

**Article VII.—PHYLOGENY OF CYNIPID GENERA AND  
BIOLOGICAL CHARACTERISTICS<sup>1</sup>**

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PLATE XXXII

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INTRODUCTION

Up to the present time the relationships of the genera or even species of the Cynipidæ (Hymenoptera) have been poorly understood. Species have been catalogued without much attempt to discover an arrangement which would indicate evolution, and the genera have been in large part unnatural groups containing large numbers of unassorted, diverse organisms. Moreover, few suggestions have hitherto been made as to the origins of the peculiar biologic phenomena so character-

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istic of the more specialized gall-wasps. Information as to the evolution of some of these phenomena is highly desirable and nothing of the biological characters of such specialized creatures can be adequately learned except as it is studied in connection with the morphological characters, careful taxonomic work, and observations of the living insects.

The data here assembled is the result of a study of the Cynipidæ of the world, actual specimens of almost ninety per cent of which have been examined. Much information has been gained by a study of living material. The conclusions reached, as yet only incompletely applied to the genera of the family, will serve as the basis for a thorough revision of the classification of the Cynipidæ which I hope to be able to publish soon.

I am under great obligation to the same friends who have aided my other studies of the gall-wasps: Dr. Wm. M. Wheeler, Prof. C. T. Brues, and Prof. Irving W. Bailey of the Bussey Institution of Harvard University; Nathan Banks of the Museum of Comparative Zoology; Charles W. Johnson of the Boston Society of Natural History; and Dr. Frank E. Lutz of The American Museum of Natural History.

#### DATA CONCERNING EVOLUTION

##### RADIAL CELL

(Table I)

The wing venation of the Cynipidæ is remarkably uniform throughout the whole range of species. Only the genus *Eschatocerus*, with one known species, shows any considerable modification from the type; in that species the first and second cubital cells are closed by the extreme reduction of the second abscissa of the radius and of the second cross-vein. The related Figitidæ show a wide range of variation from the complete cynipoid venation to a condition almost as specialized as that found in those Chalcididæ which have retained only a single vein. In the Cynipidæ the modifications are very slight, and these, e. g., the presence or absence of the areolet, the extent of the cubital vein in particular, the extent and continuity of other veins, and the angles of the veins, are characters mainly of specific or even individual worth, sometimes differing on the two sides of the same specimen.

Nevertheless, it is possible to perceive two lines of modification of the venation which seem to indicate something of group relationships: (1) the radial cell, varying from a completely closed to a wide open condition, and (2) the first abscissa of the radius, varying from an arcuate to an angulate condition.

It may be considered that the open radial cell is more highly specialized than the closed cell, for the process of opening in this instance involves the disappearance of the marginal vein and later of the extremities of the subcostal and radial veins. It would be surprising to find that species with the open radial cell had developed the veins necessary to close the cell and thus originated the closed-cell forms. Evidence of evolution based on a consideration of this point alone would be meager enough, but if it parallels the data of other sorts it will lend that much more weight to the final conclusions, and at a couple of points it will bridge gaps in the history.

From the table it will be seen that the character of the radial cell is of generic importance. Although it is true that *Aulacidea* is separated from *Aylax* primarily upon this character and that this is the best reason for considering *Aulacidea* a distinct group from and more primitive than *Aylax*, nevertheless, in many other instances where the genera are founded upon other morphological characters, it will be seen that the condition of the radial cell is as good a generic character. Thus, for instance, *Disholcaspis* is a genus founded on peculiarities of thoracic sculpture, the size and shape of the second abdominal plate, and the shape and proportions of parts of the head, among other very definite characteristics. The occurrence of the open radial cell in all the known species of that genus suggests that the genus as a unit is descended, rather indirectly, from a group with the closed cell. On the other hand, in *Rhodites*, a genus maintained likewise on abundant, definite morphological and biological characters, although thirty of the species have the cell entirely closed, six species have the cell more or less open. It seems probable that in this instance the group has originated directly from a closed-cell genus, and that comparatively recent evolution within *Rhodites* itself has given rise to the few species which possess the open cell.

The order in the accompanying table is that of the apparent order of evolution, as indicated by this sort of evidence only. Again, I acknowledge the meager value of these considerations, except they be judged in connection with the other sorts of data present in this paper.

TABLE I. RADIAL CELL

Genus	No. of Species	Nature of Radial Cell
<i>Ceroptris</i>	±16	Entirely closed
<i>Synergus</i>	±60	" "
<i>Periclistus</i>	±10	" "
<i>Aulacidea</i>	22	" "
<i>Phanacis</i>	2	" "
<i>Timaspis</i>	7	Closed in 1 sp. Partly closed in 1 sp. Entirely open in 5 sp.
<i>Diastrophus</i>	14	Closed in 1 sp. Open in 13 sp.
<i>Rhodites</i>	36	Closed in 30 sp. Open in 6 sp.
<i>Aylax</i>	26	Entirely open.
<i>Neuroterus</i>	54	±closed in 6 sp. Open in 48 sp.
<i>Cynips</i> (in European sense)		Entirely open.
<i>Disholcaspis</i>	27	" "
<i>Amphibolips</i>	25	" "
All other Cynipini		Open, usually entirely open.

## RADIAL VEIN

## Plate XXXII

The first abscissa of the radial vein of the wings of the Cynipidæ varies from an arcuate to a sharply angulate condition, some species showing a pronounced, vein-like projection into the radial cell at the apex of the angle made by the vein. Every degree of gradation between the extreme forms may be found. Indeed, so remarkably complete is the list of transitional forms that it was this exhibition which first drew my attention to the existence of evidence of the course of evolution in the group, and I have failed to find any other one line of data which offers as complete a story as that presented by these gradations in vein form. A sufficient display of this variation is shown in the wings of the forty-five species which I figure to remove any necessity for an account of the details of conditions in particular species.

It is to be remarked that no great variation in the vein is to be found among the species of a single genus, i. e., the form of the vein is a generic character, indicating the same lines of generic limits which were drawn originally after considerations of very diverse morphological characters. In the Figitidæ, in *Aulacidea*, *Aylax*, *Neuroterus*, *Disholcaspis*, *Cynips* (of European authors), and in *Amphibolips* every species which I have seen agrees in details of venation with a pattern typical for its genus.

But in *Diastrophus* and *Rhodites* we find both an arcuate and an angulate condition occurring in the same genus, though the differences between two species at the extremes of variation within the genus are not to be compared with the extreme differences which occur between the genera. Apparently the form of the first abscissa of the radius gives evidence not only of group descent but also of the evolution of the species within a genus. Such a complete set of data, interpreted in the light of other evidence, should prove of great value for discovering an arrangement of the species of the family which will indicate the natural order of relationships.

The problem with which we are now confronted is to discover where in the series was the starting point, the primitive condition—of deciding in which direction development has proceeded. If, in trying to solve this question, we seek evidence in the related families of Hymenoptera, we find that apparently very little help is to be obtained there. In the Figitidæ, which are mainly parasitic species, every species of the hundreds I have examined shows an arcuate vein, which is one of the extremes to be found in the Cynipidæ. Shall we assume that the gall-wasps have originated from the more primitive figitids or that the figitids have originated from the most highly specialized of the cynipids? I think that the story might be read with equal justice in either direction if the whole of our information came from the wing-venation. In the arcuate vein we might picture the remnants of two veins of an ancestral, a more primitive, a more abundant vein condition, the two veins still evident and not entirely fused in those species showing an angulate vein. On the contrary, it is reasonable to believe that the angulate vein is the more developed condition: if this is truly the radial vein, it is a longitudinal vein and the projection at the apex of the angle is a cross-vein even though it extends lengthwise of the wing. The addition of such cross-veins to a primitive venation is not an unknown thing, though we have not realized that such additions occur very often among the Hymenoptera. Moreover, we have no great warrant in believing that this projection on the radial vein is really a vein; it is not to be distinguished from chitinizations which occur in the wings of many other Hymenoptera, and I cannot see good reasons for believing that the projection in this case is to be considered a vein rather than some other sort of formation.

It is to be expected that, where such limited considerations are drawn upon, the interpretations may be made in diametrically opposite fashions and we need not be impressed with either set of interpretations

until one of them is supported by other sorts of evidence. The important fact is that the vein considered does clearly show a path which was taken in the evolution of the insects. That the path itself does not indicate in which direction the journey was made is no reason for ignoring the existence of the path. Other signs beside the road will supply proof enough of the direction of the movement along that road.

To anticipate the conclusions which will be drawn later, it may be said that all other considerations, without an exception, point to those insects which have the arcuate vein as being most primitive; those having the angulate vein are by all means the most specialized of the gall-wasps; and an arrangement of the groups of intermediate grades of specialization strictly parallels an arrangement of those groups on the basis of venation only. Such strict parallelism of the indications of evolution of the groups demands parallel interpretations of the direction in which the evolution has progressed. It seems that we must believe that the angulate first abscissa of the radial vein in the wings of the cynipoids has developed by gradual transitions from an arcuate vein.

#### SECOND ABDOMINAL SEGMENT

An enlarged abdominal plate may be the result of the fusion of two or more plates or the actual increase in size of that plate in the course of evolution. The primitive condition, somewhere in the more or less remote ancestry of any group of insects, showed the segments more or less equal in development, and any condition which shows a single segment especially developed is undoubtedly the result of later evolution. Whether the degeneration of a segment that has become thus specialized ever occurs is a question to be debated for each group studied.

The dorsal plate of the second segment of the abdomen of Cynipidæ is always more developed than any of the other dorsal plates and in many instances the plate has become so enlarged as to cover almost the entire abdomen. That this enlargement in the true gall-wasps is not the result of fusion is evidenced by the continued existence of the other plates underneath the enlarged plate. A study of the character of the segment among all of the gall-wasps shows it to have, very apparently, generic significance, and this has been recognized in the foundation of many of the genera. In the *Andricus-Cynips* group of wasps the stricter use of this character will help solve the true relationships.

A study of the figures on Plate XXXII will illustrate the following. In the cynipoid genus *Ibalia* the second dorsal plate does not show any special modification, the segmentation appearing of a more primitive

sort except for the great development of the sixth segment, a line of evolution not pursued elsewhere among the Cynipoidea. The genus *Aulacidea* has the second segment less developed than in any of the other genera, a fossil species showing the plate still smaller. *Timaspis* and *Aylax* show conditions intermediate to *Diastrophus*, where the segment covers about one-half of the abdomen. In *Rhodites* the segment is larger than anywhere outside the group of the oak gall-wasps, and in this genus the peculiar production of the hypopygium also indicates an advanced degree of evolution. Of the oak gall-wasps, *Neuroterus* shows the most primitive second segment. In some of the species called "Andricus" the specialization reaches its extreme.

These and other instances are of a sort which invites interpreting the less developed segment as the most primitive. And such an interpretation agrees with the information concerning evolution furnished by other lines of evidence. But, in *Amphibolips*, *Disholcaspis*, and possibly some other groups which are clearly highly specialized in many respects, it is surprising to find the segment not as greatly developed as among some less highly specialized oak gall-wasps. It is possible that a degeneration of the plate has occurred in these instances, but it is also likely that there were several lines of evolution among the oak gall-wasps, along one of which the second segment did not develop as far as along another, even though other characteristics evolved farther in the first instance.

#### HOST PLANTS OF THE CYNIPIDÆ (Table II)

About 86 per cent of the known species of gall-wasps produce galls on species of *Quercus* and are confined strictly to that single genus of plants. Another 7 per cent are confined to species of the genus *Rosa*. The remaining 7 per cent are found on plants of thirty-five different genera, ranging all the way from the monocotyledons to the highest composites. That is, the hosts of a very small percentage of the species are distributed very widely throughout the flowering plants, while 93 per cent are restricted to plants of only two genera.

