtedly very active and well supplied with nutrition for the larva. Throughout the tissue are tubes (tu) lined with cells smaller than the parenchyma cells, brown in color, and not affected by haematoxylin stain. These tubes are usually associated with small bundles of fibrous tissue and are probably important factors in the nutrition of the larva. They were not found in sections of normal stem of corresponding age.

In *Gelechia gallae-solidaginis* Fitch (Fig. 41) an elongated, hollow gall on Solidago, we find the parenchymatous tissue (pa) near the surface increased in amount, the cells larger and the walls thicker than in an unaffected stem, but no intercellular spaces such as are found in T. solidaginis. The fibro-vascular bundles (f. v. b.) undergo comparatively little change, becoming slightly flattened and thinner and with a reduction of the firmer fibrous tissue. The larva chamber (l. c.) of the gall is lined with a few layers of small parenchymatous cells (st) and is the stelar part of the stem. This parenchymatous tissue is udoubtedly used for food.

In *Cecidomyia rigidae* O. S. (Fig. 42) an elongated, hollow gall common on Salix discolor, usually near the tips of the twigs, we find considerable modification of the normal stem structure. From the examination of a number of specimens it is very clear that the enlargement of the stem is due to two factors: the formation of large intercellular spaces near the surface, similar to those in T. solidaginis (Fig. 40), and the formation of the larval chamber (l. c.) in the stelar part of the stem. The parenchymatous tissue lining the chamber is made up of cells very much smaller than those in an unaffected stem.

The Lepidopterous galls on the young stems of Acer negundo and Coleopterous galls on Rubus villosus were examined but no new points presented. I was unable to secure satisfactory specimens of stem galls of Cynipidae.

Although the study of stem galls was in many respects unsatisfactory, I feel justified in giving the following brief conclusions:

CONCLUSIONS.

1. Stem galls show less variations than any other group of galls, although they may be produced by insects from widely different orders. This is undoubtedly due to the fact that the various insects attack corresponding parts of the host plants. In proof of this fact, it will be noticed that all these insects deposit the egg within the tissues of the host plant and not on the surface.

2. The galls in general show an increase of parenchyma below the epidermis, either a thickening of cell walls or a development of intercellular spaces, a flattening of the fibro-vascular bundles, an increase of parenchyma tissue in stelar part of stem and a decrease in size of same.

Part V. Development of galls.

A very large amount of material was collected for this paper and great difficulty was experienced in getting the extremely young stages because of the fact that young specimens were difficult to recognize and identify. The material was carefully killed in either Fleming's solution or chromo-acetic, passed through the alcohols, imbedded in paraffin, sectioned on a Zimmerman microtone and stained in haematoxylin.

The galls will be considered in the same order as in Part I of this series. A consideration of the leaf structure is unnecessary since that was considered in Part I.

1. GALLS OF ACARINA.

Young galls of *Phytoptus quadripes* (Fig. 43), *P. abnormis* (Fig. 44), and *P. acericola* (Fig. 45) were studied, and all show the same developmental characters. The leaf becomes slightly pitted on one side (usually the lower) and a corresponding elevation is formed on the upper surface. This gradually enlarges until the more or less spherical gall is produced. In P. abnormis the spherical gall soon assumed an elongated form. The characteristic cell structure of the leaf is lost and the cells become very irregular in shape. The elongated character of the cells just beneath the outer epidermis appears at a later period of the development. At first the inner surface of the gall is perfectly smooth, but very soon masses of cells are formed and project into the cavity (Figs. 43 and 45). At about the same time trichomes begin to develop from the inner epidermis (Fig. 44) and project into the cavity. These trichomes grow very rapidly and almost fill the entire cavity.

In the very young galls no fibro-vascular bundles are formed, but in the older galls small bundles of fibrous tissue are numerous.

The first effect of the insect attack is undoubtedly to cause an increase in the number of cells, which is an effort on the part of the plant to heal the wound produced by the repeated puncturing

of the cells by the parasite. Since the parasite continues its attack upon different cells and the plant makes the repeated effort to heal the wound, we have the very active production of cells. The parasite making its attack upon one side of the leaf, causes the unequal growth resulting in a cavity. The increase in size of the gall causes a different tension upon the inner and outer surfaces and results in the elongation of cells near the outer surface as described in Part I.

When the galls first appear they are single, but in a very short time others are formed just outside the first, thus forming a cluster.

In *Eriocum anomalum* (Figs. 47, 48, a, b), occurring on leaves and petioles of walnut, we find a condition similar to that of the Phytoptus galls except that the parasite is on a free surface instead of in a partly closed cavity. I was able to secure a very complete series of this gall. The first indication of the gall on the petiole or rib of a leaf is the increase in the amount of parenchyma tissue between the epidermis and fibro-vascular bundles. The physiological character of this tissue is also changed to some degree, since the cells are not so easily stained with haematoxylin, have rather thick walls, and contain a considerable quantity of tannin. The epidermal cells now begin to form trichomes (Fig. 47). The parenchyma tissue and trichomes both increase in quantity, the walls of the cells become thinner (Fig. 48, a, b), and the deeper parenchyma tissue gradually loses its tannin, while the outer cells retain it in great quantities.

These galls always occur over a fibro-vascular bundle and are apparently closely associated with them. These bundles become modified to some extent.

The origin and development of these galls is the same as in the Phytoptus galls except that the parasite works upon the exposed surface instead of in a cavity. The fact that one produces a cavity lined with trichomes while the other produces a protuberance covered with trichomes, is probably due to the fact that the latter is so closely associated with the fibro-vascular bundle which prevents the curvature but causes the rapidly-formed cells to swell outward into a protuberance.

2. GALLS OF THE APHIDIDAE.

In the Aphididae galls we have a condition very similar to that just described for the Acarina galls except that the shape of the galls are far more definite and they show a higher degree of development. Trichomes are not so numerous and masses of cells projecting into the larval chamber as described for Phytoptus galls are very rare. In the youngest galls the cell structure of the leaf is modified, resulting in the formation of a large number of small, irregular cells, the same as in the Acarina galls. As the

galls grow older the cells near the outer epidermis become elongated as in the Phytoptus galls.

In *Pemphigus ulmifusus* (Walsh) Oestland (Fig. 49, a, b) on U. Americana, we have the gall originating first as a fold in the leaf which becomes developed into a conical structure. The structure of the gall shows that the characteristic structure of the leaf is at first modified into a large number of small, irregular-shaped cells (Fig. 49, b). The tendency for the cells near the outer surface to elongate parallel to the surface begins with the further development of the gall. In the very young galls the tannin is in very small quantities, but increases as the gall grows older.

In *Colopha ulmicola* Fitch (Fig. 50, a, b) we have a condition almost identical with P. ulmi-fusus. The gall first appears as a slight fold in the leaf and later develops into the characteristic cockscomb gall. The cell structure is the same as in P. ulmi-fusus.

In *Phylloxera carya-fallax* Riley (Figs. 51, 52) on H. ovata, I secured the youngest galls possible to detect and identify. These galls showed a slight projection from both surfaces of the leaf, but at first the gall was not so conical as at a later period of its development. However, the youngest galls showed the characteristic structure described in Part I of this series. The first effect of the parasite attack appears to be the formation of a large number of irregular cells. The arrangement of these cells is the same in the young gall as in the more mature, but the fibro-vascular bundles of the older specimens were not observed in the young galls.

I was not so successful in securing young specimens of P. c.-globuli Walsh (Fig. 53), but, so far as I was able to observe, the line of development coincided with P. c.-fallax. However, the upper wall of the gall is at first very thin and grows in thickness as the gall approaches maturity.

Phylloxera carya-caulis Fitch of Hickory ovata was studied very carefully from a very complete series of specimens. The material, especially the younger galls, did not cut well, and so was not satisfactory for drawings. However, the development and structure were of the typical Phylloxera type corresponding very closely with that just described for P. c.-fallax. The only marked peculiarity was the close association with fibro-vascular bundles, the galls always occurring on very young green twigs, on mid-rib or on prominent veins of the leaf.

Pemphigus populi-transversus Riley (Figs. 55, a, b, and 56, a, b) and *P. p.-caulis* Fitch (Figs. 57, a, b, c, and 58, a, b, c) of the Populus are galls growing on the petiole; the former at some point between the blade and stem, the latter at the base of the leaf. In both cases the attack is made from the outside, the same as in other Aphididae galls and in the Acarina galls. A careful

study of an excellent series of both galls shows a cell structure and development very similar to other Aphididae galls; i. e., a large number of small, irregular cells. In P. p.-transversus (Fig. 55, a, b) the gall originates as a swelling on the petiole and within this swelling is a large cavity opening to the outside through a slit. In the P. p.-caulis the same condition is true but the attack of the insect causes a one-sided growth, resulting in the petiole being twisted at right angles to the blade (Figs. 57, a, b, c, and 58, a, b, c).

A careful examination of the cell structure of P. p.-transversus (Fig. 56, a, b) and a comparison with the unaffected petiole (Fig. 54, a, b) indicated a very rapid growth, resulting in the very large number of small, irregular cells. The character of the young and of the mature gall was practically the same, and not different, as in the more highly developed galls of other orders. The fibro-vascular bundles were very slightly affected.

P. p.-caulis showed the same cell structure and development, and, judging from these points alone, one would be unable to separate these two galls.

3. GALLS OF PSYLLIDAE.

In *Pachypsylla celtidis-mamma* Riley (Figs. 59 and 60, a, b, c) of the Celtis occidentalis the youngest galls did not show a cavity, but showed a modification of the leaf by which there is formed a large number of small, irregular cells which can be readily separated into two zones; the upper made up of small, and the lower of somewhat larger cells (Fig. 59). I was unable to secure specimens intermediate between this stage and a later stage, showing the true form of the gall (Fig. 60, a, b, c) The youngest galls, showing the true form, exhibited four well-defined zones: (1) epidermis, (2) zone of large, irregular-shaped cells, (3) zone of elongated cells, (4) zone of irregular-shaped cells next to the larval cavity. Adjacent to zone (3), but derived from zones (2) and (4), are cells which even in very young galls show schlerenchyma characteristics. As the gall approaches maturity this tissue increases until in the mature gall it may be found in great abundance. This gall is undoubtedly the most highly developed of any of the Hemiptera galls which I have studied.

4. GALLS OF CECIDOMYIA

Although I have a large number of Cecidomyia leaf galls, I have succeeded in getting a series of only two species. Since the Cecidomyia show by far the greatest variation in structural characters and the smallest number of typical group characters, two species are not sufficient to draw a very definite conclusion.

In *Cecidomyia gleditsiae* O. S. (Fig. 61, a, b) the two halves of the leaflet never have an opportunity to unfold, but there is a

growth of cells allowing the leaflet to enlarge and form the larval chamber between the two halves. The cells are at first normal, but gradually lengthen in an axis at right angles to the mid-rib. This can be readily observed by comparing the section of the very young gall (Fig. 61, a, b) with the section of the mature gall (Part I, Fig. 22).

In *Cecidomyia verrucola* O. S. (Figs. 62 and 63) the youngest showed a condition in which the mesophyll part of the leaf was reduced or entirely removed by the larva. The upper epidermis and palisade cells, the lower epidermis and cells next to it, form the upper and lower walls of the larval chamber while the intermediate mesophyll is removed. The inner layers of cells, i. e., the cells next to the larval chamber, now grow and divide very rapidly, gradually filling almost the entire cavity and reducing the size of the chamber (Part I, Fig. 24). At the same time the gall is increasing rapidly in size.

5. GALLS OF THE CYNIPIDAE.

Although a large amount of material was collected, only three species were sufficiently complete to enable a satisfactory study. However, several mature galls of species not described in Part I of this series were examined, and all agreed with the statements made concerning the general structural character of this group of galls.

Callirhytis papillatus O. S. (Fig. 64) was especially difficult to collect because of its very small size and close resemblance in external appearance to other small Cynipidous galls. Examination of young Cynipidous forms, which I am reasonably certain belong to this species, show all the zones in contact (Fig. 64). As the gall develops the protective zones and parenchyma zones separate but remain connected by elongated parenchymatous cells (Part I, Fig. 30).

Dryophanta palustria O. S. (Fig. 65, a, b) appears as the leaves unfold from the bud. The youngest galls collected were not over two millimeters in diameter but showed the four zones well developed, with the second and third zones in contact, thus verifying the views expressed in Part I. The cells of the innermost, or nutritive, zone were large and very granular. Evidently this zone was almost completely reduced by the larva in the specimen from which Fig. 29 of Part I was drawn. In the next, or protective, zone the cell walls were very thick. In the parenchyma zone the innermost cells were small and numerous and the walls were thin, and in both cases the long axis of the cells were at right angles to the surface of the gall. As the gall grows older the intercellular spaces may become prominent among the cells of the parenchyma zone (Fig. 65, b). Careful examination of a large number of specimens gave conclusive proof that the separation occurs

between the protective and parenchyma zones, thus leaving the two inner zones as a small sphere rolling free within the larger sphere which is formed by the two outer zones.

In *Diastrophus siminis* Basset (Figs. 66, a, b; 67; 68, a, b, c, d; 69) we have a Cynipidous gall occurring on Nepeta glechoma. I secured a very complete series of this gall and made a very careful study of its development. In the youngest gall (Fig. 66, a, b) we have the cell character of the leaf transformed into a mass of small, irregular cells which can be readily divided into two zones, the outer of which has the larger cells. At this time the cells are very compact, but as the gall grows older intercellular spaces are developed, the entire structure becomes loose and spongy and the cells become larger.

As the galls grow older a well-defined zone of flattened cells is developed in the parenchyma near the epidermis, and fibro-vascular bundles (f. v. b.) are developed at right angles to the surface (Fig. 67). Up to this time the cells are small, irregular and compact. The epidermis (ep) and parenchyma (pa) zones are well defined, but the distinctiion between protective and nutritive zones cannot be made.

