ON THE CLASPING ORGANS ATTACHING THE HIND TO THE FORE WINGS IN HYMENOPTERA

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WITH TWO FIGURES IN THE TEXT AND FOUR PLATES

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I. Introduction

It has long been known that in many four-winged insects peculiar clasping contrivances are present which unite the fore and hind wings during flight in such a manner that they together form a homogeneous surface and act like a single wing. Thus, according to Kolbe (1893, p. 255), many crepuscular and nocturnal Lepidoptera—the Sphingids, Noctuids, Geometrids, Cheloni, and Pyralids—possess a thorn or a group of bristles on the upper side of the base of each hind wing, which inserts itself into a small band-shaped structure formed of hair-scales situated on the under side of the corresponding fore wing near its base, and thus effects the union of the two wings. In the Sesiids, Cicadids, and Trichoptera this union is brought about by the hind margin of the fore wing folding over and interlocking with the inversely folded front margin of the hind wing. The highest development of such a clasping apparatus is met with in the Hymenoptera. In these, fine chitinous hooks, arranged in a row, arise from the front margin of the central part of the hind wing and insert themselves into the involuted hind margin of the fore wing. A closer examination, particularly from the morphological point of view, has up to the present never been accorded these structures, and Professor von Lendenfeld suggested to me in the autuumn of 1902 to investigate these structures. I may be permitted here to express my sincere thanks to my highly esteemed chief and teacher, not only in giving me the inspiration for this work, but also for his friendly support during its progress, and to the Smithsonian Institution for a grant from the Hodgkins Fund of that Institution which enabled me to obtain the material and instruments necessary for the work.

II. Historical Review

In nearly all entomological text-books and monographs on Hymenoptera, the wing-clasping apparatus characteristic of this order is mentioned and its function briefly explained; but in none of these works is there a discussion of the anatomical conditions involved, nor do good figures, particularly of transverse sections, exist of these structures. Chabrier's figures (1822, pl. X, fig. 4; pl. XIII, fig. 8) of a transverse section through the fore and hind wing of a bumblebee are so primitive and diagrammatic that it is obvious that the author never saw a transverse section of a hymenopterous wing under the microscope.[1] Other figures of sections through the contact region of hymenopterous wings are unknown to me. The very small number of existing works which treat especially of the clasping hooks of the Hymenoptera are for the most part purely systematic. The best and most detailed of these is Miss Staveley's (1860, Trans. Linn. Soc., London, vol. XXIII, pp. 125-138, pls. 16, 17). She describes the shape and arrangement of the hooks of the hind wing and the groove formed by the hind margin of the fore wing, and gives, based on the morphology of the costal vein and the grouping, topographic position, form and number of the hooks, a key for determining the species which will be discussed in the systematic part of this paper. Staveley mentions (1860, p. 125) that the clasping hooks have already been described and figured by older microscopists without giving any exact bibliographical references. Two smaller treatises, by Gray (1860, p. 339-342) and Staveley (1862, p. 122-123), are only supplementary to the above-cited work. Recently the variability of the number of hooks in the bee have been studied from the biometric standpoint (Koschewnikoff, cited from Bachmetieff, 1903, p. 41-43).

[1]An instructive diagram of the wing connection (surface view) is given by Sharp (1895, p. 494).

III. Material and Methods

In my investigations I used dry, spread, material as well as material preserved in liquids; the former for surface preparations of entire wings and for sections in celloidin, the latter for the thin paraffine sections necessary for a detailed study under higher powers. Surface preparations are easily made by simply inclosing the entire wings in Canada balsam. To remove the air retained in the veins, which is very disturbing, it is advisable to boil the wings in chloroform before mounting. If this be done until no more air bubbles escape from the cut ends of the veins, and the wings are then immediately transferred to the balsam, the veins will be found free from air. To obtain sections 20 to 30 microns thick, showing the mode of connection between the fore and hind wings (pl. IX), I had to embed in celloidin, because paraffine wing-sections of this thickness fall to one side as soon as the paraffine is dissolved, the wings being very thin. The celloidin, of course, keeps these high sections, standing on edge, securely upright. The objects destined to be embedded in celloidin were treated in the following manner: The insect, killed in fumes of chloroform or cyanide, with the wings hooked together, was carefully spread and, according to its size, was dried for a half or a whole week. Then I removed the two wings, still hooked together, along with the accompanying part of the thorax, boiled them in chloroform, and brought them through absolute alchohol, ether and alcohol, and ether into celloidin. Standing proved superfluous in my celloidin sections. For the study of finer details, particularly the linking of the hooks and hairs, thinner stained paraffine sections are necessary. The most favorable specimens for this kind of examination are the still soft and pliable wings of young, newly emerged imagos. I fixed wings of this kind with good success in alcohol and sublimate and also in 4 per cent formol, and preserved them in 70 per cent alcohol. The chitin of the wings in older individuals is very hard and brittle, splinters in cutting, and rarely yields good sections. I tried several times to soften hard chitin by means of diluted nitric acid, Javelle water, and caustic potash, but had no success worthy of note. A relatively good method of making hard chitinous parts somewhat more pliable is the one used by Hoffbaner (1892, p. 583), of allowing the wings to remain in paraffine a long time. The best stains for the paraffine sections proved to be concentrated aqueous solution of eosin and concentrated alcoholic solution of safranin, which were taken up fairly well by the chitin. Hæmatoxylin (Delafield's) rendered good services in the staining of pupal wings.

LIST OF THE SPECIES OF WHICH WING SECTIONS WERE STUDIED

(Of the species printed in italics paraffine sections, permitting a closer study under higher powers, were made. Of the others, only thicker celloidin sections were studied.)

Tenthredinidæ: *Tenthredo mesomelæna L., Sirex gigas L.*

Ichneumonidæ: Exetastes fornicator Grav., Campoplex aculeator Holmgr., Dyspetes prærogator Thoms., Henicospilus ramidulus Steph., *Rhyssa persuasoria Grav., Ichneumon fusorius L.*

Formicidæ: Formica rufa L., *Camponotus ligniperdus Mayr.*

Fossores: Pompilus viaticus Fabr., Ammophila subulosa Latr., *Crabro vagus Fabr.*

Vespidæ: Vespa crabro L., *Vespa rufa L., Vespa vulgaris L.*

Anthophila: Anthrena ovina Klug., *Xylocopa violacea Latr.,* Megachile ericetorum Lep., *Bombus lapidarius Walk., Bombus terrester L., Psithyrus rupestris Lep., Apis mellifica L.*

IV. ANATOMICAL PART

HIND WING

The hind wing of Hymenoptera bears on its front margin two kinds of chitinous appendages, the clasping hooks and the marginal bristles, which, during flight, are in contact with the fore wing. Of the hooks two types, differing from each other morphologically, topographically, and in part also functionally, are to be distinguished. These have already been distinguished by Staveley as distal hooks and subbasal hooks.