It is hard to understand how this extreme specialization has come about. That the oak has advantages as a shelter for an insect is readily seen, but it belongs to a comparatively small family of plants, the genus has only a limited distribution over the world today, and, whatever the qualifications of the oaks, it is not apparent why other plants should be so completely abandoned. That these other plants are capable enough

of producing galls is evident, for other gall insects of other families produce galls upon them in abundance. But, though we cannot understand the reasons for such a condition, the fact remains that there is this great specialization in the choice of host.

It need hardly be argued that this specialization has very likely been the more recent development in the evolution of the Cynipidæ. It is not unreasonable to believe that the primitive gall-wasps inhabited a wide range of plants and that these polyphagous forms have become relatively few as the numbers of the more specialized species increased. That the small percentage of the insects which are polyphagous today, which still possess the more primitive habit, are to be considered actual remnants of the ancient forms, can be readily shown.

In the accompanying table, which shows the number of species of Cynipidæ known to occur on each of the genera of host plants, the insects are listed by tribes. These tribes are well-defined groups, characterized primarily by distinct morphological structures, especially of wing-venation and of the abdomen, and the close relationship of the species included in each of the tribes is as certain as may be desired. Now, it is conspicuous that specialization in the choice of hosts is restricted to the species of particular tribes, and that practically every species in those tribes has adopted the special host. All but one of the species of the Cynipini are found regularly on oaks and all of the species of Rhoditini are found as regularly on roses, though rarely one or two of the species of each group will produce galls on a second plant as well as upon their own hosts. Finally, it is to be seen that all of the species which inhabit the plants of the many genera belong to the one tribe Aulacini. It is evident that the specialized host was not adopted by species of the Cynipidæ severally and at different times, but at two distinct periods, by two groups of forms, at a time about coincident with the differentiation of the tribes which those two groups now constitute. And it is as clear that the Aulacini comprise forms most like the primitive polyphagous species from which the Cynipini and Rhoditini have arisen at different times.

In confirmation of this, it is significant to find that not only are the Aulacini, as a group, polyphagous but that several of the species of the group are, individually, polyphagous. These are the only species of all the gall-wasps which are known to be regularly found on plants of different genera, though most of the cynipids will produce galls on several species of plants of the same genus. *Aylax pisum* lives in galls on *Lygodesmia* and on *Stephanotis*; *Aulacidea tumida* is found on *Solidago*,

*Sonchus*, and *Lactuca*; while *Aylax hieracii* is found not only on species of *Hieracium*, *Linaria*, and *Cytisus*, but also possibly in the galls on *Triticum*.

Within the Aulacini of today, however, some degree of specialization may be noted. Over a third of all the species of the tribe are confined to plants of the rosaceous genera *Potentilla*, *Fragaria*, and *Rubus*; thirteen of these species, i. e., all but four of those found on those plants, belong to the very distinct genus *Diastrophus*, and this comprises the whole of the genus as far as known. Here again is specialization developed as the group has become morphologically distinct, but in this case the choice of hosts has not reached the extreme of specialization, nor has the morphological differentiation become more than generic from the parent forms of Aulacini.

The only other apparent case of specialized hosts in the Aulacini is in the choice of many genera of the Compositæ; but there is little significance in this fact, for the Compositæ are so predominant among plants today, both in number of species and of individuals, especially among woody-stemmed plants which offer winter shelter to insects, that a due representation of the genera of this family would always have a dominance of numbers. Moreover, there is no restriction of any one or two of the genera of the Compositæ to any single genus of the Aulacini except in instances where the number of species concerned is too small to warrant conclusions.

This immediate data, considered independently, would indicate that the following arrangement shows the order of origin of the cynipid genera:

PRIMITIVE	INCIPIENTLY SPECIALIZED	HIGHLY SPECIALIZED
Aulacini (excluding <i>Diastrophus</i> )	<i>Diastrophus</i>	Rhoditini Cynipini

TABLE II. HOSTS OF THE CYNIPIDÆ

Cynipid	Host Plant	Known No. of Species of Cynipidæ Of the World	American
Eschatocerini	Leguminosæ		
	<i>Acacia</i>	1	1
Pediaspidini	Aceraceæ		
	<i>Acer</i>	1	
Aulacini	Gramineæ		
	<i>Triticum</i>	1	
	Liliaceæ		
	<i>Smilax</i>	1	
	Papaveraceæ		
	<i>Papaver</i>	3	
	Rosaceæ		
	<i>Fragaria</i>		1
	<i>Potentilla</i>	7	8 (or 4?)
	<i>Rubus</i>	9	6
	Leguminosæ		
	<i>Cytisus</i>	1	
	Asclepiadaceæ		
	<i>Stephanotis</i>	1	
	Labiatæ		
	<i>Nepeta</i>	3	1
	<i>Phlomis</i>	1	
	<i>Salvia</i>	1	
	Serophulariaceæ		
	<i>Linaria</i>	1	
	Valerianaceæ		
	<i>Valerianella</i>	1	
	Compositæ		
	<i>Solidago</i>	1 (?)	1 (?)
	<i>Bigelowia</i>		1
	<i>Silphium</i>	4	4
	<i>Ambrosia</i>	1	1
	<i>Serratula</i>	1	
	<i>Centaurea</i>	6	
	<i>Hypochaeris</i>	2	
	<i>Urospermum</i>	1	
	<i>Picris</i>	1	
	<i>Tragopogon</i>	2	
	<i>Scorzonera</i>	1	
	<i>Taraxacum</i>	1	1
	<i>Sonchus</i>	2	1
	<i>Lactuca</i>	5	3
	<i>Lygodesmia</i>	1	1
	<i>Crepis</i>	1	
	<i>Prenanthes</i>	1	1

TABLE II. (continued)

Cynipid	Host Plant	Known No. of Species of Cynipidæ Of the World	American
	<i>Hieracium</i>	1	
Rhoditini	<i>Rosaceæ</i>		
	<i>Rubus</i>	1 (?)	2 (?)
	<i>Rosa</i>	31 = 6.0%	30 = 7.0%
Cynipini	<i>Fagaceæ</i>		
	<i>Fagus</i>	1 (?)	
	<i>Castanopsis</i>		1
	<i>Quercus</i>	436 = 84.8%	370 = 86.5%

The first set of figures is based on Dalla Torre and Kieffer's catalogue (1910) of the Cynipidæ of the world, the second set on my own catalogue of the American Cynipidæ. My catalogue includes a wider recognition of synonyms and is brought more nearly up to date than Kieffer's. I have omitted two "species" of the Cynipini—*Rhoophilus loewi* Mayr, which is evidently an inquiline in the *Rhus* gall, and *Solenozopheria vaccinii* Ashmead, which I have reason to believe is not the true maker of the huckleberry gall with which the single specimen was taken.

### GALL STRUCTURE

(Table III)

Of all plant deformations, the galls inhabited by the gall-wasps show the most astonishing of elaborate and regular designs, and many theories have been invented to explain what may be the causes of such phenomena. Apparently the secret is still far from solution. I have nothing at this time to contribute on the subject, nor is it in point here to review the work of those who have tried to solve the question. What may be offered now is material to show that all of this elaborate organization of plant tissue has arisen within the history of the Cynipidæ alone, independent of any other group of gall-making insects, since a day when the family was merely plant-tissue-inhabiting, not yet gall-producing.

That the factors responsible for the form of the deformation are specific for the insect inhabiting the gall has always been recognized. The number of designs of these galls is about as great as the number of species of insects producing them. Occasionally two apparently different species of wasps will produce galls very nearly identical,<sup>1</sup> but a careful

<sup>1</sup>For examples, *Andricus singularis* and *A. osten-sackeni*; *Amphibolips citriformis*, *A. coelebs*, and *A. ilicifoliae*; *Neuroterus batatus* and *N. noxious*; *Disholcaspis cinerea* and *D. unicolor*; *Philonix pezomachoides* and *P. hirta*, are among the few cases of close identity of galls.

study of even these instances will show that there are constant enough differences between the galls of the species. On the contrary, a few instances might be cited where the same insect is found inhabiting galls so different in form that they have been considered as distinct species. In these cases it seems that the influences of the host plant organization have come to the front, for where two galls are thus dissimilar they are found always upon host plants of different species. Thus the smooth form of the gall of *Rhodites dichlocerus* is found on species of rose whose stems are comparatively unarmed, and the very spiny form of the gall, produced by the same species, is found upon species of rose whose stems are normally more densely covered with prickles. But such cases are the exceptions. It is only rarely that the importance of the plant in determining the character of the gall becomes more than secondary; the specific qualities of the insect inhabitant are the primary factors in determining the form of the gall.

The factors inciting gall formation have more than this specific nature. They show qualities which are generic for the insect producing the gall, but not for the host plant on which the gall occurs. This fact has been vaguely recognized by students of cynipid galls for many years. It has been natural to refer to a "typical *Disholcaspis*" or a "typical *Amphibolips*" gall, but such statements have never been carried to the point of defining the characters of the galls of any of the genera of the Cynipidae. After an elaborate study of the histology of galls of many species, Melvin T. Cook (1902) arrived at the conclusion that "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 bore out the experience of all who had carefully examined galls. It was valuable to have the confirmation of an histological study, but an examination of the gross morphology of the structures offers as satisfactory information, and there seems to be no reason why it is necessary to study the microscopic structure of the gall before one can perceive its generic characters.

With such brilliant guides available to indicate generic relations of the insects, it is surprising that no student has employed gall characters on any large scale in classifying the Cynipidae. Strange inconsistencies are found in our present-day classifications which have arisen because the generic characters of the insect were not sufficiently apparent, al-

though the characters of the gall might have thrown considerable light on the question. In revising the genera of the Cynipidæ, I shall give great consideration to lines that the gall characters may indicate, then, of course, looking for confirmation of these by the less evident characters of the insect morphology.

The galls of each genus are not only of the form typical for the group, but also of a degree of complexity which is usually quite uniform within the group, with considerable variation between groups. The galls of species of a wide range of genera studied by Melvin T. Cook (1902-4), Cossens (1912), and others all show a similar differentiation of the plant tissue into three zones, the epidermal, the parenchymal, and the nutritive, with often the addition of a fourth zone, the protective. But, although all cynipid galls are formed on fundamentally the same pattern, the developments of that pattern are surely much more complex in certain cases than in others. It seems proper to call those galls most simple in which the extent of proliferation of the plant tissues is least in amount (relative to the amount in that part of the plant normally), where the separation of the zones of tissues is least definite, and where the gall is still an integral part of the host plant; and to call those galls more complex where the amount of new tissues is relatively greatest and the separation of the zones is most complete, resulting in the complete independence of some of the zones in some cases (especially in the production of a separable larval cell) and where the separation of the gall from the host is most complete, the gall in many cases becoming almost or entirely a separable organism, connected with a food supply by only a small amount of tissue or in some cases actually developing in size and in formation of new tissue after the gall has left the parent plant. Involved with these characters of complexity will also be a reduced number of cells or a single larval cell within each gall; the smaller the number of larval cells in a single gall, the greater the amount, relatively, of new tissues produced by each individual insect, and the more definite the gall structure; consequently the monothalamous gall indicates greater specialization than either the polythalamous or the agglomerate gall.

In accordance with our understanding that the galls of each genus of gall-wasps show related characters, we find (as detailed in the accompanying table) that the degree of complexity of gall structure shows the generic relations of the insects producing the galls. It is to be noted that in many of the genera the galls are all of a single degree of complexity. Without an exception, the galls of *Aulacidea* are of about one degree of

simplicity, of *Disholcaspis* of one degree and sort of complexity, of *Amphibolips* of another, etc. The absolute uniformity in these genera of the degree of complexity needs to be fully realized, for it has some significance. In several genera, *Rhodites*, *Neuroterus*, etc., there is a range, more or less wide, in the degree of complexity of the galls of a single genus and, with our present inadequate knowledge, we cannot be sure what this may mean; but such instances do not invalidate the force of the fact that in many cases the degree of complexity of gall structure is a definite indicator of the generic nature of the insect.