As the gall grows older a cleavage plane is formed in the parenchyma just inside the zone of flattened cells (Fig. 68, a). A careful examination of the parts thus cut off and surrounding the larval chamber (l. c.) shows two well-defined zones which correspond to the nutritive and protective zones described in Part I. At this time there is no marked difference in the amount of food supply of the two zones. In the outer part formed by this cleavage plane we have the parenchyma (pa) and epidermal (ep) zones (Fig. 68, c). Connecting the parenchyma and protective zones we find fibro-vascular bundles (f. v. b.) surrounded by parenchyma cells (Fig. 68, d). The character of these connecting strands is very similar to that described for H. centricola (Part I, Fig. 27) and A. inanis (Part I, Fig. 28), but contains more parenchyma tissue than either. However, the parenchyma cells are not so elongated as in C. papillatus (Part I, Fig. 30). As the gall grows older the cells of the protective zone become clear and the cell walls of the nutritive zone gradually thicken (Fig. 69), many undergoing complete degeneration, while others assume the character of the sclerenchyma.

CONCLUSIONS.

1. All conclusions given in Part I are emphasized by the study of the development of the galls.

2. In the formation of all leaf galls except the Cecidomyia galls, the normal cell structure of the leaf is first modified by the formation of a large number of small, compact, irregular-shaped cells. In the galls of Acarina and Aphididae this is followed by

a development of trichomes, especially the former. In all galls the mesophyll is subject to the greatest modification. Many small fibro-vascular bundles are formed in this modified mesophyll.

3. The Acarin may be considered the lowest group of galls, the Aphidid the next higher, the Cecidomyia galls the next higher, and the Cynipidous galls the highest. However, many of the Cecidomyia galls are lower than the Aphidid galls.

4. The galls of Acarina and Aphididae show the greatest resemblance. In these cases the method of attack is very similar and is first directed against the epidermal or adjacent layer of cells.

5. In some of the Cecidomyia galls (e. g. C. verrucola) the larva appears to make its entrance into the mesophyll before there is any pronounced modification of the cell structure. However, the Cecidomyia galls are too varied and the study too incomplete to make a positive conclusion.

6. Both Adler and Fockeu consider that after the first stages of formation, the gall becomes an independent organism growing upon the host plant. This is probably true in the highly developed galls of Aphididae, Cecidomyia and Cynipidae, but the writer is very doubtful if this is true of the less complex galls of Acarina, Aphididae and Cecidomyia.

This work was pursued during the year 1902–03, in the Biological Laboratory of DePauw University, but was under the supervision of Professor Herbert Osborn, of the Ohio State University, to whom I am indebted for many valuable suggestions. I am also indebted to two of my former students, Miss S. Emma Hickman and Miss Margaretta S. Nutt, for aid in preparing slides and making drawings. Drawings made by these two ladies are marked with their initials. I also wish to express my thanks to my many friends who have called my attention to, or have collected material for, these investigations.

LITERATURE.

New literature will not be cited at this time, but a more complete list will be given in connection with later papers upon this subject.

EXPLANATION OF PLATES.

In making the drawings a Bausch & Lomb microscope, with No. 2 ocular and 1/6 objective, and a B. & L. camera lucida were used. The drawings are, therefore, larger than those used in Parts I and II, and the reduction not so great. The diagrams are not made upon a definite scale. Drawings 34, a, b, c; 35, a, b; 37, 38, 55, a, b; 57, a, b, c, and 58, a, b, c, were made from nature, and are very little smaller than the original. The numbering of the drawings is continuous with Parts I and II.

ABBREVIATIONS.

ep.—epidermal zone.
pa —parenchyma zone.
pr.—protective zone.
nu.—nutritive zone.
f. v. b.—fibro-vascular bundles.

34. a. Bud of Hicoria ovata.
34. b, c. Holcaspis globulus on H. ovata.
35. a. Andricus seminator gall and two buds on Q. alba.
35. b. Andricus seminator gall and bud scar on Q. alba.
36, a, b. Section of Andricus seminator gall on Q. alba.
37. Cecidomyia gall on A. negundo.
38. Pachsylla c.-gemma on C. occidentalis.
39. Cross section of stem of Solidago.
40. Trypeta solidaginis on Solidago.
41. Gelechia gallae-solidaginis on Solidago.
42. Cecidomyia rigidae on Salix.
43. Phytoptus quadripes on A. saccharinum.
44. " abnormis on T. Americanum. (Two larval chambers.)
45. " acericola on A. saccharinum.
46. Petiole of Juglans nigra. (Cross section.)
47. Erineum anomalum on J. nigra. (Young gall.)
48, a, b. Erineum anomalum on J. nigra. (Mature gall.)
49, a, b. Pemphigus ulmi-fusus on U. Americana.
50, a. b. Colopha Ulmicola on U. Americana.
51. Phylloxera carya-fallax on H. ovata.
52. " " " "
53. " carya-globuli on H. ovata.
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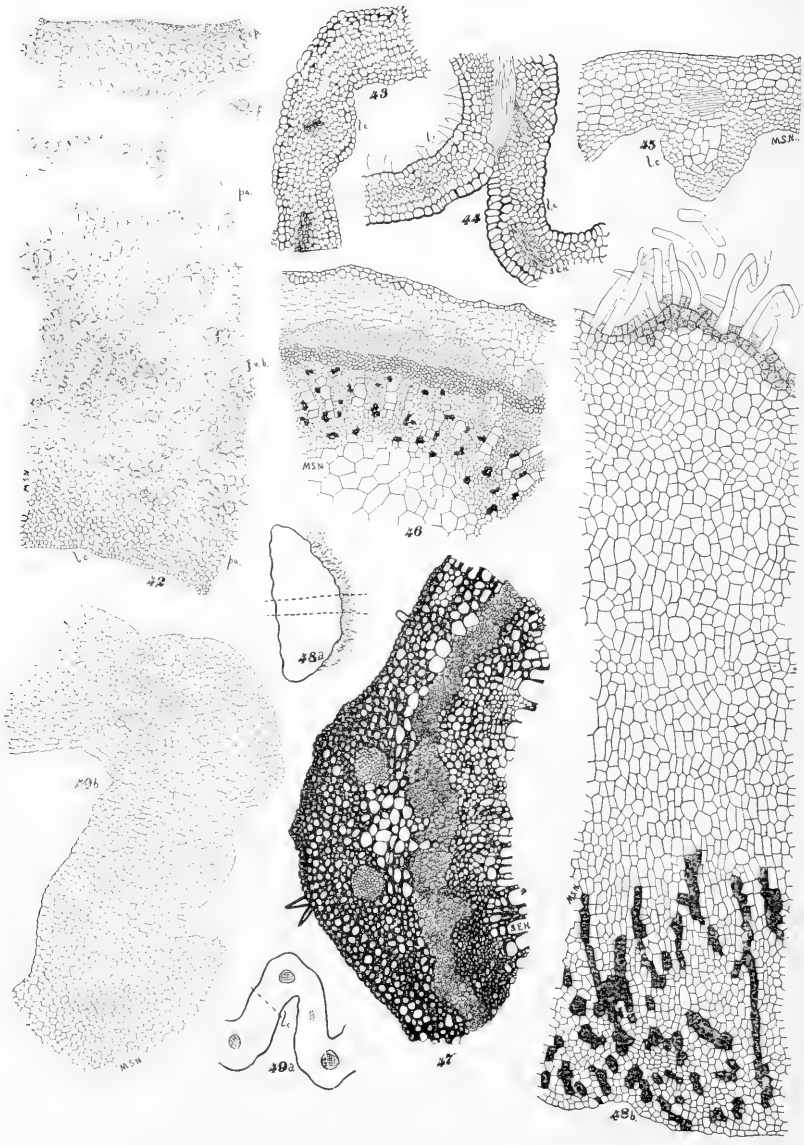
68, c. " " Epidermal and parenchyma zones.
68, d. " " Strand connecting protective and parenchyma zones.
69. " " Nutritive zone in gall almost mature.

COOK on "Galls and Insects Producing Them."



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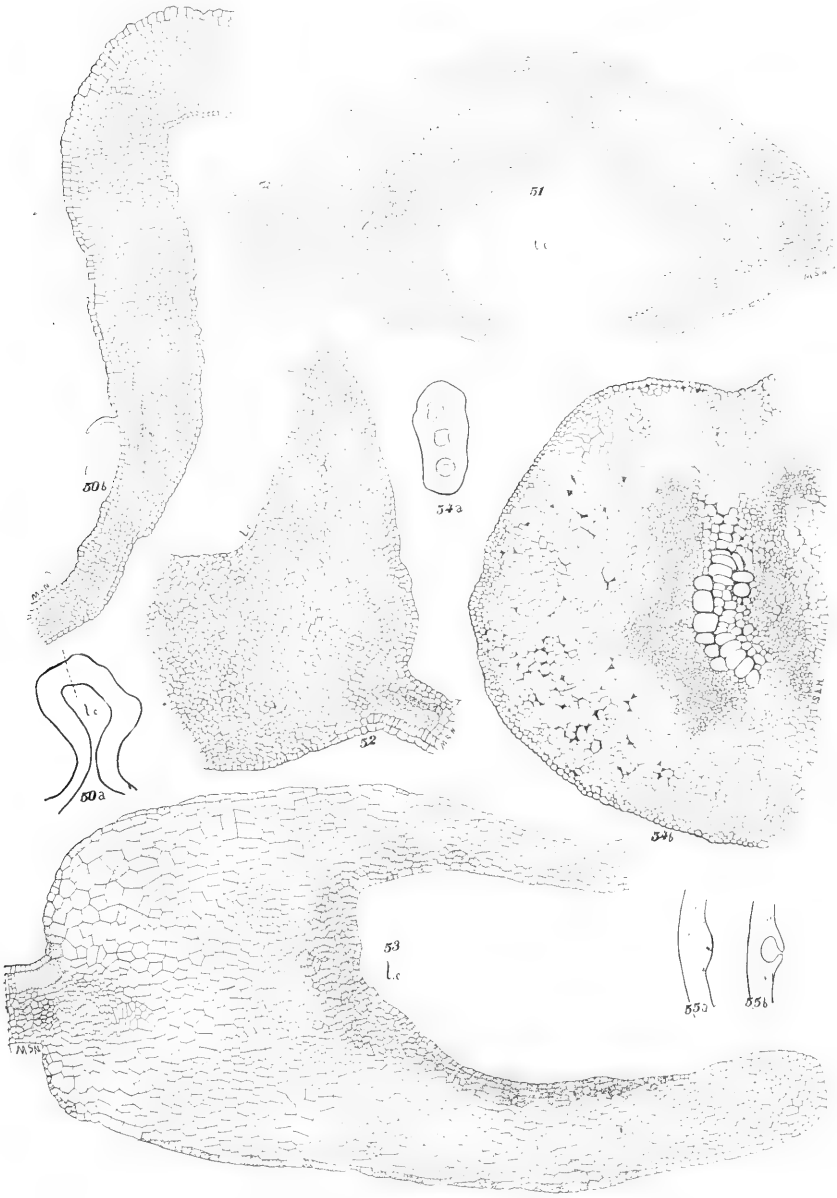
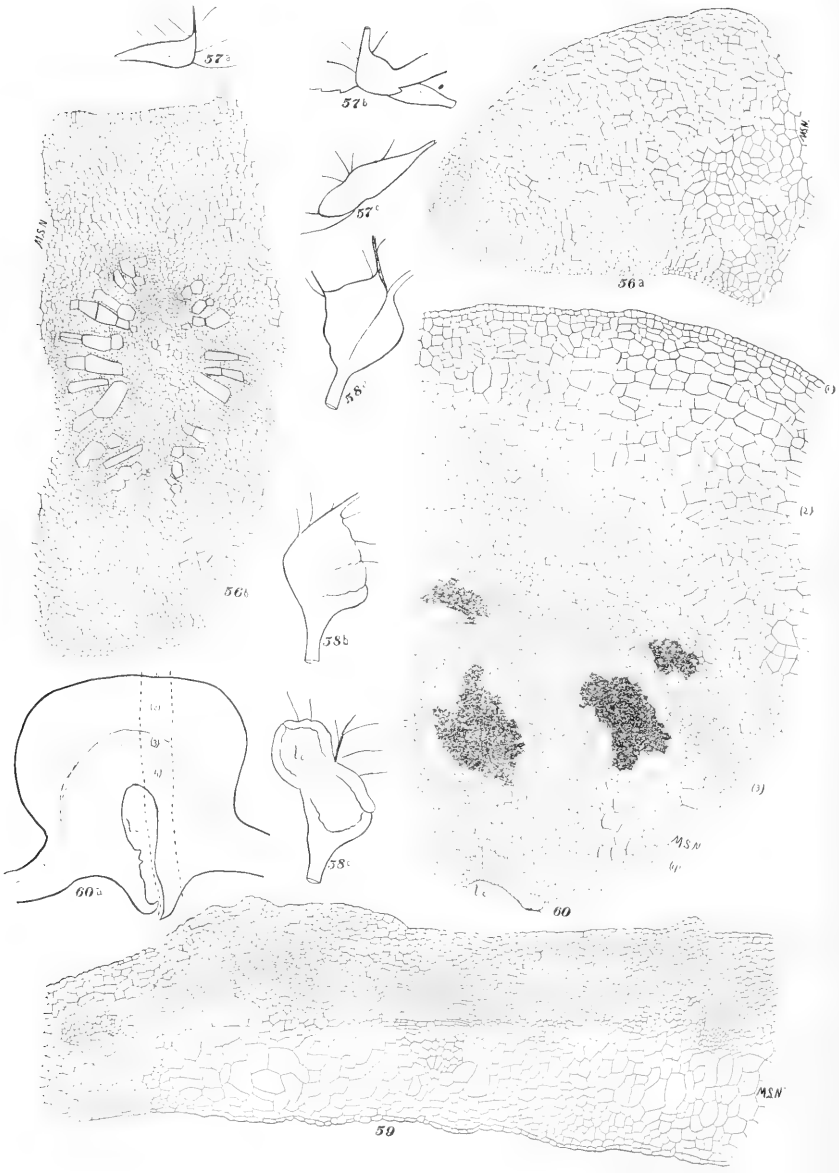


Cook on "Galls and Insects Producing Them."