The distal hooks, which play the principal rôle in uniting the wings during flight, are located on the anterior margin of the hind wing, on the upper side of the costal vein. In the Tenthredinidæ and Uroceridæ they are arranged somewhat irregularly, often appearing to form a double row (pl. VII, fig. 3); in all the other families, when present in large numbers, a single row (pl. VII, figs. 1, 2, 5, 7-9; pl. VIII, figs. 10-13). This hook-row begins, as the figures show, before, at, or behind the place where the cross-vein branches from the costal vein, and extends not quite half way of the distance between this branching and the apex of the wing. This region of the wing is commonly indicated as the frenum; therefore, instead of the not very characterizing name "distal hooks," perhaps the term "frenal hooks" could be used for these appendages. The hooks of the Tenthredinidæ and Uroceridæ do not form two strictly parallel rows, but rather a row of hooks standing in groups of twos—in large forms, also in threes. The arrangement of the individual hooks of these groups is irregular and variable, not only in different species, but also within the same species. In the forms with a single row the distal hooks usually lie in a straight line parallel to the margin of the wing; sometimes, as in many Ichneumonids, they form a gentle curve open towards the anterior margin of the wing. The intervals between the individual hooks differ greatly. In the genera *Bombus* and *Xylocopa* they are very close together, comb-like, in contact with each other at the base; in the other Anthophilids and the remaining families they are 50 to 200 microns apart. The strongest and largest hooks generally stand farthest apart, so in the Vespids the first ones and in the Ichneumonids the middle ones, but no uniformity can be recognized in this respect. The number of the distal hooks in the different species varies exceedingly, from two (*Proctotrupes*) to about 50 (*Sirex*). Even among different individuals of the same species the number of hooks is very variable. This, as well as the availability of the number and arrangement of the hooks for systematic purposes, will be dealt with below in the systematic part.

The distal hooks have the shape of rather flat bands. Only at the base, and just above it, the cross-sections are circular (pl. X, fig. 31); towards the tip, they soon become elongated, elliptical. The shape of a distal hook can be readily made out by the aid of fig. 10 on plate VIII (surface view) and fig. 22 on plate IX (transverse section). The hook describes an arc, open towards the wing surface. This arc does not, however, extend in a plane, but describes half to three-quarters of a spiral, the axis of which is parallel to the costal vein. The basal portion of the hook is inclined towards the costal vein. With this it incloses an angle of 40 to 60 degrees and with the wing surface an angle of 90 to 120 degrees. When the latter approaches 120 degrees the central parts of the hooks project beyond the anterior margin of the wing, particularly when this margin is strongly turned down, as in the flower-wasps (pl. VII, figs. 7, 9; pl. VIII, figs. 11, 12, 13). The stouter hooks of the series are particularly strongly bent. The distance between their ends and the wing surface is less than the space taken up by the corresponding part of the groove of the fore wing (made clearer by lines in pl. IX, fig. 22). As the transverse sections (pl. IX, figs. 19-25), show, the hooks are uniformly curved and, however much twisted, never, as the surface view might lead one to assume, abruptly bent at any point. If a hook were straightened out, its form would be lanceolate. It is broadest in the middle and narrows towards the apex, finally tapering to a point. A tubular cavity extending the entire length of the hook is always clearly discernible. Conforming to the shape of the hook, this cavity, in transverse section, is circular or punctiform at the base (pl. x, figs. 31, 1), and shaped like a narrow slit farther up. It appears to terminate some distance below the apex. I have never been able to see an orifice at the end of a hook. This hook-cavity is, as a rule, in open connection with the cavity of the costal vein, but this communication may be interrupted by soft matrix or chitinous layers secondarily formed. Sometimes the walls of the costal vein itself are thickened to such an extent that its lumen is obliterated and the vein itself converted into a solid rod, from which it is to be inferred that these cavities generally are not of any importance. The costal vein is sometimes considerably broadened in the frenal region, sometimes throughout the whole hook region (pl. VII, fig. 6); sometimes it is dilated at the point of insertion of each hook (pl. VII, fig. 4). In most cases, however, it shows no distinct differentiation in the hook region except a slight incurving at the base of the hooks. The distal hooks are inserted in the upper surface of its wall, either in the middle of its broad face or nearer to the wing margin (pl. x, figs. 27-29). It is interesting that the Tenthredinids and Anthophilids, which are systematically very far removed from each other, also show the greatest differences in the mode of attachment of the hooks, while in the families systematically intermediate transitional forms of hook attachment are seen. The difference in the mode of insertion of the hooks appear to be correlated to the differences in the formation of the costal vein, and not solely dependent upon differences of habit. For the investigation of these conditions in the Tenthredinids I had at my disposal, besides *Tenthredo mesomelæna* L., abundant and excellent specimens of *Sirex gigas* L., an ideal material for this work on account of its large size. In both species I found the hooks quite similarly inserted. I will therefore describe them together. *Sirex gigas* is, like the other Tenthredinids, remarkable for the thinness of the wing-lamellæ and the spacious cavities in its wing veins. Its hooks are very much flattened, distinctly ribbon-shaped. The attachment of the hooks involves considerable modifications of the wall of the costal vein at the points of insertion. The hooks are inserted in circular openings of the vein wall, the margins of which are raised up to form elevated rings, both outside and in. The outer elevation is very slight (pl. x, figs. 27, 28, 29, R), while the inner one attains considerable dimensions. These elevated rings are not cylindrical, but form semi-globular pans (pl. x, figs. 27, 28, 29, P). In sections through the wings of fully developed specimens caught on the wing the cavity of the pan is not in connection with the lumen of the vein. In young, not fully colored specimens cut out of pine wood, I found the bottom of the pan perforated; but in the center in every case there was distinguishable a differentiated bordering layer between the pan-cavity and the matrix of the costal vein (pl. x, fig. 27, Gr). In older animals also the bottom of the pan sometimes appears centrally perforated in cross-section, but in this case the edges of the opening are sharply broken, and clearly indicate that the missing piece of the bottom has broken away in sectioning, on account of the well-known brittleness of older chitin (pl. x, fig. 28). This difference between young and fully developed specimens shows that the closing of the chitinous pan is effected by chitin secreted after the formation of the wing-lamellæ. The pan is about 37 microns wide. Its outer opening is covered, like a drum, by a fine membrane, which appears as a continuation of the outer layer of the upper wing lamella (pl. x, fig. 28, Me). Centrally this membrane incloses the hook, the basal part of which projects about 15 microns into the cavity of the pan. The hook has a diameter of 22 microns. It is not thickened at the base. The lumen of the hook (pl. x, fig. 28, I) terminates basally with a funnel-shaped extension. Numerous fine, transparent chitinous threads arising from the inner wall of the pan, attach themselves to the basal end of the hook (pl. x, fig. 28, F) and hold it fast. From the central portion of the bottom of the pan no such threads arise. This contributes to the ease with which this part of the pan is broken away in sectioning.

