A STUDY OF THE WINGS OF THE TENTHREDINOIDEA. A SUPERFAMILY OF HYMENOPTERA.

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INTRODUCTION.

This is a study in the phylogeny of a group of animals based on a study of the modifications of a single organ. It is an attempt to trace the course of the changes wrought by natural selection, an effort to apply the principles of descent to taxonomy.

Classifications based on the modifications of a single organ are generally imperfect. But on no single organ of any group of animals or plants has the effects of natural selection been written so clearly as on the wings of insects. The record is spread out as on a printed page and only awaits the translator. The taxonomy of several groups of insects based on a genetic study of their wings has been published, and in every case where phylogenies based on other sets of organs have been made it has been found that they confirm the conclusions derived from a study of the wings.

The Tenthredinoidea have been carefully studied by many investigators. Several classifications have been proposed, but no attempt has been made hitherto to work out an arrangement along the lines here proposed. In previous groupings a character common to a large number of forms and not common to others has been taken as of high value, while those common to a smaller number of forms as of subordinate value. No account has been taken of the question as to whether these characters include forms of one or of many lines of descent.

At the outset I wish to express my obligations to Prof. J. H. Comstock and Dr. W. A. Riley for constant advice throughout the preparation of this paper; to the authorities of the United States National Museum for the loan of specimens from their collections not otherwise accessible to me, and to Mr. J. Chester Bradley for the privilege of examining a number of species and for looking over the manuscript.

I.-HISTORICAL."

Students of wing-venation in the past almost invariably made the mistake of considering the few-veined wing as the starting point and the many-veined wing as the acquired condition. In the Lepidoptera a wing-type like that occurring in the Noctuidae or Arctiidae was considered the generalized condition, while the many-veined wings of the Hepialidae and Micropterygidae were looked upon as being at the summit of specialization in that order. In the Diptera the wing of the Muscidae was taken as the starting point, and the extra veins found in the Tabanidae and Leptidae were considered as entirely new developments and were given special names. The same view was held by writers on the Hymenoptera, where a wing type similar to that found in the Sphecidae was made use of.

Our knowledge of the homology of the wing veins of insects is due to the work of several investigators. The first one to consider this subject was Hermann Hagen. h He published a paper Ueber rationelle Benennung des Geaders in den Flügeln der Insekten, but this had little more effect than to call attention to the importance of the subject. The first serious attempt to homologize the wing yeins of insects of all orders was not undertaken until sixteen years later when Josef Redtenbacher published a paper on a Vergleichende Studien uber das Flügelgeader der Insekten, which was an epoch-making work. Unfortunately he made the serious mistake at the beginning of his investigations of adopting the conclusions of Adolph; who, from a study of the development of wing veins, had concluded that the veins were of two distinct kinds, concave and convex. The concave veins had been produced by a thinning and the convex veins by a thickening of the wing membrane; the former by a pushing in of the trachea, the latter by the formation of chitinous lines and occupied by tracheæ only secondarily. Redtenbacher believed further that the wing was longitudinally plaited, consisting of alternate ridges and grooves, the concave or primary veins being situated at the bottom of the grooves and the convex or secondary veins along the top of the ridges. considered that in the primitive insect the two wings of each side were fan-like in form and similar in venation, like the wings of the Saltatorial Orthoptera and Ephemeridae. Starting with such a manyveined type, he was successful in homologizing the main stems of the principal veins, but through his efforts to apply the theory of Adolph,

[&]quot;For extended bibliographics of papers dealing with the wing veins of insects the following should be consulted:

H. J. Kolbe. Einführung in die Kenntniss der Insecten. 1893. Pp. 269–271.

A. S. Packard. Text-book of Entomology. 1898. Pp. 147-148.

<sup>b Hermann Hagen. Stett. Ent. Zeit., XXXI, 1870, pp. 316–320.
c Josef Redtenbacher. Ann. k. k. Naturh. Hofmus., I, 1886, pp. 153–232.</sup>

dG. Ernst Adolph. Ueber Insectenflügel. 1879.

he was led into serious errors in homologizing the tips of the veins. In comparing the few veined wings of the Lepidoptera, Diptera, and Hymenoptera, where practically all the concave veins are wanting, with his primitive fan-type of wing, he concluded that fully one-half of the veins had been lost. He was the first to devise a uniform nomenclature and to apply it to all the orders of winged insects. Beginning with the front margin of the wing, the veins were named costa, subcosta, radins, media, cubitus, and anal. The convex veins were designated by odd Roman numerals, costa by I, radius by III, media by V, cubitus by VII, and the convex analyeins by IX, XI, XIII, etc., the concave veins by even Roman numerals, subcosta by II, the concave analyeins by VIII, X, XH, etc., the concave yeins IV and VI being left unnamed. The branches of the veins were designated by Arabic numerals appended as indices to the Roman numerals the Arabic indices being odd or even in accordance with whether the veins were convex or concave.

Redtenbacher in conjunction with Brauer in Ein Beitrag zur Entwicklung des Flügelgeaders der Insekten," from a study of the development of the veins in the wing of a nymph of an Æschnid, proved that both concave and convex veins are preceded by tracheæ and are therefore similar in origin and consequently completely upset the conclusions of Adolph.

Spuler in 1892 in a paper, Zür Phylogenie und Ontogenie des Flügelgeaders der Schmetterlinge, pave the results of an investigation of the tracheæ that precede the wing veins, determined the type of the lepidopterous wing, and was the first to recognize that radius in the hind wings of this order has only two branches. A modified form of the Redtenbacher notation was adopted, the veins being numbered consecutively with Roman numerals and Arabic indices regardless of their origin, Redtenbacher's veins IV and VI being entirely disregarded. Unfortunately, however, he overlooked the trachea of costa, vein I, and began his numbers with the second of the principal veins.

The following year Comstock published the results of a general investigation of wing veins, with special reference to the Lepidoptera. From a comparative study of the wings of carboniferous insects he showed that the two pairs of wings were similar in form and venation, the most generalized forms being found among the carboniferous cockroaches, where, with one exception—the anal furrow, vein VIII—all of the veins are convex, while none of the wings are plaited. He further showed that the fan-type of wing assumed by Redtenbacher as the primitive type was an extreme type of specialization for a particular kind of flight, and that instead of regularly alternating concave

^a F. Brauer and J. Redtenbacher. Zool. Anz., X1, 1888, pp. 444–447.

^b A. Spuler. Zeit. Wiss. Zool., LIII, 1892, pp. 597-646.

^cJ. H. Comstock. Wilder Quarter-Century Book, 1893, pp. 37-113.

and convex veins the concave veins are secondary in origin, being either modified convex veins or veins that have arisen de novo. The concave veins having arisen to meet two distinct needs-first, in those insects where the wings are broadly expanded so as to fit them for a sliding flight there is a necessity for a plaiting of the wings when not in use so as not to impede locomotion on foot; and second, where the width of the wings has been greatly reduced to fit them for a rapid vigorous flight and the wings have been corrugated so as to strengthen them. The concave veins IV and VI, here named "premedia" and "postmedia," respectively, were considered as wanting not only in the Lepidoptera, but also in the primitive insect's wing. They were considered to be present only in those highly specialized wings of modern insects where a corrugation of the wing has arisen. The nomenclature of Redtenbacher was adopted in all details, except that the branches of the veins were numbered consecutively with Arabic indices regardless as to whether they were convex or concave.

Packard,^a in 1895, gave an abstract of Spuler's paper mentioned above, in which the nomenclature of Spuler is followed. Apparently, if we may judge from his labeling of a notodontid wing, he has overlooked one of the most important facts discovered by Spuler, namely, that the radius of the hind wings of the Lepidoptera consists of two branches.

In a Mannal for the Study of Insects, b published during the same year, the homology of the wing veins in the orders Lepidoptera. Diptera, and Hymenoptera was carefully determined and named in accordance with the modified Redtenbacher notation. The concave veins IV and VI were shown to be wanting in these orders, but were supposed to be present as secondary developments in those orders where the fan-type of wing existed.

In 1897 Comstock and Needham c began jointly the publication of a series of articles on the wings of insects of all orders. This investigation was developed along two distinct lines and all the accessible material of all the orders of winged insects was examined. First, wherever possible, a careful study was made of the tracheæ which precede the veins in the wings of immature insects; and, second, there was made a morphological comparison of the veins in the wings of adult insects. The following important results were reached:

First. That the concave veins IV and VI are wanting in the wings of all insects.

Second. That the primitive insect's wings had comparatively few veins. These veins were eight in number. Beginning with the front

a A. S. Packard. Psyche, VII, 1895, pp. 235–241.

^b J. H. and A. B. Comstock. Ithaca, N. Y., 1895.

^eJ. H. Comstock and J. G. Needham. The Wings of Insects, Amer. Nat., XXXII and XXXIII, 1898 and 1899.

margin of the wing, they are costa unbranched, subcosta with two branches, radius with five branches, media with four branches, cubitus with two branches, and three unbranched anal veins.

Third. That the modification in the number of wing veins of insects has proceeded along two distinct lines, the specialization of wing veins by reduction and the specialization of wing veins by addition. The former is illustrated by the wings of the orders Lepidoptera, Diptera, and Hymenoptera; and the latter by the wings of the orders Orthoptera, Ephemerida, and Neuroptera.

Fourth. The development of a hypothetical wing type, which was believed to represent the maximum number, the arrangement, and the method of branching of the veins of the primitive insect's wing. This hypothetical type was shown to be of primary importance in determining the homology of the wing veins of insects of all orders.

The terminology of Redtenbacher had been applied in so many different ways by previous investigators that these writers made use of a different system of notation. They adopted the names of the stems of the veins as used by Redtenbacher and used abbreviations of these names to designate the veins, Arabic numerals being added as indices to the abbreviations for designating the branches of the veins. The abbreviations used were the following: costa, C; subcosta, Se; radius, R; media, M; cubitus, Cu; and the anal veins as 1st A, 2d A, and 3d A.

In 1902 a Enderlein, in a discussion of an abnormal specimen of Telea polyphemus gives the results of an extended investigation of the interrelation of the wing and body trachea. The trachea of each wing is divided into two systems, the radial and the medial, the former including the costa, subcosta, and radius; the latter, media, cubitus, anal, and axillary veins. It is unfortunate that this writer did not study some of the generalized Lepidoptera, such as the Hepialida. It has been amply proven that in certain of the lower orders of insects, as the Plecoptera, there are two tracheal trunks, the anterior giving rise to costa, subcosta, radius, and media; the posterior, to cubitus and the anal veins. That this was probably the primitive condition in the Lepidoptera is shown by the adult wings of certain species of Hepialus in which media anastomoses with cubitus for a short distance, bends abruptly toward the radius, joins it, and coalesces with it to the base of the wing. In most Lepidoptera this basal connection between media and radius has been lost, but the condition found in Hepialus would seem to indicate that the arrangement of the veins into systems as shown by Enderlein was probably an acquired one. He has shown conclusively that costa of both wings is

a Dr. G. Enderlein. Eine einseitige Hemmengsbildung bei Telea polyphemus vom ontogenetischen Standpunkt. Ein Beitrag zur Kenntniss der Entwicklung der Schmetterlinge. Zool. Jahrb., XVI, 1902. Part 4.

always preceded by a trachea and that in certain cases this is the most prominent trachea in the wing. The tracheal trunks behind cubitus are divided into two groups. The anterior he has called the anal group and the posterior the axillary group. The modified Redtenbacher nomenclature used by Comstock and Needham is adopted.

From a study, extending over a period of several years, of the wing-veins of the superfamily Tenthredinoidea, which contains all the generalized wings found in the order Hymenoptera, I am convinced that the homologies established for the Hymenoptera by Comstock in his Manual for the Study of Insects, and farther elaborated by Comstock and Needham, are correct, and they are accepted and followed in this paper. An attempt will be made here to explain some details of the Hymenopterous wing as exemplified by the Tenthredinoidea and not discussed by these investigators.

II. GENERAL CONSIDERATIONS.

In determining the homology of the wing-veins of insects, conclusions are reached by two different methods. First, by a study of the ontogony of the wing-veins, which consists of a careful examination of the tracheation that precedes the veins and a comparison of it with the wing-veins of the pupa and adult. As a rule, cross-veins are not preceded by tracheæ, so that this method, where it can be applied, is of the greatest importance in determining the course and extent of the principal veins and their branches. Second, by a study of the phylogeny of the wing-veins, which consists of a careful comparison of the progressive modifications found in the wings of adult insects. By this method, the accuracy of the results depend on the skill of the investigator in deciphering the record.

It has been shown by Comstock and Needham at that an ontogenetic study of the wings of the Hymenoptera is not of any value in determining the homology of the veins, and I can not do better than quote their account:

The importance of this method of study has been well shown by the results we have obtained. But we also found that in the Trichoptera there is little correlation between the venation and the tracheation of the wings, a remarkable reduction of the wing tracheae having taken place. A similar reduction of the tracheae of the wings exists in most families of Diptera; and even when a large proportion of the tracheae are retained, as in certain Asilids, they afford little aid in the determining of the homologies of the wing-veins. For this reason we omitted a discussion of the tracheation of the wings of Diptera. Again, in the Hymenoptera we find that the courses of the tracheae can not be depended upon for determining the homologies of the wing-veins. But here, in the more generalized members of the order, we find a very complete system of wing-tracheae, and it is, therefore, incumbent on us either to point out the correspondence between the tracheae and the wing-veins, or to demonstrate that such a correspondence does not exist.

a.J. H. Comstock and J. G. Needham. Amer. Nat., XXXII, 1898, pp. 421-422.

In the Hymenoptera, as we have shown, the courses of the branches of the forked veins, in those forms where they have been preserved, have been so modified that these branches extend more or less transversely, making sharp angles with the main stems. It is not strange, therefore, that the tracheæ of the wings of the pupa lying free within the wing-sac, have not followed these changes.

It was found, however, that this is not the explanation of the change. An examination of the wings of young pupe of the honey-bee revealed the fact that in this insect the laying out of the wing-venation precedes the tracheation of the wing. After the wing-veins reach that stage of development in which they appear as pale bands, the tracheae grow out from the base of the wing into them.

It is obvious that tracheæ developed in this way will follow the paths offering the least resistance to their progress; and that it is not to be expected that the tracheæ will preserve their primitive arrangement under these conditions. This brings us to the conclusion, already announced, that in determining the homologies of the wingveins in the Hymenoptera we are forced to base our conclusions on a study of the veins themselves, and that a method of study which is of the highest importance in determining the homologies of the wing-veins in many other insects, is of little use here for this special purpose.

From the results just given it is evident that we must depend entirely on a careful comparison of the wing-veins of the Tenthredinoidea, part by part, for a determination of their homology. Before considering the special modifications of wing-veins, some discussion is necessary of the manner in which the veins may be modified or reduced in number and the resultant reduction or combination of cells,

A reduction in the number of wing-veins may take place in two ways—first, by the coalescence of two or more adjacent veins; and second, by the atrophy of a whole or a part of a vein. The first method of reduction, coalescence, may proceed in three ways—first, by the coalescence of principal veins or branches from the base of the wing toward the margin; second, by the coalescence of the tips of veins or branches from the margin of the wing toward the base; and third, by the coming together of two veins at some point more or less remote from the margin of the wing and their coalescence for a greater or less distance. This third type of coalescence is generally spoken of as anastomosis. The modern hymenopterous type of wing has been produced, as will be described later, by a combination of all three of these methods.

The second method of reduction, atrophy, or the fading out of the whole or a part of a vein, is the means by which most of the changes found in the modern hymenopterous wing are brought about.

When two or more branches or any of the principal veins coalesce, this fact is indicated by placing a plus sign (+) between the abbreviations of the veins that have combined. If, for example, R_2 and R_3 coalesce, the legend would be R_{2+3} ; while if any of the principal veins combine, as R, M, and Cu, it would be written thus: R+M+Cu. This implies that not only the branches of the same vein, but that the stems of the different veins, as well as the branches of different veins, may coalesce.

The cells of the wing are named by applying to them the abbreviations of the vein forming its front margin, the group of cells at the base of the wing (fig. 1), being designated by the abbreviations of the principal veins, while the group of cells at the apex of the wing are designated by the branches of the veins. It should be borne in mind that when the vein forming the front margin of a cell is a composite one, as R_{2+3} , the cell behind this vein is not R_{2+3} , but R_3 , the cell R_2 having been obliterated by the coalescence of the veins R_2 and R_3 . When cells are divided by a cross-vein, as cell M_2 , the basal portion is spoken of as 1st M_2 and the marginal portion as 2d M_2 . In labeling the figures of entire wings, the names of the veins are put either on the veins or near them, and an arrow placed to indicate the vein to which the name applies, or at their apices around the wing margin, while the names of the cells are placed within the cells to which they apply.

All that portion of a vein that does not coalesce with any other vein is spoken of as the free part of that vein. If media be taken as an example, then all that portion of M_1 between the point where it separates from M_2 and the margin of the wing would be the free part of M_1 . In the following pages the origin of particular veins is frequently spoken of. By this is meant the point or place where they separate or fork and does not refer to the actual point of origin. If media be taken again as an example, the point where M_1 separates from M_2 would be considered as the origin of the free part of M_1 .

Although there are no facts in support of the method here given, and although it implies a condition much more generalized than is found in the hypothetical type, yet I have always found it easier in working out the homology of veins myself, and also in explaining venational problems to others, to consider each of the branches of any vein as extending from the base to the margin of the wing. If radius and its five branches be taken as an example, the stem part, always designated as R, would be considered as being a combination of all the branches of radius, or as $R_{1+2+3+4+5}$, which divides into R_1 and R_8 . In like manner the stem of the radial sector would be considered as being a combination of all the branches of the radial sector, or as $R_{2+3+4+5}$, which divides into R_{2+3} and R_{4+5} , and these in turn into R_{2} and R₃, and R₄ and R₅, respectively. So that in tracing out the course of any of the branches of radius by drawing a pencil along them, as R. beginning at the base of the wing, we would pass first over the stem of R, then over the stem of the radial sector, then over R_{4+5} , and finally over the free part of R.

III.—THE ORIGIN OF THE HYMENOPTEROUS TYPE.

In order that the reader can follow more intelligently the later discussions, the following general description of the origin of the wing of the Hymenoptera is introduced at this point. Use has been made of the following series of hypothetical figures to show how the existing arrangement of wing-veins was in all probability developed from a wing similar to that of the Comstock and Needham hypothetical type. This series begins, therefore, with this hypothetical type and concludes with a typical generalized hymenopterons wing, which is the wing of *Macroxyela ferruginea* to which has been added the free part of Cu₂. To the hypothetical type I have added the crossveins which are present in hymenopterous wings. These cross-veins are as follows:

The radial cross-vein r, situated between R_1 and R_2 ; this is wanting in the Hymenoptera only in certain genera of the Tenthredinoidea.

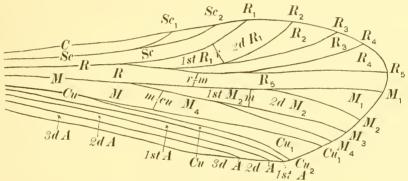


FIG. 1.—HYPOTHETICAL WING TYPE.

The radio-medial cross-vein r-m, situated between radius and media.

The medial cross-vein m, situated between M_2 and M_3 .

The medio-cubital cross-vein m-cu, situated between media and cubitus.

Beginning with the analyveins, the veins will be taken up in order, proceeding from the hind to the front margin of the wing.

The anal veins are three in number, simple, fill the anal portion of the wing, and are known as 1st A, 2d A, and 3d A. The first modification of the anal veins to be noted is the coalescence of the tips of 2d A and 3d A, resulting in the closing of the second anal cell at the margin of the wing (fig. 2). This coalescence proceeds farther and farther and the 1st A migrates toward the combined tip of 2d A and 3d A and combines with it, shoving the second anal cell toward the base of the wing and closing the first anal cell at the margin (figs. 3–4). Coincident with this apical coalescence, the base of 2d A migrates

forward to the base of 1st A, combines with it, and closes the first anal cell at base as well as at apex (figs. 4-5). The further modifications of the analyceins and cells are all the result of this coalescence continued at apex and base until the free part of 2d A appears as a cross vein just beyond the middle of the cell, while the apex of the cell bears an elongate, simple, spur-like vein formed by the combined

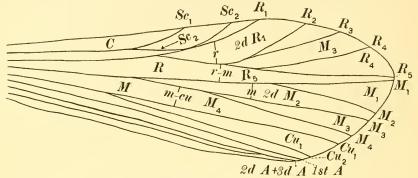


FIG. 2.-MODIFIED HYPOTHETICAL TYPE.

union of the three anal veins (figs. 7–8). We thus have formed what is known to the students of the Tenthredinoidea as the lanceolate cell, which is in reality two very different cells. The modifications of the lanceolate cell serve as excellent characters for tracing the phylogeny of the family Tenthredinidæ and for dividing it into smaller groups.

The cubitus, Cu, is a forked vein lying just in front of the three anal veins (fig. 1). The two branches of cubitus, Cu₁ and Cu₂, migrate

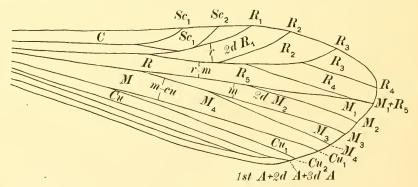


FIG. 3.—MODIFIED HYPOTHETICAL TYPE.

toward the combined tip of the anal veins (fig. 3) and coalesce with it (figs. 4-5). By this means, first, the cell Cu and then the cell Cu₁ are closed at the margin of the wing. The branches of cubitus after combining with the united tip of the anal veins, follow along the front margin of 1st A, coalescing with it more and more, and at the same time crowding the cells Cu and Cu₁ farther and farther away from the

margin of the wing (figs. 6-7). This coalescence continues until the free parts of Cu₁ and Cu₂ appear like short cross-veins near the middle of the wing. At the same time that the apices of the branches of cubitus are combining with the analyveins, the base of cubitus migrates toward the front margin of the wing, combines with the united base of radius and media (figs. 6-8), and closes the base of the cell M. With the migration forward of the base of cubitus, the combined bases of 1st A and 2d A, also migrate forward to fill the space vacated by the base of cubitus.

The media, M, lies just in front of and parallel with the cubitus (fig. 1). Near the middle of the wing it divides into two branches, each of which divides again. With the migration and coalescence of the tips of cubitus and anal veins there begins also a migration of the three posterior branches of the media (figs. 2-5). M₄ eventually combines with the combined tip of the anal veins and cubitus, closing the cell M₄ at the margin of the wing (fig. 6), migrates along this vein, and

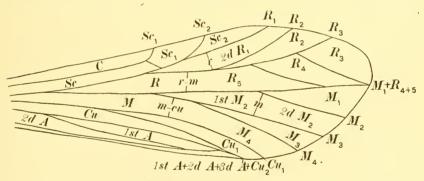


FIG. 4.—MODIFIED HYPOTHETICAL WING.

combines with the tip of the free part of Cu, crowding the cell M, back still farther from the wing margin (figs. 7-8). M₃, pulled along by the same force that combined M, with the anal veins and cubitus, migrates along the margin of the wing and combines with the tip of the spur-like vein situated at the apex of the first anal cell. In this way the cell M, is closed at the margin of the wing. The spur-like tip now consists of the combined anal, cubitus, and two posterior branches of media. The tip of the vein 1st A+2d A+3d $A+Cu_{1+2}+$ M_{3+4} has been lost, so as to permit of the folding of the posterior margin of the wing where the hooks of the hind wing are fastened. M₂, tied to M₃ by the medial cross-vein, is also pulled around the wing margin, changing from a longitudinal to a transverse position, while the medial cross-vein is transformed from a vein extending transversely to one extending longitudinally (figs. 5-7). The first branch of media maintains its primitive position near the middle of the wing throughout the entire series. The stem of media very early migrates forward and combines with the stem of radius (figs. 4-7), thus completely closing the base of the cell R. This coalescence continues until the stem of media and the stem of radius are combined for almost their entire length, while the cell R is crowded toward the middle of the wing and is found as a small trapezoidal-shaped area near the base of the stigma (figs. 7–8).

The radius, R, lies just in front of media (fig. 1). Near the middle of the wing it breaks up into five branches. In its primitive condition radius divides by a series of characteristic dichotomies, separating first into two unequal parts, R_1 , and a large part which, together with all its branches, is known as the radial sector. The radial sector divides into two equal branches, each of which in turn divide into two more branches. This characteristic dichotomy is entirely lost in the Hymenoptera. The suppression of the dichotomy of the radius has been brought about by the coalescence of the stems R_{2+3} and R_{4+5} . This coalescence has proceeded so far that the branches of the sector now arise from a common stem (figs. 2–3). With the coalescence of

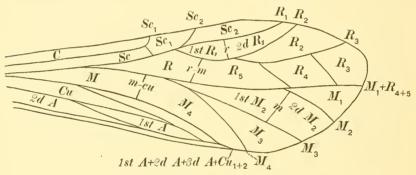


FIG. 5.-MODIFIED HYPOTHETICAL TYPE.

the stems of R_{2+3} and R_{4+5} , R_1 and R_2 begin to migrate toward the apex of the wing, to stiffen the area vacated by R_4 and R_5 , which have migrated toward the tip of M_1 (figs. 2–4). R_4 and R_5 each in turn coalesces with M_1 and closes the cells R_5 and R_4 at the margin of the wing. The coalescence proceeds farther and farther until the free parts of R_5 and R_4 appear like cross-veins extending between R_3 and M_1 , and the cells R_5 and R_4 as quadrangular areas within the disk of the wing (figs. 5–7). The primitive condition maintained by M_1 near the middle of the wing is undoubtedly due to the early coalescence of R_5 and R_4 with it and holding it in place.

The subcosta, Sc, lies just in front of the radius and parallel with it. It breaks up into two branches, Sc_1 and Sc_2 , near the margin of the wing (fig. 1). The anterior branch is preserved in practically its primitive condition throughout the series. The posterior branch bends down and touches R_1 (fig. 2), with which it anastomoses more and more (figs. 4-6), until there is only a small portion of the distal end free (fig. 7). This anastomosing of Sc_2 and R_1 divides the cell Sc_2 into

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two distinct parts, a long basal portion Sc and a small area at the apex of the small free part of the vein Sc_2 and in front of the vein R_1 . This cell in all Hymenoptera is strongly chitinized and is known as the stigma.

The costa, C, is situated on the front margin of the wing and does not undergo any marked modifications.

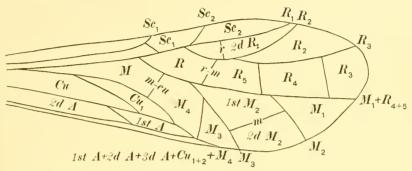
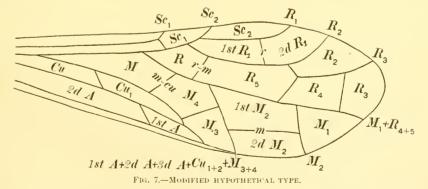


Fig. 6.—Modified hypothetical type.