OHIO NATURALIST. *Plate 16.*



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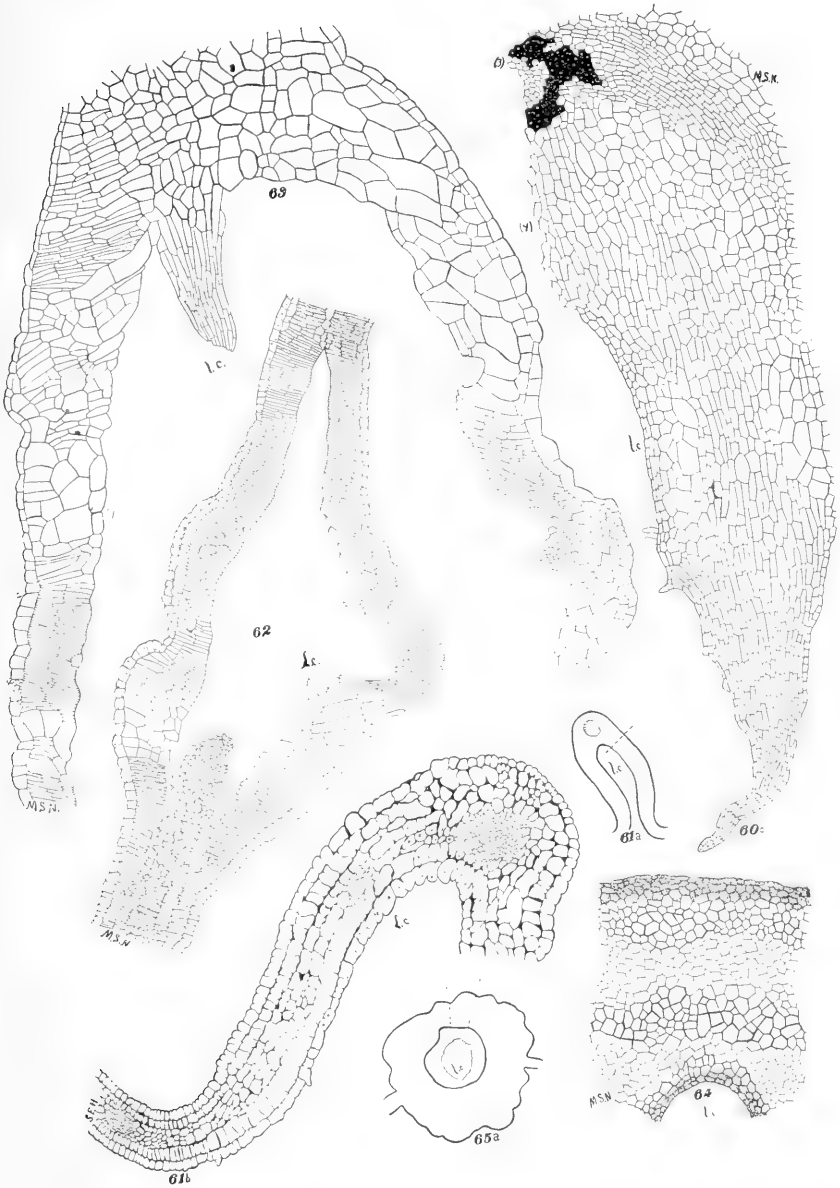
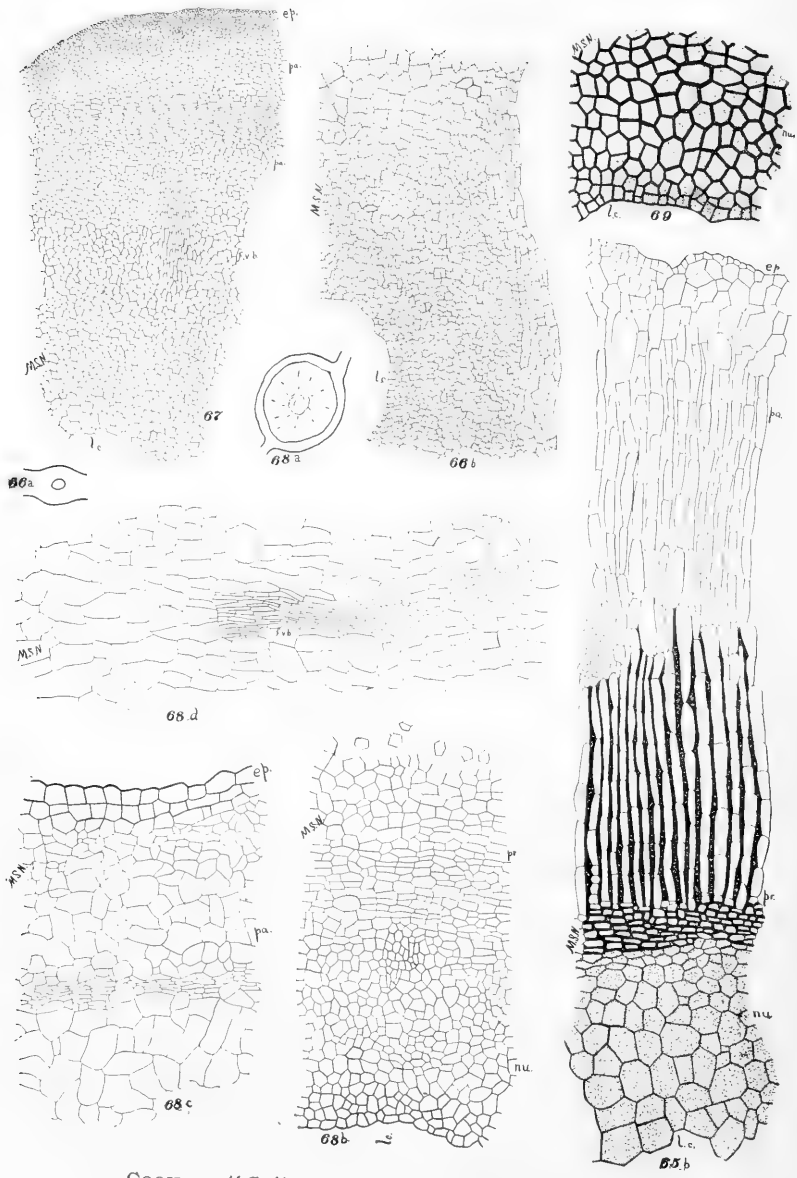


COOK on "Galls and Insects Producing Them."

OHIO NATURALIST.

Plate 18.



COOK on "Galls and Insects Producing Them."

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GALLS AND INSECTS PRODUCING THEM.*

MELVILLE THURSTON COOK.

PART VI. FLOWER AND FRUIT GALLS.

Galls affecting flowers and fruits are not so abundant as those affecting leaves, but in many cases the insect which produces flower or fruit galls also produces leaf galls. No sharp line of distinction can be drawn between flower and fruit galls, since the gall may form and mature without indication of fruit or may form in the flower and mature as the fruit develops. Thus far I have collected five species of flower and fruit galls representing three orders of insects.

1. GALLS OF THE ACARINA.

Phytoptus sp.—on Euphorbia corallata L. (Figures 70; 71a, b; 72a, b). This mite produces galls on both leaf and flower. The structure of the gall is the same in both cases and is identical with Phytoptus galls, previously described in Part I, (Figures 8–11). All my specimens of this gall were well advanced. The structure of the leaf of E. corallata (Fig. 70) is typical. When attacked by the Phytoptus the leaf becomes very much modified by thickenings, ridges and convolutions (Figures 71a, b). The palisade cells divide so that it is impossible to distinguish them from the mesophyll, and the intercellular spaces are obliterated as the result of the rapid cell division. The new cells are small and very rich in protoplasm, but gradually become filled with tannin as the gall approaches maturity. The tannin first forms in the outer and most exposed cells of the gall while the inner layers of cells retain their protoplasm very late. The Phytoptus restricts its attacks to these inner and more protected parts. From a study of these galls it is apparent that the Phytoptus is not working on

* Contributions from the Department of Zoology and Entomology, Ohio State University, under the direction of Prof. Herbert Osborn, No. 17.

all parts of the gall at the same time, but gradually moves outward over the surface of the leaf, thus increasing the size of the gall and drawing its food supply from the newer part thus formed.

When the attack is made upon the flower we have a mass of distorted tissue which is structurally the same as that produced in the leaf gall (Figures 72a, b). The floral envelopes are the first to suffer from the attack, the ovary with its contents is the next greatest sufferer, while the stamens are frequently unaffected. It is evident that the attack upon the flower must be made very early in order to cause complete destruction. Very frequently the floral envelopes will be very much deformed and the ovary and the stamens very slightly affected. In other cases the ovary will be very much enlarged and its chambers practically obliterated. It is evident that the attack upon the ovary must be made very early to produce a great deformity. The partial immunity of the stamens is probably due to their being very nearly mature before the opening of the bud.

2. GALLS OF CECIDOMYIA.

Cecidomyia anthophila O. S.—on Solidago canadense L. (Figs. 73a, b), makes the attack early and completely prevents the opening of the bud. The gall is in the form of a hollow cone. The transformation is so complete that the location is the only evidence that the gall is produced from a flower bud. A section of the gall shows the nutrient layers of the cells next to the larval chambers, large parenchyma cells near the outer epidermis, and a number of rather weak fibro-vascular bundles.

Cecidomyia sp.—on Ratibida pinnata Barnhart (Figs. 74a, b, c). The entire bud is transformed into a gall with the larva in a chamber in what was originally the ovary. All the floral parts have become modified and united to form the gall. A section of the gall (Fig. 74c) shows that the cells are more uniform in size than in the preceding galls and that the fibro-vascular bundles are practically obliterated.

Cecidomyia sp.—on Prunus virginiana L. (Figs. 75a, b). My specimens of this gall were mature. I am unable to say at what time the gall originates, but it reaches its maturity with the fruit. The gall is somewhat larger than the fruit, but otherwise resembles it closely. The larva makes its exit through an opening at one side of the stem. The larval chamber is very large, thus giving the gall a bladder-like character. The cuticle is well developed and the parenchyma cells below it are very large, while the cells next to the larval chamber are much smaller. Weak fibro-vascular bundles are also present. The wall of the gall (Fig. 75b) is much thicker than the wall of the fruit at this time (Fig. 75a), and parenchyma cells are much larger. The characteristic stone (sclerenchyma) of the fruit is never developed in the gall.

3. GALLS OF LEPIDOPTERA.

I gathered a number of Lepidopterous galls on Rudbeckia laciniata L. which I was unable to determine. These galls occur on both leaf and flower and are very large and fleshy. In fact they were so fleshy and juicy that it was very difficult to secure sections. The parenchyma cells were very large, and small fibro-vascular bundles were numerous. The larval chambers were numerous and each contained a single larva or pupa. In my specimens the larvae were far advanced, many of them in the pupa stage, but the cells next to the chambers were very rich in food supply.

PART VII. ROOT GALLS.

Amphibolips radicola Ashm. (Figs. 76a, b).—on Quercus alba L. was the only root gall that I collected. The galls were borne just under the surface of the ground at about the point of transition from stem to root. They were produced in great numbers and so closely packed together as to assume the shape of figs. Those nearest the surface of the ground and therefore slightly exposed to the light were of a rich, red color, while those deeper in the ground were almost white, slightly tinged with yellow. Each gall contained from one to five larval chambers. The younger galls showed four zones well defined (Fig. 76a). The inner or nutritive zone was thick and the cells contained abundance of protoplasm. The protective zone was thin and the cells fibrous in character rather than sclerenchymatous. The parenchyma zone was thick and composed of large parenchyma cells. The epidermal zone was relatively thick and the cells firm. As the insects approach maturity the nutritive and protective zones are entirely destroyed (Fig. 76b). The insect eventually makes its escape through an opening in the side of the gall.

PART VIII. HISTOLOGY OF GALLS.

Many of the histological characters of galls have been referred to in the preceding parts. This part has been introduced at this time for the purpose of adding a few additional facts which were not clear at the time of the writing of the preceding parts.

A. Internal Structures.

1. GALLS OF ACARINA.

These galls have been sufficiently discussed and need very little attention at this time. In general these galls may be thrown into three groups: (1) Those galls in which there is very little distortion, but a modification of the epidermis, as in the case of the Phytoptus on the beech; (2) Convolutions of the parts as in the case of P. ulmi (Fig. 8), P. abnormis (Figs. 9, 44), P. quad-

ripes (Figs. 10, 43), and P. acericola (Figs. 11, 45). These convolutions result in the formation of a more or less well defined cavity, and trichomes are developed in great abundance in the younger stages; (3) Thickening of the parts which become covered with an abundant growth of trichomes as in the case of E. anomalum (Figs. 47, 48).

The Phytoptus galls show two fairly well-defined zones, the outer made up of rather large cells and the inner of much smaller cells, which are very rich in protoplasm and which supply nourishment for the young animal (Fig. 77). As the galls approach maturity the protoplasm disappears, first from the outermost cells and lastly from the cells on the inner surface. As the protoplasm disappears the tannin accumulates in great abundance (Fig. 78).

2. GALLS OF THE APHIDIDAE.

Many of the Aphididae galls produce trichomes which soon disappear. At first all the cells contain protoplasm and divide rapidly, but as the galls approach maturity the tannin increases in abundance.

Schizoneura americana Riley (Fig. 12), Colopha ulmicola Fitch (Fig. 13), and Hormaphis hamamelis Fitch (Fig. 15) have been considered in Part I.

In Pemphigus populi-transversus (Figs. 55, 56) and P. p.-caulis (Figs. 57, 58) the thickness of the walls of the galls is much greater than any other members of this family and the cells are more uniform in character. These galls are especially well supplied with fibro-vasular bundles and are very dense.

In P. vagabundus (Fig. 112) we have a gall in which many of the cells are elongated similar to C. ulmicola and H. hamamelis. Its close structural resemblance to C. ulmicola and H. hamamelis and unlikeness to P. p.-transversus and P. p.-caulis is due to the fact that P. vagabundus, C. ulmicola, and H. hamamelis are formed on the blades of the leaves, while P. p.-transversus and P. p.-caulis are formed on the petioles which are made up largely of fibro-vascular tissue. My specimens of these galls were mature, and I am therefore unable to say anything concerning their early stages.