A type of insertion wholly different from this is found in the Anthophilids. In these Hymenoptera the wall of the costal vein is extremely thick. Sometimes the two lamellæ forming it, of which the upper is always considerably the thicker, touch each other, so that the vein lumen entirely disappears (pl. x, fig. 30). It is perhaps on account of the strength of the walls of the costal vein, that the mode of inserion of the hooks is much less complicated in the Anthophilids than in the Siricids. I particularly examined the distal clinching hooks, peculiar to the Anthophilids, in *Apis mellifica* L., *Bombus terrestris* Latr., *Bombus lapidarius* Walck., and *Megachile ericetorum* Lep. The upper lamella of the costal vein, very stout in all the species of this family, forms prominent ring-shaped thickenings round the bases of the distal hooks (pl. x, fig. 30, R), which are homologous with the elevated rings of the Tenthredinids. The prominences are centrally perforated by conical tubes into which the basal ends of the hooks are inserted. The considerably thickened basal end of each hook fits closely into this tube, so that the hooks appear firmly embedded in the costal vein (pl. x, fig. 30). The distal hooks of

Apis mellifica are at the point of insertion in the tube about 12 microns and at the basal end about 15 microns thick. The lumen of the hook, which in the Anthophilids possessing a hollow costal vein is in open communication with the lumen of the vein, does not terminate with a funnel-shaped extension ; at the most, such an extension is only slightly indicated. This anthophorid type of hook insertion possesses the decided advantage of greater strength over the tenthredinid type, but this greater strength is gained at the expense of that elasticity and movability which is attained in the Tenthredinids through the attachment by means of the drum membrane and the chitin threads. The distal hook of a bee or bumblebee can only be removed from the wall of the costal vein, without being itself broken, by shattering the costal vein to which it is attached. As a result of this, during the upward stroke of the wings, the fore wing presses principally on the central parts of the hooks in the Anthophilids, while in the Tenthredinids this pressure is transmitted to the drum membranes covering the pans and the chitin threads attached to the bases of the hooks. In accordance with this, the distal hooks of the Anthophilids are considerably broader, longer, and thicker than the typically ribbon-shaped hooks of the Tenthredinidæ. Numerous transitional forms connect these extremes. The Anthophilidæ type is by far the most common, narrowness of the lumen of the costal vein, or even solidity of it, being the rule.

Besides the distal hooks, in many Hymenoptera another kind of hook occurs—Staveley's subbasal hooks. These are situated, as the name implies, near the base of the wing, and sometimes also halfway between this and the distal hooks (pl. VII, fig. 3, SbH ; pl. VIII, figs. 14-18). They are not met with in all the families, and show great diversity in regard to number, arrangement, and development. In the Vespidæ, Formicidæ, Evaniidæ, and Proctotrupidæ they are wholly absent. In some Apids and Fossores they can be recognized as slightly curved, stump-like processes, placed midway between the basis of the wing and the distal hooks, generally nearer the latter. Many genera of these families, however, are entirely without them. It appears doubtful whether the chitinous structures of the Cynipidæ, Braconidæ, and Tenthredinidæ corresponding to the subbasal hooks of other families, should be designated as clasping organs, because they are hardly at all curved. Only in a single species of the last-named family, in *Pamphilius hypotrophicus* D. T., I discovered curved subbasal hooks. These are very peculiarly bent, about ten in number, and form a group near the base of the wing (pl. VIII, fig. 15). In *Sirex gigas* L. appendages are found in the same location, which partly resemble subbasal hooks and partly marginal bristles (pl. VIII, fig. 18). The Ichneumonidæ and Chrysididæ possess well developed, highly differentiated subbasal hooks. In the first these arise close to the base of the wing from the upper of the two branches into which the costal vein divides at its origin (pl. VIII, fig. 3; pl. VIII, fig. 16). In the Ichneumonidæ there is either only one subbasal hook or a group of hooks standing close together, while in the Chrysididæ, where always a considerable number of them is present, the hooks stand at greater and irregular intervals (pl. VIII, fig. 17). The subbasal hooks are directed obliquely towards the apex and outer side of the wing. With the costal vein they inclose an angle of about 50 to 80 degrees (pl. VIII, figs. 14-18), and with the wing surface, as the accompanying diagrammatic figure of a cross-section shows, an angle of about 140 to nearly 180 degrees. When this angle approaches 180 degrees these hooks lie almost wholly in the plane of the wing surface.

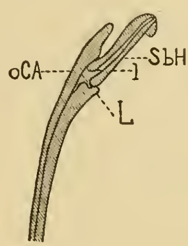


FIG. 20.

In their outward appearance the subbasal hooks differ from the costal hooks principally by their being less curved; only just below the distal end they are bent. Like the distal hooks, their transverse section is circular at the base, and narrow, elliptical distally. They arise from the upper side of the costal vein; or, when this is bifurcate, from its anterior branch, in the same manner as the distal hooks (pl. VIII, figs. 15, 16, 17, oCA). The anterior branch of the costal vein is, in the Ichneumonidæ, short and thickened in the region of the subbasal hooks. It is, as the sections show, often provided with an entirely isolated lumen. Like the distal hooks, the subbasal hooks possess a lumen, in transverse sections circular or punctiform at the base and slit-shaped distally. When the vein from which the hooks arise is hollow the hook cavity openly communicates with the vein cavity. Distally the hook cavity terminates below the pointed apex of the hook; its end is closed. The manner of insertion is the same as in the distal hooks. The points of insertions do not, however, lie central on the broad side of the costal vein, which is elliptical in cross-section, but greatly approximated to the margin of the wing; at times wholly marginal. (Compare the above diagram, fig. 20, of a cross-section through the wing of an ichneumon-wasp in the region of the subbasal hooks.)