If the gall (however it may be produced) is an expression of the physiological make-up of the insect; if the form of the gall is an expression of both the specific and generic constitution of the insect; if the degree of complexity of the gall is a definite guide to the generic nature of the insect; then we may believe that the degree of complexity of gall structure is an expression of the degree of development, evolutionarily, of the insect. Specific and generic characters are merely expressions of the relationships of the origin, in the course of evolution, of the organism, and anything which is constantly an expression of these generic qualities (as the gall structure and degree of complexity undoubtedly are) will indicate these evolutionary relationships. This is my justification for believing that the simplest galls are found among the most primitive Cynipidae, and that the most complex galls are found only among the highest Cynipidae. We must admit that there seems to be nothing known that demands that only the highest cynipids produce complex galls, but this ignorance is due, patently, to the fact that we know nothing of the way in which galls are produced. All we can say is that some activity on the part of the insect is responsible for the gall production, and it is in no wise unreasonable to think of that activity becoming more potent in its effect as the insect has evolved.

In the accompanying table of the gall characters of certain groups of Cynipidae the genera have been arranged in the order of an increasing degree of complexity of the gall, and we believe that order to be in some degree the order of origin of the genera, making due allowances for the inadequacies of a linear arrangement of an evolutionary series. We may allow details of relationships to be worked out by other lines of evidence, but we should attach some importance to the very primitive character of all the galls of *Aulacidea* (without a single exception), to the less primitive but still simple qualities of the galls of *Aylax*, *Diastrophus*, and *Neuroterus*, and to the highly developed characters of the galls of *Cynips* (European sense), of *Disholcaspis*, and of *Amphibolips*.

TABLE III. CYNIPID GALLS

Genus	Amount of Hypertrophy	Larval Cell	Order of Larval Cells	Connection with Host
<i>Aulacidea</i>	None, or small	Not distinct nor separable	Agglomerate	Not distinct, and entirely inseparable
<i>Phanacis</i>				
<i>Timaspis</i>				
<i>Aylax</i>	None, or small, or great	Distinct but inseparable	Agglomerate or polythalamous; monothalamous in 4 species	Not distinct, or not separable; separable in 3 or 4 species
<i>Rhodites</i>	Small or great	Distinct but inseparable	Agglomerate or polythalamous	Inseparable or separable
<i>Diastrophus</i>	Small	Distinct, but only slightly separable	Agglomerate or polythalamous	Inseparable
<i>Gonaspis</i>	Not very great	Distinct, only slightly attached	Monothalamous	Separable
<i>Neuroterus</i>	None, or small	More or less distinct; not separable	26 species agglomerate or polythalamous; 26 species monothalamous	30 species inseparable; 22 species separable
<i>Amphibolips</i>	Great	Very distinct, but more or less connected with the rest of the gall by strands of fibers.	Monothalamous	Entirely distinct and separable
<i>Disholcaspis</i>	Great	Entirely distinct and separable (at least in maturity)	Monothalamous	Entirely distinct and separable

## REPRODUCTION

(Table IV)

A large proportion of the Cynipidae reproduce agamically. There can be little question of the non-existence of the males of many of the species. Hartig (1840) bred almost 10,000 individuals of a single species, *Dryophanta disticha*, and secured only females. In spite of extensive collecting and breeding of many species of gall-wasps, both in Europe and America, no males have been found for some of them, and Adler (1881) and other workers have regularly secured galls and mature insects from the eggs of these agamic females.

The successive generations of some species are all similar and agamic; Adler found this to be the case with five species, each of which he bred for two successive generations—for three generations in the case of *Andricus seminationis*. In the case of other species, most likely for the

majority of the oak-gall-producing Cynipidæ, only the alternate generations are similar, every agamic generation being succeeded by a bisexual generation, which in turn produces an agamic generation. Where this heterogeny occurs the origin and development of an agamic generation has been so involved with the origin and development of the alternation of dissimilar generations that the problem is more properly discussed in the section of this paper on the alternation of generations. The simpler case, where only agamic generations exist, will be discussed here.

That agamy is a more specialized method of reproduction than a bisexual method need hardly be argued. The evolution of agamy among the Cynipidæ is easily understood, for among the species still existing today we find all gradations from the primitive bisexual to the specialized agamic condition. Among the species of *Aulacidea*, the sexes are produced in about equal numbers and normal sexual reproduction occurs. Here and in the very closely related genera are the only instances of normal sexual reproduction found in the whole family, except such as occur in the sexual generation of heterogenous species. In *Diastrophus* the male sex is much less abundant than the female, constituting only about thirty per cent of the total number of individuals, and it is therefore very likely that parthenogenetic reproduction occurs frequently in the group. But that the eggs are still often fertilized is quite certain; I have many times seen copulation in the case of *Diastrophus nebulosus*. In *Rhodites*, however, it is definitely known that for several species the parthenogenetically produced eggs are the regular means of reproduction, and Adler (1881, p. 153) went so far as to call the males of these species superfluous. Though it is still likely that the males do occasionally fertilize the females in these species, it is quite certain that, as Adler put it, "we can predict that they [the males] will probably become extinct in the course of time." In *Disholcaspis* we have instances where apparently only females are ever produced, but it is still possible that there is a bisexual, an alternate generation yet to be discovered among those species. At any rate complete agamy has been attained by at least those five species of *Andricus* studied by Adler.

The accompanying table giving some data as to the ratio of the males to females is based on my own observations, supplemented in a few cases by records from other observers. The total amount of the data is very meager, but is enough to indicate what are undoubtedly the true conditions among several of the groups. The order of the species is that of the diminishing abundance of the males. This is largely a generic arrangement of the species, which indicates that the sequence

is to some extent evolutionary, but it should be emphasized that, though a strictly agamic group is in that respect more specialized than one only partially agamic, it need not necessarily be derived from the next less strictly agamic group. Thus, though *Diastrophus* is undoubtedly derived from *Aulacidea* or related forms, as indicated by the consideration of reproduction in the group and as confirmed by several other sorts of evidence, and though *Rhodites* is undoubtedly a more highly specialized group than *Diastrophus*, it is not to be believed that *Rhodites* originated from *Diastrophus*. Other considerations indicate distinct origins of *Diastrophus* and of *Rhodites* from *Aulacidea*, rather directly in each case. That is, the agamic condition has arisen independently at least three times among the Cynipidae, not to mention its further occurrence among the forms which have an alternation of generations. And, though we do not have the transitional conditions for each of the lines of development, it seems clear that this agamic condition is the result in each case of the gradual disappearance of the males and the gradual appearance of parthenogenetic reproduction, first as an occasional phenomenon, finally as the regular and only method of reproduction.

This condition is not in the least surprising, for parthenogenesis has undoubtedly arisen independently at very many different times among a great number of the groups of the Hymenoptera.

TABLE IV. SEXES OF GALL-WASPS

Species	Individuals counted	Per cent Males
<i>Aulacidea podagræ</i>	391	55
<i>Aulacidea bicolor</i>	36	44
<i>Aulacidea nabali</i>	300	36
<i>Aulacidea annulata</i>	120	16
<i>Aulacidea tumida</i>	89	30
<i>Diastrophus kincaidi</i>	39 (Gillette '93)	36
<i>Diastrophus nebulosus</i>	192	28
<i>Rhodites ignotus</i>	37	35
<i>Rhodites dichlocerus</i>	66	8
<i>Rhodites rosæ</i>	419	1.5
<i>Rhodites bicolor</i>	14	0
<i>Disholcaspis</i> (whole genus)		0 (?)
<i>Andricus cellularius</i>	30 (Gillette '92)	0
<i>Andricus dasydactyli</i>	118 (Ashmead '96)	0

## ALTERNATION OF GENERATIONS

(Table V)

The alternate generations of certain species of gall-wasps show more remarkable differences than do the alternate generations of any other group of animals in which this heterogeneity is known to occur. Because of the careful experiments of Adler (1881) and of others, most students of biology are thoroughly familiar with the extreme differences presented by successive generations of these Cynipids. I have given detailed accounts of the life histories of some of our American species in an earlier paper; and a review of this and of Adler's work will show to what the extremes of differences amount. The galls of two successive generations may be produced on different parts of the plant and may present entirely different forms, e. g., the gall of one generation of *Andricus operator* is mainly a large mass of wool on the young stems, leaves, or aments of the oak; the second generation gall is a small, seed-like, naked capsule between the cup and the acorn. The insects of the two generations of some species may be so entirely different as to warrant believing them to belong to different genera, if the relationships of the two forms has not been discovered. In fact, Adler indicated that in practically every instance the two generations had been placed in different genera.

We have been so impressed with these extreme instances of alternation that we have failed to recognize the less remarkable cases; and the origin of the perfected phenomenon of heterogeneity has remained a riddle just because we have not paid sufficient attention to these less extreme instances.

An adequate conception of the characters of the adults and of the galls of the species concerned in this discussion can be gained only by an examination of specimens or by a careful study of the papers already referred to, Adler's paper including most of the European and my paper including most of the American species of which the life histories are known, but the accompanying table will summarize the essential characters for each species.

It is remarkable that for several of the species, all of which belong to the genus *Neuroterus* (of genetic significance), the successive generations are very similar. Indeed, the differences between the adults is so slight as to be practically indiscernible. The main difference is physiological, for one generation reproduces agamically and the other by fertilized eggs. The galls of these two forms are likewise exceedingly similar and, although they may appear quite different in most cases, they are still of fundamentally the same type. The differences in those

cases are of a sort that might be explained as due entirely to the differences in the parts of the plant affected. If it is the young, growing shoot which is affected by one generation in mid-June, and the young leaves and undeveloped stems in the buds which are attacked by the next generation early in the following May, the galls (e. g., *Neuroterus batatus* and *N. noxiosus*) may be rather different in appearance but will be of exactly the same type: an irregular swelling of the part affected, the gall quite inseparable and not even distinct from the parent plant, with the same irregular distribution of larval cells, which cells are of the same degree of complexity in the two generations. Such a case amounts to no more than a seasonal dimorphism among the adults, with the differences in the galls due to seasonal factors and, except for the more complex alternation found in others of the Cynipidæ, one would not ordinarily think of such instances as alternations of generations.

Indeed, it is hard to understand how differences in the forms of the galls of successive generations could be often avoided where the two generations of a species are produced in a single year. The part of the plant affected is usually different for each generation, for it must always be a rapidly growing part of the plant which receives the egg. This last fact explains sufficiently why different parts of the plant are attacked by the insects in the different generations. It may be too much to suggest that in all the instances of extreme differences in the successive generations the differences are due primarily to the extreme differences of the parts of the plants affected, for we do not know enough about the factors influencing gall production to compare adequately the effects; but, in the simpler cases mentioned, we feel warranted in ascribing the most of the differences which appear to this difference in the part of the plant affected. It may be possible to secure more definite information on this subject by experimentally breeding and raising the galls.

That the second generation became fixed in the life cycle of each species only after a period of struggle to find a suitable method of obtaining an existence is apparent from observations already made on two species. Adler (1881) described the way in which *Cynips pallida* (also named *Biorhiza terminalis*, and the alternate was called *Biorhiza aptera*) arrives at the successful location of the eggs of the second generation only after unsuccessful attempts to find the suitable place. The bisexual generation is developed in galls on the terminal buds of young shoots, and oviposits usually in the bark of the roots, but also in the buds and leaf petioles. Galls begin development on the buds and petioles but, as far as is known, do not reach maturity. The galls on the roots are

successful in reaching their full development and from these the alternate, the agamic generation, will be produced. A further point of interest with this species is the fact that the adults of the two generations are very similar except in size, in mode of reproduction, and in the condition of the wings: although the agamic females are always wingless and the males of the bisexual generation are winged, the bisexual females either have normal wings or have reduced wings, or are almost wingless, exhibiting in this as in other respects not well fixed and not very great differences between the alternate generations, even though at first sight the differences appear remarkable.