In the Phylloxera galls all the cells are at first rich in protoplasm and the tannin does not form in abundance until very late. The two zones are fairly prominent. In P. c.-caulus Fitch on H. ovata, a gall which forms on both blade and petiole of the leaf and also on young stems large intercellular spaces are formed near the surface.

3. GALLS OF PSYLLIDAE.

Pachypsylla c.-mamma Riley has been described in Part V (Figs. 59, 60).

4. GALLS OF CECIDOMYIA.

These galls have been described in Part I (Figs. 22, 23, 24), in Part V (Figs. 61, 62, 63), in Part VI (Figs. 73, 74, 75), and in the Appendix (Figs. 114–119). In these galls the two zones are usually fairly well defined, but the galls of this genus are so different in character that it is difficult to give a definite description. The time for the formation of the tannin is variable, but it is usually produced late and in great abundance.

5. GALLS OF THE CYNIPIDAE.

All these galls are very similar. The majority show the four zones and in most cases these zones are well defined. The outer zone is the epidermal which will be described later (Figs. 84–91). The second is the parenchyma zone; the third is the protective zone made up largely of sclerenchyma, and the fourth or innermost is the nutritive zone. In many cases the second and third zones become partially or entirely separated. This separation, however, is not between the second and third zones as previously stated by me in Parts I and V, and by Focken, but rather a separation of the tissues of the second or parenchyma zone, the greater part of this zone clinging to the epidermal zone and a few cells remaining attached to the protective zone.

Diastrophus siminis Bassett (Figs. 66–69) has been described in Part V. The four zones are distinct and each shows the character previously referred to.

Diastrophus nebulosus O. S., described in the Appendix (Figs. 129a, b), is a stem gall in which the zones are well defined, the protective zone being especially well developed. Each zone shows the characters previously referred to.

In Amphibolips confluentus Harris (Figs. 121a, b, c) the first and second zones are well developed, but the distinction between the third and fourth is not so pronounced.

In Amphibolips inanis O. S. (Fig. 28) the four zones are well defined. In the young gall (Fig. 79) the cells of the nutritive zones are very rich in protoplasm and there is very little or no distinction between the nutritive and the protective zone, but as the galls approach maturity the cells of the protective zone become very thick and are soon converted into sclerenchyma (Fig. 80).

In Callirhytis papillatus O. S. we have the four zones well defined (Fig. 30). As the gall approaches maturity the cells of the nutritive zone lose their protoplasmic contents and become very much shriveled, the protective zone is made up usually of only two or three layers of cells. Next to the protective zone are two or three layers of cells which are in reality a part of the parenchyma zone. The large intercellular spaces formed in this

zone are bridged by long unicellular threads, but no fibro-vascular bundles (Fig. 81)

Dryophanta palustris O. S. galls show the four zones well defined (Figs. 29, 65). When mature the contents of the cells of the nutritive zone has been entirely used by the insect. The protective zone consists of only two or three layers of sclerenchyma cells, to which are attached a few cells of the parenchyma zone (Fig. 82).

Andricus petiolicola Bassett (Fig. 124) produce a very hard petiole or mid-rib gall which shows the four zones well defined. There is no separation between the second and third zones. The nutritive zone is at first very prominent, but it is reduced as the gall approaches maturity. The protective zone developes its sclerenchyma character rather late (Fig. 83) and gradually merges into the two adjacent zones.

B. Epidermal Structures.

The epidermal cells vary in the size and in the thickness of the cell walls. The galls may be smooth, pubescent or covered with spiny structures. The amount of pubescence depends somewhat on the natural pubesence of the host plant. Galls on such smooth plants as Populus deltoides Marsh show very few and very small trichomes, while galls on plants that are naturally pubescent are likely to be pubescent. These trichomes vary in shape and general character and are very prominent when the gall is young. As the gall approaches maturity the trichomes usually disappear. When these trichomes drop off their place of former attachment is marked by a small mass of small cells, usually containing tannin and from which imperfect rows of cells seem to radiate (Figs. 84–90).

1. GALLS OF CYNIPIDAE.

Dryophanta palustris O. S. is very pubescent when young (Fig. 84a). In the mature gall the cells are much larger, the trichomes have disappeared and their point of attachment is made visible by the accumulation of tannin (Fig. 84b).

All my specimens of Amphibolips inanis O. S. were fully developed, but the points where the trichomes had evidently been attached were very prominent (Fig. 85). These points are the large, black spots so prominent on these large bladdery galls.

In Diastrophus siminis Bassett the trichomes are very large (Fig. 86) and drop off very readily.

In Diastrophus potentillae Bassett the trichomes are very numerous and each is at the apex of a very small elevation (Fig. 87). Examination of the epidermis of Acraspis erinacei Walsh show that its spines were due to similar but much more prominent elevations.

2. GALLS OF THE APHIDIDAE.

Galls belonging to this family are usually less pubescent than those belonging to the Cynipidae. The trichomes are usually much shorter and frequently less numerous. Each trichome is usually made up of a single cell (Fig. 88). The place where these trichomes were attached is marked by an accumulation of tannin, the same as in the Cynipidous galls (Figs. 89, 90).

Examination of the galls of the Phylloxera spinosa Shimer show that the spines were due to the same cause as in the Cynipidous galls (Fig. 87).

Galls of Pemphigus p.-transversus Riley (Fig. 91) and P. p.-caulis Fitch were perfectly smooth, but the cell walls were much thicker than in any other galls studied.

CONCLUSION.

1. The inner layer of cells (i. e., those next to the larva) are always supplied with nutriment until the insect is mature.
2. The development of the other layers of cells is for the protection of the larvae. These protective devices reach their highest development in the Cynipidous galls.
3. In the very young galls there is usually little or no distinction between the nutritive and protective zones. The time of the differentiation of the protective zones varies in different species.
4. The fibro-vascular bundles are most prominent in galls on the petiole and mid-rib.
5. Most galls are covered with trichomes which disappear as the galls approach maturity. The number of trichomes is variable in proportion to the pubescence of the host plant.
6. Spines are due to elevations composed almost entirely of epidermal cells.

PART IX. OVIPOSITORS AND MOUTHPARTS.

One of the most prominent questions concerning the formation of galls which presents itself to the students of entomology and botany and even to the most casual observer, is the exciting factor in gall production. Is the stimulus from the ovipositor or mouthparts? Is it mechanical or chemical? The author believing that the logical method of solving this problem was to first make a careful study of the morphology and development of galls has published the preceding parts of this paper. The author does not claim to have found a complete solution of the problem, but is hopeful that some of the facts stated in this series of papers may lead to more thorough and satisfactory studies of the problem. The problem presents many difficulties; the parasites and inquilines which are usually present are frequently difficult to distinguish from the real gall-maker; this is especially true when the study is confined to the larvae. In the following studies the author is reasonably certain that the determinations are correct.

OVIPOSITORS.

Gall-making insects deposit their eggs by two methods, either on the surface of the plant or within the tissues. Those insects which deposit their eggs on the surface usually have mouthparts developed for sucking, while those which deposit their eggs within the tissues usually have mouthparts developed for biting. Those which deposit their eggs on the surface of the plant are the Acarina, the Hemiptera, and the Diptera. Those which deposit their eggs within the tissues are the Hymenoptera and the Lepidoptera. In this paper we have made a careful study of the ovipositors of Cecidomyia gleditsiae, of Nematus sp———, Dryophanta palustris, Amphibolips radicola, Andricus cornigerous, A. seminator, and Rhodites radicum. A number of others were examined, but because of the uncertainty as to determination are not figured.

The Cecidomyia ovipositor (Fig. 92) is not suited to puncturing tissues. The gall is never formed until after the hatching of the larva. In this case it is evident that the stimulus, whether mechanical or chemical, is produced by the larva.

Insects belonging to the genus Nematus deposit their eggs either on the surface of the plant or in slits made by the ovipositor (Figs. 93a, b). It is said that the galls are formed from these wounds before the larva escapes from the egg, and in these cases it is claimed that the irritating cause is a drop of fluid secreted by the parent insect. Westwood claims that the egg increasing in size is a result of imbibing sap from the wound in the plant. It is well known that the eggs of some insects increase in size as a result of the growth of the embryo within the egg. I have so far been unable to make any satisfactory observations upon the Nematus galls, but it is probable that the eggs increase in size from the growth of the embryos and not as a result of the absorption of plant sap. It is also possible that the gall may be the result of the mechanical irritation of the ovipositor or the enlargement of the egg or both. The wound caused by the ovipositor of the Nematus is very much more severe than the wounds caused by the ovipositors of the Cynipidous insects.

Adler, after a careful observation on Nematus Vallisnierii, says: "This fly, which is armed with a finely serrated terebra, cuts into the tender leaves of the end of the shoot of the Salix amygdalina, and inserts her egg into the open wound, frequently placing several in the same leaf. At the same time the glandular secretion flows into the wounded leaf. A few hours after this injury the leaf surface presents an altered appearance, and new cell formation begins freely, leading to a thickening of the surrounding leaf surface. After the lapse of about fourteen days the green and red-shaped gall is fully grown. If it be now

opened the egg can still be seen lying within the cavity. The embryonic development is as yet unfinished and three weeks elapse before the larva emerges from the egg to find around it the material prepared for its nutriment. In this case the wound caused by the fly is the immediate exciting cause of cell activity, and leads to gall formation."

M. W. Beyerinck, in a paper regarding the growth of the gall of Nematus caprea on Salix amygdalina holds a similar view. I have not seen this paper, but an abstract* of it says: "The production of the gall is undoubtedly due to the matter secreted by the poison gland, which is, consequently, homologous with the poison of Hymenoptera aculeata; when the insect does not deposit an egg in the wound which it makes, the quantity of albuminous matter poured into the vesicle is always less than when an egg is deposited; by careful observation it is possible to assure oneself that the size of the gall is always proportional to the size of the wound and the quantity of albuminoid matter introduced. By an experiment in which a deposited egg was punctured by a fine needle, it was shown that the gall is due to the parent and not to the egg; but, of course, in such a case the gall remains small; neither the egg nor the larva are necessary for its production, though their presence exercises a certain influence on the regularity of their development."

The ovipositors of the Cynipidae vary in length and in the amount of coiling within the abdomen. All present the same general characters. So far I have been unable to detect any relationship between the length and character of the ovipositors and the location and complexity of the galls (Figs. 94 to 98). Adler claims that the egg is always deposited in or near the Cambium layer of the plant. I am inclined to accept this statement, but have made no special effort to verify it. If Adler's observations are correct the length of the ovipositor would be associated not with the depth of the Cambium from the surface of that part of the mature plant affected, but with the location of the Cambium at the time of oviposition and with the difficulties which the insect would experience in forcing the ovipositor to the desired point.

Oviposition usually occurs before the buds are open, and the eggs may be placed in three positions (1) in the stem, as in the case of Rhodites radicum O. S., R. globulus Beut., Andricus cornigerous O. S.; (2) in the apex of the incipient stem as in Andricus clavula Bassett, and Holcaspis globulus Fitch; or (3) in the leaves of the bud as in Rhodites bicolor Harris, Amphibolips confluentus Harris, A. inanis O. S., A. ilicifoliae Bassett, Neuroterus irregularis O. S., A. seminator, Callirhytis tumifica

*Jour. Roy. Micr. Soc., 1887, p. 746.

O. S., Holcaspis centricola O. S., Dryophanta palustris O. S., and Callirhytis papillatus O. S. In these cases it is evident that the force necessary to penetrate the bud may be as great or even greater than the force necessary to penetrate a stem. Adler's observations demonstrate that great force is used to penetrate the buds and reach the desired point for depositing the eggs.

Beyerinck has demonstrated that the fluid ejected by the ovipositor of the Cynipidae is very different from the fluid ejected from other Hymenopterous insects; that it is without taste or smell and does not irritate when injected under the skin. Adler has demonstrated that this fluid cannot be considered as the stimulus to gall production. It is probable that it may serve to attach the eggs, or as an antiseptic, or as a seal for the wound.

Since the gall does not form until after the hatching of the larva it is evident that oviposition does not furnish the stimulus unless it may be that there is cell division but no swelling of the plant tissues previous to the hatching of the larva. The author has made no observations upon this point. Adler, in discussing this question, says, in regard to Trigonaspis: "This fly pricks the leaf in May, but months pass before any trace of gall formation can be seen. It has tolerably strong ovipositor with which it cuts into the veins of the leaf, and in this way a distinct mark is left wherever an egg has been inserted. Guided by these marks it is easy to find the egg, but it is not until September that the larva leaves the egg, and then gall formation begins."

MOUTHPARTS.

Since oviposition does not give an explanation of the stimulus causing the formation of the gall it is necessary for us to turn our attention to the mouthparts.

For convenience the insects may now be divided into two groups, those with mouthparts for sucking, which make their attacks upon the outside, and those with mouthparts for biting, which make their attacks from the inside. Under the former are included the Acarina, the Hemiptera and the Diptera; under the latter are included the Lepidoptera and the Hymenoptera.

1. HEMIPTERA.

The Hemipterous insects which produce galls may be placed in the following order, with reference to the complexity of their galls, beginning with the lowest: Schizoneura, Colopha, Hormaphis, Phylloxera, Pemphigus and Pachypsylla. Mouthparts of the following were carefully examined: Schizoneura americana Riley, Colopha ulmicola Fitch (Fig. 99), Hormaphis hamamelis Fitch, Phylloxera carya-fallax Riley, P. c.-globuli Walsh, P. c.-spinosa Shimer, P. vastatrix Planchon, Pemphigus populitransversus Riley, P. p.-caulis Fitch, P. vagabundus Walsh,

Pachypsylla celtidis mamma Riley (Figs. 100a, b), and P. c.-gemma Riley.

The study of these mouthparts gave no new anatomical facts. The different genera showed considerable variation as to length of beak and setae. In general it may be said that the setae tend to increase in the distance they may be protruded beyond the tip of the beak as the galls approach complexity. This, however, cannot be considered an exact rule, since the S. americana, C. ulmicola and H. hamamelis have setae of practically the same length, although the gall produced by S. americana is much simpler than the galls produced by either C. ulmicola and H. hamamelis (Part I, Figs. 12, 13 and 15). It was impossible to make exact measurements of the distance the setae protruded beyond the tip of the beak, since it was impossible to tell whether the setae were fully extended or partially retracted. The above conclusions were reached after the examination of a large number of specimens.