Besides the distal and subbasal hooks, the anterior margin of the hind wing, as a rule, bears more or less strongly developed marginal bristles. In the Tenthredinidæ these are very poorly developed and sometimes wholly wanting; in the Ichneumonidæ and Chrysididæ they are well developed, and they are strongest and stoutest in the Vespidæ and Anthophilidæ (especially in Bombus). They usually stand in three dense, comb-like groups or rows, the first near the base of the wing (pl. VIII, fig. 16), the second before (pl. VII, figs. 1, 6 B 2, 9; pl. VIII, figs. 11, 12, 13), and the third beyond the distal hooks (pl. VII, figs. 1, 6 B 3, 9; pl. VIII, figs. 11, 12). These three groups are not always distinctly developed; the group before the distal hooks is the one most frequently observed and the most highly developed. The marginal bristles are not, like the hooks, restricted to the costal vein, but also attached to the parts of the wing membrane adjacent to the costal vein (pl. IX, fig. 26, B 2). Their direction is similar to that of the subbasal hooks; they inclose an angle of 90 to 180 degrees with the wing surface. These bristles are straight or slightly curved and twisted. In size they considerably exceed the subbasal hooks, attaining a length of 233 microns, while the subbasal hooks are at the most 57 microns long. They are inserted in low ringed ridges on the upper lamella of the wing and possess a narrow axial lumen distally closed. The chitinous spines which, in the Ichneumonidæ, Vespidæ, and Anthophilidæ, often accompany the series of hooks in the frenal region (pl. IX, figs. 20, 22, 23, Z 1), are also to be considered as marginal bristles of this kind.

FORE WING

The posterior margin of the fore wing is recurved and folded in, so as to form a groove. Into this groove the hooks of the hind wing are inserted (pl. IX, figs. 19-26, R i). In the Anthophilidæ, Fossores, and Vespidæ a convex bulging of the upper side of the wing is connected with this more or less highly developed plicature of its posterior margin (pl. IX, figs. 22-26). The plicature and the groove produced by it extend over the proximal half of the hind margin of the wing, and terminated distally at the place where the anal vein reaches the margin of the wing. Here the groove ends abruptly in a knob. Towards the wing basis this plicature flattens out. In forms possessing subbasal hooks closely approximated to the base of the wing the plicature (groove) is deeper at the place opposite these hooks, but there never is, as stated by Staveley (1860, p. 135), a second groove near the base of the wing separated from the distal one by a tract of unfolded wing margin. The plicated chitin forming the groove is much darker than that of other parts of the wing, and the parts of both the lamellæ composing the wing which form the groove are much thicker than the parts forming the wing proper (pl. IX, most plainly visible in figs. 22 and 23). From the upper convex side above the groove short, pointed, spines arise. These are particularly numerous near the margin. They correspond to the spines of a similar kind mentioned in the discussion of the hind wing, and, like these, are directed obliquely towards the apex of the wing (pl. IX, figs. 19 Z 2, 20). Therefore, as Staveley mentions (1860, p. 135), the margin of the groove appears serrate in surface views. Such spines are chiefly met with in the Tenthredinidæ and Ichneumonidæ. In the Vespidæ, most of the Fossores, and the Anthophilids these spines are less numerous, more blunt, and often absent altogether. On the other hand, most of the representatives of the last-named families possess a longitudinal ridge near the margin of the groove generally restricted to the frenal region (pl. IX, figs. 22, 23, Lg), which may be looked upon as a functional equivalent to the spines in other families.

DEVELOPMENT OF THE HOOKS AND THE GROOVES

In the autumn of 1905 I obtained some nests of *Vespa rufa* L., and their pupal inmates offered me an opportunity of investigating the development of the clasping organs, the structure of which has been described above. As unfortunately I did not succeed in obtaining an unbroken series of developmental stages and in this memoir an embryological chapter was not contemplated, I must restrict myself to describing the main features in the development of the distal hooks and the groove as observed by me. The development of the distal hooks commences simultaneously with the brown pigmentation of the eyes and the folding of the wings within the pupal envelope. It is initiated in the region of the frenum. First some hypodermal cells, lying in a row and belonging to this region of the costal vein, become considerably enlarged. In surface views these cells appear as a row of low, small elevations on the upper side of the costal vein. It is possible that the presence of larger fragments of fat body, which is always noticeable at this stage, is in some way connected with the formation of the hooks. The cells forming these elevations are the mother-cells of the hooks. From their upper side processes, resembling the necks of bottles, grow out and rise above the upper wing-lamella. These bend over arcuately, secrete a chitinous covering, and thus form the hooks. The formation of chitin is first consummated at the distal end of the hook; whereupon the tapering distal process of the mother-cell withdraws from the end of the hook. In the lumen of the fully formed hook no living substance (marrow of hypodermal matrix) is present. A regeneration of worn off hooks is therefore impossible. The cuticule of the upper wing-lamella, pierced by the hooks, sinks down around their basal ends, round which it is thickened and from which it is divided by an incision. (The depression is shown in fig. 33, the incision in fig. 32 on plate x.) On the whole the hooks are developed in the same manner as the hairs and scales of the Lepidoptera, the development of which has been described by Semper (1857, pp. 326-339). Like these unicellular structures which are fully chitinized in the developed animal, they are neither capable of secondary growth nor of regeneration.

The groove-like plicature of the posterior margin of the fore wing is formed rather late, about the time when the coloring of the body commences. The upper wing-lamella takes a more prominent part in the formation of the groove than the lower. This predominance of the upper over the lower lamella, clearly recognizable also in other respects, is particularly noticeable during development (pl. x, figs. 34, 35).

V. Function of the Clasping Apparatus

The connection established between the fore and hind wings by means of the hooks and groove is extremely close and energetically maintained. It is only with difficulty that the hind wings can be detached from the fore wings in the living animal without injuring the wings, and as soon as one lets go, the parted wings are immediately reunited by a powerful stroke. What functions pertain to the different parts of the clasping apparatus during flight and in what manner they are brought into play may be elucidated by a consideration of the wing-stroke. The position of the wings is, according to Marey (1869, p. 667), such that in the downward stroke the upper side of the wing faces obliquely forward; in the upward stroke, obliquely backward. At the same time the apex of the wing describes a line approaching the shape of the figure 8, with narrow upper loop (1872, p. 2).