Thus far there has been considered only a hypothesis as to how the most generalized hymenopterons wing known could have been formed. The data upon which this hypothesis is founded is not original with the writer but is based on facts first pointed out by Prof. J. H. Comstock in his Manual for the Study of Insects and Elements of Insects Anatomy. Let us now look at a few of these facts on which this hypothesis is based. If a careful study be made of a number of wings of the Diptera, one of the most striking facts noted will be that "there is a



marked tendency for veins to coalesce from the margin of the wing toward the base." In fact, if the wing of *Midas* (fig. 28) be examined, it will be seen that a larger proportion of the veins are coalesced at apex than in any known hymenopterous wing. If Cu₂ and 1st A be examined in the wings of *Pantarbes* (fig. 21), *Erax* (fig. 22), *Tabanus* (fig. 23), *Scenopinus* (fig. 24), *Rhamphomyia* (fig. 25), and *Musca* (fig. 26),

in the order named, there will be found a complete series showing how Cu, has combined with 1st A. It is true that only one branch of cubitus has combined with the anal vein, yet it shows how this coalescence proceeds. When the medial area of Erax (fig. 22) is examined it will be noted that M₃ and Cu₁ have coalesced at apex, crowding the cell M, back from the margin of the wing just as cell M, is pushed back in the hymenopterous wing, and it does not need a long stretch of the imagination to understand what would be the result if the vein M₃+Cu₁ were to migrate toward the apex of the vein 1st A, as has occurred in the Hymenoptera. The wing of Erax shows also how, through the combination of the apices of the veins, the medial cross-vein has been swung around from a transverse to a longitudinal position. This same condition is also shown in the wing of *Pantarbes* (fig. 21), where the medial cross vein and the first three branches of media assume a position almost identical with that found in the Hymenoptera. shows how the branches of R₅ and M₄ have coalesced, the only differ-

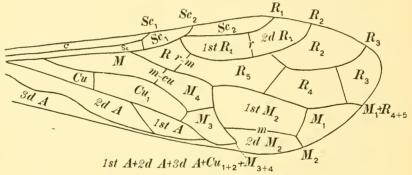


FIG. 8.—TYPICAL HYMENOPTEROUS WING.

ence in the Hymenoptera being that this condition has proceeded much farther and R₄ also has combined with M₄. This condition found in Pantarbes is not peculiar to this wing, but is also found in Pipunculus, Conops (fig. 27), most Syrphide, and many Calyptrate Muscide. wing of Midus (fig. 28) is an interesting example of how far this apical coalescence may proceed. In this wing the coalescence takes place in a different direction, but is just as pertinent to the point in hand. Here veins R₂₊₃, R₄, and R₅, have coalesced with R₁ in just the same way that R₄ and R₅ have coalesced with M₇ in the Hymenoptera, the difference being that in the Hymenoptera only two veins coalesce while in this dipterous wing three veins have coalesced and the fourth vein has migrated up to the tip of R₁. Both branches of subcosta are preserved in but very few insects and the peculiar anastomosis of Sc, and R, and the formation of the stigma are paralleled in the wings of the Plecoptera. In the genus Nemoura (fig. 29), the anastomosis extends for only a short distance, while in the genus Tachiopteryx (fig. 30), the anastomosis is for almost the entire length of Sc₂, resulting in a condition similar to that found in the generalized Tenthredinoidea.

IV .-- A STUDY OF THE WING AREAS.

As already indicated, the wings of insects may be divided into six well-marked areas, an area for each of the principal veins. It is true that these areas are closely interlocked in the Tenthredinoidea, but this seems the most logical way of approaching the subject. An attempt will be made here to describe the most important modifications found in the wings of existing genera.

1. THE FRONT WINGS.

In all insects where the wings of a side are closely fastened together for unison in flight, there is a great difference in the amount of reduction found in the two wings. It is a well-established fact that that animal whose wings approximate most nearly a triangle in outline is the most efficient flyer. For this reason it is apparent that when the wings are of this type, as in the order Hymenoptera, the hind wings are always the ones to undergo the greater amount of reduction, and consequently it has been found necessary to discuss the areas of the two wings separately.

THE COSTAL AREA.

Costa is a simple straight vein of the same width throughout in the Lydidæ (figs. 36–43), Xyelidæ (figs. 31–35), and Megalodontidæ (fig. 92). In most genera, as Dolerus (fig. 49), Pteronus (fig. 68), Blenocampa (fig. 72), and Eriocampa (fig. 47), it is decidedly thickened at apex, spatulate in outline, while in the Cimbicinæ (figs. 59–60), it is thickened throughout its entire length and lies adjacent to Sc + R + M, practically squeezing out the costal and subcostal cells.

A peculiar condition found in most of the Tenthredinoidea, though not occurring outside this superfamily, so far as I have been able to observe, is a hinge-like thinning out of the margin of the wing at the base of the stigma. It is present in all the genera except the large-bodied, active species of the family Siricidæ (figs. 86-91), and the subfamilies Cimbicinæ (figs. 59-60) and Pterygopherinæ (fig. 81). It represents the space on the margin of the wing between the apex of the costa and the point where the second branch of subcosta joins the margin. In those forms where this structure is wanting it has been chitinized secondarily, and even here its position can often be detected because the band of chitin closing the space is not so broad as it is on either side of it.

The humeral cross vein, situated at the base of the wing between costa and subcosta, is one of the most constant of the cross veins found

in the other orders of insects. In the Tenthredinoidea it is present only in *Macroxyela ferruginea*, and even here is only faintly indicated. In the Lydidæ, there is a broad thickening at the base of subcosta and a similar thickening in the Megalodontidæ (fig. 92) between costa and Se + R + M that may be homologous with this cross-vein.

THE SUBCOSTAL AREA.

Subcosta does not occur in the Hymenoptera outside the superfamily Tenthredinoidea, and here only in the families Xyelidæ (figs. 31-35) and Lydidæ (figs. 36-43). In most of the genera of these families subcosta extends midway between costa and R+M. Near its apex it divides into Sc,, which ends in the margin of the wing, and Sc,, which anastomoses with R+M and ends in the margin of the wing at the base of the stioma. Behind the stem of subcosta there is found the cell Sc and behind and beyond the vein Sc, the cell Sc,. In Megaxyela (fig. 31) and Odontophyes (fig. 32) the cell Sc, is very small, due to the great length of subcosta. Subcosta divides into Sc, and Sc, midway between the origin of media and the radial sector. In Macroxyela (fig. 33) this separation takes place just beyond the origin of media, while in the Lydidæ this separation is a considerable distance before the origin of media. These wings show that there is a progressive migration of the origin of Sc, and Sc, from near the origin of the radial sector to a position near the base of the wing. In Xyela (fig. 35) and Manoxuela (fig. 34) the stem of subcosta is closely appressed to R+M, though it is never coalesced with it, so far as I have been able to observe, almost obliterating the cell Sc and causing the branch Sc, to extend like an oblique cross-vein from R+M to the wing margin. In Neurotoma (fig. 36) the free part of Sc, has completely atrophied, while the remainder of the vein is normal. An interesting related condition is found in certain of the large species of Siricida, as Tremex columba (fig. 91), where the area of the wing situated between costa and R+M is almost as strongly chitinized as the veins themselves. In wings mounted in balsam it is possible to trace as a pale line a condition of subcosta similar to that found in Neurotoma. This seems to indicate that subcosta has been suppressed in two ways, first, by the close appression of its stem to R+M and its probable later coalescence with it, and, second, by the chitinization of the area between costa and R+M, and in this manner doing away with the necessity for a vein to stiffen this area.

In all other Tenthredinoidea, where any portion of subcosta is present, other than the apex of Sc_2 , it is the free part of Sc_1 . It extends as a cross-vein between costa and R+M, and is usually spoken of by the investigators on this superfamily as the intercostal cross-vein. It is generally situated just in front of the radial end of the mediocubital cross-vein, except in Xiphydria (fig. 85), where it is sometimes

opposite the point of origin of media, and in Dineura (fig. 63), where it is distinctly beyond the radial end of this cross-vein. An interesting modification is found in the subfamily Tenthredinina (figs. 56-58), where R+M is bent at a prominent angle at the point where it is joined by Sc, indicating a condition more closely related to the Xyelide and Lydide than is found in the other members of the family Tenthredinidæ. Sc, is best preserved in those genera where the mediocubital cross-vein and the stem of $M_{2+\epsilon}$ are strongly divergent behind. In fact, there seems to be a direct correlation between the divergence of these veins, the widening of the area between costa and Sc+R+M, and the preservation of the free part of Sc.. This is especially marked in the subfamily Nematina (fig. 68). The free part of Sc, is entirely wanting in the Cephida (figs. 93-96), Oryssida (fig. 97), Cimbicina (figs. 59-60), and numerous genera of other groups as Labidarge (fig. 78), Phyllotoma (fig. 54), Harpiphorus, and Blasticotoma (fig. 44); while in many genera, as Stromboceros (fig. 50), Dolerus (fig. 49), and Macrophya (fig. 57) there is a marked thinning out of the costal half of the vein, while in still other genera as Allantus and Athalia, there is only a slight projection on the front margin of Sc+R+M.

If the record has been correctly interpreted, the free part of Sc₁, as represented in the genus *Dineura* (fig. 63), has undergone a double migration. First, from near the stigma to the condition found in *Xyela* (fig. 35), as shown by the wings of the Xyelidæ and Lydidæ, and second, after the coalescence of the stem of subcosta with R+M, a remigration toward the stigma has resulted.

THE RADIAL AREA.

Radius divides into R_1 and the radial sector just before the stigma, of which the vein R_1 forms the hind margin, and beyond the stigma extends along just within the wing margin to or beyond the apex of R_3 .

There is only one family of Hymenoptera, the Xyelidæ (figs. 31–35), in which all the branches of radius are present. In all the families except the one named the entire free part of R_s has been obliterated.

In the genus Macroxyela (fig. 33) R_2 arises about midway between the radial cross-vein and the origin of the free part of the vein R_5 ; in Manoxyela (fig. 34) it usually arises near the apex of the cell R_5 , though in the same species it may in some specimens arise from the cell R_5 and in others be interstitial with the free part of the vein R_5 , and in Xyela (fig. 35), although it normally arises from the cell R_4 , yet it is sometimes interstitial with the free part of the vein R_5 .

The radial cross-vein is situated between the vein R_1 and the stem of the radial sector, dividing the cell R_1 into two parts. Within certain limits it is fairly constant in its position. In every case, so far as I have observed, its anterior end is joined to about the middle of

Its posterior end in the families Xvelidæ (figs. 31–35) and Cephidæ (figs. 93-96) is attached near the middle of the cell R_s; in the Megalodontide (fig. 92) and Siricide (figs. 86-91), except the genera Tremex (fig. 91) and Teredon (fig. 90), where it is joined to the cell R, it is attached just beyond the middle of the cell R; in the Lydidæ (figs. 36-43) it varies in position from just beyond the middle of the cell R_z to the apex of this cell, and in some forms is interstitial with the free part of the vein R₅, and in all other Tenthredinoidea it is attached near the middle of the cell R, except in certain species of Tenthredopsis, Scolioneura (fig. 75), Monophadnus, Lycaota (fig. 55), and Blennocampa (fig. 72), where it is interstitial with the free part of the vein R₁, and in certain species of the genus Kaliosysphinga (fig. 73), where it is attached to the cell R₃, but this latter change is not due to a shifting of the position of the radial cross-vein, but to a migration of the free part of the vein R, toward the base of the wing. The radial cross-vein is present in the wings of all Hymenoptera where the base of the radial sector is present other than those of a few groups of Tenthredinidae, Lophyrinæ (fig. 45), Nematinæ (fig. 68), Perreviina (fig. 80), Pergina (fig. 84), and Ptervgopherina (fig. 81).

The radio-medial cross-vein is rarely wanting, though in many genera it is so completely covered by a large clear spot or bulla that it is often difficult to determine whether it is present or not. This condition is well shown in many Nematina, where all stages from a distinct well-marked cross-vein to its total disappearance can be found. In other genera, as Trichiosoma (fig. 59), Clarellaria (fig. 60), Oryssus (fig. 97), Kaliosysphinga (fig. 73), Acordulecera (fig. 83), and Blusticotoma (fig. 44), all trace of the cross-vein has disappeared, while in Monoctenus (fig. 67) only the posterior half is wanting. In those genera, where this cross-vein is retained, it always appears as a transverse vein extending between the stem of the radial sector and the stem of media. In the Xyelidæ (figs. 31-35) the medial end has swung toward the base of the wing so that it appears to be a continuation of the radial sector, while a portion of the stem of the radial sector appears to be the cross-vein. In certain genera of the Siricide, as Sirex (fig. 87-88) and Tremes (fig. 91), the medial end has swung around still farther toward the base of the wing so that it arises from the angle made by the transverse and longitudinal parts of the stem of media where it is joined by the medio-cubital cross-vein, and in some species arises distinctly from the transverse part of media.

The free part of R₅ is wanting in only a very few genera, as *Dolerus* (fig. 49), *Loderus*, *Euura*, and *Tremer* (fig. 91).

The free part of R_4 so far as observed is never wanting in this superfamily. It is not so constant in position as R_5 ; in the Xyelidæ (figs.

31-35) and Lydidæ (figs. 36-43) it is an oblique transverse vein situated near the margin of the wing. In most Tenthredinidæ, as *Hoplo-*

campa (fig. 61), Cladius (fig. 66), Tenthredo (fig. 56), and Dineura (fig. 63), it is found in the apical third of the distance between the base of the stigma and the apex of the wing, while in a few genera, as Loboceras (fig. 82), Acordulecera (fig. 83), and many Hylotomine (fig. 76), it is found near the middle of this area.

In the apex of the wing of many Tenthredinoidea, as Sirex and Tremex (fig. 10, e), there is found a prominent spurlike projection from the apex of the cell R_{1+2} . The area included in front of this spur has been termed the appendiculate cell. As there is no vein forming the front margin of this cell, and as this name is in general use by the investigators on this order, it will be used here. The origin of the appendiculate cell will be more readily understood if we examine this region first in certain genera where

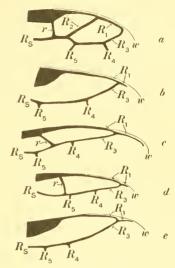


FIG. 9.—ORIGIN OF THE APPENDICULATE CELL. a, MACROXYELA FERRUGINEA; b, MONOCTENUS JUNIPERI; c, CLAVELARIA AMERINÆ; d, XIPHYDRIA CAMELUS; c, PERRYIA VITELLINA.

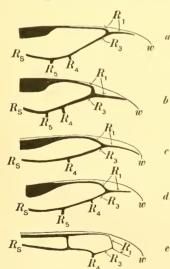


FIG. 10.—APPENDICULATE CELL. a, DIE-LOCERUS FORMONUS; b, PACHYLOTA AUDOUINI; c, PTERYGOPHORUS CINCTUS; d, LABIDARGE DIBAPHA; c, TREMEX FUSCICORNIS.

the appendiculate cell is not supposed to be present. If the front wing of almost any member of this superfamily be examined in this region, it will be noted that the portion of R, beyond the stigma does not form the margin of the wing but is set in a short distance from it. This is especially marked in the genera Macroxyela (fig. 9, a), Tenthredo (fig. 56), Monoctenus (fig. 9, b), Cladius (fig. 66), and Strongylogaster (fig. 51). It should be also noted that in all these wings R, extends beyond the point where it is joined by R₃. This is especially marked in most Cimbicina, as Clavellaria (fig. (9, c), where there is also a slight curving down of R, at the point where R, joins it. Now if this region at the apex of R. is examined in the following wings, it will be seen that the formation of the appendiculate cell is only a gradual modi-

fication of the condition existing in the wing of *Clavellaria*. In *Xiphydria* (fig. 9, d), the bending down is slightly more pronounced

yet not so prominent that systematists have ascribed an appendiculate cell to this genus. In the genera Perreyia (fig. 9, e), Dielocerus (fig. 10, a), Pterygophorus (fig. 10 e), Labidarge (fig. 10, d), Sirex (figs. 87-88), and Tremex (fig. 10, e), all of which are considered as having an appendiculate cell, there is a perfect series from the condition found in Tenthredo and Chavellaria to those genera in which the appendiculate cell is well marked. This series also shows clearly that the vein projecting from the apex of the cell 2d R₁+R₂ in Tremex is not of secondary origin but is vein R₁, which has moved in from the margin of the wing and that vein R₃ ends at the point where it joins R₁. The formation of the appendiculate cell has arisen through the necessity for a stiffening of the apex of the wing.

THE MEDIAL AREA.

The point of separation of the stem of media from radius and the position of the medio-cubital cross-vein are so intimately associated that they will be discussed together. Media is found in its most primitive condition in the wings of Manoxyela (fig. 34), where it separates from radius very nearly midway between the stigma and the base of the wing. It does not bend down at right angles, as is the case in most of the veins of the Hymenoptera, but branches off in a manner similar to that found in the branches of radius and media in the dipterous wing. This has a marked effect on the size and shape of the cell R, which is here three times as long as it is broad at its widest point. The medio-cubital cross-vein also occupies a very generalized position. It is located at the apex of the cell R, almost interstitial with the radio-medial cross-vein, while in all other Tenthredinoidea it is found at or near the base of the cell R. In Macroxyela (fig. 33) we find a slight modification of the condition found in Manoxyela. Here media has combined with radius for a greater distance, separating from radius distinctly beyond the middle of the distance between the stigma and the base of the wing, while the cell R is only about twice as long as broad. The medio-cubital cross-vein arises from near the apex of the cell R and is about the same length as the portion of media between it and radius, the two standing at about the same angle like the top of a Y. In all other Tenthredinoidea the media has coalesced with radius for a much greater distance—for at least three-fourths of that portion of radius extending between the stigma and the base of the wing. In Xiphydria (fig. 85) media arises very much as in the wings just described and the medio-cubital cross-vein is transverse and placed just before the middle of the cell R. The wing of Oryssus (fig. 97) is another interesting example. In this wing the reduction in the number of wing veins has been carried farther than in any other Tenthredinoidea, yet as regards the origin of media and the position of the medio-cubital cross-vein it is practically the

same as is found in *Xiphydria*. This is an interesting example of how very specialized a wing may be in one part while in others it may have retained a very generalized condition. In the Lydidæ (figs. 36-43) media arises in a manner similar to that just described, but the mediocubital cross-vein is always many times longer than the transverse part of media and meets it soon after it separates from radius in the genera Bactroceros (fig. 41), Cephaleia (fig. 42), Neurotoma (fig. 36), Liolyda (fig. 43), and Panaphilius (fig. 39), while in the genera Itycorsia (fig. 40), Cænolyda (fig. 38), and Lyda (fig. 37) it arises in the angle formed between radius and media. It is of interest to note that in the case of those genera where it arises in the angle between radius and media no part of the cross-vein has migrated onto radius, but that it is attached to the very base of media. In the anomalous genus Blasticotoma (fig. 44) media, after separating from radius, goes off at a right angle for a short distance and then turns abruptly toward the apex of the wing. the anterior end of the cross-vein being joined to media at the point where the abrupt bend is made and the posterior end, instead of joining cubitus almost directly behind its anterior end, as in the generalized families Xyelidæ and Lydidæ, has migrated along cubitus toward the base of the wing and extends toward media at an angle of about 45°. In most Cephidæ (figs. 93–96) media arises as in the Lydidæ and the cross-vein is in a similar position, but on first examination it appears to be very different. This is due to the migration of the basal end of the radial sector toward the radial cross-vein and the migration of the radio-medial cross-vein toward the apex of the wing, in this way greatly increasing the size of the cell R.

The modifications found in the family Tenthredinidæ (figs. 45-84) are a continuation of those just described. The cell R instead of being a large irregular area with no two sides parallel has been transformed into a small quadrangular cell with the opposite sides parallel. Media has not changed its position materially from that found in the Lydidæ and Blasticotomidæ, but the medio-cubital cross-vein is very inconstant in its location. It is usually found in a position similar to that found in *Blasticotoma* (fig. 44), extending at an angle of about 45°. The posterior or cubital end is fairly constant in position, but the anterior end, from being attached to the base of media, as in Periclista (fig. 69), swings toward the base of the wing; in Acordulecera (fig. 83), Rhadinocera (fig. 70), Loboceras (fig. 82), Monoctenus (fig. 67), and Perga (fig. 84) it is attached in the angle between radius and media; in Strongylogaster (fig. 51), Stromboceros (fig. 50), Dolerus (fig. 49), and Cladius (fig. 66) it is attached to radius just before the angle; in Macrophya (fig. 57), Pteronus (fig. 68), Hoplocampa (fig. 61), and Dineura (fig. 63) it is attached to radius for a considerable distance before the angle, and, finally, in Trichiosoma (fig. 59) and Clavellaria (fig. 60), it is attached as far distant from media as its own length, standing almost perpendicular between radius and cubitus.

In the wings just described the modifications of the origin of media and the changes in the position of the medio-cubital cross-vein marks out a distinct line of development, the changes proceeding from a

generalized to a very specialized condition.

The families Megalodontida (fig. 92) and Siricida (figs. 86-91) illustrate a very different line of specialization. In those groups, when the cross-vein reaches a position similar to that found in Xiphydria (fig. 85), it becomes fixed in its location and all further modifications are due to the migration of the base of media. With the genus Keris (fig. 89), there is a perpendicular transverse vein forming the apex of the cell M. The anterior half of this vein represents the transverse part of M and the posterior half the medio-cubital cross-vein. The peculiar condition found here has been brought about by the coalescence of the base of media with radius to a point opposite the anterior end of the medio-cubital cross-vein. This coalescence has been carried farther and farther until in the genera Tremex (fig. 91) and Megalodontes (fig. 92) the medial vein separates from radius distinctly beyond the apex of the anterior end of the medio-cubital cross-vein, while the vein forming the apex of the cell M is a fairly straight but very oblique vein with M apparently arising from its middle, as has been described.

All the branches of media are fairly constant in position and depart but little from the condition found in the typical hymenopterous wing. Only the more marked of these secondary modifications will be discussed here.

The transverse part of M, in many of the highly specialized genera of the Tenthredinidae, as Loboceras (fig. 82), Acordulecera (fig. 83), Perregia (fig. 80), and Dielocerus (fig. 79), has migrated toward the base of the wing so that the length of the medial cross-vein is greatly reduced. In Oryssus (fig. 97) the transverse part of M₂ is entirely wanting, and if it were not for the presence of the first anal cell and the interrelation of the transverse part of M and the medio-cubital cross-vein, it might be easily mistaken for the wing of a Braconid.

M₂₊₄ has undergone a slight modification in direction in many genera. This will be best understood if we look first at some of the genera of the Xyelida (figs. 31-35) and Lydida (figs. 36-43). In these genera it will be noted that if this vein were continued at the same angle to the margin of the wing that it would reach the margin at a point at or beyond the apex of the cell 1st A, while if the mediocubital cross-vein be continued it would end near the free part of 2d A. If now we examine such genera as Pteronus (fig. 68), Hoplocampa (fig. 61), Monoctenus (fig. 67), and Cladius (fig. 66), we find that with the marked migration of the cubital end of the medio-cubital cross-

vein toward the base of the wing there is a corresponding migration of the posterior end of the stem of M₃₊₄ toward the apex of the wing, and although this latter vein keeps relatively the same inclination, yet in these genera it would end at or a little before the apex of the cell 1st As was pointed out above, there seems to be a marked correlation between the divergence of these veins and the widening of the cell C, together with a usually well preserved Sc;; an exception is found in the genera Labidarge (fig. 78) and Blasticotoma (fig. 44). where the free part of Sc, is entirely wanting and cell C is hardly more than a line, but this discrepancy is due to another cause, the different way in which the stress exerted in flight is transmitted from the stioma to the anal margin of the wing, which is shown by the angulate condition of M at the origin of the stem of M_{3+4} . If now we examine another series, as Xiphydria (fig. 85) and Xeris (fig. 89), where the medio-cubital cross-vein is transverse, we find that the posterior end of the stem of M_{3+4} has migrated slightly toward the base of the wing and is parallel with the cross-vein. In Megalodontes (fig. 92), where the cross-vein is oblique, the posterior end of the stem of M₂₊₁ has migrated still farther, yet maintains its parallel course. While in such genera as Strongylogaster (fig. 51), Cephus (fig. 96), Phymatocera (fig. 71), Blennocampa (fig. 72), and Tenthredo (fig. 56), where this crossvein is strongly inclined and if continued would approximate the base of the wing, there is a corresponding migration of the posterior end of the stem of M_{3+4} toward the base of the wing which has kept pace with the cross-vein, and if it were continued it would reach the margin some distance before the apex of the first anal cell.

THE CUBITAL AREA.

The base of cubitus in most Tenthredinoidea coalesces with the combined bases of radius and media for only a very short distance, for one-fifth to one-sixth the length of the distance between the base of the wing and the apex of the cell M. The family Lydidæ (figs. 36-43) represent a marked sidewise development as regards this coalescence, where cubitus has coalesced with R+M for fully one-third of the distance between the base of the wing and the apex of the cell M.

The free part of Cu_1+M_4 is almost always found extending between the cells M_4 and 1st A. In the Lydidæ (figs. 36–43) it joins the cell M_4 at or beyond the middle and the cell 1st A on its apical third or fourth with this end always pointed toward the apex of the wing. In Manoxyela (fig. 34) it occupies a similar position except that the end joining the anal vein points toward the base of the wing, while in Macroxyela (fig. 33) it joins cell M_4 on its apical fifth and bends toward the base of the wing. It is found in Paururus (fig. 86) near the middle of the cell M_4 and on the basal third of the first anal cell; in Xeris (fig. 89) it joins the cell M_4 on its basal fourth and the

first anal cell as in Paururus; in Xiphydria (fig. 85) it joins M4 at the base, being almost interstitial with the medio-cubital cross-vein, and the first anal cell at middle; and in Tremex (fig. 91) it joins the cell M distinctly before the medio-cubital cross-vein and the first anal cell on its basal fourth. In most other Tenthredinoidea it joins the cell M, just before, at, or just beyond the middle, is either transverse or inclined toward the apex of the wing, and joins the first anal cell near the middle, except in the genus Labidarge (fig. 78), where it joins it near the apex, a secondary modification due to the coalescence of the veins at the apex of the first anal cell. In the subfamily Tenthredining it joins the cell M, at base just in front of the medio-cubital cross-vein and inclines strongly toward the apex of the wing. genera Megalodontes (fig. 92), Oryssus (fig. 97), Trichiosoma (fig. 59), and Perga (fig. 84), it is interstitial with the medio-cubital cross-vein and likewise inclined toward the apex of the wing. In the genus Perreyia (fig. 80) there is a marked convexity in the veins Cu, and M, with the convexity turned toward the analyeins, the free part of Cu, +M, starting off at the point of greatest convexity and inclining strongly toward the base of the wing. This condition seems to be characteristic of practically all the species of this subfamily.

All vestige of the free part of the vein Cu₂ is wanting except in certain species of the genera Pamphilius (fig. 39), Cephaleia (fig. 42), Bactroceros (fig. 41), Lyda (fig. 37), and Canolyda (fig. 38) of the Lydidæ, and the species of the genus Paururus (fig. 86). The position of the free part of this vein is represented in various other genera of Siricidæ, as Sirex californicus (fig. 87), by a minute spur. In the remaining genera of the family Lydidæ, where the free part of this vein is wanting, the prominent bend indicating the usual location of this vein is as prominent as in those genera where the vein is present, but even this bend is wanting in all other Tenthredinoidea.

THE ANAL AREA.

As already described, the wing area inclosed by the three anal veins has been named the lanceolate cell by the students of the Tenthredinoidea. This so-called lanceolate cell is in reality two cells, 1st A and 2d A. The front margin of the first anal cell is formed for the most part by the coalesced veins, 1st A, Cu₁, Cu₂, and M₄; its hind margin is formed by the combined 2d A and 3d A. The front margin of the second anal cell is formed for the most part by the coalesced 1st A and 2d A; its hind margin is formed by the 3d A. The cells 1st A and 2d A are separated by the free part of 2d A, which extends transversely and is generally spoken of as the cross-vein of the lanceolate cell.

The lanceolate cell is found under five different forms: First, open at the shoulder with an oblique or straight cross-vein; this is the form found in the typical hymenopterous wing and is of most frequent occurrence (fig. 11, a-d); second, open at the shoulder without a cross-vein—that is, with the free part of 2d A wanting (fig. 11, e); third, contracted at middle without a cross-vein (fig. 11, b-g); fourth, petiolate (fig. 12, a-e); and fifth, with the lanceolate cell represented only by the vein forming its front margin (fig. 81).