So far as I have been able to determine the insects do not remain attached to any one point for a great length of time. The P. c.-mamma (Figs. 100a, b) has a gall of the greatest complexity, and the insect has setae which protrude farther beyond the point of the beak than any other examined; a large number of these galls were opened and the position of the insect noted. The insect was never found attached and apparently had no definite point of attack.

The preceding observations emphasize Conclusions 6 and 8 of Part I and a statement in the first of Part V. That is, the modification of the plant tissue to form the gall is purely mechanical, being a continuous effort on the part of the plant to heal the wound produced by the repeated puncturing of the cells by the insect. When a branch is cut from a tree a growth is produced which tends to cover the wound. In this case a single wound and a single stimulus which is purely mechanical but which produces rapid growth for the purpose of covering the wound. In the case of Aphididae and the Psyllidae galls the wounds are more slight but repeated rapidly, the stimulus is mechanical and the growth rapid, tending to cover the injury.

It is possible that the setae of the various genera may stimulate different tissues and thus cause galls of varying complexity, but upon this question I am not ready to give a definite statement.

2. DIPTERA.

The Cecidomyid galls occur upon a greater variety of hosts than any other group of galls, and as previously stated in Part V, show by far the greatest variation in structural characters and the smallest number of typical characters.

The mouthparts of a number of larvae were examined (Figs. 101, 102), and all were practically the same; salivary or other gland structures could not be demonstrated.

I am inclined to believe that the Cecidomyid galls are due to purely mechanical stimuli and that the great variations are due to the different tissues upon which the larvae feed.

Mr. W. A. Cannon,* in discussing a Cecidomyid gall on the Monterey pine, says that the "larvae take their food only by absorption through the surface of the body," also that "there is no indication that the hypertrophy is either caused or affected by any substance deposited with the eggs."

3. HYMENOPTERA.

We now come to the galls of greatest complexity and also to those with which we have the greatest difficulty. These galls are so very generally infested with parasites and inquilines that it is difficult to decide which larva is the true gall producer.

A careful study of these shows that the insects have a very strong pair of mandibles (Figs. 103 to 108), each working upon two pivotal points. Some of these mandibles appear to have an opening at the tip (Figs. 104, 105), and some showed what appeared to be sacs or glands at the base (Figs. 104, 106b). In one case at least (Fig. 104) these glandular sacs appeared to be connected with the opening. The question that naturally presents itself is, are these openings for the purpose of pouring out a fluid or are they suctorial as in the case of Chrysopa and other families? In only two species was it possible to demonstrate these structures. Some light is thrown upon this by Part VIII, in which it was shown that the cell walls of the inner or nutritive zones were not destroyed, but that the contents of the cells were removed, causing them to shrivel.

The teeth of the mandibles are never on the same plane and the mandibles become more and more chitinous as the larvae approach maturity. The strength of the mandibles appears to depend upon the density of the tissue through which the insect works its way to the outside In A. inanis (104) and A. confluentus (Fig. 105) the strength of the mandibles is practically the same and the character of the galls very similar. In D. siminis (Figs. 106a, b) the mandibles are stronger and the tissues of the gall correspondingly denser. C. petiolicola (Fig. 103) is by far the strongest of those studied, and the tissues through which the insect must work its way the densest of the leaf galls (Fig. 124).

A study was made of the larvae from galls of C. papillatus. This is a small, rather dense leaf gall. Larvae of two species

*Cannon, W. A. "The Gall of the Monterey Pine." *The American Naturalist*, Vol. XXXIV, No. 406 (Oct., 1900), p. 801.

were found (Figs. 107, 108). A careful study of the mouthparts lead me to consider No. 107 as a true gallmaker and No. 108 as a parasite. The mouthparts of the one which I consider a true gallmaker were as strong as those of C. petiolicola (Fig. 103). The mandibles of the parasite (108) were equally strong and showed what appeared to be rudimentary gland structures.

Holcaspis globulus Fitch was the only bud (i. e., incipient stem gall, Part III, Fig. 34) gall examined. In the young larvae the mouthparts are weak, but as the larvae approach maturity the mandibles become very strong (Fig. 109) and well fitted to cut the opening for the escape of the insect. However, the mouthparts were not so strong as in the case of C. petiolicola, but the gall of H. globulus is not so dense as the gall of C. petiolicola.

The mouthparts of Nematus pomum Walsh (Fig. 110) were very similar to those of the Cynipidae. I am not inclined to consider the apparently glandular-like structure observed in a few species of any great importance. They may be suctorial or they may be degenerate organs. I consider the stimulus as purely mechanical. The character of the gall may depend upon the location, which would result in difference in tension in different parts of the plant on which the gall may be located and also upon the laws of natural selection, which will be considered in the latter part of this paper.

It would be interesting to know the exact time that cell division begins in the formation of a gall, but it is very difficult to make satisfactory observations upon this point. Adler has made successful observations upon this stage in Neuroterus laviusculus and Biorhiza aptera. He says: "The moment the larva has broken through the egg covering and has for the first time wounded the surrounding cells with its delicate mandibles, a rapid growth begins. This goes on so quickly that while the posterior part of the larva is still within the covering a wall of like growth of cells has already arisen in front. This rapid cell increase can be easily explained because the irritation set up by the emerging larva is exerted upon highly formative cells which collectively possess every condition of growth. The cells which are primarily around the larva cannot be distinguished from the parenchymatous cells from which they proceed."

4. LEPIDOPTERA.

A careful study was made of the mouthparts of the Gelechia solidaginis Fitch (Fig. 111) and upon an undetermined species found upon Rudbeckia laciniata (Part VI). The mandibles are larger and much stronger than in any of the Hymenopterous gallmakers which I examined. The gall is also much stronger than any of the Hymenopterous galls whose larvae were studied. No glandular structures were observed.

CONCLUSION.

1. The fluid secreted by the ovipositor is not an irritant, and therefore cannot be the stimulus for gall production.

2. Since the gall does not form, excepting the Nematus galls, until the appearance of the larvae, it is improbable if oviposition is a stimulus for gall production; and in those insects in which the egg is not deposited within the tissues of the plant it is impossible.

3. Glandular structures were observed in only a few of the Hymenopterous larvae and these were of doubtful character.

4. Since it has so far been impossible to demonstrate the presence of a chemical stimulus except in Nematus, we must consider that the stimulus is usually mechanical. As previously stated (Part I, Conclusion 3) the morphological characters of the gall depend upon the genus of the insect producing it rather than upon the plant upon which it is produced. The early history of all galls except the Cecidomyid is practically the same (Part V, Con. 2). The shape and external character of the gall probably depends upon the following: (1) The plant upon which the attack is made; (2) Upon the part upon which the attack is made; (3) Upon the tissues affected; (4) Upon possible results of natural selection.

SUMMARY OF PARTS.

Next in importance to the problem of a stimulus giving rise to a gall is the explanation of specific external characters. This question is not easily answered and at the present time any explanation must be largely theoretical.

The gall-producing insects are found in six orders, as follows: 1. Arachnida (mites); 2. Hemiptera (Aphidae and Psyllidae); 3. Diptera (Cecidomyidae and Trypetidae); 4. Hymenoptera (Cynipidae and Tenthrenidae); 5. Lepidoptera, and 6, Coleoptera. The gall-producing habit must have originated independently in each of these orders and in some orders (Diptera and Hymenoptera) it must have originated independently in each of the two families represented.

The formation of the gall is due to two primary factors; a stimulus, usually mechanical, given by the insect, and nourishment furnished by the plant.

Conclusions reached as results of previous studies and bearing on this subject are as follows:

1. "Galls may be classified into two general groups, viz.: those produced by mouthparts and those produced by oviposition. Those produced by oviposition may be considered the more highly developed." (Part I, Con. 1.)

2. "The gall does not form until the appearance of the larvae. Therefore all galls are produced by mouthparts." (Part VIII, Con. 1.) The Nematus galls are an exception.

3. "The morphological character of the gall depends upon the genus of the insect producing it rather than upon the plant on which it is produced." (Part I, Con. 3.)

4. "Within each family we find certain morphological resemblances." (Part I, Con. 4.)

5. "The families show parallel lines of development from a low form of gall structure up to a high form." (Part I, Con. 5.)

6. "The presence of at least two zones, of which the inner may be considered nutritive." (Part I, Con. 7.)

7. "The formation of the gall is probably an effort on the part of the plant to protect itself from an injury which is not sufficient to cause death. Both Adler and Focken consider that after the first stages of formation the gall becomes an independent organism growing upon the host plant. This is probably true in the highly developed galls of Aphididae, Cecidomyia, and Cynipidae, but the writer is doubtful if this is true in the less complex galls of Acarina, Aphididae and Cecidomyia." (Part I, Con. 8 and Part V, Con. 6.)

8. "In the formation of all leaf galls except the Cecidomyia galls the normal cell structure of the leaf is first modified by the formation of a large number of small, compact, irregularly shaped cells. In the galls of Acarina and Aphididae this is followed by a development of trichomes, especially in the former. In all galls the mesophyll is subject to the greatest modification. Many small fibro-vascular bundles are formed in this modified mesophyll." (Part V, Con. 2.)

9. "Trichomes are far more common in galls produced by mouthparts than in those produced by oviposition." (Part V, Con. 9, and see Summary 2.)

10. "Variation in galls is due to their being produced by insects of different orders, to their working upon different parts of the plant and upon different tissues of these parts." (Part III, Con., and Part IV, Con. 1.)

1. ARACHNIDA.

The Arachnida galls are of four types: (1) A modification in the epidermis of the leaf as in the Phytoptus galls on maple and elm; (2) A fold in the plant tissue causing a cavity filled with trichomes, among which the parasites live, as in the case of many Phytoptidi (Figs. 8, 9, 10, 11, 43, 44, 45, Parts I and V); (3) A swelling with an exposed surface covered with trichomes, among which the parasites live, as in the case of Erineum

anomalum (Part V, Figs. 47, 48); (4) The witchbroom formation, as in the case of the Phytoptus sp——, and Sphaerotheca phytoptophila Kell. and Sw. on Celtis occidentalis.

The author has studied only the second and third types. The difference between these two may be accounted for by the fact that the Phytoptus attacks the blade while the Erineum attacks the petiole, mid-rib or larger vein. The part affected undergoes a curvature in each case in the direction of the least resistance.

2. HEMIPTERA.

The method of attack by the Hemiptera is practically the same as in Arachnida, i. e., by sucking mouthparts. The galls present a complete serial line of development, the lowest form being a simple curling of the leaf as in the case of Schizoneura americana, the next higher, a simple folding of the leaf, as in the case of Colopha ulmicola, the next higher is a more complex structure, such as the Phylloxera galls and H. hamamelis, the next higher, the slightly more complex, as in the case of the Pemphigus galls (Figs. 12 to 21, and 49 to 58). The galls of the Pachypsylla (Figs. 59, 60) are the most highly developed of the entire series.

Although in this case we have a complete series, it is difficult to understand how this development has been produced. It may be that the different forms are due to the attack being made upon different tissues in each case, or to the degree in which the tissues are injured. Upon this point we have no direct proof. However, there is very little doubt that the stimulus is entirely mechanical.

3. DIPTERA.

As previously stated, the Cecidomyid galls are far more varied in location and in morphological structure than any other group of galls and show less number of characters peculiar to themselves alone. There is not sufficient data to draw even theoretical conclusions concerning the influencing causes in their development.

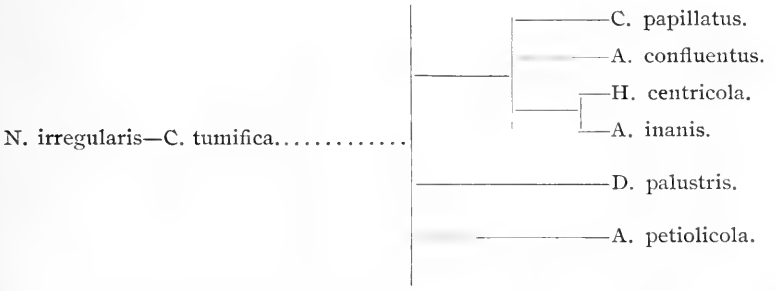
4. HYMENOPTERA.

As previously stated, the Cynipidous galls are the most highly developed and show a greater number of morphological structures peculiar to themselves than any other group (Part I, Con. 2; Part V, Con 3).

Since the gall does not begin to develop until after the hatching of the larvae, oviposition cannot be an important factor except in so far as it is necessary to have the egg placed in certain tissues.

Examination of the mouthparts show few, small and insignificant gland-like structures the character of which is doubtful. It is therefore probable that the stimulus is purely mechanical except in the Nematus. But how are we to account for the great num-

ber of specific external characters? Let us first review the structural characters of the leaf galls, since these galls show the most uniform line of development. Considering Neuroterous irregularis the gall of greatest simplicity, we can formulate the following diagram:



In N. irregularis the zones are not so well developed as in C. tumifica. In C. tumifica the zones are perfect, but in contact. In C. papillatus the protective and parenchyma zones are separated, but connected by long parenchyma cells. In H. centricola and A. inanis the protective and parenchyma zones are connected by fibro-vascular bundles. In A. confluentus they are connected both by fibro-vascular bundles and by parenchyma cells (Fig. 121). In D. palustris the parenchyma and protective zones are not connected. In A. petiolicola the zones are in contact, but the tissues are very dense, due to location in the petiole of midrib of the leaf.

If galls become independent structures they are undoubtedly subject to the same laws of natural selection as any other group of organisms, or if they be considered as parts of the plant they must also be subject to the same laws of natural selection as any other part of the plant on which they live. How, then, have these laws affected the gall? It may be a protective coloration against birds and rodents, and other insects, but this cannot be very important since many species of galls are very conspicuous. Furthermore, animals make but very little use of galls for food. So far I have observed other animals using galls for food but once and then birds were tearing open the large galls of Pemphigus vagabundus and eating the insects. The tannin which develops in such abundance in all galls as they approach maturity is probably a great protection against insectivorous animals.