I have found indications of the same sort of incomplete fixation of the habits of a generation in our common American species, *Biorhiza forticornis*. In the well-known form the adults are wingless, agamic, and emerge in December, often during very cold weather when the ground may be covered with snow. These adults are very strongly geotropic, positively, and will run down the tree to the ground, and I have succeeded in observing them oviposit in the roots or at the bases of the trunks of the white oaks. Though I have not succeeded yet in obtaining galls from these eggs, it is quite certain that a root gall does form and that these develop the adults of the bisexual generation. But, about the middle of the March following the winter emergence of the species, I found a second lot of wingless agamic females emerging from the same galls which had given the first lot of agamic adults. The insects of the two lots were not to be distinguished except by a remarkable difference in sensory reaction: these early spring adults were negatively geotropic, as I thoroughly proved by careful experiments. They climbed up the trees and oviposited in the terminal buds. Although the tree grew nicely that spring, no galls developed from these eggs. Whether galls ever develop from eggs laid by these spring forms of agamic females I cannot yet say positively. It may be that here we have another instance of the sort described by Adler for *Cynips pallida*. It is not unlikely that the fixation of the nature of the second generation for some of the species was a matter of repeated trial, and that only after some forms had failed of survival did one form finally remain and become fixed as the alternate generation. We have no way of estimating how many instances of this sort are yet to be discovered, but it is also reasonable to believe that for some species there was little or no amount of trial before a form was found which could survive.

The alternate generations of very many Cynipidae differ in their manners of reproduction, one generation reproducing agamically, the next from fertilized eggs. It will be generally believed that in such cases the sexual generation is nearer like the original form of the species. It is true that Adler argued to the contrary. He said (1881, p. 155):

(1) Some species are only propagated parthenogenetically.

(2) No species of oak gall-fly is known to propagate itself exclusively in a sexual manner. They are only known to do so alternately with an agamous generation in a generation-cycle.

Therefore it seems to me reasonable to infer that the present agamous form is either itself the original form or, if not exactly identical with it, it is at least very nearly related to it.

But such reasoning is not likely to be followed by many students. As we have shown earlier in this paper, the strictly agamic species of Cynipidae have been derived from normally bisexual species. If we were to follow Adler's reasoning, we would have to presume a group of strictly agamic Cynipids from which the dimorphic species might have arisen. But the most primitive of these dimorphic gall-wasps, species of the genus *Neuroterus*, show (in characters of radial cell, first abscissa of the radius, second segment of the abdomen, degree of complexity of gall-structure, etc.) closest relationship to the strictly bisexual genus *Aulacidea* rather than to *Diastrophus*, *Rhodites*, or other groups known to be largely agamic. Undoubtedly the bisexual form of dimorphic species is the original form.

The reason for the existence of agamic generations may be the fact that in almost every known case the agamic is the winter generation of the species. The chances of survival of this generation are naturally reduced by the vicissitudes of climatic conditions. The agamic female often appears in mid-winter when the temperature is far below freezing, or at least matures early in the spring when climatic conditions are still unfavorable. If it were necessary that the female of this winter generation meet a male of the species and that the eggs be fertilized before they were capable of developing, the chances of survival would be greatly reduced.

This may be the whole explanation of the origin of the agamic generation in these insects. If it is, the species found in warmer climates, as in southern Europe and northern Africa, and in the southern United States and Mexico, should not have an agamic generation even though there may be an alternation of generations among the species. It is highly desirable that some student experiment in such regions and solve life histories of cynipids of perpetual summer climates.

At any rate, I see no warrant for believing that the origin of the agamic condition in dimorphic species of Cynipidæ has any connection with the origin of the agamy in species, like *Rhodites* sp., which do not have an alternation of generations. If it is true that there are no such evolutionary relationships, then we may believe that the agamic condition arose independently at four different times within the family: at three points discussed in the preceding section of this paper, and in the connection in which we have discussed it here.

To summarize our conclusions concerning the origin of heterogeny among the Cynipidæ, it is suggested that the alternation of different forms of galls and of adults arose gradually, after a struggle for the fixation of the habits of each generation, among the wasps of the genus *Neuroterus* (or among allied groups), due primarily to seasonal, environmental conditions; that this alternation of generations is merely a more or less extreme type of seasonal dimorphism; and that the occurrence of agamy in one generation is mainly a result of seasonal exigencies.

TABLE V. ALTERNATE GENERATIONS

Species	Gall Begins to Develop	Gall	Adult
<i>euroterus batatus</i>			
♀rm <i>bisexualis</i>	Early May	Polythalamous swellings, young stem and petioles; inseparable; larval cells hardly distinct	Bisexual
orm <i>batatus</i>	Late June	Polythalamous swellings, main stems; inseparable; larval cells hardly distinct	Agamic. Identical with <i>bisexualis</i> , but slightly larger
<i>euroterus noxiosus</i>			
orm <i>vernalis</i>	Mid-April	Rather globular polythalamous swellings of leaf-buds, leaves, and petioles	Bisexual
orm <i>noxiosus</i>	Mid-June	Elongate, polythalamous swellings, main stem	Agamic. Quite identical with <i>vernalis</i> , but slightly larger
<i>euroterus baccarum</i>			
orm <i>baccarum</i>	Early April	Spherical, somewhat flattened, monothalamous, separable, on aments and young leaves	Bisexual
orm <i>lenticularis</i>	Mid-June	Circular, flattened, cone-shaped, monothalamous, separable, on leaves	Agamic. Rather similar to <i>baccarum</i> , differing mainly in coloring
<i>euroterus albipes</i>			
form <i>albipes</i>	Mid-March to Early April	Egg-shaped, monothalamous, on edges of leaf	Bisexual. Abdomen pedunculate
form <i>laeviculus</i>	Early June	Flattened button-shaped or shallow cup-shaped, monothalamous, on veins of leaf	Agamic. Abdomen larger, elongate. Minor color differences from <i>albipes</i>
<i>euroterus fumipennis</i>			
form <i>tricolor</i>	May	Globular, with scattered hairs, monothalamous, separable, on leaf-blade	Bisexual
form <i>fumipennis</i>	Mid-July	Circular, flattened, slightly emarginate, finely pubescent, monothalamous, separable, on leaf-blade	Agamic. Differs slightly in structure and sculpture; colors peculiarly like those of <i>tricolor</i>
<i>euroterus numismalis</i>			
form <i>vesicatrix</i>	March to April	Button-shaped, centrally depressed, covered with silky pubescence; monothalamous, on leaf; inseparable	Bisexual
form <i>numismalis</i>	Late June	Similar to gall of <i>vesicatrix</i> , but separable from leaf	Agamic. Differs in sculpture and slightly in structure

TABLE V. (continued)

Species	Gall Begins to Develop	Gall	Adult
<i>Neuroterus aprilinus</i> form <i>aprilinus</i>	July to August	Bud-gall, bud swollen, surrounded by dwarfed leaves; polythalamous	Bisexual
		On stamen; anther somewhat swollen; monothalamous	Agamic. Differs rath considerably in struc ture, sculpture, an color; smaller
<i>Chilaspis nitida</i> form <i>löwi</i>	August	Seed-like on aments, covered with hairs, monothalamous or polythalamous	Bisexual
form <i>nitida</i>	May to June	Oval, pubescent, monothalamous or polythalamous, on veins, under leaves; separable	Agamic. Differs slightl in color especially
<i>Fioriella marianii</i> form <i>meunieri</i>	March	Small, bud-like, in axils of leaves or terminal	Bisexual
		Larval cells under bark of main stems	Agamic. Similar <i>meunieri</i> , but four tim as large
<i>Cynips pallida</i> (= <i>Biorhiza terminalis</i> )	Nov. to Jan. (March ?)	Large, polythalamous masses, spherical, on twigs, mostly terminal	Bisexual. Wings lackin or reduced or short ♀, normal in ♂
form <i>aptera</i>	July	Irregularly oval, in masses, on roots	Agamic. Very similar <i>pallida</i> , but almost wingless, two times si of <i>pallida</i>
<i>Andricus ramuli</i> form <i>ramuli</i>	April	Small, oval cells in a large, dense, woolly mass, on young leaves or aments; monothalamous	Bisexual
		Bud-gall, elongate oval, surrounded by bud-scales; monothalamous	Agamic. Differs som what in structure, col and sculpture; slight larger
<i>Andricus radicis</i> form <i>trilineatus</i> (= <i>A. noduli</i> )	April to May	Slight swellings, terminal twigs or petioles; polythalamous	Bisexual
form <i>radicis</i>	Mid-August	Large swellings, potato-like, on roots or lower part of trunk; polythalamous	Agamic. In structu similar to <i>trilineatus</i> but differs in color, wi a length three tim that of <i>trilineatus</i>

TABLE V. (continued)

Species	Gall Begins to Develop	Gall	Adult
<i>Andricus collaris</i>			
form <i>curvator</i>	Early July	Irregularly globular, involving lamina of leaf	Bisexual
form <i>collaris</i>	Late June	Small, conical, appendiculate, in the winter buds	Agamic. Differs mainly in color and sculpture; somewhat larger
<i>Pediaspis aceris</i>			
form <i>aceris</i>	April	Rounded, on leaves or petiole, monothalamous	Bisexual
form <i>sorbi</i>	Early July	Pea-like, often clustered, on roots of maple; monothalamous or agglomerate	Agamic. Quite different in color, pubescence, form, structure, and sculpture
<i>Cynips folii</i>			
form <i>taschenbergi</i>	Oct. to March; usually Jan.	Elongate, rather oval, velvety; on buds on sides of twigs, or adventitious buds at base of tree; monothalamous	Bisexual
form <i>folii</i> (=C. <i>scutellaris</i> )	Late May to early June	On veins on under surfaces of leaves; large, globular; monothalamous	Agamic. Quite different in sculpture, structure, color, pubescence; quite a little larger
<i>Cynips longiventris</i>			
form <i>similis</i>	November	In buds on twigs or at base of tree; monothalamous	Bisexual
form <i>longiventris</i>	Mid-May to June	Small, globular, on leaves, underneath, on veins; monothalamous	Agamic. Differs in color, sculpture; a little larger
<i>Cynips divisa</i>			
form <i>verrucosus</i>	Oct. to Nov.	Small, globular, shot-like; on leaves, underneath, on veins; monothalamous	Bisexual
form <i>divisa</i>	Late May to early June	Long, oval, with a broad, rounded apex; on edges of leaves, or on shoots, or from buds	Agamic. Quite different in color, sculpture, and pubescence; quite a little larger
<i>Andricus futilis</i>			
form <i>futilis</i>	Late April	Blister-like, in lamina of leaf; polythalamous, larval cells distinct, joined by fine fibres to outer wall of gall	Bisexual
form <i>radicicola</i>	Mid-July	Cavities beneath bark of roots; larval cells distinct but not separable; little new tissue	Agamic. Differs in color, structure, and sculpture; two times size of <i>futilis</i>

TABLE V. (continued)