The origin of the cells of the anal area has already been discussed, and only the origin of the different types of cells will be considered here. The anal cells are found in their simplest condition in the families Xyelidæ (figs. 31–35) and Lydidæ (figs. 36–43). In these families the important points to be noted are, that the vein forming the front margin of this area is straight, while the vein forming its hind margin is straight on its apical half and has a prominent bend or

emargination on its basal half, known as the contraction of the lanceolate or second anal cell: that the anal veins have not coalesced at base; and that there is a short, oblique, transverse vein near the apex. This same type of cell is found in the genera Dolerus (fig. 49), Emphytus (fig. 46), Pseudosiobla (fig. 48), and Eriocampa (fig. 47), except that the emargination on the hind margin at base is not so deep while the cells themselves are not so In Blasticotoma (fig. 44) these cells are narrowed, but the portion of the vein on the basal side of the emargination has been enlarged shoulder-like. Among the Siricidæ there has been a gradual but marked change; in Xeris (fig. 89) and Paururus (fig. 11, b) the

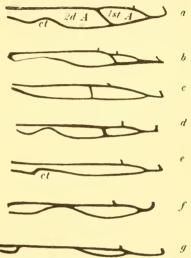


FIG. 11.—TYPES OF ANAL CELLS. α , MACRO-XYELEA FERRUGINEA; b PAURURUS CYANEUS; c, CEPHUS PYGMÆUS; d, KONOWIA WALSHII; c, STRONGYLOGASTER CINGULATUS; f, HOPLO-CAMPA FERRUGINEA; g, LABIDARGE DIBAPHA.

cells have been greatly elongated, together with a corresponding elongation of the emargination, while in *Teredon* (fig. 90) and *Tremex* (fig. 91) the emargination is so gradual that it would be overlooked if it were not for its presence in the closely related forms, while there has been developed an additional spur which extends from the apical end of the emargination toward the base and margin of the wing. In *Megalodontes* (fig. 92) these cells have been much shortened, the emargination is almost entirely wanting, while the bellying out of the third anal vein just in front of the free part of the second anal, which is only slightly indicated in the Lydida, is well marked here. In almost all those genera where there is a prominent emargination of the third anal vein at base, there is a corresponding expansion of the wing area behind the

anal veins. The Cephidæ (fig. 11, c) are an interesting example of how far the reduction of this area may be carried; in this family the emargination of the base of the third anal is entirely wanting, the free part of the second anal is perpendicular to the other veins and opposite the medio-cubital cross-vein, while the wing area behind the third anal is so greatly reduced that this vein in some species practically forms the hind margin of the wing.

The genera Derecyrta, Brachyziphus, and Konowia (fig. 11, d), of the family Xiphydriidae are described as having the free part of the second anal vein present and the third anal vein united with 1st A+2d A at the contraction of the third anal vein. The first two genera are unknown to me in nature, but the species of these genera, figured by Westwood and Kirby, show the contraction of the anal cells of the same type as found in Xiphydria (fig. 85). In Xiphydria the contraction is much deeper and the third anal approximates more closely the 1st A+2d A than in any of the other genera of the Tenthredinoidea. In Konowia walshiib the contraction is still deeper, yet the two veins do not come into actual contact with each other. Xiphydria and Konowia are of interest in showing successive stages of the anterior migration of the third anal at the contraction and to prove that at least one method of the modification of the anal cells is by the anastomosing of the veins at this point.

The anal area has been reduced in two very different ways; first, by the anastomosis of the third anal with the first and second at the contraction in the second anal cell; second, by the shortening of the free part of the second anal until the third anal comes in contact with the combined first and second anals. Thus it will be seen that in both cases the reduction is due to anastamosis, but that it takes place at a different point and in a different way.

With the exception of the genera of the family Oryssida (fig. 97), the only place where the anal area undergoes any reduction at all is in the family Tenthredinida, and even here the great majority of the genera fall under the first class. As to whether the third anal anastomoses with the combined first and second anals before or after the atrophy of the free part of the second anal, it is impossible to tell. If we base our conclusions on the Xiphydriida, the natural supposition would be that it took place before the atrophy of the free part of the second anal; but, from a careful study of this area, I have been led to conclude, because of the difference in the stages within the different families, that these modifications have arisen independently within

^aJ. O. Westwood, Thesaurus Ent. Oxoniensis, 1874. W. F. Kirby, List Hymen, Brit, Mus., Tenth. and Siric, I, 1882.

^b I am indebted to Mr. J. Chester Bradley for an opportunity to see a specimen of this species belonging to the U. S. National Museum Collections. The generic reference was made by Dr. W. H. Ashmead.

each family; and further believe, judging from the existing forms, that in the family Tenthredinidae, where there are closely related forms with and without the free part of the first anal, that this anastomosis took place after the loss of the free part of the second anal.

The type of cell, where the free part of the second anal is wanting, is illustrated by the genera *Sclandria*, *Strongylogaster* (fig. 11, e), *Stromboceros* (fig. 50), and *Thrinax* of the subfamily Sclandrina. These genera have an anal area identical with that found in the genera *Dolerus* (fig. 49), *Lophyrus* (fig. 45), *Eriocampoides* (figs. 52–53), and *Emphytus* (fig. 46), except for the atrophy of the part named, and rep-

resent the type of lanceolate cell open at the shoulder without a cross-vein.

In the genera *Hoplocampa* (fig. 11, f), Cladius (fig. 66), Monoctenus (fig. 67), Labidarge (fig. 11, a), and Hylotoma (fig. 76), the type of cells found in the Selandrina has been further modified by the anastomosis of the third anal vein with the combined first and second anal veins at the point where the third anal is deeply emarginate in the Selandrina, and consequently, with the loss of all trace of the emargination. The anastomosis varies from a short distance in Hoplocampa and Monoctenus to almost the entire length of the area in Hylotoma and Labidarge and is the type of lanceolate cell considered as being contracted at middle.

The so-called petiolate type of lanceolate cell is a direct modification of the contracted type. It is brought about

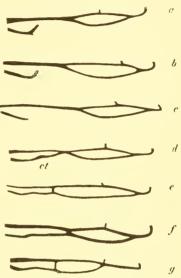


FIG. 12.—REDUCTION OF THE ANAL CELLS.

a. RHADINOCERAEA REITTERI; b. PERICLISTA MELANOCEPHALA; c. PTERONUS PAVIDUS; d. MACROPHYA ALBICINCTA; e. TENTHREDO FLAVA; f. LYCAOTA SODALIS; g. CLAVELLARIA AMERINÆ.

in two very different ways. By the atrophy of that part of the third anal vein adjacent to the basal end of the anastomosis, or by the continuation of the anastomosis of the basal part until it reaches the base of the wing. Hylotoma and Labidarge show the basal part of the second anal cell as a minute area at the extreme base of the wing while in Pachylota (fig. 77) this area is obliterated by the completion of the coalescence. Although there is no data available, yet from the shape of the anal cells in the Oryssidæ (fig. 97) it is quite probable that the reduction has taken place here in the same manner. That the petiolate type is brought about by atrophy is readily proven by an examination of the wings of Rhadinoceræa (fig. 12, a), Periclista (fig. 12, b), and Phymatocera (fig. 71), in the order named. In these wings,

the basal part of the third anal vein is preserved in every case, but is interrupted at the point where it should join the anastomosis. Pteronus (fig. 12, c) and Blennocampa (fig. 72) show a slightly later stage in which only the longitudinal part of this vein is preserved, while many genera, as Dinenra (fig. 63), show the complete atrophy of the entire basal part of the third anal, or at most it is represented only by a fold. In Perreyia (fig. 80) there is developed a peculiar spur on the posterior margin of the cell 1st A opposite the free part of M_4+Cu_1 .

The greatest reduction of the anal area is reached in the subfamilies Lobocerine (fig. 82), Pterygophorine (fig. 81), and Pergine (fig. 84), where all that remains is the simple straight vein. The members of these subfamilies, at least so far as this area is concerned, have reached the condition found in all the higher Hymenoptera. This condition has been reached by a continuation of the anastomosis found in Labidarge (fig. 78). As was shown above, the petiolate type of cell might be produced by the anastomosis of the basal part of the third anal, while the condition here is produced by anastomosis of both basal and apical parts. It is an interesting fact that the cell on the basal side of the anastomosis is bounded in front by 1st A+2d A and behind by 3d A, while the apical half is bounded in front by 1st A and behind by 2d A+3d A, so that the resulting vein is a combination of all three anal veins, which has certainly been brought about in a very roundabout manner.

The second method of the modification of the anal area, namely, by the gradual shortening of the free part of 2d A and the almost complete obliteration of the emargination of the 3d A is found only in the subfamilies Lycaotine (fig. 12, f), Tenthredinine (fig. 12, d-e), and Cimbicine (fig. 12, q). When the wings of Itycorsia (fig. 40), Lyda (fig. 37), Canolyda (fig. 38), Eriocampa (fig. 47), and Strongylogaster (fig. 51) are carefully examined there will be found at the base of the emargination a prominent shoulder, which is distinctly thickened. This shoulder is present in varying degrees in all those genera where the third anal is emarginate at base, but is especially prominent in the genera named. If, now, we examine the wings of most any member of the subfamily Tenthredinine, as Macrophya (fig. 57), we will find near the basal side of the anastomosis a slight emargination, and just beyond it a thickening. In this emargination and thickening we find the reason for our conclusions that in these subfamilies the contracted type of cells has been produced by a shortening of the free part of the second anal. This conclusion is further confirmed by the great variation in the amount of anastomosis. In the genus Macrophya alone this condition varies from a well-marked perpendicular free part of the second anal to an anastomosis for some distance. The perpendicular free part of the second anal or the anastomosis in the Tenthredinine occupies a position nearer the base of the wing than the corresponding parts in *Dolerus* or *Emphytus*, but this is undoubtedly due to the elongation and narrowing of the wing. That this position is due to the elongation of the wing is proven by the wing of *Lycatota* (fig. 55), which is broad and not at all elongated, while the anastomosis occupies a position similar to that of the free part of the second anal in *Dolerus* (fig. 49), and *Emphytus* (fig. 46). In the Cimbicina most of the genera have lost the emargination found in the Tenthredinina, but in a few genera, as *Abia*, it is prominent. Even though the emargination were wanting in all the genera of this subfamily, the general contour of the anal area in the more generalized genera, as *Cimbex* and *Trichiosoma*, would show their intimate relation to the Tenthredinina and Lycaotina. In the Cimbicina (figs. 59–60) the first anal cell is much reduced by the coalescence of the veins at its apex. In *Clavellaria* (fig. 60) this has proceeded so far that 2d A+3d A has coalesced with 1st A to just before the free part of M_4+Cu_1 .

2. THE HIND WINGS.

The hind wings of most Hymenoptera have been so greatly reduced that the primary homologies can be determined only after careful study. Once the primary homologies have been established the deter-

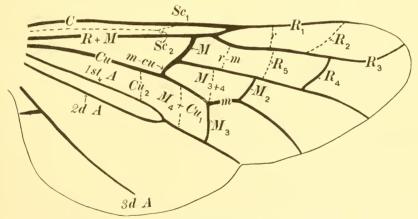


FIG. 13.—TYPICAL HIND WING WITH THE LACKING VEINS INDICATED BY DOTTED LINES.

mination of the different veins in different wings is a very simple matter. As the superfamily Tenthredinoidea contains all the hymenopterous insects in which the hind wings are at all generalized, it is apparent that a study of the wing areas of the members of this superfamily is of the first importance. Practically all the modifications found in this wing are due to the atrophy of the transverse parts of veins or to a secondary shifting of the transverse parts of veins so as to stiffen the wing more effectually. Fig. 13 represents a generalized hind wing in which the wanting veins are indicated by dotted lines.

THE COSTAL AREA.

The costal area is represented by the costa, which is present in the hind wings of practically all Tenthredinoidea as a strong vein thickened at base. So far as observed costa is wanting only in the genera Oryssus (fig. 97) and Stromboceros (fig. 50).

On the front margin of the hind wings of all Hymenoptera there is a series of hooks for fastening the two wings of a side together so that they will move as a unit during flight. These hooks are of varying extent, in the Siricidæ there is a prominent group at the base and another near the apex of Sc₂ with isolated hooks between; this same condition is found in certain Lydidæ while in others only the basal and apical areas are preserved. The Xyelidæ and Xiphydriidæ also have basal and apical areas. In the Oryssidæ there is an apical area with four or five isolated hooks just before the apical area. In most Tenthredinoidea there is only the apical area, which is likewise characteristic of the higher Hymenoptera. The apical area is of about the same extent in all the groups except the Cimbicinæ, where it extends from one-half to two-thirds the length of the cell R₁₊₂.

THE SUBCOSTAL AREA.

All vestige of the subcosta has disappeared except in the single family Lydidæ (figs. 36-43), where in the genera Lyda (fig. 37) and Buctroceros (fig. 41) it is as fully preserved as it is in the fore wing of the Lydidæ and Xyelidæ. Subcosta and its continuation, Sc., extend as a straight vein from the base of the wing to near the apex of the vein Sc₂ + R₁. The basal free part of Sc₂ is a short vein only three or four times as long as broad and in some genera, as Bactroceros, Neurotoma (fig. 36), and Pamphilius (fig. 39), it is only about as long as broad, while in the genus Cænolyda (fig. 38) it is entirely wanting. When present it is generally situated about midway of the vein R, making the cells Sc and Sc, subequal in length. The only exception observed is in the genus Neurotoma, where the free part of Se, is much nearer the apex of the wing, the cell Sc, being less than one-half the length of the cell Sc. The apical free part of Sc, has been obliterated by its coalescence with R₁ to the margin of the wing. In the genera Pamphilius, Neurotoma, Cephaleia (fig. 42), Itycorsia (fig. 40), and Lyda a considerable portion of the subcosta found between the base of the wing and the free part of Sc, has completely atrophied, the amount varying in the different genera. The conditions found in the genera just named go to show that the reduction of the subcosta in the hind wings has proceeded in a very different way from what it has in the fore wing, where the modification is clearly due to coalescence. The cell lying between costa and Sc + R + M, C+Sc+Sc₁, is broad and well marked in all the specialized Tenthredinoidea except in the family Cephidæ (figs. 93–96), where it has been completely squeezed out by the close apposition of costa and Se + R + M.

THE RADIAL AREA.

The bases of radius and media are combined in the same way as in the forewing. The single vein R+M extends to near the middle of the wing, where it divides into R_1 and R_5+M . In most specialized Tenthredinoidea the stem of R+M is only moderately thickened, but in *Oryssus* (fig. 97), the costa being wanting, the vein R+M has been excessively thickened, evidently to take up the stress that would have been transmitted along the costa.

R, combined with Sc, extends obliquely to the front margin of the wing, where it anastomosis with costa in a single point, or at most for only a very short distance, just before the apical area of hooks, then curves away from the costa and joins it again at the apex of the apical area of hooks, forming a cell Sc, homologous with the stigma of the front wings. This cell is prominent in such genera as Periclista (fig. 69), Pteronus (fig. 68), Phymatocera (fig. 71), Strongylogaster (fig. 51), Dineura (fig. 63), Dolerus (fig. 49), Tenthredo (fig. 56), and Trichiosoma (fig. 59), and is generally situated at the base of the cell R_{1+2} . In the Xyelidæ (figs. 31-35), Xiphydriidæ, Cephidæ (figs. 93-96), Megalodontide, and Blasticotomide (fig. 44), this stigma-like cell is entirely wanting, while the apical area of hooks is situated on an enlargement of the costa opposite the middle of the cell R_{1+2} . This cell is faintly indicated in the Lydidæ (figs. 36-43) and situated as in the Xvelidæ, while in the Tenthredinidæ it is generally distinct except in the more specialized subfamilies. This is especially true in those genera with an appendiculate cell. The course of the apex of R, here confirms our conclusions regarding its course around the stigma in the front wings and that the stigma is nothing more than a stronger chitinization of the wing membrane in front of R, than is found in the other cells.

The front margin of the cell R₁₊₂ in the Siricidæ (figs. 86–91), Megalodontidæ (fig. 92), Xyelidæ, Lydidæ, and Blasticotomidæ is bounded by a vein of uniform width, R₁, which, after joining the costa beyond the apex of the apical area of hooks, coalesce with it, the single vein extending along just within the front margin of the wing. It ends in the Xyelidæ (figs. 31–35), Lydidæ (figs. 36–43), Megalodontidæ and Blasticotomidæ (fig. 44), at or slightly beyond the apex of R₃ and a considerable distance before the apex of the wing. This results in a cell contour identical with that found in the front wings. In most genera of the family Tenthredinidæ, as Macrophya (fig. 56), Blennocampu (fig. 72), Stromboccros (fig. 50), Perielista (fig. 69), and Pteronus (fig. 68), R₁ likewise ends at or slightly beyond the apex of R₃, but in these genera the veins R₁ and R₃, coincident with the lengthening and nar-

rowing of the wing, have migrated to the apex of the wing, so as to stiffen it, while in the genera Blennocampa and Periclista R, extends around the apex. In the Cephidæ and Cimbicinæ R, has retained its primitive position distinctly before the apex of the wing while R, has been extended spur-like to the apex. The genus Hoplocampa (fig. 61) shows a similar condition, except that the prominent spur-like tip has not been developed. Oryssus (fig. 97), Tremer (fig. 91), Paururus (fig. 86), Monoctenus (fig. 67), Dielocerus (fig. 79), and Pachylota (fig. 77) show a modification of the condition found in Blennocampa and Periclista. In these genera R₁ and R₂ have migrated to the apex of the wing, but the apical half of the vein R, atrophied, causing the cell R_{1+2} to return to its original condition, open at the margin. The genera Xeris (fig. 89), Hylotoma (fig. 76), Labidarge (fig. 78), Perga fig. 84), Perreyia (fig. 80), and Loboceras (fig. 82) show a still different type. Here R_o ends distinctly before the margin of the wing while R, is continued to the apex, but in the course of its development was pulled away from the margin for a considerable distance, forming an appendiculate cell in the same way that it is formed in the front wing.

The second part of the vein R+M, R_s+M , very soon divides into R_s and M. In all the wings observed the free part of R_2 is wanting; also R_5 , except in the genera Megaxyela, Odontophyes, and Macoxyela. R_3 occupies a position similar to that found in the front wings; the only marked modification is the point at which it reaches the margin,

and this was fully discussed above.

The tip of the fourth branch of radius has combined with $R_5 + M_1$ as in the forewing, while the free part of R_4 is a transverse vein extending between R_3 and $R_5 + M_1$. In the Xyelidæ (figs. 31–35), Lydidæ (figs. 36–43), and Megalodontidæ (fig. 92), it is situated near the margin of the wing, but in most Tenthredinoidea it has migrated toward the base of the wing; while in such genera as Loboceras (fig. 82), Dolerus (fig. 49), Pteronus (fig. 68), and Cladius (fig. 66), it is situated in a line with the costal area of hooks. The free part of R_4 is entirely wanting in the subfamilies Blennocampinæ (fig. 72), Phyllotominæ (fig. 54), Fenusinæ (fig. 74), and the genera Tetratneura and Acidophora.

The radio-medial cross vein is wanting in all the genera observed.

THE MEDIAL AREA.

In all the wings examined, except in Sirex (figs. 87-88), and Manoxyela (fig. 34), the vein M is coalesced with the radial sector for a greater or less distance. This is very different from the conditions found in the front wing, where M always arises from R some distance before the origin of the radial sector. In Sirex and Manoxyela M arises from R distinctly before the origin of the sector, but much nearer to it than is the case in the front wings of all other Tenthredinoidea. In Paururus (fig. 86) and Xeris (fig. 89) M arises from the sector at or just beyond its origin; in Macroxyela (fig. 33) it extends

about twice as far as in Paururus; in the Lydida, Megalodontida, and most Tenthredinida it arises a considerable distance beyond the origin of the sector; while in Tremex (fig. 91), Oryssus (fig. 97), Lycaota (fig. 55), Acidophora, and the subfamily Blennocampine (fig. 72), it arises at or just before the middle of the cell R₁₊₂, but the modification found in these genera is undoubtedly due to the atrophy of the free part of R..

As soon as M separates from the radial sector it extends transversely until it joins the medio-cubital cross-vein, where it usually bends at about a right angle and extends longitudinally. About midway between its union with the medio-cubital cross-vein and the margin of the wing it divides into two branches, M, which extends direct to the wing margin, occupying a position very similar to the same vein in the front wing, and M₂, which extends transversely to near the middle of its length where it joins the medial cross-vein, from which point it extends longitudinally to the margin of the wing.

The medial cross-vein extends longitudinally toward the base of the wing, where it joins a vein which extends longitudinally or obliquely from the cubital end of the medio-cubital cross-vein. That portion of this vein which lies between the medio-cubital cross-vein and the medial cross-vein is the free parts of M₄ and Cu₁, the free part of M.+Cu, being wanting, while that portion which lies between the medial cross-yein and the tip of the analyeins is the free part of M_s. In the front wings there is a branch which extends from the stem of M and joins M, just before its union with the medial cross-vein. This is the stem of M₃₊₄ and is entirely wanting in the hind wings of all Hymenoptera. If the position of M₁, M₂, M₃, and the medial crossyein be compared with the corresponding veins in the front wings it will be seen that they occupy a similar position and are in fact the most important landmarks in homologizing the veins of the hind wings.

In Oryssus (fig. 97), Blennocampa (fig. 72), Acidophora, Perreyia, Loboceras (fig. 82), Acordulecera (fig. 83), Pterygopherus (fig. 81), and *Perga* (fig. 84), the transverse part of M, has atrophied so that the

cells M, and 1st M, are united.

The free part of M₃ in most Tenthredinoidea extends almost transversly to the margin of the wing, but in the Cephidae (figs. 93-96), Tenthredinine (figs. 56-58), and Manoxyela (fig. 34), where the anal area of the wing has been greatly reduced longitudinally, the free part of M_s has been bent abruptly toward the base of the wing. While in most genera the free parts of M₂ and M₄ are subequal in length, yet in Lobocerus (fig. 82) and Perga (fig. 84), M, is two or three times as long as M₃, while in the Cephidæ (figs. 93-96), Tremex (fig. 91), and Pterygophorus (fig. 81) M₃ is several times the length of M₄. The medial cross-vein is in most genera subequal in length with the longitudinal part of M_o, vet in Xeris (fig. 89), Tremex (fig. 91), Sericocera, and Dielocerus (fig. 79), the cross-vein is much shorter, one-third to one-fourth the length of this part of M_s.

The medio-cubital cross-vein in the generalized Tenthredinoidea is transverse and subequal in length to the transverse part of M, but there is considerable variation throughout the various genera of the other groups. Its departures from the generalized condition may be divided into five groups. In the first of these the longitudinal part of M has migrated along the transverse part of M, greatly increasing the length of the cross-vein, although the cross-vein and the transverse part of M retain relatively the same position. This is shown in the genera Trichiosoma (fig. 59), Labidarge (fig. 78), Dolerus (fig. 49), and Monoctenus (fig. 67). In the second group the length of the cross-vein has been greatly increased by the migration of the transverse part of M from its position at or near the base of the cell M₄+1st M₂ to near its middle as in the genera Tenthredo (fig. 56), Periclista (fig. 69), and Strongylogaster (fig. 51). In the Cephidae this migration has proceeded so far that the transverse part of M is joined to the cell M₄+1st M₂ near its apex. The third group is represented by the genera Xiphydria (fig. 85), Macrophya (fig. 57), Phymatocera (fig. 71), Rhadinoceræa (fig. 70), and Lucaota (fig. 55). In these genera there has been a combined migration of the longitudinal part of M along its transverse part, together with a migration of the transverse part of M toward the apex of the wing. The fourth group is represented by the genus Pterygophorus (fig. 81), where the longitudinal part of M has migrated toward M, along the mediocubital cross-vein, resulting in a distinct shortening of the crossvein. In the fifth group there has been a migration of the transverse part of M toward the apex of the wing, while the free part of M, has swung around from a longitudinal or oblique position to a transverse one. Coordinated with the change in position of the free part of M, there has been a swinging forward of the part of cubitus on the basal side of the medio-cubital cross-vein until it has come into line with the base of the longitudinal part of M, so that in this group the mediocubital cross-vein extends longitudinally instead of transversely. This is practically the same condition as is found in the higher Hymenoptera and is shown by the genera Perga (fig. 84), Perreyia (fig. 80), Acordulecera (fig. 83), and Loboceras (fig. 82).

THE CUBITAL AREA.

In the hind wings cubitus is represented by the long, straight vein extending from the base of the wing to the medio-cubital cross-vein. All trace of the free part of Cu_1 is wanting, and the same is true of Cu_2 unless we homologize the short vein found in the Xyelidæ (figs. 31-35) at the base of the wing with this vein. That this spur represents the free part of Cu_2 there can not be much doubt. That it is not

a supernumerary vein is proven by its persistence throughout all the different genera of this family. Its preservation is undoubtedly due to its position at the extreme base of the wing, and also to the fact that its anal end curves toward the base of the wing, giving it a location where its liability to be obliterated would be reduced to a minimum.

THE ANAL AREA.

The anal veins of the hind wings, like those of the fore wing, have undergone marked changes but along very different lines. Here, as in the fore wings, there has been a combination of the apices of M_3 , M_4 , Cu_1 , Cu_2 , 1st A, and 2d A, the transverse free part of the first four of these, except M_3 , being wanting. The first anal vein extends directly from the base of the wing to the transverse part of M_3 , in many cases being strongly bowed in front, and from M_3 there extends an oblique vein to or nearly to the margin of the wing. This vein is wanting in the Cephidæ (figs. 93–96), Xyelidæ (figs. 31–35), Acordulecera (fig. 83), and Blannocampa (fig. 72).

The second analyein is found in its most generalized condition in the wings of Strongylogaster (fig. 51), Tenthredo (fig. 56), Periclista (fig. 69), and Stromboceros (fig. 50), where it extends from the base of the wing as a slightly bowed vein and unites with the first analyein distinctly beyond the transverse part of M_s. In the genera *Dolerus* (fig. 49), Selandria, and Macrophya (fig. 57), the coalescence is only for a short distance in front of the transverse part of M₃. The amount of coalescence increases until in the genera Hylotoma (fig. 76) and Labidarge (fig. 78) the coalescence is for more than half the length of the anal cell. The second anal vein is entirely wanting in Xevis (fig. 89), Oryssus (fig. 97), Loboceras (fig. 82), Perga, (fig. 84), Pterygophorus (fig. 81), Perregia (fig. 80), and Acordulecera, (fig. 83). The disappearance of the second analyein is undoubtedly due to the fold in the wing just behind the line where the vein would be situated. This supposition is strengthened by the wing of *Xeris* and *Dielocerus* (fig. 79), where the transverse apical part of the stump is retained. While in Sirex albicornis (fig. 88), the basal half of the uncoalesced part is retained. In Macrosyela (fig. 33) there is a different type of modification. The second analyein is situated just in front of the furrow, is as well developed as the other veins and extends almost to the margin of the wing, where it bends abruptly forward and joins the first anal vein just before the free part of M₂. The transverse part in Manoxyela (fig. 34) is nearer the base of the wing and there has been developed in addition a secondary spur from the outer posterior angle to the margin of the wing. The Cimbicinæ (figs. 59-60) show a similar condition, except that the transverse part of the second anal is near the middle of the wing with a long spur continuous with the longitudinal part of the vein. In Macrocephus, (fig. 95) the spur is present

and the transverse part of the second anal is curved toward the base of the wing, while Cephus (fig. 96) differs only in lacking the spur.

The third anal vein is almost universally present, and extends as a slightly curved vein near the anal lobe of the wing from the base of the wing to the margin. It is represented in *Oryssus* by a fold and in *Acordulecera* by a pale band of pigment. In many of the generalized genera there is present a prominent transverse spur on its hind margin near the base of the wing, which is joined to the spiral vein, a cord-like thickening which extends along the base of the wing to the scutellum.

V.—DYNAMICAL CONTROL OF WING TYPE.

It has already been pointed out in a number of cases that certain modifications were due to mechanical causes. The wing of an adult insect is a machine purely for locomotion, and the rapidity and skill of the locomotion is directly dependent on the perfection of the machine. It is a fact that those insects are the swiftest flyers whose wings approach most nearly a triangle in outline, that is, having wings broad at base and pointed at tip. This is illustrated by the wings of the hawk-moths, the bee-flies, and the bees. The efficiency of a wing is dependent not only upon its outline but upon the arrangement and construction of its various parts. This construction consists in the arrangement of the veins in such a manner as to best fit it to withstand the stress exerted upon it in striking the air and at the same time without increasing the weight of the organ.