The greatest insect enemy with which the gall insect has to contend is the great number of parasites. The size, shape and character of the epidermal covering of the gall may be a protection against this numerous enemy. The thickness of the gall and the density of the tissues, especially the protective zone, is an

important protective device. The large intercellular chambers in the parenchyma zone place the larvae at a great distance from the surface of the gall without increasing the amount of work necessary for the mature insects to accomplish before reaching the outside; this is undoubtedly a great protection against parasites, since it increases the difficulties for the parasite in reaching the larvae with the ovipositor, The development of these protective devices is probably the result of natural selection. Since the character of the gall depends upon the insect, many variations in the gall may also depend on variations in the stimuli given by the insect. If these variations in character of epidermis, in thickness of parenchyma zone, in the formation of large intercellular spaces, in thickness and density of protective zone, are advantageous to the insect in protecting it from the numerous parasites, these characters may be perpetuated in succeeding generations and the gall may increase in complexity. Natural selection is a reasonable explanation.

It should be remembered that the plant is making an effort to resist a parasite from which it cannot escape. The gall-maker derives its nourishment without destroying its host and at the same time strives to protect itself as far as possible from the great number of parasitic enemies. The food supply first becomes a part of the gall and upon this supply which, in the case of the Cynipidae, is stored in the nutritive zone, it feeds.

Any irritation, such as the cutting or puncturing of plant tissues, may and usually does cause excessive growth. It is probable that the primitive galls were of a type similar to the simplest of the Phytoptus galls, i. e., a peculiar growth of the epidermal cells. The next step in the evolution of the gall may be represented by a type similar to Schizoneura americana, in which case the stimulus is greater, resulting in a curling of the leaf. The next step may be represented by a type similar to the more complex Phytoptus galls, H. hamamelis, C. ulmicola, the Phylloxera, the Pemphigus and the most complex of the Pachypsylla galls in which we find a series of more or less complex folds in the leaf up to the increase in amount and differentiation of the tissue as in the case of P. p.-mamma.

In the Cynipidous galls we have the greatest complexity, but also a factor somewhat different from that in the forms to which we have referred, i. e., the placing of the egg below the surface and in those tissues upon which the larva is expected to feed. It is impossible to say whether this habit of placing the egg below the surface was acquired before or after the gall-making habit, but it must be a great advantage to the insect. These galls, as previously demonstrated, show the more complex serial line of development of any of the galls, but even the simplest of these is more complex than the most complex gall produced by any other

order of insect. This very complex development is due to an early acquirement of the gall-making habit or to more rapid evolutionary development as a result of the deposition of the egg below the surface.

The greater part of the work connected with Part IX of this series was conducted at the Lake Laboratory of the Ohio State University at Sandusky, Ohio, and I am very much indebted to the Director, Professor Herbert Osborn, for valuable assistance. I also wish to express my thanks to the many friends who have collected material and otherwise aided in these studies.

This series of papers will be presented to the Faculty of the College of Arts, Philosophy and Science, of the Ohio State University, as the thesis requirement for the degree of Doctor of Philosophy, June, 1904.

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EXPLANATION OF PLATES IX–XII.

The drawings were made with a Bausch & Lomb microscope.. For Figs. 70–76 and Figs. 84–91 and Fig. 93b, a Number 2 ocular and 1/6 objective. For Figs. 77–83, a Number 2 ocular and 1/12 immersion objective. With Figs. 92–98 and Figs. 106a, 110 and 111, a 3/4 ocular and 2/3 objective. For Fig. 93 a Number 2 ocular and 2/3 objective. The reduction is not so great as in the preceding parts and therefore the figures are proportionately slightly larger. The diagrams were not made upon a definite scale. The numbering of the drawings is continuous with the preceding parts.

Abbreviations:
e. epidermis.
ep.—epidermal zone.
pa.—parenchyma zone.
p.—protective zone.
nu.—nutritive zone.
f. v. b.—fibro-vascular bundles.
l. c.—larval chambers.
sc.—sclerenchyma.

FLOWER AND FRUIT GALLS.

70. Section of leaf of Euphorbia corollata.
71a. Diagram of section of Phytoptus sp—— gall on leaf of E. corollata.
71b. Section of 71a.
72a. Section of lower part of ovary of E. corollata affected by Phytoptus sp——.

72b. Section of upper part of flower of E. corollata affected by Phytoptus sp——.
73a. Diagram of cross section of Cecidomyid bud gall on Solidago canadense.
73b. Section of same.
74a. Diagram of longitudinal section of Cecidomyid gall on Ratibida pinnata.
74b. Diagram of longitudinal section of Cecidomyid gall on Ratibida pinnata.
74c. Section of 74b.
75a. Section of unaffected fruit of Prunus virginiana.
75b. Section of Cecidomyid gall developed in fruit of P. virginiana.

ROOT GALL.

76a. Section of young gall of Amphibolips radicola.
76b. Section of mature gall of A. radicola.

HISTOLOGY.

77. Section of young gall of Phytoptus quadripes.
78. Section of young gall of Phytoptus abnormis.
79. Section of nutritive zone of young gall of Amphibolips inanis.
80. Section of mature gall of A. inanis.
81. Section of mature gall of Callirhytis papillatus. (Nutritive, protective and part of parenchyma zones.)
82. Section of mature gall of Dryophanta palustris. (Nutritive, protective and part of parenchyma zones.)
83. Section of mature gall of Andricus petiolicola.

SURFACE SECTIONS OF

84. Dryophanta palustris. (Very young gall.)
84b. Dryophanta palustris. (Mature gall.)
85. Amphibolips inanis.
86. Diastrophus siminis.
87. Diastrophus potentilla.
88. Pachypsylla c.-mamma.
89. Colopha ulmicola.
90. Phylloxera c.-globuli.
91. Pemphigus p.-transversus.

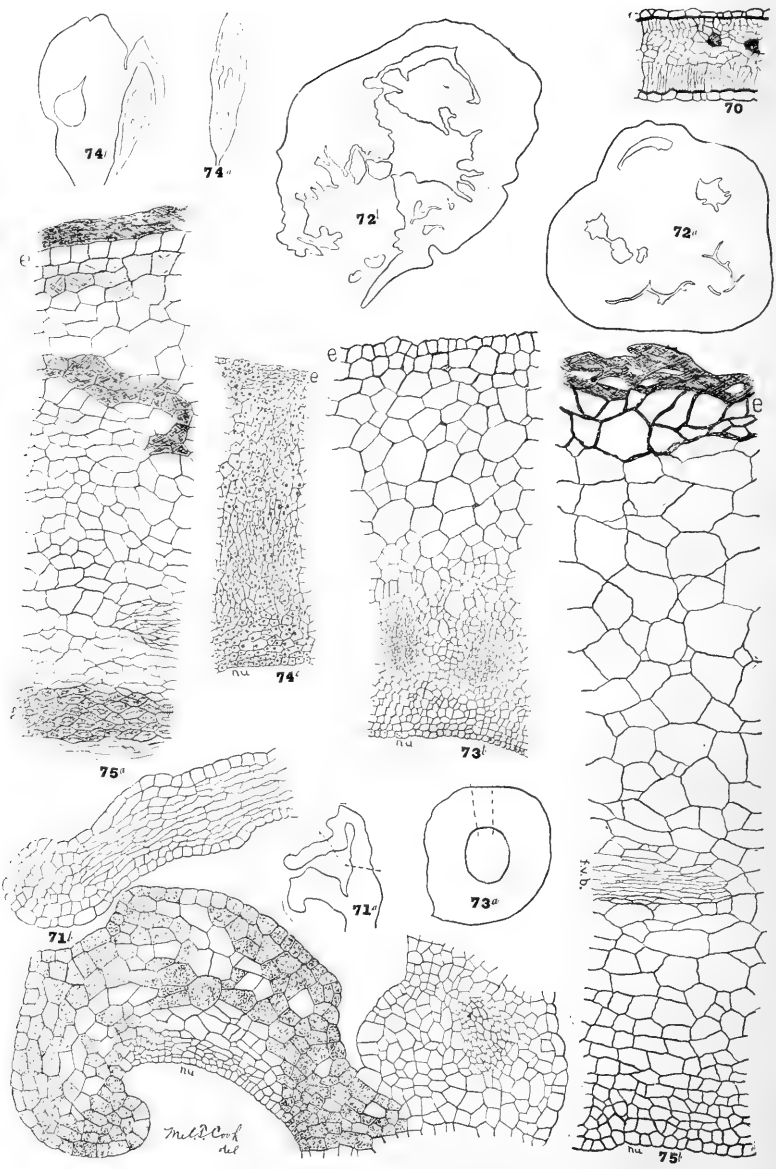
OVIPOSITORS OF

92. Cecidomyia gleditsiae.
93a. Nematus salicis-ovum.
93b. Nematus salicis-ovum.
94. Dryophanta palustris.
95. Amphibolips radicola.
96. Andricus cornigerus.
97. Andricus seminator.
98a. Rhodites radicum.
98b. Rhodites radicum.

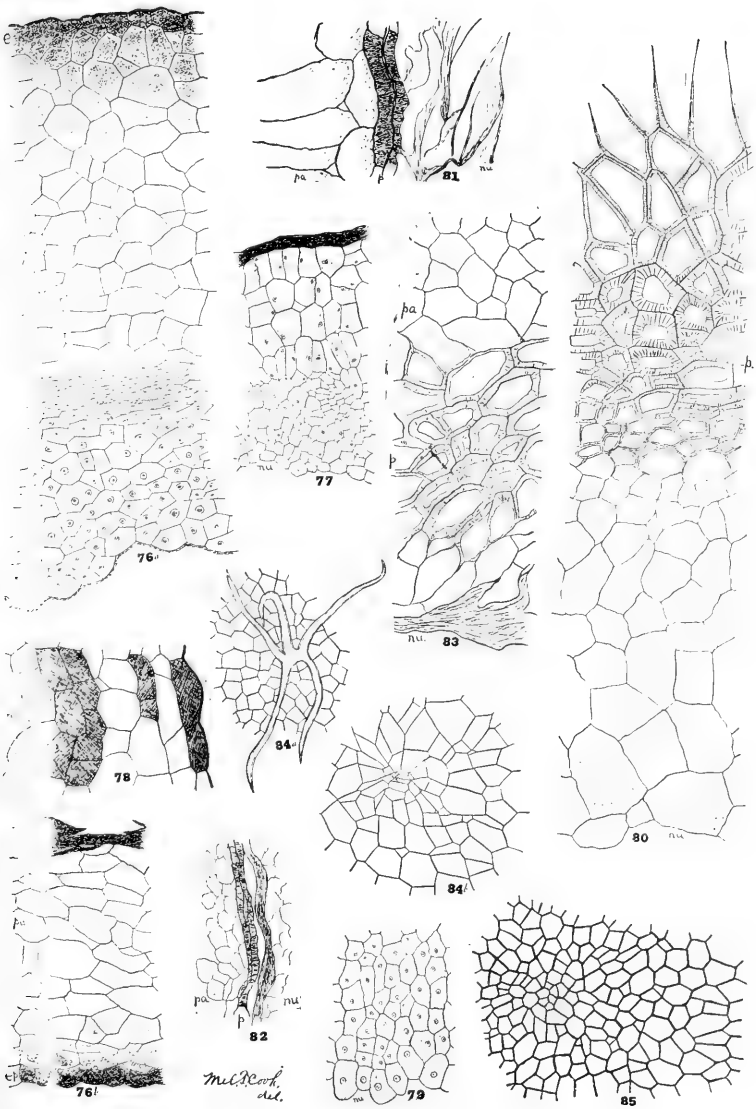
MOUTHPARTS OF

99. Colopha ulmicola.
100a. Pachypsylla c.-mamma, with setae extended.
100b. Pachypsylla c -mamma, with setae retracted.
101. Cecidomyia gleditsiae.
102. Cecidomyia pellex.
103. Andricus petiolicola.
104. Amphibolips inanis.
105. Amphibolips confluentus.
106a. Diastrophus siminis.
106b. Diastrophus siminis.
107. Callirhytis papillatus.
108. Parasite from gall of C. papillatus.
109. Holcaspis globulus.
110. Nematus pomum.
111. Gelechia gallae-solidaginis.

OHIO NATURALIST. *Plate IX.*

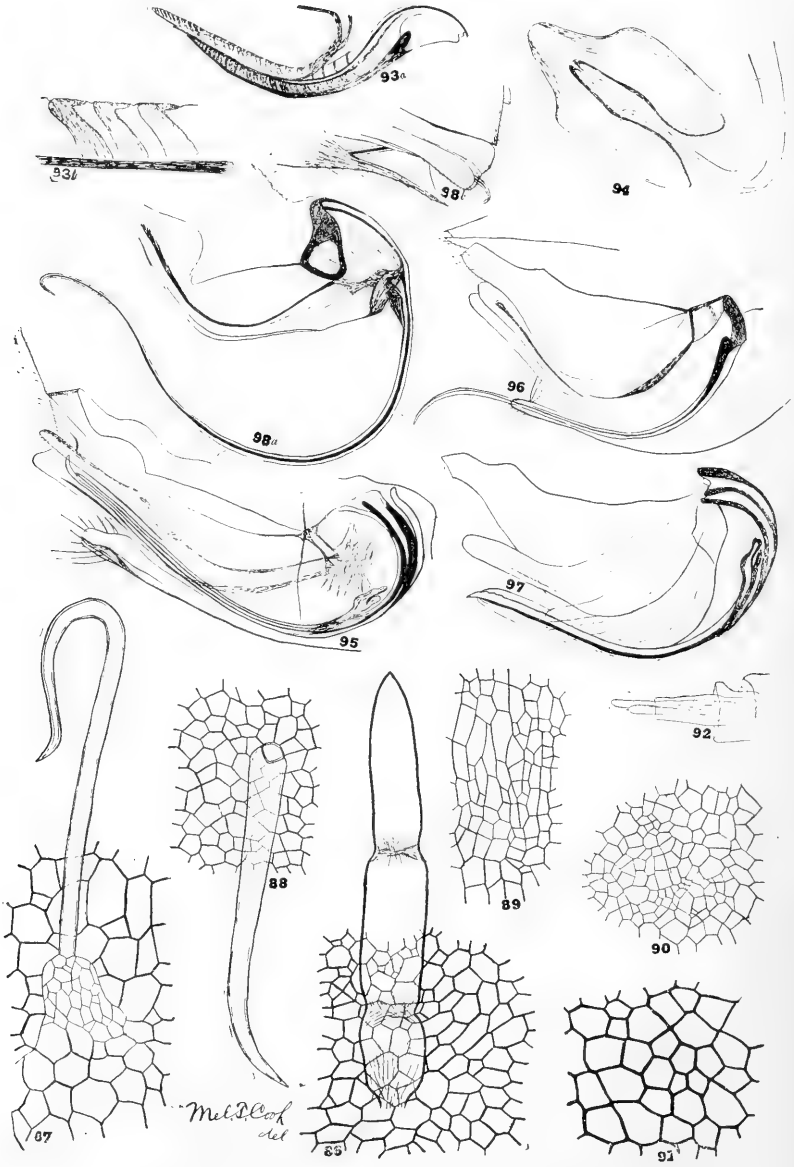


COOK on "Galls and Insects Producing Them."