The accompanying diagram shows approximately the position and direction of the two wings in the principal phases of a wing-stroke. It can be seen that, in the upward as well as in the downward stroke, the fore wing drags the hind wing after it, the latter as it were holding on to the groove of the former by means of the distal hooks. As the connection of the wings is not rigid, the hind wing forms an obtuse angle with the fore wing. Firmly clasping, stout, and strongly bent distal hooks and a deep and firm groove will be of great service in attaching the hind to the fore wing. At the points where the direction of the stroke changes, particularly at the apex of the eight, the upper loop of which, as Marey states (1872, p. 4), is usually very narrow, the wings will have the tendency to move in opposite directions and unclasp, as indicated by the small arrows in the figure. This tendency is restricted to but a moment, and probably not very strong. The wings are protected against the danger of unclasping at this point by the strong recurving of the tips of the distal hooks and strongly projecting margin of the groove (pl. IX, figs. 22, 23, are ideal examples); also the spines at the base of the hind wing and on the convex side of the groove of the fore wing may assist in the prevention of such unclasping, since, acting like rasps, they impede the relative slipping of the

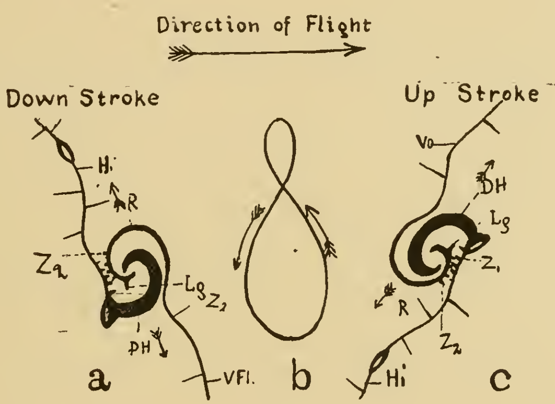
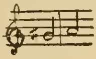
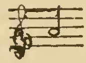
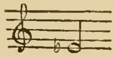
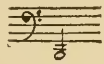


FIG. 21.

wings. The function of the subbasal hooks is the same as that of the distal hooks; they play, however, a subordinate rôle, and in many cases (particularly in the Tenthredinidæ) they pass over, morphologically as well as functionally, into the marginal bristles, which simply rest against the groove and thereby increase the elasticity of the connection. They are naturally most highly developed in forms with long wings and with the distal hooks greatly approximated to the apex of the wing, as in the Ichneumonidæ. The function of the distal hooks of the Tenthredinidæ, standing in several rows (pl. IX, fig. 19), is more difficult to explain. Those approximated to the wing margin are so strongly bent outward that the outer ones at least probably also get into the groove under certain circumstances. Their delicacy and elasticity probably enable them to do this (see above).

In reviewing the clasping arrangement in the Hymenoptera, two principal types, forming the two ends of a pretty continuous series of transitional forms, can be distinguished. The first of these types is found in the Tenthredinidæ, Ichneumonidæ, and Formicidæ; the second in the Anthophilidæ and Vespidæ. The Tenthredinidæ (pl. IX, fig. 19), Ichneumonidæ (pl. IX, fig. 20), and Formicidæ (pl. IX, fig. 21) have very flat, rather short, and only slightly bent hooks, at their bases delicate pointed spines (lacking in the Formicidæ), a widely open groove, furnished with slender spines on the outside (also lacking in the Formicidæ), no longitudinal ridge, and (as a rule wanting in the Tenthredinidæ) generally sparse, short marginal bristles. The clasping apparatus of the Tenthredinidæ is elastic and not very firm; in the Ichneumonidæ and Formicidæ it corresponds to the type described in the Anthophilids, but, in consequence of the thinness of the wall of the costal vein, it lacks the firmness peculiar to this family. Characteristic for the Anthophilidæ and Vespidæ (pl. IX, figs. 22-26) is the presence of well-developed, firm, long, and well bent distal hooks, numerous, stout, blunt spines at the bases of the hooks, and usually a longitudinal ridge on the outer side of the always deep groove, as well as long marginal bristles standing in closely crowded groups. Here the clasping apparatus is remarkably firm. On the whole, the clasping apparatus of the Anthophilids and Vespidæ is firmer than that of the Tenthredinidæ, Ichneumonidæ, and Formacidæ, and the question arises whether a correspondingly higher demand is made upon it in the former than in the latter families. The resistance of the air to the firmly joined wings principally depends upon the rapidity of the movement of the wings, *i. e.*, the number of wing-strokes executed per second and the length of the wings. According to the investigations of Marey (1886, p. 126), the bumblebee makes 240, the bee 190, the wasp 110 wing-strokes per second. No such data are available for the Tenthredinidæ, Ichneumonidæ, and Formicidæ. It is, however, possible to judge of the number of wing-strokes by the pitch of the tone produced by them in flight. Of course, no absolute data can be obtained in this manner, for errors will always creep in, caused, in accordance with Doppler's principle, by the raising of the tone when the insect approaches and its lowering when it retreats, the mingling of the tone of flight with the voice proper, etc. But these errors are not such as to preclude the possibility of deducing approximately the differences of the number of wing-strokes per second from the differences in the pitch of the tone, and it is only this that is essential here. The pitch of the wing-tone in flight is given by Landois (1867, p. 69) for *Apis* ; for *Bombus terrestris,* small male, ; for a larger male of the same species ; and for a large female of *Bombus muscorum,* . I have determined the wing-tone of *Sirex gigas* and *Rhyssa persuasoria* as . In many Ichneumonidæ, and in all Formicidæ no measurable tone of flight can be heard. These great differences in the pitch of the tone of flight of the Anthophilids and Vespidæ on the one hand and the Tenthredinidæ, Ichneumonidæ, and Formicidæ on the other, doubtless confirm the conclusion, forced upon one by a comparison of the structure of their flying organs, that the latter move the wings more slowly than the former. This difference in the rapidity of wing-movement evidently has its cause in the difference of proportion of the wing-area to the weight of the body: the Anthophilidæ and Vespidæ possess relatively much smaller wings than the Tenthredinidæ, Ichneumonidæ, and Formicidæ. If the wings of *Sirex gigas* are compared with those of *Vespa crabo,* the fore wing alone of the *Sirex* will be found to cover both wings of the larger and stouter hornet. Rapid and precise flight is probably only possible for those Hymenoptera which have firmly united fore and hind wings. Experiments made to prove this would be of doubtful value, since the removal of the hooks or the groove mutilates the wings to such an extent that it would be impossible to judge what part of the resulting peculiarities of flight should be attributed to the loss of the clasping apparatus and what part to other causes. I have several times observed bumblebees remarkable for their laborious, aimless, and wavering flight; a close examination of such always showed the hooks much injured, probably by wear.

VI. Systematic Part

The idea readily suggests itself to utilize the arrangement, number, and development of the hooks of the hind wing for systematic purposes. The first attempt in this direction, which was also the last, was made by Staveley, who ascribed a considerable systematic value to the hooks. André, who, however, otherwise does not approach the subject more closely, is very skeptical in this respect (1882, p. 65). Staveley has published a key, which, based upon the morphology of the costal vein of the hind wing and the arrangement of the distal hooks, gives in the main the following arrangement:

I.—Costal vein divided at the base.