The different kinds of insects fly in two ways—by a soaring flight, for which a broad expanse of wing is required, and by a swift dashing flight, for which a narrow, stiff wing is necessary. It is also a fact, at least so far as insects are concerned, that those species whose wings are broad and approximate closely the arrangement of the veins found in the hypothetical type are never swift flyers, while those in which there has been a marked reduction in the number of veins, together with a trussing of that part of the wing subject to the greatest stress, are always swift flyers; that is, there is always a direct correlation between the structure of a wing and its efficiency as an organ for flight.

Where insects possess four wings, the wings of a side are generally fastened together in some manner to insure a more synchronous motion. This is accomplished in the Lepidoptera by a jugum on the hind margin of the front wing, or by a frenulum on the front margin of the hind wing, or by an expansion of the front margin of the hind wing so that the two wings overlap. These fastenings are all located at the base of the wing, and consequently can not exert much influence over the course of the veins found near the middle of the wing. With the Hymenoptera in general and the Tenthredinoidea in particular the conditions are different. The wings of the Tenthredinoidea

are fastened by a series of hooks on the costal margin of the hind wing which fasten into a fold along the hind margin of the front wing. These hooks may extend from the base of the wing to near the middle of the cell R_{1+2} , they may be arranged in two groups, one near the base of the wing and another near the base of the cell R_{1+2} , or they may be arranged in a compact group near the base of the cell R_{1+2} . In all cases this latter group is always the strongest, and being situated near the middle of the wing exerts a strong influence on the course of the veins found in this region in both wings, as will be shown later.

The path of the tip of an insect's wing during flight is that of a figure 8 (fig. 14). This has been shown by Marey and other investigators. It is a well-known fact that during flight the wings go through two distinct motions, a stroke or downward motion and a recovery or upward motion. The relation of the strike and recovery are shown on

the accompanying figure copied from Marey. The up and down motion is due entirely to muscular action while the resistance of the air "effects those changes in surface obliquity which determine the formation of an 8-shaped

trajectory by the extremity of the wing."

From a mechanical standpoint, so far as insects are concerned, the act of flight is really a simple one. The wing is so constructed that there is a rigid front margin for striking the air and "a sort of flexible sail behind," which inclines the wing at the most favorable angle. This is usually about 45°. During the downward motion the wing is expanded to its fullest extent by the resistance of the air beneath it, while during its recovery it is contracted by being folded or corrugated along the lines of the wing furrows, which in this way reduce the amount



FIG. 14.—WING TRAJECTORY.

of surface of the wing and consequently reduce the resistance during recovery.

The wings of most insects are corrugated or folded along certain lines. In many orders these furrows are so persistent that they have been named. Although they are not so constant in position as the veins, yet they occupy so nearly the same relative position that it is generally possible to homologize them. The function of the furrows in an insect's wing are twofold, to strengthen it and to make it flexible. The latter function seems to be their only use in the wings of the Tenthredinoidea. In this superfamily all the following furrows are present.

The anal furrow.—This is a longitudinal furrow extending from the base of the wing to the margin just in front of the first anal vein. It is distinct in both wings. In the front wings it separates the free parts of Cu_2 , $M_4 + Cu_1$, and M_3 from the vein behind the furrow and has undoubtedly been an important factor in causing the atrophy of the free part of these veins.

The second anal furrow.—This furrow also extends from the base to the margin of the wing. It is found only in the hind wings and is situated just behind the second anal vein. It is at the end of this furrow that there is located the emargination which eventually develops into a slit, the axillary incision, which separates off the hind angle of the wing into a lobe or alula. This alula, which always contains the third anal vein, whether it is separated or not by an incision, is always turned back under the remainder of the wing.

The medial furrow.—This is a straight furrow in many Tenthredinoidea, starting in the cell R and extending along just in front of M, to near the margin of the wing. It usually bends down near the middle of the cell R₅, so that it is close to the vein. This furrow finds its greatest development in the family Tenthredinida. In most of the genera of this family it extends along close to M, until near the middle of the cell R₅, where it subdivides into two or three branches. The posterior branch crosses M_{1+2} near its origin and passes obliquely across the cells 1st M₂ and M₃. The anterior branch passes midway between M, and R₂ to near the margin of the wing; in some cases the anterior branch subdivides, one branch extends just behind R₂, while the other extends just in front of M₁. Only a casual examination is necessary to see how important the medial furrow must be in maintaining the flexibility of this area of the wing. The so-called bulla of many writers on the Tenthredinoidea are the clear spots in the yeins where these furrows cross them.

The radial furrow.—This is a short longitudinal furrow situated just in front of the radial sector and may be a branch of the medial furrow.

The costal hinge.—This is a thin area of the front margin of the wing, situated between the apex of costa and Se₂ at the base of the stigma.

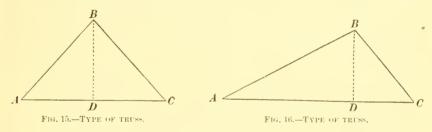
The greatest stress on a wing is always on its front or striking margin and on that part of the margin that is most prominent. In the Hymenoptera this is the region in the neighborhood of the stigma. This stress is in a plane parallel with the wing membrane. This is due to two causes, the angle at which the wing strikes the air and to the sail area—that is, approximately the posterior two-thirds of the wing, which maintains the wing-membrane at relatively the same angle. The sail area of the wing has the same effect on the wing as the tail on a kite when it is drawn rapidly through the air near the ground, causing it to maintain practically the same angle at all times.

If we examine a simple type of truss, as fig. 15, where the sides AB and BC are equal and the distance AD is equal to the distance DC, we will find that any stress exerted at the point B in the plane of the truss and perpendicular to the line AC will be equally distributed along the sides AB and BC. But if we take such a truss as fig. 16, where the

side AB is much greater than the side BC, we will find that any stress exerted at the point B will not be equally distributed, but that a much larger part of the stress would fall on the side BC than on the side AB.

We may assume that that wing is the most perfect mechanical device which approaches the closest to some type of truss. From our previous studies of the wing topography of the Tenthredinoidea we are justified in concluding that if such a thing as a truss exists in their wings it must be of the type where one side is longer than the other, for there is no point situated near the middle of the front margin of the wing to which veins converge.

Before taking up a direct comparison of the wings of the Tenthredinoidea with the types of trusses given above, we should not overlook the fact that we have to do not with a simple but with a complex type. The front wings must in reality be trussed on both sides, for the hymenopterous wing has stress exerted upon it by the air upon both front and hind margins. The primary stress is exerted at some point on the front margin where it strikes the air, while the secondary * stress is exerted on the hind margin where the hind wings are hooked



to it. This secondary stress is due to the necessity for a synchronous motion and to the fact that the hind wing must be pulled along. The force exerted on the front margin of the front wing would be a push or a force causing retardation, while the force exerted on the hind margin of the front wing and the front margin of the hind wing would be a pull or a force causing acceleration.

A clearer conception of the arrangement of the trusses in the hymenopterous wing will be had if we study first in some detail the topography of a wing in which these structures are self-evident. For this purpose a front wing of *Blennocampa alternipes* has been selected, tracings from a photograph have been made, and the trusses found in these wings marked as triangles by means of dotted lines (fig. 17). For convenience in following the course of these triangles on the figure they have been numbered, the same number being placed on each side of the same triangle. For the sake of brevity they will be referred to in the following descriptions by these numbers.

From what has already been said, it would be expected that these trusses should arrange themselves into three groups, the first strength-

ening the stigmatal region of the front wing, the second, the apex of the first anal cell of the front wing, and the third, the stigmatal region of the hind wing. The stigma, as already shown above, is the cell Sc, in which the wing membrane is almost as strongly chitinized as the veins surrounding it. In generalized genera it is a broad ovate area, which undergoes a great reduction in the highly specialized genera until it becomes a long, narrow cell, pointed at both ends. It is located at the point where the greatest stress is exerted, and is in reality a solid truss placed like a cap over this area subject to the greatest stress. So that we have in the shape of the stigma a readily observed criterion for judging the efficiency of the flight of any species, and therefore the degree of specialization to which the species has attained. Now if the stigmatal region of the front wing is examined, the following conditions are found. A large truss, truss 1, whose apex is near the middle of the stigma, with one of its basal angles at the base of the wing, and the other at the apex of R_s. Truss 2 has its apex near the

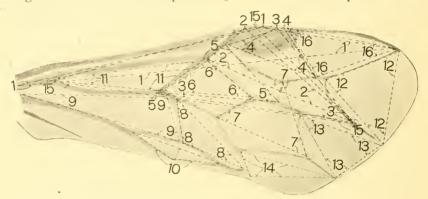


FIG. 17.—THE FRONT WING OF BLENNOCAMPA AND ITS TRUSSES.

base of the stigma, with one of its basal angles at the point of separation of R and M, and the other in the angle formed by R_4 and M_1 . Truss 3 has its apex near the middle of the stigma with one of its basal angles in the angle between the medio-cubital cross-vein and cubitus, and the other in the angle formed by R_4 and M_1 . Truss 4 has its apex near the apex of the stigma with one of its basal angles at the point of separation of R_4 and R_8 , and the other in the angle formed by the radial cross-vein and R_{3+4} . Truss 5 has its apex in the angle formed by R_4 and R_8 with one of its basal angles in the angle formed by R and M. Truss 6 has its apex in the angle formed by R and M, with one of its basal angles in the angle formed by the medio-cubital cross-vein and cubitus, and the other in the angle formed by R_4 and R_8 and R_8 with one of its basal angles in the angle formed by the medio-cubital cross-vein and cubitus, and the other in the angle formed by R_4 and R_8 and R_8 arises, with one of its basal angles in the angle formed by R_8 arises, with one of its basal angles in the angle formed by R_8 and R_8 arises, with one of its basal angles in the angle formed by R_8 and R_8 and R_8 arises, with

in the angle formed by the medial cross-vein and M_z . Of the seven trusses here enumerated, four of them have their apices in the stigma, while the remaining three have their apices so situated as to be a direct support to the trusses ending in the stigma. This does not take into account the thickened costa and the radio-medial cross-vein, which are also additional supports to this region, while truss 9, which is behind cubitus, is the main support of the stress transmitted by trusses 2, 5, and 6. Although each of these trusses is here described as a separate entity, yet the fact should not be overlooked that there is a direct interrelation between all the trusses. Each is dependent on the other. It is like the side of a bridge, composed of a complex of rods and beams that to the casual observer do not bear much relation to each other, but yet can be resolved by the engineer into a series of simple trusses, all directly interrelated in the same way as the trusses described here in this wing.

The anterior three-fourths of the wing being so strongly braced, there is no necessity for so perfect a bracing in the region of the first anal cell, because the stress exerted at this point can not be great, and in addition the stress is applied at a point where it can be easily disseminated. There are three of these trusses, though only two of them are directly connected with the anal area. Truss 10 occupies the first anal cell, with its apex directed toward the hind margin of the wing and opposite the point where the hooks of the hind wing fasten into the fold of the fore wing. Just in front of the apical half of truss 10, with its apex at the middle of the base of truss 10, is truss 8, with one of its basal angles at the apex of M3 and the other at the angle formed by M_4 and $M_4 + Cu_4$. It is of interest that the stress sustained by truss 8 is not transmitted directly to the front margin of the wing, but is disseminated over its apical two-thirds. The stress transmitted by the vein $M_1 + Cu_1$ one side of truss 8, is taken up by truss 11, which has its apex almost opposite this vein. The medio-cubital cross-vein is an excellent example of the interrelation of these trusses. It is an important factor in two trusses transmitting stress from the stigmatal region, and is equally important in transmitting stress from the anal region toward the base of the wing.

It is not necessary to discuss the trusses of the hind wings in any detail. A glance at the figure of a wing (fig. 81) is sufficient to show that all the principal trusses are behind the costal area of hooks. They are all arranged so as to spread the stress over as wide an area as possible and also to stiffen the wing membrane, for one of the principal functions of the hind wing is to furnish sail area.

In the preceding description no account has been taken of trusses 12, 13, and 14. They are not of primary importance, but serve to dissipate the stress transmitted from the stigmatal and anal regions, and to keep the membrane or sail part of the front wing expanded.

When the conditions existing in such a wing as Blennocampa alternines are compared with those found in the front wing of Macroxyela ferruginea the difference is very apparent. The trusses in the wing of Macroxyela have not been numbered. Only the most important have been indicated. From their fewness in number the reader might be led to conclude that the wing of Macroxyela had not been done full justice, but when the form of the cell areas is taken into consideration, all of them being either trapeziums or trapezoids in form, it is seen that this arrangement is one of the weakest possible. In such an arrangement as this each angle of each cell is the apex of a truss, which can have no other function than to stiffen the sail area. Consequently, if all the trusses found in the wing of Macroxyela had been indicated on the drawing, it would have resulted in this wing being apparently much more efficient, at least in number of trusses, than that of Blennocumpa. Although there are several trusses in the wing of Macroxyela, yet it is a striking fact that these trusses are not nearly

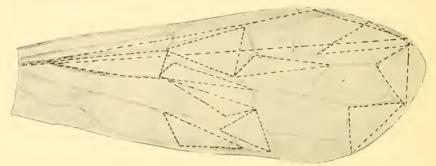


Fig. 18.—The front wing of macroxyela and its trusses.

so efficiently placed (fig. 18). There is not so great a concentration of the stress to one region. The trusses instead of stiffening a definite area are scattered over the entire wing surface. Veins that in Blennocumpa are constituents of important trusses are of little more value than to keep the wing membrane expanded in Macroxyela. Some of the most prominent differences are the position of the mediocubital cross-vein and the origin of M_1 , the course of the veins bounding the cell M_3 , the position of the radial cross-vein, the narrowing of the cells included between the veins R_3 and M_1 , and the course of the transverse part of M_1 .

The adults of *Macroxyela ferruginea* are common at Ithaea. The larvæ feed on the leaves of the numerous elms found along the walks on the campus. The adults are very inactive, so much so, in fact, that they will lie still and allow themselves to be crushed underfoot on the walks. When they are disturbed in such a way as to be compelled to use their wings, they have a slow lumbering flight and soon alight again;—that is, the generalized condition of their wings as

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regards the number and arrangement of their veins and trusses is confirmed by field observations that prove that this insect not only has wings that are poorly fitted for a rapid flight, but that in fact it is an extremely poor flyer.

If now the different groups representing families and subfamilies be examined, beginning with the more generalized, it will be found as we proceed from generalized to specialized that there is a gradual approximation to the type described for Blennocumpa, while in other groups more specialized than Blennocampa that the conditions are even more perfect than in this genus. These modifications are readily traceable in the change in position of the radial cross-vein, its posterior end swinging toward the apex of the wing and forming one side of a truss behind the stigma; the moving of the medio-cubital cross-vein from a position between media and cubitus, where it is only of secondary importance in transmitting stress, to a position between radius and cubitus, where it is of primary importance; the migration of M.+Cu, until it is practically in line with the mediocubital cross-vein; the shortening of the radio-medial cross-vein and the free parts of R₅, R₄, and R₂, in this way greatly strengthening the area lying between the most important areas of trusses, those of the stigma and those of cell M₄. The reduction of the anal cells of the front wings, the second anal cell being of only secondary importance, the base of the third analyein is gradually atrophied, and the wing membrane occupied by it reduced until the petiolate type of cell is obtained, which is gradually modified further by coalescence, and the further reduction of the wing membrane until the condition existing in the higher Hymenoptera is reached by certain subfamilies of the family Tenthredinide. The migration of the apex of R, away from the margin of the wing, forming an appendiculate cell, to a position opposite the apex of the wing. Those genera in which this type of cell has been developed have their wings greatly elongated, and the migration of R_i is to stiffen this increased sail area.

The migration of the transverse parts of the veins, due to an effort to form more efficient trusses, results in a marked modification of the position of these veins, and one of frequent occurrence. Where there is a secondary change in the position of veins, it can generally be told by a comparison with the generalized forms. This is shown in the wings of Pachylota (fig. 77), Labidarge (fig. 78), Lohoceras (fig. 82), and Perga (fig. 84), where the transverse part of M_z has migrated along $R_z + M_{z+z}$ on one side and along the medial cross-vein on the other.

When the wings of the Lydidæ (figs. 36-43) or Xyelidæ (figs. 31-35) are compared with those of *Blennocampa*, one of the most noticeable features is the great number of veins. The greater efficiency of the truss system of the wings of *Blennocampa* over that of the many

veined wings would seem to indicate that the extra veins are a hindrance rather than an aid in stiffening the wing. This is confirmed by the fact that they have been suppressed. If these superfluous yeins are a hindrance in the formation of trusses, they are also in the way in the development of wing furrows as will be seen by an examination of any of these or similar generalized forms. In the generalized wings the wing furrows are straight folds, permitting of only the minimum amount of flexibility, while in Blennocampa (fig. 72), Lucaota (fig. 55), and Labidarge (fig. 78), they have been developed to their full extent. These wing furrows are undoubtedly the primary factor in effecting the suppression of such veins as the radial crossyein, the radio-medial cross-vein, and the free part of R₅ in the front wing; and the transverse part of M, the free part of R, and the transverse part of M, in the hind wing. The way in which the radial furrow has effected the radial cross-vein is seen in the wings of *Dineura* (fig. 63), and Rhadinocerea (fig. 70), where the cross-vein is gradually losing its chitinization through the prominence of this furrow. The effect of the median furrow on the radio-medial cross-vein is seen in the wings of Eugra, Pteronus (fig. 68), Cladius (fig. 66), and Pristiphora. In this latter genus there exist all stages from a fully preserved radio-medial cross-vein to its entire disappearance. In the genera Monoctenus (fig. 67) and Lophyrus (fig. 45) an intermediate sidewise development is shown in certain species where only the posterior half of the cross-vein has atrophied, while the anterior half is fully preserved.

That the loss of the free part of Cu, is due to the anal furrow is seen by an examination of the wings of the following genera in the order named: Bactroceros (fig. 41). Pamphilius (fig. 39), Cephaleia (fig. 42), Lyda (fig. 37), Cænolyda (fig. 38), and Itycorsia (fig. 40). In these genera there is a complete series from a fully formed Cu, to a minute swelling on the side of Cu. The anal furrow is the most important as well as the most prominent and persistent furrow found in either wing. It is found in the same position throughout the entire order Hymenoptera. It is this furrow that furnishes the flexibility in movement between the two wings. Cu, having been separated from the analyeins by this furrow, could be of only secondary importance in supporting this area; in fact it is more efficiently supported in the wing of Blennocampa without it than it is in the wing of Bactroceros with it. The series here named shows that we have a gradual movement toward the assumption of the condition found in Blennocampa. This is shown in the straightening of that part of cubitus situated between the medio-cubital cross-vein and the base of the wing, and the migration of the anterior end of the medio-cubital cross-vein from a union with media to a union with radius, by this movement coming into direct line with the subtransverse part of radius. Correlated with these changes, though not necessarily due to the same cause, is the migration of the posterior end of the radial cross-vein toward the

apex of the wing.

The costal hinge as shown above is a thin place in the membrane of the wing between the apex of costa and the tip of Sc.. This is undoubtedly a weak place in the wing that has been handed down from generalized progenitors which did not require such an efficient organ for flight. That it is a weak place in the wing is shown by the fact that in those forms that are especially efficient flyers this area has been bridged over. This is the case in the Cimbicina (figs. 59-60), the Siricidæ (figs. 86-91), the Cephidæ (figs. 93-96), and in all the higher Hymenoptera. In other forms this weakness has been overcome by a decided thickening of the apex of costa, which simply rests against R.+Sc, and the stigma, but never coalesces with them. The hinge is especially prominent in those genera with a broad area between costa and Sc+R+M, and probably serves to make this region more flexible. That the prominence of the hinge in these genera is for flexibility is emphasized by the fact that the apex of the costa is not decidedly thickened. This causes a fold in the wing membrane between costa and Sc+R+M very similar to the furrow found in this same region in the Diptera, and consequently tends to stiffen it.

In the wings of *Oryssus* (fig. 97) occurs the greatest amount of reduction found in the wings of any member of the superfamily Tenthredinoidea. It is an interesting fact that the reduction found in this genus is not amenable to any of the explanations already given. In *Oryssus* the membrane of the wing has been more strongly chitinized than in the wings of other genera, and with the increased chitinization of the wing membrane the necessity of veins for stiffening the membrane has been done away with, and consequently they have gradually disappeared, being represented only by bands of pigment.

Although it is not within the scope of the present paper, yet it may not be ont of place to say something about the dynamical control of the wing type in those orders where approximately all the veins are parallel and extend lengthwise or approximately lengthwise of the wing. This is especially true of the orders Lepidoptera and Diptera.

Among the members of the order Lepidoptera the wings are broad and long. The stress exerted on the front margin of the front wings is not applied at one point as in the Hymenoptera, but is spread out along the entire front margin of the wing. Another point that must not be overlooked is the fact that there is no marked necessity for a transverse stiffening, because this is accomplished by the overlapping scales covering both surfaces, which stiffen it in the same manner that the overlapping shingles stiffen a roof. The great majority of the trusses in this order have their apices near the apex of the cell R+M and their basal angles at the margin of the wing. They serve merely

as ribs for stiffening the wing membrane and keeping the sail area of the wing expanded. If the wings of such generalized families as the Hepialide, Pyromorphide, Megalopygide, and Eucleidae be examined, it is found that this elongate type of truss is present not only on the hind but also on the front margin of the wing. But in the wings of the specialized families, Sphingide, Saturniidae, Papilionidae, and Nymphalidae, which are noted as being rapid flyers, there is a very different condition. In these families all the branches in front of vein R_5 have been crowded close to the front margin of the wing, forming a compact series of five stiff braces for supporting the area subject to the greatest stress.

In the Diptera, as in the Lepidoptera, the stress is applied along the entire front margin of the wing, but in the wings of this order the covering of overlapping scales is wanting. As there is only one wing on each side of the body, and this is sublanceolate in outline, the factor of a sailing surface is reduced to the minimum. Since the stress is applied along the entire front margin, and there is no posterior wing to exert any influence, there has not arisen any necessity for a transverse stiffening across the middle of the wing. In the generalized families the veins radiate out from the center of the wing to the margin somewhat like the spokes around the hub of a wheel. The reason for this is seen in the necessity for the stiffening of all parts of the wing. Most of the species are light bodied, and consequently the wing membrane is delicate and the wings light in weight. Those species that are predacious or hover about flowers are generally very active flyers. In these families there has been developed a marked tendency toward the coalescence of the tips of the veins, so as to prevent the fraying of the wing margin. There has also been developed along the front margin from the base to the apex of the wing a heavy vein in which the longitudinal veins terminate. This is especially marked in the families Bombyliidæ (fig. 21), Apioceridæ, and Midaidæ (fig. 28), where the tips of all the branches of radius curve forward and terminate close to the wing margin, thus accomplishing the double purpose of protecting the wing margin and at the same time stiffening that part of the wing subject to the greatest stress. The wing of Midas, which has been referred to before because of the great number of the tips of its veins that have migrated forward, illustrates this point well. It shows how the stress applied on the front margin of the wing is transmitted to the base along the radial stem, while that on the hind margin is transmitted along the medial stem. We find here the reason for the coalescence of the branches of the radial sector to R, rather than to M, as happens in the Hymenoptera; namely, because the stress in this wing is applied only on its front margin, and there is a greater need for a stiffening in this direction. That this is the correct interpretation is shown by the change in the contour of the

front margin of the wing of *Midas* as compared with that of *Pantarbes* or *Erax* (fig. 22), *Midas* showing the highest type of efficiency, a long, narrow triangle.

VI.—THE PHYLOGENY OF THE TENTHREDINOIDEA.

It is essential in determining the phylogeny of any group to ascertain what are the most primitive forms, to compare them, and to determine the ways in which they have been modified. In making these comparisons the structure of a set of organs should be studied and the phylogeny of the group determined from this study; then other sets of organs should be examined, until all the organs of the animal have been examined, phylogenies based on these studies should be made, and then compared with the phylogeny first determined. If it is found that these successive phylogenies corroborate each other, we have a demonstration of the correctness of our conclusions. If they disagree, then there is indicated a need for a further examination of the disagreeing forms, for when correctly interpreted it will be found that the different records of the action of natural selection will not contradict but confirm each other. In the following pages the first step in such an investigation, a phylogeny based on an examination of the wings of the Tenthredinoidea, is given.

There arises, in working out the phylogeny of any group, the necessity for distinguishing between different kinds of characters.

First, characters indicating difference in kind of specialization; and second, characters indicating difference in degree of specialization of the same kind. The former will indicate dichotomous divisions of lines of descent; the latter merely indicate degrees of divergence from a primitive type. Thus, it is shown that there are two distinct ways of uniting the two wings of each side in the Lepidoptera; they may be united by a frenulum, or they may be united by a jugum. These are differences in kind of specilization, and indicate two distinct lines of descent or a dichotomous division of the order. Among those Lepidoptera in which the wings are united by a frenulum great differences occur in the degree to which this organ, or a substitute for it, is developed; such differences may merely indicate the degree of divergence from a primitive type, and may need to be correlated with other characters to indicate dichotomous divisions."

There is also a necessity, as is shown by Comstock, to distinguish between the characters used by systematists merely to make it possible for students to recognize the members of a group—recognition characters and the essential characters of a group. The essential characters of a group are not necessarily dependent on the presence or absence of any character or in the form of any part of the body, but on the characteristic structure of the progenitor of the group and the direction in which the descendants of this progenitor have been specialized. Recognition characters are generally those first observed and used by the systematist. They may also be essential characters,

^a J. Il. Comstock. Evolution and Taxonomy, Wilder Quarter Century Book, p. 42.

but as a rule taxonomists search only for characters indicating a difference in kind.

Specialization may take place in two very different ways—"first, by an addition or complication of parts, specialization by addition; second, by a reduction in the number or in the complexity of parts, specialization by reduction." The specializations to be considered later are all of this latter type.

It should also be borne in mind that when an organ disappears in any phyllum or line of ascent it can not reappear in the descendants of this phyllum, though they might develop a substitute for it. Even if such a substitute should be developed, it is not probable that the substitute would resemble the organ so closely as to be mistaken for it.

In determining the phylogeny of any group, those characters indicating a difference in degree of specialization of the same kind are the most useful in allotting the rank of the different groups. Every large group has numerous characters indicating a difference in degree of specialization of the same kind. Certain of these characters show the ascent of the group as a whole, while others show only small lateral lines of ascent or a sidewise development. Characters indicating a sidewise development frequently arise independently several times, and do not indicate anything as to the line of ascent of the group as a whole. This is illustrated by the presence or absence of the radial cross-vein in the families Xiphydriida (fig. 85) and Tenthredinida. The presence or absence of this cross-vein is of value in indicating the line of ascent of the genera of each of these families, but is worthless so far as indicating any rank between the families themselves. Therefore care must be taken to differentiate between those characters that show the ascent of the group as a whole and those characters that show only a sidewise development.

The front wing of the original progenitor of the Hymenoptera, and therefore of the Tenthredinoidea, was undoubtedly very similar to the one already described as the typical hymenopterous wing (fig. 8). This wing contains not only all those parts that are generally wanting in the Hymenoptera, but the various parts are arranged in the most primitive condition known to us, as can readily be seen by comparing this wing with those of the Xyelidæ (figs. 31–35) and Lydidæ (figs. 36–43). No hymenopterous wing contains all the veins shown in the typical wing, but by combining the wings of the families just named the wanting parts can be readily supplied.

The characters that have been found the most useful in determining the ascent of the Tenthredinoidea are the position of the radial crossvein, the position of the medio-cubital cross-vein, and the reduction of the anal cells of the front wings.