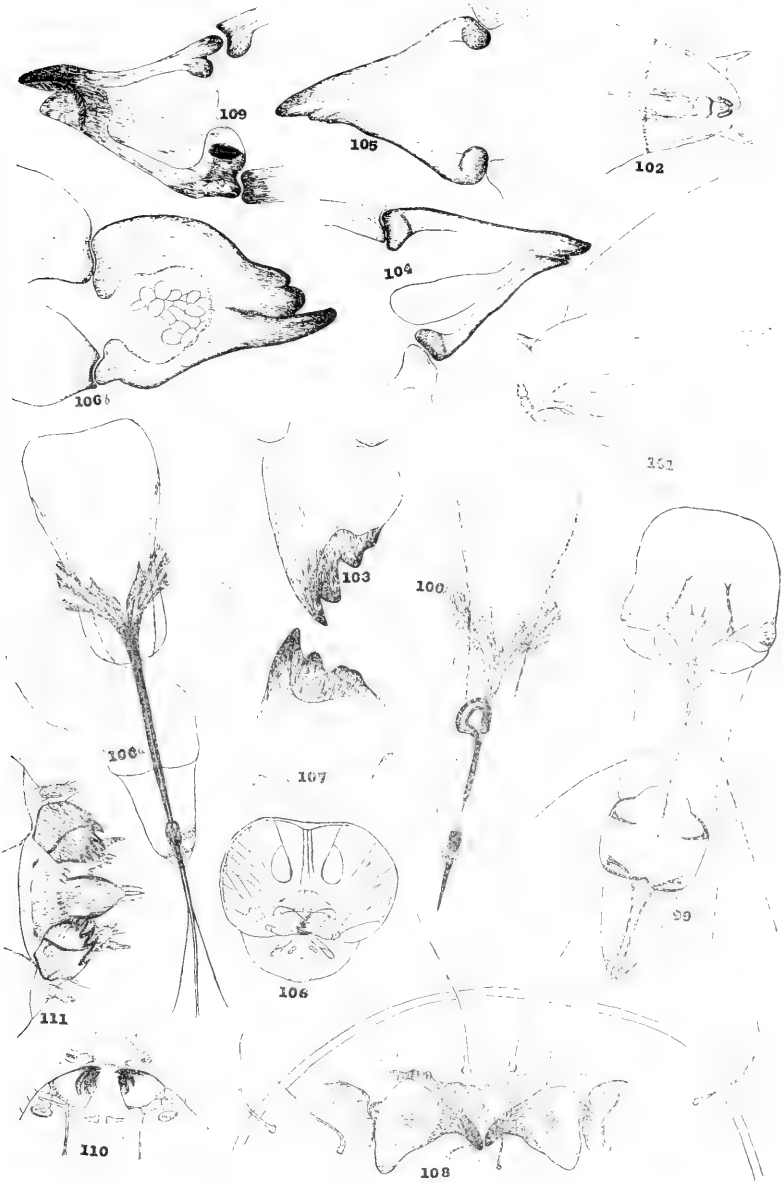


COOK on "Galls and Insects Producing Them."

OHIO NATURALIST. *Plate XI.*



COOK on "Galls and Insects Producing Them."



COOK on "Galls and Insects Producing Them."

APPENDIX I.

GALLS AND INSECTS PRODUCING THEM.

MELVILLE THURSTON COOK.

PART I. MORPHOLOGY OF LEAF GALLS.

1. GALLS OF THE APHIDIDAE.

The gall of Pemphigus vagabundus Walsh (Fig. 112) is evidently formed as a result of the distortion of a large number of bud leaves. My specimens of these galls were mature, so I was unable to follow its development. Small fibro-vascular bundles were numerous and tannin was formed in great abundance. The structure was so modified that the leaf characters were lost; the cells were uniform in character, but were slightly smaller near both the exterior and interior surfaces.

The galls of Pemphigus rhois Fitch (Fig. 113) are large, bladdery and evidently the pocketing of a single leaflet of the host plant, Rhus glabra or R. typhina. My specimens of these galls were fully mature, and I was therefore unable to follow the line of development. The leaf structure was modified into the characteristic Aphididae gall structure. Fibro-vascular bundles were numerous and near the inner surface of the gall. Opposite each bundle was a large cavity filled with some substance which I was unable to determine.

2. GALLS OF CECIDOMYIDAE.

The galls of Cecidomyia pellex O. S. (Figs. 114a, b) are formed by a thickening of the petiole, giving it the appearance of a long fleshy bean pod with a slit along the upper side. This gall shows three well defined zones; an inner nutritive zone of small cells, a parenchyma zone of larger cells and the epidermal zone. The fibro-vascular bundles are numerous and are located between the nutritive and protective zones and arranged around the larval cavity and opening, the largest one just below the larval chamber and corresponding to the mid-rib of the leaflet.

Cecidomyia impatientis O. S. (Fig, 115) is a fleshy gall occurring on the leaves of Impatiens fulva. Some of my specimens had the appearance of deformed flower buds, but upon this point I was unable to decide. This gall showed two well defined zones; a zone of small cells lining the larval chamber and making up about one half the thickness of the gall, and an outer zone of large cells. Small fibro-vascular bundles were formed between the zones.

The galls of Cecidomyia holotricha O. S. on Hicoria ovata (Figs. 116a, b, c) are small and very firm. My specimens were

mature, but the cells lining the larval chamber were well supplied with protoplasm, and numerous short trichomes were developed from the dorsal surface and extended into the chamber. Tannin was very abundant.

The gall of Cecidomyia tubicola O. S. on Hicoria ovata (Figs. 117a, b, c) is very similar to C. holotricha, except that the amount of tannin is not so great. The upper wall of the gall is much thicker than either the side or lower wall. The point of attachment is not so large, but the gall is protected by a growth producing a cup-shaped cavity in which the gall is developed (Fig. 117a). The inner layers of cells are very rich in protoplasm. The cells are elongated in the long axis of the gall and fibro-vascular bundles are more numerous than in C. holotricha, but are very small. The cup-shaped structure (117c) in which the gall is formed is composed of elongated cells. The palisade cells in that part of the leaf opposite the gall are unaffected.

Cecidomyia viticola O. S. (Fig. 118) has the same general character as C, tubicola, but is much longer.

Sciara ocellaris O. S. is one of the simplest of the Cecidomyidae galls. The larva does not penetrate the tissues of the leaf, but confines its attack to the outside, causing an indentation on one surface of the leaf and a corresponding elevation on the opposite surface (Fig. 119a) and also causing a very slight thickening. The structure (Fig, 119c) when compared with that of the normal leaf (Fig. 119b) shows the palisade transformed into ordinary mesophyll and the intercellular spaces entirely obliterated. It therefore corresponds in structure to the simple leaf-curl galls produced by some of the Aphididae (e. g., Schizoneura Americana Riley, Part 1, Fig. 12).

3. GALLS OF THE CYNIPIDAE.

My specimens of Rhodites bicolor Harris (Fig. 120) were well developed when collected. I was therefore unable to determine the early structural characters. The structure in these galls evidently does not show the four well defined zones so characteristic of this family. The inner cells are well supplied with nourishment for the large number of larvae.

The galls of Amphibolips confluentus Harris are very large and have a single larval chamber in the center. The nutritive and protective zones (Fig. 121a) can be distinguished, but are not so well defined as in the closely related species, A, inanis (Part I, Figs. 28a, b). The parenchyma and epidermal zones (Fig, 121b) are well defined and the space in the parenchyma is filled with a cottony-like substance which upon close examination is composed of fibro-vascular bundles (as in A. inanis, Figs. 28a, b, and H. centricola, Figs. 27a, b, c) and of long, unicellular threads (Fig. 121c), as in C. papillatus (Figs. 30a, b, c and 81).

My specimens of Amphibolips illicifoliae Bassett were too far advanced to admit of sectioning, but a careful examination indicated that the zones were well defined and that the space in the parenchyma zone is bridged by means of fibro-vascular bundles as in A. inanis and H. centricola.

The galls of Amphibolips prunus Walsh (Fig. 122) are very firm and all the zones are well defined except the protective zone, which is entirely absent. The parenchyma zone is very thick and probably compensates for the lack of a protective zone. There are very few small fibro-vascular bundles.

Galls of Amphibolips sculpta Bassett (Fig. 123) were more succulent than other specimens which I have examined. My specimens were mature, but the four zones were well defined. The nutritive zone was almost obliterated, due to the age of the gall. The protective zone was thin and the cell walls not very thick. The parenchyma zone was very thick and composed of large, succulent cells and was probably very important in furnishing nutriment to the larva. Near the outer surface were numerous small fibro-vascular bundles. The epidermal zone was very prominent and composed of small cells.

Andricus petiolicola Bassett is one of the firmest of the leaf galls. It is formed either on the petiole or mid-rib and is composed of very small, firm cells (Fig. 124). The four zones are well defined, but the protective zone is very thin and the cell walls but very little thicker than in the neighboring cells. The parenchyma zone is very thick, composed of very small cells with no intercellular spaces, but with many layers of long fibrous cells.

The galls of Acraspis erinacei Walsh (Fig. 125) are very conspicuous. The galls are always developed on the mid-rib of the leaf, but contain no fibro-vascular bundles. The nutritive zone is thick and very rich in protoplasm. The protective zone is also thick and gradually merges into the parenchyma zone, which is also thick. The epidermal zone is very irregular and is covered with numerous unicellular trichomes.

The galls of Biorhiza forticornis Walsh are fig-shaped and the larval chamber instead of being suspended in the center of the gall, as is many others, is placed at the apex (Fig. 126a) and the space between the protective and parenchyma zones, or rather in the parenchyma zone, extends less than half way round the larval chamber. My specimens were mature and I was unable to make a careful study of the nutritive and protective zones. However, the nutritive zone appeared to be relatively thicker, while the protective zone was thin and merged gradually into the parenchyma zone (Fig. 126b). The parenchyma zone was thick and composed of large cells (Fig. 126c). Considerably more of this zone remained attached to the protective zone than is the case with most galls where this separation occurs. The cavity formed

by the separation of the cells in this zone is bridged by numerous unicellular threads as in C. papillatus (Figs. 30a, b, c). In the outer part of the parenchyma zone, but near the cavity, are formed the fibro-vascular bundles. The epidermal zone is well defined and the trichomes on the surface are uni-cellular (Fig. 126c).

4. GALLS OF TENTHREDINIDAE.

The galls of Nematus pomum Walsh were the only leaf galls of this family that I secured and they were mature. There was no indication of a zonal structure, but the cells were very uniform in size and structure throughout the entire gall (Fig. 127). Many of the cells contained tannin and intercellular spaces were large and evenly distributed.

PART II. LATERAL BUD GALLS.

Mature specimens of Holcaspis globulus Fitch show the four well defined zones (Fig. 128). The inner nutritive zone is thick, composed of small cells and well supplied with nutriment for the larva. The protective zone is thin and composed of very small cells with thin walls. It gradually merges into the nutritive zone on the one side and the parenchyma zone on the other side. The parenchyma zone is very thick, the cell walls medium in size and the fibro-vascular bundles small and numerous. Further observations upon this gall emphasize the statement previously made that it is the enlargement of an incipient stem.

Further observations upon the gall of Andricus seminator Harris confirm the statement previously made that it is a compound gall produced by the insect depositing an egg in each element of the bud.

PART III. STEM GALLS.

The gall of Diastrophus nebulosus O. S. (Fig. 129a, b) is a very large swelling on the canes of Rubus villosus and is about two or three inches in length. It contains a large number of larval chambers each containing a single larva (Fig. 129a). The four zones are especially well defined. The nutritive and protective zones are composed of a few layers of cells while the parenchyma zone is very thick, composed of smaller cells and more dense than the corresponding zone in most galls of this family.