A.—Upper branch of the costal vein marginal, reaching to the middle of the wing, where it again unites with the lower one.

Subdivisions are distinguished according to the following principles:

Cross-vein branches from the costal vein at or behind the point of junction of the two branches of the costal vein.

Series of distal hooks beginning before, at, or behind this point of junction.

B.—Upper branch of the costal vein marginal, after a short space becoming very thin or disappearing altogether. The lower branch reaches the wing-margin behind the middle.

Subdivisions according to the following principles:

End of the upper branch of the costal vein distinct or indistinct.

Wing-membrane outside the costal vein in the region of the distal hooks visible or invisible.

II.—Costal vein not divided at the base; simple; behind the middle of the wing not marginal.

Subdivisions according to the following principles:

Cross-vein branching from the costal vein behind the middle;

Series of distal hooks begins before or at this branch.

III.—Costal vein not divided at the base; marginal; unites behind the middle of the wing with the II longitudinal vein.

A.—The two veins, after their junction, continue as one.

Series of distal hooks begins before this junction.

Subdivisions according to the following principles:

Series of hooks single or double.

B.—Costal and II longitudinal vein forming a loop by again dividing after their junction and thereupon again uniting.

Series of hooks always double.

To ascertain the family to which an undetermined Hymenopteron belongs, the table of Staveley is not suitable. The reasons for this are the following: Only a few families are restricted to one division (Vespidæ, I. A; Ichneumonidæ, I. B; Apidæ, Formicidæ, II); many families and even subfamilies are distributed over several divisions; so the Sphegidæ over I. A and I. B, the Tenthredinidæ over II., III. A, and III. B, etc. Furthermore, in some of the divisions representatives of the most heterogeneous families are united, *e. g.*, II. Apidæ, Crabronidæ, and Tenthredinidæ. Finally the number of species indicated as examined by Staveley is exceedingly small. Cynipidæ and Braconidæ are not mentioned by her at all. Moreover, no necessity exists for the use of the differences in the arrangement of the hooks, spines, etc., other much more conveniently examined characters, as the wing-venation, the structure of the legs and antennæ, etc., being amply sufficient for the determination of the families. Nor can peculiarities of the clasping arrangement be used for differentiating nearly related genera similar in their grosser characters, because such nearly always agree in the character of their clasping organs. Neither does the structure of the clasping apparatus admit of the recognition of the different sexes of the same species, males and females showing the greatest similarity in this respect. At the most, the larger females possess more hooks than the smaller males (*Bombus, Camponotus, Vespa*). The number of the hooks, of the distal as well as the subbasal rows, is by no means constant and characteristic for any one species, but varies more or less with the size of the animal, between very wide limits. Of a number of species it may be said that the number of the hooks is primarily in accordance with the size and not with the power of flight. The great variability in the number of hooks, which precludes their utilization in systematic work, may be shown by the following table, in which the results of counting the number of hooks in different specimens of three species are brought together (*l.*—left; *r.*—right wing):

Sirex gigas L.		*Rhyssa persuasoria L.*				*Vespa rufa L.*	
l.	*r.*	*l.*		*r.*		*l.*	*r.*
37	30	SbH.	D H.	SbH.	D H.	20	19
37	49	1	11	1	11	24	28
38	37	1	12	1	13	24	29
39	41	1	13	1	13	26	27
39	42	1	14	1	15	26	28
43	39	1	15	1	15	28	28
43	43	1	16	1	13	27	27
43	45	2	16	2	17	27	29
45	43					28	27
46	43					29	28
46	49					29	29
48	50					29	29
50	47					29	32
51	53					31	32
52	46						

(All the specimens of *Vespa rufa* were taken from the same nest.)

This table shows how wide the limits of variation are in this respect, even in a comparatively small number of individuals of the same species. It also shows that usually even the same individual has different numbers of hooks on the right and the left hind wing. A repetition of the same numbers in different specimens turns out to be still more rare, and was only found once in *Vespa rufa*

(29–29). The figures given prove better than a long discussion could, that the study of the number of hooks, however promising it may be to the biometrician, is of no use to the systematist.

Although it can only be conceded a very problematic value as an aid in determination, it can still be used, in most cases, as a contribution to the general characterization of the species, genera, and, with certain restrictions, also of the families, among which the Cynipidæ, Braconidæ, and the greater part the Ichneumonidæ show a pretty uniform development of the clasping organ. In so far as a characterization of this kind is possible, it is briefly offered below for the families, representatives of which I was able to examine.

I. Tenthredinidæ

The distal hooks are slender, slightly curved, typically ribbon-shaped, and very elastic. As a rule, they are arranged in double rows (pl. VII, fig. 4), placed upon the upper branch of the loop formed by the costal and subcostal vein and beginning before it. Single rows are very rare. Subbasal hooks are not always present; when developed they are generally not sharply distinguished (pl. VIII, fig. 18), only rarely well differentiated (pl. VIII, fig. 15). Marginal bristles are absent or very poorly developed.

Twenty species were examined, among them *Sirex gigas, Tenthredo mesomelæna* L., *Tenthredopsis thomsoni* in a large number of specimens.

II. Cynipidæ

The distal hooks are slender, very slightly curved, present in small number, and arranged very characteristically on the broadened end of the costal vein, where this reaches the margin (pl. VII, fig. 5). Subbasal hooks and marginal bristles cannot be distinguished from each other. They are present in very small numbers, and not well developed.

Three species were examined.

III. Ichneumonidæ

The distal hooks are long, slender, moderately curved, and placed upon the costal vein in a single row (as in all following), always beginning behind the junction of the cross-vein (pl. VII, figs. 3, 6).

Differentiated subbasal hooks, abruptly bent at the point, are always present. They are placed near the base of the wing, upon the upper branch of the forked costal vein, which branch disappears after a short course (pl. VIII, fig. 16). When present in greater number they stand at small, equal intervals. More or less robust marginal bristles are always present.

Thirty-four species were examined, among them in greater numbers *Pimpla instigator* Grav., *Rhyssa persuasoria* Grav., *Ichneumon fusorius* and *luctatorius* L.

IV. Braconidæ

The distal hooks are weak, slender, very slightly curved, and placed upon the costal vein a little behind the place where it joins the margin (pl. VII, fig. 8). The subbasal hooks are difficult to distinguish from the marginal bristles, which are more numerous than in the Cynipidæ.

Three species were examined.