Hitherto the special modifications of the wing veins of the Tenthredinoidea have been considered in detail, particularly with respect to the way in which the progressive modifications of each part has arisen. Let us now consider the interrelation of the various parts in its bearing on the phylogeny of the group as a whole, and its bearing on the relation of the Tenthredinoidea to the other superfamilies of the Hymenoptera.

The superfamily Tenthredinoidea is a homogenous group easily demarcated from all other Hymenoptera by several structural characters other than those found in the wings. The effect of natural selection on their wings has tended to modify them along so many different lines that it would be strange if we should find any single character that would circumscribe the group. This has been found to be true,

though the separation of the group is readily accomplished by the employment of several coordinate characters.

As has already been pointed out several times, the superfamily Tenthredinoidea contains all those genera of the Hymenoptera that are especially generalized, as the free part of the veins R., Cu., 2d A, and 3d A is found only within the limits of this superfamily. The great majority of the members of this superfamily can be distinguished by the presence in the front wings of either the second or third anal cells or both. In a few subfamilies of the

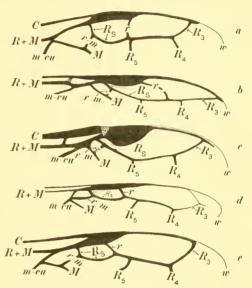


FIG. 19.—THE BASE OF THE RADIAL SECTOR. a, C.ENOLYDA SEMIDEA; b, TENTHREDO FLAVA: c, CLADIUS PECTINI-CORNIS; d, PAURURUS CYANEUS; e, MEGALODONTES SPISSI CORNIS.

family Tenthredinidæ both of these cells are wanting. But these subfamilies, Incaliinæ, Acordulecerinæ (fig. 83), Lobocerinæ (fig. 82), Pteryogphorinæ (fig. 81), and Perginæ (fig. 84), of which only the second is represented in our fauna, are easily distinguished by the position of the medio-cubital cross-vein, which always extends between radius and cubitus, while in all other Hymenoptera other than the Tenthredinoidea, and even in certain members of the Tenthredinoidea, as has already been shown, this cross-vein always extends between media and cubitus. Other minor differences that should be noted are the preservation of a much greater number of veins in the radial and medial areas of the hind wings—this is true even in those subfamilies in which the anal cells of the front wings have been suppressed—and the preservation of the third anal vein

of the hind wings, which appears to be wanting only in the genus Oryssus (fig. 97).

The most notable difference is found in the condition of the base of the radial cross-vein. The radial sector separates from R, at or before the base of the stigma. This is shown in the wings of Macroxyela (fig. 33) and Canolyda (fig. 19, a), where the radial sector, after separating from R₁, extends transversely for a considerable distance before extending longitudinally. The radial cross-vein in Macroxyela is a perpendicular vein extending from near the middle of the stigma to near the middle of the cell R_z. In Bactroceros (fig. 41) this crossvein joins the stigma near its apex and the cell R₅ near its apex. In the genus Tenthredo (fig. 19, b) the radial sector likewise arises from the base of the stigma, but differs from Macroxyela and Canolyda in that the base of the radial sector does not extend transversely, but extends from R₁ along R₃ to the margin of the wing in a continuous regular curve. The anterior end of the radial cross-vein is beyond the middle of the stigma, as in Buctroceros, and the posterior end has migrated to near the middle of the cell R₄. Cladius (fig. 19, c) shows a condition similar to that found in Tenthredo, except that the radial cross vein has atrophied, but it should be noted that in both of these genera—the one with a radial cross-vein, the other without—the radial sector arises in exactly the same manner. In Paururus (fig. 19, d) the radial sector arises in a similar manner to that of Macroxyela and Cænolyda, except that the transverse part is not so prominent. The radial cross-vein extends between the apical third of the stigma and the apical third of cell R₅. It should be noted that this cross-vein is parallel with the transverse part of the radial sector and appears to be the direct continuation of that part of the radial sector beyond it. This appearance is emphasized by the position of the posterior end of the radio-medial cross-vein, which has migrated along the base of media until it has come into line with the longitudinal part of the radial sector, so that one not very familiar with the topography of this area might easily make the mistake of considering this yein as arising at the posterior end of the radio-medial cross-vein and the basal or transverse part of the radial sector, as well as the radial cross-vein, as cross-veins.

The wings of Megalodontes (fig. 19, e) are shorter and more compact, and there has been a crowding of the cells R, R₅, 1st R₁, and M₄ into the area behind the stigma, resulting in a condition similar to that found in Panrurus. There are the following differences, however: The transverse part of the radial sector and the radial crossvein are longer; the cross-vein is more oblique, and the appearance that it is the base of R₃ is more strongly emphasized; and the radiomedial cross-vein appears to be the continuation of the vein extending from the posterior end of the radial cross-vein to the anterior end

of the radio-medial cross-vein, the entire vein appearing as a transverse vein comparable to the free part of R₅. In Macrocephus satyrns (fig. 20, a) there is a further modification of the condition found in Megalodontes; the cells 1st R₁ and R are about equal in length, so that the vein forming their outer ends, which extends from the posterior end of the radial cross-vein to the posterior end of the radio-medial cross-vein, is but little longer than the free part of R₅, and is only slightly angulate. The fact should not be lost sight of that this vein is a composite one, being made up of the radio-medial cross-vein and a part of

the radial sector. In this wing the cell 2d R, + R, is much longer, and the inclination of the radial crossvein, together with the course of the vein forming the apices of the cells R and 1st R. emphasizes the fact still more strongly that it might be the base of R_a instead of the radial cross-vein. That part of the radial sector extending from the base of the stigma to the anterior end of the radio-medial cross-vein in this wing extends almost longitudinally. In Janus cynosbati (fig. 20, b), the base of that part of the vein just described has faded out for a short distance near the stigma, while in Janus abbreviatus (fig. 20, c) the base of this vein has faded out for over half its

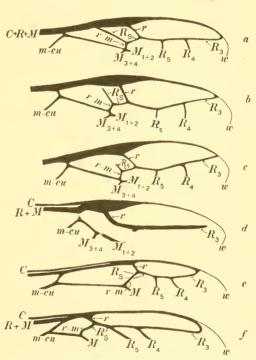


Fig. 20.—The switching of the base of the radial sector, a, Macrocephus satyrus; b, Janus cynosbati; c, Janus abbreviatus; d, Oryssus abietinus; c, Pelopæus cementarius; f, Apis mellifica.

length. If the remainder of the basal part of the radial sector should atrophy up to the point where it is joined to the anterior end of the radio-medial cross-vein, and if it were not for the successive stages just described, then the radial sector would be considered as arising from the middle of the stigma and the entire first transverse vein, as a cross-vein. This is exactly the interpretation that has been given to these veins throughout the higher Hymenoptera, where this very condition exists. The same condition is found in the Tenthredinoidea in the genus *Oryssus* (fig. 20, d), but this genus is not so interesting in this connection, because the first transverse vein, i. e., the radio-medial cross-vein plus

a part of the radial sector, has also atrophied. The atrophy of the base of the radial sector results in the union of the cells R and 1st R, a condition not found in any Tenthredinoidea other than Oryssus and Ophrynopus. This character is probably common to the other two genera of this family which are not known to the writer. That the above interpretation is the correct one is confirmed by the examination of the wings of the genera Rhogas, Anlacus, Gasteruption, Pelopaus (fig. 20, e), and Apis (fig. 20, f). If the base of the vein starting off from the stigma in the first four of these genera be examined, it is found that it extends obliquely to the first transverse vein just as in Megalodontes, Cephus, and Janus. If this vein were the base of the radial sector, it would proceed in a regular curve, as in the genera Tenthredo and Cladius. The composite nature of the first transverse vein is shown by an examination of this vein in certain specimens of Apis, where it is not straight but angular, as in Cephus. In certain genera of Apoidea, as Bombus, Psithyrus, and Osmia, and of Larridae, the base of the radial sector is preserved as a fine thread-like vein, frequently entirely colorless, while in some other genera only the transparent stubs remain.

The superfamily Tenthredinoidea can be differentiated from the other superfamilies by the presence in the front wings of one or both of the anal cells, or, if both be wanting, with the medio-cubital crossvein extending between R+M and cubitus; the cells R and 1st R_1 separated by a vein as broad as any of the others, or if not separated, with the first anal cell present.

The superfamily Tenthredinoidea is divisible into nine families. They are the Xyelidæ, Lydidæ, Blasticotomidæ, Tenthredinidæ, Xiphydriidæ, Sirieidæ, Megalodontidæ, Cephidæ, Oryssidæ. They are all represented in the American fauna except the Megalodontidæ and the Blasticotomidæ, and contain a very limited number of species except the family Tenthredinidæ, which embraces several hundred species and a large number of subfamilies.

The close relation of these families is proven by characters showing a difference in degree of specialization of the same kind, but through the loss of certain of the intermediate stages those characters indicating a difference in degree of specialization of the same kind are here just as useful as characters indicating a difference in kind of specialization for marking dichotomous divisions. Although each of these families represents a period in the development of certain characters, yet the series is not a lineal one; that is, the connecting links do not lie between the various families, but behind them. They have been developed from a common progenitor which transmitted its characters to its offspring in an elementary condition, and these offspring have developed along several parallel lines. Fortunately for our study,

these offspring have all arrived at different stages in their ascent, and by a comparative study it is possible to determine the road along which they have traveled. From this it is evident that in this superfamily those characters of value as essential characters are equally valuable as recognition characters.

The relation of the families of the Tenthredinoidea can be best shown by the following synopsis.

SYNOPSIS OF THE FAMILIES OF TENTHREDINOIDEA.

The generalized Tenthredinoidea	Xyelida.
The specialized Tenthredinoidea:	Lydidæ.
The cell R ₄ group	Blasticotomidæ.
	Tenthredinidae.
The cell R ₅ group	Xiphydriidæ.
	Siricidæ.
	Megalodontidæ.
	Cephidæ.
	Oryssidæ.

THE GENERALIZED TENTHREDINOIDEA.

The generalized Tenthredinoidea embraces two families, both of which are near the stem form of the original progenitor of the Hymenopteria. They are marked as generalized types by their short, broad, many-veined wings, in which the veins have not been arranged to the best advantage for stiffening the stigmatal and anal areas. They are further distinguished by the origin of the radial sector distinctly before the stigma, and by its prominent subtransverse bend away from the stigma. The course of the apex of the vein R_3 in both wings also demarcates them; this vein near the point of origin of the vein R_4 bends abruptly toward the margin of the wing, so that the cell on its front side, R_2 or 2d R_1+R_2 is blunt or subtruncated at apex, a condition found only in generalized genera.

This group is of particular interest to the student of phylogenies, because it approaches nearest to the typical wing in its retention of subcosta, the free part of R_2 and the free part of Cu_2 , though this latter is also found complete in one genus of Siricidæ.

Ayelidæ.—A small family embracing five genera and a limited number of species, which are confined mainly to the American fauna. It is easily separated from all other Hymenoptera by the presence in its wings of the free part of the vein R₂. The family contains, at least so far as their wing venation is concerned, the most generalized Hymenoptera known (figs. 31–35). This is shown by the origin of media near the middle of the costal area; by the perfect transverse direction of the radial cross-vein, which is situated midway between the radio-

medial cross-vein and the origin of R_2 ; by the position of the medio-cubital cross-vein near the posterior end of the radio-medial cross-vein in Manoxyela (fig. 34), its location about halfway between this cross-vein and the point of separation of media in Xyela (fig. 35), its migration toward the base of the wing until still nearer the origin of media in Megaxyela (fig. 31), and Odontophyes (fig. 32), and finally in Macroxyela (fig. 33), to a position only a very short distance before the origin of media; by the progressive migration of the free part of M_4+Cu_1 from just before the apex of the first anal cell in Xyela to just beyond the middle in Macroxyela; by the preservation of the radio-medial cross-vein in the hind wings of Megaxyela, Odontophyes, and Macroxyela; and by the location of the free part of R_4 of the hind wings near the apex of M_1 in these same genera.

It is worthy of note that the Xyelidae have departed from the type of wing assumed for the original progenitor of the Hymenoptera only in the loss of the free part of the vein Cu. It is also of interest that although their wings are distinctly generalized, yet in many ways they have undergone prominent progressive specializations, and that in each case these specializations have not proceeded in the same order. The variation in the order of specialization of the different genera will be seen in the following lists of genera which are arranged from generalized to specialized. If the modifications of the subcosta be taken they would be arranged, thus, Odontophyes, Megaryela, Macroxyela, Xyela, Manoxyela; if the shape of the stigma thus, Xyela, Manoxyela, Macroxyela, Megazyela, Odontophyes; if the position of the mediocubital cross-vein, thus, Manoxyela, Xyela, Odontophyes, Megaxyela, Macroxyela; if the position of the free part of M,+Cu, thus, Xyela, Odontophyes, Megaryela, Manoryela, Macroxyela; if the origin of media thus, Xyela, Macroxyela, Manoxyela, Odontophyes, Megaxyela. If now the position of the five genera be tabulated for the five characters given, it is found that Megazyela occupies all the positions but the first, and occupies the fourth twice, Odontophues occupies each of the five places. Macroxyela occupies the third and fifth each twice, and does not occupy either the first or fourth, Manoxyela occupies each of the five places. Xyela occupies the first place three times, and does not occupy either the third or fifth.

This family is divisible into two subfamilies on the form of the base of the subcosta of the front wings. In one subfamily, of which Macroxyela (fig. 33) may be taken as the type, the subcosta extends from the base of the wing midway between costa and R+M to beyond the origin of media, where it divides into two branches, one going to the costal margin, the other extending transversely coalesces with radius. In the other subfamily, of which Xyela (fig. 35) may be taken as the type, the base of subcosta is closely appressed to R+M but does not coalesce with it, to about the middle of the distance between

the base of the wing and the stigma, where it turns abruptly toward the margin of the wing. The free part of the vein Sc_2 and the cell Sc have been suppressed by the close approximation of the stems of Sc and R+M.

Lydidæ.—The Lydidæ is an easily circumscribed family of ten genera and about one hundred and twenty-five species which are peculiar to the northern hemisphere. This and the Xyelidæ are the only families of Hymenoptera in which subcosta has been preserved in the hind wings (figs. 36-43). In this character the Lydida are more generalized than the Xyelidæ. The series of wings here shown are of value as indicating the manner in which the subcosta of the hind wings has been suppressed, namely, by atrophy from the base toward the apex. This family is noteworthy for the retention in many species of the free part of Cu, though this character has been preserved in a limited number of species of the family Siricidæ (fig. 86). The Lydidæ have departed farther from the tyical hymenopterous wing, and are therefore more specialized than the Xyelida. This is shown by the origin of media much nearer the origin of the radial sector, so that the cell R is only about as long as wide; by the position of the posterior end of the radial cross-vein, which varies from a position on the apical two-thirds of the cell R₅ to a position interstitial with the free part of the vein R₅; by the position of the anterior end of the medio-cubital cross-vein at or just beyond the origin of the media; by the loss of the free part of R2; by the coalescence of the tip of R, for a greater distance from the margin of the wing; by the difference in the shape and position of the cell M, due to change in position of the stem of media and of the medio-cubital cross-vein; in the hind wings by the greater coalescence of the stem of media and the radial sector; and by the greater constriction of the apex of the first anal cell of the hind wings due to a coalescence of the first and second analyeins. The loss of the free part of the second branch of cubitus is a gradual one. It is complete except for the point where it is crossed by the anal furrow in Liolyda (fig. 43), Pamphilius (fig. 39), and Bactroceros (fig. 41); in Lyda (fig. 37) and Cephaleia (fig. 42) the posterior half is wanting; in Canolyda (fig. 38) it is only a small tubercle on the posterior side of cubitus, while in Neurotoma (fig. 36) and Itycorsia (fig. 40) there is left only the convexity, indicating where the free part of Cu, was situated. The Lydida differ from the specialized Tenthredinoidea in the preservation of subcosta of both wings, the origin of media, the shape of the cell 1st R₁+R₂ and the course of the radial cross-vein.

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THE SPECIALIZED TENTHREDINOIDEA.

Beginning with the families here included, there is found the first marked departure from the typical hymenopterous wing. This group is differentiated by the almost entire loss of the base of subcosta. The only exception is found in certain species of Siricidae (fig. 87), in which a subcosta of the type found in Neurotoma (fig. 36) persists. It can be traced as a pale, indistinct line through the middle of the area between costa and R+M in wings which have been cleared and mounted in Canada balsam. In addition to the loss of the base of subcosta, there is a decided shortening of cell R, due to the coalescence of radius and media to near the base of the stigma. The wings are longer, narrower, and more efficient organs of flight. The base of the radial sector has lost its prominent transverse curve, and measured along R₃ extends to the margin of the wing in a regular curve. The stigma has lost its broad quadrate outline, and, except in the genus Blasticotoma (fig. 44), it is narrow and diamond shaped.

The specialized Tenthredinoidea are divisible into two distinct phyllogenetic groups on the position of the posterior end of the radial cross-vein, in one ending in the cell R₅, in the other in the cell R₄. The position of this cross-vein, together with the position of the mediocubital cross-vein and the direction of the base of media, mark these groups as very different lines of development.

The determination of the sequence of these groups in a lineal arrangement has been a difficult one. In the answering of questions of this nature, the rule laid down by Comstock" seems the most available one:

It seems to me that the most practicable way of meeting this difficulty is to begin with the description of the most generalized form known, and to follow this with descriptions of forms representing a single line of development, passing successively to more and more specialized forms included in this line. When the treatment of one line of development has been completed take up another line, beginning with the most generalized member of that line and clearly indicating in the text that a new start has been made.

This shows clearly the method of procedure so far as the components of each line of development are concerned, but the difficulty here to be met is the determination of the sequence of the lines of development themselves. For the sake of brevity and convenience in referring to these lines of development, they may be known as the cell R_5 group and the cell R_4 group. As is indicated above, in the former the radial cross-vein ends in the cell R_5 and in the latter in the cell R_4 . Both lines contain families that are very generalized and are consequently near the stem form. In the arrangement here adopted, it has been assumed that the group that departs farthest from the condition of the original progenitor of the group should be given the highest rank, because

they have shown by the adoption of these modifications greater ability to conform to environmental modifications.

The cell R, group finds its greatest modifications in the position of the radial cross-yein, the position of the medio-cubital cross-yein between Sc+R+M and cubitus, and in the loss of the anal cells. The cell R₅ group finds its greatest modifications in the swinging of the base of media toward the apex of the wing, the atrophy of the base of the radial sector, and the loss of the second anal cell. It has been shown that the trend of modifications in these wings is toward the arrangement of the veins in such a way as to form supporting trusses in the stigmatal area. The cell R, group has accomplished this by means of the medio-cubital cross-vein alone, while the cell R₅ group has employed not only the cross-vein, but combined it with the transverse part of media. The fact that this latter type is the one preserved throughout the higher Hymenoptera would seem to indicate that it is the one that has been most successful in meeting the requirements of natural selection, and consequently must be the most efficient type. The loss of the base of the radial sector, which is peculiar to the cell R_s group, and likewise to the higher Hymenoptera, would also seem to point in this same direction. On the other hand, the cell R, group has exceeded the cell R₅ group in the loss of the anal cells, which is likewise peculiar to this group and the higher Hymenoptera; but even this condition is approximated by the cell R₅ group in the genus Oryssus (fig. 97), where the second anal cell is apparently wanting. So far as structural modifications are concerned, the weight of the evidence shows that the modifications found in the cell R₅ group have departed farthest from the primitive type, and we are therefore justified in giving it the precedence here.

Another fact that should not be overlooked, although it does not refer to structural predominance, is the number of descendants. The cell R₃ group contains five families, all of which are limited as to number of genera and species. The cell R₁ group contains two families, one containing a single species and the other many times as many genera and species as is found in all the remainder of the Tenthredinoidea together. The predominance of the cell R, group would seem to contradict our conclusions from structural superiority and therefore of efficiency of type, namely, that the predominance of indiyidnals is a direct confirmation of the superiority and efficiency of the cell R, type. This is only an apparent contradiction, for, if structural superiority and predominance of descendants are compared in other groups of animals, it is found that in those groups where there is a marked structural superiority there are a limited number of genera and species, while in those groups where there is a marked predominance of descendants, they are as a rule only mediocre so far as struc-

tural superiority is concerned.

THE CELL R4 GROUP.

It has been noted that there are two modifications in the stigmatal region that go hand in hand. The one is the progressive coalescence of the media from the middle of the costal area to near the stigma; the other is the progressive migration of the medio-cubital cross-vein from a position near the apex of the cell R to a position in the angle between R and M. In the cell R, group there is found the consummation of these modifications, the base of the media moving still nearer the stigma and the cross-vein cutting loose from media and migrating along Sc+R+M until in some genera it is more than its own length away from the media. It is doubtful that this moving of the radial end of the cross-vein toward the base of the wing is in every case a bona fide migration, and herein probably lies the explanation of why this character is of little value in certain subfamilies of the Tenthredinide. If the wings of Strongylogaster (fig. 51), Stromboceros (fig. 50), and Selandria are examined, it is found that in the first the cross-vein arises in the angle between R and M, and that radius extends toward the stigma in a regular curve; in the second the cross-vein is farthest from M, but that beyond the cross-vein radius makes a more prominent bend toward the stigma, while in the third the cross-vein is distant from M and radius makes an abrupt bend toward the stigma. The evidence here suggests that in the case of Selandria this condition was reached by a coalescence of the anterior end of the cross-vein and Sc+R+M.

This group is noteworthy as being the only one showing the different ways in which the anal area has been modified and therefore the successive changes that have resulted in the complete reduction of the anal cells.

The position of the radial and medio-cubital cross-veins marks the group as a sidewise development, this arrangement of parts being peculiar to the group. With the exception of a single case in the cell R_5 group, it is the only place where the radial cross-vein is lost. This peculiarity has arisen independently a number of times in the family Tenthredinidæ. When present, this cross-vein is always oblique to R_{3+4} and never perpendicular, as in the generalized Tenthredinoidea.

The hind wings are practically the same in venation as those of the Lydidae, except that in some forms the free part of the second anal, the free part of R_4 , and the transverse part of M_2 has atrophied.

Blasticotomidæ.—A family containing a single genus and species, found only in central and eastern Europe (fig. 44). This is an isolated archaic type. It is, in certain of its characters, closely related to the Xyelidæ and Lydidæ; in others it approximates the Tenthredinidea; that is, it is intermediate between these two groups. The area between costa and Sc+R+M is hardly more than a line and all trace of the sub-

costa is wanting. The stigma is a broad oval area like that of the Xyelida. The radial sector separates from R, distinctly before the stigma and extends to the wing margin along R, in a regular curve. The apex of the cell 2d R₁+R₂ is broadly rounded, just as in the generalized Tenthredinoidea and Megalodontidae (fig. 92). The radial cross-vein is joined to the stigma at its apical fourth and to the vein R₂₊₁ near the middle of the cell R₄. The radio-medial cross-vein is wanting. Media separates from radius a short distance in front of the radial sector; it extends transversely for a short distance, then extends in a broad bow-like bend to the point of separation of M_{1+2} and M_{3+1} , much as in Bactroceros (fig. 41) and Itycorsia (fig. 40). The anterior end of the medio-cubital cross-vein is joined to media at the posterior end of its transverse part and the posterior end of the cross-vein to cubitus just beyond its middle, the cross-vein extending from this point to media in a prominent curve, so that the cell M, is in the shape of a semicircle. The cubitus is a straight vein, closely appressed to Sc+R+M at the base of the wing, but not coalesced with it. The free part of M₁+Cu₁ is situated near M₂, as in the Lydidæ, the vein being transverse instead of oblique. The anal cell is of the form found in the typical wing. In the hind wings the cell R_{1+2} is bluntly rounded as in the fore wing and they differ from the Lydidæ only in wanting the subcostal vein and in that the transverse part of media is nearer the apex of the wing.

Almost every writer who has studied this species has located it in a different place. It has been placed in the subfamily Hylotominæ (figs. 76-79), or as a separate subfamily, or as a tribe near the generalized Tenthredinoidea. It has affinities with the generalized Tenthredinoidea in the shape of the stigma, the shape of the apex of the cell R₂, and the position of the medio-cubital cross-vein. It is allied to the family Tenthredinidæ (figs. 45-84), in the course of the base of the radial sector and in the position of the radial cross-vein. It differs from the generalized Tenthredinoidea and the generalized Tenthredinidæ in the constriction of the area between costa and Sc+R+M. These characters indicate it as a primitive form closely related to the family Tenthredinidæ, which finds its proper location as a distinct family just before the Tenthredinidæ.

Tenthredinide.—A large family with numerous subfamilies, genera, and species, found in all parts of the world. The stigma is of moderate size, ovate in outline. The costa in most of the species is distinctly thickened toward the apex. The area between costa and Sc+R+M is of varying width, the subcosta is represented only by the free part of Sc_1 , and only in rare cases is all trace of this wanting. The radial cross-vein is joined to the stigma near its apex and to R_{3+1} near the apex of the cell R_4 . The radial sector extends from the base of the stigma in a regular curve. In many genera the angle between the

stigma and the base of the radial sector has been strongly chitinized secondarily, so that the radial sector appears to arise from the base of the stigma, but it is always possible to differentiate this secondary part from the stigma and the vein because of the difference in the amount of chitinization. This condition is very prominent in *Hemichrou* (fig. 62) and *Periclista* (fig. 69). Media separates from radius near the stigma. The anterior end of the medio-cubital cross-vein may be joined to it at its origin or arise from the angle between R and M, or be joined to Sc+R+M at various distances from the origin of M. The anal cells show a marked progressive modification, but this and the other modifications can be dealt with better under the discussion of the subfamilies, and will be treated there.

It has been shown that the interrelation of the medio-cubital cross-vein and the origin of media is one of the most useful characters in indicating the sequence of the different families. Although there is quite a little modification in this region within the family Tenthredinidae, yet it is worthless for our present purpose, since it does not indicate anything as to the phylogeny of the group. The anal veins and cells maintain the same form and relation in all the families of the Tenthredinoidae except the Oryssidae and the Tenthredinidae. In the Tenthredinidae this area goes through a series of successive changes that are just as valuable in indicating the sequence of the subfamilies as the position of the medio-cubital cross-vein is in indicating the sequence of the families. Using, therefore, the anal area as a basis, this family can be divided into the following subfamilies, the relation of which can be best understood by means of the following synopsis:

SYNOPSIS OF THE SUBFAMILIE'S OF TENTIIREDINIDÆ.

Generalized Tenthredinidae	Lophyrine. Emphytine. Selandriine. Dolerine. Phyllotomine.
Specialized Tenthredinida.	
Anal cell conservers.	
Second anal vein conservers	Lycaotina. Tenthredinina. Cimbicina.
Second anal vein losers.	
Second anal cell reduced by atrophy.	
Costal area conservers.	
Radial cross-vein conscrvers.	Hoplocampinae. Dineurinae.
Radial cross-yein losers	. Monoctenine. Cladiine. Nematine.
	TACINE CITIES

Costal area losers	Blennocampinæ.
	Fenusinæ.
	Scolioneurinæ.
Second anal cell reduced by coalescence	Hylotominæ.
	Schizocerinae.
	Perreyiinæ.
Anal cell losers	Incaliinæ.
	Lobocerina.
	Acordulecerinæ.
	Pterygophorina.
	Perginae.

GENERALIZED TENTHREDINIDÆ.

The five subfamilies here included do not represent a continuous line of modification. Each subfamily is a separate entity, representing only the tip of a line of ascent. In the anal area they have retained the primitive condition of the typical wing, but in other regions they are distinctly modified. The group contains genera that have been distributed among various subfamilies. The primitive condition of the anal cells and the prominent contraction in the third anal vein shows their close relation to the generalized Tenthredinoide, their close affinity as a group, and furnishes ample reason for their inclusion as separate subfamilies in this place.