Species	Gall Begins to Develop	Gall	Adult
<i>Andricus operator</i>			
form <i>operator</i>	April to early May	Small, seed-like cells, covered with long, dense hairs to form a large, woolly mass, on terminal stems, young leaves, or aments	Bisexual
form <i>operatorolor</i>	Late June	Small, nut-like kernel at base of acorn, between cup and nut	Agamic. Different in color, structure and sculpture; larger
<i>Andricus inflator</i>			
form <i>inflator</i>	Late March to April	A swollen bud and shoot, with a foliaceous covering; monothalamous	Bisexual
form <i>globuli</i>	June to July	Globular bud-gall, surrounded by bud-scales; monothalamous	Agamic. Differs considerably in structure, sculpture, pubescence, etc.; larger
<i>Andricus fecundatrix</i>			
form <i>pilosus</i>	April	Elongate oval, covered with hairs; among anthers of aments; monothalamous	Bisexual
form <i>gemmea</i>	June	Bud-gall, with many closely imbricated scales; hop-like; monothalamous	Agamic. Differs in sculpture, structure, and color; three times size of <i>pilosus</i>
<i>Andricus testaceipes</i>			
form <i>testaceipes</i>	April to May	Small, simple thickening of mid-rib of leaf or petiole or of young twigs, 1 or 2 celled	Bisexual
form <i>sieboldii</i>	Aug. to Sept.	Good-sized, conical, ridged; arising from under bark on older twigs; monothalamous	Agamic. Differs in structure, sculpture, color, and pubescence; much larger
<i>Andricus corticis</i>			
form <i>gemmaeus</i>	April to May	Small, egg-like or bud-like, on tips of twigs or in leaf-axils	Bisexual
form <i>corticis</i>	Late July to early August	Irregular swellings in bark of roots or of old bark of trunk, containing a clustered mass of distinctly separate larval cells	Agamic. Very distinct from <i>gemmaeus</i> in every respect
<i>Andricus callidoma</i>			
form <i>cirratus</i>	April	Oval, bearing tufts of long hair, forming a dense, woolly cluster among the aments	Bisexual

TABLE V. (continued)

Species	Gall Begins to Develop	Gall	Adult
<i>orm callidoma</i>	Early June	Spindle-shaped, longitudinally ribbed, slender-stalked, in axil of leaf	Agamic. Differs from <i>cirratus</i> in every respect; three times as large
<i>udricus malpighii</i>			
<i>orm nudus</i>	April	Elongate, oval, with a depressed apex, entirely glabrous; on male catkins; monothalamous	Bisexual
<i>orm malpighii</i>	Early June	Small, spindle-shaped almost sessil, in leaf-axil; monothalamous	Agamic. Differs in every respect; two times as large
<i>udricus fulvicollis</i>			
<i>orm bicolens</i>	Early Nov.	Small, seed-like, polythalamous, in young buds, at apices or on scales	Bisexual, winged
<i>orm erinacei</i>	May	Rather large, oval, spiny, on midvein under leaf; polythalamous	Agamic. Wingless; differs in every respect
<i>ndricus palustris</i>			
<i>orm palustris</i>	March to April	Globular, hollow, succulent; the larval cell entirely free; on aments, young leaves, petioles, or stems	Bisexual; winged
<i>orm compressus</i>	May to June	Small, globular, hollow, without distinct larval cell, on veins of leaf	Agamic. Wingless; differs in every respect
<i>ynips megaptera</i>			
<i>orm megaptera</i> ( <i>=Trigonaspis crustalis</i> )	Dec. to Jan.	Rounded, pea- or cherry-like; monothalamous; on lateral buds on twigs	Bisexual. Winged
<i>orm rumin</i>	June	Small, kidney-shaped, on veins under leaves; monothalamous, separable	Agamic. Wingless; differing in color, sculpture, structure, etc.; about one-half to one-third as large as <i>megaptera</i>

## OTHER CONSIDERATIONS

We have been handicapped in discussing the phylogeny of the Cynipidæ by our lack of knowledge of fossils of the group. The only fossil gall-wasps known are three species which I have recently described. All three of these belong to the genus *Aulacidea*, but whether this is significant may not be determined on the basis of such meager data. Nevertheless, it is remarkable that no cynipid galls are described from fossil oaks. The only fossil galls known are quite certainly not cynipid. I am inclined to believe that the family Cynipidæ is of recent origin, possibly not much older than the Oligocene fossil I have described.

Certainly the family has not existed for any long time with the characteristics shown in the present day by the more specialized groups, for it is inconceivable that the insects could have survived for long any struggle for existence while impeded by the specialized habits possessed by most of the species, as the following brief data may show.

The necessity of the larva passing its life within a gall greatly reduces the parent's chance of finding the proper place in which to oviposit. The parent gall-wasps of most species must find a plant of the one genus and possibly of the one or two species of that genus on which alone it can survive. In most species, moreover, the parent must find a particular part of that special host and, failing to arrive at that spot within the very few hours of its adult life, the insect dies without effecting reproduction. Such a failure is not as likely to occur with forms which are less specialized in their choice of host and part of host affected. Insects of this latter sort are found in the genus *Aulacidea*.

Effective as a highly complex gall may prove as a protection to the larval wasp, it has evident disadvantages. It serves as a prison in which the larva is trapped. The larva has become a degenerate, legless, inactive, helpless organism; and, if once its gall defence is broken, the insect is quite at the mercy of the enemy. The defence offered by the gall itself is, I think, largely theoretical, and exists mostly in the minds of superficial observers. The hardest galls, or galls most complicated with hairs, spines, wool, loose larval cells, etc., or galls rich in tannin crystals, etc., are all abundantly parasitized and, indeed, some of the most heavily parasitized galls are those best equipped (theoretically) against enemies (e. g., *Amphibolips confluens* has 95% parasites, *Callirhytis furnessae* has 50% parasites, *Biorhiza torticornis* has 96% parasites, *Rhodites rosea* has 15% parasites, etc.). The smallest amounts of parasites usually occur with those species of *Aulacidea* which make the simplest galls.

Again, agamic reproduction has evident advantages but it is inconceivable, from what we know of reproduction among animals, that such a method of propagation, especially where agamy has become the only method, can result in anything less than a loss of vitality and the ultimate extinction of the species. This belief may be due to our inadequate knowledge of biological phenomena, but it is significant that the agamic species of cynipids (e. g., *Rhodites*, *Disholcaspis*, and the genera with an alternation of generations) more often fail to reach maturity than do species of the bisexual groups (*Aulacidea*, *Diastrophus*, etc.). It is a common experience to obtain only a score of adults from hundreds of the oak- or rose-galls, while many hundreds of adults may be secured easily from a score of galls of *Aulacidea*, for instance. The failure of those certain species to reach maturity may be due in part to their higher degree of parasitism, but it is not due entirely to that.

Still another thing which indicates decreased vitality in the oak gall-wasps is the short duration of the adult life of most species. Having observed some thousands of adults of scores of species on trees until the insects died natural deaths, I found that about two days was the average length of life for those species, while many species will die almost instantly after oviposition, even if that is only a few hours after the emergence from the gall.

The adults of most species of cynipids are very weak creatures, fatally injured by the slightest touch or by a sudden change of temperature or of humidity. One of the greatest obstacles in my experimental breeding has been the enormous amount of destruction caused if a rainy or even foggy day occurred at the time of emergence of a lot of adults. Although I kept the insects under cover, at such a time they would not oviposit or even make any attempt to climb over the trees; when the weather would become favorable in a day or two most of the wasps had lost all vitality and soon died without laying eggs.

Still another indication of the reduced vitality of most of these cynipids is the number of adults which reach maturity but then do not succeed in making (chewing) their way through the walls of the gall. It is hard to determine what percentage of adults thus fail, at the last moment, to achieve the goal of their lives, but it is apparently large, for almost any collection of galls, cut open, will show many such individuals in galls which were evidently mature before they were gathered. For instance, from one lot of galls of *Andricus pomiformis* not a single individual was bred, although at least 150 entirely mature adults were found within the galls. Osten Sacken bred only one adult from the type

galls of *Andricus pellucidus*, but from the other seven, monothalamous galls I secured seven mature adults, most of which had eaten their way through the walls of the larval cells but had then died before getting through the thinner walls of the outer gall. I gathered many adults of *Andricus tecturnarum* which had emerged through the hard walls of the galls but had then died before escaping from the coat of tangled hairs which covered the galls. Hundreds of other similar instances might be cited. It is likely that under natural conditions there is less of this sort of mortality than when the gall is gathered into breeding jars, but even this indicates an amount of vitality possessed by the insects which is none too sufficient.

On the contrary, species of *Aulacidea* are very easily bred in numbers and it is a rare thing to find adults left in the galls. The adults of these species will always live for many days. I have just found a female of *Aulacidea annulata* which was soaked in alcohol for half an hour and then glued to a cardboard point; the insect was discovered alive after ten days in a Schmitt box. Such vitality, as far as I have ever seen, is not to be found among the oak gall-wasps.

On the basis of these considerations, the Cynipidæ may be divided into two more or less distinct groups. One group, including mainly oak gall-wasps, has little vitality, possesses a mode of reproduction which would seem to guarantee a continuation of the lowering of vitality, and has a manner of living its larval life which invites a tremendous number of parasites and offers often insurmountable obstacles to the insect's growth to maturity. The other group, mainly *Aulacidea* and the allied genera, has a much larger amount of vitality, a method of reproduction (bisexual) which is fit to maintain the vitality of the group, and a mode of larval life (in simple galls or merely in stems) which offers fewer obstacles to the achievement of maturity. The first group is very apparently over-specialized and must ultimately become extinct. It is not likely that such a group could have furnished the progenitors of the second group, i. e., the Cynipini were not the ancestors of the Aulacini. This latter group possesses the far more successful mode of living and is likely to survive until it too has become specialized to the ultimate, the disastrous degree.

## PHYLOGENETIC POSITION OF GENERA

**AULACINI****AULACIDEA**

We include *Pseudaulax* Ashmead in this group. The radial cell of the wings in *Pseudaulax* is closed, which is a primitive condition found elsewhere among the true gall-wasps only in the genus *Rhodites* and in some few genera known only from a very few species.

In all the species of *Aulacidea* the first abscissa of the radius is arcuate, one of the extreme forms of that vein in this family and, although, as we have already pointed out, the arcuate is not necessarily a more or a less primitive form than an angulate form of the vein, it is definitely an extreme condition in this family. Because of the way in which all the other lines of evidence read, we consider the arcuate vein most primitive rather than most specialized. In one species, *Aulacidea annulata*, the vein is arcuate with a very slight suggestion of an angle on one side only.

The second segment of the abdomen is smaller here than in any of the other gall-wasps, and this small segment represents a more primitive condition than where the segment is enlarged to cover most of the abdomen, as in most of the genera of the family.

The hypopygium in this genus is less highly specialized than in any of the other cynipids. It has not assumed the peculiar, pointed form found in species of *Rhodites*, nor become narrow and elongate as in most of the oak gall-makers. In *Aulacidea* it is still a broad, ventral plate, very little produced.

The species of this group inhabit plants of thirteen different genera distributed widely from one of the lower monocotyledons, *Triticum*, to the highest plants, composites. This wide range of hosts is a very primitive condition, compared with the complete restriction of the greater number (93%) of the gall-wasps to plants of only two genera, and further study will undoubtedly reveal species of *Aulacidea* on many more plants than they are at present described from. Moreover, the only known instances among the Cynipidae where the same species regularly inhabits plants of different genera seem to be in this genus and in the very closely related *Aylax*. Thus, *Aulacidea tumida* is found on either *Solidago*, *Sonchus*, or *Lactuca*; several of the American species of *Aulacidea* may be found on either *Lactuca* or *Prenanthes*; and *Aylax pisum* lives on *Lygodesmia* and on *Stephanotis*; while *Aulacidea hieracii* has been reported (possibly not entirely correctly) from *Hieracium*, *Linaria*, *Cytisus*, and *Triticum*. This is a remarkable lack of specialization in the choice of host.

