

THE DEVELOPMENT OF INSECT GALLS AS ILLUSTRATED BY THE GENUS AMPHIBOLIPS.

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The study of the development of insect galls involves more complicating factors than most problems of evolution, since the host plant is forced to give both nourishment and protection to its enemy. The result of this enforced action is the formation of a structure which is normal for the parasite and pathological for the host. The histology of these gall structures presents some very interesting questions involving the point of stimulation, the character of the stimulation and the evolutionary lines along which the various species of galls have developed. For some time we have recognized that the point of stimulation is in the meristomatic tissues, and that in most cases the stimulation is not due to a glandular secretion from the parent insect.¹ However, there appears to be abundant evidence that in most cases the stimulation comes from the larva, but whether mechanical or chemical, or both, or the former in some species and the latter in others, is a practically untouched problem.

In 1902 the writer² advanced the opinion that "the morphological character of the gall depends upon the genus of the insect producing it, rather than upon the plant upon 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 difference." Further studies along this line have convinced the writer of the correctness of this view, and have also led to efforts to work out a system of classification based on the histological character of the galls which would be correlated with the classification of the insects. However, the completion of such a series of studies is largely dependent upon a more satisfactory knowledge of the taxonomic relations.

While it is true that the histological characters of the galls depend upon the insects rather than upon the host plants, it is also true that we find certain characters common to all groups. The first step in the forma-

¹ Adler & Straton. Oak Galls and Gall Flies. 1894.

² Galls and Insects Producing Them. Ohio Naturalist, II:7, p. 270. 1907.

tion of a gall is (1) the excitation of growth and cell division, (2) the failure of the cells of the affected part to differentiate into the characteristic tissues of that part, and (3) the differentiation into characteristic tissues of the gall. We also recognize certain similar lines of development in what we now consider well-defined genera. The explanation of the similarities and differences in these lines of development will depend largely upon future work in both taxonomy and histology.

It is the purpose of this paper to call attention to certain points above referred to in connection with the genus *Amphibolips*. The taxonomy of the insects of this genera have been very thoroughly studied and carefully described and arranged by Mr. Wm. Bentenmuller.³ The writer has also studied the histology of several of the galls.

The genus *Amphibolips* belongs to the family Cynipidæ, is quite distinct, and stands high in the line of development. As previously stated, the galls originate as a result of stimulation of meristomatic tissue, resulting in growth and cell division. This is followed by a differentiation of this mass of cells into the tissues characteristic of the galls. In the cynipidous galls we have the four distinct tissue zones which have been referred to by many writers, viz: (1) the epidermal zone, or outside layer of cells, (2) the parenchyma zone, which may be quite thick, either dense or loose, and in which may be found fibrous tissue radiating from the center of the gall, (3) the protective zone, composed of sclerenchyma tissue and varying in thickness in different species of galls, (4) the nutritive zone of parenchyma cells, rich in protoplasm and immediately surrounding the larval chamber. The galls belonging to this genus have the four well-defined zones, but with variation in the parenchyma and protective zones by which they may be subdivided into the following groups:

GROUP A.

Amphibolips confluens, Harris.

" *caroliniensis*, Bassett.

" *longicornis*, "

" *acuminata*, Ashmead.

³ The Species of *Amphibolips* and their Galls. Bulletin of the American Museum of Natural History, Vol. XXVI, Art. VI, pp. 47-66. 1909.

GROUP B.

- Amphibolips inanis*, O. S.
 " *ilicifoliae*, Bassett.
 " *Cocclebs*, O. S.
 " *citriformis*, Ashmead.
 " *melanocera*, "
 " *cinerea*, "
 " *cooki*, Gillette.
 " *tinctoria*, Ashmead.

GROUP C.

Division a.

- Amphibolips spinosa*, Ashmead.
 " *globulus*, Beutenmüller.

Division b.

- Amphibolips nubilipennis*, Harris.
 " *racemaria*, Ashmead.

Division c.

- Amphibolips prunus*, Walsh.
 " *guineci*, Bassett.
 " *fuliginosa*, Ashmead.
 " *palmeri*, Bassett.
 " *trizonata*, Ashmead.

The writer has previously made studies of the histology of *A. conflucus*, *A. inanis*, *A. ilicifoliae*, *A. nubilipennis*, and *A. prunus*. Taking *A. conflucus* as a type of the group A, we find the parenchyma zone very thick and composed of cells which when mature have the character of a mass of colored cotton, and among which may be found fibro-vascular bundles. The parenchyma cells, when examined under the microscope, are found to be unicellular, long and threadlike. The protective zone is comparatively thin. The nutritive zone is prominent only in the young galls. The writer has not had an opportunity to examine the other three species of this group, but from the taxonomic discussion, they appear to coincide very closely with *A. conflucus*.

In group B the writer has studied *A. inanis*, *A. ilicifoliae* and *A. cocclebs*, which, judging from Beutenmüller's description, are quite typical of the group. In these galls the parenchyma zone is characterized by large intercellular spaces. A part of the parenchyma cells remain attached to

the epidermal zone, another part to the protective zone and some to the well-defined fibro-vascular bundles which radiate from the central body to the outer part of the gall. These fibro-vascular bundles are in general much better developed than in the galls of group A. The protective zone is subject to considerable variation in the different species; it is quite prominent in *A. inanis* and practically absent in *A. coclebs*. The nutritive zone, as in the first group, is prominent only when the gall is young.

In group C the writer has studied *A. nubilipennis* and *A. prunus*. This group may be readily divided into three sub-groups as indicated above. The species of sub-group (a) because of the inner radiating and spongy substance, appear to be intermediate between group B and the other species of group C. The species of sub-group (b) are more succulent than the species of sub-group (c).

My studies of *A. nubilipennis* demonstrate a thick parenchyma zone of large succulent cells and very small fibro-vascular bundles which were most numerous near the surface of the gall. The protective zone consisted of a few layers of thin-walled cells. The nutritive zone was prominent in the young galls and persisted quite late.

My studies of *A. prunus* demonstrated a very thick parenchyma zone, much firmer and drier than in *A. nubilipennis*, and in which were very few small, fibro-vascular bundles. The protective zone was entirely absent. The nutritive zone well developed in the young galls.

In general it will be noted that in this genus we have (1) the galls originating and developing in the normal manner which results in the formation of the four zones; (2) the variation in the parenchyma and protective zones, which enables the above division and sub-divisions; (3) that group A may be considered the most highly developed and sub-group c of group C the lowest. The significance of this line of development cannot be determined until we know more about other genera of gall-makers and their galls. However, a study of the known geographical distribution of the species of this genus is interesting in connection with this study. In group A, *Amphibolips confluens* is very widely distributed over Canada, the Eastern States south to Georgia, and west to Colorado, while the other three species have much more limited ranges, two and possibly all three within the range of the first. In group B we find that *A. inanis* ranges from Canada and the Eastern States west to Iowa and south to North Carolina; *A. cooki* has almost the same range; *A. ilicifoliae*, A.

coelebs and *A. tinctoria* are included within the above range; and *A. citriformis*, *A. melanocera* and *A. cinerea* are reported from Florida. In group C, we find *A. nubilipennis* very widely distributed from New York west to Illinois and south to Pennsylvania, *A. prunus* from New England west to Colorado and south to Georgia; *A. spinosa*, *A. racemaria* in Florida, *A. fuliginosa* in Florida and Georgia, *A. globulus* in New Jersey, *A. gainesi* in Texas, *A. palmeri* in Mexico, and *A. triazonata* in Arizona.

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