Lophyring.—The broad area between costa (fig. 45) and Se+R+M, together with the distinct free part of Sc, and the origin of media from R, much as in the generalized families, denominates this group as a generalized one. It is specialized in its loss of the radial crossvein and the open condition of the apex of the cell R_{1+a} of the hind wings, in these ways surpassing all the subfamilies of the generalized Tenthredinidae. The base of the radial sector bends abruptly toward the apex of the wing, but not as abruptly as this vein bends in the Xyelidæ (figs. 31–35) and Lydidæ (figs. 36–43). The apex of the cell R_{1+2} of the front wings is moderately blunt, due to the bending of R_2 abruptly toward the wing margin at the origin of R, though pointed at its actual apex; the cell M, is about twice as long as wide; the vein M₄+Cu, is joined to the middle of the cell M₄; the medio-cubital crossvein is joined to Sc+R+M just before the origin of media, the cross vein and M₃₊₄ are slightly divergent, the free part of R₄ and the transverse part of M, of the hind wings is present, and the first anal cell is petiolated at apex for a short distance. An interesting modification is the loss of the posterior half of the radio-medial cross-vein in many species.

This subfamily as known to me contains only the genus *Lophyrus* (fig. 45). It is usually associated with the genus *Monoctenus* (fig. 67), and placed near the Hylotomina and its allies, but I believe that the most important modification that can be used in assigning a location

for a group in lineal arrangement in the family Tenthredinidæ is the condition of the anal cells, and judged by this criterion the Lophyrinæ must fall among the generalized Tenthredinidæ.

Emphytinæ.—The Emphytinæ have the area between costa (figs. 46-48) and Sc+R+M restricted, though in some genera it is fairly broad with a distinct Sc., in others it is narrow, and Sc. is only represented by a projection upon the front margin of Sc+R+M. The mediocubital cross-vein is attached in the angle between radius and media, this cross-vein and M_{3+4} are parallel. The radio-medial cross-vein is wanting in certain genera, as *Emphytus* (fig. 46) and *Pacilostomidea*, so that the cells R and R- are combined. Many writers on the Tenthredinoidea content themselves with the statement that there are three or four submarginal cells present, but it is very apparent that this does not give a hint as to what vein is wanting and therefore what cells have combined. The radial cross-vein is never wanting. The cells 2d R₁+R₂ of the fore wings and R₁₊₂ of the hind wings are distinctly pointed at apex. The free part of M4+Cu, varies as to the place at which it joins the cell M, from near the middle of the cell to a point almost interstitial with the medio-cubital cross-vein. In the hind wings the free part of R₄ is frequently wanting, while in other genera both the free part of R, and the transverse part of M, are wanting. There is considerable variation in the amount of coalescence of the first anal cell of the hind wings. In Acidophora the second anal vein separates from the first distinctly beyond the free part of M₄+Cu₄ in other genera, as *Tetratueura*, the apex of the first anal is interstitial with M₄+Cu₄, while in Eviocampa (fig. 47) the coalescence is for a considerable distance before M.+Cu. The following genera would be referred to this subfamily as here constituted: Athalia, Eriocampa, Strongglogastroidea, Pacilostomidea, Pacilostoma, Taxonus, Hypotaxonus, Hemitaxonus, Emphytus, Harpiphorus, Tetrutneura, Acidophora, Parasiobla, and Pseudosiobla.

Sclandriinæ.—A group with only a limited number of genera, but fairly rich in species. It is of especial interest, because it marks the first stage in the reduction of the anal area, the free part of the second anal vein being wanting (figs. 50–51). It is only recently that systematists have considered the loss of the free part of this vein of even generic value, but the modifications of this area are of such great phyllogenetic importance that there is not the slightest reason for not considering the loss of this vein as of subfamily value. The loss of the free part of the second analyvein marks a high specialization within the generalized Tenthredinidæ and should place this subfamily at the head of this series; but, as pointed out above, each of these subfamilies is only the tip of a line of ascent, and as the other characters of the wings ally it closely with the Emphytinæ its most natural location is after this group, where all previous systematists have placed it.

In the front wings the costal area varies from a broad prominent space to a narrow restricted area, the latter being the predominant condition. The anterior end of the medio-cubital cross-vein may arise either from the angle between radius and media or from Sc+R+M distinctly before the origin of media. This shows that in certain groups at least the location of this cross-vein at or before the origin of media does not include forms belonging to the same line of ascent, but it does show the successive modifications within this line of ascent. The other wing structures are practically the same as in the Emphytima except that, so far as observed, the free part of R_4 and the transverse part of M_2 are never wanting in the hind wings. This subfamily includes the following genera: Strongylogaster, Thrinax, Stromboceros, and Selandriat.

Polerinæ.—A subfamily (fig. 49) with a distinct habitus, closely related to the Emphytina and Selandriina. The costal area has been greatly reduced, the free part of Sc_1 is only a projection upon the front side of Sc+R+M. The costa is prominently thickened at apex. This, together with the thickening of Sc+R+M, have undoubtedly been important factors leading to the reduction of this area. The mediocubital cross-vein joins Sc+R+M just before the origin of media. This cross-vein and the stem of M_{3+4} are slightly divergent behind. The most important characters for differentiating the group from the other subfamilies of the generalized Tenthredinidae is the atrophy of the free part of M_4+Cu_1 is situated near the middle of the cell M_4 . The hind wings are of the usual form found in the generalized Tenthredinidae. This subfamily contains two genera, *Dolerus* and *Loderus*.

Ph. flotominæ.—This subfamily is distinctive in the oblique course of the medio-cubital cross-vein (fig. 52–54), which is joined to Sc+R+M distinctly before the origin of media and by the direction of the stem of M_{3+4} , which is strongly divergent from the cross-vein behind. The costal area is narrow, the free part of Sc_1 is represented by a mere projection on the front margin of Sc+R+M in Caliroa, and is entirely wanting in Phyllotoma.

The costa is broadly expanded at apex. The radial and radio-medial cross-veins are so completely covered by furrows in certain species as to be apparently wanting. The free part of M_4+Cu_1 is joined to the cell M_4 near its middle. The hind wings have undergone the greater reduction, the free part of R_4 and the transverse part of M_2 are generally wanting, though this latter vein is sometimes present. In the males there has been a peculiar change in the direction of the veins, all of them running direct to the margin, the free part of R_4 and M_3 and the transverse part of M_2 are wanting, and in their place there has been developed secondarily a vein along the margin of the wing from the apex of the cell R_{1+2} to the apex of the first anal

cell very much like the ambient vein of the Diptera. This condition can be explained in another way by assuming that the free part of R_4 , the transverse part of M_2 , and the free part of M_3 are all present, and simply have migrated to the margin of the wing. The difficulty in the way of this explanation is that the free part of R_4 is always wanting in the females of these genera. In certain species of *Phyllotoma* the free part of the second anal vein coincides with the second anal furrow and the apex of the free part has atrophied. This subfamily contains the genera, *Caliroa*, *Phyllotoma*, and *Eriocampoides*.

THE SPECIALIZED TENTHREDINIDÆ.

A group containing the greater part of the genera and species of the family Tenthredinidæ. They are differentiated from the generalized Tenthredinide through the loss of the constriction near the middle of the second anal cell. The subfamilies fall into several wellmarked lines of development. The Lycaotina (fig. 55), Tenthredinina (figs. 56-58), and Cimbicine (figs. 59-60) are the only members of this series in which the free part of the second analyein of the front wings is preserved. The marked contraction of the third analyein is represented as a slightly thickened emargination just before the free part of the second analyein, this is found only in the Lycaotine (fig. 55) and Tenthredinine. In the genera Macrophya (fig. 57) and Tenthredo (fig. 56) the presence or absence of a transverse vein between the second and third analycins is not of generic value. The Hoplocampine, Dinurine, Cladiinæ, Monocteninæ, Nematinæ, Blennocampinæ, Scolioneurinæ, and Fenusina have the anal cells either anastomosed at middle or with the basal half of the third anal vein atrophied. In the Hylotomine, Schizocerine, and Perrevine the second anal cell has been reduced by the progressive coalescence of the anastomosis to the base of the wing. In the Lobocerine, Pterygophorine, and Perreyine the anastomosis has proceeded both ways, so that both the first and second anal cells have been reduced.

Lycatoline.—This subfamily contains the single genus Lycata (fig. 55). Its location with the Tenthredinine and Cimbicine is due to the form of the anal cells, which anastomose at a single point at the usual place for the location of the free part of the second anal vein. The wings are broad and their apices are blunt. The medio-cubital crossvein arises from Sc+R+M, just before the origin of media. This cross-vein and M_{3+4} are parallel. In the hind wings the free part of R_4 is wanting and the first and second anal veins are coalesced for nearly one-half the length of the veins. This subfamily is placed as the most generalized member of the specialized Tenthredinida because of the form of the anal veins of the front wings and the position of the medio-cubital cross-vein.

Tenthredining.—The limits of this subfamily as given here is the same as that usually assigned it by systematists with the exclusion of those genera in which the free part of the second analyein appears like an oblique cross-vein. The Tenthredininæ are generalized in the preservation of the remnant of the contraction of the typical wing (figs. 56-58), the fairly broad costal area, and in the parallel medioenbital cross-vein and M₃₊₁. The medio-cubital cross-vein is oblique. and is joined to Sc+R+M a considerable distance before the origin of media. The cells between R, and R, are broad, the radial cross-vein long and bowed. The topography of the hind wings is of the ordinary type found in the Tenthredinida, except that there has been a notable reduction of the anal area of the wing, so that the lobe behind the second analyein is almost entirely wanting. In the front wings the modification of the second analyein varies from a long vein in Tenthredo (fig. 56) to a broad contraction in Pachyprotasis (fig. 58); in the hind wings the cell R_{1+2} extends to the apex of the wing R_1 , extending beyond as a short spur. Although it is impossible to put it into words, yet the general appearance of the wings of this subfamily is distinctive and easily recognized and would never be confused with those of any other group.

Cimbicinæ. - Like the preceding group, this one has the same limits as that given it by systematists. Its distinctive characters are the narrow costal area (figs. 59-60); the long, narrow-pointed stigma; the narrow-pointed area between the veins R, and R, which always ends a considerable distance before the apex of the wing, the vein R₁ being always extended for a considerable distance beyond the apex of this area; the radial cross-vein is straight and slightly oblique; the mediocubital cross-vein usually joins Sc+R+M more than its own length before the origin of media; the medial cross-vein is frequently oblique; the free part of the second anal vein may be present or its location represented by a broad anastomosis; the medio-cubital cross-vein and the stem of M₃₊₄ are divergent before; the first anal cell has been shortened at apex by the coalescence of the first anal and the combined second and third anals; the radio-medial cross-vein is wanting, so that the cells R and R₅ are coalesced. The wing area of the hind wings has not been modified from the usual type and the vein topography is the same, except that the cell R₁₊₂ ends a considerable distance before the apex of the wing, the vein R, being continued to near the apex of the wing. The apex of the free part of the second anal vein is transverse like a cross-vein, and there has been developed from the apex of the first anal cell on the hinder angle a long secondary spur to the wing margin. The costal area of hooks extends to or beyond the middle of the cell R_{1+2} .

Hoplocampine.—A small group, embracing two genera, Hoplocampa (fig. 61) and Hemichroa (fig. 62). This and the following sub-

family represents a series in which the anal veins have been modified before the loss of the radial cross-vein. In this subfamily the costal area is broad with the free part of Sc_1 distinct. The area between R_1 and R_3 is very broad, the radial cross-vein is long, straight, and slightly oblique. The area between the base of the stigma and the base of the radial sector has been chitinized so that it appears as a part of the stigma. The medio-cubital cross-vein is joined to R+M distinctly before the origin of media, usually near the free part of Sc_1 . The free part of M_4+Cu_1 is joined to the cell M_4 near its middle. The anal cells are contracted for a short distance in Hoplocampa and for a considerable distance in Hemichroa. In the hind wings the anal lobe is larger, the venation is of the usual type.

Dineurinæ.—This subfamily as generally limited contains the general Dineura (fig. 63) and Mesoneura (fig. 64). To these has been added the genus Pseudodineura (fig. 65), which is closely allied to them. The Dineurine are quite similar in wing type to the preceding subfamily, the most notable difference is in the loss of the base of the third anal vein, so that the cell included between 1st A+2d A, and 3d A has coalesced with the third anal cell. There is a notable variation in the amount of thickening of the apex of the costa, the greatest thickening being found in the genus Mesoneura. The free part of Sc. occupies a different position in each of the genera; in Mesoneura it is about its own length before the medio-cubital cross-vein, in Pseudodineura it is almost interstitial with the cross-vein, and in Dineura it is about its own length beyond it. The position of the free part of Se, is usually of but little value systematically, at least in certain groups. This is marked in *Pteronus ventralis*, one of the Nematine, where this vein is not constant within a single species, but may in different individuals occupy all three of the positions described for the genera of this subfamily. In Pseudodineura the apex of the free part of the second analyein is wanting. The hind wings are of the usual type.

Monocteninæ.—Beginning with this subfamily there is a series of three closely related subfamilies in which the loss of the radial crossvein has preceded the modifications of the analyveins. The Monocteninæ contains a single genus, Monocteninæ (fig. 67), which all systematists have agreed hitherto in associating with the genus Lophyrus (fig. 45), described above. Monoctenia is like Lophyrus in lacking the radial cross-vein and in having the costal area broad, with a prominent free part of Sc_1 . In Monoctenia the costal is slightly thickened at apex; the medio-cubital cross-vein is joined in the angle between R and M; this cross-vein and the stem of M_{3+4} are divergent behind; the anal cells are broadly anastomosed at middle; the free part of M_4 +Cu₁ joins the cell M_4 near its middle and is strongly oblique; the cell R_{1+2} is broad and pointed at apex, and the area between the base of the stigma and the radial sector is distinctly chitinized. In the hind wings the

cell R_{1+2} is broad and open at apex; the radial sector reaches the wing margin at the actual wing apex; the remainder of the wing is of the

usual type.

Cladiinæ.—The genera included in this subfamily are generally placed with the next, the Nematine. The costa is somewhat thickened at apex (fig. 66); the medio-cubital cross-vein joins Sc+R+M just before the origin of M, this cross-vein and the stem of M_{3+4} is strongly divergent behind. In the hind wings the cell R_{1+2} is broad, pointed, not open at apex, and ends on the front margin distinctly before the apex of the wing with the vein R_1 extending beyond the apex of the cell spur-like. This subfamily includes the genera Cladius, Priophorus, Trichiocampus, and Camponiscus.

Nematinæ.—A large subfamily of several genera and numerous species. The genera here included are those generally included in this subfamily, in which the base of the third analyvein has atrophied so that the cells 2d A and 3d A are coalesced (fig. 68). The costa is distinctly thickened at apex, the costal area is broad; the area between the base of the stigma and the base of the radial sector is strongly chitinized; the medio-cubital cross-vein is joined to Sc+R+M a considerable distance before the origin of media; the base of the free part of the third analyvein is wanting; the free part of R_5 is wanting in Enura; and the radio-medial cross-vein is frequently so completely covered by the radial furrow as to be partially or wholly wanting, a condition especially noticeable in the genus Pristiphora.

Fenusinæ. -- Of the genera known to me, there are two, Fenusa (fig. 74) and Kaliosysphinga (fig. 73), which would fall into this subfamily as here limited. The group is indicated by the narrow costal area; the thickened apex of the costa; the loss of all trace of Sc; the broad stigma; the subtransverse bases of the radial sector and of media; the strongly bowed medio-cubital cross-vein, which is joined either in the angle between R and M, or just before the origin of media; the strong divergence of the medio-cubital cross-vein and the stem of $M_{3\pm i}$. The radio-medial cross-vein is wanting; in Kuliosysphinga, the base of the third analyein is represented by a dark band of coloring matter, which in Fenusa is completely wanting. In the hind wings there is the atrophy of the free part of R, and the transverse part of M_s. The apical two-thirds of the second analyvein is wanting in Kaliosysphinga, and the anal area of the wings is greatly reduced. The apex of the cell R₁₊₂ is open, the vein R₃ reaching the wing margin at the actual apex of the wing.

Scolioneurinæ.—A small subfamily containing two genera, Entodecta and Scolioneura (fig. 75), which are closely related to the preceding subfamily. It differs from the Fennsine in having the free part of Sc₁ preserved as a protuberance upon the front margin of Sc+R+M, and in having the cell R₁₊₂ of the hind wings closed some distance before

the apex of the wing, the vein R_1 being continued spur-like beyond the apex of the cell. In *Scolioneura* the radial cross-vein is interstitial with the free part of R_3 , and the base of the free part of the third anal is preserved, though its connection with the other anal veins at the contraction is wanting. The radio-medial cross-vein is present, although almost entirely covered by the radial furrow. In *Entodecta* the base of the third anal vein is represented in the wing membrane as a dark, straight band.

Blennocampina.—This and the two following subfamilies begin a series in which the costal area has been greatly reduced, and the free part of Sc, is represented only by a spur (figs. 69-72). The Blennocampinæ is a large group rich in genera and species, in which systematists have placed a number of genera bearing no relation to the group at all, as here restricted. The costa is prominent and thickened at apex; the medio-cubital cross-vein is joined to radius in the angle between radius and media and is usually parallel with M₂₊₁, very slightly divergent in Rhadinocerea; the base of the third analyein is partly atrophied, different genera showing the successive stages in the atrofication of this vein; the free part of M,+Cu, varies in position from near the middle of the cell M, to a position almost interstitial with the medio-cubital cross-vein. In the hind wings the free part of R, and the transverse part of M, are wanting in certain genera; the first anal cell is of varying lengths, the first and second anal veins being coalesced from a point opposite the free part of M₂ to near the middle of the distance between the base of the wing and the free part of M_3 ; the cell R_{1+2} usually ends just before the apex of the wing, but in Periclista R₃ ends at the actual apex, the cell being closed; in the males of certain species the apex of the wing is margined by an ambient vein as in the males of certain Phyllotomina.

Hylotomine and allies.—This group (figs. 76-80) includes three subfamilies, the Hylotomine, Schizocerine, and Perrevine. As only a very limited amount of material of the last two subfamilies is at hand for study, it will be impossible to more than point out some of the more salient characters of the group, and for this reason the groups are given the same limits in the table on another page that is generally assigned them by systematists. It seems doubtful that these groups as now arranged represent natural divisions. The Hylotomina and Schizocerinæ are differentiated by the moderately broad costal area together with a well-marked Se,, which is common to the former and wanting in the latter, while both conditions are found in the Perrevinæ. The characters above given would place the genera Hylotoma (fig. 76) and Pachylota (fig. 77) in the same subfamily. In both the cell R₁₊₈ of the front wings is prominently appendiculate, but in the hind wings of Pachylota this cell is open at the apex, the veins R₁ and R₂ extending parallel to the margin of the wing. This condition is also

found in the Schizocerine, where this cell is appendiculate in Labidarge (fig. 78), and broadly open at apex in Scobina and Diclocerus (fig. 79); in fact, in Scobing this cell is not appendiculate in either wing. If the results of our studies on the other groups of this family be of any value, then the variation in the characters just cited must indicate very different lines of ascent, and be of more value than for the mere differentiation of genera. The medio-cubital cross-vein is generally joined to Sc+R+M at or very near the origin of media. Although it is not true of all the genera, yet in certain genera there seems to be a marked tendency for the migration of the free parts of R, and R, and the transverse part of M, toward the base of the wing, thus greatly increasing the size of the apical cells. The second anal cell is wanting in the Perreyina, but according to descriptions of genera may be either present or absent in both the Hylotomina and Schizocerina. This character is not of any phylogentic value, since, so far as it is concerned, these subfamilies are undergoing a progressive reduction of this cell. In the Hylotomine and Schizocerine the hind margin of the cell M, is a fairly straight vein, the free part of M,+Cu, joining it near its middle, and is either perpendicular to it or inclined toward the apex of the wing. In most Perrevine the hind margin of the cell M. is deeply curved, the free part of M₄+Cu₄ is joined to it at or before the middle, and is always strongly inclined toward the base of the wing. This is the only venational character thus far discovered that is of any value in separating the Perreying from the other two subfamilies. In the hind wings it is only with rare exception that either the free part of R, or the transverse part of M, are wanting in the Hylotominæ and Schizocerinæ, and when either of them are wanting it is always the latter. In marked contrast to this is the almost entire absence of the transverse part of M_o in the Perreyina, the free part of R, being always present, so far as can be judged from figures of wings. Here, just as in the front wings, there is a marked tendency toward the migration of the free part of R₄ and the transverse part of M₂, when it is present, toward the base of the wing. In many Tenthredinide the transverse part of M, is either interstitial, or nearly so, with the free part of R_o, but in this group it has migrated toward the base of the wing until it is near, or sometimes even before, the free part of M₃. There is also in many Tenthredinidae a prominent angle opposite the anterior end of the free part of M₂, but in this group this angle has been straightened out and cubitus appears to extend directly to the margin of the wing. The Perreyinæ are frequently separated from all the preceding subfamilies by the loss of the free part of the second analyein. It has been pointed out above that this vein is also wanting in the Phyllotomine and Fenusine, and the same condition is found in certain Schizocerina and Hylotomina. This is a character that has arisen several times in widely separated groups, and does not

appear to be of any phyllogenetic value. Although the Hylotomine, Schizocerine, and Perreyine are so closely related in their wing characters that there is a great dearth of prominent differences for dividing them, yet the Perreyine are readily separated from the other subfamilies on antennal characters.

The anal cell loosers.—The genera included under this heading are generally divided into three subfamilies, the Lobocerine, Pterygophorine, and Pergine. Such a grouping combines forms that are not closely related and they have therefore been divided into the following subfamilies: The Incaline, including the genera Incalin and Paralypia, which are limited to South America; the Lobocerine, including the genera Loboceras (fig. 82), Aulacomerus, Syzgonia, and Corynophilus, which are also limited to South America; the Acordulecerinæ, including the single genus Acordulecera (fig. 83), found in North and South America; the Pterygophorine including the genera Pterygophorus (fig. 81), Pterygophorinus, Lophyrotoma, and Philomastix, which are limited to Australasia; and the Pergina, including the genera Cerealces and Perga (fig. 84), and its subdivisions, which are limited to Australasia. It has been impossible to examine specimens of all these groups, and the writer has had to depend in many cases on figures, so that the characters given in the table on a later page may not be of any more value than to indicate the regions which are undergoing modifications. These subfamilies are set off from all the other Tenthredinide by the reduction of both anal cells of the front wings. The wings are long and slender, and the anal area of the hind wings is generally greatly reduced. In the front wings the costal area is broad. and the free part of Sc, is preserved in the Lobocerine, but in the other subfamilies the costal area is hardly more than a line, and the free part of Sc, is wanting. The radial cross-vein is wanting. The cell R₁₊₂ is appendiculate in the Incalina, Lobocerina, Pterygophorine, and Pergine, ending at or before the middle of the cell R₃, the vein R, being continued to the apex of the wing.

In the Acordulecerinæ this cell is not appendiculate, and ends distinctly beyond the middle of the cell R_3 . The medio-cubital crossvein joins Sc+R+M at or very near the origin of M. In the Pterygophorinæ the free part of R_5 is wanting, in Acordulecera and certain species of Perginæ the radio-medial cross-vein is also wanting. The free part of M_4+Cu_1 joins the cell M_4 just before the middle in the Lobocerinæ and Pterygophorinæ, and insterstitial with the medio-cubital cross-vein in the Perginæ. In the hind wings the cell R_{1+2} is appendiculate in the Perginæ and Lobocerinæ, while in the Acordulecerinæ and Pterygophorinæ it extends as a long, pointed cell to the apex of the wing. The free part of R_4 is always present, and the transverse part of M_2 always wanting. As in the Hylotominæ and its allies, the base of cubitus apparently forms a continuous vein to the

wing margin by coming into line with M_4 , the medial cross-vein, and the longitudinal part of M_2 . The medio-cabital cross-vein is longitudinal in the Incaliine, Lobocerine, and Pergine, and transverse in the Acordulecerine and Pterygophorine. The free part of M_4 is longitudinal in the Pterygophorine and only about one-third the length of the free part of M_3 , while in the Lobocerine and Pergine the free part of M_4 is transverse and two or three times as long as the free part of M_3 . This is due to the migration of the basal end of the medial cross-vein along the free part of M_3 . The free part of the second anal vein is wanting throughout the group, due to the great reduction of the anal lobe of the wing, while the second anal furrow and the axillary incision are near the first anal vein. The loss of the second anal is the consummation of a variation that has appeared sporadically in other subfamilies.

THE CELL R5 GROUP.

It has been pointed out in the case of the generalized Tenthredinoidea that the radial cross-vein always ends in the cell R_5 . In the families Xiphydriide (fig. 85), Siricide (figs. 86–91), Megalodontide (fig. 92), and Cephide (figs. 93–96) this cross-vein, with rare exceptions, also ends in the cell R_5 . In the family Orysside (fig. 97) this cross-vein is apparently wanting, but, as was shown above, the cross-vein is present and is represented by the transverse vein at the base of R_3 . The only modification in the course of the cross-vein is that its posterior end has migrated toward the apex of the wing, so that it is always oblique to R_{3+4} instead of being perpendicular.

The interrelation of the radio-medial cross-vein, the base of the radial sector, and the base of the media is a prominent characteristic of this group of families. In the Xiphydriidæ there is only a slight departure from the arrangement of parts existing in the typical wing, the base of the radial sector and the base of media being parallel, and the cross-vein perpendicular to them. In the other families, however, the posterior end of the cross-vein has swung around at such an angle as to form an apparently continuous vein with a part of the radial sector, while the basal part of the sector extends transversely between the cross-vein and the stigma like a cross-vein. As a result of this change in the direction of the veins, the cells R, 1st R_1 , and 2d $R_1 + R_2$ are arranged in a row.

The position of the medio-cubital cross-vein in those families in which the posterior end of the radial cross-vein ends in the cell R_5 is also of especial interest. In the Xiphydriidæ this cross-vein occupies practically the same position that it does in the typical wing. The Oryssidæ show a stage slightly more advanced than that of the Xiphydriidæ. The cross-vein is longer than the transverse part of media, which has been brought about by a combined migration of the anterior

end of the cross-vein along media, and by a further coalescence of media with radius until it is almost opposite the anterior end of the cross-vein. A similar condition is found in certain Cephida, the cross-vein being about three times as long as the transverse part of media. In this family the modification has been a migration of the anterior end of the cross-vein along media until in certain species, as Cephus pygmæus (fig. 96) it arises in the angle between Sc+R+M and media. In the Siricidæ and Megalodontidæ the modification has been in an entirely different direction. The cross-vein and the transverse part of media in these families are subequal in length, while the origin of media is either opposite or beyond the anterior end of the crossvein and never before it, as it is in all the forms previously described. The manner in which this arrangement of parts has arisen can be best understood if a study be made first of the condition found in the Xiphydriidæ (fig. 85). In this family the cross-vein and the transverse part of media are subequal in length, just as in the families named above. The cross-vein is distinctly bowed on the side toward the base of the wing. This bow in the cross-vein has been preserved in practically all the Siricidæ (figs. 86-91). Now, if the cross-vein maintain this same form and position, and the point of separation of media from radius be gradually changed, moving toward the apex of the wing by the coalescence of media more and more with the radius until it is opposite or beyond the anterior end of the cross vein, exactly the same condition will be had as is found in the Siricidæ. The Megalodontidæ (fig. 92) differ only in that the coalescence has proceeded farther, the transverse part of media being distinctly inclined toward the base of the wing, and the cross-vein is straight instead of being bowed.