The galls of this genus are by far the simplest known among the Cynipidae. Indeed, several species make absolutely no gall and are merely pith-inhabiting insects. *Aulacidea bicolor* has long been known to be such a species, and I have found, on investigations of dead stems, several other species of the same sort, of which I have already described *A. abdita*. Without a single exception, the galls of this genus are simple, never consisting of more than swellings of stems, agglomerate or polythalamous, without separable or even distinct larval cells, and in no case is the gall separable from the plant. As we have shown in the discussion of galls, such simple galls are primitive and indicate primitive relationships of the insects. Very interesting proof of the simple nature of even the most developed of these *Aulacidea* galls is furnished by the galls of *A. podagræ* and *A. tumida*. In each case the insect may be found in stems which show no traces of galls, although definite deformations of the pith surround the larval cells inside the stem; while, at other times, the same species (I am satisfied as to the identity after examination of large series of the insects) will produce a swelling of the stem, making a more or less conspicuous gall. It may be that the state of the plant at the time the insect's egg is laid in it, or the physiological nature of the particular plant, due to its special environment, determines the extent of the hypertrophy. In either event, it seems that the gall-producing powers of the insect are not developed enough to insure the formation of a gall except under the most favorable circumstances, although other Cynipidae, whenever they produce a gall at all, apparently always produce galls of a uniform pattern and of the same degree of complexity.

This (*Aulacidea* and most likely *Aylax* and other related genera) is the only group of the Cynipidae in which the sexes of most of the species occur in about equal numbers. Our data on this point are quite meager but seem to warrant this conclusion. The reproduction is normal, sexual reproduction, which is certainly more primitive than the partially or strictly agamic reproduction of the rest of the family.

There is apparently no alternation of generations in this genus, such as occurs in most of the oak gall-producing cynipids. Nothing that I know of from observation of the American species would indicate that there is anything but normal reproduction in the group. *Aulacidea nabali* emerges late in May and the galls are mature in September, appearing however a couple of months before that. *A. podagræ* emerges in mid-June, and the galls are good-sized by August. *A. tumida* emerges in early June; *A. annulata* emerges in early June; and the galls must develop on the plants before they have become mature, which date for

*Lactuca* is late July or early August. In all these instances there does not appear to be time enough for the development of an alternate generation in the same year between the date of emergence of the insect and the appearance of the gall of that species. More positive proof of the absence of an alternate generation is furnished by the work of Adler who secured, experimentally, the successive generations of *Aulacidea hieracii* and reported (1881) that there was no alternation of generations with that species. This absence of heterogeny is an important indicator of the lack of specialization of the group in that respect.

Our knowledge of fossil cynipids covers only three species and, with such limited knowledge, we are not warranted in drawing general conclusions. The three described fossils all belong to this genus *Aulacidea*.

The amount of vitality shown by individuals of this genus is (as I have described on p. 384) decidedly greater than that shown by the majority of cynipids, and this may be an indication of the relation of the group to the primitive, more successful insects rather than to the less vigorous, decidedly unsuccessful, more specialized forms.

We must conclude, then, on consideration of these eight or nine sorts of evidence, that this group is the most primitive in relationships of the existing Cynipidae.

#### PHANACIS

We should, undoubtedly, place this genus in as primary a position as *Aulacidea*, since the insect is morphologically as primitive and produces as primitive a gall. However, only two species of this genus are known (the gall of one is not known) and, consequently, we are not warranted in making too broad generalizations. We may not be correct in considering this genus distinct from *Aulacidea*.

#### TIMASPIS

This genus, with seven known species, is not very distinct from *Aulacidea*. The galls of the two groups are equally simple and occur on plants of many genera. An indication of higher position, evolutionarily, is seen in the radial cell, which is usually partly open; and the second segment of the abdomen, though of about the same size in the female as in *Aulacidea*, is larger in the male, there covering about one-half of the abdomen.

#### AYLAX

We would include the following as belonging to the one genus: *Aylax* Hartig (= *Aulax* Hartig), *Isocolus* Förster, *Eubothrus* Förster, *Liposthenes* Förster, *Antistrophus* Walsh, *Asclepiadiphila* Ashmead, and

*Gillettia* Ashmead. This is the synonymy recognized by Beutenmüller (1910), and is practically that adopted by Kieffer (1910). The characters by which these various groups are separated seem hardly sufficient for drawing generic lines.

The radial cell throughout this genus is open, and in many cases the limiting veins are quite considerably reduced. This, without question, is more specialized than the closed cell of *Aulacidea*.

The first abscissa of the radius is usually arcuate, the more primitive condition, or may be slightly subangulate (as in *Aylax glechomæ*), which form of the vein is somewhat more specialized than the arcuate vein found in *Aulacidea* and the other species of *Aylax*.

Other indications of some specialization in the wing-venation are (1) the reduction of the veins bounding the areolet so that this cell is closed in most of the species of this genus, and (2) the lack of pigmentation and the fine form of the veins in practically every case, this condition appearing to result ultimately in the disappearance of the veins.

In most of the species the second segment covers only about one-third of the entire abdomen, a condition as primitive as that found in *Aulacidea*. But the dorsal extent of the plate in some of the species is somewhat greater, indicating greater specialization. In *Aylax pisum* (= *A. stephanotidis* Ashmead) the plate equals two-thirds of the length of the abdomen, though it is still small in lateral extent.

The hosts of this genus are as varied as the hosts of *Aulacidea*, including plants of at least sixteen different genera of seven natural families. This is the more primitive trait in the choice of hosts, as we have pointed out before.

The galls produced by the insects of this genus vary greatly in complexity. *Aylax rufus* produces no gall at all, living in the pith of stems, in this respect resembling *Aulacidea bicolor*, *A. abdita*, and *Phanacis centaureæ*. Most of the species produce decided swellings of the part affected, which is either stem, leaf, seed-capsule, or bracts, but the gall remains an integral part of the plant, more so in some cases than in others. Still other species form galls which are more or less separable from the plant, e. g., *A. kernei*, *A. salviæ*, *A. pisum*, and occasionally *A. glechomæ* and *A. latreillei*, and this represents a more complex condition. A character which holds for most of the species of this group, and one which indicates a more complex condition than any found in any of the species of *Aulacidea*, is the formation of distinct, but still inseparable, larval cells. The galls of some of the species (those which are inseparable from the plant) are polythalamous and agglomerate; the galls of

others are agglomerate but essentially monothalamous; the galls of four of the species (the galls which are separable from the plant), *A. glechomæ*, *A. kernei*, *A. pisum*, and *A. latreillei*, are distinctly monothalamous. No species of *Aulacidea* produces a gall which is monothalamous, or separable, or which develops distinct larval cells. The galls of *Aylax* are very evidently less primitive, though not all of the galls of this genus are as complex as others.

Reproduction in this group is most likely normal, sexual reproduction. The males of most of the species (not including *A. glechomæ*) are known, and the sexes are about equally well represented in collections, but I have not had an opportunity to breed large enough numbers of any of the species of the genus to obtain reliable data as to the ratio in which the sexes exist. *A. glechomæ* may regularly reproduce agamically.

There is no alternation of generations in *Aylax glechomæ* and *Aylax papaveris* (= *A. rhæadis* Bouché), as Adler proved (1881) by experimental breeding of the insects for successive generations. Nothing of the observations made on species of the genus concerning emergence dates, etc., would seem to indicate any likelihood of heterogeny occurring anywhere in the group.

In summary, species of *Aylax* are primitive in abdominal characters choice of host plant, degree of complexity of the galls of several species, and in manner of reproduction. The genus, however, evidently includes more specialized forms than *Aulacidea*, as evidenced by the specialized wing-venation, the enlarged second segment of the abdomen of some of the species, the more complex character of the galls of most of the species, and in the possible existence of agamic reproduction in one species. *Aylax glechomæ* is in many respects the most specialized of the species of *Aylax*. But in no cases do the species show as specialized characteristics as those of most of the oak gall-producing Cynipidæ.

I believe *Aylax* was derived directly from *Aulacidea*.

#### DIASTROPHUS

The radial cell in thirteen of the fourteen known species of this genus is open, indicating some degree of specialization, but the occurrence of the closed cell in one species, *D. fragariæ*, indicates that the group is descended directly from some closed-cell genus such as *Aulacidea*.

The first abscissa of the radius for most of the species is slightly angulate, but in a few species, e. g., *Diastrophus rubi*, it is still arcuate, the primitive condition. Evidently, there has occurred some evolution

of this character within the group, but the genus is closely related to, most likely descended directly from, *Aulacidea* or *Aylax*, the only genera where this vein is always arcuate.

The second segment of the abdomen of species of *Diastrophus* covers, dorsally, more than half the whole abdomen, in this respect being more developed than in *Aulacidea*, but not as developed as in *Rhodites* or most of the oak gall-producing cynipids.

The face of the species of this genus is peculiarly marked with fan-shaped striæ. This is a sort of specialization not found elsewhere among the true gall-wasps.

The bidentate claws may be some indication of specialization. The claws of other groups of the Aulacini are simple.

The hosts of this genus are mostly plants of the family Rosaceæ. One species is on *Smilax*, a liliaceous plant. One species is found on *Fragaria*, four species are on *Potentilla*, and seven species occur on *Rubus*. Thus, the choice of host plant is rather wide, indicating a relationship to the primitive, polyphagous groups of the Aulacini. But over half of the genus is confined to *Rubus*, and another third to the related *Potentilla*, and this is a specialization of a degree much greater than that found in any of the other Aulacini, but it is not comparable with the complete specialization achieved by the Rhoditini and Cynipini.

The galls of this genus are remarkably uniform in degree of complexity of structure, all but one of the species producing galls which are agglomerate or polythalamous swellings of stems, quite inseparable from the plant, and to this extent quite primitive. But the forms of the galls are fairly definite, and the formation of larval cells which are slightly separable from the rest of the galls indicates some degree of specialization. The gall of *Diastrophus cuscuteformis* appears to be an exception to this general type, but this species may best be considered to belong to the genus *Gonaspis*. That is, the galls of *Diastrophus* indicate rather primitive, but somewhat developed, relationships.

Reproduction within the group may be normal sexual reproduction at times. I have often seen the males of *Diastrophus nebulosus* copulating with the females, and undoubtedly fertilization often occurs. But the males constitute only about thirty per cent of the total number of individuals, and it is very likely that this scarcity of males results in unfertilized eggs being laid very often, and the parthenogenetic development of these eggs is not, unlikely. Again, we find an instance of the rather primitive (bisexual) nature of the species of *Diastrophus*, showing at the same time some degree of specialization, in the gradual disappearance of the males.

It is very doubtful if there is any alternation of generations within this genus. Adler (1881) has definitely proved, by the breeding of successive generations, that *Diastrophus rubi* has no alternation of generations, and nothing known concerning emergence dates, dates of appearance of the galls, etc., indicates that we should expect heterogeny in the group. Herein these insects are more primitive, less specialized than the oak gall-wasps.

#### **GONASPIS**

This genus is clearly related to the genus *Diastrophus*, from which it is best distinguished by having the scutellum ending in a point which projects far over the metathorax. This indicates some degree of specialization beyond *Diastrophus*.

Another character which I feel is a good indication of specialization is the more complex character of the galls of *Gonaspis*. These galls are monothalamous and separable from the host plant (*Diastrophus* galls are polythalamous and inseparable) and show a considerable degree of separation of the zones, the epidermal layer in *G. potentillae* being connected with the larval cell by distinct strands of tissue.

*G. cuscuteformis* also has a monothalamous, separable gall which is complicated with spinous processes, and the species evidently belongs in this genus, where Dalla Torre and Kieffer (1910) placed it. It has a scutellum which is more specialized than is usual in the genus *Diastrophus* and, although it is not as developed as in *Gonaspis potentillae*, this character, taken in connection with the specialized gall of the insect, is enough to warrant considering the species to belong to *Gonaspis*.