V. Proctotrupidæ

Two extremely slender, very slightly curved distal hooks are present. These are placed in the middle of the anterior margin of the hind wing, in which, only at the base, an indication of a costal vein can be detected (pl. VII, fig. 2). There are sparse marginal bristles, but no subbasal hooks.

One species was examined.

VI. Chrysididæ

The distal hooks are well developed, generally very numerous, and placed upon the costal vein behind the insertion of the cross-vein.

Subbasal hooks are always present. They are well developed and placed at irregular intervals near the base of the wing (pl. VIII, fig. 17). Marginal bristles are always present before and behind the series of subbasal hooks; they are stoutest at the base of the wing.

Three species were examined.

VII. Formicidæ

The distal hooks are very slender, delicate, and slightly curved. They are placed upon the costal vein, the series beginning behind the insertion of the cross-vein (pl. VII, fig. 7). Subbasal hooks are wanting. The marginal bristles are extremely small and thin.

Seven species were examined, among them, in a larger number of specimens, *Formica rufa* L., *Camponotus ligniperdus* Mayr., and *Lasius flavus* Mayr.

VIII. Fossores

In this family such a diversity prevails that it is hardly possible to give even an approximate characterization. The distal hooks, in form and arrangement, sometimes resemble those of the Ichneumonidæ, sometimes those of the Vespidæ, and sometimes those of the Anthophilidæ. The subbasal hooks are also very diversely developed, and sometimes absent altogether. The marginal bristles are not very well developed. It is remarkable that in this family they are often found in the middle of the series of distal hooks.

Twenty-two species were examined.

IX. Vespidæ

The distal hooks are very stout, strongly curved, and numerous. The series begins before or at the point of insertion of the costal vein (pl. VII, fig. 9). Subbasal hooks are absent. The marginal bristles are always numerous and well developed.

Nine species were examined, among them a larger number of specimens of *Vespa germanica* Fabr., *Vespa vulgaris,* and *Vespa rufa* L.

X. Anthophilidæ

The distal hooks are always stout, strongly curved, and numerous. The series begins before, at, or behind the insertion of the cross-vein (pl. VII, fig. 1; pl. VIII, figs. 11, 12, 13). The subbasal hooks, wanting in many forms, when present, short, stumpy, very slightly bent, and placed at irregular intervals between the base of the wing and the series of distal hooks (pl. VIII, fig. 13). Strongly developed marginal bristles are always present.

Eighteen species were examined, among them a larger number of specimens of *Bombus terrestis, hortorum,* and *lapidarius* L., *Psithyrus rupestris* Lep., and *Apis mellifica* L.

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VIII. Explanation of Plates

All figures are photomicrographs, prepared with a Leitz microscope and a Zeiss microphotographic apparatus. Figs. 1 and 3 are taken with a Zeiss microplanar; all the others, according to magnification, with the Leitz objectives 3, 5, 8, without eye piece, partly by Welsbach light and partly by daylight.

The following abbreviations apply to all figures:

B 1, B 2, B 3.....Marginal bristles.
D H.............Costal vein; oC A, upper; u C A, lower branch.
C A............Distal hooks.
F ....Chitinous threads.
Gr ....Border layer between wing-matrix and lumen of the hook.
Hi ....Hind wing.
L ....Lumen of the costal vein.
l ....Longitudinal ridge of the groove of the fore wing.
Ma ....Matrix of the costal vein.
Me ....Drum-membrane of the "pan."
oL ....Upper wing-lamella.
P ....Pan.
R .... Annular ridge.
Ri ....Groove of the fore wing.
SbH ....Subbasal hooks.
uL ....Lower wing-lamella.
Vo ....Fore wing.
Z 1..............Tubercles at the anterior margin of the hind wing.
Z 2............. Tubercles on the outer side of the groove.

Plate VII

Figures 1-9.

All the figures are surface views.

1. Hind wing of *Bombus terrestris* L. . . . . Magnified 9
2. Distal hooks of *Proctotrupes gravidator* L. . . . . " 56
3. Hind wing of *Rhyssa persuasoria* L. . . . . " 9
4. Distal hooks of *Tenthredopsis thomsini* Knw. . . . . " 50
5. Distal hooks of *Dryophanta folii* Forst. . . . . " 130
6. Distal hooks of *Anomalon flavifrons* D. T. . . . . " 50
7. Distal hooks of *Lasius flavus* Mayr. . . . . " 56
8. Distal hooks of *Dacnusa petiolata* Hal. . . . . " 85
9. Distal hooks of *Vespa vulgaris* L. . . . . " 50

Plate VIII

Figures 10-18

All the figures are surface views.

10. Distal hooks of *Polistes galleca* Latr. . . . . Magnified 58
11. Distal hooks of *Eucera longicornis* Scop. . . . . " 45
12. Distal hooks of *Anthrena ovina* Klug. . . . . " 40
13. Distal hooks of *Halictus calceatus* D. T. . . . . " 70
    shows the peculiar arrangement of the distal hooks in groups.
14. Subbasal hooks of *Halictus levigatus* Lep. . . . . " 70
15. Subbasal hooks of *Pamphilius hypertrophicus* D. T. . . . . " 70
16. Subbasal hooks of *Henicospilus ramidulus* Steph. . . . . " 70
17. Subbasal hooks of *Holopyga amoenula* Dahlb. . . . . " 75
18. Subbasal hooks of *Sirex gigas* L. . . . . " 35

Plate IX

Figures 19-26

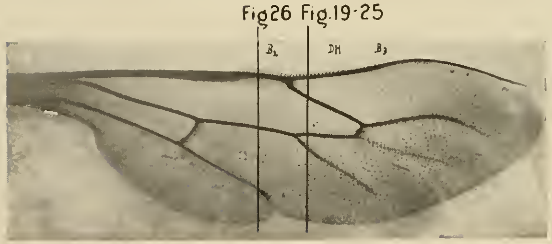
All the figures represent cross-sections through the two wings joined together. The region of the sections is approximately indicated in pl. VII, fig. 1, by vertical lines.