The only other possible solution of the arrangement of veins in the the stigmatal area of the Siricidæ would be that starting with a wing like that of Cephus pygmæus, the base of media had migrated along the cross-vein until near its middle, and that at some later time the anterior end of the combined cross-vein and media had migrated along radius toward the apex of the wing. This would give exactly the same result that has been explained above in another way. That this latter explanation can not be the correct one is proven by the relation of these veins in the Xyelidæ, Lydidæ, Cephidæ, and the Tenthredinidæ. It has been shown that in the first three of these families the tendency is for the progressive coalescence of media with radius, and coordinated with this a progressive migration of the medio-cubital cross-vein from a position near the apex of the cell R to the point of separation of media from radius. That the tendency is not for media to migrate along the cross-vein when the cross-vein reaches the angle between radius and media, as has been shown in the Tenthredinidæ, but instead that the cross-vein continues its migration toward the base

of the wing along Sc+R+M. This is conclusively shown in *Trichiosoma* (fig. 59), where the cross-vein has migrated more than its own length away from the origin of media. That this latter solution is untenable is further proven by the position of the posterior end of the radio-medial cross-vein, which in both the Siricidæ and Megalodontidæ is so near the posterior end of the transverse part of media as to preclude such a migration.

It has been shown that the preservation of the radial cross-vein as the base of R_3 , as in the Oryssidæ, is the same condition existing in all the higher Hymenoptera. It is of especial interest that the form of the medio-cubital cross-vein and the base of media is also the same arrangement of parts found in the other Hymenoptera. Both of these conditions go to show that the other superfamilies of the Hymenoptera were derived from a progenitor closely allied to the families Siricidæ, Megalodontidæ, and Oryssidæ.

Xiphydriida.—This family contains four genera and about twentyfive species, which are distributed over North and South America, Europe, and Asia. Their wing type (fig. 85) is the most generalized found in the specialized Tenthredinoidea. The front wings are long and narrow; the costal area is broad and distinct; the free part of Sc. is represented by a prominent transverse vein situated near the origin of media, which is a direct modification and migration of the condition found in Xyela (fig. 35) and Manoxyela (fig. 34); the anterior end of the radial cross-vein is situated near the apex of the stigma and its posterior end near the apex of the cell R₅ or interstitial with the free part of the vein R₅ and is either perpendicular or slightly oblique; this cross yein is wanting in the genus Derecurta. The radial sector arises at the base of the stigma and continues along R, in a regular curve. The base of the sector is subtransverse; it does not make as abrupt a bend as in the generalized Tenthredinoidea, while, on the other hand, it is not so gradual a curve as in the more specialized forms. The radiomedial cross-vein is somewhat oblique and distant from the origin of media, and is wanting in the genus Konowia. Media separates from radius but little nearer the stigma than in the Lydidæ, while the portion before the medio-cubital cross-vein is oblique, just as in Macroryela (fig. 33), though both this part of media and the cross-vein are longer than in that genus, resulting in a much wider cell M; the free part of M₄+Cu₁ is near the posterior end of the radio-medial crossvein, almost interstitial with it. In the hind wings the origin of media is distant from the origin of the radial sector, and the first anal cell is of a type similar to that found in the Lydidæ (figs. 36-43) except in Konowia, where it is open at the apex.

The migration of the apex of R_1 in the front wings away from the margin of the wing in *Xiphydria camelus*, as already described, has developed into a distinct appendiculate cell in *Derecyrta* and *Brachyxiphus*.

The venation of the wings of this family is like the typical wing in the origin of media, the location of the medio-cubital cross-vein, and the type of anal cells.

The Xiphydriidae has generally been considered by systematists as a subfamily of the family Siricidae. That it represents a distinct line of development is shown by the condition of the area between costa and Sc+R+M, which is broad, and the wing membrane not any thicker than that of any other part of the wing, while the remnant of subcosta retained is a modification of the type found in Xyela, the type found in the Siricidae, as will be shown later, is a modification of the type found in Neurotoma. That the Xiphydriidae represent a distinct line is further shown by the origin of the base of media, by the position of the radio-medial cross-vein, and by the origin of the base of media in the hind wings, which is in reality quite a specialized condition. All these characters go to show that the wings of this family are more nearly like those of the generalized Tenthredinoidea than those of the specialized Tenthredinoidea.

Siricidæ.—This family contains five genera, all of which are limited to the northern hemisphere. The Siricidæ are large, active, flying insects, and as a result their wings are long and narrow. The wings are like the typical wing (figs. 86-91) only in having homologous veins. The stigma is narrow, pointed, and eight to ten times as long as broad. The area between costa and Sc+R+M is narrow and almost as strongly chitinized as the veins themselves. The suppression of the subcosta, which is represented in some species as a pale, indistinct line, is undoubtedly due to the chitinization of the membrane of this area. In Tremex columba (fig. 91) the chitinization has proceeded so far that there is a large trachea unprotected by a vein ramifying through this area. The peculiar arrangement of the veins forming the apex of the cell M has already been discussed and need not be considered here. The posterior end of the radio-medial cross-vein joins the cell M₄ on its basal third; in Tremex fuscicornis it ends in the angle between the transverse and longitudinal parts of media, while in Sirex californicus (fig. 87) it ends on the posterior third of the transverse part of media. Correlated with the migration of the posterior end of this cross-vein there is a corresponding migration of its anterior end along the radial sector until, in Tremex fuscicornis, it arises almost at the origin of the sector, so that the cell R is hardly more than a broad line. In Tremex the radial cross-vein is situated near the apex of the cell R₅+R₄, the free part of the vein R₅ is wanting. On the apex of the front wings of all the species of the family there has been developed a large appendiculate cell, with the apex of R₁ as a prominent vein extending toward the actual apex of the wing. An especially interesting feature of the wings of the Siricidæ is the preservation of the free part of Cu, in the genus Paururus (fig. 86) and a portion of it in different species

of Sirex. This yein is found besides in the Siricidæ only in certain species of the family Lydidæ. It is noteworthy that it is situated nearer the medio-cubital cross-vein than in the Lydidæ, and that the prominent bow in the base of cubitus, so characteristic of the Lydida, is wanting in the Siricidæ. The first and second anal cells approximate the type found in the typical wing, but the emargination near the base of the third analyein, instead of being an abrupt one, as in the typical wing, is a long, continuous curve. There has also been a progressive migration of the free part of the second anal toward the apex of the wing until in Paururus and Sirex californicus it is situated midway between M₃₊₄ and the medio-cubital cross-vein. In Xeris (fig. 89) it is just beyond the cross-vein, while in Tremer it is before. In the hind wings there is in certain species a well-marked appendiculate cell, but in *Tremer* and *Paururus* the transverse part of R, has been obliterated, leaving the cell R₁₊₀ open at apex. This family is so specialized in most of its structures that it is of interest to find at least one of its characters very generalized. This is the point of origin of media, which is more primitive than the same region in the Xyelidæ (figs. 31-35). There is a progressive migration from a position distinetly before the radial sector in Sirex californicus, from the origin of the radial sector in Paururus, and finally from the radial sector distinetly beyond its origin in Tremex. We find a confirmation of the generalized condition of this character in its great variability, which is not constant even in the same species. The first anal cell in Panrurus and Sirex californicus is of the type described for the Lydidæ and Xiphydriida, but in Tremer and Xeris the free part of the second anal vein is entirely wanting. The explanation of the obliteration of this vein is found in the following species: In Sirex albicornis the basal two-thirds and the small transverse part is preserved; in Sirem flavicornis only the basal two-thirds is preserved, while in Xeris only a part of the small transverse part remains. It should be noted that in the three species just named the longitudinal part of this vein coincides with the second anal furrow, along which this part of the wing is folded, while in *Paururus*, where the entire free part of the second anal vein is preserved, that the free part of this vein is distinctly before the furrow. There is only one solution possible for the loss of this vein, and that is that it is due to the presence and location of this furrow, which has migrated forward in certain species hand in hand with the reduction of the anal area of the wing. That there is a marked migration of this furrow and reduction of the anal area will be readily seen by an examination of the wings of the different species of Tremer.

The genus Teredon a (fig. 90) possesses a number of interesting fea-

^aThe figure of *Teredon latitarsus* was enlarged from a photomicrograph of the wings of the type in the Collection of the American Entomological Society made and loaned the writer by Mr. J. Chester Bradley.

tures. The radial cross-vein is intermediate in its location between Sirex and Tremex, being almost interstitial with the free part of R₅, which is fully preserved; the transverse part of the base of media has begun to disappear and the radio-medial cross-vein to function for it; the apices of the veins forming the appendiculate cell of the front wing have faded out, so that there is found exactly the same condition in both wings that exists in Tremex; the free part of the second anal vein is preserved and the anal area of the wing is large. All these characters ally this genus more closely with a form like Sirex albicornis than with Tremex, near which it has been placed.

The Siricidæ are a well-circumscribed group, defined by the condition of the area between costa and Sc+R+M, by the relation of media and the medio-cubital cross-vein, by the position of the radio-medial cross-vein, and by the prominent appendiculate cell at the apex of the

front wing.

Megalodontidæ.—This family (fig. 92) contains four genera and about twenty-five species, and is peculiar to Europe, Asia, and north-It represents a line of specialization very similar to that found in the Siricidæ. This is shown by the condition of the base of media and the medio-cubital cross-vein. The cells R, 1st R₁, and 2d R₁+R₂ are arranged in a row. The base of the radial sector is transverse, as in the Lydidæ, but that portion of the sector between the anterior end of the radio-medial cross-vein and the posterior end of the radial cross-vein is not so strongly curved, so that the cell 1st R₁ is almost a parallelogram. The Megalodontidæ differ from the Siricidæ in that the cells R and 1st R, are subequal in size, the cell M, is proportionately much smaller, the cell 2d R₁+R₂ is of about the same length, but is much broader, while the apex of the cell is like that of the Xyelide and Lydide, and is not appendiculate. The anal cells are like those of the typical wing. The area between costa and Sc+R+M is broad, and all trace of the subcosta is wanting. The vein forming the apex of the cell M is a straight one; each of the components of this vein is not separately bowed on the basal side with an emargination between them, as is so characteristic of this vein in the Siricidæ, while it is more strongly inclined than in this latter family. The hind wings are just like those of the Lydida, except that the subcosta is wanting. generalized condition of the apex of the cell R₁₊₂, obliquely truncated and not pointed, is notable.

The forms considered here as constituting the family Megalodontide are invariably classified by systematists as a subfamily of the Lydide. That they do not have any affinities with this family is shown by the difference in the position of the medio-cubital cross-vein, by the difference in the position of the cells R and 1st R_1 , by the entire loss of the subcosta in both wings, by the loss of the free part of Cu_2 , by the straightening of the cubital vein, so that the curve so characteristic of

this vein in the Lydidæ is wanting, by the lack of coalescence between cubitus and Sc+R+M, which extends for almost one-half the length of the vein Sc+R+M in the Lydidæ, and by the difference in the shape of the cell M₄. The facts just given show conclusively that the Megalodontidæ are more closely allied to the Siricidæ than to any other family, while there are an abundance of characters for retaining them as a distinct family.

Cephida.—A family of about a dozen genera and moderately numerous in species of intercontinental distribution. It is not closely related to any of the families described hitherto. The front wings (figs. 93-96) are long and narrow, the hind wings have been remarkably reduced in the anal region, and the insects are very rapid fliers. The area between costa and Se+R+M has been eliminated in both wings. Media separates from radius distant from the stigma, in about the same region as in the Xvelidæ. The cell R is long, subequal in length to the cell R₅, and is in line with the cells 1st R₁ and 2d R₁+R₂, as in the Siricide and Megalodontide, but differs from these families in that the apex of the cell R is almost opposite the apex of the cell 1st R.. The radio-medial cross-vein is transverse. The portion of the radial sector between this cross-vein and the stigma is longitudinal, while the portion of the sector between the radio-medial cross-vein and the radial cross-vein is subtransverse, and might readily be mistaken for a part of the radio-medial cross-vein if it were not for the angle at its anterior end. The radial cross-vein is oblique and appears to be the base of R₃. The cell 2d R₁+R₂ is very long, as in the Siricidæ, but is pointed at tip. The anterior end of the medio-cubital cross-vein is joined to media in certain species distinctly beyond its origin, while in others it arises from the angle between R and M. The cell M, is as long as or longer than the cell R. The cubitus coalesces with Sc+R+M for only a very short distance at base. The cells 1st A and 2d A are subequal in width, and the free part of the second analyein is situated just beyond the middle of cubitus and is perpendicular to the first and third anal veins, while the contraction of the third anal vein is wanting. The hind wings are just as distinctive as the front wings. With the exception of the subcostal area, costa being coalesced with R+M, the number of veins is the same as in the Xiphydriidæ. The most distinctive character is in the arrangement of the cells. Beginning at the base of the wing (fig. 95) the cells 1st A, M₃+Cu+Cu₁, M₄+1st M₂, R+R₅+R₄, and R₃ are arranged in an oblique row from the base to the apex of the wing.

Practically all systematists are agreed in considering the Cephidæ as a distinct group worthy of family rank. So far as the wings are concerned, they are the most distinctive of any group of the Tenthre-dinoidea, and are only indirectly related to any of the other families. They are generalized, so far as the origin of media is concerned, but

are very specialized in the region of the radial and radio-medial crossveins and in the arrangement of the cells of the hind wings in an oblique row.

Oryssidæ. —A small family consisting of four genera and a very limited number of species found in all parts of the world. The family is known to the writer only in the genera Orussus (fig. 97), Ophrunopus, and the notes given here refer only to these genera. It has been found that as a rule the figures of wings given by writers who have not made an especial study of wing venation can not be depended upon. but, judging from such figures of species not accessible to the writer, they would seem to indicate more generalized conditions than those existing in Oryssus. The costal area is narrow; the costa is a delicate vein quite strongly thickened at base; Sc+R+M is a strong vein which functions for the costa, and at the origin of media it bends abruptly toward the stigma; eubitus and Sc+R+M are coalesced for a short distance at the base of the wing; the veins beyond and behind the stigma are nothing more than dark bands of color; the transverse part of media is almost entirely wanting; the radio-medial cross-vein, the base of the radial sector, the free part of R₅, and the transverse part of M₆ are entirely wanting. The weakening of these veins is undoubtedly due to the thickening of the wing membrane. The second anal cell has been reduced, probably by the coalescence of the third anal with the combined first and second anal. The base of R₃ is joined to the stigma by means of the radial cross-vein, as was fully described in the preceding pages. In the hind wings the costa is entirely wanting, R+M is thickened and takes the place of costa; the cubitus and the remainder of the veins are only lines of color; the second anal is entirely wanting; the third anal is preserved as a very delicate line.

So far as their wings are concerned the presence of the second anal cell in the front wings is the only structure that would place the genus *Oryssus* in the superfamily Tenthredinoidea. In their form and topography they are much more like the higher Hymenoptera than the other Tenthredinoidea. It stands at the summit of specialization, so far as this group is concerned, as an extreme isolated line of development.

VII.-SUMMARY.

In the course of the study presented in the preceding pages the following topics have been discussed:

- 1. An historical consideration of those investigations that have had to do with the development of a uniform nomenclature for the wing veins of all orders.
- 2. It has been shown how the complex hymenopterous wing has been developed from a wing of the simplest type.
- 3. How the apex of vein R₁ has been gradually pulled away from the wing margin to form an appendiculate cell.

4. The progressive coalescence of the base of media and radius toward the middle of the wing and, coordinated with this, the progressive migration of the medio-cubital cross-vem toward the point of separation of radius and media to form a transverse support for the stigma.

5. How all the types of anal cells found in the superfamily Tenthredinoidea have been developed from the form of this area found

in the generalized families.

6. The veins of the hind wing have been homologized with those of the front wing and all the marked modifications occurring in the

superfamily discussed.

7. An attempt has been made to show that all the modifications in wing topography are directly dependent on the efficiency of the wing as an organ of flight, and that this efficiency is due to the arrangement of the veins in such a manner as to stiffen the areas of the wing subject to the greatest stress.

8. The venational distinction of the Tenthredinoidea from the other

superfamilies of the Hymenoptera has been pointed our.

9. The distinctive characters of the families of the Tenthredinoidea have been considered in detail and their phylogenetic importance indicated.

- 10. The loss of the base of the radial sector and its bearing on the homology of the veins of the wings of the higher Hymenoptera has been discussed.
- 11. A classification of the superfamily Tenthredinoidea is given. The sequence of the families and subfamilies, whether generalized or specialized, has been determined by a genealogical study of the different structural modifications of the wings.
 - 12. Analytical tables are given for separating the families of the superfamily Tenthredinoidea and of the subfamilies of the family Tenthredinide. These tables are based on venational characters alone, and are examples of the value of such studies as the one given in the preceding pages.

13. Front and hind wings of all the generalized genera and examples selected from the numerous other groups are figured and their wing

veins homologized.

14. All previous classifications have been based on recognition characters and are therefore likely to be artificial. Great use has been made of the form of the antennæ and claws, modifications that have arisen independently several times. The foregoing investigation is only a beginning of what needs to be done. Phylogenetic studies should be made of all those structural parts that will indicate anything as to the complete genealogy of the group. Two such regions are the mouth parts and the structure of the thorax.

TABLE FOR SEPARATING THE FAMILIES OF THE TENTHREDINOIDEA.

- - b. Front wings with the base of subcosta present as a distinct vein....LYDIDÆ
 - bb. Front wings with the base of subcosta wanting, if present, only as a pale indistinct line; the subcosta is represented only by the free part of the vein Sc₁, which is like a cross-vein near the apex of the costal area, and even this is sometimes wanting.
 - c. Front wings with the radial cross-vein ending in the cell R₄, very rarely in the cell R₃; the medio-cubital cross-vein joined to the vein Sc+R+M or to the vein M; if joined to the vein M, the transverse part of the vein M not more than one-sixth the length of the cross-vein.

 - dd. Front wings with the medio-cubital cross-vein either joined to the vein Sc+R+M or to the vein M in the angle between radius and media; the cell 1st R₁+ R₂ always pointed at apex; the veins surrounding the front margin of the cell M₄ never semicircular but always with prominent angles before.
 TENTHREDINID.E
 - cc. Front wings with the radial cross-vein ending in the cell R₅, rarely in the cell R₄; and, if so, with the medio-cubital cross-vein joining media distinctly beyond the radius and subequal in length to the transverse part of media.
 - d. Front wings with the transverse part of the vein M₂ present.
 - e. Front wings with the medio-cubital cross-vein subequal in length with the transverse part of media; the portion of the radial sector between the stigma and the anterior end of the radio-medial cross-vein always distinctly less than the portion between this cross-vein and the posterior end of the radial cross-vein, or when the radial cross-vein is wanting, less than the portion between the radio-medial cross-vein and the anterior end of the free part of the vein R₅, resulting in the apex of the cell R extending but little beyond the base of the cell 1st R₁, or if the radio-medial cross-vein be wanting, the cell R+R₅ extending but little beyond the apex of the cell 1st R₁.
 - f. Front wings with the free part of the vein Sc₁ present and situated near the point of the separation of radius and media; the base of media extending longitudinally and separating from radius distinctly before the anterior end of the medio-cubital cross-vein; the radio-medial cross-vein, when present, transverse and not appearing as the base of the radial sector.......X1PHYDRIID.£
 - ff. Front wings with the free part of the vein Sc_I wanting; the base of media extending transversely and separating from radius either opposite or beyond the anterior end of the medio-cubital cross-vein; the radio-medial cross-vein oblique and appearing as the base of the radial sector.
 - g. Front wings with the area between costa and the vein Sc+R+M hardly more than a line; the cell 2d R₁+R₂ of both wings either appendiculate or extending to the apex of the wing; the free part of the vein M₄+Cu₁ joined to the cell 1st A near its base, never more than twice the length of the free part of the second anal vein from its base.
 SIRICID.E

gg. Front wings with the area between costa and the vein Sc+R+M broad and distinct; the cell 2d R₁+R₂ of the front wings and cell R₁₊₂ of the hind wings never appendiculate, never reaching the apex of the wing, and bluntly rounded at apex; the free part of the vein M₄+Cu₁ joined to the cell 1st A near its apex, over three times the length of the free part of the vein 2d A from its base.

MEGALODONTIDÆ

- dd. Front wings with the transverse part of the vein M_2 wanting..ORYSSIDÆ

TABLE FOR SEPARATING THE SUBFAMILIES OF THE TENTHREDINIDE.

- a. Front wings always with the first and frequently with both first and second anal cells present.
 - b. Front wings with the second anal cell contracted at middle.
 - c. Front wings with the free part of the second anal vein present.
 - d. Radial cross-vein present.
 - e. Front wings with the free part of the vein R₅ present and the cells R₅ and R₄ therefore separate.
 - f. Front wings with the medio-cubital cross-vein and the vein M₃₊₄
 parallel Emphytin.
 - ff. Front wings with the medio-cubital cross-vein and the vein M₃₊₄ strongly divergent behind Phyllotomia.
 - cc. Front wings with the free part of the second analyvein wanting. Selandrinæ bb. Front wings with the second anal cell not contracted at middle.
 - c. Radial cross-vein present.
 - d. Front wings with the medio-cubital cross-vein joined to the vein Sc+R+M at or near the origin of media, its distance from media always less than one-half the length of the cross-vein.
 - e. Front wings with the medio-cubital cross-vein and the vein M_{3+4} parallel.
 - f. Front wings with the base of the third anal vein present and the second anal cell therefore not combined with the third ...LYCAOTINE
 - ff. Front wings with the base of the third analyvein atrophied or at least in part so that the second and third analycells are combined.

BLENNOCAMPINÆ

- e. Front wings with the medio-cubital cross-vein and the vein M₃₊₄ strongly divergent behind.
 - f. Hind wings with the vein R₃ reaching the margin distinctly before the apex of the wing; the cell R₁₊₂ pointed at apex and closed.

SCOLIONEURINÆ

- ff. Hind wings with the vein R₃ reaching the margin at or beyond the apex of the wing; the cell R₁₊₂ round at apex and open ... Fenusine
- dd. Front wings with the medio-cubital cross-vein joined to the vein Sc+R+M distant from the origin of media; its distance from media always one-half or more of the length of the cross-vein.

- e. Front wings with the base of the third analyvein present and the second anal cell therefore not combined with the third.
 - f. Front wings with the medio-cubital cross-vein and the vein M_{3+4} parallel, or at least not divergent behind.
 - g. Front wings with the medio-cubital cross-vein and the vein M₃₊₄ parallel; media separating from radius at the base of the cell M₄; the radio-medial cross-vein rarely, if ever, wanting; hind wings with the cell R₁₊₂ extending to the apex of the wing...Tenthredinine.
 - ff. Front wings with the medio-cubital cross-vein and the vein M₃₊₄ strongly divergent behind HOPLOCAMPINE
- ee. Front wings with the base of the third anal vein atrophied and the second and third anal cells therefore united.......DINEURINÆ
 - d. Front wings with the third and combined first and second anal veins anastomosed at middle for a short distance, the length of the coalescence always being less than the length of the second anal cell.
 - dd. Front wings with the third and combined first and second anal veins anastomosed at middle for a considerable distance, the coalescence being two or three times the length of the second anal cell or the second anal cell wanting or combined with the third anal cell.
 - e. Front wings with the portion of the free part of M₃ situated between the apex of the vein M₃₊₄ and the basal end of the medial cross-vein always more than one-half, usually subequal, and frequently greater in length than the free part of the vein M₄, causing the cell M₄ to appear distinctly longer longitudinally than transversely; the free part of the vein M₄+Cu₁ perpendicular to the first anal vein, if oblique, inclined toward the apex of the wing.
 - f. Front wings with the free part of the vein Sc, present.

 - gg. Front wings with the cell R_{1+2} appendiculate at apex or open, never closed at the wing margin before the apex of the wing.

HYLOTOMINÆ

f. Front wings with the free part of the vein Sc₁ always wanting.

SCH1ZOCERIN.E

- aa. Front wings always with both the first and second anal cells wanting.
 - b. Front wings with the free part of the vein M₄+Cu₁ distinctly beyond the posterior end of the medio-cubital cross-vein.
 - c. Hind wings with the cell R_{1+2} distinctly appendiculate.

cc. Hind wings with the cell R_{1+2} never appendiculate, but open at apex.

d. Front wings with the cell R_{1+2} not appendiculate; hind wings with the portion of the vein R_{5+M} forming the base of the cell R_{1+2} transverse.

Acordulacerinæ

dd. Front wings with the cell R_{1+2} appendiculate; hind wings with the portion of the vein $R_{5}+M$ forming the base of the cell R_{1+2} longitudinal.

Pterygophorinæ

bb. Front wings with the free part of the vein M₄+Cu₁ interstitial with the mediocubital cross-vein, at most not more than the width of the vein beyond the cross-vein Pergine

LIST OF ABBREVIATIONS.

1st A	=First anal vein.	m-eu	=Medio-cubital cross-vein.
2d A	=Second anal vein.	R	=Stem of radius.
3d A	=Third anal vein.	r	=Radial cross-vein.
C	=Costa.	R_1	=First branch of radius.
ct	=Contraction in second anal	R_2	=Second branch of radius.
	cell.	R_3	=Third branch of radius.
Cu	=Stem of cubitus.	R_4	=Fourth branch of radius.
Cu ₁	=First branch of cubitus.	R_5	=Fifth branch of radius.
Cu_2	=Second branch of cubitus.	rf	=Radial furrow.
М	=Stem of media.	Rs	= Radial sector.
m	=Medial cross-vein,	R + M	=Combined stems of radius
M_1	=First branch of media.		and media.
M_2	=Second branch of media.	r-m·	=Radio-medial cross-vein.
M_3	=Third branch of media.	$\mathrm{R} + \mathrm{Se}_2$	=Combined radial stem and
M_4	=Fourth branch of media.		second branch of sub-
M_{1+2}	=Stem of the first and second		costa.
	branches of media.	8	=Stigma.
M_{3+4}	=Stem of the third and fourth	Se	=Stem of subcosta.
	branchas of media.	Sc_1	=First branch of subcosta.
M_4 + Cu_1	=Combined fourth medial and	Se_2	=Second branch of subcosta.
	first cubital branches.	$Se+R+\lambda$	I=Combined stems of subcosta,
$M_1 + R_{4+5}$	=Combined first medial and		radius, and media.
	fourth and fifth radial	$_{\mathrm{sp}}$	=Secondary spur.
	branches.	SV	=Spring vein.

EXPLANATION OF PLATES.

PLATE XXI.

- Fig. 21. Wing of Pantarbes capito.
 - 22. Wing of Erax furax.
 - 23. Wing of Tabanus lineola.
 - 24. Wing of Scenopinus fenestralis.
 - 25. Wing of Rhamphomyia sp.

PLATE XXII.

- Fig. 26. Wing of Musca domestica.
 - 27. Wing of Conops affinis.
 - 28. Wing of Midas militaris.
 - 29. Front wing of Nemoura completa.
 - 30. Front wing of Taniopteryx frigida.

PLATE XXIII.

- Fig. 31. Wings of Megaxyela major.
 - 32. Wings of Odontophyes avinigrata.
 - 33. Wings of Macroxyela ferruginea.

PLATE XXIV.

- Fig. 34. Wings of Manoxyela sp.
 - 35. Wings of Xyela julii.
 - 36. Wings of Neurotoma fasciata.

PLATE XXV.

- Fig. 37. Wings of Lyda erythrocephala.
 - 38. Wings of Canolyda semidea.
 - 39. Wings of Pamphilius pallimacula.

PLATE XXVI.

- Fig. 40. Wings of Itycorsia hieroglyphica.
 - 41. Wings of Bactroceros depressus.
 - 42. Wings of Cephaleia abietis.

PLATE XXVII.

- Fig. 43. Wings of Liolyda frontalis.
 - 44. Wings of Blasticotoma filiceti.
 - 45. Wings of Lophyrus sp.

PLATE XXVIII.

- Fig. 46. Wings of Emphytus balteatus.
 - 47. Wings of Eriocampa ovata.
 - 48. Wings of Pseudosiobla excarata.

PLATE XXIX.

- Fig. 49. Wings of Dolerus thomsoni.
 - 50. Wings of Stromboceros signarius.
 - 51. Wings of Strongylogaster cingulatus.

PLATE XXX.

- Fig. 52. Wings of Eriocampoides athiops female.
 - 53. Wings of Eriocampoides varipes male.
 - 54. Wings of Phyllotoma vagans.

PLATE XXXI.

- Fig. 55. Wings of Lycaota sodalis.
 - 56. Wings of Tenthredo flara.
 - 57. Wings of Macrophya albicincta.