#### **RHODITINI**

##### **RHODITES**

Including *Lytorhodites* Kieffer

The radial cell in this genus is closed in thirty species, but it is more or less open in six species, *R. arefactus* Gillette, *R. multispinosus* Gillette, *R. nebulosus* Bassett, *R. neglectus* Gillette, *R. ostensackeni* Beutenmüller, and *R. semipiceus* (Harris) [=*R. fulgens* Gillette]. The closed radial cell is found nowhere else in the family except in the group to which *Aulocidea* belongs, and it is not to be supposed that a closed-cell genus is evolved from other than a closed-celled genus. It appears that *Rhodites* is evolved, directly or indirectly, from *Aulocidea* or from a group from which they both originated. The species with the open radial cell show, in that respect, a higher development, and

give a clue to the evolution within the genus. Kieffer has established (1902, Bull. Soc. Metz, (2) X, p. 96) a distinct genus, *Lytorhodites*, for these species, but there seem hardly enough other distinctive characters to warrant making of the group more than a subgenus.

In *R. vernus* Osten Sacken (= *R. nodulosus* Beutenmüller) the first abscissa of the radius is arcuate, a primitive condition of the vein. The only other groups in the family where this vein is arcuate are some of the genera of the Aulacini, and *Rhodites* is most likely descended from one of the groups of that tribe. All the other species of the genus have developed an angulate vein, in this respect showing specialization, but even in most of these species the vein is only slightly angulate and has not developed the angle to any great degree.

The second abdominal segment throughout this genus is well developed, occupying a half to two-thirds of the whole abdomen. This is a more specialized condition of the segment than occurs in *Aulacidea* and a less specialized condition than in most of the species of oak gall-makers.

The hypopygium of the insects of this genus is a remarkably developed structure. It is broad and very acutely pointed, "plow-shaped." This is a very specialized form for that segment to assume; throughout the rest of the family it is quite inconspicuous and without a peculiar form.

The hosts of this group of gall-wasps are plants of the genus *Rosa*. Every known species of the genus occurs on roses. One species, *R. rosae*, is believed to produce a gall, rarely, on plants of the related genus *Rubus* but, although this gall does resemble the mossy gall occurring on rose, I do not know that any one has bred the adult wasps from the blackberry gall and definitely proved the identity of the maker. Other records of species of *Rhodites* occurring on *Rubus* are undoubtedly errors in the determination of the host. There is no question that the insects are remarkably specialized in their choice of hosts. Compared with the distribution of the Aulacini upon plants of thirty-five different genera, this restriction of *Rhodites* (which genus contains about half as many species as the whole tribe of the Aulacini) undoubtedly indicates a higher degree of evolutionary development, a degree matched only by the concentration of the Cynipini upon the genus *Quercus* and only less remarkable than the specialization of the oak gall-makers because the number of the species of *Rhodites* is many times less than that of the Cynipini. The degree of specialization is complete in either case.

The galls produced by the insects of this genus vary considerably in degree of complexity. The galls of *R. vernus* and of *R. fusiformans*, for instance, are comparatively simple swellings of stems, entirely inseparable from the plant, and agglomerate or polythalamous—primitive characters. On the contrary, the galls of *R. bicolor*, *R. nebulosa*, *R. rosæ*, *et al.*, are very complex developments, entirely separable from the plant, highly modified in form, and with a high development of the larval cell. All degrees of complexity between these two extremes are to be found. The larval cell is distinct in most of the galls and has a well-developed wall, but in no case that I know of is the cell separable from the rest of the gall. That is, the galls indicate a wide range in the degree of development, evolutionarily, of various species of the genus, but in no case are the galls as highly complex, i. e., as highly developed, as in some of the genera of the oak gall-makers.

The mode of reproduction within the genus undoubtedly varies considerably among the species. It would be especially interesting to observe the reproduction of a species like *R. vernus*, for instance, which in wing-venation (arcuate first abscissa of the radius) and simplicity of the gall appears to be a more primitive form. It is possible that the reproduction of that species is primitive, normal, sexual reproduction. But it appears that, on the whole, the species of this genus reproduce agamically, with the males still existent but not usually abundant enough to fertilize many, if any, of the females. As Adler stated concerning this group, "The few males that are still produced are thus superfluous, and we can predict that they will probably become extinct in the course of time" (Adler-Straton, 1894, p. 153). Males are bred much less often than are the females and, from what limited data we can gather, they appear (cf. Table IV) to constitute only about two or three per cent of the total number of individuals. But this does not always apply to the progeny of any one individual; my first breeding of *Rhodites rosæ* gave six females and seven males, although subsequent breedings of the same species have only rarely given me any males at all. Gradually the male sex is disappearing from the genus and in consequence agamic reproduction is, likewise gradually, becoming the sole means of reproduction for these insects. Adler (1880) secured normal galls and insects from the unfertilized eggs of *Rhodites rosæ* and *R. eglanteriæ*, and there is thus no doubt that these unfertilized eggs are entirely capable of maturing. This agamy, almost completely achieved, is undoubtedly more specialized, more recently evolved, than the normal, sexual means of reproduction.

Adler (1880) proved by experimentally breeding for successive generations, that *Rhodites rosæ*, *R. eglanteriae*, and *R. spinosissimæ* produce galls and adults in the second generation which entirely resemble the galls and adults of the parent generation, i. e., that there is no alternation of generations among these species such as occurs among the oak gall-makers. I have obtained a second generation of *Rhodites ignotus* which, similarly, is like the parent generation, and it is unlikely that alternation of generations occurs anywhere in the genus.

Summing our conclusions concerning the evolutionary position of *Rhodites*, we find that it shows primitive relationships in some respects but is more or less specialized in other ways. The closed radial cell of most of the species, the arcuate first abscissa of the radius of one species, and the simple galls of some species require that we derive the genus directly from some group as primitive as *Aulacidea*. However, the high specialization in the choice of host, the developed hypopygium, and the occurrence of agamy throughout the genus show a great degree of development beyond that attained by *Aulacidea*. The variation in the degree of specialization of the wing-venation and of the gall-structure indicates a considerable evolution occurring within the group itself.

### CYNIPINI

#### NEUROTERUS

This includes *Neuroterus* Hartig, *Spathegaster* Hartig, *Ameristus* A. Förster, *Manderstjernia* Radoszkowski, and *Dolichostrophus* Ashmead.

In this group of oak gall-makers the radial cell is entirely or partially closed in six species, and in the remaining forty-eight species it is entirely open. This would indicate that the group, rather directly descended from the closed-cell genera *Aulacidea* or *Rhodites*, has had considerable evolution occurring within the genus itself.

The first abscissa of the radius shows considerable variation in *Neuroterus*, from a condition almost arcuate to a form very distinctly angulate with a slight projection into the radial cell. In no case, however, that I have examined is the vein as broadly and entirely arcuate as in the genus *Aulacidea*.

The second segment of the abdomen of species of *Neuroterus* is about one-half as long as the whole abdomen, being somewhat longer dorsally in the female but with a less extent laterally, so that the segment in this genus, though larger than in the *Aulacini*, is smaller than in the other oak gall-wasps. That is, there is closer relationship to the

Aulacini than is shown by this character by other genera of the Cynipini, and this suggests that in this group are the forms most like the ancestral Cynipini.

The galls of this genus are entirely restricted to oaks, the group showing in this respect the extreme specialization of the choice of hosts which is found in all the Cynipini and which is a remarkable condition.

The galls of *Neuroterus* are, on a whole, comparatively simple but there is some degree of difference in complexity of galls of various species. The differences, however, are not nearly as great as the differences between the galls of two genera of the oak-gall-producing cynipids. The galls of twenty-six species are polythalamous and inseparable, four species have monothalamous galls which are also inseparable, while twenty-two species have monothalamous galls which are separable from the plant. The polythalamous galls (the more primitive type) are always inseparable (a more primitive character); all but a few of the monothalamous (specialized) galls are separable (a specialized character). Some of the species are so primitive as hardly to produce a gall, e. g., *Neuroterus virgens* and *N. catesbaei*. Even in the most specialized galls the structure is never highly developed; there is no separation of parts; and there is no production of any abundance of new tissue or peculiar structures. The galls never consist of more than a rather simple wall surrounding the larval cell, rarely with a little simple pubescence, slightly peculiar shape, etc. The larval cell is sometimes quite distinct from the rest of the tissue of the gall, in some species much less so than in others but in no case that I know of is it separable from the rest of the gall. Again, in gall-structure, we find proof of the primitive nature of *Neuroterus*, more primitive than in any other group of the Cynipini but within the genus showing some considerable evolution. It is likely that further study of the galls may give further warrant for dividing the group into the several genera which have already been proposed for these species.

Reproduction in this group is so closely concerned with alternation of generations that it should be considered in that connection. The life histories of seven species have been studied and in every one of these cases heterogeny has been discovered. It is very likely that in most of the other species of the genus a similar heterogeny exists, but it is extremely important to discover whether all of the species have this sort of life history. The alternate generations, as far as known, always occur on similar parts of the plant, the galls appearing, superficially, rather different, but a closer study shows that in most instances they are of very

similar pattern. The galls of four of the European species studied are leaf-galls, all these being monothalamous and separable from the plant, with differences between alternate generations amounting to differences of form and not of plan of structure. The gall of the European *Neuroterus aprilinus* is a bud-gall, the alternate of which is more distinctly different than with other species of this genus. The American species of *Neuroterus* of which the life histories are known show still less distinction between the galls of the two generations, having no greater differences than what would be necessitated by the differences in the state of the plant at the times of the year in which the galls are produced. The adults of the two generations in this genus are likewise very similar, differing primarily in being bisexual in one generation and agamic in the other. Concerning the European species Adler said (1881, p. 26): "If we compare the flies of the two generations belonging to any of the species above described, we shall find the differences at first sight very slight. The difference of colouring is unimportant, and is chiefly observable in a slight variation in the colour of the legs; nor is the size of the body very different, while the form and surface markings agree in many points." And he then pointed out that the only important differences are those of form of abdomen and of ovipositor, due to the different modes of reproduction of the two forms. Among our American species the differences between the adults of the two generations are even less marked. There is no doubt that the heterogeny found among the species of *Neuroterus* amounts to no more than seasonal dimorphism with agamic reproduction in alternate generations. This is in marked contrast to the great differentiation between alternate generations of the species of other cynipids where heterogeny occurs. No other instances of differentiation of alternate generations as slight as in *Neuroterus* are known among the other cynipids. Again we find proof that the genus *Neuroterus* is more primitive than the other oak gall-wasps.

In conclusion, we believe that *Neuroterus* is one of the most primitive groups of the Cynipini, derived rather directly from *Aulacidea*, and that a considerable evolution has occurred within the genus. Consequently, in this group we may expect to find the primitive stages of several of the biological characteristics of the oak gall-makers, and considerable attention given to the study of the life histories of species of *Neuroterus* is likely to be well repaid by discoveries which will cast light on the evolution of the highly specialized cynipids.

### DISHOLCASPIS

*Holcaspis* Mayr (not of Chaudoir) is a synonym of *Disholcaspis* Dalla Torre and Kieffer.

In this genus the radial cell is open. In most cases the apical portion of the subcosta is very short or lacking and the radius terminates a considerable distance from the margin of the wing. This is the greatest reduction, the greatest specialization, of these veins, found regularly in any genus in the family.

The first abscissa of the radius in every instance is very angulate, the angle approaching ninety degrees, and the projection into the radial cell is always very distinct. This comes very near to being an extreme of the form assumed by this vein in the Cynipidae—the extreme which we have considered the most highly specialized condition.

The second abdominal segment is not as highly developed as in many of the other oak gall-makers, though it is more developed than in the Aulacini. It regularly covers a half of the abdomen. These considerations, taken alone, would suggest that *Disholcaspis* is either more primitive than the rest of the Cynipini or that it has developed independently of most of those oak gall-makers.

The hosts of these insects is *Quercus*, these wasps showing the same extreme specialization in this choice of hosts as is characteristic of all of the Cynipini. Another sort of specialization shown by this group is the production of the galls of most of the species upon a single part of the plant—the lateral buds. It appears to be the stem that is affected, but M. T. Cook (1904, p. 143) pointed out that for at least some of the species it is really the bud that produces the gall. Most of the genera of gall-wasps include species which will attack the several parts of the plant, but in *Amphibolips*, *Cynips* (of European authors), and *Disholcaspis* the species of each genus are confined mainly to a single part of the plant. This seems to be specialization that, following generic lines, indicates something of the phylogenetic position of the group.