Andricus cornigerus O. S. (Fig. 130) produces one of the hardest of the stem galls. My specimens of this were gathered in the winter and were fully mature. The horn-like protuberance is a closed tube extending to near the center of the gall. This tube is composed of sclerenchyma tissue and evidently corresponds to the protective zone. Near the base of the tube is a thin partition forming the larval chamber. When mature the

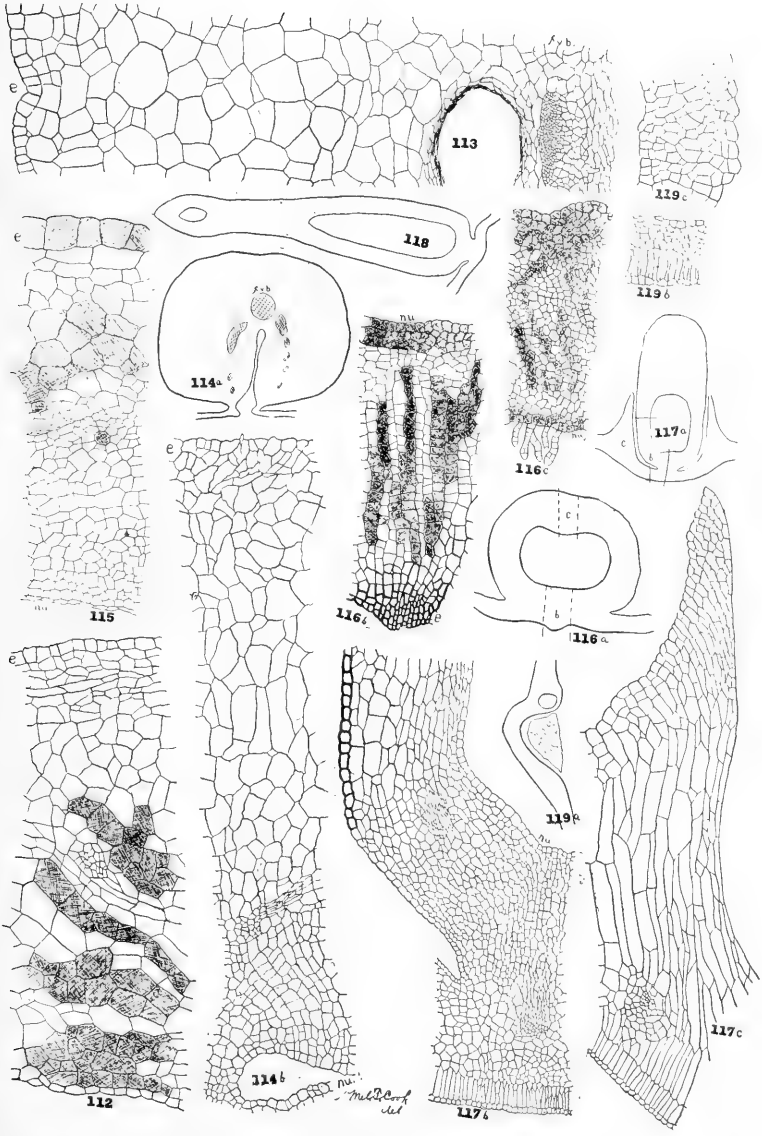
insect destroys this partition, travels to the end of the tube which projects beyond the body of the gall, and there makes an opening through either the end or the side of the tube and thus makes its escape. Examination of young specimens would probably show the four zones as well defined as in Diastrophus nebulosus.

Part IV. Development of Galls.

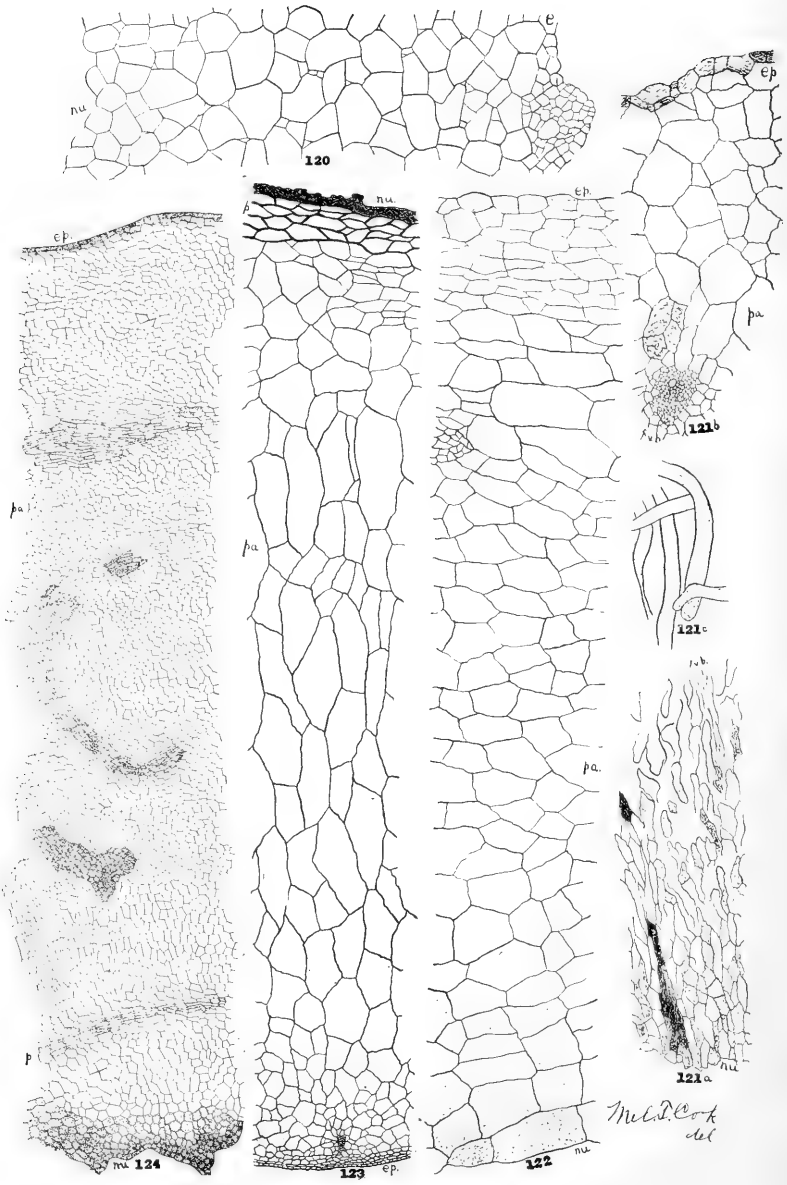
Examination of very young specimens of Andricus seminator Harris shows three well defined zones (Figs. 131a, b), the protective zone being undeveloped. The fibro-vascular bundles were very numerous and distributed just beneath the epidermal zone. I have examined a large number of these galls of various ages and have been unable to find any trace of a protective zone. Tannin develops in the outer cells very early and probably helps to form a protection for the larva.

PLATES XIII–XV.

112. Section of gall of Pemphigus vagabundus.
113. Section of gall of Pemphigus rhois.
114a. Diagram of gall of Cecidomyia pellex.
114b. Section of gall of Cecidomyia pellex.
115. Section of gall of Cecidomyia impatientis.
116a. Diagram of the gall of Cecidomyia holotricha.
116b. Section of the gall of Cecidomyia holotricha.
116c. Section of the gall of Cecidomyia holotricha.
117a. Diagram of the gall of Cecidomyia tubicola.
117b. Section of the gall of Cecidomyia tubicola.
117c. Section of the gall of Cecidomyia tubicola.
118. Diagram of the gall of Cecidomyia viticola.
119a. Diagram of the gall of Sciara ocellaris.
119b. Section of normal leaf of Maple.
119c. Section of gall of Sciara ocellaris.
120. Section of gall of Rhodites bicolor.
121a. Section of gall of Amphibolips confluentus. (Epidermal and parenchyma zones.)
121b. Section of the gall of Amphibolips confluentus. Nutritive and protective zones.)
121c. Section of gall of Amphibolips confluentus. (Elongated cells in the cavity of the parenchyma zone.)
122. Section of gall of Amphibolips prunus.
123. Section of gall of Amphibolips sculpta.
124. Section of gall of Andricus petiolicola.
125. Section of gall of Acraspis erinacei.
126a. Diagram of gall of Biorhiza forticornis.
126b. Section of gall of Biorhiza forticornis. (Nutritive and protective zones.)
126c. Section of the gall of Biorhiza forticornis. (Section of protective and epidermal zones.)
127. Section of the gall of Nematus pomum.
128. Section of the gall of Holcaspis globulus.
129a. Diagram of gall of Diastrophus nebulosus.
129b. Section of gall of Diastrophus nebulosus
130. Diagram of gall of Andricus cornigerus
131a. Diagram of cross section of gall of Andricus seminator.
131b. Section of young gall of Andricus seminator.



Cook on "Galls and Insects Producing Them."



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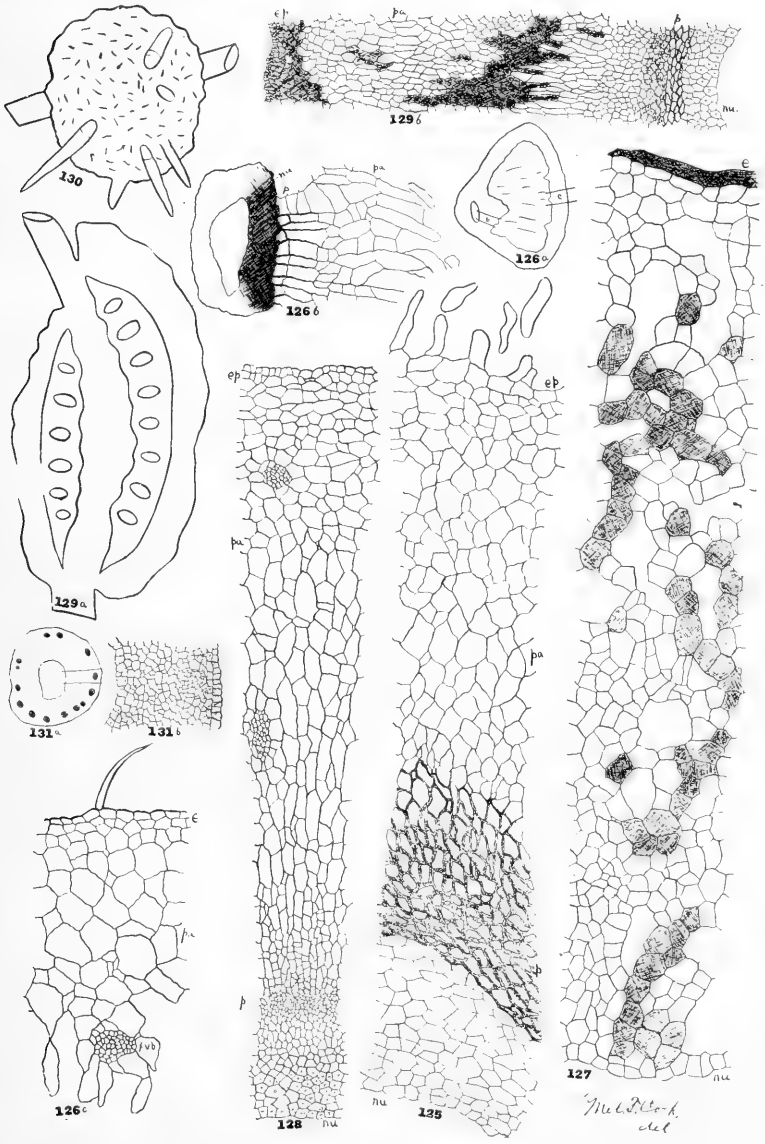

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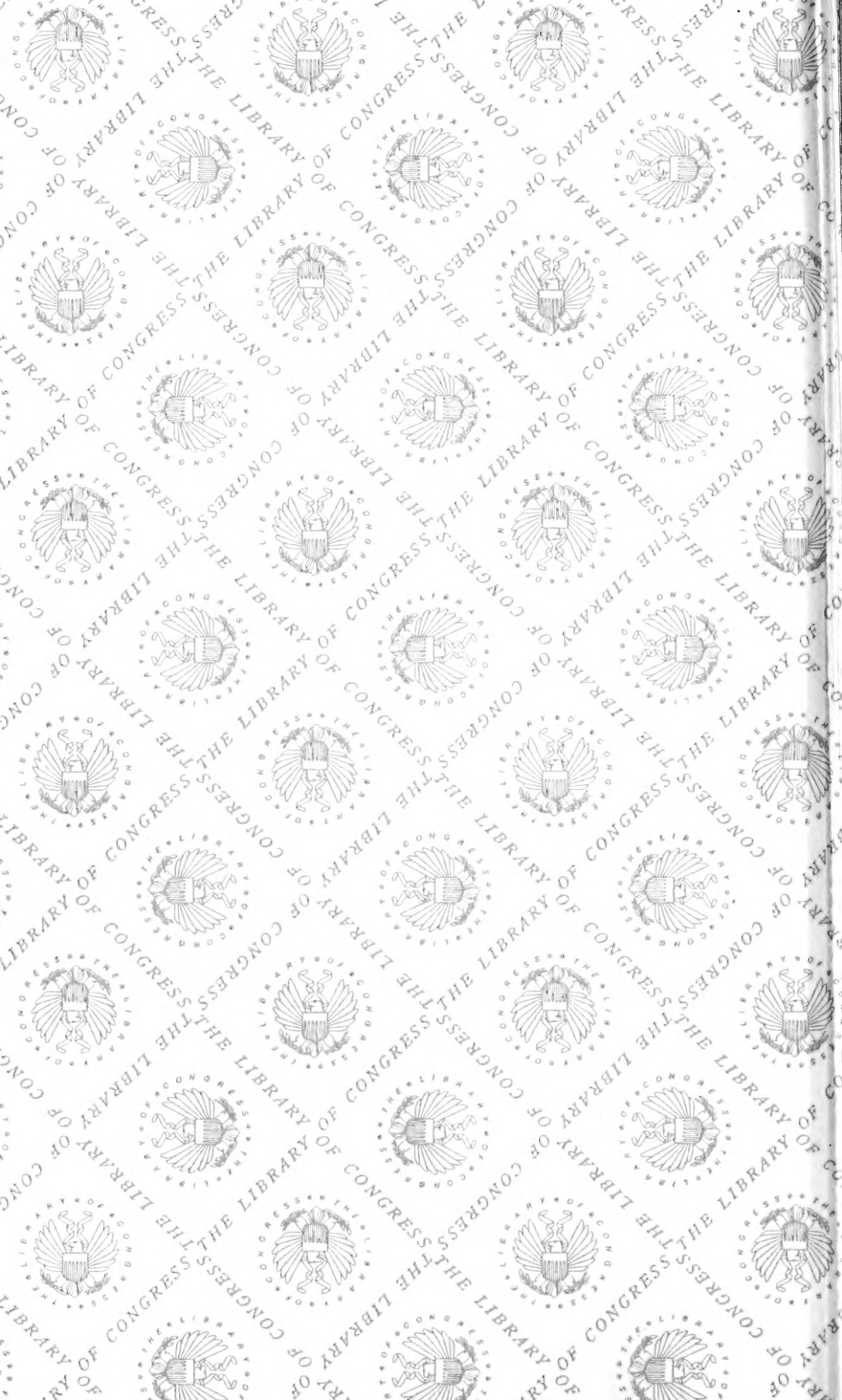
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