19. *Sirex gigas* L. . . . . Magnified 50
20. *Exetastes fornicator* Grav. . . . . " 75
21. *Formica rufa* L. . . . . " 140
22. *Vespa vulgaris* L. . . . . " 130
23. *Vespa crabro* L. . . . . " 75
24. *Apis mellifica* L. . . . . " 140
25. *Xylocopa violacea* Pr. . . . . " 45
26. *Vespa vulgaris* L. . . . . " 135

PLATE X

FIGURES 27-35

27. Cross-section through the costal vein at the place of insertion of the distal hooks of a young *Sirex gigas* L.	Magnified	280
28, 29. The same section of an older specimen of the same species	"	300
30. The same cross-section of *Apis mellifica* L.	"	300
31. Pazatangential section, through the costal vein of *Sirex gigas* L., seen from above	"	140
32. Cross-section through the costal vein at the place of insertion of the distal hooks of a young *Vespa vulgaris*	"	300
33. The same section of a pupa of *Vespa rufa* L.	"	300
34. Cross-section through the posterior margin of the fore wing of *Vespa rufa* L.	"	300
35. The same section of a young imago of *Sirex gigas* L.	"	300



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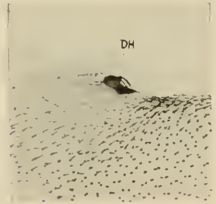

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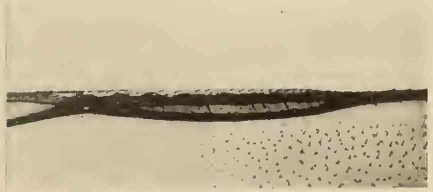

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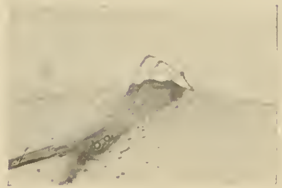

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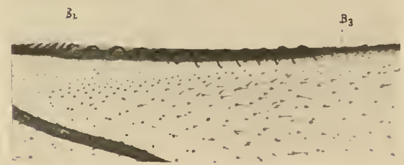

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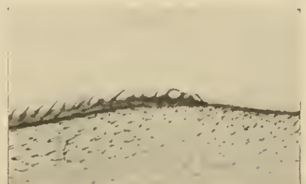

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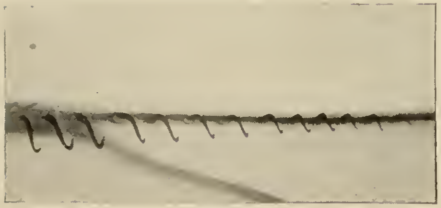
WINGS OF HYMENOPTERA



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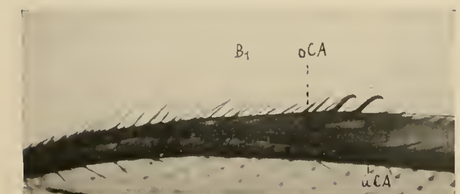

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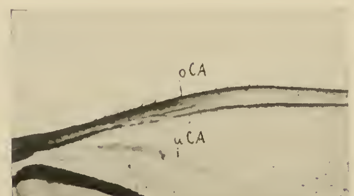

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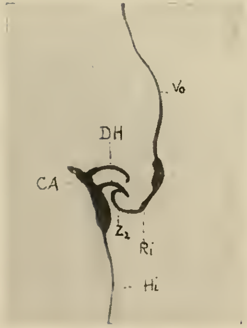
WINGS OF HYMENOPTERA



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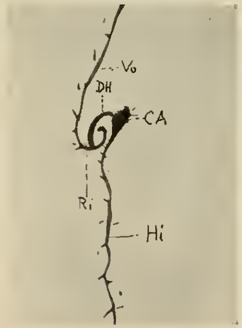

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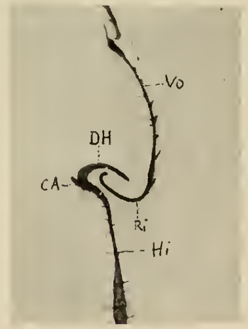

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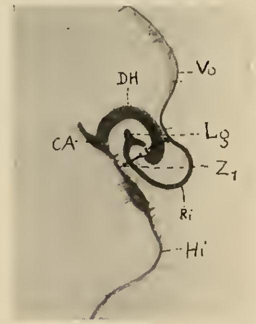

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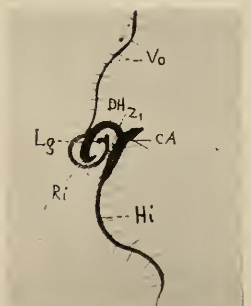

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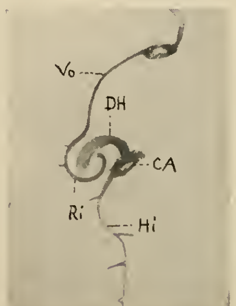

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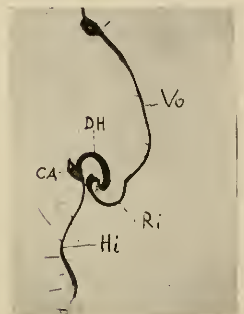

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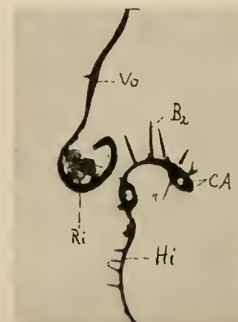

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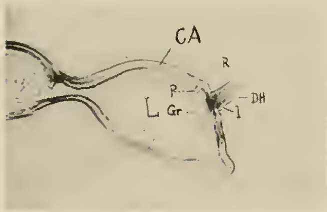
WINGS OF HYMENOPTERA



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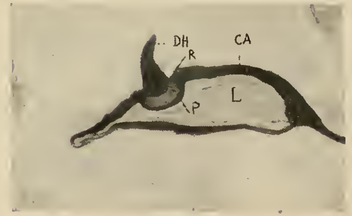

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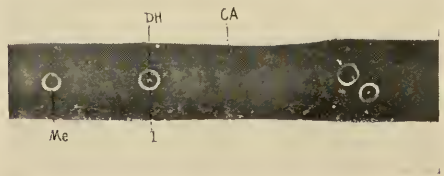

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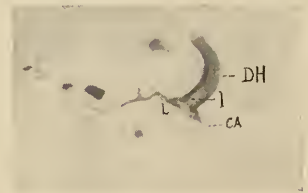

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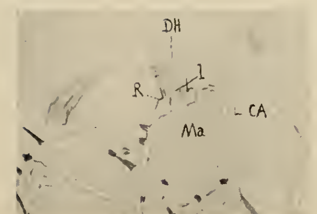

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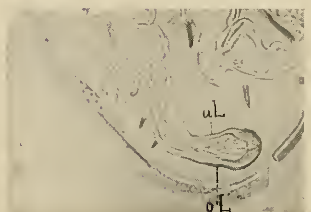

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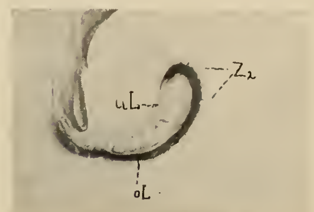

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WINGS OF HYMENOPTERA