PLATE XXXII.

- Fig. 58. Wings of Pachyprotasis rapa.
 - 59. Wings of Trichiosoma lucorum
 - 60. Wings of Clarellaria amerina.

PLATE XXXIII.

- Fig. 61. Wings of Hoplocampa ferruginea.
 - 62. Wings of Hemichroa americana.
 - 63. Wings of Dineura geeri.

PLATE XXXIV.

- Fig. 64. Wings of Mesoneura opaca.
 - 65. Wings of Pseudodineura hepatica.
 - 66. Wings of Cladius pectinicornis.

PLATE XXXV.

- Fig. 67. Wings of Monoctenus juniperi.
 - 68. Wings of Pteronus paridus.
 - 69. Wings of Periclista melanocephala.

PLATE XXXVI.

- Fig. 70. Wings of Rhadinocerwa reitteri.
 - 71. Wings of Phymatocera aterrima.
 - 72. Wings of Blennocampa alternipes.

PLATE XXXVII.

- Fig. 73. Wings of Kaliosysphinga dohrnii.
 - 74. Wings of Fenusa pygmwa.
 - 75. Wings of Scolioneura betuleti.

PLATE XXXVIII.

- Fig. 76. Wings of Hylotoma virescens.
 - 77. Wings of Pachylota audouinii.
 - 78. Wings of Labidarge dibapha.

PLATE XXXIX.

- Fig. 79. Wings of Dielocerus formosus.
 - 80. Wings of Perreyia vitellina.
 - 81. Wings of Pterygophorus cinctus.

PLATE XL.

- Fig. 82. Wings of Loboceras frater.
 - 83. Wings of Acordulecera sp.
 - 84. Wings of Perga sp.

PLATE XLI.

- Fig. 85. Wings of Xiphydria maculata.
 - 86. Wings of Paururus cyaneus.
 - 87. Wings of Sirex californicus.

PLATE XLII

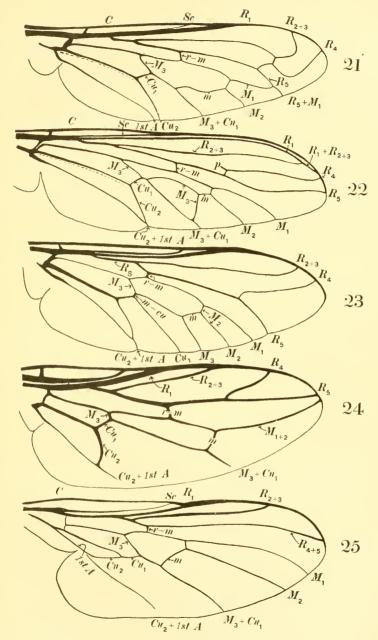
- Fig. 88. Wings of Sirex albicornis.
 - 89. Wings of Xeris spectrum.
 - 90. Wings of Teredon latitarsis.
 - 91. Wings of Tremex columba.

PLATE XLIII.

- Fig. 92. Wings of Megalodontes spissicornis.
 - 93. Wings of Janus integer.
 - 94. Wings of Janus abbreviatus.

PLATE XLIV.

- Fig. 95. Wings of Macrocephus satyrus.
 - 96. Wings of Cephus pygmaus.
 - 97. Wings of Oryssus abietinus.

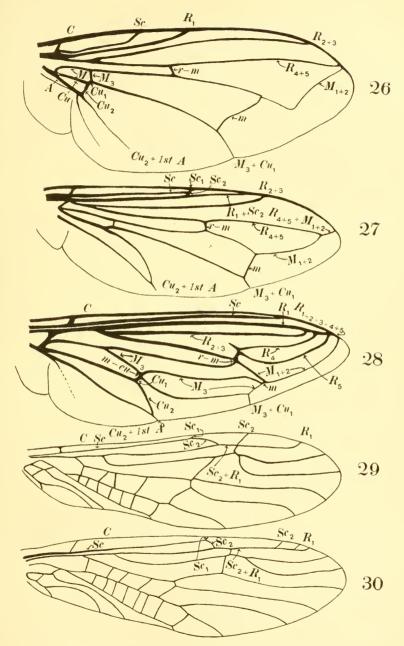


WINGS OF PANTARBES, ERAX, TABANUS, SCENOPINUS, AND RHAMPHOMYIA.

FOR EXPLANATION OF PLATE SEE PAGE 651,

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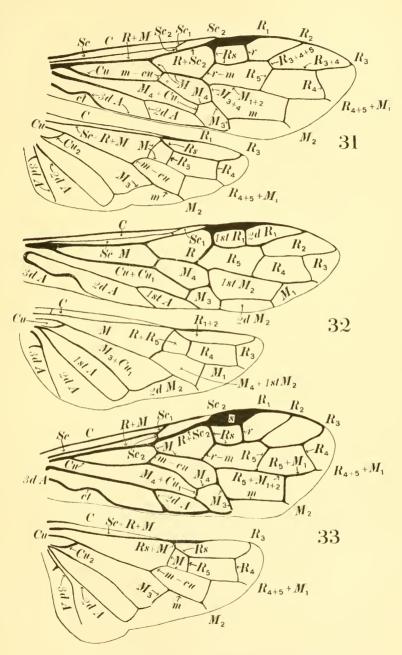




WINGS OF MUSCA, CONOPS, MIDAS, NEMOURA, AND TÆNIOPTERYX.

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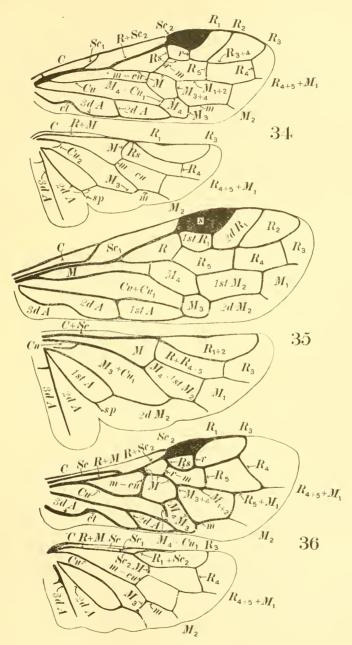




WINGS OF MEGAXYELA, ODONTOPHYES, AND MACROXYELA.

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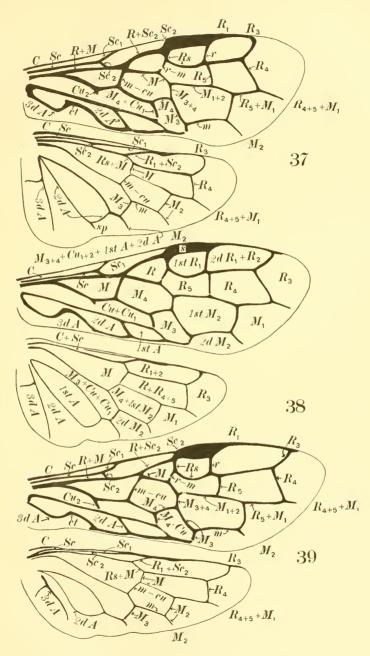




WINGS OF MANOXYELA, XYELA, AND NEUROTOMA

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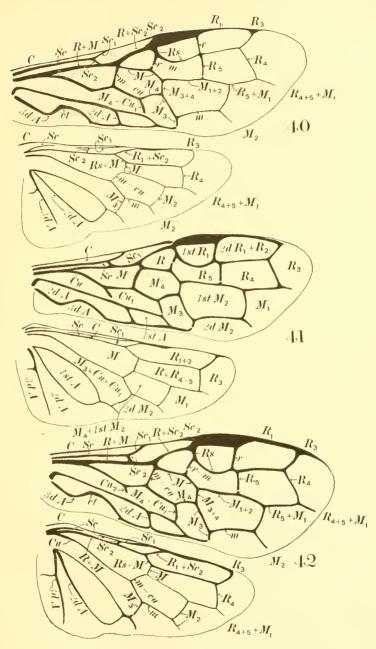




WINGS OF LYDA, CÆNOLYDA, AND PAMPHILIUS.

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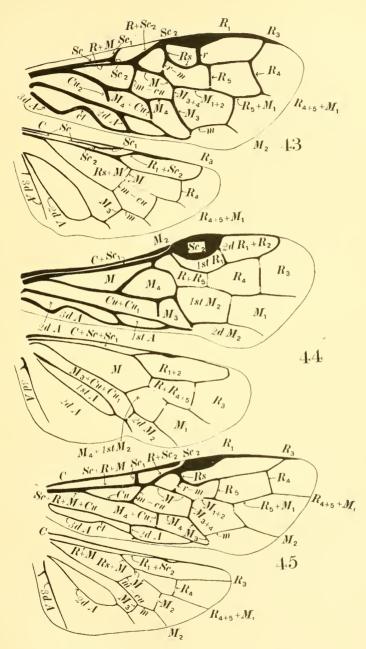




WINGS OF ITYCORSIA, BACTROCEROS, AND CEPHALEIA.

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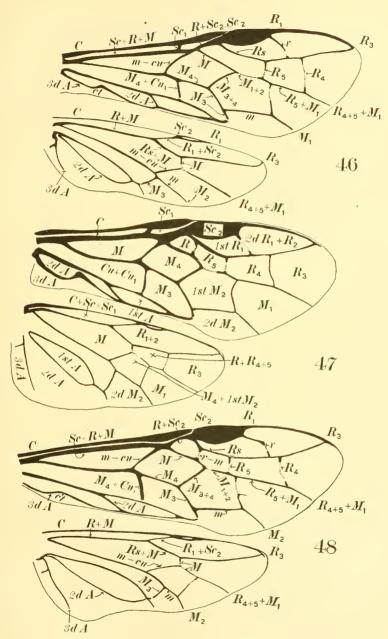




WINGS OF LIOLYDA, BLASTICOTOMA, AND LOPHYRUS.

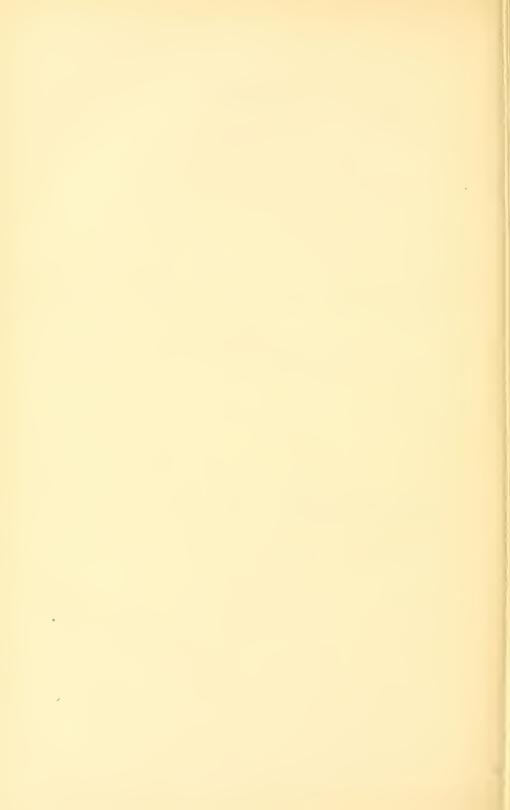
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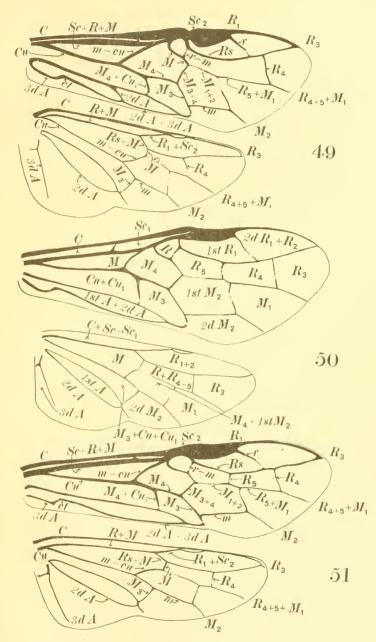




WINGS OF EMPHYTUS, ERIOCAMPA, AND PSEUDOSIOBLA.

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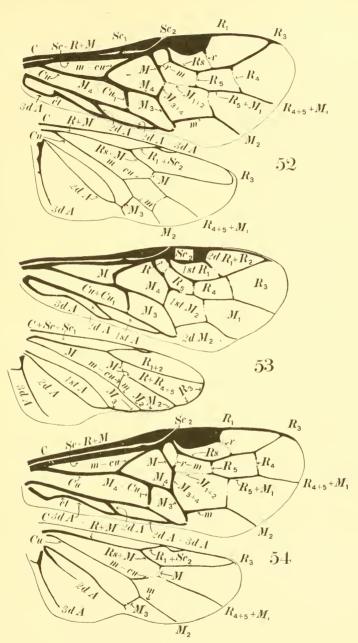




WINGS OF DOLERUS, STROMBOCEROS, AND STRONGYLOGASTER.
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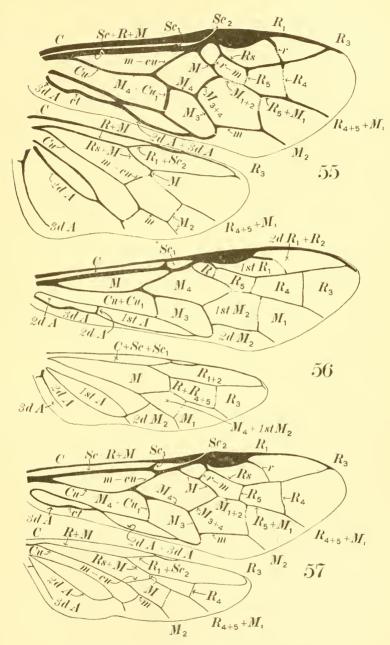




WINGS OF ERIOCAMPOIDES AND PHYLLOTOMA.

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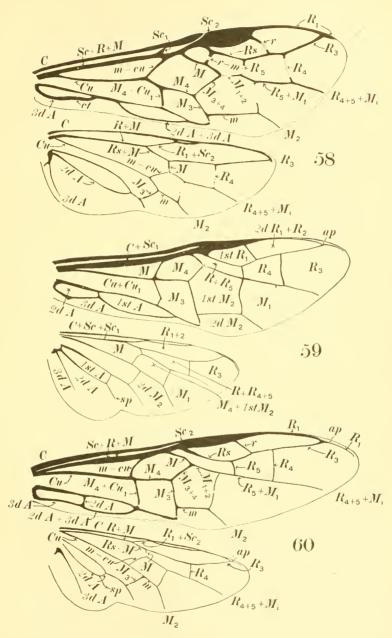




WINGS OF LYCAOTA, TENTHREDO, AND MACROPHYA.

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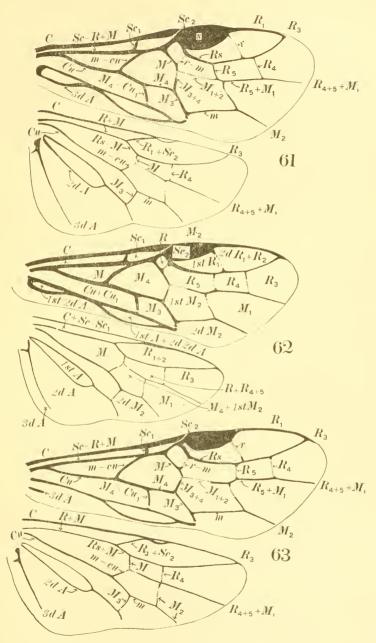




WINGS OF PACHYPROTASIS, TRICHIOSOMA, AND CLAVELLARIA.

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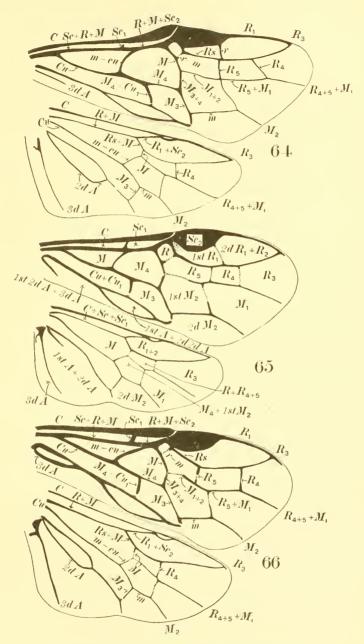




WINGS OF HOPLOCAMPA, HEMICHROA, AND DINEURA.

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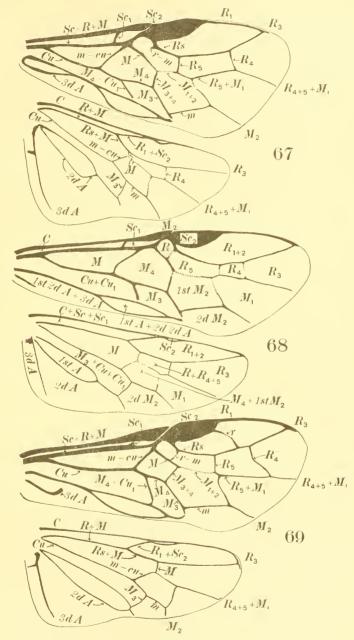




WINGS OF MESONEURA, PSEUDODINEURA, AND CLADIUS.

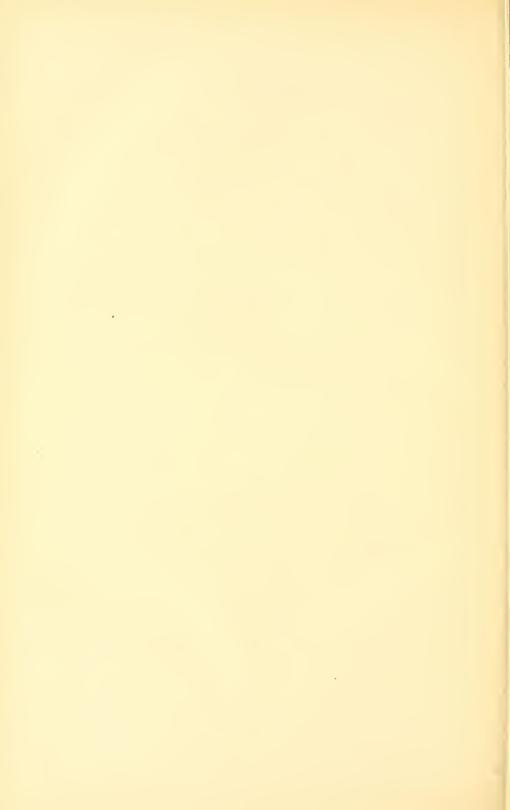
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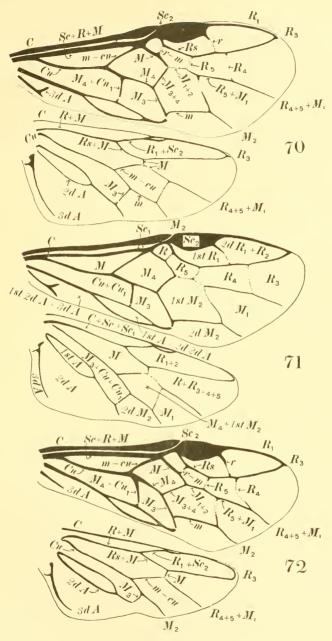




WINGS OF MONOCTENUS, PTERONUS, AND PERICLISTA.

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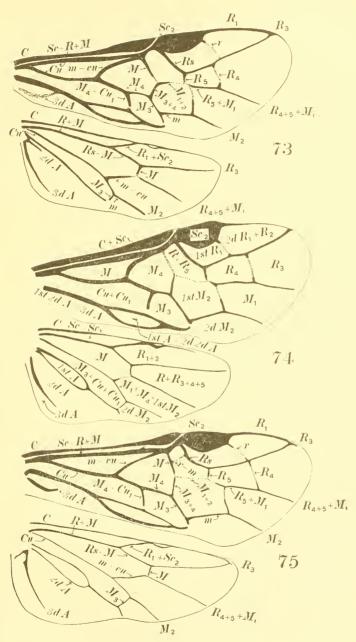




WINGS OF RHADINOCERÆA, PHYMATOCERA, AND BLENNOCAMPA.

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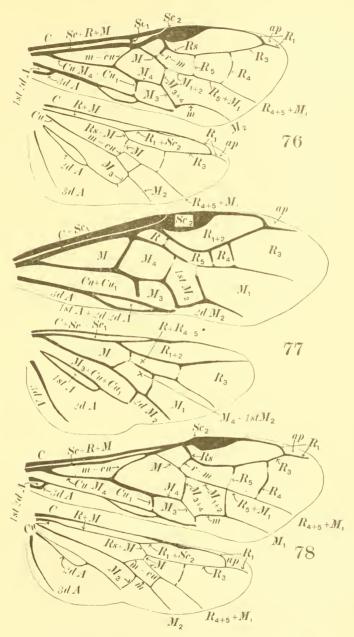


WINGS OF KALIOSYSPHINGA, FENUSA, AND SCOLIONEURA.

FOR EXPLANATION OF PLATE SEE PAGE 653.

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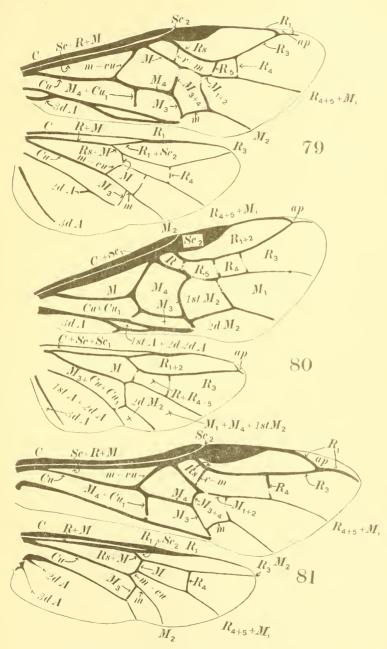




WINGS OF HYLOTOMA, PACHYLOTA, AND LABIDARGE.

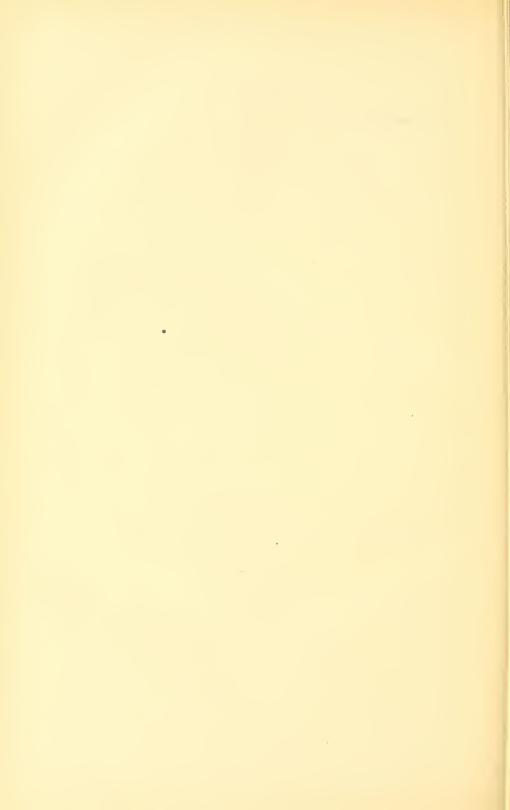
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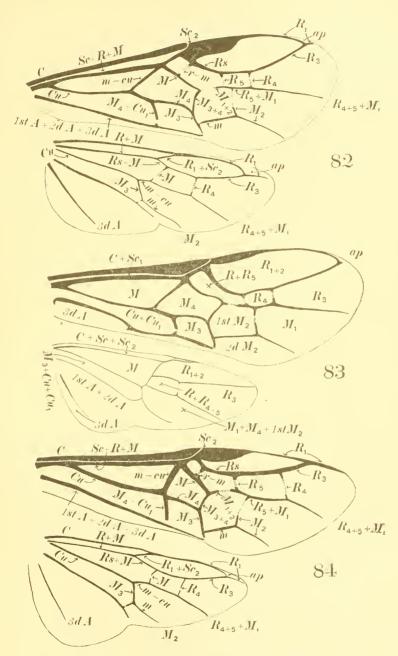




WINGS OF DIELOCERUS, PERREYIA, AND PTERYGOPHORUS.

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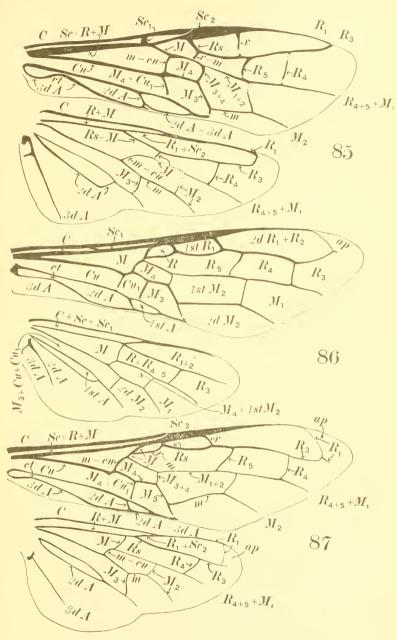




WINGS OF LOBOCERAS, ACORDULECERA, AND PERGA.

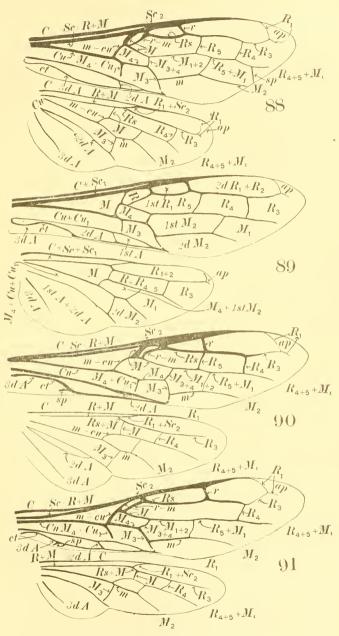
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WINGS OF XIPHYDRIA, PAURURUS, AND SIREX.
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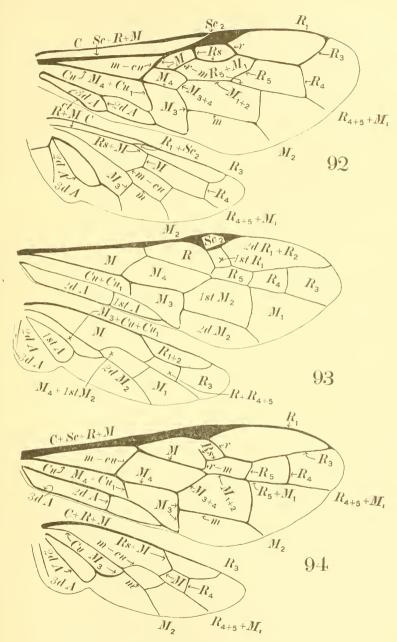




WINGS OF SIREX, XERIS, TEREDON, AND TREMEX.

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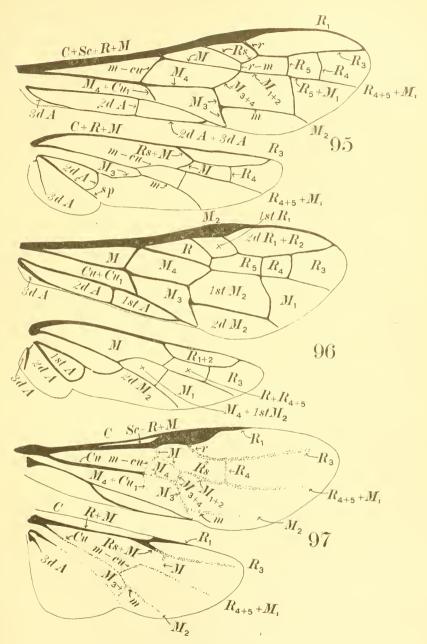




WINGS OF MEGALODONTES AND JANUS.

FOR EXPLANATION OF PLATE SEE PAGE 654.





WINGS OF MACROCEPHUS, CEPHUS, AND ORYSSUS.

FOR EXPLANATION OF PLATE SEE PAGE 654.