The galls produced by the species of *Disholcaspis* are among the most complex productions of the Cynipidae. The galls are all monothalamous; they show a distinct separation of the zones resulting especially in the formation of the very distinct, highly modified wall of the larval cell, which in most species is entirely free in the central cavity of the gall; and the galls are only very slightly connected with the plant, in many cases leaving the host long before the insect has reached maturity. These are all characters indicating a high degree of specialization. In some cases the galls assume peculiar forms (e. g., *Disholcaspis fung-*

*formis*) but the degree of complexity of plan of structure is absolutely uniform throughout the group. The only apparent exceptions to this rule are the best proof of the rule. Twenty-seven of the species are strictly of the sort described. The species called *Disholcaspis weldi*, *D. centricola*, *D. douglasi*, *D. maculipennis*, *D. brevipennata*, *D. arizonica*, and *D. truckeensis* produce galls which are very different from typical galls of *Disholcaspis*, but none of these species really belong to this group. The adults of the species *brevipennata*, *centricola*, *maculipennis*, and *weldi* have parapsidal grooves extending to the pronotum (not quite entire in *weldi*), have the second abdominal segment "tongue-shaped," i. e., produced dorsally, and in other ways are generically different from the species belonging in *Disholcaspis*, which genus was correctly limited by original definition to forms having the parapsidal grooves extending only to the middle of the mesothorax and the posterior edges of the second segment of the abdomen perpendicular or nearly so. Mayr (1902) very properly removed *centricola* and *douglasi* to the genus *Dryophanta*, with some of the species of which genus they have evident relationship; and there is as good reason for removing from *Disholcaspis* the other species listed above. Again, *arizonica*, which is apparently unknown except from the type material which I have not seen, is the only species included in *Disholcaspis* which has fifteen-jointed antennæ, and was first described (for reasons not evident from the description) as "closely related to *Cynips sulcatus* Ashmead, but differs by its much darker colour and infuscated wings. It seems to go best in *Holcaspis*" (Cockerell, 1902, p. 183). If this species differs from *Cynips sulcatus* mainly in color, it certainly does not belong to the genus *Disholcaspis*. Finally, *truckeensis* has the parapsidal grooves extending to the pronotum (only half as long in true *Disholcaspis*), has the cheeks almost as long as the compound eyes (only half as long in true *Disholcaspis*), and I have obtained it in both sexes (*Disholcaspis* is entirely agamic). That is, none of the apparent exceptions are truly exceptions to the rule of the uniformity of degree and sort of complexity of the galls of this genus. And such complete uniformity is not very likely mere coincidence but must be truly significant of the genetic relations of the insect producing the gall.

Reproduction in *Disholcaspis* must be entirely agamic. No males have ever been bred from or found in the galls of this group.

Whether alternation of generations occurs in *Disholcaspis*, with possibly bisexual reproduction in an alternate generation, is not definitely known. The genus is confined to America, so European workers have

not studied the life histories of any of the species. I have tried to breed the species for successive generations but, thus far, have not succeeded. Several of the species require two years or more for an insect to reach maturity and this makes the experimental study of these insects very difficult. All of the species, apparently, emerge in the winter. I have observed *D. globulus* ovipositing in the lateral buds of oaks but secured no galls from these buds. Whether a gall similar to that in which the parent insect matured would have resulted if the eggs had developed we cannot say positively.

*Disholcaspis*, then, is a genus which, in having an undeveloped second abdominal segment, shows what would appear to be a primitive character. But in wing-venation, restriction of the choice of host and of the part of the host affected, in the great complexity of gall-structure, and in completely agamic reproduction (in the one generation, at any rate), it shows great specialization, which is almost as great as that reached by any other genus of cynipids. It may be that the group is derived directly from the primitive oak-gall-producing Cynipidae, becoming, however, very specialized. I cannot otherwise explain the persistence of the small abdominal plate. Knowledge of the life cycle of some of the species would throw considerable light on the question.

#### SUMMARY

The following are my conclusions which apply to the true gall-wasps:

1.—The closed radial cell of the wing is more primitive than the open cell; closed-cell genera or genera containing any species with the cell closed must be derived from closed-cell genera.

2.—The arcuate first abscissa of the radius is more primitive than the angulate vein showing a projection into the radial cell; the character of this vein is of generic importance and the extent of development toward the angulate vein indicates, in general, the extent of evolution of the genus.

3.—The size of the dorsal plate of the second abdominal segment is of generic significance; the smaller plate is more primitive; but this character among some Cynipini does not always show as great specialization as other characters in a genus, indicating diverse lines of evolution within the Cynipini.

4.—The primitive Cynipidae were polyphagous; the restriction of *Diastrophus* mainly to *Potentilla* and *Rubus*, and the almost complete restriction of the Rhoditini to *Rosa* and of the Cynipini to *Quercus* show great specialization which occurred along three distinct lines of evolution.

5.—The form of the gall is an indicator of the specific nature of the insect and also of the generic relations of the insect; the degree of complexity of the gall-structure is likewise an expression of the generic position of the insect, the simplest galls being produced by the most primitive gall-wasps, and the more complex galls by more specialized wasps. The primitive cynipids were plant-tissue inhabiting, not gall-making, insects.

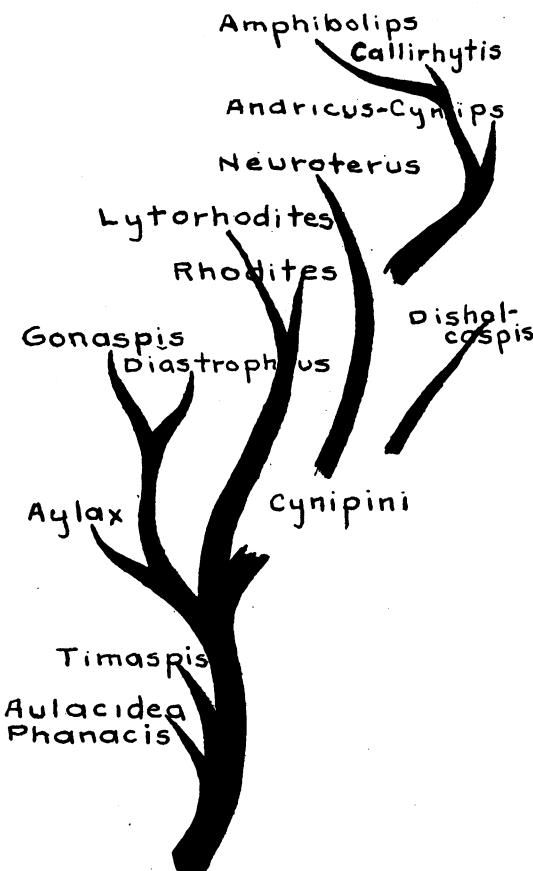


FIGURE 1. Relations of some cynipid genera.

6.—The primitive Cynipidae were bisexual species with normal, sexual reproduction. By the gradual disappearance of the male and the gradual increase of parthenogenetic reproduction, species have become agamic at several times along distinct lines of evolution within the history of the gall-wasps.

7.—Alternation of generations is a development of seasonal dimorphism, a gradual evolution incited by the differences in the nature of existence in different parts of the host plant at different seasons of the year, and achieved after a struggle for the fixation of the new generation. Agamy is not the primitive method of reproduction; it is of great advantage to the winter generation of dimorphic cynipids, and may have originated because of this.

8.—The highly specialized phenomena characteristic of the gall-wasps (gall production, agamic reproduction, and heterogeny) are of doubtful advantage, with the apparent consequences of the loss of vitality, exposure to the force of many enemies, and the ultimate extinction of the insects.

9.—*Aulacidea* and *Phanacis* are in every respect the most primitive of the *Cynipidae*.

10.—*Timaspis* is almost as primitive.

11.—*Aylax* is primitive, but shows some specialization.

12.—*Diastrophus* is derived from the *Aulacidea-Aylax* group.

13.—*Gonaspis* is a specialized development of *Diastrophus*.

14.—*Rhodites*, derived directly from *Aulacidea*, is highly specialized.

15.—*Neuroterus* is the most primitive of the *Cynipini*, and in that genus are to be discovered the incipient stages of some of the peculiar phenomena of the *Cynipidae*.

16.—*Disholcaspis*, highly specialized in most respects, shows somewhat direct relationships to more primitive groups.

The conclusions concerning the origin of the fully studied genera may be summarized as shown in figure 1.

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PLATE XXXII

Wing venation and Abdomen Characters of the Cynipidæ

First abscissa, radial vein

- Fig. 1. *Periclistus sylvestris.*
- Fig. 2. *Ceroptres cicatricula.*
- Fig. 3. *Synergus lignicola.*
- Fig. 4. *Aulacidea succinea* (fossil).
- Fig. 5. *A. bicolor.*
- Fig. 6. *A. tumida* ( $R$  = first abscissa, radial vein).
- Fig. 7. *A. annulata.*
- Fig. 8. *Aylax leavenworthi.*
- Fig. 9. *Diastrophus niger.*
- Fig. 10. *D. nebulosus.*
- Fig. 11. *D. radicum.*
- Fig. 12. *Gonaspis cuscuteformis.*
- Fig. 12a. *Neuroterus batatus bisexualis.*
- Fig. 13. *Gonaspis potentillæ.*
- Fig. 13a. *Neuroterus floccosus.*
- Fig. 14. *Rhodites multispinosus.*
- Fig. 14a. *Neuroterus vesiculosus*, ♀.
- Fig. 15. *Rhodites bicolor.*
- Fig. 15a. *Neuroterus vesiculosus*, ♂.
- Fig. 16. *Rhodites bicolor.*
- Fig. 16a. *Neuroterus irregularis.*
- Fig. 17. *Andricus coronus.*
- Fig. 18. *A. petiolicola.*
- Fig. 19. *A. furnaceus.*
- Fig. 20. *A. peredurus.*
- Fig. 21. *A. singularis.*
- Fig. 22. *A. futilis futilis.*
- Fig. 23. *A. futilis radicicola.*
- Fig. 24. *A. punctatus.*
- Fig. 25. *Dryophanta dugesii.*
- Fig. 26. *D. maculipennis.*
- Fig. 27. *D. centricola.*
- Fig. 28. *Disholcaspis globulus.*
- Fig. 29. *D. cinerea.*
- Fig. 30. *D. mamma.*
- Fig. 31. *Cynips stroblana.*
- Fig. 31a. *Andricus pomiformis.*
- Fig. 32. *Cynips caput-medusæ.*
- Fig. 32a. *Amphibolips cinerea.*
- Fig. 33. *Cynips gallæ-tinctoriae.*
- Fig. 33a. *Amphibolips gainesi.*
- Fig. 34. *Cynips calicis.*
- Fig. 34a. *Amphibolips confluens spongifi a.*
- Fig. 35. *Cynips kollaris.*
- Fig. 35a. *Amphibolips confluens aciculata.*

Abdomen of Cynipoids (II = second segment)

- Fig. 36. *Ibalia maculipennis*,  $\times 5$ .
- Fig. 37. *Aulacidea progenitrix* (fossil),  $\times 12$ .
- Fig. 38. *A. bicolor*,  $\times 25$ .
- Fig. 39. *Diastrophus nebulosus*,  $\times 16$ .
- Fig. 40. *Rhodites dichlocerus*,  $\times 20$ .
- Fig. 40a. *Neuroterus batatus bisexualis*,  $\times 25$ .
- Fig. 41a. *Amphibolips cinerea*,  $\times 10$ .
- Fig. 42. *Andricus singularis*,  $\times 20$ .

